Calendar Scale, Environmental Variation Preserved In The Skeletal Phenotype Of A Fossil Bryozoan (*Rhombopora Blakei* N. SP.), From The Mississippian Of Ireland

By: **Steven J. Hageman**, Patrick N. Wyse Jackson, Aaron R. Abernethy, and Margret Steinthorsdottir

Abstract

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CALENDAR SCALE, ENVIRONMENTAL VARIATION PRESERVED IN THE SKELETAL PHENOTYPE OF A FOSSIL BRYOZOAN (*RHOMBOPORA BLAKEI* N. SP.), FROM THE MISSISSIPPIAN OF IRELAND

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ABSTRACT—A single large colony (20 cm) of *Rhombopora blakei* n. sp. from the Hook Head Formation of Ireland (Tournaisian Stage, Mississippian) permits an analysis of within-colony variation associated with environmental change at a calendar scale (days to decades). Morphometric data for three external characters—apertures spacing along a branch and diagonal to a branch as well as lateral zooecial spacing—were collected as growth series (16–30 generations) from 13 segments within the colony. ANOVA, post-hoc means testing and graphical analysis of standardized data revealed nearest neighbor effects at the zooecial level and non-random distribution of variances across the colony. Parametric tests for sequential nonrandomness revealed cyclic variation through growth transects at three levels (23.3, 9.4 and 5.3 generations). Comparisons to growth rates of modern bryozoans suggests that the longer-term cycles are annual and that the shortest cycles may be related to lunar tidal cycles. The exceptional size and preservation of this single specimen, which is a new species of rhabdomesine Bryozoa, reinforces the importance of collecting individual morphological measurements from randomly selected and widely spaced parts of a colony for taxonomic, evolutionary and ecological applications.

INTRODUCTION

LARGE, WELL-PRESERVED specimens of modular colonial organisms such as fossil Bryozoa allow for the assessment of patterns of high-resolution paleoenvironmental variation associated with within-colony morphological variation (Fig. 1). Because individuals within a colony share a single genotype (assuming absence of significant somatic mutations) and the skeleton of each module in the colony forms under the influence of the environment prevailing at the time of its morphogenesis (Beklemishev, 1969; Boardman et al., 1970, 1973, 1983; Abbott, 1973; and Schopf, 1976), it is possible to empirically document morphological variation and infer concomitant environmental variation at a time scale equivalent to the growth of the colony. The relationship between morphology and environment has been documented in modern Bryozoa (Okamura, 1988, 1992; Okamura and Bishop, 1988; O'Dea and Okamura, 1999; O'Dea, 2003; Berning, 2007). Even when other sources of variation are present (e.g., astogenetic sensu Boardman et al. [1983] or possible morphogens of Urbanek [2004]), the environmental signal can be detected (Hageman et al., 2002, 2009; Hageman and Sawyer, 2006). Thus, environmentally induced morphological variation (e.g., size of zooecia) through a transect of the growth history of a single colony reflects some degree of changes in environmental conditions occurring during the growth of the colony.

The relationships among environmentally induced phenotypes of successive individuals (zooecia) through the growth history of a bryozoan colony can produce distinctive patterns depending on the scale and frequency of environmental changes (Fig. 2). At any given time during growth, all of the growing tips of the colony will experience the same environmental parameters such as temperature, nutrient level, salinity, etc. Environmental parameters that influence the morphology of the zooecium, e.g., temperature (O'Dea and Okamura, 2000) and nutrients (Hageman et al., 2009), will be preserved in the skeleton as morphological variation among zooecia. Therefore, within a colony (single genotype) zooecia that grew under similar environmental conditions are expected to be of similar size and shape, regardless of their absolute position in the colony. The magnitude of difference between environmental conditions during the growth of the colony will be proportionally related to the morphological differences in the zooecia that represent the different times of growth.

Potential calendar-scale (days to decades) cycles have been reported in the morphology of fossil bryozoans (Bartley and Anstey, 1987; Hickey, 1987; Hageman, 1995). A complete partitioning of morphological variance is more complex than a simple account of external environmental sources. One could also account for sources of variation caused by packing of zooecia, position relative to branching events, other positional effects within the colony, and a suite of biologic effects from pathogens to partial predation. However, with the proper experimental design (Fig. 3), general linear models such as multi-way, nested analysis of variance can be used to analyze non-genetic sources of morphological variation (e.g., Hunter and Hughes, 1994; Hermansen et al., 2001; Hageman et al., 2002, 2009).

If one measures a morphological feature of a bryozoan, say the distance between apertures in mm, and does this for say 15 times for each of 3 colonies of the same species, the variation of the 45 observations could be evaluated in two ways. First we could see if there is a difference among the three colonies (calculate the average for each colony and compare them to the average of all 45 together). Morphological differences among colonies could be caused by either genetic differences (genotypic variation) or by different environmental influences (ecophenotypic variation) expressed in the phenotypes of the three colonies during growth.

Initial studies of morphological variation in Bryozoa used analysis of variance (ANOVA) to identify the portion of the variance represented among colonies, with all of the remaining variance allocated to the residual or error sources (Schopf, 1976; Schopf and Dutton, 1976; Pachut and Anstey, 1979; Brande and Bretsky, 1982; Pachut, 1982; Key, 1987). Schopf (1976) suggested that variation among colonies (of a population) exclusively represents genetic sources and that

FIGURE 1—Exterior map of large *Rhombopora blakei* n. sp. from Hook Head Formation (Tournaisian Stage, Mississippian) of Hook Head, County Wexford, Ireland; holotype TCD.47605; measured branch segments are labeled 1–13; segments sectioned for interior analysis (acetate peels) are labeled A–C. The specimen is housed in the Geological Museum, Trinity College, Dublin.

because the within colony (residual or error) could not represent genetic variation, it must represent environmental variation developed during colony growth.

Schopf's (1976) model assumes that all variation among colonies is caused by genetic differences (Fig. 3). This model assumes that none of the morphological variation among colonies was caused by environmental effects. His model also assumes that all of the within colony variation, also referred to as "residual" or "error" in statistical texts, represents environmentally produced variation that was generated during the growth of each colony. Schopf's (1976) model (Fig. 3.1) was clarified, statistically, by Brande and Bretsky (1982), but it over simplifies the sources of variation present.

The genetic portion of among colony variation can be described by relative differences in both space and time (Fig. 3.2). Among colony variation can be due to environmental variation, which can also be subdivided both spatially and temporally (Fig. 3.2). In addition, with careful experimental design and data collection, the within colony variation can also be partitioned into several sources of small-scale environmental variation (Fig. 3.2). Within colony variation could either be temporal, the product of changing environmental conditions through the life of the colony or spatial, such as heterogeneities in substrate at the scale of an encrusting colony (e.g., composition, texture, microbial flora, presence of other encrusting competitors) as documented by Taylor and Furness (1978). Environmental difference in space at the colony scale can exist in erect forms as well, such as edge effects possibly associated with currents and nutrient access. For erect and encrusting colonies on more or less homogeneous substrates, systematic variation in zooecial characters within the colony is more likely the product of temporal environmental differences at the colony scale (Figs. 2, 3.2).

Most previous studies of morphologic variation within and among colonies have noted the relatively high portion of morphological variation present within colonies relative to among colonies: ~40–90% of total variance is accounted for by within colony variation versus ~10–60% by among colony variation (Farmer and Rowell, 1973; Schopf, 1976; Schopf and Dutton, 1976; Jackson and Cheetham, 1990; Cheetham et al., 1993, 1995; Hunter and Hughes, 1994; Hageman et al., 1999, 2002, 2009). Even when variation associated with positional effects is accounted for (e.g., patches within colonies and nearest neighbor row and column effects), the residual (within colony) variance can be as high as 18% (Hageman et al., 2002).

Evaluation of high-resolution, temporal and spatial micro-environmental variation using bryozoans is not routine because it requires large, relatively complete colonies, which are relatively rare in the fossil record. Partitioning of the different sources of variation requires nearly complete colonies with known growth histories for individual zooecia. However, such specimens are not unknown. An exceptional bryozoan specimen (Fig. 1), from the Lower Carboniferous near Hook Head, Ireland (Fig. 4), consists of a nearly complete colony of *Rhombopora blakei* n. sp., which is well preserved and largely exposed on a bedding plane. This important specimen allows for the measurement of variability of morphological characteristics through the growth history of the colony and to compare variation within and among branch segments of the fossil colony and evaluate potential cycles within colonies and other non-random variation.

Research aims.—The goals of this project are three-fold: 1) to determine whether high-resolution environmental signals are indeed detectable in the skeletal morphology of this exceptional specimen of a Mississippian Bryozoa; 2) if such signals are present, to suggest potential causal factors including spatio-temporal scales; and 3) to consider the implications of within-colony variation to bryozoan systematics and general paleoecology.

Geological setting.—The Mississippian (Tournaisian Stage) marine rocks of the Hook Head Peninsula, on the southeast coast of Ireland (Fig. 4) are comprised of the transitional Porter's Gate Formation (Sleeman, 1977) and the fully marine Hook Head Formation of Sleeman et al. (1974). The lower portion of the Hook Head Formation is equivalent to the Ballymartin Limestone Formation and its upper part to the Ballysteen Limestone Formation both of which are recognized regionally (Tietzsch-Tyler and Sleeman, 1994). The Hook

