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Introduction: The Big Picture

> The nature of life on earth and the quest for life elsewhere are two sides of the same question: the search for who we are.
> —Carl Sagan

In his book *Wonderful Life: The Burgess Shale and the Nature of History*, the paleontologist Stephen Jay Gould poses the following evolutionary thought experiment: Imagine replaying the "tape of life" from an early period in the history of animal evolution, and consider how its story would again unfurl. Would the replay result in a quintessentially alien biological world—a parade of forms that bear little resemblance to life as we know it? Or would a strikingly familiar set of anatomical designs, functional properties, and organizational patterns reemerge? The answer to this question has profound implications not only for the prospect and nature of complex life on other worlds, but also for the epistemic status of biological science itself and its potential to uncover universal laws of life.

Gould argued in *Wonderful Life*, and throughout his remaining career, that replaying the tape of life would result in radically different evolutionary outcomes. Play the tape again, and not only would no primates, mammals, and tetrapods evolve, but vertebrates and other major animal groups like mollusks, arthropods, echinoderms, annelids, and brachiopods would be relegated to the evolutionary dust heap of morphological *possibilia*, replaced by some other fortuitous set of equally workable animal designs. On this view, the familiar spate of animal body plans arose, along with many fantastical forms, in the initial explosive phases of animal evolution when developmental parameters were still largely unconstrained. These familiar forms survived the early major extinctions of animals, whereas other forms perished, for reasons unrelated to their relative functional merit. The body plans of these fortuitous survivors then solidified for the remainder of life's history due to a causal structure of embryonic development that came into effect once a certain degree of

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morphological complexity had been laid down. Existing animals thus represent but a small fraction of the set of functionally equivalent forms that either went extinct or never arose due to an unrepeatable sequence of events. If Gould is right, then history reigns supreme in macroevolution, and there is no law-like necessity to the overarching shape of animal life on Earth.

Gould's "radical contingency thesis" (RCT) and the critical attention it has received have generally focused on the replicability of complex morphology. However, the RCT is particularly provocative for the implications that it might have for the emergence of complex *cognitive* properties. Astrophysicists, especially those who have advocated the search for extraterrestrial intelligence, have long been optimistic about the frequency of intelligent life forms in the universe. Thus far, however, the cosmologist's optimism has relied mainly on general statistical principles, the ubiquity of geochemical conditions that are amenable to life, and certain (often implicit) progressivist assumptions about macroevolution, rather than from any specifically biological considerations. Gould's arguments for the primacy of contingency in macroevolution pose a formidable challenge to the view that galaxies are teaming with intelligent life, though the nature and force of this challenge has yet to be analyzed in any depth.

Is the evolution of the mind a historical accident, unlikely to be repeated in hypothetical replays of the tape of life on Earth and actual replays on Earth-like planets elsewhere? Or is mind, in any or all of its variegated forms, likely to be an evolutionarily important feature of any living world? How is the evolution of complex minds related to the evolution of complex bodies? And what does all this say about the nature of our own existence and humanity's place in the cosmos? These are big questions with correspondingly big methodological problems. Most glaring among these is the so-called $N=1$ problem: given that we are privy to but a single history of life, how can we even begin to approach let alone adjudicate questions about the contingency of bodies and minds?

Despite the seemingly intractable nature of the problem, and notwithstanding the lack of an extraterrestrial data set, biotheoretic support for the cosmologist's optimism has started to mount, and the pendulum has begun to swing away from contingency. This is due in large part to studies of "convergent evolution"—the repeated origination of similar biological forms and functions—which offers a promising avenue for empirically adjudicating the contingency question. Countless cases of sometimes striking convergence have been documented at all hierarchical levels of the biological world, from molecules and morphology to mechanisms of mind. Textbook examples of convergence include the evolution of camera-type eyes in fish (vertebrates), cephalopods (mollusks), jumping spiders (arthropods), and cubozoan jellyfish (cnidarians), lineages that diverged from a common ancestor close to 1 billion years ago in the Precambrian;

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the evolution of dolphinoid forms in porpoises (mammals) and ichthyosaurs (Mesozoic marine reptiles), whose last common ancestor was a terrestrial tetrapod that lived around 300 million years ago in the Carboniferous; and the suite of saber-toothed lion morphology that evolved separately in placental and marsupial mammals, lineages that split in the mid-Jurassic. We will encounter many such instances of evolutionary iteration over the course of this book, some of which will be analyzed in depth either to illustrate a general point or because they serve as a crucial premise in the arguments being considered.

