



# The Last Phylum: Occupation Of Bryozoa Morpho-Ecospace (Colony Growth Habits) During The Early Phase Of The Great Ordovician Biodiversification Event

By: **Steven J. Hageman** and Andrej Ernst

## Abstract

Most major phyla, and all skeletonized phyla have their first appearance in the Cambrian. The exception is the Phylum Bryozoa, which first appear in the Early Ordovician (Tremadocian 1b). Bryozoans have an excellent fossil record, due in part to their benthic marine habitat with skeletal colonies composed largely of stable, low-Magnesium calcite. These factors provide an unrivaled opportunity to observe patterns and rates of radiation of a new phylum into disparate morpho- ecospace through the Great Ordovician Biodiversification Event (GOBE). In this study, the colonial growth habits of all known skeletonized Bryozoa (181 species) from the Early and Middle Ordovician are characterized in a new classification scheme based on processes of growth, rather than their end geometry as most traditional classifications of bryozoan growth habits. These fundamental categories are: orientation, dimensions of primary growth, width of colony unit, layers of zooecia, substrate relationships, space utilization, skeleton mineralization, plus sub-categories of orientation based on their geometry. In the Early and Middle Ordovician there are 85 unique growth habits defined by these eight growth habit characters. By the end of Middle Ordovician, about 4.8% of the morpho-ecospace defined by two subsets of the characters had been occupied by five bryozoan orders (represented by 34 families, 77 genera). When plotted by Ordovician stage time-slices (ca. 2.2 my each), a sharp increase in taxonomic and growth habit occurrence is observed at the Early-Middle Ordovician transition, earlier than in other groups. Individual growth habit character states also show significant changes at this transition. In the Early Ordovician, low bryozoan taxonomic and growth habit richness is due in part to sampling bias and modified search methods are needed, however, the overall patterns (Early-Mid. Ordovician transition) observed in this study are robust and not expected to change fundamentally with additional data.

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# The last phylum: Occupation of Bryozoa morpho-ecospace (colony growth habits) during the early phase of the Great Ordovician Biodiversification Event

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## ABSTRACT

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### Keywords:

Bryozoan  
GOBE  
Biological radiation  
Colonial growth form  
Paleoecology  
Tremadocian  
Floian  
Dapingian  
Darriwilian

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In this study, the colonial growth habits of all known skeletonized Bryozoa (181 species) from the Early and Middle Ordovician are characterized in a new classification scheme based on processes of growth, rather than their end geometry as most traditional classifications of bryozoan growth habits. These fundamental categories are: orientation, dimensions of primary growth, width of colony unit, layers of zooecia, substrate relationships, space utilization, skeleton mineralization, plus sub-categories of orientation based on their geometry.

In the Early and Middle Ordovician there are 85 unique growth habits defined by these eight growth habit characters. By the end of Middle Ordovician, about 4.8% of the morpho-ecospace defined by two subsets of the characters had been occupied by five bryozoan orders (represented by 34 families, 77 genera). When plotted by Ordovician stage time-slices (ca. 2.2 my each), a sharp increase in taxonomic and growth habit occurrence is observed at the Early-Middle Ordovician transition, earlier than in other groups. Individual growth habit character states also show significant changes at this transition. In the Early Ordovician, low bryozoan taxonomic and growth habit richness is due in part to sampling bias and modified search methods are needed, however, the overall patterns (Early-Mid. Ordovician transition) observed in this study are robust and not expected to change fundamentally with additional data.

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## 1. Introduction

The phylum Bryozoa has its first appearance in the Early Ordovician (Tremadocian, time-slice 1b) (Ma et al., 2015; Ma et al., 2018), the last major phylum to appear in the fossil record (Taylor and Larwood, 1990). Reports of late Cambrian bryozoans (e.g., Landing et al., 2010) have not been demonstrated as bone fide members of the phylum (Taylor et al., 2013; Ma et al., 2015; Hageman, 2018) and are not considered in this study.

With the first record and subsequent diversification of Ordovician Bryozoa, a special opportunity exists to track not only species and higher-level taxonomic diversity through their initial radiation, but also to track their exploitation and exploration of new or unoccupied life-modes (morpho-ecospace) by tracking the appearance of fundamental

growth habit character states through time. This opportunity is made possible by the combination of 1) global and abundant shallow marine sediments of the Ordovician, 2) the concurrent timing of the diversification within many other higher invertebrate clades during the Great Ordovician Biodiversification Event (GOBE) and 3) Bryozoa's excellent fossil record, due to the stable mineral chemistry of their skeleton (low-Mg calcite).

Bryozoan growth habits, or colony forms, are phylogenetically constrained in many groups and phenotypically plastic in others. The many relationships among environmental factors and the distributions of bryozoan species (i.e., their concomitant growth habits) allows for paleoenvironmental analyses based on the occurrence of bryozoan colonial growth habits. There is a high degree of convergence and iterative evolution of bryozoan growth habit states, which necessitates the

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study of the modules (zooecia) for species-level identifications. Nevertheless, fundamental growth habit character states require an evolutionary development, often derived independently through time and space, with certain, fundamental morphogenetic processes = growth habit character states.

This study builds of the work of Taylor and Ernst (2004) and Ernst (2018), which were studies that documented the species and generic diversity of the bryozoans through the entire Ordovician. The goal of the present study is to document any patterns or trends in the early diversification of Bryozoa at the resolution of Ordovician time-slices (ca. 2.2 Myr intervals), and specifically to document any 1) times of change in frequencies of occurrence and 2) any relationships among the appearance of fundamental growth habit character states (processes) and taxonomic richness and 3) to document the occupation of subsets of morpho-ecospace through time, and finally 4) to compare any recognized patterns with trend in other biotic and physical systems through the same interval.

## 2. Materials and methods

### 2.1. Stratigraphy, distribution and resolution

The time scale of the International Commission on Stratigraphy (v2018.08) is used for global Ordovician stages and their age dates. Twelve Early-Middle Ordovician time-slices from Webby et al. (2004) based conodont and graptolite zones are used for this study. Data are plotted using the mean numerical age (mid-point) of time-slice boundaries, which were estimated from age dates of stage boundaries, divided by the number of time-slices per interval. Because time slice boundaries are biostratigraphically based, they are of unequal duration, resulting in a mean time-slice duration of 2.19 million years (Myr), range 2.97–1.35 Myr, standard deviation 0.54 Myr. The average time-slice step of 2.2 million years per data point is adequate to capture trends in Early to Middle bryozoan macroevolution.

#### 2.1.1. North American “Middle Ordovician” correlation issues

Prior to the early 2000s many wide spread North American lithostratigraphic units such as the Trenton Group, Martinsburg Formation, Decorah Shale, Ottossee Formation were correlated globally with the Middle Ordovician (e.g., Twenhofel, 1938; Ross, 1963, 1984; Karklins, 1983a). Based on chemostratigraphy of bentonites and revised biostratigraphic correlation (Bergström et al., 2004), many of these units are now correlated globally with Late Ordovician (Sandbian, or even Katian) or straddle the Middle-Upper Ordovician boundary (Leslie and Lehnert, 2005).

The primary bryozoan systematics literature prior to 2000, and summaries derived from them, e.g., Treatise (Bassler, 1953; Blake, 1983; Karklins, 1983b; Utgaard, 1983), and data in the Paleobiology Database (PDB), report the abundant bryozoan faunas from these and other units as “Middle Ordovician.” Every attempt was made to correct data for this study, but future correction of range data for impacted taxa, especially in digital databases needs to be addressed for all taxa to ensure comparable North American data with global correlation.

### 2.2. Bryozoan species list

A list of global occurrences for Early and Middle Ordovician bryozoan species was generated using six sources. 1). The primary list of bryozoan species is from author A. Ernst, which was compiled from primary data from museum specimens in European collections and summarized at the genus level in Taylor and Ernst (2004) and Ernst (2018). 2). This was supplemented from a list of Baltic Ordovician occurrences compiled by fossilid.info, Paleobiodiversity in Baltoscandia. 3). A combined list of species was generated from PDBD/Fossilworks, which aided with North American taxa, but also contained a number of erroneous entries. 4). Species occurrences were checked with

Bryozoa.net and Bryozone.org. 5). Taxonomic lists with ranges, from Bassler (1953), Astrova (1965), Utgaard (1983), Karklins (1983b) and Blake (1983). Species lists with stratigraphic occurrences from all of these sources were combined into a single data set (Supplemental Data), with the goal resolving synonymies and any discrepancies in stratigraphic ranges. 6). In addition, newly described species from recent, primary literature were added to the list. The few ctenostome bryozoans known from the Early and Middle Ordovician are not included in this analysis because they are endolithic and unskeletonized (Larwood et al., 1979).

### 2.3. Bryozoan growth habit characterization

The scheme used here to characterize bryozoan growth habits is novel in that its expressed goal is to categorize life mode strategies based on features known to be important to the ecology of individual colonies. Although previous bryozoan growth habit schemes had the goal of (paleo)environmental inference (e.g., Stach, 1936; Schopf, 1969; Nelson et al., 1988), most begin by characterizing the resulting geometric form of the colony, which often results in an indirect assessment of undifferentiated life mode characteristics and processes of growth. Although many of the character states employed in this scheme of the current study are the same as those Hageman et al. (1998), the two schemes differ philosophically. Hageman et al. (1998) attempted to create a morpho-ecospace based on character states for all member of the phylum Bryozoa, which although widely cited and technically viable (Hageman et al., 2013), for a variety of reasons has not been applied widely in case studies. The scheme employed in the current study was built first from seven fundamental categories, shared by all bryozoans. The combination of these categories in manageable groups of two or three at a time results in morpho-ecological sub-space that are recognizable geometries for users, but yet allow for partitioning and broader analysis of the fundamental biological processes of growth and feeding.