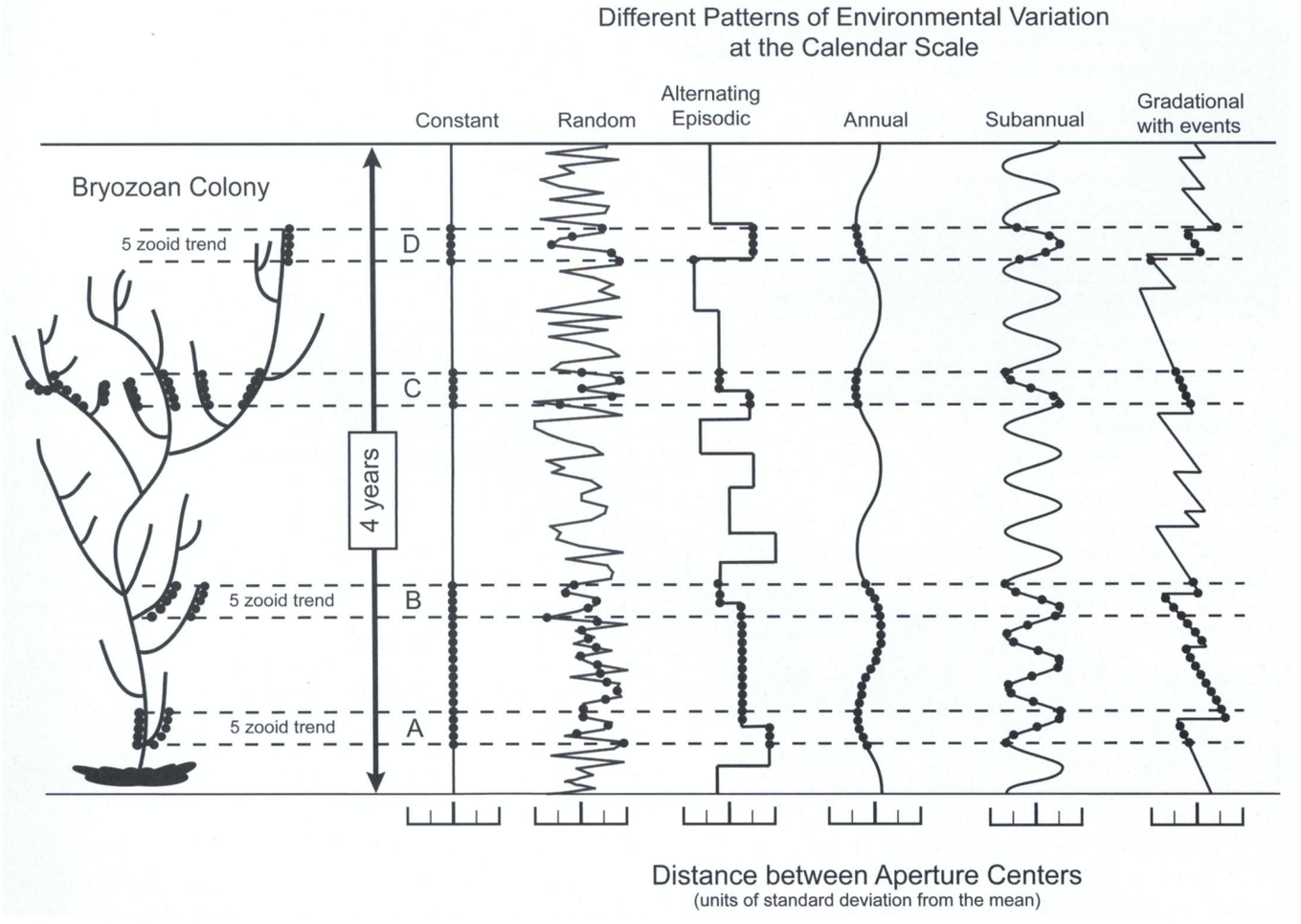

FIGURE 2—Generalized model illustrating the relationship between the spacing of apertures (distance between successive, proximal-distal, aperture centers) through a growth transect of successive generations of a mature erect bryozoan colony (~3.5 years old); example plots of five generations (zooids) shows where their values (in units of standard deviation from the mean) may plot under different, changing environmental conditions; these models assume constant growth rates and continuous growth; Constant=no environmental change during the life of the colony; Random=environmental change not associated with time; Episodic=rapid environmental changes alternating with times static environmental conditions, but neither expressed at regular intervals or durations; Annual=systematic, gradational change through one year; Subannual=two cycles of systematic, gradation change through one year (e.g., seasonal); and Gradational=directional changes (decrease in spacing) associated that are punctuated at irregular intervals by abrupt change. The model assumes no spatial environmental variation, such that all individuals in the colony experience the same environmental conditions at the same point in time.

Head Formation is a 335 m thick sequence of limestones and shales (Ausich and Sevastopulo, 1994) that is subdivided into one formal member, the Bullockpark Bay Dolomite Member (Sleeman et al., 1974), and four informal units (Smyth, 1930) (Fig. 4) that represent progressively deeper water as they get younger. These units are considered to represent carbonate and siliclastic tempestite shelf deposits (Ausich and Sevastopulo, 1994, p. 253) The lowest '*Michelinia* Beds' (correlated with the Ballymartin Limestone Formation) consist of 124 meters of tabular to lenticular crinoidal packstones and dark grey calcareous shales with robust crinoids and plentiful fenestrate bryozoans. They are overlain by the Bullockpark Bay Dolomite Member (25 meters thick), an oolitic limestone with some vertical burrows and cross stratification that represents a period of shallow marine conditions (Ausich and Sevastopulo, 1994). This distinctive unit is succeeded by the fossiliferous dark grey muddy limestone facies of the 'Supra-Dolomite Beds' (91 m) that are lithologically similar to the '*Michelinia* Beds'. Following the 'Supra-Dolomite Beds' are: the '*Linoproductus* Beds' (38 m) and the uppermost '*Chonetes* Beds' (50 m). The former contain well-preserved bryozoans and crinoids and several marker horizons with robust spinose brachiopods in life-position. The latter are less fossiliferous than older horizons and represent the deepest sedimentary environments in which the thin-walled brachiopod *Chonetes* thrived. Some beds also contain numerous *Zoophycos* burrows.

The limestones of the Hook Head Formation are highly fossiliferous, and have yielded many hundreds of generally well-preserved Mississippian taxa (M'Coy, 1844) with bryozoans (Bancroft, 1986a, 1986b, 1988; Bancroft and Wyse Jackson, 1995; Cleary and Wyse Jackson, 2007; Miller, 1961; Tavener-Smith, 1974; Wyse Jackson et al., 2006), crinoids (Austin and Austin, 1843–1849; Ausich and Sevastopulo, 1994, 2001), and brachiopods (Smyth, 1930; Mottequin, 2010) being dominant macrofaunal elements. Bivalves, trilobites (Owens, 2000), and corals (Smyth, 1928, 1930; Nudds, 1983) form a lesser component of the macrofauna, that also includes some conodonts (Johnston and Higgins, 1981) and microvertebrates (Duncan, 2003).

1 Modified Schopf Model for Zooecia-level Morphological Variation

Among Colony Variation = genetic

Residual (within colony, error) = environmental

All *Zooecia-level Morphological* Variation — Total — 100%

2 Partitioned Sources of Zooecia-level Morphological Variation

	Source	
Among Colony Variation		
Genetic Variation – among colonies	*Spatial*	*Temporal*
among species and higher taxonomic units		
within species		
within populations (biological)		
Environmental Variation – among colonies		
macro-environmental (e.g., different climate zones)		
meso-environmental (e.g. facies within climate zone)		
micro-environmental (e.g., substrates within facies)		
total Among		
Within Colony Variation	*Source*	
Astogenetic & Deterministic - subcolony		
Ontogenetic		
Polymorphic		
Budding/Packing		
Environmental		
Spatial (ultra-microenvironmental, within colony)		
Temporal (heterogeneity during colony lifespan)		
total Within		
Residual (not in model + error) (theoretical sources, somatic mutation, morphogens, taphonomy, other unknown factors, collection error)	*residual*	
All *Zooecia-level Morphological* Variation	*Total*	100%

FIGURE 3—Models for partitioning morphological variation among and within colonies. *1*, model proposed by Schopf (1976) and modified by Brande and Bretsky (1982); *2*, model to partition all sources of morphological variation at the zooecia-level among and within bryozoan colonies, not including potential interactions among sources.

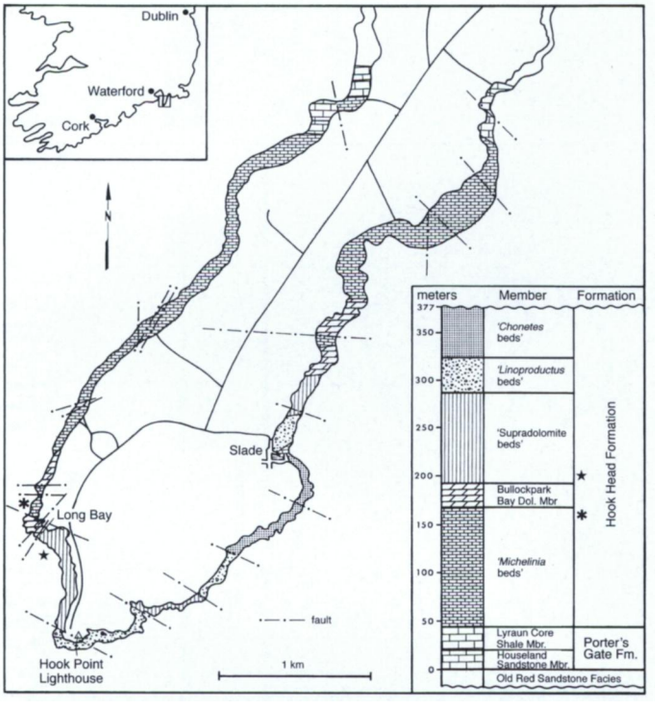

FIGURE 4—Geological map of the Hook Head Peninsula, southeast Ireland, showing collection localities of the large specimen in this study; asterisk designates locality 19a of Smyth (1930) and supplemental material for taxonomic comparison; star designates locality 64 of Dresser (1960)] in the Hook Head Formation, Tournaisian Stage, Mississippian. Modified from Ausich and Sevastopulo (2001, text-fig. 3).

MATERIALS

This study is based on a large *Rhombopora blakei* n. sp. colony (Figs. 1, 5.1–6) (TCD.47605) preserved on a limestone slab that was found as float on the southwest margin of the Hook Head Peninsula at Long Bay, approximately 1 km north of Hook Head Lighthouse, close to locality 19c of Smyth (1930) (Fig. 4). Although loose, the slab is lithologically identical to the uppermost '*Michelinia* Beds' on which it lay (Fig. 4) and there is no reason to believe that the specimen originated from any other stratum. Additional specimens (TCD.25875–77, 41782–87), collected in the late 1950s from the lowest part of the 'Supra-Dolomite Beds' (Fig. 4), provided additional systematic information. These were collected in situ approximately 100 m south of locality 19c at Little Cove (locality 64 of Dresser, 1960).

For taxonomic treatment the following morphometric characters were measured: branch diameter, autozooecia apertural length, autozooecia apertural width, interapertural wall thickness measured longitudinally, interapertural wall thickness measured transversely, basal wall length measured along axis, thickness of chamber wall in endozone, exozone wall thickness, metapore diameter, metapore depth, acanthostyle core length, acanthostyle diameter, distance between adjacent acanthostyles.

SYSTEMATIC PALEONTOLOGY

All specimens are stored in the Geological Museum, Trinity College, Dublin, Ireland (prefix TCD).

Phylum BRYOZOA Ehrenberg, 1831
Class STENOLAEMATA Borg, 1926
Order CRYPTOSTOMATA Vine, 1884
Suborder RHABDOMESINA Astrova and Morozova, 1956
Family RHOMBOPORIDAE Simpson, 1895
Genus RHOMBOPORA Meek, 1872

Type species.—*Rhombopora lepidodendroides* Meek, 1872 by original designation, from the ?Willard Shale, Pennsylvanian of Nebraska City, Otoe County, Nebraska.

Diagnosis.—Rhomboporid with erect dendroid zoaria composed of dividing cylindrical branches. Linear axis irregular. Autozooecia tubular and diverge from axis at a low to moderate angle. Hemisepta absent. Metapores rare. Diaphragms uncommon. Acanthostyles frequent with one to two proximal to autozooecial apertures; aktinotostyles common to abundant (modified after Blake, 1983, p. 577, 578; Wyse Jackson, 1996, p. 129).

