

From a draft. May differ from the published version, which appeared in *Filosofia e História da Biologia* 10, no. 1 (2015): 99–123, available from <http://www.abfhib.org/FHB/FHB-10-1/FHB-10-1-07-Sander-Gliboff.pdf>.

The Mendelian and Non-Mendelian Origins of Genetics

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Abstract. The story of Gregor Mendel's long neglect and rediscovery has been criticized for taking Mendel's paper out of context, both in 1865, when he presented it to the Naturalists' Society in Brno, and in 1900, when it became a cornerstone of genetics. But what are the proper contexts? Here a case is made for reading Mendel's paper, in both time periods, as part of a large body of nineteenth-century literature on practical plant- and animal breeding and experimental hybridization.

This literature contained a confusing and contradictory assortment of observations on heredity and preliminary laws and generalizations, some in line with Mendel's, but most not. In 1865, Mendel's paper was intended as a modest attempt to begin to bring order to this chaos, but there was little reason to celebrate it as a breakthrough: too many "non-Mendelian" cases were known.

After 1900, this literature was, in a sense, rediscovered along with Mendel, and it then played a dual role. For critics like W. F. R. Weldon, the non-Mendelian cases falsified Mendel's laws. But for Mendel's three co-rediscoverers, William Bateson, and others, they represented challenges to be met within a research program that would modify and extend Mendel's system and establish a new scientific discipline.

Keywords: Genetics, Mendelism, Gregor Mendel, Carl Correns, Hugo de Vries, Erich von Tschermak-Seysenegg, William Bateson, Germany, Austria, Britain, Early 20th Century.

Introduction

As the story is usually told, the intellectual and methodological foundations for the science now known as genetics were laid in 1865 by Gregor Mendel, an Augustinian monk, experimenting in his spare time in a monastery garden in Moravia. Supposedly, he worked in isolation, far from the major European centers of learning and without significant influences from contemporary science. His insights into heredity were ahead of his time and therefore incomprehensible and unappreciated by the few people who read his paper, and overlooked by everyone else.

Only in 1900, after thirty-five years of neglect was Mendel's paper "rediscovered." Three botanists in three different countries read it and wrote about

it: Hugo de Vries in the Netherlands, Carl Correns in Germany, and Erich Tschermak in Austria. They soon were joined by William Bateson in Britain in recognizing its importance. They accepted Mendel's basic laws of heredity and his model of paired hereditary factors, and they became the principal founders of genetics.

There are, of course, many problems with this story, not the least of which are the assumptions that Mendel was so isolated and his paper was unknown or lost on its few readers. It should be apparent from the text of Mendel's paper that he was responding to literature by academic botanists, practical breeders and experimental hybridizers, citing their results, addressing their questions, and adopting their methods.¹ It would be very odd indeed, if he did not consider his work to be part of a larger dialogue, or if his methods and concepts were alien to the nineteenth century.

It is also not clear how completely lost or unknown the paper could have been. It was formally published in a scholarly journal, the *Verhandlungen des naturforschenden Vereines in Brünn* [Proceedings of the scientific society in Brno],² admittedly not the most visible journal in the world, but still with over 300 subscribers plus honorary members and institutional exchanges.³ Major European research libraries had copies.

Bibliographies and secondary literature did their proper work of listing and referencing the paper. Pre-1900 citations and discussions of it are well known to historians. A compendium on plant hybridization by the German Wilhelm Focke and a bibliography by the American Liberty Hyde Bailey are thought

1. On Mendel's connections to experimental plant hybridization, see Robert C. Olby, *Origins of Mendelism*, 2nd ed. (Chicago: University of Chicago Press, 1985); on Mendel's academic side, Sander Gliboff, "Gregor Mendel and the Laws of Evolution," *History of Science* 37 (1999): 217–235; and on plant breeding, Roger J. Wood and Vítězslav Orel, *Genetic Prehistory in Selective Breeding: A Prelude to Mendel* (Oxford: Oxford University Press, 2001); for an overview, Sander Gliboff, "The Many Sides of Gregor Mendel," in *Outsider Scientists: Routes to Innovation in Biology*, ed. Oren Harman and Michael R. Dietrich (Chicago: University of Chicago Press, 2013).

2. Gregor Mendel, "Versuche über Pflanzenhybriden," *Verhandlungen des naturforschenden Vereines in Brünn* 4 (1865): 3–47.

3. "Verzeichnis der Mitglieder," *Verhandlungen des naturforschenden Vereines in Brünn* 4 (1865): x–xxi; "Anstalten und Vereine: Mit denen bis zum Schlusse des Jahres 1865 wissenschaftlicher Verkehr stattfand," *Verhandlungen des naturforschenden Vereines in Brünn* 4 (1865): vi–ix.

to have been particularly important in leading the rediscoverers to Mendel's paper.⁴

Let me then try to tell the story of Mendelism in a different way, under different assumptions: that his paper was not hard to find or to understand, that Mendel was involved in several overlapping botanical communities—of practical breeders, experimental hybridizers, and academics—and that twentieth-century readers were the ones who misunderstood his paper, if they read it in isolation from the larger body of nineteenth-century literature produced by those communities.

