



## Bryozoan Growth Habits: Classification And Analysis

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### Abstract

Bryozoans are an important part of the benthic marine fauna in a wide variety of modern environments and are found in rock forming abundance in a number of settings throughout much of the Phanerozoic. Bryozoologists and nonspecialists have grouped taxa into colonial growth forms (e.g., erect fenestrates or encrusting sheets), both to simplify analyses and because correlations exist between some colony growth forms and the environmental conditions in which the organism lived. These correlations allow for the possibility of paleoenvironmental analyses based on skeletons alone. Existing bryozoan colonial growth form classifications do not, however, fully exploit the ecological information present in colony form. A new scheme is proposed here (Analytical Bryozoan Growth Habit Classification), which provides a list of colony-level morphological characteristics for bryozoan growth habits. This differs from previous approaches to bryozoan growth form analysis in that it is a classification of growth habit characteristics rather than a classification of morphological groups as such. The classification is based on eleven character classes, which describe the orientation of the colony and its occupation of, and placement in space. The overall colony shape is described based on the arrangement of modules in colonial growth.

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46. Brush Creek unit exposed in Conrail RR cut at south edge of Summitville just east of Ohio Rte. 644, NW¼, SE¼, sec. 23, Franklin Twp., Columbiana Co., Ohio, Kensington 7½' quadrangle, OGS 14776.
47. Brush Creek unit exposed in roadcut on east side of Foundry Hill Rd., 0.2 km southeast of boundary line between secs. 30 and 32, NW¼, NW¼, sec. 30, Washington Twp., Columbiana Co., Ohio, Gavers 7½' quadrangle, OGS 6310, 10418, 14771.
48. Brush Creek unit exposed in roadcut on west side of Ohio Rte. 13, N½, NE¼, sec. 10, Trimble Twp., Athens Co., Ohio, Corning 7½' quadrangle, OGS 6680.
49. Pine Creek unit exposed in roadcut on north side of Rte. 28 east of Etna at intersection of 28 and Powers Run Rd., Allegheny Co., Pennsylvania, Pittsburgh East 7½' quadrangle.
50. Cambridge and Portersville units exposed in abandoned John Gress & Sons quarry, approx. 0.4 km east of New Concord and 0.5 km north of U.S. 40, Westland Twp., Guernsey Co., Ohio, New Concord 7½' quadrangle.
51. Cambridge unit exposed in abandoned quarry on north side of drive extending from Adams Twp. Rd. 6113, N½, secs. 24 and 25, Adams Twp., Guernsey Co., Ohio, Bloomfield 7½' quadrangle.
52. Portersville unit exposed on west side of run behind buildings just north of Red Head Gas Station on west side of Richland Avenue, approx. 0.5 km south of the Hocking River, Athens Twp., Athens Co., Ohio, Athens 7½' quadrangle.
53. Portersville unit exposed in first ravine north of elev. 684 on east side of Margaret Creek, approx. 1.4 km east-northeast of Hibbardville, Alexander Twp., Athens Co., Ohio, The Plains 7½' quadrangle, OGS 11249.
54. Portersville unit exposed along west side of creek back of Belle Valley, SE¼, SW¼, NE¼, sec. 20, Noble Twp., Noble Co., Ohio, Caldwell North 7½' quadrangle.
55. Portersville and Ames units exposed at an undescribed locality, NW¼, SE¼, sec. 3, Noble Twp., Noble Co., Ohio, Bylesville 7½' quadrangle.
56. Portersville unit exposed at its type locality in abandoned Wabash RR tunnel cut, SW¼, NW¼, sec. 24, Bearfield Twp., Perry Co., Ohio, Deavertown 7½' quadrangle, OGS 10375.
57. Ames unit exposed on east side of Athens Co. Rd. 17 at junction with Alexander Twp. Rd. 55, Alexander Twp., Athens Co., Ohio, Athens 7½' quadrangle, OGS 11251.
58. Ames unit exposed in roadcut on south side of U.S. 40 relocation and east of junction with Rte. 513, NW¼, sec. 25, Oxford Twp., Guernsey Co., Ohio, Antrim 7½' quadrangle.
59. Ames unit exposed on west side of Rte. 78 and directly opposite road junction with 764, sec. 2, Olive Twp., Noble Co., Ohio, Caldwell South 7½' quadrangle, OGS 15780.
60. Ames unit exposed in high roadcut on Star City Rte. 19-7 just south of the University of West Virginia near bend in road, Morgan Twp., Monongalia Co., West Virginia, Morgantown North 7½' quadrangle.
61. Ames unit exposed in roadcut on west side of U.S. 23 south of White's Creek, Boyd Co., Kentucky, Burnaugh 7½' quadrangle, 38°19'15"N, 82°34'40"W.

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## BRYOZOAN GROWTH HABITS: CLASSIFICATION AND ANALYSIS

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**ABSTRACT**—Bryozoans are an important part of the benthic marine fauna in a wide variety of modern environments and are found in rock forming abundance in a number of settings throughout much of the Phanerozoic. Bryozoologists and nonspecialists have grouped taxa into colonial growth forms (e.g., erect fenestrates or encrusting sheets), both to simplify analyses and because correlations exist between some colony growth forms and the environmental conditions in which the organism lived. These correlations allow for the possibility of paleoenvironmental analyses based on skeletons alone. Existing bryozoan colonial growth form classifications do not, however, fully exploit the ecological information present in colony form.

A new scheme is proposed here (*Analytical Bryozoan Growth Habit Classification*), which provides a list of colony-level morphological characteristics for bryozoan growth habits. This differs from previous approaches to bryozoan growth form analysis in that it is a classification of growth habit characteristics rather than a classification of morphological groups as such. The classification is based on eleven character classes, which describe the orientation of the colony and its occupation of, and placement in space. The overall colony shape is described based on the arrangement of modules in colonial growth. This classification provides a common ground for systematic comparison of character states among varied bryozoan growth habits. This approach allows for the evaluation of correlations among observed morphological character states and specific environmental conditions in which they develop. In addition, these growth habit characters can be used to recognize, characterize, evaluate, and apply more traditional growth form groups in broader studies.

### INTRODUCTION

**T**HE MORPHOLOGY of an organism can reflect adaptive evolutionary or phenotypic responses to selected environmental pressures under which the organism lives. This correlation between the morphology of an organism and the physio-chemical parameters of its environment allows for the possibility of paleoenvironmental interpretations based on the distribution of skeletal hard parts alone.

Previous studies have demonstrated that despite complexity of biological and ecological systems and potential uncertainties

in their relationships, a valuable degree of real, interpretable, ecological signals is contained in the distribution of bryozoan morpho-types (e.g., Stach, 1936; Cheetham, 1963, 1966, 1971; Lagaaij and Gautier, 1965; Cuffey, 1967; Schopf, 1969; Nelson et al., 1988; Moissette, 1988, 1989, 1993; see Hageman et al. [1997, appendix] for more complete list). The potential to make paleoenvironmental interpretations based on the skeletons of fossil organisms is a powerful tool for paleoecologists and sedimentologists and makes the pursuit of these methods worth the effort of sifting through their complexity.

A number of approaches to bryozoan growth form classification has been employed in previous studies. An expanded and more versatile approach is proposed here: *Analytical Bryozoan Growth Habit Classification*. The approach is "analytical" in that the growth habit characteristics of an organism are separated comprehensively into their constituent elements for analysis. The bryozoan growth habit classification proposed here provides for: 1) a more comprehensive characterization of growth habits, which will likely provide greater sensitivity to ecological variability; and 2) a more stringently defined classification, which will allow for more accurate and complete comparisons among forms. The purpose of this paper is to 1) briefly review previous approaches to bryozoan growth form analysis; 2) introduce this classification of bryozoan growth habit characteristics; 3) provide examples of its application; and 4) discuss its potential for broader, paleoecological applications.

#### HISTORY OF GROWTH FORM APPLICATIONS

A review of previous growth form classifications is provided here first, because an appreciation of the various features of these schemes will aid in the understanding of the rationale behind the proposed analytical approach. The new, analytical classification is described and discussed in other sections.

The term "growth habit" as used in this study is largely interchangeable with the traditional term "growth form." The primary difference between the two terms is that "habit" reflects a broader suite of zoarial characters (ecological strategies), i.e., not just overall shape or form. The term "growth form" will be used here when referring to earlier works that used this nomenclature and the term "growth habit" will be used when discussing the analytical classification and methods presented in this paper.

The ultimate goal of all growth form studies was to recognize correlations between morphology and environment. Colonial organisms, such as bryozoans, are well suited to studies which capitalize on correlations between morphological and environmental variation in paleoecological analysis. The modular nature of growth of colonial organisms allows for both: 1) phenotypic variation within one species (or specimen) in response to variable environmental conditions; and 2) a wide range of ecologically adapted, determinate, morphological types among taxa. Nomenclature, methods, and theory have developed somewhat independently among various colonial and vegetative groups (corals, sponges, plants), although common ecological principles apply to all (e.g., Ryland and Warner, 1986). Only bryozoan growth habits are treated in this study.

Methods for the application of growth forms have been developed in a number of independent studies through time (e.g., Stach, 1936; Cheetham, 1963; Lagaaij and Gautier, 1965; Schopf, 1969; Moissette, 1993). The fundamental premises upon which growth form analysis is based are straight forward (Stach, 1936): 1) define/recognize bryozoan growth forms present in a study area; 2) determine the distribution and relative importance of growth forms in study area; 3) correlate trends of growth form distributions with environmental conditions; and 4) use these growth form characteristics in predictive models in an unknown setting.

Methodological concepts for bryozoan growth form studies are more complex when actually put into application. There are many ways in which a single data set can be compiled and analyzed, but certain procedures are more attractive than others and a standardized method is proposed in Hageman et al. (1997). More information about ecological controls over growth form distributions is needed, especially changes in predominant ecological strategies through geologic time (e.g., Lidgard et al., 1993).

#### FUNCTION OF GROWTH FORM APPLICATIONS

Growth form classifications and applications serve several functions within the context of paleoenvironmental analysis. It is important to differentiate these functions in order to appreciate how classifications are derived and applied.

*Communication and generalized comparisons.*—Bryozoans can be arranged into traditional growth forms such as "fenestrates" or "cellariforms" based on shared growth habit characteristics (e.g., Schopf, 1969). Such terms provide descriptive framework with which workers can communicate and compare general morphologies of Bryozoa outside of a taxonomic context. The communicative function of a traditional growth form classification is largely a simplification or summary of a complex ecological system. The communicative function of growth form classifications can be applied independently of any environmental interpretations.

*Characterization.*—The distribution of growth habit characteristics can be documented relative to known environmental conditions. This has been done with traditional growth form groups (e.g., Lagaaij and Gautier, 1965). The more completely that growth habit character states are documented for a specimen, the more fully the ecological information contained in their distribution can be exploited. Comprehensively characterized taxa can, likewise, be grouped into categories based on shared morpho-ecological strategies. Resultant classification will be less user-friendly for communication, but this is a conscious trade off for increased ecological resolution.

*Predictive role.*—The distribution of traditional growth forms, or the distribution of growth habit characteristics, can be used to predict environmental parameters from an unknown setting (e.g., Moissette, 1993; Moissette and Saint Martin, 1995). This is the goal of paleoenvironmental analysis. Growth habit distributions must be well-characterized independently, based on known settings, before they have predictive value. It is, therefore, doubly important to differentiate between the characterization and predictive phases of growth form analysis (Hageman et al., 1997).

#### APPROACHES TO GROWTH FORM CLASSIFICATION

Informal descriptive terms for bryozoan colonial shapes and orientations have been used widely. More formal growth form classifications have arisen and evolved based on the needs of workers with broad interests (biologists, paleontologists and sedimentologists). Schopf (1969), Smith (1995), and McKinney and Jackson (1989) provide the most comprehensive examples of each of the three major approaches to classification schemes discussed here: 1) archetypal; 2) hierarchical geometry and construction; and 3) ecological. A fourth scheme, the *Analytical Bryozoan Growth Habit Classification*, which encompasses strengths of all of these classifications, is proposed here.