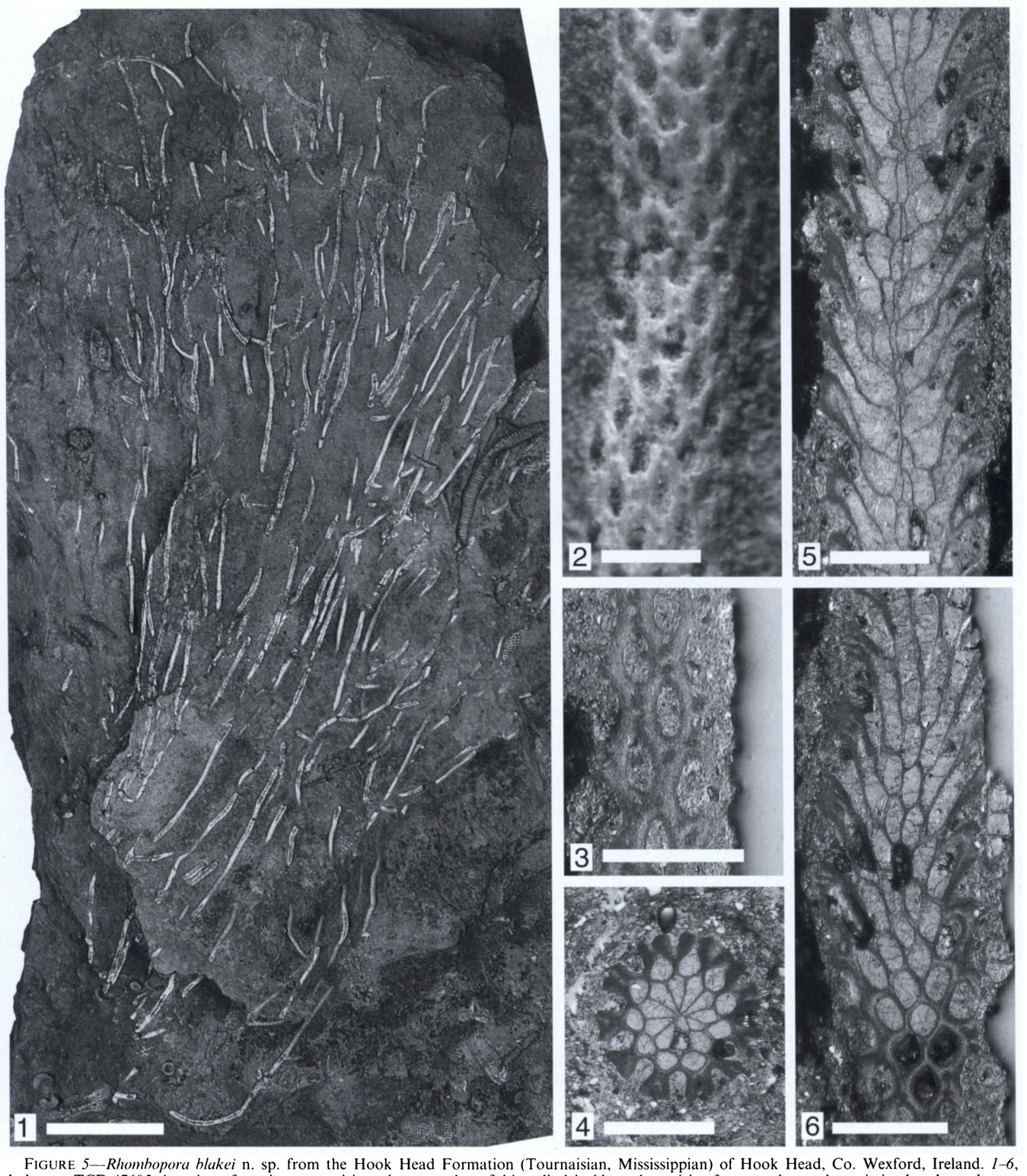

FIGURE 5—*Rhombopora blakei* n. sp. from the Hook Head Formation (Tournaisian, Mississippian) of Hook Head, Co. Wexford, Ireland. *1–6*, holotype, TCD.47605: *1*, region of zoarium comprising a large number of thin cylindrical branches arising from an obscured or missing basal attachment point, and diverging sub-parallel to each other; *2*, external view showing paired acanthostyles between oval-shaped autozooecial apertures; *3*, shallow tangential section illustrating autozooecial aperture shape and an acanthostyle situated at the distal and proximal margins of apertures; *4*, transverse section showing spiral budding pattern of autozooecia around central axis; *5*, longitudinal sectional through central axis showing autozooecial chambers, with acanthostyles in exozone and metapores; *6*, oblique longitudinal section through endozonal (at top) and exozonal portions of a branch (at bottom). Scale bars: *1*, 20 mm; *2–6*, 0.5 mm.

RHOMBOPORA BLAKEI new species
Figures 1, 5.1–6

Rhombopora sp. B. DRESSER, 1960, p. 35, fig. 40a–c.

Diagnosis.—*Rhombopora* with erect dendroid zoarium comprised of numerous long irregularly dividing cylindrical branches. Autozooecia budded in a spiral manner from a distinct central linear axis; base recumbent and inflated on budding wall, tubular through endozone; vestibule at a moderate angle to external surface. Exozone thin. Autozooecial apertures oval in shape, moderate to large in size, arranged in quincunx in longitudinal rows around branches. Metapores rare, circular, developed in exozone and situated proximal to autozooecial apertures sometimes between acanthostyles. Two acanthostyles developed proximal to autozooecial apertures.

Description.—The zoarium of *Rhombopora blakei* n. sp. comprises numerous long branches that measure 20 cm from holdfast to their distal tips; these make up a bush-like expansion with a basal diameter of 4 cm to a distal diameter of 12 cm. Branches slender, 0.793–0.815 mm (mean: 0.803 mm) in diameter, of consistent thickness along their length except immediately prior to bifurcation of lateral branch development when a slight increase in diameter occurs. Bifurcation is infrequent and irregular; lateral ramifications likewise irregular, generally deviate at moderate to high angles of between 50° and 90°; secondary branches soon assume a growth direction parallel to adjacent branches. Autozooecia are budded in a spiral fashion from an undulatory, central axis. Zooecial bases are weakly inflated, and measure 0.120–0.226 mm (mean: 0.182 mm) along the axial budding surface. In longitudinal section chambers diverge at a low angle of 20° from the axis, before bending to be orientated at 60° in their midsection where chambers are narrowest; at the exozone-endozone boundary chambers are bent proximally so that vestibules cut the zoarial surface at an angle of 30°. In cross-section chambers in the endozone are elongate-hexagonal in shape, becoming sub-pentagonal within the exozone. In the endozone chamber walls are very thin (0.005–0.010 mm [mean: 0.008 mm]), composed of a very thin granular core covered by laminated skeleton; in the exozone, walls are considerably thicker than those of the endozone, and are composed of laminated skeleton only. The exozone measures 0.114–0.144 mm (mean: 0.126 mm) and makes up just less than 50% of the branch width.

Autozooecial apertures are oval in shape, 0.164–0.194 mm (mean: 0.175 mm) long by 0.075–0.108 mm (mean: 0.089 mm) wide; regularly spaced 0.142–0.198 mm (mean: 0.171 mm) longitudinally and 0.094–0.113 mm (mean: 0.104 mm) transversely, and arranged in longitudinal rows spirally around the branch. Interapertural walls are rounded, smooth and lack stylets except for the placement of two prominent acanthostyles situated at proximal and distal ends of apertures. Acanthostyles develop from within the exozone, have a distinct core that deflects a laminar skeletal sheath. Within the core tiny dark spines are developed perpendicular to growth direction; these resemble axial spines more typically developed in aktinotostyles (Blake, 1973, 1983). In tangential section the core of acanthostyles appears as a pale spot surrounded by darker laminae. Acanthostyles measure 0.033–0.043 mm (mean: 0.039 mm) in diameter and are 0.052–0.105 mm (mean: 0.078 mm) apart. Metapores are moderately common, developed in interapertural areas either between apertures and acanthostyles or in the area between two acanthostyles. They are circular in cross-section, small 0.114–0.144 mm (mean: 0.126 mm) in diameter, and form elongate parallel-sided chambers with rounded bases when seen in longitudinal section.

In the bases and mid-sections of some chambers dark diffuse material has collected; this may be organic in origin and similar to brown-bodies seen in other stenolaemate bryozoans (Key et al., 2008).

Branching is infrequent, and branching angles increase distally, being on average 50–60° proximally and 80–90° distally.

Etymology.—Named for Daniel B. Blake, noted bryozoan paleontologist.

Types.—Holotype, TCD.47605, '*Michelinia* Beds', Hook Head Formation, Tournaisian Stage, Mississippian; Locality 19c (of Smyth, 1930), Long Bay, Hook Head Peninsula, Co. Wexford, Ireland. Paratypes, TCD.25875–77, 41782–87, 'Supra-Dolomite Beds', Hook Head Formation, Tournaisian Stage, Mississippian; Locality 64 (of Dresser, 1960), Little Cove, Hook Head Peninsula, Co. Wexford, Ireland.

Occurrence.—*Rhombopora blakei* occurs only in the Mississippian (Tournaisian Stage) of Hook Head Peninsula, Co. Wexford, Ireland.

Discussion.—In terms of preserved size, the holotype of *Rhombopora blakei* n. sp. is a unique example of a rhomboporid bryozoan. In one specimen (Figs. 1, 5.1) a largely complete zoarium comprising up to 25 branches reaching 20 cm in length is preserved. This is highly unusual as in most cases the branches of delicate cryptostomes usually become broken into short lengths prior to burial. This specimen provides a unique perspective of zoarial form, a bush-like expansion of long branches that grew broadly parallel to each other (Fig. 6), and an insight into how other cryptostome bryozoan colonies may have looked when alive.

Rhombopora blakei resembles *R. binodata* Trizna, 1958 in having two large acanthostyles developed between autozooecia. However branches are broader in *R. binodata*, the exozone is thicker, and autozooecial apertures are considerably smaller.

The proximo-distal pattern of variable angles between branches suggests that new branches were added dichotomously as primary branches at the proximal end of the colony and mainly as secondary branches distally. This dual pattern of branching is typical in the Suborder Rhabdomesoidea (Blake, 1976). Probably the first round of branching is astogenetically controlled, whereas the sharp upward turn of the secondary branches may reflect microenvironmental control, where self-recognition of already established adjacent branches is involved in preventing crowding. This suggests some modular control over growth that aims to maximize the resources available to the entire colony (Franco, 1986) and avoiding competition as if between branches from two different colonies (Buss and Jackson, 1979).

