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Kate Runciman

The College of Wooster, krunciman22@wooster.edu

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**Model of a Biotic Hard Substrate Community:
Paleoecology of Large Trepostome Bryozoans
from the Upper Ordovician (Katian) of the
Cincinnati Region, USA**



by

Kate Runciman

Written in partial fulfilment of the requirements of Senior
Independent Study at the College of Wooster

20 February 2022

Cover Photo:

Trepostome bryozoan from the upper Whitewater (Katian) of Wayne County, Indiana (N 39.78631°, W 84.90318°). Sample C/W-148-3.

ABSTRACT

The calcite skeletons of trepostome bryozoan colonies from the Upper Ordovician (Katian) of the Cincinnati region record the diverse interactions and growth responses these colonies experienced. Trepostome specimens from three Cincinnati strata; the Bellevue Member, the Bull Fork Formation, and the Whitewater Formation, were studied within this project. These three strata were deposited in a shallow epicontinental sea environment that was located in the southern subtropics, approximately 20-23°S at the time of deposition. The focus of this project was the paleoecology of large trepostome bryozoans, which was studied by examining bryozoan growth patterns, trace fossils, and sedimentation. Microscopic examination of these features was conducted by sectioning colonies and making acetate peels and thin sections. Through this examination many trace fossils were found, with *Trypanites* borings being the most common. These borings often contained calcite "ghosts" and appear to have been excavated mechanically by a worm such as a sipunculan or phoronid. A subset of the observed borings prompted growth reactions in their host bryozoan, indicating that these borings progressed through a live portion of the colony. Growth reactions served to seal the cavity and regain feeding surfaces by: (1) Zooids surrounding the cavity growing upwards and angling inwards, creating a "tent" with the cavity closed off; (2) Zooids growing laterally over the cavity opening, sealing it off with a flat "roof"; or (3) Zooids budding down into the cavity then angling upwards, filling in all open space and resuming a feeding surface above. Other features observed in the trepostomes studied include calcite tubes, which are interpreted as fossil cornulitids; a tube and holdfast, interpreted as a sphenothallid; and prismatic calcite features, which are interpreted as the remains of aragonitic shells. All colonies and trace fossils included in this study were infilled with one or more of: sparry calcite cement, dolomite rhombs, biosparite, micrite, prismatic calcite, and phosphate. This range of infilling materials suggests that infilling processes were episodic. The episodic nature of these processes allowed for the preservation of ghosts and occasionally geopetal structures. Internal surfaces were observed that indicated regions of self-overgrowth in the colony. These self-overgrowths were commonly associated with brown bodies. Work continues to combine insights provided by the trace fossils, growth responses, and infill observed in the Cincinnati trepostomes to interpret the ecology and life modes of these bryozoans.

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These individuals and this project have had a wonderful impact on my life and have helped me to find a direction for my future; I hope to continue palaeontology research at the graduate level.

INTRODUCTION

Fossil bryozoans provide a record of the environment they inhabited and the interactions they had with other organisms. Thus, these fossils provide insight into past ecosystems (Wilson, 2007). In this study, trepostome bryozoans from the Upper Ordovician (Katian) of the Cincinnati region and their trace fossils are first placed in their taxonomic, ichnotaxonomic, and stratigraphic context and then described and analyzed. The specimens examined contain an abundance of growth responses and trace fossils that communicate the interactions and relationships between trepostomes and other organisms in their environment. The shape, composition, and nature of these features are microscopically examined. Evidence of a variety of symbiotic organisms as well as several styles of growth response are found. This evidence has implications for trepostome growth and symbiotic processes.

BACKGROUND

A General Introduction to Bryozoans

Bryozoans are aquatic filter-feeding colonial invertebrates with a long evolutionary history. There are approximately 6000 modern species recognized within the Phylum Bryozoa (Taylor, 2020). Fossil evidence of this phylum begins in the early Cambrian (Zhang et al., 2021). They exist in a variety of aquatic environments and are distributed globally. Although characteristics of bryozoans can differ substantially between species, all bryozoans are aquatic invertebrates and suspension-feeders. Additionally, most or potentially all bryozoans are colonial (Taylor, 2020), which in the context of these animals means, as Taylor (2020, p. 1) explains "an aggregate of genetically identical, conjoined modules." These modules are called zooids. Zooids are small (typically less than 1mm long) and they are physically attached to the neighbouring zooids in the colony. They can die from aging or external factors, but the death of individual zooids does not result in the death of the colony (Taylor, 2020). Zooids vary in morphology depending on the species and can establish colonies in a plethora of colony-forms (shapes) and sizes. Note however, that colony-form is rarely indicative of bryozoan species (Taylor, 2020).

Individual zooids consist of a cystid (body wall), which can develop a skeleton. Within the cystid is the coelom (a fluid filled internal cavity). The coelom contains a polypide, which is an organ that collects and digests food (Taylor, 2020). The polypide has several components that facilitate this food processing. One of these components is the lophophore, a crown of tentacles used for filter-feeding (Figure 1; Taylor and Ernst, 2004). Zooids can protect their lophophore by retracting it into the cystid. After the

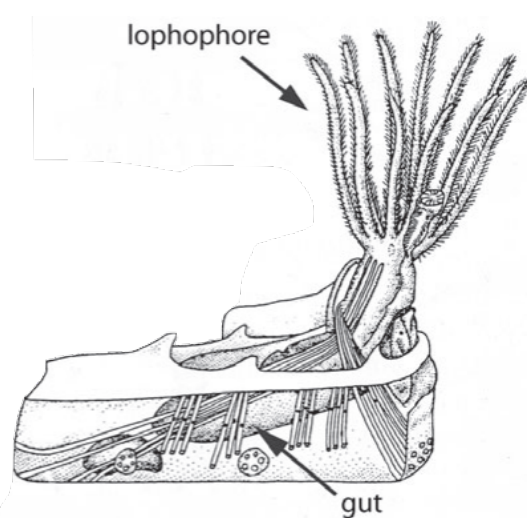


Figure 1. Diagram of a basic bryozoan zooid, showing the gut within its cystid and the lophophore extended. After Taylor et al. (2015, fig. 1).

lophophore has been retracted, it can be expanded back into the water column (Taylor, 2020). A lophophore can have as few as eight or as many as 100 or more tentacles. Tentacles have several cilia, which are hair-like structures, some of which move in such a way as to generate a small current in the surrounding water. The purpose of this current is to move water carrying phytoplankton through the lophophore for the zooid to consume. This food enters the zooid's gut for digestion through a mouth where the lophophore tentacles diverge. The mouth and gut are also part of the polypide (Taylor, 2020). A zooid's polypide regularly degenerates and is replaced through the process of polypide cycling. The remains of a degenerated polypide are called a brown body and are either kept in the coelom or defecated. In

marine bryozoans, polypide cycling is a zooid's waste removal mechanism (Taylor, 2020).

During the growth of a colony, zooids are added through mitosis in a process termed "budding." Budding usually occurs in zones, rather than throughout the entire colony at once (Taylor, 2020). To produce new colonies, bryozoans generally fertilize between colonies to produce swimming larvae. These larvae cannot eat, so they establish a colony quickly by adhering to the substrate, metamorphosing, then budding new zooids. This founding individual of a colony is called the ancestrula (Taylor, 2020). In some cases, colonies can also propagate through the fragmentation of an existing colony. Fragmented colonies are genetically identical to those they fragmented from. Generally, colonies settle on firm or hard substrates, but there are some exceptions (Taylor, 2020).

The lifespans of bryozoan colonies vary greatly. In some cases, colony ages can be estimated by seasonal, annual, or lunar/tidal growth cycles, but growth rates and patterns differ significantly between species. Some species live less than a year (Taylor, 2020), but fossil evidence indicates that colonies have lived as long as 133 years (Reid, 2014). Though some bryozoans can live for a relatively long time, they are threatened by predation. Bryozoans are preyed upon by many animals such as sea spiders and sea slugs. Predators may target the entire colony or individual zooids (Taylor, 2020).

In the study of fossil bryozoans, two principal methods are employed to determine a colony's taxonomy. In post-Paleozoic bryozoans, external morphology is most commonly used to identify the colony. By contrast, the most important methods for studying Paleozoic bryozoans are thin-sections and acetate peels. Thin sections are of higher quality but they are fragile and most or all of the sample is destroyed in their preparation. Peels are of lesser quality and cannot be used for high-magnification analysis. However, the preparation of peels is a simple process and does not consume as much of the specimen. Peels work well for carbonate fossils but are not useful for silicified or dolomitized specimens. There are three standard planes on which bryozoans are cut for thin sections or peels, these planes are transverse, longitudinal, and tangential (Figure 2). Using these three planes reveals the internal morphology of the colony in three dimensions (Ernst, 2020).

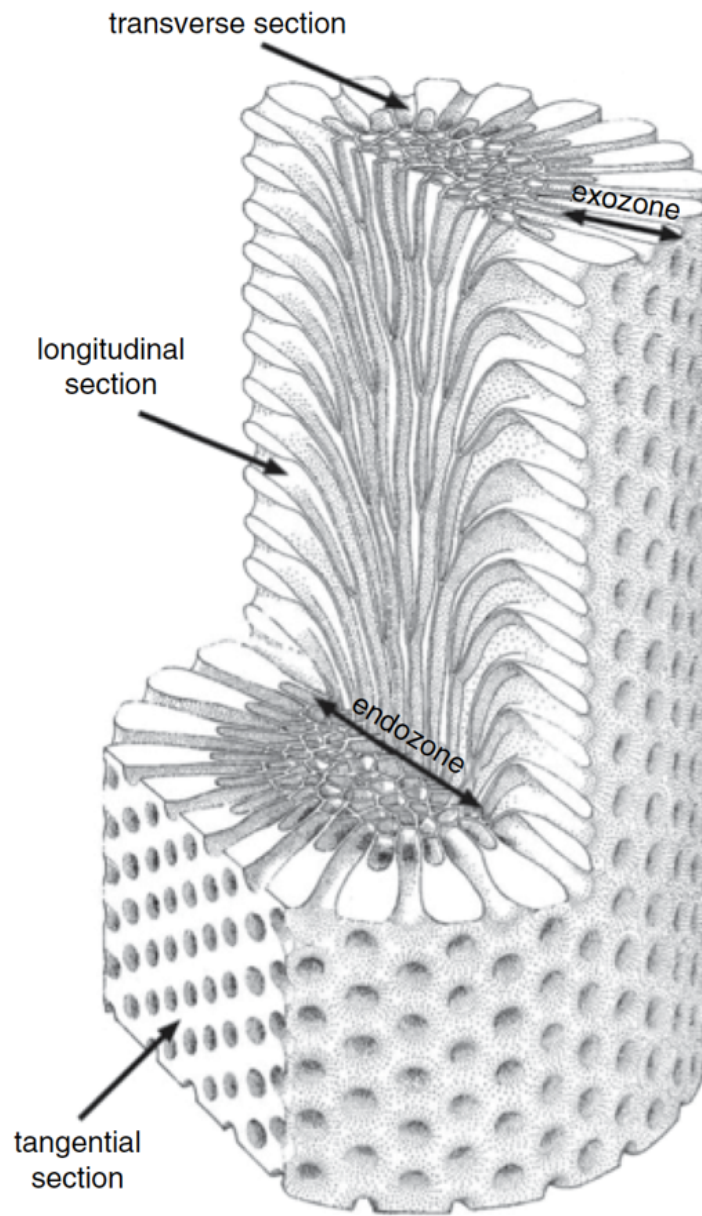


Figure 2. Diagram illustrating the three standard planes on which bryozoan thin sections and acetate peels are cut. This is a branch of a ramose trepostome colony. After Taylor (2020, fig. 1.5).

Stenolaemata

The Phylum Bryozoa is subdivided into three classes: Phylactolaemata, Gymnolaemata, and Stenolaemata (Taylor, 2020). The class Stenolaemata, which includes the order Trepostomata studied here, first appears in the fossil record in the Early Ordovician and examples of this class continue to this day. There are currently seven recognized orders of stenolaemates, of which all save one are Palaeozoic (Taylor, 2020).

There are several characteristics that stenolaemates share. For example, stenolaemate zooids have a tubular shape and a small circular lophophore. Additionally, stenolaemates all have mineralized skeletons, making them excellent candidates for fossilization. They are exclusively marine and produce a variety of colony-forms (Taylor, 2020).

Trepostomata

Trepostomata is one of seven orders in the class Stenolaemata. This order is found in the fossil record from the Ordovician to the Triassic (Taylor, 2020). The study of trepostomes began around 1900 and has continued steadily since that time (Boardman and Buttler, 2005). The features of trepostome bryozoans can vary greatly between species and even colonies of the same species, see Figure 3 for an example of a trepostome colony (Taylor, 2020). Colony lifespans differ, but the longest-lived bryozoan colony known was a trepostome from the Permian of Tasmania, which may have lived for 133 years (Reid, 2014).

Trepostome zooids can display a wide variety of morphologies. Like all stenolaemates, their zooids are tubular. However, the zooid proportions can range from squat, shallow tubes to extremely elongated ones (Taylor, 2020). Colonies can contain different types of zooids (Boardman and Buttler, 2005). The one type of zooid that all bryozoans must have are autozooids (Taylor, 2020). Autozooids are necessary for feeding and can perform all the life functions essential for a bryozoan colony. In trepostomes, autozooids are fairly evenly distributed in the colony (Boardman and Buttler, 2005). The space between the autozooids is generally filled with extrazoooidal skeleton. This skeleton functions as protection and support for the colony but it is not part of the structure of the colony's zooids (Boardman and Buttler, 2005). Some bryozoan colonies also have exterior frontal walls, but these are not present on trepostomes. Some trepostomes have a thin-walled inner section of their colony skeleton. This section is referred to as the endozone. It is contrasted with the outer exozone. Exozones are built of thicker walls and the zooids are perpendicular to their orientation in the endozone (Figure 2; Taylor, 2020). Thin-walled endozones are present in some ramose and frondose trepostome colonies but not in other bryozoans (Wyse Jackson and Key, 2007).

