



# Mendel and Darwin

Andrew Berry<sup>a,1</sup> and Janet Browne<sup>b,1</sup>

Edited by Nils Stenseth, Universitetet i Oslo, Oslo, Norway; received February 1, 2022; accepted April 30, 2022

Evolution by natural selection is an explicitly genetic theory. Darwin recognized that a working theory of inheritance was central to his theory and spent much of his scientific life seeking one. The seeds of his attempt to fill this gap, his “provisional hypothesis” of pangenesis, appear in his notebooks when he was first formulating his evolutionary ideas. Darwin, in short, desperately needed Mendel. In this paper, we set Mendel’s work in the context of experimental biology and animal/plant breeding of the period and review both the well-known story of possible contact between Mendel and Darwin and the actual contact between their ideas after their deaths. Mendel’s contributions to evolutionary biology were fortuitous. Regardless, it is Mendel’s work that completed Darwin’s theory. The modern theory based on the marriage between Mendel’s and Darwin’s ideas as forged most comprehensively by R. A. Fisher is both Darwin’s achievement and Mendel’s.

evolution | Darwin | Mendel

Too often, Gregor Mendel is relegated to the sidelines in accounts of the history of evolutionary thought. The reasons are many. There is the tantalizing “what if” relating to the possibility that Darwin may (perhaps) have had access to Mendel’s paper, now understood to be a myth. There are the efforts of Darwin and others to formulate viable theories of transmission genetics in ignorance of Mendel’s results. Then the rediscovery of Mendel’s work—or at least, an appreciation of its significance—apparently derailed evolutionary biology for the best part of a decade as the biometrician/Mendelian dispute unfolded. We lack detailed knowledge about the man himself. While Darwin and his fellow Victorians left dense paper trails—the Darwin correspondence project currently lists nearly 16,000 letters—Mendel’s life and thoughts were largely undocumented. He wrote a “short summary of his life’s history” in 1850 as part of his application to sit a teacher certification examination. This brief yet florid document, which opens “Praiseworthy Imperial and Royal Examination Committee” and in which Mendel refers to himself in the third person as “the respectfully undersigned,” is the major source of information on his early life (1). Mendel is therefore frequently characterized in popular accounts as an isolated figure, working quietly away in a scientific backwater. In fact, Brno in general, and the monastery at which he worked in particular, were scientific powerhouses, and Mendel’s work was very much part of the scientific mainstream. He was interested in the pressing scientific issues of the day. We know, for example, that he read (and carefully annotated) the second edition of the German translation of *On the Origin of Species* when it appeared in 1863 (2). There is no doubting the centrality today of Mendel’s ideas in evolutionary

biology. The current theory’s foundation, the modern synthesis, depends arguably as much on Mendel as it does on Darwin. The 200th anniversary of Mendel’s birth is thus an appropriate moment for both reevaluating and celebrating his legacy in evolutionary biology.

## Darwin and Mendel: The Not-Quite Connection

**Both Heavily Influenced by Plant and Animal Breeders.** Darwin famously began *On the Origin of Species* (3) with an account of artificial selection and of pigeon breeding in particular. For many years previously, he had assiduously explored crossing and hybridization in a huge number of species. He conducted experiments as intensively as he was able; researched an exceptional range of texts on the subject; corresponded with a variety of practical experts as he tried to nail down the causes of phenomena such as reversion, sterility, and hybrid vigor; and puzzled endlessly over possible mechanisms of inheritance and the causes of variability. To his mind, these phenomena were inextricably linked together, although he did not know exactly how, and coalesced in the processes of reproduction or, as he would have called it, “generation.” Indeed, he has been described as “a lifelong generation theorist” (4). The full extent of his interest is demonstrated on every page of his book on *Variation of Animals and Plants under Domestication*—the massively detailed two-volume work (5) that summarized and extended the research that he originally intended for the big book on species he was writing before being forced by Alfred Russel Wallace’s communication in 1858 to rush out *On the Origin of Species* instead (6). His theory was based on a fundamental analogy between the so-called artificial selection of traits in domestic organisms and the “natural” selection of variations in the wild. However, how did the variations arise in either case? He looked to breeding and all its ramifications for his answers.

Darwin’s generation theory took him into some strange quarters, or at least quarters that were strange to him. Take pigeon breeding, for instance. The production of fancy pigeons and other pedigreed animals was something of a craze in Victorian England, one that crossed class lines,

Author affiliations: <sup>a</sup>Department of Organismic & Evolutionary Biology, Harvard University, Biological Laboratories, Cambridge, MA 02138; and <sup>b</sup>Department of History of Science, Harvard University, Science Center, Cambridge, MA 02138

Author contributions: A.B. and J.B. performed research and wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

Copyright © 2022 the Author(s). Published by PNAS. This article is distributed under Creative Commons Attribution-NonCommercial-NoDerivatives License 4.0 (CC BY-NC-ND).

<sup>1</sup>To whom correspondence may be addressed. Email: berry@oeb.harvard.edu or jbrown@fas.harvard.edu.

Published July 18, 2022.

attracting enthusiasts ranging from miners and weavers to Queen Victoria herself. He started studying and breeding pigeons in 1856 and soon became very learned in the area. He entered into an enlightening correspondence with William Tegetmeier, a leading fancier, who supplied him with living specimens of different breeds (7). These birds were of course intended for experimental purposes, but this did not prevent Darwin from becoming attached to them. Among other things, he sought to recreate a living representative of the common ancestor of all domestic breeds by crossing and recrossing the varieties, and he did ultimately produce something very much like the ancestral rock pigeon. The birds were eventually killed and skeletonized to allow osteological comparison with wild pigeons: did the differences among the birds extend to changes in bone structure? From this work, Darwin felt he had gained a deep practical appreciation of the numerous small spontaneous variations that served as the raw material for selection. The work certainly established his empirical case in the *Origin of Species*. His enthusiasm for pigeons as a case study was so apparent in his manuscript for *Origin of Species* that the prepublication reviewer—who did not at all care for Darwin's secularizing account of the origin of animals and plants—recommended that Darwin write instead a short book on pigeons. "Everybody is interested in pigeons," the reviewer said (ref. 8, p. 75).

Mendel too was a lifelong generation theorist. He started early on the Moravian farm he grew up on. His father worked with the local priest on a project to improve the yield and hardiness of fruit trees through selective breeding and grafting. As many as 3,000 of the resulting trees were distributed among local farms (ref. 9, p. 105). However, it was in 1843 when he arrived at St. Thomas's Augustinian monastery in Brno that Mendel was exposed to the full impact of breeding science. Brno was the Hapsburg Empire's textile center (so much so that it was even referred to as the "Austrian Manchester" [ref. 10, p. 242]), and sheep breeding was central to attempts to improve the product.