On its face, the logic of the evidence is straightforward and compelling: convergent evolution is tantamount to natural experimental replication in the history of life; and to the extent that evolutionary replication is ubiquitous, this would seem to cast doubt on the RCT. Indeed, this is precisely how patterns of convergent evolution have been interpreted by some biologists, philosophers of science, and cosmologists. But is this reading of convergent evolution correct? Do episodes of convergence provide evidence against the RCT, and if so, under what conditions might they do so? Are certain cases of convergence more theoretically significant than others, and how might such cases be delineated in concept and identified in practice? More broadly, what mechanisms could explain these convergent regularities on Earth, and what might these patterns and mechanisms tell us about the prospect of complex bodies and minds on other worlds? This book will sharpen some critical points of the "critique from convergence" while blunting others, with the aim of developing a clearer picture of the interplay between contingency and convergence in the great dialectic of macroevolution.

To begin to work out answers to these questions, we must first have a clearly articulated account of evolutionary contingency in hand. Roughly speaking, evolutionary outcomes are radically contingent if they are historical accidents that are unlikely to be repeated across replays of the tape of life. Although the RCT has received much attention from biologists and (to a lesser extent) from philosophers of science, it remains decidedly underspecified, liable to misinterpretation, and riddled with conceptual and methodological difficulties that have only barely been explored. Furthermore, while convergent evolution constitutes a potentially fruitful source of evidence against the RCT, the logic of this evidential relationship has been underexamined. The lack of an extended analytical treatment of the theoretical relationship between contingency and convergence has hampered the design and interpretation of evolutionary research, resulting in critiques of the RCT that are less effective than they could have been. Challenges to Gould's thesis that appeal to the general frequency of convergent evolution or to specific compelling episodes of convergence have generally failed to engage with the core claims and theoretical commitments that underpin

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the RCT. By the same token, contingency theorists have yet to situate the phenomenon of convergent evolution within a broader, historically contingent view of life.

This book represents the first attempt to weave these disparate philosophical and empirical threads together into a critical discussion of the interaction between contingency and convergence in macroevolution, as it relates to both complex life in general and cognitively complex life in particular. It would clearly be impossible for a single book to treat these matters in any depth without an appropriate focus to rein it in. The present analysis is accordingly narrow but at the same time ambitious: its goal is to shed light on what the phenomenon of convergent evolution tells us about constraints on the history of life as it has unfolded on Earth, and how it might do in other nooks and crannies of the habitable universe.

This, in turn, requires that we engage with philosophical discussions not only of the central organizing concepts of contingency and convergence, but also of laws, chance, causation, constraint, explanation, evidence, and experiment as these concepts relate to the evolutionary process. As applied to mind, the contingency question compels us to wrestle with problems surrounding the nature of cognition, its phylogenetic distribution, and the circumstances and consequences of its evolution. The overarching aim of this analysis is to foreground the conceptual, methodological, and empirical problems that must be resolved if we are to assess the significance of contingency and convergence in this, or any, history of life.

Part I, "Convergent Bodies," considers what we can infer about the shape of life as we do not know it by studying patterns of convergent evolution in the history of life on Earth—and in particular, and by examining the causes that underlie these patterns. The evolutionary replicability of complex morphological outcomes hinges, of course, on the replicability of organizational stepping stones along the way, including first and foremost the evolution of life itself. We thus begin in chapter 1, "Visions of the Living Cosmos," by contrasting the emerging consensus on the cosmic replicability of basic microbial life from the greater controversy that surrounds the evolution of more complex organisms. An apparent theoretical tension between the rapid timing and singular nature of life's origin is highlighted and resolved, and the limits of coarse-grained statistical approaches to contingency questions are made clear. In particular, observer selection biases prevent us from projecting aspects of our own history of life onto other life-amenable worlds, underscoring the crucial need for biotheoretical input.

