

## An Autobiographical Anatomy

Michael T. Ghiselin

*California Academy of Sciences,  
Golden Gate Park, San Francisco,  
CA 91118, USA*

STEPHEN JAY GOULD, *The Structure of Evolutionary Theory*, Cambridge:  
Harvard University Press, 2002, xxxii + 1433 pp., illus., \$39.95.

An 'anatomy' is a literary work that treats a particular topic at great length and in minute detail. Viewed as a contribution to that genre, this massive and prolix tome may be read with patience and also with sympathy for its author. Gould died around the time that it was published, and the book is a fitting monument to his life's work. Because he goes into so much detail, providing an immense amount of background, including especially the autobiographical aspects, he provides unusual opportunities for critical analysis and commentary on matters of fundamental interest. But doing justice to the book as a whole requires familiarity with a range of subject matter that only a few of us possess. I review the work as very much an insider.

Gould and I were born at about the same time, and participated in many of the great debates about evolution that marked the second half of the twentieth century. Although he was trained as a paleontologist and I as an anatomist, we both did our graduate research on mollusks, and it was as malacologists that we first began to interact, debating the issues of gastropod origins. Both of us quite early became devoted admirers of Darwin, and Gould begins his last book with a citation of my first, to the point that what really matters is the opinions of the best minds, not the general public. Some readers may wish that more of Darwin's more or less unaffected modesty had worn off on Gould. He and I were among the first 22 to receive MacArthur Fellowships, and soon thereafter I went to Chicago to visit the Foundation's staff. When I remarked that I hoped the award would enable him to stop writing popular works and get

back to something more worthy of his talents, I was told that it had been given to him for that very reason.

Be this as it may, Gould provides me with an excuse for not being modest about one of my own major contributions to knowledge, which is the thesis that species are individuals, not classes. He devotes a chapter of some 150 pages to that idea, which is fundamental to his macroevolutionary thinking. More background details need to be filled in here. In 1971 there was a meeting in Washington, D.C. of the Geological Society of America at which there was a symposium on the general topic of 'Models in Paleobiology'. My contribution was a paper on phylogenetics. Gould and his co-author, Niles Eldredge, were both there to present the theory of 'punctuated equilibria'. I had met Eldredge when, as a graduate student, he took a course that I taught at the University of California's Bodega Marine Laboratory.

Gould had just reviewed a draft of my second book, *The Economy of Nature and the Evolution of Sex*, for Harvard University Press. It seems to have influenced his thinking more than he has been willing to admit, for it was an attack on Panglossian adaptationism and the sociobiology of E.O. Wilson. Although my book emphasized the individual organism as that which gets selected, I mentioned that species are individuals, and acknowledged that perhaps their differential survival might have some kind of long-term effect. The book was finally published in 1974, the nominal year of publication of my paper entitled 'A radical solution to the species problem'. Evidently it was Eldredge who, upon reading it, first realized the macroevolutionary implications.

If species, like organisms, are concrete particular things, then they can participate in processes including macroevolutionary ones. Species selection would therefore be a legitimate analogy with organismal selection, and it might have important long-term evolutionary consequences. Gould pushes the analogy between species and organisms somewhat further than I would. Although originally he compared the speciation process to mutation, he later realized that the correct analogy is with cell division. Unless species are individuals, species selection will not work, but the fact that they are individuals only means that the theory is not metaphysically flawed. As someone who would gain a great deal were it to be found that species play an important role in macroevolution, I have been sitting on the sidelines hopefully awaiting some empirical evidence for that. Even the most sympathetic reader of Gould's effort will probably get the impression that their role has been minor, albeit significant. Everybody seems to agree nonetheless that the discussion has been exceedingly

stimulating, although not always constructive. Persons who have wanted to discredit the ideas of Eldredge and Gould have sometimes disparaged my own.

Gould cites a few of my publications about the individuality thesis and its implications. However, my 1997 book, *Metaphysics and the Origin of Species*, is not among them. That is a shame, for had he read it his thinking might have been somewhat more profound, and he might have avoided some unfortunate mistakes. One of the most important of the implications of the individuality thesis is that it helps us to understand the roles of history and of the laws of nature in evolutionary biology. Taxonomic groups are individuals, and there are no laws of nature for any individual in any science whatsoever, including evolutionary biology. The properties of species, genera, phyla, and all other taxa are matters of contingent, historical fact. On the other hand the laws of nature in biology are all generalizations about kinds of individuals, not about particular ones. In his book *Wonderful Life* Gould emphasized, as have few authors before or since, the contingent nature of evolutionary history. Yet had Gould possessed a somewhat deeper understanding of the individuality thesis, he might have carried that line of thinking to its logical conclusion and found himself facing a dreadful dilemma. As it was he failed to realize the fundamental contradiction between his ideas about contingency and necessity, or history and law. Therefore he continued to endorse various essentialist notions, and to proclaim himself a structuralist.

