

Evolution, 56(11), 2002, pp. 2339–2345

LESS WOULD HAVE BEEN MORE¹

STEPHEN C. STEARNS

Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut 06520-8106

E-mail: stephen.stearns@yale.edu

Received August 27, 2002.

Stephen Jay Gould, remarkable paleontologist and revered popularizer of science, died of cancer on May 20, 2002. With his death, he passed into the history that he loved; a history, as he well knew, whose mills grind exceedingly fine. Those mills have started work on his writings, just as he ruminated memorably over books by Lamarck, Cuvier, Goethe, Geoffrey St. Hilaire, Darwin, Weismann, de Vries, Bateson, Fisher, Haldane, Wright, Goldschmidt, Simpson, Schindewolf, Dobzhansky, and many others. *The Structure of Evolutionary Theory*, his intellectual last will and testament, was the first book he had written for a professional audience since 1977. He worked on it intermittently for twenty years and rushed to finish, so it seems, as he saw the end nearing. It summarizes, ties together, and places in historical context his major evolutionary interests: punctuated equilibria, especially stasis; hierarchical selection, especially species selection; internalist, as opposed to externalist, explanations of evolutionary patterns; exaptations and the exaptive pool; spandrels and other avatars of constraint; evo-devo and hoxology. It does so at great, needless, and self-defeating length: at about five pounds, it is heavy enough for a stewardess to have insisted that I store it in an overhead compartment for takeoff and landing lest it endanger the passengers. It will be bought more often than read and used as a bookend more often than as a book. Much of it deserves attention, some of it is exciting, and some of it is beautiful, but the gems are hard to locate amidst the sesquipedalian verbiage.

Had you told me in 1970 that an evolutionary biologist would succeed in influencing the discourse of our field as much as Gould did for the last thirty years with so little use either of data or of equations, I would have laughed—but he did it, he did it well, and he did it primarily with rhetoric and historical analysis, tools deployed more often in the humanities than in the sciences. With those tools he helped to reinvigorate paleontology, launch macroevolution on a new course, and provide a context in which development could be integrated into evolution. Those are not minor accomplishments.

But what was his contribution to evolutionary theory, the focus of this book? Here I argue that he deserves quite a bit more credit than his severest critics would grant (zero) but less than he has here attempted to award himself (a great deal indeed).² To prepare that argument, I first consider an

aspect of his rhetorical stance that has consistently obscured the debate over his contributions and induced resistance—some needless, some appropriate—among a variety of evolutionary biologists.

Steve Gould, Revolutionary

In a revealing aside, Gould states, “if I were to cite any one factor as probably most important among the numerous influences that predisposed my own mind toward joining Niles Eldredge in the formulation of punctuated equilibrium, I would mention my reading, as a first year graduate student in 1963, of one of the twentieth century’s most influential works at the interface of philosophy, sociology, and the history of ideas: Thomas S. Kuhn’s *The Structure of Scientific Revolutions* (1962). (My friend Mike Ross, then studying with the eminent sociologist of science R.K. Merton in the building next to Columbia’s geology department, ran up to me one day in excitement, saying ‘you just have to read this book right away.’ I usually ignore such breathless admonitions, but I respected Mike’s judgement, and I’m surely glad that I followed his advice. In fact, I went right to the bookstore and bought a copy of Kuhn’s slim volume.)” (p. 967)

Gould cites Kuhn in this context specifically for the analogy that Kuhn’s punctuational change of ideas has for punctuational change of morphology in the fossil record, but I read Gould’s enthusiasm for Kuhn more broadly. His encounter with *The Structure of Scientific Revolutions* (a title meaningfully echoed in the title of this book) legitimized and intensified Gould’s predisposition to see himself as a heroic and interesting rebel against an established and boring orthodoxy. Whether or not evolutionary biology needed a revolution, whether or not the stagnation of early-sixties paleontology could be generalized to evolution as a whole, whether or not the field had been driven into a state of internal contradiction by its own results, it was going to get a revolution, and Gould was going to lead it.

