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A Philosophical Theory of Evolutionary Contingency

Stephen Jay Gould was one of the great popular science essayists of his day. His voluminous, wide-ranging, and baroque body of scholarship is known for many things, but understatement is not one of them. His views were often presented in bold terms, sometimes to the ire of his peers who cringed at the language of “revolution” or chaffed at what they saw as characterizations of evolutionary science that were either uncharitable or vulnerable to exploitation by creationist political forces. On occasion, Gould was compelled to walk back some of his more provocative assertions while still clinging to scientific vindication (see, for example, the multidecade controversy over “punctuated equilibria”). Other bastions of Gouldian thought were defended categorically and unapologetically to the very end.

The emphasis on historical contingency in evolution is one such unyielding commitment. Gould never abandoned his self-professed crusade to free biology from the yolk of physics envy by encouraging paleontologists to unabashedly seek narrativistic explanations of macroevolution. More than this, he insisted that contingency dominated at the level of scale and detail that is of the greatest interest to macroevolutionary biologists, namely at the level of form.

Yet after more than two decades, the radical contingency thesis (RCT) remains underspecified. Ambiguities in its formulation have caused ongoing confusion about the core commitments of the theory and consequently the evidence that might bear on its adjudication. Not only did Gould not attempt to define contingency in any systematic way, but he also used the term inconsistently, at times conflating the metaphysics of contingency with the epistemic consequences of contingent causal dynamics, such as in relation to prediction and explanation.

Further ambiguities abound. For instance, it is not clear which types of evolutionary outcomes the RCT is intended to capture and at what level of description. Nor is it obvious how dissimilar outcomes must be across replays of life’s tape for them to support the RCT or how this outcome dissimilarity should be measured. A further wrinkle is that contingency can only be assessed relative to

initial conditions; hence, whether an outcome is contingent or robust will depend on what we take the replay starting conditions to be. Are we contemplating replaying the tape from the origins of the first cell, the first eukaryotes, the advent of complex multicellularity, the emergence of tetrapods, the demise of the nonavian dinosaurs, and so on? An outcome may be stable across the evolution of mammals, even while it is unstable across the evolution of tetrapods, chordates, bilaterians, metazoans, or eukaryotes. Gould's Cambrian thought experiment, discussed in chapter 2, is structured in this manner, as it assumes the existence of complex multicellular organization among its initial conditions and queries whether the evolution of specific body plans and their associated regularities hold across replays of the complex multicellular tape of life.

Finally, and even more daunting from a methodologic perspective, the contingency question is one of relative frequency, in that it may apply to some evolutionary outcomes but not to others. Adjudicating the RCT requires, therefore, that we make some global judgment about the relative significance of contingency in the history of life, and as a result there is no single crucial experiment that can be performed that would refute Gould's thesis. A frustrating implication of this is that a handful of putative counterexamples can at best refute subclaims of the RCT, not the RCT as a whole. For instance, even if turns out that the mind is evolutionarily robust, as will be argued in part II, this does not preclude other major aspects of life, such as body plans, from being radically contingent. Despite these difficulties, it is nonetheless meaningful to ask whether contingency is a dominant theme in macroevolution and to investigate the specific outcomes to which it does and does not apply.

How does acknowledging outcome ambiguities, contingency gradations, spheres of application, and initial condition-relativity affect the ways in which we understand and evaluate the RCT? By sketching out an answer to this question, we can begin to develop a better sense of how the RCT hangs together with Gould's other theoretical commitments and whether it stands up to our current scientific understanding of life. Although one goal of this chapter is to tease apart the nuances of Gould's view, the primary aim here is not exegetical. It is one thing to consider what Gould might have had in mind when he described evolutionary outcomes and processes as "contingent"; it is quite another to consider which reading of contingency best conforms to the existing body of contemporary biological theory. The task of this chapter is also critical, therefore, in that it underscores a number of conceptual problems with the RCT both as Gould framed it and as it has been elaborated on in more recent philosophical scholarship. As we shall see in the next three chapters, these conceptual problems have seeded misinterpretations of Gould's thesis, which in turn have impeded evolutionary investigations that are designed to put that thesis to the test.

1. Conceptions of Evolutionary Contingency

Contingency is a conceptually fraught subject, bristling with different meanings in different literatures and contexts. For instance, in traditional philosophical discussions of laws of nature, a common view is that to satisfy the criteria for lawhood, a universal generalization must be a “contingent necessitation,” by which it is meant that laws must not be logically necessary truths. In evolutionary biology and other historical sciences, the term “contingency” takes on a very different meaning—something closer to a “formative happenstance,” or an accident that shapes or influences some relevant outcome or set of outcomes. There are many nonequivalent definitions of contingency on offer in the biological literature, and many interpretations of what Gould meant by the term. Existing accounts capture important aspects of evolutionary contingency, but, as we shall see, these accounts are ultimately incomplete.

1.1. Two Senses of Gouldian Contingency

Because Gould did not attempt a definition of evolutionary contingency, students of Gould are left to piece together a conception out of fragmented passages in Gould’s prolific corpus of scholarship. Our reconstruction project begins with philosopher John Beatty, who argues that Gould equivocates between two compatible but importantly different conceptions of contingency.¹ Although Beatty is right that these different senses of contingency can plausibly be attributed to Gould, we shall see why, taken both individually and collectively, they do not adequately capture the concept of contingency as it figures in the Gouldian view of life.

The first sense of contingency that Beatty attributes to Gould is what he calls “contingency as causal dependence.” In brief, this implies that a series of prior events (E_1, E_2, \dots, E_i) in a chain (or dynamic web) of causation are each necessary with respect to the production of an outcome O , such that if any of these events had not occurred or had occurred in a different way, O would not have occurred or would have occurred in a different way. Where such a causal structure obtains, we can say that O is contingent on E . Beatty is right to say that evolutionary contingency involves the causal dependence of evolutionary outcomes on prior events. But causal dependence *simpliciter* is vastly overinclusive, for two reasons.

First, it fails to rule out nomically expectable outcomes. If all events (E_1, E_2, \dots, E_i) along a causal chain or in dynamic causal web are highly likely to repeat, say, due to constraints of the laws of physics, then O will be virtually certain to repeat, given a replay of the system. Star formation may be contingent on inhomogeneous concentrations of matter brought about by the shock

waves of supernovae or, more distally, by quantum fluctuations in the early expanding universe, but stars cannot plausibly be considered radically contingent phenomena in the Gouldian sense because they are law-like outcomes that will reliably occur across countless replays of the tape of the cosmos. So, on Beatty's first definition, *O* may be contingent on *E* even if *E* is nomically necessary and *O*'s occurrence is, due to its lawful connections to *E*, highly replicable. This notion of contingency does not get at the causal dynamics the RCT is after.

