Three Puzzles in Hierarchical Evolution[1]

DANIEL W. MCSHEA[2,*] AND MARK A. CHANGIZI[3,†]

*Department of Biology, Duke University, Box 90338, Durham, North Carolina 27708-0338
†Department of Psychological and Brain Sciences, Duke University, Box 90086, Durham, North Carolina 27708-0086

SYNOPSIS.   The maximum degree of hierarchical structure of organisms has risen over the history of life, notably in three transitions: the origin of the eukaryotic cell from symbiotic associations of prokaryotes; the emergence of the first multicellular individuals from clones of eukaryotic cells; and the origin of the first individuated colonies from associations of multicellular organisms. The trend is obvious in the fossil record, but documenting it using a high-resolution hierarchy scale reveals three puzzles: 1) the rate of origin of new levels accelerates, at least until the early Phanerozoic; 2) after that, the trend may slow or even stop; and 3) levels may sometimes arise out of order. The three puzzles and their implications are discussed; a possible explanation is offered for the first.

INTRODUCTION

It is sometimes worthwhile to try to document the obvious. One reason is that the obvious may turn out, on close examination, to be false. Another is that even if true, the search for evidence often reveals unexpected patterns, or puzzles, which in turn can lead to deeper insights.

The obvious here is the trend over the history of life in the hierarchical structure of organisms. The trend is captured by three well-known transitions: 1) the origin of the eukaryotic cell from symbiotic associations of prokaryotes; 2) the emergence of the first multicellular individuals from clones of eukaryotic cells; and 3) the origin of the first individuated colonies from associations of multicellular organisms. In each case, the increase was hierarchical in that lower-level entities combined to form a higher-level individual. This is structural hierarchy, or hierarchy in the sense of Simon (1962), Salthe (1985), Wimsatt (1994), Valentine and May (1996), Pettersson (1996), McShea (2001a), and others. The trend is an increase in the maximum, a rise in the number of levels present in the hierarchically deepest organism in existence. And it is obvious in that the fossil record clearly reveals the three transitions occurring in the order listed.

To document the trend, one needs to establish first occurrences in the fossil record for each of the four major levels, i.e., to identify and date the first prokaryotic cell, eukaryotic cell, multicellular individual, and individuated colony. Further, to investigate the precise pattern of change, it would be helpful to add more levels, or more precisely to interpolate sublevels, in effect to increase the resolution of the hierarchy scale. One of us (DWM) did this in a recent paper (McShea, 2001a), devising a scale with four major lev-els, each subdivided into three "minor levels" based on the degree to which organisms at each level are "individuated." (See also an attempt by Pettersson, 1996.) Figure 1 shows the first known occurrence of each minor level, based on the fossil record. The scale and various terms—e.g., level, individuation—are explained briefly below, and at greater length in McShea (2001a).

The data have at least three puzzling aspects: 1) Acceleration. The figure shows a huge increase in the rate of generation of new higher levels from the origin of life in the middle Archean, 3.5 billion years ago, to the early Ordovician, about 480 million years ago. (Interpreting a trajectory on this higher-resolution hierarchy scale is actually not straightforward. As will be seen, a transformation of the data is needed to properly demonstrate an increase in rate.)

2) Possible slowing of the trend. The highest level documented was the colony level, level 4, mainly because little evidence for higher levels can be found. In the record for the past 480 million years (including the Recent), there a few good candidates for level 5 (supercolonies), but no equally convincing cases of level 6 (super-supercolonies). (Human societies are a possible exception but difficult to evaluate.) Thus, taking the record at face value (and ignoring humans), the rate of increase would seem to have slowed. Indeed, the possibility needs to be considered that an upper limit has been reached and that the trend has been truncated.

3) Order of occurrences. From certain viewpoints, the order of first occurrences is anomalous. We defer explaining this issue to the last section, because it requires a more detailed explanation of the hierarchy scale.

