# REPLAYING LIFE'S TAPE*

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It might seem self-evident that evolutionary biology is an "historical" discipline. But in the mid-to-late nineteen seventies and early eighties, a number of evolutionary biologists began to argue that the field was lacking historical perspective.[1] Among the most outspoken proponents of this view was Stephen Gould, for whom taking history seriously meant—above all—taking "contingency" seriously. As he reflected in his book *Wonderful Life*, ". . . the essence of history. Its name is contingency . . . ."[2]

To explain what he meant, Gould offered a thought experiment:

> I call this experiment "replaying life's tape." You press the rewind button and, making sure you thoroughly erase everything that actually happened, go back to any time and place in the past . . . . Then let the tape run again and see if the repetition looks at all like the original (WL, p. 48).

His expectation was that, "any replay of the tape would lead evolution down a pathway radically different from the road actually taken" (WL, p. 51).

In this paper, I will examine Gould's thesis in connection with two interestingly different attempts to test it: 1) Jonathan Losos et al., "Contingency and Determinism in Replicated Adaptive Radiations of Island Lizards," and 2) Michael Travisano et al., "Experimental Tests of the Roles of Adaptation, Chance, and History in Evolution."[3] The first is based on a macroevolutionary, "natural experiment." The second is based on a laboratory-controlled, microevolutionary experiment. There many other interesting studies that bear on Gould's views.

I have chosen to focus on these two because they explicitly address Gould's claims, and because they are very often cited in this regard (see the Appendix for a guide to the literature).

Another reason for discussing these two studies is that they are based on different interpretations of Gould's views. And yet, as I will argue, both interpretations are fair. That is, Gould—seemingly inadvertently—articulated two quite different notions of historical contingency.

To begin, I will briefly introduce and contrast the two versions of contingency that Gould articulates in *Wonderful Life*. Then I will discuss the two versions in detail in order to show more clearly how they differ, and also in order to show that they can be seen as *complementary* rather than competing accounts of contingency. For example, they play complementary roles in Gould's critique of the all-sufficiency of selectionist reasoning in evolutionary biology.

Next, I will discuss the Losos et al. and Travisano et al. studies, and how they bear upon the two versions of contingency.

Finally, in my conclusion, I will briefly suggest an additional way of reconciling Gould's two versions of contingency (i.e., in addition to stressing the complementary roles that they play in his critique of selectionist reasoning), namely, by viewing them as complementary components of narrative explanation—a form of explanation very common in history.

## I. TWO VERSIONS OF CONTINGENCY

Recall Gould's thought experiment:

> You press the rewind button and . . . go back to any time and place in the past . . . . [A]ny [such] replay of the tape would lead evolution down a pathway radically different from the road actually taken.

I will call this the "unpredictability" notion of contingency. It figures prominently in *Wonderful Life*. But if that is what contingency is all about, then it is difficult to see why Gould drew so much inspiration from the Frank Capra movie from which he took his title (WL, pp. 287-289). In the film, *It's a Wonderful Life*, George Bailey's guardian angel, Clarence, shows the despondent George what an important difference he had made in so many people's lives, by letting him see how sad life in Bedford Falls would have been without him. This is not replaying the tape of life in Bedford Falls from the same point in the past, however; this is replaying the tape from a very different point—without George! The difference that George made is not really captured by the unpredictability interpretation of contingency; it is much better captured by another version of contingency that Gould articulates. I will call this the "causal-dependence" version:

> Historical explanations take the form of narrative: E, the phenomenon to be explained, arose because D came before, preceded by C, B, and A. If any of these earlier stages had not occurred, or had transpired in a different way, then E would not exist (or would be present in a substantially altered form, E´, requiring a different explanation). Thus, E makes sense and can be explained rigorously as the outcome of A through D. . . .
>
> I am not speaking of randomness . . . , but of the central principle of all history—*contingency* . . . . A historical explanation [rests] on an unpredictable sequence of antecedent states, where any major change in any step of the sequence would have altered the final result. This final result is therefore dependent, or contingent, upon everything that came before—the unerasable and determining signature of history. (WL, p. 283)[4]

On the face of it, this would seem a very different version of contingency. On the first version, we get different, unpredictable outcomes from the same or indistinguishable prior states (Fig. 1, left).

[insert Fig. 1 around here]

Which might sound somewhat mysterious. Whereas on the second version, the particular outcome depends strongly on which particular states preceded it (Fig. 1, right). Different prior states lead to different outcomes. Which might sound somewhat trivial.

Another way of putting the difference is that on the unpredictability version, the occurrence of a particular prior state is *insufficient* to bring about a particular outcome, whereas on the causal-dependence version, the occurrence of a particular prior state is *necessary* (or strongly necessary) to bring about a particular outcome. (Yet another way of putting the difference is to note that these two versions correspond to the two colloquial uses of the term "contingent"—"contingent *per se*," and "contingent upon"—the former indicating unpredictability, and the latter causal dependence.)

These two versions of historical contingency are clearly compatible. We might even think of them as complementary components of a combined interpretation, according to which:

> a historically contingent sequence of events is one in which the prior states are *necessary* or strongly necessary (causal-dependence version), *but insufficient* (unpredictability version) to bring about the outcome.

Such a combined notion of contingency figures prominently in the literature of philosophy of history and historiography. Gould, himself an accomplished historian and philosopher of history, frequently alluded to this by referring to "historical explanation" and "historical narrative" (e.g., in the previous quotation). He might profitably have drawn more on

this literature in clarifying his position; but he did not. I will discuss his views in connection with this literature briefly in my conclusion.

In addition to the complementary roles that these notions of contingency play in philosophy of history, they also play complementary roles in Gould's critique of the all-sufficiency of selectionist reasoning, to which I will turn shortly. But the best way to make sense of their roles in Gould's critique of pan-selectionism is to continue to consider them separately. For, as I will explain, Gould presents two different critiques of selectionism, corresponding to the two versions of contingency. This way of proceeding is also useful when considering subsequent tests of Gould's views, which are sometimes aimed at one, and sometimes at the other version or component of contingency. So I will back up and consider each version and its bearing on selectionist thinking in greater detail, beginning with the unpredictability notion.

## II. THE UNPREDICTABILITY VERSION OF HISTORICAL CONTINGENCY

Gould first raised the possibility of replaying life and getting different outcomes from the same starting point as a way of understanding why, of many diverse multicellular animals that arose in the early Cambrian period (570 mya), only a small number persisted during the apparent mass extinction that followed. Why those few? Why, for instance, did *Pikaia*—the first known chordate and possibly an ancestor of vertebrates, including humans—persist, rather than *Opabinia*, *Wiwaxia*, *Hallucigenia*, *Anomalocaris* or so many of the other wonderful but extinct forms preserved in the Burgess Shale?[5]

One possibility is that the winners (including our ancestors) were much better adapted to their environments. Indeed, they were so much better adapted, that if we could put all the same Cambrian ancestors back into the same Cambrian environments, we would get the same winners over and over.

Another possibility is that the decimation that followed the Cambrian explosion was more like a "lottery" among forms that were equally well, if differently, adapted, and hence had equal chances of survival (WL, pp. 50, 239). In this case, if we replayed the tape we might end up with descendants of *Opabinia*, *Wiwaxia*, *Hallucigenia* or *Anomalocaris* instead, and perhaps *we* wouldn't be around to watch the tape play out.[6]

Generalizing, when Gould speaks of replaying the tape, with the unpredictability version of contingency in mind, he imagines what would be the evolutionary outcomes if initially indistinguishable ancestors were placed in indistinguishable environments (presumably, if the environments change, they would change at the same times and in the same ways). To the extent that natural selection within a particular environment is sufficient to determine which forms prevail, then under these circumstances, the same outcomes would prevail over and over. In denying that the same outcomes will result, Gould is not suggesting that the outcomes are inexplicable. Rather, he is denying that selection alone is sufficient to guarantee one particular outcome. Some other factors that distinguish the lineages or groups of lineages must be responsible.

