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Mapping sclerobiosis: a new method for interpreting the distribution, biological implications, and paleoenvironmental significance of sclerobionts on biotic hosts

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Abstract.—The use of sclerobiosis as a tool for paleoenvironmental and paleoecological research is undermined by a lack of comparable methods for sclerobiont data collection and analysis. We present a new method for mapping sclerobiont distributions across any host, and offer an example of how the method may be used to interpret sclerobiont data in relation to host orientation. This approach can also be used to assess the suitability of beds and fossil material for paleoenvironmental reconstruction.

A sample of 150 encrusted dorsibiconvex atrypide brachiopods were selected from six beds in the Waterways Formation (latest Givetian – Early Frasnian; Alberta, Canada). The dorsal and ventral valves of each brachiopod were photographed. Sclerobiont taxa were mapped onto the photographs, and the maps were used to create stacked images with each of the 25 brachiopod specimens from each bed. Based on the life orientation of dorsibiconvex atrypides, three zones were designated on the host: the post mortem zone, (only available to sclerobionts after death and reorientation of the host); the shaded zone (brachial valve, excluding the post mortem zone); and the exposed zone (ventral valve).

Randomization simulation results indicate that all beds likely exhibit non random encrustation patterns, and corroborate the hypotheses that: (1) much of the encrustation occurred while the hosts were alive, and (2) these beds and fossils have experienced little physical reworking or transport and would be suitable for paleoenvironmental analysis. Mapping sclerobionts across hosts can serve as a unifying method to increase the recognition and use of sclerobiosis in paleontological studies.

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Introduction

Few interactions between organisms in the fossil record are as well preserved as sclerobionts attached to biotic hosts. Sclerobionts (sensu Taylor and Wilson 2002; equivalent to "epibionts" in several modern studies) make up an important and often diverse part of marine communities both in the fossil record, and in the modern (Fenton 1937; Lescinsky 1996; McKinney 1996; Nebelsick et al. 1997; Taylor and Wilson 2003; Schneider 2013; Brett et al. 2012). The spatial distribution of sclerobionts on the host allows for examination of paleoenvironmental conditions, potential biological relationships between sclerobionts and their hosts, as well as relationships between multiple sclerobionts on the same host (Ager 1961; Kesling et al. 1980; Sparks et al. 1980; Sando 1984; Donovan 1989; Fagerstrom 1996; Peters and Bork 1998; Taylor and Wilson 2003). With such a wealth of sclerobiont information available from an assemblage of hosts, it can be difficult to determine the best methods for data collection, analysis, and interpretation. As a result, there are no unified methods for analyzing sclerobiont data, which makes large scale comparisons of sclerobiosis across host groups, time, and space exceedingly difficult (Schneider 2013). Additionally, factors such as the life status of the host at the time of encrustation further complicate paleoenvironmental and biological interpretations of sclerobiont data. The following study not only presents a unifying method for mapping sclerobiont distributions across hosts, but also examines sclerobiont distribution in relation to the host's life orientation. To demonstrate the utility of

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this method, the study examines sclerobiont distributions across a group of brachiopod hosts in which the life orientation is tightly constrained (Barclay et al. 2015). The ultimate goal of the study is to present a technique that not only will potentially capture more biologically meaningful information regarding the sclerobiont host relationship but which will also assess the degree of time averaging of the fossils within a bed, thus providing an independent means of determining whether such beds and their constituent fossils would be suitable for use in any subsequent paleoenvironmental analysis.

One of the greatest challenges facing any researcher interested in using sclerobionts to examine paleoenvironments or sclerobiont-host relationships is the life status of the host at the time of encrustation. While there are examples of direct evidence for the timing of encrustation, such as sclerobiont overgrowth of food gathering or respiration structures on the host that would have either killed the host or occurred post mortem (Ager 1961; Alvarez and Taylor 1987; Bose et al. 2011), and synchronous or directional growth of the host and sclerobionts which would indicate a live live relationship between the sclerobiont(s) and host (Alvarez and Taylor 1987; Taylor and Wilson 2003), such examples are not commonplace. Without direct evidence of the timing of encrustation, the life orientation of the host may provide insight into the biological implications of sclerobiont positions on the host, the degree of time averaging in an assemblage, and which sclerobionts and hosts may potentially represent a live live relationship.

However, it is often the position of sclerobionts on a host that is used to infer the life orientation of the host (e.g., Cuffey et al. 1995). For example, the position of sclerobionts on concavo convex brachiopods has been used as one line of evidence to infer that the brachiopods lived with the convex valve facing down into the substrate (Richards 1972; Bordeaux and Brett 1990). In contrast, Lescinsky (1995) used the position of sclerobionts to infer that the same morphology of brachiopod lived with the concave valve facing the substrate. Regardless of interpreted host orientation, in both cases there is the possibility of reorientation during the lifetime of the host, as well as post mortem transport, reorientation, and subsequent encrustation of the valve that was initially against the substrate (and therefore unavailable to sclerobionts during the host's lifetime). Substrate, ornament, and textural affinities may further complicate sclerobiont settlement patterns (Bose et al. 2011), as post mortem, concave valve interiors of modern terebratulides, which are more prone to disarticulation that atrypides, can be much more heavily encrusted than valve exteriors by both epibionts and endobionts (Rodland et al. 2004, 2006, 2014). Distinguishing hosts that were encrusted post mortem is critical to understanding sclerobiont-host relationships, as post mortem encrustation of a host does not contribute to an understanding of a biological relationship between sclerobionts and hosts. The number, or lack, of hosts encrusted post mortem may also be used for paleoenvironmental analysis, such as the amount of time averaging in an assemblage. If it can be demonstrated that hosts were heavily encrusted post mortem, then these specimens spent considerable time exposed on the surface after death, and potentially may no longer be reliable paleoenvironmental indicators. If such post mortem encrustation were widespread in a unit, then it would be more conservative to remove such specimens from the paleoenvironmental analysis.

Experimental tests of functional morphology are an independent method for biomechanically determining plausible life orientations for hosts. Biomechanical experiments on brachiopods have been particularly well documented (Alexander 1975, 1984, 1986; LaBarbera 1977, 1978; Leighton and Savarese 1996; Leighton 1998, 2005; Messina and LaBarbera 2004; Barclay et al. 2015). In a previous study by the authors, biomechanical experiments were conducted on common dorsibiconvex brachiopod hosts as a means of independently assessing the life orientation of the dorsibiconvex brachiopod morphology (Barclay et al. 2015).

