

The minor transitions in hierarchical evolution and the question of a directional bias

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Abstract

The history of life shows a clear trend in hierarchical organization, revealed by the successive emergence of organisms with ever greater numbers of levels of nestedness and greater development, or 'individuation', of the highest level. Various arguments have been offered which suggest that the trend is the result of a directional bias, or tendency, meaning that hierarchical increases are more probable than decreases among lineages, perhaps because hierarchical increases are favoured, on average, by natural selection. Further, what little evidence exists seems to point to a bias: some major increases are known – including the origin of the eukaryotic cell from prokaryotic cells and of animals, fungi and land plants from solitary eukaryotic cells – but no major decreases (except in parasitic and commensal organisms), at least at the cellular and multicellular levels. The fact of a trend, combined with the arguments and evidence, might make a bias seem beyond doubt, but here I argue that its existence is an open empirical question. Further, I show how testing is possible.

Introduction

One of the most salient and certain trends in the history of life is the increase in hierarchical structure in organisms. Figure 1 shows the approximate trajectory of the trend. The left-most data point marks the first known prokaryotic cells, the next is the origin of the first eukaryotic cell from symbiotic associations of prokaryotic cells, the third is the advent of multicellular individuals from clones of eukaryotic cells, and the last is the origin of the first colonial individual from associations of multicellular entities. The increase is hierarchical in that in each transition, a new level of nesting of entities within entities arose.

The existence of such a hierarchical trend has been widely acknowledged (e.g. Spencer, 1900, 1904; Needham, 1943; Stebbins, 1969; Wimsatt, 1976, 1994; Corning, 1983; Salthe, 1985, 1993; Buss, 1987; Bonner, 1988; Maynard Smith, 1988; Swenson & Turvey, 1991;

Maynard Smith & Szathmáry, 1995, 1999; Szathmáry & Maynard Smith, 1995; McShea, 1996a; Pettersson, 1996; Heylighen, 1999; Stewart, 2000; Wright, 2000; Knoll & Bambach, 2000). It is also – to my knowledge – unchallenged.

What is not widely agreed upon is the mechanism or dynamics of the trend, the pattern of change among lineages that accounts for it. One possibility is that change among lineages is biased, so that increases are more probable than decreases, as shown in Fig. 2(A). Such a mechanism would be consistent with the suggestion that hierarchical increases are blocked ordinarily by design limitations, by what Sterelny & Griffiths (1999) call 'right walls' on the hierarchy scale, but that very occasionally these walls are breached, producing an organism with greater hierarchical structure (Stebbins, 1969; Sterelny & Griffiths, 1999; Sterelny, 1999; Knoll & Bambach, 2000). In most versions of this mechanism, breaching of the walls is understood to be irreversible, ratchet-like, or nearly so (e.g. Maynard Smith & Szathmáry, 1995), which is equivalent to a strong directional bias. (The term bias is sometimes associated with error, and thus the phrase 'directional bias' might

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Fig. 1 First occurrences of organisms at successive hierarchical levels, based on the body fossil record. Data points correspond to the first highly individuated representative of each level, from the first free-living prokaryotic cell about 3.5 billion years ago to the first individuated colonies (bryozoans) in the early Ordovician, 480 million years ago. The grey-shaded area shows the hierarchical range occupied by all life over that time range. The black line shows the trajectory of the maximum; see text. Criteria for levels and for individuation are discussed in the text and at greater length in McShea (2001). Also see McShea (2001) for a detailed discussion of the evidence for each data point.

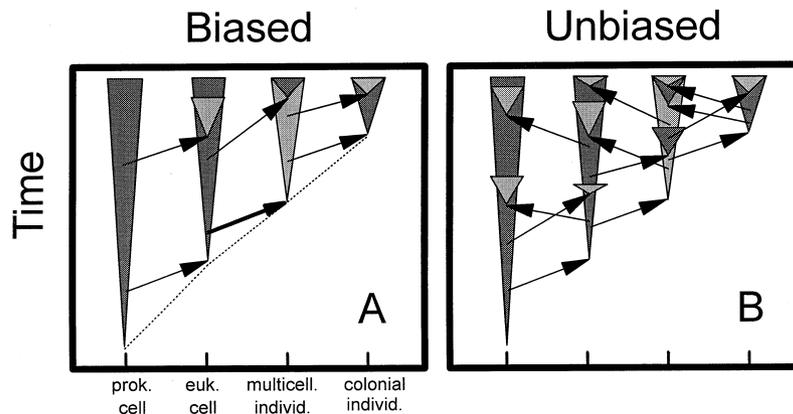
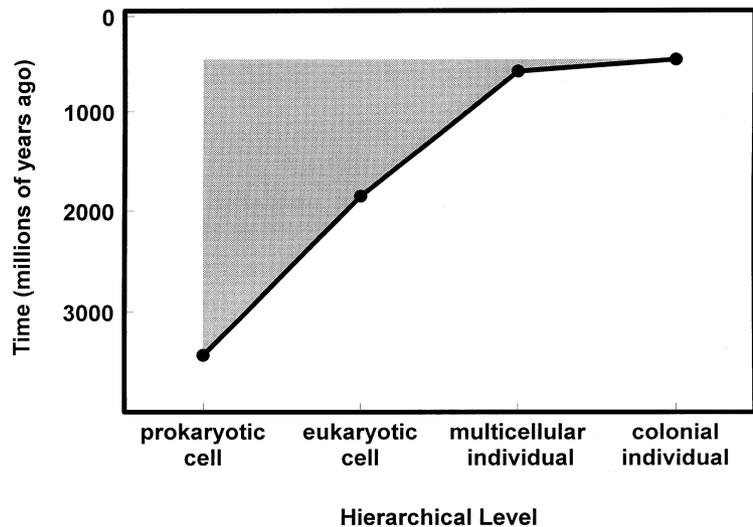


Fig. 2 Schematic representations of two alternative mechanisms underlying the increase in maximum hierarchical structuring. Each triangle represents the diversification of a group at a given level. (Differences in shading among triangles are for visual clarity and have no other significance.) Arrows show transitions from one major level to an adjacent one. Right-pointing arrows show major upward transitions (increases), i.e. the origin of groups at higher levels from ancestors at lower levels, and left arrows show major reversals or downward transitions (decreases). For example, the bold arrow in A shows the origin of a group of highly individuated multicellular organisms from a single-celled ancestor; this particular transition marks the advent of (highly individuated) multicellularity, and therefore corresponds to a rise in the maximum for life as a whole. (The dotted line in A represents the overall trajectory of the maximum.) A: all arrows point right, meaning that change is biased, with increases more probable than decreases. B: change is unbiased, meaning that increases and decreases are equally probable.

seem to imply a tendency to err in a particular direction. As used here, however, the phrase is value neutral, referring simply to a tendency to *change*, especially, a tendency to increase [see McShea, 1994, 1996a, 1998].)

Another possibility is that change is unbiased, so that increases and decreases are equally probable, as in Fig. 2(B), and that the trend is the result of passive diffusion (McShea, 1994, 1996a, 2000a; Gould, 1996; McShea *et al.*, 1999). In some versions of this mechanism, the diffusion is said to occur in the presence of a lower bound, or lower limit, on hierarchical structure, presumed to lie roughly at the level of the prokaryotic

cell (Maynard Smith, 1970; Gould, 1996; McShea, 2000a). (There are other possibilities; see below.)

