

The Tragedy of *a priori* Selectionism: Dennett and Gould on Adaptationism

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Abstract. In his recent book on Darwinism, Daniel Dennett has offered up a species of *a priori* selectionism that he calls algorithmic. He used this view to challenge a number of positions advocated by Stephen J. Gould. I examine his algorithmic conception, review his unqualified enthusiasm for the *a priori* selectionist position, challenge Dennett's main metaphors (cranes vs. skyhooks and a design space), examine ways in which his position has led him to misunderstand or misrepresent Gould (spandrels, exaptation, punctuated equilibrium, contingency and disparity), and discuss recent results in developmental biology that suggest that an *a priori* position does *not* fill the demands of an evolutionary biology. I conclude by insisting that evolutionary biology is many leveled, complicated, and is carried on an ever shifting and expanding empirical base that when disregarded results in caricature.

Key words: adaptation, algorithm, atavism, contingency, deep homology, Dennett, development, disparity, epicurean selectionism, evolution, exaptation, Gould, metaphors, punctuated equilibrium, selectionism, spandrels

From the early days of selectionist explanations there have been those who found selectionist reasoning obvious. Patrick Matthew who is credited by Darwin as anticipating his own and Wallace's view, writes;

To me the conception of this Law of nature came intuitively as a self-evident fact, almost without effort of concentrated thought. Mr. Darwin here seems to have more merit in the discovery than I have had; to me it did not appear a discovery. He seems to have worked it out by inductive reason, slowly with due caution to have made his way synthetically from fact to fact onwards; while with me it was by a general glance at the scheme of Nature that I estimated this select production of species as an *a priori* recognizable fact – an axiom requiring only to be pointed out to be admitted by unprejudiced minds of sufficient grasp.¹

Recently, Daniel Dennett has written an account of evolutionary theory that is part of this tradition (Dennett 1995). He calls his book *Darwin's Dangerous*

Idea: Evolution and the Meanings of Life (DDI). ‘Darwin’ has undergone some realignment under Dennett’s care. It might better be called *Patrick Matthew’s Dangerous Idea*, but it is Darwin whose name has been affixed to the flag under which any number of evolutionists (and evolutionary theories) have sailed (Hull 1985).

As it turns out, if we attend to all the caveats that are tucked into Dennett’s chapters we find that what he really means is something tamer than dangerous ideas. The title, *Darwin’s useful null hypothesis: adaptationism* while more descriptive has substantially less flash. Dennett claims that all selectionist accounts must be tied to optimality arguments of some kind (see especially chapters 8 and 9) though he falls short in indicating how one would choose between competing accounts. That selectionism tied to optimality arguments might serve the function of generating scenarios in which selection is the primary explanation for the distribution of characters in a population is not controversial. Whether it has been used effectively this way in particular cases is frequently argued (Orzack and Sober 1994; Orzack and Sober 1996; Brandon and Rausher 1996; Brandon 1978). Dennett’s description of neo-Darwinism is, to borrow a line from Douglas Adams, “mostly harmless” and, to the extent that DDI stimulates more interest in and discussion of evolutionary theory it is to be praised.

That said, there are two topics that I find worth examining (for a more complete review of DDI see Orr 1996b, 1996c; Dennett 1996; Orr 1996a). First is Dennett’s claim that natural selection is a substrate neutral algorithm. Second is his discussion of Stephen J. Gould’s work. The first will allow me to explore an unnecessary inversion in Dennett’s thinking. His *a priori* commitment to selection as the explanatory focus in all situations puts the cart before horse and he falls in love with the cart. I will suggest that this is due, in part, to his embrace of ubiquitous intentionality. Mark Ridley has enthused that the chapter on Stephen J. Gould’s work “should be widely read . . . and would be ideal material for graduate discussion classes” (Ridley 1995). You may think of my comments on this second topic as notes for Ridley’s graduate discussion. I will review Dennett’s metaphor of cranes and skyhooks and his notion of design space. I will step through the main topics raised in his discussion of Gould and will end by suggesting that Dennett’s description is not rich enough to reflect the interests of evolutionary biology.

Evolution as an algorithm

Dennett’s self claimed contribution to evolutionary theory is the restatement of natural selection as an ‘algorithm.’ I am sympathetic to the attempt to view biological processes computationally. But he manages to dilute the term so

much that in his own estimation, “. . . are there any limits at all on what may be considered an algorithmic process? I guess the answer is No; if you wanted to, you could treat any process at the abstract level as an algorithmic process” (p. 59). So he gets marks for honesty, but is it controversial (or a novel insight) that evolution is a process? Even insisting that Darwinian selection is a process that uses only local information and local rules is not really news. Dennett suggests that he is recovering Darwin’s actual accomplishment (i.e. that the algorithmic conception *is* Darwin’s grand project).

Dennett trades on our enthusiasm about the guaranteed results that come from (some) algorithms (the spreadsheet dutifully calculates sums, the database sorts names and addresses, etc. . . .) to lend an aura of guaranteed results to selectionism. If so, it is incumbent on Dennett to support this claim. There exist algorithms that have provably guaranteed results; some examples can be found in any introductory text (e.g. Cormen et al. 1990). It is not clear what is guaranteed by Dennett’s framing of selectionism as an algorithm. To algorithmatize specific evolutionary explanations we need to specify what kind of variance is possible, what the basis of selection is, what is being selected, and the relative fitnesses in different contexts. Even non-biological engineering problems face this challenge. The subject of “genetic” algorithms (a current vogue in computer science) is full of questions about how a problem is to be encoded and how the solution landscape is related to the “genetic” operators that are used to generate the possible solutions.²

Dennett suggests in the book and reaffirmed, in subsequent discussion, that he means to cast a wide net for ‘algorithm.’ He certainly wants to include traditional natural selection. Dennett has recently insisted that ‘algorithm’ was used in DDI to refer to the set of all Turing machines (Mulhauser 1997; Dennett 1997). This is barely helpful and is not even really true. There are many algorithms that are Turing computable that keep track of various pieces of global state information that would be rejected by the orthodox neo-Darwinism that Dennett describes; adaptations emerge solely from local population dynamics – so global state information can not be allowed.

If we were to grant a kind of loose algorithmic status to evolutionary theory then this commits Dennett to, at least, two more volumes outlining the various parameters from *the world* that are fed into the algorithm and the (deterministic?) results that come out. Let me suggest; *Darwin’s Daunting Initial Conditions* and *Darwin’s Deductive Inference*. But Dennett shows little enthusiasm to actually deliver on these implications of the algorithmic conception or to do the empirical work.

One reason for pushing an algorithmic conception is that Dennett wants to aid the strong program in Artificial Life (Alife) (for a philosophical discussion see Lange 1996). Strong Alife claims that instantiations of life can

extend to models that abstract away some essential relations from particular biochemical, physiological or ecological details. By tying 'Darwin' to the algorithmic conception Dennett hopes to establish legitimacy (through paternity) turning Alife modelers into the orthodox Darwinians. One "sign of life" has traditionally been that life evolves. In making evolution algorithmic, Dennett may be hoping for a tidy inversion as non-artificial(!) life becomes merely an instantiation of the selectionist algorithm.

Unfortunately, Dennett is not weighing in on the interesting epistemological issue of the status of abstract models. The suggestion that selectionism is ontologically prior to any particular biological details is a natural extension to his approach. As a description of scientific practice such a claim would falter on historical grounds. Biologists have not conceptualized selectionism in abstract enough terms to compare it easily with the models to which physicists often accord a higher degree of reality than the phenomenological examples they are meant to explain (e.g. lawlike statements, for a discussion see ch 12 of Hacking 1983). One could argue that just because they have not done so, does not mean they should not (for a rare exception see Williams 1970; Rosenberg 1985). Verifying an ontological commitment to selectionism is troubled by an important asymmetry. While we can, in principle, combine any particular claim of selectionism with initial conditions and other limiting constraint assumptions to derive expectations about distribution and abundance (the promise of optimality arguments) doing the inverse (logically establishing the presence of a particular selection regime by a particular distribution or abundance) is not warranted.³ This is just to say that in biology the historically contingent facts of the matter are still prior. I suspect this is largely because the gulf between the possible and the actual in biology is so vast. There are far too many worlds consistent with selectionism, so that if our concern is to explain the details of this one world we will, of necessity, make deep appeals to historical constraint (compare Beatty 1995).

