READING 33-1

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Gregor Mendel

Gregor Mendel. 1865. Experiments on plant hybrids. (Versuche uber Pflanzen-Hybriden). Verhandlungen des naturforschenden den Vereines in Brunn 4:3–47.


Gregor Mendel

Mendel's paper is a victory for human intellect, a beacon cutting through the fog of bewilderment and muddled thinking about heredity. The story of its origin, neglect, and so-called rediscovery has become a legend in biology: an obscure monk working alone in his garden discovers a great biological phenomenon, but the report is ignored for a third of a century only to be resurrected simultaneously by three scientists working independently. Recognition, alas, comes too late, for the gentle amateur died 16 years earlier.

In contrast to most romantic revisions of history where the sugar coating melts under the heat of scrutiny, the drama of Mendel intensifies rather than subsides. Indeed, the stature of Mendel as a creative thinker with profound scientific foresight grows with the passage of time. He is revealed as a 19th-century Leonardo da Vinci with broad scientific interests and shares with Albert Einstein the distinction of having failed an accreditation examination, not once but twice, and that for certification as a high school teacher. His paper, instead of being revealed fully by the discoverers, is subtly altered in interpretation and a generation of scientific endeavors is necessary to understand it completely. It yields insights still.

The prevailing view of heredity during the middle of the 19th century assumed 2 gross misconceptions: the acceptance of a blending of hereditary factors and the heritability of acquired characters. Evidence for a particulate basis for inheritance, such as the reappearance of ancestral traits, was common knowledge but considered exceptional. In fact, all the "discoveries" attributed to Mendel, such as the equivalence of reciprocal crosses, dominance, uniformity of hybrids, and segregation in the generation following hybridization, are gleanable from the pre-Mendelian literature.

Incredibly, Charles Darwin's explanation of evolution by natural selection became a well-establishd theory in the years following publication of Origin of Species in 1859 despite any factual evidence to explain either the nature or the transmission of hereditary variation. Darwin, aware that blending inheritance led to the disappearance of variation, relied on the inheritance of acquired characters to generate the variability essential to his theory. His clear but inaccurate formulation of a model of inheritance (pangenesis) which involved particles (gemmules) passing from somatic cells to reproductive cells exposed the lack of any factual basis. The concept was merely a restatement of views dating from Hippocrates in 400 BC and endlessly reformulated.

Mendel's paper describes a series of experiments involving inheritance of traits in peas and beans. Preliminary results with peas allowed Mendel to formulate and then to test laws of inheritance that involved segregation and recombination of particulate elements. The proof of the particulate nature of the elements was made possible by the nature of the plants and traits studied. The traits chosen were contrasting (e.g., yellow versus green cotyledon, tall versus dwarf plant) and constant (i.e., true breeding) after normal self-pollination in the original lines. In 7 of the 8 characters chosen for study, the hybrid trait resembled one of the parents; in one character, bloom date, the hybrid trait was intermediate. Mendel called traits that pass into hybrid association "entirely or almost entirely unchanged" as dominating and the latent trait as recessive because the trait reappeared in subsequent crosses. The phenomenon of dominance was clearly not an essential part of the particulate nature of the genetic elements but was important to classify the progeny of hybrids. The disappearance of recessive traits in hybrids and their reappearance, unchanged, in subsequent generations was striking proof that the elements responsible for the traits (now called genes) were unaffected or contaminated in their transmission through generations.

When the hybrids of plants differing by a single trait were self-pollinated, three-fourths of the progeny displayed the dominating trait and one-fourth the recessive. In the next self-generation, progeny of plants displaying the recessive trait remained constant (nonsegregating), but those with the dominant trait produced 1 of 2 patterns of inheritance. One-third were constant, as in the original parent with the dominating trait, and two-thirds were segregating as in the hybrid. Thus the 3:1 ratio in the first segregating generation (now called the F_2 generation) was broken down into a ratio of 1 (true breeding dominant) : 2 (segregating dominant as in the hybrid) :1 (true breeding recessive). The explanation proposed was that theme parental plants had paired elements (e.g., *AA* or *aa*, respectively) and the hybrids of such a cross were of the constitution *Aa*. Further, elements were distributed and to conceptualize a genetic theory that was to create a new biology. The standard approach to unravel the mysteries of heredity was to analyze the complex of characters usually from wide crosses, a method that had failed for 2000 years and was to continue to fail even when applied by the combined talents of Francis Galton and Karl Pearson.

Mendel succeeded because of his approach. His goal was grand, being no less than to obtain a "generally predictable law" of heredity. His previous crosses with ornamentals had indicated predictable patterns, and his assumption was that laws of heredity must be universal. He had reviewed the literature and noted that "of the numerous experiments, no one had been carried out to an extent or in a manner that would make it possible to determine the number of different forms in which hybrid progeny appear, permit classification of these forms in each generation with certainty, and ascertain their numerical relationships."

