Journal of Paleontology, 88(3), 2014, p. 475–487
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0022-3360/14/0088-475$03.00
DOI: 10.1666/13-138

EPIZOOZOAN TREPOSTOME BRYOZOANS ON NAUTILOIDS FROM THE UPPER ORDOVICIAN (KATIAN) OF THE CINCINNATI ARCH REGION, U.S.A.: AN ASSESSMENT OF GROWTH, FORM, AND WATER FLOW DYNAMICS

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ABSTRACT—*Spatiopora* Ulrich, 1882 is a trepostome bryozoan that is found encrusting living orthoconic nautiloids in the Upper Ordovician (Katian) of North America, as do several other bryozoans. These epizoozoan bryozoans are characterized by possessing thin unilaminate zoaria with rows of elongate maculae, which may be monticulate and aligned coaxially to the host growth axis. These develop a distinctive linear shape in response to growing on a conical host, rather than as a response to channelized water flow along the host. Monticules increase in size and spacing adorally until a maximum inter-macular area is reached that results in a decline in surface water flow efficiency, and a new monticular line is inserted. Orthocones normally swam forward at lower velocities that enabled lophophore eversion and feeding, which would have been impossible at the higher speeds reached when the host jetted backwards during escape. Monticules reduced drag and turbulence acting on the orthocones which allowed for more efficient venting of bryozoan macular excurrents. Characteristic elliptical monticule growth continued even after death of the motile host. A *Trypanites*-bryozoan-orthoconic nautiloid association shows a complex biological and taphonomic relationship between these organisms.

INTRODUCTION

THIS STUDY investigates the relationship between orthoconic nautiloids and encrusting trepostome and cystoporate bryozoans including *Spatiopora* Ulrich, 1882 from the Upper Ordovician, Katian Stage (lower part of the Cincinnatian Series of North America [Bergström et al., 2009]) of the Cincinnati Arch region, U.S.A. It primarily involves cephalopods that were fouled while alive (e.g., Landman et al., 1987) or possibly those that were necroplanktonic—dead floating shells (Davis et al., 1999) and brief comment is made on some new observations on post-mortem encrustation (e.g., Wilson and Taylor, 2012). Epizoozoans are animals that encrust a living animal substrate (Taylor and Wilson, 2002), in this case bryozoans living on orthoconic nautiloids.

Settlement of larvae on motile benthic or nektonic host substrates occurs much less frequently than on sessile epibenthic hosts or hardgrounds (Taylor, 1990). The exceptional feature of encrustation of orthoconic nautiloids in the Upper Ordovician of North America is that coverage of the host shells is typically almost complete from the apex of the phragmocone to the anterior margin of the body chamber (Fig. 1.1, 1.3). The distribution of fossil episkeletozoans (sensu Taylor and Wilson, 2002) on their hosts can provide details of lifestyles of the host, their feeding habits as well as those of the encrusting organism, and information on taphonomic processes.

Another aspect concerning fouling of cephalopods is whether encrustation occurred while the host was alive or dead. An earlier study of this topic concluded that there was evidence for the former in at least some specimens from the Upper Ordovician of the Cincinnati Arch region of Ohio, Kentucky, and Indiana (Baird et al., 1989), and we discuss this further. Evidence of *syn-vivo* encrustation includes 1) holoperipheral growth of bryozoans on host; 2) regular linear arrangement of maculae; and 3) zooids show a preferred growth direction towards the host body chamber.

Similar to these fossil nautiloids, motile hosts encrusted by modern bryozoans include sea snakes (Key et al., 1995, 1996b), king or horseshoe crabs (Key et al., 1996a, 1996b, 2000), decapod crabs (Key et al., 1999), hermit crabs (Balazy and Kuklinski, 2013), pycnogonids (Key et al., 2012), isopods (Key and Barnes, 1999), sea turtles (Frazier et al., 1992) and, by fossil bryozoans, trilobites (Key et al., 2010), cephalopods (Baird et al., 1989; Wyse Jackson and Key, 2014), and echinoderms (Schneider, 2003).

The objective of this study is not to provide a formal systematic reassessment of the type specimens of the bryozoan taxa that encrust nautiloids. However, through examination of type material in the Smithsonian Institution, Washington, DC, a number of the bryozoan specimens utilized in this study are identified with confidence to species level and this terminology is used herein; others are left in open nomenclature. Our goal is to qualitatively and quantitatively describe the interactions between cephalopods and bryozoans and the paleoecological and paleobiological inferences of such a relationship.

Additional goals of this study are to determine the morphology of these bryozoan zoaria, the morphology of orientated maculae and associated monticules, and attempt to reconstruct the water-flow regimes that were generated over the bryozoan zoaria. Maculae are clusters of macrozooecia, exilazooecia or areas of extrazooecial skeleton that define a colony-wide excurrent chimney (Banta et al., 1974; Key et al., 2002, 2011); monticules are topographically elevated expressions of maculae (Taylor, 1979), and in this study while all bryozoans are maculate not all develop monticules.

Monticule shape has been observed to change along an orthocone shell (Baird et al., 1989), but it has not been demonstrated if this change is systematic and/or significant. If

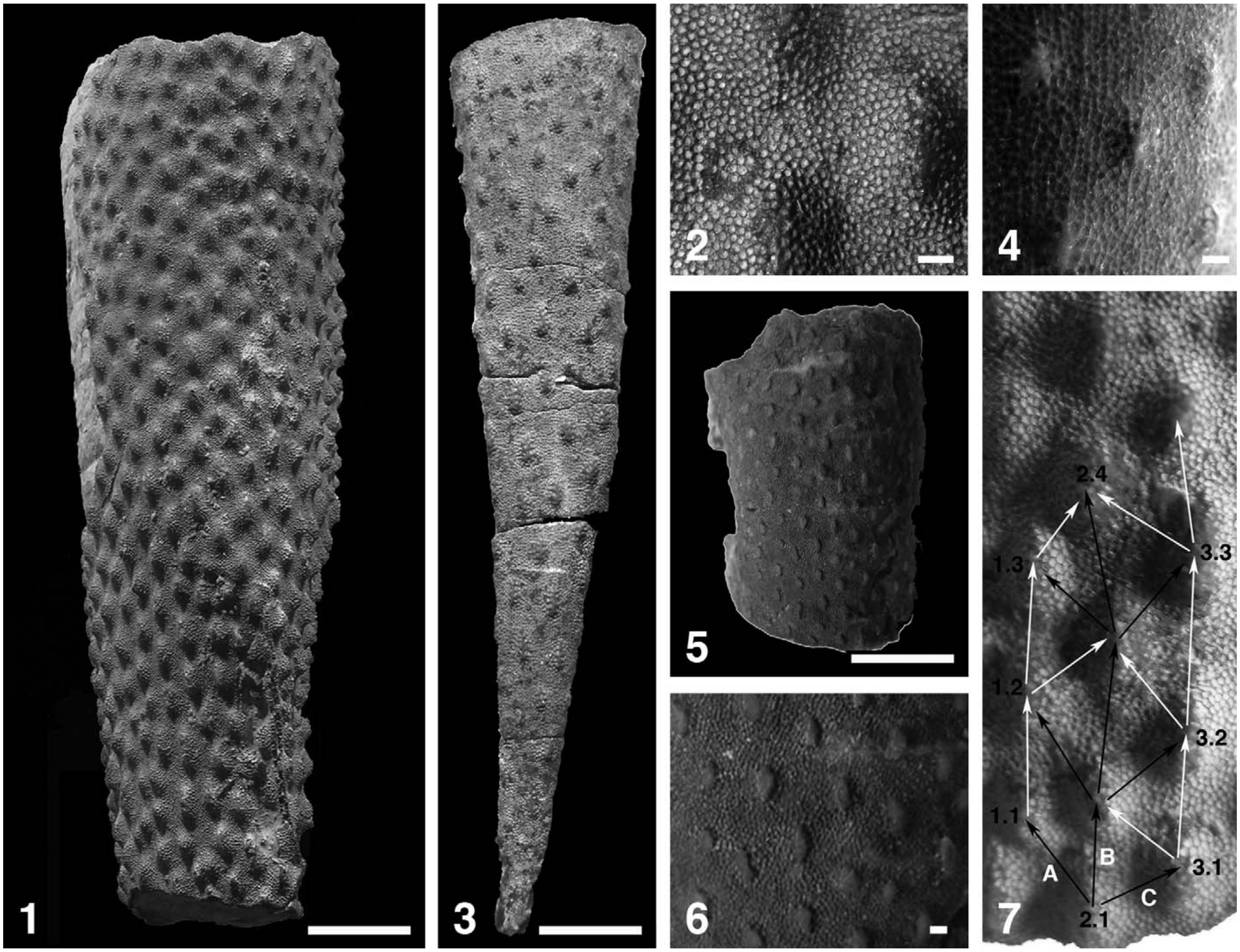


FIGURE *1*—*Spatiopora* and other trepostome bryozoans encrusting *syn-vivo* on orthoconic nautiloids. Data on macula distribution was gathered on specimens illustrated in *1–6*. *1*, *Spatiopora montifera*, specimen 8, CMC IP70086; *2*, close up view of *1* showing shape and arrangement of monticules, a basal attachment point of *Sphenothallus* [=*Dawsonia cycla*] is located above left of lower-most monticule; *3*, *Spatiopora lineata*, specimen 38, CMC IP70116; *4*, close up view of *3* showing arrangement of monticules; *5*, *Atactopora maculata*, specimen 7, CMC IP70085; *6*, close up of *5* showing arrangement of monticules; *7*, vector/grid numbering scheme adopted in this study illustrated on *Spatiopora montifera,* specimen 8, CMC IP70086. Scale bars=10 mm (*1*, *3*, *5*); 1 mm (*2*, *4*, *6, 7*).

size and shape is significantly different, could host architecture control this variation, or does the lifestyle of the host play a role? Detailed observations of monticule morphology also allows for an assessment of the efficiency of monticules as excurrent chimneys (Taylor, 1979; Key et al., 2011) along the length of the hosts.