From this launching point, we go on to reconstruct the conceptual and empirical foundations of the RCT, consider several alternative ways of understanding

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contingency in macroevolution, and examine the use of convergence as evidence against the most plausible interpretation of Gould's thesis. Chapter 2, "The Radical Contingency Thesis," discusses the epistemic role of counterfactual thinking in the historical sciences writ large before turning to Gould's "rewinding the tape" thought experiments and distilling the theoretical pillars that undergird his thesis. These premises include particular taxonomic and paleoecological interpretations of the earliest animal fauna, the role of early stochastic extinctions in the culling of higher taxa, and the developmental canalization of fortuitous surviving lineages resulting in the deep conservation of body plans at high and moderate taxonomic levels. Critiques of Gould's taxonomic and paleoecological presuppositions are considered, but deemed nonfatal and to some extent orthogonal to the core contentions of the RCT.

Chapter 3, "A Philosophical Theory of Evolutionary Contingency," offers a more sustained analysis of the concept of contingency in macroevolution. It argues that the RCT is best understood not as a series of assertions about unpredictability, chance, stochasticity, path-dependency, or repeatability per se in macroevolution, but rather as a "modal" thesis about the stability of evolutionary outcomes across possible evolutionary worlds. Contingency, it is shown, is distinct not only from the metaphysics of chance and epistemic issues of predictability, but also from questions about the existence or absence of laws in biology. Although each of these matters are related in various ways to contingency, conflating them with contingent dynamics is liable to confuse more than to illuminate. This enables us to more clearly frame the antithesis—the "robust replicability" view—whose theoretical commitments are then laid bare and distinguished from other related but distinct theses such as adaptationism.

With this account of contingency and its antithesis in hand, chapter 4, "The Critique from Convergent Evolution," canvasses a challenge to the RCT that appeals to the ubiquity of convergent evolution. It identifies several misconceptions that have prevented this critique from making contact with Gould's thesis. For instance, contingency is frequently but incorrectly equated with unpredictability or nonrepeatability, due in part to Gould's own inconsistent writings on the topic. This chapter shows that such readings do not go to heart of the RCT and have resulted in much talking at cross-purposes. Once these exegetical shortcomings are recognized, a more effective case against macroevolutionary contingency can be made.

Chapter 5, "Convergent Evolution as Natural Experiment," shows that convergence can, under certain conditions, constitute natural experimental replications that undercut the RCT. Yet not only do many cases of convergence fail to meet these experimental validity conditions, but some evolutionary iterations actually *bolster* the RCT insofar as they are caused by shared developmental

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constraints that make certain adaptive innovations more accessible to selection. Shared internal constraints undermine the independence of natural experimental replications by constricting the space of evolutionary possibility for converging lineages, which in turn limits the evolutionary robustness of the iterations observed. Such internally constrained iterations are referred to as "Gouldian repetitions," and they are distinguished from related phenomena such as "parallelisms." The key contrast, however, is between Gouldian repetitions and "true convergence"—or iteration that transcends the developmental history of the lineages involved. This chapter shows that there are significant challenges to both conceptualizing Gouldian repetitions and detecting them in practice, but that meeting these challenges is necessary if we are to establish the evidentiary relevance of convergence to the contingency debate. Because the existing body of convergence data does not discriminate between these different types of convergence, the case against the RCT remains inconclusive.

Chapter 6, "The Entanglement Problem," shows that the problem of evidential underdetermination that beleaguers the critique from convergence is simply one aspect of the broader challenge of disentangling radically contingent features of the living world from the robustly replicable features with which they are intertwined. The entanglement problem is exacerbated by the human cognitive penchant to treat familiar trait bundles as law-like clusters that can be projected outward into the cosmos. The bundling bias is counteracted, and the underdetermination problem remedied, by proposing criteria for differentiating convergent regularities based on the modal robustness of the generalizations they support. These criteria are then applied to a smattering of better and lesser-known cases of convergence, including some that prove to be particularly important for the remainder of the book. In the coda to part I, "Convergence at the Grandest Scales," special attention is given to the so-called major transitions in evolution, or key organizational shifts in the history of life that have served as structural, informational, and energetic scaffolding for the subsequent step-ups in hierarchical complexity that would ultimately lead to animal bodies and brains.