Dorsibiconvex brachiopods were abundant worldwide during the Silurian and Devonian and were common sclerobiont hosts (Copper 1966a,b, 1967, 1973, 1990, 1998; Johnson 1970, 1974; Hurst 1974; De Keyser 1977; Alexander 1986; Gibson 1992; Alexander and Gibson 1993;

Day 1990, 1992, 1996, 1998; Day and Copper 1998; Schneider and Leighton 2010; Bose et al. 2011; Bose 2012; Barclay et al. 2013; Webb and Schneider 2013). Biomechanical experiments indicated that these dorsibiconvex atrypides did not have a true hydrodynamically stable position and were at considerable risk of transport, and so probably retained a pedicle throughout their lives (Barclay et al. 2015). Therefore, they most likely lived with the posterior portion of the dorsal valve, and the tip of the umbo on the ventral valve, resting against the substrate (Barclay et al. 2015) (Fig. 1). Those parts of the brachiopod that would have rested against the substrate during life would have been unavailable for sclerobiont settlement and therefore any encrustation of those areas could only occur after significant erosion, or death, decay of the pedicle, and reorientation of the brachiopod.

Grid systems are a common method used to examine sclerobiont distributions across a host (e.g., Kesling et al. 1980; Sparks et al. 1980; Gibson 1992; Bose et al. 2010, 2011; Webb and Schneider 2013; Furlong and McRoberts 2014). However, there are many methods for developing host grids. As the use of a grid system is often associated with the use of goodness of fit tests (e.g., Chi-square test), and such tests are usually scale dependent, the choice of the number of cells in the grid can create an artifact that may bias the result. Alternatively, Lescinsky (1995) used points to represent the location of each sclerobiont on the host, but this approach ignores areal coverage of sclerobionts, and may not be able to differentiate multiple sclerobionts encrusting the same position. In addition, the problem still remains that interpretation of the biological significance of sclerobiont positions is dependent on the host's orientation.

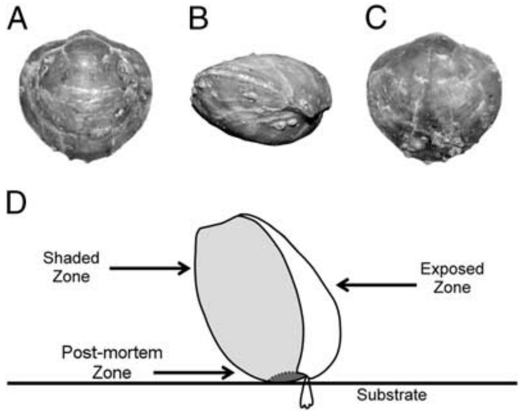

FIGURE 1. A typical encrusted dorsibiconvex atrypide brachiopod from the Waterways Formation and its probable life orientation (based on Barclay et al. 2015). A, Dorsal view; B, lateral view; C, ventral view; and D, probable life orientation, illustrated with post mortem, shaded and exposed zones, which are biologically significant areas for encrustation of the brachiopod. The post mortem zone indicates a zone of encrustation which could only occur after the death of the brachiopod, decay of the pedicle, and subsequent transport or reworking, resulting in exposure of the post mortem zone to sclerobionts.

Furthermore, without a unified method of data collection, it is difficult to compare multiple sclerobiont studies to ascertain any common or unique trends. A simple solution might be to directly map the outline of each sclerobiont exactly as it appears on each host. Retaining complex spatial outlines of sclerobionts would allow independent assessment of any patterns suggested by the original researchers. The area of the host's shell unavailable to sclerobionts during the host's lifetime would allow distinction of post mortem encrustation, which would benefit paleoenvironmental interpretations and analysis of live sclerobiont, live host relationships.

The goal of the following study is to provide a unifying method for sclerobiont studies, which may be used to: (1) map sclerobiont distributions across any host, (2) assess the potential paleoenvironmental or biological significance of sclerobiont distributions based on the host's orientation, and (3) minimally provide a new method for distinguishing post mortem encrustation of hosts, and thus an additional means of assessing time averaging.

Geologic Setting

The Waterways Formation (latest Givetian–Early Frasnian) outcrops along the Athabasca and Clearwater Rivers in northeastern Alberta, Canada (Fig. 2). The formation consists of five members, which, from oldest to youngest, include: the Firebag, Calumet (Calmut), Christina, Moberly, and Mildred Members (sensu Crickmay 1957; Norris 1963) (Fig. 3).

FIGURE 2. Paleogeography of North America during the Givetian–Frasnian with an enlarged inset of the study area. Fort McMurray is indicated by a black star. Present day geography has been inserted for reference, with Devonian land masses indicated in dark grey. The paleoequator lies in northern Canada and is indicated by a solid black line (modified from Day 1998: Fig. 1; Barclay et al. 2013).

During deposition of the Waterways Formation, northeastern Alberta lay along a passive continental margin in the tropics, south of the paleoequator (Loranger 1965; Witzke and Heckel 1988) (Fig. 2). The Waterways Formation was deposited on a shallow water platform below fair weather wave base, but above storm wave base (Oldale and Munday 1994; Schneider and Grobe 2013), with a possible offshore island arc to the present day west (Moore 1988; Wendte and Uyeno 2005; Schneider et al. 2013b). Uplift and erosion of the Ellesmerian Fold Belt (Stoakes et al. 1992; Wendte 1992) and/or the Caledonian or Franklinian orogenic belts (Moore 1988; Wendte and Uyeno 2005) to the present day northeast provided a large source of terrigenous mud influx (Wendte and Uyeno 2005; Barclay et al. 2013; Schneider et al. 2013b) (Fig. 2). The Givetian/Frasnian boundary occurs coplanar with the contact between the Firebag and Calumet Members (Braun et al. 1988). The four lower members outcrop near the city of Fort McMurray along the Athabasca and Clearwater Rivers; the upper Mildred Member is present only in the subsurface to the west of the study area.

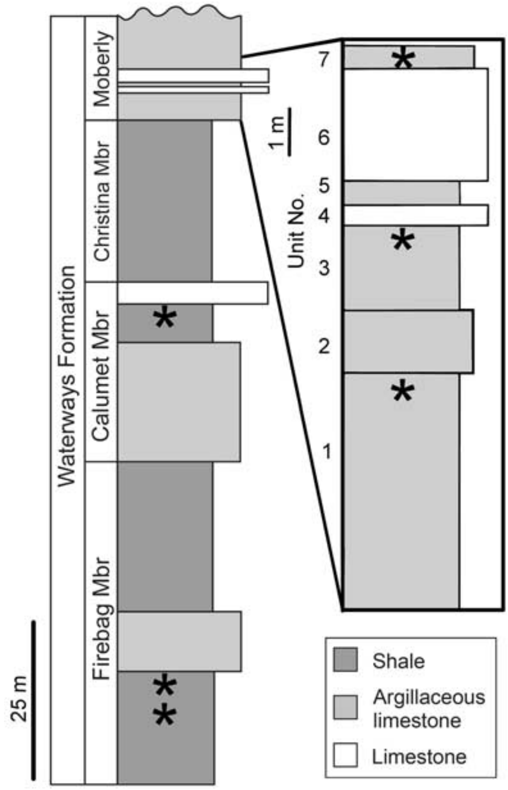

FIGURE 3. Composite stratigraphy of outcrops of the Waterways Formation along the Athabasca River near Fort McMurray, Alberta, Canada. The Givetian/Frasnian boundary is placed at the boundary between the Firebag and Calumet Members (Braun et al. 1988). The left column depicts the Waterways Formation to scale, with the right column/inset depicting an enlarged view of the lower Moberly Member. Black asterisks indicate the six stratigraphic units that were sampled for this study (modified from Schneider and Grobe 2013; Schneider et al. 2013c: Fig. 2; Barclay et al. 2015: Fig. 5).

