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ARTICLE

Mendel's reaction to Darwin's provisional hypothesis of pangenesis and the experiment that could not wait

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INTRODUCTION

In 1868 Charles Darwin published his book *The Variation of Animals and Plants Under Domestication* in short "*Variation under Domestication*" which comprised two volumes and 28 chapters, one of which presented his provisional theory of inheritance, which he called "Pangenesis". Gregor Mendel bought a copy of the German translation in early 1869. Mendel's copy is annotated with lines in the margins and underscored sentences, indicating which passages he considered important. The great majority of Mendel's annotations are found in the chapter on pangenesis. From the few comments Mendel wrote, it can be concluded that he found Darwin's ideas highly speculative. Several annotations relate to Darwin's claim that multiple pollen grains must fertilize an egg cell to form a seed. In contrast, Mendel's theory of inheritance was based on the random union of one egg cell and one pollen grain. Mendel wrote to Carl Nägeli, in Munich, that this matter was so important that he had to conduct single-grain pollination experiments in *Mirabilis* despite suffering from eye ailments. Mendel's result was consistent with his theory; in all 18 attempts, a single pollen grain was sufficient to form a seed and vigorous offspring. The following year he repeated the experiment with the same result. In addition, for Mendel's theory, no more than one pollen grain should fertilize an egg cell. Mendel tested this by conducting pollinations with two different grains simultaneously; each from a plant with different flower color. Information about the outcome of this experiment has not survived, but the design of the experiment provides an insight into Mendel's clear thinking. Here we contrast Mendel and Darwin's views of inheritance.

DARWIN'S PROVISIONAL PANGENESIS HYPOTHESIS

Charles Darwin's theory of evolution by natural selection requires both a source of heritable variation and a mechanism by which this variation is inherited. Darwin had been developing his ideas on inheritance since the 1840s (Olby 1985), and eventually he proposed a theoretical mechanism which he called pangenesis, first published in 1868 in *Variation under Domestication*:

> "In variations caused by the direct action of changed conditions, whether of a definite or indefinite nature, as with the fleeces of sheep in hot countries, with maize grown in cold countries, with inherited gout, etc., the tissues of the body, according to the doctrine of pangenesis, are directly affected by the new conditions, and consequently throw off modified gemmules, which are transmitted with their newly acquired peculiarities to the offspring". (Darwin 1868 Variation under Domestication p 394 vol 2)

Gemmules were proposed to be minute granules released by cells and which circulated freely throughout the body where they could multiply under favorable conditions. The type and quantity the various gemmules was thought to be responsible for an observed phenotype. Gemmules would accumulate in the reproductive cells and be transmitted to the offspring, hence becoming heritable. Gregor Mendel had published his "Experiments on Plant Hybrids" (Mendel 1866, 2016) two years earlier. Darwin's theory and Mendel's 1866 interpretation of inheritance have some similarities; both propose the existence of discrete determinants of character states and these can be latent, depending on the state of other determinants. There are important differences; Darwin's gemmules could be affected by the environment, Mendel's elements not. Gemmules were explicitly particles, they accumulated in vegetative buds as well as sex cells, so latent gemmules could become manifest as a somatic sector. In hybrids new types of gemmules were created. For Darwin, the quantity of gemmules was important for determining the appearance of an organism, a deficiency of gemmules led to sterility and excess to parthenogenesis. For Mendel it was the type of inherited element that mattered and whether the type(s) inherited from the male and female parent were the same or different; hybrids simply had both the maternal and paternal type of element.

For Darwin, there was no clear difference between growth, vegetative reproduction, parthenogenesis and sexual reproduction. Darwin was aware that Pangenesis was a hypothesis (even a provisional one), but in his view, it was the best explanation of a wide variety of phenomena, such as limb regrowth in amphibians, parthenogenesis, and the re-emergence of ancestral features, in one comprehensive conceptual structure.

