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Rugosans immured in Silurian *Paleofavosites;* Brassfield Formation (Llandovery) of Ohio

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ABSTRACT. The occurrence of a solitary rugose coral, *Streptelasma* sp., anchored within colonial skeleton of the tabulate coral *Paleofavosites prolificus* is here reported. Numerous specimens of *Streptelasma* were found within three coralla of this tabulate species among 55 collected from the uppermost 30 cm of the Lower Silurian (Llandovery) Brassfield Formation at Fairborn, Ohio. These rugosans are largely immured in the favositid coralla, and, as bioclaustrations, reveal important information on the paleobiology of both species. However, the immuring of some *Streptelasma* within *Paleofavosites* coralla was not complete during the life of the rugosan, as calice openings of these are present at the corallum surface. Complete immuration (or total overgrowth) indicates that the rugosan no longer competed successfully for space; whether entombment occurred after the death of the rugosan or was the cause of its death is unknown. *Streptelasma,* in assuming an epibiotic lifestyle probably benefited from the secure attachment to the larger, stable colonial form of *Paleofavosites prolificus* and were able to exist within this particular Brassfield facies interpreted to have been a vigorous, current-swept environment. These high energy environments would have been inimical to the small, light-weight rugosans living as isolated corallites. The successful settling and growth of the rugosans on the tabulate colonies reflects their higher status in an aggression hierarchy. This interspecies interaction indicates an early Paleozoic development of an aggression hierarchy of corals belonging to the Rugosa and Tabulata (Phylum Cnidaria).

KEYWORDS: *Streptelasma*, bioclaustration, aggression hierarchy, Cnidaria, epibiont.

1. Introduction

We report the occurrence of rugose corals living during the Early Silurian as epizoans on massive colonies of tabulate corals, and becoming partially or totally immured within them. Close interspecies relationships of this sort between rugose and tabulate corals are of interest for several reasons, (1) they allow understanding the corals' position in the Brassfield ecosystem, and (2) they allow us to hypothesize biological relationships between organisms of different major Paleozoic taxa of the Cnidaria. We have found only one previous reference to the occurrence of rugose corals on, or within, coralla of massive tabulate corals; that of McLean (1974) who reported a species of *Streptelasma* occurring within a tabulate colony in Lower Silurian rocks of New South Wales, Australia*.* Kershaw (1978) also reported a species of the rugosan T*ryplasma* occurring as an endobiont within the stromatoporoid sponge *Clathrodictyon* in Middle Silurian strata of Gotland.

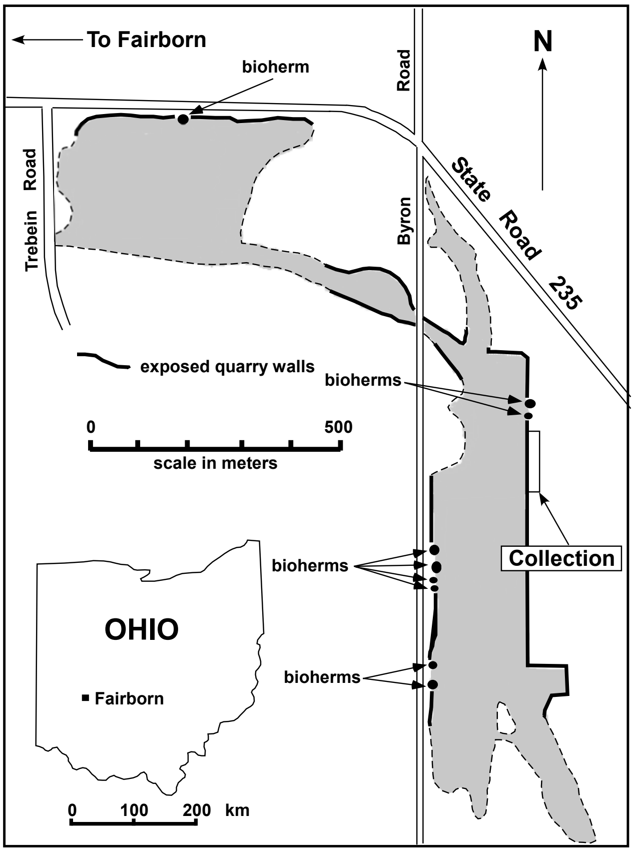

Figure 1. Map of the inactive Southwestern Portland Cement Company quarries at Fairborn, Ohio, as they existed during 1967-1975. Corals discussed in this paper came from the portion of the east quarry face labeled Collection on the map. This quarry also was Locality 7 of Laub (1979, p. 11), while newer quarrying to the south was his Locality 7a.

