

## 2

# Modern Darwinism and the Pseudo-Revolutions of Stephen Jay Gould

This critique of Gould was originally designed as the final segment of the introduction to my edition of Darwin's *On the Origin of Species* (2003). The critique was written shortly before the publication of Gould's last big book, *The Structure of Evolutionary Theory* (2002). In that book, he recapitulates the ideas and stratagems he had developed over the past three decades: anti-adaptationism, "pluralism," "punctuated equilibrium," and "spandrels." All these topics have already been adequately considered in this critique of his previous work. No good critical purpose would be served by appending a critique of his last book.

I discuss Gould's introduction to Kurtén's *Dance of the Tiger* in this vol., part 2, chapter 5.

Stephen Jay Gould is the most widely read contemporary popular commentator on evolution, and he is also the chief critic of contemporary Darwinism. He has done field work on land snails in the West Indies, has written a long series of popular essays and scholarly studies on natural history and the history of biology, and until his death in 2002 occupied something like the unofficial chair of evolutionary biology in the pages of the *New York Review of Books*. His chief claim to scientific eminence is to have proposed putative corrections and alternatives to mainstream Darwinism, especially to the idea that adaptation through natural selection is the main engine of evolutionary change. In reality, Gould has offered no truly original and genuinely significant contributions to evolutionary theory. Instead, he has created a vast rhetorical tissue of sophisticated equivocations.

If Gould has formulated no significant revisions of Darwinian theory, why is it necessary to take account of his views? Maynard Smith poses this question and provides an answer:

Gould occupies a rather curious position, particularly on his side of the Atlantic. Because of the excellence of his essays, he has come to be seen by non-biologists as the preeminent evolutionary theorist. In contrast, the evolutionary biologists with whom I have discussed his work tend to see him as a man whose ideas are so

## 228 • Literary Darwinism

confused as to be hardly worth bothering with, but as one who should not be publicly criticized because he is at least on our side against the creationists. All this would not matter, were it not that he is giving non-biologists a largely false picture of the state of evolutionary theory. (1995, p. 46)

By describing the failure of Gould's efforts to undermine the modern Darwinian synthesis, we can confirm the continuing strength of that synthesis. While examining the issues Gould has brought forward, we shall also be taking account of the current state of knowledge in evolutionary biology. We shall identify which ideas are firmly established and which still generate fruitful controversy. Gould makes frequent appeal to Darwin as an authority and example, and by assessing these appeals we shall be able to situate Darwin's own work in relation to current knowledge in evolutionary biology.

As an evolutionary theorist, Gould provides an illuminating contrast with Darwin in two ways. The sophisticated procedures through which he constructs his critique of Darwinism contrast sharply with the integrity of argument that is so signal a feature of Darwin's own work, and the pseudo-revolutions generated by these sophisticated procedures contrast sharply with the real revolution in thought and knowledge that was produced by Darwin.

Gould's claims for revolutionary revision depend on combining a few basic techniques of sophisticated argument. In its simplest version, Gould's technique involves two steps. The first is to create a straw man by giving a falsely simplified description of the received view. The second is to propose what is actually the received view and to present this standard view as if it were a revolutionary correction. In his falsely simplified representation, the Modern Synthesis and its current acolytes consist of "ultra-Darwinians" and "panadaptationists" who are oblivious to all adaptively neutral phenomena and who fervently believe that all of evolution consists in the production of maximally efficient adaptations unconstrained by inheritance or contingent historical circumstance. In order to rescue evolutionary theory from these strangely narrow and obsessive "Darwinian fundamentalists," Gould propounds an array of concepts to which, he intimates, they are strangers. These broader concepts include the observations that adaptations are not ideally perfect but only relatively, competitively perfect, that inherited structures constrain adaptive change, that previously existing structures can be modified for some new adaptive purpose, that some structures are not themselves adaptive but are nonetheless sustained by natural selection because they happen to be connected, in inheritance, with structures that are adaptive, and that evolutionary change proceeds at a varying pace, depending both on the appearance of favorable variations and on alterations in the total set of ecological conditions. In reality, all of these concepts are standard features in the complex of ideas that constitutes the Modern Synthesis.

Gould's largest rhetorical strategy is to acknowledge adaptation through natural selection but to place all his emphasis against it. He seeks to create a

pervasive rhetorical blur in which adaptation seems to be set in contrast or opposition to other elements of the total evolutionary process, and he often appeals to Darwin as a supposed precedent for this maneuver. Consider, for example, the following thumbnail sketch of modern Darwinian theory, from an essay first published in 1981:

Darwin acknowledged the provisional nature of natural selection while affirming the fact of evolution. The fruitful theoretical debate that Darwin initiated has never ceased. From the 1940s through the 1960s, Darwin's own theory of natural selection did achieve a temporary hegemony that it never enjoyed in his lifetime. But renewed debate characterizes our decade, and, while no biologist questions the importance of natural selection, many now doubt its ubiquity. In particular, many evolutionists argue that substantial amounts of genetic change may not be subject to natural selection and may spread through populations at random. Others are challenging Darwin's linking of natural selection with gradual, imperceptible change through all intermediary degrees; they are arguing that most evolutionary events may occur far more rapidly than Darwin envisioned. . . .

