

The hierarchical structure of organisms: a scale and documentation of a trend in the maximum

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Abstract.—The degree of hierarchical structure of organisms—the number of levels of nesting of lower-level entities within higher-level individuals—has apparently increased a number of times in the history of life, notably in the origin of the eukaryotic cell from an association of prokaryotic cells, of multicellular organisms from clones of eukaryotic cells, and of integrated colonies from aggregates of multicellular individuals. Arranged in order of first occurrence, these three transitions suggest a trend, in particular a trend in the maximum, or an increase in the degree of hierarchical structure present in the hierarchically deepest organism on Earth. However, no rigorous documentation of such a trend—based on operational and consistent criteria for hierarchical levels—has been attempted. Also, the trajectory of increase has not been examined in any detail. One limitation is that no hierarchy scale has been developed with sufficient resolution to document more than these three major increases. Here, a higher-resolution scale is proposed in which hierarchical structure is decomposed into levels and sublevels, with levels reflecting number of layers of nestedness, and sublevels reflecting degree of individuation at the highest level. The scale is then used, together with the body-fossil record, to plot the trajectory of the maximum. Two alternative interpretations of the record are considered, and both reveal a long-term trend extending from the Archean through the early Phanerozoic. In one, the pattern of increase was incremental, with almost all sublevels arising precisely in order. The data also raise the possibility that waiting times for transitions between sublevels may have decreased with increasing hierarchical level (and with time). These last two findings—incremental increase in level and decreasing waiting times—are tentative, pending a study of possible biases in the fossil record.

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Introduction

A good case can be made for a trend in the degree of hierarchical structuring of organisms over the history of life. The principal evidence consists of two unambiguous instances of increase: the origin of eukaryotic cells from symbiotic associations of prokaryotic cells and the emergence of multicellular organisms from clones of eukaryotic cells. And arguably there has been a third, the advent of what might be called colonial individuals, or integrated societies, from associations of multicellular individuals. This sequence may represent a trend in hierarchy in a number of senses, but here the concern is mainly with a single sense, structural hierarchy, or the number of levels of nestedness of lower-level entities within higher-level individuals, of parts within wholes. The sequence also represents a trend of a special kind, a trend in the *maximum*, that is, an increase over time in the upper limit of hierarchical structure, or in the

number of levels present in the hierarchically deepest organism on Earth.

Even a cursory review of the paleontological evidence seems to confirm that the first two increases (and probably all three) occurred in the order listed: the first prokaryotic cells appear in the fossil record before the first eukaryotic cells and these before the first eukaryotic multicellular individuals. Given this evidence, it is difficult to doubt that a trend occurred. Indeed, the existence of a hierarchical trend of some sort has been widely acknowledged in evolutionary studies for more than a century (e.g., Spencer 1900, 1904; Needham 1943; Stebbins 1969; Wimsatt 1976, 1994; Corning 1983; Salthe 1985, 1993; Buss 1987; Bonner 1988; Swenson and Turvey 1991; Maynard Smith 1988; Maynard Smith and Szathmáry 1995, 1999; Szathmáry and Maynard Smith 1995; Pettersson 1996; McShea 1996a, 1998; Heylighen 1999; McShea et al. 1999; Knoll and Bambach 2000; Wright 2000). Also, a trend has often been a background assump-

tion, or a secondary theme, in contemporary discussions of “levels of organization” or “integrative levels” (in the sense of Redfield 1942; Novikoff 1945; Fiebleman 1955; Polanyi 1968; MacMahon et al. 1978) and “levels of selection” (in the sense of Maynard Smith 1988; Brandon 1996, 1999; Keller 1999), as well as in discussions of the “major transitions” in evolution (Maynard Smith and Szathmary 1995, 1999; Szathmary and Maynard Smith 1995).

However, rigorous documentation of the trend is not straightforward and indeed, to my knowledge, has never been attempted. The main difficulty lies in developing a proper scale for measuring hierarchical structure, or more precisely, in devising a set of criteria for levels that is both operational and consistent. Operational criteria—which for fossils means morphological criteria—are required for objectivity. Without operational criteria for the multicellular level, for example, we have no way to determine objectively which fossil occurrence corresponds to the first multicellular organism. Consistency is also important. We need a single set of criteria that can be applied to organisms at all levels, across the hierarchy spectrum, from prokaryotic cells to colonies of multicellular individuals. It might be tempting to adopt a unique set of criteria for each level, for example, a nucleus and a cytoskeleton as criteria for the eukaryotic-cell level and the presence of tissues for the multicellular level. The problem with this approach is that it would leave us with no common scale, and the various transitions would not represent change in the same dimension.

Beyond these two minimal requirements, another virtue in a structural hierarchy scale would be high resolution. As conventionally configured, the scale recognizes only four hierarchical levels—at least among those for which fossil evidence of first occurrences is available—and therefore three increases over the history of life. Thus, even with operational and consistent criteria, very little could be said about the pattern of increase, about changes in rate of increase, for example.

Here I propose a scale that is operational in that the criteria on which it is based are morphological (and can therefore be applied to fossils). It is also consistent in that the criteria

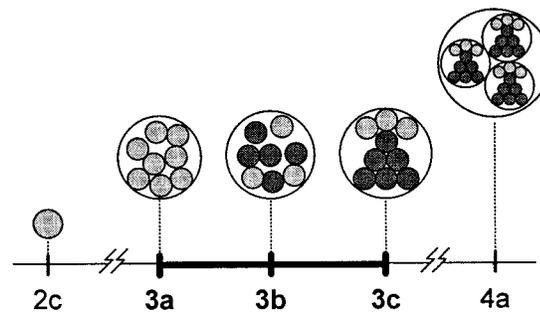


FIGURE 1. Schematic representation of the third level of nestedness (arbitrarily chosen), showing its sublevels based on degree of individuation: 3a: monomorphic aggregate of level-2 entities; 3b: differentiated aggregate of level-2 entities; 3c: differentiated aggregate of level-2 entities with intermediate-level parts. An intermediate-level part can be either a single elaborated or enlarged lower-level entity or a subgroup of two or more lower-level entities; in the figure, there are two of the latter type.

can be applied to all levels, across the hierarchy spectrum. Further, the scale offers moderately high resolution in that the four conventionally recognized levels are each subdivided into three discrete sublevels. (As will be seen, the scale also has a number of limitations.) I then use the scale to document a trend in maximum hierarchical structure using the fossil record.

It should be pointed out that a low-resolution scale has been developed recently by Pettersson (1996). His scale is based on two criteria for hierarchical levels, what he called the “compositional criterion” and the “duality criterion” (see below), both of them operational and consistently applicable. However, Pettersson provided only very rough estimates of first occurrences and did not describe the fossil evidence on which his estimates were based. (See Pettersson 1996: Fig. 2.4.) The scale I propose includes Pettersson’s criteria, among others, and thus could be understood as a further development of his approach.

