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A Revised Darwinism

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Stephen Jay Gould's last book and *magnum opus* is first and mainly a theoretical revision. The revision is of Darwinism, in both its original and Modern Synthesis formulations, of what Gould calls the "tripod of support" on which the theory of natural selection traditionally rests. This tripod consists of three major claims: (1) The sufficiency of natural selection acting at the level of the individual to explain the major features of evolution at all temporal and taxonomic scales. Gould's view is that species selection is necessary to explain most large-scale patterns. (2) A view of natural selection as creative, as supplied with variation that is copious, small in effect, and directionally unbiased (Gould's term is "isotropic"), and therefore as causal in the origin of novelty. Gould argues that variation is massively constrained, and that these constraints are a major source of creative input. (3) Evolution at the large scale – i.e., macroevolution, including large-scale trends – can be understood as the direct extrapolation of processes at the small scale, i.e., microevolution. Gould argues that different processes may operate at different scales, sometimes in opposition, or more often, orthogonally.

The book is also a work of history. It is a history of Darwinian thought from the 19th century to the 21st – a selective history to be sure, focusing on figures whose views are central to the revisions Gould proposes. And finally the book is a summation and a synthesis of Gould's life's work. He pulls together the major themes of those hundreds of *Natural History* columns and dozens of books, plus his technical papers on *Cerion*, into a single story. Like the *Origin* itself, *The Structure of Evolutionary Theory* is truly "one long argument." It is a treatise, or a kind of legal "brief" in support of the revisions Gould proposes to the conceptual tripod (although a less apt term than "brief" is hard to imagine – the book is 1343 pages long).

The book reveals all of the many Goulds who have so much enlivened evolutionary discourse in the past forty years. We see Gould the virtuoso, polymath, and show-off. He can't just explain Geoffroy's version of transcendental morphology. He has to compare Geoffroy's romantic theorizing to Don Quixote's. And Gould can't just argue that we ought to consider the social influences giving rise to Geoffroy's Naturphilosophie as independent of the reasons for its ultimate success. He has to draw parallels with Nietzsche's historical methods and with exaptation in evolution. Like Michael Jordan cutting in alone to the basket, he can't just dunk it. Hanging in mid-air, he has to pass it from one hand to the other, with eyes closed and tongue hanging out, and *then* dunk it.

We also see Gould the novelist. His history is a narrative, told with feeling and drama. And like George Eliot, he empathizes to some degree with all of his characters, from Lamarck to de Vries to Simpson, Mayr, and Dawkins, showing generosity even to those obviously wanting in manners and breeding, and to those whose views are anathema to him. The understanding and warmth that comes from his having lived briefly inside the head of all of them – through their major works – radiates from every line. And finally, inevitably, we see Gould the Bronx street-fighter. At the end of a long chapter on punctuated equilibrium, he slashes back at detractors who have accused him of dishonesty, of stealing ideas, and of having ulterior motives, accusing some of them in turn of professional jealousy. Gould, as we've long known, can hold his own with the toughest and the meanest. It's not pretty. But then street-fighting never is.

Swishes and misses

Everyone will take home something different from this large and magnificent work. And I do not presume to know what will eventually be considered the most important of his views, what will be his legacy to, say, 22nd-century evolutionary biology. But I have selected two points of his for special comment, chosen because they are relevant to my own research and because I think Gould may be wrong in ways that undermine his overall view. As will become clear, I generally support that view, indeed mostly take it for granted, although I should add that I am not an unbiased reviewer, having been raised in roughly that outlook. I have also chosen for comment two issues on which I think Gould is importantly right, in which he makes points that are central in macroevolutionary thought but that in my experience have not been widely appreciated.