The character state options for the fundamental categories listed below are provided in Fig. 1. A detailed definition, explanation and rationalization of the character states will be treated in another paper, but the fundamental biological processes involved should be evident in the descriptions below to students of bryozoan ecology.

Orientation: relates to colonies position relative to substrate-water boundary flow layers, encrusting = paralleling a surface, massive = mounding above it, or erect = growing away from it perpendicularly (see themes in Vogel, 1996).

Dimensions of growth: the primary dimensions of growth of the propagating colony front can be linear (1-D), as a runner, branch or lobe, two dimensional as spot, disk or sheet or in three dimensions as a 3-D object (Boardman and Cheetham, 1969; Hageman et al., 1998).

Width of colony unit: the hydrodynamics of bryozoan suspension feeding is greatly affected by the width of the colony unit (McKinney, 1986). In narrow colonies of three or fewer zooids across, water can pass by uninhibited, in intermediate sized colonies (approximately 4 to 13 zooids across) waste water can be expelled at the colony edges. Broader colonies require some coordinated system of excurrent chimneys, which may or may not be reflected in the skeleton of the colony (Banta et al., 1974; Cook, 1977).

Layers of zooecia: the budding pattern of bryozoan colonies provides constraints on the overall colony form and in some cases in phylogenetically controlled. This includes both the number and orientation of zooecial layers and also the degree of colonial coordination, e.g., colony wide growth of a new layer, versus uncoordinated eruption of individual zooids.

Substrate relationships: the presence of a firm substrate is required for the successful settlement and metamorphosis of all bryozoan larvae. Some bryozoans are restricted to growth with their primary exterior cuticular wall always in contact with a hard/firm substrate. Other forms can separate the primary external wall from the substrate, growing over

Fundamental Characters*	Character States* (code)	Definition	Notes
<b>Orientation</b> relative to substrate: position of active colony feeding layer relative to substrate-water boundary flow layers.	<b>encrusting</b> (1)	parallels substrate	independent of colony geometry, attachment or substrate type or number of layers
	<b>massive</b> (2)	mounds above substrate	
	<b>erect</b> (3)	extends away from substrate	
<b>Dimensions</b> of growth: primary direction(s) of colony growth.	<b>one-dimension</b> (1)	linear (branch)	independent of bifurcations
	<b>two-dimensions</b> (2)	area (sheet)	
	<b>three-dimensions</b> (3)	primary object	
<b>Width</b> of colony unit: Feeding currents necessitated by width of the colony, branch, or cornidia	<b>narrow</b> colony unit width (1)	1-3 zooecia wide (uni-, bi-, tri- serial)	independent of skeletal monticules or maculae
	<b>mid-width</b> colony unit (2)	4-12 zooecia wide (oligo-serial)	
	<b>wide</b> colony unity (3)	13 or more zooecia wide (macro-serial)	
<b>Layers</b> of zooecia: Number of layers and style of zooecial budding (growth).	<b>unilaminar</b> (1)	single layer, including primary, exterior wall or not	in addition, the relative position of primary, external wall should be noted
	<b>bilaminar</b> (2)	two layers, with back to back primary, exterior walls or not	
	<b>radial</b> (3)	radially budded from central axis	
	multilaminar, <b>self-overgrowth</b> (4)	colony thickens by layers of zooecia with exterior (primary) walls between each layer	
	multilaminar, <b>limited frontal</b> budding (5)	colony thickens by a limited number of frontally budded or elongation of zooecia	
	multilaminar, <b>coordinated vertical</b> budding (6)	colony thickens by addition of multiple layers or elongation of zooecia	
	multilaminar, <b>individual vertical</b> budding (7)	colony thickens by haphazard addition of many individual zooecia	
<b>Substrate</b> relationships: Relationship of the primary, exterior wall to the initial, firm substrate on which the ancestrula formed	<b>restricted</b> (1)	primary, exterior wall restricted to firm, primary substrate	does not grow beyond initial substrate, also includes bases for many erect cemented forms and all endolithic forms
	<b>escaped</b> (2)	primary, exterior wall can grow beyond or above firm, primary substrate	escaped portion typically with wrinkled underside
	<b>articulated</b> (3)	mineralized, attached basal holdfast with articulated colony attachment	ball and socket form
	<b>rooted</b> (4)	attached by heterozoid(s), mineralized or not	cuticular heterozoids may include skeletal internodes
	<b>regenerated</b> or budded (5)	asexually budded from a previous colony	without ancestrula
<b>Space</b> utilization: Relationship of colony perimeter to area or volume	<b>occupies</b> (1)	smooth colony perimeter	if colony is not mature, note developmental stage
	<b>mixed-use</b> (2)	generally irregular or uneven colony perimeter	
	<b>explores</b> (3)	colony extensions result in very irregular perimeter	
	<b>backfills</b> (4)	initial irregular perimeter, filled by secondary growth	
	<b>fuses</b> (5)	through growth, intra-colony units meet and fuse	
<b>Skeleton</b> mineralization	<b>unmineralized</b> (1)	only cuticle or soft tissue	independent of skeletal composition
	<b>lightly</b> mineralized (2)	flexible, lightly mineralized	
	<b>primary</b> mineralization (3)	single layer of primary skeleton	
	<b>secondary</b> mineralization (4)	skeleton thickened with secondary mineral layers	
	<b>colony-wide</b> mineralized structures (5)	significant, extra-zooecial skeleton	

\*abbreviated name for each in bold

**Fig. 1.** Categories and character states for seven fundamental growth form processes with their numerical codes. For example, a unique growth habit code of 1-2-2-1-1-1-3 represents a colony that is encrusting (parallel to substrate), 2-dimensional (sheet), mid-width (3–12 zooecia wide), unilaminar (single layer of zooecia), with primary wall restricted to its substrate, with a growth strategy that occupies space with a skeleton of primary mineralization only.

or above it.

**Space utilization:** Although not a physiological constraint, the ratio of the volume of the colony versus its surface area plays a fundamental role in how the colony occupies and uses space. End-point ecological strategies can be inferred, e.g., colonies with smooth, versus jagged outlies/surfaces and twiggy versus bushy arborescent forms.

**Skeleton mineralization:** the presence, robustness and amount of skeleton that bryozoans generate can play an important role in which overall colony forms are possible. This ranges from no mineralized skeleton to lightly and typically mineralized primary skeleton, so secondary thickening of exterior walls, to the generation of colony wide zoarial structures.

Within each of the three character states of “Orientation”, subcategories of geometric form can be designated that are commonly observed in nature. In principle, “Orientation and Geometry” could be combined into a single category, but they are kept separate in this scheme for three reasons, 1). to keep the fundamental categories simple and more direct for analysis, 2). subcategories are dependent on (can only be applied to) their parent category and thus they are not fundamental features, and 3). subcategories of geometry break from the goal of classifying *processes* rather than resulting states. Geometry states do prove useful in description and interpretation of growth habits, so they are retained as an eighth category, but are not analyzed in this study.

Undoubtedly such an approach may be required for specific faunas that could benefit from additional subdivisions, such as the many styles of root attachments in modern forms. Subcategories of “Encrusting” are based on the zooidal budding parameters of Lidgard (1985), Lidgard and Jackson (1989), which were recognized as important for colonial growth habit distributions among micro-environments by Hageman et al. (2013). Subcategories of “Massive” are based on colony width to height ratios. “Erect” sub-categories are first divided by their primary growth dimension, branch (1-D), sheet (2-D) or object (3-D). These are further subdivided as follows, “radial branches” by the nature of their central axes, “non-radial branches” and “sheets” by the curvature of their surfaces, and “3-D objects” by their overall shape. Many examples of the Geometry category are illustrated in Hageman et al. (1998).

The character states and numerical codes for “Geometry” are as follows: 1.1) encrusting intrazoooidal budding, 1.2) encrusting zooidal budding, 1.3) encrusting multizoooidal budding; 2.1) massive (medial < lateral) disk, low dome, 2.2) massive dome to hemisphere, 2.3) massive, high dome to cone, 2.4) massive ellipse-spheroid, 2.5) massive nodule, irregular, 2.6) massive, fungiform; 3.1) erect radial branch, no central axis, 3.2) erect radial branch, solid axis (variable), 3.3) erect radial branch, hollow axis (extracolony), 3.4) erect radial branch, skeletal axial (endo)zone; 4.1) erect non-radial branch, flat surface, 4.2) erect non-radial branch, angular surface, 4.3) erect non-

radial branch, curved surface; 5.1) erect sheet, flat surface, 5.2) erect sheet, curved surface, 6.1) erect, turbinate, 6.2) erect, ellipse-spheroid, 6.3) erect, irregular nodule.

This method allows for recognition of multiple growth habits for a single species, designated in this data set as “*species name* GH1”, “*species name* GH2”, etc. An example of a growth habit code in this scheme: (3, 2, 3) (2, 1, 1, 3) (5.1) = (erect, 2-dimensions of growth, wide) (bilaminar, restricted to substrate, occupies its space, with primary skeleton only; and a geometry of a flat erect sheet). An abbreviation for the full eight fundamental categories to aid in recall is:

(O, D, W) (L, Su, Sp) (Sk, G)

In some analyses it is useful to consider subsets of morpho-ecospace (fundamental categories). Two subsets are used here, 1) Orientation-Dimensions-Width and 2) Layers-Substrate-Space (Fig. 1). The unique combination of three character states within the subset of categories is considered a “form”, e.g. encrusting, 1-dimensional, un-laminar = form 1-1-1.

#### 2.4. Data collection, robustness and potential biases

Each entry in the dataset (Supplementary data) is an occurrence of a species (and growth habit if variable for a species), within one Ordovician stage time-slice. Ideally, each occurrence datum in this study is based on four items: 1) species name (and unique growth habit number if variable within species), 2) lithostratigraphic unit, 3) biozone (typically conodont or graptolite) and 4) regional stage or other stratigraphic information. No specimen abundance or biomass estimations are included. When available, information for geographic distributions and lithostratigraphy are included in the data set for future analyses, but were not used in this study. Occurrence data for bryozoan species were derived from the literature of primary taxonomic descriptions, supplemented by synthesis papers that provided credible species assemblage lists, ranges, and geographic distributions. The bibliography of sources used to construct the data set range from the early 19th Century to the present (Supplementary data).

