Two Historical Investigations in Evolutionary Biology

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1. The history of form and the forms of history: Stephen Jay Gould between D'Arcy Thompson and Charles Darwin

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> "Our greatest intellectual adventures often occur within ourselves—not in the restless search for new facts and new objects on the earth or in the stars, but from a need to expunge old prejudices and build new conceptual structures. No hunt can promise a sweeter reward, a more admirable goal, than the excitement of thoroughly revised understanding—the inward journey that thrills real scholars and scares the bejesus us out of the rest of us" (Gould 2001, p. 355).

> "Steve…was first and always a morphologist and developmentalist" (Eldredge 2013, p. 6).

Introduction: Stephen Jay Gould and the science of form

The story of Stephen Jay Gould's evolutionary philosophy has yet to be fully told, because I suspect it cannot be fully told. For one thing, there is no univocal philosophy to which Gould's name attaches (Ruse 1996, pp. 494-507, Thomas 2009). His views changed as he aged, not as a scaling-up of ancestral potentialities, but rather as a series of heterochronies involving both translocations and deletions. Some of these fell in line with broader trends in scientific thought, for instance, the surge of interest in stochasticity following MacArthur and Wilson's publication (1963, see also MacArthur & Wilson 1967). Others resonated to more idiosyncratic desires, including Gould's lifelong wish "to be seen as a major architect of evolutionary theory" (Stearns 2002, p. 2341).

Gould was a creature of his time, by deliberate choice and sustained effort. He felt the manifold pressures of his age, and adjusted his thinking as the situation seemed to demand (Prindle 2009).[1] If we could "replay the tape" of Gould—changing, perhaps, some adventitious parameter—it is entirely conceivable that a different thinker would emerge (David Sepkoski raises a number of interesting counterfactuals in his book, *Rereading the Fossil Record*). Yet in holding with another of Gould's themes, the seeming contingency of his thought does not render it unintelligible. It simply requires that we understand the man in the context of his changing concerns (see Allmon 2009, Perez 2013, Perez Sheldon 2014). The historical Gould was a multifaceted thinker, and not always self-consistent. This presents certain difficulties for the student of history, and may indicate that a synthetic portrait is an unrealistic goal (it will not be mine).

Curiously, we lack a robust account of Gould's early intellectual development, spanning his time as a graduate student and culminating in his meteoric rise during the nineteen-seventies. Part of the reason, no doubt, is Gould's own attitude towards this period, which is by turns dismissive and derogatory (see Gould 2002, pp. 41, 1183).[2] Another reason is the scholarly habit of homogenizing an author's works, by locating in a set of writings a small number of coordinating themes. Gould's writings are sufficiently consistent (enough subjects carry through his entire corpus) that the homogenizing strategy provides some genuine insights. Warren D. Allmon provides a deft analysis of Gould's career that utilizes punctuated equilibria as a coordinating theme (Allmon 2009). The political scientist David Prindle attempts a similar feat while focusing on Gould's humanism—with less success (Prindle 2009). However, neither of these authors has

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[1] I do not wish to impute to Gould any malfeasance—only to note that his thinking on biological topics not infrequently had a social dimension (see Segerstråle 2003, Prindle 2009, Perez 2013). In the words of Ullica Segerstråle: "Gould went a step further than [the majority of] his leftist colleagues" during the sociobiology debate. "Knowing the ease with which people will…employ scientific theories as a basis for their social and moral reasoning, how could one make sure that theories with potential social implications would not have adverse social consequences? Gould's solution was extraordinary. His answer to the dilemma was to deliberately develop theories that, if applied to humans and social affairs, just might lead to the "correct" political conclusions!" (Segerstråle 2003, p. 474).

[2] An exception to this is the review paper of 1966, of which Gould was justly proud, and which continues to be heavily cited (Princehouse 2009, p. 156).

much to say about the first decade of Gould's career, beyond noting the obvious influence of *On Growth and Form* (Thompson 1942, see Allmon 2009, p. 24).[1] Richard Bambach fares better on this count, but insists on reading Gould's earliest publications in light of his later theoretical commitments, suggesting, perhaps, that these existed *in potentia* all along (Bambach 2009, pp. 74-75). While this is not necessarily wrong, it forecloses the possibility that Gould's philosophy underwent a sizable shift during the nineteen-seventies. I believe that it did, and that our understanding of this episode has been hindered by a regrettable ignorance of Gould's early motivations and influences.

"Gould's laws"

This essay was motivated by one recent (and, I think, largely successful) attempt to identify a unifying thread in Gould's writings—that of the philosopher Chris Haufe (2015). As Haufe describes his project:

> Much of Stephen Jay Gould's legacy is dominated by his views on the contingency of evolutionary history expressed in his classic *Wonderful Life*. However, Gould also campaigned relentlessly for a "nomothetic" paleontology…I argue that Gould's conception of science and natural law combined with his commitment to contingency to produce an evolutionary science centered around the formulation of higher-level evolutionary laws (Haufe 2015, p. 1).

While Haufe's account is on the whole compelling, it risks oversimplification by slurring over a major change in Gould's philosophy consequent on the abandonment of his early research program. Additionally, Haufe mischaracterizes Gould's views on the nature of history (ca. 1970), as well as the function of idealized models in his proposed science of form. Much of the confusion stems from an anachronistic reading of Gould's 1970 paper, "Dollo on Dollo's law," in which the author "openly debates the question of how to

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[1] The historian Patricia Princehouse also mentions the connection between *On Growth and Form* and Gould's first study organism, *Poecilozonites*, but gets the arrow of causality backwards (Princehouse 2009, pp. 155-156). *Poecilozonites* did not lead Gould to appreciate D'Arcy Thompson; Gould's admiration for Thompson predisposed him to appreciate *Poecilozonites*.

reconcile [his nomothetic approach to science]…with undeniable nomothetic complications posed by contingency" (Haufe 2015, p. 6,). But contingency was not on Gould's mind in 1970—at least not in the sense identified by John Beatty (2006, pp. 338-340).[1] While this does not vitiate Haufe's thesis that Gould "conceived of the science of evolution as a science of laws," it does illustrate the danger of interpreting a thinker's early works in terms of a later theoretical and ideological agenda.[2]

Thompson and Darwin: a prefatory note

> "I used to think (long ago and with my strong internalist, Platonist, D'Arcy Thompsonian biases) that mass extinction was just a whiz-bang phenomenology with no lasting importance…Now you have all helped me to realize that it truly is a separate process, and a cardinal shaping force for patterns in life's history" (Gould to L. and W. Alvarez, D. Jablonski, D. Raup, A. Seilacher and J. Sepkoski, 1983, quoted in Allmon 2009, p. 55).

Presentation of the hypothesis

Doubtless there are multiple ways to approach the subject of Gould's philosophical upheaval, each with a certain claim to truth. Yet "coherence demands a synthetic theme," and this may be found, if my thesis is correct, in Gould's relation to two seminal thinkers.

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[1] In fact, Beatty identifies two versions of contingency at work within Gould's *Wonderful Life*, which he terms "unpredictability" and "causal dependence" (see Beatty 2006, pp. 338-340).

[2] Having said that, I am not at all convinced that Gould conceived of evolutionary biology as "a science of laws." A better (if less sexy) expression might be "a science of *causes*," but this is neither surprising nor original. Gould's campaign to introduce nomothetic methods (i.e., mathematical modeling) into *paleobiology* had more to do with traditional habits of thought in *paleontology* than a grand vision for *evolutionary biology*. And even within paleobiology, Gould's 'lawmaking enterprise' consisted largely of identifying nonhistoric or statistical causes of particular phenomena, for instance, clade shape and the morphologic coherence of major groups (Raup et al. 1973, Gould et al. 1977, Raup & Gould 1974). Not all causes must be *mechanisms*, after all. It is entirely legitimate to say that a particular phenomenon has a statistical, as opposed to a deterministic, cause. Yet I suspect the term "causal" did not suffice to highlight the uniqueness of the MBL approach, which sought general insights in computerized simulations. (For background on the MBL collaboration, see Raup 1977, Gould 1978a, Sepkoski 2012, Ch. 7. For Gould's defense of the term nomothetic, see Sepkoski 2012, p. 235.)

The first of these is D'Arcy Thompson, renowned polymath and Gould's "earliest intellectual hero" (Gould 1995, p. 3). The second is Charles Darwin. I propose that we can understand Gould's intellectual development as a *transit* between these counterposed intellectual spheres. To wit, the Gould of D'Arcy Thompson was a *de facto* determinist who championed "mechanical improvement" as a window to evolutionary history (Gould 1970a, pp. 108-112). He cared deeply for the professional standing of paleontology (especially invertebrate paleontology), and regarded its problematic as 'the explanation of phylogenetic events by the subsumption of their antecedent conditions under general laws' (Gould 1969a, p. 410). "Darwinian Gould," by contrast, was an outspoken indeterminist, a proponent of narrative explanation, and a staunch methodological pluralist (Gould 2002, pp. 1333, 1337). Rather than foregrounding the nomothetic aspects of inquiry, he stressed that explanations of evolutionary events must have reference to "the specific contingencies of antecedent states, which, if constituted differently, could not have produced the observed result" (p. 1333). (Careful readers will notice that the latter is not the philosophy of nature underlying "Punctuated equilibria: an alternative to phyletic gradualism" (Eldredge & Gould 1972). It was only *after* 1972 that Gould swore off his "Thompsonian biases," meaning that his most famous scientific contribution dates to the largely ignored 'prehistory' of his thought (Gould to Alvarez et al., 1983, quoted in Allmon 2009, p. 55). Surely this is reason enough to attempt an understanding of the period it on its own terms.)

Even as an undergraduate, Gould was attracted to the polymathic scholarship of D'Arcy Thompson, as a large number of twentieth century biologists have been. Thompson's was a broad and powerful mind, which moved effortlessly between natural science, mathematics and the classics (his father's vocation, delightfully described by G. Evelyn Hutchinson). In each these he was a *bona fide* expert, capable of holding a first-rate university chair. Moreover, he was a prose stylist without peer in the natural sciences, and adorned his view of nature with many a literary confection:

> [The] waves of the sea, the little ripples on the shore, the sweeping curve of the sandy bay between the headlands, the outline of the hills, the shape of the clouds, all these are so many riddles of form, so many problems of morphology, and all of them the physicist can more or less easily read and adequately solve; solving them by reference to their antecedent phenomena, and to which we interpret them as being due (Thompson 1942, p. 10).

Gould's early writing is shot through with Thompson's handsome, geometrical worldview. It was Thompson who inspired his first publication ("Form in biology," published in *The Antioch Review* (1963)), and Thompson who formed the keel of his 1966 article, "Allometry and Size in Ontogeny and Phylogeny." What's more, Gould's first essay in *Natural History* (entitled "Size and shape") is a veritable paean to Thompsonian structuralism (Gould 1974b). With it, Gould discloses the aim of his early career, which was, as he had earlier alluded, to "Darwinize" D'Arcy Thompson (see Gould 1971a). There exists a widespread belief "that the exuberant diversity of life will forever frustrate our arrogant claims to omniscience," Gould observes.

> Yet, however much we celebrate diversity and revel in the peculiarities of animals [*sic*], we must also acknowledge a striking "lawfulness" in the basic design of organisms. This regularity is most strongly evident in the correlation of size and shape (Gould 1977b, p. 171).

This statement speaks to a common theme of Gould's early work: the rendering of complexity by a small number of causal factors. Like Thompson, Gould believed that intelligibility resides in simplicity; we may get closer to the causes of form by resolving complexity into separate influences upon growth. From here, the investigator can proceed to address problems that Thompson never did, for instance, the functional significance of particular growth patterns (which is a problem separate from their derivation). But the goal of inquiry is, in a sense, unchanged. To *understand* is to relate multifarious complexity to lawlike simplicity, and such simplicity permeates the material world.

Fast-forward two decades, and Gould's affections had changed. "Many scientists, if only to coin a striking metaphor, depict a creating God as a mathematician from the realm of Plato or Pythagoras," Gould observed in 1995 (p. 3). (Immediately preceding this statement, the author had quoted from *Growth and Form*, "For the harmony of the world is made manifest in Form and Number, and the heart and soul of all poetry of Natural Philosophy are embodied in the concept of mathematical beauty" (Thompson 1942, pp. 1096-1097). Had he continued the quotation, it would have read: "…Not only the movements of the heavenly host must be determined by observation and elucidated by mathematics, but whatsoever else can be expressed by number and defined by natural law. This is the teaching of Plato and Pythagoras, and the message of Greek wisdom to mankind.") However in spite of the power of mathematics to describe certain natural phenomena, much of nature is "messy and multifarious, markedly resistant to simple mathematical expression" (Gould 1995, p. 3). "Even the preeminent field for abstract, quantified beauty [celestial mechanics]…includes ever so many awfully messy and downright inconvenient irregularities" (Gould 1995, p. 4).

This passage finds Gould at his most "Darwinian": vigorous, feisty and forever skeptical of the "narrowness of physical scientists in debasing natural history" (Gould 2002, p. 1334). Or at least this was his idiosyncratic take on Charles Darwin's worldview (see Gould 1989a, pp. 290-291, 299-301). As Gould came to understand it, Darwin lived in a world ruled by contingency, and the messy irregularities of history.[1] Indeed, Gould

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[1] "I assert the powerful role of contingency in Darwin's system not as a logical corollary of his theory, but as an explicit theme central to his own life and work," Gould wrote in *Wonderful Life.* Darwin invoked contingency "as his primary support for the fact of evolution itself…[if] whales retained no trace of terrestrial heritage, if pandas bore perfect thumbs, if life on the Galápagos neatly matched the curious local environments, then history would not inhere in the productions of nature. But contingencies of 'just history' do shape our world, and evolution lies exposed in the

went so far as to depict the *Origin*'s famous peroration as a *satire* of the claim that the physical sciences represent a pinnacle of sophistication, with natural history lagging far behind:

> Note how Darwin contrasts the dull repetitiveness of planetary cycling (despite the elegance and simplicity of its quantitative expression) with the gutsy glory of rich diversity on life's ever rising and expanding tree. Darwin even gives his metaphor a geometric flavor, as he contrasts the horizontal solar system…with the vertical tree of life, starting in utmost simplicity at the bottom, and rising right through the horizontality of this repetitive physical setting towards the heavenly heights of magnificent and ever expanding diversity (Gould 2002, p. 1334).

As bizarre as this interpretation is, it says a great deal about the sensibilities of its author. Gould had indeed traversed a great distance during the 1970s and '80s, and made a complete transit between Thompson and Darwin. In what follows, I will endeavor to give the *how* and the *why* of this transit, taking into account a number of pertinent factors. To my knowledge, this project has yet to be undertaken (although the essays of Princehouse (2009) and Thomas (2009) contain some pregnant comments). It is my hope that by addressing this crucial period in Gould's career, a richer account might emerge of his intellectual development, and of the development of twentieth century evolutionary biology.

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panoply of structures that have no other explanation than the shadow of their past" (Gould 1989a, pp. 300-301).

Life's Nature and Structure: Gould's Thompsonian program

> "Good scholars struggle to understand the world in an integral way…These visions of reality…demand our respect, for they are an intellectuals only birthright. They are often entirely wrong and always flawed in serious ways, but they must be understood honorably and not subjected to mayhem by excision of patches" (Gould 1993b, p. 136).

Evolutionary paleontology and the science of form

Stephen Jay Gould was born in 1941 in Bayside, Queens, and completed his Bachelor's degree at Antioch College in 1963.[1] His earliest intellectual hero was the Scottish polymath D'Arcy Wentworth Thompson—a talented morphologist and incomparable prose stylist (Gould 1995, p. 3). As an undergraduate, Gould admired Thompson's scholarship without measure, and made of it the subject of his senior thesis (published as "Form in Biology" in *The Antioch Review*). Probably it was Thompson's study of equiangular spirals that launched Gould on the course that would culminate in his Ph.D. dissertation. As Niles Eldredge recalls:

> Steve had discovered (or Prof. [J.F.] White had shown him) an unwrapped, unstudied collection of Bermudan Pleistocene land snails [*Poecilozonites*] in the basement of the Geology Department at Antioch…[S]mitten with the geometric growth of these well-preserved snails…[he] vowed to one day make them the subject of his doctoral dissertation (Eldredge 2013, p. 6).

Gould was as good as his word, and after "the usual scaling down of initial plans, produced a Ph.D. dissertation on the species *P. cupula* and *P. bermudensis* in 1967" (Gould 1969a, p. 409). A monograph entitled "An Evolutionary Microcosm" soon followed, at which time Gould had left Columbia University for Harvard. Through the

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[1] Antioch is a private liberal arts college in Yellow Springs, Ohio, which was "considered a bastion of progressive thought, social activism, and defense of free speech" (Perez 2013, p. 105). Its charming motto—"*Be ashamed to die until you have won some victory for humanity*"—befitted at least one of its graduates.

vicissitudes of a growing celebrity, he continued to publish morphological papers until the final years of his life, mostly on the land snail *Cerion* (e.g., Gould 1969a, 1971c, 1984, 1989b, 1997, Gould & Johnson 1986). Additionally, he co-authored with R.F. Johnson a lengthy paper advocating multivariate approaches to the study of geographical variation (Gould & Johnson 1972, see also Woodruff & Gould 1980 on speciation).[1] Although it is rarely mentioned, Gould's first empirical work was not given over entirely to the study of (ontogenetic) allometry, but concerned instead the detection of "subtle variations in morphology that characterize geographic variation and incipient differentiation within species" (Gould 1969a, p. 422).

If there is a coordinating theme of Gould's early work, it is the application of multivariate statistical analysis to the problems of paleontology (e.g., Gould 1967, 1968, 1969a, 1973b). Indeed, multivariate analysis represented, to Gould, something more than a set of techniques—it was a systematic approach to the problems of life. "[We] must emphasize the influence that this new technology, or any new technology for that matter, must have upon our approach to a problem," Gould wrote of computerized multivariate analysis in 1972. "A new method is not simply a neutral tool for the resolution of issues in well-established ways." Instead, "it imposes its capabilities upon the questions we ask and even upon the theories that support these questions" (Gould & Johnson 1972, p. 488). (Gould would make essentially the same point in "Punctuated equilibria," leveraging

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[1] Curiously, this paper, which was published in the same year as "Punctuated equilibria," closes with the confident assertion that "the allopatric orthodoxy is about to yield its exclusive and pluralistic view that welcomes and expects sympatric speciation" (Gould & Johnson 1972, p. 489). This pluralistic crusade reached the apex of its curve eight years later, where, in a famous paper, Gould urged the outright abandonment of the terms "allopatric" and "sympatric" (Gould 1980c, p. 123). Although Gould would later deny it, this was obviously an attempt to win for punctuationism some share of the microevolutionary pie.

Kuhn, Feyerabend and Hanson to argue that all scientific inquiry is colored by theory (Eldredge & Gould 1972, pp. 84-86).)[1]

Gould left Columbia as an evolutionary paleontologist of a somewhat singular persuasion. Although he did not express himself thus, his fondest hope was to furnish a Darwinian rationalization of Thompson's structuralism—a means of judging "the adaptive reasons for specific pathways in the phylogeny of form" (Gould 1970a, p. 85). This was to be achieved through "a mild mechanistic reductionism," which wed the elegance of classical morphometrics with the sophistication of multivariate statistics. "A science of form is now being forged within evolutionary theory," Gould declared in a 1970 manifesto, "Evolutionary paleontology and the science of form." "It studies adaptation by quantitative methods, using the organism-machine analogy as a guide; it seeks to reduce complex form to fewer generating factors and causal influences" (Gould 1970a, p. 77). Most importantly, it utilizes multivariate statistics, which (though long desired) have hitherto been ignored because of the sheer labor of calculation involved (Gould 1971a, p. 253). It was for precisely this reason, Gould believed, that D'Arcy Thompson's promising start had foundered:

> Unfortunately, D'Arcy Thompson was about one half-century too early. His approach to form was multivariate in conception; hence it suffered the misfortune of much prophesy—it could not be used in its own time (Gould 1971a, pp. 253-254).

With the advent of high-speed computing, Thompson's vindication appeared to be at hand (Gould 1971a, p. 254). "I am convinced that the computer can be to the science of form what the microscope, telescope and electron accelerator were to their respective fields," Gould wrote in "Evolutionary paleontology" (p. 102). His confidence stemmed from the fact that multivariate approaches had long been desired by students of form, and

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[1] I say "Gould" instead of "Eldredge and Gould," because Gould wrote the opening section of the paper, with little or no input from Eldredge.

sometimes openly advocated (e.g., Burma 1948, 1949). Bivariate methods had achieved widespread currency for reasons of simple tractability (a crucial consideration in the era of manual calculation). But this constraint had now been lifted, and biologists could look forward to an era in which important questions—hitherto intractable—could finally be posed in a meaningful way. For instance, utilizing an analog computer, David Raup had generated a four-dimensional space which contained "most of the theoretically possible [forms]" of coiled shells. (While this study did not utilize multivariate statistics, it was, like Thompson's work, 'multivariate in conception.') From here Raup proceeded to make a number of pregnant observations regarding the occupation of theoretical morphospace:

> When the geometries of naturally occurring species are plotted in [morphospace], it becomes evident that it is not evenly filled. Evolution has favored some regions while leaving others essentially empty. In the empty regions we are presumably dealing with forms which are geometrically possible but biologically impossible or functionally inefficient…It is often easier to explain the absence of forms than their presence (Raup & Michelson 1965, p. 1294).

Gould saw Raup's studies as touching a fundamental issue in the study of form, and one that resonated with his own empirical work. Consequently, he tended to cite Raup in conjunction with Thompson's vector model (1942, pp. 748-849), as well as his own work on shell morphology and allometry (e.g., Gould 1966a, 1966b, 1969a). Raup himself had earlier drawn attention to the connection with Thompson, noting that while the geometry of gastropod shells had been a popular subject for speculation in the 18th and 19th century, the meat of such discussions was synthesized by Thompson "[whose] principal thesis…is that growth in coiled forms follows rather rigid mathematical laws" (Raup 1961, pp. 602-603):

> Thompson's scheme for describing the gastropod shell does not consider such features as ornamentation, growth lines, or the form of the protoconch: it is intended only to include the basic shape upon which the complete morphology is built. As such, it is an idea which should be exceedingly attractive to the zoologist and the paleontologist. From the viewpoint of pure description it represents an attempt to

> diagnose shell form in terms of *truly natural parameters* related to growth, rather than in terms of arbitrary characters such as width of body whorl or spire height" (p. 603, emphasis added).

Although the connection between these men was not as clear as Gould liked to think, it was nonetheless deeply engrained in his mind. Gould was the chief evangel of Thompsonian biometry, and Raup was the man extending Thompson's greatest insight into new conceptual spaces (Raup 1966, 1967). Gould, in turn, was utilizing an allied approach to infer the rules of ontogenetic allometry in actual specimens (Gould 1968, 1969a, pp. 421-422).[1] Since allometry "gives insight into the relationship of form and habit," the study of ontogeny is capable of throwing light on why certain areas of morphospace are densely crowded and others scarcely occupied (see Gould 1968, p. 97, Gould and Calloway 1980, p. 395). Thus the ends meet; the inductive mode is complementary to the deductive. Additionally, as even moderately complex allometries defied deductive treatment in the 1970s, a successful science of form *required* an inductive mode, which can infer rules of growth from clusters of covarying characters. It was this inductive mode that Gould sought to develop in his *Poecilozonites* research.

Allometry and adaptation in Poecilozonites

No theme so dominated Gould's "Thompsonian period" as *allometry*: differences in shape that systematically accompany changes in size (Gould 1966a, 1966b, 1968, 1971d, 1972, 1973a, 1974a). In part, this was due to his study organism, *Poecilozonites bermudensis*, a pulmonate land snail endemic to the Bermudan archipelago. As Gould

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[1] Raup's deductive approach to the study of shell coiling relies on the isometry of spiral geometry throughout the growth process (that is, on non-allometric growth). Although simple allometries can be incorporated into his model (by redefining parameters as variables instead of constants), non-gradual and non-regular trends require inductive treatment.

quickly discovered, significant allometry occurs "during the ontogeny of every variable in *P. bermudensis*," including shell color, shell thickness, and external shape (Gould 1968, p. 81).[1] Still more interesting, however, was the natural history of the species. In a brief 300,000 years, *P.b. zonatus* gave rise, in iterative fashion, to no less than *four* paedomorphic offshoots, each of which is more weakly colored, thinner shelled and relatively wider than its parent form (Gould 1969a, p. 408).[2] Now consider the following two points, as phrased by Gould:

1. **Allometry** "often gives insight into the relationship of form and habit" (Gould 1968, p. 82), and
2. **Heterochrony** "has allometry as a necessary consequence of its occurrence" (p. 83).

How can knowledge of ontogeny provide insight into the relationship of form and habit? Gould's study of ontogenic allometry in *Poecilozonites* furnishes an excellent case study. Land snails move by gliding upon a muscular, hydrostatic foot, which exudes an adhesive mucus—source of the infamous "slime trail." If a snail grows isometrically (maintaining geometric similarity among its parts) the volume of the shell will increase faster than the surface area of the foot. Such "non-allometric" growth, if carried on long enough, will result in a situation in which the foot can no longer discharge its ancestral offices. When a snail reaches a certain weight relative the surface area of its foot, it will no longer be able to perform wet adhesion ("sticking" to a surface). This constitutes a significant impediment for the snail, as it is this faculty that enables the organism to mount vertical

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[1] Snail shells are accretionary structures, meaning that they retain a near complete record of their morphological development—even as fossils (Rudwick 1968). "If shape changes during ontogeny…then a description of the sequence of forms attained at various sizes or whorl numbers provides the basis for interpreting relationships between ontogeny and phylogeny," Gould writes. "[The] size of the origin of new features can be determined; phyletic alterations of form can be understood as the cumulative effect of ontogenetic changes in growth rates; [and] paedomorphic or recapitulatory effects can be easily spotted" (Gould 1969, p. 420).

[2] Paedomorphosis is a kind of heterochrony achieved by the speeding of sexual maturation (progenesis) or the slowing of somatic development (neoteny).

structures (Gould 1968, p. 85). Significant positive allometry of foot growth—or the development of a foot initially large enough to withstand the effects of isometric growth—is prerequisite for an adult snail to retain its ability to climb. In other words, the snail needs to grow in such a manner as maintains a favorable ratio of foot surface area to weight *if* it is to perform this behavior at adult sizes.

To Gould, this constituted a sufficient explanation of shell allometry in *Poecilozonites*. A more domed shell, produced by relative height increase (thus rounding the aperture through which the foot is extruded), "provides additional internal volume for a foot growing by positive allometry" (Gould 1968, p. 89). It is obvious enough how this could benefit a snail, by deconstraining the size of the foot. But how does this knowledge help to illuminate the phylogeny of the group? Paedomorphic land snails possess proportionally wider shells than their non-paedomorphic ancestors, which are also drabber, and paper-thin. Additionally, their apertures are condensed relative to those of non-paedomorphic adults, effectively limiting the size of the foot. On its face, both of these traits would seem to be bad news for the snail. Thin shells are more liable to break, and will sequester fewer minerals than their thickened counterparts. (Calcium limitation has been linked with decreased growth rate, survivorship and fecundity in pulmonates.) Additionally, thinner apertures afford less room for the extrusion of the foot, limiting its size and its ability to perform wet adhesion. (Of course, thinner shells are also lighter, which somewhat offsets the decrease in maximum size.) The question thus arises: why did paedomorphs repeatedly evolve (and gain a toehold during periods of glacial retreat) in spite of this apparently inferior design? Why have multiple offshoots of *P.b. zonatus* forgone the seeming benefits of ontogenetic allometry in order to assume the squat and drab morphology of ancestral juveniles? Gould's studies suggest an answer.

Utilizing Q-mode factor analysis, Gould documented four independent episodes of paedomorphosis, all of them taking place on glacial red soils. (While the inference of paedomorphosis does not require multivariate statistics, nonetheless *some* knowledge of ontogenetic allometry is required to support the hypothesis.)[1] As glacial soils are virtually lime-free, and most pulmonates build their shells from ingested limestone, Gould suggested that the adaptive significance of paedomorphosis "may be related to the advantages of thin shells in [low] calcium environments" (Gould 1969a, p. 408). In specific, he proposed that neoteny (literally 'holding onto youth') enabled snails to become established on glacial red soils by forestalling positive allometry of shell growth. (Paedomorphosis, Gould notes, "did not evolve in times of carbonate-dune depression.") Adult paedomorphs were "scaled up replicas of juvenile shells of the central stock," which achieved shell thinning by "a slowdown in retardation of rapid juvenile growth rates" (Gould 1968, p. 93). As a consequence of this slowdown, Gould speculated, features that appear late in the ontogeny of nonpaedomorphs fail to develop in paedomorphs:

> If the gonads of paedomorphs and nonpaedomorphs mature at approximately the same time after hatching, the paedomorph will be larger at this time due to its maintenance of the high juvenile growth rate. Since both paedomorphs and non-paedomorphs reach the same adult size and whorl number, features which appear late in the ontogeny of nonpaedomorphs will be so delayed in size of appearance in paedomorphs that they never develop at all (Gould 1968, p. 93).

Happily, the temporal and spatial resolution of the *Poecilozonites* data were sufficient to reveal that splitting occurred at the periphery of the species range, just as Mayr's peripatric model requires (1963, Ch. 16). This enabled Gould to account for the apparent discontinuities in the fossil record. They *were* discontinuities, Gould insisted, and they had occurred by cladogenesis (in specific, the budding off of a peripheral isolate). "The

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[1] What factor analysis enabled Gould to demonstrate was that the shape of adult paedomorphs more closely resembled the shape of juveniles of the parent stock than adults. Remarkably, the first two axes explained more than 95% of the total information (as size nearly always associates with the first principal component, data bearing on size were exempted from the analysis). Additionally, the various subspecies paedomorphs were shown to more closely resemble one another than members of the central *P.b. zonatus* stock.

proposition that two taxa, one a paedomorphic derivative of the other, inhabited Bermuda during the Shore Hills-Southampton interval is the simplest phyletic interpretation that can be given to the distribution of paedomorphic samples" (Gould 1969a, p. 473). But although this was the simplest explanation, and the one a traditional paleontologist would be most likely to give, it was dead wrong. "I found a more complex story, involving an unusually literal interpretation of paleontological data. Each of the four discontinuous occurrences represents an independent episode of paedomorphosis." (It is interesting to note that in 1968, Gould expressed surprise that his data could be interpreted so literally (p. 93). He reiterated his surprise in 1969, seemingly indicating that the mode of interpretation was not general. Presumably it was Eldredge who helped to jog him from this familiar mode of thought, although Gould later indicated that the prevalence of stasis in the fossil record had been apparent from an early date (Gould 1989c).)

One final comment is in order. Since paedomorphosis can effectively "unbind morphology from selective control" (Gould 1977a), the price of misinterpretation is strong.[1] Investigators engaged in explaining a paedomorphic event (without identifying it as paedomorphic) are likely to posit an independent selective advantage for each juvenilized character. (Recall that in *Poecilozonites*, all shell characters display significant allometry, and are therefore affected by paedomorphic events.) Alternatively, they might posit a number of correlates of a "primary adaptation" selected from a static spectrum of variation at adult sizes (Gould 1969a, p. 472). However, if the true explanation of the event involves a heterochronic change, the traditional Darwinian account is likely to misfire. Perhaps selection was merely acting on maturation time, or a single character like shell thickness (achieved not by selection from the normal spread of

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[1] The type of paedomorphosis responsible for this "unbinding" is progenesis (see Gould 1977a, p. 388).

adult phenotypes, but by changes in developmental rate).[1] It follows that only through allometric analysis can the phylogeny of a group like *Poecilozonites* be properly assessed. While there is no simple relationship between ontogeny and phylogeny, ontogenetic data *cannot be ignored* in the study of evolution—at least no more than geographic or stratigraphic data. And perhaps more importantly, multivariate analyses of form can aid in the study of evolution.

