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Testing for bias in the evolution of coloniality: a demonstration in cyclostome bryozoans

Daniel W. McShea and Edward P. Venit

Abstract.—Colonial organisms vary in the degree to which they are individuated at the colony level, i.e., in the degree to which the colony constitutes a unified whole, as opposed to a group of independent lower-level entities. Various arguments have been offered suggesting that evolutionary change along this continuum may be biased, that increases may be more probable than decreases. However, counterarguments can be devised, and the existing evidence is meager and inconclusive. In this paper, we demonstrate how the question can be addressed empirically by conducting a test for bias in a group of stenolaemate bryozoans, the cyclostomes. More specifically, we suggest three criteria for colony individuation: degree of connectedness among lower-level entities (in this case, zooids), degree of differentiation among lower-level entities, and number of intermediate-level parts. And we show how these criteria can be used together with a phylogeny and ancestral-state reconstruction methods to test for bias. In this case, results do not unambiguously support any single interpretation but are somewhat supportive of a null hypothesis of no bias in favor of increase.

As part of the demonstration, we also show how results can be transformed into a quantitative estimate of an upper limit on bias. Finally, we place the question of bias in a larger context, arguing that the same criteria and methods we employ here can be used to test for bias in other colonial taxa, and also at other hierarchical levels, for example, in the transitions from free-living eukaryotic cells to multicellular organisms.

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Introduction

Some compelling arguments suggest that the evolution of coloniality should be strongly directional, or biased. The suggestion has two components. The first is that in colonial organisms—such as bryozoans, corals, ascidians, social vertebrates, and social insects—coloniality is a matter of degree. In other words, there is variation in the degree to which the colony constitutes a unified whole as opposed to a group of independent lower-level entities, or more simply, in the degree to which the colony is ''integrated'' or ''individuated'' (Beklemishev 1969; Cowen and Rider 1972; Boardman and Cheetham 1973; Cook 1979; Boardman 1983; Boardman et al. 1983; Mackie 1986; McKinney and Jackson 1989; McShea 1996; Dewel 2000). The second component is the suggestion that in evolution, change along this continuum is biased, so that increases in colony individuation are more likely than decreases.

Two main lines of argument have been advanced in support of a bias. One is that increases in colony individuation are typically accompanied by increases in colony size, dispersal capability, resistance to physical stress, homeostasis, and division of labor, and these are all favored by natural selection (Wilson 1971, 1975; Bonner 1988; Anderson and McShea 2001). The other is that decreases in individuation, including complete reversal to a solitary condition, are blocked, ordinarily, or at least somewhat obstructed. The thinking is that as colony individuation increases, the lower-level entities become specialized—morphologically, physiologically, and behaviorally—and more dependent on the colony as a whole (Beklemishev 1969; Wilson 1971; Gadagkar 1997; Anderson and McShea 2001). If so, reversal would require these entities to regain some degree of competence for a more solitary existence, which in turn would require a long and complex series of adaptive steps.

Both points seem reasonable, but arguments against a bias can be devised. In particular, one could argue that colony individuation should track certain environmental vari-

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ables, and if these vary randomly over time, no increasing tendency is expected. For example, Dewel (2000) has suggested that high levels of predation, and other forces tending to fragment colonies, might be more dangerous to species with greater interdependence among lower-level entities, i.e., higher levels of colony individuation. Or conversely, one might also argue that the more highly individuated colonies are able to mount more coordinated responses to predators, perhaps by employing more-specialized defensive units (Mackie 1986), and therefore might be favored under high levels of predation. In either case, if colony individuation tracks predation levels, and if predation levels do not tend to increase or decrease systematically over time (but see Vermeij 1987), then individuation should show no tendency to increase or decrease in evolution, on average. Similar arguments could be developed for other ecological variables (cf. Hughes and Jackson 1990).

Further, in many colonial species, specialization of lower-level entities is incomplete, as evidenced for example by the high levels of conflict that remain in certain social-insect colonies (Keller and Reeve 1999). In these cases, lower-level entities may retain a high level of competence for independent existence, and if so, evolutionary reductions in colony individuation, or even returns to solitary existence, would be relatively easy. In any case, even where extreme specialization has occurred, it is not obvious that decreases must be more improbable than the increases that preceded them: both presumably require a long and complex series of adaptive steps. In sum, a priori, we have some reason to think that increases and decreases would be equally likely, and that selection has been equally constrained in both directions.

The empirical case for bias is also inconclusive. Increases in colony individuation are certainly common. The high level of colony individuation known as eusociality has apparently originated multiple times in a number of groups, including mammals and crustaceans (e.g., Duffy et al. 2000), as well as insects. Also, one aspect of individuation is polymorphism, or differentiation among lower-level entities (see below), and polymorphism has arisen a number of times (Harvell 1994). But decreases in colony individuation are also known. Perhaps the best known are the multiple transitions from eusociality to solitary living in the halictid bees (Danforth and Eickwort 1997; Danforth 2002). In ants, returns to a solitary condition are not known, but lesser reversals have apparently occurred, such as the loss of a differentiated queen in some ponerine ants (Gadagkar 1997). Possible cases of reduction in sociality can also be found in other insects, as well as in spiders, birds, and ascidians (Wcislo and Danforth 1997). In sum, it is clear that change in colony individuation is not ratchet-like, i.e., not irreversible. But the degree to which it is reversible is an open question.

Testing for Bias

Here, we demonstrate how the question can be addressed empirically by conducting a test for bias in a group of stenolaemate bryozoans, the cyclostomes. To conduct the test, we use five characters, that is, five morphological criteria for colony individuation, modified from schemes developed by Beklemishev (1969) and Boardman and Cheetham (1973). Then, we use a phylogeny published recently by Taylor and Weedon (2000), along with a variety of ancestral-state reconstruction methods, to estimate numbers of increases and decreases in each of the criteria. And using a method developed by Sanderson (1993), we convert these numbers to probabilities and test for bias; that is, we test whether probability of increase is significantly greater than probability of decrease. We also offer a way to assess the power of the test, specifically, to estimate quantitatively the maximum bias that is consistent with the data overall at a given level of statistical confidence. Our approach is similar to that used by Danforth (2002) to estimate number of reversals in coloniality in halictid bees, but we use different criteria for coloniality, we use a variety of ancestral-state reconstruction methods, and we go a step further, converting numbers of changes in coloniality into a test for bias in the direction of change.

Cyclostomes are colonial marine invertebrates, ranging in time from the Ordovician to the Recent (Ryland 1970; Boardman and

Cheetham 1987; McKinney and Jackson 1989). Colonies are composed of cylinder-shaped zooids, each of which presumably corresponds to a solitary multicellular individual (Boardman and Cheetham 1973; although see Dewel 2000). We chose cyclostomes because there is considerable variation in degree of coloniality within the group (Boardman and Cheetham 1973) and because a robust phylogenetic analysis has been conducted recently (Taylor and Weedon 2000) for a moderate sample of taxa (i.e., 29 taxa, most of them extant). Also, bryozoans generally, including cyclostomes, have an excellent fossil record (Foote and Sepkoski 1999), and thus fossil first occurrences can be used, in addition to standard methods, to generate plausible ancestral-state reconstructions (see below).

As will be seen, results in this case do not unambiguously support any single interpretation. However, our main goal is to offer a model for future studies. A second goal is to place the question in a larger context, suggesting that the same criteria and methods we apply here can be used to test for bias in the evolution of hierarchical structure at other levels, for example, in the transition from free-living eukaryotic cells to multicellular organisms. Thus, this paper extends the line of thought begun by McShea (2001a), which argued that (1) contrary to certain common intuitions, it is an open question whether change in hierarchical structure has been biased at the largest scale (i.e., over the history of life); and (2) the question can be addressed empirically.

This study is also relevant to the more general and ongoing discussion of coloniality in bryozoans (Cowen and Rider 1972; Boardman and Cheetham 1973; Cook 1979; Ryland 1979), as well as in marine invertebrates generally (Beklemishev 1969; Boardman et al. 1973; Larwood and Rosen 1979; Jackson et al. 1985; Mackie 1986; Harvell 1994), social insects (reviewed in Anderson and McShea 2001), vertebrates (e.g., Wilson 1975; Danchin and Wagner 1997; Kitchen and Packer 1999), and plants (e.g., Hutchings and Wijesinghe 1997). And it contributes to the discussion of the mechanisms governing the origin (and loss) of higher levels of selection (Leigh 1983, 1991; Buss 1987; Maynard Smith 1988; Sober and Wilson 1994; Maynard Smith and Szathmáry 1995; Brandon 1996, 1999; American Naturalist 1997; Keller 1999; Michod 1999).

Clarifications

Three clarifications are in order. First, the issue of bias is partly independent of the question of a trend. Given a bias, a trend is almost inevitable (assuming no upper limit is reached), but the absence of a bias does not imply the absence of a trend. A trend could also be produced, for example, by unbiased diffusion or by lower extinction rates among the more-individuated taxa (McShea 1994); other mechanisms are also possible (Alroy 2000; McShea 2000). In any case, the point is that testing for bias is not the same as testing for a trend. In cyclostomes, a trend is uncertain. Boardman and Cheetham (1973) observed that the larger group, the stenolaemates, showed no long-term trend in the maximum, but the behavior of other summary statistics, such as the mean, has not been investigated either in cyclostomes or in stenolaemates as a whole.

Second, the concern here is not with particular episodes of change in individuation, i.e., with gains or losses in particular lineages and with the unique ecological or developmental factors associated with these changes. Rather the focus is at a larger scale, on probabilities of change in higher taxa, across many lineages and spanning diverse ecological circumstances. Third, the bias issue concerns the mechanism or dynamics of change among lineages (McShea 1994), not what we commonly think of as "causes." Causes lie at a lower explanatory level. That is, a bias is consistent with a number of possible causes: for example, a bias—if present—could be caused by selection, as discussed earlier, but it could also be caused by a developmental constraint.

Methods

Criteria for Individuation

Here we adopt three criteria for colony individuation: connectedness among lower-level entities, differentiation among lower-level entities, and number of intermediate-level parts (explained later). The three are gener-

alizations of certain more-specific criteria that have figured prominently in classic studies of coloniality by Beklemishev (1969) and Boardman and Cheetham (1973; see also Cowen and Rider 1972).