Firebag Member.—The lowest Waterways member consists of an approximately 50 m thick section containing lower and upper shale units with a middle argillaceous limestone (Buschkuehle 2003; Barclay et al. 2013; Schneider and Grobe 2013). The unit is largely unfossiliferous, with distinct fossiliferous horizons that are dominated by brachiopods, but also include crinoids and bivalves. Brachiopod faunas are heavily dominated by atrypides, particularly *Desquamatia* (Barclay et al. 2013). Two fossiliferous beds along the Athabasca River, both from the lower shale unit, were sampled for this study, and will be referred to herein as Firebag Sample 1 and Firebag Sample 2 (Fig. 3).

Calumet Member.—The Calumet Member outcrops mainly along the Clearwater River east of Fort McMurray, and consists of a lower argillaceous limestone, middle shale, and upper "clean" limestone (Schneider and Grobe 2013). Fossils are again dominantly brachiopods, but throughout much of the unit consist mostly of the concavo convex *Strophodonta* and the orthide *Schizophoria*, instead of atrypides (Schneider and Grobe 2013). It is only near the top of the Calumet Member that brachiopod faunas return to an atrypide dominated assemblage, similar to those of the Firebag and Moberly Members. A series of thin horizons at the transition between the middle shale and upper limestone consisting of mostly atrypide brachiopods were sampled for this study, and will be referred to as Calumet Sample 1 (Fig. 3). The entire member is approximately 22–30 m thick in the study area (Schneider and Grobe 2013).

Christina Member.—The Christina Member consists of an approximately 25–30 m thick, unfossiliferous shale (Schneider and Grobe 2013), and was therefore not sampled.

Moberly Member.—The top of the Moberly Member is absent in parts of the study area, and overall, the member varies in thickness between 62–80 m in its entirety (Schneider and Grobe 2013). Lithology and fauna are varied throughout the member, and have been separated into 13–14 informal units (sensu Schneider et al. 2013a,c). Unit 6 is the most easily correlated unit and is an approximately 2–3 m thick biostromal rudstone consisting of massive and branching stromatoporoids and corals (Schneider and Grobe 2013; Schneider et al. 2013a,c). Three samples were collected from fossiliferous argillaceous limestones in the Moberly Member, two from the lower section of argillaceous limestone (units 1 and 3, respectively), and one from the base of unit 7, the argillaceous limestone immediately above the biostromal unit 6. These three samples will be referred to herein as Moberly Samples 1, 2, and 3 (Fig. 3). In each of the Moberly samples, atrypide brachiopods, especially *Radiatrypa*, were the most abundant fossils.

Methods and Materials

Field Methods.—Brachiopods were bulk, surface collected from individual, fossil rich horizons of the Waterways Formation exposed along the riverbanks of the Athabasca and Clearwater rivers near Fort McMurray, Alberta, Canada (Fig. 2). Samples were collected to minimally fill a one gallon bag with matrix free brachiopods (the minimum sample size was 109 brachiopods). Collected brachiopod specimens had to include the umbo and at least 50% of the brachiopod. The vast majority of the specimens found were articulated. Specimens were collected without any other bias, such as a bias toward overall preservation or encrusted/unencrusted specimens. Brachiopods in each sample were cleaned, sorted, and examined for exceptional preservation (primary shell layer mostly or entirely intact). Given the nature of this study, only brachiopod units that contained comparable, atrypide dominated assemblages were considered for examination. Additionally, atrypide brachiopods are known to have great rates of encrustation (Hurst 1974; Gibson 1992; Schneider and Leighton 2010; Bose et al. 2011; Barclay et al. 2013; Webb and Schneider 2013). Previous work within the Western Canadian Sedimentary Basin, as well as the Waterways Formation itself, also indicated that brachiopods were generally very well preserved and had abundant sclerobionts (Schneider and Leighton 2010; Barclay et al. 2013; Schneider and Grobe 2013; Schneider et al. 2013 a,c). Of all the samples collected, six beds, as described above (Firebag Samples 1 and 2, Calumet Sample 1, and Moberly Samples 1, 2, and 3) (Fig. 3), were found to contain atrypide brachiopods which met the study parameters.

Mapping Methods.—Atrypide brachiopods were cleaned and identified to genus. Any atrypide that was not identifiable, at least to genus, or comprised less than 50% of the specimen or primary shell layer, was culled from the sample set. Only articulated specimens were used. Of the atrypide brachiopods, only specimens belonging to those brachiopod taxa which fit the typical dorsibiconvex atrypide morphology and which behave similarly in flume experiments (Barclay et al. 2015) were used for mapping purposes. In the Firebag and Calumet Members, those brachiopods consisted mostly of the genera *Desquamatia* and *Pseudoatrypa*, and in the Moberly member, those brachiopods consisted of the genera *Desquamatia, Pseudoatrypa,* and *Radiatrypa*. Morphologically, these three genera are extremely similar, and are distinguished primarily on the basis of differences in ornament or the interarea.

For all six beds, the brachiopods were similar in adult size (approximately 2 cm in length). In each bed, the brachiopod specimens selected for mapping purposes were generally the largest and best preserved specimens in that assemblage, regardless of species identity. As a result of these similarities in morphology, biomechanical performance, proportional abundance in each assemblage, and size, there was no reason to assume that encrustation of the genera would be different. However, brachiopods from the six beds were analyzed separately so as to retain stratigraphic resolution and to avoid any assumption that the trends in each bed would have been the same, which is not necessarily true when examining sclerobionts and hosts from multiple assemblages (Barclay et al. 2013). As well, by keeping the six beds separate, any potential changes in sclerobiont patterns associated with proportional changes in the most common host genus would be immediately apparent.

It is important to stress that rigorous, selective choice of the brachiopod material used in the study was used to demonstrate the utility of the new sclerobiont mapping method, as is described in the following pages, and is not necessarily meant to act as a detailed, representative paleoecological analysis of sclerobiosis in the Waterways Formation. Selection of material was simply based on previous work, including independent establishment of the life orientation of dorsibiconvex brachiopods (Barclay et al. 2015), and easy access to well preserved brachiopod material. As the major goal of the study is to provide a unified method for collecting sclerobiont data, any other assemblage of different hosts in which the life orientation of the host had been previously established could have also been used.

