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

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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.

The differential importance Gould and Dawkins attach to the “historical” manifests itself in other ways as well. Dawkins is impressed by living things’ seemingly limitless ability to adapt to new challenges, especially those posed by other living things, remarking: “I believe that there’s not a lot that genes can’t achieve in the way of small-scale, gradual, step-by-step change from what’s already there” (Brockman 1995: 81). By contrast, Gould is impressed by constraints that place limits on evolutionary change, maintaining that: “There are certain pathways that are more probable, and there are certain ones that aren’t accessible, even though they might be adaptively advantageous. It really behooves us to study the influence of these structural constraints upon Darwinian and functional adaptation; these are very different views” (Brockman 1995: 53).

5 Dawkins and Gould on Chance

5.1 A Minor Ingredient in the Darwinian Recipe

The notion of *chance* is fundamental to Darwin’s conception of evolution, yet by his own admission he found it difficult to explain its precise role, thereby rendering his theory vulnerable to endless misunderstanding and misrepresentation. For example, creationists argue that “random evolution” could never explain the beautifully designed features of living things, to say nothing of uniquely human characteristics. They are right, of course, but their facile mistake, as Dawkins points out with undisguised exasperation, is “to believe that Darwinism explains living organization in terms of chance . . . alone. This belief, that Darwinian evolution is ‘random’, is not merely false. It is the exact opposite of the truth. Chance is a minor ingredient in the Darwinian recipe” (Dawkins 1986: 49). By contrast, “the most important ingredient” of Darwinian evolution, in Dawkins’ view, is *cumulative selection*, “which is quintessentially *non*random” (ibid: 49; emphases in original). Cumulative selection is simply the iterated operation of natural selection whereby the accumulation of small changes over time results in significant evolutionary change. Always armed against the doubters of Darwinism, Dawkins is concerned to show that slight, chance improvements in functionality can accumulate to produce the astoundingly complex adaptations of living things we observe. Chance variations are crucial to this process, but all the heavy lifting involved in forging adaptations is done by natural selection, a nonrandom process.

5.2 Lucky Breaks

Gould’s primary concerns lay elsewhere, in the vast expanse of the history of life, a history that is characterized by unpredictable twists and turns. In his book *Wonderful Life: The Burgess Shale and the Nature of History* (1989), he encourages readers to think of life on earth as shot through with *contingency*.[5] Fossil remains in the Burgess Shale of British Columbia reveal a bonanza of long-extinct *phyla*, the likes of which have not existed for half a billion years since the mysterious Cambrian Explosion, dubbed evolution's "big bang." Why did these bizarre body plans flourish and then suddenly vanish? No one knows. But according to Gould (1989: 47), it was a genuine *decimation* in the sense that those that left descendants were a minute, *random* sample of those that had previously flourished. An ultra-adaptationist, Gould points out, would interpret this pruning of the tree of life as yet another example of natural selection in action, no doubt insisting that "all but a small percentage of Burgess possibilities succumbed, but the losers were chaff, and predictably doomed. Survivors won for cause—and cause includes a crucial edge in anatomical complexity and competitive ability" (ibid: 48). Against this ultra-adaptationist interpretation, Gould insists, those that survived were just the beneficiaries of *lucky breaks*; consequently, their distant descendants (including us) are merely the products of "a thousand . . . happy accidents" (ibid: 48). The survival of entire phyla often depends more on *luck* than on fitness. Were it possible to restart the evolutionary process from its beginning, there is every reason to conclude that an entirely different biota would evolve. Contingency rules over Darwinian evolution.

