

Coda to Part I: Convergence at the Grandest Scales

Complex multicellularity is a precondition for nearly all of the convergent features of bodies discussed in the previous chapters. The iterated features of bodies were sculpted by selection out of highly differentiated cell types that comprise muscle, nervous, epithelial, connective, and other tissues. The evolutionary robustness of complex multicellularity in turn hinges on several earlier events in the history of life on Earth, such as the origins of the eukaryote cell and before that the simpler prokaryote cell. Several key transformations in the form and organization of life on Earth were crucial for subsequent evolutionary step-ups in hierarchical complexity; if any of these transformations are radically contingent, then all subsequent evolutionary outcomes that causally depend on them will be radically contingent as well. It would be remiss, therefore, for us not to consider the contingent nature of major transitions in the history of life.

1. Major Transitions in Evolution

In *The Major Transitions in Evolution* (1997), evolutionists John Maynard Smith and Eörs Szathmáry drew up a list of key shifts in the history of life and attempted to connect these events with a common theoretical thread.¹ Some of these transitions involve a shift from autonomous replication to cooperative group replication, in which fitness is “transferred” from lower level units to the group level, thus forging a new evolutionary individual. Other transitions involve the emergence of new systems of inheritance that allow for molecular and cellular divisions of labor, such as the separation of transcription and translation and epigenetic systems that direct cell line differentiation.

Whether Maynard Smith and Szathmáry succeeded in theoretically unifying the diverse events that they identify as major transitions is questionable.² In addition, some theorists have objected to their anthropocentric—and, more broadly, eukaryote-skewed—picture of macroevolution, which obscures the bacterial

dominance of life on Earth from its inception to the present day.³ To paraphrase microbiologist Ford Doolittle, living worlds will always be run by and for microbes. Nevertheless, the transition from microscopic to macroscopic life was of great ecological significance to the history of life on Earth, and it is especially crucial to the inquiries that preoccupy us here. Some events Maynard Smith and Szathmáry describe are the organizational building blocks upon which later complex morphological and functional iterations would be built.⁴ The replicability of certain major transitions, especially basal ones like eukaryogenesis and multicellularity, is thus pivotal to the overall story to be told in this book.

2. Iterated Transitions

Iterated major transitions enable us to avoid inductive problems that stem from observer selection effects (discussed in chapter 1). Any observer reflecting on the prospects of extraterrestrial life need not hail from a planet on which some of the major transitions that led to the observer—such as the free-living cell, multicellularity, and society—have multiple iterations. Singular transitions, on the other hand, create problems for the robust replicability thesis (RRT) precisely because they are susceptible to observer selection effects.

In recent work, Szathmáry notes that some major transitions are subject to “recursion” (read: iteration), but he does not draw out the theoretical import of this pattern, nor does he consider the implications of the lack of recursion in other transitions for the prospects of a law-like theory of macroevolution.⁵ Some major transitions in hierarchy that are perquisites for the evolution of body and mind are subject to clear iteration while others appear to be singular.

For instance, multicellularity has arisen more than two dozen times across distant branches of the eukaryote tree of life, including in animals, land plants, fungi, and various algae (brown, red, and green), with about one out of every twelve of these simple origins giving rise to complex multicellularity.⁶ Basic multicellularity requires several generic innovations, including cell-to-cell adhesive properties, systems of intercellular communication, and reproductive specialization. This last innovation is especially important, for as evolutionists Rick Michod and Matthew Herron have argued, there may be a limited number of ways that transitions to complex multicellularity can occur such that fitness is transferred from lower-level to higher-level entities.⁷ One such iterated mechanism is the evolution of the *germ–soma division*, wherein some cell lines specialize in reproduction while others specialize in the various nonreproductive functions of the organism. Once reproduction becomes specialized in this way, all cell lines of the body come to share a collective fate, and a new evolutionary individual is “born.”

Multicellularity per se does not seem particularly hard to evolve and it appears to transcend phylogenetic constraints. It has arisen many times in eukaryotes as well as in both domains of prokaryotes to produce what might loosely be called “bacterial bodies,” complete with specialized modes of adhesion, signaling, and reproduction.⁸ Nevertheless, only two multicellular lineages—animals and green plants (and to a lesser extent, fungi)—have achieved levels of cellular specialization that support truly three-dimensional body plans.

