Gregor J. Mendel – Genetics Founding Father

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Abstract

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Mendel's impact on science is overwhelming. Although based on the number of scientific papers he published he might be considered a meteorologist, his most significant contribution is his study of plant hybrids. This single work puts Mendel on a par with Darwin's evolutionary theory and establishes him firmly in the frame of today's biology. The aim of this article is to introduce the personality of Gregor Johann Mendel, focussing not just on his scientific work, but also on his background and what or who influenced him. To understand Mendel's use of quantification and mathematical analysis of obtained results, representing a radical departure from methods of his predecessors, it is important to know something about their arguments, beliefs, and practices. He designed his experiments to answer a long standing question of hybridization, not inheritance as we perceive it today, since the science of genetics was born considerably later. He studied many genera of plants, but his famous research was on garden peas. To choose a single species for his crosses was fundamental to his success, but also fuelled most of criticism at the time he presented his results. The reason for his success was partly due to being a hybrid himself: of a biological scientist, a physical scientist and a mathematician. Mendel's other fields of interest such as meteorology and bee keeping are also introduced in this article.

Keywords: heredity; hybridization; manuscript; Mendel; Pisum

Gregor Johann Mendel has left an indelible mark on the history of science. His work together with Darwin's evolutionary theory established the theoretical basis of today's biology. Many books have been written about his life, and his discoveries are recorded in almost every biology textbook. The first Mendel biography by Hugo Iltis, 1924, "Gregor Johann Mendel. Leben, Werk und Wirkung" (ILTIS 1924), later translated to English (ILTIS et al. 1932), is the basic source of information about Mendel, even today. Iltis collected historical documents connected to Mendel and used them as source for his book. The number of these historical documents is limited, but it is not true, that, as often wrongly argued, his personal belongings were burnt after his death. Anyway, the discovery of new information about Gregor Mendel is very rare and other authors can only refer

to, supplement or newly interpret what Hugo Iltis documented. The latest book about Mendel, "Solitude of a Humble Genius – Gregor Johann Mendel: Volume 1" appeared in 2013 (Klein *et al.* 2013) and took 10 years of preparation. Before commenting Mendel's work let's look at some aspects of his life.

Mendel was born, according to the birth record, on 20th of July 1822 at the small village Heinzendorf bei Odrau (then in the Silesian part of Moravia within the Austrian empire, now Hynčice u Vražného in northern Moravia in the Czech Republic) and was baptized Johann the same day. However, according to his nephew, Mendel celebrated his birthday the 22th of July. Contemporary speculations about his nationality (German, Austrian, Silesian, Moravian, Czech) overlook the fact that nationality in its present day sense was barely important in his time. Mendel

was simply a German speaking inhabitant of the Austrian empire, native to Moravia.

Mendel was involved in tending the farm and field work from early childhood. Mendel went easily through various levels of education thanks to his bright mind and ease of learning. He went to the primary school at his native village and later to the Piaristic school at Lipník nad Bečvou. He then attended the Grammar School at Opava, followed by studies at the Philosophical Institute (today Sts Cyril and Methodius Faculty of Theology of the Palacký University) at Olomouc from 1840 to 1843. He struggled with the costs of his education, but was offered to join the St. Augustine order, famous for its support of education and science, at the Moravian capital Brno. He did not hesitate and entered the order in 1843 (Figure 1). He passed a number of exams during the first years in the monastery, that were not much related to his preparation for priesthood, such as in fruit-growing and horticulture. Mendel became a respected substitute teacher at the Grammar School at Znojmo. His efforts to become a legitimate professor of biology and physics led him to take a teacher's qualification exam in 1850. Unfortunately, he did not succeed, but was recommended to study at the University. At the University of Vienna (1851 to 1853), Mendel enrolled in courses with the famous physicist Christian Doppler and the renowned mathematician Andreas von Ettingshausen. Apart from acquiring knowledge in mathematics and physics, Mendel also received education in methods of performing physical experiments, which he used in the careful planning and design of his Pisum experiments. Traditional experimentation with hybrids was based on compilation and cataloguing information, followed by drawing conclusions from observations. The radically new approach used by Mendel was the Newtonian, where first a hypothesis is formulated and experiments are then carefully designed to prove or disprove it. Orel (1984) suggests that Mendel might have learned also from a mathematical textbook of DOPPLER (1844) with a chapter, that translates "combinatorial theory and basic principles of probability calculation". Orel also argues that Mendel might have