There is considerable potential for inferring various paleobiological aspects of the corals involved in this remarkable occurrence in Lower Silurian (Llandovery) Brassfield strata near Fairborn, Ohio (Fig. 1), where individuals of the solitary rugosan, *Streptelasma* sp., occur within colonies of the tabulate *Paleofavosites prolificus* (Fig. 2). Some interspecific relationships are described below, notably observations pertaining to the spatial and biological relationships between these rugosans and tabulates. Tapanila (2005, p. 89) noted that a faunal relationship where an endobiont occurs within a host skeleton is "particularly well-suited for studying animal interactions." He also added that this relationship can produce the special group of trace fossils called bioclaustrations (Palmer & Wilson 1988; Taylor 1990), as a result of immuring of epi- or endobionts by skeletal material of the host species. Although *Streptelasma* corallites are now found partially or wholly immured within the *Paleofavosites* coralla, their living tissues were confined to the most recently formed portion of the skeleton, and that lay *on* the contemporaneous surface of the host (Fig. 2); hence they were epibionts that became immured by later tabulate skeletal growth.

Figure 2. External view of solitary corallites of *Streptelasma* sp., opening at the surface of *Paleofavosites prolificus* (PRI 64764).

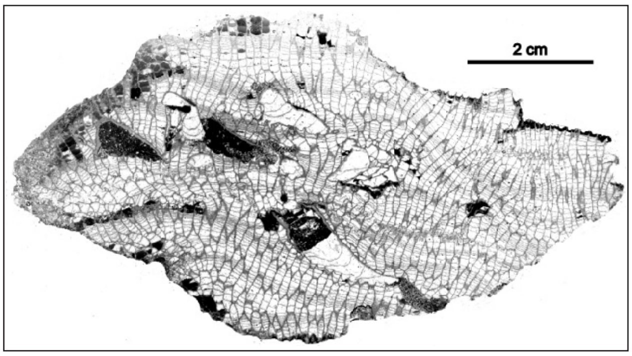

Figure 3. Transverse thin section of *Paleofavosites prolificus* containing numerous immured individual corallites of *Streptelasma* sp. (PRI 64764c). Section also shows placement of rugosans on and near zones of closely spaced tabulae in the favositid corallum. The two long *Streptelasma* corallites in the central part of this thin section are shown at greater magnification in Figures 7 and 8 below.

2. Bioimmuration, bioclaustration, and agression

A number of reports have focused on the bioimmuration of symbionts by their host organism, as here in the Brassfield where rugose corallites occur within colonies of *Paleofavosites prolificus*. Taylor (1990) surveyed paleontological occurrences of bioimmuration and suggested several types. Of these, the Brassfield occurrence is "epibiont bioimmuration," although several characteristics make this Lower Silurian occurrence somewhat special. Here there is not one organism overgrowing and encapsulating another, but rather, one organism living upon a colony of another and killing or displacing individuals of that colony to acquire living space. In addition, *Paleofavosites* does not here simply bend laterally and then overgrow the rugosan, but rather, after the rugose coral has occupied space on dead portions of its corallum (Fig. 3), with the rugosan dorsal skeletal wall intact, neighboring *Paleofavosites* polyps multiplied and overgrew the upper wall of the semi-recumbent rugosan corallite. That the rugosan deposited skeletal material, both an external wall and internal septa and tabulae makes it a special case in the spectrum of bioclaustrations reported by Palmer & Wilson (1988). The name was initially proposed for bioimmuration where an endobiont is a soft-bodied organism, one that would not otherwise have been preserved in the fossil record. Taylor later (1990, p. 4) modified the definition of the term to include skeletonized endobionts entombed by bioimmuration. It should be also emphasized that the living *Streptelasma* polyps only occupied the last formed portion of the rugosan corallite (perhaps 5 or 6 mm), so that there was not a living organism immured within the tabulate skeleton although the older portion of the *Streptelasma* corallite skeleton was surrounded and anchored within the *Paleofavosites* corallum.

