Devonian stromatoporoid interactions at the Falls of the Ohio State Park, Clarksville, Indiana

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Devonian stromatoporoid interactions at the Falls of the Ohio State Park, Clarksville, Indiana

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Thesis Submitted in Partial Fulfillment of Requirements for the Honors Program and for the Degree of Bachelor of Science

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Bellarmine University

Spring 2018
Acknowledgments

I am extremely grateful to my advisor, Dr. Bulinski, who has been so helpful and supportive throughout this process. She has enabled me to achieve my full potential, which I believe is reflected in this thesis.

Thank you also to my readers, Dr. Carlson Mazur and Dr. Challener, who have spent time editing my paper and helping me develop my thesis presentation.

I also want to acknowledge the other students involved in this research project who helped collect data and gave me new directions in which to develop my own research. Thank you, Tonya, Kendra, Alma, Zoe, and Aspen.

Lastly, I could not have finished this project without the support of my parents, Buford and Debby Hall.

Thank you!
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1. Abstract

Stromatoporoids are calcitic sponges that occurred in the fossil record from the Early Ordovician to Late Devonian period. These sponges show evidence of interaction with other organisms, especially rugose and tabulate corals. Some corals appear to benefit from the rigidity of stromatoporoids in response to turbulent marine conditions. Stromatoporoids and many corals went extinct during the Frasnian-Famennian crisis when paleoenvironmental parameters were shifting. However, factors leading up to the extinction are not well understood. For this reason, studying the relationships between these taxa may provide insight to their vulnerability during the extinction.

This research was performed at the Falls of the Ohio in the Coral Zone of the Jeffersonville Limestone, a biostrome of exposed Devonian-age fossils located in Clarksville, Indiana. Even though this is an important paleontological site that contains several hundred species of coral, no peer-reviewed paleoecological studies have been conducted here in more than fifty years. Organisms in the Coral Zone were studied using transect sampling along a portion of the bedding plane. Each fossil along the 81 meters of transect line was identified, measured, and if the fossil was elongate, a compass bearing was recorded. Stromatoporoid-coral interactions were also documented. The data were then analyzed in Excel and tables were created to summarize fossil occurrences and interactions.

Stromatoporoids accounted for 72.9% of the biomass of fossils identified, demonstrating their overwhelming dominance in the biostrome. They most commonly interacted with small rugose corals. A meta-analysis using scientific literature was also performed to compare results from the Falls of the Ohio to other Devonian systems across the world. Tabulate corals were the most common interaction, followed by rugose corals. Delicate corals were likely protected by the
rigid stromatoporoid skeleton, but endobionts also competed with their host for food and slowed its growth. For this reason, both commensal and parasitic relationships between stromatoporoids and corals are possible. By studying interactions between these organisms, their life processes, paleoecology, and vulnerability to the Frasnian-Famennian extinction can be better understood.

2. Introduction

Stromatoporoids are extinct sponges that persisted from the Early Ordovician to Late Devonian period, about 360-480 million years ago (Rigby 1987; Stock 2005; Kershaw 2013). During the Devonian period, they became more abundant and diverse contributed to reefal and biostromal frameworks with their rigid calcitic skeleton. Morphology indicates that stromatoporoids formed in warm temperatures, low latitudes, and shallow waters where turbulent conditions were common (Stock 2005). Stromatoporoid specimens around the world encrusted other organisms including rugose and tabulate corals (Kershaw 2013). These interactions were also evident in the Devonian field area at the Falls of the Ohio, Clarksville, Indiana.

In the Late Devonian period, many environmental conditions were changing. Ocean chemistry shifted from calcitic to aragonitic, atmospheric carbon dioxide levels fluctuated, global temperatures dropped, sea levels fell, and developing forests added new nutrients to the water (Copper 2011). It is hypothesized that a combination of these conditions led up to the Frasnian-Famennian extinction, around 375 million years ago (Stock 2005; Copper 2011). Many organisms including corals, brachiopods, conodonts, and trilobites disappeared at this time. Stromatoporoids went completely extinct (Stock 2005). Since these sponges frequently interacted with other fauna, it is possible that the loss of stromatoporoids influenced extinction of other organisms.
Even though stromatoporoids have been the focus of numerous studies, their interactions with other organisms have not been thoroughly analyzed, especially at the Falls of the Ohio. The purpose of this study is to bring together decades of paleontological studies on Devonian stromatoporoids, through a survey of scientific literature and online databases, and to identify the most prominent interactions. These global studies will also be compared to Devonian specimens found in a recent field study from the Falls of the Ohio biostrome. Analysis of these data will contribute to a better understanding of the kinds of organisms that interacted with stromatoporoids and whether relationships were mutual, commensal, parasitic, or some combination thereof. By examining these interactions, the life processes and paleoecology of corals and stromatoporoids can be better understood. By learning more about paleoecology, stromatoporoid interactions can also shed light on the vulnerability of Paleozoic fauna during the Frasnian-Famennian extinction.

3. Literature Review

a. Classifying Reefs

In the modern world, studying reefs is important in understanding earth processes such as climate change. Investigating ancient reefs is also important because marine organisms preserved in the fossil record provide a look at ecological conditions occurring millions of years ago (Pandolfi 2011). This can help scientists today understand how modern reefs might respond to changes in the environment. However, reef classification has been a topic of debate in scientific literature. This creates discrepancies in studies that refer to the same place using different terms. At the Falls of the Ohio, for example, some researchers refer to it as a “reef” while others use the term “biostrome.”
“Reef” are rigid, three-dimensional, wave-resistant structures shaped by living organisms and inorganic sediments (Cumings 1932; Wood 1999; Hubbard et al. 2001). Reefs form underwater ecosystems that contain large amounts of biomass and biodiversity of marine organisms. These formations are regulated by biotic and abiotic aquatic factors including waves, turbidity, light availability, and water chemistry. In general, reefs form in tropical latitudes between 30°N and 30°S but ranges have expanded and contracted throughout geologic time (Pandolfi 2011). Ancient reefs initially diversified and expanded in the Early Ordovician period and were dominated by calcitic invertebrates including cnidarians, sponges, and bryozoans (Wood 1999). Modern reefs are largely composed of corals and algae that grow by photosynthesis (Wood 1999).

“Bioherm” is another classification that has been equated with the term “reef” (Kershaw 1994). This terminology was developed to more clearly define reefs by identifying their external and internal structures (Kershaw 1994). Bioherms are made up of living organisms that accumulate vertically to form three-dimensional, moundlike frameworks (Fig. 1; Kershaw 1994).

“Biostromes” are also composed of living organisms but expand horizontally rather than vertically. These systems are structured more two-dimensionally than bioherms, and form layers or beds (Fig. 1; Cumings 1932). Most biostromes are calcareous and skeletal-dominated. Since they are typically interbedded and buried with sediment, they are less distinguishable than bioherms, which more clearly appear on the surfaces of rock formations (Kershaw 1994).
Paleoenvironmental conditions of biostrome environments are understudied, but specific cases provide possible answers. A Silurian biostrome in Gotland, Sweden formed on a flat sea floor with low sedimentation and stable sea levels. The system was stromatoporoid-dominated but was eroded by turbulent waters and storms (Sandstrom and Kershaw 2002). In contrast, a Devonian biostrome in California was largely composed of stromatoporoids and formed in shallow, muddy conditions where rapid sedimentation was periodic (Suek 1975). Kissling and Lineback (1967) classified the Falls of the Ohio as a biostrome and determined it formed in shallow waters under gentle currents and low turbulence. The thin, laminar beds lacking three-dimensional structure also support the biostrome classification (Cumings 1932; Hendricks et al. 2005).

b. Stromatoporoids

i. Taxonomy

In many biostromes, like at the Falls of the Ohio, stromatoporoids are prevalent (Kershaw 1998). These sponges are classified in Kingdom Animalia, Phylum Porifera, and Class Stromatoporoidea (Kershaw and Brunton 1999). Stearn et al. (1999) identified seven orders including Labechiida, Clathrodictyida, Actinostomatida, Stromatoporellida, Stromatoporoida, Syringostomatida, and Amphiporida. Over 100 genera have been named throughout the history of studying stromatoporoids (Stock 2001).

Variations in stromatoporoid morphology make it difficult to identify genus and species, especially without the ability to remove the organism from the fossil bed. Two thin sections of a sample are required for reliable identification (Kershaw 2013). Thin sections are slices of a specimen that are thin enough to be observed under a microscope. For this reason, genus and
species of stromatoporoids in this study were not identified. However, previous studies at the Falls of the Ohio identified *Amphipora ramosa* in the upper fossil beds (Hendricks et al. 2005).