It might seem that the evidence points clearly to a bias. At the lower hierarchical levels, we know of four likely instances of major increase, specifically, the transition from free-living prokaryotic cells to free-living eukaryotic cells and three transitions from eukaryotic cells to highly individuated multicellular organisms, i.e. those in which multicellularity is well developed, such as a mammal, a mushroom or a magnolia (animals, fungi and land plants). But we know of no major reversals, no cases in which a free-living prokaryotic cell arose from a

eukaryotic cell or a free-living eukaryotic cell arose from a highly individuated multicellular organism (Knoll & Bambach, 2000). Certain commensal and parasitic protists may have arisen in this way: e.g. myxozoans from a bilaterian stem group or from cnidarians (Siddall *et al.*, 1995; Kim *et al.*, 1999); the *Hela* cells from humans (Strathmann, 1991; Van Valen & Maiorana, 1991); also, see below. But arguably these do not count, because they are dependent on the hierarchical structuring present in the host (Heylighen, 1999). Also known are a number of transitions from simple multicellularity (e.g. cells joined in filaments) to free-living unicells, such as probably occurred in certain yeasts. But one might argue that these do not count either, because simple, filamentous forms are not highly individuated (i.e. their multicellularity is not well developed), and therefore the reversal is only partial.

Nevertheless, a case can be made for an unbiased mechanism. First, in the highest level transitions, between free-living multicellular organism and individuated colony, there is no obvious bias. Many increases have occurred, but many reversals – returns to a solitary condition – are also known, for example, in halictine bees (Wcislo & Danforth, 1997). Second, at the lower levels, few major increases are known, and therefore few reversals would need to be discovered to equalize numbers of increases and decreases. The protistan biota is not sufficiently well known, for example, that we can confidently rule out the origin of two or three free-living unicellular species – perhaps not yet discovered – from a highly individuated metazoan. In any case, absolute numbers of decreases should actually be less, even if increases and decreases were equally probable. The reason is that a decrease from any given level cannot occur until that level has first arisen. Thus, decreases have had less time, or fewer opportunities, to occur than increases. Third, unlike increases, reversals produce nothing new in hierarchical terms; they only generate more species at already-occupied levels. Thus, they might be less salient and harder to detect.

Other arguments in favour of and opposed to a bias will be discussed later. And the point will be to argue that an unbiased system is at least plausible. Assuming that it is, how could we test? Using a hierarchy scale like that in Figs 1 and 2, testing would be difficult. The problem is that with so few transitions known, a bias is difficult to demonstrate statistically. For example, for the cell-to-multicellular transitions discussed, three increases and zero decreases would not be a statistically significant bias. One solution would be to increase the sample of transitions by increasing the resolution of the scale. This could be done by devising a way to recognize and measure intermediate degrees of individuation of an organism at a given level (Salthe, 1985) or, in other words, to develop a hierarchy scale which recognizes minor as well as major transitions. For example, the transformation of a solitary cell into a simple cell

aggregate, such as a filamentous form, would be a minor transition, as would the transformation of a monomorphic aggregate into one with two cell types. In this view, multicellularity (and every other hierarchical level) is recognized as a matter of degree, rather than an all-or-none phenomenon. As shown in Fig. 3, using a higher-resolution scale, the sample of increases and decreases could be greatly increased. Criteria for individuation and the details of a higher-resolution scale based on them are discussed later.

Clarifications

Some clarifications are in order before proceeding. First, the trend of interest here is the increase in the maximum, or in the number of levels of nestedness present in the hierarchically deepest organism on Earth. In other words, it is with the rise in the outer envelope of hierarchical structuring, represented by the dark line in Fig. 1. The behaviour of other trend statistics, such as the minimum and mean, are not at issue (and are not known in any case; see below). Second, the concern is not with the unique mechanisms underlying particular transitions, such as the origin of multicellularity in the Metazoa (e.g. Maynard Smith & Szathmáry, 1995), or even with the dynamics underlying change in single transitions generally (Leigh, 1983, 1991; Michod, 1999), but at a larger scale, with possible common forces acting on structure in all (or most) transitions, across the hierarchy spectrum (see especially Bonner, 1988; Gould, 1996).

Finally, the concern here is with organisms, and thus for present purposes, I exclude the various nonorganismal hierarchical structures (Eldredge & Salthe, 1984; Gould & Lloyd, 1999), such as certain chemical systems and also ecological associations.

Terminology

Various terms have been used to describe the major hierarchical levels: they have been called 'integrative levels' or 'levels of organization' (in the sense of Redfield, 1942; Novikoff, 1945; Fiebleman, 1955; Polanyi, 1968; MacMahon *et al.*, 1978) and levels of selection (see Buss, 1987; Maynard Smith, 1988; Sober & Wilson, 1994; Brandon, 1996, 1999; Keller, 1999). And the trend has been described as an increase in hierarchical complexity (McShea, 1996a,b; Dewel, 2000) or vertical complexity (Sterelny & Griffiths, 1999; Sterelny, 1999).

Here, I use the term 'structural hierarchy', which is equivalent to what Salthe (1985, 1993) called scalar hierarchy and Valentine & May (1996) called constitutive hierarchy (see also inset 4 of the figure in Bunge, 1959; Pattee, 1970; Wimsatt, 1976, 1994; Eldredge & Salthe, 1984; McShea, 1996a,b; Pettersson, 1996; Simon, 1996). Structural hierarchy in this sense is divorced conceptually from any notion of function. The two are undoubtedly related in evolution (McShea, 2000c), but here the

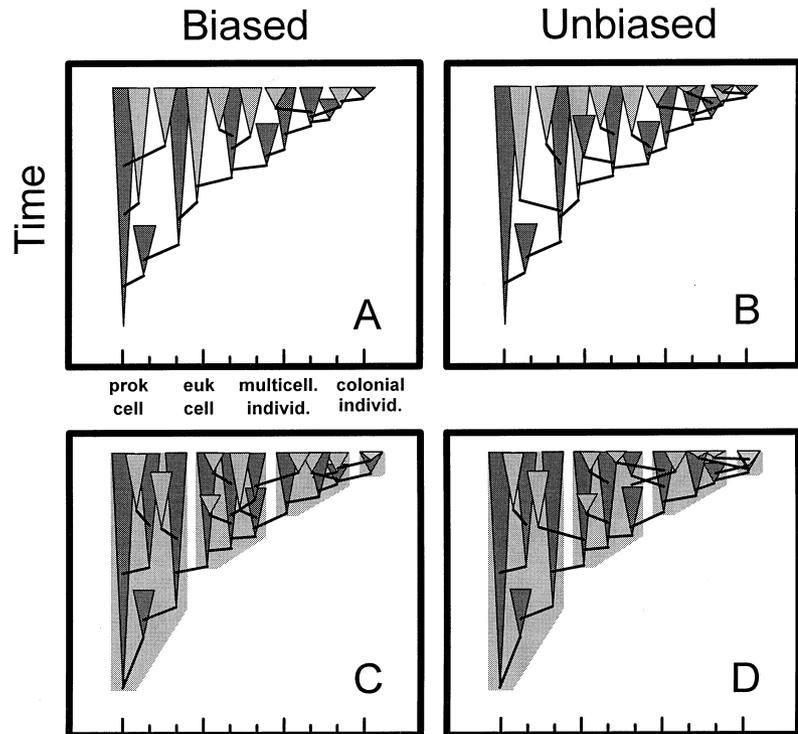


Fig. 3 Biased vs. unbiased, as in Fig. 2, but here on a scale with higher resolution, indicated by the subdivisions of the major hierarchical levels marked on the horizontal axis. (Line segments are used, rather than arrows, to show transitions.) A: biased, over all minor transitions (increases more probable than decreases); B: unbiased, over all minor transitions (increases and decreases equally probable); C: only certain minor transitions biased (between grey areas, increases more probable than decreases), others unbiased (within grey areas, increases and decreases equally probable); D: all minor transitions unbiased (both between and within grey areas).

