

# Epizoan and endoskeletozoan distribution across reassembled ramose stenolaemate bryozoan zoaria from the Upper Ordovician (Katian) of the Cincinnati Arch region, USA

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The Upper Ordovician (Katian) of the Cincinnati, Ohio, USA region has yielded bedding-plane assemblages of ramose stenolaemate bryozoans. Sixteen colonies were reassembled which provide valuable data on the settlement patterns of epizoans and endoskeletozoans, information on the timing of infestation and encrustation, and on environmental and taphonomic conditions affecting the bryozoan colonies. Various parameters were assessed: the size, incidence and position of borings; whether or not they show a regeneration rim that would indicate an in-vivo relationship between host and boring organism; and the position on branches of epizoans, measured on proximal and distal colony portions, and on the upper-facing or lower-facing sides of colonies as they lay on the substrate. Epizoans include thin adnate colonies of *Crepipora* and other unidentified cystoporate bryozoans, cornulitids, the problematicum *Hederella* and the cnidarian *Sphenothallus*. Encrustation was generally slight and in all but one colony was evenly distributed on all sides of branches indicating probable in-vivo infestation. The one exception suggests that the colony acted as a hardground once it had toppled over and was lying on the substrate. Boring into the zoarial skeleton took place both before and after death of colonies. Twice as many post-mortem borings are seen. Borings with a diameter of <0.5 mm are more frequent than larger borings. Distal halves of colonies exhibited twice the number of borings than proximal parts of colonies. Colonies from the Richmondian were less bored than older Edenian and Maysvillian counterparts, and also retained intact growing tips on two thirds of branches. In the stratigraphically older colonies growing tips were rare and just over half of broken branch tips showed excavation of the endozone by endoskeletozoans. This probably weakened branch extremities leading to breakage.

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ENDOLITHIC organisms since the Cambrian have bored into and exploited hardgrounds and skeletal materials in which to live (James & Kobluk 1977). The Ordovician saw a rapid and significant diversification of endolithic and infaunal organisms which began to exploit a range of substrates (Kobluk *et al.* 1978; Taylor & Wilson 2003; Buatois *et al.* 2016) including sediments (Droser & Bottjer 1989), hardgrounds (Wilson & Palmer 1988; Vinn *et al.* 2015) and skeletal elements (Buatois *et al.* 2016). As a result, bioturbation increased as did bioerosion (Wilson & Palmer 2006). The diversity of ichnogenera also increased significantly throughout the Ordovician, from 30 during the Tremadocian to just over 100 in the Hirnantian (Mángano & Droser 2004; Buatois *et al.* 2016).

During the Ordovician, endolithic organisms have contributed to what has become known as the ‘Ordovician Bioerosion Revolution’ (Wilson & Palmer 2001), and have produced 19 bioeroding ichnogenera by the Late Ordovician, an increase from the three known in the Cambrian (Buatois *et al.* 2016, table S6).

In the Cincinnati of the USA a rich ichnofauna of burrows and trails is known (Osgood 1970; Meyer *et al.* 2009) with over 30 ichnogenera. Five ichnogenera produced by macroborers have been reported: *Trypanites*, *Palaesabella*, *Petroxestes*, *Ropalonaria* (Pohowsky 1978; Anstey & Wilson 1996), and *Sanctum* (Wilson & Lazzari

2000; Wilson & Palmer 2006), and these occur in rugose corals (Cameron 1969; Elias 1983, 1986), stromatoporoids, molluscs, brachiopods (Pohowsky 1978; Anstey & Wilson 1996) and bryozoans (Wilson & Palmer 1988; Erickson & Bouchard 2003). They are most probably domicinia (Meyer *et al.* 2009, p. 206) and may also have served as refugia from predation for the boring organisms (Buatois *et al.* 2016). The pseudo-boring *Catellocaula vallata* is found in Cincinnati *Amplexopora* bryozoan colonies (Palmer & Wilson 1988) and superficially resembles true borings. Microendolithic organisms are diverse in the Cincinnati (Vogel & Brett 2009), but these are not documented in this study.

The literature on borings into nodular and hemispherical Paleozoic stenolaemate bryozoans is quite extensive. *Trypanites* is the most widely reported ichnogenus, found in the Middle Ordovician (Cuffey 1977; Kobluk & Nemcsok 1982; Pickerill *et al.* 1984, specifically in *Prasopora* colonies (Wyse Jackson & Key 2007)) and also in the Late Ordovician (Erickson & Bouchard 2003; Wyse Jackson & Key 2007). *Osprioides* has been recently reported from the Late Ordovician of Estonia (Vinn *et al.* 2014). Similarly, endolithic organisms have targeted stromatoporoids from the Ordovician (Tapanila *et al.* 2004), Silurian (Nield 1984), and Devonian (Pemberton *et al.* 1988) which provided morphologically similar hosts/substrates as did nodular trepostome bryozoans.

In contrast, to date there have been few studies of encrustation and borings in ramose Paleozoic stenolaemate bryozoans. Erickson & Bouchard (2003) erected the ichnogenus *Sanctum* for borings in several Cincinnatian bryozoans including *Constellaria*, *Heterotrypa*, *Monticulopora*, *Parvahallopora* and *Rhombotrypa*. This ichnogenus was identified and reinterpreted by Wyse Jackson & Key (2007) on the basis of material from the Lower Ordovician of Estonia. That study showed that a single trace maker could produce two different ichnogenera whose characteristic morphology was controlled by the skeletal architecture of the host colony. Boardman (1960) illustrated borings in ramose colonies of *Leptotrypella asterica* Boardman, 1960 from the Middle Devonian of New York (Boardman 1960, pl. 9, composite colony). However, his sample size was small, and partially based on fragmentary material assumed to be from one original colony, and the information recorded was tangential to the main taxonomic focus of his study (Boardman 1960). McKinney (1968) noted extensive borings in bifoliate zoaria of *Meekopora clausa* (Ulrich, 1884) from the Mississippian of Tennessee.

The imbalance of literature documenting borings in ramose as against nodular and hemispherical bryozoans is probably due to scale and the ease of preservation of the latter forms. Ramose colonies are more often than not preserved highly fragmented, whereas the latter colonies often remain complete, and as such boring and encrustation patterns are easier to document than in smaller zoarial fragments. Similarly, larger dome-shaped trepostomes provide a hard substrate sensu hardground for exploitation by epi- and endobionts. This study, on endoskeletozoans and borings in reassembled ramose colonies goes some way to rebalancing this situation.

Hardgrounds are examples of carbonate horizons that have become been subjected to syndimentary cementation (Wilson & Palmer 1992), and these provide surfaces for settlement by larvae of encrusting and boring organisms. In geologic history, the Ordovician was a time of extensive hardground development (Palmer 1982) produced by rapid calcite deposition during times of calcite seas (Palmer & Wilson 2004). Colonisation of hardgrounds by boring organisms commenced in the Cambrian and diversification of the communities increased into the Middle Ordovician after which diversity remained relatively static through to the Cretaceous. Aside from diversity, intensity of boring into hardgrounds increased during the Middle and Late Ordovician in North America but stayed static in Baltica (Vinn *et al.* 2015). By the Middle Ordovician, cornulitids, and encrusting cystoporate and trepostome bryozoans had appeared, and in the Upper Ordovician conularids and tabulate corals made their appearance (Palmer 1982). Hardground colonisation is prevalent in the Ordovician (Palmer & Palmer 1977; Vinn & Toom 2015) and boring organisms which dominated the communities produced ichnogenera also found in organic hard substrates such as bryozoans.

