Complexity Generated by Iteration of Hierarchical Modules in Bryozoa

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ABSTRACT

Growth in colonial organisms by iteration of modules inherently provides for an increase in available morpho-ecospace relative to their solitary relatives. Therefore, the interpretation of the functional or evolutionary significance of complexity within groups that exhibit modular growth may need to be considered under criteria modified from those used to interpret complexity in solitary organisms. Primary modules, corresponding to individuals, are the fundamental building blocks of a colonial organism. Groups of primary modules commonly form a second-order modular unit, such as a branch, which may then be iterated to form a more complex colony. Aspects of overall colony form, along with their implications for ecology and evolution, are reflected in second-order modular (structural) units to a far greater degree than by primary modular units (zooids). A colony generated by modular growth can be classified by identifying its second-order modular (structural) unit and then by characterizing the nature and relationships of these iterated units within the colony. This approach to classifying modular growth habits provides a standardized terminology and allows for direct comparison of a suite of functionally analogous character states among taxa with specific parameters of their ecology.

ARTICLE

The evolutionary threshold between solitary versus modular organisms represents a key innovation that allows for a quantum increase in available morpho-ecospace (=complexity) for modular organisms. This increase results from the great degree of variability of body forms afforded through growth by iteration of modules. Interpretation of functional or evolutionary significance of overall body/colony forms in organisms that grow by iteration of modules, therefore, needs to be tempered with an appreciation of this growth mechanism and its resulting array of body plans.

The goal of this paper is to put forward the argument that there are two aspects of modular growth relevant to arguments of complexity. In the first type, primary modules are the only unit of repetition (iteration) within the colony (Figs. 1A–B and 2A–B). Colonial organisms that are restricted to growth by iteration of primary modules tend to form simple colony forms such as encrusting runners, sheets and mounds (Fig. 1A–B). A second type of modular growth, an extension of the first, also involves primary modules, however, in this case the primary modules coordinate to form a higher level of organization = second-order modules. For example, a branch within a colony, itself composed of primary modules is a second-order modular unit (Fig. 1E, F). When second-order modules are repeated and iterated to generate a colony, the potential morpho-ecospace that the colony can occupy increases geometrically (Figs. 1C, E, G and 2C, D).
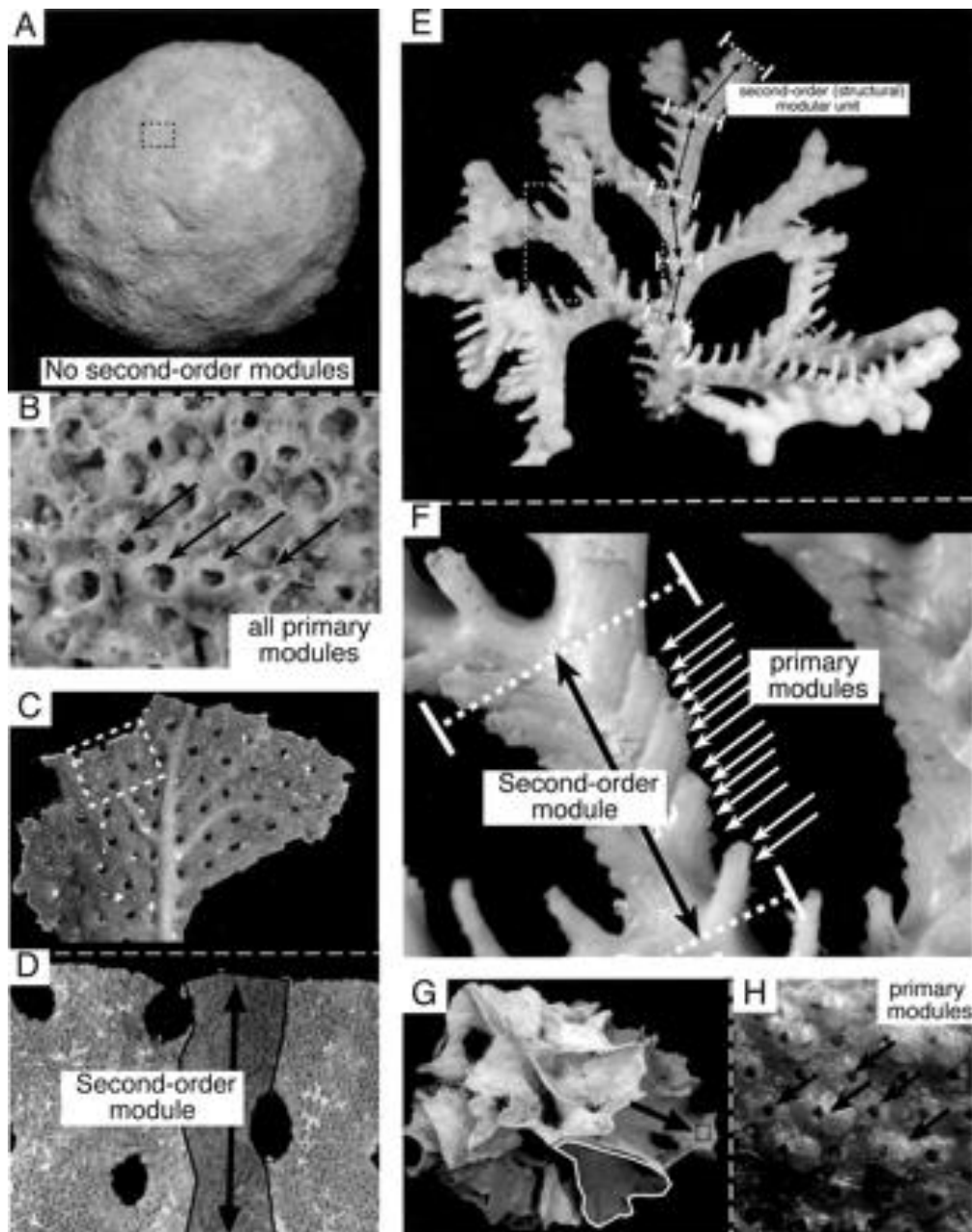
Fig. 1. Examples of bryozoan colonies illustrating the concept of iteration of primary modules and second-order modular (structural) units. A–B. A massive colony with iteration of only primary zooids. Celleporaria sp.; massive; free-living sedentary; rigid contiguous; macroserial maculate; multilaminate; no secondary skeletal thickening; solid dome; primary 3-D object; no bifurcations; no bifurcations; no connections. A. Location of 1B outlined by box, 2.3×. B. Primary modules, 35×. C–H. Bryozoan colonies with iteration of second-order modular (structural units). C–D. Adeona sp.; pedunculate; rooted; rigid contiguous; oligoserial; bilaminate; frontal secondary skeletal thickening; branch with convex surface; curved branches; very frequent bifurcations; bifurcations in one plane; laterally fused branches. C. Location of 1D outlined by box, 1×. D. Second-order module, 5×. E–F. Hornera sp.; erect; cemented; rigid contiguous; oligoserial; unilaminate; no secondary skeletal thickening; branch; angular branches; infrequent bifurcation; bifurcation in more than one plane; no lateral connection of branches. E. Location of 1F outlined by box, 8×. F. Primary and second-order modules, 40×. G–H. Schizoporella sp.; erect; cemented; rigid contiguous; macroserial non-maculate; bilaminate; no secondary skeletal thickening; sheet; curved sheets; infrequent bifurcation; bifurcation in more than one plane; fused lateral connection of sheets. G. Location of 1H outlined by box, 0.7×. H. Primary and second-order modules, 30×
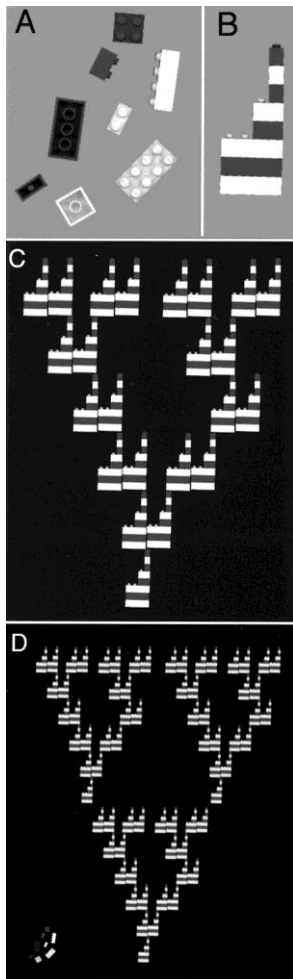

