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The Creativity of Natural Selection? Part I: Darwin, Darwinism, and the Mutationists

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Abstract. This is the first of a two-part essay on the history of debates concerning the creativity of natural selection, from Darwin through the evolutionary synthesis and up to the present. Here I focus on the mid-late nineteenth century to the early twentieth, with special emphasis on early Darwinism and its critics, the self-styled "mutationists." The second part focuses on the evolutionary synthesis and some of its critics, especially the "neutralists" and "neo-mutationists." Like Stephen Gould, I consider the creativity of natural selection to be a key component of what has traditionally counted as "Darwinism." I argue that the creativity of natural selection is best understood in terms of (1) selection *initiating evolutionary change*, and (2) selection *being responsible for the presence of the variation it acts upon*, for example by *directing the course of variation*. I consider the respects in which both of these claims sound non-Darwinian, even though they have long been understood by supporters and critics alike to be virtually constitutive of Darwinism.

Keywords: Natural selection, Creativity, Darwinism, Mutationism

Introduction

The author of a recent essay, "Correcting some common misrepresentations of evolution in textbooks and the media," targets (among other things) the alleged creativity of natural selection:

> Natural selection is not "creative."… [I]t is more accurate to say that in the struggle for existence, some individuals are weeded out before they can reproduce. This process is not creative…. And

> really, why push it? The term is anthropomorphic. Leave creativity to the artists. (Padian, 2013, p. 9)

Why push it? According to Stephen Gould, the ''creativity of natural selection'' is ''the essence of Darwinism'' (Gould, 1977, p. 44). Asking ''Why push the creativity of natural selection'' would be like asking ''Why push Darwinism?'' Note: Gould's point was that ''the *creativity* of natural selection,'' not just ''*natural selection*,'' is the essence of Darwinism.

But what does it mean to say that natural selection is ''creative?'' Minimally though importantly, the claim has served to rebut the position taken by the author above, before he sets the question aside as not worth arguing about. It is to deny that natural selection merely ''weeds out'' disadvantageous variations, or merely retains the advantageous.

The idea that selection merely eliminates or preserves the variation provided, suggests that there can be no evolution in any particular direction until variation in that direction is made available; selection must wait for variation to act upon. On the contrary, as Darwinian defenders of the creativity of natural selection have argued, it is natural selection, not the production of variation, that initiates evolutionary change. Moreover, natural selection is in an important sense responsible for the variation that it acts upon. One way in which this occurs is when selection in a particular direction results in the production of further variation in the same direction.

Both of these claims may sound surprisingly *non*-Darwinian, hardly the ''essence'' of Darwinism. First, the idea that selection, rather than the production of variation, initiates evolutionary change seems at odds with the commonly held view that evolution by natural selection is a ''two-stage'' process: the first step being the production of variation and the second being selection. But this is not so obviously true after all; or has not been so obviously true to many Darwinians (including Darwin).

As for the claim that natural selection does not merely preserve or eliminate the variation provided, but somehow provides variation for itself to preserve or eliminate – this seems to be at odds with the traditional Darwinian understanding of ''chance variation'': the idea that, whatever causes the appearance of an advantageous trait, it has nothing to do with the fact that such a trait would be selected. And yet defenders of the creativity of natural selection have seemed to suggest that selection in a particular direction increases the probability of occurrence of further variation along the same trajectory.

I'll try to make sense of these apparent inconsistencies, not to resolve them, but to explore the lines of reasoning and evidence employed by

defenders of the creativity of natural selection and their critics. This leads to a richer understanding of the history of "Darwinism," and what many critics have found objectionable about it. While my understanding of the issues involved in debates about the creativity of natural selection differs somewhat from Gould's, I nonetheless agree wholeheartedly with his view that the creativity of natural selection is constitutive of what it has meant to be a self-regarding "Darwinian." And correspondingly, the creativity of natural selection has been the *target* of many self-regarding *critics* of "Darwinism."

This paper is the first of a two-part essay on the history of debates concerning the creativity of natural selection, from Darwin through the evolutionary synthesis and up to the present. Here I focus on the mid-late nineteenth century to the early twentieth, with special emphasis on early Darwinism and its critics, the self-styled "mutationists." The second part (Beatty forthcoming) focuses on the evolutionary synthesis and some of its critics, especially the "neutralists" and "neo-mutationists." There is another (at least one other) important line of discussion/debate that I am not considering in either essay, even though it is especially dear to me: it has to do with Henri Bergson's influential critiques of the creativity of natural selection, and responses to Bergson. These debates had to do with a different (though partially overlapping) set of issues – especially indeterminism and vitalism – and a different (though partially overlapping) group of actors. I hope this will someday be the third part of the project.

Thomas Hunt Morgan is the endpoint of the present essay, and the starting point of the next. He is an especially important figure in the creativity controversies, being in many ways the most significant critic of Darwinism (again, Darwinism not just in terms of evolution by natural selection but also in terms of the creativity of natural selection) prior to the evolutionary synthesis. And he and de Vries were in turn among the most significant foils of the architects of the synthesis in their attempts to update Darwinism and improve the case for creativity.[1]

Garland Allen, to whom this paper is dedicated, has on several occasions addressed Morgan's "endless quest" to undermine the cre-

[1] My two reviewers wanted me to say more about how the issues discussed here relate to claims and counter-claims about creativity in the evolutionary synthesis and more recently. That's where I'm headed, but I have to leave that until "Part II" and try to be true in this paper to the concerns of Darwin, early Darwinians, and early critics of Darwinism. For now I'll just stress that there is indeed continuity, for example through Morgan and de Vries as critics of creativity, and subsequent criticisms of them. The several references to Ernst Mayr here (who will play a prominent role in Part II), and the quotation from Sergei Chetverikov at the very end of this paper will hopefully do for now.

ativity of natural selection (Allen, 1978, p. 315, 1980, pp. 378–379). I will address Allen's treatment of these issues in the penultimate section.

