Richard G. Delisle *Editor*

The Darwinian Tradition in Context

Research Programs in Evolutionary Biology

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Preface

In the wake of the Evolutionary Synthesis constituted in the 1930s, 1940s, and 1950s, historians and philosophers of biology have devoted considerable attention to the Darwinian tradition linking Charles Darwin to mid-twentieth-century developments in evolutionary biology. This historiographical focus may not be wholly coincidental, given the professionalization of the fields of history of science and philosophy of biology that accompanied the post-1960 era. Since then, more recent developments in evolutionary biology challenged the heritage of the Darwinian tradition as a whole or in part. Predictably, perhaps, this was followed by a historiographical "recalibration" by historians and philosophers toward other research programs and traditions since Darwin's time.

As this recalibration is going on, it is difficult not to have the impression of confusion or dismay regarding what exactly happened in evolutionary biology. In order to dispel some of this confusion, it seems timely to reunite in this volume synthetic contributions concerned with historical, philosophical, and scientific issues. It is the main goal of this volume to contextualize the Darwinian tradition by raising such questions as: How should it be defined? Did it interact with other research programs? Were there any research programs whose developments were conducted largely independently of the Darwinian tradition? Authors of this volume explicitly reflect upon the nature of the relationship between the Darwinian tradition and other parallel research traditions.

A more traditional approach to the topic might have required organizing the volume's contributions along themes like the "main Darwinian tradition," "non-Darwinian theories," "evolutionary biology in national traditions," "pre-synthetic developments," the "Evolutionary Synthesis," or "post-synthetic developments." As much as this was the editor's original intention, many contributions collected here suggested to him that historiographical studies are currently moving beyond this more traditional outlook, pointing at other intellectual avenues. In order to acknowledge this historiographical shift and foster new thinking on these matters, the papers are organized in a sequence that highlights how the boundaries of the various research programs within evolutionary biology are apparently more porous than often assumed. The papers can be meaningfully arranged into two main threads:

1. Part I: The view that sees Darwinism as either originally pluralistic or acquiring such a pluralism through modifications and borrowings over time.
2. Part II: The view blurring the boundaries between non-Darwinian and Darwinian traditions, either by holding that Darwinism itself was never quite as Darwinian as previously thought or that non-Darwinian traditions took on board some Darwinian components, when not fertilizing Darwinism directly.

Between a Darwinism reaching out to other research programs and non-Darwinian programs reaching out to Darwinism, the least that can be said is that this crisscrossing of intellectual threads blurs the historiographical field.

In Part I of this volume, Timothy Shanahan argues in "Selfish Genes and Lucky Breaks: Richard Dawkins' and Stephen Jay Gould's Divergent Darwinian Agendas" that Darwin's Darwinism was polymorphic or pluralistic enough to legitimately accommodate future developments as divergent as those opposing Dawkins's genetic reductionism and Gould's holistic hierarchical thinking. In a similar vein, John Alcock's "The Behavioral Sciences and Sociobiology: A Darwinian Approach" holds that Darwin's strong adaptationist stance has been successfully maintained in the behavioral sciences but by applying it to new phenomena, this time involving both genetic entities and individual organisms (and excluding higher entities), as seen in scholars like N. Tinbergen, W. Hamilton, E. O. Wilson, and R. Dawkins, among others. Embracing the same historiographical view, but simultaneously allowing for an expansion of Darwinism, David Depew argues in his "Darwinism in the Twentieth Century: Productive Encounters with Saltation, Acquired Characteristics, and Development" that Darwinism continually and successfully met the challenges of evolutionary developmentalism, the inheritance of acquired characteristics, and saltationism by taking on board new explanatory components but within its own ways of doing things. This evolving and flexible Darwinian tradition is presented in Massimo Pigliucci's "Darwinism after the Modern Synthesis" as having permitted the transition from the Evolutionary Synthesis to the Extended Evolutionary Synthesis—incorporating new phenomena, mechanisms, and concepts—yet without moving beyond the confines of the same paradigm. This view is also shared by Adam Van Arsdale in his "Human Evolution as a Theoretical Model for an Extended Evolutionary Synthesis," who uses the case of human evolution to reflect upon the nature of this theoretical expansion when it comes to integrating unique features such as encephalization, as well as nongenetic and flexible behaviors.

In Part II of this volume, Richard Delisle holds in "From Charles Darwin to the Evolutionary Synthesis: Weak and Diffused Connections Only" that key Darwinian scholars (including Darwin himself) and some proponents of the Evolutionary Synthesis were also simultaneously committed to ideas that were not particularly Darwinian, making the boundary between Darwinian and non-Darwinian ideas porous. Indeed, Georgy Levit and Uwe Hossfeld argue in "Major Research Traditions in Twentieth-Century Evolutionary Biology: The Relations of Germany's

Darwinism with Them" how evolutionary biology in German-speaking countries which centered around notions like "type," "monism," and "holism" variously integrated some Darwinian elements, especially as seen in E. Haeckel, L. Plate, and B. Rensch.

What used to be seen in the traditional historiography as past blind intellectual alleys are increasingly seen as possible early insights now in need of some sort of revival. In "Alternatives to Darwinism in the Early Twentieth Century," Peter Bowler expands on how important Lamarckism, Orthogenesis, and Saltationism had been for evolutionism in the late nineteenth and early twentieth centuries, some of these ideas now being reconsidered. In a similar vein, Maurizio Esposito holds in "The Organismal Synthesis: Holistic Science and Developmental Evolution in the English-Speaking World, 1915–1954," how a fairly robust tradition founded on the centrality of organismic biology persisted in the English-speaking world throughout the first half of the twentieth century—largely independently of what was perceived as a reductionistic and mechanistic neo-Darwinism—a tradition revived today in Evo-Devo under different guises. And precisely because these research programs overlap, one strain of the multifaceted, robust, and long-lasting Lamarckian movement in France paved the way for important innovations in molecular biology in the 1950s and 1960s, as argued in the "Lamarckian Research Programs in French Biology (1900–1970)" of Laurent Loison and Emily Herring. This situation erected a bridge between two movements usually opposed over the divide of "hard inheritance" (molecular biology) and "soft inheritance" (Lamarckism), Darwinism being traditionally associated more closely to the former than the latter. In "Molecularizing Evolutionary Biology," Michel Morange further reflects upon the nature of the interrelationship between molecular biology and evolutionary biology, arguing that the former has insinuated itself ever more profoundly into evolutionary questions since the 1960s, to the point of significantly modifying the character of the so-called Modern Synthesis.