As Alife models become more elaborate it may be that we will get a sense of both what is guaranteed and over what kinds of data structures selectionist algorithms illustrate those guarantees (e.g. Fontana et al. 1994). A crucial part of thinking about algorithms is defining the kind of data over which an algorithm works. What bridge principles allow me to add 1 apple to 1 apple and get 2 apples while adding 1 sand pile to 1 sand pile can result in 1 sand pile? Dennett insists that natural selection is everywhere applicable (a universal acid that dissolves everything) (this position is strongly challenged and minimal criteria for invoking a selectionist explanation are offered in Amundson 1989). The appropriate deployment of selectionist arguments seems to me to be an empirical question not dispatched by Dennett's insistence to the contrary. As some of us rush to embrace computer models as an alternate

laboratory for evolutionary and ecological questions (an interesting approach is described in Ray 1994) it is important not to assume that we have reached this goal, as the journey has just begun.

Dennett achieves his algorithmic conception (as underspecified as it is) by abstracting away from the biological description. In this way he has formulated an object for his affection. My core discomfort with this trajectory is that in making a fetish of selectionism the biology recedes too far into the background. Dennett never makes clear what we gain by embracing his attenuated and all-embracing algorithmic conception. My fear is that enormous diversity of the organic world will be missed as Dennett careens, algorithm in hand, toward “redesigning morality” (his penultimate chapter). A destination where in a Panglossian fervor that must warm the hearts of corporate polluters, he suggests that ecological disasters might be good – since they can galvanize public opinion and help us avoid other disasters in the future (p. 498 n. 4).

Learning not to worry and love adaptationism

Dennett’s enthusiasm for “the strategy of interpreting organisms as if they were artifacts” (p. 212) derives from his approach to why-questions. For Dennett, why-questions demand answers in intentional terms; i.e. what the designers had in mind. This is his ‘intentional stance.’ It just does not sit well with him to answer a why-question with an appeal to structural constraint or contingency. He is so sure that every trait is an adaptation in part because he can think of no other way to proceed. He wants to find final causes (in Aristotle’s sense, *aitia*, i.e. what is responsible). Being a modernist he can not accept external teleology (in Plato’s sense) and is relieved to be saved by Darwin’s material account of a process that *simulates* external agency (see the discussion in Lennox 1992).

Unnecessarily, he wants us to believe that just accepting ubiquitous intentionality settles the many detailed biological questions about the genesis and current distribution and abundance of organisms and their suites of traits. We do not have to accept his diagnosis. We could insist with Hobbes and Bacon that the only legitimate cause is efficient cause (Bacon called final causes “barren virgins”). We then refuse to answer why-questions and restrict ourselves to ‘how’ and ‘what.’ This seems to actually have happened in many branches of science. Alternatively, we could allow other kinds of answers, thus embracing structural constraint and historical artifact as legitimate responses to why-questions about traits and trait distributions.

Did he jump or was he pushed? Dennett would have us believe that there is no choice but to view everything in adaptationist terms (i.e. he was pushed)

(ch. 9). But what if it is Dan Dennett and not biology that demands the intentional stance (i.e. he dove in head first with eyes open). This opens the possibility that DDI is a *reductio ad absurdum* designed to show what silliness happens if you fully embrace the view that all features have a reason. If so, Dennett is not letting on. So we have to allow that he, at least, feels as if his current understanding of the subject matter pushed him to this view.

Having arrived at his stance Dennett imagines that the only problem to resolve is comfort with this position. Dennett's urging of adaptationism-tinted glasses (what he illustrates with "artifact hermeneutics" (pp. 212–220)) parallels Saint Augustine's directive, written in 397 C.E., regarding figurative expressions in biblical text; "... a rule such as this will serve, that what is read should be subjected to diligent scrutiny until an interpretation contributing to the reign of charity is produced" (Book III ch. 15 Augustine 1958). I imagine Dennett insisting that we examine the organism until an interpretation contributing to the adaptationist description is produced, or as he says, "adaptationist reasoning is not optional; it is the heart and soul of evolutionary biology" (p. 238). Dennett is distinctly uncomfortable foregrounding constraint or contingency, but happy to press these ideas into service as limits to optimality assumptions when trying his hand at reverse-engineering. He does not address typical issues in population genetics (e.g. the problem of far from equilibrium population dynamics) but would probably subsume these as just another constraint on optimality.

That we can redescribe everything around us in purely adaptationist terms is not controversial, whether we should, is. Dennett is wrong to encourage his lay audience to stick their head in the same pan-functionalist sand where he finds comfort. Even if we were to embrace thoroughgoing adaptationism, all of the same problems remain. Which scenario, which constraints, what is the relative importance in a particular situation of all the factors that could be explanatory. Dennett's insistent redescription flirts with losing natural selection as an explanation, as once we assume adaptationism we see only confirming instances. This is precisely what bothered Popper about Marxism, psychoanalysis, and individual psychology and lead him to his demand that scientific propositions be falsifiable (Popper 1962, ch. 1).

Dennett on Gould

The participants in the relatively small community of those who embrace evolutionary biology have a long tradition of sniping at each other. This may be a way to sublimate the frustration with their majority who do not find evolutionary explanations compelling or necessary. I will now turn to criticisms that Dennett has leveled at the evolutionist Stephen J. Gould.

Part of the issue is, what conditions must be obtained to give natural selection full/sole credit as the creative force in generating adaptation. A multitude of small undirected heritable variants do not, alone, give rise to cumulative adaptations. Selection, is credited with the creative power by Darwin when the variations are undirected, plentiful and small. But the dynamics of possible and actual variations available to a population are part of the explanation. Gould has defended the importance of processes that are relevant to understanding the distribution and abundance of living forms (from internal developmental constraints, to external biophysical constraints, to historical contingencies, to cooptation of functions, to large external events (meteor at the K-T boundary), to species level selection). All of these do undermine pan-selectionism and pan-functionalism. But it is the ‘pan’ that they challenge not the existence of the process or its affects.

Gould demands that focus be shifted to the many interactions, historical opportunities and constraints, and the core importance of historical contingency in explaining the details of the biological world. I will begin by reiterating those of Dennett’s themes that come up in his discussion of Gould, rehearse some of Gould’s claims, Dennett’s counter claims and hopefully clarify the gulf between them. I will end with several contemporary examples to indicate what an evolutionary biology must encompass.

Dennett’s framework: skyhooks & cranes

Dennett distinguishes evolution by skyhooks from evolution by cranes. This analogy is meant to capture some of the distinctions that were traditionally expressed in the struggle about teleology and to reemphasize the idea that evolution is profoundly myopic, constantly working with what it currently has; cranes can be used to build bigger cranes but you must **not** hope for ropes to hang from the sky to pull you up. Dennett uses this analogy to distance himself from those who would dare to appeal to anything other than cranes. Since the only option in his scheme are the skyhooks, this will turn out to be anyone who is not firmly within Dennett’s ultra-Darwinist camp.

While the skyhook and crane do allow us to distinguish externalist teleological explanations from local materialist ones, it is not in the end a particularly helpful analogy. It commits us to a currently nonexistent tension (within evolutionary biology) between those who long to explain the distribution and abundance of organisms by an appeal to volitional or providential external forces (miraculous ropes hanging from the heavens) and those who do not (only materialist cranes building on their previously built foundations). As I discuss below the real debate in evolutionary biology is, to accede to the metaphor for a moment, in the details of the ‘cranes’ and the constraints that

are offered by the previously built foundations, not in separating cranes from skyhooks.

Additionally, the word ‘crane’ suggests crane operators and a task. What task? Sometimes, I read Dennett as suggesting that sentience or even consciousness is an inevitable outcome of natural selection (pp. 306–307). If so, then maybe he means this task. Finally, it encourages the view that the structure being built has a direction, up toward the skyhooks. This implicit embrace of progressivism is surprising in a contemporary evolutionary exposition. Dennett will thankfully reject this literalized reading of his metaphor so I will not weigh down his argument with these implications, though I caution that this reading is any easy extension of his analogy.