The Huxley dimension: clades, grades and "transspecific evolution"

As late as the mid-seventies, Gould's view of life was predicated on the idea of mechanical improvement, then a commonplace among evolutionary biologists. Possibly he received this perspective from Julian Huxley, the celebrated biologist who had commissioned Gould's allometry paper of 1966. "I was just awestruck by Huxley," Gould recalled in 1998, "and so I wrote him a long letter saying how much his work had meant to me" (quoted in Princehouse 2009, p. 156). Gould was not alone in his estimation of Sir Julian. Throughout the middle of the century, Huxley was the most famous evolutionary biologist in the world, and Britain's 'Public Scientist Number One.' "A voracious reader, an international traveler, and an indefatigable promoter of science," it is easy to see what Gould found admirable in Huxley (Smocovitis 1996, p. 138). But Gould admired Huxley for many reasons, not the least of which was an important

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[1] It might be worried that there is some linguistic trickery here. After all, are not paedomorphs part of the normal spread of phenotypic variation? (An alternative is to consider them *discontinuous* variants, and thus removed from the normal spread of phenotypic variability.) And is not the target of selection the phenotypic character itself, not developmental rate? While the answer to both these questions may be 'yes,' the relevant point is that identifying a phenotype as paedomorphic adds something to the explanation over and above the claim that selection acted on an aspect of the phenotype. Moreover, as Gould was beginning to realize, developmental timing (and specifically *the timing of maturation*) is often an adaptation in itself—although this is probably irrelevant to the case of *Poecilozonites* (Gould 1976a, 1977a, p. 290).

volume, *Problems of Relative Growth,* which its author hoped might prove "a worthy offspring of *Growth and Form*" (Huxley to Thompson, 1932, quoted in Esposito 2014, p. 90).[1] The volume is accordingly dedicated to D'Arcy Thompson, with whom Huxley was in active correspondence until Thompson's death in 1948. (Interestingly, the long epigram that follows Huxley's dedication—a Thompsonian meditation on the correlation of parts—is quoted at length in "punctuated equilibria" (Eldredge & Gould 1972, p. 86).)

Huxley was neither a paleontologist nor a taxonomist, yet he made significant contributions to paleontology by proposing refinements to the theory of animal taxonomy (see Huxley 1957, 1958). Perhaps his most influential refinement was the distinction between *clades* (delimitable monophyletic units) and *grades* (assemblages of forms at a common level of adaptive organization). As Huxley observed, there are two ways of delimiting collections of species—either by propinquity of descent (monophyly) or by the possession of the similar anatomical, physiological and behavioral properties. The former strategy, when practiced exclusively, seems to leave something out: and something of major importance (biological improvement).[2] What's more, we want to be able to separate the birds from the reptiles on principled grounds, and to discuss lungfish and teleosts while excluding whales and orangutans (something that is barred on all strict versions of "phylogenetic systematics"). Huxley accordingly suggested that we supplement "the customary terminology purporting to define [monophyletic] units" with a secondary terminology "aimed at delimiting steps of anagenetic advance." "The best

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[1] Usually it is said that this book is about "allometry," and indeed this is an accurate description, although an anachronistic one. Huxley coined the term "allometry" only after the book was published, in a famous paper of 1936 (co-authored with Georges Teissier). Nonetheless he had formulated the famous "law of heterogenic growth" before *Problems of Relative Growth*, in 1924 ($y=bx^k$). Gould's first published paper, co-authored with his Antioch professor John F. White, concerns the biological interpretation of the allometric coefficient, 'k' (White & Gould 1965).

[2] As Mayr would later observe, 'If the only information one wants to retrieve from a classification is the sequence of branching points of the phylogeny, then a cladistic classification is the answer. If one wants more of the history of a group reflected in the classification, one will look for a method which does not completely disregard evolutionary divergence and autapomorph [i.e., derived] characters" (Mayr 1982, p. 230).

general term for such anagenetic units would seem to be *grade*," he wrote (perhaps in a nod to his grandfather, who had also employed the term). "I further suggest the term *clade*, to distinguish monophyletic units of whatever magnitude" (Huxley 1958, p. 27).

According to Huxley, the movement of a lineage towards a new organizational level or "grade" is achieved by a stepwise improvement in one important character after another, with each step attended by a minor radiation (Huxley 1963).[1] Once a new grade is attained, the lineage may cease to experience significant anagenetic change (improvement), but nonetheless flourish "as a result of bountiful speciation and various modification in the basic adaptive theme of the grade" (Mayr 1976a, p. 450). By this means, G.G. Simpson observed, a pioneering species (or assemblage of species) can attain to a higher taxonomic rank—but not otherwise:

> Our recognition of a higher category is *ex post facto*, as is our designation and placing of it in the [taxonomic] hierarchy. The Cricetidae (a family of mouselike rodents) are a family because they have become so extremely varied. If there were only a few genera or species of Cricetidae they would be members of the Muridae…[Likewise] if pterodactyls had persisted to become the dominant flying vertebrates, and as richly varied as birds, they would not be reptiles, but a separate class; and if birds had stopped short with *Archaeopteryx*, they would be reptiles and not a separate class (Simpson 1953, p. 342).

Given the independence of anagenesis (improvement) and cladogenesis (diversification), we should expect to find that many taxa are actually grades, having been achieved *independently* by several lineages. (That is, we should expect to find that many taxa are in fact polyphyletic grades, and *not* clades.)[2] And indeed, in the wake of Huxley

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[1] Years earlier, Gavin De Beer had lent to this process a name, "mosaic evolution," and a paradigmatic instance, the development of birds from dinosaurs via *Archaeopteryx* (de Beer 1954). It seems to have been Simpson who first perceived the connection between these two positions, writing that Huxley's grades reflect general biological improvements which evolve in a mosaic fashion in a number of related phyletic lines (Simpson 1959).

[2] In fact, this was an expectation even before Huxley's publication. Writes Simpson: "Since selection is likely to act similarly on similar populations, adaptive characters are likely to arise in parallel in several or many related lineages" (1953, p. 348). Probably the majority of higher categories "as they are actually defined and used in practice are polyphyletic in detail [with] more

publication, many paleontologists believed they had found precisely this. There is no *a priori* reason to expect that a grade should be monophyletic, after all, and still less to expect all members of a clade will occupy the same level of adaptive organization. Anagenesis followed by adaptive radiation will result in monophyletic grades, but this is not the only way in which a new grade can be achieved. In addition, an ancestral grade can give rise to multiple lineages that achieve a higher grade independently (Eldredge lists as phyla that were "found to be grades" in the wake of Huxley's publication, "the goniatites, ceratites, and ammonites among the Ammonoidea; the chondrosteans, holosteans, and teleosteans within Osteichthyes (Schaeffer 1965); the various groups of placoderms (Miles 1969); and so forth" (Eldredge 1985, p. 102)). As Mayr wrote, with characteristic certainty, "It is…quite unreasonable to demand that major levels in phyletic evolution should always coincide with the branching of lineages" (Mayr 1963, p. 609).

While this brief flowering of "gradal" classification may strike us as bizarre, it was in tune with the *Zeitgeist* of the 1950s and '60s. What the multiple evolution of grades represented was an overweening belief in the power of natural selection to forge common solutions to shared functional problems. Assuming, for instance, that mammals *do* represent an improvement over reptiles in basic design, and assuming that natural selection tends to foster biological improvement (if not invariably, at least frequently), why could not the mammalian grade have been achieved multiple times (perhaps as many as five, as Simpson once claimed)? Simpson laid bare the logic of this position in 1953. "Since selection is likely to act similarly on similar populations, adaptive characters are likely to arise in parallel in several or many related lineages" (1953, p. 348). Probably the majority of higher categories "as they are actually defined and used in practice are

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A note on "experimentation"

Among the many supporters of Huxley's gradal scheme was Bobb Schaeffer, longtime curator at the AMNH and Professor of Zoology at Columbia University. Schaeffer was an accomplished student of fossil fishes, and furnished compelling evidence of the polyphyletic nature of Actinopterygii (Schaeffer 1956). In addition, and in a rare excursion into theory, he developed the so-called "experimentation" model of adaptive radiation (actually an explanation of gradal ascent). As Schaeffer wrote in a 1965 paper, "The role of experimentation in the origin of higher levels of organization":

> The transition from one higher level of organization to another always involves some form of biological improvement for the same or a new way of life.[1] Except in rare cases when a single lineage attains a new level, the transition is expressed in terms of similar adaptations (broad adaptations) that evolve more or less in parallel in lineages of common ancestry (Schaeffer 1965, p. 318).

"In a real sense every organism is a mosaic," consisting of some combination of primitive, intermediate and advanced characters (p. 322). According to Schaeffer, these combinations represent *competitive experiments in design*, and are the cardinal means by which species probe the adaptive possibilities open to them. But experimentation is *not* about local adaptation, and does not occur within a single interbreeding population. Rather, it concerns general biological improvement and occurs within large taxonomic groups, with each lineage representing an independent experiment in design. Most of these will lineages blink out before achieving a new organizational level, but assuming that the new level represents a bona fide improvement, it is to be expected that

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[1] Note that Schaeffer restricts his comments to transitions between "higher" levels of organization (i.e., vertebrates).

"[similarities] in experimentation in related lineages [will] lead to parallelism in particular character complexes and to general adaptations representing a new organizational level."[1]

Judging from his citation record, Gould thought highly of Schaeffer's proposal, and followed him in regarding new taxa as "competitive experiments in design" (Gould 1970a, p. 111). (He did not follow him in thinking that the origin of higher taxa must represent "an extension of the mechanisms that underlie intraspecific variation, species formation and species transformation" (Schaeffer & Hecht 1965, p. 245); indeed, quite the contrary.) Beyond this, he seems to have held Schaeffer's scholarship in high regard, and to have sought his counsel on at least one occasion (Princehouse 2009, p. 157).[2] The upshot was a distinctly Schaefferian interpretation of transspecific evolution, as always, titrated with D'Arcy Thompson's structuralism:

> A quantitative and functional science of form suggests that parallelism and convergence are dominant phenomena, not mere taxonomic nuisances. Early in their history, most phyla display great diversity at high taxonomic levels. These are not classic adaptive radiations, but sets of competing experiments in basic design. Early experimentation is followed by standardization of the best mechanical designs. These are often improved in similar ways by many independent lineages. Standardization and improvement provide invertebrate life with a history; the Phanerozoic has not been a time of endless ecological variation on a static set of basic structures (Gould 1970a, p. 78).

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[1] Schaeffer adds that although "the canalization of morphogenesis appears to be a major factor in limiting experimentation, the existence of some variation in the epigenetic process provides a basis for the evolution of modified morphogenetic systems" (pp. 334-335) Canalization is responsible for evolutionary stasis (at least in part); yet the organism is not equally plastic in all directions. Rather, variation is constrained by "the limited range of viable epigenetic change," as well as the nature of the well-integrated genotype (p. 328).

[2] For instance, it was Schaeffer who advised Gould to take up *Tempo and Mode* (1944) after learning of some doubts he had developed regarding its sequel, *The Major Features of Evolution* (1953). *Tempo and Mode*, Schaeffer indicated, was a very different book than *Major Features*, and altogether more radical (Princehouse 2009, p. 157). Years later, Gould hauled Simpson over the coals for watering down his theory of quantum evolution in *Major Features*, "once his delight and greatest pride" (Gould 1980d, p. 167). Yet, in an ironic twist, it was Schaeffer that Simpson regarded as "instrumental in [the] modification of my formerly more extreme views on quantum evolution" (Simpson 1953, p. 392). Schaeffer was eleven years Simpson's junior, but radical he was not (see Colbert & Gaffney 1984).

We now have the outlines of a history, Gould declared: “the weeding out of unsuccessful designs and multiple evolution of mechanical optima” (Gould 1970a, p. 111). I will return to Gould’s view of Schaeffer’s “experimentation model” below. First it will be necessary to explore the relationship between vertebrate and invertebrate paleontology during the 1950s and ‘60s, as it was Gould’s identity as an *invertebrate* paleontologist that provides the key to understanding his early views on transspecific evolution (literally, evolution beyond the species level).

Macroevolution and the science of form

Vertebrates and invertebrates

Perched atop a forgotten review paper is an innocuous claim, no doubt hastily written and probably ignored by the majority of readers. The paper is Simpson’s “Some problems with vertebrate paleontology” (1961), and the claim is: “The study of fossil vertebrates elucidates the general principles of evolutionary biology.” Simpson’s point was an old one: namely, that experimental biology cannot reproduce the immense span of time and “complex horizontal extent of environment” to which paleontology has unique access (Simpson 1944, xxix). As a consequence, the paleontologist must play an indispensible role in the study of evolution, for it is only he who can study evolutionary rates under natural conditions, and make sense of how populations “passed from one way of living to another or failed to do so” (p. xxx). It was no publisher’s mischief that led Simpson to title a later work *The Major Features of Evolution*. While laboratory scientists may tell us how evolution works, their words are idle chatter until they are checked against the rocks.

However, while this is best understood as a plea for equality, Simpson's comments were not free of parochialism. Observe that what elucidates the general principles of evolutionary biology is "the study of fossil *vertebrates*"—not the study of fossils *in se*. But why did Simpson restrict his statement to vertebrates? One reason was the subject of the paper. Simpson was a vertebrate paleontologist tasked with reviewing problems in vertebrate paleontology (or at any rate this is where he chose to restrict his attention). But another reason, by no means trivial, was the widespread presumption that fossil vertebrates provide materials especially suited to the task of theoretically-minded paleontologists. In particular, it was fossil vertebrates that provided the means of attacking paleontology's most daunting problems, for instance:

> the rise of higher taxa and the evolutionary nature of higher categories; their duality of diversification and divergence; the occurrence of 'explosive' episodes of diversification; the prevalence of parallel evolution throughout many high taxa and problems of polyphyly arising therefrom; [and] patterns of early radiation in such groups as fishes, therapsids, and rodents (Simpson 1961, p. 1688).[1]

Additionally, the vertebrate series throws light on that defining feature of transspecific evolution: biological improvement. To quote Bobb Schaeffer, "The most convincing evidence for biological improvement through time can be found in the vertebrates, which have numerous skeletal elements associated with both feeding and locomotion…The evolution of various vertebrate groups, such as the placoderms, sharks, ray-finned fishes, labryinthodont amphibians, synapsid reptiles, and certain mammalian orders, can be visualized as a series of successive levels or grades of increasing efficiency" (1965, p. 319). The morphologically depauperate invertebrates, on the other hand, are ill-suited to

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[1] This is perhaps a good time to note that the parochialism cut both ways. Indeed, paleontologists in the 1940s and 50s were far from agreed on what constitute the most important problems in paleontology. Many believed that paleontology ought to embrace its close association with the earth sciences (biostratigraphy is "the heart of geology," J. Marvin Weller urged (quoted in Sepkoski 2012, pp. 53)). Paleontologists should avoid deluding themselves into thinking that they could solve any of biology's outstanding problems; such delusions divert from those problem areas in which paleontological research is most profitably focused (Weller 1947, pp. 572-574).

such analyses. They have, as Gould would mockingly claim, a history of diversity (splitting), but no history of form (improvement). Needless to say, Gould disdained this bit of common knowledge, but he was correct to think that the presumption was widespread.

Throughout the floruit of the modern synthesis, invertebrate paleontologists did little more than nod their silent approval, if they attended the flow of events at all (Rainger 2001). This was particularly the case at the American Museum of Natural History, where, since the reign of H.F. Osborn, vertebrate paleontologists had ruled the evolutionary roost. While Simpson was composing *Tempo and Mode in Evolution* (a composition interrupted by voluntary military service), invertebrate paleontologists were engaged in the familiar tasks of describing specimens and correlating rocks (Rainger 2001, p. 1058-1059). A large number were engaged in "economic geology" (whether in the employ of petroleum companies, or at the behest of geological surveys), and only a few harbored interests in such esoterica as the method of organic evolution. Following the publication of *Tempo and Mode* (1944), the situation began to change—albeit slowly.[1] Instrumental in this change was the young invertebrate paleontologist Norman Newell, whom Simpson recruited to the AMNH in 1947. David Sepkoski quotes from a memo that Newell distributed among his museum colleagues "in 1948 or 1949," concerning the state of pedagogy in contemporary invertebrate paleontology:

> The period between the two world wars was characterized by development in invertebrate paleontology chiefly along utilitarian lines, seemingly at the expense of fundamental progress in the science…Because of the traditional union between

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[1] In 1950, Simpson published a quantitative analysis of the recent contents of the *Journal of Paleontology* (covering the years 1939-1949) in an attempt to ascertain whether the recent ferment in paleontology might indicate "some sort of trend for paleontological research to concentrate less exclusively on routine description and nomenclature, and perhaps give more attention to such subjects as ecology, functional and broadly comparative morphology, evolutionary processes…[and] theories and principles" (Simpson 1950, p. 498). His analysis turned up no significant changes (but see Rainger 2001 for a longitudinal analysis that successfully challenges Simpson's verdict).

> invertebrate paleontology and geology it has come to be forgotten that the roots of paleontology are in biology, just as geophysics rests on physics. It is a tragedy that paleontology has at last become a "handmaiden to geology." Yet the techniques and mass of data of paleontology are now so distinct from geology and biology that the majority of biologists and geologists do not even know what constitutes urgent problems in paleontology. Although it is seldom accorded the status of a separate science, paleontology is just that (quoted in Sepkoski 2012, p. 58).

A biologist at heart, Newell was particularly sensitive to the fact that as "the majority of teachers of paleontology…[are] stratigraphers or petroleum geologists…[little] progress is being made toward an understanding and interpretation of fossils and their life environment." Yet Newell "saw an opportunity to change this at Columbia, drawing on the rich resources at the AMNH to develop 'a program of instruction in invertebrate paleontology, or paleobiology, at a professional level, adequate for the development of research specialists'" (Sepkoski 2012, p. 58). One beneficiary of Newell's efforts was Stephen Jay Gould, who came to New York to study with Newell in 1963. Niles Eldredge, an undergraduate at Columbia, joined the graduate program one year later.

To recapitulate, the 1950s and '60s witnessed a backlash against the notion that invertebrate paleontology was merely a service branch of geology, with little to contribute to evolutionary theory (see Colbert 1947, Knight 1947). "[It] is almost as if invertebrate paleontology [is] in bondage to geology," J. Brookes Knight complained in 1947 (p. 282). "[The] invertebrate paleontologist is for the most part not a paleontologist at all," he continued. "He is a geologist, a stratigraphical or 'soft rock' geologist," ill-equipped to trench upon serious evolutionary problems. The vertebrate paleontologist Edwin Colbert went still further. "[It] is not only a question of lack of interest in the subject [of evolution]," Colbert complained, "for it is a fact that most of our contemporary geologists are not even competent to take more than a superficial interest in evolutionary problems (Colbert 1947, p. 289). To be sure, the situation had improved somewhat in 1963, when Gould entered graduate school. But it was far from rectified, even in the elite centers of paleontological training. Apart from a few choice institutions, the situation in invertebrate paleontology remained much as it was during the 1930s and '40s, when invertebrate paleontology was regarded (not without justice) as a means by which rocks are better classified in time and in environment of origin (Kay 1947).

An invertebrate history of form: Gould's early writings on transspecific evolution

In 1970, Stephen Jay Gould authored a remarkable paper, grandly titled "Evolutionary paleontology and the science of form." In it, he leveraged a variety of new approaches in an attempt to restore paleontology to the status of an independent contributor to evolutionary science. He began with a subtle turn of phrase. "A science of form is now being forged *within* evolutionary theory," he observed (1970a, p. 77):

> It studies adaptation by quantitative methods, using the organism-machine analogy as a guide; it seeks to reduce complex form to fewer generating factors and causal influences. If a function can be postulated for a structure, then its optimum form, or paradigm, can be specified on mechanical grounds. The approach of a structure to its paradigm provides the elusive criterion of relative efficiency that any science of adaptation requires. Physical laws and forces also specify that form be adapted to the requirements of size (surface/volume relationships) and space (close packing criteria). When we cannot establish paradigms on deductive criteria, an experimental approach to form is appropriate. Idealized models are favored over actual specimens because they can be built to test predetermined factors. Paleontology need not remain solely a descriptive science based on observational methods, but may adopt the experimental techniques of explanatory procedures (Gould 1970a, p. 77).

Gould's proposed science of form was three-pronged, and consisted of a combination of inductive and deductive approaches. These were addressed to a pair of broad problems: firstly, *how is biological form produced* (what morphogenetic rules are implicated in the production of complex structures) and secondly, *what is the adaptive significance of observed morphological changes* (their "purpose or final cause expressed materially"

(Gould 1966a, p. 621)). In Gould's view, satisfactory explanations of phyletic history often require the investigator to address both of these problems: to resolve apparent complexity into a small number of influences on growth, *and* to specify the adaptive reason for each change in form.[1] The former can be done either inductively or deductively, by multivariate statistical analysis or Raupian theoretical morphology.

The latter, by contrast, should be carried out experimentally (assuming that this is indeed possible). Following the eclipse of functional morphology during the evolutionary synthesis, the study of adaptation has been plagued by "vague, trivial and untestable proposals," and wants for a measure of relative efficiency with which to compare allied structures (Gould 1971a, p. 256). In order to make progress in this area, it is necessary to approach adaptation in the manner of the experimentalist, using controlled scenarios in order to extract measures of relative efficiency. This was the bailiwick of the paradigm method, devised by the invertebrate paleontologist Martin Rudwick during the 1960s (Rudwick 1961, 1964).[2]

Gould called his approach *quantifunctional*—a "literary barbarism" that nonetheless sufficed to convey the flavor of his ambitions. A mature science of form needed to multivariate in conception, just as D'Arcy Thompson's structuralism had been (Gould 1971a, pp. 252-253). No less importantly, it needed to be both *quantitative* (able to probe behind appearances for reasons of analysis and comparison) and geared to produce

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[1] This distinction does not map perfectly onto Mayr's proximate-ultimate distinction, as Gould regarded his approach as "indifferent to the cause of [formal] change, to whether it be the unfolding of a genetic program in ontogeny or the alteration of that program in ontogeny" (Gould 1970a, pp. 104-105). In other words, it may be the case that the causes of formal change *differ* between ontogeny and phylogeny (the one being traceable to mechanistic causes, the other to natural or sexual selection). But it may also be the case that they are *equivalent*, for the causes of "mechanically-required adaptations" (formal changes exacted by the physics of size and shape) needn't differ between ontogeny and phylogeny (p. 109).

[2] Gould also notes that natural experiments afford an opportunity to study adaptation *in situ* without limiting ourselves to "modern manipulation" (Gould 1970a, p. 89). Here he quotes Adolph Seilacher, who put natural experiments to work in his studies of epizoans (1960) and belemnites (1968). His earlier study of parallel adaptive trends in Bermudian microgastropods utilized a similar logic (Gould 1970c).

functional explanations (with natural selection as the efficient cause of morphological change). "As a palaeontologist," Gould had earlier written, "I acknowledge a nearly complete bias for seeking causes framed in terms of adaptation" (Gould 1966a, p. 588). Yet Gould's adaptationism was a "secular" adaptationism, which is to say it concerned those physical features of organisms that fit them to their secular (abiotic) environments. Moreover, it was an adaptationism that took "fitness" to be something specifiable *a priori* for a particular environment. As Gould wrote in an early *Natural History* essay:

> In nature, A's superiority over B will be *expressed* as differential survival, but it is not *defined* by it…certain morphological, physiological, and behavioral traits should be superior a priori as designs for living in [particular] environments. These traits confer fitness by an engineer's criterion of good design, not by the empirical fact of their survival and spread (Gould 1977b, p. 42).

It is notable that the four primary protagonists of "Evolutionary paleontology and the science of form" were all invertebrate paleontologists—Gould, Raup, Rudwick and Adolph Seilacher. (These individuals commanded the most space in the text, and earned the greatest number of citations.)[1] This, of course, was no accident. In a sense, Gould had tailored his science of form to fit the unique attributes of the invertebrate fossil record. Rampant parallelism and convergence, the prevalence of size-exacted adaptations, and of mechanical and developmental correlates (exquisitely preserved in accretionary structures)—all of these are areas in which invertebrates outshine vertebrates in terms of the quantity and quality of the materials presented. But while all of these themes feature prominently in Gould's early writing, his foremost concern was to establish a single claim. This was, simply, that major invertebrate groups show clear marks of improvement over time, which lay open to the quantifunctional approach (Gould 1970a, p. 109). "Rarely do we realize how little our current perspective provides invertebrate life

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[1] Equal in citation number to Seilacher, but figuring less prominently in the text, are the vertebrate paleontologists George Simpson and Björn Kurtén.

with a history of form—defining history as directional change through time," Gould lamented. "A history of diversity it surely has, for the pulse of mass extinction established the larger divisions of history's time and still inspires paleontologists to intense debate…So too, in one sense, do we have change of form, but it is often placed in a strange static framework that recalls the steady-state of Lyell's world—change without history." Gould's later comments on Lyell notwithstanding, such steady-statism held little appeal for the Gould of D'Arcy Thompson.

What does it matter if invertebrates show clear marks of improvement over time? It matters because if the history of invertebrates is predominantly a history of diversity, unaccompanied by advancements in form, then the *real* paleontological action lies elsewhere—namely, in the vertebrate fossil record. Invertebrate paleontologists can describe and classify; they can ascertain the age of rocks by comparing fossil assemblages and they can practice functional morphology on a particular group of organisms. But of the great outstanding problems of paleontology—the problems of transspecific evolution—they can have little to say. To Gould, such defeatism was flatly unacceptable:

> I will argue that our standard picture of evolution prevents us from seeing certain key phenomena in a light that would provide invertebrate life with a history. That picture is the tree of life, a model of diversity with ever diverging branches. The phenomena are parallelism and convergence on the one hand and an aspect of "adaptive radiation" on the other…[W]hen the theme changes from branching diversity to mechanical optima and limited solutions defined in an engineer's language, then parallelism and convergence are among the normal results of adaptation and provide, moreover, a criterion for judging history: for short of being an all-knowing engineer, we must infer biological progress from the observation that, again and again, independent lineages develop the same design to perform a given function. And if parallelism and convergence are more common than we usually think, then the idea of biological improvement must be resurrected…and the notion of an invertebrate history reinstated (Gould 1970a, p. 109).

There are at least two points to notice in this passage. First, according to Gould, the ubiquity of non-divergent evolution proclaims the power of natural selection to fashion common solutions to shared functional problems. Massive parallelism and trends towards increased mechanical efficiency mark the history of vertebrates and invertebrates alike; consequently, Huxley's gradal scheme, "for all its frankness and subjectivity," has an equal claim to validity as the customary arboreal picture. As Gould wrote in 1976 (in one of his last public defenses of biological improvement):

> If efficient solutions to common problems of optimization are as limited as D'Arcy Thompson has claimed, then grades are levels of structural organization that may be reached independently by different lineages. Many higher taxa are not the monophyletic clades that most theories of classification require (or at least desire) but are grades of improvement attained in the same way by many lineages…When solutions to common problems are limited and success confers great advantages on lineages in competition, parallel evolution is rampant. A "phyletic bias"—and its metaphor, the evolutionary tree—has prevented proper assessment and understanding of the severe constraints that mechanical limits (including size itself) place on adaptive design (Gould 1976, pp. 119-120).

This leads to the second point: namely, that mechanical efficiency defines the cardinal vector of life's progress (at least within individual groups). To the extent that evolutionary history is irrevocable, as Louis Dollo argued, this improvement is not merely apparent (Gould 1970b). Time *does* have an arrow specified by a vectorial property of the organic world, which can be investigated by both deductive and inductive means. However it is not the case, as many would maintain, that macroevolution is simply microevolution extrapolated to geological timescales. Rather, "just as increase in size, of itself, subjects organisms to a different realm of forces and requires change in morphology, so also might extension in time bring emphasis to evolutionary events and processes that do not dominate at the species level. In particular, the great parallelism that occurs in independent lineages of most vertebrate classes and orders stands in contrast to the theme of splitting and diversification that predominates at lower levels" (Gould 1968, p. 97). Thus, Huxley's gradal scheme is not only an *alternative* iconography for evolutionary biology (a claim for *parity*), but also the *appropriate* iconography for the study of transspecific evolution (a claim for *priority*).

This was Gould's first attempt to show that micro- and macroevolution are conceptually distinct, and that species divergence fails as a model of transspecific evolution (Gould 1968, p. 97, Gould 1969, p. 497). As a replacement for the species divergence model, Gould insisted that macroevolution is dominated by the phenomenon of limited solutions, whether owing to mechanical necessity (all large terrestrial animals have thick legs) or constrained pathways of improvement (there are few ways of improving upon the jaw hinge of a gnawing rodent). Close convergence is therefore "less surprising and improbable than it appears under our usual views of phylogeny" (Gould 1972, p. 416). Microevolution, by contrast, is dominated by ease of genetic modification. To vary Stebbins, evolution proceeds down the genetic lines of least resistance (Stebbins 1974). Although Gould was unable to articulate precisely *why* there should be "a fundamental difference in explanation for similar events at micro- and macrolevels," yet he strongly suspected this was the case, and wasted no rhetorical power in making the point. "An incorporation of insights gained from the study of vast time spans might increase the generality of evolutionary theory in much the same way that a consideration of high velocities modified Newtonian physics" Gould 1969a, p. 410). This is no small claim, but then again, Gould was no small thinker.

Subsequent developments

Gould's enthusiasm for functional morphology continued into the mid-nineteen seventies, whereupon it quickly evaporated. As late as 1974, he saw fit to conclude an important paper (co-authored with Dave Raup) with a plea for "the devotion of more attention to the neglected but growing field of functional morphology in paleontology" (Raup & Gould 1974, p. 321).[1] The best method of studying adaptation in the fossil record does *not* begin with the identification of trends, although these command attention for other reasons. Rather, it begins with the analysis of structures in the light of operational principles (see Rudwick 1964). Likewise, in 1976, Gould advocated the use of the analog "when we study what an organ does rather than where it came from" (Gould 1976d, p. 121).[2] "Long live the analog and its science of functional morphology," Gould proclaimed:

> The analog is the paleontologist's only source of experimental material; for it is a replicate (however imperfect) in the testing of any functional hypothesis…the convergent evolution of similar structures fulfills, at least imperfectly, the criterion of independent replication that any experiment requires.

By 1980, little of Gould's initial optimism remained. Whereas once he had lauded Thompson's view that "the principles of mechanics specify a limited number of good designs for the solution of common problems" (Gould 1971a, p. 257), now he was forced to recant. To be sure, he did not abandon the belief that organisms are generally well-designed, and that their construction imparts a preferred directionality to evolutionary change (see Gould 1980a). Yet after the mid-1970s, Gould gave up the attempt to gloss phenomena like allometry in strictly functional terms, and soured on functional morphology (e.g., Gould 1982a, p. 337, Gould & Lewontin 1979, p. 591). Whatever

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[1] This claim must be read in the context of their study—a simulation purporting to show that many patterns typically interpreted as resulting from selection can be generated in "stochastic systems bounded by minimal biological constraints" (Raup and Gould 1974, p. 305). In light of their results, the authors came to doubt whether patterns of change (and statistical correlations between characters) can be used as evidence for deterministic causes (see Raup 1977, pp. 55-57). Random morphological change associated with branching events can also generate a high degree of apparent order, presumably by means of a random walk. Thus, according to Raup, "[it is] the functional analysis of morphology rather than the simple fact of correlation between characters that provides the basic evidence for adaptive evolution" (p. 57). (Given Raup's emphasis on correlation, and Gould's outstanding interest in trends, it was probably Gould that drew the moral about orthoselection.)

[2] This too was an echo of Rudwick (1961, 1964), although Rudwick emphasized that functional inference does *not* cleave narrowly to the demands of analogy.

order permeates the biological realm would not be revealed by a basically Newtonian approach: an experimental study of adaptation in fossils. “Interesting answers demand new questions, and empirical studies cast explicitly in their light,” Gould argued. Consequently:

> functional morphology will fulfill its promise when it probes the situations in which animals are *not* well designed—developmental, phyletic, and architectural constraints as marks of history. As a key issue, I suggest: why is morphological space so sparsely populated, but so clumped where it is occupied? How much of clumping and non-occupation reflects good and untenable design (Raup 1966), how much the constraints of genealogy? (Gould 1980b, p. 101)[1]

Gould goes on to state his new vision for evolutionary paleontology (now christened “paleobiology”), which differs significantly from that of the previous decade. It is illuminating to read the following passages back to back:

- **1970**: “The branching tree of life, our traditional model, has no claim to necessary superiority over its rivals—to the gradal scheme of Huxley (1958) for example. It has been preferred chiefly because we can define, document and catalog the diversity on which it is based. When we employ form only to delineate taxa, it reinforces our traditional emphases on diversity. If, on the other hand, we use it to judge the functional efficiency of structural designs, then the science of form may reinstate paleontology as a source of new themes for evolutionary theory” (Gould 1970a, p. 112).
- **1980**: “I seek a kind of ‘bounded independence’ for macroevolution—unity in a body of principles common to all levels, diversity in the different working of these principles upon the material of different levels. In any case, if species are irreducible

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[1] This too may reflect Lewontin’s influence, as Lewontin has long held that the explanation of non-existent morphologies is a key problem for evolutionary biology.

> inputs, then paleontology wins its independence as a subject for the generation and testing of evolutionary theory. The origin of species is the highest, and rarely-observed, event of microevolutionary studies. If we must start with large numbers of species and calculate their differential survival in order to understand macroevolution, then paleontology must be our primary source of information and insight" (Gould 1980b, p. 107).

