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PERSPECTIVE

METAZOAN COMPLEXITY AND EVOLUTION: IS THERE A TREND?

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Abstract.—The notion that complexity increases in evolution is widely accepted, but the best-known evidence is highly impressionistic. Here I propose a scheme for understanding complexity that provides a conceptual basis for objective measurement. The scheme also shows complexity to be a broad term covering four independent types. For each type, I describe some of the measures that have been devised and review the evidence for trends in the maximum and mean. In metazoans as a whole, there is good evidence only for an early-Phanerozoic trend, and only in one type of complexity. For each of the other types, some trends have been documented, but only in a small number of metazoan subgroups.

Key words.—Complexity, hierarchy, macroevolution, Metazoa, trends.

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The centerpiece of the case for a pervasive evolutionary trend in complexity has always been a story. Figure 1 tells one version: the first organisms were simple and single-celled. From these arose more complex multicelled invertebrates, which in turn were followed by primitive vertebrates, then mammals, and finally the most complex species of all, human beings.

Many find the story compelling, and to some it might make the existence of a trend seem too obvious to question. But there have always been reasons for doubt. First, what is complexity? Is it number of parts? Number of interactions among parts? Degree of functionality of those interactions? Or a combination of all three? The story does not say, and no general consensus exists. Even if a consensus could be reached—say, on complexity as a joint measure of number of parts and functionality—how would we demonstrate a trend? To compare parts-and-functionality in a human and a trilobite, for example, how would we proceed? These questions have no satisfactory answer, and therefore such comparisons (along with the trend inferred from them) are purely impressionistic.

Second, even if the sequence in Figure 1 *is* an increase in complexity in some sense, it documents just one case, not a pervasive trend. Many other (putative) cases of increase have been cited in the evolutionary literature (Cope 1871; Spencer 1890; Rensch 1960a), 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 either. 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 so on. Without an unbiased sample, we cannot say which, if either, predominates. Only very recently have attempts been made to sample in an unbiased way (see below).

Historically, a great many rationales have been offered to explain why complexity *should* 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 a greater division of labor among parts. Waddington (1969; Arthur 1994) 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. (Others are reviewed in McShea 1991.) The combined effect of all these speculations has undoubtedly been to reinforce the impression of a persistent trend. However, none has any solid empirical support.

For most of the history of evolutionary thought, there has been a near consensus on complexity (McShea 1991). Evolutionists who shared the impression of a general trend include Lamarck (1809), Darwin (1987), Cope (1871), Spencer

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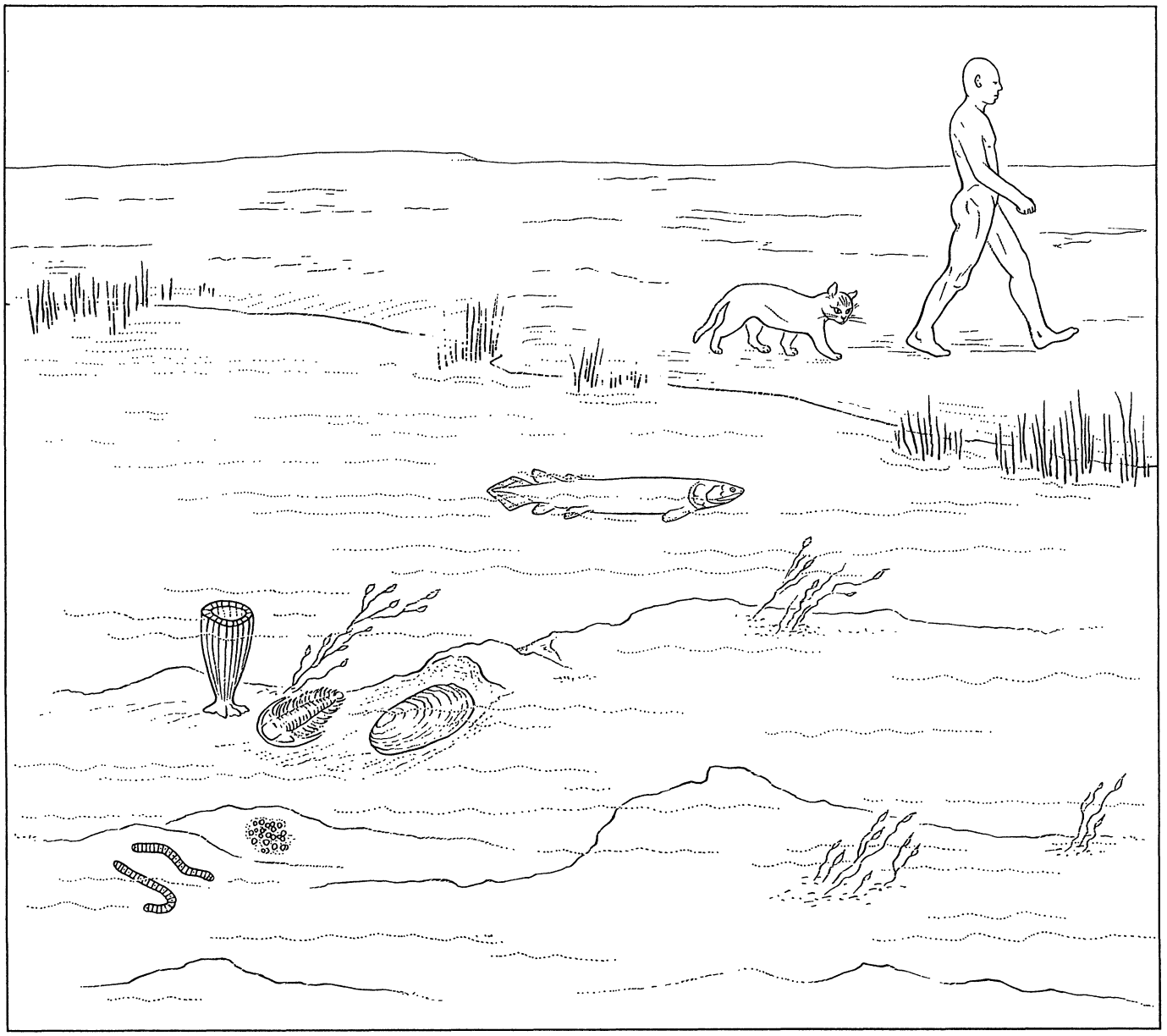

FIG. 1. Increasing complexity in evolution?