Yet amidst all this turmoil no biologist has been led to doubt the fact that evolution occurred; we are debating *how* it happened. (1984, pp. 255–256)

In such passages, Gould is trying to turn back the clock on the history of evolutionary theory, and at the same time he is attempting to depict this retrograde movement as the resumption of a basically sound tradition that includes Darwin and that was only temporarily interrupted by the Modern Synthesis. In this Gouldian version of the history of Darwinism, Darwin himself treated the theory of natural selection as only “provisional”—a word presumably signifying “hypothetical,” “tentative,” or “temporary.” His contemporaries and successors followed his lead in adopting this skeptical or diffident attitude toward natural selection, and except for the one deviant generation that produced the Modern Synthesis, all subsequent evolutionists have accepted “the fact of evolution” but have bracketed or suspended natural selection as the cause or “*how*” of evolution. This sound Darwinian tradition has consistently acknowledged a *mélange* of causal mechanisms. Some radical anti-adaptationists, among them presumably Gould himself, are even arguing that natural selection does not work through “gradual, imperceptible change through all intermediary degrees,” and if it does not work in this way, it can work only through sudden macromutational leaps or the appearance of what are known as “hopeful monsters.” (The idea of sudden macromutational leaps or “saltation” was prominent in the early decades of the twentieth century, but the proponents of the Modern Synthesis believed that it had been decisively falsified by the development of modern genetics.) Within the larger *mélange* of causal mechanisms recognized by the new, Gouldian generation, natural selection still has some indefinite “importance,” but clearly, since we are now debating

## 230 • Literary Darwinism

“*how*” evolution occurred, natural selection is no longer regarded as the central mechanism. It is once again “provisional,” and that is all to the good.

As history, this Gouldian narrative is of course quite false, and as theory it is misleading in a number of ways. It is—to adapt Gould’s disparaging term for all adaptive explanations—a “just-so story.” As any reader of the *Origin* can readily attest, Darwin himself saw nothing “provisional” or marginal about natural selection. And as anyone reading current biological theory can attest, the Modern Synthesis is in fact the dominant, mainstream view among evolutionists. Since the time of the Modern Synthesis, almost all eminent evolutionists have accepted natural selection as the central mechanism of evolutionary change. The proponents of the modern theory have assimilated the findings of Kimura and others on the evolution of adaptively neutral nucleotides—nucleotides that are by definition outside the purview of natural selection—and none of them regards this theory as a challenge to the Darwinian theory that attributes all complex functional structure to the action of natural selection. Similarly, while most evolutionists have displayed some interest in the debate over the pace of evolutionary change, almost none of them believes that this debate challenges the centrality of natural selection. And finally, no reputable current evolutionary theorist, not even Gould, overtly and unequivocally proclaims a belief in macromutational leaps as a mechanism of evolutionary change.

The term that Gould uses to link himself with Darwin and set himself and Darwin together in ostensible opposition to the Modern Synthesis is “pluralism.” By this word, Gould means a view of evolution that takes account of an array of causal mechanisms different from natural selection. Darwin himself consistently declared that adaptation through natural selection is the main but not the only mechanism of evolutionary change. In addition to natural selection, he acknowledged two other mechanisms: the inherited effects of direct environmental influence, and the inherited effects of habit or the use and disuse of organs (2003, chap. 5, pp. 178–185.) Use and disuse and the direct effect of the environment are concessions to ignorance—to what was not yet known about the mechanisms of inheritance. They are forms of what is commonly regarded as “Lamarckian” inheritance or the inheritance of acquired characteristics. Neither of these supplementary mechanisms is central to the argument of the *Origin*. In later editions, the supplementary mechanisms were given greater play as Darwin hedged against the criticisms of Fleeming Jenkin on the effects of blending inheritance and of Lord Kelvin on the extent of geological time, but natural selection remained unequivocally the core of Darwin’s argument. Later discoveries have proved that the supplementary mechanisms do not work. They can and must be eliminated from the set of recognized causal mechanisms. Fortunately for the standing of Darwin’s book as a scientific classic, dispensing with the supplementary mechanisms does no serious damage to the structure of his argument, and very little even to

the details of his exposition. The overwhelming majority of his examples and causal analyses directly concern natural selection, not the supplementary mechanisms.

There are three sophisticated twists in Gould's appeal to Darwin's "pluralism." (a) He takes Darwin's pluralism as a precedent for his own, blurring over the fact that the supplementary mechanisms Darwin acknowledged have been scientifically disconfirmed and were never, in any case, central to Darwin's argument. (b) He identifies as the constituents of his own "pluralism" ideas that are already part of the Modern Synthesis and that are either compatible with adaptation through natural selection or actually integral with it. And (c) he poses this putative "pluralism" as if it is an *alternative* to the "adaptationism" of the Modern Synthesis. The ideas that are already part of the Modern Synthesis and that are compatible with natural selection include correlated growth, adaptively neutral changes, and variable pace in evolutionary change. (Correlated growth is the idea that certain features not in themselves adaptive are linked genetically to features that are adaptive and that are thus targeted by selection. The non-adaptive features hitchhike on the adaptive features to which they are joined. Darwin cites as an example the shape of pelvises and kidneys in birds [2003, chapter 5, p. 186]. In modern genetics, correlated growth is associated with the term "pleiotropy," meaning genes that have multiple, diverse effects.) The chief idea that is actually integral with natural selection is that of inherited constraints on adaptive structure.

Gould's article "Darwinian Fundamentalism" (1997) offers a representative instance of his technique with respect to "pluralism." First, he cites a passage from the sixth and last edition of the *Origin* in which Darwin denies the charge that "I attribute the modification of species exclusively to natural selection" (p. 34). On the basis of this defensive disavowal, Gould declares that "Darwin himself strongly opposed the ultras of his own day" (p. 34). In contrast to the restrictive influence of supposed "ultra-Darwinians" such as Maynard Smith, Dawkins, and Dennett, Gould celebrates "the invigoration of modern evolutionary biology with exciting *nonselectionist and nonadaptationist* data from the three central disciplines of population genetics, developmental biology, and paleontology" (p. 34; my italics). Gould celebrates population genetics because it provides evidence of changes in adaptively neutral nucleotides; paleontology because it provides evidence for variations in the pace of evolutionary change; and developmental biology because it provides evidence for the idea of "developmental constraints," an idea Gould sets forth as clearly distinct from that of "natural selection" (pp. 35, 36). This supposedly non-adaptationist matrix of disciplines renders the 1990s "an especially unpropitious time for Darwinian fundamentalism—and seems only to reconfirm Darwin's own eminently sensible pluralism" (p. 34). In this specific article, Gould does not include pleiotropy or "correlated growth" within his canon of "nonselectionist or nonadaptationist" ideas. For the inclusion of this idea, we

## 232 • Literary Darwinism

can cite “A Hearing for Vavilov” (1984) and “The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme” (Gould and Lewontin, 1979). In the former essay, Gould presents correlated growth as an instance of “the limits placed upon selection by structure and development” (p. 144), and in the latter essay, he presents the “production of nonadaptive structures by developmental correlation” as part of his catalogue of phenomena that supposedly stand outside the scope of “the adaptationist programme” (p. 581).