Various other criteria have been developed in the theoretical literature (Campbell 1958; Hull 1980; Salthe 1985; Mishler and Brandon 1987; Bonner 1988; see also Simon 1962; Allen and Hoekstra 1992; Sober and Wilson 1994; Ghiselin 1997; Wilson 1999; Gould and Lloyd 1999; Wagner and Laubichler 2000; McShea and Venit 2001). And still others have been developed for investigating individuation empirically in particular taxa (Beklemishev 1969; Cowen and Rider 1972; Boardman and Cheetham 1973; Coates and Oliver 1973; Cook 1979; McKinney 1984; Lidgard 1985, 1986; Mackie 1986; Lidgard and Jackson 1989; McKinney and Jackson 1989; Anderson and McShea 2001). We chose these three because they are often manifest in morphology at a gross structural level, and also because they can be assessed in various ways across a range of colonial taxa (see below). Finally, the three can be used for evaluating degree of hierarchical structure in organisms at all levels, from prokaryote to integrated colony (see below).

A brief discussion of the criteria follows, along with an explanation of how each was applied in bryozoans. As will be seen, we used five characters to assess the three criteria, one each for connectedness and intermediate-level parts, and three for differentiation.

Connectedness.—The assumption here is that connectedness reflects the degree to which lower-level entities can share resources and function in a coordinated fashion, and therefore the degree to which the colony operates as a unified whole. Connectedness can take a variety of forms, including physical attachment; sharing of a gut, coelom, vascular system, or nervous system (as in some colonial invertebrates); and behavioral interactions mediated by pheromones, sound, or physical contact (as in social insects and vertebrates).

In post-Paleozoic cyclostomes, the vertical walls separating adjacent zooids have pores (Borg 1926; Ryland 1970; Nielsen and Pedersen 1979), creating narrow coelomic connections among the zooids. In the forms that are called "fixed walled," these pores constitute the only coelomic connection, because the vertical walls contact and fuse with the exterior walls which then calcify to form frontal walls (Fig. 1). But in "free-walled" forms, the frontal walls are uncalcified, and no contact is made with the vertical walls, creating a more extensive connection around the distal ends of the vertical walls (Fig. 1) (Larwood and Taylor 1979; Hayward and Ryland 1985; Taylor 2000).

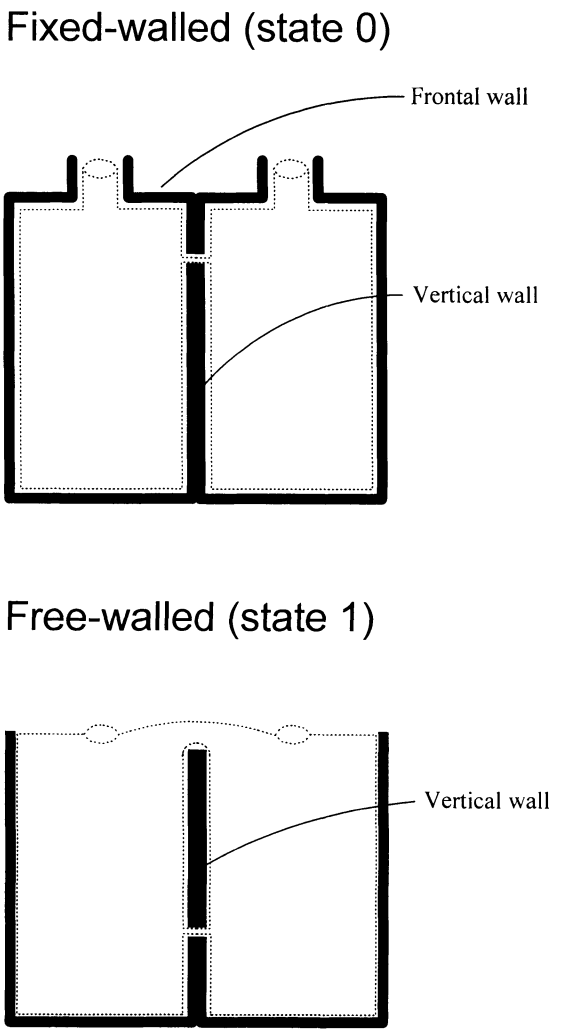

FIGURE 1. Connectedness: fixed- vs. free-walled. The dark-bordered cylinders represent zooids, and the dotted lines show their coelomic boundaries and connections. In post-Paleozoic fixed-walled taxa (top), coelomic connection is possible only through pores in the internal vertical walls separating adjacent zooids, whereas in free-walled taxa (bottom), an additional connection is present around the ends of the vertical walls.

TABLE 1. Criteria for colony individuation and character-state numbering scheme.

Criteria and character states	Description
Connectedness	
0	Fixed-walled
1	Free-walled
Differentiation	
0	Eruptive overgrowth, adventitious branching, or daughter colonies absent
1	Eruptive overgrowth, adventitious branching, or daughter colonies present
Intermediate-level parts (maculae)	
0	Maculae absent
1	Maculae present

Here, fixed-walled forms are assigned to "state 0" and free-walled forms to "state 1" (Table 1). (Fixed-walled corresponds approximately with Boardman and Cheetham's Series A, state 2, and Series B, state 3; free-walled corresponds with Series A, state 3, and Series B, state 4 [Boardman and Cheetham 1973; see also Boardman 1983].)

Differentiation.—The suggestion here is that degree of individuation of a colony increases as the morphological, physiological, or behavioral differentiation among its component lower-level entities increases (Anderson and McShea 2001). One rationale would be that greater differentiation means greater specialization and division of labor, which in turn means greater dependence of differentiated types on the whole (Beklemishev 1969). (For further discussions of differentiation in bryozoans, see Banta 1973; Cheetham 1973; Schopf 1973; Silén 1977; and Harvell 1994.) Thus, a colony with more different types of lower-level entities is more individuated than one with fewer. In principle, differentiation is a continuous variable, but here it is treated as discrete, with differences among lower-level entities assessed impressionistically (consistent with the approach to counting part types in Cisne 1974; Bonner 1988; Valentine et al. 1994; Bell and Mooers 1997).

We focused on morphological differentiation and in particular on what is called astogenetic differentiation. A cyclostome colony is founded by a larva that settles and metamorphoses into a zooid, called the ancestrula. The ancestrula gives rise to a second generation of zooids, which in turn gives rise to a third, and so on, in a process called astogeny. Astogenetic differentiation is generational variation in zooid morphology. In many species, astogenetic differentiation is limited to the proximal region of the colony, meaning to the ancestrula alone or the ancestrula plus the first few generations of zooids. This primary zone of astogenetic change is then followed by a much longer zone of repetition of zooids with essentially the same morphology (Boardman and Cheetham 1973; Taylor and Furness 1978). In some species, however, the repetition is interrupted by a secondary zone of astogenetic change (Boardman and Cheetham 1973), which is our concern here.

We considered three forms of secondary-zone change: eruptive overgrowth, adventitious branching, and daughter colonies:

1. Eruptive overgrowth occurs when a zooid or group of zooids somewhere in the zone of repetition shows an unusual amount of growth, extending above the colony surface and then budding additional zooids, which begin to overgrow the existing colony. The zooid initiating the overgrowth ("pseudoancestrula") differs morphologically from the zooids in the adjoining zone of repetition and initiates a zone of secondary astogenetic change. Among the 29 taxa considered here, eruptive overgrowth occurs in *Foricula*, *Collapora*, *Meliceritites*, and *Reptomultisparsa*.

2. In species in which the colony branches, new branches normally arise by division of a distal growing tip of an existing branch. An adventitious branch, in contrast, is one that arises from the side of an existing branch, beginning with a short series of differentiated

zooids; subsequent generations of zooids along the branch then typically return to the normal colony budding pattern. Among the taxa here, adventitious branching occurs only in *Cuffeyella*, an extinct genus from the Ordovician.

3. Daughter colonies (also called subcolonies) originate when an otherwise normal zooid at the distal growing edge of the colony differentiates in the sense that it begins to behave like an ancestrula, budding new zooids in a pattern normally associated with the initial astogeny of the colony (McKinney and Taylor 1997). Daughter colonies occur in a number of cyclostome taxa (McKinney and Taylor 1997), but among the 29 taxa considered here, only in *Plagioecia* and *Disporella*. *Disporella* has two types of daughter-colony-like structures, at least one of which may be (partly) homologous with those of *Plagioecia* (P. D. Taylor personal communication 2001); structures of the other type are maculae, of the sort discussed in the next subsection.

Here, we treat the three types of secondary astogenetic differentiation independently. For all three, state 0 corresponds to the absence of differentiation and state 1 to its presence (Table 1). (Absence of eruptive overgrowth, adventitious branching, and daughter colonies corresponds to Boardman and Cheetham's Series D, state 3, and their presence to Series D, state 4 [Boardman and Cheetham 1973; see also Boardman 1983].)

Intermediate-Level Parts.—These are colony structures that consist of either a single, enlarged lower-level entity or a collaboration of two or more lower-level entities (McShea 2001b; for a slightly broader definition, see Anderson and McShea 2001). Such structures are intermediate in level in that they are larger than a typical lower-level entity but a subset of the entire colony. On account of their large size, intermediate-level parts can perform functions on a larger scale than would be possible for a single or ordinary-sized lower-level entity, that is, on a scale that is useful to the colony as a whole. Intermediate parts correspond closely to what Beklemishev called ''cormidia'' (see also Ryland 1979). In bryozoans, these structures include maculae, narrowly construed here as a feature of skeletal morphology, in particular (following Taylor and Weedon 2000), as regularly spaced zones on the colony surface where feeding zooids are absent or less dense than in the rest of the colony. In many species, including all of the maculate taxa considered here, these zones occur as raised mounds known as monticules (Taylor 1999).

Maculae represent multizooidal collaborations in two senses. First, feeding zooids in intermonticular regions presumably collaborate in providing food for the colony as a whole, including the non-feeding zooids. And second, the groups of non-feeding zooids in the monticular regions represent a kind of collaboration for the provision of excurrent chimneys to channel food-depleted sea water away from the colony (Banta et al. 1974).

Maculae are commonly understood in a broader sense to refer to a variety of structures that function as excurrent chimneys. For example, in the disk-shaped colonies of *Plagioecia*, zooids in the center of the disk lean away from a central point, producing an excurrent chimney there (F. K. McKinney personal communication 2001). And in certain cheilostome bryozoans, maculae may occur as clusters of feeding zooids that elevate and orient their feeding organs (lophophores) so as to produce excurrent chimneys without requiring any skeletal modification (McKinney 1990). Maculae in this broad sense have arisen often in evolution (i.e., convergently) in response to the varying demands for excurrent channels that accompany changes in colony form or size (McKinney 1986, 1990; Key et al. 2001). Our use of the narrower definition, based on feeding-zooid density, increases the likelihood that maculae will be to some degree homologous across taxa.