Primary, historical stratigraphic information was correlated with global time-slices (Webby et al., 2004) in several ways, listed from most accurate to least: 1) use of biostratigraphic data based on definition of time-slices. Correlation of secondary taxa was not attempted; 2) assignment of a lithostratigraphic unit to a time-slice based on published work from other authors; 3) correlation of position within regional

stages with equivalent global stages (time-slices). Information for the fundamental growth habit category states were coded from 40 primary literature sources, each from either original or secondary species descriptions and illustrations.

The resulting data set (Supplemental data) is based on the whole of known, global information of bryozoan species occurrence in the E-M Ordovician, so it is only biased by the entirety of our collective knowledge and not the limitations of single data set. Although we believe that the global patterns presented here are robust enough for a first and meaningful analysis, we acknowledge the possible presence of the following biases: 1) due to outcrop exposure, fossil abundance and historical concentration, data are disproportionately, but not nearly exclusively, from Baltoscandia and North America. 2) Related to the previous, monographic biases concentrate our knowledge on these geographic areas. 3) A potential lithofacies contrast between the Early and Middle Ordovician may influence the distribution and preservation of Bryozoa.

##### 2.4.1. Use of non-normalized data

A well-known concern in the analysis of taxonomic occurrence (diversity) curves is the bias that is introduced by differential sampling efforts (Raup, 1975; Cooper et al., 2004; Taylor and Ernst, 2004; Alroy et al., 2008; Servais et al., 2010; Kröger and Lintulaakso, 2017). In diversity studies through time it is important to normalize observed frequencies by accounting for sample size and edge effects in taxonomic ranges (Sepkoski, 1975; Cooper et al., 2004). The primary goal of the current study is to characterize and compare the growth habit characteristics with the relative frequency abundance of the taxa from which they were observed and therefore data are not normalized. Any formal comparison of these data to measures of diversity will require their normalization *sensu* Cooper et al. (2004).

#### 2.5. Methods for analysis

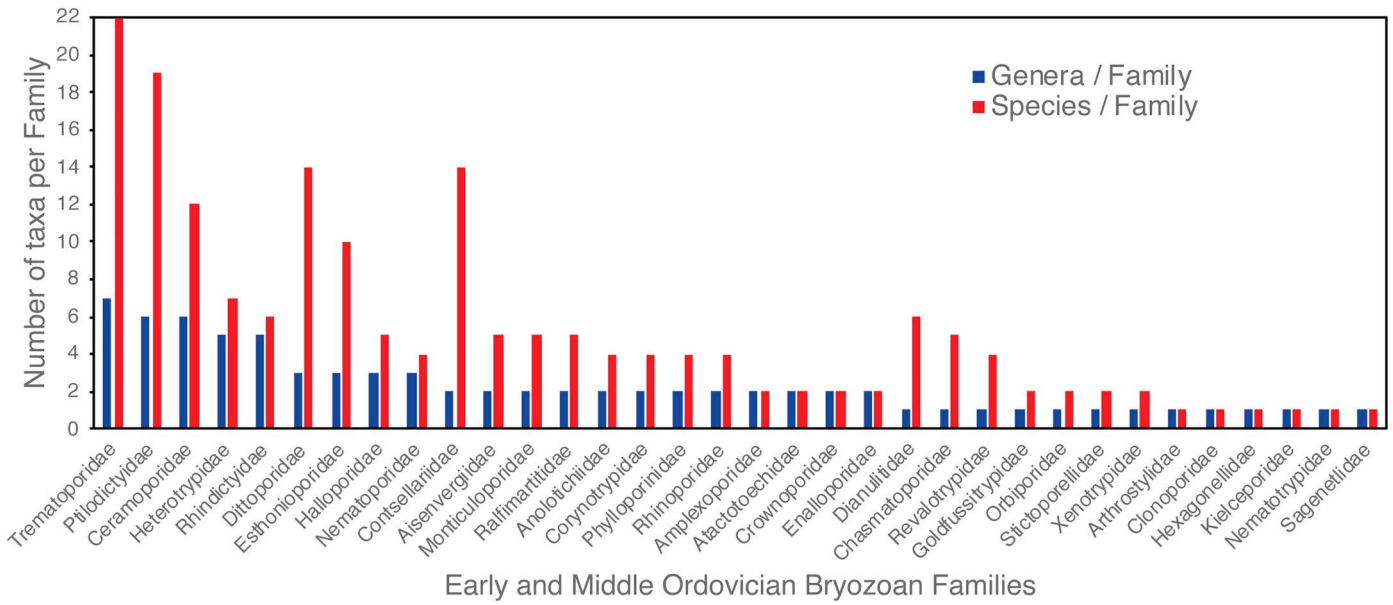
Analysis for this study consists of qualitative comparisons of the frequency (total number) of taxonomic units, unique growth habits and individual fundamental growth habit categories per Ordovician stage time-slice. What are: 1) Total number (standing richness) of bryozoan species, genera, families and unique growth habits per time-slice for the Lower and Middle Ordovician? 2) The number of new/first occurrences (FADs) of bryozoan species, genera, families and unique growth habits

**Table 1**

Taxonomic richness (occurrence frequencies) and number of first occurrences for bryozoan taxa and unique growth habits for Early to Middle Ordovician stage time-slices (1a-4c).

TS	Time Ma	Standing (total) per time-slice				New (FAD) per time-slice			
		UGH	Species	Genera	Families	UGH	Species	Genera	Families
4c	459.9	56	108	55	26	20	59	23	3
4b	462.9	41	73	34	20	8	16	8	2
4a	465.8	39	69	33	21	9	29	11	4
3b	468.0	33	57	26	19	8	18	6	3
3a	469.3	26	39	21	17	9	24	8	6
2c	471.3	17	17	12	11	6	3	2	2
2b	473.9	18	21	12	11	8	7	4	2
2a	476.4	11	14	9	8	4	6	3	2
1d	478.7	7	10	7	6	1	3	1	1
1c	480.6	8	9	7	6	6	7	6	4
1b	482.5	6	9	5	5	6	9	5	5
1a	484.4	0	0	0	0	0	0	0	0
Totals						85	181	77	34

TS, Ordovician stage time-slice; UGH, unique growth habit; FAD, first appearance datum.

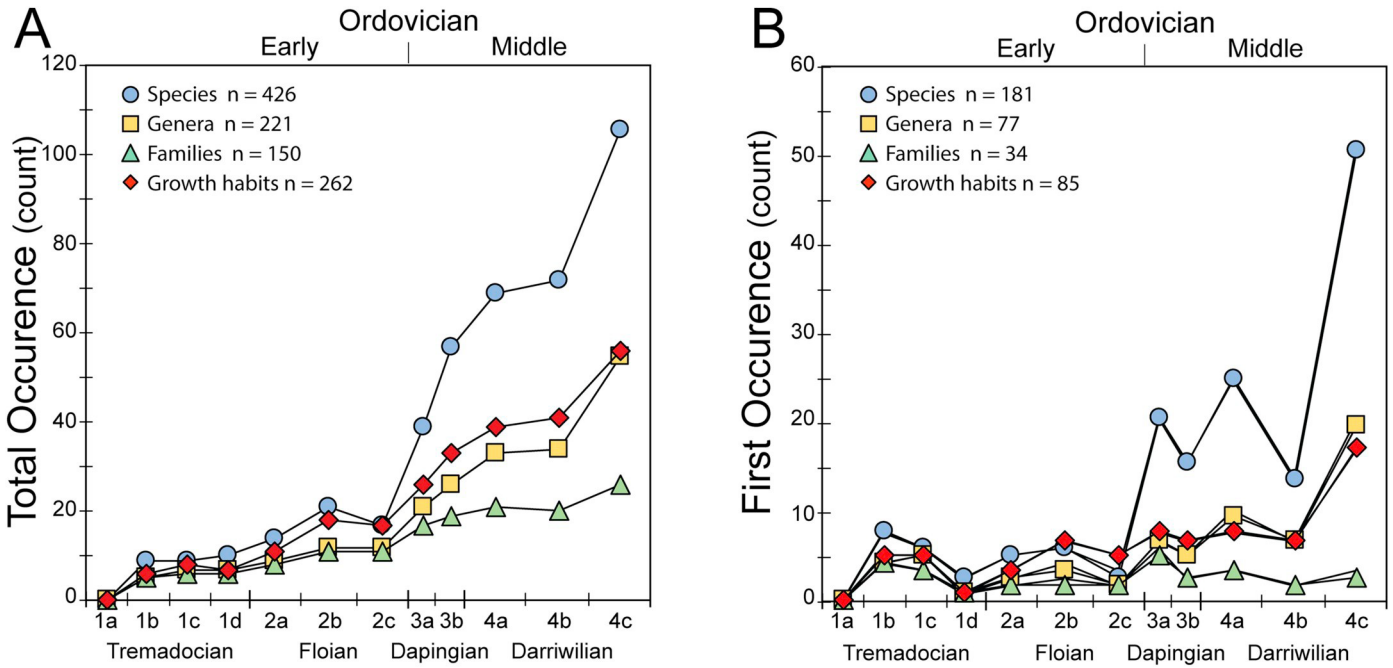


**Fig. 2.** Histograms of the frequencies of bryozoan genera per family (blue, average = 2.3, coefficient of variation = 71.6) and species per family (red, average = 5.3, coefficient of variation = 95.5). Total number of families = 34, genera = 78, species = 179. Average number of species per genus (not graphed) = 2.3, with coefficient of variation = 82.2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

