Gould's Laws

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Much of Stephen Jay Gould's legacy is dominated by his views on the contingency of evolutionary history expressed in his classic *Wonderful Life*. However, Gould also campaigned relentlessly for a "nomothetic" paleontology. How do these commitments hang together? I argue that Gould's conception of science and natural law combined with his commitment to contingency to produce an evolutionary science centered around the formulation of higher-level evolutionary laws.

1. Introduction. What could a science of evolution possibly look like if one were committed to the view that evolution does not repeat itself? Stephen Jay Gould wrestled with this question from his very first publication to his very last, which he concluded by embracing what he called the "paradoxical situation" to which his rich and varied evolutionary musings had inevitably led him (Gould 2002, 1338). His popular legacy, which he there acknowledged and endorsed, was that of champion of the uniqueness of the biological world and the high degree of contingency associated with the particular evolutionary endpoints that inhabit it. But he had also spent his entire professional career campaigning for a seat at evolutionary theory's "high table" for his own discipline of paleontology, a campaign whose success required—as it had for Darwin, Fisher, Wright, Hamilton, and the rest of the "grown-ups"—the formulation of general evolutionary laws (Maynard Smith 1984, 401). Thus, we have the following "paradox" (technically, just a prima facie inconsistent pair of commitments):

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a) Gould believed that the biological facts could have been otherwise (the "Replay Thesis");
b) Gould believed that there are evolutionary laws.

Owing in no small part to the excellent description, analysis, and extension of the Replay Thesis by John Beatty (Beatty 1995, 2006; Beatty and Desjardins 2009) and the vast literature it has inspired, we now have a deeper and more formal grasp of Gould's views on biological contingency and their significance. Little if any attention has been devoted to the positive, equally fervent views on evolutionary laws to which Gould appealed throughout his scientific career (a notable exception is Sepkoski 2012). This article aims to partially fill that gap in the record.

I argue below that Gould conceived of the science of evolution as a science of laws—distinctively evolutionary laws—and that these laws were/are seen as holding even though the biological facts that fascinate us most would have been otherwise were we to replay the tape of life. As I will show, Gould was well aware of the challenges that the Replay Thesis posed for a law-centered or "nomothetic" science of evolution. He endeavored to meet these challenges by shifting his lawmaking focus to higher-order phenomena for which the Replay Thesis did not apply—orders for which the "peculiarities of individual taxa" do not matter (Raup et al. 1973, 526). The direct result of Gould's higher-order evolutionary focus—a focus he shared with a small cadre of maverick paleontologists—was the emergence of the discipline of paleobiology and the establishment of three important ongoing research programs: (1) punctuated equilibrium, (2) diversity dynamics, and (3) the extinction of higher taxa. Each of these research programs avoids the pitfalls of the Replay Thesis by rising above the morphological cacophony at the species level to reveal a higher evolutionary order, and the latter two continue to drive much of the research in paleontology. Thus, the apparent inconsistency in the pair of statements above—Gould's "paradox"—is resolved: for Gould, evolutionary laws are higher-level laws that are not sensitive to the features of the evolutionary process that motivated his commitment to the Replay Thesis.

My argument proceeds in four steps. I begin (sec. 2) by documenting two critical and foundational features of Gould's philosophy of science: (1) his conception of science as a lawmaking enterprise, and (2) his conception of laws as spatiotemporally invariant generalizations. If he took these commitments seriously, they should have constrained his strategic response to the Replay Thesis in fairly predictable ways—namely, he should be expected to focus on features of the evolutionary process that are free from the projection-confounding properties of evolutionary contingency. The second step of the argument (sec. 3) confirms this prediction by tracing the course of development of Gould's thinking about how to confront the Replay Thesis nomothetically, a course that was paralleled independently by a number of other paleontologists working at the time.

Gould's nomothetic strategizing resulted in three distinct research programs, each of which managed the Replay Thesis in its own way. If, as Gould thought was the case, the success of an approach to evolutionary lawmaking is tied to its ability to accommodate the difficulties generated by the Replay Thesis, we should expect the degree of success achieved by these three research programs to track the different degrees to which a research program succeeds in accommodating those difficulties. As I show in section 4, the evidence in favor of this claim is persuasive.

What we will have shown at this point is that the nomological approach in evolutionary science looks precisely as Gould first envisioned it. Whether particular law statements generated by this science actually achieved the scientific goals outlined by Gould is another matter. In the final stage of my argument (sec. 5), I describe a couple of evolutionary laws that have grown out of the nomological approach pioneered by Gould and the other extraordinary paleontologists involved in what has recently been called the "Paleobiological Revolution" (Sepkoski 2012). As Gould had hoped, these laws, from all appearances, would not have been otherwise were we to replay the tape of life.