In the fossil record, only a few studies show that erect bryozoans provided niches for settlement by organisms exploiting their hard (and therefore assumed dead) surface, and gaining benefits of being elevated into the water column. In other cases, bryozoans are the encrusting organism on either motile (Key *et al.* 2010 and references therein) or sessile hosts such as crinoids (Wyse Jackson *et al.* 1999) or brachiopods (Ernst & Bohaty 2009).

## AIMS

This study focuses on epizoans and endoskeletozoans found in association with reassembled ramose fossil bryozoan colonies from the Cincinnatian (Katian) of the USA. Various questions pertaining to the interactions between the bryozoan hosts and the organisms that either encrusted or bored into their skeleton are addressed.

Specifically it aims to: (1) document the spatial distribution of borings, their morphology and size, (2) identify encrusting taxa and their spatial distribution on host colonies, (3) determine whether host colonies were encrusted or bored while alive and infer how much of the branches was covered with living tissue, (4) document whether bioerosion is responsible for patterns of breakage seen in the bryozoan colonies, (5) examine the settlement patterns of borers and encrusters on distal and proximal portions of colonies, (6) elucidate in colonies that can be shown to have toppled over and then were settled, which side of the colony was facing upwards, (7) infer general larval settlement site preferences, (8) document any differences in the incidence of boring and larval settlement in three successive stages of the Cincinnatian.

Answers to these questions could reveal information on the hydrodynamic and sedimentologic conditions affecting bryozoan life habits and preservation in the Cincinnatian, senescence in the bryozoan colonies, and the biology of the infesting organisms themselves. Bioeroders by their very activity may weaken the host skeleton into which they bore, and such activity probably contributed a considerable volume of fragmentary carbonate skeletal sediment to parts of the sedimentary record. Breakage of bryozoan colonies may be attributable to various vectors such as biostratinomic or diagenetic, but it is possible that bioerosion contributed to this breakdown.

## MATERIALS

This study was based on 16 reassembled fossil ramose stenolaemate bryozoan colonies, collected from various localities from the Upper Ordovician Katian Stage (=Edenian to Richmondian Stages in North America terminology) of the Cincinnatian Series (Table 1). The colonies come from outcrops exposed in four localities in the Cincinnati Arch region of southwestern Ohio and northern Kentucky, USA. They grew on a storm-dominated ramp in a shallow epeiric sea floor covered by mixed carbonate-siliciclastic sediments (Meyer *et al.* 2009). The 16 colonies included one cystoporate species (*Constellaria florida*) and six trepostome species (*Batostomella gracilis*, *Hallopora andrewsi*, *Homotrypa obliqua*, *Dekayella ulrichi*, *Dekayia aspera*, *Stigmatella* sp.) (Table 1).

Preservation of large, complete bryozoan colonies is rare in the fossil record with zoaria usually found highly fragmented. In rare cases some trepostome bryozoan colonies were smothered in sediment and early lithification resulted in these colonies being preserved in three dimensions. Examples of Cincinnatian colonies are present in the collections of the Cincinnati Museum of Natural History and Science's Geier Collections and Research Center, and the Natural History Museum, London. Reid (2010, fig. 4C) illustrates Permian examples of *Stenopora* colonies in situ in the field. However, removal of sediment surrounding these latter specimens is difficult and so they were of no value in the present study.

Within the Cincinnatian, some calcareous shale horizons have yielded bryozoan colonies which, while

**Table 1.** Stratigraphy, locality, and specimen identification information for the Upper Ordovician (Cincinnatian) ramose bryozoan colonies used in this study. \*CMC = Cincinnati Museum of Natural History and Science's Geier Collections and Research Center. OSUN = Ohio State University at Newark. (#1–16) = colony number for this study.

North American Stage	Formation	Member	Locality	Species	Repository ID Number* and study colony number
Richmondian	Arnheim	Sunset	Flat Run Quarry; immediately adjacent to the intersection of Ellis Road & Fry Road, far-southern Clay Township, far-southwestern Highland County, just east of Sicily, east of Mount Orab, southwestern OH, USA; 39.027933°N, 83.84745°W	<i>Batostomella gracilis</i>	OSUN 1 (#8) OSUN 2 (#9)
Maysvillian	Fairview	Mount Hope	Northwestern corner of the intersection of US Route 62/68 (Clyde T. Barbour Parkway) and Kentucky Route 3056 (Germantown Road) in Maysville, KY; on bench above Pickett Lane; 38.674014°N, 83.799353°W	<i>Constellaria florida</i>	CMC IP72750 (#2)
Edenian	Kope	McMicken	Northern corner of the intersection of Route 9 (AA Highway) and Kentucky Route 1019 (Lenoxburg Foster Road) south of Foster, KY; on bench over Route 9; 38.774825°N, 84.206678°W	<i>Hallopora andrewsi</i> <i>Homotrypa obliqua</i>	CMC IP72752 (#4) CMC IP72753 (#5) CMC IP72754 (#6)
Edenian	Kope	Southgate	Western corner of the intersection of Route 9 (AA Highway) and Kentucky Route 709 (US 27-AA Highway Connector Road) adjacent to Alexandria, KY; on slope leading down to Route 709; 38.988753°N, 84.396203°W	<i>Hallopora andrewsi</i> <i>Dekayella ulrichi</i> <i>Homotrypa obliqua</i> <i>Dekayia aspera</i> <i>Stigmatella</i> sp.	CMC IP72749 (#1) CMC IP72755 (#7) OSUN 6 (#13) CMC IP72751 (#3) OSUN 7 (#14) OSUN 8 (#15) OSUN 3 (#10) OSUN 4 (#11) OSUN 5 (#12) OSUN 9 (#16)

fragmented, remain relatively undisturbed following burial. Preservation in a low energy deep-water environment or having been rapidly buried may have produced this in situ preservation. Colonies became fragmented during diagenesis by compaction due to pressure exerted by lithostatic overburden. A number of stress relief breaks were recemented during diagenesis, but these do not affect the measurement of boring or epizoids. Careful collecting of these collapsed colonies has allowed for them to be reassembled (Cuffey & Fine 2005, 2006; Erickson & Waugh 2002; Waugh & Erickson 2002; Waugh *et al.* 2005; Key *et al.* 2016). The largest colony reassembled measured 66 cm in diameter (Cuffey & Fine 2006). In this study, we have focused on ramose bryozoan colonies rather than on frondose trepostomes which have proved in the past to be easier to reassemble (Cuffey & Fine 2005, 2006; Erickson & Waugh 2002; Waugh & Erickson 2002; Waugh *et al.* 2005). A suite of complete or reassembled ramose bryozoans had not been studied before in any meaningful manner with respect to epibiotic interactions, but a subsequent comparative study of such frondose specimens could be revealing. This is beyond the scope of this current study.