A HIERARCHY SCALE

Hierarchy as understood here has two components: first, nestedness or aggregation; and second, individuation. Aggregation refers to the number of nested levels of entities within entities that an organism contains, where the entities are present or former levels of selection (sensu Brandon, 1996). Thus, the multicellular
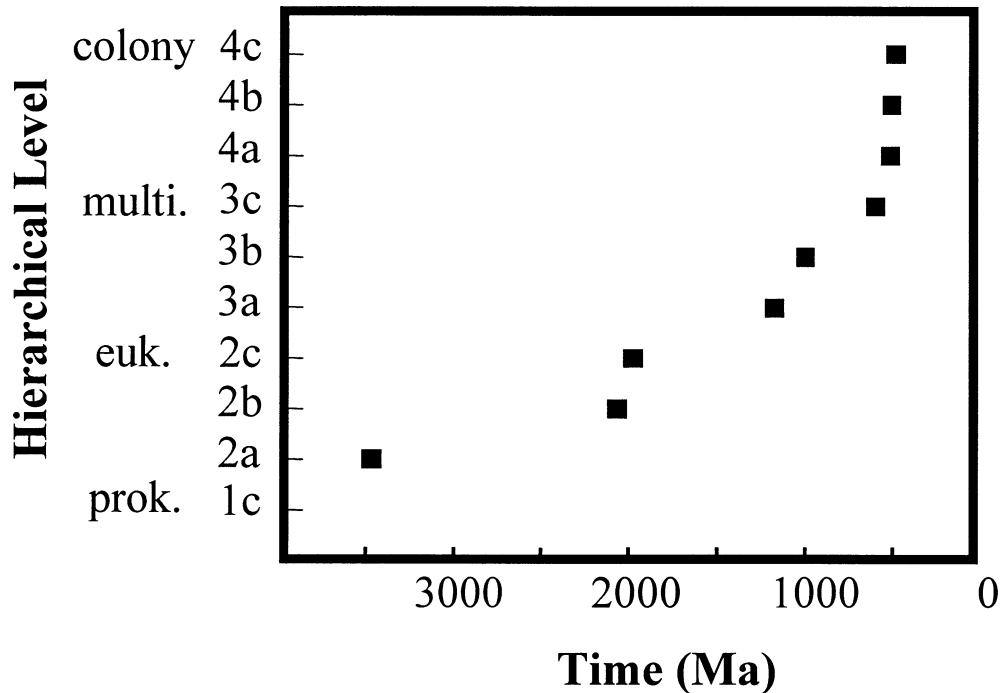
FIG. 1. First occurrences of each hierarchical level based on the fossil record. For explanation of the scale, see Figures 2 and 3 and discussion in text. Taxa and approximate age corresponding to each data point are as follows: 2a: carbonaceous cyanobacteria-like filaments, 3,465 Ma; 2b: *Archaeoellipsoides* (akinetes of nostocalean cyanobacteria), 2,065 Ma; 2c: *Grypania* (spirally coiled eukaryotic cell), 1,975 Ma; 3a: *Bangiomorpha* (bangiophyte red alga), 1,175 Ma; 3b: *Palaeovaucheria* (xanthophyte algal filaments), 1,000 Ma; 3c: *Nimbia, Vendella, & Irridinitus?* (oldest Ediacaran-like forms), 600 Ma; 4a: *Moorowipora & Arrowipora* (cerioid corals), 514.5 Ma; 4b: Dendroid graptolites, 504.5 Ma; 4c: *Dianulites* (stenolaemate bryozoan), 483 Ma. Level 1c omitted here, and in Figure 4a, because early Archean specimens are ambiguous (but see Fig. 4b). Dates are range midpoints. See McShea (2001*a*) for references and further discussion. N.B. Recently, Brasier *et al.* (2002) argued that the 3,465-Ma Apex Basalt microfossils, which here are considered the first level 2a organisms, are abiogenic (but see Schopf *et al.*, 2002). If true, they would be replaced at level 2a by slightly younger specimens from the 3,445–3,416-Ma Overwacht Formation, and the overall trajectory of first occurrences would change very little (see McShea, 2001*a*, Appendix).

green alga *Gonium* has three levels: the organism as a whole (1), which is an aggregate of eukaryotic cells (2), which in turn is an aggregate of former prokaryotic cells (3). (That is, the eukaryotic cell body is likely a former archaebacterium, and mitochondria are former eubacterial endosymbionts.) A coral colony, in contrast, is apparently an aggregate of former multi-

cellular individuals (*cf.,* Dewel, 2000), the polyps, and if so it has four levels, one level more than *Gonium*. The scale employs the following numbering system for levels of aggregation: prokaryotic cells are placed arbitrarily at major level 1; free-living eukaryotic cells such as *Amoeba* occupy level 2; multicellular eukaryotes such as *Gonium* occupy level 3; and colonial individuals such as corals occupy level 4.

