The Biology of Sclerobionts and their Hosts:
Comparing Biomechanical Experiments on Brachiopod Hosts
to Sclerobiont Distribution Maps

by

Kristina Meredith Barclay

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science

Department of Earth and Atmospheric Sciences

University of Alberta

Abstract

Sclerobionts and their host organisms provide a great deal of information for palaeoecological and palaeoenvironmental studies. However, any interpretation of sclerobiont – host relationships depends on an understanding of the host's orientation. In the past, distinction of host life and post-mortem orientations has depended on the positions of sclerobionts on hosts, but this logic is circular and has lead to multiple, opposing interpretations for the same host organism. The goals of the following thesis are to (1) biomechanically test the life orientation of a common, dorsibiconvex brachiopod host (Order Atrypida), and (2) interpret the position of sclerobionts on brachiopod hosts based on the resulting life orientation of the brachiopod, to create an independent, biologically meaningful test of the timing of encrustation that can be used for palaeoecological studies.

Two dorsibiconvex atrypides from the Waterways Formation (Givetian – Frasnian, Alberta, Canada) were modeled and biomechanically tested by placing the models in a recirculating flume in one of three initial orientations: (1) anterior commissure upstream, (2) umbo upstream, and (3) lateral (specimen perpendicular to flow). Each test was conducted with the dorsal and ventral valve topmost, and repeated on both a plexiglass and sand substrate. All scenarios were repeated five times for a total of sixty trials per specimen (120 total).

Flume trials indicate that neither brachiopod had a true hydrodynamically stable orientation. Reorientations occurred at low velocities (~0.2 m/s), with transport occurring soon after (~0.3 m/s). Assuming that a juvenile, pedunculate brachiopod would have initially

been oriented with its ventral valve topmost, the brachiopods were likely attached via pedicles throughout their lives.

Given the results from the biomechanics experiments, the brachiopods would have rested with the umbo of the ventral valve (surrounding the pedicle foramen) and the posterior portion of the dorsal valve against the substrate. This area was designated the “dead zone,” as any encrustation of that portion of the brachiopod would have only occurred after death and reorientation of the brachiopod. Assemblages of brachiopod hosts with little or no encrustation of the dead zone likely represent assemblages that were alive at the time of burial, an important distinction for palaeoecological studies. Two other areas, the shaded zone (the remaining portion of the dorsal valve), and the exposed zone (ventral valve) were also designated.

To capture the distribution of sclerobionts within the three zones, the 25 “best” encrusted atrypides were selected from each of six beds of the Waterways Formation. Sclerobionts were mapped directly onto photographs of the dorsal and ventral valves of each brachiopod. A stacked image of all of the brachiopods from each bed was created, and the amount of encrustation in each zone was noted and compared for each stratigraphic unit.

The number of brachiopods encrusted post-mortem was immediately apparent, with some assemblages having no post-mortem encrustation and therefore being potentially useful for palaeoenvironmental studies. Additionally, there was no consistent preference for shaded or exposed zones. The life orientation of hosts is therefore critical to interpret the timing and significance of encrustation in fossil assemblages.

Preface

This thesis is an original work by Kristina Barclay. No part of this thesis has been previously published.

Acknowledgments

I would like to thank the members of my supervisory committee (Drs. Lindsey Leighton, Chris Schneider, and John-Paul Zonneveld) for all of their guidance, support, and helpful comments. I credit Dr. Leighton and Dr. Schneider for my growth as a scientist, a debt that I will never be able to repay in full. This thesis is not only a document of a student's hard labours in search of new scientific knowledge, but I hope that it also reflects the difference made by sharp and supportive mentorship.

I am also grateful to Dr. Jed Day of Illinois State University for his assistance with the identification of the brachiopod specimens, and to my peers and lab mates: Ben Collins, Darrin Molinaro, and Drs. Frank Forcino, Cory Redman, Emily Stafford, and Amelinda Webb for their patience, support, and helpful discussions. I would also like to thank Drs. Leighton, Schneider, and Webb for their assistance with field-work, stratigraphy, and specimen identification.

Funding for this research was provided by an Alexander Graham Bell Canada Graduate Scholarship (Barclay) and a Discovery Grant (Leighton, student supervisor) from the Natural Sciences and Engineering Research Council of Canada, a Walter H Johns Graduate Fellowship (Barclay) from the University of Alberta, a Geological Society of America Student Research Grant (Barclay), and a Lerner Gray Memorial Fund grant from the American Museum of Natural History (Barclay).

Table of Contents

List of Tables

List of Figures

Chapter 1. Introduction

Fossil assemblages are often subject to some degree of time averaging, which makes the interpretation of organism interactions challenging, if not impossible. Unlike most fossil assemblages, sclerobionts (marine organisms that must attach to hard substrates) (Taylor and Wilson 2002), and their hosts (the organisms to which sclerobionts attach, regardless of whether the host was alive or dead) are preserved in situ, providing highly detailed palaeoecological information. The spatial distribution of sclerobionts preserved on biotic hosts, particularly brachiopods, can be used to interpret various aspects of host biology, such as the original life orientation of the host organism. However, there is little known about the biology of sclerobionts themselves. Any non-random distribution of sclerobionts on a host organism is generally accepted as biologically meaningful, but the actual significance often remains unknown, or is based on qualitative assessment that can be subject to debate. Without understanding the controls of sclerobiont distribution on a given host, any interpretation of the host's biology based on sclerobiont distribution is circular. My goal was to create independent, biomechanical tests to determine the stable orientation of brachiopod hosts in order to refine our understanding of the biological significance of sclerobiont distribution on brachiopod hosts.

Sclerobionts are usually small, suspension feeding organisms that must attach themselves to a hard substrate. In the fossil record, sclerobionts are often used to interpret the palaeoenvironment and palaeoecology of their host organisms based on the assumption that the sclerobiont larvae place themselves, or land and are able to survive, on surfaces that enable them to feed more efficiently (i.e., sclerobionts will be found in positions that are more hydrodynamically advantageous). For example, the asymmetrical distribution of sclerobionts on brachiopod hosts has been used to determine the direction of the palaeocurrent, assuming that sclerobionts are more likely to be found facing up-stream to improve their ability to feed (Ager 1961; Kesling et al. 1980). Following these same assumptions, the life orientations of hosts are often based on sclerobiont distribution (Ager 1961; Hoare and Steller 1967; Hurst 1974; Kesling et al. 1980; Sando 1984; Alexander 1986; Alvarez and Taylor 1987; Bordeaux and Brett 1990; Cuffey et al. 1995; Lescinsky 1995; Bose et al. 2011).

However, it is often difficult to distinguish whether sclerobionts were present when the host was alive, or if encrustation occurred on the host post-mortem. Sclerobionts that exhibited parallel or synchronous growth with their hosts have been used to invoke a live sclerobiont – live host relationship (Ager 1961; Alvarez and Taylor 1987; Cuffey et al. 1995). Without obvious indicators of live – live associations, it can be more difficult to determine when encrustation occurred, which casts doubt on the life orientation interpretation of hosts based on sclerobiont distribution. For example, while many researchers have used the placement of sclerobionts on concavo-convex brachiopod shells to infer that the brachiopod lived with the convex valve against the substrate (Bordeaux and Brett 1990), Lescinsky (1995) argued that the sclerobionts indicate that concavo-convex brachiopods lived with the convex valve up away from the substrate.

To attempt to solve the life orientation of sclerobiont hosts, Leighton (1998) suggested that functional morphology should be considered above sclerobiont distribution when determining brachiopod orientation, as post-mortem reorientation may confound any interpretation of life orientation based on sclerobiont placement. Therefore, the best independent test for brachiopod orientation should be a biomechanical experiment on brachiopod hosts, achieved through flume experiments on brachiopod models in order to determine the behaviour of brachiopod shells exposed to a unidirectional current. There have been many papers using both modern and fossil brachiopods in a flume to determine the specifics of brachiopod biology, such as post-mortem orientation or reorientation (Alexander 1986; Messina and LaBarbera 2004). However, the life orientation of one common and abundant group of brachiopod hosts, dorsibiconvex atrypides, is still uncertain and has not been biomechanically studied in any detail.

The goal of the second chapter of this thesis is to biomechanically assess the life orientation of dorsibiconvex brachiopods by placing realistic models in a flume. Determining the life orientation of brachiopod hosts will not only provide a biologically meaningful method for interpreting sclerobiont distributions, but will also create a new tool for palaeoenvironmental interpretation. Researchers can use the life orientation of brachiopods in an assemblage to help determine the rate of sediment deposition, and any potential transport or time-averaging of the fossil assemblage. For example, if an outcrop contains brachiopods that are not preserved in their life orientation, transport must have occurred. Producing a protocol for biomechanically testing the life orientation of brachiopods will create a tool that not only pertains to refining our understanding of brachiopod and sclerobiont biology, but will also be of great interest to the greater palaeontological and geological community as a means of assessing the palaeoenvironment of assemblages containing brachiopods.

Once a protocol has been established which allows the biomechanical testing of brachiopod host orientations, it becomes immediately apparent which sclerobionts encrusted the brachiopod post-mortem. Any area of the brachiopod that is found to rest against the substrate during its life would not be available for sclerobionts to encrust when the brachiopod host was alive. Therefore, any sclerobionts that are found to encrust that area of the brachiopod must have done so after the brachiopod had died and been removed from its original orientation. Additionally, understanding the life orientation of brachiopods allows for a biologically meaningful analysis of sclerobiont distributions on the brachiopod's shell. For example, there may be areas of the brachiopod that are more exposed to predators or water currents.

Despite the large number of sclerobiont/brachiopod host studies, there has been no unified protocol established for the collection and interpretation of sclerobiont data. Several authors have subdivided the brachiopod host into sections to determine if there were any non-random distributions of sclerobionts observed in each section on the hosts (Kesling et al. 1980; Alvarez and Taylor 1987; Gibson 1992; Bose et al. 2010, 2011). While subdividing brachiopod hosts into sections has provided interesting information, the determination of the sections is not the same between authors, and was always determined a priori via author discretion. For example, Gibson (1992) divided each type of host into different sections based on host morphology, yet Bose et al. (2010, 2011) divided each host into sections of equal area. If the determination of sclerobiont preferences relies on the differences in distribution between these sections, how can we assess which method may be more accurate? For instance, neither paper treats the two valves of the brachiopod hosts differently, yet with a live brachiopod, the valves would be in fundamentally different orientations, with at least part of one or both valves resting on or within the substrate.

Using biomechanical tests of the life orientation of potential brachiopod hosts not only indicates the amount of post-mortem encrustation of the host, but also creates a more biologically meaningful context for understanding sclerobiont distribution. Instead of simply creating zones that may or may not be biologically meaningful to sclerobionts, it may be more accurate to map the actual distribution of sclerobiont samples onto images of their brachiopod hosts. The use of mapping of fossil sclerobiont distributions onto a particular host organism provides a unifying tool for future sclerobiont research that will produce highly accurate and detailed information of use to palaeoecologists studying the timing of events within a community (i.e., post-mortem encrustation or live host – live sclerobiont relationships). As well, combining biomechanical tests on brachiopod orientation with highly precise mapping of sclerobiont distributions will result in more robust, biologically meaningful interpretations of sclerobiont location on brachiopods, and sclerobiont – brachiopod relationships.

1.1 Works Cited

Ager, D. V. 1961. The epifauna of a Devonian spiriferid. Quarterly Journal of the Geological Society 117:1–10.

Alexander, R. R. 1986. Life orientation and post-mortem reorientation of Chesterian brachiopod shells by paleocurrents. Palaios 1:303–311.

Alvarez, F., and P. D. Taylor. 1987. Epizoan ecology and interactions in the Devonian of Spain. Palaeogeography, Palaeoclimatology, Palaeoecology 61:17–31.

Bordeaux, Y. L., and C. E. Brett. 1990. Substrate specific association of epibionts on Middle Devonian brachiopods: implications for paleoecology. Historical Biology 4:203–220.

Bose, R., C. L. Schneider, P. D. Polly, and M. M. Yacobucci. 2010. Ecological interactions between *Rhipidomella* (Orthides, Brachiopoda) and its endoskeletobionts and predators from the Middle Devonian Dundee formation of Ohio, United States. Palaios 25:196–208.

Bose, R., C. L. Schneider, L. R. Leighton, and P. D. Polly. 2011. Influence of atrypid morphological shape on Devonian episkeletobiont assemblages from the lower Genshaw formation of the Traverse Group of Michigan: a geometric morphometric approach. Palaeogeography, Palaeoclimatology, Palaeoecology 310:427–441.

Cuffey, C. A., A. J. III. Robb, J. T. Lembcke, and R. J. Cuffey. 1995. Epizoic bryozoans and corals as indicators of life and post-mortem orientations of the Devonian brachiopod *Meristella*. Lethaia 28:139–153.

Gibson, M. A. 1992. Some epibiont-host and epibiont-epibiont relationships from the Birdsong shale member of the Lower Devonian Ross Formation (west-central Tennessee, U.S.A.). Historical Biology 6:113–132.

Hoare, R. D., and D. L. Steller. 1967. A Devonian brachiopod with epifauna. The Ohio Journal of Science 67:291–297.

Hurst, J. M. 1974. Selective epizoan encrustation of some Silurian brachiopods from Gotland. Palaeontology 17:423–429.

Kesling, R. V., R. D. Hoare, and D. K. Sparks. 1980. Epizoans of the middle Devonian brachiopod *Paraspirifer bownockeri*: their relationships to one another and to their host. Journal of Paleontology 54:1141–1154.

Leighton, L. R. 1998. Constraining functional hypotheses: controls on the morphology of the concavo-convex brachiopod *Rafinesquina*. Lethaia 31:293–307.

Lescinsky, H. L. 1995. The life orientation of concavo-convex brachiopods: overturning the paradigm. Paleobiology 21:520–551.

Messina, C., and M. LaBarbera. 2004. Hydrodynamic behavior of brachiopod shells: experimental estimates and field observations. Palaios 19:441–450.

Sando, W. J. 1984. Significance of epibionts on horn corals from the Chainman Shale (Upper Mississippian) of Utah. Journal of Paleontology 58:185–196.

Taylor, P. D., and M. A. Wilson. 2002. A new terminology for marine organisms inhabiting hard substrates. Palaios 17:522–525.

Chapter 2. Breaking the mold: using biomechanical experiments to assess the life orientation of dorsibiconvex brachiopods

2.1 Introduction

Examination of the original life habit or orientation of fossil organisms can not only be used to tease out biological information about the organism in question, but can also assist in the interpretation of the palaeoenvironment and palaeoecology of the assemblage from which the organism came. As one of the most abundant and environmentally diverse Palaeozoic marine clades, brachiopods and their original life orientations have been important topics for many researchers (e.g., Fenton and Fenton 1932; Copper 1966b; Ager 1967; Hoare and Steller 1967; Richards 1972; Hurst 1974; LaBarbera 1977, 1978; Rowell 1977; Kesling et al. 1980; Sparks et al. 1980; Richardson 1981b; Alexander 1984, 1986; Bordeaux and Brett 1990; Alexander and Gibson 1993; Cuffey et al. 1995; Lescinsky 1995; Fagerstrom 1996; Leighton 1998, 2005; Dattilo 2004; Messina and LaBarbera 2004; Tomašových et al. 2008; Bose et al. 2011). However, with such a broad range of morphological shapes and only a few, conservative modern analogues, it is often difficult to determine the original life orientation of extinct brachiopods. Through experiments testing the biomechanical behavior of two closely related atrypide brachiopods, we attempt to not only discern the most feasible life orientation for these two brachiopods, but also attempt to discern the biomechanical effects of small morphological changes within related brachiopod lineages.

Atrypide brachiopods (Order Atrypida) are one of the most abundant groups of marine organisms throughout the Silurian and Devonian of much of the world, and have been well studied in the past fifty years (e.g., 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). Like all brachiopods, atrypides would have lived attached to the substrate via a pedicle for at least some early portion of their lives. However, it has been suggested that some members of the Family Atrypidae experience atrophy, and/or may lose the pedicle entirely (Fenton and Fenton 1932; Copper 1966b, 1967). Additionally, the complete loss of the pedicle could potentially allow the brachiopod to reorient relative to the substrate on which it lived (Fenton and Fenton 1932; Copper 1966b, 1967). With the loss of a pedicle, atrypide brachiopods would have had to rely on other morphological features in order to maintain their sedentary life-style, such as an overall valve shape conducive to resting in sediment or resisting transport, or the development of ornamentation (i.e., frills) that would have assisted in stabilizing or anchoring the brachiopod to a soft sediment substrate (Copper 1966b; Ager 1967). While there are many examples of atrypide brachiopods that potentially fit such morphological criteria, there have been few biomechanical studies that have included any atrypides at all (e.g., Alexander 1984, 1986), and none that have used functional tests to compare different atrypide morphologies, let alone determine their original life orientation with certainty. By conducting biomechanical experiments on realistic brachiopod models placed in a flume, I aim to determine whether or not there was a stable orientation (or stable orientations) in which dorsibiconvex atrypides would have been able to survive, particularly if the pedicle was lost during the course of the brachiopod's lifetime.