"Creativity"

Part of what Gould had in mind – by emphasizing the centrality to Darwinism of the creativity of natural selection – had to do with a common conception of natural selection *prior* to Darwin (Gould, 1987, 2002, pp. 137–139). Take the case of Edward Blyth. According to his biographer Eisley (1979), Blyth was unfairly denied credit for his pre-Darwin enunciation of the principle of natural selection. Consider for example Blyth's claim:

> [A]mong animals which procure their food by means of their agility, strength, or delicacy of sense, the one best organised must always obtain the greatest quantity… and be thus enabled, by routing its opponents, to transmit its superior qualities to a greater number of offspring. (Blyth, 1835, p. 46)

However, as Gould explains, Blyth explicitly denied that species could be changed in this way. Rather, such a "struggle for existence" (Blyth's term) preserves each species in its original condition, and this is according to God's plan. "[B]y removing all [the members of a species] that deviate from their normal or healthy condition," this struggle "perpetuates the pristine characters [of the species] without a blemish or decay to their remotest posterity" (Blyth, 1837, pp. 79–80).

So according to Blyth, selection for "superior qualities" prevents change; while for Darwin, selection of fitter variations leads to directional change, divergence of species, and speciation. To say that, for Darwin, selection is *creative* serves in part to emphasize how differently he envisioned its role, compared to previous thinkers like Blyth.

Which might have settled the matter of the creativity of natural selection, except that the issue changed. The creativity question in the post-Darwin debates was a different one having to do with the relative evolutionary contribution of natural selection vs. the occurrence of variation. According to Gould, claims for the creativity of natural selection, relative to the production of variation, have rested on three assumptions: (1) that variation is "copious," and moreover "in all directions"; (2) that variation is "undirected"; and (3) that while large-scale (or discontinuous) variations may occur, the variation that serves as the material of evolutionary change is small in scale (nearly contin-

uous). I will focus on the first two assumptions (I will explain later why I am not dealing with the third). With regard to both assumptions, I believe Gould is right *in part*. He is certainly right that Darwin and Darwinians have emphasized the copiousness of variation. But he doesn't explain how, exactly, this bears on the creativity of natural selection. What he might have added is that, as long as variation is copious in all directions, then natural selection and not the appearance of variation *initiates* evolutionary change; there's no waiting. I will explain this shortly. Gould does say that if variation was not copious in all directions, then evolution by natural selection would "consume its own fuel and bring itself to an eventual halt." What he might have added is the crucial implication: namely that, should evolution by natural selection come to a halt for lack of variation, then the production of further variation would be required to *re-initiate* evolutionary change; in which case the production of variation, not natural selection, would be the initiator. Again, I will explain this in what follows.

What Gould also does not say, but what follows from the ever-present copiousness of variation in all directions, is that selection in any direction must shift the range of variation in that direction. So that in an important sense, *variation is directed* by natural selection; which seems, in the same important sense, at odds with the second assumption, namely that variation is "undirected."

My view is that the creativity of natural selection is best understood in terms of it's (1) *initiating* evolutionary change, and (2) *being responsible for the presence of the variation it acts upon*, for example by *directing the course of variation*; as oddly non-Darwinian as both of those points may sound.

Darwin

From early on Darwin was criticized, even by his strongest supporters including Asa Gray, Charles Lyell and Joseph Hooker, for exaggerating the importance of selection relative to the production of variation. How could he presume to explain the origin of all the diverse forms of life with a theory that was silent on the origin of variation and dealt only with its elimination or preservation? This was to leave out the creative part of what was supposed to be a replacement for special creation. As Lyell put it,

> If we take the three attributes of the deity of the Hindoo Triad, the Creator, Brahma, the preserver or sustainer, Vishnu, & the de-

> stroyer, Siva, Natural Selection will be a combination of the two last but without the first, or the creative power, we cannot conceive the others having any function.
>
> The destroy[ing] force is selection, the sustaining [force] preserves things,… but in order that life shd. exist where there was none before,… & mind in the course of time,… this is not selection, but creation, the variety-making not the destroying, or continuing by inheritance, power. Nothing new wd. appear if there were not the creative force.[2] (Lyell in Wilson, 1970, p. 369)

For some, like Lyell and Gray, the hole in Darwin's theory – the production of variation – was best filled by the creative power of the Creator himself. Darwin found this proposal theologically problematic to say the least; it would take a pretty capricious deity to dictate such an unpredictable process (Lennox, 2010; Beatty, 2010). Better to leave variation to chance; in which case selection, not the production of variation, is most responsible for the creation of well-adapted organisms. He made his point by comparing selection to an architect-builder (see also Beatty, 2014).

> Let an architect be compelled to build an edifice with uncut stones, fallen from a precipice. The shape of each fragment may be called accidental; yet the shape of each has been determined by the force of gravity, the nature of the rock, and the slope of the precipice, – events and circumstances, all of which depend on natural laws; but there is no relation between these laws and the purpose for which each fragment is used by the builder. In the same manner the variations of each creature are determined by fixed and immutable laws; but these bear no relation to the living structure which is slowly built up through the power of selection, whether this be natural or artificial selection. If our architect succeeded in rearing a noble edifice, using the rough wedgeshaped fragments for the arches, the longer stones for the lintels, and so forth, we should admire his skill even in a higher degree than if he had used stones shaped for the purpose. So it is with selection, whether applied by man or by nature; for though variability is indispensably necessary, yet, when we look at some highly complex and excellently adapted organism, variability sinks to a quite subordinate position in importance in comparison with selec-

[2] This is a passage from Lyell's journal in March 1860. He had most likely discussed it during a visit with Darwin in Down in the same month. See Darwin's continuation of their discussion of the "creative and sustaining powers of Brahma," Darwin to Lyell, 15 April 1860, in Darwin (1993, pp. 160–161).