Darwin was aware of the behavior of grafts in plants; he cultivated the periclinal chimera Adam's laburnum and discussed it in *Variation under Domestication* (volume 1, p 469), he also wrote to Thomas Rivers in 1862 (Darwin, 1862):

> "I want these facts partly to throw light on the marvellous Laburnum Adami—Trifacial oranges &c. That Laburnum case seems one of the strangest in physiology: I have now growing

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splendid, fertile yellow Laburnums (with long racemes like the so-called Waterer's Laburnum) from seed of yellow flowers on the L. adami".

Even in such a close association in which two species 'unite their cellular tissue' the gemmules appeared to remain distinct.

Soon after his provisional hypothesis of Pangenesis was published, Darwin's half-cousin, Francis Galton, tested the theory by performing blood transfusion experiments with rabbit breeds of different coat colors (Galton 1871). If the gemmules were in the bloodstream, the color of the fur of the offspring of transfused rabbits would be expected to show an influence of the blood donor. However, the results of these experiments were negative (Bulmer 1999). Darwin objected:

"I have not said one word about the blood, or about any fluid proper to any circulating system" and "when I used these latter words and other similar ones, I presume that I was thinking of the diffusion of the gemmules through the tissues, or from cell to cell, independently of the presence of vessels" (Darwin 1871).

Despite these obvious difficulties, Darwin was reluctant to give up Pangenesis (see also Galton 2018).

Darwin's ideas are easily compatible with a theory of blending inheritance, while Mendel's are not. These similarities and differences would have been of interest to Mendel. In 1869, Mendel obtained both volumes of the German edition of Darwin's *Variation under Domestication*, which are still present in the Mendel Museum in St. Thomas Abbey, Brno; Mendel's annotations of these were published by Richter (1943) and can be found in Fairbanks (2020). Mendel's letters to Nägeli, the Munich botany professor, published by Correns (1905) and translated into English by Piternick and Piternick (1950), also describe Mendel's reaction to Darwin's Pangenesis. Here we explore Mendel's comments on pangenesis, based on Richter (1943).

MENDEL'S MARGINALIA IN DARWIN'S *VARIATION UNDER DOMESTICATION*

Mendel's volumes of the German edition of Darwin's *Variation under Domestication* were paper-bound, and three-quarters of the pages of volume 1 have not been cut open (In Mendel's days, books were delivered with a paper binding that was often later replaced by a leather binding by a bookbinder. In the binding process, any pages that were still joined were trimmed so that they came loose. For books that were not bound, the attached pages had to be cut open to be read). Volume 2 was completely open. The chapters in the uncut pages of volume 1 on mammals (dogs, cats, rabbits, horses, and cattle) apparently did not interest Mendel.

Mendel's many annotations show that he studied the text extensively and he must have read the book before the summer of 1869 because afterward, as indicated in a letter to Nägeli, he developed eye problems that made him incapable of any exertion well into the winter. Usually, Mendel drew pencil lines in the margins; sometimes, these were double or triple, presumably reflecting their importance. Some sentences were underlined and occasionally Mendel put an exclamation mark in the margin. He wrote page numbers on the end pages, sometimes with a keyword. Very infrequently he wrote text.

The annotations to Chapter 27 on pangenesis clearly display Mendel's scepticism. Mendel put a line in the margin at the first part of the sentence:

"The existence of free gemmules is a gratuitous assumption, yet can hardly be considered as very improbable" (p 497 of the German edition, p 378 of the English).

At the bottom paragraph of this page Mendel placed three lines and an exclamation mark in the margin where the text reads:

"As each unit, or group of similar units throughout the body, casts off its gemmules, and as all are contained within the smallest egg or seed, and within each spermatozoon or pollen-grain, their number and minuteness must be something inconceivable".

Here, Mendel also wrote the only full sentence annotation he made in the book:

"*sich einem Eindrucke ohne Reflexion hingeben*" (to give in to an impression without reflection).

Mendel clearly did not like Darwin's speculations without empirical support. On segregation at the following sentence Mendel drew a single line:

"So, also, hybridized plants can be multiplied to any extent by buds, but are continually liable to reversion by seed, —that is, to the loss of their hybrid or intermediate character. I can offer no satisfactory explanation of this fact". (Vol. 2; p 519 Ger.; p 396 Eng.)

Mendel's work, of course, offered the explanation.

