

# The “Rediscovery” of Mendel’s Work

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**Abstract:** Contrary to popular belief, Mendel’s famous paper about plant breeding announced no major findings; it was known and acknowledged as “typical” science for its day. When it was “rediscovered” in 1900, Mendel’s paper became famous primarily as a result of a priority dispute between de Vries and Correns. This dispute prompted researchers to reinterpret and read importance into Mendel’s paper.

**Keywords:** Correns, de Vries, Genetics, Mendel, Tschermak

“Mendel’s 1865 report ... fell on deaf ears”. (Lander and Weinberg, 2000)

“There is not known another example of a science which sprang fully formed from the brain of one man.” (de Beer, 1965)

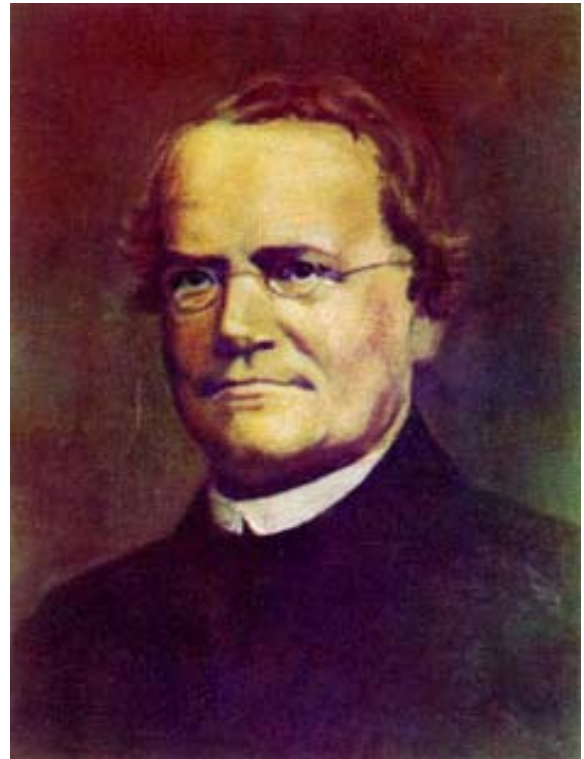
“The publication of Mendel’s paper in 1865 [sic] was the throwing of pearls before swine.” (Darbishire, 1911)

“All geneticists admitted that [Mendel’s paper] was written so perfectly that we could not – not even at present – put it down more properly ... It was a work which came prematurely but being repeated and rediscovered it became one of the immortal works of the human spirit penetrating into the mystery of life” (Nemec, 1965)

“Stolidly the audience had listened ... Not a solitary soul had understood him. Thirty-five years were to flow by and the grass on the discoverer’s grave would be green before the world of science comprehended that tremendous moment.” (Eiseley, 1959)

“[Mendel’s] laws were read back into his work and have continued to be read back in textbooks ever since”. (Bennett, 1964)

“Mendelian historiography is a continuing detective story where overstatement and misunderstanding seem to have been, and still are the fashion of the day”. (Meijer 1982)



## Introduction

Gregor Mendel (1822-1884) ranks second only to Charles Darwin on most biologists’ scales of hero worship. Mendel has been credited with discovering the first two laws of inheritance (i.e., the laws of segregation and independent assortment), which form the basis of what is now called “Mendelian genetics.” Consequently, Mendel -- like Darwin -- is included in

all courses in introductory biology; he is said to have provided the foundation of genetics, supplied the missing mechanism in the Darwinian revolution, and, in the process, changed our understanding of the world (Gliboff, 1999; Olby, 1979).

Discussions of Mendel's work are almost always accompanied by mythical stories of how Mendel's discoveries were rejected and how he died neglected, only to be resurrected as a scientific genius. Mendel's resurrection involved a "rediscovery" of his work by botanists Carl Erich Correns (1864-1933) of Tübingen (Germany), Erich Tschermak von Seysenegg (1871-1962) of Esslingen (near Vienna, Austria), and Hugo Marie de Vries (1845-1935) of Amsterdam (Netherlands), each of whom claimed to have independently rediscovered and independently published virtually the same results in early 1900 (i.e., 16 years after Mendel's death). As Tschermak (1900) himself claimed,

"The simultaneous discovery by Mendel by Correns, by de Vries, and myself appears to me especially gratifying ..."