This change reflects the consummation of a major upheaval in Gould's philosophy of nature, and likewise his philosophy of science. By an idiosyncratic detour, his affections had shifted from the laws of form to the nature of history; from "the formal content of phyletic change" (Gould 1977a, p. 4) to "the higher-level study of long times and large clades" (Gould & Eldredge 1977, p. 145). His youthful interest in Thompsonian formalism had given way to an interest in the formal properties of species and superspecific taxa. Additionally, in a parallel development, Gould began taking an ever-increasing interest in Darwin's historical methodology, as encapsulated by the claim that Darwin made history "doable for the zealous researchers of science" (Gould 1986, p. 61). The days of testing history by experimental means were over, replaced by the statistical consideration of cladal trending.

As Roger D.K. Thomas has observed, Gould's early interest in D'Arcy Thompson stemmed from a realization that "Thompson's emphasis on intrinsic formal properties of organic design was *complementary* to Darwinian evolutionary theory" (Thomas 2009, p. 281, emphasis added). I have suggested that Gould's Thompsonianism ran even deeper: that it entered as a constituent thread of his youthful worldview, coloring all of his early activities. Nonetheless I agree with Thomas's analysis of Gould's "break" with Thompson, and his adoption of contingency as the cardinal theme of life's history. As time bore on, "Steve [became] increasingly unwilling to accept the determinism that is implicit in Thompson's worldview," Thomas observes:

> [He] preferred contingency to any sort of more general determinism on personal and ideological grounds. His rich and provocative evolutionary theory—at least the key punctuational and hierarchical parts of it—does not require that the effects of natural selection, speciation, or extinction must be unbiased in their directions. But Steve's humanity, his commitment to free will and personal responsibility, did require this. It gave rise to a highly personal evolutionary synthesis in which historical contingency takes the dominant role (Thomas 2009, p. 287).

Interlude

Ontogeny and Phylogeny, and an evident paradox

Without a doubt, Gould's finest intellectual achievement was his first book, *Ontogeny and Phylogeny*—in many respects the dénouement of his early career (Gould 1977a). Today it is little read, and probably best remembered for its advocacy of the neoteny hypothesis of human evolution (Somel et al. 2009). But human neoteny is a coda rather than a *sine qua non* of the work. *Ontogeny and Phylogeny* is not primarily a treatise on human origins, nor is it a historical study of "the structural (formalist) biology tradition developed…by Continental Europeans" (Clarke and York 2011, p. 54). Rather, it is an investigation of heterochrony—of "*all* directions of change in developmental timing and their evolutionary significance" (Gould 1979, p. 126).[1] Additionally, and in spite of its

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[1] It is startling how often this is misunderstood. For instance, Joe Cain claims that *Ontogeny and Phylogeny* "attacked adaptationism" in order to promote Gould's anti-deterministic 'developmental approach' to evolution (Cain 2009, p. 350). This statement is so misguided that one is led to wonder whether Cain (an excellent historian) has actually read the second half of the book. On the other end of the spectrum, Michael Ruse writes that *Ontogeny and Phylogeny* "can with good reason be considered as one long testament to an adaptively fueled progressionism leading to humankind" (Ruse 1996, p. 497). This is a significant reach. Here we do best to take

author's false modesty, it is an attempt to weave into a synthesis over a decade of thought concerning themes of size, shape and biological improvement. Gould may not have pioneered many ideas in *Ontogeny and Phylogeny* (with the exception of the ill-fated "clock model"). But the attempt to relate paedomorphosis to particular life history theory was portentous, in spite of its limitations (pp. 292-351, see Wake 1978, pp. 97-98 for criticism). Likewise, Gould's suggestion that progenesis "unbinds morphology from its usual selective control" was remarkably pregnant:

> [Progenesis] is selected not primarily for morphology but by the need for precocious maturity as a life-history strategy. The morphology of progenetic forms is not inadaptive (the very fact that wingless aphids and paedogenetic gall-midges cannot fly keeps them in their superabundant resources and spares them the energy needed to produce "expensive" sensorimotor devices). But morphology is simply not the primary ingredient of many progenetic adaptations. The redirection of selection towards the timing of maturation might well release the rigid selection usually imposed upon morphology. Morphology would then no longer be fine tuned to a changing environment (Gould 1977a, p. 388).[1]

The composition of *Ontogeny and Phylogeny* spanned a vibrant period in Gould's career, which saw the MBL collaboration (1972-1977); the initial turbulence surrounding punctuated equilibria (1972-); the rise of taxic paleontology (1969-); and the debut of Stephen Stanley's theory of species selection (1975). In addition, three events of considerable importance occurred at Harvard University. First, Gould was awarded a full professorship in 1973, just two years after earning tenure. (His promotion was roughly coincident with his debut as a public intellectual. Gould's first essay in *Natural History* magazine appeared in January of 1974, and bore the very Thompsonian title "Size and

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Gould at face value: "[This] book is primarily one long argument for the evolutionary [i.e., adaptive] importance of heterochrony" (Gould 1977a, p. 2).

[1] The astute reader will have noticed that Gould's *Poecilozonites* monograph concerns neoteny, whereas here he speaks of progenesis. Both are forms of paedomorphosis, but whereas neoteny refers to the slowing of somatic development, progenesis refers to the speeding of sexual maturation. This difference is of the essence for Gould's argument in OP, as he related progenesis to "r-selected regimes" (where the focus of selection is rapid maturation or small body size) and neoteny to "K-selected regimes" (where the focus of selection is longevity or large body size). Only progenesis unbinds morphology from selective control; neoteny retains a "primary role for morphology in adaptation" (Gould 1977a, p. 34).

Shape.") Second, the brilliant and charismatic Richard Lewontin was hired away from the University of Chicago in 1973, whereupon he began teaching evolution with Gould (Gould 1993a, p. 320). By Gould's own admission, Lewontin was instrumental in turning him from adaptationism—a subject to which we will have occasion to return. Finally, in 1975, E.O. Wilson published his magnum opus: a glossy 600-page tome on the evolution of social behavior. Vigorously promoted by Harvard University Press, *Sociobiology* was a publication event of the first magnitude, involving "full-page advertisements in the *New York Times*, author-publisher cocktail parties, [and] prepublication reviews and interviews on television, radio, and in popular magazines" (Lewontin, Rose & Kamin 1984, p. 233). However, in spite of positive early notices (e.g., Bonner 1975, Hutchinson 1976), the final chapter on "Man" sparked heated debate, and galvanized the New Left into activity. Particularly notorious was a letter in the *New York Review of Books*, of which Gould was a signee, linking the ideology of sociobiology to Nazi war crimes:

> These theories provided an important basis for the enactment of sterilization laws and restrictive immigration laws by the United States between 1910 and 1930 and also for the eugenics policies which led to the establishment of gas chambers in Nazi Germany. The latest attempt to reinvigorate these tired ideologies comes with the alleged creation of a new discipline, sociobiology (Allen et al. 1975).

The Cambridge-based "Sociobiology Study Group" began meeting in 1975, and within a year Gould had fired the opening salvo in his personal campaign against adaptationism (Gould 1976c). Soon he would be known as sociobiology's most implacable opponent, a reputation he maintained for nearly twenty-five years (see Barash 2002, Orr 2002, Shermer 2002). However when *Ontogeny and Phylogeny* hit bookshelves in 1977, readers were greeted to an unmistakably adaptationist argument. Indeed, Arthur Cain, a forceful adaptationist if ever there was, described the book as "a fascinating attempt at a functional interpretation of those phylogenetic alterations [involving changes in developmental timing]" (Cain 1978, p. 758). (This comment is the more interesting in light of Cain's tirade against "The Spandrels of San Marco," in which he accused the authors of scientific malfeasance, stirred by ideological factors (see Segerstråle 2000, p. 109).) What accounts for this seeming anomaly: an adaptationist railing against adaptationism?

The banal answer is that *Ontogeny and Phylogeny* was conceived before the menace of sociobiology appeared. Gould began research on the book in 1972, although elements of his argument were in hand much earlier.[1] Probably it went to the publisher in early 1976 (Gould lists only two articles from 1976 in the bibliography, one of them an unpublished manuscript). Had he begun the project in 1975, it can hardly be doubted that its contents would differ considerably from what is actually on the page. Probably they would more closely resemble Gould's later interpretations of heterochrony as embodying the "major internalist themes of constraint, and structurally-enabled substantial change" (Gould 1992, p. 277).[2] At any rate, we can be certain that the theme of the book (that all heterochronic changes are selected for immediate benefit, whether morphological or maturational) would be blunted somewhat, if not outright changed.

I regard this answer as "banal" because it ignores a more interesting issue, at least in my estimation. While *Sociobiology* helped to precipitate Gould's disillusionment with

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[1] By 1968 Gould had dispatched with the chief difficulty plaguing de Beer's analysis of heterochrony: the extension of the term to cover *the introduction of new features*. The restriction of heterochrony to *character displacement in time* is the linchpin of OP's second half, and a necessary assumption of the clock model. "An overabundance of terminology, complicated by semantic arguments based on inconsistent usage among authors, has obscured the fact that heterochrony occurs in only two forms," Gould wrote in 1968. "A feature may appear earlier in the descendant's ontogeny than in that of the ancestor, producing recapitulatory effects, or later, producing paedomorphic effects" (Gould 1968, pp. 82-83). What remained to accomplish was an intensive historical survey of recapitulationism, and the formulation of the taxonomy on which the clock model was founded (Gould 1977a, pp. 246-262).

[2] This is not at all what Gould had in mind in *Ontogeny and Phylogeny*, where he argues that in order to understand heterochrony, we must understand what immediate advantages it confers (for instance, speeding maturation in *r*-selected regimes). Of course, Gould *does* note that progenesis can unbind morphology from selective control, but he treats this unbinding in the context of selection for precocious maturation; its adaptive component is therefore scarsely lessened. Implicit in his argument is the notion that selection is *always* in control of the evolutionary trajectory of a lineage, such that whatever 'channeling' occurs during the course of descent results from selection on some aspect of morphology or life history.

adaptation (Gould 1993a, pp. 319-320), there are nonetheless *major points of difference* between the "adaptationisms" of Gould and Wilson. So great are the differences, in fact, that I am hesitant to lump them together.

Two adaptationisms

What separates the adaptationisms of Gould and Wilson? In the first place, there is the question of *explananda*. During the salad days of the late sixties and early seventies, Gould's primary concern was with morphological and physiological characters—"species-universals" in the realm of basic design. Edward Wilson, by contrast, wished to explain behavioral and psychological characters—species-universals of a much shorter wavelength. It is possible (even likely) that these interests reflect different disciplinary foci. A paleontologist faces a hard row in the study of behavior and cognition; likewise a behaviorist can't say much about the origins of basic animal design. But this interpretation glosses over a deeper, and I think more important, issue.

According to Gould, the struggle over adaptation transcends biology, and instead reflects a deep rift in Western thought (Russell 1916). On the one hand, we have the functionalists, for whom adaptation mirrors the purposeful aspects of the world and its construction (Russell lists Aristotle, Cuvier and von Baer as the chief evangels of the "functional attitude").[1] On the other hand, we have the formalists: descendants of Plato and the continental idealists (Gould 1993a, p. 319).[2] Gould's idolization of D'Arcy Thompson ensured that he could never be a thoroughgoing functionalist, as Wilson most

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[1] To crib a phrase from Stephen Pepper (1942), the root metaphor of the functionalist worldview is the machine, in whose construction is revealed something of its designer's purposes. No external designer is required, of course. Aristotle's famous term *entelecheia* means, quite literally, having (*echo*) one's purpose (*telos*) within (*entos*).

[2] The root metaphor of the idealist worldview is the developing organism, superintended by some principle or "law" which ensures its continuing coherence. Clearly this was the conception of the German transcendentalists (see Russell 1916, pp. 89ff, Gould 1977a, pp. 33ff). More recently, Peter Bowler has indicated that a large number of post-Darwinian biologists, including the anatomists Richard Owen and Albert Kölliker, viewed evolution through this lens (Bowler 1983).

certainly is. From the first, Gould endeavored to meld the formalist and functionalist positions—a desideratum that set him at variance with functionalist hardliners (e.g., Dawkins 1995, p. 10). It also led him to deny several of the tenets that sociobiologists held most dear, including the fine-grained genetic control of organismal construction.

As Lewontin, Rose and Kamin observe, the claim of sociobiology to explain the entirety of the human condition enjoyed popularity far in excess of its explanatory yields. The reason, they speculate, owes to the nature of the explanation itself, "a reductionist, biologically determinist explanation of human existence" (p. 236). Such explanatory schemes tend to incite warm criticism from certain areas of the academe, but, if the *New York Times* bestseller list is any indication, they also enjoy a truly general appeal:

> The central assertion of sociobiology is that all aspects of human culture and behavior, like the behavior of all animals, are coded in the genes and have been molded by natural selection. While sociobiologists sometimes hedge on the issue of direct genetic determination of every detail of social and individual behavior, the claim for ultimate genetic control…lies at the heart of a system of explanation that cannot survive otherwise (Lewontin, Rose & Kamin 1984, pp. 235-236).

Thus sociobiology reposes upon a particular hypothesis regarding the *intensity* of genetic determination—not a mere claim for its existence. No one disputes that behaviors have *some* grounding in genetics (to say 'genes influence behavior' is to say little more than 'behavior exists'). 'Fish gotta swim, birds gotta fly' (at least some of them), and human beings must act in a manner *broadly* conducive to their survival. But a world of subtlety separates this statement from the speculations of a Dawkins or a Barash (Gould 1978c). The pertinent issue is not the *presence* of genetic influence, but rather how *fine-grained* the genetic control of the phenotype really is (see Gould 1981, pp. 325ff). Sociobiologists tend to suspect that it is very fine-grained indeed, and that psychological characters have been molded in much the same way as bodies. Gould held an almost opposite view, which he inherited from D'Arcy Thompson (Thompson 1942, pp. 783-784). As he phrased it in a *The Mismeasure of Man*, the issue was one of "biological potentiality versus biological determinism":

> Humans are animals, and everything we do is constrained, in some sense, by our biology. Some constraints are so integral to our being that we rarely even recognize them, for we never imagine that life could proceed in another way…The contentious subjects are behavior that distress us and the we struggle with difficulty to change (or enjoy and fear to abandon): aggression, xenophobia, [and] male dominance, for example (Gould 1981, pp. 328-329).

Now, all evolutionists recognize that genetic influence is "spread diffusely across many genes," such that genes "set limits to ranges; they do not provide blueprints for exact replicas." In one sense, therefore:

> the debate between sociobiologists and their critics is an argument about the breadth of ranges. For sociobiologists, ranges are narrow enough to program a specific behavior as the predictable result of possessing certain genes. Critics argue that the ranges permitted by the genetic factors are wide enough to include all behaviors that sociobiologists atomize into distinct traits coded by separate genes (Gould 1981, p. 329).

Gould and Wilson agreed that organisms tend to be well designed (and indeed who would deny it?). But to say that organisms are well designed is *not* to say that they are adaptively honed in every detail of their phenotype. What would it mean, after all, if the manifold dimensions of behavior and cognition were precisely honed, like the axial skeleton of a greyhound? It would mean, firstly, that additive genetic variance existed along all relevant phenotypic axes, and secondly, that these axes were not lashed together by copious epistatic interactions (thus limiting their independent modifiability).[1] Moreover, it would seem to require that genes encode a great deal of information

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[1] Strictly speaking, this relates only to selection and character-dissociability—not to development *in se*. But such a view seems to suggest a fine-grained genetic control of the phenotype—the more fine-grained, the more perfect the adaptation. To vary a Wilsonian expression, 'genes hold phenotypes on a tight leash' (Wilson 1978). Gould, by contrast, favored the view that "selection may set some deeply recessed generating rules; but specific behavior are epiphenomena of the rules, not objects of Darwinian attention in their own right" (Gould 1981, p. 329).

pertaining to the state of the (mental) phenotype, which is decoded over the course of ontogeny (Gould 1978c, p. 532). But such control is the abnegation of the Thompsonian position, which relies on the systematic *underdetermination* of phenotypic complexity by heredity. Writes Gould:

> It is inconceivable that each aspect of a complex form is the direct product of an individual genetic instruction. We can simplify, and thereby understand, the generation of apparent complexity by recognizing that physical forces directly influence shape and that a few simple rules can fashion some very intricate final products (Gould 1970a, p. 77).

To Gould, the reduction of complexity to "a few simple rules" is essential to the framing of a causal morphology (see also Gould 1971b, pp. 415-416). It also implied that genetic inquiry was limited in what it could say about the intricacies of human behavior (to say nothing of the organization of whole societies). Gould's argument in *Ontogeny and Phylogeny* was indeed adaptationist, and implicated natural selection as the main causal factor directing evolution. Yet all it posited was *some* degree of character dissociability, along with the genetic control of *certain aspects* of developmental timing. Of the tight control of phenotype by genotype it simply had nothing to do.

This insight provokes an interesting question. For if Gould's adaptationism was of a fundamentally different wavelength than Wilson's, why did Gould react to sociobiology by foreswearing *all* adaptationism, including his somewhat idiosyncratic Thompsonian variety? While Lewontin's influence was certainly crucial, I think the primary reason had to do with his changing views on macroevolution during the early-to-mid 1970s.[1] Thereby hangs a tale; it is the subject of the next section.

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[1] Another reason, which deserves a closer look, is Gould's changing views regarding non-morphological adaptation. Judging from his published statements, the early enunciations of life history theory signaled a turning point in Gould's thinking about adaptation (e.g., Stearns 1976, see Gould 1976a). As late as the early-1970s, Gould's notion of adaptation had earlier been dominated by *secular* adaptations—morphological characters that "fit" organisms to a particular abiotic environment. This, no doubt, can be chalked up to his paleontological training:

From Thompson to Darwin

The re-construction of punctuated equilibria

By the mid-1970s, Stephen Jay Gould was a blossoming public intellectual and co-author of a theory which, according to Steve Stanley, compelled an entirely new view of life's history (Stanley 1975). For *if* the majority of evolutionary change is cramped into speciation events, and *if* these are stochastic with respect to "long-term, net directional change" (Eldredge & Gould 1972, p. 111), then the cardinal process determining evolutionary trends must take speciation events as its basic input. Stanley christened this process "species selection," and suggested that it operates on species within higher taxa, determining statistical trends, much as natural selection acts on organisms:

> Species selection, *which must largely determine the overall course of evolution*, is most analogous to natural selection in asexual organisms. A new species, like a mutant arising in an asexual group, contributes to the future population solely through the selection of its direct descendants. The descendants form what has been traditionally been termed a clade (Stanley 1975, p. 648, emphasis added).

"Traditionally paleontology rarely [considered immediate functional significance]; it focused instead on the meaning of adaptation as a contribution to long-term evolutionary trends. And when it considered the immediate significance of adaptation at all, it did not venture beyond morphology in a 'physicalist' perspective—i.e., to what aspect of the physical environment is this structure fitted? The ecological themes of population dynamics, life history strategies and species interactions were simply not categories for consideration" (Gould 1976a, p. 233).

With this insight in tow, we can also see *Ontogeny and Phylogeny* in a new light. A large part of *Ontogeny and Phylogeny*'s second half is an argument that there is more to the study of heterochrony than retrospective assessments of evolutionary significance. Heterochronies must also confer some *immediate* advantage upon an organism lest they vanish immediately, and this will frequently be unrelated to any specific morphological structure. Indeed, adaptations may involve little more than changes in the timing of key life history events—the onset of sexual maturity, for instance. (Gould's interest in life history theory, while strong, was somewhat transient. After the mid-seventies, Gould had little more to say about theoretical ecology, and devoted increasing attention to his formal expansion of Darwinian theory (but see Gould 1976d, Gould & Eldredge 1977). An excellent account of Gould's relationship with ecology can be found in Allmon et al. (2009), but there is much more work to be done on this topic.)

Gould was greatly impressed by this proposal, and later admitted that it "developed the implications that I had been unable to articulate from our original section on evolutionary trends" (Gould 2002, p. 980). It is thus unsurprising that the sequel to "Punctuated equilibria" (subtitled "The tempo and mode of evolution reconsidered") differs markedly from its predecessor. In 1972, Eldredge and Gould argued that the stochasticity of speciation events with respect to cladal trends results from *adaptation*—specifically, the adaptation of peripheral isolates to local conditions. These episodes constitute what the authors term "'explorations' or 'experimentations' (see Schaeffer 1965)…invasions, on a stochastic basis, of new environments by peripheral isolates." There is nothing inherently directional about these invasions; they do not arise preferentially in one direction or another in conformance with ongoing evolutionary trends ("Wright's rule"). Yet "a subset of these new environments might, in the context of inherited genetic constitution in the ancestral components of a lineage, lead to new and improved efficiency," enabling the fledgling species to take root, and perhaps to usurp the parent stock. Trends can accordingly be rendered as the differential survival of species in virtue of graded improvement along a vector of functional efficiency (if trends be identified with biostratigraphic character gradients).

By 1977, it had become apparent that this interpretation was too narrow. In their original presentation, Eldredge and Gould had leaned heavily on the differential *survival* of species within clades, thus ignoring their differential *fecundity*, or propensity to speciate (Gilinsky 1981, p. 324). Moreover, their discussion had been executed in light of a belief in biological improvement, which lead them to foreground the progressive aspects of cladal trending. According to the authors, *all* speciation events involve adaptation to prevailing conditions, yet not all adaptations bootstrap directional trends. The question thus arises: 'which adaptive events are prone to bootstrap directional trends?' Gould's answer was "mechanical improvements of the engineering type," which he contrasted with "the acquisition of a limiting morphological specialization" (Gould 1968, p. 97, 1977c, pp. 22-23). (This was not an extraneous theoretical commitment grafted onto an indifferent subject matter. Rather, the appeal to improvement resolved an apparent conundrum. For if *all* speciation is adaptive in nature (which Eldredge and Gould believed), and if trends result from the differential *survival* of species (determined by the phenotypic attributes of organisms), then the determinant of long-term trends must be something beyond mere adaptation. To Gould, this 'something beyond' was mechanical improvement—a subject that had interested him since the mid-1960s. All species are adapted to their environments, but the species that have undergone biological improvement have a *primus inter parus* status. As such, they are an obvious contender to partake in evolutionary trends.)

It had long been common knowledge that specialization is the enemy of biological progress; that highly specialized lineages sacrifice evolutionary plasticity for short-term adaptive gains. However, as Julian Huxley had observed, not all adaptations consist in increased specialization for a particular way of life. In addition, there exists a class of adaptations that are *non-limiting*, and which relate to the "raising of the upper level of all-round functional efficiency" (Huxley 1963, p. 565). Such adaptations do not lead to a restriction of evolutionary potential, but rather open out expansive vistas that a lineage might subsequently colonize. It was precisely this class of adaptations that was associated with the attainment of new grades or "organizational levels"—the subjects of Schaeffer's experimentation model.[1] Additionally, it was this class of adaptations that Gould had foregrounded in his prolegomenon for evolutionary paleontology (Gould 1970a, pp. 108-112).

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[1] Recall that for Schaeffer, "vertebrate groups can be divided historically into a sequence of organizational levels [with each] succeeding level [representing] an improvement in functional efficiency" (Schaeffer 1965, p. 334). Experimentation consists in the "trying out" of various combinations of primitive, intermediate and advanced characters, occasionally resulting in the origin of new and higher organizational levels.

Given this background, it is of great interest that Eldredge and Gould chose to discuss trends in light of Schaeffer's model of biological improvement. After all, "experimentation" is *not* an explanation of local adaptation, which everyone agreed was the province of natural selection (Eldredge & Gould 1974, p. 305). Rather, it is a means of explaining how a group can achieve a new organizational level by means of the differential survival of "experiments," each of which bears a particular complement of characters.[1] The lineages that achieve the new level "form the subset of a directional trend," one might say (Gould 1977c, p. 23). (Actually, all lineages that "ascend" by successful experimentation "form the subset of a directional trend," not just those that achieve the new level.)

Let me be clear. The rendering of trends by differential species survival is *not* Schaefferian experimentation—not even close. Nonetheless, when we examine the conceptions side by side certain similarities emerge, which help us to make sense of the punctuationists' explanations of biological improvement. For instance, both figures tell the story of a unidirectional trend: Schaeffer's the ascent from one organizational level to another; Gould's the graded evolution of some morphological character.[2] Both depict directional change as resulting from a process that is prone to failure (if I may be allowed a bit of teleological language). And both depict improvement as episodic: in Schaeffer's case, as an integral of multiple "experiments," in Gould's, the integral of multiple (adaptive) speciation events. (There is an important corollary to the latter point, on which it is well to comment. In "Punctuated equilibria" (1972), the authors endeavor to explain

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[1] Actually, this is an oversimplification. According to Schaeffer, experimentation does not occur among lineages that *already possess* (for whatever reason) a particular complement of morphological characters (cf. Gould 1970a, p. 111). Rather, it involves the exploration of a "transitional space" between organizational levels by lineages that acquire particular complements of characters *during* the exploration process. Of these, only a small number are successful in leaving a posterity that includes members of the higher grade. But these can be viewed as *victors* in a competition of sorts, and Schaeffer makes clear that victory typically owes to "improvement[s] in functional efficiency" (Schaeffer 1965, p. 334).

[2] I say "Gould" instead of "Eldredge and Gould" because it was Gould who produced the illustration shown in Figure 8.

phyletic trends—'biostratigraphic character gradients' built by successive speciation events. Gould's famous illustration does *not* depict a statistical trend within a complex branching phylogeny (a *phylogenetic* trend) but rather 'anagenesis in the speciational mode' directed by differential rates of extinction. Only after Gilinsky's important paper did Gould begin stressing the importance of differential origination, which, Gilinsky notes, further decouples trends from adaptation. "Macroevolutionary trends that are powered by differential extinction can often be explained in terms of attributes of individual organisms…Trends that result from differential origination, however, cannot easily be viewed in this manner, because adaptedness of individuals to their surrounds does not in any direct way lead to speciation" (Gilinsky 1981, p. 326).)

Of course, there are key differences as well. In Schaeffer's figure, the vertical axis corresponds to organizational level; thus the ascent from rhipidistian to amphibian organization is progressive, and indicates "an increase in functional efficiency that can be defined in terms of general adaptations" (Schaeffer 1965, p. 334). Gould, on the other hand, pictures *time* on the vertical axis. His figure thus contains no explicit representation of improvement (although we can be certain that it does not occur in the vertical shafts, which correspond to morphological stasis). Probably most trends are not progressive in any meaningful sense; or at least this is true of minor (easily reversible) trends. Yet when we interpret the figure in light of the text, it is evident that the authors intend at least *some* long-trends to be ascribed to adaptive improvement (and perhaps the majority). Other contemporary writings support this conclusion, for instance, Gould's claim that the history of "major groups" often consists in mechanical improvement:

> [Major] groups often have a history that can be described on the basis of a few functional themes. "Fish, as we have said, progress to more efficient levels of feeding and locomotion [Schaeffer & Rosen 1961, Schaeffer 1965]. Spasskiy (1967) has elucidated the history of rugose corals as a series of improvements in feeding mechanisms. The main outlines of gastropod evolution involve advantages of torsion and the development of more efficient current systems (Rollins and Batten 1968).

> Mantle fusion, siphon formation, and the subsequent invasion of more protected infaunal niches is, according to Stanley, the dominant theme in bivalve evolution…Trends in Paleozoic echinoids were analyzed by Kier (1965), who wrote: 'All the changes do not seem to require a change in habit to explain their origin but resulted from the gradual improvement of the animal as a living mechanism' (Gould 1970a, pp. 111-112).

Statements like this are typical of Gould's early work, which sought nothing less than a rehabilitation of "the idea of biological improvement…in a Darwinian framework" (Gould 1970a, p. 109). (This sentence was published during the same year that "Punctuated equilibria" was drafted.) Accordingly, when we read in "Punctuated equilibria" (1972) that natural selection is responsible for "new and improved efficiency" among members of an isolate, we suspect that the authors are speaking of a limited form of progress. Moreover, when we read in Gould (1977c) that increased biomechanical efficiency represents "one pathway to adaptation," and that species that follow this path "form the subset of a directional trend," we are confident that improvement was never far from Gould's mind in the discussion of trends (see also Gould 1976d). Or at least such was the case prior to 1977.

Wright's rule and the new explanation of trends

I have yet to say much about the "reconstruction" of punctuated equilibria (ca. 1977), by which I mean the "reconstruction" of the authors' explanation of trends. Suffice it to say, this represents the beginning of Gould's break with adaptationism, and the first full-throated attempt to argue for the *necessity* of rendering evolutionary theory in a hierarchical context. The centerpiece of the reconstruction is Steve Stanley's notion of *species selection*, which "follows from the validity of two premises":

1. "[The] model of punctuated equilibrium itself," which serves to individuate species in geologic time, and

2. “[The] proposition that the set of morphologies produced by speciation events is essentially random with respect to evolutionary trends within a clade. Sewall Wright (1967) made this suggestion in explicit analogy with the lower-level phenomena of random mutation and natural selection within populations. We suggest that this proposition be termed ‘Wright’s rule,’ and that it testing be an item of high priority in paleobiology” (Gould & Eldredge 1977, pp. 139-140).

From here, Gould and Eldredge proceed to offer the following epitome of their “speciation theory of macroevolution,” namely: *punctuated equilibria* + *Wright’s rule* = *species selection*. “Previously, mutation and natural selection within populations were regarded as fully sufficient to render macroevolution,” the authors claim; “one had only to extrapolate their action to longer times and higher taxa to render all of macroevolutionary change.”

> But if we (1972) and Stanley (1975) are right, then speciation interposes itself as an intermediate level between macroevolutionary trends and evolutionary events within populations. Species become the raw material of macroevolution: they play the same role, at their level, as mutations do in local populations (Gould & Eldredge 1977, p. 140).

Stanley’s proposal was a watershed in Gould’s thinking about macroevolution. Although Gould continued to hold that the “primary events of speciation…adapt populations to local environments” (but see Gould 1982b, p. 383), he soon realized that the causes of speciation held little interest for students of long times and large clades (Gould 1977c, p. 22). What mattered were not the causes of speciation in ecological time, but rather “the deployment of species in geological time” (Gould & Eldredge 1977, p. 145). More specifically, what mattered were the processes leading to “the differential birth and death of species *considered as entities*” (Gould 1984, p. 92, emphasis added). The origin of a feature is one thing, Gould cautioned; the spread of features through large clades is another. “Macroevolution is fundamentally about the combination of features and their differential spread” (Gould 1982b, p. 385). As such, it does not take as its *explicans* the phenotypic properties of organisms (at least not exclusively), but deals in those properties of species leading to their differential fitness *qua* units. Trends can arise because one kind of species reproduces more rapidly than another kind of species within a clade; or because one kind of species is more resistant to extinction than another kind. In either case, one kind of species will increase in representation relative to another, for reasons that have little to do with the “triumph [of one species over another] in direct competition” (Gould & Eldredge 1977, p. 144).

This was the insight that Gould had been searching for since his days at Columbia—a means of establishing a principled difference between the micro and macrocosm. Once he laid hold of it, Gould did not disappoint. For the next 25 years, he poured himself increasingly into his macroevolutionary theory, culminating in a valedictory statement, *The Structure of Evolutionary Theory,* published just 60 days before his death. The book is overripe, and defies any attempt at brief description. (For reviews and criticism, see Borrello (2004), Jablonski (2002), Orr (2002), Stearns (2002), and Zimmerman (2002).) Suffice it to say, it is a conception of evolutionary theory that only a paleontologist could love. Nonetheless, the book is uniquely Gould’s, and expresses his mature philosophy as only a 1,300-page tome can. It is Gould at his most “Darwinian.”

Gould's change: a hypothesis

It remains to say what accounts for the major upheaval in Gould's thought—the 'transit' from Thompson to Darwin, as I earlier called it. Roger Thomas provided an important insight in the passage quoted above (and might have said more, as Seilacher's *konstrukionsmorphologie* doubtless played a role in the transition).[1] Yet Thomas's answer must be regarded as incomplete. While I cannot pretend to a full analysis here—such would require extensive archival work, and a better grasp of the paleontological literature than I possess—, I will close this essay by offering a tentative hypothesis. This hypothesis does not seek to account for the increased importance that Gould began assigning to contingency during the late-1970s, a development Sepkoski has convincingly traced to Gould's experience with random models (see Sepkoski 2012, pp. 264-266). Instead it concerns the all-important developments that enabled Gould to break with his Thompsonian adaptationism after 1976, and to undertake a vigorous and idiosyncratic expansion of Darwinian theory.