A particularly glaring example of Gould's metaphysical confusion is his failure to understand those fundamental concepts that we anatomists call 'homology' and 'analogy'. He gets the two backward! To be sure, something of the sort has happened to the language before, and most of what has been written about these terms is at best nugatory. Homology and analogy are both relations of correspondence (not similarity) between the parts of wholes. Homology is a relation between parts (organs) of wholes (organisms) which in turn are parts of larger wholes (lineages). It is an historical concept, one that allows us to generalize about relationships within one vast individual, which is a genealogical nexus. Analogy, on the other hand, is a relation between parts (organs) of wholes (organisms) which are members (not parts) of classes (not individuals). It is a non-historical concept, one that allows us to generalize about kinds of organs in the context of spatio-temporally unrestricted generalizations, including perhaps laws of nature. Gould however tries to make 'homology' designate the fundamentally important relationships, 'analogy' the superficial ones.

Yet there is nothing superficial about the relationships between the wing of a pterosaur, a dragonfly, an airplane, and any other such component that may have evolved or been invented on some planet several billion light-years distant from our own. They are manifestations of the fundamental laws of nature to which all beings throughout the universe conform, always have conformed, and always will conform.

Gould invokes what strikes me as an occult property, which he calls 'deep homology', to account for certain constraining influences that allow him, he thinks, to explain the order of organic nature in terms of something internal to the organisms. There has been a lot of loose and muddled talk of late about taxa being 'natural kinds', but that implies that they are classes, not individuals, and that the underlying order would have to be nomothetically necessary rather than historical and contingent. Those who have advocated that move are of course wrong. Evidently they have confused what systematists call 'conservative characters' with kinds. Conservative characters are parts that evolve very slowly if at all, either because they are not very labile or because of their conditions of existence. Their failure to change readily allows a useful amount of forecasting; but unlike the laws of nature, they allow no prediction in the sense that something must be so and cannot be otherwise. What is called 'structuralism' maintains that the properties of organisms are to be explained in terms, not of history, but of laws of nature. If species and other taxa are individuals, then the structuralists' fundamental position is untenable. For that very reason some of them have flatly rejected the individuality thesis. Gould simply misses the point about what causes the structure of organized beings, and fails to realize that he has spurned the very contingency thesis that he argues with such eloquence and force.

Given the extent to which Gould labors to expound his entire worldview, an explanation for his confusion is not far to seek. Not only does he proclaim himself a structuralist, he professes esteem for essentialism in general, and praises a long list of idealistic morphologists and others with similar intellectual tastes. His reflections on such persons are worth reading as indicative of how long, and how profoundly, *Naturphilosophie* has distorted the thinking of biologists. His discussion of Eimer, for example, stimulated me to snatch my own copy off the shelf, and to read the appended essay in which Eimer praises Lorenz Oken. It stands to reason that Gould would reject David Hull's idea that historical entities such as Darwinism do not have essences, and that he would seek for 'defining properties' of taxonomic groups. He tries to resurrect the notion of an

archetype by equating it with developmental mechanisms that (as he sees it) constrain evolution along certain lines, in turn equating the tendencies or evolutionary trends that result with orthogenesis. Darwin of course disposed of archetypes by equating them with common ancestors, which are the starting points for evolution within clades.

Gould attempts to move the Ideas in the Mind of God of which particular organisms are imperfect copies into the developmental and hereditary apparatus. That move clearly will not work, for, as has been obvious all along, the developmental and hereditary apparatus itself evolves. To lend plausibility to his view, Gould tries to make a case for treating developmental constraint as something 'positive'. Let us hope that nobody falls prey to such sophistry. Whether something is negative or positive is not necessarily either a good thing or a bad thing. Negative feedback is good because it allows a thermostat to keep the temperature of a room within certain limits. Constraint prevents things from happening, and therefore it simply must be negative. What Gould labels positive constraint is really something quite different. It is the potentiality for a particular developmental system to become modified in some respects, giving the capacity for modification and consequently for the emergence of some kind of novelty. Of course the initial organism, *i.e.*, the common ancestor, must have possessed the ability to give rise to whatever modified descendants arise from it. It is therefore unconstrained in that sense, but we would not say that it is positively constrained. Constraint of course is a very old idea, and not just in biology. Curiously, Gould treats it as if it were the contribution of structuralists like him. However, it is a functional concept, not a morphological one. After all, it was the great functionalist Cuvier who argued against evolution on the grounds that organisms are so constrained by the co-adaptations of their parts that any change would render them inviable.

