BIOTIC INTERACTIONS BETWEEN CONULARIIDS AND EPIBIONTS FROM THE SILURIAN WAUKESHA BIOTA

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ABSTRACT

Here we describe an epibiont association between conulariids and holdfast producers, with attachment scars resembling those of the tubular epibiont, *Sphenothallus*, from the Silurian (late Telychian Series) Brandon Bridge Formation, Wisconsin. The conulariid population represents the most abundant sessile organisms in the Waukesha Biota and consists of two species, *Conularia niagarensis* Hall, 1852 and *Metaconularia* cf. *manni* (Roy, 1935). Attachment scars present on the conulariid test offer a unique glimpse into the paleoecology of this Silurian benthic assemblage. However, body fossils of the attached epibiont are scarce and have not been observed attached or near conulariid

specimens. This study evaluates the identity and paleoecological relationship between the conulariids and their enigmatic epibionts. Statistical analyses of attachment trace size, frequency, and distribution on the conulariid test gives insight to the nature of their symbiotic relationship. Our results did not find any significant support for a parasitic relationship. However, commensalism cannot be ruled out and serves as an alternative explanation for the relationship between these two organisms.

INTRODUCTION

The sessile life mode of conulariids predisposed them to serve as a hard substrate for colonization by epibiont or other holdfast-bearing organisms. Among the taxa reported attaching to conulariids are cnidarians, principally *Sphenothallus* (Van Iten et al. 1996; John et al. 2010); brachiopods, including orbiculoids and rhynchonelloids (Babcock and Feldmann 1986a; Van Iten et al. 2016, 2018); edrioasteroids (Van Iten et al. 2018); other conulariids (Van Iten et al. 2016); microconchids (Brood 1995); and holdfast structures with unknown affinity (Babcock and Feldmann 1986a, 1986b; Van Iten et al. 2018).

Within the Waukesha Biota, conulariids are among the few preserved sessile organisms that could have served as a hard substrate in life (Miller et al. 2022). Though other sessile taxa have been documented from the assemblage, they are rare, and include orbiculoid brachiopods and a single specimen of *Sphenothallus* sp. (Wendruff et al. 2020). Whether either taxon was the producer of the holdfasts on the conulariids remains to be determined. Conulariids and *Sphenothallus* are well known to co-occur in similar paleoenvironments and geological formations throughout the Paleozoic (Van Iten et al. 1992a, 1996, 2013, 2016; Brabcová and

Kraft 2003; Botting and Muir 2012), though this alone is not indicative of such an association for the material documented herein.

Though epibiont associations with conulariids have been well documented, assessment of the host/epibiont interaction, particularly the degree of aggregation and distribution across and between individual hosts, has not previously been quantified. However, epibionts are purported to have attached to their conulariid hosts to benefit from (1) better access to food suspended higher in the water column; (2) opportunistic feeding from currents produced by the conulariid (assuming both organisms are filter feeders) (Neal and Hannibal 2000); and (3) avoiding predators on the seafloor surface (Sendino and Bochmann 2021).

The material herein presents an opportunity to investigate conulariid/epibiont dynamics and infer the nature of their relationship. Based on the disruption of the ornament around attachment surfaces and continued thecal growth we argue that the conulariid host and their epibionts shared a long-term relationship. Possible explanations for such a relationship include parasitism (i.e., a negative impact for the host but positive for the epibiont), mutualism (i.e., a positive impact on both host and epibiont) and commensalism (i.e., no impact for host but positive for the epibiont) (Zapalski 2011; Topper et al. 2014; Robin 2021). Due to the ambiguity in identifying mutualism and commensalism based on fossil data (Zapalski 2011), we conducted several analyses specifically to test for a parasitic relationship between conulariids and their epibionts. The relationships between host size and shape relative to attachment scar presence and abundance, as well as the distribution and size of the traces across the conulariid test were examined. This work aims to address the following questions: (1) what is the most parsimonious taxonomic affinity of the epibionts attached to conulariid specimens in the Waukesha Biota; (2) how do abundance and spatial distribution of attachment scars relate to the host’s body size or shape; and (3) to what degree do the size and distribution of the attachment scars reflect epibiont recruitment throughout conulariid ontogeny and the nature of their interaction?