*Classifications based on informal descriptors.*—A number of informal terms have been used to describe bryozoan growth forms, which are based primarily on the overall colonial geometry. Examples of these informal descriptors included: stick-bryozoans or sheet-bryozoans, twiggy or fenestrate forms, buttons, and spots. General descriptors such as delicate or robust, as well as encrusting or erect are commonly used. Many other descriptive terms are used informally.

These informal descriptors are useful and appropriate for the level of resolution generally available during field-work. These terms are somewhat subjective and generally used by individual workers within the context of the fauna with which they are dealing. The informal nature of these terms means that a proper formalization of this scheme would not be desirable. This "quick and dirty" approach to growth form analysis can, however, carry

pertinent ecological signals within local studies. However, workers should be cautious of broad comparisons and oversimplifications using informal terms.

*Classifications based on archetypes.*—In archetypal classifications, the name of a growth form is based on genus or family that typifies a distinctive form. For example “cellariform” (articulated cylindrical branches) is typified by members of the genus *Cellaria*. More than twenty archetypal growth forms have received common usage, and many more have been proposed. Studies that have contributed to archetypal growth form classifications include: Canu and Bassler (1920), Stach (1936), Brown (1952), Lagaaij and Gautier (1965) and Brood (1972). These are summarized in Schopf (1969).

An advantage of using archetypal names for growth forms is that a single word (distinction) can be used to carry a great deal of information about morphology, construction and ecology. For those familiar with basic bryozoan groups (typically familial level), a term such as “catenicelliform” or even “cats” clearly brings to mind images of flexible bushes of articulated zooids, rooted to their substrate. An obvious disadvantage of archetypal names is that the term “catenicelliform” means nothing to a person who is not familiar with the characteristics of the family Catenicellidae. The esoteric and technical nature of this classification may prove daunting to nonspecialists.

A potentially greater disadvantage of the archetypal approach to growth form classification is that it is based on differences among discrete groups. That is, each archetype is recognized based on its own characteristic features, with little recognition of shared or nonunique characters. This is illustrated in Figure 1, in which 17 classic archetypal growth forms are characterized based on the characters by which they were originally defined (from Schopf, 1969). Character states not mentioned in original descriptions are left blank in Figure 1. Note that functional or ecological evaluation of more than one growth form at a time results in “apple and orange” comparisons of character classes (e.g., cellariforms and conescharelliniforms can be compared directly based on their “Attachment to substrate” and shape of “Structural units”, but remaining comparisons are of “Orientation” and “Construction” of cellariforms versus “Arrangement of frontal surfaces” of conescharelliniforms. Obviously, each growth form possesses characteristics for (and distribution is controlled by) all of these features. Conclusions for archetypal growth form analysis are directly inferred, however, only from those features listed. The character states for the other features are unknown and, in many cases, variable within archetypal groups.

Another difficulty encountered with the present archetypal classification is that there are not enough described categories available to accommodate the diversity of observed forms. Some archetypal categories therefore include multiple ecologic strategies, and there are forms with no existing archetypal category. Nevertheless, the value of archetypal terms, which have the ability to carry information about a great number of complex character states, should not be dismissed. Even workers who are critical of these terms find themselves using them regularly (if only informally) as a direct result of their convenience (communicative function of growth forms).

*Hierarchical classifications based on geometry and construction.*—In a hierarchical classification, growth forms are grouped based on similar characteristics. For example, all forms might be grouped first as to whether they are encrusting or erect. Secondly they might be subgrouped by other characteristics such as branch shape or flexibility. This strategy allows for more direct comparison of characteristics and their environmental distributions (e.g., encrusting versus erect). Examples of hierarchical growth form applications and classifications include: Lagaaij

	Orientation	Attachment	Construction	Rows of zoecia	Layers of zoecia	Shape	Skeletal thickening	Substrate type
<i>Adeoniform</i>	erect	firmly attached	rigid		bilamellar	lobate	calcareous base	solid
<i>Catenicelliform</i>	erect	rootlets	flexible, jointed	few individuals				red algae
<i>Cellariform</i>	erect	rootlets	flexible, jointed	numerous indiv.	on all faces	cylindrical		variable
<i>Celliporiform</i>					multilaminar	variable		flexible
<i>Conescharelliform</i>		chitinous tubes			radial	spherical or conical		
<i>Eschariform</i>		radicles or direct	strongly calcified	macroserial	bilamellar	foliaceous	frontal	
<i>Flustriform</i>	erect		very flexible					
<i>Hemescharan</i>	erect				unilamellar			
<i>Lichenoporiform</i>	erect, stalked					conical		unmineralized
<i>Lunulitiform</i>		free living			outer face	disk or thimble		sandy bottoms
<i>Membraniporiform A</i>	encrusting		entirely calcified		unilamellar			solid substratum
<i>Membraniporiform B</i>	encrusting		poorly calcified		unilamellar			flat, flexible substr.
<i>Petrilitiform</i>		rootlets			unilamellar			
<i>Pseudovinculariform</i>	erect				unilamellar	hollow cylinder		algal stem
<i>Reteporiform</i>	erect	firmly attached	rigid			fenestrate/reticulate	strongly calcified	solid substrate
<i>Setoselliform</i>	encrusting					spiral growth		small objects
<i>Vinculariform</i>	erect	firmly attached	rigid		all sides	subcylindrical	calcareous base	solid substrate

FIGURE 1—Bryozoan growth forms and character states from Schopf (1969).

and Gautier (1965), Nelson et al. (1988), Viskova (1992), Bone and James (1993), Smith (1995).

There are several advantages of a hierarchical approach to growth form classification. These classifications use descriptive names that have meaning for, and can be applied by, non-bryozoologists (e.g., erect rigid branches). In addition, these classifications are based on similarities among growth forms that allow for direct comparison of characters with ecological significance.

Existing hierarchical growth form classifications have emphasized overall colonial shape. This has arisen from the goal to develop classifications accessible to non-bryozoologists. Frequently, however, function and correlative ecological significance can not be interpreted directly from shape alone. This results in grouping of ecologically unrelated forms based on their superficial form (e.g., the many similar-looking discoidal forms, which can represent quite different growth habits: Free-living avicularia supported, Free-living sedentary, and a variety of Rooted and Pedunculate forms).

Existing hierarchical growth form classifications have not been comprehensive in their treatment of characters. Theoretically, it should be possible to devise a hierarchical classification that encompasses every conceivable growth form. Attempts at expanded hierarchical classifications (e.g., Hageman et al., 1997; Hageman, unpub. data) have proven to be of limited value, primarily for two reasons. Firstly, iterative, convergent evolution means that subcategories have to be duplicated under different primary headings (e.g., subtypes of attachment methods may be included repeatedly under various higher categories of colonial shape). Although this makes the classification complex, it does not necessarily render it unusable. The greater problem is that with any hierarchical classification, by definition, some characters must be deemed more important than others (cf. example above; subtypes of colonial shapes may alternatively be included repeatedly under various higher categories of attachment methods). Different workers may have significantly different views as to the relative importance of growth form characters. Each may be appropriate for their line of questioning, but results and conclusions derived from different hierarchical classifications are not directly comparable.

*Classifications based on ecological principles.*—Variable morphologies may be viewed as different evolutionary or phenotypic responses to environmental pressures within phylogenetically constrained biomechanical limits (e.g., Rider and Cowen, 1977; Jackson, 1979; Cook, 1981; McKinney, 1986a; Jackson and McKinney, 1990). Thus, an ecological parameter may be recognized first in the development of a growth form classification (e.g., feeding strategies) and then morphologic expressions can be evaluated as responses to the related ecological pressures. For example, during filter feeding in bryozoans, there is a trade off between the need to generate a frontal current to bring food into the colony surface versus the need to dispose of equal volumes of waste water. Many of the characteristics of branch size and shape are related to resolving this problem (Winston, 1977, 1979, 1981; McKinney, 1986a; McKinney and Jackson, 1989). Characteristics of branch size and shape are, however, ultimately affiliated with colony shape. Many growth form studies have placed significance on the presence of fenestrate growth forms in a given environment (e.g., Stach, 1936; Lagaaij and Gautier, 1965). There is strong evidence, however, that the fenestrate growth form is simply one of many logical resolutions to the problem of unilaminar branch width versus feeding current generation (McKinney, 1986b).

The advantage of this ecological approach to growth form

classification is that conclusions are more soundly based in ecological theory and observations rather than in speculative or uncertain correlations. There are several disadvantages to the ecological approach. First, our current state of knowledge is concentrated in microenvironmental processes. Macroenvironmental processes and interactions, which are the focus in most traditional growth form studies, are more poorly understood. Next, observations based on modern ecological material do not always translate to the paleontologic record. An additional disadvantage is that an a priori interpretation of ecological strategy may not be the sole factor governing the expression of a morphological characteristic. Until we know a great deal more about these morpho-ecological relationships, workers are encouraged to independently test existing ideas of ecological function and significance of morphological characters. Nevertheless, a greater component of ecological theory needs to be incorporated into the all growth form analyses, as that is the ultimate ground upon which all interpretations are based.

#### ANALYTICAL GROWTH HABIT CLASSIFICATION

The goal of *Analytical Bryozoan Growth Habit Classification* (Fig. 2) is to provide a comprehensive list of characters that can be used to systematically describe the growth habit of every known bryozoan using the same set of criteria. This list of standardized growth habit characters allows for character state comparisons within and among groups of bryozoans, whether the groups be defined by taxonomy-phylogeny, form-function, environment-ecology, or geography-stratigraphy or any combination thereof. These growth habit characters may, in addition, be used to recognize, characterize and analyze groups (e.g., traditional archetypal growth forms), but the classification does not in itself define or classify growth form groups.

*Development of the analytical bryozoan growth habit classification.*—The proposed classification is based on seven basic modifications and adaptations of previous approaches to growth form classifications (cf. Fig. 1 vs. Fig. 2).

1) Individual characteristics used to describe traditional growth forms (Schopf, 1969) are grouped into eight character classes based on form, function, and ecological relationships (Fig. 1).

2) Two additional character classes are included in the new classification (Fig. 2). *Arrangement of zooecial series* is related to strategies of both feeding and growth. *Secondary skeletal thickening* is related to several different strategies of growth and structural reinforcement of the colony.

3) The character class for "Shape" is expanded from one character in traditional classifications (Fig. 1) to five character classes in the new classification based on the concepts of modular growth (structural units and their arrangement).

4) The character class for "Substrate type" is moved to a secondary status. Deemphasis of this category is based on the circularity of this character for the interpretation of environments and the difficulty associated with its diagnosis from fossil material (see discussion below).

The result of these first four modifications is a list of eleven growth habit character classes (Fig. 2). Further modifications deal with how the character states of each of these character classes are treated.

5) Within each of these eleven character classes a list of potential character states is provided (Fig. 2). Descriptive terms are used for character states and the number of categories has been expanded beyond previous classifications in order to provide greater differentiation of forms.

