BOOKS: EVOLUTION

Stephen Jay Gould à la recherche du temps perdu

Douglas J. Futuyma

Although he is the most widely known evolutionary biologist since T. H. Huxley, vicar of Darwin to the literate public, defender of evolution in courts of law, sometime Wunderkind of paleontology, and primus inter pares as champion of macroevolution's place at high table, few match Stephen Jay Gould as object of professional controversy. It has been 25 years since his first and, until now, only book directed at his peers. Now (after a labor perhaps comparable in time and magnitude of product to Wagner's on *Der Ring des Nibelungen*, Goethe's on *Faust*, or Proust's on his search for time past), he has rendered a synthesis of the themes that have preoccupied him, and have evoked hundreds of pages of commentary ranging from scholarly debate to outraged fulmination, since Niles Eldredge and he punctuated a contented, placid—dare we say static?—theory 30 years ago.

The Structure of Evolutionary Theory
by Stephen Jay Gould
Belknap (Harvard University Press), Cambridge, MA, 2002. 1457 pp. $39.95, £27.50, €45.90. ISBN 0-674-00613-5.

The Structure of Evolutionary Theory presents the structure that, Gould envisions, must account for macroevolution; the details of genetic drift, modes of selection, or genetic architecture are not his concern. The book consists of a 169-page prolegomenon, six chapters that trace the history of the ideas with which he is concerned, and five that argue for expansion of Darwinism—not replacement, but nevertheless a "wrenching from several key assumptions." Gould's themes are that selection operates not only among organisms within species, but also at other levels (especially among species, thus accounting for macroevolutionary trends); that the heritable phenotypic variation arising within species is not "isotropic" but biased in certain directions, providing "positive constraints" on the direction of evolution; and that the vectors of change within species are cancelled by selection (or "sorting") at higher "tiers," chiefly by species selection and by mass extinctions. He articulates in extenso these familiar arguments in his familiar style, cementing them by empirical case histories and occasionally adding a gargoyle or two to face down his critics.

Others must judge his treatment of the early history of the field, but his portrayal of the "evolutionary synthesis" strikes me as generally sound—although like most of us he can be too eager to contrast the novelty of his ideas with the staleness of his predecessors'. (For instance, he quotes a passage from Ernst Mayr's *Animal Species and Evolution* that seems to deny catastrophic extinction; yet in the same passage, Mayr acknowledges mass extinctions and, citing Gould's mentor Norman Newell, attributes them to sea-level regression.) Nonetheless, having been reared on the same evolutionary literature as Gould, I agree that the postsynthesis era was one in which individual (organismal) selection was considered a sufficient cause of almost all of evolution; there was little sense that macroevolution posed any challenging or even interesting questions.

Among the three major themes, Gould's short treatment of the role of catastrophic extinction is, I think, unexceptionable, at least as a principle. Perhaps the most successful of the more substantial chapters concern the second theme: structural, or formal, approaches to the origin of morphology that emphasize, inter alia, the role of constraints. Gould's excitement (which I share) about contemporary "evo-devo" is palpable: his prose rises to lyrical heights as he summons "hoxology" and other developmental genetic homologies to attest to the roles that common ancestry and contingency play in phenotypic evolution. Treating the role of historical constraint in a purported analogue of the classical symphony (perhaps confounded with the sonata form of a single classical movement), Gould (to my delight) assigns saltation to the scherzo (joke): "[W]e must ask whether saltational themes...can also advance a strong case for a rehearing. My own conclusions are primarily negative...." Thus this rough magic doth he here abjure, and deeper than did ever plummet sound, he'll drown his book (or at least an infamous 1980 paper in which he tarred himself with Goldschmidt's brush). As Gould shows, parallel evolution, based on homologous developmental genetic foundations, illustrates the constraining, or at least biasing, role of development. (I, however, do not agree that the convergence of vertebrate and cephalopod eyes, in which some "master" genes play common roles, has lost its role as testament to the power of natural selection.) These chapters include a strong case for the ubiquity and importance of "spandrels" (nonadaptive by-products of form) and a worthy call to study their contribution to "evolvability." Alas, spandrels now are accompanied by pharaonic bricks, miltons, and other aspirants for our jargon. *Dum spirat, sperabit*—but I fear Gould hopes in vain.

The book's core, its heart of hearts, is the 279-page chapter on punctuated equilibrium, because it is the concept of static species that undergirds "the central proposition of macroevolution, that species play the same role of fundamental individual that organisms assume in microevolution." "Species sorting,"

Learning from old shells. For his frontispiece, Gould has adapted this illustration from Filippo Buonanni's *Ricreatione dell'occhio e della mente nell'osservation delle Chiocciole* (Rome, 1681), the oldest known book devoted to conchology.

