

Paleoecology of an Upper Ordovician submarine cave-dwelling bryozoan fauna and its exposed equivalents in northern Kentucky, USA

Caroline J. Buttler¹ and Mark A. Wilson²

¹Department of Natural Sciences, Amgueddfa Cymru – National Museum Wales, Cathays Park, Cardiff CF10 3NP, Wales, UK
{Caroline.Buttler@museumwales.ac.uk}

²Department of Geology, The College of Wooster, Ohio 44691, USA {mwilson@wooster.edu}

Abstract.—A bryozoan-dominated fauna that inhabited small caves underneath a carbonate hardground is here described from the Corryville Formation (Upper Ordovician, Katian) exposed near Washington, Mason County, Kentucky, USA. The dominant bryozoan, *Stigmatella personata* (a trepostome), is found both growing downwards from the cave ceilings and upwards on the exposed hardground surface above. Another trepostome, *Monticulipora*, is a minor component of the cave fauna. There are few discernible anatomical differences between the bryozoan colonies that grew upwards in presumably well-lit waters and those that grew downwards in the gloomy caves. The pendant, cave-dwelling *S. personata* in some cases appears to have longer zoecial tubes than its exposed equivalent. The colonies of *S. personata* are rounded mounds with multiple layers formed by self-overgrowth. The overgrowths in both downward and upward growing forms are marked by thin layers of sediment infilling the upper zoecial chambers in the older portion of the colony. We suggest that biofilms developed on patches of the colony where the zooids had died. Sediment adhered to these surfaces and the colony then overgrew the patches, trapping sediment within the skeleton. The bryozoan zoaria and the carbonate hardground are extensively bored by the cylindrical ichnogenus *Trypanites* that occasionally contain cylindrical calcite-filled tubes similar to “ghosts” of organic materials. Bioclastrations are present in some of the bryozoan skeletons. This cave fauna is one of few submarine examples known from the Paleozoic. It supports the hypothesis that early cave-dwelling organisms were little differentiated from their exposed counterparts.

Introduction

Fossil submarine cave faunas are relatively rare, especially in the Paleozoic (for reviews see Kobluk, 1981; Taylor and Palmer, 1994; Taylor and Wilson, 2003). This paper describes an Upper Ordovician (Katian) cave system underneath a carbonate hardground with trepostome bryozoans attached to the ceiling. The bryozoans contain abundant borings, bioclastrations, and organic remains within their zoaria. The dominant bryozoan species, the massive calcitic *Stigmatella personata*, is also found on the upper exposed surface of the hardground, enabling us to directly compare exposed and cryptic, upside-down varieties of this bryozoan. Study of this fossil assemblage thus gives us early examples of cave-dwelling bryozoans that are elsewhere known from the Jurassic (Palmer and Fürsich, 1974; Wilson, 1998), Neogene (Rosso et al., 2015), and Recent (Harmelin, 1986, 1997, 2000; Rosso et al., 2013). New information is gained about bioerosion during the Ordovician Bioerosion Revolution (Wilson and Palmer, 2006; Buatois et al., 2016), preservation by bioclastration (Taylor, 1990) within bryozoan skeletons, and the distribution of preserved bryozoan polypides called “brown bodies” (Boardman, 1999).

Geological setting

Locality.—The carbonate hardground and associated cave fauna were found and collected in 1999 south of Maysville, Mason County, Kentucky (38.609352°N, 83.810973°W; College of Wooster location C/W-10). It was exposed for many meters on both sides of US Highway 68, 0.2 km south of its junction with US Highway 62/KY 1236. The cave portion of the hardground was destroyed by later road work, but parts of the hardground itself are still in place. The hardground is within the Corryville Formation of the Upper Ordovician Katian Stage (Fig. 1). It is ~2.2 meters above road level. The bryozoans at this location were previously described as “reefs” by Cuffey (1998), who believed the outcrops had been destroyed by road construction between 1992 and 1998. Cuffey (1998) at the time of his collections, did not note the caves or pendant bryozoans (Fig. 2), so they were likely not exposed during his visits.

Stratigraphy.—The Corryville is a formation (sometimes referred to as a member of the Grant Lake Formation) within the type Cincinnati Series exposed in southeastern Indiana, southwestern Ohio, and central Kentucky. It is Katian (Late Ordovician) in age and within the Cincinnati Sequence C3

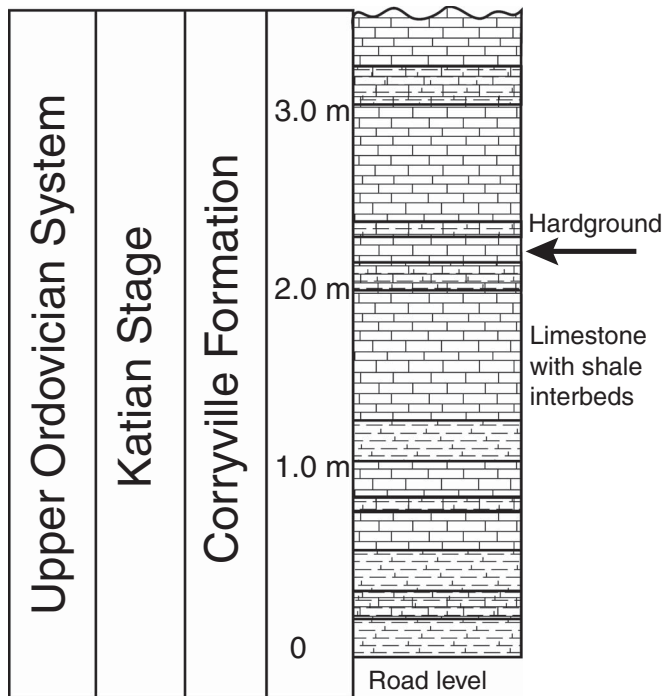


Figure 1. Location of the hardground within the Corryville Formation.

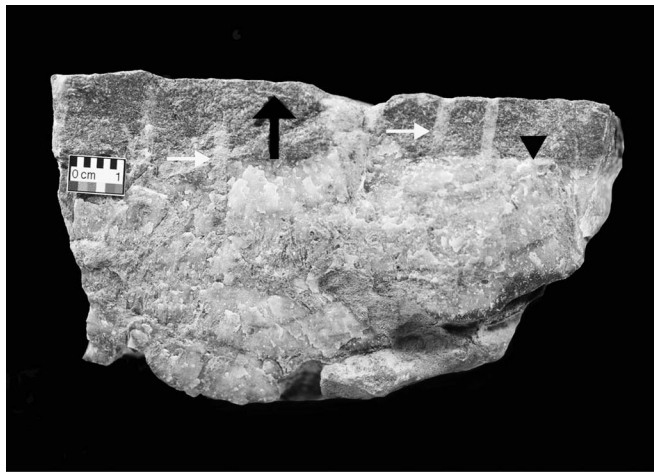


Figure 2. Large colony of *Stigmatella personata* (NMW 2017.9G.1.1) growing downwards from the hardground (black triangle), both the bryozoan and substrate extensively bored (white arrows). Black arrow indicates the way up of sediments.