The necessity of alternative hierarchies. Gould's view of evolution is hierarchical, and he is clear that the units in his hierarchy are individuals, physically nested one within another. This is hierarchy in the sense of Simon (1969), Vrba and Eldredge (1984), Salthe (1985), Eldredge (1985), Wimsatt

(1994), Valentine and May (1996), and McShea (2001). Gould considers the various difficulties in identifying levels, and then argues for a single hierarchy of individuals: gene, cell, multicellular organism, deme, species, and higher monophyletic taxa. He acknowledges that others have settled on other schemes, in particular, that Eldredge (1985; Eldredge and Salthe 1984) has argued for two parallel and partly overlapping hierarchies, a genealogical one, (genes, chromosomes, organisms, demes, species, monophyletic taxa) and an economic or ecological one (molecules, organelles, cells, tissues, organs, organ systems, organisms, populations, certain ecological units). For comparison with Hull's (1980) well-known conceptual scheme, the genealogical hierarchy is roughly a hierarchy of "replicators," and "interactors" are a subset of the ecological hierarchy. But Gould rejects this dual scheme – noting that this is the single major issue on which he has differed with Eldredge over the years – seeking instead a hierarchy of individuals that are both replicators and interactors, i.e., the levels of selection.

Contrary to Gould, I see no real disagreement. For certain purposes – for example, to ask questions about levels of selection – something like Gould's univariate scheme is obviously useful. But for other purposes, it is helpful to separate the two. For example, we may be interested in genealogy-independent relationships among entities within organisms. We might ask what is the relationship between number of cell types and number of tissues types in multicellular organisms? Or, under what circumstances do teams and task groups arise in colonial individuals? (For other such questions, see Anderson and McShea 2001.) To ask these, we need a hierarchical scheme that recognizes entities such as tissues and organs, entities that are not now and have never been levels of selection.

A related complaint is that in Gould's scheme, entities consisting of associations of genealogically disparate individuals – i.e., symbioses and ecological associations of various kinds – are excluded. He acknowledges they exist, notably the ecological association of prokaryotes that historically produced the eukaryotic cell and Wilson-and-Sober's phoretic associations (multispecies associations of mites, nematodes, fungi, and so on that move together from resource patch to resources patch on the back on an insect; Wilson and Sober 1989). But Gould excludes them from his hierarchy on account of their supposed rarity. I think it is currently unclear how common such associations are. But these aside, why exclude the more conventional and indisputably ubiquitous ecological associations, from microbial mats to ecosystem-scale units? I would think that the degree to which these qualify as replicators and interactors (and therefore as levels of selection) is presently an unresolved empirical matter. Perhaps they are not organisms, but it does not follow that they are not evolutionary individuals, albeit individuals that are not well bounded and therefore are difficult for us to perceive as unified. Here I take my lead directly from Gould and Lloyd (1999): these could well be individuals with some distinctly un-organism-like properties.

The questionable necessity of punctuated equilibrium. I have never been able to understand why species selection requires punctuated equilibrium. (Although I worry that this failure is my own obtuseness, because Gould and others seem so sure of the connection.) Clearly, species selection requires that species be evolutionary individuals, but why must they originate rapidly and then remain static? One rationale is that a rapid birth makes them stand out clearly as individuals by drawing attention to their boundedness in time, an essential criterion of individuality, many have argued. In contrast, individuality is less obvious if species arise anagenetically, by gradual transformation of pre-existing species, with old species grading insensibly into new ones. With no discrete, or quasi-discrete, moment of birth, their individuality is certainly less striking.