Dennett’s framework: design space

Dennett sees evolution as a process of exploring “design space” an abstract (possibly platonic) multidimensional space that has designs in it. We should prefer ‘morphospace,’ leaving designs and all of the functionalism that they imply as hypotheses to be deployed critically (see the discussion of spandrels below). Design space sounds so end-directed and final. Positing a design space takes for granted part of what selectionist theories are meant to explain. If everything selected is designed and selection is then used to explain design we have the kind of trivial conclusion that we depend on philosophers to save us from. A change to ‘morphospace’ takes some of the shine off the skyhook/crane analogy but redirects us to a more important question; what variation is there for selection to act on?

Universal selectionists, like Dennett, are not usually making claims about the details of morphological variation. Their (appropriate) emphasis on precisely that variation that is available to selection in a local population (a charitable reading of the admonition – “no skyhooks”) can give the impression that there is some kind of normally distributed variance over all morphological variables. The traditional picture of bell curves with selection acting to shift the population mean illustrates and reinforces this notion. However, the neighborhood in morphospace that is actually explored by a given population is due to a complicated mix of mutations, translocations, inversions and other genetic events that have anything but uniform effects on morphology as they affect different regulatory and structural genes (a dichotomy that sounds more absolute than it is, compare Nijhout 1990). These, in turn, participate in developmental systems that facilitate and resist changes in morphospace and have norms of reaction that can result in very different morphologies in different environmental contexts (another dichotomy, environmental/physiological, that implies a divide that is difficult to sustain

on close examination (this topic has a large literature, but see Gray 1992)). Understanding the variance and covariance of traits is a major project in quantitative genetics (a good introductory discussion is Murphy 1979), and no amount of armchair biology can stand in for it.

The design-space that Dennett asks us to imagine is closely tied to his description of genotype space. To illustrate a genotype space, he borrows Borges' metaphor of a library that contains books with every permutation of letters and thus all possible books; every edition and every draft, every argument and every response (Borges 1962b), and rechristens it Mendel's library. He then conceives evolution as a voyage from one volume (sequence) to another. Borges realized that an exhaustive library of possibilities does not generate meaning.

I know of districts where the youth prostrate themselves before books and barbarously kiss the pages, though they do not know how to make out a single letter. Epidemics, heretical disagreements, the pilgrimages which inevitably degenerate into banditry, have decimated the population. I believe I have mentioned the suicides, more frequent each year (Borges 1962b, p. 87).

Dennett borrows the metaphor but leaves Borges' pessimistic moral behind. By not focusing on the relationship between the transition from genotype to phenotype Mendel's library becomes deceptively under-powered in Dennett's hands.

Dennett's enthusiasm for both Mendel's library and a Design space comes from linking the two. The allure of a 'space' comes from the sense that there is a meaningful way to deliver on our intuition of distance. A space has some kind of metric that lets me say A is closer to B than it is to C, but as has long been known; some points distant in genotype space result in similar phenotypes (i.e. convergence), some points close in genotype space result in large differences in phenotype space (e.g. homeotic genes), and environment influences phenotype (an environment that includes other evolved organisms). Darwin was especially sensitive to the last of these as his discussion of orchids and their pollinators will attest (Darwin, 1892). In addition, the movement through the genotype space can be somewhat abrupt (there are inversions, translocations, chromosome doubling, and chromosome loss, and so on). These complications arise just in connecting a genotype space to a morphological space. Such problems are compounded for a "design-space". Even if we were to supply all of the bridge principles, elaborating Mendel's library to include all of the context, environment, population size and distribution, and detailed history it would become no more than a way of bookkeeping. The history of life can be seen as a set of trajectories through

genotype space, but this focus on sequences is not explanatory (gene-centrism has been criticized in this way by Sober and Lewontin 1982).

To reiterate, if we do not really know what designs are close to others or if we are continuously surprised by how accessible one design is from another, then our space will have an unusable metric and we may prefer to simply make an exhaustive list. It may be that ‘space’ (design, morphological, or genotype) is just Dennett’s way of discussing a point set and that there is no need to have any sense of distance (a metric). If so, this loses an interesting and important intuition. Dennett has been pressed on design-space (Mulhauser 1997; Dennett 1997) and has let the concept collapse into the self-referential “everything ‘designed’ is related by descent to some product of natural selection.”

Dennett would have done better to borrow from another Borges story in the same volume, in which a novel and a labyrinth are joined as “The Garden of Forking Paths” (Borges 1962a). This invention illustrates the teeming possibilities that result from attending to innumerable historical alternatives. When the alternatives are taken together they result in a pullulation of possible worlds, “a dizzily growing, ever spreading network of diverging, converging and parallel times.”

Folk selectionism

Dennett’s selectionism is Darwinism as seen through the dramatic irony that is found in Richard Dawkins’ writings (Dawkins 1982; Dawkins 1986; Dawkins 1989; Dawkins 1995). Dawkins has cautioned me not to view Dennett as his acolyte (Dawkins 1996), but clearly Dennett has adopted many (if not all) of Dawkins’ provocative predilections. We should recall that Dawkins, in his more reflective moments, suggests that gene centrism is but one way to see the world, a way that he claims will illuminate problems, and is only as important as the new hypotheses it generates (Dawkins 1982, p. 1). Dawkins, as we know, is not always so cautious. His unapologetic use of volitional terms, for example, came under strong criticism (Midgley 1979; Dawkins 1981; Midgley 1983; Rodd 1987).⁴ Dennett misunderstands these criticisms (p. 328) as Dawkins did. Formally, Dawkins is free to use words as labels without the demand that their usual meanings transport constraints on his model. But this approach means that it is up to others to remind unsuspecting audiences of the unfortunate switch of the formal for the familiar. Dennett and Dawkins dismiss discomfort with the use of familiar volitional terms because they claim that no one should believe that, for example, genes can act in their own interests and insist that the borrowing of ordinary language is only a (technical) short hand for retrospective evaluation. ‘Extant genes duplicated

themselves for the sake of surviving’ means something like ‘genes that were not duplicated did not survive.’ The criticism, however, is precisely that readers unencumbered by years of biological knowledge might be confused and that this language invites infelicitous conclusions.

Dennett has turned Dawkins’ preferences into a fundamentalist orthodoxy. I suspect that even Dawkins may, in time, find this cloying. The reasons for the embrace of an ultra-selectionist caricature by Dennett and Dawkins is somewhat different. Where Dennett believes he has found an analytic truth in selectionism, one that both transcends any detailed knowledge of the world and is required to understand the world, Dawkins (and J. Maynard-Smith and G.C. Williams) think that they have found the right place to start. “It [today’s theory of natural selection] may not, in any absolute or permanent sense, represent the truth, but I am convinced it is the light and the way” (Williams 1966).

Sober has argued that deploying hypotheses is in itself an adaptive heuristic (Sober 1994b). He makes the case that early commitment to the reality of theoretical terms allows science to flourish. Briefly, Sober argues that if you insist that your sense impressions are caused by an external reality then you can start making abductions and this is a much more helpful heuristic for generating hypotheses than solely inducing over statistical correlations in sense impressions. Dennett makes a similar point in trying to validate folk psychology as explanatory, with a kind of pragmatic it-works-and-lets-me-predict criterion (Dennett 1991; Dennett 1987). Should we see Dennett’s approach as a promiscuous folk selectionism that merely allows abduction to begin?

In this view, Dennett’s actual claim about universal selectionism should be that it is a folk evolutionism; a workable caricature that allows good guesses much of the time. As evolutionists, it is difficult to evaluate our guesses. Much of evolutionary biology is an *ex post facto* enterprise. This results in the temptation to confuse a selectionist rationalization with what actually happened (see the discussion of the spandrels paper below). It is not surprising then that working biologists require more than a folk evolutionism in their attempt to make reasonable inferences about evolutionary history.