Complexity.—Hierarchical structure is an aspect of complexity, which in turn is often understood in a broad sense as a kind of summary term for organismal features associated with adaptedness, sophistication, intelligence, or progress generally (e.g., Wright 2000). My concern is only with complexity in a narrow sense, having to do with physical structure, or with what I have elsewhere called “object

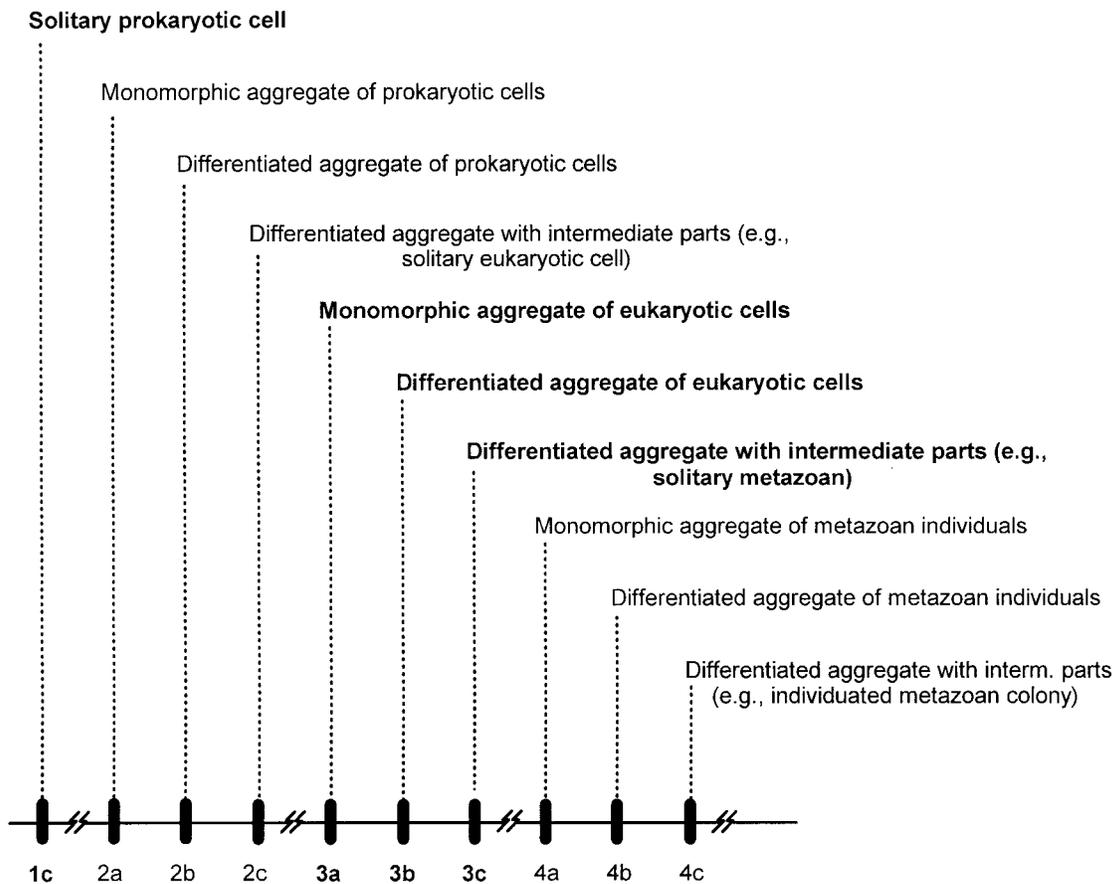


FIGURE 2. An expansion of Figure 1, showing the hierarchical range considered here, with examples of organisms occupying each level. Criteria for sublevels, examples, and interpretative conventions are as follows: (1) Level a: monomorphic aggregates. These are aggregates of two or more lower-level entities that remain reliably attached over some significant portion of their existence, e.g., longer than the time required for mating. Examples: 2a: filamentous cyanobacteria (e.g., *Oscillatoria*) in which all cells in the filament have approximately the same morphology; 3a: undifferentiated aggregates of eukaryotic cells (*Gonium*); 4a: colonies of the major zoantharian coral groups, in which polyps and corallites are essentially undifferentiated. (2) Level b: differentiated aggregates. These are attached aggregates with two or more different morphological types. (Convention: as in various studies of numbers of part types, degree of differentiation among types is assessed subjectively [Cisne 1974; Bonner 1988; Valentine et al. 1994].) Examples: 2b: heterocystous cyanobacteria (*Anabaena*); 3b: various multicellular algae, such as the xanthophycean *Vaucheria*, which has differentiated vegetative cells and spores; 4b: dendroid graptolites, which had two or more zooid types. (Convention: haploid cells, such as sex cells, in diploid organisms do not count as differentiated types.) (3) Level c: differentiated aggregates with intermediate-level parts. To qualify, parts may consist either of a subgroup of two or more lower-level entities or a single lower-level entity that is hypertrophied or elaborated in various ways. Examples: 2c: modern eukaryotic cells; the portion of the cell that is homologous with the original archaeobacterial host plus structural additions, including microtubular structures, intracellular membranes, etc., but excluding former endosymbionts (e.g., mitochondria, chloroplasts), is an elaborated lower-level entity; 3c: tissue- and organ-grade metazoans, with tissues and organs constituting subgroups of cells; 4c: cyclostome bryozoan species with clusters of nonfeeding zooids (or lower densities of feeding zooids), called maculae (Boardman and Cheetham 1987; Taylor 1999), possibly functioning as excurrent chimneys for the colony as a whole (Banta et al. 1974). (Convention: in prokaryotic cells, identifying intermediate-level parts is not straightforward, but subjectively the cells are highly individuated and therefore assigned to level 1c, rather than 1a or 1b.)

complexity" (McShea 1996a,b). Further, it is only with the hierarchical aspect of structure, or what Sterelny (1999; see also Sterelny and Griffiths 1999) has called "vertical complexity," and not (directly) with "horizontal com-

plexity," number of types of parts at a given level (e.g., Cisne 1974; Bonner 1988; McShea 1993; Valentine et al. 1994).

The exclusive focus on structure may strike some as overly limiting, especially insofar as

it overlooks the developmental or genetic processes involved in the generation of structural hierarchy (many of them also hierarchical, but in a different sense [see Salthe 1993; Raff 1996; McShea 1996a,b; Arthur 1997]) and the ecological circumstances in which hierarchical structure arises. However, the omission reflects a deliberate strategy of avoiding compound concepts, of keeping variables distinct, which is necessary initially in order ultimately to study the relationships among them. For example, to investigate the relationship between the structural and developmental hierarchies in organisms, we would need to be able to assess each independently. Thus, the treatment here could be understood as a first step in a number of such investigations, offering a way to measure objectively one of the relevant variables, structural hierarchy.

Related Work.—This treatment differs from the various studies of particular episodes of hierarchical increase, such as the origin of the eukaryotic cell. Here the focus is at a larger scale, on features common to all hierarchical transitions. It also differs from the various studies of the mechanism involved in transitions (e.g., Leigh 1983, 1991; Salthe 1993; Maynard Smith and Szathmáry 1995; Szathmáry and Maynard Smith 1995; Michod 1999), because my concern is with the detection and measurement of hierarchical structure rather than how it arises.

Finally, an important difference with the conceptual scheme developed recently by Maynard Smith and Szathmáry (1995, 1999; Szathmáry and Maynard Smith 1995) needs to be pointed out. They offered a list of eight “major transitions,” including the three discussed above, most (but not all) of which involve lower-level entities joining to form a higher-level individual, i.e., increases in structural hierarchy. However, another common feature of most of their transitions, and the one to which they drew attention, was that lower-level entities lose the ability to replicate independently. Based on *this* criterion, their scheme constitutes what might be called a process hierarchy (McShea 1996a,b) or a control hierarchy, rather than a structural hierarchy; in other words, their concern is with a fundamentally different phenomenon.

A Hierarchy Scale

The scale is based on a conceptual decomposition of hierarchical structure into two components, number of levels of nestedness and degree of individuation of the entity at the highest level.

Nestedness.—Nestedness refers to physical containment or inclusion: a higher-level individual contains entities from the next lower level, and includes them as parts. Thus, the nestedness criterion is comparable to Pettersson’s (1996) “compositional criterion,” which requires that higher-level entities materially consist mainly of entities at the next lower level. (See also inset 4 of the figure in Bunge 1959; Simon 1962; Pattee 1970; Salthe 1985, 1993; Valentine and May 1996; McShea 1996a,b.) To this I add a requirement that lower-level entities be bounded, and also a further requirement that lower-level entities be spatially aggregated and attached to each other, an indication that they interact in some way and that their behaviors are correlated (Campbell 1958; McShea and Venit 2001). The effect of both requirements is to limit consideration to higher-level individuals that are manifest as objects and in which nestedness is a directly observable topological relationship.