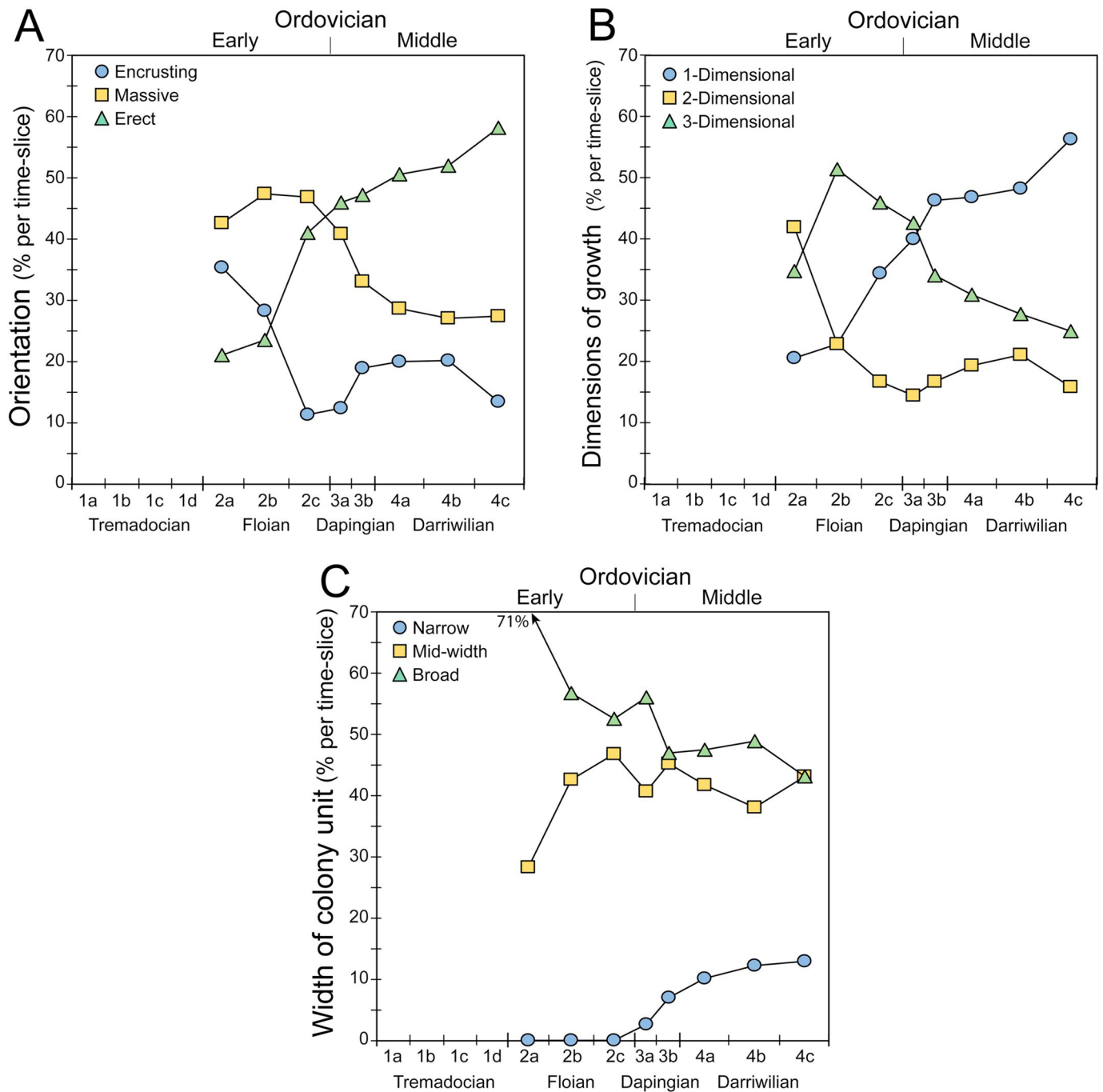
per stage time slice for the Lower and Middle Ordovician? 3) The total number (standing richness) and new/first occurrences (FADs) of each of the seven fundamental bryozoan growth habit categories for the Lower and Middle Ordovician? 4) Heat-maps of occurrence data for two combinations of fundamental growth habit categories for each time-slice are generated. Both directional trends and the timing of changes in

slope/rates are identified. Quantitative testing of potential relationships is not a goal of this phase of study.

There is no a priori expectation of evenness across taxonomic ranks (e.g., approximately the equivalent number of genera recognized among all families). It is broadly recognized, however, that phylogenetic relationships among early bryozoans are in need of reevaluation.



**Fig. 3.** Taxonomic richness (count) per Ordovician time-slice for species, genera, families, and unique growth habits. A. Cumulative totals, B. First stratigraphic occurrences.



**Fig. 4.** Relative abundance, percent of occurrences within time-slices (Floian to Darriwilian) for three fundamental growth habit categories, A. Orientation, B. Dimension of growth, and C. Width of colony unit. Each time-slice totals 100%, n (total) = 408 occurrences, n for each time-slice: 2a = 14, 2b = 21, 2c = 17, 3a = 39, 3b = 57, 4a = 69, 4b = 73 and 4c = 108. Categories and character states are defined in Fig. 1.

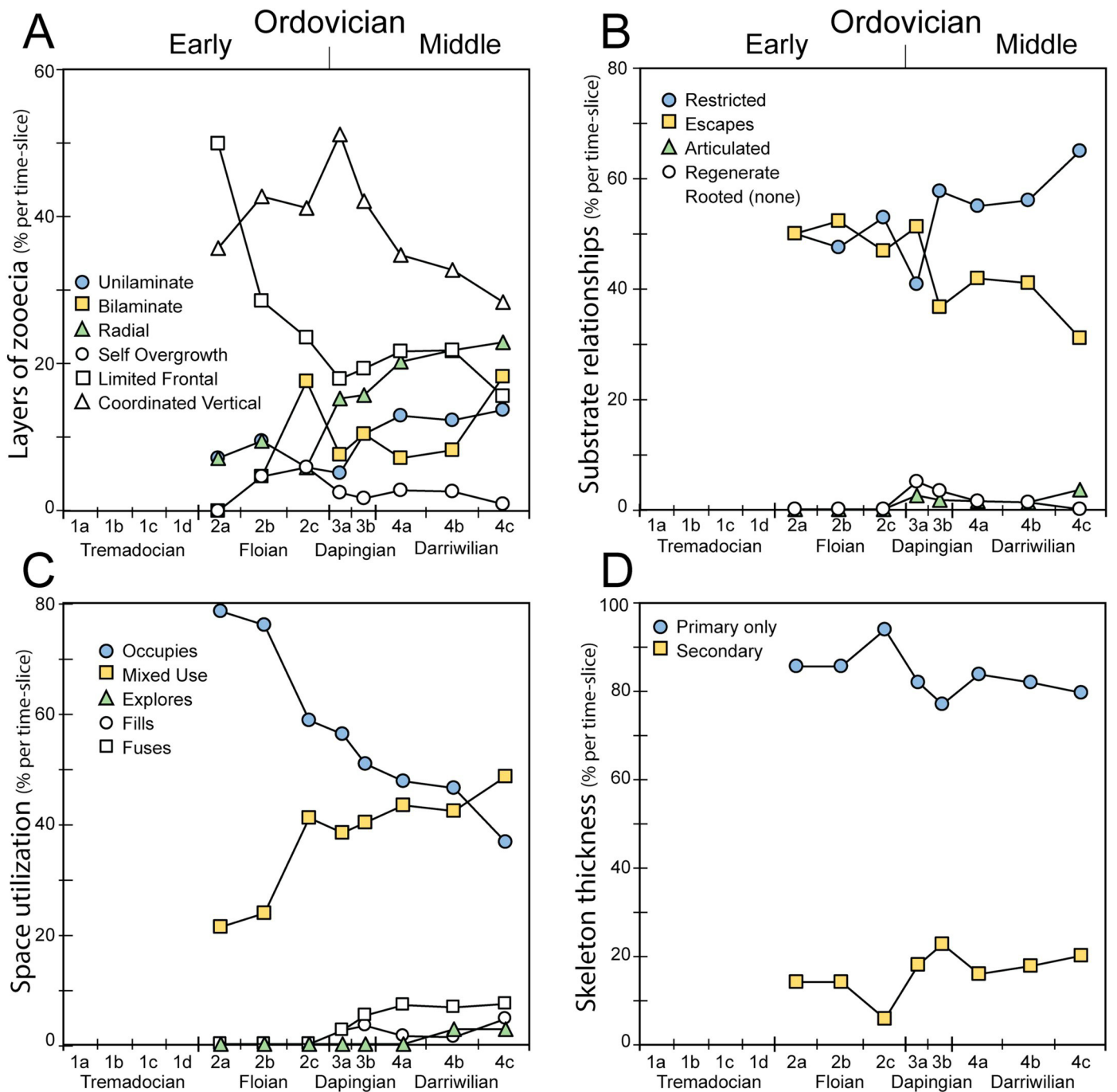
A summary of the evenness of bryozoan families, genera and species is presented, but macroevolutionary patterns within and among clades remains preliminary.

### 3. Results

The data set for Early to Middle bryozoan species occurrences and their fundamental growth habit categories are in the Supplemental data. Table 1 provides a summary of the taxonomic richness, first

occurrences and growth habit characteristic frequencies and first appearances. These data are used in scatter plots throughout this paper. Both the Supplemental Data and Table 1 serve as working hypothesis to be refined, not as final conclusions.

Taxonomic evenness of the data (Fig. 2) shows that 13 of the 34 families in the study are monogeneric, 11 have two genera defined and five families have 5 or more genera. The number of species per family ranges from one to twenty.