Were the bryozoans commensal, i.e., did they settle and grow during the life-time of their hosts? Did it become maculate/monticulate on orthocones only and not when encrusting other substrates? Additionally the study briefly outlines cephalopod-bryozoan interactions in the Ordovician fossil record.

SPATIOPORA ULRICH, 1882 AND OTHER EPIZOOZOAN BRYOZOANS ON UPPER ORDOVICIAN CEPHALOPODS OF THE CINCINNATI ARCH REGION

Cephalopods have a long geological history ranging from the Cambrian to the Recent, and have provided substrates for many encrusting skeletobionts (see reviews in Taylor and Wilson, 2003; Wyse Jackson and Key, 2014). Generally, encrustation of cephalopods is rare due to a number of factors including the presence of an organic layer in some nautiloids, or the ability of the cephalopod to ‘clean’ its shell surface; this rarity may also be due to the failure to recognize or simply report encrustation (Davis et al., 1999).

In the Upper Ordovician, the instances where bryozoans and cephalopods are found in association with each other are more common than at any other time in the geological record (Wyse Jackson and Key, 2014).

Of those bryozoans reported attached to the exterior surfaces of Cincinnatian cephalopods, and as a result considered to be potentially *syn-vivo* encrustation, *Spatiopora* (Fig. 1) is by far the most common (Ulrich, 1883; Foord, 1883; Baird et al., 1989). Originally erected by Ulrich (1882) who designated *S. aspera* from the Upper Ordovician of Ohio as type species (Ulrich, 1883), Ulrich remained non-committal about the familial placement of the genus, but later it was placed in the Family Ceramoporidae of the Order Cystoporata (Bassler, 1915, 1953) and subsequently regarded as belonging to the Order Trepostomata (Utgaard, 1968, 1983).

The genus *Spatiopora* was defined as being “Incrusting, and forming very thin, large expansions, with a smooth or strongly tuberculated surface. Cells shallow, with oblong and irregular apertures. Interstitial cells sparingly developed. Spiniform tubuli generally of considerable size" (Ulrich, 1882, p. 155). Initially Ulrich (1883) considered the genus to contain seven species from the Ordovician, and he later added another two species and one subspecies from Minnesota (Ulrich, 1893). *Spatiopora* is now represented in the literature by 18 species and three subspecies that range from the Ordovician into the Silurian (Wyse Jackson and Key, 2014). The collections of the Natural History Museum, London include a number of specimens purchased from Ulrich in 1898 from the Upper Ordovician (Cincinnatian) of Ohio to which he applied four manuscript species names that he subsequently never published. Matching specimens and other undescribed species are also in the USNM (labeled by R. S. Bassler). These questionable specimens have not been examined for this current study, and their taxonomic status remains unclear.

In the Upper Ordovician of the Cincinnati Arch area, and elsewhere in Iowa, Minnesota, New York, and Ontario, the bulk of *Spatiopora* species encrust orthoconic nautiloid shells, but rarely cyrtoconic nautiloid shells, and the majority are monticulate (Wyse Jackson and Key, 2014). Other bryozoans fouling nautiloids in the Cincinnatian include the trepostomes *Atactopora hirsuta* Ulrich, 1879 (Ruedemann, 1925), *Atactopora maculata* Ulrich, 1879 (Baird et al., 1989), *Atactoporella multigranosa* (Ulrich, 1879), *Leptotrypa minima* Ulrich, 1883 (Ruedemann, 1925), the cystoporate *Crepipora solida* Ulrich, 1890, and an undetermined taxon (Specimens 15, 17, 42 [see Appendix]), which are all maculate, and *Leptotrypa cortex* Ulrich, 1883 and *Paleschara beani* (James, 1878, 1884; Bassler, 1906, 1915) which are non-maculate.

Settlement on orthocones may be simply a function of their abundance in successions such as the *Treptoceras duseri* shale of the Waynesville Formation where they make up 89 percent of the nautiloid fauna (Frey, 1988, 1989), and thus provide a common substrate, as indicated with over 50 percent carrying episkeletozoans (Frey, 1989). While much of the sediment being deposited at this time in the Cincinnati Arch area was muddy (Cuffey, 1998) and eventually became lithified as the shaly units, there are tens of ramose erect bryozoan species described from the Upper Ordovician of the Cincinnati Arch region (see listing in Dalvé, 1948), and settling larvae of these must have found a suitable non-nautiloid hard substrate on which to settle and grow.

For *Spatiopora* it is possible that the association between encrusting bryozoan and orthoconic nautiloid was site specific and obligate in the Cincinnati Arch basin, although this would be difficult to prove, and is questionable given that rare occurrences on other substrates are known from elsewhere: asaphid trilobites (Oakley, 1938) and the sponge *Pasceolus* (Foord, 1883), and even quartz pebbles (Astrova, 1965). *Spatiopora* reported from the Silurian occurs on substrates other than orthoconic nautiloids: tabulate corals, gastropods, stromatoporids, and brachiopods, and this suggests that the orthocone-bryozoan association is a specialist association restricted to the Upper Ordovician basins of mid and north-eastern North America. Mark Wilson (personal commun., 2013), who has collected extensively in these Upper Ordovician successions, has not encountered *Spatiopora* on substrates other than orthoconic nautiloids, nor have the authors during collecting in the field and during examination of large collections in museums. Pachut and Fisherkeller (2010) have argued, on the basis of ancestrula dimensions and a restricted distribution in North America, that a number of species of ten genera probably produced larvae that were lecithotrophic and non-planktotropic. These larvae had to settle fast, which accounts for the limited distribution of the taxa. While ancestrulae have not been identified in any *Spatiopora* species, given the prevalence of the genus in the Upper Ordovician of the Cincinnati Arch region it is possible that their larvae were also lecithotrophic.

An alternative to site-specificity for *Spatiopora*, given the plasticity of zoarial form exhibited by some bryozoans, is that a number of the *Spatiopora* species are in fact other species of other genera which attach to varied substrates that controlled their resultant zoarial form. Other trepostome bryozoans *Atactopora* and *Leptotrypa*, for example, are represented in the Cincinnatian as both ramose colonies growing on hard-grounds, and as encrusters on nautiloids. *Leioclema* in the Mississippian of north Wales exhibited several zoarial forms that were controlled by various ecological parameters (Wyse Jackson et al., 1991). *Spatiopora* may well be exhibiting a zoarial form determined by its host's architecture.

In many cases post-mortem encrustation by bryozoans occurs on the internal molds of nautiloids, a preservation pattern common in the Upper Ordovician of the Cincinnati Arch region, and in the Kanosh Shale (Whiterockian, Lower Ordovician) of Utah (Wilson et al., 1992), and generally takes two forms. The interior of body chambers provided cryptic niches for the runner-like forms *Cuffeyella* and *Corynotrypa* as well as for other adnate taxa (Taylor and Wilson, 1994; Wilson et al., 1994), whereas internal molds where the external shell has dissolved away provide hardgrounds (Palmer and Wilson, 2004) which may be subsequently colonized.

Although *Treptoceras* survived the late Ordovican extinction, Silurian forms in the Brassfield Formation of southwestern Ohio are not encrusted with *Spatiopora* (R.C. Frey, personal commun., 2013). During the Silurian, the relative ratio of orthocones to curved and coiled nautiloids changed, with curved forms becoming more dominant but still very rare (Barskov et al., 2008). As with earlier Ordovician forms cyrtoconic nautiloids favored reefal settings or may have stayed close to, or crawled along, the sediment surface, in contrast to actively swimming longiconic forms that kept to open water (Meyer and Davis, 2009), but neither groups are encrusted. This suggests that post-Ordovician larvae and their post-settlement colony survival on various hard substrates may have differed from those that evolved during the Ordovician.

