Philosophica 59 (1997, 1) pp. 79-112

COMPLEXITY IN EVOLUTION: A SKEPTICAL ASSESSMENT

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ABSTRACT

A survey in the imagination of the history of multicellular animals suggests to many that *something* has increased. Is it complexity? Here, in a skeptical approach to this question, I give four operational definitions of complexity, and then show how each has been applied to organisms to test for a trend. Some evidence for increase exists for all four, although arguably not enough to make a conclusive case, which raises the question of whether the apparent increase has anything to do with complexity.

1. *Introduction*

"One of the most striking features of evolution is that it tends to produce organisms which are more and more complex" (Saunders and Ho, 1976, p. 375). The claim may sound plausible, perhaps even obviously true. But suppose we wanted to investigate it, that is, suppose we wanted to study seriously the problem of what it means for complexity to increase and to examine empirically its pattern of change over the history of life, or some large portion of it. How would we proceed? I can imagine two radically different approaches.

One would be to start with the widely shared intuition that *something* has increased in evolution, and to assign the word "complexity" to this unspecified something. We could then examine the history of life to try to determine precisely what the something is, in other words, to discover what complexity is. The approach seems reasonable, first because the impression of a trend seems to be a strong one for many people: modern organisms (notably, human beings) are often said to be more advanced, or more sophisticated, in some sense, than ancient ones (say, an early sponge species). Second, because we are unable at present to say exactly what feature is supposed to be increasing, the word that we choose for it should be somewhat vague and yet carry overtones of advancement, sophistication, and so on. For that purpose, complexity is almost ideal.

The approach might be characterized as "exploratory." A trend of some sort is assumed, and the goal is to *discover* what feature of organisms is increasing. Much of the substantial literature on evolutionary "progress" could be interpreted as an exploratory exercise of this sort, as an attempt to discover what it is that increased (e.g., Huxley, 1942, 1953; Simpson, 1967; Nitecki, 1988; see Ruse, 1996, for an historical treatment). And indeed, the word complexity is often used — at least in casual conversation — as a synonym for progress. (Often, I think, it is used as a kind of code word for progress, especially now that the term progress has been decried as unscientific [Gould, 1988a].)

An alternative approach is to define complexity *a priori*, and then to use this definition to examine patterns of change or to test for a trend over the history of life. This is the approach that is adopted in this review, and that is implicit in recent empirical studies of complexity (see below). For this approach to work, the definition of complexity chosen must be operational, that is, chosen in such a way as to make complexity measurable in organisms. For example, we might define complexity as number of different types of parts at a given hierarchical level. At the cellular level, this might be number of different cell types. Then, if we could establish cell-type numbers in ancient and modern organisms, we could test for a trend.

This second approach might be characterized as "skeptical." No trend is assumed. Rather, the point is to test whether or not a trend occurred specifically in complexity, as defined *a priori*.

Generally speaking, the skeptical approach sets a high standard of proof and takes a neutral stance (at least initially) on the subject of whether or not a trend in complexity occurred. More specifically, it adopts the following tactics: 1) It takes seriously the problem of sampling in an unbiased way. A case for increasing complexity has often been made by citing numerous instances of increase (e.g., Spencer, 1890; Rensch, 1960b), such as the increase in segment differentiation in arthropods, in folding of the vertebrate brain, and so on. But marshaling cases does not document a pervasive trend. The many increases could well be offset by an equal (or greater) number of decreases (McCoy, 1977), such as the loss of parts in the evolution of many parasites, the reduction in number of skull bones in vertebrates, and even reductions in behavioral (Sturmbauer et al., 1996) and brain complexity (e.g., Schmidt and Wake, 1997) in certain groups. To avoid this problem, the skeptic chooses organisms and structures to be compared randomly, which is to say, without regard for whether they will show an increase, decrease, or no change in complexity at all. (This is the tactic appropriate for investigating a trend in the mean; testing for a trend in the maximum would proceed differently: see below.)

2) The skeptic ignores the reigning consensus on complexity. Historically, a great many evolutionists have proposed that complexity increases, including Lamarck (1809), Darwin (1987), Spencer (1893), Rensch (1960a, b), Stebbins (1969), Saunders and Ho (1976, 1981), Bonner (1988), Arthur (1984, 1988), Heylighen (in press), and many others. However, the basis for the suggestion has usually been either wholly impressionistic or based on lists of instances of increase marshaled to build a case. In other words, the evidence has not been gathered in the skeptical mode. Indeed, some evolutionists have questioned recently whether the consensus has any solid empirical basis (Williams, 1966; Lewontin, 1968; Levins and Lewontin, 1985; McShea, 1991).

3) Finally, the skeptical approach allows only a very limited role for theory. A great many rationales have been offered for why complexity *ought* to increase in evolution. For example, Rensch (1960a, b; Bonner, 1988) argued that complexity should be favored by natural selection, because complex organisms are mechanically more efficient, having more parts and presumably greater division of labor among parts. Waddington (1969; Arthur, 1994; Heylighen, in press) suggested that as diversity increases, niches become more complex, and more complex niches are then filled by more complex organisms. Saunders and Ho (1976; Katz, 1987) contend that component additions are more likely than deletions, because additions are less likely to disrupt normal function. Various rationales based on thermodynamic principles have also been offered (Brooks et al., 1989; Weber et al., 1989). (Others are reviewed in McShea, 1991; In press.) The combined effect of all of these speculations has undoubtedly been to reinforce the impression of a trend, but the skeptic points out that they provide no support for the empirical claim that a trend in fact occurred.

Theory is nevertheless important in the skeptical approach. For one thing, it may play a role in choosing an operational definition; ideally we would measure some feature of organisms that our theories about organismal complexity predict will be significant in evolution.

1.1 Relative Merits of the Two Approaches

The exploratory and skeptical approaches are not mutually exclusive; both can be profitably pursued at the same time. In a sense, they are complementary. Of course, confusion is likely to result if we are not explicit in our analyses about how the term complexity is being used, about whether it is intended as a temporary name tag in an exploratory treatment or as a technical term with a precise meaning in a skeptical treatment.