Rhombopora blakei is only the third accepted species of *Rhombopora* from the Mississippian of Ireland and Britain, the previously described species being *R. cylindrica* Wyse Jackson, 1996 (=*R. similis* [Phillips, 1841] of some earlier authors) and *R. hexagona* Wyse Jackson, 1996. Owen (1966) decribed *R. radialis* from Derbyshire but this has been shown to synonomous with *Pseudonematopora turkestanica* (Nikiforova, 1948) (Wyse Jackson, 1996, p. 127). *Rhombopora blakei* differs from other Mississippian species from the British Isles in usually possessing two large acanthostyles between adjacent autozooecia whereas *R. cylindrica* one acanthostyle is usually located at autozooecal apices, while in *R. hexagona* acanthostyles are absent and smaller heterostyles are arranged in a

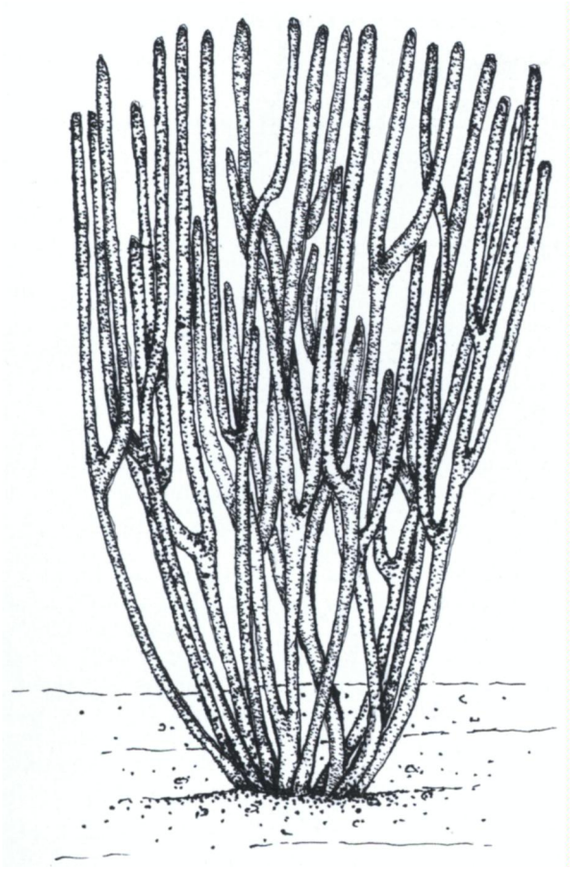

FIGURE 6—Reconstruction showing gross form of a young colony of *Rhombopora blakei* n. sp. approximately 10 cm tall in life position.

hexagonal pattern around autozooecial apertures (Wyse Jackson, 1996).

METHODS

Because the data of interest are preserved in the skeletal phenotype, analytical methods for within-colony variation apply to both modern and fossil material is used and to both erect and encrusting colony growth forms. An ideal data set for this study would consist of a suite of measurements for external and internal characters collected from each zooecium through multiple lineal budding sequences, beginning in the zone of astogenetic repetition and continuing to the growing tip of a branch. Inevitable taphonomic events, such as fragmentation, mean that even exceptionally well preserved fossil specimens can produce a data set that only approaches the ideal. In this study, our goals was to collect measurements for a limited number of exterior characters from sequentially budded zooecia in segments of the colony representing different phases of the colony's growth history.

Taphonomic analysis.—In order to determine whether the specimen represented segments of a single colony, rather than multiple colonies, it was examined visually using the following qualitative criteria:

1) orientation of all branches:
   1. consistent with a single proximal distal growth direction, vs.
   2. multiple growth trajectories, resulting from multiple colonies, vs.
   3. random or indeterminate, resulting from disturbance or transport.

2) continuity of branch segments:
   1. likelihood that proximo-distally adjacent fractured branches physically align, vs.
   2. branch segments with no apparent matching counterpart, or
   3. likelihood that sediment covered portions of branches trace to proximo-distally adjacent branches, vs.
   4. covered branch segments with no apparent matching counterpart.

3) ancestrulae and colony form:
   1. distribution of branches consistent with a single colony form, with proximal regions converging on a single ancestural, vs.
   2. the potential for multiple colonies, growing from different ancestrulae.

This evaluation was qualitative but required careful examination of the entire colony which was accomplished by creating a digital image map. Using the best preserved branches, the specimen was placed under an Olympus SZX 12 microscope with an Olympus CC12 digital video camera attached. Successive digital images of the colony were taken at the zooecial level along selected branches. The images were transferred to Adobe Photoshop 5.0 and zooids were aligned within branch segments. Segment composite images were fused creating a replica of each branch studied (Fig. 7).

Material for detailed study.—After performing a taphonomic analysis of the specimen, thirteen branches (Fig. 1) were chosen for further study based on: 1) the quality of preservation (some parts of colony are more abraded, fractured and covered by sediment than others); and 2) the length (i.e., the number of generations displayed).

Morphological characteristics for study.—Three morphological characteristics were chosen for measurement (Fig. 7): the distance between approximated centers of apertures along a branch (AB); the distance between the centers of apertures measured diagonally across a branch (DB) and the lateral spacing of zooecia (LB). Although it was likely that DB would be correlated with AB, LB or both, the nature of these relationships could not be known a priori. These morphological characteristics are correlated with both zooid size and spacing (Winston, 1976, 1977). Each zooecium was given a serial number according to branch segment, photo, and position, respectively. Calibrated measurements for the three characters were collected with Olympus Microsuite-Basic software. Branch segments ranged from 16 to 32 serial zooecia in length, with an average 22.6 zooecia per segment.

Summary statistics were calculated for each branch and Pearson's correlation coefficient was calculated for each pair of characters. Unless otherwise noted, analyses are based on standardized data [Z-score = $(X_i - \mu)/s$] where X_i is the i^{th} data point, μ is the mean and s = the standard deviation for all observations (Zar, 1999, p. 83). Data are available from the journal's supplemental data archive (http://www.journalofpaleontology.org).

Graphical view of variation among and within branch segments.—Standardized data were plotted as XY scatter plots for paired combinations of the three characters. Data points were coded by their branch segment number in order to examine patterns of within colony variation. If variation was randomly distributed, all data points would form a single, mixed, data cloud.

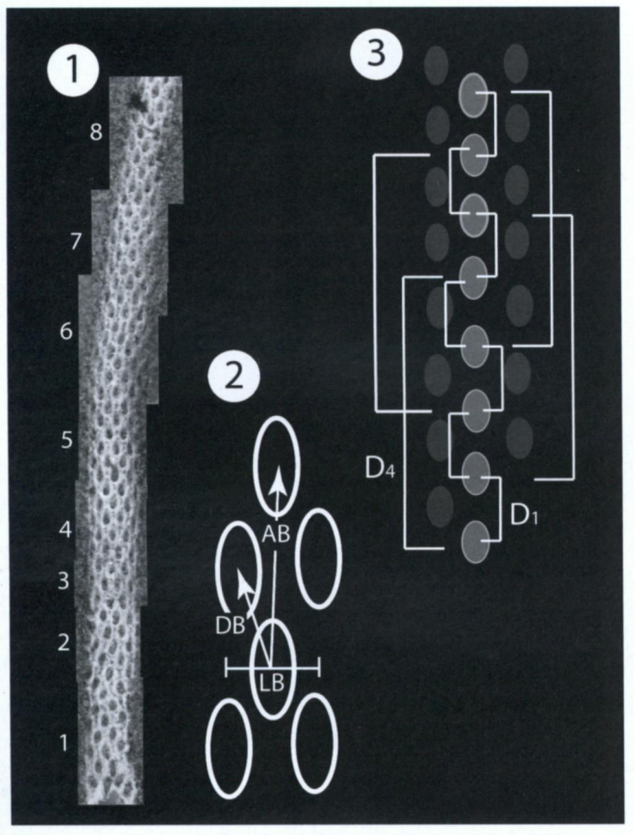

FIGURE 7—*1*, composite of eight images for branch-segment-7, images, ×22.5; *2*, morphometric characteristics chosen for study: AB=aperture centers along branch vertically, DB=aperture centers along branch diagonally, and LB=lateral spacing of zooecia; *3*, example of comparisons separated by D_1=one generation and D_i=four generations, values were averaged over all thirteen segments for each generational comparison between D_1 and D_{18} (Fig. *8*).

Analysis of within-colony variation.—In order to test whether morphological variation is non-randomly distributed within the colony (i.e., zooecia within branch segments are more similar to each other than to those among branches), data were subjected to a single-factor analysis of variance (JMP® 8.0.1). For each of the morphological characters studied (AB, DB, LB) a one-way analysis of variance was performed, in which the null hypothesis of each test was that the mean values of each of the thirteen branches do not differ:

$$H_o: \mu_1 = \mu_2 = \mu_3 = \mu_4 \ldots = \mu_{13}$$

A post-hoc comparison of means using Student's t was performed to test for significant differences between pairs of branch segments (JMP® 8.0.1).

Weighted moving average of sequential observations through segments.—Standardized data for three morphological characters from 13 colony segments (294 observations measured to 0.001 mm) were used. Standardization of data results in a series with a mean of zero and a standard deviation of one across all branch segments. Moving averages for each character were calculated within each branch segment using a weighting of 1:2:1 in order to smooth noise out of a potentially broader signal. For example if the first raw values observed in a branch were:

0.5, 0.7, 0.6, 0.8, 0.7

the first value in the weighted moving average would be:

$$0.625 = (0.5 + (2 * 0.7) + 0.6)/4$$

the second value in the weighted moving average would be:

$$0.675 = (0.7 + (2 * 0.6) + 0.8)/4$$

and so on through all available data points for each segment. This procedure resulted in a series of (n–2) data points for each segment.

Evaluating cyclicity within a colony.—Three methods were employed to explore for potential cyclic variation in zooecia size and spacing during the growth of a colony. The first was a graphical exploration where data from weighted running averages were plotted in series as scatter plots. In order to simplify graphs for evaluation, characters AB and DB (aperture spacing along branch and diagonal to branch, found to be strongly correlated) were combined into a single value [AS=(AB + DB)/2] representing the average aperture spacing.

The second method was to perform a non-parametric runs test for serial non- randomness (Zar, 1999, p. 416), for which the null hypothesis is that the distribution of directional changes is random. For example, if the size of a character from two successive zooecia in a branch segment increased it was scored a "+,"whereas a decrease was score "−."Two extremes (i.e., non-random) would be 1) too many runs or 2) too few runs as compared to that expected from a random distribution.

1) + − + − + − + − + − + − + − + − + − + − + − + − +
2) + + + + + + + + + + + + + − − − − − − − − − − − −

If n_1=the total number of "+" and n_2=the total number of "−,"and u=the number of runs, the critical values for u at a probability level of α can be read directly from Table B.28 in Zar (1999). An approximation for critical values for large n is also provided in Zar (1999, p. 417).

The third method to test for within colony cycles used the parametric test of serial randomness (Zar, 1999). The null hypothesis was that there is no difference in a measure of successive positions in a series, or:

> *Ho*: Consecutive measurements of a zooecial character through sequential budding generations of a branch segment varies randomly.
> *HA*: Consecutive measurements of a zooecial character through sequential budding generations of a branch segment vary non-randomly and are serially correlated.

The null hypothesis can be tested with a mean square successive difference test (Zar, 1999, p. 418) in which the variance between successive observations (s^2_*) is compared to the variance of observations from the population mean (s^2). A function of this ratio yields a test statistic C, which can be evaluated at critical probability levels for different sample sizes (Zar, 1999, table B.29). Both of the tests for serial non-randomness were performed on weighted running averages of standardized data, independently for each of the three characters through each of the thirteen segments.

Characterizing potential cycles.—The colony does not carry direct information about the timing of growth (i.e., no clear annual growth checks are present) and branch segments cannot be aligned temporally (i.e., a lower branch at the edge

of the colony may have formed later and in a different microenvironment than a branch near the top). Therefore mathematical analyses such as time-series and wavelets are not appropriate for analyzing the significance of potential cycles in zooecial size during the growth of the colony. Any inference about the causes and implications of potential cycles must be based on: 1) number of zooecia (generations) per cycle; 2) typical growth rates of bryozoans with similar lifestyles; 3) environmental controls on zooecial size and growth rates; and 4) timing of growth (i.e., continuous vs. punctuated and constant vs. variable rate).