A second problem with conceiving of evolutionary contingency as mere causal dependence, in the way that Beatty does, is that it does not enable us to locate the source of the disagreement between the RCT and its detractor theories. It cannot be that contingency in the Gouldian sense entails that *any* change in initial conditions will tend to produce *any* change in outcome. Without saying something more definitive about the kind of causal dependence that is actually in dispute, we are liable to wind up talking at cross purposes or addressing straw man versions of opposing views—which, as we shall see in the next chapter, has in fact occurred.

The second sense of contingency that Beatty attributes to Gould is what Beatty calls “contingency as unpredictability.” This entails that identical initial conditions do not suffice to produce the same outcome. This definition seems to accord with Gould's various “rewind the tape” thought experiments, whereby we go back in time to key junctures in animal evolution and let life march forward once again, only to find that it does so to a very different macroevolutionary tune. As we saw in chapter 2, Gould does gloss the RCT in terms of unpredictability, an epistemic state that he attributes to the “ecological handicapper” in his macroevolutionary thought experiments. Although there is a textual basis in Gould's work for interpreting contingency in terms of unpredictability, there is a major exegetical problem with this interpretation, as well as an even more serious conceptual problem with such an account.

The exegetical problem is that this notion of contingency would seem, on its face, to commit Gould to the metaphysical thesis of indeterminism because by definition “contingency-as-unpredictability” requires that the *same* initial conditions produce *disparate* outcomes—a physical impossibility if determinism obtains for biological systems. Beatty expressly disavows the inference from contingency-as-unpredictability to indeterminism,² and rightfully so given that Gould explicitly divorced randomness from contingency.³ The difficulty for Beatty's reading, however, is that if determinism is true, then Gould's rewinding-the-tape thought experiments are trivial exercises, for they will always play out in precisely the same way. In a “deterministic” universe, any state of the world is necessitated or determined by a previous state together

with the laws of nature. French mathematician Pierre-Simon Laplace eloquently describes such a universe:

We ought to regard the present state of the universe as the effect of its antecedent state and as the cause of the state that is to follow. An intelligence knowing all the forces acting in nature at a given instant, as well as the momentary positions of all things in the universe, would be able to comprehend in one single formula the motions of the largest bodies as well as the lightest atoms in the world, provided that its intellect were sufficiently powerful to subject all data to analysis; to it nothing would be uncertain, the future as well as the past would be present to its eyes.⁴

Like Laplace, Gould entwined the metaphysical thesis of determinism with the epistemic state of predictability. As the philosopher Yemima Ben-Menahem points out, the literature on historical contingency tends to conflate chance (indeterminism) and contingency, even though the two concepts are clearly severable.⁵ Indeed, not only are the concepts of contingency and predictability severable, they describe *entirely different categories of thing*: metaphysical states of the universe, on the one hand, and knowledge states about metaphysical states of the universe, on the other. Although determinism and predictability bear important relations to one another, it is also easy to see how the two come apart and why their conflation is problematic.

For instance, chaotic dynamical systems are deterministic, yet they are in principle unpredictable; quantum mechanical systems are irreducibly indeterministic, yet they support the greatest predictive precision ever achieved by a human science. Even comparatively simple deterministic systems will support prediction only to the extent that the laws of nature can be known, present states ascertained, and future states computed by the cognizer in question. The “*n*-body problem” in physics shows that even for Newtonian systems involving only three bodies moving solely under the effects of mutual gravitation, attempts to derive future states of the system can be intractable. Thus, whether the universe or some relevant subset of it is deterministic is a metaphysical question that is wholly distinct from the question of whether future states can be predicted by any given cognizer. It follows that whether macroevolution is radically contingent is a metaphysical question that is decidedly not determined by the knowledge state of any observer. Were it so determined, then a system could at the same time be radically contingent for one observer and not for another, depending on their respective computational capacities, knowledge of initial conditions, and understandings of nature’s laws.

Imagine, for example, a late-Cretaceous observer—whom we will refer to as the Cretaceous Daemon—who has a profoundly deep understanding of Mesozoic marine and terrestrial ecosystems, as well as an awareness of the

position and velocity of all kill-grade celestial objects in the solar system. Imagine also that our idealized observer, upon witnessing a gravitational disturbance in the Kuiper Belt or the Oort Cloud, calculates the projected impact angle and energy of the bolide that will deterministically careen thousands of years hence into the shallow, sulfur-rich sea beds of the Yucatán Peninsula. From there our Daemon derives the likely geological, climatological, and ecological aftermath of this event, predicting the global wildfires borne of raining impact ejecta, the blanketing of the planet in sulfuric acid aerosols that would cause global temperatures to plummet and trigger acidification of the oceans, the plunging of the Earth into global darkness and cooling that shut down photosynthesis and result in catastrophic losses to phytoplankton and plant species, which in turn would trigger a collapse of Cretaceous ecosystems and usher in a new climatic regime on Earth. What's more, our Cretaceous Daemon can calculate the extinction probability distribution for lineages that are likely to be severely depleted or extinguished in this biotic crisis based on factors such as their geographic distribution, trophic position, biomass, speciosity, feeding ecology, body size, species-typical behaviors, coevolutionary interactions, and so on, allowing the Daemon to foretell the radiation of surviving mammals into the vacated archosaurian niches.

Even if our idealized Cretaceous observer were capable of such preternatural epistemic feats, the dinosaur-mammal succession *would still be radically contingent*. For it is not the amenability of this outcome to prediction but rather its causal structure that makes it contingent. This means that the RCT is at bottom a metaphysical thesis, not an epistemic one. It holds that certain macroevolutionary outcomes are sensitive to low probability events that are unlikely to be replicated across the vast majority of alternative evolutionary histories. In Gould's own words, "alter any early event, ever so slightly and without apparent importance at the time, and evolution cascades into a radically different channel."⁶ Here again Gould can be found tying the metaphysics of contingency to epistemic states ("apparent importance"). But whether the metaphysics of contingency translates into *ex ante* unpredictability is simply irrelevant for purposes of characterizing these causal dynamics.

In *The Structure of Evolutionary Theory*, Gould abetted the confusion on these points by contrasting the "contingent phenomenology" of natural history with Laplacean-style determinism.⁷ Yet, as we have seen, if determinism is true, then rewinding the tape of life would be a trivial exercise because the trajectory of life would unfold in precisely the same manner. If determinism obtains, then the same set of initial conditions *must* result in the same outcome. How then can we make sense of Beatty's claim that what Gould meant by

“contingency” is that different outcomes follow on from the same initial conditions? It seems we have two options.