Abbot Cyrill Napp (1792 to 1867), the son of a glovemaking, embodies perfectly the region's embrace of technology and innovation. After all, the finances of the monastery were closely tied to wool, the primary agricultural product of the monastery's lands. Napp created an extraordinary, almost university-like, atmosphere at St. Thomas's, encouraging the exploration of the scientific and technical issues of the day. Indeed, the church authorities were deeply suspicious of Napp's secular undertakings in Brno.

Despite showing considerable promise as a teacher at the Technical School in Brno, Mendel failed his teacher qualification examination. Napp's first critical intervention was to ensure that Mendel spend some time at the University of Vienna in order to be ideally prepared to retake the examination. The Napp-gifted 2 y in Vienna, 1851 to 1853, surely hold the key to Mendel's intellectual development. One of his instructors in biology was Franz Unger (1800 to 1870) (ref. 9, p. 109), an early proponent of cell theory. The idea that the cell is a fundamental unit of biological organization seems today to be self-evident, but, for Unger and his contemporaries, it was still controversial. What happened at plant fertilization? Did the pollen tube transport a tiny preformed embryo, or rather, was the formation of

the embryo initiated by the fusion of cells? University records indicate that Mendel most distinguished himself in the physics institute, where he was appointed student demonstrator. Surely Mendel's exposure to statistical and combinatorial thinking was critical when it came to making sense of the patterns that he observed from generation to generation in pea plants. Mendel's work was arguably an early instance of what has become a recurrent feature of biology: insight into hitherto intractable problems using methods and rigor borrowed from the physical sciences.

Whatever the virtues of Mendel's Viennese education, he again failed the high school certification examination in 1856. By then he was back in Brno at the Technical School, and there he stayed, although never formally qualified, until, in 1868, he was promoted to abbot of St. Thomas's.

Prompted by Napp, Mendel undertook his own experiments on plant hybridization. It is still a matter of debate the extent to which he may have been concerned with the role of hybridism in evolutionary change. Schooled in the traditions of plant and animal breeding, he recognized that breeders were invested in identifying and isolating a trait of interest and then, typically through some kind of inbreeding process, ensuring the continuity and maintenance of the trait-enhanced line. These, in the language of the modern geneticist, are pure breeding lines that are fixed for the trait—green peas, or yellow peas, say—in question.

Mendel therefore sought out simple traits that were available in pure breeding lines supplied by breeders. He may have started with mice, planning to investigate the inheritance of coat colors, but the prospect of a colony of copulating rodents in the chaste confines of the monastery was not well received (ref. 11, pp. 92 and 105). Mendel needed an alternative model organism. The English plant breeder, Thomas Knight (1759 to 1838), who had pioneered methods of artificial fertilization in plants, worked on many plant species including peas. In 1799, in fact, Knight had crossed two pea lines and recovered just one form (the phenotype determined by the dominant allele) before obtaining individuals of the recessive phenotype by crossing the hybrid individuals to the recessive parental line (ref. 12, p. 70), i.e., in modern terms, via a back cross. The distinguished scholar of plant hybridization, Joseph Gottlieb Kölreuter, was also a fan of the pea as an experimental organism. As a long-domesticated plant, peas had for centuries attracted breeders interested in unusual traits. For example, one of the characters that Mendel used is white flower color, a trait described as early as the 14th century in Pietro de Crescenzi's agricultural manual. Again, there were longstanding variants available from seed suppliers: Mendel stated in his 1866 paper that he ordered 34 varieties of *Pisum sativum* from several seed suppliers (13). He is known to have purchased seeds later on from the seed merchant Ernst Benary, located in Erfurt, in Germany (ref. 14, p. 17).

Variability from one individual to the next was for Mendel and Darwin and their contemporaries a puzzle. It seemed in some way to be integral to reproduction and heredity, but how? It is hard for us today to recapture that mindset: because we are so familiar with modern genetics, we are able mentally to separate the processes underpinning the production of variation (mutation and recombination) from

transmission itself. Many 19th century naturalists believed that hybridization between species and cross-fertilization between varieties were much the same thing and must somehow generate new or different qualities in offspring. Crossing was, to them, a two-pronged tool, useful both for exploring where new species came from and for looking for profitable new breeds of plant or domestic animal (15).

Leaders in the field included Charles Naudin, who conducted experiments on hybridization, variability, and the acclimatization of plants, at first in the *Museum Nationale d'Histoire Naturelle* in Paris and then in the French town of Antibes. Similarly, the work of master gardeners in the renowned Vilmorin seed company was widely appreciated. Noted philosophical botanists, such as Carl Friedrich von Gaertner, worked on the problem too. Gaertner's *Versuche und Beobachtungen* (1849) (16) defended the stability of species, showing that, contra Linnaeus, they did not, for the most part, produce fertile offspring when crossed. Darwin criticized these views. However, Mendel was impressed: he seems to have prepared his experiments after carefully reading and annotating Gaertner's *Versuche und Beobachtungen*. His annotated copy of the book is now on display in the Mendel Museum at St. Thomas's Abbey, Brno (ref. 17, p. 50).

Probably the single most significant direct influence on Mendel was the prominent Swiss biologist Carl Nägeli, whose work as professor at the University of Munich ranged from microscopical studies of cell division, protoplasm, and cellular anatomy to theories of inheritance. During the 1840s and 1850s, huge advances had been made in the elucidation of the various parts of the cell with early discoveries made by Hugo von Mohl, Matthias Schleiden, Eduard von Benenden, and Theodor Schwann. Nägeli built on these to propose that cells contained their hereditary properties in a distinct part of the protoplasm that he called the idioplasm, which was passed from cell to cell in the process of reproduction. There is still debate about whether he associated this hereditary material with the cell nucleus or even recognized the significance of the nucleus in general. Either way, he ignored Mendel's experimental demonstration of the particulate transmission of inherited traits. It is clear from correspondence from 1866 to 1873 that Nägeli was unimpressed by Mendel's experiments (ref. 11, pp. 190–193). It is not clear what impact this discouragement had on Mendel. Mendel was promoted unexpectedly to abbot in 1868 and rapidly found himself embroiled in legal cases involving the tax status of the monastery. He continued to do some science—meteorology and beekeeping being his two main interests—but his research was largely eclipsed by his administrative work. Nägeli made no mention of Mendel in his *Mechanisch-Physiologische Theorie der Abstammungslehre* (*A Mechanico-Physiological Theory of Organic Evolution*) (18) published in 1884, the year of Mendel's death. Interestingly, Nägeli also corresponded with Darwin, but their letters were exclusively about Nägeli's determined rejection of natural selection.

Darwin and Mendel were products of this culture of experimental breeding: they both capitalized on the efforts of the breeders who came before them.