Many reasons have been given for the alleged neglect of Mendel's paper, including that it was not distributed to Mendel's contemporaries, that it was overshadowed by Darwin's work, that it was a "duplication of previous research," that it was based on a "forbidding mathematical approach," that it was "premature" and that "the time was not yet ripe" for Mendel's ideas, that it was done by an amateur scientist, and that it was published in an obscure journal (e.g., see Gliboff, 1999; Iltis, 1932; Gasking, 1959; Orel and Kupstor, 1982; Barber, 1961; and references therein). Some of these claims are true; for example, Mendel was an amateur scientist and he did publish his work in a relatively obscure journal. However, these facts alone do not validate the many claims that Mendel's work was unknown or neglected. Moreover, there is an alternate hypothesis; namely, that 1) Mendel's work was known and acknowledged as "typical" science that was not revolutionary when viewed in the context of its time (Olby, 1979), and 2) Mendel's work became famous not only for its content, but also as a result of a priority dispute among its "rediscoverers." In this paper, I will develop this alternate hypothesis.

### Mendel's Paper

On 8 February and 8 March of 1865, Mendel described his research at consecutive monthly meetings of the Brunn Natural Science Society (Orel 1984).<sup>1</sup> Although the "Mendel mythology" claims that there were no questions or discussion after either presentation, the facts are different: both presentations generated "lively discussions" (e.g., see Henig 2000, Orel 1973, Olby and Gautrey 1968). Mendel's talks

were received favorably and were reported in Brunn's daily newspaper (*Tagesbote*) and in Czech and German newspapers as contributions to hybridization (Brannigan 1981). The following year, Mendel (1866) published his now famous (but seldom read) 48-page paper in the society's journal of its proceedings, *Proceedings of the Brunn Society for the Study of Natural Science*. That paper reported research done by Mendel from 1854-1863 (after he abandoned his mice-breeding experiments) involving almost 28,000 plants, of which he "carefully examined" 12,835 plants.<sup>2</sup> Mendel's key experiments involved crossing two pure-breeding varieties of garden pea (*Pisum sativum*) that differed in easily distinguishable ways (e.g., the shape and color of seeds). Mendel confirmed his findings by testing his crosses through at least four generations.

About Mendel's paper:

- Mendel's paper was about speciation and hybridization, not heredity; it did not even include the words *heredity* or *inheritance*. On the contrary, Mendel was trying to find "a generally applicable law governing the formation and development of hybrids." Similarly, the discussions following Mendel's presentations to the Brunn Natural Science Society in 1865 (see above) were about hybridization, not heredity. These results suggest that Mendel's contemporaries may have understood the purpose of Mendel's paper better than did those who "rediscovered" it in 1900 (Corcos and Monaghan, 1990).
- Mendel never mentioned the now-famous 9:3:3:1 ratio in his paper.
- Mendel often used italics to announce what he felt were important findings. For example, Mendel used italics to note that "*the behavior of each pair of differing traits in a hybrid association is independent of all other differences in the two parental plants*".
- This phrase – the climax of his paper -- would later be developed by the "rediscoverers" and others into Mendel's Law of Independent Assortment. Contrary to numerous claims (e.g., that Mendel "discerned several fundamental laws of heredity"; Lander and Weinberg 2000), Mendel's paper announced no major discoveries and did not state any of "Mendel's laws." Those laws were proposed by Mendel's successors.
- Although Mendel's influence on biology is undeniable, the aims and results of his 1866 paper were not as grand as has sometimes been claimed (Simmons, 1996; Orel, 1996 and references therein).<sup>3</sup> Mendel's work includes no evidence that Mendel had any concept of particulate determiners, either paired or unpaired. Mendel never described the nature of

a gene, nor did he describe the equivalence between character pairs and pairs of factors of inheritance. In that regard, Mendel was not a Mendelian (see Olby, 1979). Correns, not Mendel, was the first to introduce the concept of equivalence.

- Mendel used the cell theory of fertilization to explain why some offspring of hybrids breed true and others do not (he wanted to “throw light on the composition of the egg cells and pollen cells in hybrids”). Mendel didn’t use this theory to locate genes; he had no concept of genes, and his work does not mention two (and only two) mutually exclusive factors or elements in heredity. Mendel did discover the composition of egg and pollen cells, but he did so without invoking the idea of segregation or, for two or more traits, independent assortment. Mendel was studying the numbers and types of progeny produced by self-fertilized hybrids, not the inheritance of characters.
- Mendel used two different words that are both often translated as “character trait”: but which, in fact, have different meanings. *Merkmal* refers to a feature that one can see or recognize; that is, a “trait.” Mendel used *Merkmal* more than 150 times in his paper; in the “rediscovery” papers of 1900, this word often was translated as “factor” or “determinant.” However, Mendel also used the word *Elemente*, which has a meaning similar to its English cognate, *element*; Mendel used *Elemente* to refer to unknown substances that might produce *Merkmal*. Mendel’s 10 uses of *Elemente* were always plural and were restricted to his paper’s conclusion, where he deduced elements from the way that traits had moved from one generation to the next. The 20<sup>th</sup>-century hindsight enjoyed by Mendel’s rediscoverers may have prompted them to use more biologically-modern words (e.g., “factor”) and, in the process, make it seem that Mendel was closer to the gene concept than he really was (see discussion in Henig 2000).
- Mendel was the first to describe hybrids with double letters (e.g., Aa), suggests he knew that hybrids carried two different character traits. However, he used only one letter for pure-breeding stocks (e.g., his description was A:2Aa:a). Perhaps Mendel believed that pure-breeding plants had only one such character, or, more likely, he may not have thought that his letters represented any sort of physical structure at all (e.g., see Henig 2000).
- Mendel explained his results mathematically as a “series.” This enabled him to see the constancy of the various types of progeny, as well as that this constancy could be used to understand the results of his many different

