

Complexity and Evolution: What Everybody Knows

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ABSTRACT: The consensus among evolutionists seems to be (and has been for at least a century) that the morphological complexity of organisms increases in evolution, although almost no empirical evidence for such a trend exists. Most studies of complexity have been theoretical, and the few empirical studies have not, with the exception of certain recent ones, been especially rigorous; reviews are presented of both the theoretical and empirical literature. The paucity of evidence raises the question of what sustains the consensus, and a number of suggestions are offered, including the possibility that certain cultural and/or perceptual biases are at work. In addition, a shift in emphasis from theoretical to empirical inquiry is recommended for the study of complexity, and guidelines for future empirical studies are proposed.

KEY WORDS: Complexity, entropy, evolution, evolutionary trends, Herbert Spencer, progress.

A CONSENSUS ON COMPLEXITY

Everybody seems to know that complexity increases in evolution. Darwin¹ thought it does, as did E.D. Cope, Herbert Spencer, and most of the Anglo-American paleontological community from the last decade of the nineteenth century through the first three of this one (Swetlitz 1989). At mid-century, the consensus was still intact. Some of the major Modern Synthesis authors, notably Huxley (1953), Rensch (1960), and Simpson (1961)², said that complexity increases; and Goudge, in his 1961 book *The Ascent of Life*, included increasing complexity in a list of large-scale evolutionary patterns widely accepted among evolutionary biologists.

More recently, some have expressed doubts (Williams 1966; Lewontin 1968; Hinegardner and Engelberg, 1983), but increasing complexity is still the conventional wisdom. Clear statements that complexity increases can be found in the work of Stebbins (1969), Denbigh (1975), Papentin (1980), Saunders and Ho (1976, 1981), Wake et al. (1986), Bonner (1988), and others. And lately the new thermodynamic school of thought has added its voice to the chorus: Wicken (1979, 1987), Brooks and Wiley (1988), and Maze and Scagel (1983) have all argued that complexity ought to and does increase in evolution. In my own

experience, the consensus extends well beyond evolutionary biology and professional scientists. People seem to know that complexity increases as surely as they know that evolution has occurred. (For a recent declaration from the mainstream press, see Wright (1990).)

Does complexity *in fact* increase? Is the conventional wisdom true? Very little evidence exists. Empirical inquiries have been few; instead of gathering and evaluating data, students of complexity have been preoccupied with theorizing, with developing rationales for why escalating complexity is the expectation. Further, both empirical and theoretical studies have lacked rigor; for example, missing from most (until recently) have been clear discussions of what complexity means.

I will begin with a discussion of the modern solution to the question of meaning. Then, capitulating to the historical dominance of theory over evidence, I will discuss the various rationales that have been offered for why complexity ought to increase. Turning to the evidence, I will argue that not enough evidence exists to make an empirical case either for or against increase. Finally, guidelines for future empirical studies will be suggested and some explanations offered for what has sustained the consensus on complexity in the absence of evidence.

A preliminary word on progress in evolution: this discussion both is and is not about progress. It is not, because despite the historical connection between progress and complexity, the two should be divorced, as I will argue later. For now, I simply ask the reader not to equate complexity with progress. However, progress *is* relevant here on account of its historical association with other apparent evolutionary trends, such as increasing adaptability and increasing control by organisms over their environment (discussed by Simpson 1949). On the basis of my limited investigation, I strongly suspect that the critique of complexity offered here could be applied to most other aspects of progress with little revision.

WHAT IS COMPLEXITY

Until recently, the word complexity has been used casually in the evolutionary literature, and interchangeably with "order" and "organization", to denote properties of organisms that seem to improve or progress in evolution. In the past 30 years, however, as students of information theory have begun to apply their concepts and formalisms to living systems, some essential clarifications have been made. There is some consensus now that the structural or morphological complexity of a system (biological or otherwise) is some function of the number of different parts it has and the irregularity of their arrangement (Kampis and Csányi 1987; Hinegardner and Engelberg 1983; Wicken 1979, 1987; Saunders and Ho 1976). Thus, heterogeneous, elaborate, or patternless systems are complex.

Order is the opposite of complexity (Wicken 1979). An ordered system has

few different kinds of parts arranged in such a way that the pattern is easily specified. Homogeneous, redundant, or regular systems are ordered, such as the atoms in a crystal lattice or wallpaper patterns. Organisms have sometimes been described as well ordered, and for some the central problem in biology has been explaining the generation of order (e.g., Needham 1936), meaning the origin and subsequent evolution of life. However, in the modern definitional scheme, organisms are not especially well ordered (although they are well organized, as discussed below).

Organization refers to the degree of structuring of a system for some function, independent of its complexity and order (Wicken 1979; although see Atlan 1974). Complex systems may be organized, as an automobile is, or disorganized, as a junk heap is (ordinarily). Both the automobile and the junk heap are complex, because they have many parts and the parts are irregularly arranged. This conceptual separation of complexity (a structural property) and organization (a functional property) is important, because we want to be able to evaluate structure even if we know little about function. The junk heap may be functional: for example, it may function as a work of art (perhaps one requiring a very specific arrangement of parts). On the other hand, it may be a haphazard pile of parts with no function. The point is that we do not have to know anything about its function in order to judge that its structure is complex.

In this definitional scheme, there is no necessary connection between complexity and organization. In evolution, however, complexity and organization probably *are* connected, because more complex organisms need more organization in order to survive (Saunders and Ho 1976).

Complexity has been discussed recently in a number of different contexts. For example, much has been written about the complexity of number sequences and geometric patterns (for recent commentaries, see Landauer (1988) and Maddox (1990)). In biology, some current topics are the complexity of biological hierarchies (Salthe 1985), of evolutionary clades (Brooks and Wiley 1988), and of genetic systems (see Subba Rao et al. (1982) and Gatlin (1972) on genome "information content," which is a kind of complexity).