6) In growth habit descriptions, character states are included (filled in) for all of the blank spaces in Figure 1, as well as the two new character classes. This produces a complete description

<b>1. Orientation relative to substrate</b>	A	B	<b>7. Structural units</b>	A	B
Encrusting	1	1	Single zoecium	1	32
Massive	2	2	Cluster of 2-5 zooecia	2	33
Erect-continuous	3	3	Runner-Branch with flat surface	3	34
Pedunculate	4	4	Runner-Branch with convex surface	4	35
Fungiform	5	5	Sheet	5	36
			Lobe	6	37
<b>2. Attachment to substrate</b>			Disc	7	38
Cemented	1	6	Solid Cylinder	8	39
Rooted	2	7	Hollow Cylinder	9	40
Free-living, sedentary or tumbled	3	8	Solid Cone-Cap-Dome	10	41
Free-living, avicularia supported	4	9	Hollow Cone-Cap-Dome	11	42
Endolithic	5	10	Sheroid to Ellipsoid	12	43
Regenerated (erect)	6	11	Nodule	13	44
<b>3. Construction</b>			<b>8. Dimensions of structural units</b>		
Rigid contiguous	1	12	Straight or Flat	1	45
Articulated, indeterminant cuticular connections	2	13	Curved or Folded	2	46
Articulated, determinant cuticular joints	3	14	Primary 3-D object	3	47
Flexible weakly-calcified	4	15			
Uncalcified	5	16	<b>9. Frequency of bifurcation</b>		
			No bifucations	1	48
<b>4. Arrangement of zoecial series</b>			Infrequent bifucations (1-2 from primary)	2	49
Uniserial	1	17	Frequent bifucations (3-5 from primary)	3	50
Biserial	2	18	Very frequent bifucations (6 or more)	4	51
Oligoserial (3~12)	3	19			
Macroserial nonmaculate	4	20	<b>10. Dimensions of bifurcation</b>		
Macroserial maculate	5	21	No bifucations	1	52
			Bifurcation in one plane (fan)	2	53
<b>5. Arrangement of frontal surfaces</b>			Bifurcation in more than one plane (bush)	3	54
Unilaminate	1	22			
Bilaminate	2	23	<b>11. Connection of structural units</b>		
Trilaminate	3	24	No lateral connections	1	55
Quadrate	4	25	Fused structural units	2	56
Radial	5	26	Extrazoecial skeletal connections	3	57
Multilaminate	6	27	Cuticular tubes connecting structural units	4	58
			Stolonate connection of zoecial units	5	59
<b>6. Secondary skeletal thickening</b>			Calcified tubes connecting zoecial units	6	60
No secondary skeletal thickening	1	28			
Frontal/obverse skeletal thickening	2	29	Substrate type		
Basal/reverse skeletal thickening	3	30	Hard primary substrate		
Frontal and basal skeletal thickening	4	31	Hard secondary substrate		
			Particulate substrate		
			Live organic substrate		

FIGURE 2—Analytical Bryozoan Growth Habit Classification. Seven character classes, with hierarchical character states. Character codes in column A are for states taken within each of the eleven character classes. Character codes in column B are for all 60 character states used independently (present absent).

for each colony and allows for comprehensive comparisons among all colonies.

7) Character states for each character class are recognized in an ecological context wherever possible. That is, one or more ecological strategies related to physio-bio-chemical conditions can be hypothesized for each character-state listed in Figure 2. It should be emphasized, however, that the classification is intentionally descriptive and not directly interpretive. Actual ecological controls over the distribution of these features must be tested further before generalized models can be adopted. A fully interpretive classification of growth habits will undoubtedly take a different form.

It is not the goal of this classification to fully differentiate the morphology of every bryozoan colony. Bryozoan workers will invariably be able to subdivide proposed character states to account for variation within their group of speciality. The goal of this classification is to provide a list of character classes that are common across all Bryozoa with approximately equal ecological "difference/distance" between character states within a character class. Note that some obvious distinctions are not made directly, but are accounted for by a combination of character classes. For example, the difference between free-living sedentary and free-living tumbled is not distinguished by separate categories of substrate attachment. Their forms are, however, distinguished by the shape category, conical versus nodular. Specialists are encouraged, however, to develop standardized subcategories of existing characters to further differentiate their groups. Such characters can be incorporated into growth habit analyses, given proper coding/weighting for numerical analyses.

This classification was tested and refined using Modern marine bryozoans from the southern margin of Australia (330 species, from 191 genera, from 77 families and four orders/suborders). Although not comprehensive, consideration was also given to deep sea forms (Cook, 1981; Gordon, 1987), tropical non-reefal forms (Canu and Bassler, 1929; Cheetham, 1963), ctenostomes (Hayward, 1985), Paleozoic cryptostomes (Blake, 1983; Karklins, 1983), cystoporates (Utgaard, 1983) and trepostomes (Bassler, 1953).

*Advantages.*—The greatest advantage of this scheme is that it allows for more comprehensive and systematic analysis of relationships among morphological growth habit characteristics and the environmental conditions in which they are distributed. This is in contrast to other methods in which the overall growth form name represents some variable combination of known and unknown characters. As correlations between individual growth habit characters and their environments become better understood, relationships between overall zoarial morphology and environment will have greater significance.

The proposed scheme is versatile and allows for comparisons among varied forms based on standardized descriptors. Virtually any growth form can be described under this scheme (Paleozoic timanodictyid to a modern ctenostome).

Taken as a whole, Figure 2 is an approximation of the morpho-ecospace occupied by Bryozoa zoaria. This multidimensional space, defined by growth habit characters, can be used to compare morphological diversity and disparity through time and environments. Growth habit characters can also be compared with, or independent from, the phylogenetic affinities of taxa. This allows for the tracking of ecological and/or macroevolutionary trends through space and time.

*Disadvantages.*—The complexity of this analytical growth habit scheme undoubtedly generates points for criticism, but this is a direct result of the complexity of the biological system. This method may appear to approach a complete description of a taxon. However, only colony-level characters are employed here. With the exception of avicularia supported free-living forms, no

zoecial, heteromorphic or reproductive characters are included. Comprehensive descriptions of bryozoan zoaria and their growth habit strategies are more complex than has been previously acknowledged.

A potential criticism of the method is that its complexity does not allow for easy naming of growth forms for communication purposes. Although the goal of *Analytical Growth Habit Analysis* is one of completeness and not convenience for its own sake, there are ways in which this classification may be modified for more general purposes. Growth habit terms may be used as modifiers to well established archetypal names. For example, "reteporiform" refers to cemented fenestrate forms, but modifiers can be added to differentiate among: 1) cemented and rooted fenestrate forms; 2) unilaminar and bilaminar fenestrate forms; and 3) rigid and weakly-calcified flexible fenestrate forms. Although this may be useful for isolated comparisons, it is evident that even in this example, we are quickly approaching the analytical growth habit approach simply by differentiating various "reteporiform" bryozoans.

A second approach is to use only a select subgroup of the eleven fundamental characteristics. For example, a study could be performed using only characteristics of *Orientation relative to substrate*, *Attachment to substrate* and *Structural units*, in a hierarchical classification (e.g., erect-rooted-sheet). If such subgroup classifications are used, however, workers should clearly justify their selection criteria, and acknowledge restrictions for broader comparisons.

This classification does not take full advantage of ecological strategies recognized primarily for encrusting forms such as budding patterns (Lidgard, 1985; Lidgard and Jackson, 1989). For example, distinctions among intrazoooidal, zoooidal, and multi-zoooidal, as well as lineal and non-lineal budding are not made here. Although budding parameters are important for overall colonial growth strategies, in many cases, they require a specialist to establish (recognize) the character-state. In addition, bryozoan budding parameters have not been fully explored in erect forms. Nevertheless, budding strategies, and other zoecial characters such as the distribution of polymorphs (Schopf, 1973), reproductive strategies (Jackson and Coates, 1986; Herrera and Jackson, 1996) and overall colonial integration (Boardman and Cheetham, 1973) are all growth habit characters that could be treated by methods similar to those presented here and tested for their significance as environmental indicators.

#### PRESENTATION OF THE ANALYTICAL BRYOZOAN GROWTH HABIT CLASSIFICATION

Characters of the *Analytical Bryozoan Growth Habit Classification* are presented and discussed in the following section. The potential ecological significance of character classes is discussed in the text, but detailed review of ecological strategies associated with every character state is beyond this paper (see Gautier, 1962; Blake, 1981; McKinney and Jackson, 1989; and references therein). Character states illustrated in Figures 3 and 4 are intentionally idealized in order to convey the overall concept of a character-state rather than to represent an example from a single species. A variety of examples is presented in Figures 5 and 6, with growth habits of each specimen fully characterized in the Appendix.

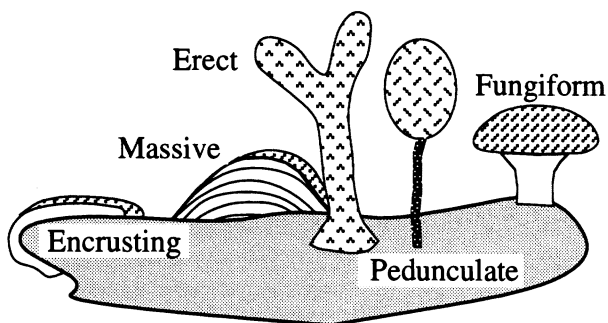
#### ORIENTATION RELATIVE TO SUBSTRATE

Orientation refers to the orientation of the feeding surface of a colony relative to its substrate. Different growth and feeding strategies may apply depending on whether a colony's surface is very near or has risen above the substrate (Fig. 3.1).

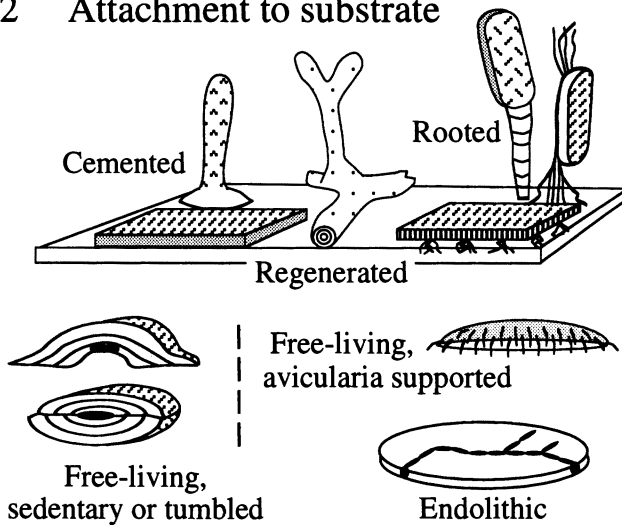
*Encrusting.*—Bryozoan colonies that provide a thin cover over their substrate are known as encrusting forms. Encrusting



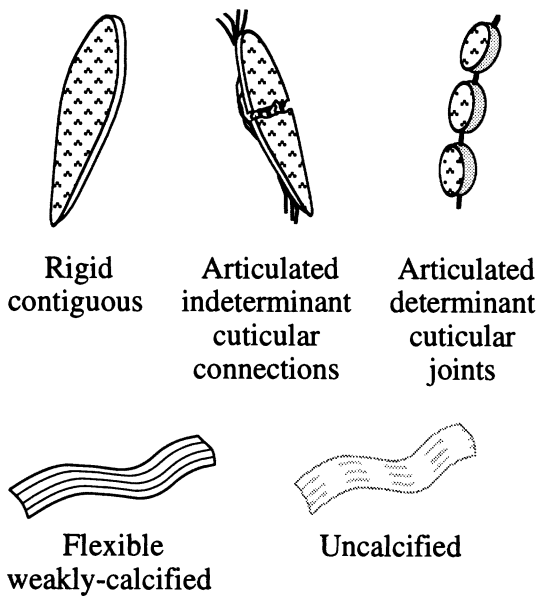
1 Orientation relative to substrate



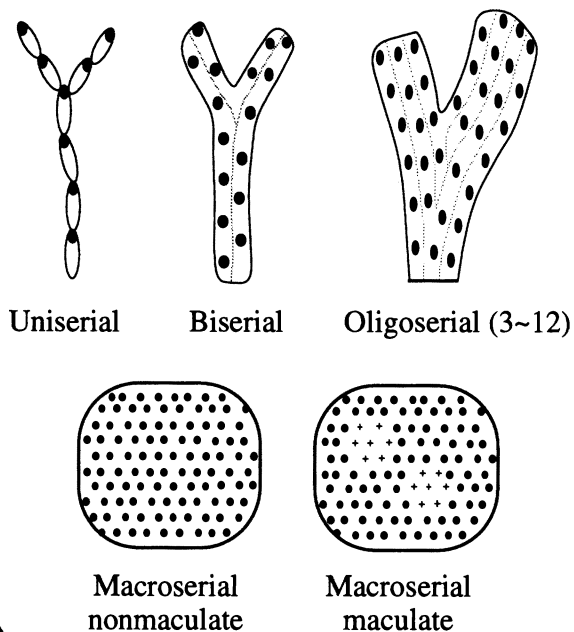
2 Attachment to substrate



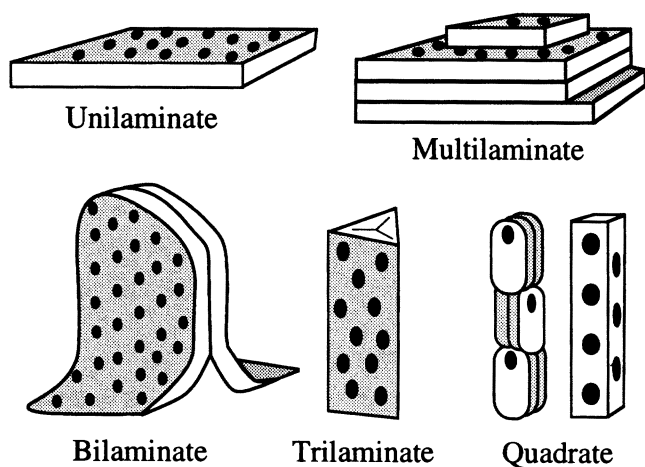
3 Construction



4 Arrangement of zooecial series



5 Arrangement of frontal surfaces



6 Secondary skeletal thickening

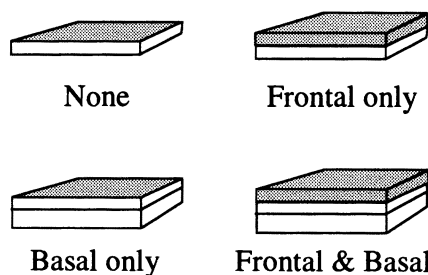


FIGURE 3—Idealized examples of character states for bryozoan growth habits for character classes related to the orientation of the colony and its occupation of space (growth).



colonies generally result in flat or irregular runners, strips, or sheets. Encrusting forms are confined to the environmental conditions at the substrate-water interface (Vogel, 1981). The term "encrusting" does not relate to method of attachment (i.e., encrusting forms may be cemented or rooted to any type of substrate). Note also that life position is irrespective of absolute orientation (i.e., a colony may encrust a vertical wall).