crosses. Although Mendel was one of the first biologists to use generalizations involving binomials and mathematical symbols, his work was not based on overly difficult math.

- Mendel’s experiments involved 34 different seed-types that Mendel assumed were *Pisum sativum*, but there were probably other species as well (e.g., *P. quatratum*, *P. saccharatum*; see Henig 2000). Mendel wasn’t overly concerned about their precise classification, noting that it was “just as impossible to draw a sharp line between species and varieties themselves.” Mendel believed that this line was “quite immaterial” to his experimental goals; all he wanted was pure-breeding plants (Henig, 2000).



Mendel’s contemporaries considered Mendel’s work to be about hybridization, not heredity. For example, a letter by Iltis and Tschermak in 1907 to potential donors for a Mendel monument stated that “the discovery and actual determination of the hybridization laws indeed opened and enabled a new, unusually fertile era of experimental research of heredity of individual traits ...” (Orel, 1973). This claim that Mendel’s studies of hybrids indirectly produced an understanding of heredity also appears in a textbook published in 1914, and in 1922. Correns noted that the laws of heredity were “not formulated by Mendel himself, but were derived from reality only at their rediscovery” (Correns 1922).

After publishing his work, Mendel was urged by botanist Carl von Nägeli to study hawkweed (*Hieracium*). Unbeknownst to Mendel, hawkweeds have an unusual means of reproduction: they are apomictic, meaning that they appear to cross-fertilize

but, in fact, reproduce asexually (their seeds are of maternal origin; see Brannigan 1981, Corcos and Monaghan 1990). Although Mendel could not repeat his *Pisum* results with hawkweed, he reported his results to the Brünn Society for the Study of Natural Science in June of 1869, and published his results the next year. However, unlike with his *Pisum* work, Mendel ordered no reprints and sent no letters describing his work (e.g., see Henig, 2000). Mendel soon lost confidence and abandoned most of his botanical research. Only years later did he resume this research, studying apples and pears. Those studies were solid work, but produced nothing remarkable.<sup>4</sup>

### Was Mendel's Work Known to His Peers?

Mendel's paper was sent to more than 100 individuals and libraries (Orel, 1984; Brannigan, 1981). Thereafter, it was cited (as a contribution to hybridization, not heredity) in papers, books, and bibliographic guides throughout the world (including America, England, Middle Europe, Russia, and Sweden) as a contribution to the understanding of hybridization (Olby, 1979; Dorsey, 1944). These citations did not mention that Mendel's work was revolutionary or even out of the ordinary; they were "typical" citations, suggesting that his contemporaries had not misread Mendel's work. Similarly, Mendel's obituaries recognized his work with hybrids (Orel, 1984), but did not indicate that the work was revolutionary. Taken together, these observations indicate that Mendel was not an obscure figure in 1865. Although Mendel's work did not break new ground when it was published, it was known to many of Mendel's contemporaries. In this regard, the alleged "neglect" of Mendel's paper becomes a moot issue, for any "neglect" would be a problem only if Mendel's paper had been considered a pioneering paper by Mendel's contemporaries. It was not; Mendel's paper was merely one of many excellent studies of hybridization.

Mendel had no collaborators to help him and no students to carry on his work; Mendel's only associates lived in the next century (Eiseley, 1959). Mendel did little to promote his work; he did not republish his conclusions, nor did he do a barnstorming tour to promote his work. Mendel, a humble monk, merely announced his results and left the stage.

### How Was Mendel's Work Rediscovered?

In early 1900 de Vries, Correns, and Tschermak each published at least one paper in which they noted a 3:1 ratio in the distribution of characteristics in hybrids; these are the papers that comprise the "rediscovery" of Mendel's work. In 1959, Robert Platt (1959) became the first to question the independence of the "rediscovery" of Mendel's paper by de Vries, Correns, and Tschermak:

"It is usually reported that they all independently rediscovered the Mendelian laws, but as each one quotes the work of Mendel, it seemed to me that it would be interesting to find out ... how far they had gone with their own experiences before being enlightened by Mendel's genius."

