

of public-private partnerships for malaria action have been explored (4). New possibilities, involving joint action between research-based pharmaceutical companies, the academic sector, and governments, are now being developed. This raises many difficult issues, particularly those relating to intellectual property, that have yet to be addressed.

Within developing countries, the private sector (whether in the form of a licensed medical practitioner, private pharmacy, or traditional healer) is very often the main source of advice and treatment for all people, including the poor. Government health services will need to acknowledge this and develop better ways of working with and regulating the different types of practitioners to provide essential public health services.

Most health-related decisions are made in the home, not in the health center. However, as we all know from our own experience, people do not always choose to live in ways that preserve their health. Often this is because they do not know what is for the best. Even when they do, they may not be able to access the services they need and benefit from them. Roll Back Malaria will have to increase the availability of good-quality information and services. Information and education will not only mean that men and women will make more appropriate choices, it will also create

a climate of expectation that demands improved services.

The Next Steps

Roll Back Malaria will not be a "one-time" project. Sustained effort and financing will be required over the next two decades. It will be a global initiative, adapted to the needs of regions and countries. It will respond to climatic and environmental changes, human migration and displacement, and the development of resistance to antimalarial medication and insecticides. It will do this from within the health sector but will recognize that in practice many people get the health care they need in the home, from private (rather than public) services. The details of the initiative have yet to be determined.

Over the next few months, Brundtland and her team will develop the mechanisms that will allow WHO to work effectively with other partners in the Roll Back Malaria initiative. She will find ways to reinforce the links between the several WHO programs that focus on malaria and between WHO activity at headquarters, regional, and national levels. This united WHO should be a good candidate to lead a partnership of national governments, multilateral agencies (such as UNICEF), development banks (particularly the World Bank), providers of bilateral assistance (such as the United Kingdom, the United States,

and Japan), the international research community, and private sector companies.

Getting these systems right and developing the capacity to implement effective action will be crucial, and it will inevitably take time. There will not be much new activity on the ground within the next few months. Activities will be apparent from next year onward, building on what has been done before and developing new approaches to the provision of health services. This will revolutionize malaria control and set the direction for more integrated health action in other priority areas, such as tuberculosis and safe motherhood.

Rolling back malaria is not going to be easy. The aspiration of halving malaria deaths by 2010 and halving them again by 2015 will not be achieved without sustained and broad-based commitment. However, the potential is there, and if the scientific and technical inputs can be channeled through effective health systems and supported by adequate finances and political commitment, the benefits for the poor of the world will be enormous.

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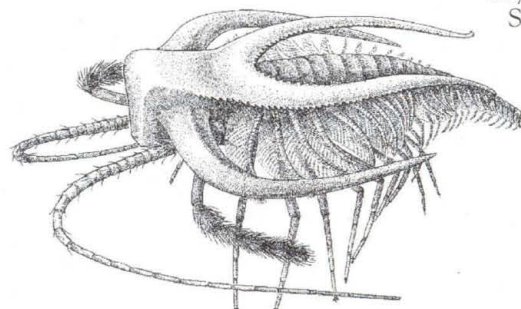
BOOKS: EVOLUTIONARY BIOLOGY

Contingency and Convergence

Mike Foote

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



First found. The first sketch of the primitive arthropod *Marrella splendens*, the most abundant animal from the Burgess Shale, appeared in Charles Walcott's field notes for 31 August 1909, recording the discovery of this soft-bodied fauna.

(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 exist-

ence 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 (preadaptations, 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