Stephen Jay Gould, as Dave Sepkoski notes, was a radical in the venerable sense of

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[1] After studying under Gould at Harvard, Thomas went on to become one of the leading advocates of *konstructionsmorphologie* in the United States. But he did not receive this perspective from Gould (Thomas, personal communication). Indeed, Gould seems not to have cared much for *konstructionsmorphologie* in the early 1970s, or even to have understood it. In 1971, reporting on the Tübingen Meeting on Form, Gould mildly chided his Teutonic colleagues for their "reluctance to grant Darwinian processes a complete role in the explanation of form (obvious adaptations to definite environments, yes of course; basic *Baupläne* perhaps not)" (Gould 1971e, p. 1042). Such comments notwithstanding, this brief notice is a treasure-trove of minor revelations, and includes one of the first discussion of "constraints" as Gould would come to understand them:

"It is perhaps ironic, perhaps enlightening, that a theoretical perspective to our own (and therefore 'wrong' in our eyes) should inspire such excellent work; for it is clear that German paleontology is far ahead of ours or anyone else's in its attention to form (thought not to variation)…Yet is it this very 'incorrect' perspective that inspires such a detailed attention to form; for we, when we don't understand a structure, tend to think: 'I know it's adaptive even if I don't know, so I'll move on to something else,' whereas a German, in a similar dilemma, is inspired to continue his study because he has no set answer and because the allocation of structures to adaptive and non-adaptive categories remains a theoretical pursuit of high importance….The challenge for us, I think, is to incorporate our colleagues' superb feeling for form within the context of our preferred theories that I for one, in my own narrowness, will continue to espouse, at least for the moment" (Gould 1971e, pp. 1042-1043).

‘considering things from their root [*radix*]’ (Sepkoski 2009b, p. 335). Already by 1972, he had taken up the cudgels against ‘stale’ orthodoxies—the branching view of life’s history, and the dogma of phyletic gradualism. In addition, he had published a commentary on uniformitarianism in *The American Journal of Science* (1965), railed against biological determinism (Gould 1974c), and complained about “vague, trivial and untestable” adaptive hypotheses within evolutionary paleontology (Gould 1971a, p. 254). His first book, *Ontogeny and Phylogeny*, was an attempt to reclaim for evolutionary biology a vast reservoir of forgotten data, the importance of which had been obscured by ritualized prejudice. And the MBL collaboration—so rich in potential implications—furnished morals about philosophic determinism (Gould et al. 1977, p. 23), responsible paleontological praxis (pp., 24-25, 35), and the aptness of Lyell’s “steady state metaphor” for describing the evolution’s uneasy panorama (p. 39).

Gould preferred no role to ‘the champion of the underdog,’ and the 1970s saw him playing it with increasing vigor. Probably this owed to his success as a public intellectual—a role that fosters principled opposition to the status quo (Gouldner 1979). Throughout his career, Gould worked hard to maintain his public persona, which Perez Sheldon describes as “a sage yet relatable man, filled with a wisdom for the ages, even the cosmos” (Perez 2013, p. 108). Yet beneath this placid surface existed a current of genuine subversiveness, which ran as a coordinating thread through his many activities. Gould delighted in posing uncomfortable questions, in confronting “orthodoxy” with tales of the oppressed, and in perfuming his criticisms with an overwrought *savior-vivre*. If scientific criticism is an art, then Gould must be recognized as a great past master. While he lacked the harness of the finest of scientific critics (men like T.H. Huxley and P.B. Medawar), yet few scientists have so seamlessly melded their critical and “positive” programs, all while maintaining a keen philosophic vigil. Perhaps Dana Geary said it best—“People like Steve don’t come along very often” (Geary 2009, p. 140).

Given what has just been said, it is tempting to ascribe Gould's philosophic change to his subversive streak, which kicked into high gear following the publication of *Sociobiology*.[1] But such would be an impoverished analysis of a rich and variegated period in Gould's career, and in evolutionary biology writ large. In what follows, I discuss five pertinent considerations that bear on Gould's transit between Thompson and Darwin (ca. 1972-1977). Some of these considerations are new; others are recapitulations of earlier points. To insure intelligibility, I will follow my enumeration with a brief attempt at a summary and a synthesis. —What points must we hold in mind if we wish to comprehend Gould's change?

1. *Gould's adaptationism could have survived the Wilsonian menace.*

As we've seen, Gould's early adaptationism accorded him ample room to criticize Wilson while yielding little ground to his opponent. Gould's disagreement with sociobiology, after all, did not concern the presence of *adaptation* so much as the question: 'how fine-grained is the genetic control of the phenotype?' (The presence of "adaptation, in humans, is neither an adequate, nor even a good argument for genetic influence," Gould wrote in *The Mismeasure of Man* (p. 327).) Accordingly, Gould could easily have maintained a limited adaptationism at the same time that he took sociobiologists to task on issues of methodology and ideology (see Gould 1977b, p. 255). Yet after meeting Wilson on the battlefield, Gould abandoned citadel after citadel, presumably of his own volition. Why was this the case?

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[1] H. Allen Orr comes close to supporting this interpretation in his review of *Structure* (2002). Other authors, like Barash (2002) and Prindle (2009), have supported the thesis that Gould's politics was the tail wagging the dog of his science; but this is not the same thesis, and at any rate is incorrect.

2. *Gould came to regard adaptation as pernicious around the same time he realized that his macroevolutionary theory could do without it.*

The answer to the above question has two components: one (primarily) social, the other (primarily) pragmatic. First, Lewontin convinced Gould that the besetting sin of sociobiology is *adaptationism*, a point Gould had yet to appreciate during the mid-1970s (Segerstråle 2000, p. 118). It follows that the true menace to evolutionary biology was not overheated sociobiologists, but rather the "adaptationist programme," of which sociobiology was but a local recrudescence (see Lewontin 1978). Fair enough—but Gould's adaptationism was defensible from many of charges that Lewontin hurled at sociobiologists (for instance, that they regard *all* traits as adaptive, and view them as essentially *disjunct* from other characters). At the very least we might have expected some hemming and hawing from Gould, if not a period of equivocation. But this does not seem to have occurred. Again we must ask why this was the case.

The reason, I think, is that after 1976, *adaptation was no longer required to round out Gould's macroevolutionary theory*. For one, computer simulations had revealed that apparently directed trends could be generated in stochastic systems bounded by minimal biological constraints (Raup & Gould 1974).[1] While this did not tell against the importance of "conventional Darwinian selection [acting on individual organisms]," it did suggest that over long stretches of time, "*undirected* selection may be the rule rather than the exception in nature" (Raup & Gould 1974, p. 321, emphasis added). More importantly, Steve Stanley had shown that punctuated equilibria *entails* an autonomous realm of macroevolutionary processes, in which species-individuals serve as the primary actors. Evolution in the phyletic mode, *sans* speciation, was simply too slow to account for the rates of evolution recorded in the fossil record—something more was needed. This "something more" was selection operating on rapid speciation events: "species selection."

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[1] The same can be said of non-directed cladistic patterns (Raup et al. 1973).

No longer was it desirable, or even appropriate, to invoke directional natural selection as the cause of "long-term, net directional change" (or, more to the point, differential species success within large clades); the cause did not match the effect. Gould embraced this argument around the same time he came to see adaptationism as pernicious. Within several years, adaptation had been redacted more or less completely his macroevolutionary theory.

3. *The invertebrate factor: changing audiences, changing identities.*

Gould's "science of form" had as its object to raise the status of invertebrate paleontology within the evolutionary disciplines, and thus to score a victory for paleontology as a whole. Not only do invertebrates possess a *history of form*, susceptible of functional explanation, but this history is capable of suggesting new insights into paleontology's unique domain: "transspecific evolution and major patterns in the history of life" (Gould 1970a, p. 80). For instance, the science of form affirmed the theoretic importance of parallelism, convergence and iterative evolution, and pointed to the necessity of recognizing 'limited solutions to common problems' as a major theme in transspecific evolution (see Gould 1971a, p. 257). It also suggested new data collection practices, and encouraged the adoption of a multivariate approach, which had at last become feasible with the advent of mainframe computers.

Gould began pleading his case in the late 1960s, at which point he would have been regarded as a promising young paleontologist, trained by Norman Newell and John Imbrie. Although his allometry review had been a watershed, Gould was not yet widely known outside of his immediate professional community; certainly no one viewed him as an up and coming *evolutionary theorist*. Accordingly, he addressed himself primarily to paleontologists, by urging internal reforms that, with luck, might reverberate in larger biological spaces.

"Punctuated equilibria" changed everything (Sepkoski 2009a). Throughout the 1970s Gould's star was on the rise, and his audience began to swell. But more importantly, the makeup of his readership changed. All of the sudden, Gould had the ears not only of paleontologists, but of *all* evolutionary biologists. The majority of these readers were uninterested in the second-class status of invertebrate paleontologists within geology departments—to them, Gould was simply a *paleontologist*. Embracing this new and broader identity, Gould ceased worrying over what invertebrate paleontology could offer to paleontology writ large, and began angling for a distinctive paleontological contribution to evolutionary theory. By the early 1980s, Gould was one of the most controversial figures in all of evolutionary biology, and a man whose rhetorical pyrotechnics "[call] for serious attention by students of evolution" (Charlesworth et al. 1982, p. 474). He was also fully committed to reforming evolutionary theory along hierarchical lines. When set against this promise (to affirm paleontology as a generator of "testable *and irreducible* theories about pattern in the history of life"), the science of form must have appeared a rather meager prize.

4. *The subversive streak, and the strategic devaluation of natural selection.*

How does one win for paleontology a seat at the evolutionary high table? One strategy involves questioning how adequately conventional evolutionary theory accounts for the major features of evolution, including (most importantly) evolutionary trends and patterns. Gould had learnt from Raup how fruitful it could be to remove natural selection from the field of evolutionary causes, at least as a heuristic exercise (Sepkoski 2012, p. 223). Much of the order traditionally ascribed to selection can be recovered in stochastic simulations, employing a minimum of "biological" assumptions:

> The morphological order of evolutionary trees has been the traditional argument for the operation of directional causes in macroevolution…Our simulations display most

> of the ordered features generally associated with uni-directional selection: morphological coherence of monophyletic groups and incomplete filling of “morphological space”; regular “unfolding” of morphology…; marked evolutionary “trends”; [etc.]…We attribute much of this order to abstract topological properties of the tree itself and urge that the data for inferences about directional causes be sought elsewhere (in functional morphology, for example)” (Raup & Gould 1974, p. 305).

Needless to say, Gould had no interest in repudiating natural selection, a move that would send him careening toward the lunatic fringe with iconoclasts like Søren Løvtrup and Brian Goodwin. Nonetheless he wished to knock it from its pedestal as the *sole* factor lending to evolution its direction and its intensity (cf. Simpson 1953, p. 140). Given what paleontologists had discovered during the 1970s, it was incumbent upon them to see how much (macro)evolutionary order could be recovered without recourse to natural selection (as well as other causes operative within local populations). Gould suspected it was quite a lot, and issued the exploration of “unorthodox” factors as a direct challenge to paleobiology:

> The evolutionary ideas that most paleontologists employ are extensions by simple extrapolation, to vast times and large groups, of processes that operate in local populations over a few generations. But our tendency for uncritical extrapolation is bound often to lead us astray, unless reductionism is a valid approach and evolutionary processes display no hierarchical structure (with different styles of explanation emerging at higher levels). Our conventional reliance upon microevolutionary processes as a source of paleontological explanation has impeded the formulation of an adequate theory of macroevolution. We extrapolate so automatically that we scarcely recognize and ponder what we do; hence we often do not even realize alternatives (Gould & Calloway 1980, pp. 393-394).

5. *The moral factor.*

Finally, I wish to offer a brief statement on the relationship between Gould’s critical program and his philosophy of nature (for more thorough analyses, see Segerstråle 2003, Perez 2013). To Gould, much of science resonated in the moral sphere, which—like all products of the mind—is a human construction. Yet Gould was no relativist concerning the products of scientific inquiry, notwithstanding his interest in the limitations of human mentation ("the inherent structural baggage that Kant called the *synthetic a priori*"). Science is *progressive* in the sense that contemporary scientists know more about the furniture of the world (and the household economy) than 18th century natural philosophers. But its progress is not an upward sweep that proceeds ineluctably from ignorance to unambiguous truth. Instead, it is a tortuous and largely abortive process, wherein most suggestions are stillborn and all manner of prejudice and persuasion influence its course. This perspective saturates Gould's writings and deeply informed his science, in particular, his view that good science entails an element of social criticism ("debunking," Gould wrote, "[is] positive science"). Here as elsewhere, Ullica Segerstråle's perspective is worth attending carefully:

> Unlike many modern scientists who saw their task as limited to the strict pursuit of knowledge, leaving it to the political process to decide about the uses of science, Gould pursued a combined scientific and moral/political agenda. Gould's science was typically "engaged"; it was science for a purpose. And the purpose was to make this world a better place to live for society's less privileged members. Coming from an immigrant background himself, keenly aware of his family history and alert to the fact that scientific findings could be used to legitimize social discrimination, he saw as his mission to identify and debunk potentially dangerous scientific claims about the biological makeup of humans. This is why he devoted a great deal of his time during the last quarter-century to criticizing IQ research and sociobiology (Segerstråle 2003, p. 469).

Segerstråle has described Gould's political philosophy as a kind of "intuitive" (as opposed to doctrinaire) Marxism: a flexible, "gut-level" philosophy which "predisposed him to 'antiestablishment'-type explanations" (Segerstråle 2003, p. 468). I would add that it predisposed him to a particular view of the uses and functions of science within democratic society. A keen student of history, Gould was well aware of the manifold *uses* of science, many of which were retrograde in their influence on social affairs. But given that all science has an ideological dimension, it is impossible to sort the wheat from the chaff based on some measure of ideological taint. What can be controlled is how useful science is to members of the power elite. In other words, scientists can (and must) control the *function* of science—or at least police it. If it is undesirable that science should echo the sentiments of the powerful, then scientists must pursue inquiry against a background that is unlikely to produce adverse social consequences. This does not mean manipulating results or suppressing research, but rather ensuring that science does not become an instrument of social oppression, by rooting out prejudice to the best of our abilities.

Perhaps this can be stated more baldly without losing hold of the guiding thread. To Gould, it was simply unthinkable that "good science" would conflict with the worldview at which he had so fitfully arrived. Of course, science is fated to produce uncomfortable results, some of which will strain our psyches to their breaking points (see Gould 1996). But science done for the right reasons will not lend itself easily to social abuse. Conversely, if scientific researches *are* susceptible of such abuse, it is probable that they represent "bad science" or subliminal bias (Gould 1978b, 1981). At the very least, they must be regarded with the utmost suspicion.

Gould's reasoning, as I have depicted it, is circular, but it is predicated on an independent claim concerning the function of scientific inquiry. Good science does not prostrate itself before the power elite.[1] To the extent that science has a function within democratic society (as opposed to mere uses) the safeguarding of the status quo is opposed to it. The way to avoid retrograde influences is to remain self-critical, and to harness the moral purview of science to desirable ends. A racist society will produce racist science, even if it is filled with upstanding empiricists (Gould 1981). Yet by the same lights, a society committed to the ideal of social equality will produce science that furthers humanitarian causes and combats inter-group prejudice. (To complicate matters, these societies may employ similar, or even *equivalent*, methodologies. What differs between them is not a matter of art, but concerns the matrix of factors that determine how

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[1] This is true even of politically charged areas of research, like studies of human intelligence, which Gould defended in a limited way (see Luria, Gould & Singer 1981, p. 308).

and when a particular methodology is employed, and how relevant data are identified and interpreted. In other words, what differs are their largely-unanalyzed background assumptions.) —It was by this route that Gould came to support many "causes," including anti-adaptationism and anti-progressionism, such that "his methodological and philosophical stance always buttressed his political views and vice-versa" (Prindle 2009, p. 17). Gould's critical program had a strong moral component. Probably this crystalized after Richard Lewontin's arrival at Harvard in 1973 (although it was not unique to this period).

* * *

What accounts for Gould's change? Here is my hypothesis. I think that the early MBL papers (i.e., Raup et al. 1973, Raup & Gould 1974), and especially Steve Stanley's "widely discussed *PNAS* article of 1975," exercised a powerful and lasting effect on Gould's thought (see Gould 2002, p. 980). After experimenting with stochastic models, and having absorbed the argument for the autonomy of species-level processes, Gould wished to discover how much macroevolutionary order could be explained on principles other than "conventional Darwinian selection" (Gould & Lewontin 1979, p. 593). "Macroevolutionary stochasticity," directional speciation, species selection, and various types of constraint *all* seemed competent to produce effects which tradition ascribed to orthoselection (e.g., Simpson 1953, Hecht 1965). Moreover, and quite happily, *all* these mechanisms fell within the ambit of evolutionary paleontology, and suggested new and fruitful directions for paleobiological research (Gould 1980b, 1985, Gould & Calloway 1980). With such conceptions in tow, adventurous paleontologists could look forward to a far richer future than had previously been the case. The macroevolutionary playground had been opened: "[If] evolution works on a hierarchy of levels (as it does), and if emerging theories of macroevolution have an independent status within evolutionary theory (as they do) then paleontology may [at last] become an equal partner among the evolutionary disciplines" (Gould 1980b, p. 78).

The best years of Gould's professional life were spent in pursuit of several goals, foremost among them the raising the status of paleontology among the evolutionary sciences (see Sepkoski 2012). As Grantham observes, "Gould hoped that paleontology would make a *distinctive* contribution to evolutionary theory"—which meant unearthing new causes or mechanisms, even if these causes were 'just' statistical (Grantham 2009, p. 232). "Although the ultimate aim was to produce a genuine synthesis of micro- and macroevolution [as indicated by Gould's persistent interest in ontogeny], paleobiology first needed to establish a robust realm of macroevolutionary phenomena that are not adequately captured by microevolutionary approaches—an idea that was sure to ruffle some feathers." And ruffle them it did, particularly in light of Gould's seemingly tireless manufacture of new causes of punctuation and stasis. Factor in Gould's flamboyant critical program (adorned with all manner of literary confection), and there was little chance that his macroevolutionary theory would gain significant traction outside of paleobiology.

In discussing Stephen Jay Gould, the foremost difficulty to be avoided is holding too fast to any one factor as sufficient to account for his thought. Such conditioning factors will only get us so far if we fail to understand the deeper currents on which they are imposed. What moved Gould were those elements of orderliness that provided history with its shape and its texture—as well as their limitations. Whether in thrall to Thompson or Darwin, it was *grand narratives* that appealed most strongly to his heart, and which gave to "lovely particulars" their savor and their consequence. Gould had a gift for seeing the beauty incarnate in an equiangular spiral, a tiny wrist-bone, a Cambrian priapulid.

And, of course, he had a knack for expressing it. In the end, he earned the same homage that G. Evelyn Hutchinson paid to D'Arcy Thompson:

> What he wrote brings home to the scientific mind, perhaps better than the work of any other writer, what it means to be civilized; the splendor of the panorama that he has presented gives value to what we try to do, and in giving us this he achieved a reward given to few men (Hutchinson 1948, p. 604).

2. The Problem of Beginnings: “Mivart’s dilemma” and the direction of 19th century evolutionary studies

Max W. Dresow

I.

Introduction

“The two greatest problems in history,” a famous Romanist once declared, “are how to account for the rise of Rome, and how to account for her fall” (Reid 1911, p. 54). The student of 19th century biology might render a similar verdict with respect to Darwinism. Of course, the selection theory did not ‘fall’ in the sense of ‘going to pieces’ (see Largent 2009). As the 19th century drew to a close, the followers of Darwin remained in the majority among students of evolution, and the theory of selection was anything but abandoned. Yet as the bacteriologist Herbert Conn observed in 1900, “while scientists are agreed to-day…that the theory of descent represents the actual history of the organic world,” yet it is “probably not incorrect to say that upon the question of method [mechanism] there is to-day greater uncertainty of opinion and greater confusion than at any previous time” (Conn 1900, pp. 10, 11). Conn continues (with his trademark optimism): “This is not…because we know less of the subject, but because we know more. It is because the problem has not proved to be the simple one at first conceived, but to have many factors entering into it not at first expected” (p. 11).

It is a measure of Darwin’s influence that he continued to exert a powerful sway over biological thought even during the period of his “eclipse” (Bowler 1983). While non-Darwinian theories were prevalent during the 19th century, most took their rise from some difficulty on the selection theory, and derived their explanatory power from an ability to overcome it. A leading difficulty, which had exercised Darwinists since St. George

Mivart's *On the Genesis of Species* (1871), concerned the incipient stages of useful structures. How can development get started along a particular line when the early stages of modification are so trifling as to make no difference to welfare on the organism? To this problem biologists addressed a great diversity of hypotheses, none of which sufficed to dispel the difficulty (Cock 1973, p. 8).[1] However the failure to forge a consensus on the method of origination should not detract from the broader point that the *problem* of novel structures was burning during the latter 19th century. It seems to me a good time to revisit this fascinating period in history, as the problem of novel structures is burning once more (Wagner 2011, Brigandt & Love 2012, Wagner 2014).

Evolutionary thinking traced an extraordinary arc during the nineteenth century. From the introduction of Lamarck's transformist doctrine in 1800, to the publication of *Die Mutationstheorie* in 1901, the science of descent attained to a remarkable degree of sophistication within a mere hundred years. Setting aside Darwin's private jottings (which constitute an era unto themselves), the majority of this development was crowded into four decades at the end of the century (1859-1900). This was the *belle époque* of classical Darwinism, and the beginning of its "eclipse." Historians of science have concentrated largely on the former episode, encompassing the formulation of Darwin's theory and its early career (see Kohn 1985, Glick 1988 for early essays in these areas; Ghiselin 2009 for a guide to the formidable secondary literature; Desmond & Moore 1991, 2009, Hodge 2009 for important recent contributions). By contrast, my interest lies

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[1] As many have noted, Anton Dohrn's principle of *Functionswechsel* (or 'function-change') greatly dulls Mivart's objection (Cock 1973, p. 8, Gould 1991, Bowler 1996, pp. 162-163). The principle of *Functionswechsel* (according to Caianiello, a "radically functionalist" extension of Darwin's proposal that organs may undergo a 'conversion from one function to another' (1872, p. 147)) states that novel structures arise by 'priority changes' within preexisting multifunctional structures (Caianiello 2015). (This circumvents Mivart's dilemma by denying that *there have ever been* rudimentary, non-functional organs.) However, as Cock observes, the crucial point is *not* whether a 'correct' solution to the problem of incipient structures was lighted upon during the 19th century. Rather, what matters is contemporary opinion regarding the adequacy of proposed solutions. Given Weismann's repeated attempts to solve the difficulty during the 1890s, we can safely say that even dogmatic selectionists did not see the issue as resolved around the turn of the century (Weismann 1904, p. 132).

in the latter 19th century: specifically, in the crisis of faith concerning the method of organic evolution.

There is nowadays considerable scorn to be earned for generalizing over broad periods of time, as well as multiple national, disciplinary and institutional contexts. Once, Peter Bowler could strike a blow against orthodoxy by doing little more than documenting "the temporary explosion of interest in non-Darwinian ideas of evolutionism in the late nineteenth century" (see Bowler 1983, 1988). (Bowler may not have been a young Turk historian, but the project was nonetheless exceptional in its concentration on 'failed' scientific theories.) Now, the hypothesis of an "eclipse" is just one more orthodoxy to be resisted—the newest set of blinders preventing a proper appraisal of the era. Mark Largent goes so far as to compare the propagandistic function of "the eclipse of Darwinism" with the "Dark Ages," and recommends its abandonment forthwith (Largent 2009). I will advocate a different tack—an understanding of the "eclipse" in terms of the problems deemed worthy of attention by various research communities.

I make no pretense of completeness with respect to my undertaking; in fact, I am quite unqualified to mount a frontal assault on this enormous problem. Instead, I have endeavored to follow out a single thread: the "problem of beginnings" as it developed in the non-Darwinian literature.[1] As a means of accessing this issue, I have concentrated especially on the dilemma of incipient structures, hereafter "Mivart's dilemma." My thesis is that Mivart's dilemma played a critical role in structuring post-Darwinian biology, most importantly by drawing attention to cases where an incompatibility exists between the cause assigned (natural selection) and the outcome (a particular structure or transformation). I will *not* concentrate on how research into these problems was shaped

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[1] The term "problem of beginnings" belongs to Vernon Kellogg, an eminent (and eminently level-headed) Darwinian entomologist who spent the majority of his career at Stanford (e.g., Kellogg 1907, p. 35).

by particular institutional and disciplinary contexts.[1] This massive project must be left for those with abler pens; Nyhart (1995) and Desmond (1996) have made promising starts on the problem, but much work remains to be done.

A note on St. George Jackson Mivart

My essay has no protagonist, but it does have a central figure, the Darwinian excommunicate St. George Jackson Mivart. Although not a scientific behemoth like his mentor, T.H. Huxley, he was nonetheless a person of considerable importance: a credentialed anatomist and prolific author of both professional and popular texts (see Gruber 1960). In addition, it was Mivart who first brought attention to a number of the objections "that would later be exploited during the eclipse of Darwinism" (Bowler 1983, pp. 22-23). These gained widespread currency with the publication of his first book, *On the Genesis of Species* (1871)—in particular, his eponymous "dilemma":

> "Natural selection," simply and by itself, is potent to explain the maintenance or the further extension or development of favorable variations, which are at once sufficiently considerable to be useful from the first to the individual possessing them. But Natural Selection utterly fails to account for the construction and development of the minute and rudimentary beginnings, the slight and infinitesimal commencements of structures, however useful those structures may afterwards become (Mivart 1871, p. 23)

While no longer regarded as worrisome (but see Gould 1980d, p. 167), Mivart's dilemma made great waves during the post-Darwinian period (Desmond 1982, pp. 180-181, Gould 2002, pp. 1219-1220). William Bateson referred to it as *by far* the most serious objection yet brought against the theory of natural selection (1894, pp. 15-16, see also Bateson 1900). T.H. Morgan called it "a veritable stumbling block [for Darwin's] theory," and

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[1] The reason for this is personal incapacity; I do not wish to pass judgment on social or disciplinary factors, other than to say that I consider them *exceedingly* important. An important early study of the social and political context of Mivart's science is Adrian Desmond's *Archetypes and Ancestors* (1982).

proceeded to discuss Mivart's attack of Darwinism at some length (Morgan 1903, pp. 132-138). Vernon Kellogg devoted much space in *Darwinism To-day* to that "basic problem of evolution"—the problem of beginnings—and worried incessantly over the early initial stages of modification (Kellogg 1907, pp. 35, 49). And R.S. Lull traced the entire body of orthogenetic literature to "the difficulty of explaining the beginnings of advantageous modifications…by the selection of individual variations" (Lull 1920, p. 175). Darwin may have provided a cogent answer to Mivart's dilemma in 1872 (Ch. 5, 7), but this did not dispel the problem in the eyes of many researchers.

"The life of St. George Mivart fits the Victorian era," writes Jacob Gruber. "In all his life, in the work he did and in the controversies in which he engaged, he reflected the conflicting currents of thought and feeling which marked the age" (Gruber 1960, p. 2). St. George was born under the sign of the pound sterling, in November of 1827. His father was James Edward Mivart, socialite and proprietor of the famous Mivart's Hotel in Brook Street (now Claridge's). From an early date, James kindled and expedited his son's intellectual endeavors, to which St. George responded with undying affection. "It was something more than stereotyped filial devotion which prompted [St. George]…to dedicate one of his last books *To the dear memory of my father James Edward Mivart, who by his toil freed me from sordid cares while he ever encouraged me to love and work for science*. Here, as in many cases, the boy was the father to the man" (Gruber 1960, p. 6).

Mivart's life was forever changed in 1844, when the sixteen year-old entered St. Chad's Cathedral and declared his faith in the Roman Catholic Church. Following his conversion, Mivart defended his adopted faith with tremendous energy, eventually becoming one of the more influential lay Catholics in Great Britain. Yet he remained forever a freethinker, and ended life as an apostate, casting vitriolic aspersions on the throne of St. Peter (Root 1985). In a sense, it was a fitting end to a long and tempestuous existence. Mivart's long-standing piety had been sincere, and had formed the mainspring of his life's ambitions witness his many articles in *The Nineteenth Century*, and *The American Catholic Quarterly Review*). But it concealed a rebelliousness which lay near the heart of his manifold excursions in science and philosophy. "What is surprising is not that Mivart ended his life as a heretic," Gruber muses, "but that the always uneasy alliance between him and the Church should have lasted so long" (Gruber 1960, p. 144). (This is true, but only to the extent that "Church" is read as "Roman Catholic Church," not as a synonym for "Theism.")

Professionally, Mivart was a comparative anatomist specializing in the osteology of primates. His work was well-regarded, particularly prior to the mid-1870s, and Darwin cited it in *The Descent of Man*. Perhaps his best-known researchers concerned the osteology of lemurs, but he also deserves credit for supporting the "lateral fold" hypothesis regarding the origin of paired fins (Mivart 1877). He died in London in 1900.

Plan of the essay

The goal of this essay is to demonstrate the prominence of Mivart's dilemma within late 19th century evolutionary studies. Specifically, I will argue that by directing attention to "the problem of beginnings," Mivart played a crucial role in structuring the problem horizon of the eclipse period. It should be noted, however, that Mivart's dilemma was but a single facet of a larger critique. As R.C. Punnett complained in 1911: "[The] function of natural selection is selection and not creation. It has nothing to do with the formation of new variation. It merely decides whether it is to survive or to be eliminated" (p. 175). Likewise T.H. Morgan: "[Selection] has not produced anything new, but only more of certain kinds of individuals. Evolution, however, means producing *more new things*, not more of what already exists" (Morgan 1916, p. 154, emphasis added). Quotations like these could be multiplied *ad infinitum*; at any rate, the general tenor of the argument is clear.

To Punnett and Morgan, it was simply inconceivable that selection should be credited with *originating* anything (see also Delage 1903, p. 843, De Vries 1905, p. 7, Bateson 1909, p. 96). Selection can prune and suppress; it can keep the fittest in trim whilst condemning the inferior to extinction. But it is impotent in creation. As a jaundiced Theodor Eimer wrote, mere months before his premature death:

> I must, in fact, reiterate again and again that natural selection can under no circumstances create anything new. It can only work with existing material, and it cannot even use that until it has attained a certain perfection, until it is already useful. Selection can only remove what is downright injurious, and preserve what is useful. By always selecting the useful it will strengthen its development, but the facts prove that even this can take place only in a restricted measure. Primarily, therefore, the importance of selection consists not its being an active and principal agency in the transmutation of forms but in its being at most a simple collateral instrument in this process (Eimer 1898, p. 21).

This is a broader argument than Mivart's, one that denies to gradual natural selection any creative function whatsoever. But while Mivart agreed with this position, "Mivart's dilemma," as I have defined it, is *not* the suggestion that natural selection is a purely destructive force. Instead, it concerns the question of how natural selection can account for those transitions in which the initial stages confer no adaptive benefit (thus ceding the point that selection can explain transitions in which all stages confer a benefit).[1] Crucially, Mivart's dilemma does *not* concern the inability of selection to explain the origin of the variants it fosters. (Mivart was well aware that this was not Darwin's problem, although he did view it as a problem.) Rather, it concerns the "impotence" of

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[1] While Mivart believed that all consequential variation was determinate, this is irrelevant to the issue at hand. Nonetheless, we can rephrase Mivart's dilemma so as to give a pointer to his preferred solution: determinate variation achieved by leaps. Mivart reasoned as follows. If the early stages in a proposed transition are not beneficial to the organism, then they cannot be systematically preserved. In other words, *there is no handle for natural selection* in this scenario—another cause must be provided. We will examine a number of proposed solutions to this quandary below.

natural selection (*qua* cause) to produce a certain class of effect (i.e., transformations that confer no benefits in their incipient stages).

My study will proceed in two steps. In the first place, I will examine criticisms of natural selection concerning the "problem of beginnings," with special attention paid to Mivart's dilemma. Following this, I will offer some preliminary comments on the "problem horizon" of late 19th century evolutionary studies: *what* questions were burning at this time and *why*? In the second place, I will examine two broad attempts to grapple with the problem of beginnings: "directed evolutionism" (orthogenesis) and "discontinuous evolutionism" (saltationism). In each case, I will aim to show the importance of Mivart's dilemma in compelling the search for non-Darwinian modes of origination (constrained variation and saltation, respectively). Several important thinkers will feature prominently my account, most notably, Theodor Eimer and William Bateson. Approaching these researchers in light of the problem of beginnings is not only valid, I argue, but also highly suggestive, as each authored a major treatise on the subject of evolutionary novelty. Although much scholarship has focused on the extra-scientific causation of the so-called "eclipse of Darwinism," not enough has considered the scientific underpinnings of non-Darwinian arguments. It is my hope to rectify this situation, in however small a way.

Mr. Darwin's critics: The Jenkin episode and Mivart's dilemma

The Jenkin episode

The initial resistance to Darwinism has almost always been treated as ideological, and therefore as hindering the forthright discussion of evolutionary factors (Nordenskiöld

1928, pp. 477-485, Mayr 1972, Ghiselin 2003).[1] In the uncharitable words of Delage and Goldsmith: "We can truthfully say that all [Darwin's] opponents were, in the last analysis, swayed consciously or unconsciously by one of two motives, their theological turn of mind or their hatred for all general ideas in science" (Delage & Goldsmith 1912, pp. 43). Only *after* the historicity of descent had been established were disputants freed to concentrate on questions of causality and mode, such as agitated the later century. These discussions began in earnest in the 1860s, and rose to a fever pitch in the following decades (see Vorzimmer 1970, Ruse 1979, Ch. 8).