*Massive.*—The distinction between encrusting and erect forms is somewhat arbitrary in the case of thick, multilaminar, massive colonies. During early colonial development, massive forms are effectively encrusting their substrate. However, some multilaminar colonies build en masse eventually to produce significant relief from their original substrate. Because mature massive forms have escaped their primary substrate, yet do not have determinate erect growth, a distinction is made here for massive forms.

*Erect-continuous.*—Some Bryozoa have the ability to bud in a manner that allows the colony to rise above the substrate in a self-supported, erect form. The term "erect" refers to growth away from a substrate and may result in forms growing horizontally or even downward. A distinction is made here between erect forms that have zooecial apertures (active or dormant), from the base to the tip of the colony (erect-continuous), and those that do not (pedunculate, or fungiform). An *Erect-continuous* growth habit allows the colony to minimize competition for substrate and to access nutrients higher in the water column.

*Pedunculate.*—Many erect bryozoans are supported above their substrate by long barren sections of their colony that contain no feeding zooids. This barren section (peduncle or stalk) allows the main feeding region of the colony to be supported above the substrate. Although peduncles are all typically constructed of kenozooids (nonfeeding polymorphic zooids), peduncles may range from articulated calcareous plates (e.g., *Adeona*), to a bundle of cuticular kenozooids, to a single, large, soft rootlet. Pedunculate forms come in a wide variety of colony shapes and constructions (e.g., bilaminar sheets of *Parmularia*, multilaminar spheres and nodules of *Sphaeropora*).

*Fungiform.*—Some forms develop continuous, calcareous stems, with zooids concentrated at typically flaring ends. Fungiform growth allows feeding zooids to be concentrated above the substrate in a manner similar to pedunculate forms. Barren regions (stems) of fungiforms are usually constructed of exterior skeletal walls. Fungiforms are typical of several early Paleozoic trepostome and a number of post Paleozoic tubuliporate (=cyclostome) groups.

#### ATTACHMENT TO SUBSTRATE

The relationship between bryozoan colonies and their substrate (method of attachment) has been largely neglected in bryozoan growth form studies, yet it is very important for paleoecological reconstructions (Figure 3.2). The method of attachment may not be evident from single colonial skeletal fragments, but it is generally consistent within clades (generic and often family-level). Substratal relationships can usually be inferred for a fossil species from detailed morphological studies of populations.

*Cemented.*—The term "cemented" applies to all bryozoans attached directly to any substrate (i.e., not just solid, hard substrates). No distinction is made here between forms that cement over their entire basal surface versus those that have multiple contact points. The concept of a "calcareous basal structures" of Schopf (1969) for certain erect cemented forms is treated here under the category of Secondary skeletal thickening.

*Rooted.*—Many bryozoans are rooted to their substrate. These rootlets, called radicles by some early authors, attach to a wide

range of substrate types, including plant and animal hosts. Different types of rooting structures have developed, independently, in several clades. Cuticular kenozooids vary in size and rigidity among taxa. In some taxa rootlets are similar to bundles of small, firm tubes (e.g., *Catenicella* and *Cellaria*). In others, numerous rootlets are thin, like hairs (e.g., *Hiantopora*). Another, independently developed rooting system consists of soft, turgid, extrazoidal tubes (e.g., *Sphaeropora* and *Parmularia*). Other forms are attached by rooting structures consisting of calcareous plates articulated by cuticle (e.g., *Adeona*, *Crisia*).

Distinctions are not made in this classification among various types of root formation. A potentially more informative ecological characteristic is the distinction between forms that merely attach to a hard or firm substrate and those that allow for stabilization of unconsolidated sediment. Recognizing rooting structures of any type from fossil or dead modern material is not always easy. Diagnosis of rooting attachment is typically based on taxonomic uniformitarianism. However, distinctive morphological characteristics are present in these forms that do allow specialists to verify rooting life habits.

*Free-living sedentary or tumbled.*—Several groups of bryozoans have independently developed the ability to grow on soft, particulate substrates. Virtually all bryozoans require a solid substrate on which to metamorphose (although see Håkansson, 1975). Free-living forms are able to subsequently grow beyond (incorporate into their skeleton) their original, sand-sized, hard substrate. Mature colonies may become several orders of magnitude larger than their nuclear substrate and are essentially unattached or free-living. These free-living, sedentary forms are typically tabular or hemispherical and commonly have imbricated margins that have grown out over soft sediment (*Celleporaria*). In higher energy environments free-living forms may be intermittently overturned. Alternative growth on either side of these tumbled forms results in fusiform or nodular colonies, with their small original substrate (litho- or bioclasts) as a core. These are the ectoproctoliths of Rider and Enrico (1979).

*Free-living avicularia supported.*—A number of unattached forms are actually supported above their substrate by the long mandibles of marginal avicularia (Cook and Chimonides, 1978). These forms are usually discoidal or cap shaped (lunulitiform), but are distinguished by their conspicuous marginal avicularia (e.g., *Lunularia*, *Cupuladria*, and *Otionella*). In all of these forms, avicularia can remove sediment from the surface of the colony, unbury the colony from a moderate sedimentary depositional event, and stabilize the colony position above the substrate (McKinney and Jackson, 1989). Many taxa can reorient the colony after it has been overturned using the mandibles. The genus *Selenaria* is even motile, using avicularian mandibles to skip along the substrate (Cook and Chimonides, 1978). Although this character state (Free-living avicularia supported) is largely based on the presence of the long mandibles of marginal avicularia, it is recognized separately from other free-living forms because: 1) it has developed independently in at least two different clades; and 2) it represents a fundamentally different life mode, with a rich and diverse record.

*Endolithic.*—Endolithic forms bore into hard substrates, commonly calcareous shells. They are typically small, simple colonies in the form of uniserial runners or branches, with or without stolons. Endolithic forms are potentially important paleoecological indicators (Boekschoten, 1966), but they are not major contributors to bioerosion in comparison with algae or sponges.

*Regenerated (erect).*—Forms that regenerate after the original colony has been removed from its substratal attachment are technically neither attached nor free-living. For example, a branch may be broken off an erect form in a storm and transported some

distance. Subsequently, if the fragment is large enough to provide a stable base, an erect colony of the same genotype may grow from the unattached fragment. Regenerated forms are included here as a separate category because it is a common occurrence in some taxa and may be a strategy for propagation (Blake, 1976; McKinney, 1983; Winston, 1983).

#### CONSTRUCTION

Construction has been an important character in previous growth form classifications (Fig. 3.3). Construction is generally used as a proxy for flexibility and is related to suitability for life in a region of high wave/current energy and/or rapid sedimentation rate, where the ability to slough sediment is a great advantage (Lagaaij and Gautier, 1965).

*Rigid contiguous.*—Many bryozoan colonies are composed of rigid (inflexible), contiguous calcium carbonate skeletons. Rigid colonies can range from delicate and brittle, to strong and robust.

Robustness, which is not the same as rigidity, is a function of the thickness of the zooecial walls, degree of secondary skeletal thickening, arrangement and relative number of zooecial rows and layers, and overall colony shape and construction. Relative robustness is, therefore, represented by a combination of these characters and not treated as a separate category here.

*Articulated, indeterminate cuticular connections.*—Some colonies with otherwise rigid continuous segments also have supplementary bundles of long, cuticular tubes (kenozooids) that support the colony on the reverse or lateral sides of the branch. Such colonies generally do not have predetermined points of articulation. However, if a colony is fractured during life, flexible connections result at points where the rigid branches break (e.g., *Caberea*, *Menipea*).

*Articulated, determinate cuticular joints.*—Some bryozoan colonies are constructed with rigid segments that are connected by flexible joints (e.g., *Catenicella*, *Cellaria*). Cuticular joints pass between distal and proximal pores of successive segments. Articulated skeletons are generally quite flexible and may even appear soft.

*Flexible, weakly-calcified.*—Some bryozoans have flexible colonies as a result of incomplete or weak calcification. These colonies generally have not played an important role in sedimentologic, bryozoan growth form analyses because their skeletons are poorly preserved. They are, however, ecologically important in modern settings. Flexible, weakly-calcified bryozoans have a wide range of colonial shapes (e.g., *Membranipora* and *Carbasea*).

*Uncalcified.*—Many bryozoans (primarily ctenostomes and a few cheilostomes) are uncalcified. Although these forms are of minimal interest as body fossils, uncalcified bryozoans are often important as host substrates for abundant, calcified epibiotic bryozoans (Hageman et al., 1996). Uncalcified forms are often well preserved as bioimmured specimens (Todd, 1994).

#### ARRANGEMENT OF ZOOECIAL SERIES

Bryozoan colonies grow by asexual budding of individual zooids. The way in which they propagate these units reflects adaptive ecological strategies for growth and influences generation of feeding currents (Winston, 1979; McKinney, 1986b). Feeding strategies can be inferred from skeletons based on how many zooids there are across a branch (approximates degree of interaction imposed on neighboring lophophores). Five categories of branch width are recognized here (Figure 3.4).

*Uniserial.*—Uniserial budding produces a chain (runner or branch) one zooid wide.

*Biserial.*—In colonies that are biserial, zooids share one wall and result in a strip two zooids wide. Uniserial and biserial forms

can be either encrusting or erect and are typified by rapid extension of colony and independently feeding polyps (McKinney and Jackson 1989).

*Oligoserial (3~12).*—Colonies that grow by budding several zooids along a growing margin are oligoserial. An upper limit of approximately 12 zooecial rows across the branch is placed on oligoserial colonies. In examples of bryozoan feeding behavior given in Winston (1977, 1979, 1981) and McKinney (1986), no zooecium is typically more than six zooecial positions away from an excurrent chimney or colony edge. This is the approximate width at which each zooid may still expel water from the edge of a flat colony without having to develop an integrated, communal feeding strategy. Oligoserial forms can be encrusting to erect, and are typically narrow strips, branches or cylinders.

*Macroserial non-maculate.*—When colonies are wider than approximately 12-zooids, they must develop an integrated, communal feeding strategy or be subjected to feeding stresses arising from interfering feeding currents. Communal feeding strategies (cooperative feeding currents) may not be reflected in the skeleton of the colony (Winston, 1979; McKinney, 1986a) resulting in skeletal surfaces of undifferentiated zooids. These forms are called nonmaculate. The subjective cut off of 12-zooids is based on observations of published illustrations for many broad branched non-maculate and maculate specimens.

*Macroserial maculate.*—Macroserial colonies with surfaces that have differentiated regions for water current outflow (e.g., clusters of nonfeeding polymorphs), barren extrazooecial regions or oriented apertural structures (lacunae) are *maculate* forms. Both types of macroserial forms may be encrusting to erect, and of various shapes such as wide strips, thick cylinders or broad sheets. Macroserial forms are generally found in more stable microenvironments and are committed to a local microhabitat.