The construction of an epicurean selectionism can start from either end. Start with caricature and then add filigrees until the full complexity of the theory stretches from one horizon to the other, or dispense with the exclusive emphasis on selectionism (happy to be spared from the excesses of just-so stories, false implications of gradualism, politically expedient sociobiology, . . .) and build the story back up with a contemporary take on heritability, development, and the dynamics of a genome? The theoretical entities in the second approach are more detailed and models built from them may be

more intricate. This does not make this approach superior. Cladistics, for example, has had a terrific effect on systematics (and slowly taxonomy) with its, admittedly, caricature models of trait state changes (Sober 1984; Wiley et al. 1991). (Why prefer the shortest tree?) The theoretical terms you cleave to can depend on the problem you are working on and a judgment on what will expedite your work. However, to the extent that Dennett insists that adaptationist models are always to be favored he is well outside any actual methodological debate in evolutionary biology, where detailed biological description is the starting point favored by almost everyone.

Gould's resistance

Understanding what kind of variation is possible and at what level selection occurs over those variations is what has driven the conversation about evolutionary biology at least since Darwin. Dennett places his emphasis on a divide between evil skyhook believers and righteous crane trusters. The discussion in evolutionary biology is actually (to use Dennett-speak) how are the cranes made (in detail!) and what is the accessible neighborhood from a particular point in morphospace. In these debates Gould and others have weighed in. Dennett realizes that Gould's positions push back against the story that he wants to tell, so he aims to undermine some of Gould's proposals.

Dennett correctly notes Gould's resistance to ultra-Darwinism. Dennett synonymizes his own no-skyhooks Darwinism with the ultra-Darwinist stance, as elaborated by John Maynard-Smith, G.C. Williams and Richard Dawkins (see discussion in Eldredge 1995). We are told that Gould rejects "the very idea that evolution is, in the end an algorithmic process" (p. 266). Given Dennett's attenuated all-inclusive sense of algorithm, what does this mean? I have already registered my concern that an algorithmic conception needs far more definition before it can even be evaluated.

Dennett writes, "The uncompromising 'no skyhooks-allowed' Darwinism I have presented is, by Gould's lights, hyper-Darwinism, an extremist view that needs overthrowing" (p. 264). This sentence implies that Gould's description is pro-skyhooks, that hyper-Darwinism is identical with Dennett's earlier presentation of neo-Darwinism, and that Gould buys this arrangement of the furniture. I do not think that most fair readers would find in Gould a sky-hooks-allowed or -encouraged philosophy. Throughout, Dennett seems to suggest that contemporary Darwinism is so free of empirical content that *a priori* no-skyhooks selectionism is all there is to it.

It is important to recognize that some of Gould's distinctions were intended as therapeutic, designed to challenge careless habits. Dennett in firm possession of a purely formal adaptationism might not make any of these mistakes

and so may not need the correctives. While Dennett may believe that biologists long for a crystal palace of pristine adaptationism, many biologists glory in the exquisite mix of contingency, adaptation and constraint that is in evidence in the uncountable compromises that result in a particular ecosystem on a particular day. As Ernst Mayr insisted more than thirty years ago; the evolutionary biologist “is impressed by the enormous diversity of the organic world. He wants to know the reasons for this diversity as well as the pathway by which it has been achieved” (Mayr 1961; an embrace of this intricacy is offered by Rice 1996).

Spandrels and adaptationism

In 1979 Gould and Lewontin wrote a memorable article that is often referred to as the spandrels paper (Gould and Lewontin 1979). It is a forceful statement against explaining every feature of an organism as an adaptation. They noted that there are architectural byproducts of particular structures. These byproducts are often integrated into the visual presentation of the artwork that decorates the design. Sometimes the integration is so natural and appropriate one might be tempted to think that the artistic design came first and the structure was made to fit that need. Their example is the iconography that decorates the “spandrels” in the great dome of St. Mark’s Cathedral in Venice. Spandrels are the triangular space between the exterior curve of an arch and the rectangular framework surrounding it. Dennett has discovered that the structure that Gould and Lewontin refer to, the triangular section of vaulting between the rim of a dome and the adjacent pair of the arches, are called *pendentives*.

Dennett lets himself get distracted by a long explanation of how domes could be placed on walls without forming pendentives (but see Mark 1996). After several pages he ends by concluding that in fact not all features are adaptations; “Natural selection could still be the ‘exclusive agent’ of evolutionary change even though many features of organisms were not adaptations” (p. 277). This simply moves the goal post. If we synonymize ‘evolutionary change’ with ‘natural selection’ then sentences like the above are not very interesting. Dennett’s discussion of the spandrels paper shows an obsessive attention to the wrong details. His *discovery* of pendentives causes him to miss the point of this argument; the temptation to explain every feature as the best possible (reminiscent of Voltaire’s Dr. Pangloss) is great and must be self-consciously stemmed.

In his discussion of adaptationism Dennett allows that, “Adaptationists are masters of the retrospective rationale. . . . But before we decide that this is a *flaw* in adaptationist character or method, we should remind ourselves

that this . . . is the way Mother Nature herself operates. Adaptationists should hardly be faulted for being unable to predict the brilliant moves that Mother Nature herself was oblivious of until she'd stumbled upon them" (pp. 251–252). I am not prepared to promote unbounded retrospective rationalization just because structures are coopted for new uses in unpredictable ways. If Dennett is arguing that previous adaptations plus environmental pressure are not sufficient to allow us to predict (or retrodict) the adaptive outcome then *he* is making Gould and Lewontin's point. Robert Brandon is right to understand the spandrels paper to be arguing for a pluralism of causal agents (Brandon and Mishler 1987). A pluralism that allows arguments about which agent or combination of agents is most explanatory in a particular case.

This approach is neatly captured by Amundson's discussion of the explanatory force of an explanation (Amundson 1989). Natural selection depends on sorting through variants. Central to this kind of explanation is the historically realized sequence of variants. Selection shares explanatory force with the dynamics of variation. We give more or less credit to the selective component of natural selection as a function of how undirected, abundant, and heritable the available variation is. This is an empirical question whose details can vary with each set of features being described.

Dennett prefers a monistic stance, quickly insisting that understanding mechanical (and other constraints) has always been a necessary part of adaptationist storytelling but that selection is always the main part of the explanation. That constraints are a constitutive part of selectionism is surely welcome news to Gould and Lewontin, who made the argument about spandrels in the first place. Their paper is frequently used to encourage students to avoid explaining every biological detail as an adaptation and to attend to the many ways that variation is not spontaneous, persistent, abundant and small. This pedagogical use suggests that the paper's conclusions do find a ready audience who agree with a spirit of caution when deploying an adaptationist story. Maynard-Smith, for example, allows that, "By and large, I think their paper had a healthy effect. There are plenty of bad adaptive stories. . . . Their critique forced us to clean up our act and to provide evidence for our stories" (Maynard-Smith 1995). Dennett quotes a similar sentiment but does not seem to attend to it, *contra* Maynard-Smith he claims that Gould was preaching to the converted and no competent adaptationist story went to the excesses that the Panglossian adjective implied (some agreement can be found in Queller 1995). Dennett does nothing to show that the paper's main points lacked a referent in evolutionary biology practice. If anything, his quoting of Maynard-Smith indicates the opposite.

The challenge is to evaluate claims like this one, "Half of the North American Lepidoptera species, and the three largest families (Noctuidae,

Geometridae, and Pyralidae), have ears, a testimonial to the voracious appetite of bats” (Scott 1986, p. 96). A testimonial maybe, but not the sole cause. Are ears a shared ancestral character (symplesiomorphy)? Did they evolve in parallel? And how shall we go about finding out? Are bats an ubiquitous feature of these moths’ habitats? Dennett would happily have us start with this adaptationist claim, but what would motivate him to do more than tell this story?

Dennett is content to assert (with a quote from Cronin) that all adaptive characteristics are the result of natural selection – but not all characteristics are adaptive. Does this solve our problem? We still have to sort them out, and we do not really have a good sense of which dominates in a particular situation. Dennett finds it difficult to separate adaptations from spandrels. There is no shame in that. This is a difficult problem. Even the initial recognition and atomization of an organism into traits offers a great challenge. That these challenges are usually glossed over does not dilute their importance (for a contemporary flirtation with the “just so” tradition see Thornhill and Gangestad 1996). We are asserting something about the way a particular structure came to be when we name it an adaptation. We are suggesting a causal history that involves variance, heritability, and disproportionate success of those who carried the variant. Dennett seems to want permission to hold that this is the default position until shown otherwise. Gould (and others) would hold that this is an irresponsible default position – preferring to withhold ‘adaptation’ until detailed selectionist criteria have been shown to have obtained.