Since the seminal work by Lang (1973), numerous authors have reported on mutual aggression between different coral species (Bak et al., 1982; Chornesky, 1983, etc.), especially reef-dwelling corals. These relationships have been summarized by Lang & Chornesky (1990) and further expanded by many authors since that date (summarized in Barnes & Hughes, 1999). Lang (1973) determined experimentally that each coral species attacked only certain other species, and each was itself only attacked by some others, providing a coral "aggression pecking order." She also determined that scleractinian corals extruded their mesentarial filaments both orally and through temporary openings in the polyp wall to digest the flesh of neighboring coral species externally (Lang, 1973). Among other authors, Chornesky (1983) observed that all modern coral polyps have such mesenterial filaments, but that additionally, some species develop sweeper tentacles. These are specialized tentacles that commonly appear on polyps adjacent to areas where mesenterial filaments are attacking adjacent coral soft tissues (Chornesky, 1983, p. 570), are larger than normal and more heavily armored than usual and extend farther into neighboring space (Bak, et al, 1983).

Evidence for this aggressive behavior between the Brassfield species of *Streptelasma* sp. on the tabulate species *Paleofavosites prolificus* is discussed below.

Materials and methods

Upper Brassfield strata in the inactive quarries of the Southwestern Portland Cement Company, east of Fairborn, Ohio (Fig. 1) were examined in detail and more than 2800 m of linear exposures were surveyed in the summers of 1967 and 1968. All *in situ* corals and stromatoporoids were either collected or identified in place and their locations, stratigraphic positions, axial dimensions, and burial orientations recorded. The Brassfield Limestone here is comprised of three distinct facies; (1) bioherms, (2) interbioherm strata, and (3) hardground (Kissling, 1977).

A specific collection of 203 corals from the uppermost 30 cm of the Brassfield from high-energy, current-deposited strata along 110 m of the east wall of the southern quarry extension (Fig. 1, labeled "Collection") includes three coralla of the tabulate species *Paleofavosites prolificus* that contain rugose corals. The total number of specimens and species of this limited 110 m collection includes the following: 19 *Paleofavosites prolificus*, 80 *Favosites favosus*, 8 *Halysites* sp., 7 *Heliolites* sp., and 89 solitary rugosans (Table 1). The total counts from seven collecting sites (six sites plus those noted above) of this uppermost zone in the south quarry (encompassing 354 m of quarry wall) are listed below and compared with the stromatoporoid sponge and coral fauna of both bioherms and contemporaneous interbioherm strata. Note that *Clathrodictyon vesiculosum,* although very abundant, is the sole stromatoporoid sponge taxon at this locality.

The three assemblages are distinct in terms of proportional representation of constituents. Of the total 274 *Paleofavosites prolificus* (Billings) colonies collected, slabbed, and examined throughout the quarry, only three coralla from the hardground high-energy facies exhibit infestation by rugosans. Nearly all *Paleofavosites prolificus* colonies collected from the bioherm and hardground facies (170 and 55 specimens, respectively) were sawn parallel to the vertical growth axis, polished, etched and reproduced as acetate peels to record annual growth increments and presumed ages of each to reconstruct age-frequency population structures for these distinct populations (Kissling, 1977). A series of 18 large thin sections

	Hardground	**Bioherms**	**Interbioherms**
Lateral coverage along quarry walls	354 m	149 m	2326 m
Taxon			
Clathrodictyon vesiculosum	124	59	45
Paleofavosites prolificus	55	173	46
Favosites favosus	137	588	96
Halysites	10	4	19
Heliolites	13	2	0
Alveolites	2	1	3
Solitary rugosans	140	106	25
Colonial rugosans	2	28	11

Table 1. Taxonomy and numbers of corals and stromatoporoids collected from the three facies of the Brassfield Formation studied on the east wall of the southern quarry at Fairborn, Ohio.

spaced approximately 10 mm apart and oriented in the plane of growth, were prepared from the largest of the three coralla, one which possessed a low domal, nearly tabular form. Similarly, four thin sections spaced 10 mm apart were prepared from a smaller, ellipsoidal corallum of *P. prolificus*. The third infested *Paleofavosites* corallum was not sectioned, but it does display six *Streptelasma* calices opening at its surface (Fig. 2). Detailed study of the small rugosans immured within the host *Paleofavosites* were carried out by microscopic examination of thin sections, which also furnished the photographic figures presented in this paper. All specimens are reposited in the Paleontological Research Institution collections at Ithaca, New York, USA, numbered PRI #64764a-64764n, 64765a-64765d, and 64766a-67466d respectively, for sections from the three colonies.