5.3 Convergence

In response, Dawkins essentially accused Gould of grossly exaggerating the significance of some well-known facts. In a withering review of *Wonderful Life*, first published in 1990, Dawkins (2003: 205) writes: "Since, for Gould, the Cambrian was peopled with a greater cast of phyla than now exist, we must be wonderfully lucky survivors. It could have been our ancestors who went extinct…. We came 'that close' to not being here. Gould expects us to be surprised. Why? The view that he is attacking—that evolution marches inexorably towards a pinnacle such as man—has not been believed for years." Elsewhere Dawkins (1986) had already considered, and rejected, the claim that, were the evolutionary process to be restarted from its beginning, an *entirely* different biota would evolve. On the contrary, he noted: "It is . . . a striking testimony to the power of natural selection . . . that numerous examples can be found in real nature, in which independent lines of evolution appear to have converged, from very different starting points, on what looks like the same endpoint" (Dawkins 1986: 94). In *Climbing Mount Improbable* (1996: 19–22), Dawkins argues that eyes have evolved independently a number of times because organs for seeing are likely to be useful under a wide array of

[5]Later, in his final major work, Gould (2002: 47) defines "contingency" as "the tendency of complex systems with substantial stochastic components, and intricate nonlinear interactions among components, to be unpredictable in principle from full knowledge of antecedent conditions, but fully explainable after time's actual unfoldings" [*sic*].

recurring circumstances. Replay life's tape and it is indeed unlikely that the same *species* would evolve again, but it is overwhelmingly likely that evolution would again produce organisms with organs for detecting light—*and* functional types such as autotrophs, herbivores, carnivores, scavengers, parasites, etc. In his view, Gould fails to understand that the fundamental nature of Darwinian evolution makes it likely that organisms playing the same ecological roles would invariably arise again because selection channels chance variations into broadly predictable paths. In Dawkins' view, the conclusions that Gould draws from his "replaying the tape of life" thought experiment simply do not follow from, and indeed are contradicted by, the basic principles of Darwinian evolution.

6 Dawkins and Gould on Progress

6.1 A Noxious Idea

Darwin's view of evolutionary progress is best described as *guarded*. He was confident that natural selection improves the beings on which it operates, making organisms that appear later in an evolving lineage "higher" in the scale of nature than their predecessors in the same lineage. But he was contemptuous of a Lamarckian "tendency to progression" and consequently dismissive of any attempt to rank as higher or lower organisms of different "types." Still, he believed that he discerned a real, if qualified, sense in which evolution manifests progress (Shanahan 2000). Gould entertains no such qualifications. As he explains in the first sentence of one essay, "Progress is a noxious, culturally embedded, untestable, nonoperational, intractable idea that must be replaced if we wish to understand the patterns of history" (Gould 1988: 319). Writing eight years later, he adamantly denies "that progress characterizes the history of life as a whole, or even represents an orienting force in evolution at all" (Gould 1996: 3). At least five distinct arguments for these claims can be extracted from the latter work.

First, we humans have a lamentable, albeit understandable, tendency to place ourselves atop nature's hierarchy and to arrange all other living things somewhere down the evolutionary ladder. The very fact that we are so predisposed to believe in progress, and to place ourselves at evolution's pinnacle, should render this belief deeply suspect. Second, there is nothing about the evolutionary process *per se* that would make progress inevitable, or even likely. Instead, the history of life is rife with chance, contingency, and historicity, making each stage in the process utterly unpredictable given what came before. Third, because life necessarily began in a simple, relatively uncomplicated form, the only regions of morphospace available for colonization were those for more complex organisms. Organisms became more complex, not because increased complexity was "better," but just because there was nothing else to do *but* to become (on average) more complex. Fourth, evolutionary progress is an illusion because bacteria and insects far outnumber mammals.

Finally, evolution should be viewed as "a history of change as the increase or contraction of variation in an entire system (a 'full house'), rather than as a 'thing' moving somewhere" (Gould 1996: 146). In short, progress is an illusion, albeit a seductive one.