Among the 29 taxa considered, maculae are present at least occasionally in *Foricula*, *Disporella*, *Patinella*, *Favosipora*, *Borgiola*, and all three species of *Heteropora*. State 0 corresponds to the absence of maculae and state 1 to their presence (Table 1). (Maculae might be understood as interruptions in the astogenetic pattern, in which case their absence would correspond with Boardman and Cheetham's Series D, state 3, and presence with Series D, state 4. Or they might be construed as non-as-

togenetic differentiation, and then their absence would correspond with Boardman and Cheetham's Series E, state 1, and presence with Series E, states 3–4 [Boardman and Cheetham 1973; see also Boardman 1983].)

Relationships among the Criteria.—The three criteria are conceptually independent but nevertheless seem to be somewhat correlated in colonial organisms. For example, in ant colonies, high levels of polymorphism (i.e., differentiation) are associated with the performance of many tasks by teams (i.e., intermediate-level parts), rather than by individuals. A likely explanation is that team tasks require some division of labor, which in turn is facilitated by differentiation among lower-level entities. See Anderson and McShea 2001 for a longer discussion of features shared by highly individuated colonies (or what they call complex colonies; see Bourke 1999) and of the possible correlations among them.

Connectedness is somewhat more problematic. It seems clear that connectedness in some form must increase in the transition from solitary to colonial living. For one thing, connectedness in the form of resource sharing is necessary to support lower-level entities that do not feed; and more generally, connections are necessary to coordinate behavior among lower-level entities. However, it is possible that the positive relationship between connectedness and colony individuation has limits. That is, after a certain point, further connectedness may tend to undermine colony individuation. One possible reason comes from theory: Kauffman (1993) has investigated networks of interacting components, what he calls N-K Boolean networks, in which each component receives inputs from K other components, on average, and the state of each component at a given time—on or off—is a function of the states of its inputs at the previous time. Kauffman found that in large arrays of connected components, complex and stable patterns of activation emerge only at intermediate levels of connectedness, especially at $K = 2$. At higher K, arrays behave chaotically, with most components turning on and off in no particular pattern, whereas at $K = 1$ arrays tend to freeze, with most components in either the on or off state. The relevance of this finding to the relationship between connectivity among components and the performance of functions by the whole would be worth exploring further.

Second, and more concretely, the development and maintenance of differentiation among lower-level entities may require some degree of mutual isolation, or of what has been called in marine organisms, compartmentalization. Cheilostome bryozoans are polymorphic and also highly compartmentalized, whereas in both phylactolaemate bryozoans and ascidians, polymorphism is absent and compartmentalization is absent or much reduced (Ryland 1979; Boardman 1983; Mackie 1986; Harvell 1994). On the other hand, compartmentalization is low and polymorphism high in two cnidarian groups, the hydroids and siphonophores (Harvell 1994). In any case, as a result of these ambiguities, a necessary assumption here is that in cyclostomes, overall connectedness among zooids (by all routes, not just coelomic connections) is relatively low, and therefore that higher levels of coelomic connectedness do reflect higher levels of colony individuation.

Taxa and Data

The Taylor and Weedon (2000) tree was based on 46 skeletal characters in 29 taxa. They used *Cuffeyella* as an outgroup (see Taylor and Wilson 1996) and found a single most parsimonious tree. Taylor and Weedon argue that the living cyclostomes are a monophyletic group (see also Taylor 2000; but see Boardman 1998) and that the taxa they selected are a representative sample. The data for our analysis—character states for colony individuation—were obtained from the Taylor and Weedon (2000) study and personal communications from F. K. McKinney and P. D. Taylor, as well as various sources in the general literature. These data are shown in Figures 2–6, mapped onto the Taylor and Weedon tree.

Two of our five characters were also used by Taylor and Weedon in generating the tree: fixed-walled versus free-walled (connectedness) and presence versus absence of maculae (intermediate-level parts). To investigate the possibility of circularity, we used PAUP (version 4 [Swofford 1998]) to reconstruct the tree

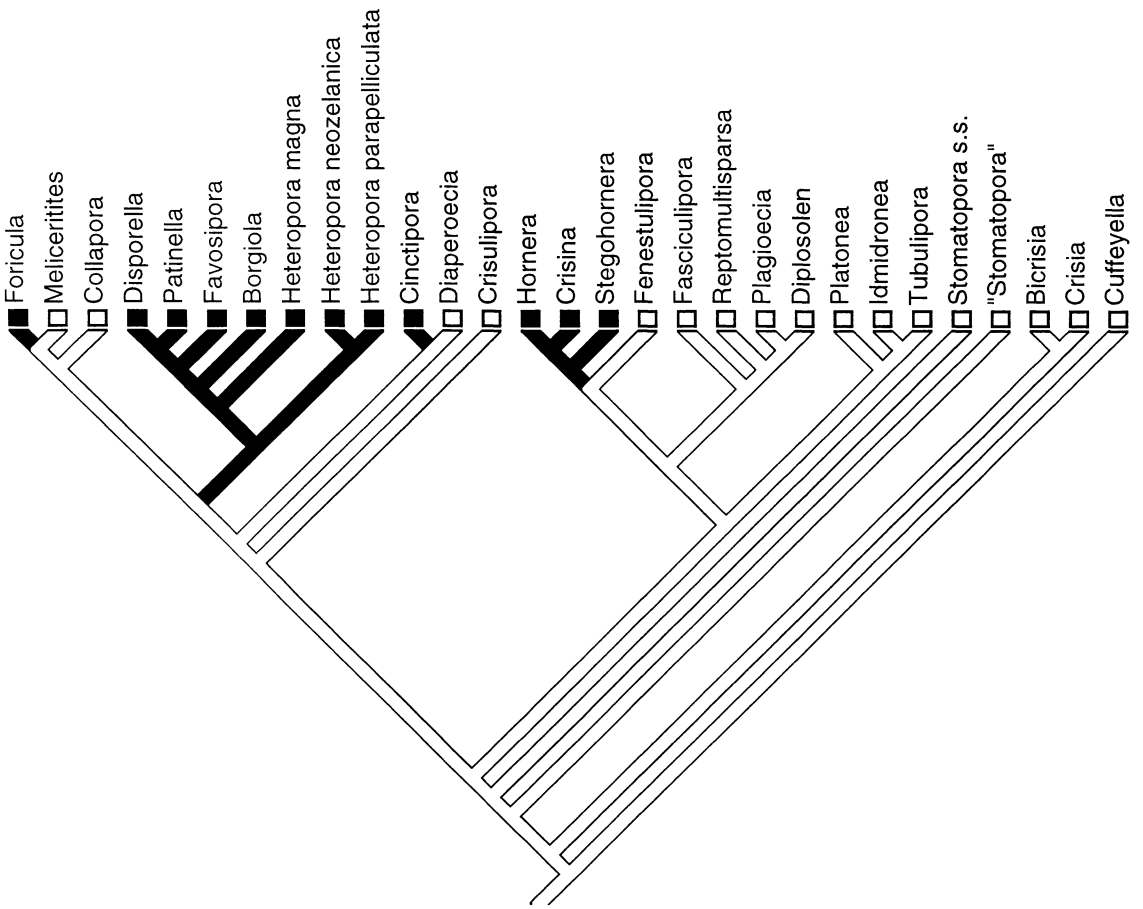

FIGURE 2. Most parsimonious tree for 29 cyclostome taxa (modified from Taylor and Weedon 2000). Reconstruction shown here is for connectedness; see text. White = fixed-walled (state 0); black = free-walled (state 1). All reconstructions in Figures 2–6 are based on parsimony.

using the Taylor and Weedon data set with wall structure and maculae removed. Following the Taylor and Weedon procedure, we used a heuristic search with ten random addition sequences. With the two characters removed, we found 51 equally parsimonious trees. A consensus tree was somewhat less resolved than the Taylor and Weedon tree, with one eightfold polytomy, but was otherwise completely consistent with it.

Estimating Bias

Overview.—We took two different approaches to estimating bias in bryozoans. In both, the five characters were treated independently. In the first approach, the character states of nodes within the tree, or ancestral states, were reconstructed using a maximum-parsimony method, a one-rate maximum-likelihood method, and also a method based on fossil first occurrences. For each method, counts of increases and decreases were generated by comparing states at adjacent nodes (i.e., in ancestor-descendant pairs). For the most part, we counted only unambiguous transitions, those in which both nodes could be assigned states by the method. Finally, following a method developed by Sanderson (1993), we normalized these counts by dividing by number of opportunities for change, thus generating probabilities of increase and decrease.

