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The Critique from Convergent Evolution

Darwin's mentor and the founder of modern geology, Charles Lyell, was skeptical of the notion that species changed over time and that new species arose from existing ones through natural, rather than miraculous, means. Yet Lyell had begun to recognize, as much as anybody of his day, that many of the creatures represented in the fossil record have no analogs among living species. The signature of extinction grew ever stronger in Lyell's time, to the point that its theoretical importance became impossible to deny. In an effort to reconcile clear patterns of extinction in the fossil record with the doctrine of divine creation, Lyell postulated a theory of "cyclical return."¹ On this view, species are immutable for the duration of their existence but bound for extinction as their habitats inevitably deteriorate until they can no longer support their particular lifeways. Lyell hypothesized that the origin of taxa would track global cycles in climate, with the reiteration of species corresponding to ecologically propitious stages in the cycle. Because he believed that climatic change was cyclical, and because the origin of species was thought to depend on the presence of environmental conditions that corresponded to specific ways of life, Lyell believed that extinct forms were destined for reiteration.

Writing in a colder, drier period of Earth's history (the Cenozoic Era), Lyell argued that if the conditions of existence were to return to the temperature and moisture levels that typified the Mesozoic, we might then expect "those genera of animals return, of which the memorials are preserved in the ancient rocks of our continents. The huge iguanodon might reappear in the woods, and the ichthyosaur in the sea, while the pterodactyle might flit again through umbrageous groves of tree-ferns."² Lyell was well aware that the Earth's climate did not cycle precisely, so he conceded that iguanodon-the-resurrected would be sufficiently different from iguanodon-the-original to recognize it as a distinct species—though he thought the two taxa would be similar enough to fall under the same genus (based on overall similarity, of course—cladistic principles would not emerge for more than a century). In contemplating a naturalistic

ground for cyclical return, Darwin wrote to Lyell in 1859 (the same year that the *Origin of Species* was published) that although it is possible in theory that natural selection could produce identical forms over deep evolutionary time, this is so astronomically improbable that it can safely be ignored by evolutionary theory.³ For Darwin, the stamp of phylogenetic history is indelible, even when lineages are subject to the same selection pressures.

Lyell's theory of cyclical return has a certain aesthetic appeal to the nostalgic among us who long to commune with living worlds that have been lost forever to the strata of geological time. At the time of Lyell's writing, however, there was no evidence for cyclical return. To the contrary, there was every indication that extinction is forever. Nevertheless, Lyell's view, so viciously mocked by his contemporaries and so thoroughly eclipsed by the Darwinian revolution, may have some nuggets of truth after all. The aim of this book is to determine how substantial these nuggets may be and to gauge the pressure they put on the Gouldian view of life.

1. Is Extinction Forever?

At the very outset of this investigation, we flagged the legitimate worry that the contingency dispute, though philosophically intriguing, might be empirically intractable. Some of this intractability stems, as we saw in chapter 3, from problems that are conceptual in nature. But even if these conceptual problems could be ironed out, adjudicating the radical contingency thesis (RCT) would still face sizable methodological challenges. The most glaring among these is the sample size problem noted in the introduction: we are working with a single history of life.

Because we cannot literally rewind the tape of life to see how outcomes hold up against perturbations in initial conditions at different junctures in life's history, it is only by consulting extraterrestrial data sets that we could decisively distinguish accidental from law-like features of the living world. We would begin by observing numerous alien histories of life, each beginning from a different set of initial conditions with respect to geophysical and climatic variables, the ordering of mutations, developmental configurations, ecological relations, and so forth. With these data in hand, we would then search for nonaccidental regularities that allow us to infer cosmic frequency distributions and the macroevolutionary processes that underpin them. To the extent that such regularities existed and could be identified, they would allow us to make predictions about how life will tend to unfold on the grandest of scales.

Unfortunately, the “ $N=1$ ” situation prevents us from investigating the stability of evolutionary outcomes in this way. Even just one example of an alien

tree of life would probably tell us more about the prospects of cosmic biology—and about the status of biological laws—than any amount of theorizing on the basis of a single sample. What could we possibly learn about the nature of other living worlds by studying life as we know it on Earth?

1.1 Finding Empirical Traction

Gould's macroevolutionary thought experiments, explored in the previous two chapters, are designed to circumvent the $N=1$ problem. But such exercises of the imagination are empirically inconclusive. Perhaps in the vast majority of close possible Cambrian worlds, the vertebrate clade survives and thrives in the wake of the end-Cambrian extinctions; perhaps it survives but does not thrive, its elimination simply delayed rather than indefinitely staid; or perhaps it is eliminated and nothing like it ever arises again. We simply do not know the frequency distribution of these outcomes with any reasonable levels of confidence. The same is true for the persistence and replicability of other animal body plans. Gould's thought experiments are effective when it comes to posing critical research questions, but less so when it comes to answering them.

Other investigations of evolutionary contingency tackle the question of replication more directly. These experiments include controlled manipulations of evolving microbial populations,⁴ longitudinal studies of selection in the wild,⁵ and evolutionary simulations.⁶ As ingenious as these studies are, they do not generalize to patterns in eukaryotic evolution that only manifest over immense timescales, and so they do not speak to key claims of the RCT.

Take, for instance, Richard Lenski's pioneering Long-Term Experimental Evolution (LTEE) project. Lenski and his collaborators have investigated evolutionary contingency by cloning twelve populations of *E. coli* bacteria and observing how they respond to identical selective environments over tens of thousands of generations (the experiment is currently at 60,000 generations and counting). As part of the study, researchers froze a time slice of each population every 500 generations, so that replays from various stages of evolution could be carried out. If selection were the dominant force acting on these separate populations, they would be expected to evolve in parallel; if chance or history were dominant, then the populations would be expected to diverge even under common selective regimes. This setup accords with Beatty's “contingency-as-unpredictability” formulation of Gouldian contingency, as discussed in chapter 3, wherein the same starting conditions result in different outcomes or, alternatively, the same selection pressures are insufficient to guarantee the same outcomes. It also accords with “radical contingency” as positively formulated in the same chapter, wherein small and in some cases imperceptible perturbations (such as stochastic events like mutation and drift) cause substantial differences in outcomes.