(1893), Huxley (1953), Rensch (1960a,b), Stebbins (1969), Saunders and Ho (1976, 1981), Wake et al. (1986), Bonner (1988), Ayala (1988), Arthur (1984, 1988), Lewin (1992), Valentine et al. (1993), and many others. But in recent decades, some have expressed skepticism, including Williams (1966), Lewontin (1968), Levins and Lewontin (1985), Gould (1985), and Slobodkin (1992), perhaps a sign that the consensus is coming apart.

Rising doubts about trends offers an opportunity now to reformulate concepts and to evaluate the evidence neutrally. The mood of this paper is skeptical, but the point is *not* to make a case that complexity has not increased. Possibly it has, in some sense. Rather, the point is to rescue the study of biological complexity from a swamp of impressionistic evaluations, biased samples, and theoretical speculations, and to try to place it on more solid empirical ground. The immediate goal is to determine what we can say now and with confidence about trends, and what evidence is still needed.

Trends in Means and Maxima

A preliminary issue concerns the distinctions among trends. A trend might refer to directional change in a single lineage, such as the increase in brain size from *Homo habilis* to *Homo sapiens*, or in the mean in a diversifying group of lineages, such as the increase in mean brain size in primates. This paper is concerned mainly with trends in the mean, in particular, mean complexity for multicellular animals (metazoans) over the Phanerozoic Era, essentially their entire history. Some closely related topics are not covered, such as trends in plants and trends at the scale of ecosystems.

Also of interest will be a trend in the maximum, in other words, in the complexity of the most complex metazoan. Maxima are of special interest, because a leveling off of the maximum in a diversifying group suggests the presence of a boundary, or an upper limit to complexity. In principle, means and maxima are independent; thus, here they are treated separately.

Definitions, Evidence, Causes, and Limits

This paper has four parts: (1) First, I propose a narrow definition and a general scheme for understanding complexity. The scheme reveals complexity to be a compound concept encompassing four independent aspects or types. Thus, 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. Some evidence exists for an early-Phanerozoic trend in the metazoan maximum and mean, but only for one type of complexity and only at one scale. For other types and scales, trends have been documented but only in subgroups within the Metazoa.

(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). 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.

Defining Complexity

The word complexity has been applied to various objects and processes, or more generally, systems. The weather, a watch, and the world economy are said to be complex systems. In biology, DNA, the human brain, and rain forests are usually considered complex. In search of a common theme, 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) and the length of the shortest algorithm that will generate it (Kolmogorov 1965; Chaitin 1975). (For others, see Bennett 1988, 1990.) Each may be useful in some context. But no broad definition has been offered that is both operational, in the sense that it indicates unambiguously how to measure complexity in real systems, and universal, in the sense that it can be applied to all systems. What is the length of the shortest algorithm that will generate an actual rain forest?

A Narrower View

Thus, in order to study complexity empirically—to measure it, test for trends, and investigate its properties—some evolutionists have adopted a narrower view: the more differentiated a system is, the more complex it is. More precisely, 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 different parts, while a raindrop and a rubber ball are simple. This narrow view has been advocated by some theoreticians in biology (Hinegardner and Engelberg 1983; Katz 1986, 1988; Kampis and Csányi 1987; Wicken 1987; Slobodkin 1992) and is implicit in recent empirical studies (Cisne 1974; Boyajian and Lutz 1992; McShea 1993; Valentine et al. 1993).

The narrow view is purely "structural," in that complexity depends only on number of different parts and interactions and not on their functionality. 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. To many this view will seem wrong-headed, to miss the essence of complexity by failing to distinguish between a functional differentiated structure like an automobile and the (ordinarily) functionless heap of parts in a demolished one. The complaint is serious and will be addressed later. I will argue that *not* making this distinction is *essential* for certain research agendas.

Order and Organization.—These words have been used casually in biology, and interchangeably with complexity, creating much confusion. Order is especially troublesome, because simple systems like crystals and complex ones like organisms are both said to be highly ordered. Some have suggested that organization should denote degree of functionality (Atlan 1974; Wicken 1979; McShea 1993), independent of complexity, but this usage is not yet widely accepted. For clarity, neither word will be used in this discussion.

Four Types of Complexity

Even narrowly defined, complexity is still a compound term; it is composed of four distinct types, based on two dichotomies: object versus process, and hierarchical versus nonhierarchical structure (McShea, in press). The four possible combinations of these terms generate the four types: (1) Nonhierarchical object complexity; (2) nonhierarchical 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 different interactions among them. For processes, a collision between two billiard balls is simple, whereas 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; one part may participate in essentially one (major) interaction, as does a heart, or many, as does a liver. In Figure 2, 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 or physiological, and the component interactions might be morphogenetic events and metabolic