Sanderson developed his method for character sets with only two possible transitions (e.g., gain and loss), and the use of his method here, along with the choice of a two-state (0,1) scale, might seem to imply that we consider transitions to other states—e.g., a state of connectedness higher than that designated here

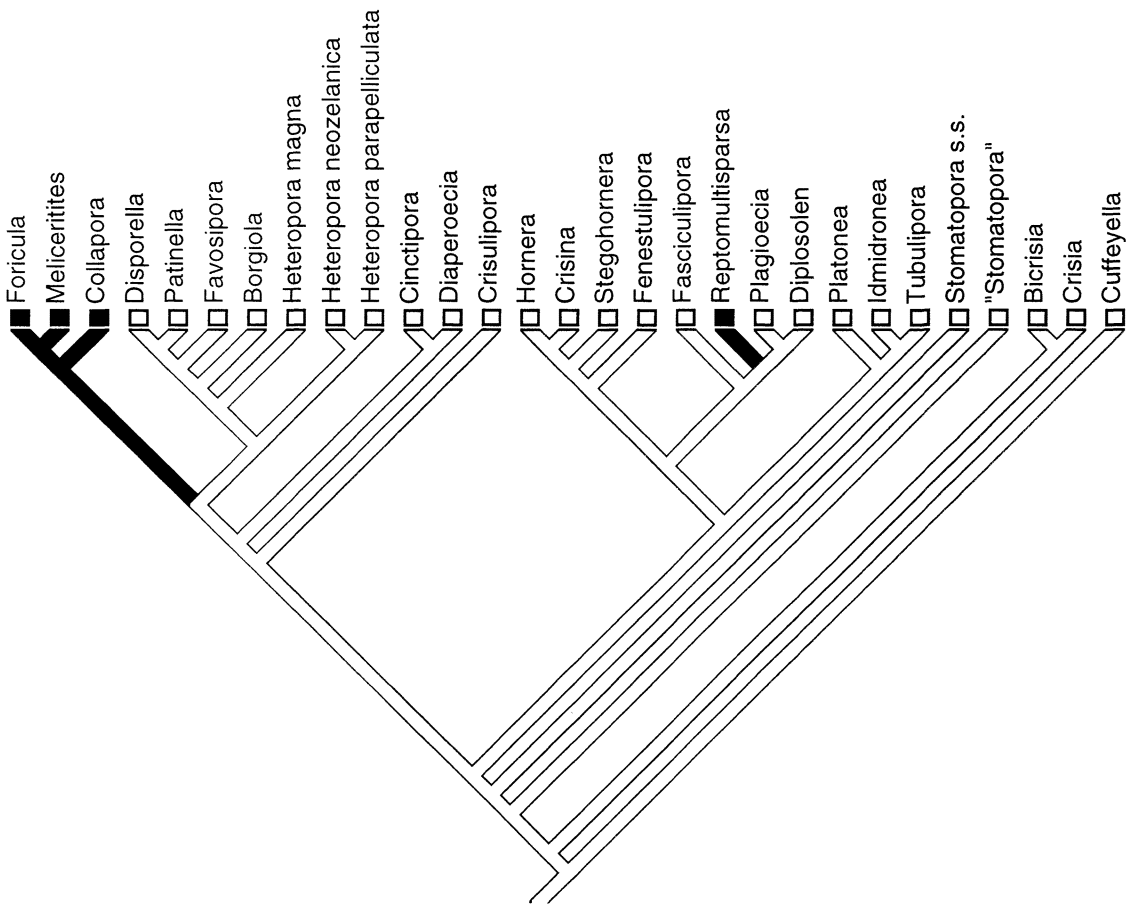

FIGURE 3. Differentiation: eruptive overgrowth. White = absent (state 0); black = present (state 1).

by state 1 or lower than that designated by state 0—to be impossible. Actually, this is not the case. Rather, the choice of scale reflects a deliberate tactic of focusing exclusively on changes visible in certain small ''windows'' along the individuation continuum, or in other words, across a series of small morphological gaps, whose endpoints are arbitrarily labeled 0 and 1. Thus, transitions to adjacent states, both higher and lower, outside these windows are possible but are not considered. For example, a connectedness state lower than what is here called state 0 might be one in which mural pores between adjacent zooids—as well as coelomic connections—are absent. In the cyclostomes considered here, the probability of a transition to this state from state 0 would seem to be quite low, in that no such transitions occurred, despite many opportunities. (Interestingly, communication pores were apparently absent in many Paleozoic fixed-walled taxa [Boardman and Cheetham 1987], which establishes the theoretical possibility of below-state-0 connectivity.) In any case, such a transition lies outside the chosen window, and thus its probability is not evaluated.

The second approach was based on rates of change generated by using a two-rate maximum likelihood model and is explained later.

Parsimony.—We used MacClade 3.01 (Maddison and Maddison 1992); the shading of branches in Figures 2–6 shows the resulting ancestral-state reconstructions. Two necessary assumptions are that rates of change were low and constant throughout the tree. (For others, see Schluter et al. 1997; Omland 1999.) We weighted increases and decreases equally (see below), essentially assuming a null hypothesis of equal probability of change

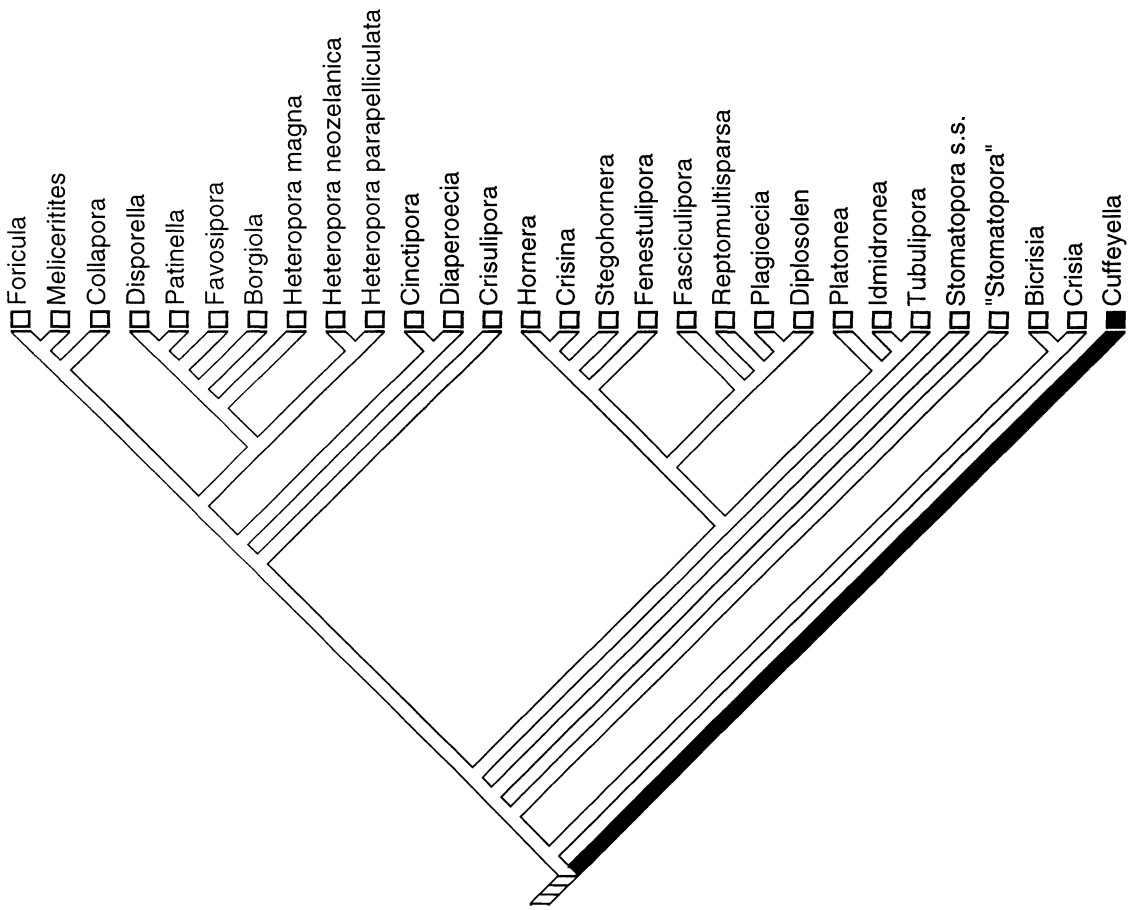

FIGURE 4. Differentiation: adventitious branching. White = absent (state 0); black = present (state 1); cross-hatched = state uncertain.

in both directions. For four characters (all except adventitious branching), the reconstructed state of the deepest node on the tree was the same as that of the outgroup, *Cuffeyella*; for adventitious branching, the deepest node was ambiguous (with equal weighting). All other nodes, for all characters, were reconstructed unambiguously.

Maximum Likelihood.—We used a maximum likelihood model, Discrete 1.01a (Pagel 1994, 1997), to reconstruct states at internal nodes. In particular, we used a one-rate model, which is generally preferable for moderate-size trees (Mooers and Schluter 1999). In a one-rate model, a single overall transition rate is assumed, i.e., $\alpha = \beta$, where α is the rate of transition from state 0 to state 1 and β is the rate of transition from 1 to 0. We assumed equal branch lengths (branch-length estimates unavailable), equivalent to assuming a punctuated model of evolutionary change. Implicit in the use of the model is an assumption that rates were stochastically constant over time and over all branches; see Pagel (1994, 1997) and Schluter et al. (1997) for other assumptions.

Our method follows Mooers and Schluter (1999; cf. Pagel 1999): for each character, we used Discrete to compute the overall transition rate. Then for each node, we reran the program with this rate fixed to compute the likelihood of the actual character-state distribution, first with that node fixed in state 0 and then with the same node fixed in state 1. The maximum likelihood state for that node is the one that produces the greater likelihood value. The procedure was repeated for each node, using the same overall rate, to produce a com-

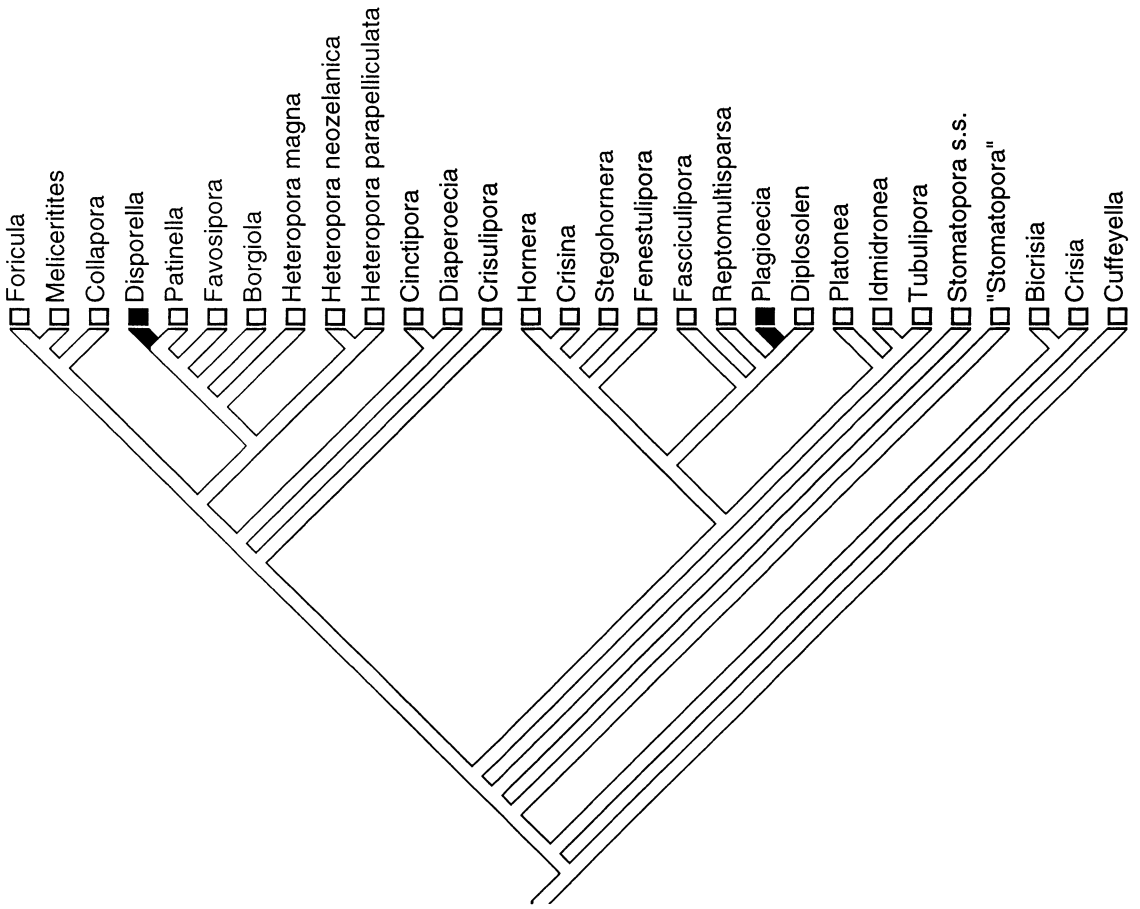

FIGURE 5. Differentiation: daughter colonies. White = absent (state 0); black = present (state 1).