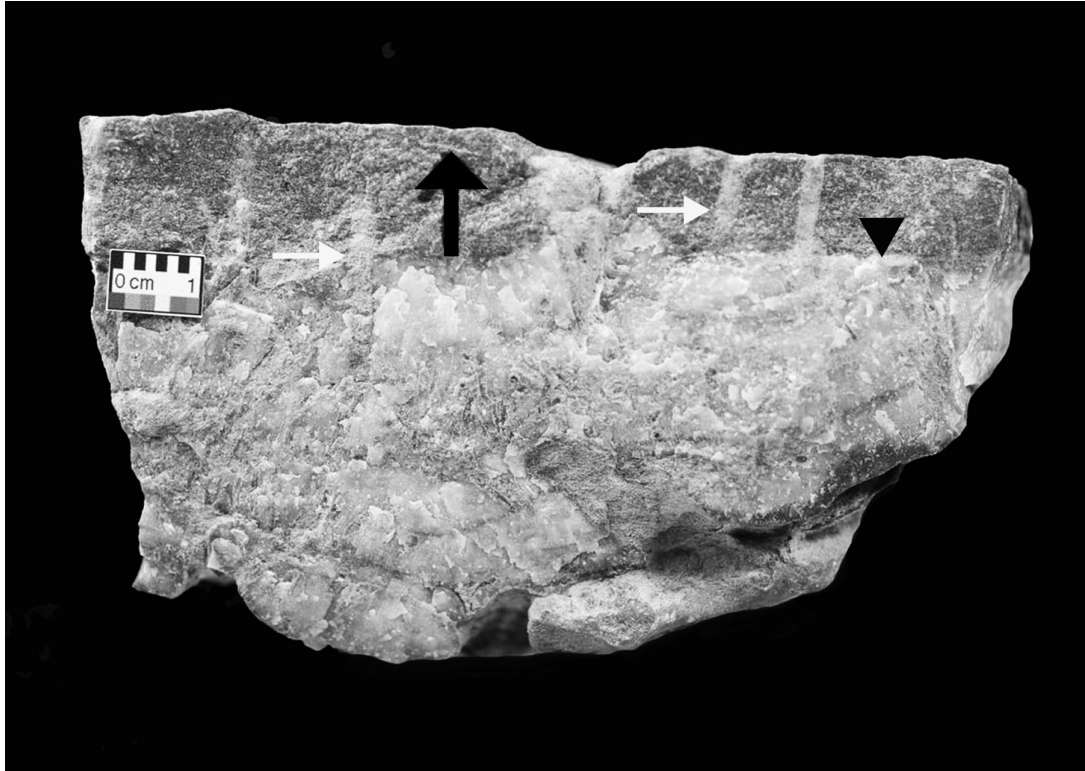


Figure 3. A large Upper Ordovician trepostome colony of the species *Stigmatella personata*. This particular specimen grew upside-down in a small cave. The black arrow indicates the way up of sediments. The black triangle denotes the hardground-colony boundary, the white arrows indicate *Trypanites* borings. After Buttler and Wilson (2018, fig. 2).

As mentioned above, bryozoans can contain different types of zooids. Different zooids perform different functions in the colony, resulting in polymorphism, i.e. zooids having different morphology (Taylor, 2020). Polymorphism is common in trepostomes. Typical trepostome polymorphs are mesozooids and exilazooids. Neither of these polymorphs contain brown bodies, which suggests that they did not have polypides (Taylor, 2020). Additionally, mesozooids and exilazooids are typically smaller than autozooids and can have different cross-sectional shape, depending on the species. These polymorphs are dispersed between autozooids. Their function is debated, but it is likely that they served a predominantly structural purpose, regulating gaps between autozooids (Taylor, 2020).

Trepostomes can produce a wide range of colony-forms. A colony-form begins to develop when a larva attaches to a substrate and forms a dome-shaped structure called a protoecium. The protoecium is the initial component of the ancestrula. A zooid emerges from the protoecium, followed by one to three more zooids (Taylor, 2020). In trepostomes, the ancestrula typically buds three autozooids. After these primary zooids have budded, the ancestrula walls can thicken, making a distinctive flange around the colony in a V or U shape (Figure 4; Pachut and Fisherkeller, 2011). As zooids bud, they

initially form a cone shape with the ancestrula at the centre. As the colony continues to grow from this structure, colony-form will differ depending on the location, direction, and rate of budding (Pachut and Fisherkeller, 2011).

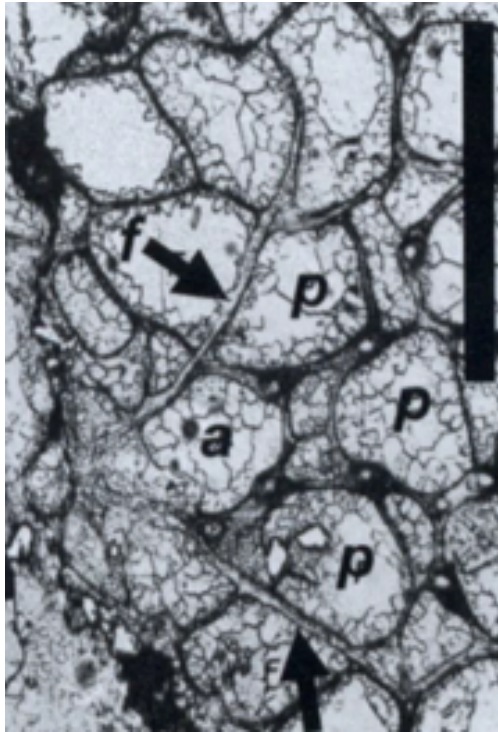


Figure 4. A thin section of a trepostome colony, showing the ancestrula (a) and three primary zooids (p) that budded from it. A characteristic V-shaped flange (f) then formed around these founding components of the colony. Scale bar = 0.5mm. After Pachut and Fisherkeller (2011, fig. 2.1).

Borings

Trepostome colonies interacted with other organisms and some of these interactions are recorded in the colony skeleton as trace fossils. Trepostome colonies commonly contain borings. This type of trace fossil is formed when an organism excavates a hard substrate, such as a bryozoan colony (Wilson, 2007; Wyse Jackson and Key, 2007). Excavation is conducted by chemical and/or mechanical erosion of a substrate. Both of these methods are types of bioerosion, which is defined as the "biological erosion of a substrate" (Wilson, 2007, p. 356). Often, bryozoan colonies were used as a substrate by organisms that produced macroborings. Macroborings are a type of boring that can be seen with the unaided eye, typically 1mm and greater in diameter (Figures 3 and 5; Wyse Jackson and Key, 2007; Wilson, 2007). Macroborings are an important part of the fossil record because they record specific behaviours over time, thus indicating evolutionary change (Wilson, 2007; Mángano et al., 2016).

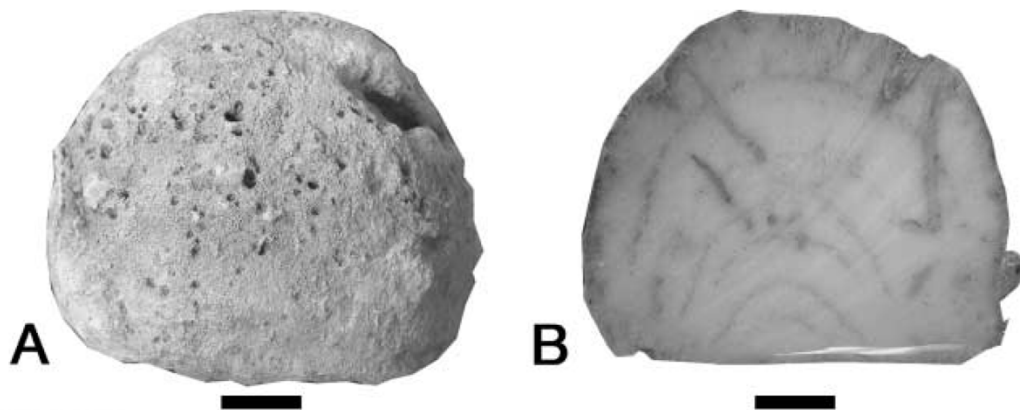


Figure 5. *Trypanites* macroborings in a hemispherical trepostome colony from the Upper Ordovician of Estonia, shown on (A) the exterior of the colony and (B) in longitudinal section. Scale bars = 10mm. After Wyse Jackson and Key (2007, fig. 4).

There are many organisms that produce borings, and these organisms have changed through geologic time. It is impossible to examine a boring and determine the organism that excavated it, so trace fossils are categorized by their morphology into ichnotaxa. An ichnogenus describes the shape and features of a trace fossil rather than the organism that created it (Wyse Jackson and Key, 2007). For example, the ichnogenus *Trypanites* refers to a cylindrical unbranched boring normal to the substrate surface (Figure 5). Many organisms have been responsible for this type of boring (Wilson, 2007).

The earliest borings are Precambrian, found in grains like ooids and pisoids. The Ordovician saw an increase in the diversity and abundance of borings that was so pronounced it has been termed the Ordovician Bioerosion Revolution (Wilson and Palmer, 2006; Mángano et al., 2016). This event represents niche diversification during this period. Overall, macroborings experienced three major diversification events, each corresponding to a general evolutionary radiation of marine organisms. These events occurred in the Ordovician, Devonian, and Jurassic (Wilson, 2007).

The most common boring found in trepostomes is *Trypanites*. As mentioned above, it is a simple cylindrical, unbranched boring that can reach impressive lengths of up to 50 times its width. This ichnogenus ranges from the Cambrian to Recent and was first described by Mägdefrau in 1932. *Trypanites* is one of only two Cambrian macroborings and one of the most common Ordovician borings (Wilson, 2007). It is a typical boring of worms and worm-like animals, though many other taxa have also been postulated as *Trypanites* borers (Wyse Jackson and Key, 2007).

Another macroboring found in trepostomes is *Sanctum*. This ichnogenus is unique to Ordovician ramose and frondose trepostomes. Like *Trypanites*, it has a circular opening, but it expands into a chamber in the bryozoan's endozone. This chamber can be a variety of shapes (Erickson and Bouchard, 2003). Wyse Jackson and Key (2007) propose that the *Trypanites* and *Sanctum* borings in their Ordovician trepostomes were excavated by the same animal. They suggest that the different boring shapes are simply a function of

the substrate. The thin endozones found in particular trepostomes would have been relatively easy for the borer to erode, giving rise to the *Sanctum* chamber shape that is only found in endozones.

The third macroboring that is found in trepostome bryozoans is *Palaeosabella*. This ichnogenus shares many similarities with *Trypanites*, so these two ichnogenera are often confused. Both have an unbranched, cylindrical shape, but *Palaeosabella* has a swollen distal end that can be described as clavate. Therefore, *Palaeosabella* and *Trypanites* are differentiated by the shape of their distal ends. The two are indistinguishable when viewed from the exterior of the substrate. *Palaeosabella* ranges from Ordovician to Recent (Wilson, 2007).

The boring *Petroxestes* is also found in trepostome bryozoans. Unlike the other three borings discussed, *Petroxestes* is slot shaped. It is defined by its elongated shape, its rounded base, and its depth that varies from shallow to deep (Wilson and Palmer, 1988). The bivalve *Corallidomus scobina* is known to have mechanically excavated these borings for domiciles, although *C. scobina* may not have been the only organism responsible for *Petroxestes* (Wilson and Palmer, 1988). *C. scobina* has been linked to *Petroxestes* because it has been found in life position in samples of these borings (Pojeta and Palmer, 1976). *Petroxestes* ranges from the Ordovician to the Miocene and is abundant in the Cincinnati Series (Wilson, 2007; Wilson and Palmer, 1988).

Trepostome bryozoans have been found with borings that do not fit the descriptions of any of these four trace fossils. Bowl-shaped borings, small cylindrical borings, and boring networks or intersecting borings have all been found in trepostomes but have yet to be identified (Vinn et al., 2022).

The macroborings found in trepostomes were excavated to form domiciles, not for predation. When boring organisms excavated bryozoans, they truncated the zooid walls that intersected their borings. As a result, these zooids must have been dead before boring or killed during the process. Boring into live zooids would not have had a serious impact on the colony because it is typically only a small portion of the colony that is bored. However, it is possible that too many borings in one colony could reduce the structural stability of the bryozoan. Additionally, if the borer was a filter-feeder, it could have impeded the ability of nearby zooids to filter-feed (Wyse Jackson and Key, 2007).

The borers likely lived in both dead and live bryozoan colonies. This deduction is evidenced by the presence of borings at all levels of the bryozoan skeleton, from the colony surface to far within the colony (Vinn et al., 2022). Additionally, repair tissue has been observed adjacent to some borings, indicating that the bryozoan was alive when it was bored. Some trepostome colonies were bored on their basal surface, which suggests that they rolled on the substrate during storms. It is reasonable to assume that zooids would die if they rested too long on the substrate (Wyse Jackson and Key, 2007). Wyse Jackson and Key (2007) suggest that due to these conditions, some borers eroded parts of the colony surface that did not contain living zooids, though other parts of the colony were alive.

To understand the borings found in trepostome colonies, these borings are examined in a variety of ways. The colonies are often sectioned longitudinally. They can also be sectioned obliquely and transversely, or left un-sectioned for examination of the colony surface. From the colony sections, borings can be counted, though this provides an underestimate of the true number of borings in a colony. Boring length, maximum width,

and cross-sectional area can also be measured, but length and cross-sectional area are underestimates as well. By contrast, maximum width can be a particularly useful measurement. Wyse Jackson and Key (2007) argue that the width of the boring represents the width of the borer, so a maximum width measurement should indicate the size of the boring organism. Qualitative characteristics are also often recorded (Wyse Jackson and Key, 2007).