**ii. Morphology**

Even though it is difficult to identify taxonomy because of variations in morphology, stromatoporoids did have common features. They were ancient sponges made up of calcite, a form of calcium carbonate (Kershaw 2013). These sponges were sessile and benthic, meaning they were immobile and attached to the sea floor. They did not have the spicules that are characteristic of modern sponges, and they ate by suspension feeding (Kershaw 2013).

Their calcitic skeleton is called a *coenosteum*. Stromatoporoid surfaces were smooth or covered with small bumps called *mamelons* (Fig 2; Rigby 1987). On top of mamelons, *astrorhizae* discharged water from the surface. *Laminae* were smooth fingerprint-like patterns that expanded as bands of growth (Fig 2; Kershaw and Brunton 1999). These are thought to reflect environmental changes including tides, seasons, climate, or food sources (Rigby 1987). A group of laminae made up a *latilamina*. *Galleries* were spaces between laminae while *pillars* were perpendicular to laminae (Fig. 2; Rigby 1987).
Growth formations have been classified as low or high profile *dendroid, laminar, domical, tabular,* and *bulbous* based on vertical height, basal diameter, width, and qualitative observations. These different growth patterns created stability of the organism and contributed to reef, bioherm, or biostromate structures (Kershaw 1984). Other researchers use more generalized terminology to describe forms including *encrusting, branching, mat,* and *mound* shapes (Greb et al. 1993).

Stromatoporoids exhibited these different forms based on a combination of genetic and environmental conditions. Some species conformed to a specific growth pattern in response to accessible nutrients, sedimentation, available space, and water conditions (Kershaw 1984). Therefore, it is possible to reconstruct paleoenvironmental conditions by inferring environmental parameters based on growth structure. For example, *Amphipora* stromatoporoids of the Devonian period were branching forms. Their delicate morphology could not have tolerated turbulent water conditions, so they most likely lived in lagoons. Paleontologists studying *Amphipora* can infer their environment was low in wave energy (Stearn 1982).

The branching *Amphipora ramosa* is found in the upper beds of the Falls of the Ohio as well. Other stromatoporoid forms found here are mat and mound shapes that likely bound

![Figure 3. A stromatoporoid at the Falls of the Ohio. It resembles a “cow patty” due to crusty silicification (photo by M.S. Hall).](image)
sediments in the biostrome. Their encrusting habits and large biomass contributed to the biostrome structure (Hendricks et al. 2005). At these Devonian fossil beds, stromatoporoids can be identified by their resemblance to “cow patties.” They are silicified and covered in crusty brown rock (Fig. 3; Greb et al. 1993).

iii. Interactions

1. Classifying Interactions

Stromatoporoids were known to interact with a variety of organisms, whether by encrusting other organisms or by hosting endobionts that were embedded in the surface of the sponge (Fig. 4; Kershaw 2013). The most common intergrowths found within stromatoporoids were rugose corals, tabulate corals, and tube fossils that are suspected worms (Kershaw 2013). By studying their relationships, life processes of these organisms can be better comprehended.

However, the relationships between stromatoporoids and the organisms that dwelled inside them are not fully understood. Sometimes, the method of interaction was unclear. The sponge may have encrusted the other organism (Fig. 4), or the other organism may have settled into the sponge. Most stromatoporoids with endobionts embedded in the surface had distinct laminae shaped around the encrusted organism, but this would have happened in either interaction (Tapanila 2005). If the sponge grew over the organism, its

Figure 4. Stromatoporoids often encrusted other organisms. Growth bands seen on the surface and surrounding endobionts can indicate if the sponge was negatively affected by interacting organisms (Greb et al. 1993).
laminae would change shape around the organism. If the organism settled into the host, the stromatoporoid skeleton would still be altered around the animal (Tapanila 2005).

When endobionts settled into the host’s skeleton, *bioclaustrations* were formed. These small holes have been used to measure the interactions or associations between ancient and modern organisms (Tapanila 2005). Bioclaustrations were first observed in the Late Ordovician period in corals, bryozoans, and crinoids. Throughout the Silurian and Devonian, they increased in number and were found in a wider variety of organisms including stromatoporoids, chaetetid sponges, and brachiopods (Tapanila 2005). These interactions, especially between corals and stromatoporoids, started to decline in the Middle Devonian until the the Frasnian-Famennian extinction (Tapanila 2005).

*Caunopores* are an example of bioclaustrations. These were specific intergrowths of the tabulate coral *Syringopora* within a stromatoporoid (Tapanila 2005; Taylor 2015). Caunopore associations have been noted at the Falls of the Ohio in Kissling and Lineback (1967). A commensal relationship, where one organism benefits while the other is neutrally affected, is possible here. The fragile branches of the *Syringopora* coral were protected by the rigid stromatoporoid with little effect on sponge’s growth (Kissling and Lineback 1967; Kershaw 1998).

Parasitic relationships, in contrast, negatively affect one organism while benefitting the other. These interactions are recognized by changes in size, growth rate, or morphology of the host organism. Growth bands would be smaller if growth was slowed (Taylor 2015). In a Middle Devonian system in France, a tubeworm embedded in a stromatoporoid apparently slowed the growth rate of its host. The sponge’s growth bands were bent down around the tubeworm,
indicating a slowed growth pattern. Access to food sources and a more stable habitat may have benefitted the parasite while harming its host (Zapalski and Hubert 2011).

Similarly, worm-stromatoporoid interactions found in a Late Silurian biostrome in Estonia may have benefitted the worm with negative consequences to the sponge. The endobionts were possibly protected from predators and gained a platform that benefitted their suspension feeding and reduced feeding efficiency of their host (Vinn and Motus 2014). Especially when stromatoporoids were already experiencing harmful effects due to changing environmental conditions, it is possible that parasites would have further worsened their ability to survive these conditions.

2. Rugose Corals

One of the most frequent organisms that stromatoporoids encrusted or hosted in their skeletons were rugose corals. These corals are classified under Phylum Cnidaria and Class Anthozoa (Taylor and Lewis 2005). Rugosa appeared in the fossil record from the Middle Ordovician to the Late Permian period. These corals had morphology similar to the modern Scleractinia and have been misidentified as such but they are actually not closely related (Taylor and Lewis 2005). Rugosa were calcitic while Scleractinia are aragonitic. Septa, which are skeletal plates circularly radiating inside the coral’s wall (Fig. 5), are arranged differently and are therefore used to differentiate the two orders. Rugose corals were bilaterally symmetrical while scleractinian corals are radially symmetrical (Oliver and Coates 1987).

Rugosa commonly had a distinctive horn shape that is thought to be related to water energy, as bends in the skeleton would have stabilized against turbulent conditions (Scrutton 1999). Genera of rugose corals were about two-thirds solitary and one-third colonial (Fig. 6).
Solitary species had diameters up to 14 cm, while colonial species had diameters up to 400 cm (Oliver and Coates 1987). Colonial corals had individual corallites. The external wall of both solitary and colonial corals is called the epitheca (Fig. 5; Scrutton 1999).

![Figure 5](image)

**Figure 5. Three examples of Paleozoic corals and their anatomy.** A) A solitary rugose coral, *Heterophrentis*, that contained septa and an epitheca. B) A colonial rugose coral, *Eridophyllum*. It had septa, epitheca, and individual corallites. C) A tabulate coral, *Favosites*. The individual corallites were inside the epitheca wall. There were no septa (modified from Greb et al. 1993).

3. Tabulate Corals

Stromatoporoids also frequently interacted with tabulate corals. Tabulata have been recorded from the Early Ordovician to Late Permian period. These corals were calcitic, monophyletic, and radially symmetrical (Scrutton 1999). They lacked septa unlike rugose corals. Species were colonial (Fig. 6) and they contained corallites and epitheca (Fig. 5; Scrutton 1999).
Like stromatoporoids, Tabulata have been documented encrusting other organisms. Morphological terms are similar to stromatoporoid terminology as colonies can be described as massive, laminar, tabular, domical, and bulbous (Scrutton 1999). Examples of common tabulate corals include *Halysites, Heliolites, Favosites,* and *Syringopora* (Taylor and Lewis 2005).

iv. Paleoecology

1. Rugose and Tabulate Corals

Paleozoic corals thrived in shallow-water bioherms and biostromes around mid-low latitudes and occasionally higher latitudes (Scrutton 1999). Solitary corals often lived freely and unattached to surfaces while colonial corals sometimes encrusted other organisms in their ecosystem. Corals were able to grow and spread rapidly on flat surfaces lacking sedimentation. High sedimentation rates sometimes buried corals but also created more stable substrate for colonies to grow on (Scrutton 1999). Corals also tended to be distributed endemically, meaning certain species were concentrated in specific areas. This is significant because corals can be used...
to reconstruct geography of the Devonian period based on where they are found today (Oliver and Coates 1987).

However, reconstructing the exact paleoecological role of the Rugosa and Tabulata is sometimes difficult because it is unknown whether they contained zooxanthellae. Zooxanthellae are photosynthetic algae that grow symbiotically with modern corals. Coral metabolism rates are increased when this symbiotic relationship is present (Oliver and Coates 1987).