> tion, in the same manner as the shape of each fragment used by our supposed architect is unimportant in comparison with his skill. (Darwin, 1868, vol. 2, pp. 248–249)

This is rightly considered Darwin's most carefully articulated understanding of chance or "accidental" variation, and the conception of chance variation that remains current.[3] To say that the production of variation is a matter of chance is to say that whatever causes the appearance of a new variation, it has nothing to do with whether the variation will prove useful and be selected. But there is much more to the analogy than just what is meant by chance variation. Although Darwin does not explicitly refer to "creativity" here, he does compare evolution by natural selection to a creative process, and aspects of this comparison figure centrally in the subsequent creativity debates, especially with regard to the role of selection in initiating evolutionary change. Note that the construction of the "edifice" is initiated by the architect. The building materials were just sitting there prior to his employment of them; they might have been sitting there for millennia. The architect does not wait to begin, and having begun, never stops and waits for additional material in order to continue.

If this point – about selection initiating the process – seems just plain wrong – so wrong that you cannot even momentarily entertain it – this may be because evolution is so often portrayed as a "two-stage process," a linked sequence of events that starts with the occurrence of variation, followed by natural selection of that variation. For example, as Ernst Mayr famously put it:

> Let us remember that evolutionary change is a two-factor process. One stage consists in the generation of genetic variation. It is on this level that chance reigns supreme. The second stage is concerned in the choosing of genotypes that will produce the next generation. On this level natural selection reigns supreme and chance plays a far less important (although not negligible) role. (Mayr, 1963, p. 214; see also Mayr, 1970, p. 128)[4]

[3] E.g., "Mutation is random in [the sense] that the chance that a specific mutation will occur is not affected by how useful that mutation would be" (Futuyma, 1986, p. 78).

[4] Interestingly, here and elsewhere Mayr seems unsure whether to characterize evolution by natural selection as a two-"factor" or a two-"stage" process. It's the *two-stage* characterization – which suggests that the chance production of variation comes first, followed by natural selection – that concerns me here. As I'll discuss in Part II, Mayr's own defense of the creativity of natural selection doesn't fit well with the two-stage model.

But for Darwin this was just one possible sequence of events. In the *Origin*, he illustrated evolution by natural selection with two alternative scenarios. In the first he imagines a population of wolves in which there is at first considerable standing variation with regard to body proportions and speed, but no evolutionary change. Evolution commences only when there is a change in the environment – specifically, a reduction in the number of prey (deer) – that leaves the faster and slimmer wolves better off. In the second example, he again imagines a population of wolves. But here evolution does not commence until the appearance of a favorable variation (in this case a new dietary preference) that was not previously present. The new variation confers greater survival ability and is subsequently accumulated by natural selection (Darwin, 1859, pp. 90–91).

The first narrative is like the architect scenario, where the building materials are just sitting there until the architect initiates construction. It is not at all clear that there is, in this case, a coherent process that begins with the appearance of some traits that only later – perhaps much, much later – prove advantageous and are subsequently selected. The second narrative is not at all like the architect analogy. In this case, evolutionary change is more straightforwardly triggered by the occurrence of the new advantageous trait. The appearance of the new trait also plays an important directing role; evolution by natural selection takes-off in *that* direction.

This difference was resolved in the fifth edition of the *Origin*, published two years after the architect analogy. There, Darwin deleted the second illustration, the one where evolution commences with the appearance of a new variation and then proceeds in that direction. He did not cite inconsistency with the architect analogy as the reason, which would have been a weak reason indeed. Rather he made the change, he explained, in response to Fleeming Jenkin's extremely critical review of the *Origin* (Jenkin, 1867; Darwin, 1869, pp. 103–104). Among other things, Jenkin pointed out a problem in thinking that that evolution begins with the appearance of a new beneficial variation. The problem was Darwin's ''blending'' theory of inheritance, according to which parents who differ with respect to some trait would give rise to offspring intermediate between them. The possessor of a single, new advantageous variation would thus not pass the same trait to its offspring; rather, the trait – along with its degree of advantage – would be diluted through mating with an organism of the previously prevailing type. And over and over in succeeding generations, until the trait and its advantage had almost entirely disappeared. Darwin answered Jenkin in part by dropping the idea that selection acts on new variations as they

arise, and by supposing instead that there is always considerable variation present for natural selection to act on; and by supposing further that the variations that ultimately prove advantageous will be sufficiently numerous, and their possessors will mate with each other sufficiently often, that blending will not prevent their accumulation (see the excellent, nuanced discussion of this historical episode in Gayon, 1998, pp. 85–102).

This was a capitulation of sorts, but the effect was to make natural selection a more important evolutionary factor than would be the case if selection waited for advantageous variations to arise. There is thus a double meaning to the appreciation that Darwin expressed in correspondence to Hooker: ''Fleeming Jenkin has given me much trouble, but has been of more real use than any other essay or review'' (16 January 1869, in Darwin 2009, pp. 20–21).

Darwinism

So in an important sense selection, not the production of variation, initiates or originates evolutionary change, according to Darwin. And this would be a contentious issue in the creativity debates that followed. Another contested issue would be whether and in what sense selection is responsible for the variation that it acts upon; for example, whether and in what sense selection in a particular direction results in the production of further variation along the same lines. Here is another surprising position for Darwin and Darwinians to take, especially given their notion of chance variation.

For Darwin, this was related to the ''accumulative'' power of selection. At the beginning of Chapter 4 of the *Origin*, where Darwin lists the conditions for natural selection, he carelessly concludes, ''This preservation of favourable variations and rejection of injurious variations, I call Natural Selection'' (1859, p. 81). I say this was careless because throughout the *Origin* and elsewhere Darwin emphasizes the eliminative, preservative, and *accumulative* power of selection. By selective ''accumulation,'' he did not just mean increasing the proportion of an advantageous trait within a species, as for example when an ancestral flying squirrel is born with a flap of skin between it's fore- and hind-flanks that is larger (say $x+$) than the flap possessed by other members of its species (say x), and the initially rare $x+$ variation becomes more and more common. Rather, he was referring to the way in which selection in favor of larger flaps increases the mean flap volume from x,

to $x+$, to $x++$, to $x+++$, etc. And the important point here is that, as evolution by natural selection proceeds in the direction of larger flap volumes, *ever larger variations become available for natural selection to act upon*.