(Patzkowsky and Holland, 1996). In the North American stage terminology it is Maysvillian.

The Corryville consists of very fossiliferous limestones (packstones and wackestones) and shales deposited on a carbonate-siliciclastic ramp under considerable storm influence (Holland, 1993). The sediments accumulated in a deep subtidal environment (between fair-weather wavebase and storm wavebase) on the paleocontinent Laurentia $\sim 20^\circ\text{S}$ of the paleoequator (Holland and Patzkowsky, 2007; Vogel and Brett, 2009, fig. 2).

Hardground and cave development

Hardgrounds are symsedimentarily cemented, in situ, rocky seafloors (Wilson and Palmer, 1992; Taylor and Wilson, 2003).

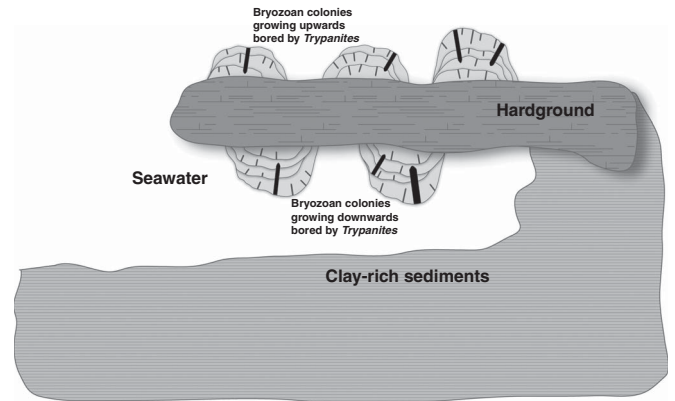


Figure 3. Reconstruction of living positions of bryozoan colonies of *Stigmatella personata*.

They are common throughout the Cincinnati Series, especially in limestones formed in subtidal paleoenvironments (Palmer, 1982). Typical hardgrounds, such as the Corryville example in this study, are only a few centimeters thick and have less-indurated sediments above and below. They are thus commonly found as shelf-like projections from outcrops or loose slabs, allowing easy access to their bored and encrusted surfaces.

This Corryville hardground was at some point exposed on the seafloor and currents washed away large patches of soft clay underneath it, forming cavities 5–20 cm high (based on field measurements) with the hardground as a solid roof. Bryozoans then occupied the ceilings of the cavity below the hardgrounds as well as the hardground upper surfaces, producing the cryptic and exposed communities we see today on the tops and bottoms of the Corryville hardground slabs (Fig. 3). The same phenomenon has been documented with hardgrounds exposed in the Middle Jurassic of Utah (Wilson, 1998). We do not know how long these small caves remained open and connected to normal marine circulation, but we suspect a substantial interval because the cryptic bryozoans hanging pendants from the ceilings grew to considerable sizes—up to 93 mm in diameter and 50 mm high.

Materials and methods

The specimens (NMW 2017.9G.1-7) forming the basis of this work were collected from exposures in 1999 (38.609352°N latitude, 83.810973°W). Longitudinally oriented thin sections were prepared to examine internal structures and photographed using a Canon 70D on a Leica Z6 microscope. Colony measurements are given in Table 1.

Repository and institutional abbreviation.—NMW – Amgueddfa Cymru – National Museum Wales, Cardiff, UK.

Systematic paleontology

Phylum Bryozoa Ehrenberg, 1831

Class Stenolaemata Borg, 1926

Superorder Palaeostomata Ma, Buttler, and Taylor, 2014

Order Trepostomata Ulrich, 1882

Table 1. Measurements of *Stigmatella personata* colonies; mean averages, ranges, number of measurements given in brackets.

	Height of colony (mm)	Width of colony (mm)	Length of zooeical tubes (mm)	Max width of autozooeical chamber (mm)	Max width of autozooeical chamber in maculae (mm)	Diaphragm spacing (mm)
Colonies growing upward	19.59 11–32 (6)	63.25 52–80 (4)	5.58 1.17–16.60 (26)	0.23 0.17–0.28 (17)	0.38 0.34–0.45 (6)	19.1 3–82 (211)
Colonies growing down	46.6 43–50 (5)	83 76–93 (3)	10.6 3.7–22.5 (10)	0.23 0.19–0.26 (20)	0.36 0.31–0.40 (10)	19.6 5–70 (207)

