

Wonderful Life Revisited: Chance and contingency in the Ediacaran-Cambrian radiation

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ABSTRACT - In his 1989 book *Wonderful Life* Stephen Jay Gould employed the fossils of the middle Cambrian Burgess Shale to argue for a pervasive role of contingency in the history of life. But Gould wrote at the advent of an explosion of research in the Ediacaran-Cambrian diversification of animals, before ‘tree-thinking’ had made great inroads into the reconstruction of phylogeny, and with just the first glimmer of data on the remarkable conservation of developmental genes across major animal clades. More than twenty years on, not only have views of the Burgess Shale fossils undergone considerable change, but the role of contingency has become more widely accepted among paleobiologists. Yet much of Gould’s argument that if one ‘played the tape again’ the outcome would differ is difficult to accept. In this contribution I review new views of the Ediacaran-Cambrian explosion relevant to the role of chance in evolution as an example of a larger tension between historicity and laws in evolution.

Introduction

Although the importance of determinism versus chance was not one of the ‘eternal metaphors’ in Stephen Jay Gould’s essay of the same name (Gould, 1977), but it might well have been, for the debate over how much of the history of life is deterministic, the result of physical processes, scaling laws or various biological constraints, versus how much of it reflects either chance or just one of many possible evolutionary histories (contingency) dates at least to Darwin (Beatty, 2008). Although the topic became less prominent with the Modern Synthesis, chance and necessity served as the title of Monod’s eponymous book (Monod, 1972), arose as ‘frozen accidents’ in Crick’s early discussion of the structure of the genetic code (Crick, 1968), and played a significant role in Kauffman arguments that many aspects of evolution may be ‘frozen accidents’, preserved not for their adaptive value but rather because they generate complexity which is subsequently preserved (Kauffman, 1993). The tension between determinism and chance continues today (Carroll, 2001). It appears in discussions over the ubiquity of allometric scaling relationships (Brown et al., 2004) and in structuralist arguments for the importance of physical forces (Salazar-Ciudad et al., 2003). In astrobiology a fundamental assumption is that sufficient regularities exist in the history of life that studies on Earth will have implications for life elsewhere in the Universe. The ubiquity of convergence of morphological form has often been used as evidence against contingency (Conway Morris 2003, McGhee, 2011), generating a suite of issues. But chance and contingency are different issues. Since 1989 the much of focus of this tension over chance,

contingency, convergence and determinism and has revolved around Gould's book *Wonderful Life* (Gould, 1989), his recounting of the history of research into the extraordinary fossils of the Burgess Shale and their implications for the history of life.

As I discuss further below, one of the meanings of contingency involves the unpredictability of evolutionary history. Let me state at the outset that there seems little point in disputing this facet of life. My favorite example comes not from the Burgess Shale or the Cambrian, but from the great end-Permian mass extinction 252 million years ago (Ma) when over half of all families and perhaps 90% of marine species disappeared (Erwin, 2006b). Echinoids (sea urchins, sand dollars and their allies) were a relatively insignificant component of Paleozoic marine ecosystems with perhaps eight genera in the Permian. Based on phylogenetic analysis of echinoids only one or two species of echinoid appear to have survived the mass extinction, but these gave rise to the incredible diversity and morphologic range of post-Paleozoic echinoids with almost one thousand living species. I see no way to reject the view that the survival of echinoids was fortuitous and illustrates the role contingency can play in the history of life. More interesting perhaps, is how contingency plays out at different levels of evolution and the tradeoffs with deterministic processes.

Gould published *Wonderful Life* in the early years of a tremendous increase of research interest in the Cambrian Explosion of animal life, which coupled with the spread of new, more rigorous methods of phylogenetic reconstruction through cladistic methods, considerably altered our understanding of many of the empirical issues raised by Gould. To take a few examples of changes that occurred within a few years of the publication of *Wonderful Life*, our understanding of the phylogenetic relationships among animal clades was fundamentally altered by new techniques in phylogenetic analysis (Jefferies, 1979) particularly the introduction of molecular data (Field et al., 1988), and the application of molecular clocks (Runnegar, 1982; Wray et al., 1996). New radiometric dates began to emerge in the early 1990s, changing our understanding of the tempo of the Cambrian explosion and the association between the earlier Ediacaran macrofossils and the Cambrian (Bowering et al., 1993). The Chengjiang Fauna had been discovered by Hou Xianguang in 1984, providing a slightly older, early Cambrian Chinese analog to the Burgess Shale (Hou et al., 1991) but most publications of the new taxa came during the 1990s and continue today. Many other new fossil discoveries have occurred as well. New techniques were developed to deal with many issues of macroevolutionary dynamics, such as quantitative approaches to the study of morphologic disparity (Briggs et al., 1992; Foote, 1992) in direct response to the claims made by Gould. Finally, the growth of comparative evolutionary developmental biology ("evo-devo") has shown that many of developmental genes responsible for body plan formation in animals are broadly shared across the major clades, and thus must have been present early in animal history. In short, since 1989 almost every aspect of our understanding of the early history of animals and the Cambrian Explosion has been fundamentally altered, and recent descriptions of the Cambrian Explosion are much different than those of the late 1980s or early 1990s (Erwin et al., 2011; Erwin and Valentine, 2013). These developments have altered, often significantly, the evidentiary basis for his arguments.

The theoretical framework of Gould's argument has changed as well. The arguments for contingency that Gould advanced in *Wonderful Life* were only a part of a larger landscape of his scholarship on the role of history in evolution. Indeed, there is a curious and I think largely unresolved tension in Gould's work between his earlier interest the role of law-like processes (Gould, 1970; Raup et al., 1973a; Raup and Gould, 1974; Raup et al., 1973b), and later papers addressing how historical constraints may limit the power of adaptive evolution (Gould and Lewontin, 1979). A central theme in this later phase is limits to the role of natural selection in structuring the waxing and waning of diversity in different clades of organisms. These threads were the focus of a 1980 *Paleobiology* article in which Gould explicitly addressed the tension between idiographic studies (descriptions of historically unique events) versus nomothetic research (the search for general principles or laws) (Gould, 1980). Gould later returned to the theme, arguing for the importance of mass extinctions in limiting the power of adaptive evolutionary trends (Gould, 1985). (See also discussions in Baron, 2009; Beatty and Desjardins, 2009; Sepkoski, 2012; Sepkoski and Ruse, 2009; the philosopher Chris Haufe is currently studying this issue) There can be of course, no certain resolution to idiographic versus nomothetic approaches, or to the tension between historicity and a search for general laws. As Gould realized, paleontology is a combination of both idiographic and nomothetic approaches. Each approach plays an important role in understanding aspects of the history of life, and both have been addressed in many discussions of macroevolution since 1989, as well as in papers by a number of philosophers and historians.

