

# 1 The Miscellaneous Transitions in Evolution

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In Mark Twain's *Letters from the Earth*, his sardonic alter ego Puddin'head Wilson reflects that if the Eiffel Tower represented the history of the world, and the skin of paint atop the knob at the pinnacle were the portion of that history in which humans have existed, "anybody would perceive that that skin was what the tower was built for. I reckon they would, I dunno" (Twain 1962, 226).

Twain was being facetious, of course, but taken at face value the remark does reflect a common intuition that people are special, that their existence reflects something profound about the evolutionary process, that evolution somehow culminates in them, that they are what evolution at the largest scale—all life over its entire 3.5 billion-year history, the whole Eiffel Tower—is all about. In the spirit of Puddin'head's remark, a modern analyst could choose to scorn this intuition as an expression of our natural human infatuation with ourselves. Alternatively, but equally skeptically, a hard-headed contemporary might treat this intuition as a cultural residue of our two-thousand-year-old obsession with the Great Chain of Being, the notion—dating back to Aristotle—that there is an ordering among organisms, from lower to higher, from monad to man.

But another avenue is open to us. We could, instead, take the widely shared impression of an ordering seriously. We could conjecture that the Great Chain represents a direct but difficult-to-articulate insight—perhaps partly confused, or perhaps only partly correct—into a true natural ordering of some kind. Of course, a modern Great Chain would include a time component, identifying not just a set of organisms but a set of transitions: bacterium to protist to multicellular animal, or more recently, within chordates, fish to reptile to mammal to human. In other words, we could take seriously the idea that an updated Great Chain reflects an actual ascent of some kind, an increase in some objective and important property or quantity over the history of life. And we could then investigate to discover what that property is. Our project would be to discover what we will call the "theoretical unity" that links the transitions leading to people. So, for example, we would ask what is the variable that increases in the transitions from fish to human? On what scale do reptiles score higher than fish and lower than mammals? Is it intelligence, energy intensiveness, or maybe fitness? The search would be open-ended. The goal would be to determine what it is that our

intuition has grasped, to figure out how to say, in scientific language, what we already think we know prescientifically. If the Great Chain is real, even in part, what is it that is increasing as we move up it?

In this project, testing would be crucial. We would want to operationalize each of the candidate variables, and then to make some measurements. Probably most candidates would turn out to be false leads in the sense that they do not produce the right trajectory, that is, they do not increase consistently up the Great Chain. Or they might fail in not placing people at the top. For example, body size is a candidate variable, increasing over at least the early transitions. But it fails at the end because people are smaller than blue whales (and many other mammals). In this approach, many variables might have to be considered before we found one that actually did increase in a way that captured the central intuition. But finally, when we have located the right variable, we could proceed to investigate the dynamics of the trend, its causes, its various exceptions, and so on.

Alternatively, there is another project we could pursue, one that is more in keeping with the spirit of Puddin'head's remark. We could set aside the Great Chain and our intuition that people are special. Then, turning to evolutionary theory, we could ask what variable we *expect* to increase over the history of life. Again, the trend might be noisy, the pattern imperfect. And if that variable can be operationalized, we can then investigate its pattern of change. In this approach, there is no intuited a priori set of transitions to be connected somehow, no trend with humans at its endpoint. Instead, beginning with some variable chosen based on theory, we would determine *empirically* what the major steps upward have been. If theory predicts that maximum body size should increase in evolution, say, on account of the advantages of large size, then we would investigate to discover whether or not the predicted trend occurs, and if it does, what are its properties. We could do this independently for any number of variables—perhaps fitness and complexity, as well as body size—that are predicted to increase in evolution at the large scale. In this project, the question is not about the Great Chain, but about directionality more generally: “What is it that is increasing over the history of life?”

In this project, unlike the first, we would be undaunted by the discovery that humans are not the culmination of a trend. Indeed, this project leaves open the possibility that we are not the culmination of a trend in any variable, at least not in evolution at large scale. (At smaller scales, of course, many species arising later in time will turn out to be local maxima in some variable or other, if only because the evolutionary branching process is Markovian, making humans—and indeed every other species—the local maximum of *some* sort, in *some* variable.)

The Great Chain is in bad odor these days, at least officially, which would make it easy to scorn the first project as unscientific. But we think it is not. For one thing, our prescientific intuitions could be right. For another, there is nothing wrong with focusing on people and the steps leading to us. We are interesting to ourselves. And there is nothing unscientific about pursuing that interest, about seeking the evolutionary sources of human nature

in deep time. It would be of considerable general interest to know whether there is some variable that is changing directionally over the grand sweep of evolutionary time, some trend that makes humans—or something like us—likely. Of course, in a modern discussion, our notion of a trend would have to be updated. Evolution is not a linear ascent. Any trend, however central to the process as a whole, will experience local reversals and be subject to numerous exceptions. But the primary intuition underlying the Great Chain could be right. If so, it would be important to show that evolutionary theory predicts, however roughly, the series of transitions it represents. Such a project could be partially revisionary. Our prior, intuitive conception of the scale might have to be revised during investigation.