Fig. 2. Traditional Lego™ blocks provide a simple model for modular growth. (A) single blocks represent primary modules (solitary or disassociated from a colony), which can be assembled into a second-order modular unit (B), which when iterated (repeated) can generate a complete colony form (C). Complex colony forms can be generated by iteration of higher order modular units (D)

Increased morphological diversity and disparity (=complexity), within a clade of modular organisms, relative to their most close solitary relatives, is an expected consequence of the acquisition of the growth mode itself. That is, the transition from (1) an ancestral solitary organism, to (2) a colonial descendant with growth by iteration of primary modules alone is a relatively rare evolutionary event (only occurring a single to a few times within certain phyla). However, the transition from (2) iteration of only primary modules to form colonies, to (3) the iteration of second-order (and higher) modular units to generate complex colonies has occurred repeatedly within groups. Thus, the range of morphological complexity within groups that exhibit modular growth needs to be considered under different criteria from comparisons of relative complexity made among these modular organisms and organisms that do not display modular growth.

INDIVIDUALS, COLONIES, CLONES AND MODULES

The concept of iterative growth of hierarchical, modular units is common among diverse groups such as plants and many invertebrate phyla. A rich literature exists relating to topics of asexual growth and clonal propagation (Boardman and Cheetham, 1973; Coates and Jackson, 1985; Cook, 1985; Harper, 1985; Hughes and Cancino, 1985; Jackson, 1985; Pitelka and Ashmun, 1985; Waller and Steingraeber, 1985; Bell, 1986; Hallé, 1986; Mackie, 1986; Ryland and Warner, 1986; Trinci and Cutter, 1986; Williams, 1986). Application of terminology for modular growth is generally well established within taxonomic groups. Unfortunately, among specialized workers, the disparity of these taxonomic groups has resulted in inconsistent use of terminology and independent descriptive concepts for similar ecological/morphological features. A brief review is provided below with the goal of illustrating the broader applicability of concepts of coloniality and modular growth that are shared among a variety of taxonomic groups. Figure 3 represents a general consensus (though not unanimity) for usage of terms among all authors cited here.

	Solitary animals individuals unconnected & without communication	Colonial animals individuals either connected or functionally interdependent	Plants vegetative growth, module defined as interval between branching events
Clonal capable of asexual reproduction	some ascidians, parthenogenic aphids, polyembryonic opossums	Bryozoa, many corals, some ascidians *individuals potentially autonomous or specialized*	modules (ramets) are fully functional & potentially autonomous e.g., *strawberries*
Aclonal sexual reproduction predominates	many common invertebrate, and vertebrate animals	social insects, some higher vertebrates?	modular subunits incapable of independence

Fig. 3. Definitions and examples for clonal versus aclonal for solitary and colonial animals and plants.

Definitions and concepts

The distinction between clonal and aclonal organism is based on the predominance of one mode of replication (Hughes, 1989). Many animals, otherwise considered to be aclonal, are capable of clonal reproductive processes, e.g., production of identical siblings in mammals through polyembryony.

Clonal reproduction: any of the many forms of reproduction that results in generation of offspring with genotypes that are identical to the parent (baring somatic mutation), = asexual reproduction. Processes include fission, autotomy, laceration, budding, parthenogenesis, polyembryony, gemmulation (Hughes and Cancino, 1985). Most clonal organisms exhibit aclonal reproduction at some point in their overall life history.