6.2 Dyed-in-the-Wool Progress

In a scathing review of Gould's *Full House*, Dawkins agrees that "complexity, braininess and other particular qualities dear to the human ego should not necessarily be expected to increase progressively in a majority of lineages" (Dawkins 1997: 1018), but nonetheless finds fault with Gould's broader critique of evolutionary progress: "Why should any thoughtful Darwinian have expected a majority of lineages to increase in anatomical complexity? Certainly it is not clear that anybody inspired by adaptationist philosophy would" (ibid: 1017). In his view, "Gould is wrong to say that the appearance of progress in evolution is a statistical illusion" (ibid: 1018) because there is an alternative, and far more plausible, way of construing evolutionary progress, namely, as "a tendency for lineages to improve cumulatively their adaptive fit to their particular way of life, by increasing the numbers of features which combine together in adaptive complexes" (ibid: 1016). "By this definition," Dawkins writes, "adaptive evolution is not just incidentally progressive, it is deeply, dyed-in-the-wool, indispensably progressive" (ibid: 1017). For example, "The evolution of the vertebrate eye *must* have been progressivee.... Without stirring from our armchair, we can see that it must be so" (ibid: 1018; emphasis in original). Evolutionary progress, which does not require the baggage Gould attempts to saddle it with, is thus quite real.

6.3 Not Evolution's Defining Feature

The Gould–Dawkins debate over evolutionary progress may be a classic case of interpreting the same facts through the lenses of two different conceptual frameworks. For his part, Gould (1996: 197) grudgingly acknowledges the fact of increasing *complexity* in the history of life, but insists that this should not be regarded as evolution's "defining feature," for two reasons. First, although increasing complexity (on average) *is* an undeniable a feature of evolution, it is not a pervasive feature of most lineages. Second, increasing complexity, where it occurs, arises as an incidental by-product of processes whose causes do not include a mechanism for progress or increased complexity. Dawkins, likewise, believes that complexity (on average) has increased over time but interprets this increase as an inevitable consequence of a mechanism, natural selection, which may bias evolution in that direction. Consequently, while agreeing on many of the *facts*, Dawkins and Gould nonetheless fundamentally disagree on the *significance* of these facts for understanding Darwinian evolution. Perhaps more clearly than in any other area, their dispute over the reality of evolutionary progress demonstrates that simple appeals in science to "the evidence" are sometimes insufficient to resolve fundamental theoretical issues because it is precisely the *interpretation* of the evidence that is at issue.

7 Dawkins, Gould, and Darwinian Traditions in the Twentieth Century

So far we have considered Dawkins' and Gould's alternative, and often diametrically opposed, views on a range of fundamental issues concerning evolution, along with their stated reasons for holding such views. Without in the least minimizing the importance of those reasons, we can also delve more deeply into the different contextual factors and associated methodological agendas that contribute to such divergent interpretations and applications of Darwinism.[6] Chief among these factors are different disciplinary priorities and culturally inflected research agendas.

7.1 Disciplinary Priorities and Culturally Inflected Research Agendas

In the 1960s, Dawkins was a student in Oxford of Niko Tinbergen (1907–1988), one of the founders of ethology, a biological subdiscipline that aims to understand the adaptive significance of animal behavior in the context of an animal's natural environment, and hence a field of inquiry that takes adaptationism as a central organizing principle. Its limitations (e.g., as pointed out by Gould and Lewontin) notwithstanding, adaptationism is unarguably a powerful heuristic in the study of animal behavior—one that Dawkins thoroughly absorbed in his scientific training. He was also ideally situated to inherit an exciting new set of ideas strongly associated with late mid-century British evolutionary theorizing. He credits William D. Hamilton (1936–2000) and John Maynard Smith (1920–2004), in particular, for introducing him to the ideas of inclusive fitness and evolutionarily stable strategies, respectively—ideas around which much of *The Selfish Gene* is organized. Dawkins' work also reflects key ideas and ideals associated with fellow Englishman Ronald A. Fisher (1890–1962), whom Dawkins once lauded as "the greatest biologist since Darwin."[7] Fisher's "Fundamental Theorem of Natural Selection" states that, in an infinite population, "The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time" (Fisher 1930: 35).