It would also be easy to laud the second project as a kind of scientific ideal. What could be more in keeping with the spirit of objective inquiry than a priori agnosticism about the standing of humans, combined with dismissal of the Great Chain? But there is a concern that needs to be addressed here. Behind an official agnosticism, one suspects an agenda of demoting the importance of people, an agenda that could easily bias the investigator against a finding of a trend culminating in humans, even if one had actually occurred. And therefore in this project, the investigator would need to be careful to let the data speak, to leave open the possibility that humans might really be the culmination of a large-scale trend, at least for certain variables (perhaps, say, ability to control the environment, if it could be operationalized). Properly understood, the main point of this second project is not to understand the evolution of humans at all. But it does not rule out any particular finding about us. Insofar as this project would concern us at all, the point would be simply to find out objectively, neutrally, where we stand.

## Two Projects

A possible example of the first project is Francisco Ayala's 1974 treatment of biological progress. Ayala is interested in what he calls "a 'ladder of life' rising from amoeba to man" (Ayala 1974, 339), an updated Great Chain (although he does not use this phrase). His project seems to be to examine a number of candidates for the critical variable that underlies ascent up the ladder, including increasing adaptedness and the accumulation of genetic information, ultimately rejecting them in favor what he calls "ability to obtain and process information about the environment" (Ayala 1974, 349). On this scale, Ayala argues, animals generally score higher than plants, vertebrates higher than invertebrates, mammals than reptiles, and humans than all other species. The match to the Great Chain would seem to be very good.

Now there are reasons to be skeptical of Ayala's result. He has not found a way to operationalize "ability to gather and process information" in a way that would make them objectively measurable. His assessments are impressionistic. But there is nothing wrong

with his project, even by modern standards, insofar as it represents an attempt to find the key variable that underlies an updated Great Chain sequence. It is a bit like the project of finding a formula underlying a sequence of numbers that we have prior reason to think are the result of some underlying process, such as 2, 3, 4, 8, 14, 21, 34, 52, which is very nearly a Fibonacci series. Both for evolution and for a number sequence, the search for an underlying formula seems scientifically reasonable, provided we are able to test our hypotheses objectively, and provided, too, we are prepared to give up a preferred hypothesis that on close study is discovered to fit the sequence poorly.

An example of the second project is George Gaylord Simpson's chapter on evolutionary progress in his mid-twentieth-century, semipopular *The Meaning of Evolution* (Simpson 1967). Essentially, Simpson was seeking the key feature of organisms that accounts for what he thought of as the obvious directionality in the history of life. He considered a number of possibilities, including adaptedness, efficiency, specialization, independence from the environment, control over the environment, complexity, energy intensiveness, and others. In the end, the project failed, and he despaired of finding a single variable (aside from the general tendency for life to expand), concluding that there was not one but many sorts of progress. Significantly, and consistent with his overall strategy, Simpson began his treatment by recognizing the potential for anthropocentric bias in such an investigation, but admonished us not to reject out of hand the possibility that humans may rank highest. He considered our status, like that of every other species, an open question, something to be discovered in the course of investigation. In this second project, the important species and the transitions to them are the outcome of the investigation, not—as in the first project—the standard by which the success of the investigation is to be judged.

### **Theoretical Unity versus History as One Damn Thing after Another**

The two projects are very different, the first focusing on the Great Chain and the second on the history of life, ignoring the Great Chain. But they have something in common, namely, a search for theoretical unity, for a common thread running through the history of life. They share a hope that the search for a common thread will reveal something about the evolutionary process, about its robustness perhaps, its repeatability, or the nature of the forces guiding it. The first project starts with an intuited series of transitions and asks what is the theoretical unity behind them. The second starts with a theoretical unity—some variable predicted to increase by evolutionary theory—and asks what series of transitions (if any) it predicts.

Theoretical unity is a big part of what makes history interesting. History becomes much more intellectually satisfying when we can explain a series of apparently disparate events by citing a common underlying cause. Consider the following major events in mid-twentieth-century world history: the overthrow of the democratically elected government of Iran in 1953, the building of the Berlin Wall in 1961, the Soviet invasion of Czechoslo-

vakia in 1968, the U.S. involvement in Vietnam in the 1960s and 1970s, and the Soviet war in Afghanistan in the 1970s and 1980s. All of these events are explained by a common cause: the escalating Cold War between the United States and the Soviet Union from the end of World War II until the collapse of the Soviet Union. In other words, the Cold War provides the theoretical unity that explains and makes sense of an otherwise disparate series of events.