It was a mistake for historians to searching the literature too narrowly for pre-1900 references to Mendel or for cases of apparent Mendelian dominance or segregation. This has detracted from our picture of both Mendel and many authors not named Mendel. When not completely neglected, these authors have been treated mainly as “forerunners” or “precursors” of Mendel, but only insofar as their results agreed with his. The earliest histories of genetics by Hans Stubbe or H. F. Roberts, for example, treated them in this manner. To be sure, they did anticipate and maybe influence Mendel in some ways, for example by breaking down the overall appearance of the plant or animal into individual characteristics as was usual in practical breeding. Some also arranged their experimental characteristics in opposing pairs, or crossed varieties that differed in one or a small number of chosen characteristics, as Mendel did. Several extolled the special virtues of the pea plant as an experimental organism that could easily be either crossed or self-pollinated.

There are even reports of what appear in retrospect to be Mendelian dominance and segregation. Thomas Andrew Knight, John Goss, and Thomas Laxton in England, Giorgio Gallesio in Italy, Augustin Sageret, Charles Naudin, and Louis and Henry Vilmorin in France, and others, found that the first hybrid generation was uniform and either resembled one parent or the other in the trait of interest or else took on a consistent intermediate form. They also found that this uniform generation would give rise to a mixture of the parental traits in the next generation. Some even used comparable language to Mendel's for these two phenomena. Sageret and Gallesio spoke of one trait “dominating” the other in the hybrid; Naudin of the “disjunction” of the parental essences in

4. Olby, 115; Conway Zirkle, “The Role of Liberty Hyde Bailey and Hugo de Vries in the Rediscovery of Mendelism,” *Journal of the History of Biology* 1, no. 2 (1968): 205–218; Åke Gustafsson, “The Life of Gregor Johann Mendel—Tragic or Not?” *Hereditas* 62, nos. 1–2 (1969): 239–258.

the second generation.⁵

But that is only half the story. The focus on only what was most Mendel-like in their methods and results obscures their original purposes and implies that they were flawed scientists or shortsighted ones who could not see what was obvious to Mendel. It also gives a distorted view of the intellectual and disciplinary context in which Mendel worked and to which he was trying to contribute. A less selective presentation of pre-Mendelian breeding and hybridization, and their contradictory and confusing results would show why Mendel's paper would not have looked like a great breakthrough. Too many "non-Mendelian" cases were known: too many counterexamples to Mendel's generalizations or, indeed, to any proposed law of heredity.

But the nineteenth-century breeding- and hybridization literature also had a role to play in the early twentieth-century. Things moved very fast after 1900, and the debate over Mendel did not wait for new experimental results to be published, but required a fresh look at old data. Many nineteenth-century non-Mendels were plucked from an obscurity as deep or deeper than Mendel's own, their results put to new work and given new interpretations. In a sense they were "co-rediscovered" with him.

When the British zoologist and biometrician W. F. R. Weldon led the attack against Mendelism in 1902, he combed the older literature for cases that seemed to falsify Mendel's laws. Curiously, the pro-Mendelian side—for present purposes, mainly the three co-rediscovers plus Weldon's leading opponent, William Bateson—took an equally strong interest in that literature and began rediscovering it for their own purposes. They were looking, of course for confirmatory cases, but not exclusively. They also studied the counter-cases for ideas on how to improve on Mendel's laws and for research opportunities within the basic Mendelian framework.

Mendel's paper had already hinted at ways of investigating some of the recalcitrant cases and gradually modifying and extending his proposed laws. That is what most distinguished Mendel from the other authors and that is what caught the attention of his twentieth-century supporters: his choice of a simple set of experimental crosses as a starting point or exemplar, and the

5. Hans Stubbe, *History of Genetics: From Prehistoric Times to the Rediscovery of Mendel's Laws*, trans. T. R. W. Waters (1965; repr., Cambridge: MIT Press, 1972), Ch. 6; Herbert F. Roberts, *Plant Hybridization before Mendel* (Princeton: Princeton University Press, 1929), 85–93, 104–110 & 120–136; see also Conway Zirkle, *The Beginnings of Plant Hybridization* (Philadelphia: University of Pennsylvania Press, 1935); Conway Zirkle, "Gregor Mendel and his Precursors," *Isis* 42 (1951): 97–104.

extensibility of his system of explanatory laws and mechanisms.⁶ Unfortunately, he carried out very little of this program himself. It, too, had to be rediscovered and resumed.

Mendel's Program

Mendel had discussed many apparent violations of his own laws, such as hybrids that were known to breed true like new varieties instead of segregating out into parental types. As an example, he cited willow hybrids studied by Max Wichura.⁷

Mendel also noted several complications or exceptions in his own experiments on peas. There was a case of what we might now call pleiotropic effects: one of his experimental factors determined the colors of the seed covering, the petals, and part of the stem, all at the same time. He acknowledged that hybrids often exhibited a “middle form [*Mittelbildung*]” in-between certain parental characteristics, such as size or shape of the leaves, instead of complete dominance or recessiveness. And he had a case of what we might now call overdominance, in which the hybrid of the tall and short varieties was actually taller than the tall.⁸

Mendel claimed only partial success in replicating his results in other plants. For example, he described white-flowered and purple-red-flowered string beans, whose hybrid segregated into a spectrum of floral colors from purple-red to pale violet, with an occasional white, when his laws would have predicted the two parental colors in 3:1 ratios.