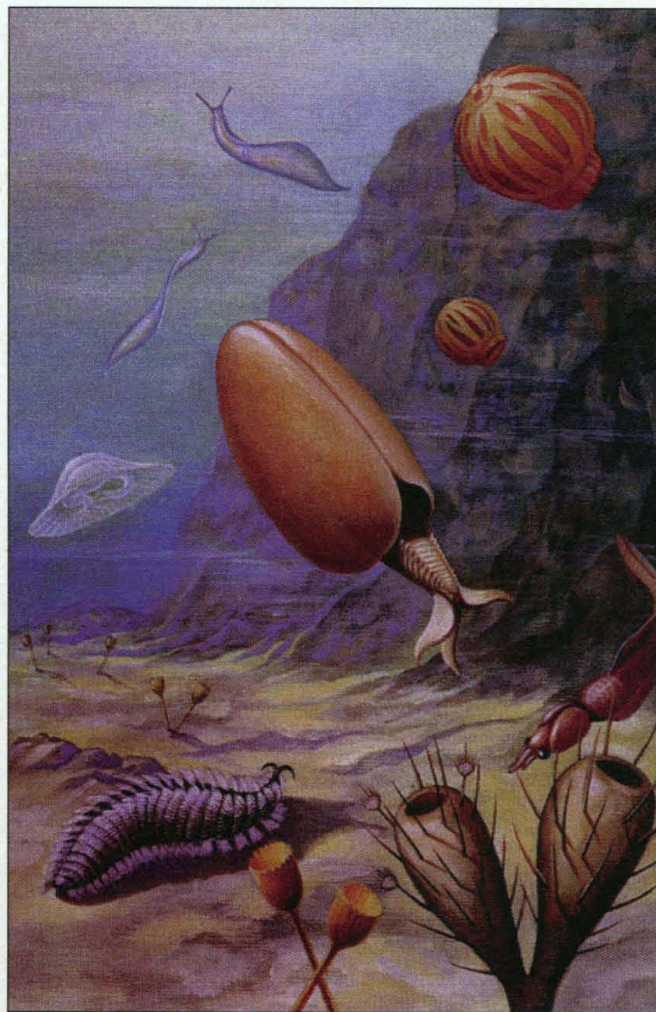
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conclusion that mass extinctions, with their consequent, profound changes in the biotic composition of the world, may not be mere intensifications of normal environmental stress, but rather may select for completely different properties than are favored 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 Mor-



Above the Burgess seabed. The arthropod *Odaria* (center), the chordate *Pikaia* (top left), the ctenophore *Ctenorhabdodus* (top right), the possible echinoderm *Eldonia* (translucent disk), and the enigmatic *Nectocaris* (right edge) were among the swimmers and floaters of the Middle Cambrian.

ris'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.

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Browsings

Emerging Infections. Richard M. Krause, Ed. Academic Press, San Diego, CA, 1998. 527 pp., illus. \$84.95. ISBN 0-12-425930-8. Biomedical Research Reports.

After introductory chapters on emerging infectious diseases and the analysis of epidemics, contributors cover the population, evolutionary, and medical biology of new and recurrent bacterial, viral, and parasitic infections including tuberculosis, influenza, dengue, malaria, Hantavirus, Ebola virus, and Lyme disease.

The Gospel of Germs. Men, Women, and the Microbe in American Life. Nancy Tomes. Harvard University Press, Cambridge, MA, 1998. 366 pp., illus. \$29.95. ISBN 0-674-35707-8.

Aided by public health reformers and home economists, the findings of late 19th-century bacteriologists were transformed into a popular obsession with germs. Tomes'

narrative suggests that the legacies of that earlier phobia still affect infectious disease control today.

Perceiving Talking Faces. From Speech Perception to a Behavioral Principle. Dominic W. Massaro. MIT Press, Cambridge, MA, 1998. 507 pp., illus., with CD-ROM. \$55. ISBN 0-262-13337-7.

To consider the bimodal (auditory and visual) processing of speech, the author combines theory, empirical results, and the construction and testing of mathematical models. The talking-head technology used in many of the experiments is described in detail, and the accompanying CD-ROM allows readers to experience the phenomena under consideration.

Science Incarnate. Historical Embodiments of Natural Knowledge. Christopher Lawrence and Steven Shapin, Eds. University of Chicago Press, Chicago, 1998. 350 pp., illus. \$55. ISBN

0-226-47012-1. Paper, \$19 or £15.25. ISBN 0-226-47014-8.

Through considerations of the habits and practices of individuals (including René Descartes, Isaac Newton, Ada Lovelace, and Charles Darwin), the essays in this collection explore connections between human bodies and our body of knowledge.