Individuation refers to the degree to which the top-level entity (*i.e.,* the organism or colony) constitutes a unified whole. Here, degree of individuation is operationalized using two criteria: 1) degree of differentiation of the lower-level entities; and 2) number of what are called intermediate-level parts. (Degree of connectedness among lower-level entities is also important, and even implicit in the notion of aggregation, but will not be further considered here; see McShea 2001*a*.) Figure 2 shows how the criteria are used. *Gonium* is poorly individuated in that it is undifferentiated, *i.e.,* all cells are the same type (in the vegetative phase). In contrast, the xanothophycean alga *Vaucheria* has two cells types, and thus *Vaucheria* is more individuated than *Gonium*. In the level-labeling system used for minor levels, *Gonium* occupies level 3a and *Vaucheria* occupies level 3b. More generally, organisms at the "a" levels on the scale are undifferentiated
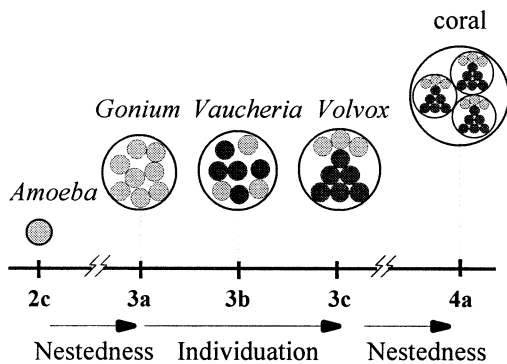

FIG. 2. Schematic representation of a portion of the hierarchy scale (arbitrarily chosen), showing major levels based on aggregation (2, 3, and 4) and sublevels based on degree of individuation (a, b, and c). The level 3 sublevels are 3a: monomorphic aggregate of level-2 entities; 3b: differentiated aggregate of level-2 entities; 3c: differentiated aggregate of level-2 entities with intermediate-level parts.
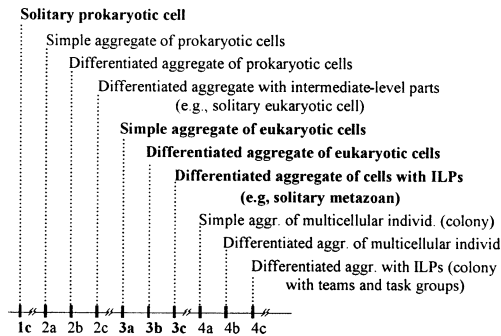
Solitary prokaryotic cell
Simple aggregate of prokaryotic cells
Differentiated aggregate of prokaryotic cells
Differentiated aggregate with intermediate-level parts
(e.g., solitary eukaryotic cell)
Simple aggregate of eukaryotic cells
Differentiated aggregate of eukaryotic cells
Differentiated aggregate of cells with ILPs
(e.g, solitary metazoan)
Simple aggr. of multicellular individ. (colony)
Differentiated aggr. of multicellular individ
Differentiated aggr. with ILPs (colony
with teams and task groups)

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

Fig. 3. An expansion of Figure 2, showing a large portion of the hierarchy scale.

aggregates of entities at the next lower level, while those at the "b" levels are differentiated into two or more lower-level types.

Level "c" organisms have two or more lower-level types too, but they also have one or more "intermediate-level parts" (McShea, 2001a). These can be understood (for present purposes) as collaborations of lower-level entities that are subsets of the whole organism. They are intermediate in that they occupy a hierarchical level between the lower level and the whole. (For a broader notion of intermediate-level parts, see McShea, 2001a; Anderson and McShea, 2001.) For example, Volvox has two cell types (in the vegetative phase), like Vaucheria, but unlike Vaucheria, a subset of the lower-level entities in Volvox is organized collaboratively. Specifically, the flagellated cells are organized to form an outer shell, which propels the organism. Thus, Volvox occupies level 3c. Most tissues and organs in multicellular organisms are collaborations of this sort. (Note that in Volvox and in Fig. 2, intermediate parts are composed of lower-level units of the same type; this is a special case, used here for clarity of illustration. In fact, intermediate parts may be collaborations of many different lower-level types.)

In sum, the scale consists of numbered major levels, corresponding to present or former levels of selection, subdivided into letter-labeled minor levels, corresponding to degrees of individuation of the top-level entity. Figure 3 shows the scale over the range of interest here.

Certain clarifications may be helpful here; see McShea (2001a) for others. 1) The concern is only with biological individuals, with what Valentine and May (1996) called constitutive hierarchies, excluding ecological associations. In principle such associations could be included, but in practice they are difficult to detect in the record. 2) The concern is only with structure, and thus for present purposes, other considerations such as the functional capabilities of an individual, the hierarchical organization of its development, and phylogenetic relationships among its components, are not directly relevant (cf., Knoll and Bambach, 2000). Also not directly relevant are the precise mechanisms by which the various levels have aris-

en (cf., Maynard Smith and Szathmáry, 1995). 3) The scale is somewhat crude in that it does not make distinctions at higher levels of individuation. That is, a simple alga like Volvox and a complex metazoan like an octopus both occupy the same sublevel (3c). Both have two or more cell types and one or more intermediate-level parts. (However, the scale could be modified to capture such differences.)