The present discussion is concerned only with morphological complexity, which is a property of physical systems like organisms (as opposed to abstract systems like number sequences). More specifically, the focus is the morphological complexity of biological individuals (as opposed to, say, genomes or ecosystems). I leave it to others to discover the extent to which my remarks apply in other complexity domains.

MECHANISMS FOR INCREASING COMPLEXITY

Most theories of complexity increase can be classified as either internalist or externalist. (This division follows Gould's (1977a) classification of theories of directional evolutionary change.) Internalist theories conclude that complexity increase is driven by inherent properties of either complex systems generally or

of organisms in particular – their design, genetics, and development. Externalist theories invoke natural selection or some aspect of the environment. A few remaining theories invoke no driving force at all.

Internalist Mechanisms

1. *Invisible fluids.* Lamarck (1809) believed that simple organisms arise spontaneously and that their lineages transform over time in the direction of increasing complexity. Driving these transformations are invisible fluids, present initially in the environment and kept in constant motion by the sun's energy. Somehow these fluids become bottled up inside of organisms, and once there, they act internally. Lamarck writes:

... when reflecting upon the power of the movement of the fluids in the very supple parts which contain them, I soon became convinced that, according as this movement is accelerated, the fluids modify the cellular tissue in which they move, open passages in them, form various canals, and finally create different organs, ... (Lamarck 1809, p. 2).

The effect of adding new canals, organs, and so forth is to enhance complexity. The effect of the environment is mainly to deflect or retard the process.

2. *The instability of the homogeneous.* Spencer (1890) argues that dynamic systems tend to become more concentrated and heterogeneous as they evolve. He calls this tendency the Law of Evolution, although by "evolution" he means directional change in a wide variety of dynamic systems, not just living ones. The abstract argument is this: given a homogeneous and diffuse collection of identical particles, let the collection begin to aggregate under the influence of various natural forces (such as gravity). As it does so, particles in different positions within the aggregate will find themselves in different environments (inside as opposed to outside, for example) and thus will experience different forces. Differences among the forces cause differentiation among the particles, thus increasing the heterogeneity or complexity of the whole system.

The law has a corollary: when fully aggregated and fairly homogeneous systems do manage to arise, they are unstable, because they are unable (in the long run) to maintain the identity and internal relations of their parts in the face of external perturbations. The instability is not exactly driven. It is not that of a stick balanced on its end, Spencer explains, but rather that of balanced scales, which eventually become unbalanced due to rust, abrasion, wind, and such.

Spencer's Law is clearly internalist. The corollary relies on external perturbations to trigger differentiation, but the instability which makes change possible is an internal condition. His law is supposed to capture a universal developmental principle, in the tradition of the *Naturphilosophen*, and its debt is to von Baer in particular (Gould 1977b).

3. *Repetition and differentiation of parts.* Cope (1871) offers a mechanism derived from Haeckel's principle that evolution occurs by the acceleration of

ontogenies (the speeding up of organismal development) and the terminal addition of parts (Richardson and Kane 1988; Gould 1977b). In Cope's mechanism, acceleration results in the repetition of existing parts, and their subsequent differentiation produces complexity, with both processes driven by an internal "growth force." Cope acknowledges another ontogenetic mechanism, retardation, which can (and frequently does) decrease complexity, but on average parts and differences accumulate and complexity increases.

Gregory (1934, 1935a, 1935b, 1951a) offers a similar mechanism: evolution occurs mainly by duplication of parts, producing a morphological condition he calls polyisomerism, and differentiation of parts, producing anisomerism. Gregory uses language that suggests his mechanism is internalist, consciously adopting Cope's phrase "anteroposterior repetitive acceleration" to describe one kind of polyisomerism (Gregory, 1934), and referring at one point to polyisomerism as "an inherent property of protoplasm" (Gregory 1935a). He is cagier, however, about the forces of anisomerism; his remarks on the subject are few (Gregory 1935a, 1951a) and open to either internalist or externalist interpretation.

4. *The path of least resistance.* Saunders and Ho (1976, 1981) suggest that component additions are easier to achieve in development than component deletions, because components already present will tend to have been integrated into developmental pathways and thus will be hard to remove. The asymmetry is slight but sufficient to drive an evolutionary trend in complexity, they aver (but see Castrodeza 1978).

5. *Complexity from entropy.* There is currently much enthusiasm for the view that rising complexity has something to do with the Second Law of Thermodynamics. However, while much has been said about the role of non-equilibrium principles in complexity increase in prebiotic evolution (Prigogine et al. 1972; Wicken 1979, 1987), organismal ontogeny (Robson et al. 1988), speciation and diversification (Brooks and Wiley 1988), and ecological succession (Salthe 1985; Wicken 1987), clear discussions explicitly linking the Second Law and *morphological* complexity are hard to find. From what *has* been said, I have pieced together two possible versions of a thermodynamic argument.

One version begins with the observation that dynamic systems far from thermodynamic equilibrium spontaneously develop complex structure and that complexity increases as the systems grow and age (Salthe 1985; Wicken 1987). If evolutionary lineages are also far-from-equilibrium systems, then structural complexity might be expected to rise in all of them. Here the connection between the non-equilibrium condition and complexity is purely empirical. A mechanism is presumed to exist, but it is not known in any detail.

In a second version, entropic change would lead to morphological complexity by promoting what Wicken calls "configurational disorder" (Wicken 1987, p. 179). This disorder would have two consequences in evolutionary lineages: the building up of some morphologies by the addition of components (along

with the breakdown of some others); and the scrambling of arrangements of existing components (in all lineages). Most disorderings in most lineages would be disadvantageous, but some would be functional improvements, and these would tend to be preserved. Increasing complexity, in this version, consists of a raising of the upper level of functional disorder.