[6]For a more detailed analysis of such factors, see Shanahan (2001).

[7]http://edge.org/conversation/who-is-the-greatest-biologist-of-all-time

Although there are (as Fisher recognized) conditions under which this prediction will not be borne out (since all real biological populations are finite), the theorem nonetheless provides a basis for an inherent directionality in evolution. Not coincidentally, Fisher was also a staunch believer in evolutionary progress. Indeed, Ruse (2006: 147) describes Fisher's *The Genetical Theory Natural Selection* (1930) as "a hymn to evolutionary progress." Dawkins' belief that evolution *must* be progressive has a strong Fisherian flavor. Like Fisher, Dawkins begins with an idealized conception of the evolutionary process as adaptive change powered by natural selection and logically deduces the necessary consequence: organisms will become progressively better adapted to their specific conditions of life.

Other seminal influences on Dawkins are less direct but no less consequential. Julian Huxley (1887–1975) managed to surpass even Fisher as an enthusiast for evolutionary progress. Like Dawkins, he studied and then taught at Oxford University. From his earliest writings (Huxley 1912: 114–115) straight through to his later writings (Huxley 1953: 31), he emphasized the objective reality of evolutionary progress and the importance of co-evolutionary arms races for understanding progressive evolution—a topic on which Dawkins would later conduct original research (Dawkins and Krebs 1979). Eventually, Huxley (1954: 11) defined evolutionary progress as consisting in the appearance of biological innovations that make possible further progress—an idea that strikingly presages Dawkins' (1989b) idea of the "evolution of evolvability." Dawkins' emphasis on arms races, adaptation, progress, and the evolution of evolvability, as well as his highly public role in the promotion of science, are all themes with striking Huxlean precedents.[8] In myriad ways, Dawkins sports a distinctively English neo-Darwinian pedigree (Kohn 2004).

Gould's Darwinian pedigree is strikingly different. In 1967, he completed a doctorate at Columbia University in evolutionary biology and paleontology—the latter a discipline that aims to understand patterns of change and diversification among (overwhelmingly extinct) biological lineages during the last 550 million years. Gould became a paleontologist at a time when paleontology still labored under a second-class professional status within evolutionary biology, being overshadowed first by population genetics in the 1940s and then by molecular biology in the 1950s. The former situation had begun to be rectified during Gould's childhood by the American paleontologist George Gaylord Simpson (1902–1984) who, in *Tempo and Mode in Evolution* (1944), sought to integrate paleontology into the congealing "modern synthesis." Simpson also combatted what he saw as the naïve anthropocentricism of evolutionary progressionists like Huxley by arguing in *The Meaning of Evolution* (1949) that "The [fossil] record has demonstrated that evolution is not some over-all cosmic influence that has been changing all living things in a regular way throughout the periods of the earth's history" (Simpson 1949: 97).

[8]What has been said about Huxley could with equal justice be said about Dawkins: "Huxley's contributions of new knowledge were far less important than his infectious enthusiasm and encouragement, as well as his ability to combine scattered concepts or ideas into general principles and meaningful visions" (Cain 2009a: 649).

Supposed instances of progression in the fossil record are merely artifacts of selective and faulty analysis of the paleontological data. In his view, the "tempo" of evolution is characterized by a diversity of evolutionary rhythms varying from one evolutionary branch and geological period to another, with contingent historical factors playing a crucial role.