The Trend

Figure 1 was generated by surveying the paleontological literature to produce a list of candidates for first occurrences. Each candidate was assigned a hierarchical level based on descriptions of its morphology, in some cases relying on analogies with extant organisms. Where hierarchical levels could not be unambiguously determined, candidates were assigned a range of possible levels. For example, the remains of Grypania, the first known fossil eukaryotic organism, do not unambiguously indicate whether it is a solitary unicell, at level 2c, or an undifferentiated multicellular filament, at level 3a (Han and Runnegar, 1992), and thus here it was assigned a range, 2c to 3a. To estimate the trajectory of the maximum, two alternative protocols were used: in the first, each candidate was assigned to the lowest hierarchical level in its range, so that the resulting trend represents a kind of "restrictive view" of the history of hierarchy. In the second, each candidate was assigned to the highest level in its range, producing a "permissive view." Finally, for each view, candidates were ordered in time, using dates also drawn from the literature, and the list was culled to leave only first occurrences.

The two views are presented side-by-side in Figure 4 to convey some idea of the error in the vertical dimension, i.e., hierarchical level. The error bars in the left graph show date ranges for two taxa, offered here as an indicator of error in the horizontal dimension, time.

Puzzle 1: Acceleration

The dominant feature of Figures 1 and 4 is an acceleration in the rate of origin of new levels from the Archean to the Ordovician, about 500 million years ago, including a dramatic increase in rate in the last 100 million years of that period. Arguably, however, the increase in rate cannot be read directly from the graphs in Figure 4, because successive increments on the hierarchy scale are not comparable. For example, a transition from level 2a to 2b (an origin of differentiation) represents a different sort of morphological change than the transition from 2b to 2c (the advent of an intermediate-level part), and thus the rates of the two sorts of transition are not comparable in any simple way. Thus, to see the increase in rates, we ought to only compare transitions of the same type. Figure 5 shows the distribution of waiting times for each transition type (a-to-b, b-to-c, and c-to-a), based on the restrictive data, as a function of hierarchical level. Clearly, waiting times decrease as hierarchical level
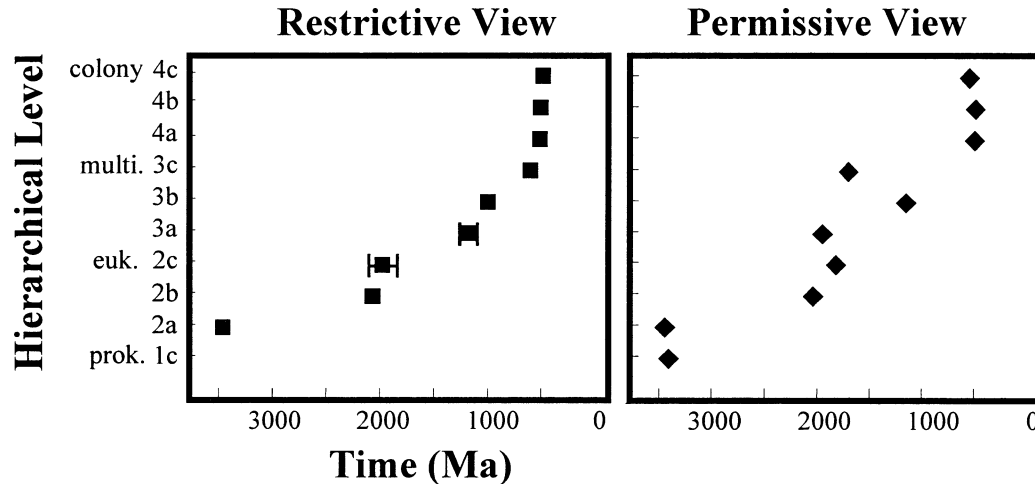
FIG. 4. First occurrences of hierarchical levels based on a restrictive view of the data (left; identical to Fig. 1) and a permissive view (right); see text for explanation of these two terms. Together the two graphs are intended to convey a rough notion of the error involved in assigning fossil specimens to a hierarchical level. The error bars in the left graph show temporal ranges for two taxa, intended to illustrate error in time.

increases. A similar trend emerges when waiting times are plotted against absolute time (not shown).

There are good reasons to be skeptical of these data. In addition to the inevitable errors in identifying hierarchical level and estimating age, trajectories of first occurrences are expected to be sensitive to sample size, and the density of fossil occurrences is very uneven in the early record (Archean and Proterozoic). However, there are also good reasons to think the acceleration is real. In particular, even spacing of first occurrences, with no increase in rate, would require implausible range extensions for certain hierarchical levels. For example, with even spacing, the first highly individuated multicellular organism (level 3c) would have to have arisen more than 1.6 billion years ago, a range extension of about a billion years.