CREDIT: FROM FILIPPO BUONANNI, *RICREATIONE DELL'OCCHIO E DELLA MENTE NELL'OSSERVATION DELLE CHIOCCIOLE* (ROME, 1681)

including species selection (based on emergent characters or fitness of species), generates a trend in a character that is correlated with speciation or extinction rate, but "directional speciation"—biased production of offspring species, which can be produced by selection toward the same distant optimum within each of a number of successively originating species—renders species selection unnecessary. Gould accepts that directional speciation is probably common, and he also notes that the relatively small number of species available for species selection can vitiate its evolutionary impact. (This problem especially

The author is in the Department of Ecology and Evolution, State University of New York at Stony Brook, 650 Life Sciences Building, South Loop Drive, Stony Brook, NY 11794–5245, USA. E-mail: futuyma@life.bio.sunysb.edu.

limits the number of characters that can shift directionally by species selection, if they are neither genetically correlated nor correlationally selected within and among species.)

Eldredge and Gould originally explained the pattern of punctuated equilibrium (rapid shifts between long-continuing, nearly static phenotypes) by a causal hypothesis (also called punctuated equilibrium) borrowed from Mayr, namely that new phenotypes represent reproductively isolated species that arose by "genetic revolutions" in small populations. (Gould rightly points out that this hypothesis never included macromutational saltation, despite this frequent, and continuing, misunderstanding.) The only truly objectionable element in their hypothesis was their postulate that genetic homeostasis prevents evolution except during speciation. Neo-Darwinians who, on the basis of theory and evidence, rightly rejected this explanation of stasis naturally also rejected the hypothesis that speciation is required for phenotypic evolution.

Nota bene: Gould now acknowledges population genetic theory and evidence; admits that "Eldredge and I made a major error by advocating, in the original formulation of our theory, a direct acceleration of evolutionary rate by the processes of speciation"; and abandons the notion that stasis is due to internal resistance to natural selection. But, he says, "*Eppur non si muove*." Stasis is still real, species still don't "move." So what can explain stasis and the punctuated equilibrium pattern? Gould adopts a solution that I proposed in 1987: If a character has multiple equilibrial states, perhaps as adaptations to different resources or habitats, evolution from the ancestral state z_0 to one such state, z_k, may readily occur in population k. However, the divergence will eventually be undone when the population's geographic distribution is altered and it interbreeds with conspecific populations that have retained z_0. Only reproductive isolation confers long-term integrity, enabling the character change to persist long enough to be registered in the fossil record and, moreover, to be ratcheted toward a more extreme state in later evolution. Thus phenotypic evolution is associated with speciation because reproductive isolation confers permanence on what would otherwise be an ephemeral change. Stasis, then, represents the time-averaging of populations that make only temporary slight excursions from z_0 and are soon homogenized by gene flow. Excursions will be especially ephemeral when environments are highly unstable, so (as noted by Peter Sheldon) a punctuated equilibrium pattern may be associated with unstable climatic conditions, and gradual evolution with environmental constancy.

This hypothesis applies only when there are multiple optimal states or adaptive peaks, and so may be far from general. Furthermore, it does not predict constancy over very short time spans. Thus, although I am gratified that Gould has adopted my suggestion, I believe that in its light some of the implications drawn from the original theory of punctuated equilibrium require more reformulation than Gould provides. For example, species selection will not be the engine of trends for characters that do not fit this model's assumptions; I don't think the reformulated punctuated equilibrium theory predicts phenotypic constancy in such a short term as the last 40,000 years' history of *Homo sapiens*; and I cannot agree that "evolutionary change itself must be reconceptualized as the infrequent breaking of a conventional and expected state." However, I certainly do agree with Gould that empirical study of the fossil record must tell us whether phenotypic evolution is commonly associated with speciation (when gene flow would otherwise reverse divergence) or not (when species undergo a long-term approach toward a single optimum). The critical test, as Gould has long argued, is whether or not ancestral phenotypes usually persist along with new, divergent descendants. Gould recounts a goodly number of cases that meet this criterion, but he does not provide a quantitative tabulation of the empirical literature (which may prove ambiguous at best).

