

2 The Radical Contingency Thesis

On June 28, 1914, Archduke Franz Ferdinand, heir to the Austro-Hungarian Empire, traveled with his pregnant wife Sophie by royal car down the streets of Sarajevo, a Bosnian city stoked with Slavic nationalism and stirring with rebellion. The archduke and his family had successfully evaded an assassination attempt in the form of a lobbed grenade only hours earlier during their trip to city hall, and the return journey took the royal procession along the same fateful route. In the “shot heard round the world,” the archduke and his wife were murdered in their vehicle by an assassin who fired two single shots from his pistol.

The archduke had been an influential moderating force in attempts to diffuse the growing prospect of military conflict between the European powers, and his assassination greatly affected the psychology of the Austro-Hungarian leadership. The chain of events that ensued was complex, unpredictable, and formative of global events for generations to come. The assassination had been organized by a secret Serbian military society and was bankrolled by the government of Serbia, which led the leaders of Austro-Hungary and Germany to issue an ultimatum to Serbia—worded in a way that made Serbia likely to reject it.

The assassination bolstered the case for war that was being made by hawkish elements within the empire, and it served as the ideal pretext for an aggressive attack on Serbia. If Russia chose to intervene on Serbia’s behalf, Kaiser Wilhelm II, the German emperor, would then be absolved of any blame for escalating the conflict. Upon Serbia’s partial rejection of the ultimatum, Austro-Hungary declared war on Serbia, and under the terms of a secret pact, Russia and France were compelled to enter the war on Serbia’s side. This, in turn, triggered the military mobilization of the Austro-Hungarian Empire and its invasion of neutral Belgium, with the aim of decisively defeating France to avoid a two-front war. This then brought Britain into the war on the side of France and Russia.

In a matter of weeks, nearly all major world powers (save for the United States, whose entry would come later) had entered into a war that would take the lives of 40 million people and culminate in the signing of the punitive Versailles Treaty. This draconian treaty would sow the seeds for a second and even more devastating world war and its unparalleled war crimes and genocides, which would follow only two decades later. The resolution of this second global catastrophe would be followed by the Cold War, the collapse of the Soviet Union, and solidification of U.S. geopolitical hegemony—a sequence of events that some historians take to be so causally intertwined that they constitute a single, protracted, historical episode: all emanating from a single assassin's bullet.

As the *New York Times* presciently reported just one year after the archduke's assassination,

Those two shots brought the world to arms, and the war that followed ... brought devastation upon three continents and profoundly affected two others.... Nation after nation has been drawn into the whirlpool, and more are drawing toward it, and the end is far off. What face the world will wear when it is all over no man can predict, but it will be greatly changed, and not geographically alone.¹

The assassination of Archduke Ferdinand and the ensuing descent into global catastrophe is perhaps the most famous illustration of the role of contingency in human affairs. Had a breeze or tremor of the hand caused the assassin's bullet to miss the archduke's jugular vein, or had the conspiracy been foiled, then World War I could very well have been avoided—and had it been avoided, then the geopolitical landscape of the contemporary world would have assumed a dramatically different shape. There is nothing inevitable about the forces and pathways that led to our particular political world.

The same may be said of more recent world-shaping historical events, such as the 9/11 attacks by Al-Qaeda on New York City and Washington, DC, which garnered support for the 2003 U.S. invasion of Iraq. Postwar mismanagement of the Iraqi army opened up a power vacuum in the Levant in which the Islamic State could recruit and operate; this then created fertile grounds for a cascade of rebellions that comprised the Arab Spring, resulting in the catastrophic collapse of Syria into a multidimensional civil war. Syria then became the epicenter of a massive refugee crisis that stirred the extreme nationalism, nativism, and xenophobia that helped bring about the Russia-assisted Trump presidency and the ascendancy of similarly authoritarian political parties in Europe and around the world, as well as the destabilization of NATO and the European Union. Like the *New York Times* in 1915, contemporary policy makers, journalists, historians, political scientists, and international relations theorists can scarcely make out the shape of the global geopolitical landscape even just one decade out.

As counterfactual historian Richard Ned Lebow has put it, “a small and credible re-write of history has the potential over time to bring about a very different world.”² One reason for this is that human historical trajectories are sensitive to “micro” events, such as the quirky beliefs and desires—or more reductively, brain states—of executive leadership, be they presidents, prime ministers, generals, directors, advisors, experts, or policymakers, who sit at or near the apex of organizational hierarchies and thus have a ramifying causal influence. If these executive levers of causal influence are pressed, they can drive the system into unlikely historical terrain. It is for this reason that we have difficulty predicting the human historical future, even while history can be forensically pieced together once it has been made.

In his book *1776*, historian David McCullough describes the outcome of the American Revolution, and the shape of history that unfolded from it, in beautifully contingent terms: “Especially for those who had been with Washington and who knew what a close call it was at the beginning—how often circumstance, storms, contrary winds, the oddities or strengths of individual character had made the difference—the outcome seemed little short of a miracle.”³

Is the history of life on Earth similarly contingent? If so, what features of the evolutionary process are responsible for these dynamics? We will begin by reconstructing the most influential argument for contingency in macroevolution: Stephen Jay Gould’s analysis of early animal evolution in the Cambrian period and the philosophical lessons he draws therefrom. Before taking a deep dive into counterfactual Cambrian seas, however, let us first unpack some of the challenges that face counterfactual reasoning in the historical sciences more broadly, as this will portend some of the difficulties that confront the adjudication of Gould’s thesis.

1. Counterfactuals in the Historical Sciences

In his epic and ruminating tome *The Structure of Evolutionary Theory*, published around the time of his death, Stephen Jay Gould noted that it was his admiration for the study of history in the broadest sense that compelled him to investigate the role of contingency in evolution.⁴ The counterfactual investigation of human history—studies of how history would have unfolded had certain events not occurred or occurred in a different way—has enjoyed something of a renaissance in recent research, though many historians remain skeptical that such an approach can rise to the level of serious scholarship.⁵ This skepticism is understandable, for as with the history of life on Earth, we cannot rewind the tape of human history, induce a few choice perturbations

while holding other variables constant, and observe how these perturbations affect the unfolding of the system. The worry is that counterfactual history is at best methodologically problematic and at worst a parlor game in which ideological penchants and flights of fancy substitute for sound science.

And yet counterfactual thinking is inescapable in historical scholarship. Historical accounts would be disjointed litanies of facts, not narratives, if they did not weave a tapestry of causal claims about beliefs, intentions, desires, actions, influences, *zeitgeists*, environmental conditions, economic factors, institutional contexts, and so on. And the grounding of causal claims (and for some, the metaphysics of causation itself) is widely thought to hinge on counterfactual analysis (see chapter 5 for further discussion). This is as true for history as it is for the physical sciences. When historians assert that Lee Harvey Oswald shot President John F. Kennedy, that Hitler was responsible for the Holocaust, or that Osama bin Laden funded and directed the 9/11 attacks, they mean that the assassination of JFK, the Holocaust, and the 9/11 attacks would not have happened, would have been far less likely to happen, or would have happened in a different manner were it not for the deliberate actions taken by Oswald, Hitler, and bin Laden in furtherance of their respective ideological goals. If historical narratives are to be meaningful and coherent, they have no choice but to indulge in causes, which in turn requires that they indulge (at least implicitly) in counterfactuals.

The value of counterfactual thinking in human history goes beyond substantiating specific causal claims. It is also necessary for establishing which historical outcomes and trends are robust against minor perturbations, and which are sensitive to small-scale events that could easily have been otherwise. Let us first consider outcomes. World War II historian Andrew Roberts dedicates the final chapter of a recent book, *The Storm of War*, to counterfactual analyses of the war in order to show that Hitler's defeat was guaranteed once Germany, fueled by Nazi racial ideology and buoyed by its lightning quick defeat of France and the British Expeditionary Force, invaded the Soviet Union.⁶ In most historical accounts of the war, the Soviets would eventually have captured Berlin whether or not the D-Day landings had been successful and a second front was opened up against the Axis powers. Asking how alternative wartime decisions, operations, and allocations would have affected the shape of the war is a useful way of discerning the causal structure of Allied victory and teasing apart robust and contingent features of the war.