Gould’s implied contrast between the various ideas he describes and the adaptationism and selectionism of the Modern Synthesis is transparently but breathtakingly bogus. In the case of variations in the pace of evolutionary change, the evolution of adaptively neutral nucleotides, and correlated growth, the contrast is bogus because none of these processes has any bearing on the evolution of complex functional structure, and that is the one central feature of evolution that adaptation by means of natural selection is designed to explain. Only natural selection produces complex functional structure, and in this sense it is the only answer to “*how*” evolution occurred. In the case of inherited constraints on functional structure, the supposed contrast is bogus because inherited constraint is an integral and indispensable *component* of natural selection.

Darwin’s supposed “pluralism” consists of one major and two minor mechanisms for the creation of adaptive structure. In addition to these mechanisms, Darwin acknowledges the whole array of phenomena that Gould identifies as the key components of his own pluralism, and these components are also standard parts of modern evolutionary theory as it was constituted by the Modern Synthesis. In speaking of “Organs of little apparent importance,” in chapter 6, “Difficulties on Theory,” Darwin gives full consideration to the existence of nonfunctional structures:

I fully admit that many structures are of no direct use to their possessors. . . . Correlation of growth has no doubt played a most important part, and a useful modification of one part will often have entailed on other parts diversified changes of no direct use. So again characters which formerly were useful, or which formerly had arisen from correlation of growth, or from other unknown causes, may reappear from the law of reversion, though now of no direct use. . . . But by far the most important consideration is that the chief part of the organisation of every being is simply due to inheritance; and consequently, though each being assuredly is well fitted for its place in nature, many structures now have no direct relation to the habits of life of each species. . . . We cannot believe that the same bones in the arm of the monkey, in the fore-leg of the horse, in the wing of the bat, and in the flipper of the seal, are of special use to these animals. (2003, chap. 6, pp. 219–220)

Darwin’s argument for adaptation through natural selection explains both complex functional structure and also the limitations on maximal efficiency

that flow necessarily from the constraints of inheritance. The constraint of inheritance is an overt and pervasive theme in the *Origin*, and indeed it is formulated as an explicit and emphatic thesis in both of Darwin's early sketches of his theory in 1842 and 1844 (Darwin and Wallace, 1958, pp. 78, 170). This theme is equally overt and pervasive in the work of virtually all prominent contemporary Darwinians. It is for example one of Richard Dawkins' constant themes, and Dawkins is one of the most prominent of the evolutionists whom Gould identifies as "ultra-Darwinians." Following in the line of Darwin's own logic, Dawkins observes that "evolution never starts from a clean drawing board. It has to start from what is already there" (1987, p. 92). One result is that many designs are not optimally efficient. As an instance of imperfect design, Dawkins' describes the wiring of the optic nerve in the vertebrate eye. One of the consequences of building step by step is that all previous steps constrain succeeding developments. In the case of the eye, Dawkins observes, one previous step, so far back in evolutionary time as to be lost to explanation, has resulted in a tiny but ubiquitous imperfection of design. "Each photocell is, in effect, wired in backwards," and this arrangement, of no apparent adaptive utility, produces an untidy and inefficient tangle of nerves (p. 93). The idea of inherited constraint, with all its attendant imperfections, is central to Darwin's own logic; it is one of his chief forms of proof for natural selection, and it is a constant feature in the entire subsequent history of Darwinian adaptationist thinking.

Dawkins' choice of the eye to illustrate imperfection in design is particularly felicitous in that, among adaptationists, the eye is the most prominently and frequently cited instance of an organ that displays complex functional structure. Paley takes the eye as a central exhibit in his argument for the existence of a divine designer, and Darwin, G. G. Simpson, and Dawkins all take it as a challenge to the proposition that any complex organ can be built up by infinitesimally small steps, beginning, in this case, with nothing more than a light-sensitive nerve. In "The Psychological Foundations of Culture" (1992)—an essay that has already achieved something like canonical status in modern evolutionary psychology—Tooby and Cosmides make the mechanics of vision a central illustration for the idea that complex functional structure is the key indicator of adaptation through natural selection. In *How the Mind Works* (1997b), an exposition that integrates evolutionary psychology with cognitive neuroscience, Steven Pinker analyzes the mechanics of sight at a length and with a precision of detail that would weary an ophthalmologist.