The first option is to maintain that Gould was, despite protestations to the contrary, committed to the metaphysical indeterminism of evolutionary biological systems. Biological indeterminism is not, substantively speaking, an implausible position, as irreducibly chancy events may very well “percolate up” from the quantum level to affect evolutionary trajectories. This percolation may occur, for example, through proton tunneling that affects which mutations arise or in what order they do so. Or it may occur through quantum alterations of microscopic initial conditions on which chaotic geophysical systems (such as weather, climate, tectonics, etc.) are sensitively dependent, with chaotic dynamics magnifying these events to the point that they influence large-scale selective environments. Nevertheless, because Gould was explicit about not equating contingency with indeterminism, it is best to opt for another interpretation.

According to this different interpretation, Gould is either explicitly excluding certain evolutionary boundary conditions from the “same initial conditions” or else referring to an epistemically equivalent (but metaphysically nonequivalent) set of boundary conditions, wherein the undetected nonequivalent conditions are responsible for the disparity in outcomes. Let us call this latter view the “hidden variables” reading of contingency-as-unpredictability. It bears noting that Gould at no time explicitly excludes any classes of initial conditions—and neither does Beatty in his interpretation of Gould—and it is unclear what principled rationale could justify such an exclusion. But the hidden variables account is the more plausible reading of the two more plausible readings of Beatty’s second formulation of Gouldian contingency.

Nevertheless, there is a fundamental problem with this interpretation as well. The problem is that the issues of determinism-versus-indeterminism and predictability-versus-unpredictability are red herrings because they tell us nothing about the accidental or law-like nature of macroevolutionary outcomes—which is what the RCT is arguably all about. Accidental outcomes remain accidents, and law-like outcomes retain their nomic necessity, regardless of whether they are part of a deterministically or indeterministically configured universe, and regardless of whether they are amenable or recalcitrant to prediction. The RCT is best understood, I submit, as a “modal” thesis that describes the sensitive causal dependency of evolutionary outcomes on small changes in initial conditions. If this is correct, then the RCT hypothesizes a causal structure of life that can only be revealed through analyses of possible evolutionary worlds.

1.2 Contingency, Stochasticity, and Path Dependence

Before canvassing this positive view, let us briefly consider two other philosophical accounts of Gouldian contingency and their limitations as doing so will further motivate the view that I want to defend. In chapter 2, we saw that stochastic or pseudo-stochastic extinction plays an important role in the RCT. The sampling of Cambrian body plans for reasons unrelated to long-term functional merit is one of the two major pillars on which the RCT rests, the other being the developmental entrenchment of the body plans that fortuitously survived these perturbations. Philosophical accounts of Gouldian contingency have been influenced by each of these pillars, though as we shall now see they come up short of a full-fledged theory.

For instance, the philosopher Derek Turner has argued that we should conceive of Gouldian contingency as a claim about macroevolutionary stochasticity. Turner maintains that “for Gould, evolutionary contingency is the random or unbiased sorting of entire lineages. It just is the macroevolutionary analogue of random drift.”⁸ In a similar vein, Beatty is puzzled by Gould’s decision not to include stochastic processes in his concept of contingency, given that “Gould acknowledged [these phenomena] as sources of historical contingency.”⁹ Turner’s recommendation that we think of Gouldian contingency in explicitly macroevolutionary terms is on the right track. But focusing exclusively on stochasticity is problematic for several reasons.

First, as we saw in the previous chapter, many lineage culling episodes may be selective and thus not genuinely stochastic, even if the selective regimes imposed are too fleeting and sporadic to permit the construction of macroevolutionary adaptations. The key characteristic of these sorting episodes is not that they are stochastic, but that the sorting is unrelated to the relative *long-term* functional merits of the sorted lineages. Another way of putting the point is that these sorting events are stochastic *with respect to body plans*, which merely come along for the ride with other population-level or organism-level traits that are fortuitously connected to clade survival during mass extinctions.

Second, as we also saw in the last chapter, the RCT presupposes constraints on the ability of evolution to “correct” for mass extinction perturbations in the enormous intervening timespans between major extinction events. It thus requires a developmental constraints component to ensure that stochastic or pseudo-stochastic episodes of sorting have permanent effects on the shape of life. And constrained evolutionary trajectories, whether due to selection or to the internal biases of development, are inconsistent with genuinely stochastic patterns like random walks because the latter entail equiprobable sampling probabilities at every branching point.¹⁰ In contrast, the very gist of constraints

is that they bound the space of evolutionary possibility, making some outcomes more likely than others. Thus, stochasticity alone cannot explain the bounded variation observed in between mass extinction perturbations, which is a crucial element of Gould's thesis.

A third problem with equating contingency and stochastic lineage sorting is that doing so fails to distinguish the sources of radical contingency from the contingent dynamics themselves. Drift, mutation, and stochastic fluctuations of ecological environments are all potential sources or causes of evolutionary contingency (more on these causes later); however, the *causes* of evolutionary contingency should not be incorporated into our *definition* of contingency, lest they be prevented from serving in explanations of contingent dynamics. If contingency is a multiply realizable phenomenon, then no single cause or causes should be incorporated into its definition, lest this obscure its diverse causal base. So, although stochastic or pseudo-stochastic sampling at the lineage level may be a source of contingency and figure in explanations of the same, these processes should not be equated or conflated with contingent phenomena.

A similar problem arises for philosophical accounts that equate contingency with path dependence. Philosopher Eric Desjardins (a former student of Beatty's) conceives of contingency in terms of "historicity," which he cashes out in terms of causal dependence on the past.¹¹ Evolutionist Eörs Szathmáry describes the notion of path dependence this way: "Path dependence entails that the probability of going back to some previous state decreases with time, or that switching to a state that could have easily been reached, had the population taken a different turn previously, is becoming increasingly improbable as time goes on."¹² Desjardins's contribution is to formalize the notion of path dependence, or the causal structure that, he argues, makes history matter.

The explanatory primacy of history figures prominently in Gould's work, from his decimation-diversification hypothesis about the early origins and subsequent canalization of body plan disparity (discussed in chapter 2), to his advocacy of concepts like "exaptation" and "spandrels" that figure in his broader critique of adaptationism. Path dependence explains why species that adapt to the same external environments never evolve the exact same solutions, and why traces of the unique, contingent histories of converging lineages are never fully erased (see chapter 4).¹³ Here is a simple analogy: In the early building phases, a house can take on many different configurations. Halfway through construction, however, the possible functional outcome space has narrowed considerably; because of accumulated and convoluted structural interdependencies, certain designs are now off-limits—unless one scraps the entire project and starts over, which unlike foresighted human engineers natural selection cannot do. For example, in the early stages of their evolution, plants came

to rely on growth, rather than on neural-muscular systems, as their primary means of movement. This irreversible evolutionary “choice” imposed significant constraints on how plants could respond to predation, foraging, and mating tasks that have since arisen in the course of their evolution.

