

**SHOWDOWN ON THE BURGESS SHALE.** *Simon Conway Morris; Stephen Jay Gould.*  
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**Abstract:** Stephen Jay Gould published "Wonderful Life: The Burgess Shale and the Nature of History." His observations on the diversity of fossils found in Canadian shale and made conclusions on evolution. However, many of Gould's interpretations may be flawed. A participant in the research reevaluates and challenges some confusions.

Almost a decade ago, Harvard paleontologist and *Natural History* columnist Stephen Jay Gould published *Wonderful Life: The Burgess Shale and the Nature of History* (W. W. Norton and Company, 1989). In addition to chronicling ongoing work on the Burgess creatures, Gould used these fascinating fossils to exemplify his view of evolution. A few months ago, in *The Crucible of Creation: The Burgess Shale and the Rise of Animals* (Oxford University Press, 1998), invertebrate paleontologist Simon Conway Morris, of Cambridge University, a key player in Burgess research, challenged Gould's interpretations. We invited Conway Morris to summarize his argument, which we publish here, along with Gould's reply.

### The Challenge

Few books on paleontology have achieved the wide readership of Stephen Jay Gould's *Wonderful Life*, which popularized research spearheaded by Harry Whittington at Cambridge on the 520-million-year-old Burgess Shale, found between two peaks in the Canadian Rockies near Banff. But Gould did much more than chronicle discoveries concerning these Cambrian fossils; he also set forth his own deeply held views on the mechanisms and nature of evolution--and even on humankind's place in the universe--as the "lessons" to be drawn from the Burgess Shale.

In my new book, *The Crucible of Creation*, I argue that the major premises and conclusions of *Wonderful Life* must be seriously challenged. Let me begin with some matters of interpretation of patterns in the fossil record, then move on to paleontological particulars, and finally offer different "lessons" on what the Burgess Shale means in the larger reading of evolutionary history.

Gould emphasizes, above all, the apparent weirdness and diversity of the Burgess fossils. How, he asks, was such an extraordinary range of anatomies produced, and all apparently in a blink of geological time? He hints at a special mechanism at work--some unusual genetic happenstance gone wild--that might account for the production of so many biological novelties in such a startlingly short period of time, perhaps only a few million years. And what if we could "rerun the tape" so that the subsequent history of this maelstrom of diversification would have taken a different course? We would still have a planet full of life, he argues, but surely one utterly different from our familiar world. Notably, this new trajectory of evolution would probably not have led to the human species and its unique form of consciousness and self-awareness, which emerged through a series of contingent accidents in a unique, unrepeatable sequence.

Gould also charges that Charles D. Walcott, the discoverer of the Burgess Shale, was ill equipped to appreciate how diverse these novel phyla of sea creatures really were. Committed to the orthodox view that the range of life-forms must become ever greater over time, Walcott, in Gould's view, was unprepared to confront a world in which the proliferation of different kinds of life-forms (phyla) was much greater in the distant past

than in, say, the age of dinosaurs or the more recent age of mammals. Therefore, he argues, Walcott attempted to "shoehorn" a range of previously unknown creatures into a few familiar categories to fit his preconceptions. Gould asserts that paleontologists have only just begun to appreciate the ever-expanding catalog of bizarre "dead-end experiments" conducted by nature in ancient seas.

Looking back at the Cambridge group's classifications of the Burgess Shale, undertaken many decades after Walcott's pioneering work, my colleagues and I can see that we made some mistakes. Too often, we thought we had stumbled across yet another novel body plan (phylum, if you will), and in a few crucial instances, we did not realize that seemingly unrelated fossils were actually fragments of a single organism. With the benefit of hindsight, we can see that we had exaggerated the diversity of these supposedly bizarre fossils and needed to reconsider their evolutionary relationships. Recent discoveries in southern China (Yunnan) and northern Greenland (Peary Land) have provided links that join several of these previously unconnected fossils and establish them in recognizable phyla.