METHODS

Geological Setting

The Silurian (Llandovery Series; late Telychian Stage) Brandon Bridge Formation and associated basal Waukesha Lagerstätte crops out as a shallow, southward dipping unit in south-east Wisconsin. The succession represents a mixed carbonate-siliciclasitc transgressive sequence package overlying a locally irregular, karstified ravinement surface of the Manistique Formation that wedges out on the western side of the Michigan Basin (Kluessendorf and Mikulic 1996; Grathoff and Moore 2002). The lithology and sequence stratigraphic context of the unit has been documented in detail previously (Mikulic 1977; Mikulic et al. 1985a, 1985b; Kluessendorf 1990; Kluessendorf and Mikulic 1996).; Pulsipher et al. *in press*). The accumulation of soft-bodied fossils within the Waukesha Lagerstätte has been attributed to anoxic conditions formed locally within hydrodynamic traps across the irregular paleoscarp surface in conjunction with entombment via microbial films (Kluessendorf 1990; Wendruff et al. 2020; Anderson et al. 2021).

A comprehensive systematic and taphonomic assessment of the two conulariid taxa—*Conularia niagarensis* Hall, 1852 and *Metaconularia* cf. *manni* (Roy, 1935)—from the Waukasha Biota has been provided by Miller et al. (2022) wherein the conulariids are reported as a dominant constituent of the sessile fauna within the fossil assemblage, but among the few to maintain evidence of biomineralization. Preservation of the conulariids is consistent with minimal post-mortem transport, as evidenced by a conspicuous lack of theca breakage or abrasion of fine external ornament, though the energy and duration of transportation has been suggested as sufficient to remove or dislodge attached epibionts (Miller et al. 2022). Post-burial taphonomic pathways demonstrate varying degrees of demineralization in response to changing pH conditions followed by compression and kerogenization of the conulariid theca. The result is a spectrum of taphomorphs from compressed forms with recrystallized thecae composed of francolite to carbonaceous films and kerogenous patches left on impressions or molds of the theca within the matrix (Miller et al. 2022).

Morphometric Data

Conulariid specimens examined in the present study are housed in the invertebrate paleontology collection of the University of Wisconsin-Madison Geology Museum (UWGM). Different conventions exist for the terminology of conulariid morphologies, herein we use that employed by Sinclair (1952), Moore and Harrington (1956), and Van Iten et al. (1996). Moreover, the terminology used herein concerning modes of attachment to hard substrates follows the conventions summarized in Bromley and Heinburg (2006). Of the total 40 conulariid specimens measured, we analyzed 33 (excluding counterparts and folded specimens) to characterize body size and shape. Among those analyzed, 562 attachment scars were measured on 20 conulariid individuals. Specimens were examined and photographed using a GIGAMacro Magnify2 Robotic Imaging System with Canon EOS Rebel T6i DSLR to acquire gigapixel resolution photomosaics with a T1 x1 and x3 Nikon objective. Morphological data of conulariid body size and associated attachment scar dimensions and distributions were then measured using the free image processing software package Fiji (Schindelin et al. 2012; http://imagej.net). Conulariid body size was measured based on the maximum length from aperture to apex along the corner groove and the maximum width of the aperture (Fig. 1A). Width measurements represent half the perimeter of the aperture (equivalent to the width of two faces) rather than the true width across one face due to the compression of the samples. For incomplete specimens on the apical end, length was estimated based on the projected apical angle of the lateral corner grooves on either edge of the specimen. The estimated width was based on the measured distance from the outer edge of the corner grove at the aperture to the intersection with the projected corner groove based on the apical angle (Fig. 1A). To examine the spatial distribution of the attachment sites across conulariid individuals, the distance of each trace to the aperture was measured (Fig. 1B).

Attachment scar morphology exhibits two discernible types depending on whether they are preserved on the internal or external surface. Those on the outer surface of the conulariid that preserve on the calcium phosphate test have a shallow circular depression with an outer rim that is fabric destructive relative to the external ornament (nodes, longitudinal striae, interspaces, and transverse ribs), herein referred to as type 1 (Fig. 1C, 1D). Traces visible on the internal surface of the conulariid take on two forms. Type 2a is the moldic counterpart of a type 1 depression and instead exhibits a positive circular feature (Fig. 1E, 1F). Type 2b lacks a positive mold and rather exhibits a faint circular feature often surrounded by a darker carbonaceous rim in the area outside of fabric destruction. Trace dimensions were measured as the maximum diameter and the maximum length perpendicular to the maximum diameter. For type 1 this is represented by the extent of the circular depression; if this was not present the extent of the outer rim was used. For type 2a, the diameter of the raised mold was measured. For type 2b, the faint circular feature was measured; however, in the absence of this feature the extent of fabric destruction was measured in its place (Fig. 1G, 1H).