The approach taken here was to identify *potential* cycles by examining the magnitude of differences between character measurements separated by differing numbers of generations (i.e., through a linear growth sequence of zooecia). For example, D_1 = the average difference between a character for adjacent zooecia in a budding series;

$$D_1 = \Sigma\left(x_i - x_{(i+1)}\right)$$

for all comparisons across all branch segments;

and in general D_g = the average difference between a character for every combination of zooecia separated by *g* generations;

$$D_g = \Sigma\left(x_i - x_{(i+g)}\right)$$

for all comparisons across all branch segments;

These examples are illustrated in Figure 7.3. Average D-values (using weighted moving average of standardized data) were calculated for differences ranging between one to eighteen generations; standard deviations were calculated for D-values for each generational difference (g = 1 to g = 18). Larger average D-values indicate greater differences between observations separated by *g* generations. Smaller standard deviations highlight more consistent generational differences. Scatter plots of both values were used to identify potential cycles.

Estimating absolute scale of cyclicity.—The scale of cyclicity in real time can be estimated by using some known values and bounding several variables by extreme constraints. Because these processes might have variable rates (e.g., dormant growth intervals within a year) and could be asymmetrical (e.g., rise and fall at different rates), one should be cautious in ascribing true cyclic processes with perfect periodicity to causal mechanisms. However, based on earlier analysis of morphological patterns within growth series that appear to be cyclic, we will attempt to explain the observed patterns from known cyclic phenomena, including diurnal (daily), lunar (~28 day), annual/seasonal (yearly), and oceanographic (e.g., ENSO ~4 yr). For any specimen we know the overall colony length and average spacing between apertures (AB), from which one can approximate the total number of generations present in a complete lineal budding sequence. Having estimated the number of generations present in a first level cycle (previous section), one can estimate the number of 1st level cycles present throughout the entire colony growth sequence. With that knowledge one can hypothesize the scale of the driving factor for the 1st level cycle (e.g., as either daily or annual). From this one can approximate the age of the colony (in years) and the rate of growth (mm per year) required to account for the observations. These can then be compared to growth rates in modern bryozoans. One can only say that the hypothesized rate is unreasonably fast or unreasonably slow and thus bracket a most likely scale for the cycle. Because these are order-of-magnitude estimates, we are not concerned with temporal variation in orbital parameters (e.g., exact duration of a late Paleozoic lunar month).

RESULTS

Taphonomic description and conclusions.—All observations based on the orientation and continuity of branches and colony form support the hypothesis that the specimen was originally a single contiguous colony (Fig. 1). Branches are all oriented proximo-distally in the general direction of growth, expanding bush-like toward the top and converging toward the bottom (Figs. 1, 6). No ancestrula or hold-fast is preserved on the specimen but neither is there evidence for the origins of multiple colonies. In many places, the fractures between adjacent segments visibly align and exposed branch lengths can be traced beneath a thin cover of sediment (Fig. 5.1). Cut and sanded faces along the edges of the slab show that branches of the ostensible colony extend about one cm into the sediment with the same density as seen on the surface, as could be expected from a colony toppled into sediment. This is in contrast to alternatives of a lag of fragments concentrated at the surface or a random distribution of segments throughout the thickness of the block. Although we cannot say with certainty that this specimen represents a single genotype (one colony), based on all evidence, the hypothesis cannot be rejected.

Descriptive statistics.—Descriptive statistical summaries for each of the three characteristics from the thirteen branch segments are presented in Table 1. The coefficients of variation (CV) for each character among all branch segments are of similar magnitude (Table 1), ranging from 9.5 for aperture spacing along branch (AB) to 11.8 for lateral zooecia spacing (LB).

Graphical view of variation among and within branch segments.—When standardized data are labeled by the branch segment from which they were measured and plotted on XY scatter plots, several patterns are evident. Similar patterns and trends are exhibited by all combinations of branch segments, but four segments are highlighted to serve as an example (Fig. 8). First, the characters aperture spacing along branch (AB) and diagonally across branch (DB) are positively correlated (Fig. 8.1; Pearson Correlation Coefficient r = 0.637; significant at $P < 0.0001$). Secondly, when either AB or DB is plotted against LB (lateral zooecia spacing), branch segments may be differentiated in three ways: 1) branch segments are completely discrete from other segments, such as Segment–3 (Fig. 8.2, gray diamonds); 2) mean values for branch segments are clearly separated, but distributions partially overlap in morphospace, such as Segment–1 (circles) and Segment-4 (triangles) in Figure 8.2; and 3) segments with distinct mean values, but whose distributions largely overlap other branch segments in morphospace, such as Segment-1 (circles) and Segment-5 (squares) in Figure 8.2.

Thus, some regions of the colony have a morphology that is different from other parts of the colony, while other regions share a similar morphology even though they might have come from different positions within the colony and grew at different times.

Analysis of variance.—The ANOVA summary (Table 2), confirms that significant differences exist in the mean values among branch segments for each of the three characteristics (p-values $\ll 0.0001$ for each). The F statistics of the apertures along branch (AB) and the apertures diagonally (DB) were similar; however, lateral spacing of zooecia (LB) displayed a significantly larger value for its F statistics (otherwise same parameters, Table 2).

TABLE 1—Descriptive statistics for each branch segment (mm) for the distance between aperture centers along a branch (AB), the distance between aperture centers diagonally across branch (DB), and the lateral distance between zooecia (LB), see Fig. 4.3 for placement of measurements. Abbreviations include the character (Char), average (Ave), standard deviation (SD), coefficient of variation (CV), maximum (Max), minimum (Min), and number of apertures measured (N).

Segment	Char	Ave	SD	CV	Max	Min	N
1	AB	0.436	0.022	5.0	0.485	0.397	29
2	AB	0.418	0.023	5.5	0.483	0.372	30
3	AB	0.400	0.045	11.2	0.474	0.321	17
4	AB	0.385	0.035	9.0	0.465	0.322	25
5	AB	0.432	0.052	11.9	0.521	0.347	16
6	AB	0.386	0.029	7.4	0.443	0.344	23
7	AB	0.429	0.041	9.7	0.528	0.355	26
8	AB	0.363	0.027	7.5	0.421	0.326	20
9	AB	0.400	0.022	5.5	0.441	0.356	21
10	AB	0.389	0.037	9.6	0.467	0.322	24
11	AB	0.393	0.033	8.5	0.449	0.315	19
12	AB	0.405	0.034	8.4	0.464	0.343	26
13	AB	0.393	0.027	6.9	0.449	0.361	18
All	**AB**	**0.403**	**0.038**	**9.5**	**0.528**	**0.315**	**294**
1	DB	0.252	0.015	5.9	0.283	0.217	29
2	DB	0.248	0.019	7.7	0.285	0.211	30
3	DB	0.244	0.023	9.3	0.287	0.196	17
4	DB	0.208	0.026	12.6	0.249	0.160	25
5	DB	0.231	0.036	15.7	0.306	0.161	16
6	DB	0.222	0.018	8.0	0.266	0.193	23
7	DB	0.241	0.020	8.2	0.283	0.206	26
8	DB	0.232	0.017	7.3	0.276	0.211	20
9	DB	0.236	0.023	9.6	0.277	0.197	21
10	DB	0.234	0.020	8.5	0.262	0.188	24
11	DB	0.230	0.022	9.4	0.267	0.196	19
12	DB	0.251	0.028	11.0	0.297	0.208	26
13	DB	0.234	0.017	7.4	0.283	0.205	18
All	**DB**	**0.236**	**0.025**	**10.5**	**0.306**	**0.160**	**294**
1	LB	0.201	0.015	7.6	0.227	0.163	29
2	LB	0.213	0.016	7.5	0.237	0.178	30
3	LB	0.264	0.011	4.3	0.287	0.246	17
4	LB	0.207	0.014	6.6	0.222	0.159	25
5	LB	0.210	0.011	5.4	0.234	0.191	16
6	LB	0.223	0.020	9.1	0.269	0.202	23
7	LB	0.234	0.017	7.4	0.268	0.200	26
8	LB	0.264	0.011	4.2	0.286	0.243	20
9	LB	0.242	0.015	6.0	0.268	0.209	21
10	LB	0.196	0.013	6.4	0.217	0.164	24
11	LB	0.201	0.022	11.0	0.279	0.179	19
12	LB	0.237	0.023	9.7	0.279	0.176	26
13	LB	0.216	0.010	4.6	0.233	0.198	18
All	**LB**	**0.222**	**0.026**	**11.8**	**0.287**	**0.159**	**294**

For the characters AB and DB, the specific branch segment accounted for approximately 21% of the variance, leaving a relatively large proportion unaccounted for in the residual, or within branch segment variation. In contrast, the branch segment accounted for ~66% of the total variance for lateral zooecial spacing (LB). That is, a larger proportion of the variance for LB is accounted for among branch segments than within branches.

A post-hoc comparison of branch segment means for each character supports these observations (Fig. 9), with significant differences among groups for the characters AB and DB (Fig. 9.1, 9.2), but even greater discriminatory value among branch segments for lateral spacing of zooecia (LB, Fig. 9.3).

Evaluating cyclicity within a colony.—Plots of weighted moving averages of standardized data for average aperture spacing (average value of AB and DB) and lateral zooecia spacing (LB, Fig. 10) reveals potential cyclicity in zooecial dimensions through growth series across all segments. Curves appear to either change direction or slope every 3 to 5 generations. Although patterns invite interpretation, they are not regular enough nor are the series of long enough duration to permit quantitative time series analysis.

A non-parametric runs test performed on each segment did not reject the null hypothesis that consecutive positive and negative changes in character dimension through a growth series were random. However, the length of each segment is limited (maximum 30) and longer segments might have approached significance.

A parametric test for serial randomness includes the magnitude of successive differences (the mean square successive difference test), revealed significant deviations from random distributions for many branch segments and for both characters using standardized data (Table 3). For example, significant differences occurred across all three characters in branch Segments 3, 4 and 11 (Table 3; Fig. 10). Lateral zooecia spacing (LB) displayed more non-randomness (potentially cyclicity) than the other two characters, as indicated by significant differences in nine of the 13 segments (Table 3).

When the weighted moving average data were analyzed with mean square successive difference test, all characters were significantly non-random in their growth series (Table 4). Furthermore, 30 of 39 tests were very highly significant at $P \leq 0.0001$. A comparison of Tables 3 and 4 shows that the 1-2-1 weighted moving average enhances the non-randomness of standardized data.

Identifying internal intervals of cyclicity.—Because no absolute time markers can be identified within the colony, the potential durations of cycles of morphological variation (Fig. 10) can be expressed only in units of zooecial generations. Comparison among generations of zooecia (average of absolute values) from successively greater generational intervals (Fig. 7.3) provides graphical information about nearest neighbor effects, cycles within colonies, and overall maximum variation (Fig. 11).