4. Geological setting

The Brassfield Formation of Late Llandovery Age (*Monograptus sedgwicki* Zone) represents basal Silurian limestone and dolomite throughout most of the western Cincinnati Arch region of Ohio, Indiana, Kentucky and Tennessee. Regionally the base and top of the formation are diachronous, the formation becoming older and thicker towards the east and southeast as it grades into the Tuscarora Sandstone in the Appalachian Basin.

At Fairborn, Ohio the Brassfield is unconformable on the Late Ordovician Elkhorn Formation, and measures 12 m thick. Local quarry workings were confined to the upper 4 m of the Brassfield which here contain numerous richly fossiliferous, argillaceous bioherms surrounded by thick-bedded coarse, crinoidal grainstones. Thin beds of crinoid grainstone interbedded with greenish gray, calcareous shale bearing abundant corals and stromatoporoids mark the uppermost part of the formation along the eastern wall of the southern quarry where this thin interval overlies a well marked discontinuity or hardground. In turn, this unit is overlain unconformably by the Dayton Limestone, locally dolomite, comprised of crinoid-brachiopod-bryozoan packstones. The uppermost Brassfield, with its crinoid grainstones, is interpreted to have represented wave-swept, high-energy, hardground environments that experienced episodes both of deposition and of erosion. This upper zone, a maximum 0.30 m thick, is marked by the presence of numerous lithic clasts, rotatory coralla of *Favosites favosus* (or circumrotatory, the term used by Kissling), well-abraded large, solitary rugosans, and some *F. favosus* coralla cemented to a lithified substratum (Kissling, 1973, p. 53). This thin unit, lying between erosional discontinuities at the top of the Brassfield Formation, was studied along a distance of 250 m along the eastern wall of the southern quarry, where all *in situ* fossils exposed were collected or recorded. It is absent where the two discontinuities merge. These observations serve to suggest that the numerous corals and stromatoporoids recovered *in situ* from the hardground facies had inhabited shallow, turbulent waters.

5. Discussion

5.1 The host

Paleofavosites prolificus. Of the many *Paleofavosites prolificus* coralla from the Brassfield that were sectioned and studied (274 coralla, 55 in the hardground facies above the recognizable lower disconformity), only three were infested by rugosans, each with multiple rugosans. These are numerous small, solitary streptelasmatid corals whose larvae settled on the tabulate colonies while the latter were still alive and secreting skeleton. Three-fourths of the 285 corals and stromatoporoids for which burial orientations could be established were seen to retain their original growth orientation; 80% of such specimens were encountered in bioherms, 75% in interbiohermal strata, and 67% on the hardground. This suggests that bioherms were the least turbulent and the hardground was the most turbulent of the habitats preserved in the upper Brassfield. Numerically, *Clathrodictyon vesiculosum* possessed the most stable form (as indicated by their having remained in growth position), while of corals present in these environments, *Paleofavosites prolificus* provided the most easily disoriented or overturned colony form. Only 58% of *Paleofavosites prolificus* colonies from all three habitats (as interpreted) were oriented in their growth position. Colony stability was dependent on their ability to adhere to the substratum or their capacity to adopt growth forms compatible with water turbulence. The premise that local environmental conditions influence the development of specific growth forms in organisms with accretionary skeletons is generally accepted.

The growth forms of large *P. prolificus* coralla are possibly the most indicative of habitat conditions. Shapes of 340 colonies were categorized as tabular (or low-mounded), hemispherical and columnar by measuring three perpendicular intercepts for each colony (one intercept coinciding with the growth axis), and transforming measurements to percentages. Columnar colonies are absent in the uppermost unit (hardground), whereas 95% of *P. prolificus* colonies have low-mounded, tabular forms in this facies, displayed by 75% of specimens from interbiohermal facies and by 70% of specimens from all bioherms.