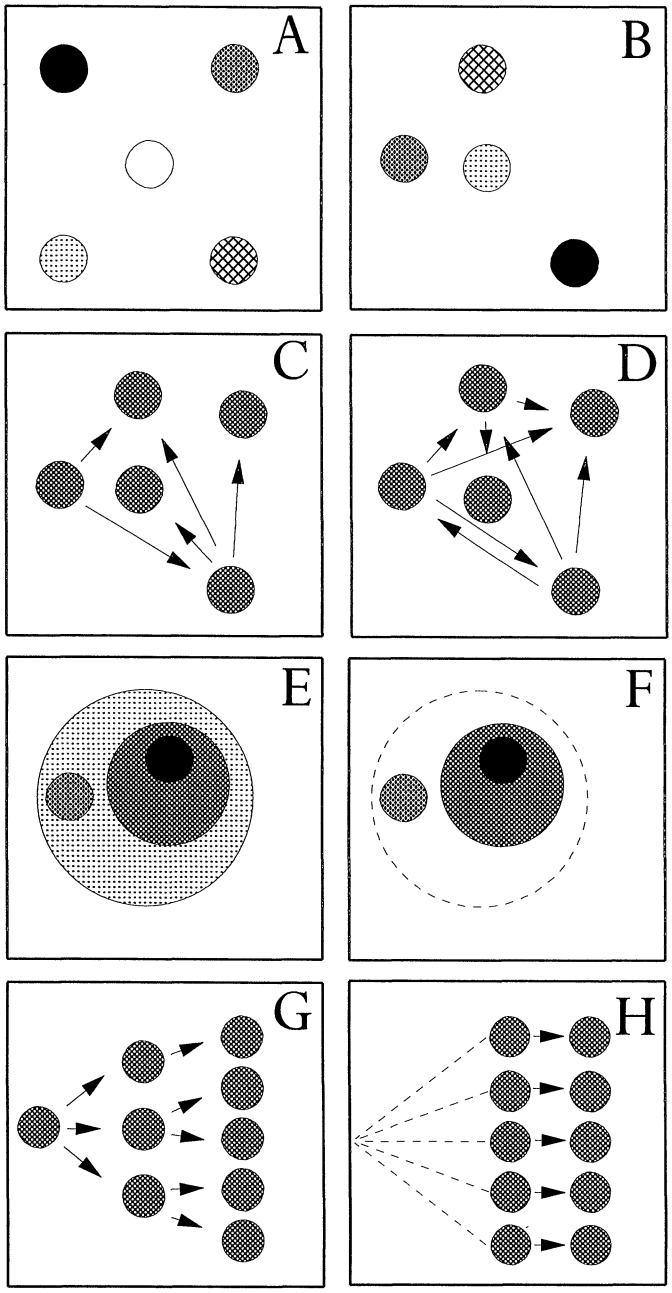

FIG. 2. Systems (squares) of parts (circles) and interactions (arrows), illustrating the various types of complexity. (A, B) object complexity (A > B); (C, D) process complexity (D > C); (E, F) hierarchical object complexity (E > F); (G, H) hierarchical process complexity (G > H). (The dashed lines in H are a reminder 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.)

steps, respectively. Here, only morphology will be considered under the heading of object complexity, and only development under process complexity.

Hierarchical and Nonhierarchical Structure.—Hierarchical object complexity is the number of levels of nestedness of parts within wholes. A possible object hierarchy in biology is the series: . . . organelle, cell, organ, organism . . . , a sequence of what have classically been called "levels of organization." Upper-level entities or individuals physically contain the lower and constrain their behavior somewhat (Eldredge and Salthe 1984; Salthe 1985, 1993; O'Neil et al. 1986). In Figure 2, E and F appear to have the same number of levels, but in E the upper level (the large circle) is more completely "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). (For further discussion, see McShea, in press.) The arrangement of interactions is hierarchical in Figure 2G but nonhierarchical in Figure 2H.

Nonhierarchical complexity is the number of parts or interactions 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 nonhierarchical 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, independent of their differentiation (Katz 1986). For example, a parade is typically highly differentiated, consisting of many differently dressed individuals, but configurationally simple, in that individuals march in regular rows. (In Fig. 2, A is more differentiated than B but less complex configurationally.) This dichotomy introduces four more types of complexity, a configurational version of each of the four above. However, the configurational types have received little attention in biology (but see Yagil 1985; McShea 1992), and will not be considered here.

Overall Complexity.—Is a human more complex than a trilobite *overall*? The question seems unanswerable in principle because the types of complexity are conceptually independent. The aspects of other measures, such as size, have this same independence: a balloon can be larger than a cannonball in volume but smaller in mass. Likewise, a trilobite might have fewer parts but more interactions among parts. Thus, it is hard to imagine how a useful notion of overall complexity could be devised. This is not to deny that the types might be related empirically. Just as volume is often correlated with mass, so morphological and developmental complexity might turn out to be correlated.

Objections to the Narrow View

Complexity and Randomness.—Three senses of randomness are relevant here. (1) Colloquially, in calling a compost heap random, we might mean that its composition has no functional significance. Accordingly, it might seem appropriate to define complexity so as to exclude systems, or those

portions of them, that have no function. However, our ignorance of function is profound in biology, and the attempt to separate the functional from the "random" 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 the narrow view is that complexity can be measured while judgments about function are deferred.

(2) The narrow view might seem to equate complexity with entropy, another sort of randomness. 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). However, calling a compost heap complex for this reason would be a category mistake. Entropy is a relationship between microstates and macrostate, whereas complexity in the narrow view is a property of a single microstate, of one specific composition and configuration, and thus involves no such relationship (Wicken 1987). In the narrow view, complexity is not entropy.

(3) Some have argued that systems contain both a "regular" and a "random" component (Crutchfield and Young 1989; Crutchfield 1991) and that only the differentiation of the regular portion ought to contribute to complexity. Here, random refers to the unique features of systems, such as the precise number of hairs on the arm of a particular human individual, while regular refers to shared features, such as a five-fingered hand. The intent is to restrict complexity to features that are "rule-based," in other words, to features produced either by natural law acting in the present or by irrevocable, contingent events in the past (frozen accidents) (Gell-Mann 1994). This approach is actually consistent with the narrow view. 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.

Dependence on Descriptive Frame.—The number of parts in a system depends on scale, as discussed, but also on descriptive frame, in other words, on how we define a part at a given scale (Kampis and Csányi 1987). The choice may seem arbitrary, which will make complexity measures seem arbitrary as well. One solution might be to define parts functionally, based on the plausible notion that distinctiveness of parts in organisms is the evolutionary result of selection for functionality (Wagner 1995). The problem is that identifying function is difficult, especially for parts that are no longer functional.

Alternatively, parts could be defined as regularities, in the sense discussed. Elegant algorithms have been devised for discovering regularities in bit strings (Crutchfield 1991), and in principle, these could be applied to organisms. However, the algorithms make assumptions, such as statistical stationarity, that have not yet been justified for organisms. At present, our best strategy is probably to proceed intuitively, that is, to identify parts and discover regularities using our precognitive perceptual skills. We are obviously sensitive to many cues, such as boundaries and morphological commonalities among parts. We can articulate only some of them, but this does not make the partitioning arbitrary. The complexity studies reviewed below apply this method opportunistically. Scalar levels and organisms (or their substructures) are selected in such a way that the partitioning is intuitively unambiguous.

Differing Research Agendas.—A view that classifies a demolished car as complex will seem somewhat perverse to those with certain research agendas. In particular, a goal for many students of complexity has been to find the critical structural and dynamical commonalities among systems that are known to be highly functional, in the sense that they are able to self-organize, compute, evolve, and so on. For example, in Boolean networks (Kauffman 1993) and cellular automata (Packard 1988; Langton 1990), high levels of functionality seem to occur when some frozen structure is present but change occurs as well, in the middle range between monotonous regularity and chaotic irregularity (cf. Mitchell et al. 1993). And accordingly, an appropriate complexity scale would seem to be one on which middle-range systems score highly. In effect, the point of this research agenda is to discover the essence of complexity by investigating the common features of highly functional systems. This is very much science in the exploratory mode.