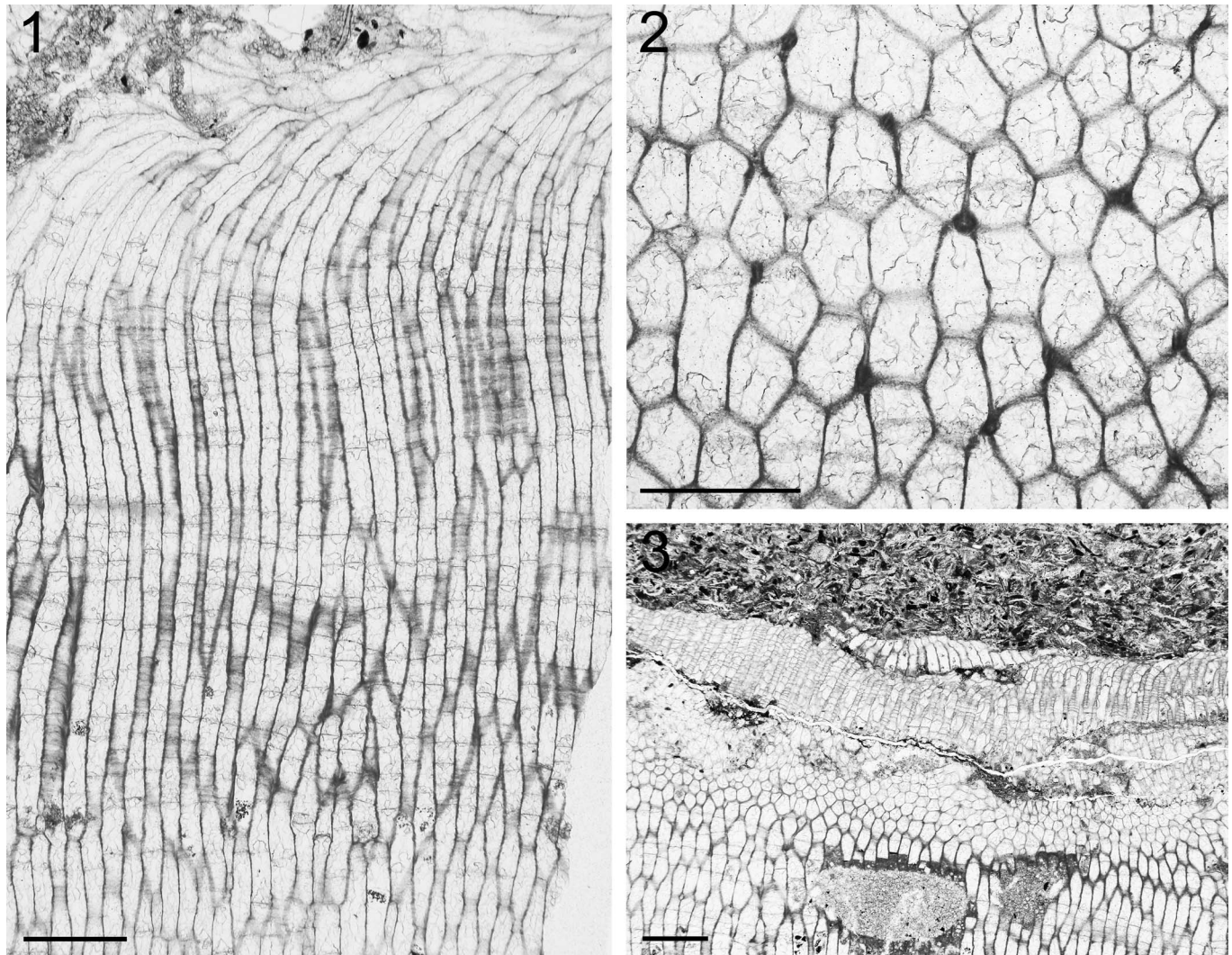


Figure 4. (1) NMW 2017.9G.2, Long zooeical chambers of *Stigmatella personata* colony growing downwards, longitudinal section; (2) NMW 2017.9G.1.2, polygonal zooeical chambers of *S. personata* with styles in walls, tangential section; (3) NMW 2017.9G.1.2, *Monticulipora* colony growing downwards overgrown by *S. personata* colony. Scale bars (1, 3) = 1 mm; (2) = 0.5 mm.

Family Heterotrypidae Ulrich, 1890
Genus *Stigmatella* Ulrich and Bassler, 1904

Type species.—*Stigmatella crenulata* Ulrich and Bassler, 1904

Stigmatella personata Ulrich and Bassler, 1904
Figures 4.1, 4.2, 5.1–5.6

1904 *Stigmatella personata* Ulrich and Bassler, 1904, p. 35.
1925 *Stigmatella personata lobata* Dyer, p. 72.

1964 *Stigmatella personata* Ulrich and Bassler; Utgaard and Perry, p. 82.

1973 *Stigmatella personata lobata* Dyer; Fritz, p. 17.

Holotype.—USNM 43.201 from the Richmond Formation, Hanover, Ohio (Ulrich and Bassler, 1904).

Diagnosis.—Zoaria branching or massive, formed by multiple overgrowths. Maculae composed of macrozooeica.

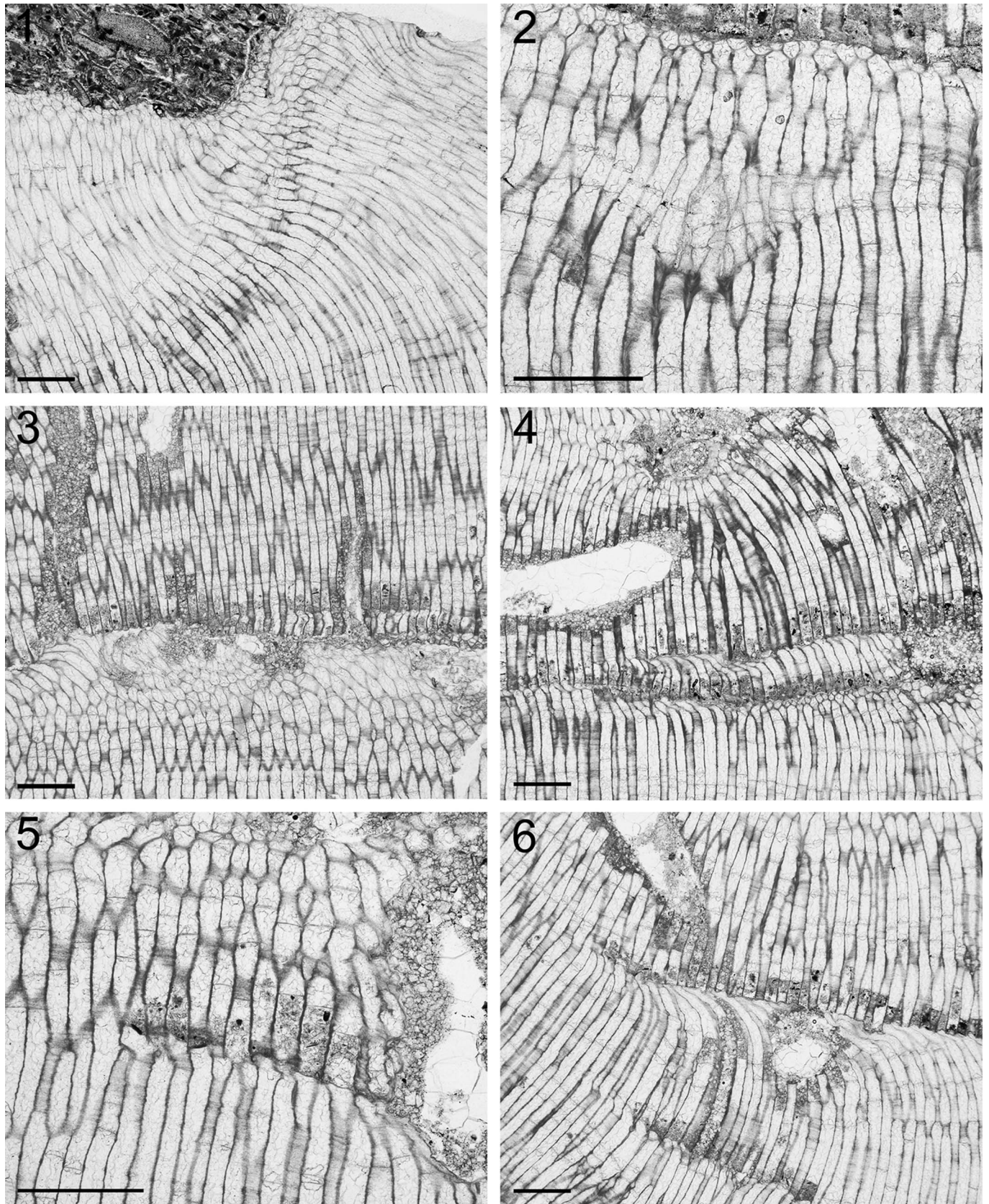


Figure 5. *Stigmatella personata*: (1) NMW 2017.9G.2.2, long zoecial tubes showing a gradual change in orientation; (2) NMW 2017.9G.1.2, localized development of styles in autozoecial wall; (3) NMW 2017.9G.2.2, large multi-layered colonies formed by self-overgrowth; (4) NMW 2017.9G.1.2, overgrowths marked by sediment infilling the zoecial chambers in the older part of the colony; (5) NMW 2017.9G.2.2, localized overgrowth; (6) NMW 2017.9G.2.2, intracolony nature of the overgrowths recognized by uninterrupted zoecial chambers adjacent to those overgrowing part of the colony. Longitudinal sections; scale bars = 1 mm.