Simpson's influence on Gould was profound. Like Simpson, Gould spent most of his career at the American Museum of Natural History in New York and at the Museum of Comparative Zoology at Harvard. (Prior to joining the American Museum, Simpson was a professor at Columbia University, Gould's alma mater.) Like Simpson, Gould rails against popular but (in his view) mistaken progressionist conceptions of evolution and aims to demonstrate that a critical interpretation of the fossil record renders such popular beliefs empirically untenable. Gould's deep admiration for the work of Simpson is clearly evident in his assessment of Simpson's contribution to the modern synthesis (e.g., in Gould 1980b: 120). Also, "This View of Life"—the title of Gould's long-running monthly column in *Natural History* magazine—is the title of one of Simpson's books (Simpson 1964). Indeed, at times Gould's prose is virtually indistinguishable from Simpson's. Compare Gould's denial "that progress characterizes the history of life as a whole, or even represents an orienting force in evolution at all" (Gould 1996: 3) with Simpson's nearly identical claim that "evolution is not invariably accompanied by progress, nor does it really seem to be characterized by progress as an essential feature" (Simpson 1949: 262). In crucial respects, Gould trod in Simpson's influential footsteps.[9]

Gould's understanding of evolution also owes a powerful debt to the American population geneticist Sewall Wright (1889–1988). Wright was suspicious of mathematical models that treat populations as infinite and as lacking significant internal structure and that treat chance events as relatively unimportant (Provine 1986). In Wright's view, random genetic drift—a process that characterizes all real, finite populations—may underlie the ability of biological populations to cross genetic valleys and thereby to ascend higher adaptive peaks. Gould followed Wright in his suspicion of models that fail to acknowledge the multitude of complicating factors to which real biological systems are always subject, that fail to consider the evolutionary history of evolved entities, and that downplay the pervasiveness of chance factors in evolution. The theory of punctuated equilibrium—the scientific idea for which Gould is best known—owes much to Wright's notion (later given greater prominence by Ernst Mayr via his model of allopatric speciation) that speciation may be favored by the subdivision of populations by random genetic drift into reproductive isolates that continue to diverge until new species formation is complete (Turner 2017). In these and other ways (e.g., his frequent allusions to baseball to drive home key points), Gould is a product of distinctly American influences.

[9]In time, however, Gould sought to distance his views from those of Simpson. As Cain (2009b) discusses, Gould later embarked on a campaign of "ritual patricide" against his one-time hero.

7.2 Dawkins and Gould as "Darwinians"

Despite their methodological and substantive disagreements, Dawkins and Gould each sees himself as representing authentic "Darwinism" and each enthusiastically (albeit selectively) appropriates Darwin for his own purposes—a rhetorical strategy that Darwin facilitated through his polymorphic theorizing. Recall the two great principles that Darwin explains and defends in the *Origin*: natural selection and descent with modification. To a first approximation, Dawkins and Gould each can be viewed as prioritizing one of Darwin's great principles over the other. For Dawkins, the most striking feature of living things requiring cogent explanation—namely, their complex organization—requires understanding how natural selection could have forged such remarkable design: "The problem is one of complex design…. Complicated things, everywhere, deserve a very special kind of explanation. We want to know how they came into existence and why they are so complicated" (Dawkins 1986: ix, 1). The answer, of course, is natural selection. For Gould, by contrast, the most important features of living things requiring explanation are patterns of similarity and diversity over immense periods of time, e.g., as evident in the fossil record. These are characteristics of biological lineages, not individual organisms, and therefore require first and foremost understanding historical patterns and processes of descent with modification: "In our Darwinian traditions, we focus too narrowly on the adaptive nature of organic form, and too little on the quirks and oddities encoded into every animal by history" (Gould 1995: 371). (See Shanahan 2011 for how Darwin attempted to reconcile these themes.)

Like observers attending to different aspects of the same Gestalt image, Dawkins and Gould naturally privilege different elements of Darwin's theory, with consequences for their respective self-identifications with "the Darwinian tradition." Dawkins, it is fair to say, always sees himself as carrying on the scientific tradition inaugurated by Darwin. He wears the "Darwinian" mantle with obvious pride while recognizing that biologists have learned much that Darwin necessarily could not have known. In his view, the most important piece missing from Darwin's understanding of evolution is modern genetics: "If only Darwin had read Mendel! A gigantic piece of the jigsaw puzzle would have clicked into place…. Darwin would have been delighted and astounded by the population genetics, the neo-Darwinism of the 1930s. It's also nice to think that he might have been pleased about kin selection and selfish genes as well" (Brockman 1995: 75). Kin selection and selfish genes are, of course, central to Dawkins' own interpretation of evolutionary theory. By judging that Darwin would have approved of these ideas, Dawkins thereby situates himself as heir to a Darwinian tradition stretching back to, and deriving authentication from, the great man himself.

