

Darwin's Influence on Mendel: Evidence from a New Translation of Mendel's Paper

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ABSTRACT Gregor Mendel's classic paper, *Versuche über Pflanzen-Hybriden* (Experiments on Plant Hybrids), was published in 1866, hence 2016 is its sesquicentennial. Mendel completed his experiments in 1863 and shortly thereafter began compiling the results and writing his paper, which he presented in meetings of the Natural Science Society in Brünn in February and March of 1865. Mendel owned a personal copy of Darwin's *Origin of Species*, a German translation published in 1863, and it contains his marginalia. Its publication date indicates that Mendel's study of Darwin's book could have had no influence while he was conducting his experiments but its publication date coincided with the period of time when he was preparing his paper, making it possible that Darwin's writings influenced Mendel's interpretations and theory. Based on this premise, we prepared a [Darwinized English translation of Mendel's paper](#) by comparing German terms Mendel employed with the same terms in the German translation of *Origin of Species* in his possession, then using Darwin's counterpart English words and phrases as much as possible in our translation. We found a substantially higher use of these terms in the final two (10th and 11th) sections of Mendel's paper, particularly in one key paragraph, where Mendel reflects on evolutionary issues, providing strong evidence of Darwin's influence on Mendel.

A few pages into the first chapter of the 1859 first edition of Darwin's *Origin of Species*, readers encounter a sentence that succinctly states what was true at the time: "The laws governing inheritance are quite unknown" (Darwin 1859, p. 13). Ten years later, in the fifth edition, Darwin slightly altered the wording: "The laws of inheritance are for the most part unknown" (Darwin 1869, p. 14). By this time Mendel's classic paper *Versuche über Pflanzen-Hybriden* (Experiments on Plant Hybrids) had been in print for slightly more than 2 years. Yet, there is compelling evidence that Darwin knew nothing of Mendel then, or at any time of his life, in spite of much speculation to the contrary. Some historians have lamented that had Darwin read Mendel's paper, a "meeting of the minds" between the two might have ensued that would have dramatically altered the course of modern biology; others counter that their views were too divergent for them to have found common ground (for reviews, see Olby 1985, Sapp 1990, Orel 1996, and Fairbanks and Rytting 2001).

This lament that Darwin knew nothing of Mendel has unfortunately eclipsed evidence that Mendel, by contrast,

was well acquainted with Darwin's writings. Although Mendel probably knew little about Darwin when conducting his pea experiments, the situation abruptly changed when he obtained a copy of *Origin of Species* in 1863, the final year of these experiments. It was a German edition, translated by H. G. Bronn, and Mendel marked a number of passages in it (Figure 1). Mendel's marginalia offer strong circumstantial evidence that he read *Origin of Species* while composing his classic paper from 1863 to early 1865, and that it may have influenced him. We will augment this here with further evidence of Darwin's influence from Mendel's paper itself, and discuss the new Darwinized translation of Mendel's paper we have prepared.

English Translations of Mendel's Paper

It is well known that Mendel's discoveries languished in near obscurity for 35 years, from the time he presented them in 1865 until the first months of the 20th century. In 1900, Hugo de Vries, Carl Correns, and Erich Tschermak von Seysenegg published the results of experiments they independently carried out, confirming the principles Mendel had discovered and rapidly elevating Mendel's paper from its long neglect to widespread fame. This event is known as "the rediscovery," although to what extent de Vries, Correns, and Tschermak

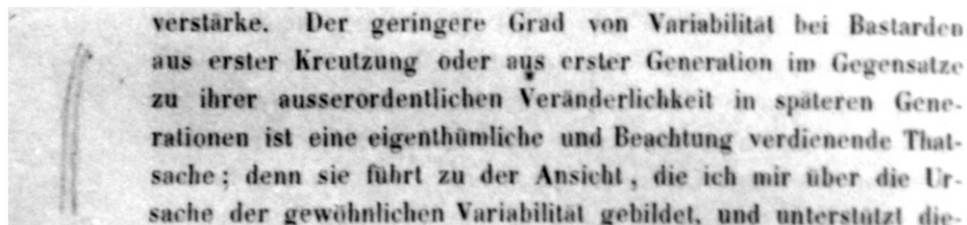


Figure 1 Example of a passage in *Origin of Species* marked by Mendel. In Darwin's original English, this passage reads, "The slight degree of variability in hybrids from the first cross or in the first generation, in contrast with their extreme variability in the succeeding generations, is a curious fact and deserves attention." For commentary regarding Mendel's marginalia in *Origin of Species*, see Fairbanks and Rytting (2001).

actually *rediscovered* Mendel's principles of inheritance has been disputed in light of evidence that Correns and de Vries may have read Mendel's paper before arriving at their conclusions, and that Tschermak may not have fully understood Mendel's interpretations (Zirkle 1964; Olby 1985; Reinberger 1999).

