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Contingency and Convergence

A review by **Mike Foote**

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The Crucible of Creation. The Burgess Shale and the Rise of Animals. SIMON CONWAY MORRIS. Oxford University Press, Oxford, 1998. xxxiv, 242 pp., illus. $30. ISBN 0-19-850256-7.

Which features of the history of life are (practically speaking) inevitable, which are highly contingent, and how can we know the difference? The eternal discussion of chance and necessity has found a new focus in the evolutionary implications of the Cambrian Explosion, the burst of animal disparity (that is, the variety of anatomical designs) that occurred over the span of just a few million years, some half billion years ago. Analysis of this diversification has largely centered on the fossil faunas captured in the famous Burgess Shale and related deposits. According to the view promoted by Stephen Jay Gould (1), chance elements may have been so important that the survivors of this initial radiation--and therefore the long-term course of subsequent biotic evolution--could not have been predicted by a Cambrian observer, even a very smart or knowing one. It is probable that certain general products of evolution are essentially predictable (say, the existence of carnivores that harvest lower-level consumers), while the particular details (say, predatory snails such as *Conus* species that stun their prey with toxins) rely on a string of unique historical events (2). Some of these events are extrinsic to the lineages involved (the catastrophic extinction of a competitor, for example), while some are intrinsic (preaptations, the prior evolution of organs that are later modified or co-opted).

Simon Conway Morris, who has expertly studied Cambrian faunas for over 25 years, gives excellent overviews of the anatomy and ecology of the Burgess Shale animals, the faunas of other Burgess-like deposits, and the resolution of some morphological and genealogical puzzles. Amidst these discussions lies a perspective on the importance of evolutionary contingency that differs from that of Gould. Gould's emphasis on the contingent partly reflects a theme found in many of his writings, that culturally laden ideas--such as progress, the scale of nature, and the primacy of humans at the pinnacle of that scale--have stifled our understanding of evolution. But his emphasis also reflects recent developments in paleobiological research, such as the conclusion that mass extinctions, with their consequent, profound changes in the biotic composition of the world, may not be mere intensifications of normal environmental stress, but rather may select for completely different properties than are favored during most of Earth's history (3). Conway Morris finds this emphasis on the contingent to be "trivial" (p. 200). His point is to dispute not the fact but the importance of contingency. Replay life's

tape (to use Gould's metaphor) and you may not get *Conus* again, but you will probably get benthic marine predators. Conway Morris sees convergence, not contingency, as the more compelling theme of evolution.

In some sense, the disagreement reflects a mixing of categories--the contingency of details and the inevitability of properties--and an exaggerated dichotomy. One way to circumvent both problems would be to assess, quantitatively if possible, the degree of contingency of properties. How might we do this? An obvious, operational approach would be to compare the net amount of time during which environmental conditions, in the broadest sense, have been favorable (or at least not unfavorable) to a certain biological property with the net amount of time during which that property has existed. Leaving aside the complications involved in assessing the favorability of conditions, we can suggest that the higher the ratio of potential to actual existence of a property, the more contingent the property. Long lags between the creation of an ecological opportunity and its exploitation would be evidence for contingency; short lags would suggest relative inevitability. The properties considered need not be limited to ecological or functional features of organisms; they may be aspects of ecosystem structure, patterns of biogeographic distribution, and so on. And, of course, waiting time would need to be weighted by taxonomic diversity or taxonomic origination rate to reflect better the number of opportunities available for a property to evolve.

Consider two classic cases. (i) Consciousness is often seen as a fine example of contingency, depending not only on unique evolutionary events (1), but--more speculatively--perhaps even on recent events in human history that favored consciousness as a learned style of mental function (4). Although we cannot discount Conway Morris's suggestion that consciousness may be as common in the future as it has been rare in the past, the present evidence suggests that consciousness has not been around for long. It satisfies our operational notion of a highly contingent property. (ii) Reefs, heterogeneous in composition but sharing certain ecological and structural features, are a common theme in the history of marine ecosystems. Once established, they tend to last until decimated by extinction events. In the wake of such crises, the evolution of new reefs may take many millions of years (5). Thus, much, but not all, of Phanerozoic time is marked by well-developed reefs, which therefore are features of intermediate contingency.

Regarding an example that is less frequently discussed, Conway Morris suggests that although the existence of whales may be highly contingent, the existence of large, fast, filter-feeding animals is rather inevitable. If he is correct, then why did whale-like creatures take so long to evolve? In this case, unlike that of large terrestrial herbivores, we probably cannot argue that reptiles filled this role during the Mesozoic, only to be replaced by mammals following the end-Cretaceous mass extinction (6). Instead, it seems plausible that by completely closing off access from mouth to lungs, certain mammalian adaptations related to suckling were co-opted to enable the kind of high-speed, open-mouthed feeding that would drown a reptile (6). Thus the evolution of whales or their analogues may be more contingent than Conway Morris suggests.

The foregoing examples are perhaps trivially simple, but the same approach could be applied to more complicated cases. And surely, much more useful measures of the degree of contingency will be found. The goal, however, should not be the mere tabulation of cases. Rather, operationalizing the dual notion of contingency and inevitability will enable us to explore temporal and phylogenetic trends in the degree of contingency in evolution. To take a rather obvious example, the increase in ecological "packing" that has taken place over Phanerozoic time (7) might suggest that any available ecological opportunity would be increasingly quickly exploited, leading to shorter lag times. On the

other hand, the apparent tightening of developmental and genetic systems (7) might hinder the evolutionary change needed to exploit such opportunities, leading to longer lag times. These and other evolutionary hypotheses are testable in principle. Just as Gould's book helped to promote a renewed investigation of the evolution of biological disparity, so should Conway Morris's book help to bring us beyond the standard catalogue of cases of convergence (such as marsupial and placental wolves) toward a fresh look at the role of contingency in evolution and--perhaps more importantly--the evolution of contingency itself.

References and Notes

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*The author is in the Department of the Geophysical Sciences, University of Chicago, Chicago, IL 60637, USA. E-mail: m**foote**@midway.uchicago.edu*

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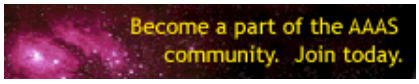

PAGE TOP