Each brachiopod was examined under a 10–40× binocular microscope (Leica) for sclerobionts. Brachiopods that had sclerobionts were sorted from those that were unencrusted. Of the encrusted specimens, the 25 best brachiopods from each of the six beds (those that were similar and typical in size for adult brachiopods of the Waterways Formation, the most complete, had little or no deformation, and had the majority of the primary shell layer preserved) were selected for mapping purposes, for a total sample of 150 specimens. While this reduced the overall potential data, the approach ensured that high quality specimens were consistently used; studies of sclerobiosis require excellent preservation. Samples were unbiased with regard to anything other than the quality of the material. If there were more than 25 brachiopod specimens per bed that fit the study criteria, the largest and smallest of the eligible brachiopods were removed until the sample was reduced to 25 specimens. A sample of 25 specimens per bed was deemed adequate for the testing of this hypothesis, as the goal was to demonstrate the utility of the mapping method, and then determine if each individual brachiopod had evidence of post mortem encrustation. Logistically, the sample size was limited by Calumet Sample 1, which only had 25 encrusted brachiopods that were sufficiently large and well preserved enough to be considered for the study. Despite this constraint, the present work constitutes the most detailed mapping of fossil sclerobionts that has been conducted up to now.

Two high resolution photographs, a dorsal and ventral view, were taken of each specimen. A metric scale card was used to retain size data for each brachiopod. Each photograph was then opened in GIMP 2.8 (a free graphic editing software program), and the brachiopod was simultaneously examined under a microscope. The outline of the brachiopod was drawn onto the photograph, and all sclerobionts were then identified to the lowest taxonomic level possible under the microscope. A separate image layer was created for every sclerobiont taxon present, and the outline of each individual sclerobiont was drawn directly on the image of the brachiopod, using the microscope as an aid. This produced two maps of each brachiopod (dorsal and ventral views) in which the original photo could be removed so that only the outline of the brachiopod and each sclerobiont remained (Fig. 4). Once every sclerobiont had been mapped onto the photographs, there were 50 maps from each bed (25 each of the dorsal and ventral views). For each bed, the 25 dorsal or ventral valve images were scaled, rotated, and stacked onto one another, by aligning specimens across the hingeline and median plane of symmetry, so that a detailed, stacked map was created of the sclerobionts on each of the 25 brachiopod dorsal and ventral valves, in which the 25 layers could be hidden or viewed (Fig. 4). The final result was two separate maps for each of the six beds, one each of both the dorsal and ventral valves, or 12 maps in total (Fig. 5). Given the similarity in morphology between the dorsibioconvex atrypides included in the study, the following method also standardizes for surface area of the host. Standardization of surface area of different host taxa is an important consideration for future studies that may compare different host taxa.

Analyses.—Given that the probable life orientation of dorsibiconvex atrypides had been previous established (Barclay et al. 2015), three zones were identified: the post mortem, shaded, and exposed zones (Fig. 1). The size of the post mortem zone was based on the amount of the dorsal valve that rested against a firm surface when the umbo/pedicle foramen was placed against that surface (about 6% of the brachiopod's total surface area). These zones allow for the distinction between post mortem, and potential life associated encrustation of the brachiopods. Instead of creating an arbitrary grid scheme on the brachiopod host, the present zonation, based on existing information regarding the life orientation of the brachiopod, allowed for a potentially more biologically meaningful visual examination of sclerobiont distributions on brachiopod hosts.

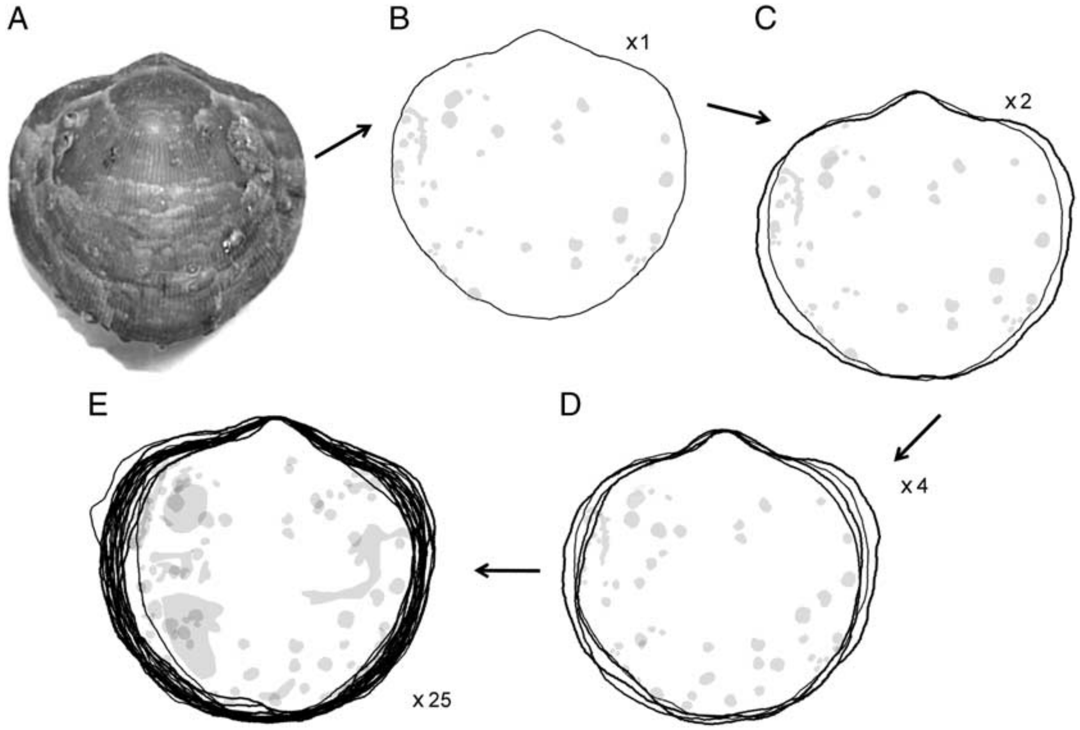

FIGURE 4. Illustration of the sclerobiont mapping process. A, Two photos are taken of each brachiopod specimen (dorsal and ventral views). Here, the dorsal view is shown. B, The brachiopod's outline, and the outline of each sclerobiont are mapped onto the photograph. C, D, E, Each brachiopod is mapped, and the mapped images are scaled and stacked on top of one another until there is an image with 25 maps.

