

Understanding Palaeozoic stromatoporoid growth

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Abstract

Stromatoporoids were abundant components of reefs, reef complexes and associated facies for ca. 100 million years between Middle Ordovician and end-Devonian time. A lot of environmental information stored in their skeletons may be used to develop: a) understanding of stromatoporoid growth controls; and b) interpretations of sedimentary environments in which they lived. General patterns of stromatoporoid distribution are well known, but knowledge of detailed interactions between stromatoporoids and their environments is poorly developed and under-used, potentially of great value in analysis of facies and palaeoecology. From a pool of several thousand specimens examined over four decades, this study identifies four key attributes of stromatoporoids that may be applied to enhance broad-scale knowledge of these fossils and their environments: **1) Substrates:** Most stromatoporoids grew directly on wackestone to packstone substrates comprising micrite, clay and bioclasts. Evidence from the relationship between stromatoporoids and sediments demonstrates they were able to grow on soft substrates, but also leads to interpretation of partial lithification of the sea floor (and/or stabilisation by microbial filaments that may not be preserved) in mid-Palaeozoic carbonate facies, with potential implications for models of oceanic carbonate cycling. **2) Growth interruption:** Almost all stromatoporoids examined show growth interruption, mostly caused by sedimentation and movement. Stromatoporoids normally recovered quickly and completely from interruption, thus were resilient to interruption events; **3) Associated organisms:** Stromatoporoids have abundant associated organisms in two groups: (i) epibiotic encrusters and borers; and (ii) endobiotic organisms embedded in their structure, alive as the stromatoporoids grew. Epibionts used stromatoporoid surfaces that are presumed dead in almost all cases; some are associated with interruption events, but in most cases those were overgrown by successive stromatoporoid growth. Endobionts (mostly corals, plus spirorbids and others) are common to abundant in many stromatoporoid taxa. Stromatoporoid growth was little affected by presence of endobionts but in many cases (commonly restricted to certain stromatoporoid taxa) there was a complex biological interaction valuable in understanding controls on stromatoporoid development. **4) Growth form and taxonomy:** Stromatoporoid assemblages are low diversity in almost all cases, regardless of age and facies, with two or three taxa much more abundant than the others. Some stromatoporoid taxa are limited

46 to certain growth forms, thus taxonomic information is very important for facies
47 analysis and palaeobiological interpretations.

48 Stromatoporoids occur commonly with rugose and tabulate corals, both of
49 which could also live on unconsolidated fine-grained substrates, therefore
50 sediment-tolerance cannot be the only reason for stromatoporoid ability to
51 outgrow corals in reefs. Arguments in the literature for photosymbiosis in both
52 stromatoporoids and Palaeozoic corals are currently inconclusive for both fossil
53 groups. Nevertheless, the sum of evidence indicates stromatoporoids were fast-
54 growing, resilient and flexible benthic organisms, in a range of water depths,
55 capable of dealing with soft substrates and largely unaffected by presence of
56 endobionts. These characteristics are interpreted to have made stromatoporoids
57 successful during mid-Palaeozoic time and valuable as tools in facies analysis.
58 Recognition of the four key attributes which encompass all aspects of
59 stromatoporoid growth controls makes palaeobiological study of stromatoporoids,
60 in palaeoenvironmental reconstructions where they occur, readily accessible to
61 researchers.

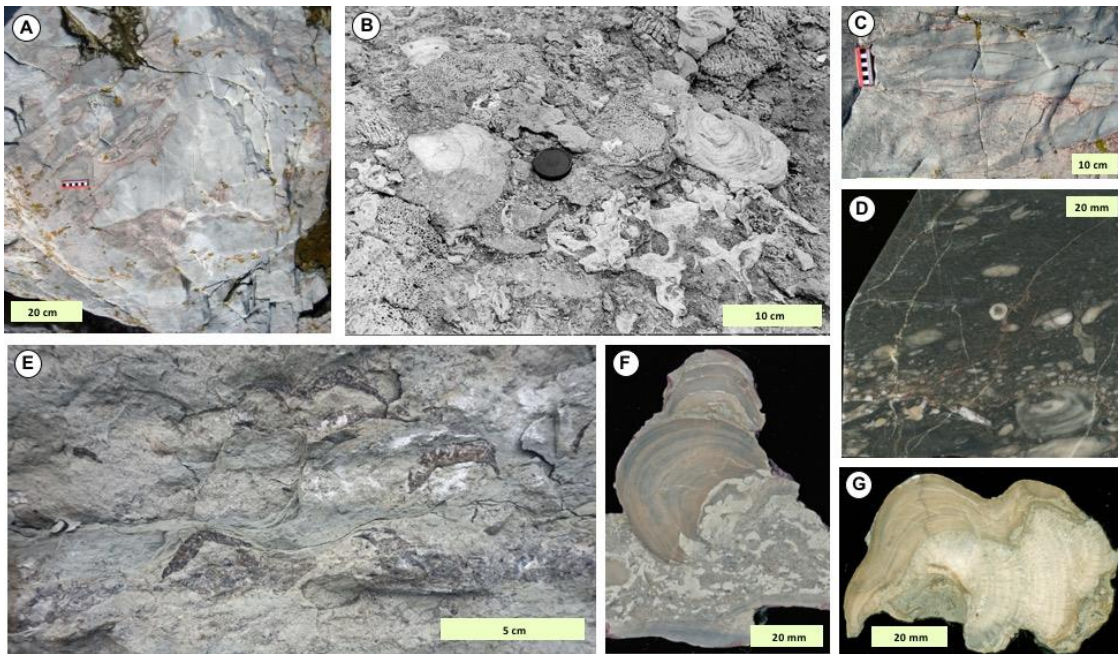
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63 **Key words:** stromatoporoids; corals; symbionts; sedimentation; substrates;
64 Palaeozoic

65 66 67 **1. Introduction and aims**

68 Palaeozoic stromatoporoids (hypercalcified sponges, Stearn, 2015a,
69 p417) were abundant in reefs (including individual reefs on platforms, reef
70 margins and entire reef complexes) and associated facies in carbonate
71 environments throughout the ca. 100 million years from the advent of large reefs
72 in the late Darriwilian Epoch (Middle Ordovician) Great Ordovician
73 Biodiversification Event (Webby 2004) to their collapse at the end-Devonian
74 Hangenberg mass extinction (Stearn, 2015b, p599). During this interval,
75 stromatoporoids were key components in reefs on a global scale, with large
76 extensive reef complexes influencing huge areas of shallow-marine platforms
77 (e.g. Copper, 2011). Thus, it has long been recognised that stromatoporoids are
78 valuable environmental indicators, based on their growth forms and interactions
79 with the sedimentary environments in which they grew (e.g. Kershaw, 1998, 2012,
80 2013; Da Silva *et al.*, 2011a, b; Webby and Kershaw 2015 and references
81 therein). However, although much is published on the patterns of growth and
82 distribution of stromatoporoids, understanding the cause of their great success in
83 Palaeozoic shallow-marine environments continues to be a challenge.
84 Furthermore, a lot of information is present in the growth history of individual
85 stromatoporoids that may be used to analyse patterns of responses to their
86 environments; but this information is under-utilised in facies and palaeoecological
87 studies where stromatoporoids are present.

88 The aim of this paper is to provide an updated view of the growth
89 attributes of stromatoporoids and to develop their use to assist sedimentary
90 facies analysis and palaeoecological interpretations. Of particular importance, we
91 have identified four attributes of stromatoporoid growth that encompass all

92 aspects of their application relevant to facies analysis, in an attempt to provide
 93 researchers with tools to fully utilise stromatoporoids in studies of rocks that
 94 contain them. Review papers commonly display palaeogeographic maps, range
 95 charts, data compilations and summative model drawings. For stromatoporoids,
 96 there are several such presentations in published literature of recent years that
 97 we do not want to repeat (several chapters in the Treatise on Palaeontology, Part
 98 E, edited by Selden, 2015), so our approach here is to augment literature
 99 information with a range of new material not previously published. Thus we view
 100 this paper not as a review, but as a synthesis of stromatoporoid growth attributes
 101 and their applications. We present a distillation of detailed evidence derived from
 102 examination of several thousand stromatoporoids in Middle Ordovician to Late
 103 Devonian outcrops, polished blocks and thin sections, assembled since 1975.
 104 Fig. 1 shows the range of appearance of stromatoporoids in Palaeozoic rocks,
 105 illustrating variations in size, morphology and facies relationships that this paper
 106 explores.
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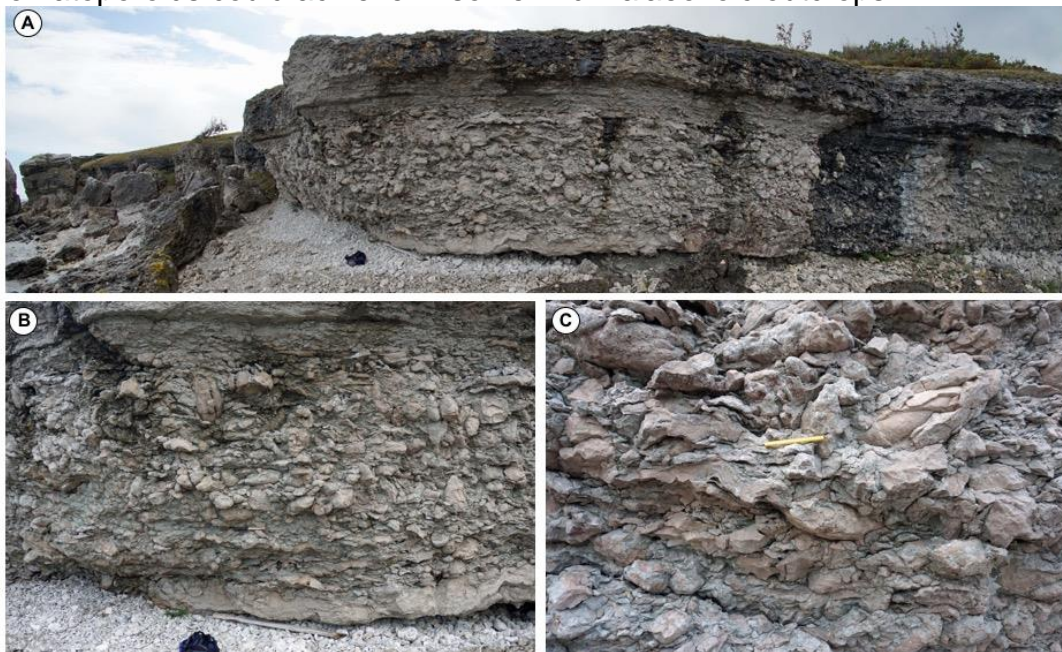


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 109 Fig.1. Examples of stromatoporoids and corals to show key growth features. A)
 110 Large domical reef-building stromatoporoids (grey colour, in pink matrix of
 111 bioclastic debris and micrite), typical of the large size of stromatoporoids in
 112 Palaeozoic reefs. Walls Hill Limestone Fm, Givetian, Devonian; Long Quarry
 113 Point, Devon, UK (Scrutton, 1977). B) Reef framework of a dense accumulation
 114 of stromatoporoids and corals, Braksøya Fm, Wenlock, Silurian; Gåserumpa
 115 Island, Oslo Fjord, Norway (Worsley et al., 1983). C) Interdigitations between
 116 reef stromatoporoid margins (grey colour) and sediment, site as in A. D) Small
 117 bulbous and dendroid stromatoporoids together with branching tabulate corals in
 118 dark micrite, back-reef facies. Ashburton Limestone, Eifelian-Givetian, Devonian;
 119 Ashburton, Devon, UK (Scrutton, 1977). E) Small domical-form stromatoporoids
 120 and corals in open-shelf marls, typical of their appearance in bedded limestones.
 121 F) Domical stromatoporoid in wackestones, showing movement and re-

122 encrustation by further stromatoporoid and coral growth. G) Domical
123 stromatoporoid encrusting an overturned favositid tabulate. E-G from Upper
124 Visby Fm, Wenlock, Silurian; Ireviken, Gotland, Sweden (Calner et al., 2004).

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127 Figure 2 shows the abundance of stromatoporoids in one of the most dense
128 accumulations, as an illustration of the large extent to which stromatoporoids
129 were able to develop in Palaeozoic deposits under the appropriate conditions.
130 The example in Figure 2 is part of a biostromal unit covering several tens of
131 square kilometres. Almost all the densely packed fossils shown in these
132 photographs are stromatoporoids, with a range of growth forms from laminar to
133 tall domical types, with a mixture of in-place and locally transported specimens.
134 In this assemblage *ca.* 70% of the numbers of specimens are represented by
135 three taxa, described by Kershaw (1990), a low diversity that is typical of
136 stromatoporoid assemblages. Abundance of stromatoporoids in this example is
137 greater than many other occurrences (such as most of the large Devonian reef
138 complexes in Canada and Australia), and demonstrates the volume that
139 stromatoporoids could achieve in some mid-Palaeozoic outcrops.



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141 Fig. 2. Example of a dense stromatoporoid accumulation, in a biostrome,
142 showing high abundance of specimens, with varying growth forms and sizes.
143 Backpack in A and B is 0.5 m long; yellow scale in C is 20 cm long. For
144 descriptions of the faunas and facies of this site see Kershaw (1981, 1987, 1990)
145 and of the wider area see Sandström and Kershaw (2002, 2008). Hemse Group,
146 middle Ludlow, Silurian; Kuppen, Gotland, Sweden.

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150 2. Materials, methods and study issues

151 Traditionally, stromatoporoid studies focused on taxonomy, for which
152 samples from the interior of a specimen are used to make microscope sections.
153 Vertical thin sections at 90 degrees to the growth layers, and tangential (often
154 called transverse) sections parallel to growth layers, are used to provide full
155 taxonomic information. Stromatoporoids normally cannot be identified fully
156 without both thin-section views. Acetate peels have limited use in
157 stromatoporoids; because of density contrast issues, only a few taxa can be
158 studied with peels. A complete compendium of study methods is given by Stearn
159 (2015e).

160 As a result of the tradition of taxonomic focus, published photographs of
161 stromatoporoid thin sections are usually of small areas of the interior of a sample
162 in vertical and tangential views, so that most of the information uses selected and
163 limited observations. This practice is useful for much taxonomic work, but larger
164 thin-section views are often significantly beneficial. Furthermore, the study of
165 stromatoporoid palaeobiology and applications in facies analysis require more
166 information, and needs the basal part, margins and top as well as the interior of
167 samples in order to demonstrate all aspects of skeleton growth and associations
168 with other organisms. Ideally, microscope sections of the entire fossil can provide
169 the maximum information, but these are constrained because: 1) reef
170 stromatoporoids and corals are usually too large for single thin sections; 2)
171 contemporaneous erosion of margins of corals and stromatoporoids in reefs
172 reduces the amount of information at the margins; and 3) in reefs in particular,
173 the effects of pressure solution dissolving stromatoporoid margins degrades the
174 samples and may be a significant problem in reconstructing the growth history of
175 these fossils in rocks strongly affected by pressure solution. Vertical sections
176 through the centre of a stromatoporoid, revealing base, top and margins, provide
177 the most useful information of the growth and microfacies history of a specimen.
178 Tangential sections are valuable for study of endosymbiont distributions. Oblique
179 cuts are rarely of value in stromatoporoid work.

180 Because most stromatoporoid studies have not focused on orientated
181 sections through entire specimens, and parts critical for growth analysis, the
182 result is that comprehensive statistics on growth features of stromatoporoids (and
183 corals) are subject to unavoidable bias. Nevertheless, as an approach to obtain
184 the best material for study, effort was made to assemble a sample set of
185 complete specimens, and where this was not possible, appropriate portions of
186 stromatoporoids were selected to view the key aspects for this study, with
187 attention paid to bases, margins and tops of stromatoporoids. A lot of information
188 came from stromatoporoids of the Upper Visby Fm, in the Silurian of Gotland,
189 where entire small stromatoporoids are easily extracted from calcareous
190 mudstones. Other samples from a variety of selected Silurian and Devonian sites
191 are illustrated here; they contain features of all four attributes recognisable
192 across the Palaeozoic stromatoporoids. Large thin sections of many individual
193 fossils are included, mostly vertical thin sections because they show the growth
194 history of individuals. A subsample selected for SEM study of the relationship
195 between stromatoporoid bases and their substrates is also included.

196 Thin sections provide two-dimensional views of a structure, but
197 stromatoporoids vary in three dimensions. In most studies, it is impractical to
198 undertake large-scale serial sectioning of samples to examine the structure in
199 three dimensions. However, three-dimensional variation within specimens is
200 needed. In this study, three approaches were used to examine stromatoporoids
201 in three dimensions: 1) Some representative complete specimens were cut
202 vertically with two cuts at 90 degrees through the centre of the sample, dividing
203 the stromatoporoid into quarters, and all the faces then polished to allow the
204 structure to be studied in three dimensions. 2) Most specimens for which thin
205 sections were made were cut into at least three pieces by two vertical parallel
206 cuts, one through the central point of the specimen, and the other close to the
207 centre through the flanks. In some cases the sample was cut into four slices, to
208 create two slices in the central area, from which thin sections were made, and
209 the other pieces show sections through the flanks of the sample. In a few
210 specimens two thin sections were made within 1 cm of each other in the central
211 part of the stromatoporoid. The remaining slices were again polished so that in
212 some cases we have two thin sections plus six polished faces of vertical cuts to
213 study the structure. 3) Large stromatoporoids cannot be studied in single thin
214 sections so samples were cut into blocks with sides up to ca 10 cm, some
215 rectangular and others odd-shaped, with appropriate cut orientations aimed at
216 revealing the structure in three dimensions; each cut surface was polished so
217 details could be examined with the hand lens and imaged using a document
218 scanner, with thin sections made as required. These three approaches are easy
219 to achieve at low cost, reveal a lot of three-dimensional information and are
220 recommended to researchers wishing to study stromatoporoids. Thus serial thin-
221 sectioning is not needed to extract most three-dimensional information from
222 stromatoporoids.

223 Because the majority of stromatoporoids are too large to collect entire,
224 and/or affected by pressure solution destroying essential information at their
225 bases, tops and margins, numerical analysis of their growth histories is
226 problematic. Instead, generalisation into Rare, Common and Abundant
227 categories is applied. Indeed, each stromatoporoid is a unique construction; not
228 all attributes are visible in each specimen, and the expression of each attribute
229 varies between samples. Some attributes are subject to interpretation that is not
230 always resolved. However, studies of stromatoporoid growth form and taxonomy
231 is more amenable to numerical analysis in cases where growth forms are
232 sufficiently preserved and where the taxa can be satisfactorily identified (true of
233 most stromatoporoids), although the number of published studies is limited (see
234 Kershaw, 2012 for review).