My objective here is to reconsider the arguments Gould makes in *Wonderful Life* in light of the discoveries and conceptual advances since 1989, both on the Burgess Shale fossils specifically as well as the Cambrian Explosion more generally. I begin with a summary of the principle arguments that Gould developed in *Wonderful Life*, focusing on those associated with the role of contingency. I turn next to a necessarily abbreviated discussion of the scientific developments on the events of the Ediacaran and Cambrian since 1989 before assessing the status of Gould's arguments in *Wonderful Life*. The issues of contingency raised by Gould have received extensive discussion by philosophers and historians of science. Lacking a union card for either discipline I will confine my comments to those issues where knowledge of the fossil record or evolution is relevant.

Major Arguments of *Wonderful Life*

In *Wonderful Life* Gould employed the fossils of the Burgess Shale and the history of research on the fossils to further his arguments for the importance of historical contingency relative to selection and adaptation in the history of life. Gould made three primary, albeit overlapping, arguments: First, that rather than the 'cone of increasing diversity', which he describes as the primary iconography of evolution, the fauna of the Burgess Shale supports a model of rapid increase in morphologic diversity or disparity, followed by elimination of many lineages and diversification of the successful lineages. His critical point here is that maximal morphologic disparity was a primary feature of the Cambrian metazoan radiation, not a consequence of subsequent evolutionary history. Thus evolutionary innovation was primarily focused in the events of the Cambrian, with

later history largely, in Gould's view, "generating endless variants upon a few surviving models" (Gould, 1989, p. 47). He describes this as a model of decimation and diversification. The book as a whole celebrates the incredible morphologic disparity of the Burgess Shale fossils, suggesting at one point that in addition to the thirty or so animal phyla recognized in 1989:

"the Burgess Shale, one small quarry in British Columbia, contains the remains of some fifteen to twenty organisms so different one from the other, and so unlike anything now living, that each ought to rank as a separate phylum.... The fifteen to twenty unique Burgess designs are phyla by virtue of anatomical uniqueness." (Gould 1989, p 99-100).

This statement accurately captures the zeitgeist of the times. As a personal example, Jim Valentine and I made approximately the same estimate of phyla and new classes (Valentine and Erwin, 1987), and Conway Morris and others made similar arguments.

The model of maximal increase in morphologic diversity (now described as disparity) early in the history of Metazoa as a whole, and of specific clades leads naturally to the second major argument of the book: Gould's highly contentious thought experiment of 'playing the tape of life again'. (The metaphor of 'playing the tape of life again' as applied to the Cambrian actually originated with Conway Morris (1985).) If the rate of evolutionary experimentation documented by the fossils of the Burgess Shale was as high as claimed by Gould, and if the success of different clades was based on factors other than adaptive value, indeed if success were largely a contingent phenomenon, then an Ordovician ocean could have been composed of very different clades. But as Gould recognized, this argument depends upon the survivors having greater morphologic complexity and competitive ability. Gould's argument represents the acme of his fight against adaptive storytelling and inferred evolutionary progress. In a critical passage in *Wonderful Life* Gould argues for an alternative view:

"...any replay of the tape would lead evolution down a pathway radically different from the road actually taken. But the consequent differences in outcome do not imply that evolution is senseless, and without meaningful pattern; the divergent route of the replay would be just as interpretable, just as explainable *after* the fact, as the actual road. But the diversity of possible itineraries does demonstrate that eventual results cannot be predicted at the outset. Each step proceeds for cause, but no finale can be specified at the start and none would even occur a second time in the same way, because any pathway proceeds through thousands of improbable stages. Alter any early event, ever so slightly and without apparent importance at the time, and evolution cascades into a radically different channel" (Gould, 1989, p. 51).

For Gould this is the essence of contingency, in which the outcome of any historical process is dependent upon a sequence of largely unpredictable prior events. [Gould's discussion of *post hoc* evolutionary explanations is described by Taleb (2010) as the 'narrative fallacy'; see also Kahneman, (2011)]. Gould contrasted the fate of priapulids, a

group of carnivorous worms that persist today but at very low diversity, with the polychaete annelids, the clade that includes earthworms and is today a major component of animal biodiversity. Although priapulids are today ecologically insignificant, they were far more abundant than annelids among the fauna of the Burgess Shale specimens, and there are five species of each clade (Briggs et al., 1994).

Near the end of *Wonderful Life* Gould considers other examples that illustrate the power of contingency, events where the history of life might have turned out differently: the diversification of large flightless birds versus placental mammals after the end-Cretaceous mass extinction, survival during mass extinctions, the evolution of the eukaryotic cell, the failure of the Ediacara fauna of soft-bodied animals that serves as the prelude to the Cambrian explosion, the small shelly fossils of the earliest Cambrian, terrestrial vertebrates, mammals and finally humans.

Finally, Gould's third argument in *Wonderful Life* builds from the pattern of disparity and the ubiquity of contingency to conclude that selection and adaptation play a much less significant role, at least over the great spans of deep time, than acknowledged by many evolutionary biologists. This theme was first enunciated in the *Spandrels of San Marco* paper (Gould and Lewontin, 1979) and developed through much of the middle part of Gould's career. Gould's views on adaptation figure in evaluating just what he meant by contingency.