The findings thus far have been mixed, with some bacterial populations evolving in parallel along a number of dimensions (e.g., metabolic capacity, cell size, growth rates, gene expression, etc.), and others diverging from one another due to a combination of chance and history that is difficult to parse.⁷ For example, researchers found that after some 30,000 generations of constant exposure to a challenging metabolic substrate (e.g., citrate), only a tiny fraction of the populations evolved the ability to metabolize the substrate, even though doing so was significantly fitness enhancing and clearly within the evolvability space of all the lineages exposed (as a few managed to achieve it). The LTEE researchers inferred from these nonreplications that numerous mutations must be in place at the same time for certain salutary traits to emerge, whereas each of these necessary mutations is not selectively beneficial on its own nor is some subset of them. This “macromutation problem” could prevent incremental selection from reliably driving lineages toward advantageous outcomes. It may also explain the significant delay that is often observed in the fossil record between the presence of a particular ecological regime and successful evolutionary responses to it.⁸

Does the LTEE project actually test the RCT, even in a highly localized bacterial setting? As just noted, the Lenski studies do seem to probe Beatty’s conception of contingency-as-unpredictability, wherein the same initial conditions result in disparate evolutionary outcomes. This is achieved by isolating cloned populations and subjecting them to identical ecological regimes. The differences in outcome could then be explained by the vagaries of chance or the constraints of history. As we saw in chapter 3, however, there are good reasons not to conceive of Gouldian contingency in this way, and there are several reasons why the LTEE study does not in fact test the RCT, properly construed.

First, it is important to note that these experiments do not support the robust replicability thesis (RRT). To do so, they would need to show not parallel evolution *geometrically* conceived—wherein two populations evolve along some character dimension in the same direction from the same starting point, producing a geometrically parallel set of trajectories—but rather, proper *convergence*, wherein two lineages arrive at a structurally similar solution from *highly disparate starting points* (particularly as it relates to their initial developmental/phylogenetic conditions). Because the LTEE observes the evolution of bacterial lineages from identical or highly similar starting points, it does not provide evidence for the RRT.

Neither, however, is the study clearly in tension with Gould’s thesis. For as we saw in the previous two chapters, the RCT is a non-uniformitarian theory that does not treat all time frames in the history of life, at all phylogenetic

grains of resolution, as chaotic or unpredictable. In chapter 2 we saw that the developmental component of the RCT holds that the causal topography of gene-regulatory networks constrains the space of evolutionary solutions that a lineage can deploy in solving its ecological design problems. If any such Gouldian constraints are in operation, they will not be detected by subjecting identical populations to the same selection pressures, as the LTEE has done. Studies of convergence that are designed to test the RCT are vulnerable to a similar critique, as we shall soon see.

Another reason that the LTEE studies fail to test the RCT's core claims is that their findings are not generalizable to macro-morphological evolution—though, to be fair, they never claimed to be. The marvelous advantage of experimental evolutionary work on prokaryotes is that tens of thousands of bacterial generations can be explored within a single human scientific career (indeed, within a single graduate student's fellowship)—a feat that is impossible for studies of animals or even unicellular eukaryotes, which have vastly longer generation times and cannot be cloned as readily as bacteria. Exploiting this advantage, however, limits our ability to generalize from these experiments to the kinds of patterns that Gould was trying to explain.

This is not to say that the evolution of microbial metabolic innovation is a trivial feat; but at bottom, the contingency debate concerns the broadest brush strokes on the canvas of animal form, not the capacity to digest a challenging substrate. Just as importantly, it is plausible that historical constraints will be far more pronounced in macro-morphological evolution than they will be in the evolution of bacterial metabolism, given the more intricate interlocking of gene-regulatory networks and phenotypic components that are involved in the production of body plans. If the RCT is to be put to the test, it will have to be through the examination of large-scale patterns in the history of life on Earth.

1.2 The “N=Many” Scenario

Chapter 1 argued that purely statistical approaches to cosmic biology, such as applications of the Copernican principle, are theoretically unmoored, infected with observer selection biases, and too coarse-grained to draw any meaningful conclusions about life on other worlds. Chapters 2 and 3 showed that the nomic structure of biological science does not, on its face, support any specific biological laws of form and function; in addition, the universality of radically contingent dynamics would seem to preclude the possibility of making any specific projections from the shape of life as we know it to life as it might exist on other worlds. Very generic universal predictions are easy to make: life will metabolize, it will reproduce, it will have a digital genetic code, it will form adaptations under the guidance of natural selection, it will exhibit certain

trophic ecosystem structures, and so on. But any more contentful predictions about macroscopic form, in the absence of an extraterrestrial data set, will be on far shakier epistemic ground.

Not everyone agrees with this gloomy characterization. Some theorists reject the seemingly uncontroversial claim that $N=1$. Their assertion is not that we have actually discovered instances of extraterrestrial life from which we can begin to glean the laws of life. Nor do they assert that we have found independent trees of life that arose on Earth. Rather, the “ $N=\text{many}$ ” claim is premised on the idea that the history of life on Earth contains within it countless replays of the tape of life that hint at the existence of evolutionary regularities that, taken together, cast doubt on the RCT. Thus, a distinctively macroevolutionary argument against the RCT is now taking shape.