Second Nature. Environmental Enrichment for Captive Animals. David J. Sheperdson, Jill D. Mellen, and Michael Hutchins, Eds. Smithsonian Institution Press, Washington, DC, 1998. 370 pp., illus. \$32.50. ISBN 1-56098-745-6.

Contributors to this volume explore a range of approaches for addressing the psychological needs of captive animals (primarily mammals, mainly in zoos). By stimulating more diverse natural behaviors, managers can improve the physical well-being of these animals, facilitate breeding and reintroduction efforts, and help educate visitors.

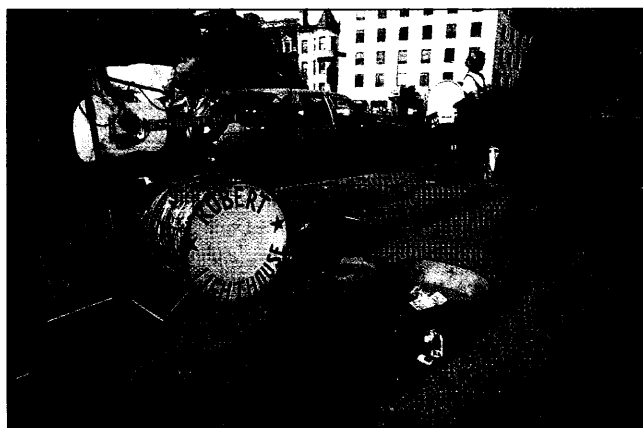
RESEARCH: GAME THEORY

Give and Ye Shall Be Recognized

Claus Wedekind

Students often share a flat because it is too expensive to rent one alone. Later, their flat sharing may include reciprocal shopping, cooking, cleaning, and household chores. Such cooperative behavior can be seen as a form of reciprocal altruism ("I scratch your back, you scratch mine"). Humans, however, are frequently altruistic even if the altruistic act is not likely to be returned by the recipient. In the June 11 issue of *Nature*, Nowak and Sigmund (1) explain why such behavior can pay off in the long run and so be evolutionarily stable. According to their main idea, whether an individual helps others determines his or her social status in the group. Indirect reciprocity can evolve if the others take this information into account in future social interactions.

Those with experience in flat sharing know that reciprocal altruism is not the whole story. Unfortunately, it is tempting for each of the occupants to do a little bit less than the others, just as it is tempting for industries to discharge radioactive or chemical wastes into the common instead of using a cleaner but more costly solution, or for fishermen to catch more than their fair share of fish (2). Game theory is a branch of



Social climbing. Acts of apparent altruism, such as donations to a street musician, may not actually be so selfless if the generous act increases the donor's social status.

mathematics devoted to such problems—to problems of cooperation and conflict in social situations (3). This is a broad area. It is in fact difficult to think of any form of social behavior, be it simple or complex, that is neither cooperative nor competitive. The breadth of this problem has kept sociologists, psychologists, economists, and biologists working for decades, using game theory as their basis.

Previous theoretical work suggested that direct reciprocity readily leads to the evolu-

tion of cooperation (4–6), but only in very small groups (7, 8). Thus, the fact that humans sometimes cooperate in large groups of unrelated individuals has been an evolutionary puzzle. This puzzle may have been caused partly by the way people thought about social dilemmas. Dilemmas have been described mostly as two

player or n-player matrices. For example, in the two-player "Prisoner's Dilemma" matrix, each player gets more if both cooperate than if both defect, but if one cooperates while the other does not, the cheater gets most and the betrayed least. Played only once, the evolutionary stable strategy for both players is to defect. This way they achieve less than if they had cooperated. If repeated, however, this game usually leads to rather cooperative solutions (6–10). In

multiplayer Prisoner's Dilemma games the solutions are less cooperative (7, 8).

There are everyday situations that are not easily approximated by such games. If you meet, for example, a street musician you have two options: either to give some money or not to give anything. Of theoretical interest is that this decision will, in most cases, not have any impact on whether the musician continues to play or not. The situation can be seen as a two-player game in which one party decides whether to lose

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