Bioclaustration

Bioclaustration is a type of trace fossil that is easily mistaken for a boring. However, bioclaustration does not involve excavation, instead it occurs when an organism settles to the surface of a living host and the host then grows around the infesting organism, entombing it. Hosts need to be skeletal for this interaction to appear in the fossil record (Palmer and Wilson, 1988). When bioclaustration was first described by Palmer and Wilson (1988), the term was only applied if the infester was soft-bodied. Taylor (1990) then expanded the definition to also include skeletal infesters. These skeletal infesters include organism such as cornulitids, tabulates, and rugose corals (Vinn et al., 2021).

In fossils, bioclaustrations appear as holes in the host's skeleton. These holes may be partially or completely sealed off by the skeleton. Bioclaustration can be found in bryozoan skeletons and provides an excellent record of the biological interactions between organisms and their hosts (Palmer and Wilson, 1988; Vinn et al., 2021). This trace fossil can be distinguished from borings by the distortion of the host skeleton around the hole, rather than the truncation of the skeleton at the edges of the hole (Figure 6). The shape of the hole reflects the shape of the infester; essentially the process of bioclaustration forms an external mould of the infester through the growth of the host (Palmer and Wilson, 1988).

Bioclaustrations record not only the external morphology of the infester, but also the interaction between the infester and the host. The infester would settle on a live portion of the colony surface and in some cases, begin to grow across the surface of the bryozoan. On bryozoans, this initial settlement would interrupt the growth of the zooids below and the adjacent zooids would begin to outgrow the infester. If the host reacted quickly, it could outgrow the infester before that organism was able to expand across the colony (Palmer and Wilson, 1988). The longer it takes for a host to overgrow an infester, the more likely it is that the host will suffer serious harm from this interaction (Taylor, 1990). This harm comes as a result of several detrimental impacts the infester and its growth may have on the host. These impacts include the reduction of food supply, interfering with budding, and the initiation of a required growth response (Palmer and Wilson, 1988). In contrast, the infester likely benefited from this relationship. The bryozoan skeleton could provide protection from predation and stable substrates (Vinn et al., 2022). Given these consequences that are brought on by the infester, it is very likely that bioclaustration was a parasitic relationship.

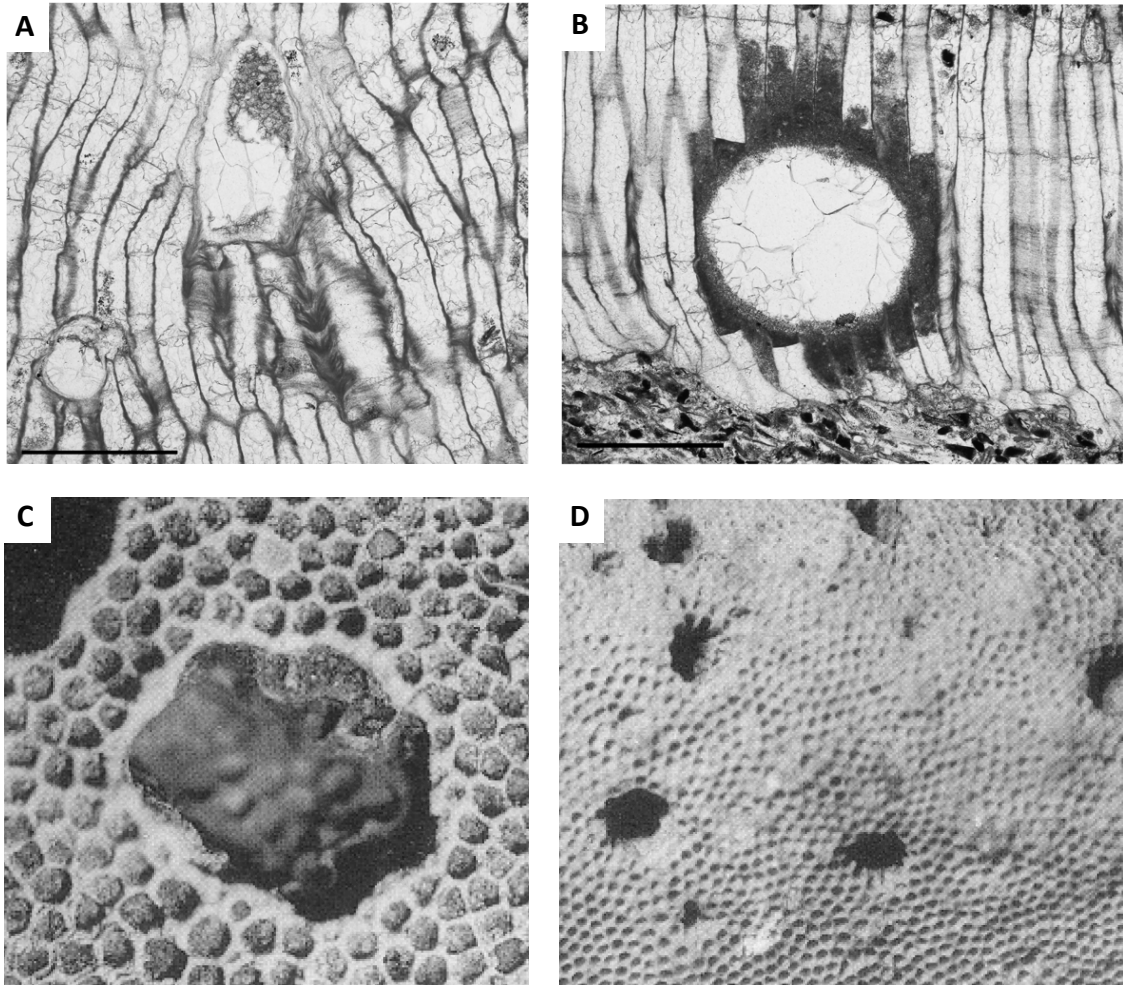


Figure 6. Differences between bioclaustration and boring as seen in Upper Ordovician trepostomes. (A) An example of bioclaustration in longitudinal section; notice how the zooids grew around the infester; (B) *Trypanites* boring in longitudinal section, where the zooid walls have been truncated; this boring has been infilled with micrite and contains a calcite tube (a ghost); (C) surface of a bryozoan colony with a depression that was originally occupied by a soft-bodied infester; this depression is an example of bioclaustration; none of the zooids are truncated; (D) surface of a bryozoan colony with *Trypanites* borings; zooid walls are truncated at the edge of the borings. (A, B) Trepostomes from the Corryville Formation of Kentucky; after Buttler and Wilson (2018, fig. 6 and fig. 7); (C, D) trepostomes from the Kope Formation of Ohio; after Palmer and Wilson (1988, fig. 1). (A, B) Scale bars = 1mm.

Ghosts and Biofilms

Ghosts are sometimes found in trace fossils, but they are not trace fossils themselves. Wyse Jackson and Key (2007, p. 240) define ghosts as "sparry cement-filled voids within larger matrix-filled borings" (Figure 6B). For ghosts to form, a boring is filled with sediment while the borer is inside. This process kills the boring organism, which then decays, leaving a void. The void is later filled with diagenetic cement. Therefore, ghosts are a cast of the borer.

Ghosts are smaller than their borings. In a study of Ordovician trepostomes and their trace fossils, Wyse Jackson and Key (2007) calculated and compared the mean boring width in their sample and the mean ghost width. They found a mean boring width of 2.3mm, which was notably wider than the mean ghost width of 1.2mm. Wyse Jackson and Key (2007) argue that this discrepancy did not exist between living borers and their borings. Rather, the width difference is the result of post-mortem shrinkage of the borer.

Like ghosts, biofilms are not trace fossils. Biofilms are the residue of organic material (Figure 7). They developed in trepostome colonies when thin layers of sediment infilled zooecial chambers, sealing the chambers. These biofilms were likely left by decaying zooids and associated decomposing bacteria and fungi. It is probable that the zooids were not alive when their chambers were sealed. After the chambers were closed off, the colony would overgrow these areas (Buttler and Wilson, 2018).

The creation of both ghosts and biofilms requires the influx of sediment. For ghosts, storms are likely the mechanism through which sediment reached and filled the borings

(Wyse Jackson and Key, 2007). In the case of biofilms, it is improbable that storms were responsible for the sediment influx. Storm sediment would be expected to coat a large portion of the bryozoan; however, where biofilms formed, only small sections of the colonies are affected. Additionally, sediment infilled chambers that are known to have been suspended from a cave ceiling. In this setting, storm sediments would be expected to dislodge as a result of gravity. Instead of storms, it is possible that the sediment influx occurred when dead areas of the colony became coated in biofilms such as bacteria or fungi. Sediment would then adhere to the biofilm and become sealed in the colony skeleton as the bryozoan grew (Buttler and Wilson, 2018).

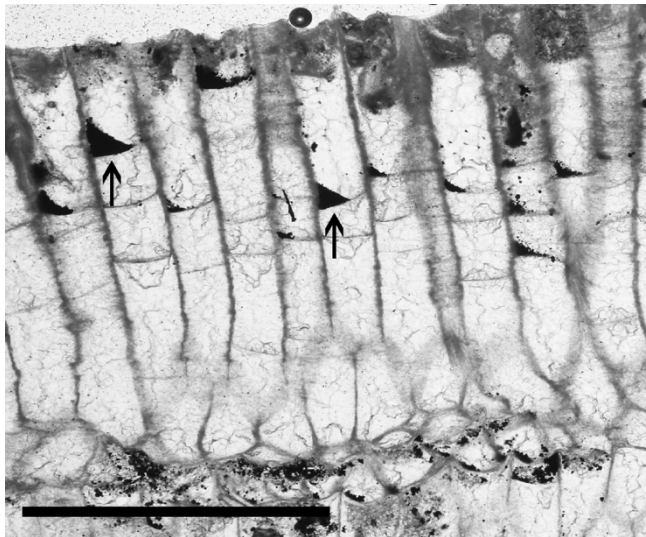


Figure 7. Biofilms sealed into the zooecial chambers of an Upper Ordovician trepostome colony from Kentucky. Biofilms are indicated with black arrows. Longitudinal section; scale bar = 1mm. After Buttler and Wilson (2018, fig. 8).

STRATIGRAPHY

Overview

In this project, trepostome bryozoan samples from three Ordovician strata were examined. These strata are the Bellevue Member, the Bull Fork Formation, and the Whitewater Formation, all of which are found in the Cincinnati Series (Upper Ordovician) of the Cincinnati Arch region (midwestern USA). The Cincinnati Series is exposed in southwestern Ohio through southeastern Indiana and north-central Kentucky. It is comprised of three stages; the Edenian Stage, the Maysvillian Stage, and the Richmondian Stage.

The Bellevue Member, Bull Fork Formation, and Whitewater Formation are fossiliferous and known to contain trepostome bryozoans (Brett et al., 2019; Singh, 1979; Utgaard and Perry, 1964).

When the Cincinnati Series was deposited, it was in a very different environment than its current setting. These strata date to the Katian stage of the Upper Ordovician. At this time, the Cincinnati region was located at a latitude approximately 20-23°S in the southern subtropics. In this position, the climate of the region was temperate to warm, occasionally semi-arid, and gave rise to large tropical storms. The region was covered by a shallow epicontinental sea that contained cool water despite its location, likely due to water at higher latitudes entering the sea through upwelling processes. The Cincinnati Arch area contained shallow subtidal through peritidal (intertidal and supratidal) environments, with the subtidal facies found in the north of its modern-day position and the peritidal to the south (Figures 8 and 9; Brett et al., 2019).

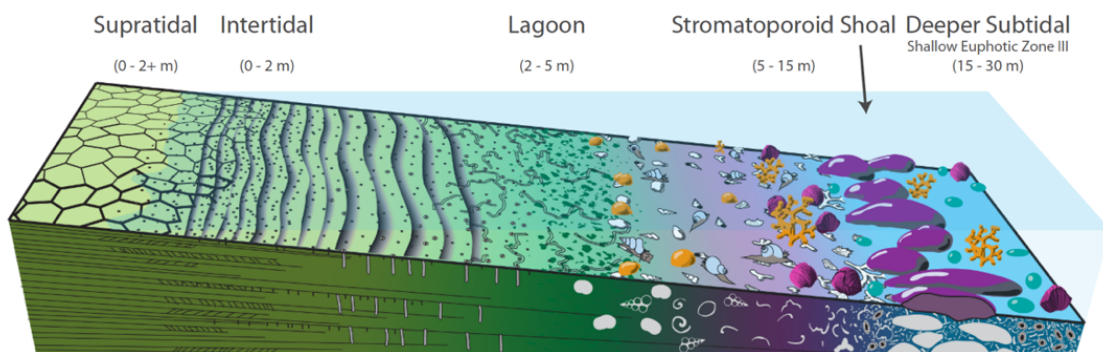


Figure 8. Simplified cross-section of the Cincinnati paleoenvironments. North is to the left of this diagram, progressing southward to the right. After Brett et al. (2019, fig. 2).