Let's begin with the animal *Wiwaxia*. In *Wonderful Life*, it is described as "another Burgess oddball, perhaps closer to the Mollusca than to any other modern phylum ... but probably not very close." Ironically, the first breakthrough in establishing *Wiwaxia*'s affinities came from a postgraduate paleontologist at Harvard who was inspired by Gould's lectures a decade or so ago. This young researcher, Nick Butterfield, managed to extract pieces of scalelike armor from the fossilized creature. When Butterfield studied their microstructure, he noticed immediately that it was the same as that of the chitinous bristles (chaetae) that project from the bodies of such modern annelids as earthworms. His conclusion, published in 1990, was that *Wiwaxia* was not a mollusk at all but an annelid. Yet this was what Walcott had claimed in 1911. In at least this case, Butterfield concluded, Walcott was not "shoehorning" bizarre animals into familiar phyla, as Gould had charged; Walcott had got it right the first time.

Another recent discovery, in which I was fortunate to play a role, sheds further light on the place of certain Burgess animals in evolutionary history. On July 9, 1989, I was with a team in northern Greenland, collecting at a site containing fauna from Sirius Passet, a regional variant of the Burgess Shale. It was our first day at the site, and almost immediately we found an extraordinarily complete fossil of a halkieriid--an armored slug with a trig shell at either end. We wondered whether this organism--with such a weird anatomy, apparently so different from any other animal's--represented yet another new phylum. But that was only at first sight. Until then, halkieriids had been known only from the evidence of isolated scales; with our discovery of this and other complete specimens, however, we were able to confirm that the creature was in reality closely related to *Wiwaxia*.

In making that connection, we were moving toward resolving a fundamental problem in evolution: How are body plans constructed, and how do new phyla actually emerge? To get from halkieriids, well represented as Lower Cambrian fossils, to *Wiwaxia*, which thrived in the Middle Cambrian, there is no need to postulate macroevolutionary jumps or some sort of genetic revolution. The halkieriids are not only older than *Wiwaxia* but also clearly more primitive. In life, halkieriids crawled across the seabed, their scales forming a beautifully arranged protective armor. *Wiwaxia* looked somewhat similar, but as

Butterfield showed, its scales evolved into chaetae. So is *Wiwaxia* an annelid? It is really a matter of definition, but in my opinion, *Wiwaxia* is a member of the annelid stem group--a creature still in the process of becoming an annelid. Once scrutinized, the *wiwaxiids* and the *halkieriids*, despite their seemingly great differences, are closely related. They may be connected by two simple steps: the scales of *halkieriids* are transformed into *wiwaxiid* chaetae, and lobate, leglike extensions develop so that the style of locomotion changes from crawling to a kind of stepping.

In recent years, the techniques of molecular biology have profoundly influenced paleontology in ways that bear on Gould's premise that the Burgess Shale was a seemingly inexplicable explosion of hundreds of bizarre life-forms, unrelated to anything familiar. One major surprise concerns the evolutionary position of the phylum Brachiopoda, a group with bivalved shells. Molecular data, quite unexpectedly, shows brachiopods to be closely related to annelids. Functional morphology also indicates that the shells of brachiopods must have originated as two separate valves; clams, in contrast, derived their familiar double shells from an ancestor with a single plate, across which developed a narrow zone of weakness, which became the hinge. Projecting from the margin of both valves of a brachiopod are delicate, chitinous bristles--identical to those of annelids. *Halkieriids* also have two prominent shells. In the pre-brachiopods, I believe, the two shells were probably close to each other, back to back. To produce a true brachiopod, all that was necessary was to fold one shell beneath the other. And, interestingly, exactly this process can be seen in the embryological development of certain primitive, living brachiopods. So what was once a worm is transformed into a bivalved animal, the familiar brachiopod. Nor does the story finish here. If the scales of *halkieriids* can become chaetae, surely they can also evolve into the structurally identical chitinous bristles of a brachiopod. Of course, the origin of brachiopods is not so simple, but such transformations are functionally plausible and historically believable. Although constrained by genetic possibilities, they are products of convergent evolution. Similar environmental selection pressures, acting on differing anatomies, can create convergent or parallel adaptations.