**A Meeting (for Real or of Minds)?** As previously mentioned, there is speculation about whether or not Darwin had

access to Mendel's results. There is no evidence to support this. Yet the counterfactual is enticing: if Darwin had read (and, importantly, understood) Mendel, would the history of science have been very different? Would the modern synthesis—the modern theory of evolution that is essentially a marriage of Mendel's and Darwin's ideas—have occurred decades earlier than it did? William Bateson, who became Mendel's champion in the English-speaking world, was pondering this scenario as early as 1902: “Had Mendel's work come into the hands of Darwin, it is not too much to say that the history of the development of evolutionary philosophy would have been very different from that which we have witnessed” (ref. 19, p. 39).

While Mendel and Darwin never met, they could have. The story is worth telling not because of the fun engendered by trying to imagine the conversation between them (Mendel's command of English was presumably limited, and Darwin was famously averse to German) but because the possibility that such a conversation could have occurred helps us appreciate more fully the extent to which the vision of him as an isolated backwater country friar is a mischaracterization.

Mendel visited Paris and London. In August 1862, he traveled on a special chartered train with 157 others from Vienna to Paris and London, with the party's main goal being the International Exhibition in London. This was high-end travel, a “pleasure train” (*Vergnügungszug*) designed for the elite (ref. 20, p. 7). A news report details the visit to London, “The Viennese travel group had its headquarters in the London Pavilion, Music Hall and Dining saloons, Tichborne Street, between Regents Street and Haymarket, where breakfast and dinner were served for the whole group. Additional sleeping arrangements were in furnished rooms in the surrounding area. This location was chosen perfectly, right at the heart of metropolitan traffic, on the mainline from the city to the exhibition building” (ref. 20, p. 13). The exhibition was held in the Crystal Palace, the glass and iron structure originally constructed for the first world exhibition in Hyde Park, London, in 1851, which had been moved to Sydenham, south London. The relocated Crystal Palace and Darwin's home, Down House, are not far apart—about 13 km as the crow flies. Did Mendel take the opportunity to visit? There is no evidence that he did. Darwin's correspondence (21) indicates that one of Darwin's children and his wife Emma were sick with scarlet fever. There would have been no visitors to the house. It seems that 13 km is as close to each other as they ever got.

However, what about a paper-mediated meeting of the minds? One scenario suggests that Mendel sent Darwin a copy of his publication, but it remained, its pages uncut, on the shelves of Darwin's library. Like most anecdotes, this is not as simple as it looks. The story gains added piquancy from the suggestion that Darwin might have failed to appreciate its significance. We find the second part of this conjecture eminently plausible. First, Darwin's struggle with scientific German suggests that he might not have done the paper justice even if he did “read” it. Second, the combinatorial logic that Mendel lays out is, as anyone who teaches introductory genetics will affirm, not remotely intuitive. Surely one of the reasons that Mendel's work was overlooked for so long is that it is hard to understand, requiring as it does biologists to

bring an often-unfamiliar quantitative dimension to their thinking. This would have been an especially big ask of Darwin, who was not by any standards a mathematician or even comfortable with mathematical arguments. Writing in 1828 to a high school friend while in university and supposedly cramming for an impending examination, Darwin confessed, "I am idle as idle as can be: one of the causes you have hit on, viz irresolution the other is being made fully aware that my noddle is not capacious enough to retain or comprehend Mathematics" (22).

Some historians have suggested that Mendel sent Darwin a copy in the mail. These claims are impossible to substantiate, although we know that Mendel did distribute 40 copies to European colleagues at his own expense (23). There is no copy of the offprint in the existing Darwin archive (24). Kerner von Marilaun, who had been one of Mendel's teachers at Vienna University, received one that was evidently unread because the pages are uncut. Interestingly, another copy, now in the Institute of Botany in the University of Amsterdam, is the one that Hugo De Vries read in 1900 (ref. 17, p. 70, and ref. 25).

What is easier to substantiate is that in 1881, Darwin did have access to a comprehensive published account of research into hybridity in which Mendel's work was mentioned. This book (26), by Wilhelm Olbers Focke (1881), was a useful compendium of works on hybridization. Darwin lent his copy to George Romanes who was then writing an article on hybridism for the ninth edition of the *Encyclopedia Britannica* (27, 28). Focke remains in Darwin's library, preserved in Cambridge, United Kingdom. Tellingly, this too has never been read because the pages retain the original uncut edges (29). Mendel's work was literally a closed book to Darwin.

If Mendel's work was a closed book to Darwin, the reverse was certainly not true (29). Mendel read Darwin's *Origin of Species* in the second German edition of 1863 and there are suggestions that his later experiments may have been set up to explore Darwin's evolutionary proposals more generally in the manner of Karl F. Gaertner or Charles Naudin, both of whom were cited by Darwin as fine experimentalists in plant hybridization (30). It seems that Mendel read Darwin's *The Variation of Animals and Plants under Domestication* (1868) that was published in German translation that same year (ref. 11, p. 103, and ref. 14, p. 29). His copy of *Variation* is in the abbey library. He mentioned "the spirit of the Darwinian teaching" in his 1870 paper "On Hieracium hybrids obtained through artificial fertilisation" and referenced Darwin three times in letters to Carl von Nägeli, also all in 1870. However, Mendel did not set out to break the constitution of plants to produce "sports" that might represent a new kind of organism or to produce new species through hybridization as might be expected from an exploration of commonly understood Darwinian proposals. Instead, he was interested in the stability, disappearance, and reappearance of traits over several generations. He chose well (and was lucky in those choices), using pure-breeding lines and focusing on simple binary characters like wrinkled/round and green/yellow that could be easily scored and did not intergrade. Apparently, he did not formulate his experimental questions as direct contributions to contemporary debate over the possible roles of sports or hybrids in generating new species.

Another interesting avenue remains to be explored: could Darwin have discovered Mendel's ideas by himself? Given the centrality of transmission genetics to natural selection and Darwin's awareness of the need to provide a robust model of inheritance, the question is whether Darwin could have devised Mendel's ideas without Mendel? This is not as far-fetched as it may sound. After all, as we have seen, Darwin was extremely well versed in the animal/plant breeding literature and—think pigeons—was immersed in parts of that world. Anyone who has conscientiously plowed all the way through *The Variation of Animals and Plants under Domestication* will have a deep respect for Darwin's monumental capacity for documenting the outcomes of breeding experiments. Even Darwin recognized that the book is not a page turner. He wrote in 1867 to his botanical colleague, Joseph Hooker, prior to its publication: "About my book, I will give you a bit of advice, skip the whole of Vol I, except last Chapt. (& that need only be skimmed) & skip largely in 2d. vol., & then you will say it is very good book" (31). Darwin even discussed variation in the garden pea in this book, among his many instances of variation under domestication, and illustrated four pea-pods (ref. 5, vol. 1, p. 328).