## METHODS

Colony fragments were carefully collected from exposed bedding surfaces, ultrasonically cleaned and dried. Fragments were then sorted according to branch diameter, and adjacent broken surfaces matched up. These were then glued together and the colony reassembled following the five-step process outlined in Key *et al.* (2016). Colonies were carefully reassembled incorporating 3–34 fragments (mean: 12.4, standard deviation: 9.3), but unlike some earlier studies (Waugh & Erickson 2002) were not reconstructed in any way through the addition of fillers to replicate missing portions of colonies. None of the colonies were complete as some contained broken distal branch tips or were lacking basal attachments. No colonies were

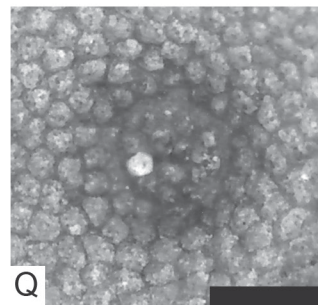
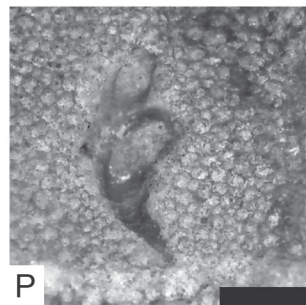
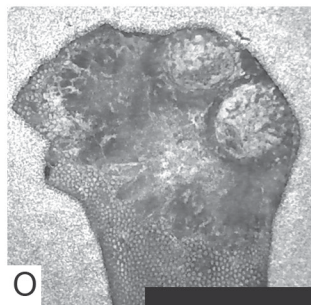
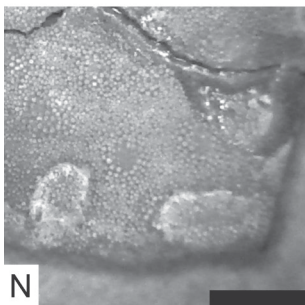
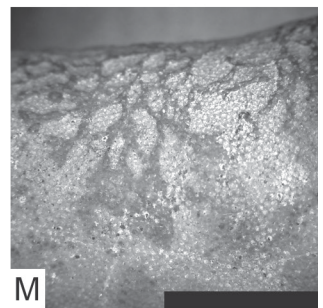
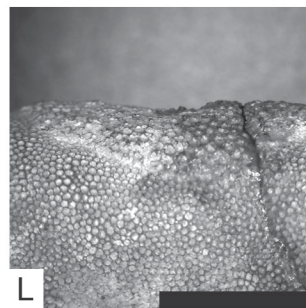
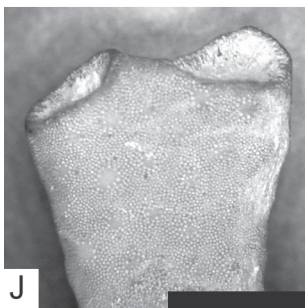
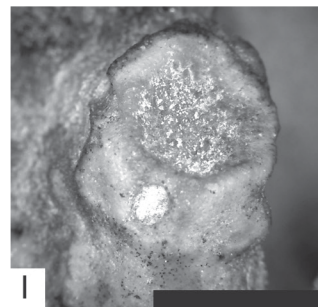
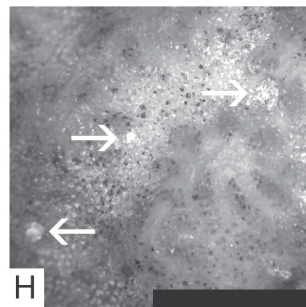
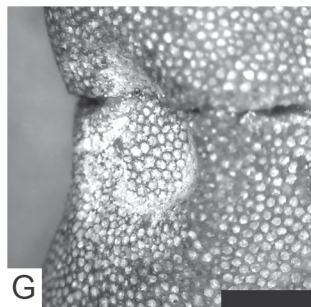
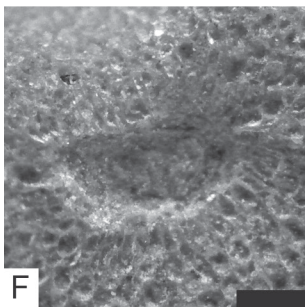
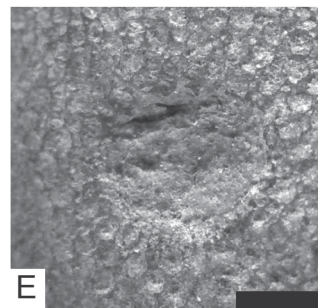
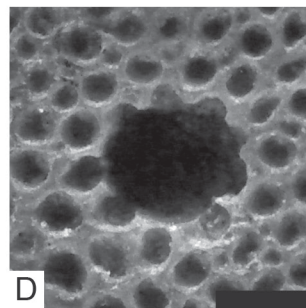
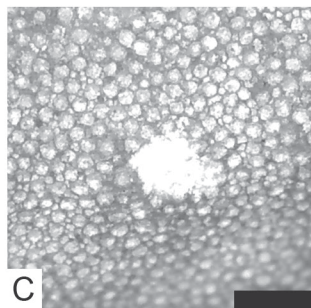
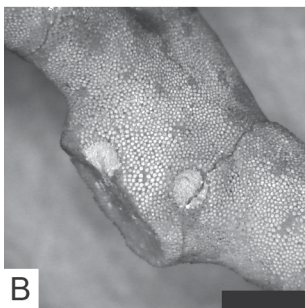
sectioned, and details of the internal mined out endozones were derived from examination of the broken fragment ends before their reassembly, or from abraded tips of branches (Fig. 1I, J) subsequent to reassembly.

In general terms the colonies did not develop bush-like spherical shapes in life, but were broadly planar in form. This form seen in the reassembled fossils is not as a result of diagenetic flattening (see above). Reassembled colonies were laid flat and photographed and then turned over and a second photograph obtained. These images were printed to 215.9 mm × 279.4 mm size, and these sheets were marked up to record the position of borings and encrusts. Additional features of note such as the position of abraded surfaces or sediment occlusion were also recorded on the sheets. Examination of the bryozoans was undertaken utilising a standard biological stereoscope microscope with magnification up to ×100.

Additional digital images of features of interest were photographed at magnifications of up to ×200 using a Dino-Lite AM4013MT camera mounted on a stand, and imported into Adobe Photoshop for later use.

Each host bryozoan colony was identified to genus and species level where possible. Only one was left in open nomenclature. The following characters were measured and recorded; the number of large borings of diameter >0.5 mm with regenerative margins (Fig. 1E, F) indicating that boring occurred into a surface covered by living tissue, and the number of large borings of diameter >0.5 mm with sharp margins (Fig. 1B–D) indicating boring was into dead skeleton. Likewise the number of small borings with a diameter of <0.5 mm with regenerative margins (Fig. 1H) and sharp margins. The presence and number of encrusting bryozoans (Fig. 1L–N), encrusting cornulitids (Fig. 1P), encrusting *Hederella* and encrusting *Sphenothallus* bases (Fig. 1Q) were noted. Observations were made on the occurrence of worn abraded surfaces, sediment covered surfaces, and self-overgrowth by bryozoans. The number and percent of borings/encrusts in distal and proximal





halves of colonies, and the number of intact growing tips in colonies characterised by having a hemispherical pristine growing tip, sensu Key (1990, fig. 1) (Fig. 1K) and number of broken growing tips in colonies were also recorded. Broken branch tips mined or unmined were noted. Those mined are recognised in the colonies by the bluish-gray matrix infilling of the endozonal domichnia of the endoskeletozoan that made the ichnofossil *Sanctum laurentiensis* (Erickson & Bouchard 2003; Wyse Jackson & Key 2007) (Fig. 1I, J). Mined out breaks have a distinctive concave, indented, dimpled shape (Fig. 1I, J) (Erickson & Bouchard 2003, figs 2.6, 2.15 of longitudinal cross-section) indicative of healing and continued post-breakage growth of the branch. The orientation of branch surfaces was determined in colonies that lay horizontally on substrate. The 'top' and 'bottom' sides of colonies were determined visually in three ways. Firstly, the upper surfaces were largely clean of adhering fine grained mud and lighter in colour, whereas the opposite held for the lower surfaces. This cleaning of the upper surfaces took place once the overlying muds were removed as the Cincinnati horizons were revealed through rapid recent erosion (Ohio Department of Transportation 2011). Secondly, in some colonies, notably #5 and #16, abrasion and erosion surfaces, which would have been uppermost, are lighter in colour than the unabraded surfaces, and have been worn down to the endozone in most cases. Thirdly, the orientation of stress-related breaks that indicated the direction of compaction pressure of overlying sediment from above could be determined in 12 of the 16 colonies studied.