The dorsibiconvex brachiopod morphology (dorsal valve is inflated and more convex in comparison to the ventral valve) is common among groups such as spiriferides, orthides, and particularly atrypides. Despite their abundance, the dorsibiconvex morphology is rather conservative, especially throughout the evolutionary history of the atrypides (Copper 1966a, b, 1973, 1990, 1998; Day 1998; Day and Copper 1998), (Fig. 2.1). However, atrypides varied considerably in shell ornament, and in more subtle differences of the overall dorsibiconvex morphology, such as the length and curvature of the hinge, degree of valve convexity, and strength or absence of a fold and sulcus. These variations in morphology are apparent between closely related atrypides, sometimes even among members of the same genus or species. As a result, taxonomic identification is often difficult, and the taxonomy of the group has been reworked several times (Copper 1973, 1990; Day and Copper 1998). During the Silurian and Devonian of North America, brachiopod assemblages are often dominated by members of the Family Atrypidae, including genera such as *Spinatrypa, Spinatrypina, Desquamatia, Pseudoatrypa,* and *Radiatrypa* (e.g., Johnson 1962; 1970; Copper 1966a, 1973, 1990, 1998; De Keyser 1977; Day 1992, 1996, 1998; Day and Copper 1998; Bose et al. 2011; Bose 2012; Barclay et al. 2013; Webb and Schneider 2013). With the exception of *Spinatrypa* and *Spinatrypina*, which are readily distinguished based on their regular, spine-forming and frilly growth lamellae, respectively, other members of the Family Atrypidae, mainly *Desquamatia, Pseudoatrypa,* and *Radiatrypa*, have, to the non-expert, very similar shell ornament and “shield-shaped,” dorsibiconvex morphologies.

Dorsibiconvex atrypides are abundant in many different environments (Copper 1966a; Day 1998; Barclay et al. 2013). With frills absent in some species, and poorly preserved or questionable in others, it can be challenging to attempt to correlate frills or ornament with environment. In the Western Canadian Sedimentary Basin, even members of the same species, *Radiatrypa clarkei*, are found in both “muddy” and “clean” carbonates. However, there is a level of plasticity within some dorsibiconvex species that suggests a functional difference between morphologies that is potentially correlated with environment. As well, given the lack of clear evidence for a large or functioning pedicle (Copper 1966b, 1967), it is difficult to discern how such brachiopods lived relative to the substrate. In order to determine any stable orientation, or whether it is even possible for a dorsibiconvex brachiopod to survive without a pedicle, biomechanical experiments examining the behavior of these shell morphologies are essential, yet this has never been done for this group of brachiopods.

In the past, there have been several lines of evidence that have been used to infer the life orientation of brachiopods. Taphonomic indicators, such as shell abrasion (Alexander 1986; Alexander and Gibson 1993), are one such line of evidence. Alexander and Gibson (1993) used taphonomy as an indicator of life orientation of various brachiopods from the Devonian of Tennessee, inferred from the type of compaction patterns observed on the brachiopods. In this study, they observed one atrypide, *Atrypa reticularis*, with a “splaying” pattern in which the ventral valve was commonly flattened relative to the more convex dorsal valve (Alexander and Gibson 1993). They concluded this “splaying” pattern indicated that the brachiopod lived reclining on one valve (Alexander and Gibson 1993). While this method has many useful applications, it is difficult to use when a fossil assemblage shows little or no taphonomic compaction of brachiopod specimens.

Another method that has been used to determine the life orientation for a broad range of brachiopods and other organisms is the position of epibionts, also known as sclerobionts

(Taylor and Wilson 2002), on their host organisms (Ager 1961; Hoare and Steller 1967; Richards 1972; Hurst 1974; LaBarbera 1977; Pitrat and Rogers 1978; Kesling et al. 1980; Sparks et al. 1980; Sando 1984; Alvarez and Taylor 1987; Donovan 1989; Alexander and Scharpf 1990; Bordeaux and Brett 1990; Alexander 1994; Cuffey et al. 1995; Lescinsky 1995, 1996; Fagerstrom 1996; Nebelsick et al. 1997; Taylor and Wilson 2003; Bose et al. 2010, 2011). For example, Sando (1984) used the position of sclerobionts on the concave and upper-half of coral polyps (*Barytichisma*) to infer that the polyps toppled from their original upright position, and rested on their side, with the coral polyp growing upwards. In the modern, epibiont positions on brachiopod hosts have been used to infer current direction with great success, as the hypothesis could be directly tested by determining the direction of current flow where the brachiopods were found to live (LaBarbera 1977). Sclerobionts on fossil brachiopods hosts have been well studied, particularly in the Devonian, but determining the life orientation of brachiopods based on the position of sclerobionts on brachiopod shells is not as clear in the fossil record. For example, it is generally assumed that concavo-convex brachiopods, such as strophomenides, lived with the convex valve resting down into a soft substrate (Alexander 1984; Bordeaux and Brett 1990; Leighton 1998, 2005) and therefore, any encrustation of the convex valve must have occurred after post-mortem reorientation of the shell (Bordeaux and Brett 1990). However, Lescinsky (1995) suggested that the opposite was true, in that such brachiopods lived with the convex valve facing away from a firmer substrate and encrustation of the convex valve represented a live-host, live-epibiont relationship. With such potentially ambiguous sclerobiont data, Leighton (1998, 2005) suggested that functional morphology should be of primary concern when trying to determine the life orientation of brachiopods.

Functional morphology has received limited use as a means for testing brachiopod life-orientation, especially among the atrypides. However, even seemingly small morphological variations can have a large effect on the hydrodynamic stability or behavior of brachiopod shells, which can then potentially be correlated to other environmental factors, such as sediment type or current strength (Alexander 1975, 1984). Flume studies have been particularly insightful when examining shell behavior under a variety of settings. LaBarbera (1977, 1978) conducted flume experiments on live brachiopods, and then compared these results to both empty shells, and live, in situ brachiopods. Alexander (1975, 1984, 1986) conducted flume experiments to test many different brachiopod morphologies under a variety of conditions, and was one of the first researchers to test brachiopods with experimental models (1986). As well, Alexander's 1984 study includes the only example of an atrypide brachiopod (*Atrypa*) to be examined experimentally in a flume.

The following study attempts to use more realistic models of two atrypide brachiopods, each of which represents an end-member morphology of the taxon *Radiatrypa clarkei*, to (1) determine the most plausible life orientation for each brachiopod morphology, and whether or not each could survive without a pedicle, and (2) examine the functional effects of subtle differences in shape between two similar brachiopod morphologies.

2.2 Methods

2.2.1 Modeling Procedure

Two very well preserved, articulated specimens of *Radiatrypa clarkei*, representative of the two "end-member" morphologies or morphotypes within the atrypide clade, were selected for all modeling and experimental purposes (Fig. 2.1). The specimens were arbitrarily assigned as “Morph A” and “Morph B,” and were collected from the Moberly and Calumet Members of the Waterways Formation (Early Frasnian, Western Canadian Sedimentary Basin), respectively. Morph A represents the more dorsibiconvex, inflated, sulcate morphotype, with a shorter, more rounded hingeline and slightly finer ribbing (Fig. 2.1). Morph B is the more convexoplane specimen, with an almost flat ventral valve, no sulcus, a longer hingeline with a characteristic “shield-shape” appearance, and slightly coarser ribbing (Fig. 2.1). Both specimens represent average adult sized brachiopods for this species.

Specimens of the two morphotypes were selected for lack of taphonomic distortion and excellent preservation of external ornament. Both specimens were approximately the same size (about 30 mm at the widest point on the shell parallel to the hingeline). However, while the dorsal valves of the two morphotypes were almost identical in terms of surface area, there was a difference in the convexity of the two ventral valves. The surface areas of the ventral valves were slightly different, with the more convex ventral valve of Morph A being about 9 mm longer than the more planar ventral valve of Morph B. As a result, the original living Morph B brachiopod’s ventral valve would have weighed less, proportionally, than the ventral valve of Morph A.

Silicone-rubber molds were cast from the exterior of both brachiopod morphotypes. Each mold was made in two parts, one for each valve, which interlocked to form a tight seal. From these external molds, wax replicas were made of the articulated brachiopods. The wax brachiopods were carefully examined under a microscope, and any impressions of sclerobionts or debris were gently removed with a dental pick. External ornament and shell detail were then carefully reshaped using the dental pick. Silicone-rubber molds of each brachiopod valve were again cast from the cleaned and retouched wax brachiopods.

Once the external molds of each retouched brachiopod valve had cured, a thin layer of plasticine (about 2 mm thick) was formed into the mold to create a temporary cast of each individual brachiopod valve. Thickness of the plasticine valve casts was approximated by taking thickness measurements at several points on disarticulated *R. clarkei* specimens that were approximately the same size as the model specimens. More silicone-rubber was poured on top of the existing molds and plasticine to create four two-piece molds, one for each of the two brachiopod's valves.

Casts of each brachiopod valve were made from a liquid casting plastic (SMOOTH-CAST 200 Series) mixed with enough iron filings to match the specific gravity of calcium carbonate (2.7), which would closely match the original specific gravity and mass of the brachiopod's shell. A strong magnet was applied to either side of the mold in order to keep the iron filings evenly distributed within the liquid plastic as it cured. Any imperfections or rough edges of each brachiopod valve were retouched with a dremel. The dremel was also used to gently sand the interior of each valve to an even, accurate thickness, as indicated by disarticulated fossil specimens of approximately the same size. The final product was two realistic replicas of the shells of the brachiopods as they would have been during life, or prior to fossilization.

2.2.2 Experimental Procedure

A recirculating flume was used to test the biomechanical behavior of the two brachiopod models experimentally (Fig. 2.2). The flow chamber (3.50 m by 0.27 m) was filled with room temperature tap water, and during the experiments, was filled to a depth of 0.25 meters. Each brachiopod model was placed in the flume, allowed to completely fill with water, and then a small amount of plasticine (< 0.01 g) was used to create a seal around the entire margin of the commissure. Experimental trials were conducted separately for each brachiopod model using multiple starting orientations, and the trials were run five times for each orientation/model combination to ensure accuracy and consistency of each trial.

In order to determine if the brachiopod models had a stable orientation, each model was placed in the flume with the velocity at 0 m/s in one of three different predetermined orientations: (1) anterior commissure facing upstream, (2) umbo facing upstream, and (3) lateral (anterior – posterior length was perpendicular to flow). These three orientations were repeated with the position of the valves reversed relative to the substrate, i.e., one set with the dorsal valve topmost, and one with the ventral valve topmost, for a total of 6 experimental sets for each brachiopod model. Two different types of substrate were used in the experiments: smooth plexiglass, and sand (grain size, $\phi = 2.56$). All twelve experimental sets were conducted once on the plexiglass, and once on the sand substrate. Each experimental set was repeated for a total of 120 experimental trials.

Along with each of the experimental conditions, if a situation arose where, in life, it would have been impossible for a live brachiopod to feed (and so would probably have resulted in death), the time and flow velocity were recorded, and the experiment was stopped. These conditions were: (1) burial of the commissure in sand, or (2) entrainment or transport.

The models were placed in the centre of the flow chamber, 1.25 meters away from the inflow pipe (Fig. 2.2). Free-stream flow velocity of the flume was then increased incrementally at a rate of approximately 0.01 m/s every 30 seconds so as to maintain relatively laminar flow within the flow chamber and thereby prevent any vortices or surges within the flow chamber. If at any point the model began to move or reorient itself, the velocity and change in orientation were noted. The flow velocity was then held for a minimum of one minute, or until any movement had ceased for an additional 30 seconds. The flow velocity was increased until the brachiopod model became entrained or was swept towards the end of the flow chamber, indicating destabilization that would also have resulted in the death of the brachiopod, and ending the trial. If a model was noted to remain in a specific orientation until it began to move towards the end of the flume, or until the end of the trial, this was recorded as the brachiopod's "semi-stable" orientation. The velocity at which each brachiopod model began transport was also noted. Video recordings and photographs of each experimental trial were also taken for further review.

In this study, the use of closed brachiopod models (as opposed to gaping models) to determine the original life orientation or habit of dorsibiconvex brachiopods can be considered conservative with regards to the flow velocities in which transport of the models occurred. It is likely that a gaping brachiopod model would produce more turbulence and lift at the same flow velocities, therefore increasing the likelihood of destabilization at comparable, or lower flow velocities. In other words, a gaping model is more likely to destabilize at a lower flow velocity than a closed model. The laminar flow produced by the flume was also deemed conservative with regards to flow velocities, as oscillatory flow would increase turbulence, and therefore increase the likelihood of destabilization at comparable flow velocities.

2.2.3 Analyses

Two-tailed Student's *t*-tests were run to determine if there was a statistically significant difference in the flow velocities at which reorientation and transport occurred between the two models.

2.3 Results

2.3.1 Morph A

Reorientation of the model from its original experimental orientation occurred in 39 out of 60 trials. Regardless of the original orientation of the model, either with respect to flow direction or to which valve was topmost, of the 60 original experimental trials on this model, there were only two "semi-stable" orientations that occurred before destabilization or movement down the flume. In 41 of the experimental trials, the model ended oriented with the dorsal valve topmost, and the umbo facing upstream (Fig. 2.3A). In the other 19 trials, the model ended oriented with the ventral valve topmost, the commissure inclined roughly vertically, and the umbo facing upstream (Table 1, Fig. 2.3B).

Reorientation of the model on the plexiglass substrate, for all trials in which there was reorientation, occurred at approximately 0.12 – 0.13 m/s in all orientations, with transport occurring at approximately 0.21 m/s. On the sand substrate, reorientation occurred at approximately 0.20 – 0.21 m/s, and transport occurred at approximately 0.31 – 0.32 m/s. At free-stream velocities of 0.2 m/s, the boundary layer was calculated to be 12.5 mm thick, indicating that the majority of both brachiopod models would have been experiencing free-stream flow velocities just prior to transport. The scour that occurred around the brachiopod models (Fig. 2.4) indicates that these results are conservative in that scour was produced at velocities below 0.2 m/s.

2.3.2 Morph B

Reorientation of the model occurred in 33 of 60 trials. There were two common “semi-stable” orientations, but three other orientations occurred in 7 of the trials (Table 1). In 28 of 60 trials, the model ended with the dorsal valve topmost and the anterior – posterior commissure facing perpendicular to flow (Fig. 2.3C). In 25 of the trials, the model ended with the ventral valve topmost, the anterior commissure perpendicular to flow, and the brachiopod leaning with the downstream side of the commissure and hingeline resting gently on the substrate (Fig. 2.3D). However, unlike the first morphotype, the initial orientation with respect to which valve was topmost did have an effect on the final orientation. For instance, the brachiopod model only flipped over once to rest on the other valve. In this trial, the model flipped over to rest on the ventral valve when it had originally been oriented with the ventral valve facing away from the substrate. In 25 of the remaining instances, the model remained with the ventral valve topmost, and the commissure turned perpendicular to flow. If the dorsal valve was topmost, it remained that way, and turned laterally in all but three trials, wherein the brachiopod did not reorient. There were only four instances where the model did not end in the lateral orientation.

Reorientation for all trials in which reorientation occurred and transport free-stream flow velocities were comparable to Morph A. The average flow velocity of reorientation on the plexiglass substrate was approximately 0.18 – 0.19 m/s, with transport occurring at approximately 0.21 – 0.22 m/s. Reorientation of Morph B on the sand substrate occurred at approximately 0.21 – 0.22 m/s, and transport at approximately 0.31 – 0.32 m/s.

2.3.3 Comparison of the Morphotypes

A two-tailed *t*-test, assuming unequal variances, found no statistically significant difference in the free-stream flow velocities at which both reorientation and transportation of the models occurred. For both models, no true hydrodynamically stable orientation was observed, as transport occurred in all trials at relatively slow flow velocities. However, it is most likely that Morph A will orient itself with the umbo upstream, and Morph B will orient itself laterally, regardless of which valve faces the substrate. In general, Morph B was slightly more stable, as Morph A had a tendency to wobble and flip over during reorientation, while Morph B remained fairly stationary until transport. Morph A “wobbled” and rotated during transport, whereas Morph B simply slid towards the end of the flume.