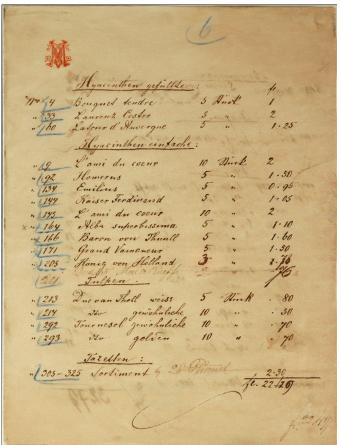


Figure 1. The Old Brno Augustinians; arrow points to Mendel

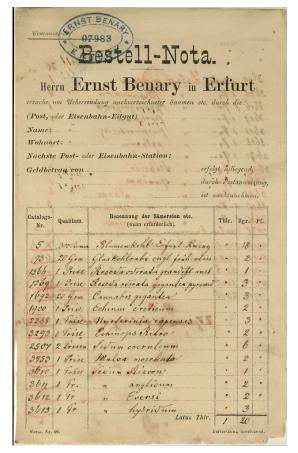
known J. J. LITTROW's (1833) booklet, that translates "Probability Calculation as Used in Scientific Life", that helped him to compile meteorological records and to make weather forecasts. Mendel finished his studies in 1853. In 1855 he again failed in the teacher's qualification exam and could therefore work only as a substitute teacher at the German Grammar School in Brno. Around 1854 he started experiments to answer a long standing question of hybridization, not inheritance itself as we perceive it today, since the science of genetics was born later. This is reflected in the title of Mendels famous "Versuche über Plfanzen-Hybriden" ("Experiments in Plant Hybrids") (MENDEL 1866). Hybridisation experiments can be traced back to Rudolph Jacob Camerer (1694), but systematic research by crossing plants considered as distinct varieties or species started with Joseph Gottlieb Kölreuter (1733–1806), followed by Carl Friedrich von Gärtner (1772–1850). In general, such research was mainly focused on the variation or stability of natural forms and the physiology behind the transfer of plant traits between generations. Especially, the extent by which parents contribute to the characters of the offspring, if both parents influence the offspring traits in a similar way and how the inherited traits develop in the offspring. Distant crosses, often used in such studies, were largely unsuited to observe the transmission of traits between generations due to impaired fertility. The current scientific opinions were, that

- (a) hybrids represented an equal or near equal mix of parental traits,
- (b) that interspecific hybrids are generally infertile, except from closely related species, that show some degree of fertility,
- (c) that a few offspring of fertile hybrids revert to the hybrid form, whereas most revert to the grandparent forms; and
- (d) that the expression of traits in the hybrids is related to the strength of "essence" of the species, as thought at that time (WYNN 2007).

Mendel honestly confronted the current opinions with his results in two lectures in 1865. According to Mendel's own account, his findings were considered controversial because of their unorthodoxy and none of the Society's members felt they were sufficiently important to replicate them (ILTIS et al. 1932). The reason for his success is in part the result of Mendel



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Figure 2. A	seed order	for Men	del	