The upshot of part I is that convergent regularities vary in the temporal and phylogenetic depth of the evolutionary "rewinds" across which they remain modally stable. For instance, some iterations only hold up across the evolution of mammals, tetrapods, or vertebrates, while others appear to be stable across "deeper" rewinds such as the evolution of animals, eukaryotes, and perhaps even life itself (with caveats for some known unknowns). The origins of eukaryote-grade life (complex cells) as well as animals with guts and neurons remain two nagging pressure points in the case for contingency with respect to which the convergence data are presently inconclusive.

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Does this analysis ultimately vindicate or rebuff Gould's thesis? The short answer is that it does both. Important elements of the RCT survive, including its claims about the radical contingency of animal body plans and the evolutionary iterations that causally hinge on them. However, other evolutionary outcomes look to be robustly replicable, and perhaps even law-like, at a level of detail that begins to put significant pressure on the RCT. This is true for some of the increases in hierarchical complexity upon which sophisticated sensory, neural, cognitive, behavioral, and social systems have been built, as well as for some of these systems themselves.

This partial defense of the RCT in part I paves the way for a substantive critique to follow in part II, "Convergent Minds," where the focus shifts from complex life in general to complex *cognitive* life in particular. Among those evolutionary outcomes that might defy the RCT, cognition is particularly important, not only for human-specific inquiries into the evolution of intelligence and consciousness but also for the large-scale ecological organization of living worlds. What do patterns of cognitive convergence, and the lack thereof, tell us about the nature of mind, its evolution, and its place in the universe?

The evolution of mind starts with the senses, and in particular, with image-forming sensory modalities. The investigation of convergent minds thus begins in chapter 7, "Convergent Ways of Seeing," by exploring the convergent evolution of three image-forming sensory modalities: vision, echolocation, and electrolocation. These three modes of "seeing," despite their different energetic bases, representational capacities, and phenomenological qualities, allow organisms to construct rich three-dimensional scenes of their surrounding world. From these diverse modes of seeing we can glean some general lessons about the universal constraints on image-forming organs as well as their evolvability and ecological utility. This chapter argues that due to the laws of physics, there are a limited number of waveform energies that organisms can use to produce informationally rich, real-time, ecologically relevant images of the kind that can support active, goal-directed behavior in a three-dimensional world. These energies include light, sound, and electromagnetism—all potential reservoirs of detailed spatial information that evolution has tapped repeatedly in distant groups. This suggests that image formation is widely accessible, multiply realizable, and confined to a small number of possible solutions—properties that smack of law-like-ness. Furthermore, the evolution of object perception in different modalities requires convergent solutions to a similar set of cognitive problems, such as how to bind properties, valences, and identities to objects, and how to produce a stable, unified model of the surrounding world.

Chapter 8, "Convergent Evolution of the Umwelt," argues that image-forming sensory systems serve as the gateway to the emergence of intelligent

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life. As their perceptual acuity was honed, image-forming sensory organs—in particular, convergent visual systems—would have generated selection pressures for increasingly sophisticated cognitive mechanisms and their associated neural architectures, enabling organisms to make adaptive use of the valuable information that such sensory systems afford. These neural-cognitive mechanisms and honed optical functions would have then fed back into the evolution of sensory, motor, and proprioceptive systems in a complexifying feedback loop that resulted in the convergent evolution of the Umwelt. Adapting what was originally a nonevolutionary concept in German biology, the "Umwelt" is understood here as a unified phenomenal world of spatially distributed, bound, and meaningful (valenced) objects with the body and/or subject of experience at its center. Although the Umwelt can be conceived in wholly cognitive (e.g., representational) terms, the subjective quality of the Umwelt is also taken seriously as an evolutionary explanandum.

Does Umweltian cognition and consciousness reflect a deep structure of mind that is likely to be found elsewhere in the living cosmos? This is the central question taken up over the next two chapters, which explore the distribution of mind in nature. Although mind cannot be observed directly, its causal signature can be inferred from two mutually informing lines of evidence: brains and behavior, which, when taken in the light of evolution, permit us to draw inferences about the replicability of mind on Earth and beyond.