On the back of the inside page of volume 2, Mendel wrote "*524 Wichtig*" (important); and on page 524 the following passage is marked with black and red lines in the margin (Vol.2; p 400 Eng.):

"Each organic unit in a hybrid must throw off, according to the doctrine of pangenesis, an abundance of hybridized gemmules, for crossed plants can be readily and largely propagated by buds; but by the same hypothesis there will likewise be present dormant gemmules derived from both pure parent-forms; and as these latter retain their normal condition, they would, it is probable, be enabled to multiply largely during the lifetime of each hybrid. Consequently the sexual elements of a hybrid will include both pure and hybridized gemmules; and when two hybrids pair, the combination of pure gemmules derived from the one hybrid with the pure gemmules of the same parts derived from the other would necessarily lead to complete reversion of character; and it is, perhaps, not too bold a supposition that unmodified and undeteriorated gemmules of the same nature would be especially apt to combine. Pure gemmules in combination with hybridized gemmules would lead to partial reversion. And lastly, hybridized gemmules derived from both parent-hybrids would simply reproduce the original hybrid form".

We can only speculate on what Mendel would have thought about this. Perhaps he wondered whether Darwin's proposed gemmules might be reconciled with his elements. Mendel did not state explicitly where his elements were located in the plant body, but his emphasis on cell biology suggests Mendel considered the elements to be the properties of cells:

"With regard to those hybrids whose progeny are variable, one might perhaps assume that between the differing elements of the germ and pollen cell a mediation presumably occurs as well in so far as the formation of a cell serving as the foundation of the hybrid still becomes possible; yet that the compromise between the opposing elements is only a transient one and does not extend beyond the life of the hybrid plant. Since no changes in its habitus are perceptible during the whole vegetation period, we would have to conclude further, that the differing elements only succeed to step out of their enforced association during the development of the fertilization cells. In the formation of these cells, all the elements participate in a totally free and uniform arrangement, while only the differing ones mutually exclude each other. In this way, the formation of as many kinds of germ and pollen cells would be enabled as there are combinations allowed for by the elements capable of development". (BSHS p 42, our emphasis).

He had shown however that the elements are unchanged in the hybrid and that only one of each pure breeding type is found in the reproductive cells. That the hybrids did not have a new type of element was an important conclusion from Mendel's work. Mendel did not say how many of each element was present in a reproductive cell, only that there is just one type of element (obviously the simplest explanation is that there is in fact just one). Mendel's proposed elements are much more constrained than Darwin's gemmules, and they behave in a way that is statistically predictable.

THE EXPERIMENT THAT COULD NOT WAIT

Mendel's strongest annotations refer to Darwin's statement that multiple pollen grains were needed to produce a single seed, and Darwin's suggestion that the "quantity of formative matter" was important. In the back endpapers of volume two of his copy of *Variation under Domestication*, three page numbers are listed next to the written word "*Quantität*" (quantity), referring to the number of pollen grains needed to fertilize an egg cell to produce a seed (Box 1)

These annotations highlight Mendel's disagreement with two of Darwin's claims; Mendel considered that:

Box 1. Details on Mendel's annotations concerning the number of pollen grains needed to fertilize an egg cell and the relevant passage from Mendel (1866)

1. p363 (German p478), marked with a double line in the margin:

"This last careful observer [Gärtner] found, after making successive trials on a Malva with more and more pollen-grains, that even *thirty grains* [underlined by Mendel] did not fertilize a single seed; but when forty grains were applied to the stigma, a few seeds of small size were formed. The pollen-grains of Mirabilis are extraordinarily large, and the ovarium contains only a single ovule; and these circumstances led Naudin to make the following interesting experiments: a flower was fertilized by three grains and succeeded perfectly; twelve flowers were fertilized by two grains, and seventeen flowers by a single grain, and of these one flower alone in each lot perfected its seed; and it deserves especial notice that the plants produced by these two seeds never attained their proper dimensions, and bore flowers of remarkably small size".