Real systems are hierarchically deep, perhaps bottomless, and therefore a count of number of levels of nestedness must be relative to some arbitrarily chosen starting point. Here, the starting point is the prokaryotic cell and its level of nestedness arbitrarily designated level 1. The second level of nestedness, level 2, is occupied by aggregates of prokaryotic cells (e.g., eukaryotic cells), level 3 by aggregates of level-2 organisms (e.g., eukaryotic multicellular organisms), and level 4 by aggregates of level-3 organisms (e.g., colonial individuals).

Implicit in this numbering scheme is a requirement that lower-level entities must be homologous with organisms in a free-living state, either extant or extinct. (This requirement appears to correspond closely with Pettersson’s [1996] “duality criterion” and has the effect of limiting occupation of levels of nestedness to present and former “levels of selection,” in Brandon’s [1999] sense.) A conse-

quence is that certain sorts of intermediate-level parts that might seem to represent levels of nestedness are deemed to lie between numbered levels and thus are not assigned levels of their own. For example, in a multicellular organism, a segment, tissue, or organ that has been interpolated between a multicellular individual and the cell is not assigned to a level of nestedness. However, as will be seen, these structures do contribute to the individuation of entities at the next highest level, in this case the multicellular level.

Notice that the numbering scheme above would need to be realigned if actual, historical sequences of hierarchical change were discovered to differ in critical ways from the conventional view (as has been suggested by Dewel [2000]). For example, if a segment in an arthropod is actually homologous with some ancient multicellular organism at level 3, then an arthropod as a whole would constitute a highly individuated colony at level 4.

Two further points need to be made in connection with these criteria, the first concerning the requirement that lower-level entities be organized as attached aggregates. (The boundeness requirement is discussed later.) A higher-level individual could be present even where lower-level entities are unattached and somewhat dispersed (Gould and Lloyd 1999; McShea and Venit 2001), as in a social insect colony and perhaps in certain multispecies ecological associations (e.g., stromatolites). However, the pattern of interaction among parts that confers individuality at the higher level will generally be difficult to detect in fossils. For this practical reason, such somewhat dispersed colonies and ecological associations are excluded here (although including them may be possible in examinations of hierarchy in modern organisms).

The second point is that attached aggregates of lower-level entities may arise by any evolutionary route. They can arise by aggregation of independent lower-level entities, as probably occurred in the origin of the eukaryotic cell from disparate prokaryotic species. (Notice that members of an aggregate need not be related; the concern here is with what Eldredge and Salthe [1984] called the "ecological hierarchy" rather than the "genealogical hierar-

chy.") Aggregates can also arise by replication of a lower-level entity and continued association of its progeny, as may have occurred in the origin of the first aggregates of eukaryotic cells. Finally, they can arise by enlargement and partitioning of a single lower-level entity.

Individuation.—For each level of nestedness, we can recognize degrees of "individuation" (Salthe 1985) at the highest level, or the degree to which the highest-level entity in a nested sequence constitutes a unified whole. In principle, to operationalize "individuation," criteria could be drawn from those that have been devised on the basis of theory, such as connectedness (or integration), cohesiveness, isolation, the ability of entities at a given level to serve as boundary conditions for lower-level entities, and so on (Campbell 1958; Simon 1962; Hull 1980; Allen and Starr 1982; Salthe 1985; Mishler and Brandon 1987; Ghiselin 1997; Gould and Lloyd 1999; Wagner and Laubichler 2000; McShea and Venit 2001). However, many of these are difficult to measure using morphology alone. An alternative approach is to draw criteria from phenomenological studies of hierarchical transitions. Here I drew three from Beklemishev's (1969; see also Boardman and Cheetham 1973) list of morphological transformations involved in the emergence of colonial individuals, mainly in marine invertebrate colonies. Generalized to make them applicable to all levels, the selected criteria are: (1) connectedness (a generalization of what Beklemishev calls "integration"), (2) differentiation ("polymorphism"), and (3) the presence of intermediate-level parts ("cormidia"). In adopting these, the assumption is that they are correlates of the theoretical criteria.

Notice that other criteria could have been chosen from Beklemishev's list, or from other treatments of colony individuation (Boardman and Cheetham 1973; Coates and Oliver 1973; Cook 1979; Lidgard 1985, 1986; Lidgard and Jackson 1989); an expanded set of criteria might prove useful in future studies. Also, notice that the set of criteria adopted here is broader than that in an earlier paper (McShea 1996a), where individuation was a function of connectedness alone.

Figure 1 shows how these three individua-

tion criteria are used to define three sublevels, a, b, and c. Figure 2 and its caption provide examples and describe certain interpretative conventions.

The first and lowest sublevel, a, is occupied by undifferentiated (monomorphic) aggregates of lower-level entities in which the entities are attached, with attachment interpreted in this context as an indicator of at least minimal connectedness (first criterion above). The second sublevel, b, is occupied by connected aggregates in which the lower-level entities are differentiated (second criterion) into at least two different types. And at the third, c, are differentiated aggregates with intermediate-level parts (third criterion), or structures that are larger than a typical lower-level entity but a subset of the entire aggregate (Anderson and McShea in press).

For present purposes, intermediate-level parts are limited to those that contain at least one lower-level entity. Such a part might consist either of a subgroup of two or more lower-level entities or of a single lower-level entity that is enlarged or elaborated in various ways. Thus, certain intermediate-level objects are excluded, in particular those that do not contain even one lower-level entity, or what have also been called "extrazoooidal parts" (Boardman and Cheetham 1973). Examples are the sheaths enclosing cyanobacterial filaments and the mucilaginous masses embedding certain aggregates of eukaryotic cells (e.g., *Proterospongia*, a choanoflagellate).

Among the three criteria, connectedness is a special case. One reason is that attachment, a criterion for nestedness, is also treated as an indicator of connectedness, a criterion for individuation. A consequence is that, in effect, the individuation of a higher level of nestedness begins at the moment of its formation (Fig. 1).

Connectedness is also a special case in that, unlike differentiation and intermediate parts, we have prior reason to think that its relationship with individuation may not be monotonic. That is, while individuation presumably rises with moderate increases in connectedness—including increases beyond mere attachment, such as the advent of new channels for signaling or nutrient sharing (not consid-

ered here)—extreme connectedness may tend to undermine individuation and thus to undermine hierarchical structure (Wimsatt 1974; Anderson and McShea in press). It was for this reason that boundedness of lower-level entities was required for nestedness, to reduce the likelihood of *overconnectedness*. A consequence of this requirement is that multinucleate (coenocytic) eukaryotic cells—in which boundaries among nuclei are absent and connectedness is presumably extreme—are assigned to the same hierarchical level as mononucleate cells, even those multinucleate forms with structurally complex thalli (e.g., some dasyclad algae).

Alternative Theoretical Bases for the Scale.—The aggregation-differentiation-intermediate-parts sequence is an expected consequence of the emergence of a higher level of selection (in Brandon's [1999] sense), or in other words, of selection acting on a higher-level entity. (For general discussions, see Corning 1983, 1997; Leigh 1983, 1991; Buss 1987; Bonner 1988, 1998; Maynard Smith 1988; Sober and Wilson 1994; Brandon 1996, 1999; Keller 1999; Michod 1999; also see a recent special issue of *American Naturalist* [1997].) In particular, Bonner (1988) argued that the emergence of a higher-level individual is favored by selection for large size and further that size increase favors division of labor and therefore differentiation among lower-level entities (see also Corning 1983; Buss 1987; Bell and Mooers 1997). This argument might be extended to predict intermediate-level parts: as the size of the higher-level individual increases, the size of any single lower-level entity relative to the whole decreases, and therefore its ability to effectively perform functions for the whole, working alone, declines (Anderson and McShea in press). Thus, selection might favor collaborations among groups of lower-level entities, or enlargements and elaborations of single ones, i.e., intermediate-level parts.

