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Myth 18: That Darwin's theory would have become more widely accepted immediately had he read Mendel's paper

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> Q: What would have happened if Darwin had read Mendel's work?
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> A: He would have been overjoyed, because it solved the greatest weakness of natural selection: it did not work under the theories of inheritance at the time. The most common theory was "blended inheritance" and natural selection cannot work under it… Mendelian genetics is one of [the] pillars of [the] Modern Synthesis (neo-Darwinism) formulated in the 1940s.
>
> *Quorum.com*, top answer in 2022

> There was no denying Jenkin's inescapable logic: to salvage Darwin's theory of evolution, he needed a congruent theory of heredity…. [For Darwin, reading Mendel's] study might have provided the final critical insight to understand his own theory of evolution. He would have been fascinated by its implications, moved by the tenderness of its labor, and struck by its strange explanatory power. Darwin's incisive intellect would quickly have grasped its implications for the understanding of evolution.
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> Siddhartha Mukherjee, *The Gene: An Intimate History* (2016)[1]

Introduction

Myth 18 is actually two myths wrapped together:

[1] Epigraphs from, respectively, https://www.quora.com/What-would-have-happened-if-Darwin-had-read-Mendels-work (accessed 8 September 2022) and Siddhartha Mukherjee, *The Gene: An Intimate History* (London: Bodley Head, 2016), p. 46.

• The myth that Darwin's theory of natural selection was unworkable and so unconvincing until integrated with Mendel's theory of inheritance.

• The myth that, had Darwin read Mendel's 1866 paper on his experiments with crossbred peas, the needed integration would have taken place around 1870 rather than around 1940.

Let us call these the "Darwin needed Mendel" myth and the "decades wasted" myth, respectively. In what follows I shall consider each in turn, taking them in that order because, for the most part, the idea that Darwin's theory had a Mendel-sized gap in it (the "Darwin needed Mendel" myth) is what has prompted some Darwinians to lament the fact that Darwin never read Mendel, on the view that, had Darwin done so, he would have plugged the gap himself and so sped up acceptance of his theory by decades (the "decades wasted" myth). But the historical record, always full of surprises, shows that in fact a version of the "decades wasted" myth predates the "Darwin needed Mendel" myth. Even more surprisingly, this if-only-Darwin-had-read-Mendel lament came not from a champion of Darwinian natural selection but from an *opponent*, who made his lament not in the wake of the successful integration of natural selection theory and Mendelian genetics—the "Modern Synthesis" of the 1930s and 40s, after which Darwinian theory went fully mainstream—but in the early twentieth century, when there was so much controversy over natural selection that the period was later dubbed the "eclipse of Darwinism."[2]

Our counterfactually minded anti-Darwinian was the most fervent Mendelian who ever lived, the Cambridge biologist William Bateson. "Had Mendel's work come into the hands of Darwin," wrote Bateson in *Mendel's Principles of Heredity: A Defence*, published

[2] The phrases "Modern Synthesis" and "eclipse of Darwinism" both come from Julian Huxley, *Evolution: The Modern Synthesis* (London: Allen & Unwin).

in 1902, just two years after Mendel's paper had become an unexpected talking point in European botany, "it is not too much to say that the history of the development of evolutionary philosophy would have been very different from what we have witnessed." Bateson here emphatically did not mean: if only Darwin had read Mendel, then biologists would have embraced the theory of natural selection more strongly and swiftly. Before 1900, Bateson was best known for arguing that evolutionary theorizing had taken a wrong turn with Darwin's *Origin of Species*, since, in Bateson's view, the evidence showed that new species evolve from existing ones not, as Darwin had thought, by gradual adaptive change driven by natural selection, but by non-adaptive jumps from one stable form to another. For Bateson, reading Mendel's paper would have alerted Darwin to his error. His corrected theory would then have redirected his followers towards Mendel-style experimental hybridizing with all-or-nothing "unit" characters as the best way to understand the discontinuous nature of the origin of species. When Bateson imagined Mendel's paper coming into Darwin's hands, it was to help twentieth-century biologists rid their science of natural selection theory for good.[3]