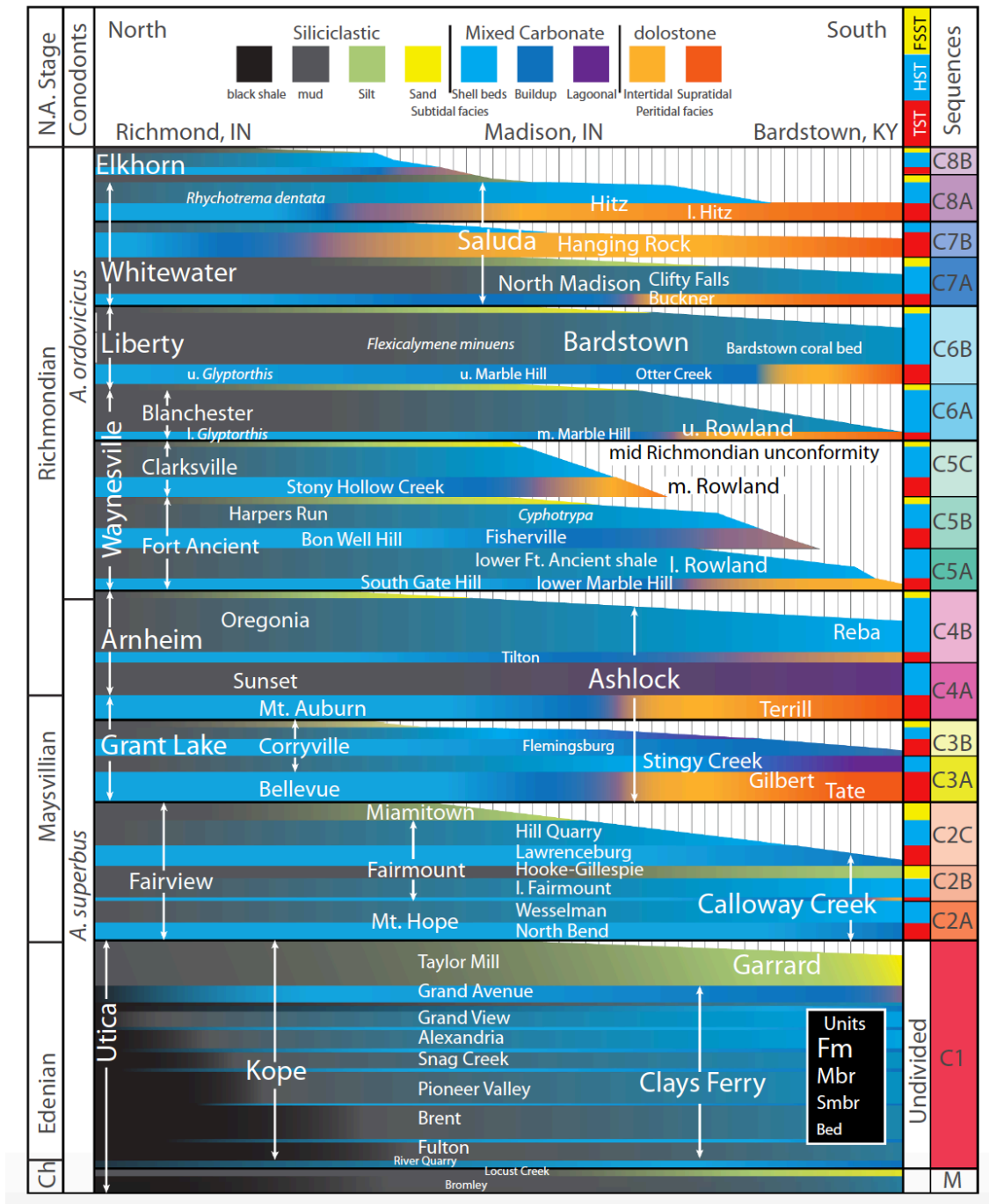


Figure 9. Sequence stratigraphy of the upper Katian of the Cincinnati Arch area. Notice the facies of the Bellevue Member (sequence C3A), the Bull Fork Formation (sequence C5A), and the Whitewater Formation (sequence C7A and C7B). Abbreviations: Fm: Formation; FSST: falling stage systems tract; HST: highstand systems tract; l: lower; m: middle; Mbr: Member; Smbr: Submember; TST: transgressive systems tract; u: upper. After Brett et al. (2019, fig. 8).

The Bellevue Member of the Grant Lake Formation

The Bellevue Member is the oldest strata from which samples originated, being part of the Grant Lake Formation, in the Maysvillian Stage (Figure 10). Note that the Maysvillian was formerly known as the MacMillan Formation in the Cincinnati region (Brett et al., 2019). The Grant Lake Formation is divided into three members; the Bellevue Member, the Corryville Member, and the Mount Auburn Member, each named for a hill in the Cincinnati area. The Bellevue Member is situated at the base of the Grant Lake Formation, between the Fairmount Member of the Fairview Formation or in some regions the Miamitown Shale, and the overlying Corryville Member (Figure 10). To the south, the Bellevue meets the thick dolomitic siltstones of the Tate Member, the Bellevue's equivalent in the Ashlock Formation (Brett et al., 2019). Of these boundaries, the contact between the Bellevue Member and the Fairmount Member is the most distinct.

The contact between the Bellevue Member and the Fairmount Member is an unconformity. This erosional surface is considered a major sequence boundary (Brett et al., 2019). The Bellevue and the Fairmount have very different characteristics. The Fairmount is composed predominantly of sparsely fossiliferous, planar-bedded limestone, with approximately 50% shale. By contrast, the Bellevue is fossiliferous limestone, with wavy to irregular bedding. It also contains less shale (17-47%) than the Fairmount (Schumacher et al., 1991).

The rocks that form the Bellevue Member have many noteworthy characteristics. These rocks are generally grainstones and packstones, with some shale (Brett et al., 2019). The Bellevue limestones vary from thin to thick and the shale is thin. Overall, the Bellevue Member's thickness ranges from less than 6m to greater than 21m. The thickness is generally uniform but thickens to the east and southeast (Schumacher et al., 1991). The Bellevue facies is subtidal (Figures 8 and 9), roughly 5-10m below wavebase. Additionally, this stratum shows occasional high-energy sediment disturbance. It is a fossiliferous member, containing invertebrate fossils such as bryozoans, brachiopods, edrioasteroids, tubeworms, and crinoids. Additionally, many tempestites have been found in the Bellevue Member, indicating that there were large tropical storms during its formation (Shroat-Lewis et al., 2011). Northwest of the Cincinnati Arch, the Bellevue contains crinoidal grainstones with some herringbone cross bedding and oncolites. These deposits indicate marine transgression and therefore relative sea level rise during the time of deposition. Following this change, sea level rise rates decreased in the Corryville Member, showing regression (Brett et al., 2019).

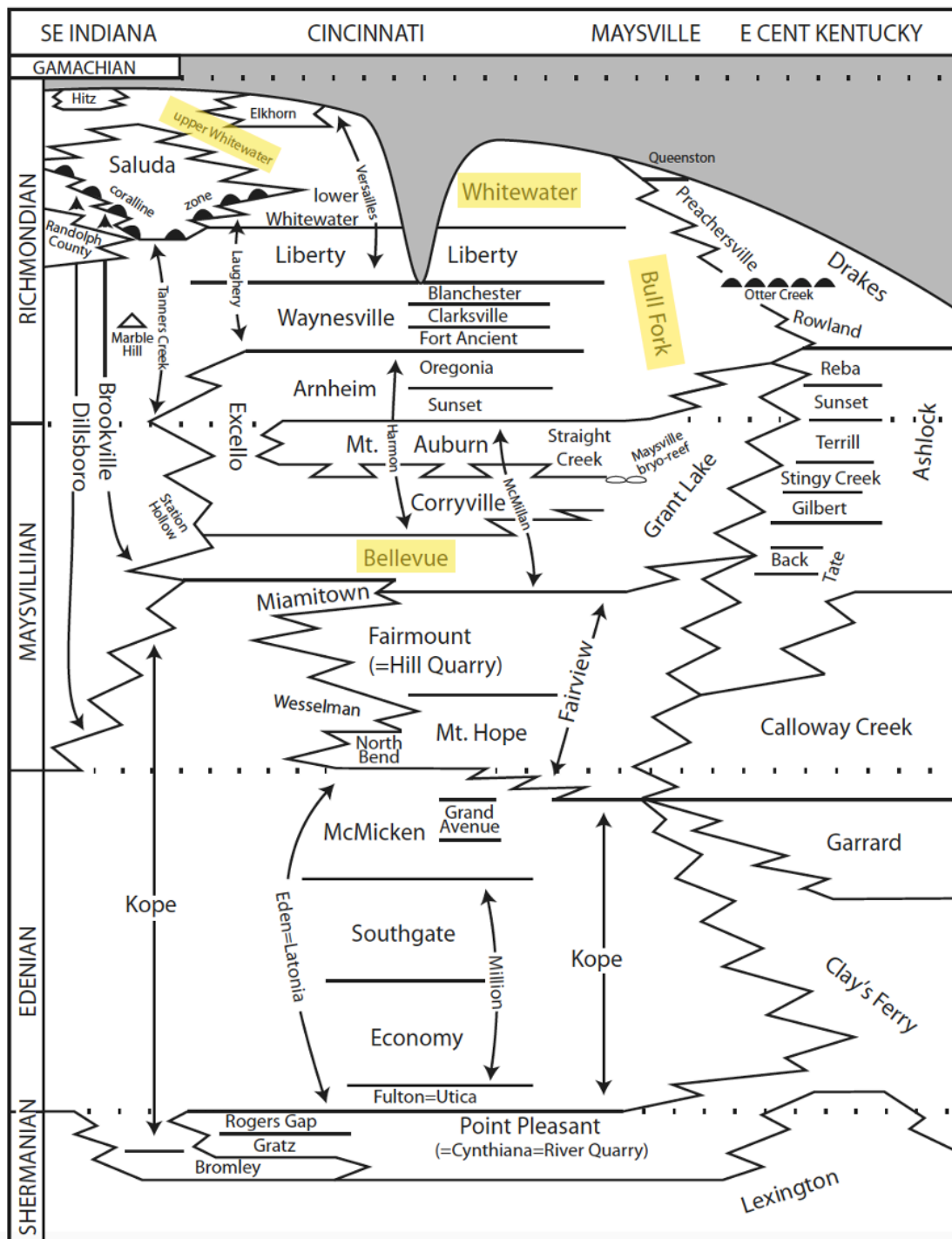


Figure 10. Cross-sectional diagram of the Cincinnati strata. The strata from which samples for this study were taken are highlighted in yellow. After Brett et al. (2019, fig. 4).

Towards the upper reaches of the Bellevue Member, there are several features that differentiate it from the overlying Corryville Member. Besides the transgression present in the Bellevue Member and the regression in the Corryville Member, the deposits also have different proportions of shale. Like the Bellevue, the Corryville is composed predominantly of limestone and shale, however the Corryville Member has a greater shale content (34-74%), compared to the 17-47% shale in the Bellevue. Furthermore, the Corryville shale is much less fossiliferous than that of the Bellevue Member. The Bellevue comprises wavy to irregularly bedded limestone or fissile-parted shale, whereas the Corryville contains limestone with planar or lenticular bedding or platy-parted shale. This difference leads to a sharp contact between the two in some areas (Schumacher et al., 1991). Brett et al. (2019) suggest that this boundary is particularly pronounced due to flooding and sediment starvation. However, the contact is not distinct for its entire extent. There is some intertonguing between the Bellevue Member and the Corryville Member. Additionally, in some areas the contact is gradational, with a 0.3-2m transition zone. Where this is the case, the contact is arbitrarily assigned to the middle of this zone (Schumacher et al., 1991).

The Bull Fork Formation

The Bull Fork Formation is a Richmondian stratum found on the eastern side of the Cincinnati Arch. This formation is equivalent to the lower Rowland to the west and the Arnheim and Waynesville Formations of Ohio (Brett et al., 2015; Brett et al., 2019). The formation is well exposed on the southwestern edge of the Cincinnati Arch (from Mount Sterling to Flemingsburg Kentucky) and thins abruptly to the south (from Owingsville to Mount Sterling Kentucky). This thinning is possibly a regionally angular unconformity (Brett et al., 2015).

The Bull Fork sediments were deposited in a distal foreland basin that was subdivided by a platform (the Lexington Platform). Due to this platform, the sediments accumulated on a gentle slope. The sediments are composed of mixed siliciclastic-carbonate rocks. Siliciclastics originate from areas uplifted during the Taconic Orogeny. Carbonates developed locally. The formation represents peritidal facies to the south, progressing through shoal and relatively deep ramp environments to the north (Brett et al., 2015).

The Bull Fork Formation is a highly fossiliferous stratum of mixed composition. Its carbonate deposits grade from micritic wackestones, through skeletal grainstones, mudstones, muddy packstones, and occasionally grainstones. These deposits represent shallow marine facies, through ramp facies, to facies below wavebase. The base of the formation is comprised of a shale interval, the *Cyphotrypa* shale, named for this interval's abundance of the small bryozoan *Cyphotrypa clarksvillensis*. This layer also contains brachiopods and bivalves, but apart from *Cyphotrypa* bryozoans, it is sparsely fossiliferous. This shale is overlain by 15-20cm of packstone, the upper surface of which is almost entirely coated in *C. clarksvillensis*. This surface is therefore referred to as the "ball bryozoan bed." These bryozoans were most often attached to bivalves, evidenced by the external moulds of bivalves found on the base of bryozoan colonies. The ball bryozoan bed is overlain by a poorly exposed, fossiliferous dolomitic mudstone interval, especially rich in bryozoans and the brachiopod *Hebertella*. The limestones of the Bull

Fork Formation are exceptionally rich in bryozoans (particularly *Cyphotrypa*), colonial corals, stromatoporoids, brachiopods, and oncolites (Brett et al., 2015).

The Whitewater Formation

The Whitewater Formation is part of the Upper Richmondian (Katian). This formation lies with the Liberty Formation below and the Elkhorn Formation above, (Figure 10; Brett et al., 2019).

The Whitewater Formation took its name from the Whitewater River, along which sections of the formation are exposed at Richmond, Indiana. The formation is found in Ohio and Indiana and it is subdivided into three members. The oldest member is the lower Whitewater member, above which is the Saluda Member, followed by the upper Whitewater member (Brett et al., 2019). The Saluda Member extends farther laterally than the lower and upper Whitewater members, essentially wedging between them (Browne, 1964). Beyond the lower and upper Whitewater members, the Saluda Member becomes large enough to be its own formation. The Saluda member corresponds to merely the uppermost member of the Saluda Formation, therefore the Saluda Member and Saluda Formation are only partially equivalent (Brett et al., 2019).

The Whitewater Formation is complex with a number of unconformities. Within the formation, eight subaerial erosional surfaces are recognized. One prominent unconformity exists at the base of the formation. For 1-3m directly above the Liberty-Whitewater contact, there are "abundant reworked concretions and limestone clasts" (Brett et al., 2019, p. 24), indicating substantial erosion. Above this bed are 2-3m of limestones, after which the dolomitic wackestones of the Saluda Member begin (Brett et al., 2019). This member is approximately 9m thick but thins southward (Browne, 1964). The upper Whitewater is roughly 8-10m thick and is composed primarily of grainstones-packstones (Brett et al., 2019).