Whether or not the Darwinian/non-Darwinian divide is judged to have been more porous than often assumed, some research programs managed to grow without much contact with Darwinism, until recent bridges were established. In "Cells, Development, and Evolution: Teeth Studies at the Intersection of Fields," Kate MacCord and Jane Maienschein offer an alternative to the narrative of a "gene-centered" evolutionary biology by recounting how development, evolution, and cells were brought together throughout the twentieth century. In a different case study, Ulrich Kutschera's "Symbiogenesis and Cell Evolution: an Anti-Darwinian Research Agenda?" explains how the research program on the rise of more complex cells in the early history of life (the symbiogenesis theory) was for too long conducted from the viewpoint of an anti-Darwinian agenda.

Just as the first two contributions to this volume argued that Darwinism's original pluralism was sufficient to explain a wide scope of evolutionary phenomena, so the volume closes with Derek Turner's analysis in "Paleobiology's Uneasy Relationship with the Darwinian Tradition: Stasis as Data" in which he holds that Darwinism today has been destabilized by what paleobiology brought to evolutionary studies since the 1970s.

Irrespective of how one understands the Darwinian tradition, most contributions to this volume show the extent to which the various research programs in evolutionary biology are deeply pluralistic, often being composed of many overlapping or semi-distinct intellectual strains, suggesting an overall picture of a tight and complex network of ideas across evolutionary biology.

Lethbridge, Canada Richard G. Delisle

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Introduction: Darwinism or a Kaleidoscope of Research Programs and Ideas?

Richard G. Delisle

Who controls the past controls the future: who controls the present controls the past.
George Orwell, Nineteen Eighty-Four (1949)

The Preface to this volume has provided an exposition of the project, the rationale for the order of presentation of the papers, and a brief description of each paper. In this introductory chapter, I would like to embrace a more personal view about what seems to have emerged in this research area with the assistance of insights provided by some of the contributions included here.[1]

We know too well that history is continually being rewritten in light of a changing present. The current turmoil in evolutionary biology about evo-devo, epigenetic inheritance, holistic manifestations, and stochastic modes of change, for example, can only serve as a stimulus for revisiting the past in search of antecedents. Yet, ironically, this salutary quest under way reveals that what we thought were novel claims may not be entirely so. Indeed, if the currently sought pluralism for accommodating recent developments in evolutionary biology is found to have existed in the past, then the past and the present of evolutionary biology cannot be entirely incommensurable with one another. I would argue that the current phase in evolutionary biology may be characterized as follows: after initial claims of novelties proclaimed during the last decades, historians and philosophers are in the process of researching the past in order to see how the pieces of the overall puzzle fit together. Suddenly, it seems, the past comes hunting for the present, generating complex interactions between the two. The jury is still out on what the outcome of these reflections will be. Darwinism, today, has never been more of a "moving target" (Burian 1988: 250).

[1]The view presented here is solely my own. The reader is strongly encouraged to discover what other authors have had to say for themselves in this regard beyond the brief summary already presented in the Preface.

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In a sense, evolutionary biology today fell victim to events occurring between the 1930s and the early 1960s, known collectively as the Evolutionary Synthesis. The synthesists proclaimed themselves to have reached a theoretical unity of unprecedented breadth, and, serendipitously, the newly rising professionalization of history and philosophy of biology offered the synthesists an amplifier for their voice. As Mark Largent (2009: 4, 8) writes:

> The architects of the modern evolutionary synthesis and the historians who followed them constructed a discontinuous history of their discipline... By unquestionably interpreting early twentieth-century evolutionary biology through the lenses of the triumphalist synthesizers, [historians of biology] distort our understanding... and commit a historiographical blunder... We need to go back to the generation prior to synthesis... and free ourselves from the propagandistic claims made by the mid-twentieth century synthesizers.

The Evolutionary Synthesis stands in the middle of twentieth century like a horizontal cut, defining what came before and after. In fact, the horizontality of the standard view is such that distinct yet overlapping intellectual layers have been proposed: the first synthesis (mathematical population genetics plus selectionism in the 1920s and 1930s), the second synthesis (adding organismic biology in the late 1930s and 1940s), and the hardening of the synthesis (focusing nearly exclusively on selectionism in the 1950s and after). The first and second phases are sometimes reunited together under the epithet of the "pluralistic phase of the synthesis," in opposition to its hardened and later phase (Provine 1985; Gould 1983; Mayr 1982).

It is not my aim to criticize the historians and philosophers of the first generation: after all, we are largely building upon their work. Rather, I am merely raising the obvious historiographical point that if the Evolutionary Synthesis is not what has been advertised, it is only natural that what has been left out of the official story needs to be reinserted into the narrative. As much as the Evolutionary Synthesis seems to be an established reality in the mind of many scholars, it should be noted that a small but significant number of them question its historiographical reality. The following quotes will make this point more obvious:

> There was more to the synthesis project than work done by the so-called architects or the supposed merger of Mendelian genetics and selection theory via mathematical theory. The evolution books of the revived Columbia Biological Series have been far too dominant in the synthesis historiography. There was more—much more—to evolutionary studies in the 1920s and 1930s than is suggested in the mainline narratives of the period... I propose we abandon the unit concept of 'the evolutionary synthesis'... What do we find when we remove the organization this master narrative imposes? What is gained if we presume the unit concept 'the evolutionary synthesis' obscures more than it clarifies (Cain 2009: 621, 622, 625).

> [O]ur analysis of Rensch's theoretical work can be seen as a case study of the heterogeneity of the Modern Synthesis. The scale of this heterogeneity is, in fact, so significant that the picture of the Synthesis as a unified movement needs to be deconstructed. The idea that the Synthesis is an interdependent body of beliefs covering not only all major branches of empirical biology, but also the general questions of methodology, history, and philosophy of science, collapses in front of such hardly compatible world views as Rensch's and Mayr's. It is also important to remark that all parts of their theoretical constructions were equally important for their arguments in favor of Darwinism... Rensch's holistic

> theoretical system is in almost direct opposition to Mayr's philosophy, coinciding with it only on the purely phenomenological level and in empirically testable explanations. Indeed, beyond the elementary level of accepting mutation, recombination, geographical isolation, and natural selection as the most important factors of evolution, there is little that unites them considering deep philosophical differences between their systems. This makes the picture of the Synthesis as an amalgamation of closely interrelated theoretical systems very questionable (Levit et al. 2008: 320–321).