The "Darwin needed Mendel" myth

It is by no means clear that Darwin needed *any* theory of inheritance, whether Mendel's or anyone else's. Consider that, on Darwin's presentation of his theory, natural selection will take place whenever three conditions are satisfied: first, there is variation among individual organisms; second, there is a Malthusian "struggle for existence" sufficiently intense that only some of those organisms will survive to reproduce; and third, the offspring of the

[3] William Bateson, *Mendel's Principles of Heredity: A Defence* (Cambridge: Cambridge University Press), pp. 37–39, quotation on 39. For Bateson on species, see his *Materials for the Study of Evolution Treated with Especial Regard to Discontinuity in the Origin of Species* (London: Macmillan, 1894). For further discussion of Bateson's counterfactual see Gregory Radick, *Disputed Inheritance: The Battle over Mendel and the Future of Biology* (Chicago: University of Chicago Press, 2023), pp. 293, 295–96.

survivors on the whole inherit the adaptive variations that caused their parents to become survivors. In Darwin's view, the evidence in support of nature's fulfilling these conditions was overwhelming. Indeed, in the first chapter of the *Origin*, in the sole extended discussion of inheritance per se in the book, he wrote that it was only "theoretical writers" who had ever doubted that "like produces like." By contrast, he went on, the two kinds of practical men whose occupations gave them the largest scope to observe parents and offspring up close – namely, breeders and doctors – took the principle utterly for granted. For Darwin's own theoretical purposes, then, he needed only for offspring to inherit their parents' distinctive characteristics; and he took it to be an incontrovertibly well-evidenced fact that, in general, that was what happened.[4]

The theory of natural selection nevertheless came to acquire a reputation for needing a theory of inheritance – indeed, a better theory than Darwin came up with in his ignorance of Mendel's paper – because of a review of the *Origin* that appeared in 1867 in the *North British Review* by the Scottish engineer Fleeming Jenkin. In this review, Jenkin drew attention to what he declared to be a fatal problem for Darwin's theory, in the form of an imperial fantasy. Imagine, wrote Jenkin, that a male colonist ends up on an island and begins reproducing prodigiously with the native women. Imagine further that, in terms of the struggle for existence, the colonist is superior to the natives. According to Jenkin, the children will inherit not the colonist's advantageous variations but, because of the native mothers, a watered-down version of them, so that whatever advantage the variations brought the colonist will, on average, be halved. Jenkin went on to show that, even taking into account the tendency of the colonist-native offspring to survive disproportionately, and so to

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[4] Charles Darwin, *On the Origin of Species by Means of Natural Selection* (London: John Murray, 1859), pp. 12–14, quotations on 12. For further discussion see Gregory Radick, "How Breeders Work Their Magic: Ch. 1 — Variation under Domestication." In *Teaching and Learning Evolution with Darwin: Reading the* Origin *in a Contextual Science Education*, ed. Maria Elice de Brzezinski Prestes. Springer (Cham: In press).

be represented disproportionately among the parents of the next generation, within a short while, the colonist's advantageous variations will be utterly swamped. On Jenkin's calculations, then, it appeared that, far from inheritance preserving the advantageous variations which natural selection then amplified and accumulated, as Darwin had supposed, inheritance blended advantageous variations away into nothing.[5]

For anyone impressed with Jenkin's swamping argument, the theory of natural selection appeared to be a bust, due to Darwin's failure to bolster it with a theory of inheritance that explained (as the Mendelian theory would eventually do) why advantageous variations will not be blended into oblivion. But for anyone who had read—let alone written—the *Origin*, there was an obvious objection. As an empirically well-attested matter of fact, under artificial selection, advantageous variations *do* accumulate, with the result that wild progenitor species become modified. On the farm, in the garden, and in the aviary, human breeders consistently avoid the potential for swamping identified by Jenkin by iteratively mating the best males not with the average females, but with the best ones. For Darwin, in nature, a comparable situation obtains, since the struggle for existence—the natural counterpart to the human breeder—ruthlessly culls all potential mates except for those that vary most fully in the directions favored under the prevailing conditions of life. In nature as under domestication, then, the scenario under which Jenkin-style swamping is a threat rarely if ever actually arises. Accordingly, Darwin regarded Jenkin's critique not as landing a devastating blow to the theory of natural selection but, when it came to variation and inheritance, as providing an occasion to state more clearly what Darwin already believed. Previously Darwin had doubted that what he called "sports"—individuals that, by the accidents of birth, differ dramatically from the rest of their generation—could be anything