The approach outlined here supposes a very different agenda. The criteria for complexity are fixed in advance, and the point is to measure the complexity of systems (and thus to *discover* which are complex) and then to test empirically for trends and for relationships with other variables (e.g., stability). In principle, this tactic leaves open the possibility that humans, for example, will prove not to be especially complex relative to other species. However unlikely such a finding may seem, the existence of the in-principle possibility is essential for getting nontrivial answers to questions about trends. In the exploratory agenda, however, the criteria for complexity are sought with the capabilities of highly functional systems, such as humans, in mind, and thus a trend with humans at or near the zenith is virtually inevitable.

Notice that the narrow, a priori definition of complexity advocated in this agenda (or some close analogue of it) is essential for investigating the relation between complexity and other variables. Is complexity correlated with intelligence? Are complex organisms more evolvable? To answer such questions, we must be able to measure the two variables involved—complexity and intelligence, or complexity and evolvability—*independently.* Only then can we plot one against the other and find out if the suspected relationship really exists. This agenda is very much science in the hypothesis-testing mode. Both agendas are worthwhile and they need not conflict.

Complexity and Generating Processes.—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 be 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 very complex recipe (Rombauer and Becker, 1974). Finally, we would like to learn how complexity of systems and complexity of their generating processes are related empirically,

and defining one in terms of the other permanently obscures that relation.

In early studies of DNA complexity, the more "advanced" organisms (such as humans) were assumed to be more complex, in some unspecified sense, and the expectation was that generating their greater complexity would require more genes and larger genomes (Britten and Davidson 1969; Sparrow et al. 1972). For the most part, expectations have been frustrated. Based on limited data (Cavalier-Smith 1985; Szathmáry and Maynard Smith 1995), the correlation between "advancement" and genome size (also called C value) is poor. The correlation with gene number is better, but current estimates place humans in the same range as lungfish (Szathmáry and Maynard Smith 1995).

The unruly behavior of these variables has been called the "C-value paradox," but for complexity no paradox exists. Indeed, the absence of a correlation between structure and generating mechanism is unsurprising, especially across the wide scalar gap that separates DNA molecules and whole-organism morphology. (Conversely, the possibility should not be brushed aside that lungfish and other high-C-value species *are* both complex and "advanced" in some respect still undiagnosed. Impressionistic assessments of "advancement" could be wildly off.)

Evidence for Trends

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 nonhierarchical morphological complexity (see below). The alternative is to develop a variety of metrics, each targeting a specific group *within* the Metazoa. If a trend occurred in the Metazoa, it should emerge as a statistical regularity or bias, that is, significantly more groups should show increases than decreases. (A limitation of this approach is discussed below, under "causes.") The recent studies reviewed below fit neatly into this strategy.

Nonhierarchical Morphological Complexity

Measures.—Various approaches to counting parts are possible. For example, Thomas and Reif (1991, 1993) devised an ingenious classification of design elements. Using their "skeleton space," the complexity of an organism might be just the number of different elements it contains. For greater resolution, parts can be weighted by frequency of occurrence using formulas from information theory (e.g., Gatlin 1972; 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 (Bookstein et al. 1985), 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 (Sneath 1964; Bonner 1988). They plotted cell types for modern species against time of origin for their bodyplans (Fig. 3), using only modern species that are 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 because the minimum is stable (at one cell type), a trend in the mean seems inevitable as well.

The method seems very promising, but the data so far (Fig. 3) are 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. 3). 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) used limb-pair heterogeneity as a measure of complexity in free-living aquatic arthropods. Figure 4 shows that a trend in the mean and maximum occurred over about the first half of the Phanerozoic, and then both leveled off.

(3) I used two measures to study complexity in the vertebral column: the (size-corrected) range of variation along a column (R); and the (size-corrected) average absolute difference between each vertebra and the mean (C, see Fig. 5), a variance analogue (McShea 1992, 1993). In most ancient and modern fish, vertebrae vary relatively little in any dimension from one end of the column to other, while in mammals variation is considerable (shown for one dimension in Fig. 5). Using a larger sample, these differences have been shown to be significant for both R and C in several dimensions, which implies a trend in the vertebrate maximum and almost certainly in the mean as well (McShea 1993).

Nonhierarchical Developmental Complexity

Measures.—For development, nonhierarchical 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; 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 metrics are 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

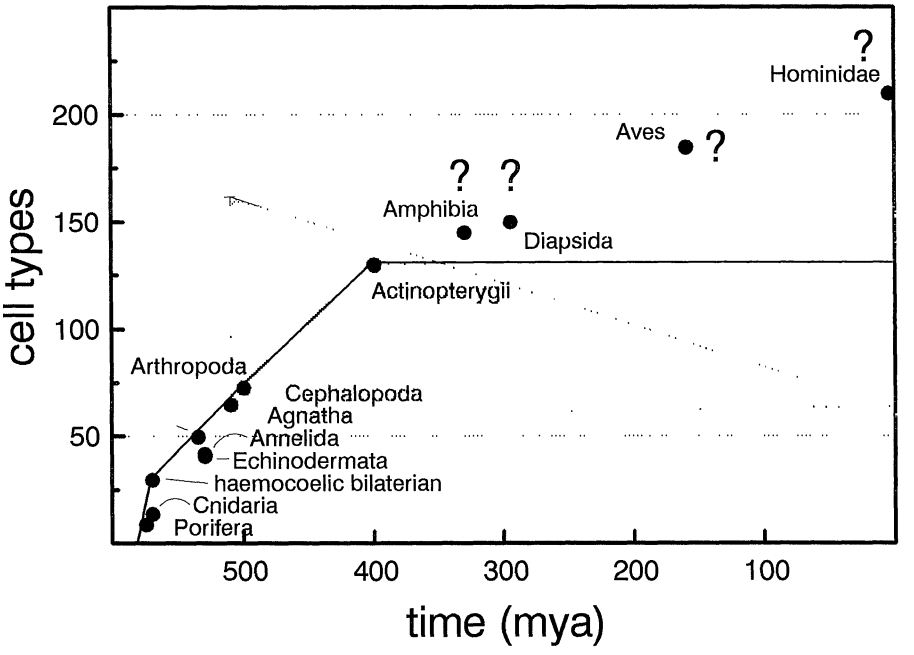

FIG. 3. Cell-type counts for modern primitive members of certain groups, each plotted against time of origin for the group's bodyplan (Valentine et al. 1993). The data are intended to show the trajectory of the maximum number of cell types (see text). Some annotations have been added: the question marks indicate taxa for which estimates are probably 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.)