Externalist Mechanisms

1. *Selection for complexity.* Rensch (1960) suggests that the addition of parts permits more division of labor among the parts, and that therefore complex organisms are more efficient. The superior efficiency of complex organisms gives them a selective advantage, and this advantage drives complexity upward in evolution. Bonner (1988) makes this same argument and extends it: selection not only directly favors greater efficiency (which can be achieved by increasing complexity) but also favors large size, which may in some cases demand more efficiency, which in turn may require more complexity.

2. *Selection for other features.* Complexity itself may not be advantageous and yet may increase passively as a consequence of natural selection for other characters. In particular, selection for large size can permit increases (e.g., Rensch 1960; Katz 1987). Accompanying greater size may be greater cell numbers or tissue bulk beyond what is functionally necessary, thus freeing the redundant cells and tissue to vary. The resulting variation, or differentiation, is complexity. Rensch's version of this mechanism has a Spencerian spin: increase in body size makes possible a greater range of variation in environments within an organism. Different environments make different demands on local cells, leading (via natural selection) to cellular differentiation.

More generally, redundant parts, whether produced by selection for large size or any other process, are free to be modified by selection, and their modification has the incidental consequence of greater morphological complexity. Darwin expressed the principle nicely, in passing, in a discussion of morphology:

We have formerly seen that parts many times repeated are eminently liable to vary in number and structure; consequently it is quite probable that natural selection, during a long-continued course of modification, should have seized on a certain number of the primordially similar elements, many times repeated, and have adapted them to the most diverse purposes (Darwin 1859, pp. 437–438).

Here, selection drives the adaptive modification of parts, which results in complexity, but complexity itself is not directly favored.

3. *Niche partitioning.* Waddington (1969) suggests that as organismal diversity increases, niches become more complex. The more complex niches are then filled by more complex organisms, which further increases niche complexity (because niches are partly defined by these organisms), thus sustaining a cycle of ever-increasing complexity.

Undriven Mechanisms

1. *Random walk.* Fisher (1986) proposes two mechanisms for producing any sort of evolutionary trend, both requiring no driving force at all. One is simple luck: most evolutionary lineages could, by chance alone, happen to wander in the direction of higher complexity.

2. *Diffusion.* Fisher further suggests that if complexity in every lineage follows a random walk, decreasing as often as it increases on average, and if there is a complexity floor (a minimum below which no lineage can go), then the mean complexity of all lineages is expected to go up. Stanley (1973) offers the same logic as an explanation for the evolutionary trend in size described by Cope's Rule.

Maynard Smith (1970) makes the suggestion that if the first organisms were and had to be simple, then later ones could only have been more complex. The reasoning is the same as Fisher's but considers only a limiting case, namely the first moments of evolution when the only existing lineages sat right on the complexity floor and had nowhere to go but up.

3. *The ratchet.* Stebbins (1969) proposes that major evolutionary jumps in complexity occur occasionally in the adaptive radiations accompanying the invasion of new habitats. The complexity increase in such adaptive radiations is not inevitable, not the consequence of relentless driving forces, but rather is contingent on the prior existence of promising morphological specializations in the radiating group. New levels of complex organization achieved in these occasionally successful radiations are conserved, however, and lay the foundation for future jumps. Over the long haul of evolution, the result is a ratcheting upward of the upper limit of complexity.

The main purpose of this list is to document the heavy emphasis on theorizing. The list recalls the characterization by Vogt and Holden (1979) of the superabundance of theorizing in the dinosaur extinction debate as a case of "the multiple working hypotheses method gone mad." As in the dinosaur case, few of the hypotheses or mechanisms have been refuted. (Lamarck's mechanism especially sounds false, but the major fault may be simply his language, invisible fluids now being unfashionable.) Unlike the dinosaur case, the main problem is a paucity of data, as I argue below.

The list is also a small data set for further study of the relationships among the mechanisms. In particular, the mechanisms share many similarities, some offering about the same product but in different packages. Consider Spencer's instability of the homogeneous, which predicts an increase in complexity in an aggregating system by the accumulation of perturbations. This sounds a lot like complexity from entropy and also a lot like complexity permitted by size increase. Consider the Saunders and Ho argument that deletions are less likely on account of their developmental entrenchment. This sounds like selection against deletions, selection that acts at the embryo stage; they intend their

mechanism to be internalist, but it has an externalist interpretation too. Even Lamarck's mechanism may be redundant: in some lights it looks vaguely thermodynamic. Finally, where the products seem to differ, they share many of the same ingredients. For example, most depend on some kind of ratcheting process, and most can be construed as variations on the repetition-and-differentiation-of-parts theme. Considering the large number of striking similarities among these mechanisms, the possibility seems worth investigating that they are all, at bottom, the same.

THE EVIDENCE ON COMPLEXITY

In what follows, I characterize and critique the empirical evidence that exists on complexity change, covering mainly the work of the principal students of complexity since Darwin: three internalists – Spencer, Cope, and (probably) Gregory; two externalists – Rensch and Stebbins; and the several moderns. Broader coverage is unnecessary, because most of the remaining evidence in the literature consists of isolated and casually treated examples of increase. The literature is baroquely ornamented with these examples, and while together they add much to the apparent bulk of the evidence, they add little to its mass.

The purpose of critiquing the work of these serious students of complexity is not to diminish it. For one thing, the point is more to discover if enough evidence exists to make a case today than to prove a case has not been properly made in the past. For another, some of the work considered is only secondarily concerned with complexity; its authors had more general concerns, such as evolutionary progress, and can hardly be faulted if they failed to make a different point than they intended. Finally, the purpose of any such critique is to learn lessons from the inevitable mistakes attending all first efforts. We applaud those efforts for their courage rather than damn them for their errors.