I argued in the last chapter, and in publications going back to 2007, that a crucial component of the RCT is the developmental entrenchment of stochastic (or pseudo-stochastic) bouts of lineage sorting—particularly at the body plan level of morphological organization. The notion of path dependence can reasonably encompass internal constraints that are imposed by the causal topography of development (as discussed in chapter 2). However, without the stochastic or pseudo-stochastic culling component, the path-dependency view glosses over why the RCT presents as the antithesis of progressivist views of macroevolution. If globally optimal animal designs arose in the Cambrian and steadily out-competed their functionally inferior counterparts, then it would be of little theoretical consequence if these forms exhibited path dependence within the parameters of their own evolution. When path dependency is combined with non-merit-based culling at the lineage level, however, it begins to capture the Gouldian view of life.

Although macroevolutionary stochasticity and path dependence in combination go a long way toward *explaining* contingent dynamics, they are not equivalent to them. It is only when contingency is framed not in terms of mechanisms or processes but as a modal claim about the stability of evolutionary outcomes across initial conditions that we can then go on to formulate hypotheses about the causes and relative frequency of contingency. Stochasticity and path dependence are both plausible causes of modal instability, but they are not equivalent to it.

Defining contingency in terms of stochasticity or path dependence or both misses the mark for another crucial reason: evolution is neither wholly stochastic nor wholly path dependent, and the extent to which it is either depends on the grain of resolution at which we examine its processes and products. This issue proves critical to understanding the RCT, for reasons that will be unpacked over the next three chapters. For now, it is enough to note that evolutionary systems can exhibit path *independence* (and hence modal stability) at finer grains of phylogenetic resolution, while exhibiting path dependence (and hence modal instability) at coarser grains. Accounts that reduce the RCT to stochasticity or path dependence or to other features of the evolutionary process overlook this textured feature of Gould’s view of life. I will argue later that such a mixed contingent/convergent system is not only consistent with but actually a direct entailment of the RCT.

1.3 Contingency as Sensitive Dependence

I will now sketch an alternative conception of contingency that I think better suits the role that the concept plays in the RCT, and that can make sense of its variable usages both in Gould's work and in the broader literature on the topic. The conception of macroevolutionary contingency that I will defend is drawn from an account I have developed in a series of papers.¹⁴ Once this account has been laid on the table, I will go on to consider how it interacts with other areas of philosophical research, such as biological laws and explanation. I will refer to this account, both here and throughout the remainder of the book, as *radical contingency*. The working definition is as follows: Outcome O is radically contingent if and only if a marginal change in some initial condition I_1, \dots, I_n would tend to result in Outcome O^* in any physically possible world, where O^* is radically disparate from O . There is much to unpack here and many ambiguities to tackle, but let us begin with an exegetical defense of this formulation.

The origins of radical contingency can be found in some of Gould's earliest writings on the subject, where he describes the quintessential case of contingency as one in which "*small and apparently insignificant changes* ... lead to cascades of accumulating difference," yielding entirely different evolutionary outcomes.¹⁵ Gould hints again at this interpretation of contingency when he draws an analogy to the dynamics of human history, surmising that if we were to rewind the tape of the American Civil War, "with just a few *small and judicious changes* (plus their cascade of consequences), a different outcome, including the *opposite resolution*, might have occurred with equal relentlessness."¹⁶ Consistent with Beatty's pluralism thesis, however, Gould can also be found associating contingency with "an *unpredictable* sequence of antecedent states, where any *major change* in any step of the sequence would have altered the final result."¹⁷ Instead of quibbling over interpretations of Gould's voluminous work, it is more productive to focus on the virtues of conceiving of contingency in the way outlined here, as compared to the alternative accounts discussed in the previous two sections.

The first thing to note about this account of radical contingency is that it describes a counterfactual causal structure. This accomplishes four useful things. First, it separates the metaphysical dimensions of contingency from the epistemic consequences of contingent causal dynamics, thus eschewing problems that confront epistemic characterizations of the thesis (such as Beatty's second definition). Second, by focusing on evolutionary modality, or the stability of evolutionary outcomes across nomically possible biological worlds, radical contingency has the luxury of remaining agnostic to metaphysical debates over determinism versus indeterminism in biology and beyond. The

reason it can remain agnostic to those metaphysical questions is that on the account proposed, the perturbations in initial conditions can be either actual (e.g., via percolating quantum events) or idealized (e.g., had such and such initial developmental conditions been different, a disparate outcome would have ensued). Third, radical contingency allows contingent phenomena to be explained by various mechanisms and processes, such as stochasticity and path dependency, without being identified with or reduced to those mechanisms and processes. Any attempt to define contingency in terms of mechanisms and processes will forego these explanatory virtues.

Fourth, radical contingency does a good job of explaining, and goes some way toward unifying, the two versions of contingency that Beatty has identified, in addition to the accounts of Turner and Desjardins, all of which capture important dimensions of Gouldian contingency but are, in and of themselves, incomplete. Radical contingency accounts for Beatty's notion of "contingency as causal dependence" because it describes the causal dependence of particular outcomes on changes in particular initial conditions. However, radical contingency picks out a *particular sort* of causal dependency—namely, a sensitive dependence on small changes in initial conditions, which allows it to home in on the sort of counterfactual instabilities that lie at the heart of the RCT. This sensitive dependency implies that relatively small changes in boundary conditions, including geophysical, biochemical, developmental, phylogenetic, and ecological conditions, will substantially affect long-term evolutionary outcomes. Radical contingency also helps to make sense of Beatty's notion of "contingency as unpredictability," as well as the common entanglement of the distinct but causally related metaphysical and epistemic aspects of contingent systems. The behavior of radically contingent systems will be hard to predict because their trajectories are easily derailed by small perturbations along the way. Radically contingent systems magnify small differences in initial conditions, resulting in disparate outcomes from initial conditions that are *for all practical purposes identical*. Radical contingency can thus account for the hidden variables reading of contingency as unpredictability.