2. p385 (German, pp505–506), with a single score in the margin, and the last part with an exclamation mark:

"We may conclude from the fact of a single spermatozoon or pollen-grain being insufficient for impregnation, that a certain number of gemmules derived from each cell or unit are required for the development of each part. From the occurrence of parthenogenesis, more especially in the case of the silk-moth, in which the embryo is often partially formed, we may also infer that the female element includes nearly sufficient gemmules of all kinds for independent development so that when united with the male element the gemmules must be superabundant".

3. p401 (German, p525), with single score in the margin:

"*A certain number of gemmules being requisite for the development of each character* [underlined by Mendel with a wavy line], as is known to be the case from several spermatozoa or pollen-grains being necessary for fertilization, and time favouring their multiplication, will together account for the curious cases, insisted on by Mr. Sedgwick, of certain diseases regularly appearing in alternate generations".

In the 1866 paper, Mendel wrote:

"It is entirely left to chance which of the two pollen kinds joins with each individual germ cell.

However, according to the rules of probability it will always occur on the average of many cases that each pollen form *A* and *a* unites equally often with each germ form *A* and *a*; one of the two pollen cells *A* will therefore come together with a germ cell *A*, the other with a germ cell *a* in fertilization, and in the same manner a pollen cell *a* will be joined with a germ cell *A*, and the other with *a*". [Mendel 2016; BSHS translation, p29]

1. One pollen grain was sufficient for fertilization
2. The amount of fertilizing material had no effect on the quality of the offspring.

Since the mid-1850s, it was generally accepted that the plant embryo developed from the egg cell after contact with the pollen tube, but it was not known how fertilization took place in detail. It was suspected that a fertilizing liquid diffused from the pollen tube into the egg cell (Sachs 1875, 1890). The union of sperm and the egg cell nuclei was discovered much later by Eduard Strasburger (1884). In microscopic studies, several pollen tubes were frequently observed in the vicinity of the egg cell. Given the idea of a diffusing fertilizing fluid, fertilization by only a single pollen grain was not a foregone conclusion.

For Mendel's explanation of the patterns of inheritance, the fertilization of an egg cell by a single pollen grain was fundamental. This makes a clear and testable difference between Mendel's and Darwin's theories. In the summer of 1869, Mendel eyes were suffering from a serious problem caused by the bright light he used in his intense microscopical work with *Hieracium* florets. Despite this, but because of the importance of the problem, Mendel carried out experiments using single pollen grains for fertilization in *Mirabilis*.

In his letter to Nägeli dated July 3, 1870, Mendel wrote:

> "Because of my eye ailment I was not able to start any other hybridization experiments last year. But one experiment seemed to me to be so important that I could not bring myself to postpone it to some later date. It concerns the opinion of Naudin and Darwin that a single pollen grain does not suffice for fertilization of the ovule". (see also Supplementary information; Piternick and Piternick (1950), p 26)

Charles Naudin (1815–1899) was a French botanist who, like Mendel, was occupied with crossing experiments. He published his work in the Treatises of the National Museum of Natural History and was a member of the Academy of Sciences in Paris and he corresponded extensively with Darwin. Most of Naudin's crosses were between species. Although he arrived at a segregation hypothesis, he made no quantitative analysis of the progeny types and did not formulate rules of inheritance the way Mendel did.

Mendel conducted two kinds of experiments:

i. Pollination with a single pollen grain as Naudin had done previously (see below).
ii. Pollination with two pollen grains, each from a variety with different flower color (double mixed pollination).

This experimental design shows the clarity of Mendel's thinking. He realized that the experiments with a single pollen grain would show only that a single pollen was sufficient for fertilization, but he also needed to show that two pollen grains could not both be involved in fertilization; the condition of his theory was that *only* one pollen grain fertilized (see Fig. 1):

Naudin's experiments with the ornamental species *Mirabilis* were described by Darwin. The ovule of *Mirabilis* contains only one egg cell, and the pollen grains are very large (>100 µm). Single pollen grain pollination could be effected in this species using a needle and a magnifying glass. Naudin concluded: "With a single grain of pollen, fertilization is still possible, but it becomes more and more uncertain". In addition, Naudin felt that the experiments should be repeated (Naudin 1862). Darwin's account of Naudin's experiments was correct on p478, but not on pages 505 and 525. Mendel relied on Darwin's erroneous second and third interpretation of Naudin's experiments.