#### Potential errors or limitations to methodology

Key *et al.* (2016) have outlined limitations to the measurement of colony size and quantification of branching styles in these specimens. However, while this earlier study relates to branching morphologies and frequencies, in the present study the only major linear measurement required was to partition the colony into proximal and distal portions. This was done by simply measuring the maximum height of colonies, measured as the linear distance from the base of the colony to the distal end of the longest branch, and dividing the result by two. The encrusting base was preserved in only one specimen (#16) (Fig. 1A, bottom right colony) while in two others (#8 and 9) the distal tips of branches were largely intact (Fig. 1, last two colonies on upper right, 2K). The remaining specimens constituted a portion of once larger colonies whose actual size was unknown, and it was impossible to determine the ratio of distal:proximal portions when they were alive. A smallish colony could be a distal portion of a much larger colony. However, when collected on bedding planes, it was clear that the fragments had not been transported post-mortem,

and the reconstructed colonies must represent most of the original colony. Where basal portions were not preserved a 50:50 ratio is assumed. While recognising that the lack of proximal and distal terminations in most of these colonies might be problematic, we anticipate that this will not adversely affect the findings on endoskeletozoan and epizoan distribution.

## RESULTS AND DISCUSSION

Data is presented in several tables: Table 1 gives stratigraphic, locality and taxonomic information; Table 2A provides data on proximal versus distally placed features and Table 2B gives numbers of borings, encrusters and other features on the 'top' and 'bottom' of branches. Detailed data on the numbers of branch tips broken and interiors mined is provided in Key *et al.* (2016, table 2) but data of specific relevance to this study are summarised below. Results of this study are discussed in respect of the eight aims outlined above.

In total 252 features were documented on the 16 bryozoan colonies examined in this study (Table 2), which demonstrates the complexities of interactions between bryozoan colonies as hosts and encrusting and boring organisms.

#### Size distribution of borings

In the two Richmondian colonies, few borings were found, with only six large (>0.5 mm) examples and no small (<0.5 mm) examples. This contrasts starkly with the situation in the 14 Edenian/Maysvillian colonies with 69 large borings and 75 small borings recorded. Of the latter, over a third were observed in *Constellaria florida*, the only cystoporate sampled (Fig. 1H). These were largely situated on the tops of the star-shaped monticules, which is surprising as this area is the most heavily calcified. It is probable that the boring organism targeted these locations to exploit residual food remaining in exhalant currents, unless the maculae were reverse chimneys centered on inhalant currents (e.g. Anstey 1981).

#### Encrusting taxa

Of the epizoic organisms encrusting the host colonies, these were dominated by bryozoans (n=36) which comprised both thin adnate cystoporates and trepostomes (including *Crepiopora* sp. (Fig. 1L)), and runner-like cyclostomes (*Corynotrypa* sp. and *Cuffeyella arachnoidea* (Fig. 1M)). The enigmatic runner *Hederella* was present as a single occurrence only on colony #12. *Sphenothallus*, which has been interpreted to be an alga (Neal & Hannibal 2000) but is more probably a medusozoan cnidarian (Vinn & Kirsimäe 2015; Van Iten *et al.* 2016), occurs sparingly

**Figure 1 (opposite).** A, Sixteen reassembled colonies used in this study. From top left, colonies #1 to #9; from bottom left, colonies #10 to #16. B–Q, Details of borings, encrusters and overgrowths. Geological horizons given in Table 1. B, CMC IP72749 (#1): branch with two large borings. C, OSUN 9 (#16): large boring in dead skeleton. D, OSUN 3 (#10): large boring in dead skeleton showing sharp edges. E, F, OSUN 6 (#13): large borings with regeneration of zoarium around rim. G, OSUN 3 (#10): large boring over which bryozoan has regrown and closed off. H, CMC IP72750 (#2): small borings (arrowed) situated in stellate maculae. I, CMC IP72750 (#2): mined and rounded broken branch tip showing regeneration with large boring on one side. J, OSUN 9 (#16): mined and broken branch tips showing regeneration. K, OSUN 2 (#9): colony with pristine branch tips. L, OSUN 3 (#10): Encrusting cystoporate bryozoan *Crepiopora* overgrowing *Homotrypa obliqua*. M, CMC IP72752 (#4): Encrusting cyclostome bryozoan *Cuffeyella* overgrowing *Hallopora andrewsi*. N, OSUN 9 (#16): Self-overgrowth in *Stigmatella* sp. O, OSUN 3 (#10): Rugose coral encrusting around broken branch tips. P, OSUN 7 (#14): Encrusting cornulitids. Q, OSUN 1 (#8): *Sphenothallus* base. Scale bars: 10 mm (K, J, O); 5 mm (A, B, I, L, M, N); 2 mm (H); 1 mm (Q); 0.5 mm (C, D, E, F, G, P).



**Table 2A.** Summary statistics for proximal:distal distribution of encrusters/borings. Abbreviations: R=Richmondian; M=Maysvillian; E=Edenian; (B) = Large boring of diameter >0.5 mm with regenerative margin (Fig. 1E, F) indicating that boring occurred into surface covered by living tissue; B = Large boring of diameter >0.5 mm with sharp margin (Fig. 1B–D) indicating boring was into dead skeleton; (b) = Small boring of diameter <0.5 mm with regenerative margin (Fig. 1H) indicating that boring occurred on surface covered by living tissue; b = Small boring of diameter <0.5 mm with sharp margin indicating boring took place into dead skeleton; EnBr = Encrusting bryozoan (Fig. 1L–N); Total number and % of borings/encrusters in distal and proximal halves of colonies.

Colony #	Stage	Colony height (mm)	# (B), (b)		# B, b		EnBr		Total # features incl. non-bryozoan encrusters		% features		Mean link length (mm) [data from Key <i>et al.</i> (2016)]	Shreve's (1967) branching ratio	# features on distal half correcting for Shreve's (1967) branching ratio
			Dist.	Prox.	Dist.	Prox.	Dist.	Prox.	Dist.	Prox.	Dist.	Prox.			
8	R	83.3	1	0	1	0	0	0	3	3	50	50	11.6	4.3	0.7
9	R	92.2	1	4	0	0	0	0	2	4	33	67	8.5	5.7	0.4
2	M	85.6	17	2	27	0	0	0	45	2	96	4	20.9	2.0	22.5
1	E	138.7	2	7	1	1	8	0	13	8	62	38	17.4	2.8	4.6
3	E	86.8	3	3	0	0	5	0	8	3	73	27	11.4	3.0	2.7
4	E	77.1	9	3	8	4	4	1	23	10	70	30	14.5	3.3	7.0
5	E	71.3	0	1	1	4	0	1	1	6	14	86	12.8	2.3	0.4
6	E	64.1	0	0	2	0	0	0	2	0	100	0	8.8	2.3	0.9
7	E	66.0	0	2	1	1	0	1	1	4	20	80	16.8	4.0	0.3
10	E	100.1	1	2	11	2	4	0	18	4	82	18	18.6	5.0	3.6
11	E	86.9	0	0	8	0	0	0	9	0	100	0	16.9	2.9	3.1
12	E	95.1	0	0	7	10	0	0	7	11	39	61	16.6	3.5	2.0
13	E	67.4	5	1	0	0	0	0	5	4	56	44	12.2	2.7	1.9
14	E	87.9	0	0	1	10	4	0	5	15	25	75	15.7	3.0	1.7
15	E	61.3	0	0	1	4	1	0	2	4	33	67	14.3	4.0	0.5
16	E	152.2	0	0	5	9	4	3	12	18	40	60	24.3	2.9	4.1
SUM			39	25	74	45	30	6	156	96					