A clarification: the issue here is not simply the Cambrian explosion and its possible causes. First, what the figures document is an acceleration in *hierarchy,* and the Cambrian explosion has been understood mostly as an accelerated increase in diversity, disparity, or complexity in any of a number of non-hierarchical
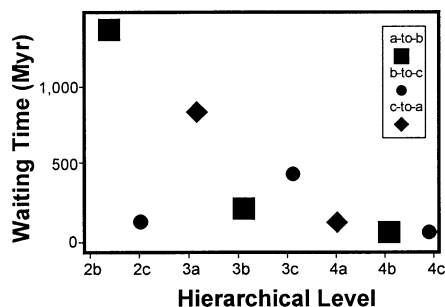

FIG. 5. Relationship between waiting time and hierarchical level (restrictive view only), sorted according to transitions of different types—a to b, b to c, and c to a. Waiting time for a given sublevel is the difference in time between its first occurrence and the first occurrence of the next lowest sublevel.

senses (Valentine, 2002), not hierarchy (*cf., Dewel, 2000). Second, the acceleration begins in the Archean, and therefore none of the various explanations that have been offered for the Cambrian explosion will suffice, at least by themselves. However, as we will argue, the explosion could well be relevant in that common causes could be at work.

A selective mechanism

We offer three possible explanations for the rise in rate, all interrelated. First, it may be that hierarchy is advantageous. For example, Bonner (1988) has argued that hierarchical structure is a route to large size and that large size is favored ordinarily by natural selection (see also Boraas *et al.*, 1998). Selection of this sort might explain a hierarchy increase, but for an increase in rate arguably we need a rise in selection intensity. Such a rise might have been produced, for example, by two surges in atmospheric oxygen, one about 2 billion years ago and the other in the late Proterozoic (Knoll and Carroll, 1999). Increases in oxygen could have been especially favorable to size increases, and therefore perhaps to hierarchy. Alternatively, the acceleration could have been triggered by a one-time increase in rate of generation of novel morphologies, especially in the Metazoa, presumably made possible by the origin of new developmental control systems (Valentine *et al.*, 1999; Peterson and Davidson, 2000; Valentine, 2003), and perhaps linked to an environmental change (Knoll and Carroll, 1999).

A diffusive mechanism

Instead of selection, the rise in the maximum could have been the result of diffusion, the random movement of lineages in hierarchy morphospace, coupled with an increase in diversity (Gould, 1996; McShea, 2001*b*; *cf.,* Knoll and Bambach, 2000). And indeed, at least the last third of the hierarchy trajectory roughly

coincides with the increase in global diversity attending the rise of the Ediacaran fauna and the Cambrian explosion. A problem with this mechanism is that in a diffusive system, an ordinary exponential increase in diversity apparently produces a trajectory for morphological maxima that is concave down, with the slope decreasing over time, at least under certain plausible parameter configurations (Valentine *et al.*, 1994). However, the actual trajectory is concave up (Fig. 4). A purely diffusive mechanism is still possible but would require hyperexponential growth in diversity in the late Proterozoic. This is plausible, although to my knowledge no quantitative estimate of the diversity trajectory for this period has been attempted.

A combinatoric mechanism

The acceleration could be the result of a positive feedback based on hierarchy itself. The underlying principle is simple combinatorics, which we illustrate here with a toy model. We explain the model using biological terms, describing the various entities as cells and organisms, but the purpose is only to illustrate a mathematical principle, not to offer an actual history of life.

Imagine that at some early stage of hierarchical evolution, the highest level achieved is, say, solitary eukaryotic cells. Further imagine that the developmental-genetic architecture of these cells is able to generate some number of cell types, C. Then, suppose that as a result of one or more evolutionary innovations, a new major level arises, that is, aggregates of cells, then differentiated aggregates, and finally differentiated aggregates with intermediate-level parts (*i.e.,* individuated multicellular organisms). Now, within such organisms, suppose that cell types combine to perform functions, and that each function requires, on average, L_1 cells. Then the number of functions that can be performed (across all organisms) is the number of possible cell types (again across all organisms) raised to the power of the number of cells combining (L_1), or C^{L_1}. Thus, in principle, if there are 4 possible cell types and if functions are performed by collaborations of 3 cells, a total of 4^3 or 64 different functions are available to multicellular individuals. One can think of the units performing functions as tissues or organs (or more generally, intermediate-level parts), and a multicellular individual as a package of these, each drawn from the combinations available. (Notice that if the relationship between cell types and functions is to be combinatorial, it must be that $L_1 > 1$. If $L_1 = 1$, the relationship is one of simple proportionality.) In this scheme, the pool of functions available to all multicellular organisms can be increased either by increasing the number of cell types or the number of cells per function. We use the term "innovation" to describe new functions arising in this way.