Scour occurred in a crescent shape upstream of both models when placed on the sand substrate (Fig. 2.4). Scour patterns were very similar between the two morphs, with slightly deeper scouring occurring around Morph A. With Morph A, the scour caused a pedestal-like formation to occur underneath the model, which eventually collapsed (Fig. 2.4A). The brachiopod model then destabilized and slid rapidly down the flume for a short distance, until it came to a rest, and the process was repeated. While the same scour pattern occurred with Morph B, the scour and destabilization process that occurred in Morph A was not as pronounced with Morph B, and Morph B simply slid down the flume during transport (Fig. 2.4B). The appearance of the scour patterns, as well as the aforementioned destabilization process that occurred on the sand substrate, was very similar to the scour patterns and destabilization of brachiopod specimens observed by other authors (Alexander 1984, 1986; Messina and LaBarbera 2004).

2.4 Discussion

2.4.1 Implications for Once-Living Brachiopods

Given the low free-stream flow velocities (≤0.3 m/s) at which transport of the brachiopod models occurred, and the lack of a true hydrodynamically stable position, there are two possibilities for the once living brachiopods: either (1) the brachiopods retained a strong pedicle throughout their lives to serve as a strong attachment point on the substrate; or (2) the brachiopods may have lost the pedicle but lived in a quiet water environment, with flow velocities well below 0.3 m/s.

The latter situation seems highly unlikely, as there are many examples of these dorsibiconvex brachiopod morphologies in high-energy environments (e.g., Copper 1966a, b; 1973; De Keyser 1977; Alexander 1984, 1986; Gibson 1992; Alexander and Gibson 1993; Day 1992, 1996, 1998; Day and Copper 1998; Buschkuehle 2003; Ma et al. 2008). However, this is not to say that dorsibiconvex brachiopods are not found in low energy environments as well. If it were possible that these brachiopod morphotypes were found to live in undisturbed, low energy environments and lost their pedicles, then reorientation is certainly plausible, with several possible life orientations on the substrate, including a reversal of which valve rested against the substrate. For example, Fenton and Fenton (1932), and Copper (1967) have suggested that the hydrodynamically stable orientation for atrypides would be to rest with the more planar, or ventral valve, to rest against the substrate. Based on the flume experiments, this would certainly be possible for both morphotypes. Alternatively, Lamont (1934, in

Copper 1967) suggested that atrypides likely lived with the dorsal valve partially buried, and the ventral valve acting as a “shovel.” Again, based on the flume experiments, this is also plausible for both morphotypes, but only in palaeoenvironments characterized by consistently low flow-velocities well below 0.3 m/s.

However, if it is likely that dorsibiconvex brachiopods, at least those of a similar size and/or mass, retained a strong pedicle throughout their lives, any discussion of potential pedicle loss and reorientation is seemingly irrelevant. While atrypide brachiopods lacked pedicle adjustor muscles and were incapable of resorbing shell material around the pedicle foramen during growth to accommodate a growing pedicle (Copper 1967), it seems much more likely that some sort of pedicle was retained throughout their lives, one which would have been strong enough to keep the brachiopod in place at flow velocities of approximately 0.3 m/s or greater. Copper (1967) suggested that the pedunculate atrypides, such as *Desquamatia,* may or may not have had a “functional” (i.e., muscular) pedicle, but perhaps at least retained the pedicle, and partially supported their weight against the substrate. Studies of modern brachiopods indicate that there is no correlation between the size of the pedicle foramen, and the strength of the pedicle, or pedicle attachment (Thayer 1975; Richardson 1981a). It is therefore incorrect to assume that a reduced or small pedicle foramen in atrypides, or indeed any other group of brachiopods, would automatically indicate that the adult brachiopod was living with an atrophied pedicle, or without a pedicle altogether.

2.4.2 Environmental Implications for Atrypide Morphotypes

A brachiopod living attached by its pedicle, but potentially supporting some of its mass by resting against the substrate, would most likely have lived in an orientation where the pedicle foramen was relatively close to the substrate. This would suggest that dorsibiconvex atrypides would have rested with the posterior portion of the dorsal valve against the substrate, and the commissure inclined away from the substrate (Fig. 2.3B). There is no discernible evidence from the flume experiments to indicate a preferential or hydrodynamically stable orientation relative to the direction of flow, but it certainly seems plausible that Morph B may have been more commonly aligned with the anterior-posterior axis perpendicular to flow, as has been observed with some modern brachiopods (LaBarbera 1977, 1978; Richardson et al. 2007). However, unlike modern brachiopods, without pedicle adjustor muscles, the pedicle on atrypide brachiopods would not have been capable of reorientation/pivoting of the shell, and would have primarily served as an attachment point to the substrate (Copper 1966b, 1967; Rudwick 1970). Differences in the convexity of the valves between morphotypes would change the position of the commissure relative to the substrate. As well, the presence or strength of a fold and sulcus changes the position of the commissure.

Within the Western Canadian Sedimentary Basin, dorsibiconvex brachiopods, especially atrypides are by far the most abundant brachiopod, with both atrypide end-member morphotypes present. The Waterways Formation is one of the thicker, geographically extensive, and more fossiliferous units, and is separated into five members (Fig. 2.5). The planoconvex Morph B was selected from the transition between the shale and upper limestone in the Calumet Member, and Morph A was selected from an argillaceous limestone below a biostromal unit in the Moberly Member (Fig. 2.5).

Morph A, which was generally less stable than Morph B, is abundant in high energy environments and a pedicle therefore seems undeniable. The brachiopod likely rested with its commissure steeply inclined, between 70 – 90 degrees, relative to the substrate (Fig. 2.3B). The large fold and sulcus would have allowed for better separation of the inhalant and exhalant flow chambers within the brachiopod.

If attached via a pedicle, Morph B would have sat with the commissure approximately perpendicular to the substrate. The lengthened, straighter hinge (relative to Morph A), would have provided a wider surface area for the shell to rest against the substrate, especially when occurring on softer or muddier substrates. The nearly vertical orientation of the commissure would have allowed for maximum separation of inhalant and exhalant flow within the water column, which would have been beneficial for feeding and excretory purposes. As suggested by Lamont (1934, in Copper 1967), it is also possible that this morph may have lived with the dorsal valve partially buried, but given the patterns of scour observed in the experiments of this study, the pedicle would have still served as an important stabilization point, especially in higher energy settings.

Within the atrypides, ornament has often been suggested as a means of stabilization (Copper 1966b, 1990; Ager 1967; Leighton 2000). Ornament such as spines (mainly *Spinatrypa*) and frills (many of the Atrypidae) are thought to provide anchorage and/or stability in softer substrates, as in the manner of many spinose productidines (Grant 1966, 1968; Rudwick 1970; Leighton 2000). However, Atrypide frills are not usually preserved, and it is believed that frills are highly plastic and can be altogether absent, even within members of the same genus. As *Radiatrypa clarkei* is not frilled, and there are generally no large frills or spines observed within brachiopod assemblages in the Mid – Late Devonian of the Western Canadian Sedimentary Basin, testing the hydrodynamic behavior of frills was deemed less conservative for addressing the overall stability of the dorsibiconvex brachiopod morphology.

Based on the experimental results observed, the use of modeling materials that closely resemble the mass of the original shell material are integral for an accurate interpretation of the original life habit of the organism in question. While flume experiments and modeling techniques provide excellent insight into the hydrodynamic behavior of brachiopod shells, the use of materials resembling the original mass and density of the brachiopods probably generated more realistic and robust results in regards to the life orientation of atrypides, and by extension, potentially several other dorsibiconvex brachiopods, such as many orthides and spiriferides.

2.5 Conclusions

(1) Using appropriate and realistic modeling materials is an important consideration when attempting to discern the life habit or orientation of any organism. While using fossils and other models in flume experiments has produced important information about the hydrodynamic behavior of those fossils, a brachiopod fossil that is completely infilled with sediment will weigh much more than the actual animal. Producing a realistic model of fossil brachiopods is a relatively simple process that should be used in functional morphology studies of life habit or orientation.

(2) Dorsibiconvex atrypide brachiopods, such as *Radiatrypa clarkei*, most likely lived attached by a pedicle of some form. There is also the more unlikely possibility (given their broad palaeoenvironmental distribution) that these brachiopods were capable of living

without the pedicle, perhaps in a different orientation, but would be restricted to environments in which the maximum flow velocities were well below 0.3 m/s.

(3) Any discussion of dorsibiconvex brachiopods, at least those of similar size and original mass to the two specimens in this study, should likely assume that the brachiopod was attached via a pedicle, unless a biomechanical test of the hydrodynamic stability of the shell proves otherwise.

2.6 Works Cited

Ager, D. V. 1961. The epifauna of a Devonian spiriferid. Quarterly Journal of the Geological Society 117:1–10.

——— 1967. Brachiopod palaeoecology. Earth-Science Reviews 3:157–179.

Alexander, R. R. 1975. Phenotypic lability of the brachiopod *Rafinesquina alternata* (Ordovician) and its correlation with the sedimentologic regime. Journal of Paleontology 49:607–618.

——— 1984. Comparative hydrodynamic stability of brachiopod shells on current-scoured arenaceous substrates. Lethaia 17:17–32.

——— 1986. Life orientation and post-mortem reorientation of Chesterian brachiopod shells by paleocurrents. Palaios 1:303–311.

——— 1994. Distribution of pedicle boring traces and the life habit of Late Paleozoic leiorhynchid brachiopods from dysoxic habitats. Lethaia 27:227–234.

Alexander, R. R., and M. A. Gibson. 1993. Paleozoic brachiopod autecology based on taphonomy: example from the Devonian Ross Formation of Tennessee (USA). Palaeogeography, Palaeoclimatology, Palaeoecology 100:25–35.

Alexander, R. R., and C. D. Scharpf. 1990. Epizoans on Late Ordovician brachiopods from southeastern Indiana. Historical Biology 4:179–202.

Alvarez, F., and P. D. Taylor. 1987. Epizoan ecology and interactions in the Devonian of Spain. Palaeogeography, Palaeoclimatology, Palaeoecology 61:17–31.

Barclay, K. M., C. L. Schneider, and L. R. Leighton. 2013. Palaeoecology of Devonian sclerobionts and their brachiopod hosts from the Western Canadian Sedimentary Basin. Palaeogeography, Palaeoclimatology, Palaeoecology 383–384:79–91.

Bordeaux, Y. L., and C. E. Brett. 1990. Substrate specific association of epibionts on Middle Devonian brachiopods: implications for paleoecology. Historical Biology 4:203–220.

Bose, R. 2012. A new morphometric model in distinguishing two closely related extinct brachiopod species. Historical Biology 24:655–664.

Bose, R., C. L. Schneider, P. D. Polly, and M. M. Yacobucci. 2010. Ecological interactions between *Rhipidomella* (Orthides, Brachiopoda) and its endoskeletobionts and predators from the middle Devonian Dundee formation of Ohio, United States. Palaios 25:196–208.

Bose, R., C. L. Schneider, L. R. Leighton, and P. D. Polly. 2011. Influence of atrypid morphological shape on Devonian episkeletobiont assemblages from the lower Genshaw formation of the Traverse Group of Michigan: a geometric morphometric approach. Palaeogeography, Palaeoclimatology, Palaeoecology 310:427–441.

Buschkuehle, B. E. 2003. Sedimentology and stratigraphy of middle and upper Devonian carbonates in Northern Alberta: a contribution to the carbonate-hosted Pb-Zn (MVT) target geosciences initiative. EUB/AGS Geo-Note 2002 14:1–14.

Copper, P. 1966a. Ecological distributions of Devonian atrypid brachiopods. Palaeogeography, Palaeoclimatology, Palaeoecology 2:245–266.

——— 1966b. Adaptations and life habits of Devonian atrypid brachiopods. Palaeogeography, Palaeoclimatology, Palaeoecology 3:363–379.

——— 1967. Pedicle morphology in Devonian atrypid brachiopods. Journal of Paleontology 41:1166–1175.

——— 1973. New Siluro-Devonian Atrypoid brachiopods. Journal of Paleontology 47:484–500.

——— 1990. Evolution of the atrypid brachiopods. Pp. 35–40 *in* D.I. MacKinnon, D.E. Lee, and J.D. Campbell eds. Brachiopods through time: proceedings of the 2nd international brachiopod congress, University of Otago, Dunedin, New Zealand.

——— 1998. Evaluating the Frasnian-Famennian mass extinction: comparing brachiopod faunas. Acta Palaeontologica Polonica 43:137–154.

Cuffey, C. A., A. J. III. Robb, J. T. Lembcke, and R. J. Cuffey. 1995. Epizoic bryozoans and corals as indicators of life and post-mortem orientations of the Devonian brachiopod *Meristella*. Lethaia 28:139–153.

Dattilo, B. F. 2004. A new angle on Strophomenid paleoecology: trace-fossil evidence of an escape response for the Plectambonitoid brachiopod *Sowerbyella rugosa* from a tempestite in the upper Ordovician Kope formation (Edenian) of northern Kentucky. Palaios 19:332–348.

Day, J. 1990. The Upper Devonian (Frasnian) conodont sequence in the Lime Creek Formation of North-Central Iowa and comparison with Lime Creek ammonoid, brachiopod, foraminifer, and gastropod sequences. Journal of Paleontology 64:614–628.

——— 1992. Middle-Upper Devonian (Late Givetian – Early Frasnian) brachiopod sequence in the Cedar Valley Group of Central and Eastern Iowa. Pp. 53–105 *in* J. Day, and B.J. Bunker, eds. The stratigraphy, paleontology, depositional and diagenetic history of the Middle-Upper Devonian Cedar Valley Group of Central and Eastern Iowa. Guidebook Series No. 16. Iowa Department of Natural Resources, Iowa City, Iowa.

——— 1996. Faunal signatures of Middle-Upper Devonian depositional sequences and sea level fluctuations in the Iowa Basin: U.S. Midcontinent. Geological Society of America Special Papers 306:277–300.

——— 1998. Distribution of latest Givetian-Frasnian Atrypida (Brachiopoda) in central and western North America. Acta Palaeontological Polonica 43:205–240.

Day, J., and P. Copper. 1998. Revision of the latest Givetian – Frasnian Atrypida (Brachiopoda) from central North America. Acta Palaeontologica Polonica 43:155–204.

De Keyser, T. L. 1977. Late Devonian (Frasnian) brachiopod community patterns in Western Canada and Iowa. Journal of Paleontology 51:181–196.

Donovan, S. K. 1989. Taphonomic significance of the encrustation of the dead shell of recent *Spirula spirula* (Linné) (Cephalopoda: Coleoidea) by *Lepas anatifera* Linné (Cirripedia: Thoracia). Journal of Paleontology 63:698–702.

Fagerstrom, J. A. 1996. Paleozoic brachiopod symbioses: testing the limits of modern analogues in paleoecology. Geological Society of America Bulletin 108:1393–1403.

Fenton, C. L., and M. A. Fenton. 1932. Orientation and injury in the genus *Atrypa*. American Midland Naturalist 13:63–74.

Gibson, M. A. 1992. Some epibiont-host and epibiont-epibiont relationships from the Birdsong shale member of the Lower Devonian Ross Formation (west-central Tennessee, U.S.A.). Historical Biology 6:113–132.

Grant, R. E. 1966. A Permian Productoid brachiopod: life history. Science 152:660–662.

——— 1968. Structural adaptation in two Permian brachiopod genera, Salt Range, West Pakistan. Journal of Paleontology 42:1–32.

Hoare, R. D., and D. L. Steller. 1967. A Devonian brachiopod with epifauna. The Ohio Journal of Science 67:291–297.

Hurst, J. M. 1974. Selective epizoan encrustation of some Silurian brachiopods from Gotland. Palaeontology 17:423–429.

Johnson, J. G. 1962. Brachiopod faunas of the Nevada Formation (Devonian) in central Nevada. Journal of Paleontology 36:165–169.

——— 1970. Early middle Devonian brachiopods from central Nevada. Journal of Paleontology 44:252–264.

——— 1974. Early Devonian brachiopod biofacies of western and arctic North America. Journal of Paleontology 48:809–819.

Kesling, R. V., R. D. Hoare, and D. K. Sparks. 1980. Epizoans of the middle Devonian brachiopod *Paraspirifer bownockeri*: their relationships to one another and to their host. Journal of Paleontology 54:1141–1154.

LaBarbera, M. 1977. Brachiopod orientation to water movement. 1. Theory, laboratory behavior, and field orientations. Paleobiology 3:270–287.

——— 1978. Brachiopod orientation to water movement: functional morphology. Lethaia 11:67–79.

Lamont, A. 1934. Brachiopod morphology in relation to environment. Cement Lime Gravel 8:216–219.

Leighton, L. R. 1998. Constraining functional hypotheses: controls on the morphology of the concavo-convex brachiopod *Rafinesquina*. Lethaia 31:293–307.

——— 2000. Environmental distribution of spinose brachiopods from the Devonian of New York: test of the soft-substrate hypothesis. Palaios 15:184–193.