Still, we can compare them. The skeptical approach has the advantage that its usage of the term complexity is clear and operational. A consequence is that in addition to testing for trends, other questions can be addressed objectively, such as whether complexity is correlated with size (Bonner, 1988; Bell and Mooers, 1997), taxonomic longevity (e.g., Boyajian and Lutz, 1992; Saunders and Work, 1997), or various environmental factors (Hughes and Jackson, 1990).

The skeptical approach has the disadvantage that the *a priori*, operational definitions it employs strike many people as shallow or incomplete; a common reaction is that complexity surely means more than just, for example, numbers of part types. The skeptic acknowledges this defect, but points out that it can be overcome if the investigator is persistent. That is, if a trend is not found in number of part types, the skeptic would try alternative operational definitions, such as complexity as number of functions, as computational ability (if it can be operationalized), and so on. The goal of these repeated efforts would be to find a biologically interesting definition, one that shows a trend, or at least captures complexity in the sense in which it is relevant to organisms and to their evolution. Thus, in the long run, the skeptical approach becomes — in its systematic elimination of alternatives — exploratory.

1.2 A Focal Question

This goal of this review is more limited. It is essentially a progress report on the skeptical approach, an assessment of where we stand presently in the skeptical project of testing for a trend in complexity. Four alternative (but related) operational definitions of complexity will be considered. The focus will be on multicellular animals (metazoans) over the Phanerozoic Eon — about the past 540 million years and the bulk of metazoan history for which we have substantial fossil evidence. The concern will be only with the complexity of organisms, and not of species or ecosystems. The goal is to assess the evidence for a trend in the mean for the Metazoa as a whole, although in pursuit of such evidence, patterns of change in various metazoan subgroups will be relevant also. A secondary focus will be the question of a trend in the maximum, of an increase over time in the complexity of the most complex metazoan species in existence.

1.3 Definitions, Evidence, Causes, and Limits

The paper has four parts: 1) First, I propose a general scheme for understanding complexity, and then four different *a priori* definitions — four types of complexity — based on it. Thus, in this scheme, the question of a trend will ultimately have four answers, not one. 2) Then, I describe some of the measures that have been devised for the four types and review the evidence for trends in each.

3) Another issue concerns the causes of trends, if trends in fact occurred. The standard explanation has been general tendencies driven by the supposed selective advantages of complex structure and development (Gould, 1994, 1996). But trends can also occur "passively," even if complexity is not generally advantageous. In this section, I explain these two categories of causes further and consider the evidence for each. 4) Finally, if trends occurred, they may have been short-lived; in other words, limits may have been reached, perhaps long ago. Here I review the available evidence.

This essay draws heavily upon, and updates, my earlier review (McShea, 1996a).

2. *A Priori Definitions*

Some broad definitions of complexity have been proposed. For example, the complexity of a system has been defined as the length of the shortest complete description of it (Löfgren, 1977; Papentin, 1980, 1982) or the length of the shortest algorithm that will generate it (Kolmogorov, 1965;

Chaitin, 1975). (For others, see Bennett, 1988, 1990.) For present purposes, however, all are too broad, or too general, to be sufficiently operational; none indicates unambiguously how to measure complexity in actual organisms. How would we calculate the length of the shortest algorithm that will generate a sponge?

The skeptic adopts a narrower view: the complexity of a system is some increasing function of the number of different types of parts or interactions it has. The opposite of complexity is simplicity; systems with few types of parts or interactions are simple. Thus, an organism and an automobile are both complex, both having many parts and interactions, while a raindrop and a rubber ball are simple. A similar view has been advocated by some theoreticians in biology (Hinegardner and Engelberg, 1983; Katz, 1986, 1988; Kampis and Csányi, 1987; Wicken, 1987; Heylighen, in press).

Notice that this view treats complexity as a purely "structural" property, in that complexity depends only on number of parts and interactions and not on their ability to perform functions. Thus, a working automobile and a demolished one, a live organism and a dead one, and a natural community and a compost heap, are all complex.

As it turns out, we have abundant theoretical justification for adopting a definition based on numbers of parts and interactions. That is, various theories have been proposed in which such numbers are taken to be significant for organisms: for example, number of parts might be correlated with number of functions (e.g., Heylighen, in press; also see McShea, 1991). But *conceptually*, complexity and functionality are still independent.

The words "order" and "organization" have often been used interchangeably with complexity, creating much confusion. For clarity, neither word will be used in this discussion.

2.1 Four Types of Complexity

Even narrowly defined as above, complexity is still not quite operational. To make it so, we can break it down into four types, based on two dichotomies: object versus process, and hierarchical versus non-hierarchical structure (McShea, 1996b). Thus, the four types are: 1) Non-hierarchical object complexity; 2) non-hierarchical process complexity; 3) hierarchical object complexity; and 4) hierarchical process complexity.

Objects and processes. Object complexity refers to the number of different physical parts in a system, and process complexity to the number of interactions among them. For processes, a collision between two billiard balls is simple, while an avalanche is complex. Parts do the interacting, but the interactions can be considered on their own, independent of the parts. Indeed, there is no necessary correlation; a single part may participate in essentially one interaction or many. In Figure 1, A has greater object complexity than B, because it has more different parts. C and D have the same object complexity, but D has greater process complexity.

In biology, the object might be the genome, and the parts genes or nucleotides, or it might be the entire organism (its entire morphology), and the parts cells or organs. Processes might be developmental, physiological, or behavioral and the component interactions might be morphogenetic events, metabolic steps, or individual behaviors, respectively. Here, object complexity refers mainly to morphology, and process complexity refers to development. For interesting treatments of behavioral complexity, see Pringle (1951), Cole (1985), and Sturmbauer et al. (1996).

Hierarchical and non-hierarchical structure. Hierarchical object complexity is the number of levels of nestedness of parts within wholes. A possible object hierarchy in biology is the sequence: ... organelle, cell, organ, organism ..., or what have classically been called "levels of organization." Upper-level entities or individuals physically contain the lower (Eldredge and Salthe, 1984; Salthe, 1985, 1993; O'Neil et al., 1986). In Figure 1, E and F might seem to have the same number of levels, but in E the upper level (large circle) is more "individuated" (see below), and thus E has (fractionally) more levels.