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236 **3. Background information on stromatoporoids**

237 Stromatoporoids (and corals) grew on carbonate-dominated sediments
238 and are abundant in pure carbonate sediments, and in marls (carbonate &
239 siliciclastic mud mixtures), but rare in pure siliciclastic mud or sand. In some
240 cases the substrate is composed of only micrite (carbonate) with clay. Kershaw
241 (1998) argued that stromatoporoids were successful in the Palaeozoic because

242 they were able to deal with fine-grained sediment substrates. Thus, in contrast to
243 modern corals and calcified sponges, fossil stromatoporoids seemed to have
244 been able to tolerate siliciclastic mud as long as it was mixed with carbonate.

245 Most stromatoporoid-rich reef deposits contain a variety of stromatoporoid
246 growth forms, which largely range from laminar sheets to domical forms. A
247 comprehensive description of the range of stromatoporoid forms is given by
248 Webby and Kershaw (2015). Palaeozoic stromatoporoids are much larger than
249 modern calcified sponges, which are their counterparts and grow to only a few
250 cm diameter (e.g. Wörheide, 1998), while stromatoporoids may reach several
251 metres across. Modern calcified sponges are cryptic, outcompeted by fast-
252 growing zooxanthellate scleractinian corals, not least because such sponges
253 grow very slowly, at rates of approximately 0.1 mm/year (Benavidas and Druffel,
254 1986; Dustan and Sacco, 1982), with some variation between taxa, a range of
255 0.05 to 0.4 mm/year (Grottoli et al., 2010). In contrast, the larger size of
256 Palaeozoic stromatoporoids is evidence that they grew faster because if they
257 grew at the low rates of modern calcified sponges it is difficult to accept that they
258 could have become so large in the active environments of shallow-marine
259 conditions. However, no physical structures that would indicate a photosynthetic
260 ability, nor symbiosis with photosynthetic organisms, are known in
261 stromatoporoids (Kershaw, 2013). Nevertheless, stromatoporoids demonstrate
262 geotropic growth, easily appreciated from the common domical forms illustrated
263 in Figures 1E-G and 3B. Some stromatoporoids have columnar growth
264 protrusions on their upper surfaces; these columns are always vertically
265 orientated, notable in stromatoporoids that grew on sloping substrates (see
266 photographs in Kershaw, 2013). Stromatoporoids became the dominant reef-
267 builders in most Silurian and Devonian reef settings. In cases where the reef
268 sequence shows shallowing-up facies (e.g. the Höglint reefs, Wenlock, Gotland)
269 stromatoporoids become progressively larger and more abundant than corals as
270 the water shallowed (Watts, 1988; Riding and Watts, 2000). Large size and
271 geotropic growth are circumstantial evidence that stromatoporoids may have
272 been photoresponsive. For comparison, there is a range of published evidence
273 supporting photoresponsiveness in corals (e.g. Frankowiak et al., 2016;
274 Tornabene et al., 2017; Zapalski et al., 2017a, 2017b), including data from
275 isotopes for tabulates (Zapalski, 2014), although Jakubowicz et al. (2015) drew
276 attention to the problems of diagenetic alteration of isotopes in Palaeozoic corals;
277 thus none of these ideas are proven, and in reefs corals are generally smaller
278 and less abundant than stromatoporoids. Copper and Scotese (2003, p. 223)
279 argued for photoresponse in reef-building corals and stromatoporoids, but
280 recognised that this is unconfirmed. There is much greater confidence that
281 photosymbiosis in corals evolved in the Middle Triassic when scleractinians
282 appeared (Stanley, 2003). Detailed discussion of the issue of photosymbiosis in
283 Palaeozoic stromatoporoids by Stearn (2015f, p. 556-560) demonstrated the lack
284 of clear evidence that would lead to a conclusion as to whether stromatoporoids
285 were photoresponsive or not. Nevertheless, the fact remains that
286 stromatoporoids were more abundant than tabulate corals in Palaeozoic reefs,

287 demonstrating an ability amongst the stromatoporoids to dominate these
288 environments.

289 Growth rate studies in stromatoporoids are problematic, as discussed by
290 Young and Kershaw (2005), and we point out that the often-cited work by Gao and
291 Copper (1997) did not examine the margins of stromatoporoids, that we consider
292 to be essential in relating growth attributes to environmental aspects, particularly
293 sedimentation, and the possibility of annual banding. Platy corals in deeper-water
294 facies have been interpreted to indicate photosymbiosis (e.g. Zapalski et al.,
295 2017b) but this is problematic. Kershaw (1998, text-fig. 9E) noted that
296 laminar/tabular stromatoporoids in deeper water were considered by other authors
297 as indicating photosensitivity, but in order to investigate this it is necessary to relate
298 taxonomy to growth form to show that platy forms in deeper water are the same
299 taxa as those in shallow water. Such information might add to the circumstantial
300 evidence of a photoresponse in stromatoporoids, but there are no studies which
301 demonstrate such a relationship. We stress that stromatoporoids were shallow-
302 water organisms; although water depth is difficult to estimate, it is clear that
303 stromatoporoid abundance was low and size was small in deeper settings (e.g.
304 Cockbain, 1984; Da Silva et al., 2011b). Stromatoporoids built reefs only in shallow
305 waters, of depths likely approximately equivalent to modern coral reefs.

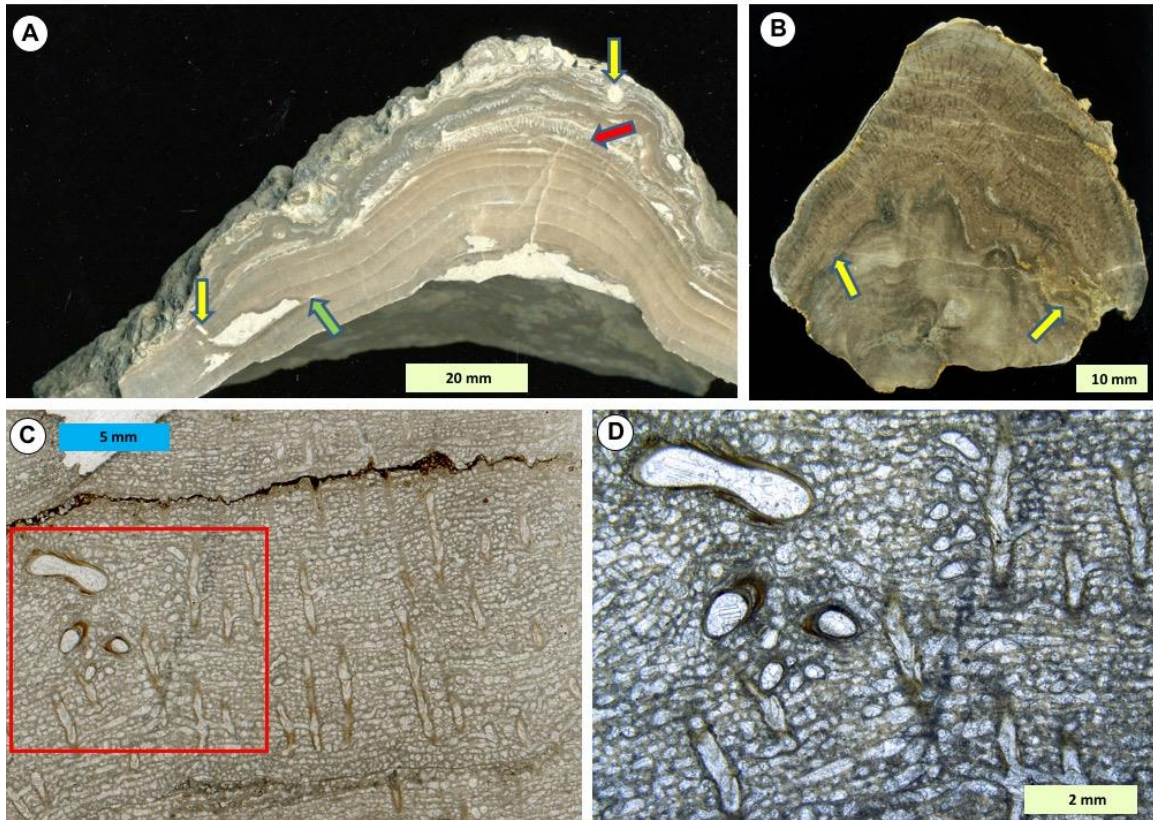
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308 **4. Stromatoporoid growth attributes**

309 The four key attributes of stromatoporoids (see Fig. 3) that may be applied to
310 understand their growth controls and associated environmental processes are: 1)
311 the relationship between the basal portions of their growth and the substrate on
312 which they grew; 2) growth histories and the importance of their reaction to
313 growth interruption events; 3) interactions with symbiotic organisms during
314 stromatoporoid lives and shortly after their death; and 4) the relationship between
315 growth form and taxonomy. This paper does not address the details of skeletal
316 architecture of stromatoporoids; this topic is dealt with comprehensively in the
317 recent Treatise on hypercalcified sponges (Stearn, 2015c and d); instead we
318 examine the relationship between growth and the environmental factors, and
319 interactions amongst stromatoporoids and associated organisms.

320 Stromatoporoids co-existed with rugose and tabulate corals and heliolitids
321 (considered by many coral workers to be separate from the tabulates), and in
322 many cases these fossil groups show similar responses to environmental factors.
323 Where appropriate, we draw parallels between stromatoporoids and the coral
324 groups (e.g. Scrutton, 1998; Young and Scrutton, 1991).

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 329 Fig. 3. Photographs illustrating the four growth attributes of stromatoporoids,
 330 identified in this paper as important for understanding stromatoporoid growth. A)
 331 Small stromatoporoid grew on fine-grained marly sediment on a small
 332 topographic high on the sediment surface, the most common substrate
 333 relationship in stromatoporoids. This sample also shows growth interruption
 334 surfaces within its life, including sediment layers (one surface is labelled with a
 335 green arrow) and encrusting corals (red arrow), but also shows portions where
 336 the interruption cannot be easily traced laterally across the sample. Small borings
 337 entered from the top surface (yellow arrows), likely after the stromatoporoid died.
 338 The fourth growth attribute (growth form and taxonomy) is partly represented in
 339 A, wherein the lower stromatoporoid (in this case *Pseudolabechia hesslandi*)
 340 always occurs as a low-profile form. Upper Visby Fm, Wenlock, Silurian;
 341 Häftingsklint, Gotland, Sweden (Calner et al., 2004). B) Two unidentified
 342 stromatoporoid taxa, the upper one using the lower as a substrate; yellow arrows
 343 mark the base of the upper stromatoporoid. The lower stromatoporoid shows two
 344 geotropic growth columns developing in its structure. The upper stromatoporoid
 345 shows geotropic growth and also has symbiotic syringoporid corals throughout its
 346 structure, common in some stromatoporoid taxa. A thin light-coloured sediment
 347 layer separates the two stromatoporoids, indicating that the top surface of the
 348 lower stromatoporoid is a growth interruption surface. C) Vertical thin section of
 349 an unidentified stromatoporoid containing two endobiont taxa: syringoporid
 350 tabulate and probable spirorbid worm. The two dark irregular lines are
 351 interruption surfaces where sediment accumulated, here affected by pressure

352 solution creating stylolites, common in stromatoporoids. D) Enlarged area of red
353 box in C, showing details of the relationship between the stromatoporoid and the
354 two endobionts. There is little variation of the effect of endobionts on the
355 stromatoporoid structure, which is typical for stromatoporoid-endobiont
356 interactions. The spirorbid likely began growth on the living stromatoporoid
357 surface and does not extend down to its base; its tube is associated with
358 prominent upbending of stromatoporoid laminae around the tube. However,
359 down-bending of stromatoporoid laminae, commonly seen in hosts with
360 endobionts (e.g. Tapanila, 2005) is not present in all stromatoporoid laminae in
361 this photograph. B-D: Santa Lucía Fm, Emsian (Lower Devonian); El Millar,
362 Cantabrian Mountains, northern Spain (Fernandez et al., 1995; Mendez-Bedia et
363 al., 1994).

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5. Substrate relationships in stromatoporoids and their importance in facies analysis

370 Although observations of stromatoporoids from Middle Ordovician to end-
371 Devonian age rocks show that stromatoporoids are found mostly on sediment
372 substrates (see Figs. 3A and 4A for examples), the problem of understanding the
373 nature of their growth relationship with the substrate remains. Evidence that
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376 Fig. 4. Outcrop photographs of small stromatoporoids and a coral in bedded
377 wackestones, demonstrating the ability of stromatoporoids to grow on fine-
378 grained sediment. A) Stromatoporoids apparently grew directly on sediment
379 surface. B) Coral (halysitid) apparently grew on sediment (very common in
380 tabulate corals) but adjacent stromatoporoid grew on a gastropod shell. C) The
381 larger stromatoporoid (left) has a smoothly curved base, consistent with growth
382 on a shell, possibly a nautiloid subsequently lost in diagenesis. This
383 stromatoporoid overturned twice, and either continued growth or the skeleton
384 was used by later stromatoporoid growth. See also Fig. 5. Upper Visby Fm,
385 Wenlock, Silurian; Halls Huk, Gotland, Sweden (Calner et al., 2004).

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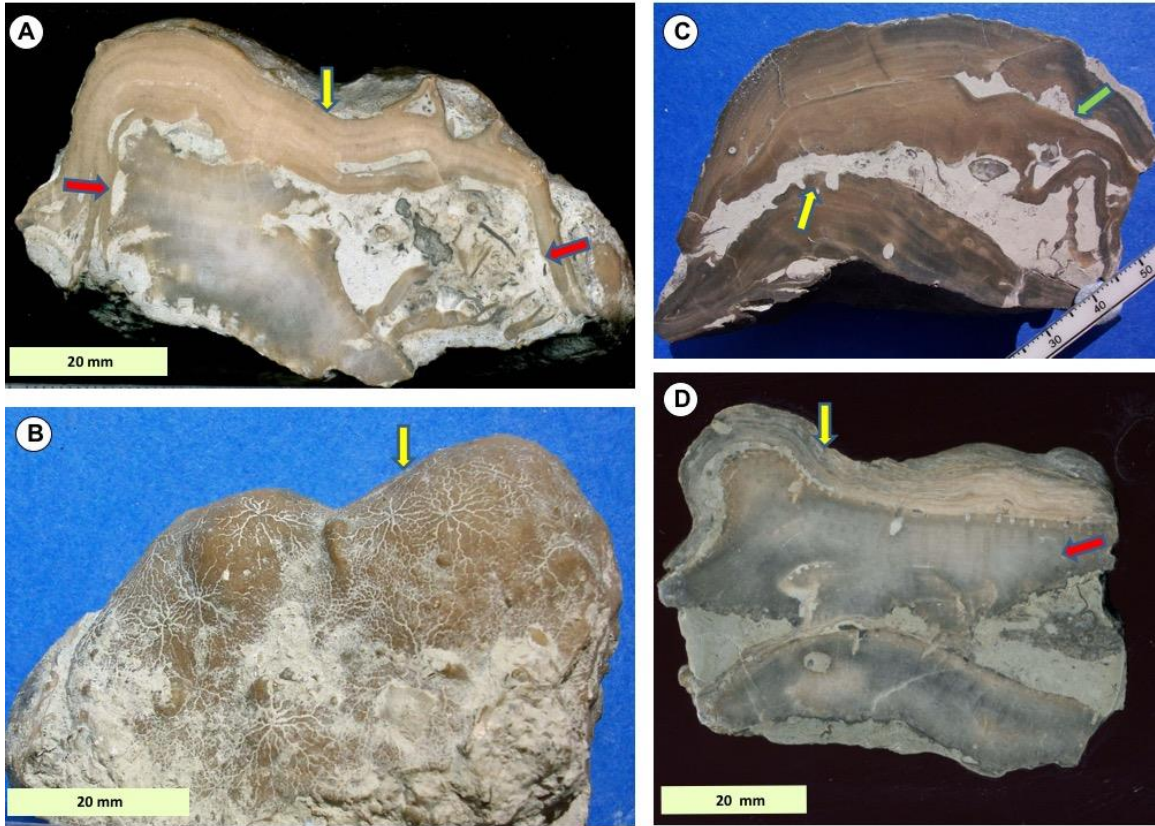
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388 stromatoporoids were moved on the substrate prior to burial (Fig. 1F, see also
389 Kershaw, 1980, 1984) means that for any individual stromatoporoid it is
390 necessary to determine whether a) it is preserved on sediment that it grew on, b)
391 formed a primary cavity below its base that was later infilled, or c) was moved
392 before burial and now lies on sediment unrelated to its original growth. Such
393 information is highly valuable in facies analysis where stromatoporoids are used
394 to interpret palaeoenvironmental changes. Given that many stromatoporoid
395 substrates are marls, the possibility that compaction closed a primary cavity must
396 also be considered, although cases of preservation of geopetal sediment with
397 cement infilling the remaining space are very rare. Segars and Liddell (1988)
398 interpreted primary cavities below stromatoporoids on level substrates, to
399 account for cryptic encrusters; one problem is that encrusters commonly occur
400 across much of stromatoporoid bases, leading to difficulty of understanding how
401 the stromatoporoid could have created a cavity without movement. However,
402 Wood (1999, page 74) demonstrated that some *in situ* stromatoporoids in
403 Devonian back-reef facies of the Canning Basin, Australia, could develop primary
404 cavities that had pendant, downward-growing microbial forms on their bases.
405 Building on Wood's work, Kershaw et al. (2006) explored this relationship more
406 widely in stromatoporoids and discovered in many cases that there is great
407 difficulty of interpreting whether growth occurred directly on the soft sediment
408 substrate of clay-rich micrites, or formed primary cavities that are not preserved.
409 Nevertheless, in a large number of other cases, growth directly on sediment is
410 demonstrable (Fig. 3A). Stromatoporoids that grew on the dead skeletons of
411 other organisms (Fig. 1G and likely Figs. 4B, C) clearly used these as hard
412 substrates, but in many cases there is a thin layer of clay-rich micrite covering
413 the dead skeleton; thus stromatoporoids were able to grow on such sediment
414 surfaces. In other cases the substrate comprises several cm of wackestone.
415 Whether this sediment was unconsolidated at the time of beginning of growth
416 remains unclear in many stromatoporoids but in others there is good reason to
417 interpret a stabilised surface (Fig. 5A and C and photographs in Kershaw et al.,
418 2006) that may have been partially lithified and/or stabilised by microbial
419 filaments (see Bosence et al., 2015, also Hillgärtner et al., 2001) that are not
420 preserved.

421 The issues outlined above mean that classification of the consistency of
422 the original substrate is not reliable because of the various interpretations that
423 can be applied. We therefore envisage several possible alternative substrate
424 conditions that a stromatoporoid may have grown on:

- 425 1) Growth directly on fine-grained sediment that may have been
426 unconsolidated at the time;
- 427 2) Growth on stabilised sediment;
- 428 3) Growth on hard substrates (hardgrounds);
- 429 4) Growth on skeletons of dead organisms (prior stromatoporoids, corals,
430 brachiopods, orthoconic nautiloids, gastropods).