Exaptation and adaptation

‘Exaptation’ was introduced to describe traits that were adapted for a different purpose than the function they currently perform (Gould and Vrba 1982). The desire to separate current utility from the process that lead to this use runs through Gould’s discussion of adaptations. Dennett’s treatment of Gould and Vrba is curious. He seems to buy (completely) the notion of appropriation of features that were not performing their current use. In fact, his no-skyhooks rule requires this of him. He suggests that “you will find that every adaptation has developed out of predecessor structures each of which had some other use or no use at all” (p. 281). In this way he concludes that the category for features not evolved under natural selection for their current use is unnecessary. Does allowing this formal notion (every adaptation is an exaptation) gut the distinction being made? No, we do want to distinguish between current utility and a previous different use. Gould and Vrba insist that they are interested in historical genesis and so their focus on a distinction between traits shaped by natural selection for their current function (adaptations) and

those contributing to fitness regardless of origin (exaptations) is central to their concern. The previous discussion of spandrels should also alert us to those traits whose previous use was no use at all.

Exaptation has had a curious history. It was intended to separate traits initially shaped by natural selection for the current function from those that were not. But exaptation really covers two distinct notions; those traits that have been coopted from traits with a different function for which natural selection was involved (e.g. scales to thermoregulatory feathers to feathers used in flight in the bird lineage) and those traits that were nonadaptive in origin. The first of these were long recognized and unfortunately called pre-adaptations. There is wide agreement that 'pre-adaptation' was a term that had to go. However, simply replacing 'pre-adaptation' with 'exaptation' overshadows the kind of exaptation that is captured in the spandrel analogy.

Dan Fisher raises an important concern about Gould and Vrba's use, one that applies to Dennett as well. Fisher wants to emphasize that adaptation is both a state and a process and while he acknowledges the distinction being drawn by Gould and Vrba he worries that in defining adaptations as created by natural selection an important connotation is lost. "Darwin's intent, despite some heterogeneity in usage (Burian 1983), was clearly to offer the process of natural selection as an explanation for features and relationships that can be observed in the world today (not to mention those represented by fossils). It is quite a different matter to assert by *definition* that adaptations are created by natural selection for current function" (Fisher 1985). The concern is that this allows selectionism to become self referentially sealed from challenge; natural selection being that which generates adaptations and adaptations being what natural selection has wrought. As he mentions, Gould and Vrba have subsequently avoided this problem by changing the explanandum and allowing for a plurality of explanations for particular *aptations* (characters fit for their current role). But this does require recasting 'adaptation' to the point that when compared to previous uses of the term Gould and Vrba may be talking apples and oranges, or at least orange slices and oranges. Dennett's approach does nothing to avoid Fisher's concern.

Let me illustrate an exaptation with an example from protein evolution (Gould and Vrba have had plenty to say about organ-level exaptations). I will describe a pair of homologous proteins that while structurally similar have evolved very different binding sites. These proteins show how available structures can be coopted for different functions. Studying proteins is a dizzying exercise in the complexities of function assignment. This is readily seen after a particular function has been identified (e.g. the fibroblast growth factor receptor) and then it turns out that you find that molecule interacting in ways you had not imagined when it was named (e.g. novel ligands for

the FGF receptor Kinoshita et al. 1995). Having been warned, let us push ahead.

A protein involved in transporting soluble antibodies from mother's milk across the lumen of the gut in mice and rats is called FcRn. It binds (is a Receptor for) the constant portion of the antibody molecule (dubbed *Fc*, as it was the crystallizable fragment), and is expressed by cells of the intestinal lumen in the *neonate*, thus FcRn. This protein is a heterodimer. The heavy chain consists of three globular domains ($\alpha 1$, $\alpha 2$, and $\alpha 3$) and is homologous (specifically paralogous⁵) to the MHC class I proteins. The class I proteins that present short peptides to T-cell receptors. The light chain is another well known molecule, $\beta 2$ microglobulin. There is some evidence that FcRn and MHC heavy chains diverged around the time of the most recent common ancestor to lizards and mammals (Ahouse et al. 1993; Kandil et al. 1995; Simister and Ahouse 1996). The two molecules while very similar in structure (Figure 1) interact with their ligands using different faces of the molecule. MHC binds short peptides between the two helices at the "top" of the molecule. FcRn's major contact areas with antibody involve the side of $\alpha 1$ and $\alpha 2$ and the N-terminal portion of the light chain (Burmeister et al. 1994b; Burmeister et al. 1994a).

If the common ancestor of FcRn and MHC class I performed the peptide binding function of current MHC then the binding domain of FcRn is an example of what Gould and Vrba call "... features of organisms [that] are non-adapted, but available for useful cooptation in descendants" (Gould and Vrba 1982), an *exaptation*. The domain that is coopted for the function of binding in FcRn is not used, as far as we know, for any kind of binding activity in the protein that it was derived from. In this context 'exaptation' does make a useful distinction (for more discussion of the nature of convergent function in protein evolution see Doolittle 1994).

Punctuated equilibrium

The ideas labeled 'punctuated equilibrium' (P.E.) have generated much discussion (Eldredge and Gould 1972; Gould and Eldredge 1993; Prothero 1992). P.E. begins with a straightforward central claim; morphological stasis is found throughout the fossil record. Adaptive gradualism does not lead us to expect this. This point is generally summed up as "stasis is data." Dennett confuses the issue (as others have) by focusing on the punctuations not the equilibrium. It is stasis that is surprising in a gradualist all features optimizing world. Dennett takes pride in proving that Darwin never believed in constant speedism (i.e. that all morphological change in every lineage occurs at the same rate). Unfortunately, this is not even remotely part of the punctuated equilibrium

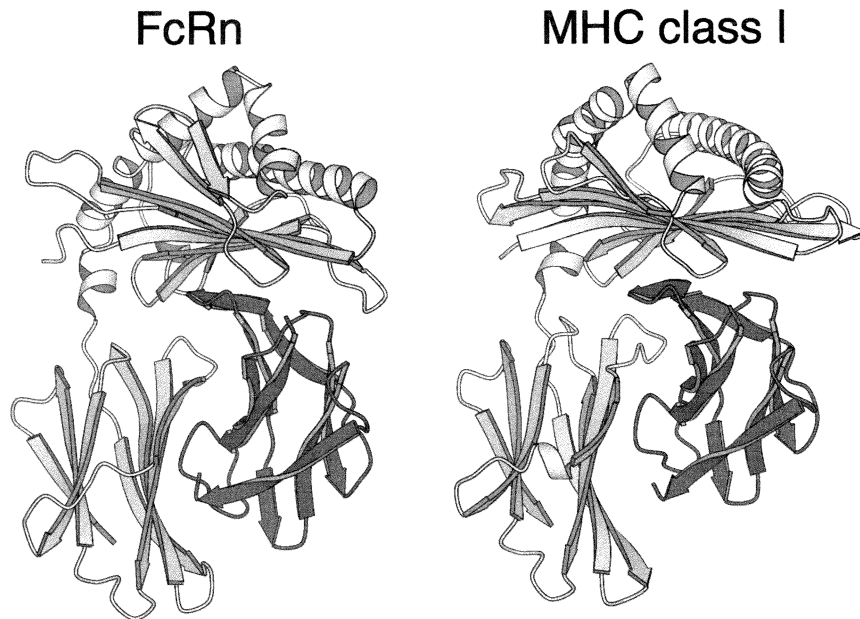


Figure 1. The FcRn and MHC class I heavy chains share a great deal of structural similarity. They both form heterodimers with $\beta 2$ microglobulin (the more darkly shaded smaller molecule), however the ligands they interact with when performing their primary function are very different. FcRn binds a portion of immunoglobulin G (a soluble antibody molecule) for transcytosis across a tight epithelium. Class I presents a short peptide to the T-cell receptor. The actual surface that interacts with ligand is completely different for the two molecules (see text). This illustrates one way that structures are coopted during evolution. (PDB files were aligned with *O* (Jones et al., 1991) and rendered with *MolScript* (Kraulis 1991).)

debate. How are we to explain stasis if we do not appeal to constraints in variation? One possibility is some form of stabilizing selection. But claiming that all stasis is due to stabilizing selection would be a controversial move. Dennett avoids it and offers instead the idea that species are intrinsically conservative, that species are tracking stable environments, and that stasis is due to a purely theoretical explanation (he does not elaborate). From this we are to conclude that, “It is quite clear, then, that equilibrium is no more a problem for the neo-Darwinian than punctuation” (p. 294). To the extent that Dennett is attempting to capture developmental constraints with his suggestion that species are intrinsically conservative he, again, embraces a position that Gould and others have articulated (Gould 1977; Hall 1992; Raff 1996).