2. The Scientific Significance of Natural Law. Shortly after beginning his graduate training, Gould wrote a short article entitled "Is Uniformitarianism Necessary?," which addressed a particular conceptual confusion that had plagued the literature in geology for over a century. Published in 1965 in the *American Journal of Science*, the article pointed to two uses of the term "uniformitarianism" in the geological literature—one substantive, one methodological—that had often been pitted against one another in a senseless debate that simultaneously undermined scientific progress within geology and the image of geology within the sciences generally. Here he argued that *substantive uniformitarianism*, the empirical claim that the rates of geological change had been constant throughout history, "has not withstood the test of new data and can no longer be maintained in any strict manner" (Gould 1965, 226), a development that Gould attributed to the growing research program on mass extinction led by his thesis advisor Norman Newell and German paleontologist Otto Schindewolf. On the other hand, *methodological uniformitarianism*, the assumption that the laws of nature remain constant across time and space, "remains vital to geologic inquiry" (226).

The importance of methodological uniformitarianism for geology has its roots in Lyell, from whom Gould approvingly quotes the following:

> Our estimate indeed, of the value of all geological evidence, and the interest derived from the investigation of the earth's history, must depend

> entirely on the degree of confidence which we feel in regard to the permanency of the laws of nature. (Lyell 1830–33, 1:165; quoted in Gould 1965, 224)

He goes on to provide interpretation and defense, in what would come to be the first of many a dramatic flair:

> Once accepted, this uniformity ended the dichotomy between a contemporary world operating under constant and verifiable natural laws and a past incapable of purely scientific explanation. The entire geologic record, with all its evidence of vast upheaval and mass extinction, was, for the first time, integrated within the sphere of empirical investigation. (Gould 1965, 224)

What the assumption of nomic spatiotemporal invariance provides—what makes the scientifically impossible possible—is the warrant for projecting observed regularities to unexamined cases. But, argues Gould, there is nothing special about geology's commitment to methodological uniformitarianism. It is, after all, nothing more than "a statement of proper scientific procedure in general, independent of any particular substantive theory" (224):

> The assumption of spatial and temporal invariance of natural laws is by no means unique to geology since it amounts to a warrant for inductive inference which, as Bacon showed nearly four hundred years ago, is the basic mode of reasoning in empirical science. Without assuming this spatial and temporal invariance, we have no basis for extrapolating from the known to the unknown and, therefore, no way of reaching general conclusions from a finite number of observations. (226)

Another feature of methodological uniformitarianism, one that requires but is not grounded in the assumption of nomic spatiotemporal invariance, is the notion that "reference need only be made to presently-observable causes in explaining past changes" (227). This is, of course, the famous *vera causae* principle upon which Lyell had so heavily insisted. Thus, methodological uniformitarianism turns out to be the claim that all and only the known laws of nature are projectable. In Gould's words,

> Methodological uniformitarianism amounts to an affirmation of induction and simplicity. But since these principles belong to the modern definition of empirical science in general, uniformitarianism is subsumed in the simple statement: "geology is a science." But since we consider geology a science, this affirmation has already been made by definition. Saying it again is at best superfluous and at worst confusing since it leads to the inference that our science has a powerful and unique guiding principle all its own.

> The unity of procedural assumptions, which binds the empirical sciences together, should not be obscured by terminology specific to one discipline. (227)

For Gould (at least, in 1965), to be a science is to use laws of nature in order to project from examined cases to unexamined cases. In this respect, geology is just like any other science.

One arresting feature of Gould's essay is his interpretation of the phrase "geology is a science." Conceiving of science as projection to unobserved cases on the basis of spatiotemporally invariant laws implies certain things for how scientific work is to be undertaken. Since the paleontologist's scientific goal is to understand unobserved (because ancient) life, and since the only way to learn about unobserved cases is to use our knowledge of observed cases to make inferences about them, and since the only inferential mechanism capable of underwriting the application of present knowledge to unobserved cases is the assumption of nomic spatiotemporal invariance, it follows that the only way for the paleontologist to achieve his scientific goal is to reason on the basis of laws of nature. Now, some fossil phenomena (e.g., finely graduated, continuous morphological series) may be subsumable under known laws (e.g., Darwinian gradualism). In those cases, argues Gould, the methodological precept of simplicity bids that we appeal to those laws known to be operative. However, when fossil phenomena like great leaps across morphospace resist subsumption under known laws, the paleontologist's ability to do science depends on his ability to discover new laws of nature that can account for the recalcitrant fossil evidence. For Gould, then, fossil phenomena not subsumable under Darwinian gradualism translate into an opportunity—indeed, a mandate implied by the very definition of science itself—to discover the laws governing those phenomena.

The image of Stephen Jay Gould as a hard-core nomothetic scientist is not one with which most of us are familiar, nor indeed is it one that comports well with his popular persona as the progenitor of what is known in evolutionary biology and in the philosophy of science as the Evolutionary Contingency Thesis (after Beatty 1995). Given that this occurred at the earliest identifiable point in his scientific career and that his focus on contingency grew with his stature as a professional scientist, we might plausibly conclude that Gould gradually outgrew the nomothetic approach as his understanding of the evolutionary process matured (Sepkoski 2012, particularly chap. 10, endorses this view). That would suggest, at a minimum, that Gould's stress on nomothetic science and his stress on evolutionary contingency should be anticorrelated to some degree. But this prediction is not born out by the historical record. This 1965 expression of the nomothetic approach is the first in a career-long history of attempts to convert paleontology into a nomothetic discipline.