The three criteria and their ordering are also consistent with the predictions of Spencer's (1904) metaphysic, with the logic of what he calls "general evolution." Spencer argued that systems of elements in which the dominant forces are aggregative tend to become differentiated as aggregation proceeds. One

reason is that elements within the aggregate are subject to different forces by virtue of their differing locations within the whole—e.g., internal versus external—and these differences in forces produce differentiation. His argument also predicts local integration of groups of similarly differentiated elemental types, a process that he calls segregation, and that could be construed to account for at least some kinds of intermediate parts.

Properties of the Scale.—1. The sublevels are designed as a logically dependent sequence, meaning that individuals meeting the criteria for a given sublevel also meet the criteria for all lower sublevels at the same level of nestedness. In other words, to qualify as a differentiated aggregate with intermediate parts (level Xc, where X is an integer), an organism must also be a differentiated aggregate (level Xb). And obviously, to be a differentiated aggregate, an organism must at least be an aggregate (level Xa).

However, logical dependence among the sublevels does not cross the boundaries between levels of nestedness; level X individuals need not be composed of level (X - 1)c entities but could instead be composed of (X - 1)b or (X - 1)a entities. More concretely, a kind of meta-association of bacterial cells—a simple aggregate of aggregates—would (if it existed) occupy level 3a, along with undifferentiated aggregates of eukaryotic cells, such as *Gonium* (in its vegetative phase) (see Kirk 1998; see also Fig. 2 caption). Thus, Figure 1 is misleading in that it creates the visual impression that the scale represents a single dimension. In fact, it has two dimensions, nesting and individuation.

Interestingly, however, in my review of the fossil record (see below), all organisms considered, at all levels (Xa, Xb, Xc), seemed to be composed of highly individuated lower-level entities, level (X - 1)c, or at least no exceptions were recognized. (Exceptions doubtless exist, but their rarity is, so far as I know, unexplained. Perceptual biases may be at work, but biological constraints may be worth investigating as well.) Thus, absent independent variation in nestedness and individuation, it seemed reasonable to collapse the two dimensions into a single scale. However, the breaks

in the horizontal axes in the figures are an acknowledgment and a reminder of the fact that two dimensions are represented.

2. The scale imposes no requirement on the evolutionary route that organisms must follow to reach a given level (logical dependence notwithstanding). In particular, there is no requirement that higher-level organisms arise in evolution by ascending the hierarchy scale one level or sublevel at a time. It should be obvious that sublevels can be skipped. For example, in the origin of the eukaryotic cell, probably a level-2b individual arose directly from level-1c individuals. At a higher level of nestedness, an analogous hierarchical transition occurs when a free-living eukaryotic cell adopts a eukaryotic cell of another species as an endosymbiont (Delwiche 1999), a jump from level 2c to 3b.

In contrast, skipping of whole levels of nestedness might seem impossible, in that the origin of a new higher level would seem to depend on the prior existence of entities at the next lower level. In fact, this is not the case; in principle, an individual at level of nestedness X could give rise directly to another at level X + 2, although the mechanistic barriers to such a transition are undoubtedly enormous. Of course, such an extraordinary event would not be classified as a two-level jump until an individual from level X + 1 assumed a free-living existence, but in principle this could happen later. The point is that, as a matter of logic, the order of first occurrences of levels is completely unconstrained.

3. The various sublevels are defined by different criteria, and therefore do not capture individuation in exactly the same sense. A consequence is that the “distances” between adjacent sublevels are not the same in any sense.

4. Finally, in this scheme, levels are not defined by organisms (Salthe 1985). For example, level 2c is not *defined* as the eukaryotic-cell level; rather, eukaryotic cells are said to *occupy* it. As will be seen, the first level-2c organism recognizable in the fossil record is a eukaryotic cell, but in principle it could have been a non-eukaryotic occupant of that level. Indeed, prokaryotes meeting the level-2c criteria are known today; for example, in the myxobacte-

rium *Chondromyces*, cells aggregate and differentiate to form a stalked fruiting body (e.g., Kaiser and Losick 1993). The stalk, for example, is an intermediate-level part, and therefore *Chondromyces* occupies level 2c.

It is worth recalling in this context that the scale and its criteria are concerned only with structural hierarchy, and therefore many of the key innovations exhibited by organisms, including many with profound functional significance, will not be directly relevant in assessing the hierarchical level they occupy. Or at least, any significance they have as indicators of structural hierarchy is not a direct consequence of their functional significance. For example, many innovations occurred in the evolution of the eukaryotic cell, but only two are relevant here for assessing its hierarchical level: (1) symbiotic association of distinct species of prokaryotic cells to produce, in effect, a differentiated prokaryotic aggregate; and (2) elaboration of one of the symbionts, the archaeobacterial host, with internal membranes, cytoskeleton, etc., to the point where the host qualified as an intermediate-level part. The cytoskeleton, for example, may have represented a key innovation in functional terms, but in structural-hierarchical terms it constituted only one element among many in the elaboration of the host.

Limitations.—1. Some aspects, or dimensions, of hierarchical structuring are not captured by the scale. In particular, consideration is limited to cases in which the entities forming aggregates are of similar hierarchical depth: prokaryotic cells forming aggregates with other prokaryotic cells, eukaryotic cells with other eukaryotic cells, etc. Thus, hierarchical organization that is produced by aggregates of individuals of *differing* hierarchical structure—such as associations between vertebrates or insects and their gut bacteria—is overlooked. Further, the scale, as understood here, is insensitive to certain topological differences that might seem hierarchically significant. For example, two very different topologies can be found at level 2c: eukaryotic cells in which some members of the aggregate lie inside another, and colonial myxobacteria, in which all members are external to each other.

2. Evaluation of hierarchical sublevel is

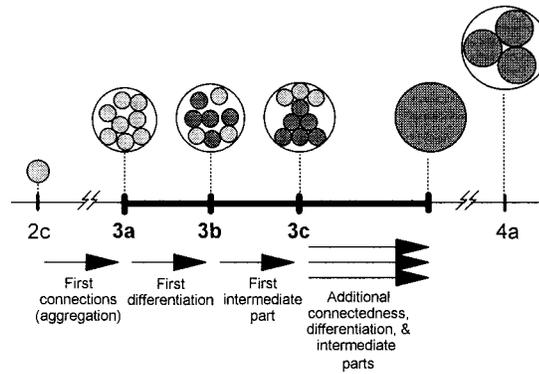


FIGURE 3. A possible expansion of the portion of the scale shown in Figure 1. On this modified scale, higher levels of individuation can be assessed, i.e., space is created to the right of sublevel 3c in which to plot organisms with greater connectedness than that required for aggregation and attachment, with differentiation of lower-level entities into more than two types, or with more than one intermediate-level part; see text. Thus, the circle at level 3c might represent *Volvox*, a cell aggregate with two cell types and a single intermediate part (vegetative cells organized to form a flagellated shell), while the fully shaded circle to the right might represent a more individuated multicellular organism such as a mollusk or an echinoderm, i.e., one with greater connectedness, more cell types, and more intermediate parts. The scale for levels 1, 2, and 4 could be expanded in the same way.

based on degree of individuation only at the highest level, and therefore losses at lower levels—e.g., losses of differentiated parts in the cells of multicellular organisms (e.g., human hemocytes) (McShea in press)—do not register.

3. The scale, as configured in Figures 1 and 2, captures only the initial steps in the formation of hierarchical structure, the first formation of connections (i.e., aggregation), the first incidence of differentiation, and the first intermediate part. And thus further increases in connectedness, differentiation, and intermediate structuring are overlooked. As a result, a highly individuated bilaterian, such as an octopus, registers as no more complex hierarchically than an anemone; both lie at level 3c. Figure 3 shows one way that the scale could be expanded to distinguish higher levels of individuation. Also, the scale overlooks other indicators of increased individuation, such as the advent of extrazoidal parts (see above). In principle, other indicators could be incorporated either by increasing the dimen-

sionality of the scale or, if logical dependence could be preserved, by adding further sublevels—d, e, f, etc.