**Table 2B.** Summary statistics for 'top'/'bottom' of branch distribution of encrusters/borings. Abbreviations: R=Richmondian; M=Maysvillian; E=Edenian; (B) = Large boring of diameter >0.5 mm with regenerative margin (Fig. 1E, F) indicating that boring occurred into surface covered by living tissue; B = Large boring of diameter >0.5 mm with sharp margin (Fig. 1B–D) indicating boring was into dead skeleton; (b) = Small boring of diameter <0.5 mm with regenerative margin (Fig. 1H) indicating that boring occurred on surface covered by living tissue; b = Small boring of diameter <0.5 mm with sharp margin indicating boring took place into dead skeleton; EnBr = Encrusting bryozoan (Fig. 1L–N); EnC = encrusting cornulitids. EnS = encrusting *Sphenothallus* base (Fig. 1Q); EnH = encrusting *Hederella*. Self-overgrowth by bryozoan.

Colony #	Stage	Colony height (mm)	# (B), (b)		# B, b features		EnBr		EnC		EnS		EnH		Bryozoan overgrowth	
			Top	Bottom	Top	Bottom	Top	Bottom	Top	Bottom	Top	Bottom	Top	Bottom	Top	Bottom
8	R	83.3	1	0	1	0	0	0	0	1	1	2	0	0	0	0
9	R	92.2	2	3	0	0	0	0	1	0	0	0	0	0	0	0
2	M	85.6	1	18	13	15	0	0	0	0	0	0	0	0	0	0
1	E	138.7	2	7	2	0	6	2	1	0	0	0	0	0	1	0
3	E	86.8	2	4	0	0	2	3	0	0	0	0	0	0	0	0
4	E	77.1	6	6	5	7	2	3	2	0	0	0	0	0	1	1
5	E	71.3	1	0	2	3	0	1	0	0	0	0	0	0	0	0
6	E	64.1	0	0	2	0	0	0	0	0	0	0	0	0	0	0
7	E	66.0	2	0	1	1	1	0	0	0	0	0	0	0	0	0
10	E	100.1	1	2	7	6	3	1	0	0	0	0	0	0	0	0
11	E	86.9	0	0	4	4	0	0	0	0	0	0	0	0	0	0
12	E	95.1	0	0	2	15	0	0	0	0	0	0	1	0	0	0
13	E	67.4	2	4	0	0	0	0	3	0	0	0	0	0	0	0
14	E	87.9	0	0	3	8	2	2	0	5	0	0	0	0	0	0
15	E	61.3	0	0	5	0	1	0	0	0	0	0	0	0	0	0
16	E	152.2	0	0	1	13	5	2	7	1	0	0	0	0	0	1
SUM			20	44	48	72	22	14	11	9	1	2	1	0	2	2

(n=3) only on colony #8 from the Richmondian. It is easily recognised on account of the characteristic imprint made by its holdfast (Fig. 1Q). Cornulitids (Fig. 1P) (n=19) were located on seven colonies and were most abundant on colonies #13, 14 and 16 from the Southgate Member of the Kope Formation (Edenian). It has been postulated that cornulitids were opportunistic filter feeders (Vinn & Toom 2015), some in symbiotic relationships with sponges, corals

and bryozoans (Vinn 2016). As such, some observed in this study may have benefited from the filter feeding currents generated by their host bryozoans. In the Richmondian a number of epizoans including cornulitids are pyritised and such preservation is not seen in the Edenian or Maysvillian colonies. The larvae of some Recent bryozoans such as *Membranipora membranacea* show preferential settlement on elevated portions of hard substrata (Walters 1992).

A similar settlement preference for monticules by larvae of small endoskeletozoans only occurred with *Constellaria florida*, and systematic encrustation on elevated portions of colonies in other taxa was not observed in this study.

### Were colonies encrusted or bored while alive and how much of the branches were covered with living tissue?

In general terms encrustation of the majority of colony surfaces was generally slight (<5%) but reached approximately 25% and 30% respectively in two colonies (#3 and #14) of *Dekayella ulrichi* from the Kope, and 40% on *Homotrypa obliqua* (colony #5) also from the Kope. In all colonies, older proximal portions appear to be less targeted by settling larvae of other bryozoans than were distal branches (proximal  $n=6$  (17%); distal  $n=30$  (83%)). This may be counter-intuitive as one would expect the older portions of colonies to be more fouled and bored. That they are not could be explained if the proximal areas had developed secondary calcification, as occurs in many bryozoan colonies during ontogeny (Cheetham 1986; Smith *et al.* 2001); however, no evidence of such additional skeletal material was observed. The patterns of larval settlement in proximal and distal portions of colonies may be a function of the concentration of sediment in the water closest to the sea floor, or differences in horizontal flow regimes over the length of the colony, both of which may lower the ability of larvae to settle on proximal parts of colonies. The differences in distal–proximal patterns could also be explained by the fact that a larger number of branches are developed in the younger parts of colonies away from the point of origin (Key *et al.* 2016).

Similar trends were observed in the settlement of endoskeletozoans (proximal  $n=70$  (38%); distal=113 (62%)). Of these 183 borings 35% ( $n=64$ ) were considered, on the basis of regrowth rims around boring margins (Fig. 1E, F), to have bored into living tissue. Similar stellate structures were described in *Leptotrypella asterica* Boardman, 1960 from the Middle Devonian of New York (Boardman 1960, pl. 9, figs 1h, i). These may also be regeneration structures following boring into living colonies. The remaining 65% ( $n=119$ ) borings penetrated exozonal walls that we inferred were not covered by living epithelial tissue as the borings had characteristic sharp margins (Fig. 1C, D). This demonstrated that the endoskeletozoans had bored into parts of the colony that were dead.

Precisely what the nature of the symbiotic relationship between the endoskeletozoan and the living bryozoan colony was can only be suggested as the biological affinity of the boring animals is not known. Wyse Jackson & Key (2007), in a study of borings in Ordovician bryozoans from Estonia, provided evidence that polychaete worms were responsible for at least some of the borings. If this is also the case in the colonies penetrated in this study, then the living host bryozoan polypides may have enhanced feeding capability for the endoskeletozoan. This relationship offers no obvious benefit to the bryozoan host.

Determining the extent of the living tissue in these bryozoans is difficult. The distribution of borings through skeleton either covered by living epithelium or considered dead between proximal and distal portions of colonies might yield data of interest in this regard: proximally located borings ( $n=70$ ), through dead skeleton (64%,  $n=45$ ) and borings through live skeleton (36%,  $n=25$ );

distally located borings ( $n=113$ ), through dead skeleton (65%,  $n=74$ ), borings through live skeleton (35%,  $n=39$ ) (Table 2A). The mean dead to alive ratio of borings is 1.8 in proximal portions of the colony and 1.9 in distal regions. It is probable that boring activity in a colony took place over its whole life span so that areas that were living were bored and that boring continued after these areas no longer supported living polypides. Unravelling senescence in these bryozoans remains problematic.