Long autozoecia with diaphragms along length. Styles present in patches, mesopores absent.

Occurrence.—Ordovician, Katian, midwestern USA (Ohio, Indiana, Kentucky).

Description.—The zooaria are massive in form and multi-laminar with the new parts of the colony overgrowing older ones. They range in size and are up to 93 mm in diameter and 50 mm in height. Monticules of clusters of larger autozoecial chambers form regular conical structures on colony surface. Endozones restricted to short recumbent autozoecia budded from exterior basal colony walls. In exozones, autozoecial boundaries polygonal in cross-section. Autozoecia in disordered pattern on colony surface. Zoecial walls thin, cortex thickness regular throughout exozone; microstructure poorly preserved. Zoecia polygonal in transverse section, 0.23 mm maximum mean diameter and 0.38 mm maximum mean diameter in monticules. Thin basal diaphragms abundant in some parts of zoecial chambers and lacking in others, spaced on mean average 0.19 mm. Styles are observed in localized patches. Mesopores are absent.

Remarks.—*Stigmatella personata* was originally described by Ulrich and Bassler (1904) as a smooth branching colony characterized by having no mesopores and few styles. Dyer (1925) proposed *S. personata lobata*, which differed in colony morphology, forming irregular lobate masses covered by low monticules. Utgaard and Perry (1964) regarded the differences between *S. personata lobata* and the type species as variations in growth form. Fritz (1973) however disagreed and considered there was a significant difference in the numbers of styles between the two. The colonies from the Corryville Formation show variation of style number within the colony. Encrusting trepostome colonies are known to develop erect branches, so species cannot be distinguished by external morphological form.

Bryozoan colonies

Taxonomy and form.—The bryozoan colonies are recognized as having lived on an exposed hardground surface and having inhabited small caves beneath it. The Corryville Formation is estimated to have been deposited below the fair-weather wave-base and above the storm wavebase, and so well within the photic zone (Holland and Patzkowsky, 2007). We investigated as to whether there were differences between those that grew upwards in presumably well-lit waters and those that grew downwards from the ceilings in the darker, light-restricted caves. There would have been differences in the water currents in the two environments and colony growth may have been affected by gravity.

Taxonomically no differences were recognized between the upwards-growing, exposed bryozoans and those living pendently in the caves. All the large colonies are identified as the trepostome *Stigmatella personata* Ulrich and Bassler, 1904 (Fig. 4.1, 4.2) regardless of their growth orientation. Only one other encrusting trepostome species is recognized; one small colony of *Monticulipora* is observed growing partly over a small single layer of *S. personata* and the ceiling of the cave

(Fig. 4.3). This colony is in turn overgrown by a large *S. personata*.

There are few discernible anatomical differences between the bryozoan colonies from the two locations. The pendant, cave-dwelling *S. personata* on average has longer zoecial tubes than its exposed equivalent, possibly caused by environmental factors in the different locations. A maximum zoecial length of 22.5 mm and was measured in colonies growing downwards and 16.5 mm in those growing upwards. The mean average of the downward growth is 10.6 mm (range 3.7–22.5 mm; SD 4.96 mm) and upward 5.6 mm (range 0.89–16.6 mm; SD 4.14 mm).

The spacing between diaphragms in the zoecial chambers was measured to determine if there is a difference between the colonies in different orientations. The diaphragms are commonly widely spaced, but in some locations are found closer together. The intervals between the first five diaphragms from the zoecial opening at the colony surface or at the point of overgrowth were measured over 200 times in colonies growing up and growing down (~420 measurements). The results showed there was only a difference of 0.005 mm in growth direction, a mean average of 0.196 mm recorded for the colonies in caves and 0.191 mm for those on the hardgrounds. However, within one colony the distances are variable as can be seen in Figure 4.1.

Growth and overgrowths of colonies.—The autozoecial chambers in the colony generally grew long, up to 22.5 mm, and straight, but can be seen to have localized changes in direction of colony growth (Figs. 4.1, 5.1). Thickening of the zoecial walls and the localized development of styles can also occur (Fig. 5.2), sometimes accompanying a change in growth direction. These developments may be controlled by external microenvironmental effects.

Discussion

The colonies of *Stigmatella personata* are multi-layered because of self-overgrowth (Fig. 5.3). The intracolony nature of the overgrowths is recognized in thin section (Fig. 5.4) by uninterrupted zoecial chambers adjacent to those overgrowing part of the colony, which has sediment that infills zoecia. This suggests the zooids in the overgrown part of the colony died and the living zooids overgrew them. The area of overgrowth can be localized or extend over most of the colony (Fig. 5.3, 5.5, 5.6). The death of parts of the colony may be due to localized predation, although no evidence can be seen in the skeletal walls. Modern-day cyclostome bryozoans are predated by a variety of organisms, including echinoderms, nudibranch sea slugs, pycnogonids, small crustaceans, and fish (Hayward and Ryland, 1985; Lidgard, 2008). The colonies living in the cave environment may have had some protection from predation compared to those growing in exposed environments. This may be the reason that longer autozoecial tubes are recognized in the bryozoans growing down in caves.

In colonies growing upwards and those growing down, the overgrowths are marked by sediment infilling the zoecial chambers in the older part of the colony (Fig. 5.4). Lev et al. (1993) observed ‘clay drapes’ on the top of colony-wide bands

in colonies of *Prasopora* from the Middle Ordovician Martinsburg Formation of south-central Pennsylvania. They suggested that these represent a turbidity episode in which fine-grained particles smothered the colony. This was then followed by a regeneration of zooids. In the colonies from Kentucky, we consider that an influx of sediment may not be responsible for killing parts of the colony by smothering because often only localized sections are affected. Modern colonies are known to be able to clean the surface of sediment. Polypides in the colony generate water currents to feed and to remove sediment and waste (Lidgard, 1981), and there are examples of zooids cleaning the colony using tentacles (Dick, 1984). It is probable that the areas that had chambers infilled with sediment had no living animals inside.