There is evidence that Paleozoic corals likely did not have the algae because they exhibited slow growth rates of about 10 millimeters per year (Taylor and Lewis 2005). In comparison, modern corals with zooxanthellae can grow up to 100 millimeters per year (Taylor and Lewis 2005). Also, little difference has been found in growth rates between Paleozoic corals that grew in shallow waters versus deeper waters, indicating that photosynthesis did not influence their growth (Taylor and Lewis 2005). On the other hand, the pattern of growth bands and large sizes of some corals suggest they did adapt to light. This could indicate zooxanthellae symbiosis, but the exact relationship is still unknown (Stanley 2001).

2. Stromatoporoids

Similar to Paleozoic corals, stromatoporoids had an affinity for subtropical and tropical latitudes. Warm temperatures were needed to secrete their calcium carbonate skeletons (Stock 2005). The majority of stromatoporoids inhabited carbonate banks and skeletal-dominated reefs or biostromes (Kershaw and Brunton 1999). Unlike modern sponges of similar growth form, stromatoporoids were tolerant of fine-grained sediment. This is supported because they grew on a wide range of substrate compositions, from skeletal debris to fine particles of mud (Kershaw 1998).
Stromatoporoids also occupied shallow seas where turbulent water conditions and tropical storms were frequent. These conditions were erosive to the sponges, often breaking them apart and causing fragments to appear in areas where they did not originally form (Kershaw and Brunton 1999). When faced with changing environmental conditions such as falling sea levels, this shallow environment could have been disadvantageous to stromatoporoid communities by further exposing them to unfavorable conditions (Kershaw 1998).

v. Extinction

During the Frasnian-Famennian extinction at the end of the Devonian period, many corals and most stromatoporoids died off. It appeared that smaller dendroid stromatoporoids were most affected by the crisis whereas mounded and flat forms were less vulnerable (Copper 1994). Some sponges recovered during the Famennian age in the form of small patch reefs (Copper 2011; Morrow et al. 2011). Specifically, Order Labechiida recovered until stromatoporoids went entirely extinct at the end of the Famennian age (Stock 2005). In general, stromatoporoids diversified in the Early Ordovician period and disappeared at the end of the Devonian period (Fig. 7).

Figure 7. Stromatoporoid diversity leading up to the Frasnian-Famennian extinction. Genera increased until the end of the Devonian period. Data from the Paleobiology Database (PBDB) are voluntarily entered by researchers, so this only represents a portion of stromatoporoids that actually existed (graph generated by author using PBDB).
The Frasnian-Famennian extinction marked the end of “true” stromatoporoids according to Stock (2001). Some post-Devonian sponges have been called stromatoporoids but they are likely misidentified because they are polyphyletic and distinct in their morphology and paleoecology (Stock 2001).

d. Ancient Environmental Conditions

i. Rise and Fall of Skeletal-Dominated Reefs

Prior to the Frasnian-Famennian extinction, many environmental conditions were changing. Reefs shifted from large microbial-dominated systems to smaller skeletal-dominated reefs in the Middle-Late Ordovician period (Kiessling 2011). During this transition, skeletal organisms such as bryozoans and stromatoporoids diversified and caused reef ecosystems to expand. These taxa encrusted other organisms and the biological interactions contributed to new habitats that stimulated evolution of new organisms (Adachi et al. 2011). In the Devonian period especially, skeletal systems flourished in the form of coral-stromatoporoid reefs like the biostrome at the Falls of the Ohio (Joachimski et al. 2009).

The change in dominance of reef building organisms was important because these two types of reefs responded differently to environmental changes. In microbial reefs, calcification was non-enzymatic, meaning it was triggered by the microbes but not controlled by them. In skeletal reefs, calcification was enzymatic, meaning it was both triggered and controlled by the organisms (Kiessling 2011). Therefore, microbial systems could recover from chemical changes like ocean acidification once chemistry returned to a level where calcification could resume. In contrast, biota that were impacted by acidification in skeletal systems would take much longer to recover since these organisms controlled calcification (Kiessling 2011). This relates to the
Frasnian-Famennian extinction because skeletal reefs that fostered stromatoporoids and corals were more vulnerable to shifting environmental conditions and therefore required more time to recover. After the extinction, microbial-dominated reefs took over again (Joachimski et al. 2009).

ii. Shift in Geochemistry: Aragonite to Calcite

Since microbes and skeletal organisms absorbed and secreted different minerals, the shift in reef dominance correlated to changes in ocean chemistry (Kiessling 2011). Aragonite and calcite are two forms of calcium carbonate, differing in their crystal structure, secreted by marine life. These minerals develop under specific chemical and physical conditions. Aragonite forms in warm temperatures and in waters with high calcium carbonate concentrations, so this influences how aragonitic organisms form (Hallock 2001). Calcitic seas require high levels of atmospheric CO$_2$ that can be detrimental to the shells of aragonitic organisms (Stanley and Hardie 1998).

Oceans shifted from aragonite to calcite when microbial-dominated frameworks became skeletal-dominated in the Early Paleozoic (Fig. 8; Kiessling 2011). Reefs in this period were made up of calcitic rugose and tabulate corals as well as calcitic stromatoporoids. In general, these calcitic fossils are better preserved than aragonitic taxa because aragonite dissolves more easily in water, especially when calcium carbonate concentrations are lowered. In the later Paleozoic through the Mesozoic era, aragonitic conditions returned and reefs were again abundant with aragonitic sponges, scleractinian corals, and algae (Fig. 8; Stanley and Hardie 1998).

iii. Shift in Atmospheric CO$_2$, Climate, and Sea Levels

Changes in ocean chemistry were correlated with changes in atmospheric chemistry. Joachimski et al. (2009) suggests Early Devonian CO$_2$ levels were 2000 ppm and decreased to
900 ppm in the Middle Devonian. Since atmospheric gases trap heat from the sun, CO₂ levels also corresponded to changes in climate. Joachimski et al. (2009) calculated ancient sea surface temperatures (SSTs) based on oxygen isotope composition of apatite phosphate from conodont fossils. Late Silurian to Early Devonian periods were about 30-32°C in low latitudes where reefs were evolving. SSTs in the Early Devonian to Middle Devonian period decreased to about 22°C then increased again in the Late Devonian to 30-32°C (Joachimski et al. 2009).

This long phase of high global temperatures was classified as a greenhouse period (Fig. 8). Glaciation was minimal during this warm interval and kept seas at higher levels (Copper 2011). The end of the Devonian period marked the end of stromatoporoids when the earth was transitioning back to an icehouse period (Fig. 8). There was a return to widespread glaciation which lowered sea levels (Copper 2011). Stromatoporoids briefly returned as patch reefs during this time but disappeared again before the Carboniferous period (Copper 2011).
e. Frasnian-Famennian Extinction

True stromatoporoids went extinct at the end of the Devonian period during the Frasnian-Famennian extinction. Corals, brachiopods, conodonts, trilobites, and other organisms were also impacted by the extinction (Stock 2005). In total, 57% of genera went extinct (Wood 1999). More specifically, corals decreased by over 50%, brachiopods by 70%, and stromatoporoids by 72% between the Frasnian and Famennian ages (Copper 2001). Stromatoporoids were completely gone before the end of the Devonian period (Copper 2001).

Kiessling (2011) classified this period as a “reef crisis” rather than a “mass extinction.” The difference between the terms lies in their causes. Most reef crises corresponded with increasing CO₂ concentrations and global warming. These factors influenced chemical changes in the ocean and decreased carbonate production in reefs. Consequently, biomineralization of reefal organisms was affected, which likely contributed to their vulnerability and may have lead to a mass extinction. A “mass extinction,” is identified by high rates of extinction and could be caused by a reef crisis (Kiessling 2011).

There are many speculations about causes of the Frasnian-Famennian extinction. Shifting environmental conditions including sea level fluctuations, mountain building, glaciation, global cooling, global warming, ocean anoxia, meteor impact, and nutrient changes caused by developing forests have all been postulated as potential causes (Stock 2005; Copper 2011). Most likely, it was a mixture of multiple factors.

Joachimski et al. (2009) asserted that coral-stromatoporoid reefs probably had a low tolerance for high temperatures, which explains their vulnerability to rising sea surface
temperatures in the Late Devonian period. They claimed that short periods of cooling followed by global warming influenced the extinction of stromatoporoids in this time period.

Copper (2011) attributed the extinction to global cooling and glaciation in the Frasnian age. The Rheic Ocean, which separated two continents in the Paleozoic era, closed and changed ocean circulation. This event redistributed cold water and affected organisms intolerant of cold conditions. It is also possible that the expanding tropical rainforests heightened oxygen concentrations and increased rock weathering. Newly eroded nutrients flowing into the ocean may have changed water chemistry and made organisms more vulnerable to extinction (Copper 2011).