What other factors? Gould did not, to the best of my knowledge, offer a systematic account of the sorts of factors that would lead to different evolutionary outcomes given initially indistinguishable ancestral lineages and indistinguishable environments. But he did emphasize one important class of factors that I would like to discuss briefly. And then I will also briefly discuss another class of factors that one might think he had in mind (especially given the Burgess Shale example), but that he explicitly excluded from the category of "historically contingent" factors.

In his discussions of contingency in the unpredictability sense, Gould often invoked Charles Darwin's distinction between what is predictable about evolutionary outcomes on the

basis of general laws, and the unpredictable "details . . . [which are] left to the working out of what we may call chance."[7] What is predictable, from Darwin's point of view, is that evolution by natural selection will result in well-adapted forms. What is unpredictable is whether evolution by natural selection will result in this particular adaptive form or that. And the reason is what Darwin called "accidental" variation, and what we call "random" variation or random mutation.

To predict what particular forms life will take, we would need to know more than just the generalization that adaptively more valuable variations and combinations of variations will be selected; we would also need to know what particular variations will arise, and in what particular order. Two initially identical populations inhabiting identical environments will not have simultaneous, identical mutational histories, and as a result they may diverge evolutionarily.

For example, imagine two populations homogeneous for a gene $X_1$. Suppose the environment of each population changes, but in precisely the same respects. Mutations occur in each population, mostly disadvantageous. But ultimately an advantageous mutation—say, $X_5$—occurs in the first population and increases in frequency. In the second population, a different advantageous mutation—$X_{12}$—occurs and increases in frequency.

It might be argued that this divergence would be temporary at best. Eventually, $X_{12}$ will occur in the first population and will increase in frequency if it is more advantageous than $X_5$. Or else $X_5$ will occur in the second population and increase in frequency if it is more advantageous than $X_{12}$. In either case, the two populations will eventually converge evolutionarily.

But even if the two populations underwent the same mutations in the long run—at one particular locus—and even if one of those mutations was significantly more advantageous than the rest, the populations might still diverge, depending on differences in their mutational histories at other loci. The problem gets much more interesting when we consider the timing and order of

mutations at multiple loci, and the possibility (known as "epistasis") that whether a mutation at one locus is advantageous depends on what genes it is teamed-up with at other loci.

To see how this might happen, return to the previous example, and imagine what is happening at a second locus. Suppose the initially identical populations are homogeneous for $X_1$ and $Y_1$ (Fig. 2).

[insert Fig. 2 around here]

Following the mutations at locus $X$, $X_5Y_1$ prevails in the first population, while $X_{12}Y_1$ prevails in the second population. Now suppose that $Y_4$ occurs in each population. Suppose further that the $X_5Y_4$ combination is less advantageous than $X_5Y_1$, so that $X_5Y_1$ continues to prevail in the first population; whereas, the $X_{12}Y_4$ combination is more advantageous than $X_{12}Y_1$, so that $X_{12}Y_4$ increases in frequency in the second population.[8]

Add more epistatic loci to the example and the difference in evolutionary outcomes will be even greater.

One of Gould's—and Darwin's—favorite examples of the unpredictability of evolution (based on the unpredictability of mutations and mutational order) concerns the evolution of the ichneumonids (parasitic wasps). One might well predict ahead of time that the reproductive behaviors and life histories of organisms would be adaptive. But could one have predicted the succession of mutually adaptive mutations leading to the ichneumonids, which insert their eggs into the bodies of living caterpillars where the eggs develop into larvae that consume the caterpillar from the inside-out, eventually emerging (à la *Alien*, the movie), and then living as pupae attached to the empty caterpillar carcass, until they emerge as wasps to repeat the hoary cycle?

The ichneumonids were especially telling for Darwin. While he could possibly imagine that God had designed the general laws of nature, like evolution by natural selection, he strongly

resisted the thought that God might have foreseen, and have either intended or allowed that particular variations would occur in a particular order leading, for instance, to the repugnant ichneumonids. Darwin preferred to think that God had let variation occur randomly. That is why he spoke of the "details, *whether good or bad*, [which are] left to the workings out of what we may call chance" (my emphasis). For Gould, as for Darwin, those "details" were a source of considerable unpredictability.

The class of factors that one might have expected Gould to invoke in order to account for contingency in the unpredictability sense is a kind of factor that evolutionary biologists have long invoked to this end, namely, sampling error. The paradigmatic case involves heterozygotes—organisms that have two different genes for a trait instead of two copies of the same gene—just by chance passing down more of one gene than the other to their offspring, thus resulting in an evolutionary change—a "random drift"—in the frequencies of those two genes.

Sampling error leading to random drift of gene frequencies is usually depicted with a common ancestral starting point—a common gene frequency—and a common environment, but with disparate evolutionary outcomes. Figure 3 is a typical example.

[insert Fig. 3 around here]

This looks a lot like the unpredictability version of contingency (just turned on its side). But Gould explicitly excluded sampling error and random drift from the category of historical contingency. In his own words, he distinguished what he called "stochastic effects" like random drift from "history," "the contingencies of history," and "the happenstances of history."[9] This is a somewhat confusing distinction, since random mutation and mutational order, which Gould acknowledged as sources of historical contingency, are themselves stochastic processes. Gould did not provide any sort of analytical grounds for this distinction.

I will have a bit more to say about this later. But I cannot go on without noting that this distinction—between stochastic effects like random drift due to sampling error, on the one hand, and historical contingency, on the other hand—does not square very well with Gould's own account of the persistence of some forms rather than others following the Cambrian explosion. According to Gould, that outcome was highly contingent and could well have turned out otherwise because it had so little to do with differences in adaptive fit and was more like a lottery. Which sounds a lot like sampling error at the level of lineages. And Gould was certainly friendly to the idea of analogous evolutionary processes taking place at multiple levels of the genealogical hierarchy.[10]

Anyway, to summarize concerning the unpredictability version of contingency—before turning to the causal-dependence version—it is not tantamount to any mysterious sort of indeterminism. It does not deny that evolutionary outcomes can be explained. It merely denies that evolution by natural selection is sufficient to guarantee the same evolutionary outcome, even given initially indistinguishable ancestral lineages and indistinguishable environments, and even excluding stochastic processes like random drift.

## III. THE CAUSAL-DEPENDENCE VERSION OF HISTORICAL CONTINGENCY

While the first version of contingency emphasizes the unpredictability of evolutionary outcomes, the second version emphasizes the causal dependence of outcomes on prior circumstances, which might seem obvious enough, but which is intended in a way that is not trivial.

Consider that a marble in the bottom of a bowl could have rolled there from anywhere inside the lip (Fig. 4).

[insert Fig. 4 around here]

Its present position is, in this sense, not dependent on its particular prior position and carries no trace of its past. The physics of the situation leads inexorably from any starting point inside the lip to the same position at the bottom.