Statistical Analyses

Analyses were conducted and figures were produced in *R* (*R* Core Team 2014; Version 1.2.1335) using the packages *ggplot2* (Wickham 2016) and *vegan* (Oksanen et al. 2020). We conducted correlation analyses and linear regression models to characterize conulariid size, shape, and ontogeny. The first model compared $\log_{10}$-transformed conulariid length and width, the second compared the geometric mean of $\log_{10}$-transformed length and width (as a body size proxy) to apical angle, and a third compared the same body size proxy as the previous model with the number of attachment scars.

Frequency distributions of the intensity of attachment scars on conulariid individuals were examined to determine if the relationship between the epibiont and host was consistent with that of a parasitic relationship. We performed a Wilcoxon test to determine the difference in median body size between conulariids with and without traces. We also conducted a non-Metric Multidimensional Scaling (NMDS) ordination on conulariid specimens using length, width, apical angle, and the number of transverse ribs per centimeter to assess how body size and shape relate to the number of attachment sites present. The NMDS reduced the data set to two dimensions, used a Euclidean dissimilarity index, and was performed using the metaMDS function in the *vegan* package (Oksanen et al. 2020).

Finally, correlation analyses were used to determine if the attachment scars show any preference toward grouping on a particular area of the conulariid. The first analysis compared trace size to the distance of the attachment site to the aperture. The second analysis conducted a similar analysis except attachment site distance was expressed as a proportion of conulariid length. The potential values of the latter range from zero (positioned at the apex) to 1.0 (positioned at the aperture). Raw data and *R* scripts are available in the Supplementary Material.

RESULTS

In sum, 32 specimens of *Conularia niagarensis* and 1 specimen of *Metaconularia* cf. *manni* were included in statistical analyses, of which, 20 had attachment scars. Trace-bearing specimens have between 9 and 47 attachment scars with a median value of 24.5. The maximum diameters of the inner pit and outer rims are 0.59 mm and 1.62 mm, respectively depending on the expression of the trace type identified. There is a significant and positive log-linear relationship between conulariid length and width ($r_{\text{Pearson}} = 0.92$, $p<0.001$) (Fig. 2A). The linear regression model characterized the relationship between the two variables as Width = 0.53 * Length + 3.86. Furthermore, *M.* cf. *manni* appears indistinguishable from the pattern dominated by *C. niagarensis*. There is a significant and negative correlation between conulariid body size (geometric mean of length and width) and apical angle ($r_{\text{Pearson}} = -0.45$, $p = 0.036$) (Fig. 2B). The linear regression model characterizes this relationship as Apical Angle = -0.145 * Geometric Mean + 27.51. The single specimen of *Metaconularia cf. manni* included in the model is characterized by a much narrower apical angle than similarly sized *C. niagarensis* specimens and we consider it to be an outlier.

There is a significant positive correlation between conulariid body size and number of attachment sites (Spearman rho = 0.61, $p = 0.0002$) (Fig. 2C). Note that there are no traces present on small (geometric mean of length and width less than 10) conulariids while larger specimens have a mix of conulariids with and without attachment scars (Fig. 2C). Frequency distributions were plotted to show the density of attachment sites on the conulariids. Specifically, the frequency distribution of the number of attachment scars on individual conulariids is strongly right-skewed (variance:mean ratio is 16.2:1) (Fig. 3A). The Wilcoxon test suggests there is a significant (*p* = 0.005) difference in median body size between conulariids with (21.6 mm) and without (14.6 mm) attachment scars (Fig. 3B). This pattern holds when the single specimen of *M.* cf. *manni* is removed, and only *C. niagarensis* is analyzed. In this case, the Wilcoxon test suggests a significant (*p* = 0.008) difference in median body size between conulariids with (20.9 mm) and conulariids without (14.6 mm) attachment scars.