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[5] [H.C.F. Jenkin], "The *Origin of Species*," *North British Review* 46 (1867): 277–318, reprinted in David L. Hull, *Darwin and His Critics* (Cambridge, MA: Harvard University Press, 1973), pp. 302–44.

like as evolutionarily consequential as individuals that were un-dramatically superior thanks to inborn variations that made them incrementally faster, taller, smarter etc. Now, thanks to Jenkin's mathematical underscoring of the point, Darwin saw that even the minimal role he had grudgingly assigned to sports in adaptive evolution was unnecessary. In the next, fifth edition of the *Origin*, he wrote sports out of the picture entirely, acknowledging his debt to Jenkin for the intellectual favor.[6]

At the time, Jenkin's critique was regarded as but one of many challenges raised against the theory of natural selection.[7] Notwithstanding such challenges, neither the theory nor the idea of the branching tree of life—which Darwin represented in the *Origin* as following from the theory—went into "eclipse." When Bateson in 1902 expressed his wish that Darwin counterfactually had read Mendel, it was precisely because he was exasperated by the prevalence of Darwinian theorizing around him. A notable irritation for Bateson was the Oxford biologist Walter Frank Raphael Weldon, whose critique of Mendel had provoked Bateson into writing his *Defence*. Weldon's enthusiasm for Darwinian natural selection extended to pioneering empirical studies that sought, via statistical analysis and other means, to catch selection in action in the changing dimensions of crab shells and snail shells. At his death in 1906, Weldon left unfinished a manuscript setting out an alternative to Mendelian theory stressing the extent to which bits of chromosome have variable effects on bodies depending on internal and external contexts. This went against the emphasis in Mendelian theory on dominance as a property that certain character versions have or do not have, categorically (in pea seeds, for example, yellowness and roundness have it and greenness and

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[6] For further discussion of Darwin's response to Jenkin, see, e.g., Susan W. Morris, "Fleeming Jenkin and *The Origin of Species*: A Reassessment," *British Journal for the History of Science* 27 (1994): 313–43; Tim Lewens, "Natural Selection Then and Now," *Biological Reviews* 85 (2010): 829–35.

[7] The best survey of the challenges to the theory of natural selection remains Peter J. Bowler, *The Eclipse of Darwinism: Anti-Darwinian Evolution Theories in the Decades around 1900* (Baltimore: Johns Hopkins, 1983/1992).

wrinkledness do not). Even after Weldon's death, Oxford remained a place where natural selection theory, often wedded to Weldonian emphases, thrived.[8]

So how did Jenkin's review nevertheless come to be remembered as stopping Darwinism in its tracks for decades? The answer lies with a book by the greatest theorist of natural selection in the generation after Weldon's, the English mathematician Ronald Fisher. Fisher's *The Genetical Theory of Natural Selection*, published in 1930, was, along with contemporary work by the English geneticist J. B. S. Haldane and the American geneticist Sewall Wright, what laid the foundations for the Mendelized natural selection of the Modern Synthesis. The book begins with a chapter entitled "The Nature of Inheritance" in which Fisher identified Darwin's commitment to blending inheritance as a weakness built into the theory of natural selection when, with seemingly no other option available, Darwin signed up to the general consensus in his era about how inheritance worked. Fully aware of the problem he thus created for himself in explaining how advantageous variations might be preserved and so accumulated by natural selection, Darwin was forced, on Fisher's reconstruction, into the very unsatisfactory position of supposing that, thanks to environmental changes inducing high levels of variability, advantageous variations are not so much preserved as constantly generated anew. As Fisher wrote to Darwin's son Leonard in 1932, "I do not believe that your father would ever have ascribed the great variability of domesticated races to the effect of their environment on their mutation rates, had he not thought that variations were continually dissipated by blending." In the *Genetical Theory*, Fisher even speculated that had Darwin or anyone else only thought harder about the possibility that inheritance might be non-blending or "particulate," they could have arrived at

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[8] On Weldon and his work and legacies, see Radick, *Disputed Inheritance*. On the Oxford tradition in theoretical and empirical studies of adaptive evolution by natural selection, from the era of Weldon and E. B. Poulton to that of E. B. Ford and beyond, see Michael Ruse, *Monad To Man: The Concept of Progress in Evolutionary Biology* (Cambridge, MA: Harvard University Press, 1996).