Overall, the Whitewater Formation is predominantly limestone. Sediments in the Whitewater Formation are a mixture of carbonates from the epicontinental sea basin and sediments transported into the region from mountains (the Taconic Mountains; Figure 9). In the lower Whitewater, there is evidence of a moderate rise in carbon-13, called the Whitewater excursion. In the upper Whitewater, carbon-13 levels began a more pronounced increase that continued into the Elkhorn Formation and is therefore termed the Elkhorn excursion (Brett et al., 2019).

The epicontinental sea environment was conducive to Ordovician marine life and led to an exceptional fossil record being conserved in the Whitewater strata. The Whitewater Formation is highly fossiliferous, containing remarkably well-preserved invertebrate fossils. The reworked sediments of the lower Whitewater contain most notably bryozoans, corals, and edrioasteroids. The Saluda Member is less fossiliferous, containing moderate amounts of invertebrate fossils, most prominently molluscs and corals (Brett et al., 2019; Browne, 1964). The upper Whitewater is rich in brachiopods and bryozoans. Overall, this formation houses a variety of other fossils, including trilobites, gastropods, and ostracods (Brett et al., 2019; Browne, 1964). Desiccation cracks are also found in the Whitewater (Brett et al., 2019). The Whitewater Formation contains an excellent record of Katian marine systems and organisms.

METHODS

Macrophotography

Bryozoan samples used in this study were photographed before they were prepared for analysis. Photographs were taken in the College of Wooster Earth Sciences photography lab using a Nikon Coolpix B700 camera. Employing Preview software, digital scale bars were added to these photographs. In some cases, colour balance was adjusted to most accurately depict the appearance of the samples.

Identification

Specimens were identified using acetate peels of the colonies in tangential section. Tangential peels were obtained by grinding an external edge of the colony and preparing the ground surface as described below. The acetate peel was then examined under the microscope, using the 4x and 10x objectives. Subsequently, the peel was compared to standards for a variety of trepostome species, using descriptions and microscope images found in Singh (1979) for the Bellevue samples, Brown and Daly (1985) for the Bull Fork sample, and Utgaard and Perry (1964) for the Whitewater samples.

Acetate Peels

To examine the internal morphology and trace fossils present in trepostomes, acetate peels were made from trepostome specimens. Acetate peels are detailed replicas of surfaces on or within a sample that allow these surfaces to be studied microscopically (Wilson and Palmer, 1989). To make an acetate peel, first a flat surface was made by either sawing through the sample or grinding an external edge of the sample. The flat surface was then polished using a slurry of water and 3.0 μ m aluminum oxide on a glass plate. Next, the sample was washed to remove any grit. After washing, the polished surface was suspended in a solution of 5% hydrochloric acid for approximately 15 seconds, etching the polished surface. The specimen was then removed from the acid and promptly dunked in water. Specimens were then left to dry. Once dry, the etched surface of the specimen was flooded with acetone and covered with a thin piece of acetate (sold as 0.003 inches thick). Specimens were let sit for at least five minutes before removing the acetate. The piece of acetate was left with an impression of the etched surface. This acetate impression could then be examined microscopically. In order to perform this microscopic examination, the acetate was trimmed to size and sandwiched between two glass slides. The slides were secured together with tape and then labelled (Wilson and Palmer, 1989). Each peel was labelled with a unique code that indicated the locality from which the specimen originated and the sample from which the peel was taken.

Microscopic Examination

Acetate peels were examined microscopically using a Nikon Eclipse E400 POL petrographic microscope at various magnifications. Areas of interest were photographed using an Infinity 5 Teledyne Lumenera camera and Infinity Analyze software. Where peels had particular features of interest, their associated sample was mailed to Quality Thin Sections, where they were made into thin sections. These thin sections were then microscopically examined in the same manner as the peels.

SAMPLES AND LOCALITIES

Five colonies were cut and examined for their growth patterns and evidence of interaction with other organisms. These colonies were collected from the Whitewater Formation, Bellevue Member, and Bull Fork Formation at three separate localities (Table 1; Figure 11). They were retained in the College of Wooster collection. The colonies are all massive trepostomes except for sample C/W-148-2, which is a bifoliate trepostome that had overgrown a ramose colony (Figure 12). The massive colonies generally grew outwards in all directions (Figure 13). Five species were represented in this study.

Table 1. Locality and taxonomic identification of trepostome colonies analyzed in this study. Taxonomic identification was determined by comparing acetate peels of tangential sections to descriptions and images in Utgaard and Perry (1964; samples C/W-148-1, C/W-148-2), Singh (1979; samples C/W-152-1 and C/W-152-2), and Brown and Daly (1985; sample C/W-153-1).

Colony ID	Formation and Locality	Species
C/W-152-1	Bellevue Member; Boone County, Kentucky (N 39.08121°, W 84.79230°)	<i>Amplexopora robusta</i>
C/W-152-2	Bellevue Member; Boone County, Kentucky (N 39.08121°, W 84.79230°)	<i>Amplexopora (?) filiasa</i>
C/W-153-1	Bull Fork Formation; Mason County, Kentucky (N 38.58518°, W 83.70157°)	<i>Dekayia stidhami</i>
C/W-148-1	Upper Whitewater; Wayne County, Indiana (N 39.78631°, W 84.90318°)	<i>Monticulipora epidermata</i>
C/W-148-2	Upper Whitewater; Wayne County, Indiana (N 39.78631°, W 84.90318°)	<i>Peronopora pachymura</i>

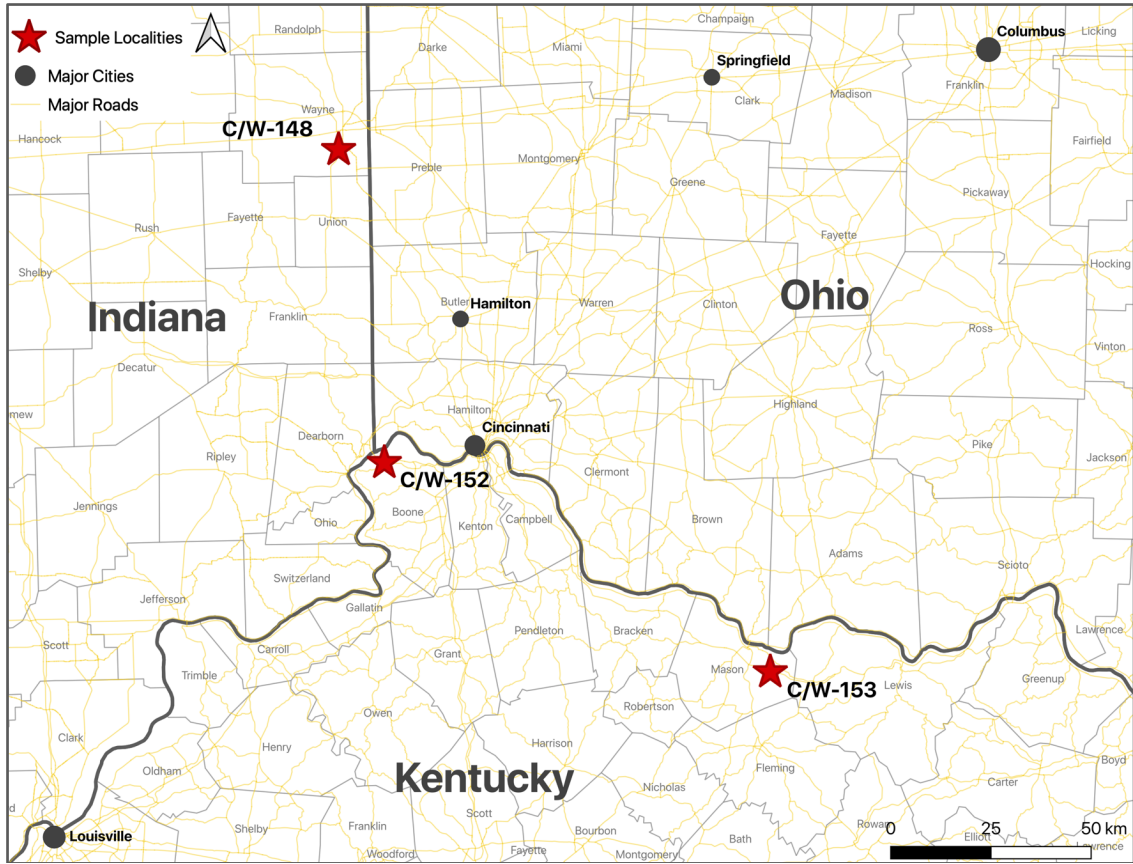


Figure 11. Locality map. Upper Whitewater samples originate from C/W-148, Bellevue Member samples from C/W-152, and the Bull Fork sample from C/W-153. Map projection: WGS 84 / UTM zone 16N. Created using QGIS software and data from the National Atlas of the United States (2014) and United States Census Bureau (2018).



Figure 12. Trepostome bryozoan colonies. (A) Sample C/W-153-1, one of the massive trepostomes examined in this study; *Dekayia stidhami* from the Bull Fork Formation; (B) sample C/W-148-2, a bifoliate trepostome (*Peronopora pachymura*) from the Whitewater Formation. Notice the ramose bryozoan that was overgrown by this bifoliate colony.

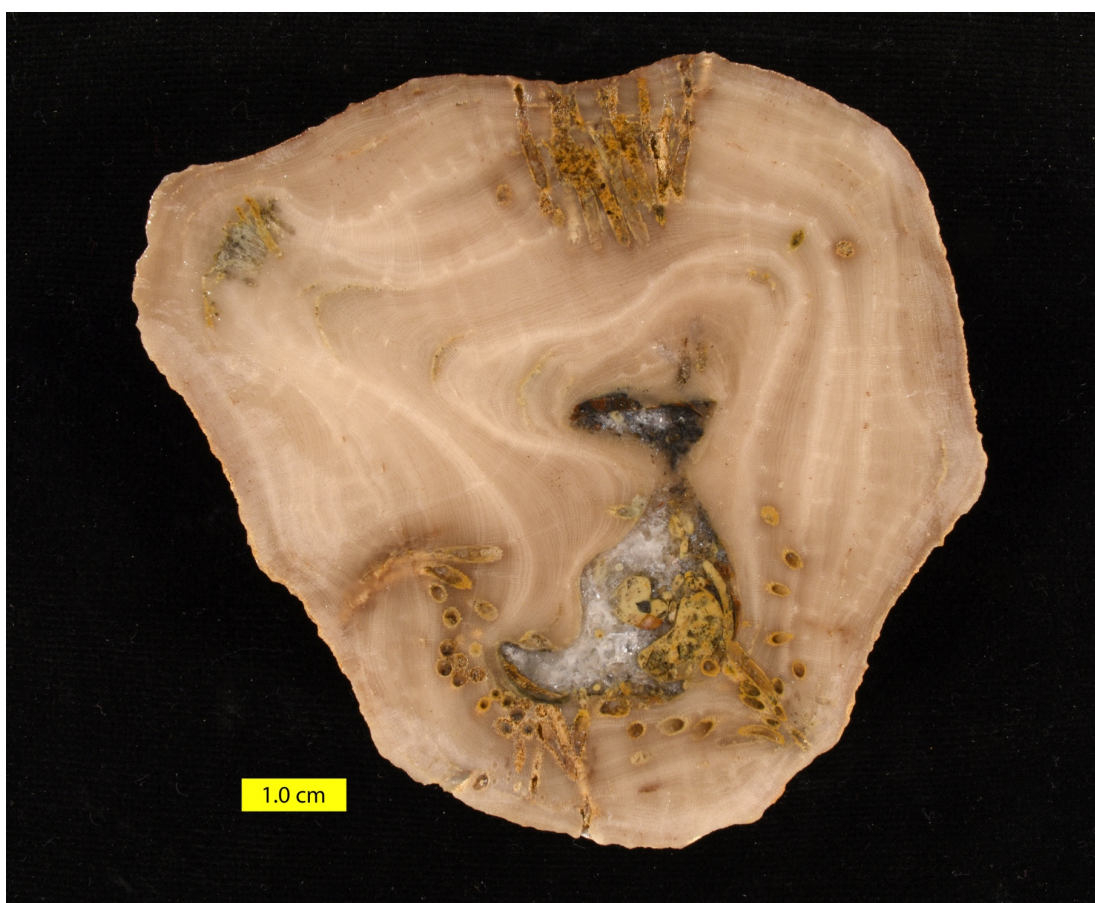


Figure 13. Section through sample C/W-152-1; *Amplexopora robusta* from the Bellevue Member. This colony grew outwards in all directions. Photo by Mark Wilson, 2021.

RESULTS

Growth Patterns

The bryozoan colonies record the history of their growth. In some areas of the colonies, the growth was uniform. In other areas, the growth was chaotic with many different directions of growth.

Changes in growth were typically observed in conjunction with damage or disturbance to the bryozoan skeleton. One such growth pattern involves the colony growing laterally over a disturbance such as a boring, essentially roofing over that disturbance (Figure 14). These "roofing structures" were the most common reaction to damage found in this study and were observed in samples C/W-148-1, C/W-152-2, and C/W-153-1.

A similar growth structure is formed by zooids budding into a cavity, then angling upwards to resume normal growth (Figure 14). Unlike roofing structures, this type of growth fills in the cavity. Examples of this structure were observed in this samples C/W-152-1 and C/W-152-2.

Wilson et al. (2021) describe three trepostome growth responses to damage. These include the roofing and infilling structures described above, as well as a third, tent-like structure. This structure occurs as the zooids grow upwards and inwards over a disturbance, sealing a cavity in the skeleton. No tent-like structures were uncovered in this study.