Whether animal-style multicellularity, which includes a body with differentiated tissues and a digestive cavity, arose once or multiple times is less clear. If radical contingency is going to outflank the evolution of complex bodies and minds, the origin of the animal gut is a promising point of attack. The metabolic challenge for animal evolution lies in switching from a basic eukaryote mode of feeding—intracellular phagocytosis (wherein nutrients are “swallowed” and digested within the cell)—to one in which cells give up their feeding capacity in order to form specialized digestive tracks that serve the higher-level unit of selection.⁹

The lack of clarity about how many times animal-grade complexity evolved is due to two uncertainties: (1) the phylogenetic position of the enigmatic “Ediacaran fauna” (a global multicellular fauna that preceded the Cambrian explosion by some 40 million years), and (2) the uncertain phylogenetic position of ctenophores (comb jellies). Paleontologist Adolf Seilacher has argued that discrepancies between Ediacaran and Cambrian modes of body construction, behavior, and ecology point to the Ediacaran fauna as a separate origin of multicellular animal life.¹⁰ This view remains controversial, however, and the now prevailing interpretation, based on recent morphological and molecular fossil analyses, is that some animal-like Ediacaran forms, such as *Kimberella* and *Dickinsonia*, are in fact “stem” taxa of later metazoans, harkening back to the cladistic reinterpretation of the Cambrian critters discussed in chapter 2.¹¹ Even so, if comb jellies turn out to be more basal than sponges, as some recent research suggests, then this would indicate multiple origins of guts as well as of nervous and motor systems (more on this in chapter 9). If, on the other hand, sponges are the most basal animal, then we are looking at a single origin of some of the key bilaterian traits on which the subsequent shape of animal life would be built. Our picture of animal evolution continues to evolve, but at present it points to a single origin of animal-grade multicellularity, even though organ-grade multicellularity per se appears to be a robustly replicable outcome.

Coloniality is another major transition listed by Maynard Smith and Szathmáry that has numerous iterations, in this case across multicellular and unicellular lineages. Among colonial organizations, caste-based eusociality comes closest to the formation of a new evolutionary individual. Eusocial societies are less physically integrated than complex multicellular organisms, but in some cases

they are highly differentiated and involve reproductive specialization into sterile and reproductive castes that resemble the germ–soma differentiation in transitions to multicellularity. Although humans are capable of cooperative feats that surpass even those of the eusocial insects (see the coda to part II), though it does not seem that human societies do not rise to the level of a new individual or super-organism. In any case, the evolution of eusociality, though ecologically significant¹² and deeply iterated,¹³ does not bear directly on the evolution of bodies and minds in multicellular organisms, so we will not explore it further here.

3. Singular Transitions

Let us assume for the sake of argument that some major transitions are law-like, or even “natural kinds” in the parlance of philosophy of science. If these outcomes hinge on earlier transitions that are radically contingent, then we have a situation where certain law-like generalizations only obtain given certain accidental antecedents. For reasons discussed in chapter 3, this scenario not only undermines the cosmic replicability of these transitions, but in addition it is plausibly consistent with the radical contingency thesis (RCT) depending on what the RCT takes as its initial conditions. Apart from the evolution of key animal features (which we will revisit in part II), which major events, given their lack of iteration, might undermine the cosmic projectibility of complex bodies?

Chapter 1 dispelled some concerns surrounding the apparently singular origin of the DNA code and offered reasons to think that protocells evolved more than once on Earth. The transitions to complex multicellularity and society also look to be evolutionarily robust, though there are several complications that may affect our credence in this conclusion. One is the prospect, already mentioned, of a single origin of animals. Another is the apparently singular origin of eukaryote-grade *cellular* complexity. “Eukaryogenesis” refers to the emergence of complex cells packed with distinct organelles dedicated to specialized functions. The origin of the eukaryote cell was a necessary condition—structurally, informationally, and energetically—for the emergence of all subsequent levels of hierarchy built upon it, including complex multicellular lineages like animals and green plants. Eukaryogenesis is thus a linchpin in the prospect of a cosmic biology, and yet it appears on all counts to be a nonrepeated event.