Alfred Russel Wallace expressed this best in response to the Duke of Argyll's contention that evolution by natural selection could not go on for long in the same direction – there could be no accumulative selection – unless the Creator continually supplies variation along that path. But Wallace, echoing Darwin, replied that breeding shows otherwise. As long as a breeder's stock is not too small, variations in the desired direction continue to arise. Ditto for nature, he insisted. Making the point about the copiousness of variation, he also drew the important implication that plentiful variation in all directions, at every stage of evolution by natural selection, requires shifting the range of variation accordingly. This occurs without God's intervention; selection itself does the trick. Wallace referred to this as a "law."

> Universal variability, – small in amount but in every direction, *ever fluctuating about a mean condition until made to advance in a given direction by "selection"* natural or artificial, – is the simple basis for the indefinite modification of the forms of life.... (Wallace, 1867, pp. 484–485; my emphasis)

Note that Wallace attributes to selection not just a change in the direction of the mean, but a shift in the "fluctuating" variability surrounding the mean.

This is perhaps the outlook that Theodor Eimer had in mind when he objected that Darwinians went too far in supposing that selection was responsible for the variation that it acted upon. Selection cannot explain the "origin of new characters."

> [I]t was the most zealous adherents of Darwin who made, and still make, the great mistake of treating the selection depending on utility as the power which by its own action brings forth those variations of the characters of the organism which afford the possibility of that selection; or at least, the mistake of not perceiving clearly how far selection, how far Darwinism as a whole, is from being able to explain these variations.
>
> The Darwinian principle of utility, the selection of the useful in the struggle for existence, does not explain the first origin of new characters. (Eimer, 1890 [1888], p. 2)

One might well sympathize with Eimer's complaint. Whichever Darwinians he had in mind might seem to have overlooked the basic Darwinian point that variation is accidental in the sense that its production is independent of the direction of selection. How then could selection in a particular direction extend the range of variation in that direction? Wouldn't that contradict the thesis that variation is accidental?

August Weismann responded by trying to explain that there is a sense in which variation is accidental, and a sense in which it is not. It is accidental whether variations occur to the "plus" or "minus" side of the parents' traits, but the mean *and range* of variation is "directed" by selection over the course of generations. This is simply a "fact" established by breeders seeking to augment a trait, say tail-feather length. They begin with birds whose mean tail-feather length is x, and whose range of feather lengths is $\{x-$ to $x+\}$. They select for the birds with feathers of length $x+$. As the mean length is shifted from $x-$ to $x+$, the range of variation around the mean also shifts and is now $\{x$ to $x++\}$. Birds with tail-feathers of length $x++$ are then selected, increasing the mean tail length and shifting the range of variation further in that direction, so that eventually birds with tail-feathers of length $x+++$ arise and are selected. And so on, and so on. That there are now Japanese cocks with tail-feathers six feet in length is due to selection shifting the range of variation from which breeders could select, and "not at all to the circumstance that at some period of the race's history a cock with tail-feathers six feet in length suddenly and spasmodically appeared" (Weismann, 1902 [1896], p. 34).

This is the sense in which selection is "actually competent to create new properties" (ibid., p. 24); the sense in which selection itself is responsible for the variations it selects.

> [T]hrough selection the zero-point, about which, figuratively speaking, the organ may be said to oscillate in its plus and minus variations, is displaced upwards or downwards. Darwin himself assumed that the variations oscillated about a mean point, and the statistical researches of Galton, Weldon, and others have furnished a proof of the assumption. If selection, now, always picks out the plus variations for imitation [i.e., reproduction], perforce, then, the mean or zero-point will be displaced in the upward direction, and the variations of the following generation will oscillate about a higher mean than before. (ibid., p. 36)

But Weismann was concerned that this fact was hardly guaranteed. Why after all should selection shift the range and not just the mean of variation? He sought a deeper grounding.

> There is involved here, however, an assumption which is by no means self-evident, that every advancement gained by the variation in question constitutes a new centre for the variations occurring in the following generation. That this is a fact, is proved by such actual results of selection as are obtained in the case of the Japanese cock. But the question remains, Why is this the fact? (ibid.)

To this end, Weismann offered what he termed an "interior mechanism" ("interior" to the organism) for the production of variation in the direction of selection. This involved supplementing selection at the level of individuals with intra-individual "germinal selection," which takes place among components of germplasm (through competion for nutrients/resources within the individual). Here is the gist of the idea:

> [A]s soon as personal selection favors the more powerful variations of a determinant [a component of the germplasm], the moment that these come to predominate in the germ-plasm of the species, at once the tendency must arise for them to vary still more strongly in the plus direction, not solely because the zero-point [mean of variation] has been pushed farther upwards, but because they themselves now oppose a relatively more powerful front to their neighbors, that is, actively absorb more nutriment, and upon the whole increase in vigor and produce more robust descendants. From the relative vigor or dynamic status of the particles of the germ-plasm, thus, will issue spontaneously an ascending line of variation, precisely as the facts of evolution require….
>
> Thus, I think, may be explained how personal selection imparts the initial impulse to processes in the germ-plasm, which, when they are once set agoing, persist of themselves in the same direction…. (ibid., pp. 44–45)

I will not attempt to elaborate upon the mechanism.[5] My concern here is just to emphasize Weismann's attitude that there must be some means by which natural selection is responsible for the variation that it subsequently acts upon, as seemingly non-Darwinian as that might sound.

[5] I recommend consulting interpretations of the mechanism by Churchill (2015), Bowler (1979) and Winther (2001).