> [B]eneath a superficial appearance of unity among neo-Darwinians [like J.S. Huxley, Th. Dobzhansky, B. Rensch, G.G. Simpson, and E. Mayr] lies genuine *foundational* oppositions in the epistemological and metaphysical choices made by them… (1) oppositions in the predominate epistemology (descriptive/synthetic, ontological monism, or etiological); (2) oppositions in the interpretation given to the direction of evolution; (3) oppositions in the scope of application of the evolutionary principles (to the biological realm only or to the entire cosmos); (4) oppositions in the nature of the evolutionary process in time (open-ended, cyclical, or stagnating)… [N]eo-Darwinism… is not a movement from which all neo-Darwinians sprung, but is rather a meeting place from which each drew evolutionary mechanisms in order to insert them in distinct and quasi-incommensurable… frameworks (Delisle 2009a: 120).

In addition to what has already been said, one will find among the various implicit and explicit points made by Mark Largent (2009), Joe Cain (2009), George Levit, Michal Simunek, and Uwe Hossfeld (2008), and Richard Delisle (2008, 2009a, b, 2011, 2017) the following:

1. Substantial synthetic work was already conducted before the Evolutionary Synthesis (ES) by evolutionists, although these were excluded from the ES by its official promoters.
2. The synthesists retroactively created an intellectual vacuum and a discontinuity before the Evolutionary Synthesis, presenting many pre-1930 ideas as misguided.
3. Architects of the Evolutionary Synthesis were actively engaged in rhetorical arguments, a kind of self-promotion: they advanced a certain narrative regarding what they believed themselves to have achieved, which was later taken up and echoed by subsequent historians and philosophers.
4. The Evolutionary Synthesis may well be better conceived as a political or sociological event than as a conceptual one.
5. The Evolutionary Synthesis became a straw man for its post-1960 opponents, thus reinforcing its political utility. It is indeed always useful to have an enemy against whom one can formulate opposite ideas, even if that enemy does not exist.

In short, skeptics[2] of the Evolutionary Synthesis have raised doubts about both its internal/conceptual coherence and its external/contextual isolation from the rest

[2]By referring to my colleagues Mark Largent, Joe Cain, George Levit, Michal Simunek, and Uwe Hossfeld, as "skeptics" of the Evolutionary Synthesis, I am not trying to co-opt their views or subsume them under my own understanding of the issues. Nor do I pretend there exists a single and unified front against the traditional historiography. Ultimately, only additional concerted work

of the field of evolutionary biology. Whether or not one is prepared to follow these analyses to their logical conclusion—the abandonment of the notion of an "Evolutionary Synthesis"—it seems to this author that a call for a historiographical shift is at least not only reasonable but also an emergent reality of recent studies. This proposed shift would move us from an evolutionary biology conceived around temporal horizontal cuts or layers (Darwinian revolution, eclipse of Darwinism, phases of the Evolutionary Synthesis, post-synthetic developments) to an analysis of vertical intellectual movements and ideas evolving in parallel and interacting in complex ways. Indeed, this shift toward historiographical continuity is supported by a fascinating crisscrossing of intellectual threads in evolutionary studies: while some scholars argue that Darwinism evolves by co-opting ideas from competing research programs, others hold that non-Darwinian programs have availed themselves of Darwinian explanatory components. For instance, David Depew (2017) argues in this volume that:

> Darwinism's continued dominance in evolutionary science reflects its proven ability to interact productively with these other traditions, an ability impressed on it by its founder's example. Evolution by sudden leaps (saltations) is alien to the spirit of Darwinism, but Darwinism advanced its own agenda by incorporating and subverting saltationist themes. Similarly, Lamarckism's belief in the heritability of acquired characteristics has been discredited, but some of the facts to which it seems congenial reappear in genetic Darwinism as phenotypic plasticity and niche construction.

The contribution of Massimo Pigliucci (2017) to this volume is of a similar spirit, promoting what he calls an Extended Evolutionary Synthesis which incorporates within Darwinism explanations about processes such as epigenetic inheritance, self-organizing biological phenomena, and self-emergent properties.

Now, looking at things from the viewpoint of non-Darwinian theories, Peter Bowler (2017) writes in this volume:

> When the author of this chapter first began to study the 'eclipse of Darwinism' in the 1980s the triumph of the modern Darwinian theory made it easy to dismiss the alternatives as blind alleys into which scientists had been led temporarily... In recent decades our interpretation of this episode has been transformed by the emergence of evolutionary developmental biology. This has reopened issues once marginalized by genetics and the modern Darwinian synthesis. Some enthusiasts see 'evo-devo' as reintroducing a role for non-selectionist factors such as Lamarckism, while even those skeptical of this view acknowledge that the older theories were not as wide of the mark as was once claimed... We can now appreciate that this concern was not merely a distraction from the main business of evolutionary biology... The historians who look back at these early non-Darwinian theories can, perhaps, see evidence of ideas being explored that may once again come to play a role in evolution theory.

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along these lines could clarify this question; organizing a symposium in a near future may be a timely idea. This being said, it is interesting to note that, to my knowledge at least, many "skeptics" have arrived at similar conclusions independently of each other. Apparently, the time is ripe for a questioning of the historiography.

Similarly, documenting the existence of a robust research tradition concerned with organismic biology in the first half of the twentieth century, Maurizio Esposito (2017) notes in this volume:

> [T]he developmentalist perspective advanced by these "romanticists" was neither equivalent with Ernst Haeckel's biogenetic law nor represented a variant of orthogenetic evolution, but rather endorsed Walter Garstang's idea according to which ontogeny does not recapitulate phylogeny, it creates it... In that sense, this perspective is closer to contemporary evo-devo than 19th century recapitulationist theories... Now, if after the 1940s, the "romanticists'" views gradually fell in the background, in favor of neo-Darwinian hypotheses... then the question is: why did that happen? The question is particularly relevant because, in the last few decades, the consensus about the neo-Darwinian synthesis has been eroded in favor of a new form of developmental evolutionism (evo-devo) and novel versions of organicist philosophies have again entered onto the stage... The overreaching perspective offered by the developmental system theory, or by the complex epigenetical models of gene expression, are certainly closer to the systemic view of the "romanticists" than the adaptationist models of the modern synthesizers.