Only two instances were found of the bioeroded bryozoan overgrowing and closing over the boring entrance (Fig. 1G), and there is clear evidence of skeletal regeneration around some openings (Fig. 1E, F), which indicates an in-vivo response of the bryozoan host. No examples of overgrowth of borings by surface encrusting bryozoan colonies were seen. However, thin-section studies would be necessary to rule out such interactions.

Host–epizoan in-vivo synergies include the one instance of *Sphenothallus* found fouling the zoarial surface, where only slight reactive growth was noted, unlike examples from the Upper Ordovician Dillboro Formation in Indiana reported by Bodenbender *et al.* (1989). In the current example, the size of autozooecea immediately surrounding the cnidarian basal disc is smaller than those further away; this smaller size is a consequence of the encrustation (Fig. 1Q). Another synergy is that of the rare incidence of bioclaustration formed by the overgrowth of cornulitid tubeworms by *Hallopora andrewsi* (colonies #4 and #13) in the Kope. Cornulitids probably benefitted symbiotically from the generation of food-bearing inhalant currents generated by the bryozoan host (see Vinn 2016). Similarly, the endoskeletozoan that produced the small borings associated with maculae in *Constellaria florida* (colony #2) discussed above did so when the host was alive.

### Distribution of endoskeletozoans and epizoans — indicators of the orientation of colonies

Several earlier studies have focused on the distribution of epizoans as indicators of whether the hosts are preserved in life or post-mortem positions. However, unlike this current study, these focused on brachiopods (Cuffey *et al.* 1995; Barclay *et al.* 2015). Spatial distribution of endoskeletozoans and epizoans may indicate whether bryozoan colonies were infested in their erect upright, and assumed living, orientation, or when lying horizontally on the sediment surface.

In all but two colonies (#6 and #15) encrustation and borings were distributed on all sides ('top' and 'bottom' of branches) (Table 2B) indicating probable in-vivo infestation. Cumulatively more than twice as many borings were recorded on the 'bottom' underside of branches (71%,  $n=116$ ) as on the 'top' of branches (29%,  $n=48$ ) (Table 2B). While the larval settlement preferences of marine invertebrates may be influenced by light, gravity, salinity, fluid flow energy, and swimming ability (Butman 1987; see McKinney & McKinney 1993 for a review of these and other factors affecting distribution of bryozoan larvae), the pattern of encrustation by endobionts in this study suggests a hydrological regime in which erect bryozoan colonies were growing in an environment with a dominant prevailing unidirectional current. Bryozoan colonies would have acted as baffles resulting in a calm area of reduced flow energy on the leeward side of branches, where preferential settlement of larvae occurred. Subsequently colonies when

toppled were most likely fall onto the side away from the prevailing current direction, which is suggestive of the higher infestation on the 'bottom' surfaces observed in this study. An alternative hypothesis is that colonies were relatively unfouled when living, and after they fell over, larvae in a phototactic or geotactic response preferentially settled on the underside of branches not touching or buried in sediment.

In colony #5 encrusting cystoporate Bryozoa have grown around branches which later toppled over and were abraded on their 'top' surface. Encrusting zoaria are present on the 'bottom' surface which therefore must have been upright when encrusted. Evidence for encrusting while the colony was upright (and assumed to be alive) can be demonstrated in colony #14 where cyclostome and cystoporate bryozoans have grown around the complete circumference of branches. *Dekayella ulrichi* (colony #3) showed encrustation by bryozoans on the upper surface and growth of the colony stops on the underside suggesting that the branch was lying in sediment. This evidence together with that discussed above provides good 'way-up' documentation. It is likely that boring could only have taken place when the colony was erect, or that it was initiated on the upper sides of fallen colonies. Once these colonies had fallen over it is difficult to ascertain whether they remained alive on their 'top' surfaces or whether encrustation of dead skeletal surfaces continued. Colony #15 was probably infested after it had fallen over as the 'bottom' surface lacks any borings or epizoans while there are six such examples on the 'top' surface (Table 2B).

### Is bioerosion is responsible for patterns of breakage seen in the bryozoan colonies?

In total 204 terminal branches in the 16 colonies were present (Key *et al.* 2016) and of these 38% were freshly broken, 91 (48%) had an old broken tip that had started to heal and regrow, and only 29 (14%) had a pristine growing tip preserved. Seventy one percent of the branches in the two Richmondian colonies had branches terminated by a pristine growing tip (Fig. 1K) which may reflect a different environmental regime to that of the older Edenian and Maysvillian colonies whose terminations were more frequently damaged with only 6% of tips intact. However, the Sunset Member of the Arnheim Formation (from where the Richmondian colonies were collected) has been interpreted as having a shallower palaeobathymetry and therefore higher energy regime than the Kope Formation, where all but one of the Edenian to Maysvillian colonies originate (Holland 1993, fig. 8; Vogel & Brett 2009, fig. 5; Smrecak & Brett 2014, fig. 1).

Damage in the older colonies from the deeper, calmer environmental settings in the Kope, may be as a result of higher frequency of boring and mining of endozonal interiors of branches leading to a weakening of branch terminations. On average, 33% of the endozones of broken branches from the Richmondian colonies were mined out, whereas 63% of the endozones of broken branches from the Edenian to Maysvillian colonies were mined out. The numbers of borings in the Richmondian specimens averaged 6.5 borings (of all sizes observed) per colony whereas the average in the Edenian to Maysvillian colonies is 8.2. This suggests that the *Sanctum*-producing endoskeletozoan(s) became less abundant in the Richmondian. The decline in observed sclerobiont intensity in this study from the Edenian to the Richmondian is a reverse of what has been

previously reported for microendoliths that bored into shells over the same geological interval in the same area (Vogel & Brett 2009). While light penetration has been cited as a major factor affecting the distribution of the smaller boring organisms, it is not a dominant factor in the distribution of larger endoskeletozoans that targeted bryozoan hosts. Alternatively, it is likely that the skeletal architecture of *Batostomella gracilis* (Fig. 1K) in the Richmondian was more difficult to penetrate than that of the trepostome and cystoporate species in the Edenian/Maysvillian. This hypothesis has not been tested here, but is the focus of a further study (Wyse Jackson *et al.* 2019).

## CONCLUSIONS

Reassembled ramose bryozoan colonies from the Upper Ordovician (Katian) of the Cincinnati Arch region, USA are subjected to encrustation by epizoans and are bored by endolithic organisms both when colonies were alive and after death. Infestation generally occurred while colonies were still upright in the water column.

Epizoan coverage is slight, but diverse with cystoporate, trepostome, and cyclostome bryozoans recorded, as well as rare rugose corals, *Sphenothallus*, and cornulitids.

Post-mortem boring into zoaria is twice as prevalent as in-vivo borings, and distal portions of colonies are also more frequently bored. The latter situation may be due to the development of more branches in the younger parts of colonies away from the point of origin, or to environmental factors influencing settlement of larvae.

Richmondian colonies are less bored and bioeroded, with more growing tips preserved than in older Edenian and Maysvillian examples. This may reflect differences in environmental conditions, bioerosion-resistance branch architecture or variation in the numbers of endolithic organisms in the two stages. In the stratigraphically older colonies extensive mining of the endozone lead to a weakening and breaking of branches, some of which exhibit repair tissue around margins.