The Mutationists

Among the most influential critics of Darwinism in the early twentieth century were so-called "mutationists" like Hugo de Vries and Thomas Hunt Morgan (see Stoltzfus and Cable, 2014 for an excellent discussion of the centrality of the creativity critique to the very identity of Mendelism-mutationism). Their problem with Darwinism was not evolution by natural selection *per se*, which Morgan took to be a truism. It was rather the Darwinians' emphasis on natural selection of ever-present variation:

> A mutationist might well insist that the essential part of Darwin's theory of natural selection is not survival [i.e., "survival of the fittest"], but Darwin's postulate that the individual variations, everywhere present, furnish the raw materials for evolution. This the mutationist would deny.[6] (Morgan, 1935, pp. 109–110)

They championed instead evolution by natural selection of "mutations," understood as alterations to Mendelian genes. Mutational variations were, most significantly, *not* ever-present; they occurred only occasionally, indeed infrequently.

> The origin of these types [due to mutations] – the real creative steps – not the preservation of certain of them after they have appeared, might rather be regarded as the essential phenomenon of evolution. If so, "the struggle for existence" and "the survival of the fittest" may express only a sort of truism or metaphor, and have nothing to do with the origination of new types out of antecedent ones. (Morgan, 1935, p. 110)

Mutations were initially understood to be large-scale, but were later taken to include variants that lie on or barely outside the limits of standing variation (e.g., Morgan, 1925, p. 129). This is why I am not concerned here with Gould's third criterion for the creativity of natural selection: that selection acts mainly on small-scale, nearly continuous variations (see also Stoltzfus and Cable, 2014 in this regard). Morgan and de Vries ultimately granted that selection acted on small-scale variations. To be sure, if natural selection were creative by whatever other criteria, then it would be considered *even more creative* for fash-

[6] This is not far from Gould's position that the essence of Darwinism is not natural selection *per se*, but rather the creativity of natural selection, which for Darwin and some Darwinians was bound-up with the idea that variation was ever-present; which in turn went hand-in-hand with the idea that selection in a particular direction slides the range of available variation along with the mean in that direction.

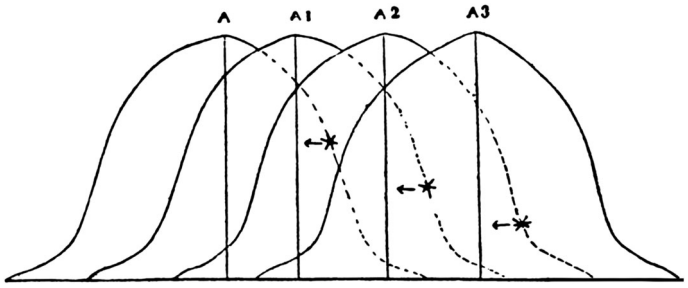

Figure 1. Selection shifts the range along with the mean of variation (See text).

ioning adaptations step-by-step, rather than simply increasing the proportion of nearly-fully-formed-appearing-all-at-once adaptive traits. But this was not the foremost concern of mutationists like de Vries and Morgan who questioned the creativity of natural selection on other grounds.

Their main objection was, again, the assumption of ever-present variation for selection to act upon and the sometimes implicit, sometimes explicit implication that selection itself shifts the range of variation, along with the mean of variation, thus ensuring that there is always further variation available, and selection never has to wait. The implication was, as de Vries put it, "that variation in a given direction can be increased by selection in that [same] direction" (1909–1910 [1901–1903], vol. 1, pp. 88, 119). Figure 1 is Morgan's graphic representation of the problematic premise. As selection shifts the mean of variation to the right, it simultaneously shifts the distribution of variation, thus ensuring that there will continue to be variation in the favored direction for selection to act upon, as well as variation in other directions in case the environment, and the direction of selection, should change. Morgan referred to this as the "sliding scale" doctrine:

> Darwin himself was extraordinarily careful, however, in the statements he made in this connection, and it is rather by implication than by actual reference that one can ascribe this meaning to his views. Some of his contemporaries and many of his followers, however, appear to have accepted this *sliding scale* interpretation as the cardinal doctrine of evolution. (Morgan, 1925, p. 128)

Note: "the cardinal doctrine of evolution."

Morgan was perhaps being generous (from his point of view) in not definitively attributing this position to Darwin, but just to his "followers." We have seen how Darwin came very close to adopting it in response to Jenkin, and in his emphasis on the accumulative power of

natural selection. And we have seen how Wallace and Weismann explicitly defended it. de Vries was as generous as he could be in blaming Jenkin for Darwin having adopted it (1909–1910 [1901–1903], vol. 1, pp. 37–39). And elsewhere Morgan seems to attribute the view to Darwin, also blaming Jenkin (Morgan, 1925, p. 139).

Were it really the case that variation is ever-present by virtue of selection always shifting the range along with the mean of variation, that would certainly make natural selection creative, as de Vries and Morgan conceded hypothetically. "[I]f the survivors produce offspring that vary further in the direction of selection, a creative process appears to have been discovered capable of explaining the evolution of life in all of its ramifications" (Morgan, 1935, p. 130).

But evolution by natural selection does *not* work like this. The quotation from Morgan continues:

> When, however, we attempt to go behind the assumptions in the last statement, we see that one of the basic ideas, namely, that this process of variation would go on indefinitely under the guidance of selection, is open to question. The implication in the theory of natural selection, that by selecting the more extreme individuals of the population, the next generation will be moved further in the same direction, is now known to be wrong. (Morgan, 1935, p. 130)

To back up this point, Morgan and de Vries invoked artificial selection plateaus, as illustrated in Figure 2. While artificial selection on existing variation results in evolution in the desired direction, sooner or later the existing variation is depleted and evolution comes to a halt. Up to this point – prior to the plateau – selection has only increased the frequency of already existing variations. There is no further change until a new, useful mutation appears and initiates an additional round of evolutionary change. de Vries made the same point:

> It is often stated that variation in a given direction can be increased by selection in that direction. Observations, or exact information in support of this statement are not given. There is of course an appearance of change owing to the elimination of the less valuable individuals. As a matter of fact in accurately recorded cases the very reverse is found to be the case; that is to say, that it becomes gradually more difficult to effect any change until finally it becomes impossible. (de Vries, 1909–1910 [1901–1903], vol. 1, p. 119).