Dawkins' treatment of the eye follows the pattern set by Darwin. Complex functional structure can be produced only by adaptation through natural selection, but adaptations are only relatively "perfect." And indeed, by reconstructing the evolutionary history in the development of the eye, any evolutionist tacitly acknowledges that at earlier evolutionary periods the eyes of various ancestral organisms were less efficient, less complex and less capable of various

## 234 • Literary Darwinism

kinds of visual resolution, than the organs of their descendants. Simpson brings this implication clearly into the open. He identifies various, currently existing levels of complexity and functional efficiency in the eyes of various organisms, and he situates these organs of sight on a scale, from simple to complex, that helps to us to understand the evolution of vision as a series of increments in structural complexity (1967, pp. 168–176). If the eyes of ancestral organisms were less efficient than those of at least some of their descendants, there could be no reason to assume that the eye of any organism is now truly “perfect” and could not, at some future point, become still more complex and efficient. No Darwinian would make so absurd an assumption. Nor would any Darwinian deny that it is equally possible that in cases in which eyes have ceased to be adaptive and have hence ceased to be targeted by natural selection—as in the case of animals living deep in caves—the eyes can degenerate over evolutionary time and become less efficient than those of ancestral organisms. “Panadaptationism” or “ultra-Darwinism” are thus chimeras of Gould’s own imagining. Or, more precisely, they are figments of his rhetorical procedures. The purpose of the procedure is to attach a stigma to all adaptationist explanation, and the means to accomplish this purpose is to attribute to evolutionists a proclivity for gross fallacies that in reality and in the simple logic of the case—the logic of adaptationist reasoning—they virtually never display.

The two ideas for which Gould has generated the most publicity are “punctuated equilibrium” and “spandrels.” The elements in these two ideas that are substantive and valid were integral parts of Darwinism before Gould formulated them, associated them spuriously with anti-adaptationist intimations, and popularized them with catchy phrases. Gould’s own distinctive contribution to these two concepts, insofar as they have consisted of ideas that were substantive and that were not already part of the Darwinian synthesis, have proven to be either compatible with mainstream adaptationist thinking, relatively unimportant, or simply wrong.

Punctuated equilibrium has taken diverse forms over the years, but the different versions can be located on a scale between the strong and weak forms of the theory. The form that is specific and peculiar to Gould is the strong form; this form involves “saltation” or “big jumps” in the evolutionary process—speciation through macromutations. The idea of saltation appears in Gould’s thumbnail sketch of modern Darwinian theory cited above, but it appears there only as an idea that Gould attributes to some unidentified speculators: “Others are challenging Darwin’s linking of natural selection with gradual, imperceptible change through all intermediary degrees; they are arguing that most evolutionary events may occur far more rapidly than Darwin envisioned” (1984, p. 255). Despite the link between saltation and certain unidentified paleontologists who are questioning the pace of evolution, Gould does not quite overtly declare himself as one of this speculative band who are challenging Darwin’s core theory. The idea of saltation as an idea that Gould him-



self embraces and does not merely attribute to unidentified others who look like him makes a more distinct appearance in an essay of 1980, "Is a New and General Theory of Evolution Emerging?" In this essay, Gould correctly characterizes the standard view of speciation as "a cumulative and sequential process powered by selection through large numbers of generations" (p. 122), and he clearly positions himself apart from this standard view. "I have no doubt that many species originate in this way; but it now appears that many, perhaps most, do not" (p. 122). He invokes new models of evolutionary change that involve "nonadaptive" processes, and he maintains that speciation represents a "discontinuity in our hierarchy of explanations" (pp. 122, 123). In these remarkable statements, Gould radically and openly subverts the core elements of Darwin's theory of descent with modification by means of natural selection. He explicitly affirms the proposition that species originate not through small, incremental changes that are adaptive in character but through processes that are nonadaptive and discontinuous.

The claims made in this essay of 1980 constituted a truly bold and startling move—too bold and too startling. Segregating himself so decisively from the central Darwinian tradition did not serve Gould's purposes. He wished only to be considered as at best an original theorist and at worst a gadfly, in no case as a mere crank on the fringe of legitimate evolutionary theory. He quickly backed off from saltation (the production of a new species within a single generation), and since this early, indiscreet foray into overt anti-Darwinism Gould's program has claimed (equivocally, but primarily) only to be "expanding" mainstream Darwinism, not replacing it. This program of expansion has had one main substantive element—an inflated claim for the significance of selection operating at the level of whole species rather than at the level of individual organisms. Gould has continued to suggest or hint at macromutation, but only by the rhetorical devices of blending it into selection at the level of species and by speaking of geologically "instantaneous" moments (that is, thousands of generations) as if these ideas somehow radically challenged Darwinian notions of "gradualism" (that is, the incremental change of species through micromutations introduced in a long series of generations).

Saltation is now almost universally regarded as biologically impossible. Species selection—natural selection operating at the level of species rather than that of individual organisms within species—is possible, but it is probably not a major factor in evolutionary change, and it is in any case not incompatible with the Darwinian theory of adaptation through natural selection. Mark Ridley (1983, pp. 136–140), Maynard Smith (1989, pp. 129, 140–141, 154), and E. O. Wilson (1992, pp. 89–92)—all eminent mainstream Darwinians—make it clear that (a) selection at the level of species is not nonadaptationist, and (b) there are no significant forms of species selection that do not work through the selection of individual organisms. Hence it does not, as Gould suggests, decouple microevolution from macroevolution.

## 236 • Literary Darwinism

In its weak form, punctuated equilibrium means only that the pace of evolution varies, that some species can remain in stasis for long periods, probably by means of stabilizing selection, while others evolve rapidly (perhaps under the stress of changing environmental conditions). This idea appears prominently in Darwin's own work (2003, chap. 10, pp. 289–292) and in that of G. G. Simpson, the most distinguished representative of the Modern Synthesis in the paleontological area (1967, pp. 20–22, 98). As Dawkins (1987, pp. 241–248) and several other writers have explained—trying to clear up some of the confusion generated by Gould—the idea of varying pace in evolutionary change is in no way opposed to Darwinian gradualism. Gradualism means change through a long sequence of micromutations. It is thus set in opposition to the idea of saltational change or the change from one species to another through macromutations. The *pace* of these changes is not at issue.