4. Even using morphological criteria, hierarchical classification of certain organisms will inevitably be somewhat subjective. Developing a perfectly operational scale would be easy if organisms were organized like certain artificial systems, especially those in which hierarchical structure has been engineered, such as nested boxes. However, organisms are hierarchically complex to some extent (Wimsatt 1974), in ways that will occasionally confound any morphology-based scheme, including this one. Given these limitations, it is worth emphasizing that the scale is a first attempt, and that others are possible, some perhaps less problematic.

A Trend in the Maximum

The following procedure was used to document a trend in the maximum. A list of candidates for first occurrences (not shown) was drawn from the paleontological literature, and each was assigned to a hierarchical level based on its morphology. Then the list was ordered according to time of first occurrence and culled to leave only first occurrences for each level (Table 1; see Appendix for rationales for level assignments).

Only body fossils were considered. And inferences regarding the structure of fossil species were in many cases based on analogy with modern representatives. For some first occurrences, other methods could have been used. For example, molecular clocks have been used to date the origin of the Metazoa (Wray et al. 1996), and molecular markers have been used to establish the first occurrence of organisms with certain features of eukaryotic chemistry (Brocks et al. 1999), and therefore possibly the first occurrence of eukaryotic cells. However, for consistency—so that all data would be subject to the same sources of error—the body-fossil record was not supplemented with inferences based on these methods.

Owing to imperfect preservation, some candidates for first occurrences could not be assigned with confidence to any single hierarchical level, especially those that may have no

modern analogue. In these cases, a range of possible hierarchical levels was assigned. For example, the Ediacaran *Rangia* has been interpreted as a pennatulacean octocoral (Jenkins 1985) (level 4c). But the Ediacaran frondlike forms as a group have also been interpreted as having a quilted, pneumatic structure (Seilacher 1989), hierarchically equivalent to a multinucleate eukaryotic cell (level 2c). To take these uncertainties into account, two lists of possible first occurrences were compiled, one by assigning each candidate to the highest hierarchical level in its range, i.e., taking a “permissive” view of its morphology (left group of columns in Table 1), and the other by assigning each to the lowest level in its range, i.e., a “restrictive” view (right group).

First occurrences for the permissive and restrictive views are graphed in Figure 4. Both sets of data points show a long-term trend, a pattern of increase in hierarchical structure extending over the Precambrian and into the early Phanerozoic. The lines in the figure are outer envelopes that show the trajectory of the maximum on the assumption that a hierarchical level, once achieved, was never lost. Extinction is common and the loss of all species occupying a level is always a possibility, but the protocol is probably appropriate for the Archean and Proterozoic in which absence from the record is likely to be an especially poor indicator of real absence. Notice that the fitting of outer envelopes eliminates decreases, forcing the trajectories to be monotonic, but that all increases are real (i.e., not produced by the method). Thus, the observed trajectories are evidence against a number of possible alternatives, such as an early, rapid increase in maximum hierarchical structure followed by long-term stasis.

The difference between the permissive and restrictive envelopes shows the uncertainty associated with assigning hierarchical level. But it should be noted that there are other sources of error, such as that associated with dating fossil specimens (although accuracy and precision have improved in recent years [Bowring and Erwin 1998]). Also, the maximum is a statistic that is very sensitive to sample size, and the density of fossil occurrences is extremely uneven over the Precambrian

TABLE 1. Possible first occurrences of hierarchical levels.

Hierarchical level	Level description (principal occupants)	Permissive view				
		Description	Alternative interpretations	Source for interpretation	Stratigraphic unit	Date (Ma) (source)
1c	Solitary prokaryotic cell	Spheroids resembling cyanobacteria	Nonfossils	Walsh 1992	Onverwacht Group, Barberton Mountain Land, South Africa	3445 to 3416 (Walsh 1992)
2a	Monomorphic aggregate of prokaryotic cells	Carbonaceous filaments		Schopf and Packer 1987	Apex Basalt, Warrawoona Group, Western Australia	3465 (Schopf 1993)
2b	Differentiated aggregate of prokaryotic cells	<i>Archaeoellipsoides</i> ; akinetes of nostocalean cyanobacteria		Amard and Bertrand-Sarfati 1997	Franceville Group, Gabon	2065 (Amard and Bertrand-Sarfati 1997)
2c	Diff. aggr. with intermediate parts (euk. cell)	<i>Kildinosphaera</i> , <i>Leiosphaeridia</i> ; sphaeromorph acritarchs	2a	Zhang 1986	Chuanlinggou Fm., North China	1900 to 1800 (Knoll 1992; Porter and Knoll 2000)
3a	Monomorphic aggregate (simple euk. cell aggr.)	<i>Grypania</i> ; spirally coiled eukaryotic cell	2c	Han and Runnegar 1992	Negaunee Fm., Michigan	2100 (Han and Runnegar 1992) to 1850 (Porter and Knoll 2000)
3b	Differentiated aggregate (diff. euk. cell aggr.)	Bangiophyte red alga; unbranched uniseriate filaments	3a	Butterfield et al. 1990	Hunting Fm., Somerset Island, Canada	1250 to 1100 (Kah et al. 1999)
3c	Diff. aggr. with intermediate parts (multicellular individual)	Megascopic, carbonaceous, leaf-shaped algae	?	Zhu and Chen 1995	Tuanshanzi Fm., North China	1850 to 1600 (Zhu and Chen 1995)
4a	Monomorphic aggregate (simple colony)	Moorowipora, Arrowipora; cerioid corals		Sorauf and Savarese 1995; Scrutton 1997	Lower Cambrian (Botomian), Moorowie Fm., South Australia	519 to 510 (Bowring and Erwin 1998)
4b	Differentiated aggregate (differentiated colony)	Dendroid graptolites		Berry 1987	Various Middle Cambrian	509 to 500 (Bowring and Erwin 1998)
4c	Diff. aggr. with intermediate parts (colonial individual)	Charniodiscus, e.g., frondose pennatulacean octocorals	2c	Jenkins 1992; also Jenkins and Gehling 1978; Conway Morris 1993	Mistaken Point, Newfoundland, Canada	565 (Grotinger et al. 1995)

TABLE 1. Extended.

Restrictive view				
Description	Alternative interpretations	Source for interpretation	Stratigraphic unit	Date (Ma) (source)
Carbonaceous filaments		Schopf and Packer 1987	Apex Basalt, Warrawoona Group, Western Australia	3465 (Schopf 1993)
<i>Archaeoellipsoides</i> ; akinetes of nostocalean cyanobacteria		Amard and Bertrand-Sarfati 1997	Franceville Group, Gabon	2065 (Amard and Bertrand-Sarfati 1997)
<i>Grypania</i> ; spirally coiled eukaryotic cell	3a	Han and Runnegar 1992	Negaunee Fm., Michigan	2100 (Han and Runnegar 1992) to 1850 (Porter and Knoll 2000)
Bangiophyte red alga; unbranched uniseriate filaments	3b	Butterfield et al. 1990	Hunting Fm., Somerset Island, Canada	1250 to 1100 (Kah et al. 1999)
<i>Palaevaucheria</i> ; xanthophyte algal filaments with septate termini		Woods et al. 1998	Lakhanda Fm., Siberia	>1000 (Rainbird et al. 1998)
<i>Nimbia</i> , <i>Vendella</i> , <i>Irridinitus</i> ?; oldest Ediacaran-like forms		Hofmann et al. 1990	Twitya Fm., NW Canada	600 (Hofmann et al. 1990; Grotzinger et al. 1995; see text)
<i>Moorowipora</i> , <i>Arrowwipora</i> ; cerioid corals		Sorauf and Savarese 1995; Scrutton 1997	Lower Cambrian (Botomian), Moorowie Fm., South Australia	519 to 510 (Bowring and Erwin 1998)
Dendroid graptolites		Berry 1987	Various Middle Cambrian	509 to 500 (Bowring and Erwin 1998)
<i>Dianulites</i> ; stenolaemate bryozoan		Taylor and Wilson 1999	Lower Ordovician (Arenigian), Fillmore Fm., Utah	483 (Bowring and Erwin 1998)