Stock (2005) considered a transcontinental barrier that disconnected two large marine habitats known as Eastern Americas Realm and the Old-World Realm. The barrier separated marine fauna in these habitats so that they grew and diversified separately. Once the sea level rose high enough in the late Givetian age, the two habitats conjoined and fauna mixed together. When sea levels fell again around the time of the Frasnian-Famennian extinction, stromatoporoids competed with new fauna in smaller spaces. Organisms were also exposed to even shallower seas, which provided less protection against temperature changes in this period of rapid global cooling. Though this is a speculation, it shows how a mixture of conditions such as changing ocean chemistry, fluctuating temperatures, and falling sea levels could have contributed to extinction of stromatoporoids and other Paleozoic fauna (Stock 2005).

Ancient reef systems were evidently affected by these changing environmental conditions that led up to the Frasnian-Famennian extinction. Organisms that were interacting within these ecosystems suffered as a result (Stock 2005; Copper 2011). Though they were directly affected by their environment, it is possible that the mutual, commensal, or parasitic relationships
between organisms also made them more vulnerable to the extinction (Kershaw 1998; Tapanila 2005). This hypothesis was explored by identifying and analyzing the types of interactions between stromatoporoids and other fauna at the Falls of the Ohio and in other Devonian systems across the world.

4. Field of Study

a. Falls of the Ohio

i. Modern Location

The Falls of the Ohio is a 220-acre area (DNR 2018) of exposed Devonian fossil beds ranging from 350 to 425 million years old (Greb et al. 1993) Located in Clarksville, Indiana, across from Louisville, Kentucky, the fossil beds extend from the banks of the Ohio River (Fig. 9). The fossils are submerged under water most of the year except for August-October when river levels are lowest.

Figure 9. Devonian fossil beds at the Falls of the Ohio State Park. These extend from the banks of the Ohio River (photo by M.S. Hall).
(DNR 2018). The “Falls” refer to the rapids in the river that presented an obstacle to well-known explorers including Lewis and Clark in the early 1800’s (Greb et al. 1993).

ii. Fossils

Over 600 species of fossils have been documented at the Falls of the Ohio. Stromatoporoids are just one of the many fossils found here. Other organisms include brachiopods, bivalves, trilobites, rugose corals, tabulate corals, gastropods, echinoderms, crinoids, and rostroconchs (Greb et al. 1993).

Solitary rugose corals at the Falls of the Ohio include the exceptionally large genus Siphonophrentis that has been documented at the Falls at over 120 cm long and 10 cm wide (Hendricks et al. 2005). Eridophyllum is a colonial rugose species also found at the Falls. Its corallites grew larger when facing south, possibly because water currents came from a southern direction and corals fed on organisms carried by the water (Hendricks et al. 2005). Other rugose corals common in the area include Heliophyllum, Prismatophyllum, Cystiphylloides, Tabulophyllum, and Acinophyllum (Greb et al. 1993).

Tabulate corals are also frequent in this location. A few species found here include Thamnopora (Hendricks et al. 2005), Favosites, Aulopora, Syringopora (Kissling and Lineback 1967), Emmonsia, Cladopora, Pleurodictyum, and Halysites (Greb et al. 1993).

Some taxa found in this study have not been previously documented in published work at the Falls of the Ohio. Future research should use systematics to confirm identifications.
iii. Paleogeography

During the Devonian period, the Falls of the Ohio was located at 41.1° South, 34.5° West (PBDBa). This means that it formed under subtropical conditions. However, fossils found today are not in the same location as they were millions of years ago. Plate tectonics and continental drift shifted land masses and seas over time (Greb et al. 1993). The Middle-Late Devonian period included huge floods that created shallow inland seas and provided new niches for organisms such as stromatoporoids to diversify (Copper 2011). The Falls location was an inland sea, which accounts for the diverse group of fossils found here today (Greb et al. 1993).

iv. Past Research

Research began at the Falls of the Ohio in 1820 when paleontologists C.S. Rafinesque and J. D. Clifford identified different species of corals. In the 1880’s, geologists James Hall and William J. Davis published illustrations and photographs of fossils found at the Falls (Greb et al. 1993). Throughout the first half of the 20th century, geologists and paleontologists continued to research fossils here (Greb et al. 1993).

In 1964, paleontologist Edward Stumm published a significant compilation of species identified at the Falls. At this point, nearly 600 different species had been documented but many were misidentified (Greb et al. 1993). Stumm confirmed over 400 specimens in his document, 30% of which were discovered for the first time in the world. Some of the original fossil specimens used for these identifications reside in museums and institutions today, including the University of Louisville, University of Kentucky, and national museums in the U.S., Canada, Germany, and France (Greb et al. 1993).
Kissling and Lineback (1967) described the Coral Zone of the Jeffersonville Limestone. This was the only peer-reviewed paleoecological study published on the Falls of the Ohio. Fossils larger than 4 cm were analyzed in terms of abundance, sizes, and compass bearings. These patterns of distribution were then used to interpret the paleoenvironment. Tabulate corals made up over 70% of the fauna and Favosites were especially abundant in this study. Tabulata and stromatoporoids were linearly distributed north-south while rugose corals were distributed more randomly. Sediments were brought in from the ocean rather than land and caused moderate turbidity (Kissling and Lineback 1967). They also concluded that an east-west tidal current was responsible for the orientations of the fossils studied.

For nearly fifty years, however, little research was performed at the Falls of the Ohio. Though there were some informal, unpublished studies, research has been lacking in peer-reviewed and published work. This study is an initiative to update research at the Falls through field work that will also lead to future studies. By focusing on stromatoporoids and their interactions at the Falls of the Ohio, this study will also contribute to understanding the role of these organisms in this ancient ecosystem.

b. The Jeffersonville Limestone

The Falls of the Ohio contains a Devonian bedrock layer called the Jeffersonville Limestone. This is made up of three facies, which are rock formations...
with distinct characteristics. These facies include a southern portion at the Falls of the Ohio, the Geneva Dolomite Member, and the Vernon Fork Member. At the Falls of the Ohio, 0-200 feet of Emsian and Eifelian (Early-Middle Devonian) aged rock is exposed. This portion is also divided into five biozones (Fig. 10), distinguished by differences in fossil assemblages (Droste and Shaver 1975).

i. The Coral Zone

Five biozones make up the Jeffersonville Limestone facies at the Falls of the Ohio (Fig. 10). The Coral Zone is the lowest zone with a thickness of 9.9 feet. Fossil fauna found here include solitary and colonial corals, crinoid fragments, and mound-shaped stromatoporoids (Hendricks et al. 2005).

The northeast corner of the Coral Zone was the selected field of study in this project (Fig. 11) because of the flat and accessible surface. Studying an area with sloped rock would have involved examining different time periods. The flat surface assured that all fossils existed at more or less the same time period as the rock’s sediment was forming.

**Figure 11. Geography of the Falls of the Ohio fossil beds.** The Coral Zone of the Jeffersonville Limestone was the location of research, indicated by the red diamond. This area was easily identifiable so the team could find the same spot throughout the field season (Greb et al. 1993).
ii. Other Biozones

The Amphipora zone is the second oldest zone in this formation. The stromatoporoid Amphipora ramosa is common here along with solitary corals, colonial corals, and other types of stromatoporoids (Hendricks et al. 2005). The Brevispirifer gregarius zone includes crinoid fragments, charophytes, and a few corals along with abundant silicified Brevispirifer brachiopods. On top of this zone is the Fenestrate-Brachiopod zone, which is rich with crinoids, echinoderms, bryozoans, brachiopods, and corals. The youngest zone is the Paraspirifer acuminatus zone and contains bryozoans, brachiopods, and crinoids (Fig. 10; Hendricks et al. 2005).

iii. Lithology

Kissling and Lineback (1967) described the Coral Zone as biomicrite and biosparite limestone. Bronner (1981) also classifies the lithofacies as “coralline biomicrite.” Micrite is a type of sediment classified by having clay-sized particles of calcium carbonate (Fichter 2000). Biomicrite refers to micritic sediment with embedded fossils (Fichter 2000). Biosparite pertains to the cement that holds these sediments together (Fichter 2000).

Kissling and Lineback (1967) also identified 30 dolomitic pebbles sized 3 to 6 cm in diameter. It was deduced that the source of these pebbles was the Geneva Dolomite—another limestone facies existing about 13 miles northeast of the Falls of the Ohio (Kissling and Lineback 1967).

Other authors have identified the lithology as predominantly packstones, grainstones, and rudstones within the fossiliferous limestone, which are terms that describe the density of fossil distribution within the rocks (Hendricks et al. 2005).
iv. Paleoenvironmental Interpretations

The micritic sediment in the Coral Zone suggests environmental conditions of gentle currents and low turbulence (Kissling and Lineback 1967). The variability of fossil orientations found by Kissling and Lineback (1967) also supports the possibility of gentle currents and calm waters. This study concluded the most likely force influencing fossil orientations was an east-west tidal current with a stronger east current.