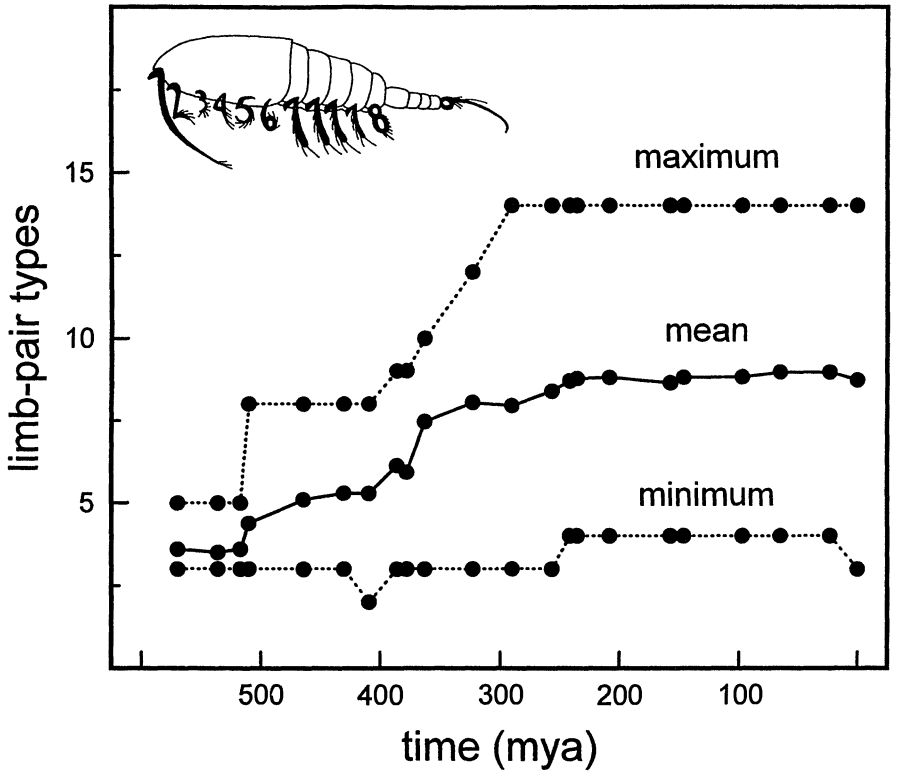

FIG. 4. Change in maximum, mean, and minimum number of leg-pair types in free-living aquatic arthropods over the Phanerozoic. Cisne measured complexity as a function of both leg-pair types and the number of each type (tagmosis), but here only number of each type is plotted. The Burgess Shale problematic taxa are omitted. (Inset figure reproduced with permission.) (Data are from Cisne 1974.)

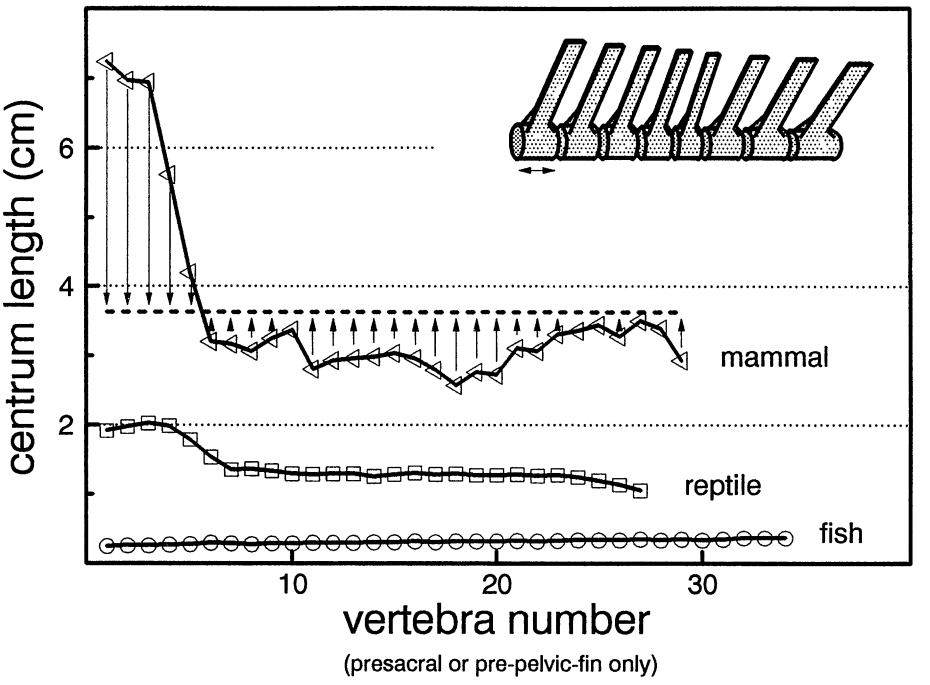

FIG. 5. Variation in one vertebral dimension, centrum length, along the vertebral column in three modern taxa, a fish (*Oncorhynchus*), a reptile (*Varanus*), and a mammal (*Equus*). The two complexity measures are univariate: for centrum length, the range of variation (R, not shown) is just the (size-corrected) difference between the longest vertebra and the shortest. C is the (size-corrected) average absolute difference from the mean (dashed line), which is the average length of the arrows. The inset shows a sequence of vertebrae from the middle portion of the mammal column in which centrum length (double-headed arrow) decreases then increases again.

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. Since Vermeij, there has been some discussion of functional correlates of nonhierarchical complexity (e.g., Lauder 1981); compelling arguments have been developed for why we ought to expect increases (Riska 1986) or decreases (Riedl 1977) to predominate in evolution; and trends have been investigated at a low taxonomic level (e.g., Kurtén 1988; McShea et al. 1995). But at a high taxonomic level, neither a trend nor its absence has been documented.

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 and counting them is straightforward. But many natural systems appear to occupy a much smoother continuum of levels (Salthe 1985), from the atomic level (and below) to the level of the universe as a whole (and perhaps above). An organism, for example, has atoms as components and is itself a component of the universe, with an indefinitely large number of levels intervening in both directions. 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 measure 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. 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 a high level of cohesiveness or connectedness (Hull 1980) among the parts, which corresponds closely with morphological integration in Olson and Miller's (1958) sense. Thus, one measure of individuation at some scalar level might be simply the number of interactions among the parts at a 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, such as spatial or temporal localization (Hull 1980; see Beklemishev 1969; Varela et al. 1974; Salthe 1985). If so, the metric may have to be modified to capture individuation in its fullest sense.