Second, let us consider trends. Historical trajectories that are driven by population-level or "deep structural" forces tend to be robust against micro-level perturbations. This is the explanatory approach taken by Jared Diamond in his justly famous book *Guns, Germs, and Steel*, in which he develops a

deep structural explanation as to why peoples descending from agricultural populations in Eurasia ultimately displaced indigenous populations around the world.⁷ Diamond argues that systematic differences in climate and geography resulted in technical advancements in plant and animal domestication in certain regions of the world and the absence of such innovations in others; these agricultural innovations, in turn, supported larger populations with highly differentiated systems of labor, advanced weapons manufacture, and unwitting pathogen transmission capabilities, all of which facilitated the “displacement” of indigenous populations. Whether it was the Spanish, Dutch, British, or Ottoman empires that did the displacing in any given case may be historically contingent, but the deep structural nature of Diamond’s explanation means that the trend is highly replicable across reasonably close possible worlds. The same may be said for the rise of markets, currencies, military hierarchies, minimal states, and the like, which can be explained by “invisible hand”-like forces without appealing to the specific beliefs, desires, or actions of executive agents. As philosopher of biology Kim Sterelny has pointed out, trajectories driven by population-level mechanisms can be realized by numerous microstate configurations and pathways, and it is this massive multiple realizability that gives them their counterfactual stability.⁸

Another important function of counterfactual reasoning in history is to disabuse us of the fallacious notion that certain historical outcomes are inevitable. As historian Philip Tetlock and coauthors put it, counterfactual thinking about human history can liberate us

from the cognitive tyranny of hindsight bias: to prevent the world that did happen from obstructing our view of the panorama of possible worlds that could have sprung up into being but for tiny twists of fate, to sharpen our appreciation of how uncertain almost everyone was about what would happen before they learned what did happen, and to sensitize us to the intricate complexity and probabilistic character of the causal processes that produced the world we happen to inhabit.⁹

In short, counterfactual thinking is inescapable if we are to recognize a contingently configured world. As we shall now see, this is as true for natural history as it is for human history.

2. Counterfactuals in Animal Evolution

In his acclaimed book *Wonderful Life: The Burgess Shale and the Nature of History*, Stephen Jay Gould proposes a series of macroevolutionary thought experiments designed to probe the contingent nature of life’s history.¹⁰ He imagines rewinding the “tape of life” to various critical junctures in the history

of animal evolution and then considers how life's story would again unfurl. Gould argues that replaying the tape of animal life would result in a radically different set of macroevolutionary outcomes—a morphological menagerie bearing little resemblance to animal life as we know it. Not only would no humans, mammals, or vertebrates evolve, but neither would any creatures even approximating them. In fact, for Gould, contingency is not merely a characteristic of animal evolution; it is a pervasive feature of the evolutionary process. In one of his more hyperbolic moments, Gould exclaims that “almost every interesting event of life's history falls into the realm of contingency.”¹¹ I will refer to this view of life, both here and throughout the book, as the “radical contingency thesis” (RCT).

Gould's most crucial replay concerned the dynamics and long-term aftermath of a critical episode in the history of animal life known as the “Cambrian explosion.” This event marks the geologically abrupt emergence, about 545 million years ago, of the vast majority of animal body plans that comprise *Bilateria*: bilaterally symmetric animals with digestive tracks and a separate mouth and anus. The first detailed picture of this event came from the fossil *lagerstätten* of the Burgess Shale, located in Yoho National Park in the Canadian Rockies.

These fossil beds are located in one of the most sublime landscapes in North America (see figure 2.1). They are famous not for their idyllic setting, however, but for their remarkable preservation of the soft bodies of the first bilaterians, most of which had no skeletonized parts and whose physical forms had, as a result, long remained a mystery (only about 3% of Cambrian taxa had mineralized skeletons, and most of these were trilobites). The diagnostic hard parts of the major bilaterian clades—such as the exoskeletons of arthropods, the shells of mollusks and brachiopods, and the backbones of chordates—all had yet to form. The Burgess Shale provided the first clear window into the morphological and ecological diversity of the earliest bilaterians, as well as the tempo and mode of their evolution. Similar fossil assemblages have since been found in China and Greenland (most recently, the Qingjiang biota *lagerstätte* from south China¹²), showing definitively that the critters of the Burgess Shale were indeed a global fauna.

In addition to some familiar sights (like trilobites, brachiopods, and priapulid worms), many fantastical animal designs appear among the early Cambrian fauna and then vanish in the extinction crises that punctuate the same period. Gould was especially taken by the strangeness of *Opabinia*, a soft-bodied animal with five stalked eyes, a backward-facing mouth, and a hollow, flexible, vacuum cleaner-like proboscis with a grasping claw at the end (figure 2.2)—so much so, that he nearly named his book *Wonderful Life* “Homage to *Opabinia*” but was wisely talked out of this by his editor. Although *Opabinia* had some affinities



Figure 2.1

The Burgess Shale and surrounds. (*Top*) Waterfalls cascading down Michael Peak just after emerging onto the Burgess Highline from Yoho Pass. (*Middle*) View of Emerald Lake from Burgess Highline just past the switchbacks leading to the Burgess Shale. (*Bottom*) Guided group ascending to the Walcott Quarry outcrop, taken from the southern portion of the Burgess Highline. Photos by author.

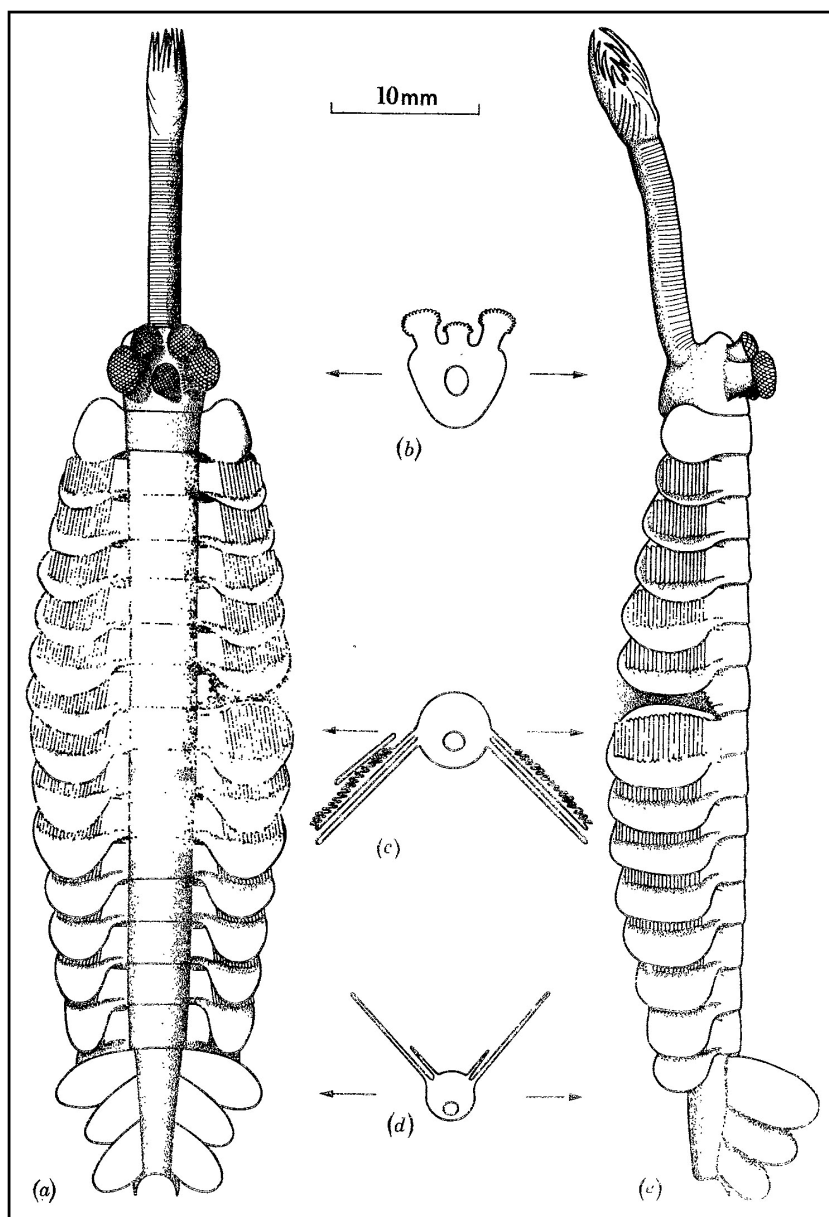


Figure 2.2

Dorsal and lateral views of *Opabinia*. From H. B. Whittington, "The Enigmatic Animal *Opabinia Regalis*, Middle Cambrian, Burgess Shale, British Columbia," *Philosophical Transactions of the Royal Society of London. B, Biological Sciences* 271, no. 910 (1975): 1–43.

to arthropods, it did not have a jointed exoskeleton, and there is nothing in existing arthropods that resembles its grasping hose-like appendage or its set of five stalked eyes. Legend has it that when Harry Whittington, one of the scientific heroes of *Wonderful Life*, unveiled the first reconstructed image of *Opabinia* to an audience of paleontologists, it was greeted with the laughter of disbelief.

Opabinia was not alone. The Burgess Shale pageant included many other science-fictionary forms, like *Wiwaxia*, *Hallucigenia*, and *Anomalocaris*, which like their contemporary *Opabinia* did not, at the time of Gould's writing, fit neatly into any known animal phyla. Taxonomically challenging critters of the Cambrian have emerged at a regular pace ever since. Recent additions to the pageant include two curious filter-feeding luolishaniid lobopodians, a paraphyletic group of wormlike creatures that fed on larvae in the water column; the first is a superarmored worm nicknamed "Collin's monster" after its eponymous discoverer,¹³ and the second has been dubbed the "ovation worm" for its inferred upward limb-waving posture.¹⁴

These "mind-bending problematica," in the words of paleogeologist Andrew Knoll, shared the early Cambrian seas with many representatives of familiar body plans such as cnidarians, sponges, mollusks, priapulids, comb jellies, basal chordates, and traditional arthropods like trilobites.¹⁵ This led Gould to surmise that an alternative set of body plans could very well have emerged as the evolutionary victors of the Cambrian—that if events had played out just a little bit differently, familiar animal forms might have been relegated to the realm of the fantastic while the weird wonders of the Burgess Shale inherited the Earth. This, for Gould, was the deep significance of these fossils. Whereas many have come to view the Cambrian explosion as the ultimate arena of animal experimentation, for Gould it represented an early crossroads pregnant with alternative macroevolutionary possibility. The Burgess Shale did not reveal an early phase of evolutionary experimentation in which bizarre and inferior designs were driven to extinction in the unrelenting crucible of natural selection; rather, they offered a window into what alternative—and equally functional—histories of life on Earth might have looked like.