At this point we make an assumption (which we will later relax), namely that number of types of multicellular individual scales proportionally with number of functions. That is, if the number of possible functions doubles, the number of types of multicellular individual also doubles. More abstractly, the assumption is that $T_1 \sim C^{L_1}$, where T_1 is the number of possible multicellular types. (Notice that T_1 is related to, but not identical with, taxonomic diversity. One reason is that distinct taxa need not have different functions, different innovations. Also, conversely, some distinct multicellular types will be differentiated entities within the same colony, and therefore members of the same taxon.)

Now consider the effect of adding another hierarchical level, that is, combining multicellular individuals in colonies, ultimately colonies with differentiation and intermediate-level parts. In such colonies, suppose that functions are performed by collaborations among the multicellular individuals that constitute it, and that these collaborate in groups of size L_2, on average. Then the number of functions available at the colony level is proportional to the number of types of multicellular individuals, C^{L_1}, raised to the power of L_2, which is $(C^{L_1})^{L_2}$ or $C^{(L_1 L_2)}$. (As above, for the relationship to be combinatorial, it must be that $L_2 > 1$.) Thus, among all colonial organisms, the pool of available innovations can be increased by increasing number of cell types (C), number of cells per function at the multicellular level (L_1), or number of multicellular individuals per function at the colony level (L_2). Finally, we assume that number of colony types scales proportionally with number of colony functions, $T_2 \sim C^{(L_1 L_2)}$, where T_2 is the number of possible colony types.

Regarding the acceleration in hierarchy, our suggestion is that the advent of a new hierarchical level should be followed by an enormous increase in innovation. That is, the magnitude of the bursts of functional innovation following the addition of each successive level should follow a power law in which exponents for successive levels are multiplied. Assume further that the discovery of new hierarchical levels requires innovations of some kind, *i.e.,* that the rate of discovery of new levels is correlated with the size of innovative bursts. If so, then an accelerating rate of discovery of new hierarchical levels is expected.

Notice that this reasoning does not depend on the earlier assumption that multicellular types increase proportionally with number of innovations. In particular, suppose that innovations instead unite combinatorially to make different types of multicellulars. The effect would be to introduce an additional hierarchical level between the cell level and the multicellular level, so that $T_1 \sim (C^{L_1})^{L_{1A}}$ or $T_1 \sim C^{(L_1 L_{1A})}$, where L_{1A} is the number of innovations combining to produce a multicellular type and $L_{1A} > 1$. Similarly, $T_2 \sim C^{(L_1 L_{1A})(L_2 L_{2A})}$ or $T_2 \sim C^{(L_1 L_{1A} L_2 L_{2A})}$, where L_{2A} is the effective number of functions per colony type and $L_{2A} > 1$. The effect is to increase all exponents and thus to increase the acceleration of the combinatorial explosion.

The toy model requires tremendous simplification, obviously, and for greater realism, the equations would

need some adjusting. First, the developmental-genetic architecture of multicellular organisms presumably imposes certain constraints or "rules" limiting which cell-type combinations can be generated. And other combinations will be possible from a generative standpoint but not functional, *i.e.,* would be opposed by natural selection. As a result, the actual exponent will be less than the theoretical one, or in other words, C^{d_1} for multicellulars, and $C^{(d_1 d_2)}$ for colonies, where $d_1 < L_1$ and $d_2 < L_2$. Also, other generative and functional constraints reduce the magnitudes of the expressions overall by some fraction ($\propto$). Thus, number of functions is $\propto_1 C^{d_1}$ for multicellulars and $\propto_2 C^{(d_1 d_2)}$ for colonies, where $\propto_1, \propto_2 < 1$.

The principle here comes from a more general scheme relating parts and wholes developed by one of us (MAC; Changizi, 2001*a, b*, 2003; Changizi *et al.*, 2002). And a similar principle was invoked by Valentine (2000) at the molecular level. Valentine argued that in multicellular invertebrates, relatively few genes are needed to generate high levels of morphological complexity, because complexity is generated combinatorially, by regulatory interactions in which each gene is used many times, in many different ways. Here we (partly) formalize this principle, using a scheme based on morphology rather than genes, and also show the consequences of extending it hierarchically.

