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REVIEW ARTICLE

Demystifying the mythical Mendel: a biographical review

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Gregor Mendel is widely recognised as the founder of genetics. His experiments led him to devise an enduring theory, often distilled into what are now known as the principles of segregation and independent assortment. Although he clearly articulated these principles, his theory is considerably richer, encompassing the nature of fertilisation, the role of hybridisation in evolution, and aspects often considered as exceptions or extensions, such as pleiotropy, incomplete dominance, and epistasis. In an admirable attempt to formulate a more expansive theory, he researched hybridisation in at least twenty plant genera, intentionally choosing some species whose inheritance he knew would deviate from the patterns he observed in the garden pea (*Pisum sativum*). Regrettably, he published the results of only a few of these additional experiments; evidence of them is largely confined to letters he wrote to Carl von Nägeli. Because most original documentation is lost or destroyed, scholars have attempted to reconstruct his history and achievements from fragmentary evidence, a situation that has led to unfortunate omissions, errors, and speculations. These range from historical uncertainties, such as what motivated his experiments, to unfounded suppositions regarding his discoveries, including assertions that he never articulated the principles ascribed to him, staunchly opposed Darwinism, fictitiously recounted experiments, and falsified data to better accord with his theory. In this review, I have integrated historical and scientific evidence within a biographical framework to dispel misconceptions and provide a clearer and more complete view of who Mendel was and what he accomplished.

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INTRODUCTION

The year 2022 marks the bicentennial of Gregor Mendel's birth. He rose from an impoverished childhood in a small village to become a successful teacher, scientist, priest, and ultimately prelate and abbot. His discoveries and interpretations of elegant symmetrical patterns of inheritance in the garden pea (*Pisum sativum* L.) led him to develop a theory of inheritance that has endured with little change. No one, including Mendel, recognised the importance of his theory in his day; it languished mostly unnoticed until its dramatic rediscovery founded the science of genetics at the beginning of the twentieth century. The fragmentary evidence of Mendel's history has left much room for speculation and conjecture. Inevitably, misunderstandings, myths, omissions, and rumours have become part of popular and scholarly accounts of his accomplishments and history. Some mysteries may never be resolved due to the absence of sufficient evidence. In this review, I examine within a biographical framework the scientific and historical evidence to clarify some of the most important Mendelian misconceptions.

MENDEL'S YOUTH AND EARLY EDUCATION

Johann Mendel was born in July 1822 in the village of Heinzendorf (Hynčice)[1] in Austrian Silesia (currently in the Czech Republic); his parents were Rosina Schwirtlich and Anton Mendel. When he became a friar in 1843, he took on the monastic name Gregor. The first of several historical misconceptions is the day of his birth, disputed as July 20 or 22. Some authors, mostly in popular online biographies, have attempted to resolve this discrepancy by speculating that he was born on July 20 and baptised on July 22. However, the evidence contradicts this presumption. The parish birth register lists the date of his birth and baptism as July 20 (Moravian Museum 1965). After pointing out several discrepancies in the birth register, Klein and Klein (2013) noted, "Another peculiarity of the register is that all seven children born in 1822 were baptized on the day of their birth" (p. 123), suggesting that the dates may be incorrect because, at the time, infants were rarely born and baptised on the same day. Mendel himself consistently listed his birthdate as July 22 on all known

[1]When naming cities and places, I have used the Anglicised name if it is available (for example Moravia instead of Mähren or Morava). Because many of the places associated with Mendel are now in the Czech Republic and bear Czech names, but were known by both their German and Czech names in his day, and he typically used their German names, I have included the German name first in each instance, followed by the Czech name in parentheses, and used only the German name for each subsequent use.

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documents. His nephew, Alois Schindler, wrote that his uncle Gregor and his mother Theresia insisted that the correct birthdate was July 22, the feastday of St. Mary Magdalene. Schindler further reasoned, "Perhaps the parish dates were recorded belatedly and incorrectly" (translated from the original 1902 German in Kříženecký 1965, p. 80).

Although writers often state that Johann had two siblings, probably based on Iltis (1924, 1966), in fact he was the second of five children in the family. Two of his sisters, Veronika and Theresia, lived to adulthood. Two other sisters, both named Rosina, died as children, one as a toddler the other as an infant (Klein and Klein 2013). Theresia lived to see her late brother Gregor attain fame as the founder of genetics in the early twentieth century. She provided some of the most important information of his early history based on her recollections and documents she retained. Two of her sons, Alois and Ferdinand Schindler, recorded her reminiscences along with their own (Kříženecký 1965).

Johann and his sisters attended classes in a small schoolhouse a short walk from their home. His teachers arranged for him to attend boarding school for gifted children in Leipnik (Lipník) where he studied for one academic year (1833–34). He received admission to the Troppau (Opava) Gymnasium where he would continue his schooling for six academic years, graduating in 1840. He then attended the Olmütz (Olomouc) Philosophical Institute, graduating in 1843. Once while he was in Troppau and again while he was in Olmütz, he suffered episodes of nervous illness so severe that he had to retreat home for months to recuperate, the second time costing him a year of his schooling. Despite these prolonged illnesses, his performance was outstanding at all three schools.