By contrast, Gould's self-conception in relation to "the Darwinian tradition" is more ambiguous. Early in his career he declared that "the essence of Darwinism lies in its claim that natural selection creates the fit. Variation is ubiquitous and random in direction. It supplies the raw material only" (Gould 1977: 44). Later he came to characterize "strict Darwinism" as a rigid ideology according to which natural selection is regarded as the only important cause of evolutionary change, organisms are infinitely malleable under the influence of natural selection, micro-evolutionary processes can be extrapolated to explain all macro-evolutionary phenomena, and the history of life as a whole can be defined by a drive toward better, more complex organisms. Indeed, it is vital for "strict Darwinism" that selection operating on individual bodies explains "all major patterning forces in the history of life.... unless you can argue that Darwinian selection on bodies is, by extrapolation, the cause of evolutionary trends and of the major waxing and waning of groups through time, then you don't have a fully Darwinian explanation for life's history" (Brockman 1995: 63). Gould obviously does not consider himself a Darwinian in this "strict" (i.e., constricted) sense. Indeed, in this constricted sense, he says, even "Darwin is not a strict Darwinian" (Brockman 1995: 53). At various times, Gould (1980b, 1997b, respectively) has prophesized the demise of strict Darwinism and contrasted it with a more open, pluralistic attitude toward evolutionary principles that, he says characterized Darwin's own work.

Gould considers himself a "Darwinian" in this more expansive, pluralistic sense and speculates that were Darwin to learn of asteroid impacts, mass extinctions, and even punctuated equilibrium, he would be open to such ideas (Brockman 1995: 64). With respect to his own distinctive views on contingency and biological oddities, however, he opines that Darwin would be *fully* on board: "Darwin invoked contingency in a fascinating way as his *primary support* for the fact of evolution.... One might think that the best evidence for evolution would reside in those exquisite examples of optimal adaptation presumably wrought by natural selection.... Yet Darwin recognized that ... *the primary evidence for evolution* must be sought in quirks, oddities, and imperfections that lay bare the pathways of history" (Gould 1989: 300; emphases added).

Likewise, Gould interprets Darwin's view of evolutionary progress as virtually indistinguishable from his own, although given the social milieu in which he lived Darwin was forced to disguise his doubts about the inevitability of progress. Therefore, when Darwin expresses progressionist sentiments, they should not be understood to represent his *real* views, but rather as concessions to the then-prevailing *Zeitgeist* that had enshrined "progress" as an inevitable social law. In Gould's view, although Darwin categorically rejected any notion of evolutionary progress, he nonetheless sometimes weakened and included progressionist language in his writings so as to not upset the status quo of which he was such an indisputable beneficiary: "Darwin, the social conservative, could not undermine the defining principle of a culture ... to which he felt such loyalty, and in which he dwelt with such comfort" (Gould 1996: 141).

7.3 What Is "Darwinism"?

The fact that Dawkins and Gould can each think of himself as a "Darwinian," and that each can justify such self-identification by citing Darwin himself, while nonetheless holding such different views from one another, raises more general questions about the nature of "Darwinism" and "the Darwinian tradition." What *is*

"Darwinism"? Does it have defining features? If so, what are they? What constitutes "the Darwinian tradition"? Is it uniform or it is, like Darwin's own theorizing, polymorphic? Are "Darwinism" and "the Darwinian tradition" co-extensive, or distinct?