If Mendel's paper represented "typical science" when it was published, how was it "rediscovered," and why did it only then become so popular? Although cytology and the germplasm theory in the late 19<sup>th</sup>-century provided a new context for Mendel's work,<sup>5</sup> its "rediscovery" resulted primarily from a priority dispute among the people who "rediscovered" Mendel's work (e.g., see Locke 1992; Brannigan 1981).

In 1900, Tschermak was a 26-year-old graduate student. His "rediscovery" paper (Tschermak, 1900) was a seven-page summary of his doctoral thesis which noted that Mendel's "premise of regular unequal quantivalency of traits for heredity is fully confirmed in my experiments ... and in the observations of Körnicke, Correns, and de Vries in *Zea mays*, and in de Vries' interspecific crosses, and is shown to be of the utmost importance in the science of heredity in general." Tschermak (1900) reported an F<sub>2</sub> ratio of "about 3 to 1" for monohybrids (his results were only slightly closer to a 3:1 ratio than they were to a 2:1 ratio) and a 1:1 ratio in progeny of the backcross. He thus confirmed Mendel's work, but he never generalized principles, nor did he recognize the importance of Mendel's work or the 3:1 ratio. Tschermak did not understand the nature of dominance and recessiveness, nor did he understand the importance of theoretical ratios. Tschermak's understanding of dominance differed from that of Mendel, and his explanation of the concept was inconsistent and contradictory. For example, Tschermak (1900) claimed that in his F<sub>2</sub> offspring,

"Regularly, one character in question ... comes exclusively into expression (dominating character according to Mendel) in contrast to the recessive character..."

Later in the same paragraph, however, Tschermak contradicts himself:

"The appearance of the dominating and the recessive character is not a purely exclusive one. In individual cases, I could, on the contrary, detect with certainty a simultaneous appearance of both, that is to say, of transition stages."

This statement contradicts Tschermak's earlier statement as well as Mendel's statement (1866) that,

"Transitional forms were not observed in any experiment."

Moreover, Tschermak did not discuss why a 3:1 ratio should have appeared, nor did he discuss how segregation could produce a 3:1 ratio. Clearly, Tschermak did not understand that the appearance of transitional forms implies the lack of dominance (also see Monaghan and Corcos, 1987).

Although Tschermak mentioned a ratio of 9:3:3:1 (probably as a result of his reading Correns' paper; see below), his data did not support such an interpretation. This led Stern and Sherwood (1966) to conclude that "Tschermak was 'an experimenter whose understanding ... had fallen short of the essential discovery,'" "Tschermak's designation as a rediscoverer of Mendel has only limited validity," and that Tschermak's "papers not only lack fundamental analysis of his breeding results, but clearly show that he had not developed any interpretation." Others have also rejected the alleged independence of the triple rediscovery (e.g., Olby, 1985).



The priority dispute that elevated Mendel's work was primarily between de Vries and Correns:

- Near the end of the 19<sup>th</sup>-century, de Vries began studying hybridization and became convinced that traits were inherited as independent units. For example, in 1893 de Vries gathered data showing that crosses of hairy and hairless species of *Lychnis* produced all hairy hybrids, but the following year he described the F<sub>2</sub> generation as consisting of hairy:hairless plants in a ratio of 2:1 (de Vries, 1899). Like Mendel before him, de Vries had been quantifying his results.
- On 26 March 1900, the 52-year-old de Vries presented a paper entitled "On the law of

segregation in hybrids" at the *Académie des Sciences*; this paper (which described hybridization in more than 80 species) was published soon thereafter (in French) and was remarkably similar to Mendel's paper (de Vries, 1990a; see translation in Stern and Sherwood, 1966). For example, in his previous papers, de Vries always used the terms *active* and *latent*, but in 1900 he abruptly began using Mendel's terms (*dominant*, *recessive*; see below), yet did not mention Mendel or cite Mendel's work. de Vries, who was studying starchy and sugary fruits of corn, did not mention anything about a law of segregation or a 9:3:3:1 ratio, but elevated Mendel's inconspicuous 3:1 ratio to a law when he reported that "about one-quarter of the grains were sugary; the other three-quarters were starchy."