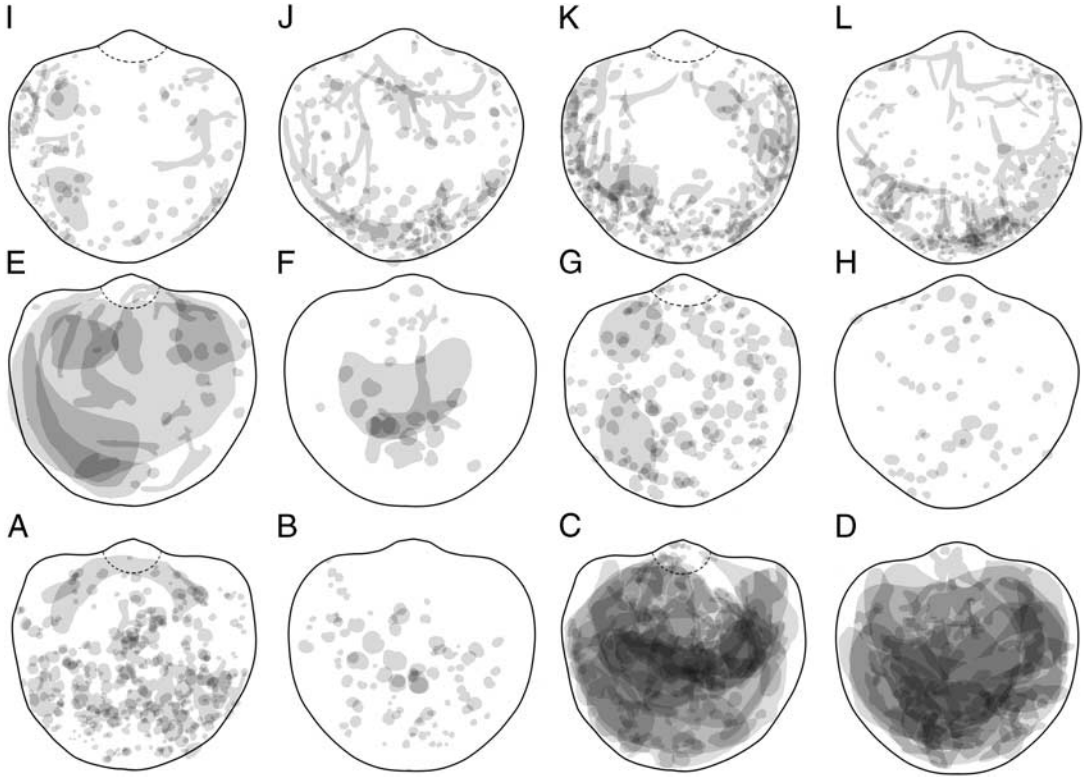

FIGURE 5. Stacked sclerobiont maps for each of the six sampled units. Sclerobionts were lightly shaded so as to produce a type of heat map in which darker shading indicates greater occurrences of sclerobionts in any given area. Columns 1 and 3 (left to right) are dorsal valve maps, and columns 2 and 4 are ventral valve maps. Each of the twelve maps is a stack of 25 brachiopod images. The individual outlines of each brachiopod have been removed and replaced with an 'idealized' outline to better capture sclerobionts near the margins of the brachiopod. In the first and third columns, the dashed line indicates the outline of the post mortem zone on the dorsal valve. A–B, Firebag Sample 1; C–D, Firebag Sample 2; E–F, Calumet Sample 1; G–H, Moberly Sample 1; I–J, Moberly Sample 2; and K– L, Moberly Sample 3.

Distinction of the shaded and exposed zones not only allowed for a comparison of the extent of encrustation on the dorsal (shaded) and ventral (exposed) valves (excluding the post mortem zone on the dorsal valve), but it also allowed for a potentially biologically significant interpretation of encrustation within each zone. Given the life orientation of the host (Fig. 1), the shaded zone on the dorsal valve was somewhat more sheltered from currents and grazing predators (e.g. Taylor and Wilson 2003), whereas the ventral valve was more exposed to fairly high energy flow velocities, which would have often exceeded flow rates of 0.3 m/s (Barclay et al. 2015), hence the terms 'shaded' and 'exposed'.

Any brachiopod that had a sclerobiont within the post mortem zone was considered dead at the time of encrustation, as encrustation of the post mortem zone could only occur after the brachiopod had died, the pedicle had decayed, and subsequent transport or reorientation had exposed the post mortem zone for sclerobiont settlement, meaning that at least some encrustation of that brachiopod had occurred post mortem. The number of brachiopods encrusted post mortem in each of the six beds was then noted. Those brachiopods that did not have sclerobionts within the post mortem zone were more likely to represent brachiopods that were encrusted while they were still alive. By distinguishing the number of brachiopods encrusted post mortem in any sclerobiont/brachiopod study, those particular brachiopod specimens can minimally be excluded from analyses of host or sclerobiont preferences, as post mortem encrustation would not contribute to any potential patterns of a live host live sclerobiont relationship.

As an additional precaution, all mapped sclerobionts were cross checked with the original specimen to ensure that the sclerobiont's position had not been distorted from its original position on the actual specimen, as the projection of a three dimensional object onto a two dimensional map sometimes meant that some spatial data was lost.

While it is possible that the absence of sclerobionts from the post mortem zone is due to random chance and has nothing to do with the life status of the host at the time of encrustation, the presence of an encruster in this zone would have been difficult to impossible while the animal was alive; thus, this method minimally provides a way to identify those hosts that experienced some post mortem encrustation, which in and of itself is useful for both paleoecological and sclerobiont studies. However, to assess whether the brachiopods within a given bed were sclerobiont free within a given zone due to random chance, we also performed a Monte Carlo randomization simulation. The post mortem zone comprises roughly 10% of the dorsal valve surface area. For the simulation, 25 hypothetical brachial valves (the same number of actual valves) in a bed were each divided into ten equal area zones, each of the same approximate surface area as the post mortem zone, for a total of 250 zones across all 25 specimens in a bed. The simulation then randomly assigned encrusters to these 250 zones. Based on the observed data, which indicated an average of 150 sclerobionts across 25 hosts in a bed, each zone on each specimen was given a 60% chance of containing an encruster. Subsequent to this random assignment of the encrusters, each zone was examined across all 25 host specimens, and the number of host specimens for which that zone was empty (unencrusted) was tabulated. This procedure was repeated for each zone. This approach is conservative—if any zone, whether the post mortem zone or not, was repeatedly empty, it would suggest that it was possible to generate an empty zone across 25 specimens by random chance alone. The entire process was iterated 1000 times to demonstrate the likelihoods (realized p-values) of observing X number of host specimens in a bed with the same unencrusted zone due to random chance, where X was the number of such host specimens actually observed in one of the study fossil beds.

On each map, the area covered by each sclerobiont was lightly shaded so that the amount of encrustation on any particular area of the shell could be visualized by increasing opacity of the maps on more heavily encrusted areas (i.e., a hot spot of encrustation versus a lightly shaded to blank cold spot of sclerobiont avoidance) (Fig. 4). Each sclerobiont map was not only a visualization tool for sclerobiont distribution patterns, but it also enabled simple sclerobiont abundance counts to be taken. Two by two chi-square tests were conducted to compare the abundance of sclerobionts in the shaded and exposed zones, taking into account the proportion of brachiopod shell in each zone available to sclerobionts.

Results

All Samples.—The mapping method produced highly detailed sclerobiont distribution maps, which clearly retained spatial information between sclerobionts, sclerobiont areal coverage, and allowed visual assessment of host areas with abundant or scarce encrustation. There were four taxonomic groups of sclerobionts found on brachiopods across the six beds: *Ascodictyon* (*incertae sedis,* see Wilson and Taylor 2014), *Microconchus* (Tentaculita, see Zatoń and Krawczyński 2011), *Hederella* (possible phoronid, see Taylor and Wilson 2008), and craniid brachiopods (Fig. 6).