431 Of potential importance in understanding the relationship between
432 stromatoporoids and their substrates is the initial attachment point of an
433 individual stromatoporoid. The first growth of a stromatoporoid individual may be
434 expected to define its ability to develop and survive. In the process of this study,
435 numerous hand specimens were found where the base can be easily completely
436 exposed by washing the uncemented sediment off the base, or were found in
437 outcrop with sediment fully removed by weathering. These show excellent
438 preservation of the basal surface of the stromatoporoids, which therefore seem to
439 have grown on unconsolidated sediment and were selected for careful sectioning
440 to try to locate the first growth point of the specimen. Other samples where
441 sediment below the stromatoporoid was lithified sediment with shell material
442 were sectioned vertically through the central part in an attempt to relate the early
443 growth to substrate. This effort resulted in recognition that the first point of
444 attachment of a new stromatoporoid to its substrate is not identifiable. Instead, in
445 all samples studied, the basal portion of a stromatoporoid extended itself across
446 the substrate to form an initial very thin laminar sheet as the basis for further
447 growth. Good examples are in vertical sections in Figures 5, 6 and 7. Kershaw
448 (1990) identified lateral merging of neighbouring individuals of the same taxon as
449 a means of occupying space on the substrate, termed coalescence by Kershaw
450 (1990). In some cases the stromatoporoid died before it could develop further
451 (e.g. Fig. 8D where the initial attachment cannot be identified).
452



453
 454 Fig. 5. Further examples of stromatoporoids from bedded wackestones. A) and
 455 B), Vertical and surface views of the same sample of *Eostromatopora impexa*
 456 (yellow arrow), showing growth on a topographic high of coral-bearing
 457 wackestone, with the stromatoporoid growth down each side of the sediment
 458 surface (red arrows on A). The shape of the stromatoporoid base and lack of
 459 geopetal sediment makes this difficult to interpret as having had a primary cavity.
 460 Furthermore, the steep sediment surface and close fit of the irregularly-shaped
 461 stromatoporoid base with the sediment is inconsistent with growth on
 462 unconsolidated sediment, and is interpreted here as evidence of partial
 463 lithification and erosion of the substrate before stromatoporoid growth. This kind
 464 of relationship is very common in stromatoporoids. C) Two specimens of the
 465 same taxon of stromatoporoid (*Densastroma pexisum*); the lower specimen was
 466 bored on its top surface before burial (yellow arrow) and the upper shows an
 467 irregular base directly on sediment without geopetal cement, another example of
 468 evidence of growth directly on sediment. Growth interruption on the right side
 469 (green arrow) shows recovery, again with an irregular base. D) Upper part is a
 470 stromatoporoid (*Petridiostroma simplex*, yellow arrow) growth on tabulate coral
 471 (red arrow), with the righthand two thirds of the stromatoporoid directly on the
 472 coral, and the lefthand third on micrite that coated the coral surface, a common
 473 feature in stromatoporoids; see Fig. 6 for details of a similar sample in thin
 474 section. Upper Visby Fm, Wenlock, Silurian; A and B: Ireviken; C-D: Häftingsklint,
 475 Gotland, Sweden (Calner et al., 2004).
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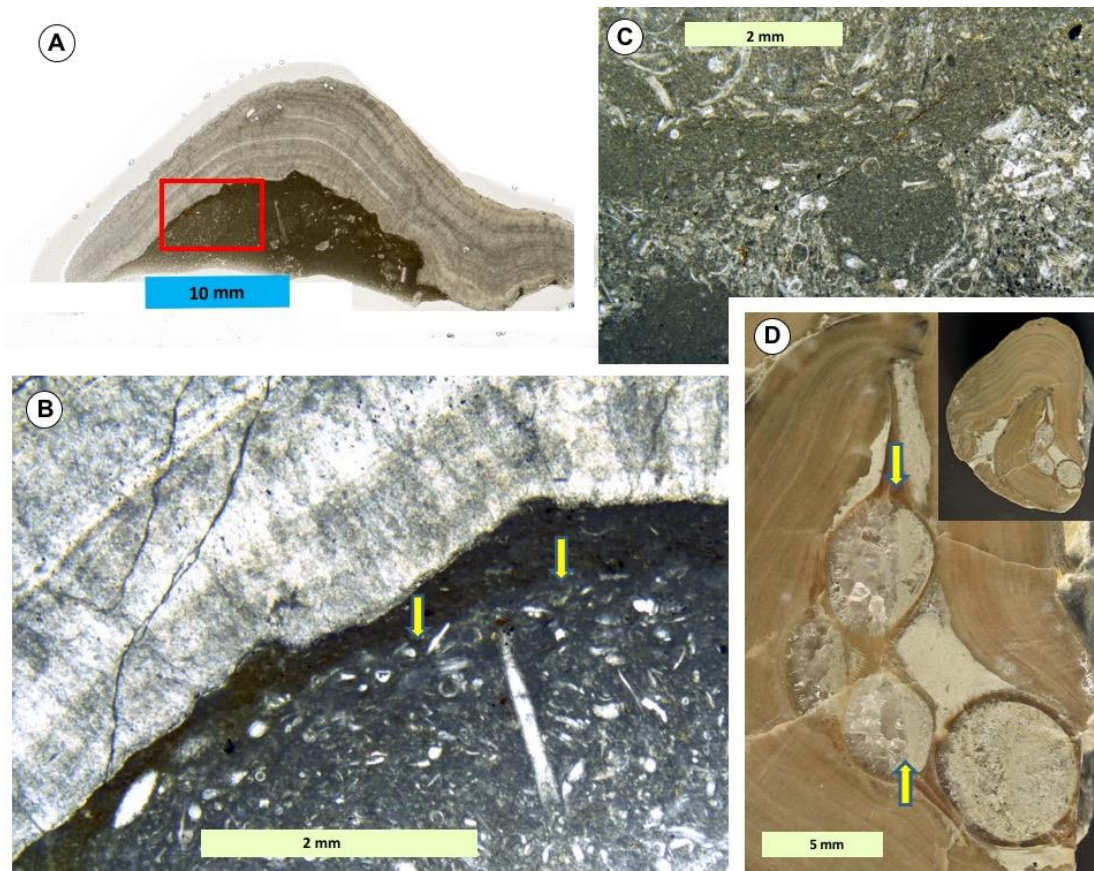
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Examination of the basal surface of a stromatoporoid cut in vertical section shows that the relationship between the early part of the growth and its substrate is indistinguishable from later parts of the growth and its substrate (Figs. 6 and 7A, B are examples). Furthermore, perhaps the most valuable aspect of stromatoporoid base-substrate relationships is that sedimentation rate must have been effectively zero for the initial growth to be uninterrupted.



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Fig. 6. Vertical thin section of a stromatoporoid (*Densastroma pexisum*) growth on a tabulate coral with sediment layer (lower yellow arrow), crinoid holdfast (red arrow), and recovery from interruption (upper yellow arrow). The lower coral in this picture grew at least partly directly on the sediment (composed of micrite) surface, similar to the stromatoporoid, and is representative of Palaeozoic corals. Note the presence of a few spiral intergrown tubes in the stromatoporoid (small white areas), discussed later. Upper Visby Fm, Wenlock, Silurian; Ireviken, Gotland, Sweden (Calner et al., 2004).

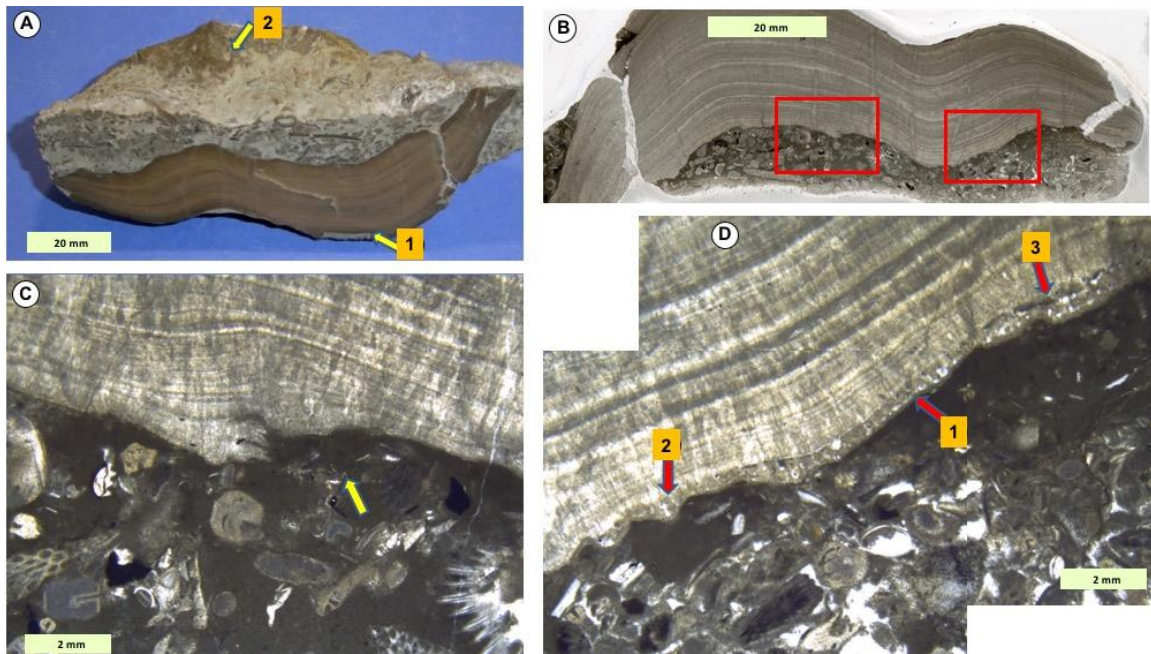


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 497 Fig. 7. Evidence of partly lithified sediments used by stromatoporoids, in this
 498 case all are *Densastroma pexisum*. A) and B) Thin-section views of a small
 499 stromatoporoid that grew on a topographic high; red box shows approximately
 500 the position of B. B) Thin section from another section from this sample, showing
 501 a sharp boundary of a burrow in sediment below the stromatoporoid indicating
 502 firm sediment that may have been partially lithified; thus the very dark layer
 503 directly below the stromatoporoid is the sediment upon which it grew; the sharp
 504 boundary with lighter sediment rich in bioclasts is the upper edge of the burrow
 505 (yellow arrows). C) Thin section of another sediment sample shows burrowing of
 506 wackestone, with sharp burrow boundary (lower centre), indicating partly lithified
 507 sediment. D) Polished vertical section of a reorientated stromatoporoid, wherein
 508 the first growth occurred on a gastropod; note the geopetal infill in the gastropod
 509 (yellow arrows mark the boundary between the sediment and cement, here
 510 vertically orientated) was sufficiently stabilised prior to movement to prevent re-
 511 settling of sediment, indicating at least partial lithification before reorientation and
 512 regrowth occurred. Note in A, the presence of a few spiral intergrown tubes
 513 (small white areas), discussed later. Upper Visby Fm, Wenlock, Silurian; A-C:
 514 Ygne, D: Ireviken, Gotland, Sweden (Calner et al., 2004).

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517 Figure 8 shows details of a sequence of development of two
 518 stromatoporoids, with evidence of soft sediment as substrate. Figure 9 gives
 519 proof of stromatoporoids that grew on topographic highs but were then moved, to

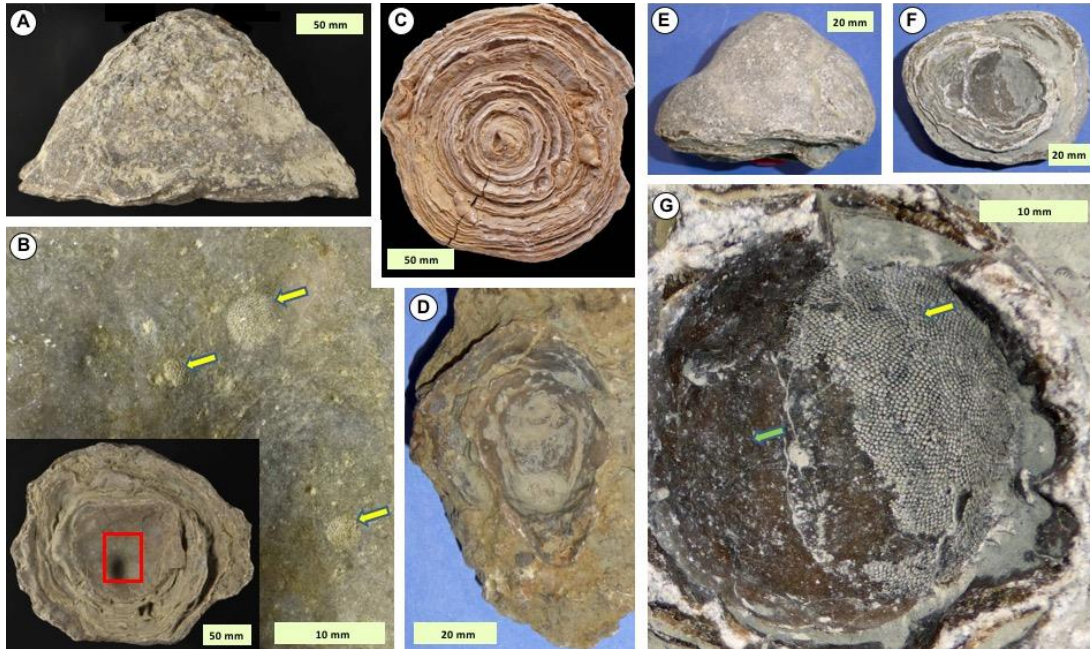
520 allow encrusters to attach to their bases. Overall, Figures 4 to 9 provide an
 521 overview of the variety of relationships between stromatoporoid bases and their
 522 substrates. However, difficulty remains in distinguishing between growth directly
 523 on substrate, and growth to form a primary cavity that was backfilled to occlude
 524 any geopetal structures. Extensive searching in thin sections and SEM has not
 525 produced any criteria to recognise fully-backfilled primary cavities. We stress, as
 526 mentioned above, that although primary cavities were proved in Devonian
 527 stromatoporoids found in growth position (Wood, 1999) with downward-growing
 528 cryptic biotas on their bases, these are rare in stromatoporoids. Nevertheless, as
 529 indicated above, stromatoporoids commonly have basal encrusters. Kershaw
 530 (1980) showed that such encrusters are not common on the upper surfaces of
 531 the stromatoporoids, indicating the encrusters were likely to be cryptic. If they
 532 were not encrusting the roofs of primary cavities, for reasons argued above, an
 533 alternative interpretation is that the stromatoporoids were moved by physical
 534 disturbance, caused by water turbulence or possibly mobile animals, creating
 535 small cavities (e.g. Fig. 9; also see Kershaw 1998 for more discussion, including
 536 report of laboratory experiments with model stromatoporoids that show they were
 537 relatively easy to move on the substrate, to create secondary cavities).
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 542 Fig. 8. Stromatoporoid bioconstruction composed of two taxa, showing evidence
 543 consistent with growth directly on sediment. A) Oblique basal view of one half of
 544 a stromatoporoid sectioned vertically along its midline, showing growth on
 545 topographic high (stromatoporoid curves over underlying sediment, indicated by
 546 arrow 2). Also note this specimen shows contemporaneous damage (arrow 1).
 547 B). Vertical section parallel and close to the line of section of A, shown in upright
 548 orientation illustrating the uneven base and locations of details in thin sections C
 549 and D. C) Basal part of stromatoporoid showing very small-scale sediment

550 interdigitation, evidence that this part of the stromatoporoid grew on
 551 unconsolidated sediment. D) Very thin (0.3 mm thick) laminar stromatoporoid of a
 552 different taxon (*Eostromatopora impexa*) grew first directly on sediment (1), then
 553 was overgrown by the upper stromatoporoid (2) (*Densastroma pexisum*) and a
 554 thin lens of sediment (3), evidence that the lower stromatoporoid died before the
 555 upper one grew. Upper Visby Fm, Wenlock, Silurian; Ygne, Gotland, Sweden
 556 (Calner et al., 2004).

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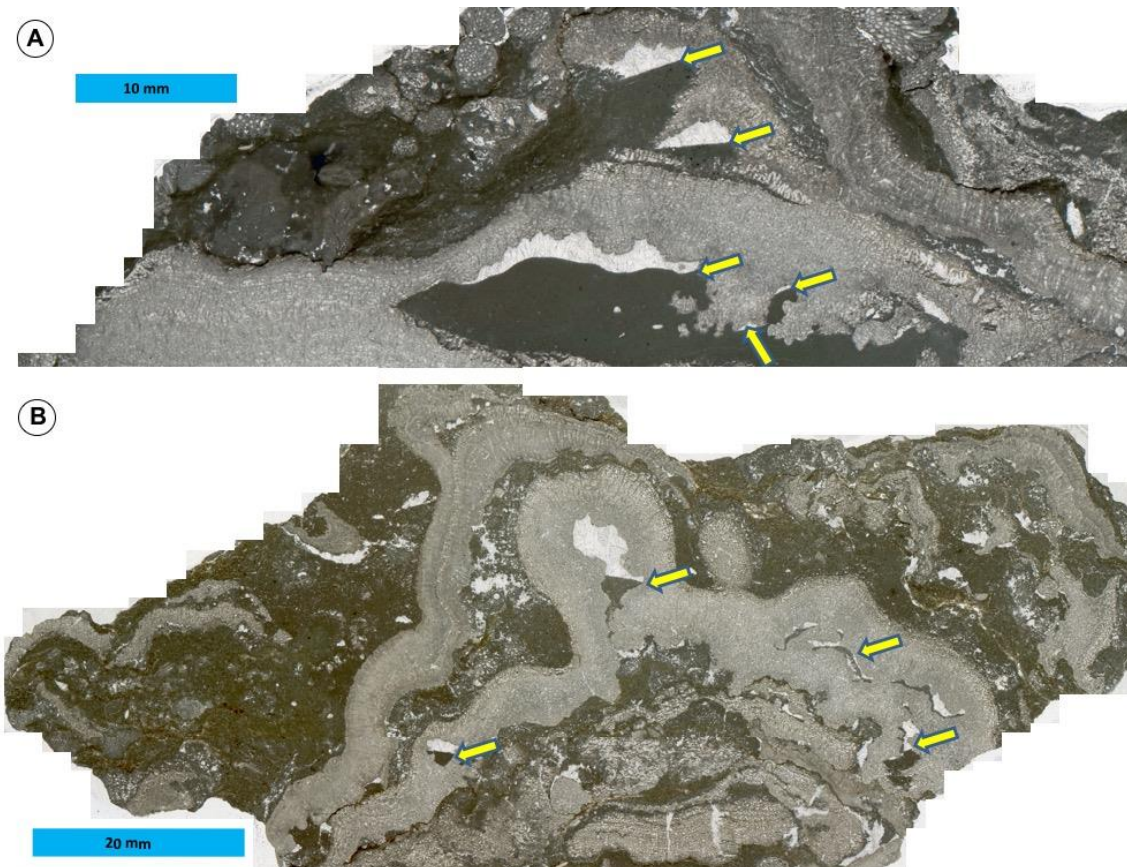
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 561 Fig. 9. Bases of unidentified stromatoporoids showing evidence of having grown
 562 initially on unconsolidated substrates because the entire base is visible, having
 563 been moved on the substrate. A-B) Side view and base of large specimen with
 564 encrusting bryozoa on the base (arrows in B). C) Basal view of another specimen
 565 showing several shells that lay on the sea floor, over which the stromatoporoid
 566 grew. D) Basal view showing growth was on an ovoidal object, likely an
 567 oncocerid cephalopod (see photographs in Stridsberg 1985). E-G) Small
 568 specimen (E is a side view, F and G are basal views) with large encrusting
 569 bryozoan in the basal cavity (yellow arrow in G) on the stromatoporoid basal
 570 surface (green arrow); likely this stromatoporoid grew on a shell, separated by a
 571 thin layer of soft sediment, and the base was exposed by storm action before the
 572 bryozoan attached. A, B and D-G from the Upper Visby Fm; C from the
 573 Klinteberg Fm, Wenlock, Silurian, Gotland, Sweden (Calner et al., 2004).