Hierarchical process complexity is the number of levels in a causal specification hierarchy (Salthe, 1993). An army chain of command is such a hierarchy, with the highest ranking officers issuing the most general orders, causing the lower ranks to give more specific orders. Likewise, development is (partly) a causal hierarchy (Arthur, 1988; Gould, 1993; Salthe, 1993). (See McShea [1996b] for further discussion.) In Figure 1, the arrangement of interactions is hierarchical in G but non-hierarchical in H.

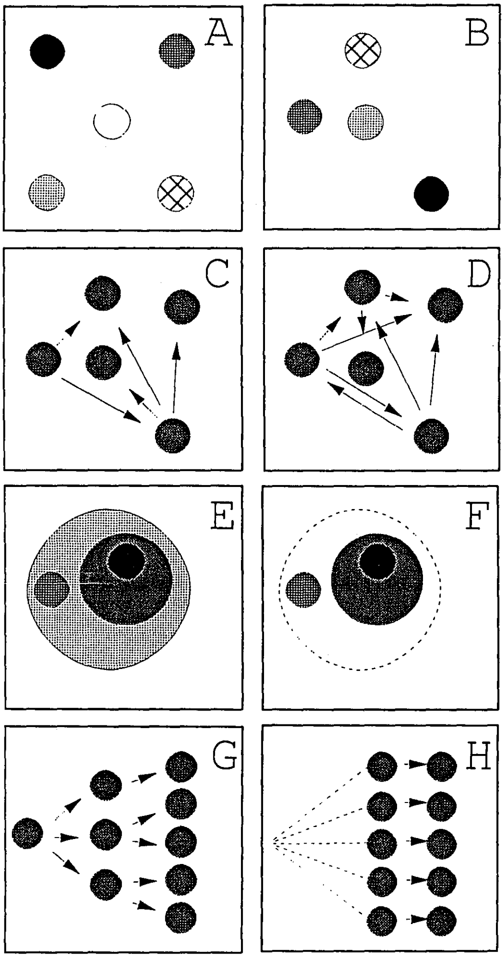

Figure 1. Types of complexity. A and B: object complexity (A>B); C and D: process complexity (D>C); E and F: hierarchical object complexity (E>F); G and H: hierarchical process complexity (G>H). (The dashed lines in H indicate that, in developmental systems at least, pathways may tend to converge to one or a small number of initiating events, and to the extent that this occurs, such systems are partly hierarchical. Still, at shorter time scales, interactions may occur independently, in parallel, as shown.)

Non-hierarchical object and process complexity refer to the number of parts and interactions, respectively, at a given spatial or temporal scale. It is thus a scale-relative property. No scalar level is privileged *a priori* (Salthe, 1985), and thus no system has a single true or essential non-hierarchical complexity. In particular, the molecular or genetic level in organisms is no more privileged than any other.

Configurational complexity. A third dichotomy could be recognized also, differentiation versus configuration. The four types of complexity above are differentiational; configurational complexity is irregularity of arrangement of parts and interactions (Katz, 1986). However, the configurational types have received little attention in biology (but see Yagil, 1985, 1995; McShea, 1992), and will not be considered here.

2.2 Objections

Complexity and function. Some will think it odd that complexity is not restricted to parts and interactions that are *functional*. However, our ignorance of function is profound in biology, and the attempt to separate the functional from the non-functional would be frequently frustrated. We do not know, for example, whether the placement of the human heart on the left or the number of fingers in the hand is functionally significant. One virtue of a purely structural definition is that complexity can be measured while judgments about function are deferred.

Also, a common notion is that functionality is most likely to occur in complex systems whose dynamics and structure occupy a middle range between monotonous regularity and chaotic irregularity (Kauffman, 1993; Packard, 1988; Langton, 1990). Accordingly, a complexity scale with some promise of biological relevance might be one on which such middle-range systems score highly. In principle, this notion could provide the basis for an *a priori* definition, but the skeptic can make no use of it until operational metrics applicable directly to organisms have been developed; so far, to my knowledge, they have not.

Complexity and entropy. The four definitions might seem to equate complexity with entropy. A compost heap is entropic in that a large number of different microstates (possible combinations and configurations of parts) correspond to the same macrostate, the same compost heap. But calling a compost heap complex for this reason would be a category mistake. (It *is* complex, as discussed earlier, but not *for this reason*.)

Entropy is a relationship between microstates and macrostates, while complexity is a property of a single microstate, of one specific composition and configuration, and involves no such relationship (Wicken, 1987). Complexity is not entropy.

Complexity and randomness. Some have argued that systems contain both a "regular" or rule-based component, and a "random" or arbitrary component (Crutchfield, 1991) and that only the differentiation of the rule-based portion ought to contribute to complexity. The precise number of hairs on a human arm is probably arbitrary, while a five-fingered hand is rule-based. This approach is actually consistent with a definition of complexity as number of types of parts or interactions. For example, to identify types of parts is to discern first-order regularities. More concretely, a decision that two cells are the same type can be construed as a decision that their similarities are rule-based and their differences not.

Complexity and generating mechanism. One suggestion has been that the complexity of a system ought to be a function of the process that generated it (e.g., Lloyd and Pagels, 1988). In biology, a common notion is that the complexity of an organism is the information content of its DNA, which is assumed to constitute a kind of generating mechanism. One problem is that much of the information in development is cytoplasmic and not present in DNA. Another is that simple systems can have complex generating mechanisms, and vice versa. For example, mayonnaise is a simple, homogeneous substance (at ordinary scales of observation), but it has a somewhat complex recipe (Rombauer and Becker, 1974). See McShea (1996a) for a discussion of DNA complexity and of the so-called "C-value paradox."

Other potential difficulties, such as the dependence of complexity on scale and on descriptive frame are also discussed in McShea (1996a).

3. *Evidence for Trends*

3.1 A Research Strategy

For investigating a trend in the mean, ideally a metric applicable to all metazoans would be developed for each type of complexity. However, a (nearly) universal metric has been devised only for non-hierarchical morphological complexity (number of cell types; see below). The alternative is to develop a variety of metrics, each targeting a specific group *within* the Metazoa. If a trend in the mean occurred in the Metazoa, it might emerge as a statistical regularity or bias, that is, significantly more groups might show increases than decreases. Most of the studies reviewed below fit neatly into this strategy.