The Coral Zone thins towards the north and the east, which is also the relative location of the Geneva Dolomite. Based on the dolomitic pebbles found in the Coral Zone, it was also inferred that there was an eastern shoreline beyond the Jeffersonville outcrop and the pebbles washed in from that direction. Based on these postulations, the flood tide consisted of the eastward tidal flow while the ebb tide consisted of the westward tidal flow. These tidal currents most likely contributed to the orientation of fossils found in the Coral Zone (Kissling and Lineback 1967)

5. Methods

a. Field Work

i. Data Collection

The purpose of this study was to identify fossils and their interactions at the Falls of the Ohio, to explore what these fossils can tell us about the past, and to compare this system to others that existed in geologic history. This was done through identifying and measuring organisms in a selected area. Data collection occurred between August-October 2017 when the Ohio River was low enough to expose the Coral Zone fossil beds at the Falls of the Ohio. Dr. Kate Bulinski from Bellarmine University led a team of research students who aided in data
collection. The Coral Zone was the interval selected because of the flat surface, distinguishable features, and proximity to the park’s visitor center.

Transect sampling was used to collect fossil data (Fig. 12). 1-20-meter lines were laid out using measuring tape. Only fossils touching the left side of the transect line were sampled to avoid bias. Transect D was oriented at 235 degrees and created a 20-meter baseline for the other transects, which were oriented at 325 degrees. 10-meter transects A, B, C, E, and F were completed at the beginning of field work. 1-meter transects G-Q were completed at the end of the field season when it was unclear whether there was enough time to complete 10-meter transects. The transects perpendicular to transect D were 1-meter apart from each other, with the exception of a gap between transect C and Q (Fig. 12). This area was not studied because it was covered in spring-fed puddles and was not easily accessible.

Mud was cleared off the area of study prior to sampling using brooms, small brushes, buckets of river water, and pressurized river water. Some fossil beds were pooled with water.

*Figure 12. A diagram of the transects sampled in the Coral Zone at the Falls of the Ohio. This method was a quick and organized way of identifying fossils (schematic diagrammed by Dr. Bulinski).*
from recent rain events and buckets were used to clear out the excess water. Once the fossils were cleaned, Dr. Bulinski identified each fossil touching the transect line that was larger than 1 cm. Any organisms smaller than 1 cm were recorded as “fragments.” After each identification, the length and width of each fossil was recorded. If the fossil was elongate (i.e., length was greater than width), the compass bearing of the fossil was recorded 0-360° (which was later standardized to a bearing between 0 and 180°). If an organism had a large bend, two compass bearings were taken for each end of the fossil. No compass bearing was taken for fossils without a clear orientation such as stromatoporoids, mounded colonial corals, and end views of rugose corals. In addition to the collection of these data, additional notable observations were recorded and the transects were photographed. The field season ended when the river rose high enough to flood the fossil beds.

ii. Data Analysis

Once data collection was complete, Dr. Bulinski standardized the taxonomy of the entries to make the data as consistent as possible. Additionally, since bearings of elongate fossils have two directions (i.e., a long straight fossil can point east on one end and west on the other), compass bearings were standardized by subtracting 180° from each bearing greater than 180°. A column was also added for “biomass,” which was calculated using the following equation:

\[
\text{Biomass} = \text{length of fossil} \times \text{width of fossil}
\]

Biomass could only be calculated for fully measurable organisms. Some margins were unclear, especially for a few stromatoporoids, which prevented them from being included in biomass calculations.
Stromatoporoids were then quantified by percentage of organisms, percentage of transect, and percentage of biomass of all data. These calculations were performed using the following equations:

\[
\text{Percentage of stromatoporoids} = \frac{\text{Number of stromatoporoids}}{\text{Total number of organisms}} \times 100\%
\]

\[
\text{Percentage of stromatoporoids on the transect} = \frac{\sum (\text{Transact length of individual strom.})}{\text{Total transect length}} \times 100\%
\]

\[
\text{Percentage of stromatoporoid biomass} = \frac{\text{Total stromatoporoid biomass}}{\text{Total organism biomass}} \times 100\%
\]

Field work data were also used to identify fossils interacting with stromatoporoids, which were any organisms embedded in the surface of the sponge. Interactions were noted in field descriptions and were summarized. Top-views of corals seen in stromatoporoids were difficult to identify. Therefore, five categories of interacting corals were classified as “unknown coral,” “unknown rugose,” “solitary rugose,” “colonial rugose,” and “tabulate.” The number of occurrences for each interaction was quantified.

iii. Specimen Analysis

A stromatoporoid specimen was also collected from the Falls of the Ohio with the park’s permission. The rock was found near the area of study as a piece broken off the fossil beds and likely came from the Coral Zone. In the lab, the sample was measured by length, width, and biomass. Interacting organisms were observed when there were small circles embedded in the surface of the sponge. These organisms were counted and observed more closely using a magnifying light. Tiny rugose corals were identified based on presence of septa.
b. Meta-Analysis

i. Literature Review Database

In addition to the dataset generated by field work, a database was compiled by the author using peer-reviewed literature. This database included information about Devonian stromatoporoid interactions across the world. Throughout the literature review process, entries were logged in Excel to summarize and later quantify stromatoporoid interactions. Data were entered only if the reference specifically stated that an organism was intergrown, encrusting, or being encrusted by a stromatoporoid. Unclear language including “associations” and “coexisting organisms” was not included. Location of study, interacting organisms, Devonian series, author interpretation, and reference were listed for each entry. Online databases contributed information about stromatoporoids such as location, paleoenvironment, and time periods. However, online databases do not provide information about stromatoporoid interactions. This is why literature review was necessary for studying the interactions.

Five types of interactions were identified in the database, based on specific language used in each reference. Most authors speculated on whether interactions were commensal, mutual, or parasitic, but did not come to a conclusion. Therefore, “endobiont” was identified as any organism boring into or embedded within the stromatoporoid. “Organism encrusted stromatoporoid” denoted that the interacting organism grew over the sponge. “Stromatoporoid encrusted organism” means the stromatoporoid overgrew the organism. “Stromatoporoid encrusted stromatoporoid” identified specimens overgrowing each other. “Mutual encrustation” means the organism and stromatoporoid mutually overgrew each other. These interactions were summarized in a data table.
Since coral-stromatoporoid interactions were found at the Falls of the Ohio, these relationships were the focus of the literature review analysis. From all data found in the scientific literature, corals were separated in another table. This second summary table allowed for specification of coral genus, suborder, or order based on information found in literature and were comparable to data from the Falls of the Ohio. Some authors described corals to genera but many authors only listed suborder or order. However, some genera were found consistently so they were still separated by the order to which they belong. For example, *Syringopora* is a genus under the order Auloporida, but these categories were separated into “*Syringopora*” and “Other Auloporida.” This is because the genus was frequent enough to be its own category. This is also true for genus *Thamnopora*, which is classified under suborder Favositina and closely related to genus *Cladopora*, which was found in the field study.

ii. Paleobiology Database (PBDB)

Another source of data in the meta-analysis was the online Paleobiology Database (PBDB). This database lists fossil occurrences around the world. PBDB members include nearly 400 scientists from 24 countries. These scientists contribute data from their own research and from other paleontology literature by manual voluntary entry (PBDBb). The website lists 1,355,662 occurrences from 65,168 references as of December 2017. Since this is such a large database, many other online databases of fossil information cross-reference and link back to the PBDB.

A disadvantage to relying on voluntary manual entry is the inherent bias because the database does not represent all fossils that have been studied. Therefore, organisms listed will be concentrated only in the areas that contributing scientists have studied. The database also does not provide much specific information about the fossil data, so literature had to be more closely
examined to find stromatoporoid interactions and other relevant information. The PBDB did provide references to literature that were valuable when creating the literature review database.

The PBDB also includes an interactive global map where users can select time, taxa, and stratigraphy to refine their search. For the purposes of this study, the search was refined to class *Stromatoporoidea* in the Devonian period. References were selected from a variety of locations on the map to ensure a more comprehensive global analysis. From the map data, a diversity curve was also generated that demonstrates the radiation and extinction of stromatoporoids.