Buried in the pages of *Variation*, in fact, lies what might be regarded as Darwin's discovery of Mendel's famous 3:1 ratio (32). In a crossing study of the snapdragon *Antirrhinum*, which he had carried out in his own garden, Darwin produced an F2 generation derived from two pure breeding lines, one for a recessive phenotype, the other for a dominant one, after noting that all flowers had the dominant phenotype in the F1. The F2 numbers for dominant/recessive phenotype were 88:37. It is not exactly 3:1, but any undergraduate genetics student would today see this today as the Mendelian ratio, with a little stochastic overlay. Darwin made nothing of this outcome in *Variation*. Rather, he moved on to proffer his decidedly non-Mendelian theory of inheritance.

Why did Darwin choose not to follow up on this snapdragon result? As Howard (32) has argued, Darwin was focused on a model of variation (and selection) that insisted that the differences among variants were infinitesimal. Ever a keen disciple of Lyell's uniformitarian doctrine, he envisaged gradual evolution in response to selection on continuously varying traits. He famously had a dispute with his own most prominent disciple, T. H. Huxley, on the subject, insisting that "Natura non facit saltum." The phrase appears many times in Darwin's *Origin of Species*. Darwin was in many ways justified in this belief by the variation he saw as a naturalist: traits were continuously distributed, rather than being carved into discrete Mendelian states. People range continuously in height: it is not as though we are all 5', 5'6", or 6' tall; height varies across the spectrum continuously, with intervals being infinitesimal. For Darwin, then, discrete traits were a peculiarity, something of interest to plant breeders, maybe, but of no general relevance to the variation in nature that mattered, the kind on which natural selection operated.

This, then, adds a third reason (beyond the German language and Darwin's amathematical "noddle") for assuming that Darwin would not have appreciated the significance of Mendel's paper even if he had read it from cover to cover: he was wed to an infinitesimal variation model that

supposed that the kind of discrete variation exploited in his experiments by Mendel was uninteresting. To Darwin, the paper would have appeared as a statistical contribution to plant breeding rather than the founding document in transmission genetics.

## Pangeneses

In *The Variation of Animals and Plants under Domestication*, Darwin proposed what he called “pangeneses,” a theory suggesting that the hereditary material was contained in “gemmules” that circulated through the body. Early in his evolutionary thinking, he had recognized that any natural selection-like theory required a component addressing the transmission of traits from one generation to the next. Jonathan Hodge (33) has traced the origin of pangeneses to Darwin’s notebooks in 1841, during the time he was formulating his evolutionary ideas (he produced the first short sketch of these ideas in 1842). Natural selection is indeed, in today’s terms, an explicitly genetic theory: its core is the differential probabilities of genetic variations being passed on. Today, knowledge of how those variations are passed on is woven into the theory. However, Mendel-less, Darwin was content to consign the mechanics of inheritance to a black box in which parental input was somehow converted into offspring output. All that was required for natural selection to work was that the black box generated offspring bearing their parents’ traits—that, in short, variations are inherited. Darwin addressed the inheritance issue in the first two chapters of *Origin* but ultimately rather finessed it, reckoning that the observations of both breeder and naturalist were a sufficient grounding for his theory: “No breeder doubts how strong is the tendency to inheritance: that like produces like is his fundamental belief” (ref. 3, p. 12).

Darwin was, however, criticized for presenting natural selection without a model of transmission genetics. His work on pangeneses shows how he sought to address this criticism. The then-standard understanding of inheritance, that offspring are a blend of their parents, failed to explain some important observations. Some characters did not blend and indeed exhibited an inexplicable facility for reappearing in a second generation after disappearing in the first (cf. the snapdragon experiment referred to above). In essence, these were the occasional monogenic characters with simple dominance relations that Mendel studied. In 1866, Darwin wrote to A. R. Wallace on the subject (34):

I do not think you understand what I mean by the non-blending of certain varieties. It does not refer to fertility; an instance I will explain. I crossed the Painted Lady and Purple sweetpeas [*Lathyrus odoratus*], which are very differently coloured varieties, and got, even out of the same pod, both varieties perfect but not intermediate.

Then there was the problem implicit to blending inheritance: the inevitable loss of variation. In principle, assuming random mating and blending inheritance, a bell curve of variation of a given trait would progressively narrow over the generations, converging ultimately on the mean. The only way to preserve the extremes of the range of variation,

after all, would be through a mating of two individuals with the same extreme phenotype. On average, extreme individuals would mate with individuals closer to the mean, producing, under blending inheritance, offspring half way between the two parents. Blending inheritance and the maintenance of genetic variation in populations were antithetical. This issue was a prominent feature of the 1867 critique of natural selection by Scottish engineer, Fleming Jenkin (1833 to 1885), who pointed out that a beneficial new mutation would be diluted away over a few generations of blending inheritance (ref. 35; for commentary, see ref. 36). Darwin was impressed, writing to Wallace in 1869, “Fleming Jenkin’s (sic) arguments have convinced me” (37), but as noted above, he had started to work on his solution to the problem that Jenkin described decades earlier.

For Darwin, pangeneses was a big departure from his normal style of science. He was a naturalist, an observer, but here he was taking a deep dive into the unseen: the field biologist becomes molecular biologist. He was uncomfortable doing this, saddling his idea with the qualifier “provisional,” when he first launched it as chapter 27 of *Variation* that he titled “The Provisional Hypothesis of Pangeneses.” He had sought reassurance from T. H. Huxley earlier, sending him in 1865 a 30-page manuscript on the subject. Huxley’s response was not sufficiently enthusiastic: he pointed out the similarities of Darwin’s ideas to those of past thinkers wed to the inheritance of acquired characters. However, he nevertheless encouraged Darwin to publish: “Somebody rummaging among your papers half a century hence will find Pangeneses & say ‘See this wonderful anticipation of our modern Theories—and that stupid as, Huxley, prevented his publishing them’” (38).

Darwin never quite decided if his gemmules were capable of blending or not. However, at least they offered the possibility of particulate—nonblending—inheritance. Particles—nonblending ones—would not inevitably converge on the mean of a distribution but could retain their own discrete identities. Darwin suggested that some gemmules could remain latent for several generations (explaining the reappearance of characters that had apparently disappeared in intervening generations), while others could blend, and yet others could possibly pick up the effects of the external environment (allowing for the inheritance of acquired characters). In short, Darwin hoped that his provisional hypothesis would prove to be a general-purpose solution to many biological conundrums he had encountered in the breeding literature.