However, not all historical sequences have this unified structure. Let's move to a smaller time scale: I leave my house in a hurry one morning, forgetting my bag lunch at home. So for lunch I go to a restaurant instead, there by chance encountering a colleague who apprises me of a talk on campus later that afternoon. The talk is to be held in a building on a part of campus that is distant from my office, so I drive there, and after the talk head directly home, which requires me to take a different route home than usual. On my way home by this unusual route, I run over a rake on the highway puncturing two tires. This was an eventful day. Each event is directly connected to and depends on the one before it. Each is a necessary part of the explanation of my arrival home in a tow truck, with my incapacitated car riding atop, and atop, on its flatbed.

Now these events are causally connected and dependent on each other. But there is no theoretical unity. Unity does not demand a single unifying factor. Our Iran to Afghanistan macro-narrative would be unified even if the narrative depended on, say, an interaction between the Cold War and world population growth. But in the story of this eventful day, there is no unified analysis even of this more complex kind. Notice too that there are no general lessons to be learned from this story, say, about the importance of not forgetting one's lunch or about not taking unusual routes home. After all, forgetting my lunch could just as easily have eventuated in me finding a \$20 bill on the sidewalk outside the restaurant, and no punctured tires later. From this history we learn only what happened to me that day, which while fascinating (and frustrating) to me, entertaining to my family over dinner, and briefly amusing to my friends perhaps, contains little of general interest. Each event has its own unique cause. Of course, history of this sort does have a sort of fascination, of the kind offered by certain adventure stories, page-turners that are hard to put down because of the rapid flow of improbable events. We gobble up such stories like we eat peanuts, never completely satiated and not at all edified. This is history without theoretical unity, history as a series of miscellaneous transitions, history as Henry Ford saw it, "one damn thing after another."

Of course, it could be that real life is really like this. Many historians study history under the assumption that there are no general principles. In biology, Gould (1989) has defended a view of evolution as the product of chance, with no governing large-scale regularities, at least in the features of organisms. And this view could be right. But surely it is too soon to decide that. In any case, both of the projects outlined above start with the view that the search for regularity is worthwhile, that there could be some theoretical unity in the history of life, and that the goal of discovering it, if it is there, is worthy.

### The Miscellaneous Transitions

Since the mid-twentieth century, most studies of large-scale directionality have involved one of the two projects, or a combination of them. Many of these have revolved around the idea of progress. We have already mentioned Ayala's and Simpson's treatments. There is also Vermeij's (1987) argument that the history of life is characterized by organisms with ever-greater energy intensiveness, Van Valen's (1989) suggestion that absolute fitness increases, Knoll and Bambach's (2000) suggestion that what is increasing is diversity and occupation of ecospace, and others (see lists in McShea 1998 and Rosslenbroich 2006). In some cases, it is clear that the project is of the second sort, that the variable of interest arose from theory (e.g., absolute fitness). In others, it seems likely that the project is of the first sort, an attempt to find the variable underlying a set of preconceived transitions (e.g., Ayala). But all share the virtue of searching for theoretical unity.

However, there have also been some instructive exceptions, and we briefly outline three of them here. The first appears to be a case where a theoretical unity was sought, and almost—but not quite—found. (As it turns out, however, this project might be retrospectively salvageable.) The last two seem to us to be failures, cases in which theoretical unity was sought only halfheartedly, if at all. In both cases, none was found, not surprisingly. These projects do not seem salvageable.

### Huxley and the Basis for “Higher” and “Lower”

In a chapter on evolutionary progress in his mid-twentieth century, semipopular *Evolution in Action*, Julian Huxley (1942) sought the variable that underlies our notions of “higher” and “lower.” His goal was to find a theoretical unity, that is, to find the variable that changes directionally in evolution as higher organisms evolve from lower. His treatment was not explicitly about the Great Chain, but “higher” and “lower” are key words in Great Chain discourse, and it is clear throughout that the transitions he was seeking to explain are the standard ones—the more complex crustaceans succeeding the trilobites, the jawless fishes succeeding the marine arthropods, followed by the amphibians, reptiles, and so on. Huxley's Great Chain branched a great deal, as any modern version must, with insects pursuing their own ascent from higher to lower in parallel with the chordates, for example. But the location of people at the top, as the most dominant species of all time, was unquestioned and indeed was a big part of what was to be explained.