Mendel indicated how his rules and explanations might be revised and extended to cover these kinds of cases. For example, a small revision would allow him to account for the string-bean flowers. One had only to allow a single trait to be determined by multiple factors (as in polygenic inheritance). He remarked that it would be very rewarding if one could research the matter further,⁹ which I take as an additional indication that he was keeping track of exceptions and saving them for future investigation. The one that he did

6. For a philosophical treatment of geneticists' strategies for expanding the scope and complexity of the gene concept see Lindley Darden, *Theory Change in Science: Strategies from Mendelian Genetics* (New York: Oxford University Press, 1991).

7. Mendel, “Versuche über Pflanzenhybriden,” 38, 40.

8. *Ibid.*, 8, 10, 11.

9. *Ibid.*, 33–36.

manage to take up was the category of hybrids like the willows that bred true instead of segregating. That was the subject of his second and last article on hybridization, a study of the hawkweed.¹⁰ What other ideas and studies might he have had in the pipeline?

Accounts of Mendel's unpublished research are sketchy at best, but he is said to have bred different colored mice,¹¹ conceivably with the aim of extending his laws to animals. He is known to have taken a special interest in bees and tried to perform crosses with them, which was not easy. He had to shoo his selected queen and drones into a specially made mating cage on the monastery grounds, apparently without much success.¹²

The trouble he took suggests that he had special questions about the bees, possibly in connection with the new (in 1854) and controversial idea that the drones were generated parthenogenetically. That would have given him reason to reconsider whether his hereditary factors always had to occur in pairs.¹³

Finally, one of the minor mysteries in the Mendel literature is whether he should not have encountered linkage, given that he chose seven traits for his experiments in a species with seven pairs of chromosomes. Was it just a coincidence that he observed only independent assortment, or did he present his results selectively and not quite honestly?¹⁴ Modern estimates vary considerably, but most give him pretty good odds of *not* detecting linkage, given the small number of tests he reported and their sample sizes.¹⁵ On the other hand,

10. Gregor Mendel, "Ueber einige aus künstlicher Befruchtung gewonnenen Hieracium-Bastarde," *Verhandlungen des naturforschenden Vereines in Brünn* 8 (1869): 26–31.

11. Hugo Iltis, *The Life of Mendel* (New York: W. W. Norton, 1932), 92 & 105.

12. Letter to a beekeeper, 1880, quoted in Vítězslav Orel, *Gregor Mendel: The First Geneticist*, trans. Stephen Finn (Oxford and New York: Oxford University Press, 1996), 233.

13. Iltis, 212; Zirkle, "Gregor Mendel and his Precursors," 100–102.

14. L. C. Dunn, *A Short History of Genetics* (New York: McGraw-Hill, 1965), 12.

15. L. Douglas and E. Novitski, "What Chance did Mendel's Experiments Give Him of Noticing Linkage?" *Heredity* 38, no. 2 (1977): 253–257; see also R. A. Fisher, "Has Mendel's Work Been Rediscovered?" *Annals of Science* 1 (1936): 115–137; Daniel J. Fairbanks and Bryce Rytting, "Mendelian Controversies: A Botanical and Historical Review," *American Journal of Botany*

he might well have detected linkage, but set it aside as a complication to be introduced later in the program.

Pre- and Non-Mendelian Heredity

Even more complications can be found in the wider breeding- and hybridization literature. Some involved correlations between characteristics. Also widely discussed were a variety of effects usually subsumed under the concept of “prepotency”: something about a particular parent—perhaps its sex, physiological constitution, variety, or ancestry—that gave it more power than its mate to transmit its own characteristics to the offspring.

Some experimental hybridization work partially reproduced Mendel’s findings. The grain breeder Wilhelm Rimpau, for example, systematically hybridized a large number of wheat, rye, barley, and oat varieties and sometimes observed dominance and segregation, but not consistently enough for him to deem them general rules. They seemed to him to apply only to particular traits in particular varieties.¹⁶

The zoologist Wilhelm Haacke performed crossing experiments with mice, with the aim of falsifying August Weismann’s germplasm theory, and he, too, described dominance in the hybrid and the separating out of the parental influences in the next generation. This was interpreted initially as undermining Weismann’s ideas about the gradual diminution of ancestral contributions to the germplasm, but it soon would be seen to have a bearing on Mendelism.

In response to Haacke, Georg von Guaita, working in Weismann’s laboratory, investigated the mouse crosses further. He, too observed dominance and segregation, albeit with complications. Crosses of white mice with Japanese waltzing mice yielded exclusively grey (i.e., wild-type coat color), non-waltzing offspring. When these hybrid mice were crossed, six different colors emerged, and the ratio of normal to waltzing was reported to be 36:8 or 4.5:1.¹⁷

88, no. 5 (2001): 737–752.

16. Wilhelm Rimpau, “Kreuzungsprodukte landwirtschaftlicher Kulturpflanzen,” *Landwirtschaftliche Jahrbücher* 20 (1891): 335–371; on Rimpau and other grain hybridizers, see also Thomas Wieland, “Scientific Theory and Agricultural Practice: Plant Breeding in Germany from the Late 19th to the Early 20th Century,” in “Biology and Agriculture,” *Journal of the History of Biology* 39, no. 2 (2006): 309–343.