Aclonal reproduction: involves meiotic processes with a recombination of genetic material (=sexual reproduction) and retains minimal potential for, or expression of clonal processes.

Individual: two primary usages, (1) any unit that is the result of either an aclonal or clonal reproductive event (regardless of its functionality) = definition used in this paper; or (2) used synonymously with a single "solitary organism" defined below.

Solitary or unitary organism: any organism that can be recognized as physically separate from others (regardless of its genetic distinctiveness). For example, all aclonal invertebrate and vertebrate organisms, plus individual organisms that are produced through clonal mechanisms, but are physically separated from their parent.

Colonial organism: organisms that produce clonal replicates that remain physically connected. A degree of physiological communication among individuals within a colony is usually expected, but may not occur in all examples. Although found in a separate body of literature from marine invertebrates and plants, social insects such as ants, termites, bees and wasps can be considered as an example of aclonal colonies if the definition of colonial is expanded to include groups of individuals that are highly specialized to the degree that the life history of the individual is functionally dependent on the fitness of the overall collective (Keller, 1998).

Clone, genet, or soma: the complete product of all asexual reproduction from a single zygote = sexually produced parent. That is, all individuals that share an identical gene line (applied here to eukaryotes only). A clone, genet or soma may consist of groups of physically connected, budded individuals (colony), or multiple groups of individuals separated from each other (colonies derived from fission or fracture of a parent are members of the same clone), or solitary individuals or colonies derived from regeneration of a parent or parthenogenesis (individuals of an ancestral lineage may be long dead). All members of a clone, whether physically connected or not, share an identical genotype that has not experienced sexual recombination.

Module or ramet: Modules are the iterated building blocks of the colony. All colonial organisms exhibit modular growth, however, not all clonal organisms are modular (Fig. 3). Note that "module" is the term that receives the most variable usage among workers. Some treat a

module as the smallest fully functioning (autonomous) unit in a colony (Ryland and Warner, 1986; Williams, 1986).

In this paper, the concept of modularity is expanded to include (1) primary modules, the fundamental unit resulting from an asexual reproductive event in colonial organisms, regardless of its functionality, and (2) second- (and higher) order modules, themselves assemblages of primary modules. The logic in this application is that all specialized individuals (polymorphs) are derivatives of fully functioning individuals. Thus, primary modules are the smallest unit of a colony, whether they are capable of physio-ecological independence, or only perform a subset of functions.

Because the concept of hierarchical organization has broad applicability in the organic world (McShea, 2001a), the concept of a "modular organism" has lost its specificity since Huxley (1851) used it in an analysis of Salpa (Ryland and Warner, 1986; Williams, 1986). Developmental biologists have co-opted the term "modular organism" to include any solitary organisms that has the ability to dissociate developmental processes, e.g., serially homologous structures of the Bilateria (Wagner, 1996; Carroll, 2001; Galis et al., 2001; Magwene, 2001). Modularity is also applied as units of cellular, physiological and ecological hierarchy (McShea, 2001a, b). Thus, there is the need for students of modular growth to clearly define the context in which they are working.

Ecological significance of modular growth

The concept of growth of colonies through iteration of modules does require erection of novel concepts not otherwise considered for solitary organisms. Examples include: Growth: occupation of space (Gardiner and Taylor, 1982; McKinney and Raup, 1982; Cheetham and Hayek, 1983; Waller and Steingraeber, 1985); growth habit plasticity in response to local environmental variation (Stach, 1936; Pandolfi and Burke, 1989; Marfenin, 1997); repair and recovery through regeneration (Coates and Jackson, 1985; Oren et al., 2001); potential for isometric scaling from small to large colonies (Kim and Lasker, 1998). Resources: acquisition and partitioning of resources across locally heterogeneous space (Harper, 1985; Colasanti and Hunt, 1997; Jackson, 1985); generation and maintenance of colony-wide structures not identified with an individual (Boardman and Cheetham, 1973; Coates and Jackson, 1985). Integration and polymorphism: degree of autonomy of individual versus integration of specialized individuals, relative degrees of fitness (Boardman and Cheetham, 1973; Schopf, 1973; Bates and Kirk, 1985; Pitelka and Ashmun, 1985; Mackie, 1986). Reproduction, life cycles and mortality: reproduction through fission, and fracture (Jackson and Winston, 1981; Hughes and Cancino, 1985; Håkannson and Thomsen, 2001); astogeny and ontogeny (Boardman and Cheetham, 1973); degeneration and regeneration of polypides within modules (Jackson and Winston, 1981); cost benefit analysis (Cook, 1985). Selection pressures: selection on colony vs. selection on individual (Schopf, 1973; Hughes and Cancino, 1985; Tuomi and Vuorisalo, 1989; Pedersen and Tuomi, 1995); indeterminate growth and problems of self crowding (Jackson, 1985; Bates and Kirk, 1985; Lazo and Chapman, 1998).

Complexity, polymorphism and colonial integration

Complexity in colonial organisms is often equated with the degree of integration in polymorphs (Jackson, 1985). A colony with a low degree of integration is one in which the modules are identical, fully autonomous units (isomorphs) that share structural walls with minimal or no communication (e.g., occupants sharing an apartment building). Whereas, a highly integrated colony consists of specialized individuals (e.g., separate feeding, defensive, and reproductive roles) whose interdependence and great degree of communication among modules results in a super-organism, such as Portuguese man-o-war (Bates and Kirk, 1985).

It is argued here that although integration of polymorphs is an important part of the history of complexity for colonial organisms, the overall colony form is the component of complexity that initially confronts a worker when surveying a suite of organisms. Thus, constructural complexity is an important factor for consideration, regardless of polymorphism and integration.

MODEL FOR GROWTH BY ITERATION OF HIERARCHICAL MODULES

Old fashioned Lego™ blocks can be used as a simple model to conceptualize growth in modular, colonial organisms. Note that most contemporary Lego™ toys are highly specialized kits designed for the construction of a predetermined object (e.g., robot or dinosaur). In contrast, the original rectangular block design encouraged the user to construct any number of shapes or objects out of the same set of blocks. For example, the eight blocks shown in Figure 2A represent eight primary modules. In Figure 2A these eight units are separate, representing either eight solitary organisms or eight disassociated individuals of a colony. These eight primary modules can be assembled to form a colony as in Figure 2B.