The Internalists. – Spencer (1893) considers the evidence from the plant and animal kingdoms separately, but finds the same pattern of complexity change in both. His strategy is to arrange a number of existing plant and animal species along a scale according to their relative degrees of integration, which for Spencer encompasses degree of autonomy of wholes from their parts (organisms from organs, organs from cells, etc.), degree of physical cohesion among parts (mainly cells), depth of hierarchical organization (number of levels of subunits within subunits), and degree of interdependence of parts. Protozoans, for example, he describes as mere aggregates of protoplasm and assigns to the first order of integration, while sponges, coelenterates, and others are aggregates of first-order aggregates and thus belong to a second order. He assumes that the more highly integrated organisms arose from the less, and in accordance with his Law, these will also be the more highly differentiated and thus the more complex.

Spencer gives numerous other examples of evolutionary (biological sense) transformations that agree with his principle (Spencer 1890). Using worms as

ancestors of crustaceans, insects, and arachnids, he points out that the transformation involved an aggregation of body segments to produce a smaller number of more integrated units. Using trilobites as ancestors of the crustaceans, he notes a progressive differentiation of the limbs; among the vertebrates, the transformation from fish to reptiles to mammals and birds is marked by increasing heterogeneity of the vertebral column. This is only a small sample of his biological examples; he also gives innumerable examples from other realms, invoking the same principle to explain the differentiation of the planets in the Solar System from a homogeneous nebula, of social roles in advanced societies, of words in modern languages, and much more.

Cope's discussion centers on differentiation in the elements of homologous series, such as limb bones, teeth, and vertebrae (Cope 1871), while Gregory's major example is the reduction and differentiation of the skull bones in the evolution of the vertebrates (Gregory 1935b). For both, these are just focal cases among many; their discussions are shorter than Spencer's but no less densely packed with examples.

All three use examples of the same sort, and their evidence shares the same major weakness. That is, the examples were deliberately chosen in order to make a case for what we might call uniform complexity increase, and no finite list can make that case. Explaining this point first requires a distinction: Ayala (1974) distinguished uniform progress, or progress which occurs in all lineages at all times, from net progress, or progress occurring occasionally or only in some lineages (resulting in an increase in the mean). A similar distinction can usefully be made for complexity. Spencer and Cope both posit developmental laws or forces that act pervasively, and for Gregory the forces producing polyisomerism and anisomerism, whatever their origin, act in a wide variety of contexts. All three expect complexity to rise in all or most lineages, something more like uniform increase than net increase.

Now the point: instances chosen and marshalled in order to prove that a principle operates everywhere and always can do no better than to show that it has operated in those instances. Ten, a hundred, even a thousand photos of blue-eyed unicorns do not make the case that unicorns are uniformly (or even predominantly) blue-eyed if those animals were picked and photographed just to build that case.

For complexity, a long list of instances in which developmental forces have acted may *seem* to build a case, but really it cannot show that the forces have acted in all, most, or even a sizable percentage of lineages. Good evidence would consist either of a complete list of all instances, or more practically, of an arbitrary or random sample. In a large random sample, robust patterns of change should emerge as statistical regularities (Gould et al. 1987).

The Externalists. – Stebbins (1969) identifies eight grades of "complexity of organization," the lowest being the earliest self-reproducing organic systems, followed by the prokaryotes, the single-celled eukaryotes, the simple multicelled eukaryotes, organisms with differentiated tissues and organs, organisms with well-developed limbs and nervous systems, homeotherms, and finally human

beings. He then observes that the order of levels corresponds well with time of appearance in the fossil record, suggesting a progressive increase in maximum complexity of organization. Rensch (1960) uses roughly the same strategy, but his grades are mainly levels of functional sophistication (e.g., in digestion or vision) rather than structural organization.

Stebbins and Rensch, unlike the internalists, use evidence appropriate to their cases. They seek to demonstrate only a net trend, a raising of the upper level, and they properly do so by trying to document the transitions in which net increase occurred. Nevertheless, their evidence does little to help support a case for increasing complexity. For Stebbins, the complexity of an organism seems to be its hierarchical depth (number of levels of nested subunits), but he is not consistent. On this understanding, it seems clear enough that multicelled organisms are more complex than single-celled and that those with cells grouped into tissues and organs are more complex yet. However, the later transitions, to better nervous systems and then to homeothermy, do not seem to increase hierarchical depth. For these changes, Stebbins appears to have a different idea of complexity, and his ordering is strongly reminiscent of the old *Scala Naturae*.

Maynard Smith (1988) has assembled a similar list showing changes in hierarchical organization, a list which also seems reasonable up to the point of multicellularity. His next two organizational levels, demes and then species, however, do not correspond to evolutionary transformations in time.

Rensch is more consistent, but his evidence is no more helpful for present purposes. He is interested mainly in evolutionary progress, which he calls anagenesis, only one aspect of which is increasing complexity; other aspects are increasing rationalization of structure and function, increasing plasticity, and so on. A rise in any one of these constitutes anagenesis, although he clearly thinks they are somewhat correlated, and so the instances that constitute his evidence for anagenesis do not by themselves support a case for complexity increase. (Where he discusses complexity alone, his few examples do more to show what he means by complexity than to document major evolutionary transitions.)

The Skeptics. – Williams (1966) questions whether recent animals are more complex than Paleozoic members of the same taxa, noting that, for example, the skulls of Devonian fishes had far more bony elements and thus were far more complex than the human skull. He also points out that some organisms typically considered “low” or “simple”, such as the liver fluke, have enormously complex life cycles in which they take on a large diversity of forms.³ His message is that decreases are common, complexity is difficult to measure, and the risk of gross error in making casual assessments is high. The more recent skeptics (e.g., McCoy 1977; Hinegardner and Engelberg 1983) give a few, somewhat different, examples but make the same points.