There was one taxon in particular among this motley Cambrian menagerie that caught Gould's eye, one that was of particular significance for its apparent insignificance. This is *Pikaia*: a relatively understated creature in terms of its ecology and anatomical complexity, but one that is by most accounts a close relative to the ancestor of all modern vertebrates. *Pikaia* is a leaf-shaped animal that vaguely resembles jawless chordates such as the lancelet; it has blocks of segmented skeletal muscles similar to the myomeres of fish, with two tentacles on its eyeless, protohead. The macroevolutionary moral Gould draws from

Pikaia is this: had conditions at the end of the Cambrian been just a little bit different, then *Pikaia* and other nascent taxa might not have survived, and the morphological landscape of life on Earth would have assumed a markedly different shape.¹⁶ If no *Pikaia* (and its contemporaneous ilk), then no vertebrates. If no vertebrates, then no tetrapods. If no tetrapods, then no mammals. If no mammals, then no humans. If no humans, then no self-consciousness. If this reading of animal evolution is correct, it offers perhaps the strongest basis yet for the SETI skepticism that swells among the ranks of evolutionary biologists (as discussed in chapter 1). If intelligent life is unlikely to be replicated were the tape of animal life to be replayed on Earth, then there is little reason to think it would arise in a predictable or law-like way throughout the cosmos.

Gould's counterfactual analysis of macroevolution was not limited to the origins and evolution of bilaterian phyla in the Cambrian. He also considered replays in relation to more fine-grained taxonomic events, such as the seemingly improbable survival of the lobe-finned fishes that gave rise to tetrapods (four-limbed vertebrates) as well as the extinction of the long-dominant nonavian dinosaurs, which cleared the way for the unlikely radiation of mammals and their eventual rise to macro-faunal dominance in the Cenozoic. Gould argued that were we to replay the tape of life in each of these cases, evolution would be channeled into a different pathway, resulting in outcomes that bear little resemblance to the history of life as we know it.

It is no accident that Gould entertained this particular set of evolutionary counterfactuals out of the vast number of evolutionary counterfactuals that he could have entertained. For both the evolution of tetrapods and the dinosaur-mammal succession were crucial junctures in the seemingly improbable chain of events that led to human beings. If any one of these links in the chain did not occur, so the argument goes, we would not be here, nor would any creatures even remotely like us. Had the understated *Pikaia* and its close chordate relatives been wiped out in the Cambrian, then vertebrates as we know them would never have arisen. Had a quirky lineage of lobe-finned fish in the Devonian drawn the short evolutionary straw, then tetrapods would have remained hypothetical forms of possible evolutionary worlds. Had a massive asteroid missed the Earth rather than careening obliquely into the Yucatan Peninsula some 65 million years ago, mammals would still be scurrying under the toes of sleeping dinosaurs, and no animals on Earth would be capable of reading these words or thinking these thoughts. By running these counterfactuals, Gould invites us to question the necessity of our living world and, by implication, the precariousness of our own existence.

Contingency is a ubiquitous feature of our personal worlds. My great grandmother, who fled pogroms in the Ukraine to settle in New York City as a

teenager, landed her first paying job in the United States at the Triangle Waist Company factory in Greenwich Village. On March 25, 1911, a man she was casually dating (who would later become my great grandfather) invited her to lunch. She snuck out of work to meet him just after noon, and they had such a good time that she decided to skip out on the rest of the workday. The infamous Triangle Shirtwaist fire broke out in the mid-afternoon that day, killing 146 garment workers, most of them Jewish and Italian immigrants. Had my great grandmother not gone out for lunch, I would probably not be here today. This example is a particularly dramatic one, but similar stories of contingency, both existential and mundane, are part of everyone's life. A key question before us is whether natural history is amenable to similar sorts of contingency narratives, in which respects, and why.

3. The Radical Contingency Thesis

Let us now begin to unpack the various theoretical components of the RCT. When Gould looked at the distribution of existing animal body plans, he saw islands of form amid a vast and largely unoccupied theoretical "morphospace," with huge gaps between the islands. Mollusks, arthropods, vertebrates, echinoderms, annelids, brachiopods, nematodes, priapulids, and other bilaterian animal phyla are diverse groups (some more so than others), yet all this diversity is clustered within each respective "island" or body plan. We do not observe a smooth gradation of forms bridging the rather substantial morphological gaps between body plans. Gould's Cambrian thought experiment asks whether this clumpy distribution of form in an otherwise vast and uncharted morphospace is the result of a replicable optimizing process—one that drives evolution toward certain global attractors—or rather the product of quirky, causally formative events that took place early in the history of animal evolution.¹⁷ How we answer this question will have profound implications for the astrobiological questions posed at the outset of this book.

Gould's contention is that small changes in early Cambrian conditions would have led to a very different initial occupation of morphospace and hence history of life. There are two theoretical pillars that undergird this claim.¹⁸ The first relates to the stochastic (or pseudo-stochastic) nature of mass extinctions, with the Cambrian extinctions being the most causally formative of these culling episodes. The second concerns the developmental entrenchment or "freezing" of the body plans that survive these bouts of lineage sampling, which ensure that the gaps between morphological islands are never crossed. Neither subthesis is, on its own, sufficient to establish the RCT, but together they provide the bulwark for Gould's view of life.

3.1 Stochastic Extinction

The Phanerozoic Eon, which began 541 million years ago and continues to the present day, is punctuated by at least five major extinction pulses in which a large proportion of species and higher taxa were wiped out. In the aftermath of these extinction events, a previously dominant faunal assemblage is replaced by an entirely different biota, which radiates to fill the ecospace vacated by the decimated incumbents. Take, for example, the most extreme episode of extinction in the history of animal life: the end-Permian crisis, which took place about 250 million years ago, in which it is estimated that a staggering 95 percent of living species were extinguished.¹⁹ This event, which coincided with the greatest volume of volcanism in the Phanerozoic,²⁰ eliminated some of the most successful groups of all time, such as the trilobites, while it brought to prominence other lineages such as bivalves, gastropods, fishes, and echinoids, which until the Permian extinction had been only marginal players in marine ecosystems dominated by brachiopods, crinoids, and bryozoans.²¹ Many of the lineages that rose to dominance in the wake of the Permian catastrophe radiated from only a handful of surviving species. This pattern, which is replicated in other major extinctions, suggests that had things played out a little bit differently, these groups also would have perished, leaving the vacated niches to be occupied by other fortuitous and theretofore unassuming groups.

Reflecting on these patterns, paleobiologist Doug Erwin and his collaborators remark that mass extinctions “not only punctuate the history of life, they also forever alter its trajectory.”²² Part of the trajectory-altering power of mass extinctions comes from the fact that they are not merely temporary intensifications of background extinction rates.²³ Rather, they are macroevolutionary game changers—events that briefly but significantly alter the rules of survivorship that obtain in more halcyon times, upending successful incumbents and in some cases triggering a climatic overhaul that shapes the nature of postextinction recovery.

How precisely are the dynamics of mass extinction related to the RCT? Gould appears to reason as follows: the extinctions that filtered out the Cambrian *Problematica* either (1) were truly stochastic, in which case there was no rhyme or reason (or more precisely, no dominant explanatory cause or causes) for the observed patterns of taxa survivorship, and thus no reason to believe these patterns would be replicated if the tape of animal life were replayed under slightly different conditions; or (2) were selective and thus to some extent replicable, but in a sense that cannot be traced to any long-term functional superiority of the surviving groups.

Groups may have certain traits that make them more likely to survive the ravages of a given mass extinction, such as a wider geographic range, patchy population structure, smaller body size, burrowing capacity, generalist feeding ecology, higher fecundity, smaller generation time, higher intraspecific variation, or greater evolvability, to name a few candidates. But none of the traits that plausibly confer advantages during mass extinctions (or in selection among species to the extent this occurs) relate to the clusters of features that are associated with specific animal body plans.²⁴ Moreover, traits that confer differential survival in mass extinctions may not be properly characterized as adaptively superior traits or even as adaptations at all, because they are only causally connected to differential clade persistence in rare geological moments of mass perturbation, when the global biota is temporarily strained. The fraction of the Phanerozoic during which mass extinction conditions prevail is a miniscule proportion of the eon, spaced out by scores or even hundreds of millions of intervening years, during which time the ordinary “background rules” of clade survivorship govern. This, in turn, prevents adaptations to mass extinction conditions from accumulating.

