



The Major Transitions of Evolution. by John Maynard Smith; Eors Szathmary

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simple conditions of life, and in some cases will even degrade or simplify the organisation, yet leaving such degraded beings better fitted for their new walks of life. (p. 330)

So-called living fossils, like the coelacanth, reveal that degree of morphological "complexity" can remain unchanged for long periods of time. Secondly eyeless cave-dwellers and secondarily flightless birds demonstrate that evolution can also involve decreases in morphological "complexity." Goodwin's theory of evolution cannot account for any of these phenomena.

It is incredible that someone who seeks to revolutionize the central organizing principle of biology should be so misinformed about the field. Goodwin selectively uses biological examples, while ignoring relevant data on the origin of spatial coordinates in embryos, the ubiquity of genetic variation, and the efficacy of natural selection. His implicit assumption that the developmental process itself requires no explanation reveals that he does not seek to explain complexity, but assumes it as a starting point. His logical fallacy of assuming that similarity of pattern demonstrates unity of mechanism reveals an underlying belief that only the simplest explanation can be correct. The subtitle of Goodwin's book—*The Evolution of Complexity*—is quite ironic, for the author leaves us with a greatly simplified view of evolution. In fact, A. C. Doyle's intuition appears to have been more accurate: "Life is infinitely stranger than anything which the mind of man could invent. We would not dare to conceive the things which are really mere commonplaces of existence" (1891, p. 31). In an effort to understand nature, we cannot be content merely to sit before computers and devise simple, appealing ways of explaining evolution.

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THE MAJOR TRANSITIONS OF EVOLUTION

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In their new book, Maynard Smith and Szathmáry take an approach that may change the face of evolutionary theory. They focus on the major transitions of evolution, such as the origin of life, and the evolution of eukaryotes, multicellular organisms, animal and human societies. In each of these tran-

sitions, smaller parts, already tested by the struggle for existence, join into larger wholes that become units of selection in their own right. Focusing on these transitions should reorient evolutionary theory in ways that will relate it more obviously to the rest of biology, and make it much easier to teach. This may be the most important book on evolution since Fisher's (1930) *Genetical Theory of Natural Selection*: there is every reason to hope that its impact will be far more immediate.

Analyzing these major transitions to learn how, in each case, parts are joined into larger wholes, may help biologists

¹ *The Major Transitions of Evolution*. John Maynard Smith and Eörs Szathmáry. W. H. Freeman, New York. 1995. xiv + 346 pp. \$29.95 paper.

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deal with creationists. I dwell on this topic because I consider that the vigor of creationism reflects a confusion and malaise within evolutionary theory (which this book should help cure). The thrust of creationism is primarily negative, as if, once natural selection were driven from the field, creationism would be accepted by default. Thus, creationists concentrate on denying that natural selection of such chance improvements as random mutation offers could possibly lead to the marvels of biochemical, morphological, and behavioral adaptation manifested by modern organisms. In fact, impugning the efficacy of natural selection cannot unseat the evidence for evolution. Indeed, Darwin's (1859) *Origin of Species* showed that if God did create the universe at one go some thousands of years ago, He clearly wanted us to think that the universe was much older, and that all living things descended from a common ancestor. Nonetheless, the creationists' approach works all too well: their ranks are swelled by fellow travelers put off by the way evolution was taught to them in school.

In reading this book, two methods of attacking the problem come to mind. One is to construct plausible scenarios for the pivotal events of macroevolution. A convincing explanatory account of how natural selection shaped the progress from nonlife to life, from prokaryotes to eukaryotes, from single-celled to multicellular organisms, and the like, could deprive creationism of many of its fellow travelers. Second, even if such a convincing explanatory account is beyond our reach, one can search for unmistakable footprints of the decisive role of natural selection in evolution. What could serve as such a "footprint"? Suppose, for example, that Fisher (1930) had succeeded in showing that the only advantage to recombination was that it permitted the simultaneous fixation of different favorable mutations, while many advantages accrued from diminishing or eliminating recombination. Then the prevalence of recombination would be unquestionable evidence of the vital importance of facilitating the spread of favorable mutations. This would be just the sort of unmistakable footprint I have in mind. Moreover, the prevalence of recombination would also suggest that new favorable mutations occur quite often enough to fuel adaptive evolution—a conclusion that should interest those creationists willing and able to follow this argument. In fact, the validity of Fisher's argument is far from settled, even though 65 years have elapsed since he presented it. Nonetheless, Maynard Smith and Szathmáry's comparisons of the means by which individual advantage was reconciled with or subordinated to the good of the group during these various transitions, will uncover other clear footprints of the importance of natural selection in evolution.