MATERIALS

This study is based on a suite of 59 specimens given to the authors by the late Ken McKinney, who received them from Carlton Brett, second author on the ground-breaking paper by Baird et al. (1989). A number of these specimens were examined and illustrated by Baird et al. (1989) who noted that they had been deposited in the University of Rochester collections (although they did not carry accession numbers). Most of the Rochester paleontology collections were passed onto the Paleontological Research Institute, Ithaca, New York, but following agreement with Carlton Brett, we have deposited the specimens studied here in the Cincinnati Museum of Natural History (accession numbers CMC IP70079–CMC IP70137). The specimens were collected from localities in Indiana, Kentucky, and Ohio from the Kope Formation (Edenian Stage) (specimens 1–5; CMC IP70079–83), unnamed units in the Maysvillian Stage (specimens 6, 7; CMC IP70084–5), to the younger Waynesville Formation (Richmondian Stage) (specimens 8–59; CMC IP70086–137) of the Katian Stage in current global Ordovician nomenclature (ICS, 2013). Frey (1995) and Key et al. (2010) provide information on the stratigraphical succession of the Cincinnati Arch region, and Hansen (1997) correlates older stratigraphical terminology with modern equivalents.

Stratigraphic and locality details for the study material are listed in the Appendix. We have also examined type and non-type specimens of *Spatiopora* species and other examples of bryozoans encrusting nautiloids in the collections of the United States Natural History Museum, Smithsonian Institution (USNM).

METHODS

Three host orthoconic nautiloids were selected for the morphometric part of this study: Specimen 7 *Atactopora maculata*; Maysville Group, specimen 8 *Spatiopora montifera*; Fort Ancient Member, Waynesville Formation, and specimen 38 *Spatiopora lineata*; *Treptoceras duseri* shale, Fort Ancient Member, lower Waynesville Formation (Fig. 1.1–1.6). These specimens were picked to maximize first the completeness of the orthocone, second purported bryozoan species diversity, and finally preservation of well-defined monticules. According to Frey (1989) *Treptoceras duseri* is the most commonly *Spatiopora*-encrusted nautiloid. This bryozoan was also found on *Geisonoceras* from the Utica Shale of New York by Ruedemann (1925) who also reported the occurrence of *Atactopora hirsuta* on *Paractinoceras* and *Leptotrypa minima* on specimens of the nautiloid genus *Actinoceras* from the same horizion.

To test for systematic variation of monticule morphology, we measured monticule length, width, and area, as well as intermonticule distance and area (Fig. 1.7). We defined the lateral extent of monticules as the azooecial, aperture-free, mesa-like, elevated surface. The length was measured parallel to the growth axis of the host, and width was measured perpendicular to this. Monticule area was calculate assuming a rectangle from length times width.

As the monticules were arranged in lines parallel to the long axis of the host and in order to establish a framework for monticule spacing, one monticule at the apical, narrower end of the host, was selected and numbered 1.1. Three vectors were drawn using the Annotate function in the computer programme Preview (Apple Mac, 2002–2009). The vectors were drawn in an adoral direction from the center of the monticule to the center of three nearest adoral neighbors. The left vector was designated "A", the central vector (drawn coaxial to shell length) was designated "B", and the right vector was designated "C". The same treatment was applied to subsequent monticules, moving adorally along the "B" vector line and labeling each sequentially (e.g., 1.2, 1.3, 1.4, etc.) (Fig. 1.7). The result is a series of ABC vectors which, when applied to the lines of monticules along the host, establish a framework that allows identification of a monticule and corresponding measurement by counting along the line. Though the measurements are shown in plan view (Fig. 1.7), they were taken line by line while rotating the host to minimize the distortion caused by the curvature of the host's conical shell. Intermonticule distance was defined as the length of the B vector. Intermonticule area was defined by two times the area of the triangle created by the A and B vectors of one monticule and the C vector of the following monticule. This serves as a simple rough proxy for the areal extent of the autozooecia contributing filtered water to the monticule's excurrent chimney. All measurements were made to the nearest 0.0001 mm using version 1.42q of the computer program ImageJ (Rasband, 1997–2012).

Secondly, all specimens were qualitatively examined for growth patterns, macule and monticule morphology, overgrowths, and the relationship of the episkeletobionts to the nautiloid shells and to each other.

RESULTS

Host size and tapering ratio.—Morphometric statistics are summarized in Table 1. All three of the orthoconic nautiloids were partial specimens and did not completely extend from the apex to the adoral end of the body chamber. The nautiloids ranged in length from 43.8 mm (specimen 7) to 87.5 mm (specimen 38). They ranged in diameter from 3.3 mm (specimen 38) to 39.1 mm (specimen 8). Their tapering ratio (i.e., diameter/length) ranged from 0.15 (specimen 8) to 0.19 (specimen 38). Variation in orthocone size resulted in a range of two to five lines and ten to twenty monticules per line being measured.

Variation in monticule size and spacing between specimens.—As the three orthocones represented different portions of complete specimens, all data were plotted in relative position along the host in an adoral direction (i.e., from the apex to the body chamber). This was done assuming the unique tapering ratio mentioned above for each of the three orthocones was constant along its length.

The shortest, thinnest, and smallest area monticules were formed by *Atactopora maculata* on specimen 7 and *Spatiopora lineata* on specimen 38, the largest by *Spatiopora montifera* on specimen 8 (Table 1). The qualitative character of the monticules also differs. *Atactopora maculata* has flatter monticule surfaces. *Spatiopora montifera* and *Spatiopora lineata* both have more peaked monticular apices. *Spatiopora montifera* exhibits more autozooecial apertures on the sides of its monticules. *Spatiopora lineata*'s monticules exhibit subtle radiating buttresses with intermediate relief that may be analogous to the branching macular channels documented by Key et al. (2011), albeit on a smaller scale.

Corresponding with monticule size, the most closely spaced monticules as defined by smallest intermonticule distance and intermonticule area were formed by *Atactopora maculata* on specimen 7, the most widely spaced by *Spatiopora montifera* on specimen 8 (Table 1).

Variation in monticule size and spacing within specimens.—To test for systematic and significant patterns in monticule size and spacing along the long axis of the host, we averaged the measurements across lines (e.g., the length measurements of the first monticule in each line [i.e., 1.1, 2.1, 3.1, etc.] were averaged) to produce a mean value of each monticule in a sequence along the long axis of the host. On each orthocone, mean monticule length shows a signficant (regression analysis; $P<0.05$) linear increase in the adoral direction followed by an equally significant linear decrease (Fig. 2.1). The same pattern holds true for mean monticule width (Fig. 2.2) and mean monticule area (Fig. 2.3). On each orthocone, intermonticule distance shows a signficant (regression analysis; $P<0.05$) linear increase in the adoral direction followed by an equally significant linear decrease, except for the decreasing slope of specimen 7 is not signficant (regression analysis; $P>0.05$) (Fig. 2.4). The same pattern holds true for intermonticule area (Fig. 2.5). The lack of significance of the decreasing slopes in intermonticule distance and area in specimen 7 is attributed to small sample size (i.e., there were only four monticules in that section of the pattern).

For each of the morphometric parameters, the change in slope on an orthocone occurs at the same place (i.e., at 163 mm from the apex in specimen 7, at 217 mm in specimen 8, and at 72 mm in specimen 38). The change in slope on all three orthocones co-occurs with the development of a new monticule at that point in the colony. The new monticule starts a new line of monticules that continue as the bryozoan colony grows towards the aperture of the cephalopod. When the monticules reach a certain size (i.e., the point where the slopes change sign, the monticule size and spacing begins to decrease in response to the new line [Fig. 2.6]). The negative slope is steeper than the positive slope in 12 of the 15

TABLE 1—Summary morphometric statistics of the host orthoconic nautiloids and bryozoan monticules.

Specimen number from Appendix	7	8	38
Bryozoan species	*Atactopora maculata*	*Spatiopora montifera*	*Spatiopora lineata*
Host length (mm)	43.8	85.6	87.5
Host diameter range (mm)	24.1–31.8	26.1–39.1	3.3–20.1
Host tapering rate (diameter/length)	0.18	0.15	0.19
Number of lines of monticules measured	5	4	2
Monticule length			
Number of measurements	45	55	34
Range (mm)	0.84–1.57	1.45–5.74	0.85–2.01
Mean (mm)	1.20	4.01	1.29
Standard deviation (mm)	0.20	0.80	0.32
Monticule width			
Number of measurements	45	35	34
Range (mm)	0.37–0.76	1.75–3.56	0.37–1.26
Mean (mm)	0.56	2.42	0.68
Standard deviation (mm)	0.10	0.46	0.21
Monticule area			
Number of measurements	11	20	17
Range (mm^2)	0.46–0.88	5.70–17.92	0.38–1.93
Mean (mm^2)	0.68	10.41	0.90
Standard deviation (mm^2)	0.12	3.10	0.39
Intermonticule distance			
Number of measurements	10	20	17
Range (mm)	2.46–3.80	3.65–6.92	3.33–5.84
Mean (mm)	3.16	5.24	4.58
Standard deviation (mm)	0.33	0.71	0.74
Intermonticule area			
Number of measurements	10	19	17
Range (mm^2)	5.98–9.47	11.32–22.17	6.68–15.90
Mean (mm^2)	7.53	16.85	12.73
Standard deviation (mm^2)	0.94	3.29	2.56

(80%) comparisons (i.e., three specimens × five morphometric parameters). This indicates that the adoral rate of change of increasing monticule size and spacing is usually less than the rate of decrease following the insertion of a new monticule line.