3. Gould between Contingency and Necessity

> There are nomothetic undertones to the results of evolution—the principle of natural selection is among them—and it is here that our laws must be formulated. They must be based on immanent processes that produce events, not on the events themselves. (Gould 1970a, 209)

Gould frequently lamented the narrow focus within paleontology on what he called "inductivism"—the view that describing fossils is as much science as a paleontologist need bother with. For interesting reasons to be described below, Gould saw this as an impediment to paleontology's ability to mature scientifically, not because describing the world is not science, but because it is not a reliable strategy for formulating laws.

Gould set out to cast the problem of inductivism in a new problematic light in his historical study of "Dollo's law," named for Swiss naturalist Louis Dollo (1857–1931). For us, the real value of this study lies not in what it tells us about Dollo but in what it tells us about Gould, for it is here that all of the notable streams of Gould's scientific thought come together: laws, contingency, anti-inductivism, hypothesis testing—each of them woven into an impressively coherent narrative that sheds significant light on Gould's philosophy of science, his scientific method, and the "paradoxical situation" to which he alludes in the final pages of *The Structure of Evolutionary Theory*. Gould (1970a) openly debates the question of how to reconcile the aims of science as he saw them in 1965 with undeniable nomothetic complications posed by contingency. Here, as in later years, the problem he faced was not one of whether to (1) approach science nomothetically or (2) acknowledge evolutionary contingency. The problem, rather, was how to do evolutionary science nomothetically given contingency, and it was a problem with which a number of other paleontologists were grappling at the time. If, as I have claimed, Gould continued to hold that to do science was to search for spatiotemporally invariant laws, we would expect to see this reflected in his understanding of how evolutionary contingency affects the search for evolutionary laws. As I show, this 1970 paper explicitly endorses a reconciliation strategy that maintains a commitment to nomic spatiotemporal invariance by searching for levels of biological organization that are insensitive to the sort of biological variation that had hampered paleontologists' lawmaking efforts. The same strategy was simultaneously and independently endorsed by several other leading paleontologists, whose efforts I describe at the end of this section.

The purpose of the essay titled "Dollo on Dollo's Law: Irreversibility and the Status of Evolutionary Laws" is to correct various misinterpretations of Dollo's claims concerning the irreversibility of evolution and then bring the correct interpretation to bear on the study of evolution. Dollo claimed that physical structures do not evolve more than once, a fact that he (channeled through Gould) attributed to the physical complexity of organisms. Given that each specific morphological change in a lineage is a very low probability event, the probability of the same structure evolving twice on a lineage is negligible. Thus, we have Dollo's law: morphological changes along a lineage are irreversible, and so "a whole organism never reverts completely to a prior phylogenetic stage" (Gould 1970a, 201). Here Gould argues that Dollo's law of the irreversibility of evolution was not an empirical generalization derived from the fossil record but rather a special case of the principle that

> when a phenomenon reaches a sufficient degree of complexity, requiring a sufficient number of independent steps for its realization, repetition becomes "absolutely unimaginable—there are too many other possibilities, the probability is nil." (Gould 1970a, 199)

Readers familiar with Gould's work on contingency will instantly recognize what Gould found important about Dollo's law, for it serves as the conceptual basis for his views about contingency of evolutionary history. Gould's favorite metaphor for the history of life was that of a "tape" that, if erased, rewound, and replayed, would thrust life in an entirely new direction, resulting in a different panoply of phenotypes. It is Dollo's law—the principle that Markov chains of complex events are not repeatable—that supports the evolutionary intuitions evoked by "replaying the tape of life."

But Gould saw the significance of Dollo's law as extending beyond its biological meaning. As he observed,

> Dollo's law is not an adjunct of evolutionary theory. It is a statement, framed in terms of animals and their evolution, of the nature of history; or, put another way, it is an affirmation of the historical nature of evolutionary events. (Gould 1970a, 208)

For Gould, this affirmation held implications for "the entire enterprise of lawmaking for phylogenetic results" and, consequently, for how a science of paleontology ought to look (209). Fossils record historical events, and history does not repeat itself. Each fossil records a highly improbable sequence of events that could have been otherwise—indeed, would have been otherwise—were we to "replay the tape of life." When we attempt to formulate laws on the basis of the physical features of particular fossils, we succeed only in describing what a bunch of historical accidents have in common. But there is nothing lawlike about the highly contingent phenotypic states recorded by the fossil record since, ex hypothesi, they could (would) have been otherwise. In effect, the truth of Dollo's law implies that an "enterprise of lawmaking for phenotypic results" is doomed to fail, since laws must describe states that could not have been otherwise, and Dollo's law implies that phenotypic states would have been otherwise. Here is Gould at his best:

