# How far does contingency rule?[1,2]

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Although it almost doesn't get around to discussing the subject directly, this is a book on the nature of science. Rather, on one of the natures of science -- Gould celebrates diversity in diverse ways. As one might expect, the writing is accessible to the uninitiated, and I have heard that the book has even been a best-seller. Don't let that put you off; this isn't sugar-tinged pablum but an intellectually important and intricately woven argument. It doesn't compromise its conceptual depth by being understandable.

Real science is supposed to consist of general laws, according to the lawgivers of Science. And just how many general laws can you think of in your field? Of course they may be more prevalent than we know; the evolutionary half of biology has its own cultural traditions which have inhibited much exploration in this direction. This culture itself has a real basis, though. A large part of evolution does proceed as a result of local idiosyncracies of one sort or another, from mutation and meiosis to bolides and drifting plates. That there are sometimes regularities in whole classes of such idiosyncracies doesn't prevent each from having a potentially irreversible effect. For want of a nail the shoe was lost, etc., even though nails fall out of horseshoes, I suppose, with some definable frequency distribution.

It is easy to look at any sequence of anything and, retrospectively, find some sort of regularity in it. It is equally easy to elevate such apparent regularities into claims of the existence of laws. If there isn't another sequence or twenty available to test them, such claims may have a weak apparent plausibility even if they lack a reasonable mechanism. The proposal of such pseudo-laws used to be a popular after-dinner sport in evolutionary biology, especially when one started with an implicit or explicit assumption of progress in evolution toward our own species. A minor theme of Gould's book is a documentation of the widespread belief in such progress, and the resulting pseudo-laws dependent on the existence of that particular species or its immediate relatives. It is unclear how many such pseudo-laws would carry over into a world where intelligence evolved but from a different phyletic source.

Historical events and continua like those of evolution have causes, and the causes are caused. It is at such lower levels that laws are more prevalent, as I argued in 1972. For astronomy the connection between these laws and the historical processes is, or seems to

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[1]Contribution 104, Lothlorien Laboratory of Evolutionary Biology

[2]**Wonderful Life**: The Burgess Shale and the Nature of History.
**Stephen Jay Gould.** 1989. Norton. 0 + 347 pp. Apparently acid paper. ISBN 0-393-02705-8. Hardbound. $19.95.

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be, closer than it is for evolution or human history, with historical geology being intermediate. To the extent that an event depends on a sufficiently local interaction of causes it is unpredictable, idiosyncratic, quasirandom, contingent, quirky. (Does anyone but Gould use this last word? He almost avoids it in this book.)

In Gould's reiterated image, play the tape of history again, presumably with some apparently irrelevant initial difference (or perhaps not detectably so, with the blossoming of chaos), and the result is a progressively widening divergence from our world, as the differences in the paths themselves cause further divergence. The paths are partly autocatalytic cascades which take quasirandom walks in too many dimensions for them to meet again.

Play the tape a few more times, though. We see similar melodic elements appearing in each, and the overall structure may often be quite similar. The extent to which this is the case will depend on (1) how much the later physical environment, hypothetically identical in the replays except for (in some ways major) feedback from the biota, determines the course of evolution, and (2) how much it is that evolution has its own laws. We can't approximate the importance of either of these classes of influence yet, so we have no reasonable idea of the extent to which the tapes would be repeatable. The book doesn't go into these problems, and so its message of the overwhelming importance of contingency is stronger for its effect but weaker in its substance.

A major reason for such myopia is the conventional and usually implicit equating of evolution with what happens to lineages, clades, etc., of organisms, the view from genealogy. Here we do have good reason to opt for a great preponderance of contingency. There are just too many variables which have to go the same way to get repetition. Rather less often, but still within the scope of the book, we consider the evolution of traits themselves independent of what lineage they happen to be in. Convergence comes in here, as does the genuinely different and still rather mysterious phenomenon of parallelism. Parallelism remains mysterious because it is causally grounded in development, which is still too much of a black box. Parallelism comes from similar developmental control of responses to similar selection, while convergence is the triumph of selection over differences in developmental systems. (Gould and I are both skeptical of the robustness, to future discoveries, of existing cladograms of Burgess Shale arthropods. Our doubt comes from the apparent prevalence of parallelism over convergence in their evolution. As Gould puts it, it is to some extent as though the animals were randomly drawn from a basket of traits and we see whatever was viable.)

There would probably still be eukaryotic cells even if our particular ancestral host bacterium, a cousin of the archaebacteria, had succeeded in digesting our equally ancestral purple bacterium instead of marrying it; there are even similar symbioses with other components today. There could be intelligence without us, although here we can only guess. And so on. To some extent there are repeatable patterns in the evolution of traits, but again contingency has the upper hand. There are often many ways to solve a problem in adaptation, or it may not be solved at all: in evolution one can't always get there from here, especially if there isn't much time. (And time should often not matter. In my prelims as a graduate student, one question was how similar to Earthly life would life be on another planet. A while later two members of the committee, Simpson and Dobzhansky, published papers on this subject.)