If narrativistic explanations are to be intelligible, they must provide causal explanations (see chapter 2), and making good on causal claims may require appealing, if tacitly, to laws that explain the interactions identified. But any laws lurking in the background of narrativistic explanations will not significantly constrain the long-term behavior of the system, and thus will not provide the predictability that is associated with nomological styles of explanation. As Gould put it, "the contingency of history guarantees that any body of theory will underdetermine important details, and even general flows, in the realized pageant of life's phylogeny on Earth."¹⁸

Much ambiguity remains. It is unclear, for example, how small the changes in initial conditions and how large the outcome disturbances must be in order for a system to count as radically contingent. Some cases are clear-cut; the ordering of mutations in a lineage surely counts as a small perturbation, and if this ordering substantially affects the stability of a given evolutionary outcome, then that outcome is radically contingent. Other cases of radical contingency involve large perturbations that are themselves contingent on small perturbations. The K-Pg impact event, for example, clearly constitutes a large perturbation of late Mesozoic ecosystems, but the impact can be traced to negligible changes and interactions in the positions of objects orbiting the sun, which ensured that a 10- to 15-kilometer bolide would collide with the Earth at a particular place, time, and angle—details that would determine the shape of the resultant biotic crisis and its aftermath. If events that occur with some regularity over the course of any history of life, such as magmatic activity, bolide impacts, or continental collisions, have the potential to substantially and permanently alter large-scale evolutionary outcomes depending on when and how they manifest, and if the occurrence or nonoccurrence of these events can be traced to small changes in initial conditions, then the system can be properly characterized as radically contingent.

1.4 Characterizing Radical Contingency

In short, the RCT is best understood as a universal biological claim about the sensitivity of large-scale evolutionary outcomes to initial conditions. The claim is universal because it cites causal mechanisms and processes that are applicable to the history of life on Earth and to all nomically possible histories. These include stochastic or pseudo-stochastic bouts of extinction and a causal topography of development that makes upstream components of development resistant to modification, resulting in the entrenchment of non-merit-based episodes of lineage-level sorting. There is no reason to think that the causal geometry of development and the constraints it imposes on macroevolutionary search space would be different on other life worlds. Evolution everywhere will build incrementally on existing gene-regulatory networks, resulting in the entrenchment of phylogenetically and ontogenetically earlier components.

Also likely to be universal is the non-meritorious culling power of mass extinctions. Life will tend to evolve on geophysically dynamic planets,¹⁹ and the downside of living on a geophysically dynamic planet is that it comes with the occasional mass perturbation due to volcanism, tectonic movements, asteroid impact, climatic change, and the like. And once we add strategic evolutionary interactions and ecological dependencies among living lineages into the

mix, the prospect of mass perturbations increases substantially. Note that the *content* of background fitness conditions on any given life world does not matter for the point being made here—what matters is that this content will be rapidly and dramatically altered for brief punctuations, resulting in biotic crises and faunal turnovers which, when combined with developmental entrenchment, give rise to radical contingency. Thus, although the RCT issues a profound challenge to the project of a contentful universal biology, it also offers some properly cosmic lessons of its own.

Let us elaborate further on the notion of radical contingency by returning to the modal dimensions of the concept. The set of initial conditions upon which an evolutionary outcome is sensitively dependent must contain “non-replicable” members. That is to say, it is necessary that this set contains events that are essentially accidental. For instance, the origin of life may be contingent (in the simple causal sense) on the precise positioning of a planet within the “goldilocks zone” of its host star or of the solar system within the so-called galactic habitable zone. Yet causal dependence on goldilocks positions does not make the origins of life radically contingent. For although worlds within the goldilocks zone may be somewhat rare, current astronomical research suggests that an appreciable fraction of rocky planets are likely to fall within the habitable range. This is our first clue that radical contingency is closely connected to cosmic frequencies, a connection we will return to shortly.

Likewise, it is important to be clear about the nature of the outcome at issue. For instance, the formation of a *token* star, such as our own Sun, may be radically contingent: had a supernova not occurred or occurred in a different way, then the ensuing collapse of the interstellar molecular cloud that led to the formation of our solar system would either not have occurred or would have taken a different form, and a different type of star in a different place and time would have formed. But the formation of stars and planets *qua entity types* is highly robust, much like the positioning of worlds within the stellar or galactic habitable zones.

1.5 A Problem with a Solution

This brings us to a problem with the notion of radical contingency as it has thus far been framed. The problem is that as a thesis about evolutionary patterns throughout the Phanerozoic, radical contingency is quite obviously false. Much of evolution is clearly not sensitively dependent on initial conditions. Indeed, it is largely through the efforts of Gould and his collaborators that the nonrandom clustering of organismic form within discrete body plans was foregrounded as an important explanandum in macroevolutionary theory. It is precisely this explanandum—bounded variation within body plans—that is

underscored in Gould's decimation-diversification hypothesis (see chapter 2). The shape of life is not incomprehensibly chaotic as one might expect if evolution was thoroughly radically contingent. How do we square this with the RCT?

A closer look at Gould's view of life reveals that it does not entail evolutionary chaos at all. On the contrary, the developmental pillar of the RCT holds that internal constraints due to the causal topography of development impose significant order and predictability on the actual occupation of morphospace once the initial crop of body plans had congealed. Take any two animal clades, such as mammalian vertebrates and bivalve mollusks: no matter what their ecological conditions and selective regimes, these lineages will not, according to the RCT, escape the architectural confines of the vertebrate and mollusk body plans, respectively. Nor are these lineages capable of transcending the developmentally "midstream" anatomical parameters of their respective mammalian and bivalve organizations. In other words, they will never venture down "radically different" evolutionary paths, where this refers to alternative occupations of morphospace at phyletic and perhaps class-based levels of organization. These are the crucial contrast classes against which outcome similarity and dissimilarity should be measured.

On this view, the reason why lineages do not venture beyond their initial body plan parameters is not because the existing clumps in morphospace are perched atop globally optimal fitness peaks, with natural selection having culled suboptimal forms that wandered into what paleobiologist Simon Conway Morris memorably calls "the howling wilderness of the non-adaptive."²⁰ Rather, it is because internal constraints prevent lineages from traversing these regions of morphospace even when doing so would (*ceteris paribus*) be evolutionarily beneficial.

In short, the "sensitive dependence" component of the RCT is not intended to describe the evolutionary behavior of existing lineages *within the confines of their own body plans*. On the most plausible reading of Gould, much of evolution is constrained and predictable—but these constraints are essentially "internal" and embedded in a deeper causal framework of sensitive dependence. This claim will be fleshed out and defended in the chapters to come.

2. Radical Contingency and the Laws of Life

Contingency is frequently contrasted with necessity, and necessity is often associated with laws of nature. Given this, one might think that adjudicating the RCT will boil down to whether there are biological laws describing the relevant sorts of evolutionary outcomes—that if such laws can be found, then

Gould's thesis will have been refuted. Indeed, Gould attributed evolutionary contingency to the lack of invariant biological laws.²¹ Nevertheless, the RCT is not in tension with the existence of evolutionary laws *tout court*. And as we shall see, depending on how one conceptualizes laws of nature, the RCT may even be consistent with the existence of specific laws of form and function. The upshot is that questions about contingency ought to be decoupled from questions about laws.