The NMDS of individual conulariid specimens comparing body size and apical angle has a stress value of 0.030 (Fig. 3C). NMDS1 is interpreted as an inverse proxy of conulariid body size (larger specimens with negative values and smaller specimens with positive values). NMDS2 is interpreted as a proxy for shape that is positively correlated with apical angle (relatively wider aperture with positive NMDS2 values, relatively narrower aperture with negative NMDS2 values) and negatively correlated with density of ribs (lower density of ribs with positive NMDS2 values and higher density of ribs with negative NMDS values).

The Pearson correlation analysis resulted in a significant positive correlation between attachment scar size and distance to aperture (r = 0.145, *p* = 0.0014, n = 562) (Fig. 4A). There is no significant correlation between the trace size and proportional position of the attachment site (r = 0.073, *p* = 0.112, n = 562) (Fig. 4B). The smallest conulariids have small traces that are relatively close to the aperture (Proportional Position of Attachment Site >0.5). Larger conulariids have a broad range of trace sizes at low proportional positions (<0.5) and have very few small traces (i.e., mostly larger ones) closer to the aperture (>0.5).

DISCUSSION

Trace Morphology and Epibiont Affinities

Our material shows three main types of attachment scar morphologies. Though invariably some of the morphological variation observed relates to the vagaries of taphonomy, generally the traces can be simply characterized as circular in nature with an outer rim. While no attached epibiont body fossil has been observed in direct association with a conulariid, the most likely epibiont would be found within the Waukesha Biota. We also think these attachment scars were produced *syn-vivo* based on their presence on all faces of the conulariid test. In select specimens (UWGM 2754 and 4006) we see both type 1 attachment traces on the outer test and type 2a or 2b attachment traces on the opposing face. Furthermore, transverse rib ornamentation is disrupted in type 1 attachment traces suggesting that the epibiont stayed attached to the conulariid theca for an extended period of time, if not throughout both organisms' lives. Though raised bumps within the host rock and underlying fossils could be microbially-induced gas escape structures, type 2a attachment traces appear to be biologically induced structures and are produced antemortem (Wendruff et al. 2020).

Attachment traces on conulariid specimens that resemble those seen on our material have been described and figured without assigning an affinity, but could represent *Sphenothallus* holdfasts (Van Iten et al. 2018, fig. 5C–E; Sendino and Bochmann 2021, fig. 11). Furthermore, several studies have identified *Sphenothallus* attachment scars that bear a striking resemblance to what we describe as type 1 attachment traces (compare Fig. 1C, 1D to: Bodenbender et al. 1989, fig. 3; Neil and Hannibal 2000, figs 6, 7; Lerner and Lucas 2011, fig. 2; Zicha et al. 2020, fig. 3p, 3q; Bruthansová and Van Iten 2020, fig. 11a). *Sphenothallus* holdfasts and traces are often seen without any body fossils still attached to the host organism (Lerner and Lucas 2011), though phosphatic residues from the Silurian (Llandovery Series, early Aeronian Stage) Cape Schuchert Formation, Washington Land, North Greenland reveal well-preserved specimens of

Sphenothallus sp. holdfasts, attachment discs, and basal portions of the tube (Peel 2021). *Sphenothallus* holdfasts are characterized as conical with circular to elliptical outline ranging between 0.3–2 mm in diameter (Bodenbender et al. 1989; Peel 2021). The underside of the holdfast structure in loose phosphatic specimens shows a funnel-shaped smooth transition into the tube interior (Peel 2021, fig. 2B, 2C, 2K, 2P). Holdfasts preserved *in situ* attached to the host tend to lack the body tube, but show a raised phosphatic rim with a roughly circular pit in the center (Bodenbender et al. 1989; Neal and Hannibal 2000, fig. 6), while attachment scars attributed to members of the genus are also associated with circular outlines and interior depressions. Our material is small, averaging 0.6 mm in diameter for the outer ring with the center pit measuring 0.2 mm in diameter, which approximates dimensions of holdfast material documented from the Cape Schuchert Formation (Peel 2021).