One distinctive aspect of the strong form of punctuated equilibrium is the idea that change can occur *only* during speciation events. This claim has been proven to be empirically incorrect. (See Mark Ridley, 1983, pp. 121–133.) In its weak form, punctuated equilibrium incorporates an idea that was put forward by Darwin (2003, chap. 4, pp. 157–161; chap. 6, p. 204) and given prominence by Ernst Mayr—the idea that speciation events can be facilitated by the isolation of small populations. The question of whether speciation can take place *only* through the isolation of small populations remains a live issue subject to empirical study. The best evidence seems to suggest that this is not in fact the case. (See Ridley, 1983, chap. 8.) E. O. Wilson summarizes the long debate over punctuated equilibrium and makes it clear that once the false claims and confusions have been cleared away, little of substance remains:

[The argument for punctuated equilibrium] claims that not only does evolution periodically bound forward but it tends to flow to a virtual halt at other times. Species emerge quickly and fully formed after a rapid burst of evolution, then persist almost unchanged for millions of years. And, conversely, rapid evolution is driven mostly or entirely during species formation. The alternation between leaps and pauses creates a jerky pattern, a punctuated equilibrium, so extreme as to point to novel processes of evolution beyond the natural selection of genes and chromosomes. Macroevolution, the reasoning in its most radical form concludes, is in some fashion unique, not the same as microevolution. (1992, pp. 88–89)

Wilson explains that the theory “was at first promoted as a challenge to the neo-Darwinian theory of evolution” and that it was presented as “in effect, a new theory of evolution,” but that claim, he observes “has been abandoned by most of its proponents. The fossil evidence for the widespread occurrence of jerky patterns proved weak, and most examples put forth at the outset were discredited” (p. 89). He notes that standard Darwinian theory already took account of the varying pace of evolution, so that those parts of the theory that were correct

were not new, whereas those parts that were new were not correct. Macroevolution has not been decoupled, as Gould wished, from microevolution.

Gould's one other big idea is that of "spandrels" or nonadaptive structures. "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme" is probably Gould's best-known essay—so well known that an entire book of essays in rhetorical analysis has been devoted to it (Selzer, 1993). In this essay, Gould, in company with Richard Lewontin, explains that spandrels are "the tapering triangular spaces formed by the intersection of two rounded arches at right angles" (1979, p. 581). Such spaces are "necessary architectural by-products of mounting a dome on rounded arches." The arches provide structural support for the dome, and the "tapering triangular spaces" (the spandrels) that are produced by this support structure are walled in. The resulting surfaces are often decorated, and in Saint Marks Church in Venice, they are covered with gold mosaic. The point of the metaphor is that not every feature of a complex structure is adaptive. Some features, like the areas of wall between the arches, are side effects or byproducts of some structural feature—in this case, the feature of intersecting arches. The spandrel walls are not created, Gould and Lewontin argue, to provide a surface for the application of gold mosaic. The areas of wall just happen to be there, but since they are there, some use is found for them.

In making spandrels into a biological metaphor, Gould blends two legitimate Darwinian concepts, but he spuriously represents this blended concept as an alternative or supplement to the idea of adaptation through natural selection. One of these legitimate Darwinian concepts is pleiotropy or multiple genic effects: what Darwin calls correlated growth. The other legitimate Darwinian concept is the idea that previously existing structures can be altered through natural selection to fulfill adaptive functions. Darwin offers as an example the swim bladder that in the course of evolution is transformed into a lung (2003, chap. 6, p. 214). The tetrapod body plan also caught Darwin's attention (pp. 219–220) and has remained a favorite example among evolutionists. The forelimbs evolve from fins to legs, and from legs sometimes to wings and sometimes to flippers. Another favorite example, discovered after Darwin's time, is that of the reptilian jaw bones that have been transformed into the mammalian ossicles—the bones of the inner ear. (See Young, 1992, pp. 185–186; Moore, 1993, pp. 176–177, 412–414.) For adaptations that use either previous adaptive structures or previous structures of no adaptive value, Gould and Vrba (1982) have invented the term "exaptation." This term is a variant of a term that was previously current—"preadaptation"—and the concept is itself a commonplace in standard Darwinian theory.

If we examine the metaphor of architectural spandrels more closely, we shall see—contrary to the implications in the argument presented by Gould and Lewontin—that "spandrels" are in fact an integral part of an adaptive design. If the spandrels were not walled in—if the architect chose to leave triangular holes in the walls below the dome—the architectural effect would be

## 238 • Literary Darwinism

absurd, both eccentric in appearance and unpleasantly drafty. In the degree to which the architect operates within the range of architectural good sense and thus does not choose to create a perforated building, spandrel walls are a necessary part of the larger structure—a dome supported on arches. If a dome supported on arches is the adaptive target structure, in the degree to which the spandrels are a necessary part of that structure they are themselves an integral part of the adaptation. Spandrels are in this respect like the whiteness of bone. The bone could be any color, so far as color is concerned. But it could not be composed of any mineral. For the sake of hardness, a bone needs to be composed of calcium, and calcium, as it happens, is white. In that nontrivial sense, then, whiteness is an indispensable component of the whole adaptive design of bones. No whiteness, no calcium; no calcium, no hardness. Hardness is the target feature, but calcium, which happens to be white, is the means through which this feature is realized.

It would be unwise to make too much of the architectural metaphor. All metaphors contain adventitious and misleading associations, and they can be treacherous guides in the construction of scientific hypotheses. But for what it is worth, we can draw out an implication of the spandrels metaphor that is almost the opposite of that which Gould intends. Spandrels can be taken to illustrate the opportunistic process through which natural selection uses whatever structures are available to gain some advantage for an organism. Unless we choose to produce perforated buildings, spandrel walls inevitably accompany arches, and since they are there, they might as well be used, even if only for ornamentation. But is ornamentation adventitious or irrelevant to the functions of architecture? Both Dissanayake (1995b, p. 230) and Dennett (1995, pp. 273–274) go so far as to claim that ornamentation is itself the central target feature for selection. What purpose does a dome itself have other than to produce an aesthetic effect? In any case, ornamentation is integral with the total set of aesthetic and cultural functions a Byzantine-style church is designed to fulfill. The spandrel walls are there, as a byproduct of a structural feature, and they are then adapted to fulfill at least one of the functions appropriate to the church. They are, metaphorically, adaptive.