17. Wilhelm Haacke, *Gestaltung und Vererbung: Eine Entwicklungsmechanik der Organismen* (Leipzig: T. O. Weigel Nachfolger, 1893), 102–103

Other pre-rediscovery authors, whose work would receive new scrutiny after 1900, were also using quantitative and experimental methods comparable to Mendel's, but getting contrasting results. A certain H. Crampe hybridized wild, grey rats with domesticated color-variants in the 1870s and 1880s and reported that the offspring always took after the wild parent, regardless of whether it was the mother or the father.¹⁸

Yet another good example is Johann von Fischer, of St. Petersburg, who found that the parent's sex, rather than its wildness or domesticity, was the decisive factor. In his crosses between varieties of several species of rodent, the offspring always took after the father in coat color.¹⁹

It was also frequently reported that hybrids bred true instead of segregating into the parental types, as in Mendel's hawkweeds or Wichura's willows. Closer to the rediscovery period, in 1894, the work of Alexis Millardet on the so-called "false hybrids" of strawberries called renewed attention to such puzzling cases, especially those in which one parent seemed to transmit little or nothing to the hybrid. They were to occupy geneticists for years after the rediscovery.²⁰

& 238–240; Georg von Guaita, "Versuche mit Kreuzungen von verschiedenen Rassen der Hausmaus," *Berichte der Naturforschenden Gesellschaft zu Freiburg i. Br.* 10, no. 1 (1897): 317–331.

18. H. Crampe, "Zucht-Versuche mit zahmen Wanderratten, 1: Resultate der Zucht in Verwandtschaft," *Landwirthschaftliche Jahrbücher* 12 (1883): 389–449; H. Crampe, "Zucht-Versuche mit zahmen Wanderratten, 2: Resultate der Kreuzung der zahmen Ratten mit wilden," *Landwirthschaftliche Jahrbücher* 13 (1884): 699–754; H. Crampe, "Untersuchungen über die Vererbung der Farbe und über die Beziehungen zwischen der Farbe und dem Geschlecht bei Pferden," *Landwirthschaftliche Jahrbücher* 13 (1884): 949–956.

19. Johann von Fischer, "Die Säugethiere des St. Petersburger Gouvernements," *Der Zoologische Garten: Zeitschrift für Beobachtung, Pflege und Zucht der Thiere* 10 (1869): 336–343; Johann von Fischer, "Beobachtungen über Kreuzungen verschiedener Farbenspielarten innerhalb einer Species," *Der Zoologische Garten: Zeitschrift für Beobachtung, Pflege und Zucht der Thiere* 15 (1874): 361–374.

20. E.g., A. J. Mangelsdorf and E. M. East, "Studies on the Genetics of *Fragaria*," *Genetics* 12 (1927): 307–339.

Rediscovery Revisited

Aware of much of this literature, Mendel's rediscoverers approached Mendel with varying degrees of caution. De Vries was boldest and most provocative in his initial announcements of Mendel's laws, but even he explicitly limited their realm of applicability: "According to my experiments, they have general validity for the true hybrids,"²¹ in other words, not for the false hybrids of Millardet or comparable cases in which the hybrid bred true like a new species.

In his conclusion, however, de Vries omitted the qualification and claimed "that the *law of segregation of hybrids* found by Mendel in peas finds general application in the plant kingdom, and that it has a quite fundamental significance for the study of the units of which species characteristics are composed."²² Later in 1900, after reading more cautious accounts by his co-rediscoverers, de Vries remained firm in his rhetoric about Mendel's general applicability,²³ but also began making a greater effort to acknowledge more kinds of aberrant cases and to try to accommodate them within Mendel's general framework.

In particular, he discussed cases in which the paired elements of the hybrid did not segregate into equal percentages of the sex cells. Mendel, he argued, just happened to choose cases in which the two factors turned out to be equivalent in their segregating behavior. "But such an equivalence," he wrote, "is in no way a necessity. The traits can, in other cases, also be non-equivalent in segregation. They would then either not separate or follow other rules upon their separation."²⁴ This unequal distribution of factors to the gametes could generate other segregation ratios than Mendel's 3:1. It could also make Mendel's hawkweeds or Millardet's false hybrids, which did not segregate at all, into just one extreme on a modified Mendelian spectrum. In other words, de Vries thus made Mendel's law of segregation into a special case of a more general model.

21. Hugo de Vries, "Das Spaltungsgesetz der Bastarde: Vorläufige Mittheilung" (1900), in *Fundamenta Genetica: The Revised Edition of Mendel's Classic Paper, With a Collection of 27 Original Papers Published During the Rediscovery Era*, ed. Jaroslav Kříženecký, with an intro. by Bohumil Němec (Prague: Czechoslovak Academy of Sciences, 1965), 97.

22. *Ibid.*, 102, emphasis original.

23. Hugo de Vries, "Ueber erbungleiche Kreuzungen: (Vorläufige Mittheilung)," *Berichte der Deutschen Botanischen Gesellschaft* 18, no. 9 (1900): 435–443, on 435–436.

24. *Ibid.*, 436.

De Vries then went on to describe mutations, latent traits, and atavisms, and other unequal or atypical segregation rules. Despite his opening reassertion of the generality of Mendel's laws, de Vries was soon directing most of his efforts at investigating non-Mendelian cases, and trying to apply the Mendelian explanatory framework to them.