plete set of ancestral states. Here, a state was considered ''unambiguous'' if half the difference in tree likelihood between the two alternative states, 0 and 1, exceeded two natural-log units (Mooers and Schluter 1999). Only transitions between unambiguous nodes were considered.

Fossil First Occurrences.—Each node in the tree was assigned the same state as the descendant genus with the earliest first occurrence. (The method is a modification of one used by Alroy [1998; see also Wagner and Erwin 1995; Wagner 1996].) For example, in Figure 2, the ancestor of *Foricula* and *Meliceritites* was inferred to be fixed-walled, because that is the state of *Meliceritites*, the genus with the earlier first occurrence of the two. Likewise, the ancestor of *Collapora* and the *Foricula–Meliceritites* subclade was also inferred to be fixed-walled, because that is the state of *Collapora*, the genus with the earliest first occurrence of that node's three descendant genera. Notice that there is no required assumption here that the modern representatives used in the analysis to represent the genus are primitive in all respects, only that they have the character in question in its primitive state. Notice, too, that first occurrences are being used only to assign states at ancestral nodes, not to evaluate the topology of the tree (cf. Huelsenbeck 1994).

This method has a number of possible sources of error (see Alroy 1998 for further discussion): (1) Fossil first-occurrences do not correspond to true first occurrences because the record is incomplete, although the bryozoan record may be more complete than average (Foote and Sepkoski 1999). (2) Using genera rather than species means that state changes at the species level will be overlooked;

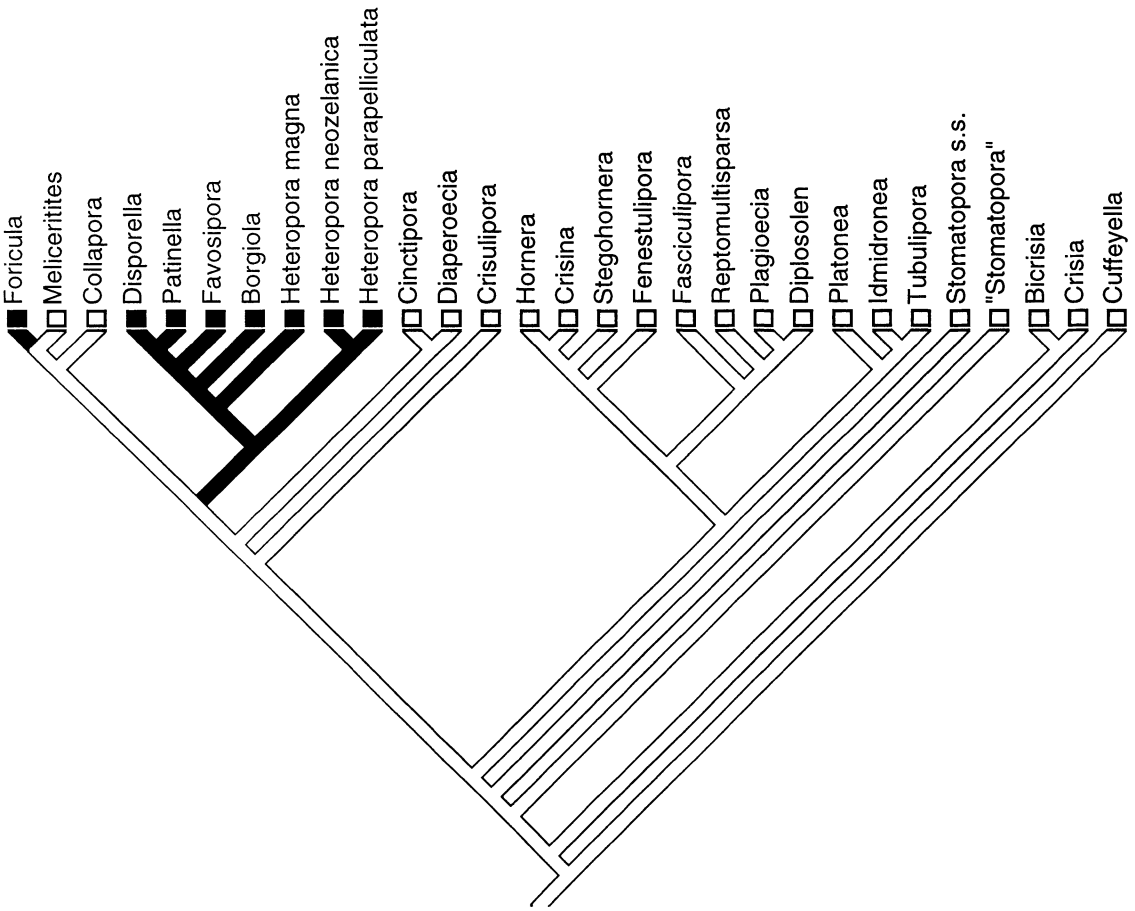

FIGURE 6. Intermediate-level parts: maculae. White = absent (state 0); black = present (state 1).

in other words, an internal node might be in a different state than a terminal taxon of the same genus. (3) The common classification practice of placing fossil species in extant genera produces an artificial extension of modern genus ranges (pointed out by C. R. Marshall personal communication 2001). All of these are significant sources of error, but they are not expected to bias results toward either increase or decrease. Therefore, they can be treated as random noise, whose main effect is to decrease the power of the test (see below).

First-occurrences were based on J. J. Sepkoski's genus-level compendium of stratigraphic ranges (unpublished, but see Appendix), supplemented by personal communications from F. K. McKinney and P. D. Taylor. The analysis was limited to the 23 cyclostome genera for which reasonably reliable estimates of stratigraphic ranges were available (see Appendix).

Two-Rate Model.—In the second approach, we used a two-rate maximum likelihood model ($\alpha \neq \beta$) to compute rates of increase (α) and decrease (β) directly, and we interpreted these values directly as estimators of transition probability. For each character, the significance of the difference between α and β was evaluated with a likelihood ratio test: $LR = -2\ln(H_0/H_1)$, where H_1 is the likelihood of the data (the states of the terminal taxa) using the two-rate model ($\alpha \neq \beta$) and H_0 is the likelihood using a one-rate model ($\alpha = \beta$) (Pagel 1997; Schluter et al. 1997; Ree and Donoghue 1999). LR is distributed as χ^2 with one degree of freedom.

Results

Results for the various ancestral-state reconstruction methods (i.e., the first approach

TABLE 2. Results using three ancestral-state reconstruction methods: maximum parsimony, maximum likelihood ($\alpha = \beta$, with 2-ln-unit cutoff; see text), and fossil first occurrences. The four "transitions" columns show numbers of transitions of each type between adjacent nodes on the reconstructed tree. Following Sanderson (1993), p(I) is probability of increase, or number of 0-to-1 transitions divided by the sum of 0-to-0 and 0-to-1 transitions: (0-to-1)/(0-to-0 + 0-to-1); p(D) is probability of decrease: (1-to-0)/(1-to-1 + 1-to-0). The "bias" column indicates which has greater probability, increase or decrease. p is overall probability of change, or (0-to-1 + 1-to-0)/(0-to-0 + 0-to-1 + 1-to-0 + 1-to-1). $G = -2*\log(LR)$, where LR is the likelihood-ratio, or p/p(I) when p(I) > p(D), and p/p(D) when p(D) > p(I). For trees as small as 32 taxa, G is distributed approximately as χ^2 (1 degree of freedom). Here $n = 29$ taxa for maximum likelihood and parsimony reconstructions; $n = 25$ for the fossil reconstructions; assuming the test is valid for these, none are significant at the 0.05 level (i.e., $G < 3.84$, in all cases); see text.

	Transitions								
	0 to 0	0 to 1	1 to 0	1 to 1	p(I)	p(D)	bias	p	G
Connectedness									
Parsimony	36	4	0	16	0.100	0.000	I	0.071	0.292
Max. likelihood	28	1	0	16	0.034	0.000	I	0.022	0.382
Fossils	25	3	3	17	0.107	0.150	D	0.125	0.158
Differentiation: eruptive overgrowth									
Parsimony	50	2	0	4	0.038	0.000	I	0.036	0.064
Max. likelihood	50	2	0	4	0.038	0.000	I	0.036	0.064
Fossils	32	2	5	9	0.059	0.357	D	0.146	0.778
Differentiation: adventitious branching									
Parsimony	(no unambiguous changes)								
Max. likelihood	(no unambiguous changes)								
Fossils	46	0	1	1	0.000	0.500	D	0.021	2.760
Differentiation: daughter colonies									
Parsimony	54	2	0	0	0.036				
Max. likelihood	54	2	0	0	0.036				
Fossils	42	2	2	2	0.045	0.500	D	0.083	1.556
Intermediate-level parts: maculae									
Parsimony	42	2	0	12	0.045	0.000	I	0.036	0.209
Max. likelihood	42	2	0	12	0.045	0.000	I	0.036	0.209
Fossils	32	2	3	11	0.059	0.214	D	0.104	0.627

above) are presented in Table 2. For parsimony, probability of increase exceeded probability of decrease for three characters: connectedness, one type of differentiation (eruptive overgrowth), and intermediate-level parts (maculae). Relative probabilities could not be assessed for adventitious branching and daughter colonies, in the former case because no unambiguous changes could be identified in the reconstructed tree, and in the latter because there were no opportunities for decrease and thus probability of decrease could not be computed.