Evolutionary biologists and philosophers of science have begun to pay increasing attention to the theoretical importance of a phenomenon known as “convergent evolution”—the independent origination of similar biological forms and functions. Convergence has been interpreted by many theorists as tantamount to natural experimental replication in the history of life, and thus as a promising source of evidence for investigating the contingency question. If this interpretation is correct, and our single history of life contains numerous replays, the results of which can be analyzed and generalizations drawn therefrom, then the sample size is actually far greater than 1. Perhaps the contingency dispute is empirically tractable after all.⁹

Unlike controlled evolutionary experiments on prokaryotes in the laboratory or observations of natural selection in the field, studies of convergent evolution can draw upon a voluminous database of natural history to make inferences about the robustness of evolutionary processes operating over vast timescales and across immense phylogenetic gaps. We cannot literally replay the tape of life on Earth from different starting points, but we can infer the existence of natural replays by consulting “phylogenetic reconstructions” that reflect our best current hypotheses about the evolutionary relationships among animal groups. Sophisticated methods of evolutionary tree reconstruction (including parsimony, likelihood, and Bayesian statistical frameworks) are painting an increasingly precise picture of how evolutionary outcomes are distributed in space and time. The question that will preoccupy us in this and the next two chapters is this: Can evolutionary repetitions revealed through phylogenetic analyses be marshaled into an argument against the RCT?

1.3 The Case for Convergence

Several biologists have compiled expansive evidence bases of convergent phenomena with the aim of debunking, or casting doubt on, Gould’s thesis. The seminal treatment of convergence as evidence against the RCT is Simon

Conway Morris's *Life's Solution: Inevitable Humans in a Lonely Universe*.¹⁰ A more recent monograph defending the same theoretical reading of convergence came from George McGhee, whose *Convergent Evolution: Limited Forms Most Beautiful* makes a comprehensive case for the ubiquity of convergent evolution.¹¹ Both of these authors have documented an impressive body of convergence to be mined by future researchers, and their books are brimming with many fascinating and underappreciated examples of convergence. Convergence has been established at all levels of the biological hierarchy, from molecules and morphology to functions and lifeways. McGhee, for instance, reviews convergence on animal swimming, flying, walking, burrowing, and other locomotion-related morphologies, sensory modalities, masticatory apparatuses (e.g., teeth, beaks, and claws), poison-injection systems, digestive capabilities, defensive structures, reproductive strategies (e.g., live birth), and so on. He does the same for plants, where he documents convergence in tree and leaf morphologies, water-transport modes, root systems, seeds, and seed-dispersal mechanisms. How should we interpret this body of convergence?

"All observation must be for or against some view if it is to be of any service," Darwin remarked in an 1861 letter to economist Henry Fawcett. Convergent events are compiled by the above authors with the aim of testing a theory, namely the RCT, which the convergence data is then interpreted as refuting. This "critique from convergence" (CFC), as we shall call it, strikes back at the RCT and the supposed "nomological vacuum" of biology by arguing that patterns of evolutionary repetition demonstrate the modal robustness of highly specific evolutionary outcomes across vast timescales and phylogenetic histories. The signal of convergence is taken to suggest that over the macro-evolutionary long haul, convergence will overcome the constraints of history and the derailing tendencies of stochastic processes to ensure the reliable (re) production of evolutionary outcomes. And *contra* the nomological vacuum characterization, the CFC argues that we can infer from patterns of evolutionary iteration that there are, in fact, specific (nongeneric) biological laws of general, perhaps even universal, projectibility lurking beneath the surface of what would otherwise appear to be a nomically unconstrained domain. Although these specific laws of life have yet to be articulated with any rigor, patterns of convergence intimate that they exist and are waiting to be described.

Some cases of convergence are not only striking, but even "eerie," as Conway Morris describes them. Two naturalistic reasons for this eeriness come to mind. One is that on the face of things, there is nothing in the known laws of biology that predicts the occurrence of such repetitions or explains why they should occur. In this respect, convergence presents as a scientific "anomaly," or an observation that is in tension with our existing body of theory, requiring either the modification of existing theories or the development of new ones.

Selection to a common ecological regime is undoubtedly *part* of the explanation of convergence; but why should this result in *similar functional forms* rather than *similarly functional but morphologically divergent* forms? The principle of natural selection, when framed as a general law, does not enlighten us. There must be other causes and laws operating in the background that account for convergent outcomes. A key question for the next two chapters is what if anything can we say about these other causes and how they bear on the contingency debate. A second reason why some cases of convergence might present as eerie is that evolutionary replications are often close but rarely exact, resulting in an “uncanny valley” experience that we interpret as “creepy.”¹² In the case of eerie convergence, it is the signature of history that is responsible for the partial failure of resemblance, though the outcomes are close enough to fall within the uncanny valley.

The CFC is not merely on a negative mission to defeat Gould’s thesis, however. It is also marshaled in support of a positive theory, namely the claim that patterns of convergent evolution indicate that rerunning the tape of life, even from disparate starting points, would produce a set of macroevolutionary outcomes that is substantially similar to the shape of life as we know it. This, of course, is the “robust replicability thesis” (RRT) discussed in chapter 3. The RRT is most prominently defended by Conway Morris, both in his pioneering work on convergence and in his public debates with Gould.¹³ Similar appeals to patterns of convergence in support of the broad replicability of evolutionary history are made by biologists George McGhee,¹⁴ Geerat Vermeij,¹⁵ and Jonathan Losos,¹⁶ as well as paleontologist Larry Martin¹⁷ and philosopher Daniel Dennett,¹⁸ to name a few.

In his book *The Crucible of Creation*, Conway Morris argues that patterns of convergence show that contingent processes are irrelevant so far as the history of life is concerned. He contends that major evolutionary outcomes will, despite the meanderings of their actual sequence, inevitably manifest in the unfolding of macroevolutionary time. He concludes with a bold cosmic prediction: “Although any history is necessarily unique, the resultant complex end-form is not simply the contingent upshot of local and effectively random processes. On any other suitable planet there will I suggest be animals very much like mammals, and mammals much like apes. Not identical, but surprisingly similar.”¹⁹ Although the phrase “surprisingly similar” is not quantified by Conway Morris, we can take it to mean something like a cosmic uncanny valley. Philosopher Daniel Dennett likewise holds that “convergence … is the fatal weakness in [the] case for contingency.”²⁰ In discussing the Cambrian experiment in animal evolution, Dennett contends that “whichever lineage happens to survive will gravitate toward the Good Moves in Design Space....