In the time preceding the summer of 1841, he faced a pivotal decision. His father, crippled by an accident three years earlier, could no longer manage the farm. Johann, now at his nineteenth birthday, had to decide whether to take over the family farm or continue his education. A document from the time makes it clear that by the end of that summer he had decided to enter the priesthood. Respecting that decision, his father sold the farmstead to Alois Sturm, Veronika's husband, with the following provision: "The purchaser shall pay to the son of the seller, Johann by name, if the latter as he now designs should enter the priesthood, or should he in any other way begin to earn an independent livelihood, the sum of 100 fl. … and shall also defray all expenses connected with the first mass" (Iltis 1966, p. 39). Johann's physics professor in Olmütz, Friedrich Franz, highly recommended him for admission to the Augustinian order in the St. Thomas monastery in Brünn (Brno), the capital of Moravia. Mendel was officially admitted to the order on October 9, 1843 (Iltis 1966, p. 43).

FRIAR, SCIENTIST, AND TEACHER

The group of Augustinians Mendel joined in October 1843 was extraordinary. Although often identified as a monk, he was a friar, which is an important distinction. The mendicant orders, including Augustinians, consist of friars in that their members openly serve the community, leading much less cloistered lives than traditional monks. Several of the St. Thomas friars were highly educated, serving as teachers and professors, conducting scholarly research in the sciences, arts, and humanities, and holding prestigious administrative positions in commerce and academic societies. They were especially dedicated to secular academic teaching and research, a situation that often placed them in conflict with their ecclesiastical superiors beyond the monastery.

The abbot, Cyrill Franz Napp, was a highly respected scholar characterised by a fellow friar as "a famous prelate, scientist, secret freethinker, and patriot, and expert in state affairs and economy" (Matalová 1973, p. 252). Prior to his abbacy, Napp taught at the Brünn Theological Institute. The monastery had large agricultural holdings, and Napp was committed to implementing scientific advances in agriculture. He was an influential member of the Moravian-Silesian Agricultural Society, especially in the society's sheep breeding and pomological associations. With Napp's encouragement, Mendel took classes in scientific agriculture at the Brünn Philosophical Institute and was elected to membership in the Agricultural Society in 1851 (Matalová and Matalová 2022).

Mendel's close friend and mentor during these early years was his fellow friar Matouš František Klácel, a philosopher specialising in the writings of Georg Wilhelm Friedrich Hegel and a self-described freethinker who was constantly at odds with church authorities beyond the monastery. Shortly after Mendel arrived, Bishop Anton Ernst Schaffgotsch dismissed Klácel from his teaching position at the Brünn Theological Institute for teaching "pantheism and other heresies related to Hegelianism" (Peaslee and Orel 2007, p. 152).

Revolutionary sentiment swept much of Europe in 1848 and was especially forceful in Vienna, spilling over into Brünn. The St. Thomas friars supported revolutionary reforms, with Napp's enthusiastic encouragement. Klácel seized the opportunity to compose a petition demanding greater freedom for friars from religious duties, allowing them to devote themselves more fully to secular research and teaching. The wording of the petition was scathing, its content overflowing with hyperbole. It concluded, "the undersigned professors and pastoral workers in the Order of St. Augustine in Altbrünn take the liberty of appealing to the imperial parliament to <u>grant them constitutional civil rights</u>, and request to be allowed to devote their entire efforts, according to their abilities and past services, to public teaching institutions and to free, united, and <u>indivisible citizenship</u> … [and] make it respectfully their missions to promote science and humanity…" (<u>underlining in the original</u>, Klein and Klein 2013, p. 281). Mendel was one of six friars who signed the petition.

Several premature deaths in the 1840s created a shortage of parish priests, leading Napp to recommend Mendel's ordination at the earliest possible date. Napp assigned Mendel to serve as a parish priest but soon discovered that he was poorly suited to this role. In a letter, Napp informed Schaffgotsch that he had relieved Mendel of his ecclesiastical duties because he was "much less fitted for work as a parish priest, the reason being that he is seized with an unconquerable timidity when he has to visit a sick-bed or to see anyone ill and in pain" (Iltis 1966, p. 58). Napp, as administrator over Moravian schools, arranged for Mendel to instead assume a teaching position at the Znaim (Znojmo) Gymnasium, southwest of Brünn.

Mendel immediately proved to be an exemplary teacher, loved by his students, and praised by his colleagues. A newly implemented law, however, required that teachers be certified through a gruelling series of examinations. Accordingly, Mendel applied in 1850 to be certified in physics and natural history. He received the first part of the examination, a homework portion that he was to complete by writing two essays in response to questions, one on physics and the other on natural history. His essay on natural history contains his first known allusion to evolution, a part of which reads, "The vegetable and animal life developed more and more richly; its oldest forms disappeared in part to make way for new and more perfect ones" (Fairbanks 2020).

The examiner for physics, Andreas von Baumgartner, found Mendel's essay on this topic to be informed and well written. However, Rudolf Kner, the examiner for natural history, determined that Mendel's essay on this subject was deficient. Both examiners, however, recommended him for the next part known as the *Klausurprüfung*, an on-site written examination in a locked room at the University of Vienna with no access to resources. Mendel's written answers this time were less than favourable. His examiners, nonetheless, allowed him to proceed to the *viva voce* (oral) portion. Here he faced a commission, among them the famed physicist Christian Doppler, after whom the Doppler effect is named. His physics examiners evaluated him as “unqualified to teach physics….” and Kner wrote that “he is not yet competent to become a teacher” (Iltis 1966, p. 72). The written report languished in bureaucracy as it bounced from one administrative office to another, finally reaching Napp and Mendel in August 1851, almost a year after the examination in Vienna.