"*Verachtet mir die Meister nicht*" [scorn not the masters] counsels the wise cobbler in Wagner's *Die Meistersinger von Nürnberg*, the musical revolutionary's tribute to tradition. By accommodating my suggested revision of punctuated equilibrium, by admitting the probable prevalence of "directional speciation" (i.e., traditional response to organismal selection), and by restricting the scope of species selection chiefly to differential speciation rather than differential extinction (because the latter seldom stems from emergent species-level characters), Gould approaches traditional neo-Darwinism far more closely than he explicitly admits. Because the chief implication of punctuated equilibrium is an autonomous macroevolutionary theory of trends, and because Gould details several reasons why species selection might be less likely to generate trends than the "hard" punctuated equilibrium hypothesis originally suggested, perhaps we should pose the empirical question of just how common trends are. If they can be only rarely discerned amidst the thickets of adaptive radiation, a selection theory beyond the neo-Darwinian may prove more needed in principle than in practice.

The Structure of Evolutionary Theory will doubtless be roundly criticized. It omits vast fields and perspectives in evolutionary biology and advocates positions that few will embrace in toto. But grant the hyperbole and the flaws in Gould's argument; grant that he might have thought to warn all but the most persistent readers, "*Lasciate ogni speranza, voi ch'entrate*"; grant even his self-description as "the most arrogant of literati." It is nonetheless the case that evolutionary biology today has an immensely broader perspec-

BROWSINGS

The Sport of Life and Death. The Mesoamerican Ballgame. *E. Michael Whittington, Ed.* Thames & Hudson, New York, 2001. 288 pp. $50. ISBN 0-500-05108-9.

The Sport of Life and Death. The Mesoamerican Ballgame. *E. Michael Whittington, curator.* An exhibit organized by the Mint Museum of Art, Charlotte, NC, where it closed 6 January 2002. At the New Orleans Museum of Art, New Orleans, LA, through 28 April; the Joslyn Museum of Art, Omaha, NE, 8 June to 1 September; and the Newark Museum, Newark, NJ, 1 October to 29 December.

During the two-and-a-half millennia preceding the Spanish Conquest, team games involving a rubber ball were played on courts at sites ranging from Honduras to Arizona and east to Puerto Rico. Combining athletic skills and ritual spectacle, the games were vested with religious and political symbolism. The exhibit and catalog sample the diverse artwork inspired by the games, including tiny jade carvings of Olmec player kings, the stone goals of Aztec ball courts, and this ceramic figurine of an elite Late Classic Maya ballplayer from Campeche, Mexico (left). Essays in the catalog discuss various aspects of the games and their cultural background.

CREDIT: THE ART MUSEUM, PRINCETON UNIVERSITY tive than 30 years ago; that we recognize stasis, constraints, multiple levels of selection, differential clade diversification, and historical contingency as valid principles worthy of research; and that Gould has played a leading role in bringing about these changes, in part by arguments retold in this, his *apologia pro vita sua*. He can exasperate but also charm, for as Homer said so memorably, τοῦ καὶ ἀπὸ γλώσσης μέλιτος γλυκίων ῥέεν αὐδή [and from his tongue flowed words sweeter than honey].

BOOKS: HISTORY OF SCIENCE

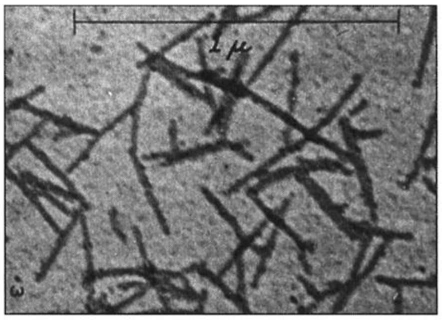
TMV in the Lab and Life Sciences

Soraya de Chadarevian

In 1935, in the pages of this journal, Wendell M. Stanley from the Division of Plant Pathology at the Rockefeller Institute in Princeton announced that he had isolated the virus responsible for mosaic disease in tobacco (TMV) as needle-shaped crystals of pure protein. The paper created a scientific sensation. Stanley's feat demonstrated that viruses, the invisible agents responsible for some of the most damaging diseases in plants, animals, and humans, could be treated like a chemical substance. The evidence that TMV was a protein, but one which could reproduce itself, led to heated debates about the role of viruses in the origin of life. On a more general level, it confirmed expectations that proteins represented the material basis of heredity. Subsequent corrections of Stanley's claim not withstanding—the virus was recognized as a nucleoprotein rather than pure protein—the 1935 paper quickly received canonical status in virus research, and Stanley received many awards, including the 1946 Nobel Prize in chemistry.

