BOOK REVIEWS

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WONDERFUL CRUCIBLE[1]

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Paleontologists do not always get the respect they deserve. Luis Alvarez, physicist, Nobel Laureate, and originator of the impact hypothesis for the disappearance of the dinosaurs, told the *New York Times*, "I don't like to say bad things about paleontologists, but they're really not very good scientists." While most readers of *Evolution* probably would not be quite so outspoken, there is nevertheless a faint antipaleontology snobbishness among those of us who study evolution by sequencing *Drosophila* DNA or by counting the number of grubs picked up off a conveyor belt by a hungry starling. After all, our organisms are three dimensional, complete, and alive, while theirs are usually squashed, partial, and always long dead. We can sample and experiment as much as we like, while they are stuck with the unlucky few that got caught up in a Silurian mud slide. Ours, we congratulate ourselves, is an experimental science, while theirs is merely descriptive.

Our snobbishness is of course ridiculous: fossils supply us with our only direct glimpse of the history of life. We are reasonably good (and getting better, courtesy of DNA) at inferring what went on in the past by studying what we have with us today, but there is no substitute for that direct view into the Permian. There are aspects of the history of life that simply cannot be reconstructed from contemporary organisms. Imagine a world without fossils. Dinosaurs? Even the most imaginative of herpetologists on the fossil-free planet would have a hard time convincing their colleagues that the gap between modern lizards and birds was once occupied by reptiles as big as barns.

The Cambrian explosion—that sudden appearance of many major animal groups in one seemingly frenzied burst of evolutionary innovation—eclipses even dinosaurs in the paleontological pantheon of evolutionary events that we would never have been able to reconstruct in the absence of fossils. The earliest known metazoan animals were probably diploblastic, belonging to the Ediacaran fauna that dates from about 620 to 550 million years ago (MYA). Triploblastic organisms have recently been found in China (Xiao et al. 1998) dating from as early as 570 MYA, and there is an anomalous subsequent set of fossils known informatively as the small shelly fauna. Then, come the Lower Cambrian, at about 530 MYA, the explosion occurs: a quantum leap in the biological colonization of the planet. No longer are we looking at bizarre worm-like Ediacaran forms or that nondescript small shelly fauna; animals—in just the sense we think of them today—have arrived. Not only is a wide taxonomic range represented—priapulids, annelids, arthropods, even chordates—but there is considerable morphological diversity within some of these groups. And the world has suddenly gotten ecologically diverse, too; animals are no longer a bunch of inert filter feeders but have branched out into more ambitious trophic domains, including predation. Such is the complexity of this early Cambrian marine environment that I suspect that a future Martian paleontologist presented with early Cambrian fossils and with fossils from some contemporary marine community would be hard pushed to determine which of the two faunas is most "primitive"; the animal world has gone from simple, ancient to complex, modern in a single step.

Here, of course, is the power of fossils. No analysis of modern arthropods, priapulids, annelids, chordates could ever even hint at the apparent suddenness of their origins.

The most famous of all fossil deposits from this period is the Burgess Shale, which dates from about 510 MYA. Discovered in 1909 by Charles Doolittle Walcott high in the Canadian Rockies, the Burgess Shale has yielded the majority of the material on which our views of the Cambrian explosion are based. For reasons which will probably remain forever conjectural, preservation is excellent in the Burgess Shale. The Burgess Shale, however, is not alone; one of things I learned from Simon Conway Morris's new book, *The Crucible of Creation*, is that there are number of other early- to mid-Cambrian deposits that have yielded (and are yielding) further evidence of the Cambrian explosion, and several of these are markedly earlier than the Burgess. Conway Morris specifically discusses two such deposits, the Sirius Passet of Greenland, and the Chengjiang of China, both of which are 10–20 million years older than the Burgess.