Mendel's correct theory of inheritance with no need of the experiments that Mendel did – and so, at a stroke, could have resolved the difficulty that blending inheritance posed for the theory of natural selection.[9]

By the early 1950s, the Fisherian notion that Jenkin had exposed the fatal flaw in the pre-Mendelian theory of natural selection was becoming a commonplace.[10] And so was born the familiar version of our second myth.

The "decades wasted" myth

Although, as mentioned above, the "Darwin needed Mendel" myth seems to imply the "decades wasted" myth, only commentators at a much greater distance from Darwin's writings than the likes of Fisher have judged the latter plausible. In the *Genetical Theory*, Fisher never raised the question of whether Darwin might have jettisoned his ideas on inheritance had he only read Mendel's paper. Thirty years later, the English biologist Julian Huxley did consider it, but only because others by then had done so. He concluded that almost certainly Darwin would have been un-moved, in part because the form of Mendelism that proved amenable to synthesis with Darwinism itself took decades to develop, and in part because Darwin would have regarded Mendel's paper as dealing not with inheritance in general but with a special case. It is worth quoting Huxley at length, beginning with his ringing endorsement of the "Darwin needed Mendel" myth. Note too Huxley's identifying the inheritance of acquired characters as another position that Darwin was forced into supporting to overcome Jenkin's analysis:

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[9] Ronald Fisher, *The Genetical Theory of Natural Selection* (Oxford: Clarendon Press, 1930), ch. 1; letter from Fisher to L. Darwin, 14 October 1932, in *Natural Selection, Heredity, and Eugenics*, ed. J. H.Bennett (Oxford: Clarendon Press, 1983), pp. 154–55, quotation on 155.
[10] Morris, "Fleeming Jenkin," p. 317.

Fleeming Jenkin pointed out in 1867 that, on the current theory of blending inheritance, even favourable new variations would tend to be swamped out of effective existence by crossing, if heritable variation in general was rare and infrequent. It was to provide for sources of more abundant variation that Darwin came to ascribe increasing importance to the evolutionary role of "acquired characters." Only when the actual genetic mechanism had been discovered and its particulate (non-blending) nature had been established, could it be shown – notably by R. A. Fisher – that Lamarckian … theories of evolution were not only unnecessary but inherently incorrect and impossible…. It has been suggested that Darwin would have avoided falling into these pitfalls if only he had paid attention to Mendel's work, which was published in 1865 [sic], in plenty of time for Darwin to amend his views in later editions of the *Origin*. I do not think this is so. It needed nearly twenty years of intensive research on suitable material such as [the fruit fly] *Drosophila* before the findings of genetics could be fruitfully integrated with evolutionary theory. Before that, most geneticists, obsessed by the obvious mutations with large effects which they naturally first studied, were led to anti-selectionist views and to the idea that evolution would normally take place by discontinuous steps [recall Bateson] …. I suspect that if [Darwin] had known of Mendel's results he would have regarded them as interesting but exceptional and relatively unimportant for evolution, as he had already done for other cases of large mutations and sharp segregation. A premature attempt at generalizing Mendelian principles would merely have weakened the central Darwinian principle of gradual slow change.[11]

[11] Julian Huxley, "The Emergence of Darwinism," in *Essays of a Humanist* (London: Pelican, 1969), pp. 13–38, quotation on 30; first published in 1960.

That was in 1960. From then to now, the scholarly consensus has sided with Huxley.[12] It is nevertheless valuable to look in a little more detail at quite why reading Mendel's paper would probably not have prompted any big changes of mind in Darwin. Here are three considerations that stand out to me.