- Before 1900, de Vries did not think in Mendelian terms, nor had he reported his F<sub>2</sub> results in a 3:1 ratio; he had merely listed or described his F<sub>2</sub> data in a non-Mendelian way. However, de Vries' data for F<sub>2</sub> generations of hybrids changed to 3:1 ratios after 1900. For example, his 2/3 hairy:1/3 nonhairy F<sub>2</sub> ratio for *Lychnis* in 1897 became 3/4:1/4 when they were published in 1900, although the actual data (i.e., 99 hairy vs. 54 nonhairy) were closer to a 2:1 ratio than a 3:1 ratio (Corcos and Monaghan, 1985b).<sup>6</sup> Although de Vries (1900b) gave no explanation for his results, his data could not have led him to the law of segregation (de Vries even claimed that the F<sub>2</sub> data consisted of "the most varied combinations and mixtures"). Similarly, in 1897 de Vries reported a 80:20 ratio for flower-color in *Linaria vulgaris*; by 1903, de Vries had changed this ratio to 3:1, despite the fact that he had reported that there were three phenotypes ("the great majority were purple, some were white, others dark red ..."; see de Vries 1900d). This suggests that de Vries did not develop his theory of segregation independently of Mendel, although he asserted, from 1900 on, that he had discovered Mendel's laws in 1896 (see Kottler, 1979; Stomps, 1954). As Zirkle (1968) noted, "de Vries either had not read Mendel's paper until a short time before he announced its discovery, or that if he knew of its contents earlier, he had not recognized its importance ... de Vries could have gotten his 3:1 ratio either by reading Mendel or by counting his own plants. His own plants, however, did not give a 3:1 ratio."
- In 1889 de Vries claimed that pangenes could readily change from active to latent forms (de Vries 1889). In 1903, de Vries claimed that pangenes were virtually invariant (Theunissen, 1994). Similarly, de Vries' theory of inheritance

became semi-Mendelian only after 1900 (Corcos and Monaghan, 1985b).

- Campbell (1980) has also noted that de Vries' ideas about inheritance changed dramatically in 1900. Before 1900, de Vries repeatedly claimed that all of a species' hereditary traits are borne in germ cells; after 1900, he embraced paired units and claimed that each pollen grain and egg cell received but one of the two traits. Corcos and Monaghan (1985a & b; 1987a-c) and Monaghan and Corcos (1986, 1987) have noted that none of the "rediscoverers ever made a Mendelian interpretation of the data from their hybridizing experiments before 1900." Each tried to do so only after reading Mendel's paper, thus questioning their claims that they had discovered Mendelism independently of Mendel.
- Correns received a copy of de Vries' paper on 21 April 1900. Although Correns' research had a different purpose and was based on different data (i.e., how pollen affects seed color) than Mendel's work, Correns was familiar with Mendel's work; he had published a paper in December, 1899 (Correns, 1899) that mentioned Mendel's research (i.e., that some hybrids have characteristics of their parents). Correns mailed his "rediscovery" paper on 22 April 1900 (i.e., the day after he received de Vries' paper) to *Berichte der deutschen botanischen Gesellschaft*, the most prestigious botany journal in Germany. In that paper, Correns (1900a) inferred that Mendelian segregation and assortment occurred in the nucleus, thereby shifting the focus from theory to mechanism (Gliboff, 1999).
- Although Correns' rediscovery paper was largely an attempt to explain Mendel's paper, it was nevertheless remarkable (Orel, 1996):
  - Correns discovered the 9:3:3:1 ratio for offspring of crosses differing in two traits. Although this suggests that Correns understood the independent assortment of two pairs of genes (with dominance), he never stated such independence.
  - Correns explained Mendel's theory as the determination of each trait by two hereditary units. Bateson later would call these traits allomorphos, then alleles (Bateson, 1894).
  - Unlike de Vries and Tschermak, Correns thoroughly understood Mendel's work (Corcos and Monaghan 1987c). Correns' data (which included tabular results for experiments with *Pisum* and *Zea*) and explanations are more complete and more convincing than are those of either Tschermak, Mendel, or de Vries. Moreover, Correns' discussion went far beyond Mendel's original idea; Correns even suggested a theory of inheritance that is a simple version of what we now call Mendelian genetics. Correns supported his 9:3:3:1 discovery by showing that his data from *Zea* and Mendel's data gave "a good approximation of the ratio."
    - Although Mendel had used the German word *Merkmal* to describe what his rediscoverers later translated as "factor," Correns used *Anlage* – a word that, unlike *Merkmal* and *Elemente*, described a discrete determinant that could move from parent to offspring. In this sense, *Anlage* was much closer to our understanding of a gene than was Mendel's *Merkmal*. *Anlage* also implies that it is not the trait itself, but instead codes for events that lead to the trait (Henig 2000). According to Correns' thinking, each trait had a single *Anlage*, which was either dominant or recessive, whereas hybrids have one of each form. The dominant *Anlage* suppresses the recessive *Anlage*, but doesn't change it.
    - Correns was the first to explicitly link one factor of inheritance with one character; to report cases of linkage; to see that the four different phenotypes produced by a dihybrid cross "must occur in a ratio of 9:3:3:1," and to suggest that segregation was due to meiosis: "The earliest time at which this separation might occur is the time of formation of the primordial *anlage* of both the seed and the anthers. The numerical ratio of 1:1 strongly suggests that the separation occurs during a nuclear division, the reductive division of Weisman..."
    - Moreover, Correns suggested that an organism's entire set of *Anlagen* was in its cells' nuclei (Henig, 2000). These observations question the claim (e.g., Lander and Weinberg, 2000) that Correns' paper "revealed little more than what Mendel had found 35 years earlier."
    - Correns suggested that every trait is based on an *anlage*, which is a hypothetical nuclear unit that causes the trait to be expressed. This explained segregation, dominance, and recessiveness; since hybrids express only one trait, one *anlage* must suppress the expression of another (Corcos and Monaghan, 1990). Correns was the first to suggest that a pair of characters are determined by a pair of *anlagen*, noting that "A complete