Sediment could have entered the cave environment during a storm episode, but why was it retained on the colony surface and not dislodged due to gravity? Alternatively, it is possible that dead parts of the colony had become covered in biofilms. Gerdes et al. (2005) recognized that bryozoans represented a common settling ground for a wide range of epizoid biofilms, including cyanobacteria and fungi. Sediment may have adhered to the surface of the biofilm, trapping it between the layers when the colony overgrew.

Borings

All colonies in both growth orientations have been extensively bored (Fig. 6.1–6.6). The borings are located throughout the colony and can also be seen in the hardground substrate (Fig. 2). They all have a similar form: straight with a cylindrical cross section. Two different types are recognized, but both are identified as *Trypanites* Magdefrau, 1932. This trace fossil, which is known from throughout the Phanerozoic, was extremely common during the Late Ordovician when it was a significant bioeroder of hard substrates (Wilson and Palmer, 2006). The two types are found in the exposed and cave environment.

Trypanites boring Type A.—These are the smaller of the two varieties (Fig. 6.1) and have a slightly different structure, depending upon the whether they are boring into the bryozoan colonies or into the hardground substrate. The tubes range in diameter from 0.74 mm to 1.62 mm, with a mean diameter of 1.25 mm, and the maximum length measured is 16 mm.

These borings are confined to a single overgrowth within the bryozoan colonies. The borings are often covered over by subsequent layers of the colony (Fig. 6.2). This suggests that the borings were not occupied by living organisms at this time; possibly they had died in a storm-sedimentation event.

Type A borings appear circular in cross section in hand specimens with straight sides to the tube. When observed in transverse sections of the bryozoan colony (Fig. 6.1), the borings are bounded by the calcite walls, which creates a polygonal rather than circular structure (Fig. 6.3). Even though calcite colony walls were eroded in the boring process, excavating the cylindrical cavity parallel to the walls was the way of least resistance for the borer. This was also observed by Wyse Jackson and Key (2007) in Ordovician bryozoans from Estonia. They found the borings oriented roughly perpendicular to the colony surface minimized intersection with skeletal walls

of the bryozoan zooecia. The strength of the calcite diaphragms within the bryozoan colony also resulted in a structure with a stepped appearance when they appear to form a more resistant barrier and cause the burrow to be offset to the adjacent chamber (Fig. 6.2). There are some Type A borings that cut through zooecial chambers at a 90° angle.

Type A borings are commonly infilled with micrite. Some contain an additional cylindrical tube of calcite (Fig. 6.4). These appear to be similar to the ‘ghosts’ of organic material described by Wyse Jackson and Key (2007). They interpreted the ghosts as the sparry cement-filled cast of the boring organism that was killed by infilling of matrix into the larger boring it had excavated. This may have occurred during a storm event that buried the host colony. This is consistent with evidence for the colonies being covered in sediment and disrupting the growth.

Trypanites boring Type B.—The second variety has a larger tube size; these tubes range in diameter from 2.4 mm to 3.2 mm, with a mean diameter of 2.9 mm and the maximum length measured is 39 mm. These cut through several layers of overgrowth (Fig. 6.5). The borings are infilled with various sediments, some containing numerous dolomite rhombs and others with larger fossil fragments, including cryptostome bryozoans, brachiopod shell, and echinoderm fragments (Fig. 6.6). There are no cylindrical calcite ‘ghosts’ present in these structures.

Bioclaustration

The primary bryozoan in this study, *Stigmatella personata*, hosts several bioclaustration structures (Figs. 7.1, 7.2). Bioclaustration was originally described by Palmer and Wilson (1988) as a process by which soft-bodied symbionts are entombed within the growing skeletons of other organisms. Taylor (1990) expanded the definition to include the embedment of skeletal organisms as well. There are only four bioclaustration ichnotaxa formally described in Paleozoic bryozoans: *Anoigmaichnus odinsholmensis* Vinn et al., 2014, from the Middle Ordovician (Darrivilian) of Estonia; *Catellocaula val-lata* Palmer and Wilson, 1988, in Upper Ordovician (Katian) trepostomes; *Caupokeras calyptos* McKinney, 2009, in Middle Devonian fenestrates (see also Suárez Andrés, 2014); and *Chaetosalpinx tapanilai* Ernst et al., 2014, in Middle Devonian cystoporates.

The bioclaustration structures in *S. personata* are flat-bottomed tubular structures. They appear to represent soft-bodied fouling organisms that spread across the apertures of three to six zooecia, effectively halting their growth. Neighboring zooecia grew up and eventually overtopped them, forming keyhole-like cross-sections, as in Figure 7.1. Patches of sparry calcite and sediment appear to be additional examples of “ghosts” of soft tissues (Fig. 7.1). In some bioclaustration structures, there is a hint of a recrystallized skeleton for the embedded organism (Fig. 7.2).

The bioclaustration structures in *S. personata* do not fit the descriptions of current ichnotaxa, but with only cross-sections, we do not have enough information to erect a new ichnotaxon. We also cannot identify the symbiont that left these features. We know enough, though, to classify these bioclaustrations within