Evolution, Gould argued, is not like that. Nothing, not even natural selection, leads inexorably from any starting point to the same outcome—not even in indistinguishable environments. Present (and future) forms of lineages are highly dependent upon their prior ancestral states. The main reason for this, according to Gould, involves what he called "historical constraints." These are factors "internal" to the ancestors of a lineage that restrict the range of variations upon which natural selection can act to further modify the lineage. In Gould's terms, historical constraints "restrict the freedom of natural selection to establish and control the direction of evolution" (*ibid.*, p. 1028). Historical constraints ensure that future forms of a lineage are inscribed with the "unerasable signatures" of past forms—i.e., unerasable by natural selection (WL, p. 283).

For example, neither whales nor fish have legs, and from an adaptive point of view, it is sufficiently clear why. But the four-legged ancestors of whales provided very different variations for natural selection to act upon than did the legless ancestors of fish. And this difference in variations available to natural selection is evident in the different outcomes. Whales may no longer have legs, but they carry around rudimentary pelvises that natural selection has not completely erased. The exact outcome of whale evolution is thus historically contingent in the sense of being causally dependent on the ancestral state of whales.[11]

Before moving on to the empirical tests of Gould's views, it is worth pausing to note that, while the unpredictability and causal-dependence versions of historical contingency make different points, they are similar in at least one respect. That is, they make the same general point

vis-à-vis evolution by natural selection. Together, they rule out the sort of evolutionary inexorability portrayed in Figure 5.

[insert Fig. 5 around here]

That is, they rule out the idea that evolution by natural selection in a specified environment will result in a predictable outcome *regardless of ancestral starting point*. (And what's more, this non-inexorable nature of evolution has nothing to do with sampling error and random drift.)

Nonetheless, interesting and important differences between the two versions of historical contingency remain. The sources of contingency in the unpredictability sense—random mutation and mutational order—render the future somewhat independent of the past. While the sources of contingency in the causal-dependence sense—historical constraints on variation—inscribe the future with the past.

Differences between the two versions are also important to keep in mind in considering attempts to test Gould's view(s) on contingency.

## IV. TESTING GOULD'S VIEWS: A MACROEVOLUTIONARY "NATURAL EXPERIMENT"

Toward the end of *Wonderful Life*, Gould mused, regretfully, that of course the tape can never be replayed. There can never be a controlled experiment to confirm or disconfirm the contingency of an evolutionary outcome. However, as he more cheerfully noted, nature sometimes presents us with fairly well designed evolutionary experiments featuring closely related—and hence similar, if not indistinguishable—lineages inhabiting fairly similar environments over long periods of time (WL, pp. 297-299). Let's now consider one of those "natural experiments," as analyzed by Losos et al. (*op. cit.*). And then finally I will consider

something like an actual replaying of the tape as designed and analyzed by Travisano et al. (*op. cit.*)

Losos et al. were primarily concerned to put the causal-dependence version of historical contingency to the test. And this is reflected in the first sentence of their paper: "The theory of historical contingency proposes that unique past events have a large influence on subsequent evolution" (*op. cit.*, p. 2115). But their study actually bears on both versions of contingency, and there are indications in their article that this was not entirely inadvertent. For example, their title, "Contingency and Determinism in Replicated Adaptive Radiations . . ." suggests that they were addressing the unpredictability interpretation, by pursuing the question whether the outcomes of replicated radiations are contingent, or predictable. The first sentence of their abstract suggests the same:

> The vagaries of history lead to the prediction that repeated instances of evolutionary diversification will lead to disparate outcomes even if starting conditions are similar." (*op. cit.*, p. 2115)[12]

Losos and his colleagues studied the evolutionary diversification of lizards of the genus *Anolis* on four islands in the Caribbean: Cuba, Hispaniola, Jamaica and Puerto Rico. No single species occurs on more than one island, but the same "ecomorphic" *types* of species occur over and over (an "ecomorph" is a type of species that is adapted to a particular niche). For example, each island has its own "twig ecomorph" species of *Anolis* that is well adapted to living on and navigating narrow twigs. These lizards have relatively short legs and well developed toe pads (they also have a slow, searching form of foraging behavior, and rely primarily on cryptic coloration combined with stillness for defense against their own predators). And each island has its own "trunk-ground ecomorph" species that is well adapted to life on tree trunks and the ground. These lizards have longer limbs and less well developed toe pads (and they run and grab

moving prey, and run to escape their own predators). There are also two other ecomorphs on each island, adapted to life on two other parts of trees. The adaptive fit of the various ecomorphs to their preferred habitats has been well studied, for example, by "chasing" different types of lizards along rods of different diameters, and measuring their speed and agility.[13]

How did it come to be that each island has its own representative of each of these four ecomorphs? One extreme possibility is that each island was originally colonized by the same ecomorph. And then from that type of ancestor, the other three ecomorphs evolved independently on each island. This sounds somewhat like the opposite of Gould's replay expectation, in that basically the same evolutionary outcome would have occurred four times (that is to say, on four islands) from basically the same ancestral starting point, and in basically the same environmental conditions. In this case, one could even say that the *same four outcomes* (the same four ecomorphs) would have occurred *four times* (on four islands), under basically the same environmental conditions.

Another extreme scenario is the Gouldian possibility that each ecomorph arose only once, as one of many, equally satisfactory ways of adapting to a Caribbean environment. Descendants of each original ecomorphic species then made their way around to the various Caribbean islands (by dispersal or vicariance) and survived there nicely.

Losos et al. attempted to distinguish between these extreme possibilities by reconstructing and analyzing the evolutionary relationships of the species in question (based on mitochondrial DNA sequences). On the first hypothesis, the species living on any one island, although representing four different ecomorphs, should be more closely related to each other than to species on any other island (Fig. 6, top). On the second hypothesis, the species within any one ecomorphic group, while inhabiting separate islands, should be more closely related to each

other than to species within any other ecomorphic group, even species on the same island (Fig 6, bottom).

[insert Fig. 6 around here]

In fact, their phylogenetic analysis revealed that species on each island were more closely related to each other than to species on any other island, strongly suggesting that each ecomorphic species arose on each island: four replays of the evolution of the same four ecomorphs.

With one interesting difference: the evolutionary relationships of the ecomorphs were different on each island (Fig. 7).

[insert Fig. 7 around here]

Losos et al. suggested that these differences could be understood as differences in the temporal order of evolution on each island, which in turn could be due to contingency in the causal-dependence sense. As they reasoned, the niches (or ecomorphic opportunities) available at any one time on an island depend on which ecomorphs have already arrived or evolved there.[14]

So Losos et al.'s study bears on the causal-dependence version of contingency, since they were addressing the extent to which differences in outcome are attributable to different ancestral states. But their work also bears strongly on the unpredictability interpretation of contingency, since their phylogenetic analysis is consistent with the possibility that, from basically the same starting point (the same ancestral ecomorph), the same outcome (the same derived ecomorphs) repeatedly result.

It is worth mentioning one other respect in which the Losos et al. study addressed and ruled-out historical contingency in the causal-dependence sense. That is, they raised the possibility that the ancestral lineages that originally colonized the islands were either negatively constrained from producing any ecomorphs other than the set of ecomorphic variants seen there,

or positively constrained to produce just those types. In this case, the repeated evolutionary outcomes would have been contingent—in the causal-dependence sense—on the prior state of the ancestral lineage and could not be explained solely in terms of adaptive fit. They ruled out this possibility on the grounds that the colonists presumably arrived from the mainland, and on the mainland there is a wider range of ecomorphs than is found on the islands.