separation of the two *anlagen* ... so that one half of the reproductive nuclei receive the *anlage* for the recessive trait, ... the other half the *anlage* for the dominating trait.”

- The random recombination of these *anlagen* in zygotes gave Correns an explanation of how the parental types could be recovered from hybrids.
- Of the three rediscoverers, only Correns fully understood Mendel’s paper (e.g., Corcos and Monaghan 1990). Correns’ conclusion was bold: “*This I call Mendel’s Principle ... Everything else may be derived from it.*”
- Another paper written by Correns published in 1900 (Correns, 1900b) involving *Levkojen* hybrids defined two Mendelian principles and showed the linkage of some traits. Correns used a footnote to add that Mendel had earlier noted the association of different features (e.g., coloration of seed coat, flowers, and pigmentation of leaf axils).
- Correns claimed to have figured out the explanation of the 3:1 ratio in October 1899, several weeks before he read Mendel’s paper, but he did not mention this explanation in the paper that he published in December (Correns 1899). In 1900 (Correns, 1900a), Correns did not cite Mendel’s paper, but he did refer to Mendel’s earlier discovery: “... the behaviour is the same as that found when yellow and green pea seeds are bastardized, as has been correctly pointed out by Darwin and Mendel.”
- When Correns saw de Vries’ paper, he suspected that de Vries’ wanted to hide Mendel’s earlier discovery of the 3:1 segregation ratio. In his “rediscovery” paper, Correns (1900a) used sarcasm and understatement to point out de Vries’ use of Mendel’s terms (Stern and Sherwood, 1966; emphasis in original): “This one may be called the **dominating**, the other one the **recessive** anlage. Mendel named them in this way, and by a strange coincidence, de Vries now does likewise.”
- This was no coincidence, for de Vries had learned of Mendel’s paper (that notes a 1:2:1 ratio in F<sub>2</sub> progeny) in 1892 from a bibliography of L.H. Bailey (1892). This may account for de Vries’ mention of a “1:2:1 law” for pangenesis in hybridization in some of his correspondence before 1900 (Zevenhuizen, 1996). As de Vries later noted in a letter to Bailey (Edwardson, 1962), “Many years ago you had the kindness to send me your article on “Cross-breeding and hybridization” of 1892; and I hope it will interest you to know that it was by means of your bibliography therein that I learnt some

years afterwards of the existence of Mendel’s papers, which now are becoming to so high credit.”

- Just as Correns had de Vries’ paper available before he wrote his rediscovery paper, so too did Tschermak have the papers of both de Vries and Correns in hand when he wrote his rediscovery paper. Tschermak (1958) later claimed that when he visited de Vries in Amsterdam in 1898, de Vries knew of Mendel’s work and was verifying the results in other hybrids. Such observations have prompted Meijer (1982) to conclude that de Vries – like many others -- knew of Mendel’s work before 1900, but “failed to understand its full extent” (also see Corcos and Monaghan, 1987a & b).



- After seeing de Vries’ paper (de Vries, 1900a), Correns realized that he’d lost the priority of the discovery of the 3:1 ratio. Rather than allow de Vries to get credit for the discovery, Correns quickly wrote a paper that gave Mendel credit for de Vries’ findings (Correns, 1900a). Correns went out of his way to show readers that de Vries’ claims were, in fact, made decades earlier by Mendel: “*After my discovery of the law of behaviour and its explanation ... I have experienced what apparently de Vries experiences now: I thought it was something new.* But then I had to convince myself that the abbot Gregor Mendel in Brünn, during the sixties, had not only come up with the same results as de Vries and I, through his elaborate experiments over many years with peas, but that he had also given the same explanation, as far as that was possible in 1866.” (emphasis Correns’)

- In the next line, Correns further praised Mendel's work by proclaiming that "Mendel's paper is among the best that have ever been written about hybrids ..."
- Correns, who had learned of Mendel's work from his teacher Nägeli (Roberts, 1929), used his paper's title to cite Mendel and elevate Mendel's findings to a "law": "G. Mendel's Law on the Behaviour of Progeny of Variable Hybrids" (Correns, 1990a). Rather than give de Vries credit for Mendel's work, Correns cited Mendel's work as the original idea, and then made himself one of Mendel's prophets (Brannigan, 1981).