The skeptics do a good job of illustrating the difficulties in many analyses of complexity, such as the lack of objective measures, but they provide us with no evidentiary case against the existence of a trend. A case against a *net* trend in complexity would require at a minimum a demonstration that the major transitions cited by Rensch, Stebbins, and others do not constitute increases; for

that purpose, the skeptics examine the wrong examples and treat them too briefly. For a uniform trend, a series of deliberately chosen examples, such as the comparison of fish and human skulls, no more weighs against than the lists of the internalists weigh in favor.

The Moderns. – Cisne (1974) studied evolutionary changes in limb tagmosis (complexity) of free-living aquatic arthropods. He defined tagmosis as the amount of information needed to specify the diversity of limb-pair types and calculated it (using an expression from information theory) as a function of the total number of limb-pairs and the number of each type. Cisne compared tagmosis values in a series of four malacostracan crustacean groups that may correspond roughly to an evolutionary lineage, and found a pattern of continuous increase. He also plotted mean values for all orders worldwide against time and found a trend in the shape of a logistic curve spanning the past 600 million years.

Cisne's result has a number of difficulties. For example, Van Valen (personal communication) has shown that if complexity is measured with a simple count of number of different leg-pair types (rather than the information-theory metric), complexity still increases, but the logistic curve disappears. And Raup (personal communication) has shown that the monotonic trend is an artifact. That is, the arthropod orders fall into two groups, an earlier one (trilobites) with low tagmosis values and a later one with higher values; the monotonic trend is a consequence of averaging in the time period of overlap, the later Paleozoic. Cisne's data show, therefore, not a pattern of continuous increase, but a single increase in the later Paleozoic.

The approach has considerable merit, however. First, Cisne provides a clear, operational definition of complexity. Second, he does not seem to have chosen arthropod limb types for the reason that they help make a case for complexity increase; more likely, his metric required easily differentiable, serial structures, and arthropod limbs were convenient. If so, then arthropod limb types are an arbitrary sample of all possible characters in all groups, and his study does provide some evidence for uniform increase. His sample size, a single character in a single group, is of course quite small.

Bonner (1988) measured the complexity of an organism as the number of different cell types it has. The measure has the drawback that cell types are difficult to distinguish without careful histological studies and only very approximate counts are possible presently for organisms with more than about 10. The metric has the virtue, however, that it captures the complexity of a whole organism, rather than of just one or several structures. Also, it will work with almost all taxa, thus allowing comparisons of organisms as different as fungi and frogs.

Bonner did not try directly to show ascending complexity with time; rather, he showed that the size of the largest organisms increases and that complexity correlates with size. However, as he admitted, the correlation with size is weak, with some groups (e.g., vertebrates with 120 cell types and higher plants with 30 cell types) having size ranges spanning about 10 orders of magnitude and

broadly overlapping each other. The correlation between number of cell types and *maximum* size is better but still quite rough.

Consider one final empirical study, this one my own. From among a number of different analyses,⁴ I have deliberately chosen one that shows a decrease in complexity. This is hardly in keeping with the spirit of disinterested inquiry advocated earlier; I present it here mainly to offset the impression doubtless left by the discussion of Cisne's and Bonner's work that the modern studies show nothing but rising complexity.

Following Cisne, complexity is understood in this analysis as the amount of differentiation within a homologous series of elements. A different metric has been adopted, however, in order to accommodate series in which change in the shape of elements along the series is continuous and in which the elements therefore do not fall neatly into discrete types. The vertebral column is an example of such a series and the focus of my analysis. Figure 1 shows drawings of the vertebral columns of a lion and of a finback whale. Figure 2 shows a schematic drawing of a typical vertebra indicating the vertebral dimensions relevant to the analysis.

Complexity is measured as a function of the amount of variation along a column in a single vertebral dimension. (Figure 3 shows artificial data for centrum length in a short imaginary series of 10 vertebrae.) Actually, three different functions are used in order to capture three different aspects of that variation:

1. Range of variation (R). R captures complexity as the maximum difference between elements, or as the difference between the two elements that are most different (Figure 3).
2. Polarization, or overall complexity (C). C captures complexity as the average difference between the elements and their mean (Figure 3). The word polarization is appropriate because C is maximal when half of the elements lie at each of the two extremes of the range, that is, when all the elements are as different as possible from the mean.
3. Irregularity (C_m). C_m captures complexity as the average difference between adjacent elements. C_m values reflect the number and magnitude of reversals in the direction of change along the column, or in other words, the bumpiness of the curve in Figure 3.

Precise formulae for computing R, C, and C_m from raw vertebral column measurements appear in the caption to Figure 3, along with a summary of the various transformations used to correct for size differences and to remove redundancies among the complexity measures.⁵

The analysis consists of a comparison between certain aquatic mammals and their terrestrial ancestors, or more precisely, surrogates for those ancestors. Sufficiently complete vertebral columns for directly ancestral species have not been discovered, so their complexities are estimated using average values for a diverse assemblage of living terrestrial taxa. The substitution is reasonable, because what fossil vertebral material exists suggest that the ancestors of these