Baird et al. (1989) reported a decrease in linearity of the shape of the monticules in the adoral direction along specimen 38. We tested this using the ratio of monticule length/monticule width as a proxy for monticule linearity. We also found a significantly decreasing trend in only our longest host (specimen 38) (regression analysis, m=–0.0085, R^2=0.5684, *P*=0.0005).

DISCUSSION

Variation in monticule size and spacing.—The bryozoan species with the largest monticules has the most widely spaced monticules (*Spatiopora montifera*), whereas the bryozoan species with the smallest monticules has the most closely spaced monticules (*Atactopora maculata*). This suggests there is a consistent relationship between monticule size and monticule spacing. Previous authors have argued for an optimal incurrent area (here defined as intermonticule area) for a given excurrent macula size (here defined as monticule area) (see review in Key et al., 2011). Our results support this.

It is interesting to note that the orthocone with the lowest tapering ratio (specimen 8) also has the largest, most widely spaced monticules. This could simply be a coincidence as they all roughly had the same tapering ratio, 0.2. We need more measurements on more orthocones of different tapering ratios to resolve this but it raises the question of whether monticule size and spacing is an interspecific (i.e., genetically controlled) character of the bryozoan or an ecophenotypic character of the bryozoan that is environmentally induced by zoarial growth on the expanding conical host substrate. Resolving this question could only be achieved through a systematic revision of the taxa to determine which if any are morphotaxa, and such a revision is outside the scope of this project.

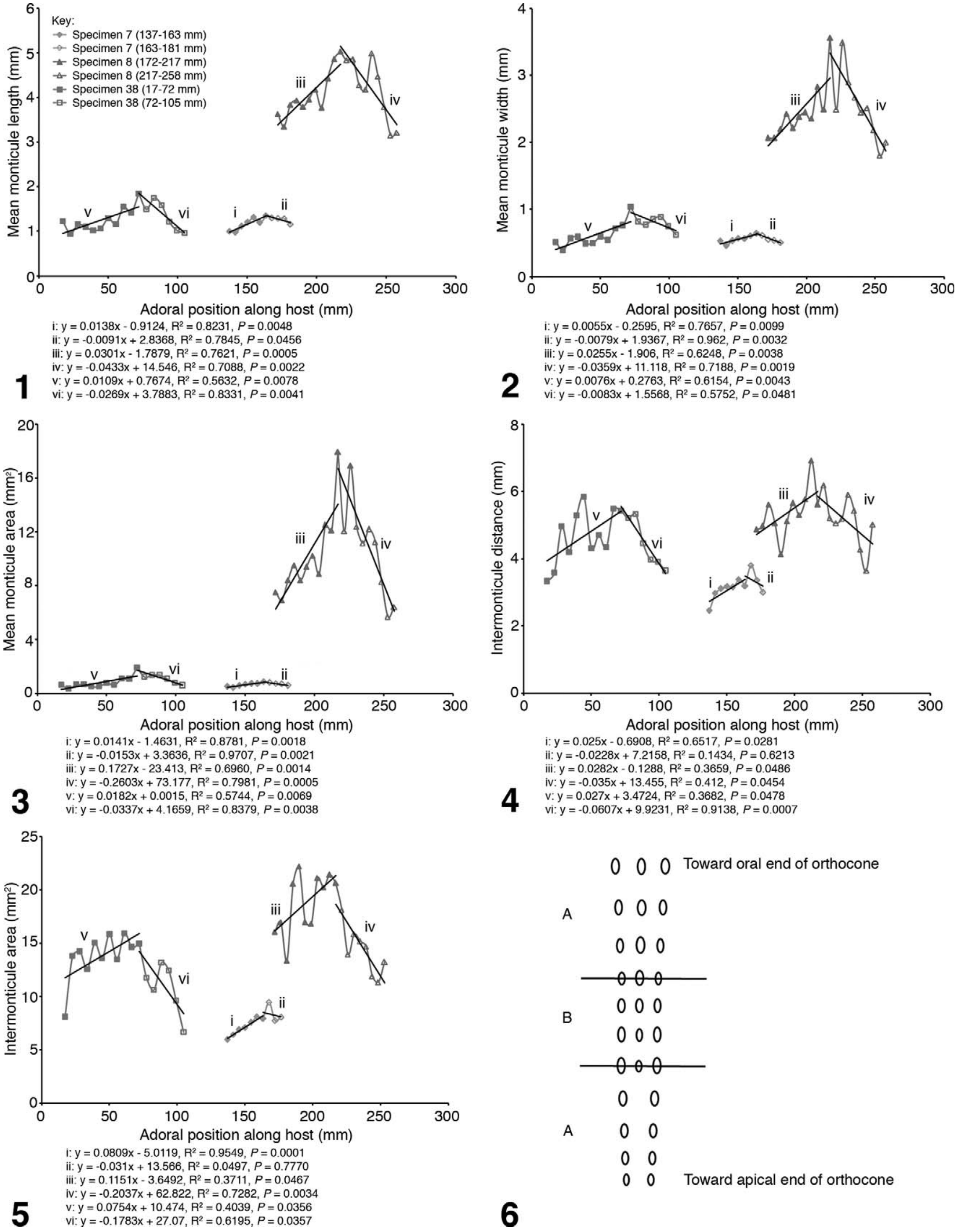
We hypothesize that the increase–decrease pattern would have repeated all along the host, and the segments of the hosts we have preserved simply record different parts of the pattern. We interpret the insertion of a new monticule line to be in response to the increasing circumference of the expanding conical substrate of the host.

We interpret that adoral rate of change of increased size and spacing following the insertion of a new monticule line to mean that if we had a complete record along a long host, we would see longer, lower, positive slopes of increasing monticule size and spacing followed by shorter, steeper, negatives slopes of decreasing monticule size and spacing. Despite the insertion of the new monticule line with its expanding monticules, the two adjacent lines are contracting so the sequential mean decreases.

The decreasing trend in linearity observed in specimen 38 may be due to the increasing diameter of the orthocone creating in effect a more planar substrate where a more circular monticule is expected (Taylor, 1979; McKinney, 1986; Key et al., 2002). The problems with this interpretation are that specimen 38 is the narrowest orthocone, and specimens 7 and 8 have either a significantly or insignificantly positive trend, respectively.

Growth orientation of Spatiopora *colonies*.—Ruedemann (1925), Baird et al. (1989), Frey (1989), and Kröger et al. (2009) observed adoral growth of bryozoans encrusting nautiloids. Although difficult to determine from the surface features of a number of *Spatiopora* species, a preferred directional growth is certainly obvious in the cystoporate bryozoan *Crepipora solida* Ulrich, 1890 in which the autozooecial apertures are partially closed by a semi-circular lunarium that has the effect of directing lophophores towards the adoral end of the orthocone (Fig. 3.2). In cross-section, growth direction is easier to ascertain as the attitude of autozooecial chambers which bud from a thin basal layer become recumbent in the endozone towards the adoral end of the shell (Fig. 4.3, 4.5). In most species the outermost portion of the autozooecial chamber in the exozone is orientated normal to the host's growth axis.

However, apical-directed growth can be detected in some colonies. Where two colonies meet (see below) one must have been growing towards the apex of the host. In *Leptotrypa minima* the apical termination (orthocone tip) of colony growth in at least one specimen, USNM 43676 (Fig. 3.4), is marked by a monticule,



1

i: y = 0.0138x - 0.9124, $R^2 = 0.8231$, $P = 0.0048$
ii: y = -0.0091x + 2.8368, $R^2 = 0.7845$, $P = 0.0456$
iii: y = 0.0301x - 1.7879, $R^2 = 0.7621$, $P = 0.0005$
iv: y = -0.0433x + 14.546, $R^2 = 0.7088$, $P = 0.0022$
v: y = 0.0109x + 0.7674, $R^2 = 0.5632$, $P = 0.0078$
vi: y = -0.0269x + 3.7883, $R^2 = 0.8331$, $P = 0.0041$

2

i: y = 0.0055x - 0.2595, $R^2 = 0.7657$, $P = 0.0099$
ii: y = -0.0079x + 1.9367, $R^2 = 0.962$, $P = 0.0032$
iii: y = 0.0255x - 1.906, $R^2 = 0.6248$, $P = 0.0038$
iv: y = -0.0359x + 11.118, $R^2 = 0.7188$, $P = 0.0019$
v: y = 0.0076x + 0.2763, $R^2 = 0.6154$, $P = 0.0043$
vi: y = -0.0083x + 1.5568, $R^2 = 0.5752$, $P = 0.0481$