These observations are consistent with Mendel's fame being largely due to how Mendel's work was used by others (e.g., Correns and de Vries) to promote themselves in a priority dispute. Indeed, Correns ensured that Mendel, not de Vries, would get credit for the 3:1 ratio, and thereby played a major role in transforming Mendel's results into Mendel's laws. Correns' paper read importance back into Mendel's original work, and was a critical step in the "rediscovery" of Mendel (MacRoberts, 1985).

Unbeknownst to Correns, de Vries had written another paper -- one of three that he wrote in 12 days (de Vries, 1900b; also see Zirkle, 1968; Roberts, 1929). This was the only one of de Vries' "rediscovery papers" in which de Vries discussed the results of his dihybrid crosses. In that paper (written in German and submitted for publication on 14 March 1900), de Vries promoted his theory of pangensis. He also mentioned Mendel:

"From these and other numerous experiments I conclude that the law of segregation of hybrids as discovered by Mendel for peas has a very general application in the plant kingdom, and has a basic significance for the study of the units of which the specific characters are composed."

Contrary to this claim by de Vries, Mendel never stated a law of segregation; de Vries must have inferred it from Mendel's paper (consistent with this is the fact that de Vries stated it differently in each of his "rediscovery" papers). de Vries noted that recessive traits in his crosses accounted for 22-28% of hybrids' progeny, and that back-crosses yielded a segregation ratio of 1:1 (de Vries 1990b). de Vries used a footnote to add that Mendel's work "is so rarely quoted that I myself did not become acquainted with it until I had concluded most of my experiments, and had independently deduced the above propositions." Neither Mendel nor de Vries ever mentioned that there is one unit of heredity in sex cells or that there are two in vegetative cells.

de Vries' appreciation of Mendel's ideas was short-lived, however. After initially believing that Mendel's work supported his theory of pangensis, de Vries subordinated Mendel's theory to his own theory of mutation, despite the fact that his explanations entangled him in many contradictions (e.g., Stamhuis, et al., 1999). de Vries claimed that Mendel's data were for a "special case" (Meijer, 1982; MacRoberts, 1985; Olby, 1985),

"The essential parts of these principles ... have been formulated already by Mendel a long time ago for a special case (peas). They went into oblivion ... and were overlooked."

In a third paper, also published in 1900, de Vries (1900c) summarized how his experiments with hybrids related to his theory of intracellular pangensis. de Vries concluded that,

"This law is not new. It was stated more than thirty years ago, for a particular case (the garden pea). Gregor Mendel formulated it in a memoir entitled "Versuche über Planzaenhybriden" in the Proceedings of the Brünnner Society. Mendel here has shown the results not only for monohybrids, but also for dihybrids."<sup>8</sup>

William Bateson, a Cambridge zoologist who rejected Darwin's ideas about gradualism, learned of Mendel's work by reading de Vries' and Correns' "rediscovery" papers. On 8 May 1900, while aboard a Great Eastern Railway train to the meeting of the Royal Horticultural Society in Liverpool, the 40-year-old Bateson read Mendel's paper and recognized its significance (Bateson's wife remarked that it was as though "with a very long line to hoe, one suddenly finds a great part of it already done by someone else.") Bateson rewrote his lecture to feature Mendel's work. Bateson, who later extended the validity of Mendel's theory to the animal kingdom (Bateson and Saunders, 1902), believed that Mendel's work confirmed his concept of discontinuous variation (Bateson, 1894). Soon after reading Mendel's paper, Bateson used Mendel's work to proclaim the birth of a new science -- he termed it *genetics* -- that was in total opposition to Darwin's ideas. Bateson also noted that some of the key findings in the papers by de Vries and Correns were made by Mendel (MacRoberts, 1985; Olby, 1985). Bateson and several others had Mendel's paper re-published in several English-language journals and books (Brannigan, 1979 & 1981), thereby completing the promotion and accompanying "rediscovery" of Mendel's work.

Perhaps de Vries did not consider the Mendelian discovery to be important as he pursued his own research (Stamhuis, 1995). Nevertheless, de Vries continued to downplay Mendel's contributions



(Theunissen, 1994; Stamhuis et al, 1999 and references therein). In late 1901, de Vries continued his efforts to convince Bateson that Mendelism “is an exception to the general role of crossing” and claimed that the separation of hereditary factors does not occur in Mendelian crosses (Stamhuis et al., 1999). Later, de Vries refused to sign a petition calling for the construction of a memorial to Mendel in Brunn, and even rejected an invitation to attend a 1922 celebration of Mendel’s work. As he explained to his friend F.A.F.C. Went in September of that year (Stamhuis et al., 1999),

“To my regret I cannot accede to your request. I just don’t understand why the academy would be so interested in the Mendel celebrations. The honoring of Mendel is a matter of fashion which everyone, also those without much understanding, can share; this fashion is bound to disappear. The celebration in Brunn is nationalistic and anti-English, directed especially against Darwin and

thus unsympathetic to my mind but, therefore, also very popular.”