According to most accounts, natural selection received its heaviest blow from H. Fleeming Jenkin, a celebrated polymath and intimate of William Thomson (see Morris 1994, pp. 320-328).[2] In Jenkin's view, the evidence from domestic productions militated against the notion that nature has "the power indefinitely to magnify the peculiarities which distinguish [her] breeds from the original stock" (Jenkin 1867, pp. 278-279):

> A given animal or plant appears to be contained, as it were, within a sphere of variation: one individual lies near one portion of the surface, another individual, of the same species, near another part of the surface; the average animal at the center…There is no reason to believe that a fresh variability is acquired by long selection of one form; on the contrary, we know that with the oldest breeds it is easier

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[1] Olivier Rieppel's volume, *Evolutionary Theory and the Creationism Controversy* (2011), is a recent scion of this tradition, but it is to be hoped that with an increased recognition of the currency and diversity of transformist thinking during the early 19th century (e.g., Corsi 2005, Richards 2008), such narrow accounts will lose their grip.

[2] As Darwin wrote to J.D. Hooker, "Fleming Jenkyns [review] has given me much trouble, but has been of more real use to me than any other" (quoted in Morris 1994, p. 315). Many of Darwin's contemporaries took notice of the "trouble" without sensing its putatively constructive sequel (e.g., Romanes 1886, p. 339-340). As Adrian Desmond records, Darwin suffered considerably from "the mutually reinforcing positions of Mivart and Jenkin," which appeared in rapid succession during the late 1860s (Desmond 1982, p. 180). Indeed, "Jenkin's cruelly logical *North British Review* article (1867) silenced even a usually noisy Huxley—who admitted its 'real and permanent value,' and then promptly dropped the subject." Apropos of these dramatics, the 'Jenkin episode' has attracted a large amount of historical interest (perhaps in a degree disproportionate with its actual importance). Examples of publications addressing the episode include Brooks 1883, Poulton 1908, Willis 1940, Eiseley 1958, Hardin 1959, Vorzimmer 1963, Olby 1963, Geison 1969, Burchfield 1974, Ruse 1979, Bowler 1989, Richards 1989, Gould 1991b, Morris 1994, Gayon 1998, Bulmer 2004, and Olby 2009. Bowler (1988) was an early advocate of the view that its importance has been overstated (pp. 91-92).

> to bring about a diminution than an increase in the points of excellence. The sphere of variation is a simile embodying this view (Jenkin 1867, pp. 282, 286).

Jenkin further suggested that while an individual "may produce descendants varying in any direction, [it] is more likely to produce descendants varying towards the centre of the sphere" (p. 282). This tendency to normalization indicated that interbreeding should continuously obviate deviations from the norm, resulting in a backsliding towards the modal character of the race (see Jenkin 1867, pp. 289-290). Thus was the "paint-pot problem of heredity" born; many drops of gray paint can be stirred into a pot of white without altering the hue of the mixture (Hardin 1959, see also Bulmer 2004). Something more than the summation of favorable increments was needed to account for the origin of species, Jenkin divined. Substantial morphological changes must occur by the occasional production of true-breeding sports, which are at once stamped with a kind of "perfection" (see Jenkin 1867, p. 287). Indeed, Jenkin was convinced that *only* a saltational mechanism could account for the origin of new types given the time allotted by the ripe age of the Earth (somewhere in the neighborhood of 100 million years).[1] Arguments to this effect remained in good standing well into the 20th century (e.g., de Vries 1919).

Why was Jenkin's review so successful? A number of reasons can be brought forward, not the least of which was Jenkin's easy and congenial style (paired with some genuine touches of humor).[2] What's more, as Susan Morris notes, Jenkin grounded his argument in the apparent security of physical law, not in the monotonous accumulation of

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[1] The question of the age of the Earth, and the length of time available to evolutionary processes, was, in Morris's view, Jenkin's primary concern in his *North British Review* article (Morris 1994, pp. 315-316). It was also the leading reason that Darwin rated the review so highly. Many scholars have misconstrued this point, Morris claims, and focused undue attention on Jenkin's treatment of variation and inheritance (the so-called "swamping argument"). My reason for perpetuating this error—if indeed I have—is that it is *the response of biologists to the review*, and not Darwin's appraisal of its value, that interests to me. When thus framed, the swamping argument is of greater moment than its thermodynamic sequel, although both arguments retained their relevance well into the twentieth century (see Burchfield 1974).

[2] The racism that so offends the modern reader was unexceptional during the 1860s, and would not have detracted from the article's appeal.

facts, as Darwin had (Morris 1994, pp. 329-330). This allowed Jenkin to concede various empirical matters, and even to admit a certain amount of biological ignorance, while yielding nothing to his illustrious opponent (see Jenkin 1867, p. 278). Simultaneously, it enabled him to occupy the high ground of apparent nomologic inference which had attained to ascendency through Newton's celebrated labors. Thus, Jenkin could readily grant that Darwin had identified a feature of the world that arose in a law-like fashion from natural processes, while nonetheless complaining that he had not posited a law *of* selection—"for there is no single, universal law that is to natural selection as the Newtonian inverse square law is to gravitational force" (Hodge 2000, p. 40). To the extent that this was regarded as a failing, natural selection did not attain to the epistemic value of (for instance) the second law of thermodynamics, upon which Jenkin heavily relied.[1]

Mivart's dilemma

Jenkin's essay appeared in *The North British Review* in June of 1867, under the veil of anonymity. "It would be about a year and a half before Darwin would learn that the engineer Fleeming Jenkin had written the essay," Susan Morris relates. "By then Darwin had concluded that the critique was the most valuable he had ever read on *The Origin of Species*" (Morris 1994, p. 313). The same year, a cognate article appeared in the Catholic periodical *The Month,* entitled "Difficulties of the Theory of Natural Selection" (1869). Like Jenkin's review, its authorship was undisclosed (although it soon became evident who had written the piece). Consisting of three parts, the article was St. George Mivart's

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[1] It is notable that the declining century would host many attempts to discover laws *of* evolution (which operated in the same epistemic space as the inverse square law). The orthogeneticists—who sought to frame 'laws' of forthright progressive advance (see Berg 1969, Ch. 3), and the saltationists—who attempted to discover "the laws to which the origin of new species conform" (de Vries 1909, p. 6), both attempted to usurp Darwinism by this epistemic maneuver. These attempts will be examined in greater depth below.

first attack on Darwinism, and began with a laundry list of criticism. The most famous of these was the dilemma of incipient structures, which Mivart stated as follows:

> What we have now to bring forward may be summed up as follows…That though potent to explain the maintenance of further extension of favourable variations, the theory [of selection] fails to account for the conservation and development of the first beginnings of such (Mivart 1869, p. 41).

Unlike many of Darwin's critics, St. George Mivart was a learned and capable scientist, having read anatomy under T.H. Huxley at the Royal School of Mines. Following his matriculation in 1861, Mivart formed "an intimate acquaintance with his teacher," who joined with Sir Richard Owen in securing him an appointment at St. Mary's Hospital in London (Richards 1989, p. 354). It was during these early years that Mivart began making a name for himself as a skilled researcher in the field of comparative osteology. In the words of his biographer, Jacob Gruber:

> The decade after his first real association with Huxley marks a period of growth during which Mivart secured by patient and painstaking research the reputation from which his later more controversial—and more speculative—pronouncements derived their support and authority…While the diffuse and often superficial character of many of his later writings could lead with some justification to the charge that he wrote "for mere effect," his articles and monographs of the 1860s were solid contributions to both the descriptive and theoretical aspects of biology (Gruber 1960, p. 27).

The estrangement of student and teacher commenced in 1869, agitated by profound differences in worldview. It was exacerbated two years later when Mivart debuted his new compendium of anti-Darwinian arguments, obnoxiously entitled *On the Genesis of Species*. As he writes in the book's introduction, the theory of evolution has "steadily gained ground" since its introduction in 1859, and it can be predicted "that the number of facts which can be brought forward in its support will, in a few years, be vastly augmented" (Mivart 1871, p. 5). Yet the "special Darwinian hypothesis," which many suppose to account for these facts, is beset with insuperable difficulties. It is the object of the present volume, he declares:

> to maintain the position that "Natural Selection" acts, and indeed must act; but that…in order to account for the production of known kinds of animals and plants, it requires to be supplemented by the action of some other natural law or laws as yet undiscovered. Also, that the consequences which have been drawn from Evolution, whether exclusively Darwinian or not, to the prejudice of religion, by no means follow from it, and are in fact illegitimate (Mivart 1871, p. 5).

The most important argument contained in the *Genesis of Species* is the aforementioned dilemma of incipient structures (Mivart's dilemma). Mivart could not imagine how gradual selection could have originated features like complex mimesis in butterflies, limbs and prehensile tails in vertebrates, whalebone in Mysticeti, mammary glands in mammals, the laryngeal structures of new-born kangaroos, rattles in pit vipers, the pedicellariae of echinoderms, et cetera.[1] Time and again he implies that only a saltational mechanism is capable of overcoming these difficulties, as natural selection cannot work on that which is of no benefit to the organism (Mivart 1871, p. 264). However, as Mivart correctly notes, this suggestion is profoundly anti-Darwinian:

> The theory of "Natural Selection" excludes the notion of a *sudden* resemblance [of, e.g., an insect] to a leaf or a bamboo. Any spontaneous tendency in such directions is similarly and equally excluded, through the impossibility of explaining such cases by "community of descent" (Mivart 1869, p. 45).

Mivart's dilemma is sometimes described as the thesis that "organs of extreme perfection" cannot arise by natural selection (the canonical example being the vertebrate

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[1] Darwin endeavored to answer these criticisms in a chapter added to the sixth edition of the *Origin* (Chapter VII: "Miscellaneous Objections to the Theory of Natural Selection"). As always, he prosecuted his task with considerable ingenuity, and in some cases his answers are quite convincing (e.g., whalebone, prehensile tails, pedicellariae). In other case he does not succeed nearly so well, or leans heavily on Lamarckian factors (e.g., flatfish eyes, mammary glands). What is most important for our purposes is that neither Darwin's response, nor Dohrn's "principle of function change," sufficed to dispel Mivart's dilemma in the eyes of the biological community. *Why* they did not suffice is an interesting and important question—but it is not *my* question. (For a recent analysis of Darwin and Dohrn's responses to the *Genesis of Species*, see Caianiello 2015.)

eye). If, in order to function, a large number of parts must collaborate in a precise and coordinated manner, then the organ could not have originated by the preservation of minute variations. I hope I have made clear that this is *not* Mivart's dilemma, but rather one particular extension of it. Arguments pertaining to "organs of extreme perfection" play a subordinate role in the *Genesis of Species*, and are best discussed under the heading of "coadaptation," which Mark Ridley defines as such:

> Coadaptation meant the exact mutual adjustment of the different parts of the body to each other. For example, the skeletal, muscular, nervous and circulator systems must all be of the correct relative sizes or none of them will work. Therefore, any evolutionary change of a coadapted system would require synchronous changes, all of exactly the right amount, in all the coadapted parts…Unless all the variants arose together, natural selection would oppose change, not favour it. So coadaptations would have to be explained by some factor other than natural selection (Ridley 1982, p. 46).

As Ridley observes, coadaptation is but a single dimension of a large and convoluted debate regarding the efficacy of natural selection in species-change (p. 45). And while Mivart had recourse to the coadaptation argument (e.g., 1871, pp. 58-60), it is preferable to define his "dilemma" more generally, in holding with the author's own enunciations (Mivart 1869, p. 41; 1871, pp. 251-252). An example will illustrate the distinction.

One of the strongest arguments adduced in the *Genesis of Species* concerns the "wandering eye" of pleuronectiform flatfishes (Mivart 1871, pp. 41-43). Larval flatfish are largely symmetrical—"[they] have a similar range in shapes, sizes and anatomical variability as the rest of the teleosts" (Geffen et al. 2007, p. 35). Yet during larval metamorphosis, one eye migrates upwards, eventually settling next to the other eye. Thereafter the flatfish foregoes perpendicular life (having rotated 90° about its dorsal plane), and lives on its side with *both* eyes facing upwards. Mivart wondered how this situation could have come about by the accumulation of petty differences, each benefitting its possessor. "If this condition had appeared all at once…then the perpetuation of such a transformation by the action of 'Natural Selection' is conceivable enough," Mivart admits. But this is *not* the Darwinian view of transformation (p. 42).[1] Here "Mivart's dilemma" concerns the riddle of how an eye can wander from one side of the head to the other when the first stages of modification leave the eye pretty much where it began.[2]

It bears repeating that Mivart's dilemma has to do with the capacity of a cause (natural selection) to produce its supposed effect. Recognizing the potential for confusion so often realized in debates over evolution, Mivart takes pains to emphasize that this is an *ontological*, not merely an *epistemological*, argument. "It may be objected," he writes, "that [the difficulties here mentioned] are difficulties of ignorance—that we cannot explain them because we do not know enough of the animals [*sic*]" (Mivart 1871, p. 59). But this is not Mivart's complaint. "[It] is not that we merely fail to see *how* Natural Selection acted, but that *there is a positive incompatibility between the cause assigned and the results*" (p. 59, emphasis added). Later commenters would develop this criticism more robustly, and in ways that wed its ontological and epistemological components. For instance, Bateson argued that the presupposition of utility effectively precludes the consideration of alternative explanations, as the failure to prove utility cannot *refute* the selection hypothesis (see Provine 1986, p. 221). In A.J. Cain's words: "it is doubtful whether any examples of variation in Nature can be so completely analyzed that, after selective effects have been estimated, the residual variation can be ascribed with confidence to [stochastic phenomena]. There is always the possibility, indeed the

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[1] Interestingly, two apparently transitional flatfishes have recently been described, *Heteronectes* and *Amphistium*, wherein the wandering eye assumes an intermediate position near the top of the head. This strongly suggests an incremental (if not necessary gradual) evolution of the craniofacial complex.

[2] As with the "co-adaptation argument," the inference that natural selection is incompetent to produce this transformation depends on the claim that the earliest stages of modification could *not* have conferred a benefit upon the organism. The explanation, however, does not have to do with the interaction of parts in a mechanism (unless the mechanism is taken to be the entire organism). Rather, it concerns the impossibility of accounting for the beginnings of modification by the selection of minute variations.

likelihood, that the analysis of selective effects was not complete" (Cain 1951, p. 1049). Consequently, the Darwinist is discouraged from even *recognizing* the incommensurability between cause and effect.[1] In a similar vein, E.B. Poulton did not think it probable that many characters were without utility:

> The more we study the characters of animals in general, even though we at first can see no utility, the more we come to admit this principle, and to believe that either now or in some past time, the characters have been useful. I can certainly say of many characters which I have studied in some of my investigations, that at first they seemed to be meaningless, but afterwards appeared to be of much importance in the struggle for existence. I think we may safely assume with regards to many characters of which we can now see no explanation that ultimately the explanation will be forthcoming (Poulton 1908, pp. 106-107).

Needless to say, many biologists in the late 19th century did not share Poulton's optimism.[2]

S*pecific genesis*

> "Owen…spread abroad in England the perception that a deep significance underlies the structure of animals—a significance for which no stress or strain and no influence of heredity, and certainly no mere practical utility, can account. The temporary overclouding of this perception through the retrograde influence of Darwin's hypothesis of "natural selection" is now slowly but surely beginning to pass away" (from an 1893 statement by Mivart, quoted in Gould 2002, p. 329).

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[1] Indeed, Mivart recognized this point perfectly well, even if he did not lay great emphasis on it in the *Genesis*. Writing in 1872, in response to Chauncey Wright's criticisms in *The North American Review* (1871), Mivart stressed the irrefutability of selection hypotheses (and, what is unique, the equally insulated position occupied by the opponents of selection): "Natural Selection can never be completely proved or disproved by [natural] science in *a posteriori* investigation; for it will always be open to one side to say, the utility not yet shown in any given structure will be shown later, and to the other side to say, whatever utility you show, though existing in an organ, was not the cause of that organ" (Mivart 1872, pp. 463-464).

[2] This is not to say that the average anti-selectionist believed *most* characters to be useless (although some did believe this). Nor is it to make the claim that the parts of the organic mechanism have *no use*—a remarkable accusation, but one that was occasionally leveled at Mivart. In response to Chauncey Wright's barb (accusing Mivart of denying the giraffe neck any special utility), Mivart exclaims: "can Mr. Wright suppose that I ever dreamed that the structures of animals are not useful to them[?]" "Apparently possessed with some such idea, Mr. Wright proceeds to exhibit the giraffe's neck in the character of a 'watch-tower.' But this leaves the question just where it was before. Of course I concede [that]…the long neck is most useful *when you have got it*; but the question is how it *arose*, and in this species *alone*" (Mivart 1872, p. 463).

Perhaps it owed to a lifelong interest in philosophy, perhaps to a tendency to hair-split, but Mivart understood the epistemic difficulties faced by the Darwinists. Writing in 1896, just four years before his death, he inquired whether specific characters are the result of natural selection. His response is revealing, both as regards its presentation and its conclusion:

> Dr. Wallace affirmed that "no other agency" than "natural selection" has been shown as a probable cause of specific characters—and therefore of species.[1] Possibly not. But if an asserted cause (X) has been shown to be incapable of producing a certain effect, it is of no use to say: "It must be (X) because you cannot bring forward any definite (not X) as efficient to produce that effect." Surely it is enough to reply: "The cause you assert is insufficient, and we must therefore remain in an attitude of doubt and expectancy" (Mivart 1896, p. 247).

Needless to say, doubt and expectancy were not Mivart's usual condition. If anything, he suffered from near pathological levels of confidence, which afforded a constant outlet for his disputative nature. It was thus inevitable that he would propose his own *not-X*, and defend it with all the powers at his command. In his best-known work, he christened it "specific genesis" (1871) and defended it against attack the following year (1872).

Much like Richard Owen, Mivart struggled to enunciate his alternative to Darwinism, probably because he could offer no clear "mechanism." Ultimately, he opted for a view wherein external potentiators join with internal forces to produce "changes which are harmonious and symmetrical"—fresh chords in the harmony of nature (Mivart 1871, p. 261).[2] These changes affected at once all parts of the organism, just as "the internal nature of vibrating plates causes sand grains scattered over them to assume definite and symmetrical figures when made to oscillate in different ways." Mivart completes the

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[1] Mivart might also have said, 'a probable cause of characters with no adaptive value in their incipient condition.' Specific characters needn't be such, but the logic of his argument is the same in both cases.

[2] He compares these – in a lurid, if somewhat confusing, analogy – to the patterns assumed by sand grains on a vibrating plate (see Mivart 1871, pp. 261-262)

analogy in a manner that anticipates the morphogenetic field (albeit in a perfunctory manner):

> The results of these combined internal powers and external influences might be represented under the symbols of complex series of vibrations (analogous to those of sound or light) forming a most complex harmony or a display of most varied colours. In such a way the reparation of local injuries might be symbolized as a filling-up and completion of an interrupted rhythm. Thus also monstrous aberrations from typical structures might correspond to a discord, and sterility from crossing be compared with the darkness resulting from the interference of waves of light (Mivart 1871, p. 261).

As befit a disciple of Owen, Mivart's thinking on transmutation was dominated by the idea of homology: the relation between organic parts that "may be said [to be] 'the same,' or at least 'of similar nature'" (Mivart 1871, p. 177). Indeed, there is hardly a publication on biological topics "in which he does not stress the importance of this concept for an understanding of the origin of species" (Gruber 1960, p. 19). In defense of its theoretic importance, Mivart scoured the literature of pathology and teratology for insights regarding animal symmetries, particularly in his best-loved field of osteology. What he uncovered dealt a fatal blow "to any purely utilitarian, environmental, or secular explanation of the organization and development of the organism" (Gruber 1960, p. 19):

> Altogether, then, it appears that each organism has an innate tendency to develop in a symmetrical manner, and that this tendency is controlled and subordinated by the action of external conditions, and not that this symmetry is superinduced only *ab externo*. In fact, [each] organism has its own internal and special laws of growth and development. [If] it is still necessary to conceive an internal law or "substantial form," moulding each organic being and directing its development as a crystal is built up, only in an indefinitely more complex manner, it is congruous to imagine the existence of some internal law accounting at the same time for specific divergence as well as for specific identity (Mivart 1871, p. 210).

Writing to Owen in 1871, Mivart confessed: "The more I think over natural philosophy the more I feel that it is *necessary* to ascribe to bodies the possession of some *internal* principle regulating their evolution."[1] Yet he took it for granted "that the law itself was a consequence of 'that innate potentiality which God has implanted' in living matter"—or, we might rather say, in the totality of the cosmic system (Desmond 1982, p. 181). Not unexpectedly, few professional scientists were convinced. However, while "specific genesis" may have had a fugitive existence, the same cannot be said of his critique of Darwinism. According to Gruber, each of the objections in the *Genesis* "represents an area [of inquiry] which was to inspire a host of future biological researches" (1960, p. 56). (Of course, Mivart cannot be credited with *spawning* these diverse areas of study, and the extent of his direct influence may rightly be questioned. But his arguments were not easily discredited, and gained in importance as non-Darwinian scientists began agitating for status.) Thus did a Catholic anatomist, destined for excommunication, influence the course and content of evolutionary studies.

An interlude on the troubled life of St. George Mivart

> "If a man never had faith he cannot either have lost it or abandoned it. They all say that he who has faith feels 'certainty' & that I certainly never have felt" (Mivart to E. Green, 3/29/1900, quoted in Root 1985, p. 22)

Although Mivart was an able scientist and critic, he was seemingly unable to keep out of trouble. Perhaps this owed to some deficiency in his character (Darwin's view), or maybe he was genuinely unaware of the tone he struck. As evidence of the latter position, Mivart appears to have been surprised by the reception of several offending statements, in

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[1] Just as serial, lateral and vertical homologies testify to a principle at work within the organism (and directing change down preexistent channels of potentiality), so do the homologies between species "testify to some similar [or identical] guiding plan throughout the organic universe" (Gruber 1960, p. 16). As Mivart wrote in his *Lessons from Nature*:

"At the close of the preceding chapter, the outcome was glanced at of those lessons which had already been gathered from nature. They were recognised as teaching that there exists in each animal and plant a unity of force corresponding with its unity of frame, each living organism manifesting, by unmistakable external signs, the presence of such internal power the mysterious nature of which it was sought to bring home by a consideration of those deep-lying tendencies revealed in the facts of serial and other homology" (Mivart 1876a, p. 280).

particular, an 1874 slur of Charles's second son George Darwin.[1] Had this been an isolated incident in an otherwise stainless career, it is possible that the elder Darwin might have overlooked it, and that Mivart's reputation might have remained intact. As it were, the *ad hominem* attack was just the latest in a series of missteps, the first of which was a belligerent review of the *Descent of Man* published in the *Quarterly.* As Gruber notes, this marked a turning point in Mivart's already strained relationship with the Darwinists:[2]

> The tone of the article is different from that of the *Genesis*. Where the latter, even at its most critical, was warm, friendly, and congenial, the former was bitter, overbearing, and condemnatory. While only tinges of the personal appear in the *Genesis*, the review is saturated with personal bias. This difference, both in tone and in argumentative approach, reflects Mivart's decision to combat the false application of Darwinism to man with every weapon at his disposal (Gruber 1960, p. 79).

After slandering George Darwin (again in the *Quarterly*), the fallout was quick and severe. Huxley cut off all communication with his former student after hauling him over the coals in a letter. Their friendship would not resume for a further ten years, and never again transcended simple pleasantries.[3] Others, like Joseph Hooker, never forgave him, as evidenced by his efforts to bar Mivart from the Athenaeum club. Writes Desmond:

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[1] If his letters are to be believed, Mivart deeply admired Charles Darwin, and was forever desirous of the older man's favor. This makes his published output all the more puzzling, as he frequently worked himself into a lather complaining about the moral consequences of "pure Darwinism." (Although this position is often imputed to Charles Darwin, Mivart's strongest comments were reserved for the so-called "Teutonic Darwinians," for instance, Ernst Haeckel and August Weismann.)

[2] This was the same publication that had earlier engaged Bishop Wilberforce to review the *Origin of Species* in 1859.

[3] Mivart attempted to appease his old mentor in his typical cloying manner. He seems unaware of the degree to which his libel had incensed Huxley, who days earlier had written to Hooker: "I will not leave a square inch of unwaled skin upon his idolatrous carcass before I have done with him." Huxley replied to Mivart with a *de facto* notice of anathematization. "[It] will be obvious to you that our views on those questions which *I* hold to be the most important of all mankind are too hopelessly divergent to make familiar intercourse between us pleasant and advisable" (quoted in Gruber 1960, pp. 106-107).

Mivart was deeply wounded by this letter, and persisted in currying Huxley's favor until the latter's death in 1895. Mivart's letters to Huxley are frequently pathetic, and often heartrending. "I *read* you when the opportunity offers, as, in old times, I used to *hear* you," Mivart wrote to

> The punishment would have been out of all proportion had the crime been solely scientific. But Mivart's untimely and unexpected pledge of support of the despised Platonism stabbed at the very heart of the new movement; a fact made worse by his almost becoming one of Darwin's inner circle. His precipitous desertion called for a show of strength, as much to warn the faithful as frighten the offender. Mivart thus found himself excommunicated by bell, book (*The Origin*) and candle, as he was later to be by the church himself (Desmond 1982, p. 141).

The flogging Mivart suffered at the hands of the Darwinists left gaping wounds, which did not heal for a great many years. But evolution had never been the mainspring of his philosophy. This honor fell to Catholicism. Following his youthful conversion in 1844, Mivart devoted the best years of his life to a staunch defense of the faith, in particular, its compatibility with modern science (see Mivart 1900a). His philosophy was not typical Catholic fare, but instead represented a mystic idealism that fused Platonic and naturalistic elements (it is here that Owen's influence is particularly clear). Ultimately it pleased no-one. First Mivart was marginalized from mainstream British science, as his philosophic conceptions came to impinge ever more on his work. Several decades later, following a series of fiery polemics, he broke with the church (Root 1985). "Catholics, to be logical, must say to any Roman congregation which should attempt to lay down the law about any branch of science: 'You have blundered once, and we can never trust you again in any scientific matter," Mivart raged:

> You may be right in your dicta, but also you may be wrong. The only authority in science is the authority of those who have studied the matter and are "men in the know." As to all that comes within reach of inductive research, you must humbly accept the teachings of science, and nothing but science. And for this you should be grateful (Mivart 1900b, pp. 61-62).

It is befitting that a wrangler like Mivart should go out on his own terms, having alienated both colleagues and coreligionists. Following the Dreyfus affair—which roused

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Huxley in 1886. "Do you recollect you said you used to call me your 'constant reader'?" (quoted in Gruber 1960, p. 24).

him to righteous indignation—he abandoned by turns the doctrine of infallibilism (Mivart 1887), the Catholic dogma of Hell (Mivart 1892), the Christian code of ethics and finally, the belief in the divinity of Christ (Gruber 1960, p. 212).[1] "*Liberavi animam meam*," Mivart declared: "I have freed my mind and my spirit" (p. 210). In the ruins of his life's work, amid the pale embers of a dying faith, Mivart had found peace.

The post-Darwinian problem horizon

Beyond Mivart's dilemma

It is a measure of Darwin's importance that he continued to exert a guiding influence over biological thought even during the period of his "eclipse" (Bowler 2009, p. 565). Throughout this interval, non-Darwinian theories derived a goodly amount of explanatory power *not* from the strength of novel premises, but rather by pointing a way around some difficulty on the selection theory. Chief among these was Mivart's dilemma—"The incompetency of Natural Selection to account for the incipient stages of useful structures" (1871, p. 23). But there were other factors that called into question natural selection's creative efficacy, and thus its sufficiency as a causo-mechanistic theory of descent.[2] Two in particular warrant mentioning, namely:

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[1] "As to the character of Jesus Christ," Mivart wrote to Alice Meynell, "I have during my long illness made as careful a study of it as I could, and I think the sentiment so many feel about it is due to traditional reverence and what they have been taught from infancy. What *God incarnate* did and said I used to reverence as divine and never criticized. But calm judgment of Jesus Christ as a mere man is a different matter. St. John's account I put aside as ideal and fictitious. Of what we read in the Synoptics how much is *true* history? But if we accept most of it, it seems to me that certain parts are admirable, some teaching distinctly immoral, and other parts ignorant and foolish. Altogether had I lived then, I do not think he would have attracted me" (Mivart to Meynell, 1900, quoted in Gruber 1960, p. 212).

[2] Here I am ignoring Jenkin's "swamping argument"—for a time 'the most celebrated difficulty' of Darwinian evolution (see Herdman 1889, p. 5). I gave it brief notice above in virtue of its tremendous importance and wide circulation; indeed, to bypass it would have been irresponsible. But being as it has been much-discussed in the historical literature, there is little more I can add that has not already been said.

- **“Spencer’s difficulty”** concerning the supposed impossibility of accounting for complex co-adaptation by means of the piecemeal modification of parts (Spencer 1864, pp. 450-457; see also Mivart 1871, pp. 58-60, Brooks 1883, pp. 281-289, Carpenter 1888, p. 681, Weismann 1909, pp. 32ff, Ridley 1982, p. 46).[1] As Spencer states his case (referring to congenital modifications): “among any organs which habitually act in concert, an increase of one can be of no service unless [to the organism] there is a concomitant increase of the rest” (Spencer 1864, p. 451). Stronger muscles require stronger bones to resist contraction, thicker ligaments to secure articulation, larger nerves to transmit stimuli, a greater blood supply, etc. The question thus arises: “[will] spontaneous variation occur simultaneously in all these co-operative parts? Have we any reason to think that they spontaneously increase or decrease together?” Spencer viewed the prospect as dim.

The logic of Spencer’s argument was ably summarized by the Scottish polymath J.J. Murphy (for biographic details see Duddy 2002, pp. 259-262):

“The higher the organization, whether of an entire organism or of a single organ, the greater is the number of the parts that co-operate, and the more perfect is their co-operation; and consequently the more necessity there is for corresponding variations to take place in all the co-operating parts at once, and the more useless will be any variation whatever unless it is accompanied by corresponding variation in the co-operating parts; while it is obvious that the greater the number of variations which are needed in order to effect an

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[1] The family of coadaptation arguments was not the exclusive possession of anti-Darwinian biologists. For instance, A.R. Wallace used a kind of coadaptation argument to downplay the importance (by questioning the viability) of saltatory variation (Wallace 1869, quoted in Mivart 1871, p. 117).

improvement, the less will be the probability of their all occurring at once" (Murphy 1869, p. 319).

(The problem of "coadaptation" has been expertly treated in Mark Ridley's paper "Coadaptation and the inadequacy of natural selection," published in *The British Journal for the History of Science* (1982). In spite of this, at least one recent commenter has persisted in identifying Mivart's dilemma with "the coadaptation of parts" (Caianiello 2015, p. 339). While it is true that Mivart employed this argument, I must stress again that coadaptation was a *facet* of Mivart's dilemma—it was not its nucleating center.)

. **Nägeli's argument** regarding the "negativity" of selection (Nägeli 1865, 1884 [cited in Morgan 1916, p. 35]; see also Jenkin 1867, p. 282, Mivart 1876a, p. 300, Cope 1887, pp. 14-16, Eimer 1898, p. 21, Korschinsky 1899, Berg 1969, pp. 57-59). According this popular argument, selection is powerless in creation because it cannot account for the origin of the variants it preserves (Delage & Goldsmith 1912, p. 250). The argument differs from Mivart's—which concerns the initial development of useful structures—by stressing the logical status of selection with respect to the origin of variation.[1] Purveyors of Nägeli's argument ask the question: 'what, in evolution, *originates* structures,' and reason that it cannot be selection, which is "wholly a restraining and cutting-back factor, not at all a formative one" (Korschinsky 1899, cited in Kellogg 1907, p. 333). In the words of E.D. Cope: "nothing ever originated by natural selection…It is to the great causative forces as are the gutters and channels which conduct the water in

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[1] Nonetheless many thinkers run the two arguments together, for instance, E.D. Cope, who additionally suggests that natural selection "fails to account for many characters which express the relations of *homology* and *parallelism* [two pillars of Mivart's *Genesis*], and is almost confined in its exhibitions to features which express teleology" (Cope 1887, p. 15).

comparison with the pump and the man who pumps it" (Cope 1887, p. 16). (As I have discussed this argument above, I will say no more of it here.)