The null hypothesis here is no bias in favor of increase, and therefore equal weighting of increases and decreases is appropriate in the sense that it does not bias the analysis in favor of rejection (Cunningham et al. 1998; Cunningham 1999). Still, some consideration of the sensitivity of results to transition weighting, or transition "costs," is in order (Omland 1997). As will be seen, the overall result here—two moderately well supported decreases (see below)—is consistent with the null hypothesis. So in this case, increasing the cost of increase would only tend to produce more decreases, reinforcing this result. However, increasing costs of decrease (i.e., favoring increase) has the potential to produce higher probabilities of increase in one character, adventitious branching: a decrease-to-increase cost ratio of 2-to-1 was sufficient to fix the basal node of the tree in the "branching absent" state, changing the lone transition from "ambiguous" to an increase. However, this possibility is contradicted by the fact that the outgroup, *Cuffeyella*, is an early Paleozoic form that long predates the 28 other taxa considered and therefore is more likely to exhibit the primitive state (i.e., adventitious branching present; see below).

For maximum likelihood, results were es-

TABLE 3. Estimates of rate of increase and decrease using a one-rate maximum likelihood model; see text. Column 2 = overall rate from one-rate model ($\alpha = \beta$); column 4 = α (rate of increase) from one-rate model, and column 5 = β (rate of decrease) also from one-rate model. Column 6 (bias) indicates in which direction the transition rate was higher using the one-rate model, increase (I) or decrease (D). Significance of the difference between rates of increase and decrease was assessed using a likelihood ratio test: $LR = -2\ln(H_0/H_1)$, where H_0 is the likelihood of the data using a one-rate model (column 3) and H_1 is the likelihood using a two-rate model (column 7); see text. LR is distributed as χ^2 (column 8) with one degree of freedom; significant differences ($P \leq 0.05$; $\chi^2 \geq 3.84$) are marked with an asterisk in column 6.

Individuation criterion	Overall rate ($\alpha = \beta$)	$-\ln(H_0)$	Rates of increase or decrease ($\alpha \neq \beta$)		Bias	$-\ln(H_1)$	χ^2
			α	β			
Connectedness: fixed- vs. free-walled	0.0947	27.337	0.1103	0.0006	I	25.614	3.45
Differentiation:							
Eruptive overgrowth	0.0397	17.013	0.0401	0.0008	I	16.881	0.26
Adventitious branching	0.0186	8.627	0.0001	0.7256	D*	2.076	13.10
Daughter colonies	0.0388	17.096	1.9034	25.6959	D*	13.169	7.85
Intermediate-level parts:							
Maculae	0.0404	16.942	0.0483	0.0010	I	16.190	1.50

sentially the same as for parsimony: probability of increase was greater for connectedness, eruptive overgrowth, and maculae, and relative probabilities could not be assessed for adventitious branching or daughter colonies.

Results for the fossil-based method differed systematically from the others in that they show a greater probability of decrease for all characters. The main reason is that the method produced moderately unparsimonious patterns of gains and losses, i.e., more total increases and decreases. As a result, the numerators of the ratios used to calculate both $p(I)$ and $p(D)$—number of 0-to-1 and 1-to-0 transitions, respectively—were both larger. However, the denominator of $p(D)$ is smaller for all characters, because the "1" state was rarer, or in other words, opportunities for decrease were always fewer. And thus the net effect was a greater increase in p(D).

This observation draws attention to a general phenomenon, namely that adding equal numbers of increases and decreases—such as might be effected by adding unbiased noise—will tend to increase the probability of the transition toward the more common character state. Importantly, however, this does not mean that the results from the fossil-based method constitute noise and can be discounted; indeed, the unparsimonious distributions of character states these results support may reflect reality.

Finally, results for the two-rate maximum likelihood approach (i.e., the second approach above) are shown in Table 3. The difference between rates of increase and decrease using a two-rate model reached statistical significance ($p \leq .05$; $\chi^2 \geq 3.84$) for adventitious branching and daughter colonies and nearly reached significance for connectedness among zooids (see caption and last column in Table 3). For both adventitious branching and daughter colonies, $\beta > \alpha$, meaning that decrease was more probable. These findings support the fossil-based results in the two cases for which relative probabilities could not be assessed using the other two ancestral-state reconstruction methods.

An apparent oddity in the maximum likelihood results for daughter colonies might need some explanation: the parsimony analysis suggested only two changes, both of them gains (Fig. 5), but the two-rate maximum likelihood algorithm inferred a higher rate of decrease, i.e., a high probability of loss. Actually, this sort of result is not unexpected in a maximum likelihood analysis when the character state in question is present (state 1) only in a small number of isolated terminal taxa. One way to explain it is that a very high rate of loss insures that any chance gains occurring low in the tree will be reversed, thus making a terminal distribution with few 1s—like the target distribution—relatively likely. In contrast, with a low rate of loss, any gains occurring low in the tree are unlikely to be reversed (C.

W. Cunningham personal communication 2001; see also discussion in Pagel 1999).

Discussion and Conclusion

The data do not provide strong evidence either for or against a bias. In Table 2, none of the results for any single aspect of colony individuation attained statistical significance ($p \leq 0.05$; $G \geq 3.84$; last column). Further, the various methods did not produce fully concordant results for any character.

Still, it is worth pointing out that for two characters, adventitious branching and daughter colonies, the decreases found using the fossil-based method attained the highest levels of significance (highest *G*-values; see Table 2) of all of the comparisons. Further, these two decreases did reach statistical significance in the two-rate maximum likelihood approach (Table 3), and they were at least not contradicted by the other two ancestor-reconstruction methods (in that these methods produced no interpretable result). In other words, two results might be considered moderately well supported, both decreases.

The higher probability of decrease in adventitious branching raises an important issue. The parsimony analysis (Fig. 4) shows that adventitious branching was present in the Paleozoic outgroup, *Cuffeyella*, and that it failed to arise despite numerous opportunities in the 28 post-Paleozoic taxa (46 opportunities; see Table 2). (Actually, adventitious branching does occur in at least two other post-Paleozoic cyclostome genera not considered here [P. D. Taylor personal communication 2001].) One could argue that this interpretation prejudices the result against increases by overstating the number of opportunities. That is, some taxa have a colony form that does not permit branching (e.g., circular or subcircular encrusters, such as *Plagioecia*), or in other words, adventitious branching cannot arise in these, at least not without a prior change in colony form. However, the viewpoint adopted here is that colony form constitutes a part of the *explanation* for the failure of adventitious branching to arise, not a factor tending to distort the results. In other words, the constraint imposed by colony form underlies and (in part) explains the low probability of change revealed by the analysis. The same argument applies to other characters that cannot occur in certain colony forms (e.g., maculae, which cannot occur in a biserial form, such as *Crisia*, without a prior change in colony form).

Another issue concerns the choice of outgroup. We used the outgroup chosen by Taylor and Weedon, the Ordovician genus *Cuffeyella*, which was poorly individuated in four of the five criteria. However, it is possible that early post-Paleozoic cyclostomes were more individuated, on average. (For example, *Disporella* from the Cretaceous may have been highly individuated by three out of five criteria.) To address this possibility, we evaluated the effect of removing *Cuffeyella* and substituting an unspecified taxon with the more individuated state for the four criteria. (We considered only the effect on the probability calculations not on the cladogram, i.e., the effect on each of the four criteria of changing one 0-to-0 transition to a 1-to-0 transition in Table 2). The obvious net effect was to shift the results in the direction of greater probability of decrease. Specifically, after we made the changes, all entries under ''bias'' in Table 2 were decreases (including the two entries for daughter colonies that were previously incalculable), except for connectedness-parsimony (which remained an increase) and the two reconstructions for adventitious branching (which still produced no unambiguous changes). Still, none of the results in Table 2 achieved statistical significance.

Estimating Maximum Bias

Even when significant results are few, they can be transformed into an estimate of ''maximum bias.'' In other words, an upper bound—at some preselected confidence level—on the magnitude of a bias can be computed.

We begin by defining the underlying bias in a clade as b, the actual probability that a change in colony individuation, when one occurs, will be an increase; $1 - b$ is the probability of decrease. Thus, $b = 1$ for irreversible increase, a positive ratchet; $b = 0$ for irreversible decrease; and $b = 0.5$ for an unbiased system. Now consider the results above, zero increases and two decreases, out of two mod-

erately well supported results. If the underlying dynamic were unbiased, with $b = 0.5$, such a result would occur only one time in four, and therefore we can rule out the possibility that $b = 0.5$ with probability $(1 - b)^2$, or 0.25, corresponding to a confidence level of 75%. To achieve 95% confidence, a higher b-value must be allowed:

$$(1 - b)^2 > 0.05, \text{ or } b < 0.77.$$

The maximum bias is thus 0.77, or, in other words, we can rule out with 95% confidence the existence of a bias toward increase of 0.77 or greater.

More generally, for any combination of N results, consisting of I increases and D decreases, where $N = I + D$, the maximum bias b, at confidence level $1 - p$ (in the case above, $p = 0.05$), can be computed as the solution to the binomial equation:

$$\sum_{j=D}^{j=N} [N!/j!(N - j)!][b^{N-j}(1 - b)^j] > p$$

It should be emphasized that these findings depend on the correctness of the tree on which the results are based. Any random error in the structure of the tree will be manifest as random error in the results, which in turn will favor the null hypothesis, i.e., will tend to produce an estimate of b closer to 0.5.

In this case, the findings—$b < 0.77$—fall short of establishing that the evolution of colony individuation in cyclostomes is unbiased, but they do weigh against the possibility of an extremely strong bias toward increase. Further tests, based on larger samples, may be able to establish a lower ceiling, a lower maximum bias.

Larger-Scale Investigations

We intend this treatment as a model for investigating bias in the evolution of coloniality, not only in bryozoans but in other taxa as well. Indeed, the three criteria for individuation were chosen in part because of the ease with which they can be applied in other taxa. Consider ant colonies, for example. Connectedness might be measured as some function of the number of pairs of individuals that interact relative to the number of possible interacting pairs, also called ''average system connectedness'' (Moritz and Southwick 1992); differentiation could be measured as the number of morphological castes; and intermediate-level parts as the number of types of groups or teams in which multiple individuals cooperate in the performance of tasks. (For a longer discussion, see Anderson and McShea 2001, and references therein.)