Replay the tape a thousand times,” Dennett claims, “and the Good Tricks will be found again and again.”²¹

On these views, successful animal groups are not the fortunate winners of an early extinction lottery, as Gould’s theory would have it. Instead, surviving lineages represent a globally optimal set of solutions among the set of theoretically possible alternatives that were experimented with and discarded by natural selection, particularly and most spectacularly in the early phases of animal evolution when the great branches of animal evolution congealed.

Some evolutionists, like George McGhee, go even further to defend a quasi-essentialist reading of convergence, analogizing between the periodic table of atomic elements and the limited set of organismic forms that can be inferred from patterns of convergent evolution. McGhee suspects that “the modern scientific discipline of evolutionary biology is in a similar position as the scientific discipline of chemistry before the discovery of the periodic table of elements.”²² Given certain physical conditions, we can expect the law-like emergence of particular atomic elements with predictable sets of physical properties. Likewise, given certain ecological conditions, we can expect the emergence of particular biological forms with predictable sets of morpho-functional properties. On this view, historical contingencies recede to the explanatory background and convergence dominates over deep evolutionary timescales.

Darwin for his part believed that high degrees of convergence are so unlikely as to warrant ignoring this possibility for the purposes of taxonomy. But if convergence is as powerful and ubiquitous as the above authors suggest, then it could impede our ability to construct phylogenetic histories, for it would call into question approaches to phylogenetic reconstruction (such as parsimony) that operate on the assumption that the single origin of a complex trait is more probable than multiple origins. Indeed, it could lead one to be suspicious of the cladistics enterprise itself. This may sound like a radical inference to draw from convergence data, but it would explain why in Conway Morris’s leading study of convergence there is not a single cladogram to be found—and why McGhee’s work, though it makes extensive use of cladograms, defends an “atomic elements” analogy that could call into question the motivations for cladism. Nevertheless, the signatures of history that result in the uncanny valley make phylogenetic reconstruction possible, and this in turn permits reliable inferences of iterated origins.

Even theorists who are largely sympathetic to Gould’s view of life and to the role of narrative explanation in the sciences more broadly, such as John Beatty,²³ interpret convergent evolution as undercutting the RCT. Cosmologists, too, have jumped on the convergence bandwagon, which they view as lending distinctively biological support to the justification of SETI-like

programs.²⁴ In short, the CFC argues that, given enough time and the presence of certain environmental conditions, similar biological forms will emerge over and over again. If so, then perhaps in a meaningful sense Lyell was right: extinction is not forever.

1.4 Convergence as Evidence

If destiny and predictability are balms to human psychology, then contingency chaffs at the soul. Psychological palatability is not, however, a virtue of theories that aim to describe the causal structure of the world. Scientific theories stand or fall on their empirical adequacy. Although much research has been devoted to documenting the phenomenon of convergence, the logic of convergence as evidence remains critically underexplored.

On its face, the evidential relation between convergence and the RCT/RRT debate seems straightforward and compelling: convergent evolution is tantamount to natural experimental replication in the history of life. And to the extent that macroevolutionary replication is ubiquitous, this would seem to cast doubt on the RCT and corroborate the RRT. Even if our explanations of convergence in general are not fully fleshed out, and even if the adaptive motivations for particular cases of convergence are unclear, patterns of convergence can nonetheless support the evolutionary robustness of certain outcomes, which is ultimately what the RCT/RRT debate is all about.

For instance, the fact that the “saber-toothed lion” ecomorph evolved at least four times in mammals, three times within the placentals, and once between placentals and marsupials, gives us *prima facie* reason to think that this complex suite of cranial modifications is adaptive and evolutionarily replicable, even if we are not entirely certain about what its function was (e.g., predation, sexual selection, etc.). The “sabertooth syndrome” includes a generally catlike appearance with the elongation and lateral compression of the upper canines (which are bladelike in contrast to the conical canines of modern cats), robust forelimbs for grasping prey, and dozens of iterated cranial features (such as a massively reduced coronoid process of the mandible) that allow for increased gape and bite force.²⁵ The balance of evidence suggests that the sabertooth morphology is a highly specialized feeding adaptation. The point, however, is that we can be confident in an inference of *replicability* without being confident in any particular adaptive hypothesis.

Indeed, there are a host of challenges that confront specific functional attributions, even for cases in which we are confident that a trait is an adaptation. These challenges arise from the fact that adaptationist claims are claims about selection histories, and selection histories can be difficult to piece together due to our limited epistemic access to the past. As Richard Lewontin notes, we

may never know whether Stegosaur plates *originally* evolved to deflect the teeth of their theropod predators, to regulate heat, or to signal to mates and other conspecifics, because the information necessary for making such inferences may be irretrievably lost to the crumbling geological record.²⁶ We should not underestimate the diverse epistemic toolkit that paleobiologists have at their disposal to test and adjudicate such theories,²⁷ but the point is we can be confident that complex structures like stegosaur plates are adaptations while being uncertain as to their specific function.

Nevertheless, convergent evolution is generally thought to offer some of the strongest evidence we have for adaptation, and indeed for specific functional attributions. The fact that ichthyosaurs, dolphins, plesiosaurs, pinnipeds, sea turtles, and sea snakes all evolved flippers or paddles in an aquatic environment overwhelmingly suggests that these features were shaped by selection to meet a similar functional demand: locomotion of a macrobe in an aqueous medium. A more detailed swimming convergence is the iterated evolution of the high-powered “thunniform” swimming style in four distant groups of vertebrates, including (in order of evolutionary appearance): ichthyosaurs (~250 mya), tuna (~55 mya), lamnid sharks (~50 mya), and dolphins (~45 mya) (see figure 4.1).²⁸ The same goes for other strongly functionally constrained structures, such as wings and eyes, which like paddles are unambiguous cases of adaptive convergence.