Conway Morris started studying Burgess "worms" as a graduate student in the early 1970s under Harry Whittington at Cambridge, United Kingdom, and has since, along with a few others, most notably Derek Briggs and Des Collins, gone on to become the recognized authority on early- to mid-Cambrian animals in general, and on the explosion in particular. Given the apparent importance of the Cambrian explosion in the evolution of animals, and the amount of work Conway Morris has done on it, a book comes as no surprise. However, he is not motivated solely by a desire to tell the world about the wonders of the Burgess; his book is largely a response to Stephen Jay Gould's *Wonderful Life* (1989), which also showcased the Burgess. It might have taken him nine years to get his response out, but *Crucible of Creation* is nevertheless a direct reply to Gould. Conway Morris finds a lot to disagree with in *Wonderful Life*. He even manages to find grounds for a dispute before the Burgess Shale comes

[1] *The Crucible of Creation: The Burgess Shale and the Rise of Animals.* Simon Conway Morris. 1998. Oxford University Press, New York. 242 pp. HB $30.00, ISBN 0-19-850256-7.

over the geological horizon. Whereas Gould endorses Dolf Seilacher's view that the Ediacaran fauna is a "failed experiment" in the history of life, a dead end, Conway Morris makes the case that Ediacaran animals, or at least their descendants, are alive and well in the Cambrian, and indeed today, as cnidarians.

On the surface at least, Conway Morris's response to Gould is of a "biting the hand that feeds" kind. Conway Morris—or the "Simon" whose name is sprinkled liberally throughout Gould's text—is essentially the hero of Gould's book, the brilliant young paleontologist who, in his reanalysis of Walcott's fossils, has overthrown Walcott's conservative and sometimes erroneous classification of the material. Gould even goes so far as to say that it was a paper of Conway Morris's that inspired him to write *Wonderful Life*. Conway Morris delivers a polite, "his writings have done much to sharpen my appreciation of the issues involved," on the first page of his preface, and then rolls his sleeves up; he doesn't then have a great deal that is nice to say about Gould or *Wonderful Life*. "Gould announces to the awestruck onlookers that our present understanding of evolutionary processes is dangerously deficient and the theory is perhaps in its death throes. We look beyond the exponent of doom, and there standing in the sunlight is the edifice of evolutionary theory, little changed."

Their disagreement even extends to the details. Whereas Gould refers to Walcott's photographs of the fossils as "egregiously retouched," Conway Morris seems to approve of Walcott's practice: "In his time, the standard of photography was less impressive than today, and Walcott routinely retouched the photographs, the better to do justice to the amazing fossils."

What's going on? Both authors are dealing with the same material and asking more or less the same questions. Is this simply a case of academic sour grapes, or are there genuine biological issues at stake? It's certainly not sour grapes—I definitely don't get the sense that Conway Morris is in the least territorial about the Burgess—but I don't think, ultimately, that the issues are entirely biological, either. Fossils provide just enough data to fuel a debate but not enough to resolve it. The interpretation one puts on the Burgess and on biological events in the Cambrian is therefore somewhat a matter of preference, and Gould and Conway Morris come at the Burgess from very different philosophical positions.

The first question, which is addressed most fully by Conway Morris, is whether the Cambrian explosion is real or not. Maybe the suddenness of the appearance of the fossils is artifactual; there have been plenty of suggestions that, combined, the antiquity of the period in question (i.e., the low probability of finding any early Cambrian fossils at all) and the rareness of instances in which soft parts are mineralized even in comparatively recent fossil faunas (i.e., the low probability of soft-body fossilization) would result in a vanishingly low chance of our ever finding a fossil early Cambrian soft-body fauna. If the event is very rare and is poisson distributed, then, if we're lucky, we might see one instance, but probably not more. According to this explosion-as-artifact argument, the Burgess Shale is that one fortuitous event. Of course, therefore, it's remarkable; virtually all the evolution that went before it is missing from the fossil record. Hardly surprising, therefore, that the Burgess gives the impression of extraordinary evolutionary events if everything that went before was not documented in the record. Maybe we would be talking about a "Jurassic explosion" if, for whatever reason, all Triassic and earlier fossils had been subducted in some frenzy of tectonic activity: there are no fossils, and then, suddenly, we have a fossil record boasting a bunch of dinosaurs.