——— 2005. Comment: A new angle on Strophomenid paleoecology: trace-fossil evidence of an escape response for the Plectambonitoid brachiopod *Sowerbyella rugosa* from a tempestite in the upper Ordovivian Kope formation (Edenian) of Northern Kentucky (Dattilo, 2004). Palaios 20:596–600.

Lescinsky, H. L. 1995. The life orientation of concavo-convex brachiopods: overturning the paradigm. Paleobiology 21:520–551.

——— 1996. Don't overlook the epibionts! Palaios 11:495–496.

Ma, X., V. Ebbighausen, and R. T. Becker. 2008. *Desquamatia* and related atrypid brachiopods from the Frasnian (Upper Devoninan) of Bergisches Land, Germany. Canadian Journal of Earth Sciences 45:121–134.

Messina, C., and M. LaBarbera. 2004. Hydrodynamic behavior of brachiopod shells: experimental estimates and field observations. Palaios 19:441–450.

Molinaro, D. J., B. M. J. Collins, M. E. Burns, E. S. Stafford, and L. R. Leighton. 2013. Do predatory drill holes influence the transport and deposition of gastropod shells? Lethaia 46:508–517.

Nebelsick, J. H., B. Schmid, and M. Stachowitsch. 1997. The encrustation of fossil and recent sea-urchin tests: ecological and taphonomic significance. Lethaia 30:271–284.

Pitrat, C. W., and F. S. Rogers. 1978. *Spinocyrtina* and its epibionts in the Traverse group (Devonian) of Michigan. Journal of Paleontology 52:1315–1324.

Richards, R. P. 1972. Autecology of Richmondian brachiopods (Late Ordovician of Indiana and Ohio). Journal of Paleontology 46:386–405.

Richardson, J. R. 1981a. Brachiopods and pedicles. Paleobiology 7:87–95.

——— 1981b. Brachiopods in mud: resolution of a dilemma. Science 211:1161–1163.

Richardson, J. R., A. E. Aldgridge, and I. D. Endersby. 2007. Post settlement behaviour of brachiopods on hard and soft substrates. New Zealand Journal of Zoology 34:43–49.

Rowell, A. J. 1977. Valve orientation and functional morphology of the foramen siphonotretacean and acrotretacean brachiopods. Lethaia 10:43–50.

Rudwick, M. J. S. 1970. Living and fossil brachiopods. Hutchison, London.

Sando, W. J. 1984. Significance of epibionts on horn corals from the Chainman Shale (Upper Mississippian) of Utah. Journal of Paleontology 58:185–196.

Schneider, C. L., and L. R. Leighton. 2010. Epizoans and predation traces of Devonian Hay River Formation brachiopods: indicators of complex ecosystems and ties to the Iowa Basin. GeoCanada 2010 – Working with the Earth, Conference Abstracts.

Sparks, D. K., R. D. Hoare, and R. V. Kesling. 1980. Epizoans on the Brachiopod *Paraspirifer bownockeri* (Stewart) from the middle Devonian of Ohio. Papers on Paleontology 23:1–108.

Taylor, P. D., and M. A. Wilson. 2003. Palaeoecology and evolution of marine hard substrate communities. Earth-Science Reviews 62:1–103.

Thayer, C. W. 1975. Strength of pedicle attachment in articulate brachiopods: ecologic and paleoecologic significance. Paleobiology 1:388–399.

Tomašových, A., S. J. Carlson, and M. LaBarbera. 2008. Ontogenetic niche shift in the brachiopod *Terebratalia transversa*: relationship between the loss of rotation ability and allometric growth. Palaeontology 51:1471–1496.

Webb, A. E., and C. L. Schneider. 2013. Ecology of an encrusting fauna on *Desquamatia* (Atrypida, Brachiopoda) from Cedar Valley formation (Givetian, Devonian) of Iowa, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 377:102–109.

Table 2.1. Summary of the final orientations for each of the flume trials. Reorientation and transport flow velocities were not statistically different between the two morphologies.

Final Orientation	Morph A	Morph B
Dorsal valve topmost, anterior commissure upstream	0	0
Dorsal valve topmost, umbo upstream	41	3
Dorsal valve topmost, Lateral	0	28
Ventral valve topmost, anterior commissure upstream	0	2
Ventral valve topmost, umbo upstream	19	2
Ventral valve topmost, Lateral	0	25

Figure 2.1. Two representative dorsibiconvex brachiopod morphologies (*Radiatrypa clarkei*) from the Waterways Formation of the Western Canadian Sedimentary Basin. (A i – iii) Morph A is inflated, sulcate, strongly dorsibiconvex, and has a reduced hingeline. (B i – iii) Morph B is more planoconvex, has a longer hingeline, and is very weakly sulcate. (A, B i) dorsal view, (A, B ii) ventral view, (A, B iii) lateral view. Scale bar is 1 cm.

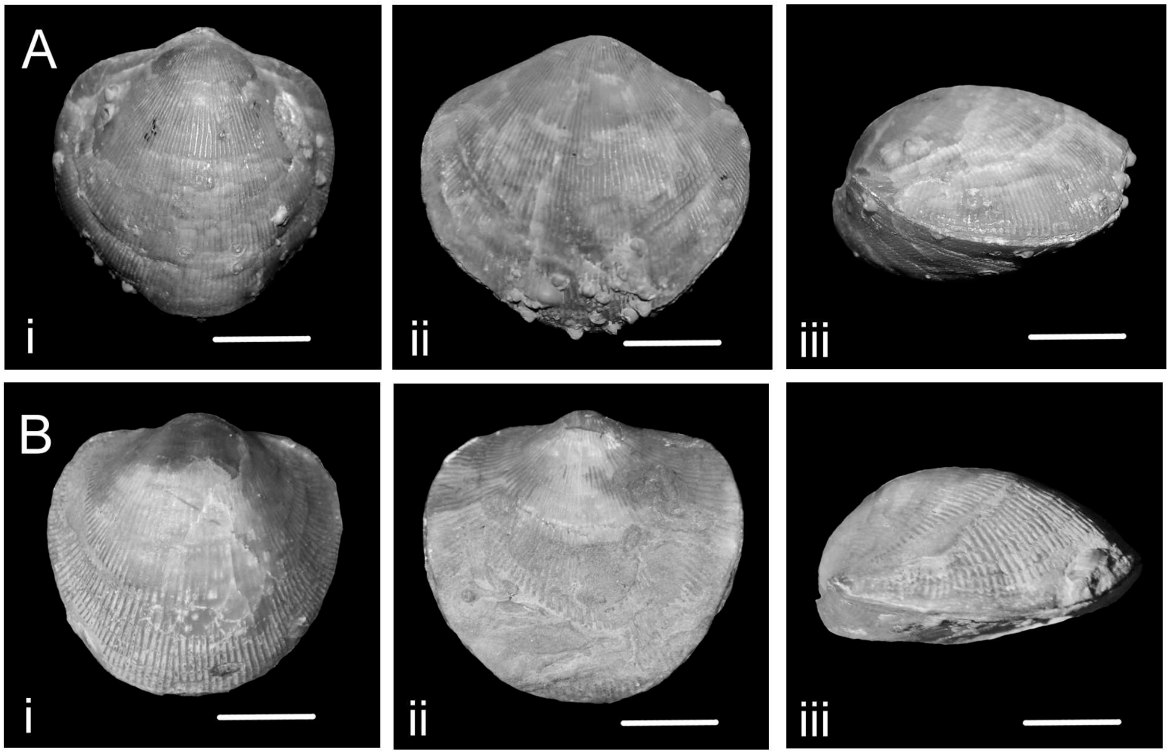


Figure 2.2. Schematic of the recirculating flume tank used in experimental trials. Specimens were placed downstream of the flow straightener, within the working chamber of the flume, as indicated by the “bulls-eye” in the diagram. (Image modified from Molinaro et al. 2013).

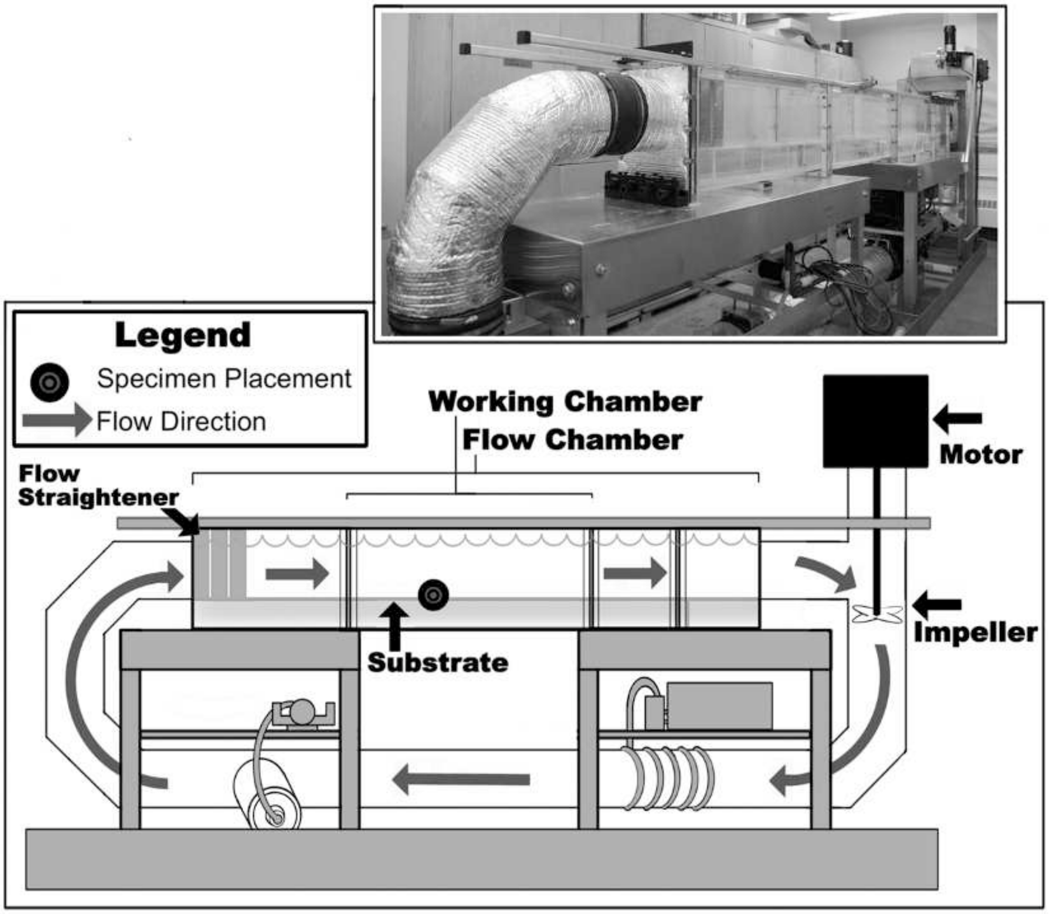


Figure 2.3. The most common final orientations for the experimental trials. Direction of flow is from left – right in all pictures. (A) Morph A orientation with dorsal valve topmost and umbo upstream. (B) Morph A orientation with ventral valve topmost, commissure inclined, and umbo upstream. (C) Morph B with dorsal valve topmost, and anterior-posterior axis perpendicular to flow. (D) Morph B with ventral valve topmost, commissure inclined away from flow, and anterior-posterior axis perpendicular to flow.

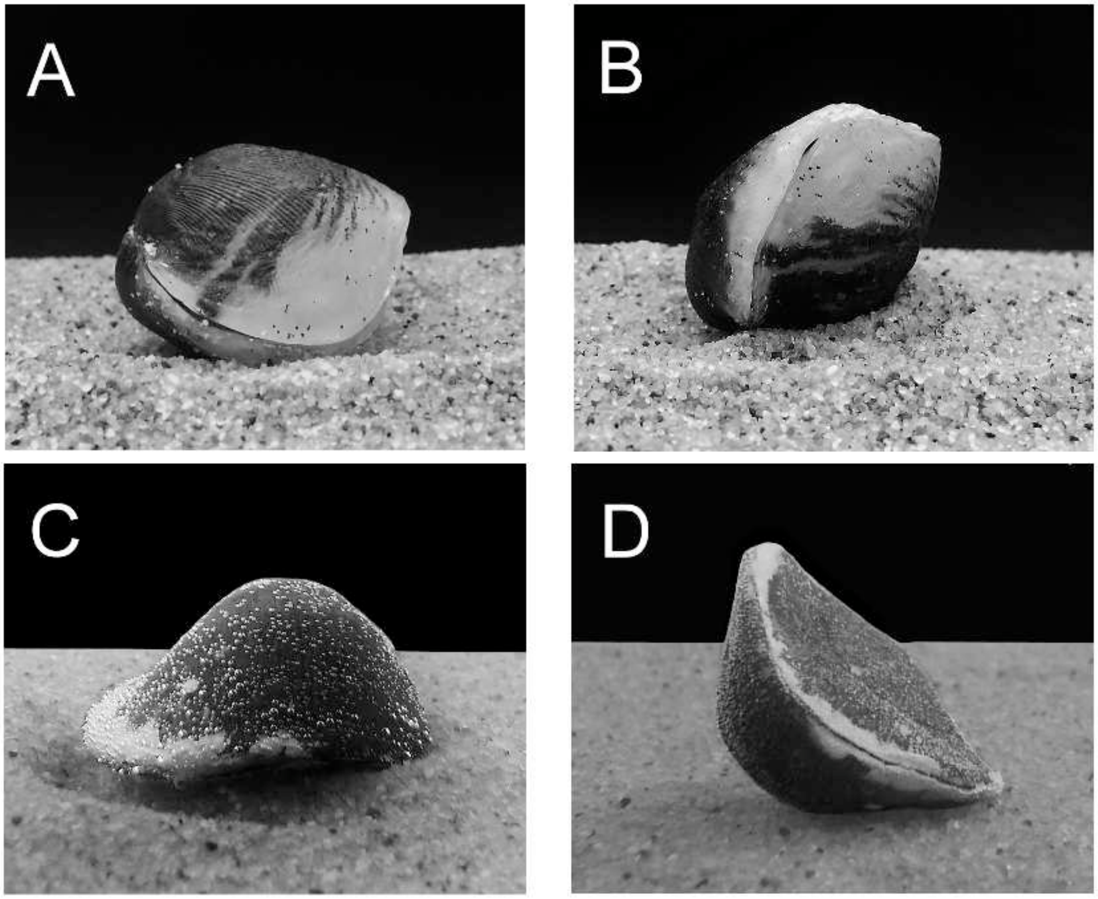


Figure 2.4. Scour patterns for both brachiopod models. Scour marks occurred as crescent shapes upstream around the margin of the shell. (A) Scour pattern around Morph A. (B) Scour pattern around Morph B.