For lateral spacing of zooecia (LB, Fig. 11.1) the average difference between generations increases rapidly from D_1 to D_4. That is, throughout all segments of the colony, adjacent zooecia are more similar in size to each other than they are (on average) to any other zooecia in the colony. This size similarity is true for zooecia two generations apart and even three, and four generations apart. Thus, there is a strong pattern of nearest neighbor similarity is sustained for about four generations.

From comparisons D_4 through D_{10} there is a linear relationship between generational difference and magnitude of average difference between generations (Fig. 11.1). That is, zooecia separated by successively greater generational distances are progressively more different, but diverge at a slower rate, which appears to be constant ($y = 0.024x + 0.04$). The average difference between generations peaks at D_{11} and decreases slightly from D_{12} to D_{14}, reaching a slightly variable plateau at D_{15} to D_{18}. This means that zooecia separated by about 14 generations are actually more similar to each other on average than those separated by 9 to 13 generations. It also means that the colony attains an overall maximal difference (i.e., divergence does not increase indefinitely).

Similar patterns exist in the magnitude of the standard deviation for absolute values of comparisons at successive generational distances (Fig. 11.1). Variation increases rapidly from D_1 to D_4, is relatively constant from D_5 to D_8, increases again from D_9 to D_{11}, and then decreases from D_{11} to D_{16}, and rises again. This means that zooecia differ from each other at about the same amount from D_4 to D_7 as compared to D_9 to D_{11} where they not only have greater, but more variable, differences.

Similar patterns also exist in the average aperture spacing (AB and DB) (Fig. 11.2). This can be summarized as: a rapid

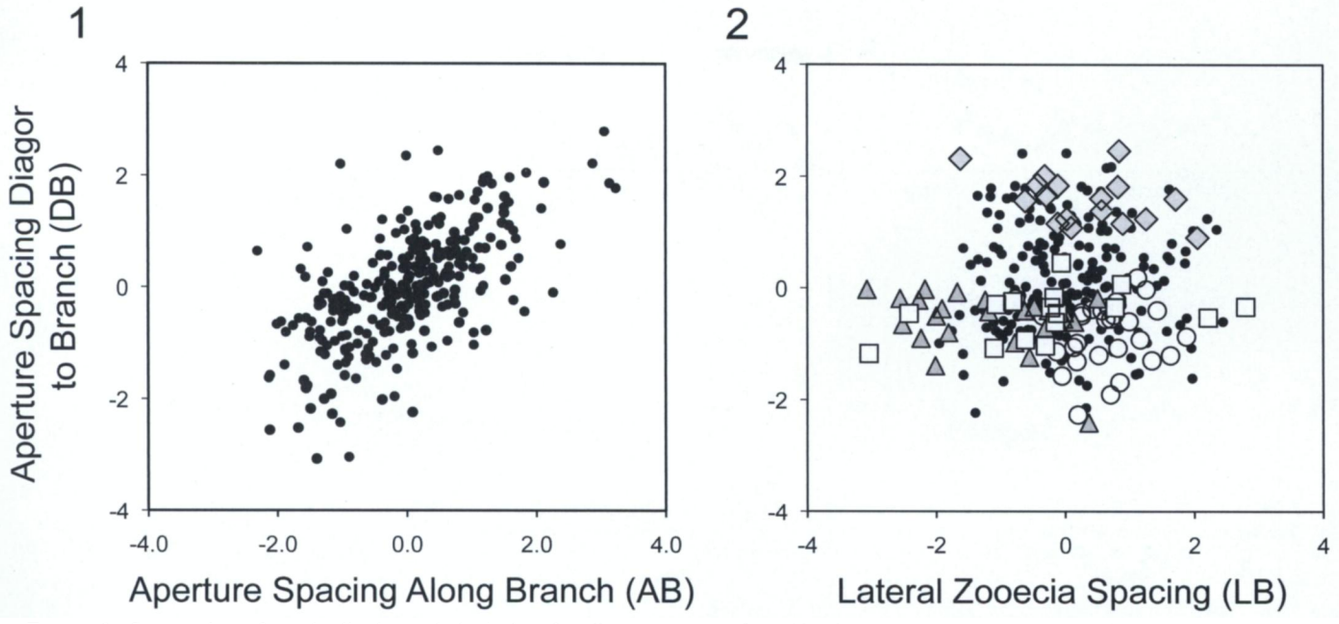

FIGURE 8—Scatter plots of standardized morphologic data for all measurements from 13 colony segments. *1*, aperture spacing along a branch versus diagonal to branch shows a strong positive correlation; *2*, lateral zooecia spacing versus aperture spacing diagonal to branch. Open circles=Segment-1; gray diamonds=Segment-3; open triangles=Segment-5; open squares=Segment-5; and solid small circles=nine other branch segments.

TABLE 2—Summary of one-way analysis of variance testes (ANOVA) among 13 branch segments for AB (aperture centers along branch), DB (diagonal aperture spacing) and LB (lateral zooecia spacing). The abbreviations are character (char), degrees of freedom (df), sum of squares (SoS), Mean squares (Ms), F test-statistic (F), probability that null hypothesis is true (p-value), absolute variance (S^2_A), and the percentage of total variance (%var). See Table 1 for N of each branch segment.

char	Source	df	SoS	Ms	F	P-value	S^2_A	%var
AB	Segments	12	113752	9479	6.61	$p \ll 0.0001$	370.2	20.5
AB	Residual	270	387088	1434			1434.0	79.5
AB	Total	282	500840				1804.2	100.0
DB	Segments	12	47890.5	3990	6.83	$p \ll 0.0001$	156.8	21.2
DB	Residual	270	157723.8	584			584.2	78.84
DB	Total	282	205614.3				741.0	100.0
LB	Segments	12	151374	12614	43.04	$p \ll 0.0001$	567.0	65.9
LB	Residual	270	79140	293			293.0	34.01
LB	Total	282	230514				860.0	100.0

increase in average spacing from D_1 to D_3, a variable plateau from D_4 to D_9, another increase to an overall maximum from D_9 to D_{12}, and finally a decrease from D_{12} to D_{18}. Thus, on average, aperture spacing for zooecia separated by 18 generations are more similar to each other than those separated by three generations. Similar trends are apparent for the variability of generational differences (standard deviation, Fig. 8.2), but three trends of increasing and decreasing variability are present from D_3 to D_{14}.

Potential cycles were identified based on three criteria presented in Table 5 as estimates to the nearest one tenth zooecial generation. Three cycles were identified with an average of 23.3, 9.4 and 5.3 generations per cycle, respectively (Fig. 11).

Estimating absolute scale of cyclicity.—The overall colony length is ~200 mm and the average aperture spacing along a branch is 0.403 mm, which means that there are approximately 500 zooids in the lineal budding sequence along the entire colony length. The duration of the first level cycle was estimated to have been 23.3 generations long (Table 4; Fig. 11). From this we can compare multiple scenarios based on different estimates of the age of the colony. For example if the entire colony grew in one year, the growth rate would be

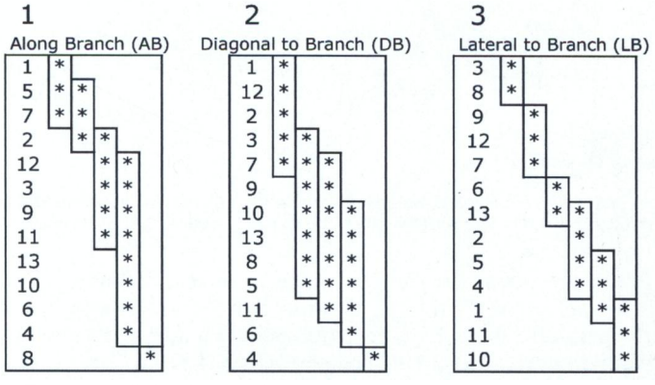

FIGURE 9—Pair-wise post-hoc comparison of means using Student's t. Numbers in columns correspond to branch segment numbers. Shaded bars represent combinations of branch means that are not significantly different at $P \leq 0.05$; *1*, results for aperture spacing along branch (AB); *2*, results for aperture spacing diagonal to branch (DB); and *3*, results for zooecia spacing lateral to branch (LB); see Figure *4.3* for placement of characters.

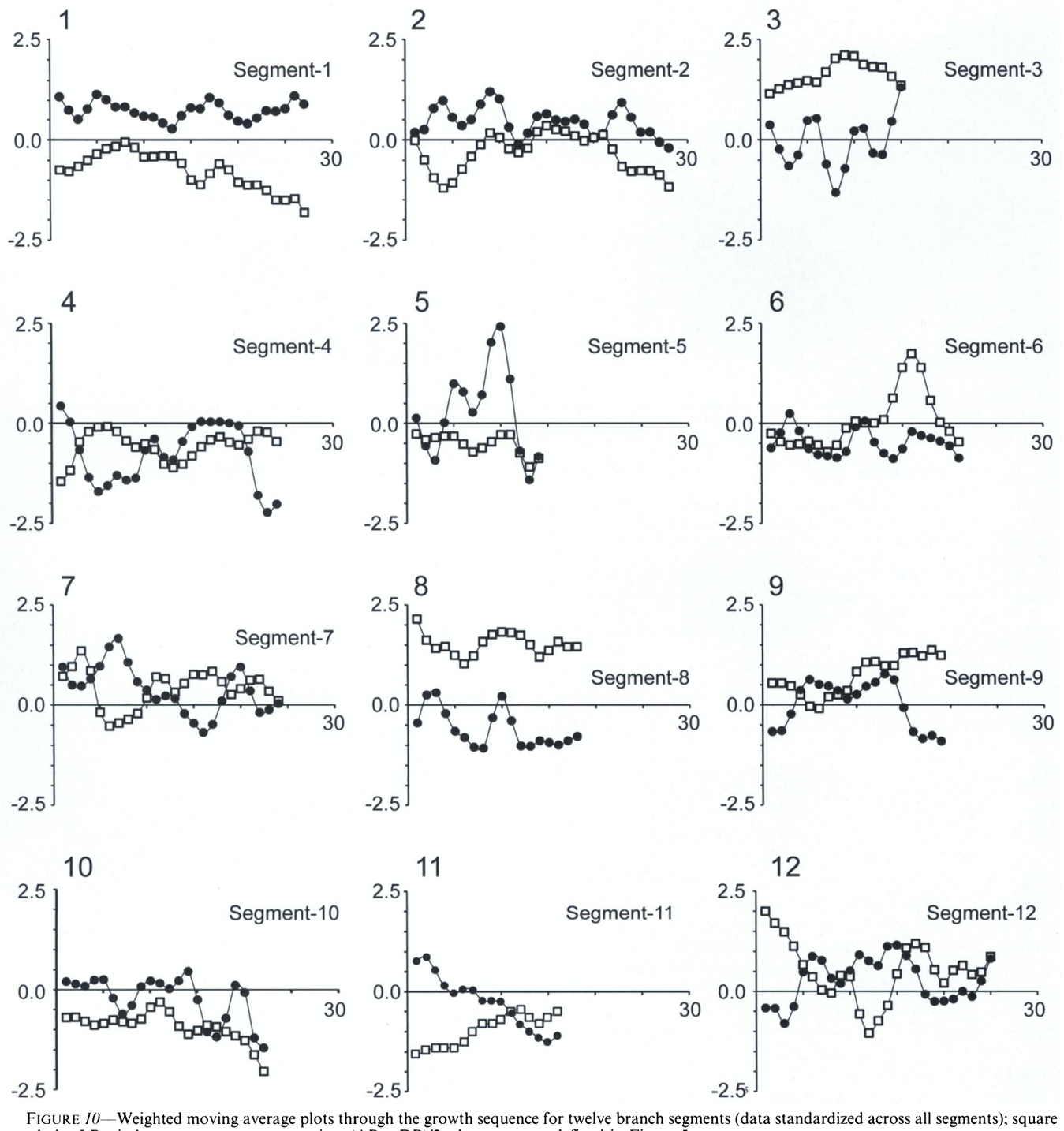

FIGURE *10*—Weighted moving average plots through the growth sequence for twelve branch segments (data standardized across all segments); square symbols=LB; circles=average aperture spacing, (AB + DB)/2; characters are defined in Figure *5*.