If one is to provide convincing scenarios of the pivotal events of macroevolution, it is crucial to make sense of the origin of life. A third of this book is devoted to this topic. It seems clear that life derived from entities where RNA served as both replicators and catalysts: the division of labor by which DNA serves as replicator and proteins as catalysts came later. Moreover, the origin of life must have involved various forms of complementation and cooperation between different RNA elements. This book's account of life's origin includes some superb Just-so stories, which give the reader a good sense of the nature of adaptation. Their account of

how and why the properties of the genetic code and the size of its alphabet came to be, is particularly lovely. Nevertheless, the treatment is so condensed, and presupposes so detailed a knowledge of biology and biochemistry, that much of it was lost on me. To summarize, the belief that we can eventually construct a "mechanistic" account of the "self-organization" of life from compounds in prebiotic "soups," droplets, or surface films is still most decidedly an act of faith. With an honesty worthy of Darwin himself, the authors point out that the gaps in their story are abundant, and some of them dismayingly wide. Even so, this faith is now appearing progressively more reasonable as new facts come to light.

This book does provide a coherent, if sketchy, account of mechanisms that can trigger and control differentiation. I can remember when it seemed impossible perhaps even in principle to explain how the mitotic multiplication of a zygote into genetically identical cells could cause morphogenesis and the differentiation of tissues. Deciphering that puzzle must be the most spectacular of the triumphs of molecular biology during the past 10 or 20 years.

At the moment, however, a convincing scenario of the evolution of human intelligence and reason seems further off than ever. We haven't the vaguest notion how to speak of the evolution of consciousness or self-awareness. Moreover, it is not yet clear whether evolutionary theory can "answer Kant's riddle as to how anything in the mind can be a representation of anything outside the mind" (Putnam 1992, p. 34). Wisely, the authors pass these questions by.

Looking for clear footprints of the role played by natural selection in the major transitions of evolution yields more immediate profit. To make sense of these transitions, we must learn how the entities involved benefited by joining in groups. Moreover, we must discover the means by which the common interest among a group's members prevailed over the dysfunctional behavior of "selfish" individuals, for only when natural selection "sides with" the common interest can it shape these groups into integral wholes. Buss (1987) showed how considering the means of suppressing potential conflicts between a cell and the multicellular organism to which it belongs could illuminate comparisons of morphogenesis and development among different phyla. Comparisons among all the major transitions of evolution—drawing, in effect, from all the stunning diversity of life—provide scope for comprehensive tests of hypotheses concerning evolutionary mechanism, which may help us identify the desired footprints of the decisive role of natural selection.

Thus, we are reminded that nowadays, as in Aristotle's time, biology draws its strength from comparisons. To show how Maynard Smith and Szathmáry deploy the comparative method, consider how they answer Fisher's (1930) question of why, in sexual organisms, the sexes are nearly always two. Theory shows that selection on organelles is more nearly subordinated to the good of their hosts if each host inherits all representatives of a given kind of organelle from one parent (see below). Are the sexes only two because this facilitates the uniparental transmission of organelles? They deduce the likelihood of this proposition by observing that the species which have many mating types never exchange cytoplasm or organelles when they mate. Hypotrichs "mate"

both by the fusion of gametes to form zygotes and by the exchange of nuclei during "conjugation." No cytoplasm is exchanged during conjugation, so there are many "conjugation types," but the gametes occur in just two sexes.