> Simpson has distinguished immanent from configurational properties of the universe (the former as “the unchanging properties of matter and energy and the likewise unchanging processes and principles arising therefrom”; the latter as “the actual state of the universe or of any part of it at a given time”). Laws are framed for immanent properties: we are not interested in the melting behavior of a particular ice cube but in the properties of water in general. Physics rarely deals with the configurational; if its formal structure is lawlike, this is because it has excluded the configurational from its domain. The error made by reductionists who attempted to formulate laws for the results of evolution was that they assumed a similar focus for biology and physics. But biology often deals with the configurational and the search for so-called historical laws among such properties is not a fruitful endeavor. (Gould 1970b, 209)

The difference between physical science and biological science, as he saw it, was primarily a matter of “difference in emphasis,” and the emphasis within paleontology on “the configurational”—contingent evolutionary outcomes—had inhibited our ability to discover laws.

But if the laws are not to be found among the fossils, then where? His prescribed remedy was for our lawmaking efforts to be “based on the immanent processes that produce events, not on the events themselves” (209). And how are we supposed to do that, exactly? The emphasis on “the configurational” was, for Gould, a symptom of paleontology’s addiction to “inductivism,” a refusal to venture outside “the observational mode of traditional natural history” (Gould 1970a, 88). Consequently, he saw the success of lawmaking endeavors in paleontology as hinging on a shift away from an observational style of inquiry—describing fossils and the like—to an approach that focused on constructing models of evolutionary processes and using fossils to test those models. There is thus an impressively straight line from Gould’s embrace of the contingency of evolutionary results to his embrace of modeling as the most fruitful approach to paleontological inquiry.

Gould’s articulation of his vision for a higher-order evolutionary theory followed and was deeply influenced by the equilibrium approach to island biogeography that had recently been anointed by Robert MacArthur and E. O. Wilson (1963; see Sepkoski 2012, chap. 4). Famously, the MacArthur-Wilson model describes how the number of species on an island achieves an equilibrium value through the counterbalancing forces of migration and extinction alone, regardless of what is migrating and what is going extinct. The potential of this model for ameliorating the nomothetic challenges posed by the Replay Thesis was not lost on other paleontologists, who began mounting their own conceptually independent arguments for a nomothetic approach to paleontology that was unburdened by the quirks of individual species. Irrespective of Gould’s complaints about evolutionary noise, for example, his colleague Thomas Schopf's concern had been that species actually become biologically insignificant at larger timescales. Schopf contrasted two conceptions of "community" in biology: one according to which a community is merely a collection of particular species at a given point in history, the other according to which a community is a "general environment" that persists for millions of years and sees the appearance and disappearance of untold numbers of species. He called the latter conception the "equilibrium view" of biological communities and likened it to "a gas law in which the state of any particular molecule is immaterial to the general description of the behavior of the volume as a whole." In contrast to the historical view of communities, here "the particular history of species may be immaterial"—"in some important senses, every species is 'equally good'" (Schopf 1972, 12–13).

Adding to the case against species was the result, obtained by Leigh Van Valen in 1973, that a taxon's age has no effect on its probability of extinction. Here is how his argument works. Take any taxonomic group (say, a family). Calculate the longevity for each subgroup by measuring the distance in years from its historical origination time to its historical extinction time. Now plot each of these subgroup longevities starting at year "0," so that all subgroups exist at year "0" and no subgroups exist after the extinction of the longest-lived subgroup. The conventional expectation was that, as we get further and further away from year "0," we should see an increase in the percentage of subgroups that go extinct in a given time interval. This corresponds to the view that a taxon's probability of extinction increases with age: when taxa are young, their extinction probability is low, and so years nearer to "0" should see relatively small percentages of subgroups lost to extinction. As taxa get older, their extinction probability rises, and so subsequent years should see subgroups lost in relatively greater proportions. The extinction probability can thus be thought of as the "mortality rate" for a given age.

What Van Valen actually found was that the percentage of extinctions per unit age remained constant across ages within a group—for all groups examined. If the frequency distribution of extinction events is the same for all ages, then each age has the same mortality rate. Thus, the probability of extinction does not vary with age. With respect to taxon age, then, extinction is "a randomly acting process" (Van Valen 1973, 17). (An analogous situation would be a case where we found that the human mortality rate was the same for all ages. If the probability of dying is the same no matter how old one is, then death does not discriminate between ages [although it might still discriminate based on other factors, such as diet].)

This result added a critical empirical dimension to the philosophical campaign against species. By showing that extinction actually was a randomly acting process in a very surprising and important respect, Leigh Van Valen had proven that there was more to the move to higher levels of evolutionary analysis than a mere shift in perspective (a la Schopf) or the in-principle recognition that species do not record evolutionary generalities—that, in fact, the Reaper just does not care how long a species is around. Now, this did not show that extinction was totally random, or anything close to that. But what it suggested was that extinction was random along a dimension in which we expected it on Darwinian grounds to be highly discriminatory.