Conway Morris counters the explosion-as-artifact argument in two ways. First, as exemplified by the Sirius Passet and Chengjiang faunas, apparently fossilization of these soft-bodied faunas did occur at a respectable rate. The Burgess is not, after all, unique. He goes further, demonstrating that known early Cambrian localities are predictably arrayed around the perimeter of the Cambrian supercontinent, Laurentia. This suggests that future sites can be found by searching in a more systematic, less haphazard way. Second, Conway Morris points out that the early Cambrian sees a vast increase in the number and complexity of trace fossils, especially burrows and tracks. Thus, it appears that the behavioral complexity of animals was increasing at the same time as their morphological complexity. Note that the chances of fossilization of a track through mud are independent of the kind of animal, hard- or soft-bodied, that made it. The parallel explosion of trace fossils therefore argues that the Cambrian event is not an artifact of, for example, the recent acquisition by animals of hard (and occasionally fossilizable) exoskeletons. The Cambrian explosion is real enough. True, we're talking "explosion" in geological terms, but it appears nevertheless that the animal world went within a relatively short space of time from a dull place rather short on diversity to something not too different in gross terms from what we have today.

The next issue, surely, is what caused the explosion. Surprisingly, given that the cause of the Cambrian explosion is one of those perennial two-or-more evolutionary-biologists-in-a-bar topics, neither Gould nor Conway Morris devote a great many pages to the subject. Gould, in fact, explicitly steers clear of it, choosing, as he puts it, to "shamelessly bypass" the issue, though he cannot resist presenting a brief summary of some alternative hypotheses in the process. Conway Morris rather wishes that Gould had been more explicit, because he clearly wants Gould to insist on "some novel type of evolutionary mechanism" to account for the explosiveness of the Cambrian metazoan evolution; some off-the-wall conjecture that he can shoot down in flames. While Conway Morris can easily find an embrace of such mechanisms in Gould's writing—there was, for example, that dalliance with Richard Goldschmidt's hopeful monsters—he won't find it in *Wonderful Life*.

Gould presents what he perceives to be Conway Morris's point of view, which he dubs "conventional" and "too sensible to dismiss," though he then refers to a "gut feeling" that the "Cambrian explosion was too big, too different, and too exclusive" for it to be a complete explanation. Essentially it is an ecological argument. Having established the developmental wherewithal to create complex bodies, animals underwent a spectacular adaptive radiation. It's the same scenario as the arrival of, say, the original honeycreeper on the Hawaiian Islands, only writ global and much larger. For the first and only time in the history of life, metazoans were presented with what in effect was a huge range of unoccupied niches; an evolutionary bonanza if ever there were one. I for one have no gut feeling that this admittedly boringly orthodox model is anything but the right one. A theory isn't wrong simply because it's the standard one.

Conway Morris is more explicit about the ecological processes that resulted in the Cambrian explosion. He cites predation. He argues that the it was the "invention" of predation that drove diversification. *Anomalocaris*, a predatory early Cambrian arthropod which looks like a hybrid between a lobster and a vacuum cleaner, certainly demonstrates that predation had become a major component of the ecological landscape, and we know from removal experiments that top predators can be important determinants of ecological diversity.