Orbiculoid and rhynchonellid brachiopods are also known to attach to conulariids (and *vice versa*), however they often remain affixed after burial and consequently their attachment scars are rarely observed. Brachiopod attachment scars appear as lopsided circular to ovular depressions without any interior features (Zatoń and Wrzołek 2020, fig. 5B), unlike those examined in our material that are characterized by an inner pit surrounded by an outer ring. Attachment scars of unidentified brachiopods affixed to conulariid specimens were figured by Bruthansová and Van Iten (2020, fig. 12A, 12B) which bear no resemblance to the traces seen on our material. Furthermore, a figured conulariid specimen from the Skaneateles Formation, Middle Devonian, Cazenovia, New York is preserved with subcircular pits that were the attachment sites of orbiculoid brachiopods on the test face (Babcock and Feldmann 1986c, fig. 2I). However, these pits are very large, measuring 8–10 mm in diameter, far exceeding the maximum dimensions of the Waukesha Lagerstätte material.

Sphenothallus is perhaps the most parsimonious candidate for producing the observed traces, particularly given the overlapping dimensions and its contemporaneous occurrence within the Waukesha Biota (albeit only a single specimen has been confidently figured; see Wendruff et al. 2020, fig. 6C). The apparent absence of directly associated body fossils or holdfasts could be justified as taphonomic bias. This may be explained by potentially three scenarios that are not necessarily mutually exclusive. First, the epibionts were initially removed from the host through abrasive processes as a consequence of pre-burial transportation. Second, the attachment mechanism between the holdfast or attachment disc of *Sphenothallus* and adjacent theca detached at some point during conulariid growth or was degraded relatively rapidly post-mortem. Third, the very thin test of *Sphenothallus* was predisposed to enhanced demineralization pre- and post-burial , which may assist in explaining the rarity of *Sphenothallus* body fossils in the assemblage (Miller et al. 2022). Nevertheless, a soft-bodied organism cannot be ruled out, given that several taxa, including algae, annelids, ciliates, hydrozoans, select bryozoans, and sponges present in the modern day are known to adopt this epibiont habit (Waugh et al. 2004). This could also account for the absence of a physical holdfast, which have been reported previously in association with *Sphenothallus* (Mason and Yochelson 1985; Neal and Hannibal 2000).

Conulariid Size and Epibiont Abundance

Trends in conulariid shape and size are inherent to their growth habit—centripetal accretion (Van Iten 1992)—involving gradual thickening of two macrolamella zones on the inner surface of the periderm (Ford et al. 2016). Marginal accretion is produced by progressive mineralization of the test along weakly to non-mineralized lamellae close to the apertural margin (Mergl et al. 2016). Based on the specimens measured herein, we observed a strong positive correlation between length and width (Fig. 2A). Though this might initially suggest isometric growth, caution is required when interpreting this result as it is influenced by the method used to measure width, equating to two faces, as opposed to one. Moreover, the body size (geometric mean of length and width) scales negatively with apical angle, implying the angle becomes narrower and therefore that the rate of aperture expansion reduces throughout ontogeny (Fig. 2B). This is more suggestive of allometric growth.

Determining the morphological trends of the host throughout ontogeny is relevant to understanding the relationship between the host and epibiont throughout their respective lifecycles. Assuming smaller conulariids correspond to younger individuals we hypothesize that individuals with attachment scars are, in general, larger than those without them, and our results support this pattern (Fig. 3B). Among specimens with attachment scars present, larger specimens (i.e., with a body size greater than 10 mm, Fig. 2C) tend to possess more epibionts. This suggests that larger and presumably older specimens have more attachment scars, which would be consistent with the accumulation of parasites or epibionts throughout ontogeny (Huntley and Scarponi 2021). Frequency distributions corroborate this finding. The distribution of attachment sites among the conulariid population is strongly right skewed (Fig. 3A) with the many of conulariids lacking attachment scars while those possessing traces display a wider distribution (Fig. 3B). Other host-sclerobiont associations demonstrate comparable trends that have been explained by a prolonged availability of substrate and greater surface area for settling larvae on larger hosts as opposed to smaller ones (Webb and Schneider 2013). This type of distribution is also common among macroparasites (Shaw and Dobson 1995; Wilson et al. 1998) but is not definitive of a parasite-host interaction.