A different sampling strategy is required in order to document a trend in the maximum, that is, an increase over time in the most complex metazoan in existence. Specifically, one might identify the instances in which the maximum is thought to have increased, and show that each in fact corresponds to an increase in complexity according to the *a priori* definition adopted. As for means, however, most of the studies reviewed below focus on trends within metazoan groups, rather than is the Metazoa as a whole.

3.2 Non-hierarchical Morphological Complexity

Measures. One measure is simply a count of number of different part types. For greater resolution, parts can be weighted by frequency of occurrence (e.g., Cisne, 1974). Where variation is continuous and types intergrade, complexity is degree of differentiation among parts, which is measurable using the range of variation, the variance, or a variance analogue (McShea, 1992). As a complexity measure, a variance could be construed as a way of counting parts that weights each according to its distinctiveness from a typical part, the mean.

Evidence. 1. Valentine et al. (1993) used cells as parts and measured complexity as number of cell types (see also Bonner, 1988). They plotted cell types for modern species against time of origin for their bodyplans (Fig. 2), using only modern species that were thought to be primitive representatives of their bodyplans. Only maxima were plotted, that is, only those primitive taxa that were thought to break the existing cell-type record at the time of origin of their bodyplan. The maximum increases, and since the minimum is stable (at one cell type), a trend in the mean seems inevitable as well.

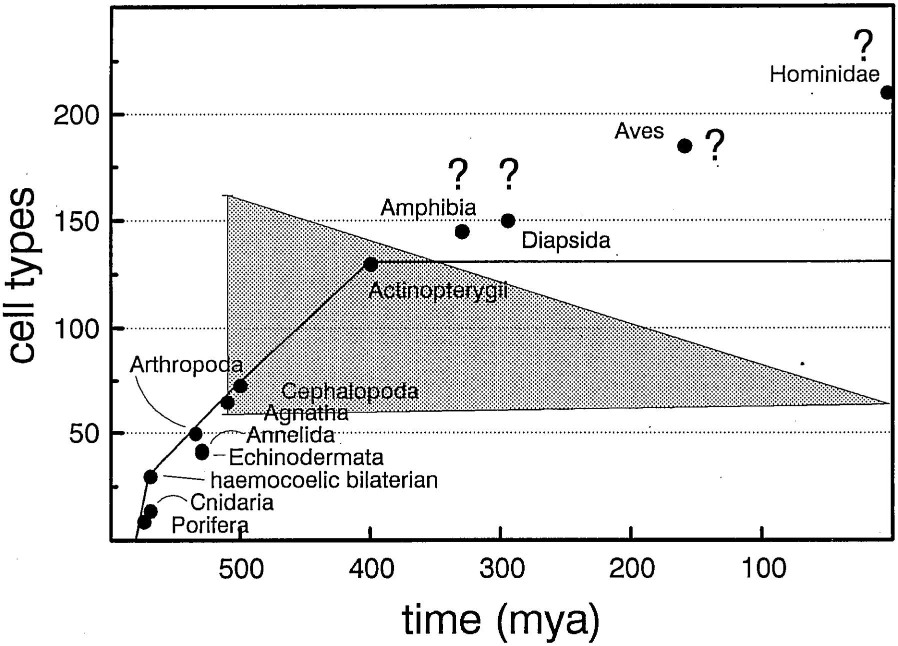

Figure 2. Cell-type counts for modern primitive members of certain groups, each plotted against time of origin for the group's bodyplan. Valentine et al. (1993) argue that the data show change in maximum number of cell types over time. Some annotations have been added: the question marks indicate taxa for which estimates may be too high because their cells have been studied much more intensively. The solid line shows the trajectory of the maximum with these points eliminated. The range bar and shaded area have been added for one group to draw attention to the fact that the data can be expected to underestimate maxima for any group in which maximum numbers of cell types decreased, if any such exist. (The length of the bar and the choice of agnathans were arbitrary.)

The method seems very promising, but the data so far may be misleading. First, vertebrates (especially humans) have been studied far more intensively than other organisms, and subtler differences among cell types have probably been discerned, leading to higher counts. Second, counts are based on modern organisms and therefore underestimate maxima in groups in which maxima declined, if any such exist (Fig. 2). This raises the possibility that the true curve arcs upward more steeply, and perhaps higher, than the data suggest. In sum, the data are consistent with many patterns, including a burgeoning of cell types in the early Phanerozoic, with little change in the maximum (or in the mean) after that. More counts, revealing distributions within bodyplans, might help to reduce the uncertainties.

2. Cisne (1974; see also Flessa et al., 1975) studied free-living aquatic arthropods and used a weighted function of limb-pair diversity in a given organism as a measure of its complexity. He found a trend in the mean and maximum over about the first half of the Phanerozoic, after which both leveled off.

3. I used two measures to study complexity in the vertebral column: 1) the (size-corrected) range of variation in various vertebral dimensions along a column (R); and 2) the (size-corrected) average absolute difference between each vertebra and the mean, a variance analogue (McShea, 1992, 1993). In most ancient and modern fish, vertebrae vary relatively little in certain dimensions from one end of the column to other, while in mammals variation is considerable. Using a larger sample, I showed these differences to be significant in several dimensions, which implies a trend in the vertebrate maximum, from fish to mammal, and almost certainly in the mean as well (McShea, 1993, 1994).

3.3 Non-hierarchical Developmental Complexity

Measures. For development, non-hierarchical complexity might be the number of independent interactions, or factors, controlling form. Where interactions are correlated, complexity is the total amount of residual independence after redundancy has been removed (what Van Valen [1974] called information). For example, with two measured dimensions, independence could be calculated as two minus the squared correlation coefficient (Van Valen, 1974; see also McShea et al., 1995). Other metrics might be developed using an inverse function of degree of integration (Olson and Miller, 1958; Wagner, 1990). The approach is indirect in that the metric is based on measurements of morphology, and thus morphology is used as a proxy for developmental interactions.