The Ediacaran-Cambrian Radiation since *Wonderful Life*

Although *Wonderful Life* was intended as much for a general as a professional audience, publication led to considerable controversy among paleontologists over Gould's interpretations of the fossil data, among evolutionary biologists and philosophers over his claims for the role of contingency, and among many scholars about the nature of contingency itself. In this section my interest is in how subsequent research on both the Burgess Shale and more broadly on the Cambrian Explosion have affected Gould's conclusions.

Several decades of work on fossil and geological data through the Ediacaran (635-541 Ma) and Cambrian (541-489 Ma) have established that the Ediacaran-Cambrian Radiation (ECR) began with the appearance of the first soft-bodied Ediacaran macrofossils after 579 Ma. The suite of Ediacara fossils includes a variety of different clades, likely of metazoan affinities but lacking obvious guts, appendages or other features characteristic of post-Cambrian metazoan clades (Erwin et al., 2011; Xiao and Laflamme, 2008). The Cambrian explosion itself begins after 542 Ma with the appearance in the fossil record of a diverse array of bilaterian groups including arthropods, molluscs, and most other major clades of marine animals. This evolutionary diversification clearly encompasses more than just bilaterian animals, however, as it is associated with the appearance of a diversity of sponges (Botting and Butterfield, 2005), organic walled microfossils (Butterfield, 2001), and a diverse array of burrows and other trace fossils (Jensen et al., 2005). With additional study of the fossil record and new radiometric dating the abruptness of the fossil appearances has only increased (Erwin et al., 2011).

Our understanding of the morphologic breadth of the Cambrian explosion has been greatly enhanced by numerous occurrences of extraordinary preservation where soft-bodied organisms have been exquisitely preserved. The Burgess Shale was just first of these to be discovered. It is now dated to Cambrian Stage 5, about 511 Ma. In particular the Chengjiang fauna contains many fossils representing taxa very similar to the Burgess Shale, as well as some new forms (Hou et al., 2004).

The chordate *Pikaia* is the final taxon discussed in *Wonderful Life*, with Gould claiming that he “saved the best for last” (Gould, 1989, p. 321). Recognizing the apparent segmentation, Walcott had placed it among the polychaete annelids, but as a graduate student Conway Morris had recognized it as the earliest-known chordate. Following a rather prolonged gestation, the paper redescribing *Pikaia* recently appeared (Conway Morris and Caron, 2012). Gould closes the book with the following rumination, worth quoting at some length:

“I do not, of course, claim that *Pikaia* itself is the actual ancestor of vertebrates, nor would I be foolish enough to state that all opportunity for a chordate future resided with *Pikaia* in the Middle Cambrian; other chordates, as yet undiscovered, must have inhabited Cambrian seas. But I suspect from the rarity of *Pikaia* in the Burgess and the absence of chordates in other Lower Paleozoic *Lagerstätten*, that our phylum did not rank among the great Cambrian success stories, and that chordates faced a tenuous future in Burgess times.

Pikaia is the missing and final link in our story of contingency—the direct connection between Burgess decimation and eventual human evolution.... Wind the tape of life back to Burgess times, and let it play again. If *Pikaia* does not survive in the replay we are wiped out of future history—all of us, from shark to robin to orangutan. And I don’t think that any handicapper, given the Burgess evidence as known today, would have granted very favorable odds for the persistence of *Pikaia*.” (p. 322-333)

I wish I had taken the bet, for Gould’s suspicion that other chordates inhabited Cambrian seas has been abundantly confirmed by the Chengjiang biota (Chen, 2008; Shu et al., 2010). Representatives of each of the extant chordate subphyla have been described from the Chengjiang, including vertebrates. *Cathymyrus* is, like *Pikaia* a cephalochordate (Shu et al., 1996), several craniates have been described as well as *Shankouclava*, a urochordate. Other clades of crown or stem-group chordates are also known, including vetulicolids and the more problematic yunnanozoans. And several of these, such as *Haikouichthys*, a jawless fish, are far from rare. As a good Bayesian, this forces me to recalculate the odds on the persistence, if not of *Pikaia*, than chordates as a clade and they certainly seem a great bit higher.

The evidence for relatively abrupt diversification of Cambrian contrasts sharply with evidence from molecular clock studies, which compare DNA sequences of living taxa, calibrated against divergence times estimated from the fossil record, to estimate older

divergence estimates. The rigor of such analyses has improved greatly in the past decade, and in a recent study we estimated the origin of animals at about 780 Ma and of bilaterians at about 660 Ma (Erwin et al., 2011). These results indicate a long, largely hidden history of early metazoan radiation, but the molecular clock study also confirms a burst of diversification of crown group bilaterians during the late Ediacaran and Cambrian, consistent with fossil evidence. Thus we appear to have evidence for both a 200 million year early history of animals, and a burst of diversification associated with the ECR. The resolution of the apparent conflict between the fossil and molecular clock model can be found in a model of gradual divergence of metazoan lineages up to the Ediacaran, followed by the rapid establishment of a variety of larger, macroscopic stem and crown-group bilaterian clades in the latest Ediacaran and early Cambrian (Erwin and Valentine, 2013). Thus the Cambrian Explosion is a real and significant macroevolutionary event, but it is not the same thing as the origin and early diversification of Metazoa, a process that played out over some 150 million years during the Cryogenian and early Ediacaran.

Molecular methods have also revolutionized our understanding of the overall topology of metazoan relationships, such that current views of a tripartite division of bilaterians among deuterostomes, lophotrochozoans and ecdysozoans (Aguinaldo et al., 1997; Halanych, 2004) bears little relationship to the views of the late 1980s (e.g. Erwin and Valentine, 2013). For example Walcott, Whittington and Gould each accepted a fairly close relationship between arthropods and annelids, yet molecular data has since shown that the two clades are distantly related, belonging to the Ecdysozoa and Lophotrochozoa respectively.