200 mm/yr with 500 zooecia budded per year, covering 21.5 first-level cycles (Table 5). Alternatively, if the colony were 10 years old, the calculated parameters would be: 20 mm/yr, 50 zooecia/yr, and 2.1 cycles per year (Table 5). As a final example, if the colony required 50 years to grow, the growth rate=4 mm/yr, 10 zooids/yr, and 0.43 cycles per year or one cycle every 2.33 years (Table 5).

Using these parameters, one can work backwards and estimate the age of the colony and its respective growth rate assuming that the first level cycles were due to either lunar-scale, annual-scale, or ENSO-scale phenomena. Estimates for these values are presented in bold in Table 6.

DISCUSSION

Presence of within colony morphological cycles.—Regardless of whether the environmental driving forces are identified or not, it is important to note that morphological variation in this bryozoan colony is not random, nor is it a simple unidirectional gradient. Any study that incorporates morphological variation (evolutionary, ecological, or systematic) must

TABLE 3—Mean square successive difference test - C values (standardized data). Characters AB, DB, LB defined in Figure 7. Probability levels for critical values (0.05, 0.005 and 0.0005) are indicated by symbols. The number of cases at each probability level is given in parentheses.

Segment	N	AB	DB	LB
1	29	−0.157	−0.281	0.728•••
2	30	−0.064	0.101	0.624•••
3†	17	0.476•	0.528•	0.306•
4†	25	0.620•••	0.646•••	0.591•••
5	16	0.450•	0.517•	0.241
6	23	−0.091	−0.119	0.762•••
7	26	0.247^	0.418•	0.267^
8	20	0.440•	0.287^	0.391•
9	21	0.620•••	0.685•••	0.009
10	24	0.434•	0.225	0.764•••
11†	18	0.834•••	0.476•	0.671•••
12	27	0.274^	0.140	0.605•••
13	18	0.392•	0.218	0.326^

^ approaching significance ($P \leq 0.1$).
• $0.05 \geq P > 0.005$ (11 cases).
•• $0.005 \geq P > 0.0005$ (0 cases).
••• $0.0005 \geq P$ (12 cases).
† all three characters significant for the segment.

consider how potential non-random variation can affect expected results.

Age of colony.—Any interpretation of the causal factors of within colony morphologic cyclicity will be contingent upon an estimate of the age of the colony. In modern bryozoans, more is know about growth rates than about absolute age of colonies (Table 7). In polar settings, the observed growth rates range from ~2.5–10 generations (lineal budded zooecia) per year (Table 7). Typical growth rates in the temperate settings are 15–50 generations per year (Table 7). Growth rates reported for tropical bryozoans are much higher, many consisting of 100 generations per year (Table 7), but reports for tropical bryozoans are for lightly calcified encrusting forms, expected to have a higher growth rate. Growth rates are not known for modern taxa closely most closely related to *Rhombopora*, i.e., erect stenolaemate cyclostome bryozoans.

Based on a sub-storm wave base, tropical setting for this specimen (~4° South, Falcon-Lang, 1999), a reasonable estimate for its growth rate is ~40–80 generations per year (Table 6, e.g., *Cellaria sinuosa, Pentapora foliacea,* and *Pentapora fascialis* not at fresh water seeps). This estimate is based on broad averages and clearly values might differ depending on local conditions. Growth rates of significantly greater than 100 generations per year typical of shallow tropical encrusting forms (Table 7) or less than 10 generations per year typical of cold water forms (Table 7) are unlikely for this setting.

TABLE 4—Mean square successive difference test - C values (weighted moving average of standardized data). Characters AB, DB, LB defined in Figure 7. Probability levels for critical values (0.05, 0.005 and 0.0005) are indicated by symbols. The number of cases at each probability level is given in parentheses.

Segment	N	AB	DB	LB
1†	27	0.640•••	0.569•••	0.926•••
2†	28	0.663•••	0.690•••	0.863•••
3	15	0.486•	0.512•	0.864•••
4†	23	0.814•••	0.836•••	0.748•••
5	14	0.648••	0.712••	0.676••
6	21	0.551••	0.624••	0.872•••
5†	24	0.842•••	0.728•••	0.744•••
8	18	0.727•••	0.579••	0.655••
6†	19	0.816•••	0.869•••	0.920•••
10	22	0.611••	0.781•••	0.873•••
11†	16	0.934•••	0.914•••	0.936•••
12†	25	0.849•••	0.709•••	0.843•••
13	16	0.900•••	0.683••	0.494•

• $0.05 \geq P > 0.005$ (3 cases).
•• $0.005 \geq P > 0.0005$ (9 cases).
••• $0.0005 \geq P$ (30 cases).
† all three characters very highly significant for the segment.

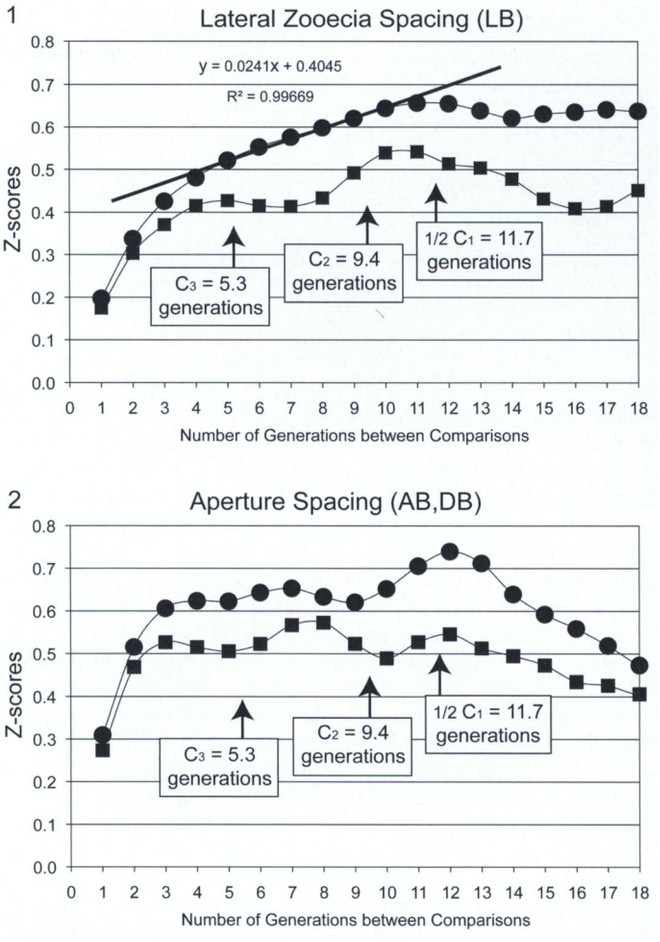

FIGURE 11—Comparison of average differences between characters measured at successively distant generations; circles are averages, squares are standard deviations; *1*, lateral zooecia spacing; *2*, average aperture spacing (AB + DB)/2.

Cause of 1st level cycles in the specimen.—If the 1st level cycles (~23 generations) were driven by lunar, fortnightly, tidal cycles, its growth rate would have been 280 generations per year (Table 6). Even for a tropical erect form this growth rate seems too high. The entire 20 cm tall colony would have grown in less than two years.

If the 1st level cycles were driven by annual cycles, the growth rate would have been 23 generations per year (Table 6). This growth rate is considerably slower than expected for shallow water, encrusting bryozoans but is comparable to growth rates of temperate forms. An annual scale appears reasonable for a sub-tidal habitat and would have required ~22 years to complete colony growth.

If the 1st level cycles were driven by multi-year climate oscillations, such as ENSO, NAO, or SAM (Barnes et al., 2006b) the annual growth rates would have to been much slower. For example if a climate oscillation occurred approximately every four years, the growth rate would be 5.6 generations per year requiring 90 years for colony growth (Table 6).

TABLE 5—Estimation of cycle length based on empirical patterns. Bold=observed values from trends in Figure 8; italic=values calculated (halved or doubled) from observations. Average values of three inferred levels of cyclicity are labeled on Figure 11. Start, end, and cycle duration are all expressed in units of generations (successive zooecia in linear budding sequences).

Character	Trend	Start	End	1/2 cycle	Full cycle	Inferred level
Lateral	Ave. overall maximum	0	11.3	**11.3**	*22.6*	1
Lateral	Ave. inflection to linear	0	4.8	**4.8**	*9.6*	2
Lateral	SD maximum to maximum	4.6	10.5	*2.95*	**5.9**	3
Lateral	SD minimum to minimum	6.7	16.4	*4.85*	**9.7**	2
Aperture	Ave. overall maximum	0	12.0	**12.0**	*24.0*	1
Aperture	Ave. inflection to linear	0	4.0	**4.0**	*8.0*	2
Aperture	SD maximum to maximum	3.0	7.7	*2.35*	**4.7**	3
Aperture	SD minimum to minimum	5.0	15.2	*5.1*	**10.2**	2
	Average			11.65	22.3	1
	Average			4.69	9.4	2
	Average			2.65	5.3	3

The most likely duration for a 1st order cycle of ~23 generations is annual. In a tropical setting the cycle was most likely driven by seasonal monsoons, the evidence for which (same geologic time and setting) have been documented in fossil tree rings (Falcon-Lang, 1999). Variation in zooecia size may be related to the presence or absence of suspended nutrients associated with monsoons (Hageman et al., 2009) or to temperature fluctuations associated with annual upwelling or other major oceanographic currents (O'Dea, 2003).

Cause of 2nd and 3rd level cycles in the specimen.—It is more difficult to constrain the scale of lower level cycles because so little is know about the variability of growth rates within a year. If rates were absolutely constant, then 2nd level cycles (9.4 generations) would be 40% of a year or about 160 days (396 days per year in (Courceyan–Arundian)). Third level cycles (5.3 generations) would comprise 22% of a year or about 90 days. Neither of these values have an apparent celestial or oceanographic driving mechanism. It seems more likely that colonies experienced a time of slower growth and times of more rapid growth associated with the annual events.

TABLE 6—Bracketing values for scale of within colony cyclicity. Known values: colony length (~200 mm), average aperture spacing along branch (0.403 mm), approximate number of zooids (lineal budding sequence) along entire colony length (~500), and 1st level cycle=23.3 generations (zooecia).