**Fig. 5.** Relative abundance, percent of occurrences within time-slices (Floian to Darriwilian) for four fundamental growth habit categories, A. layers of zooecia, B. substrate relationships, C. space utilization and D. skeleton mineralization. Each time-slice totals 100%, n (total) = 408 occurrences, n for each time-slice: 2a = 14, 2b = 21, 2c = 17, 3a = 39, 3b = 57, 4a = 69, 4b = 73 and 4c = 108. Categories and character states are defined in Fig. 1.

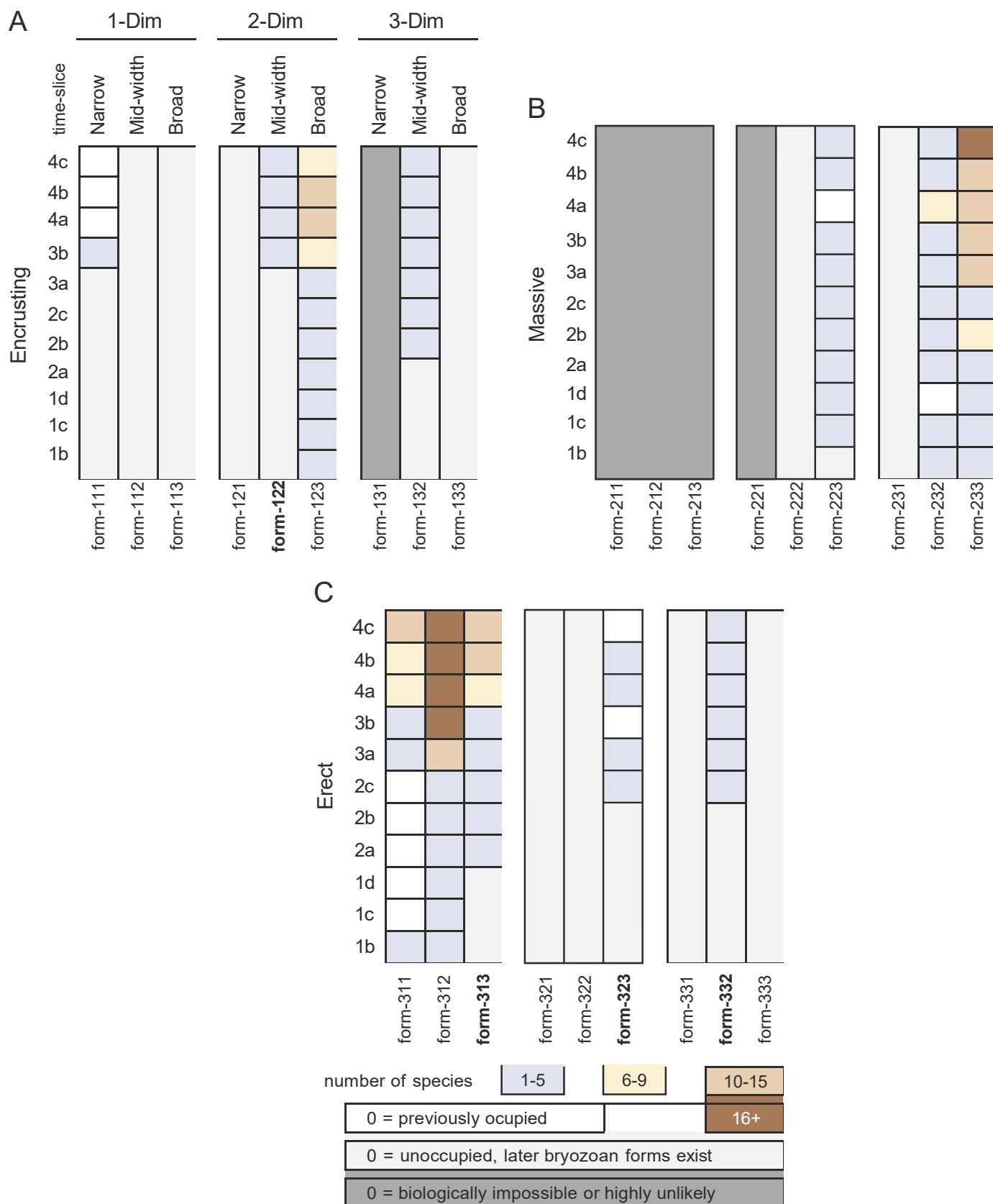
### 3.1. Standing (total) taxonomic and growth habit richness per time-slice

The total number of Early and Middle Ordovician bryozoan species is 181, with 77 genera and 34 families (Table 1). The number of species, genera and families (taxonomic richness) for each time-slice (Fig. 3A) illustrates two general trends, one of gradual increase through the Early Ordovician (time-slices 1b – 2c), with a marked increase in species richness in successive Middle Ordovician time-slices (Fig. 3A). The rate of increase for species is about twice that of genera, which is about

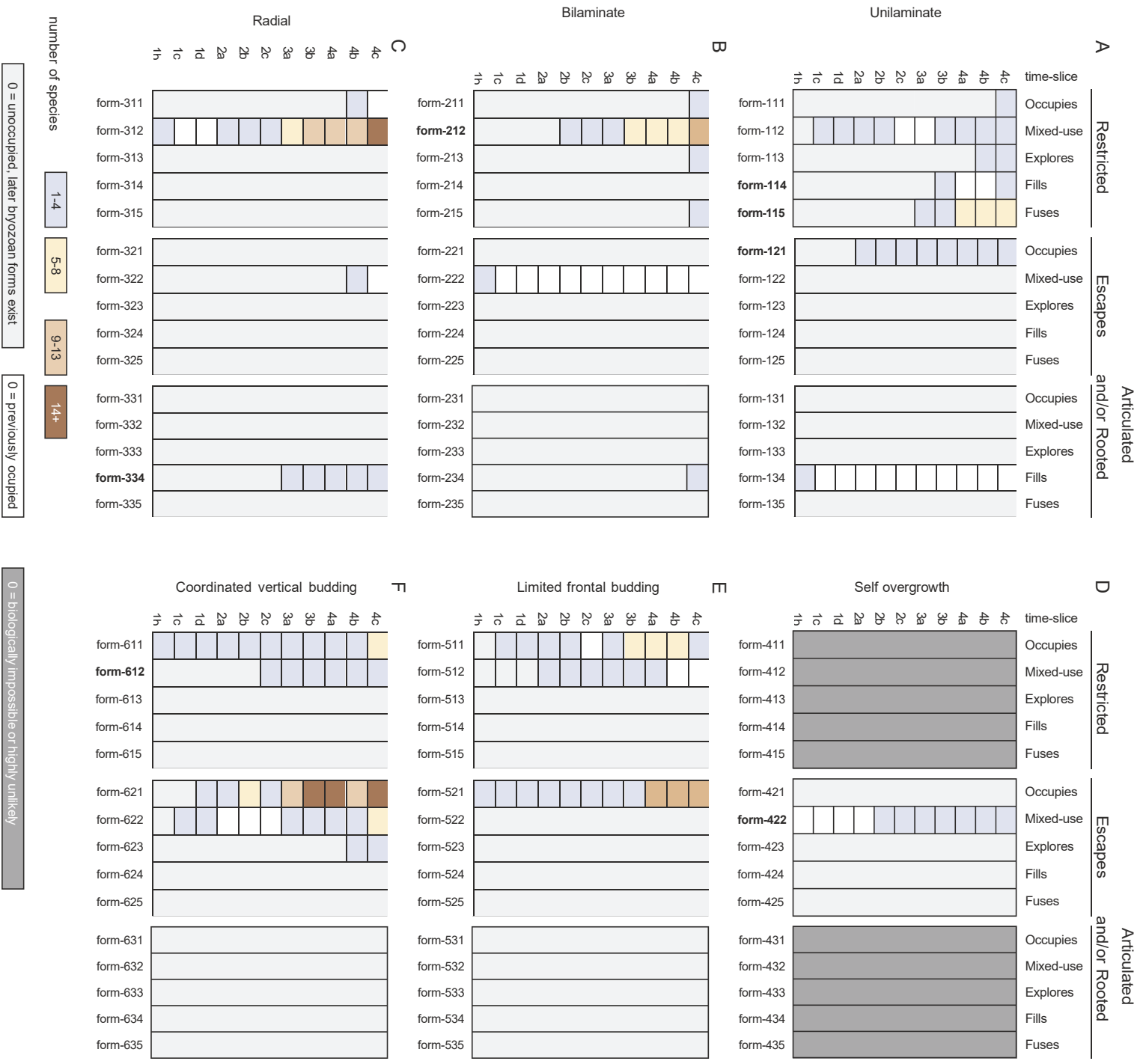
twice that of families. The only exception is the latest Early Ordovician (Floian, time-slice 2c), which is represented by a slight decrease in the number of species and a plateau for generic and family-level richness. There is also an apparent increase in taxonomic richness at all levels in the late Middle Ordovician (Darriwilian, time-slices 4b to 4c), Fig. 3A. The significance of this potential trend can only be resolved with data crossing into the early Late Ordovician.

A total of 85 unique bryozoan growth habits are present in the Early to Middle Ordovician (Table 1). A trend in the increase in the number of





**Fig. 6.** Heat-map (occurrence frequency per time slice) of occupied morpho-ecospace defined by a subset of the first three fundamental categories, orientation, dimensions of growth, and width of the colony unit (see Fig. 1 for definition of character states). Bold forms are examples from text.



**Fig. 7.** Heat-map (occurrence frequency per time slice) of occupied morpho-ecospace defined by the second subset of three fundamental characters, Layers of zoecia, Substrate relationships, and Space utilization (see Fig. 1 for definition of character states). Bold forms are examples from text.

**Table 2**

The most common growth habit character states for Early versus Middle Ordovician Bryozoa.