The existence of selection plateaus was understood in terms of the accumulation of Mendelian genes at relevant loci, until all the members

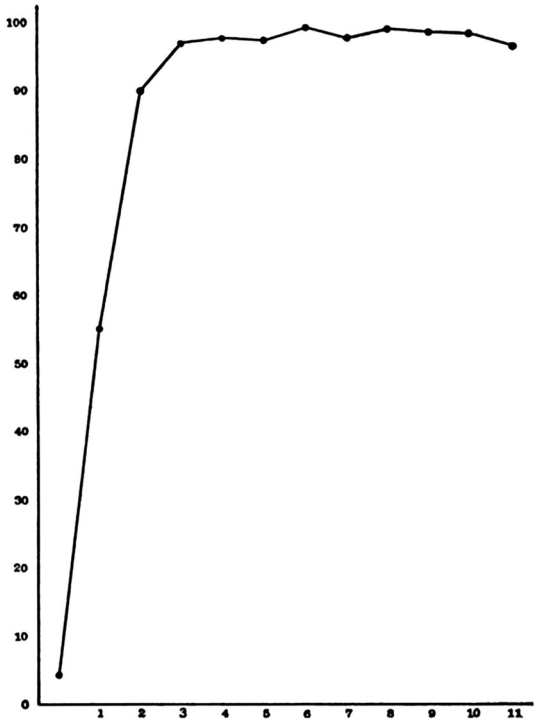

Figure 2. Artificial selection plateau (See text).

of the population in question were homozygous at each of those positions; at which point there would be no more evolution at those loci until mutations occurred there. Moreover, de Vries and Morgan insisted that much of the Darwinians' vaunted, ever-present variation was not inheritable and hence not selectable. Much of that variation was due to differences in environment rather than genetic differences.

To be sure, they argued, the range of selectable variation in any one trait at any one time can be extensive, due to genetic differences at many contributing loci. But again, selection in any one direction will reduce the range of selectable variation until all the members of a population are homozygous at *all* the relevant loci. At which point evolutionary change will come to an end, until new beneficial mutations appear.

William Castle, who considered himself a "Mendelian" – but of the Darwinian rather than the mutationist sort – carried out artificial selection experiments on coat color in rats and was able to obtain by gradual evolutionary change entirely white and entirely black rats from black-"hooded" ancestors (see Figure 3 from Castle, 1914). He initially argued that the trait "hoodedness" was due to differences in a single

Mendelian "factor" (allele) at a single locus, and that selection in the direction of more fully hooded rats (or alternatively, no hood) had actually modified, not just accumulated, the gene in question. This demonstrated the "creativity" of selection to "create" the genetic variation that it subsequently acts upon (e.g., Castle, 1912, pp. 353–354).[7] Mutationist-Mendelian doubters, he argued, had not been patient or determined enough with their own selection experiments, mistakenly assuming that temporary slowdowns indicated a depletion of inheritable variation, when in fact selection was slowly modifying the material that it acted upon. Ultimately, though, Castle conceded his results could be better explained in terms of selection eliminating variation at multiple loci (Allen, 1978, pp. 264–268).

Thus, a central difference between the Darwinians and the mutationists was that according to the former, selection brings about directional change all the while *shifting and preserving* a wide range of selectable variation. Whereas according to the mutationists, directional evolution takes place at the *expense* of selectable variation: natural selection *reduces* the range of variation that it can act upon. And this has consequences with regard to the creativity of mutation relative to natural selection. First, it is mutation that initiates evolutionary change, or re-initiates evolutionary change when it stalls due to there being no further beneficial variation. It cannot be natural selection or a change in the environment that initiates evolutionary change when there is no variation left to select. Moreover, the mutation that starts or restarts the change also directs it – evolution by natural selection takes-off in *that* direction – just as in Darwin's second hypothetical scenario, the one he abandoned in response to Jenkin. The mutation that initiates or re-initiates evolution by natural selection may be in the same direction that evolution by natural selection had been going, but there is no *further* evolution in that direction without that mutational event.

In addition to this argument against the sliding-scale thesis and its bearing on the creativity issue, de Vries and Morgan raised an additional objection. This one was based on an assumption that they considered to have originally been constitutive of Darwinism, but that had seemingly been abandoned by Darwin, or at least by his most ardent followers: namely, the idea that the production of variation is a matter of chance, meaning that, whatever causes a new variation to appear, it

[7] This is somewhat reminiscent of Weismann's attempt to demonstrate a *mechanism* by which selection in a particular direction simultaneously by shifts range of variation and guarantees the occurrence of future variation in that direction, thus clearly exemplifying the "creativity" of natural selection (see earlier in the text).

has nothing to do with whether the variation will be beneficial and subsequently selected. The question as to how variations arise should be kept separate from the question as to whether they will be selected or not. But this did not sit comfortably with the other core Darwinian assumption that variation was ever-present; which implies that selection shifts the range along with the mean of variation, further implying that the direction of variation is not independent of the direction of selection after all. de Vries and Morgan were at pains to school Darwinians on their supposed allegiance to chance variation, and to the two-step view of evolution by natural selection that it involved: *first* chance variation arises, *followed by* non-chance natural selection. The sliding-scale idea muddles the two stages temporally and conceptually by suggesting that new variation appears *coincident* with selection, and its appearance is somehow *due* to natural selection rather than being a matter of chance. Instead, they argued (it may be hard to imagine a Darwinian needing to hear this, nonetheless…), a beneficial variation appears first, by a process that has nothing to do with its being beneficial, followed by its selection, which of course has everything to do with its being beneficial.