Similar experiments were carried out by later researchers (Correns 1900, Harland and Haigh 1927, Niesenbaum 1999) but

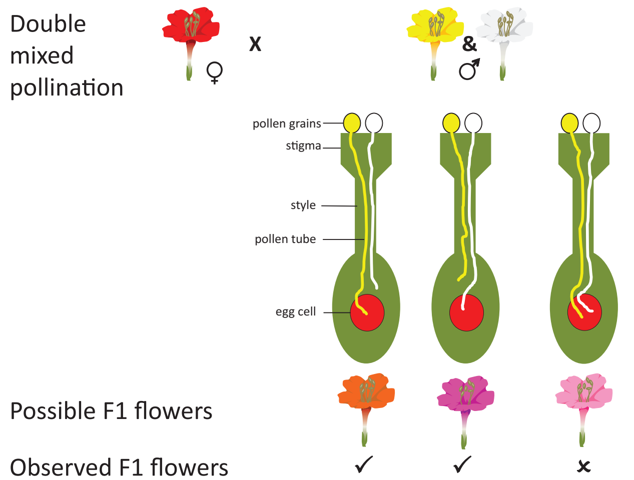

Fig. 1 Mendel's double mixed *Mirabilis* pollination experiment. The color of the pollen and the egg cell represent the flower color of the parents and the color of the egg cell represents the flower color of the female parent. The (imaginary) flower colors of the hybrids are shown below because this unpublished experiment was described only briefly in letters. There are three possible outcomes: if only a single pollen grain fertilized then the flowers of the hybrids would have the colors known from the two crosses where there was a single male parent. If two pollen grains fertilized an egg cell simultaneously, then a new third color would have appeared.

without cross referencing each other or Mendel. Only Niesenbaum (1999) failed to show that a single pollen grain was sufficient.

It is probable that Mendel was aware of Knight's experiments on superfoetation in pea (Knight 1799), and the logic of using more than one distinguishable male parent to investigate the process of fertilization would have suggested an extension to the single pollen grain fertilization experiment. In this same letter to Nägeli, Mendel also described the double mixed pollination experiment (see also Supplementary information):

> "Under way is another experiment with Mirabilis, designed to find out also whether two pollen grains may simultaneously participate in fertilization. The varieties with crimson red, yellow, and white, flowers, respectively are constant when raised from seed, as I know from experience, and the hybrids which first result from the crosses crimson+yellow and crimson +white show no variations in their characteristic coloration. Both fertilizations succeed equally well and thus no differences in the degree of relationship [among the three varieties] is apparent. In the crimson variety a fairly large number of fertilizations was undertaken in such a way that two pollen grains were simultaneously put on each stigma, one of the yellow, and one of the white variety. Since the resultant flower colors of the crosses crimson+yellow and crimson+white are known, it will be shown next year whether in addition to the hybrid colors still a third color will appear, one explainable by joint action of the two pollen grains". (Mendel's letter to Nägeli September 27, 1870; Piternick and Piternick (1950), p 29)

If, in a tri-parental cross, simultaneous fertilization by two or more pollen grains could occur, then the proportions of the offspring types would not follow Mendelian ratios (see Supplementary information) and there would be at least one additional class of F1 (Fig. 1). Mendel knew that the outcome of two-parent crosses in *Mirabilis* was the same as in *Pisum* (apart from the lack of dominance).

Mendel's interpretation of his data in the 1866 *Pisum* paper explained the composition of the progenies of his crosses and selfings by the fertilization of each egg cell by a single pollen grain. In his *Mirabilis* experiments, he demonstrated that a single pollen grain was sufficient for fertilization, but the competition experiment would also have shown, that no more than one pollen grain was actually involved. If an egg cell were pollinated by two different pollen grains, intermediate forms would arise and segregation ratios would be disrupted.