The reception was mixed. It is nicely typified by A. R. Wallace. He was initially extremely enthusiastic (ref. 39, vol. 1, p. 422):

I am reading Darwin’s book (“Animals and Plants under Domestication”), and have read the “Pangeneses” chapter first, for I could not wait. The hypothesis is *sublime* in its simplicity and the wonderful manner in which it explains the most mysterious of the phenomena of life. To me it is *satisfying* in the extreme. I feel I can never give it up, unless it be *positively* disproved, which is impossible, or replaced by one which better explains the facts, which is highly improbable... I consider it the most wonderful thing he has given us, but it will not be generally appreciated.

However, the initial enthusiasm did not last. In 1905 (ref. 39, vol. 2, p. 21), looking back, Wallace provided a post mortem on Darwin's pet theory:

I never imagined that it could be directly disproved, but Mr. F. Galton's experiments of transfusing a large quantity of the blood of rabbits into other individuals of quite different breeds, and afterwards finding that the progeny was not in the slightest degree altered, did seem to me to be very nearly a disproof, although Darwin did not accept it as such. But when, at a much later period, Dr. Weismann showed that there is actually no valid evidence for the transmission of such characters, and when he further set forth a mass of evidence in support of his theory of the continuity of the germ-plasm, the "better theory" was found, and I finally gave up pangenesis as untenable.

The experiments by Francis Galton (1822 to 1911) that Wallace refers to involved transfusing blood between differently colored rabbits to see if the transfused blood containing, supposedly, color-specifying gemmules affected the color of the offspring produced by the transfusion recipients. There was no effect. The recipient rabbits produced offspring completely lacking even a hint of the donor rabbits' color. A period of family awkwardness ensued—Darwin and Galton were cousins—with Darwin publishing a response to Galton in *Nature* (40) insisting that he had never specified that gemmules would be blood-borne as they traveled from every part of the body to the gonads: "I have not said one word about the blood, or about any fluid proper to any circulating system. It is, indeed, obvious that the presence of gemmules in the blood can form no necessary part of my hypothesis; for I refer in illustration of it to the lowest animals, such as the Protozoa, which do not possess blood or any vessels; and I refer to plants in which the fluid, when present in the vessels, cannot be considered as true blood."

## Heredity

Until the later 19th century, questions about heredity usually ran along lines separate from the problem of the origin of species. In the 1880s, for example, Galton, whose primary focus was heredity, proposed that offspring inherited equal portions of their heritable characteristics from each parent, who in turn had inherited equal portions from their parents, and so on back through the ancestral line. In more statistical terms, this meant that parents contributed one-half of the total heritage of the offspring; grandparents, one-quarter; and so on. This so-called law of ancestral heredity explained traits that ran in families as well as the appearance of only some of the parental qualities in successive generations. It proved a popular, commonsensical scheme and one, furthermore, readily amenable to statistical analysis. In the last decade of the century, evolutionary biologists W. F. R. Weldon (1860 to 1906) and Karl Pearson (1857 to 1936) merged these ideas with their own meticulous observations on variation and evolutionary change. They followed Darwin's precepts, and more directly walked in Galton's footsteps, in developing the field of biometry, in which they measured small, almost continuous changes in

organisms, deeming these to be the material on which natural selection went to work.

Other leading biologists were at the same time exploring other ideas about inheritance that depended on the transmission of discrete material from parent to offspring. In 1883, August Weismann (1834 to 1914) famously proposed that the heritable material ("germ-plasm") existed in what he called "germ-cells" that were entirely separate from ordinary somatic cells and transmitted independently and unchanged from generation to generation. He located these germ cells in the reproductive parts of the body, the gonads of multicellular organisms. Weismann rejected Darwin's suggestion of pangenesis, but was nevertheless an advocate of Darwinian evolution by natural selection. By the end of the 19th century his theory of germ-plasm had become the most widely accepted way to understand heredity. In Weismann's opinion the largely random process of mutation in the germ cells in the production of gametes supplied the only source of transmissible change for natural selection to work on.

The Dutch botanist Hugo De Vries (1848 to 1935) was prominent in bringing about this latter shift in perspective, emphasizing the importance of sports or macromutations in generating new species. His embrace of Darwinism led him to modify Darwin's theory of pangenesis. He suggested that the inheritance of traits in organisms was specified by inherited particles that he called "pangenes," a term that 20 y later was shortened to "genes" by Wilhelm Johannsen. Yet he was ambivalent about the power of natural selection to do all that was promised by Darwin and Wallace. In 1886 he discovered new forms of evening primrose (*Oenothera lamarckiana*) growing wild in an abandoned potato field near his research station in the Netherlands. Taking seeds from these spontaneous sports, he found that they produced many new varieties in his experimental gardens, some of them so different from each other and their parent as to appear to be distinct species. He defined these as mutations. In his two-volume 1901 to 1903 publication *Die Mutationstheorie* (41), De Vries proposed that new species might appear more frequently from such large-scale changes than from gradualistic Darwinian processes.

This mutation theory did not stand the test of time. *Oenothera*, it turns out, is thoroughly atypical: unusual features of its chromosomal organization mean that it is particularly prone to meiotic disruptions. Many of the "new species" prized by De Vries were polyploids—individuals with extra sets of chromosomes. Not surprisingly, De Vries's project was undone by its lack of generality: other organisms did not produce *Oenothera*-type macromutations. By 1915, the mutation theory had begun to lose its grip on the biological community, and, by the time of De Vries's death in 1935, it was almost completely abandoned (42). Yet, during the first decade of the 20th century it achieved an enormous popularity because it seemed to offer something that many sought: a Mendelian approach to understanding the evolutionary process.

## Rediscovery

De Vries began a systematic program of plant breeding in 1892 to support his theory of pangenes, in which he hybridized varieties of several plant species. Unaware of

Mendel's work, he found that in peas the inheritance of characters occurred in a 3:1 ratio in the second generation. When it came time to publish his work some years later, he became aware of Mendel's paper of 1866 and altered his terminology to match. He seems to have thought of Mendel's work merely as an earlier empirical instance of what he was doing and that it confirmed his results. When he published the results of his own experiments in the French journal *Comptes Rendus de l'Académie des Sciences* in 1900, De Vries neglected to mention Mendel's work (43); only after criticism by Carl Correns did he concede Mendel's priority—in a German translation of the same article published a few weeks later.

This moment can be formulated not just in terms of rediscovery but also as a case of disputed priority. Correns claimed to have discovered the 3:1 ratio in 1899 when he was doing crossing experiments in peas and maize. In his article, Correns thanked De Vries for sending him the *Comptes Rendus* article and stated that he achieved the same result. He went on to say that Mendel preceded them both (44). He evidently came across Mendel from reading Focke (26), the handy list of all 19th century hybridizers that had been available to Darwin. Correns's article in the *Deutschen Botanischen Gesellschaft* was therefore explicitly about bringing Mendel back into circulation. Weirdly, then, the fabled rediscovery was initially fueled by two biologists' desire to one up each other: Mendel was just a weapon in the precedence war (45).