Both Gould and Conway Morris manage to avoid getting stranded in a favorite backwater in those bar-room conversations: developmental genetics. Conway Morris sees ecology as the primary determinant of diversification, and Gould (1998) has in fact recently explicitly (if indirectly) denied a role for developmental genetics in the generation of the Cambrian explosion. In commenting on Greg Wray et al.'s (1996) conclusion from molecular data that the protostome/deuterostome lineages diverged more than a billion years ago (i.e., a long time—even in geological terms—before the appearance of even the Ediacaran fauna), Gould claims that the result, if true, does not render the Cambrian explosion any less interesting: "In fact, I don't see that it matters one whit . . . whether one wormlike species carrying the ancestry of all later animals, or ten similar wormlike species representing the lineages of ten subsequent phyla, crossed the great divide from an earlier Precambrian history." But it makes a big difference so far as possible mechanisms for the explosion are concerned. If there were indeed just one worm (i.e., Wray et al. are wrong, as is suggested by a number of other studies, notably Ayala et al. [1998] and Doolittle et al. [1996]), then the potential exists for an important role for developmental innovation in the explosion. Imagine that our one worm evolves hox genes. Couple the acquisition of the resulting capacity for segmentation and segmental variation to the ecological opportunity discussed above, and we have a truly explosive mix. If, however, Wray et al. are right, and it was ten long-diverged worms that wandered into the Cambrian, then it is unlikely that each group would have convergently evolved developmental processes that could facilitate such a bout of spectacular diversification, and we are left with ecology as our only explanation of the explosion.

The remaining issue raised by the Cambrian explosion, and the one most thoroughly explored by Gould, is the fate of those Cambrian lineages. It is here that Gould seems to have trodden most thoroughly on Conway Morris's toes. Conway Morris sees Gould's insistence on the history of life being governed by contingency, "one colossal lottery," as buttressing "an ideological viewpoint." Ideology? Gould, we learn early in Conway Morris's book, is a devotee of Marxism, "the greatest of twentieth-century pseudoreligions," and this apparently informs much of his science. Conway Morris, on the other hand, hints occasionally at his sympathy for some kind of theism. He suggests that Neanderthals, as judged from their burial practices, developed "some sort of sense of an afterlife." "Materialists," he writes, "will scoff at this as a shared delusion, but there are metaphysical alternatives that are perhaps more fruitful."

I hate to be prosaic in the midst of a contest between religion and pseudoreligion, but I think the difference in interpretation has much more mundane origins. Gould essentially sees chance as playing a major role in the history of life, whereas Conway Morris, who never denies some role for contingency, sees the history of life through a deterministic lens. Stochasticity versus determinism is one of the oldest evolutionary debates around. It's currently alive and well in population genetics in the form of the neutralist-selectionist debate. Interestingly, your choice of camp is somewhat determined by which side of the Atlantic you were born on. British evolutionists have tended to follow Fisher and his deterministic vision, whereas American evolutionists have been raised in the Wrightian tradition, with its emphasis on drift processes. This is obviously a ridiculous oversimplification that fails to do Conway Morris and Gould, major thinkers both, justice. But the fact remains that the argument between them is essentially the same as the Fisher/Wright argument, only on a much larger scale. I find the invocation of Marx and other "non-pseudo" factors merely to distract from what are interesting and important biological issues.

Gould's famous metaphor is "re-running the tape of life." Do that, and Gould claims that what we get will be very different from what we have on this particular run of the tape. Conway Morris, on the other hand, reckons that things won't be too different: "within certain limits the outcome of evolutionary processes might be rather predictable." "What we are interested in," he goes on, "is not the origin, destiny, or fate of a particular lineage, but the likelihood of the emergence of a particular property, say consciousness."

Convergent evolution is the vehicle of this vision of Conway Morris's, and the independent evolution of a marsupial saber tooth tiger in South America is held up as evidence of the power of convergence. I certainly would not dispute the power of natural selection to promote convergent solutions to common problems, but I think that Conway Morris rather overrates its generality. His approach of comparing two geographically isolated faunas will of course furnish many examples of convergence, but there are many more examples of differences between the faunas. Gould, for example, reminds us of the giant South American ground birds, the phorohacids, which were ferocious predators—a very different solution to the "top predator" problem to the one we see in operation on, for example, the plains of Africa today. Therefore, if Conway Morris's "particular property" is a general ecological attribute (e.g., grazer, scavenger, predator, top predator), then, yes, evolution is predictable: each time the tape is run, we're going to wind up with grazers, scavengers, predators, top predators. The process, however, is scale dependent: if Conway Morris wants to get more specific (e.g., in insisting that top predators should all have fang-like canines), I'm not sure that the power of convergence is enough to guarantee similar outcomes on each run.