New discoveries and interpretations have altered our view of arthropod evolution as well. The biggest surprise is *Hallucigenia*, exemplar of the bizarre. Or is it? Recent finds from the Chinese deposit of Chengjiang reveal that my original reconstruction of this odd-looking, spiky animal had but one simple mistake: I had envisioned it upside down. *Hallucigenia* (a name coined by a colleague and me in an attempt to capture its dreamlike appearance) may still look strange, but with new discoveries, especially from southern China, *Hallucigenia* is now seen to belong to a group of primitive arthropods. And what about the famous *Anomalocaris*, another of Gould's star oddballs? "Nothing ... about *Anomalocaris* suggests a linkage with arthropods," he writes. Now we know better. The discovery, in different species, of lobopod-like legs and jointed appendages along the length of the body not only establishes a link between *Anomalocaris* and the more primitive *Hallucigenia* but also is crucial for understanding the appearance of the first arthropods--a group that would eventually radiate into crabs, spiders, and the millions of species of insects.

So the Burgess creatures do not form an exception to the orthodox mechanisms and patterns of evolution, as I believe Gould has implied. The new evidence suggests that not only did the sheer number of species increase since the Cambrian (as nearly everyone agrees), but, more significantly, the total number of phyla has been maintained and has not, contrary to what Gould has written, shown a catastrophic decline. But now we come

to the most egregious misinterpretation of the Burgess Shale in Gould's book--a conclusion drawn not from the evidence of paleontology but from Gould's personal credo about the nature of the evolutionary process.

Gould sees contingency--evolutionary history based on the luck of the draw--as the major lesson of the Burgess Shale. If you rerun the tape of evolution, he says, the results would surely come out differently. Some creature similar to Pikaia, a small eel-like animal with a rudimentary head, may have survived in Cambrian seas to become the ancestor of all vertebrates. If it hadn't, Gould says, perhaps other--entirely different--major animal groups would have evolved instead from one of the Burgess Shale's other "weird" body plans. Such a view, with its emphasis on chance and accident, obscures the reality of evolutionary convergence. Given certain environmental forces, life will shape itself to adapt. History is constrained, and not all things are possible.

To understand how creatures that are descended from very different groups can evolve similar forms and functions, consider that dolphins, which evolved from doglike mammals, are shaped like fish because there exists an optimal shape for moving through water--a classic example of convergent evolution. Or consider another example: both placental mammals and marsupials produced a large, saber-toothed carnivore on separate continents. If such a quality as intelligence can arise both in human beings and in the octopus--an eight-armed sea animal without a bone in its body--then perhaps there is a course and a direction to evolution that would be achieved despite diverse anatomical starting points.

Contingency or no, I believe that a creature with intelligence and self-awareness on a level with our own would surely have evolved--although perhaps not from a tailless, upright ape. Almost any planet with life, in my view, will produce living creatures we would recognize as parallel in form and function to our own biota. But first, life must arise, and we have no idea how rare an event that might be. If we are honest, despite our exciting fancies about extraterrestrials, we must admit the real possibility that life arose but once, and that we are alone and unique in the cosmos--with an awesome and, to many, unanticipated role as stewards of all other living things. But were we to let evolution take another route than it did, why not grant (as Gould will not) that another kind of being would have evolved to fill our special place in nature?

### The Reply

The recorded history of life on earth extends from 3.5-billion-year-old bacteria to our modern biota of oak trees, great white sharks, people, and many other organisms of stunning diversity. If evolution had followed a path of smoothly rising complexity, then our cultural preferences for progress would be fulfilled and paleontology would validate our deepest hopes and expectations. But life's bumpy and unpredictable course challenges us at every turn. Why did unicellular organisms of bacterial grade hold exclusive sway for nearly 2 billion years--more half of life's duration on earth? When multicellular animals of modern design finally entered the fossil record, why did nearly all phyla make their initial appearance in an interval so brief (perhaps no more than 5 to 10 million years) that paleontologists call this episode the Cambrian explosion?

The Burgess Shale, in the Canadian Rockies, contains the world's most important fossil fauna--a detailed and exquisite record (with rarely preserved soft parts included) of marine

life about 520 million years ago, just following the Cambrian explosion and therefore permitting us to census the results of this seminal episode in the history of animal life on earth.