At much the same time, Erich von Tschermak-Seysenegg (known as Tschermak, 1871 to 1962) at the Academy of Agriculture in Vienna also became aware of Mendel's work. Tschermak was an agronomist, and his hybridization experiments aimed at improving crops such as wheat, barley, and oats. Coincidentally, his maternal grandfather was Eduard Fenzl, who had been one of Mendel's botany professors during his student days in Vienna. In January 1900, Tschermak wrote his PhD thesis on the inheritance of seed colors and shapes in pea hybrids (his "Habilitationsschrift"). Apparently, he saw a reference to Mendel's work and had the 1866 paper in *Verhandlungen des Naturforschenden Vereines* sent to him from the library of the University of Vienna. He found that Mendel's work with the garden pea duplicated and, in some ways, superseded his own. His article (46), published in June 1900, was written after he had read both De Vries and Correns (ref. 11, pp. 303–310). This calls into question Tschermak's membership of the rediscovery club. Moreover, Tschermak's place in the club has also been challenged on the grounds that he misunderstood the fundamentals of Mendel's arguments and interpreted Mendelian phenomena within a pre-Mendelian concept of heredity (ref. 42, p. 114).

Since the 1950s, questions have regularly arisen concerning both the chronology and the specific contributions of each of the three rediscoverers. Not only the independence but also the parallelism needs to be analyzed in the context of the individual research programs of all three. Also, perhaps the three-way focus needs to be reevaluated. Simunek et al. (47), for example, point out that Tschermak's contributions were heavily influenced by his older brother, Armin von Tschermak-Seysenegg (1870 to 1952). These questions are important. We need to look

carefully at the key overlapping influences operating in each case to understand what social, technical, and political factors conspired to bring Mendel so dramatically into the limelight.

## The First Mendelians

The rediscovery ushered Mendel into a contested area of biology. There was an ongoing debate about the nature of variation—was it a seamless continuum of minor (even infinitesimal) differences, as Darwin had proposed, or did it occur predominantly as sports of nature? How did it arise, and how was it transmitted? Was it particulate? If yes, the suggestion was that the discrete particles could be freely mixed or recombined (not blended).

Mendel's work was taken up by a group of biologists vigorously engaged in defending mutation theory, among them the Cambridge naturalist William Bateson (1861 to 1926), who believed that mutation was the most likely source of evolutionary innovation. Bateson's first book *Materials for the Study of Variation*, published in 1894 (48), was written directly in opposition to the work of the evolutionists gathered around Pearson and Weldon in London. This latter group, who self-identified as "biometricians," regarded themselves as the true apostles of Darwinism by exploring small, continuous variations. Pearson measured traits in animal populations and showed that they generally graphed as a smooth or continuous distribution. For 10 y or more, this intense debate—that began some years before Mendel's paper resurfaced—juxtaposed individuals who, to a man, sincerely believed in evolution yet opposed each other over the question of whether it proceeds by jumps or gradually, via continuous variation.

Mendel's rediscovered work accordingly stumbled into an ongoing controversy to which it seemed to speak directly. There is a story that, in May 1900, Bateson was on the train from Cambridge to London to give a lecture at the Royal Horticultural Society when he read Mendel's work. Recognizing Mendel's significance as support for his own saltationist point of view, Bateson immediately modified his speech to incorporate the new vision. Attractive as it is, this story is apocryphal (49). Regardless, Bateson rapidly became the most prominent proponent of Mendelian inheritance and soon published a translation of Mendel's paper into English (50) and *Mendel's Principles of Heredity: A Defence* (19). Mendel was, for Bateson, a useful means of self-promotion as well: Bateson could style himself the noble champion of the neglected underdog. He suggested using the word "genetics" (from the Greek "to give birth") to describe the science of variation and inheritance and first used the term at the Third International Conference on Plant Hybridization in London in 1906. At Cambridge University he led the first department of genetics in the country. Between 1900 and 1910 he directed a program of research at Cambridge into plant genetics mostly undertaken by young women trained at Newnham College, the first college for women at the university (51).

In effect, Bateson harnessed Mendel to promote his own world view and what he regarded as a new dawn in the study of variation. According to Arthur Koestler, he even named his son Gregory after him (ref. 52, p. 54).

Bateson and others cemented their self-perceived status as leaders of the new science in a wave of celebrations marking the revolution in biology. In 1909, in Cambridge, United Kingdom, Bateson was the leading figure in commemorating the 50th anniversary of the publication of Darwin's *Origin of Species*: Darwin's sons attended, as did Hugo De Vries. Then, in 1910, Bateson delivered a speech at the international gathering in Brno to memorialize Mendel and erect a statue outside the abbey. A small Museum Mendelianum was set up in the abbey in 1922.

Darwin's death in 1882 deprives us of the opportunity to learn what he would have made of these developments. However, we can gauge his likely response from that of A. R. Wallace, who lived until 1913. Darwin and Wallace disagreed on plenty of topics—most notably whether or not natural selection was sufficient to account for the evolution of our own species—but Wallace was nevertheless a keen defender of what he insisted modestly was Darwinian orthodoxy. We can observe two phases in Wallace's response. First, prerediscovery, came the macromutational perspective of Bateson, as laid out in Bateson's 1894 book, *Materials for the Study of Variation Treated with Especial Regard to Discontinuity in the Origin of Species* (48). In his review, Wallace pointed out that Darwin had already dealt with the issue (ref. 53, p. 216): "Darwin, while always believing that individual differences played the most important part in the origin of species, did not altogether exclude sports or discontinuous variations, but he soon became convinced that these latter were quite unimportant, and that they rarely, if ever, served to originate new species."

Wallace then supplied a number of objections to Bateson's belief in the centrality of sports in the generation of evolutionary novelty, noting that despite the catalog of mutant forms that Bateson presented, the key consideration is that they tend not to survive in the wild, leading us to "conclude that all these irregularities and monstrosities are in a high degree disadvantageous" (ref. 53, p. 221).

What of Mendelism? Again, Wallace had a response (ref. 54, p. 137):

The curious phenomena that present themselves when these [mutants] are crossed with allied forms either domesticated or natural, though they may be of considerable interest as furnishing materials for the study of the theory of heredity, have absolutely nothing whatever to do with the origin or modification of species.

Wallace here clearly articulated the key disconnect: that the sciences of heredity and of evolution are in some way independent of each other. Wallace was pigeonholing the theory of heredity as some kind of special case involving the transmission of discrete characters; for him, it was distinct from the kind of inheritance that generates bell curves of individuals whose differences are infinitesimal. Wallace, like many of Darwin's heirs, failed to recognize that Mendelian transmission is not a special case; rather, the special cases are those simple monogenic polymorphisms that permit the process to be observed directly.