Eldredge and Gould’s use of the term (and the resultant focus on) ‘punctuation’ may have been ill-advised. This word and Gould’s historical interest in Goldschmidt and Goldschmidt’s suggestion of large scale changes in morphology (hopeful monsters) has prompted some to conclude that saltationism

is an integral part of punctuated equilibrium. But simultaneous interests do not make a theory. It is important to distinguish gradualism in populations from the emergence of novel forms in individuals. There is strong consensus that, in sexual organisms, population variables change slowly as mutations, even those with a dramatic phenotype, sweep through the population. The textbook example of evolution, industrial melanism in the peppered moth (Kettlewell 1973), does not require that all individuals in the population are slightly darker in each generation. Rather, the claim is that the distribution of individuals in the population shifts from mostly light to mostly dark. While there are examples of “instantaneous” reproductive isolation in plants whose chromosome number changes and so lose the ability to cross with members of the parent population, this does not challenge the general consensus that most changes sweep through a sexual population over a number of generations. Any talk of group saltation has been *non sequitur* throughout this debate. Punctuation emphasizes the stability of characters for more than 90% of the time that a form is recognized in the fossil record.

Gould and others have taken the observation about stasis to make plausible “species sorting” as an explanation in macroevolutionary dynamics (Gould and Eldredge 1993; Gould 1994b). The important contention of punctuated equilibrium is what it has to say about trends in the fossil record. Gould and Eldredge claim that anagenesis, directional morphological change, “is only accumulated cladogenesis filtered through the directing force of species selection” (Gould and Eldredge 1977). Dennett lets himself get caught in a *cul-de-sac*, arguing about macromutational jumps and misses the argument about trends completely. Now Gould and Eldredge may be wrong to demand that their claim about rates (P.E.) is necessarily connected to their claim about macroevolutionary change. Species selection could, in principle, direct accumulated cladogenesis even if we did not have long periods of stasis. Still, it is easy to see how the pattern of stasis with interruptions motivates their macroevolutionary claim.

Punctuated equilibrium is one side of an argument about the connection of microevolutionary changes and macroevolutionary ones. It is not an argument about saltationism. The discussion regarding species selection is ongoing and enthusiasm for or against it seems to have everything to do with what scale you are examining. In explaining the diversity and abundance of various forms at a particular time and place we press a number of explanatory machines into service. Dennett, it seems, would insist that every (evolutionary?) feature of distribution and abundance is best explained by local adaptation. Is this true? Certainly not. We are then left with the issue of deciding what features to foreground as we tell the story of life (for an analysis of the struggle to tell this history well see O’Hara 1992). Parts of that story invite highlighting

gradual phyletic change where anagenesis is accumulated microevolutionary changes (e.g. the changes in primate limb structure, Fleagle 1988) others macroevolutionary dynamics (e.g. extinctions in the marine fossil record, Raup and Sepkoski 1982).

Contingency, disparity and the Burgess Shale

In describing Gould's Burgess Shale book (Gould 1989), Dennett writes;

Gould speaks here not just of unpredictability but of the power of contemporary events and personalities to 'shape and direct the actual path' of evolution. This echoes exactly the hope that drove James Mark Baldwin to discover the effect now named for him: somehow we have to get personalities – consciousness, intelligence, agency – back in the driver's seat. If we can just have contingency – this will give the mind some elbow room so it can act, and be responsible for its own destiny, instead of being the mere effect of a mindless cascade of mechanical processes! This conclusion, I suggest, is Gould's ultimate destination, revealed in the paths he has most recently explored (p. 300).

This does not resonate with my take on Gould's project. Contingency could just as easily be taken to undermine the best laid plans, defeating any personal agenda. All of this driver's seat talk seems misdirected.

It misses the breadth of Gould's Burgess Shale book to touch on only two topics. But we will follow Dennett as he focuses on contingency and disparity. Contingency in these debates refers to the crucial importance of historical "accidents" in explaining the distribution of life. Dennett takes this claim as obvious, implying that Gould is trading in trivialities. Gould compiled several examples of inevitable progressivist human (male) centric iconography, at the outset of *Wonderful Life*. That these examples are so readily available seems to justify making the point about contingency to his lay audience and possibly to his professional audience as well.

I arrived at my lab on a recent Sunday morning to a scene of fire fighters, tractors and trucks from the gas company blocking off the road to the university. The campus safety officer, who ushered me through, told me that a squirrel climbing on power lines was "zapped" by the main transformer. It fell to the ground in flames. There was a small gas leak from the gas main, at the spot where the squirrel came to rest. The gas caught on fire and an explosion was feared. The fire department and the gas company were called in and the street upstream of the fire was eventually dug up. A power spike associated with these events started every alarm (freezers, incubators, . . .) on my floor ringing and many computers went down. Strong contingency,

is in part the claim that “flaming squirrels” are important in explaining the distribution and abundance of organisms through the history of life.

The issue of disparity arises when we want to assess the direction and magnitude of morphological change through time. More generally, what are the dynamics of variation in the lineages in the tree of life? Mark Ridley in his review of *Wonderful Life* complained that Gould had energized his argument (that the diversity of fauna in the Burgess shale is greater than what we see between extant lineages) with a mistaken criterion; the use of higher taxonomic categories (Ridley 1990). I agree with the point that Ridley raises. This problem in systematics (what, if anything do grade based higher level taxa mean) is still open (dive into this discussion with de Queiroz and Gauthier 1990). Gould claims to have other criteria (Gould 1991b). Among these he notes that cladograms for these groups use a large number of loss-of-feature character state transitions. In doing so he implicitly raises the thorny issue of character weighting in a cladistic framework. Both sides of this debate are worth spending time with (Ridley 1993; Gould 1993b; McShea 1993). I would encourage anyone even casually interested in this issue to get a copy of the wonderful coffee table book on the Burgess (Briggs et al. 1994) and see how *you* would classify this fauna (then compare the claim that “the problematic Cambrian taxa do not show any remarkable morphological separation [from “unproblematic” lineages]” (Briggs and Fortey 1989, p. 243)).

Dennett does not address any of the issues raised under the term “disparity.” He does, however, hammer away at contingency (which, remember, he thinks is a trivial point); “evolution can be an algorithm, and evolution can have produced us by an algorithmic process, without it being true that evolution is an algorithm for producing us” (p. 308). If you are attracted to his use of the word algorithm to mean process then once again he is falling into line with Gould, though you would not gather this from his tone. I think it falls to Dennett to show that the lay audience for Gould’s books have all long ago rejected any teleological leanings and so do not need to be reminded that humans are not the point of the nature’s narrative. Even more important, there is no narrative in the traditional sense (see discussion in O’Hara 1992). This is what Gould, who knows how to tell a good story, must grapple with. How do you deliver in an engaging way the message that there is no simple narrative, no simple moral to be drawn from the history of life?

Gould and Dennett share the desire to remove the comfort of the idea that the world exists solely for us and that humans are the inevitable result of evolution. Though (*contra* Gould) Dennett may be suggesting that “air-breathing, land-inhabiting vertebrates” that are “intelligent, language-using, technology-inventing, culture-creating beings” are inevitable (p. 307). Though he avoids committing himself to the latter.