How reliable the inference from convergence to adaptation is will depend on the complexity of the underlying trait and how clearly the trait is matched to a common ecological regime.²⁹ With respect to simple (low-dimensional) traits, some degree of convergence can be expected *as a simple matter of chance*—that is, under the influence of stochastic processes alone.³⁰ The more structurally complex a trait, however, the less likely it is to arise *repeatedly* due to chance, particularly if it solves an ecological design problem. Adaptation is thus implicated in cases of complex functional match that have been arrived at independently, and many cases of convergence documented in the literature fit this bill.

Recall, however, that adaptationism alone does not get us all the way to the RRT. Selection could be a dominant force in evolution and yet the multiple realizability of fitness and function could undermine evolutionarily replicability. Thus, it is critical that convergence support three additional, more philosophically onerous assertions that underpin the RRT. First, convergence must indicate that certain design problems are pervasive in any history of life. If the conditions that precipitate convergent episodes are restricted to extremely rare circumstances, they will have very low replicability across life worlds (more on this in chapter 6). Second, convergence must indicate that the set of

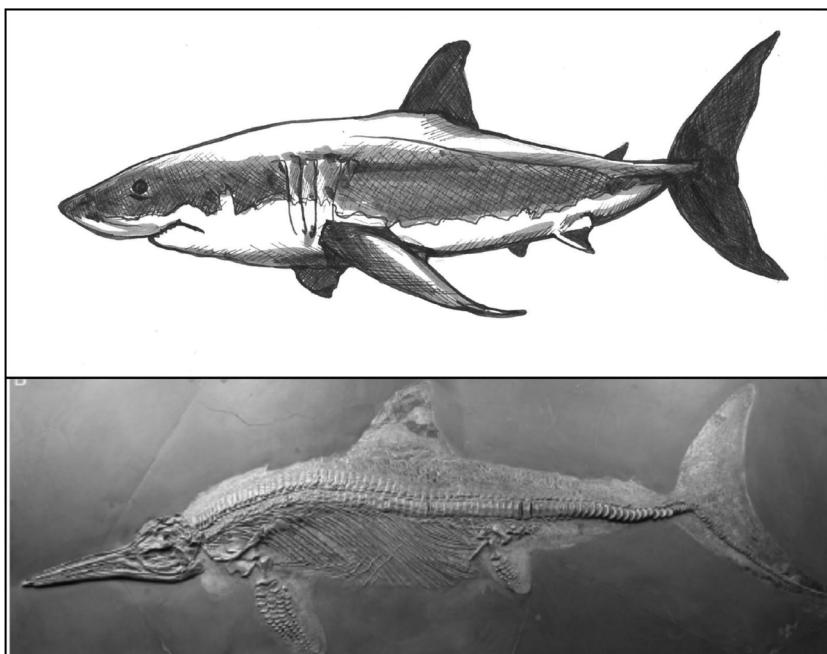


Figure 4.1

The great white shark (*Carcharodon carcharias*, top sketch, a fish) and the ichthyosaur (*Stenopterygius quadriscissus*, bottom photo, a Mesozoic marine reptile) have converged on numerous features of the body plan, including a teardrop shape, a heavy dorsal fin and high-aspect-ratio caudal fin for swimming at speed, and a crossed-fibered architecture of the skin composed of the same chemical fibers, as well as a specialized caudal peduncle and ligament force-transmission system. Redrawn from T. Lingham-Soliar, “Convergence in Thunniform Anatomy in Lamnid Sharks and Jurassic Ichthyosaurs,” *Integrative and Comparative Biology* 56, no. 6 (2016): 1323–1336. Photo of specimen in Senckenberg Museum, Germany. Courtesy of Wikimedia Commons.

adaptive solutions to these pervasive ecological design problems is highly circumscribed. If there is an unmanageably large number of equally good solutions to pervasive ecological problems, then there is no reason to think that any particular outcomes will (re)occur at predictable frequencies. Third, and most crucially, convergence must indicate that these few optimal solutions to pervasive design problems are accessible to selection notwithstanding, and irrespective of, the internal constraints of phylogeny.

In other words, convergence must not only show that lineages can navigate to these solutions from very distant developmental starting points, but also that the solutions themselves are not contingent on body plan parameters that could easily have been otherwise. If Good Tricks (in Dennett’s terminology) are not accessible from distant evolutionary trajectories, or if they are only

“Good” in the context of accidental developmental parameters, then there is no reason to think that they would be subject to repetition across deep replays of the tape of life on Earth or independent replays of the tape on other worlds. As we will see in the next two chapters, drawing each of these inferences from existing data on convergent evolution can be highly problematic.

2. Matters of (Mis)interpretation

Before delving into these evidential matters further, however, let us foreground several interpretive confusions that have prevented the CFC from making contact with key claims of the RCT. Some of these exegetical misreadings of Gould are understandable, given the lack of detail and rhetorical variability in Gould’s expressions of the thesis (see chapter 3). Still, it is a useful exercise to consider what claims the RCT might be making and determine which of these claims is subject to refutation by convergence data. At the end of the day, however, the problems we are wrestling with are not exegetical but epistemic and ontological: they concern our best understanding of the nomological structure of the biological world regardless of what Gould or anybody else thought on the matter.