Evidence. Vermeij (1971, 1974) has documented an increase in the maximum number of coiling parameters in gastropods, especially in the early Paleozoic transitions from uncoiled to planispiral to conispiral shells. In each transition, another dimension of variability, and thus another degree of independence, was added. Vermeij (1973, 1974) cited other possible instances of increase (e.g., land plants, actinopterygian fishes), but acknowledged that limits may exist and that larger, unbiased samples are needed to document a trend.

3.4 Hierarchical Morphological Complexity

Measures. Hierarchical morphological complexity is the number of levels of nesting of parts within wholes. For some artificial systems, such as nested boxes, levels are well defined (e.g., Simon, 1969) and counting them is straightforward. But many natural systems appear to occupy a continuum of levels (Salthe, 1985). Further, the degree to which natural systems are integrated at each level — what will here be called degree of individuation (see below) — varies across the scalar hierarchy (Wimsatt, 1976). In such a situation, counting levels is difficult.

One solution is to focus only on the instances in which the addition of levels is arguably unambiguous, such as the formation of the first eukaryotic cells from a symbiotic association of prokaryotes, or the emergence of multicellular organisms from clones of free-living, eukaryotic cells. A study by Maynard Smith and Szathmáry (see number 1 below, under "evidence") implicitly adopts this tactic, in that they consider only what they call the "major transitions" in hierarchical organization.

Another solution — which I explore in the remainder of this section — is to evaluate hierarchical complexity only in a relative sense. In particular, we might assume that the hierarchical complexity of all metazoans is about the same up to the level of the multicellular individual (for aclonal species) or module (for clonal species). We can then ask to what degree some higher level, such as the society or colony, is individuated (see numbers 2 and 3 below, under "evidence"). Species that are more individuated at the higher level could be said to have fractionally more levels and thus greater hierarchical morphological complexity.

An individual is understood here as a system of parts which together form a unified whole. A central feature of that unity is the cohesiveness or connectedness among the parts (Hull, 1980; Mishler and Brandon, 1987). Thus, one measure of individuation at some hierarchical level might be simply the number of interactions among the parts at the next lower level. For greater resolution, interactions might be weighted by their intensities, using correlation coefficients or covariances among parts as proxies (Olson and Miller, 1958; Cheverud, 1995). I advance this approach tentatively, because individuation may turn out on closer examination to have other features that are important in this context (Hull, 1980; Salthe, 1985; Mishler and Brandon, 1987). If so, the metric may have to be modified to capture individuation in its fullest sense.

Consistent with the purely structural view of complexity adopted here, only structural aspects of individuation will be considered relevant. Thus, excluded are features of colonial organisms that indicate higher-level functionality (or superorganism status), such as the presence of colony-level parts, differentiation among colony members, and the degree to which growth is controlled by the colony as a whole.

Evidence. 1. Maynard Smith and Szathmáry (1995) document a series of eight "major transitions" in evolution: 1) early replicating molecules to populations of molecules in compartments; 2) unlinked replicators to replicator linkage in chromosomes; 3) the origin of the genetic code and of translation; 4) prokaryote to eukaryote; 5) asexual to sexual reproduction; 6) single-celled existence to multicellularity; 7) solitary existence to coloniality; and 8) the emergence of human social organization based on language.

The common theme in most of these transitions is the emergence of a higher level of nesting of parts within wholes (see also Stebbins, 1969; Pettersson, 1996), and therefore an increase in hierarchical complexity. In Maynard Smith and Szathmáry's terms, what we see is the emergence of new "levels of organization" or new levels of selection (Maynard Smith, 1988). "Entities that were capable of independent replication before the transition can replicate only as part of a larger whole after it" (Maynard Smith and Szathmáry, 1995, p. 6).

The list convincingly documents a trend, at least in maximum hierarchical complexity, and probably in the mean as well. Notice that the last two transitions occurred within (and since the origin of) the Metazoa, both of them (at least partly) in the Phanerozoic. However, notice too that the last transition differs from the others. Human social organization is the result of interactions among metazoan individuals, and therefore would seem to occur at a level precisely parallel to that of social insect colonies or marine invertebrate colonies. Human language is certainly a unique mode of interaction, doubtless lending a special character to the social integration it facilitates, but it is hard to see how it adds a level above that of the colony.

Interestingly, if we remove this last transition, the list documents only a single origin of a new level, the colony, within the Metazoa. Then, arguably, instead of suggesting a pattern of relentless addition of new levels over time, the list raises the question of why only a single level has arisen in the half billion to a billion years since the Metazoa arose. Of course, the degree of individuation of the colony level may have increased, which is the subject of the next two empirical treatments.

2. Boardman and Cheetham (1973) used the absence and incompleteness of the walls separating modules as a measure of connectedness in fossil and modern bryozoans. They reported a trend in the maximum in Mesozoic and Cenozoic cheilostomes, but none in the (mainly) Paleozoic stenolaemates, which apparently were highly integrated at their first appearance (Boardman and Cheetham, 1973). In a second measure, the number and directness of soft-tissue connections among modules (which in fossils could only be inferred), the cheilostomes showed no trend. Jackson and McKinney (1990) found that, in the Mesozoic and Cenozoic, communication among zooids was more extensive in cheilostomes than in cyclostomes and that cheilostomes largely replace cyclostomes, which implies a trend in mean degree of individuation for bryozoans as a whole.

3. Coloniality itself is a crude indicator of individuation, in that connectedness among modules in colonies is more likely than among solitary individuals. Coates and Oliver (1973) noted that the first corals were already colonial and that percent coloniality among genera (and thus the mean) showed a net decline over the Phanerozoic. Wood et al. (1992) reported that early Phanerozoic sponges were mainly solitary, while most modern sponge species are modular, which implies a trend in mean coloniality. At least a brief trend in insect coloniality and colony individuation also seems likely, in that the first fossil representative of a modern eusocial group (Martínez-Delclòs and Martinell, 1995) appeared about 250 million years after the first insects (Labandeira, 1994).