The probability that our world is as we find it is, depending on one's temper, either one, close to zero or just a badly formed problem. My temper is with James who suggests that we must not assign probability to events that have occurred (James' response to Shaler on this point was discussed in Gould 1991a). Dennett suggests that Alife models, "which do allow us to rewind the tape again and again," is a way out of this problem (p. 305). Surely Dennett is not suggesting that we are in a position to model the wholly contingent elaborate tree of life. The computational effort for this endeavor is easily NP-complete and the input to this problem is huge. It is not clear to me what he has in mind. Even elaborate cellular automata or huge Alife simulations would not resolve the issue, whether they showed the importance of history in long range dynamics or not.

In making the case against teleology and inevitable progress Gould insinuates these ideas more gently, without insisting that his religious colleagues are lazy and dishonest; compare "those evolutionists who see no conflict between evolution and their religious beliefs have been careful not to look as closely as we have been looking, or else hold a religious view that gives God what might we call a merely ceremonial role to play" (p. 310). This gratuitous slap at the symbolic and mythic traditions that many people use to find personal (and importantly, social) identity and meaning has no bearing on the evolutionary questions under discussion and is simply part of Dennett's speculative and impoverished reconstruction of Gould's "religious yearnings."

Attention to contingency does challenge certain notions of progress. If this challenge stands, it would undermine an important aspect of Dennett's algorithmic conception. Dennett would be left to argue that to realize a particular design, he must wait for "diffusion" through Mendel's library to generate morphotypes that bump into the relevant part of design-space and instantiate his adaptation. This process looks progressive only if you retroactively attend solely to the specific history that led to your adaptation (e.g. composite flowers or Dennett-like philosophers). I read Dennett as preferring a selection driven process that results, frequently (inevitably?), in the emergence of robust and complex designs. If I am misreading and his attraction to 'algorithm' demands far less than this and so reduces to merely a 90s cyberpunk way of saying 'process' then there is not even a tempest in this teapot. Certainly the computer engineering community hopes that optimization using local hill climbing (for problems where a fitness function can be specified) will generate beautifully crafted solutions (by loose analogy with nature). This is an interesting possibility but the proof will be in working implementations not in simplifying nature until the caricature is suggestive of the current computer model.

Dennett has yet to demonstrate that the larger population of biologists, Gould's lay audience or engineers who wish to emulate evolution have nothing to learn from spandrels, exaptation, punctuated equilibrium, or an emphasis on contingency. Additionally he will need to argue more convincingly that Gould's "mild correctives" were an extant and vivid part of the synthesis to make his criticisms stick.

The morphological neighborhood and the adaptationist tale

I have insisted that to understand evolution we have to attend to the dynamics of the genotype and the relationship between genotype and phenotype. What do we know about genic variation and the resultant accessible morphological neighborhood? The last few years have yielded a bounty of information. Much of this work has come thanks to years of *Drosophila* genetics. That this work has such wide application is itself a testament to the deep homologies in the tree of life.

One of the important parts of the adaptationist tale has been the idea that similar environments can generate similar solutions (convergence). Dennett even takes convergence to be an example of replaying the tape of life (p. 306). Examples that are often marched out involve the similar forms of marsupial and placental mammals (the placental rabbit that moves just like a kangaroo, the marsupial saber-toothed cat, . . .) or the streamlining that is shared by dolphins and tuna. A recent example is the variation of Malaysian pit viper venom tied to local prey availability (Daltry et al. 1996). Not bad examples. The other side offers long lists of organisms that do not have convergent partners, my favorite is the woodpecker. What happens when one of our favorite examples from one column is yanked into the other?

The evolution of the eye

The evolution of the eye stood for years as a paradigmatic example of independent evolutionary paths fulfilling the same need. Vertebrates and mollusks have single lens eyes (though the photoreceptive cells under the lens have opposite orientation) while insects have compound eyes. These differences had been taken to imply that the eye evolved (independently) numerous times (Salvini-Plawen and Mayr 1977). Now it looks (pun!) as if the large morphological differences share a common developmental pathway for eye morphogenesis. The evidence for homology in the developmental pathways comes from looking at the orthologous protein in mammals and flies (discussed in Halder et al. 1995; Gould, 1994a). This particular protein, called

eyeless for its mutant phenotype in fruit flies, was shown to give rise to eyes on wings and legs when expressed ectopically. So it must be near the top of the developmental hierarchy for eye development. A mutation in the orthologous protein in mammals results in abnormal formations of the eye. The mouse protein, when expressed ectopically in the fly, also results in production of fly eyes! The original report indicating homology between mouse (*Pax6*) and fly (*eyeless*) (Quiring et al. 1994) has been reinforced by careful examination of the role of *Pax6* in development (Quinn et al. 1996). What do we take from this deep homology? Does this mean that there is no selection – of course not! But it does sensitize us to the importance of the lineage. It suggests that if there is even the slightest backdrop that can be utilized in a new context it will be. Maybe selection does not have the latitude that we often give it. If the *Pax6* cascade had not been extant in the lineage that led to insects, chordates and mollusks would there have been eyes in these lineages?

Not everyone has embraced this reading of the *eyeless* homology. It has been argued that the position I reviewed “does not consider convergence (analogy) as an alternative to conservation (homology) in attempting to account for the strikingly similar roles, in eye development, of *eyeless* in *Drosophila* and its homologs in vertebrates” (Dickinson and Seger 1996). That the proteins from mouse and fly are interchangeable, that they share splice sites, and that they share much of their sequence strongly argues for homology (Gehring 1996).

The breakdown of the standard story about independent origination and convergence during adaptive radiations is being noticed frequently in developmental evolutionary genetics from the well known homeotic genes (Carroll 1995) to the *Pax6/eyeless* story. We are looking at situations where identical ancestral conditions seem to facilitate subsequent adaptations, we might call this facilitated parallelism. I suspect that this will become an ever more important part of evolutionary explanations.

The evolution of the ear and other atavisms

Can the variation that selection operates on include a visit to the past? Anyone interested in animal development these days will find themselves learning about a group of genes called the *Hox* genes. Originally identified by transformations of body segments, these mutants underline the ability of small genetic changes to have profound morphological consequences (not news – but underlined nonetheless). Even more fascinating is recent work showing that changes in some *Hox* genes can result in ancestral morphologies reemerging (atavism). The ancestral condition for the mammalian ear ossicles is a single bone homologous to the stapes (stirrup). The familiar

malleus (hammer) and incus (anvil) are derived from the articular (lower jaw) and quadrate (upper jaw). Scrambling the *Hoxa-2* gene in mice changes the pharyngeal arches during development resulting in morphology much like the ancestral condition (Lufkin et al. 1992). A similar thing is seen in *Hoxb-8* and *Hoxc-8* manipulations where rib and vertebral atavisms are seen (Pollock et al. 1995). The ancestral one wing per segment can be seen in manipulations of insect *Hox* genes (Carroll et al. 1995). The hypothesis that flowers derived from leaf tissue is lent support by plant mutants that show whole flower structures where anthers, stamens, petals and sepals can be replaced by leaf tissue (Weigel and Meyerowitz 1994). This should not be taken to imply that the intricate derived states (getting the four whorls of flower tissue from leaf tissue) are only a couple of mutations away from the ancestral condition, rather these mutations emphasize that certain (surprising?) forms are close (only a few mutations away) to extant forms and evolutionary dynamics may be dependent on the possibilities that are “stored” in these developmental pathways (for an introduction to atavisms see Day 1995).

I raise the examples of deep homology and atavism to remind you where one of the foci of current discussion in evolutionary biology rests. The argument is not in some kind of tension between mystics and realists. It is hard to cram all of these details in to a hyper-selectionist framework. Adding the many facets required by these new observations and experiments demands the a more elaborate often perplexing position. Gould has been working from the paleontological end to widen evolutionism (in both the patterns we recognize and then need to explain and in the tentative explanations we deploy). This task has been joined by the developmental geneticists who are struggling to understand the way small steps through genotype space result in both large and small steps in morphospace.