1. Fossilworks

Fossilworks is another resource used in this research. Dr. John Alroy created this portal to the Paleobiology Database in 1998 and servers are held at Macquarie University in Sydney, Australia (Fossilworks). This website has the advantage of summarizing data from the PBDB. Summary tables are generated through the user’s choice of parameters including location, age, lithology, paleoenvironment, and more. Additional analysis tools include counting taxa, finding common taxa in specific locations or time periods, calculating first appearance, generating a diversity curve, analyzing abundance, analyzing taxonomic ranges, and analyzing stratigraphy (Fossilworks). These data contributed to the meta-analysis by highlighting where stromatoporoid research has been most common. A summary table was generated to evaluate what kind of paleoenvironments stromatoporoids were associated with during the Devonian period. Fossilworks was also used as a resource throughout the literature review process for information about certain coral and stromatoporoid taxa.
iii. PaleoReefs Database (PARED)

The PaleoReefs Database has been developed by Professor Wolfgang Kiessling since 1995 to compile data on Phanerozoic reefs. PARED includes data from the “best developed reef,” which standardizes frequently studied areas with understudied areas to decrease bias in locations that might generate duplicate entries (Kiessling 2011). The database includes country, age of rock, latitude and longitude, main biota, and has a link back to the PBDB reference. The PaleoReefs Database adds context to the information reported from the Paleobiology Database by using a “remarks” column that provides additional notes on interacting organisms, lithology, ecological settings, and interpretations. This column was reviewed and sources with information relating to stromatoporoid interactions were studied further and added to the literature review database. Altogether, 234 Devonian stromatoporoid entries were found in this database.

6. Results

a. Field Work

i. Total Organisms Identified

In total, 4109 entries were recorded in the field work study. Of these entries, there were 2434 identifiable organisms. The remaining 1675 entries were fragments of fossils that were smaller than 1 centimeter. In addition to fragmentation, many corals were overturned. In order from greatest to least occurrences, the top seven organisms found were: *Heliophyllum*, *Cladopora*, *Favosites*, *Acinophyllum*, *Cystiphylloides*, *Tabulophyllum*, and Stromatoporoid (Fig. 13). Some of these taxa, however, have not been documented at the Falls of the Ohio before and therefore require future work using systematics to confirm identifications.
ii. Stromatoporoid Data

In the area of study, 170 stromatoporoids were found, accounting for about 7% of organisms identified (not including fragments). The total length of transects used for transect sampling was 8100 cm. Stromatoporoids accounted for 1223.7 cm of the transect, which was 15.1% of the total transect.

Biomass of all measurable organisms was 70274.2 cm$^2$ and stromatoporoid biomass was 51240.2 cm$^2$. Therefore, stromatoporoid biomass made up 72.9% of the area studied (Fig. 14). It is important to recognize that biomass was calculated only for measurable organisms. Fragments and some stromatoporoids had unclear margins that prevented them from being measured and
therefore included in calculations of biomass. Since some stromatoporoids were unmeasurable, they actually accounted for even more of the percent biomass than calculated; thus, this estimation of biomass is conservative. Calculations of the surface area occupied by stromatoporoids are also not exact representations of biomass because they do not have straight edges.

**Figure 14. Biomass proportions of fossils identified at the Falls of the Ohio.** Stromatoporoids accounted for the largest percentage of biomass, followed by *Heliophyllum* and *Favosites.*
iii. Stromatoporoid Interactions

In some stromatoporoids at the Falls of the Ohio, interactions were clearly evident. The most frequently occurring interaction was with small rugose corals (Table 1). Interacting solitary rugose corals included *Tabulophyllum* and *Heliophyllum*. The interacting colonial rugose coral was *Acinophyllum*. Tabulate corals interactions included *Syringopora*, *Favosites*, and *Cladopora*. Other stromatoporoid-coral interactions were evident but sometimes unidentifiable.

<table>
<thead>
<tr>
<th>Type of coral</th>
<th>Number of interacting stromatoporoids</th>
</tr>
</thead>
<tbody>
<tr>
<td>Unknown coral</td>
<td>6 (20.0%)</td>
</tr>
<tr>
<td>Unknown rugose</td>
<td>8 (26.7%)</td>
</tr>
<tr>
<td>Solitary rugose</td>
<td>7 (23.3%)</td>
</tr>
<tr>
<td>Colonial rugose</td>
<td>1 (3.3%)</td>
</tr>
<tr>
<td>Tabulate</td>
<td>8 (26.7%)</td>
</tr>
<tr>
<td>Total</td>
<td>30 (100%)</td>
</tr>
</tbody>
</table>

Table 1. Stromatoporoid-coral interactions at the Falls of the Ohio. Many corals were unidentifiable. Small rugose corals were most frequently seen interacting with stromatoporoids.

iv. Stromatoporoid Specimen

The stromatoporoid sample obtained from the field area measured 46.2 cm by 41.7 cm and constituted a biomass of 1926.5 cm² (Fig. 15). This was representative of other individual specimens found during the study. There were 114 organisms embedded in the stromatoporoid surface. These organisms were difficult to identify but were mostly small rugose corals, based on the presence of septa. A magnified view of the sample shows how the sponge’s laminae grew concentrically around an interacting coral (Fig. 16).
b. Meta-Analysis

i. Literature Review Database

The literature review database was made up of 76 entries consisting of stromatoporoid interactions from 17 different locations around the world. The locations included Alaska/Canada border, Australia, Belgium, California, Canada, China, Czech Republic, France, Indiana, Iowa, Michigan, Morocco, New York, Pakistan, Poland, Spain, and Virginia.

From the references analyzed, 14 types of organisms interacted with stromatoporoids. The groups of organisms included brachiopods, bryozoans, chaetetid sponges, colonial rugose
corals, crinoids, cyanobacteria, gastropods, molluscs, polychaetes, rhodophyta, stromatoporoids, solitary rugose corals, tabulate corals, and tentaculitids (Table 2).

Tabulate corals including *Syringopora*, other *Auloporida, Thamnopora*, other *Favositina, Alveolitina*, and *Heliolitida* were the most frequently interacting organism (Table 3). Nine tabulate corals were endobionts, eight encrusted a stromatoporoid, and eight were encrusted by a stromatoporoid. In one case, a suborder of *Favositida*, *Alveolitina*, was found both encrusting and being encrusted by a stromatoporoid (Table 2; Table 3). This interaction occurred in a Frasnian system in Iowa.

Rugose corals were the second most frequently interacting organism. Seven colonial rugose corals were represented by *Prismatophyllum, Acinophyllum, Eridophyllum, Xystriphyllum, Spongophyllum*, and *Hexagonaria* (Table 3). Four solitary rugose corals were unknown species except for *Acanthophyllum* (Table 3).

Following corals, cyanobacteria had nine interactions, seven of which were the organism encrusting the stromatoporoid. Stromatoporoids were also found encrusting each other nine times (Table 2). Polychaete, which are worms, were also notable interactions with five entries, four of which were endobionts (Table 2).
Table 2. Summary of organisms interacting with stromatoporoids from a sample of Devonian systems across the world. Tabulate corals, which are colonial, were the most frequently interacting organism. The most frequent type of interaction was endobiotic where the organism lived within the tissue of the stromatoporoid.

<table>
<thead>
<tr>
<th>Interacting organism</th>
<th>Endobiont</th>
<th>Organism encrusted stromatoporoid</th>
<th>Stromatoporoid encrusted organism</th>
<th>Stromatoporoid encrusted stromatoporoid</th>
<th>Mutual encrustation</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brachiopod</td>
<td>2 (2.6%)</td>
<td>--</td>
<td>1 (1.3%)</td>
<td>--</td>
<td>--</td>
<td>3 (3.9%)</td>
</tr>
<tr>
<td>Bryozoan</td>
<td>1 (1.3%)</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>1 (1.3%)</td>
</tr>
<tr>
<td>Chaetetid</td>
<td>--</td>
<td>1 (1.3%)</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>1 (1.3%)</td>
</tr>
<tr>
<td>Crinoid</td>
<td>2 (2.6%)</td>
<td>--</td>
<td>1 (1.3%)</td>
<td>--</td>
<td>--</td>
<td>3 (3.9%)</td>
</tr>
<tr>
<td>Cyanobacteria</td>
<td>1 (1.3%)</td>
<td>7 (9.2%)</td>
<td>1 (1.3%)</td>
<td>--</td>
<td>--</td>
<td>9 (11.8%)</td>
</tr>
<tr>
<td>Gastropod</td>
<td>1 (1.3%)</td>
<td>--</td>
<td>2 (2.6%)</td>
<td>--</td>
<td>--</td>
<td>3 (3.9%)</td>
</tr>
<tr>
<td>Mollusc</td>
<td>--</td>
<td>--</td>
<td>2 (2.6%)</td>
<td>--</td>
<td>--</td>
<td>2 (2.6%)</td>
</tr>
<tr>
<td>Polychaete</td>
<td>4 (5.3%)</td>
<td>1 (1.3%)</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>5 (6.6%)</td>
</tr>
<tr>
<td>Rhodophyta</td>
<td>--</td>
<td>1 (1.3%)</td>
<td>1 (1.3%)</td>
<td>--</td>
<td>--</td>
<td>2 (2.6%)</td>
</tr>
<tr>
<td>Rugose coral (colonial)</td>
<td>--</td>
<td>4 (5.3%)</td>
<td>3 (3.9%)</td>
<td>--</td>
<td>--</td>
<td>7 (9.2%)</td>
</tr>
<tr>
<td>Rugose coral (solitary)</td>
<td>3 (3.9%)</td>
<td>--</td>
<td>1 (1.3%)</td>
<td>--</td>
<td>--</td>
<td>4 (5.3%)</td>
</tr>
<tr>
<td>Stromatoporoid</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>9 (11.8%)</td>
<td>--</td>
<td>9 (11.8%)</td>
</tr>
<tr>
<td>Tabulate coral</td>
<td>9 (11.8%)</td>
<td>7 (9.2%)</td>
<td>8 (10.5%)</td>
<td>--</td>
<td>1 (1.3%)</td>
<td>25 (32.9%)</td>
</tr>
<tr>
<td>Tentaculitid</td>
<td>2 (2.6%)</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>2 (2.6%)</td>
</tr>
<tr>
<td>Total</td>
<td>25 (32.9%)</td>
<td>21 (27.6%)</td>
<td>20 (26.3%)</td>
<td>9 (11.8%)</td>
<td>1 (1.3%)</td>
<td>76 (100%)</td>
</tr>
</tbody>
</table>
Table 3. Detailed summary of corals interacting with stromatoporoids found in literature review. Colonial rugose corals, solitary rugose corals, and tabulate corals from Table 2 are specified by genus, suborder, or order based on information provided by scientific literature.