Macroevolutionist David Jablonski has referred to extinction dynamics of this sort as “nonconstructive selectivity,”²⁵ a notion that is broadly similar to David Raup’s concept of “wanton extinction.”²⁶ I will refer to it here as “pseudo-stochastic” sampling because, although the sampling patterns are not truly random, they are both less obvious and more fleeting than those that might underwrite competitive replacements in normal times. Pseudo-stochastic extinctions are not truly stochastic like lightning strikes or David Raup’s “field of bullets” scenario, in which all lineages have the same chance of being sampled (or persisting into some future geological period). The difference between pseudo-stochastic and merit-based models of extinction is not that one involves lineage sampling that is driven by fitness differences whereas the other is fitness neutral. The difference, rather, is that in one case the fitness conditions imposed are not stable for a sufficient amount of time to allow for a macroevolutionary response to selection—either at the level of individual organisms or at the level of lineages. The staggered and precipitous nature of these perturbations means that adaptations to mass extinctions will either fail to accrue or else come undone by countervailing selection and drift in the protracted intervening timespans in which ordinary selection regimes prevail.

Both mass-extinction scenarios—a truly random sampling of the biota and the episodic imposition of different rules governing clade survivorship—undermine the prospects for any long-term competitive replacement of functionally inferior lineages by superior ones, at least in terms of the cluster of

traits that comprise animal body plans. If long-term competitive interaction is the most plausible driver of macroevolutionary replicability, then stochastic and pseudo-stochastic patterns of extinction cut deeply into the possibility of a law-like shape of life.

3.2 Faunal Turnover

There is a close relationship between macroevolutionary competition narratives and the progressivist readings of life that Gould had long sought to dethrone. Paleontologist Steven Stanley remarked that “paleontologists have almost universally accepted the idea that certain body plans have been rendered obsolete during modernization of the world’s ecosystems.”²⁷ Implicit in such talk of obsolescence is the notion that there are competitive interactions between taxa in which some have a distinct fitness advantage over others. These repeated rounds of interaction, so the logic goes, explains the waxing of one clade and the waning of another, until the functionally superior clade fully supplants the inferior one. Although plausible *a priori*, there is currently little evidence to indicate that major²⁸ and moderate²⁹ faunal turnovers—situations in which one faunal assemblage is succeeded by another—can be explained by the long-term competitive superiority of the succeeding faunas.³⁰

What evidence is there that the faunal turnover that marked the end of the fantastic phase of animal evolution in the Cambrian was more like a lottery than a merit-based competition? Gould draws this ontological conclusion from an epistemic premise, namely that no biologist without the benefit of hindsight could have predicted the actual patterns of Cambrian survivorship on the basis of any plausibly relevant traits, such as anatomical complexity or ecological prominence. The fact that no evolutionary handicapper worth her salt would have predicted which designs would survive the end-Cambrian extinctions is then taken to indicate that early bilaterian extinctions were essentially haphazard—and thus counterfactually unstable.

For Gould, then, the Cambrian explosion does not simply recount “a unique and peculiar episode of possibilities gone wild”—it reveals a deeper truth about the contingent topography of complex life as we know it.³¹ Because there was no necessity to the patterns of survivorship in the Cambrian, there is no necessity to the actual shape of animal life, whose parameters are bounded by the confines of surviving body plans. Before elaborating on this boundedness, let us consider other prominent faunal turnovers that might support a Gouldian view of life.

Just as no good evolutionary handicapper would have bet on the unassuming *Pikaia* and its kin to squeak through the Cambrian extinctions and go on to establish the vertebrate clade (but see section 4.2 of this chapter), so too would

no late-Cretaceous handicapper have predicted that mammals would supplant the dominant *Dinosauria* as the Earth's prevailing megafauna courtesy of "one terrible day in the history of the Earth."³² Mammalian diversity (species richness) and disparity (the breadth of functional anatomical designs) were largely suppressed throughout the Mesozoic era, an approximately 185-million-year period (from 250 million to 65 million years ago) during which time dinosaurs were by far the most salient terrestrial vertebrate fauna. The suppression of mammals is generally attributed to the success of the incumbent dinosaurs and other archosaurs (such as pterosaurs and crocodilians), which packed available niches and relegated mammals to nocturnal, insectivorous, rodent-like forms that generally weighed less than 4 kilos. After the sudden bolide-induced mass extinction that claimed the nonavian dinosaurs, pterosaurs, and apex marine reptiles (such as the mosasaurs and plesiosaurs) and nearly extinguished birds and crocodilians, therian mammals (which include placentals and marsupials) radiated rapidly and dramatically to fill the emptied niches.³³ Bats took to the sky and whales to the sea like pterosaurs and mosasaurs before them, and large predatory bear-like mammals (such as *Titanoides*) hunted in the same forests and grasslands that were stalked by tyrannosaurs not long before.³⁴ These magical worlds were separated by a geologically short span of time punctuated by a single apocalyptic event.

This now-canonical picture of the dinosaur–mammal succession serves as an effective antidote to the long-standing progressivist narrative that had wily mammals outsmarting and thus replacing their fiercer but dimwitted dinosaurian counterparts. It is rather like the classic fable of David and Goliath, but with Goliath dropping dead from a heart attack and David moving unopposed into his house. However, as is so often the case in science, the reality turns out to be more complicated. Multituberculate mammals—an extinct group of rodent-like mammals with molar-like teeth—appear to have radiated some 20 million years *prior* to the Cretaceous-Paleogene (or "K-Pg") boundary (formerly known as the "K-T boundary"). Multituberculates ate insects, and they appear to have diversified along with the proliferation of angiosperms (flowering plants) and their coevolving pollinators up to and even through the K-Pg boundary.³⁵ Nevertheless, all fossils that exhibit traits characteristic of modern mammalian orders appear after—not before—the K-Pg boundary.³⁶ There is no reason to think that multituberculates were outcompeting dinosaurs or played any role in their demise.

There are two additional wrinkles in the standard dinosaur–mammal succession picture. First, there are indications that therian mammals (not just multituberculates) may have begun to diversify before the end-Cretaceous extinction.³⁷ Second, there is now some data suggesting that nonavian dinosaurs had already

begun their broad decline tens of millions of years before the K-Pg event. Data on dinosaur diversity and disparity during the last few million years of the Cretaceous comes almost entirely from the Hell Creek formation in the western interior of North America. Studies of Hell Creek have generally found many dinosaur clades (as well as other archosaurs, such as pterosaurs) doing well right up until the K-Pg boundary, beyond which no nonavian dinosaurs have ever been found.³⁸ However, a recent statistical analysis of speciation rates suggests that all three major dinosaur groups—sauropods, theropods, and ornithischians—were on the whole declining for more than 40 million years before the boundary, with net speciation rates being exceeded by extinction rates in the middle-early Cretaceous (this does not appear to be true for ceratopsians and hadrosaurs, however).³⁹

Even if a broad dinosaurian decline were borne out, this still does not support a competitive replacement scenario in which ecologically superior mammals gradually dislodged their inferior dinosaur counterparts from their niches. Such a scenario predicts that we should see the allegedly superior group diversifying as its weaker competitor declines. This coordinated waxing and waning of fauna is pictorially depicted by Gould and Calloway's classic "double-wedge" pattern.⁴⁰ The double-wedge model contrasts with what paleontologist Michael Benton calls the "mass extinction" pattern,⁴¹ in which the incumbent holds steady until the extinction boundary, with the successor remaining at low levels of diversity until the incumbent lineage goes extinct or suffers a severe depletion (figure 2.3).

Even if dinosaur diversity (net speciation) had long been in decline, at the time of the end-Cretaceous extinction event, they were still far and away the most ecologically diverse terrestrial vertebrates on Earth. Dinosaur abundance and functional diversity was thriving, and dinosaur ecosystems were bustling, right up to the boundary—until glass beads (tektites) and other impact ejecta are found clogging up the gills of fish struggling in the first hours after the impact.⁴² It was only after the severe archosaurian depletion at the K-Pg boundary that mammals could radiate into their modern forms and massively increase in body size. Recent modeling work by Graham Slater supports the archosaurian suppression of mammalian diversity throughout the Mesozoic, followed by mammalian disparification at the boundary coinciding with the release of ecological constraints.⁴³ This picture does not fit the double-wedge model. Neither, however, does it perfectly fit the mass extinction pattern, given both the long-term diversity decline of *Dinosauria* and the pre-K-Pg radiations of mammals.