However, one feature that might seem relevant, functionality, is deliberately excluded (Hull 1980). Functional, higher-level individuals are commonly called superorganisms (Seeley 1989; Wilson and Sober 1989), and their functional aspects include the ability to self-organize and self-maintain, the division of labor and differentiation among parts, and so on. But consistent with the narrow view of complexity, only

the structural aspects of individuality—the degree to which parts interact to produce a unified whole—are relevant here. As argued earlier, by keeping structure and function separate, it becomes possible to investigate empirically the relationship between them, in this case between individuation and superorganism status. Some correlation seems likely, because selection for functionality is likely the main *cause* of higher-level individuation (Buss 1987; Wilson and Sober 1989). But the correlation is probably imperfect. An organism (or superorganism) cannot be completely unified structurally, because some internal independence—some structural disunity—is probably essential for it to function.

Among the colonial invertebrates, trends have been documented in a variety of features that are properly associated with "integration" in some sense, such as the presence of extramodular parts (Boardman and Cheetham 1973; Coates and Oliver 1973; Coates and Jackson 1985), differentiation among modules (Boardman and Cheetham 1973: Jackson and McKinney 1990), and the degree to which growth is controlled by the colony as a whole (Lidgard 1986; Lidgard and Jackson 1989). But these are (tentatively) excluded here, because they seem to be more directly connected with colony function than with structural individuation per se.

Choice of Levels.—The level of the society or colony is a natural choice to study for two reasons. First, a pre-Phanerozoic trend in maximum (and probably mean) hierarchical complexity for life as a whole is uncontroversial. Eukaryotic cells arose as unions of prokaryotic cells, and multicellular eukaryotes (including metazoans) arose by the adhesion and integration of eukaryotic clones. In each case, a new higher-level individual was formed. But the existence of a trend at the next level is not so obvious, and thus seems worth investigating. Second, the fact that societies and colonies are neatly decomposable into well-individuated components, multicellular individuals, makes analysis at this level easier (Simon 1969; Wimsatt 1974). As it turns out, almost all empirical treatments have targeted the colony level.

Trends in individuation could occur at other levels as well, perhaps at the level of the cell (or lower) or at the level of the ecosystem (or higher). Alternatively, it is possible that increases occur sequentially, at higher and higher levels (Buss 1987), or perhaps by the interpolation of newly individuated levels between existing levels. Finally, trends could occur in multispecies coevolutionary groups, such as phoretic associations (Wilson and Sober 1989). However, to my knowledge, empirical investigation of such trends—using clear criteria for individuation consistently applied—has not been attempted.

Evidence.—(1) 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.

(2) Coloniality itself is an (indirect) 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 percentage of 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, whereas most modern sponge species are modular, which implies a trend in mean coloniality. A trend in insect coloniality and colony individuation might also seem 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). But we do not know whether the first insects were social; while functional features such as caste differentiation can be inferred in some fossil specimens (Wilson 1987), inferring connectedness among individuals is more difficult. Many other modern species seem to be highly individuated at the colony level, including some siphonophores (Wilson 1975) and even human beings (White 1975), but the fossil record of their individuation is poor (or absent), and thus trends are difficult to document.

(3) Boyajian and Lutz (1992) documented patterns in hierarchical complexity 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 (Fig. 6). 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; Figure 6 shows that mean and maximum fractal dimension increased initially, over about the first half of ammonoid history, but later the mean decreased slightly and the maximum leveled off.

Hierarchical Developmental Complexity

Measures.—One measure of hierarchical process complexity is just the number of links or levels in the causal chain (two, in Fig. 2G), or the average number where causal nodes are disjunct. Counting levels in development is difficult, but a relative 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). One problem is that declining variability might have other causes, such as increases in the intensity of selection (Ridley 1993; see also Valentine 1995). Measurement protocols are discussed in Briggs et al. (1992), and Wills et al. (1994). Once again the method is indirect in that morphology is used as a proxy for development.

Evidence.—Evidence for a trend comes from the arthropods of the early Phanerozoic Burgess Shale (Gould 1991, 1993; Briggs et al. 1992). In a comparison of Burgess arthropods with a sample of modern ones, character variability

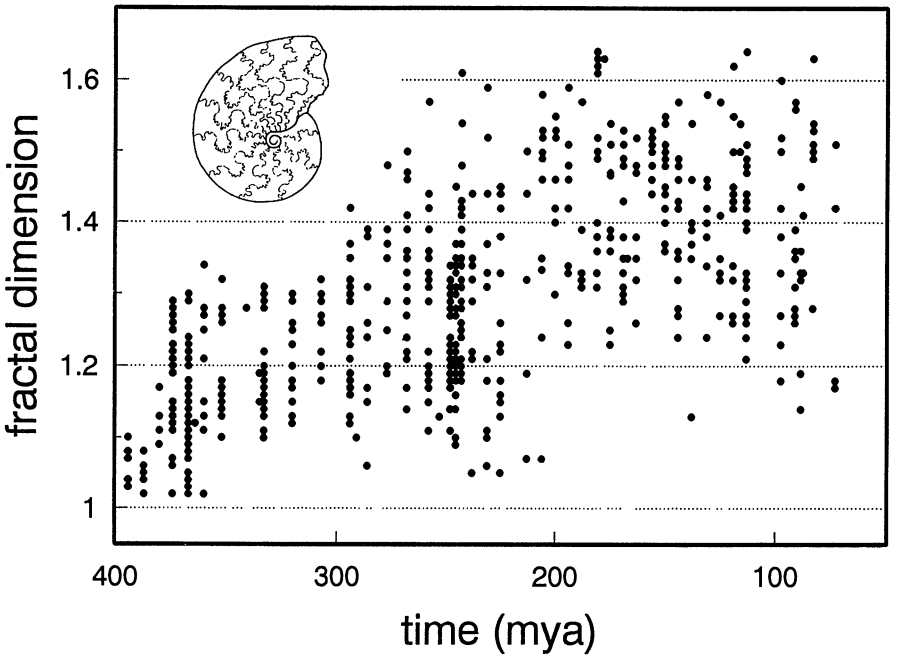

FIG. 6. Sutural fractal dimension (see text) in a sample of ammonoid species spanning the history of the group.

was found to be about the same (Briggs et al. 1992; Wills et al. 1994). Thus, modern species achieved about the same variability in 450 million years (since Burgess times) that Burgess species achieved in 50 million years (from the origin of arthropods). This implies a major reduction in the rate of morphological change (Foote and Gould 1992). Similarly, over the Paleozoic, variability 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).