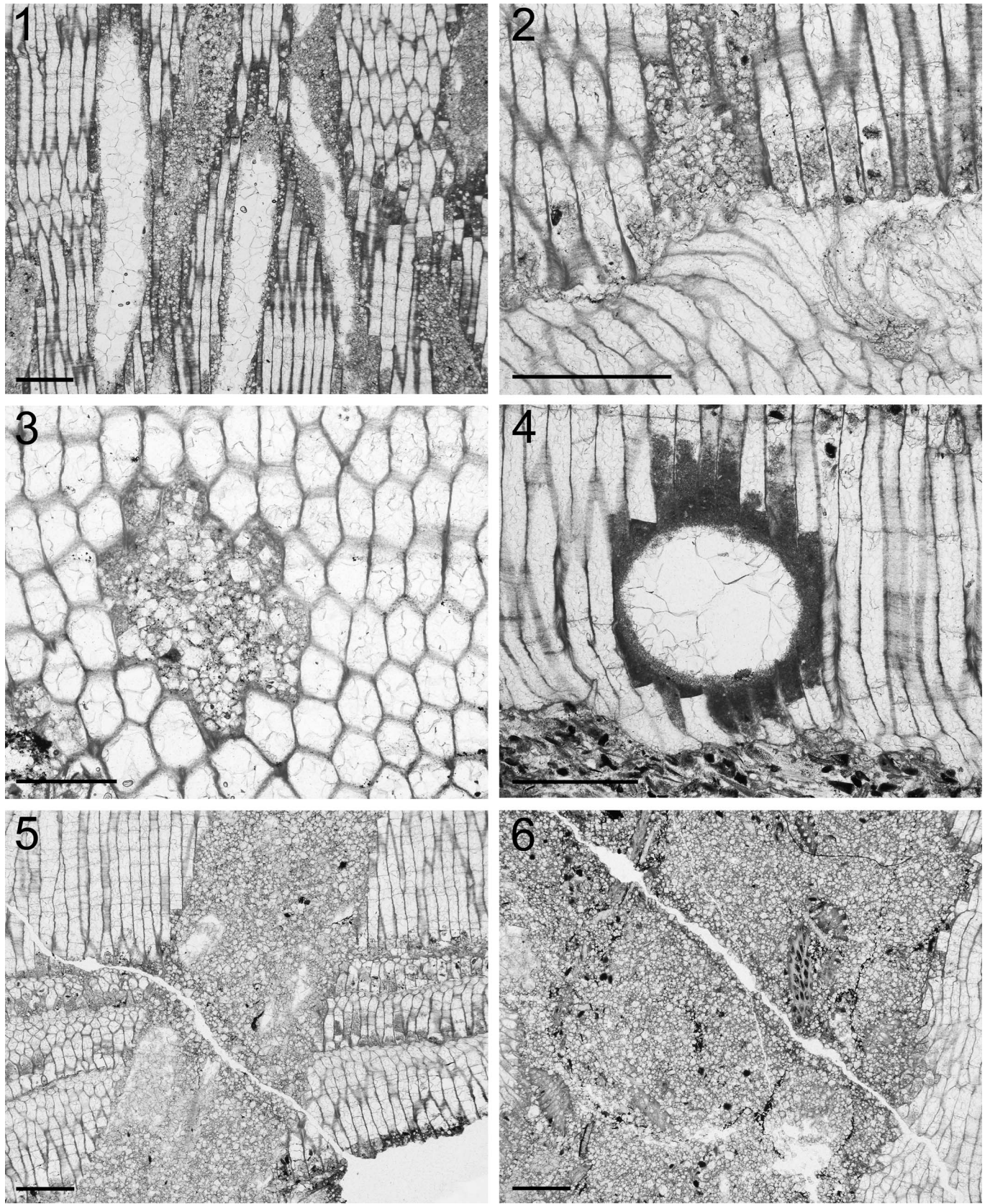


Figure 6. *Trypanites* borings: (1) NMW 2017.9G.1.2, colony extensively bored by *Trypanites* type A; (2) NMW 2017.9G.2.2, *Trypanites* type A overgrown by *Stigmatella* colony; (3) NMW 2017.9G.1.3, *Trypanites* type A polygonal in transverse section; (4) NMW 2017.9G.3.2, *Trypanites* type A infilled with micrite and containing cylindrical tubes of calcite, possible evidence of boring animal; (5) NMW 2017.9G.1.2, *Trypanites* type B cutting through multiple layers of *Stigmatella* colony; (6) NMW 2017.9G.1.2, *Trypanites* type B infilled with sediment containing dolomite rhombs and fragments of cryptostome bryozoans. (1, 2, 4–6) longitudinal sections; scale bars = 1 mm; (3) tangential section; scale bar = 0.5 mm.

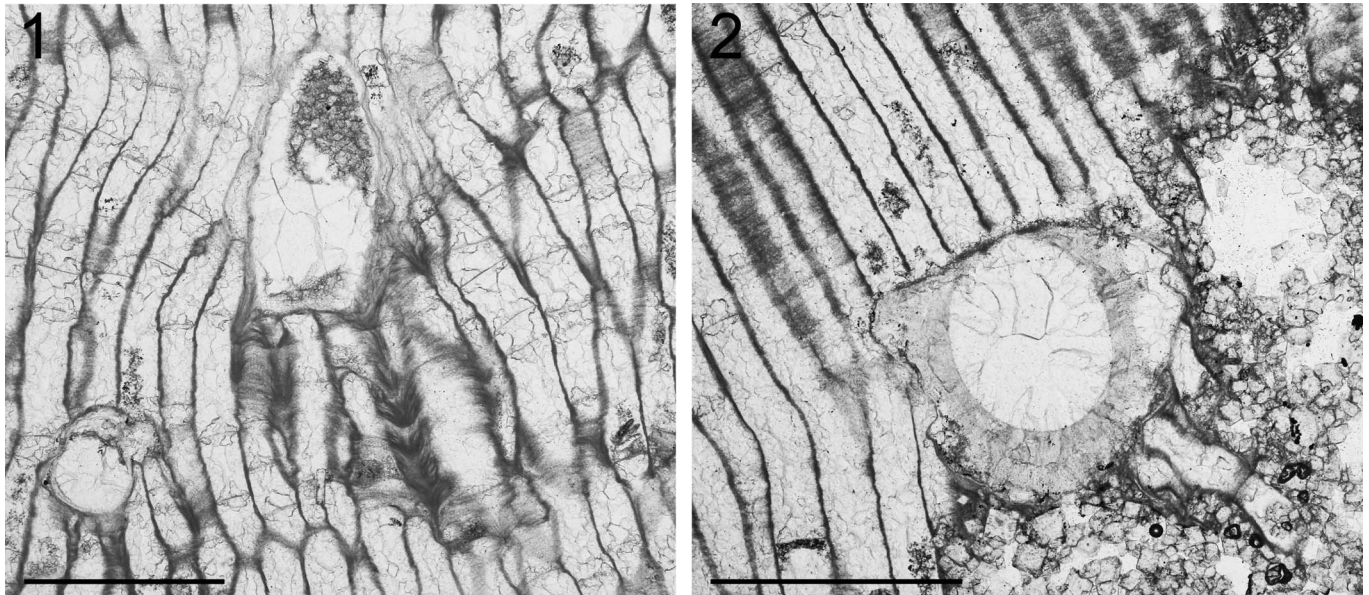


Figure 7. Bioclastration: (1) NMW 2017.9G.2.2, void with thickened wall overgrown by colony; (2) NMW 2017.9G.1.2, thickened wall grown around tubular structure. Longitudinal sections; scale bars = 1 mm.

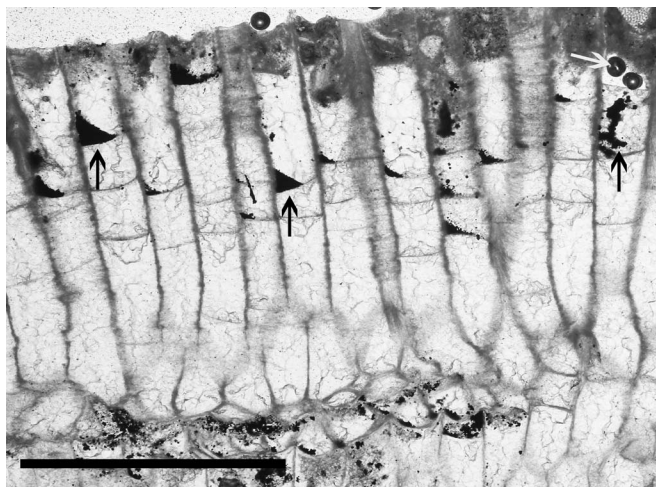


Figure 8. NMW 2017.9G.3.2, Longitudinal section growing upwards showing the dark remains of organic material (black arrows) above diaphragms in zoecial chambers (white arrow indicating air bubbles). Longitudinal section; scale bar = 1 mm.

the category *Impedichnia* (Tapanila, 2005) because they impeded the normal growth of *Stigmatella personata*.