THE UNIVERSITY OF VIENNA AND THE MOTIVATION FOR MENDEL’S EXPERIMENTS

By the time the examination report finally arrived, Napp was already arranging for Mendel to study at the University of Vienna in preparation for a teaching career. The wheels of bureaucracy again turned slowly, and when Mendel finally departed for Vienna, he was five weeks late for the beginning of the 1851 fall term. Serendipitously, due to delays in renovation of the physics laboratory, the experimental physics course began at the same time as Mendel’s arrival. This was his only course that fall term, and it was influential, taught by Doppler to thirteen students. For the 1852 spring term, Mendel again enrolled in Doppler’s course, with additional courses in other subjects. Doppler departed that summer for Italy to recuperate from an illness and died soon thereafter, so Mendel was one of his last students. Although Mendel was originally scheduled to spend a year at university, he remained for almost two years, taking advanced courses in physics, mathematics, chemistry, botany, zoology, and palaeontology, and assisting with entomological research in an extracurricular setting.

Some have argued that Mendel was a staunch anti-evolutionist and adherent of the doctrine of special creation (Callender 1988; Bishop 1996). There is ample evidence, however, to contradict these views, beginning with Mendel’s studies at the University of Vienna. Pre-Darwinian evolutionary theory was prominent at the time, and Mendel studied it in courses on botany, zoology, and palaeontology. One of his most influential professors was Franz Unger, a botanist and palaeontologist. Unger popularised evolution for the public through a series of newspaper articles later compiled as a book (Unger 1852). He also published a popular book with hand-tinted lithographs of geological periods dating from the present to hundreds of millions of years ago (Unger 1851). Unger’s conception of evolution was remarkably like Darwin’s, even though Origin of Species was still eight years from publication. Gliboff (1998) thoroughly reviewed Unger’s evolutionary theory, titling it the “theory of universal common descent” (p. 223). Unger’s development of this theory reached its peak while Mendel was studying with him in Vienna.

At the time Mendel was attending Unger’s lectures, he witnessed first-hand a series of anti-evolutionary attacks pitting Catholicism against evolution. Sebastian Brunner was a prominent Catholic priest, a prolific author and orator, purveyor of religious orthodoxy, and anti-Semite, known by the epithet *Malleus episcoporum*, the bishop’s hammer (Gliboff 1998). Brunner publicly singled out Unger in his attacks, which began two days before Mendel’s arrival in Vienna in October of 1851. These attacks persisted unabated until the spring of 1856, approximately a year and a half after Mendel had returned to the monastery. Brunner named Unger in a newspaper headline as “Isis Priest and Philistine” and in another article as “a man who openly denied the creation and the Creator” (Olby 1985, pp. 202–203). In his most sarcastic article, Brunner wrote that Vienna’s botanists “do everything they can to make themselves into plants of botanical learning that can be smelt from afar—and place themselves voluntarily into the eternally stinking dung-bed of the pantheistic world view, which nevertheless fosters a certain richness of blossoms” (Fairbanks 2020, p. 265).

By the time Brunner wrote these words, Mendel had been officially appointed as one of these Viennese botanists. In 1853, his professors and colleagues elected him to full membership in the Imperial-Royal Zoological-Botanical Society in Vienna. Some have erroneously surmised that Mendel’s classic 1866 paper was his first scientific publication when, in fact, it was the third of eight (Mendel 1853, 1854, 1866, 1870, 1871, 1879a, 1879b, 1882). Much of his focus was on physics, which led him to pursue meteorology as one of his principal research activities throughout the remainder of his life. If his published compilations of meteorological data are added to the list, the number of his scientific journal publications totals fourteen. Mendel presented a scientific paper to the Imperial-Royal Zoological-Botanical Society in Vienna in 1853 on lepidopteran predation in radishes. This paper became his first scientific publication when it appeared in the society’s journal (Mendel 1853). In 1854, he submitted another paper based on microscopic examination of the pea weevil and its infestation of pea seeds, which Vincenz Kollar, one of his professors, presented to the society in Mendel’s absence. It too was published in the society’s journal (Mendel 1854).

Mendel returned from the University of Vienna to the monastery in the summer of 1853. By then, Pope Pius IX had issued an edict that Austrian monasteries be investigated for secularism and neglect of religious piety. Cardinal Schwartzenberg in Prague appointed Bishop Schaffgotsch in Brünn to investigate the St. Thomas monastery. The investigation concluded with a formal visitation in early June 1854. At the time, Mendel had recently accepted a teaching appointment at the Realschule, a school focused on training students in their adolescent years in science, mathematics, and technical subjects. This teaching assignment prompted Schaffgotsch to accuse Mendel of studying “profane sciences at a worldly establishment in Vienna at the expense of the monastery to become a professor of said sciences at a state institution” (Klein and Klein 2013, p. 295). At the conclusion of his report, Schaffgotsch recommended dissolution of the order, determining that “any hopes that the spirit could be exorcized and the order returned to a conscientious observance of its rules and constitutions must be given up” (Klein and Klein 2013, p. 295). The report made its way to the Vatican. Although no actions were taken, and Mendel’s monasterial community remained intact, the friars lived under a cloud knowing that dissolution could be imminent.