Chapter 9, "Finding Minds: Evidence from Neuroanatomy," reviews evidence for the convergent evolution of brains in animals, as well as the muddled evolutionary history of the neuron. It first wrestles with an apparent evidential conflict: on the one hand, phylogenetic and fossil data point to at least three separate origins of brains as the most parsimonious explanation of observed patterns of neuroanatomy; on the other hand, there are genetic, structural, and developmental data that seem to indicate one brain origin and numerous brain losses. If the latter "brain homology" hypothesis were true, it would entail more than a dozen losses of head/brain/eye complexes and the corresponding reorganization of body plans and lifeways in many animal groups. This chapter concludes that, all things considered, the brain homology hypothesis is less plausible than the brain convergence scenario, which suggests that vertebrates, cephalopod mollusks, and arthropods (the group that includes insects, arachnids, myriapods, and crustaceans) independently evolved central nervous systems. The chapter goes on to examine the even harder-to-parse phylogeny and evolvability of the neuron cell type, as well as the signaling systems and action potentials that allow for sophisticated information transfer in organisms that lack proper nervous systems, such as in green plants.

Even if brains originated multiple times, this does not necessarily imply that minds arose multiple times, because the connection between brains and minds

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is not clear-cut. Central nervous systems may or may not generate cognitive mechanisms that rise to the level of what we would want to call "mind." To better interpret the neuroanatomical data, therefore, we need to look for the behavioral signatures of cognitive functions that are linked to intelligence, thinking, planning, concept formation, spatial cognition, and other mind-like properties. Chapter 10, "Finding Minds: Evidence from Behavior," reviews the behavioral evidence for sophisticated forms of perception and cognition in invertebrates. The chapter focuses on invertebrates because it is only across the great phylogenetic chasms of animal evolution—in lineages in which brains arose separately and independently—that the robust replicability of the Umweltian minds can be established. The chapter begins with a review of the comparatively limited but better-known research on cephalopods, and then moves into a lengthy exploration of the stunning body of research on arthropod perception, cognition, and behavior.

Work with bees has replicated many of the complex learning tasks that have been demonstrated for "advanced" vertebrates like mammals and birds. The bulk of chapter 10 is dedicated to making the case for holistic perception and object recognition in insects as well as examining their ability to categorize objects, learn abstract concepts, perform complex unnatural motor sequences, reason about causes, plan routes, perceive time, count, and learn through observations of conspecifics. Evidence for attentional processes, emotional states, and even consciousness in arthropods is also reviewed. Taken in conjunction with neuroanatomical and evolutionary data, this work suggests that the Umwelt has arisen at least three times in the history of animal life. The chapter concludes by considering how the Umwelt turbo-charged goal-directed behavior and, in so doing, ushered in the modern era of animal ecology.

Part II concludes that if complex bodies are common in the universe, then complex minds are probably common as well. This raises the prospect, to borrow Stuart Kauffman's felicitous phrase, that mind may one day yet find itself "at home in the universe." In the coda to part II, "Homage to *Homo Sapiens*," the pendulum swings back once again toward contingency, as the discussion moves away from the convergent and toward the singular. Despite convergence on complex cognition, social learning, and tool use, cumulative cultural species are likely to be extremely rare due to the peculiar suite of phylogenetic and ecological contingencies that make the evolution of robust technological taxa possible. The key to robust technology is the evolution of cumulative culture, which allows for the maintenance, incremental improvement, and reliable transmission of complex technical designs.

What accounts for the striking lack of convergence on cumulative culture in nonhuman animals? Part of the puzzle is that there is a sizable temporal gap between the origins in early humans of the cognitive and cultural capacities

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that are implicated in cumulative technology—such as language, morality, causal reasoning, foresight, coordinated intentions, and culturally constructed learning environments—and the origins of cumulative culture, which occurred only quite recently in human evolutionary history. Moreover, many of the traits that underwrite this complexly configured adaptation are uniquely human, even if some of their building blocks can be found scattered among nonhuman animals. Unlike the Umwelt, which is likely to have evolved in positive feedback with image-forming sensory modalities and motor systems, the evolution of cumulative technological capacities appears to occur only when a suite of largely orthogonal factors, each with a low probability of occurring, are simultaneously in place.

This investigation of contingency and convergence in the history of life leads, therefore, to an unexpected conclusion. Although there are distinctively biological reasons to believe that intelligent life is common in the universe wherever microbial life evolves and is sustained for billions of years, exceedingly few of these intelligent species will ever develop robust technological capacities with signatures that are detectable across the immensity of space and time. Wherefore an eerie silence above, a mindful cacophony below.

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Contingency and Convergence

Toward a Cosmic Biology of Body and Mind

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