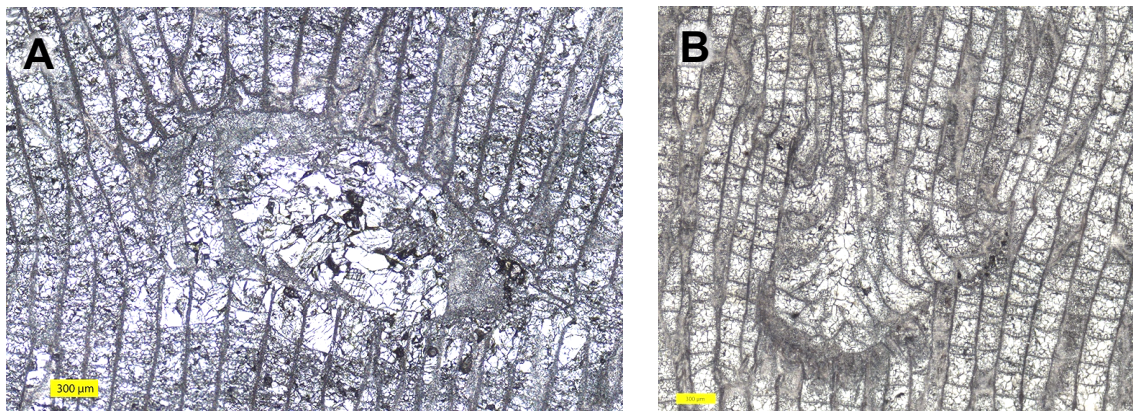


Figure 14. (A) Longitudinal section through a "roofing structure," zooids were budded across the top of the disturbance, sealing it in the colony skeleton; sample C/W-152-2, longitudinal section; (B) a growth structure where the zooids angled inwards to fill a cavity; sample C/W-152-1, longitudinal section. Scale bars = 300µm.

There is one final growth pattern that was observed several times in this study. This structure is formed by zooids that appear to radiate from a disturbance such as a boring (Figure 15). This radiating structure was found in samples C/W-152-2 and C/W-153-1.

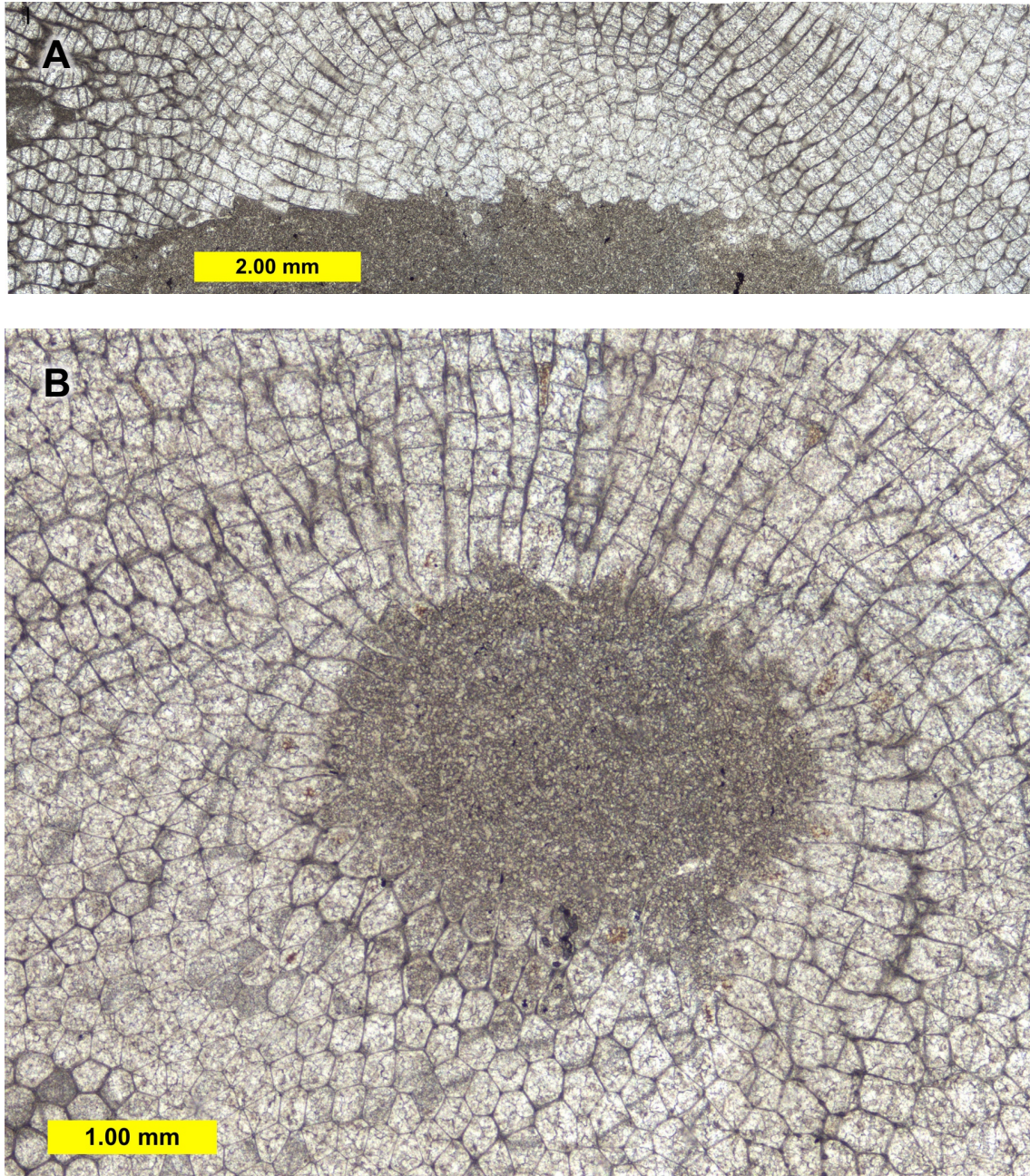


Figure 15. Structures of zooids radiating from borings. (A) Sample C/W-152-2; (B) sample C/W-153-1.

Borings

In this examination of Ordovician trepostome colonies, many borings were observed. The most common borings were *Trypanites*, which were observed in every sample (Figure 16). Additionally, several branched cylindrical borings were observed, but only in sample C/W-153-1 (Figure 17). A wide range of boring sizes were present. Though it is difficult to quantify boring size due to the restrictions of a planar cut through a non-planar boring, the borings appeared to vary from 200 μ m to 9000 μ m in diameter.

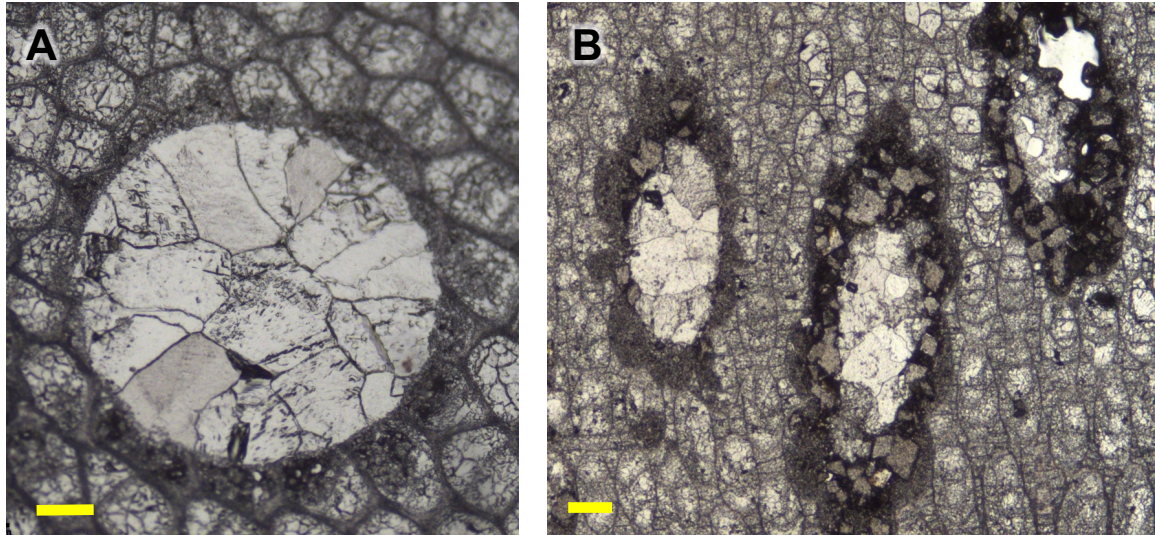


Figure 16. *Trypanites* borings with calcite ghosts. (A) *Trypanites* boring in cross-section, sample C/W-152-1; (B) sample C/W-148-2, oblique section. Scale bars = 200 μ m.

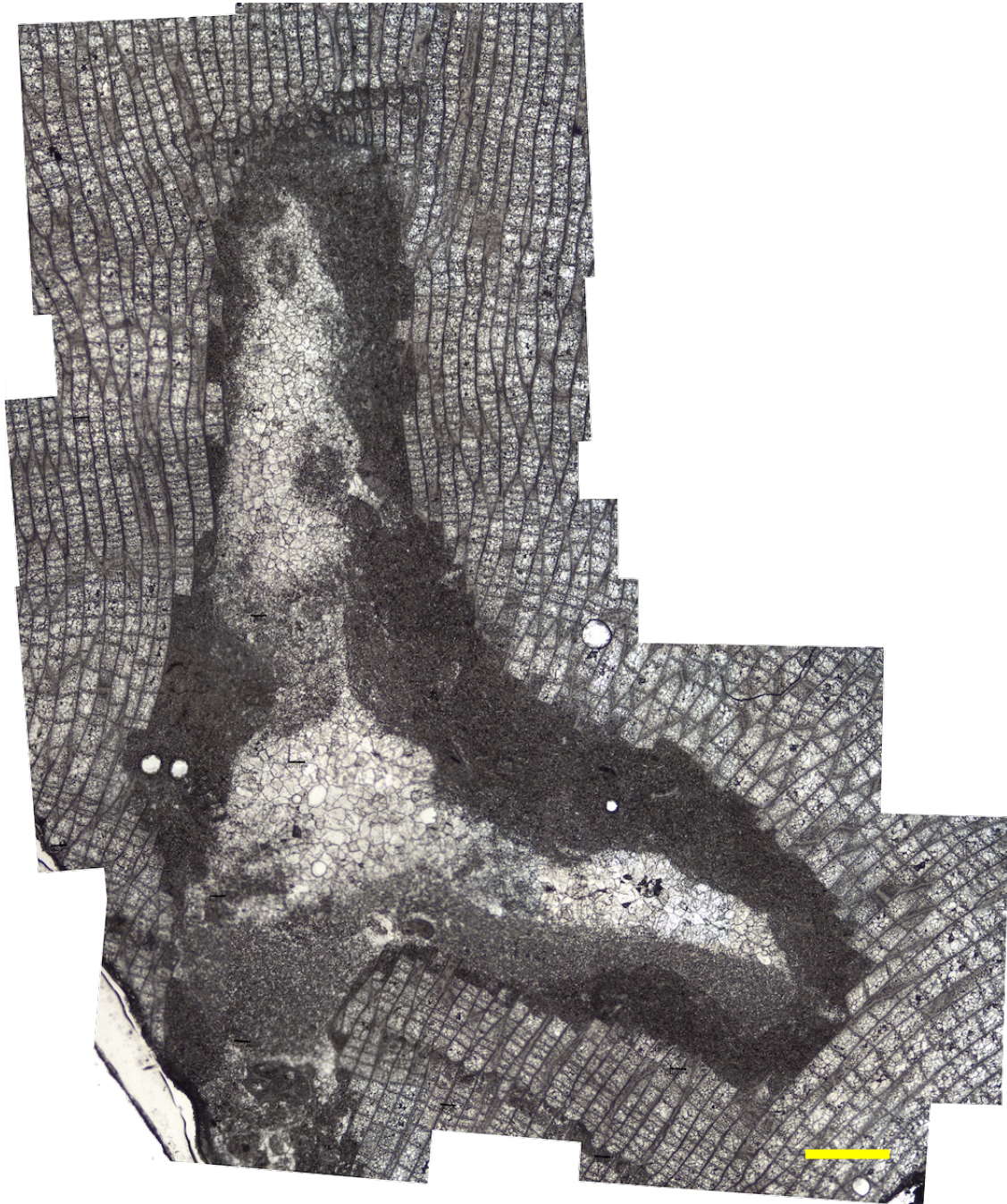


Figure 17. Branched boring with calcite ghost. Notice the dark sediment surrounding the ghost and the lighter sediment at the base of the ghost. See also the roofing structure above the boring. Sample C/W-153-1, longitudinal section. Scale bar = 1mm.

Some borings were associated with changes in bryozoan growth, others were not. Some borings cut roughly through the bryozoan skeleton, with no associated change in bryozoan growth. These borings were rimmed by roughly broken zooecial walls, with the boring cavity ending at zooecial diaphragms (Figure 18). Conversely, other borings were associated with changes in growth. These changes include the roofing and radiating structures described above. Additionally, some borings were encompassed by terminal diaphragms and basal laminae (Figure 18). These structures were accompanied by thickened zooecial walls near the boring.

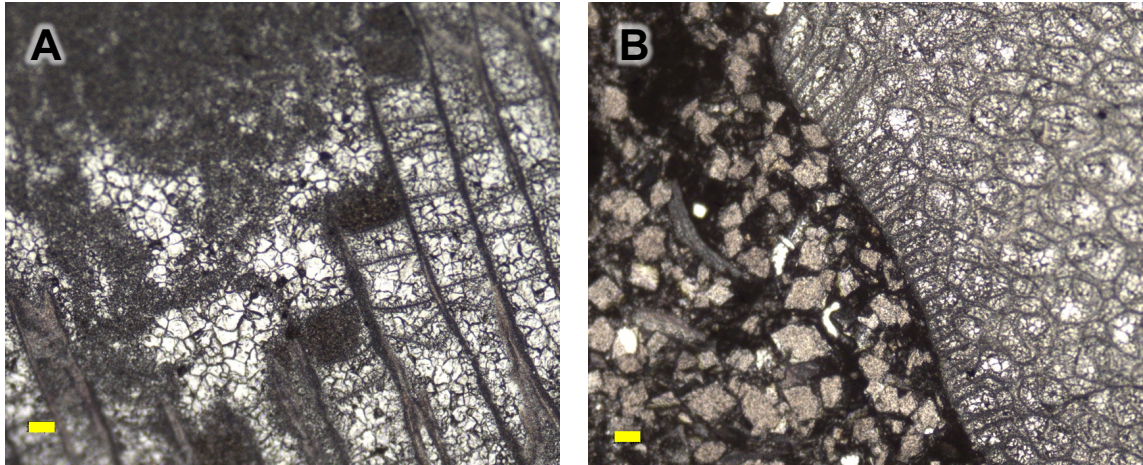


Figure 18. Boundaries between borings and zooecial chambers. (A) Roughly broken zooecial walls with the boring cavity ending at diaphragms; sample C/W-153-1, longitudinal section; (B) smooth boundary with terminal diaphragms and thickened zooecial walls; sample C/W-148-2, oblique section. Scale bars = 100 μ m.