4. Boyajian and Lutz (1992) found a trend in hierarchical complexity of another sort, at a smaller scale, within a substructure in the extinct ammonoids. Ammonoids secreted a coiled, chambered shell as they grew, and septa separating the chambers are visible externally in many fossil specimens as curvy lines or sutures. In many later species, the sutures became quite complex, sporting sharp curves, curves within curves, and so on. A measure of the average depth of nesting of curves within curves is the fractal dimension: Boyajian and Lutz found an increase in mean, maximum, and minimum fractal dimension of sutures over about the first half of ammonoid history, from about 400 to 230 million years ago (see also, Saunders and Work, 1997), but later the mean decreased slightly and the maximum leveled off, until their extinction 65 million years ago.

Using a different measure of sutural complexity, Saunders and Work (1996) have documented multiple independent increases in sutural complexity in ammonoid lineages during the Upper Carboniferous, about 300 million years ago. At this finer temporal scale, the increase in the mean was accompanied by both an increase in maximum complexity and a decrease in the minimum.

3.5 Hierarchical Developmental Complexity

Measures. One measure of hierarchical process complexity is just the number of links or levels in a causal chain (two, in Fig. 1G), or the average number where causal nodes are disjunct. Counting levels in development is difficult, but a measure might be based on degree of character entrenchment (Wimsatt, 1986). In principle, the variability of the most deeply entrenched characters (those of the bodyplan) should decrease as the number of developmental interactions dependent on them increases (Wimsatt, 1986; Gould, 1993). Further, as variability declines, the rate at which species in a group diverge from each other morphologically, or become morphologically more "disparate," should decline. Thus, increases in hierarchical developmental complexity might be manifest as decreases in rates of change in morphological disparity. (See McShea, In press, for a review of the various rationales that have been developed for why this sort of complexity might be expected to increase.) One way to measure the disparity of a group of taxa is as their average distance from their centroid in some suitable morphospace (e.g., Foote, 1993). Other protocols are discussed in Briggs et al. (1992), Wills et al.

(1994), Jernvall et al. (1996), and Foote (1997).

One problem with this approach is that declining variability might have other causes, such as increases in the intensity of selection (Ridley, 1993; Valentine, 1995). And once again the method is indirect in that morphology is used as a proxy for development.

Evidence. Some evidence for a trend comes from the arthropods of the early Phanerozoic Burgess Shale (Gould, 1989, 1991, 1993; Briggs et al., 1992). In a comparison of Burgess arthropods with a sample of modern ones, morphological disparity was found to be about the same (Briggs et al., 1992; Wills et al., 1994). Thus, from the origin of arthropods, presumably sometime in the 500 million years before the start of the Phanerozoic, until Burgess times, arthropod disparity increased considerably (from zero to some high level). But in the 500 million years of so after that, disparity apparently changed little, which seems to imply a major reduction in the rate of morphological change (Foote and Gould, 1992). Also, over the Paleozoic, disparity among genera peaked early (relative to diversity) in blastozoan echinoderms (Foote, 1992). Both patterns are consistent with an increase in entrenchment. On the other hand, certain subgroups — trilobites and blastoids — showed the opposite pattern (Foote, 1993).

Finally, the data in Jernvall et al. (1996) show a rapid increase in disparity among crown types of molar teeth in ungulates during their initial Paleocene-Eocene radiation followed by a pattern of slower, more gradual increase after that. This pattern too is consistent with an increase in hierarchical developmental complexity.

3.6 Weaknesses of the Recent Studies

Despite the use of operational metrics, a skeptic would have reason to be concerned about many of these studies. In many cases, a trend was foreseeable before the metrics were applied, leaving open the possibility that prior impressions may have (unconsciously) influenced the choice of group, or even motivated the study in the first place. Further, the arthropod-limb, vertebral-column, and ammonoid-suture studies rely on an unsupported assumption. Measuring complexity requires sets of comparable parts, but other than cells, no such sets are obvious in whole organisms. These studies avoid the problem by measuring complexity in substructures with comparable parts, and by making the assumption that complexity change in a substructure will reflect that in the whole organism. The assumption has not been tested.

4. *Causes*

4.1 Passive and Driven

Here I introduce a scheme for classifying possible causes of trends in cases where species diversity increases, a scheme that is based on differences in underlying trend dynamics. Consider Figures 3A and 3B: both show trends over time (vertical axis) in complexity (horizontal axis) in diversifying groups. In Figure 3A, change is biased so that increases occur more often than decreases within lineages. The trend is "driven" (McShea, 1994, 1998), or more informally, the lineages have a "general tendency" to increase. In Figure 3B, half the changes within lineages are increases and half decreases, but the whole group is constrained by a boundary (Stanley, 1973; Fisher, 1986; Gould, 1988b, 1996; McKinney, 1990). If the figure represents the diversification of all life, then the boundary might correspond to the complexity of the simplest possible organism (Maynard Smith, 1970). The trend might be called diffusive or "passive" to emphasize that it occurs without any biasing or driving forces.

Most explanations that have been proposed for complexity trends implicitly invoke biases and thus are driven. A number were listed in the introduction; see also McShea (1991). In contrast, little has been said about possible causes of boundaries (although see Heylighen, in press), a subject which is ripe for theoretical investigation.

Figure 3F shows what might be called a “null model,” or a case in which diversification occurs in the absence of any boundary or bias.