Charles D. Walcott, a great American paleontologist, discovered the Burgess Shale early in our century but failed to appreciate its full significance. Beginning in the 1960s, Cambridge University paleontologist Harry Whittington, in eventual partnership with two remarkable graduate students, Derek Briggs and Simon Conway Morris, restudied Walcott's extensive collection in conjunction with new material from their own fieldwork and developed a novel interpretation with profound implications for our understanding of evolution and the history of life. I told the story, following their views of the Burgess fauna quite strictly (while presenting my own best judgment about larger implications), in my book *Wonderful Life*. Simon Conway Morris (who has since rejected his original interpretation and reached a nearly opposite conclusion--in general, an admirable stance for a scientist, although in this particular case, I think that Conway Morris was right the first time around) recently challenged my reading in *The Crucible of Creation*, the impetus for this dialogue.

Interpreting the fauna of the Cambrian explosion raises two deep and distinct issues, often confused in Conway Morris's commentary but providing a good framework for exemplifying our differences. First, a question of origins: How could so much anatomical variety evolve so quickly? In particular, must novel evolutionary mechanisms be proposed for such a burst of activity? Second, a question of consequences: How many distinct lineages arose in the Cambrian explosion? How many survived to leave modern organisms as descendants? Why have no new animal phyla (with the single exception of Bryozoa) evolved in more than 500 million years since the Cambrian explosion? Did surviving lineages prevail for predictable reasons of superior biomechanical design or ecological adaptation? Or did nature (to speak metaphorically) play a grand lottery with this initial diversity, issuing just a few winning tickets effectively at random--thus implying that modern groups, including our own lineage of vertebrates, owe their current success to an initial luck of the draw, combined with good fortune along the meandering paths of history's later contingencies?

The question of origins: I devoted only a few pages to this fascinating topic in *Wonderful Life* because so little meaningful evidence exists, and fruitful science must be defined by palpable and potentially decisive data, not by our subjective sense of intrigue or importance. (For this reason, questions about intelligent extraterrestrial life remain scientifically vacuous, although no issue could be more important in principle.)

As a framework for tackling the puzzle of why so much anatomical variety arose so rapidly at this unique time, I suggested that two basic approaches should be explored (with a full answer undoubtedly requiring a balance of both). An "external," or ecological, perspective would focus upon the uniquely "empty" ecological barrel of potential environments for mobile multicellular animals at the dawn of Cambrian time; almost any "experiment" might work for a while during an initial "filling"--at least until Darwinian forces sorted the workable from the suboptimal and placed a brake upon subsequent change of such magnitude. By contrast, an "internal" genetic or developmental perspective might view the Cambrian as a time of unique flexibility, before definite patterns of growth from egg to adult became so locked into the embryology of complex organisms that fundamental reconstructions became nearly impossible.

I suggested in *Wonderful Life* (and still maintain) that scientists should devote more attention to the unconventional internal arguments than to the more familiar ecological claims. I proposed no bizarre or novel evolutionary mechanisms but only emphasized a potentially greater efficacy for ordinary processes at a unique time of organic flexibility, before major developmental pathways became irrevocably set. I therefore feel that Conway Morris has misrepresented my views by vague allusion (for he can cite no true source for arguments I never made) when he states that I hint "at a special mechanism at work--some unusual genetic happenstance gone wild" or when he floats an even vaguer charge about unorthodox mechanisms that he "believes" I have "implied."

The question of consequences: This second key issue does call upon a large and juicy reservoir of testable evidence and therefore does become subject to scientific adjudication and fruitful debate. I based *Wonderful Life* almost exclusively upon this issue. Two basic questions, with different judgments and implications, have been widely debated within this general theme:

1. How much anatomical variety did the Cambrian explosion generate? Did the number of early experiments exceed (or overshoot) our current range of organic architecture? *Wonderful Life* argues for greater disparity during the explosion, with subsequent trimming on the "lottery model"--thus raising the interesting implication (and central theme of my book) that if we could perform the great undoable thought experiment of "rewinding the tape of life" back to the Cambrian and "distributing the lottery tickets" at random a second time, the history of animals would follow an entirely different but equally "sensible" course that would almost surely not generate a humanoid creature with self-conscious intelligence.

Most of Conway Morris's commentary properly focuses on a crucial and testable point. He denies my claim for a Cambrian overshoot by arguing that most Burgess "oddballs" really belong to modern groups (or to formative stages of modern designs) when properly interpreted. Therefore, the Cambrian did not generate enough anatomical variety to fuel a markedly different outcome for any hypothetical replay of life's tape.