Doing so required that the orthodoxy of the Modern Synthesis first be made excruciatingly clear so that the heterodoxy of the rebels could stand out in sharp relief. The dominant population geneticists had to be trimmed down to size to free up enough space at the core of evolutionary theory for the new ideas. Because modern evolutionary theory was moving fast and presented an inconveniently sophisticated target, it made sense to cast the argument in the broad historical context and concentrate on Darwin’s century-old deficiencies, particularly the gradualism and uniformitarianism he had absorbed from Lyell, in the process letting Gould

¹ *The Structure of Evolutionary Theory*. Stephen Jay Gould. 2002. Harvard University Press, Cambridge, Massachusetts. xxii + 1433 pp. HB \$39.95, ISBN 0-674-00613-5.

² For briefer reviews, with both of which I completely agree, see Wake (2002) and Futuyma (2002). Of the many obituaries that had appeared as of this writing, Carol Kaesuk Yoon’s front-page obit in the New York Times (May 21, 2002) remains the best I have seen.

climb onto the stage with the most distinguished evolutionist of them all. It was a bold strategy. And it worked.

But these moves raised hackles, for many who saw themselves as open-minded, flexible, and perhaps even a bit revolutionary did not appreciate being tarred with the brush of orthodoxy and dipped in the paint of a stodgy intellectual conservatism they themselves disdained. Nor did they—nor did the real conservatives—necessarily buy the argument that evolution was in a state of intellectual crisis that could only be resolved with a paradigm-shifting revolution. In attacking the extreme with a vigor that was often inappropriately indiscriminate and exaggerated, Gould alienated the moderates and induced much more resistance than was warranted by the bare bones of the facts to which he pointed and the logic he deployed. Although his attack reached the peak of intensity two decades ago (Gould 1980), and while he has moderated his stance since then and in this book, emphasizing that he seeks to extend, not to overthrow, a Darwinism he respects, much of the revolutionary rhetoric remains, scattered in strata of text twenty years deep, and reminding the reader frequently of a subtext that has been modified extensively but never discarded. Gould cherished and advertised his self-image as a revolutionary opposing stodgy orthodoxy to the end.

Thus Gould's style, as much as his message, provoked opposition. With that on the table, let us consider Gould's major scientific preoccupations: hierarchical selection, punctuated equilibria, and internalist explanations from the point of view of standard realist science. Are they logical, what problems do they solve, and do we need them badly enough to keep them around?

Hierarchy, Hierarchy, Hierarchy

I have no trouble at all with the idea that selection can work simultaneously at several levels of a hierarchy, nor do many other evolutionary biologists. Gould seems to have thought to the end that this was a revolutionary idea, but he did not invent it, and he was preaching to the choir for at least the last decade and in some cases for much longer than that. Price (1970, 1972) published the idea about the same time that Eldredge and Gould came up with punctuated equilibria, admittedly as a somewhat impenetrable equation, but Price did have the good grace to state the principle simply in English: "effect of selection = intensity of selection \times variation on which selection acts" (Price 1972, p. 488) for all levels of a nested hierarchy. Price's covariance mathematics formalized well-known examples with a much longer history, such as meiotic drive and the evolution of virulence in myxomatosis in rabbits in Australia (see references in Lewontin 1970). His formulation of the relative strength of selection at two levels is critical for our understanding of multilevel selection and genomic conflict, one of the more fascinating recent developments in microevolutionary theory (e.g., Haig 1992; Hurst et al. 1996).

The idea of multilevel selection is now a well enough established part of the orthodoxy to appear even in an elementary text:

Organisms consist of a hierarchy of replication levels, at each of which natural selection may occur simultaneously. Organisms occur in groups, and under some

conditions groups are also subject to natural selection, for they may form new groups and disappear at different rates, depending on their composition. Replicating units that occur in few copies and whose replication and segregation are strictly controlled, such as cell nuclei and their chromosomal genes, do not easily cause genomic conflicts. Replicating units that occur in many copies and whose replication and segregation are not strictly controlled, such as cytoplasmic genetic elements, more easily cause genomic conflict. Sexual organisms are more prone to experience genomic conflict than asexual organisms. Genomic conflicts can generate evolutionary change and may have been involved in several key evolutionary events, such as the evolution of the male-female distinction. Genomic conflicts can also account for uniparental inheritance of cytoplasmic genomes, male sterility in plants, and genomic imprinting of growth genes in mammals. Whether they can account for speciation . . . is not yet clear. (Stearns and Hoekstra 2001, p. 212)

Note that we did not mention species selection, which at the time we did not think was very important but is the level of the hierarchy that Gould emphasizes. Nor did Gould cite Haig or Hurst, who had provided him with outstanding examples of multilevel selection operating in systems that can be studied in the laboratory and whose dynamics is readily analyzable with standard microevolutionary tools. That mutual lack of communication is easily understandable because of what each person was trying to explain—genomic conflict for Stearns and Hoekstra, macroevolutionary patterns and trends for Gould. While we were aware of Gould's position on species selection, we did not mention it because we did not think it contributed to the analysis of adaptation and were insensitive to its potential role in shaping macroevolutionary patterns. Although Gould was aware of Price's formulation (p. 663) and Lewontin's review (p. 657), he chose not to push the analogy of abundant examples of multilevel selection at levels below that of the species, perhaps because he simply was not very interested in evolutionary processes within species.