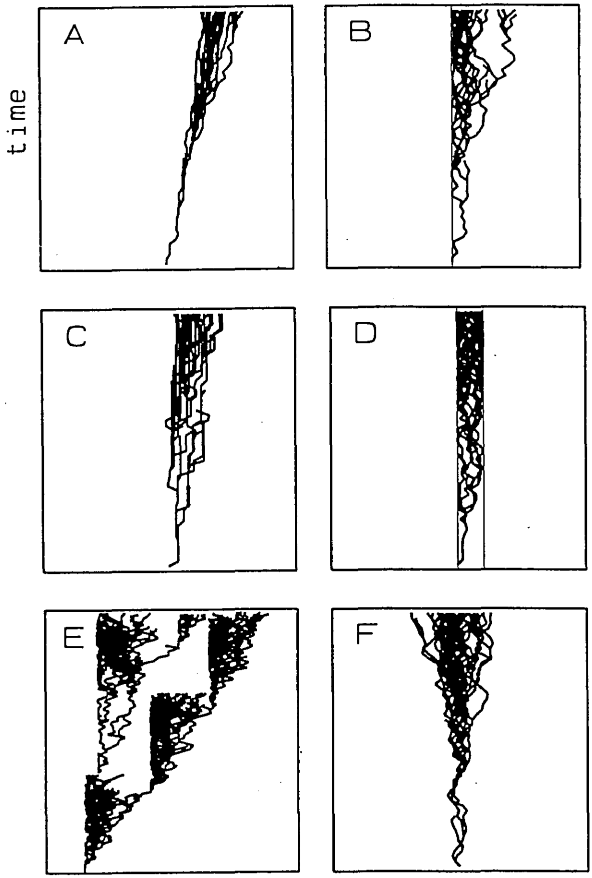

Figure 3. Output of a computer model for simulating complexity change (horizontal axis) in evolution. In each figure, a group begins as a single lineage. In every time step, each lineage has the opportunity to increase or decrease in complexity, to speciate, and to become extinct, each occurring with some fixed probability. If boundaries are present (vertical lines in B and D), changes that would cause lineages to cross them are nullified. See McShea (1994) for further details of the model. A: Driven trend -- no boundary, strong bias. B: Passive trend -- lower boundary, no bias. C: Weakly driven trend -- no boundary, weak bias. D: No trend -- upper and lower boundary, no bias. E: Driven, at the large scale (in that an increasing bias is present in the origin of groups, although change within groups is passive -- no boundary, strong bias (although one that is invoked only occasionally). F: No trend -- no boundary, no bias

4.2 Behavior of Maxima

The main virtue of this outlook for present purposes is that it helps us to focus on what sort of patterns require explanation, and to imagine alternatives. First, consider the behavior of maxima. In the null model (Fig. 3F), the maximum is expected to increase. Indeed, the maximum is expected to increase in five of the six cases illustrated in Figure 3. The point is that an increase in the maximum requires no special explanation, either in terms of selection or boundaries.

Thus, for example, Maynard Smith and Szathmáry's finding that maximum hierarchical complexity has increased is a very weak claim, at least in dynamical terms. (Their claim that the increase is episodic is much stronger, of course, in that it implies two distinct causal regimes, one operating during major transitions and another between, as in Figure 3E.) In dynamical terms, the more interesting and as-yet-unaddressed issue would be whether the origin of levels is biased or not, that is, whether lower levels ever arise from upper, and if they do, whether they do so as often as the reverse.

This is not to say that maxima are irrelevant. For example, a long-term leveling off of maxima would certainly require special explanation, perhaps one that predicts the existence of an upper bound of some sort (Fig. 3D).

4.3 Behavior of Minima

The null model (Fig. 3F) also shows that, in the absence of boundaries, the minimum is expected to decrease. However, no theoretical treatment I know predicts a long-term decrease in minimum complexity. Rather, the assumption in most hypotheses (often implicit) is that the minimum has not changed. Notice that while a stable minimum might seem to suggest the existence of a boundary and therefore a passive mechanism, this is not the case: a stable minimum can be produced in either a passive (Fig. 3B) or a weakly driven system (Fig. 3C). In other words, a stable minimum is not by itself conclusive evidence for either passive or driven.

4.4 Tests and Evidence

Passive and driven are broad categories of causes; biases and boundaries both have a number of possible more-specific underlying causes. (For example, a bias might be caused by selection; and a boundary might result from a developmental constraint.) Thus, distinguishing passive and driven in trend data would not identify a specific cause, but would narrow the field somewhat. Several tests are known (McShea, 1994). One is based on the behavior of the minimum. The test is asymmetrical in that the minimum can remain stable in either passive or driven trends (Figs. 3B and 3C), but if it increases, a trend is probably driven (Fig. 3A). The test assumes increasing diversity.

A second test is based on a comparison of ancestors and descendants (McShea, 1994). In a passive trend, increases and decreases should be equally frequent among ancestor-descendant pairs (at least in a sample far from any possible lower bound), while in a driven trend, increases should outnumber decreases.

(It is worth recalling here the strategy we are using to detect trends in the Metazoa: testing for a statistical bias in the direction of complexity changes among metazoan subgroups. Notice now that this strategy in effect applies the ancestor-descendant test but for a different purpose, to test for a trend rather than to analyze the causes of a trend already documented. Notice too that only a driven trend can be detected in this way. If no bias is found, a passive trend is not ruled out.)

At the scale of the Metazoa, we have little evidence regarding causes. The cell-type minimum remained constant, consistent with either passive or driven (although Valentine et al. [1993] suggest passive on other grounds). Within groups, the minimum increased (temporarily) in arthropod limb types, which suggests driven. The minimum in the vertebral column remained roughly stable (at the fish level of differentiation), and in an ancestor-descendant test, no bias was found, which implies passive (McShea, 1993, 1994). The initial increase in suture complexity in ammonoids seems to have been a driven trend: at least in the initial diversification, the minimum rose and ancestor-descendant comparisons reveal a preponderance of increases (Saunders and Work, 1997). The non-hierarchical complexity increase documented by Vermeij and the hierarchical morphological complexity increase documented by Maynard Smith and Szathmáry are consistent with both passive and driven mechanisms. Finally, some compelling theoretical arguments have been offered that explain why the trends in bryozoans and corals (Lidgard, 1986; Jackson and McKinney, 1990) and in developmental hierarchies (Riedl, 1977; Wimsatt, 1986; Salthe, 1993) are expected to have been driven, but the data are not conclusive. On the whole, the evidence is scanty, and much more is needed to raise the study of causes above the level of speculation.

4.5 Upper Limits

Most rationales for a trend allow complexity to increase indefinitely, but there are theoretical reasons to think that upper limits might exist. For example, selection might oppose greater complexity when added parts begin to interfere with proper function (Castrodeza, 1978). Also, increase might be limited if highly complex systems are regularly displaced by more sophisticated, simpler ones (Arthur, 1994). And overly connected systems might tend to behave chaotically (Kauffman, 1993) and thus to be unstable.