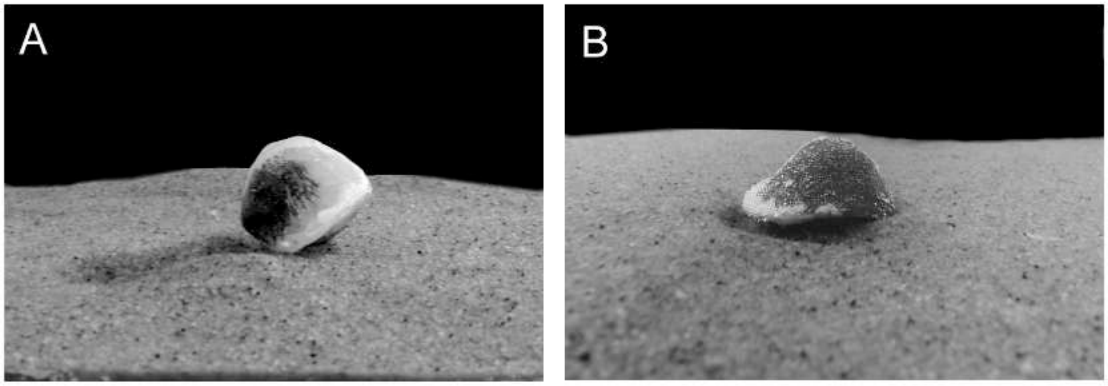
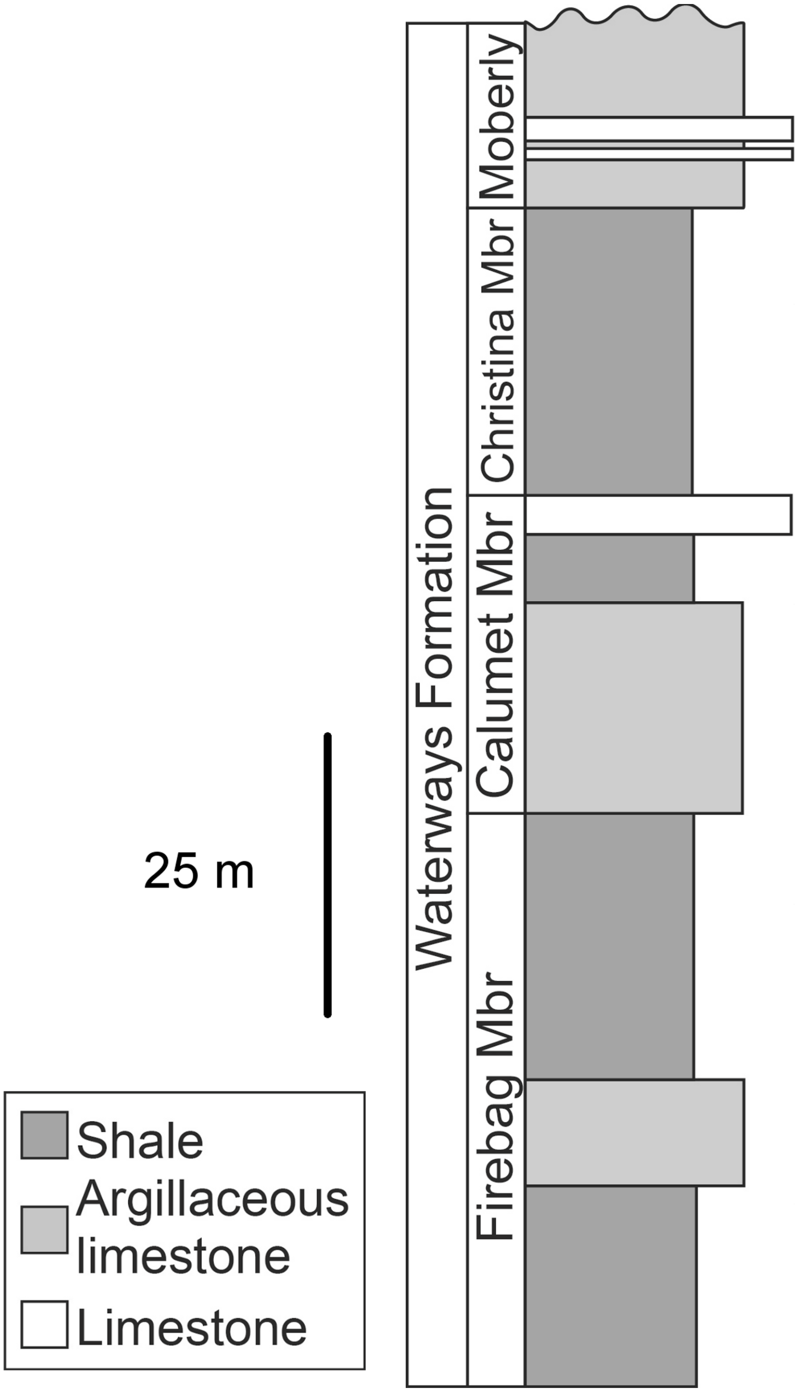


Figure 2.5. Stratigraphy of the Waterways Formation from Alberta, Canada (latest Givetian – middle Frasnian).



Chapter 3. A new method for assessing the biological significance of sclerobiont distributions on atrypide brachiopod hosts (Waterways Formation, Givetian – Frasnian, Alberta, Canada)

3.1 Introduction

In the fossil record, few interactions between organisms are as well preserved as epibionts attached to biotic hosts. Epibionts, also known as sclerobionts in palaeontological studies (sensu Taylor and Wilson 2002), make up an important and often diverse part of marine communities both in the modern and in the fossil record (Fenton and Fenton 1932; Fenton 1937; Ager 1961; Hoare and Steller 1967; Hurst 1974; Thayer 1974; LaBarbera 1977; Pitrat and Rogers 1978; Sparks et al. 1980; Sando 1984; Alvarez and Taylor 1987; Donovan 1989; Bordeaux and Brett 1990; Alexander and Scharpf 1990; Gibson 1992; Cuffey et al. 1995; Lescinsky 1995, 1996, 1997; Fagerstrom 1996; McKinney 1996; Nebelsick et al. 1997; Peters and Bork 1998; Lescinsky et al. 2002; Taylor and Wilson 2002, 2003, 2008; Schneider 2003, 2013; Rodland et al. 2004, 2006; Zapalski 2005; Bose et al. 2010, 2011; Schneider and Leighton 2010; Brett et al. 2011, 2012; Zatoń and Krawczyński 2011; Zatoń et al. 2011; Barclay et al. 2013). In the fossil record, retention of the spatial distribution of sclerobionts on the host allows for examination of palaeoenvironmental conditions, as well as potential biological relationships between sclerobionts and their hosts. However, any biological or palaeoenvironmental interpretation using sclerobionts and their hosts must assume that encrustation occurred when the host was alive. While there are some instances where post-mortem or live encrustation is obvious (Alvarez and Taylor 1987; Bose et al. 2011), the timing of encrustation must usually rely on an understanding of either the sclerobiont's or host’s biology. For example, during any host’s lifetime, there would have been areas of its body that would have been either covered in soft tissue, or resting against the substrate, and therefore unavailable to sclerobionts while the host was alive. Problematically, it is often the position of sclerobionts on the host that is used to determine the life orientation of the host. The following study uses the life orientation of a common brachiopod host, independently established in a previous study (Chapter 2), to determine (1) the amount of post-mortem encrustation of the host, and (2) any true biological preferences for sclerobiont positions on the brachiopod hosts.

The unique preservation of highly detailed spatial information of sclerobionts on their hosts permits the study of organism interactions in a way that is normally impossible in the fossil record. As a result, it is possible to ascertain biological information, such as potentially symbiotic or parasitic relationships between sclerobionts and their hosts, sclerobiont preferences for host type or location on a host, or the life orientation of the host (e.g., Ager 1961; Thayer 1974; Kesling et al. 1980; Alvarez and Taylor 1987; Baumiller 1990, 1993; Bordeaux and Brett 1990; Alexander and Scharpf 1990; Lescinsky 1995; Bose et al. 2011; Webb and Schneider 2013). Researchers can also interpret palaeoenvironmental information, such as current direction, firmness of the substrate, and the amount of time averaging in an assemblage (e.g., Kesling et al. 1980; Sparks et al. 1980; Lescinsky 1996; Peters and Bork 1998; Taylor and Wilson 2003; Schneider 2013). However, one of the greatest challenges facing any researcher interested in sclerobiosis is the life status of the host at the time of encrustation.

In palaeontological studies, the term “sclerobiont” (Taylor and Wilson 2002) is used specifically to address uncertainties in the life status of the host organism at the time of encrustation. Any hypothesis involving the nature of the relationship between sclerobionts and their hosts, or sclerobiont/host "preferences" must be able to determine whether or not the host was alive 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, it is still important to determine the life orientation of the host in order to understand the biological implications of sclerobiont positions on the host, and which sclerobionts and hosts 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. 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 brachiopod lived with the concave valve facing the substrate. Regardless of interpreted host orientation, in both cases there is the possibility of 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). Post-mortem encrustation of a host does not contribute to an understanding of a biological relationship between sclerobionts and hosts, and can potentially obscure any true biological signal. Distinguishing between a live and dead host is therefore critical to understanding sclerobiont – host relationships.

In order to avoid potentially circular reasoning, the life orientation of sclerobiont hosts must be derived independently of sclerobiont positions. One independent method is to test the functional morphology of the potential sclerobiont host biomechanically (Alexander 1975, 1984, 1986; LaBarbera 1977, 1978; Leighton 1998, 2005; Messina and LaBarbera 2004). Biomechanical experiments on brachiopods have been particularly well documented (Alexander 1975, 1984, 1986; LaBarbera 1977, 1978; Leighton 1998, 2005; Messina and LaBarbera 2004). In an unpublished study, biomechanical experiments were conducted on common dorsibiconvex brachiopod hosts from the Late Givetian – Frasnian of the Western Canadian Sedimentary Basin as a means of independently assessing the life orientation of the dorsibiconvex brachiopod morphology (Chapter 2).

Dorsibiconvex brachiopods were abundant worldwide during the Silurian and Devonian (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), and were common sclerobiont hosts (Hurst 1974; Gibson 1992; Schneider and Leighton 2010; Bose et al. 2011; Barclay et al. 2013; Webb and Schneider 2013), however, their life orientation remains poorly understood (Fenton and Fenton 1932; Copper 1966b). The 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 (Chapter 2). 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 (Fig. 3.1). By determining the life orientation of these common brachiopod hosts, an independent method for assessing the amount of post-mortem encrustation can be implemented; those parts of the brachiopod that would have been resting against the substrate during life would have been unavailable for sclerobiont settlement and therefore any encrustation of those areas could only have occurred after death, decay of the pedicle, and reorientation of the brachiopod.

Once the probable life orientation of a sclerobiont host has been determined, not only can the extent of post-mortem encrustation of the host be distinguished, but an attempt can also be made to determine the biological significance of sclerobiont positions on the potentially live hosts. For example, sclerobiont positions may indicate a preference for a less exposed area of the host (area that would have been adjacent to the substrate) that may not have been evident if the analysis also included hosts that displayed post-mortem encrustation.

There have been many different methods for determining sclerobiont "preferences" in the past (e.g., Hurst 1974; Thayer 1974; Kesling et al. 1980; Sparks et al. 1980; Alvarez and Taylor 1987; Gibson 1992; Lescinsky 1995; Bose et al. 2010, 2011; Webb and Schneider 2013). A commonly used method to quantify the amount of encrustation across a host is to create a grid or zonation system to divide the host into sections and compare the amount of encrustation in each section (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 different ways of developing a grid system on a host. For example, Kesling et al. (1980) devised a grid system that separated spiriferide brachiopod hosts into 41 sections on each valve, taking into account proximity to the hingeline, commissure, and fold/sulcus. Gibson (1992) placed an emphasis on the commissure and fold/sulcus, but used fewer grid sections that were not as uniform in shape. Other methods have used a grid system with fewer sections (Bose et al. 2010, 2011; Webb and Schneider 2013), and some have had different grid sections for each valve (Sparks et al. 1980). If each method was used on the same sclerobiont data set, each would produce different results, but it is not clear as to whether any one of these approaches is “better” than the others. In addition, as the use of a zonation system may be 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/zones in the grid can create an artifact that may bias the result. An alternative approach has been to do away with a grid system altogether, and instead use a symbol or dot to represent the exact location of each sclerobiont on the host’s shell (Lescinsky 1995). While this method potentially provides more detailed spatial relationships between sclerobionts, the challenge becomes dealing with sclerobionts that cover large areas of the host’s shell, or grow in complicated branching patterns. Additionally, the “dot” method may not be able to differentiate multiple sclerobionts that have encrusted the same position on the host’s shell. With any one of the grid methods, or the “dot” method, the problem still remains that any interpretation of the biological significance of sclerobiont positions is dependent on the orientation of the host, an issue that is not usually addressed in these types of sclerobiont studies.

Without a unified method of data collection, it is difficult to compare or contrast sclerobiont studies to ascertain any common or unique trends. Furthermore, any assumption of the biological significance of sclerobiont distribution across the host is potentially meaningless without corroborating the life orientation of the host. Instead of devising a complex grid system, or using dots to represent potentially complicated sclerobionts, one of the simplest solutions might be to directly map the outline of each sclerobiont exactly as it appears on each host. The only zone that would need to be created would be the “dead zone”, or area of the host’s shell that would be against the substrate during life and would therefore only be encrusted after post-mortem transport and/or reorientation. A map of sclerobiont outlines would create a kind of heat map in which one could examine any “hot spots” of encrustation, percent areal coverage, and the amount of post-mortem encrustation. Other biologically meaningful zonation schemes could be developed either before or after sclerobiont mapping, but the actual mapping of sclerobionts would not be affected. Retaining the complex spatial outlines of each sclerobiont would also allow others to independently assess any “zones” or preferences that were suggested by the original researchers. The direct mapping method takes into account the orientation of the host organism to understand sclerobiont distribution better, and minimally provides a method for distinguishing those hosts which were encrusted post-mortem. For example, if a brachiopod specimen has a sclerobiont within the “dead zone”, it was clearly encrusted post-mortem, and would therefore be unsuited for use in an analysis of either host, or depending on the hypothesis, even sclerobiont, biology.

The goals of the following study are to: (1) use the inferred life orientation of atrypide brachiopod hosts to distinguish between which brachiopods are encrusted post-mortem, and which might provide palaeoenvironmental data and biologically meaningful information on the relationships between sclerobionts and hosts, and (2) create maps of sclerobiont positions on each brachiopod host in order to determine any potential biological trends on those brachiopod hosts that are not encrusted within the “dead zone”.

3.2 Geology

The Waterways Formation (latest Givetian – Early Frasnian) outcrops along the Athabasca and Clearwater Rivers in northeastern Alberta, Canada. 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. 3.2). During deposition of the Waterways Formation, northeastern Alberta lay along a passive continental margin in the tropics, south of the palaeoequator (Loranger 1965; Witzke and Heckel 1988) (Fig. 3.3). The Waterways Formation was deposited on a shallow water platform (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. 3.3). 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.

3.2.1 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, but there are distinct fossiliferous horizons that are dominated by brachiopods, but also include crinoids and bivalves. Brachiopod faunas are heavily dominated by atypides, particularly *Desquamatia* (Barclay et al. 2013). Two fossiliferous units along the Athabasca River, one at the transition between the lower shale and middle argillaceous limestone, and one at the transition between the middle argillaceous limestone and upper shale, were sampled for this study, and will be referred to herein as Firebag Sample 1 and Firebag Sample 2 (Fig. 3.2).

3.2.2 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* (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. 3.2). The entire member is approximately 22 - 30 m thick in the study area (Schneider and Grobe 2013).

3.2.3 Christina Member

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

3.2.4 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 limestone beds 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. 3.2). In each of the Moberly samples, atrypide brachiopods, especially *Radiatrypa*, were the most abundant fossils.

3.3 Methods

3.3.1 Field Methods

Brachiopods were surface collected from horizons of the Waterways Formation near Fort McMurray, Alberta, Canada (Fig. 3.3). The samples were collected from six beds as described above (Firebag Samples 1 and 2, Calumet Sample 1, and Moberly Samples 1, 2, and 3) (Fig. 3.2), chosen specifically for high quality preservation required for the detailed sclerobiont analysis required for this study. 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).

3.3.2 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, was culled from the sample set. Of the atrypide brachiopods, only those brachiopods which fit the typical dorsibiconvex atrypide morphology and which behaved similarly in flume experiments (Chapter 2) were used for mapping purposes. In the Firebag Member, those brachiopods belonged to the genus *Desquamatia*, and in the Calumet and Moberly members, those brachiopods belonged to the genus *Radiatrypa*.

For all six beds, the brachiopods were similar in both morphology and size (about 2 cm in length). In each bed, the genus selected for mapping purposes was also the largest and most abundant brachiopod in that assemblage. 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 two genera would be different. However, brachiopods from the six beds were analysed separately so as to maintain the highest possible 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 the change in host genus would be immediately apparent.

Each brachiopod was then examined under a 10 – 40x microscope for sclerobionts. Brachiopods that had sclerobionts were sorted from those that were not encrusted. 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), for a total sample of 150 specimens, were selected for mapping purposes. A sample of 25 specimens per bed was deemed adequate for testing this hypothesis, as the goal was to determine if each individual brachiopod was alive or dead at the time of encrustation. For example, if 23 of 25 brachiopods had no sclerobionts within the dead zone, this would be a representative “live” sample in which the two “dead” brachiopods could be removed from any subsequent analysis.

Two high-resolution photographs, a dorsal and ventral view, were taken of each specimen. Each photograph was then opened in GIMP 2.8, 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 genus 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 (both a dorsal and ventral view map) in which the original photo could be removed so that only the outline of the brachiopod and each sclerobiont remained (Fig. 3.4). 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 so that a detailed, stacked map was created of the sclerobionts on each of the 25 brachiopod valves, in which the 25 layers could be hidden or viewed (Fig. 3.4). The final result was 2 maps for each of the six beds, one each of both the dorsal and ventral valves, or 12 maps in total (Fig. 3.5).

3.3.3 Analyses

Given that the life orientation of dorsibiconvex atrypides had been established in a previous unpublished study (Chapter 2), three zones were identified: the dead, shaded, and exposed zones (Fig. 3.1). The size of the dead 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 distinction between post-mortem, and potential life-associated encrustation of the brachiopods. Instead of creating a 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 distribution on brachiopod hosts.

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 dead zone on the dorsal valve), but it also allowed for a biologically significant interpretation of encrustation within each zone. Given the life orientation of the host (Fig. 3.1), the shaded zone on the dorsal valve was somewhat more sheltered from currents and grazing predators (see Taylor and Wilson 2003 for a detail list of 'cryptic' encrustation through time), whereas the ventral valve was more exposed (hence the terms 'shaded' and 'exposed').