Organic remains

Remains found within the living chambers of Cincinnatian trepostomes have been interpreted as preserved indications of polypides. These were first identified by Cummings and Gallo-way in 1915, who recognized brown granular material that was present in autozooids, but never in mesopores. The degenerated cells that result from the normal degeneration-regeneration cycles of living bryozoan polypides are known as brown bodies (Boardman, 1999). The fossilized remains of organic material that may have been brown bodies are referred to as brown deposits (Boardman and Cheetham, 1983; Key et al., 2008).

In one specimen from Kentucky growing upwards on the exposed surface, brown deposits are found on the upper surfaces of diaphragms (Fig. 8). These do not have any indications of polypide anatomy similar to those recognized in other lower Paleozoic trepostomes from North America (Boardman, 1999).

Conclusions

This cave fauna is one of few submarine examples known in the Paleozoic. The distribution of organisms in and outside the caves supports the hypothesis that early cave-dwelling organisms were little differentiated from their exposed counterparts (see Taylor and Wilson, 2003). Mesozoic cave and other cavity faunas, in contrast, usually had distinct polarization between cryptic and exposed communities (Palmer and Fürsich, 1974; Palmer and Wilson, 1990; Taylor and Palmer, 1994; Wilson, 1998). This fauna represents a community of large bryozoan colonies bored by two distinct organisms, with symbionts growing on the surface and biofilms developing on the dead parts of the colony.

Acknowledgments

We thank A.J. Valentine-Baars (Amgueddfa Cymru) for preparing the thin sections and J. Turner (Amgueddfa Cymru) for assistance with photography. The Luce Fund at The College of Wooster generously provided funds for the fieldwork. M.M. Key Jr., P.N. Wyse Jackson, and A. Ernst provided very helpful reviews.

References

- Boardman, R.S., 1999, Indications of polypides in feeding zooids and polymorphs in Lower Paleozoic Trepostomata (Bryozoa): *Journal of Paleontology*, v. 73, p. 803–815.
- Boardman, R.S., and Cheetham, A.H., 1983, Glossary of morphologic terms, in Robison, R.A., ed., *Treatise on Invertebrate Paleontology*, Pt. G, Bryozoa,