Species Selection

Species selection is a central element of Gould's macroevolutionary theory. He needs punctuation and stasis to give him a clear definition of species in the fossil record, and he needs species to be regarded as individuals rather than collectivities for species selection to work. Wake (2002), who knows a species when he sees one, doubts that many species can be usefully characterized as individuals—their spatial and temporal genetic borders are too fuzzy—and sees greater hope for clade than for species selection. Gould held the opposite view—species selection must be strong and real to have produced the macroevolutionary patterns that we see, whereas clade selection is probably too weak to have had much effect. (Both Wake and Gould could be right with an appropriate adjustment of the unit of selection. What paleontologists perceive as species in the fossil record might have been species swarms with fuzzy edges. One would then talk about selection of species swarms rather than species.)

The proper criteria by which to judge the strength and importance of species selection were laid out by Price (1970). Two concepts and a link between them explain both adaptive and neutral evolution. The two concepts are heritable variation in traits and variation in reproductive success. The link is the correlation between the two. When the correlation between reproductive success and a trait is significantly positive or negative, natural selection is operating; when that correlation is zero, selection disappears, even though variation in reproductive success remains, and what is left is neutral evolution. Thus drift is not only a property of small populations, for it works in large populations whenever the correlation between the effect of a gene on the phenotype and reproductive success is zero. If that were not the case, molecular evolution as we interpret it would not work. For species selection, variation in reproductive success results from variation in speciation and extinction rates. Whereas individual selection often consists of millions or billions of events, species selection consists of many fewer. The sample sizes involved differ by orders of magnitude. That is the point, as Gould acknowledges, that Fisher (1930) emphasized when he pointed out that adaptations result from very large numbers of selective events.

When we look at species selection this way, several points become a bit clearer. First, as Gould points out, species selection does not produce the polish, efficiency, and elegant design that we associate with adaptations: it takes millions, not hundreds or thousands, of selective events to do that. Millions of selective events (births and deaths) are readily present in the family histories of organisms and genes; they are not present in the family histories of species. Second, drift at the species and clade level produces the arbitrariness of history: that is much of what macroevolution generates. Gould acknowledges that, but it is not what interests him. He wants species selection to create macroevolutionary trends and patterns. Well, third, the ability of species selection to create macroevolutionary trends depends on the magnitude and significance of the correlation coefficient between variation in the trait involved in the trend and variation in species reproductive success. For species selection to be effective, that correlation must be large and significant.

That is an empirical issue. When such data are produced, and agreement is reached on their quality and admissibility, and when they show a strong and significant correlation between a species-level trait like geographic range and species reproductive success, then species selection is producing a macroevolutionary trend. I have no problem with that, and I do not want to fault Gould for not citing more data of that nature, for such data are hard to get. We do have Jablonski's (1987) correlation between geographic range and species duration in Cretaceous mollusks and Wagner's (1996) analysis of the roles of individual selection, constraints, and differential extinction in shaping shell morphology in early Paleozoic gastropods. But at the moment, it is fair to say that we do not have evidence that forces us to conclude that species selection has produced very many striking macroevolutionary trends. More such work is needed.

What about other patterns? What about the fact that some clades are speciose and others impoverished? What about the species richness of beetles and snails and the species poverty

of priapulids and phoronids? Is that not evidence of the power of species selection to shape a major feature of "life's elegant tapestry"? Gould claims that it is, but look at what he is saying: clades in which speciation rates exceed extinction rates become more speciose; those in which speciation and extinction are balanced tend to remain impoverished; those in which extinction rates exceed speciation rates disappear. That is true enough, but it is neither surprising nor striking. Thus species selection could contribute to trends, but we do not know if it does; it generates variation in the species richness of clades, but that is elementary.