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576 As stated above, stromatoporoids have rare geopetal structures that might
 577 have been primary cavities below their bases (e.g. Kershaw et al., 2006; Nestor
 578 et al., 2010, Fig. 7, Plate 15a & b), but these lack encrusters that would
 579 strengthen recognition of primary cavities. The typical appearance of such

580 cavities is shown in Figure 10A, which is an excellent illustration of the problem
581 of determining whether a primary cavity existed below a stromatoporoid base or
582 not. If those specimens grew on sediment that was then partly removed to leave
583 geopetals, there is a problem to explain the irregular shape of the sediment
584 surface, particularly in the centre of Figure 10B, if the micrite was
585 unconsolidated. If the micrite was partially lithified then there is a further problem
586 of how to explain how such a small irregular protrusion of sediment was created
587 on the sea bed; erosion of lithified sediment on the sea floor would not be
588 expected to produce such a structure.

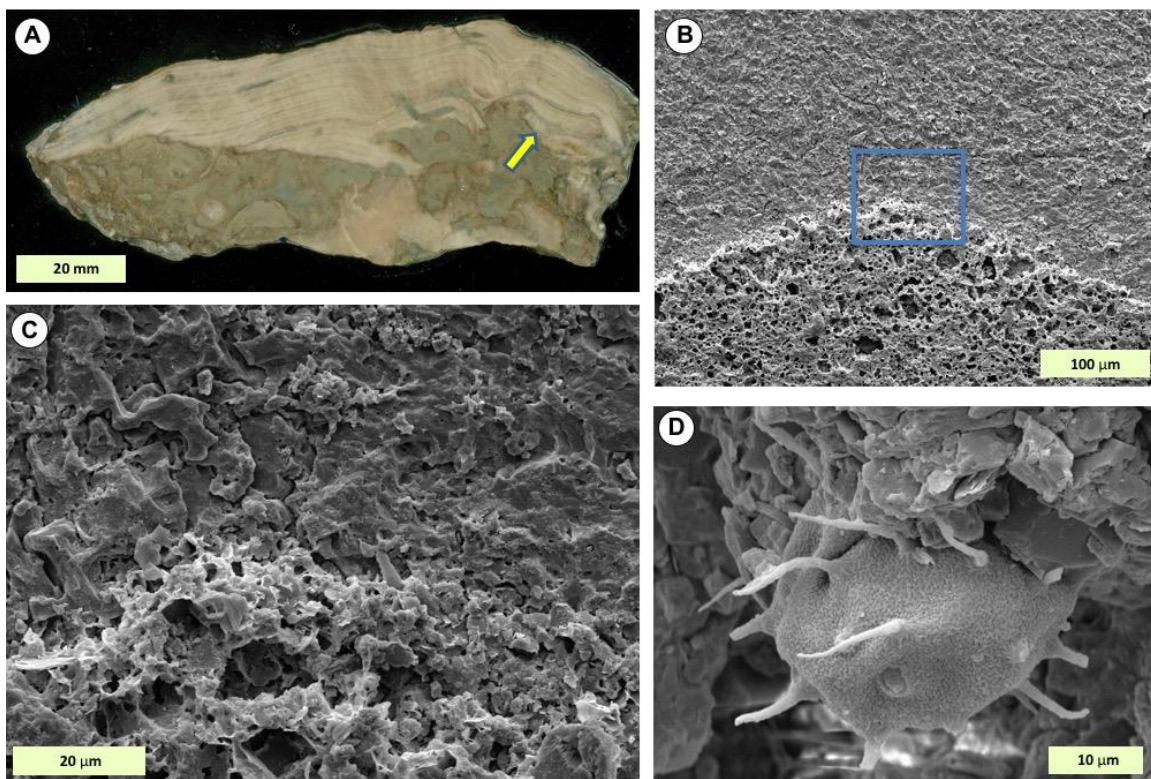
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592 Fig. 10. A) and B) Stromatoporoids showing irregular bases, but with rare display
593 of geopetal sediments, illustrating the problem of interpreting geopetals in
594 stromatoporoids. Both stromatoporoids show the irregularity of basal surfaces
595 that is common in stromatoporoids that grew on sediment (compare the basal
596 surfaces of the stromatoporoids in this figure with those in Figs. 5 and 7 where
597 there is no cavity). In each example, the main stromatoporoid is *Actinodictyon*
598 *nestori*, and the upper thin laminar stromatoporoid is *Syringostromella yavorskyi*
599 (see Mori, 1969). Högklint Fm, Wenlock, Silurian; Kopparsvik Quarry, Gotland,
600 Sweden (Calner et al., 2004; Watts and Riding, 2000).

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604 However, although such examples invite alternative explanations, our detailed
605 examination of stromatoporoid bases reveals a repeated pattern of gently curving
606 concave-down bases that are commonly very irregular and are evidence of
607 growth on topographic highs. Samples illustrated in Figs. 5, 6, 7 and 9 are only a
608 few of many hundreds of specimens that show concave-down bases. Those with
609 smooth bases can be linked to growth on individual large shell bioclasts (e.g. Fig.
610 9D, in which the ovoidal cavity is one example of many that is consistent with
611 oncocerid orthocones as bases, see Stridsberg, 1985). We emphasise that
612 detailed investigation using SEM has not revealed any evidence to counter the
613 interpretation that stromatoporoids could grow on soft sediment, but in many
614 cases determination of substrate consistency remains inconclusive;
615 representative photographs are shown in Figure 11.
616



617 Fig. 11. Scanning electron microscope study of a small part of a stromatoporoid
618 base (arrow in the vertical cut surface in A) reveals growth directly on sediment
619 surface (B and C), found repeatedly in SEM study. The blue box in B is enlarged
620 in C. D) An uncompact acritarch in the sediment shows early partial
621 lithification, evidence that the stromatoporoid grew on either unconsolidated
622 sediment that was subsequently lithified at an early stage, perhaps while the
623 stromatoporoid was still alive, or partly lithified sediment. *Densastroma pexisum*,
624 Much Wenlock Limestone Fm, Wenlock, Silurian; Penny Hill Quarry, near
625 Malvern, Worcestershire, UK (Bassett, 1974).
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629 The interpretation of the relationship between stromatoporoids and their
630 substrates, based on illustrations in this paper, requires a case-by-case
631 approach, but the bulk of evidence is that while some stromatoporoids grew on
632 dead shells, they were fully capable of growing directly on sediment, including
633 soft substrates. However, as shown here, there are numerous cases where we
634 interpret that they took advantage of early sediment stabilisation that may have
635 been partial sediment lithification. Whether this stabilisation occurred directly on
636 the sea floor or occurred a short distance below it (with soft sediment removed by
637 water turbulence) is undetermined, but the sediment became sufficiently firm at
638 an early stage to leave evidence in stromatoporoid samples (e.g. Fig. 5A and B).
639 Later physical disturbance commonly turned over the stromatoporoids followed
640 by regrowth by: 1) continued growth of living parts of the overturned
641 stromatoporoid; 2) new stromatoporoid of same or different species. Illustrations
642 here demonstrate this pattern for the Upper Visby Fm (Wenlock) on Gotland; we
643 also recognise this habit in calcareous mudstones of the Ludlow Hemse Group
644 (informally called Hemse Marl) on Gotland, and in Wenlock age limestones in
645 England (not illustrated here). Stromatoporoids were easily overturned and
646 moved, but clearly capable of recovery.

647 On the larger scale of stromatoporoid geological history we interpret that
648 throughout Middle Ordovician to end-Devonian time, very early sea-floor
649 stabilisation was common, which, as far as we know, is the first recognition of
650 this aspect of middle Palaeozoic sea floors from stromatoporoid evidence.
651 Perhaps it is not surprising that carbonate-rich sediments on the sea floor may
652 have been easily stabilised and partly lithified because the concept of intraclasts
653 is a prime component of limestone classifications that indicate erosion of early
654 lithified sediment. On the broad scale of Phanerozoic ocean history, there is
655 general agreement that the period when Palaeozoic stromatoporoids lived was a
656 time of calcite seas (e.g. Balthasar and Cusack, 2014), high level of ocean-
657 atmosphere carbon dioxide (e.g. Zeebe, 2012), high sea-surface temperatures of
658 ca 30 degrees C with reefs at palaeolatitudes as high as 45-55 degrees (Copper,
659 2011) and high levels of carbonate accumulation in shallow seas (Ridgewell,
660 2005). Munnecke et al. (1997) presented evidence from SEM and isotope work
661 that early formation of calcite microspar was a feature of the shallow marine
662 sediments, and that transformation of original aragonite muds to calcite cements
663 occurred early in the history of the sediments. Evidence in our samples of early
664 lithification of sediments directly below stromatoporoids is augmented by
665 presence of undeformed acritarchs (Fig. 11).

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668 **6. Stromatoporoid growth histories and the importance of growth-** 669 **interruption events**

670 Stromatoporoids are well-known to be potentially useful tools for
671 environmental analysis because of the changes recorded in their skeletons
672 (Webby and Kershaw, 2015). Thus, recognition of interruptions and their causes
673 is the second of the four attributes we regard as essential to understanding

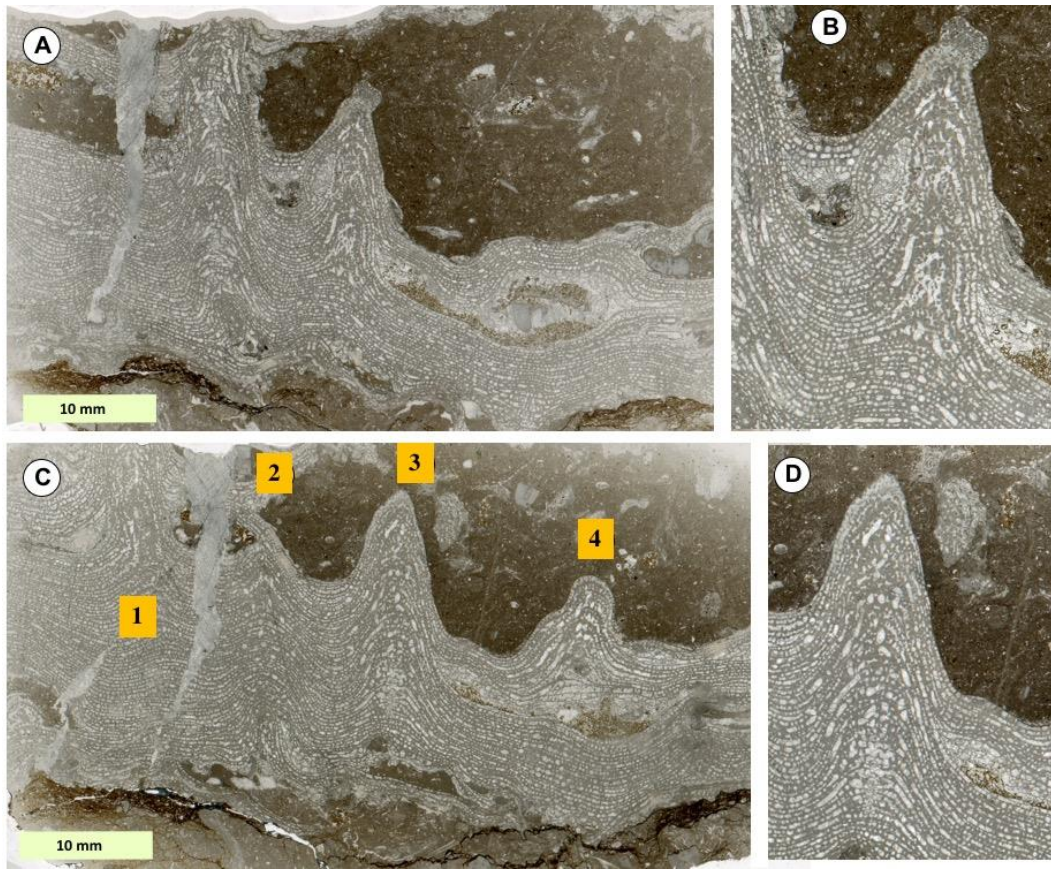
674 stromatoporoid growth and to utilising these fossils in facies analysis. Evidence
675 of growth interruption in stromatoporoids (and also tabulate corals) is present in
676 every specimen we studied as part of this work. Of all the stromatoporoids in the
677 previous figures (Figs. 1 to 11) only one specimen (Fig. 7A, B) is not affected by
678 growth interruption during its life, but it may have died as a result of the ultimate
679 interruption of being buried so deeply it could not recover, which might explain
680 why it is a small fossil (stromatoporoid in Fig. 7A is only 33 mm in basal
681 diameter). Therefore, understanding growth interruption is very important. Further
682 evidence of growth interruption is illustrated in Fig. 12; in this sample interruption
683 affected the lower portions of a laminar stromatoporoid but had little impact on
684 the columnar projections rising vertically from the surface. The features of Figure
685 12 are here interpreted as evidence for sedimentation as cause of the
686 interruption, wherein the columns were above the level of the sediment and were
687 little affected. If a different process caused the interruption, then there is difficulty
688 to explain why the tops of the columnar projections were little affected by the
689 interruption in contrast to major interruption of the topographically lower parts. In
690 contrast, the stromatoporoid in Figure 13 is significantly more complex and has
691 several interruptions in its lower portion, with minor sediment wedges in the lower
692 flanks on both sides (Fig. 13A) that can be traced as banding through the
693 specimen. Approximately two-thirds up the sample has a major interruption that
694 comprises three sub-events which overlap. In this case, the interruption affects
695 the topographically highest part of the surface while the left lower flank is barely
696 affected. This situation is common amongst interruption surfaces in
697 stromatoporoids and creates a problem of explaining how they occur. Evidently
698 sediment has accumulated on the stromatoporoid surface but is concentrated in
699 one area. We consider the most likely interpretation of this feature is that the
700 interruption was caused by sedimentation across much of the stromatoporoid
701 surface, but the stromatoporoid soft tissue was able to self-clear much of the
702 sediment, perhaps where it was a thin layer, allowing an area of live sponge
703 tissue from which recovery could occur. Experimental work on modern sponge
704 tolerance to sediment by Strehlow et al. (2017) shows that living sponges have
705 efficient sediment-clearing mechanisms capable of removing all sediment from a
706 sedimentation event off the living surface within three days, but when
707 sedimentation was chronic, removal took 14 days or more. Nevertheless the
708 sponges survived and recovered. If Palaeozoic stromatoporoids possessed this
709 ability, then it is likely that the majority of growth interruption events can be
710 attributed to sedimentation, which may be due to local sediment reworking by
711 transient currents.

712 Following growth interruption in any stromatoporoid, it is possible that the
713 soft tissue became dormant for a short time, before recovery, thus leaving a
714 prominent disruption visible in vertical sections. However, there are no features
715 described in publications or in any of our material indicative of dormant periods.
716 Nevertheless, modern non-calcified sponges have dormant phases when
717 gemmules (bud-like cells) form during adverse conditions (e.g. Frost, 1991;
718 Harrison and Cowden, 1976). In modern *calcified* sponges, dormant
719 pseudogemmules are known in *Acanthochaetetes wellsi* (West et al., 2013, p2).

720 Work on Lower Devonian laminar stromatoporoids by Adachi et al. (2006)
721 interpreted repeated harsh conditions for growth interruptions in stromatoporoids,
722 which recovered when the adverse conditions ended, circumstantial evidence for
723 dormancy in fossil stromatoporoids.