3

i: y = 0.0141x - 1.4631, $R^2 = 0.8781$, $P = 0.0018$
ii: y = -0.0153x + 3.3636, $R^2 = 0.9707$, $P = 0.0021$
iii: y = 0.1727x - 23.413, $R^2 = 0.6960$, $P = 0.0014$
iv: y = -0.2603x + 73.177, $R^2 = 0.7981$, $P = 0.0005$
v: y = 0.0182x + 0.0015, $R^2 = 0.5744$, $P = 0.0069$
vi: y = -0.0337x + 4.1659, $R^2 = 0.8379$, $P = 0.0038$

4

i: y = 0.025x - 0.6908, $R^2 = 0.6517$, $P = 0.0281$
ii: y = -0.0228x + 7.2158, $R^2 = 0.1434$, $P = 0.6213$
iii: y = 0.0282x - 0.1288, $R^2 = 0.3659$, $P = 0.0486$
iv: y = -0.035x + 13.455, $R^2 = 0.412$, $P = 0.0454$
v: y = 0.027x + 3.4724, $R^2 = 0.3682$, $P = 0.0478$
vi: y = -0.0607x + 9.9231, $R^2 = 0.9138$, $P = 0.0007$

5

i: y = 0.0809x - 5.0119, $R^2 = 0.9549$, $P = 0.0001$
ii: y = -0.031x + 13.566, $R^2 = 0.0497$, $P = 0.7770$
iii: y = 0.1151x - 3.6492, $R^2 = 0.3711$, $P = 0.0467$
iv: y = -0.2037x + 62.822, $R^2 = 0.7282$, $P = 0.0034$
v: y = 0.0754x + 10.474, $R^2 = 0.4039$, $P = 0.0356$
vi: y = -0.1783x + 27.07, $R^2 = 0.6195$, $P = 0.0357$

6

FIGURE 2—Variation in monticule size and spacing within specimens 7, 8, and 38. Key in *1* applies to symbols also used in *2*–*5*. Regression line statistics provided beneath each graph for the two lines in each of the three specimens (i–vi). *1*, mean monticule length shows a signficant linear increase in the adoral direction followed by an equally significant linear decrease; *2*, mean monticule width shows a similar pattern; *3*, mean monticule area also shows a similar pattern; *4*, intermonticule distance in each orthocone displays a linear increase in the adoral direction followed by an equally significant linear decrease, except for the decreasing slope of specimen 7 which is not signficant; *5*, intermonticule area displays the same pattern as *4*; *6*, stylized model showing intraspecimen variation in monticule size and spacing. Monticule size and spacing begins to decrease in response to the intercalation of a new line of monticules, assuming monticule length=2× width is constant throughout. Abbreviations: A=longer phase of slower increase in size and spacing; B=shorter phase of faster decrease in size and spacing.

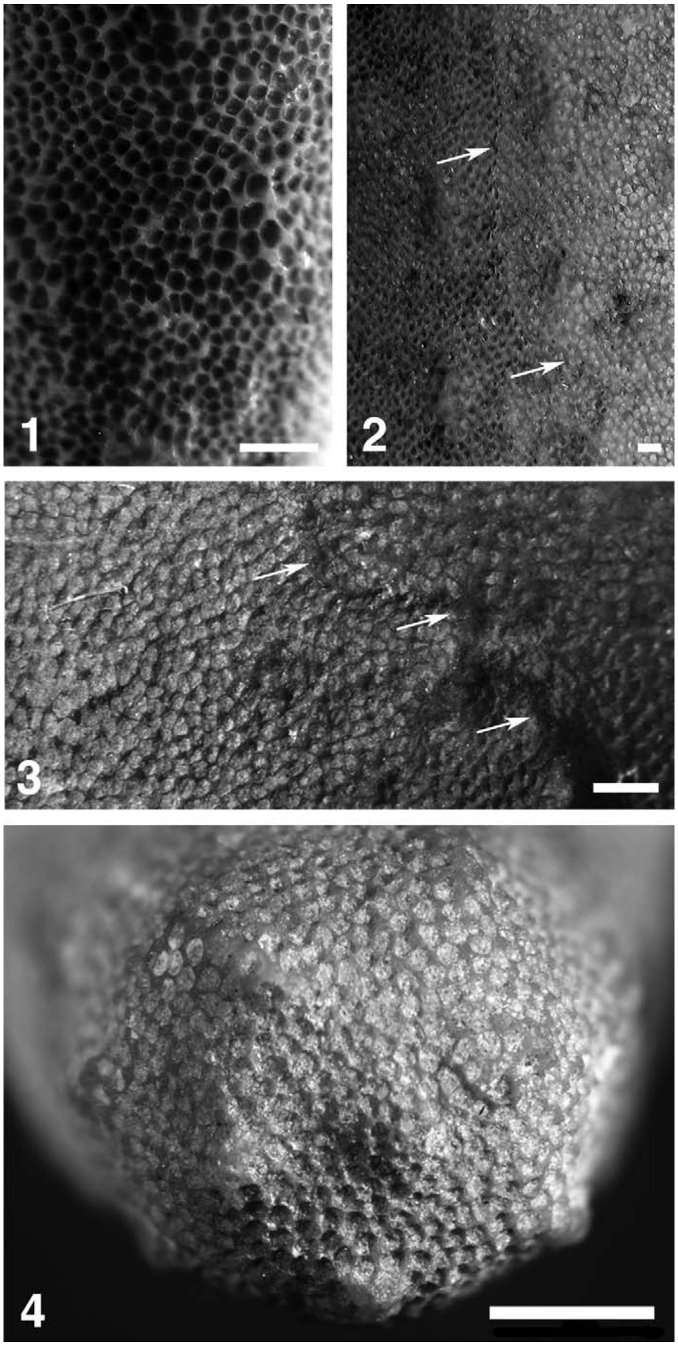


FIGURE 3—*Spatiopora* and other trepostome bryozoans encrusting *syn-vivo* on orthoconic nautiloids. *1*, isolated *Leptotrypa minima* colonies, some circular in outline, growing close to the apical end of an orthocone (specimen 5, CMC IP70083) and merging to form a unilaminar sheet; *2*, *Spatiopora* sp. and the cystoporate bryozoan *Crepipora solida* growing side-by-side on an orthocone (junction arrowed), *C. solida* (on the left) has autozooecial apertures partially closed by a semi-circular lunarium that directs lophophores towards the adoral end of the orthocone, specimen 44, CMC IP70122; *3*, *Spatiopora aspera* showing junction between two adjacent colonies marked by the development of a rim (arrowed), USNM 43254; *4*, *Leptotrypa minima*, USNM 43676, showing apical orientated encrustation of broken apex of phragmocone with regular monticule development. Scale bars=1 mm (*1–4*).