Far from always being segregated, competing research programs are intellectually fertilized by each other. Laurent Loison and Emily Herring (2017) describe in this volume how this happened during the transition from Lamarckism to Darwinism:

> We describe how Teissier and L'Héritier's interests, ideas and conjectures, despite their Darwinian inclinations, were influenced by the Lamarckian atmosphere of French biology. This example perfectly shows how non-Darwinian ideas influenced the development of the Modern Synthesis... Despite their indisputable commitment to Darwinism, Teissier and L'Héritier also showed interest in certain aspects of inheritance and evolution that did not belong to the classical Mendelian-Darwinian account of evolution. Here, we would like to briefly sketch these unorthodox dimensions of their work and emphasize their connections with the predominantly Lamarckian atmosphere of French zoology during the 1930s and 1940s... L'Hérititier's and Teissier's heterodox position underlines the specificity of the French context: at the time of the Synthesis, French biology was under the domination of Lamarckian-Bergsonian thought which prioritized the separation between adaptation and true evolution and which tended to favor non-Mendelian modes of heredity: these two main characteristics were central to L'Héritier's and Teissier's rethinking of the structure of the Evolutionary Synthesis.

As we dig deeper into the annals of evolutionary biology, the task of clearly distinguishing between the various research programs does not get any easier. Presenting in this volume what was once called "Old-Darwinism," Georgy Levit and Uwe Hossfeld (2017) write (see also Levit and Hossfeld 2006):

> 'Old-Darwinism' in its fully established and explicit form cannot be reduced to any other theoretical school. The specificity of this theory lay to combine the 'standard' Darwinian factors of evolution (mutation, recombination, geographic isolation, natural selection) with the neo-Lamarckian and orthogenetic mechanisms in order to define the exact role of all these mechanisms in evolutionary process proceeding from the whole complex of biosciences including genetics. Old-Darwinians legitimately insisted that they follow the initial ideas of Darwin, who assumed some roles for Lamarckian mechanisms as well as for the auxiliary hypothesis of constraints. The very idea of combining various evolutionary mechanisms was wide spread at that time within various cultural contexts... In addition to Darwin, Haeckel and himself, Plate counted Richard Semon (1859–1919), Wilhelm Roux (1850–1924), Richard von Hertwig (1850–1937), Fritz v. Wettstein (1895–1945), Berthold Hatschek (1854–1941), Jan Paulus Lotsy (1867–1941), Franz Weidenreich (1873–1948)

> and the future "co-architect" of the Evolutionary Synthesis, Bernhard Rensch, among the old-Darwinians… In Plate's later works (Plate 1932–1938) we find all the basic factors of evolution later adapted by the Evolutionary Synthesis. Thus, Plate claimed that random mutations and recombination deliver the bulk of raw material for evolution. Natural selection and geographical isolation perform a major role in evolution… Also, what is now known as 'population thinking' is of great importance for Plate as he analyses the 'laws of populations' with some mathematics… Yet Plate also admitted other evolutionary mechanisms going beyond the basic tenets of the Synthetic Theory of Evolution. Plate accepted both macro- and directed- mutations, orthogenesis and the inheritance of acquired characters.

The closer we study the development of evolutionary biology, the more the overall picture seems to be blurred and networklike, rendering the neat separation of research programs and historical periods somewhat difficult (see also Levit and Hossfeld 2011). The obvious question to ask at this stage is whether or not distinguishing research programs from one another is even possible. I, myself, do not know the answer, given the current state of our knowledge. However, the apparently obvious solution, that of identifying research programs by their distinct "hard cores," is no panacea. Assuming that research in any particular area consists in a continually evolving quest—research programs are historical entities, to use familiar terminology—must we assume also that such an area is accompanied by an explanatory hard core? Let us take Darwinism as an example. If one answers "yes," then one is committed to the "multilevel model" of science which promotes an explanatory structure positioning the cause (i.e., natural selection) in a privileged hierarchical position relative to other components or fields being explained by that cause or hard core.

There exists, however, an alternative view of science and Darwinism: it consists in arguing that Darwinism was never quite as advertised in the traditional historiography. Already, John C. Greene (1981, 1999) argued for a Darwinism that is intimately connected with so many ontological and metaphysical issues as to make the traditional view centered around selective mechanisms a pale representation of its multidimensional complexion. No surprise, then, that Ernst Mayr (1986) expressed frustrations at Greene's depiction of Darwinism, busy as the former was in representing it as a pure product of positivistic science (Delisle 2009c). Moving away from the "mechanism-centered" bias of the historiography allows for the uncovering of self-proclaimed rhetorical arguments in favor of Darwinism during its two main phases: Darwin's *Origin of Species* and the Evolutionary Synthesis (Delisle 2008, 2009b, c, 2011, 2014, 2017). Several of these so-called Darwinians (including Darwin himself) are committed to so many distinct and competing empirical, conceptual, ontological, and metaphysical choices that they are unable to use the concept of natural selection without significant distortion. On this view, "Darwinians" are not truly bound together under a strong and common intellectual thread; rather, they each exploit some Darwinian components in a piecemeal fashion only by inserting them in distinct research entities. The dissolution of Darwinism, under this thesis, expresses itself through the weak and diffused spread of "Darwinian" explanatory components among a wide scope of evolutionary views, irrespective of how we call them. This alternative view appeals to a "reticulate model" of science founded on a diffused and flexible explanatory structure, with no privileging of causal components over more descriptive ones, and no hierarchical organization of disciplines over others (explanatory core versus explained periphery), in contradiction to the multilevel model of science. In other words, the reticulate model holds that Darwinism has no real hard core, and without it, the task of segregating research programs from one another becomes nearly impossible.

Without a doubt, the debate is an open and fascinating one. Irrespective of which thesis one favors, studies in evolutionary biology tend to show that this area is a kaleidoscope of research entities and ideas, an ever thicker and complex intellectual network. One thing is sure, though: much work remains to be done regarding the development of evolutionary biology. I, for one, once thought that the main events of its development had already been fairly well established. I no longer think this to be the case. New research perspectives and new material are what the future will be made of. "Who controls the past controls the future: who controls the present controls the past," wrote George Orwell in his 1949 novel. I would like to close by extending a plea to historians and historically inclined philosophers: let us prove Orwell's motto wrong in its second half, and true in its first. New viewpoints about the development of evolutionary biology need not always wait for the Whig judgment of a changing present.