Character	Ordovician	
	Early	Middle
Orientation:	Massive	– Erect
Dimensions:	3-D growth	– 1-D growth
Width:	Broad	– Mid-width narrow
Layers:	Limited frontal coordinate vertical	– Radial unilaminate
Substrate:	Escapes	– Restricted
Space:	Occupies	– Mixed use fused
Skeleton:	Primary	– Primary

unique growth habits through this interval (Fig. 3A, red diamonds), shows the same inflection as the taxonomic richness at the Early-Middle Ordovician transition (Fig. 3A). The number of unique growth habits most closely tracks the number of genera per time-slice. A slight drop in the number of unique growth habits at Floian, time-slice 2c, and increase at Darriwilian, time-slice 4c parallels the trends in taxonomic richness.

### 3.2. First occurrence of taxa and growth habits per time-slice

The number of new taxa per time-slice (Fig. 3B) shows that the number of new species, genera, families and growth habits roughly parallel each from their first appearance (Tremadocian, time-slice 1b) up to the late Early Ordovician (Floian, time-slice 2c), with an average of 5.8 new species per time-slice (Table 1). At the beginning of the Middle Ordovician (Dapingian, time-slice 3a), the rate of new species addition increases disproportionately from that of new higher level taxa and growth habits. In addition, an apparent increase in rate of addition of new species, genera and growth forms is present in the latest Middle Ordovician (Darriwilian, time-slice 4c), however the rate of new families is relatively unchanged at this interval (Fig. 3B).

### 3.3. Occurrence of fundamental growth habit character states

The number of occurrences of the seven growth habit characteristics is reported in Figs. 4 and 5. Values are relative percentages of occurrences for each feature within a time-slice (sum to 100 within each time-slice). Data for the early Early Ordovician (Tremadocian, time-slices 1a–1d) are omitted from graphs because the small sample size results in extreme fluctuations that are not likely representative of long term trends.

For each of the seven fundamental growth habit categories, there is some change in the distribution at the Early to Middle Ordovician transition (Figs. 4 and 5), which represents change in relative frequency of character occurrence, not an artifact of increased species richness.

Orientation of colony: from the Early to Middle Ordovician, there is a trend of increasing importance of erect forms and a relative decrease in both massive and encrusting forms (Fig. 4A). The cross-over and inflection point for these trends is between the Lower and Middle Ordovician (Floian, time-slice 2c to Dapingian, time-slice 3a).

Dimensions of growth: the pattern of relative importance of primary growth dimensions in bryozoans parallels that of Orientation (Fig. 4A and B) from the Early to Middle Ordovician. The occurrence of 1-Dimensional colonies increases as that of 3-Dimensional colonies diminishes, with the cross over at the Lower and Middle Ordovician transition (Floian, time-slice 2c to Dapingian, time-slice 3a). Two-Dimensional colonies remain relatively steady after this transition.

Width of colony unit: Broad and Mid-width colonies essentially converge in relative importance at the Floian, time-slice 2c to Dapingian, time-slice 3a transition (Fig. 4C). Narrow colonies (three-zoecial wide or fewer) appear at this transition to Dapingian, time-

**Table 3**

Occurrence of bryozoan taxa and unique colony growth habits within each Tremadocian time-slice and the totals for the entire stage.

Category	Tremadocian time-slices			
	1b	1c	1d	Total 1b-d
Orders	4	3	4	5
Families	5	7	6	10
Genera	5	7	7	12
Species	9	9	10	19
Unique growth habits	6	8	10	13

slice 3a and then plateau in the middle and late Darriwilian – a single Tremadocian, time-slice 1b species, *Heminematopora* sp., does have a narrow colony unit width.

Layers of zooecia: trends for zooecial layers are not simple, but can be summarized as, an overall decrease in Limited Frontal budding and Coordinated vertical budding, with an overall increase in unilaminate, bilaminate and radial budding forms (Fig. 5A). Although there are both deviations in the trends and timing of inflections, the transition from Early to Middle Ordovician (Fig. 5A) remains a theme in the occurrence of zooecial layers.

Substrate relationships: the frequency of substrate relationships is counter to that of colony unit width (cf. Figs. 5B and 3C). For substrate relationships, there is a divergence between forms restricted to the substrate and those that escape the substrate at this transition from Early to Middle Ordovician (Fig. 5B).

Space utilization: the pattern of space use corresponds to that of colony unit width (cf. Figs. 5C and 3C), with colonies that occupy space (smooth colony outline) converging in relative importance with those of mixed-use (few branches) (Fig. 5C). Although of minor relative importance, colonies that fuse first appear at the Early to Middle Ordovician transition, and those that explore first appear in the late Middle Ordovician (Darriwilian, time-slice 4b).

Skeleton mineralization: the pattern for skeletal thickening differs from the other fundamental categories, in part because only two of the five options were occupied during this interval (Fig. 5D). The relative importance of primary skeleton only is represented in about 80% to 85% of the occurrences and secondary skeletal thickening in the complementary 15% to 20%. The only minor deviation is at the end of Early Ordovician (Floian, time-slice 2c) where the relative number of occurrences for Primary skeleton rises at the expense of Secondary (Fig. 5D).

Geometry of colony forms: the eighth category, which is a subdivision of first (Orientation), is included in this study as a feature in the characterization of unique growth habits, however, the details and analysis of its distribution through the Early-Middle Ordovician are not included in this study because patterns display complexity worthy of their own study.

### 3.4. Morpho-ecospace occupation through time

Two subsets of morpho-ecospace, defined by a combination of three fundamental growth habit categories each, are coded, and the number occurrences per time-slice of each are shown in heat-maps (Figs. 6 and 7). Growth habits with few occurrences per time-slice are blue, common forms are yellow, abundant forms are light-red, and those with exceptional numbers are shaded brownish-red. This allows for casual identification of the morpho-ecospace for gradients, maxima, gaps and for unoccupied (empty) morpho-ecospace that is represented by forms later in the Phanerozoic.

In the defined morpho-ecospace, for Fig. 6 there are 22 possible combinations ( $3 \times 3 \times 3 = 27$  possible states). By the end of the Middle Ordovician, 12 of these had been occupied, or about 54.5% of

**Table 4**

Examples of growth habit character state combinations (forms defined by combination of three character states), that have a delayed first appearance (compare to Figs. 6 and 7).

First appearance time-slice	Orientation	Dimensions	Width	Form, figure	Example
2a	Erect	1-Dim	Broad	313, Fig. 6C	<i>Stictopora labyrinthica</i>
2c	Erect	3-Dim	Mid-width	332, Fig. 6C	<i>Xenotrypa primaeva</i>
2c	Erect	2-Dim	Broad	323, Fig. 6C	<i>Rhinopora prima</i>
3b	Encrusting	2-Dim	Mid-width	122, Fig. 6A	<i>Constellaria vesiculosa</i>

First appearance time-slice	Layers	Substrate	Space use	Form, figure	Example
2a	Unilaminar	Escapes	Occupies	121, Fig. 7A	<i>Revalotrypa gibbosa</i>
2b	Bilaminar	Restricted	Mixed-use	212, Fig. 7B	<i>Phaenopora gregaria</i>
2b	Self over-growth	Escapes	Mixed-use	422, Fig. 7D	<i>Pakridictya maculata</i>
2c	Coordinated vertical	Escapes	Mixed-use	612, Fig. 7F	<i>Dittopora sokolovi</i>
3a	Radial	Articulated	Fills	334, Fig. 7C	<i>Arthroclema vescum</i>
3a	Unilaminar	Restricted	Fuses	115, Fig. 7A	<i>Chasmatopora furcata</i>
3b	Unilaminar	Restricted	Fills	114, Fig. 7A	<i>Goryunovia hemiseptata</i>

total possible. For Fig. 7 there are 80 possible combinations ( $6 \times 3 \times 5-10 = 80$  possible states). By the end of the Middle Ordovician, 26 of these had been occupied, or 32.5% of total possible. The morpho-ecospace defined by the combination of these six characters has not been evaluated, but would have 1760 possibilities ( $22 \times 80$ ) not reduced for biologically impossible combinations. Thus, given the *maximum* number of combination of the two spaces and the observed 85 unique growth habits (combinations), bryozoans had occupied 4.8% ( $85/1760$ ) of the total defined morpho-ecospace by just the end of Middle Ordovician.

#### 4. Discussion

Results from this study support previous observations about early bryozoan taxonomic diversity (Anstey and Pachut, 1995; Taylor and Ernst, 2004, fig. 16.3), that there is a pulse of bryozoan diversification that begins in the Middle Ordovician and continues into the Late Ordovician. New information is provided in this study by: 1) inclusion of more Early Ordovician taxa from recent discoveries, 2) characterization of fundamental colony growth habit categories, that can be assessed individually or in combination by stage time-slice, 3) comparison of the distribution of colony growth habit features with taxonomic, and eventually phylogenetic, temporal trends. Although these data provide a benchmark for comparison, caution should be exercised in any analysis of broader phylogenetic trends, due to the need for comprehensive review of taxonomic concepts for a number of the families, and the fact that all of the data include first and early occurrences at all taxonomic levels during the initial radiation of a phylum.

##### 4.1. Viability of colonial growth habit characterization to Paleozoic bryozoans

Although existing classification schemes for bryozoan colonial growth habits can be superimposed onto Paleozoic stenolaemate bryozoans (Hageman et al., 1998), in practice, all schemes were developed for and using Post-Paleozoic cheilostomes and cyclostomes (e.g., Stach, 1936; Schopf, 1969; Nelson et al., 1988). The generation and successful application of a growth habit classification scheme to early Paleozoic bryozoans is significant in its self, even without any analysis of macroevolutionary patterns. In addition, this classification is based on fundamental growth processes (categories), which are applicable throughout the phylum, fossil to recent.

The purpose of this paper is to identify patterns and relationships among Early to Middle Ordovician bryozoan taxonomic and growth

habit occurrences, i.e., generate hypotheses for future testing. In this section, possible inferences about controlling factors for the data are posed, but it is beyond the scope of this paper to test each.