1. Darwin had done experiments like Mendel's, and even, sometimes, got results like Mendel's—but never regarded them as clues to some larger new truth about the nature of inheritance. At its most elementary, Mendel's method was to cross two pure-bred varieties, examine the character of the hybrid offspring, then examine the character of the offspring of the offspring. That method led him to his discovery that, for example, when a yellow-seeded variety of garden pea was crossed with a green-seeded variety, all the offspring plants had yellow seeds, but that, in the next generation, green seeds come back in the famous ratio of 3 yellow seeds to 1 white seed. (For Mendel, "dominant" just meant: visible in the hybrid generation, as distinct from the "recessive" character version.)[13] But in the first chapter of the *Origin*, Darwin reported similar experiments with pigeons—and the results did not much resemble Mendel's. Crossing "some uniformly white fantails" and "some uniformly black barbs" had produced birds that were neither all-white nor all-black but "mottled brown and black." Crossing those together had yielded a bird with the blue colour and black-and-white markings of a wild rock pigeon – something Darwin interpreted as a "reversion" to the wild ancestral form from which, he reckoned, all domesticated pigeons derive. In the early 1860s, he undertook a crossing experiment using two varieties of snapdragon, one with normal flowers (the "common" form), the other with abnormally shaped or "peloric"-form flowers.

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[12] For a recent consensus-affirming paper see Pablo Lorenzano, "What Would Have Happened if Darwin had known Mendel (or Mendel's Work)?", *History and Philosophy of the Life Sciences* 33 (2011): 3–48.

[13] Gregor Mendel, "Experiments on Plant Hybrids" (1866), translation with commentary by Staffan Müller-Wille and Kersten Hall. *BSHS Translations* 2016.

As described in his 1868 book *The Variation of Animals and Plants Under Domestication*, all of the offspring looked like the common-form parent; and when Darwin allowed them to self-fertilize, the 127 seedlings produced grew into 88 common-form snapdragons and 37 peloric snapdragons. So close to the 3-to-1 ratio of dominant to recessive! Yet for Darwin, the pattern was but an instance of "prepotency": when, in the offspring of a cross, one parent's character is visible and the other's is not, though the causal ingredients for the latter can nevertheless be transmitted. The snapdragon pattern was just one of the many possible patterns of inheritance, of no special importance except for illustrating the general truth that manifesting a character and transmitting its causal ingredients are separate things. We should note too that, in an un-Mendelian way, Darwin additionally reported that among the grandchildren snapdragons were two flowers "in an intermediate condition between the peloric and the normal state."[14]

2. Darwin's "provisional hypothesis of pangenesis," which he used to explain inheritance patterns and much else, was not a late arrival in his theorizing, hastily put together in desperation at Jenkin's review; furthermore, in the year Mendel published, Darwin found new evidence for it – and from someone whose own work on crossbred peas, also published in that year, in no way supported Mendel's conclusions. The penultimate chapter of the *Variation* set out what Darwin called his "provisional hypothesis of pangenesis." On this hypothesis, all parts of an adult body constantly shed microscopic buds called "gemmules" which, in sexual organisms, collect in the sperm or pollen and eggs and then, after reproduction, cause the parts that they came from to develop in the offspring (or else to remain latent).[15] It is often remembered as Darwin's worst theory, with the embarrassment for Darwin's admirers made the more acute by the thought that it could have

[14] Darwin, *Origin*, p. 23; Charles Darwin, *The Variation of Animals and Plants Under Domestication*, 2 vols (London: John Murray, 1868), vol. 2, pp. 70–1.
[15] Darwin, *Variation*, vol. 2, ch. 27.

been avoided, had Darwin only followed up the references to Mendel in books on the shelf at Down House…[16] But part of the attraction of pangenesis for Darwin was that, as he saw it, the many and varied patterns of inheritance—including, yes, the inheritance of the effects of the use or disuse of limbs and organs, or so-called "Lamarckian" inheritance, after the French naturalist Jean-Baptiste de Lamarck (see Burkhardt, this volume)—were thereby explained. Better still, they were explained by the same ideas that also explained a remarkably wide range of other patterns to do with living tissue, from healing and regeneration to the curiously independent lives that parts of the body sometimes seemed to lead. Darwin found it hard to believe that an idea that brought explanatory order to so much diverse evidence could be wrong. Indeed, for all that he had been nurturing pangenesis for decades, new evidence still came in. In 1866, Darwin was delighted to read that a breeder of peas, Thomas Laxton, had found that when he transferred pollen to a female pea plant, the paternal influence was visible not just in the offspring but on the maternal plant: yet another of the patterns that Darwin held pangenesis to explain. And that year, Laxton published a paper on his observations about seed color and seed shape in experimental crosses he had done with his garden peas. Unlike Mendel, Laxton found that pretty much anything could happen – a conclusion that Darwin would have been prepared to accept partly from his own impressions of how unruly inheritance could be, and partly from his positive regard for Laxton's abilities. (He was one of the most successful breeders of the Victorian era.)[17]