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Part I
From a Pluralistic Darwinism to an Ever More Inclusive Darwinism

Selfish Genes and Lucky Breaks: Richard Dawkins' and Stephen Jay Gould's Divergent Darwinian Agendas

Timothy Shanahan

Abstract Darwin expressed alternative theoretical perspectives on a range of issues fundamental to our understanding of evolution, thereby making it possible for his intellectual descendants to develop his ideas in markedly different and even incompatible directions while still promoting their views as authentically "Darwinian." The long-running and well-publicized scientific rivalry between Richard Dawkins and Stephen Jay Gould is a striking case in point. In elegantly written books and essays spanning the last quarter of the twentieth century, they developed and defended diametrically opposed views on the units of selection, the scope and depth of adaptation, the significance of chance events, and the reality and meaning of evolutionary progress—each explicitly juxtaposing his own views against those of the other while insisting that his own conclusions represent the genuinely "Darwinian" view. These skirmishes raise many questions. If there is just one world, why do they reach such different conclusions about it? Does each have an equally good claim to represent authentic "Darwinism"? Are they best viewed as defending different interpretations of a *single* Darwinian tradition, or as representing alternative (e.g., competing) Darwinian *traditions*? More generally, is a scientific tradition best characterized by a set of propositions that define its essence, or by causal interactions providing cohesiveness in terms of self-identification, social relations, and historical continuity? An analysis of the Dawkins–Gould rivalry provides a fertile opportunity to address these and other questions concerning "the Darwinian tradition" in the twentieth century.

Keywords Charles Darwin • Richard Dawkins • Stephen Jay Gould • Evolution • Natural selection • Adaptation • Constraints • Convergence • Contingency • Progress • Darwinism • Research programs

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1 Introduction

Richard Dawkins (b. 1941) and Stephen Jay Gould (1941–2002) are among the best-known evolutionists of the last half-century, each having produced an impressive stream of scholarly and popular works intended to educate readers about the nature of science and to persuade them to accept their respective interpretations of evolution. Although they agree on many issues, they disagree in significant ways on a range of issues fundamental to our understanding of evolution.[1] A critical comparison of their strikingly different views promises to illuminate not only the character of the Darwinian tradition (or traditions) in the twentieth century but also the interpretive nature of scientific knowledge more generally.

Understanding Dawkins' and Gould's divergent Darwinian agendas requires situating them in relation to a pair of parallel, culturally inflected research traditions descended from Darwin's own polymorphic evolutionary theorizing. Darwin expressed his understanding of evolution in ways that (like species diverging from a common ancestor) permitted subsequent theorists to develop his ideas in markedly different directions while viewing themselves as remaining within the Darwinian clade. As Delisle (2017) observes, "Darwin does not provide for the evolutionists of the future a unified view of evolution, but instead offers a whole range of tools and concepts from which one can individually pick." Consequently, identifying some of the theoretical branching points in Darwin's view (in Sect. 2) will prove useful for comparing, contrasting, and explaining their differential expressions in the work of Dawkins and Gould (Sects. 3, 4, 5 and 6). We can then draw upon these comparative analyses to assess the significance of the Dawkins–Gould dispute for understanding the nature of the Darwinian tradition in the twentieth century and for the interpretive nature of scientific knowledge more generally (Sect. 7). I will argue that the Darwinian tradition has a distinctive "hard core" that differentiates it from other approaches to understanding life but also possesses ample conceptual resources to permit biologists to develop this tradition in divergent ways while legitimately representing themselves as carrying on and extending Darwin's seminal work, thereby endowing "Darwinism" with a remarkable capacity to continually adapt and evolve.

2 Darwin's Polymorphic Theorizing

Depending upon how generously one understands the extension of the word "evolution," theories of biological evolution predate publication of *On the Origin of Species* (1859) anywhere from decades to millennia. By the mid-nineteenth century, a belief in the *fact* of evolution, in some form, was common. Darwin's most important contribution was the idea of *natural selection* and his detailed argument, supported by facts

[1]Although Gould died in 2002, for consistency I will continue to refer to both biologists in the present tense.

culled from diverse domains, that it offers the best explanation for organisms' remarkable appearance of having been intelligently designed (and, significantly, for *deviations* from perfection) and for the tendency of new species to arise from preexisting species via a gradual process of "descent with modification." The basic idea is simple enough (in retrospect). Living things tend to differ slightly from one another in ways that confer on some a small advantage in the struggle for survival and reproduction. Some of these characteristics are heritable and are passed on to offspring, who in turn exhibit differential fitness with respect to their own (often slightly different) environments. Over time, kinds of living things become better adapted to their diverse environments and tend to further diverge from one another. Adaptation and diversification are thereby explained by appeal to natural causes alone.

That bare-bones outline is accepted by all Darwinians, yet it embodies many unresolved puzzles, the pursuit of solutions to which has been the driving force in the development of evolutionary biology since Darwin. Among these puzzles are fundamental questions concerning the units of natural selection, the scope of adaptation, the significance of chance, and the reality of evolutionary progress (see Shanahan 2004). A brief review of Darwin's views on these issues is essential for understanding their subsequent differential development in the work of Richard Dawkins and Stephen Jay Gould.

2.1 Darwin on Natural Selection

First, consider Darwin's characterization of *natural selection*. In all six editions of the *Origin*, he maintains that "natural selection works solely by and for the good of each being" (Darwin 1859: 489; 1959: 758). But for the good of *which being(s)* does natural selection work? There are many kinds of biological entities, from cells to organisms to species to ecosystems. Darwin generally thought of natural selection as discriminating among, and thereby ultimately being for the good of, *individual organisms*. In a pack of wolves, for example, the swiftest and slimmest will be the most effective predators, and hence selection will favor individual wolves possessing such characteristics (Darwin 1859: 90). But Darwin realized that explanations in terms of individual advantage alone are limited. For example, in Chapter VII of the *Origin*, he considers "one special difficulty, which at first appeared to me insuperable, and actually fatal to my whole theory. I allude to the neuters or sterile females in insect-communities" (Darwin 1859: 236). Why this should be a problem for Darwin's theory is clear. Sterile individuals, by definition, do not reproduce. Instead, they appear to sacrifice their reproductive interests to serve the interests of the hive or colony. If natural selection can operate only on individuals that pass on their characteristics, it is difficult to see how sterile castes can be products of evolution. Yet eusocial insects, with their sterile castes, are among the most widespread and successful living systems on earth—a great puzzle, indeed.

Despite the serious threat it appeared to pose to his theory, Darwin thought that the problem of sterile castes could be handled rather easily: “[I]f such insects had been social, and it had been *profitable to the community* that a number should have been annually born capable of work, but incapable of procreation, I can see no very great difficulty in this being effected by natural selection” (Darwin 1859: 236; emphasis added). Here, at least, Darwin was willing to entertain the idea that there could be selection for characteristics beneficial to the community, even though they were of no use (and actually detrimental) to the fitness of the individuals possessing those characteristics. Whether this process involved selection operating at the individual level, or a special form of selection operating on more inclusive organizational levels, remained unclear (perhaps even to Darwin himself) and was left for others to work out.