Things get more interesting when Gould discusses general features of species that predispose them to high or low speciation or extinction rates. Here we have to deal with the possibility that variation in the trait at the species level and in the speciation and extinction rates are byproducts of processes at the individual level (Vrba's effect hypothesis). Gould concludes that species extinction must often be a byproduct of individual fitness, that differential extinction is therefore not a strong motor of species selection, and that differential speciation must account for most of it. Although he acknowledges such connections between micro- and macroevolution, and moved, in this respect as in many others, a long way from his initial positions, Gould remained committed to the end to a separate realm of macroevolutionary causation with a clear break from microevolutionary causation. He did so because he wanted paleontology to be an independent and important source of evolutionary explanation and because he wanted to be seen as a major architect of evolutionary theory, not because he was driven logically to that position by a paradox in the data that could only be solved by that adjustment of the theory.

That may be understandable from a feisty paleontologist seeking legitimacy for his field, but it results in an unproductive and inappropriate strategy for chunking reality and defining big problems. If we want to understand life as a whole, not in separate compartments of paleontology and neontology, macro- and microevolution, then the links between those compartments become as fascinating and as crucial as what goes on within them. I say that not in the belief that a proper study of the links will reduce macro- to microevolution completely, although I think it will do so partially. Nor do I rule out an important macroevolutionary influence, driven by species selection, on some species-level characteristics of great interest to microevolutionists, such as sexual versus asexual reproduction, semelparity versus iteroparity, ecological specialization versus ecological generalization, or selection of a narrow versus a broad range of habitats in which to settle. All those distinctions would plausibly impact the vital rates of species, and it will be interesting to see if they do.

No, the reason I find the interaction of micro- with macroevolution important and do not want it defined out of existence by walling the two off from each other is that in other cases of multilevel selection (meiotic drive, male sterility, uniparental inheritance, intragenomic conflict over parental investment), the interaction between levels has been crucial to our understanding, the quantitative balance of selection forces at the higher and lower level have been decisive for the outcome, and if we had ignored those interactions we

would have understood very little about what was going on. I hope that anyone willing to ignore intellectual turf wars and to use any useful tool, intellectual or material, to get at the truth without regard for disciplinary boundaries, is inclined to agree.

Stasis Is Data

This Eldredge-Gould mantra was coined in the seventies to emphasize the empirical basis of their hypothesis of punctuated equilibria: stasis is data, stasis is data. I agree completely, consider the observation well founded, and think this is one of the most important points that Eldredge and Gould uncovered. Why do many, but by no means all, species not change for very long periods of time, and why do ancestral species persist unchanged after daughter species have formed and diverged, as shown, for example, by Jackson and Cheetham (1999)?

At least two answers can be given: an externalist or selectionist answer and an internalist or structuralist answer. Gould draws this distinction and I agree that it is useful. The externalist answer suggests that young organisms select the habitats in which they live, that they thereby select the selection pressures they will experience as adults, that virtually only adult morphologies are fossilized, that the selection pressures operating on the adults are stabilizing, and that all this is particularly important in the marine invertebrates with larval stages that dominate the fossil record and provide the best evidence for stasis. Thus the externalist answer is, stasis results from stabilizing selection as a byproduct of faithful and precise habitat selection. This may be plausible, but I do not know how to test it in the fossil record.

The internalist answer can take at least two forms. The first says many traits are internally connected. When such connections exist, it is often the case that the fitness gained when one trait changes is compensated by a fitness loss when other, connected traits change. Such connections can cause stabilizing selection on the traits involved. When they are present, and they appear to be omnipresent, stasis arises and persists as a result of stabilizing selection that exists for internal, not external, reasons. The most important part of the environment of a trait is thus its connections to other traits, not the external environment with which the whole organism interacts. When stasis is caused by internal connectedness, it is not particularly surprising that morphology persists unchanged through periods of rapid change in the external environment, for that is not the part of the environment of the traits that matters most. Such is the first internalist explanation, and it is not Gould's, it is mine (see also Schwenk and Wagner 2001).

The second internalist explanation is based on developmental constraints and supported by the abundant recent data on deeply conserved developmental control genes, to which Gould enthusiastically refers as hoxology (although the field studies many genes outside the hox cluster). The idea is that the genetic and developmental control networks that specify the basic features of body plans are incredibly ancient and broadly shared. They can be modified in interesting ways, but in general they appear to have served as constraints on the kinds of organisms that evolution can produce and can

thus explain why phenotypes are clumped in morphospace. Gould was not concrete about how that could explain stasis, and for good reason: we do not yet know.