Importantly, in proceeding this way there is no implicit assumption that the evolutionary constraints are the same in ants and bryozoans, nor that both will show the same evolutionary patterns. For example, a bias could be absent in bryozoans but present in ants. Rather, the assumption is that the same criteria play similar roles in colonial organization in both groups—that connectedness, for example, is relevant to coloniality in the same way in both—and that these common roles can be captured with different characters (e.g., fixed- vs. free-walled in bryozoans, average system connectedness in ants).

This study can also be understood as part of an investigation of bias at a larger scale, in the hierarchical structure of organisms generally over the entire history of life. Four major hierarchical levels can be discerned in the fossil record: prokaryotic cells, eukaryotic cells (which historically are associations of prokaryotic cells), multicellular eukaryotes, and colonies. And within these levels, there are differences in individuation that can be assessed on the basis of differences in connectedness, differentiation, and number of intermediate-level parts. For example, at the multicellular level, the green alga *Gonium* (a close relative of *Volvox*) is poorly individuated in that it consists entirely of cells of the same type. In contrast, *Volvox* is better individuated in that it has two cell types (in its vegetative state) and an intermediate-level part (vegetative cells organized to form a flagellated sphere).

Is there a bias in the evolution of individuation generally, at all major levels, across the hierarchy spectrum? As for the colony level, arguments both for (e.g., Bonner 1998) and against (e.g., Gould 1996) a bias have been offered, and the evidence one way or the other is meager and inconclusive (McShea 2001a;

McShea et al. 1999). One way to test for bias would be to assess probabilities of increase and decrease in connectedness, differentiation, and intermediate-level parts in a sample of clades distributed widely across the hierarchy spectrum, from the prokaryote level to the colony level (McShea 2001a: Fig. 6). In such a project, the present study constitutes a single data point, an investigation of bias in a single clade located at the high end of the spectrum.

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Literature Cited

Allen, T. F. H., and T. W. Hoekstra. 1992. Toward a unified ecology. Columbia University Press, New York.

Alroy, J. 1998. Cope's rule and the dynamics of body mass evolution in North American fossil mammals. Science 280:731–734.

———. 2000. Understanding the dynamics of trends within evolving lineages. Paleobiology 26:319–329.

American Naturalist. 1997. Multilevel selection: a symposium organized by David Sloan Wilson. American Naturalist 150(Suppl.).

Anderson, C., and D. W. McShea. 2001. Individual versus social complexity, with particular reference to ant colonies. Biological Reviews 76:211–237.

Banta, W. C. 1973. Evolution of avicularia in cheilostome Bryozoa. Pp. 295–303 *in* Boardman et al. 1973.

Banta, W. C., F. K. McKinney, and R. L. Zimmer. 1974. Bryozoan monticules: excurrent water outlets? Science 185:783–784.

Beklemishev, W. N. 1969. Principles of comparative anatomy of invertebrates. *In* Z. Kabata, ed. Translated by J. M. MacLennan. Propmorphology. Vol. I. University of Chicago Press, Chicago.

Bell, G., and A. O. Mooers. 1997. Size and complexity among multicellular organisms. Biological Journal of the Linnean Society 60:345–363.

Boardman, R. S. 1983. General features of the class Stenolaemata. Pp. 49–137 *in* R. S. Boardman et al. Bryozoa. Part G of R. A. Robison, ed. Treatise on invertebrate paleontology. Geological Society of America, Boulder, Colo., and University of Kansas, Lawrence.

———. 1998. Reflections on the morphology, anatomy, evolution, and classification of the class Stenolaemata (Bryozoa). Smithsonian Contributions to Paleobiology No. 86.

Boardman, R. S., and A. H. Cheetham. 1973. Degrees of colony dominance in stenolaemate and gymnolaemate Bryozoa. Pp. 121–220 *in* Boardman et al. 1973.

———. 1987. Phylum Bryozoa. Pp. 497–549 *in* R. S. Boardman, A. H. Cheetham, and A. J. Rowell, eds. Fossil invertebrates. Blackwell Scientific, Palo Alto, Calif.

Boardman, R. S., A. H. Cheetham, and W. A. Oliver Jr., eds. 1973. Animal colonies: development and function through time. Dowden, Hutchinson, and Ross, Stroudsburg, Penn.

Boardman, R. S., A. H. Cheetham, and P. L. Cook. 1983. Introduction to the Bryozoa. Pp. 3–48 *in* R. S. Boardman et al. Bryozoa. Part G of R. A. Robison, ed. Treatise on invertebrate paleontology. Geological Society of America, Boulder, Colo., and University of Kansas, Lawrence.

Bonner, J. T. 1988. The evolution of complexity. Princeton University, Princeton, N.J.

———. 1998. The origins of multicellularity. Integrative Biology 1:27–36.

Borg, F. 1926. Studies on recent cyclostomatous Bryozoa. Zoologiska Bidrag från Uppsala 10:181–507.

Bourke, A. F. G. 1999. Colony size, social complexity and reproductive conflict in social insects. Journal of Evolutionary Biology 12:245–257.

Brandon, R. N. 1996. Concepts and methods in evolutionary biology. Cambridge University Press, Cambridge.

———. 1999. The units of selection revisited: the modules of selection. Biology and Philosophy 14:167–180.

Buss, L. W. 1987. The evolution of individuality. Princeton University Press, Princeton, N.J.

Campbell, D. T. 1958. Common fate, similarity, and other indices of the status of aggregates of persons as social entities. Behavioral Sciences 3:14–25.

Cheetham, A. H. 1973. Study of cheilostome polymorphism using principal components analysis. Pp. 385–409 *in* G. P. Larwood, ed. Living and fossil Bryozoa. Academic Press, London.

Cisne, J. L. 1974. Evolution of the world fauna of aquatic free-living arthropods. Evolution 28:337–366.

Coates, A. G., and W. A. Oliver Jr. 1973. Coloniality in zoantharian corals. Pp. 3–27 *in* Boardman et al. 1973.

Cook, P. L. 1979. Some problems in interpretation of heteromorphy and colony integration in Bryozoa. Pp. 3–27 *in* Larwood and Rosen 1979.

Cowen, R., and J. Rider. 1972. Functional analysis of fenestellid bryozoans. Lethaia 5:145–164.

Cunningham, C. W. 1999. Some limitations of ancestral character-state reconstruction when testing evolutionary hypotheses. Systematic Biology 48:665–674.

———, K. E. Omland, and T. H. Oakley. 1998. Reconstructing ancestral character states: a critical reappraisal. Trends in Ecology and Evolution 13:361–366.

Danchin, E., and R. H. Wagner. 1997. The evolution of coloniality: the emergence of new perspectives. Trends in Ecology and Evolution 12:342–347.

Danforth, B. N. 2002. Evolution of sociality in a primitively eusocial lineage of bees. Proceedings of the National Academy of Sciences USA 99:286–290.

Danforth, B. N., and G. C. Eickwort. 1997. The evolution of social behavior in the augochlorine sweat bees (Hymenoptera: Halictidae) based on a phylogenetic analysis of the genera. Pp. 270–292 *in* J. C. Choe and B. J. Crespi, eds. The evolution of social behavior in insects and arachnids. Cambridge University Press, Cambridge.