Shortly after the rediscovery, William Bateson arranged for the Royal Horticultural Society of London to commission and publish an English translation of Mendel's paper (Mendel 1901). Bateson soon thereafter became embroiled in a high-profile public debate with W. F. R. Weldon over the validity of Mendel's discoveries (Radick 2015), which drew widespread attention to Mendel's paper in the scientific community. An article by Weldon (1902) criticizing Mendel's experiments prompted Bateson to publish a book titled *Mendel's Principles of Heredity: A Defence* (Bateson 1902). In it, Bateson fanned the flames of controversy with sarcastic attacks against Weldon, such as his claim that Weldon was "about as likely to light a fire with a wet dish-clout as to kindle interest in Mendel's discoveries by his tempered appreciation" (Bateson 1902, p. 208). The book included the full text of the Royal Horticultural Society translation, which rapidly became the standard source in English. It soon was reprinted in several subsequent books, continuing throughout the remainder of the 20th century, and more recently online. British poet, author, and botanist Charles Thomas Druery was principal translator of the first draft (Olby 2000), but was not acknowledged in the published translation. In recognition of Druery's contribution, commentators have in recent years referred to it as the Druery–Bateson translation (Hartl and Fairbanks 2007; Franklin *et al.* 2008), which we also will do hereafter. In spite of serious flaws and inaccuracies, it has endured as the principal source of Mendel's paper in English for more than a century.

At the centennial of Mendel's paper in 1966, Curt Stern and Eva Sherwood published a book titled *The Origin of Genetics: A Mendel Source Book*, which includes a collection of reprinted and translated documents relevant to Mendel (Stern and Sherwood 1966). Stern, who was a native German speaker, recruited Eva Sherwood, also a native German speaker, as principal translator for a new English version of Mendel's paper, which they undertook because they felt that the Druery–Bateson translation was seriously flawed (Stern and Sherwood 1966), a view with which we concur. We refer

to their version as the Sherwood–Stern translation to maintain consistency with the first version by naming the principal translator first.

This second translation is generally accepted as the more accurate of the two and is often quoted in scholarly articles. The Bateson–Druery translation nonetheless has continued to attract widespread use, both in scholarly publications and in popular references to Mendel, for at least two principal reasons. First, it is in the public domain and is freely available online in stand-alone websites and in books whose copyrights have expired and have been posted online. The Sherwood–Stern translation is not as readily available because it remains under copyright, preventing unrestricted dissemination, and Stern and Sherwood's book is currently out of print.

Second, much of the published commentary on Mendel's paper consists of articles addressing the Mendel–Fisher controversy, based on a 1936 paper, "Has Mendel's work been rediscovered?" by the famed statistician and population geneticist Ronald Fisher (Fisher 1936). His paper consists of a mostly successful attempt to reconstruct Mendel's experiments, and to place Mendel's discoveries in the context of Darwinian thought. Fisher's admiration for Mendel is evident throughout the paper, which he concluded with the observation that Mendel had published "experimental researches conclusive in their results, faultlessly lucid in presentation, and vital to the understanding not of one problem of current interest, but of many" (Fisher 1936, p. 137). The paper, however, is remembered not for Fisher's praise of Mendel but for his application of Pearson's chi-square goodness-of-fit test to Mendel's data, and his inference that "the data of most, if not all, of the experiments have been falsified so as to agree closely with Mendel's expectations (Fisher 1936, p. 132). In correspondence with the journal's editor, E. B. Ford, Fisher referred to this inference as an "abominable discovery," yet could not convince himself that Mendel would commit scientific fraud, presuming instead "that Mendel was deceived by some assistant who knew too well what was expected" (Fisher 1936, p. 132).

Although Fisher's paper was published in 1936, the controversy it generated only began in earnest in the mid-1960s, shortly after Fisher's death. It consists of numerous articles and book chapters spanning nearly a half century, debating the validity of Fisher's claim that Mendel's data had been falsified. It faded in 2008 when a book titled *Ending the*

Mendel-Fisher Controversy (Franklin *et al.* 2008) essentially accomplished what its title purported to do. Throughout the years of the controversy, authors who addressed it repeatedly cited the Druery–Bateson translation because Fisher used it exclusively when referring to Mendel, never questioning its accuracy nor referring to the original German when dealing with critical passages. In fact, some aspects of the Mendel–Fisher controversy may be attributed to Fisher’s reliance on this translation (Fairbanks and Rytting 2001).