One of the most profound changes impacting Gould's arguments was the introduction of cladistics or phylogenetic methods for rigorously assessing the evolutionary relationships among taxa. The introduction of cladistics or phylogenetic analysis was in its infancy in the 1980s and in fact neither word appears in the index to Gould's book. Today most researchers would rightly criticize a revision of Burgess Shale taxa, or a description of new species, that did not include at least an initial phylogenetic analysis. Early in *Wonderful Life* Gould claimed that the intellectual straightjacket of the cone of increasing diversity necessarily forced Walcott to classify the fossils of the Burgess Shale "... either as primitive forms within modern groups, or as ancestral animals that might, with increased complexity, progress to some familiar form of the modern seas" (p. 46). Much of the middle part of the book describes (as an 'intellectual revolution') the changes brought about by Whittington, Briggs and Conway Morris and the recognition that many of the Burgess animals represented 'weird wonders' unlike any modern phyla. But in a turnaround that many of the critics of *Wonderful Life* must relish, the introduction of phylogenetic methods has altered the perspective of paleontologists yet again, with many seemingly distinct phyla now recognized as stem lineages of extant clades. Clades are defined as monophyletic groups of taxa, incorporating an ancestor and all of its descendants. This is a very different (and far more useful) approach than reliance upon some poorly characterized inference of 'morphologic distinctiveness' as a basis for distinguishing taxa. As a consequence of this emphasis on 'tree-thinking' the 1980s boom

in extinct phyla and classes was replaced by a focus on phylogeny, and the identification of stem- and crown-groups. The morphologies of these groups are no less distinctive but the evolutionary relationships of most of the Burgess Shale and Chengjiang fauna are now well established.

Stem groups are extinct representatives from the early in the history of a clade, branching before the crown group. The crown group, in contrast, represents the last common ancestor of the *living* members of a clade, and all of its descendants both extinct and living (Jefferies, 1979). The total group comprises the crown group plus various stem groups back to the last common ancestor of all members of the clade. Derek Briggs (one of the chief protagonists of *Wonderful Life*) was the principle advocate for the introduction of phylogenetic methods to the study of the Burgess Shale (Briggs and Fortey, 1989). Brysse (2008) presents a discussion of the impact of this development on interpretations of the Burgess Shale. As she emphasizes, many of the Burgess arthropods, while clearly arthropods, possessed combinations of morphological characters that were otherwise unknown and thus had proved impossible to classify. The introduction of phylogenetic analysis and the recognition of stem and crown-groups focused attention on shared morphologic characters and led to the recognition that most of the canonical 'weird wonders' of the Burgess Shale represent stem-groups of well-established clades. Thus *Opabinia*, the various anomalocarids, and some arthropods such as *Marrella*, *Yohoia*, and *Naraoia* represent various basal stem groups of the Panarthropoda (Daley et al., 2009; Edgecombe, 2010). With *Hallucigenia* joining *Ayschaesia* as a lobopodian, relatives of the extant Onychophora, and the discovery of many lobopodians among the Chengjiang biota (Liu et al., 2008) it became apparent that the diversity of Cambrian lobopodians was much greater than previously realized. Subsequent studies have suggested that the lobopods form a paraphyletic grade leading to the base of the Panarthropoda (Budd, 1996, 1999; Edgecombe, 2010).

This cladistic approach to phylogeny has by now decisively replaced the earlier approach, known as evolutionary systematics, in which morphologic distinctiveness often played a significant role in taxonomic assignments. As Brysse (2008) observes, Gould might well have rejected a cladistic approach because it focused on shared derived characters and rejected the use of unique morphological features (apomorphies). This was a point of serious contention through the 1980s and into the 1990s, but eventually faded with the introduction of quantitative techniques to assess morphological diversity, better known now as disparity.

Through the 1980s paleontologists and many evolutionary biologists used taxonomic ranks as a rough proxy for morphologic disparity (e.g. Erwin et al., (1987)). Paleontologists were not unaware of the limitations of such an approach, but the combination of the development of quantitative morphometrics during the 1980s (Benson et al., 1982; Bookstein et al., 1985) and the controversies engendered by the publication of *Wonderful Life* led directly to quantitative methods to assess morphologic disparity (Briggs and Fortey, 2005; Briggs et al., 1992; Foote, 1992, 1993; Fortey et al., 1996; McShea, 1993; Wills, 1998; reviewed by Erwin, 2007; Foote, 1997). When

combined with phylogenetic analyses, such approaches constitute a powerful suite of methods with which to analyze the occupation of evolutionary space. Although the early studies by Briggs, Fortey and colleagues were intended to refute Gould's claims about disparity, the general conclusion from a variety of studies (reviewed by Erwin (2007), Foote (1997)) has been that many large clades, particularly those involved in the Cambrian Explosion, rapidly defined the morphospace occupied by the clade (early maximal disparity), followed by subsequent filling out of the space through taxonomic diversification. This pattern is not universal, however. Post-Cambrian priapulids, for example, appear to occupy a morphospace adjacent to the Cambrian representatives (Wills, 1998; Wills et al., 2012). Thus Gould's claims that Cambrian morphospace was larger than later in the Phanerozoic have not been supported by subsequent studies, but these studies have not supported the 'cone of expanding diversity' model that Gould questioned. Gould deserves credit (along with Valentine and others who made similar observations (Valentine, 1980)) for driving this conceptual shift in macroevolution.

The discovery of highly conserved developmental regulatory genes has also dramatically altered our understanding of the ECR, with implications for some of the arguments about contingency in *Wonderful Life*. Briefly, analysis of the genomic basis of development in many living animals has revealed that they share a common 'developmental toolkit' of genes responsible for patterning the developing embryo. These shared genes are generally transcription factors or elements of signaling pathways and including the HOX genes as well as others involved in anterior-posterior and dorsal-ventral patterning and the formation of eyes, brains, heart, appendages, the gut (Carroll, 2008; Carroll et al., 2001; Davidson and Erwin, 2010b; Erwin, 2006a; Erwin and Davidson, 2002; Knoll and Carroll, 1999). In contrast to views of development through the 1980s, these discoveries reveal a common developmental underpinning shared among all bilaterian animals, and extending into basal clades such as cnidarians and even sponges. Consequently, similarities in developmental patterning (for example, limb development in lobopodians and arthropods) often reflect shared developmental mechanisms. The critical issue here for discussions of contingency is that although the morphologic expression of eyes, appendages, etc. may have arisen independently in different clades (after all, the eyes of a cat and a fly share few similarities) the underlying developmental foundation is shared. This raises some tricky issues for assessing claims of historical uniqueness versus convergence, for even distantly related groups may share common developmental pathways.