Now let us return to our major theme: How were groups of formerly independent entities transformed into integral wholes during major evolutionary transitions? For these transitions to occur, members of these groups had to share an identifiable common interest, and these groups had to be organized in a way that lent effectiveness to their common interest. In some transitions, groups become coherent wholes once the failure to cooperate becomes self-punishing. The authors show, for example, that once the ancestors of mitochondria could reproduce only by being transmitted "vertically" to their hosts' offspring, then an endosymbiont of this species that injures its host diminishes its own reproduction. Once these endosymbionts' reproduction depended so utterly on their hosts' welfare, their transformation into integral parts of their hosts was only a matter of time. Price's extension of Fisher's fundamental theorem of natural selection to compare the contribution to evolution of genetic variance among, relative to that within, groups, allows us to calculate how limited "horizontal" transmission of endosymbionts must be for selection among endosymbionts to be subordinated to their hosts' good (Crow and Aoki 1982; Leigh 1983; Frank 1994). I find it gratifying that Fisher's fundamental theorem turns out to be so helpful in analyzing the conditions under which selection within groups is subordinated to selection among groups. The ways by which conflicts between cells and their organelles are suppressed, and more generally, the means by which organisms suppress intragenomic conflict, provide clear footprints of natural selection's importance. To complete our understanding of the transition to eukaryotes, we need to learn how the ancestral mitochondria or chloroplasts trapped themselves, or were trapped, into their dependence on host reproduction. Did ancestral mitochondria "garrison" their host cells against invading conspecifics, as a house cat defends the house whose family it is "taking over" against other house cats (Gallico and Szasz 1985)? If their "territoriality" eventually eliminated opportunities for "horizontal transmission," it thereby helped to subject these ancestral mitochondria to selection in their host cells' interest.

In other transitions, some group members can force others to cooperate. Maynard Smith and Szathmáry tell how the queen of a honeybee colony "loses" if a worker diverts some of its colony's energy to rearing its own young rather than the queen's. By mating many times, the queen bee ensures that the overwhelming majority of a worker's comrades are half-sisters which share their queen's interest in suppressing that worker's reproduction, and express it by eating any eggs she does lay. More generally, they conclude (p. 258) that "To the extent that individual bees, ants and termites have lost the capacity to reproduce, they can propagate their genes only by ensuring the success of their colony, just as somatic cells can only propagate theirs by ensuring the success of the organism." (On p. 245, they criticize Leo Buss for thinking that sequestering the germ line helps enfeeble a metazoan's somatic cells to the good of their organism: I find this contradiction as incomprehensible as it is uncharacteristic). The

fact that really complex insect societies, such as honeybees or leafcutter ants, are societies where cheating is no longer a viable option, and where workers treat their queen as a valued resource rather than as a rival (Hölldobler and Wilson 1990) strikes me as another clear footprint of natural selection's importance.

In some groups, enforcement of cooperation is less "authoritarian." Maynard Smith and Szathmáry explain how, among sexual organisms, a segregation-distorter allele which spreads a harmful phenotypic defect through a population by biasing meiotic segregation-ratio in its own favor, injures both the individuals carrying this allele, and alleles at unlinked loci which cannot spread in linkage with the distorter but which suffer from the damage inflicted on the vehicles for their replication. The common interest of the genome in honest meiosis, which allows alleles to become more common only if they benefit their carriers, is enforced by natural selection for mutants at unlinked loci which suppress this segregation-distortion.

One of their transitions seems to require no enforcement at all. Maynard Smith and Szathmáry consider the evolution of sexual reproduction to be a major transition. Here, two individuals cooperate to produce more varied offspring, instead of each one "cloning" itself. This transition must have been a pivotal event which greatly speeded the rate of evolution. Nonetheless, comparing this transition with the others raises a host of questions. Whose interest does sexual reproduction represent: the interest of each reproducing individual, or a wider common interest? If we are dealing with a common interest, is it that of the mating couple, the species, or a higher-order phylad? What entity suffers if an individual clones itself rather than reproducing sexually? Who retaliates against parthenogens? Since a successful sperm contributes as many genes to future generations as a successful egg, half a population's reproductive effort is devoted to male functions. Anisogamy, however, allows males to contribute nothing but genes to their offspring. Thus sexual reproduction often imposes a 50% cost on its practitioners. It has been quite a struggle to show that sexual reproduction prevails if and when it is advantageous to its individual practitioners, but this seems to be true. It appears, moreover, that once sexual reproduction evolves, species may benefit from features that may prevent reversion to parthenogenesis. Thus mammals have certain tissues where, at some loci, only paternal genes are expressed, while among gymnosperms, chloroplasts are inherited through pollen. Nevertheless, sexual reproduction stands out as a case where cooperation evolved in the absence of mechanisms to prevent or punish noncooperation.