<table>
<thead>
<tr>
<th>Interacting coral</th>
<th>Endobiont</th>
<th>Organism encrusted stromatoporoid</th>
<th>Stromatoporoid encrusted organism</th>
<th>Mutual encrustation</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Rugose coral (colonial)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Prismatophyllum</em></td>
<td>--</td>
<td>--</td>
<td>1 (2.8%)</td>
<td>--</td>
<td>1 (2.8%)</td>
</tr>
<tr>
<td><em>Acinophyllum</em></td>
<td>--</td>
<td>1 (2.8%)</td>
<td>--</td>
<td>--</td>
<td>1 (2.8%)</td>
</tr>
<tr>
<td><em>Eridophyllum</em></td>
<td>--</td>
<td>1 (2.8%)</td>
<td>--</td>
<td>--</td>
<td>1 (2.8%)</td>
</tr>
<tr>
<td><em>Xystriphyllum</em></td>
<td>--</td>
<td>1 (2.8%)</td>
<td>--</td>
<td>--</td>
<td>1 (2.8%)</td>
</tr>
<tr>
<td><em>Spongophyllum</em></td>
<td>--</td>
<td>1 (2.8%)</td>
<td>--</td>
<td>--</td>
<td>1 (2.8%)</td>
</tr>
<tr>
<td><em>Hexagonaria</em></td>
<td>--</td>
<td>--</td>
<td>1 (2.8%)</td>
<td>--</td>
<td>1 (2.8%)</td>
</tr>
<tr>
<td><em>Unknown</em></td>
<td>--</td>
<td>--</td>
<td>1 (2.8%)</td>
<td>--</td>
<td>1 (2.8%)</td>
</tr>
<tr>
<td><strong>Rugose coral (solitary)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Acanthophyllum</em></td>
<td>1 (2.8%)</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>1 (2.8%)</td>
</tr>
<tr>
<td><em>Unknown</em></td>
<td>2 (5.6%)</td>
<td>--</td>
<td>1 (2.8%)</td>
<td>--</td>
<td>3 (8.3%)</td>
</tr>
<tr>
<td><strong>Tabulate coral</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Syringopora</em></td>
<td>7 (19.4%)</td>
<td>--</td>
<td>--</td>
<td>--</td>
<td>7 (19.4%)</td>
</tr>
<tr>
<td>Other <em>Auloporida</em></td>
<td>--</td>
<td>1 (2.8%)</td>
<td>1 (2.8%)</td>
<td>--</td>
<td>2 (5.6%)</td>
</tr>
<tr>
<td><em>Thamnopora</em></td>
<td>--</td>
<td>1 (2.8%)</td>
<td>1 (2.8%)</td>
<td>--</td>
<td>2 (5.6%)</td>
</tr>
<tr>
<td>Other <em>Favositina</em></td>
<td>1 (2.8%)</td>
<td>3 (8.3%)</td>
<td>1 (2.8%)</td>
<td>--</td>
<td>5 (13.9%)</td>
</tr>
<tr>
<td><em>Alveolitina</em></td>
<td>--</td>
<td>1 (2.8%)</td>
<td>3 (8.3%)</td>
<td>1 (2.8%)</td>
<td>5 (13.9%)</td>
</tr>
<tr>
<td><em>Heliolitida</em></td>
<td>--</td>
<td>1 (2.8%)</td>
<td>1 (2.8%)</td>
<td>--</td>
<td>2 (5.6%)</td>
</tr>
<tr>
<td><em>Unknown</em></td>
<td>1 (2.8%)</td>
<td>--</td>
<td>1 (2.8%)</td>
<td>--</td>
<td>2 (5.6%)</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>12 (33.3%)</td>
<td>11 (30.6%)</td>
<td>12 (33.3%)</td>
<td>1 (2.8%)</td>
<td>36 (100%)</td>
</tr>
</tbody>
</table>
ii. Fossilworks

The paleoenvironments of Devonian stromatoporoids was summarized using a Fossilworks summary table. A reef, buildup, or bioherm is by far the most common paleoenvironment that stromatoporoids existed in, with 1690 frequencies out of 2878 total, accounting for 58.7% of the occurrences (Table 4). Other frequent paleoenvironments include shallow areas.

<table>
<thead>
<tr>
<th>Paleoenvironment</th>
<th>Devonian stromatoporoid occurrences</th>
<th>Percent total (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Reef, buildup or bioherm</td>
<td>1690</td>
<td>58.7</td>
</tr>
<tr>
<td>Perireef or subreef</td>
<td>377</td>
<td>13.1</td>
</tr>
<tr>
<td>Marine indet.</td>
<td>331</td>
<td>11.5</td>
</tr>
<tr>
<td>Shallow subtidal indet.</td>
<td>169</td>
<td>5.9</td>
</tr>
<tr>
<td>Lagoonal/restricted shallow subtidal</td>
<td>110</td>
<td>3.8</td>
</tr>
<tr>
<td>Open shallow subtidal</td>
<td>51</td>
<td>1.8</td>
</tr>
<tr>
<td>Deep subtidal shelf</td>
<td>45</td>
<td>1.6</td>
</tr>
<tr>
<td>Carbonate indet.</td>
<td>36</td>
<td>1.3</td>
</tr>
<tr>
<td>Coastal indet.</td>
<td>20</td>
<td>0.7</td>
</tr>
<tr>
<td>Other</td>
<td>49</td>
<td>1.7</td>
</tr>
<tr>
<td>Total</td>
<td>2878</td>
<td>100</td>
</tr>
</tbody>
</table>
7. Discussion

a. Field Work

All fossils identified through transect sampling in the Coral Zone at the Falls of the Ohio were rugose or tabulate corals, except for stromatoporoids. The abundance of these organisms implies they were significant contributors to the structure of the Coral Zone. Stromatoporoids were the seventh most frequent organism identified, but they made up 72.9% of biomass (Fig. 14), showing that these sponges were especially important in the Devonian system.

This paleoenvironment can be confidently identified as a “biostrome,” in agreement with Cumings (1932), Kissling and Lineback (1967), and Hendricks et al. (2005). In contrast to a “bioherm” or “reef,” the Coral Zone is structured in layers, especially due to the presence of mat-shaped stromatoporoids that encrusted other fossils laminarly.

The abundance of rugose corals, tabulate corals, and stromatoporoids suggests a particular paleoenvironment as well. In general, these Paleozoic taxa shared similar paleoenvironments including mid to low latitudes (Scrutton 1999; Stock 2005) and shallow seas (Kershaw and Brunton 1999; Scrutton 1999). The presence of these fossils in the Coral Zone indicates the biostrome formed in tropical or subtropical latitudes, which is confirmed by the Paleobiology Database (Table 4). The shallow sea environment is also supported by these data.