Despite the confusions and ambiguities introduced through the architectural metaphor, none of the implications in the idea of spandrels is in any way contrary to standard adaptationist thinking. What Gould and Lewontin have attempted to do, though, is to use the metaphor to suggest, without quite saying it, that major features of complex functional structures have been produced independently of adaptive processes. Put this baldly, the claim is simply and obviously false, but unless it is put this way, the claim has no actual content that is not already part and parcel of standard Darwinian thinking. Since the time of his youthful foray into saltation, Gould himself has usually been careful, whenever he implies or suggests this false idea, also to say that he recognizes that complex functional designs result from adaptation, or that adap-

tation through natural selection is an “important” feature of the evolutionary process. The false and obfusatory implications in the more radical understanding of “spandrels” are nonetheless its *raison d’être*, its chief purpose and function. It subserves the larger Gouldian program of minimizing in whatever way he can the general significance of adaptation through natural selection.

In order to achieve their aim of minimizing the significance of adaptation through natural selection without clearly and decisively cutting themselves off from mainstream Darwinism, Gould and Lewontin are driven to the necessity of perpetual equivocation, and the equivocation is rendered all the more impenetrable by being commingled with a pseudo-concept produced by breaking a single, valid concept into two parts and representing these parts as antithetical. The single, valid concept is that of “selection,” and the two parts are “selective force” and “constraints.” We shall begin with the equivocation and then consider the pseudo-concept. Spuriously invoking Darwin as an antecedent for their own anti-adaptationism, Gould and Lewontin repudiate the idea that Darwin was himself “a radical selectionist at heart who invoked other mechanisms only in retreat, and only as a result of his age’s own lamented ignorance about the mechanisms of heredity” (1979, p. 589). “This view,” they declare, “is false.” But then they also declare, in the very next sentence, that “Darwin regarded selection as the most important of evolutionary mechanisms. As do we.” *As do we*. Strange, then, that the whole thrust of their essay should be toward the conclusion that “constraints restrict possible paths and modes of change so strongly that the constraints themselves become much the most interesting aspect of evolution” (p. 594). Or as they explain in the head note to the essay, “the constraints themselves become more interesting in delimiting pathways of change than the selective force that may mediate change when it occurs” (p. 581). Selection is the most important mechanism, but despite its importance, it is still not very interesting, somehow, not nearly so interesting as other things that are not so important.

The idea of a selective force operating independently of constraints—the idea of selection operating in a vacuum, independently of all actually existing conditions—is something like the idea of one hand clapping. When the idea of selection is placed in antithesis to the idea of constraints, it ceases altogether to be an intelligible idea. It becomes a pseudo-concept, a rhetorical term that is devoid of any conceptual content other than the confusion caused by the faulty way in which it is formulated. One might suppose that this feature of the concept—its lack of any content other than the confusion generated by the way it is formulated—would help to explain why it is so uninteresting, but it could hardly also explain why it is still “important.” Gould and Lewontin have here drifted into a very strange region of “thought,” a region much more familiar within the confines of postmodern literary theory than within those of evolutionary biology. Like Derrida or Foucault, Gould and Lewontin bring to bear sophisticated analytic and rhetorical skills, but these skills are oriented

## 240 • Literary Darwinism

not to the production of clear and distinct ideas but to exactly the opposite, to the construction of pseudo-concepts that obstruct clear thinking.

There is one chief difference between the work of Gould/Lewontin and that of the postmodernists. Derrida, Foucault, and their many acolytes overtly declare irrationalism as their creed. It is the substance and burden of their theory, and in this sense their central theoretical claims are integral with their rhetorical methods. Gould and Lewontin use the techniques of sophisticated equivocation in a virtuoso way, but they do not overtly and forthrightly declare that their purpose is to suspend the capacity for rational thought. There is, in that respect, something less complete and robust about their work. It is a sort of hybrid between sophistry and science.

Confusion is not itself the targeted feature under selection in "The Spanrels of San Marco." It is a means to an end, and that end is to achieve the appearance of revolutionary transformation without formulating ideas that are clear and distinct enough to be vulnerable to refutation. Since Gould and Lewontin are arguing only about degrees of difference ("so strongly") in subjective responses ("most interesting"), they cannot be held to have affirmed any specific proposition. Because they have produced no clear and distinct ideas, their claims cannot be falsified. They have nonetheless created a rhetorical facsimile of contrasting theoretical positions, and they can thus present themselves as having constructed a solid foundation for a revolutionary transformation of "the adaptationist programme" (1979, p. 581).

In his eagerness to minimize the significance of adaptation through natural selection, Gould is, in wish and emphasis, anti-Darwinian. But since, within the range of scientifically reputable evolutionary theory, there is no actual alternative to Darwinism—no alternative, that is, to adaptation through natural selection as an explanation for complex functional structure—Gould can never say fully what he wants to say. His plight recalls that of "Atticus" in Alexander Pope's "An Epistle from Mr. Pope to Dr. Arbuthnot." In Pope's depiction, Atticus (Addison) wished to satisfy envy and spite without making himself vulnerable through open attack. He thus developed a proto-Gouldian rhetorical technique that enabled him to "Damn with faint praise, assent with civil leer, / And without sneering, teach the rest to sneer; / Willing to wound, and yet afraid to strike, / Just hint a fault, and hesitate dislike" (1969, ll. 201–204).

In an article that offers a thorough and precise analysis of Gould's rhetorical strategies, John Alcock identifies a number of Gould's feints and dodges, and he observes that, while Gould frequently makes pretenses of affirming the centrality of adaptation, he also perpetually employs sophisticated formulations intended to eliminate adaptation from the conceptual repertory of evolutionary biology. With respect to one such formulation, Alcock notes that "by 'adaptation'" Gould "means a trait that evolved without historical constraints,

which means that almost no trait qualifies for the title. And I think that this is essentially what Stephen Jay Gould has in mind” (1998, p. 332).

