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# The Many Sides of Gregor Mendel

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**Abstract.** Gregor Mendel (1822–1884) was a man of many talents, interests, and social roles, some of which took him inside the mainstream of the academic life sciences, and some of which kept him aloof and gave him his unique and innovative perspective.

Historians of science used to see him as a tragic figure, because his forays into the study of heredity went unappreciated—either they were too far ahead of their time, or emanated from too far outside the centers of European science. But that was a view from inside the ivory tower, which ignored the non-academic sides of Mendel and most of what he did and valued. Here I would like to paint a more comprehensive picture, in which he is successful at many things, draws on varied intellectual and practical resources, and addresses other audiences than just the geneticists of the future.

Far from being designed only for the ages, Mendel's celebrated experiments on hybridization in peas addressed the interests of contemporary breeders, plant hybridizers, Mendel's teachers in Vienna, brothers at the monastery, and colleagues at the Brünn Society. It was the work of a man with many sides, who belonged to many communities.

**Keywords:** Genetics, Mendelism, Plant Breeding, Gregor Mendel, Biography, Austrian Empire, 19$^{th}$ Century.

## Introduction

Gregor Mendel (1822–1884) was longviewed as the ultimate scientific outsider. After all, he was not celebrated as the founder of genetics until sixteen years after his death. He was not a professional researcher by any definition, but a monk and a schoolteacher, later an abbot. He lived and worked far from the great European intellectual centers of his day, in Brünn, provincial capital of Moravia, then part of the Austrian Empire (Brno, in Czech; since 1993, part of the Czech Republic).[1] He presented the results of his experimental crosses of pea plants, along with the foundational ideas of genetics, only at his local scientific society in 1865. His now-famous article on the subject came out in

1. Throughout this paper, I use the German place-names, as Mendel would have done.

the *Proceedings* of the society in 1866,[2] not the most conspicuous place for it, and, indeed, little notice was taken of it at first. It took until 1900 for it to be "rediscovered" and recognized as a cornerstone of the emerging science of genetics. Only then did Mendel find a place among the scientific insiders, or so it seemed to early geneticists.

The geneticists quickly embraced Mendel as one of their own. His name was given to "Mendel's laws," traits that "Mendelize," "Mendelism" as a theory of heredity, and "Mendelism" as a theory of evolution. Geneticists from all over the world donated money for a Mendel monument in Brünn. Mendel's work seemed to fit in so well in twentieth-century science that it was hard to imagine him ever belonging anywhere else, and the image developed of Mendel as a man so far ahead of his time that he had no intellectual company, no peers, no teachers. Unencumbered by old-fashioned preconceptions or intellectual commitments, he could see ahead to future problems and solve them, while his shorter-sighted contemporaries would not have seen the point of his work, had they even read it.

The blinkered view of Mendel as a figure without peers is reflected in one of the best-known photographs of him (Figure 1), which is actually a detail from a group portrait. The corresponding narrative of the lone and unrecognized genius is told most eloquently by Loren Eisley. Here is how he describes Mendel's 1865 presentation to the Brünn Society of Naturalists:

> Stolidly the audience had listened. Just as stolidly it had risen and dispersed down the cold, moonlit streets of Brünn. No one had ventured a question, not a single heartbeat had quickened. In the little schoolroom one of the greatest scientific discoveries of the nineteenth century had just been enunciated by a professional teacher with an elaborate array of evidence. Not a solitary soul had understood him.
>
> Thirty-five years were to flow by and the grass on the discoverer's grave would be green before the world of science comprehended that tremendous moment. Aged survivors from the little audience would then be importuned for their memories. Few would have any.

2. Gregor Mendel, "Versuche über Pflanzenhybriden," *Verhandlungen des naturforschenden Vereines in Brünn* 4 (1865): 3–47; also available in English and online: Curt Stern and Eva R. Sherwood, eds., *The Origin of Genetics: A Mendel Source Book* (San Francisco: W. H. Freeman, 1966); Gregor Mendel, "Experiments in Plant Hybridization," MendelWeb, URL: `http://www.mendelweb.org/MWpaptoc.html`.