Dewel, R. A. 2000. Colonial origin for Eumetazoa: major mor-

phological transitions and the origin of bilaterian complexity. Journal of Morphology 243:35–74.
Duffy, J. E., C. L. Morrison, and R. Ríos. 2000. Multiple origins of eusociality among sponge-dwelling shrimps (*Synalpheus*). Evolution 54:503–516.
Foote, M., and J. J. Sepkoski Jr. 1999. Absolute measures of completeness of the fossil record. Nature 398:415–417.
Gadagkar, R. 1997. Social evolution—has nature ever rewound the tape? Current Science 72:950–956.
Ghiselin, M. T. 1997. Metaphysics and the origin of species. State University of New York Press, Albany.
Gould, S. J. 1996. Full house: the spread of excellence from Plato to Darwin. Harmony Books, New York.
———, and E. A. Lloyd. 1999. Individuality and adaptation across levels of selection: how shall we name and generalize the unit of Darwinism. Proceedings of the National Academy of Sciences USA 96:11904–11909.
Harvell, C. D. 1994. The evolution of polymorphism in colonial invertebrates and social insects. Quarterly Review of Biology 69:155–185.
Hayward, P. J., and J. S. Ryland. 1985. Cyclostome bryozoans. Synopses of the British Fauna (New Series), No. 34. Bath Press, Avon, England.
Huelsenbeck, J. P. 1994. Comparing the stratigraphic record to estimates of phylogeny. Paleobiology 20:470–483.
Hughes, D. J., and J. B. C. Jackson. 1990. Do constant environments promote complexity of form? The distribution of bryozoan polymorphism as a test of hypotheses. Evolution 44:889–905.
Hull, D. L. 1980. Individuality and selection. Annual Review of Ecology and Systematics 11:311–332.
Hutchings, M. J., and D. K. Wijesinghe. 1997. Patchy habitats, division of labour and growth dividends in clonal plants. Trends in Ecology and Evolution 12:390–394.
Jackson, J. B. C., L. W. Buss, and R. E. Cook, eds. 1985. Population biology and evolution of clonal organisms. Yale University Press, New Haven, Conn.
Kauffman, S. A. 1993. The origins of order. Oxford University Press, New York.
Keller, L., ed. 1999. Levels of selection in evolution. Princeton University Press, Princeton, N.J.
Keller, L., and H. K. Reeve. 1999. Dynamics of conflict within insect societies. Pp. 153–175 *in* Keller 1999.
Key, M. M., Jr., L. Thrane, and J. A. Collins. 2001. Functional morphology of maculae in a giant ramose bryozoan from the Permian of Greenland. *In* P. N. Wyse Jackson, C. J. Butler, and M. S. Jones, eds. Bryozoan studies 2001. Balkema, Rotterdam (in press).
Kitchen, D. M., and C. Packer. 1999. Complexity in vertebrate societies. Pp. 176–196 *in* Keller 1999.
Larwood, G., and B. R. Rosen, eds. 1979. Biology and systematics of colonial organisms. Systematics Association Special Volume 11. Academic Press, London.
Larwood, G. P., and P. D. Taylor. 1979. Early structural diversification and ecological diversification in the Bryozoa. *In* M. R. House, ed. The origin of the major invertebrate groups. Systematics Association Special Volume 12:209–234. Academic Press, London.
Leigh, E. G., Jr. 1983. When does the good of the group override the advantage of the individual? Proceedings of the National Academy of Sciences USA 80:2985–2989.
———. 1991. Genes, bees and ecosystems: the evolution of a common interest among individuals. Trends in Ecology and Evolution 6:257–262.
Lidgard, S. 1985. Zooid and colony growth in encrusting bryozoans. Palaeontology 28:255–291.
———. 1986. Ontogeny in animal colonies: a persistent trend in the bryozoan fossil record. Science 232:230–232.
———, and J. B. C. Jackson. 1989. Growth in encrusting cheilostome bryozoans. I. Evolutionary trends. Paleobiology 15: 255–282.
Mackie, G. O. 1986. From aggregates to integrates: physiological aspects of modularity in colonial animals. Philosophical Transactions of the Royal Society of London B 313:175–196.
Maddison, W. P., and D. R. Maddison. 1992. MacClade: analysis of phylogeny and character evolution, Version 3.0. Sinauer, Sunderland, Mass.
Maynard Smith, J. 1988. Evolutionary progress and levels of selection. Pp. 219–230 *in* M. H. Nitecki, ed. Evolutionary progress. University of Chicago Press, Chicago.
Maynard Smith, J., and E. Szathmáry. 1995. The major transitions in evolution. W. H. Freeman, Oxford.
McKinney, F. K. 1984. Feeding currents of gymnolaemate bryozoans: better organization with higher colonial integration. Bulletin of Marine Sciences 34:315–319.
———. 1986. Historical record of erect bryozoan growth forms. Proceedings of the Royal Society of London B 228:133–149.
———. 1990. Feeding and associated colonial morphology in marine bryozoans. Reviews in Aquatic Sciences 2:255–280.
———, and J. B. C. Jackson. 1989. Bryozoan evolution. University of Chicago Press, Chicago.
———, and P. D. Taylor. 1997. Life histories of some Mesozoic encrusting cyclostome bryozoans. Palaeontology 40:515–556.
McShea, D. W. 1994. Mechanisms of large-scale trends. Evolution 48:1747–1763.
———. 1996. Metazoan complexity and evolution: is there a trend? Evolution 50:477–492.
———. 2000. Trends, tools, and terminology. Paleobiology 26: 330–333.
———. 2001a. The ''minor transitions'' in hierarchical evolution and the question of directional bias. Journal of Evolutionary Biology 14:502–518.
———. 2001b. Hierarchical complexity of organisms: a scale and documentation of a trend in the maximum. Paleobiology 27:405–423.
———, and E. P. Venit. 2001. What is a part? Pp. 259–284 *in* G. P. Wagner, ed. The character concept in evolutionary biology. Academic Press, San Diego.
———, ———, and V. Simon. 1999. Hierarchical complexity of organisms: dynamics of a well-known trend. Geological Society of America Abstracts with Programs 31:A171.
Michod, R. E. 1999. Darwinian dynamics: evolutionary transitions in fitness and individuality. Princeton University Press, Princeton, N.J.
Mishler, B. D., and R. N. Brandon. 1987. Individuality, pluralism, and the phylogenetic species concept. Biology and Philosophy 2:397–414.
Mooers, A. Ø., and D. Schluter. 1999. Reconstructing ancestor states with maximum likelihood: support for one- and two-rate models. Systematic Biology 48:623–633.
Moritz, R. F. A., and E. E. Southwick. 1992. Bees as superorganisms. Springer, Berlin.
Nielsen, C., and K. J. Pedersen. 1979. Cystid structure and protrusion of the polypide in *Crisia* (Bryozoa, Cyclostomata). Acta Zoologica (Stockholm) 60:65–88.
Omland, K. E. 1997. Examining two standard assumptions of ancestral reconstructions: repeated loss of dichromatism in dabbling duck (Anatini). Evolution 51:1636–1646.
———. 1999. The assumptions and challenges of ancestral state reconstructions. Systematic Biology 48:604–611.
Pagel, M. 1994. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. Proceedings of the Royal Society of London B 255: 37–45.
———. 1997. Inferring evolutionary processes from phylogenies. Zoologica Scripta 26:331–348.

———. 1999. The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. Systematic Biology 48:612–622.

Ree, R. H., and M. J. Donoghue. 1999. Inferring rates of change in flower symmetry in asterid angiosperms. Systematic Biology 48:633–641.

Ryland, J. S. 1970. Bryozoans. Hutchinson, London.

———. 1979. Structural and physiological aspects of coloniality in Bryozoa. Pp. 211–242 *in* Larwood and Rosen 1979.

Salthe, S. N. 1985. Evolving hierarchical systems. Columbia University Press, New York.

Sanderson, M. J. 1993. Reversibility in evolution: a maximum likelihood approach to character gain/loss bias in phylogenies. Evolution 47:236–252.

Schluter, D., T. Price, A. Ø. Mooers, and D. Ludwig. 1997. Likelihood of ancestor states in adaptive radiation. Evolution 51: 1699–1711.

Schopf, T. J. M. 1973. Ergonomics of polymorphism: its relation to the colony as the unit of natural selection in species of the phylum Ectoprocta. Pp. 247–294 *in* Boardman et al. 1973.

Silén, L. 1977. Polymorphism. Pp. 183–231 *in* R. M. Woollacott and R. L. Zimmer, eds. Biology of bryozoans. Academic Press, New York.

Simon, H. A. 1962. The architecture of complexity. Proceedings of the American Philosophical Society 106:467–482.

Sober, E., and D. S. Wilson. 1994. A critical review of the philosophical work on the units of selection problem. Philosophy of Science 61:534–555.

Swofford, D. L. 1998. PAUP*. Phylogenetic analysis using parsimony (*and other methods), Version 4. Sinauer, Sunderland, Mass.

Taylor, P. D. 1999. Bryozoans. Pp. 623–646 *in* E. Savazzi, ed. Functional morphology of the invertebrate skeleton. Wiley, New York.

Taylor, P. D. 2000. Cyclostome systematics: Phylogeny, suborders, and the problem of skeletal organization. Pp. 87–103 *in* A. Herrera-Cubilla and J. B. C. Jackson, eds. Proceedings of the 11th International Bryozoology Association Conference. Smithsonian Tropical Research Institute, Balboa, Republic of Panama.

Taylor, P. D., and R. W. Furness. 1978. Astogenetic and environmental variation of zooid size within colonies of Jurassic *Stomatopora* (Bryozoa, Cyclostomata). Journal of Paleontology 52: 1093–1102.

Taylor, P. D., and M. J. Weedon. 2000. Skeletal ultrastructure and phylogeny of cyclostome bryozoans. Zoological Journal of the Linnean Society 128:337–399.

Taylor, P. D., and M. A. Wilson. 1996. *Cuffeyella*, a new bryozoan genus from the Late Ordovician of North America, and its bearing on the origin of post-Paleozoic cyclostomates. Pp. 351–360 *in* D. P. Gordon, A. M. Smith, and J. A. Grant-Mackie, eds. Bryozoans in space and time. NIWA, Wellington, New Zealand.

Valentine, J. W., A. G. Collins, and C. P. Meyer. 1994. Morphological complexity increase in metazoans. Paleobiology 20: 131–142.

Vermeij, G. J. 1987. Evolution and escalation. Princeton University Press, Princeton, N.J.

Wagner, G. P., and M. D. Laubichler. 2000. Character identification in evolutionary biology: the role of the organism. Theory in Biosciences 119:20–40.

Wagner, P. J. 1996. Contrasting the underlying patterns of active trends in morphologic evolution. Evolution 50:990–1007.

Wagner, P. J., and D. H. Erwin. 1995. Phylogenetic patterns as tests of speciation models. Pp. 87–122 *in* D. H. Erwin and R. L. Anstey, eds. New approaches to speciation in the fossil record. Columbia University Press, New York.

Wcislo, W. T., and B. N. Danforth. 1997. Secondarily solitary: the evolutionary loss of social behavior. Trends in Ecology and Evolution 12:468–474.

Wilson, E. O. 1971. The insect societies. Harvard University Press, Cambridge.

———. 1975. Sociobiology: the new synthesis. Harvard University Press, Cambridge.

Wilson, J. 1999. Biological individuality: the identity and persistence of living entities. Cambridge University Press, Cambridge.

Appendix

Stratigraphic range estimates for the 23 cyclostome genera used to reconstruct ancestral states. (The three species of *Heteropora* were all assigned the same range; reasonably reliable range estimates were unavailable for *Patinella, Favosipora, Diaperoecia,* and "*Stomatopora.*") Abbreviations: Ord = Ordovician; Sil = Silurian; Dev = Devonian; Tr = Triassic; J = Jurassic; K = Cretaceous; T = Tertiary. Abbreviated names of stratigraphic stages appear in parentheses.

Genus	Stratigraphic range	First occurrence (Ma)	Last occurrence (Ma)
Foricula	K (Alb)–K (u. Maes)	112	65
Meliceritites	K (l. Barr)–K (u. Maes)	127	65
Collapora	J (Aale)–K (Ceno)	180	93.5
Disporella	K (Coni)–R	89	0
Borgiola	T (l. Mio)–R?	23.8	0
Heteropora	J (Aal)–R	180	0
Cinctipora	T (Than)–R	57.9	0
Crisulipora	T (l. Ol)–R	33.7	0
Hornera	T (l. Eo)–R	54.8	0
Crisina	T (?)–R	65?	0
Stegohornera	R	0	0
Fenestulipora	R	0	0
Fasciculipora	J (u. Bath)–R	169	0
Reptomultisparsa	Tr (Nori)–R	221	0
Plagioecia	J (Bajo)–R	176	0
Diplosolen	K (Coni)–R	89	0
Platonea	T (u. Eo)–R	37	0
Idmidronea	K (l. Camp)–R	83.5	0
Tubulipora	K (l. Camp)?–R	83.5	0
Stomatopora	Tr (Carn)–R	227	0
Bicrisia	T (l. Eo)–R	54.8	0
Crisia	K (Val/Haut)–R	137	0
Cuffeyella	Ord (Cara–Ash)–Sil/Dev?	458	417?