As research on the ECR has progressed there are two components, discussed in the final chapter of *Wonderful Life*, that might seem even better exemplars of the role of contingency than the animals of the Burgess Shale: the soft-bodied forms of the Ediacaran fauna (579-542 Ma) and the small shelly fossils that dominated the earliest Cambrian (542- ~520 Ma). The Ediacara macrofossils encompass a diverse array of centimeter to meter-sized fronds, disks and more complex architectures, some vaguely resembling bilaterians (Fedonkin et al., 2007; Xiao and Laflamme, 2008). Although many exhibit bilateral symmetry, none show evidence of appendages, eyes, a gut or other

bilaterian features, which has led to a long history of controversy over their phylogenetic affinities (discussed by Erwin and Valentine 2013). Gould relied on Seilacher's re-interpretation of the Ediacara fossils as a separate and independent multicellular clade (Seilacher, 1984). Seilacher's novel perspective, while insightful, has relatively few adherents today (see discussion in Erwin and Valentine, 2013). Laflamme's recent analysis suggests there are perhaps six different clades of Ediacarans distributed across the Metazoan tree, as well as a number of as yet unresolved groups (Laflamme in prep, and Erwin et al. 2011). One of the clades includes *Kimberella* and likely represents a molluscan stem-group. The causes of the disappearance of the Ediacara fossils remains unclear (Laflamme et al., 2013), but Gould suggests that in an alternative world we might wind up with nothing but Ediacarans. I think we can now reject this possibility. Molecular clock evidence indicates that many metazoans, including bilaterian clades were present during the Ediacaran, although most are not represented in the Ediacara macrofauna. But once the physical environment and ecological interactions triggered the Cambrian Explosion the majority of the Ediacara clades were done for – predation alone would have seen to their disappearance. So if one is resetting the clock to the Ediacaran, evolution might have played out much the way it did, at least at the macroscale.

The small shelly fossils (SSFs) are assemblages of minute (<2mm) plates, spines, tubes and other fossils. Some of these skeletal elements are the shells of whole animals, but many represent parts (sclerites) of larger animals; when the sclerites are preserved as part of the whole animal rather than disarticulated they are described as the scleritome. The spines of *Hallucigenia* from the Burgess Shale, if disarticulated, would be SSF elements, for example. A great diversity of SSF has been described appearing near the base of the Cambrian and increasing steadily in diversity through stages 1 and 2 (Bengtson, 2005; Kouchinsky et al., 2011; Li et al., 2007; Maloof et al., 2010). The SSF represent many different clades of lophotrochozoans and some ecdysozoans; deuterostomes seem to be poorly represented. But the numerous clades of SSF provide us many phylogenetically independent tests of Gould's claims for contingency – and relatively few passed. Having a multi-plate scleritome just doesn't seem to have been a viable strategy in the face of increased predation, particularly when most of these clades were capable of forming a single larger and more protective, shell.

Thus the Ediacara macrofossils and the SSF share many similarities with Burgess Shale-type faunas: Both exhibit high degrees of disparity with relatively low diversity (although assessing taxonomic diversity in the SSF is hampered by disarticulation); their preservation has been strongly influenced by rather narrow taphonomic windows, from microbial mats for Ediacara fossils (Gehling, 1999; Laflamme et al., 2010) and an abundance of phosphate deposits for the SSF (Porter, 2004). The 'disappearance' of both groups from the fossil record at least partly reflects these preservational issues, clouding their true evolutionary duration. The recent report of an anomalocarid from the Lower Ordovician of Morocco (Van Roy and Briggs, 2011) revealed that some of the Burgess Shale lineages may have had quite respectable durations but are simply not well represented in the fossil record. Nonetheless, for both the Ediacara macrofossils and the

small shelly fossils at the macroscale a pure contingency argument seems difficult to sustain.

In summary, research into the ECR since the publication of *Wonderful Life* has altered the empirical foundation for some but not all of Gould's arguments. Phylogenetic methods have made most if not all of the 'weird wonders' less weird as they have found homes as stem groups of larger clades. This even extends to such peculiar forms as *Opabinia*. Quantitative assessments of morphologic disparity, however, have largely confirmed much of Gould's argument about maximal early disparity and the limitations of 'the cone of expanding diversity' as an appropriate metaphor for the history of life. As Conway-Morris during the 1980s, Valentine and I, and many others argued, the ECR was an interval of extraordinary morphologic innovation. Indeed evidence from the body and trace fossil record and the molecular clock estimates of divergences of crown-group bilaterians independently support the conclusion that the Cambrian explosion was a significant and rapid episode of evolutionary innovation. The completely unexpected discovery of deep conservation of developmental pathways across all major clades of animals has recast arguments about morphological patterning. The early origin of much of the developmental toolkit required to construct bilaterians (probably by about 680 Ma: Erwin et al. 2011), strongly suggests that the Cambrian explosion of bilaterian forms in the fossil record reflects ecological feedbacks and possibly environmental changes (Erwin and Valentine 2013).

Contingency

In Chapter 3 of *Wonderful Life* Gould focuses his argument for the contingent nature of life on the more iconic specimens, particularly the arthropods *Marrella*, *Yohoia*, *Naraoia*, *Sanctacaris*, and some of the bivalve arthropods, as well as *Pikaia*, *Opabinia*, *Aysheaia*, *Anomalocaris* and *Wiwaxia*. This argument is central to his thesis and has generated considerable controversy and discussion among paleontologists, evolutionary biologists and philosophers. Here I want to sharpen my evaluation of Gould's claims in light of the discussions over the nature of contingency.