Tubes

Some tube-shaped disturbances to bryozoan growth were found in samples CW-148-1, C/W-152-2, and C/W-153-1. These tubes have relatively thick walls and the insides of the tubes are filled with sparry calcite (Figure 19). Tubes sectioned lengthwise appeared to have jagged edges (Figure 19). The tubes found in this project occurred in conjunction with changes in bryozoan growth, including terminal diaphragms, thickened zooecial walls, and roofing structures. Similar calcite-filled tubes were discussed by Holland (1988) in his investigation of Ordovician brachiopods.

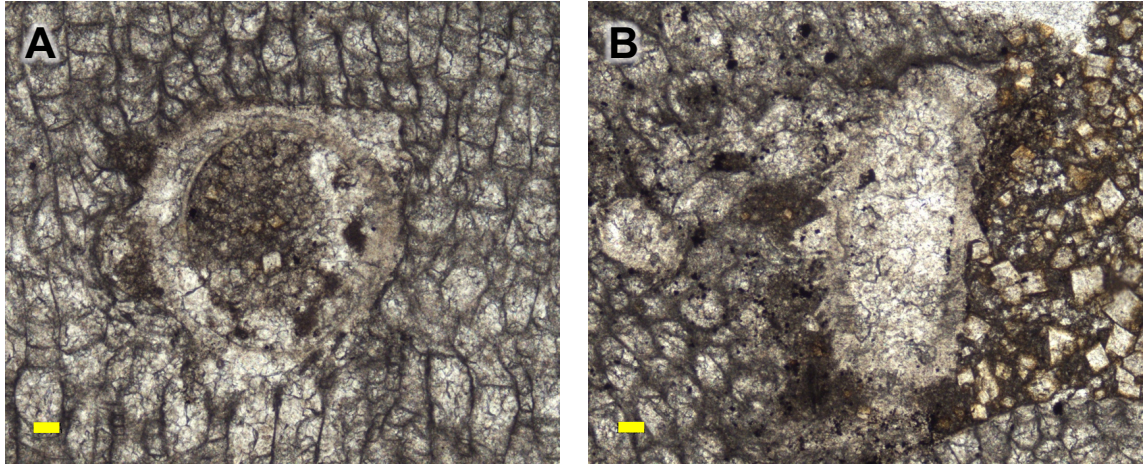


Figure 19. Calcite tube-shaped disturbances; (A) with roofing structure above; (B) with jagged edges. (A, B) Sample C/W-148-1, longitudinal section. Scale bars = 100 μ m.

An additional tube-shaped structure was found in this study. Only one example of this structure was observed, it was found in sample C/W-152-2. It is a holdfast and tube structure, which comprises a flat-topped tube emerging from a small cavity in the colony skeleton (Figure 20).

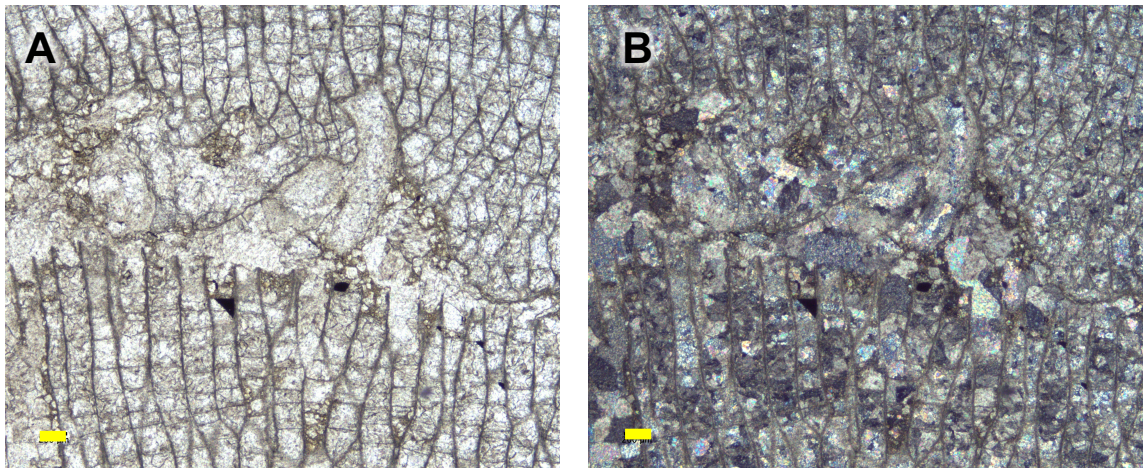


Figure 20. Holdfast and tube structure; (A) PPL; (B) XPL. (A, B) Sample C/W-152-2, longitudinal section. Scale bars = 200 μ m.

Infilling Materials

The borings and other disturbances were all infilled. A number of different infilling materials were observed. These materials were sparry calcite cement (all samples), dolomite rhombs (all samples), biosparite (samples C/W-148-1 and C/W-148-2), micrite (all samples), prismatic calcite (samples C/W-148-1, C/W-152-1, and C/W-153-1), and rarely calcium phosphate (samples C/W-152-2, C/W-153-1; Figures 21 and 22). Cavities in the skeleton were observed to contain any one of these materials, or a combination thereof.

Like the borings, the calcite ghosts found in these borings were typically cylindrical with rounded ends (Figures 16 and 17). Some non-cylindrical ghost shapes were found, but these non-cylindrical shapes were unique and were not found repeated within or between colonies.

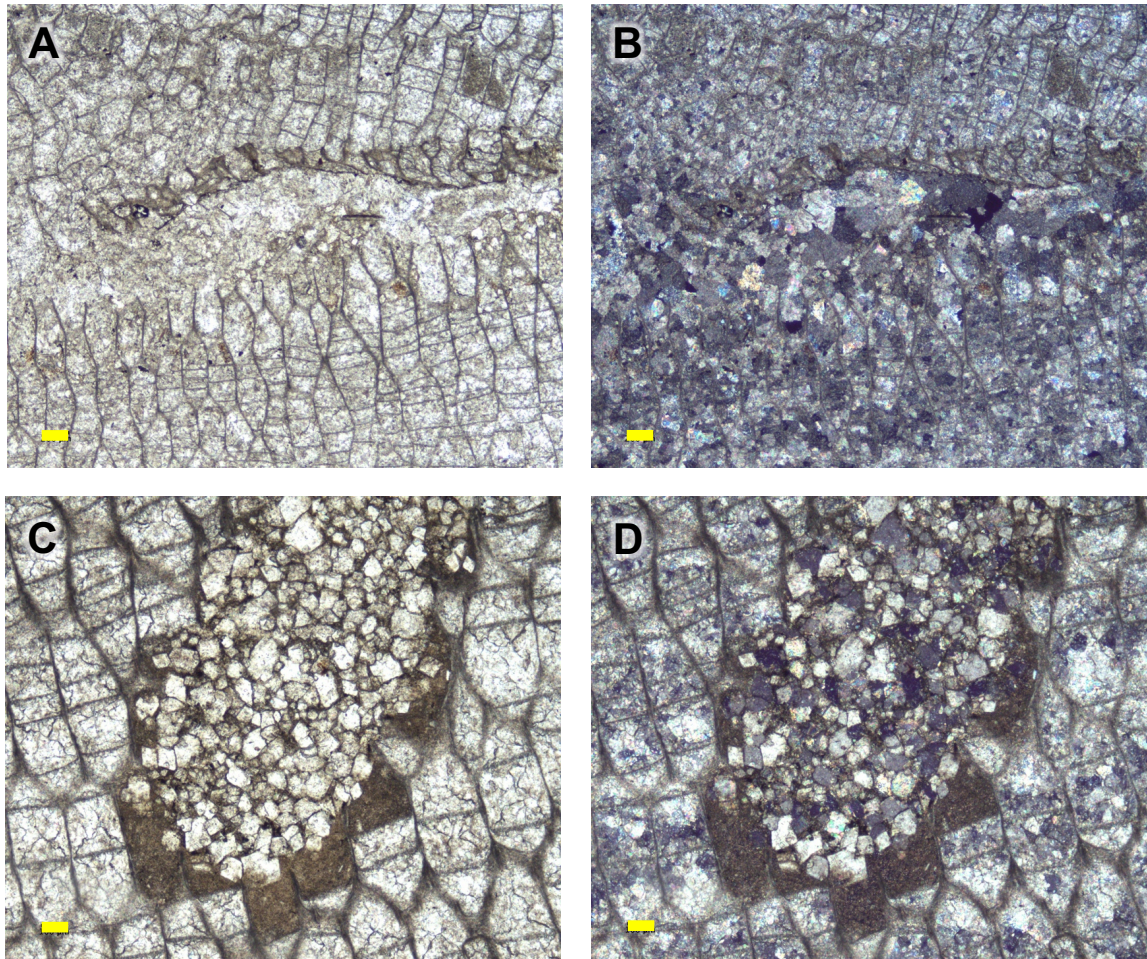


Figure 21. Infilling materials. (A) Calcite cement in PPL and (B) XPL; sample C/W-152-2, longitudinal section; (C) boring containing dolomite rhomb fill and calcium phosphate margins in PPL and (D) XPL; sample C/W-152-2, oblique section. Scale bars (A, B) = 200 μ m; (C, D) = 100 μ m.

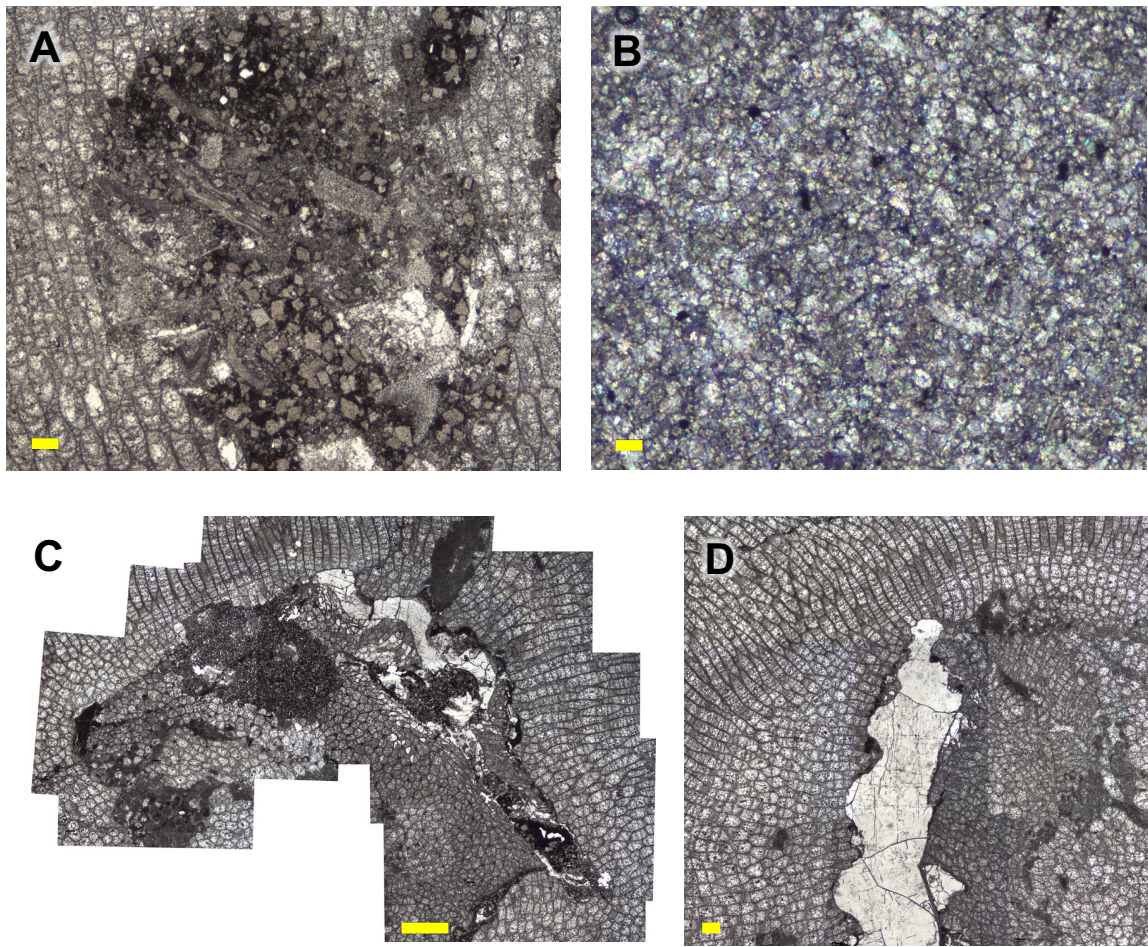


Figure 22. Infilling materials. (A) Biosparite; sample C/W-148-2, oblique section; (B) micrite; sample C/W-153-1; (C, D) prismatic calcite; sample C/W-153-1. Scale bars (A, D) = 200 μ m; (B) = 40 μ m; (C) = 1.0 mm.

Sparry calcite was often found in conjunction with other infilling materials. These materials often surrounded calcite ghosts, filling in the space between the ghosts and the boring walls. Sediments also appeared within the ghosts (Figures 16 and 17).