This threat coincided with Mendel’s earliest known pea experiments (Mendel 1854, 1866; Stern and Sherwood 1966; Orel 1996; Klein and Klein 2013). There is little evidence, however, to indicate the extent to which this threat had any influence on his experimental approach. Some have speculated that this and later threats from ecclesiastical superiors led Mendel to carefully avoid naming controversial evolutionary biologists, such as Darwin and Unger, in his printed publications, but nonetheless showing how his research contributed to evolutionary theory (Klein and Klein 2013; Fairbanks 2020). Mendel more overtly expressed his Darwinian views in his private correspondence than in his published writings (Iltis 1966; Fairbanks 2020).

In 1855, Mendel arranged to retake his teacher certification examination. He completed the homework portion at an unknown date then during the first week in May 1856 he travelled to Vienna for the on-site written and oral portions. Fragmentary accounts of what transpired have provoked exaggerated myths regarding Mendel and his motivations for his famous experiments.

In the early part of the twentieth century, Hugo Iltis (1924, 1966) interviewed one of Mendel’s school colleagues who recalled that when Mendel returned from the examination, he was “very much out of humour” because “he had a very sharp difference of opinion with the examiner in botany, and had stubbornly maintained his own point of view” (Iltis 1966, p. 95). This account has morphed into the notion that the unnamed examiner was Eduard Fenzl, one of Mendel’s botany professors. Mendel purportedly insisted during the examination that heredity was biparental whereas Fenzl authoritatively proclaimed that it was purely paternal, the female parent serving merely as a nurse to the pollen (Wunderlich 1982; Olby 1985; Orel 1996; Klein and Klein 2013). According to Iltis (1966), Mendel's school colleague believed that "this dispute with the examiner led Mendel to begin his experiments" (p. 95).

A letter from Klácel, written immediately after Mendel's return from the fateful examination, provides a contemporary and much more accurate account of what transpired:

> Although he [Mendel] drew easy questions, he fell ill during the first Klausurprüfung and as a consequence was unable to write. He seems to have problems with his nerves generally since he endured several such insidious attacks already and they say that in his youth he suffered from epilepsy. The day passed and nothing was achieved. One has to feel sorry for him, since his homework etc. was graded as excellent. But formalities are formalities; in this case it was not possible to continue. Afraid that further attacks might continue, he returned home without accomplishing anything. (Klein and Klein 2013, p. 364)

This account makes it clear that Mendel had performed well in the homework portion, but he experienced yet another nervous attack early during the Klausurprüfung (locked-room, written portion) and "was unable to write". Because he abandoned the examination before the oral portion, he could not have confronted Fenzl. Mendel then rescheduled the examination for August but there is no record that he travelled to Vienna for it.

Further evidence shows that the abandoned examination could not have motivated Mendel's experiments. Although he began his pea hybridisations that same spring in 1856, he probably planted the parental varieties at least a month earlier. Importantly, he already had his experiments in mind two years earlier, having conducted essential preliminary experiments with the commercial pea varieties during the summers of 1854 and 1855 to ensure that they were true-breeding and to determine which of them were most suitable for his hybridisation experiments.

Although anachronisms dispel the notion that the abandoned examination motivated Mendel's experiments, an earlier dispute between Unger and Fenzl may have played a role (Olby 1985). Cell theory was a rapidly developing discipline at the time, and Unger and Fenzl were two of its leading researchers. They debated the nature of fertilisation, based in part on their interpretations of competing hypotheses of Matthias Jakob Schleiden and Giovanni Battista Amici (Olby 1985; Orel 1996; Klein and Klein 2013). Mendel was undoubtedly familiar with the Unger-Fenzl dispute long before this examination. Several aspects of his experimental design directly addressed this dispute and conclusively resolved it.

MENDEL'S EXPERIMENTS AND THEORY

Mendel carried out his hybridisation experiments over eight years (1856–63), then presented them as two lectures in 1865 and published them in his classic paper the following year (Mendel 1866). Two recent English translations are freely available online, one by Abbott and Fairbanks (2016) and the other by Müller-Wille and Hall (Mendel 2016). My focus here is on misconceptions, myths, controversies, and omissions shrouding his experiments, discoveries, and theory.

One of Mendel's most important contributions, often omitted from accounts in textbooks and articles, is his definitive resolution of the Unger-Fenzl dispute. At the time, competing hypotheses regarding fertilisation and inheritance included strict uniparental inheritance, some form of unequal biparental inheritance, or strict biparental equality. Mendel's definitive resolution of the issue in terms of cell theory is evident in a passage that Sekerák (2017) highlighted as the place where "Mendel reveals the generally valid essence of the reproduction of living organisms" (p. 65). Here Mendel concluded that "one germ cell and one pollen cell unite into a single cell that is able to develop into an independent organism through the uptake of matter and the formation of new cells. This development takes place according to a constant law that is founded in the material nature and arrangement of the elements" (Abbott and Fairbanks 2016, p. 420).