The NMDS ordination shows that conulariids without attachment scars tend to have narrower apical angles (Fig. 3C). This suggests that individuals with a smaller apical angle and body size are less likely to be colonized. Of the specimens examined, ~60% possessed attachment scars, which represents a moderate frequency of encrustation. However, given that approximately 40% of the conulariid specimens examined remained epibiont-free with potential space for attachment, there must have been limiting factors within the environment on epibiont recruitment (e.g., turbidity, depth, energy) (Taylor 2016). Furthermore, colonization methods employed by the epibiont likely impacted their settlement among the conulariid population, including such factors as the size of the larva, use of chemical signaling, and preferences in surface microtopography (Agostini et al. 2017; Bruthansová and Van Iten 2020). In our case, without knowing exactly what the epibiont is, it is problematic to infer the methods of recruitment. Nevertheless, we can infer the pattern of epibiont recruitment would have generally followed the patterns noted above (Carrera 2000; Taylor 2016; Agostini et al. 2017; Bruthansová and Van Iten 2020).

We must also be cautious in the interpretation of our data, as taphonomic and sampling biases could underrepresent the number of epibionts on individuals. For instance, the 2D compression of the conulariid specimens usually limits our sample set to one half (or two faces) of the organism. Moreover, prior dissolution of the theca during preservation or mechanical breakage of the test during sampling will further remove morphological data (Miller et al. 2022). Notably, the best-preserved examples of attachment scars are observed as type 1 traces on phosphatic test material, though frequently these show a very thin layer of phosphate or the underlying matrix compared to uncolonized test surface, suggesting the theca was particularly thin at the site of the scar. This may be a consequence of etching of the adjacent theca beneath the epibiont attachment in conjunction with increased proclivity towards pre-and post-burial dissolution (Bromley and Heinburg 2006).

Aggregation and Distribution of Epibionts

To determine the motive behind attachment, we assessed the relative position and distribution of the attachment sites across the host (Fig. 4A, 4B). A major assumption made in the interpretation of these results was that the attaching epibiont was the filter/suspension-feeding organism *Sphenothallus*, competing for resources in a kleptoparasitic fashion. As such, we hypothesized that young *Sphenothallus* would preferentially settle close to the aperture to gain access to the strongest feeding currents—a characteristic of kleptoparasitism (Morris 1981; Iyengar 2008; Zhang et al. 2020). Given this long-term, *syn-vivo* association, as the conulariid grows, *Sphenothallus* must grow to stay close to the aperture of the conulariid to maintain access to the feeding current. Older *Sphenothallus* would be larger with correspondingly large basal attachments that would be located closer to the apex compared to new, ontogenetically younger *Sphenothallus* settling near the aperture. In this case, we would expect to see a positive correlation between *Sphenothallus* basal attachment size and distance from the aperture. Moreover, we would expect to see few small/young *Sphenothallus* far from the growing margin.

The results of our analyses found a significant correlation between the distance from the aperture and the size of the associated attachment scar (Fig. 4A), though not for trace size and proportional distance (Fig. 4B). Given the significant correlation has a very low r value and is based on a very large sample size, even the statistical significant test may not reflect much true, ecological significance. Consequently, the weak relationship between these two variables suggests that conulariids and *Sphenothallus* may not have shared a kleptoparasitic relationship. Indeed, in larger conulariid specimens, few small attachment scars are found near the aperture, as would be expected with kleptoparasitism. Instead, conulariids and *Sphenothallus* could share a commensal relationship in which *Sphenothallus* was using the conulariid theca as an attachment surface to feed independently. However, testing for commensalism is presented with several challenges.

The argument for commensalism is often presented as follows: if the host tolerates large numbers of symbionts, (1) they must be harmless (Browne and Kingsford 2005; Dvoretsky and Dvoretsky 2009); (2) there is very little cost to the host (Goto et al. 2007; Lee et al. 2009); or (3) there is a positive effect for the symbiont and an undetectable positive or negative effect for the host in which a neutral effect is assumed (Mosher and Watling 2009; Torres-Martínez et al. 2021; Zapalski 2011). There are issues with each argument presented for commensalism in the fossil record. For instance, the first argument is problematic because parasites can be tolerated by the host in large quantities with no apparent effect (Miller et al. 2005; Zapalski 2011). It has also been argued that commensal relationships can become parasitic as the interaction between host and symbiont can fluctuate over time with external environmental influences (Miller et al. 2006; Lee et al. 2009; Zapalski 2011). Our material is not evidently parasitic; hence we propose that a commensal relationship is most appropriate, one in which there is a positive gain for the epibionts and negligible detectable effect on the host organisms. Nevertheless, we concede this interpretation is based on a lack of negative evidence, given the aforementioned limitations on the interpretations of commensalism in the fossil record.