##### 4.2. Early to Middle Ordovician change in taxonomic richness and growth habit disparity

Bryozoa taxonomic and growth habit occurrence frequencies change at the Early to Middle Ordovician transition (Floian, time-slice 2c to Dapingian, time-slice 3a) (Figs. 3 and 4). The timing of this apparent change is earlier than for other phyla (Fig. 8), which generally begin an increase in slope at the Dapingian, time-slice 3b to Darriwilian, time-slice 4a transition. The start of increased richness for bryozoans, relative to other benthic invertebrates, may be an artifact of non-normalization of the data, or it may be a real signal that invites further investigation. This Floian to Dapingian transition is also important in the relative abundance (occurrences) of six of the seven fundamental growth habit categories (Fig. 3, transition from time-slice 2c to 3a).

Through the Early Ordovician (Tremadocian, time-slice 1b to Floian, time-slice 2c), the number of new unique bryozoan growth habits does not correspond to the number of new species during the key interval the change (Fig. 3B). From the early to mid- Middle Ordovician (Dapingian, time-slice 3a to Darriwilian, time-slice 4b) the rate of new growth habit appearances remains relatively constant, whereas the number of new species increases (Fig. 3B). This illustrates that species concepts (characteristics used for diagnosis and identification) for Bryozoa are decoupled from the growth habit characteristics defined here (Fig. 1). It is well known that bryozoan species concepts are based on zoecial (module) features rather than colony form, but one of the questions in this study is whether an increase colonial morpho-ecospace, also results in a diversification in new species within those forms. It is possible that in the final time-slice in the Middle Ordovician (Darriwilian, time-slice 4c, Fig. 3B) that the sharp increase in new species, corresponds to the sharp rise in new growth habits. Additional data into the Late Ordovician are needed to test this idea.

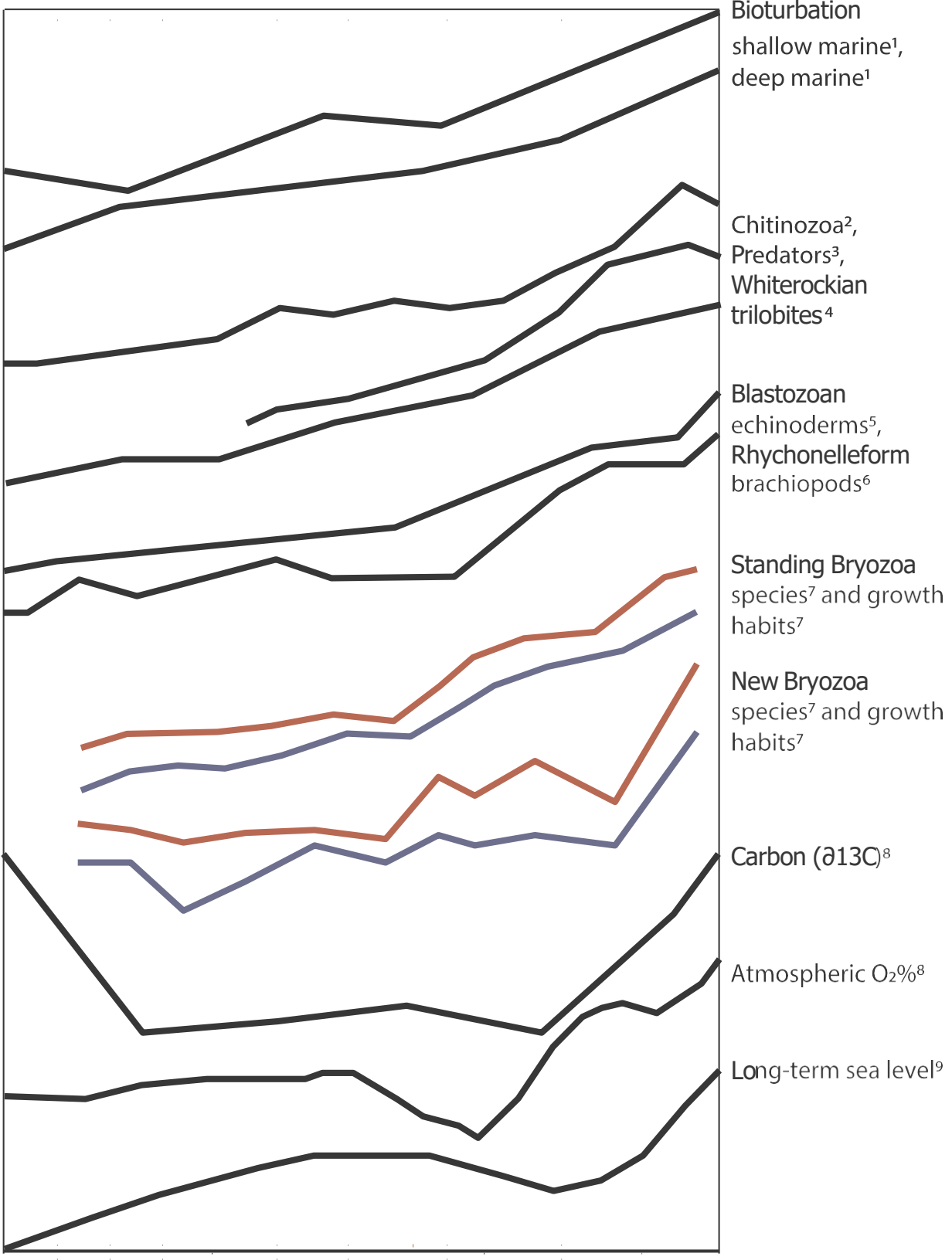
In general, the number of new growth habits throughout the Early to Middle Ordovician, most closely corresponds to the number of new genera recognized per time-slice. Future studies could compare a compilation of characters diagnostic for these genera in order to determine of what role colony growth form features play in generic concepts and whether these are justifiable phylogenetically.

# Ordovician

Early Middle

Tremadocian Floian Dapingian Darriwilian

1a 1b 1c 1d 2a 2b 2c 3a 3b 4a 4b 4c



(caption on next page)

**Fig. 8.** Summary of other biotic and physical trends through the Early and Middle Ordovician that roughly correspond to those observed in Bryozoa. Trend lines are from references cited and all are scaled to equal height across the maximum of the presented range, regardless of units. Data are from <sup>1</sup>Buatois et al. (2016), <sup>2</sup>Paris et al. (2004), <sup>3</sup>Kröger et al. (2009), <sup>4</sup>Adrain et al. (2004), <sup>5</sup>Nardin and Lefebvre (2010), <sup>6</sup>Harper et al. (2004), <sup>7</sup>this study, <sup>8</sup>Edwards et al. (2017), <sup>9</sup>Haq and Shutter (2009), and summarized in Servais et al. (2010).

#### 4.3. Individual growth habit characteristics

As summarized in the Results section, patterns for relative frequency of fundamental growth habit categories do display general trends, most of which have a nexus at the E-M Ord. boundary (Figs. 4 and 5). Hypothetical forms generated from the most common character states for each of the seven fundamental categories (Table 2), the Early Ordovician is characterized by massive, hemispherical domes with coordinated 3-D budding that escape their original substrate (e.g., *Esthoniopora*, *Orbipora*, and *Stigmatella*). For the Middle Ordovician, the most common composite is erect, radial branches with one dimensional growth restricted to their substrate by a holdfast (e.g., *Aostipora*, *Batostoma*, *Dittopora*). To a bryozoologist, these results are not revelatory, however the totality of character states in Figs. 4 and 5 place these colony archetypes in temporal context with many other forms that are present, albeit with lower species richness per form.

A noteworthy latecomer bryozoan growth habit character state is that of Narrow colony unit width (Fig. 4C). This corresponds to the origin and rise of fenestrate and thin rhabdomesid bryozoans. Through the Early Ordovician, there is only one known described, erect bryozoan with preservable skeletons. The character state of Fused branched in space utilization (Fig. 5C) corresponds to the same, later origination. For substrate relationships, articulated and regenerated forms are not known until the beginning of the Middle Ordovician (Dapingian 3a), but these remain of minor importance through the rest of Middle Ordovician.

The following growth habit character states are missing from the Ordovician: forms rooted to their substrate (very important in the Cenozoic), those uncalcified or lightly calcified skeletons (quite possibly missing for taphonomic reasons), as well as those with colony scale skeletal structures (important in mid-late Paleozoic fenestrates among others).

#### 4.4. The earliest bryozoans (Tremadocian and Floian)

The taxonomic richness of Tremadocian, time-slice 1b bryozoans (Ma et al., 2015; Ma et al., 2018), relative to the number of occurrences (e.g., nine species among five genera and five families in four orders), has several implications for the origin of the phylum. Bryozoan lineages were already quite diverse (multiple higher taxa) in the Early Ordovician when they are first observed in the fossil record. This supports the long held expectation that the phylum Bryozoa had its origin well before, in the Cambrian or earlier, and their first appearance in the fossil record is related to the advent of skeletalization. This timing parallels patterns in the early Cambrian where multiple clades independently evolve skeletal hard parts over a short interval, presumable in response to extrinsic factors (Servais et al., 2010; Edwards et al., 2017).

Data for the Tremadocian (Table 3) and to a lesser extent the Floian, demonstrate that the interval is under-sampled with respect to bryozoan occurrences. This is evident in Table 3, where the occurrence of multiple families (and genera) shows ghost lineages for groups found in the early Early Ordovician. Although the morpho-ecospace of Figs. 6 and 7 in no way imply phylogenetic continuity (e.g., states may be derived individually through convergence), that fact that there are more missing growth habit character states in late Tremadocian and Floian also suggests Early Ordovician under sampling. Presumably, representative members for some of these missing growth habit character states could be found with sampling methods equivalent to those of Ma et al. (2015) and Ma et al. (2018) in Tremadocian, time-slice 1b,

where the earliest bryozoan specimens are being discovered in bulk rock sampling, with extensive, exploratory slabbing and thin sectioning.