The Life of a Virus
Tobacco Mosaic Virus as an Experimental Model, 1930–1965
by Angela N. H. Creager
University of Chicago Press, Chicago, 2002. 412 pp. $75, £47.50. ISBN 0-226-12025-2. Paper, $27.50, £16. ISBN 0-226-12026-0.

This event, Angela Creager eloquently tells us in *The Life of a Virus*, marked only the beginning of an immensely successful laboratory career of TMV. The virus, inscribed in a changing set of experimental systems, became a model not just for the study of other viruses but for a wide range of questions of 20th-century life sciences as well. A series of firsts kept it at the forefront of research. After its identification as a protein, TMV became the first virus prepared by sedimentation in an ultracentrifuge. These pioneering investigations, performed in a collaboration between Stanley and Ralph Wyckoff, not only changed the representation of TMV but also triggered the development of ultracentrifuges from analytical to preparative instruments and thus to a much wider range of applications. A few years later, German researchers collaborating with Siemens to develop the first commercial electron microscope published an electron micrograph of TMV, making it the first virus to be so visualized. The electron microscope was used in much subsequent work under Gerhad Schramm at Tübingen as well as in Stanley's new Virus Laboratory at Berkeley (the main focus of Creager's study). Their efforts were aimed at defining the size and shape of the virus. TMV became the first virus for which a subunit structure was postulated. Chemical data together with evidence from x-ray crystallography (based especially on the work of Rosalind Franklin) provided support for this hypothesis and established that TMV was built of protein subunits that form a hollow cylinder around a helical strand of RNA. The isolation of its parts was followed by attempts to reconstitute the virus in vitro. The 1955 announcement by Heinz Fraenkel-Conrat and Robley Williams, members of Stanley's lab, that an infective TMV had been assembled from its purified parts stirred media interest much like the coverage following Stanley's original crystallization of the virus.



Early electron micrograph. Wendell Stanley and Thomas Anderson used electron microscopy to confirm the size and shape of TMV.

CREDIT: W. M. STANLEY AND T. F. ANDERSON, JOURNAL OF BIOLOGICAL CHEMISTRY 139 (1941), 325-38

Closely connected to its model roles in research concerning the nature and structure of viruses and in the development of representation technologies, TMV played a pivotal role in investigations central to the emerging field of molecular biology. Although virus researchers were slow in attributing an infective function to the viral RNA, during 1952–53 James Watson studied TMV at Cambridge in the hope of elucidating the structure and function of RNA. With the ready availability of mutants and the early sequencing of its protein subunits, TMV joined bacteriophage as a prime model organism for studies on the genetic code (though in the end the code was instead deciphered in a cell-free translation system with synthetic RNA polymers).

Creager, a historian of science at Princeton University, firmly places TMV among the few laboratory organisms that have served as model systems for 20th-century bioscience. She offers thoughtful reflections on how such systems guide research and what can be gained by focusing on the laboratory practices that sustain them. By emphasizing TMV's role as an exemplar rather than as a standardized prototype (as has been done for other model organisms), Creager aims to underline the changing nature of TMV and the many ways in which TMV research could be adapted to new contexts.

Perhaps because TMV served primarily as a (changeable) "point of reference," it does not seem to have inspired the creation of a community (with centralized services, a newsletter, and specialized meetings) like those that grew up around the fruit fly and the mouse. Yet the widespread reference to TMV allows Creager to draw connections between apparently separated endeavors and to offer new perspectives on some much-studied historical events. One point in particular seems of wide-ranging importance. The most enduring legacy of World War II for the life sciences, Creager argues, was not the influx of physicists but the rise of public expectations for and lay activists' funding of biomedical research. The TMV story demonstrates that medical concerns and funding also underpinned much of the early research in molecular biology. The impact of funding for cancer research (including the search for cancer viruses) by government and the cancer societies springs to mind. But Creager bases her argument especially on the case of the National Foundation of Infantile Paralysis, whose financial support for biomedical research rose sharply in the 1940s and 1950s. In the "war against polio" declared by this volunteer-based organization and the sustained effort to develop a vaccine against the feared disease, TMV served both as a substitute and as an exemplar guiding much research on the polio virus itself. The polio virus was crystallized in Stanley's laboratory in 1955, an achievement overshadowed by Jonas Salk's development of a polio vaccine in the same year.

Thoroughly researched and well presented, *The Life of a Virus* turns the career of TMV into a rich portrait of the changing practices and images of mid-20th-century life sciences.

The author is in the Department of History and Philosophy of Science, Cambridge University, Free School Lane, Cambridge CB2 3RH, UK. E-mail: sd10016@hermes.cam.ac.uk