Gould's analysis of the Burgess Shale takes his claims of contingency to a level beyond the "re-run-the-tape" thought experiment. He contends that the range of morphological diversity was actually greater in the Burgess than it is today, and that what we see today is the product of an essentially random winnowing process he refers to as decimation. Note the randomness of that winnowing process; Gould's world is not the meritocratic competitive one of Darwin. There are two matters at issue here. The first is empirical: how does Burgess diversity measure up to today's? The second is less concrete: what ever happened to that Burgess diversity (or lack of it)?

Gould makes a great deal of the phylum-busting Burgess taxa. Here, apparently, were a bunch of invertebrates so bizarre and so bereft of affinities to known phyla that we must be dealing with a radiation of phylum-level diversity. The traditional adaptive radiation of island biology with its generation of new species is subverted in the early Cambrian to generate not species but phyla. This is not the place to get into what precisely constitutes a phylum (i.e., when is one bauplan sufficiently distinct from another?), but distinct phyla can nevertheless be taken to represent a high degree of differentiation. Gould, in his tabulation of Burgess fossils subjected to the Cambridge group's reanalysis, claims that they include representatives of nine previously undescribed phyla; that's nine out of 28 taxa total. When you consider there are currently some 35 phyla, it's apparent that nine new ones from a sample of 28 fossils represents a pretty high rate of new-phylum discovery. Unfortunately, Conway Morris does not supply a comparable table, but he makes the general point that the more we have learned about these bizarre fossils, the more we find that they do in fact have affinities with known groups. Thus *Hallucigenia*, once the pinup of Burgess weirdness, has been down graded to a mere onychophoran now that it has been recognized that it was originally reconstructed upside down. Further, Conway Morris hypothesizes that *Wiwaxia* and the halkieriids, which he describes as armored slugs, no longer merit phyla of their own, but are in fact intermediate between Annelids and Brachiopods. Conway Morris is, in short, doing the opposite of Gould. Where Gould highlighted differences, Conway Morris seeks similarities.

The irony is that *Wonderful Life* is Gould's celebration of Conway Morris's facility for recognizing weird things for what they are, that is, weird, rather than trying, to use Gould's term, to "shoehorn" them into established groups, just as *Wonderful Life*'s villain, Walcott, did when he carried out the original descriptive work on the Burgess material. If we are to believe Gould's characterization of him, Conway Morris seems to have shifted from Walcott nemesis to Walcott disciple. Indeed, *Wiwaxia* ("new phylum" in Gould's table) was classified by Walcott as an annelid, and is now placed by Conway Morris close to the annelids. Conway Morris would, I think, say that his apparent shift in orientation is no such thing, but merely reflects the outcome of further study of the fossils. His general conclusion, then, is that the Burgess fauna isn't nearly as oddball as Gould would have us believe. Does this affect the initial claim about the diversity of the Burgess fauna? I think not. Even if every second fossil is not after all a new phylum, the Burgess nevertheless contains an extraordinary range of morphologies. Remember what came before it: the squidgy diploblastic Ediacaran animals and those unclassifiable small shelly things.

Does high morphological diversity early in metazoan evolution necessarily imply, as it does to Gould, that the subsequent history of life is as much, or more, about the random pruning of the tree of life as about ramification and diversification? Conway Morris thinks not, and I'm with him on this one. Yes, there was some serious trimming of the bush in the early Cambrian as various newly evolved body plans made competing bids for evolutionary posterity, but after that there was a lot of straight forward diversification to look forward to. Land and air would each witness their own subsequent radiations. Gould shies away from any notion of competitive displacement, resorting to the crapshoot he is comfortable with. Conway Morris lacks these inhibitions. Some things are better than others at doing certain tasks; that's natural selection. He sees no reason why we shouldn't apply the basic competitive principles underlying contemporary community ecology to the Cambrian.