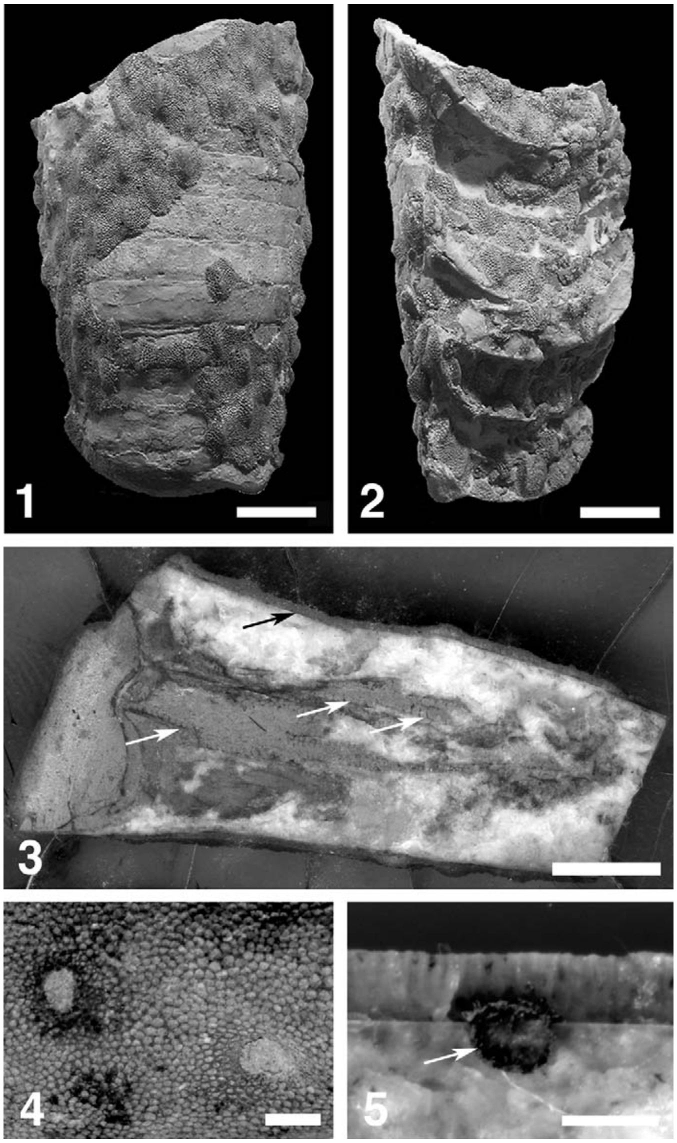


FIGURE 4—*Spatiopora* encrusting dead orthoconic nautiloids. *1*, *2*, *Spatiopora* sp., specimen 43, CMC IP70121, growing on an internal mold where the external shell of the nautiloid has dissolved away (*1*), and across the septa on the other side where more skeletal material including septal walls have been partially removed; the regular pattern of monticules is maintained on both surfaces (*2*); *3*, telescoping of nautiloids: small orthocones (white arrows) with encrustation of internal surfaces of body chambers by *Spatiopora aspera* situated within the body chamber of a larger orthocone that is encrusted on its outer surface (black arrow), specimen 19, CMC IP70097; *4*, *5*, *Trypanites*-bryozoan-orthocone association, Fort Ancient Member, Waynesville Formation, specimen 15, CMC IP70093; *4*, view of two circular *Trypanites* openings with reaction rims produced by living bryozoan; *5*, cross-section of *Trypanites* boring infilled with sediment (arrowed) showing it cross-cutting encrusting trepostome bryozoan (top) and sparry calcite-infilled chamber of phragmocone (bottom). Scale bars=10 mm (*1*, *2*); 5 mm (*3*); 1 mm (*4*, *5*).

and such a development would not have occurred at this point if it had been the position of the ancestrula. This confirms that apical growth could occur.

Monticule shape and inferences for orthocone swimming behavior.—The preferred growth direction of bryozoans towards the host body chamber lends support to the observations that Ordovician orthoconic cephalopods moved in an adoral direction rather than backwards or adapically (Kröger et al., 2009). Modern *Nautilus* can move backwards at speeds of up to 0.25 m/sec (Ward et al., 1977) through jetting water from its hyponome, but this may simply be an escape mechanism, and the flying squid *Ommastrephes bartrami* can swim backwards so fast that they fly out of the water to avoid predators. The architecture of some Cambrian cephalopods shows that they were ill-equipped to swim rapidly by jetting (Mutvei et al., 2007). Slow forward-movement in *Nautilus* can be achieved through use of its tentacles (Bidder, 1962), and Monks (2010) has postulated that Paleozoic orthocones and other cephalopods could move slowly in a similar direction. Holland (1984) has argued that some Silurian orthocones could bend their hyponomes adapically to move forward adorally by jetting, and Hauschke et al. (2011) have inferred a similiar forward swimming direction through the growth position of a stalked cirriped on the shells of Cretaceous heteromorphic orthoconic ammonites.

Orthoconic nautiloids maintain bouyancy in the water column by means of gas-filled chambers in the phragmocone, and it has been argued that a horizontal position is maintained through selective weighting of the ventral part of the shell with cameral deposits (Fischer and Teichert, 1969; Holland, 1984). An alternative viewpoint suggests that a horizontal position is not possible due to the hydrodynamics of the conical shape of shells whose centers of gravity and bouyancy are close together, and so they adopted a downward facing position in the water column (Ebel, 1999). If such a position was the norm, one might expect monticules to grow at an angle somewhat transverse to the orthocone long axis, but this pattern is not observed. The development of elongated monticules in *Spatiopora* aligned coaxially to the long axis of orthcone shells lends support to the observation that these animals in the Cincinnatian did maintain a horizontal position in the water column.

We believe that the development of linear maculae and monticules is largely controlled by the physical architecture of the conical host on which it lives, and not, or perhaps to a lesser extent, to the movement of that host through the water column. This is borne out by our observations of *Spatiopora* on dead orthocones (see below) and by their regularity of form on living shells. Due to the small fragmentary size of colonies on other substrates, it is difficult to determine with any certainty if the regular maculae/monticule pattern found on orthocones also occurs on other substrates. However, we suspect that such consistency is not prevalent on other substrates.

Orthocone truncation.—In a number of specimens, bryozoans have grown over septa where a portion of the apical end of the orthocone was missing. Interestingly, monticule development is noted to be regular even in an example (USNM 43676) where the host shell diameter is only 5 mm (Fig. 3.4). Baird et al. (1989) attribute this non-lethal phragmocone damage to predation or collision. Alternatively, the septal surface may have been exposed through the process of truncation that is known from several nautiloids including the ascocerids from the Ordovician of Estonia (Kröger, 2007) and *Sphooceras* in the Silurian of the Prague Basin (Turek and Manda, 2012). Although the diagnostic skeletal pattern seen on the exposed septum in the Silurian example would be obscured by encrusting bryozoans in the examples under study here, it is possible that the Cincinnatian occurrences of shortened orthocones represents another example of this biological process in cephalopods.

In some living and fossil molluscs, the presence of epizoans has resulted in modification of the host's shell growth patterns or rates (Seilacher, 1960; Wahl, 1996; Rakociński, 2011), which has affected buoyancy (Checa et al., 2002). No such modification in predicted and natural growth patterns were found in this study, and it is clear that encrustation by *Spatiopora* and other adnate bryozoans of nautiloids in the Upper Ordovician is not detrimental in this manner.

Multiple or single colonies and overgrowths.—Earlier authors have not detected multiple bryozoan colonies on individual orthocones which, if correct, would suggest that initial encrustation by bryozoans took place when the orthocone was a juvenile and that growth of the colony kept pace with the growth of the host. Frey (1989) suggested that initial colonization occurred at the apices of orthocones. While this may be so in some cases, it is unlikely that bryozoan larvae were initially selectively drawn to the narrower ends of orthocones unless they were encrusting juveniles. In this study, however, multiple colonies are discernable on several orthocones. In the holotype of *Spatiopora aspera* (USNM 43254), two adjacent colonies merged and developed a rim at their line of contact (Fig. 3.3). Similar intracolony contact is seen in *Leptotrypa minima* from the Bellevue Member (CMC IP70083) on an orthocone from the upper Kope Formation (specimen 5) where a number of small circular colonies merge resulting in disruption of their radial growth patterns (Fig. 3.1).

Specimen 44 from the Blanchester Member, upper Waynesville Formation, is encrusted with colonies of two different monticulate bryozoan genera, *Spatiopora* and *Crepipora*, growing against each other without disruption to the monticule spacing (Fig. 3.2). Similarly, specimen 59 from the same horizon contains two different *Spatiopora* species growing alongside each other.

Baird et al. (1989) observed irregular overgrowth patterns in *Atactopora maculata*. It is clear from their illustration that the positioning of monticules on the lower bryozoan surface remains constant in the overlying upper zoarium. This is probably due to regeneration of the colony following a period of senescence, rather than overgrowth of the old colony by a new colony developing laterally over it. We observed in *Leptotrypa minima* (USNM 43676) this regularity in monticule arrangement that continues across a colony boundary into the adjacent colony. We interpret this as further evidence that the main constraint on the monticule pattern is simply growth on an expanding conical host.

On only one of the 59 specimens studied were bryozoans overgrown by themselves (i.e., intracolony overgrowths—*Spatiopora montifera* on specimen 40). On only three other specimens were bryozoans encrusted with examples of smaller colonies belonging to other taxa: specimens 40 (unidentified bryozoan on *S. montifera*), 6, and 46 (*Atactoporella maculata* encrusting *S. lineata*). Most (93%) orthocones were simply encrusted by thin, unilaminar colonies of a single species.

Modern nautiloids can live for up to 20 years (Saunders, 1984), which is in broad agreement with some Silurian orthoconic nautiloids that lived for over 15 years (Hewitt, 1984). If Ordovician forms also had similar lifespans, this would provide more than adequate time for bryozoans to completely colonize the surface, as is seen in many specimens—approximately 88 percent of the hosts examined are completely covered by bryozoans, and 12 percent of specimens were not completely covered due to spalling of colony portions from the surface (e.g., upper left edge of Fig. 1.1). One might then wonder why overgrowths are not observed. It is probable that the zoaria contained living polypides for most of their life and over most of the colony surface, that they may have been long-lived, and that this discouraged settlement of other larvae. Otherwise we should see more episkeletobionts of non-bryozoan species and more bryozoan overgrowth.

Monticule form in Spatiopora *encrusting dead orthocone shells*.—The development of elongate maculae and monticules is not dependent on the orthoconic nautiloid being alive when encrusted. The skeleton of specimens 40, 43, and 59 were diagenetically altered following death, through dissolution, or collapse, of the outer wall of the nautiloid, and collapse of the internal septal walls. Infilling by sediment or early sparry calcitic cement in these specimens provided an internal mold on which encrustation has taken place. *Spatiopora* larvae settled on the steinkerns and zoaria grew across this mold surface, any fragments of remaining outer shell walls, and any exposed septal walls and maintained the regular monticule morphology and pattern observed in *syn-vivo* encrustation (Fig. 4.1, 4.2). This post-mortem morphological pattern of growth adds further support to our conclusion that the host morphology is the overriding influence on monticule shape and form.