2.2 Darwin on Adaptation

Second, consider Darwin’s treatment of *adaptation*. Natural selection is said by him to work “for the good of each being.” But as resulting from a blind, unguided process, *how good* should one expect the products of such adaptation to be? On the one hand, Darwin was fond of describing adaptations as “perfect” when he wanted to emphasize “the beauty and infinite complexity of the coadaptations between all organic beings, one with another and with their physical conditions of life, which may be effected in the long course of time by nature’s power of selection” (Darwin 1859: 109). Indeed, sometimes when he used the word “perfection” he meant it *literally*. In the *Origin*’s chapter on “Instinct,” he devotes twelve pages to providing a speculative reconstruction of the evolution of the cell-making instinct of hive-bees. Such bees have succeeded in solving a difficult mathematical problem—that of constructing a hive that will hold the greatest quantity of honey while using the least amount of wax. They solved the problem by constructing hexagonal cells that fit together with no wasted intercellular spaces. As Darwin (1859: 235) remarks, “Beyond this stage of perfection in architecture, natural selection could not lead; for the comb of the hive-bee, as far as we can see, is absolutely perfect in economizing wax.” On the other hand, he was aware that living things generally will *not* attain biological perfection and indeed in many instances fall far short of this high standard. Vestigial and rudimentary organs (e.g., the human appendix and male nipples) are classic examples. Indeed, “Organs or parts in this strange condition, bearing the stamp of inutility, are extremely common throughout nature” (Darwin 1859: 450). Therein lay the puzzle: Why does selection produce absolute perfection in some cases but not in others? What degree of perfection should we expect, and what factors prevent some living things from achieving perfection? Again, Darwin begat the problem but ultimately left it unresolved.

2.3 Darwin on Chance

Third, consider Darwin's understanding of the role of *chance* in evolution. What many of his contemporaries found most objectionable about his theory was not evolution *per se* or even natural selection, but rather the idea that the entire process depends on *chance* variations, thus leaving evolution bereft of a preordained goal or even an inherent direction. Darwin seemed to make evolution more haphazard than anyone before him had dared to imagine (Shanahan 1991).

"Chance" also enters his theory in another important way, one that underscores the *historical* nature of evolution. As he inferred from his biogeographical studies, present-day organisms bear the marks of contingent historical events. That long ago one or a few birds were blown off course during a storm and were stranded on a remote island was a purely contingent event; no law of nature dictates that this must happen. But given the right conditions and sufficient time, such accidental colonizers may evolve into distinct species. Thus, the origin of new species will be *governed* by natural laws, but will not be *predictable* from the knowledge of such laws, as Darwin explained using a striking simile: "Throw up a handful of feathers, and all must fall to the ground according to definite laws; but how simple is the problem where each shall fall compared to the action and reaction of the innumerable plants and animals which have determined, in the course of centuries, the proportional numbers and kinds of trees now growing on the old Indian ruins!" (Darwin 1959: 75). What is true for those trees growing on the old Indian ruins is true in spades for species over millions of years of undirected evolution. Evolutionary change is both lawlike *and* subject to innumerable historical, chance events. Yet, although the notion of chance is fundamental to Darwin's theory, by his own admission he had difficulty grasping its precise role. In a 22 May 1860 letter to the American botanist Asa Gray, he confided: "I am inclined to look at everything as resulting from designed laws, with the details, whether good or bad, left to the working out of what we may call chance. Not that this notion *at all* satisfies me. I feel most deeply that the whole subject is too profound for the human intellect. A dog might as well speculate on the mind of Newton" (Darwin 1993, vol. 8: 224). Darwin recognized this basic property of evolution but never fully explained *which* features of the evolutionary process are predictable and which are contingent and in principle unpredictable.

2.4 Darwin on Evolutionary Progress

Finally, consider *evolutionary progress*. On the one hand, Darwin again and again expresses confidence that "natural selection is . . . silently and insensibly working, whenever and wherever opportunity offers, at the *improvement* of each organic being in relation to its organic and inorganic conditions of life" (Darwin 1859: 84; emphasis added). Indeed, "The inhabitants of each successive period in the world's history have beaten their predecessors in the race for life, and are, in so far, *higher* in the scale of nature"—a fact which accounts for "that . . . sentiment, felt by many paleontologists, that organization on the whole has progressed" (Darwin 1859: 345; emphasis added). On the other hand, he also seems to categorically *reject* talk of "higher" and "lower." In the third edition of the *Origin* (1861), he rhetorically asks: "[W]ho will decide whether a cuttle-fish be higher than a bee?" (Darwin 1959: 550). By the sixth edition (1872), he was prepared to answer that question with a degree of confidence that seems to leave no doubt about his position: "To attempt to compare members of distinct types in the scale of highness seems hopeless; who will decide whether a cuttle-fish be higher than a bee, that insect which the great Von Baer believed to be 'in fact more highly organized than a fish, although upon another type'?" (Darwin 1959: 550) Moreover, he was very much concerned to distance his view from Lamarck's "law of progressive development." In an 11 January 1844 letter to Joseph Hooker, he wrote: "Forfend me from Lamarck nonsense of a 'tendency to progression'! But the conclusions I am led to are not widely different from his; though the means of change are wholly so" (Darwin and Seward 1903, vol. I: 41). Statements like these clearly illustrate the problem concerning evolutionary progress bequeathed by Darwin to later biologists. Progress is real (in some hard-to-define sense), but its nature and causes are wholly different from those previously attributed to it.

2.5 Darwinian Puzzles

All of the unresolved theoretical issues just briefly discussed are summed up in Darwin's remarkable claim, expressed *verbatim* in all six editions of the *Origin*, that "As natural selection works solely by and for the good of each being, all corporeal and mental endowments will tend to progress towards perfection" (Darwin 1859: 489, 1959: 758). This is a stirring summary statement of astounding scope and significance. But it leaves many questions of fundamental importance unresolved. *For the good of which being*(*s*) does natural selection work? *How perfectly adapted* should we expect these beings to be? How should we understand the relationship between lawlike and chance *tendencies* in evolutionary change? How, if at all, should *evolutionary progress* be characterized? To point out that there are unresolved issues in Darwin's view is not to criticize his magnificent accomplishment. On the contrary, it reflects the fact that in forging a novel perspective, some of his ideas were bound to be inchoate. Moreover, the fact that biologists continue to debate these issues suggests that nature itself speaks ambiguously on them. As we shall see, Dawkins' and Gould's disagreements about each of these issues reflect divergent interpretations of Darwin's polymorphic theorizing.