Even if the impact event had never occurred, it is possible that the dinosaurs would have still declined to extinction over a longer time frame, due (say) to

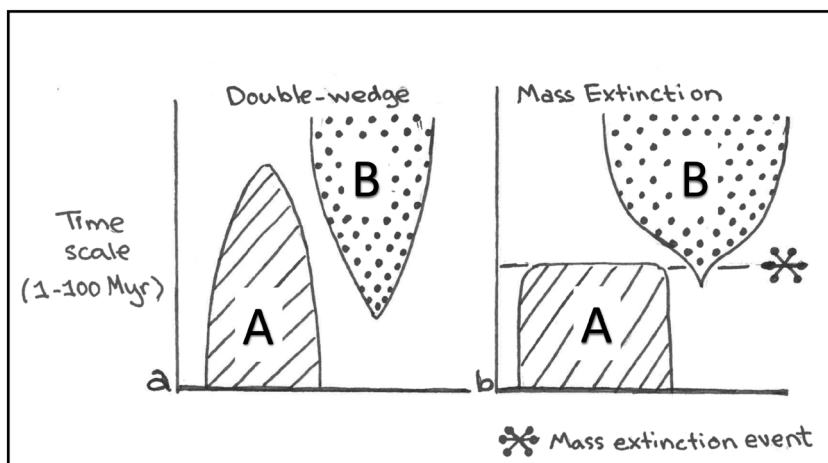


Figure 2.3

(a) Double-wedge diversity pattern, with one clade replaced by another through competitive interactions. (b) Mass extinction diversity pattern, in which one clade is extinguished or severely depleted in a major biotic perturbation and only then replaced by another clade. Redrawn from M. J. Benton, “The Late Triassic Tetrapod Extinction Events,” in *The Beginning of the Age of Dinosaurs: Faunal Change across the Triassic-Jurassic Boundary*, ed. K. Padian, 303–320 (Cambridge University Press, 1986).

endothermic inefficiencies that made them poorly suited to a cooler world, while mammals would have continued to diversify during this drawn-out dinosaurian decline. It is also possible, perhaps even likely, that dinosaurs would have continued into the Paleogene to the present day—which would amount to only a small extension of their total reign—adapting to a new climatic regime and the restructuring of Mesozoic ecosystems thanks to the rise of angiosperms. In any case, other taxa, such as endothermically efficient birds, were also “waiting in the wings” and seem to have been equally amenable to a post-K-Pg radiation. Why then did mammals radiate when they did, whereas birds failed to re-evolve guilds of dinosaurian megafauna?

In the three decades since *Wonderful Life* was published, studies of faunal turnover have extended Gould’s contingency counterfactual to the rise of *Dinosauria* itself. One might conclude from the remarkable evolutionary success—and astronomically bad luck—of the dinosaurs that the rise of this noble clade must have been due to its adaptive edge over the primitive reptile fauna that preceded it. In fact, the adaptive radiation of *Dinosauria* in the wake of the end-Triassic mass extinction, and its displacement of the formerly dominant crurotarsans (crocodile-like archosaurs), exhibits the same noncompetitive, contingent dynamics that we see with the rise of mammals 170 million

years later. Like the Mesozoic mammals, dinosaurs during the Triassic were relatively marginal players that just happened to be in the right place at the right time with the right equipment and raw evolvability to support an adaptive radiation in the aftermath of a major biotic crisis.

Dinosaurs originated in the middle Triassic, entering a Mesozoic world in which the incumbent crurotarsans were more disparate, more diverse, and more ecologically prominent. Studying the range of morphospace occupation over the Triassic and Jurassic, paleontologist Steve Brusatte and colleagues found a classic mass extinction pattern: the crurotarsans had twice the diversity in body plans, lifestyles, and diets as dinosaurs throughout the Triassic, holding steady and continuing to overshadow them until the great perturbation at the end of the Triassic—at which point the morphospace curves reverse, with the once marginal dinosaurs doubling the crurotarsans in all measures of evolutionary success.⁴⁴ There is no evidence that dinosaurs gradually outcompeted the crurotarsans or otherwise competitively drove them to extinction. In a remark that is reminiscent of Gould’s handicapper claim about the Cambrian, Brusatte noted, “If we were standing in the Late Triassic, 210 million years ago or so, and had to bet on which group would eventually dominate ecosystems, all reasonable gamblers would go with the crurotarsans.” In a final twist, the crurotarsans themselves rose to prominence along with other archosaurs in the wake of the end-Permian extinction, where they replaced apex predators like the “stem” mammal gorgonopsians (therapsids), which perished along with 96 percent of species in the greatest biotic crisis of all time. Perhaps some understated fauna waiting in the wings will eventually replace therian mammals in the wake of the next mass extinction.

The dinosaur–mammal, crurotarsan–dinosaur, and therapsid–crurotarsan successions represent only a tiny handful of the faunal turnovers that have occurred in the history of animal life, though they are particularly relevant to the contingency of our own evolutionary history. Still, the overwhelming majority of animals are not vertebrates (let alone tetrapods), and the extent to which the above turnover dynamics generalize to other episodes in animal evolution is unclear. The aim here is not to provide an exhaustive review of this phenomenon so much as to appreciate the central role it played in the intellectual development of Gould’s thesis.

3.3 Developmental Entrenchment

The stochastic or pseudo-stochastic sampling of lineages in mass extinction events, followed by the adaptive radiation of surviving clades into newly emptied ecospace, gets us only part of the way to the RCT. For it still leaves open the

possibility that, in the intervening time between these perturbations, life will reliably gravitate back toward the optimal attractors in morphospace.

For instance, even if *Pikaia* and its proto-chordate ilk had perished in the Cambrian, perhaps “vertebrates” in some broad functional sense would have arisen again over deep time. And perhaps this “evolutionary overdetermination” goes for other bilaterian body plans. And perhaps within each of these body plan attractors there are still more fine-grained morphological attractors. For example, perhaps within the “mollusk” attractor there are “bivalve,” “gastropod,” and “cephalopod” attractors, such that once the mollusk plan emerges, these forms are, given enough time and a diversity of selection pressures, likely to emerge as well. Whether these sorts of attractors exist, how broadly defined they might be, and the crucial matter of their underlying causes will be investigated in the chapters to come. The point here is that the extinction/turnover dynamic, without more, does not rule out the possibility of global attractor repopulation.

Enter the second theoretical pillar on which the RCT stands: developmental entrenchment. It is the internal structure of development which ensures that bouts of non-merit-based sampling will have permanent effects on the future of animal life. To see how this might be so, let us return once again to the Cambrian. Gould’s hypothesis is that once the early pages of the book of animal life were written in the Cambrian, they significantly constrained the form and content of subsequent chapters due to the entrenched nature of development.

“Development” refers to the patterns, processes, and mechanisms that characterize the maturation of a multicellular organism from zygote to death. One of the great mysteries of biology, now being slowly unraveled, is how a single cell—the embryo—can reliably give rise to an adult organism with trillions of cells, numerous cell types, and countless functionalities that comprise the tissues, organs, and organ systems of animals. The challenge is to understand how the descendants of a single cell are programmed to guide cellular differentiation and the formation of body parts depending on their location in space and time to the axes of the developing bilaterian body.

Gould’s idea is that once the overarching developmental parameters of a lineage are laid down in the early history of a clade, they become highly impervious to selective modification due to their being causally bound-up with many interacting genes and functional pathways that lie “downstream” in the developmental cascade leading to the phenotype. Writing with fellow Harvard biologist Richard Lewontin in 1979, Gould surmised that “in complex organisms, early stages of ontogeny are remarkably refractory to evolutionary change, presumably because the differentiation of organ systems and their integration

into a functioning body is such a delicate process, so easily derailed by early errors with accumulating effects.”⁴⁵ In *The Structure of Evolutionary Theory*, Gould drew upon cutting-edge work in developmental biology to support this crucial claim about the conservation of body plans.⁴⁶

3.4 The Causal Topography of Development

Gould’s developmental hypotheses have been given a philosophical gloss by Jeffrey Schank and Bill Wimsatt, whose notion of “pleiotropic entrenchment” provides a conceptual model of the processes that might result in the conservation of “upstream” components in the developmental cascade.⁴⁷ These same developmental dynamics also bias evolutionary change toward the modification of factors that occur in the temporal tips, as it were, of the unfolding phenotype. Their rather plausible idea is that genes and regulatory networks that act early on in the developmental cascade tend to have collateral, knock-on effects vis-à-vis downstream structural and regulatory genes, and these “pleiotropic” effects make upstream components harder for selection to modify.

As a result of this causal topography, early developmental structures fail to meet the two necessary criteria for adaptation identified by Richard Lewontin in his classic paper in *Scientific American*: “quasi-independence” and “incrementality.”⁴⁸ The quasi-independence criterion is violated: due to downstream pleiotropy, early ontogenetic structures cannot be modified independently of many other features of the organism, and the combination of blind variation and natural selection cannot coordinate the mutations necessary to modify all of these variables at once in a way that would result in a functionally viable outcome. The incrementality criterion is also violated: any alteration of upstream developmental components, again due to pleiotropic effects, are likely to result in morphological saltations (leaps), rather than incremental adjustments. And saltations are extremely unlikely to catch the gradient of a fitness peak in a “rugged adaptive landscape”; instead they are far more likely to land in a valley or plain. Any significant alterations of the upstream components of a gene regulatory network are likely to produce a “hopeless monster.” Thus, while selection can *conserve* body plan features—and is probably a necessary force in their conservation—once these upstream structures are laid down and connected up to midstream and downstream components, they cannot be further *shaped* by selection even if such modifications would, *ceteris paribus*, be beneficial in any given case.⁴⁹

Empirical research in the intervening years has more or less confirmed Gould’s suspicions about the evolutionary developmental structure of animal body plans. Gene regulatory networks are among the most complex systems known in nature. They are informationally dynamic, controlling the expression

and interaction of thousands of genes, proteins, and nongenetic components over the course of ontogeny to ensure the reliable unfolding of the phenotype. Precisely how phenotypic information is represented in “cis-regulatory” circuits, in which noncoding regions of the genome control the transcription of nearby structural genes by acting as binding sites for transcription factors, is not well understood and remains a source of ongoing investigation. Whatever the mechanisms involved, innovations in gene-regulatory networks undoubtedly played a crucial role in the evolution of complex multicellularity, including the emergence of bilaterian body plans.