Although there were plenty of suggestions during the first part of the 20th century that inheritance-writ-large and Mendelism were in fact the same thing, R. A. Fisher

(1890 to 1962) deserves the credit for making the connection (55). The vaunted bell curve and Mendel's wrinkled/round peas were in fact produced by the same processes: the bell curve, with its infinitesimal individual-to-individual gradations, was born of multiple Mendelian factors (genes) combining to affect a trait, along with input from the environment, which smears genotypic categories one into another.

## Eugenics

The elephant in the room was the question of human heredity. The possibility of directing the future evolution of human beings through the application of eugenics had been discussed widely since 1883, when Francis Galton first articulated the term. With the arrival of Mendel's insights, a new rigorous vision of eugenics beckoned: human traits, including inheritable medical conditions, could perhaps be understood in terms of the particulate inheritance of dominant and recessive Mendelian factors. Galton, whose original 1865 work had focused on the inheritance of hereditary genius in families, now had a new paradigm in which to continue his exploration (56). The project soon took on a life of its own. The fusion of Mendelian transmission genetics with eugenical ideas about the improvement or eradication of traits in humans was one of the most conspicuous aspects of biology in the first several decades of the 20th century. Eugenics was coconstructed, one might say, with the rise in biological determinism and was responsible for the troubling and ultimately disastrous trends in the application of biology to social policy (57).

By the 1920s, eugenics was a well-established field of inquiry in Europe and North America and would soon have a truly global reach (58). That identifiable traits like eye and hair color, or medical conditions such as albinism, apparently followed Mendelian patterns of inheritance bestowed credibility on the burgeoning social-cum-scientific movement. In the hands of early activists such as Charles Davenport, pedigree analysis of the transmission of Mendelian factors was trumpeted as the way to understand and control human biology. In 1904, Davenport became director of Cold Spring Harbor Laboratory, NY, where he founded the Eugenics Record Office in 1910. There, he and his team generated pedigree charts showing the transmission of scores of what they believed to be inheritable traits like alcoholism, pellagra (later shown to be due to a vitamin deficiency), criminality, feeble-mindedness, bad temper, intelligence, and manic depression. The premise was simple: having identified the patterns of inheritance, society should prevent the "unfit" from passing on their flawed genetic heritage to the next generation. The extent to which the eugenic pedigree-builders overlooked the obvious impacts of rearing environments is remarkable. Davenport's colleague Harry H. Laughlin analyzed the inheritance of boat-building skills in Rhode Island's Herreshoff family. It did not occur to Laughlin and Davenport that being raised by a boat-builder might influence an individual's decision to join that very trade. Laughlin also produced a chart showing the intellectual abilities of members of the Darwin-Wedgwood-Galton clan for display at the Third International Congress of Eugenics in 1932 at the American Museum of Natural History, NY. Galton, who was immensely proud of his connection to Darwin, would have loved it.



It was not just the Mendelians. Leading biometricians such as Pearson were closely connected to socialist eugenic groups in the United Kingdom. In fact, Pearson's views on statistics, eugenics, race, empire, and evolution were irrevocably intertwined. Eugenics provided him with a language to express his racist and political views. Galton had in fact given Pearson the foundations of his statistical method, his commitment to evolution, and his belief in eugenic advance. In a way he was Galton's intellectual heir.

However, when Galton died in 1911, he had no literal heir. Ironically, the father of eugenics had failed to contribute genetically to the human future. Who was the beneficiary? He left the balance of his considerable fortune to University College London, to finance a university eugenics department. Pearson was named the first Galton Professor in National Eugenics, a position that exists today as the Galton Chair of Genetics. Ronald Fisher was Pearson's successor both as the Galton Chair of Eugenics at University College London and as editor of the *Annals of Eugenics*. In 2022, University College London removed Galton and Pearson's names from three of its buildings.

## Conclusion

History tells us that great ideas are often not recognized or accepted in their own time. Mendel's findings are a classic example of this, in the sense that his work is said to have been "forgotten" or "neglected" and then "rediscovered" independently by three biologists. Mendel's modern fame is due to figures who were initially unaware of his work but then saw how it could be appropriated and turned to personal advantage in a post-Darwinian debate about the

mechanism of evolutionary change. To be a Mendelian in the early years of the 20th century was to promote saltation and to downplay or even ignore the role of selection in favor of mutation and evolution by jumps. To others, such as the biometricians, Mendel's findings were meaningless in a world where natural selection acted on minute distinctions. This surprisingly bitter impasse between saltationists and gradualists was only resolved with Fisher's 1918 mathematical formalization (55) of the observation that a continuous distribution can readily be derived from underlying discontinuous variation at multiple contributing loci coupled with environmental variation.

It is impossible to overstate the significance of Fisher's insight. It set the stage for the emergence of theoretical population and quantitative genetics, which in turn reestablished natural selection as the main driver of evolutionary processes, very much in the way that Darwin had envisaged. Building on the simple logic of Mendel and its application to populations, population genetics provided an understanding of the engine that drives the evolutionary process. Courtesy of Fisher's bridging insight, the modern theory of evolution truly is a marriage of Darwin's ideas and Mendel's. Mendel himself was perhaps an early evolutionist (29), but unbeknownst to him, his role was much more central than that: he provided the crucial insight that subsequently transformed Darwin's ideas from uncomfortably incomplete into a comprehensive theory of evolution by natural selection. Friar Mendel stands right there, front and center, beside Darwin in the pantheon of key contributors to evolutionary thought.