3 Dawkins and Gould on Natural Selection

3.1 Selfish Genes

Evolutionists since Darwin generally have followed him in viewing natural selection as operating primarily on individual organisms, and *perhaps* occasionally on groups of organisms as well, with a few biologists (e.g., Wynne-Edwards 1962) taking group selection to be both common and important. Richard Dawkins argues that there is a more penetrating and powerful view, namely, that *genes*—not organisms, and certainly not groups or species—are the "beings" (to use Darwin's term) for whose good natural selection works. As he memorably puts it in one essay: "Birds' wings are obviously 'for' flying, spider webs are for catching insects, chlorophyll molecules are for photosynthesis, DNA molecules are for... What *are* DNA molecules for? .... [This] is the forbidden question. DNA is not 'for' anything.... all adaptations are for the preservation of DNA; DNA just *is*" (Dawkins 1982a: 45). Previously some biologists (e.g., Williams 1966) had explicitly proposed such a view, and it was perhaps implicit in the seminal work of R. A. Fisher (1930), but in *The Selfish Gene* (1989a) Dawkins made it into a powerful organizing first principle for addressing a range of biological puzzles, from the origin of life to altruism to the social behaviors of animals (see also Alcock 2017). He deployed two kinds of arguments in support of the "selfish gene" view.

First, according to Dawkins, only genes have the requisite properties to function as "units of selection" and thereby to be the ultimate beneficiaries of natural selection. Genes (usually) replicate faithfully, exist in large numbers in virtue of their many copies in a population, and persist for long periods of time. Genotypes, organisms, and groups, by contrast, are ephemeral, short-lived entities whose components are repeatedly reshuffled, exist in far fewer numbers, and can be said to replicate in only a very loose sense. According to Dawkins (1989a: 34), "[T]he individual [organism] is too large and too temporary a genetic unit to qualify as a unit of natural selection. The group of individuals is an even larger unit. Genetically speaking, individuals and groups are like clouds in the sky or duststorms in the desert. They are temporary aggregations or federations." Only genes are preserved intact from one generation to the next; hence, only genes have the properties necessary to be the units of selection.

Second, the selfish gene view has unrivaled explanatory *power* and *scope*. Darwin struggled to explain the existence of sterile castes in the eusocial insects by a vague appeal to what would be "profitable to the community." But William D. Hamilton (1964), one of Dawkins' intellectual heroes, showed how sterile insect castes could evolve and be maintained in terms of selection operating at the level of shared genes within the peculiar haplo-diploid reproductive systems of eusocial insects. Hamilton's key insight was that these sterile individuals are unusually closely related to fertile members of the colony. Although themselves reproductively sterile, by helping their fertile relatives to survive and reproduce they assist in the propagation of copies of their own *genes*, many of which are shared with close relatives. Such a process [later dubbed "kin selection" by John Maynard Smith (1964)] obviates the need to postulate selection at some higher biological level. Dawkins' insight was to realize that this striking explanatory success has far-reaching implications. Whereas only *some* biological phenomena can be explained in terms of selection operating at the level of organisms, *every* such phenomenon, Dawkins contends, can be explained in terms of selection operating at the level of genes. The selfish gene view therefore provides a *deeper explanation* and a *more general theoretical perspective* than any of its theoretical alternatives (see Shanahan 1997).

3.2 The Invisibility of Genes

Across the Atlantic, Gould was not convinced. He claimed to find an elementary flaw in the selfish gene theory: "No matter how much power Dawkins wishes to assign to genes, there is one thing he cannot give them—direct visibility to natural selection. Selection simply cannot see genes and pick among them directly. It must use bodies as an intermediary. A gene is a bit of DNA hidden within a cell. Selection views bodies" (Gould 1980a: 90). Moreover, Gould claimed that the selfish gene view grossly misconstrues the relationship between genes and bodies: "Bodies cannot be atomized into parts, each constructed by an individual gene" (Gould 1980a: 91).[2] Even if the one gene/one body part view *were* true, the selfish gene view would still be flawed, Gould contended, because it is the whole organism, rather than the individual gene, that is naturally selected. Gould attributed the fascination generated by Dawkins' view to "some bad habits of Western scientific thought—from attitudes . . . that we call atomism, reductionism, and determinism" (Gould 1980a: 91–92). By contrast, his own evolutionary perspective is proudly hierarchical: "The world of objects can be ordered into a hierarchy of ascending levels. . .. Different forces work at different levels" (Gould 1980a: 85). Insofar as Darwin (usually) thought of selection as operating on individual organisms rather than on discrete units of heredity (of which he knew nothing), Gould could claim to be more "Darwinian" than Dawkins on this point. Indeed, Gould saw himself as restoring the organism to the central role assigned to it by "the orthodox, Darwinian view" (Gould 1980a: 85). Endorsing David Hull's (1976) pithy formulation, he declared that "genes mutate, organisms are selected, and species evolve" (Gould 1980a: 85). Fifteen years later, Gould was still chastising Dawkins as a "strict Darwinian zealot . . . who's convinced that everything out there is adaptive and a function of genes struggling. That's just plain wrong, for a whole variety of complex reasons" (Brockman 1995: 63). The battle between "orthodox" and "zealous" [latter dubbed by Gould (1997a) "fundamentalist"] Darwinian visions was well under way.

[2]See MacCord and Maienschein (2017) for a contemporary critique of the overemphasis on the role of genes as the locus of explanation for development and evolution.

3.3 Replicators and Vehicles

It did not take long for Dawkins (1982a: 47) to strike back, emphasizing that insisting on the causal primacy of genes "does not mean, of course, that genes … literally face the cutting edge of natural selection. It is their phenotypic effects that are the proximal subjects of selection." Differences in genes give rise to differences at the phenotypic level, resulting in the differential propagation of the genes responsible for those phenotypes. Natural selection operates directly on "vehicles" (i.e., phenotypes), but it is the indirect effects on the differential fate of "replicators" (i.e., genes) that is crucial for understanding evolutionary change. Evolution is essentially a contest in which genetic replicators vie with each other by constructing bodies by which they lever themselves into subsequent generations. Moreover, Dawkins disavowed the idea that the selfish gene theory requires that there be a simplistic one-to-one mapping of genes to phenotypic characteristics. It is quite enough, he pointed out, that *differences* among genes be responsible for *differences* at the phenotypic level.