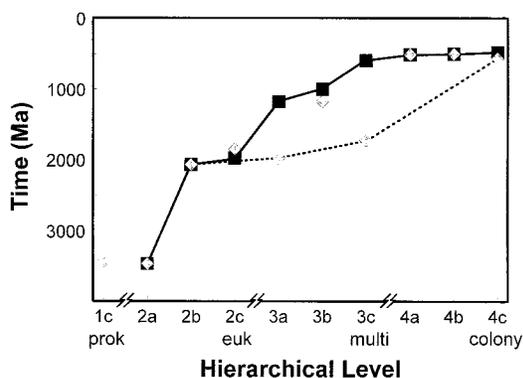


FIGURE 4. The trajectory of maximum hierarchical structure (horizontal axis) over time (vertical axis). Absolute ages are based on recent published estimates for the stratigraphic unit in which the specimen was found (see Table 1); uncertainties in dating were accommodated using range midpoints. The diamonds show first occurrences based on a permissive view, with each candidate organism assigned to the highest hierarchical level in its range; the squares shows the trajectory based on a restrictive view, with each assigned to the lowest level in its range (see text). The data points coincide in cases where the same taxon qualified in both views as a first occurrence of the same level (levels 2a, 2b, 4a, 4b). The lines are outer envelopes showing the trajectories on the assumption that the maximum did not decrease, i.e., that a hierarchical level, once achieved, was never lost: dotted line = permissive; solid line = restrictive; see text. The first data point, for solitary prokaryotic cells (level 1c), was not included in either outer envelope, because its first known occurrence slightly postdates the first prokaryotic filaments (level 2a).

(Schopf 1992a). Thus, the data set should also be taken as a first attempt, one that will doubtless need to be modified in light of future fossil finds and reinterpretations.

The possibility of systematic bias also gives some reason for skepticism. For example, suppose that the highest level considered here, 4c, had actually arisen very early (contrary to Figure 4), perhaps in a series of rapid steps early in the Archean, with the maximum remaining stable since that time. Further suppose that the probability of any given organism appearing in the fossil record has increased over time (perhaps because of an increase in preserved volume of sedimentary rock) and that species at higher levels tend to have much smaller population sizes than those at lower levels. In that case, the sparse early record might contain only representatives of the large-population taxa at low hierarchical levels, the more complete later record might contain the entire range of levels, and the maximum would ap-

pear to increase over time. It would be very surprising if this or any other bias was sufficient to produce the appearance of a trend where none existed. However, pending a study of possible biases, all interpretations of the details of the pattern in Figure 4, including those that follow, should be considered tentative.

These problems acknowledged, suppose that the data do accurately report the timing of first occurrences. First, notice that all sublevels between solitary prokaryotic cell (level 1c) and colonial individual (level 4c) are occupied. This need not have been the case, because sublevels can be skipped in evolution, as discussed. Second, notice that the levels of nestedness arise in order; i.e., level 2a predates level 3a, which in turn predates level 4a. This was not logically necessary, as discussed, but it is unsurprising on the assumption that a higher-level individual at any given level of nestedness would arise most readily as an aggregate of entities from the next lower level. What is more surprising is that, at least in the restrictive view, *sublevel* first occurrences also fall (almost) in order. (Level 1c is the lone exception.) One obvious explanation is that for individuation as well as for nestedness, skipping of levels occurs with much lower probability than incremental (single-sublevel) increases.

Interestingly, this incremental increase in the maximum is not produced by a single lineage. In other words, there is no single extreme lineage that mounts the hierarchical ladder one rung at a time, producing an incremental rise in the maximum with each step. Rather, most first occurrences appear to be representatives of different and often distantly related groups. For example, in the restrictive view, the first representative of level 4a is a coral, but the first representative of 4b is a graptolite, and the first 4c is from yet another group, the bryozoans. One possible explanation is that the rise in the maximum is a mass effect, i.e., produced by many lineages, each occasionally increasing (and perhaps decreasing) in hierarchical structure, such that no single lineage is able to dominate the maximum consistently. (See the discussion in Gould [1996] of "ladders" and "bushes" as alterna-

tive representations of trend dynamics.) Further investigation of the precise dynamics underlying the trend would require examining the transitions involved at the lineage level, i.e., in a phylogenetic context.

Three cautionary notes are in order regarding Figure 4. First, the overall shapes of the envelopes are not meaningful, because the distances between adjacent sublevels on the horizontal axis are not comparable, as discussed. Second, the termination of the trend at level 4c, in the early Phanerozoic, has no significance, because the possibility of organisms at levels higher than 4—aggregates of colonial individuals, differentiated aggregates of colonial individuals, etc.—was not considered. Thus, the data convey no information relevant to such interesting questions as whether or not an upper limit of hierarchy has been reached (McShea 1996a).

Third, a current issue in the literature has been whether or not hierarchical change at the lineage level is directional, whether or not hierarchical increases are more probable than decreases among lineages. Various arguments have been offered that suggest a directional bias, including the suggestion that increase is more probable because it is expected to be favored by selection (e.g., Bonner 1988, 1998; see also Sterelny 1999; Sterelny and Griffiths 1999; Knoll and Bambach 2000). However, the suggestion has also been made that change is unbiased, and that the increase in the maximum is a result of diffusion, perhaps in the presence of a lower bound (Gould 1996; McShea 1994, 1996a, 2000; cf. McShea et al. 1999). The point to be made here is that an increase in the maximum is consistent with both possibilities and provides no evidence one way or the other.

Waiting Times.—Based on the restrictive-view data, the time between successive hierarchical maxima, or “waiting times” for transitions between sublevels, decreases with increasing hierarchical structure (Fig. 5) and with time (not shown). (In the permissive view, many of the waiting times could not be computed, because first occurrences of higher sublevels preceded those for adjacent lower sublevels.) In principle, the decrease could be mainly an artifact of the decline in completeness of the fossil record with age. On the other

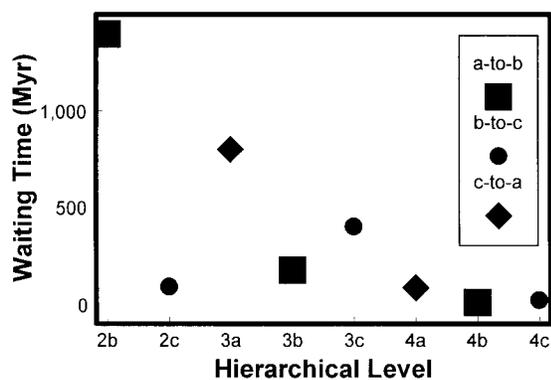


FIGURE 5. Relationship between waiting time and hierarchical level (restrictive view only), where waiting time for a given sublevel is the difference in time between its first occurrence and the first occurrence of the next lowest sublevel. Different symbols are used for the three different types of transition—a to b, b to c, and c to a.

hand, the null alternative—that average waiting times for both lower-level (earlier) and higher-level (later) transitions do not differ from the overall average for all transitions—seems unlikely. The average waiting time for the last three increases (3c to 4a, 4a to 4b, and 4b to 4c) is 39 million years. For new fossil finds to increase this value to reach the overall average for all transitions—368 million years—such finds would have to extend the range of highly individuated multicellular organisms (level 3c) back to about 1.6 billion years ago, a range extension of about 1 billion years.