2.1 Misconception 1: Contingency ⇒ Nonrepetition

A general problem with the CFC is that it has often mischaracterized the RCT, dismantling “straw man” versions of Gould’s thesis. By engaging with easy-to-refute characterizations, proponents of the CFC have tended to gloss over important nuances of Gould’s view of life and how it might accommodate convergent phenomena. For example, McGhee in his leading review of convergent evolution aims to refute several claims that he attributes to Gould, but which Gould almost certainly did not hold.³¹ The first is “the view that the evolutionary process is nonrepeating.”³² This misinterpretation of the RCT, which we shall refer to as “M1,” is by no means unique to McGhee. We can infer that other convergence proponents, such as Conway Morris and Dennett, also endorse M1 because they take the entire unqualified body of convergence data, including any and all evolutionary repetitions, to militate against the Gouldian view of life. Biologist Zachary Blount, a researcher on the LTEE studies (see section 1.1 in this chapter), likewise holds that contingency should preclude evolutionary repeatability, citing Gould’s *Wonderful Life* and *The Structure of Evolutionary Theory*.³³ This (mis)reading might explain why the LTEE studies, which are designed to test the RCT, are structured in the way that they are (see section 1.1). Much of the philosophical attention to

Gould's thesis has likewise focused on its implications for the nonrepeatability—and, as we shall see, unpredictability—of evolutionary outcomes.

The first thing to say about M1 is that it is demonstrably false. If the RCT did entail M1, then, as McGhee argues, it too would be demonstrably false. Yet numerous impressive examples of convergence have long been documented. If M1 accurately described Gould's thesis, then McGhee's systematic review of convergent phenomenon would not be needed to refute it. Rather, a single or a few well-documented cases of convergence would suffice. There is simply no way that Gould, well aware of the phenomenon of convergence, would embrace such an obviously falsified thesis. We can make M1 more plausible by rephrasing it to express a *relative frequency* claim rather than a *categorical denial* regarding evolutionary repetition. This revised (mis)interpretation, which we can refer to as "M1.1," might hold that "the evolutionary process is *rarely* repeating." Refuting this claim is no longer a trivial exercise and justifies the systematic review that Conway Morris, McGhee, and others have diligently carried out. However, M1.1 still misses the mark because at bottom the contingency debate is not a relative frequency dispute about *evolutionary repetition per se*—rather, it is a dispute over the *nature and causes of those repetitions*. Or so I will argue over this and the next two chapters.

There is in fact ample room within the Gouldian view of life for a great deal of evolutionary iteration and predictability. What is glossed over by M1 and M1.1 is the role of internal developmental constraints in the RCT and how they figure in the possibility space of life as we know it. By giving theoretical primacy to developmental constraints, the RCT in fact predicts certain kinds of repetition, namely repetitions that result from entrenched developmental systems that make certain adaptive outcomes more likely due to their accessibility to selection.

One might reply that I am drawing entailments of Gould's theory that he personally did not entertain, even if these entailments are theoretically justified. This is not so. In *The Structure of Evolutionary Theory*, Gould's last and most comprehensive monograph, Gould maintains that "Homologous developmental pathways can also be employed ... as active facilitators of homoplastic adaptations that might otherwise be very difficult, if not impossible, to construct in such strikingly similar form from such different starting points across such immense phyletic gaps."³⁴ Thus, although many authors cite *Structure* for the claim that Gouldian contingency is inconsistent with evolutionary repeatability, this is an erroneous reading of that text and of Gould's overarching view of macroevolution. It is through the causal explanatory role of developmental constraints that Gould's view of life can accommodate certain kinds of evolutionary repetition. In the rest of this book, we will explore just how

far this accommodation can go before the weight of convergence data bends Gould's theory to the breaking point.

2.2 Two Readings of Developmental Constraint

To understand how the RCT might accommodate evolutionary repetition, it is important to distinguish between negative and positive readings of developmental constraint. As we saw in chapter 2, the RCT maintains that once animal body plans congealed in the early stages of animal evolution, the causal topography of development restricted the subsequent exploration of morphospace, leaving ever larger and unbridgeable gaps between body plans as some were culled in stochastic (or pseudo-stochastic) extinction events. In this account, developmental constraint is read in the "negative" sense as confining or restricting the adaptive search of morphospace, preventing selection from journeying beyond the confines of the body plan. This negative framing is consistent with the canonical definition, which holds that "developmental constraint" refers to "biases on the production of variant phenotypes, or limitations on phenotypic variability, caused by the structure, character, composition or dynamics of the developmental system."³⁵

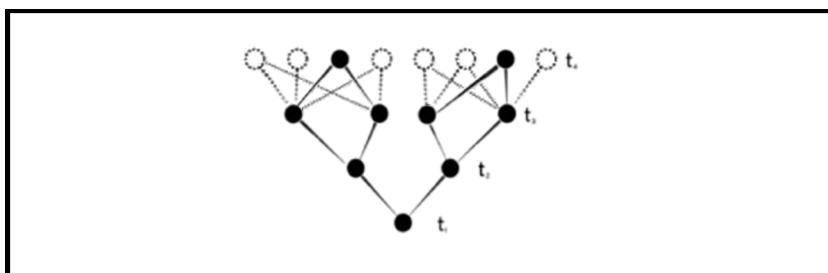
We can distinguish these "internal" developmental constraints on form from the "external" constraints imposed by the optimizing agency of natural selection working to solve ecological design problems within the confines of physical and chemical laws.³⁶ The basic Gouldian idea is that internal developmental constraint, not the external optimizing force of natural selection, is the fundamental cause of "clumpy" morphospace occupation. *Within* these clumps (or islands) of form, natural selection can be a difference-making cause of evolutionary change; yet the ultimate bounds of that restricted space are determined not by selection but by the frozen accidents of developmental parameters. On this picture, developmental constraints are more causally important than selection in determining morphospace occupation, because they are a greater determinant of where in a vast morphospace a particular lineage lies. Whereas selection explains, for example, why a lineage occupies one of two close regions of morphospace within a body plan, developmental constraints explain why selection is confined to discriminating between those close regions out of the vast theoretical space of possible forms. This appears to be the logic behind Gould and Lewontin's conjecture that "developmental constraints ... may hold the most powerful rein of all over possible evolutionary pathways."³⁷