The assembled group of primary modules in Figure 2B, when taken as a whole, can be considered a second-order modular unit. If this second-order module is repeated a larger, more complex colony results (Fig. 2C). Once the evolutionary potential for iteration of second-order modules has been achieved, even higher order levels of modularity are possible. For example, the colony form shown in Figure 2C can itself be iterated as a third-order module, resulting in the colony form illustrated in Figure 2D (original eight primary modules included for scale).

Although the perceived increase in complexity from the colony forms from Figure 2B to Figure 2D may appear great, the more significant evolutionary event is represented by the transition from Figure 2A to Figure 2B, the acquisition of modular growth. Once the potential for modular growth has been achieved, iteration of second-order (and higher) modules, and concomitant complexity, is virtually inevitable.

Modularity and inherent potential for variation

Primary modules in Figure 2A could be assembled in many different ways other than the one shown in Figure 2B (e.g., a straight ladder, cris-crossed, or spiral tower; as a flat sheet, a mound, or a linear string). It is this level of variation among primary modules that is generally highlighted in analyses of modular growth (e.g., Coates and Jackson, 1985; Ryland and Warner, 1986). Note however, that Figure 2C also illustrates only one of a vast number of potential colony patterns that could result from the iteration of the second-order module in Figure 2B. In the same way, the object in Figure 2D is a very simple expression of the iteration of the form in Figure 2C. The third-order module of Figure 2C could easily have been swept into a complete radial colony, and a simple twist between each iteration would produce a three dimensional bush. In addition, variation in the sequence of assembly of units within and/or among the modules is not present in the examples shown. More complex forms can be generated from non-linear rules of assembly and/or random perturbations of primary or higher-order modules.

DESCRIBING AND QUANTIFYING SHAPE

Shape can be approached by erecting discrete categories into which objects must be fit (e.g., a cube versus a sphere versus an arborescent tree). Alternatively, a mathematical model can be developed to describe a continuum of forms (McKinney and Raup, 1982; Pandolfi and Burke, 1989; Waller and Steingraeber, 1985; Bell, 1986 and examples therein). An intermediate approach was developed to describe colonial forms of Bryozoa generated through iteration of second-order (and higher) modular units (Hageman et al., 1998).

As with the Lego™ block example, a second-order modular unit is recognized as a functional level in a hierarchy, above the primary module (zooid or polymorph), but below the colony as a whole. In the terminology of Hageman et al. (1998), second-order modular units are called structural units. Structural units (second-order modules), such as a branch or a sheet are comprised of multiple primary modules, and a colony is comprised of multiple structural units (Fig. 1E–F). In general, a second-order modular (structural) unit is defined as the region of a colony between branching events. Therefore, nonbranching colonies are made up of a single second-order modular (structural) unit. Complex colonies may have several segments (articulated subunits) between branching events. The scheme presented here was developed to acknowledge both the variable position of modular units within the hierarchy and to be flexible enough to accommodate them without the user specifically having to define their position in the hierarchy.

The concept of colonies being composed of multiple structures, possibly in hierarchical arrangement is not new (Hallé et al., 1978; Waller and Steingraeber, 1985; Hallé, 1986). The hierarchy for modular growth in tropical trees (Hallé, 1986) consists of "units of morphogenesis," "modules," and "architectural models," which roughly correspond to primary modules, second-order modular (structural) units, and colony growth habits respectively in this paper. Prescribed rules for construction, i.e., assembly of units and modules (Reffye, 1983), have been used to describe two dozen architectural models for observed growth in tropical trees (Hallé et al.,

1978). The classification for colonial growth habits summarized here is far more comprehensive in its ability to describe features of complex growth habits than previous models. This is accomplished by maintaining relatively simple rules of assembly of modular units, while providing generalized options for the characteristics of the structural units. This generalized approach allows for description and direct comparison of character states across the broadest range of growth habits. Comparison of more subtle differences among functionally, closely related colonial habits requires simple modification of the existing scheme to account for the desired detail.

BRYOZOA GROWTH HABIT CLASSIFICATION

Bryozoa is the only phylum for which all of its members are colonial. Individuals within all bryozoan colonies are relatively small (typically 0.1 to 1 mm). Most marine forms have calcified skeletons (a box or tube for each primary module), covered by a common tissue, with varying degrees of communication among individuals within a colony. Bryozoan colonies range from simple lineal strands of connected, clonal, autonomous individuals, to highly integrated colonies with determinant growth and coordinated behavior (Jackson, 1985). Because of these characteristics, Bryozoa are commonly used as model organisms in studies of coloniality, modularity, integration and individuation.

Aspects of overall colony form, along with their implications for ecology and evolution, are reflected in second-order modular (structural) units to a far greater degree than by primary modular units (zooids). The goal of this classification is to break down overall colony form in order to recognize its second-order modular (structural) unit, if present, and then characterize the nature and relationships of these iterated units within the colony (Hageman et al., 1998). For example, a single unilaminate branch of an erect arborescent colony (Fig. 1E–F) is a second-order modular (structural) unit. This classification was developed for Bryozoa, but the principles have general applicability.

The classification of modular growth forms of Hageman et al. (1998) is summarized below. The illustrated concepts are intentionally idealized in order to provide a model with the greatest breadth of application. In application, for any given specimen (colony), a single, most appropriate second-order modular (structural) unit can be selected (Fig. 4). Additional features of the overall colony form can be accounted for by variation of a relatively small number of fundamental characteristics, such as the orientation and construction, of the structural units (Figs. 5, 6 and 7). This classification provides a checklist, whereby workers can select the most appropriate idealized state within each fundamental character, subheadings below. Examples of some character states are illustrated in specimens of Figure 1. More complete examples are illustrated in Hageman et al. (1998).