Huxley proceeded by considering two candidate variables, ultimately rejecting both of them: ability to survive (rejected because the organisms we recognize as higher seem not to be especially extinction resistant) and complexity (rejected because many lower organisms are quite complex). He then considered and accepted a variable he called “dominance,” and argued that dominant groups (i.e., higher groups) might be those with traits that give them greater control over and independence from the environment. In the Paleozoic, large predatory arthropods, eurypterids, were more powerful swimmers than the tri-

lobites they evolved from. And later fish were more efficient swimmers than their earlier relatives. Both of these represent increases in a kind of environmental control, in the ability of these aquatic animals to manipulate or make use of the medium in which they live. And humans, of course, are the apotheosis of environmental control. In other cases, however, it is not environmental control that increases from “lower” to “higher” but internal homeostasis, that is, independence from the environment. Lower marine animals, he argues, are in diffusional equilibrium with the surrounding sea water, whereas fish are able to regulate their internal chemistry somewhat. The evolution of a shelled egg liberated reptiles from their ancestor’s dependence on water in early development, and endothermy in birds and mammals produced some measure of independence from temperature variability in the environment.

If these examples, and others that Huxley cites, are granted, it would seem that he has found not *one* but *two* variables that increase up a modern Great Chain—control over the environment and independence from the environment—with some transitions marked by one and some by the other. And so we think we must judge this result a failure in the search for theoretical unity. In making this judgment, we do not deny that both environmental control and independence could be important in the history of life. Nor do we deny that one or the other underlies all of the major transitions picked out by the Great Chain, some transitions marked by increase in environmental control, some by increase in independence from the environment, and some by both. But his failure to find a single variable that underlies all transitions implies that “lower” and “higher” mean different things in different contexts, that the Great Chain is not unified. In effect there are at least two Great Chains, one for control and one for independence. This could be the case, a fact of the world, but we accept it at the price of rejecting, or at least revising, the intuition that motivated the project in the first place.

On the other hand, Huxley’s result may yet be salvageable, if only we could find a way to unify control and independence. Is there some single factor that these two variables represent alternative manifestations of? The answer could be no. It’s easy to see an exoskeleton, a shelled egg, or life cycle with resting-cyst stage as ways to achieve some degree of independence from the external environment. But it is difficult to see them as control over the external environment in the same sense in which, say, a beaver or a human building a dam is. On the other hand, both control and independence have to do with the organism-environment relationship, and more specifically with the ability of organisms to develop and function under conditions of their own making. Somewhere in that concept there may be a single variable that underlies the ascent from lower to higher (and, indeed, Laland, Odlong-Smee, and Feldman [2001] treat these as different aspects of so-called niche construction).

It is worth noting here that some promising conceptual work along these lines has been done by Rosslenbroich (in preparation; see also Rosslenbroich 2005, 2006). In particular, he develops a notion of organismal “autonomy,” and shows in a compelling way how

autonomy seems to have increased in each of the transitions along a standard Great-Chain-like sequence, bacterium to protist to multicellular individual, and so on.

### **Stebbins and the Eight Major Levels of Organization**

The results of Ledyard Stebbins's 1969 study of progress are less promising. Stebbins identifies eight "major levels of organization" in evolution. How are these levels to be understood? He wrote:

In the long run, organisms repeatedly have evolved new ways of exploiting . . . environments. In doing so, their bodies have from time to time evolved new levels in the hierarchy of complexity from macromolecule to organelle, cell, tissue, organ, and organ system. Achieving these levels required the accumulation of new genetic information, concerned largely with the integration of development and metabolism and with regulating the translation of genetic information into form and function. (Stebbins 1969, 29)

And here is his list of levels (Stebbins 1969, 30):

1. Earliest self-reproducing organic systems (free-living viroids, none still living).
2. Surrounding cell membrane with selective permeability and active transport of metabolites (prokaryotes).
3. Division of labor between nuclear, cytoplasm organelles (flagellates, other protozoa (eukaryotes)).
4. Multicellular organisms with some cellular differentiation (sponges, algae, fungi).
5. Differentiated systems of organs and tissues (coelenterates, flatworms, higher plants).
6. Organized central nervous system, well developed sense organs, limbs (arthropods, vertebrates).
7. Homeothermic metabolism (warm blood) (mammals, birds).
8. Dominance of tool using and conscious planning (man).

Let us ask just what is increasing here. Stebbins uses the term "complexity," which he seems to understand as hierarchy, the number of levels of organization, or parts within wholes. Earlier in his book a short section describes the hierarchical structure of a simple muscle fiber, starting with a whole muscle tissue and descending in a series of steps through fiber group, single fiber, fibril, and down to a single actin-myosin subunit. Most of his list of eight levels makes sense if complexity is understood in precisely this way, as nested objects within objects or, in evolutionary terms, as the progressive origin of ever higher levels of aggregation. Certainly the transition from level 2, prokaryotic cell, to level 3, solitary eukaryotic cell, can be understood in this way, the eukaryotic cell having arisen historically as an association between (at least) two prokaryotes, an archaeobacterium and a eubacterium. Likewise, the level 3 to level 4 transition—solitary eukaryotic cell to multicellular eukaryote—is obviously the origin of a new level. The next transition, from 4 to 5, is somewhat problematic, in that although a new level arises, it does so in a different way than in the earlier transitions. Tissues and organs arise not by aggregation of lower-level entities but by interpolation, so to speak, between existing levels, between the level of the multicellular whole and the level of the cell. Still, hierarchical structure does increase.