When we take a broader view, the role of contingency diminishes. Look at the tape as a whole. It resembles in some ways a symphony, although its orchestration is internal and caused largely by the interactions of the many melodic strands. Patterns here tend to have causes which don't depend crucially on the specific organisms involved. The fact that there are such patterns, in macroevolution, in communities, in ecosystems, shows that biotas aren't an arbitrary mixture of independently evolving units. Biotas have several sorts of structure, and this structure itself is subject to evolution. Such biotal evolution is as worthy of study as is the evolution of organisms themselves. Even in biotal evolution, though, contingency is important; mass extinctions are one sort of example, and the possibility (less likely to me than an Earth without life, *contra* Gould) of prokaryotes never forming eukaryotes in a replaying is another sort of example.

So. Contingency is important in evolution. How do we know this? Not by doing experiments, as the lawgivers would have it. (At least not mostly. Some low-level aspects, like the refaunated islets of Simberloffia or the interaction between selection and drift, are amenable, and natural experiments grade into the next method.) The comparative method, or class of methods, are basic here, and we see them paradigmatically used in the various subjects we call natural history. Or at least paradigmatically in biology: they also provide the scientific base for the study of human history. Science is not just the discovery of general laws, although those of us in contingency-dominated fields do tend to overlook even the possibility of laws. Science is equally the understanding of what has happened, and the often unpredictable and local and even unreachable reasons why.

And the Burgess Shale? Actually the direct subject of most of the book is this great window on the early flowering of metazoans. The odder animals, and some of the less odd, each have a vignette, all done in the context of the history of their discovery. This history itself forms a shifting background for the paleontology, although I think it is a distortion to portray Walcott as scientifically superficial, damned with the praise of being a good administrator. The three themes, of philosophy, science, and history of discovery, are skilfully interwoven, with each emerging as dominant at appropriate points. This is itself an interesting accomplishment and the metaphor of a symphony is again relevant.

An unexpected bonus in the book is a series of stylistically and anatomically excellent drawings of reconstructions of many of the Burgess animals, by Marianne Collins. They are much the best available and contrast with muddy reproductions of some historical photographs, one (p. 27) even cropped so much that its legend is inaccurate.

The bilateral animals of the Burgess Shale (the sponges are almost predictable, and a paleobotanist should look at the algae sometime, and has anyone thought of looking for microorganisms?) are indeed a wonder to our eyes. I remain to be convinced, though, that they were as diverse as Gould and others have made them, and also that they provide real evidence on the contingency of evolution. I therefore doubt both of Gould's main points with respect to the fauna itself, although his conclusions may eventually prove to be right.

I have argued the first point elsewhere (Van Valen, 1989), although without knowledge of Gould's work, and summarize a plausible alternative here, one that indeed seems to me a bit the most likely. It is plausible that early in metazoan evolution it was relatively easy to change morphological development. Later modifications and new structures must evolve so as to be developmentally compatible with what is retained of the old, a phenomenon which I have called internal coadaptation, Riedl has called burden, and Wimsatt has called entrenchment. If there is little internal coadaptation the evolution of adaptively useful new structures can proceed readily, given a path in the evolution of variation. This hypothesis is purely developmental and is compatible with diverse genetic and ecological situations. Developmental buffering against developmental and environmental stresses may also not have been well developed at this time, permitting larger morphological change from the same degree of program change

(McNamara, 1986). On this general view many of the diverse morphologies we see in the Cambrian are closer to each other developmentally than are disparate members of single phyla today. Foote (1989) has found that even in the Ordovician, trilobites were distributed less continuously in morphospace than they had been in the Cambrian.

In addition, we impose on the Cambrian a classification based on what best separates later forms. What would a Cambrian taxonomist do? We can approximate a Cambrian taxonomist by trying to forget about everything later and examining the Cambrian animals by themselves. This is a difficult exercise, partly because of our mental baggage and partly from our incomplete knowledge, but more so because of the apparently rampant parallel evolution then, which low internal coadaptation should facilitate. There is a running controversy on contemporaneous vs. retrospective interpretation of diversification for the Echinodermata, and it may exemplify a broader problem. (Historians will be reminded of the whiggery issue, itself with more than two poles. For nonhistorians, this is the question of whether, and if so how much and in what way, to let present views influence how we interpret the past. I would like to know, e.g., whether Oken's apparently bizarre theoretical morphology was good science for its time. This is an entirely distinct question from Oken's influence, and is outside current approaches to historiography.)

Take tagmosis, the pattern of fusion of body segments. It is one of the basic character groups in arthropod classification. Primarily because of it various Burgess arthropods are separated from groups they resemble in some ways. We infer their pattern of tagmosis by where limbs emerge from the body. Yet this is hardly an infallible criterion; it is violated whenever a pair of limbs is lost. Arthropods do lose limbs now and then in their evolution; an obvious example is most of the insect abdomen, even if insects were derived paedomorphically from hexapod juveniles of myriapods, and there are other cases less generally familiar. Why not in the Cambrian, when it perhaps was easier? Possibly even tagmosis itself, as distinct from our evidence for it, was a rather minor feature then: we don't know. The importance of characters itself evolves, and any taxonomist knows cases of low-level variation of characters which separate higher taxa elsewhere.