Losos et al.'s work was not discussed in print by Gould. But Losos recollects hearing second hand, through a *Science* reporter, that Gould was not moved by their results:

> My recollection is that his response was that the phenomena he was talking about pertained to events deep in evolutionary time (perhaps referring explicitly to the Cambrian Explosion) and that our lizard work was on recently diverged events.[15]

## V. TESTING GOULD'S VIEWS: A MICROEVOLUTIONARY, LABORATORY EXPERIMENT

Given Gould's reaction to Losos et al.'s *macroevolutionary* study, it is perhaps not too surprising that he had no detailed response to Travisano et al.'s *microevolutionary* experiment. But, for reasons that I will discuss, Gould might also have felt that he and they were talking past each other somewhat.

While Losos et al. focused on the causal-dependence version of contingency, Travisano et al. explicitly focused on the unpredictability interpretation. They designed and ran experiments to mimic as closely as possible actual replayings of the evolutionary—albeit microevolutionary—tape. As they explained their intent,

> S. J. Gould has argued for the great importance of historical contingency. He has presented a gedanken experiment of "replaying life's tape" to test the repeatability of evolution and thereby evaluate the roles of adaptation, chance and history. Of course,

> one cannot perform an actual experiment on the grand scale envisioned by Gould, but one can perform rigorous experiments, of shorter duration and in simpler environments, to quantify the roles of adaptation, chance, and history in evolution. Instead of replaying life's tape sequentially, one can achieve the same objective by doing an experiment in which replicate populations are propagated simultaneously. (Travisano et. al., *op. cit.*, p. 87)

This sounds promising. Recall that Gould also distinguished between adaptation, "stochastic" factors and historical contingency. So this experiment might seem to be right on the mark. However Travisano et al. did not distinguish between "chance" and "history" in the same manner that Gould distinguished between "stochastic" factors and "historical contingency." Gould conceived of random mutation and mutational order as sources of historical contingency, and he contrasted historical contingency with stochastic effects like random drift due to sampling error. Travisano et al., in a more traditional manner, included in the category "chance" *both* sampling error leading to random drift, *and* random mutation and mutational order. (Although, as we shall see, in further studies Travisano, Lenski and their colleagues tried to tease apart the contributions of sampling error and random mutation in ways that Gould would probably have appreciated.) Moreover, they invoked "history" only in those cases where different evolutionary outcomes resulted from different ancestral states (*op. cit.*, p. 87), which corresponds to Gould's causal-dependence version of historical contingency. Although, it was the unpredictability version of historical contingency that they had set out to investigate.

I will discuss two of the four experiments that Travisano et al. reported. Each of these experiments had two stages (Fig. 8).

[insert Fig. 8 around here]

In the first stage, they cloned 12 copies of a single genotype of *E. coli* to establish 12 genetically identical populations. Then they grew these populations separately in a glucose-limited environment for 2,000 generations, and measured the derived phenotypes that resulted (I will discuss the phenotypes in question shortly). Following that stage, they cloned 3 copies of one individual from each of the 12 populations to produce 36 populations (of 12 different genotypes), and grew these separately for 1,000 generations in a maltose-limited environment, and then measured the derived phenotypes.

They interpreted the results with the help of the following analytical scenarios, beginning with possible outcomes of the first stage (Fig. 9; *ibid.*).[16]

[insert Fig. 9 around here]

NB: Travisano et al. did not address the role of history in the first stage. Indeed, given what they meant by "history," there was no history in the first stage to address.

In the first scenario (Fig. 9, top), from the same ancestral state, in the same environment, the same particular form is derived every time. This, they argued, would be best interpreted solely in terms of adaptation—selection in favor of a greater value of the phenotypic variable—with no role for chance (*ibid.*).

In the second scenario (Fig. 9, middle), from the same ancestral state, in the same environment, a range of forms around the mean of the ancestral form are derived. This purely dispersing effect, they argued, would be best interpreted solely in terms of chance, with no role for natural selection (*ibid.*). Recall that they included in the category "chance" not only random drift due to sampling error, but also random mutation, which Gould associated with historical contingency in the unpredictability sense. So "chance" for them overlaps one of Gould's sources of historical contingency.

The third scenario (Fig. 9, bottom), they argued, is best interpreted in terms of selection in favor of an optimal phenotype, together with the dispersing effects of chance (*ibid.*).

Moving now to the analytical scenarios for interpreting the second stage of the experiment (Fig. 10).

[insert Fig. 10 around here]

In the first scenario of the second stage (Fig. 10, top), from widely different starting points, a much narrower range of outcomes results. Travisano et al. suggested that in this case, "an initial effect due to history is eliminated by subsequent effects due to chance and adaptation" (*ibid.*). Recall that they associated "history" with differences in ancestral states; history has a role when differences in evolutionary outcomes are due in part to differences in ancestral states. Clearly history as such has no role in this scenario.

In the second scenario (Fig. 10, bottom), Travisano et al. suggested that, "an initial effect due to history is maintained with subsequent effects due to chance and adaptation superimposed" (*ibid.*).

Again, the sort of "history" that Travisano et al. are looking for with this sort of experiment, and this sort of analysis, is historical contingency in the causal-dependence sense. Although, it was the unpredictability version of historical contingency that they reported to be the focus of their study.

The actual results of their experiments are extremely interesting. They studied two phenotypes, cell size, which they had prior reason to believe was only weakly correlated with fitness, and fitness itself as measured by ability to compete for resources.

I will focus on the results of the fitness experiment. At the end of the first stage, in the glucose-limited environment, the 12 populations had very similar fitness values suggesting (not surprisingly) a significant role for adaptation. However, when those 12 derived populations were

*initially* placed in the maltose-limited environment (at the beginning of stage 2), their fitnesses were found to diverge considerably, although these differences were subsequently erased, suggesting again a significant role for adaptation.

But what about those initial differences in fitness in the second, maltose-limited environment? This finding was investigated further in a separate paper, which concluded that considerable genetic differences underlay the similarities in fitness that had developed in the glucose-limited environment, and that the different genotypes represented equally adaptive outcomes within that environment.[17] Brief mention was made of the extent to which random mutation and mutational order might be involved in the differences that occurred at the genetic level.[18]

This finding quite clearly bears on Gould's unpredictability notion of historical contingency, since at least at the genetic level, different outcomes resulted from identical ancestral states in identical environments. Other studies by the Lenski group delved more deeply still into the role of random mutation and mutational order in the unpredictability of evolutionary outcomes.[19] Moreover, in these studies, random mutation and mutational order were sometimes referred to not only as chance events, but also as historically contingent factors—as for example when Lenski and Travisano referred to "the crucial role of chance events (historical accidents) in adaptive evolution" (*ibid.*, p. 6813).

Although Gould never commented in detail on the Travisano et al. study, he did refer to it briefly, in a footnote, in his last book, *The Structure of Evolutionary Theory* (*op. cit.*). There he also discussed (at greater length) the study by Lenski and Travisano that I just mentioned and will now describe in more detail. The Lenski and Travisano experiment corresponded to the first stage of the Travisano et al. experiment, extended from 2,000 to 10,000 generations in the glucose-limited environment. Somewhat surprisingly, the fitness values of the 12 populations,

which were similar after 2,000 generations, were still *only similar* after 10,000 generations. Why after 10,000 generations in exactly the same environment had not all of the populations evolved the same ability to compete for the resources available in that environment? Lenski and Travisano suggested that the residual differences in fitness reflected underlying genetic differences, which had in turn resulted from the different order of mutations occurring in the 12 populations, compounded by epistasis (*op. cit.*, p. 6813). They concluded that, "our experiment demonstrates the crucial role of chance events (*historical accidents*) in adaptive evolution" (*ibid.*; my emphasis).