Monte Carlo simulations indicated that across all 25 specimens in a bed, fewer than 9 sclerobionts within any one simulation zone would be significant (realized $p = 0.032$). This also indicates that an observation that 17 or more of the 25 hosts had the exact same zone unencrusted would likely be a non random result (while it is possible for more than one sclerobiont to appear in a zone, both in reality and in the simulation, such occurrences are

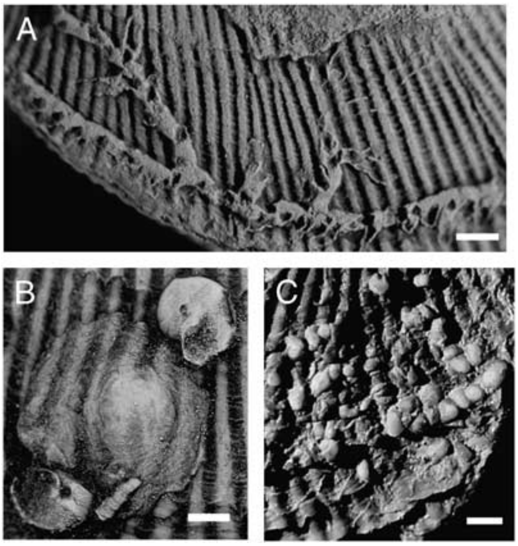

FIGURE 6. Representative specimens of sclerobiont taxa from the Waterways Formation. A, *Hederella*; B, a craniid brachiopod (middle) with two *Microconchus*; and C, *Ascodictyon*.

relatively uncommon). No iteration of the simulation ever produced a result with more than 20 hosts with the same zone unencrusted.

Firebag Sample 1.—In this sample, there were no sclerobionts within the post mortem zone (all 25 hosts had unencrusted post mortem zones, realized $p << 0.001$) (Table 1, Fig. 5A and B). Two sclerobionts appeared to fall within the post mortem zone on the two dimensional map, but an examination of the original specimens showed that these sclerobionts actually fell outside of the post mortem zone (Fig. 5A). The brachiopod specimens were greatly convex, and very slightly distorted posteriorly, resulting in the projection of the sclerobionts within the post mortem zone, an unavoidable problem when a three dimensional object is projected onto a two dimensional surface (e.g., a map of the earth). Interestingly, the one sclerobiont was an *Ascodictyon* that appeared to perfectly surround or skirt the area, which had been designated as the post mortem zone (Fig. 5A). Chi square tests also indicate a strong preference for the shaded zone (dorsal valve excluding the post mortem zone) ($p < 0.01$) (Table 1). Sclerobiont taxa included *Microconchus*, *Hederella*, *Ascodictyon*, and a single craniid brachiopod (Table 2, Fig. 6). The ventral valve was encrusted solely by *Microconchus* (Table 2).

TABLE 1. Summary results of sclerobiont distributions based on the life orientation of the dorsibiconvex atrypide host. The number of brachiopods with encrustation of the post mortem zone are noted for each unit. Zone preference was calculated using a 2 × 2 chi square test comparing the frequency of sclerobionts in the shaded vs. exposed zones based on the proportional surface area of each zone (Shaded = approx. 55%, Exposed = approx. 39%, Post mortem = approx. 6%).

Sample Unit	# Brachiopods encrusted post mortem	Zone Preference
Firebag Sample 1	0/25	Shaded ($p < 0.01$)
Firebag Sample 2	7/25	None
Calumet Sample 1	2/25	None
Moberly Sample 1	3/25	Shaded ($p < 0.01$)
Moberly Sample 2	0/25	Exposed ($p < 0.01$)
Moberly Sample 3	1/25	None

Firebag Sample 2.—Of the 25 brachiopods from Firebag Sample 2, seven had sclerobionts within the post mortem zone (18 of 25 hosts had unencrusted post mortem zones, realized $p = 0.008$) (Table 1, Fig. 5C,D). Chi square tests revealed no preference between the remaining shaded and exposed zones (Table 1). Sclerobiont taxa included *Ascodictyon*, *Hederella*, and *Microconchus* (Table 2, Fig. 6).

Calumet Sample 1.—Calumet Sample 1 had two brachiopods that had sclerobionts within the post mortem zone (23 of 25 hosts had unencrusted post mortem zones, realized $p << 0.001$) (Table 1, Fig. 5E,F). There was no valve preference, and sclerobiont taxa included *Ascodictyon*, *Hederella*, and *Microconchus* (Table 2, Fig. 6).

Moberly Sample 1.—Moberly Sample 1 had three brachiopods that were encrusted within the post mortem zone (22 of 25 hosts had unencrusted post mortem zones, realized $p << 0.001$) (Table 1, Fig. 5G,H). Chi-square tests also indicate that there was a preference for the shaded zone ($p < 0.01$) (Table 1). Sclerobiont taxa include *Microconchus*, craniid brachiopods, and a single *Hederella* on the dorsal valve (Table 2, Fig. 6).

Moberly Sample 2.—Moberly Sample 2 had no brachiopods encrusted within the post mortem zone (realized $p << 0.001$), but unlike Firebag

Table 2. Abundances of each sclerobiont taxon from all six of the sampled units. Brachiopods which had encrustation within the post mortem zone were conservatively considered dead at the time of any encrustation, including those sclerobionts which were on a brachiopod with post mortem encrustation, but which did not fall within the post mortem zone themselves. The number of sclerobionts on post mortem encrusted brachiopods were reported under the rows "Post mortem (overall)".

Sclerobiont	Firebag Sample 1	Firebag Sample 2	Calumet Sample 1	Moberly Sample 1	Moberly Sample 2	Moberly Sample 3
Ascodictyon						
Post mortem (overall)	0	9	1	0	0	0
Shaded	2	7	6	0	0	0
Exposed	0	8	2	0	0	0
Hederella						
Post mortem (overall)	0	15	1	1	0	0
Shaded	4	13	5	1	18	30
Exposed	0	11	2	0	22	30
Microconchus						
Post mortem (overall)	0	44	0	26	0	54
Shaded	287	6	18	127	85	155
Exposed	91	4	25	48	109	145
Craniid						
Post mortem (overall)	0	0	0	1	0	0
Shaded	1	0	0	1	2	3
Exposed	0	0	0	1	5	1

Sample 1 and Moberly Sample 1, there was a strong preference for the exposed (ventral) zone ($p < 0.01$) (Table 1, Fig. 5I,J). Sclerobiont taxa included *Hederella, Microconchus,* and craniid brachiopods (Table 2, Fig. 6).

Moberly Sample 3.—Moberly Sample 3 had only one brachiopod encrusted post mortem, with a single *Microconchus* encrusting that brachiopod specimen within the post mortem zone (realized $p << 0.001$) (Table 1, Fig. 5K,L). There was no valve preference, and sclerobiont taxa included *Microconchus*, *Hederella*, and craniid brachiopods (only on the dorsal valve) (Tables 1 and 2, Fig. 6).