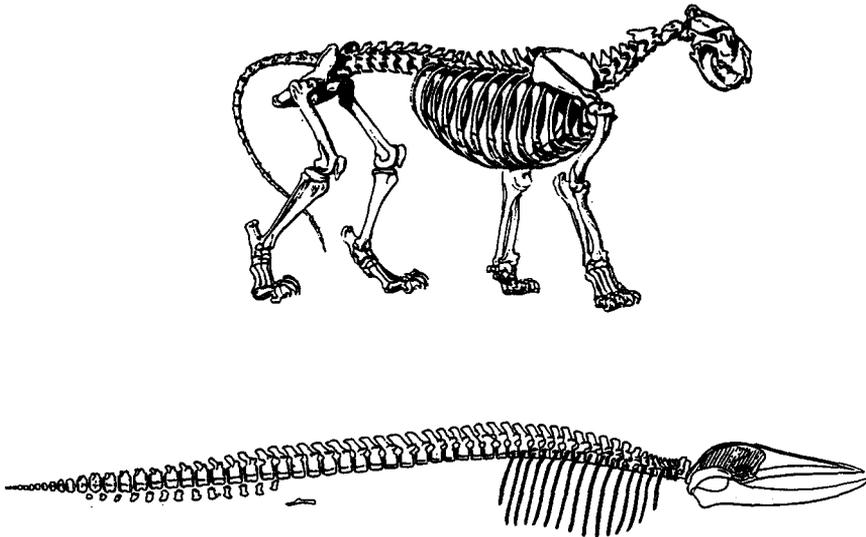


Fig. 1. Drawings (not to scale) of the skeletons of a lion (modified from Owen 1866, p. 493) and a finback whale (modified from Gregory 1951b, p. 899), showing their vertebral columns.

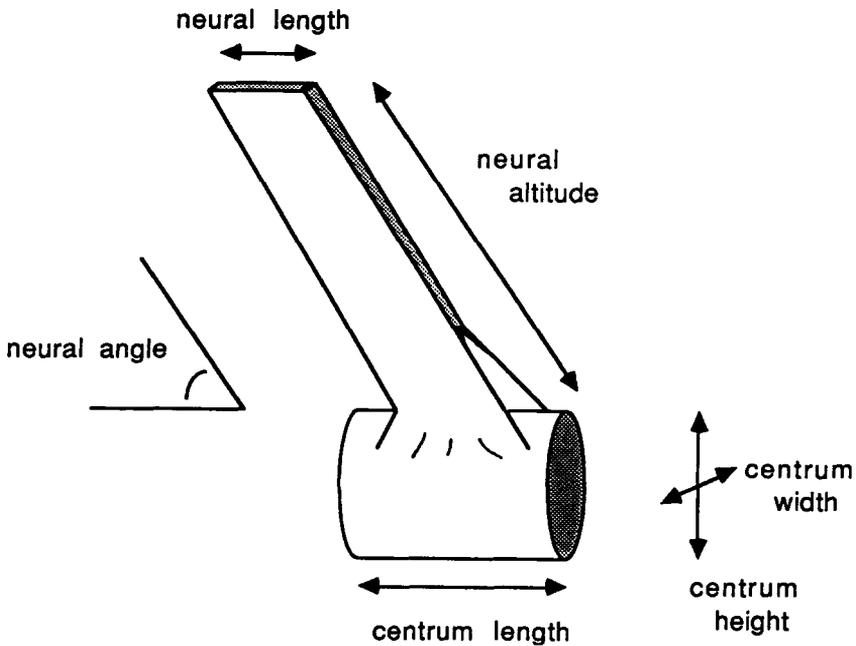


Fig. 2. A schematic drawing of a typical vertebra showing the vertebral dimensions relevant to the analysis.

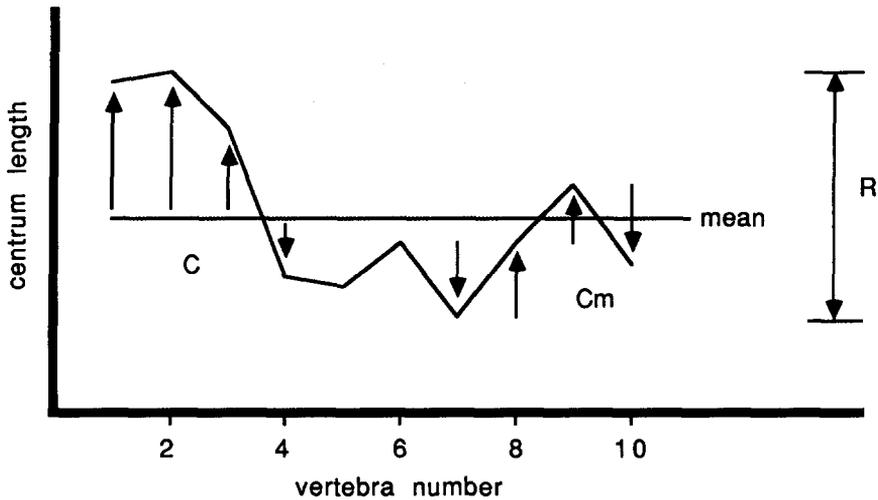


Fig. 3. A plot showing artificial centrum-length data for an imaginary column of 10 vertebrae, and the way in which the range (R), polarization (C), and irregularity (C_m) are calculated. R : the absolute difference between the longest and the shortest vertebrae (illustrated by the double-headed arrow on the right); C : the average absolute difference between each vertebra and the mean (shown for four vertebrae by arrows on the left); C_m : the average absolute difference between each vertebra and the one before it (illustrated for four vertebrae by the arrows on the right). In real columns, averages are computed over all vertebrae from the second cervical (the axis) to the last presacral (just ahead of the hip), inclusive. The formulae are as follows:

$$R = \log [X(\max) - X(\min)];$$

$$C = \log [2 \sum |X_i - \bar{X}| / N];$$

$$C_m = \log [\sum |X_{i+1} - X_i| / (N-1)],$$

where X_i is the raw measurement for the i th vertebra, \bar{X} is the mean, and N is the number of vertebrae. Size correction is necessary for comparison among taxa: size-corrected R , C , and C_m values are estimated as residuals from a reduced-major-axis, best-fit line in a plot of C values against the log of a size factor (in this case, average posterior-centrum area). R , C , and C_m are strongly correlated, so to remove redundancies, R' and C_m' are substituted for R and C_m , computed respectively as residuals from reduced-major-axis, best-fit lines in plots of R and C_m against C .

aquatic species (among the early Carnivora for the otter and the pinnipeds and among the Condylarthra for the whale and the manatee) had vertebral columns generally similar to modern terrestrial mammals. The reason for the similarity is that terrestrial support and locomotion is associated with a characteristic pattern of variation in the direction and magnitude of forces acting along the column, and to accommodate these forces, the columns of most terrestrial mammals must be differentiated in broadly similar ways.