concern is only with structure. A consequence is that gains or losses of function that are not accompanied by change in hierarchical structure do not count as hierarchical changes. (And, conversely, changes in hierarchical structure not accompanied by gain or loss of function *do* count.) Thus, structural hierarchy as understood here overlaps with but is narrower than the dimension considered by Knoll & Bambach (2000), which is a combination of structural hierarchy and ability to occupy new ecospace.

Importantly, my concern is also not (directly) with process or control hierarchies, such as those that have been implicated in organismal development (Riedl, 1978; Wimsatt, 1986; Valentine & Erwin, 1987; Salthe, 1993; Raff, 1996; Arthur, 1997). A developmental program might be said to be hierarchical to the extent that later steps, or causal events, are dependent on earlier steps, and to the extent that there is a many-to-one relationship between later and earlier steps (McShea, 1996a,b). (An army chain of command is strongly hierarchical in both senses.) While there may be some relationship in evolution between the structural and developmental hierarchies, they are conceptually distinct. For example, in principle, at least, a structurally deep organism could have a developmental program with relatively little temporal dependence, i.e. it could be hierarchically flat.

Along the same lines, the concern here is with what Eldredge & Salthe (1984) called the 'ecological hierarchy'

rather than the 'genealogical hierarchy'. A consequence is that the lower-level entities that constitute a higher-level entity need not be closely related. Thus, a eukaryotic cell, in which the component entities are unrelated prokaryotic species, is hierarchically structured in the same sense as a colonial myxobacterium, in which the cells are a clone.

I adopt Maynard Smith and Szathmáry's phrase 'major transition' to refer to a change from a highly individuated organism at one level to a highly individuated organism at an adjacent level. And the term 'minor transition' is coined to refer to smaller changes in hierarchy on a higher-resolution scale. One can think of the minor transitions as subdivisions of the major transitions, or at least of the three major transitions represented in the fossil record. However, a possible difference in usage needs to be pointed out. Maynard Smith & Szathmáry (1995) offered a list of eight 'major transitions', including the three discussed above, most of which involve increases in structural hierarchy. However, the common feature of these eight to which they drew attention was not the increase in structural hierarchy but the loss of independent replication ability in lower-level entities. In other words, their concern seems to be with a kind of control hierarchy (the control of higher levels over lower-level replication), rather than with structural hierarchy *per se*; if so, my use of the term 'major transition' is somewhat different.

Overview

Hierarchical structuring is an aspect of organismal complexity generally, perhaps its most commonly recognized aspect. Other aspects include number of different types of parts at a given level and number of interactions among them, as well as hierarchical organization in development, physiology and behaviour (McShea, 1996b). For most of these, no long-term trend has been documented. However, for structural hierarchy, a trend is almost undeniable – at least from the origin of life through the first individuated colonies in the early Phanerozoic (McShea, 1996a, 2001). Indeed, the possibility is worth considering that it is mainly the structural-hierarchical trend that underlies and supports the widespread impression that complexity increases in evolution.

The fact of a trend, combined with the various arguments that have been offered in support of a bias, might make the existence of such a bias seem obvious. Gould (1988, 1996) discusses the conceptual and historical roots of the apparent connection between trends and biases. In this paper, I argue that the presently available evidence and arguments are not conclusive and that the existence of a bias is an open empirical question. Further, I show that an avenue for testing is available. The paper is organized as follows: In the first section below, I present the main arguments for and against a bias and discuss the other mechanisms that might be responsible for the trend. The second section describes a possible higher-resolution hierarchy scale, and the third explains how the scale can be used to test for bias. The fourth illustrates how the test could be done, presenting a sample of preliminary results drawn from a more comprehensive study currently underway.

Trend mechanisms

Biased vs. unbiased

At issue is the mechanism, or the pattern of change among lineages, underlying a large-scale trend, i.e. a trend in some summary statistic for a state variable (McKinney, 1990) in a diversifying clade. Here, the summary statistic is the maximum, the state variable is the degree of hierarchical structure and the clade is all of life.

The increase in the maximum could be the result of a bias, as discussed, and a bias can take a number of different forms. It could be pervasive, that is, present across the state space, so that all lineages, at all hierarchical levels and at all times, have a greater probability of increasing than of decreasing (e.g. Fig. 3A). Or biases might be distributed diffusely over a subset of lineages, hierarchical levels and times. Another possibility is that a bias is present in some transitions and absent in others (e.g. Fig. 3C).

Alternatively, if no bias is present, the trend might be the result of simple diffusion, of the increase in variance

that accompanies increases in diversity (e.g. Fig. 3B) (Stanley, 1973; Fisher, 1986; Gould, 1988, 1996; McShea, 1994, 1998). Or, what is equivalent, many different lower-level dynamics – including, perhaps, both increasing and decreasing biases – might be present and distributed randomly throughout the space, producing no net increasing tendency, and allowing the maximum to increase diffusively. Notice that the maximum is expected to rise even with a pervasive *decreasing* bias (Gould, 1996), provided the bias is not sufficiently strong to overcome the upward diffusion.

Further, the trend could be the result of neither bias nor diffusion, but instead of various nonbias, lower-level dynamics, such as variation in speciation or extinction rate over state space (McShea, 1994). For example, a trend in the maximum would be expected if speciation rates were higher (or extinction rates lower) for species with greater hierarchical structuring. Other, more complex mechanisms – many discussed by Alroy (2000; see also McShea, 2000b) – are also possible. Here, for simplicity, the focus is on two alternatives, increasing bias vs. unbiased, but it should be kept in mind that there are many other possibilities.

Three clarifications are needed here. First, the issue of mechanism has to do with the pattern of change among lineages, and thus any given trend mechanism is consistent with a number of possible underlying causes (McShea, 1994). For example, a biased mechanism could be the result of selection for increasing hierarchical structure, but in principle, it could equally well be the result of an internal (i.e. developmental) bias in the production of new forms. Second, the concern is with mechanism at the largest scale, in the clade of life as a whole. Thus, a finding that an unbiased mechanism has operated would not deny that selection may have been involved at a smaller scale, in particular transitions. Indeed, in principle, in an unbiased system, every increase and every decrease could be selection driven.

