Book Review

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The Structure of Evolutionary Theory.
Stephen Jay Gould (2002, Belknap Press.) Hardback, 1433 pages.

Since the publication of *The Origin of Species* nearly 150 years ago, Darwinism has been an integral part of not just biological theory but contemporary scientific and even popular culture, as relevant today as when we were first introduced to the concept of natural selection. This continuing relevance is apparent from such recent movements as neo-Darwinism, sociobiology, and of course artificial life. In his magnum opus, *The Structure of Evolutionary Theory*, Stephen Jay Gould draws together the themes of a long and illustrious career in palaeontology and evolutionary theory into a single constructive critique of Darwinism and natural selection.

Throughout its long history, of course, Darwinism has been subjected to extensive debate, and reformulations both successful and abortive, but perhaps nothing on the scale of the reform Gould proposes with his book. Gould identifies his critique as reformulating the three key claims of Darwinism: the effectiveness and the predominant role of natural selection in directing evolution, and the ability of natural selection at this level to explain all macroevolutionary trends, such as speciation, extinction, and the diversity of life, through extrapolation from this fundamental mode of operation. The reformulations Gould proposes, which he claims strengthen Darwinism while leaving its central character intact, are: the notion of constraints on evolution that limit or channel natural selection's ability to adapt evolutionary individuals, the introduction of hierarchical selection at levels both below the organism (for example, the gene) and above (demes and species, among others), and the existence of a hierarchy of qualitatively different time scales, each with different causal mechanisms affecting evolution's history.

To provide a context for his critique, Gould first presents a history and commentary on the genesis of Darwinism, and the major developments and events in its subsequent history. As Gould says, "I can only hope that this . . . will strike some readers as enlightening for the 'quick entrée' thus provided into the essential work of the people who led, and the concepts that defined, the history of the greatest and most consequential revolution in the history of biological science." At nearly half of a very lengthy book, this 'quick entrée' makes fascinating reading for anyone interested in the history of explanations for life as we know it, ranging as it does from the pre-evolutionary thought of Paley, Geoffrey, and others, through Darwin's revelation in the *Origin*, to the pan-adaptationism of the Modern Synthesis via the rediscovery of Mendelian genet-

ics and the work of such well-known figures as Fisher, Haldane, and Simpson. Theories relevant to all three pillars of Darwinian theory, whether proposed before of after the publication of the *Origin*, are presented. For the effectiveness of natural selection, constraint and channels are considered, from Geoffrey and Owen's archetypes to Goethe's leaves, from the saltation and macromutation of Galton and Bateson to de Vries, including Goldschmidt's hopeful monsters. For the exclusivity of selection at the level of the organism the historical debate begins with Lamarck and ends with Weismann's spectacular reversal from supporting initial exclusivity to formulating germinal selection, while for extrapolation into geological time the main attack comes from Kelvin's estimate of an earth far too young to have allowed natural selection to generate life as we know it.

Having thus set the stage, Gould is ready to launch into the main theme of the book, as suggested by its title, describing a revised structure for evolutionary theory. Gould draws together a life's work to present reformulations on each of Darwinism's three pillars. In response to Darwin's claim for the organism as the exclusive focus of natural selection, Gould presents his proposal for a six-tiered hierarchy of selective levels: gene, cell lineage, organism, deme, species, and clade. Gould argues that each level of this hierarchy is characterized by the different effects natural selection can produce at it, and the controls that one level can impose on another. For example, Gould proposes that while natural selection can operate at the level of the gene or cell-line individual, the functionally integrated organism at a higher level must impose controls on these lower levels if it is to survive, because the consequence of runaway evolutionary success at one of these lower levels is usually highly detrimental or even lethal (for example, Down's syndrome at the gene level or cancer at the cell-line level). In contrast, the species individual, which is not functionally integrated, is quite able to accommodate the runaway evolutionary success of a mutant organism individual within it. To validate this hierarchical approach to macroevolution Gould presents his theory of punctuated equilibrium and argues that the predominance of stasis in species, punctuated by rapid periods of evolutionary change resulting in the formation of new species, is best explained by selection at the species level, also arguing that the punctuated mode undermines the Darwinian strategy of explaining macroevolutionary patterning by extrapolation from microevolutionary processes.