### Summary

The history of science includes many famous priority disputes (e.g., Leibniz and Newton about calculus; discovery of the AIDS virus; see Hellman, 1998). Similarly, many important findings have been known but ignored for decades (e.g., Barbara McClintock’s discovery of transposons). Many aspects of the “rediscovery story” of Mendel’s paper are inaccurate. Mendel’s original paper announced no major findings; it was known and acknowledged as “typical” science for its day. When it was “rediscovered,” Mendel’s paper became famous as a result of a priority dispute between de Vries and Correns. This dispute prompted researchers to reinterpret and read importance into Mendel’s paper.



### Footnotes

1. Since 1918, Brunn has been known by its Czech name Brno.
2. To deduce “true numerical ratios,” Mendel knew that large sample-sizes were essential; as he explained, “the greater the number, the more effectively will mere chance be eliminated.” Mendel, who hand-pollinated his plants, was also keenly aware of the tedium that these large samples produced; as he noted, “It requires indeed some courage to undertake a labor of such far-reaching extent; this appears, however, to be the only right way by which we can finally reach the solution of a question the importance of which cannot be overestimated in connection with the history of the development of organic forms” (see Simmons, 1996). The methods that Mendel used to design his experiments and interpret his results were influenced by his studies of math and physics when he attended the University of Vienna. Until 1854, Mendel had studied breeding mice. However, the church didn’t like this work, and Mendel was encouraged to change his research. Thus, when Bishop

- Anton Ernst Schaffgotsch visited Mendel in Brunn in 1854, Mendel agreed to begin growing plants. He later noted, “the bishop didn’t understand that plants also have sex” (Henig, 2000).
3. Although Mendel may have had other important insights, we’ll never know; his experimental notebooks were destroyed after he died.
  4. Contrary to myth, Mendel was not a shy, secluded person; he traveled, was active in several professional societies, directed an organization for deaf and mute children, and was chairman of mortgage bank (Iltis, 1932). In addition to working in the monastery’s garden and 550-year-old glasshouse, Mendel devoted much of his time to bee-keeping and meteorology; for almost 30 years, Mendel collected weather data three times per day, and during his lifetime, Mendel was more famous for forecasting the weather than for breeding plants (Orel, 1996). Mendel also spent a lot of time doing the administrative chores that accompanied his appointment on 30 March 1868 as abbot of the modest St. Thomas monastery. Near the end of his life, Mendel’s administrative duties embroiled him in a bitter tax-dispute with the government, and he isolated himself from most people. He then developed heart disease and kidney problems, and began smoking 20 cigars per day. He spent his last days sitting on a couch with his feet in bandages (Simmons, 1996). For more about Mendel’s life, see Orel (1996) and <http://www.stg.brown.edu/MendelWeb/>
  5. For example, new ideas from cytology led de Vries to his theory of intracellular pangenesis. de Vries rejected much of Darwin’s “gemmules” hypothesis, and renamed the carriers of heredity *pangenes* (de Vries, 1889).
  6. Before 1900, de Vries reported his data as raw data, not ratios. This is consistent with de Vries not having had a Mendelian perspective before 1900. Indeed, there is a big difference between reporting numbers of plants having different characteristics, discerning a similar ratio, and deducing a theoretical ratio that leads to a fundamental understanding of biology.
  7. Before 1900, de Vries did not claim (as he did in 1900) that *anlagen* are side-by-side in hybrids and separate in egg and pollen. Instead, de Vries used a model of an urn with black and white balls, from which came two balls represented the formation of offspring.
  8. In fact, Mendel (1866) performed seven monohybrid studies, two dihybrid studies, and one trihybrid study.
  9. Bateson later rejected and campaigned against the chromosomal theory of heredity (Olby, 1985). Bateson’s vigorous promotion of Mendelism (and his rejection of Darwinian evolution) hindered the development of genetics in Great Britain (Olby, 1985). At the end of his life, Bateson admitted to his son Gregory (named after Mendel) that his devotion to Mendelism “was a mistake,” for it was “a blind alley which would not throw any light on the differentiation of species, nor on evolution in general” (Koestler, 1971)

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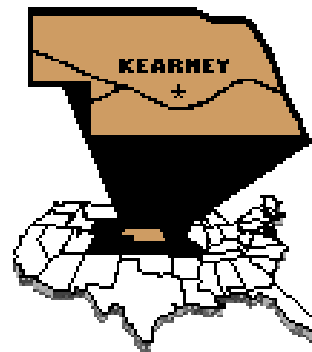
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