

The Evolution of Tolerance

Wonderful Life: The Burgess Shale and the Nature of History

by Stephen Jay Gould, *Hutchinson Radius*, 1990. £14.95 hbk (346 pages) ISBN 0 09 174271 4

Gould's *Wonderful Life* is a seductively provocative book, undermining the popular but misguided view that the march of darwinian evolution is inexorably up and out. Organisms might look as if they were designed by committee but, if evolution is the sole responsibility of natural selection, then no opportunity is supposed to have been lost in the unceasing business of fine-tuning that honed life's fragile beginners into the glorious mean gene machines we know today. Can there be any doubt that the perceived functionally harmonious successors – strutting their stuff at the very tips of the Tree of Life – were the deserved fruits of a 3000-million-year war of attrition?

In challenging this view, Gould rests his case on the unexpected hypervariability of Cambrian life forms, where 'weirdness', 'comicality' and functional 'illogicality' are the unavoidable descriptions from minds and eyes too used to the narrow permutations of contemporaneous forms.

Can there be any readers left who have not heard the story of the Burgess Shale – the Canadian quarry that preserved the treasure trove of some of the earliest animal body plans? The drama of the Burgess Shale fauna and that of the 'Cambrian explosion' is encapsulated by the words of Conway Morris¹ who writes that the period rapidly produced 'an astonishing riot of morphological designs', so distinct that 'it is difficult to avoid the sobriquet of extinct phylum'. There are 120 genera falling into 12 major groups of animals, which have been defined from approximately 73 300 specimens. Amongst these 12 groups, the dustbin group of 'incertae sedis' itself comprises at least 12 distinct body plans that are as different from each other as any of the remaining phyla in the fauna'. Within the arthropods alone (one of the 12 major groups) 'the cavalcade of morphologies [20–30 different kinds not to be found in any of the four 'modern' categories] seems to be inexhaustible'.

We are in a world in which arthropods 'seemed to be built from a grab-bag of characters – as though the Burgess architect owned a sack of all possible arthropod structures, and reached in at random to pick one variation upon each necessary part, whenever he wanted to build a new

organism' (Gould). What is more, these assemblages represent functionally successful entities, stable for millions of years and extending around the world from Canada to China^{1,2}. By the monotonous standards of today's life forms, the great Architect is no longer 'the *enfant terrible* of a brave new multicellular world, fashioning *Anomalocaris* with a hint of arthropod, *Wiwaxia* with a whiff of mollusk, *Nectocaris* with an amalgam of arthropod and vertebrate'.

What, then, are we to make of the morphological and behavioural ingenuity of the first multicellular organisms, waiting for 1.4 billion years to enter the world's stage after the advent of eukaryotic cells? Why the delay if complexity offers such rewards, and why the Cambrian in which to juggle and recruit characters from the arthropod grabbag? And what of life today: are extant phyla the legitimate survivors with just the requisite anatomical deftness and competitive edge?

For Gould there are no invariant 'basic laws (natural selection, mechanical superiority in anatomical design)' by which the winners and losers could be guaranteed. Our current impoverished pattern of anatomical disparity is largely in the lap of 'historical contingency', the small chance steps acquiring unforeseen major significance, as time's arrow flies. For Conway Morris, the Cambrian Explosion is basically an 'adaptive radiation' of untried multicellular novelties filling out an empty ecological barrel, vacated with the (inexplicable) extinction of the previous Ediacaran fauna, with rediversification among surviving clades a consequence of random extinction of intermediates and the subsequent establishment of strongly defended adaptive peaks.

As Gould recognizes, there are some general laws of nature that arise out of principles of self-organization and the physics of surfaces and volumes. However, at this level of D'Arcy Thompsonism there is little argument, and prediction is relatively trivial. The main argument lies elsewhere and rests on Gould's contention that the new (post-Burgess) view of our modern order of life is rooted in contingency, in contrast to the older view that our modern world was guaranteed by timeless laws of natural selection and mechanical superiority in design. For Gould, the 'ultimate question of questions boils down to the placement of the boundary between predictability under invariant law and the multifarious possibilities of historical contingency'. In the now famous image of

the replay of life's erased tape, Gould rightly emphasizes that evolution would proceed down a pathway radically different from the road actually taken.

My quibble is whether the local and particular occurrence of natural selection (that passive outcome of differentials between never-to-be-repeated phenotypes in their interactions with the never-to-be-repeated microenvironment at any given generation) is anything but contingent on the accidents of genetic variation and the chaotic vagaries of ecology. Although there is a widespread tendency to regard selection as an 'active' principle of evolution (biology's triumphant 'law' on par with the laws of physics), the comparison is patently false because, unlike physics, there are no regularities of occurrence of events from which predictions can be made. We can predict the behaviour of a jugfull of water molecules; we can't do the same for a population of individuals. The case for contingency is pervasive whether evolution proceeds in the selective mode or not³. It is highly improbable that evolution will proceed down any given path (determined with hindsight); but there is a probability of one, given the nature of the internal and external forces at play in living systems, that it will proceed down some path which, as Gould concludes, would be 'just as interpretable, just as explainable *after* the fact, as the actual path'.

If all evolutionary processes are essentially random walks, the 'question of questions' is perhaps not so much predictability versus contingency, but where to place the boundary between the external and internal phenomena that affect both the appearance and disappearance of organisms. The 'empty barrel' idea and the imagery of 'adaptive radiations' place their emphasis on the external ecological parameters which, Gould argues, would have to be peculiarly unique to the early Cambrian, because subsequent extinctions (for example, the Permian debacle) did not lead to any major structural novelties.