Five different senses of contingency have been identified: 1) *drift or sampling error*, which Gould explicitly rejected as a form of contingency, although not always to the satisfaction of some (Beatty, 2006; Travisano et al., 1995). 2) *Unpredictability*, in which the outcome of a process cannot be determined from a prior state (Beatty, 2006). 3) *Causal dependence* or sensitivity to initial conditions in which a prior state is necessary to reach a particular outcome (Beatty, 2006; Ben-Menahem, 1997, 2009); Turner (2011) suggests that contingency as causal insufficiency might be a better term. Beatty (2006) argued that although unpredictability and causal dependence can be complementary, Gould failed to distinguish between them and often conflated the two. 4) *Sensitivity to external disturbance*, which is related to the resilience of a historical process and is distinct from sensitivity to initial conditions (Inkpen and Turner, 2012). 5) *Macroevolutionary stochasticity*. Turner (2011), in a discussion of Beatty (2006) suggested that Gould's argument in *Wonderful Life* is largely focused on macroevolutionary sorting among species, and that he viewed contingency as an issue of unbiased species sorting, rather than the

sampling error problem in point 1) above. Turner claimed: "...evolutionary contingency is the random or unbiased sorting of entire lineages. It just *is* the macroevolutionary analogue of random drift." (p. 69, emphasis in original). Finally, Inkpen and Turner (2012) offered a preliminary discussion of how the 'topography' of historical contingency may change over time. This seems quite probable, and they discuss how history might involve conditional inevitability (a concept originally introduced by Sterelny (2005)). This important issue is one that has received too little attention (Erwin, 2011).

Although Gould viewed testing his contingency hypothesis as difficult, several different groups have attempted just that using a variety of theoretical, field-based and experimental approaches. For example, Fontana and Buss (1994) applied λ -calculus, a form of abstract chemistry, and concluded that general patterns of self-organization would emerge even in the absence of selection. Fontana and Buss suggest that these results are applicable to early stages in the history of life, perhaps up to the origin of eukaryotes. The structure of repeated adaptive radiation on islands provides an interesting 'natural' experiment of Gould's contingency hypothesis, for ecologists expect similar ecological communities to arise in similar environments. Losos and colleagues used their studies of repeated production of *Anolis* lizards in the Caribbean to evaluate the predictability or determinism of adaptive radiations (Losos et al., 1998). The similarity of ecomorphs on different islands suggested that contingency was less significant than ecologically generated constraints, although within a single island the order of evolution of ecomorphs did constrain the available evolutionary options for other species. A recent paper evaluated replicate radiations of *Anolis* across Caribbean islands, including unique species, to evaluate the overall convergence using a model of the adaptive landscape (Mahler et al., 2013). The results showed that convergence of morphologies onto shared adaptive peaks was the most favored model. This suggests that the adaptive landscape has persisted for perhaps 30-40 million years, more than long enough to influence macroevolutionary patterns. A similar pattern ecomorphologic constraint has been found among the various ecomorphs of the spider *Tetragnatha* in Hawaii (Gillespie, 2004) and Losos (2010) evaluates other cases. The implications of these highly structured radiations for Gould's argument is mixed, for while they strongly support a deterministic view, the radiations are also confined to closely related species which share common developmental and genetic systems (Losos 2010), a situation most unlike the Cambrian explosion. Beatty (2006) reports that Losos heard that Gould was unimpressed by their initial results, suggesting that such recent divergences had little relevance for the Cambrian Explosion. If true (and I suspect it was), this may provide further insight into Gould's perspective and support Turner's argument for the relevance of macroevolution sorting to the contingency argument in *Wonderful Life*.

Lenski's long-term experimental evolution with *E. coli* project was in part intended to rest Gould's assertions. In Lenski and Travisano (1994) and Travisano et al., (1995) they conducted several experiments to test the role of contingency and showed that different evolutionary outcomes could result from the effects of random mutation and the order of mutation (Beatty and Desjardins (2009) discuss these issues as well). Thus in contrast to the ecological studies reported by Losos, in Lenski's experimental work where the *E. coli*

populations were in identical environments, different clones exhibited very different evolutionary trajectories. These results seem to support Gould's arguments for contingency, but as Turner (2011) points out, as beautiful as the work of Lenski and Travisano has been, it really does not address the issue of macroevolutionary sorting that is at the heart of Gould's argument.

A more macroevolutionary critique of Gould's contingency argument by Vermeij (2006) utilized a compilation of both unique or singular and repeated evolutionary innovations, ranging from the origins of the genetic code and arthropod wings to vertebrate teeth and plant alkaloids. Vermeij acknowledges that contingency (in Beatty's sense of unpredictability) is "an essentially universal property of dynamic systems" (p. 1804), but suggests that an examination of unique evolutionary innovations provides an opportunity to examine the ubiquity of contingency. According to Vermeij, unique innovations support claims of contingency, but if innovations occurred multiple times this supports a more deterministic system in which the innovation would occur eventually, even if in a different clade. Vermeij shows that the 'purportedly unique' innovations are significantly older than those that occurred multiple times. However, he concludes that this pattern is more likely to reflect the loss of information from other clades; with a more complete record many of these unique innovations would be revealed to have occurred several times as well. Vermeij's list of both singular and repeated innovations seems highly idiosyncratic, however, reflecting the absence of a metric for evolutionary innovations and difficulty in granularity. Thus bilaterian pattern formation is counted as a singular innovation but eyes as a repeated innovation since the phenotypic expression has arisen multiple times. More problematic is the inclusion of many items among the repeated innovations (e.g. a gastropod labral tooth) that seems incommensurate with the origin of eukaryotes, or of sex. Vermeij concludes that most innovations arise multiple times in many clades because their adaptive value is sufficiently high that selection will favor their development even if the pathways to produce the innovations differ in their particulars.