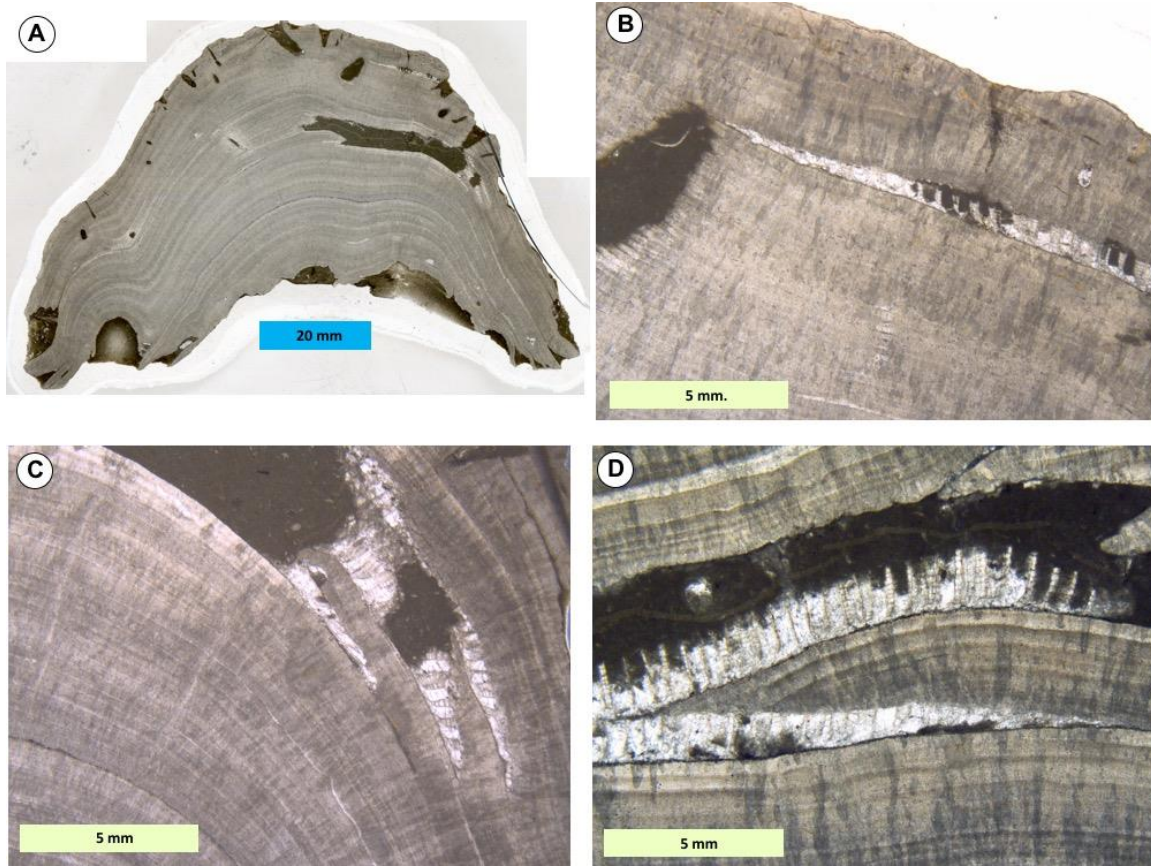
724 Growth interruptions also seem to relate to growth banding in
725 stromatoporoids (Figs. 5A, 11A and 13A are good examples). Young and
726 Kershaw (2005) attempted the first comprehensive approach to understanding
727 growth banding in stromatoporoids and corals. They showed that in almost all
728 cases, stromatoporoids did not exhibit growth banding, instead banding was
729 created by interruption of growth. A major outcome of that study is the need to
730 view the margin of a stromatoporoid, to identify the nature of the contact between
731 the skeleton and the sedimentary deposits collecting around it as it grew. Overall,
732 as argued above, growth interruptions in stromatoporoids that have not been
733 dislocated and re-orientated are generally interpretable as related to
734 sedimentation, consistent with the irregularity of banding in many
735 stromatoporoids. However, stromatoporoids commonly show regular banding,
736 evidence that growth rates of individual stromatoporoids varied on a regular
737 pulse, so the possibility exists that the stromatoporoid stopped or slowed growing
738 episodically, perhaps regularly, and allowed sediment to collect. Evidence in the
739 primitive stromatoporoid, *Pulchrilamina*, indicates it paused regularly in growth
740 (Adachi et al., 2012). Growth banding may thus be a real phenomenon in
741 stromatoporoids, and growth rates interpreted by some authors (e.g. Gao and
742 Copper, 1997) of about 3 mm/year may be accurate estimates. The issue that
743 remains is to prove the growth banding is due to annual variation of
744 stromatoporoid growth, that future work may succeed in solving.

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Fig. 12. Two vertical thin sections, cut parallel to each other and *ca* 2 cm apart, from one laminar-form unidentified stromatoporoid, showing variations in details of growth. Both sections show: i) negative geotropic growth in the columnar projections from the upper surface; and ii) the effects of the same growth interruptions. Lower topographic parts of the specimens were affected by interruption, whereas the upper parts of the columnar protrusions show minimal influence of the interruption; A) has two prominent geotropic columns in the plane of section. B) Enlargement of righthand projection in A, showing no evidence of growth interruption in the central upper part, but do on the flanks. C) A different plane of section showing four geotropic columns (numbered). D) Enlargement of projection 3 in C, showing only the flanks are affected by interruption. Preservation of the base of the stromatoporoid is affected by pressure solution. Santa Lucía Fm, Emsian, Lower Devonian; El Millar, Cantabrian Mountains, northern Spain (Fernandez et al., 1995; Mendez-Bedia et al., 1994).



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 765 Fig. 13. Growth interruption accompanied by encrusting bryozoans in a
 766 stromatoporoid that recovered from the interruption. A) Whole stromatoporoid in
 767 vertical thin section, showing concave irregular base interpreted as growth
 768 directly on an eroded sediment surface. Several interruption surfaces are visible,
 769 detailed in B-D, but note the left side of the sample shows almost no evidence of
 770 the interruptions. B) Detail of upper right hand part of A, showing a *Trypanites*
 771 boring that penetrated the stromatoporoid at a growth interruption surface, and
 772 an encrusting bryozoan on the same interruption surface. The bryozoan has
 773 sediment deposited in its zooecia, indicating it was killed before overgrowth by
 774 the recovery of the stromatoporoid, interpreted as evidence of a notable length of
 775 time of the interruption prior to new growth of the same stromatoporoid taxon. C)
 776 Enlargement of right side of A, showing three closely spaced overlapping
 777 interruptions, with bryozoan growth on the interrupted surfaces. D) Detail,
 778 from another thin section of the same sample, cut 1 cm parallel to the thin section
 779 figured in A-C; D shows two interruptions of stromatoporoid growth accompanied
 780 by bryozoan encrustation, stromatoporoid recovery and sedimentation.
 781 *Densastroma pexisum*, Upper Visby Fm, Wenlock, Silurian; Häftingsklint,
 782 Gotland, Sweden (Calner et al., 2004).

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7. Organisms associated with stromatoporoids and their importance in environmental analysis

787 The third of our four key attributes of stromatoporoids relates to numerous
788 studies which describe organisms associated with stromatoporoids, from the
789 early work by Nicholson (1885-1892) to modern papers (e.g. Mori, 1970; Nield,
790 1986; Tapanila, 2005 for bioclustrations; Stearn, 2015c; Vinn, 2016 and
791 references therein for other symbionts in stromatoporoids). There are two groups
792 of associations with stromatoporoids that are easily recognisable in hand
793 specimens, thin sections and some also clearly visible in outcrop; they are
794 surface-associated organisms (epibionts) and internally-associated organisms
795 (endobionts).

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798 7.1. Surface-associated organisms (epibionts)

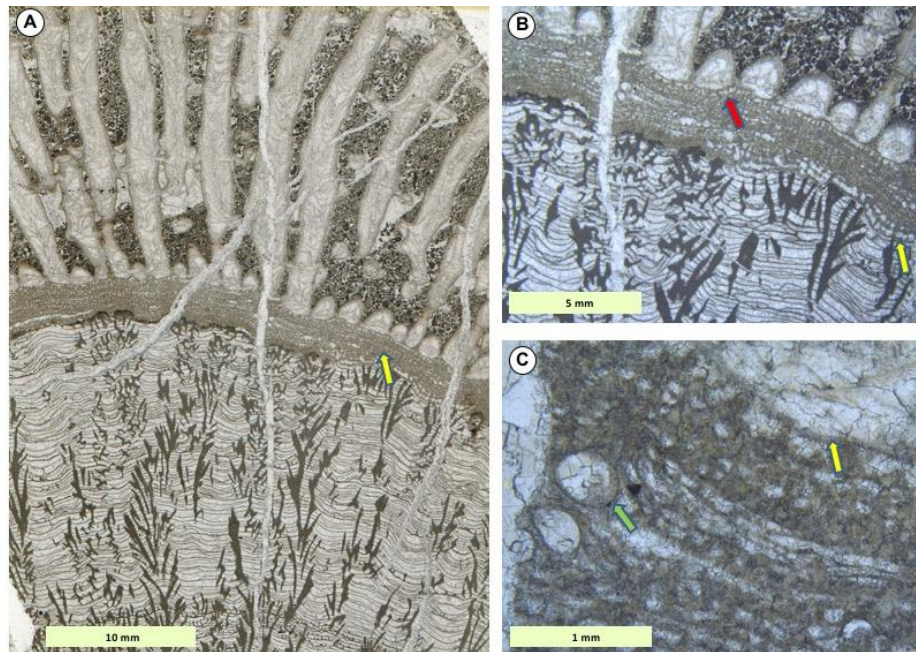
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800 Epibionts are organisms associated with both the upper and lower surfaces of
801 stromatoporoids, and include encrusters and borers. Borers are classed here as
802 surface-associated organisms because they entered stromatoporoids from their
803 surfaces. In examples of unconsolidated sediments, where stromatoporoid
804 surfaces can be cleaned of sediment in the laboratory, epibiotic organisms can
805 be found in many cases to be abundant on both upper and lower stromatoporoid
806 surfaces (e.g. Nield, 1986). It is highly likely that the majority of encrusters and
807 borers colonised the surfaces after death of the stromatoporoid, because
808 stromatoporoids show no reaction to their presence, in contrast to endobionts.
809 Examples of epibionts are bryozoans (Figs. 3A, 9 and 13), *Trypanites* borings
810 (Figs. 3A, 4C, 5C and 13), crinoids, spirorbid worms, corals and brachiopods.

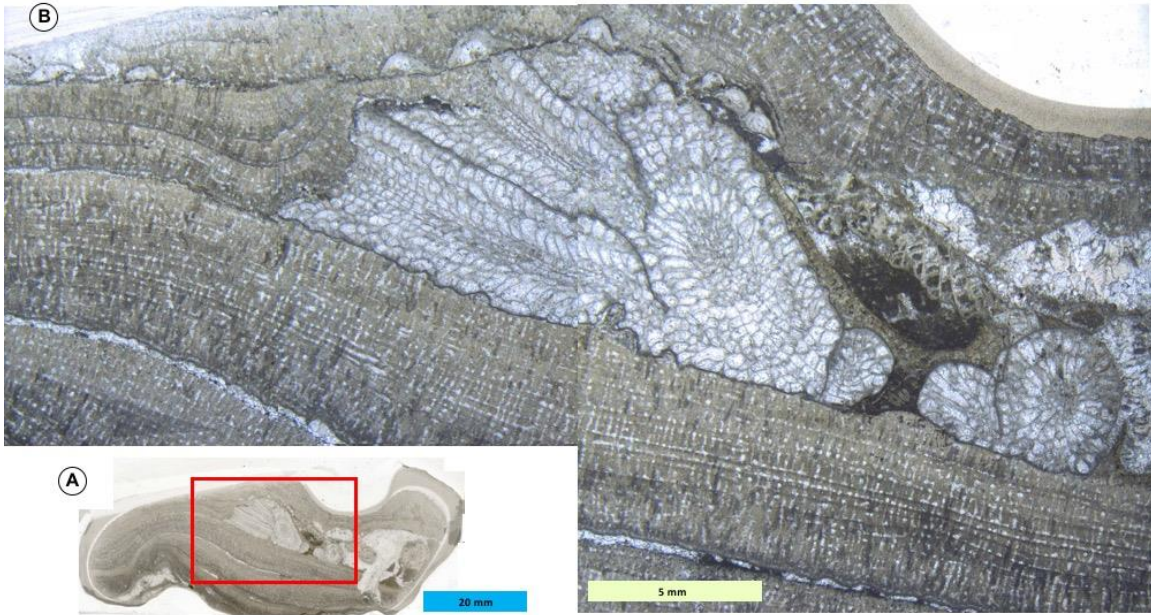
811 The application of epibionts in analysis of stromatoporoids and facies
812 depends on understanding the nature of the relationship. Regarding epibionts on
813 the growth (upper) surface of stromatoporoids, because in almost all cases the
814 stromatoporoids were dead before epibiont growth, there must have been a time
815 difference between stromatoporoid death and colonisation. The length of this
816 time is not determinable, of course, but it is reasonable to presume that a greater
817 density of epibionts is likely to indicate a longer time for the surface to have been
818 available, during which there was presumably little or no sedimentation.
819 Abundant epibionts on stromatoporoid bases may have attached after
820 stromatoporoids were moved by water turbulence (or possibly dislodged by
821 mobile organisms on the substrate or nekton), and it is unknown whether the
822 stromatoporoids were alive or not at the time of epibiont attachment.
823 Nevertheless, stromatoporoid-rich deposits with abundant epibionts reflect the
824 episodic nature of sedimentation in those settings, and may be consistent with
825 abundance of growth interruption during the life of the stromatoporoid.

826 Excellent examples of epibiont associations with stromatoporoids studied
827 as part of this work are the marls of the Upper Visby Formation (Wenlock,
828 Silurian) and the Hemse Group marls (Ludlow, Silurian) of Gotland, Sweden,
829 because in both cases, stromatoporoids can be extracted whole. For
830 stromatoporoids enclosed in cemented limestones, therefore often in reef
831 structures, stromatoporoid surfaces are less available, normally visible only as
832 cross sections in cliff faces, making assessments of abundance of epibionts

833 difficult. Most stromatoporoid-bearing deposits we studied have at least some
 834 epibionts on stromatoporoids and reflect the episodic nature of sedimentation, as
 835 would be expected given that stromatoporoids themselves clearly required
 836 conditions of low sedimentation to grow. Figures 14 and 15 show examples of
 837 epibionts on both stromatoporoids and corals that are typical in reef systems,
 838 where these two groups of organisms grew in close association as part of reef
 839 construction.
 840



841
 842 Fig. 14. Two stromatoporoids and a syringoporid tabulate coral forming a growth
 843 sequence. A) The lower stromatoporoid (*Platiferostroma chaetetiporoides*) is
 844 encrusted by an unidentified laminar stromatoporoid (yellow arrow) and the
 845 syringoporid directly encrusted the upper stromatoporoid. B) Enlargement of the
 846 central part of A showing more detail of encrustation of the upper stromatoporoid
 847 on *P. chaetetiporoides* (yellow arrow), but also shows the syringoporid is partly
 848 embedded into the surface of the upper stromatoporoid (red arrow), raising a
 849 question as to whether the upper stromatoporoid was still alive when the
 850 syringoporid encrusted. C) Detail of the upper central part of B, showing tubes of
 851 a symbiotic worm (green arrow) and the base of the syringoporid (yellow arrow).
 852 Topmost part of Changtanzi Fm, Famennian, Devonian; Gui Xi area, western
 853 Sichuan (Rong, 1988). (Specimen provided by Yue Li, Nanjing).
 854



855
 856 Fig. 15. Vertical thin section of a stromatoporoid ("*Stromatopora*" *bekkeri*, a taxon
 857 awaiting confirmation of identity) from the biostrome shown in Fig. 2. At least two
 858 interruption surfaces are recognisable. The main interruption surface (with a coral
 859 encrusting it) seems to have been modified by pressure solution, but the effect is
 860 small, not laterally continuous and does not prevent the interpretation that the
 861 coral encrusted the stromatoporoid surface after growth interruption. Above the
 862 coral is an upper interruption surface that was colonised by auloporid and other
 863 tabulate corals. Hemse Group, middle Ludlow, Silurian; Kuppen biostrome,
 864 Gotland, Sweden (Calner et al., 2004).

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869 7.2. Internally-associated organisms (endobionts, including bioclaustrations)

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871 Endobionts are organisms that grew within stromatoporoids as the
 872 stromatoporoids developed (see Figs. 3 and 16). This is therefore a live-live
 873 relationship where the stromatoporoid showed reaction to the presence of the
 874 endobiont by changes preserved in its adjacent skeleton. Examples include
 875 tabulate and rugose corals, and spiral and straight tubes of worms and
 876 spirorbids; these all have shells against which the stromatoporoid laminae abut.
 877 Those without shells are called bioclaustrations, considered by Tapanila (2005)
 878 to be trace fossils. Vinn (2016) and Stearn (2015c) provided very useful
 879 overviews of the intergrowths between stromatoporoids and other organisms.
 880 Vinn and Motus (2014a) analysed the relationship between rugose corals and a
 881 stromatoporoid; and Vinn and Motus (2014b) and Tourneur et al. (1994)
 882 described intergrowths of worms in stromatoporoids. Powell (1991) described a
 883 rare association between a stromatoporoid and algae. Symbionts are rare before
 884 the early Silurian, so their utility is effectively limited to Silurian and Devonian

885 stromatoporoids. Some endobionts are illustrated in Figures 3B-D (syringoporid
886 tabulate and spiral tubes), 6 and 7A (small spiral tubes).

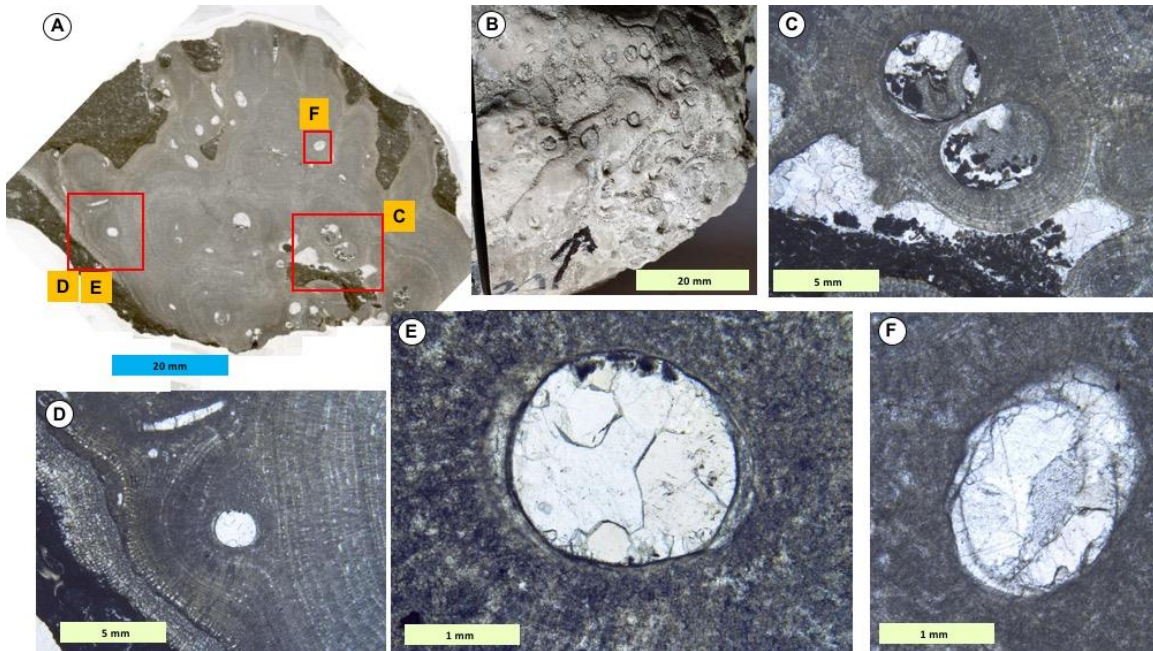
887 Intergrown organisms are most commonly found in reef environments,
888 which may be due to higher energies of reefs encouraging the more delicate
889 corals and other tube-secreting organisms to seek shelter (discussed further
890 below). In contrast, examples illustrated in this paper from the Upper Visby
891 stromatoporoids and corals, lower Wenlock of Gotland, Sweden, contain no
892 intergrown corals, but there are some occasional spiral tubes. Figure 16 shows
893 an unusual case of abundant spiral tubes, which contrasts their rarity in more
894 typical cases illustrated in Figure 3.