In any case, proceeding as above, putting aside the uncertainty introduced by an incomplete record, suppose that the waiting times in Figure 5 are roughly accurate. One possible reason for the decline is diversity increase. The probability of increase in the maximum at any given time must be at least partly a function of the number of species available at that time to generate higher hierarchical levels. To examine this possibility further, we would need at least an approximate diversity curve, similar to those that have been produced for the Phanerozoic but for all life, extending back to the Archean.

Also, in the restrictive view, there are at least two notable declines in waiting time, one in the transition to level 2c and the other beginning with the transition to level 4a. These

are manifest in Figure 4 as decreases in slope (restrictive view) at about 2000 and 600 Ma (waiting times in Figure 5 are just the slopes of the line segments in Figure 4). These decreases correspond roughly with major increases in atmospheric oxygen, raising the possibility that oxygen was a trigger for hierarchical reorganization (A. H. Knoll personal communication 1999; Knoll and Bambach 2000).

Finally, Figure 5 reveals no obvious association between waiting time and type of transition. That is, no single type of transition—a-to-b, b-to-c, or c-to-a—stands out as requiring more time, on average, to occur than the others.

Discussion and Summary

The body-fossil record shows a long-term increase in maximum hierarchical structuring over the history of life. Further, in one of two alternative interpretations of the morphological evidence, the pattern of increase in the maximum was stepwise over time, with all sublevels except the first arising precisely in order. Under the same interpretation, waiting times between hierarchical transitions declined, both with increasing hierarchical structure and with time. It should be stressed that, given the enormous uncertainties in these data, all of these findings except the occurrence of the trend itself are highly tentative. Still, they do raise possibilities, some perhaps worth further investigation.

For most senses of complexity—such as complexity as number of different part types or depth of causal chains in development—I have argued elsewhere that there are reasons for skepticism about the existence of a trend at the scale of life as a whole (McShea 1996a). But for hierarchical complexity, a long-term trend—at least in the maximum—seems inescapable.

Still, it is worth pointing out that there is very little else that we can say with confidence about this system. The trajectories of other trend statistics, such as the minimum and the mean, are virtually unknown. Consider the minimum. Conventionally it is assumed that prokaryotic cells arose from chemical systems at lower hierarchical levels, which in turn

arose from systems at still lower levels, and so on (e.g., Maynard Smith and Szathmáry 1995). However, we do not know whether such lower-level systems have persisted, or whether they have been consumed or perhaps out-competed over time by higher-level systems, and thus, we do not know whether the minimum has remained stable or has increased. Even a *decrease* in the minimum, however improbable sounding, cannot be ruled out.

Our knowledge of the behavior of the mean is similarly meager. To estimate it, we would need approximate numbers of taxa occupying each hierarchical sublevel in a series of time slices spanning the history of life.

Also unknown is the underlying pattern of change among lineages. Some specific questions have been raised already, regarding the mechanism that underlies the incremental increase in the maximum and the existence of a directional bias at the lineage level in the direction of change. More generally, it would be interesting to know whether there are common patterns *within* levels of nestedness, for example, whether the hierarchical changes within level 2 (2a-to-2b and 2b-to-2c) have any common features, and if so, whether they differ in some systematic way from those within level 3 (3a-to-3b and 3b-to-3c). Also of interest is the possibility of common patterns *across* levels of nestedness, among transitions of particular types, for example, the possibility that certain ecological conditions might be required for the origin of differentiation among lower-level entities (the Xa-to-Xb transition). Addressing both of these broader issues would require a finer-scale examination of hierarchical changes than has been attempted here, i.e., again, examining change at the lineage level and in a phylogenetic context.

But a prerequisite, indeed a starting point, for investigating these unknowns is a way to assess degree of hierarchical structuring in organisms, a hierarchy scale. The scale developed here is a possible starting point.

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Appendix

Discussion of First Occurrences (Table 1)

Level 1c. Solitary prokaryote.—Walsh (1992) described spheroids from the Onverwacht Group, South Africa, in a size range similar to that of coccoidal cyanobacteria (level 1c) and larger ellipsoids and spheroids that could be either large solitary bacteria (1c) or sheaths of cyanobacterial colonies (2a). However, their simple morphology leaves open the possibility that they are abiogenic (Walsh 1992). Possible filamentous bacteria have also been found in the Onverwacht (Walsh and Lowe 1985); the filaments are nonseptate, which raises the possibility that they are elongated prokaryotic cells (1c), but regular breaks in the filaments suggests a series of cells within a sheath (2a) (Schopf 1992b). Other possible solitary bacteria of about the same age are also known (reviewed by Schopf and Walter 1983; see also Schopf 1992a).

Level 2a. Monomorphic aggregate of prokaryotes.—The carbonaceous filaments from the Apex Basalt, Western Australia, described by Schopf and Packer (1987; see also Schopf 1992a, 1993) are monomorphic (2a) and cyanobacteria-like. As noted, the Onverwacht filaments could be monomorphic colonies at level 2a, but the Apex specimens predate them in any case (Table 1), and thus the latter represents the first occurrence of this level in both the permissive and restrictive views.

Level 2b. Differentiated aggregate of prokaryotes.—Probable akinetes of nostocalean cyanobacteria occur in 2065-Ma cherts of the Franceville Group, Gabon (Amard and Bertrand-Sarfati 1997). The fossils are solitary cells but they resemble the spores of modern filamentous heterocystous cyanobacteria (e.g., *Anabaena*). Filaments in these prokaryotes have three cell types (including akinetes), one of them—called a heterocyst—specialized for nitrogen fixation (see also Golubic et al. 1995).

Level 2c. Differentiated aggregate of prokaryotes with intermediate-level parts (solitary eukaryotic cell).—In the permissive view, the first eukaryotic cells are the organic-walled microfossils, or acritarchs (Schopf 1992b), of the Chuanlinggou Formation, North China (Zhang 1986); the spirally coiled, carbonaceous megafossil, *Grypania*, of the Negaunee-Iron Formation, Michigan, is older, but in the permissive view occupies level 3a (see below). In the restrictive view, the Chuanlinggou acritarchs would be con-

sidered large prokaryotic cells or envelopes of prokaryotic colonies, leaving *Grypania* as the first occurrence of level 2c (assuming that it is unicellular [Han and Runnegar 1992]). (The 2000-Ma Gunflint forms are of uncertain affinity [Knoll 1992] and are excluded.)

Level 3a. Monomorphic aggregate of eukaryotic cells.—Specimens of *Grypania* that are younger than the Negaunee specimens show transverse markings suggestive of cell boundaries (Runnegar 1994). Thus, in the permissive view, *Grypania* is multicellular and occupies level 3a. In the restrictive view, the first level-3a organism is a red alga described by Butterfield et al. (1990) from the Hunting Formation (1250–1100 Ma) in arctic Canada. The alga is a bangiophyte, consisting of disk-shaped cells in either a uniseriate or multiseriate filament, with a multicellular attachment structure. The alga occupies level 3a only on the assumption that the cells of the attachment structure are not a distinct morphological type.

An older candidate for the first occurrence of level 3a was the possible *Hormosira*-like brown alga described by Grey and Williams (1990; see also Knoll 1992) from the Stag Arrow Formation of Western Australia and by Horodyski (1982, 1992) from the Appekunny Argillite of Montana (1400 to 1200 Ma [Yochelson et al. 1993]). However, these fossils—described as strings of cell-sized beads—are only impressions, not body fossils; in any case, their temporal range overlaps with that of the bangiophyte alga, and substituting them as first occurrences of this level would change the trajectory of the trend in Figure 4 very little.