Perhaps the most sustained critique of Gould's contingency argument has come from Simon Conway Morris and his proposals that the ubiquity of convergence suggests that despite apparent contingency, long-term determinism regulates patterns of evolutionary change (Conway Morris, 2000, 2004, 2009). Conway Morris' argument rests on the ubiquity of convergence – the appearance of similar patterns in different groups. He has exhaustively compiled examples of convergence and employed them to argue that evolution is far more deterministic than admitted by Gould. Curiously, some of the best evidence for the extent of convergence come from phylogenetic analyses, yet Conway Morris has consistently, and somewhat perversely, refused to use such examples. As several authors have noted, it is often difficult to discriminate between convergence between unrelated taxa and parallelism (Pearce, 2012; Powell, 2012). The tension between chance versus determinacy is plagued by issues of granularity as well. At a coarse-grained level two features may seem convergent, while they look very different in a more fine-grained analysis, as both Sterelny (2005) and Inkpen and Turner (2012) suggest for Conway Morris's (2004) discussion of agriculture in humans and leafcutter ants. In the absence of a concrete metrics for the evaluation of apparent convergence, in

terms of phylogenetic distance, morphologic similarity (or similarity of other features), and developmental similarity, it seems difficult to adjudicate competing claims.

I think Conway Morris too readily dismissed the issues raised by the discovery of deep homology underlying developmental mechanisms in distantly related animal groups. Work over the past two decades has challenged distinctions between convergence and parallelism and led to both scientific and philosophic discussions about the nature of homology (Abouheif, 1999; Arendt and Reznick, 2008; Hall, 2007; Losos, 2011; Pearce, 2012; Wake et al., 2011). Reliably discriminating between convergence and parallelism is critical to evaluating claims of contingency, since convergence focuses attention on the power of external selection while parallelism emphasize the power of internal developmental mechanisms and constraints on the generation of variation. In a sense, developmental patterning may impose a structure on available evolutionary variation not unlike the ecological landscape of Losos's *Anolis* lizards and similarly support deterministic processes. Unfortunately, clearly identifying developmental homologies is difficult, particularly with increasing focus on developmental gene regulatory networks (Arendt and Reznick, 2008). Pearce (2012) proposes a 'neo-Gouldian' approach, emphasizing morphology in distinguishing between homology and homoplasy, and development in separating convergence and parallelism. He suggests: "...convergent traits are realized by non-homologous underlying generators, whereas parallel traits are realized by homologous underlying generators." (p. 445). Understanding where within a hierarchical GRN developmental changes lie may provide a mechanistic basis for Pearce's generators (Davidson and Erwin, 2010a, b; Erwin and Davidson, 2009). There may be no final resolution to the debate over deep homology and how it applies to convergence versus parallelism in part because researcher's use of the terms may often reflect differing rhetorical strategies.

With these discussions of contingency in hand we are now in a position to evaluate Gould's discussion of the Burgess Shale and the Cambrian Explosion in light of the five different definitions identified at the beginning of this section.

Gould dismissed the issue of sampling error as contingency with some justification, as sampling error, drift and similar problems did not really encompass the issues that he wanted to address. But I want to raise the sampling issue because it may be relevant for some of Gould's claims. Raup distinguished between three different modes of extinction selectivity: a 'field of bullets' scenario in which extinction is random without regard to differences in fitness; the 'fair game' scenario in which extinction selectivity is Darwinian, based on differential fitness or adaptation, and promoting long-term increases in same; and 'wanton extinction' where extinction is selective, but not based on factors other than those which promote survival in a species' normal environment (Raup, 1991). For example, during many mass extinctions (but not during background intervals) geographic range at the generic level increases survival probability (Jablonski, 1986).

Gould's discussion of the 'decimation' of the Burgess Shale fauna in *Wonderful life* (pages 233-239) contrasts assumptions of that survival was based on 'superior competitive ability'

versus his suggestion that widespread evolutionary experimentation led to contingent survival (see also Turner's (2011) discussion of the differential sorting of the Burgess Shale fossils as a lottery). Gould argues: "But if we face the Burgess fauna honestly, we must admit that we have no evidence whatsoever – not a shred – that losers in the great decimation were systematically inferior in adaptive design to those that survived" (p 236) (I'll address the issue of competitive ability again below). But in Raup's field of bullets scenario extinction selectivity is a function of the species diversity of a group, or abundance of a species, depending on the level of analysis and many of the 'weird wonders' of the Burgess were very rare. Very few specimens of *Aysheaia*, *Hallucigenia* or *Opabinia* are found in the collections at the Smithsonian while over 9000 individuals of *Marrella* (closely related to trilobites) were recovered by Walcott. Thus even if *Hallucigenia* and *Marella*, or one of the abundant euarthropods, had equivalent competitive abilities, and if the fossil abundances are a reasonable proxy for abundances of living species (correcting for arthropod molts, and time-averaging of sediment, for example), we would expect the persistence of the more abundant group on purely statistical grounds. And the more abundant or diverse a group is, and the longer it persists, the more likely it is to leave descendants rather than go extinct. Gould I think rightly questioned the assumption of superior competitive ability as an explanation for selective extinction (Raup's 'fair game' scenario), but does not seem to have considered whether sampling effects might be a sufficient explanation for the pattern observed. I do not want to argue that sampling effects are sufficient to explain the disappearance of the Burgess fauna as a whole. Because the fossil record preserves very few Burgess Shale-type exceptionally preserved faunas we have little information on when the more extraordinary organisms of the Burgess died out. Thus the question of extinction is essentially unresolvable with current data, but is likely more complex than Gould described.

I accept Beatty's argument that Gould used contingency in both the sense of unpredictability and causal dependence on initial conditions, although I think he largely intended it in the former sense. Inkpen and Turner (2012) suggest that contingency could also apply to sensitive dependence to external disturbance (developing the perceptive argument of Ben-Menahem (1997)). While they are correct that this is one compelling use of the term contingency, it is not obvious that this applies to Gould's claims for the Cambrian (and since we have no data on the extinction of these groups we can't apply it in any case).