#### ARRANGEMENT OF FRONTAL SURFACES

This growth habit character class reflects various strategies bryozoans use to occupy space. Growth is accomplished by adding zooecial units in various budding directions and orientations (Figure 3.5).

*Unilaminate.*—Colonies that grow as a single layer of zooids are unilaminate. Unilaminate forms may be encrusting or erect and uniserial to broad sheets.

*Bilaminate.*—Colonies that grow erect in two back-to-back layers are bilaminate. Some bilaminate colonies arise from two essentially unilaminate sheets encountering and supporting each other (same or different colony or species). Other bilaminate colonies arise from a much more determinate growth (e.g., minor, early encrusting phase as a precursor to predetermined erect growth).

*Trilaminate.*—Some unusual forms are three-sided prisms (e.g., *Prismopora*).

*Quadrangle.*—Some specialized forms are four-sided, narrow branches that are essentially alternating pairs of back to back units (Figure 3.5)

*Radial.*—Many cylindrical forms arise from a single layer of zooids budded in a radial pattern (wagon wheel transverse section). These can be thin narrow branches or thick, macroserial branches.

*Multilaminate.*—Colonies that result in multiple layers of zooids, either by frontal budding or self-overgrowth, are multilaminate. Note that all multilaminate colonies begin as another category in this class early in their development (e.g., unilaminate or radial). No differentiation is made here among multilaminate forms.

## SECONDARY SKELETAL THICKENING

Secondary, multizooecial thickening of the skeleton is an important structural component of many bryozoans (Cheetham et al., 1981). Secondary thickening serves to support larger erect forms and/or to make them more resistant to higher energy environments. As many workers have noted (e.g., Wass, 1991), secondary skeletal thickening may also profoundly affect the exterior appearance of colonies through their development. Many bryozoan groups exhibit *No secondary skeletal thickening* (Fig. 3.6). Other groups exhibit thickening on the *Frontal-obverse surface only*; *Basal-reverse surface only*; or on *Both the frontal and basal surfaces*.

## COMPONENTS OF OVERALL COLONY SHAPE

The overall shape of bryozoan colonies has been emphasized in most growth form classifications. The topic of shape can be addressed from two end points on a continuum. One approach to shape is the recognition of discrete forms or categories (e.g., a cube versus a sphere versus a tree), which has been the approach used in traditional growth form analyses. The alternative approach is to describe shapes in a mathematical context based on parameters of geometric growth. This has been used effectively in modeling bryozoan growth, especially in branching forms (Cheetham and Thomsen, 1981; Cheetham et al., 1981; McKinney and Raup, 1982; Gardiner and Taylor, 1982; Bell, 1986; Callaghan et al., 1990). Complex plant forms, similar to those of bryozoans, have been modeled exquisitely using Lindenmayer systems and other modeling languages (Prusinkiewicz and Lindenmayer, 1990). Ecological principles or attributes are usually associated with parameters for mathematical models, and these models are useful in interpreting theoretical growth strategies and/or restrictions. However, mathematical models do not lend themselves to viable classifications and simple interpretations primarily because they emphasize similarities among innumerable intermediate forms. The ecological significance between closely related forms becomes blurred.

An intermediate approach is applied here. The category of "shape" is divided into five character classes based on concept of modular growth of a colony. In this classification, the basic module is the *Structural unit* (e.g., branch or sheet). In general, the structural unit is defined as the region of a colony between bifurcation events. Thus, nonbranching colonies are made up of a single structural unit. However, articulated colonies may have several segments (subunits) between bifurcation events. By convention, discrete segments of articulated forms are considered structural units (one node of *Cellaria*, *Crisia* or *Catenicella*). Structural units are difficult to define in stolonate forms such as *Aetea*, or sheets comprised of interconnected zooids such as *Retevirgula*. In such cases, the individual zooecium is considered the structural unit.

The hierarchical aspect of modular growth in bryozoans introduces great complexity into the description of colony shape. This scheme was developed to acknowledge both the variable position of structural units within the hierarchy of modules and to be flexible enough to accommodate them, but without the user specifically having to define their hierarchical position.

Once the structural unit has been recognized, additional character classes provide description of the dimensions, arrangement and connection of the units. This approach provides for accurate descriptions of complex forms and allows for comparison of subcategories within overall shape (e.g., straight cylindrical branches with many bifurcations in a single plane (fan), versus straight cylindrical branches with many bifurcations in multiple planes (bush), all in the context of simultaneous comparison of many other varied forms). As a consequence, this method does

not necessarily provide for optimal descriptive convenience (communication function). Some workers may choose to combine these four categories into a single shape character using traditional terms. It should be noted, however, that some discrete traditional categories are much more similar to each other morphologically and ecologically than others. For example, the difference between a unilaminar fenestrate sheet and anastomosing, dendritic branches is really just a matter of whether adjacent branches fuse or not (Gordon, 1989, p. 75, description of *Reteporella*; McKinney, 1986b). This five-part approach to shape both emphasizes the similarities and highlights the similarities and differences among growth and form (cf. Thompson, 1917).

## STRUCTURAL UNITS

Although there is an infinite range of potential colony shapes, discrete categories have been established here (Fig. 4.1) based on observed bryozoan forms and ecological strategies associated with them. This classification may not characterize every colonial shape to its fullest, however, a single most appropriate category should be evident for virtually every form.

*Single zooecium*.—In the case of many stolonate forms and quasi-sheet forms (e.g., *Retevirgula*), single zooids serve as structural units. These units are then connected by stolons (calcareous or not), or thin lateral tubes. Some articulate zooidal forms are also considered to have a single (autozooecial) structural unit.

*Cluster of 2–5 zooecia*.—A structural unit comprised of a small cluster of zooids (2–5) is typical of articulated forms such as *Catenicella*. Some mature encrusting colonies are comprised of a cluster of a small number of zooids. Clusters are also typical of small, deep sea and interstitial rooted forms.

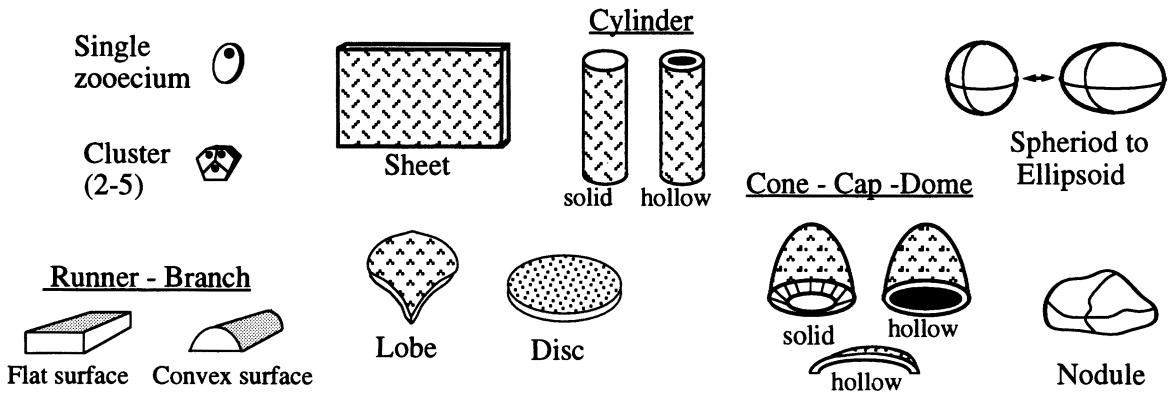
*Runner-branch*.—Any structural unit comprised of a narrow to broad band or strip of zooids is placed under a single category. The term runner is typically applied to encrusting forms and branch to erect forms. All of these names, as well as thin thread-like and broader ribbon-like forms apply to the concept of elongate strips (other characters describe their width and thickness). Two categories of *Runner-Branch* are recognized here, based on whether their surfaces are predominantly *Flat*, or *Convex*.

*Sheet*.—A structural unit comprised of a broad, primarily two-dimensional expanse of zooids is a sheet. A sheet can be either encrusting or erect and of variable thickness, number and shape (see below). A semantic problem may arise in distinguishing between: 1) a continuous sheet of zooids; and 2) a series of anastomosing branches that result in essentially a fenestrated sheet. Because this category defines a structural unit, a fenestrate colony is treated as a series of branches, based on its morphogenesis.

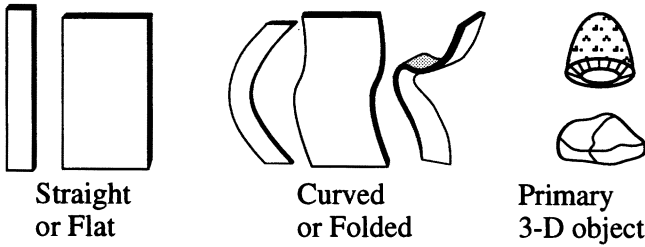
*Lobe*.—Structural units that are intermediate between strips and sheets arise from cases where a narrow strip expands systematically to a broader sheet, resulting in a lobe. Although potentially part of a continuum, a separate category is included here because some taxa clearly have determinate lobe shapes (many encrusting tubuliporates). This category is also appropriate for some erect forms with narrow bases and broadly expanding branches.

*Disc*.—A special case of growth for a sheet arises from a radial budding pattern from the ancestrula, resulting in a disc. A semantic problem arises in that many encrusting sheets display a disc or spot shape in early colony development. The term disc should be reserved for forms that display a clearly determinate circular shape in mature stages of development (as observed from populations). Discs are known primarily from encrusting species, but some very flat, unattached "cones" and "caps" have been referred to as "discs" in other classifications.

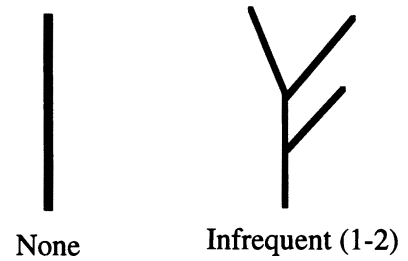
1 Structural units



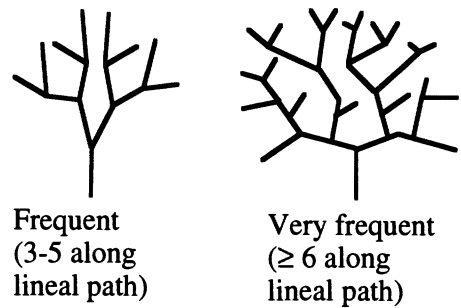
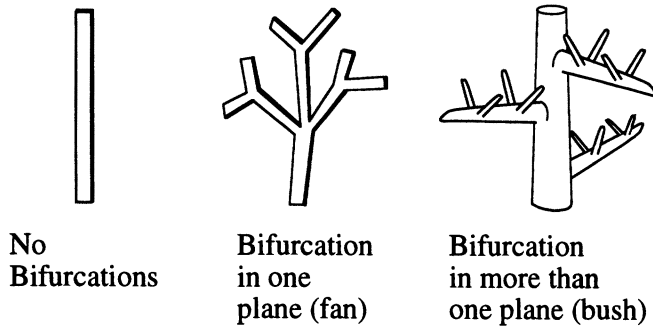
2 Dimensions of structural units



3 Frequency of bifurcation



4 Dimensions of bifurcation



5 Connection of structural units

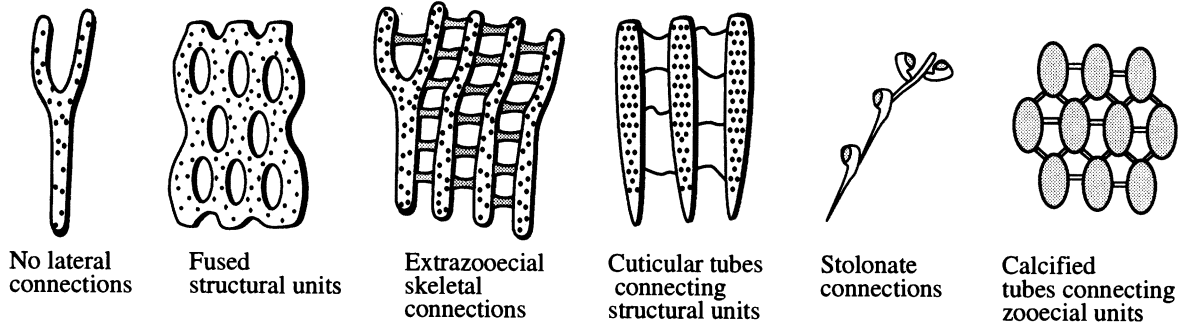


FIGURE 4—Idealized examples of character states for bryozoan growth habits for character classes related to the over all shape of the colony based on the arrangement of modules (structural units).