Alcock persuasively argues that one animating motive in Gould’s campaign against adaptation is his commitment to Marxist ideology. From a Marxist perspective, to affirm adaptive design is to acknowledge that the existing structure of social and political power is constrained in some way by the nature of things, and to acknowledge that much is to come too close, the Marxist feels, to justifying the existing social order. Marxist utopianism requires that human beings not be constrained by evolved motives; “human nature” is to consist in little more than a capacity for culture that entails infinite flexibility. It is certainly the case that from the very beginning Gould’s ideological career has been punctuated repeatedly by attacks on human sociobiology and evolutionary psychology, and it seems more than probable that this social and political animus has helped to shape his formulations of general evolutionary theory, even when that theory directly concerns only insects, snails, pandas, flamingoes, horses, dinosaurs, and Cambrian phyla, not human beings. (On Gould’s ideological motives, also see Gross, 2002.)

Gould’s primary field of specialization is paleontology, and for a paleontologist the one most significant modern find—the one find that offers the greatest opportunity for drawing conclusions of broad general import in the field of evolutionary theory—are the fossils of the Burgess shale. Gould gives a historical and theoretical account of the Burgess fossils in his popular book *Wonderful Life: The Burgess Shale and the Nature of History* (1989). He uses the fossils to support his claim that evolution is wholly “contingent.” By totalizing and hypostatizing this word—that is, by treating “contingency” as a distinct, substantive entity rather than a logical category—he creates the impression that evolution is altogether unpredictable and chaotic. The idea of contingency as *events resulting from unforeseen causal relations* bleeds over, in Gould’s formulations, into the idea of contingency as *events happening in ways that are not subject to causal analysis because they happen without cause*. The idea of contingency as somehow distinct from adaptation is closely affiliated with the idea of constraints that are somehow more interesting than the selection that works on them. Insofar as it is not merely a form of obfuscation, this notion of contingency is a form of mysticism or irrationalism. We hear again the sound of one hand clapping.

Simon Conway Morris is a Cambridge paleontologist who performed an important part of the primary scientific work on the Burgess shale fossils. In *Wonderful Life*, Gould gives Conway Morris good press, but he does not thereby succeed in blunting the edge of the criticism that Conway Morris levels at him in his own subsequent book. In *The Crucible of Creation* (1998), Conway Morris opposes Gould’s interpretation of the Burgess fossils on two main counts: the relative diversity of Burgess and modern phyla, and the

## 242 • Literary Darwinism

significance of constraints. He argues that Gould is wrong in claiming that the Burgess animals displayed greater disparity of body form and a larger number of phyla than present animals. The appearance of greater disparity, he argues, is an artifact of classification (pp. 205–206, 218; also see Mark Ridley's (1990) review of *Wonderful Life*). Like Gould, Conway Morris emphasizes constraints, but he draws a radically different inference from them. One major feature of evolution, convergent evolution, powerfully supports the idea that viable forms are constrained in certain directions by the conditions of life on earth. Organisms that display convergent evolution have functionally similar adaptations that have evolved independently in distinct phylogenetic lineages. Signal instances include the eyes of insects, vertebrates, and cephalopods (squids), and the wings of birds, insects, and bats. By emphasizing the significance of the constraints evidenced by convergent evolution, Conway Morris undermines Gould's claims for unpredictability (pp. 139, 201–202).

David Hull, a leading figure in the history and philosophy of biology, takes Gould as an illustration of his thesis that "scientists are engaged in the ongoing process of jockeying for recognition in science" (1988, p. 202). Hull treats of science chiefly as an institutional and social process, and the "process" he describes consists largely in choosing strategies for the advancement of scientific careers. There are two basic strategies. Scientists can present themselves as adherents to the received view, contributing only refinements of technical detail, or they can present themselves as radical revolutionaries. "The choice is between a safe strategy with a minor payoff versus a very dangerous strategy that promises great rewards" (p. 203). In biology, for instance, scientists can choose to "exaggerate their differences with the received view to emphasize how original their contributions are," or they can "exaggerate the similarities between their views and those of contemporary Darwinians in order to throw the mantle of the great Darwin round their own shoulders" (p. 202). Gould has found a way to combine these two strategies. He presents himself as a radical opponent of the received view but—apart from his youthful fling with overt saltation—also as a Darwinist more truly Darwinian than the "Darwinian fundamentalists." He has found a way to seek great rewards with little risk, but the method he has chosen for thus maximizing his strategic advantages is to abandon any effort to produce substantive contributions to scientific knowledge and instead to generate verbal problematics.

There is a cost to the strategy Gould has adopted, even in the purely careerist terms described by Hull. As Alcock observes, "Gould's debating tactics may make his essays persuasive to a general audience, but rhetoric alone cannot overcome the research record established by persons willing to put their ideas about the adaptive design of traits on the table for honest testing" (1998, p. 335). In an exchange with Gould over evolutionary psychology, Steven



Pinker makes a similar appeal to positive research findings and cites an illustrative range of psychological topics:

The adaptationist approach has, for over a century, driven the most rigorous, elegant, and empirically rich branch of psychology, perception. Today it is spawning new insights and intensive modeling and data-gathering on every other aspect of the mind, including reasoning, mental imagery, memory, language, beauty, sexual desire, autism, emotions such as fear and disgust, violence, the numerical abilities of children and animals, and the shaping of personality.” (1997a, p. 56)

Alcock and Pinker both believe in the ultimate integrity of the scientific process. On the basis of this belief, Alcock declares, “I am confident that, in the long run, Gould’s polemical essays will be just an odd footnote in the history of evolutionary thought, a history that has been shaped in a wonderfully productive manner by the adaptationist perspective” (p. 335). Gould’s situation is something like that in the story of the man, hungry for fame, who made a particularly ingenious bargain with the devil—ingenious, that is, on the devil’s side. In return for his soul, the man would be famous in his own day, but only on the condition that after his death all trace of his works would be eradicated from the memory of men.