Weaknesses of the Recent Studies

The use of operational metrics in the recent studies is an improvement over impressionistic assessments, but reasons for concern remain. In most 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 solve 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.

CAUSES

Passive and Driven

Figure 7A–B show trends in complexity (horizontal axis) in diversifying groups. In Figure 7A, change is biased so that increases occur more often than decreases within lineages. The trend is "driven" (McShea 1994), or more informally, the lineages have a "general tendency" to increase. In Figure 7B, 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; 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.

Colloquially, a distinction is sometimes made between occasional and necessary increase. Ordinarily, the point is that increases in complexity occur occasionally, accounting for the apparent rise in the maximum over the history of life, but that increase is not necessary, accounting for a stable minimum, that is, the persistence of seemingly simple forms such as prokaryotes. In the present scheme, the distinction is not especially useful. First, occasional increases occur in all systems, whether passive or driven, even in those with no trend at all (Fig. 7F). Second, occasional-but-not-necessary increase would be classified as just another kind of driven trend, perhaps like the one in Figure 7E. Trends may or may not occur within groups (in the figure, they do), but either way, the transitions between groups are usually increases in complexity. The trend at the largest scale is driven, because it is caused by a bias, albeit a bias which is expressed infrequently.

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, a subject which is ripe for deeper theoretical investigation (see below).

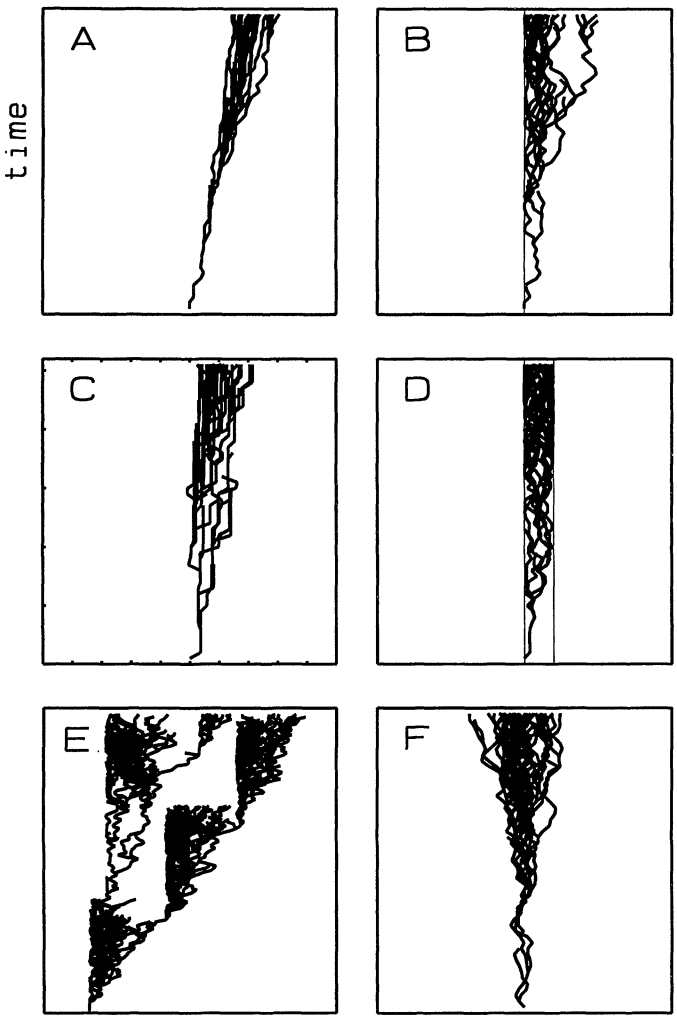

FIG. 7. Output of a computer model for simulating the diversification of a group. The horizontal axis is complexity. In each figure, a group begins as a single lineage. In every time step, each lineage has the opportunity to increase or decrease in complexity, to speciate, and to become extinct, each 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—no boundary, strong bias. (B) Passive—lower boundary, no bias. (C) Weakly driven—no boundary, weak bias. (D) No trend—upper and lower boundary, no bias. (E) Driven (at the large scale)—no boundary, strong bias (but invoked only occasionally). (F) No trend—no boundary, no bias.

Tests and Evidence

Passive and driven are broad categories of causes. Thus, distinguishing them in trend data would not identify a precise 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. 7B and 7C), but if it increases, a trend is probably driven (Fig. 7A). The test assumes increasing diversity. (If diversity decreases, however, a rising minimum is expected in either passive or driven trends.)

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 the lower bound), whereas in a driven trend, increases should outnumber decreases. Recall the strategy employed here 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 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 (Fig. 4), 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). Minimum suture complexity in ammonoids increased slightly during the initial trend, but Boyajian and Lutz (1992) argue that the trend was passive (based on the behavior of the variance). 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.

LIMITS

Most rationales for a trend allow complexity to increase indefinitely, but there are theoretical reasons to think that 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. 7A–C,F), but a failure of the maximum to increase (Fig. 7D), or a leveling of the maximum, suggests an upper limit. (On the other hand, a declining maximum is expected if diversity decreases.) Stable maxima occurred in arthropod limb types and possibly in cell types, both concurrently with increasing diversity. For other types of complexity, additional data and analysis are needed, in particular, high-resolution comparisons of temporal patterns in diversity and maxima.

DISCUSSION AND SUMMARY

Complexity and the Great Chain of Being

Figure 1 looks like an excerpt from a (temporalized) Great Chain of Being (Lovejoy 1936), an ancient scheme for or-

TABLE 1. Two modern views of the rise in "complexity" in the history of life. Neither applies a consistent understanding of complexity, and both are reminiscent of a (temporalized) Great Chain of Being.