These popular arguments (together with those of Jenkin (1867) and Mivart (1871)) influenced the development of four distinct but interpenetrating problem areas, each with its own set of (non-mutually exclusive) questions:

1. *What is the mechanism of heredity?* —How do we conceive of heredity and variation; when and why do organisms become variable (i.e., what are the "laws" of variability); how is variation to be analyzed; how are we to distinguish between heritable and non-heritable characters (and can under what conditions can the latter *become* heritable); to what extent are heritable characters dissociable; etc.
2. *When and how do novel characters originate?* —What is the nature and mode of variation; when in the life-cycle do novel characters appear; where is one most likely to find them (geographically, or in conjunction with what conditions); what rules or laws superintend the introduction of new forms; etc.
3. *What course has life's history travelled heretofore?* —How are groups of organisms related to one another in time; how did extant groups come to occupy their present ecological and geographical stations; what patterns or laws dominate the history of life (e.g., Cope's rule of phyletic size increase, Williston's law of specialization); etc.[1]

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[1] In *Life's Splendid Drama,* which treats the early research program in evolutionary morphology (and post-Darwinian paleontology), Peter Bowler lists a number of additional questions, for instance: "What is the relationship between classification and phylogeny, and how does one define a 'natural' group? How does the biologist adjudicate between different lines of evidence bearing on the question of origins, when the implications seem to contradict one another? To what extent must theories on the nature of the evolutionary mechanism influence our ideas about the possible relationships between groups?" (Bowler 1996, p. 98). To Bowler, these questions pierce near the

4. *What is the predominant mode of phyletic advance (i.e., progressive evolution)?* —Is evolution gradual or episodic; what is the tempo of organic change, and what is its "motor"; to what laws or spatiotemporal invariabilities does progressive evolution conform; what is the role of natural selection in species-forming (if it has any role at all); etc.

Attention to these problem areas was ubiquitous in evolutionary studies between 1875 and 1900. Granting this—and realizing that Mendelism would eventually disclose the "secret" of evolutionary creativity—students of the period have devoted a great deal of attention to the first and fourth areas, the problems of heredity and mode. Bowler's volume, *Life's Splendid Drama*, was intended to redress the relative neglect of the third area (see Bowler 1996, pp. 2-4); in addition, the topic of evolutionary biogeography has received some attention following Browne's *The Secular Ark* (1983).

By contrast, the second problem area has been slow to be recognized. Possibly this is because it is difficult to separate from (1) and (3). (In fact, *none* of the aforementioned problem areas can be reasonably decoupled from the others. The nature of heredity bears on the problem of variation; the nature of variation provides the channel(s) by which novelty is generated; and the generation of novelty entrains the process of descent. How easy, then, to slur over the problem of origination, especially considering that few undertook to study it directly.) I wish to suggest that we should regard origination as its own problem area. For instance, research into (2) needn't involve a hypothesis as to (1);[1] nor is it necessary to study origination in conjunction with (4) (although the two were often connected). Additionally, one could study (1) (as the biometricians did) without a

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heart of evolutionary biology, in part, because they are questions that could not have been formulated during the bad old days of idealistic morphology.

[1] It might be noted that in William Bateson's monumental study of variation (1894), the author advocates the abandonment of the term *heredity*, as nothing like the vertical transmission of property can be plausibly held to occur during reproduction.

strong hypothesis as to (2), and without any interest in (3). Finally, many paleontologists studied (3), and were led to speculate on (2) and (4), while showing only a superficial interest in (1).

What follows is an examination of two groups of thinkers in light of the problem of beginnings: the so-called “orthogeneticists” and “saltationists,” respectively. These variegated movements were *not* merely efforts to refute the selection theory, as a distressing amount of secondary literature seems to imply. Of course, they were partially this, but they were also frank attempts to address several burning biological problems: for instance, how do novel features arise during the course of descent, and what is the bearing of this process on the general features of evolution? My contention is that Mivart’s dilemma played an important role in structuring the discussion surrounding these topics, and in determining the sorts of explanations of origination that researchers found compelling. Mivart’s dilemma was thus a touchstone for theories of origination—one that can help us to make sense of a debate fractured in a thousand ways by deep veins of ideology and prejudice.

II.

Introduction

Herbert William Conn was born in January of 1859, in the evening of the pre-Darwinian world. As a young man he read morphology at Johns Hopkins, became interested in evolution, and helped to found the Society for American Microbiologists (now the American Society for Microbiology). In addition, he penned one of the most thoughtful treatments of evolutionary theory to appear during the early century, *The Method of Evolution* (1900). This work was Darwinian to the hilt—a considerable change from his earlier survey, *Evolution of Today*, wherein it was written that "Natural selection, or Darwinism, is…almost everywhere acknowledged as insufficient to meet the facts of nature, since many features of life are not explained by it" (Conn 1887, p. 243).[1] Further, and while it was conceived for a lay audience, yet it contained a rich and sophisticated account of natural selection as understood by 19th century scientists (Conn 1900, pp. 13-50). This included a description of those criticisms of natural selection that still loomed at the turn of the century (see also Conn 1887, pp. 212-243, Kellogg 1907, Ch. 3-5).

A leading criticism of the selection theory (which we have now considered at length) was Mivart's dilemma of incipient structures (Mivart 1871, p. 26, Conn 1887, p. 259). Having experienced the evolutionary debates of previous decades, Conn was well aware of the importance of the dilemma, and its continuing relevance:

> From the very outset of the discussion aroused by the theory of natural selection, it has appeared that one of the most serious difficulties in the way of accepting natural selection as a satisfactory solution of descent is the seeming impossibility of

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[1] Conn continues by stating that this fact "does not detract from the importance of the principle, which still remains as one of the most important laws regulating organic life...No one would be inclined to-day to deny that natural selection is a law of nature, and that many changes are induced by it. But while some believe it to be the all-important law of organic life, others would consider it a secondary and very subordinate principle whose effect is of little importance. Between these two extremes all grades can be found (Conn, pp. 243, 245)." (Compare to Conn 1900 pp. 394-403.)

> accounting for the beginning of organs. Selection explains elimination and the moulding of organs to new functions, but it doesn't explain origin. This difficulty appealed to Darwin and he candidly discussed it, suggesting various facts looking toward a solution of the difficulty. But the same question has been raised by nearly everyone who has discussed selection, and it has been studied from various standpoints (Conn 1900, p. 134).

The usual response to Mivart's dilemma was to assert that organs, while always functional, may nonetheless change their *primary* function over time. Thus fins became tetrapod limbs became flippers (or wings)—but never is a limb uni-functional (or without functional importance). For instance, a proto-wing may continue to function as an arm, or may confer some other benefit(s) besides. This argument, which debuted in the *Origin of Species* (1859, p. 191, 1872, Ch. 7), was codified and extended by Anton Dohrn in his *Der Ursprung der Wirbelthiere* of 1875:

> The transformation of an organ occurs through the succession of functions, the bearer of which remains one and the same organ. Each function is a resultant of many components, of which one forms the main, or primary function, while the others represent subsidiary, or secondary functions. The sinking of the main function and the rising of a subsidiary function changes the total function. The subsidiary function gradually becomes the main function, the total function becomes another one, and the result of the entire process is the transformation of the organ (Dohrn 1875, p. 60, quoted in Bowler 1996, p. 163).

It is possible that Dohrn slowed the acceptance of his principle of *Functionswechsel* (function-change) by debuting it in conjunction with a bizarre argument concerning the derivation of vertebrate penises from annelid gills (Dohrn 1875, p. 67).[1] In any event—and notwithstanding its subsequent triumph—the idea of co-option did not dispel Mivart's dilemma entirely. Of course, every evolutionist recognized that wings are modified limbs, which in their ancestral state were adapted to non-aerial functions.

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[1] Paradoxically, this great student of novelty was deeply suspicious of genuine origination, which he compared to the unacceptable doctrine of spontaneous generation (Dohrn 1875, p. 21). His view of evolution was thus dominated by *Functionswechsel*—that is, the co-option of structures by formerly "subsidiary" functions. It also led him to posit, perhaps not unreasonably, that most organs are multifunctional (see Caianiello 2015).

Likewise, everyone believed that the tetrapod limb began as a fin, and had to acquire its capacity as a load-bearing structure. But how did appendages originate in the first place? Many had ventured hypotheses, including such luminaries as Oken (1843), Owen (1849), Gegenbaur (1870), Huxley (1876), and Balfour (1878). (Incidentally, Mivart came out in support of James Thatcher's 'lateral fin fold hypothesis' [1877]—also supported by Balfour—in 1879, and is now recognized as an important architect of that theory.) Thus was Conn led to observe, twenty-five years after Dohrn's publication, that "in spite of all that has been said it can hardly be claimed by anyone that these difficulties have been removed by one or all the considerations that have been urged":

> How an organ could ever get started is a mystery. It certainly cannot fall under the explanation of the selection of variations around a mean, for until an organ has made its appearance in some form it cannot show variations…This fact has led some of our most thoughtful and observant naturalists to question seriously whether selection can be regarded as a *vera causa*, while it has convinced others that we can never find the explanation of descent by the study of natural selection, no matter how vigorously we pursue the subject, and that the only chance for further progress is in the study of variations themselves (Conn 1900, p. 135).

This statement might easily have been penned by William Bateson, whom we shall encounter presently. First, however, we will examine one other noteworthy attempt to grapple with Mivart's dilemma—that of the directed evolutionists.

Constrained novelty: directed evolution and Mivart's dilemma

"Orthogenesis"

Considered in their manifold details, the theories of orthogenesis formed a disorderly multitude, replete with all manner of philosophic artifice and linguistic treachery. But common to all theories was the conviction that evolution is, at its core, an orderly phenomenon, dependent in some manner upon the organization of living things or their germs. Such orderliness finds its expression in patterns of morphological transformation, which unfurl in relative isolation from the exigencies of local ecology (Bowler 1983, p. 141). Theodor Eimer, the great student of animal coloration, expressed his position thus:

> Orthogenesis is a universal law. It holds, as I have long insisted, not only for the markings, but also for the other morphological characters of animals, and also for those of plants. Even in the latter, as my personal observations have convinced me, the markings of the blossoms and the shape of the leaves follow, in rigorous conformity to law, a *few* definite directions (Eimer 1898, p. 21).

As Eimer's statement brings out, the chief attraction of the orthogenetic doctrine was its promise to replace Darwin's "empire of accident" with an unshakable rule of law (see also Eimer 1890, p 1). The saltationists had similar ambitions, of course, as did the neo-Lamarckians. But the students of directed evolution were on the whole unsurpassed in their commitment to a law-bound transformism and a nomothetic biological science. In light of this philosophy, the activity of natural selection was tightly circumscribed, often to the point of outright dismissal (Nägeli 1884, p. 285, Mivart 1896, p. 246, Eimer 1898, p. 54, Berg 1967, p. 51). It was no mere idiosyncrasy that led Eimer to subtitle his capstone publication *On Orthogenesis:* "and the impotence of natural selection in species formation" (1898). (Interestingly, the term "impotence" also features centrally in Mivart's *On Genesis of Species*. Let our Freudian colleagues make of this what they may.)

The directed evolutionists were a mixed lot, and came of a distinctly motley tradition. The earliest representatives were theistic evolutionists like Mivart and Edward Drinker Cope (see Cope 1868, Mivart 1876b). Later in the century, an increasing number of secular biologists joined the fray, for instance, Theodor Eimer, H.F. Osborn and C.O. Whitman (see Eimer 1890, Osborn 1894, 1912, Whitman 1919). Most had an especial interest in morphology, whether animal or vegetable (Levit & Olsson 2006). Some were paleontologists (e.g., Cope 1871, Hyatt 1884, Scott 1894); a great number were

Lamarckians (e.g., Mivart 1884, Cunningham 1895, Delage 1895); a few appealed to saltational mechanisms (Huxley 1896, p. 223, Eimer 1898, pp. 33-34, Thompson 1942, pp. 1094-1095); and others flaunted all rules of scientific decorum (Nägeli 1884, Pfeffer 1895).[1] Thankfully, this clutter does not render the position unintelligible. As Kellogg writes in *Darwinism To-day*:

> Many biologists see in variation and in species-forming certain determinate characteristics exhibited by, or lines or paths being followed by all or most of the individuals of successive generations; and see in descent *certain phenomena of forthright progressive movement* which they find selection based on utility unable to explain (Kellogg 1907, p. 275, emphasis added).

This is as pithy a summary of directed evolutionism as can be found in the evolutionary literature. It lacks only reference to "biological laws" to round it out as a complete statement of the position.[2] The paleontologist R.S. Lull draws attention to the nomologic dimension in his popular textbook, *Organic Evolution* (1920). Like Kellogg, he emphasizes the supposed capacity of orthogenesis to surmount one or more difficulties on the selection theory—most notably, Mivart's dilemma. Unlike Kellogg, he suggests that this is *raison d'etre* of the theory:

> Orthogenesis (Gr., ὀρθός, straight, γένεσις, production) is the theory that variations and hence evolutionary change occur along certain definite lines impelled by laws of which we know not the cause. *This theory has arisen mainly from the difficulty of explaining the beginnings of advantageous modifications or of new organs by the selection of individual variations occurring in every direction of change.* It is evident that unless a structure appeared at once in a degree of development to give it a "selection value," it would be difficult to account for its beginning, but the very teaching of the Neo-Darwinians postulates the selection of minute Darwinian variations and not such saltations as the idea just advanced would imply. There are also recorded apparent instances of the existence of determinate variation, such as those along fixed and apparently not advantageous lines, and the definite cases of over-development of parts beyond the point of advantage (Lull 1920, p. 175).

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[1] A thorough review of the orthogenetic literature of the early 20th century can be found in Glenn Jepsen's paper, "Selection, 'Orthogenesis,' and the Fossil Record" (1949, pp. 490ff).

[2] For a sensitive account of early "Platonic" evolutionary theories—which also had appeal to directed causes—Desmond's *Archetypes and Ancestors* remains unsurpassed. Bowler has also discussed these conceptions under the heading "theistic evolutionism" (e.g., 1983, Ch. 3).

In this section, I will follow Lull in regarding "orthogenesis" as a relatively coherent school of thought in spite of its factional nature (but see Jordan & Kellogg 1907, p. 113). Moreover, I will consider as an "orthogeneticist" any who regards variation as pursuing a definite course *in relative independence of environmental conditions* (in particular, the pressure of population on the means of existence).[1]

Haacke and Eimer

The term orthogenesis—nowadays taken to cover all theories of directed evolution—was coined by Wilhelm Haacke in 1893, and co-opted by Theodor Eimer two years later. To both of these thinkers, the phenomena of orthogenesis depend upon the presence of powerful constraints on variation, acting in concert with strong environmental potentiators. In Haacke's view, constraints on variation result from the geometrical properties of hereditary particles called "*gemmae*" (Levit & Olsson 2006, p. 101).[2] As the *gemmae* "tend to assume certain relations of equilibrium" in cells and organisms (which may nonetheless be upset by external influences), it follows that evolution consists in the transformation of *gemmaria* from one point of stability to another (Hartog 1913, p. 76).

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[1] It may be profitable to subjoin a more modern definition of orthogenesis, framed by a professional historian. Bowler's 1983 chapter entitled "Orthogenesis" is a useful introduction to the topic (and should be read in conjunction with the preceding chapter, entitled "The American School"), but more sympathetic is Levit and Olsson's 2006 article, cleverly titled "Evolution on Rails." Their definition of orthogenesis is as follows:

"Considering its history, orthogenesis can in general terms be defined as a concept of interior or exterior constraints restricting variation in such a way that evolution will be canalized in a certain, theoretically explicable, and therefore predictable direction. In a more narrow sense…orthogenesis means that fundamental organismic structures exist, which predispose living beings to vary only in certain directions. In the majority of theories, orthogenesis is opposed to the idea of evolution as an immediate and permanent adaptation of organisms to their environments, although there is no logical necessity for orthogenetic evolution to be non-adaptive, as was shown by Berg…Rather, orthogenesis implies that there are trends in development and evolution, which can be seen as non-adaptive considering the immediate needs of the organisms" (Levit & Olsson 2006, pp. 128-129).

[2] This is opposed to the Darwinian concept of "amphigenesis," or undirected variability (Haacke 1893, p. 32).

These points of stability are not random, but follow each other in lawful (i.e., deterministic) procession. It is this geometrical process that is responsible, in Haacke's view, for all forthright trends of phyletic advance.[1]

In addition to the concept of constrained variation (which implies no principle of evolutionary progress), Haacke subjoined the notion of "epimorphism," or "[the] increasing degree of developmental perfection, which comes into being in the course of phylogenetic history" (Haacke 1893, p. 204). As with orthogenesis, the processes generating epimorphism derive ultimately from the geometry of the heredity materials (in conjunction with external circumstance). But the two types of modification are conceptually distinct (Levit & Olsson 2006, p. 103). Where they converge is in the supposition that organisms are only modifiable *in toto*—that is, through an externally induced restructuring of the hereditary system. Thus, when we come to examine evolution as a whole, the strands of orthogenesis and progressivism are deeply—and perhaps inextricably—interwoven (Haacke 1893, pp. 33-34).

Wilhelm Haacke was a minor figure in the span of 19th century biology. Better known was Gustav Heinrich Theodor Eimer, Kölliker's pupil and the author of influential studies on the wall lizard (*Lacerta muralis*) and swallowtail butterflies (genus *Papilio*). An early convert to Lamarckism, Eimer's enthusiasm for "definitely directed evolution" did not crest until the final decades of his life, at which point he had set his sights on the

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[1] Haacke regarded the vertebrate eye as a paradigm instance of orthogenetic progression (Grehan & Ainsworth 1985). During the long course of its evolution, the eye developed from a simple pigmented cup "towards a more and more advanced sensory tool," finally attaining to a high pitch of perfection in raptorial birds (Haacke 1893, p. 32). This is a clear instance of a trend directed by constraints on variability, Haacke thinks. But the attainment of perfection is not a phyletic inevitability. Sometimes the progression is suspended—a condition frequently observed in troglodytes (wherein eyes tend to assume a vestigial condition). At other times it is terminated outright. However—and here we come to Haacke's point—eyeless organisms rarely, if ever, re-evolve their ancestral condition in all its delicacy (see Gould 1970). From this and similar phenomena, Haacke concluded that evolution is constrained to flow in a single direction. "It was to facilitate the discovery of this kind of phenomena that Haacke coined the term orthogenesis," Levit and Olsson explain (2006, pp. 102). Haacke was more dogmatic. "Within each phylogenetic line the development has always proceeded only in one specific direction. Orthogenesis has taken place everywhere" (p. 32).

destruction of Weismannism (Bowler 1983, pp. 153-154). But Eimer's orthogenesis was not *merely* an attempt to confute Weismann—his one-time teacher and, by 1890, the most influential Darwinist in Germany. His finest volume, ponderously titled *Organic evolution as the result of the inheritance of acquired characters according to the laws of organic growth*, begins with an illuminating passage:

> It seemed to me long ago of the greatest importance to undertake an investigation of the question whether the modification (variation) of the species of animals is not governed by definite laws. It had previously been assumed that variation occurred quite irregularly, in the most diverse directions, that it was abandoned completely to chance; in fact, the origin of species according to the Darwinian explanation is left entirely to chance…If, as I acknowledge, the principles of Darwinism are true because they can be shown to follow from natural laws, then it was to be expected that obedience to laws would also be discovered in that province which Darwin had surrendered to chance. But if variation were shown to follow certain laws, the same demonstration would apply to the origin of species (Eimer 1890, p. 1).

Of course, Eimer was not so unprejudiced as he would have his readers believe. Indeed, he was convinced that *if* natural selection were efficacious in species-forming, evolution would at once strike off along "all sorts of heterogeneous and radiating lines" (Kellogg 1907, p. 282)—a position no Darwinist would support.[1] Having thus rigged the game, it was his pleasure to lay about Darwinism with spiteful blows, in particular, the Darwinism of August Weismann. Criticizing natural selection served the needs of his orthogenetic thesis, which made heavy weather of the problem of beginnings. But Eimer also had an axe to grind, and made no effort to conceal it. Probably this cost him dearly in the court of public opinion.

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[1] Compare to Haacke's claim that, under Darwinian assumptions, reversion should be as frequent as phyletic advance.

Eimer on variation: directions and causes

So far as Eimer could tell, variation does not take place "in all kinds of directions irregularly, but always in definite directions, and [usually] only in a few" (1890, p. 20). In order to bring this insight in line with scientific materialism, he was forced to play nomenclator (a game for which he had startlingly little talent). However notwithstanding these exercises, Eimer made little attempt to conceal his sympathies with Lorenz Oken (author of the *Grundriss der Naturphilosophie*), leading Bowler to assert that his true purpose was "the imposition of a transcendental order upon the apparent chaos of nature" (Bowler 1983, p. 153). As Bowler writes in an early study of Eimer's orthogenesis:

> There is little doubt that Eimer himself found the Darwinian world view unacceptable for broadly philosophical reasons, and the same must be true to some extent of his followers…Those who wished to restore to the evolutionary process the element of regularity denied by the materialism of Darwin's theory would inevitably tend to opt for orthogenesis. In Eimer's case, the expectation that nature ought to exhibit a regular pattern of development seems to represent the last phase in the influence of the old idealist world view of *Naturphilosophie* (Bowler 1979, pp. 71-72).

Probably this statement contains a kernel of truth, but it is doubtful whether so strong a line can be drawn between Darwin and Eimer's "materialism," and the moral implications they entrain. Although much has been made of Darwin's metaphysic, the Englishman was not Friedrich Engels (see Sloan 1985, 2005, Richards 1992). Moreover, while Eimer was indeed an organicist after the old German fashion, the charges of mysticism or romantic idealism do not stick. Eimer's resistance to Darwinism was in large part a resistance to "the Darwinian principle of utility," which at the time of his training "still exclusively prevailed among zoologists in Germany" (Eimer 1890, p. 21).[1]

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[1] There are strong reasons to believe that Eimer overstates his case with regards to the popularity of "utilitarianism" in Germany (c. 1875). Although German biology was strongly mechanistic and Darwinian at this time, its "mechanism" was laced with psychical elements, and its "Darwinism" was filtered through Haeckel, in particular, the *Generelle Morphologie der Organismen* (see Corsi & Weindling 1985).

Already in 1874, Eimer had gathered under three heads the difficulties that non-adaptive characters raise for a panselectionist research program, all well grounded in the knowledge of the day:

1. "From internal causes conditions of organisation may arise…which are just as useful to the organism as if they had been due to the struggle for existence. In this case the claims of the principle of utility are accidentally satisfied by the results of evolution from internal causes, and the importance of that principle remains therefore undiminished.
2. "From internal causes characters which are indifferent for the success of the organism [may arise], and
3. "[Even] harmful characters may arise…But organisms burdened with harmful characters can only maintain themselves, and only transmit their peculiarities through future generations when such characters are inconsiderable in comparison with the useful ones also present, or when such characters stand in correlation with others whose usefulness is greater than their harmfulness" (Eimer 1874, quoted in Eimer 1890, p. 21).

The important point is that even in the throes of his youthful idealism, Eimer's perspective did not exclude selection, or view it with hostility. Yet as his personal animosities mounted over the course of the 1880s and '90s, his resistance to Darwinism hardened. When *Die Entstehung der Arten* appeared in 1888, Eimer was still willing to concede that "organic growth" furnished the materials 'from which the struggle for existence makes its selection.' By 1898, however, nothing of his earlier evenhandedness remained:

> The law of definitely directed evolution or orthogenesis, not that of natural selection, dominates in its entirety the transformation of the animate world. The fact that the variation of living being follow in perfect conformity to law a few definite directions…shatters irreparably the foundations of the Darwinian doctrine. For Darwin's doctrine must always have a most varied assortment of variations ready to hand if selection is to play a determinative part in the production of forms (Eimer 1898, p. 21).

Whereas once directed causes furnished the raw materials for selection, now it is orthogenesis that 'dominates in its entirety the transformation of the organic world.' Its causes are contained "in the effects produced by outward circumstances and influences such as climate and nutrition upon the constitution of a given organism" (p. 22). In past ages, these have resulted in such novelties as organismality, multicellularity, excitability, spontaneous movement, striated and non-striated muscle tissue, nervous organization and verbal communication (Eimer 1890, pp. 315-378). Yet while these may appear as contingent developments (which is to say: 'selected from a vast universe of possibilities,' many of them unrealized), in fact development is guided down a small number of pathways, determined in their course by the material composition of bodies. Importantly, Eimer denies that utility plays any role in the process by which rudimentary characters are graduated into distinct structures (see Eimer 1898, p. 48).

In Eimer's view, evolution is compelled down steeply banked channels by the stress of outward circumstances on the physico-chemical processes of growth. What brings forth novelties is *not* the nature of the environmental stressor, or selection on the basis of utility. Rather, it is the structure of the growth channels, which "force" variations to take particular forms. But the chemical determination of growth was *not* the subject of Eimer's investigations. Eimer performed no transplantation experiments and made no attempt to systematically intervene upon the processes of growth. (Additionally, while he subscribed wholeheartedly to the doctrine of the inheritance of acquired characters, he did not undertake to study it directly—or even indirectly.) By contrast, Eimer studied the results of presumptive transformations as a means of addressing a particular hypothesis. Since it is inconceivable that natural selection has originated all of the properties of organisms (by the cumulation of useful increments (Eimer 1898, p. 21)), could it not be the case that evolution sometimes moves along definite channels, which selection for utility is powerless to modify? And if this is the case, could not definitely directed variation account for that greatest of evolutionary quandaries: the problem of beginnings?

Eimer and the problem of beginnings

As Mark Ulett (2014) argues, Eimer's emphasis on novelty was the cornerstone of his project, and keyed his broader rhetorical strategy. Aware of Mivart's dilemma and cognate considerations, Eimer leveraged "the general explanatory strengths of orthogenesis and the weaknesses of natural selection" by focusing on Darwin's oldest bugbear: "the origin of novel characteristics" (Ulett 2014, p. 126). In so doing, "He was not quibbling over small details or academic minutiae" but focusing instead "on the 'big picture' of evolution"—those aspects of phyletic advance that *most demanded* explanation by a theory of descent. "Eimer knew that evolutionary theories emphasizing natural selection could not easily account for incipient features and the evolution of underdeveloped characters, a problem that Darwin…and many others had [commented] on (Mivart 1871)." He thus proposed to study the problem of beginnings *directly*, by an exhaustive investigation of a single genus.[1]

The first model that Eimer employed was the wide-ranging European wall lizard *Lacerta* (now *Podarcis*) *muralis*, a species that also attracted the attention of A.R. Wallace (Eimer 1875, see also Cope 1890, Bowler 1979, pp. 46-47). Later he proceeded to investigate color variation in caterpillars, and the wings of *Papilio* butterflies. These researches were soon to become his primary evidence for definitely directed evolution, and featured centrally in his *Die Artbildung und Verwandtschaft bei den Schmetterlingen* (1889) and in *Orthogenesis bei Schmetterlingen* (1897)—each of which contains full color plates (some of which are reproduced in *On Orthogenesis*).

Eimer worked by arranging his specimens into series of presumptive modifications, beginning with a fundamental form, *Papilio podalirius*, featuring eleven longitudinal bands running parallel to the main axis of the body. Thereafter he attempted to infer the

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[1] "This was not a side argument in *Organic Evolution*," Ulett adds—"the origin of novel characteristics accounts for 40% of the entire volume (Ulett 2014, p. 126).

laws of transformation, in effect, reading the laws of evolution directly from the wings. His clear wish was to see evolution in action—a wish that he shared with Bateson and a host of disillusioned morphologists. Yet his studies were hindered by the contemporaneous nature of his materials, which forced him to employ *ad hoc* hypotheses about (e.g.) the "standstill of development at definite stages [‘*epistasis*’]." While such hypotheses enabled him to interpret certain extant species as the ancestors of others, its arbitrary nature was readily apparent to his critics, including Weismann and Charles Minot, whose exchange with the Countess von Linden (published in *Science*) is highly revealing as regards Eimer's methodology.[1] Von Linden was Eimer's assistant, and believed entirely in the validity of his methods (most notably, the arranging contemporaneous species into *actual* (formal) series of descent):

> This short exposition of the direction of evolution in the genus *Papilio* seems to me to show that it was not arbitrariness on Eimer's part to select *Papilio Podalirius* as the ancestral form of his group of butterflies. He has shown, by his study of the markings of one series of forms, that those of all its members can be reduced to one and the same scheme, and that aberrations from the forms which are nearest to this original scheme of markings vary so as to form transitions to nearly allied species, which again are connected with more distant species, and the conclusions drawn from the study of these phenomena are confirmed by the results of geographical distribution. This being so, I cannot understand how Minot can doubt that Eimer's assertions are correct (von Linden 1897, p. 311).

Minot's reply is painfully terse, and cuts straight to the quick of Eimer's approach:

> All of Eimer's evidence is essentially that he *asserts* that of a group of living species a certain form or certain forms are ancestral types. If one denies that assertion Eimer cannot *prove* that it is correct, but unless he *proves* it his deductions remain hypotheses. The reader is asked to consider whether Countess von Linden offers proof that a certain species in any given case is the ancestral race (Minot 1897, p. 313).

Just as systematic practice was predicated on the intuition of specialists regarding the

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[1] Quite possibly Eimer's familiarity with his materials led him to believe that he could make these inferences non-arbitrarily; there is, at any rate, little evidence to suggest that he recognized any legitimacy in Weismann's criticisms.

probable affinity of organisms, so Eimer believed his intuitions to be sound regarding the ancestral condition of *Papilio*. But intuitions are not proof, and this was indeed the Achilles heel of his method. All Eimer could do was point to other instances whereby modification seemed to follow the same basic rules (he provides ostensible corroboration in reptiles, birds and mammals). Yet these corroborating instances, *even if* they are granted as genuine, do not touch to core issue as identified by Minot. For who is to say that Eimer's sequences are not determined by natural selection: if not selection acting on the marking themselves, perhaps selection acting on some physiological process that has the markings as a correlate?

Again, Countess von Linden's comments are helpful. "On the basis of arguments which have hitherto been considered customary and convincing in biology, I believe I have shown that Eimer [is] far from rejecting Darwin's theory…because 'it does not explain the origin of variations' [Minot's claim]":

> He knows as well as Minot that Darwin does not even attempt an explanation of the origin of new characters, Darwin has not, as Eimer shows, explained that which he wished to explain. As, however, *the theory of the origin of species demands an explanation of the origin of new characters,* Darwin has not, as Eimer shows, explained that which he wished to explain. Eimer, on the contrary, shows in [*Die Artbildung und Verwandtschaft bei den Schmetterlingen*] how new qualities develop; he explains the causes of their formation and traces the laws of their development (von Linden 1897, p 312).

Thus, to von Linden, Eimer's results deserve the benefit of the doubt because they—unlike Darwin's researchers—at least *attempt* an explanation of that most important of evolutionary riddles: the origin of new characters.

Summary

Eimer wished to discover the laws to which variations answer by examining sequences of transformation in living organisms. Unlike his paleontological colleagues, he was suspicious of the fossil record, or at least of its capacity to disclose the kinds of variations that interested him. (Eimer cited Hyatt and Cope favorably, but greatly preferred the evidence from extant productions.) Having thus forsworn the insights of vast times, he immersed himself completely in "the study of a single living being, in order to penetrate into its nature as deeply as possible" (Eimer 1890, p. 3). His approach was not unlike that which utilizes model organisms to probe general principles. In Eimer's words, "If we could know all the natural laws which have operated in the evolution, and which operate in the existence of a single animal or a single plant, we should understand the laws of the organic world altogether." What is true of *Papilio* is true of the elephant!

Eimer's method of arranging specimens into graded series left much to intuition, but it was nonetheless a creative approach to the problem of beginnings.[1] More importantly, it was unlike anything found within the Darwinian canon. In the *Origin,* Darwin had attempted to rationalize the history of complex adaptations by arranging known structures into graded series. But his purpose was to demonstrate that complex adaptations *can* be evolved in a stepwise manner, not that they had evolved in this or that *particular* manner. His successors often restricted their attention to particular groups, but with an eye to the reconstruction of life's history (e.g., Müller 1864, Dohrn 1868, Kowalevsky 1874). Usually this meant searching for homologies among extant groups, a strategy not wholly disjunct from Eimer's. Yet Eimer sought *to rationalize the transit between forms* (viz., by seeking the laws that superintend the transformation). Although few would accept his solution, nonetheless he recognized the need to address this problem at a time when most

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[1] Jepsen notes that this approach was once popular among neontologists, and lists over twenty studies—published between 1899 and 1939—in which authors "have arranged their materials in graded fashion…either in support of orthogenesis or to discredit it" (Jepsen 1949, p. 490). "Frequently one end of the layout is selected as the more primitive and is hence said to be a relict survivor or "structural ancestor" which is unchanged from the ancestral form that gave rise to the next step in the array, and so on, as a series of step-projections from the past to the present."

biologists were unwilling or unable to offer compelling functional explanations of phyletic history (Bowler 1996, pp. 250-258).