Second-order modular (structural) units

Single
individual

Cluster
of individuals

Sheet

Cylinder

solid   hollow

Spheriod to Ellipsoid

Runner - Branch

Flat
surface

Convex
surface

Lobe
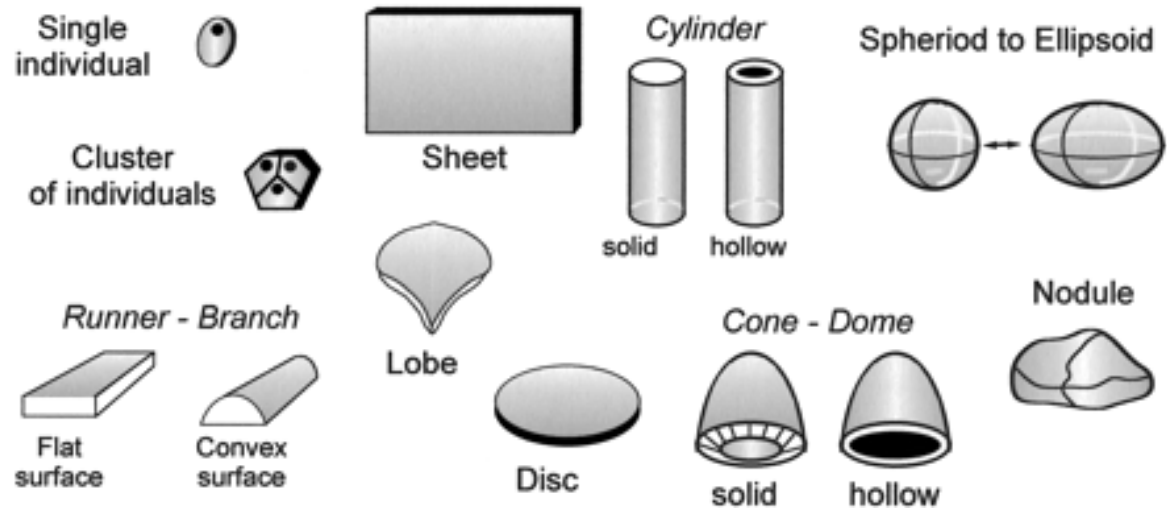
Disc

Nodule

Cone - Dome

solid   hollow

Fig. 4. Examples of the most common second-order modular (structural) units recognized in bryozoans from empirical examples. Second-order modular (structural) units are constructed by multiple primary modules (zooids)
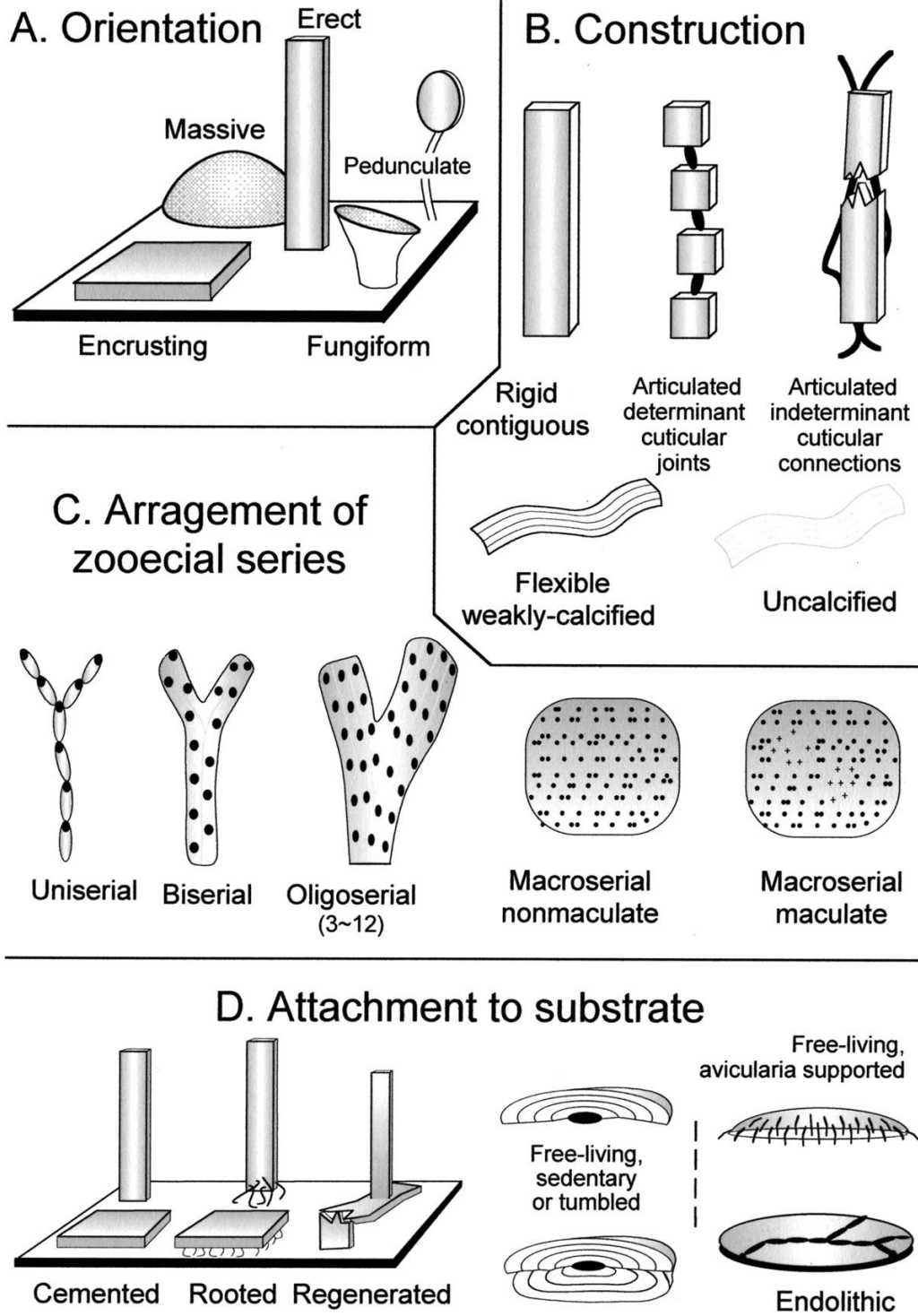