But these are psychological phenomena. Rapid birth and stasis are ideal conditions for detecting individuality. But nothing in our notion of individuality requires it in principle (even by Gould's own criteria). Consider these counter-examples. A human settlement may grow gradually over centuries from a single farmhouse to a city of millions, with no single stage or period of growth clearly identifiable as the episode of its birth as a city. Yet a city is an individual. Hurricanes too are individuals, even though they grow and develop gradually and typically dissipate rapidly (when they track over land), with no clear period of stasis. And consider a more conventional biological example. We routinely recognize what might be called degrees of multicellularity. *Gonium* is a green alga consisting of simple association of cells of a single cell type. It is multicellular. But so is an octopus, and intuitively the octopus has achieved multicellularity more fully, or more deeply, or at a higher level. In what has recently become a fairly precise technical language for hierarchy, octopuses are said to be more "individuated" at the multicellular level, and criteria have been devised to assess degree of individuation, at least in qualitative terms (see references in the last paragraph). The point is that the transition from less to more individuation is gradual and continuous – conceptually and also probably actually, in the history of life – but this continuity does not compromise the individuality of octopuses in the slightest. More generally, individuality does not require discrete origins.

In addition to conferring individuality on species, Gould thinks punctuated equilibrium is important because it guarantees the existence of higher-level causes in evolution (critical to his revision of the first leg of the tripod), and because it precludes the notion that macroevolution is a simple extrapolation

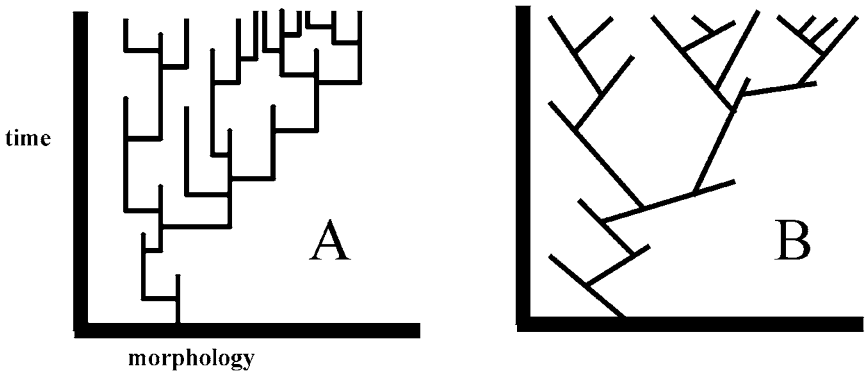

Figure 1. A trend in morphology produced by species selection, in this case, a higher speciation rate for lineages with higher values of the (here unspecified) variable on the morphology axis. (A): A punctuated version, with changed unbiased, meaning that speciation events producing increases about as often as they produce decreases. (B): A gradualistic version, in which species change anagenetically, but as in A, not in any preferred direction.

of microevolution (critical to his revision of the third leg). My understanding of his thinking is that in the punctuational mode, microevolutionary processes act below the species level, but because species are stable entities, evolution at higher levels must be explained by other processes (such as species selection). In this view, species-level stasis is necessary to insulate higher levels from lower-level causes, in a sense, to produce causal independence among levels.

This logic seems faulty to me. Consider a canonical case of punctuational change and species selection shown in Figure 1A. The assumption here is that selection acts on organisms but produces no net change, on average, within a species. The trend – represented here as an increase in some aspect of aspect of morphology – is produced by species selection, or in this case, a greater speciation rate at higher values of the morphological variable. Species on the right speciate more than species on the left. But consider the equivalent gradualistic case in Figure 1B. Again, only organismic selection operates within species, but here it produces anagenetic change, and does so in every lineage. However, no trend results at the clade level, because anagenesis occurs equally in both directions. The trend at the clade level is produced by differential speciation, just as in the punctuational case. In other words, causal insulation can be achieved in gradualistic mode, without stasis. (See also Vrba's [1980] argument that stasis is not required for species individuality.)