I accept and applaud some of Conway Morris's arguments, while regarding the tone of his rhetoric as peculiar in several key places. Why, for example, does he label as ironic the fact that Butterfield's more orthodox reinterpretation of *Wiwaxia* began with an interest in my lectures? I don't know what could bring a scientist greater pleasure--the very antithesis of irony--than the honor of having his ideas act as a spur to important advances in knowledge, whatever the impact upon any initially favored and necessarily tentative hypothesis. And why does Conway Morris imply that I have been soft-pedaling the revised interpretation of *Hallucigenia*, when I applauded this discovery as soon as it was announced by writing an entire essay for this magazine entitled "The Reversal of *Hallucigenia*" (January 1992)?

Nonetheless, I think my central argument has fared well in the decade since the publication of *Wonderful Life*, for both a general and a specific reason. For the general argument, my colleague Mike Foote, of the University of Chicago, and I engaged in a technical debate with Conway Morris's colleagues (published in our major professional journal *Paleobiology*) on the quantitative assessment of comparative degrees of anatomical variety in the Burgess Shale versus modern oceans. Even our staunchest critics agreed that the Burgess range equaled the modern scope (while we argued for a greater variety in

Burgess times). In other words, even our strongest opponents admit that in less than 20 million years from the inception of the Cambrian explosion to the deposition of the Burgess Shale, marine invertebrate life reached a fully modern range--and that more than 500 million years of subsequent evolution has not at all enlarged the scope of basic anatomical variety. In this context, how can the early Cambrian be viewed as anything other than a unique time of explosive and unparalleled diversification?

For the specific argument, I believe that many Burgess and other early Cambrian creatures are weirder than Conway Morris allows and that several of his linkages to modern groups remain fanciful at best. For example, he blithely speaks about connecting wiwaxiids and halkieriids--rather dissimilar creatures, to my eyes--by "two simple steps" that seem both complex and improbable to me. How can Conway Morris view the evolution of lobopods (leglike extensions present in halkieriids but not in wiwaxiids) from no prior structure at all in supposedly ancestral halkieriids as a simple and obvious step? I am even more surprised by Conway Morris's confidence that the two plates at either end of an elongated Halkieria can overcome their several centimeters of separation to become the two connected valves of a brachiopod.

(I must also ask readers' indulgence for a paragraph that Robert's Rules of Order would call a "point of personal privilege": Conway Morris has chosen, less in this article than in his book, to be imperiously dismissive of my ideas, as if no sensible or experienced person could ever advocate such prejudiced nonsense. But he never tells us that *Wonderful Life* treats him, in his radical days as a graduate student, as an intellectual hero. I developed my views on contingency and the expanded range of Burgess diversity directly from Conway Morris's work and explicit claims, and I both acknowledged my debt and praised him unstintingly in my book. I even suggested--although it's surely none of my business--that Whittington, Conway Morris, and Briggs should receive the Nobel Prize for their exemplary work. Conway Morris is certainly free to change his mind, as he has done. Indeed, such flexibility can only be viewed as admirable in science. But it is a bit unseemly never to state that you once held radically different opinions and to brand as benighted, in some obvious and permanent sense, a colleague who holds the views you once espoused. I do therefore object to Conway Morris's strategy of working out his own ontogenetic issues at my expense. Lest readers think I am being either peevish or idiosyncratic, may I cite our British colleague Richard Fortey, who generally sides with Conway Morris on the scientific debate, from the October 10 issue of the *London Review of Books*: "What is peculiar about [The Crucible of Creation] is that the casual reader ... would never guess from it that Conway Morris ever entertained views different from those he now holds.... It is this selective amnesia which accounts for the passion of his disillusion with Gould, for Gould has preserved in the print of a best-seller ideas that Conway Morris ... now repudiates. He is furious that his past misinterpretations have been so eloquently placed on record.... The way Conway Morris goes about biting the hand that once fed him would make a shoal of piranha seem decorous.")