Turner's (2011) suggestion that Gould's discussion of contingency needs to be seen as a macroevolutionary phenomenon, and allied to issues of species selection and clade sorting, is an interesting one. Turner relies overly much on a suite of papers written by Raup, Gould, Schopf and Simberloff during the 1970s for support of his thesis, evidently unaware that since Stanley et al. (1981) paleontologists have largely discounted the significance of these models because of the scaling problems (although see Slowinski and Guyer (1989) for an improved approach). Nonetheless, Turner is at least partly correct that Gould's discussion of contingency focuses on the differential success of clades (priapulids vs. annellids, or euarthropods vs. onychophorans) but focusing entirely on the macroevolutionary aspect of contingency would ignore Gould's longstanding critique of

adaptationism, which is better encompassed by uses 2 and 3. But I do not view Turner's macroevolutionary stochasticity as entirely separate from Beatty's unpredictability and causal dependence. Rather, in a hierarchical view of evolution with sorting and (less frequently) selection at many levels from genes through populations to species and clades (Jablonski, 2007), contingency may arise at different levels. The contingency of Travisano and Lenski applies to genes, Losos's studies to species, and Vermeij's at the level of macroevolutionary innovations among clades. Thus the question of "contingency versus determinism" is poorly posed. More accurately, the issue is the relative importance of contingency and determinism at a particular focal level. In any case, as Turner points out, Gould provides no operational means to evaluate unbiased versus biased sorting among the Burgess Shale taxa, and this remains a compelling research question.

In the case of the Ediacara macrofossils and the small shelly fossils of the early Cambrian I have argued that there are fairly good reasons for thinking that both groups would have disappeared in any alternative worlds in which active, particularly predatory, animals appeared. Thus Gould's claims of contingency would be limited to some suite of alternative worlds in which metazoan evolution for some reason stops with either of these assemblages (a fairly unlikely scenario).

Evaluating the claims of contingency for the Burgess Shale is more difficult. While I think it is plausible that contingency in the sense of both unpredictability and causal dependence are involved in aspects of the Cambrian Explosion (see Erwin 2015), the appropriate focal level for reconsidering *Wonderful Life* is the differential success of various clades of early metazoans. Here I think Gould's claims run into three critical difficulties: First, as described above, the apparently low diversity and low abundance of some of the more unusual forms of the Burgess Shale renders their long-term success implausible simply on statistical grounds, with no need to consider other factors. Second, the adoption of a cladistic approach to systematics, and particularly the concept of stem-clades has generated phylogenetic homes for most, if not all, of the 'weird wonders' of the late 1980s. This reduces the number of independent phylum-grade lineages and considerably alters the evaluation of claims of contingency. With the identification of many lobopod lineages, their close association with *Opabinia*, *Anomalocaris* and related forms, and with basal arthropods, the evaluation of their differential success becomes more interesting. Third, key to Gould's claims for contingency is his claim of "apparently equivalent anatomical promise – over twenty arthropod designs later decimated to four survivors, perhaps fifteen or more unique anatomies available for recruitment as major branches, or phyla, of life's tree..." (p. 288). The recognition of stem clades has already made a hash of the claims of "fifteen or more unique anatomies", but what of the claims for "apparently equivalent anatomical promise"? In my discussion of the Ediacara macrofossils and the small shelly fossils I suggested that it was difficult to argue that either clade was adaptively superior to later evolving bilaterians, particularly in the face of increased predation. Gould's argument is also difficult to sustain for some of the other Burgess organisms. Rigorously formulating such an argument would require functional studies, but euarthropods do share a number of important adaptations (jointed appendages, for example) that might have enhanced their 'anatomical promise'.

Discussion

The debate over contingency versus determinism touches another fundamental issue in evolution – why is there such a phenomenal underdispersion of genetic, developmental and morphological possibilities? Although Gould barely touched on the issue, Carroll (2001) posed the question of why morphological complexity is so much less than what seems possible based on the number of genes and their possible developmental deployment. Following the logic of Kauffman (1995), a genome of 25,000 genes with two inputs per gene, has $2^{25,000}$ possible states. Although accounting for the hierarchical structure of developmental regulatory interactions would reduce this state space, the fact remains that evolutionary complexity at all levels is so much less than the possible. Lewontin (2003) viewed the underdispersion of morphologies as one of the great unresolved problems in evolution. How much of this reflects determinism, and how much chance or contingency? Koonin usefully rephrased the question as one about “the fraction of all possible trajectories in the genotype space that are open for exploration by the evolutionary process” (2012: p. 405). In many molecular settings the range of possible pathways may be very limited, yielding what appears to be fairly deterministic pathways. More importantly, Koonin argues that the balance between contingency and determinism is critically dependent upon the selection pressure and thus population size. With sufficiently large populations evolution may be largely deterministic, while contingency will become increasingly important with smaller population sizes.

It seems unlikely that there is will be any general answer to questions over the role of contingency versus necessity in evolution, either with the Burgess Shale fossils and the Cambrian radiation specifically, or more generally in the history of life, in large part because at such a coarse level the question is mis-specified. The relative importance of contingency depends upon whether one is interested in molecular processes, development, phenotype or macroevolutionary patterns, and the answer may differ at these different levels, even for the same event.

The role of contingency versus historical laws in evolutionary processes is of great interest not only in understanding the trajectories of the history of life on the Earth, but critical for the nascent field of astrobiology. Essential to astrobiology as a field of inquiry is the assumption that there are sufficient underlying generalities to the history of life, a ‘Book of Rules’, if you will, to guide an exploration strategy. Among these assumptions are that life beyond Earth will be carbon-based, rely on aqueous chemistry, and employ metabolic other ecological and evolutionary principles that evolutionary biologists have established here, such as natural selection. Any of these assumptions might be false: life could be silicon-based, live in gaseous clouds in some non-cellular form and employ a truly Lamarckian evolutionary scheme. For a variety of chemical and biological reasons the likelihood of any of these alternatives is low relative to the probability of carbon and water based life. Thus the astrobiology community has focused attention and their exploration strategy on the more reasonable assumptions. Much astrobiological research, either explicitly or implicitly, assumes the nature of chance and contingency facing life on other planets is largely confined to particular domains.

In trying to understand the roles of chance and of contingency in evolution more generally (either on Earth or elsewhere) we can distinguish between a set of questions where laws or laws are likely to play a major role in controlling general patterns, and a domain where chance and contingency are likely to play an important role; there is also a set of questions where we currently lack sufficient information to be able to allot them to these two different domains.

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