Like Gould, I'm concerned about evolutionary explanations that rely solely on special external factors (something in the Cambrian water!), as if organisms and their genetic constitutions are mere putty in the hands of The Great Selective Moulder beyond. It is too simple to reduce the complex dynamics of the living world to a process by which genetically endowed individuals are dragged, screaming and kicking, towards pre-established niches. Organisms

themselves play an active role in the establishment of the complex sets of interactions that make up local ecologies, a point actively pursued by Lewontin⁴. This realism – what Gould calls the ‘dialectics of inside and outside’ – somewhat dispels Kauffman’s idea⁵ (cited and supported by Gould) that major innovation inevitably gets harder as organisms find themselves on higher and higher adaptive peaks, with nowhere to go but down. The new ‘dialectics’ surely suggests that the sizes and numbers of adaptive peaks are as changing as the surface of the ocean. We have yet to unravel, when looking at a contented organism functionally at peace with its environment, how much of this momentary tranquillity is the result of three potential contributing processes: adaptation, exaptation⁶, and adoption³.

In thinking indirectly about the last two, Gould takes up a point of Valentine’s (see Ref. 7) that perhaps Cambrian genomes were smaller and more flexible, and that over time genetic systems became ‘less forgiving of major restructuring’. However, the absence of any consistent correlation between genome size and evolutionary advance, makes me uncomfortable with the idea that early metazoan genomes were small. Some of the greatest fluctuations in genome size occur amongst unicellular organisms, indicating that, at least for the modern representatives of pre-Cambrian forms, mechanisms of genomic turnover and their evolutionary consequences were well in place and have remained active ever since, leaving the questions still begging: why wait for the Cambrian and why only in the Cambrian?

The answers might lie in the major biological transition from unicellular to multicellular organization, coupled to what is currently known about the genetics of multicellular development. This is not the place to expand on the latter except to emphasize that there are two significant findings that might help in understanding the rise, persistence and unrepeatability of the Burgess bestiary. The first concerns the widespread presence of homeotic genes in unrelated metazoa which, in their ability to transform one body part to another, very much lessen the surprise of mosaic organisms grabbed from a bag of existing parts. Is the chimaeric *Nectocaris*, that amalgam of arthropod and chordate, seducing us into conclusions that homeotic genes were up and running before the subsequent divergence of these phyla? Is this why modern representatives of these phyla share the same linear order and

spatial expression of such key genes? The embryology of *Nectocaris* would have been fascinating to dissect, or even imagine!

The second finding shows that pattern, shape and form are not necessarily the emergent properties of multicellular tissues obeying underlying physical principles of organization (‘developmental fields’) but are the accidental outcome of very local cell–cell interactions, effected by specific signalling and communication molecules^{8,9}. Evidence is accumulating that the primary aim of a cell is more to put out peace overtures to its neighbours than to worry about the Grand Design of the organism.

It might not be unrealistic to imagine an early metazoan world in which, for example, the genes for body-part identity and cell–cell interactions were groping their way to their later role in life as the first unicellular progenitors were learning to live together in the multicellular conglomerates. The same could be true for haploid genomes coexisting in the diploid state, during the first sexual fumbings. This might have been a time for unprecedented experimentation for ultimately comfortable combinations and interactions, producing along the way an unexpected diversity and ‘weirdness’ of forms. Such oddballs would have been successful just because of the high levels of tolerances between molecules within the organisms and between them and their environment in this early experimental phase. Ontogenetic and evolutionary success is all about tolerance. If genetic systems and their products manage to turn a unicellular zygote into a multicellular adult, it might not matter overmuch whether the product *exactly* fits some prescribed niche.

Successful molecular and ecological interactions are more than simply an outcome of selectively engineered entities of matching locks and keys, honed to perfection by the eternal struggle for survival in overpopulated communities.

As J.B.S. Haldane wrote, ‘I have no doubt that in reality the future will be vastly more surprising than anything I can imagine. Now my own suspicion is that the universe is not only queerer than we suppose but queerer than we can suppose’¹⁰. The variety of permutations between the three major processes of evolutionary change and the emergence of a rounded evolutionary theory are beginning to come within reach of our own imaginations and suppositions. The Burgess bestiary demands an explanation.

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Palaeozoic Tetrapods

The Dicynodonts: A Study in Palaeobiology

by Gillian King, *Chapman & Hall, 1990. £35.00 hbk (xi + 233 pages) ISBN 0 412 33080 6*

Dicynodonts were a group of specialist reptilian herbivores (indeed they were the first terrestrial vertebrate herbivores) that grew to predominance during the Permian period, suffered a drastic reduction during the end-Permian extinctions, rallied during the middle Triassic, but became extinct at the end of that period. Despite their abundance, dicynodonts are a neglected group in the public

imagination. They are neither fierce nor exceptionally large. Yet, unlike most predominantly Palaeozoic tetrapods, dicynodonts yield information on questions such as group behaviour, sexual dimorphism and growth series. Because of their abundance, we can approach questions of ecology and behaviour with information comparable to that from the dinosaurs.

Gillian King is one of the world’s leading authorities on the group, and she has done a splendid job. Beginning with an introduction on how to recognize a dicynodont, she goes on to show the general principles by