There were also arguments against the focus on species that were purely methodological, making no reference to their importance or visibility to the evolutionary process. Rather, the worries raised here concerned the abysmal state of the fossil record for species. For example, by 1972, David Raup could already claim that

> there is no disagreement on the proposition that the number of taxa known from the fossil record is less than the number that actually lived. This stems simply from the fact that some taxa (particularly at the species level) are rarely or never preserved. (Raup 1972, 1067)

Even if species were the most appropriate unit of evolutionary analysis, and even if we had (contra Van Valen) no reason to think that evolution ignored some particularly salient species properties, the species level was still a poor choice for studying evolution through the fossil record. Since everyone agrees that the species record is woefully incomplete, we have no choice but to base our inferences on the fossil record for higher taxa (specifically families, orders, and genera).

Within a few years of the Van Valen results, J. John “Jack” Sepkoski Jr. would publish the results of a computer simulation that indicated that the incompleteness of the species record was really nothing to worry about. While acknowledging that the claims about species diversity “ideally should be tested with data on species themselves,” Sepkoski went on to demonstrate that inferences from patterns exhibited by higher taxa to patterns exhibited by species would generally be valid, in the sense that higher taxonomic diversity patterns could be expected to reflect diversity patterns at the species level. Thus, although a reliable direct measurement of species diversity was, “as is well known, . . . rarely possible in paleontology,” it was also not necessary (Sepkoski 1978, 237). We could learn whatever we wanted to learn about diversity over time from the study of patterns at higher taxonomic levels.

By 1978, then, paleontologists could point to a whole litany of higher-order insights, each of which would have been by itself sufficient to warrant an exclusive focus on higher taxa. For Gould, if paleontology was to be a science, it would need to discover evolutionary laws, and there are no evolutionary laws at the species level. For Schopf, paleontology was a science of evolution on large timescales, scales at which the idiosyncrasies of individual species do not matter. For Raup and Sepkoski (respectively), paleontologists' ability to sample the species record was neither sufficient nor necessary for understanding the evolutionary history of biodiversity. Add to this the fact that species extinction and species adaptedness did not appear to relate to each other in precisely the manner we would have expected, and we have a complete argument for an approach to solving evolutionary problems posed by the fossil record that treats "species as particles"—one that could be articulated along philosophical (Gould), theoretical (Gould), metaphysical (Schopf), evidentiary (Raup), methodological (Raup and Sepkoski), and epistemic (Sepkoski) grounds.

The suite of independent arguments for a shift to generating laws above the species level strongly suggests that Gould's views about the necessity of nomothetic science and the spatiotemporally invariant character of natural law were widely shared across the discipline. While each argument presents its own justification for moving beyond species, at bottom the basic motivation to move beyond species originated out of the need to reconcile the nomothetic demands of science with evolutionary contingency. Because of the pervasiveness of this sentiment, a variety of nomothetic research programs began to emerge, each with the aim of inoculating paleontology against the "rule-breaking capabilities of evolutionary change" (Beatty 1995, 51). This trend continues to the present day (Jablonski 2009).

4. The Comparative Success of Gould's Nomothetic Research Programs.

In this section I survey three programmatic instantiations of Gould's evolutionary lawmaking strategy. Each of these research programs was a self-conscious attempt by Gould to introduce a way of doing paleontology that would allow researchers to partake of the bountiful scientific yield that was characteristic of a law-centered approach to scientific inquiry. Some were more successful than others, and I argue below that their success is positively correlated with the degree to which they avoided the disturbing effects of the Replay Thesis.

4.1. The Science of Form.

The first of these attempts was the "science of form," Gould's early adaptationist effort to bring quantitative modeling to paleontology. The initial idea had been to use the power function $y = bx^k$ as a constraint on what sorts of morphological changes we could expect to see along a lineage. Since many physiological functions require a constant surface area–to–volume (A/V) ratio, we should expect natural selection to favor morphological changes that preserve this ratio at the cost of changes in shape, rather than favoring preservation of prevailing body shape at the cost of changes in A/V ratio (Gould 1966). Gould would later expand the science of form beyond allometry to cover all of evolutionary morphology; the power function was, after all, just one way of generating quantitative predictions for morphology. The broader strategy (outlined by Rudwick 1964) was to identify evolutionary functions that could then be subject to optimality modeling, ultimately resulting in predictions for what sorts of structures we should expect to see if those structures were designed by natural selection for performing the identified functions.

Had it been successful, the optimality approach would have allowed paleontologists to ignore species peculiarities by highlighting those of their features that we should expect purely from the optimizing process. These are the features that we should expect to see across repeated replays of the tape of life because they are rendered highly probable by the evolutionary process itself, regardless of what it is that's evolving. Thus, all the family baggage that a species brings to the evolutionary process is revealed in the form of deviations from certain optima. In the ideal case, the case I believe Gould envisioned as the mature version of the science of form, optimality modeling would succeed in turning the study of morphology into the study of optimized structures. In Gould's words, "idealized models are favored over actual specimens," a methodological shift that was supposed to make it possible to study generalized features of the selective process by ignoring "configurational properties"—contingent events in the history of life on earth that ultimately tell us nothing about how evolutionary systems operate in and of themselves (Gould 1970a, 209; 1970b, 77). The morphological peculiarities of individual taxa (i.e., actual specimens) are rendered explanatorily superfluous because they, unlike idealized models, are highly imperfect representations of the effects of general evolutionary processes. We learn more about evolution by abstracting from those peculiarities, that is, by treating species as particles subject to certain (evolutionary) pressures.