The features composed of prismatic calcite formed a variety of shapes, the majority of which had ridges (Figure 22).

Phosphate was observed in samples C/W-152-2 and C/W-153-1. It appeared to fill zooid chambers immediately surrounding skeletal disturbances (Figure 21).

Self-Overgrowths and Brown Bodies

Self-overgrowths were common in the trepostomes studied and were observed in every sample. These surfaces are an area where bryozoan growth halted and the zooecial chambers terminated, then the colony overgrew these surfaces (Figure 23). The earlier

growth and overgrowth are frequently separated by a thin layer of sediment. Additionally, they often grow in different directions.

Brown bodies were often seen in the zooecial chambers directly below self-overgrowths (Figure 23). Brown bodies form where organic material (i.e. the zooid) was sealed into the zooecial chamber (Buttler and Wilson, 2018). Though brown bodies were typically found beneath self-overgrowths, they were not limited to these settings. The brown bodies were generally located in the centre of the zooecial chamber.

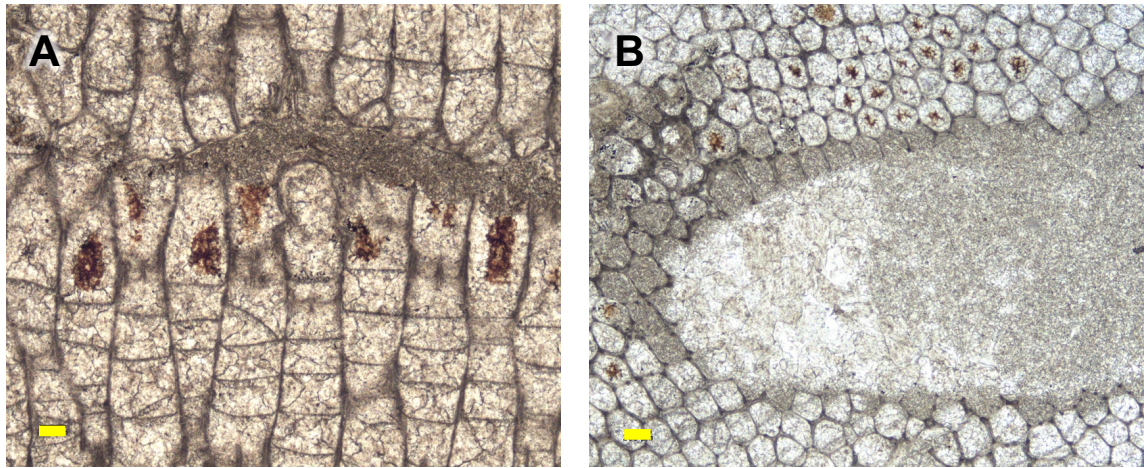


Figure 23. Brown bodies present at the centre of zooecial chambers. (A) Self-overgrowth with brown bodies below; notice the sediment coating the overgrowth surface; sample C/W-153-1, longitudinal section; (B) sample C/W-153-2, transverse section. Scale bars (A) = 100 μ m; (B) = 200 μ m.

DISCUSSION

Colony Disturbance and Damage Control

Many borings cut roughly through the trepostome colonies with no associated change in colony growth. The rough edges of these borings indicate that they were excavated mechanically rather than chemically. The lack of bryozoan response to this type of boring suggests that these borings, or at least the parts of the borings through which the colonies were sectioned, were excavated into an area without live zooids.

In other instances, colony disturbances were associated with changes in bryozoan growth. This association suggests that the disturbance affected a living surface of the colony and prompted a growth reaction from the bryozoan. In each example, the growth response closed a cavity created by the disturbance. Except examples where zooids infilled the cavity entirely, the cavities were preserved in the bryozoan skeleton. These cavities are therefore a form of bioclaustration.

Sedimentation

Given the presence of multiple varieties of sediment within individual disturbances, it appears that infilling occurred in multiple steps. The first generation of sediment appears to have been deposited while the boring was occupied, filling the space around the occupant. Then the occupant would die, leaving an external mould in that sediment. A second generation of sediment might then enter that void and partially fill the mould. Subsequently, the bryozoan would overgrow the boring. Eventually, calcite cement would fill the bryozoan and boring, creating a ghost (Figures 17 and 24).

Multiple generations of sediment functioned as geopetal structures. The second generation of sediment collected in the bottom of the boring at the time of deposition. The spheroidal shape of certain trepostome species, where the zooids grew out from the interior in all directions, suggests that the orientation of the colonies was not constant during their lifetimes. The geopetal structures support this interpretation of trepostome life modes, but the occurrence of these structures was too rare to provide conclusive evidence. Understanding of trepostome life modes could benefit from future investigation of geopetal borings.

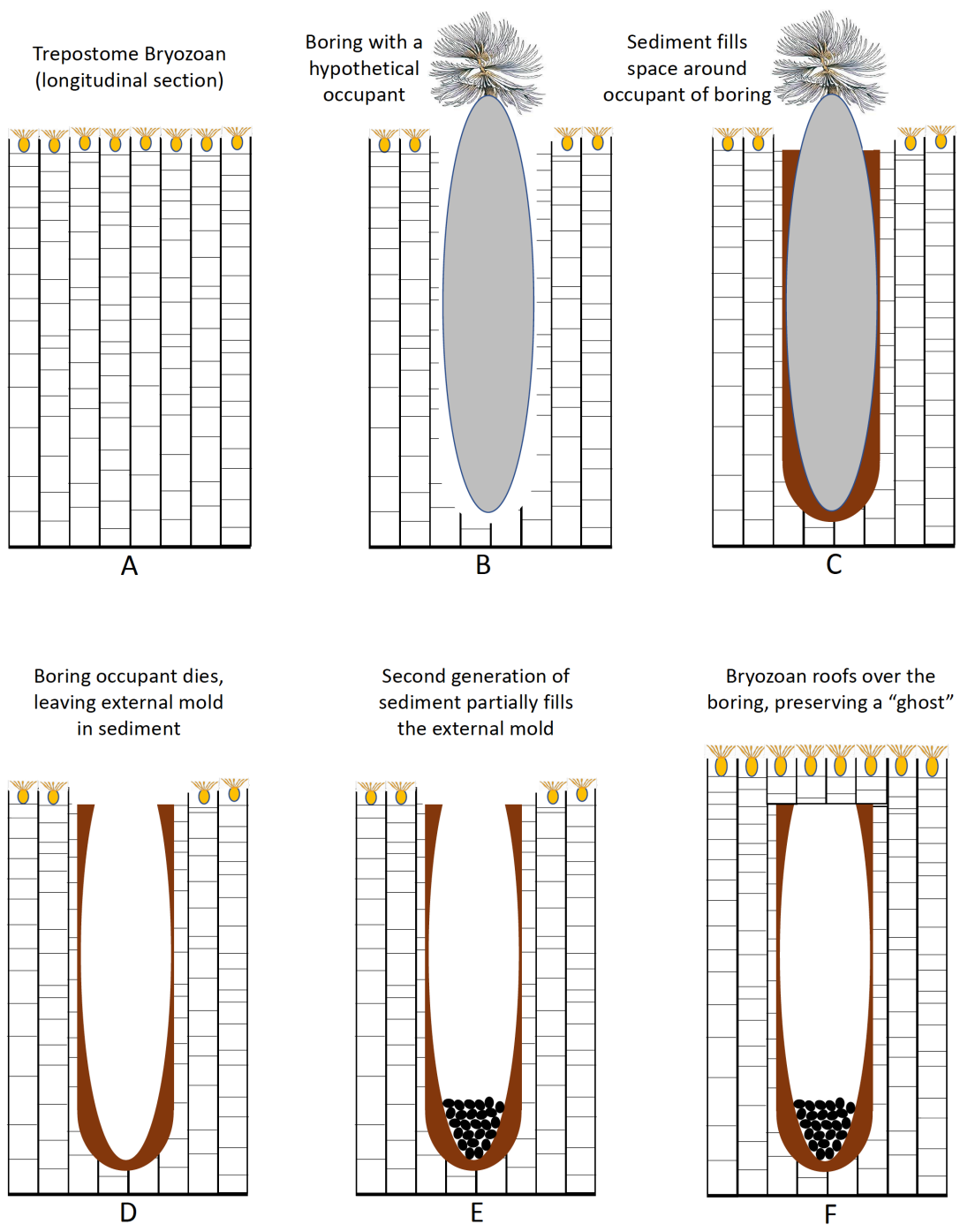


Figure 24. Diagrams illustrating the sedimentation process interpreted from borings with multiple generations of sediment. Diagrams by Mark Wilson, 2021.

Incongruous Features

The most common ghost shape, cylindrical with rounded ends, indicates that the boring occupants were a type of worm. Wisshak et al. (2017) argued that a single entrance trace fossil was more likely to have been created by a worm with both the mouth and anus located at its anterior, rather than a worm with mouth and anus at opposing ends. This reasoning holds true for the *Trypanites* borings as well as the *Lapispecus* trace fossils studied by Wisshak et al. (2017). In both cases, "the single entrance is in good accordance with the body plan of either a sipunculan (the so-called "peanut worms"; > 100 extant species), or a phoronid (the so-called "horseshoe worms"; ~ 10 extant species)" (Wisshak et al., 2017, p. 173). These two taxa are probable creators of the single-entry *Trypanites* borings.

Though the majority of borings were unbranched *Trypanites*, several branched borings were also observed. Branched macroborings are not generally found in Ordovician specimens (Wilson, 2007). Therefore the branched borings found in this study likely represent multiple generations of boring (compound borings). It is plausible that these branched borings were not excavated with multiple branches but were instead intersecting unbranched borings that were excavated separately.

Another unusual feature found in the trepostomes was a structure of zooids appearing to radiate from a boring. It is possible that these structures record the bryozoan overgrowing the boring, but further work would be required to properly interpret these features.

Given the composition and shapes of the prismatic calcite features found in the bryozoans studied, these features are likely the remains of aragonitic shells, such as brachiopod shells.

The nature of the phosphate observed remains unknown. A variety of Ordovician taxa had phosphatic hard parts or precipitated phosphate (Lowenstam, 1972). Therefore, it is possible that this material was organically derived, especially given its association with skeletal disturbances.

Some of the trepostome colonies also contained calcite tube-shaped features. These tube-shaped features often prompted growth responses in the bryozoan. Holland (1988) found similar calcite-filled tubes in Upper Ordovician brachiopods. Holland (1988) suggested that these tubes were unfilled burrows that were later filled by calcite cement. Dixon (2010) also investigated similar tube-shaped structures in Upper Ordovician corals, identifying those structures as species of cornulitid. In the trepostomes, tubes sectioned lengthwise appeared to have jagged edges, making their morphology accordant with fossil cornulitids. These tubes were more consistent with the tubes discussed by Dixon (2010) than those discussed by Holland (1988). Thus, the tube structures are interpreted to be the remains of cornulitids.

The tube and holdfast structure was likely a small organism that attached to the bryozoan colony. The feature resembles examples from the genus *Sphenothallus*. The ecology of *Sphenothallus* is poorly known and there is considerable variation in size and proportions within this genus (Vinn and Kirsimäe, 2015; Neal and Hannibal, 2000). However, the general layout of the observed feature, with gently bending tube connected to a base shaped like an upside-down cup, is consistent with a sphenothallid tube and holdfast (Peel, 2021; Neal and Hannibal, 2000). The feature is oriented such that the

widest part of the holdfast sits directly atop bryozoan skeleton, which aligns with the orientation in which sphenothallids would encrust their substrates (Van Iten et al., 1991). Furthermore, *Sphenothallus* is known to occur in Ordovician strata of the Cincinnati Arch area (Neal and Hannibal, 2000). Due to these similarities, it is probable that this structure is a bioclastration of a sphenothallid tube and holdfast.

Brown Bodies

The position of the brown bodies has implications for the cementation processes of the colonies. Had the calcite been deposited in the chambers or progressed laterally through the colonies, the brown bodies would most likely be situated against the chamber wall. However, this was not the case. The brown bodies were situated in the centre of the zooecial chamber, which indicates that the calcite cement that now fills the colonies formed first at the zooecial walls and then grew inwards.

CONCLUSIONS

1. The paleoecology of large trepostome bryozoans from the Upper Ordovician (Katian) of the Cincinnati region (USA) was studied using bryozoan growth patterns, trace fossils, and sedimentation.
2. *Trypanites* borings were abundant in the colonies sampled. These borings appear to have been bored mechanically and were probably produced by a type of worm, most likely a sipunculan or phoronid. Borings often contained calcite ghosts.
3. Some borings prompted growth reactions in their host bryozoan, indicating that boring progressed through a living portion of the colony. The growth reactions served to seal the cavity and regain feeding surfaces, typically a form of bioclastration. The growth reactions observed included roofing and infilling structures.
4. Calcite tubes were found in the bryozoans and are interpreted as fossil cornulitids.
5. A tube and holdfast structure was found and interpreted as a bioclastration of a sphenothallid.
6. Disturbances composed of prismatic calcite occurred in a variety of shapes, often with ridges. These features are interpreted as remains of aragonitic shells, such as brachiopod shells.
7. Colonies and trace fossils were all infilled. Infilling materials were one or more of: sparry calcite cement, dolomite rhombs, biosparite, micrite, prismatic calcite, and phosphate. Varieties of infilling materials indicate that infilling progressed episodically. This progression allowed for the preservation of ghosts and occasionally geopetal structures.
8. Calcium phosphate was found associated with skeletal disturbances. This phosphate is possibly of organic origin.
9. Self-overgrowths were common within the colonies and were often associated with brown bodies. Brown bodies were located at the centre of the zooecial chamber, indicating that the calcite cement formed first at the skeletal walls and built inwards into the chambers.
10. Structures of radiating zooids were found but require further investigation.
11. Spheroidal colony shapes suggest that colony living orientation was not constant. Further investigation of trace fossils, infill, and growth responses could provide insight into the orientation and life modes of trepostome bryozoans.

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