Mendel's next surviving letter to Nägeli is dated three years later, in November 1873, contains no information about the results of the double mixed *Mirabilis* pollination experiment. Probably multiple letters, including the one discussing the results of the *Mirabilis* experiment, are lost. (We know from Nägeli's notes that at least one letter which Mendel wrote in the spring of 1873 did not reach him. The record of communication between Nägeli and Mendel is far from complete, and it seems that Nägeli did not keep all of Mendel's letters, and may have kept only those that discuss *Hieracium*). Even though the results of these experiments are not known, there is no doubt that Mendel was right: had Mendel obtained data from the double mixed pollination experiment, these would have shown that no more than a single pollen grain was involved in fertilization.

Fourteen years after Strasburger's discovery of the union of the sperm and the egg cell nuclei, in 1898, Sergei Nawaschin and Léon Guignard independently discovered double fertilization in flowering plants. It turned out that the pollen tube contained two sperm nuclei, one fertilizing the egg cell, giving rise to the embryo, and the other fertilizing other central cell, giving rise to the endosperm, a tissue that nourishes the developing embryo. Polyspermy is the fertilization of the egg cell or central cell by two pollen nuclei. Recently some data about the occurrence of polyspermy have been published. In maize, mixed pollination experiments with pollen from plants with different endosperm markers have shown that polyspermy of the central cell can occur at frequencies up to 4% (Dresselhaus and Johnson 2018). Polyspermy of the egg cell is much rarer than that of the central cell. Grossniklaus (2017) detected only one egg cell fertilized by two sperm nuclei out of 50,000 analyzed. Nakel et al. (2017) used a two-component transgenic resistance system in the plant species *Arabidopsis thaliana* to detect extremely rare polyspermy. The frequency of polyspermy was estimated to be 1.2 in 10,000 fertilizations, which is much too low a frequency to have any noticeable disturbing effect on Mendelian segregation ratios.

CONCLUSION

Darwin's ideas about the number of pollen grains and the amount of formative matter needed to fertilize an egg cell differed markedly from Mendel's. How this quantity was proposed to affect the quality of the offspring is characteristic of Darwin's thinking in terms of continuous variation. Despite their different views, Darwin was interested in the same transmission problem that Mendel was studying in pea (see Supplementary information). In describing the white flower and associated white seed coat color which Mendel studied in reciprocal crosses and where he had already shown the white flower color to be recessive, Darwin interpreted the result not in terms of latency but as "weakness of transmission in peas" (second edition of *Variation under Domestication*, Darwin 1875, p 464). The contrast between Darwin and Mendel could hardly be greater.

POSTSCRIPT

While we were completing the revision of this manuscript, a publication appeared on Mendel's *Mirabilis* experiments in *Hereditas*: "Mendel's controlled pollination experiments in *Mirabilis jalapa* confirmed his discovery of the gamete theory of inheritance in *Pisum*", by Zhang H, Zhao X, Zhao F et al. *Hereditas* 159, 19 (2022) https://doi.org/10.1186/s41065-022-00232-1.

From the letters to Nägeli of July 2 and September 27, 1870, we read that Mendel had repeated the single pollen experiment, and a double mixed experiment was underway. However, the authors of the *Hereditas* article concluded from the same passages that Mendel had self-fertilized the F1 plants obtained from the single and double mixed pollen experiments and had analyzed the resulting F2 for flower color segregation. Mendel, though, wrote, “it will be shown *next year* whether in addition to the hybrid colors still a third color will appear, one explainable by joint action of the two pollen grains” (our emphasis). The results of the double mixed experiments would, therefore, not be available until 1871 (in agreement with Zhang et al., Table 1). Contrary to Zhang et al., we do not see any report from Mendel on the F2 of the single pollen grain fertilizations in Mendel’s letters to Nägeli. Mendel’s following (and final) surviving letter is dated 1873 and contains no information about the results of his *Mirabilis* experiments. Nevertheless, we completely agree with Zhang et al. that it is ‘fortunate’ that we have a record of Mendel’s *Mirabilis* experiments and experimental plans, as these are highly informative about Mendel’s thinking.