Again, this would seem to bear quite directly on Gould's unpredictability version of contingency. Interestingly, Lenski and Travisano did not cite Gould's views on historical contingency in this particular paper. But Gould certainly saw the connection himself. As he reported their results:

> The general path of increase [e.g., in fitness] followed the same trajectory in all populations, but with fascinating differences of both form and genetics in each case [presumably referring to the genetic differences underlying the similar fitnesses]—a remarkable commentary, at such a small and well-controlled scale, of the roles of detailed contingency and broad predictability in evolution. (Gould, 2002, *op. cit.*, p. 932)

The "remarkable commentary" was not further articulated.

Apparently, sometime just before the 2002 book went to print, Gould also added a footnote concerning the Travisano et al. experiments, which he took as support for the significance of contingency, but without elaborating why (2002, *op. cit.*, pp. 932-933).[20] He did not refer to the ways in which Travisano et al. distinguished between adaptation, chance and history. This would not have been something that he could have discussed briefly![21]

It is interesting that Gould's discussion of Lenski and Travisano, and his footnote on the Travisano et. al. experiments, was in the context of their bearing on punctuated equilibrium—not contingency *per se*. He seemed most interested in the patterns of punctuated evolution in their results. Perhaps this helps to explain why Gould seemed to have a fairly positive view of the Lenski group's microevolutionary studies, relative to his slightly negative view of the Losos group's macroevolutionary studies. Recall his reported critique of the Losos group: that their study did not extend sufficiently deep into evolutionary time.

## VI. CONCLUSION

By way of conclusion, I would like to return briefly to two issues, and raise a third anew. First, what are we to make of the two versions of historical contingency? Do we need both? Or does one version have a better claim to the title? There is no question that in ordinary language, "contingent" is used to refer to unpredictable outcomes ("contingent" *per se*) and also to the causal dependence of particular outcomes on prior events (as in "contingent upon;" see, e.g., *Merriam-Webster*). But perhaps more importantly, there is a tradition in historiography and philosophy of history of viewing these two notions of contingency as complementary components of historical narratives. W.B. Gallie often made this point:

> In general, the possibility of prediction figures in stories very much as it does in most of our thinking about everyday life. There is a dominant sense of alternative possibilities: events in train are felt to admit of different possible outcomes—particularly those events that count, that evoke praise or blame, that deserve to be recorded, that could be the pivot of a good story. But side by side with this there is the recognition that many events, or aspects of events, are predictable either exactly or approximately. But, although recognized, this predictable aspect of life is, so to speak, recessive or in shadow.

> It is in contrast to the generally recognized realm of predictable uniformities that the unpredictable developments of a story stand out, as worth making a story of, and as worth following.
>
> We should notice here that perhaps of greater importance for stories than the predictability relation between events is the converse relation which enables us to see, not indeed that some earlier event necessitated a later one, but that a later event required, as its necessary condition, some earlier one. More simply, almost every incident in a story requires, as a necessary condition of its intelligibility, its acceptability, some indication of the kind of event or context which occasioned or evoked it, or, at the very least, made it possible. This relation, rather than the predictability of certain events given the occurrence of others, is the main bond of logical continuity in any story.[22]

In a nutshell: if the outcome of a historical narrative were predictable from the outset, or at any point, there would be no need to include any further events—i.e., no need for the rest of the narrative. So the early and intermediate events in a narrative should be insufficient to make sense of the outcome. Of the intermediate events that *are* included, at least some should have a causal bearing on the outcome—otherwise, why include them? So a good, self-contained narrative should be constructed out of events that are insufficient but necessary for the outcome.

But even if there is good reason to stick with a dual notion of contingency, rather than viewing one or the other version as *the* correct account, still, it helps to state clearly which version is at issue in discussions and empirical investigations of contingency. This helps, for instance, in appreciating how the Losos et al. study bears on more than just the causal-dependence version of historical contingency, and how the Travisano et al. experiments bear on more than just the unpredictability version.

The second point to which I would like to return briefly concerns the distinction between historical contingency and chance. How should that distinction be drawn? Some will find Travisano et al.'s distinction more compelling than Gould's. Recall that Travisano et al. included random variation and random drift in the "chance" category, while Gould put random variation in the "historical contingency" category, leaving random drift in the "stochastic" category. The emphasis on "random" may suggest a natural link that Gould artificially severed. It may be that he was thinking along the following lines (I am not trying to defend his distinction here; for the time being I just want to understand it). Random variation and historical constraints, for all their differences, both have to do with the *origin and direction* of variation, whether random or constrained. Evolution by natural selection and sampling error leading to random drift, for all their differences, both have to do with the *differential persistence of existing variation*. By emphasizing the importance of historical contingency relative to evolution by natural selection and random drift, then, Gould may have intended to emphasize the need to take into account the origin and direction and not just the persistence of variation in explaining evolutionary outcomes.

But who really cares whether, for instance, random mutation and mutational order go into the category of "historical contingency," or into the category of "chance?" Why don't we just investigate, for instance, the relative extents to which random mutation and mutational order, vs. random drift, vs. adaptive evolution are responsible for evolutionary outcomes? Interestingly, while Lenski and Travisano (*op. cit.*) include random mutation, mutational order and random drift all in the "chance" category, nonetheless they distinguish between the effects of random mutation and mutational order on the one hand, and random drift on the other, and argue that the former is more important in explaining the divergence of populations in the 10,000 generation experiment.

Why place so much emphasis on the distinction between historical contingency and chance? I suspect we will be in a better position to answer that question when we understand why, beginning in the mid-late nineteen seventies and early eighties, there was so much concern to emphasize the importance of "history," not only in evolutionary biology, but also in other areas of biology like ecology, biogeography, conservation biology and systematics, and in the social sciences as well (see note 1).

Finally, it is important to consider what the issues concerning Gould's views of historical contingency have in common with so many other issues in biology, and what will make the issues concerning contingency difficult to resolve long after we have sorted out the conceptual issues at stake. This is the problem of extrapolating from the importance of an evolutionary factor in one or a few, or even many cases, to its overall importance. What does one study, or one hundred, or even one thousand tell us about the overall importance of historical contingency in either or both of the senses that Gould articulated? Of course, Gould did write that "*any* replay of the tape would lead evolution down a pathway radically different from the one taken" (WL, p. 51; my emphasis). In principle, one negative case would undermine his position (at least with regard to one of the versions of contingency). But we should not forget that Gould was also the co-author of that famous line in "Spandrels of San Marco:"

> In natural history, all possible things happen sometimes; you generally do not support your favoured phenomenon by declaring rivals impossible in theory. Rather, you acknowledge the rival, but circumscribe its domain of action so narrowly that it cannot have any importance in the affairs of nature. Then, you often congratulate yourself for being such an ecumenical chap.[23]

Surely, like so many disputes in biology, the issue will become one of the *relative significance*—rather than the *universality*—of historical contingency.[24] Losos charitably

acknowledges that so far the evidence bearing on Gould's position is "anecdotal."[25] What sorts of studies, short of a complete tally of evolutionary episodes, will give us more than anecdotal insight into the overall importance of historical contingency?[26]

## FIGURES

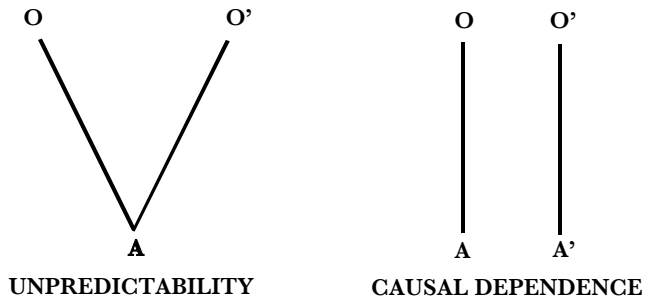


Fig. 1. The two versions of historical contingency. The unpredictability version: from the same starting point A (A for ancestral), evolution leads unpredictably to different outcomes O and O'. The causal-dependence version: depending on the starting point, A or A', evolution leads to O or O'. See text.