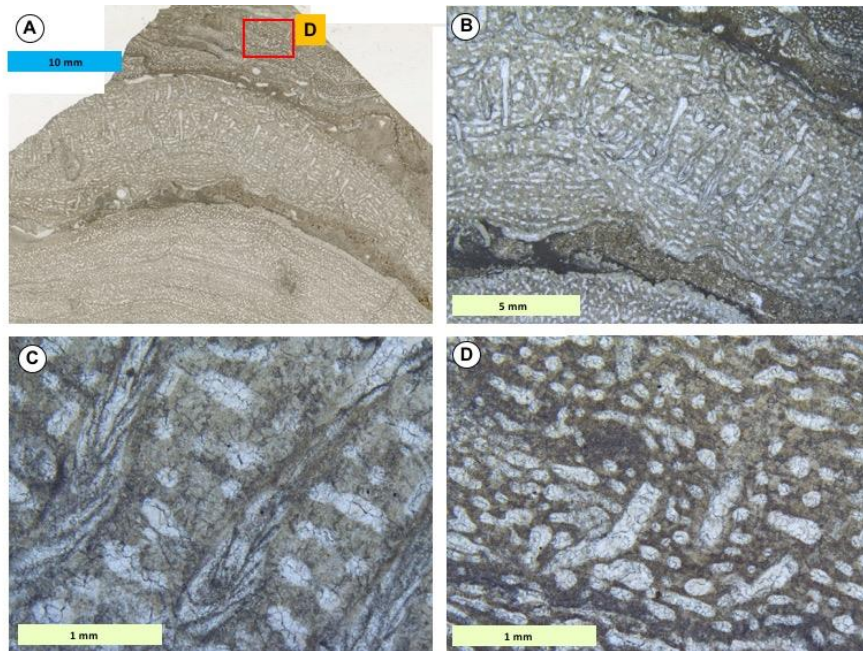
895 Fig. 16. Vertical thin section of a unidentified stromatoporoid with abundant
896 intergrown calcified tubes. Abundant tubes in a single stromatoporoid, particularly
897 in bedded limestones, is very rare; in almost all cases, normally only one or two
898 tubes occur in one stromatoporoid. This suggests a mass of larvae encountered
899 a stromatoporoid in this case. Much Wenlock Limestone Fm, Wenlock, Silurian;
900 Blakeway Hollow, Wenlock Edge, UK (Bassett, 1989).

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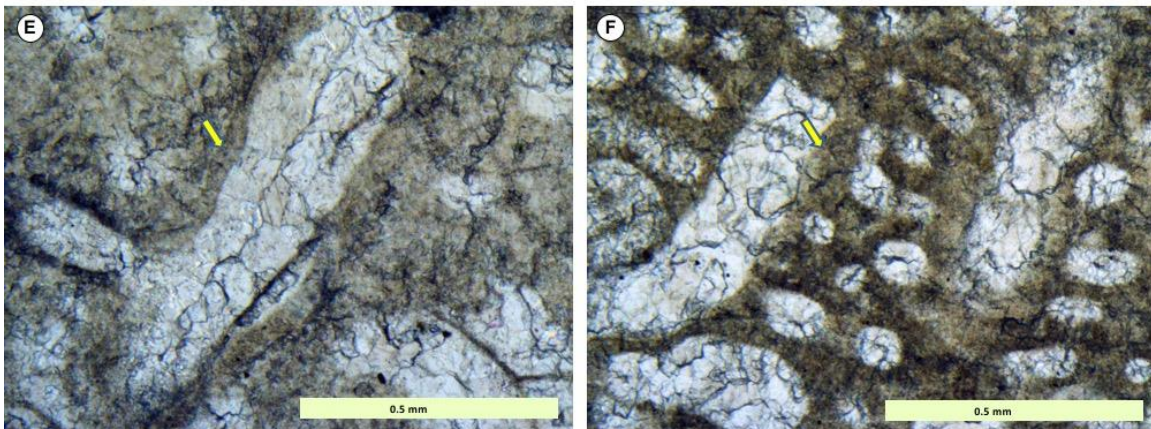
Understanding relationships between stromatoporoids and their
endobionts gives valuable information about growth characteristics of
stromatoporoids, and augments environmental analysis. However, care is
needed to discriminate between endosymbiont skeleton and the components of
the stromatoporoid. Although in Figure 17, the distinction between
stromatoporoid and endosymbiont tubes is unquestioned, this is contrasted by
Figure 18 which shows an example where the stromatoporoid skeleton can be
potentially confused with an endosymbiont. Fortunately such cases are not
common.



914
 915 Fig. 17. Calcified tubes of uncertain affinity encrusted by stromatoporoid
 916 *Syringostromella yavorskyi* (see Mori, 1969). A) Vertical thin section of whole
 917 stromatoporoid that has geotropic columnar growth in its upper part. B) Surface
 918 view showing tubes encased in stromatoporoid. C-F) Details of tubes, shown in E
 919 and F to be lined with thin shell material, separating the tube soft tissue from the
 920 stromatoporoid. In C, the tube infill is a mixture of bioclasts, matrix and cement.
 921 Höglint Fm, Wenlock, Silurian; Kopparsvik Quarry, Gotland, Sweden (Calner et
 922 al., 2004; Watts and Riding, 2000).
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Fig. 18. Vertical thin section containing three stromatoporoid taxa (unidentified), with growth interruption events at the top of the lower and middle stromatoporoids; the middle taxon contains intergrown syringoporids, missing from the other two. A) and B) All three taxa showing the historical development of the stromatoporoid. C-F) These illustrate the problem of interpretation of some tubular structures in stromatoporoids that have the appearance of intergrown organisms but lack a shell wall. Thus in C and E, the syringopridor tabulate has a coral wall that the stromatoporoid skeleton touches, while in D and F, the prominent linear cavities are lined by only stromatoporoid skeleton, creating uncertainty about whether this is part of the stromatoporoid structure or

940 represents a bioclaustration. Shiniulan Fm, Llandovery, Silurian; Qijiang,
 941 Sichuan, China (Jin et al., 1982). (Specimen provided by Yue Li, Nanjing).
 942

943 Table 1 shows a numerical compilation from Mori (1970), demonstrating the
 944 close relationship between certain stromatoporoid taxa and coral intergrowths.
 945 Mori (1970) collected 707 specimens and found 38 species, of which 11 species
 946 contain intergrown corals in 303 specimens, so 43% of all his samples contain
 947 intergrown corals. However, note that Kershaw (1990) in one biostrome found
 948 that all of the 31 samples of *Petridiostroma convictum* (previously called
 949 *Clathrodictyon convictum*) collected contain intergrown syringoporoids. These data
 950 indicate that the relationship between stromatoporoid and endobionts is
 951 biologically complex and not simple to interpret.

Stromatoporoid Taxon	No. of stromatoporoids with commensal <i>Syringopora</i> *	No. of stromatoporoids with commensal rugose corals*	Total no. of stromatoporoids	Notes "- " = No data
<i>Petridiostroma convictum</i> Yavorsky	13	3	19	Previously <i>Clathrodictyon convictum</i>
<i>Ecclimadictyon robustum</i> Nestor	4	-	26	
<i>Simplexodictyon yavorskyi</i> Nestor	4	6	8	Previously <i>Diplostroma yavorskyi</i>
" <i>Stromatopora</i> " <i>bekkeri</i> Nestor	1	1	10	Awaiting formal definition
<i>Stromatopora carteri</i> Nicholson	3	3	13	
<i>Stromatopora discoidea</i> (Lonsdale)	1	-	1	
<i>Stromatopora cf. Pseudotuberculata</i> Riabinin	2	-	12	
<i>Stromatopora venukovi</i> Yavorsky	13	3	22	
<i>Parallelostroma tenellum</i> Mori	3	-	9	
<i>Parallelostroma typicum</i> (Rosen)	2	2	97	
<i>Plectostroma scaniense</i> Mori	-	10	86	

952
 953 Table 1. Compilation of sample counts from Mori's (1970) classic study of
 954 Silurian stromatoporoids from Gotland, showing the preference of corals for
 955 certain taxa of stromatoporoids. Mori's data show that not all of these
 956 stromatoporoid taxa have intergrown corals.

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959 7.3. Stromatoporoid growth, endobionts and facies; case studies

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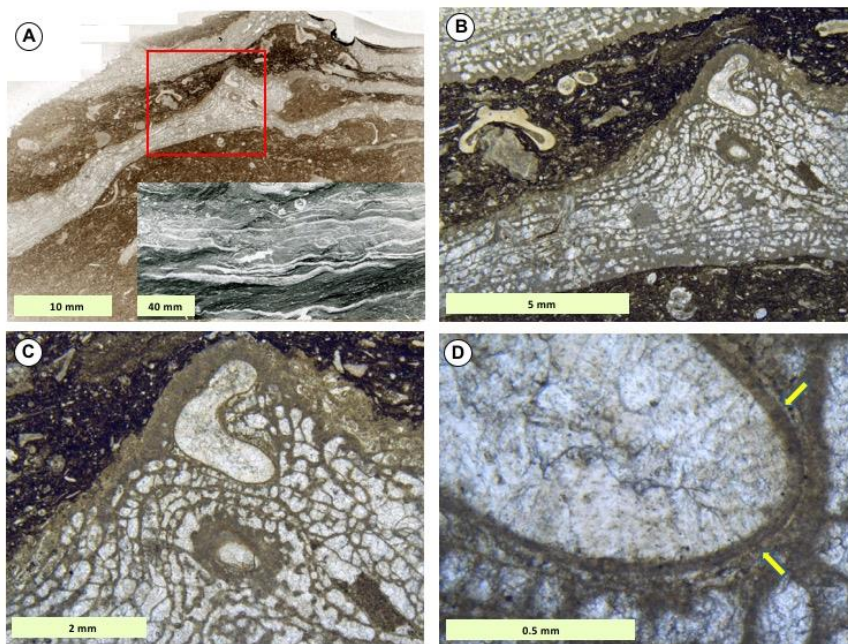
961 In this section case studies explore the utility of endobionts in stromatoporoid
 962 growth study, and demonstrate their variability and complexity.

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964 *7.3.1. Case 1: laminar stromatoporoids in calcareous mudstones*

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Endobionts in thin laminar stromatoporoids demonstrate that even in thin laminar stromatoporoids, endobionts took advantage of their presence. In the Middle Devonian case shown in Figure 19 from an open-shelf setting (Mabille and Boulvain, 2007), the facies illustrated comprises apparently organic-rich sediment that emitted a strong organic smell when thin sections were prepared, and raises a question about the low oxygen tolerance of stromatoporoids. Of course the organic matter may be a later influx during burial, but the possibility of low oxygen tolerance exists. Lee and Riding (2018, p. 111) discussed the oxygen tolerance of sponges in the Ordovician and drew attention to the fact that modern sponges can live in low oxygen conditions. As Lee and Riding (2018) noted, stromatoporoids are generally recognised as having lived in normal oxygenated environments, but the tolerance of stromatoporoids to lower oxygen levels has not been investigated. The example illustrated here may indicate some stromatoporoids had a low oxygen tolerance, and if that was the case, then the symbiont did also. Oxygenation aspects of stromatoporoid growth requires further investigation in future work.



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Fig. 19. A) Laminar stromatoporoid in open-shelf fine-grained sediments, with intergrown shelly organisms, probably gastropods, together with bioclastic debris deposited presumably by storm action. Inset in A shows vertical section of field view. B) Enlargement of red box in upper central part of A, showing spiral endosymbiotic tube. C) Detail of B, demonstrating the disruption to the stromatoporoid skeleton, presumably caused by the presence of the spiral tube, considered by some authors as evidence of parasitism of the stromatoporoid by the endosymbiont, discussed in the text. D) Detail of the endosymbiont tube in C, showing its shell structure (yellow arrows) adjacent to the stromatoporoid skeleton. Hanonet Fm, Couvinian-Givetian, Devonian; La Couvinoise (previously

994 called Haine) Quarry, near Couvin, southern Belgium (Mabille and Boulvain,
995 2007).

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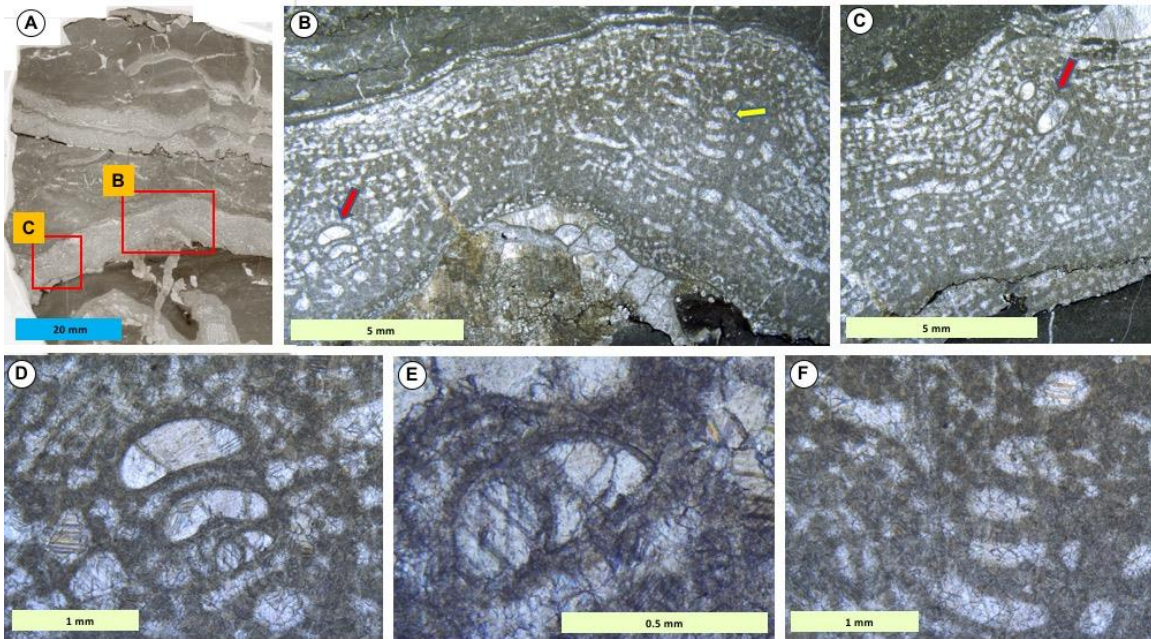
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998 Upper Devonian laminar stromatoporoids in the well-known site at Tailfer,

999 southern Belgium (Da Silva et al. 2011b), certainly formed in oxygenated

1000 conditions, and show some spiral tubes within the stromatoporoid structure (Fig.

1001 20).



1002

1003 Fig. 20. Calcified spiral tubes in laminar unidentified stromatoporoids of open-
1004 shelf facies. In most stromatoporoids such spiral tubes are rare, but there are
1005 several in this sample. A) Thin section of laminar-shaped stromatoporoids in
1006 micrite. B) and C) Enlargements of red boxes labelled in A, with spiral tubes and
1007 stromatoporoid skeletal structure (red and yellow arrows). D) Enlargement of
1008 spiral tube in the lower left part of B, showing disruption of the stromatoporoid
1009 skeleton around the tube. E) Enlargement of a spiral tube not present in B or C.
1010 F) Enlargement of stromatoporoid skeleton in the right-hand part of B, showing
1011 this is not a shelly endosymbiont but is part of the stromatoporoid structure
1012 (contrast with D and E in which the endosymbiont tubes both have shell walls).
1013 As in Fig. 18F, the possibility exists that this structure may be a bioclaustration.
1014 Lustin Fm, Frasnian, Devonian; Tailfer Quarry, near Dinant, southern Belgium
1015 (Da Silva et al., 2011b).

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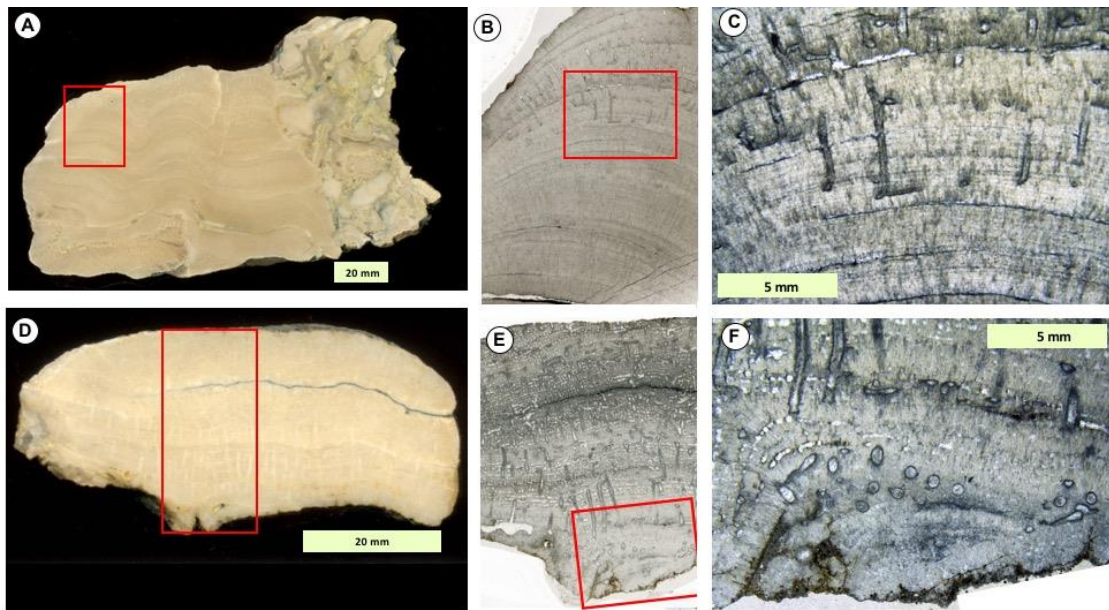
1018 7.3.2. Case 2: Timing of endosymbiont development in stromatoporoids

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1020 As far as we know, this is the first study of endosymbionts in stromatoporoids
1021 that includes the examination of entire stromatoporoids, and allows exploration of
1022 the history of the endosymbiont growth within individual stromatoporoids. In our
1023 study of a large sample, it is clear that the timing of growth of endosymbionts in a

1024 stromatoporoid structure is highly variable. A good example of this variation is
 1025 shown in the differences between the two cases in Figure 21, of syringoporids in
 1026 two specimens from the same biostrome. In Figure 21A-C two-thirds of the
 1027 stromatoporoid had grown before syringoporids appeared within its skeleton in
 1028 the plane of section illustrated, which is very unusual; in contrast, Figure 21D-F
 1029 shows the more normally encountered situation where syringoporid growth
 1030 appeared in the skeleton a short distance above the base of the stromatoporoid
 1031 in this plane of section. The situation in Figure 21D-F is a repeated observation
 1032 throughout almost all the Silurian and Devonian material examined in this study
 1033 and is discussed later.