Postscript: the many faces of orthogenesis

Throughout the post-Darwinian period, a large number of scientists sought to discern the broad contours of descent, hoping that it would throw light on the method of evolution. Absorbed in minutiae but desirous of generality, they sought the security of higher ground, hoping that the elevation would help them to see farther. Eimer, by contrast, narrowed his gaze in order that he might glimpse broader vistas; "For the more an investigator devotes himself to a fruitful object, the richer it appears to his eyes, the more it shows new properties, the more it acquires living interest and importance, and the more do all its characters and the relations of its life show themselves to be governed by law" (Eimer 1890, p. 3). Eimer squinted in order to see general principles, and in this important respect anticipated the mood and method of the new experimentalism.

The theory of orthogenesis comes down to us as a peculiarity; a strange admixture of wish thinking and interpolation, cut with a perhaps too-healthy dose of the idealist metaphysic. This is probably unfair. As Gar Allen explains, by 1900, many biologists had adopted the orthogenetic doctrine in one form or another (Allen 1969, p. 77).[1] These men were by no means unanimously opposed to the theory of selection (in fact, Plate and Whitman were among Darwin's foremost supporters during the early century). Nor were they a coalition of reactionaries, as Mayr was fond of implying (e.g., 1982, p. 50). Whatever the case, the orthogeneticists were united in the belief that selection required a menial in the production of those rectilinear lines of descent that were their great

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[1] "Among those explicitly advocating such ideas," Allen writes, "were F.B. Loomis, S. Korschinsky, Carl von Nägeli, O.F. Cook, George Pfeffer, Bashford Dean, Ludwig Plate, T.H. Eimer and C.O. Whitman" (Allen 1969, p. 77). To this list may be added the names of A. von Kölliker, T.H. Huxley, E.D. Cope, Alpheus Hyatt, Alpheus Packard, Wilhelm Waagen, W.B. Scott, H. Gadow, Yves Delage, H.F. Osborn, Arthur Dendy, W.D. Lang, Othenio Abel, G.A. Boulenger and Edwin Hennig.

obsession. Some (perhaps most) overstated their case, thus marginalizing selection within the field of evolutionary factors. Yet others, like Charles Whitman, remained equitable, and de-emphasizing “the unifying aspect of orthogenesis as promoted by Eimer” (Bowler 1979), avoided alienating excesses:

> I take exception…to the implication that a definite variation-tendency must be considered to be teleological because it is not ‘orderless.’ I venture to assert that variation is sometimes orderly and at other times rather disorderly, and that the one is just as free from teleology as the other. In our aversion to the old teleology, so effectually banished from science by Darwin, we should not forget that the world is full of order, the organic no less than the inorganic. Indeed, what is the whole development of an organism if not strictly and marvelously orderly?...If variations are deviations in the directions of the developmental processes, what wonder is there if in some directions there is less resistance to variation than others? (Whitman 1919, p. 11).

Leapfrogging Mivart: the saltationist alternative

Discontinuous evolution

Of orthogenesis and discontinuous evolutionism, it was the latter that posed the strongest challenge to Darwinism around the turn of the century, and the latter that won the lion’s share of adherents. Although saltationism would enter upon a fallow period following the decline of de Vriesian mutationism (ca. 1910-1915), the notion that evolution might proceed discontinuously was common fare during the post-Darwinian period. The high-water mark, of course, was de Vries:

> At the present moment, probably because of a strong reaction against the too blind acceptance and general overemphasis of the selection doctrines, and because, too, of the unusually extensive character of de Vries’s experimentation and observation, and his trenchant criticism of the weak places in the other theories, with the generally weighty character of his work and reputation, because of all this the theory of species-forming by mutation has at the present moment a fairly large body of adherents among reputable biologists (Jordan & Kellogg 1907, p. 115).

But while de Vries represented the zenith of the saltationist curve, his theory had forerunners in T.H. Huxley (1860), Richard Owen (1860) and Albert von Kölliker (1864) (as well as in Heer (1865), Cope (1871), Dall (1877), Brooks (1883), Galton (1889), Eimer (1890), Dollo (1893), Emery (1893), Bateson (1894) and Korschinsky [sometimes Korzhinskii] (1899)). The discontinuous evolutionists were a mixed lot, but were united in the belief that new varieties are produced "by certain leaps" (*stufenweise*) akin to the saltations of old (de Vries 1905, p. vii). Such saltatory evolution had been discussed and discarded by Darwin, who regarded it as at best an infrequent factor in species-modification (Darwin 1859, p. 194; 1872, pp. 201-202).[1] But by 1894, William Bateson had marshaled a wide range of evidence in its favor, and—after lavishing criticism on the selection theory—concluded that the gaps between species are an expression of the discontinuity of variation (e.g., Bateson 1894, pp. 68-69). "[The] existence of sudden and discontinuous Variation…that is to say, of new forms having from their first beginning more or less of the kind of *perfection* that we associate with normality, is a fact that disposes, once and for all, of the attempt to interpret all perfection and definiteness of form as the work of Selection. The study of Variation leads us into the presence of whole classes of phenomena that are plainly incapable of such interpretation" (Bateson 1894 p. 568).

What is discontinuous evolution (neé saltationism)? In essence, it is a theory of phylogenesis that avoids the most conspicuous difficulties on the selection theory while considerably speeding the rate of evolution. The crux of the proposal is that evolution

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[1] Why should not Nature have taken a leap from structure to structure?" Darwin asked in *The Origin of Species*. "On the theory of natural selection, we can clearly understand why she should not: for natural selection can act only by taking advantage of slight successive variations; she can never take a leap, but must advance by the slowest and shortest steps" (Darwin 1859, p. 194). Of course, it is well known that many biologists (including some of Darwin's closest colleagues) did not share this perspective. "I think *transmutation* may take place without *transition*," Huxley wrote to Lyell (Huxley to Lyell 1859, cited in Lyons 1995, p. 491). Still, around the time of Darwin's death, the notion that evolution proceeds by the summation of tiny increments did not lack for supporters, and was common fare at leading centers of biological education like Cambridge.

proceeds (at least some of the time) *per saltum*—by discontinuous steps which have at once some degree of perfection (or "completeness"). Discontinuous evolutionism recommended itself for two primary reasons, each related to a popular criticism of the selection theory:

(1) *The incipient stages of certain useful structures confer no benefit on their possessors (Mivart's dilemma).*

. Consider the case of mimesis in butterflies. Surely the first fleck of cryptic coloration on a butterfly's wing can serve no protective function (Turner 1983, but see Fisher 1927, Poulton 1931). Only such variation as generates a non-trivial likeness between model and mimic can benefit the latter—specifically, by thwarting would-be predators. From here one can imagine the gradual refinement of mimesis under a selection regime of varying intensity—but, as Mivart observed, there is again a difficulty in accounting for the 'last touches of perfection in the mimicry.' (Ironically, this difficulty—although not well founded—seems to have driven some evolutionists to deny to selection *any* role in the forging of complex mimesis. Eimer, for instance, adopted this perspective, charging the students of mimesis with anthropocentric bias. "What is the utility of the general sculpturing, marking, and coloring of shell snails which during their whole lifetime are usually covered with mud or dirt and of which the delicate features of marking and coloring often do not appear until after polishing," he queried. "Nothing could be more magnificent than the play of color of Labradorite. Is this brilliant display useful to the stone[?]")

(2) *The constitution of a species limits its variability.*

> . Species are not indefinitely modifiable; barring a significant disruption of "normal specific stability" (Mivart 1871, p. 143), the selection of individuals can produce only geographic races, not new types. It requires a genuine *leap* to break through a species' "sphere of variation," or to cause the "polygonal slab" of Galton to overpass the limits of a facet and tumble into a new position. (Stephen Jay Gould provides a deft analysis of these issues in his *Structure of Evolutionary Theory* (Ch. 5)—in particular, the "coagulation" of structuralist themes into "implicating sets…[for instance] structurally-based correlation, evolution by internally generated sources of variation, and suspicion of adaptational scenarios as primary explanations for basic organic design" (Gould 2002, p. 397). His "exegesis" of Bateson's *Materials* (pp. 396ff) is particularly on the nose, especially the section entitled "The physical basis of discontinuity" (pp. 403-404).)

In the *Origin of Species*, Darwin wrote, "If it could be demonstrated that any complex organ existed which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down" (Darwin 1859, p. 189). The discontinuarians believed they had identified many such organs, a goodly number of which were not even "complex." Taking Darwin at his word, this seemed to compel the abandonment of absolute gradualism (but see Wallace 1895, pp. 219-223). "[N]umerous, successive, slight modifications" are *not* a prerequisite of evolution, the discontinuarians argued, echoing Huxley (1860). Perhaps they are even irrelevant to progressive evolution. In any event, the dogma of Darwinian utilitarianism must be abandoned if the science of evolution is to advance. *A priori* considerations speak against it, and empirical results disclaim its all-sufficiency (Bateson 1894, Ch. 1).

According to Garland Allen (1969), two issues were "constantly intertwined" during the post-Darwinian period—"the nature and origin of variation, and the role of selection in producing new species" (p. 69). These issues, in turn, were closely related to another: the question of whether selection is wholly eliminative, or whether it plays a *creative* role in evolutionary change (Gould 2002, p. 397). As selection operates on differences between members of a population, it is clear that the issue of creativity cannot be separated from the question of what generates these differences.[1] The relationship between selection and variation can nonetheless be pictured in a variety of ways. As Kellogg writes in *Darwinism To-day* (probably with de Vries in mind):

> The meaning of heterogenesis [saltationism] in connection with species-forming and descent is essentially this: whereas by the Darwinian theory species are transformed slowly and by slight changes in at first one or two or a few and only later in more parts…by the theory of heterogenesis new species appear suddenly, not by a selective choosing among the slight fluctuating Darwinian variations, but independently of selection, and largely independently of the so-called Darwinian variations, by the appearance in fixed definite form of several to many slight to considerable variations, which give the new species definite characteristics differentiating it often in many particulars from the old species (Kellogg 1907, p. 328).

Given a modern slant, the question is basically this. Is the evolutionist warranted in defining natural selection *broadly*, so as to enfold all the processes implicated in the generation of genotypic diversity? Certainly natural selection has a hand in determining the contents of the gamete pool, as do mutation, recombination and migration. (This broad definition leaves no doubt that natural selection is the primary creative factor in evolution, although it purchases this certainty by way definitional fiat—that is, by using "selection" as a synonym for "selective evolution.") Or, alternatively, is natural selection to be considered *narrowly*, as no more than character-fitness covariance (interpreted causally)? Such a definition does not preclude one from interpreting natural selection as

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[1] A latter-twentieth century biologist would list mutation, recombination, natural selection, migration and genetic drift as factors contributing to the generation of variability in local populations.

creative, although it does call for a more restrained interpretation of selection's creative writ. (Sewall Wright, for instance, considered even extinction to be creative. Obviously, this is not the notion of creativity that the critics of selection's creative writ had in mind!)

The idea of discontinuous evolution sprang up a number of times during the nineteenth century. With the notable exception of Galton (and perhaps Bateson), the saltationists were most successful as critics. Still, they were not altogether lacking in positive suggestions for evolutionary science. Specifically, the notion that variation might leapfrog the first beginnings of organs was a powerful idea, and suggested a research program geared towards investigating large-scale variations. That he initiated this program was Bateson's great contribution to evolutionary studies—an episode to which we shall return below.

Kölliker's heterogenesis, and the negation of novelty

The term *heterogene Erzeugung* ("heterogeneous production" or "heterogenesis") owes its coinage to Albert von Kölliker, who in 1864 attempted to resuscitate Geoffroy's saltationism under a new name (see Di Gregorio 2005, pp. 301-305). According to Kölliker, evolution is basically determinate—"The [core] of this hypothesis is that under the influence of a general law of development [*Entwickelungsgesetz*] organisms bring forth other kinds differing from them out of the germs produced by them" (Kölliker 1864, p. 10).[1] In the words of William H. Montgomery:

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[1] This, it ought to be noted, was not quite Geoffroy's vision. In Geoffroy's view, saltational events owe their origin to environmental stresses acting *directly* on the embryo; "a picture of progressive evolution," Morgan notes, "that carries with it an idea of mechanical necessity" (Morgan 1903, p. 28). A important memoir of 1833 bears the title "Memoir on the Degree to Which the Environment Influences Animal Form; the Interesting Question of the Origin of Teleosaurian and Modern Species." "Here, and in his 1831 book on the 'great saurians,' [Geoffroy] argued that reptile and bird respiratory systems had been changed by an environment that was 'all-powerful in modifying organized bodies,' especially during their embryonic phase" (Reid 2004, p. 9). These modifications occurred by means of 'new births' or 'creations.' Kölliker, by contrast, was a thoroughgoing internalist. His primary complaint with Darwinism concerned the prevalence of

> This process would not be dependent on the external environment, but would function according to a general developmental law. Kölliker explained the functioning of this law by analogy to the alteration of generations and embryonic recapitulation. It seemed to him that a mammal embryo required only a slight modification in order to produce a different form. This idea was somewhat vague, but Kölliker imagined that it might eventually be explain in terms of natural laws (Montgomery 1988, p. 98).

Kölliker lists and assesses eight criticisms that have been brought to bear on Darwinism, which we needn't bother to enumerate. Some he rejects, others are pedantic, and still others suggest a willful misreading of the *Origin of Species* (see Huxley 1864 for discussion). More interest attaches to the analogy Kölliker draws between saltation and "agamogenesis" (reproduction without the fusing of gametes), alluded to above:

> The fundamental conception of this hypothesis is, that, under the influence of a general law of development, the germs of organisms produce others different from themselves. This might happen (1) by the fecundated [fertilized] ova passing, in the course of their development, under particular circumstances, into higher forms; (2) by the primitive and later organisms producing other organisms without fecundation, out of germs or eggs (Kölliker 1864, cited in Huxley 1864, p. 574).

Let us take these mechanisms one at a time. With respect to the first (the direct analogy with agamogenesis), Huxley experienced no difficulty in revealing many points of disanalogy (Huxley 1964, pp. 574-575, see also Owen 1854, 1858). These are sufficiently obvious that Kölliker must have been aware of them; however given his perverse reading of the *Origin* (and the fact that "heterogenesis" was first presented during a public lecture), perhaps precision was not his first priority. Huxley is kinder to his second mechanism: the mysterious birth of saltated forms from fertilized eggs, perhaps under

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non-adaptive characters, and the notion that the struggle for existence can exert a selective pressure *at all*. Moreover, he thought the phenomenon of hybrid infertility weighed heavily against the plausibility of gradualistic evolution (see Glick 1988, p. 99).

conditions of environmental stress.[1] Though Kölliker brought no observations to bear on this proposal, he nonetheless "thought it likely that the embryo of a higher animal could be jogged from its usual path of development early on so as to head in a different direction and thus produce a new species" (Nyhart 1995, pp. 125-126). His view was bolstered by Kölliker's belief that "organic development worked almost completely through causes operating *within* the organism"(p. 126, emphasis added). All possible routes of development were thus present *in potentia* within the "the original, primitive seed of all organisms" (Kölliker 1872, p. 223). According to Robert J. Richards:

> Kölliker assumed that "at the foundation of the origin of the whole organized world lay a great developmental plan that rove to simplest forms to ever more variable unfolding" [Kölliker 1864, p. 184]. Obviously, Kölliker has yet to abandon a teleological foundation for his conception of species change.

It is important to stress the latter point, for without it, my account tempts the interpretation of Kölliker as a forerunner of twentieth century macromutationists (e.g., Richard Goldschmidt). This is true only at the most superficial level. As E.S. Russell explains in *Form and Function*, "Kölliker's attitude is typical of that taken up by many of the morphologists of the day. He accepts evolution completely, but rejects Darwinism because it recognises no *Entwickelungsgesetz*, or principle of evolution" (Russell 1916, p. 243). For the fortuitous variations of Darwin, Russell continues, Kölliker would substitute "the theory of evolution through sudden, large variations, brought about by the influence of a general law of evolution." However:

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[1] It should be remembered that Huxley was himself a saltationist, and that he possessed considerable regard for Kölliker. Although he had little positive to say about "heterogeneous generation," Huxley somewhat unexpectedly tempers his criticisms with a confessional—"we have always thought that Mr. Darwin has unnecessarily hampered himself by adhering so strictly to his favourite 'Natura non facit saltum.' We greatly suspect that she does make considerable jumps in the way of variation now and then, and that these variations give rise to some of the gaps which appear to exist in the series of known forms" (Huxley 1864, pp. 575-576).

> It is to be noticed that Kölliker laid more stress upon the *Entwickelungsgesetz* that upon the saltatory nature of variation, for he says a few pages further on—"the notion at the base of my theory is that a great evolutionary plan underlies the development of the whole organised world, and urges on the simpler forms towards ever higher stages of complexity" [p. 184]. Saltatory evolution was *not* the essential point of the theory: —"Another difference between the Darwinian hypothesis and mine is that I postulate many saltatory changes, but I will not and indeed cannot lay the chief stress upon this point, for I have not intended to maintain that the general law of evolution which I hold to be the cause of the creation of organisms, and which alone manifests itself in the activity of generation, cannot also act that from one form others quite gradually arise" [p. 185] (Russell 1916, p. 243, emphasis added).

Kölliker, he concludes, "put forward the hypothesis of saltatory variation because it seemed to him to lighten many of the difficulties of Darwinism" (he mentions "the lack of transition forms, [and] the enormous time required for evolution"). This sentiment is echoed by Montgomery (Montgomery 1988, pp. 98-99) and by Lynn Nyhart, in *Biology Takes Form* (Nyhart 1995, pp. 126-127). Curiously, however, Kölliker did not attempt to replace natural selection with his own novelty-producing mechanism (as later saltationists would repeatedly attempt). Rather, he responded to the shortcomings of Darwinism by denying novelty *tout court*! "[Kölliker] seems not to have believed in true novelty," Nyhart writes—his notion of internal causation admitted of changes *only within* the channels prescribed by the potentialities of the system (1995, p. 127). As befit a German scientist of his age, Kölliker did not regard this conception as teleologic, and claimed no supernatural sanction for his *Entwickelungsgesetz*.[1] Nonetheless, his old-fashioned heterogenesis found little sail in the exuberant 1870s, when Darwinism was sweeping Germany. What small influence it had can be attributed to the prestige of its author, and the prominence of his position in the Würzburg medical faculty (Nyhart 1995, p. 108).

This is one way to have done with Mivart's dilemma: namely, to deny the very *possibility* of evolutionary novelty. But to many in the 19th century, evolution was *defined*

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[1] In this way, he was like Karl von Nägeli, who resolutely maintained the "mechanistic" credentials of his "mechanico-physiological theory of organic evolution" (1884).

as ‘the development of novel structures.’ To say that something was ‘evolving’ was to claim that it was becoming something new (certainly planets are not “evolving” when they turn in their orbits!).[1] The question thus arises: how are we to study this?

I will close this essay by examining the first concerted attempt to found a science of evolutionary novelty: that of William Bateson. It can hardly be accidental that the champion of the science of novelty set great store by Mivart’s dilemma. To Bateson, natural selection simply could not explain that which an evolutionary theory *must* explain: the major steps in progressive evolution. Accordingly, a different approach was required—one capable of illuminating the causes of progressive evolution. Moreover, it must avoid the difficulties that bedevil the historical approach, which studies novelty by searching out rudimentary adaptations in the presumptive ancestors of a taxon (or by identifying supposed homologies). (It is ironic that Bateson later turned to a hypothesis similar to Kölliker’s in order to account for evolutionary novelty (Bateson 1914, pp. 17-18). This, however, belongs to a later period in Bateson’s life, and one that I will not consider in this essay.)

Usually, it has been supposed that Bateson became disillusioned with evolutionary morphology in virtue of a “lack of hard evidence [from the fossil record] to confirm or refute the various mutually inconsistent hypotheses of vertebrate origins” (Bowler 1996, p. 187). While it is doubtless true that Bateson came to regard such parlor-room phylogenizing as stale and arbitrary, I wish to suggest that his disillusionment stemmed from the inability of scientists to infer the *mechanism* of transmutation from the products of history, considered as static bits of anatomy (Bateson 1928, pp. 19-20, 30-31). This hypothesis is implicit in many historical treatments of Bateson (e.g., Bowler 1988, p. 121,

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[1] Indeed, Darwin’s term “descent with modification” captures this sentiment perfectly. Change is prosaic—only a philosopher or a madman would deny it. Yet some changes are more momentous than others. Darwin’s great achievement was to realize that such change as we observe in natural populations can open onto new and previously undisclosed possibilities—*this* was groundstuff of evolution.

1996, p. 187, Gould 2002, p. 399). In accordance with the broader themes of this essay, I wish to make it explicit.

William Bateson: background

William Bateson began his career as an upstanding Darwinist, trained by the leading embryologist of the day, Francis Balfour. Though known as a talented investigator, Bateson owed his reputation to his remarkable industry and the keenness of his critical faculties (Crowther 1952, pp. 254-255). Perhaps the dearest service he rendered on biology was his lusty skepticism, which poured forth at every stage of his career, even the earliest (Bowler 1992, p. xix). Yet Bateson was not the antique Bantam cock that historians have sometimes portrayed.[1] Of course, he was partially this, but he was also an ambitious and multifaceted iconoclast—certainly "strong-willed and disputative, but also equipped with a strong sense of fun" (Bateson 2002, p. 57). "No one more delightful to work with than Bateson could be imagined," R.C. Punnett recalled in 1950 (quoted in Bateson 2002, p. 56). (For a lively account of Bateson's early life and career, see J.G. Crowther's *British Scientists of the Twentieth Century* (1952, pp. 248-310).[2] Alan Cock and Donald Forsdyke have recently published a much richer biography (2008).)

While still a young and relatively unheralded morphologist, Bateson undertook a pilgrimage across the Asian Steppes with the intention of investigating the origin of the

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[1] For instance, according to Mayr, Bateson's most persistent critic, "Bateson was pig-headed, intemperate, and intolerant...quite incapable of understanding the nature of natural populations (in spite of his field work in Asia, and his great horticultural experience)" (Mayr 1973, p. 146). Likewise, Fisher reprimanded Bateson for his excessive sarcasm and "zealous partisan[ship]" in denigrating Darwinian theory (e.g., Fisher 1936).

[2] Crowther's account is distinguished by its emphasis on the social dimension of Bateson's unorthodox biological views (e.g., pp. 256, 289). Yet it is marred by its gratuitous adulation of Trofim Lysenko, which reads almost as parody. "Lysenko's biological approach, his capacity for interesting the people in biology and helping them to use it for changing the climate and characteristics of the country, are essential in [the recent 'tenfold increase' in "the people's activity in biology]. He has succeeded in creating a biology with a meaning deeper and wider than that of Mendel-Morgan genetics" (Crowther 1952, p. 303).

Aral Sea basin lakes (Bateson 1928, Peterson 2008, p. 277).[1] Although this goal was thwarted, Bateson nonetheless perceived that the lakes afforded an ideal opportunity to test the principles of local adaptation in invertebrates (specifically, the effects of salinity on freshwater mollusks). Apropos of his training, he anticipated that organismal characteristics would display a close correlation with ambient conditions, thus testifying to the power of natural selection in forging precise adaptations (Cock & Forsdyke 2008, p. 28). Yet Bateson's investigations failed to uncover any strong evidence that the properties of organisms graduate in sympathy with environmental conditions. While the action of selection could explain *some* of the correlations he had documented (variation in certain species of cockle along an environmental gradient), selection seemed unable to account for the preponderance of data he had collected (Peterson 2008, p. 283). Further study turned up other instances in which natural selection seemed impotent to account for the observed structures (e.g., Bateson & Bateson 1891). This suggested that the preponderance of characters come into being *discontinuously*—for reasons having to do with their intrinsic "stability," not their usefulness in the struggle for existence:

> It may be observed at this stage that in proportion as the process of Evolution shall be found to be discontinuous the necessity for supposing each structure to have been gradually modeled under the influence of Natural Selection is lessened, and a way is suggested by which it may be found possible to escape from one cardinal difficulty in the comprehension of Natural Selection…This difficulty, which is well known, may be stated thus. If the process of Variation is supposed to have been continuous, it cannot be supposed that the mechanism was at all periods of its evolution so beneficial as to be selected (Bateson & Bateson 1891, p. 388).

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[1] As Bateson wrote in a letter to His Excellency, The Governor General of the Province of Turkestan (on whose territory he had accidentally trespassed): "It is no doubt well known to you that it is generally held by geologists that the whole plain in which these seas exist,…in past times formed one sea, which probably communicated with the Arctic Ocean. Upon the drying up of the sea for some unexplained reason, it is to be expected that the marine animals inhabiting it would be isolated in the various basins which would then be separated. The question, then, that I am engaged in investigating is firstly, whether such traces of marine life do exist in these waters, and secondly what variations they have undergone. This is to be determined by a comparison of the existing forms in various waters with each other, and with such sub-fossil remains as can be found" (quoted in Cock & Forsdyke 2008, pp. 22-23).

To Bateson, "discontinuity" is the key to evolution; that is, the insight that series of descent are graded, not intergrading. A modern form is *not* separated from its ancestors by an unbroken chain of intermediates, each of which *actually existed* at some point in the past. Rather, a modern form represents the last term in a graded series, which exists in virtue of "[the] determinateness of *Stability* in its various manifestations" (Bateson 1897, quoted in Cock & Forsdyke 2008, p. 139). Accordingly, it is the nature of the organism that determines the kinds of transformations it can undergo, just as the nature of a molecule determines the kinds of reactions in which it can partake.[1] Bateson elaborated on this topic in a lecture of 1899:

> Think of what organisms are—complex systems of chemical and molecular actions. We are asked to suppose that they have no natural or inherent order—that without Selection or environmental control they would be *Chaotic*. But when [we] turn to the facts of variation [it is] not necessary to suppose any such thing" (Bateson 1899 [lecture], quoted in Cock & Forsdyke 2008, p. 140).

According to Bateson, natural selection is impotent to explain the major features of evolution, including the novelties that adorn each branch of the tree of life (Bateson 1909, p. 96). Although selection is certainly competent to decide between discrete varieties, it has nothing to do with the *origin* of these varieties, nor their definiteness and distinctness (see, e.g., Bateson 1894, pp. 64-65, 266, 417ff). The conclusion cannot be avoided: we must attempt to study variation directly.

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[1] In fact, this was something more than an analogy, as Bateson was given to arguing that many variations (for instance, "variation in Colour") "may be an index of serious changes in the chemical economy of the body" (Bateson 1894, p. 73). This fact is often overlooked, Bateson complained, "[by] those who have attempted to reconcile the phenomena of Colour with the hypothesis of Natural Selection."

Bateson on adaptation

By the late 1880s, Bateson had grown deeply suspicious of the study of adaptation, as well as the speculative phylogenizing it tended to service. Not only are "its results meager and its conclusions unsound," but the whole enterprise is beset with epistemic difficulties of a high caliber (Bateson 1894, p. 12). The chief problem lies with the fact that "there are a hundred ways in which [a particular variation] may be beneficial or detrimental," and no principled means of choosing between them (p. 79). In order for a Darwinian explanation to attain to scientific status, the investigator must do more than indicate how a trait *can* benefit an organism in its struggle with the local environment. In addition, he or she must ascertain *how* the presence of a character affects "the profit and loss account" of the organism in question. "To know that the presence of a certain organ may lead to the preservation of a race is useless if we cannot tell how much preservation it can effect"—that is, "how many individuals it can save that would otherwise be lost" (p. 12). In the absence of "such correct and final estimates of utility," Bateson scolds, "we must never use the *utility* of a structure as a point of departure in considering the manner of its origin":

> for though we can see that it is, or may be, useful, yet a little reflexion will shew that it is, or may be harmful, but whether on the whole it is useful or on the whole harmful, can only be guessed at. It thus happens that we can only get an indefinite knowledge of Adaptation, which for the purposes of our problem is not an advance beyond the original knowledge that organisms are all *more or less* adapted to their circumstances (Bateson 1894, pp. 12-13).

What accounts for Bateson's anti-adaptationism? Was it his personality, his desire for scientific fame, his Liberal *rentier* upbringing, or perhaps his not-so-latent romantic idealism? I think that all of these factors must be admitted, but that no factor was more important than his desire to provide *causal* explanations of apparent evolutionary novelties. Bateson may have given up on speculative phylogenizing, but he retained his interest in the formal content of phyletic advance (in other words, the major steps in progressive evolution). In the next section, I will attempt to show how his interest in the basic organizational motifs of animals and plants—combined with a deep appreciation of Mivart's dilemma (to Bateson, "an almost fatal objection" to the selection theory)—joined to produce the first research program self-consciously addressed to the study of evolutionary novelties.

The variation problematic: Bateson's science of beginnings

Much like St. George Mivart, Bateson was obsessed with symmetry, which he called "a particular case" of a more general phenomenon: the "Repetition of Parts" (Bateson 1894, p. 569).[1] The subject appears in his earliest scientific publications, including the concluding entry in a four-paper series on the "barnacle tongue," *Balanoglossus* (Bateson 1886). In this classic of evolutionary morphology, Bateson predicated his rejection of the annelid theory of vertebrate origins on "the common tendency to repeat parts already present, which tendency occurs more or less in almost all animals" (p. 539). Already disillusioned with evolutionary morphology, it is not irrational to regard this paper, first and foremost, as a youthful meditation on the evolutionary importance of segmentation:

> In the following pages it is proposed to examine the propriety of employing the character of metameric segmentation as one of first importance in forming a phylogeny of [vertebrates and their prevertebrate ancestors]. And before referring to the evidence derived from the fact that the three characteristic features of Chordata are found in Tunicata and Enteropneusta, which are unsegmented forms, it will be best first to discuss the meaning of the phenomenon—"segmentation"—for if resolved into its elements it will be found to be by no means a peculiar feature of a few groups, but rather the full expression of a tendency which is almost universally present (Bateson 1886, p. 538).

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[1] Unlike Mivart, Bateson thought very little of the concept of "homology," and even suggested that the term, as usually defined, clashed with the known facts of development "and is founded on assumptions that are not justified" (Bateson 1892, p. 114).

To Bateson, the "Repetition of Parts" was the tail that wagged the dog of evolutionary morphology (Bateson 1928, p. v). It featured prominently in his application for the Linacre Professorship at Oxford, wherein he proposed to gather facts bearing on "The Variation of Multiple Parts and of Symmetry," which serve as "evidence of the magnitude of the integral steps by which Variation proceeds and of the control which the symmetry of the body exercises over these variations." And it only gained in importance as he began composing *Materials for the Study of Variation*, published in 1894. In *Materials*, Bateson toyed with the notion that symmetry might form the basis of *all* biological order, being the inevitable by-product of basic ontogenetic processes. "That which is most important…is to note the almost universal presence of Symmetry and of Repetition of Parts among living things," he mused. "Both are the almost invariable consequence of division and differentiation, which are fundamental characters without which Life is not known" (Bateson 1894, p. 21). In his later publications, Bateson would stress the degree to which animal and plant symmetries approximated to wave and vibrational phenomena (much as Mivart and Hering had several decades earlier):

> If anyone will compare one of our animal patterns, say that of a zebra's hide, with patterns known to be of a purely mechanical production, he will need no argument to convince him that there must be an essential similarity between the processes by which the two kinds of patterns were made…With a little research we can find among the ripples marks [on a beach], and in other patterns produced by simple physical means, the closest parallels to all the phenomena of striping as we see in animals (Bateson 1913, p. 36).

Bateson's interest in "the nature of the organism" was the coordinating theme of his early work, and persisted into his final publication (Cock & Forsdyke 2008, p. 139). In order to understand how organisms "come to be what they are," Bateson wrote in *Materials*, the investigator must confront the familiar question of "the origin and meaning of patterns…the outward and visible expression of that order and completeness which inseparably belongs to the phenomenon of Life." He continues:

> If anyone will take into his hand some complex piece of living structure, a Passion-flower, a Peacock's feather, a Cockle-shell, or the like, and will ask how it has come to be so, the part of the answer that he will find it hardest to give, is that which relates to the perfection of its pattern. And it is not only these large and tangible structures that the question arises, for the same challenge is presented in the most minute and seemingly trifling details. In the skeleton of a Diatom or of a Radiolarian, the scale of a Butterfly, the sculpture on a pollen-grain or on an egg-shell, in the wreaths and stars of nuclear division, such patterns again and again recur, and again and again the question of their significance goes unanswered (Bateson 1894, pp. 21-22).