Discussion

Mapping Method.—Comparison of sclerobiont studies has been hampered by the diverse methods used to collect and analyze sclerobiont data, which makes large scale analysis of sclerobiosis across time and space difficult (Schneider 2013). Despite the extensive wealth of sclerobiont research, as well as both the demonstrated and potential utility of sclerobionts in paleoenvironmental and paleoecological studies (e.g., Taylor and Wilson 2003), sclerobiosis remains a fairly obscure and specialized topic. By creating a unified method for the collection of sclerobiont data, we aim to provide a tool which will help bring sclerobiosis to the forefront of paleoecological and paleoenvironmental research.

Implementation of sclerobiont distribution maps is straightforward, and maps can be created using many different image processing software packages. The use of a map, by identifying explicit locations of sclerobionts, also avoids the biases generated by a grid system, and allows independent assessment of sclerobiont distributions by other researchers. For example, while the remainder of this discussion examines the potential implications of sclerobiont distributions across the hosts within the context of the host's life orientation, anyone may examine the raw sclerobiont distribution maps (Fig. 5, Supplementary Appendix 1) to verify or challenge any biological interpretations made herein.

Post mortem Zone Implications.—In most fossil assemblages, there is a degree of time averaging. Even in modern assemblages of bivalves or brachiopods, there are invariably dead individuals amongst live individuals (e.g., Richardson 1981). An easy way to assess the number of individuals dead at the time of encrustation is to examine the number of specimens that have sclerobionts on the inside of the valves where soft tissue would have occurred during life, or those individuals that have sclerobionts growing over anatomical features necessary to maintain the life of the host, such as the commissure. However, such cases are relatively rare, especially for brachiopods with cyrtomatodont hingelines (Alexander and Gibson 1993), suggesting the need for an additional tool, such as the one suggested herein.

By using the life orientation to distinguish a post mortem zone on the host, the amount of post mortem host encrustation in each of the six beds was immediately apparent. There are two major outcomes of this distinction of a post mortem zone: (1) brachiopod specimens with encrustation of the post mortem zone can be removed from any analysis of sclerobiont host relationships, and (2) those assemblages which have few brachiopod hosts that were encrusted post mortem are more likely to indicate an assemblage that had experienced little post mortem time averaging at the time of burial and therefore are more reliable for any paleoenvironmental or sclerobiont host study in which temporal resolution should be constrained.

The life orientation of sclerobiont hosts is critical to understanding the relationship sclerobionts would have had with their hosts. For example, any inference of shaded or exposed zones would potentially be subjective or circular without an independent means of testing the life orientation of the brachiopod. The same could be said of other brachiopod morphologies as well. However, independent evidence of host life orientation, such as the biomechanical behavior of the host, allows corroboration of any biological interpretations of sclerobiont placement.

Assessing post mortem encrustation is not always straightforward in the fossil record. The differentiation of the post mortem zone on dorsibiconvex brachiopods, such as *Desquamatia*, *Pseudoatrypa*, and *Radiatrypa*, allowed for a simple method to infer the minimum proportion of brachiopods in an assemblage that were encrusted post mortem. While some encrustation outside of the post mortem zone could have potentially occurred post mortem, encrustation of the post mortem zone identifies a minimum number of brachiopods that were dead at the time of encrustation within an assemblage. Based on this evidence, it is assumed that at least some encrustation on that brachiopod occurred post mortem, although it is also possible that a host with no sclerobionts in the post mortem zone experienced some, or complete, post mortem encrustation. However, given the results of the Monte Carlo simulations, those brachiopods that do not have any sclerobionts within the post mortem zone are more likely to have been encrusted while the brachiopod was still alive. The simulations also reinforce the proposed identification of the post mortem zone. Based on the simulation results, the likelihood that any one simulation zone equivalent in area to the post mortem zone, let alone specifically the post mortem zone, would remain empty of sclerobionts across more than 20 of the 25 hosts in a bed due entirely to random chance is extremely small (realized $p << 0.001$). In fact, no iteration of the simulation ever produced such a result. Yet, such a result was observed in five of the six samples from the Waterways Formation, and the result was observed in the specific area proposed to be a post mortem zone, a zone that would be inaccessible to sclerobionts during the life of the host. The simulation and fossil results are consistent with the proposed post mortem zone suggested by biomechanical experiments in Barclay et al. (2015).

The allocation of the post mortem zone was independently supported by the spatial distribution of several sclerobionts which appeared to border the post mortem zone, such as certain specimens of *Ascodictyon* in both Firebag samples and the Calumet sample, as well as at least four *Microconchus* in Moberly Sample 1 (Fig. 5A,C,E,G). The number of brachiopods encrusted within the post mortem zone also serves as an indicator of which assemblages as a whole may or may not be useful for sclerobiont host studies. For example, Firebag Sample 2 had at least seven of

25 (28%) brachiopods that were encrusted post mortem. This suggests that close to a third of the entire assemblage was likely encrusted after death and so might not be a reliable source of information of sclerobiont host interactions. However, Firebag Sample 1, and Moberly Sample 2 had no encrustation of the post mortem zone, so are therefore more likely to represent live sclerobiont live host relationships. Even Moberly Sample 3, which had a single *Microconchus* in the post mortem zone, likely indicates that the majority of the brachiopods in the assemblage were encrusted during the lifetime of the brachiopod.

Greater frequencies of post mortem encrustation likely indicate a greater degree of time averaging (however, see Rodland et al. 2006, 2014 for alternative results). Therefore, those assemblages with large amounts of post mortem encrustation would not be reliable in terms of assessing biologically meaningful relationships between sclerobionts and hosts, or for that matter, any other paleoenvironmental interpretation that relies on the assumption of live individuals at the time of encrustation. A fundamental assumption of using fossils in paleoenvironmental reconstruction is that the fossils present in a bed are of organisms that lived in the associated environment. This assumption may be violated if time averaging and transport are extensive. An exploratory analysis of post mortem sclerobiosis provides a conservative assessment of whether fossil specimens should be part of a subsequent paleoenvironmental analysis.

In the present study, all six of the samples exhibited encrustation rates in the post mortem zone lower than would be expected by random chance (realized p-values all <0.01) and two of the six samples contained no sclerobionts in the post mortem zone at all. Given these results, fossils (or at least the atrypides) from these beds in the Waterways Formation, with the possible exception of Firebag Sample 2, would be suitable for use in paleoenvironmental reconstruction (the fossil assemblages likely experienced little or no reworking). We conclude that understanding the life orientation/post mortem zone provides an important method for culling those brachiopods which were encrusted post mortem from a sample, and assessing which assemblages of hosts are worthwhile to examine for live sclerobiont live host relationships or for paleoenvironmental reconstruction.

Sclerobiont Distribution.—Understanding the life orientation of the host organism is also critical to interpret the biological significance of sclerobiont distribution across the host's shell. For those brachiopod specimens that did not have encrustation within the post mortem zone, directly mapping the position of sclerobionts on the brachiopod shells allowed for a visual map of hot and cold spots of encrustation across the shell that could be analyzed quantitatively, and more importantly, interpreted within a biologically significant context. For example, sclerobiont preferences for shaded or exposed areas of the shell could be assessed for each of the six units. Additional visual distributions, such as sclerobiont preferences for the fold/sulcus or commissure can also be easily distinguished and interpreted, and each sclerobiont taxon could be assessed independently.