REFERENCES

Bulmer M (1999) The development of Francis Galton’s ideas on the mechanism of heredity. J Hist Biol 32:263–292

Correns CE (1900) Über den Einfluss, welchen die Zahl der zu Bestäubung verwendeten Pollenkörner auf die Nachkommenschaft hat. Ber Deut Bot Ges 18:422–435

Correns CE (1905) Gregor Mendels Briefe an Carl Nägeli, 1866-1873. Abhandlungen der Mathematisch-Physischen Kl der Königlich Sächsischen Ges der Wissenschaften 29:189–265

Darwin C (1862) https://www.darwinproject.ac.uk/letter/?docId=letters/DCP-LETT-3879.xml (Accessed 19 Jan 22)

Darwin C (1868) The Variation of Animals and Plants Under Domestication. John Murray London available online at http://darwin-online.org.uk/ *Das Variiren der Thiere und Pflanzen im Zustande der Domestication* (Vols. I and II). Translated by JV Carus. E. Schweizerbart’sche Verlagshandlung, Stuttgart

Darwin C (1875) The variation of animals and plants under domestication. Second revised edition. John Murray, London, http://darwin-online.org.uk/

Darwin C, Pangenesis Nature 3:502–503 available online at http://darwin-online.org.uk/

Dresselhaus T, Johnson MA (2018) Reproduction: Plant Parentage à Trois. Curr Biol 28: R28–R30

Fairbanks DM (2020) Mendel and Darwin: untangling a persistent enigma. Heredity 124:263–273

Galton F (1871) Experiments in Pangenesis, by breeding from rabbits of a pure variety, into whose circulation blood taken from other varieties had previously been largely transfused. Proc R Soc Lond 19:123–129

Galton DJ (2018) Standing on the shoulders of Darwin and Mendel CRC Press. Taylor and Francis, Boca Raton

Grossniklaus U (2017) Polyspermy produces tri-parental seeds in maize (*Zea mays*). Curr Biol 27:R1300–R1302

Harland SC, Haigh JC (1927) Counted grain pollinations in *Mirabilis jalapa*, L. Am Nat 61:95–96

Knight TA (1799) An account of some experiments on the fecundation of vegetables. Philos Trans R Soc Lond 89:195–204

Mendel G (1866) Versuche über Pflanzen-Hybriden. Verhandlungen des naturforschenden Vereines, Abhandlungen, Brünn 4:3–47

Mendel G (2016) Experiments on Plant Hybrids (1866). Translation and commentary by Staffan Müller-Wille and Kersten Hall. British Society for the History of Science Translation Series. http://www.bshs.org.uk/bshs-translations/mendel

Nakel T, Tekleyohans DG, Mao Y, Fuchert G, Vo D, Groß-Hardt R (2017) Triparental plants provide direct evidence for polyspermy induced polyploidy. Nat Comm 8:1033

Naudin C (1862) Nouvelles recherches sur l’hybridité dans les végétaux. No 5. Fécondation par un et deux grains de pollen dans le genre Mirabilis. Nouvelles Archives du Muséum Tome I, Paris

Niesenbaum RA (1999) The effects of pollen load size and donor diversity on pollen performance, selective abortion, and progeny vigor in *Mirabilis jalapa* (Nyctaginaceae). Am J Bot 86:261–268

Olby R (1985) Origins of Mendelism. University of Chicago Press, Chicago

Piternick LK, Piternick G (1950) Gregor Mendel’s letters to Carl Nägeli. Genetics 35:1–29. http://www.esp.org/foundations/genetics/classical/holdings/m/gm-let.pdf

Richter O (1943) Johann Gregor Mendel wie er wirklich war. Verhandlungen des Naturforschenden Vereines Brünn 74:1–263

Sachs J (1875) Geschichte der Botanik vom 16. Jahrhundert bis 1860. Oldenbourg, Munich

Sachs J (1890) History of Botany (1530-1860), Translated by HEF Garnsey and IB Balfour. Clarendon Press, Oxford

Strasburger E (1884) Neue Untersuchungen über den Befruchtungsvorgang bei den Phanerogamen als Grundlage für eine Theorie der Zeugung. Verlag von Gustav Fischer, Jena, Germany

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AUTHOR CONTRIBUTIONS

PVD was responsible for researching the original German texts. NE and PVD wrote the manuscript together.

COMPETING INTERESTS

The authors declare no competing interests.

ADDITIONAL INFORMATION

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41437-022-00546-w.

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