A New Darwinized Translation of Mendel’s Paper

Both the Druery–Bateson and Sherwood–Stern translations share a serious shortcoming: both lack the Darwinian influence that a careful reading and analysis of Mendel’s original German article reveal. Given the strong circumstantial evidence that Mendel studied *Origin of Species* while preparing his manuscript, the case for inclusion of Darwinian phraseology when translating Mendel’s paper into English, is compelling, as discussed below, and served as the initial premise for our translation.

This translation has two principal objectives. First, we intend it to be more accurate than the Druery–Bateson translation and more accessible than the Sherwood–Stern translation. To maximize accessibility, we have made it freely available online through open-access format with no restrictions on reproduction in whole or in part other than appropriate citation (<http://www.genetics.org/content/204/2/407>). Second, given that a German translation of *Origin of Species* was probably the only source originally written in English that influenced Mendel at the time he drafted his paper, we made an exhaustive effort to employ Darwin’s phraseology from *Origin of Species* when choosing English words in the translation. This provides it with a decidedly 19th century Darwinian tone, which, of course, is consistent with the time when Mendel presented and published his paper. Lastly, its publication celebrates the sesquicentennial of Mendel’s paper.

Both the Druery–Bateson and Sherwood–Stern translations were the products of two-person teams in which one individual produced an initial draft of the translation (Druery and Sherwood), and the other was a geneticist who was fully familiar with Mendel’s research (Bateson and Stern). Our collaboration mirrors these. S.A. is a scholar of 19th and 20th century German literature who specializes in German–English translation, including German medical documents coincident with Mendel’s presentation in 1865 (Carter *et al.* 1995). D.J.F. is a geneticist with an academic background in plant genetics who has published on Mendel and the Mendel–Fisher controversy (Fairbanks and Rytting 2001; Hartl and Fairbanks 2007; Fairbanks and Schaalje 2007; Franklin *et al.* 2008; Westerlund and Fairbanks 2010). To ensure that previous translations would not unduly influence ours, Abbott produced the first draft as an entirely “clean” translation, without consulting other translations. Fairbanks then reviewed the draft for botanical accuracy, comparing

Mendel’s botanical German with English counterparts, and making appropriate corrections. We then together set about Darwinizing the translation by exhaustively cross-comparing German words and phrases in Mendel’s paper with those in the Bronn translation of *Origin of Species*, then identified the corresponding words or phrases in Darwin’s original English. We used the corresponding English phraseology employed by Darwin in our translation, except in those instances when doing so would deviate from Mendel’s obvious intended meaning, when Bronn’s translation was erroneous, or when doing so resulted in awkward English.

Evidence of Darwin’s Influence on Mendel

An important discovery that emerged from this effort was strong evidence of Darwin’s influence on Mendel’s writing. Under the premise that the passages Mendel marked in *Origin of Species* may have preferentially influenced his writing, we color-coded words and phrases in his original German paper that matched words and phrases from the passages Mendel marked in his German translation of *Origin of Species* (excluding common words whose function is more grammatical than substantive). We then used a different color to denote words and phrases not in the passages Mendel marked but found elsewhere in *Origin of Species*. Both types of phraseology were collectively abundant in the paper.

This color coding revealed that phraseology from the passages Mendel marked in *Origin of Species* are more frequent and more diverse in the final two (10th and 11th) sections of his paper. In particular, such terms overwhelmingly clustered in one paragraph just prior to the final section, subtitled “Concluding Remarks.” This observation offers particularly strong evidence that Darwin’s book influenced Mendel’s writing. Fisher likewise noted the Darwinian nature of this paragraph when quoting a portion of it, then commenting, “The reflection of Darwin’s thought is unmistakable and Mendel’s comment is extremely pertinent, though it seems to have been overlooked” (Fisher 1936, p. 134). The following is our English translation of the latter (most Darwinian) portion of this paragraph. Words corresponding to German words found in Mendel’s copy of *Origin of Species* are in boldface type; those from the passages in *Origin of Species* marked by Mendel are also underlined. Those labeled with asterisks are cases in which the German word appeared in *Origin of Species* but we chose an English word not used by Darwin (for reasons stated earlier), in which case, we note the Darwinian term in brackets. Words in italics correspond to German words that we searched in Bronn’s translation but did not find.