There are two features of the evolution of the eukaryote-grade cell that are hard to reconcile with the RRT. First, as just noted, it arose only once in the entire history of life.¹⁴ Second, it took nearly 2.5 billion years to do so after life had gained a permanent foothold on the planet. There are two alternative explanations of eukaryogenesis. The first, known as the “autogenous” hypothesis, holds

that the eukaryote cell was fashioned from a single prokaryote ancestor through accumulated mutations that produced invaginations of the cell membrane, which resulted in the various organelles such as the endoplasmic reticulum and golgi. This hypothesis is now largely rejected for the mitochondrion as well as for the chloroplast in plant and algal cells, which are both understood to be the descendants of once free-living bacteria that were acquired in endosymbiotic events. The second, “exogenous” account of eukaryogenesis hypothesizes that an ancestral prokaryote—probably an archaean—somehow (despite the lack of phagocytosis) engulfed and maintained a bacterium that would become the mitochondrion, and that this energetic upgrade in turn set the stage for eukaryogenesis. Proponents of this hypothesis, such as biologists Nick Lane and William Martin, reason that the increased energy production that came from the addition of mitochondrial membranes was crucial for the energetically costly expression of larger, informationally capacious genomes, which in turn supported the internal differentiation of the eukaryote cell.

What can we say about the contingency or robustness of this event, which served as the scaffolding for countless morphological convergences over the subsequent history of life? If we presuppose, as many believe, that the endosymbiotic acquisition of the mitochondrion was the chief evolvability hurdle to genomic and therefore morphological complexification, then there is some reason for optimism. For although the mitochondrion was acquired only once, the endosymbiotic acquisition of free-living prokaryotes for metabolic functions has occurred over and over again, including not only in the case of the chloroplast (mentioned earlier) but also in many secondary and tertiary plastid endosymbioses as well.

What’s more, the citric acid cycle itself—the metabolic pathway through which aerobic respiration is carried out in the mitochondrion—may have evolved numerous times in prokaryotes due to its global adaptive efficiency,¹⁵ using the smallest number of chemical steps to produce the highest energy yield.¹⁶ The biochemical constraints on aerobic respiration, along with phylogenetic variability in citric acid cycle intermediates that appear to have been recruited from different subcellular functions, raise the possibility that aerobic respiration has arisen multiple times. This would not be surprising, given that prokaryote metabolic innovation is among the most versatile and evolvable properties in the biosphere.

What about the great delay before the emergence of eukaryotes? And why did prokaryotes not subsequently re-evolve eukaryote-grade complexity? One reason for the delay in the origin of the eukaryote cell, which could also account for its subsequent nonreplication, is an evolutionary catch-22: engulfing a fellow prokaryote (like the mitochondrion) requires sophisticated cellular capacities,

but by Lane and Martin's calculations these cellular capacities could not have evolved without the added mitochondrial power. How this happened remains one of the great mysteries in biology, though there is recent evidence to suggest that phagocytosis evolved before the acquisition of the mitochondrion.¹⁷ A much better understanding of the ecological conditions, genetic innovations, and metabolic mechanisms that precipitated these events and precluded their iteration is needed before we can draw any definitive conclusions. In the meantime, the replicability of our complex living world hangs in the balance.

4. Summary of Part I

Let us now distill the main takeaways of part I. Patterns of convergent evolution offer a promising source of evidence for adjudicating the contingency debate. They also provide a way around observer selection effects that would otherwise prevent us from projecting earthly outcomes out into the cosmos. Until they are parsed in accordance with their underlying causes, however, convergence data cannot establish the replicability of animal forms across deep rewinds of the tape of life on Earth, let alone support Simon Conway Morris's stronger assertion that "the nodes of [morphospace] occupation were effectively predetermined from the big bang."¹⁸ This is because some iterations are consistent with, and could be read as corroborating, a broadly contingent view of life in which internal constraints set the channels for evolutionary innovation, repetition, and predictability. Once we begin the project of parsing convergent events, we find that many iterations are the result of body plan parameters that are likely to be radically contingent and thus do not speak to the replicability depths and global optimization narratives that Gould's contingency thesis denies.

At the same time, we also found that some iterations that implicate shared developmental mechanisms (like deep homologs) are nevertheless genuine cases of convergence. In disentangling robustly replicable features from radically contingent ones in "bundled" evolutionary outcomes, we can identify repetitions that are more clearly in tension with the RCT. Radical contingency remains a very real possibility, however, for some singular major transitions and key innovations out of which animal forms have been built. At this stage in the investigation, what we can say with confidence is that some specific forms (though not body plans)—and many more generic forms and functions—are robust probably across the evolution of animal-grade morphological complexity, quite possibly across the evolution of eukaryote-grade cellular complexity, and perhaps across the evolution of life itself. We have thus begun to build a case for a cosmic biology of bodies. Part II will mount a similar case for minds.

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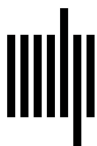
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