*Solid cylinder.*—Structural units that are elongate and round (radial) in cross section are cylinders. Cylinders typically have zooids on surfaces all the way around. Technically however, some specialized unilaminate and bilaminate branches may approximate cylindrical cross sections (as a result of secondary, skeletal thickening), resulting in arbitrary distinctions through a continuum. However, a large number of erect forms have determinate, solid cylindrical growth.

*Hollow cylinder.*—Hollow cylinders are typically the result of encrusting forms that completely surround the stem of a host plant or animal substrate. Erect self-supported growth of hollow branches is common in some mature forms that grow beyond the limits of their original host organic substrates in a determinate manner.

*Solid cone-cap-dome.*—A variety of growth habit strategies result in colonies (single structural units) that are cones, caps, or domes. These can be high-peaked conical, hemispherical, or low-peaked nearing discoidal. Solid forms are typically rooted (by their apex) or are unattached and sedentary.

*Hollow cone-cap-dome.*—This category is comprised of colonies with single structural units in the form of cones, caps, or domes that are hollow (convexo-concave). These forms are typically unattached motile or sedentary, although some are rooted.

*Spheroid to ellipsoid.*—This category encompasses a range of three-dimensional, morphologically continuous, single objects. These subcategories may be separated at a later date if distinctions among them proves viable and useful. These forms are typical of some modern rooted forms (*Sphaeropora*) and of some unattached, tumbled forms. Spherical colonies are also typical of some small encrusting epibiontic forms that have very small attachment sites.

*Nodule.*—Nodular colonies are irregular three-dimensional objects, which are typical of unattached, tumbled forms (ectoprocoliths) and multilaminate, epibiontic encrusting forms (i.e., over grown irregular, hollow cylinder).

#### DIMENSIONS OF STRUCTURAL UNITS

Bryozoans have developed different degrees to which they can occupy three-dimensional space, which are primarily limited by their budding loci (Blake, 1980). Bryozoans that are restricted to growth (budding at a leading edge) in approximately a single plane are recognized as *Straight or Flat* (Fig. 4.2). Those forms that grow out of their primary plane are *Curved or Folded*. A third category is recognized for *Primary three-dimensional objects*. Encrusting forms conform indiscriminately to the dimensions of their substrate. Therefore, all encrusting forms are registered, as a convention, as straight or flat (as if encrusting a plane). These character states represent a significant, but necessary simplification of the complex nature of bryozoan growth.

#### FREQUENCY OF BIFURCATIONS

Bifurcation, or production of multiple structural units through branching, applies to both linear branches and runners, and to planar sheets. No distinction is made here between dichotomous bifurcation at growing tips and secondary lateral budding of branches. Ultimately, this character class is a proxy for the efficiency with which a branching colony can cover the total surface area (or volume) that the maximum limits of the colony occupy. At one extreme of a continuum, we would have a fan comprised of many bifurcating branches with short segments and at the other a twiggy arborescent form with a few long branches (same branch width and total number of zooids).

It would be desirable to have a simple, objective method with which to place forms into a number of discrete categories along

this continuum. Although the geometry involved in growth models is well established (Cheetham et al., 1981; Gardiner and Taylor, 1982), measurement and calculation for all parameters are not practical. Parameters include variable lengths of segments between bifurcations and variable bifurcation angles. In addition, the width of a branch segment influences the perception of relative branch frequencies.

Branch frequency here is based on the number of bifurcation events throughout the length of a complete branch path, base to tip or from the primary lineal branch (Fig. 4.3). If there are one or two branch points along the path then there are *Infrequent bifurcations*; if three to five events are present then bifurcations are *Frequent* and if there are six or more present, bifurcations are *Very frequent*. These distinctions are based on the integer cut-off values of the log(n) of the number of branches produced by an increasing series of bifurcation events (Fibonacci series). In colonies with trifurcating branching events, these cut off values are adjusted; one to two trifurcations in a series is *Frequent* and three or more is *Very frequent*.

#### DIMENSIONS OF BIFURCATIONS

Although bryozoans can occupy space by budding in three dimensions to produce curved or primary three-dimensional objects (Dimensions of structural units), it is also common for these growth strategies to be implemented at points of new branch formation (Fig. 4.4). Those forms that are restricted to a *single plane* of budding at bifurcations result in planar fans. Those forms that branch in *more than one plane* result in three-dimensional bushes. Note that higher dimensions of shape can also be superimposed on these, such as curved fans (e.g., *Caberea* and *Lyropora*), but these differences are not accommodated in this scheme.

#### CONNECTION OF STRUCTURAL UNITS

In more complex colonies, multiple structural units are connected by various mechanisms (Fig. 4.5). The primary purpose for connections is to provide additional structural support. Connecting mechanisms often prove very efficient in that they allow colonies to grow beyond the size to which they would be limited based on the strength of the primary colony alone. Bryozoans with no branches are placed in the same category as branched forms that do not have any lateral connecting structures.

*Fused structural units.*—In some bryozoans, two branches that meet may fuse to provide continuous skeleton across the boundary. This behavior may be relatively random, as in the three-dimensional boxwork of some celeropariids, or may be very deterministic as in many reticulate forms such as phylloporinids and phidoloporids.

*Extrazooecial skeletal connections.*—Highly coordinated skeletal growth is seen in many fenestrate bryozoans, where cross bars of extrazooecial skeleton connect branches in a very regular form.

*Cuticular tubes connecting structural units.*—Some rooted forms develop cuticular connections between lateral branches (e.g., some cellarids and caberids). This allows radiating, planar branches to become connected as fronds.

*Stolonate connections.*—There is a wide range of structures that connect individual or small clusters of zooids. Some of these are long extensions of the zooecium of an autozooid, whereas other connecting mechanisms are constructed by heterozooids.

*Calcified connecting tubes.*—A number of encrusting forms are essentially separate zooecia that are connected by calcareous tubes (e.g., *Retevirgula*).

## SUBSTRATE TYPE

The type of substrate on which a bryozoan lives (lived) is an important character for paleoenvironmental reconstruction and has been used as a character in some growth forms classifications. However, substrate type is not included as a formal character class here for two reasons. First, it is not a morphological characteristic and therefore invites circularity in ecological interpretations. Secondly, this character can usually only be determined with confidence by direct observation from live material. Nevertheless, substratal information is so valuable for developing ecological models for growth habit distributions, that it is worth recording whenever possible. A list of substrate types is provided here for the local substratum on which the bryozoan is actually living (regional substrate may be different).

**Hard primary substrate.**—Hard or firm sea-floor such as primary bedrock or cemented hardgrounds provide favored substrates for many bryozoans. Primary substrates are lithologic in origin. The size limit used to distinguish between small primary substrates (boulders, lithoclasts) and large particles (gravel, cobble) is subjective and is partially dictated by the relative size of the bryozoan colony.

**Hard secondary substrate.**—Many bryozoans live on hard objects that are large enough to provide suitable substrate, but are not of lithologic origin. These include dead biogenic structures such as shells and skeletons, and objects produced by humans, such as glass, plastic and metal refuse and building structures. Distinctions between bryozoans originally growing on dead shells (secondary substrate) and those growing on shells with live occupants (epizoans) may be difficult to establish with fossil material, but the ecological significance between the two is more than just conceptual (i.e., ecological relationships of fouling, commensalism and symbiosis versus nonselective settlement on a stable, inert substrate).

**Particulate substrate.**—Some bryozoans have the ability to grow on unconsolidated particulate substrates. Many of these forms are members of the "sand fauna" discussed by Cook (1965, 1966, 1979). This category includes all ranges of sediment grain sizes from mud and silt to sand and gravel.

**Live organic substrate.**—Some Bryozoa have the ability to attach themselves to living plants and animals. These forms are epibionts. Epibionts have the advantages of increased available space to occupy and access to currents and nutrients higher in the water column, regardless of the shape of the colony. Forms living on *animals* are epizoans and those that live on *plants* are epiphytes. It is difficult to distinguish between epiphytes and epizoans in the fossil record, but criteria for recognizing epibionts in general are discussed in Hageman et al. (1996) and Voigt (1956, 1973).

## APPLICATION OF GROWTH HABIT CLASSIFICATION

This classification is flexible in that it can be used to characterize the growth habit characteristics of any individual specimen or group of bryozoans (species or higher taxo-ecological group). Greatest ecological resolution is obtained by specimen-level characterization, but it is left up to the user to decide how specimens/taxa should be grouped for analysis (e.g., potentially

by families or traditional growth forms). Methods of growth habit analysis are discussed in the next section, but all applications are based on the principle that the growth habit for any bryozoan can be represented by at least one character state selected for each of the eleven character classes (Fig. 2).

**Variability of growth habit characteristics.**—Character states within a character class may be unique (single state) or variable (multiple states). The uniqueness or variability of growth habit character states within character class type depends on: 1) whether the characterization is based on an observed occurrence or represents potential growth habit states of the specimen/group; 2) the hierarchical level of the group under consideration; and 3) the inherent range of ecological variation in the bryozoan under consideration. Empirically observed character states will tend to be less variable and contain more detailed ecological information than more generalized, range of potential character states for a taxon. Growth habit characterization for lower taxonomic levels (individual specimens and species) are typically less varied than for higher taxonomic levels (genera and families).

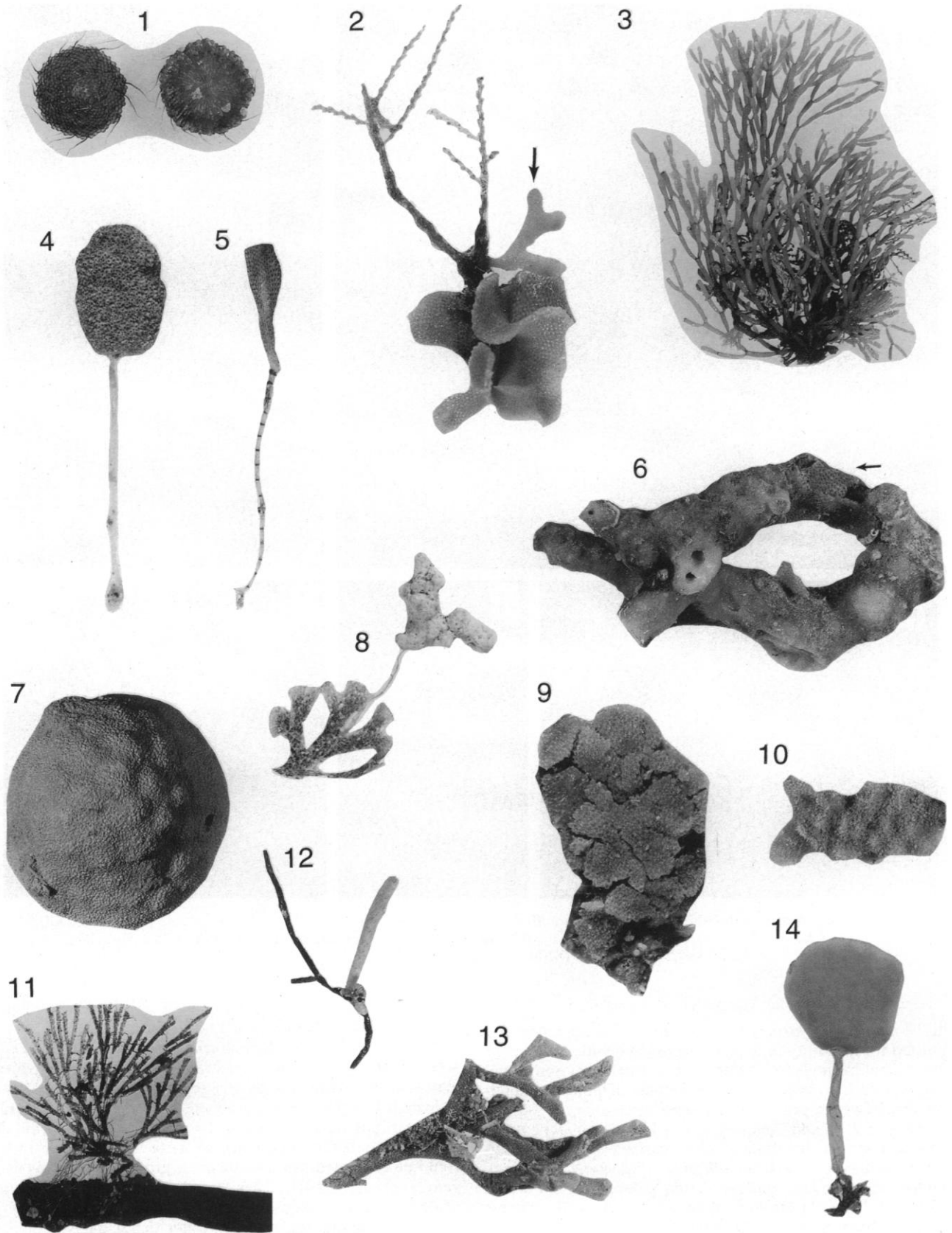
Some bryozoan species (specimens) can modify their morphology (growth habit) in order to adapt to local environmental conditions (Stach, 1935, 1937). For example, some bryozoan species display intraspecific, morphologic plasticity, varying from encrusting unilaminar sheets, to erect bilaminar sheets, to broad bilaminar branches, to delicate cylindrical branches (e.g., *Caleshara denticulata*). Other bryozoan species are morphologically determinant, with each species having a more genetically dictated growth habit (e.g., *Conescharellina biarmata*). Thus, with morphologically conservative species, growth form variation among environments is interspecific. The difference between intraspecific and interspecific growth habit variation is very important when developing concepts for ecological analyses (Hageman et al., 1997).