Mendel clearly knew what he wanted to do and his method was precisely appropriate. His achievement was no serendipitous discovery. He was the consummate experimentalist, fully aware that the "value and validity of any experiment is determined by the suitability of the means as well as by the way they are applied." He defined the system. Plant material must possess constant differing traits which do not disturb fertility in further generations and must remain free from pollen contamination (outcrossing). All the progeny, without expectation, must be observed.

The experimental organism, the garden pea, was a perfect choice. Mendel procured 34 cultivars from seedsmen, tested their uniformity over 2 years, and selected 22 for hybridization experiments. Results from preliminary crosses indicated that common traits were transmitted unchanged to progeny but that contrasting traits may form a new hybrid trait that changes in subsequent generations. A series of experiments followed traits carefully selected for discontinuity to permit definite and sharp classification rather than "more-or-less" distinctions. This was a key decision.

Mendel restricted his attention to individual traits for each cross, avoiding the "noise" of extraneous characters. His analysis was quantitative and he displayed a mathematical sense in the analysis of data and the design of experiments. Mendel had a clear feeling for probability and was not put off by large deviations in small samples.

Mendel was a meticulous researcher. The sheer mass of his data is impressive and his experiments build from the simple to the complex. His clarity of thought is mirrored by a felicity of expression. His prose is straightforward, free of unnecessary arguments and obfuscation, faults that make many of the papers of his contemporaries almost incomprehensible.

The story of his paper has some interesting twists and turns that are important because they bear on the relation of progress in science and scientific publication. Mendel presented his paper in 2 oral sessions of the Brunn Society for the Study of Natural Sciences (February 8 and March 8, 1865) and it was published in the Proceedings of the Brunn Society for the Study of Natural History in 1865, which appeared in 1866. The paper made no impact on the scientific establishment. In 1966 it was discovered that the 2 lectures received an enthusiastic but anonymous review in a daily newspaper in Brunn, the only positive feedback that Mendel was to receive. Mendel's published paper was distributed to about 120 libraries throughout the world through the exchange list of the Brunn Society and was available in England and the United States. The paper was listed in the Royal Society (England) Catalogue of Scientific Papers for 1866 and referred to without comment in a paper on beans by H. Hoffmann in 1869. The only substantial reference was in the 590-page treatise on plant hybrids by W.O. Focke in 1881; Mendel's name is mentioned 17 times, but it is clear that Focke did not understand Mendel. In the critical passage he writes: "Mendel's numerous crossings gave results which were quite similar to those of [Thomas Andrew] Knight but Mendel believed he found constant numerical relationships between the types of the crosses." R.A. Fisher's comment on Focke's treatise in his famous 1936 paper ("Has Mendel's Work Been Rediscovered?") is priceless: "The fatigued tone of the opening remarks would scarcely arouse the curiosity of any reader, and in all he has to say, Focke's vagueness and caution have eliminated every point of scientific interest."

Focke's mention of Mendel did have repercussions. It was probably the basis for Mendel being listed as a plant hybridizer in the 9th edition of the *Encyclopaedia Britannica* (1881–1885) in an article by G.J. Romanes. Mendel's paper was also cited from Focke, but unread, by Liberty Hyde Bailey in an 1892 paper, "Cross Breeding and Hybridization," which according to 1 account by Hugo De Vries, may be the source of De Vries's introduction to Mendel. Focke's reference to Mendel was also picked up by Carl Correns and Erich von Tschermak when they began their research with peas.

In a book published in 1885 by Nageli and Peter entitled *Die Hieracien Mitteleuropas*, Mendel's paper is cited out of context, lumped with his other inheritance paper on Hieracien. The relation between Mendel and Nageli (analogous in many ways to Mozart and Salieri) is a shameful episode for academic science. Carl Wilhehn Nageli (1817–1891), a distinguished botany professor at the University of Munich, corresponded with Mendel and received Mendel's reprints, a reformulated explanation, packets of seed of peas with notes by Mendel, but he could not or would not understand the paper. His eternal punishment is that he may only be remembered for this fact.

There are other curious references. The Russian botanist I.F. Shmalhausen (1849–1894) appears to have read and appreciated Mendel's results. Mendel is cited as a footnote to a literature review of his 1874 Master's thesis but incorporated in the thesis *after* printing! The thesis was translated into German and appeared in *Botanishe Zeitung*, but the chapter with the historical review was omitted.

Finally, Hugo Iltis, Mendel's biographer, admits to having read Mendel's paper in 1899 when a high school student. "Amazed and puzzled" by the mixture of botany and mathematics, he brought the paper to an unnamed professor of natural history, who also proved uncomprehending.

Mendel received 40 separates of his paper, of which 3 have been traced. One went to Nageli at Munich, one to Anton Kerner von Marilaun at Innsbruck (found after his death, uncut), and one turned up in the hands of M.J. Beijerinck, who sent it to Hugo De Vries, undoubtedly the true source of De Vries' introduction to Mendel.