This, anyway, had been Gould's initial motivation for pursuing the science of form as an opportunity to formulate higher-level evolutionary laws. However, by 1980, he had pronounced the program effectively dead, citing a number of problems that led to its demise. One problem was the fact that designing the quantitative optimality model against which to test an evolutionary function hypothesis required "specifying function a priori," and that is very difficult to do (Gould 1980, 102). In addition, the research program seemed in his estimation simply to restate the obvious fact that "animals tend to be well-designed" (102).

The deeper reason for the program's demise can be related directly to the Replay Thesis and its important foundational role in the critique of adaptationism. The mistaken presupposition of the science of form was that history posed no impediment to phyletic optimization: that (1) the right variants could always be expected to arise, (2) the strength of natural selection's optimizing power made the historical order in which variants arise irrelevant, and (3) adaptive optima are sparse, timeless, objective points in morphospace—quite generally, the only thing that mattered for a lineage's evolutionary trajectory was its one true adaptive optimum. The success of the science of form as a program capable of generating evolutionary laws depended on the irrelevance of history, on morphological structures turning out the same on each replay of the tape of life. But by the mid-1970s Gould could clearly see how important history was for phyletic evolution and, consequently, for the prospects of adaptationism. Indeed, this mistake had been so obvious in hindsight that Gould amusingly suggested in *The Structure of Evolutionary Theory* that one of his early publications on the science of form, which he described as "a ringing paean to selectionist absolutism" that endeavored to "prove panadaptationism even for fossils that could not be run through the hoops of actual experiments," be "wipe[d] . . . of the face of the earth and out of all memory" (Gould 2002, 41).

4.2. Punctuated Equilibrium. Gould's most well-known campaign for the importance of distinctively paleontological contributions to evolutionary theory came in the form of his promotion of the theory of punctuated equilibrium. In brief, this theory argued that the geological column's record of sudden leaps across morphospace followed by long-term stability reflects the operation of allopatric speciation, and that this was in fact how most evolutionary change occurs: if allopatry is the dominant mode of speciation, and speciation is followed only by long-term stasis, then evolutionary change only occurs when allopatric speciation occurs (Eldredge and Gould 1972; Gould and Eldredge 1977).

The punctuated equilibrium saga represents another, reasonably more mature attempt to understand evolution "by constructing a model that makes no reference to the peculiarities of individual taxa" (Raup et al. 1973, 526). Like the science of form, the theory of punctuated equilibrium was intended to describe a general feature of the evolutionary process that was insensitive to differences at the species level. Consider the following: if allopatric speciation is where species come from in general, then species peculiarities clearly cannot matter to how speciation generally works. If we are to expect species to arise via allopatry in this way no matter what they are like, and if allopatric speciation necessarily involves rapid evolutionary change following long-term stasis (as Eldredge and Gould thought it did), then none of a species' peculiarities matter a jot to whether it will evolve via allopatry followed by long-term stasis. The presence of the species-as-particles perspective here is unavoidable: general theories of speciation apply to all species, regardless of what is biologically distinctive about them. (At least) one thing they all have in common is that they are species.

Gould, of course, never wavered in his esteem for punctuated equilibrium, and it continues to be an important idea in paleontology. But it is now widely recognized that punctuated change is not the only kind of evolutionary change that occurs, not least because speciation is not the only opportunity for evolutionary change to occur. Other evolutionary mechanisms, like directional selection and random walk, can produce consistent, measurable phenotypic change. Now, speciation remains a plausible explanation for punctuated change when punctuated change occurs. In that, it retains some of the basis for Gould's original enthusiasm: plausibly, when punctuated change occurs, the process by which it occurs is insensitive to the idiosyncrasies of particular species. Therefore, the general shape of punctuated evolutionary change would look the same, were we to replay the tape of life (see, e.g., Futuyma 1987; Eldredge et al. 2005). However, punctuated change is now seen as one of a variety of types of evolutionary change, and there is no reason to think that the lineages that have undergone punctuated change during this run of the tape of life would do so on replay (mutatis mutandis for lineages that have not undergone punctuated change). Again, as with the science of form, the degree of success achieved by punctuated equilibrium as a research program is explicable in terms of the degree to which it describes an evolutionary process that is not endangered by the Replay Thesis.