All *P. prolificus* colonies exhibit well developed growth banding expressed as alternating zones of close-spaced tabulae and widely spaced tabulae; the couplet presumed to represent one year of skeletal secretion in which bands of close-spaced tabulae may signify seasonal conditions less conducive to skeletal growth than those of widely spaced tabulae (Kissling, 1977). Successful settling of the rugosan *Streptelasma* sp. and competition for space on the living surface of the host tabulate corals was most frequently accomplished either during the onset or within the midst of the "slow growth season." The poor growth conditions resulting in closely-spaced tabulae may also indicate that tabulate polyps were little able to fend off settling *Streptelasma* larvae at these times. Growth banding in *P. prolificus* does demonstrate that these widely differing corals grew simultaneously, but also that most of the individual rugosans were eventually outpaced in their upward growth and enveloped by host skeleton within several years after settlement. The presence of *Streptelasma* in the tabulate colonies was restricted to the uppermost, hardground facies.

Streptelasma sp. immured in *P. prolificus* skeletal tissue are bioclaustrations as described by Palmer & Wilson (1988), although here there is rugosan skeletal material present. These also vary from classic bioclaustrations in that there is no deflection of skeletal growth to surround the entombed species. Rather, in this case, mortality of *Paleofavosites* polyps occurred beneath the rugosans; later colonial skeletal growth overlapped and eventually covered the rugosan skeletons. The rugosan presence suggests that their polyps had a higher position in an aggression hierarchy (Lang, 1973, Bak et al, 1982, and others) than did the *Paleofavosites* polyps. By analogy to modern Scleractinia, cnidoblast-laden tentacles of smaller polyps (here of the tabulate) would have lacked the reach to dissuade the larger rugosans.

We consider encroachment onto the favositid surface by larvae of the epibiont rugosans and subsequent post-larval growth to result from rugosan requirements for living space on a hard

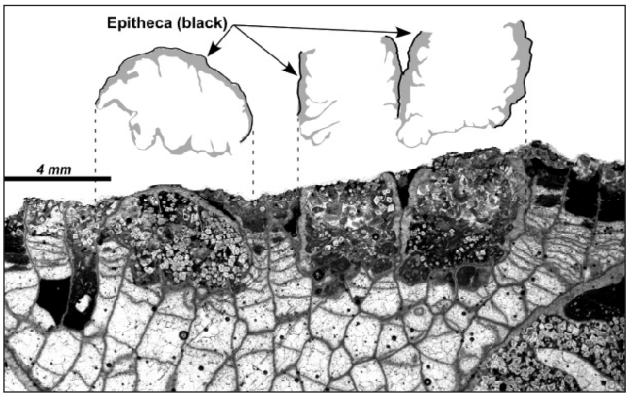

Figure 4. Thin section and drawing of *Streptelasma* corallites at surface of *Paleofavosites* (PRI 64764e). Note that growth orientation of the rugosans is here roughly parallel to the upper surface of the tabulate, and that their ventral wall is non-epithecate and incomplete. Note that the two corallites on the right side have been eroded, thus their epitheca and wall have been removed at the top of their sections.

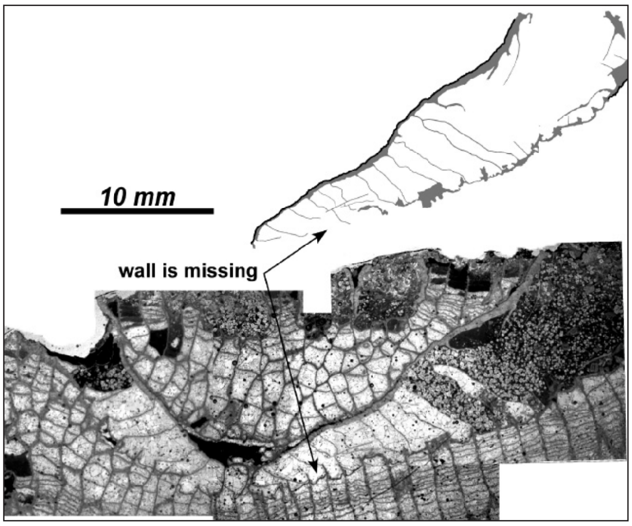

Figure 5. Corallites of *Streptelasma* sp. in longitudinal section immured within favositid (PRI64764d) along with drawing of corallite at right. Note that the dorsal wall of the right hand corallite is epithecate, but that the ventral wall is absent or composed of thin stereome only where the rugosan was in contact with the tabulate skeleton.

substrate. It appears that individual polyps of *Paleofavosites* were killed due to their position in proximity to growing *Streptelasma* polyps. Colonial growth of *P. prolificus* corallites to encapsulate the rugosan skeletons was due to later corallite budding and corallum expansion over the individual corallites. Foremost of the needs of the rugosans was shelter from high-energy current action and improvement of feeding conditions. The survey by Tapanilla (2005) of bioclaustration taxa in a literature review, reported 43 bioclaustrations occurring in corals, and 38 of these occurred in Tabulata and Heliolitida. Surprisingly, of this group of 38, half are reported as occurring in the Favositidae, and 17 of these are reported to occur in either *Favosites* or *Paleofavosites*. Clearly, these were corals that provided a convenient place for settling organisms.