Not to be outdone by de Vries, Correns responded to the former's first rediscovery paper by asserting that he had known about Mendel and his laws already²⁵ and that de Vries did not have anything original to say about hybridization. He also raised the stakes by endorsing a physical interpretation of Mendel's laws in terms of paired developmental rudiments—*Anlagen*, as he called them—in the cell nuclei: “As an explanation, one must assume, with Mendel, that after the sex-cell nuclei unite, the *Anlage* for the one character, the ‘recessive’ one, . . . is prevented from unfolding by the other *Anlage*, for the ‘dominating’ characteristic. . . .”²⁶

Nonetheless, Correns, too, was cautious about the generality of Mendel's laws. In a review of the evidence for and against Mendel, Correns recommended that we not speak of his “laws” at all, but only of lawlike behaviors in particular crosses.²⁷ Correns proposed further modifications of Mendel's laws that would improve their generality. He took on cases in which the parent seemed to exert an influence on the transmission of its traits, and also cases where two traits tended to be inherited together.

In Correns' stocks (*Matthiola*), for example, the sex of the parent influenced the transmission of its traits, contrary to what Mendel observed: “*In their color, on average, the seeds thus resembled their respective mother more than their father.*”²⁸

25. Indeed he seems to have read Mendel as early as 1896, without making much of him: Hans-Jörg Rheinberger, “When Did Carl Correns Read Gregor Mendel's Paper?” *Isis* 86 (1985): 612–616.

26. Carl Correns, “G. Mendel's Regel über das Verhalten der Nachkommenschaft der Rassenbastarde” (1900), in Kříženecký, 108–109.

27. Carl Correns, “Gregor Mendel's ‘Versuche über Pflanzen-Hybriden’ und die Bestätigung ihrer Ergebnisse durch die neuesten Untersuchungen,” *Botanische Zeitung* 58/2, no. 15 (1900): 229–235, on 233; on Correns' continuing dissatisfaction with Mendel's original formulations and his search for a more general theory, see also Margaret Saha, “Carl Correns and an Alternative Approach to Genetics: The Study of Heredity in Germany Between 1880 and 1930” (PhD Diss., Michigan State University, 1984).

28. Carl Correns, “Ueber Levkojenbastarde: Zur Kenntniss der Grenzen

Correns argued that parental effects of this sort could be accommodated under Mendel's system, if they came into play while the embryo was still in the maternal flower. In that environment, Correns argued, the hybrid embryo might pick up different pigments in different proportions, depending on the maternal floral color.

Not all of the correlations could be accounted for by influences from the maternal flower, however. Correns therefore suggested that when the Mendelian factors were distributed into the reproductive cells, they did not always assort independently, as in Mendel's experiments, but stuck together in groups. In other words, the *Anlagen* were somehow "coupled," "conjugated," or in modern terms, "linked."²⁹ With that, Mendel's law of independent assortment was rejected, yet the system as a whole was strengthened and extended to explain more kinds of cases.

The most cautious of the three co-rediscovers was Tschermak, who for several years avoided discussing the physical reality of Mendel's paired, segregating, and reassorting hereditary particles or Correns' *Anlagen*. He did not even use the word "segregation" [*Spaltung*] in his 1900 paper, but opted for a noncommittal terminology of his own, which his detractors take as evidence of his failure to understand Mendel's paper properly.³⁰

The reason for Tschermak's reservations about segregation and the underlying model of paired elements can be found in his deep knowledge of the late nineteenth-century hybridization literature, especially the work of Rimpau. That literature gave only incomplete support to Mendel. Tschermak's own data were also somewhat ambiguous. Although he often observed 3:1 segregation ratios in his pea crosses, he did not get the same ratios as Mendel in the backcrosses of the hybrid with the recessive parent. These should have yielded dominants and recessives in 1:1 ratios, according to Mendel, but Tschermak

der Mendel'schen Regeln," *Botanisches Centralblatt* 84 (1900): 97–113, 101, emphasis original.

29. Correns, "Ueber Levkojenbastarde," 106–108.

30. Curt Stern and Eva R. Sherwood, eds., *The Origin of Genetics: A Mendel Source Book* (San Francisco: W. H. Freeman, 1966), xi–xii; Floyd Monaghan and Alain Corcos, "Tschermak: A Non-Discoverer of Mendelism, I: An Historical Note," *Journal of Heredity* 77 (1986): 468–469; Floyd Monaghan and Alain Corcos, "Tschermak: A Non-Discoverer of Mendelism, II: A Critique," *Journal of Heredity* 78 (1987): 208–210; for a more nuanced, but still skeptical view of Tschermak's understanding, see also Olby, 120–124.

observed ratios of 1.2:1 and 1.75:1 in his only two test cases.³¹ By distancing himself from any physical model of segregating particles, Tschermak could allow for a range of possible behaviors and segregation ratios, among which Mendel's 3:1 and 1:1 were just two points on a large range.³²

Weldon's Critique

No doubt encouraged by Tschermak's apparent reservations about Mendel's laws, Weldon decided in 1901 to consult him before going to press with his big critique of Mendelism. Weldon had been collecting exceptions and counterexamples from the breeding- and hybridizing literature and wanted Tschermak's opinion on them, but he also asked Tschermak for more detail about how the traits actually looked on the pea plants.