To the term "single cell" in this passage, Mendel appended a footnote that unambiguously addressed the dispute between Unger and Fenzl, albeit without naming either:

> With Pisum it is shown without doubt that there must be a complete union of the elements of both fertilising cells for the formation of the new embryo. How could one otherwise explain that among the progeny of hybrids both original forms reappear in equal number and with all their peculiarities? If the influence of the germ cell on the pollen cell were only external, if it were given only the role of a nurse, then the result of every artificial fertilisation could be only that the developed hybrid was exclusively like the pollen plant or was very similar to it. In no manner have experiments until now confirmed that. Fundamental evidence for the complete union of the contents of both cells lies in the universally confirmed experience that it is unimportant for the form of the hybrid which of the original forms was the seed or the pollen plant. (Abbott and Fairbanks 2016, p. 420)

A few years later, in 1869, while reading the chapter on pangenesis in a German translation of Darwin's Variation of Animals and Plants Under Domestication (Darwin 1868b), Mendel encountered Darwin's supposition that fertilisation of a single germ cell requires more than one pollen grain. Mendel annotated a passage (Fairbanks 2020), which reads in Darwin's original English:

> 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 fertilised by three grains and succeeded perfectly; twelve flowers were fertilised 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. (Darwin 1868a, p. 364)

This passage compelled Mendel to carry out an experiment, the importance of which is evident in his description of it in an 1870 letter to Carl von Nägeli:

> 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. I used *Mirabilis jalappa* for an experimental plant, as Naudin had done; the result of my experiment, however, is completely different. From fertilization with single pollen grains, I obtained 18 well developed seeds, and from these an equal number of plants, of which 10 are already in bloom. … According to Naudin, at least three [pollen grains] are needed! (Stern and Sherwood 1966, pp. 92–93)

Later observations by microscopists solidified the fundamental concept that two gametes unite at fertilisation to form a zygote. Rarely, however, is Mendel credited with the definitive experimental confirmation of this concept, or the fact that he viewed this discovery as one of his most important achievements.

Of the many misunderstandings and myths obscuring Mendel's experimental approach are assertions that his description of his experiments was fictitious, that he never articulated the laws of segregation and independent assortment, and that his data were falsified to more closely approximate expectation. Moreover, some phenomena Mendel addressed in his paper are not attributed to him, instead considered as extensions or exceptions to his laws. I will briefly address these issues here. For extensive reviews of them, see Sapp (1990), Hartl and Orel (1992), Orel (1996), Fairbanks and Rytting (2001), Westerlund and Fairbanks (2004), Hartl and Fairbanks (2007), and Franklin et al. (2008).

The claim that Mendel's description of his experiments was fictitious dates to Bateson (1902), who speculated that "it is very unlikely that Mendel could have had seven pairs of varieties such that the members of each pair differed from each other in only one considerable character" (p. 59). Fisher (1936) quoted Bateson's claim and dismissed it: "there can, I believe, be no doubt whatever that his report is to be taken entirely literally, and that his experiments were carried out in just the way and in much the order that they are recounted" (p. 132). Corcos and Monaghan (1984) resurrected Bateson's claim, then di Trocchio (1991) amplified it, proposing that Mendel hybridised the 22 parental pea varieties he had chosen as parents in all possible combinations then disaggregated the data into fictitious experiments to make his presentations more understandable. Such assertions, however, directly contradict the words Mendel chose to succinctly describe his monohybrid experiments: "[parental] plants were used that differed in only one essential character" (Abbott and Fairbanks 2016, p. 412). After examining published characteristics of nineteenth century pea varieties, Fairbanks and Rytting (2001) determined that "the nature of variation in pea varieties (both old and modern) facilitates, rather than prevents, the construction of monohybrid experiments" (p. 744) and "Mendel's account describes a well-conceived experimental design that would not have been difficult for him to perform" (p. 745).

Claims that Mendel did not conceive the laws of segregation and independent assortment date at least to Callender (1988) who referred to "the myth of 'Mendel's Law of Segregation'; a law not to be found in either of Mendel's papers, nor in his scientific correspondence, nor in any statement that can be unambiguously attributed to him" (pp. 41–42), and Monaghan and Corcos (1990) who contended that "the traditional Mendelian laws of segregation and independent assortment are not given in the paper" (p. 268). Although Mendel did not directly articulate segregation and independent assortment as distinct and separate laws, they are evident in the theory he derived as a "constant law that is founded in the material nature and arrangement of the elements" (Abbott and Fairbanks 2016, p. 420). In a passage appearing shortly after introducing this theory, he lucidly articulated what we can now phrase in modern terms as the pairing of differing alleles of a gene in heterozygotes and their segregation during meiosis:

> In relation to those hybrids whose progeny are variable, one might perhaps assume that there is an intervention between the differing elements of the germ and pollen cells so that the formation of a cell as the foundation of the hybrid becomes possible; however, the counterbalance of opposing elements is only temporary and does not extend beyond the life of the hybrid plant. Because no changes are perceptible in the general appearance of the plant throughout the vegetative period, we must further infer that the differing elements succeed in emerging from their compulsory association only during development of the reproductive cells. In the formation of these cells, all existing elements act in a completely free and uniform arrangement in which only the differing ones reciprocally segregate themselves. In this manner the production of as many germ and pollen cells would be allowed as there are combinations of formative elements. (Abbott and Fairbanks 2016, p. 420)

A key phrase in this passage is "reciprocally segregate themselves" from Mendel's "*sich gegenseitig ausschliessen*". This phrase was translated by Müller-Wille and Hall (Mendel 2016) as "mutually exclude each other" (p. 42), by Stern and Sherwood (1966) as "separate from each other" (p. 43), and by Druery and Bateson (Bateson 1902) as "mutually separate themselves" (p. 89). Mendel's explanation of "differing elements" paired in "compulsory association" that "reciprocally segregate themselves" "only during the development of the reproductive cells" clearly reflects the modern concept of paired allelic segregation during meiosis.