**Data Availability.** There are no data underlying this work.

1. H. Iltis, *Gregor Johann Mendel, Leben, Werk und Wirkung* (Julius Springer, 1924).
2. D. J. Fairbanks, S. Abbott, Darwin's influence on Mendel: Evidence from a new translation of Mendel's paper. *Genetics* **204**, 401–405 (2016).
3. C. R. Darwin, *On the Origin of Species* (John Murray) 1859).
4. M. J. S. Hodge, "Darwin as a lifelong generation theorist" in *The Darwinian Heritage*, D. Kohn, Ed. (Princeton University Press, 1988), pp. 207–244.
5. C. R. Darwin, *The Variation of Animals and Plants under Domestication* (John Murray, 1868).
6. A. Berry, J. Browne, The other beetle-hunter. *Nature* **453**, 1188–1190 (2008).
7. J. A. Secord, Nature's fancy: Charles Darwin and the breeding of pigeons. *Isis* **72**, 163–186 (1981).
8. J. Browne, *The Power of Place* (A Biography of Charles Darwin, Princeton University Press, 2002), vol. 2.
9. J. Endersby, *A Guinea Pig's History of Biology* (Harvard University Press, 2007).
10. R. J. Wood, V. Orel, Scientific breeding in Central Europe during the early nineteenth century: Background to Mendel's later work. *J. Hist. Biol.* **38**, 239–272 (2005).
11. H. Iltis, *Life of Mendel* (Allen and Unwin, 1932).
12. C. Zirkle, Gregor Mendel & his precursors. *Isis* **42**, 97–104 (1951).
13. G. Mendel, "Versuche über Pflanzenhybriden" in *Verhandlungen des naturforschenden Vereines in Brünn*, Bd. IV für das Jahr 1865, Abhandlungen, 3–47 (1866).
14. C. Albano, M. Wallace, *The Genius of Genetics; A Celebration of Gregor Mendel through Art and Science* (Vereinigung zur Förderung der Genomforschung, 2002).
15. H. F. Roberts, *Plant Hybridization Before Mendel* (Princeton University Press, 1929).
16. K. F. Gaertner, *Versuche und Beobachtungen über die Bastardzeugung im Pflanzenreich* (K.F. Hering, 1849).
17. S. Mawer, *Gregor Mendel: Planting the Seeds of Genetics* (Abrams, 2006).
18. C. Nägeli, *Mechanisch-Physiologische Theorie der Abstammungslehre* (R. Oldenbourg, 1884).
19. W. Bateson, *Mendel's Principles of Heredity: A Defence* (Cambridge University Press, 1902).
20. P. Van Dijk, N. Ellis, Mendel's journey to Paris and London: Context and significance for the origin of genetics. *Folia Mendeliana* **56**, 5–47 (2021).
21. Darwin Correspondence Project LETT-3724. <https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-3724.xml>. Accessed 24 January 2022.
22. Darwin Correspondence Project LETT-45A. <https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-45A.xml>. Accessed 24 January 2022.
23. R. Olby, P. J. Gautry, Eleven references to Mendel before 1900. *Ann. Sci.* **24**, 7–20 (1968).
24. M. Di Gregorio, N. W. Gill, *Charles Darwin's Marginalia* (Garland, 1990).
25. E. Posner, J. Skutil, The great neglect: The fate of Mendel's classic paper between 1865 and 1900. *Med. Hist.* **12**, 122–136 (1968).
26. W. O. Focke, *Die Pflanzen-Mischung* (Borntraeger, 1881).
27. G. Romanes, Hybridism. *Encyclopedia Britannica* **12**, 422–426 (1881).
28. Darwin Correspondence Project LETT-12814. <https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-12814.xml>. Accessed 24 January 2022.
29. D. J. Fairbanks, Mendel and Darwin: Untangling a persistent enigma. *Heredity* **124**, 263–273 (2020).
30. R. A. Fisher, *Experiments in Plant Hybridization by Gregor Mendel* (Oliver & Boyd, 1965).
31. Darwin Correspondence Project LETT-5680. <https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-5680.xml>. Accessed 24 January 2022.
32. J. C. Howard, Why didn't Darwin discover Mendel's laws? *J. Biol.* **8**, 15 (2009).
33. J. Hodge, The Darwin of pangenesis. *C. R. Biol.* **333**, 129–133 (2010).
34. Darwin Correspondence Project LETT-4989. <https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-4989.xml>. Accessed 24 January 2022.
35. F. Jenkin, Review of 'The origin of species'. *N. Br. Rev.* **46**, 277–318 (1867).
36. M. Bulmer, Did Jenkin's swamping argument invalidate Darwin's theory of natural selection? *Br. J. Hist. Sci.* **37**, 281–297 (2004).
37. Darwin Correspondence Project LETT-6567. <https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-6567.xml>. Accessed 24 January 2022.
38. Darwin Correspondence Project LETT-4875. <https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-4875.xml>. Accessed 24 January 2022.
39. A. R. Wallace, *My Life: A Record of Events and Opinions* (Chapman and Hall, 1905).

40. C. R. Darwin, Pangenesis. *Nature* **3**, 502–503 (1871).
41. H. De Vries, *Die Mutationstheorie. Versuche und Beobachtungen über die Entstehung von Arten im Pflanzenreich*. (Veit & Co., 1901–1903).
42. P. J. Bowler, *The Mendelian Revolution: The Emergence of Hereditarian Concepts in Modern Science and Society* (Johns Hopkins University Press, 1989).
43. H. De Vries, Sur la loi de disjonction des hybrides. *C. R. Acad. Sci.*, **130**, 845–847 (1900).
44. C. Correns, Mendel's regel über das Verhalten der Nachkommenschaft der Rassenbastarde. *Ber. Dtsch. Bot. Ges.* **18**, 158–168 (1900).
45. J. Sapp, "The nine lives of Gregor Mendel" in *Experimental Inquiries*, H. E. Le Grand, Ed. (Kluwer Academic Publishers, 1990), pp. 137–166.
46. E. Von Tschermak, Ueber die künstliche Kreuzung von *Pisum sativum*. *Ber. Dtsch. Bot. Ges.* **18**, 232–239 (1900).
47. M. V. Simunek, M. Mielewczik, G. S. Levit, U. Hossfeld, Armin von Tschermak-Seysenegg (1870–1952): Physiologist and co-'rediscoverer' of Mendel's laws. *Theory Biosci.* **136**, 59–67 (2017).
48. W. Bateson, *Materials for the Study of Variation Treated with Especial Regard to Discontinuity in the Origin of Species* (Macmillan, 1894).
49. R. Olby, William Bateson's introduction of Mendelism to England: A reassessment. *Br. J. Hist. Sci.* **20**, 399–420 (1987).
50. G. Mendel, Experiments in plant hybridization. Translation with an introductory note by W. Bateson. *J. R. Hort. Soc.* **26**, 1–32 (1901).
51. M. L. Richmond, Women in the early history of genetics. William Bateson and the Newnham College Mendelians, 1900–1910. *Isis* **92**, 55–90 (2001).
52. A. Koestler, *The Case of the Midwife Toad* (Hutchinson, 1971).
53. A. R. Wallace, The method of organic evolution. *Fortnightly Rev.* **57**, 211–224 (1895).
54. A. R. Wallace, The present position of Darwinism. *Contemp. Rev.* **94**, 129–141 (1908).
55. R. A. Fisher, The correlation between relatives on the supposition of Mendelian inheritance. *Trans. R. Soc. Edinb.* **52**, 399–433 (1918).
56. F. Galton, Hereditary talent and character. *Macmillans Mag.* **12**, 157–166, 318–327 (1865).
57. D. J. Kevles, *In the Name of Eugenics* (Harvard University Press, 1988).
58. A. Bashford, P. Levine, Eds., *The Oxford Handbook of the History of Eugenics* (Oxford University Press, 2010).