CONCLUSIONS

Numerous attachment scars are present in over half of the conulariid specimens sampled from the Waukesha Biota, though the body fossils of the epibiont are scarce and have thus far eluded preservation *in situ*. We suggest the attachment scars present on the conulariid test were produced *syn-vivo* based on the presence of attachment sites on all conulariid faces and disrupted transverse rib ornamentation which indicates a long-term living relationship between epibiont and host. The attachment scars found on Waukesha conulariids bear a close morphological resemblance to *Sphenothallus* scars described in published literature, though the physical holdfast has not been found preserved. Principally, the presence of a circular to elliptical rim with a centralized pit distinguishes the scars from other potential attaching organisms such as orbiculoid brachiopods also found preserved in the Waukesha Biota. Concerning the nature of the relationship between host and epibiont throughout their respective lifecycles, our analysis found that larger conulariids, both in terms of size and apical angle, tend to have possessed more attachment scars. Given the moderate rate of encrustation within the population, recruitment of epibionts on the hosts was likely being impacted by other environmental or biological factors. Frequency distributions are strongly right skewed indicating an aggregated distribution of attachment scars among the conulariid population. This pattern is common among macroparasites; however, it is not definitive of a parasite-host interaction. Assessment of the relative position and distribution of attachment sites across the conulariid test did not find a strong relationship between trace size and distance to the aperture. In the absence of strongly significant evidence of a parasitic relationship, we consider commensalism an alternative explanation for the relationship between conulariid and epibiont.

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FIG. 1.—Measurements on *C. niagarensis*. **A)** UWGM 3021 showing measurements for length (white) and width (yellow) and apical angle (black). **B)** UWGM 2754 showing measured distance of the attachment scar center to the aperture. **C–H)** Examples of attachment sites in *C. niagarensis* showing corresponding measurements of maximum diameter (white) and length perpendicular to maximum diameter (yellow). **C–D)** Type 1 attachment scars on the exterior face of the conulariid test showing a small inner pit with a larger outer ring. **C)** UWGM 4011. **D)** UWGM 4006. **E–F)** Type 2a attachment scars on the exterior mold of the conulariid test expressed as a raised protrusion. **E)** UWGM 3185. **F)** UWGM 3054. **G–H)** Type 2b attachment scars on the interior surface of the conulariid test showing a shallow circular depression with a dark carbonized rim. **G)** UWGM 3172. **H)** UWGM 3966. Scale bars A and B = 2mm, C–H = 0.5 mm.

FIG. 2.—Results for a correlation analyses and linear regression models characterizing conulariid size, shape, and ontogeny. A) Relationship between conulariid length and aperture width. The x- and y-axes are $\log_{10}$ plots. **B)** Relationship between body size and apical angle of face. The x-axis is a $\log_{10}$ plot. Blue line = linear regression model. **C)** Correlation analysis showing the relationship between conulariid body size and the number of attachment scars on each specimen. The x-axis is a $\log_{10}$ plot.

FIG. **3.— Results for the distribution of the intensity of attachment scars on the conulariid test to determine the nature of the relationship between host and epibiont. A)** Frequency distribution of attachment scars on conulariids. The variance:mean ratio of the number of attachment scars is 16.3. **B)** Frequency distribution of conulariid body size. Stacked bars are color-coded to indicate the presence or absence of attachment scars. The median size values of the two groups are shown by thin vertical lines. **C)** Results of a non-metric multidimensional scaling (NMDS) ordination of individual *C. niagarensis* specimens for which measurements of the following were available: Length, Width, Apical Angle, and Ribs per cm. Size of circle corresponds to the number of traces on each specimen (n = 23). Small red circles indicate the position of the original variables in the nMDS-defined space and serve as a key to its interpretation.

FIG. **4.—Results for correlation analyses used to determine if there is a preference for epibiont grouping on the conulariid test. A)** Compares attachment scar size and actual distance of the attachment site to the conulariid aperture. The x- and y-axes are $\log_{10}$-transformed. **B)** Compares attachment scar size to the proportional position of the attachment site to the conulariid aperture. The x-axis is log transformed.