A few years ago in a memorial issue for one of Gould's longtime opponents, the distinguished Polish paleontologist Toni Hoffman, I suggested a scenario (Stearns 1994) that could form part of the answer: A developmental control system evolves in a distant ancestral species. Whether it gets canalized, or you get "canalization for free" out of its structure (Wagner 1996), is not known and is not critical for the next step. The essential starting point is that basic developmental control is somehow constrained not to change. The traits within the lineage that are still variable then co-evolve relatively rapidly with the relatively slowly changing developmental control system. "This step embeds the [developmental control system] in a network of interactions with other traits in such a way that the continued successful function of the organisms depends upon that [system] remaining canalized" (Stearns 1994, p. 221). Constraints result because the invariant developmental system cannot now be changed without incurring costs too high to be paid in the fitness contributions of the still-variable traits. "If this process is repeated many times, one trait after another will be canalized and then fixed by a web of developmental, physiological, and biomechanical interactions" (Stearns 1994, p. 221). This embedding process is one way to go in principle from the observation of deeply conserved developmental control genes to the observation of shorter-term, more superficial stasis in the external morphology of a single species over a couple of million years (see also Reidl 1978).

Such an embedding process creates as many problems for punctuation as it solves for equilibria. How can you have strong internal constraint causing stasis for a long period of time followed by a quick relaxation of internal constraint during a speciation episode? This scenario is a better explanation of the long-term evolutionary channeling discussed in the next section, than of stasis within species, for which stabilizing selection resulting from a combination of habitat selection and internal trade-offs still seems the most plausible explanation currently available. Gould agreed: "I now believe . . . that the theme of constraint, while not irrelevant to the causes of stasis in punctuated equilibrium, does not play the strong role that I initially advocated. (However—and perverse as this may seem to some detractors—my conviction about the general importance of constraint vs. adaptationism at other more appropriate scales has only intensified, particularly in the context of revolutionary findings in developmental genetics—see Chapter 10)" (p. 880).

Internalism (Structuralism) versus Externalism (Selectionism)

Internalist explanations for evolutionary patterns were a dominant feature of nineteenth-century thought. They reached an early peak in the concept of orthogenesis—rejected by the Modern Synthesis for its lack of mechanism and tinge of vitalism—and a later peak in structuralism. Gould felt that orthogenesis and structuralism both contain an element of truth that was unwisely discarded in the heat of earlier controversies: he sought to retrieve the baby from

the discarded bathwater. There is more to structuralism than extreme selectionists believe and less than its advocates claim. Here is the part that I find plausible.

First, structuralism sheds useful light on the meaning of the word “random” when we say that mutations occur at random and selection weeds out the ones that do not work. The many possible meanings of the word “random” have proven a persistent bugbear in communicating the essence of natural selection. “Random” in this context does not mean “randomly drawn from the space of all possible phenotypes”; it means “random with respect to fitness benefit.” The scope of possible phenotypic effect of all mutations is profoundly restricted by the development and physiology of the organisms in which they occur. Mutations in beetles will yield variations on beetles; mutations in tigers will yield variations on tigers; but mutations in beetles will not yield variations on tigers. That is elementary and important.

Second, much of the restriction in scope of possible phenotypic effect results from the effects of developmental control systems on body plans and the interactions those control systems have with the range of phenotypic effects that can be elicited by mutations. No system currently under study better clarifies that interaction than the butterfly wing patterns studied by Nijhout, Brakefield, Carroll, French, Monteiro, Beldade, and their colleagues. The number of such systems is increasing. Their general message may be this: any deeply conserved developmental pattern can often be tweaked to elicit an impressive array of variation in local phenotype space, but it is much rarer that it can be fundamentally remodeled in ways that can send evolution on a trajectory into distant phenotype space (cf. Wray on echinoderms). There have been no such fundamental remodelings of developmental systems, at least in animals, for hundreds of millions of years: much of the evolution of the animal phyla in the Phanerozoic can be understood as local variations on basic body plans controlled by deeply conserved developmental systems that extend back at least to the Cambrian and Ordovician. That gives internalist structuralism a large role in the generation of macroevolutionary patterns: it has held phenotypes within the basic body plans of the major phyla.