FIG. 5. Characteristics of second-order modular (structural) units of bryozoans, Orientation, Construction, Arrangement of frontal surfaces, Arrangement of zooecial series and Secondary skeletal thickening
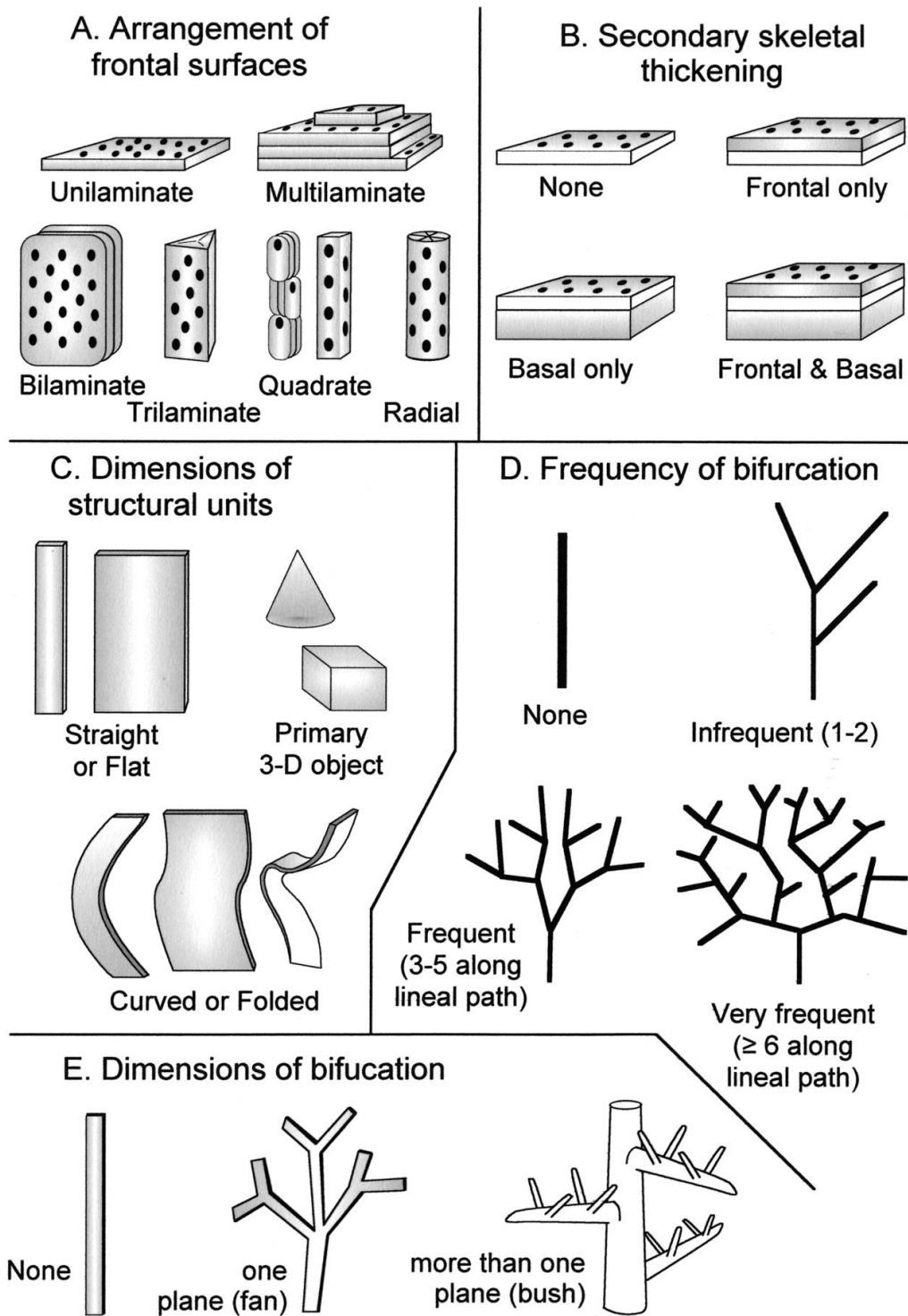
Fig. 6. Parameters describing how second-order modular (structural) units occupy space in bryozoans, Dimensions of growth, Frequency of branching, and Dimensions of branching
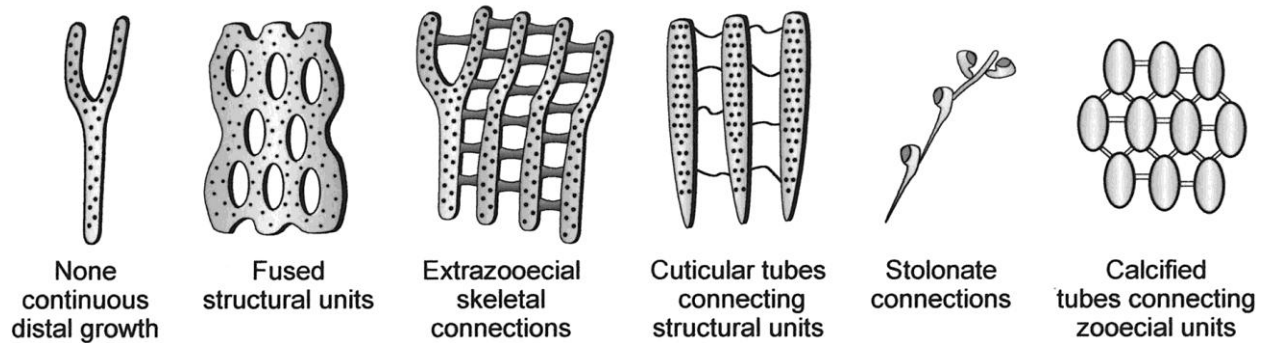
Connection of structural units

Fig. 7. Methods for connecting second-order modular (structural) units in bryozoan colony growth.