**Growth habit descriptions and character coding.**—There are two ways in which this classification can be applied. First, the eleven character classes can be treated as primary characters and a single character-state can be selected and coded for each (e.g., *Orientation relative to the substrate* = 1. encrusting; 2. massive; 3. erect; 4. pedunculate; or 5. fungiform). This works well in a descriptive format for growth habits, especially at the specimen level and for morphologically conservative taxa. If each character class has a single state (value), then a code of 11 numbers can be used directly in numerical analysis (Fig. 2, column A; e.g., Fig. 5.1, *Selenaria* sp. = 2, 4, 1, 4, 1, 3, 11, 3, 1, 1, 1). Examples are provided in the Appendix for the 21 specimens in Figures 5 and 6.

In an alternative coding method, each of the 60 character states (Fig. 2, column B) can be treated as a discrete character and coded as 0 (absent) or 1 (present). This coding method is highly flexible and allows for documentation of a range of variation; at one end, a unique character set describing observed states from a single specimen, and at the other end, general characterizations of ecologically variable, higher taxa.

FIGURE 5—Various bryozoan growth habits. 1–6 and 8–14 modern specimens from the Great Australian Bight; 7, Middle Miocene, Murray Basin, Australia. All specimens  $\times 1$ . 1, *Selenaria* sp., SAM L728; 2, arrow designates *Adeonellopsis* sp., SAM L729, lower, folded sheet is *Caleshara denticulata*, SAM L730; 3, *Cellaria rigida*, SAM L731; 4, *Sphaeropora* sp., SAM L732; 5, *Adeona* sp. immature, SAM L733; 6, large hollow branch is *Celleporaria* sp. A, SAM L734, arrow designates encrusting *Fenestrulina* sp., SAM L735; 7, *Celleporaria* sp. B, SAM L736; 8, *Retiflustra reticulum*, SAM L737; 9, *Hiantopora ferox*, SAM L738; 10, *Celleporaria* sp. C, SAM L739; 11, *Canda arachnoides*, SAM L740; 12, *Porina gracilis*, SAM L740; 13, *Hiantopora* sp., SAM L741; 14, *Parmularia reniformis*, SAM L742. Specimens in the South Australian Museum (SAM) collection, Adelaide.







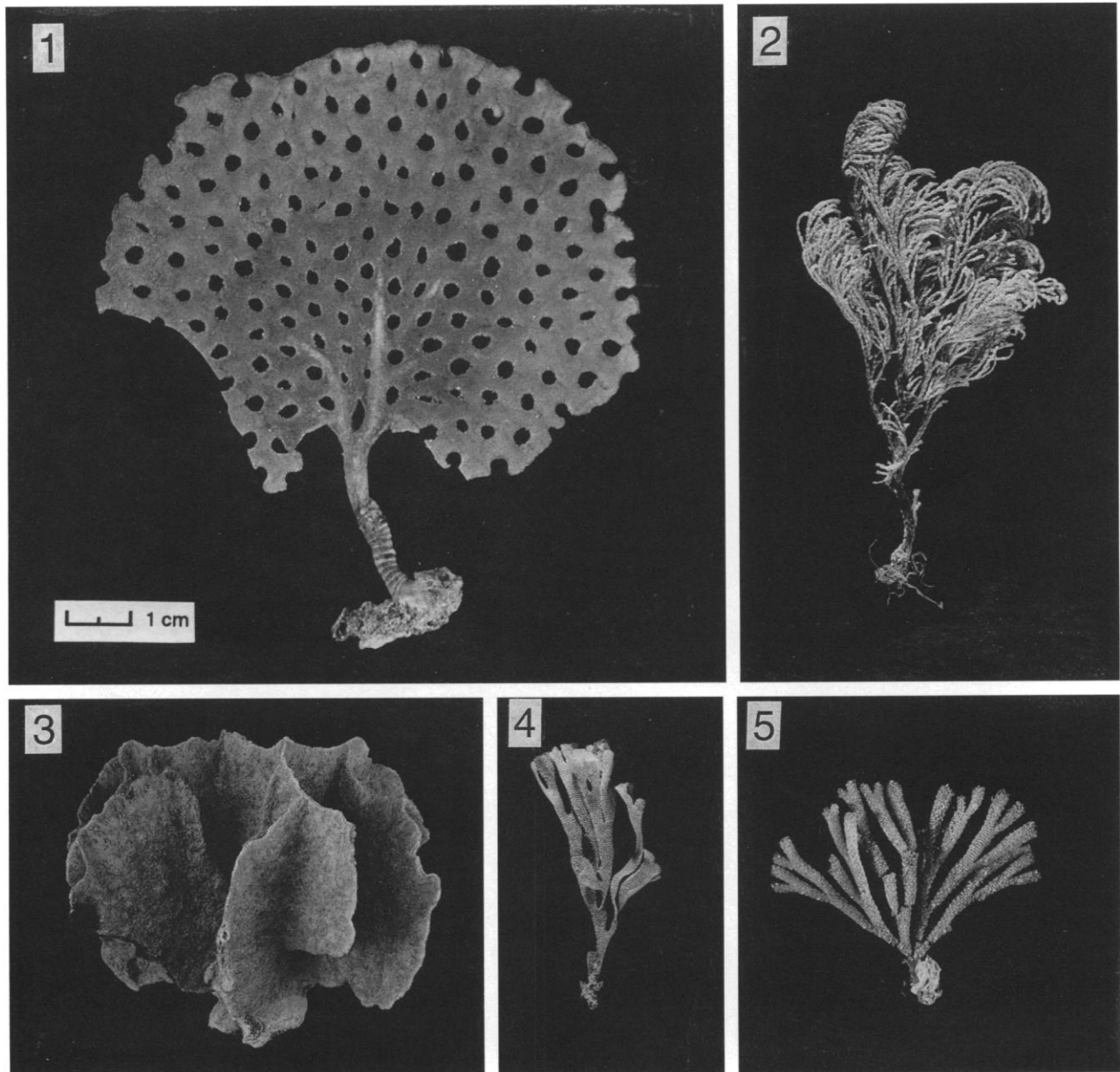


FIGURE 6—Various bryozoan growth habits, all specimens are Modern from the Great Australian Bight. 1, *Adeona* sp., mature,  $\times 1$ , SAM L743; 2, *Cribricellina rufa*,  $\times 2$ , SAM L744; 3, *Cigclisula verticalis*,  $\times 0.5$ , SAM L745; 4, *Flustra denticulata*,  $\times 1$ , SAM L746; 5, *Caberea grandis*,  $\times 2$ , SAM L742. Specimens in the South Australian Museum (SAM) collection, Adelaide.

#### ANALYSIS OF BRYOZOAN GROWTH HABITS

This *Analytical Bryozoan Growth Habit Classification* has been tested for its ability to document growth habits of observed specimens, but methods for its application to paleoenvironmental analysis are still in development. Examples of potential applications are, however, provided here with discussion.

*Characterization and comparison.*—Although analytical descriptions of growth habits may carry variable taxonomic significance, inclusion of such growth habit characterizations (i.e., Appendix) in systematic biological and paleontological works would be of value for surveys of broader ecological patterns. Systematic synopses of growth habit character states allow for direct comparisons within and among taxa and also provide an introduction to the ecology of a group to specialists and non-specialists alike.

*Modified traditional growth form analysis.*—Each unique set of growth habit characters may be treated as a highly refined growth form in the traditional sense. For example, in the characterization of 330 Great Australian Bight bryozoan species, there are approximately 80 discrete combinations of observed growth habit characters (=refined growth forms). Abundance data have not yet been compiled for these forms, but the distribution and relative importance of these 80-some growth habits could be evaluated using methods of growth form analysis (Hageman et al., 1997). These methods evaluate relationships among the distributions of growth habits and various physio-ecological parameters, such as water depth, physiographic location, and substrate type.

*Evaluation of morpho-ecospace.*—The growth habit characterization of individual specimens (or higher-level groups) can

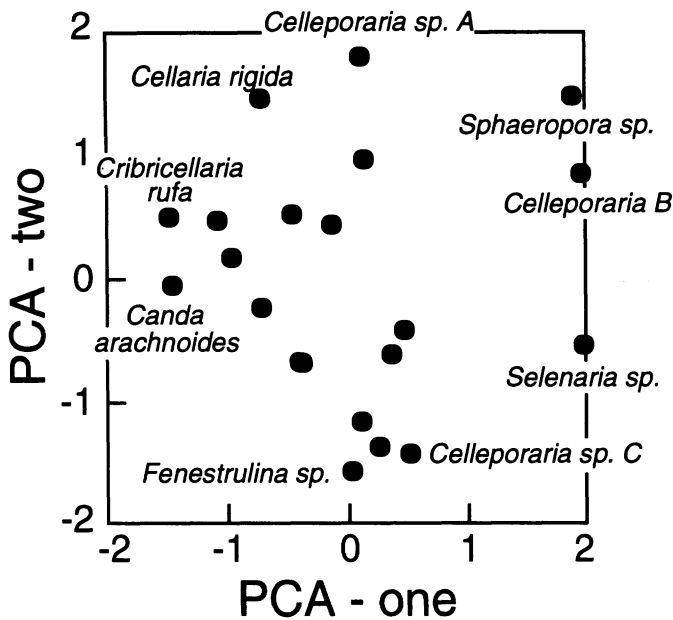


FIGURE 7—Principal component analysis employing specimens in Figures 5 and 6; data coded in the Appendix.

be plotted in a multidimensional space defined by growth habit characteristics. This can be done with either 11 dimensional character classes (e.g., Appendix) or the full list of 60 characters, which allows for more flexible coding. Detailed evaluation of the morpho-ecospace occupied by the entire Great Australian Bight data set is beyond the boundaries of this study. As an example for proposed methods, however, the 21 specimens in Figures 5 and 6 are plotted on the first two principle components, based on 11 character classes using data coded in the Appendix (Fig. 7). Results from this analysis are inconsequential because specimens are an unnatural assemblage selected to exemplify a range of growth habit variation. Nevertheless, the extremes of the distribution can be summarized as follows: 1) far left (Low on PCA-1) = rooted bushy forms; 2) far right (High on PCA-1) = free-living and rooted cones and spheres; 3) center = various rooted and cemented erect branches and sheets, 4) bottom (Low on PCA-2) = encrusting, nonbranching forms; 5) top (High on PCA-2) = large macroserial and erect multilaminar forms.