In response to the claim for the predominant status of natural selection in driving evolution Gould provides an extensive consideration of constraints, both negative and positive. By negative constraint, Gould means the traditional idea of limitation in the variability upon which natural selection can operate, through lack of the necessary genetic mutations to give rise to some useful adaptation. More interesting is the concept of a positive constraint, which channels the operation of natural selection by providing variability only in certain directions. Gould identifies the importance of development in providing positive constraints for natural selection, through examples of evolutionary trends that result in progressive juvenilization of adult forms, and through examples of strikingly similar developmental mechanisms across separate phyla. It is this latter point that is particularly interesting, and Gould's detailed consideration of the different explanations for similarities in form between species and phyla, convergence to an optimal design or commonly inherited developmental building blocks, is illustrated by fascinating reference to instances of such common inheritance as the Hox genes, whose occurrence in insects and animals provide evidence of a common ancestor of the arthropods and vertebrates in the distant past exhibiting, in its complete form, one of the developmental mechanisms fundamental to both phyla. Gould rounds off his discussion of constraint with his idea of exaptation, in which a trait arising for non-adaptive reasons at the level of selection, for example a product of gene-level selection becoming visible at the organismal level, or a physical side effect of an adaptation that

natural selection established, can subsequently be recruited by natural selection and turned into an adaptation.

Finally, and in contrast to the preceding pillars, the Darwinian claim for the ability to explain macroevolutionary phenomena by extrapolation of microevolution into geological time receives a brief treatment. Gould's approach here is again hierarchical, and he proposes that there are at least three different "tiers" of time each with different evolutionary impulses, from the time scale of ordinary natural selection on organisms at the first tier, to the time scale of macroevolution through punctuated equilibrium at the second tier, and finally to the time scale of catastrophes such as large meteorite impacts that set evolution along entirely new tracks, by changing the environment so significantly that species and clades previously dominant in the old environment can be replaced by previously insignificant lineages with newfound advantages in the new environment.

Throughout the book, Gould's presentation of the ideas involved is coherent if lengthy, and his arguments persuasive. Certainly the breadth of knowledge he displays makes this an authoritative work, although in some areas there is a suspicion of selective presentation. Indeed, from my own largely "Dawkinsian" perspective I do not consider the case for hierarchical selection, at least at certain levels of the hierarchy, to be closed. It does seem that the presentation of arguments regarding group selection is not entirely balanced, and by Gould's own admission some of his examples of higher-level selection can be explained in terms of organismal selection. Perhaps then we should not throw away the Necker cube just yet.

Beyond the numerous concepts of general interest briefly summarized above, there are some interesting perspectives for artificial life and related disciplines. Of particular interest is Gould's contrast of the cultural atmosphere surrounding Darwin's formulation of natural selection in *The Origin of Species*, and that surrounding his own reformulation through this book. Whereas Darwin's ideas matured in Victorian England, surrounded by ideas of reductionism, progress, and improvement that informed his theorizing on nature, Gould considers that the culture of the last several decades, with its emphasis on complexity and interactions as epitomized by fields of study such as complex adaptive systems, allowed the conception of such theories as punctuated equilibrium and hierarchical selection. More interesting still are some of the words of naturalists and philosophers that Gould chooses to highlight, words written hundreds of years ago whose ideas will resonate with the student of artificial life today. I conclude this review by leaving you with one striking example; in 1787 Goethe wrote thus to a friend regarding his idea for an archetypal plant: "With this model and the key to it, one will be able to invent plants. . . which, even if they do not actually exist, nevertheless might exist and which are not merely picturesque or poetic visions and illusions, but have inner truth and logic. The same law will permit itself to be applied to everything that is living." For our discipline, whose age is measured in mere decades, it is worth remembering that perhaps there really is nothing new under the sun.