Consider too the converse point, shown in Figure 2. Here a trend at the level of the clade is the result of what Gould calls "directed speciation." Change is punctuational, but organism-level selection acting in peripatric populations during speciation events consistently produces increases,

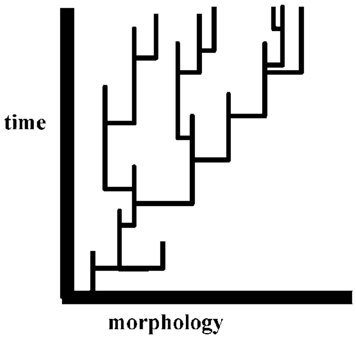

Figure 2. A trend produced by directed speciation in the punctuational mode. In speciation events, the morphological variable increases more often than it decreases, as a result of selection at the level of the individual acting in peripatric populations.

presumably because higher values are advantageous to individual organisms (at least in peripatric populations), with the result that most new species have higher values of the morphological variable than their ancestors. The clade trend then is the direct result of microevolutionary change occurring during speciation events. The point is that the punctuational mode is no guarantee of causal insulation.

The worry here is that in committing himself to punctuated equilibrium in this way, Gould may have put the entire notion of causal independence at risk. After all, punctuated equilibrium could turn out to be wrong, at least as a general statement of the predominant mode of change at the species level. (I am not arguing that it is.) And in that case, according to Gould's logic, causal independence seems to fall with it. I would argue that there is no necessary connection, despite the fact that punctuated equilibrium may have been important historically for psychological reasons, providing a way to *see* species as individuals and to *see* the sense in which hierarchical independence is possible. The worry and the irony is that in connecting causal independence to punctuated equilibrium in this way, Gould may have "loaded [himself] with an unnecessary difficulty." The irony, of course, is that the words are T.H. Huxley's (quoted in Gould, p. 151), expressing his worry about Darwin's commitment to gradualism.

Processes manifest differently at different levels. Return for a moment to the two trends in Figure 1, concentrating for the moment on the changes occurring within lineages and ignoring the species selection at the clade level. Suppose that in both, selection acts and acts powerfully at the organism level. In Figure 1A, it might do so only in peripatric populations, in some cases producing increases in the morphological variable during speciation events and in others producing decreases. In Figure 1B, it apparently does so across whole species producing anagenetic increases under some ecological circumstances and decreases under others. Now if ecology is complex, so that many different factors affecting the evolution of a given species are in play at any given moment (as predicted by Darwin's complex web of relations), then the net result in both scenarios will be randomness at the clade level. More precisely, the result will be pseudorandomness, in which outcomes – here increases and decreases – are understood as the deterministic result of many causes complexly configured. Coin flips are generally understood to be random in this way.

The point is one that Gould makes forcefully and eloquently in his treatment of hierarchy. It is not the obvious one, that processes acting at one level can have effects at higher ones. It is the less obvious point that lower-level effects can be manifest *differently* at higher levels, that their effects may be the opposite in terms of evolutionary mechanisms. In Figure 1, change controlled by selection on organisms at the lower level propagates to the higher-level as randomness in the direction of change within lineages. Now let's bring species selection back into the picture. It is randomness at the lineage level that provides the chance variation required for higher-level selection, i.e., for species selection. Those species that by *chance* have higher values of the morphological variable tend to produce more daughter species than those with smaller values. The generally under-appreciated point is that organismal selection and species selection are not alternative explanations, in some cases at least. Selection can act powerfully at the organism level, producing adaptation to local ecological circumstances, *and* simultaneously it can act at the species level, producing differential reproduction or differential survival of species based on different properties.

Selection as conservative. In the timeless selection-versus-constraint debate, selection is ordinarily cast as a creative force and constraint as conservative, with the debate centering on the relative strength of each in evolution. Gould and others have long argued that constraint has a flip-side, that it can for a number of reasons be understood as creative as well as conservative. One reason has to do with the role of constraint in exaptation, the transformation of features arising in one context to perform a novel function in a new one. One role for constraint, in this view, is to conserve useless structures, or even moderately disadvantageous ones (if they are developmentally linked to advantageous ones), thereby increasing the number of opportunities, over time, for them to be coopted in novel ways. This creative role for constraint has been well understood (if not accepted, perhaps) for some time. What is less well appreciated is that selection too has a flip-side, in principle, and for the same reasons. To the extent that organisms are well adapted, to the extent that they consist solely of selectively advantageous structures, i.e., with no spandrels, opportunities for exaptive reorganization are reduced. And in this sense, selection's role can be understood as conservative.