Independent assortment, implied by Mendel in the last sentence of this passage, is more fully clarified in other passages, such as the following: "the behaviour of each pair of differing characters in hybrid union is independent of the other differences between the two original plants and, further, that the hybrid produces as many types of germ and pollen cells as there are possible constant combination forms" (Abbott and Fairbanks 2016, p. 421).

Aspects that Mendel included in his paper, often stated as extensions or exceptions to his laws, include pleiotropy, incomplete dominance, and epistasis. He described a case of pleiotropy for seed coat colour, flower colour, and axillary pigmentation as follows: "The difference in the colour of the seed coat … is either coloured white, a character consistently associated with white flower colour, or it is grey, grey-brown, or leather brown with or without violet spots, in which case the colour of the standard petal appears violet, that of the wings purple, and the stem at the base of the leaf axils is tinged reddish" (Abbott and Fairbanks 2016, p. 408). As reviewed by Hartl and Fairbanks (2007), this pleiotropic association clarifies some perplexing questions about Mendel's experimental design, such as his reason for choosing seed-coat colour as the third character in his trihybrid experiment.

Mendel's comparison of full and incomplete dominance is evident in the following sentences:

> The experiments conducted with ornamental plants in past years already produced evidence that hybrids, as a rule, do not represent the precise intermediate form between the original parents. With individual characters that are particularly noticeable, like those related to the form and size of the leaves and to the pubescence of the individual parts, the intermediate form is in fact almost always apparent; in other cases, however, one of the two original parental characters possesses such an overwhelming dominance that it is difficult or quite impossible to find the other in the hybrid. (Abbott and Fairbanks 2016, p. 409)

Mendel's inference of what is now known as epistasis is near the end of his paper in an experiment with flower colour in the common bean (*Phaseolus*). From an interspecific cross between *P. nanus* L. (with white flowers) and *P. multifloris* W. (with coloured flowers), he noted partial dominance for flower colour and reduced fertility in the F_1 hybrids. Of the 31 F_2 plants that flowered, one had white flowers, and 30 displayed varying shades of coloured flowers. He attempted to interpret this result in the context of what he had observed in *Pisum*, speculating that if two "independent characters" (as he put it) influenced flower colour, a 15:1 ratio is expected, whereas if three did so, a 63:1 ratio is expected. He astutely added the caveat, "It must not be forgotten, however, that the explanation proposed here is based only on a mere supposition that has no other support than the very imperfect result of the experiment just discussed" (Abbott and Fairbanks 2016, p. 418). The ratios he proposed reflect what is now designated as recessive epistasis.

No Mendelian controversy has generated as much debate as the accusation that Mendel's data were falsified to more closely approximate expectation. Weldon was the first to raise questions, privately writing to Pearson in 1901 that Mendel had "cooked his figures, but that he was *substantially* right" (Mangello 2004, p. 23, italics in original). After applying Pearson's newly developed chi-squared test to Mendel's data, Weldon (1902) did not overtly claim in print that Mendel manipulated the data but dangled the possibility in several statements, one of which reads, "the odds against a result as good as this or better are 20 to 1" (p. 235). Fisher, probably influenced by Weldon's paper, famously stated in a 1911 lecture, "It may just have been luck, or it may be that the worthy German abbot, in his ignorance of probable error, unconsciously placed doubtful plants on the side which favoured his hypothesis" (Norton and Pearson 1976, p. 160). The controversy, now known as the Mendel-Fisher controversy, is based largely on an article by Fisher (1936) wherein he famously wrote, "the data of most, if not all, of the experiments have been falsified so as to agree closely with Mendel's expectations" (p. 132).

This assertion is, in fact, less incriminatory than it may seem when viewed in context of Fisher's overall paper. Fisher presumed that an assistant, rather than Mendel, must have manipulated the data, and he dedicated only a relatively small part of the paper to evidence of questionable data. Fisher's admiration for Mendel is evident in the conclusion where he referred to Mendel's paper as "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).

After its publication, Fisher's paper received little attention until the centennial of Mendel's lectures in 1965 when the controversy began in earnest. It lasted for more than forty years in numerous articles and books whose authors drew a wide range of conclusions based on analyses examining essentially every conceivable aspect of Mendel's experiments. Allan Franklin's introductory essay in Franklin et al. (2008) is the most exhaustive and definitive review of the Mendel-Fisher controversy. After evaluating the complex statistical, historical, and botanical aspects of the many published analyses of Mendel's data, Franklin concluded that "the experiments that had initially triggered Fisher's suspicions can be explained without any fraud," but "the issue of the 'too-good-to-be-true' aspect of Mendel's data found by Fisher still stands". Finally, he urged, "It is time to end the controversy" (Franklin et al., 2008, p. 68). Fortunately, most scholars have heeded this plea.