3. *On reading Mendel's paper, Darwin would have found himself the unnamed target of Mendel's criticisms of the belief – dear to Darwin – that under domestication, plants and animals become far more variable than they are in a natural state: a line of argument not*

[16] See, e.g., Mario Livio, *Brilliant Blunders: From Darwin to Einstein – Colossal Mistakes by Great Scientists that Changed Our Understanding of Life and the Universe* (London: Simon and Schuster, 2013), esp. chs. 2 and 3.
[17] For Darwin and Laxton on pangenesis and peas, see Radick, *Disputed Inheritance*, ch. 1.

calculated to make Darwin embrace Mendel. It has long been known that, although Darwin did not read Mendel, Mendel read Darwin. A close analysis by the biologist-historian Daniel Fairbanks comparing Mendel's annotations in his copy of a German translation of the *Origin* with Mendel's 1866 paper shows that Mendel's language becomes most strikingly Darwinian when, in the conclusion of the paper, he takes up the question of whether cultivated plants should be thought of as so variable as beyond the scope of natural law. Darwin of course, in stating that organisms became more variable when conditions change, and that domestication, involving the imposition of maximally changed conditions, brought on maximal variability, never meant thereby to suggest that cultivated plants were lawless. But that seems to be how Mendel understood him. And since Mendel's entire project in the paper concerns natural law governing the fate of hybrid characters in a certain class of cultivated plants, Mendel responded as if that project's possibility was under threat. The result is the one part of the paper where Mendel is almost sarcastic. It is hard to imagine Darwin reading it and feeling overjoyed.[18]

Conclusions

At the John Innes Centre in Norwich, England, there is a copy of Bateson's *Defence* with annotations from the Austrian breeder Erich von Tschermak, one of the 1900 "re-discoverers" of Mendel's work, and from his older brother Armin. Next to Bateson's speculation about the history-altering consequences of Darwin reading Mendel, one of the Tschermaks scribbled: "Ich glaube nicht"—"I don't think so."[19] As we have seen, subsequent historical scholarship bears out this skepticism. But so what? Does it really

[18] Daniel J. Fairbanks, "Mendel and Darwin: Untangling a Persistent Enigma," *Heredity* 124 (2020): 263–73.
[19] Thanks to Kersten Hall for this information.

matter that old myths about Darwin, Mendel, and the former needing the latter live on? How does the continued circulation of these myths leave us worse off? I want to suggest in closing that it does matter—that their anachronism is not merely false but impoverishing, and in two directions.

When the myths inflect our thinking about Darwin, they encourage us to be incurious about his perspective on his theorizing, not least his much-derided pangenesis hypothesis. That incuriosity in turn deprives us not just of deeper understanding of a thinker that so many of us (including readers of this volume) profess to admire, but of the pleasure that can come from inhabiting an alien point of view and, at least temporarily, finding oneself at home in it. Turn yourself into a half-decent applier and defender of pangenesis, and your relationship with it, and with Darwin, will be forever different—and deeper.

When, in the other direction, the myths inflect our thinking about Mendel, we potentially lose out in even more consequential ways. Nowhere in our culture is the mythic treatment of Mendel as the be-all and end-all on inheritance more pronounced than in education. As many commentators have noted, in the standard genetics curriculum, elementary Mendelian examples typically have a prominence that, from the standpoint of twenty-first-century biology, look downright misleading. Some years ago, I led a project to teach introductory genetics in a more "Weldonian" way, frontloading multifactorial causation and the variability it brings about. What my colleagues and I found was that, where students taking a traditional Mendelian course were on average as determinist about genes at the end of teaching as they were from the start, students on our Weldonian course were on average less determinist.[20] Helping present-day students understand inheritance in an up-to-date way

[20] Annie Jamieson and Gregory Radick, "Genetic Determinism in the Genetics Curriculum: An Exploratory Study of the Effects of Mendelian and Weldonian Emphases," *Science and Education* 26 (2017): 1261–90.

may thus depend in part on liberating ourselves far more completely from the grip of a historical myth about what would have happened had Darwin read Mendel.

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