So conceived, the role of developmental constraints is glossed entirely in the negative—it is intended to explain where selection cannot go, and why. Yet as Gould's remarks in *Structure* suggest, not all biases of development

should be thought of in terms of hindering selectively superior outcomes or rendering them off-limits. As developmental evolutionary biologist Günter Wagner has shown, by restricting the space of possibility to a handful of locally optimal solutions, internal constraints make certain solutions more accessible to selection, allowing them to be arrived at over and over again whenever suitable environments arise.³⁸ Although it is true that selection is partly causally responsible for these iterations, the reason why these particular solutions are locally optimal and thus repeatedly accessible to selection is due to the internal biases of developmental systems. Indeed, given that genetic search space is hyper-astronomical,³⁹ with more gene combinations than subatomic particles in the visible universe, how is it that any adaptive variation is ever present for selection? Developmental biases must be an integral part of this constructive story.⁴⁰

This “positive” reading of internal constraint as channels facilitating adaptive change can be found in Gould’s work on snails in the late 1980s, where he defines constraint as the “channeling [of] phenotypic change in a direction set by past history or formal structure rather than by current adaptation.”⁴¹ The idea is that internal parameters of development impose strong biases on the probabilities of different evolutionary outcomes, making some propitious outcomes highly likely (the positive reading) and others unlikely or even astronomically improbable (the negative reading). Later, in *Structure*,⁴² Gould illustrates the positive reading of constraint-as-internal-facilitation with the repeated evolution of maxillipeds in crustacean arthropods. Maxillipeds are feeding appendages that evolved multiple times from anterior walking legs via the repeated selective deployment of homologous developmental pathways (in particular, *Hox* genes). Developmental constraints make evolutionary iterations such as these possible, even if the crustacean body plan parameters that set local optimality are themselves radically contingent.

In his discussion of path dependency in evolution, Eric Desjardins (see chapter 3) considers the example of stick insects (phasmids), which evolved from a flying ancestor, subsequently lost their wings, and in a few cases regained them.⁴³ It may only take a single mutation in a complex gene network to render these insects wingless, whereas producing flight from scratch is likely to require numerous coordinated mutations affecting major limb structures as well as nervous and muscular functionalities. If a large proportion of the necessary genetic-developmental machinery for wings is conserved in wingless stick insects, then there is a reasonable likelihood that wings—and even a particular type of wing—could repeat in this clade. Given certain conserved developmental parameters in phasmids that shape the probability distribution of evolutionary outcomes, wing iteration may be highly accessible

**Figure 4.2**

A mixed contingent-convergent system that exhibits path independence and predictability at finer grains of taxonomic resolution, but path dependence and unpredictability at coarser grains. For comparison and discussion, see figure 3.1. 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.

to selection and thus more likely to occur, and to occur in particular ways, than functional alternatives.

The stick insect example hints at what it would mean for certain phenotypic potentials to be genetically conserved in a clade, an important aspect of iteration that we will return to in the next chapter. The key point here is that radically contingent developmental parameters can set the channels for evolutionary iteration. Such a mixed contingent-convergent scenario, inspired by a positive reading of developmental constraint, can be illustrated in schematic form by a system that exhibits convergence at finer grains of phylogenetic resolution but path dependence at coarser grains (see figure 4.2).⁴⁴

We can now distill the crux of the first misconception. The contingency dispute turns not on the existence of evolutionary repetitions per se, but on the *causes* of evolutionary repetition and whether they support the deep evolutionary robustness of the outcomes observed. What contingency theorists like Gould reject is the proposition that the driving forces behind convergence transcend the contingently entrenched developmental plans of particular lineages. The main question, therefore, is whether instances of evolutionary iteration reflect this transcendence—and the problem is that whether they do, as we shall see in chapter 5, is underdetermined by convergence data as it has thus far been collected and analyzed. A more general problem is that it is not entirely clear what such “transcendence” would look like. The very notion of external constraints on form may be incoherent unless it is indexed to the particular developmental systems of evolving lineages. We will return to these matters shortly. For the moment, let us press on to the second misconception that has prevented the CFC from properly engaging with the RCT.

2.3 Misconception 2: Contingency ⇒ Unpredictability

A second common mischaracterization of Gould's thesis, which is related to but distinct from the first, is the notion that the RCT entails unpredictability. McGhee, for instance, attributes to Gould the proposition that "evolution is entirely historically contingent and thus unpredictable."⁴⁵ We saw in chapter 3 that it is a mistake to equate the metaphysics of contingency with epistemic facts about predictability, even if Gould was occasionally guilty of doing so. However, we might charitably interpret McGhee not as conflating contingency with unpredictability or attributing this conflation to Gould, but instead as purporting to test an apparent entailment of Gould's theory: if macroevolution is indeed sensitively dependent on small changes in initial conditions, then evolution should proceed in an unpredictable manner.

Yet studies of convergence clearly show that selection does often drive lineages to similar evolutionary outcomes in ways that plausibly admit of prediction. For instance, tetrapods making the "fin-to-limb-to-fin" transition, such as ichthyosaurs and whales, evolve in predictable ways. Precisely why it is that some lineages end up making this transition but others do not, and why some (such as ichthyosaurs and whales) make the full transition but others (such as plesiosaurs and pinnipeds) make only partial transitions, may be harder to predict and may hinge on the contingent quirks of their respective histories. But *when* these full and partial transitions are made, the CFC argues, they will tend to come with a predictable suite of features. Thus, an entailment of the RCT—that evolutionary trajectories will not admit of prediction—is demonstrably false, and hence the RCT is refuted.