Encrustation of internal shell surfaces and telescoping of orthcones.—In rare cases the internal surface of body chambers are encrusted by bryozoans, which can only occur after death of the host. In specimens 18 and 19 from the Fort Ancient Member of the Waynesville Formation, *Spatiopora aspera* forms unilaminar sheets encrusting inside the body chamber of small orthocones; they themselves are telescoped inside the body chamber of a larger orthocone that is encrusted only on its exterior surface (Fig. 4.3). It is not known if the internally-encrusting bryozoan colonies are monticulate as they were only observed in longitudinal section. Telescoping of cephalopods is not common (Tasch, 1955; Ferretti and Kříž, 1995; Histon, 2002) and occurs following transportation and concentration of shells. The pattern of telescoping observed in the Cincinnatian is similar to those documented occurrences that suggest that post-mortem transport took place in a low energy regime (Histon, 2002). The interrelationships between bryozoans and cephalopods demonstrates a complex ecological, biostratinomic and sedimentologic sequence in the Cincinatian.

FEEDING EFFICIENCIES AND MOTILE SUBSTRATES

Filter feeders that spent their lives attached to living or floating shells probably benefitted in being lifted off the seafloor out of the bottom boundary layer. Commensal bryozoans, being filter feeders that could generate their own incurrents that enhanced feeding, would have been subject to different water regimes between those in their normal benthic position attached at the seabed as against those that adopted a pelagic mode of life attached to living cephalopods. Water movement is low at the sediment-water boundary layer (Caldwell and Chriss, 1979), and so it is beneficial for benthic organisms to get into faster moving water.

Spatiopora and other encrusting bryozoans had to contend with potential difficulties in that they grow on a motile substrate, and the speed of that substrate through the water could disrupt the preferential hydrological regime for feeding by bryozoans. How do maculae and in particular monticules function in this association? Does increased water flow over bryozoan colonies adversely effect the ability of autozooids to feed?

Macula and monticule function.—Bryozoans are filter feeders that can generate colony-wide feeding currents by beating cilia on the tentacles of their lophophores (McKinney, 1990) which exploit the water in a slow moving boundary layer (Lidgard, 1981) just above the colony surface. Through filtering, the incurrents are depleted of food, and water is pushed below the lophophores across the colony surface to the edge of the colony or to an excurrent chimney/macula. There a strong excurrent, which may also be carrying waste materials, is expelled out beyond the boundary layer (at an average of 21.2 mm/s in *Membranipora* [Lidgard, 1981]), where it can then be removed by free stream water some distance above the zoarial surface. Reduction of turbulence through an irregular monticulate surface on the smooth orthoconic nautiloid may serve to widen the surface boundary layer and therefore improve feeding efficiency.

Maculae and monticules are loci of excurrents that are ejected from the zoarial surface (Banta et al., 1974; Taylor, 1979; Key et al., 2011). A number of macular forms are present in Paleozoic bryozoans from linear strips in *Meekoporella* (Wyse Jackson et al., 1999), to those with stellate outlines (Key et al., 2011) and all shapes between. The maculae may be elevated into monticules that extend above the zoarial surface, and these may be circular in outline, stellate as in the cystoporate *Constellaria* from the Cincinnatian, or elongate as in *Spatiopora*. Lidgard (1981) demonstrated that the excurrent flow velocity in *Membranipora* drops considerably 2 mm above the colony surface from ~21 mm/s to ~8 mm/s. The development of high monticules in *Spatiopora* (~2 mm high in *S. montifera*) may be an attempt by the colony to increase excurrent flow efficiency as it would require a lower flow force for the excurrent to break through the boundary layer.

In *S. lineata* and *Leptotrypa minima*, macrozooecia are associated with monticules where they are located close to the crests; these zooecia have a larger diameter than autozooecia and have been shown by Boardman and Buttler (2005) to have contained polypides. They contend that they may have been the locus of incurrents on monticules as suggested by Anstey (1981), but these findings are not backed up by studies of monticule dynamics elsewhere. We suggest that these macrozooecia may have had the ability to enhance the outgoing excurrents just as they emerge from the tops of monticules and thus increasing their ability to penetrate the boundary layer. Alternatively they may perform another function not associated with the expulsion of waste materials. It has been suggested that the macrozooecia aided the dispersal of gametes or larvae (Taylor, 1979; Key et al., 2002); perhaps they were gonozooids that produced or stored these reproductive elements.

Anstey (1981) argued that elongate monticules in *Spatiopora* functioned to channel the water down the long axis of the host, across the colony surface and that these currents bypassed the monticules, leaving the lophophores to passively feed in the nautiloid-induced parallel flow. For this to operate efficiently, the everted lophophores would need to be directed towards the adoral end of the orthocone. In *Spatiopora* lophophores are held normal to the zoarial surface as discussed above, so incurrents and excurrents are surmised to be normal to that surface too. In *Leptotrypa minima,* lophophores may be slightly directed adorally and this taxon may have utilized the nautiloid-induced flow to enhance feeding efficiency. Anstey's (1981) model also presents problems relating to the disposal of waste material and the replenishment of food-laden water in those adapically-placed autozooids. They would be filtering food-depleted channelized water.

In this study we have seen that as the orthocone expands adorally, the intermonticule distance in the encrusting bryozoan expands to a point where the ability to generate an adequate excurrent drops and a new macula and associated monticule is generated, intermonticular area and other monticule parameters decrease, and excurrent flow and efficiency is restored. The same pattern occurs in *Meekoporella* where linear maculae drain inverted cones. As the cone widens a new linear macula is inserted when intermacular distance increases beyond efficient levels (Wyse Jackson et al., 1999, fig. 4c, 4e).

Feeding ability of bryozoans on moving substrates.—Although there is no data on how fast extinct Paleozoic orthoconic nautiloids swam, modern *Nautilus* can attain maximum speeds of 25 cm/s when escaping predators. Speed of a motile host and its direction of movement could have a profound effect on the ability of encrusting bryozoans to feed. A number of studies (Lidgard, 1981; Okamura, 1985; Pratt, 2008) have examined the effects of water flow on feeding efficiencies by encrusting bryozoans; of particular relevance to this study are the findings of Okamura (1985) and Pratt (2008) who both examined the effects of different flow velocities on an autozooid's ability to feed. Although the evidence (above) leads to the supposition that orthoconic nautiloids moved slowly through the water, examination of the feeding capability of *Spatiopora* at various flow velocities could constrain the speed at which orthocones normally moved. The capacity for this Ordovician bryozoan to feed at different flow regimes is estimated from studies of modern bryozoans which we have taken to act as proxies for lower Paleozoic hydrological dynamics acting on orthoconic nautiloids.

Okamura (1985) subjected the encrusting modern bryozoan *Conopeum reticulum* to three flow velocities (1–2 cm/s, 4–6 cm/s, and 10–12 cm/s) and showed that feeding efficiency fell drastically at the higher velocity regardless of the size of the colony. Pratt (2008) showed that the ability of the encrusting modern bryozoan *Membranipora* to feed at a velocity of 7 cm/s was low, and the encruster *Cellepora* had a low feeding capability at velocities of less than 1 cm/s. If *Conopeum* and *Membranipora* could not feed at flow velocities of 12 cm/s, we infer that *Spatiopora* could not do so either when attached to nautiloids that moved even at half the speed of its modern counterpart *Nautilus*. This conclusion lends further credence that *Spatiopora* fed in slow-moving ambient flow velocities generated as their host swam slowly forward or passively drifted.

A NEW TRACE FOSSIL ASSOCIATION

Hard-grounds and shelly-material are frequently bored by a variety of organisms which produce an array of ichnogenera, that in the Cincinnatian of the U.S.A. include *Trypanites*, *Petroxestes*, and *Ropalonaria* (Hannibal, 1996) and *Sanctum* (Erickson and Bouchard, 2003). Those with circular openings are *Sanctum* Erickson and Bouchard, 2003 and *Trypanites* Mägdefrau, 1932. The former is characterized by excavation of the endozone of trepostomes (Erickson and Bouchard, 2003; Wyse Jackson and Key, 2007), whereas the latter takes the form of elongate tubes.

Herein we report for the first time the association of *Trypanites* with an unidentified adnate bryozoan encrusting an unidentified orthocone (specimen 15) from the Fort Ancient Member, Waynesville Formation of Cincinnati, Ohio (Fig. 4.4, 4.5). *Trypanites* is quite commonly encountered on internal molds of dead orthoconic nautiloids in the Cincinnatian (Palmer and Wilson, 2004). Ekdale and Bromley (2001) illustrated *Gastrochaenolites* borings through an orthoconic nautiloid shell from the Early Ordovician of Sweden, but in this case the orthocone was not encrusted by bryozoans.