5.2 The epibiont

Streptelasma sp. - The solitary rugosan here reported as associated with *Paleofavosites prolificus* in the uppermost wave-swept hardground facies of the Brassfield is identified by us as *Streptelasma* sp. Laub (1979, p. 62) has reported a species of this genus, *S. scoleciforme* Laub, occurring in the upper unit of the Brassfield at its type locality in Kentucky (Laub, 1979, section 1). The individuals of *Streptelasma* sp. seen at Fairborn, here associated with *Paleofavosites*, cannot be identified with total confidence as *S. scoleciforme* Laub, as corallite morphologies differ, apparently due to incomplete development of skeleton here, with septa commonly lacking on the side adjacent to the tabulate colony, and wall either partially or totally absent where the rugosan lay directly on tabulate skeleton. The Laub species is the proper size and shape to be identical to the Fairborn species, but is characterized by often incomplete tabulae, while those in the latter are virtually all complete. This material from the Brassfield at Fairborn was previously misidentified as *Tryplasma* in a prior report (Sorauf & Kissling, 2011).

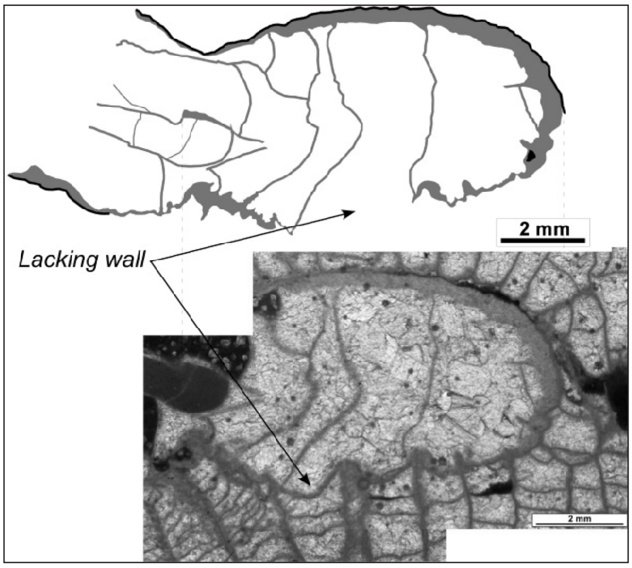

Figure 6. *Streptelasma* sp. with ventral wall lacking or very thin, with minor amounts of stereome deposited on tabulate skeleton (PRI64764e). The wall is thick and epithecate on the dorsal side where it presumably was exposed to sea water prior to being overgrown by the favositid.

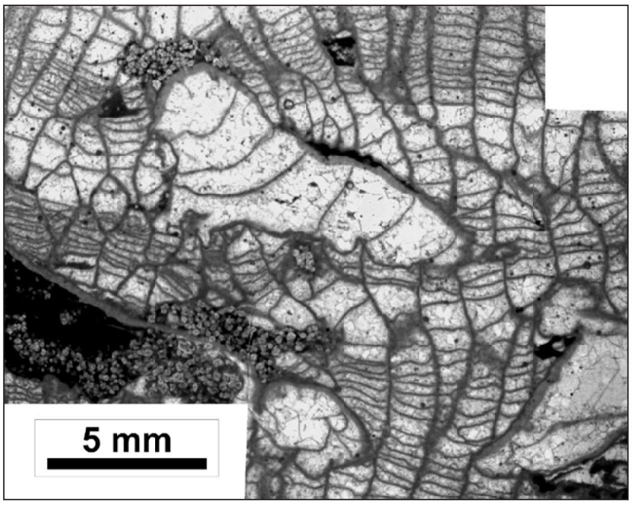

Figure 7. Corallites of *Streptelasma* sp. immured within *Paleofavosites prolificus* (PRI64764c). Note the occurrences within zones of varying growth as reflected by closely and widely spaced tabulae within the tabulate corallites. The large corallite at the upper central position here lacks wall between the rugosan and the tabulate skeleton. The apparent termination of the rugosan is apparently due to deflection of its growth direction out of the plane of the thin section.