So far so good (or at least, good enough), but in the 5-to-6 transition, the scheme breaks down. Central nervous systems, sense organs, and limbs are just organs and organ systems, the same sort of entities that arose in the transition from 4 to 5. Undoubtedly, there is something special about them, but it is surely *not* that they represent either the addition or the interpolation of a new level. The same goes for the transition from level 6 to 7. Homeothermy may be an advance in some sense—for example, in Huxley’s sense, providing increased independence from the environment—but it adds no new level of hierarchy. And as for the evolution of humans, it could be argued that they represent a higher level of nesting than a solitary multicellular individual, because we are social, and sociality is the aggregation of lower-level individuals. (And in that case, sociality should replace sense organs and limbs as level 6, and the list should end there.) But corals are also social, consisting of multiple multicellular polyps, and so are many insects and vertebrates, forming societies consisting of multiple multicellular individuals. Therefore, if the criterion for new levels is hierarchy, there is no obvious reason to pick humans as representative of the social level, tool use and conscious planning notwithstanding.

Stebbins left some wiggle room in his understanding of levels, with his mention of accumulation of genetic information, integration of development and metabolism, and increasing regulation of form and function. Possibly his claim is that the evolution of brains, homeothermy, and humans—levels 5, 6, and 7—involved increases in all or some of these. But these are things that he says are *required* for the evolution of new levels of organization, not constitutive of or definitive of them. Thus, even if these things could be shown to have increased in the last transitions, it would still remain to be shown the sense in which they constitute increases in hierarchy. Stebbins did not do so, and it is not at all obvious how it could be done.

On its face, Stebbins’s list of eight levels looks like an attempt to justify the Great Chain, to find the variable that underlies it, project 1. If so, then this worthy project failed, because no common variable was found. On the other hand, suppose that his project was really to trace the trajectory of levels of organization wherever it would have led him, that is, project 2. But in that case, his project also failed, in that he abandoned the notion of levels at the higher levels. In particular, humans do not seem to be hierarchically above other social multicellulars. Either way, no theoretical unity has been found. If this were the only way of reconstructing history, it would be revealed to be a series of miscellaneous events, on the long road to human beings, one damn thing after another.

### **Maynard Smith’s “Levels of Selection” and Maynard Smith and Szathmáry’s “Major Transitions”**

Two 1995 publications by John Maynard Smith and Eörs Szathmáry—a book and a *Nature* paper—have attracted considerable attention from molecular evolutionists, macroevolutionists, and philosophers of biology, and have helped propel a long-overdue resurgence of interest in the evolution of hierarchy (Griesemer 2001; Jablonka 1994; McShea 2001; Michod 1997, 1999; Michod and Roze 1997; Queller 2000). The issue they address is the

evolution of higher-level wholes from lower-level individuals, the emergence in evolution of new and higher levels of selection (Michod 1999; Michod et al. 2006). And they address it by examining what they call the “major transitions” in evolution, identifying eight of them, and discussing possible mechanisms by which they arose.

The *Nature* paper contains the clearer general statement of their project, so we will focus on that. It begins by directing the reader to a list of major evolutionary transitions in their table 1 (Szathmáry and Maynard Smith 1995, 228):

1. Replicating molecules to populations of molecules in compartments
2. Unlinked replicators to chromosomes
3. RNA as gene and enzyme to DNA and protein (genetic code)
4. Prokaryotes to eukaryotes
5. Asexual clones to sexual populations
6. Protists to animals, plants and fungi (cell differentiation)
7. Solitary individuals to colonies (non-reproductive castes)
8. Primate societies to human societies (language)

It then goes on to say:

There are common features that recur in many of the transitions: (1) Entities that were capable of independent replication before the transition can only replicate as parts of a larger unit after it. For example, free-living bacteria evolved into organelles. (2) The division of labor: as [Adam] Smith pointed out, increased efficiency can result from task specialization. . . . For example, in ribo-organisms nucleic acids played two roles, as genetic material and enzymes, whereas today most enzymes are proteins. (3) There have been changes in language, information storage and transmission. Examples include the origin of the genetic code, of sexual reproduction, of epigenetic inheritance and of human language. (Szathmáry and Maynard Smith 1995, 227)

There follows a short section about complexity, especially genetic complexity. Unfortunately, there is no clear statement of how complexity is to be understood, and the connections among complexity, the major transitions, and the common features of the transitions are never discussed. Their discussion has a second theme, having to do with the flow of information across the generations, in particular the notion that the fidelity and bandwidth of inheritance has increased; but again the relationships with complexity and the common features of the transitions are not clear. In any case, complexity and bandwidth aside, it seems clear that their major interest is the first criterion above, the increase in hierarchical structure in evolution and the origins of new levels of selection. Almost all of the subsequent discussion in the literature has focused on this aspect of their project, taking the trend in levels to be its centerpiece. We will read their project this way, too.