2.1 The Nomological Vacuum of Biology

The notion that there is a “nomological vacuum” in biology—a stark absence of laws of life—was first systematically argued by John Beatty.²² Beatty's core contention is that unlike thoroughly nomological disciplines like physics and chemistry, biology has no distinctive generalizations that are both exceptionless and universal. The reason for this, Beatty contends, can be found in the contingent nature of the evolutionary process. Even biological generalizations of the widest scope—such as the “laws” of Mendelian inheritance or the ubiquitous citric acid cycle (the series of chemical reactions involved in carbohydrate metabolism in aerobic respiration)—appear to be merely accidental. Although these traits are pervasive on Earth due to their unbroken descent from a common ancestor that possessed them, they are not subject to lawful generalizations in the strict sense for several reasons.

First, they are riddled with exceptions, whereas laws of nature are supposed to describe necessary relations that are invariant. For instance, not all organisms, nor even all animals, have Mendelian-style diploid inheritance, and those that do have numerous exceptions. Meiotic drive, for example, breaks Mendel's fair (50/50) segregation rule. The same is true of aerobic respiration: not all organisms on Earth use aerobic respiration; among those organisms in which the citric acid cycle is conserved, there is significant variability in the enzymes that are deployed in the cycle. Why are there invariably exceptions to even the most ubiquitous biological regularities? The reason for this, Beatty contends, is that all biological regularities are the product of an evolutionary process, and the same process that produces these regularities (via directional selection) and sustains them over evolutionary time (via stabilizing selection) will inevitably break them down by generating counterexamples. Beatty refers to these tendencies as the “rule-making” and “rule-breaking” capacities of evolution.

A second reason for the nomological vacuum is provided by philosopher Alexander Rosenberg, who notes that biological fitness and function are multiply realizable. Fitness, or expected reproductive success, “supervenes on” (roughly, is determined by) a vast heterogeneous base of intrinsic and relational

properties of the organism.²³ Fitness, in other words, is massively multiply realizable—and a consequence of this massive multiple realizability is that there is no handful of traits that we can identify as being the fit ones. For instance, sometimes being more intelligent increases survival, but in other developmental and ecological contexts selection favors reduced intelligence (as with the evolution of herbivory in a formerly carnivorous lineage); and ditto for morphological complexity (for example, in the context of the evolution of parasitism). In addition, specific biological functions may themselves be multiply realizable, and selection is unable to discriminate among different structures that realize the same function. Perhaps the citric acid cycle is only one of many possible chemical pathways that can extract energy from carbohydrates. If there are many structural realizations of a given function, then this bodes poorly for the prospect of developing a workable set of contentful biological laws.

A third reason for the nomological vacuum, also discussed by Rosenberg, concerns the ubiquity of evolutionary arms races that can destabilize evolutionary outcomes. Adaptations are constructed in local selective environments that are subject to fluctuation; these fluctuations arise not only from changes in the abiotic environment but also from biotic interactions between coevolving lineages. Even the most successful adaptations are destined for obsolescence in the unrelenting arms race of natural selection, wherein one lineage's solution becomes another's design problem and vice versa.²⁴ It is only a matter of time (barring constraints and trade-offs) before lions evolve trichromatic color vision that makes the zebra's black and white stripes pop out as clear as day on the African Savannah—and if that day did come, then zebras would likely respond by evolving less conspicuous patterns of pigmentation. And if that happened, then so much for the “law-like” generalizations “zebras have black and white stripes” and “lions have dichromatic vision.”

The macroevolutionary implications of interbiotic arms races are illustrated by Leigh Van Valen's “Red Queen” hypothesis. According to the Red Queen hypothesis, lineages must keep “running in place” (much like the theory's eponymous Lewis Carol character) merely to remain where they are—that is, to maintain their present fitness levels. “Running” here is a metaphor for adaptively evolving, and this evolvability is necessary if lineages are to respond effectively to strategic moves and countermoves of coevolving lineages (e.g., predator and prey, host and parasite, competitors, etc.). Van Valen offered the Red Queen hypothesis as an explanation of his “Law of Extinction,” or the stunning observation that the stochastic probability of a lineage going extinct does not vary with its taxonomic age, even in stable abiotic environments.²⁵ In other words, Red Queen dynamics might explain why it is that lineages do not get better at not going extinct over time as one might expect they would if

evolution were a gradual optimizing process and lineages evolved to better match their niches. In sum, due to the multiple realizability of fitness and function and the ubiquity of evolutionary arms races, biological generalizations tend to lack the necessity, stability, and projectibility that is characteristic of natural laws.

Some laws of nature are formulated with explicit or implicit *ceteris paribus* qualifications, or provisos, which specify disturbing conditions under which the law does not apply, thereby preventing its falsification when application conditions are not right. For instance, we might say that *ceteris paribus*, planets have elliptical orbits, demand increases the price of goods, meiosis exhibits fair segregation, and so on. But the “*ceteris paribus*” strategy does not work for biology because we cannot even begin to parse the application conditions that would need to be packed into the proviso in order to make contentful biological generalizations true, exceptionless, and, most importantly, nonaccidental.

One reason for the failure of the *ceteris paribus* strategy in biology is the evolutionary metaphysics of radical contingency. If a minimally different set of initial conditions would have resulted in substantially different patterns of inheritance, then any forms of inheritance that are currently ubiquitous in our biological world will be accidental regularities. On the traditional view, laws do not describe true accidental generalizations but rather outcomes or relations that are *necessarily true* given the nomic structure of the universe. Philosopher of science Bas van Fraassen illustrates the distinction between laws and accidents by comparing the generalization “there are no solid spheres of gold greater than one mile in diameter” with the generalization “there are no solid spheres of enriched uranium greater than one mile in diameter.”²⁶ The first is an accidental generalization, as nothing prohibits large gold spheres from existing (e.g., intelligent spacefaring aliens could compile one if they were so inclined); the second is a lawful necessity due to the critical instability of uranium bodies that exceed a certain mass. Beatty and Rosenberg contend, in essence, that all biological generalizations are like van Fraassen’s first generalization: they are only accidentally true. Thus, biological generalizations formulated in terms of universals are either false, analytically rather than empirically true (such as idealized models of population genetics), or else describe historically contingent outcomes of the evolutionary process and thus lack the necessity of physical laws.

2.2 The Case for Biological Laws

Although these are all good reasons for thinking that the structure of evolutionary theory precludes the existence of law-like regularities in biology, they do not make a slam dunk case for the nomological vacuum—even if we assume strict, traditional criteria for lawhood modeled on physics. For starters, there

are strong cases to be made that the principles of natural selection²⁷ and drift²⁸ are both laws in the strict sense. There is ongoing debate about whether the principle of natural selection, when formulated as a general law, has empirical content, and whether drift is a disturbing condition for natural selection.²⁹ But the generic conditions for natural selection and drift (which refers to deviations from expected frequencies in the sampling of finite populations) will exist wherever life is found because these are the very conditions that make the origin and evolution of life possible in the first place.