Any brachiopod that had a sclerobiont within the dead zone was considered dead at the time of encrustation, as encrustation of the dead zone would only occur after the brachiopod had died, the pedicle had decayed away, and subsequent transport or reorientation had exposed the dead zone for sclerobiont settlement, meaning that at least some encrustation of that brachiopod had occurred post-mortem. The number of dead brachiopods in each of the six beds was then noted. Those brachiopods that did not have sclerobionts within the dead zone were more likely to represent brachiopods that were encrusted while they were still alive. By distinguishing the number of dead brachiopods in any sclerobiont/brachiopod study, those particular 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 a 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 meant that some spatial data was lost.

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. 3.4). 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.

3.4 Results

3.4.1 Firebag Sample 1

Of the 25 brachiopods from Firebag Sample 1, 7 had sclerobionts within the dead zone (Table 3.1, Fig. 3.5A and B). Chi-square tests revealed no preference between the remaining shaded and exposed zones (Table 1). Sclerobiont taxa included *Ascodictyon, Hederella,* and *Microconchus* (Table 3.2, Fig. 3.6).

3.4.2 Firebag Sample 2

In this sample, there were no sclerobionts within the dead zone (Fig. 3.5C and D). Two sclerobionts appeared to fall within the dead zone on the two-dimensional map, but an examination of the original specimens showed that these sclerobionts actually fell outside of the dead zone (Fig. 3.5C). The brachiopod specimens were greatly convex, and very slightly distorted posteriorly, resulting in the projection of the sclerobionts within the dead 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 that had been designated as the dead zone (Fig. 3.5C). Chi-square tests also indicate a strong preference for the shaded zone (dorsal valve excluding the dead zone) ($p < 0.01$) (Table 3.1). Sclerobiont taxa included *Microconchus, Hederella, Ascodictyon,* and a single craniid brachiopod (Table 3.2, Fig. 3.6). The ventral valve was encrusted solely by *Microconchus* (Table 3.2).

3.4.3 Calumet Sample 1

Calumet Sample 1 had 2 brachiopods that had sclerobionts within the dead zone (Table 3.1, Fig. 3.5E and F). There was no valve preference, and sclerobiont taxa included *Ascodictyon, Hederella,* and *Microconchus* (Table 3.2, Fig. 3.6).

3.4.4 Moberly Sample 1

Moberly Sample 1 had 3 brachiopods that were encrusted within the dead zone (Table 3.1, Fig. 3.5G and H). Chi-square tests also indicate that there was a preference for the shaded zone ($p < 0.01$) (Table 3.1). Sclerobiont taxa include *Microconchus*, craniid brachiopods, and a single *Hederella* on the dorsal valve (Table 3.2, Fig. 3.6).

3.4.5 Moberly Sample 2

Moberly Sample 2 had no dead brachiopods, but unlike Firebag Sample 2 and Moberly Sample 1, there was a strong preference for the exposed (ventral) zone ($p < 0.01$) (Table 3.1, Fig. 3.5I and J). Sclerobiont taxa included *Hederella, Microconchus,* and craniid brachiopods (Table 3.2, Fig. 3.6).

3.4.6 Moberly Sample 3

Moberly Sample 3 had a single *Microconchus* encrusting one brachiopod post-mortem (Table 3.1, Fig. 3.5K and L). There was no valve preference, and sclerobiont taxa included *Microconchus*, *Hederella*, and craniid brachiopods (only on the dorsal valve) (Table 3.2, Fig. 3.6).

3.5 Discussion

3.5.1 Dead Zone Implications

By using the life orientation to distinguish a dead 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 dead zone: (1) brachiopod specimens with encrustation of the dead zone can be removed from any analysis of sclerobiont-host relationships and palaeoenvironmental data; (2) those assemblages which have few brachiopod hosts that were encrusted post-mortem are more likely to indicate an assemblage that was alive at the time of burial and therefore are more reliable for any palaeoenvironmental or sclerobiont – host study.

The life orientation of sclerobiont hosts is critical to understanding the relationship sclerobionts would have had with their hosts. With brachiopod hosts, such as dorsibiconvex atrypides, on which both valves can be equally encrusted, sclerobiont placement by itself should not be used to infer the life orientation of the brachiopod. In turn, the biological significance of sclerobiont positions on a brachiopod host cannot be understood unless the life orientation of the host is understood. For example, any inference of shaded or exposed zones would be subjective without an independent means of testing the life orientation of the brachiopod. The same could be said of other brachiopod morphologies as well. However, when the life orientation of the host is determined based on an understanding of the biomechanical behaviour of the host, this independent evidence corroborates any biological interpretations of sclerobiont placement. Thus, the preference of a sclerobiont for the shaded zone can be distinguished from the exposed zone, and the encrustation of a live host can be distinguished from post-mortem encrustation.

Assessing post-mortem encrustation is not always clear in the fossil record. For atrypide brachiopods, disarticulation of the valves is rare due to their cyrtomatodont hingeline, which is not prone to disarticulation (Alexander and Gibson 1993). It is therefore critical that the life orientation of the potential host should be understood to assess post-mortem encrustation. The differentiation of the "dead zone" on dorsibiconvex brachiopods, such as *Desquamatia* and *Radiatrypa* allowed for a quick and simple method for calculating the number of "dead" brachiopods in an assemblage. While some encrustation outside of the dead zone could have potentially occurred post-mortem, encrustation of the dead zone provides a minimum number of "dead" brachiopods in an assemblage. Based on this evidence, it is assumed that at least some encrustation on that brachiopod occurred post-mortem. Those brachiopods that do not have any sclerobionts within the dead zone are therefore more likely to have been encrusted while the brachiopod was still alive.

The allocation of the dead zone was independently supported by several sclerobionts which appeared to perfectly border the dead zone, such as certain specimens of *Ascodictyon* in both Firebag samples and the Calumet sample, as well as a number of *Microconchus* in Moberly Sample 1 (Fig. 3.5A, C, E, and G). The number of brachiopods encrusted within the dead 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 1 had at least 7 of 25 brachiopods that were encrusted post-mortem, or 28% post-mortem encrustation. This indicates that at least a third of the entire assemblage was likely encrusted after death and would not be a reliable source of information of sclerobiont – host interactions. However, Firebag Sample 2, and Moberly Sample 2 had no encrustation of the dead zone, so are therefore more likely to represent live sclerobiont – live host relationships. Even Moberly

Sample 3, which had a single *Microconchus* in the dead zone, likely indicates that the majority of the brachiopods in the assemblage were encrusted during the lifetime of the brachiopod.

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. An easy way to assess the number of dead individuals 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. Greater rates of post-mortem encrustation likely indicate a greater degree of time averaging. 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 palaeoenvironmental interpretation that relies on the assumption of live individuals. I conclude that understanding the life orientation/dead zone provides a simple method for culling “dead” brachiopods from a sample, and assessing which assemblages of hosts are worthwhile to examine for live sclerobiont – live host relationships or palaeoenvironmental data.

3.5.2 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 dead 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 analysed 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 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 1, which had the greatest amount of post-mortem encrustation, was also the most heavily encrusted assemblage in terms of sclerobiont areal coverage (Fig. 3.5A and B). Assuming that greater amounts of post-mortem encrustation indicates a greater degree of time averaging, 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. 3.5I – L), which could potentially support past suggestions that sclerobionts might take advantage of their hosts 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 (Fig. 3.1). 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 (Bishop 1988; Taylor and Wilson 2003).

In the past, it has been suggested that dorsibiconvex 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. As mentioned previously, using the position of sclerobionts to assess the life orientation of the host is circular, and it is best to derive the life orientation of the host independent of sclerobiont distribution. 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. The distinction of those brachiopod specimens that were encrusted post-mortem would also refine the results of these studies by removing those dead specimens that could have potentially obscured true biological preferences.

However, for the purposes of this study, there are clear inconsistencies with sclerobiont “preferences” for location on the brachiopods between the six assemblages, even amongst individual sclerobiont taxa. Three assemblages (Firebag Sample 1, Calumet Sample

1, and Moberly Sample 3) showed no valve preference, two assemblages (Firebag Sample 2, and Moberly Sample 1) showed a preference for the shaded zone, and Moberly Sample 2 showed a preference for the exposed zone. There was no correlation between zone preference (or lack thereof) and the number of “dead” brachiopods. 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, and examination of sclerobionts “preferences” should be performed 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.

3.6 Conclusions

(1) Independently assessing the life orientation of sclerobiont hosts is critical to the interpretation of sclerobiont positions on those hosts. Any use of sclerobionts to determine the life orientation of the host invokes circular reasoning that can lead to problems with sclerobiont-host relationship assessments. 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 (Chapter 2). Not only does this life orientation suggest a shaded

and exposed area for sclerobionts on the host, but it also indicates that the portion of the brachiopod that would be resting against the substrate would never be available for sclerobionts during the brachiopod's lifetime. Encrustation of this "dead zone" could only occur after post-mortem decay of the pedicle and transport/reorientation out of life orientation.

(2) Assessing the amount of encrustation within the dead zone allows for differentiation between those brachiopod hosts that were encrusted after death and those that were more likely to have been encrusted while they were still alive. Additionally, the number of brachiopods that have post-mortem encrustation can be used to assess how reliable that assemblage may be when examining palaeoenvironmental data or sclerobiont-host relationships, as only assemblages in which encrustation of the host occurred while it was alive would contribute meaningful information to palaeoenvironmental and biological studies.

(3) Sclerobiont "preferences" are not consistent between assemblages and are not associated with the amount of post-mortem encrustation. Any sclerobiont trends should therefore be examined with great scrutiny and at the highest stratigraphic resolution possible 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).

(4) Mapping sclerobionts directly onto photographs of their brachiopod hosts allows for detailed examination of sclerobiont placement on the brachiopod. These mapping techniques, along with the designation of a "dead zone", can be easily applied to help answer a variety of questions, and should serve as a unifying method for future sclerobiont studies.

3.7 Works Cited

Ager, D. V. 1961. The epifauna of a Devonian spiriferid. Quarterly Journal of the Geological Society 117:1–10.

Alexander, R. R. 1975. Phenotypic lability of the brachiopod *Rafinesquina alternata* (Ordovician) and its correlation with the sedimentologic regime. Journal of Paleontology 49:607–618.

——— 1984. Comparative hydrodynamic stability of brachiopod shells on current-scoured arenaceous substrates. Lethaia 17:17–32.

——— 1986. Life orientation and post-mortem reorientation of Chesterian brachiopod shells by paleocurrents. Palaios 1:303–311.

Alexander, R. R., and M. A. Gibson. 1993. Paleozoic brachiopod autecology based on taphonomy: example from the Devonian Ross Formation of Tennessee (USA). Palaeogeography, Palaeoclimatology, Palaeoecology 100:25–35.

Alexander, R. R., and C. D. Scharpf. 1990. Epizoans on Late Ordovician brachiopods from southeastern Indiana. Historical Biology 4:179–202.

Alvarez, F., and P. D. Taylor. 1987. Epizoan ecology and interactions in the Devonian of Spain. Palaeogeography, Palaeoclimatology, Palaeoecology 61:17–31.

Barclay, K. M., C. L. Schneider, and L. R. Leighton. 2013. Palaeoecology of Devonian sclerobionts and their brachiopod hosts from the Western Canadian Sedimentary Basin. Palaeogeography, Palaeoclimatology, Palaeoecology 383–384:79–91.

Baumiller, T. K. 1990. Non-predatory drilling of Mississippian crinoids by platyceratid gastropods. Palaeontology. 33:743–748.

——— 1993. Boreholes in Devonian blastoids and their implications for boring by platyceratids. Lethaia 26:41–47.

Bishop, J. D. D. 1988. Disarticulated bivalve shells as substrates for encrustation by the bryozoan *Cribrilina puncturata* in the Plio-Pleistocene Red Crag of eastern England. Palaeontology 31:237–253.

Bordeaux, Y. L., and C. E. Brett. 1990. Substrate specific association of epibionts on Middle Devonian brachiopods: implications for paleoecology. Historical Biology 4:203–220.

Bose, R. 2012. A new morphometric model in distinguishing two closely related extinct brachiopod species. Historical Biology 24:655–664.

Bose, R., C. L. Schneider, P. D. Polly, and M. M. Yacobucci. 2010. Ecological interactions between *Rhipidomella* (Orthides, Brachiopoda) and its endoskeletobionts and predators from the middle Devonian Dundee formation of Ohio, United States. Palaios 25:196–208.

Bose, R., C. L. Schneider, L. R. Leighton, and P. D. Polly. 2011. Influence of atrypid morphological shape on Devonian episkeletobiont assemblages from the lower Genshaw formation of the Traverse Group of Michigan: a geometric morphometric approach. Palaeogeography, Palaeoclimatology, Palaeoecology 310:427–441.

Bowsher, A. L. 1955. Origin and adaptation of platyceratid gastropods. University of Kansas Paleontological Contributions, Mollusca Article 5:1–11.

Braun, W. E., A. W. Norris, and T. T. Uyeno. 1988. Late Givetian to early Frasnian biostratigraphy of Western Canada. Devonian System of the World, Canadian Society of Petroleum Geologists, Second International Symposium on the Devonian System 3:93–111.

Brett, C. E., K. M. Parsons-Hubbard, S. E. Walker, C. Ferguson, E. N. Powell, G. Staff, K. A. Ashton-Alcox, and A. Raymond. 2011. Gradients and patterns of sclerobionts on experimentally deployed bivalve shells: synopsis of bathymetric and temporal trends on a decadal time scale. Palaeogeography, Palaeoclimatology, Palaeoecology 312:278–304.

Brett, C. E., T. Smrecak, K. Parsons-Hubbard, and S. Walker. 2012. Marine Sclerobiofacies: encrusting and endolithic communities on shells through time and space. Pp. 129–157 *in* J. A. Talent, ed. Earth and Life: International Year of Planet Earth. Springer Science + Business Media, New York.

Buschkuehle, B. E. 2003. Sedimentology and stratigraphy of Middle and Upper Devonian carbonates in northern Alberta: a contribution to the carbonate-hosted Pb-Zn (MVT) Targeted Geoscience Initiative. Alberta Energy and Utilities Board, EUB/AGS Geo-Note 2002-14.

Copper, P. 1966a. Ecological distributions of Devonian atrypid brachiopods. Palaeogeography, Palaeoclimatology, Palaeoecology 2:245–266.

——— 1966b. Adaptations and life habits of Devonian atrypid brachiopods. Palaeogeography, Palaeoclimatology, Palaeoecology 3:363–379.

——— 1967. Pedicle morphology in Devonian atrypid brachiopods. Journal of Paleontology 41:1166–1175.

——— 1973. New Siluro-Devonian Atrypoid brachiopods. Journal of Paleontology 47:484–500.

——— 1990. Evolution of the atrypid brachiopods. Pp. 35–40 *in* D.I. MacKinnon, D.E. Lee, and J.D. Campbell eds. Brachiopods through time: proceedings of the 2nd international brachiopod congress, University of Otago, Dunedin, New Zealand.

——— 1998. Evaluating the Frasnian-Famennian mass extinction: comparing brachiopod faunas. Acta Palaeontologica Polonica 43:137–154.

Crickmay, C. H. 1957. Elucidation of some Western Canadian Devonian Formations. Imperial Oil Limited, Calgary 15p.

Cuffey, C. A., A. J. III. Robb, J. T. Lembcke, and R. J. Cuffey. 1995. Epizoic bryozoans and corals as indicators of life and post-mortem orientations of the Devonian brachiopod *Meristella*. Lethaia 28:139–153.

Day, J. 1990. The Upper Devonian (Frasnian) conodont sequence in the Lime Creek Formation of North-Central Iowa and comparison with Lime Creek ammonoid, brachiopod, foraminifer, and gastropod sequences. Journal of Paleontology 64:614–628.

——— 1992. Middle-Upper Devonian (Late Givetian – Early Frasnian) brachiopod sequence in the Cedar Valley Group of Central and Eastern Iowa. Pp. 53–105 *in* J. Day, and B.J. Bunker, eds. The stratigraphy, paleontology, depositional and diagenetic history of the Middle-Upper Devonian Cedar Valley Group of Central and Eastern Iowa. Guidebook Series No. 16. Iowa Department of Natural Resources, Iowa City, Iowa.

——— 1996. Faunal signatures of Middle-Upper Devonian depositional sequences and sea level fluctuations in the Iowa Basin: U.S. Midcontinent. Geological Society of America Special Papers 306:277–300.

——— 1998. Distribution of latest Givetian-Frasnian Atrypida (Brachiopoda) in central and western North America. Acta Palaeontological Polonica 43:205–240.

Day, J., and P. Copper. 1998. Revision of the latest Givetian – Frasnian Atrypida (Brachiopoda) from central North America. Acta Palaeontologica Polonica 43:155–204.