No one will **seriously assert** that the **development of plants** in a **natural*** [free] **landscape** is **governed** by **different laws** than in a **garden bed**. Here, just as there, **typical variations** must **appear** if the **conditions of life** are **changed** for a **species**, and it **has** the **ability** to **adapt** to the **new conditions**. It is **freely admitted*** [looked], through **cultivation** the **production** of **new varieties** is **favoured**, and by the **hand** of **man** **many** a **variation** is **preserved** that

would have failed in the wild* [free] state, but nothing gives us the right to assume that the tendency for new varieties to form is so extremely augmented that species soon lose all stability and that their offspring break up into an infinite array of highly variable forms. If the change in the conditions of vegetation were the sole cause of variability, then one would be justified in expecting that those domesticated plants cultivated under almost the same conditions for centuries would have acquired stability. As is well known, this is not the case, for especially among them not only the most different but also the most variable forms are found. Only the Leguminosae, like Pisum, Phaseolus, Lens, whose organs of fructification are protected by a keel, constitute* [make] an appreciable exception. Even for these, numerous varieties have arisen during cultivation for more than 1000 years under the most diversified conditions; however, under the same permanent conditions of life, they retain stability similar to that of species growing in the wild.

A majority of Darwinian terms in this paragraph are from passages Mendel marked, and several illustrate the effect of Darwinization on our translation. The most obvious is the term *Lebensbedingungen*, which Mendel used twice in his paper, both instances in this paragraph. *Lebensbedingungen* appears three times in passages Mendel marked in *Origin of Species*, in each case corresponding to Darwin's "conditions of life," which is a quintessentially Darwinian phrase, appearing 107 times in *Origin of Species*. Bronn consistently translated it as *Lebensbedingungen*, *Lebens-Bedingungen*, or *Lebens Bedingungen*. In the Sherwood–Stern translation, this term is translated both times as "living conditions," whereas in the Druery–Bateson translation, it is translated as "conditions of life" in the first instance and "environments" in the second.

Although this paragraph appears very near the end of Mendel's paper, there are several terms from the passages Mendel marked in *Origin of Species* which, like *Lebensbedingungen*, he used for the first time in this paragraph, and nowhere else in his paper. Examples include *anzupassen* = "to adapt," *Variabilität* = "variability," and *Fähigkeit* = "ability." Moreover, other terms from the passages Mendel marked appear for the first time in this paragraph, and then again shortly thereafter in subsequent paragraphs, such as *Entstehung* = "production," *auseinander* = "break up," and variants of *veränderlich* = "variable." Notably, Mendel appears to have consciously or unconsciously reserved these terms for the conclusion, having used synonyms of some of them in earlier sections.

A key Darwinian term employed by Mendel 10 times, yet only in the "Concluding Remarks" section of his paper, is the German word *Element*, which is unambiguously translatable to English as "element." In every instance, Mendel used it to refer to his conception of material hereditary units that are variable and distinctly genotypic, what geneticists now refer to as alleles or variants. There is good reason to surmise that *Origin of Species* may have influenced Mendel's choice of this term. Although by 1868, Darwin began describing underlying hereditary units as "gemmules" when proposing his

"provisional hypothesis of pangenesis" (Darwin 1868), he consistently used the English word "element" to denote hereditary material in *Origin of Species*, which Bronn translated in almost every case as *Element*. For example, Darwin's first use of this term in *Origin of Species* appears in Chapter 1 as "the male and female reproductive elements" near a passage Mendel marked (Darwin 1859, p. 14). Lest anyone question whether Darwin used "elements" to refer to reproductive organs rather than the material hereditary content of gametes, he made his intent quite clear in the statement "the two sexual elements which go to form the embryo" (Darwin 1859, p. 246), and, in reference to attempted hybridization of reproductively incompatible plant species (also near a passage Mendel marked): "There must sometimes be a physical impossibility in the male element reaching the ovule, as would be the case with a plant having a pistil too long for the pollen-tubes to reach the ovarium" (Darwin 1859, p. 263).

Conclusion

What might have happened if Darwin had known of Mendel is a matter for speculation. On the other hand, there is no question that Mendel was well aware of Darwin. His overt references to Darwin postdate his classic 1866 paper. He mentioned "the spirit of the Darwinian teaching" in his 1870 paper "On *Hieracium* hybrids obtained through artificial fertilisation" (Stern and Sherwood 1966, p. 51), and referenced Darwin three times in letters to Carl von Nägeli, also all in 1870 (Fairbanks and Rytting 2001). Though he never mentioned Darwin by name in his classic 1866 paper "Experiments on plant hybrids," he probably read *Origin of Species* while composing the manuscript. Our new translation of Mendel's paper offers strong evidence of Darwin's influence. Mendel preferentially employed terms from passages he marked in his German translation of *Origin of Species* in the final two sections of this paper where he addressed the role of hybridization in evolution. This is especially the case in one key paragraph where Mendel discussed how "conditions of life" (*Lebensbedingungen*) affect the evolution of cultivated plants. To what extent Mendel accepted Darwinism at the time remains an open question. The evidence from our translation, however, supports Fisher's assertion that in the conclusion of Mendel's paper "the reflection of Darwin's thought is unmistakable" (Fisher 1936, p. 134).

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