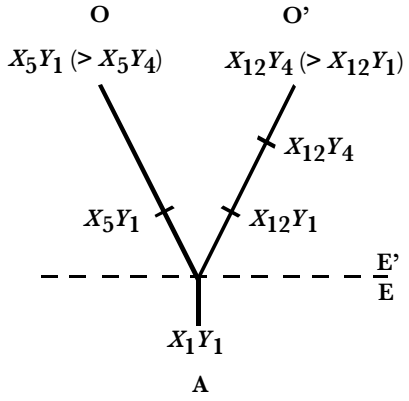


Fig. 2. Evolutionary divergence from the same starting point, due to changes in mutational order and epistasis. See text.

Fig. 3. Random drift of gene frequencies leads to two different outcomes from the same starting point (no selection, population size 100; generated by Donald Alstad's *Populus* software). See text.

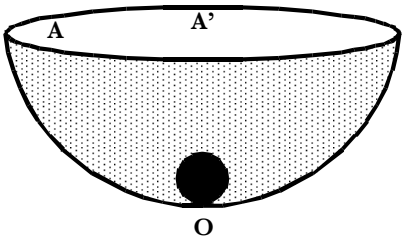


Fig. 4. An outcome that carries no trace of its past. See text.

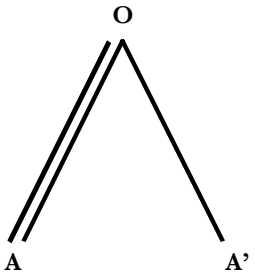


Fig. 5. What the two versions of historical contingency, together, rule out: namely that the same evolutionary outcome would result twice from the same ancestral starting point, and even from different starting points, presumably due to the overwhelming influence of natural selection. See text.

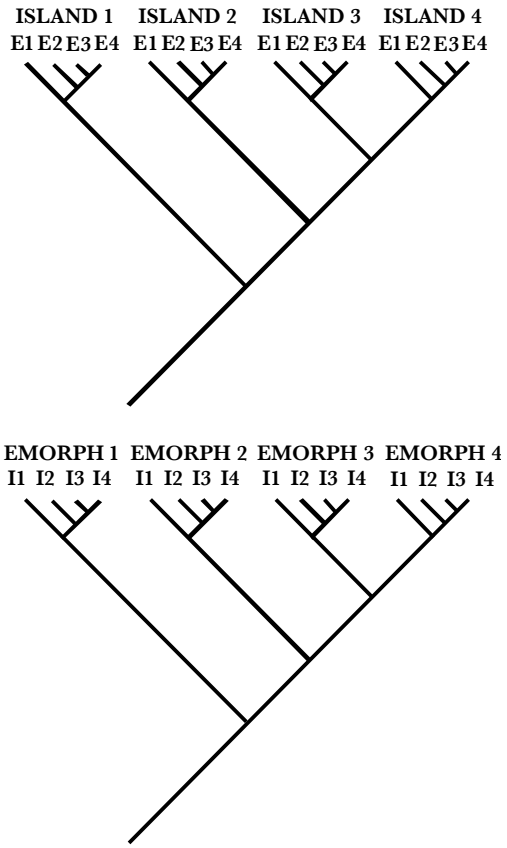


Fig. 6. Hypothetical phylogenetic scenarios for investigating the role of historical contingency in Losos et al. (*op. cit.*; much simplified by the author). *Top*: From the same ecomorphic ancestor, the same four ecomorphs ($E_1$ - $E_4$) evolved independently on each island. *Bottom*: Each ecomorph arose once; descendants of each ecomorph then eventually colonized each island ($I_1$ - $I_4$). See text.

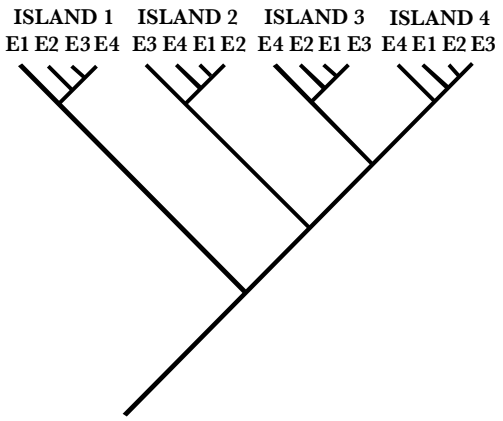


Fig. 7. Phylogenetic results of Losos et al. (*op. cit.*; much simplified by the author). See text.

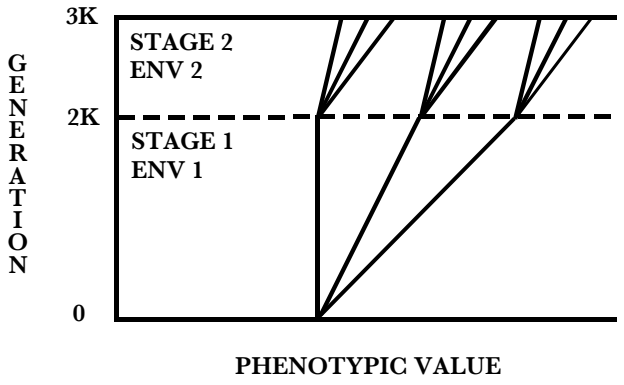


Fig. 8. Two stages of the experiments reported in Travisano et al. (*op. cit.*). See text.

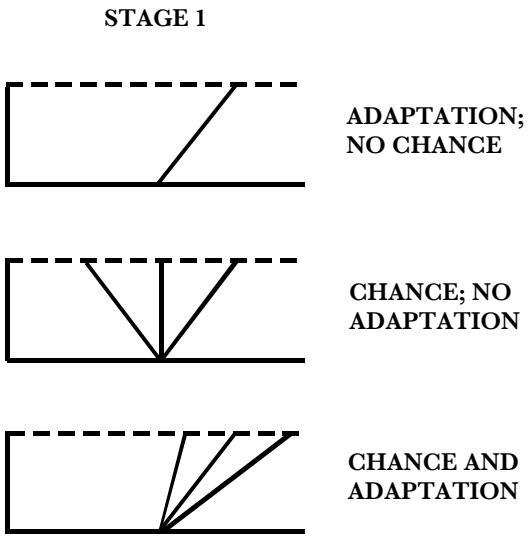


Fig. 9. Analytical scenarios for investigating the roles of "adaptation," "history" and "chance" in the first stage of the experiments reported in Travisano et al. (*op. cit.*; redrawn slightly in order to make them more consistent with other representations in this paper). NB: Travisano et al. do not address the role of history in the first stage. *Top*: From the same ancestral state, in the same environment, the same form is derived every time; this is a sign of adaptation alone with no role for chance. *Middle*: From the same ancestral state, in the same environment, a range of forms around the ancestral mean is derived; this is a sign of chance, with no role for adaptation. *Bottom*: From the same ancestral state, in the same environment, a range of forms around a new mean is derived; this is a sign of adaptation plus chance. See text.