As a staunch defender of continuous and blending variation, and especially of the idea of ancestral influences on present variation (Francis Galton's theory of ancestral heredity), Weldon wanted to see for himself how uniform and discrete the pea colors really were:

The shades of colour which become so important in the discussions of Mendel's Law are especially hard to follow from verbal descriptions, if one is not familiar with the varieties spoken of, —and I am so ignorant of horticulture that most or all of the varieties you have used are unknown to me.³³

This question of the continuity of hereditary variation would soon take center stage in the well-known Mendelian-biometrician dispute,³⁴ but it was not the only issue.

31. Erich Tschermak, "Ueber künstliche Kreuzung bei *Pisum sativum*," *Zeitschrift für das landwirtschaftliche Versuchswesen in Österreich* 3 (1900): 544.

32. For more on Tschermak and his interpretations and applications of Mendelism: Sander Gliboff, "Breeding Better Peas, Pumpkins, and Peasants: The Practical Mendelism of Erich Tschermak," in *New Perspectives on the History of Life Sciences and Agriculture*, ed. Denise Phillips and Sharon E. Kingsland (Springer-Verlag, 2015).

33. W. F. R. Weldon to Erich von Tschermak-Seysenegg, autograph letter signed, Merton Lea, Oxford, Oct. 26, 1901, Nachlaß Erich von Tschermak-Seysenegg, Archiv der Österreichischen Akademie der Wissenschaften, Vienna (henceforth cited as Tschermak Papers), box 4, folder 84.

34. William B. Provine, *The Origins of Theoretical Population Genetics*

Weldon also objected to dominance, because it implied that one did not have to know anything about a parent's ancestry in order to predict how its traits would be transmitted. So he questioned Tschermak about that matter as well. He brought up Correns' reports of variation in a trait's degree of dominance in maize, along with cases of prepotency from Crampe and von Fischer that seemed to show the influence of sex or ancestry on the expression of a trait.

He evidently expected Tschermak to agree that such influences were both common and incompatible with Mendel's conception of dominance:

I feel here that in similar cases among animals the power of dominance is often, as Correns says it is in *Zea*, an individual peculiarity. Do you know in this connection Crampe's work on rats?—von Fischer of St. Petersburg says that when white (albino) rats are paired with wild individuals, the offspring are always like the *father* in color. Crampe made the cross both ways, and the young were always like the *wild* parent, whether σ or φ .—Similar contradictions abound and many will no doubt occur to you.³⁵

In the published critique, Weldon capitalized on the scope and inconsistency of pre-1900 empirical knowledge to sow doubt about the generality of Mendel's laws: "There is so much contradiction between the results obtained by different observers, that the evidence available is difficult to appreciate."³⁶ He made no attempt to discredit Mendel directly, but gave a fair and even favorable account of his particular findings, while denying their generalizability. He cautioned against jumping to the conclusion that Mendel's "statements are applicable to a wider range of cases than those he actually observed."³⁷

In order to help him blur the distinction between dominance and recessiveness, he turned to many of our familiar "forerunners of Mendel," including Gärtner (who had been cited prominently by Mendel himself), Laxton, Rimpau, Goss, Naudin, and Knight. But of course, instead of focusing selectively

(Chicago and London: University of Chicago Press, 1971); Alan G. Cock, "William Bateson, Mendelism and Biometry," *Journal of the History of Biology* 6 (1973): 1–36.

35. W. F. R. Weldon to Erich von Tschermak-Seysenegg, autograph letter signed, Merton Lea, Oxford, Nov. 21, 1901, Tschermak Papers, box 4, folder 84, emphasis original.

36. W. F. R. Weldon, "Mendel's Laws of Alternative Heredity in Peas," *Biometrika* 1 (1902): 228.

37. *Ibid.*, 232.

on their observations of dominance, Weldon looked for reports of incomplete dominance, variation in the shading of supposedly dominant colors, and cases where green peas dominated over yellow, instead of yellow over green, as in Mendel's crosses.³⁸

Crampe and von Fischer, along with the more recent experiments on mice by Haacke and von Guaita came into play as well, as Weldon's primary counterexamples from animals. He used them to illustrate the need to allow for parental influences on dominance:

I would only add one case among animals, in which the evidence concerning the inheritance of colour is affected by the ancestry of the varieties used In both rats and mice von Fischer says that piebald rats crossed with albino varieties of their species, give piebald young if the father only is piebald, white young if the mother only is piebald.

Weldon juxtaposed von Fischer's results with a collection of seemingly contradictory cases of coat color inheritance in mice, including some from Haacke and von Guaita, and inferred that dominance could not be as simple a matter as Mendel imagined:

Results such as those which Crampe records in rats are commonly obtained when piebald and albino mice are paired; but both Haacke . . . and von Guaita . . . find that when the ordinary European albino mouse is paired with the piebald Japanese "dancing" mouse, the offspring are either like wild mice in colour, or almost completely black.³⁹

Weldon used similar tactics to dispute the generality of Mendelian segregation, working through a selection of cases from the older authorities, particularly Laxton, in which uniform hybrids sometimes segregated neatly into dominants and recessives in the predicted 3:1 ratios, and sometimes did not:

The phenomena of inheritance in cross-bred Peas, as Laxton observed them, were far more complex than those described by Mendel; but they do not preclude the possibility of a simple segregation, such as Mendel describes, in particular cases.⁴⁰

Mendel and most early Mendelians could hardly have disagreed about the complexity of the phenomena, but Weldon wanted to use them to falsify

38. Weldon, "Mendel's Laws of Alternative Heredity in Peas," 237.

39. *Ibid.*, 244.