4 Dawkins and Gould on Adaptation

4.1 Spandrels and the Panglossian Paradigm

Darwin was convinced that natural selection is a perfecting agent, yet left unresolved the issue of *how* perfect one should expect the products of natural selection to be. At least two questions in this regard need to be distinguished, pertaining to the *scope* and the *depth* of adaptation. First, should *every* phenotypic characteristic be considered an adaptation? Second, is every bona fide adaptation *optimal*?[3] In a widely cited paper, "The Spandrels of San Marco and the Panglossian Paradigm: A Critique of the Adaptationist Programme" (1979) (coauthored with his Harvard colleague Richard Lewontin), Gould answers both questions with a resounding "No." The first part of the paper's title comes from a comparison of some organismal traits to certain architectural features of St. Mark's Basilica in Venice. Spandrels are described by Gould as the tapering triangular spaces that arise as the necessary architectural by-products of mounting a dome on rounded arches meeting at right angles. Each of the spandrels in St. Mark's is decorated with a Christian motif. One ignorant of architectural necessity might suppose that the spandrels exist in order to provide spaces for the depiction of religious themes. But according to Gould, one would be dead wrong. The spandrels came into existence for inescapable architectural reasons and were *then* pressed into service for religious purposes; the fact that they provide suitable surfaces for religious iconography in no way *explains* their existence. Gould claims that biologists make an

[3]Other questions include whether biological entities above or below the level of the individual organism can be, and sometimes are, the *bearers* or "owners" of adaptations.

analogous mistake in their analysis of organisms when they uncritically assume that every phenotypic characteristic exists because it serves some adaptive purpose, thereby ignoring the "architectural constraints" that delimit the structures of organisms. By simply assuming that all characteristics are adaptive, "ultra-adaptationists" (like Dawkins) fail to distinguish between the current utility of a phenotypic characteristic and the real evolutionary reasons for that characteristic's existence in the first place.

The second part of the title of the "Spandrels" paper refers to Dr. Pangloss in Voltaire's satire, *Candide*, who assumed that whatever exists (e.g., earthquakes and all the rest) does so because it is for the best. So too, Gould maintains, evolutionary biologists are prone to exhibit unlimited "faith in natural selection as an optimizing agent" (Gould and Lewontin 1979: 147). The only brake ever admitted on the perfection of each trait consists in trade-offs among competing selection pressures: "Any suboptimality of a part is explained as its contribution to the best possible design for the whole. The notion that suboptimality might represent anything other than the immediate work of natural selection is usually not entertained" (ibid: 151). Even non-optimality is thereby accounted for in terms of selection-driven adaptation. Moreover, "This program regards natural selection as so powerful and the constraints upon it so few that direct production of adaptation through its operation becomes the primary cause of nearly all organic form, function, and behavior" (ibid: 150–151). A telltale symptom of this unquestioned assumption is the failure to even consider various non-adaptationist explanations for biological structures. Gould also hints at his preferred alternative approach, one with a distinguished European pedigree (Levit and Hossfeld 2017). Instead of viewing organisms as suites of interchangeable, atomized characteristics, he maintains that "organisms must be analyzed as integrated wholes, with *Baupläne* (fundamental body plans) so constrained by phyletic heritage, pathways of development, and general architecture that the constraints themselves become more interesting and more important in delimiting pathways of change than the selective force that may mediate change when it occurs" (ibid: 147). Significantly for the broader concerns of the present paper, Gould explicitly associates this perspective with "Darwin's own pluralistic approach to identifying the agents of evolutionary change" (ibid: 147).

4.2 Adaptationism Reasserted

Dawkins is not cited in the Spandrels paper, but he may well have taken his own approach to be among the primary targets of its pointed criticisms. Only a few years after that paper appeared, he explicitly addressed the issue of "Constraints on Perfection" in his book *The Extended Phenotype* (1982b), mentioning the authors of the Spandrels paper in the very first paragraph and then responding to them, singularly and together, throughout. He argues on theoretical grounds that we should *not* expect optimal adaptations, nor is such optimality empirically confirmed. Living things are, after all, products of blind processes. Although Darwin is not explicitly referenced, Dawkins' conclusion is exactly the same as *one* of Darwin's, with which he was surely familiar: "Natural selection will not produce absolute perfection, nor do we always meet, as far as we can judge, with this high standard under nature" (Darwin 1859: 202). (For further discussion, see Shanahan 2008.)

Having explained why one should *not* embrace the form of ultra-adaptationism critiqued by Gould, Dawkins nevertheless emphasizes in subsequent works that the adaptations of living things are, far more often than is generally appreciated, incredibly well designed. For example, the chapter entitled "Good Design" in *The Blind Watchmaker* (1986) is a *tour de force* in conveying the stupefyingly impressive adaptations that permit insectivorous bats to locate and capture prey. Natural theologians like the Rev. William Paley, author of *Natural Theology, or Evidences of the Existence and Attributes of the Deity* (1802), sought to show that a careful examination of living things provides indisputable proof of a divine Designer. Dawkins, of course, rejects Paley's specific explanation for the appearance of design. But he nonetheless thinks that Paley was right to emphasize living things' *appearance* of having been intelligently designed. The emphasis throughout the chapter and indeed the entire book is on the fact that living things have the sort of astonishingly complex "design" (i.e., adaptations) that an intelligent designer *would* impart if such a being was trying to make a nearly perfect machine of that sort; yet such astounding results have been achieved without any conscious agency whatsoever.[4]

4.3 Odd Arrangements and Funny Solutions

Whereas for Dawkins complex organic "design" is *the* preeminent biological datum requiring scientific explanation, Gould finds biological *oddity* and *poor design* to be far more significant for understanding the nature of Darwinian evolution. His essay "The Panda's Thumb" is a striking case study in historically constrained biological *imperfection* that is said to provide powerful evidence for Darwinian evolution—precisely *because* the panda's "thumb" (an extension of the radial sesamoid bone) manifests biological imperfection. In stark contrast to Dawkins' perspective, Gould writes that: "[I]deal design is a lousy argument for evolution, for it mimics the postulated action of an omnipotent creator. Odd arrangements and funny solutions are the proof of evolution—paths that a sensible God would never tread but that a natural process, constrained by history, follows perforce" (Gould 1980a: 20–21). In another essay, he explains: "[Y]ou cannot demonstrate evolution with perfection because perfection need not have a history" (Gould 1980a: 28). For Gould, historical factors trump functional factors in explaining the most interesting aspects of life.

[4]Segerstråle (2006, p. 88) interprets *The Blind Watchmaker* as a whole as Dawkins' response to Gould's critique of adaptationism. This may be going too far, but Gould is certainly *a* target.