Second-order modular (structural) units (Fig. 4)

The theoretical range of architecture of second-order modular (structural) units is virtually limitless. Empirically, however, a very large percentage of bryozoan colony forms seen in nature can be accounted for with the structural units shown in Figure 4. Idealized second-order modular (structural) units for Bryozoa include a small cluster of individuals, a linear branch or runner which may have either a flat surface (Fig. 1C) or a convex surface (Fig. 1E), a broad sheet (Fig. 1G), or determinate disk or expanding lobe, a solid or hollow cylinder, a solid or hollow cone or dome (Fig. 1A), spheroids, ellipsoids and nodules.

Orientation relative to substrate (Fig. 5A)

Orientation refers to the orientation of the feeding surface of a colony relative to its substrate. Colonies that produce a thin cover over their substrate are known as encrusting forms, regardless of the nature of its structural unit (e.g., narrow runner or broad sheet) or mode of attachment (e.g., cemented or rooted). Many mature multilaminate colonies escaped their primary substrate, yet do not have determinate erect growth, therefore, a distinction is made here for massive forms (Fig. 1A). Colonies that rise above the substrate in a self-supported form are erect-continuous form (Fig. 1C, E, G) (growth away from a substrate regardless of direction, e.g., vertical, horizontal or even downward). Some erect bryozoans are supported above their substrate by long barren sections (peduncle or stalk). These are known as pedunculate. Colonies that develop continuous, calcareous stems, with zooids concentrated at typically flaring ends are fungiform.

Construction (Fig. 5B)

Construction is generally used as a proxy for flexibility and is strongly related to environmental parameters such as wave agitation and sedimentation sloughing. Bryozoans with rigid (inflexible), contiguous calcium carbonate skeletons are common in the marine setting and are called rigid contiguous, whether they be delicate or robust (all specimens of Fig. 1). Some colonies with otherwise rigid continuous segments also have supplementary bundles of long, cuticular tubes that support the colony. Such colonies generally do not have predetermined points of articulation, however, flexible connections result at points where a rigid branch breaks (articulated, indeterminate cuticular connections). Some bryozoan colonies are constructed with rigid segments that are connected by flexible joints (articulated, determinate cuticular joints). Some bryozoans have flexible colonies as a result of incomplete or weak calcification, whereas others are entirely uncalcified.

Arrangement of zooecial series (Fig. 5C)

Five categories of branch width are recognized here. Uniserial budding produces a chain (runner or branch) one zooid wide, whereas, colonies that are biserial, zooids share one wall and result in a strip two zooids wide. Oligoserial is an ad hoc category for colonies with three to approximately 12 individuals across their surface (Fig. 1C, E). This upper boundary has functional significance in the hydrodynamics of feeding. Colonies with greater than 12 individuals across, may have fixed water excurrent chimneys reflected in the skeleton (macroserial maculate, Fig. 1A). Broad colonies with no skeletal evidence of excurrent water chimneys are macroserial non-maculate (Fig. 1G).

Attachment to substrate (Fig. 5D)

The relationship between bryozoan colonies and their substrate (method of attachment) may not be evident from single colonial skeletal fragments, but it is generally consistent within clades (generic and often family-level) and can often be inferred. Colonies that adhere directly to their substrate, whatever its composition, in part or in whole, are considered cemented (Fig. 1E, G). Colonies that attach to their substrate by cuticular rootles are rooted (Fig. 1C). Some colonies have the ability to grow beyond a small, initial hard substrate, and overgrow a particulate substrate. These are called free-living forms, which under various environmental conditions my either be sedentary (Fig. 1A) or tumbled. Several unusual groups have developed a free living life mode, where the colony is physically supported by specialized modules (polymorphs), avicularia supported. Colonies that bore into hard substrates are considered endolithic and erect forms that develop from asexual budding of a toppled fragment of a parent colony are regenerated.

Arrangement of frontal surfaces (Fig. 6A)

This growth habit character class reflects various strategies bryozoans use to place their feeding surfaces in space. Colonies that grow as a single layer of individuals are unilaminate (Fig. 1E). Colonies that grow erect in two back-to-back layers are bilaminate (Fig. 1C, G) and rare forms are three sided prisms, trilaminate. Some colonies with narrow branches are essentially alternating pairs of back to back units (quadrate). Cylindrical forms may arise from a single layer of zooids budded in a radial pattern. Colonies that result in multiple layers of zooids, either by frontal budding or self-overgrowth, are multilaminate (Fig. 1A).

Secondary skeletal thickening (Fig. 6B)

Secondary thickening of the skeleton is an important structural component in some bryozoans. This thickening may be restricted to the frontal surface (Fig. 1C), or the reverse surface, or may be present on both surfaces, or not present at all (Fig. 1A, E, G).

Dimensions of structural units (Fig. 6C)

Bryozoans have developed different degrees to which they can occupy three-dimensional space. Those that are restricted to growth in approximately a single plane are considered straight or flat (Fig. 1E). Those forms that grow out of their primary plane are curved or folded (Fig. 1C, G). Other colonies develop as primary three-dimensional objects (Fig. 1A). Because encrusting forms conform to the dimensions of their substrate, by convention all encrusting forms are registered as straight or flat (as if encrusting a plane).

Frequency of bifurcations (Fig. 6D)

The generation of multiple structural units through branching applies to both linear branches and runners, and to planar sheets. Branching frequency is categorized here as an index of none (Fig. 1A), infrequent, frequent (Fig. 1E, G) and very frequent (Fig. 1C) based on the number of branching events through the length of a complete branch path; one-two, three-five, six or more (values of the log (n) of the number of branches produced by an increasing series of bifurcation events = Fibonacci series).