Third, a matter of purely technical interest: in recent work on large-scale trends, various schemes for classifying trend mechanisms have been proposed (e.g. Wagner, 1996; Trammer & Kaim, 1999; Alroy, 2000). In my own scheme (McShea, 1994, 1998), I made a distinction between 'passive' and 'driven' trends; the distinction here between biased and unbiased is somewhat different. On a low-resolution scale (e.g. Fig. 2), a trend produced by a bias would be driven and an unbiased trend would be passive (assuming a lower bound is present; see below). But at higher resolution, the situation is more complicated, with homogeneous distributions of bias corresponding to driven (Fig. 3A) and heterogeneous distributions to passive (Fig. 3C).

Arguments

Various arguments have been advanced which suggest a bias, most formulated with a low-resolution scale (e.g.

Fig. 2) in mind. Bonner (1988, 1998) has argued that hierarchical increase is a route to size increase and that size increase is favoured, on average, by selection (see also Corning, 1983; Bell, 1985; Buss, 1987; Bell & Mooers, 1997). He also points out that there are always ecological opportunities at larger sizes and therefore at higher hierarchical levels, or in his words, 'there is always room at the top' (Bonner, 1998, p. 27). By itself, this notion is consistent with, even suggestive of, an unbiased mechanism. However, Bonner adds that niches at lower hierarchical levels – i.e. those below the uppermost – will tend to be occupied, which implies that invasion of these levels from above is to some degree limited and therefore that change is biased upward.

Upward transitions might be hard to reverse for other reasons. As a higher-level organism arises, the lower-level entities that constitute it may become specialized and lose the ability to function as solitary individuals (Maynard Smith & Szathmáry, 1995; McShea 2000a; Knoll & Bambach, 2000). If so, reverse transitions would require a long and complex series of adaptive steps and therefore should occur less frequently than forward transitions.

Other sources of bias have been proposed: selection might favour transitions to higher levels over the reverse because co-operation is more advantageous for lower-level organisms, on average, than solitary living (Corning, 1983, 1997; see also Bell & Mooers, 1997; Stewart, 2000). Also, a bias might be expected on account of the greater contribution of higher-level organisms (relative to that of their components) to dissipating energy gradients (Swenson & Turvey, 1991). Finally, if higher-level organisms are structurally more complex than lower-level organisms, they might offer more opportunities for combining with each other – more ways to accommodate each other structurally or to 'fit together' – to produce yet higher levels (Heylighen, 1999).

These arguments are plausible, but presently all have very limited empirical support. The advantages of co-operative existence are clear in particular cases, but no on-average advantage of co-operation over solitary existence has been demonstrated empirically. And the selective advantages of size increase over size decrease have not been demonstrated on the scale of life as a whole (see review by Jablonski, 1996).

Against the second part of Bonner's argument, that niches may be limited at lower levels, one might raise the possibility that ecological constraints exist but are not sufficiently limiting. To generate a bias in major transitions, packing of species at lower hierarchical levels would have to have been so consistently and unyieldingly dense over the history of life that even occasional major transitions downward were blocked. This is required because few major upward transitions are known, and therefore even a few major downward ones would eliminate a bias. Indeed, it seems likely that ecological opportunities across the hierarchical spectrum

have opened up frequently, especially during mass extinctions.

Also, the evolutionary changes required for a reverse transition – for a lower-level entity in an organism to regain competence for a free-living existence – may be improbable, but major forward transitions have apparently been quite rare and therefore are also presumably improbable. Thus, a priori, we have little reason to think that the two sorts of transition would not be equally difficult, and selection equally constrained, in both directions. Against Heylighen's argument that each successive hierarchical level is structurally more complex and therefore offers more combinatorial possibilities for further increase, one could point out that greater complexity offers more possibilities for disassembly, for hierarchical loss, as well.

Further, it should be noted that major reversal can occur by various routes, and need not involve backtracking along the forward route. I can think of only one example; it is speculative and involves a parasitic form, but it may suffice to make the point. Yang (1996) described a tumour cell lineage in dogs – presumably derived from an ancestral canid cell – that is transmissible among individuals. The cells are parasites, so the transition relies on the hierarchical structure present in the host and thus arguably does not by itself constitute a hierarchical loss. But acquiring the ability to survive in foreign and hostile environments – the tissues of individuals with alien genotypes and competent immune systems – does seem like a promising first step en route to free-living existence.

Importantly, the claim here is *not* that hierarchical change is unbiased. Rather it is that presently available arguments and evidence for a bias are inconclusive, and an unbiased mechanism is therefore plausible. Consistent with this view, I should point out that the positive case for an unbiased mechanism is also inconclusive. The case relies on two observations: that the hierarchically lowest organism is and has always been a prokaryote, which suggests a lower bound on hierarchical structuring at or just below the prokaryote level; and that the distribution of hierarchical structuring is and has always been right-skewed, with a mode at the prokaryote level. Gould (1996) pointed out – in the context of a general discussion of evolutionary progress, rather than of hierarchy *per se* – that these two observations are consistent with, and present a circumstantial case for, an unbiased mechanism. Both seem plausible, although it is worth noting that the existence of hierarchically subprokaryotic organisms – now or in the past – is not ruled out in principle. Also, while it seems likely that the modal *organism* on Earth is and has always been a prokaryote, the distribution of *species* among hierarchical levels is essentially unknown. In any case, the point to be made here is that the existence of a lower bound and a right-skewed distribution would not settle the matter, as Gould acknowledged, because both are also the expectation for

a weakly biased system; see McShea (1994) for further discussion.

Two other arguments deserve some mention, both suggesting the existence of a bias in favour of losses. First, on the assumption that most mutations are deleterious, one might suspect that it would be easier to render a structure nonfunctional in evolution than to confer functionality on it, creating a bias toward loss. However, recall that the concern here is not with function but only with structure, and more narrowly with the hierarchical aspect of structure; with this in mind, it is not clear that the average effect of mutation will be to remove rather than to add. Further, the time scale of interest is the history of life as a whole, and on such a long time scale, any mutation-driven bias could well be overridden by other forces (e.g. selection).

The second argument for loss is based on the evolution of parasitism. If structural losses constitute hierarchical losses (see below), then any tendency for organisms to lose structures when they become parasitic should produce at least a slight bias toward hierarchical decrease over the history of life, assuming no other biases exist (Gould, 1996). This argument is also plausible, but a counter-argument can be devised. As noted earlier, losses in parasites are dependent on the hierarchical structuring in the host (Heylighen, 1999). But more than this, from the viewpoint of the host, a parasite might constitute an *addition* to hierarchical structure. (Recall that there is no requirement that gains in hierarchical structure be functional, i.e. advantageous, for the organism.) Thus, whether parasitism tends to produce a net gain or a net loss is unclear.

A hierarchy scale

The scale decomposes the hierarchical structure of organisms into two components: (1) number of levels of *nestedness* of entities within entities; and (2) degree of *individuation* of the top-level entity (Salthe, 1985; McShea, 2001). A brief explanation of these terms follows. For more detail, including a discussion of justification and limitations, see McShea (2001; see also Anderson & McShea, in press).