This interpretation is consistent with three pieces of evidence: First, a discussion follows immediately of the first shared feature of the transitions, namely, “that entities capable of independent replication before the transition can only replicate as parts of a larger whole

afterwards.” In other words, a higher-level entity arises from an integration of lower-level units, from either an ecological association or a clonal aggregate of them. And it is fairly clear that Szathmáry and Maynard Smith understand it to arise as the result of higher-level selection.

Second, a central concern in both the 1995 paper and the book is the problem of cheaters, lower-level individuals that pursue their Darwinian self-interest at the expense of the higher-level whole. The question raised is how are higher levels able to persist when selection would seem to favor cheaters that undermine them? To say this question has been focal in the literature on levels of selection would be an understatement. Interest in it has been almost obsessive, to the point that other questions have been nearly ignored (cf. Calcott 2008).

Third, Maynard Smith published a paper in 1988 that is undoubtedly an intellectual precursor to his part of the 1995 paper and book. And that earlier paper was explicitly devoted to the increase in “complexity” in evolution, this time more clearly conceived as the origin of new levels of selection. He also offered a table that is remarkably similar to the 1995 table. The earlier table differs in a few ways, notably in the identification of the penultimate level as occupied by “demes,” as well as by social groups, and in the designation of an extra level—the species level—between demic-social and human culture. The inclusion of demes and species confirms the diagnosis. Maynard Smith understood the increase in complexity in the conventional way, as an increasing trend in hierarchy, understood as parts within wholes (Eldredge and Salthe 1984).

Assuming the conjecture is true, that the major transitions are to be understood mainly as increases in hierarchy, the decision to include human society as the eighth and last transition is a departure, a violation of Maynard Smith’s own criteria for what the sequence of transitions represents. A human society would seem to be just that, a society, not an even higher level of selection. It would seem to occupy the same hierarchical level as a social insect society (achieved already in the seventh transition) or a primate society (present already at the start of the eighth). Each human is a multicellular eukaryotic individual, and a human society would appear to be just another association of multicellular eukaryotic individuals. To be sure, our societies are different in detail from ant and baboon societies. Ours are also unique in a number of ways. But social organization in every multicellular species is different in detail from every other, and more different with greater taxonomic distance. Likewise, every species is unique. But that does not make us a higher level.

What is the next highest level, the level above the social? From first principles, it would seem to be an association of societies, a metasociety or supersociety of some sort. Now among nonhuman animals, at least, there seem not to be any supersocieties, either extant or in the fossil record (McShea and Changizi 2003), at least none that are individuated to the extent that organisms or even societies are. There is, in the Recent, an invasive species of ant in which clusters of colonies can be identified, but there is no division of labor among colonies as there is among well-individuated members of colonies at the next level down.

What about humans? Identifying levels in human societies is problematic, because—at least in modern societies—we associate in so many different ways, as members of so many different social units, with no clean hierarchical structure to them. Associations are crosscutting, so that a member of a village can also be a member of a guild that includes people from a number of villages, and also a member of a family or kin group that seems to crosscut both. This does not rule out the possibility that humans form super-societies; it simply means that there is some conceptual and empirical work to be done—finding ways to assess and locate hierarchical structure—before such a higher level can be claimed.

Another tactic might be to argue that our societies occupy the same level as ant and baboon societies but are more individuated at that level. In other words, all or most animal societies occupy the same level of selection, but in the human case, selection has operated more powerfully, more efficaciously, to produce greater individuation, evidenced perhaps by our greater division of labor among individuals, the development of intermediate-less associations such as teams and groups (the equivalent of tissues and organs), and so on. In other words, the suggestion is that humans are social just like ants and baboons, but that we are more *intensely* social, that we occupy the social level more fully. Again, arguing this requires some work, if only because, intuitively, the eusocial insects seem to be *more* intensely social than people, at least on account of having castes marked by phenotypic, as well as behavioral, differentiation. More generally, ants do seem to be more committed to social living than people.