Pioneering work in developmental biology has shown that gene-regulatory networks are hierarchical, just as Gould conjectured, with earlier or more central causal nodes having greater pleiotropic effects than the distal, more fine-grained terminal processes that guide cellular differentiation.⁵⁰ Upstream developmental components control the parameters of the body plan by specifying the spatial regulatory state of progenitor fields which, through localized cell signaling, guide the differentiation of specific organ systems and body parts. Upstream networks also guide the integration of phenotypic components at midstream positions in the developmental cascade. These upstream subcircuits—which biologists Eric Davidson and Doug Erwin have dubbed “kernels”—specify the general spatial configuration of the body parts of the developing organism.⁵¹ Because kernels are “recursively wired”—that is, their cis-regulatory modules are linked together in feedback loops—interference with any single kernel gene can destroy the subcircuit’s function altogether, resulting in catastrophic consequences for the phenotype such as blocking the development of major body parts.

In short, the regulatory output of an upstream circuit serves as a crucial component of the circuit below it and so on down the chain, making it difficult to modify upstream components without wreaking havoc on the phenotype. Because the phenotypic effects of mutations in developmentally upstream components like kernels are rarely linear or modular, they will often damage not only the structures that are directly implicated by the mutation but distant collateral traits as well.⁵² This causal topography places a substantial and perhaps prohibitive evolutionary premium on the selective modification of kernel elements. This, in turn, explains the deep phylogenetic conservation of upstream components that specify limb coordinates, nervous system patterning, gastrulation, and many other key characteristics of bilaterian body plans. And it does so without adverting to the relative functional superiority of conserved body plans over hypothetical or extinct alternatives.

Take, for instance, the “through gut” that connects an anterior mouth to a posterior anus in all bilaterian animals. One might conclude from its ubiquity

among animals that this design is optimal in some “global” sense—that it is a superior solution among all nomically possible animal designs and thus likely to be replicated on other living worlds where complex, multicellular life forms evolve. Yet the gut appears, on most counts, to have arisen only once in the history of life and to have been conserved in *Bilateria* ever since. Current debates over the phylogenetic position of ctenophores (comb jellies), discussed in chapter 9, leave open the possibility that the gut evolved twice in animals, which would substantially increase our credence in its replicability.

For the moment, however, let us presume that the single origin hypothesis is correct. Now add to this the additional premise that the causal topography of development is such that the gut will be conserved even if a functionally superior configuration is theoretically realizable, because any modification of the kernels that specify the axes of development will prove catastrophic for the phenotype. Given the conjunction of these two premises, there is no reason to suppose that this conserved design is optimal among all morphologically possible designs, or even that it is superior to most. Perhaps the gut is a frozen accident. This is why evolutionary iteration (of the right sort) is so important to the case against contingency.

In sum, the causal topography of gene-regulatory systems explains why bilaterian animal body plans have changed very little since their emergence in the base of the Cambrian, and why the diversification that has occurred has been restricted primarily to tinkering with downstream nodes of the morphogenetic-regulatory network.⁵³ “Body plans” refer, roughly, to the overarching morphological configuration of higher animal taxa, as quintessentially reflected by the “phyla” and “superphyla” Linnaean ranks (but potentially also referring to class and order-level organization). If body plans are specified by kernels, and if kernels are recalcitrant to modification once they become developmentally entrenched in a lineage, then it follows that the body plans of lineages that survive stochastic or pseudo-stochastic extinctions will effectively become locked in place.

Selection will thereafter be limited to tinkering with downstream or distal components of gene-regulatory networks, such as the “gene batteries” that control cellular differentiation, which can be altered incrementally (through changes in sequence, timing, intensity, etc.) without disturbing other critical elements of the organism. This allows for morphological divergence in lower taxa notwithstanding the conservation of phyletic parameters themselves. This is not to understate the amount of morphological change that can occur within phyla and even within midrange Linnaean taxa: mammals, you will recall, “disparified” from a small-bodied, rodent-like critter in the Cretaceous to the wide range of mammalian forms and lifeways we see today. But the fundamental

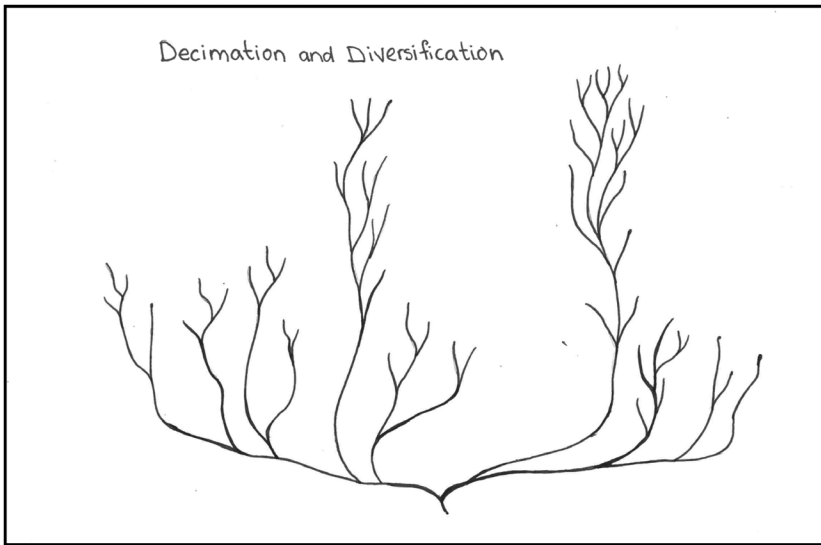
organization of the body plan remains the center of gravity for vertebrate evolution ever since it congealed in the Cambrian, much as it has for all other animal groups.

3.5 Decimation and Diversification

We can now import this thinking about the causal structure of development back into Gould's original reading of the Cambrian. The fantastical parade of forms that emerged during the Cambrian explosion was only possible because upstream developmental components had yet to be hooked up to downstream batteries of genes that guide more fine-grained structural differentiation. Once these terminal portions of the circuitry were in place, the kernels of surviving animal body plans were locked in, stabilized by selection, and buffered by canalized developmental systems to maintain the integrity of the phenotype. The development entrenchment of body plans ensured that the effects of stochastic or pseudo-stochastic patterns of extinction would be felt for the remainder of life's history. Once the initial crop of body plans had been culled, large regions of evolutionary possibility were rendered permanently off limits. Postextinction recovery and diversification would forever after be confined to the body plans of surviving higher taxa. The accidental Cambrian survivors became, in effect, frozen accidents.

This picture supports the "decimation-diversification" theory that Gould sketched in *Wonderful Life*.⁵⁴ According to that hypothesis, animal life began with only loose developmental constraints, and thus it had the potential for an explosive bout of body plan-level diversification that Gould called "disparification." The explosive evolution of body plans could only occur once the genetic regulatory innovations necessary to support the development of complex phenotypic structures were in place. However, once the various body plan parameters were laid down, they became recalcitrant to modification due to their cascading causal connections to downstream components of the phenotype. Little to no disparity is therefore added in subsequent phases of the history of animal life, even while lineages continue to diversify within their plans, increasing in lower-taxonomic richness. Over time, mass extinctions whittled down the breadth of morphospace occupation that was established in the Cambrian, eliminating some islands of form and leaving increasingly large and unbridgeable gaps between the remaining islands (see figure 2.4). Virtually all post-Cambrian disparification and diversification, so the theory goes, would take place *within* surviving body plans.

In effect, Gould is proposing a "non-uniformitarian" theory of macroevolutionary change. The term "uniformitarianism," coined by the English polymath William Whewell, holds roughly that the fundamental mechanisms, laws, and

**Figure 2.4**

Decimation-diversification pattern showing large gaps in extant morphospace occupation due to early extinction events. Redrawn from S. J. Gould, *Wonderful Life: The Burgess Shale and the Nature of History* (Norton, 1989).

processes that presently govern our world are the same as those that governed our world in the past. Conceived methodologically, uniformitarianism holds that we should proceed as if the metaphysical assumption of uniformity were true. This assumption, which rings of Copernicanism, may have served science well at times in the past. As Doug Erwin has noted, “a uniformitarian approach may have been politically necessary early in the history of evolutionary thought as a counterweight to various non-Darwinian approaches to evolution.”⁵⁵ But uniformitarianism should be treated as a working hypothesis, not a bedrock ontological or methodological commitment of any field of science. This is particularly so for biology, given the many empirical and theoretical reasons we have to doubt the uniformity of process and outcome in evolution (see chapter 1 for a discussion).

Studies of the fossil record, aided by quantitative analyses of morphological disparity developed by paleontologist Michael Foote and others, have more or less confirmed Gould’s suspicions about disparity, lending credence to the notion that macroevolution is not merely “scaled-up” or aggregated microevolutionary processes.⁵⁶ At a very coarse grain of description, biology is uniformitarian: the same forces and tendencies, such as selection, drift, and mutation, are in operation at all biological times and in all biological places. However, this glosses over more contentful processes and patterns that exhibit a

nonuniformitarian character, such as the evolution of morphological disparity. The present is not always a key to the past.