Although the anatomy and physiology of the ancestral creature do not constrain their descendants to evolve novelty, they do facilitate the emergence of such novelty because they present opportunities for it. Gould rightly emphasizes the opportunistic nature of evolutionary change, including what has been called its 'preadaptive' aspect. His historical treatment of it, however, is fragmentary and self-serving. He does consider how Darwin responded to Mivart, who had argued that the origin of new structures constituted a problem. Yet Gould ignores the contributions of Darwin's followers, especially Anton Dohrn, who introduced the concept of *Functionswechsel*. We are told nothing about the rich literature on such topics. Hence the reader is apt to get

the impression that Gould introduced something more than jargon into a traditional area of research.

There are serious problems with Gould's efforts to reconstruct Darwin's evolutionary ecology, and here too his idealistic proclivities would seem to have distorted his thinking. Gould is quite right in observing that Darwin tried to explain the evolution of human social traits as a consequence of competition between tribes. Why Darwin did not invoke artificial selection or reciprocity has always been something of a puzzle to me. Perhaps it was by extrapolation from social insects, for Darwin explained their neuter castes on the basis of families being individuals and being selected as such. Curiously, Gould maintains that Darwin explained, as have I, such phenomena on the basis of advantage to the queen. That would have made him an advocate of parental exploitation rather than familial selection. I cannot reconcile that interpretation with the Darwinian texts. With respect to the geometry of bees' cells, Gould suggests that the explanation lies in the physical necessity that results from packing them closely together. Yet Darwin himself came up with a much better explanation, and backed it up with comparative data. The hexagonal structure allows the maximum amount of honey to be contained with the minimum of wax. As with so much of his work, Darwin's explanation turns out to have been an economic one.

Not surprisingly Gould, however misguided, is by no means inconsistent in failing to understand Darwin's economic thinking in general. He not only fails to understand competition, he misinterprets it, and treats it as if it were some kind of direct physical interaction among the competitors. Gould's sympathies always lay with the nineteenth century anarchist Prince Kropotkin, rather than with Malthus or Darwin. Gould was notorious for having proclaimed that he learned his Marxism at his 'daddy's knee' yet nonetheless refusing to go public with respect to his real convictions about that belief system. Here, he declares it a private matter. In spite of that a sort of rationale for his behavior is not far to seek. Gould represents a mildly idiosyncratic variant upon the traditional theme of essentialist historicism as exemplified by Plato, Hegel and of course Marx. The Platonism is particularly evident in his esteem for D'Arcy Thompson. Marxism tried to replace the interplay of ideas with the interplay of material beings as the rationale for a metaphysical system in which the drift of history is in a predetermined direction. Gould seems to have recognized that above the organismal level in the hierarchy of individuals, the evident contingency of things tends to rule out that kind of historicism. And yet he hoped to salvage it at the level of the

developing organism. Evidently it was not obvious to him that the effort was futile, for reasons that have already been stated above. Such being the case we can read the long excursus on contemporary developments in embryology with the deepest interest, with considerable return upon the time invested, and with the highest esteem for the author's erudition. But the data presented can better be interpreted as showing that contingency reigns all the way down. The premises may be true, but the conclusion does not follow. Gould missed an opportunity to turn half of his own argument on its head and modify his views so as to become, at last, a real Darwinian.

Gould considers at some length what he thinks it means to be a Darwinian and his efforts to find something like an essence for it are perhaps as good as anybody's. He also presents some reflections upon Darwinian methodology including my suggestion that Darwin's method was hypothetico-deductive rather than the sort of approach that naïve inductionists have advocated. He does not think that adequate to characterize Darwin's accomplishment, however, and neither have I. Gould interprets *The Origin of Species* as an effort to develop a methodology for historical biology. This is certainly an important aspect of that work, which was an effort to explain a new paradigm and to justify it by means of illustrative examples. Darwin's later publications such as those on the behavior of both plants and animals help to provide further illustration. And yet, Darwin's science, however idiographic it may have been, was also nomothetic. His research program was aimed at discovering not just the history of life, but also the laws of nature that govern it and have governed it through time. He used the one to test and to develop the other. Even his monograph on barnacles, which established a genealogy and provided narratives, gave him insights about such phenomena as the prevalence of sex. The result was not just some brilliant comparative functional anatomy that made the teleological interpretation of flowers look silly. It included a great deal of experimental work on selfing and crossing. There was a remarkable unity to Darwin's thinking. As a consequence the various aspects of his science were mutually supportive, not contradictory, and he was able to see larger connections where others saw mere curiosities. Once again Gould's treatment of the Darwinian method is rather superficial, and it tells us more about Gould than it tells us about Darwin.