De Keyser, T. L. 1977. Late Devonian (Frasnian) brachiopod community patterns in Western Canada and Iowa. Journal of Paleontology 51:181–196.

Donovan, S. K. 1989. Taphonomic significance of the encrustation of the dead shell of recent *Spirula spirula* (Linné) (Cephalopoda: Coleoidea) by *Lepas anatifera* Linné (Cirripedia: Thoracia). Journal of Paleontology 63:698–702.

Fagerstrom, J. A. 1996. Paleozoic brachiopod symbioses: testing the limits of modern analogues in paleoecology. Geological Society of America Bulletin 108:1393–1403.

Fenton, C. L., and M. A. Fenton. 1932. Orientation and injury in the genus *Atrypa*. American Midland Naturalist 13:63–74.

Fenton, M. A. 1937. Species of *Aulopora* from the Traverse and Hamilton Groups. American Midland Naturalist 18:115–119.

Furlong, C. M., and C. A. McRoberts. 2014. Commensal borings from the Middle Devonian of central New York: ecologic and taxonomic review of *Clionoides*, *Clionolithes*, and *Canaliparva* n. ichnogen. Journal of Paleontology 88:130–144.

Gibson, M. A. 1992. Some epibiont-host and epibiont-epibiont relationships from the Birdsong shale member of the Lower Devonian Ross Formation (west-central Tennessee, U.S.A.). Historical Biology 6:113–132.

Hoare, R. D., and D. L. Steller. 1967. A Devonian brachiopod with epifauna. The Ohio Journal of Science 67:291–297.

Hurst, J. M. 1974. Selective epizoan encrustation of some Silurian brachiopods from Gotland. Palaeontology 17:423–429.

Johnson, J. G. 1970. Early middle Devonian brachiopods from central Nevada. Journal of Paleontology 44:252–264.

——— 1974. Early Devonian brachiopod biofacies of western and arctic North America. Journal of Paleontology 48:809–819.

Kesling, R. V., R. D. Hoare, and D. K. Sparks. 1980. Epizoans of the middle Devonian brachiopod *Paraspirifer bownockeri*: their relationships to one another and to their host. Journal of Paleontology 54:1141–1154.

Keyes, C. R. 1890. Synopsis of American Carbonic Calyptraeidae. Proceedings of the Academy of Natural Sciences of Philadelphia 42:150–181.

LaBarbera, M. 1977. Brachiopod orientation to water movement. 1. Theory, laboratory behavior, and field orientations. Paleobiology 3:270–287.

——— 1978. Brachiopod orientation to water movement: functional morphology. Lethaia 11:67–79.

Leighton, L. R. 1998. Constraining functional hypotheses: controls on the morphology of the concavo-convex brachiopod *Rafinesquina*. Lethaia 31:293–307.

——— 2005. Comment: A new angle on Strophomenid paleoecology: trace-fossil evidence of an escape response for the Plectambonitoid brachiopod *Sowerbyella rugosa* from a tempestite in the upper Ordovivian Kope formation (Edenian) of Northern Kentucky (Dattilo, 2004). Palaios 20:596–600.

Lescinsky, H. L. 1995. The life orientation of concavo-convex brachiopods: overturning the paradigm. Paleobiology 21:520–551.

——— 1996. Don’t overlook the epibionts! Palaios 11:495–496.

——— 1997. Epibiont communities: recruitment and competition on North American Carboniferous brachiopods. Journal of Paleontology 71:34–53.

Lescinsky, H. L., E. Edinger, and M. J. Risk. 2002. Mollusc shell encrustation and bioerosion rates in a modern epeiric sea: taphonomy experiments in the Java Sea, Indonesia. Palaios 17:171–191.

Loranger, D. M. 1965. Devonian paleoecology of northeastern Alberta. Journal of Sedimentary Petrology 35:818–837.

McKinney, F. K. 1996. Encrusting organisms on co-occurring disarticulated valves of two marine bivalves: comparison of living assemblages and skeletal residues. Paleobiology 4:543–567.

Messina, C., and M. LaBarbera. 2004. Hydrodynamic behavior of brachiopod shells: experimental estimates and field observations. Palaios 19:441–450.

Moore, P. F. 1988. Devonian geohistory of the western interior of Canada. Devonian of the world: proceedings of the Second International Symposium of the Devonian System 1:67–83.

Nebelsick, J. H., B. Schmid, and M. Stachowitsch. 1997. The encrustation of fossil and recent sea-urchin tests: ecological and taphonomic significance. Lethaia 30:271–284.

Norris, A. W. 1963. Devonian stratigraphy of northeastern Alberta and northwestern Saskatchewan. Geological Survey of Canada, Memoir 313 168p.

Oldale, R. S., and R. J. Munday. 1994. Devonian Beaverhill Lake Group of the Western Canada

Sedimentary Basin. Pp.149–163 *in* Mossop, G. D., and I. Shetsen, comps., Geological Atlas of the Western Canada Sedimentary Basin. Canadian Society of Petroleum Geologists and Alberta Research Council, Calgary, Alberta.

Peters, S. E., and K. B. Bork. 1998. Secondary tiering on crinoids from the Waldron Shale (Silurian: Wendlockian) of Indiana. Journal of Paleontology 72:887–894.

Pitrat, C. W., and F. S. Rogers. 1978. *Spinocyrtina* and its epibionts in the Traverse group (Devonian) of Michigan. Journal of Paleontology 52:1315–1324.

Richards, R. P. 1972. Autecology of Richmondian brachiopods (Late Ordovician of Indiana and Ohio). Journal of Paleontology 46:386–405.

Rodland, D. L., M. Kowalewski, M. Carroll, and M. G. Simões. 2004. Colonization of a 'Lost World': encrustation patterns in modern subtropical brachiopod assemblages. Palaios 19:381–395.

——— 2006. The temporal resolution of sclerobiont assemblages: are they ecological snapshots or overexposures? Journal of Geology 114:313–324.

Rudwick, M. J. S. 1970. Living and fossil brachiopods. Hutchison, London.

Sando, W. J. 1984. Significance of epibionts on horn corals from the Chainman Shale (Upper Mississippian) of Utah. Journal of Paleontology 58:185–196.

Schneider, C. L. 2003. Hitchiking on Pennsylvanian echinoids: epibionts on *Archaeocidaris*. Palaios 18:435–444.

——— 2013. Epibiosis across the Late Devonian biotic crisis: a review. Proceedings of the Geologists' Association 124:893–909.

Schneider, C. L., and L. R. Leighton. 2010. Epizoans and predation traces of Devonian Hay River Formation brachiopods: indicators of complex ecosystems and ties to the Iowa Basin. GeoCanada 2010 – Working with the Earth, Conference Abstracts.

Schneider, C. L., and M. Grobe. 2013. Regional cross-sections of Devonian stratigraphy in Northeastern Alberta (NTS 74D, E). Alberta Energy Regulator, AER/AGS Open File Report 2013-05:25p.

Schneider, C. L., M. Grobe, L. R. Leighton, and T. Hauck. 2013a. From subsurface to outcrop: the Devonian Moberly Member (Waterways Formation) of the Athabasca Oil Sands region. GeoConvention 2013: Investigation, Conference Abstracts.

Schneider, C. L., T. Hauck, M. Grobe. 2013b (in press). Sequence Stratrigraphy and architecture of the Beaverhill Lake Sequence, Western Canada Sedimentary Basin: the influences of changing sedimentological and climatological regimes. SEPM Special Publication: Deposits, Architecture and Controls of Carbonate Margin, Slope, and Basin Systems.

Schneider, C. L., M. Grobe, L. R. Leighton, T. E. Hauck, and F. Forcino. 2013c (in press). Outcrops of the Moberly Member, Waterways Formation, north of Fort McMurray on the Athabasca River (NTS 74D/14, 74E/3, and 74E/4). Alberta Energy Regulator, AER/AGS.

Sparks, D. K., R. D. Hoare, and R. V. Kesling. 1980. Epizoans on the Brachiopod *Paraspirifer bownockeri* (Stewart) from the middle Devonian of Ohio. Papers on Paleontology 23:1–108.

Stoakes, F. A., J. C. Wendte, and C. V. Campbell. 1992. Summary *in* Wendte, J. C., F. A. Stoakes, and C. V. Campbell, eds. Devonian – Early Mississippian Carbonates of the

Western Canadian Sedimentary Basin: a Sequence Stratigraphic Framework: Society for Sedimentary Geology Short Course 28:215–255.

Taylor, P. D., and M. A. Wilson. 2002. A new terminology for marine organisms inhabiting hard substrates. Palaios 17:522–525.

——— 2003. Palaeoecology and evolution of marine hard substrate communities. Earth-Science Reviews 62:1–103.

——— 2008. Morphology and affinities of hederelloid “bryozoans”. Virginia Museum of Natural History, Special Publication 15:301–309.

Thayer, C. W. 1974. Substrate specificity of Devonian epizoa. Journal of Paleontology 48:881–894.

Webb, A. E., and C. L. Schneider. 2013. Ecology of an encrusting fauna on *Desquamatia* (Atrypida, Brachiopoda) from Cedar Valley formation (Givetian, Devonian) of Iowa, USA. Palaeogeography, Palaeoclimatology, Palaeoecology 377:102–109.

Wendte, J. C. 1992. Cyclicity of Devonian strata in the Western Canada sedimentary basin. SEPM Short Course Notes 28:25–39.

Wendte, J. C., and T. Uyeno. 2005. Sequence stratigraphy and evolution of Middle to Upper Devonian Beaverhill Lake strata, south-central Alberta. Bulletin of Canadian Petroleum Geology 53:250–354.

Witzke, B. J., and P. H. Heckel. 1988. Paleoclimatic indicators and inferred Devonian paleolatitudes of Euramerica. Devonian of the World: Proceedings of the Second International Symposium of the Devonian System 1:49–63.

Zapalski, M. K. 2005. Paleoecology of Auloporida: an example from the Devonian of the Holy Cross Mts., Poland. Geobios 38:677–683.

Zatoń, A. M., and W. Krawczyński. 2011. Microconchid tubeworms across the Upper Frasnian – Lower Famennian interval in the Central Devonian Field, Russia. Palaeontology 54:1455–1473.

Zatoń, M., M. A. Wilson, and E. Zavar. 2011. Diverse sclerozoan assemblages encrusting large bivalve shells from the Callovian (Middle Jurassic) of southern Poland. Palaeogeography, Palaeoclimatology, Palaeoecology 307:232–244.

Table 3.1. Summary results of sclerobiont distributions based on the life orientation of the dorsibiconvex atrypide host. The number of brachiopods with encrustation of the dead zone are noted for each unit. Zone preference was calculated using a 2x2 chi-square test comparing the frequency of sclerobionts in the shaded vs. exposed zones based on the proportional surface area of each zone.

Sample Unit	**# Dead Brachiopods**	**Zone Preference**
Firebag Sample 1	7/25	None
Firebag Sample 2	0/25	Shaded ($p < 0.01$)
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

Table 3.2. Abundances of each sclerobiont taxon from all six of the sampled units. Brachiopods which had encrustation within the dead zone were conservatively considered dead at the time of any encrustation, including those sclerobionts which were on a 'dead' brachiopod, but did not fall within the dead zone. The number of sclerobionts on dead brachiopods were reported under the rows "Dead (overall)".

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

Figure 3.1. A typical encrusted dorsibiconvex atrypide brachiopod from the Waterways Formation and its probable life orientation. (A) Dorsal view; (B) lateral view; (C) ventral view; and (D) probable life orientation, and illustrated with dead, shaded and exposed zones, which are biologically significant areas for encrustation of the brachiopod. Because the brachiopod must have remained attached to the substrate via a pedicle, the dead zone indicates a zone of encrustation which could only occur after the death of the brachiopod, decay of the pedicle, and subsequent transport, resulting in exposure of the dead zone to sclerobionts.

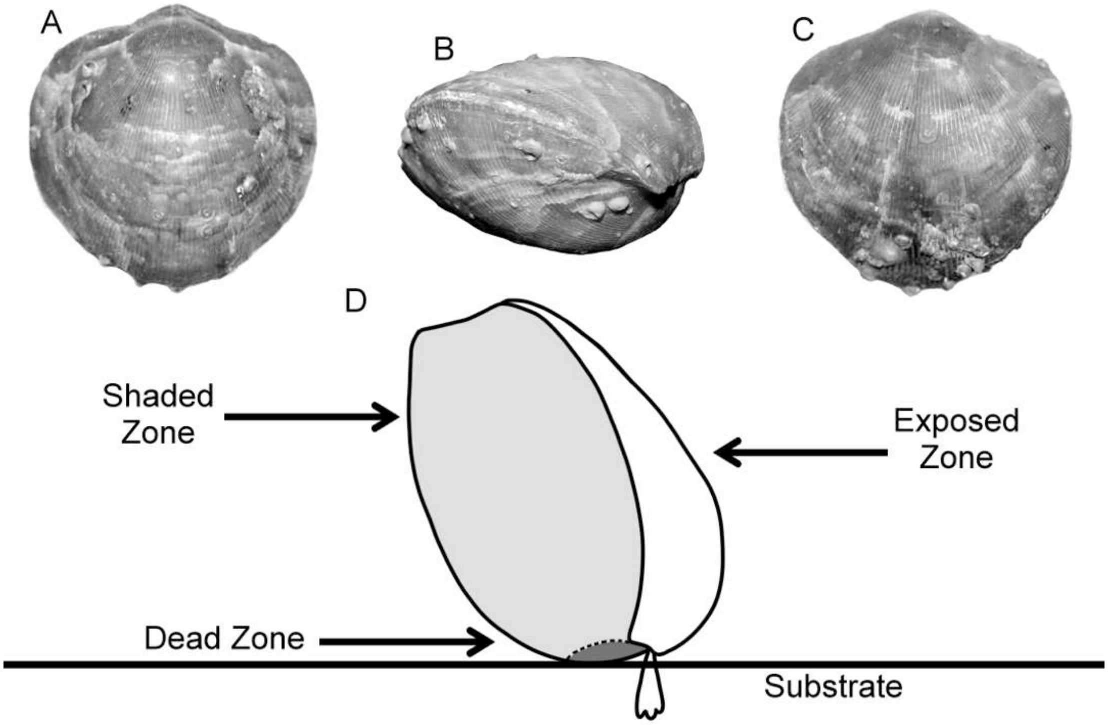


Figure 3.2. Composite stratigraphy of outcrops of the Waterways Formation along the Athabasca River near Fort McMurray, Alberta, Canada. The Givetian – Frasnian boundary is placed at the boundary between the Firebag and Calumet Members (Braun et al. 1988). The left column depicts the Waterways Formation 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; Fig. 2 of Schneider et al. 2013c).

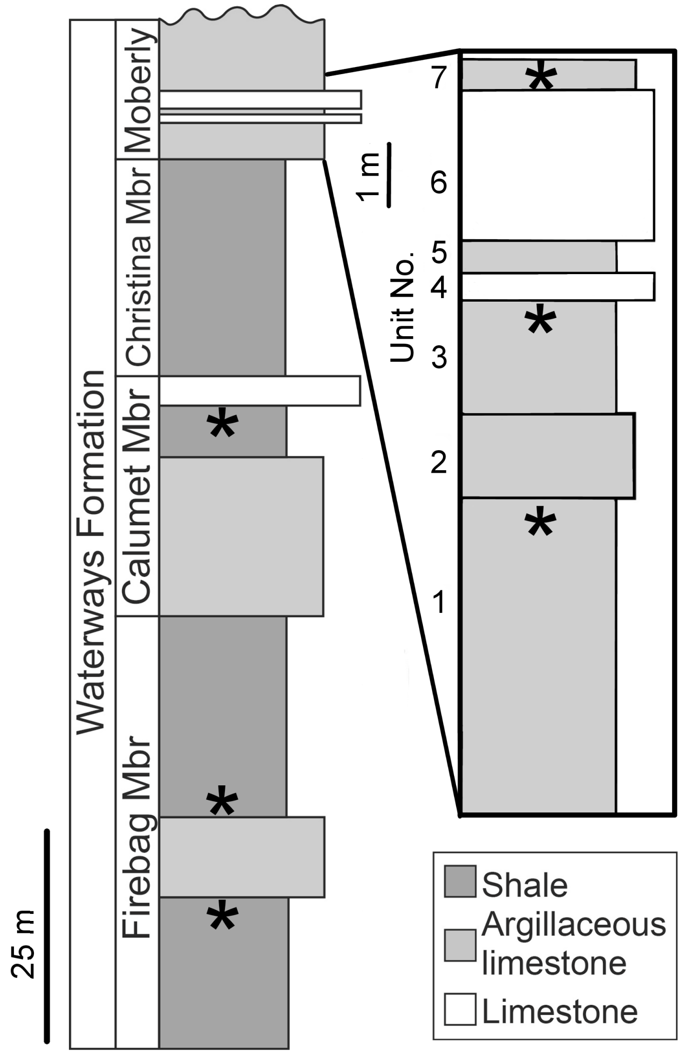


Figure 3.3. Palaeogeography of North America during the Givetian – Frasnian with an enlarged inset of the study area. Fort McMurray is indicated by a black star. Present-day geography has been inserted for reference, with Devonian land masses indicated in dark grey. The palaeoequator lies in northern Canada and is indicated by a solid black line (modified from Fig. 1 of Day 1998; Barclay et al. 2013).