Importantly, the suggestion is not that innovations actually arise in combinatorial fashion, by trying out combinations of lower-level units. Rather, the combinations represent the potentials of the underlying developmental-genetic mechanisms, and innovations are the novel combinations that remain after those potentials have been culled by natural selection. Second, this view does not contradict any of the various ecological mechanisms that have been proposed for the Cambrian explosion or other bursts of innovation such as the one that produced the Ediacaran fauna. Nor does it contradict any of the hypotheses based on the advent of new developmental-genetic regulatory mechanisms. Rather, these mechanisms presumably made the combinatorial buildup of multicellularity, and ultimately colonies, possible. Another way to frame our suggestion is this: when ecology and internal mechanisms are not limiting, combinatorics will drive the system.

Predictions

Our conjecture is that cells are used combinatorially in the production of new functions in multicellular individuals, and multicellular individuals are used combinatorially in the production of new types of colony function. If so, three predictions follow. First, within a multicellular group, such as metazoans, a log-log plot of number of functions the group is capable of performing at a given time *versus* number of cell types extant in the group at that time should have a slope that is everywhere greater than one.

Cell types can be estimated from available data (Valentine *et al.*, 1994; Bell and Mooers, 1997). Number of functions might be estimated as the number of

"part" types present in the group, in this case tissue/ organ types (McShea and Venit, 2001). Alternatively, biomass might be used as a proxy for number of functions, on the assumption that size increases require increases in number of functional capabilities (Bonner, 1988; also Changizi *et al.*, 2002). Here, biomass is the sum of the masses of all metazoan taxa, with each taxon represented by a single individual.

The second prediction is that the same sorts of relationships should exist at the colony level. That is, on a log-log plot, number of colony functions should be linearly related to number of cell types, with slope everywhere greater than one. As above, proxies are available for number of colony functions, such as number of colony-level intermediate parts (Anderson and McShea, 2001) and colony biomass (again with each taxon represented by a single colonial individual).

The third prediction is that, if higher hierarchical levels are produced combinatorially as conjectured here, the slope at the colony level will be greater than the slope at the multicellular level at all times. The reason is that exponents are always greater than one, and exponents are multiplied in transiting levels.

PUZZLE 2: A SLOWING OF THE TREND?

The record for levels above 4 is unclear. A few candidates for level 5 supercolonies are known. Certain cyclostome bryozoan species produce daughter colonies that remain attached to the parent and therefore qualify as level 5a, undifferentiated aggregates of colonies (*e.g.,* at least some species of *Plagioecia*, first known from the Jurassic, about 170 million years ago). In the Recent, other candidates can be found, but only in taxa that typically fossilize poorly, so first occurrences cannot be dated with confidence. For example, Beklemishev (1969) describes supercolonies in the siphonophores. Also, reduced intercolony aggression has been noted in populations of a modern ant species, *Linepithema humile* (Tsutsui *et al.*, 2000). And reduced aggression might be considered a first step toward cooperative interaction, and therefore toward aggregation at level 5 (Queller, 2000).

Humans present an extreme example of sociality, but the hierarchical structure of our societies is unclear and difficult to evaluate objectively. Various levels of aggregation can be identified—*e.g.,* family, clan, village, nation state—but it is not obvious which if any are present or former levels of selection. Complicating any assessment is the possibility that the selected units have shifted over historical time. Also, there are many ways to parse human associations, with the result that there is no single, obvious, clean hierarchical series. For example, clans can cross village and even nation-state boundaries. As a result, it is difficult to know what level human society reaches. It might seem that we are strongly hierarchical, perhaps reaching level 6, or perhaps much higher. But at present it is difficult to rule out the possibility that we aggregate in colonies only at level 4. We could be complex in many respects (perhaps in terms of division of labor and number of

types of interactions), without being especially deep hierarchically. In sum, there is little we can say with confidence about the trajectory of hierarchy after level 4 based on the fossil and modern record.

Another approach is to extrapolate using the curve in Figure 1. The extrapolation can be done in various ways. One is to compute the velocity of the last transition, the one to level 4 (v_4, in levels per year), and the average acceleration over the history of life (a, in levels per year^2). Then the expected hierarchical maximum reached in the Recent would be $H_{Recent} = 4 + v_4t + (1/2)at^2$, where t is the time since the last data point, level 4c ($t = 483$ million years). In this case, using different temporal scales produces different values of H_{Recent}. At a coarse scale, consider first the major-level transitions 2c-to-3c and 3c-to-4c. Based on the data in the Figure 1 caption, the average velocity of the last transition, 3c-to-4c, was 8.5×10^{-9} levels/year, and the average acceleration over both transitions was 1.1×10^{-18} levels/year^2, yielding $H_{Recent} = 10.2$. For the major transitions between the ''b'' levels, $H_{Recent} = 5.9$, and for those between the ''a'' levels, $H_{Recent} = 5.5$. Using mean values for v_4 and a yields $H_{Recent} = 6.4$.