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 1037 Fig. 21. Vertical sections of two stromatoporoids (A-C and D-F) with symbiotic
 1038 syringoporids from a biostrome. In both cases, in the planes of section of these
 1039 samples, the corals appear in the plane of section after the stromatoporoid were
 1040 established. In A-C, the coral intergrowth developed after about two-thirds of
 1041 stromatoporoid growth, in contrast to D-F, where the corals appear shortly after
 1042 the stromatoporoid base had developed. In F, the lowermost coral tubes are
 1043 horizontally orientated, shown as circles in cross section. Klinteberg Group,
 1044 Wenlock, Silurian; Vivungs, Gotland, Sweden (Calner et al., 2004).

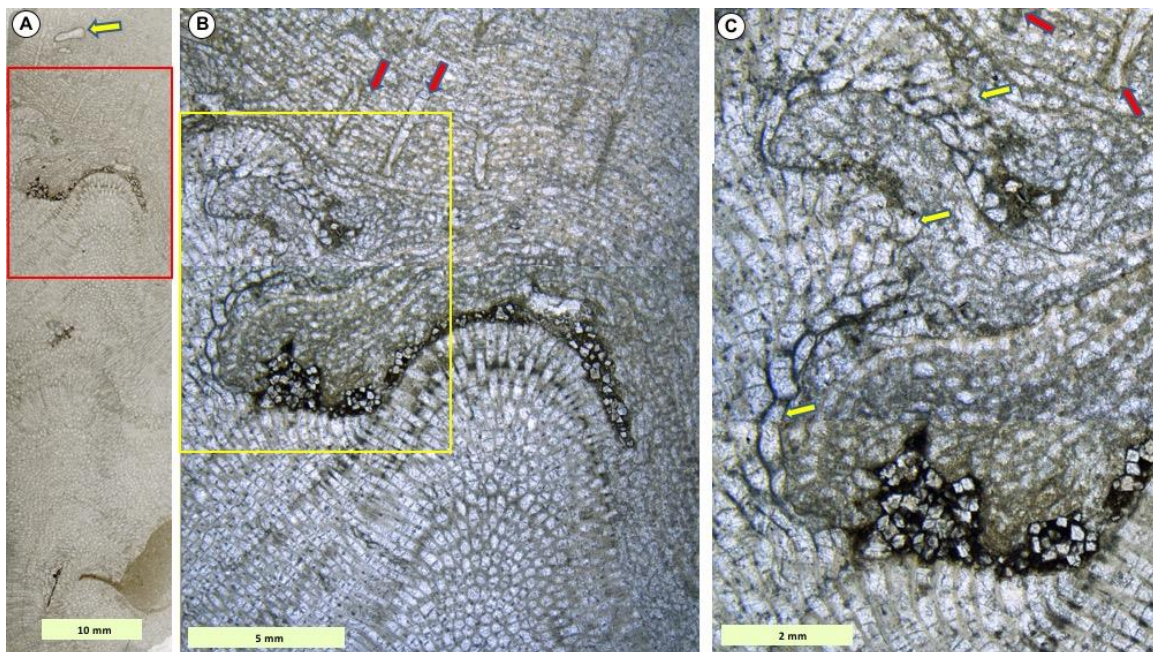
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7.3.3. Case 3: Stromatoporoids and corals in competition, together with endosymbionts

1050 In some examples, stromatoporoids clearly had a complex relationship with
 1051 nearby organisms, exemplified by Figure 22, which shows a stromatoporoid and
 1052 tabulate coral apparently competing, presumably for space. Also, the
 1053 stromatoporoid has intergrown corals, so the stromatoporoid during its life was

1054 dealing with both possible competition and the intergrowth. Note that competition
1055 between two organisms of different phyla with different ecological requirements is
1056 an interesting issue. It may be argued that corals and stromatoporoid sponges
1057 lived in different ecological niches and this may influence the concept of
1058 competition. However, evidence from examples such as in Figure 22
1059 demonstrate the two organisms grew at the same time in the same place; they
1060 both required space on the sea floor, and lived in the same conditions of
1061 turbulence and sedimentation. Although they likely ate different food (carnivorous
1062 corals versus filter-feeding sponges) there must have been considerable overlap
1063 of their environmental requirements. Therefore, we interpret that competition
1064 between these two organism types was a real feature of the ancient sea floor.

1065 Work on modern sponge-coral interactions in Colombia (e.g. Aerts and
1066 van Soest, 1979) shows that sponges were highly competitive and commonly
1067 overgrew corals, although in other work, Aerts (2000) showed competitive stand-
1068 off between corals and sponges was also common. In both these two modern
1069 examples, the sponges are non-calcifying, but given that Palaeozoic
1070 stromatoporoids likely grew faster than their modern counterparts, discussed
1071 earlier, the issue of competition between corals and sponges has similarities
1072 between the ancient and modern. However, recognition of competition between
1073 benthic clonal-colonial organisms is normally problematic because of the difficulty
1074 in most cases of proving that neighbouring organisms were alive at the same
1075 time (Fagerstrom et al., 2000); thus the uncommon example in Figure 22
1076 provides information that may not be always obtainable. Finally, modern sponges
1077 may use toxins in competitive interactions (e.g. de Voogd et al., 2004) for which
1078 there is currently no evidence in the skeletal structure of stromatoporoids or the
1079 organisms with which they competed, an area for potential future investigation.
1080



1081 Fig. 22. Vertical thin section views of apparent competitive intergrowth between
1082 tabulate coral and stromatoporoid. A) The tabulate occupies the lower two-thirds
1083

1084 of the thin section, B and C show details from the upper part. Note the intergrown
1085 large tube in A (yellow arrow), which may be a calcified worm. B) Enlargement of
1086 red box in A showing close apparent competitive growth between coral (left) and
1087 stromatoporoid (right); and endosymbiont syringoporid tubes (red arrows). C)
1088 Enlargement of yellow box in B, showing symbiotic syringoporid coral tubes (red
1089 arrows) and more detail of competitive reaction between the coral and
1090 stromatoporoid (yellow arrows). The dark material along the contact between the
1091 coral and stromatoporoid, seen in detail in B and C, is matrix with dolomite
1092 rhombs. Santa Lucía Fm, Emsian, Lower Devonian; El Millar, Cantabrian
1093 Mountains, northern Spain (Fernandez et al., 1995).
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1096 7.4. stromatoporoid-symbiont interactions and interruption surfaces

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1098 As described in Section 6, growth interruption surfaces are common in
1099 Ordovician to Devonian stromatoporoids. Such surfaces are sporadically
1100 distributed through the vertical section of the skeleton and may be primarily
1101 caused by sedimentation, as discussed above. Endosymbionts are common in
1102 stromatoporoids with interruption surfaces, so to explore the relationship between
1103 growth interruption and endosymbionts in more detail, we chose two cases of
1104 stromatoporoids from the Silurian of Gotland, Sweden. The first is from bedded
1105 limestones of the Wenlock age Halla Formation. The second is from the Ludlow
1106 age Hemse Group biostromes illustrated in Figure 2, because they are one of the
1107 densest accumulations of stromatoporoids known and have a significant
1108 component of stromatoporoids with intergrown corals.

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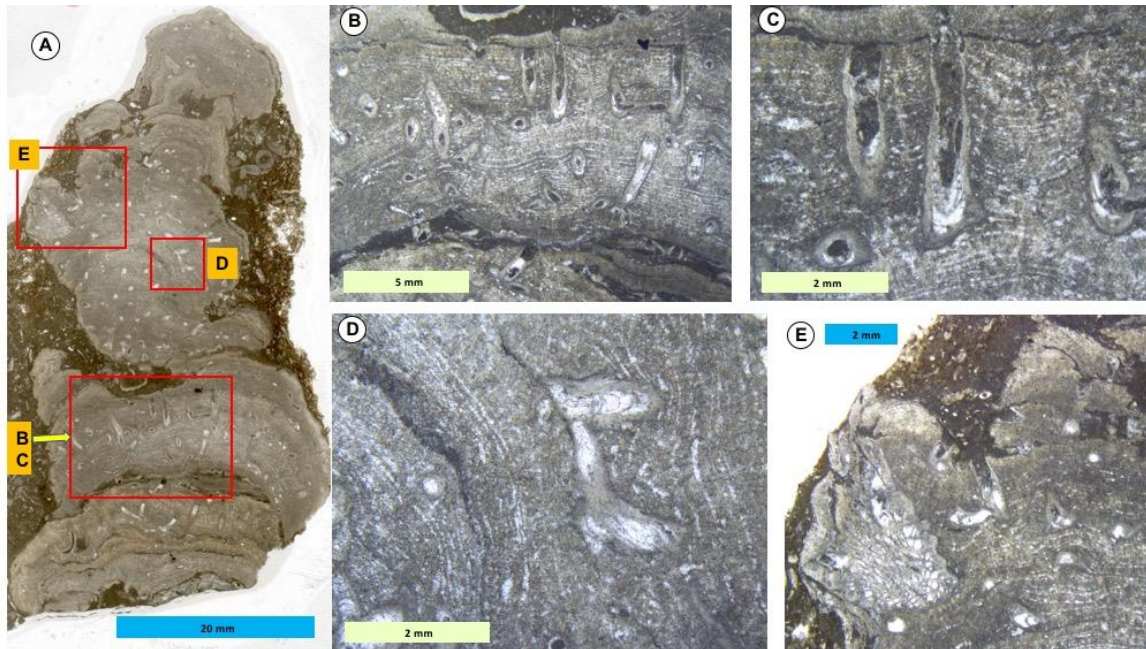
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1111 *7.4.1. Case 1: Wenlock bedded sediments*

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1113 The effect of growth interruption on the intergrowth between corals and
1114 stromatoporoids in the Upper Wenlock Halla Fm in eastern Gotland, in a low
1115 energy environment, is shown in Figure 23. The syringoporids are not evenly
1116 distributed through the stromatoporoid, indicating a dynamic relationship existed
1117 between stromatoporoid and its intergrown corals in relation to environmental
1118 change.

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Fig. 23. Stomatoporoid with intergrown corals and repeated interruption events. A) shows the overall history of interruption and coral intergrowth. B and C) show details of intergrown corals; sediment has entered the coral tubes from the interruption surface near the top of C. D) Intergrown corals developed after the stromatoporoid growth began. E) Solitary rugose coral grew on the stromatoporoid surface and was partly enveloped by continued stromatoporoid growth. Klinteberg Group, Wenlock, Silurian; Gothemshammar site, Gotland, Sweden (Calner et al., 2004).

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7.4.2. Case 2: Ludlow biostromes

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Previous work (e.g. Mori, 1970; Kershaw, 1987; Kano, 1990) highlighted the consistency of symbionts in certain taxa, in particular the stromatoporoid *Petridiostroma convictum*, which makes up about 10% of the stromatoporoid assemblage of the Hemse Group biostromes and always contains symbiotic syringoporids, often together with branching rugose corals (see Table 1). Figure 24 shows a typical example from a suite of samples of *P. convictum* showing the progression of change of the relationship between stromatoporoid host and syringoporid coral endobionts.

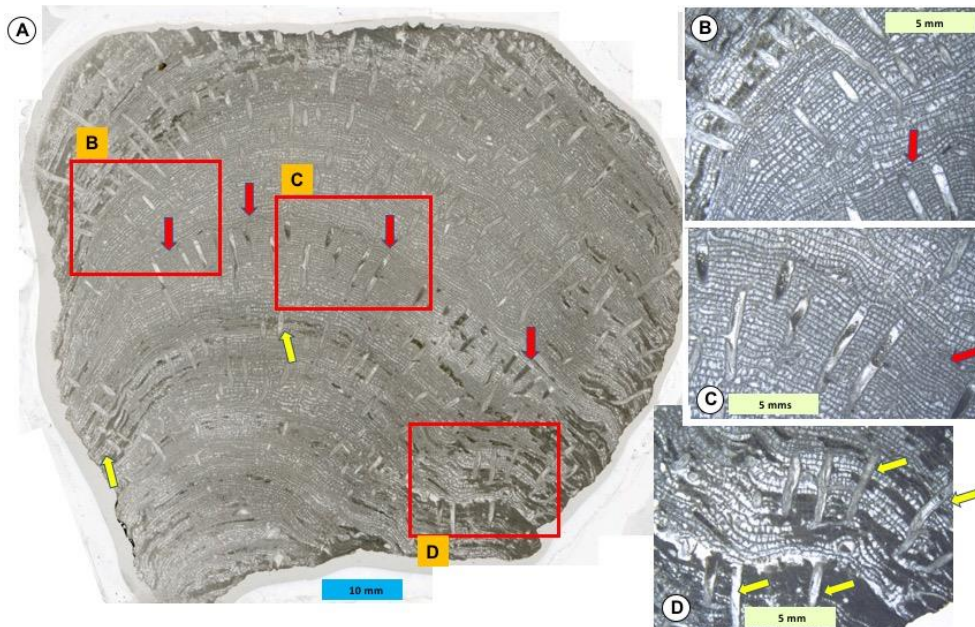
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At the margins and tops of *P. convictum*, some cases show local sedimentation that inundated the stromatoporoid galleries between laminae (Fig. 24), presumably either killing the stromatoporoid tissue locally or simply infilling dead areas of skeleton; sediment also entered some of the symbiont coral tubes (Fig. 24C). In a few samples (e.g. Fig. 24B) *P. convictum* shows a short vertical segment where laminae were strongly disrupted, an interruption event in the life of the stromatoporoid. Endosymbiont corals were also normally terminated at the same level; coral death can be distinguished in thin sections from tubes that pass out of the plane of section, because the latter taper, while the former simply

1150 terminate at the interruption surface and may collect sediment, demonstrating the
1151 corals died (e.g. Fig. 24C and D). Subsequent stromatoporoid growth recovery in
1152 almost all cases initially lacks coral symbionts in the plane of section viewed, but
1153 they were seemingly soon re-established on the stromatoporoid surface,
1154 following the same pattern as at the base of the stromatoporoid.

1155 In some cases, syringoporid corals survived sediment inputs and
1156 continued growth (Fig. 24B, D). Such cases are in contrast to the apparent death
1157 of other corals at growth interruption surfaces, and therefore show the complexity
1158 of growth of both the stromatoporoids and their endosymbiotic guests and their
1159 ability to survive interruption events. In these cases, the stromatoporoid was re-
1160 established, leading to return to the normal endosymbiotic relationship.

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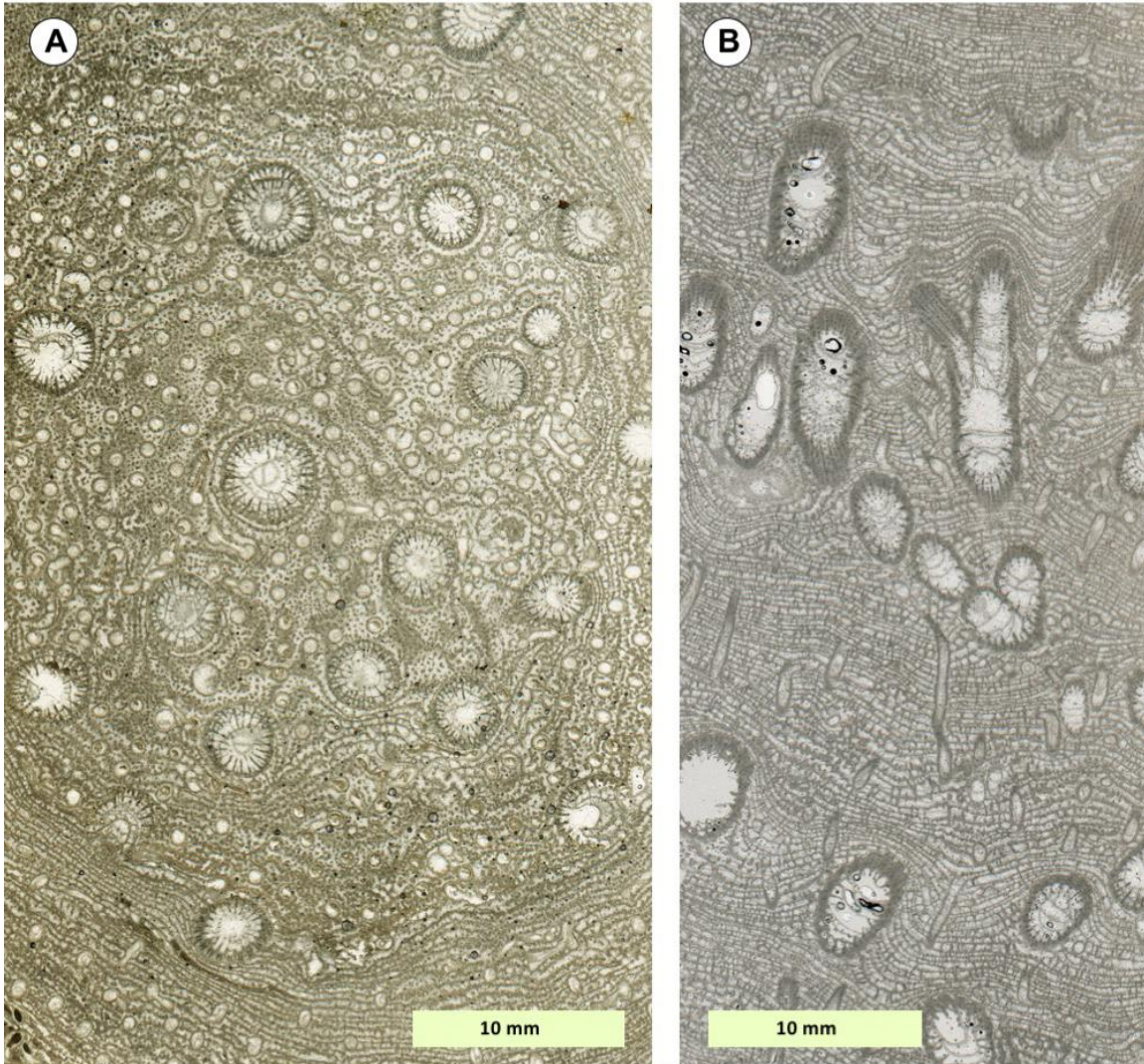
1165 Fig. 24. Vertical thin section of an almost entire stromatoporoid (*Petridiostroma*
1166 *convictum*, only part of its top surface is missing) with symbiotic syringoporid
1167 corals, from the biostrome shown in Fig. 2. A) Numerous interruption events
1168 occurred through the life of this specimen, highlighted by sediment intrusions of
1169 the margins, yet these sediment layers show very little evidence of interruption in
1170 the interior of the stromatoporoid. Note the prominent growth interruption event in
1171 the centre of the stromatoporoid. Note the prominent growth interruption event in
1172 the centre of the stromatoporoid, accompanied by termination of coral growth
1173 (red arrows). Yellow arrows mark an earlier interruption event, accompanied by
1174 sediment preserved in the stromatoporoid, but the corals survived this. B and C)
1175 Enlargements of labeled red boxes in A, showing details of the central
1176 interruption surface in A (red arrows). Note that on the left edge of both A and B,
1177 syringoporid tubes grew through a growth interruption and were apparently not
1178 affected by it. D) Enlargement of the labelled red box in lower part of A show that
1179 the earlier interruption is actually several events, possibly caused by

1180 sedimentation, but the syringoporids appear to have survived (yellow arrows). In
1181 C, sediment-filled syringoporids terminate at the stromatoporoid interruption
1182 surface (red arrow), indicating simultaneous interruption and presumed death of
1183 these corals. In B and C, stromatoporoid recovery occurred before the corals
1184 reappeared in this plane of section of the stromatoporoid skeleton, a feature
1185 present in almost all stromatoporoids with intergrowths studied here. This may be
1186 evidence that stromatoporoid recovery from interruption occurred more rapidly
1187 than coral recovery. This sample demonstrates the complexity of interruptions
1188 and intergrowths in stromatoporoids, and highlights that every stromatoporoid is
1189 unique. Hemse Group, middle Ludlow, Silurian; Kuppen biostrome, Gotland,
1190 Sweden (Sandström and Kershaw, 2002, 2008).