This characterization of the RCT, call it "M2," also misses the mark. Like M1, M2 is framed in implausible categorical terms that make it vulnerable to refutation by a single counterexample. This problem can be cured, as with M1, by modifying it to address a relative significance claim. But this more plausible reading, call it "M2.1," falters as well for a simple reason: the lack of predictability is not an entailment of the RCT. As we have seen, there is plenty of room in the Gouldian picture for certain kinds of repeatability. Indeed, the RCT is consistent with, and arguably confirmed by, what we might call "bounded repeatability"—or *repetitions within the bounds of, and caused by, internal developmental constraints*. Simply put, the RCT does not imply chaos and unpredictability at all phylogenetic and temporal scales in macroevolution, as M2 and M2.1 would suggest.

Nor does Gould intend that his contingency claims apply to all levels of trait description. In a passage from *Wonderful Life* worth quoting at length, Gould states in no uncertain terms that he is not arguing that all of evolution is historically contingent and unpredictable:

Am I really arguing that nothing about life's history could be predicted, or might follow directly from general laws of nature? Of course not; the question that we face is one of scale, or level of focus. Life exhibits a structure obedient to physical principles. We do not live amidst a chaos of historical circumstance.... Much about the basic form of multicellular organisms must be constrained by rules of construction and good design.... Invariant laws of nature impact the general forms and functions of organisms; they set the channels in which organic design must evolve. But the channels are so broad relative to the details that fascinate us! ... When we set our focus upon the level of detail that regulates most common questions about the history of life, contingency dominates and the predictability of general form recedes to an irrelevant background ... almost every interesting event of life's history falls into the realm of contingency.⁴⁶

It seems that Gould would be happy to grant that, for example, the fusiform (tapered) body shape is an evolutionarily robust feature of fast-moving, large-bodied aquatic life wherever it evolves. What he would deny is that the specific parameters of body plans and the locally optimal iterations that hinge on them are robust features of complex multicellular evolution. Convergence on fusiform morphology does little to detract from this conclusion.

There is a weak point in the above excerpt that is worth drawing attention to, however, and that is Gould's relative interest claim. Why should universal biomechanical constraints on the evolution of form not be as interesting to biologists as the quirky, more detailed outcomes of evolution? Gould offers no argument to support this assertion. Indeed, Gould's push for an autonomous, law-like paleontology shows that he was committed to the idea that a central goal of science, and indeed, of paleobiology, is to uncover spatiotemporally invariant laws.⁴⁷ Whatever one makes of Gould's advocacy of narrativistic explanation, it is hard to defend the claim that universal constraints on the evolution of form are objectively uninteresting, even if they are not among the details that some find most fascinating.

In effect, Gould is making a rhetorical move here similar to one that he (writing with Richard Lewontin) famously excoriated in connection with adaptationist explanations:

In natural history, all possible things happen sometimes; you generally do not support your favoured phenomenon by declaring rivals impossible in theory. Rather, you acknowledge the rival, but circumscribe its domain of action so narrowly that it cannot have any importance in the affairs of nature. Then, you often congratulate yourself for being such an undogmatic and ecumenical chap.⁴⁸

Gould seems to be engaging in the very mode of argument for which he chastises adaptationists. He acknowledges there are some robustly replicable outcomes in evolution, but he relegates these to theoretically uninteresting

phenomena in the history of life. It is best to avoid quibbling over which biological phenomena are the most “interesting,” and instead pose the question this way: Given our current understanding of convergence, which features of the shape of life are likely to be radically contingent, and which features are likely to be robustly replicable?

3. Macroevolutionary Overdetermination

How might proponents of the RRT make sense of the ostensibly contingent patterns of extinction and faunal turnover on which much of the Gouldian view rests? One way they might attempt to do so is by arguing for the “overdetermination” of major evolutionary outcomes. For example, Dennett claims that even if *Pikaia* and its proto-chordate ilk had been felled with other *Problematica* in the Cambrian, some other lineage in the future history of life would have hit upon the good “vertebrate” trick and thereby refilled the “vertebrate” attractor in morphospace. With vertebrates surviving and thriving throughout the Phanerozoic Eon, however, the vertebrate niche has remained packed and thus unrefillable, in accordance with incumbent advantage and ecological exclusion theory. Were the vertebrate niche to empty due to some unprecedented biotic crisis, then it would, over the long haul, be refilled by something close enough to warrant the “vertebrate-like” label.

The macroevolutionary overdetermination thesis is not incoherent, but it is underevidenced. There are simply no indications of convergence on the bundle of traits that comprise phyla or subphyla such as “vertebrates.” And relying on an incumbent advantage theory (discussed in chapters 1 and 2) to explain this lack of repetition is also problematic. If incumbent advantage did not prevent the staggering multitude of convergences documented by the CRC, why then would it preclude iterations of major body plans? The RRT has no obvious rejoinder to this query. In contrast, the developmental pillar of the RCT (see chapter 2) offers a non-ad hoc explanation of this asymmetry in iteration: the causal topography of development precludes certain iterations but permits (and even facilitates) others.

It is now time to tie the threads of the argument together. Certain exegetical problems have prevented the CFC from making contact with the key theoretical framing assumptions that underpin Gould’s thesis. As we have seen, the RCT is more capable of handling repetition and predictability than its detractors (and even its sympathizers) have acknowledged. First, critics have failed to recognize that the crux of the contingency dispute turns not on repeatability or predictability per se in evolution, but on the *causes* of observed iterations and whether

they indicate the evolutionary robustness of the regularities observed. Second, the RCT is aimed at specific levels of morphological description, and thus pointing to convergence on more generic evolutionary phenomena does not cut to the heart of Gould's argument. Finally, RRT proponents have failed to provide an adequate explanation of the lack of repetition at the level of animal body plans. The next two chapters will elaborate on each of these points by taking a closer look at the evidentiary significance of convergence.

Contingency and Convergence

Toward a Cosmic Biology of Body and Mind

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