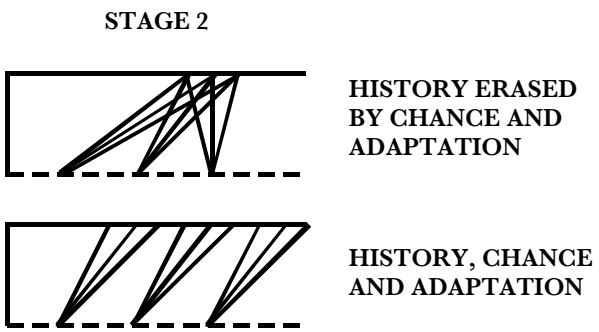


Fig. 10. Analytical scenarios for investigating the roles of "adaptation," "history" and "chance" in the second stage of the experiments reported in Travisano et al. (*op. cit.*; redrawn slightly in order to make them more consistent with other representations in this paper). *Top*: "An initial effect due to history is eliminated by subsequent effects due to chance and adaptation." *Bottom*: "An initial effect due to history is maintained with subsequent effects due to chance and adaptation superimposed." See text.

## APPENDIX

For references to Losos et al. and Travisano et al. in connection with Gould's views, see S. B. Emerson, "A Macroevolutionary Study of Historical Contingency in the Fanged Frogs of Southeast Asia," *Biological Journal of the Linnean Society* LXXIII (2001): 139-151; P. H. Harvey and L. Partridge, "Different Routes to Similar Ends," *Nature* CCCXCII (1998): 552-553; R. B. Huey, G. W. Gilchrist, M. L. Carlson, D. Berrigan, and L. Serra, "Rapid Evolution of a Geographic Cline in Size in an Introduced Fly," *Science* CCLXXXVII (2000): 308-309; R. C. MacLean and G. Bell, "Divergent Evolution during an Experimental Adaptive Radiation," *Proceedings of the Royal Society of London B* CCLXX (2003): 1645-1650; M. Matos, T. Avelar, and M. R. Rose, "Variation in the Rate of Convergent Evolution: Adaptation to a Laboratory Environment in *Drosophila subobscura*," *Journal of Evolutionary Biology* XV (2002): 673-682; E. B. Taylor and J. D. McPhail, "Historical Contingency and Ecological Determinism Interact to Prime Speciation in Sticklebacks, *Gasterosteus*," *Proceedings of the Royal Society of London B* CCLXVII (2000): 2375-2384; and B. Vanhooydonck and D. J. Irschick, "Is Evolution Predictable? Evolutionary Relationships of Divergence in Ecology, Performance and Morphology in Old and New World Lizard Radiations," in *Topics in Functional and Ecological Vertebrate Morphology*, P. Aerts, A. D'Août and R. Van Damme, eds. (Maastricht: Shaker, 2002).

For an interesting contrast with the natural and laboratory experiments reported by Losos et al. and Travisano et al., see the artificial life experiments of G. Yedid and G. Bell, "Macroevolution Simulated with Autonomously Replicating Computer Programs," *Nature* CDXX (2002): 810-812; and D. Wagenaar and C. Adami, "Influence of Chance, History and Adaptation on Evolution in *Digitalia*," *Artificial Life* X (2004): 181-190. Both explicitly address Gould's views on contingency.

Another major research program that has clear bearing on Gould's views—but that is not explicitly cast in those terms—is Dolph Schluter and his colleagues' investigations of parallel, seemingly replayable, adaptive radiations in threespine sticklebacks: D. Schluter and J. D. McPhail, "Ecological Character Displacement and Speciation in Sticklebacks," *American Naturalist* CXL (1992): 85-108; D. Schluter, "Adaptive Radiation in Sticklebacks: Size, Shape, and Habitat Use Efficiency," *Ecology* LXXIV (1993): 699-709; D. Schluter, "Experimental Evidence that Competition Promotes Divergence in Adaptive Radiation," *Science* CCLXVI (1994): 798-801; and H. D. Rundle, L. Nagel, J. W. Boughman, and D. Schluter, "Natural Selection and Parallel Speciation in Sympatric Sticklebacks," *Science* CCLXXXVII (2000): 306-308.

## NOTES

* This paper is dedicated to the memory of Steve Gould, who was so thoughtful, constructive, and generous in his engagements with historians and philosophers of science. The paper was originally prepared for a special session in his honor at the 2002 Philosophy of Science Association meetings. I am grateful to the PSA Program Committee for the invitation. I am also grateful to Jonathan Losos, Richard Lenski, Michael Travisano, Michael Whitlock, Sally Otto, Sandra Mitchell, Philip Kitcher, Elliott Sober, Marc Ereshevsky, Maggie Osler, Roberta Millstein, Sahotra Sarkar, Scott Anderson, Catherine Wilson, Alan Richardson, Chris Stevens, Mohan Matthen, and Ori Simchen, for comments and criticisms.

[1] There had been earlier attempts to stress the importance of "history" in evolutionary biology, e.g., R. C. Lewontin, "The Principle of Historicity in Evolution, in *Mathematical Challenges to the Neo-Darwinian Interpretation of Evolution* (Philadelphia: Wistar Institute, 1967). But something like a "movement" developed in the nineteen seventies and eighties. There were also, around this time, calls for greater attention to history in systematics, biogeography, ecology, and conservation biology (for an insightful overview, see S. E. Kingsland, "Afterword," in *Modeling Nature: Episodes in the History of Population Ecology* (Chicago: University of Chicago Press, 1995). There were calls for taking history more seriously in the social sciences as well. See, e.g., J. H. Goldthorpe, "The Uses of History in Sociology: Reflections on Some Recent Tendencies," *British Journal of Sociology* XLII (1991): 211-230; and J. M. Bryant, "Evidence and Explanation in History and Sociology: Critical Reflections on Goldthorpe's Critique of Historical Sociology," *British Journal of Sociology* LXV (1994): 3-19. It would be very interesting to investigate the various concepts of "history" involved,

and the reasons why history became so important in so many areas at this time. My aims here are much narrower.

[2] S. J. Gould, *Wonderful Life: The Burgess Shale and the Nature of History* (hereafter in citations WL) (New York: Norton), p. 51.

[3] J. B. Losos, T. R. Jackman, A. Larson, K. de Queiroz, and L. Rodríguez-Schettino, "Contingency and Determinism in Replicated Adaptive Radiations of Island Lizards," *Science*, CCLXXIX (1998): 2115-2118. M. Travisano, J. A. Mongold, A. F. Bennett, and R. E. Lenski, "Experimental Tests of the Roles of Adaptation, Chance, and History in Evolution," *Science* CCLXVII (1995): 87-90.

[4] In the passage just cited, Gould states that "E *had* to arise, as a consequence of A through D" (my emphasis). Here he seems to contradict his own position on the unpredictability of evolutionary outcomes. In this paper, I am treating this apparent contradiction as a misstatement.

[5] See the illustrations throughout *Wonderful Life*. See also http://www.nmnh.si.edu/paleo/shale/index.html.

[6] The analogy of "replaying the tape" is similar to an analogy used earlier by Simon Conway Morris in contemplating the same phenomena:

> . . . if the clock was turned back so metazoan diversification was allowed to rerun across the Precambrian-Cambrian boundary, it seems possible that the successful body plans emerging from this initial burst of evolution may have included wiwaxids rather than mollusks.