Nestedness

A nested system is one in which entities at one level are composed of two or more entities from the next lower level. In other words, the relationship between lower level and upper level is that of parts to whole. A further requirement for a nested relationship is that the parts interact in some way, that they are connected, so that their behaviours are correlated (Campbell, 1958; McShea & Venit, 2001). Interaction could take the form of physical attachment, so that lower-level entities form an aggregate, as in a coral colony, but aggregation is not required; lower-level entities may be physically separate

with correlations in behaviour among them achieved by signals, as in a social insect colony. (For studies of fossil organisms, in which the only available evidence for hierarchical level is morphological, a narrower standard – which excludes physically separate lower-level entities – could be used [e.g. McShea, 2001].) Some contrasts between lower and higher levels of nestedness include: a solitary cyanobacterium vs. a filamentous form, with many cells occupying a single sheath; a solitary eukaryotic cell, such as *Chlamydomonas*, vs. a monomorphic cell aggregate, such as *Gonium*; and a solitary insect vs. a social insect colony. See Bonner's (1998) discussion of the multiple origins of multicellularity for other examples of evolutionary increases in nestedness.

Individuation

Individuation refers to the degree to which an entity constitutes a unit, or a whole, as opposed to a collection of independent lower-level units. Abstract criteria for individuation have been developed in the theoretical literature (Campbell, 1958; Hull, 1980; Salthe, 1985; Mishler & Brandon, 1987; see also Allen & Hoekstra, 1992; Sober & Wilson, 1994; Simon, 1996; Ghiselin, 1997; Gould & Lloyd, 1999; Wagner & Laubichler 2000; McShea & Venit, 2001). For the present purposes, however, criteria were drawn from phenomenological studies, in particular Beklemishev's (1969) study of the emergence of colonial individuals, mainly in marine invertebrate colonies, and Boardman & Cheetham's (1973) study of colony integration in bryozoans. Modified to make them applicable to all hierarchical levels, the selected criteria are: connectedness, differentiation and number of intermediate-level part types. (See McShea, 2001, for a discussion of possible theoretical bases for these criteria.)

Connectedness

Lower-level entities are connected if they interact in a stable way, as discussed. The association with individuation arises from the assumption that connectedness among lower-level entities reflects the degree to which those entities operate or behave in a coordinated way, and therefore the degree to which the larger organism behaves as a unified whole. In evolution, connectedness can increase either by the addition of specialized channels or by the breakdown of barriers among lower-level entities. Examples of increase would include the advent of nervous and circulatory systems connecting cells in multicellular organisms, of chemical signals connecting individuals in social insect colonies, or of shared coeloms, shared vascular systems, and common guts connecting individuals in marine-invertebrate colonies (Harvell, 1994). A possible problem with this criterion is that, arguably, increases in connectedness produce increases in individuation only up to a point. For example, in extreme cases, where connectedness is very high (e.g. in

cell–cell fusions or in the origin of syncytial forms), individuation may be very low by other criteria (differentiation, intermediate parts). This issue would bear closer study (e.g. Kauffman, 1993); in any case, the assumption here is that in the transitions of interest, all increases occur at the low end of the connectedness spectrum and therefore do represent increases in individuation.

Notice that an increase in nestedness, as defined above, requires at least a small increase in connectedness, and that therefore the individuation of an upper-level entity begins at the moment of its formation.

Differentiation

The individuation of an organism is also partly a function of the degree of physiological, behavioural, or morphological differentiation among its component lower-level entities (McShea, 2001; Anderson & McShea, in press). Thus, individuation increases as the number of types of lower-level entity increases. In principle, differentiation is a continuous variable, but here – for the purpose of determining number of types – it is treated as discrete, with differences among lower-level entities assessed impressionistically (see approach of Cisne, 1974; Bonner, 1988; Valentine *et al.*, 1994; Bell & Mooers, 1997). Examples of contrasts in degree of differentiation include: a monomorphic, filamentous cyanobacterium, such as *Oscillatoria*, vs. a differentiated filamentous form, such as *Anabaena*, which has two vegetative-cell types; a monomorphic eukaryotic aggregate, such as *Gonium*, vs. *Vaucheria*, an alga with two cell types; and the essentially undifferentiated colonies of the major zoantharian coral groups vs. dendroid graptolites, which have two or more zooid types.

Intermediate-level parts

Finally, the degree of individuation of an organism is partly a function of the number of types of intermediate-level parts it contains. Intermediate parts are structures that are larger than a typical single lower-level entity but are still a subset of the organism as a whole (McShea, 2001; Anderson & McShea, in press). One way an intermediate-level part can occur is as a connected group, a subgroup, of lower-level entities. For example, most metazoan tissues and organs qualify as intermediate-level parts. Alternatively, an intermediate part may consist of a single lower-level entity which is hypertrophied or elaborated in various ways to attain intermediate size. For example, the portion of the eukaryotic cell that is homologous with the original archaeobacterial host plus subsequent structural additions – including microtubular structures, intracellular membranes, and so on, but excluding the former endosymbionts (e.g. mitochondria) – constitutes an elaborated lower-level entity and thus is an intermediate part. At a higher level, chondrophorines are colonial hydroids in which a ring of medusa-shaped gonozooids are attached to a large central

gastrozooid, which supports a large pneumatophore, or float (Hyman, 1940; Kozloff, 1990). The gastrozooid is an enlarged, elaborated single zooid and thus constitutes an intermediate part.

The hierarchy scale is presented schematically in Fig. 4. In Fig. 4(A), circles on the same horizontal level represent organisms at the same level of nestedness, and thus the first arrow – a minor transition – is an increase in nestedness. The other arrows, which also represent minor transitions, show increases in individuation within a level. In particular, the second arrow shows the advent of differentiation, and the third is the origin of the first intermediate part. The group of three arrows to the right shows further increases in connectedness, differentiation and intermediate-level parts. Figure 5 shows the scale over the entire range of interest here and gives examples of the types of organism occupying each level. The choice of the individuated colony as the highest level is arbitrary. The scale could be extended to include higher levels yet, e.g. colonies of colonies or ‘supercolonies’ (Queller, 2000; Tsutsui *et al.*, 2000).

Notice that in this scheme, hierarchical levels are not defined by specific groups of organisms (Salthe, 1985), but rather organisms are said to occupy levels. That is, a hierarchical level is not a taxonomic designation but is rather a function purely of nestedness and individuation. Thus, any prokaryotic aggregate with the same degree of individuation as a solitary eukaryotic cell occupies the same level as a eukaryotic cell. For example, the myxobacterium *Chondromyces*, in which cells are differentiated and form intermediate parts, such as the stalk and fruiting body (Kaiser & Losick, 1993), might occupy a level very near to that occupied by a eukaryotic cell.

Also notice that by the criteria above, many – but not all – losses and gains of structure count as hierarchical changes. For example, in a multicellular organism, the loss of a cell type is a decrease in differentiation, the loss of an organ type would count as a loss of an intermediate-level part, and therefore either would constitute a loss of individuation at the multicellular level. On the other hand, a loss of a number of cells of the same type would not constitute a decrease in differentiation if at least one cell of that type remains, nor would the loss of a number of serially repeated intermediate parts of the same type (e.g. vertebrae) constitute a loss if at least one of the same type remains.