TABLE 1

Results of comparisons of complexity values (R' , C , and Cm') for aquatic mammals with those of their terrestrial ancestors (estimated using average values for an assemblage of 24 diverse, extant terrestrial taxa). Aquatic descendants considered are an otter, a finback whale, a group of three pinnipeds (seal, sea lion, walrus; an average value for the three is used), and a manatee. Entries in the table indicate whether the complexity value for an aquatic mammal represents an increase (I) or a decrease (D) from the ancestral average. Significant differences ($p < 0.05$; marked with an asterisk) were identified using a bootstrap of the mean of the 24 terrestrials (and in the case of the pinnipeds, a simultaneous bootstrap of the mean for the three).

Descendants		Centrum height	Centrum length	Centrum width	Neural altitude	Neural length	Neural angle
Otter	R'	D*	D*	I*	D*	D	D*
	C	D*	D*	D*	D	D	I
	Cm'	I	D	I*	I	D*	D*
Finback whale	R'	D*	D*	D	D*	D*	no data
	C	D*	D	D*	D*	I*	no data
	C'	D*	D*	D*	D*	D*	no data
Pinnipeds	R'	I	D	D	D	D	I
	C	D	D*	D*	D*	D*	D*
	Cm'	I	D	D	D	D	D
Manatee	R'	D*	D*	D*	D*	D*	D*
	C	I*	I	I	D*	D*	D*
	Cm'	D	D*	D*	D*	D*	I

Table 1 shows the results of the comparisons. For all three aspects of complexity, most of the changes are decreases. Among the changes judged significant ($p \leq 0.05$), all but four are decreases. The table contains some redundancy: each vertebral dimension represents an independent test only to the extent that complexity values are uncorrelated, and while most pairwise correlation coefficients are low (only 6 out of 45 greater than 0.5), many are significant (14 out of 45, $p \leq 0.05$).

The decrease in complexity is almost certainly a consequence of adaptive modification of the vertebral column for life in the water. In terrestrial mammals, variation along the column in the forces associated with support and locomotion is quite high, so the columns of terrestrial mammals are highly differentiated, i.e., quite complex. Aquatic mammals are weightless in water, thus eliminating gravity as a source of stress on the column, at least for most aquatics (the otter and the pinnipeds are partly terrestrial). Further, they propel themselves mainly with simple fish-like undulations of the body (or tail), which produce a more symmetrical distribution of forces than does quadrupedal walking or running, for example. The vertebral columns of these aquatic mammals apparently evolved to accommodate the new regime of forces, their columns becoming simpler and more fish-like, especially in the case of the whale (Figure 1).

COMMENTARY AND RECOMMENDATIONS

To fill the (near) data vacuum, I encourage a shift in emphasis for the field of complexity studies from the theoretical to the empirical. Further, a high degree of rigor will be essential for future work, rigor which was largely absent in studies prior to Cisne's. For example, these studies do not define complexity operationally. That is, they give no careful explanation for how complexity is to be understood (or measured) that would enable anyone to repeat the analysis or to conduct a similar analysis independently.

Despite the recent consensus on meaning, specifying an operational metric remains a difficult problem. Useful metrics have been devised for whole organisms by Schopf et al. (1975) and Bonner (1988), for organic molecules by Papentin (1982) and Yagil (1985), for behavior by Cole (1985), and for nucleotide sequences by Gatlin (1972). Others are needed, especially ones applicable to whole organisms across a wide range of taxa.

Further, most temporal studies have not examined complexity change in true ancestor-descendant lineages, mainly because few fossils of directly ancestral species have been discovered (or have been identified as such). Rather, they substitute either a complexity value for a related species or an average value for a more inclusive taxonomic group of which the ancestor was presumably a member. No general alternative solution to this problem has been found, but close attention to the phylogenetic relationships among the taxa compared will be desirable in future studies.

A few other lessons follow from past work. Tests for uniform or overall complexity trends should cover a random sample of lineages and characters. And documenting net increase will require a more-than-casual study of the major transitions, with serious attention to the precise *nature* of the morphological changes occurring as well as the *sense* in which they constitute complexity increase. Finally, as Fisher (1986) and Gould (1988) note in their discussion of trends generally, patterns of change may vary with temporal and physical scale and may also have varied in absolute time, over the course of the history of life. As a consequence, a number of different kinds of empirical studies may be necessary before any generalizations can be made about patterns of complexity change. More detailed discussions of empirical approaches to the study of directionality in general, as well as the pitfalls of these approaches, can be found in Gould (1988), Hull (1988), Fisher (1986), and Raup (1977).

WHENCE THE CONSENSUS?

The case for increasing complexity in multicellular organisms is weak. Complexity must have increased early in the history of life, as Maynard Smith argues, if the first organisms were very simple, and the early transitions from unicellularity to multicellularity seem to be indisputable leaps in complexity. Since then, however, the only evidence is the trend Cisne found in a putative

lineage of malacostracan free-living arthropods, and the difference he demonstrates between trilobites and later arthropods. On the other hand, the evidence against a trend is also pretty thin.