Hypothetical age of colony in years	Growth rate mm per year	Lineal zooecia per year	Number of 1st level cycles per year	
1	200.0	500	21.5	
0.56	**111.8**	**280**	**12.0**	**~Lunar scale**
2	100.0	250	10.7	
3	66.7	167	7.2	
4	50.0	125	5.4	
5	40.0	100	4.3	
6	*33.3*	*83*	*3.6*	*range for*
7	*28.6*	*71*	*3.1*	*temperate*
8	*25.0*	*63*	*2.7*	*modern, erect*
9	*22.2*	*56*	*2.4*	*cheilostome*
10	*20.0*	*50*	*2.1*	*bryozoans*
12	16.7	42	1.8	*(Table 7)*
14	14.3	36	1.5	
16	12.5	31	1.3	
18	11.1	28	1.2	
20	10.0	25	1.1	
22.3	**9.0**	**23.3**	**1.00**	**~Annual scale**
25	8.0	20.0	0.86	
30	6.7	16.7	0.72	
35	5.7	14.3	0.61	
40	5.0	12.5	0.54	
50	4.0	10.0	0.43	
60	3.3	8.3	0.36	
90	**2.2**	**5.6**	**0.24**	**~ENSO scale**
120	1.7	4.2	0.18	

We suggest that the 3rd level cycles might represent fortnightly lunar tidal cycles, which could have influenced suspended nutrient concentrations. This scale is proposed because a diurnal scale would require multiple generations per day, which is not supported by other growth rate estimates. The 2nd level cycles (9.4 generations) may reflect an offset 3rd level cycle (i.e., harmonics) or may represent and average of multiple climatic evens within the year (e.g., major storm events).

Possible morphological cycles from previous studies.—Earlier studies of morphological variation that occurs during growth in bryozoans each display trends consistent with the calendar scale of cyclicity observed in this study. Elias (1964, plate 1, fig. 2) meticulously documented variation in fenestrule length across a large frond by color-coding a map of the specimen. Cycles of large and small fenestrules are evident at the scale of about six fenestrules. Schopf (1976) documented zooecial sizes in the growth of the living deep sea bryozoan *Euginoma* sp. Its opesial width displays possible cyclicity at the scale of about eight zooecia in a series (Schopf, 1976, fig. 4). In a study of the encrusting runner-like Jurassic bryozoan *Stomatopora* (Cyclostomata) Taylor and Furness (1978, fig. 3) illustrated potential cycles in zooecial size within both the zones of astogenetic change and astogenetic repetition. Hageman (1995, fig. 4) documented variation in six morphologic characters (canonical variate analysis) through growth transects of four late Paleozoic colonies of *Streblotrypa* (Rhabdomesina) and suggested that lunar cycles were present (eight serial zooecia). O'Dea and Jackson (2002, figs. 4, 5) illustrated potential cycles in zooecial size (area) through growth transects of modern, free-living bryozoans *Cupuladria* and *Discoporella*. The potential cyclic signal is more pronounced in specimens from the Gulf of Panama (Pacific) than at Bocas del Toro (Caribbean) and is on the scale of eight serial zooecia. Each of these examples would require detailed study to document the presence of non-random variation in the form of cyclicity, but they serve as guides for the potential broader significance of patterns documented in this study.

Patterns of within colony variation (patchiness of similar and varied morphologies) observed by Holdener and Hageman (1998) in a large late Paleozoic fenestrate bryozoan by Hageman and Sawyer (2006) in trepostome bryozoan colonies, and by Hageman et al. (2002) in modern cheilostome bryozoans are consistent with the pattern and scale of morphologic cyclicity observed in this study.

Potential cycles have also been observed at the scale of skeletal growth within individual zooecia. Tavener-Smith (1969) suggested that crystallites in the lamellar skeleton of stenolaemate bryozoans formed at a diurnal scale and as a result, permitting estimates of specimen age in days by

TABLE 7—Summary of modern bryozoan growth rates (mm/yr) taken from the literature. Polar: mean (4.83), median (4.35), minimum and (2.63), maximum (11.70). Zooecium lengths are from Hayward (1995) except Winston (1983). Temperate: mean (35), median (33), minimum (13), maximum (1,125). Zooecium length from Hayward and Ryland (1998) except Smith et al. (2001) and Pätzold et al. (1987). Tropical: mean (250), median (180), minimum (56), maximum (600). Zooecium length from Osborn (1940) except *Membranipora*=for genus. Colony forms erect (eR) and encrusting (eN).

Taxa	Growth mm/yr	Max. age	Growth rate source	Zooecia length mm	Generations/year	Colony form
Polar						
Cellarinella foveolata	5.0	12	Winston (1983)	1.4	3.57	eR
Cellarinella margueritae	3.4	15	Barnes et al. (2007)	1.4	2.43	eR
Cellarinella margueritae	5.6	10	Winston (1983)	1.4	4.00	eR
Cellarinella njegovanae	4.4	18	Winston (1983)	1.0–1.4	3.14–4.4	eR
Cellarinella nodulata	5.2	14	Barnes et al. (2007)	1.6	3.25	eR
Cellarinella nodulata	4.4	11	Winston (1983)	1.6	2.75	eR
Cellarinella nutti	3.4	23	Barnes et al. (2006a)	1.0	3.44	eR
Cellarinella nutti	5.2	11	Winston (1983)	1.0	5.18	eR
Cellarinella rogickae	4.6	15	Barnes et al. (2007)	1.0	4.60	eR
Cellarinella rossi	4.3	14	Winston (1983)	0.8–1.0	4.30–5.36	eR
Cellarinella sp. M	5.4	20	Winston (1983)	0.75	7.20	eR
Cellarinella watersi	4.1	11	Barnes et al. (2007)	1.4	2.93	eR
Cellarinella watersi	5.0	9	Barnes (1995)	1.4	3.57	eR
Cellaria incula	8.2	14	Brey et al. (1999)	0.7–0.8	10.25–11.7	eR
Melicerita obliqua	4.9	32	Barnes et al. (2007)	0.9	4.9	eR
Melicerita obliqua	3.0	22	Winston (1983)	0.9	3.0	eR
Melicerita obliqua	4.5	45	Brey et al. (1998)	0.9	4.5	eR
Melicerita obliqua	1.25–8.09	45	Bader and Schäfer (2004)	1.04	2–10	eR
Stomhypselosaria watersi	4.5	15	Barnes et al. (2007)	0.75–0.85	5.7–6.0	eR
Temperate						
Adeonellopsis sp. (total)	6.9	20	Smith et al. (2001)	0.5	13.8	eR
Adeonellopsis sp. (summer/fall)	10.4	20	Smith et al. (2001)	0.5	20.8	eR
Adeonellopsis sp. (winter/spring)	3.6	20	Smith et al. (2001)	0.5	7.2	eR
Cellaria sinuosa	40	1.5	Bader (2000)	0.5	80	eR
Pentapora fascialis	2–980	•	Cocito et al. (2006)	0.7–0.9	1,125	eR
Pentapora foliacea	20	10	Pätzold et al. (1987)	0.8–0.9	33.3–40	eR
Pentapora fascialis	30.5–35.9	•	Cocito and Ferdeghini (1998)	0.7–0.9	33.9–51.3	eR
Pentapora fascialis	20.7–29.3	•	Lombardi et al. (2006)	0.7–0.9	23.0–41.9	eR
Flustra foliacea	12	12	Stebbing (1971)	0.4	30	eR
Tropical						
Electra bengalensis	239.0	•	Udhayakumar and Karande (1989)	0.4	597.6	En
Acanthodesia sp.	59.1	•	Udhayakumar and Karande (1989)	0.5	118.2	En
Membranipora annae	208.5	•	Udhayakumar and Karande (1989)	0.5	416.9	En
Membranipora tenuis	133.8	•	Udhayakumar and Karande (1989)	0.5	267.6	En
Membranipora savartii	92.1	•	Udhayakumar and Karande (1989)	0.5	184.2	En
Hippoporina indica	59.1	•	Udhayakumar and Karande (1989)	0.45	131.4	En
Hippopodina feegeensis	38.1	•	Udhayakumar and Karande (1989)	0.68	56.1	En

counting laminae. Tavener-Smith (1969) illustrated this in specimens of the modern cyclostome *Hornera*, and Newton (1971) applied the concept to estimate that a Paleozoic specimen of *Rhombopora* lived approximately 325–380 days. This estimate may be reasonable for the active growth of a particular section of the colony, but may not represent the age of an entire colony. In large colonies, proximal regions often reach a terminal size, become dormant, or are even non-living. Other cycles in skeletal microstructure or zooecial level structures have been proposed for bead-like swellings in the walls of *Tabulipora* (Bartley and Anstey, 1987), and for cystiphragm deposition in *Peronopora* (Hickey, 1987), all possibly associated with fortnightly lunar cycles. Repeated endozone-exozone couplets in *Peronopora* may represent annual cycles (Hickey, 1987). It is likely that all of the features discussed above reflect cycles of the same scale as those observed in this study.

Implications for future studies.—The potential presence of calendar scale cycles within bryozoan colonies highlights the importance of avoiding small fragments or making clustered measurements within larger colonies, as proxies for characterizing colony wide morphologic variation (Hageman et al., 2002). Zooecia-level morphologic data should be collected randomly across the entire extent of available skeletal material. This is true whether the purpose be for systematics and taxonomy, for studies of rates of microevolution (Cheetham et al., 1993, 1995), or for ecological analysis such as MART (O'Dea and Okamura, 2000). The nearest neighbor effects documented here (Figs. 10, 11) and in previous studies (Hageman, 1995; Holdener and Hageman, 1998; Hageman et al., 2002; Hageman and Sawyer, 2006; Hageman et al., 2009) means that morphologic data collected from adjacent or nearby zooecia are biased and underestimate the total within colony variance.

It may be possible to analyze systematic geochemical variation within the skeleton during colony growth, e.g., Mg concentrations, to determine growth rates and to test the hypotheses such as the 23.3 zooecia per annum in this specimen.

SUMMARY

A large well-preserved single colony of *Rhombopora blakei* n. sp. (Bryozoa, Rhabdomesina) from the Hook Head Formation, Tournaisian Stage, Mississippian of southeastern Ireland, provides an opportunity to evaluate within colony variation associated with environmental change over the scale of days to decades. Three external skeletal characters associated with aperture spacing and zooecial size exhibit non-random variation within the colony.

Strong nearest neighbor effects are evident and potentially cyclic variation is evident at three scales: approximately every 23.3, 9.4 and 5.3 zooecia in a budded series. Based on known growth rates of modern bryozoans, the most likely scale of the cycles is annual for the first level (23.3 zooecia) and lunar/tidal for the third level (5.3 zooecia). Assuming that these cycles are appropriate, the large colony would have been approximately 20 years old at time of death. Similar scales of cyclicity have been proposed, but not tested statistically, in other studies of within colony variation.

Results have implications for taxonomic, evolutionary, and ecological studies based on within colony morphologic variation. Clustered measurements within a colony (or colony fragment) under estimate total within colony variation. Although it is unlikely that calendar scale variation within a single bryozoan colony can provide for high resolution documentation of environmental variation on the scale of a precise time-series, the study and application systematic variation within colonies shows promise in reconstructing paleoenvironments and their changes through relatively short time intervals.

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