being in his skills a hybrid himself: partly biological scientist, physical scientist, and mathematician. Once his observations were quantified and the relationship between the characters described in quality and quantity, Mendel turned to combinatorics and probability to provide arguments supporting the claims made from inductive reasoning, that the characters he is examining remain fixed over generations and are randomly combined in the progeny, following the well known mathematical rules of combinatorics. He used deductive principles of mathematics to present this relationship as a law of nature. To describe biological phenomena by a mathematical model, such as the famous (A + 2Aa + a), was absolutely new in science, but became the basic principle of modern scientific research in any natural science. Such an innovative approach to science sounded strange and unfamiliar to Mendel's hybridist audience (WYNN 2007) and hard to accept. Although the Society members found Mendel's results controversial at best, forgettable at worst, his complete lecture was published in the "Verhandlungen des Naturforschenden Vereins in Brünn" (Proceedings of the Natural Science Society at Brünn) in 1866 and sent to dozens of institutions across Europe. Of this group of influential and scientifically inclined biological researchers, Carl von Nägeli was the only one known to have fully read, considered, and responded to Mendel's work. The correspondence between the two suggests that Mendel's expressed interest in the *Hieracium* experiments was an important factor in Nägeli's motivation to write back. In his response to Mendel's article and initial letter, the only existing communication of Nägeli's to Mendel, Nägeli writes at length about *Hieracium* and asks for Mendel's help in doing some breeding experiments. Nägeli argued that Mendel cannot assume that his belief in the inalterability of traits is good in all cases, he asked to test it on more species.

Mendel continued with experiments on other plants, but a significant change happened in 1868, when he became abbot and had to manage the Abbey. He nevertheless continued his research on bees, built in 1871 an apiary and made crosses of various bee lineages. He was also known as a meteorologist, recorded sunspots and made the first ever scientific description of a tornado (Mendel 1871), that swept through Brno in October 1870 and caused considerable damage. Mendel held also surprising positions,

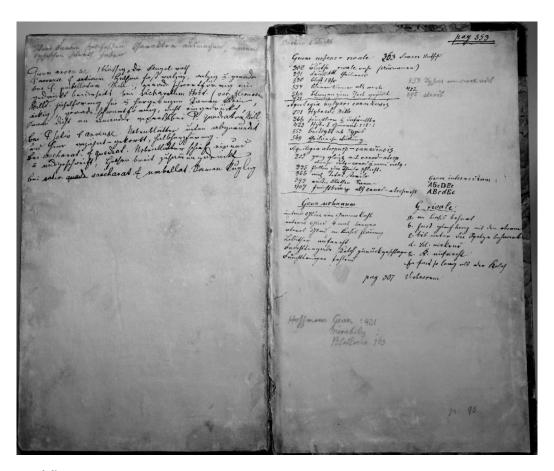


Figure 3. Mendel's notes

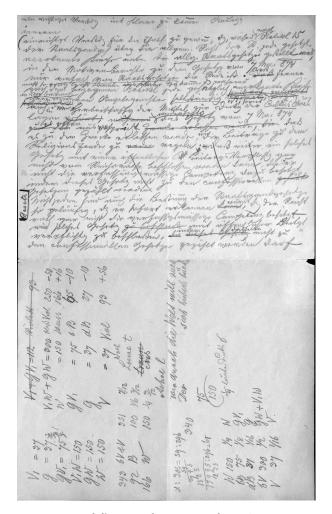


Figure 4. Mendel's notes about research on Geum

such as being director of the Moravian Mortgage Bank from the 1870's. He died from a kidney infection on 6th of January 1884 after a short illness. He was a respected personality in his town and the famous Czech composer Leoš Janáček played the organ at his funeral.

Let us now consider two contrasting questions connected with Mendel's "Experiments with Plant Hybrids":

- (a) why were Mendel's findings so boldly ignored by his contemporaries? and
- (b) why were Mendel's findings so compelling to 20th century biologists?

Darwin's evolution theory held that species varied over time, what was also a common opinion among breeders. In an apparent contradiction to it, Mendel believed that the hereditary elements of a species remained constant. Wynn (2007) argued that at least in part, Mendel's use of mathematical principles was rejected by his contemporaries because of the general opinion, that inherited characters are not stable and,

therefore, their transfer to subsequent generations cannot be described by discrete mathematical methods such as probability and combinatorics.