This passage is not simply a reverie on form, in the grand traditional of D'Arcy Thompson. By contrast, it is an ingenious argument for the ascendancy of pattern over utility in the study of evolution. Of course, Bateson does not deny that "minute and seemingly trifling details" may have their uses (although the aforementioned epistemic difficulties attach to all efforts to ascertain them). Yet by enfolding the minutiae of design within the broader phenomenology of developmental patterning, Bateson indicates that *after* utility has been demonstrated, it remains for the investigator to account for the problem of origination:

> There are many suggestions, some plausible enough, as to why the tail of a Peacock is gaudy, why the coat of a pollen-grain should be rough, and so forth, *but the significance of patterns is untouched by these*. Nevertheless, repetitions arranged in pattern exist throughout organized Nature…as a property or attribute of Life, scarcely less universal than the function of respiration or metabolism itself (p. 22, emphasis added).

Bateson's meaning, though obscured by his prose, is basically this. It is the patternedness of life that is its central riddle, not the benefits conferred by this or that structure (the riddle of adaptation). Accordingly, to account for evolution is to account for the "coming to be" of patterns—not their differential survival or elimination (p. 571). Much like Mivart, Bateson did not deny that structures *have* certain uses, and that these can be guessed at in many instances. But to discover the uses of a structure is to leave the heart of the matter untouched (see Mivart 1872, pp. 462-464). To explain evolution, one must explain the origin of new characters, and the coming to be of new patterns. As Samuel Butler quipped, “The ‘Origin of Variation,’ whatever it is, is the only true ‘Origin of Species’” (1878, quoted in Bateson 1909, p. 99).

The plan of ‘Materials’

The celebration of symmetry and pattern not only set the course for *Materials*—it also demanded that the author assign to “Discontinuous Variation” a predominant role in phyletic advance. Bateson’s argument for the evolutionary importance of discontinuity is not hard to follow (Gould provides an admirable synopsis in *The Structure of Evolutionary Theory* (pp. 396ff)). However, as it has often been caricatured, it is well to lay bare its essential elements:

1. *Symmetry and repetition are universal.* The repetition of parts, of which symmetry constitutes “a particular case,” is an almost invariable consequence of ontogeny (i.e., division and differentiation). As such, it is a universal feature of animals and plants, coextensive with life:

   “Whoever will discover by what physical process an ovum segments will give us the key to the problem of the segmentation of tissues into Series of Multiple Parts; and though we are far enough from having any such knowledge, we should at least recognize that this is the problem to be dealt with” (Bateson 1892, p. 114).
2. *Symmetries are the result of discontinuous variations*. As symmetries possess a certain omnipresent ‘perfection of form,’ changes in the state of symmetrical organization must constitute genuine discontinuities (p. 61). Consider that in moving from three-fold to four-fold symmetry, the organism will not pass through a phase of three-and-a-half-fold symmetry. “The resulting form [will

possess] the character of division into four no less completely and perfectly than its parent possessed the character of division into three" (p. 61).

Additionally, as symmetries are more-or-less "complete" and "definite" from first beginnings, they are *not* subject to Mivart's dilemma (to Bateson, "an almost fatal objection" to the selection theory (p. 69)). In other words, symmetries do not pass through a phase of "incipient minute beginnings" on their way to integral completeness. It is a basic theme of meristic variation, Gould writes, that segments "must be conceptualized as discrete anatomical forms, and supernumeraries (or deletions) are therefore usually complete (or entirely suppressed)" (Gould 2002, p. 401).

3. *It follows that...* The addition of parts to a linear series must proceed discontinuously, by the addition or subtraction of whole segments. Segments are not built up by accretion, as quartz crystal grow by the capture of silicon and oxygen molecules. Although a great many instances of "imperfect variation" can be pointed to (Bateson describes "a remarkable group of cases of *imperfect* segmentation" in arthropods), these are, "in their several degrees," discontinuous, and serve mainly to underscore the necessity of recognizing discontinuity in the origins of metamerism (pp. 156, 168).
4. *Discontinuous variations produce their effects independently of natural selection.* It follows from the foregoing considerations that new symmetries (and additions to linear series) are *not* gradually evolved on the basis of incremental advantages. Instead, they are definite and complete from the first, which is to say, their completeness *antedates selection*. "[The] principles of Symmetry…prove that there are modes in which Variation may be controlled and may produce a result which has the utility of regularity and order of form independently of the guidance of Natural Selection," Bateson wrote at the close of a long section on

"digital Variation" (p. 408). Elsewhere he states: "it is quite certain that the distinctness and Discontinuity of many characters is in some unknown way a part of their nature, and is not directly dependent upon Natural Selection at all" (p. 573).

5. *Thus: Symmetry and repetition hold the key to understanding evolution.* This rather grandiose claim consists of two parts. In the first place, "to solve the problem of Symmetry," Bateson claims, "…[is to lay] a sure foundation from which to attack the higher problem of Variation" (p. 36). The most important transitions in a progressive series are discontinuous—they are novelties that take hold because they possess a certain degree of "perfection" or "completeness" at the onset. New symmetries display this kind of completeness, as do additions to linear series. Bateson continues to detail the importance of "perfect Variation" for organic evolution:

    "We know that certain devices and mechanisms are useful to their possessors; but from our knowledge of Natural History we are led to think that their usefulness is consequent on the degree of perfection in which they exist, and that if they were at all imperfect, they would not be useful. Now it is clear that in any continuous process of Evolution such stages of imperfection must occur, and the objection has been raised that Natural Selection cannot protect such imperfect mechanisms so as to lift them into perfection [e.g., Mivart 1871]. Of the objections which have been brought against the Theory of Natural Selection this is by far the most serious" (Bateson 1894, pp. 15-16).

    From here, Bateson proceeds to assert the necessity of recognizing discontinuous changes to account for the paired phenomena of organic stability and progress (he does *not* offer a relative frequency argument concerning their incidence). In Bateson's words: "it is manifestly impossible to suppose that the

> perfection of a variety, discontinuously and suddenly occurring, is the result of Selection" (a point Francis Galton had earlier codified in his metaphor of the tumbling stone). Accordingly, "if it may be seen thus clearly that the perfection and Symmetry of a *variety* is not the work of Selection, this fact raises a serious doubt that perhaps the similar perfection and Symmetry of the *type* did not owe its origin to Selection either" (p. 68, emphasis added). Selection can explain the perpetuation of a type, but not its origins. Consequently, discontinuous variations hold the greatest potential for evolutionary progress, and "the road through the mystery of Species may thus be found in the facts of Symmetry" (p. 36).

To employ the language of a later age, William Bateson was interested in the formal content of transspecific evolution. Evolution, to him, implied a "transition from one form to another by means of a progressive series" (Galton 1894, pp. 369-370). He had little patience for the minutiae of local adaptation, electing instead to emphasize those variations that sound the very depths of organic design (Gates 1914). This led him into a study of "monstrosities," not for their intrinsic fascination, but for what they revealed about the nature of animal and plant construction. It was the origins of these designs that formed his basic problematic, and which set the course of his science of beginnings:

> The question, then, which Zoology proposes to solve is this: what have been the steps by which animals have acquired the forms which they present, and what will be the future of their development?…When we shall know the nature of the variations which are now occurring in animals, and the steps by which they are now progressing before our eyes, we shall be in a position to surmise what their past has been; for we shall then know what changes are possible to them and what are not. Until the modes of Variation are known and classified no real advance can be made in the study of Zoology (Bateson 1890, quoted in Cock & Forsdyke 2008, p. 86).

Passages such as this reveal an important point. Bateson was intolerant of continuous variations *not* because they could never accumulate within phyletic lineages, but because they were powerless to explain the major features of progressive evolution. This is why Mivart's dilemma made so strong an appeal to him. Mivart was a comparative anatomist interested in the broad outlines of organic design. His complaint was not that selection could not *act*, but rather that it could not achieve what was claimed for it: the fashioning of each major step in progressive evolution. For all his defects, Bateson appreciated the force of this difficulty, and attempted to build a science of variation that begun almost with first principles (i.e., basic symmetries). That he failed does not speak against the justice of his undertaking, only its feasibility.

Summary

Bateson viewed the problem of beginnings from a different vantage than Eimer, but like Eimer his wish was to scrutinize entire *series* of variations in as complete a state as possible. "In Variation, we look to see Evolution rolling out before our eyes," he wrote in *Materials*. However, as this is not generally feasible, it is necessary to make the best of the resources we possess in abundance:

> The Study of Variation is essentially a study of differences between organisms, so far each observation of Variation at least two substantive organisms are required for comparison. It is proposed to confine the present treatment of the subject to a consideration of the integral steps by which Variation may proceed; hence it is desirable that the two organisms compared should be parent and offspring (Bateson 1894, p. 17).

Bateson believed that certain "terms" in a series would frequently reappear in virtue of the organizational principle of the type—that is, the manner in which an organism is constructed by the sequential fabrication of its parts and symmetries. He did *not* partake in the Eimerian practice of arranging contemporaneous forms in a supposed series of descent (Eimer's confidence in this procedure stemmed from his "discovery" of *genepistasis*—"the halting of single forms at definite stages in the path of development whilst others move forward" (Eimer 1897, p. 30).) Yet he *was* interested in seeking out "complete series" of morphological conditions within known (i.e., extant) forms, and made no bones about their usefulness in comprehending the workings of evolution. Bateson, therefore, was quite serious about watching evolution unfold before his eyes, even if he lacked Eimer's interest in relating the production of novelties to actual species in nature.

Insofar as evolution traffics in the *new*, there is much to be learned from the study of how parts are added to the complex manifold of ontogeny. Further, if evolution proceeds "discontinuously" (by large variations that are relatively stable at first appearance), then it is *here* we must begin in our attempt to grasp the major features of evolution. While it is unclear what exactly is intended by the statement that "variations [are] due to Stability" (or that "the system of an organised being is such that the result of its disturbance may be *specific*"), it is nonetheless clear that adaptation is a partial explanation of descent, and one that elevates fancy over level-headed empiricism (see Cock & Forsdyke 2008, p. 139, Bateson 1894, p. 74). Indeed, to begin with utility, while regarding all variation as arising *par hasard*, is to relinquish to speculation what belongs to the science of variation.

Novelty in the new century: an epilog on the mutation theory

In the wake of Materials

Bateson's opus, *Materials for the Study of Variation*, was a monumental achievement. In it, the author cataloged 886 instances of discontinuous variation, many of them unfamiliar to naturalists of the period. Herbert Conn described it as "the only systematic attempt yet made to study variations themselves" (Conn 1894, p. 23). C.B. Davenport ranked it with the *Variation of Animals and Plants Under Domestication* as a watershed publication in the science of variability (Davenport 1900, p. 865). The British popular press reported, quite accurately, that "since the publication of the *Origin of Species* there has scarcely appeared another such monument to individual labor" (quoted in Cock & Forsdyke 2008, p. 96). And T.H. Morgan, reflecting on the deceased Bateson's career, reported that *Materials* "has recently been called Bateson's most important work" (Morgan 1926, p. 532).

These praises, however, were the exception, not the rule. Most reviews of *Materials* were critical, particularly as regards its theoretical contributions. Some even verged on savagery (Peterson 2008, pp. 289ff). While the book helped secure Bateson an FRS, sales were so meager that he abandoned his plans for a sequel, to be addressed to the subject of substantive variation (Allen 1969, p. 65). His *coup d'état* had failed. As the new century dawned, the most palpable feeling surrounding evolutionary studies was one of dissatisfaction and uncertainty. The debates that so fractured the previous generation appeared to many as interminable, and it was evident that no amount of theoretical disputation would suffice to resolve them.

Following the turn of the century, however, a number of striking researches vaulted discontinuity to the forefront of evolutionary thought. The most dramatic of these belonged to the Danish plant physiologist Hugo de Vries, a one-time student of Julius Sachs and author of the classic treatise *Intercellular Pangenesis* (1889). De Vries was aware that the foremost difficulty facing contemporary evolutionary studies was the speculative nature of its guiding theories (de Vries 1902). What was needed was an experimental program to complement and inform theoretical activity—a means of subjecting evolution to controlled observation and test.[1] It was thus with considerable

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[1] Incidentally, the lack of experimental corroboration was also the foremost difficulty facing his theory of intracellular pangenesis, which had debuted in 1889 (see Stamhuis 2003, 119-121). De Vries wished to address this by conducting hybridization experiments, the goal of which was to reveal the decomposability of species into discrete hereditary factors (each corresponding to a

zeal that de Vries began cultivating the large-flowered evening primrose, *Oenothera lamarckiana*, which he had discovered near Hilversum in 'a state of mutability' (de Vries 1905, p. 27). "This interesting plant," de Vries beamed, has "afforded me the means of observing directly how new species originate, and of studying the laws [governing] these changes." His results were to carry him to the heights of scientific celebrity, and to wash the biological world in the excitement of controversy (Allen 1969, Magnus 2000).

The mutation theory, as developed by de Vries, had a number of selling points, but its chief advantage was its concrete, experimental nature. "One of the greatest values of de Vries's work," C.S. Gager proclaimed, "was in the fact that he was *present* when the transition took place, and gives, not a theory at all but the record of a fact observed again and again" (Gager 1906, p. 86, emphasis added). This epistemic virtue counterbalanced the theory's admittedly paltry corroboration; a shortcoming that stirred much passionate debate during the first decade of the twentieth century (see Merriam 1906, pp. 242-243, Ortmann 1906). De Vries, after all, had been privy to the mutable period of a single species, and this a *rara avis,* chromosomally speaking (de Vries 1901, p. 205-207, Davis 1910).[1] Moreover, he had not so much exercised *control* over mutability as he had opportunistically *domesticated* it, utilizing the method of pedigree-culture (see Jordan 1906 for criticism).

Yet in spite of these shortcomings, de Vries was attuned to the epistemic currents of his age, which upheld controlled experimentation as a privileged means of producing knowledge (Gager 1906, p. 89). By the turn of the century, what was desired of an

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particular characteristic). To de Vries, changes in these factors were the stuff of evolutionary progress (Stamhuis *et al.* 1999, p. 257).

[1] De Vries was aware of the scarcity of direct evidence supporting his theory. He was thus forced to argue that mutability is (1) a rare enough phenomenon to have escaped most competent observers, but (2) not so rare as to make of it an aberration. *If* mutability were a mere freak occurrence, he suggested, "it would be far too rare to be disclosed by the investigation of a small number of plants from a limited area" (de Vries 1905, p. 687). Needless to say, de Vries's critics were not assuaged by this argument, and poured forth their criticisms in copious print (see Magnus 2000 for an account of the clashing epistemologies evidenced in this debate).

evolutionary theory was not comprehensive scope, but instead empirical rigor. The theoretical debates of past years had landed evolutionary studies in a linguistic and conceptual morass from which the only escape was careful experimentation and controlled observation. By no other means could an approach be made upon that most difficult of problems: elucidating "the laws to which the origin of new species conform" (de Vries 1909, p. 6).

De Vries on evolution

In de Vries's view, the organism may be visualized as a complex mosaic of characters, its attributes comprising "distinct, separate and independent units" (de Vries 1909, p. 3). Evolution consists in the wholesale change of these units (mutation), or perhaps a change in their numerical quantity. The essential characteristic of fluctuating variability is a "heaping up" of slight deviations around a mean such that the entire series obeys Quetelet's law of probability (de Vries 1905, p. 569). This framing suggests that fluctuations are simply fortuitous deviations from the status quo—the over or underdevelopment of particular organs, occurring always "in a *linear* direction" (de Vries 1909, p. 150, emphasis added). Fluctuations have no evolutionary moment. In the words a sympathetic reviewer, they are "inadequate even to make a single step along the great lines of evolution" (Spaulding 1905, p. 355). Although the natural selection of fluctuating variations can produce well-defined geographic races, it is powerless to strike off in *new* directions, or to forge genuine evolutionary novelty. It is thus a non-factor in the process of species formation.[1]

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[1] De Vries himself was well aware of Mivart's dilemma, and believed that his mutation theory "eliminated the objection that the first almost imperceptible changes [in a novel trait] could scarcely have any beneficial significance for their bearers" (de Vries 1919, p. 213). This was more a happy benefit than an essential theoretic component, however. The mutation theory was not addressed primarily to Mivart's dilemma, or the cognate difficulties of Jenkin and Nägeli. Instead, de Vries was principally concerned to bring the process of species formation into the ambit of

With mutation, however, the situation is different. Mutations "constitute divergence in *new* directions," at once transgressing the bounds of ancestral variability (de Vries 1909, p. 150, emphasis added). The progeny of mutant individuals do not regress towards the mean of their grandparents (not even in degrees), but are instead scattered about the mean of their parents—"the type of the new elementary species" (de Vries 1905, p. 570).[1] This conclusion agrees with the best practices of scientific breeding, de Vries boasted, a practice that depends for its success on the choice of an appropriate foundation stock:

> The improvement of cultivated plants must obviously begin with already existing forms. This is true of old cultivated sorts as well as for recent introductions. In either case the starting-point is as important as the improvement, or rather the results depend in a far higher degree on the adequate choice of the initial material than on the methodological treatment of the chosen varieties (de Vries 1905, p. 92).

De Vries knew from an extensive study of animal and plant breeding that mass selection is often frustrated when carried out for an extended period of time (see also Lerner 1954). He suggested, therefore, that the principal task of the breeder consists in establishing a profitable elementary species, after which time mass selection could be employed as a fine-tuning measure, further refining the stock. However, it is crucial for de Vries that man does not *produce* elementary species; this is the work of nature alone. Man produces only "improvements" (an insight he attributes to the plant breeder Kurt von Rümker). It follows that species-forming is achieved without the help of natural selection, and an elementary species, once formed, "[is] at once perfect, [needing] no smoothing, no correction" (de Vries 1902, p. 725).

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laboratory experimentation and control. Mivart's dilemma was nonetheless well known around the turn of the century, and contributed to the popularity of the mutation theory in certain circles.

[1] It should be noted how closely this accords with Galton's own view of progressive evolution, which is predicated on occasional saltations defeating the so-called 'regression to mediocrity' (a mode of variation that Galton termed "transilient").

The triumph of de Vries was the zenith of Darwinism's "eclipse" (Bowler 1978). It was also the point at which Mivart's ghost came closest to smashing the idol of neo-Darwinism:

> There must, however, be for every variation a stage of development in which it has as yet no decisive biological importance, and this stage need not by any means be so insignificant that we cannot see it, or can hardly do so: in other words, there are characters which have arisen through germinal selection, which are of purely morphological importance (Weismann 1904, p. 122).

It was not lost on Darwin's opponents that Weismann had capitulated to the gravity of Mivart's dilemma, and fallen back on *ad hoc* hypotheses rooted in the struggle between protoplasmic units (determinants) for nourishment. In Weismann's view, selection between determinants 'bootstraps' selection between organisms by enabling variation to strike off in particular directions. Of course, germinal selection was believed to do much else besides (and it was precisely this versatility that recommended it to Weismann). But to those unwilling to grant Weismann's assumptions concerning the structure of the protoplasm, germinal selection could only testify to the constitutional weakness of the Darwinian hypothesis. As de Vries presented experiments meticulously performed over two decades, Weismann piled assumption on assumption, seemingly dead to the epistemic currents that enveloped him. Weismann's recapitulation—however ingenious—was Mivart's victory.

Mivart's (short) victory

According to Jacob Gruber, Mivart's criticisms of the selection theory fell under six heads: (1) The inability of natural selection to account for the incipient stages of useful structures (Mivart's dilemma); (2) The problem of the independent origin of similar structures [given the "accidental" nature of variability]; (3) The necessity of recognizing saltations in evolution; (4) The problem of non-adaptational differences between species;

(5) The dilemmas of specific stability and apparently directed variation; and (6) The unity of the organism (Gruber 1960, pp. 52-56). In this short list can be found most of the objections raised against Darwinism during the period between 1870 and 1905 (the year de Vries's *Species and Varieties* appeared). Together they represented a cumulative critique that cast significant doubt on the efficacy of natural selection in species-forming (Provine 1985, p. 839).

Of course, it was one thing to say this, and quite another to offer a reasonable replacement. As we've seen, Mivart's theistic suggestion sunk without a trace, as did the whole of theistic evolutionism (Bowler 1983, pp. 55-57). Yet his numerous successors experienced success in various degrees, culminating in the international phenomenon of *Die mutationstheorie*. "[No] work since the publication of Darwin's *Origin of Species* has produced such a profound sensation in the biological world" F.C. Baker wrote in that long-time organ of neo-Lamarckism, *The American Naturalist* (Baker 1906, p. 327). Charles Benedict Davenport agreed:

> De Vries's great work 'Die Mutationstheorie' marks an epoch in biology as truly as did Darwin's 'Origin of Species.' The revolution that it is working is less complete, perhaps, because there has remained no such important doctrine as that of [organic] continuity to be established. But there was need of a revolution in our method of attacking the problems of evolution. Ever since Darwin's time most biologists have been content to *discuss* and argue on the *modus operandi* of evolution. The data collected by Darwin have been quoted like scriptural texts to prove the truth of the most opposed doctrines. We have seen biologists divided into opposing camps in defense of various isms, but of the collection of new data, and above all, of experimentation we have had little. The great service of de Vries' work is that, being founded on experimentation, it challenges to experimentation as the only judge of its merits. It will attain its highest usefulness only if it creates a widespread stimulus to the experimental investigation of evolution (Davenport 1905, p. 369).

According to de Vries, the mutation theory "reduced the time necessary for the evolution of life on earth…explained the appearance of the numerous useless qualities of animals and plants, and eliminated the objection that the first almost imperceptible changes could scarsely have any beneficial significance for their bearers" (de Vries 1919, p. 213). Here were all the criticisms of Mivart, marshaled into a powerful negative argument. Although by 1919 the mutation theory had been thoroughly debunked, the embattled botanist went to his grave believing that none of Mivart's criticisms were answerable on the Darwinian hypothesis. Many prior to 1920 shared his conviction, including Bateson, whose 1922 paper "Evolutionary Faith and Modern Doubts" sounded the dourest note imaginable on the eve of the evolutionary synthesis.

Then a curious thing happened. One by one, Mivart's criticisms fell. First, mathematical geneticists, led by R.A. Fisher, demonstrated that even small selection forces can push alleles to fixation under certain conditions (Fisher 1930). (Although this did not dispatch with Mivart's dilemma, nonetheless it eased the pressure that it had once exerted. An increased recognition of the importance of "function-change," as outlined by Darwin and Dohrn, further alleviated the condition.) Thereafter, parallelism and convergence were called as witnesses of the power of selection—they were no longer embarrassments to Darwinism, as Mivart had believed (see Huxley 1957, Mayr 1963). With the foregoing difficulties removed, saltations no longer seemed a theoretic necessity. Nature might avail herself of large modifications, but there was no reason to suspect this to be the predominant mode of phyletic advance. Indeed, plausible gradualist accounts were becoming available for even the main planks of Mivart's argument, for instance, complex mimesis in butterflies (see Fisher 1927, Turner 1983). What's more, the notion that the majority of "specific characters" are useless (a commonplace of the 19th century) fell from grace with the rise of the British school of ecological genetics, and the reinterpretation of classical studies like Dobzhansky's work on chromosome inversion frequencies in *D. pseudoobscura* (see Provine 1985, p. 857, Dobzhansky 1951, p. 118-121). Finally, the issue of directed variation lost control of what had been its last bastion—paleontology (Jepsen 1949). This owed in no small part to George Simpson's pioneering work, *Tempo and Mode in Evolution* (1944).[1]

Of course, this is a superficial account of a rich and vibrant period, bristling with all manner of complexity and intrigue. Yet it suffices to illustrate a more or less rapid change in the disposition of biologists over the first half of the 20th century. With Mivart's critical program in shambles, the architects of the modern synthesis were able to consolidate their gains atop a powerful theoretical apparatus. Once again, evolutionary studies buzzed with excitement; the "eclipse of Darwinism" was over.

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[1] Incidentally, in its sequel, *The Major Features of Evolution* (1953), Simpson writes of Mivart's dilemma that "[while it] long seemed an extremely forceful argument...it can now be dismissed with little serious discussion." His rationale is evident when he turns to consider the knobby skulls of the enormous titanotheres, rhino-like ungulates that H.F. Osborn had famously monographed in 1929. Writes Simpson: "[If] an animal butts others with its head, as titanotheres surely did, the slightest thickening as presage of later horns already reduced danger of fractures by however small an amount. [This is probably in response to Osborn's claim that tiny modifications, e.g., of horn rudiments, or tooth cusps, can make no difference in the struggle for existence (Osborn 1934).] That the amount in a given case is too small for selection to act upon *is an opinion now quite unjustified in view of the demonstrated great effectiveness of genetical selection in most situations*. It is certain that if we can see any advantage whatever in a small variation (and sometimes even if we cannot), selection sees more" (Simpson 1953, pp. 270-271, emphasis added).

A coda on the meaning of Darwinism

Introduction

In a paper concerned largely with non-Darwinian interpretations of evolution, it is worthwhile to reflect on the precise meaning of the term "Darwinism." I do not propose to review the voluminous literature on the subject; to do so would require another long (and tedious) paper. Instead, I will subjoin a few remarks that, I think, cut to the heart of the matter.

"Darwinism"

Can Darwinism be concisely defined? Many have tried, but the term is so freighted with history that no resolution is forthcoming (Bowler 1988, pp. 7-10). What we can say for certain is that throughout the 19th century, Darwinism "meant much more than natural selection—it referred to a whole complex of ideas that challenged the traditional view of nature" (Bowler 1985, p. 650).[1] Perhaps, as Hull suggests, it is best construed as a *lineage*: a braid of social and scientific filiation which lacks altogether a singular essence (Hull 1985). Although I appreciate the advantages that accrue to such a model, I will here attempt a non-historical sketch of Darwinism in the hopes that it might illuminate what exactly was "eclipsed" during the period of 1885-1920.

To begin with the basics, when speaking of "Darwinism," let us intend the notion of evolution by means of natural selection, or "the preservation of favoured races in the struggle for life." A Darwinist, then, is one who regards evolution as proceeding naturalistically, by the piecemeal modification of phyletic lineages (Wallace 1895, Rhodes 1987). He or she needn't be an 'uncompromising utilitarian,' as Bowler

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[1] This assertion might be questioned on the grounds that there has *never* been a univocal view of nature, whether in Britain or elsewhere (see Knoepflmacher & Tennyson 1977, Corsi 2005). Moreover, in running together Darwinism and the more inclusive category of "evolutionism," the investigator tempts considerable confusion (Richards 1992). Notwithstanding these difficulties, it is clear that Darwinism stands for something more specific than a mere belief in transformism.

somewhat uncharitably claims for Darwin (Bowler 1985, p. 648, cf. Darwin 1859, p. 170). However, a Darwinist must regard evolution as oriented, in the main, by adaptive processes, and thus indirectly by the constraints of local environments. Several other points warrant mentioning in order to lend color to this basic picture:

> *i. Size of variation.* As regards the magnitude of individual variations, it is necessary that this be "small"—perhaps not so small as that imagined by Darwin (he mentions in a letter to Lyell "a beak 1-100th of an inch longer than usual" (Darwin 1887, p. 33)), but nonetheless relatively inconspicuous. It is asking too much that a Darwinist "go whole hog" with respect to the master's infintesimalism, and lean heavily on "barely perceptible [deviations]" of structure and habit (Darwin 1844, p. 152, 1861, p. 214; see Wallace 1895, pp. 213ff, of a defense of the Darwinian's right to invoke discontinuous variations). Indeed, some measure of saltationism is acceptable in a Darwinist so long as it is admitted that gradual modification *can*, under certain circumstances, result in species-formation. (This may open the door wide enough for the admittance of T.H. Huxley.) Yet in cases like Francis Galton's—where the possibility of gradual evolution is admitted, but accorded no theoretic importance—the title of "Darwinist" is rightly withheld.[1]

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[1] Darwin's cousin is remembered, among other things, for his sponsorship of *transilient variation* resulting in evolution "by a leap from one position of organic stability to another" (Pearson 1930, p. 85). Yet he admits in *Natural Inheritance* that "a new type can [also] be reached without any large single stride, but through a fortunate and rapid succession of many small ones" (Galton 1889, p. 26). This statement is a polite nod to the Darwinian view of evolution, yet I think it is appropriate to question the degree to which Galton believed in what he was writing (see Crow 1993, Maynard Smith 1993, Gillham 2001).

The argument for withholding the mantle of "Darwinian" from Galton (and similar thinkers, like William Bateson) rests on an issue of emphasis. For it is apparent that Galton looked upon Darwinian gradualism as an altogether infrequent mode of evolution, and perhaps even an unlikely one (Galton 1894, pp. 369-370, but see Bowler 2014 for a nuanced perspective). It follows that while Galton's writings can be massaged so as to make him appear as a Darwinist—albeit a somewhat unconventional one—his vision of evolution differed sharply from that of his cousin. This seems to me reason enough to draw a distinction between the two men's views, although I agree with Peterson (2008) that it is not grounds for assuming a sharp dichotomy.

ii. Direction of variation. There is no requirement that variations be entirely unbiased in their occurrence, or absolutely indifferent with respect to the requirements of life (see Brooks 1883, pp. 276-277 for commentary). That said, for a theory to be called "Darwinian," it cannot be the case that the variation upon which it relies is *foresighted*, or oriented in a non-trivial degree by intrinsic or transcendental processes. A Darwinist must believe that variation is largely haphazard, and that major trends are *not* oriented by the nature of ontogeny, but by selection on the basis of utility. (Observe that this is not the same thing as saying that all characters are adaptive.)

iii. Divergence. Lastly, the Darwinist must see evolution as a branching process in which lineages are determined in their course by an unremitting struggle for life, at great waste and slaughter. While "the struggle for existence" was accorded a diminished role by 20th century biologists, it is hard to imagine a 19th century Darwinist who did not regard it as an important consideration (see Wallace 1889, Ch. 2). After all, the apparatus of competition was no mere watchword for Darwin—it was the linchpin of his theoretical system. As he writes in the *Origin*: "unless [the struggle for life] be thoroughly ingrained in the mind, the whole economy of nature, with every fact on distribution, rarity, abundance, extinction, and variation, will be dimly seen or quite misunderstood" (Darwin 1859, p. 62). This entrained (through somewhat opaque means) the *tendency* of populations to diverge at their margins: another key component of the Darwinian picture.

It is worthwhile to attempt a recapitulation of the previous points. The question I have set before us is simple: 'What is Darwinism?' In summarizing my answer, I will vary the words of the historian James Moore (interpreting Yvette Conry's *L'introduction du darwinisme en France au XIX siècle*):

> *Darwinism is an etiology of descent, stemming from the problematic of adaptation, by the method of natural selection, and presupposing (1) haphazard variation (usually of a minor caliber), (2) an unremitting struggle for life (resulting in the survival of organisms best fitted to their conditions of life) and (3) a tendency of lineages to bifurcate (by the divergent adaptation of their members).*

If I were to be bold, I would claim that agreement with this statement is both necessary and sufficient to pick out a Darwinist during the 19th century.

"Anti-Darwinism"

All non-Darwinian interpretations contravened one or more of the above-mentioned tenets. The orthogeneticists set great store by the internal channeling of evolutionary trajectories, and consequently downplayed the haphazardness of variation and the importance of population pressure (Olsson & Levit 2006). They doubted whether external constraints can mold and shepherd the great lines of descent, and dismissed more extreme notions of piecemeal modification as naïve (see, for instance, Eimer 1898, p. 56). Heterogeneticists, for their part, attached little importance to variations of a minor caliber, which occasioned much fruitful speculation as to the predominant mode of phyletic advance. To the average saltationist, the materials of evolution were *not* omnipresent in natural populations (forming, as it were, 'a dense and isotropic sphere of potentiality about the modal form of a species' (Gould 2002)). Instead, variations are visited capriciously on individuals, transporting them at once past the morphologic horizon of the parent form. Viewed through this lens, not only gradualism but also piecemeal modification appeared as dubious:

> If a man were asked to make a wax model of the skeleton of one animal from a wax model of a skeleton of another, he would perhaps set about it by making small additions to and subtractions from its several parts; but the natural process differs in

> one essential way from this. For in Nature the body of one individual has never *been* the body of its parent, and is not formed by a plastic operation from it; but the new body is made again from the beginning, just as if the wax model had gone back into the melting pot before the new model was begun (Bateson 1894, p. 33).

The Lamarckian school was by no means wholly distinct from the diffuse schools of orthogenesis and saltationism (nor were orthogenesis and saltationism distinct from one another). We may nonetheless say, without great distortion, that the principal demur of the Lamarckians concerned no one matter of principle (at least before Weismann galvanized them into resistance (see Pfeifer 1965, Cook 1999, Persell 1999)). Rather, Lamarckians tended to doubt how well Darwin's collocation of factors accounted for the broad phenomena of descent (see Packard 1901, p. 398). As Delage and Goldsmith write, "Natural selection did not seem to the Neo-Lamarckians an adequate explanation of evolution, as it does not account for the origins of the variations which it fosters. They preferred to attribute the origin of those variations to the direct action of the environment," to the effects of use and disuse, or to global phenomena of development like acceleration and retardation (Delage & Goldsmith 1912, p. 250, Gould 1977a, Ch. 4).

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