4.3. The Marine Biological Laboratory Simulations. The Marine Biological Laboratory (MBL) project of the mid-1970s was an effort to generalize the species-as-particles approach by stepping away from particular kinds of fossil patterns and asking what, in general, the fossil record would look like if species actually were evolutionary particles—i.e., if the evolutionary forces responsible for producing the fossil record did not discriminate between lower-level taxa. As they described their mission,

> We are convinced that sequences of unique historical events have strong general components (regulated by laws that are independent of time, space and taxonomic group)—and that it is the (heretofore neglected) task of paleontology to discover them (not by induction from empirical catalogues, but by attempts to model results with relatively simple systems). (Raup and Gould 1974, 321–22)

To accomplish this task, the MBL group (consisting of Raup, Gould, Schopf, Simberloff, and Sepkoski) had a computer simulate the kinds of patterns that would be generated if lineages had an equal probability of surviving, going extinct, or branching at all times. To the astonishment of the group's members, the simulations were able to reproduce most of the evolutionary-significant fossil phenomena. In some cases, the MBL group took the simulations' ability to reproduce these phenomena as evidence that a demonstration of natural selection from the fossil record required more than merely pointing to differences in clade shape—for these differences could be generated merely through chance. At other times, the MBL group adopted a stronger interpretation of the results, suggesting that the reason the simulations looked so much like the actual fossil record was because species peculiarities actually were invisible to the evolutionary process.

Most critically, the species-as-particles approach allowed MBL to make predictions about "the shape of evolution" that could not have been made with population genetic theory. Whether or not these predictions turned out to be true, the mere ability to make them would have established the species-as-particles approach as both a source of new evolutionary problems—a new strategy for suggesting and identifying genuine evolutionary phenomena that population genetics was powerless to explain—and a unique form of solution to those problems, one that could legitimately claim explanatory hegemony over a particular domain of biological facts. Under the kind of paleontology suggested by the MBL project, the solutions to those evolutionary problems—old as well as new—would take the form of genuine laws of nature that operate "independent of time, space and taxonomic group." Because of their freedom from the "peculiarities of individual taxa" (not to mention the ever-burdensome time and space), these laws would describe evolutionary processes that were thoroughly insensitive to the contingency inherent to the phenotypic level.

To the extent that the MBL research program can be characterized as an approach to evolution that searches for patterns and processes that are "independent of time, space and taxonomic group," the spirit of MBL pervades today's theoretical paleontology. If we follow Gould's argument for how to reconcile a science of paleontology with the Replay Thesis, this development should not be surprising. The key difference between the truly revolutionary MBL-style models and the more measured success of punctuated equilibrium is that MBL-style approaches are designed to rule out contingency from the start. When these models produce results that fit fossil trends, there is warrant for inferring that those trends were produced by general evolutionary processes, processes that would appear again and again no matter how many times we replay the tape of life. In this way, the taxon-neutral MBL approach exemplifies the sort of Replay-resistant lawmaking strategy envisioned by Gould in the early 1970s.

5. The Nomothetics of Extinction and Diversity. By 1985, Gould could (and did) triumphantly and correctly claim that paleontologists had "affirmed the theoretical independence of [their] discipline" (Gould 1985), a view that he shared with population geneticist John Maynard Smith (1984). In addition, both men recognized the pivotal role of extinction studies in particular in making this claim credible. Given the close temporal association between major extinction events and major increases in biodiversity, extinction studies naturally raised allied questions regarding how extinction causally relates to diversity. I conclude my argument for the claim that Gould's conception of evolutionary science results in laws that hold independently of time, space, and taxonomic group by describing the theoretical work on extinction and diversity that he praises in the final pages of *The Structure of Evolutionary Theory*. I then show how this work exemplifies Gould's Replay-proof ideal for evolutionary science.

To understand and appreciate the triumph of paleontology in these areas, we must first reacquaint ourselves with the Darwinian model of extinction, which dominated evolutionary thinking from 1859 until it was overturned by paleontologists in the 1970s, particularly through the work of David Raup. The model of extinction presented by Darwin in *On the Origin of Species* (1859/1962) is one in which progressively more adapted forms drive their parent forms to extinction as the lineage approaches perfection, with this process occurring both within and between evolutionary groups. The particular process described by Darwin is regarded as progressive because it favors organisms that outcompete others with respect to achieving some goal made relevant by the "conditions of existence," that is, by the normal environment to which they are adapted. As long as nature does not move the goalposts too quickly, a lineage can by this process improve its degree of adaptedness in its environment. On this view, the peculiarities of individual taxa are highly significant, because it is a taxon's peculiarities that determine the degree of fit with its environment, which in turn determines the probability that the taxon will be represented in the next generation. As nature patiently favors some peculiarities over others, eventually all but the most perfect will be filtered out of the population.