Although several different theories have been advanced among historians (ILTIS et al. 1932; OREL 1984; Henig 2000), most historians held that Mendel supported the idea that populations of organisms varied over time (ILTIS et al. 1932; HENIG 2000). Despite evidence suggesting that Mendel's work supported the Darwinian concept of transmutation of species, closer examination of Mendel's own words suggests otherwise, that he was more interested in proving that characters did not change over time, as was shown by OREL (2003). Mendel divided his scientific paper, based on experiments conducted from 1850 to 1864, into several parts. The largest section deals with experiments with *Pisum*, another part deals with other genera such as Phaseolus and the last section contains his concluding remarks. Mendel chose the genus *Pisum* deliberately, since it fulfilled his three basic requirements for his experimental plants (simplified): constancy of characters over generations (true breeding), protection from foreign pollen during flowering and undisturbed fertility of hybrids and offspring. Mendel tested 34 pea varieties during two years and selected 22 for further examination. He noticed also the problems with separation of species or subspecies, but considered this irrelevant for the experiments. He carefully chose characters, that were easily observable and clearly distinguished the tested varieties, such as flower, seed and pod characters. Mendel grew plants in garden beds and a small proportion in pots. Control plants of each experiment were kept in a greenhouse. Mendel accurately described the individual experiments and the distribution of particular characters in each generation. He examined first plants differing in one and then in two or more characters. Mendel certainly made more experiments than were published and chose the most representative experiments for publication. Mendel lectured about peas already before his experimental work. He studied a total of 15 genera of plants and obtained seeds from colleagues or ordered them. One such order is on display at the Mendel Museum at Brno (Figure 2). Mendel exchanged a series of letters with the recognised Swiss professor Carl Wilhelm von Nägeli, who became a critical judge of his work. Mendel wrote Nägeli about his appointment as abbot and about hopes to find eventually more time for his experiments. This, unfortunately, never happened. Mendel finished his experiments around 1870. Perhaps for lack of time

or problems with vision resulting from stress during artificial pollination of pea flowers. Few of Mendel's written notes are preserved. Worthy of mention is a piece of paper with remarks on experiments dealing with flower colour together with editing remarks for a sermon (Figure 3). Mendel's notes are also preserved on the cover of a book by Gärtner, mentioning the genus Geum, one of many objects of Mendel's interest (Figure 4). The notes and Mendel's Manuscript on peas (Figure 5) are on display at the Mendel Museum in Brno. A priority dispute between Hugo De Vries, Carl Correns, and Erich von Tschermak in 1900 over who was the first to discover the 3:1 and 1:2:1 segregation ratios lifted Mendel's largely forgotten paper back into public awareness. Once revealed, it required the efforts of the English biologist William Bateson (BATESON 1913), who defended Mendel's theory vigorously, coined the terms "genetics" and "allele" and petitioned renowned institutions such as the Royal Society to fund further research, before Mendel's theory spread among scientists. But only after Thomas Hunt Morgan (MORGAN 1916) integrated Mendel's theoretical model with the chromosome theory of inheritance, in which the chromosomes

within cells were thought to carry Mendel's "factors", was classical genetics born and Mendel's place in history fixed. Mendel's principles of heredity now belong to general education and are found in every biology textbook.

The basic principles, discovered by Mendel, can be summarised as follows:

The characters of plants are not inherited continuously, but in discrete units, he called "factors", now called genes. There are two alternative forms of a factor for each character. For example, the factor (gene) for flower colour in pea plants exists in two forms, one for purple and the other for white. The forms are now called alleles. For each character there are two alleles of the respective factor (gene) present in the same plant, one from each parent. The expression of a single character depends on the combination of its two alleles. One of the alleles suppresses the effect of the other allele and is called the dominant allele. The other allele, called recessive, is expressed only in the absence of the dominant allele.

This was later declared as the Law of Dominance. The alleles of a gene thus can be the same (homozygous) or different (heterozygous).