Moreover, as we saw in chapter 2, the RCT is predicated on universal biological properties, namely the dynamics of mass extinction and the causal geometry of development. It is also consistent with a wide range of candidate biological laws that are equally nonspecific in that they do not predict any details of form and function. For instance, the RCT is consistent with the Zero Force Evolutionary Law (ZFEL) as described by Robert Brandon and Daniel McShea, which refers to the tendency of biological systems to depart from a preexisting trajectory or to increase in diversity over time in the absence of biological forces or constraints.³⁰ It is also consistent with laws governing the trophic structure of ecosystems, such as those which explain why apex predators will always be relatively rare in a community.

Thus, it is not the existence of macroevolutionary laws per se that would pose a problem for the RCT. What would pose a problem is the existence of generalizations describing the evolution of specific form and function that are universally projectible and hold up across deep rewinds of the tape of life. At least two robust morphological trends in the history of life on Earth have been convincingly identified: a trend toward increasing maximum body size,³¹ and a trend toward increasing maximum hierarchy (or the “nestedness” of parts within parts, which serves as a rough marker of complexity).³² It is unclear whether these trends are driven by selection or the result of “diffusion” from a minimal complexity boundary leaving nowhere to go but “up,” so to speak. Regardless of their causes, generalizations like “over the course of evolution, life will tend to increase in body size and hierarchy” are strong candidates for biological laws; as we shall see, however, they are insufficiently specific to fall within the crosshairs of the RCT. A greater threat to Gould’s thesis comes from laws intimated by patterns of convergent evolution, which we will investigate throughout this book. The point for now is that not all strict biological laws are equally in tension with the RCT.

In any case, not all philosophers of science operate with the strict sense of lawhood that Beatty, Rosenberg, and others have presupposed. There are many philosophical accounts of laws of nature, and these differing conceptions of lawhood have different implications for the logical relation between the

existence of biological laws on the one hand, and the viability of the RCT on the other. Many theorists maintain that stricter conceptions of laws modeled on those in physics are a poor fit for the production of scientific knowledge in biology, psychology, and the social sciences. Some have argued, for instance, that generalizations do not need to be exceptionless or even have empirical content to be proper scientific laws. Others have advocated laxer accounts of lawhood that allow radically contingent antecedent conditions to be incorporated into law-like statements. The latter sorts of biological laws do not pose a problem for the RCT even if they describe highly specific evolutionary outcomes.

For instance, philosopher of biology Elliott Sober has argued that generalizations formulated in terms of counterfactual conditionals with historically contingent antecedents can satisfy the desiderata for lawhood because, so formulated, they are exceptionless and universal.³³ Sober offers the following law-like schematic (*L*): If *I* (a given set of contingent initial conditions) obtains at one time, then the generalization [if *P* then *Q*] will hold thereafter. Framed in this manner, law-like generalizations state that wherever such and such application conditions are met (e.g., where diploid genetics obtain), then some rule will hold (e.g., fair meiosis, the Hardy Weinberg equilibrium, etc.). The fact that the application conditions are themselves radically contingent does not show that the broader generalization, *L*, is accidental. Sober is right to say that the relations described by such counterfactual conditionals are not in themselves radically contingent, but if they contain antecedent conditions that are radically contingent (such as the evolution of diploid genetics), then this will undermine the modal stability (and hence cosmic projectibility) of the outcomes they describe. The existence of laws on these more permissive accounts of lawhood is thus not in conflict with the RCT.

Sober's analysis shows that many nonaccidental biological generalizations obtain only if certain accidental conditions obtain; yet the accidental nature of these antecedents infects the whole generalization, such that laws framed in this manner are, in effect, *accidental nonaccidental generalizations*. For instance, there is a sense in which it is no accident that all life on Earth shares the same DNA code, for this is both the result of faithful replication from a common ancestor and the expectable result of communal innovation pools dominated by lateral gene transfer in the early phases of life (see chapter 1). But the specific code that all known life shares may be a radically contingent, frozen accident that is not replicated on any other epistemically accessible life world. The fact that humans share a specific genetic code with plants, protists, and prokaryotes is an accidental nonaccidental generalization. In contrast, the fact that all known life has a digital (nonanalog) molecular basis of inheritance is, in all probability, a nonaccidental generalization full stop. Framing both of these as nonaccidental

generalizations would be misleading. Given the diversity of thinking about laws, linking the soundness of the RCT to a verdict on the nomological vacuum of biology is liable to confuse more than it is to illuminate.

2.3 Modal Frequencies

Let us move the discussion away from laws of nature and their associated notions of inviolability and inevitability to focus instead on *modal frequencies*—the distribution of particular outcomes across possible evolutionary histories. Low-probability outcomes become probable given a sufficiently large population of chance setups. “Chance setups” are iterations of a process that produces token outcomes, such as coin flips (heads or tails), lottery draws (win or lose), and habitable worlds (life or no life). On standard interpretations of chance, frequencies apply to outcomes, whereas explanations of those frequencies lie in the causal structure of the chance setups in conjunction with the laws of nature. From the fact that it has occurred, we know that the history of life as it has unfolded on Earth is, at the very least, *consistent* with the laws of nature. But due to observer selection effects (see chapter 1), we do not know how replicable particular aspects of that history are likely to be.

If the universe is effectively infinite, as standard cosmologies assume—this means that there are an effectively infinite number of chance setups, and thus an effectively infinite number of life worlds, and an effectively infinite histories of life that play out in precisely the same way as our own. Whether there are histories of life somewhere in an infinite universe that mirror the history of life on Earth is not the crux of the issue. The issue is whether a single history of life constitutes a sufficiently large population of chance setups to make certain low-probability outcomes probable. In other words, radically contingent traits should be vanishingly rare in the cosmic horizon—not merely *within* life worlds, but also *across* them.

Gould appears to be making a frequency claim of this sort when, for example, he discusses the contingency of human evolution:

If life started with all its models present, and constructed a later history from just a few survivors, then we face a disturbing possibility. Suppose that only a few will prevail, but all have an equal chance. The history of any surviving set is sensible, but each leads to a world thoroughly different from any other. If the human mind is a product of only one such set, then we may not be randomly evolved in the sense of coin flipping, but our origin is the product of massive historical contingency, and we would probably never arise again even if life’s tape could be replayed a thousand times.³⁴

Gould is arguing that due to the metaphysics of radical contingency, many evolutionary outcomes would occur only very infrequently across alternative evolutionary histories, whether hypothetical or actual.