Third, the information stored in genes directs the construction of material organisms. The properties of the materials out of which life is built, and the ways in which those materials are organized to interact with each other, come with important properties. The ability of a broken bone to remodel during repair along lines of stress comes largely with the choice of hydroxyapatite in a protein matrix; it is not specified in the genes, which do not code for appropriate repair of all possible breaks in bones. Genes get a lot for free out of materials. D’Arcy Thompson was right about that.

This is a part of evolution that Gould thought was very important and lacking in the Modern Synthesis, and he was right. His role in getting it more heavily emphasized in evolutionary thought, mostly through his 1977 book *Ontogeny and Phylogeny* but also here through his analysis of D’Arcy Thompson’s *On Growth and Form*, provided an important impetus, but the exciting results came from molecular developmental genetics, not from evolutionary biology and structural morphology. Gould did play an important role in preparing the anglophone community to receive the results,

to know why they were important, and to place them in the context of historically significant questions. However in continental Europe, particularly in Germany, no preparation by Gould was necessary—they were on top of the history and issues from other sources already. Therefore if he had never existed, I suspect the field of evo-devo would have been in approximately the state today that it actually finds itself in, busily connecting deeply conserved developmental control systems with broad phylogenetic patterns and exploring how far such systems can be fine-tuned to produce observed phenotypic variation. But much of the charm of history is its particularity, and the history of evo-devo that we experienced was significantly shaped and supported by Gould: it was a more interesting and colorful history because of him even if we could have gotten here without him.

Trade-Offs and Constraints in the Exaptive Pool

Gould and Vrba (1982) believed that exaptations form a reservoir of variability that can be tapped to produce innovations. Species with a large exaptive pool are more evolvable than species with a small exaptive pool. I like the idea of exaptations and think Gould’s suggestion is reasonable, but I would like to raise a point about the dynamics of exaptations. The point holds for the class of exaptations that are neutral at all levels of selection prior to being commandeered as raw material for innovations. It does not hold for traits that might be considered exaptations at a higher level but are adaptations under active selection at a lower level.

According to microevolution a trait no longer under selection will be eroded by mutations unless it is connected to or a byproduct of other traits or processes that continue to experience selection. One thinks of the eroded visual function of cave salamanders and crickets. One also thinks of the compensatory evolution of antibiotic resistance in bacteria (Schrag and Perrot 1996). If antibiotic resistance is costly when the antibiotic is not present, it will disappear rapidly from the bacterial population when the antibiotic is withdrawn, with clearly positive epidemiological consequences. If, however, compensatory evolution occurs during the period when the bacterial population is under selection from antibiotic treatment, then the cost of resistance can be modified, even to the point where resistance becomes neutral rather than costly when the antibiotic is withdrawn, and it takes a neutral trait much longer, in microevolutionary time, to disappear from a large population than it takes for a costly trait to disappear.

These quintessentially microevolutionary ideas are relevant to the plausibility of a macroevolutionary exaptive pool, for they help to define the conditions under which we can expect a neutral trait to stick around for a long time. If the trait became neutral because it underwent compensatory evolution before a selection pressure disappeared, then it will remain longer in the exaptive pool than it would have if a cost appeared when selection shifted. If it is a byproduct of a process or connected to a trait still under positive selection, then we can expect it to stick around even longer than if it is neutral, but in that case the connections it has to other traits will decrease the degrees of freedom available to use it in new contexts. Otherwise we should expect it to disappear

and be only briefly available in the exaptive pool on a macroevolutionary time scale.

The half-lives, indeed the entire distribution of residence times, of traits in the exaptive pool thus become of interest. Some spandrels will have dynamics; some (such as the gastropod umbilicus) that result from geometry and architecture may not. It will be hard to measure the dynamics, first because it is hard to assess the reliability of a claim that something is an exaptation rather than an adaptation, second because the time spans involved will often be geological rather than ecological. Those facts do not detract from the basic logical point: if you are going to use exaptations as a source of variation in macroevolutionary theory, then you need to understand their dynamics, not just their existence, for the same reasons that one needs to know the average residence time of a mutation in a Mendelian population in microevolutionary theory. Dynamics makes an important difference to our quantitative understanding of rates and potentials.