The abundance of broken, fragmented, and overturned corals implies turbulent water conditions were present, which is another sign of a shallow ocean environment. Kissling and Lineback (1967) concluded the paleoenvironment accrued under non-turbulent conditions, which is inconsistent with this conclusion. However, this study identified fossils larger than 1 cm while
Kissling and Lineback (1967) identified fossils larger than 4 cm, which would have included less broken and fragmented fossils that are characteristic of turbulent conditions.

b. Stromatoporoid Interactions

Stromatoporoids and corals were frequently interacting in the Coral Zone, recognized by corals embedded in the surface of the sponge. This indicates a relationship between the taxa in this particular location. It was difficult to identify corals more specifically than Rugosa or Tabulata due to the encrusting nature of sponges that covered potential defining features of the corals. However, rugose corals were found interacting with stromatoporoids more frequently than tabulate corals (Table 1). It is possible that this is due to the higher frequency of rugose corals at the Falls of the Ohio. Of the top six organisms identified, Rugosa (Heliophyllum, Acinophyllum, Cystiphylloides, Tabulophyllum) made up four of the most abundant taxa while Tabulata (Cladopora, Favosites) made up the remaining two spots (Fig. 13). Therefore, even though rugose corals more frequently interacted with stromatoporoids, they were also more abundant in the overall dataset than tabulate corals.

Stromatoporoid-coral relationships were also evident in other Devonian systems across the world that were identified in the literature review database. However, tabulate corals were more frequently interacting than rugose corals (Table 2). Both types of corals still made up the most commonly interacting organisms followed by cyanobacteria, stromatoporoids, and polychaetes. The abundance of tabulate corals suggests a particular relationship between stromatoporoids and tabulate corals in the Devonian period. Syringopora was the top interacting tabulate coral (Table 3), which was a specific coral of interest in studies including Kissling and Lineback (1967), Stearn (1983), and Hubmann and Gaetani (2007).
There is no strong evidence about whether stromatoporoid-coral relationships were mutual, commensal, or parasitic. However, in Kissling and Lineback (1967), a commensal relationship was interpreted between *Syringopora* and stromatoporoids at the Falls of the Ohio. This tabulate coral has delicate branches that may have been protected from high-energy water conditions by the rigid stromatoporoid. If a turbulent environment was in fact present at the Falls of the Ohio, this could be true for other interacting corals found in the field of study. The *Syringopora* coral also had little effect on the sponge, further indicating a non-parasitic relationship (Kissling and Lineback 1967). Commensal interactions between *Syringopora* and stromatoporoids were also described in Devonian systems in Arctic Canada (Stearn 1983) and Northern Pakistan (Hubmann and Gaetani 2007).

A similar interpretation can be made for the rugose corals found in the stromatoporoid specimen taken from the Coral Zone of the Falls of the Ohio. The surface of the sponge was altered by the interacting corals, which could indicate a parasitic relationship (Taylor 2015). However, unlike a parasitic interaction, the stromatoporoid growth bands that enveloped interacting organisms were the same width as growth bands distant from the corals (Fig. 16). The lack of growth interruption caused by corals in this specimen supports that it was a commensal relationship. The corals in this stromatoporoid were also very small and were potentially vulnerable to turbulent water currents on their own. The rigid calcitic skeleton of the sponge may have protected these delicate corals with little effect on the stromatoporoid itself.

However, parasitic interactions have been interpreted in other regions. Zapalski and Hubert (2011) provide evidence of a parasitic relationship in a *Torquaysalpinx*-stromatoporoid interaction in Givetian rock from France. The laminae of the sponge were seen to grow smaller around the endobiont, indicating the parasite may have been feeding on the sponge (Zapalski and
Hubert 2011). Endobiotic worms, rugose corals, and syringoporids were also discovered in stromatoporoids of a Late Silurian system in Estonia (Vinn and Motus 2014). The suspension-feeding worms that were protected by the sponge’s skeleton might have competed with its host for food, resulting in a parasitic relationship. The loss of surface area available to the stromatoporoid would also reduce its feeding efficiency, considering it is a suspension feeder (Vinn and Motus 2014).

Since both commensal and parasitic relationships are evident between stromatoporoids and their symbionts, both of these interactions likely happened throughout time. For this reason, stromatoporoids and corals can not be classified as commensal organisms or parasitic organisms in general because relationships differ from location to location. Individual interactions must be studied for a better idea of the association taking place. Paleoenvironmental interpretations are also important in studying relationships between organisms because the environment influenced their interactions as well as their vulnerability to extinction.

c. Vulnerability to Extinction

The vulnerability of stromatoporoids and corals during the Frasnian-Famennian extinction may be explained by their relationships. Both organisms may have evolved to become reliant on each other for survivability, especially in the case of commensal interactions. Bioclaustations that characterize these interactions increased in abundance and diversity throughout the Silurian and Early Devonian periods but declined in the Middle Devonian. They disappeared at the end of this period, in correlation with the organisms affected by the Frasnian-Famennian extinction (Tapanila 2005). Explanations of the crisis include new nutrients introduced to oceans due to developing forests, fluctuating atmospheric CO$_2$, dropping sea temperatures, and falling sea levels (Stock 2005; Joachimski et al. 2009; Copper 2011).
Considering the shallow, often turbulent paleoenvironments of stromatoporoids (Table 4; Kershaw and Brunton 1999), shifting environmental conditions would have considerable effects on these sponges and their endobionts. In a commensal relationship, once these factors began affecting one taxon, the other organism would become more vulnerable as well. Without the protection of the sponge’s rigid skeleton, endobiotic corals would be increasingly susceptible to changing temperatures, sea levels, and water chemistry. Additionally, parasitic corals would have already weakened their host by slowing its growth rate or reducing its feeding efficiency. Combined with these negative interactions, stromatoporoids would have heightened sensitivity to environmental fluctuations. Though the environmental conditions most likely caused the extinction, relationships between Paleozoic stromatoporoids, corals, and other organisms influenced their vulnerability.

8. Conclusion

Stromatoporoids were important organisms of the Paleozoic era. Their morphology and diversity formed large biostromes (Hendricks et al. 2005). These systems are studied to better understand ancient ecosystems and relationships between Paleozoic organisms. At the Falls of the Ohio, stromatoporoids made up 72.9% of the area studied in the Coral Zone. In other studies, such as Kissling and Lineback (1967), these sponges were also significant to the biostrome structure. This fauna combined with rugose and tabulate corals help conclude that the Falls formed in mid-low latitudes and shallow seas where turbulent waters were common.

Examining morphology of stromatoporoids and interacting organisms helps classify their relationships. For example, delicate features of corals combined with unaltered sizes of stromatoporoid growth bands indicate that associations between corals and stromatoporoids were commensal, specifically at the Falls of the Ohio and in other Devonian systems in Arctic Canada.
and Northern Pakistan (Kissling and Lineback 1967; Stearn 1983; Hubmann and Gaetani 2007). However, some studies suggest parasitic interactions when an endobiont caused a slowed growth rate or reduced feeding efficiency of its host (Zapalski and Hubert 2011; Vinn and Motus 2014). These different cases demonstrate that multiple classifications are valid in interpreting associations between stromatoporoids and other organisms.

Examining the commensal and parasitic interactions between stromatoporoids, corals, and other organisms help indicate their vulnerability to the Frasnian-Famennian extinction that killed 57% of genera (Wood 1999). It is known that fluctuating ocean chemistry, new nutrients, dropping temperatures, and falling sea levels lead up to this crisis (Copper 2011). Compared to communities in deeper waters, these environmental conditions would have greater effects on communities in shallow waters, where stromatoporoids and their endobionts were abundant (Kershaw 1998). If parasites were already harming stromatoporoids, these sponges would be more susceptible to extinction. When stromatoporoids began to die from environmental changes, their inhabitants were left without the protection and advantages of a symbiotic relationship. Examining relationships between the fundamental organisms of this time period shows how symbiosis can contribute to the vulnerability of animals facing extinction, especially when combined with shifting environmental conditions.

a. Future Work

Limitations to this research include the small time frame available for data collection. Since fossil beds are only exposed at the Falls of the Ohio for less than three months, data should continue to be collected in following years. This will provide a more comprehensive analysis of fossils that can lead to better interpretations of their paleoenvironment. Further research will also help confirm the identifications of taxa found in this study.
Data collected at the Falls of the Ohio should also be entered into the Paleobiology Database. By adding our research to the database, future studies will be able to use our data. This will also update the list of fossils found around the world, which will offer more accurate analyses for scientists using the PBDB.

Research should also be continued on organisms found interacting in the fossil record. Another limitation to this research was the lack of literature specifically focusing on these interactions. Relationships between ancient organisms can provide insight into their life processes, which advances paleontological and geological research. Mass extinctions can also be better understood through recognizing how interactions can influence vulnerability of species to extinction.

Stromatoporoid interactions should specifically be studied further to better understand mutual, commensal, or parasitic relationships and how they were related to the Frasnian-Famennian extinction. Since these sponges were significant Paleozoic reef, bioherm, and biostrome builders, understanding their interactions would contribute to a variety of paleoecological studies.

Lastly, paleontologists should also develop more clear terminology about interactions. “Associations” and “coexisting organisms” made it unclear whether organisms were found interacting or adjacent to one another. Considering these interactions can be significant to understanding the fossil record, it is necessary to convey details in a more accessible way.
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