Current work on the geological and genetic fossil records of animals confirms that nearly all body plan–level characteristics—traits that are diagnostic of modern animal phyla—arose more than 500 million years ago, with subsequent morphological diversification occurring within, rather than among, those plans. Obstacles remain to the measurement of morphospace occupation, which make the decimation-diversification hypothesis difficult to test.⁵⁷ If the hypothesis is correct, however, it provides a formidable answer to the query with which we began the previous subsection: Why, in the intervening period between mass extinctions, does natural selection not return to globally optimal attractors in morphospace? Decimation-diversification is therefore both a signature of, and a plausible explanatory framework for, contingent dynamics at work in macroevolution.

Before moving on, it is worth underscoring a point about biological universality that is lurking in the background of this discussion. The constraints on body plan modifiability that are imposed by the causal geometry of development appear, on all counts, to be law-like. That is, they seem to be a general feature of the evolution of complex, multicellular life anywhere in the cosmos. Although Gould to my knowledge never made this point, if he is right, then it is due to universal features of biology that there are no specific laws of form, and the most we can infer about complex multicellular life elsewhere in the universe is that it will be as historically contingent as our own.

4. Two Empirical Critiques

How much of the evidence that Gould relied upon has withstood the test of time? We have already seen that Gould's core claims about the evolution of body plan disparity have been largely corroborated, as have his (and Lewontin's) perspicacious theories about the causal structure of development and the constraints it imposes on morphological evolution. Ditto for Gould's views on the dynamics of mass extinction and faunal turnovers. Other recent work in evolutionary biology, however, has begun to put pressure on various components of the RCT. We will take up what I think is the most formidable of these challenges—the critique from convergent evolution—after the concept of Gouldian contingency has been more systematically examined in the next chapter. Let us briefly consider here two current lines of criticism—one taxonomic and the other ecological—that take aim specifically at Gould's reading of the Cambrian fauna. Whether or not these criticisms are ultimately persuasive, they will help us to discern additional contours of Gould's thesis.

4.1 The Critique from Taxonomy

The first challenge to the RCT takes aim at Gould's taxonomic reading of the Burgess Shale. In *Wonderful Life*, Gould makes much of the fact that many of the Burgess Shale critters that had been "shoehorned" by their discoverer (paleontologist Charles Walcott) into familiar phyla were, upon closer examination by arthropod expert Harry Whittington and his team in the 1970s, determined not to fit neatly into any extant taxonomic groups. This classification conundrum led Gould to suppose that if *Opabinia* and its ilk had survived the Cambrian extinctions while chordates had perished—which seemed like an eminently plausible possibility—then the history of life would have taken a science fiction–like turn. Of course, to an observer emerging from any such alternative history of life, the sci-fi and the familiar would be reversed, and proto-vertebrates would be among the weird wonders whose reconstructed image would provoke laughter from an audience of five-eyed geologists.

In the light of modern cladistics, however, the Cambrian fauna are less recalcitrant to classification than Gould had believed. As paleontologist Graham Budd and his colleagues have convincingly shown, many of the seemingly bizarre Cambrian taxa that inspired the RCT can be recognized under modern phylogenetic classification systems as "stem" taxa—extinct basal lineages on the stems of crown groups.⁵⁸ "Crown" groups are the groups represented by extant phyla and all their ancestors, leading back to their common ancestor. The notion of stem and crown taxa were first introduced by paleontologist Richard Jefferies to little fanfare, only to be rejuvenated by Budd and his collaborators at the beginning of the new millennium.⁵⁹ Together, the stem and crown groups comprise a "pan" taxa, which includes the crown group and all extinct lineages that are more closely related to the crown group than to any other extant groups (see figure 2.5).

On this cladistic approach to phyletic classification, body plans are defined not in terms of broad morphological or developmental parameters but rather as "set[s] of features plesiomorphically [i.e., ancestrally] shared by extant taxa in a monophyletic clade."⁶⁰ There are two things to note about this definition. First, because it is neutral to taxonomic-level, "body plan" in this sense need not specify distinctive phyla-level traits; it could refer to ancestral similarities at any phylogenetic grain of description. Second, and as a result of this phylogenetic grain-neutrality, the cladistic conception of the body plan does little to convey the notion of developmental constraint that is so prominent in the traditional study of *Baupläne* (German (pl.), body plans) that influenced Gould's evolutionary thought. We will return to this point shortly.

Conceived cladistically, there is nothing about the origins of disparate body plans or their conservation that requires special explanation. The cladist can

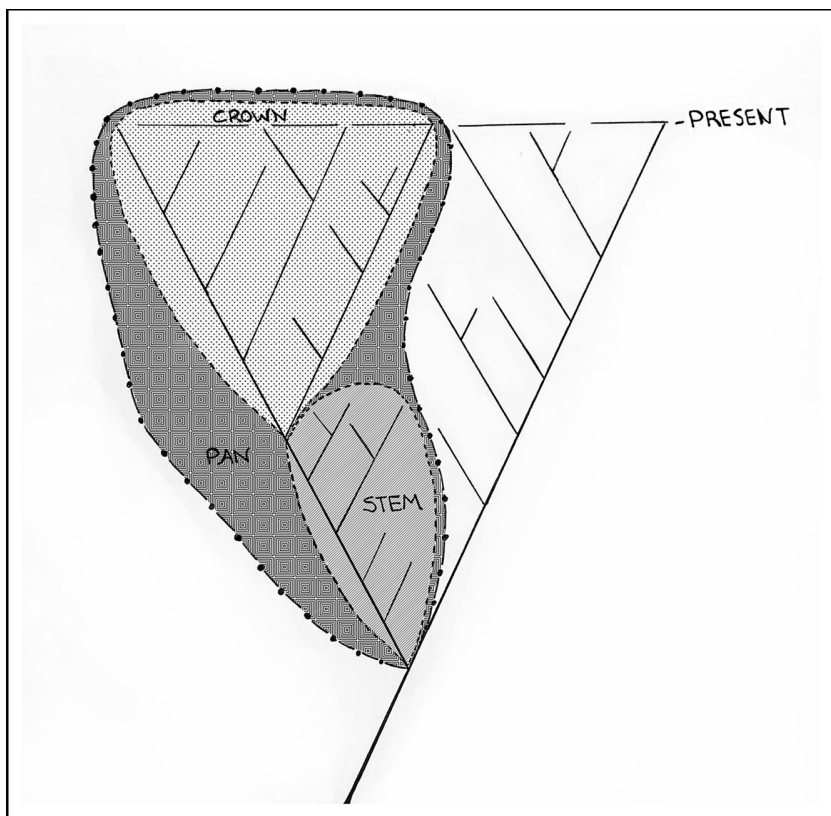


Figure 2.5

Illustration of the “stem taxa” concept in cladistic approaches to taxonomy, which can accommodate many of the Cambrian *Problematica* as members of the total (or pan) group that branched off before divergence of the crown group. Redrawn from R. P. S. Jefferies, “The Origin of Chordates—a Methodological Essay,” in *The Origin of Major Invertebrate Groups*, ed. M. R. House, 443–477 (Academic Press, 1979).

acknowledge that there are few representatives of modern body plans *sensu stricto* among the Cambrian fauna, but there is nothing anomalous about this fact—indeed, it is an expectable result of the structure of clade diversification. Once morphological disparity and phylogenetic affinities are decoupled in our system of classification—a feat that cladistics achieves—the taxonomic challenges of the early Cambrian can be “explained away” as an artifact of clade geometry and intuition-based approaches to classification that rely on subjectively chosen phenotypic traits. In essence, the stem/crown group formalization allows us to establish phylogenetic affinities of the Cambrian fauna before

true body plans emerged. What we call “phyla” actually originated deeper in evolutionary history than the crown group.

Opabinia and *Anomalocaris*, for instance, are in all probability stem arthropods, and part of panarthropoda, even if they lack the traditionally diagnostic features of the arthropod body plan such as a jointed exoskeleton and biramous limbs (though recent findings suggest that they did have compound eyes). There is no need to assign these lineages to their own phyla simply because they lack characters that are diagnostic of the modern arthropod body plan. Likewise, the famously bizarre *Hallucigenia* has been reinterpreted as a stem onychophoran (velvet worm), a group that is likely the sister taxa of [arthropods + tardigrades].⁶¹ The pan-phylum placement of other stem taxa, such as the wiwaxiids—which possess features of both polychaete worms (chitinous scales and spines) and mollusks (foot and radula)—remains unclear.⁶² The cladistic approach may illuminate some even larger phylogenetic puzzles in the origins of animals, such as the nebulous relation between the late Ediacaran fauna and the metazoans. It could suggest, for example, that the Ediacaran fauna constitutes a stem bilaterian lacking gastrulation and other diagnostic metazoan features.⁶³

Although Cambrian taxonomic challenges remain, the point is that with the concepts of stem and crown group at our disposal, there is no need to populate the early history of life with numerous, subjectively delineated phyla. Before body plans in their modern forms congealed in the later Cambrian, closely related lineages shared numerous features with one another even though they do not fit tidily into any modern groups. By decoupling phylogenetic affinities from body plans, cladistics allows us to construct a treelike picture of early animal diversification, crown and stems and all, before modern developmental organizations arose. No further evolutionary processes are needed, so the cladistic argument goes, to explain the putative Cambrian anomalies. And thus, one major pillar on which the RCT rests has been explained away by modern phylogenetic analysis. Taxonomic mystery solved. RCT refuted?