In the example illustrated here, there is evidence that the bryozoan was living while bored, but that the orthoconic nautiloid was not. The shell of the orthocone has been partially replaced by calcite, and the phragmacone chambers have been infilled with sparry calcite. The bryozoan colony shows reaction rims around *Trypanites* borings (Fig. 4.4). This strongly suggests the following sequence of biological and taphonomic events: the orthoconic nautiloid died and its conch settled on the substrate where rapid replacement of the shell and infilling of the chambers with sparry calcite occurred. The surfaces was colonized by an non-monticulate encrusting trepostome bryozoan, and while alive was bored by the *Trypanites*-maker which resulted in the bryozoan producing a narrow skeletal reaction rim around the circular bored openings. The *Trypanites* borings penetrated the interior sparry calcite, and the boring tubes then became infilled with sediment (Fig. 4.5). The *Trypanites*-bryozoan-orthocone complex provides unequivical evidence that the boring animal did not bore into living orthocone chambers, and that early cementation and diagenesis must have occurred in the Ordovician Calcite Sea (Palmer and Wilson, 2004).

CONCLUSIONS

We agree with Baird et al. (1989) who found that in most instances the trepostome bryozoan *Spatiopora* Ulrich, 1882 encrusted cephalopod hosts while they were alive. This is suggested by the holoperipheral growth of bryozoans bearing aligned monticules and maculae and the consistent adoral growth of zoaria. The development of elongate maculae and monticules coaxially to their host length is primarily an adaptation to the conical shape of the host and less to water currents passing longitudinally along the orthocones. Maculae/monticules are arranged in lines along the host, and they increased adorally in size and spacing, until their efficiency as excurrent chimneys dropped, and another new macula/monticule line was inserted. At that point the maculae/monticules in the older two lines continued to decrease in size for a short distance before increasing in size and spacing again, and the pattern was repeated.

Reduction of turbulence by the production by the encrusting bryozoans of a monticulate surface on the smooth orthoconic nautiloid may serve to widen the surface boundary layer and therefore increase feeding efficiency for the bryozoans. Equally, high, blade-like monticules enable the excurrent flow to be ejected beyond a thickened boundary layer.

Spatiopora and other monticulate bryozoan taxa in the Upper Ordovician of the Cincinnati Arch region attached themselves to passive drifting or slowly forward swimming orthoconic nautiloids. They would probably not have been capable of feeding if the host swam at speeds of over 12 cm/s.

The prevalence of encrustation on orthoconic nautiloids by *Spatiopora* as opposed to other motile or fixed substrates might suggest an obligate relationship.

A new association of the ichnogenus *Trypanites* Mägdefrau, 1932 with epizoozoan bryozoans on orthconic nautiloids is documented.

ACKNOWLEDGMENTS

We are most grateful to the late F. K. McKinney who provided the material on which this study is conducted. For most helpful advice and comments on this paper we are grateful to R. J. Cuffey, A. Ernst, D. Evans, R. C. Frey, S. J. Hageman, E. Håkansson, K. Histon, C. H. Holland, M. Wilson, and an anonymous reviewer. We thank J. Sanner (Washington, DC) for providing access to type material and for photographing some specimens, and M. Hanratty who also photographed a number of specimens. This research was partially carried out at Dickinson College when PNWJ was on sabbatical leave and who thanks their Center for Global Study and Engagement for their invaluable support.

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ACCEPTED 8 SEPTEMBER 2013

APPENDIX

Stratigraphic and locality information for the specimens used in this study

Katian Stage (Edenian)

1 (CMC IP70079): *Spatiopora* sp.; Economy Member, Kope Formation; Roadcut by Kentucky Route 8 below I-275 bridge over Ohio river near Newport, Kentucky.

2 (CMC IP70080): *Spatiopora* sp.; upper Kope Formation; I-275 W of Licking River, N side of highway, near Newport, Kentucky.

3–4 (CMC IP70081–2): *Spatiopora* sp.; uppermost Kope Formation; Rest stop on east bound lane of I-275 at Mount Carmel, Ohio.

5 (CMC IP70083): *Leptotrypa minima*; uppermost Kope Formation; Rest stop on north bound lane (E side) of I-275 at Mount Carmel, Ohio.

Katian Stage (Maysville)

6–7 (CMC IP70084–5): *Atactopora maculata*; I-471, S of Kentucky route 27, Southgate, Kentucky, 2nd exposure after intersection. Bryozoan with small cluster of cornulitids.

Katian Stage (Richmondian)

8 (CMC IP70086): *Spatiopora montifera*; Fort Ancient Member, Waynesville Formation; Cincinnati, Ohio.

9–14 (CMC IP70087–92): *Spatiopora lineata*; Fort Ancient Member, Waynesville Formation; Cincinnati, Ohio.

15 (CMC IP70093): Undetermined trepostome and *Trypanites* borings; Fort Ancient Member, Waynesville Formation; Cincinnati, Ohio.

16 (CMC IP70094): *Crepipora solida*; Fort Ancient Member, Waynesville Formation; Cincinnati, Ohio.

17 (CMC IP70095): Undetermined trepostome; Fort Ancient Member, Waynesville Formation; Cincinnati, Ohio.

18–19 (CMC IP70096–7): *Spatiopora aspera*; Fort Ancient Member, Waynesville Formation; Cincinnati, Ohio. Smaller orthocones in body chamber and post-mortem encrustation of internal surfaces.

20–34 (CMC IP70098–112): *Spatiopora lineata*; *Treptoceras duseri* shale, Fort Ancient Member, lower Waynesville Formation; Tributary to Olive Branch Creek, E of Oregonia, Warren Co., Ohio.

35–37 (CMC IP70113–5): *Spatiopora lineata*; *Treptoceras duseri* shale, Fort Ancient Member, lower Waynesville Formation; Turkey Run, Camp Whip-Poor-Will, near Rochester, Warren Co., Ohio.

38 (CMC IP70116): *Spatiopora lineata*; *Treptoceras duseri* shale, Fort Ancient Member, lower Waynesville Formation; south branch of the Turkey Run, Camp Whip-Poor-Will, near Rochester, Warren Co., Ohio.

39 (CMC IP70117): *Spatiopora* sp.; *Spatiopora* shale, Blanchester Member, upper Waynesville Formation; "Grey specimen"=Creek near Clifton, Indiana.

40 (CMC IP70118): *Spatiopora montifera*; *Spatiopora* shale, Blanchester Member, upper Waynesville Formation; "Yellow Specimen"=Bon Well Hill Cut, near Brookville, Indiana. Post-mortem encrustation of septal walls.

41 (CMC IP70119): *Leptotrypa minima*; *Spatiopora* shale, Blanchester Member, upper Waynesville Formation; Fairfield Causeway Roadcut by Lake Brookfield, Fairfield, Indiana.

42 (CMC IP70120): Undetermined trepostome; *Spatiopora* shale, Blanchester Member, upper Waynesville Formation; Fairfield Causeway Roadcut by Lake Brookfield, Fairfield, Indiana. [Same taxon as #17].

43 (CMC IP70121): *Spatiopora montifera* sp.; *Spatiopora* shale, Blanchester Member, upper Waynesville Formation; Creek 1 mile W of Liberty, Indiana.

44 (CMC IP70122): *Spatiopora* sp. and *Crepipora solida*; *Spatiopora* shale, Blanchester Member, upper Waynesville Formation; Creek, 3 miles W of Liberty, Indiana.

45–46 (CMC IP70123–24): *Spatiopora montifera*; *Spatiopora* shale, Blanchester Member, upper Waynesville Formation; Creek, 3 miles W of Liberty, Indiana.

47 (CMC IP70125): *Spatiopora lineata* with cornulitids also encrusting as well as a number of small *Atactopora* colonies; *Spatiopora* shale, Blanchester Member, upper Waynesville Formation; Unnamed creek, 3.5 miles W of Liberty, Indiana.

48–54 (CMC IP70126–32): *Spatiopora lineata*; *Spatiopora* shale, Blanchester Member, upper Waynesville Formation; Unnamed creek, 3.5 miles W of Liberty, Indiana.

55 (CMC IP70133): *Crepipora solida*; *Spatiopora* shale, Blanchester Member, upper Waynesville Formation; Unnamed creek, 3.5 miles W of Liberty, Indiana.

56 (CMC IP70134): *Spatiopora* sp.; *Spatiopora* shale, Blanchester Member, upper Waynesville Formation; Unnamed creek, 3.5 miles W of Liberty, Indiana.

57 (CMC IP70135): *Spatiopora lineata*; upper Waynesville Formation; Clifton Creek, 1.1 mile W of Clifton, Union Co., Indiana.

58 (CMC IP70136): *Spatiopora montifera*; upper Waynesville Formation; Bon Well Hill roadcuts, NE of Brookville, Indiana.

59 (CMC IP70137): *Spatiopora lineata* and *Spatiopora* sp.; probably *Spatiopora* shale, Blanchester Member, upper Waynesville Formation; locality unknown.