Thus it is possible, but by no means indicated by current knowledge, that the real basic morphological diversity in the Cambrian was greater than at later times. Many animals don't fit into known phyla. This doesn't by itself, though, mean that they represent phyla otherwise unknown. Gould himself notes this for *Aysheaia*, which, although marine, is barely outside the known morphology of the recent Onychophora and easily fits into that phyletic-adaptive cluster at well below the phylum level.

In order to make a balanced interpretation of the oddities, we need first a reasonable estimation of their phyletic relationships, and then a judgment of the adaptive and developmental-morphological differences from their relatives. Even for phyla alive today modern methods are suggesting some lumping (and, for the Mesozoa, perhaps splitting) at this level. So it may alternatively be that the real basic morphological diversity in the Cambrian was unusually low, as it was for placental mammals in the Paleocene despite the occurrence of several rather short-lived orders then. For the Cambrian we don't know yet.

Does the Burgess fauna support the importance of contingency in evolution? Here again I find myself straddling the fence for lack of adequate evidence. We don't know why *Anomalocaris* or *Wiwaxia* or even *Branchiocaris* became extinct. So what? That just means we don't know. As I noted in 1966, we also don't understand functionally why the multituberculate mammals became extinct, although they had some traits apparently inferior (and others superior) to contemporary therians; monotremes do manage to persist in a marsupial-infested Australia. There are nevertheless several kinds of evidence that multituberculate extinction was caused by slow competition with placentals, by a form of group selection.

To conclude that our lack of such evidence for the Cambrian fauna indicates that the extinctions were more or less random is a qualitative example of the Fallacy of Null Hypotheses (see Van Valen, 1982, 1985). In statistical tests the null hypothesis is conventionally accepted unless "disproved" at some arbitrary significance level. This acceptance is a methodological procedure, not something which is supposed to give us positive information about the real world without corroboration. Lack of knowledge is not knowledge of lack.

There is in fact some weak evidence for a major selective component in the attrition of the Cambrian fauna. (That it was an attrition rather than a decimation is shown by the survival of a few clades of oddities much later.) One of the surprises in the Burgess Shale is the prevalence of animals, not all of them arthropods as the phylum now stands, with a pair of unusually large jointed appendages on their head or headlike region. Others (in a broad sense including the snout of the Carboniferous *Tullimonstrum*) have a single hydroskeletal appendage there. None seem to have survived the Paleozoic, and most were extinct before the Devonian. (The paucity of soft-bodied faunas precludes more precise statements.) It is therefore plausible, and would be confirmed by a statistical test except that the hypothesis is derived from the data, that the presence of one or a pair of large appendages on the head was selectively disadvantageous in post-Cambrian Paleozoic seas. Maybe someone will be able to retrodict this pattern functionally. But even so, it could have been causally minor or irrelevant in the actual attrition. (Some eurypterids and the marine scorpions did have sizeable appendages on their anterior prosoma in the middle Paleozoic, but they too disappeared.) The Mesozoic evolution of crabs and such suggests that the phenomenon isn't inherently fatal, even though their chelipeds are the first thoracic appendages.

I don't mean the head-appendage hypothesis above to be taken as more than a suggestion. Even a multiple-comparisons test would, as usual in its post-hoc applications, suffer the fatal defect of a lack of a precise (and here even approximate) reference set. What I do want to emphasize, though, is that we have no basis at all for denying a purely selective and even repeatable attrition. Run the tape again, and how many of the instruments are the same? We just can't say.

The book itself ends with *Pikaia*, the Burgess cephalochordate. Here the two biological themes merge, with I think no better success than before. Whether cephalochordate survival was due to the quasi-luck of quite special adaptations, or to the quasi-determinism of more general adaptations, remains as elusive as with the rest. And are we descended from such cephalochordates then, so that we wouldn't be here if they had succumbed? There are two problems. One is the reduction of the head in the modern amphioxus, just the opposite trend from vertebrates and still unclear, from what I have seen, for *Pikaia*. (Collins's drawing coyly hides the head.) The other problem is the relationships of the Conodonta, abundant through the Triassic and now with pretty good evidence, which Gould disputes without saying why, that they were derived from somewhere near the divergence of cephalochordates and vertebrates. If so, their exuberant survival would give us (or whatever) another chance.

We advance in our science by the development and investigation of new concepts, derived in diverse ways. Often they are new ways of looking at the old, as Whittington's group looked at the Burgess Shale material in new ways and has given us a new and mind-stretching fauna. It is ironic that the Philosophical Transactions of the Royal Society, where most of their work has been published, has just changed its publication policy so as to prohibit most monographs. There are now alternative outlets, but the change is symptomatic of the problems systematics is facing, not merely in Britain. Will most readers of this book even realize that they are looking at systematics, unless they pay close attention?

Gould has a remarkable talent for seeing the "essence beneath externality" (p. 84). We don't always agree, but it is a wonderful book.

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