Not quite. *Wonderful Life* can still be a “homage to *Opabinia*” even if this creature and other oddballs of the Cambrian turn out to be stem taxa of familiar clades. Whereas Gould was fascinated by the *Problematica* because of their unique features and combinations, cladistic analysis ignores these unique features and instead uses shared derived characters to situate the Cambrian taxa unproblematically in relation to modern phyla. Yet in doing so, as philosopher Keynyn Brysse has pointed out, the cladistic reconstruction of Cambrian phylogeny simply bypasses the big theoretical questions that preoccupied Gould, such as in relation to patterns of morphological disparity and extinction and their implications for the contingent nature of macroevolution.⁶⁴ In essence, cladistics conceptually guts the *Bauplan*. This is a mere nominal victory, however,

because it leaves intact the key research questions that the Bauplan construct is designed to probe. The cladistic reinterpretation of the early Cambrian fauna solves a problem, but not the one that Gould had underscored.

Simply stated, cladistics is pursuing a different set of research questions than Gould was pursuing. Gould uses taxonomy as a proxy for morphospace occupation in exploring possible evolutionary worlds—an exercise that is orthogonal to the cladistics project. Gould's claims are not about taxonomy per se but about the traits that traditional taxonomy is intended to capture. Trilobites, anomalocarids, opabinids, and the like may all be diagnosable arthropods on the cladistic scheme, but there is no reason to think that the modern arthropod body plan (which includes a jointed exoskeleton and biramous limbs) was an inevitable or robustly replicable result of early arthropod evolution. The sheer dominance and diversity of arthropods in the Cambrian seas makes the survival of this clade into subsequent geological periods highly likely, but this does not mean that the distinctive characters of the arthropod body plan are themselves stable across possible Cambrian worlds.

The point is not simply that cladistics is concerned with establishing patterns of genealogy rather than the mechanisms or processes underlying those patterns. The point is that cladistics misses important patterns themselves. Recognizing this can help reconcile discord between molecular and fossil data about when major animal groups diverged. Crown groups, for example, appear to have diverged genetically as early as the end of the Ediacaran (about 545 million years ago), but this genetic divergence did not result in morphological innovations that reflect our modern range of animal phyla until later in the Cambrian. The same pattern is true, for example, of therian mammal diversification between the Cretaceous and Paleogene. This further underscores the importance of distinguishing taxonomic divergence from the morphological and ecological innovations that are relevant to Gouldian questions. In short, the cladistic reinterpretation of the Burgess Shale leaves the RCT unscathed. The fact that the Cambrian *Problematica* can be accommodated as stem taxa (rather than freestanding phyla) does no damage whatsoever to Gould's decimation-diversification hypothesis, to his claims about the developmental mechanisms that underwrite nonuniformitarian patterns of morphological evolution, or to his readings of mass extinction and faunal turnover.

This brings us to a point that has been glossed over in critical discussions of the RCT. Making this point requires telegraphing material that will be elaborated on in chapters to come, so I ask that the reader forgive the brevity of the treatment here. Let us assume, for the sake of argument, that the early Cambrian fauna did not reflect the broad range of forms that Gould believed them to. This would not, in fact, support the antithetical view of life, namely

the notion that macroevolutionary outcomes are robustly replicable. The reason for this is that the latter requires a “global” merit-based competition among early animal lineages—and such a competition could not have taken place if only a small, contingent subset of possible forms arose. It is not enough for selection to optimize body plans that did arise; if it is to achieve anything approaching global optimality, selection must cull functionally inferior plans from a wide assortment of alternative designs, many of which need to be vetted and eliminated by selection as doomed experiments in living. Thus, the lack of an early experimentation phase—especially when combined with the absence of later disparification—does little to refute the RCT.

4.2 The Critique from Paleocology

A second recent challenge is aimed at Gould’s ecological reading of the Burgess Shale fauna. Recall that the main metaphysical conclusion of Gould’s Cambrian thought experiment is that the shape of animal life is radically contingent. By this, he means that the actual distribution of body plans occupies only one of many equally functional configurations in a vast morphospace of evolutionary *possibilia*. Remember also that Gould drew this inference on the basis of an epistemic assertion: that no evolutionary-ecological handicapper worth her salt would have successfully predicted which lineages would survive the Cambrian extinctions. Although Gould was impressed by many of the Cambrian critters, he was particularly enamored of *Pikaia*, a close relative of the last common ancestor of all chordates, mainly for reasons of anthropocentric relevance: had *Pikaia* and other proto-chordates been eliminated in the luck of the draw, we—and perhaps nothing like us—would be here today.

At the time of Gould’s writing, *Pikaia* was portrayed as a relatively understated lineage that could easily have gotten lost in the blooming buzzing confusion of the Cambrian seas. Our knowledge of early Cambrian fauna at that time was limited to the Burgess Shale. Since that time, however, similar fossil lagerstätten have been found in the People’s Republic of China (and also in Greenland), including the now famous Chengjiang assemblage of the Maotianshan Shales. Like the Burgess Shale, the Chengjiang assemblage contains exquisitely preserved, non-mineralized (soft) tissues of Cambrian animals, including all the Burgess Shale groups in addition to many previously unknown lineages. The rich Chengjiang record confirms that the Burgess Shale biota was indeed a global fauna, and it strengthens the case for the geologically abrupt origin of animals—a fact that is not critical to the RCT, but which is often incorrectly thought to be. It also paints a fuller picture of the structure of Cambrian ecosystems, including the ecological role played by early chordates. Eight new candidate chordates have been discovered, includ-

ing possible 530-million-year-old craniates—chordates with a notochord and distinct head—such as *Myllokunmingia* and *Haikouichthys*.⁶⁵ Similar basal chordates have recently been found in newly uncovered deposits in the Canadian Rockies, such as in the Marble Canyon site of Kootenay National Park, which includes among its spectacular assemblage a primitive jawless fish with discernable tail and camera-type eye (*Metaspriggina*).⁶⁶

What are the implications of these findings for Gould's thesis? The first thing to note is that Gould's analysis of *Pikaia* and its implications for the contingency of vertebrate history do not rely on the claim that *Pikaia* was a *direct* ancestor of modern vertebrates—such that, had *Pikaia* gone extinct in the Cambrian, vertebrates would never have come to be. Gould was well aware of the incompleteness of the fossil record, especially of the earliest soft-bodied animals, and he no doubt presumed that *Pikaia* was not the lone proto-vertebrate lineage in the Cambrian. Nor does Gould's account rely on the claim that *Pikaia* and its ilk were ecologically *irrelevant*; the taxon's repeated preservation among Cambrian assemblages indicates that it was commonplace enough to be recorded in the fossil record, if comparatively less frequently than some other lineages. Instead, Gould's rhetorical use of *Pikaia* hinges only on the assertion that vertebrates were an *evolutionary undercard* in the Cambrian.

As Doug Erwin noted in his recent reevaluation of *Wonderful Life*,⁶⁷ new findings from the Canadian and Chinese assemblages show that basal chordates were in fact a more diverse clade, with a cosmopolitan distribution and a greater ecological presence, than the original Burgess Shale data led Gould to believe. Because prevalence is a significant determinant of survivorship in mass extinctions, the new Cambrian chordate data calls into question Gould's epistemic premise that no good evolutionary handicapper would have bet that chordates would go on to become a permanent fixture of the Phanerozoic Eon.

Even so, I do not see this adjustment to the subjective probability of early chordate elimination doing any real damage to the extinction component of the RCT. Erwin is right that it would not be unreasonable to bet on chordate survival in the Cambrian. Yet while geographical range and ecological significance are statistically relevant to the chances of survival, they are not decisive determinants of survival in the end-Cambrian or any other mass extinction. For as we have seen, many of the most diverse and dominant clades on Earth either perished or were permanently cut down in mass extinctions, paving the way for the rise of less prominent (if not ecologically negligible) clades.

The Cambrian extinctions culled lineages that were more prominent than basal chordates, including many of the critters that Gould conjectured could have been early nodes of alternative histories of life of Earth. The fact that *Pikaia* turns out to be part of a more diverse clade may make it more likely

that chordates survive into the Ordovician—but it does little to support a merit-based account of Cambrian survivorship. Gould’s point about contingency in faunal turnovers remains, even if chordates were not quite the “Cinderella taxa” that Gould imagined them to be. Once surviving Cambrian phyla underwent substantial diversification in the Paleozoic, it became unlikely that any would vanish entirely in a subsequent extinction event. Not so, however, for the weird wonders of the Cambrian, which lived during the most perilous time for body plans in the history of life.

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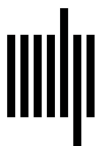
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