S. Conway Morris, "The Middle Cambrian Metazoan *Wiwaxia corrugata* (Matthew) from the Burgess Shale and *Ogygopsis* Shale, British Columbia, Canada," *Philosophical Transactions of the Royal Society*, London B CCCVII (1985): 507-582, p. 572; quoted by Gould, WL, p. 238.

[7] C. Darwin to A. Gray, 22 May 1860, in C. Darwin, *The Correspondence of Charles Darwin, Volume 8, 1860*, F. Burkhardt, J. Browne, D. M. Porter and M. Richmond, eds. (Cambridge: Cambridge University Press, 1993), pp. 223-224. See also WL, 290; and S. J. Gould, "Boyle's Law and Darwin's Details," *Natural History* CIV (1995): 8-11, 68-71, esp. pp. 69-71.

[8] Here is an admittedly fictional, but hopefully not overly contrived example of the abstract scenario just described. (This example is inspired by the study of Losos et al. to which I will turn shortly.) Suppose there are two very similar species of lizards living on different islands, but in very similar environments, spending most of their time on the ground and running to escape predators. Suppose also that the environment on each island changes in the same way, such that it is advantageous (let's imagine equally advantageous) to occupy either trees or bushes. The bushes, with their narrower stems and branches, are more difficult to run along, but suppose that they have some other advantage that makes them as advantageous a habitat as trees. Because of random mutation and differences in the order of mutation on the two islands, the lizards on one island evolve to become tree dwellers, while on the other island, they evolve to become bush dwellers. The tree lizards might well continue to run to escape their predators; that is, tree dwelling and running for protection might be a good combination. Whereas the bush lizards, which run at best haphazardly, might evolve alternative means of protection, e.g., cryptic coloration, along with the instinct to freeze whenever a predator is near.

[9] Gould and D. S. Woodruff, "History as a Cause of Area Effects: An Illustration from *Cerion* on Great Inagua, Bahamas," *British Journal of the Linnean Society* XL (1990): 67-98.

[10] E.g., S. J. Gould, *The Structure of Evolutionary Theory* (Cambridge, MA: Harvard University Press, 2002), *passim*.

[11] When Gould discussed the causal dependence of evolutionary outcomes on prior states, he usually (as I noted earlier) emphasized historical constraints on the range and direction of variation. This is, at least on the face of it, a very different source of contingency than random mutation and mutational order, which he emphasized in connection with the unpredictability of evolutionary outcomes. But it is worth noting briefly that random mutation and mutational order are not only a source of unpredictability, but also a reason for causal dependence of outcomes on prior states. Consider the scenario in Figure 2 that I discussed earlier. Here the difference in outcomes is dependent on the difference in prior states, $X_5Y_1$ and $X_{12}Y_1$, a difference that was unpredictable given ancestral state A ($X_1Y_1$) and the environment inhabited by each population. Moreover, it might be argued that as the initial differences are compounded by further differences in the order of mutation, and epistatic interactions with yet other traits, then the descendants of each lineage will eventually differ enough that they will offer quite different ranges of variation for further evolution by natural selection. In this way, random mutation and mutational order might give rise to different historical constraints.

[12] The first two sentences of the body of their paper suggest that the two versions are logically related—that the unpredictability interpretation follows from the causal-dependence version:

> The theory of historical contingency proposes that unique past events have a large influence on subsequent evolution. A corollary is that repeated occurrences of an evolutionary event would result in radically different outcomes. (Losos et al., *op. cit.*, p. 2115)

If the corollary is that replays from identical starting points in identical environments lead to different outcomes (leave the "radically" aside), then of course it does not follow. However, Losos (personal communication, 3 August 2004) confirms that the second sentence should be interpreted as making a point more in keeping with the first—something like: replays from different starting conditions, even in *similar* environmental conditions, will lead to different outcomes. His point is that, in the real world, environments are at best similar, never identical.

[13] J. B. Losos and B. Sinervo, "The Effects of Morphology and Perch Diameter on Sprint Performance of *Anolis* Lizards," *Journal of Experimental Biology* CXLV (1989): 25-30. For an overview of these ecomorphs, see E. E. Williams, "Ecomorphs, Faunas, Island Size, and Diverse End Points in Island Radiations," in *Lizard Ecology: Studies of a Model Organism*, R. B. Huey, E. R. Pianka and T. W. Schoener, eds. (Cambridge, MA: Harvard University Press, 1983). For photos of the ecomorphs, see P. H. Harvey and L. Partridge, "Different Routes to Similar Ends," *Nature* CCCXCII (1998): 552-553; and Todd Jackman's Anole page at http://www87.homepage.villanova.edu/todd.jackman/anolis/anolis.html).

[14] Although, Losos stresses that the inference from phylogeny to temporal order is not straightforward (personal communication, 3 August 2004).

[15] Personal communication, 15 October 2002. Perhaps Gould had the then-recent Losos et al. study in mind when he proposed a qualified version of the replay metaphor in 1990: "What would happen if we could rewind the tape of life to some moment in the fairly distant past and simply let it run again?" From S. J. Gould, *The Individual in Darwin's World: The Second Edinburgh Medal Address* (Edinburgh: Edinburgh University Press, 1990), p. 7.

[16] I have redrawn these scenarios somewhat in order to make them more comparable with the other figures in this paper. I do not believe that I have altered their content.

[17] M. Travisano, F. Vasi, and R. E. Lenski, "Long-Term Experimental Evolution in *Escherichia coli*. III. Variation among the Replicate Populations in Correlated Responses to Novel Environments," *Evolution* XLIX (1995): 189-200.

[18] See their reference to G. S. Mani and B. C. Clarke, "Mutational Order: A Major Stochastic Process in Evolution," *Proceedings of the Royal Society of London B* CCXL (1990): 29-37.

[19] R. E. Lenski and M. Travisano, "Dynamics of Adaptation and Diversification: A 10,000 Generation Experiment with Bacterial Populations," *Proceedings of the National Academy of Sciences of the United States of America* XCI (1994): 6808-6814; and P. A. Johnson, R. E. Lenski, and F. C. Hoppensteadt, "Theoretical Analysis of Divergence in Mean Fitness between Initially Identical Populations," *Proceedings of the Royal Society of London B* CCLIX (1995): 125-130.

[20] Concerning the seeming *non-sequitur* that concludes Gould's footnote, I think it makes more sense if you replace "Apparently" with "Moreover."

[21] Travisano believes that an historical accident of sorts may explain why Gould discovered the Travisano et al. experiment at such a late stage in the writing of his book. Due to a publisher's snafu, the Travisano et al. article was not actually listed in the table of contents of the issue of *Science* in which it appeared. Another article was listed in its place. So Gould may have overlooked it, and then may not have been able to find it even when it was first brought to his attention (personal communication, 25 October 2003; this confused me as well, the first time I tried to track down the paper).

[22] W. B. Gallie, *Philosophy and the Historical Understanding* (New York: Schocken, 1964), p. 26.

[23] S. J. Gould and R. C. Lewontin, "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme. *Proceedings of the Royal Society of London B* CCV (1979): 581-598, p. 585.

[24] J. Beatty, "Why Do Biologists Argue Like They Do?" *Philosophy of Science S* LXVI (1997): 231-242.

[25] Personal communication 27 September 2002.

[26] And even if historical contingency is somehow determined to play a role in most every case, there will still be questions about how big a role relative to simultaneously coacting factors. See S. Mitchell, "On Pluralism and Competition in Evolutionary Explanations," *American Zoologist* XXXII (1992): 135-144.