The problem for this model is the nature of higher-taxon death during mass extinction. While Darwin's understanding of how extinction works might be extended to explain the death of higher taxa for isolated cases, the pattern of extinction that characterizes mass extinctions—the simultaneous death of many higher taxa—is not within its reach. But the modern acceptance of evolutionary catastrophes in the history of life—something to which Darwin was philosophically opposed—has made the explanation of this phenomenon much easier, and theoretical research on higher-taxon extinction and origination has dominated the paleobiological literature since shortly after that time. Raup had begun articulating alternative models in the late 1970s and was in possession of a plausible mass extinction mechanism by the mid-1980s. In place of the competitive extinction model, Raup proposed a mechanism for killing lots of higher taxa all at once that is triggered by the sort of dramatic environmental perturbation that preceded the dinosaur extinction. Under this scenario, the peculiarities of individual taxa still matter, but not because of their degree of fit with the environment to which a taxon is adapted. This would be a case where the environment changes radically over a short period of time, thus changing, perhaps equally radically, which peculiarities are favored in that area. The shift in the sorts of peculiarities that are favored will be associated with a corresponding shift in the direction in which adaptive progress proceeds. Whereas in times prior natural selection was pushing a particular taxon toward more and more improved versions of one peculiarity, after the environmental perturbation this same taxon will find itself being driven toward better versions of some other peculiarity. Because the environmental change occurs so rapidly, those previously at the top of the heap might suddenly find themselves hopelessly maladapted to the new conditions, with extinction right around the corner. The relevance of competition to extinction here is marginal at best. Those organisms that are caught off guard by catastrophic environmental change would be ill-fated even with infinite resources available to them (Raup 1991 is particularly helpful on this topic). Raup dubbed this mode of extinction "wanton extinction."

This rapid transition to "different rules" (to put it in Gould's terms) for adaptedness is the only widely accepted explanation for the simultaneous extinction of lots of higher taxa that occurs during mass extinction, and in Gould's estimation it exemplified the most important contribution to date that paleontology had made to general evolutionary theory:

> The influence of the "different rules" model in helping to explain the waxing and waning of taxa in macroevolution represents the most interesting and far-reaching modification of Darwinian expectations unleashed by catastrophism's renewed respectability, and by the resulting inadequacy of uniformitarian extrapolation from Darwinian microevolution to supply a full explanation for the causes of pattern in life's history. (Gould 2002, 1317)

Any history of life that contained the simultaneous death of higher taxa would, according to this model, have to include a rapid shift in the rules for adaptedness.

This result naturally leads to the search for what David Jablonski calls "general survivorship rules," as well as for generalities in the ensuing diversity dynamics. Since the 1980s (Jablonski 1986), Jablonski has argued persuasively for the principle that a clade's having a broad geographic range increases its probability of surviving a mass extinction—a fact that holds regardless of the breadth of constituent species' geographic ranges. (Call this principle "Jablonski's law.")

Since mass extinctions favor the breadth of a clade's geographic range, not the adaptedness of its constituent species, it is probable that

> even well-established clades and adaptations could be lost during these episodes, simply because they were not associated with the features that enhanced survivorship during these unusual and geologically brief events. (Jablosnki 2005, 197)

The tendency of mass extinction events to deny exceedingly well adapted species the preferential evolutionary treatment to which they have grown accustomed during background times has the effect of leveling the adaptive topography in a region, allowing for the “subsequent diversification of formerly marginal taxa” (197).

Gould was clearly enamored of Jablonski’s law, represented by his thorough explication of it and by his taking multiple opportunities to counterpose it to Darwinian expectations. “These generalities,” he remarked, “enter the corpus of macroevolutionary theory” and “must play a major role in the most general patterning of life’s history” (Gould 2002, 1319). Jablonski’s law is a nice example of the sort of law that Gould must have imagined would characterize a future paleontology, one that describes a general feature of the evolutionary process, brutally insensitive to the phenotypic properties: no matter how many times we replay the tape of life, clades with large geographic range always have a better chance of surviving a mass extinction. At the same time, it countenances the Replay Thesis’s implication that, even though wide-ranging clades always do better when we replay the tape of life, those clades may be composed of entirely different species for each replay.

6. Conclusion.

The strategy behind Gould’s early shift to the species-as-particles approach captures the essence of the lawmaking enterprise, in biology and beyond: if individual differences among entities at one level are hampering your ability to formulate laws at that level, shift to another level.[1] Treat the sets of those entities as ensembles, and then see whether anything general can be said about the behavior of those ensembles. Just as any lineage proceeds along a highly contingent trajectory in morphospace, so too does each molecule in a gas travel along a path that could have been otherwise—indeed, would have been otherwise; knocking an individual molecule off of its current path requires far less than shifting the local evolutionary optima. Like the way in which we approach the study of molecules in a gas, the key to understanding the behavior of evolutionary ensembles such as populations and species is to see what the group-level properties of the ensembles tell us about their projected long-term states. Many of the group-level properties that allow us to make interesting long-term projections about these evolutionary ensembles may themselves fail to qualify as biological enough for Beatty’s (and others’) tastes. But if these properties are what allow us to understand evolution, then we will need to either revise our sense of what it is for something to be *biological* or give up the notion that evolution is a distinctively biological phenomenon. Perhaps what the species-as-particles

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[1] Morrison (2007) explains how early twentieth-century population geneticists were motivated by the tension between the scientific goal of nomic generalization and the biological fact of impracticable variation.

approach reveals, in much the same way that population genetics (or, for that matter, Darwin) revealed, is that much of life itself may not be all that biological.

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