> The duality of the evolution process from the point of view of natural selection has not always been sufficiently emphasized. A series of events that can be given a strictly causal interpretation leads to the occurrence of a new individual, which, through other properties inherent in living matter, can reproduce a group of individuals like itself. Another and entirely unconnected series of events in the outer world has produced [a change in the environment]. If the new type happens to come into relation with the new world it may perpetuate itself there. This is adaptation – the fortuitous coming together of the results of two processes that have developed independently of each other…. The central idea of natural selection, as generally understood at the present time, is that the relation is purely fortuitous. (Morgan, 1925, pp. 150–151)

Note: ''The central idea of natural selection,'' which was supposedly not appreciated by many leading Darwinians.

de Vries and Morgan came to propose mutationism as competitor only to a degenerate form of Darwinism, and as a ''firmer foundation'' for Darwinism proper. Mutations took over the role of the chance element in evolution by natural selection, in contrast to the standing variation itself that was somehow to be moved along in the direction of selection.

> The mutation theory may seem to be today its [Darwinism's] only vigorous competitor, yet de Vries, the author of the mutation theory, stated that it was not in opposition to natural selection, but, on the contrary, helped to put natural selection on a firmer foundation. (Morgan, 1935, p. 109; see also Morgan, 1925, p. 111)

We are now in a position to appreciate more fully the most famous critique of the creativity of natural selection – to this day – namely, de Vries' comparison of natural selection to a sieve.[8] There is so much more going on here than is commonly noted. de Vries proposed the comparison in order to emphasize that, like a sieve, selection reduces the range of variation, rather than preserving and shifting it as many Darwinians supposed. And like a sieve, selection requires additional input from time to time when the range of variation has been depleted. This may sound like a trivial point, but it is not; it was a contested point at the time, and would later be strongly contested by contributors to the evolutionary synthesis (Part II).

In addition, the sieve analogy was intended to underscore a point that Darwin had originally insisted upon, but that seemed (to de Vries and Morgan) to have been forgotten or rejected. That is, in the case of selection as in the case of a sieve, the process by which particular variations are made available is both conceptually and temporally distinct from the process by which those variations are either accumulated or eliminated. This is in contrast to the suggestion by many Darwinians that selection itself gives rise to the variation that it sorts. It is worth quoting de Vries at length, starting a little earlier in the passage than is usual, and with some clarifications (in brackets). Speaking of "how far Darwin's adherents have departed from the views actually expressed by him," de Vries continued:

> To DARWIN'S mind the essential point was that the struggle for existence should have to select from material supplied by an indeterminate [i.e., chance] variability. Natural selection is a sieve. It creates nothing, as is so often assumed [assumed, that is, by Darwinians who think that selection shifts the range of variation along with the mean]; it only sifts [i.e., eliminates or preserves variation; it is not responsible for the mutations that go into it]. [And a second point…] It retains only what variability [i.e., the mutation process, which contributes variants from outside the

[8] Surely someone has pointed out previously that sieves were used to sort larger from smaller grains; the former were then sown (rather than consumed). de Vries discusses this in 1909–1910 [1901–1903], vol. 1, pp. 107, 129.

> range of standing variation] puts into the sieve [so that the outcome will be adaptive to be sure but will be further determined by whatever particular mutations happen to arise]. Whence the material comes that is put into it, should be kept separate from the theory of its selection. How the struggle for existence sifts is one question; how that which is sifted arose is another. In both respects, DARWIN'S original view is still the best, but the point at issue has been often obscured by later writers. (de Vries, 1909–1910 [1901–1903], vol. 2, pp. 609–611, 1906, pp. 6–7, 570–574)

Looking Back

Allen writes of Morgan's "endless quest to make certain that no one viewed natural selection as 'creating' any new variations (1978, p. 315)." He also argues that this attitude toward the creativity of natural selection was an important factor in Morgan's lingering "ambivalence" toward, and "misgivings" about Darwinism (*ibid.*, pp. 314–316; see also Allen, 1980, pp. 363, 378–379). I think Allen is exactly right to connect these issues. But I want to take the opportunity here to go further.

First, it is important to explain more clearly why Morgan associated the creativity of natural selection with Darwinism. It helps to begin with Gould's suggestion that the creativity of natural selection, not natural selection *per se*, is the essence of Darwinism. Morgan made a similar point in claiming (full quotation above) that the "essential part of Darwin's theory of natural selection is not survival" but rather the assumption that "variations, everywhere present, furnish the raw materials for evolution." As I explained earlier, this postulate was taken to imply that natural selection in any particular direction shifts the range of variation in that direction, otherwise there would not be variation "everywhere present" for further selection to act upon. Morgan denied that selection could create new variation in this way; which was to deny a major tenet of Darwinism.

Second, if the tight connection between Darwinism and the creativity issue is not clearly explained, and attributed, then contemporary readers may get the impression that Morgan (and de Vries) simply did not understand evolution by natural selection. Or that they were responding to some unnamed (e.g., by Allen) figures who did not understand the subject matter. Or even a straw man. After all, we are taught over and over that evolution by natural selection is a two-step/stage process that begins with mutation and is followed by the selective preservation or

elimination of that mutation. And we are also taught that the question of how and why new variations arise is entirely separate from the question of whether and why those variations are maintained. How then, or in response to what clueless or made-up thinkers could Morgan and de Vries so naively employ this conventional understanding of evolution by natural selection *against* Darwinism? As if Darwinians worthy of the name would confuse the two steps/stages, or the two questions, and presume instead that natural selection brings about the variation that it subsequently acts upon. It is worthwhile making clear that leading Darwinians of the stature of Wallace and Weismann (and more, e.g., Castle) actually held the positions that Morgan and de Vries were at pains to refute.