Gould as Historian of His Own Research Field

It is standard practice to spin the history of a topic in the introduction to a research paper to make clear to the reader that serious deficiencies desperately need precisely the remedy that one is about to provide with the results and analysis hereinafter presented. This is a widely recognized *petit mignon*, normally tolerated with amusement and compensated for by readers almost unconsciously. In this book Gould makes this move on unprecedented scale. For over 500 pages he takes us through a close reading of the development of evolutionary thought from Cuvier, Lamarck, and Geoffrey St. Hilaire to Fisher, Haldane, Wright, Dobzhansky, Mayr, and Simpson. His reading has a subtext: to expose major deficiencies that he would later remedy with punctuated equilibria and species selection. He presents an extended brief for the importance of his own interests.

Of course he is entitled to do it. And in the process he delivers lots of insights—on the influence of Adam Smith on Darwin, on Cuvier's treatment of Lamarck, on Herbert Spencer's logorrhea (sic!), and a nice compare-and-contrast of Geoffrey St. Hilaire versus Cuvier, Goethe versus Paley, Owen versus Darwin, Goldschmidt versus Dobzhansky, and Gould versus Dawkins to demonstrate the depth and persistence of the parallel contrasts represented by those pairs. I greatly enjoyed parts of this historical prelude to the logic of evolutionary theory. But I kept noticing that Gould was selecting topics to build the historical argument for the importance of his own interests, I found that sensation uncomfortable, and I do not trust this account as a balanced—although it is an interesting—intellectual history of nineteenth- and twentieth-century evolutionary thought.

Some Relevant Things Gould Missed

It is difficult to believe that in 1343 pages Gould did not cover all the relevant material, but I found omissions of things that would have supported his major arguments. First, he did not discuss Vavilov's (1922) Law of Homologous Series, clear and early documentation that mutational variation is channeled within a clade, that closely related species have mutations with strikingly parallel phenotypic effect. Vavi-

lov's evidence supports Gould's emphasis on internal factors in evolution and should be better known. It is a classic. Second, he did not discuss Stebbins and Basile (1986), who reviewed cases in which species could be induced to phenocopy morphological features of distantly related extant taxa (teeth induced in chickens, radial symmetry induced in liverworts, leafy shoots induced in flowering plants that do not normally develop them) and invented the term "phyletic phenocopies" to cover this broad and interesting range of phenomena. Phyletic phenocopies are relevant both to evo-devo and to the exaptive pool and are also good evidence for the importance of internal factors in evolution.

But those are relative details. Two major things are missing from the book: an engagement with population genetics serious enough to have internalized what it has to say about speciation, and an overview of much of the recent literature (with the exception of evo-devo, on which he was up-to-date). Gould's argument was predominantly with the past as expressed in the state of the field at the time he was in graduate school in the early sixties. Had he stayed on top of the developing field, he would have had less and less to argue with, in part because of his own influence, which brings us to my next point.

On the Astute Creation and Exploitation of Scientific Controversies

In her incisive analysis of the sociobiology debate, *Defenders of the Truth*, Ullica Segerstråle (2000) points out that both sides used the debate to increase their publication rates, their public exposure, and their reputations as holding politically correct positions, at least for the audience to which they were playing (naturally different for Gould than for Dawkins or Wilson). In her opinion, Gould did this better than any of the other participants. He did precisely the same thing in the debates over evolutionary theory. He says himself that he used the columns in *Natural History* as "a bully pulpit" from which to spread his views, and their impact was amplified many-fold when they were packaged and marketed as a highly successful series of popular books.

As a result of his public positions on sociobiology, on IQ and race (in *The Mismeasure of Man*), and on creation science, he earned great standing as a Man of the Left, a socially engaged scholar who defended liberal positions and reaped liberal reverence, who lent the intellectual respectability of the academy to popular positions. His death prompted reminiscences in *The Nation* and a very balanced editorial, as well as a front-page obituary, in *The New York Times*. It reminds me of the funeral of Victor Hugo, when thousands lined the streets of Paris as much for the social and political positions that Hugo had defended as for the quality of his literary production.

Public awareness and reverence extended, moreover, well beyond the liberal left. I was astounded, when I returned to this country after 17 years in Switzerland, both at the degree to which evolution had been accepted by the intelligentsia (if not by the general public) as something that had really happened, and at the degree to which it was generally seen through Gould's macroevolutionary eyes. This was, on the one hand, a great service to science vis-à-vis creationism and

to the status of evolution in general, and at the same time a great miscommunication of the nature of evolutionary theory to the general public. I now frequently encounter biology undergraduates, nonacademics, and even some nonevolutionary biologists who have read Gould and carry quite alarming misapprehensions about natural selection, adaptation, and microevolutionary mechanisms, but insist that they have understood evolution at the hand of a master and need go no further.