Focusing on claims about modal frequency allows us to home in on what is actually at stake in the contingency debate. The existence of law-like evolutionary outcomes with very low modal frequencies—that is, outcomes that obtain necessarily or with high probability but do so only under conditions that are astronomically uncommon in the universe—do not undermine the RCT or support its antithesis (see below) because such features cannot be “mainstreamed” or projected onto a broad spectrum of epistemically accessible life worlds. A central task of the next three chapters is to determine whether, and if so under what circumstances, convergent evolution can be taken as evidence for the higher modal frequencies of evolutionary outcomes. Before we can tackle this question, however, we first need to have a clearer picture of the RCT’s antithesis and its own peculiar set of theoretical commitments.

3. Framing the Antithesis: Robust Replicability

The foregoing analysis of radical contingency helps to frame its contrast class. Gouldian contingency is often framed in opposition to repeatability (a common misinterpretation of the RCT that will be discussed in chapter 4). Yet recall that if determinism is true, then the tape of life would be perfectly repeatable and hence a trivial thought experiment. It is therefore not repeatability per se but rather *robust repeatability* that properly characterizes the antipodal view of life, where “robustness” relates to the stability of an outcome over a wide range of initial conditions. In other words, the antithesis to the RCT is the view that rerunning the tape of life from disparate initial conditions and under diverse perturbing influences would nevertheless produce highly similar macroevolutionary outcomes (figure 3.1). Let us call this view the “robust replicability thesis” (RRT).

3.1 The Robust Replicability Thesis

Beatty rightly suggests that any notion of evolutionary contingency should rule out a “robust equilibrium” explanation of macroevolution, in which disparate starting points lead reliably to a small set of attractors. Note, however, that the radical contingency debate is not about the evolutionary robustness of *specific taxa* at particular spatiotemporal locations in the history of life. The RRT does not claim, for instance, that replaying life’s tape from different starting points would produce vertebrates per se, with all the traits that vertebrates possess, at a particular spatiotemporal location. The claim, rather, is that what would be reproduced is not vertebrates (sans quotation marks, denoting a spatiotemporally restricted clade on Earth), but “vertebrates” (with quotation

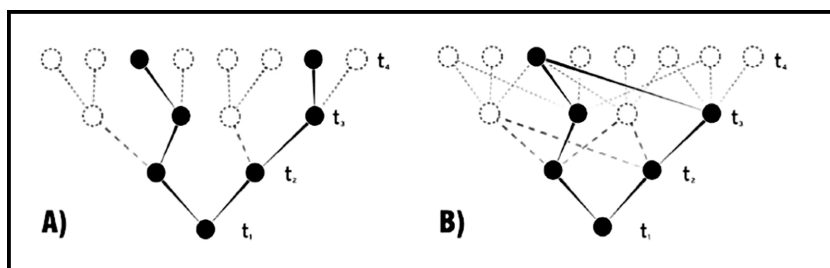


Figure 3.1

(a) A radically contingent system in which paths not taken at earlier times (dotted lines) cause evolutionary outcomes to become inaccessible at later times. (b) A convergent system in which many outcomes remain accessible from even distant evolutionary trajectories. From R. Powell and C. Mariscal, “Convergent Evolution as Natural Experiment: The Tape of Life Reconsidered,” *Journal of the Royal Society Interface Focus* 5, no. 6 (2015): 1–13.

marks, denoting a morphofunctional kind). The idea is that, over the long haul, the evolutionary crank will tend to churn out highly similar animal forms. Thus, according to the RRT, even if some features of lineages are radically contingent, enough of their basic elements will be reproduced so as to result in forms that are fundamentally familiar.

We will examine this view of life and its evidential bases in the next chapter. The lesson for the time being is that the RCT-RRT debate does not turn on genealogy or identity, but rather on whether there are nontrivial bundles of specific properties that, like their celestial counterparts, exhibit a truly robust range of counterfactual stability. These two views of life sit at opposing ends of what is surely a continuum of views on the balance of contingency and robustness in the history of life. The aim here is to set up the dialectical space necessary to stake out a position that falls in between the extremes.

3.2 Robust Adaptationism

The only known mechanism that could repeatedly drive lineages toward complex functional attractors in morphospace and keep them there is natural selection. For this to happen, it is not enough that selection is an important evolutionary mechanism. Rather, it must overwhelm other evolutionary factors that tend to divert away from the paths leading to these attractors. The RRT is therefore committed to “strong adaptationism”: the view that in the long run selection will tend to overpower perturbing evolutionary forces, constraints, and tendencies that would otherwise undermine robustness.

On this view, successful animal body plans are not the fortunate winners of a macroevolutionary lottery locked in by developmental constraints, as the

RCT would have it. Instead, they represent a superior set of solutions carved out of the vast set of ecologically possible but functionally suboptimal alternatives, many of which would have been experimented with and discarded by natural selection in the early phases of animal evolution. This view is not far removed from one that Gould spent much of his career excoriating, namely the “Panglossian” notion of the best-of-all-possible functional worlds.³⁵

The connection between strong adaptationism and the RRT is clear enough. Indeed, Beatty even frames an alternative version of his notion of “contingency-as-predictability” in terms of a denial of strong adaptationism. But even if strong adaptationism were true, and selection were in fact sufficient to guarantee a particular outcome in a given case, this does not get us to the RRT. For in addition to showing that selection reigns supreme and that macroevolutionary success is determined by a merit-based competition, the RRT must also convince us that *there are only a limited number of ways to succeed in this competition*. Without the latter qualification, there is no reason to think that selection would proceed to the same set of outcomes from disparate initial conditions, and thus strong adaptationism alone gives us no reason to think that macroevolutionary pattern would be robustly replicable. The mere predominance of selection does not imply that there is a limited number of solutions to common design problems, even if selection ruthlessly adjudicates on the merits between solutions that happen to arise. In addition, therefore, the RRT must show that the set of optimal solutions is manageably small—a premise that is not contained in the thesis of strong adaptationism.

Strong adaptationism has been subjected to its fair share of criticism, yet the evidentiary burden is even weightier for the RRT. For it turns not only on whether selection is at the helm of macroevolution but also on whether there is a limited number of destinations to which it can proceed. If there are such limitations, they will not be set by natural selection alone. For as we saw in chapter 1, the principle of natural selection, when formulated as a general law, has nothing specific to say about the sorts of evolutionary outcomes we can expect unless we plug in extensive—and for all we know, accidental—developmental details about the lineages in question. What reason, then, do we have to believe that there are contentful morphological regularities that hold up across deep rewinds of the tape of life? This brings us to the striking phenomenon of convergent evolution.

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Contingency and Convergence

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