The idea that Morgan did not understand evolution by natural selection might in some readers's minds be reinforced by Mayr's frequent criticisms of Morgan's (mis)understanding of evolutionary biology. For example, Mayr charged Morgan with "resistance against the acceptance of natural selection" on account of his denial of the creativity of selection and his adoption of the sieve analogy (e.g., Mayr, 1980, pp. 24–25). But Morgan was hardly resistant to natural selection, unless the concept of natural selection is extended to include shifting the range of variation in the direction of usefulness. It was that extension – which Morgan took to be, not the essence of natural selection, but the essence of Darwinism as insisted upon by Darwin's followers – that Morgan resisted. Mayr also attributed Morgan's failure to understand the two-step process of natural selection to his denial of the creativity of selection (e.g., Mayr, 1982, p. 591). But Morgan took himself to be a *defender* of the two-step conception against those Darwinians who seemed to overlook the first stage altogether, and to assume instead that selection, not the appearance of variation, initiates evolutionary change.

That Morgan's critiques of the creativity of natural selection might have been due to more general conceptual misunderstandings of the process might also be reinforced by the criticisms levelled by his own students, especially H.J. Muller and Alfred Sturtevant (Allen, 1978, pp. 308–315, 1980, pp. 378–379). But Morgan knew what he was talking about when he linked Darwinism to the idea that natural selection is responsible for the variation it acts upon. He may have been wrong to deny that selection is in some sense responsible after all (Part II). But he did not misinterpret the targets of his criticism, and it is important to appreciate his views in connection with theirs.

A third and closely related respect in which Allen has well instructed us, but where I would like to go further, has to do with another of Morgan's dissatisfactions with Darwinism: namely, his suspicion that

there was a purposeful element to evolution by natural selection (Allen, 1978, pp. 115–116, 314, 1980, pp. 365–366). This is one of the issues about which Morgan was criticized by Muller and Sturtevant. Allen quotes Sturtevant:

> There *was* one respect in which Muller and I had to "educate" Morgan. He was never fully happy abut natural selection, since it seemed to him to open the door to explanations in terms of purpose. We convinced him that there was nothing teleological or contrary to Mendelism in natural selection – but he remained unhappy with it, and arguments had to be repeated again and again – an experience that I think was good for both Muller and me in that it made us very careful about how we stated the case for selection. (Allen, 1978, p. 314)

Allen treats this separately from Morgan's concerns about the alleged creativity of natural selection. But they go hand-in-hand. The connection has to do with Morgan's insistence on the chance character of mutations, in contrast to what he considered a reversal on the issue by prominent Darwinians.

Morgan admired Darwin for his idea of chance variation, and he was often concerned to explain what Darwin meant by this, or more precisely what, according to Darwin, chance variation was *not* due to: "above all not to purpose either from within or from without" (Morgan, 1925, p. 14). By denying that variations arise purposefully, Morgan meant more specifically that they do not arise because of their usefulness or adaptiveness; they are not directed in this manner:

> Whether definite variations are by chance useful, or whether they are purposeful are the contrasting views of modern speculation. The philosophic zoologist of to-day has made his choice. He has chosen undirected variations as furnishing the materials for natural selection…. [H]e is inclined to question the assumption that adaptive variations arise because of their adaptiveness. (Morgan, 1909, p. 380)

This does indeed sound like Darwin – at least the Darwin of the architect analogy. But for reasons discussed above, Morgan felt that subsequent Darwinians (maybe even Darwin himself) had gone off-course by insisting that selection in a particular direction moves the range and not just the mean of variation further along the axis of usefulness. This *would* have made the process of variation "purposeful" as Morgan used that term. And at the same time it *would* have made

selection creative. Recall: "*[I]f* the survivors produce offspring that vary further in the direction of selection, a creative process appears to have been discovered capable of explaining the evolution of life in all of its ramifications" (Morgan, 1935, p. 130; my emphasis). Denying the antecedent of that conditional was, for Morgan, tantamount to denying the purposefulness of the production of variation. Perhaps Sturtevant (and Muller) did not fully understand what was bothering Morgan in this regard.

Looking Forward

Allen quotes a letter from Mayr: "'Morgan's opinions… impeded the eventual synthesis' of genetic and evolutionary theory" (Allen, 1980, p. 356). I can see why Mayr would have felt that way. And I would suppose that it had a lot, perhaps everything, to do with Morgan's denial of the creativity of natural selection. As I will argue in the second part of this two-part project, the creativity of natural selection was part-and-parcel of the evolutionary synthesis. It was an updated case, but the main points were the same: it is selection, not the appearance of new variation, that initiates evolutionary change, and selection is in an important sense responsible for the variation that it acts upon.

In his discussion of Morgan's views on the creativity of selection, Allen claims that, "By 1932, no Darwinian claimed that selection itself was a creative principle (though a few had made this claim in the early years of the century); that is, it somehow actively created new variations in a particular direction" (Allen, 1980, p. 379). That's not quite right, as we'll see, though it may be the case that Morgan's foils had mostly disappeared by that time, perhaps due to his and de Vries's own efforts in this regard. But it was a short term victory. Architects of the synthesis would press the case for creativity with vigor.

Just one example for now, from Sergei Chetverikov's "On certain aspects of the evolutionary process from the standpoint of modern genetics" ([1926] 1961). The penultimate section begins,

> It is impossible to end an essay on the role of natural selection in the evolutionary process without touching upon one important question, which has seriously preoccupied biologists in recent times and which is not completely clear even to many specialists in genetics. What is the role of selection in the progressive process of evolution? Is it only a passive factor, eliminating, eradicating the less fit genes, and protecting, on the contrary, those which have an

> advantage in the struggle for existence? Or does it create its own material, actively entering into the evolutionary process, directing variability into definite channels? (p. 189)

Chetverikov proceeded to acknowledge the role of Morgan in promoting the first, anti-creative position, and his success in doing so. "Nevertheless," he continued, "a weakness is beginning to show up…" (ibid.). Stay tuned for Part II.

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