40. *Ibid.*, 251.

Mendel's laws and discredit the whole enterprise. To the Mendelian side, in contrast, they suggested new lines of research and new opportunities for expanding Mendel's system.

Bateson's Response to Weldon

Even before responding to Weldon, Bateson had been studying much of the same breeding- and hybridization literature himself. His first major review of Mendelism, with co-author Edith Saunders, asserted that the rediscovery of Mendel would force a re-evaluation of all the old empirical findings: "The whole problem of heredity has undergone a complete revolution. . . ." ⁴¹

This first of their reports to the Royal Society organizes the historical results (along with new observations) according to whether they are readily explicable by Mendel's laws or not, and tries to assess how much of heredity is Mendelian and how good the prospects were for expanding Mendelism into a general account. For the Mendelian side they claimed many of the same breeders and hybridizers who Weldon was about to use as non-Mendelians:

The literature of breeding teems with facts now palpably Mendelian. Gärtner, Godron, Laxton, even Darwin himself, must have been many times on the brink of the discovery.

Looking now at such experiments as those of Rimpau with wheat, &c, of Laxton with *Pisum*, Godron with *Datura*, of Darwin with *Antirrhinum* and sweet pease, we can hardly understand how the conclusion was missed. ⁴²

They picked out examples of dominance from the work of Rimpau, Naudin, von Guaita, Haacke, and Darwin, and added a few more from cattle-breeders' and seed-dealers' records. ⁴³ Conflicting cases did not trouble them. They would be explained later: "It is certain that these exceptions at all events indicate the existence of other principles which we cannot yet formulate." ⁴⁴ These other principles would not replace Mendel's system, but extend it.

41. "Experiments Undertaken by W. Bateson, FRS and Miss E. R. Saunders," in *Reports to the Evolution Committee of the Royal Society*, Report I (London: Harrison & Sons, 1902), 4. The report was handed in to the Committee on 17 December 1901, before the appearance of Weldon's critique.

42. *Ibid.*, 6.

43. *Ibid.*, 138–145.

44. *Ibid.*, 152.

Writing separately from Saunders, Bateson soon responded to Weldon's examples of non-Mendelian heredity, including the mice and rats of Crampe, von Fischer, Haacke, von Guaita, and others. Crampe was not difficult to bring into line with Mendel's principles. Bateson argued that the wild color-type in Crampe's experiment was expressed preferentially in the hybrids not because of the wildness and prepotency of the parent, as Crampe and Weldon had it, but because of its dominance in the ordinary Mendelian sense.⁴⁵

In contrast, Bateson opted to attack von Fischer's credibility. Von Fischer had found coat color in rats always to be inherited from the father, which, Weldon had argued, undermined the concept of dominance. Rather than discuss the data, as he had done in the case of Crampe, Bateson subjected von Fischer's larger research program to ridicule.

Von Fischer offered an easy target, because of his views on the differences between species and varieties. In making a distinction between interspecific and intervarietal hybrids, he had argued that the father *always* determined coat color in the latter. Hence, one could use coat-color inheritance as a diagnostic tool for species- vs. variety status:

*If the product of a cross between parents of questionable species status carries the coloration of the father, then those parents belong to one and the same species. But if the product is intermediate or otherwise deviates from the father, then the parents are specifically different.*⁴⁶

Bateson emphasized the implausibility of von Fischer's claim that there were no exceptions to the rule that the father's coat color was always decisive when mere varieties were crossed. Indeed when von Fischer did encounter exceptions, he could often explain them away by reclassifying them as interspecific crosses. At this, Bateson sneered,

The reader may have already gathered that we have here that bane of the advocate—the witness who proves too much. But why does Professor Weldon confine von Fischer to the few modest words recited above [i.e., leaving out the discussion of species status]?

45. William Bateson, *Mendel's Principles of Heredity: A Defence: With a Translation of Mendel's Original Papers on Hybridization* (Cambridge: Cambridge University Press, 1902), 174; William Bateson, "The Present State of Knowledge of Colour-Heredity in Mice and Rats," *Proceedings of the Zoological Society of London* 72, no. 2 (1903): 83–89.

46. Fischer, "Beobachtungen über Kreuzungen verschiedener Farbenspielarten innerhalb einer Species," 373. Emphasis original.

That author has—so far as colour is concerned—a complete law of heredity supported by copious “observations.”⁴⁷

For the most part, however, Bateson (with and without Saunders) did what the rediscoverers were already doing: try to explain non-Mendelian phenomena by proposing more and more extensions and variations on Mendel’s original theory. But a funny thing happened as they did so. Instead of attacking Bateson for clinging unreasonably to his Mendelism, Weldon started attacking him for not being as good a Mendelian as advertised. Weldon was trying to falsify Mendel’s theory, but instead of bringing the theory down, the counterexamples were inspiring new research directions that would extend and strengthen it.⁴⁸ The theory was evolving before his eyes and evading his efforts.