A comprehensive view

Some may complain that little in this book is new, and that few of the ideas are uniquely and originally Gould's. But originality takes various forms. There's the originality of the inventor, who takes raw materials and generates something discontinuously different, with properties unimagined. In the histories I've read, Thomas Edison was original in this way. Then there's the originality of the novel application, of taking notions from one context and showing how – with modification – they can be applied in a new one to solve problems otherwise unsolvable. Darwin's originality was partly in doing this with Malthus' ideas. And then there's the originality of the leader, who takes ideas we've always known but to which we did not pay enough attention, and who shows us how to use them to solve old problems in new ways, and to solve new problems that we never knew we had. Gould is original in this way.

So one answer to the charge that Gould's work is derivative is that it is deliberately derivative. His originality lies in showing us how certain conceptual pieces from Darwin, the Modern Synthesis, and their opponents (e.g., hierarchy, stasis, and constraint) can be recombined to produce a new view of life, a view so comprehensive that, even if it has not convinced everyone (or even most?), it nevertheless set the terms of debate in evolutionary biology and paleontology in the latter half of the 20th century (and perhaps for some time into the 21st). Another answer is that to advance this view in a scientific culture that is resistant to change (like all cultures), one of Gould's principal tactics over the past forty years has been repetition, making the same points over and over, albeit in different ways in different contexts. So if in reading his *magnum opus*, we are often struck by the thought that all of this sounds familiar, that we've always known this, and that we've heard it all before, it's because we have. From him.

Acknowledgments

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References

Anderson, C. and McShea, D.W.: 2001, ‘Individual versus Social Complexity, with Particular Reference to Ant Colonies’, *Biological Reviews (of the Cambridge Philosophical Society)* **76**, 211–237.

Eldredge, N.: 1985, *Unfinished Synthesis*, Oxford University Press, New York.

Eldredge, N. and Salthe, S.N.: 1984, ‘Hierarchy and Evolution’, *Oxford Surveys in Evolutionary Biology* **1**, 184–208.

Gould, S.J. and Lloyd, E.A.: 1999, ‘Individuality and Adaptation Across Levels of Selection: How Shall We Name and Generalize the Unit of Darwinism’, *Proceedings of the National Academy of Sciences* **96**, 11904–11909.

Hull, D.L.: 1980, ‘Individuality and Selection’, *Annual Review of Ecology and Systematics* **11**, 311–332.

McShea, D.W.: 2001, ‘The Hierarchical Structure of Organisms: A Scale and Documentation of a Trend in the Maximum’, *Paleobiology* **27**, 405–423.

Salthe, S.N.: 1985, *Evolving Hierarchical Systems*, Columbia University, New York.

Simon, H.A.: 1969, *The Sciences of the Artificial*, The MIT Press, Cambridge.

Valentine, J.W. and May, C.L.: 1996, ‘Hierarchies in Biology and Paleontology’, *Paleobiology* **22**, 23–33.

Vrba, E.S.: 1980, ‘Evolution, Species and Fossils: How Does Life Evolve?’, *South African Journal of Science* **76**, 61–84.

Vrba, E.S. and Eldredge, N.: 1984, ‘Individuals, Hierarchies and Processes: Towards a More Complete Evolutionary Theory’, *Paleobiology* **10**, 217–228.

Wilson, D.S. and Sober, E.: 1989, ‘Reviving the Superorganism’, *Journal of Theoretical Biology* **136**, 337–356.

Wimsatt, W.C.: 1994, ‘The Ontology of Complex Systems: Levels of Organization, Perspectives, and Causal Thickets’, *Canadian Journal of Philosophy* **20**(Supplementary Volume), 207–274.