Dimensions of bifurcations (Fig. 5E)

Branching events that are restricted to a single plane result in planar fans (Fig. 1C). Those forms that branch in more than one plane result in three-dimensional bushes (Fig. 1E, G).

Connection of structural units (Fig. 6)

In more complex forms, reiterated structural units can be connected by a variety of mechanisms (primarily for additional structural support). Forms with no branches are treated as if they have no connections (Fig. 1A, E). Branches within a colony may fuse when they meet, resulting in continuous skeleton across the boundary (Fig. 1C, G). Highly coordinated growth displayed in some bryozoans, results in cross bars of skeleton that connect branches in a very regular form. Note that these extrazooecial skeletal connections can not be attributed to any given individual in the colony. Cuticular connections between lateral branches develop in some forms, which allow radiating, planner branches to become connected as fronds. Linear tubes or extents that connect individuals in some colonies are known as stolons. Some forms connect individual modules by calcified connecting tubes.

APPLICATION OF CLASSIFICATION

Modular growth in colonial organisms is the source of raw variation in colony form and provides a wealth of data that can potentially address fundamental questions of complexity related to phylogeny, ecology, and macroevolutionary trends. This approach to classifying modular growth habits provides a standardized terminology in which to address these questions. Comprehensive comparisons of colony form character states were not possible with previous classification schemes that relied on archetypal and incomplete descriptive concepts (Hageman et al., 1998). The classification summarized here allows for direct comparison of colony-form character states among specimens/taxa. The viability of this classification in practical application has been demonstrated in an ongoing paleoecological study of 143 Eocene cheilostomate bryozoan species (data set of Cheetham, 1963), each of which has had its colony form characterized using this scheme (Hageman, 2001).

The prime benefit of standardized descriptions of colony-form character states is the ability to make meaningful comparisons, taxonomic and ecological. This classification (Figs. 4–7) provides a multidimensional morpho-ecospace that can be applied in comparisons of modular colony form with features of its ecology. It allows for direct comparison of a suite of functionally analogous character states between any two specimens or among many taxa. The distribution of modular-growth character states can be tested for significant correlation with the organism's specific environmental parameters (e.g., temperature or nutrient concentration), geographic distribution or associated biota. In addition, all of these features can be evaluated in the context of temporal variation, e.g., neo-ecology to macroevolutionary patterns. The classification can also contribute to the study of processes involved in the phenomenon of modularity itself.

At this time our knowledge of the ecological, functional and evolutionary significance of various colonial growth form character states is not adequate to allow for speculation regarding their polarization in terms of complexity. The most important distinction that can be made now is between colonies restricted to iteration of only primary modules (e.g., single sheet, branch mound, Fig. 1A) versus those that have iterated second-order (or higher) modular units (Fig. 1C, E, G). Second and higher orders of modularity provide for more "parts" on which selection may

act. Therefore, growth through propagation of second-order modules will generally be perceived as representing a greater degree of complexity than those with few parts, i.e., iteration of only primary modules. In addition, modular growth of any kind allows for occupation and utilization of space and physical environments that may not be available to solitary individuals. Thus, with additional life modes comes greater diversity (number of ways of making a living), which is another informal measure of complexity.

Radiation of growth habit complexity in Bryozoa

Bryozoa is the only major phylum that does not have a fossil record in the Cambrian (Taylor, 1993). Earliest examples of bryozoan colonies from the early Ordovician are generally simple mounds or encrusting runners (Taylor and Cope, 1986; Hu and Spjeldnaes, 1991; Taylor and Rozhnov, 1996). These colonies were restricted to iteration of primary modules. However, by the middle Ordovician, a diverse array of growth habits were present that display modular growth by iteration of second-order modules. These represent five orders within a single dominant class, Stenolaemata (Taylor and Cope, 1986; Taylor, 1993; Taylor and Rozhnov, 1996; Hageman and McKinney, unpublished data). A systematic description of colony growth habits has not been completed for Ordovician Bryozoa, but the pattern of rapid radiation of diverse growth forms is striking. Many of what would be considered fundamental architectures of modern bryozoan colony forms had already been explored by Bryozoa by the end of the Ordovician (Hageman and McKinney, unpublished data).

A similar macroevolutionary pattern is evident in the history of the dominant group of bryozoans, the modern seas, cheilostomatids, of the class Gymnolaemata. Cheilostomes first appear as simple encrusting sheets and runners in the Jurassic (Taylor and Larwood, 1990). Like the early history of stenolaemates, the interval of time during which these forms were restricted to growth by iteration of only primary modules was relatively short, followed by a rapid increase in the diversity of growth forms in the Cretaceous resulting from colony growth by iteration of second-order (and higher) modular units.

Colonial growth habits have been "reinvented" numerous times within and among bryozoan clades. Pervasive convergent and iterative evolution is a common theme in bryozoans. This consequence of modularity has contributed to the problems encountered by non-specialists who are often overly influenced by colony form in their attempts to identify bryozoans (Hageman, 1991). Even complex, seemingly improbable growth habits such as helical coiling have been developed at least five times in four different orders among two classes in Bryozoa (McGhee and McKinney, 2000; McKinney, personal communication).

Disjunct levels of selection

Overall colony (body) form in Bryozoa is little constrained by ecological features that affect the individual (primary module). This apparently provides two, disjunct(?) sets of characters for evolutionary selection to act upon, (1) primary modules (zooids and polymorphs) and (2) those

associated with modularity responsible for generation of overall colony form. Characteristics associated with variation in primary modules (zooids) have greater phylogenetic significance, and those associated with the second set have greater ecological significance. These are well known characteristics of Bryozoa, however, the potentially disjunct relationships among evolutionary processes acting on these two sets of characteristics have not been adequately explored.

Although Carroll was writing in reference to modularity in the context of the development of solitary organisms, his (Carroll, 2001) observations hold true for the entire spectrum of modularity: "… one of the most important features that has facilitated the evolution of plant and animal complexity and diversity is the modularity of their construction from reiterated, differentiated parts."

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Footnotes

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