Even if the evidence is negligible, we must still account for the impression, the gestalt, of increasing complexity that many experience in thinking about the history of life. To some extent, the conventional wisdom must be sustained by this gestalt; I suggest (without exploring) a few of its possible sources:

One is that complexity does increase, and that we unconsciously compute complexity differences between earlier and later organisms with some innate, cognitive algorithm, or even perceive differences directly, in ways that we simply cannot yet articulate. If so, then our only project is to discover how to say what we already know.

On the other hand, properties other than complexity might cause the gestalt. Comparing a cat with a clam, for example, many will get a vague impression that "something more" is going on in the cat. Is the "something more" greater complexity or is it greater intelligence, greater mobility, or greater similarity to us? Hard to say. Complexity has to do with number of different kinds of parts and the irregularity of their arrangement, and comparing parts and arrangements in cats and clams is not straightforward. They are anatomically *very* different animals. If cats seem to have more parts, it could be just that they are larger (on average), with parts that are easier to see and more familiar.⁶ (Recall Williams's warning.) Possibly, as one reviewer suggested, organisms simply look more and more *different* from modern ones as we scan further and further back in time; if the moderns are assumed to be very complex, then less familiar might be mistaken for less complex. The human perspective, like any other, has its biases.

Other possibilities: maybe the few spectacular (or even just clearcut) cases of complexity increase, such as the transitions to multicellularity, so dominate our reflections on evolution as to create the impression of a pervasive, long-term trend. Or we may simply read into evolution the trend in technology toward increasing complexity of devices.⁷

Another cultural bias may also be at work. We have the double tendency to read progress into evolution (see discussions in Ruse (1988) and Gould (1988)) and to connect complexity with progress. More complex organisms, like more complex machines, are commonly thought to have progressive qualities like efficiency or sophistication. I suspect that these connections enable us, by a kind of reciprocal reinforcement, to comfortably maintain (without close examination) pet notions of progressive evolution and complexity increase. On the one hand, complexity must increase because selection favors progressive qualities like efficiency. On the other, the "observed" increase in complexity in evolution provides an objective basis for a belief in progress. These connections may seem so obvious as not to require demonstration, but in the absence of demonstration it is reasonable to ask if they are real.

The point has been made that progress is a poorly defined concept because it is heterogeneous, encompassing such diverse elements as organismal efficiency, intelligence, autonomy, and so forth (Fisher 1986) and that this fault, along with

an inescapable evaluative or axiological component (Ayala 1974), make it unsuitable for empirical inquiry. Complexity is more specific, more concrete, and therefore more tractable, but on account of its historical and still-commonplace association with progress, it carries the axiological taint. This is unfortunate, partly because the taint will tend to spoil empirical analyses that are otherwise reasonably value-neutral. More importantly, even if a hint of the axiological were welcome, the connection is poorly thought out and may well be baseless; the complex may not be better, in any sense.

The gestalt of increasing complexity that emerges from an overview of the history of life is an unwavering one. We know, however, that gestalts, even steady ones, can mislead, and thus a study of its possible sources in perceptual or cultural biases seems worthwhile. In the meantime, some evidence on complexity change from the natural world would do much to clarify matters.

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NOTES

¹ Darwin did not discuss his views on large-scale evolutionary patterns of complexity change in the *Origin* but did so in his Notebook E (Darwin 1987, p. 422). His mechanism is similar to one proposed more formally by Waddington (see my discussion here under the heading "Externalist Mechanisms").

² Simpson is known for his skepticism on complexity, especially for his apt remark that "It would be a brave anatomist who would attempt to prove that Recent man is more complicated than a Devonian ostracoderm." (Simpson 1949, p. 252). However, he is forthright elsewhere: "Perhaps the most common assumption about evolutionary sequences is that they tend to proceed from the simple to the complex. Such an over-all trend has certainly characterized the progression of evolution *as a whole*." (italics original; Simpson 1961, p. 97).

³ Williams' example is salutary; it has become almost obligatory in discussions of complexity to make parenthetical mention of what is supposed to be an obvious decrease in complexity in the evolution of parasites.

⁴ Most of my analyses have been ancestor-descendant comparisons in mammalian lineages. Specifically, I compared modern squirrels, ruminants, camels, whales, and pangolins with their ancestors in a number of vertebral dimensions and found no tendency for complexity to increase. In fact, the number of complexity increases was about equal to the number of decreases for all three complexity metrics (see text).

⁵ The metrics are based on a view of morphological differences as built up of small, standard units of difference. (These units are just heuristics, and their absolute size need not be specified.) Thus, a large difference is composed of proportionally more standard-difference units than a small one – it has more parts, in a sense – and thus it is proportionally more complex. A more important justification, however, is that the metrics cor-

respond roughly to our intuitive idea of complexity. The correspondence is good, but not perfect: an alternating series, for example, has very high C_m but strikes most people as fairly simple. Fortunately, alternating series (and other series that would fool the metrics) are rare in vertebral columns.

⁶ Schopf et al. (1975) measure the complexity of a variety of taxa by counting the number of morphological terms used for each by anatomists. Mammals have about three times as many total terms as bivalves (which include the clams), and about three times as many terms per genus, which suggests that cats really are more complex. The metric is ingenious, but I think it does not overcome the human bias. Mammals might have more terms just because many more people, with interests spanning a wider range, have spent more total time studying them.

⁷ This suggestion is a modification of an argument by Ruse (1988) that evolutionists tend to read into evolution the *progress* that seems evident in technology and science. The trend in technological *complexity* is almost as salient, although some counter-examples come to mind: ramjet engines are at least superficially simpler than gasoline engines (in propeller-driven aircraft), and steel-beam arches seem simpler than the stone arches they succeed. The complexity trend in technology (like the one in evolution) might be worth closer examination. Has this been done?

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