2. How repeatable is the history of life? In particular, did lineages that survived after Burgess times prevail for predictable reasons of adaptive superiority or by the luck of the draw? If we could replay life's history from Burgess beginnings, would the same trends occur, and would a self-conscious species arise again on earth? Conway Morris rests his claim for substantial predictability upon the important evolutionary phenomenon of convergence, or the independent origins of similar and highly adaptive designs in separate lineages--with the wings of bats, birds, and pterosaurs (flying reptiles of dinosaur times) or

the eyes of squid and vertebrates as classic examples. But I think that Conway Morris has given too prominent a role to an admittedly interesting principle for three reasons:

a) As a striking phenomenon, convergence draws our attention, but I think that we often overestimate its sway. Nearly all textbooks stress the admittedly remarkable convergences of several Australian mammals with their independently evolved counterparts in northern continents (for example, the marsupial "mole" with the denizens of our gardens, and the extinct Australian marsupial thylacine, otherwise known as the Tasmanian wolf, with doglike carnivores). When I first visited Australia, I expected to be overwhelmed by these demonstrations of convergence, but I encountered just the opposite phenomenon: uniqueness and difference, with convergence as an oddity singled out for textbook illustration. The mammalian fauna of Australia, after all, is dominated by upright and effectively "three-legged" herbivores known as kangaroos--a group with no evolved counterpart elsewhere.

b) Most outstanding examples of convergence build upon an inherited anatomical substrate that evolved by ordinary routes of highly contingent and unrepeatable historical circumstance. For example, the wings of bats, birds and pterosaurs are convergent, but all these structures evolved from vertebrate forelimbs of similar inherited design, not from scratch. In replaying life's tape from Burgess beginnings, what odds would anyone place on the evolution of such forelimbs if no ancestral creature had the precursors for these structures?

c) Evidence for convergence requires multiple cases of independent evolution, while the example that we all carry closest to our hearts (and that engenders the emotional oomph in this debate)--the evolution of consciousness in *Homo sapiens*--remains an outstanding singleton in the only history of life we know: the story of our own planet. (I am not impressed by Conway Morris's citation of octopuses, a group that I deeply admire and respect but that hasn't, and presumably can't, return the compliment via any higher mental functioning of its own.) Consciousness at our level of language and conceptual abstraction has evolved but once on earth--in a small lineage of primates (some 200 species), within a small lineage of mammals (some 4,000 species, while the more successful beetles now number more than half a million), within a phylum that prevailed by contingent good fortune from the Burgess draw. If complex consciousness has evolved but once in the admittedly limited domain of known evidence, how can anyone defend the inevitability of its convergent evolution?

Finally, Conway Morris charges that my arguments for contingency arise "not from the evidence of paleontology but from Gould's personal credo about the nature of the evolutionary process." This claim, however ungenerously stated, is--and must be--true, true, for any general view of life must read evidence in the light of a favored theory. I would, however, label my view as a valid reading of paleontological evidence in the context of a theory about life's evolution and history that I have worked out by considerable thought, practice, and intellectual struggle, and that I always explicitly identify as tentative, undoubtedly wrong in places (but not, I hope, in general approach), and embedded (as all ideas must be) in my own personal and social context.

I am puzzled that Conway Morris apparently doesn't grasp the equally strong (and inevitable) personal preferences embedded in his own view of life--especially when he ends his commentary with the highly idiosyncratic argument that life might be unique to

Earth in the cosmos, but that intelligence at a human level will predictably follow if life has arisen anywhere else. Most people, including me, would make the opposite argument based on usual interpretations of probability: The origin of life seems reasonably predictable on planets of earthlike composition, while any particular pathway, including consciousness at our level, seems highly contingent and chancy. I don't know how else to interpret the cardinal fact that life did originate on earth almost as soon as environmental conditions permitted such an event--an indication, although surely not a proof, of reasonable expectation and predictability; whereas consciousness has evolved only once, and in a marginal lineage among so many million that have graced our planet's history--an indication, although again not a proof, that such a phenomenon is not inevitably meant to be.

Conway Morris's peculiar and undefended reversal of these usual arguments about probability can arise only from a "personal credo"--and I would value his explicit attention to the sources of his own unexamined beliefs. All scientific greatness must integrate external data with the internal power of a fruitful view of life--the more iconoclastic the better, for Lord only knows that hidebound tradition and stupidity stand as the greatest barriers to enlarged understanding. But we cannot appreciate and use our own mental power if we do not follow the earliest and greatest advice of our classical forebears: Know thyself.