Successive levels of "Complexity" Stebbins (1969)	Major transitions in "Complexity" Maynard Smith and Szathmáry (1995)
Self-replicating molecules	Replicating molecules → Populations of molecules in compartments
Prokaryotes	Independent replicators → Chromosomes
Single-celled eukaryotes	RNA as gene and enzyme → DNA + protein
Multicelled eukaryotes with cellular differentiation	Prokaryotes → Eukaryotes
Organisms with differentiated tissues and organs	Asexual clones → Sexual populations
Organisms with well developed limbs and nervous systems	Protists → Animals, plants, fungi (cell differentiation)
Homeotherms	Solitary individuals → Colonies (non-reproductive castes)
Human beings	Primate societies → Human societies (language)

dering natural entities according to their degree of "perfection." It could also show "evolutionary progress," a preoccupation of evolutionists through the mid-twentieth century, and perhaps even today (Ruse, in press). Typically, rankings on both scales have been crudely anthropocentric, with organisms ordered roughly according to their similarity or proximity to human beings (e.g., Huxley 1942; Rensch 1960b, Stebbins 1969). The Great Chain was ostensibly abandoned long ago in biology, and progress has been decried in recent years as a value-laden and culturally embedded notion (Gould 1988a). But the impression of an ordering along the same lines—from bacterium to human (Fig. 1)—is still widespread (Ruse, in press; Lewin 1994). And with the older terms now recognized as unscientific, it is reasonable to wonder whether the word "complexity" (as it is commonly used) is just a modern substitute, a kind of code word for perfection, progress, and proximity to us.

Indeed, the word has proved vague enough to accommodate the subtle shifts in meaning needed to make a bacterium-to-human sequence cohere and appear to meet a more contemporary standard. For example, Stebbins (1969) discerned a "complexity" trend in the sequence in Table 1. He does not clearly say what he means by complexity, but in the early transitions, it seems to be physical nestedness. Self-replicating molecules are physically nested within prokaryotic cells, for example. But organisms with tissues are not nested within organisms with nervous systems. The vagueness of the word complexity makes it possible to shift unnoticed to a different standard in order to justify the next step toward human beings.

Szathmáry and Maynard Smith (1995; Maynard Smith and Szathmáry 1995) compose a similar list of transitions in "complexity" (Table 1) and argue that each transition "depended on" changes in the way information is transmitted. However, they do not explain the sense in which each transition *is* an increase in complexity; they simply assert that it is. They note that some transitions share certain features, such as nestedness of parts and division of labor. However, no one feature or set of features characterizes all transitions. These transitions undoubtedly occurred and the explanations offered are plausible and provocative, but it is not clear that any consistent standard of complexity—other than proximity to humans—is being applied.

The notion that humans are especially complex either morphologically or developmentally, hierarchically or nonhierarchically, is not warranted by any reliable evidence I know. It would be surprising if the human *brain* were not extraordinarily complex, in some sense and at some scale (Katz 1987). On the other hand, great complexity might be expected in any hypertrophied and specialized structure. It would be equally surprising if the magnificent arborescent tentacles of sabellid annelids were not more complex than those of other annelids. I do not assert that tentacles add as much to sabellid complexity as the brain adds to human complexity; no basis for comparison presently exists. The purpose of the example is to disturb complacent imaginations, and to suggest that with all specializations taken into account, it is not at all obvious that humans are more complex than other species.

What Is Complexity?

If studies of trends in complexity are going to amount to more than ad hoc justifications for a temporalized Great Chain of Being or a belief in progress, then explicit, operational standards (consistently applied) are essential. A basis for such standards is provided by the narrow view, in which the complexity of a system is an increasing function of the number of its parts or interactions. For organisms, at least four types of complexity can be distinguished: nonhierarchical morphological, nonhierarchical developmental, hierarchical morphological, and hierarchical developmental. The types are conceptually independent and each requires a different sort of metric.

The narrow view also makes it possible to address questions about the relationship between complexity and other variables. Are complex organisms more specialized and therefore more prone to extinction (see studies by Flessa et al. 1975; Schopf et al. 1975; Anstey 1978; Boyajian and Lutz 1992)? What sort of environments favor the evolution of complex structure (Hughes and Jackson 1990)? Are complex organisms more or less evolvable (Wagner and Altenberg, in press)? With complexity defined broadly or vaguely, only rhetorical answers are possible. But with the four types clearly distinguished and operational metrics devised for each, wide avenues of research are opened.

Intuition and Evidence

Has there been a trend in metazoan complexity? 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, the current evidence is not much more helpful. At least an early Phanerozoic trend occurred in mean and maximum nonhierarchical 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 using metrics tailored to each group. If a (driven) trend occurred in metazoans, then increases should predominate among groups.

For nonhierarchical 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 nonhierarchical development, an early Phanerozoic trend (at least) occurred in gastropods. For hierarchical morphological complexity, mean individuation at the colony level 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. The mean complexity of a substructure increased in ammonoids over the first part of their history, but declined after that. For hierarchical development, trends in variability are consistent with increasing depth of developmental interactions (although other explanations cannot be ruled out) in arthropods and blastozoans, but not in trilobites and blastoids.

An Emphatic Agnosticism

Increasing complexity has been a recurrent and central theme in evolutionary studies for almost two centuries (see Lamarck 1809). On a matter of such long standing and of such moment, it is tempting to take a stand either for or against the traditional view. And if a choice had to be made now, we would have to conclude, I think, that the mean and maximum for at least some types of metazoan complexity increased over the Phanerozoic, although not consistently and in some perhaps not lately. Only a few groups at most have been examined for each type, but a trend was found in most cases. And even if no tendency to increase among groups is detected ultimately, the possibility of a passive trend remains.

However, if we take our biases seriously, then trend documentation should meet a higher standard of proof. My own view is that the cell-type data are too sparse and too ambiguous, and the sample of metazoan subgroups studied is too small, to justify either accepting or rejecting the traditional view—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. From this viewpoint, the evidence so far supports only agnosticism, indeed it supports an emphatic agnosticism.

What, if Anything, Is Increasing?

A survey in the imagination of the history of life suggests to many people that *something* has increased. In the *Origin of Species*, Darwin called it "organisation." He wrote:

> "The inhabitants of each successive period in the world's history have beaten their predecessors in the race for life, and are, in so far, higher in the scale of nature; and this may account for that vague yet ill-defined sentiment, felt by many paleontologists, that organisation on the whole has progressed" (Darwin 1859:345).

The ill-defined sentiment persists. Since Darwin, many other candidates for the "something" have been proposed, including ability to obtain and process information about the environment (Ayala 1974), independence from the environment (Wake et al. 1986), energy intensiveness (Vermeij 1987), entropy (Brooks et al. 1989; Weber et al. 1989; Swenson and Turvey 1991), and others (Fisher 1986; Nitecki 1988; Raup 1988). Given the historical background and the power of culture to penetrate perception, it is reasonable to wonder whether this impression of large-scale directionality is anything more than a mass illusion. Still, the point here is not to deny that directionality exists. Something may be increasing. But is it *complexity*?

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