Too many of the comparisons this book offers are inadequately exploited. Their chapter 11 on symbiosis is based on a game-theoretic model which seems to have circumscribed their imaginations. The dominant concern of this chapter is how cheaters can be punished. In many mutualisms, however, punishment of cheaters is a small part of the story (although preventing cheating often bulked much larger during the origin of many of these mutualisms, and the mechanisms that render cheating self-defeating are clear footprints of the ghost of natural selection past). In particular, sexual reproduction is a form of cooperation that evolved without any provision

for punishing parthenogens. There is an abundance of “open” mutualisms, moreover, where each generation of hosts calls forth the guests they need from the environment. It is thus that trees acquire mycorrhizae, vestimentiferan worms their sulphur bacteria, and many corals their zooxanthellae. What keeps these mutualisms honest, if not a genuine community of interest between host and guest? Although such mutualisms of common interest are treated as enigmas in chapter 11, they are discussed with perspicacity and insight in chapter 16 on animal societies. Here, the authors distinguish between “sculling games,” where failure to cooperate leaves the cheater something valuable to “parasitize” if it stays in the group, and “rowing games,” where failure to cooperate destroys the group’s function.

With admirable courage, the authors extend their comparison to include the bases of cooperation in human societies. They begin with a model of a “social contract,” showing that cooperation is viable only if group members combine to punish noncooperators *and* anyone else who does not join in punishing these noncooperators. They recognize, however, that fear of punishment is rarely the primary reason for obeying social norms.

Two capacities play an essential role in the maintenance of human society. The first is self-awareness, which enables its possessor to “put itself in the shoes of others” in order to predict their behavior. Although the deceptions practiced by some apes on each other, and on their handlers, may provide the best evidence of self-awareness in nonhumans (Jolly 1991), the authors recognize its importance in a cooperative society. They say little about it, perhaps because it is difficult to test for in nonhumans, perhaps because it is hard to imagine a material basis for it.

The other requisite for human social behavior is language, which is also the most objectively measurable reason for the superiority of human mental capacity over that of apes (Jackendoff 1994). Maynard Smith and Szathmáry provide a charming and utterly fascinating account of the “ready-made structures” in children’s minds that allow them to learn languages so easily, that is to say, to organize the sounds they hear and the ideas thus represented into language, a skill which allows children to transform “pidgin” into a true “creole” language (Jackendoff 1994). The gift for language is truly a wondrous business. Kant claimed that three-dimensional space represents the mode, the “form” by which our minds perceive and organize spatial information (Weyl 1922, p. 3). The demonstration by Noam Chomsky and his co-workers that many of our thought patterns are “hard-wired” into our brains in the structures that allow us to learn languages (Jackendoff 1994) seems to illustrate “forms” by which we organize all kinds of information. From various mutants that affect language ability, Maynard Smith and Szathmáry infer that the capacity for language could evolve by stages, each advantageous in itself, so language could be the outcome of natural selection. This argument is hard to evaluate because our capacity to learn language is so elaborately “perfected” that it is hard to imagine intermediate stages.