MENDEL AND DARWIN

Mendel became well acquainted with biological evolution from his university studies years before he learned of Darwin. Although Mendel and Darwin were contemporaries, it is unlikely that Mendel learned of Darwin until 1863, the final year of his *Pisum* experiments. Darwin published Origin of Species in 1859, the fourth year of Mendel's experiments, but Mendel obtained his German translation of the book in 1863. It contains his hand annotations, published by Fairbanks and Rytting (2001) as an online supplement. By the time Mendel presented his lectures in 1865, Darwin's Origin of Species was widely known and popular. In the January 1865 monthly meeting of the Natural Science Society in Brünn, Mendel's friend and fellow teacher, Alexander Makowsky lectured on Origin of Species, addressing some of the same topics that Mendel addressed in the next two monthly meetings in February and March.

The existing evidence of Mendel's acquaintance with Darwin's theory and books, as well as Mendel's statements referencing Darwin, strongly counter claims that Mendel was "in favor of the orthodox doctrine of special creation" (Bishop 1996, p. 212) and "an opponent of descent with modification" (Callender 1988, p. 41). The cumulative evidence suggests that Mendel had strong interest in Darwin's writings and their relevance to his research, but that he did not become an avid promoter of Darwinism (Fairbanks 2020). Those who knew Mendel who lived into the twentieth century to share their recollections, independently confirmed this impression (Iltis 1966; Coleman 1967).

Although Mendel was thoroughly acquainted with Darwin's writings, there is no evidence that Darwin knew anything about Mendel. A common rumour purports that Darwin owned an offprint of Mendel's 1866 paper but that it was uncut. For example, Hennig (2000) wrote, "Another uncut reprint was found in the library of Charles Darwin, so Mendel must have sent him a copy, too" (p. 143). Despite several similar claims, there is no evidence that Darwin owned an offprint by Mendel (Lorenzano 2011). In fact, there is evidence to dispel the common notion that Mendel sent uncut offprints. The offprints contain several typesetter errors, which are hand-corrected in the same places and in the same manner in the offprints Mendel sent, evidence that Mendel made the corrections rather than later readers, which he could do only if the offprints were cut (Müller-Wille and Hall 2016; Fairbanks 2022).

Darwin owned two books with brief references to Mendel's experiments. One is a book by Hoffmann (1869), which contains short and essentially uninformative references, not likely to lead Darwin to seek Mendel's paper (Olby 1985). The other is a book by Focke (1881), published the year before Darwin's death, which Darwin loaned to a friend. The pages in this book with references to Mendel remain uncut to this day, possibly the source of the rumour of uncut offprints (Lorenzano 2011).

MENDEL'S SUBSEQUENT EXPERIMENTS AND LETTERS TO NäGELI

Mendel sent an offprint to Carl von Nägeli, a renowned botanist whom Unger often praised, on December 31, 1866 with a detailed accompanying letter. Fortunately, Nägeli retained Mendel's letters, although at least one is missing, and a page from another may also be missing (van Dijk and Ellis 2016). Mendel's letters to Nägeli provide important and detailed information of his research after 1866. Cautious about drawing sweeping conclusions, Mendel conducted hybridisation experiments in other plant species. These experiments were much more extensive than is often portrayed. Mendel recounted experiments with numerous plant genera, among them *Hieracium*, *Circium*, *Geum*, *Linaria*, *Calceolaria*, *Zea*, *Ipomoea*, *Cheiranthus*, *Antirrhinum*, *Tropaeolum*, *Veronica*, *Viola*, *Potentilla*, *Carex*, *Verbascum*, *Mirabilis*, *Aquilegia*, *Lychnis*, and *Matthiola*. The letters contain detailed results for several of these genera, especially *Hieracium*, *Circium*, *Geum*, *Linaria*, *Verbascum*, *Mirabilis*, *Matthiola*, and *Zea*. Mendel noted that the progeny from hybrids in *Matthiola*, *Zea*, and *Mirabilis* "behave exactly like those of *Pisum*" (Stern and Sherwood 1966, p. 93).

In his classic 1866 paper, Mendel classified hybrids into two types: those that produce variable progeny (as was the case with *Pisum* and *Phaseolus*), and those that produce constant progeny, meaning that all the progeny uniformly and consistently retain the characters of the hybrid parent through repeated generations of self-fertilisation. In his experiments with other plant species, he intentionally included genera that he expected to be variable and others that he expected to be constant. For example, he wrote to Nägeli that *Geum* "belongs to the few known hybrids that produce nonvariable progeny as long as they remain self-pollinated" (Stern and Sherwood 1966, pp. 58–59). By researching both types, Mendel hoped to develop a more expansive theory to explain inheritance and speciation in the progeny of hybrids.