Evidence that limits might exist comes from the behavior of maxima: a rising maximum is expected in all diversifying systems (Fig. 3A-C, 3F), but a *failure* of the maximum to increase (Fig. 3D), or a leveling of the maximum, suggests an upper limit. In non-hierarchical morphological complexity, stable maxima occurred in arthropod limb types and possibly in cell types. In hierarchical morphological complexity, apparently no full levels have been added since the origin of the Metazoa, although consolidation of the last-added level, the colony level, may have increased, at least in bryozoans. All of these possibly-stable maxima seem to have occurred while diversity increased, at least on average. However, for all types of complexity, closer analysis is needed, in particular, high-resolution comparisons of temporal patterns in diversity and maxima.

5. *Discussion and Summary*

5.1 Complexity, Human Beings, and the Great Chain of Being

The Great Chain of Being is an ancient scheme for ordering natural entities according to their degree of "perfection" (Lovejoy, 1936). Historically, in biology, the ordering has been crudely anthropocentric, with organisms ranked roughly according to their similarity or proximity to human beings (e.g., see ordering in Bowler, 1989). Our high ranking doubtless reflects our impression that we are special in some way, that humans stand apart from the rest of the living world, an impression that we think justified on account of our impressive (to us) mental capabilities, social organization, technology, and so on. The Great Chain was ostensibly abandoned long ago in biology, but the impression of a ranking along the same lines — from bacterium to human — is still widespread (Ruse, 1996).

If humans are special, in some sense, does that specialness have anything to do with complexity? In the exploratory approach, we might define complexity as that which makes human special, and then a connection would exist by definition. But operating in the skeptical mode, the situation is not so clear: "special" and "impressive" are not the same as complex.

Human behavior does seem quite diverse and differentiated, and therefore complex in the present view. And perhaps complex behavior also requires complex brain structure (Godfrey Smith, 1996). (Although it is not completely clear that complex behavior, even complex thought, cannot be produced by a very *simple* brain structure.) But behavior in eusocial insects also seems remarkably diverse and differentiated. And perhaps they also have complex brains.

I do not assert that honey bee behavior or brain structure is as complex as that of humans. The purpose of the comparison is to disturb complacent imaginations, and to raise the possibility that even if our brain structure, mental processes, and behavior do set us apart in some away, it is not at all obvious that they do so on account of their *complexity*.

5.2 Intuition and Evidence

Has there been a trend toward increasing complexity in metazoans? For many, a trend is intuitively obvious. Modern organisms do seem to be extraordinarily complex in all four senses. And at least morphologically, their ancient ancestors seem less elaborate, their structure less finely and crisply detailed. But perhaps the ancestors are just smaller, with parts that are also smaller and thus more easily overlooked. Also, we know them only as fossils. If they were more complex, most of their complexity would have been lost. On this question, intuition is probably a poor guide.

Unfortunately, at present the evidence is not much more helpful. At least an early Phanerozoic trend occurred in mean and maximum non-hierarchical morphological complexity, as measured by number of cell types. But no metric applicable to all metazoans has been devised for scales above or below the cell, nor for any other type of complexity at any scale. Thus, a statistical approach is required, in which a sample of metazoan groups is examined; if a (driven) trend occurred in metazoans, then increases should predominate among groups.

What do we see? For non-hierarchical morphological complexity, two trends in the mean and maximum have been documented in organismal substructures, one in arthropod limb types and one in the vertebral column. For development, an early Phanerozoic trend (at least) occurred in gastropods.

For hierarchical morphological complexity, new levels have arisen in the history of life, but it is not clear that more than one — the colony level — has been added in the history of the Metazoa. Within the colony level, mean individuation increased in bryozoans as a whole. Maximum individuation increased (by one measure) in cheilostomes but not in stenolaemates. Mean coloniality increased in sponges, but declined in corals; at least the maximum increased in insects. In any case, even if an increasing tendency can be documented convincingly at the colony level, arguably individuation has not progressed very far at that level, in any group, in the past half billion years or more. Even in the eusocial insects, colony individuation seems not to have reached the intensity that was reached long ago one level down, in the consolidation of the eukaryotic multicellular individual.

Also hierarchically, in ammonoids, a driven trend in complexity of sutures occurred, at least early in the history of the group.

Finally, for hierarchical development, decreasing rates of increase in disparity in arthropods and blastozoans, and also in mammal teeth, are consistent with increasing depth of developmental interactions. However, an alternative cause — increasing selection pressures — cannot be ruled out.

Given what we know now, the only defensible conclusion of a skeptical treatment of evolutionary trends in complexity in metazoans is, I think, agnosticism. It is true that some types of complexity increased over the Phanerozoic, although not consistently and some perhaps not lately. It is also true that while only a few groups (at most) have been examined for each type, a trend was found in most cases. Finally, even if no tendency to increase among groups is detected ultimately, the possibility of a passive trend remains.

However, the skeptical approach sets a high standard of proof. The cell-type data seem too sparse and the sample of metazoan subgroups studied too small to reach a conclusion for any type of complexity. More cases of decrease may yet emerge and even equal or outnumber increases. And the possibility that limits exist and have been reached remains to be addressed.

5.3 What, If Anything, Is Increasing?

Some will still feel the need to account for the impression that *something* has increased in the history of the Metazoa. And we could take an exploratory approach, as discussed, and define complexity as whatever-it-is that increases. But if we take a skeptical approach, it seems reasonable to ask at this point — having investigated four kinds of complexity — whether complexity has anything to do with the apparent trend. For one thing, there are many other candidates for the "something" besides complexity, such as ability to obtain and process information about the environment (Ayala, 1974), ability to control the environment, energy intensiveness (Vermeij, 1987), absolute fitness, and specialization. Still others can be imagined (see Fisher, 1986; Nitecki, 1988; Raup, 1988; McShea, In press). For most of these, hardly any skeptical investigations have been done. Also, the possibility should be considered that the appearance of a trend of any sort is an illusion, a trick of the imagination (McShea, 1991). Thus, at least at present, given the state of our knowledge, we would seem to have little basis for concluding that the "something" is complexity.

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Acknowledgments: I thank J. Valentine for contributing his data, D. Ritchie for a thoughtful reading of the manuscript, and L. Altenberg, J. Crutchfield, J. Hanson, M. Mitchell, and J. Valentine for helpful discussions.

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