Some scholars maintain that "Darwinism" has something like an essential nature that distinguishes it from other understandings of evolution, e.g., those promulgated in the years following Darwin's death and right into the early twentieth century (see Bowler 2017). James Lennox (2015), for example, maintains that "Darwinism" consists in a distinctive set of concepts, principles, and methodological maxims concerning the history and diversity of life on earth, centering on five themes: (1) probability and chance; (2) the nature, power, and scope of selection; (3) adaptation and teleology; (4) nominalism vs. essentialism about species; and (5) the tempo and mode of evolutionary change. According to Lennox, it is possible to identify the Darwinian position with regard to each of the foregoing issues; Darwin and his contemporaries recognized the distinctiveness of Darwin's position on each of these topics; and these elements continue to differentiate Darwinism from rival views of evolution. Such an approach aims to distill the essence of Darwinism in all its fullness into a comprehensive but finite set of theses.

A comparatively stripped-down but still essentialist approach is taken by David Depew (2017), who takes "Darwinism" to refer to "Darwin's claim that gradual natural selection is the primary (but not the only) cause of evolutionary diversification." Absent from this spare conception is any reference to chance, the units of selection, adaptation, the nature of species, and whether evolution itself (as distinct from natural selection) is gradual. What makes something "Darwinian" on this view is just the central importance attributed to natural selection in accounting for life's diversity. As Depew recognizes, in his view T. H. Huxley, Darwin's most formidable advocate in the years following the *Origin*, yet who always doubted the paramount power of natural selection, would fail to qualify as a "Darwinian." Presumably all biologists who consider natural selection to be "*the* fundamental idea in biological evolution" (Pigliucci 2017), despite their other differences, would qualify as Darwinians in the fullest sense of that term. Dawkins almost certainly would be included; Gould, most likely, would not.

An even more liberal approach is taken by Richard Delisle (2011: 57) who treats "Darwinism broadly construed [as] any evolutionary approach that appeals to natural selection." Here, natural selection need not even be the primary explanatory concept. This inclusivist strategy permits biologists as diverse in their understandings of the evolutionary process and its implications as Julian Huxley and George Gaylord Simpson, or Richard Dawkins and Stephen Jay Gould, to equally represent "Darwinism" while differing on many fundamental issues. Likewise, various neo-Lamarckian, neo-vitalist, and "romanticist" biological theories that flourished in the early years of the twentieth century would qualify as *fully* "Darwinian" on this liberal account inasmuch as their proponents generally attributed *some* role to natural selection (Esposito 2017). Only those approaches that deny or fail to mention *any* role for natural selection would remain outside, e.g., those forms of Lamarckism that flourished in France right through the mid-twentieth century (Loison and Herring 2017). More problematic cases include creationists who grudgingly accept some role for natural selection (typically restricted to microevolution) and extraterrestrial biologists who (we might suppose) have never heard of Charles Darwin, yet nonetheless embrace the *principle* of natural selection without, presumably, calling it that.[10]

An even more accommodating approach would be to include within the Darwinian fold all those biological theories that are *compatible* with Darwin's emphasis on the importance of natural selection, even if the proponents of those theories did not see it that way. Understood in this way, "Darwinism" might encompass some theories explicitly put forth as *anti*-Darwinian (Kutschera 2017) so long as, with hindsight, logical compatibility can be established.

The foregoing approaches all seek to characterize "Darwinism" conceptually, sometimes treating "Darwinian" and "Darwinism" as logically co-extensive. David Hull (1985: 809) distinguishes between "the Darwinians" as a *social group* and "Darwinism" as a *conceptual system* and maintains that a scientist can be a Darwinian without accepting all or even a large proportion of tenets identified with Darwinism; conversely, a scientist can accept the tenets of Darwinism without being a Darwinian. For example, in various ways Thomas Henry Huxley, Asa Gray, Alfred Russel Wallace, Ernst Haeckel, Charles Lyell, and Herbert Spencer could be considered "Darwinians" inasmuch as each accepted and promoted elements of Darwin's theory. But each also *rejected* important elements of Darwin's views. Huxley preferred saltationism to Darwin's gradualist perspective. Gray reserved a place for divine guidance in the evolutionary process. Lyell could never bring himself to extend evolutionary theory to include human beings. Even Wallace, the co-discoverer of natural selection, eventually came to doubt the power of selection to account for man's spiritual nature. Michael Ruse (1979: 203) had earlier suggested that a Darwinian is "someone who identifies with Darwin, not necessarily someone who accepted all of Darwin's ideas." In this view, one can be a "Darwinian" without accepting even key elements of "Darwinism" (whatever those may be).