Examples of minor reversals

Consider again the problem that no major reversals are known across the gap between highly individuated multicellular organisms and solitary eukaryotic cells, or between eukaryotic and prokaryotic cells. The more highly resolved scale suggests an argument in support of the notion that such decreases, although yet undetected, have nevertheless occurred. The argument begins with

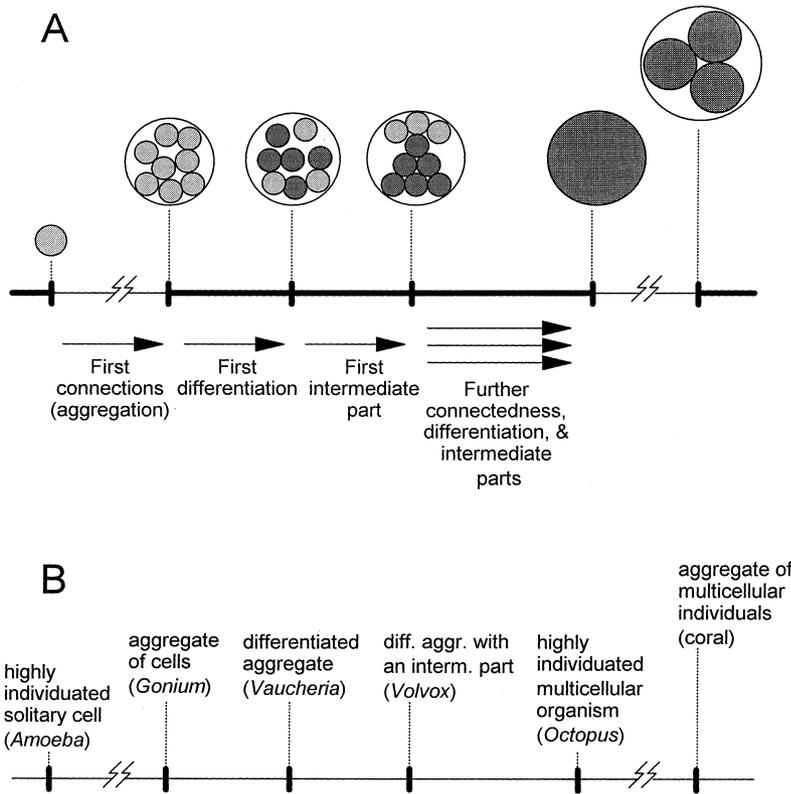


Fig. 4 A hierarchy scale. A: one segment of the scale, showing the minor transitions (arrows) that constitute a major transition. From left to right: first arrow = an increase in nestedness and connectedness resulting from the aggregation of lower-level entities; second arrow = first occurrence of differentiation; third arrow = first occurrence of an intermediate-level part. The group of three arrows to the right represents further increases in connectedness, differentiation and/or intermediate-level parts. B: The same segment of the scale, annotated with examples.

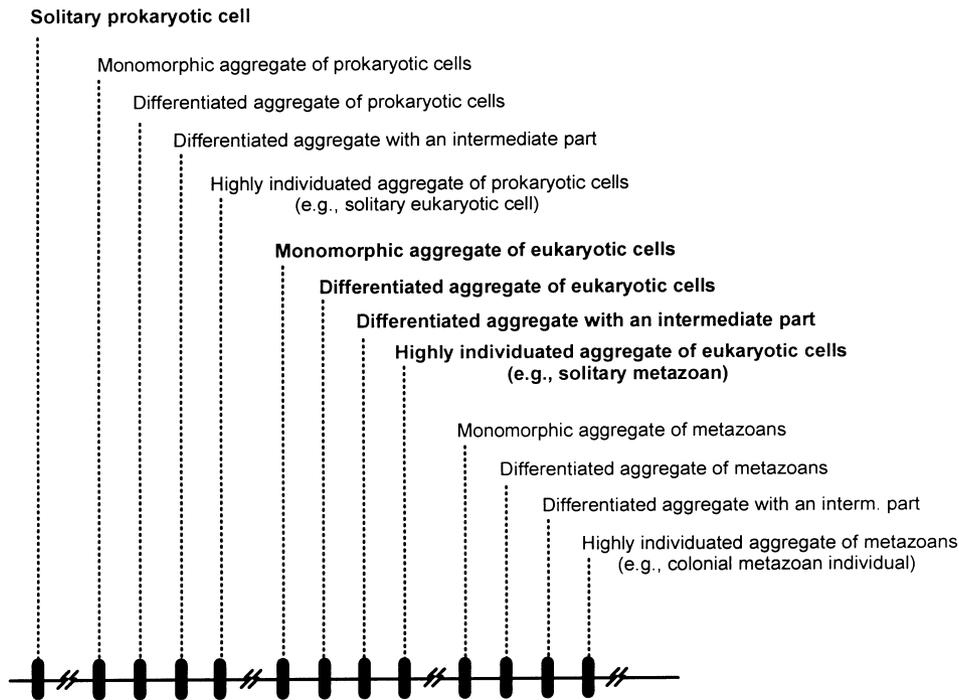


Fig. 5 The hierarchy scale, showing a range from solitary prokaryotic cell to highly individuated colony of multicellular organisms.

the observation that many cases of *minor* reversal are known:

1 Recent evidence suggests that a number of hierarchical reversals may have occurred in the volvocine algae (Kirk, 1998), in particular that forms *without* terminally differentiated somatic cells, such as *Pandorina*, may have arisen from differentiated *Volvox*-like ancestors (Larson *et al.*, 1992; Kirk, 1998). The possibility has even been raised that some solitary strains in the genus *Chlamydomonas* have arisen from multicellular forms (Kirk, 1998).

2 The evolution of flatworms may have involved the loss of a coelom (Balavoine, 1998), an intermediate-level part type. Losses of various tissue and organ types may have occurred a number of times in the evolution of the pseudocoelomate groups (Adoutte *et al.*, 1999; see also Dewel, 2000), as well as among the meiofaunal representatives of many other multicellular invertebrate taxa (Swedmark, 1964; Westheide, 1987; Hanken & Wake, 1993; although many of these have also gained parts as specialization's for interstitial existence).

3 In some protistan lineages, such as the diplomonads, mitochondria are absent and may have been lost in evolution (Katz, 1998; Roger, 1999). Many of these organisms are parasitic or commensal, but some are free living (e.g. the diplomonad *Trepomonas agilis*) and may constitute reversals from the level of the eukaryotic cell. Of course, losses of mitochondria represent reductions in nestedness only if no other former endosymbionts are present in these cells. Only with the loss of its last former endosymbiont is a eukaryotic cell host transformed into a solitary entity at the next lower level, the level occupied by prokaryotes. These are not prokaryotes, of course, but that level is not limited to prokaryotes.

The point of these examples is that minor decreases in hierarchical structure could be common in evolution. If they are, it seems likely that at least occasionally in the long history of life, several of them would have occurred in the same lineage producing a major downward transition.