We expect, however, that although a global preservational bias may exist between the Early and later Ordovician, a concentrated sampling effort for bryozoans in the Early Ordovician will fill in gaps of growth habit disparity and higher level taxonomic richness, but will not substantially increase the species richness or change the overall pattern of lower occurrence frequencies in the Early Ordovician, with a sharp change (increase) at the Lower and Middle Ordovician boundary will persist.

#### 4.5. Morpho-ecospace occupation

In order to provide simple, direct analysis, the growth habit morpho-ecospace is divided into two subsets of three features each (Fig. 1). Several patterns can be observed from the frequency heat maps (Figs. 6 and 7). First, some unique growth habits begin early and gradually increase in importance through the Early and Middle Ordovician (blue to dark-red). For example, character subset-1 (Orientation, Dimensions, Width), Fig. 6A: erect, 1-dimensional, mid-width, form 1-1-2; Fig. 6B: massive, 3-dimensional, broad, form 2-3-3; and Fig. 6C: encrusting, 2-dimensional, broad, form 3-2-3. Additional examples from character subset-2 (Layers, Substrate, Space) include: Fig. 7C: radial, restricted, mixed-use, form 3-1-2; Fig. 7E: limited frontal, escapes, occupies, form 5-2-1; and Fig. 7F: coordinated vertical, escapes, occupies, form 6-2-1.

Although morphospace for Fig. 6 is independent of that for Fig. 7 (membership in one does not automatically predict membership in another), a unique growth habit is defined by a combination of the two and in the present example of an early origin with gradationally increasing importance, three unique growth habits are involved and can be summarize in more general terms. 1) Orientation = erect, Dimensions = 1-dimension, Width = mid-width, Layers = radial, Substrate = restricted, Space = mixed-use, form 3-1-2-3-1-2 (e.g., erect, tree-like forms with moderate number and sized, radial branches, cemented to their substrate by a holdfast, such as *Aostipora*, *Batostoma* and *Dittopora*). 2) Orientation = massive, Dimensions = 3-dimensions, Width = wide, Layers = coordinated vertical, Substrate = escaped, Space = occupies, form 2-3-3-6-2-1 (e.g., massive, large, hemispherical, multilaminar, smooth mounds with that grow beyond their primary substrate, such as *Esthoniopora*, *Orbipora* and *Stigmatella*). 3) Orientation = encrusting, Dimensions = 2-dimensions, Width = wide, Layers = coordinated vertical, Substrate = escaped, Space = occupies, form 1-2-3-6-2-1 (e.g., broad, nodular sheets of limited thickness, with smooth colony margins, that grow beyond their primary substrate, such as *Ceramopora*, *Lichenalia* and *Rhinopora*).

A second common pattern is the delay of the first appearance of a combination of fundamental growth habit character states. This is quite common and includes the following, sorted by time-slice (Table 4). With careful analysis it may be possible to connect the distribution of these early growth forms to external biological or physical causes, and/or to taxonomic diversification within bryozoan clades associated with the appearance of key character states.

The absence of entries in the morpho-ecospace defined in Figs. 6 and 7 indicates one of four things. A small amount of the space (dark gray) is topologically impossible or biologically so unlikely that it can be considered un-occupiable space. The remaining space, light gray, is that which bryozoans *could* occupy, but do not, i.e., empty space. There

are three kinds of unoccupied space, 1) that which is not occupied by any bryozoan in the Early to Middle Ordovician, but most of which is occupied by some bryozoan form in the rest of the Phanerozoic; 2) unoccupied space that is stratigraphically below the first appearance of the character trait, that is, first occupied in the Early to Middle Ordovician; 3) cells for which traits have been recognized stratigraphically earlier, but are not observed in that time-slice (white fill). This could indicate unsampled morpho-ecospace, or true extinction/absence of all lineages displaying that morphology, with subsequent, independent evolution of the character state later. These are testable ideas, but cannot be resolved with the current data.

The likely under-sampling of Early Ordovician bryozoans has been discussed, but it is noteworthy that there are a number growth habit character states that are observed in the early Tremadocian, time-slice 1b, (Unilaminar, Articulated, Fills and Bilaminar, Escapes, Mixed-use) that are not present in the rest of the record presented here (Fig. 7A, form 1-3-4 and Fig. 7B, form 2-2-2). However, this potential anomaly actually highlights one of the goals of the system, to investigate trends, which also includes recognizing and accounting for outliers.

#### 4.6. Comparison to other Early to Middle Ordovician biotic and physical trends: in search of causal factors

Previous explanations for the Great Ordovician Biodiversity Event (GOBE) are summarized in Servais et al. (2010), Harper et al. (2015, table 1) and Edwards et al. (2017) and include: global cooling related decreased CO<sub>2</sub>, possibly associated with increased phytoplankton, increased predators, increased oxygen, asteroid strike effects, erosion rates, high sea levels, substrate change, volcanic and super-plume activity, tectonics and a non-event that represents a continuation of the Cambrian explosion. Clearly, a qualitative matching trend does not demonstrate correlation and, as always, correlation does not demonstrate causation. Fig. 8 shows a variety of GOBE trends for which the bryozoan data presented here have broad correspondence and can provide working hypotheses from which these relationships can be evaluated.

Edwards et al. (2017, fig. 3) show that atmospheric oxygen concentrations began to increase sharply at the Early-Middle Ordovician transition, from the 10–13% in the Early Ordovician to 24% by the middle of the Late Ordovician. For all of the geochemical proxies reviewed for this study, the trend of oxygen concentrations most closely matches the bryozoan data reported here, suggesting that absolute concentration of dissolved oxygen available in water masses and/or marine environments expanded to suitable minimum oxygen levels (Edwards et al., 2017) might be directly or indirectly associated with bryozoan taxonomic richness and growth habit disparity. Most changes in bryozoan trends begin prior to that of oxygen (Fig. 8).

Servais et al. (2010, figs. 4 and 5) summarized abundance curves for the common marine biota and life modes through the Ordovician. Although taxonomic levels of comparison vary among groups, the sessile benthic suspension feeders of blastozoans and brachiopods match the bryozoan trends reported here (inflection of increased frequency beginning at the Early-Middle Ordovician transition). This pattern is shared with chitinozoan zooplankton, Whiteoakian trilobite fauna and predators (Servais et al. 2010, fig. 4) (Fig. 8).

An important environmental feature that changes during the Ordovician is substrate composition (Taylor and Wilson, 2003). Especially important is the appearance and subsequent expansion of carbonate hard grounds (Brett and Brookfield, 1984; Ekdale and Bromley, 2001; Taylor and Wilson, 2003; Palmer and Wilson, 2004). Data are not available at this time for a direct comparison of bryozoan taxonomic and growth habit richness versus global trends in carbonate sedimentation at the resolution of time-slices.

Bryozoan distributions reported here do not generally correspond to trends summarized by Servais et al. (2010, figs. 4 and 5) for phytoplankton, graptolites, radiolaria, mobile benthos of ostracodes and

Ibexian trilobite fauna, sponges, bivalves and gastropods. The E-M Ordovician transition for the following data do not show significant change as in the bryozoan data or trends noted in Section 4.2:  $\delta^{13}\text{C}$  global curve (Bergström et al., 2009), long-term global sea level change (Haq and Schutter, 2008), <sup>87</sup>Sr/<sup>86</sup>Sr global curve (Shields and Veizer, 2004).

## 5. Conclusions

The new classification of bryozoan colony growth habits based on fundamental processes of growth proves viable for characterizing Early and Middle Ordovician bryozoans. A data set consisting of occurrences of both species and growth habit characteristics demonstrates that taxonomic richness and growth habit variety of bryozoans is low but relatively constant through the Tremadocian and Floian, but begins a sharp increase at the Early-Middle Ordovician transition, and increases throughout the Middle Ordovician (Floian–Dapingian boundary). This trend begins slightly earlier (ca. 5 Myr) than has been observed in other bryozoan and sessile suspension feeding benthic invertebrates data sets, whose rise is typically marked as Darriwilian. Apparently, the rise in overall richness is decoupled between species and higher taxa plus unique growth habits. That is, although overall richness rises through the Middle Ordovician, the number of new genera, families and growth habits per time-slice remains relatively constant, whereas the standing number new species increases per time-slice increases significantly. It is possible that discovery of new bryozoan taxa and species occurrences in this under-sampled interval, could change conclusions from the observed patterns. However, results from this study provide a strong benchmark for future comparisons, i.e., is the pattern of decoupling at the Middle Ordovician of taxonomic rates of evolution between the species level (sharp increase) and higher taxa, new genera, families and new growth habits (constant rate) real and a reflection of extrinsic forces, or somehow a function of sampling?

The limited number of species, plus gaps in fundamental colony growth habit character states suggest that the Tremadocian and Floian are under-sampled for bryozoans. Although occurrences are expectedly rare during this interval, many of the earliest bryozoan specimens have been discovered in bulk rock sampling, with extensive, exploratory thin sectioning. If such methods are employed more broadly on Early Ordovician rocks, we expect that more concentrated global collecting will increase in disparity of Early Ordovician growth habits (filling in of morpho-ecospace) and higher-level taxonomic richness. Roughly, 4.8% of the morpho-ecospace as defined by the six of the fundamental growth habit categories is occupied by bryozoans by the end of the Middle Ordovician. This is a relatively large number considering that only 25 Myr since the first appearance of the phylum in the fossil record. This invites explanation. It is possible that, 1) phylogenetic diversification with respect to potential for varied growth habits are canalized, but must have evolved prior to the appearance of skeletal hard parts in the phylum; or 2) developmental controls over growth habit characters were weak during the early history of the phylum. That is, the evolution of growth habit character states was rapid and repeatedly reversible, with inevitable variety and apparent complexity).

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