The so-called rediscovery of Mendelism by Hugo De Vries (1848–1935), Carl Correns (1864–1933), and Erich von Tschermak (1871–1962) was a consequence of independent investigation, although the almost simultaneous publications were related by events. The first published indication that Mendel's paper was understood occurred when Correns, ironically, a student of Nageli, obliquely cited both Mendel and Darwin in a paper on xenia published January 25, 1900. In March, De Vries completed 3 papers on his research, submitting them to 3 journals! Incredibly, the 1st paper to appear in print, a note in the *Comptes Rendus* of the Paris Academy of Science, did not mention Mendel but used the terms "dominance" and "recessive." Receipt of the reprint by Correns (April 21) triggered an immediate rejoinder in the form of a paper (April 22!) giving due credit to Mendel. Although the other 2 papers by De Vries did in fact mention Mendel, there is evidence that these references were second thoughts and were made in proof. Tschermak's 1st paper, which appeared in June 1900, refers to Mendel but showed a weaker grasp of its essentials than De Vries or Correns; both the De Vries and Correns papers were cited in a postscript added in proof.

None of the rediscovers' papers was in the class of Mendel's paper in terms of either analysis or style. De Vries was vague on the role of dominance and Corren was convinced that the law of segregation cannot be applied universally. Tschermak's paper reported the 3:1 ratio in the1st segregation generation but did not interpret the backcross of the hybrid to the recessive parent as a 1:1 ratio, casting doubt of his complete understanding at that time.

Why was Mendel's paper, despite its clarity and incisiveness, ignored for 35 years? The best explanation is that Mendel was ahead of his time and it took that long for the scientific community to catch up. Remarkably, Mendel's paper was precytological and the cytological discoveries that were to provide a physical basis for heredity were published between 1882 and 1903. 19th-century biology was not ready for Mendel. Part of the reason is that science then, as now, is conservative. New ideas are absorbed with difficulty and old ones discarded only reluctantly. One paper is not enough. The human qualities that made Mendel admirable as a person-modesty and reticence-worked against his receiving personal acclaim and fame during his lifetime.

The origins of the modern science of genetics are to be found in a small monastery garden cultivated by one who would worship at the altar of horticulture and science. Johann Mendel (the name "Gregor" was taken at his ordination), the child of peasants, was born in 1822 in Heinzendorf, a small village in a corner of Moravia. The boy, enamored of learning, was attracted to the monastery out of financial considerations. According to his autobiographical essay submitted for entrance to St. Thomas, the Augustine monastery of Brunn (now Brno, Czechoslovakia), his choice of vocation was influenced by his desire to be freed from the "perpetual anxiety about a choice of livelihood." He was accepted as a novice in 1843 and received a classical theological education at the local seminary. After ordination in 1847, he spent a year as a parish priest but proved to be emotionally unsuited, becoming physically ill in the presence of sickness and pain. He was offered a post to teach mathematics and Greek in the local school, a position for which although technically unqualified, he performed with distinction. Despite his lack of university training, he took the qualifying examination for teachers but failed-the question that tripped him up was the classification of mammals-the specialty of the examiner.

His monastery sent Mendel to the University of Vienna to spend 3 years studying science. In 1854 he was appointed supply (substitute?) teacher in Brunn Modern School, teaching physics and natural history to the lower school, a position he retained for 14 years. Incredibly, he again failed his accreditation exam, probably because of a dispute with his botany examiner, an event speculated to be connected with the initiation of his intensive experimental activities with peas the same year. His talents, however, were not lost on his fellow monks, who elected him prelate (for life) in 1868. The move proved to be a personal tragedy, for it caused him to withdraw from scientific work, and a bitter tax dispute between his monastery and the Austrian government embittered the last decade of his life. He died in 1884.

It is clear that St. Thomas was not a cloistered retreat with silent, tonsured monks in sandals and hairshirts but a vibrant community of scholars and artists. Mendel was neither ascetic nor reclusive and his writings are devoid of any religiosity, whatsoever. Politically, he was antiauthoritarian—a 19th-century liberal. He loved good food (he grew quite corpulent) and fine cigars (20 a day). As prelate of a wealthy monastery, he lived the busy life of an administrator, housed in elegant style and traveling widely, serving on committees and boards. He managed farms, became chairman of the Moravian mortgage bank, and even founded a volunteer fire department. He served as officer of the Brunn Society for the Study of Natural Sciences, but after 1870 he switched allegiance to the Royal Agriculture Society, serving for 2 years as acting chairman. One of his duties was that of examiner for fruit and vegetable growers. Mendel's passions were science and agriculture. In addition to being a superb horticulturist, he was an accomplished meteorologist. He wrote a definitive description of a tornado that tore through the monastery. Ironically, this published report was also ignored; a 1917 treatise by A. Wegener which describes 258 tornadoes in Europe contains no reference to Mendel. Mendel kept records of such diverse phenomena as groundwater, sunspots, and ozone levels. Tragically, most of his scientific notes and correspondence were burned at his death.

Although his scientific career was unrecognized in his lifetime-due in part to his self-effacing style-his fame soared after the rediscovery and the legend of Mendel contributed much to the feverish genetic activity from 1900 to 1925, probably making up for lost time. His subsequent fame as the Father of Genetics has obscured the fact that Mendel was primarily a horticultural scientist. His paper, the most famous horticultural paper written, may be the most famous single paper in biology.

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