Gould makes a great deal of mass extinctions, those great "random" events so important in restructuring biological communities. While it's true that plenty of higher taxa have bitten the dust over the years—I have yet to see a living trilobite or ammonite—I find it striking that recognized phyla seem as a rule to survive. Even the obscure little wormy phyla that first appear in the Cambrian are still with us today. Take the priapulids. These most-unhappily-named-of-all-invertebrates were a major component of the Burgess fauna but today are minor players on any criterion of biological diversity (whether species number, or range of morphology), and tend to exist only in marginal habitats. They've been displaced from the plum habitats by polychaetes and echinoderms. But nevertheless they've survived the five "big" mass extinctions that have occurred between the Cambrian and today. Chance inevitably plays a role, but, as the small-time drama of the priapulids shows, the signal of deterministic evolutionary processes is by no means swamped by the noise of contingency.

Conway Morris has produced a slightly strange book, but one that is nevertheless an engaging and illuminating read. It is pitched at a popular audience, which most the time is conscientiously addressed: UV radiation "from the Sun is of course responsible for sunburn." Occasionally, however, Conway Morris, professional biologist, gets the better of Conway Morris, popular writer, and we find the text cluttered with the likes of "palmate sclerites" and "neurochaetae." He by no means limits himself to fossils: postmodernism takes a passing knee to the groin when he condemns "the poisonous ideas of such individuals as Derrida." He additionally proves himself a living contradiction of the claim that any foe of Stephen Jay Gould is a friend of Richard Dawkins, whose "world view is not so much wrong, as simply seriously incomplete."

The guts of the book consist of an attempt to bring the Burgess fauna to life by taking an imaginary trip back in time to view *Hallucigenia* and friends gamboling around on the Cambrian ocean floor. I'm afraid that this device is not a huge success; although I appreciate the value of communicating some sense of the animals beyond the dry reconstructions that reside in academic monographs, Conway Morris's time-machine-cum-submersible is merely irritating. His job is not made any easier by his illustrations. The book contains drawings culled, I take it, from those monographs, plus a set of color plates featuring paintings of the organisms in their natural habitats, all of them paraded in those absurdly overcrowded environments so beloved by illustratrators of the prehistoric world. Perhaps carried away with his time machine, Conway Morris decides, in a brief afterword, to take on the rest of the universe. I'm not sure that a book on the Burgess Shale deserves a discussion of the chances of there being extraterrestrial life out there, and I'm not sure that all of extraterrestrial life deserves only a page and a half. It's a strange way to finish.

While Gould is partially responsible for paleontology's current prominence in evolutionary debate, he's also managed to alienate plenty of his nonpaleontological colleagues with his forceful advocacy of his heterodox interpretations of fossil data. Conway Morris serves as an excellent antidote: at ease with his orthodox Darwinian heritage, his insistence that even what is arguably paleontology's most spectacular asset, the Cambrian explosion, sits squarely beside *Drosophila* DNA sequence and starling optimal foraging in the mainstream of evolutionary biology reminds me, for one, what a great subject this journal is devoted to. Those same simple processes that we see in operation in natural populations today were, half a billion years ago, responsible for that extraordinary Cambrian orgy of evolutionary creativity.

Literature Cited

Ayala, F. J., A. Rzhetsky, and F. J. Ayala. 1998. Origin of the metazoan phyla: molecular clocks confirm paleontological estimates. Proc. Natl. Acad. Sci. 95:606–611.

Doolittle, R. F., D. F. Feng, S. Tsang, G. Cho, and E. Little. 1996. Determining divergence times of the major kingdoms of living organisms with a protein clock. Science 271:470–477.

Gould, S. J. 1989. Wonderful life. Norton, New York.

———. 1998. On embryos and ancestors. Nat. Hist. 8/98:20–65.

Wray, G. A., J. S. Levinton, and L. H. Shapiro. 1996. Molecular evidence for deep Precambrian divergences among metazoan phyla. Science 274:568–573.

Xiao, S., Y. Zhang, and A. H. Knoll. 1998. Three-dimensional preservation of algae and animal embryos in a Neoproterozoic phosphorite. Nature 391:553–58.

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