Mendel's choice to research *Hieracium* is often portrayed as disastrous, as is evident in the following excerpts: "the worst possible choice" (Sturtevant 1965, p. 11), "shattered the hopes he had entertained of finding a confirmation" (Iltis 1966, p. 174), "a completely misguided choice" (Hennig 2000, p. 159), and "the results were a mess" (Mukherjee 2016, p. 55). However, a detailed examination of Mendel's *Hieracium* research in his letters to Nägeli, and in the paper he published on *Hieracium* (Mendel 1870), reveals extensive and productive research. Orel (1996) characterised Mendel's choice as "in no way unfortunate", and "a logical step forward" (p. 184). Disparagement of Mendel's choice is based on the misguided presumption that all species of *Hieracium* reproduce exclusively through apomixis, seemingly ensuring uniparental-maternal inheritance and preventing artificial hybridisation. In fact, the genus *Hieracium* is extraordinarily diverse (one of the reasons Mendel chose it), and its reproductive mechanisms include varying degrees of apomixis, self-fertilisation, self-incompatibility, and cross-fertilisation, as well as a powerful influence of polyploidy on apomixis (Bicknell et al. 2016; Mráz and Zdvořák 2019; Underwood et al. 2022). Mendel's accounts make it clear that he, like other researchers, obtained true *Hieracium* hybrids, albeit not without considerable effort. He speculated that the progeny of *Hieracium* hybrids might remain constant, as in *Geum*, but he was not initially sure. His decision to choose genera that he suspected would behave differently than *Pisum* is admirable; it was his intentional attempt to better understand the complexity of hybridisation in nature.

In his brief paper on *Hieracium*, Mendel (1870) determined that "we do not possess a complete theory of hybridisation and we may be led into erroneous conclusions if we take rules deduced from observations of certain other hybrids to be Laws of hybridisation and try to apply them to *Hieracium* without further consideration" (Stern and Sherwood 1966, p. 52). Mendel observed that the F_1 hybrid plants obtained from apparently true-breeding parents tended to vary among themselves, but that their F_2 progeny from apparent self-fertilisation remained constant. He clearly stated the inevitable conclusion: "In *Pisum* the hybrids, obtained from the immediate crossing of two forms, have the same type, but their posterity, on the contrary, are variable and follow a definite law in their variations. In *Hieracium* according to the present experiments exactly the opposite phenomenon seems to be exhibited" (Stern and Sherwood 1966, p. 55). He then noted that *Hieracium* was not the only genus to display such behaviour, citing the research of Wichura indicating that *Salix* behaved similarly.

Mendel's observations were probably due to natural heterozygosity and polyploidy in the parental plants, which appeared to him to breed true due to apomixis. When he successfully hybridised them, the F_1 progeny displayed variability due to parental heterozygosity and possible variations in ploidy, then the F_2 progeny remained constant, resembling the original F_1 parents, due again to apomixis (Bicknell et al. 2016; Mráz and Zdvořák 2019). These observations revealed "exactly the opposite" of his observations in *Pisum*. The fact that he observed concordance with *Pisum* in several genera and a range of patterns in *Hieracium* and other genera neither surprised nor misled him. The only true misfortune is that he published only a fraction of what he had discovered.

MENDEL'S ABBACY AND DEATH

After Napp's death, Mendel was elected abbot in 1868. This change in status did not initially deter him from research; his letters to Nägeli reveal extensive hybridisation research for the next five years (1868–73). However, in his last letter to Nägeli, Mendel lamented that "I am really unhappy about having to neglect my plants and my bees so completely" (Stern and Sherwood 1966, p. 97). By then, a bitter dispute over monastery taxation was overwhelming him. He sent his *Hieracium* plants and herbarium specimens to Nägeli, essentially bringing his hybridisation research to a close.

Mendel died on January 6, 1884. Had he published the enormous data he collected on plant hybridisation, his work might have been more broadly known. Why he did not do so has been a matter of speculation. One of the young friars in the monastery, Prior Alphonsus Tkadlec, recalled years later that Mendel "was even attacked and his theory suspected of being contrary to the revealed truths of the Christian religion…. In bitterness he burned everything which reminded him of his previous activity" (Orel 1996, p. 195). Mendel's nephew, Ferdinand Schindler, provided a contradictory account: "He often said to us nephews, that we shall find at his heritage, papers for publication, that he could not publish in his life. But we did not receive anything from the cloister, not even a thing for remembrance" (Coleman 1967, p. 10). Antonín Doupovec, who attended to the aging abbot with his mother, remembered, "thousands of sheets of paper covered with scientific notes and data were found after his death" (Orel, 1971, p. 270). Another young friar, Pater Clemens Janetschek claimed that most of Mendel's papers were burned after his death, only the bound books retained (Iltis 1966, p. 281). It is fortunate that Nägeli and his heirs preserved Mendel's letters. Otherwise, much of his extensive research after 1866 would have remained unknown.

CONCLUSION

Mendel's classic 1866 paper remains one of the finest examples of the nature of science, a detailed and lucid presentation of extensive data exemplifying careful experimental design, hypothesis testing, and the development of an enduring theory of heredity. His paper, as the founding document for the science of genetics, is much enhanced when viewed in the context of his life, his choices, and those who influenced him at one the most extraordinary times in the history of science. In this review, I have attempted to demystify key events in his history and scientific approach to hopefully provide a clearer view of who he was and what he accomplished as we commemorate the bicentennial of his birth.

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ADDITIONAL INFORMATION

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