Granted self-awareness and language, how can social norms of human behavior be instilled or enforced? This question in human sociobiology has proved a snare for May-

nard Smith and Szathmáry, as it has for famous predecessors. Their discussion of this question begins on page 272 by quoting a rather cynical passage concerning the role of ritual in instilling social norms. After discussing briefly why humans need such rituals, they ask, “Why *Macbeth*, and the biblical story of Cain and Abel, instead of, or as well as, the simple rule ‘thou shalt not kill’?” They have confused Story and Ritual in a rather odd way. Story *explains* why these injunctions matter, not just for society, but for the potential violator. We normally show the rationale, in the guise of the experimental basis, of Newton’s laws of motion when they are taught in physics class: why separate moral injunctions from stories that illustrate the self-destructiveness of violating them? After all, Shakespeare’s plays are considered marvelous studies of human nature. Is the willingness to confuse Story and Ritual a hangover from the days of “fact/value” distinctions? This distinction blurs when one remembers that facts are “theory-laden” and the process of forming theory necessarily “value-laden” (Polanyi 1962; Putnam 1990, 1992). In a less resolutely scientific age, however, one would attack this distinction by haling forth many of Shakespeare’s tragedies and histories as examples of *reasonable* explanations of the dangers to the agent of violating various social norms. Nor did Shakespeare invent the business of providing reasonable explanations for social norms. Plato’s *Republic* argues in places that it pays the individual to obey social norms of honesty and charitableness, lest he raise up a thicket of enemies waiting for the chance to avenge themselves, a message employed today in classes on conflict resolution. Just as facts do not exist quite independently of values, so social norms are not arbitrary edicts beyond the reach of reason. It is fair to ask how much reason, as reflected in Story, needs assistance from Ritual in instilling social norms, but it does not help to confuse the two.

It seems to me, however, that there are biological parallels that would illumine the study of human societies. Maynard Smith and Szathmáry discuss “hypercycles” where A catalyzes B, B catalyzes C, and C, A; they remark that selection favors a mutant A’ that catalyzes B more effectively, only if the resulting increase in B, and therefore C, is so localized that A’ benefits more than “the average A” from the increase (the importance of David Sloan Wilson’s [1980] “trait-group mathematics” is the spotlighting of ecological circumstances where agents benefit from increasing the abundance of organisms on which they depend). There is a clearly applicable parallel between the advantage of compartmentalization for hypercycles and the advantages of stable, heritable land tenure for small-holders, which allow a farmer and his progeny to benefit *differentially* from treating their land better (Netting 1989). In a similar vein, the fairness of meiosis reminds us that “free” competition among individuals benefits their group only when the common interest of the group is sufficiently coherent, and effectively enough enforced, to suppress dysfunctional forms of competition. Indeed, a sufficiently coherent, effective common interest can maintain the integrity of a commons (Netting 1976). One does not have to be a biological determinist to see parallels between the ways of reconciling an individual’s advantage with the good of its group during the major tran-

sitions of evolution, and how they are, or might be, reconciled in human societies.

Despite the inevitable flaws in a pioneering project, I find this book enormously exciting. It is a decisive turning point. To begin with, one can no longer argue that the decisive role of natural selection in evolution is an untestable proposition. If natural selection were irrelevant to evolution, one would not find footprints of its role in the pivotal transitions of macroevolution. By the same token, the thesis that natural selection is irrelevant to macroevolution is no longer believable. Charlesworth et al. (1982) mounted a valiant attack on that proposition. Nonetheless, by focusing on the major transitions of evolution, Maynard Smith and Szathmáry laid the axe to the root of that particular tree with devastating effect.

Moreover, their explanation of these major transitions hinges on the evolution of cooperation, whose importance they also consider in more commonplace contexts. Understanding more clearly how an individual's advantage is related to the various larger groups to which it belongs, would help reconcile the approaches of community ecologists who think in terms of natural selection among individuals with those of ecosystems analysts who think in terms of the good of the community as a whole, as David Sloan Wilson (1980) emphasized long ago.

Finally, their synoptic vision of the major transitions of evolution draws on the various branches of biology—molecular biology, microbiology, genetics, developmental biology and ethology—to illumine the study of evolutionary mechanism. By so doing, they weld these major branches of biology more nearly into the common enterprise they should be. They have brought nearer Haldane's (1932) goal of making sense of evolution in terms of observable processes and come close to fulfilling Fisher's (1930) program of identifying unmistakable footprints of the decisive role of natural selection in evolution.

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