Selected morpho-ecospace can be evaluated based on occupied and vacant regions through modern environments and through geological time (Fig. 7). This will provide an improved understanding of ecological and macroevolutionary significance of growth habit strategies. Subsets of character classes can also be evaluated, such as: *Orientation*, *Construction* and *Attachment*. Evaluation of growth habit character distributions may also provide insight into patterns of evolution (e.g., key innovations and adaptive radiations) through the evolutionary history of major bryozoan clades.

*Correlations among growth habit characteristics and environmental parameters.*—Traditional growth form analysis is based on the comparison of a growth form such as catenicelliform (composite of many growth habit characteristics) with a major environmental factor such as water depth (composite of several physio-chemical conditions). This results in a “filtered” comparison of the true components of these two larger factors (Fig. 8). The goal here is to evaluate the distribution of actual growth habit characteristics that make up the “growth forms”

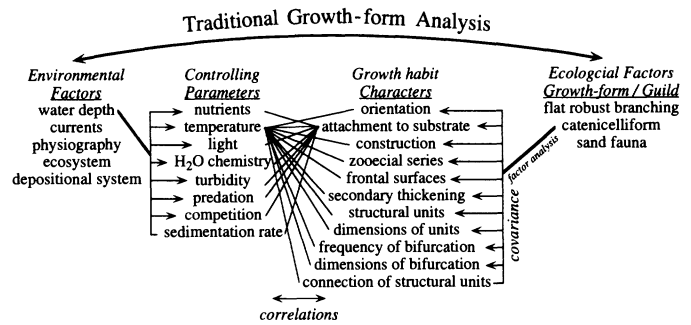


FIGURE 8—Parameters of bryozoan growth form analysis: left, environmental controlling factors and their parameters, and right, co-occurring groups of growth habits and their characteristics.

relative to measured physical parameters representing major environmental factors. If the growth habit characteristics were known for all taxa in a study and the environmental parameters listed in Figure 8 were known for each sample locality, valuable comparisons could be made such as: 1) correlation of growth habit characters and environmental parameters; 2) covariance of growth habit characteristics associated with co-occurring groups of traditional growth forms 3) covariance of individual environmental parameters associated with major environmental factors. The goal of these analyses is to bring us back to a comparison of the distribution of naturally occurring groups of growth habits, versus major environmental factors. This is, after all, the level of resolution available for most, general paleoenvironmental analyses. Obviously this can not all be accomplished in single study, but the framework and expertise exist to make great advances in this field.

#### SUMMARY

1. The *Analytical Bryozoan Growth Habit Classification* proposed here can be used to characterize the growth habit of any bryozoan, based on eleven zoarial character classes. Character classes include: 1) *Orientation relative to the substrate*; 2) *Attachment to substrate*; 3) *Construction*; 4) *Arrangement of zoecial series*; 5) *Arrangement of frontal surfaces*; 6) *Secondary skeletal thickening*; 7) *Structure of units*; 8) *Dimensions of structural units*; 9) *Frequency of bifurcation*; 10) *Dimensions of bifurcation*; and 11) *Connection of structural units*.
2. This classification has been tested on 330 ecologically diverse bryozoan species. The classification provides a common ground for systematic comparison of character states among bryozoan growth habits and allows for evaluation of correlations between observed morpho-ecological character states, and specific environmental conditions in which they live.
3. Bryozoan colonial growth habits (growth forms) can be used as paleoenvironmental indicators because many morphological parameters are often correlated with the environmental conditions in which the animals lived.
4. Growth habit strategies can be further evaluated by mapping distributions and trends in a selected multidimensional morpho-ecological space defined by the growth habit characters in the classification.
5. These approaches provide great opportunities for application of bryozoan growth habit analyses to paleoecological, paleoenvironmental and evolutionary studies.

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## APPENDIX

Specimens from Figures 5 and 6, with character states listed for each of the character classes and character states coded from the *Analytical Bryozoan Growth Habit Classification* in Figure 2: Specimen name; orientation; attachment; construction; arrangement of zooecial series; arrangement of frontal surfaces; secondary skeletal thickening; structural units; dimensions of structural units; frequency of bifurcation; dimensions of bifurcation; connection of structural units; (character codes, Fig. 2, column A). Character states are labeled in sequence of Figure 2, but could be reordered to smooth the descriptive flow.

- Selenaria* sp. (Fig. 5.1, SAM L728); massive; free-living, avicularia supported; rigid contiguous; macroserial nonmaculate; unilaminate; basal skeletal thickening; hollow cap; primary 3-D object; no bifurcations; no bifurcations; no connections; (2, 4, 1, 4, 1, 3, 11, 3, 1, 1, 1); collected from particulate substrate.
- Adeonellopsis* sp. (Fig. 5.2, SAM L729); erect; cemented; rigid contiguous; oligoserial; bilaminate; frontal skeletal thickening; branch with flat surface; straight branches; infrequent bifurcations; bifurcations in one plane; no lateral connection of branches; (3, 1, 1, 3, 2, 2, 3, 1, 2, 2, 1); collected from live animal substrate (hydroid).
- Caleshara denticulata* (Fig. 5.2, SAM L730); erect; cemented; rigid contiguous; macroserial nonmaculate; bilaminate; no secondary skeletal thickening; sheet; folded sheet; infrequent bifurcations; bifurcations in more than one plane; no lateral connection of sheets; (3, 1, 1, 4, 2, 1, 5, 2, 2, 3, 1); collected from live animal substrate (hydroid).
- Cellaria rigida* (Fig. 5.3, SAM L731); erect; rooted; articulated determinant cuticular joints; oligoserial; radial; no secondary skeletal thickening; solid cylinder; straight cylinder; very frequent bifurcations; bifurcations in more than one plane; no lateral connection of cylinders; (3, 2, 3, 3, 5, 1, 8, 1, 4, 3, 1); collected from hard secondary substrate.
- Sphaeropora* sp. (Fig. 5.4, SAM L732); pedunculate; rooted; rigid contiguous; macroserial maculate; multilaminate; no secondary skeletal thickening; ellipsoid; primary 3-D object; no bifurcations; no bifurcations; no connections of object; (4, 2, 1, 5, 6, 1, 12, 3, 1, 1, 1); collected from particulate substrate.
- Adeona* sp., immature (Fig. 5.5, SAM L733); pedunculate; rooted; rigid contiguous; oligoserial; bilaminate; frontal secondary skeletal thickening; branch with flat surface; curved branch; no bifurcations; no bifurcations; no connection of branch; (4, 2, 1, 3, 2, 2, 3, 2, 1, 1, 1); collected from particulate substrate.

- Celleporaria* sp. A (Fig. 5.6, SAM L734); erect; cemented; rigid contiguous; macroserial nonmaculate; multilaminar; no secondary skeletal thickening; hollow cylinder; curved branches; frequent bifurcation in more than one plane; fused branches; (3, 1, 1, 4, 6, 1, 9, 2, 3, 3, 2); collected from live animal substrate (sponge).
- Fenestrulina* sp. (Fig. 5.6, SAM L735); encrusting; cemented; rigid contiguous; oligoserial; unilaminar; no secondary skeletal thickening; sheet; flat sheet; no bifurcations; no bifurcations; no connections; (1, 1, 1, 3, 1, 1, 5, 1, 1, 1, 1); collected from hard secondary substrate.
- Celleporaria* sp. B (Fig. 5.7, SAM L736); massive; free-living sedentary; rigid contiguous; macroserial maculate; multilaminar; no secondary skeletal thickening; solid dome; primary 3-D object; no bifurcations; no bifurcations; no connections; (2, 3, 1, 5, 6, 1, 10, 3, 1, 1, 1); collected from particulate substrate.
- Retiflustra reticulum* (Fig. 5.8, SAM L737); encrusting; rooted; flexible weakly-calcified; oligoserial; unilaminar; no secondary skeletal thickening; branch with flat surface; curved branches; frequent bifurcations; bifurcations in one plane; no lateral connection of branches; (1, 2, 4, 3, 1, 1, 3, 2, 3, 2, 1); collected from particulate substrate.
- Hiantopora ferox* (Fig. 5.9, SAM L738); encrusting; rooted; articulated, indeterminate cuticular connections; macroserial nonmaculate; unilaminar; no secondary skeletal thickening; sheet; flat sheet; no bifurcations; no bifurcations; no connections; (1, 2, 2, 4, 1, 1, 5, 1, 1, 1, 1); collected from live plant substrate (red algae).
- Celleporaria* sp. C (Fig. 5.10, SAM L739); encrusting; cemented; rigid contiguous; macroserial maculate; unilaminar; no secondary skeletal thickening; sheet; flat sheet; no bifurcations; no bifurcations; no connections; (1, 1, 1, 5, 1, 1, 5, 1, 1, 1, 1, 1); collected from live animal substrate (hydroid).
- Canda arachnoides* (Fig. 5.11, SAM L740); erect; rooted; articulated, indeterminate cuticular connections; biserial; unilaminar; no secondary skeletal thickening; branch with flat surface; straight branch; frequent bifurcations; bifurcations in one plane; cuticular tubes connecting structural units; (3, 2, 2, 2, 1, 1, 3, 1, 3, 2, 4); collected from live animal substrate (sponge).
- Porina gracilis* (Fig. 5.12, SAM L740); erect; cemented; rigid contiguous; oligoserial; bilaminar; frontal secondary skeletal thickening; branch with convex surface; straight branch; no bifurcations; no bifurcations; no bifurcations; (3, 1, 1, 3, 2, 2, 4, 1, 1, 1, 1); collected from live animal substrate (bryozoan).
- Hiantopora* sp.; (Fig. 5.13, SAM L741); encrusting; rooted; articulated, indeterminate cuticular connections; macroserial nonmaculate; unilaminar; no secondary skeletal thickening; branch with convex surface; straight branches; frequent bifurcations; bifurcations in one plane; no lateral connection of branches; (1, 2, 2, 4, 1, 1, 4, 1, 3, 2, 1); collected from particulate substrate.
- Parmularia reniformis* (Fig. 5.14, SAM L742); pedunculate; rooted; rigid contiguous; macroserial nonmaculate; bilaminar; no secondary skeletal thickening; lobe; flat lobe; no bifurcations; no bifurcations; no lateral connections; (4, 2, 1, 4, 2, 1, 6, 1, 1, 1, 1); collected from particulate substrate.
- Adeona* sp., mature (Fig. 6.1, SAM L743); pedunculate; rooted; rigid contiguous; oligoserial; bilaminar; frontal secondary skeletal thickening; branch with convex surface; curved branches; very frequent bifurcations; bifurcations in one plane; laterally fused branches; (4, 2, 1, 3, 2, 2, 4, 2, 4, 2, 2); collected from particulate substrate.
- Cribricellina rufa* (Fig. 6.2, SAM L744); erect; rooted; articulated, determinate cuticular joints; biserial; unilaminar; no secondary skeletal thickening; cluster of zooecia; curved compound branches; very frequent bifurcations; bifurcation in more than one plane; no lateral connections between branches; (3, 2, 3, 2, 1, 1, 2, 2, 4, 3, 1); collected from particulate substrate.
- Cigclisula verticalis* (Fig. 6.3, SAM L745); erect; cemented; rigid contiguous; macroserial maculate; multilaminar; no secondary skeletal thickening; sheet; flat sheets; infrequent bifurcation; bifurcation in more than one plane; no lateral connection of sheets; (3, 1, 1, 5, 6, 1, 5, 1, 2, 3, 1); collected from hard secondary substrate.
- Flustra denticulata* (Fig. 6.4, SAM L746); erect; cemented; flexible weakly-calcified; oligoserial; bilaminar; no secondary skeletal thickening; branch with flat surface; curved branch; infrequent bifurcations; bifurcation in more than one plane; no lateral connection of branches; (3, 1, 4, 3, 2, 1, 3, 2, 2, 3, 1); collected from particulate substrate.
- Caberea grandis* (Fig. 6.5, SAM L742); erect; rooted; articulated, indeterminate cuticular connections; oligoserial; unilaminar; no secondary skeletal thickening; branch with convex surfaces; straight branches; frequent bifurcations; bifurcations in one plane; no lateral connection of branches (3, 2, 2, 3, 1, 1, 4, 1, 3, 2, 1); collected from hard secondary substrate.