The possibility of local biases

The higher-resolution scale suggests another possible type of bias, in addition to those discussed earlier. In particular, increases and decreases might be equally probable for some minor transitions but biased for others. For example, transitions in nestedness, connectedness and intermediate-level parts might be unbiased but transitions in differentiation might be irreversible. Figure 3(C) shows a case in which change within certain ranges on the hierarchy scale (grey shaded regions) is unbiased but change between these ranges is biased. Notice that this mechanism is consistent with that in Fig. 2(A) but that the higher resolution enables us to discern the placement on the hierarchy scale of the right walls separating major levels. Figure 3(D) shows an alternative, in which no bias is present at any point along the scale.

Testing for bias: a method

In order to determine whether a pervasive bias toward increase has been present, one way to proceed would be to identify a large sample of ancestor–descendant species pairs, randomly distributed over the hierarchy spectrum and over time, and to compare degree of hierarchical structure in ancestor and descendant in each pair (McShea, 1994; Alroy, 2000). In this approach, a pervasive bias, if one exists, would emerge as a statistical tendency, a significant predominance of increases over decreases among pairs. Further, given a sufficiently dense distribution of ancestor–descendant pairs, it would also be possible to detect local biases, i.e. those limited to certain times or certain types of minor transition.

Equivalently, rather than use ancestor–descendant pairs, one could select a series of clades, randomly distributed over the hierarchy spectrum and over time (Fig. 6), with each spanning one or more minor transitions. Within each clade, the degree of hierarchical structure of taxa at internal nodes, i.e. ancestral states, can be reconstructed using various methods (see below), thus generating a sample of ancestor–descendant comparisons and a count of number of increases and decreases. Raw counts can then be normalized (see below) to generate a probability of increase and a probability of decrease for each clade, and these two probabilities can be compared. In this approach, a pervasive bias would emerge as a significantly greater frequency of clades in which probability of increase exceeds probability of decrease. As above, any local biases that are present could also be identified, given sufficiently dense sampling.

Testing for bias: a demonstration

Here I offer a demonstration, based on a hybrid of these two methods, using two clades: a diatom group and a bryozoan group. Obviously, two groups cannot provide a robust test for pervasive bias; for that purpose, many more groups, spanning a greater range of time and of the hierarchy spectrum, would be needed (Fig. 6). The point is to illustrate the testing procedure.

Actually, the requirements for a robust test are violated here in another way: the groups were selected not at random but very deliberately, because they produced results consistent with an unbiased mechanism. The intent is to offer a kind of counterweight to the common intuition that a bias exists.

Diatoms

Diatoms are freshwater and marine protists, mostly photosynthetic, with elaborately ornamented bivalved shells (Margulis & Schwartz, 1988; Round & Crawford, 1990). In many species, the cells are solitary, but in

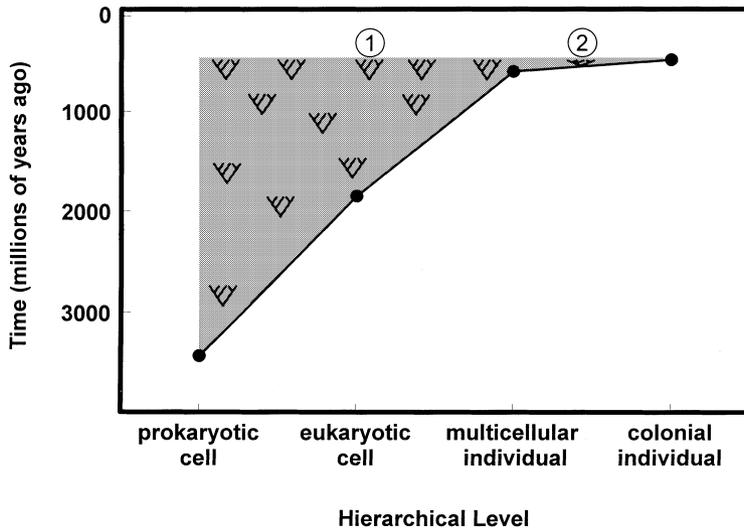


Fig. 6 Test structure. Figure 1 is reproduced with the addition of a number of phylogenetic trees scattered in time and along the hierarchical spectrum. Each tree is a clade spanning a small range of minor hierarchical transitions and of time; each is examined for bias using methods explained in the text. Given a sufficiently large and randomly distributed sample of trees, the distribution of biases could be mapped, and a test for a pervasive bias could be performed. The two numbered trees correspond roughly to the positions of the two clades analysed here, a diatom group (1) and a bryozoan group (2).

others they form ribbons, chains, filaments or have other colonial configurations. Thus, the group shows variation in nestedness (i.e. first arrow in Fig. 4), spanning the minor transition between the solitary-eukaryotic-cell and the cell-aggregate levels (Fig. 6). Recently, Medlin *et al.* (1996) undertook a phylogenetic study of the group based on small-subunit ribosomal RNA sequences in 29 extant diatom taxa, combining a number of phylogenetic methods (e.g. maximum likelihood and weighted maximum parsimony) to produce a single tree (rooted with four outgroup taxa, including the chromophyte *Pelagomonas*). For the analysis here, I assigned taxa to one of two character states, state 0 for those in which all or some individuals are solitary unicells, and state 1 for those which are entirely colonial (ribbons, chains, etc.) (Table 1). For consistency, assignments were based mainly on a single source (Tomas, 1997). The states were mapped onto the Medlin *et al.* tree, as shown in Fig. 7. (Some taxa were not included, namely those for which the character state could not be determined, reducing the group to 25.)

Cyclostome bryozoans

The cyclostome bryozoans are a group of colonial marine invertebrates in which the colony is composed of a number of cylinder-shaped zooids. (For further descriptions, see Ryland, 1970, and Boardman & Cheetham, 1987.) Each zooid is considered a multicellular entity, and there is variation among species in colony-level individuation, that is, in the degree of connectedness and differentiation among zooids, as well as in number of intermediate-level parts. Thus, the group lies in the range between an aggregate of multicellular individuals and an individuated colony (Fig. 6). A phylogenetic analysis of the group was conducted recently by Taylor & Weedon (2000), based on 46 skeletal characters in 29 genera, most of them extant (Fig. 8). Character states for taxa were obtained from the Taylor & Weedon study and also from a literature search (mainly by E. P. Venit) and personal communications from F. K. McKinney, P. D. Taylor and A. H. Cheetham. A brief review of the relevant characters follows; see Boardman & Cheetham (1973) for further discussion.

Taxon	Hierarchical range	Nestedness or aspect of individuation	Character states	
			0	1
Diatoms	solitary euk. cell to cell aggregate	nestedness	solitary	colonial (chain, filament, etc.)
Cyclostome bryozoans	multicell. individ. to individuated colony	connectedness	fixed-walled	free-walled
		differentiation	adventitious branching absent	adventitious branching present
		intermediate part	maculae absent	maculae present

Table 1 Taxa and characters.