Another species of *Streptelasma, S. recisum* McLean (1974, p. 41, pl. 1), has been reported as occurring embedded within a tabulate coral in Lower Silurian strata of New South Wales, Australia. McLean's species was found in the tabulate *Priscosolenia* and is fully developed in a rounded shape with a full complement of septa (26 – 30) and it has complete tabulae that are flat or somewhat sagging in the axial portion of the corallite. This Australian species is virtually identical in longitudinal section to the Fairborn material, except that the Ohio corals have an incomplete skeleton.

Because the Brassfield association is unique, normal taxonomy with respect to the rugosan is somewhat problematical. As shown in Figs 4-7, the Brassfield rugosan *Streptelasma* sp. here lacks some characteristics of the genus and, in fact, lacks some characters of rugosans in general, especially by lacking radial symmetry. Alteration of its morphology was apparently due to its having lived in a close relationship with, and being partially immured in *Paleofavosites*. As a result, the coral only developed the upper half of its semi-recumbent form, there retaining its normal, epithecate wall, with thin, sparse septa and complete tabulae. Dissepiments are totally lacking throughout the corallite (as in the genus). There is the appearance of sparse septal ridges in its calice, as expressed by those at the surface of the *Paleofavosites* colony (Fig. 2). It appears that modification of what would have been more typical rugosan morphology in the epibiont form is commonly expressed by, 1) a lack of septa in the lower half of the corallite, and 2) partial absence of the rugosan corallite wall in basal portions of it (ventral wall in a recumbent corallite). This lack of skeletal elements may have resulted simply from their position, lying on unoccupied tabulate corallites. It might also have had a more complex origin, a reflection of polypal skeleton modification resulting from continuing aggressive activity. Foremost of the needs of the rugosans was shelter from high-energy current action with its resulting improved feeding conditions. There was progressive

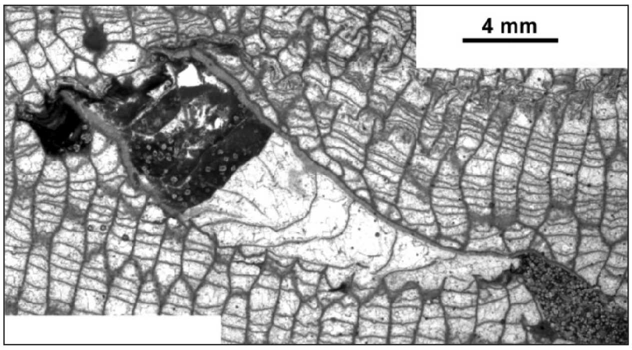

Figure 8. Immured individual of *Streptelasma* sp. lacking a ventral wall within corallum of *Paleofavosites prolificus* (PRI64764c). Note that the termination of growth of the rugosan appears to have preceded overgrowth of its calice, as the rugosan corallite was filled with sediment prior to being immured. Note also that some stereome of *Streptelasma* was deposited directly on the tabulate skeleton in the early stages of growth of the rugosan.

transgression by the growing rugosan along the tops of vacated tabulate corallites. The rugosan thus grew and secreted skeleton with sufficient rapidity to maintain the position of its polyp at the surface of the tabulate colony, avoiding for a time its complete immuration by skeletal growth of *Paleofavosites prolificus*.

The *Streptelasma* species, with its incomplete skeleton, most pronounced at its lower or ventral surface, may also reflect problems during growth of *Streptelasma* individuals with continuing contact with live tabulate polyps. One result may have been the internal rearrangement of *Streptelasma* mesenteries, with a resulting lack of septa and/or ventral wall on their undersurface. The incompleteness of the rugosan corallites also could be no more than conservation of energy, in that a wall (epithecal or not) was truly not needed on its ventral side because inert skeleton (of *P. prolificus*) was already there. Where the wall is absent however, some individuals did deposit a layer of stereome of varying thickness directly on tabulate skeletal elements (Figs 6, 8).