- Revised: Boulder, Colorado and Lawrence, Kansas, Geological Society of America and University of Kansas Press, p. G304–G320.
- Borg, F., 1926, Studies on Recent cyclostomatous Bryozoa: Zoologiska Bidrag från Uppsala, v. 10, p. 181–507.
- Buatois, L.A., Mángano, M.G., Olea, R.A., and Wilson, M.A., 2016, Decoupled evolution of soft and hard substrate communities during the Cambrian Explosion and Ordovician Biodiversification Event: Proceedings of the National Academy of Sciences, v. 113, p. 6945–6948.
- Cuffey, R.J., 1998, The Maysville bryozoan reef mounds in the Grant Lake Limestone (Upper Ordovician) of north-central Kentucky, in Davis, A., and Cuffey, R.J., eds., Sampling the layer cake that isn't: the stratigraphy and paleontology of the type-Cincinnatian: Ohio Department of Natural Resources Guidebook v. 13, p. 38–44.
- Cummings, E.R., and Galloway, J.J., 1915, Studies of the morphology and histology of the Trepostomata or Monticliporids: Proceedings of the Paleontological Society, v. 26, p. 349–374.
- Dick, M.W., 1984, Bryozoan behavior in relation to autocleaning in *Holoporella brunnea* (Hincks): Northwest Science, v. 58, p. 195–207.
- Dyer, W.S., 1925, The stratigraphy and paleontology of Toronto and vicinity. Part V. The paleontology of the Credit River section: Report of Ontario Department of Mines, v. 32, p. 47–88.
- Ehrenberg, C.G., 1831, Symbolae Physicae, seu Icones et descriptiones Corporum Naturalium novorum aut minus cognitorum, quae ex itineribus per Libyam, Aegyptum, Nubiam, Dongaliam, Syriam, Arabiam et Habessiniam, studia anni 1820–25, redirent. — Pars Zoologica, 4, Animalia Evertebrata exclusis Insectis: Berolini, Mittler, 10 pls.
- Ernst, A., Taylor, P.D., and Bohaty, J., 2014, A new Middle Devonian cystoporate bryozoan from Germany containing a new symbiont bioclaustration: Acta Palaeontologica Polonica, v. 59, p. 173–183.
- Fritz, M.A., 1973, Redescription of type specimens of bryozoan *Stigmatella* from the Upper Ordovician of the Toronto Region, Ontario: Life Sciences Contribution, Royal Ontario: Museum, v. 87, p. 1–31.
- Gerdes, G., Kaselowsky, J., Lauer, A., Mawatari, S.F., and Scholz, J., 2005, Taxonomic composition and structure of bryozoan-associated biofilms from Japan and New Zealand, in Moyano G.H.I., Cancino, J.M., and Wyse Jackson, P.N., eds., Bryozoan Studies 2004: London, A.A. Balkema Publishers, p. 69–82.
- Harmelin, J.-G., 1986, Patterns in the distribution of bryozoans in the Mediterranean marine caves: Stylogogia, v. 2, p. 10–25.
- Harmelin, J.-G., 1997, Diversity of bryozoans in a Mediterranean sublittoral cave with bathyal-like conditions: role of dispersal processes and local factors: Marine Ecology Progress Series, v. 153, p. 139–152.
- Harmelin, J.-G., 2000, Ecology of cave and cavity dwelling bryozoans, in Herrera Cubilla, A., and Jackson, J.B.C., eds., Proceedings of the 11th International Bryozoology Association Conference: Balboa, Republic of Panama, Smithsonian Tropical Research Institute, p. 38–55.
- Hayward, P.J., and Ryland, J.S., 1985, Cyclostome bryozoans: keys and notes for the identification of the species: Synopses of the British fauna (New series), v. 34, p. 147. [London, Published for the Linnean Society of London and the Estuarine and Brackish-Water Sciences Association by E.J. Brill/W. Backhuys].
- Holland, S.M., 1993, Sequence stratigraphy of a carbonate-clastic ramp: the Cincinnatian Series (Upper Ordovician) in its type area: Geological Society of America Bulletin, v. 105, p. 306–322.
- Holland, S.M., and Patzkowsky, M.E., 2007, Gradient ecology of a biotic invasion: biofacies of the type Cincinnatian Series (Upper Ordovician), Cincinnati, Ohio region, USA: Palaios, v. 22, p. 392–407.
- Key, M.M. Jr., Wyse Jackson, P.N., Miller, K.E., and Patterson, W.P., 2008, A stable isotope test for the origin of fossil brown bodies in trepostome bryozoans from the Ordovician of Estonia, in Hageman, S.J., Key, M.M., Jr., and Winston, J.E., eds., Bryozoan Studies 2007: Martinsville, Virginia, Virginia Museum of Natural History Special Publication no. 15, p. 75–84.
- Kobluk, D.R., 1981, The record of cavity-dwelling (coelobiontic) organisms in the Paleozoic: Canadian Journal of Earth Sciences, v. 18, p. 181–190.
- Lev, S.M., Key, M.M. Jr., and Lighthart, A., 1993, A paleobiologic test for diastems using the internal stratigraphy of trepostome bryozoans: Journal of the Pennsylvania Academy of Science, v. 67, p. 32–37.
- Lidgard, S., 1981, Water flow, feeding, and colony form in an encrusting cheilostome, in Larwood, G.P., and Nielsen, C., eds., Recent and Fossil Bryozoa: Fredensborg, Denmark, Olsen and Olsen, p. 135–142.
- Lidgard, S., 2008, Predation on marine bryozoan colonies: taxa, traits and trophic groups: Marine Ecology Progress Series, v. 359, p. 117–131.
- Ma, J.-Y., Buttler, C.J., and Taylor, P.D., 2014, Cladistic analysis of the 'trepostome' Suborder Esthonioporina and the systematics of Palaeozoic bryozoans: Studi Trentini di Scienze Naturali, v. 94, p. 153–161.
- Mägdefrau, K., 1932, Über einige Bohrgänge aus dem Unteren Muschelkalk von Jena: Paläontologische Zeitschrift, v. 14, p. 150–160.
- McKinney, F.K., 2009, Bryozoan-hyroid symbiosis and a new ichnogenus: *Caupokeras*: Ichnos, v. 16, p. 193–201.
- Palmer, T.J., 1982, Cambrian to Cretaceous changes in hardground communities: Lethaia, v. 15, p. 309–323.
- Palmer, T.J., and Fürsich, F.T., 1974, The ecology of a Middle Jurassic hardground and crevice fauna: Palaeontology, v. 17, p. 507–524.
- Palmer, T.J., and Wilson, M.A., 1988, Parasitism of Ordovician bryozoans and the origin of pseudoborings: Palaeontology, v. 31, p. 939–949.
- Palmer, T.J., and Wilson, M.A., 1990, Growth of ferruginous oncoliths in the Bajocian (Middle Jurassic) of Europe: Terra Nova, v. 2, p. 142–147.
- Patzkowsky, M.E., and Holland, S.M., 1996, Extinction, invasion, and sequence stratigraphy: patterns of faunal change in the Middle and Upper Ordovician of the eastern United States, in Witzke, B.J., Ludvigsen, G.A., and Day, J.E., eds., Paleozoic Sequence Stratigraphy: Views from the North American Craton: Geological Society of America Special Paper, Boulder, Colorado, v. 306, p. 131–142.
- Rosso, A., Sanfilippo, R., Taddei Ruggiero, E., and Di Martino, E., 2013, Faunas and ecological groups of Serpuloidea, Bryozoa and Brachiopoda from submarine caves in Sicily (Mediterranean Sea): Bollettino della Società Paleontologica Italiana, v. 52, p. 167–176.
- Rosso, A., Sanfilippo, R., Ruggieri, R., Maniscalco, R., and Vertino, A., 2015, Exceptional record of submarine cave communities from the Pleistocene of Sicily (Italy): Lethaia, v. 48, p. 133–144.
- Suárez Andrés, J.L., 2014, Bioclaustration in Devonian fenestrate bryozoans. The ichnogenus *Caupokeras* McKinney, 2009: Spanish Journal of Paleontology, v. 29, p. 5–14.
- Tapanila, L., 2005, Palaeoecology and diversity of endosymbionts in Palaeozoic marine invertebrates: trace fossil evidence: Lethaia, v. 38, p. 89–99.
- Taylor, P.D., 1990, Preservation of soft-bodied and other organisms by bioimmuration—a review: Palaeontology, v. 33, p. 1–17.
- Taylor, P.D., and Palmer, T.J., 1994, Submarine caves in a Jurassic reef (La Rochelle, France) and the evolution of cave biotas: Naturwissenschaften, v. 81, p. 357–360.
- Taylor, P.D., and Wilson, M.A., 2003, Palaeoecology and evolution of marine hard substrate communities: Earth-Science Reviews, v. 62, p. 1–103.
- Ulrich, E.O., 1882, American Palaeozoic Bryozoa: The Journal of the Cincinnati Society of Natural History, v. 5, p. 121–175, 233–257.
- Ulrich, E.O., 1890, Part II. Palaeontology of Illinois. Section VI. Palaeozoic Bryozoa: Report of the Geological Survey of Illinois, v. 8, p. 283–688.
- Ulrich, E.O., and Bassler, R.S., 1904, A revision of Paleozoic Bryozoa Part II: Smithsonian Miscellaneous Collections, v. 47, p. 15–55.
- Utgaard, J., and Perry, T.G., 1964, Trepostomatous bryozoan fauna of the upper part of the Whitewater Formation (Cincinnatian) of eastern Indiana and western Ohio: Indiana Geological Survey Bulletin, v. 33, p. 1–111.
- Vinn, O., Wilson, M.A., Mõtus, M.-A., and Toom, U., 2014, The earliest bryozoan parasite: Middle Ordovician (Darrivilian) of Osmussaar Island, Estonia: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 414, p. 129–132.
- Vogel, K., and Brett, C.E., 2009, Record of microendoliths in different facies of the Upper Ordovician in the Cincinnati Arch region USA: the early history of light-related microendolithic zonation: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 281, p. 1–24.
- Wilson, M.A., 1998, Succession in a Jurassic marine cavity community and the evolution of cryptic marine faunas: Geology, v. 26, p. 379–381.
- Wilson, M.A., and Palmer, T.J., 1992, Hardgrounds and hardground faunas: University of Wales, Aberystwyth, Institute of Earth Studies Publications, v. 9, p. 1–131.
- Wilson, M.A., and Palmer, T.J., 2006, Patterns and processes in the Ordovician bioerosion revolution: Ichnos, v. 13, p. 109–112.
- Wyse Jackson, P.N., and Key, M.M. Jr., 2007, Borings in trepostome bryozoans from the Ordovician of Estonia: two ichnogenes produced by a single maker, a case of host morphology control: Lethaia, v. 40, p. 237–252.

Accepted 30 September 2017