Dennett’s immoderate “falsehoods”

I will end where Dennett begins his chapter on Gould;

If you believe: (1) that adaptationism has been refuted or relegated to a minor role in evolutionary biology, or (2) that since adaptationism is ‘the central intellectual flaw of sociobiology’ (Gould 1993a, p. 319), sociobiology has been utterly discredited as a scientific discipline, or (3) that Gould and Eldredge’s hypothesis of punctuated equilibrium overthrew orthodox neo-Darwinism, or (4) that Gould has shown that the fact of mass extinction refutes the ‘extrapolationism’ that is the Achilles heel of orthodox neo-Darwinism, *then what you believe is a falsehood*” (p. 265) [emphasis in the original].

It is relevant to note that, in Dennett's words, "The real Gould has made major contributions to evolutionary thinking, correcting a variety of serious and widespread misapprehensions, but the mythical Gould has been created out of the yearnings of many Darwin-dreaders, feeding on Gould's highly charged words, and this has encouraged, in turn, his own aspirations to bring down 'Ultra-Darwinism,' leading him into some misbegotten claims" (pp. 265–266). Dennett is suggesting that there is a flow of ideas and attitude between the real and mythical Gould.

My experience does not include Gould as the anti-Darwinian pied piper. To the extent that I see mythic confusion it is members of the cult of the gene, who have gone even(!) beyond Dawkins with single genes for rape, sexual orientation, IQ, obesity . . . (for an attempt to stem this see Rose 1995). None of these one simple gene: one complex trait world-views is required by ultra-selectionism. If you make your notion of traits and 'gene' intricate enough you can salvage the excesses of gene-centrism. They are, however, the result of popularized reductionist pan-selectionism much sooner than anti-Darwinism is the result of Gould's writings.

By way of review let us examine the falsehoods in order:

- (1) Gould has argued that adaptationism is less important than pan-adaptationists would claim. Dennett thinks that adaptationism is the only game in town, provided you make adaptationists sure to avoid just-so stories, admit that everything is an exaptation, and allow numerous historical, developmental and structural constraints.
- (2) Gould has argued strongly against prejudice masked as science in sociobiology. Dennett may or may not think that sociobiology is flawed, but (surprisingly?) does not think that sloppy hyperadaptationism (what Gould clearly means by 'adaptationism') is its chief problem. He does not tell us what the central intellectual flaw is. Maybe he thinks there are so many flaws that identifying a central one is a waste of time.
- (3) Did Gould and Eldredge really claim that punctuated equilibrium overthrew neo-Darwinism? This depends in part on how 'neo' you go. Dennett is happy to filigree adaptationism to include any new information. If you are going to argue that an ever expanding neo-Darwinism holds every new observation then this does become a strongly historical debate. Was stasis really a vivid prediction of the gradualist world view? Giving a name (punctuated equilibrium) to a common pattern (stasis) in the fossil record has required additional hypotheses to be deployed by gradualists. A discussion about the dynamics of morphological change is precisely what Gould and Eldredge wanted to bring about.
- (4) Does Dennett mean that extrapolationism is not an Achilles heel for adaptationism or that mass extinctions are not the way to show this? I think

even Gould would be happy to grant that mass extinctions due to external causes (meteors etc. . . .) are obvious ways to undermine a cluster of adaptations. While these events do undercut extrapolationism this is not nearly as interesting as the claims about developmental constraints and canalization that make extrapolationism so difficult to sustain. Maybe Dennett wants to argue that successful extrapolationism should not be used to judge the success of neo-Darwinism. If so, he is again agreeing with Gould. Precious few biologists think that you can predict future shapes and adaptations using only natural selection. Maybe armchair biologist-philosophers are more sanguine about the possibility of predicting without reference to an empirical base. I hope that my comments about the intricacies of developmental genetics have helped to disabuse the discussion of this hope (an historical review of the relationship between development and evolution can be found in Gottlieb 1992).

As we reposition these “devastating” falsehoods on a more sober foundation, it is clear that Gould has had a salutary effect on these debates, even though he has not necessarily won them. Many others have also worked to elaborate these issues (for a recent discussion see Eldredge 1995). So while I agree that Gould has not proved Dennett’s falsehoods, I am not impressed by this claim. Dennett has chosen to argue the overstated. Are the bystanders, who Dennett thinks believe the four false hoods as presented, served by his intemperate critique? I would suggest that Gould himself has given a more nuanced reading to these topics. There is no need to become “pan-Gouldian” in the face of Dennett’s excessive criticism of Gould’s doppelgänger. At the same time the suggestion that these issues are resolved by the *a priori* commitment to all-explanatory selectionism is foolish. We can keep the salutary materialization of teleology offered by selectionism even as we develop a selectionist model that is open to a number of levels, as is appropriate for the traits under consideration. We can insist that the details of genetics, embryology and ecology are important. We can attend to the many ways that all things are not equal or at equilibrium and engage the contingent nature of the evolutionary process (for examples of attempts to do this see Waddington 1959; Amundson 1989). This has consistently been the position of interested biologists, even as emphasis has flowed from one area to another (Depew and Weber 1995).

I should add that I do not believe Gould intends to prove Dennett’s falsehoods, so his failure to do so is not particularly damning. Dennett might agree but insist that the “interested bystanders” believe Gould has proved them and so now Gould is responsible for leading them back from these shrill misreadings. According to Dennett, Gould has abdicated this responsibility and so Dennett must take up the task. This line of reasoning really does hinge

on showing that Gould's writings have been thus (mis) perceived. Even if it were the case, Dennett's chapter does not seek to help readers understand the "falsehoods" in a way that gives them a sense of the scientific issues that are under discussion. If he were really interested in allaying the public's confusion then this chapter is an opportunity squandered.

While I share Dennett's enthusiasm for the wonderful possibilities that natural selection suggests, I do not share his willingness to push an anemic folk selectionism as a universal explanation for the distribution, abundance and dynamics of living forms (compare more nuanced and careful examples found in Keller and Lloyd 1992; Sober 1994a; Brandon 1990). I do not want to blunt Dennett's enthusiasm for evolutionary biology – champions are to be prized. Though I fear that his *a priori* commitment to context-free selectionist theories induces him to walk in with too much baggage. "The action of thought is excited by the initiation of doubt, and ceases when belief is attained . . ." (Peirce 1932). My hope is that he can find a way to put some of those bags down, sit a spell, luxuriate in the intricacies of the biological world and let a little doubt shine in.

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Notes

¹ Matthew's passage is reprinted in the Historical Sketch found in Darwin's *Origin*, from the third edition onward (Darwin, 1866).

² To get a sense of what is currently happening in the artificial life, genetic algorithm, cellular automaton communities visit <http://www.krl.caltech.edu/~brown/alife/>, <http://alife.santafe.edu/>.

³ Jonathon Roughgarden makes a similar point for ecology; "Competition models, if ever fully validated, license an inference in one direction only. The models have the logical form 'if competition and A, then P,' where A represents some additional premises and P represents some predictions, usually pertaining to whether coexistence between certain species is possible and, if so, to the degree to which they use the same resources. Current theory does not license the converse inference, that is, inferences of the form 'if P, then competition.' No competition model has yet predicted a pattern of species competition that is logically diagnostic of competition" (Roughgarden 1986, p. 493).

⁴ Lest you wonder whether such language exists let me remind you. “On the one hand we have the beguiling image of independent DNA replicators, skipping like chamois, free and untrammelled down the generations, temporarily brought together in throwaway survival machines, immortal coils shuffling off an endless succession of mortal ones as they forge towards their separate eternities. On the other hand we look at the individual bodies themselves and each one is obviously a coherent, integrated, immensely complicated machine, with a conspicuous unity of purpose. A body doesn’t look like the product of a loose and temporary federation of warring genetic agents who hardly have time to get acquainted before embarking in sperm or egg for the next leg of the great genetic diaspora” (Dawkins 1989, p. 234).

⁵ The paralogy and orthology distinction was introduced 25 years ago to distinguish two kinds of homology in proteins (Fitch, 1970). While orthology has the traditional meaning of morphological homology, paralogy is meant to cover those situations when a gene duplication allows related proteins to evolve independently within the same lineage. Orthologs are found in different individuals and paralogs can be found in the same individual (this distinction is reviewed in Patterson 1987).

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