Level 3b. Differentiated aggregate of eukaryotic cells.—If the cells of the attachment structure of the Butterfield et al. (1990) algae are differentiated (Butterfield 2000), then the organism has at least two cell types, and therefore occupies level 3b in the permissive view. Otherwise, in the restrictive view, the first differentiated aggregate of eukaryotic cells would be *Palaeovaucheria*, a xanthophyte alga from the Lakhanda Formation (>1000 Ma, but plotted at that date in Fig. 4) described by Woods et al. (1998). Filaments are coenocytic but septate at their termini, suggesting distinct cell types, possibly zoospores. Certain carbonaceous megafossils, *Chuarina* and *Taovia* and related taxa, were also candidates at this level, because they have been interpreted as metazoans (Hofmann 1994; Sun 1994). However, distinct cell types have not been described in these taxa, and therefore here they are elevated in the permissive view only to level 3a (at which they are predated by *Grypania*).

Level 3c. Differentiated aggregate of eukaryotic cells with intermediate-level parts (solitary multicellular individual).—In the permissive view, the first occurrence at this level could be the leaf-shaped, carbonaceous megafossils of the Tuanshanzi Formation, North China (1850–1600 Ma), described by Zhu and Chen (1995). The Tuanshanzi specimens consist of sheetlike blades with short stipes. They have internal features that Zhu and Chen described as “multicellular structures” and marginal features that they interpret as possible sporangia. If so, these features qualify as intermediate structures parts, placing the specimens at level 3c. However, evaluation of these observations is problematic in that I have been unable to find any substantial discussion of the degree of variability among the specimens, and to my knowledge no critical review has been published. Pending such a review, the assignment of these specimens to level 3c is tentative.

If the Tuanshanzi specimens are ultimately interpreted as belonging to a lower level, the time of first occurrence of level 3c (permissive view) would change dramatically. In that case, the first occurrence could be *Sinosabellidites* (Sun et al. 1986) from the Liulaobei Formation of eastern China (890–840 Ma, based on Piper and Zhang 1997), a carbonaceous compression with wormlike annulations. However, it too is problematic, its affinities controversial (Cloud 1986; Sun 1986, 1987; Sun et al. 1986; Glaessner 1987; Vidal and Moczydlowska 1987; Hofmann 1994).

If *Sinosabellidites* were also ultimately assigned to a lower level, the first occurrence of level 3c (again, permissive view only) would be the sausage-shaped *Valkyria* described by Butterfield et al. (1994) from the Svanbergfjellet Formation (800–700 Ma), Spitsbergen. The specimens appear to contain at least six cell types and perhaps multicellular structures, which they describe as possible tissues (and which would constitute intermediate parts).

For the restrictive view, the first level-3c organisms could be the small, Ediacaran-like disks of the Twitya Formation, northwestern Canada, described by Hofmann et al. (1990). They identified three forms, which they assigned to the genera *Nimbia*, *Vendella*, and *Irridinitus?*, and which, according to Narbonne et al. (1994), are similar to later medusoid forms widely acknowledged as cnidarian. For example, *Nimbia* has been compared with modern trachylinid hydrozoans, and *Vendella* with later Ediacaran medusoids, especially *Medusinites* (Hofmann et al. 1990), which Glaessner and Wade (1966) classified as a (presumably cnidarian) coelenterate. Consistent with this, Seilacher (1992) assigned a number of Ediacaran forms that others have also called medusoid—and which could conceivably include the Twitya forms—to the corals, the Psammocorallia. In any case, if the Twitya taxa are cnidarian, then they presumably had intermediate parts (e.g., tentacles, gastrodermis). Hofmann et al. correlate the Twitya formation roughly with the start of the Varanger glaciation, to which Grotzinger et al. (1995) assign a maximum age of 600 Ma.

The possibility that the Twitya forms are prokaryotic aggregates cannot be ruled out (Hofmann et al. 1990). If excluded on that basis, they would be replaced as the first occurrence of level 3c (restrictive view) by multicellular forms of about the same age, namely the algal thalli described by Xiao et al. (1998; see also Zhang 1989; Zhang and Yuan 1992) from the Doushantuo Formation (590–550 Ma), South China. The specimens—considered to be multicellular red algae—exhibit cell differentiation as well as distinct tissue types and multicellular reproductive structures (both of which are considered intermediate parts).

Level 4a. Monomorphic aggregate of multicellular individuals.—Following Hartman and Reisswig (1973; see also Simpson 1973), sponges are regarded here as noncolonial, and therefore the recently described demosponges from the 590–550-Ma Doushantuo Formation, South China (Li et al. 1998), attain only level 3c. As a result, the first occurrences of level 4a—monomorphic aggregates of multicellular individuals—are *Moorowipora* and *Arrowipora*, both cerioid colonies and probable corals from the Lower Cambrian (Botomian, 519–510 Ma) Moorowie Formation, South Australia (Savarese et al. 1993; Sorauf and Savarese 1995; Scrutton 1997). Another probable coral, *Tabulaconus*, a dendroid form from Western Canada and Alaska, occurred at about the same time (Handfield 1969; Debrenne et al. 1987; Scrutton 1997).

Certain of the frondose Ediacaran forms could be interpreted as undifferentiated (4a) or differentiated (4b) colonies, but the protocols adopted here consider only the two extreme interpretations: Seilacherian pneu structures (Seilacher 1989, 1992; see below), in which case they would be classified as large, syncytial eukaryotic cells (2c; or perhaps cell aggregates, 3a); and pennatulacean octocorals (see below), in which case they would be aggregates of multicellular individuals with intermediate parts (4c).

Level 4b. Differentiated aggregate of multicellular individuals.—Dendroid graptolites (e.g., *Dendrograptus*) with differentiated thecae—e.g., autothecae, bithecae—have been found in the Middle Cambrian (509–500) (Bulman 1970; see also Rickards 1979; Berry 1987).

Level 4c. Differentiated aggregate of multicellular individuals with intermediate-level parts (solitary colonial individual).—In the permissive view, the first level-4c organisms could be certain fronds of the Ediacaran fauna, for example *Rangaea* or *Charniodiscus*, which have been interpreted as pennatulacean octocorals (e.g., Jenkins and Gehling 1978; Jenkins 1985; Norris 1989; Conway Morris 1993; see also Dewel 2000). Modern pennatulaceans (sea pens) occupy level 4c in that they contain multiple zooid types (e.g., autozooids, siphonozooids), one of which constitutes an intermediate-level part, the single enlarged axial polyp that is modified to form the stem and base (Hyman 1940). Frondlike forms occur in the earliest post-Varanger Ediacaran assemblages (Jenkins 1992; Narbonne et al. 1994) at about 565 Ma (Grotzinger et al. 1995). The Ediacarans include other possible level-4c organisms, such as *Eoporpita*, *Chondroplon*, and *Ovatoscutum*, which have been interpreted as chondrophorine hydrozoans (Wade 1971, 1972; Jenkins 1984, 1992; Stanley 1986). In modern chondrophorines, such as *Velilla* and *Porpita*, the large central gastrozoid is an intermediate-level part, as discussed.

As mentioned, Seilacher (1989, 1992) argued that the Ediacaran fronds are not octocorals, but rather are quilted, pneu structures with no close modern relatives. And the affinities of the putative chondrophorines have also been questioned (Hofmann 1988; Norris 1989). Thus, in the restrictive view, these are replaced as the first occurrence of level 4c by the Early Ordovician (~483 Ma) stenolaemate bryozoan *Dianulites* from the Fillmore Formation, Utah (Taylor and Wilson 1999). *Dianulites* seems not to have had functionally differentiated polymorphs (Taylor and Wilson 1999), but some degree of differentiation among generations of zooids seems to be present in all stenolaemates (Boardman and Cheetham 1973); at very least, presumably the colony founder, the ancestrula, differed from later generations of zooids. Also, in *Dianulites*, there is evidence of intermediate-level parts in the form of maculae (see Fig. 2 caption).