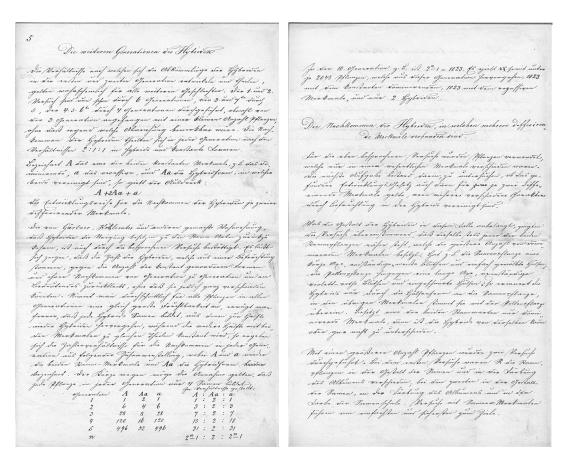
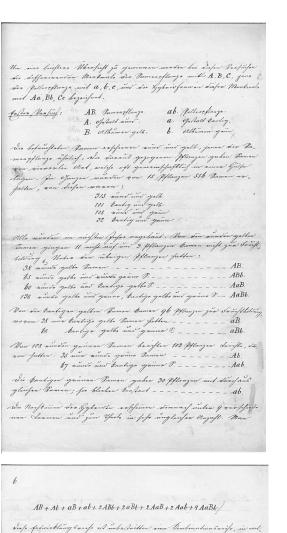


Figure 5. Mendel's manuscript; the middle part of his work on peas



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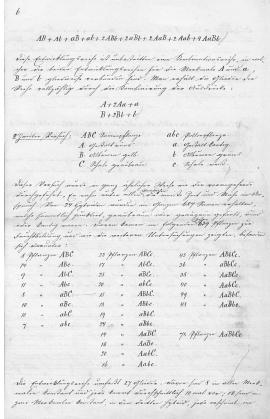
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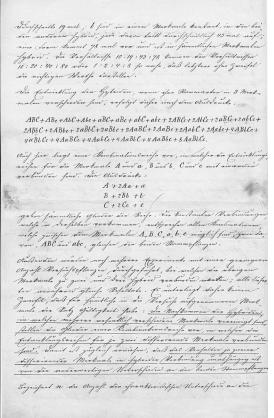


Figure 5. Mendel's manuscript; the middle part of his work on peas (continuation)

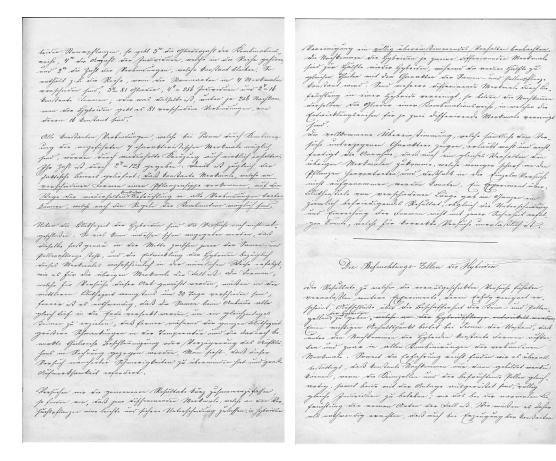


Figure 5. Mendel's manuscript; the middle part of his work on peas (continuation)

In symbolic writing, using "A" and "a" for the dominant and the recessive allele, respectively, there are four possible combinations: AA, Aa, aA and aa. The first three combinations look the same (for example purple) due to the presence of the dominant allele, while the last combination looks different (for example white).

The progeny of AA consists entirely of AA individuals and the progeny of aa entirely of aa individuals. The progeny of Aa or aA consists of randomly distributed individuals of all four categories. If we join the categories Aa and aA, the frequency of the categories in the progeny conforms to the famous formula 1AA:2Aa:1aa.

This was later declared as the Law of Segregation. During the formation of gametes (eggs and pollen) each gamete receives randomly one of the two alleles of each gene. During fertilisation (fusion of the egg with the pollen) the number two of alleles is again restored and the alleles in the hybrid results from the combination of two random gametes.

This was later declared as the Law of Independent Assortment.

Mendel himself did not formulate these laws.

As was written in an obituary of G. Mendel – Direct, epochal significance, however, he had through his research about plant hybrids. What he did and created, remains an immortal monument!

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