Overall, there was a decrease in the absolute number of *Ascodictyon* from the oldest to youngest members of the Waterways Formation, and there was an increase in the number of craniid brachiopods. Firebag Sample 2, which had the greatest frequency of post mortem encrustation, was also the most heavily encrusted assemblage in terms of sclerobiont areal coverage (Fig. 5C,D). Assuming that greater frequencies of post mortem encrustation indicate a greater degree of time averaging, all other things being equal, we would expect that there would be more encrustation, as the brachiopod hosts would have been exposed longer before their final burial.

In Moberly Samples 2 and 3, there appears to be a greater amount of encrustation along the commissure, particularly around the medial sulcus on the ventral valve (Fig. 5I–L), which could potentially support past suggestions that sclerobionts might take advantage of their host's feeding/waste currents (Ager 1961; Hoare and Steller 1967; Pitrat and Rogers 1978; Alvarez and Taylor 1987; Baumiller 1990, 1993; Alexander and Sharpf 1990). Given the inferred life orientation of the brachiopod hosts in this study, the medial anterior commissure would have been placed highest in the water column (Barclay et al. 2015) (Fig. 1). Additionally, it is generally agreed that the fold/sulcus area on atrypide brachiopods represents the area of exhalant flow (Rudwick 1970), potentially implying that the clustering of sclerobionts around the sulcus of the ventral valve would be the most optimal placement if the sclerobionts were taking advantage of the brachiopod's exhalant current. Coprophagy has been suggested for platyceratid gastropods that are often found latched onto the anuses of crinoids and blastoids (Keyes 1890; Bowsher 1955; Baumiller 1990, 1993), although kleptoparasitism has also been suggested for platyceratids (Baumiller 1990, 1993). Additionally, placement of sclerobionts at the highest point on the brachiopod's shell could indicate a preference for faster moving waters, away from sediment influx near the substrate (c.f. Bishop 1988; Taylor and Wilson 2003).

In the past, it has been suggested that some dorsibiconvex atrypide brachiopods lost their pedicles and consequently came to rest on their ventral valve, leaving the dorsal valve more exposed for sclerobionts (Fenton and Fenton 1932, Copper 1966b). Increased encrustation of the dorsal valve has also been observed for other atrypides (Bose et al. 2011, Webb and Schneider 2013). However, the biological significance of increased encrustation of the dorsal valve in these studies is ultimately tied to an understanding of the life orientation of the brachiopod. For any one of the aforementioned studies, greater rates of encrustation of the dorsal valve might indicate a preference for shaded areas of the brachiopod host, a pattern that has been identified for encrusters of some modern and fossil hosts (e.g., Nebelsick et al. 1997; Taylor and Wilson 2003). The distinction of those brachiopod specimens that were encrusted post mortem would also refine the results of these studies by removing specimens that were encrusted post mortem and which could have potentially obscured biological preferences.

In the present study, there are clear inconsistencies with sclerobiont preferences for location on the brachiopods between the six assemblages, even amongst individual sclerobiont taxa. While it is perhaps unsurprising that location preferences would vary among different sclerobiont taxa, the fact that preferences for the shaded or exposed surfaces of the host varied from bed to bed is more difficult to understand. There was no correlation between zone preference (or lack thereof) and the number of brachiopods encrusted post mortem. Given the sample size of only 25 hosts per bed, it is possible that the sample size is not sufficiently representative to capture sclerobiont preferences across the Waterways Formation. However, given the statistical results, this is unlikely, and overturning the observations would require not only much larger sample sizes, but would also require that in some cases, the additional material exhibited preferences completely opposite to the ones observed herein. Regardless, the lack of a consistent pattern of sclerobiont preferences without any correlation to the amount of post mortem encrustation indicates that overall sclerobiont trends should never be assumed from a single bed, and examination of sclerobionts preferences should be performed across multiple samples, and at the highest stratigraphic resolution possible. A previous study, which included other stratigraphic sections from the Western Canadian Sedimentary Basin, also found that there was a lack of a consistent sclerobiont preference for brachiopod host valve (Barclay et al. 2013). Sclerobiont biology is clearly more complex than is often considered, and future studies should always keep stratigraphic resolution in mind when considering sclerobiont preferences. In any case, sclerobionts should not be used to assess the life orientation or biology of their hosts when the biology of the sclerobionts themselves has not been clearly established.

The specific analysis of sclerobionts in the context of host orientation, as demonstrated in the following study, is merely one example of how a direct sclerobiont distribution map may be used for paleoecological assessment of sclerobiont host relationships. There are seemingly limitless other applications for this mapping method. For example, sclerobiont distribution maps could be used in conjunction with host growth models to examine sclerobiont preferences for location and size of hosts. Relationships between sclerobionts, such as overgrowing and spatial competition, could also be examined. Assessment of post mortem encrustation and time averaging could be applied to paleoenvironmental studies of fossil assemblages. Most importantly, a unified method for the collection of sclerobiont distribution data would allow large scale assessments of sclerobiosis through time and space, which could be used to investigate the possibility of sclerobionts as indicators of recurring paleoenvironmental conditions, or ecosystem evolution, health, and/or stability.

Conclusions

Mapping sclerobionts exactly as they appear on hosts is a relatively simple and straightforward process that can be used to produce powerful results. Even from the specific host and sclerobiont material examined in the study, there are several conclusions that can be made:

1. Mapping sclerobionts directly onto photographs of their brachiopod hosts provides a unifying method for the collection, analysis, and interpretation of sclerobiont data. These mapping techniques can be easily applied to any type of host, and can be used to widen the utility of sclerobiont data in paleoenvironmental and paleoecological studies.
2. Independently assessing the life orientation of sclerobiont hosts is critical to the interpretation of sclerobiont positions on those hosts. Prior biomechanical tests of dorsibiconvex brachiopods indicate that the brachiopods were pedunculate, and would therefore live with the tip of the ventral valve (surrounding the pedicle foramen) and the posterior portion of the dorsal valve resting against the substrate (Barclay et al. 2015), allowing distinction of post mortem, shaded, and exposed zones. Encrustation of the post mortem zone could only occur after post mortem decay of the pedicle and transport/reorientation out of life orientation, and any hosts with sclerobionts encrusting the post mortem zone should be removed from further analyses of live sclerobiont, live host relationships.
3. Waterways Formation atrypides exhibited significantly lower encrustation of the post mortem zone than expected under a model assuming random sclerobiont distribution, suggesting that post mortem encrustation and time averaging/reworking were relatively low for the sampled beds. As such, these fossils, and probably their associated beds, are suitable for further paleoecological analysis.
4. In the Waterways Formation, sclerobiont preferences are not consistent between assemblages and are not associated with the amount of post mortem encrustation. Any sclerobiont trends in other locales should therefore be examined with great scrutiny and across multiple samples to avoid any false assumptions of sclerobiont biology. This is consistent with other studies of sclerobionts within the Western Canadian Sedimentary Basin (Barclay et al. 2013).

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