There are other ways to try to argue this. One might say that human societies are more complex, not because we occupy the social level more fully, but because our societies involve more interactions than ant societies, more types of interaction, more social roles, and so on. But this is complexity in a very different sense from that being invoked in the rest of the list of major transitions. Unless one could defend a sharp distinction between kin selection and group selection, and argue that only humans are strongly group selected, human social complexity is not complexity in the sense of hierarchy, of higher levels of selection. Alternatively, one might focus on language and culture, as Maynard Smith and Szathmáry did, with both understood as novel modes of information transfer and inheritance. But while the human mode of cultural transmission is unique, it is not obvious that it produces a higher level of selection. No such argument has been made for other epigenetic information transmission mechanisms. For example, diffusible morphogens in animal development are certainly epigenetic, but their role is mainly to organize lower-level units (cells) within a higher-level whole (a multicellular individual). No one would claim that this mechanism produces an even higher individual, above that of the multicellular individual. Likewise, cultural transmission might be said to organize lower-level human individuals within a higher-level society. But it is hard to see how it produces a whole at an even higher level. (It is worth noting that Richerson and Boyd [2001] have argued that cultural transmission explains the between-group differences and within-group similarities that make group se-

lection important in human evolution. But this argument does not lead in any obvious way to a higher-level whole, that is, to a metasociety of any kind.)

In any case, though it might be possible to argue that we occupy the level of selection above other animal societies, or that our societies are more individuated at the social level, Maynard Smith and Szathmáry do not even attempt it. Indeed, in the 1995 paper and book, the ascent from one level of selection to another is claimed only for *many* of the transitions, not for all, in particular for numbers 2, 4, 5, 6, and 7. They seem aware of their theoretical inconsistency, aware that including transition number 8, the transition to humans, requires understanding the notion of a “major transition” in a different sense. It is a change in mode of information transmission, not an increase in hierarchy.

Finally, we note that, consistent with our claim of theoretical disunity, the features that separate the transition to human society from the ones just before it (change in mode of information transmission versus increase in hierarchy) have had different and independent impacts in the literature. And interestingly, these impacts roughly parallel the two projects outlined above. First, the Maynard-Smith and Szathmáry notion of change in mode of information transmission has had some impact on studies of the evolution of human language and culture (e.g., Laland et al. 2001). It fits nicely with current thinking about language and culture as epigenetic, as information-transmission systems that have been built “on top,” so to speak, of the older, DNA-based genetic system. And in its strong focus on humans, this work is somewhat allied to project 1. The issue in this area is not hierarchy, or the common themes of the evolutionary process, generally. Instead it is that last and very special transition to humans. But the major impact has been on thinking about hierarchy, evident especially in the work of Michod (e.g., 1997, 1999) on what he calls evolutionary transitions in individuality and on how these transitions come about. This work is strongly allied to project 2, the search for large-scale directionality, with no particular focus on humans. For the trend in individuality, humans are relevant but they are definitely not the zenith.

In sum, we cannot find any theoretical unity in the Maynard Smith and Szathmáry list of major transitions. The list needs revision, or the project (or projects) needs to be redefined, and not in terms of hierarchical complexity. One could argue that theoretical unity is not their goal, that they are being held to an inappropriate standard. But then we are entitled to ask, what is the point of collecting these transitions together? Can it be just their importance as milestones on the road to us? In that case, the major transitions story would be like a “story of my day,” how it all started with the forgetting of a lunch and how it ended with a trip home in a tow truck. It would be the story of how life began, some 3.5 billion years ago, what happened next, and next, and next. It is a story that takes us from the origin of life (genes, DNA) to the transitions in level of selection (bacterium, protist, multicellular individual, colony) to the origin of human beings (in particular, our language), a series of miscellaneous transitions with no obvious unity beyond their salience for us.

It could be, of course, that humans are special, independent of whether or not we are a higher level of selection. That skin of paint atop the Eiffel Tower could really be the most

interesting feature of the tower. (Is that skin of paint a different color from the rest of the tower? Is there a transmitter of some kind embedded in it?) And yet it could still be that no theoretical unity underlies both us and the other “major transitions,” however defined. But in that case, treatments such as those of Stebbins and Maynard Smith and Szathmáry are not just failures to find a theoretical unity, they are distractions. To force humans into the same theoretical box with other transitions is to overlook whatever it is that actually makes us special.

### Afterthoughts

There is something philosophically muddled and scientifically casual, about these three treatments of evolution at the largest scale. And we would argue, somewhat impatiently, that the time for getting serious about evolution at the largest scale is long past. We have had the tools for understanding large-scale trends for decades. And for much longer, we have demanded theoretical consistency in the study of trends. No one in modern biology would study the evolution of body size in any taxonomic group without adopting a single, operational definition of body size and applying it in a consistent way to all specimens considered. And there is no reason to settle for a lower standard in our treatment of the history of life at the largest scale. To be clear, the villain has not been the Great Chain, for some version of it could reflect a real insight, and it could be treated seriously. Neither has the problem been the notion that the history of life might be governed by chance, that no unity in fact exists, because that too is a possible truth of the world. The fault has been the yielding to theoretical inconsistency. Enough is enough.