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## REFERENCES

- ANSTEY, R.L., 1981. Zooid orientation structures and water flow patterns in Paleozoic bryozoan colonies. *Lethaia* 14(4), 287–302.
- ANSTEY, R.L. & WILSON, M.A., 1996. Phylum Bryozoa. *Ohio Division of Geological Survey Bulletin* 70, 196–209.
- BARCLAY, K.M., SCHNEIDER, C.L. & LEIGHTON, L.R., 2015. Mapping sclerobiosis: a new method for interpreting the distribution, biological implications, and paleoenvironmental significance of sclerobionts on biotic hosts. *Paleobiology* 41(4), 592–609.
- BOARDMAN, R.S., 1960. Trepostomatous Bryozoa of the Hamilton Group of New York State. *U.S. Geological Survey Professional Paper* 340, 1–87.



- BODENBENDER, B.E., WILSON, M.A. & PALMER, T.J., 1989. Paleoecology of *Sphenothallus* on an Upper Ordovician hardground. *Lethaia* 22(2), 217–225.
- BUATOIS, L.A., MÁNGANO, M.G., OLEA, R.A. & WILSON, M.A., 2016. Decoupled evolution of soft and hard substrate communities during the Cambrian Explosion and Great Ordovician Biodiversification Event. *PNAS* 113(25), 6945–6948.
- BUTMAN, C.A., 1987. Larval settlement in soft-sediment invertebrates: the spatial scales of pattern explained by active habitat selection and the energy role of hydrodynamic processes. *Oceanography and Marine Biology: an Annual Review* 25, 113–165.
- CAMERON, B., 1969. Paleozoic shell-boring annelids and their trace fossils. *American Zoologist* 9, 689–703.
- CHEETHAM, A.H., 1986. Branching, biomechanics and bryozoan evolution. *Proceedings of the Royal Society of London, Series B, Biological Sciences* 228, 151–171.
- CUFFEY, C.A., ROBB, A.J., III, LEMBCKE, J.T. & CUFFEY, R.J., 1995. Epizoid bryozoans and corals as indicators of life and post-mortem orientations of the Devonian brachiopod *Meristella*. *Lethaia* 28(2), 139–153.
- CUFFEY, R.J., 1977. Mid-Ordovician bryozoan reefs in western Newfoundland. *Geological Society of America, Abstracts with Programs* 9, 253.
- CUFFEY, R.J. & FINE, R.L., 2005. The largest known fossil bryozoan reassembled from near Cincinnati. *Ohio Geology* 2005(1), 3–4.
- CUFFEY, R.J. & FINE, R.L., 2006. Reassembled trepostomes and the search for the largest bryozoan colonies. *International Bryozoology Association Bulletin* 2(1), 13–15.
- DROSER, M.L. & BOTTJER, D.J., 1989. Ordovician increase in extent and depth of bioturbation: implications for understanding early Paleozoic ecospace utilization. *Geology* 17, 850–852.
- ELIAS, R.J., 1983. Middle and Late Ordovician solitary rugose corals of the Cincinnati Arch region. *U.S. Geological Survey Professional Paper* 1066-N, 1–13.
- ELIAS, R.J., 1986. Symbiotic relationships between worms and solitary rugose corals in the Late Ordovician. *Paleobiology* 12, 32–45.
- ERICKSON, J.M. & BOUCHARD, T.D., 2003. Description and interpretation of *Sanctum laurentiensis*, new ichnogenus and ichnospecies, a domichnium mined into late Ordovician (Cincinnatian) ramose bryozoan colonies. *Journal of Paleontology* 77, 1002–1010.
- ERICKSON, J.M. & WAUGH, D.A., 2002. Colony morphologies and missed opportunities during the Cincinnati (Late Ordovician) bryozoan radiation: examples from *Heterotrypa frondosa* and *Monticulipora mammulata*. 101–107 in Wyse Jackson, P.N., Buttler, C.J. & Spencer Jones, M.E. (eds), *Bryozoan Studies 2001*. Balkema Publishers, Lisse, The Netherlands.
- ERNST, A. & BOHATÝ, J., 2009. *Schischcatella* (Fenestrata, Bryozoa) from the Devonian of the Rhenish Massif, Germany. *Palaeontology* 52, 1291–1310.
- HOLLAND, S.M., 1993. Sequence stratigraphy of a carbonate-clastic ramp: the Cincinnati Series (Upper Ordovician) in its type area. *Geological Society of America Bulletin* 105, 306–322.
- JAMES, N.P. & KOBLUK, D.R., 1977. The oldest macroborers: Lower Cambrian of Labrador. *Science* 197, 980–983.
- KEY, M.M., JR., 1990. Intracolony variation in skeletal growth rates in Paleozoic ramose trepostome bryozoans. *Paleobiology* 16(4), 483–491.
- KEY, M.M., JR., SCHUMACHER, G.A., BABCOCK, L.E., FREY, R.C., HEIMBROCK, W.P., FELTON, S.H., COOPER, D.L., GIBSON, W.B., SCHEID, D.G. & SCHUMACHER, S.A., 2010. Paleoecology of commensal epizoids fouling *Calymene* (Trilobita) from the Upper Ordovician, Cincinnati Arch region, USA. *Journal of Paleontology* 84, 1121–1134.
- KEY, M.M., JR., WYSE JACKSON, P.N. & FELTON, S.H., 2016. Intracolony variation in colony morphology in reassembled fossil ramose stenolaemate bryozoans from the Upper Ordovician (Katian) of the Cincinnati Arch region, USA. *Journal of Paleontology* 90, 400–412.
- KOBLUK, D.R., JAMES, N.P. & PEMBERTON, S.G., 1978. Initial diversification of macroboring ichnofossils and exploitation of the macroboring niche in the lower Paleozoic. *Paleobiology* 4, 163–170.
- KOBLUK, D.R. & NEMCSOK, S., 1982. The macroboring ichnofossil *Trypanites* in colonies of the Middle Ordovician bryozoan *Prasopora*: population behaviour and reaction to environment. *Canadian Journal of Earth Sciences* 19, 679–688.
- MCKINNEY, F.K., 1968. A bored ectoproct from the Middle Mississippian of Tennessee. *Southeastern Geology* 9, 165–170.
- MCKINNEY, F.K. & MCKINNEY, M.J., 1993. Larval behaviour and choice of settlement site: Correlation with environmental distribution pattern in an erect bryozoan. *Facies* 29(1), 119–131.
- MÁNGANO, M.G. & DROSER, M.L., 2004. The ichnologic record of the Ordovician radiation. 369–379 in Webby, B.D., Paris, F., Droser, M.L. & Percival, I.G. (eds), *The Great Ordovician Biodiversification Event*. Columbia University Press, New York.
- MEYER, D.L., DAVIS, R.A. & HOLLAND, S.M., 2009. *A Sea without Fish — Life in the Ordovician Sea of the Cincinnati Region*. Indiana University Press, Bloomington. 346 p.
- NEAL, M.L. & HANNIBAL, J.T., 2000. Paleoecologic and taxonomic implications of *Sphenothallus* and *Sphenothallus*-like specimens from Ohio and areas adjacent to Ohio. *Journal of Paleontology* 74, 369–380.
- NIELD, E.W., 1984. The boring of Silurian stromatoporoids — towards an understanding of larval behaviour in the *Trypanites* organism. *Palaeogeography, Palaeoclimatology, Palaeoecology* 48, 229–243.
- OHIO DEPARTMENT OF TRANSPORTATION, 2011. Rock Slope Design Guide. [http://www.dot.state.oh.us/divisions/engineering/geotechnical/geotechnical\\_documents/rock\\_slope\\_design\\_guide.pdf](http://www.dot.state.oh.us/divisions/engineering/geotechnical/geotechnical_documents/rock_slope_design_guide.pdf)
- OSGOOD, R.G., JR., 1970. Trace fossils of the Cincinnati area. *Paleontographica Americana* 6, 279–444.
- PALMER T.J., 1982. Cambrian to Cretaceous hardground communities. *Lethaia* 15, 309–323.
- PALMER, T.J. & PALMER, C.D., 1977. Faunal distribution and colonization strategy in a mid-Ordovician hardground community. *Lethaia* 10, 179–200.
- PALMER T.J. & WILSON, M.A., 1988. Parasitism of Ordovician bryozoans and the origin of pseudoborings. *Palaeontology* 31, 939–949.
- PALMER T.J. & WILSON, M.A., 2004. Calcite precipitation and dissolution of biogenic aragonite in shallow Ordovician calcite seas. *Lethaia* 37, 417–427.
- PEMBERTON, S.G., JONES, B. & EDGEcombe, G., 1988. The influence of *Trypanites* in the diagenesis of Devonian stromatoporoids. *Journal of Paleontology* 62, 22–31.
- PICKERILL, R.K., FILLION, D. & HARLAND, T.L., 1984. Middle Ordovician trace fossils in carbonates of the Trenton Group between Montreal and Quebec City, St. Lawrence Lowland, eastern Canada. *Journal of Paleontology* 58, 416–439.
- POHOWSKY, R.A., 1978. The boring ctenostomate Bryozoa: taxonomy and paleobiology based on cavities in calcareous substrata. *Bulletins of American Paleontology* 73, 1–192.