Post-1902 Developments

The three rediscoverers and Bateson soon expressed satisfaction with their ability to adapt and extend Mendel. Reviewing the state of the effort in 1902, Tschermak saw no problem with the many known non-Mendelian cases: “That with these complications . . . the fundamental significance of Mendel’s work and the general validity of his basic idea are least of all to be denied, I, along with Bateson, have emphasized repeatedly.”⁴⁹

In a 1903 review, Correns granted readily that Mendel’s laws were not universal, but did not think that should be an issue: “*In principle*,” Correns wrote, “the question of the general validity of the Mendelian rules already has been answered *negatively*, as even Bateson admits.” The part that was still open, and the essence of Bateson’s dispute with Weldon, was whether a general theory could be made of them: “[Bateson] hopes to expand its limits even further than, at this time, the other authors.”⁵⁰

Bateson’s hopes proved to be well founded, as Mendelism and the new science of “genetics,” as he himself dubbed it in 1906, steadily expanded their

47. Bateson, *Mendel’s Principles of Heredity*, 176.

48. W. F. R. Weldon, “Mr Bateson’s Revisions of Mendel’s Theory of Heredity,” *Biometrika* 2 (1903): 286–298.

49. Erich Tschermak, “Der gegenwärtige Stand der Mendel’schen Lehre und die Arbeiten von W. Bateson,” *Zeitschrift für das landwirtschaftliche Versuchswesen in Österreich* 5 (1902): 1365–1392, on 1388.

50. Carl Correns, “Neue Untersuchungen auf dem Gebiete der Bastardierungslehre: (Herbst 1901 bis Herbst 1902): Sammelreferat,” *Botanische Zeitung* 61, no. 8 (1903): 113–126, on 116, emphasis original.

horizons. By 1902, for example, cytologists were making connections from Mendel's abstract model of segregating and re-assorting elements of unspecified nature, to Correns's more explicitly material and particulate *Anlagen* that occurred in linkage groups, and thence to the Boveri-Sutton theory that located the hereditary factors on the chromosomes.⁵¹ This not only established a physical basis for Mendel's theory, but also predicted and explained linkage and other non-Mendelian cases, and suggested future lines of research into chromosomal mutations and linkage mapping.

The search was also on for influences on the expression of a Mendelian factor, or "gene," as it came to be called after 1909, that could be more complex than mere dominance of one factor over its pair.

Tschermak had observed, for example, that a certain white-flowered variety of stock produced white flowers when self-fertilized, but violet ones when hybridized with other white-flowered varieties. The first variety had had the violet factor all along, so his explanation went, but the presence (or perhaps absence) of other factors had been suppressing it as long as it was inbred.⁵²

This kind of suppression or masking of a factor's effects was not an isolated phenomenon, but was also recognized by other authors. R. H. Lock, too, discussed a case where a "character was unable to manifest itself except in the presence of another character."⁵³ Bateson soon offered a general theory and terminology for such cases of "epistasis,"⁵⁴ and George H. Shull compiled and classified a larger variety of interactions that could suppress a trait—interactions not only among hereditary factors, but between the factors and the environment.⁵⁵

51. Alice Baxter and John Farley, "Mendel and Meiosis," *Journal of the History of Biology* 12, no. 1 (1979): 137–173.

52. Erich Tschermak, "Die Theorie der Kryptomerie und des Kryptohybridismus: I. Mitteilung: Über die Existenz kryptomerer Pflanzenformen," *Beihefte zum Botanischen Centralblatt* 16 (1904): 11–35.

53. R. H. Lock, "Studies in Plant Breeding in the Tropics, 1: Introductory: The Work of Mendel and an Account of Recent Progress on the Same Lines; With Some New Illustrations," *Annals of the Royal Botanic Gardens, Peradeniya* 2 (1904): 299–356.

54. William Bateson, "Facts Limiting the Theory of Heredity," *Science* (1907): 653.

55. George Harrison Shull, "A New Mendelian Ratio and Several Types of Latency," *American Naturalist* 42 (1908): 433–451.

In short, within just a few years of Mendel's rediscovery in 1900, the theory had risen to numerous challenges and was enriched and extended with concepts and studies of linkage, epistatic interactions, pleiotropic effects, polygenic inheritance, maternal effects, sex-limited characteristics, sex determination, and mutation—all things that had been absent or barely touched upon in Mendel's paper.

Conclusion

In contrast to the classic story of Mendel's isolation, neglect, and rediscovery, I have offered an account of him as a member of a community and a contributor to a larger body of literature on breeding and hybridization. All that other literature at first obscured Mendel's significance, because it offered at best only partial verification of his laws of heredity. After 1900, this literature functioned now as data against which to test Mendel's laws or proposed extensions of them, now as a foil to Mendel, now as a source of new challenges and research opportunities.

What we now celebrate as Mendel's rediscovery was the decision by a few individuals in 1900 to start small—with perhaps a few dozen traits in hardly two dozen species that they knew definitely followed Mendel's laws—and systematically extend and modify Mendel's system to make it account for more and more phenomena previously classed as non-Mendelian. That appears also to have been Mendel's own unrealized strategy. Mendel provided not a finished theory to be rediscovered, but a theory to work on.

The decision to continue Mendel's work came perhaps more easily to the rediscoverers and Bateson than to earlier authors, because they had been observing dominance, segregation, and 3:1 ratios in their own experiments in the 1890s, and knew that these phenomena had been observed sporadically before. What they needed Mendel for was the suggestion that these be taken as the starting points for a research program. But in addition to the theory to work on, they drew much more from the nineteenth-century literature. For testing Mendel's generality and for mapping out future research directions, crucial data and clues came from numerous neglected non-Mendels, who were rediscovered with him.

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