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1193 Some stromatoporoids show high abundance of endosymbionts,
1194 apparently without being adversely influenced by their presence. Figure 25
1195 shows a very good example of presence of two endosymbiont taxa in a single
1196 stromatoporoid, in the taxon *Petridiostroma convictum* in the Ludlow biostromes
1197 of Gotland (see Kershaw, 1987).



1198
 1199 Fig. 25. A and B. Transverse (A) and vertical (B) thin-section views of
 1200 *Petridiostroma convictum*, demonstrating the abundance of both syringoporid
 1201 tabulate and branching rugose corals within a single stromatoporoid. The
 1202 syringoporid is evenly distributed throughout the stromatoporoid, particularly
 1203 visible in the central part of A, while the rugose coral was branching and is less
 1204 evenly distributed. These examples demonstrate the ability of stromatoporoids to
 1205 grow with abundant endosymbionts, and emphasises the complexity of the
 1206 relationship between them. Hemse Group, middle Ludlow, Silurian; Kuppen
 1207 biostrome, Gotland, Sweden (Sandström and Kershaw, 2002, 2008).

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1211 7.5. Discussion of endosymbiosis in stromatoporoids and its applications in
 1212 palaeoenvironmental interpretation

1213
 1214 Kershaw (1987), Mori (1970) and Vinn (2016) give examples of studies that
 1215 interpreted the intergrowths to have been most likely a commensal-style

1216 relationship, in which the stromatoporoid did not benefit from the relationship,
1217 while the symbionts were interpreted to have received physical protection from
1218 the environment. However, Zapalski (2011) regarded commensalism as a term of
1219 little value because it indicates a lack of interaction that cannot be proven due to
1220 the absence of skeletal change in the stromatoporoid structure adjacent to the
1221 enclosed tube. In cases where the stromatoporoid shows profound change in
1222 response to the tube, then parasitism may explain the response of the
1223 stromatoporoid. Zapalski and Hubert (2010) interpreted parasitism in one case of
1224 an intergrowth from Devonian stromatoporoids, based on downbending of
1225 stromatoporoid laminae in the vicinity of the intergrown tubes, common in
1226 stromatoporoids with endosymbionts, yet the stromatoporoids clearly grew
1227 successfully (see also Da Silva et al., 2011b). Downbending might be caused by
1228 the endosymbiont inhibiting stromatoporoid growth in the few mm around the
1229 symbiont tube, but whether this can be classified as parasitism is an open
1230 question. Furthermore, bending of stromatoporoid laminae is not always
1231 consistent; Figure 3 shows variations within one stromatoporoid, with
1232 downbending laminae against some tubes but normal to the tube wall in others.
1233 Kershaw (2013, his fig. 12G) illustrated similar variations in a Silurian example in
1234 England, where stromatoporoid laminae adjacent to different levels of the same
1235 tube show downbent and unaffected laminae. Vinn (2016, Fig. 1) and Figures
1236 23C and 25B show cases where the laminae bend up to meet the symbiont
1237 tubes. Deflection of stromatoporoid laminae occurs only in areas close to the
1238 symbiont tubes, so most of the stromatoporoid was seemingly unaffected. Thus,
1239 if parasitism existed, it has not left evidence of significant impact on growth of the
1240 stromatoporoids. In the light of Zapalski's (2011) discussion, perhaps a more
1241 appropriate approach is to describe an interpreted commensal relationship as
1242 unproven, but not likely parasitic.

1243 Regarding the timing of the relationship between stromatoporoids and
1244 endosymbionts: A) stromatoporoids with the basal part preserved show that, in
1245 almost all cases of the planes of sections examined, the stromatoporoid began
1246 growth before the syringoporid and rugose corals appeared within the
1247 stromatoporoid skeleton (a point recognised by Pope, 1986, and by Young and
1248 Noble, 1991, in eastern Canadian Silurian sites); B) the level within the
1249 stromatoporoid at which the corals first appear varies between samples. In many
1250 cases, the corals appear after only a few laminae of stromatoporoid grew (e.g.
1251 Fig. 21F), in other cases corals appear after many laminae. Rarely do the corals
1252 appear at the base of the stromatoporoid growth. Furthermore, in almost all
1253 planes of section examined in this study the syringoporids appeared at the same
1254 horizon across the stromatoporoid, in only a few cases the syringoporid began
1255 growth in one place and then spread through the stromatoporoid (appearing at
1256 successively higher levels in different parts of the stromatoporoid, indicating
1257 expanding growth of the coral as the stromatoporoid developed). If it is possible
1258 to prove that corals appear at one horizon in any particular stromatoporoid, the
1259 concept of coral spawning events, that led to apparent simultaneous coral
1260 colonisation across the entire surface of a living stromatoporoid, is one possible
1261 avenue of investigation. However, serial sectioning of a representative sample

1262 set is likely needed to prove simultaneous appearance of coral tubes, and such
1263 work would further develop understanding of the biological nature of the
1264 relationship.

1265 The interpretation of the energy levels of a deposit where endosymbionts
1266 occur in stromatoporoids requires careful consideration. In the case of the
1267 Silurian biostrome of Figures 2 and 23, previous work (e.g. Kershaw, 1987)
1268 interpreted high water energy as the reason for growth of presumably delicate
1269 branching corals within stromatoporoids. Intergrown syringoporids are well-
1270 known from the shallow-water reef complexes of Silurian and Devonian facies
1271 (see Mistiaen, 1984 for a compilation). However, several more recent studies
1272 contradict the perception of high energy as the prime cause of the association.
1273 Throughout the Hemse biostromes of Gotland (Fig. 2, see also Kershaw, 1990;
1274 Sandström and Kershaw, 2002, 2008), evidence from the stromatoporoids and
1275 the largely fine-grained sediment between them indicated that the energy was
1276 likely to have been generally low, interspersed by high energy events, because of
1277 the common presence of tall columnar stromatoporoids, that were almost always
1278 found lying on their sides, and layers of crinoidal debris in the biostromes
1279 (Kershaw, 1990). That biostrome complex has thus been reinterpreted to have
1280 formed in low energy, but shallow marine, possibly as a back-barrier system (see
1281 Sandström and Kershaw, 2002 for discussion). Thus, endosymbiont corals
1282 occupied the stromatoporoids for reasons other than energy levels, and promote
1283 focus on the biological relationship between the stromatoporoids and their guest
1284 corals. Although not illustrated here, other samples from sparsely accessible
1285 marly sediment (low-energy environment) beneath the biostrome (recessed area
1286 at the base of the cliff in Fig. 2A & B) include the same key taxa present in the
1287 biostrome above. Several samples from this marl of *P. convictum* containing both
1288 syringoporids and rugose coral endobionts emphasise the potential importance
1289 of the biology of the corals and stromatoporoids in the nature of the relationship.
1290 Support for these interpretations comes from other work: Young and Noble
1291 (1991) described a case of a low-energy setting for other examples of
1292 intergrowths, while Da Silva et al. (2011a) found syringoporid intergrowths in
1293 Devonian mound environments in Belgium, supporting the concept of a low-
1294 energy setting. Thus, studies where stromatoporoid endobionts are present must
1295 take account of the potentially complex nature of the relationship; therefore,
1296 simple interpretations of energy levels are not necessarily viable and the
1297 intergrowths must be considered carefully in facies analysis.

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1299

1300 **8. Stromatoporoid growth form and taxonomy**

1301 The fourth and final stromatoporoid attribute addressed in this study is generally
1302 considered the most problematic, for two reasons: 1) growth forms are often only
1303 broadly recognisable in cemented limestone outcrops because much depends on
1304 the nature of the exposure, thus only broad appreciation of growth forms is
1305 commonly obtainable, and detailed assembly of measurements is often not
1306 possible. Growth form in stromatoporoids in drill cores is normally not available;
1307 2) stromatoporoid identification requires two orientated thin sections, and

1308 experience that most researchers do not develop. Nevertheless, growth form
1309 alone can be utilised in a facies study because stromatoporoids were subject to
1310 environmental energy and sedimentation and much of the microfacies can be
1311 analysed using growth form alone, where it is clearly visible. However, the
1312 relationship between growth form and taxonomy underlies the application of
1313 stromatoporoids in facies analysis and, the research is significantly enhanced if
1314 taxonomic information is available. Furthermore, most stromatoporoids in any
1315 one suite of samples can be relatively easily identified, and an excellent recent
1316 taxonomic tool has been made available in the 2015 Treatise on Paleontology
1317 (various authors in Selden, 2015) contain updated descriptions of all
1318 stromatoporoid taxa. Therefore the inclusion of stromatoporoid taxonomic data in
1319 facies analysis is not as problematic as often perceived.

1320 Although most stromatoporoid taxa exhibit a range of growth forms, it has
1321 long been recognised that certain taxa occur in particular forms (Nicholson,
1322 1885-1982), the iconic example being the branching stromatoporoid *Amphipora*
1323 *ramosa* (e.g. Stearn, 1997) which is very abundant in Devonian reefs. Others are
1324 found as only laminar forms (e.g. the Upper Silurian taxon *Lophiostroma*
1325 *schmidti*; Mori, 1970). In some cases, distinct differences in form occurs amongst
1326 stromatoporoid taxa that lived together in the same environment (e.g. Kershaw
1327 and Motus, 2016 in a study that also included corals). Kershaw (1990) showed
1328 that some individuals with a range of forms from laminar to tall domical within one
1329 locality began life as laminar forms but grew upwards into tall domical shapes, so
1330 that the shape of a stromatoporoid relates to both its genetics and its growth
1331 history. Such studies require sufficient numbers of samples to determine whether
1332 growth form variation is related to the taxonomy or not.

1333 Stromatoporoid assemblages studied in detail for taxonomy reveal a
1334 consistent pattern: within any assemblage, taxonomic diversity is normally low,
1335 with two or three taxa commonly the most abundant stromatoporoids in the
1336 assemblage, the remaining taxa being present in much lower numbers. Most
1337 stromatoporoid assemblages do not have more than about 20 taxa and normally
1338 less. This pattern is present in Ordovician, Silurian and Devonian
1339 stromatoporoids, and also holds for assemblages in both reef and bedded
1340 limestone facies (e.g. Kapp, 1974; Kapp and Stearn, 1975 for Ordovician;
1341 Kershaw, 1984, 1990; Mori, 1969, 1970 for Silurian; and Da Silva et al., 2011a,b;
1342 MacNeil and Jones, 2016; Zapalski et al., 2007 for Devonian). Kershaw (2013)
1343 summarised current knowledge about the mineralogy of stromatoporoids, which
1344 is not known for certain. Although stromatoporoids are always recrystallised to
1345 some extent, evidence that they were not low-magnesium calcite, they are less
1346 affected than known aragonitic organisms such as molluscs in the same
1347 environments (which are commonly dissolved and preserved only as moulds). In
1348 diagenesis, stromatoporoids behaved differently from high-Mg calcite skeletons
1349 such as crinoids in the same sites and cannot be reliably linked to a high-Mg
1350 calcite composition. Nevertheless, it is clear that stromatoporoid assemblages
1351 have suffered very little diagenetic loss of specimens, indicating that the fossils
1352 found are representative of the living assemblages.

1353 In order to demonstrate the combined value of taxonomic and growth form
1354 information, we complete this survey of the four attributes of stromatoporoids with
1355 examples of major studies of palaeoecology of Palaeozoic stromatoporoids that
1356 combine growth form and taxa.

- 1357 1. Darriwilian (Middle Ordovician) stromatoporoids from North America
1358 described by Kapp (1974) and Kapp and Stearn (1975) revealed laminar
1359 to domical forms of three genera (*Pseudostylodictyon*, *Pachystylostroma*
1360 and *Labechia*), showing that they grew directly on the substrate and
1361 formed reefs, the first development of stromatoporoids as reef builders.
1362 The low profile growth form of these stromatoporoid taxa is likely to have
1363 significantly assisted their reef-developing abilities.
- 1364 2. Wenlock (middle Silurian) stromatoporoids from bedded marls of Gotland
1365 (Kershaw, 1984) show that only one taxon, *Densastroma pexisum*, is
1366 abundant, and the remaining 4 taxa are much less common. *D. pexisum*
1367 formed tall domical shapes when fully grown, which may have given it a
1368 greater survival potential in the level-bottom marly facies where it is found.
1369 The consequence of survival allows individual stromatoporoids to record
1370 substantial amounts of information in their skeletons for use in
1371 palaeoenvironmental interpretation.
- 1372 3. Ludlow (upper Silurian) stromatoporoids from biostromes on Gotland are
1373 likely the densest accumulations of stromatoporoids on Earth (Kano, 1990;
1374 Sandström and Kershaw 2008). Although they contain approximately 20
1375 genera, only three are abundant in any one deposit, and they represent
1376 low diversity despite their abundance. The most abundant taxa in these
1377 environments are present as low profile forms capable of spreading
1378 rapidly across the substrate, which may indicate they took advantage of
1379 low sedimentation rates.
- 1380 4. Givetian and Frasnian (Middle and Upper Devonian) stromatoporoids of
1381 southern Belgium contain a diverse suite of biohermal reefs and mounds,
1382 and bedded sediments (including biostromes of reef debris) representative
1383 of the rich diversity of Devonian stromatoporoid faunas (Cornet, 1975).
1384 Da Silva et al. (2011a,b) identified nine genera but the distribution of
1385 stromatoporoids across the range of facies, and range of growth forms far
1386 exceeds those of the Silurian. Da Silva et al. (2011a,b) interpreted that
1387 taxa which formed lower profile forms to have been important in sediment
1388 stabilisation of Frasnian reef complexes and mounds in Belgium, although
1389 the most abundant stromatoporoids in those settings are fragmented
1390 branching forms that are presumed to have formed in low energy
1391 conditions and transported by high energy events such as storms.
1392 MacNeil and Jones (2016) compiled stromatoporoid growth forms for 10
1393 genera identified in an Upper Devonian reef in Canada and demonstrated
1394 the range of laminar, domical, branching, multicolumnar platy as well as
1395 whorl-shaped stromatoporoids. Wood (1999) illustrated a similar range in
1396 the Givetian and Frasnian of the Canning Basin of western Australia.
1397 Devonian stromatoporoid forms are significantly more complex and
1398 variable than in either Ordovician or Silurian deposits. Note that Devonian

1399 stromatoporoid reefs are described as megareefs by Copper and Scotese
1400 (2003), with the Givetian stage as the time of greatest stromatoporoid
1401 abundance, diversity and growth form worldwide.

1402 A general outcome of studying taxonomy in relation to stromatoporoid growth
1403 forms is the recognition that those taxa which developed low profile shapes likely
1404 had an advantage in their survival and ability to build reefs and dominate reef
1405 complexes.

1406

1407

1408 **9. Conclusions**

1409 This overview of Palaeozoic stromatoporoids addresses processes controlling
1410 the growth of stromatoporoids, and shows how they may be used in carbonate
1411 facies analysis and palaeoecological interpretation. Using a large sample studied
1412 in detail the outcomes are:

1413

1414 1. Four attributes of stromatoporoids valuable as analytical tools are: a)
1415 relationship with their substrates; b) the results of interruption of their growth; c)
1416 relationship with associated organisms; and d) the relationship between
1417 stromatoporoid growth form and taxonomy, which influences the other three
1418 attributes because some taxa are limited to certain growth forms. Identification of
1419 four attributes that cover the range of growth features in stromatoporoids
1420 simplifies their study and makes the understanding of stromatoporoids more
1421 accessible to researchers.

1422

1423 2. Study of stromatoporoid growth and its applications is significantly enhanced if
1424 the margins of samples are available for analysis, including the base and top of
1425 specimens, but is best if whole stromatoporoids can be studied (impractical in
1426 large samples). Because of their commonly large size and difficulty of extraction
1427 from limestone, incomplete specimens are the normal material for stromatoporoid
1428 work. Stromatoporoids in reefs are also commonly affected by pressure solution
1429 on their margins, degrading the quality of information, and making it difficult to
1430 apply numerical analysis, hence the semi-quantitative approach of Rare,
1431 Common and Abundant is applied here.

1432

1433 3. Stromatoporoids are commonly associated with substrates rich in micrite and
1434 clays, and published interpretation that stromatoporoids were capable of dealing
1435 with unconsolidated substrates is fully supported in this paper, from study
1436 throughout their stratigraphic range of Middle Ordovician to end-Devonian rocks.
1437 Stromatoporoids also grew on shelly skeletal material on the sea floor and are
1438 interpreted to have grown on surfaces of stabilised sediment that may have been
1439 partly lithified.

1440

1441 4. Tabulate corals and heliolitids found in abundance with stromatoporoids were
1442 similarly capable of growing on soft substrates, and overlap with stromatoporoids
1443 in terms of their palaeoecology. Combined studies of stromatoporoids and corals

1444 would therefore be valuable, and there is considerable scope to expand this area
1445 of research.

1446

1447 5. Almost all stromatoporoids examined during this study show growth
1448 interruption, from which they were able to recover quickly and completely, and
1449 record environmental change in their skeletons.

1450

1451 6. Stromatoporoids have abundant associated organisms, as epibiotic encrusters
1452 and borers, and as endobiotic symbionts. The relationships between endobionts
1453 and their hosts enhance understanding of stromatoporoid growth.

1454

1455 7. Evidence from our large sample points to stromatoporoids as benthic
1456 organisms with rapid growth capability and resilient to environmental events.
1457 They grew in a range of water depths, were capable of dealing with soft
1458 substrates and were largely unaffected by endobionts. The result of these
1459 attributes is interpreted here to have made them successful for 100 million years
1460 during the mid-Palaeozoic and makes them valuable in facies analysis and
1461 palaeoenvironmental studies. An interesting parallel exists in modern (non-
1462 calcified) sponges, which are likewise considered to be resilient and flexible
1463 benthos, thus some attributes of the biology of Palaeozoic stromatoporoids may
1464 have continued to the present day.

1465

1466

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1480

1481

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