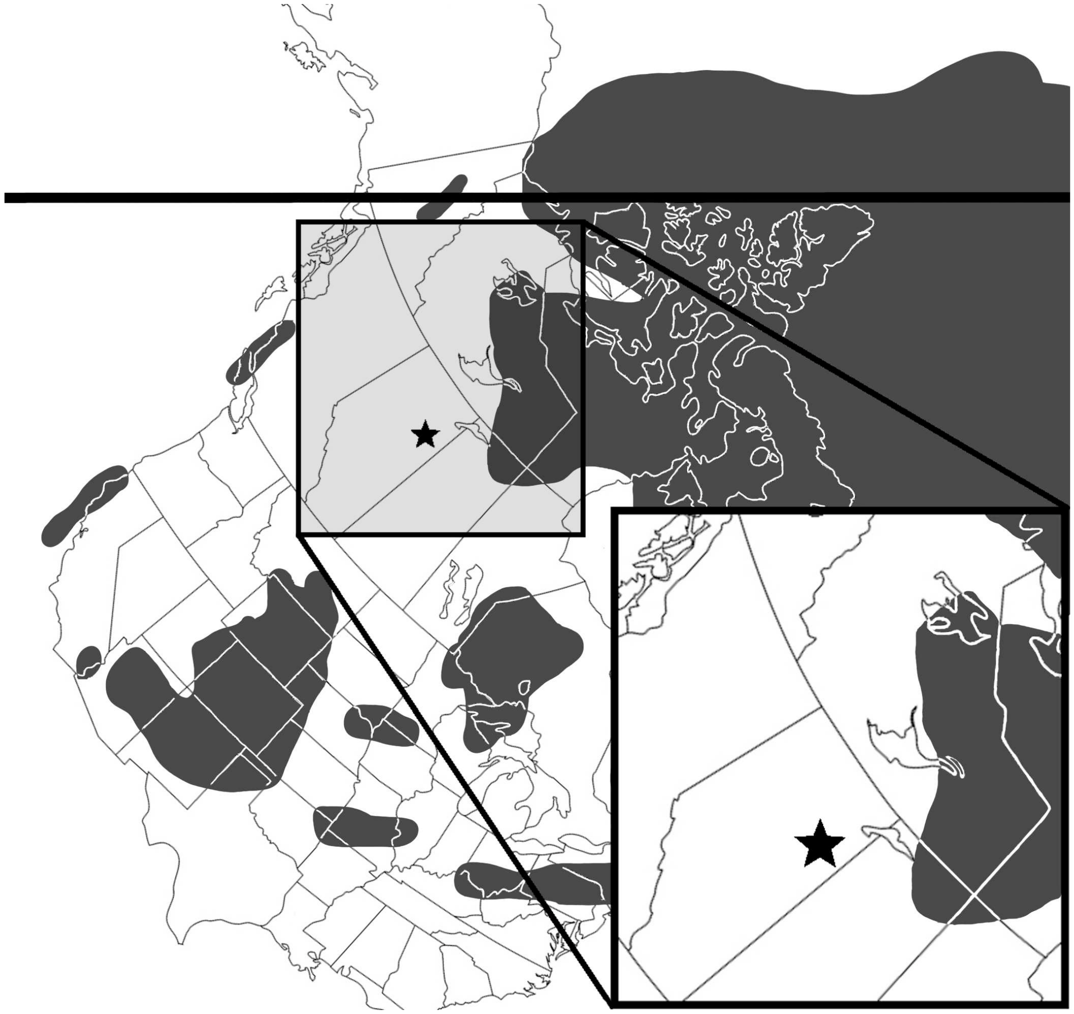


Figure 3.4. Illustration of the sclerobiont mapping process. (A) Two photos are taken of each brachiopod specimen (dorsal and ventral views). Here, the dorsal view is shown. (B) The brachiopod's outline, and the outline of each sclerobiont is mapped onto the photograph. (C, D, E) Each brachiopod is mapped, and the mapped images are scaled and stacked on top of one another until there is an image with 25 maps.

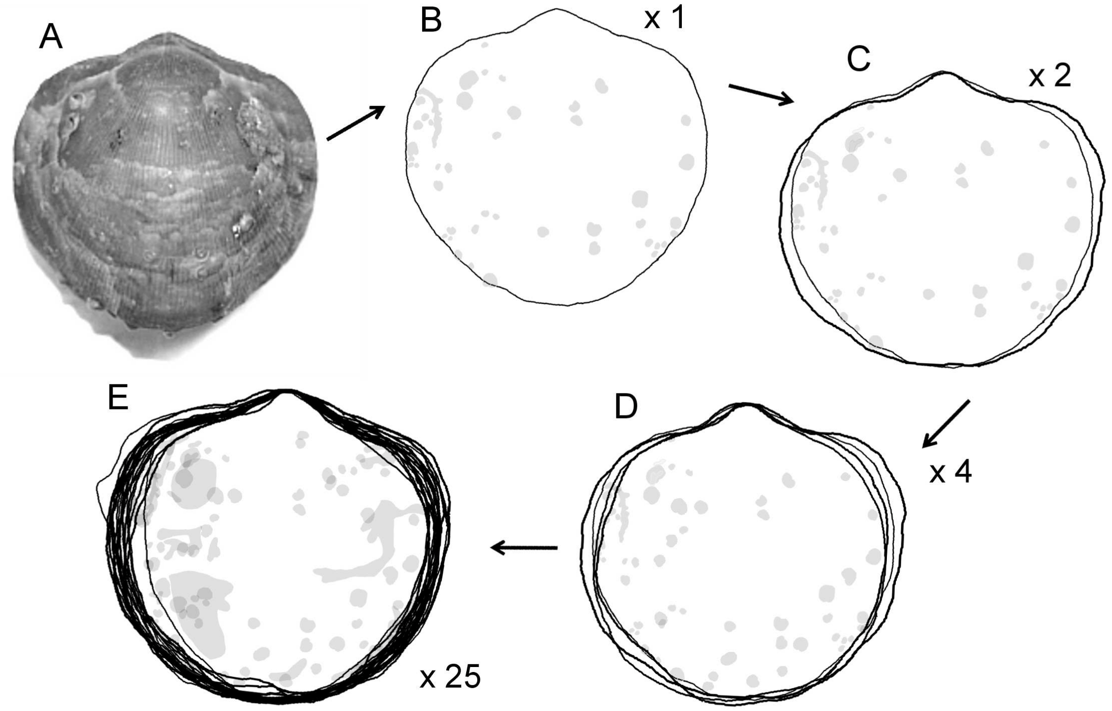


Figure 3.5. Stacked sclerobiont maps for each of the six sampled units. Sclerobionts were lightly shaded so as to produce a type of "heat map" in which darker shading indicates greater occurrences of sclerobionts in any given area. Columns 1 and 3 (left to right) are dorsal valve maps, and columns 2 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 dead 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.

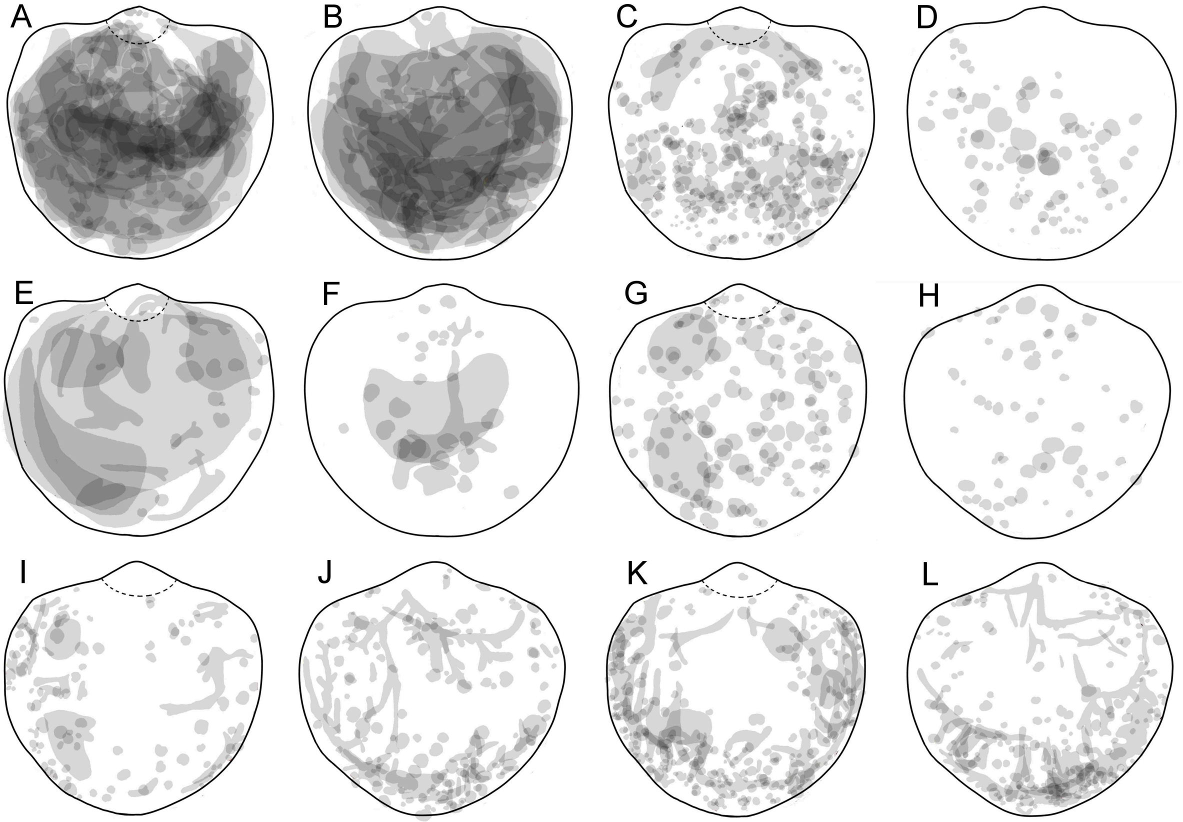
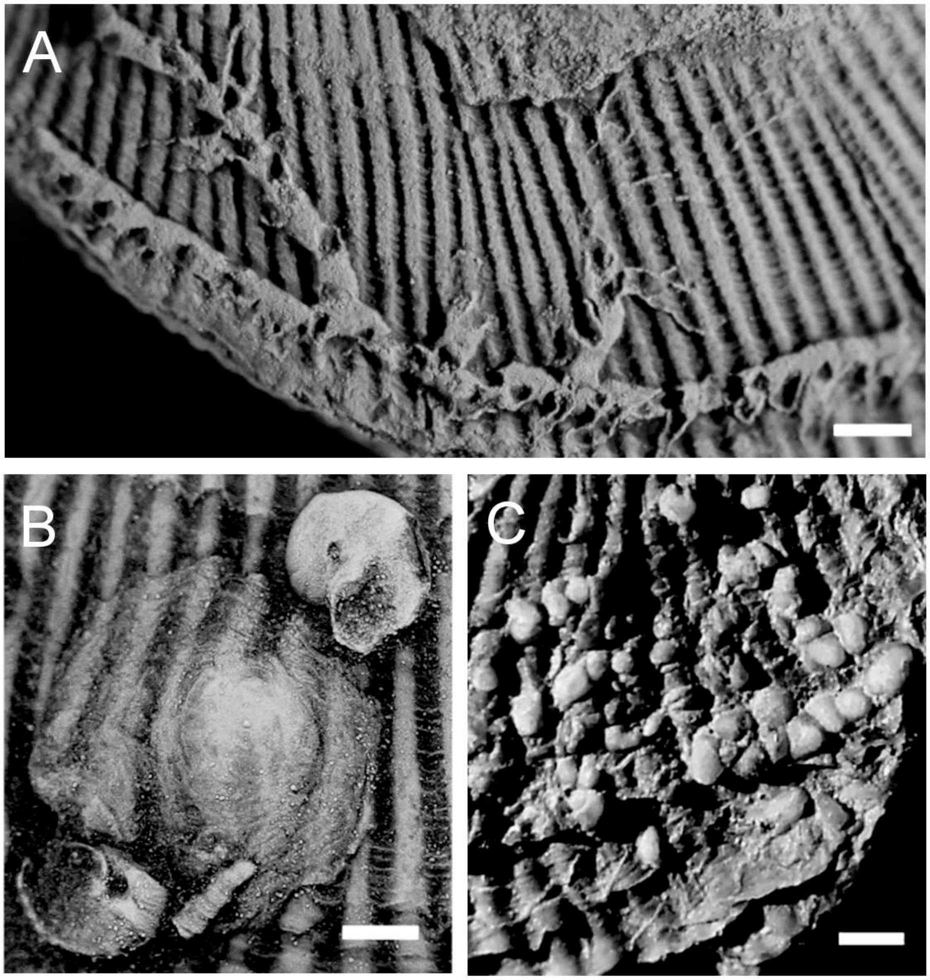


Figure 3.6. Representative specimens of sclerobiont taxa from the Waterways Formation. (A) *Hederella*; (B) a craniid brachiopod (middle) with two *Microconchus*; and (C) *Ascodictyon*.



Chapter 4. Conclusions

Sclerobionts and their hosts provide a great wealth of information that can be used to assess palaeoenvironmental conditions as well as biological interactions between sclerobionts and their hosts. However, such interpretations must assume that both the life status and orientation of the host is known. Any inference of the host's biology based on the position of sclerobionts on that host is circular, as the biological significance of sclerobiont placement on the host is dependent on how the host was positioned in life (i.e., shaded an exposed areas of the host). During the Devonian, dorsibiconvex atrypide brachiopods are one of the most abundant and commonly encrusted host organisms, yet their life orientation is poorly understood. The goal of this thesis was to devise an independent means of assessing the life orientation of these brachiopod hosts in order to refine our understanding of sclerobiont positions on these hosts. There are several important conclusions to this research:

(1) The use of realistic models in biomechanical studies allows more precise interpretation of the biology of dorsibiconvex brachiopods, and can be easily applied to functional studies of most other fossil organisms.

(2) Biomechanical tests on dorsibiconvex atrypides reveal that these brachiopods most likely retained a pedicle throughout their lives, and would therefore have rested with the posterior portion of the dorsal valve and the ventral umbo/pedicle foramen against the substrate surface.

(3) Independent evidence of a host's life orientation can be used to assess the biological significance of sclerobiont placement on the host. By mapping the outline of sclerobionts directly onto an image of the host, a detailed and biologically meaningful map of

sclerobiont distributions across hosts can be created. This method provides a biologically meaningful platform that can be used for other host organisms. As an example, dorsibiconvex atrypide hosts were divided into three zones (dead, shaded, and exposed) that might indicate a biological significance to sclerobiont location on the host. Most importantly, any area of the host that would have rested against the substrate during the host's lifetime could only become available to sclerobionts after the host had died and been transported out of its life position. Additionally, sclerobiont preferences for a location on the host can be interpreted biologically, such as preferences for areas of the host that would have been adjacent to the substrate (shaded), or exposed areas that would have been higher in the water column.

(4) Distinction of a dead zone provides a clear method for distinguishing the amount of post-mortem host encrustation. Minimally, those host specimens that are encrusted post-mortem can be removed from any analysis of sclerobiont-host relationships. Furthermore, the amount of post-mortem encrustation reveals which assemblages may be more or less reliable for both palaeoenvironmental and sclerobiont-host studies; those assemblages which have greater rates of post-mortem encrustation may indicate a greater amount of time-averaging whereas those assemblages that have few or no hosts encrusted post-mortem may indicate a true live assemblage that would provide more accurate palaeoenvironmental and palaeoecological information.

(5) From the brachiopod assemblages studied, there is no consistent sclerobiont preference for any one location on the brachiopod hosts. This suggests that sclerobiont biology is much more complex than is usually assumed, and that great care should be taken

to examine sclerobionts – host assemblages at the highest resolution possible. Overall assumptions of sclerobiont preferences or trends should be examined with great scrutiny.

In closing, this project refined our understanding of biology of both atrypide brachiopods and their sclerobionts. Additionally, the methods designed here can provide a foundation for future researcher examining either the functional behaviour of fossil organisms or the biological/palaeoenvironmental significance of sclerobiont distributions on biotic substrates.