Fig. 7 Phylogenetic tree for 25 diatom taxa (modified from Medlin *et al.*, 1996; see text), showing degree of nestedness (white = solitary; black = colonial; hatched = uncertain) for each. Character states at internal nodes and on branches were reconstructed using maximum parsimony (MacClade 3.01). Probabilities of change (Table 2) were computed based on counts of numbers of transitions of each type (Sanderson, 1993); only unambiguous transitions were considered. Here, there were four 0-to-0, zero 0-to-1, four 1-to-0 and 36 1-to-1 transitions, which gives a probability of increase of $0/(4 + 0) = 0$, and a probability of decrease of $4/(36 + 4) = 0.10$.



Fig. 8 Phylogenetic tree for 29 cyclostome genera (modified from Taylor & Weedon, 2000). The shading shows character states for connectedness only (white = fixed-walled; black = free-walled; see text). Character states at internal nodes and on branches were reconstructed using maximum parsimony (MacClade 3.01).



Connectedness

Two character states are considered, fixed walled and free walled. All post-Palaeozoic cyclostomes have interzooidal connections via pores in the vertical walls separating adjacent zooids (Borg, 1926; Ryland, 1970; Nielsen & Pedersen, 1979). In the fixed-walled forms, these narrow pores constitute the only coelomic connection, because the vertical walls contact and fuse with the calcified,

exterior frontal walls. However, in free-walled forms, the frontal walls are uncalcified, and no contact is made with the vertical walls, creating a wider coelomic connection around the distal ends of the vertical walls (Larwood & Taylor, 1979; Hayward & Ryland, 1985; Taylor, 2000). Thus, the free-walled state is more connected. Here, fixed-walled forms are assigned to 'state 0' and free-walled forms to 'state 1' (Table 1).

Differentiation

A colony is founded by a larva which settles and metamorphoses into a zooid, 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. Generational variation among zooids is called astogenetic differentiation. In all species, there is a primary zone of differentiation, which is limited to the first few generations and followed by a much longer zone of repetition of nearly identical zooids. In some species, however, there is a secondary differentiated zone, which can take various forms (Boardman & Cheetham, 1973); only one form is considered here: adventitious branching. 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, a secondary zone. 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. State 0 refers to the absence of branching (and therefore the absence of differentiation) and state 1 to its presence (Table 1).

Intermediate-level parts

Only one type of intermediate-level part is considered, structures known as maculae, which here are understood (following Taylor & Weedon, 2000) as regularly spaced zones on the colony surface where feeding-zooid apertures are less dense than on the rest of the colony or are absent altogether. In many species, including all of the maculate taxa considered here, these zones occur as raised mounds known as monticules (Taylor, 1999). Maculae represent multizoooidal collaborations in two senses. First, feeding zooids in intermonticular regions presumably collaborate in providing food for the colony as a whole, including the nonfeeding zooids. And second, the groups of nonfeeding zooids in the monticular regions represent collaborations for the provision

of excurrent chimneys to channel seawater from which food particles have been extracted away from the colony (Banta *et al.*, 1974). State 0 corresponds to absence of maculae and state 1 to presence (Table 1).

Methods and results

For both diatoms and cyclostome bryozoans, ancestral states were reconstructed using maximum parsimony (MacClade 3.01; Maddison & Maddison, 1992). For ancestral-state reconstruction, two necessary assumptions are that rates of change were low and constant throughout the tree. (For others, see Schluter *et al.*, 1997; Omland, 1999) Here, increases and decreases were weighted equally (see below). Figure 7 shows the reconstruction for nestedness in diatoms. Figure 8 shows the reconstruction for connectedness in cyclostomes; reconstructions for other cyclostome characters are not shown. For connectedness and intermediate-level parts, the state at the deepest node on the tree was the same as that of the outgroup, *Cuffeyella*; for differentiation (adventitious branching), the deepest node was ambiguous (with equal weighting), so it was fixed manually in *Cuffeyella*'s state, i.e. adventitious branching present.

Counts of increases and decreases were generated by comparing states at adjacent nodes. Only unambiguous transitions were counted. (In the diatom tree, some nodes remained ambiguous.) Then, following a method developed by Sanderson (1993), these counts were normalized by dividing by number of opportunities for change, generating probabilities of increase and decrease (see caption to Fig. 7).

Counts and probabilities are shown in Table 2: probability of increase exceeded probability of decrease for two minor transitions in cyclostomes: connectedness and intermediate-level parts (maculae). Probability of decrease was higher for two minor transitions: for nestedness in diatoms and for differentiation in cyclostomes (adventitious branching).

A robust test for a pervasive bias would differ from the demonstration above in a number of ways. For example,

	Transitions				$P(I)^*$	$P(D)^\dagger$	bias‡
	0-0	0-1	1-0	1-1			
Diatoms							
nestedness	4	0	4	36	0.00	0.10	D
Cyclostome bryozoans							
connectedness	36	4	0	16	0.10	0.00	I
differentiation: advent. branching	54	0	1	1	0.00	0.50	D
intermediate structures: maculae	42	2	0	12	0.05	0.00	I

Table 2 Results.

* $P(I)$ = probability of increase (computed as described in Fig. 7 caption). † $P(D)$ = probability of decrease. ‡I = probability of increase greater; D = probability of decrease greater.

in a maximum-parsimony analysis, some consideration of the sensitivity of the result to transition-weighting is in order (Omland, 1997; Cunningham *et al.*, 1998; Cunningham, 1999). Also, all presently available ancestral-state reconstruction methods are problematic in various ways (Cunningham *et al.*, 1998; see also a series of seven papers on ancestral-state reconstruction in *Systematic Biology* 1999, Vol. 48, issue no. 3). Thus a robust test might employ multiple methods, including, for example, a maximum-likelihood approach (Pagel, 1994, 1997; Schluter *et al.*, 1997).

Finally, tests for statistical significance of reconstructions (e.g. Schluter *et al.*, 1997) and of probability values (Sanderson, 1993) are available and could be applied.

The results here – two cases in which probability of increase was greater and two in which probability of decrease was greater – are consistent with and support the null hypothesis that increases and decreases are equally probable (or would if they had been randomly chosen). Of course, consistency is not confirmation, and if a more robust test also reveals no bias, an assessment of the power of the test would be desirable as well.

Summary

The history of life shows a clear trend in structural hierarchy, revealed by the successive emergence of organisms with ever greater numbers of levels of nestedness and greater degrees of individuation at the highest level. This successive emergence documents a trend in the hierarchical maximum, in the degree of structuring present in the hierarchically deepest organism on Earth. Regarding the trend mechanism – the pattern of change among lineages that has produced a rise in the maximum – many arguments have been offered which suggest that change among lineages is biased, that hierarchical increases are more probable than decreases, including the suggestion that increases are favoured on average by selection. Further, what little evidence exists seems to suggest a bias: a number of major hierarchical increases are known but no major decreases are known (except in parasitic and commensal organisms). The goal here has been to raise an alternative mechanism, an unbiased or diffusive mechanism, to the level of plausibility and to show how empirical testing is possible. Notice that the argument is not that no bias exists; indeed, even a strong bias is a live possibility. Rather, the point is that the existence of a bias is an open question.

A final cautionary note: the implication of an unbiased mechanism, if found to have operated, would be that no increasing tendency exists. But such a finding would not deny the efficacy of selection. Indeed, it would be consistent with the notion that selection has been equally effective in both directions, producing decrease as often as increase, as opportunities for each arose.

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