Several eminent evolutionists have reflected on the quality of sophistry that pervades Gould’s theoretical writing. Daniel Dennett, Richard Dawkins, Simon Conway Morris, and E. O. Wilson have all described the way in which Gould exaggerates the revolutionary significance of his ideas. In a chapter of *Darwin’s Dangerous Idea: Evolution and the Meanings of Life* (1995), Dennett gives a penetrating and comprehensive critique of Gould’s theoretical career and describes it, correctly, as a series of factitious revolutions. One of the chapter sections is tellingly titled “The Boy Who Cried Wolf.” Summarizing his chapter, Dennett concludes, “*Gould’s self-styled revolutions, against adaptationism, gradualism, and extrapolationism, and for ‘radical contingency,’ all evaporate, their good points already firmly incorporated into the modern synthesis, and their mistaken points dismissed. Darwin’s dangerous idea emerges strengthened, its dominion over every corner of biology more secure than ever*” (p. 312). Rather more bluntly, Dawkins complains that “Gould seems to be saying things that are more radical than they really are. He pretends” (1995, p. 84). Dawkins is openly hostile toward Gould, and he gives his reasons. “I’m extremely hostile towards any sort of obscurantism, pretension. If I think somebody’s a fake, if somebody isn’t genuinely concerned about what actually is true but is instead doing something for some other motive, if somebody is trying to appear like an intellectual, or trying to appear more profound than he is, or more mysterious than he is, I’m very hostile to that” (p. 85). As we have seen, Conway Morris provides a sober specialist critique of Gould’s conclusions about the fossils of the Burgess shale, but he also fashions an evocative

and humorous image of Gould's whole career as an ostensible post-adaptationist founder of new evolutionary theories:

Again and again Gould has been seen to charge into battle, sometimes hardly visible in the struggling mass. Strangely immune to seemingly lethal lunges he finally re-emerges. Eventually the dust and confusion die down. Gould announces to the awestruck onlookers that our present understanding of evolutionary processes is dangerously deficient and the theory is perhaps in its death throes. We look beyond the exponent of doom, and there standing in the sunlight is the edifice of evolutionary theory, little changed. (1998, p. 10)

In a similar vein, commenting specifically on the debate over punctuated equilibrium, E. O. Wilson suggests that Gould's claims for revolutionary novelty were more a matter of rhetorical posturing than of substantive conceptual proposals. "Neo-Darwinian theory was not challenged in substance, only semantically—a renaming, so to speak, as opposed to a reinventing of the wheel" (1992, p. 89). The term "punctuated equilibrium" has survived, but it "is now used mostly as a descriptive term for a pattern of alternating rapid and slow evolution, especially when the rapid phase is accompanied by species formation. Its fate illustrates the principle that in science failed ideas live on as ghosts in the glossaries of the survivors."

Early in his career as the boy who cried wolf, Gould responded to the complaint that he is generating confusion by creating pseudo-issues. Backing off from the strong, saltational version of punctuated equilibrium, he acknowledged that punctuated equilibrium "may not be directed at the heart of natural selection," but he still claimed that "it remains an important critique of the Darwinian tradition" (1982, p. 383). His supporting inference for the importance of his idea is that "the world is not inhabited exclusively by fools, and when a subject arouses intense interest and debate, as this one has, something other than semantics is usually at stake" (p. 383). Evolutionary biologists do not tend to be fools, but they do tend to be ingenuously straightforward, and they are often poorly equipped to deal with provocative challenges wrapped in obfuscatory equivocation. Gould's pluralism, his punctuationism, and his spandrels can be likened to the eggs of a cuckoo in the nest of evolutionary biology. The eggs look enough like legitimate eggs to cause consternation in the minds of the parent birds, but targeted birds eventually evolve defenses against the cuckoo's parasitism. They count eggs or assess size, and oust the illegitimate intruders. The affair costs them some little effort, but it hardly seems fair for the cuckoo then to proclaim that the effort taken to oust his illegitimate offspring constitutes evidence of his own legitimacy.

Among Darwin's contemporaries, the one figure who most resembles Gould in his use of sophisticated equivocation is the paleontologist Richard Owen (1804–1892), who wished, on the one hand, to affirm that animal forms are determined by "archetypes" that are not related to one another by lineage

and, on the other, to represent himself as having originated proto-Darwinian evolutionary ideas. Darwin responds to Owen's equivocations in the historical sketch appended to the third edition of the *Origin*, and he comes closer there to a snort of satirical contempt than he ever comes in responding to any other writer, even to Lamarck. "It is consolatory to me that others find Professor Owen's controversial writings as difficult to understand and to reconcile with each other, as I do" (2003, p. 84). Darwin himself operates in good faith, and his overriding assumption is that others do also, even when he fundamentally disagrees with them. In his *Autobiography*, he remarks, "I have almost always been treated honestly by my reviewers, passing over those without scientific knowledge as not worthy of notice" (1958, p. 125). Coming from a man who had received so many violently hostile reviews, this remark reflects a presumption of good faith so ingenuous in its benignity as to fall little short of the sublime. But Owen is so flagrantly and unmistakably not operating in good faith that even Darwin's simplicity of good will is finally roused to an awareness of Owen's deviousness and duplicity. One can only speculate how Darwin would have responded to Gould. He might well have wondered whether Gould is, as Maynard Smith characterizes him, merely confused, or, as Dawkins characterizes him, downright dishonest. To my own eye, it seems evident that Gould is not himself confused, though it is his purpose that his readers should be.