This discussion may seem uncharitable, especially in its treatment of Maynard Smith and Szathmáry, whose work has been so well received. So let us add that many aspects of the Maynard Smith and Szathmáry study may be real contributions, especially in the insights it offers into the possible mechanisms underlying some of the more puzzling big events in early evolution, such as the evolution of genetic code. And considerable praise is due to everyone who takes on the daunting project of searching for pattern at the scale of life’s history. The goal of finding a unity in that history hovers above evolutionary discourse as the moon once did above Earth, inviting the bold to explore the limits of what we can know and learn. Whatever the faults of their findings, explorers in this area deserve credit for their audacity. If they deserve any blame, it is only for a last-minute faintness of heart, for conceding failure too easily after having boldly traveled so far.

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## References

- Ayala, F. J. (1974). The concept of biological progress. In F. J. Ayala and T. Dobzhansky (eds.), *Studies in the Philosophy of Biology* (pp. 339–355). New York: Macmillan.
- Calcott, B. (2008). The other cooperation problem: Generating benefit. *Biology and Philosophy* 23: 179–203.
- Eldredge, N., and S. N. Salthe. (1984). Hierarchy and evolution. In R. Dawkins and M. Ridley (eds.), *Oxford Surveys in Evolutionary Biology*, Vol. 1. (pp. 184–208). Oxford: Oxford University Press.
- Gould, S. J. (1989). *Wonderful Life*. New York: W. W. Norton.
- Griesemer, J. (2001). The units of evolutionary transition. *Selection* 1(1): 67–80.
- Huxley, J. (1942). *Evolution in Action*. New York: Harper.
- Jablonka, E. (1994). Inheritance systems and the evolution of new levels of individuality. *Journal of Theoretical Biology* 170(3): 301–309.
- Knoll, A. H., and R. K. Bambach. (2000). Directionality in the history of life: Diffusion from the left wall or repeated scaling of the right? *Paleobiology* 26(suppl.): 1–14.
- Laland, K. N., J. Odling-Smee, and M. W. Feldman. (2001). Niche construction, biological evolution, and cultural change. *Behavioral and Brain Sciences* 23: 131–146.
- Maynard Smith, J. (1988). Evolutionary progress and Levels of selection. In M. Nitecki (ed.), *Evolutionary Progress* (pp. 219–230). Chicago: University of Chicago Press.
- Maynard Smith, J., and E. Szathmáry. (1995). *The Major Transitions in Evolution*. New York: Oxford University Press.
- McShea, D. W. (1998). Possible largest-scale trends in organismal evolution: Eight “live hypotheses.” *Annual Review of Ecology and Systematics* 29: 293–318.
- McShea, D. W. (2001). The minor transitions in hierarchical evolution and the question of a directional bias. *Journal of Evolutionary Biology* 14(3): 502–518.
- McShea, D. W., and M. A. Changizi. (2003). Three puzzles in hierarchical evolution. *Integrative and Comparative Biology* 43: 74–81.
- Michod, R. E. (1997). Evolution of the individual. *American Naturalist* 150: S5–S21.
- Michod, R. E. (1999). *Darwinian Dynamics: Evolutionary Transitions in Fitness and Individuality*. Princeton, NJ: Princeton University Press.
- Michod, R. E., and D. Roze. (1997). Transitions in individuality. *Proceedings of the Royal Society of London Series B, Biological Sciences* 264(1383): 853–857.
- Michod, R. E., Y. Viosat, C. A. Solari, M. Hurand, and A. M. Nedelcu. (2006). Life-history evolution and the origin of multicellularity. *Journal of Theoretical Biology* 239(2): 257–272.
- Queller, D. C. (2000). Relatedness and the fraternal major transitions. *Philosophical Transactions: Biological Sciences* 355(1403): 1647–1655.
- Richerson, P., and R. Boyd. (2001). Built for speed, not for comfort. *History and Philosophy of the Life Sciences* 23: 423–463.
- Rosslenbroich, B. (2005). The evolution of multicellularity in animals as a shift in biological autonomy. *Theory in Biosciences* 123: 243–262.
- Rosslenbroich, B. (2006). The notion of progress in evolutionary biology—the unresolved problem and an empirical suggestion. *Biology and Philosophy* 21: 41–70.
- Simpson, G. G. (1967). *The Meaning of Evolution*. New Haven, CT: Yale University Press.
- Stebbins, G. L. (1969). *The Basis of Progressive Evolution*. Chapel Hill: University of North Carolina Press.
- Szathmáry, E., and J. Maynard Smith. (1995). The major evolutionary transitions. *Nature* 374: 227–232.
- Twain, M. (1962). *Letters from the Earth*. New York: Harper & Row.
- Van Valen, L. M. (1989). Three paradigms of evolution. *Evolutionary Theory* 9(1): 1–17.
- Vermeij, G. (1987). *Evolution and Escalation*. Princeton, NJ: Princeton University Press.