Gould's Greatest Contribution

The complacency and rigidity of evolutionary biology in the 1960s were real. The *consistency* of evolutionary phenomena with population genetics was incorrectly extended to a general belief that population genetics was *sufficient* to account for evolution. This gave population genetics a privileged position as the standard against which evolutionary thought should be measured, and it created an atmosphere in which important evolutionary phenomena not directly tied to genetic mechanisms were often defined away or ignored, to the great frustration of those interested in them. Those important phenomena included innovations, constraints, stasis, and macroevolutionary trends. Gould's greatest contribution was his effectiveness in shattering the complacency of the field and broadening the range of respected discourse. He had to fight hard to do so, and the fact that he was not alone in that fight detracts neither from his independence, nor from his courage, nor from his contribution. He was a real leader in opening our minds to important things that had been missed, and he did our field a great service in reminding the public that there is more to biology than molecular biology and that there are interesting unanswered problems whose solutions will not require DNA sequences.

ACKNOWLEDGMENTS

Many thanks to D. Futuyma, B. Stearns, G. Wagner, and J. Powell, who commented constructively on a draft. All positions expressed are my own.

LITERATURE CITED

- Fisher, R. A. 1930. The genetical theory of natural selection. Oxford Univ. Press, Oxford, U.K.
- Futuyma, D. J. 2002. Stephen Jay Gould à la recherche du temps perdu. *Science* 296:661–663.
- Gould, S. J. 1980. Is a new and general theory of evolution emerging? *Paleobiology* 6:119–130.
- Gould, S. J., and E. Vrba. 1982. Exaptation—a missing term in the science of form. *Paleobiology* 8:4–15.
- Haig, D. 1992. Genomic imprinting and the theory of parent-offspring conflict. *Semin. Dev. Biol.* 3:153–60.
- Hurst, L. D., A. Atlan, and B. O. Bengtsson. 1996. Genetic conflicts. *Q. Rev. Biol.* 71:317–364.
- Jablonski, D. 1987. Heritability at the species level: analysis of geographic ranges of Cretaceous mollusks. *Science* 238:360–363.
- Jackson, J. B. C., and A. H. Cheetham. 1999. Tempo and mode of speciation in the sea. *Trends Ecol. Evol.* 14:72–77.
- Lewontin, R. C. 1970. The units of selection. *Annu. Rev. Ecol. Syst.* 1:1–18.
- Price, G. R. 1970. Selection and covariance. *Nature* 227:520–521.
- Price, G. R. 1972. Extension of covariance selection mathematics. *Ann. Hum. Genet.* 35:485–490.
- Riedl, R. 1978. Order in living organisms: a systems analysis of evolution. John Wiley and Sons, New York.
- Schrag, S., and V. Perrot. 1996. Reducing antibiotic resistance. *Nature* 381:120–121.
- Schwenk, K., and G. P. Wagner. 2002. Function and the evolution of phenotypic stability: Connecting pattern to process. *Am. Zool.* 41:552–563.
- Segerstrale, U. 2000. Defenders of the truth: The sociobiology debate. Oxford Univ. Press, Oxford, U.K.
- Stearns, S. C. 1994. The evolutionary links between fixed and variable traits. *Acta Paleontol. Pol.* 38:215–232.
- Stearns, S. C., and R. F. Hoekstra. 2001. Evolution: an introduction. Oxford Univ. Press, Oxford, U.K.
- Stebbins, G. L. and D. V. Basile. 1986. Phyletic phenocopies: A useful technique for probing the genetic and developmental basis of evolutionary change. *Evolution* 40:422–425.
- Vavilov, N. I. 1922. The law of homologous series in variation. *J. Genet.* 12:47–89.
- Wagner, A. 1996. Does evolutionary plasticity evolve? *Evolution* 50:1008–1023.
- Wagner, P. J. 1996. Contrasting the underlying patterns of active trends in morphologic evolution. *Evolution* 50:990–1007.
- Wake, D. B. 2002. A few words about evolution: building a hierarchical framework on the foundations of Darwinism. *Nature* 416:787–788.

Book Review Editor: D. Futuyma