- REID, C.M., 2010. Environmental controls on the distribution of Late Paleozoic bryozoan colony morphotypes: an example from the Permian of Tasmania, Australia. *Palaaios* 25, 692–702.
- SMITH, A.M., STEWART, B., KEY, M.M., JR & JAMET, C.M., 2001. Growth and carbonate production by *Adeonellopsis* (Bryozoa: Cheilostomata) in Doubtful Sound, New Zealand. *Palaeogeography, Palaeoclimatology, Palaeoecology* 175, 201–210.
- SMRECAK, T.A. & BRETT, C.E., 2014. Establishing patterns in sclerobiont distribution in a Late Ordovician (Cincinnatian) depth gradient: toward a sclerobiofacies model. *Palaaios* 29, 74–85.
- TAPANILA, L., COPPER, P. & EDINGER, E., 2004. Environmental and substrate control on Paleozoic bioerosion in corals and stromatoporoids, Anticosti Island, Eastern Canada. *Palaaios* 19, 292–306.
- TAYLOR, P.D. & WILSON, M.A., 2003. Palaeoecology and evolution of marine hard substrate communities. *Earth-Science Reviews* 62, 1–103.
- ULRICH, E.O., 1884. American Palaeozoic Bryozoa. *Journal of the Cincinnati Society of Natural History* 7, 26–33.
- VAN ITEN, H., MUIR, L., SIMÕES, M.G., LEME, J.M., MARQUES, A.C. & YODER, N., 2016. Palaeobiogeography, palaeoecology and evolution of Lower Ordovician conulariids and *Sphenothallus* (Medusozoa, Cnidaria), with emphasis on the Fezouata Shale of southeastern Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology* 460, 170–178.
- VINN, O., 2016. Tentaculitoid tubeworms as endobiotic symbionts of Paleozoic corals and sponges. *Palaaios* 31, 440–446.
- VINN, O. & KIRSIMÄE, K., 2015. Alleged cnidarian *Sphenothallus* in the Late Ordovician of Baltica, its mineral composition and microstructure. *Acta Palaeontologica Polonica* 60(4), 1001–1008.
- VINN, O. & TOOM, U., 2015. Some encrusted hardgrounds from the Ordovician of Estonia (Baltica). *Carnets de Géologie [Notebooks on Geology]* 15(7), 63–70.
- VINN, O., WILSON, M.A. & MOTUS, M.-A., 2014. The earliest giant *Osprioneides* borings from the Sandbian (Late Ordovician) of Estonia. *PLOS one* 9, 1–6.
- VINN, O., WILSON, M.A. & TOOM, U., 2015. Bioerosion of inorganic hard substrates in the Ordovician of Estonia (Baltica). *PLOS one* 10(7), 1–17.
- VOGEL, K. & 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* 281, 1–24.
- WALTERS, L.J., 1992. Field settlement locations on subtidal marine hard substrata: is active larval exploration involved? *Limnology and Oceanography* 37(5), 1001–1007.
- WAUGH, D.A. & ERICKSON, J.M., 2002. Functional morphology of the anastomosing frondose growth form reported in *Heterotrypa frondosa* (d'Orbigny) (Bryozoa: Trepostomata) from the Cincinnati (Late Ordovician) of Ohio. 331–338 in Wyse Jackson, P.N., Buttler, C.J. & Spencer Jones, M.E. (eds), *Bryozoan Studies 2001*. Balkema Publishers, Lisse, The Netherlands.
- WAUGH, D.A., ERICKSON, J.M. & CRAWFORD, R.S., 2005. Two growth forms of *Heterotrypa* Nicholson, 1879 (Bryozoan: Trepostomata) from the type-Cincinnati: Putting the pieces back together. *The Compass* 78(3), 97–112.
- WILSON, M.A. & LAZZURI, J.E., 2000. Paleocology of borings and pseudoborings in the Cincinnati (Late Ordovician) of the North American Midcontinent. *Geological Society of America Abstracts with Programs* 32(4), A68.
- WILSON, M.A. & PALMER, T.J., 1988. Nomenclature of a bivalve boring from the Upper Ordovician of the Midwestern United States. *Journal of Paleontology* 62, 306–308.
- WILSON, M.A. & PALMER, T.J., 1992. Hardgrounds and hardground faunas. *University of Wales, Aberystwyth, Institute of Earth Studies Publications* 9, 1–131.
- WILSON, M.A. & PALMER, T.J., 2001. The Ordovician bioerosion revolution. *Geological Society of America, Abstracts with Programs* 33(6), A248.
- WILSON, M.A. & PALMER, T.J., 2006. Patterns and Processes in the Ordovician Bioerosion Revolution. *Ichnos* 13, 109–112.
- WYSE JACKSON, P.N. & KEY, M.M., JR, 2007. Borings in trepostome bryozoans from the Ordovician of Estonia: two genera produced by a single maker, a case of host morphology control. *Lethaia* 40(3), 237–252.
- WYSE JACKSON, P.N., KEY, M.M., JR & REID, C.M. 2019. Bryozoan Skeletal Index (BSI): a measure of the degree of calcification in stenolaemate bryozoans. In Zagorsek, K. & Wyse Jackson, P.N. (eds), *Bryozoan Studies 2019*. Czech Geological Survey, Prague.
- WYSE JACKSON, P.N., TAYLOR, P.D. & TILSLEY, J.W., 1999. The 'Balladoole Coral' re-interpreted as the unusual cystoporate bryozoan *Meekoporella* Moore and Dudley, 1944 from the Lower Carboniferous of the British Isles. *Proceedings of the Yorkshire Geological Society* 52, 257–268.