At a finer temporal scale, we can extrapolate using rates and accelerations for just the minor transitions, for example the two c-to-a transitions (2c-to-3a and 3c-to-4a). The formula must be modified slightly to take into account that there are three minor levels per major level, so that $H_{Recent} = 4 + [v_4t + (1/2)at^2]/3$. The average velocity of the last minor transition (3c-to-4a) was 1.2×10^{-8} minor levels/year, and the average acceleration over both minor transitions was 1.0×10^{-17} minor levels/year^2, yielding $H_{Recent} = 6.3$. Using the three b-to-c transitions (2b-to-2c, 3b-to-3c, and 4b-to-4c), $H_{Recent} = 17.1$, and using the three a-to-b transitions, $H_{Recent} = 26.4$. With mean values for v_4 and a, $H_{Recent} = 16.6$. In sum, the expected hierarchical maximum in the Recent probably ranges somewhere between 6 and 17, but could be as low as 5 or as high as 26.

Combining the extrapolation results with what little can be inferred from the record suggests two very different interpretations of the recent history of hierarchy. One is that higher levels have arisen, as expected, but that they become increasingly difficult to detect. Perhaps at higher levels, connections among components tend to be weaker (Wimsatt, 1994), and therefore less visible in the fossil record. Consistent with this, in social insects and social vertebrates (including humans), the connections among components are mainly behavioral, and therefore not so well preserved as the structural linkages in colonial marine invertebrates. Also, higher-level entities might tend to take the form of multispecies ecological associations, in which again the associations are often not structural and thus are harder to detect. In this view, the expected rise in the maximum occurred but was hard to detect.

A second interpretation is that the origin of new higher levels slowed dramatically (or even halted) after the early Ordovician, 480 million years ago. In this view, it resumed only in the Recent, again assuming humans are hierarchically deep, or perhaps did not resume at all, if humans are shallow. Importantly, the suggestion here is that the rate of origin slowed for levels of selection, not necessarily for intermediate levels (*e.g.,* the tissues and organ levels). Indeed, it seems likely that metazoans at least underwent considerable elaboration at these levels.

In any case, if slowing occurred, it raises some interesting possibilities. The rise in hierarchy might have been thwarted by certain environmental changes (*e.g.,* perhaps an increase in frequency of mass extinction?). Or there might be limits of some kind to hierarchical structure. Perhaps the highest levels are unstable or hard to generate. Why might this be so?

Puzzle 3: Order of Origin

The restrictive view of the data in Figure 4a shows all levels and sublevels arising precisely in order. If the pattern is real, it might seem odd, first because skipping levels is possible. That is, nothing in the structure of the scale requires that higher-level organisms arise in evolution by ascending the hierarchy scale one minor level at a time. Second, at least one skip is known to have occurred, in the origin of eukaryotic cell. At some point in that transition, two level-1c organisms, both free-living prokaryotes, combined to form (minimally) a level-2b organism directly, skipping level 2a, the undifferentiated-aggregate stage. Third, the quality of the record is quite poor over most of the Precambrian, so that some *apparent* skips might be expected even if none occurred in evolution.

The absence of skips is less surprising, however, when one considers that the trend is not produced by a progression within a single lineage. Rather, it is the result of a multilineage diversification in which different taxa successively occupy the top hierarchical level. Thus, in principle, the maximum could increase incrementally even if skips were numerous within lineages. The absence of skips is also not very surprising because it suggests—in agreement with intuition—that skipping of levels occurs with lower probability than incremental increases.

The pattern revealed by the permissive view of the data in Figure 4B is potentially more interesting. If true, there were four skips: aggregates of prokaryotes (2a) arose before solitary prokaryotes (1c); aggregates of eukaryotic cells (3a) arose before solitary ones (2c); highly individuated multicellular organisms with intermediate-level parts (3c) arose before differentiated aggregates with two or more cell types (3b); and highly individuated colonies (4c) arose before less individuated ones (4a and 4b). Again, there are good reasons to be skeptical. For example, the first is the oldest transition known and the most likely to be an artifact of an imperfect record. And the hierarchical status of the level-3c specimens on which the third is based is suspect (see McShea, 2001*a*). But accepting the data at

face value raises the interesting possibility that hierarchy may be quite labile, that hierarchical saltations may be relatively easy in evolution. It also raises the possibility that lower levels might arise sometimes—perhaps frequently—as reversals from higher-level organisms (Dewel, 2000; McShea, 2001*b*).

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