Hull's bifurcation distinguishes "the Darwinians" as a social group from "Darwinism" as a conceptual system. Given some of the difficulties of defining "Darwinism" conceptually, it may be tempting to collapse Hull's distinction by treating "Darwinism" as whatever it is that unites Darwinians into a cohesive social group, thereby obviating the need to define "Darwinism." As Richard Delisle (2011: 50) observes, however, the dominant historiography of evolutionary biology since Darwin classifies biologists as belonging to one or the other side of a Darwinian versus non-Darwinian divide, thereby requiring historians of biology to wield *some* principle, explicitly or implicitly, for deciding who belongs in which camp—which returns us once again to the question of what is distinctive of "Darwinism."

[10]It is worth noting that Delisle (2017) expresses skepticism about the "extreme pluralism" that Darwin presents in the *Origin* as "being reducible to a sort of neat, compact, and abstract theoretical construct."

A view that seems to capture what is usually meant by "Darwinism," without leading to counterintuitive consequences (e.g., extraterrestrial Darwinians), treats it as a scientific research program roughly as described by Imre Lakatos (1970) as consisting of an incorrigible "hard core" that distinguishes that program from competing programs, surrounded by a malleable "protective belt" that permits considerable modification of the theory's "auxiliary hypotheses." The hard core of Darwinism is the central importance accorded to natural selection. That was Darwin's most novel, influential, and enduring contribution to evolutionary theorizing. But Darwinism as a research program consists of more than that. It consists of those evolutionists, their professional affiliations, research activities, products, and beliefs that constitute a nexus of causal interactions centered on a shared recognition of the fundamental importance of the seminal scientific ideas of Charles Darwin. In this view, the evolutionary theorizing and research activities of almost all mid- to late-twentieth-century biologists, Dawkins and Gould included, constitute "Darwinism." It also includes the theorizing and research activities of virtually all contemporary evolutionists, but not that of creationists nor (presumably) that of extraterrestrial biologists. "Darwinism" in this sense can be understood as a historically evolving approach to understanding life that takes Darwin's emphasis on natural selection as its origin and point of departure, but that given Darwin's pluralistic theorizing can be, has been, and presumably will continue to be, developed in significantly different ways.

8 Conclusions

Construing Darwinism as a scientific research program leaves open the question of precisely how many Darwinian traditions there are. As in biological systematics, so, too, in the history of science, there are "lumpers" and "splitters." Lumpers who emphasize commonalities will see just one, albeit multiform, Darwinian tradition. Splitters who emphasize differences may see two or more divergent Darwinian traditions. What our discussion of the Dawkins–Gould rivalry should make clear is the fact that *scientists* often care a great deal about whether their view is, or seen to be, part of a specific scientific tradition. This fact signals something important about the power of the *idea* of such traditions to shape scientific rhetoric and research agendas. "Darwinism" as a pluralistic scientific research program that can encompass a number of identifiable Darwinian traditions is flexible enough to undergo significant additions, alterations, and adjustments while retaining its distinctive identity. Consequently, reports of the *de facto* or imminent "dissolution of Darwinism" (a phrase which, shorn of its scholarly qualifications, can easily be exploited by those promoting an anti-science agenda) at present seem premature. If the past is any guide, then barring any truly revolutionary developments, Darwinism will continue to evolve in response to the multiplicity of demands placed upon it.

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