5.3 Symbiosis and Aggression

The relationship between the host colonies of *Paleofavosites* and the epibiont *Streptelasma* sp. was most likely not mutually beneficial. The only conceivable benefit the rugosan presence might have bestowed on the tabulate colonies would have been the presence of cnidarians with more potent cnidoblasts at the surface positions occupied. This is apparently negated by the vast majority of *Paleofavosites* colonies that existed in this facies without any symbionts being present (52 of 55 coralla).

The most obvious benefit to the rugosans would have been the anchoring of the fragile solitary corals in a high-energy environment where continuous currents could furnish an abundance of food. The hard-ground facies, apparently formed in shallow, turbulent environments late in the deposition of the Brassfield Formation, was likely subjected to episodic erosion and intermittent sediment accumulation. Being partially lodged within the tabulate colonial skeleton resulted in increased stability in currents afforded by the larger mass of the tabulate. The rugosans had to maintain growth rates sufficient to maintain their calices at the colony surface of the tabulate corallum, and those that were not able to maintain this position were simply overgrown and entombed, in most cases within a few years. Kershaw (1978, p. 379), noting the preference of *Tryplasma flexuosum* for *Clathrodictyon convictum* in the Middle Silurian Hemse Beds of Gotland, suggested that the preference here may have been largely due to selection of a stromatoporoid species with growth rates that were most comparable to the growth rate of the rugosan. His opinion also was that the *Tryplasma* individuals there chose stromatoporoids that adopted a relatively high profile, but inhabited high-energy environments that the solitary rugosan was too fragile to occupy otherwise.

It is uncertain whether there were other benefits to living as epibionts, in addition to the size and stability of the larger, stable, and broad-based tabulate colony in a high-energy and high-nutrient environment. The presence of the Brassfield species of *Streptelasma* as an epibiont clearly indicates that the rugosan was higher in the Paleozoic coral aggression hierarchy (Lang & Chornesky, 1990) than was *Paleofavosites prolificus*. It is unclear exactly what transpired to result in the lack of skeletal wall material of *Streptelasma* where the rugosan wall should have separated the soft tissues of the two disparate coral taxa.

The Brassfield rusosans apparently settled on and lived partially enveloped by tabulate skeleton; thus were anchored in low domal, hydrodynamically stable coralla of *Paleofavosites prolificus.* Thus they were able to inhabit high-energy, current-swept environments in Early Silurian time.

6. Conclusions

From this study, we are able to conclude the following:

1. The presence of the rugosan, *Streptelasma* sp., within coralla of *Paleofavosites proflificus* indicates that the rugosan occupied a higher position in the coral aggression hierarchy, presumably by possessing more powerful toxins and a superior means of delivering such toxins, perhaps analogous to those aggressive mechanisms (cnidoblasts, extrusion of digestive filaments) found among modern scleractinian corals, as described by Lang & Chornesky (1990).

2. The solitary corals, as indicated by their skeletons, were deformed where their lower surface was in contact with the *Paleofavosites* skeleton. The lower hemisphere of the roughly horizontal corallites generally shows a total lack of septa, and in places lacks walls, both epitheca and accompanying fibrous stereome, between the rugosan interior and the vacant tabulate skeleton. The lack of septa indicates a major reorganization of the rugosan polyp interior, a reflection of the mesenteries subdividing its gut. The lack of wall skeleton between the two greatly differing coral polyps suggests that the rugosans did not require additional protection from external forces in these locations, and also that *Paleofavosites* polyps were lacking beneath the rugosan polyps.

3. Partial bioclaustration or bioimmurration of the rugosans permitted these small, fragile, free-living corals to live anchored in a high-energy environment. This was due to the large size and hydrodynamically stable form of the tabulate colonies, as indicated by their abundance in the hardground portion of the upper Brassfield. This access to favorable feeding environments for the small, usually free-living corals provided a sufficient reward for their occurrence here as epibionts.

4. There appears to have been no particular benefit to the favositids, and they eventually overgrew and entombed the rugosans.

Favositid tabulate corals are common host organisms for epi- and endobionts as indicated by the occurrence of Paleozoic bioimmurrations. It appears clear that these small polyps were easily victimized by larger and more aggressive solitary rugosan polyps, and were situated lower on a Paleozoic coral aggression hierarchy. This occurrence in the Silurian Brassfield Formation provides us with the results of aggression of *Streptelasma* sp. on polyps of *Paleofavosites prolificus*, and is an expression of Silurian cnidarian behavior similar to that recognized in modern scleractinians.

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