Figure 1: Mendel, the isolated geneticist, a widely reproduced detail from a group portrait, which first appeared as the frontispiece to William Bateson's 1909 book, *Mendel's Principles of Heredity.* Bateson used an oval frame to help obliterate the monk seated at the lower right, but this rectangular version (from the Curt Stern Papers at the American Philosophical Society Library in Philadelphia) shows more extensive retouching. The group portrait can be seen in its entirety in Figure 2, on p. 17.

A few pages later, Eisley offers this judgment about Mendel's place in history:

> Mendel is a curious wraith in history. His associates, his followers, are all in the next century. That is when his influence began . . . . Gregor Mendel had a strange fate: he was destined to live one life painfully in the flesh at Brünn and another, the intellectual life of which he dreamed, in the following century.[3]

It is a tragic tale indeed. But cheer up, I am going to tell it a little differently, by drawing on more recent historical research that has found some company for Mendel, some associates, audiences, and influences.

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3. Loren Eisley, *Darwin's Century: Evolution and the Men Who Discovered It*, 2nd ed. (Garden City, NY: Anchor Books, 1961), 206 & 211.

Geneticists and historians alike have spun the Mendel story for a variety of rhetorical purposes.[4] Versions like Eisley's, which emphasize the long neglect and isolation, tend to aggrandize twentieth-century Mendelians for their greater openness to new ideas and their superior understanding of Mendel's paper, while the idea of a rediscovery reassures us that science is self-correcting and sooner or later will give credit where credit is due. But we should also make allowances for the lack of information about Mendel's community and context available to the rediscoverers. For them it was hardly unreasonable to infer that his monastic life and teaching duties precluded full-time research and close contacts to the international scientific community, or that the long neglect of his paper was good *prima facie* evidence that he had been misunderstood in Moravia and ignored everywhere else.

But now, more information is available and it has become clear that, for all the modernity of his scientific thinking, Mendel was also rooted in the nineteenth century: in the intellectual, economic, and religious life of Brünn, in the pure and applied sciences of the Austrian Empire (especially meteorology, biogeography, plant breeding, and evolution) and in European science generally. Several separate lines of post-Eisley research have recovered other sides of the historical Mendel than just the misplaced geneticist. I will try here to merges these lines into a more complete portrait and to show how his many sides also enrich our understanding of his famous paper.

Recent historical research also recognizes multiple nineteenth-century sources for later ideas about heredity. Far from springing fully formed from Mendel's head, genetics is beginning to look like a synthesis of many lines of thinking, not only in biology, but also medicine, agriculture, law, and other spheres.[5] From this point of view, the many-sided Mendel to be developed here, with his multiple affiliations, audiences, and intellectual resources, makes a much more plausible founding figure than the lone outsider. His achievement then emerges less as a crossing of existing disciplinary boundaries than as a merger of disciplines into something new.

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4. For a thorough survey, see Jan Sapp, "The Nine Lives of Gregor Mendel," in *Experimental Inquiries*, ed. H. E. Le Grand (Dordrecht: Kluwer Academic Publishers, 1990).

5. Staffan Müller-Wille and Hans-Jörg Rheinberger, eds., *Heredity Produced: At the Crossroads of Biology, Politics, and Culture, 1500-1870* (Cambridge, MA: MIT Press, 2007), especially the editors' introduction, "Heredity—The Formation of an Epistemic Space."

## Historical and Political Background

In the eighteenth century, some eighty years before Mendel's birth, the Habsburg dynasty ruled over a sprawling multi-national, multi-cultural realm in Central and Eastern Europe, comprising what is now Austria, Hungary, the Czech Republic, Slovakia, Croatia, Slovenia, Bosnia and Herzegovina, Romania, and parts of Poland and Italy. Along with Russia, France, and Britain (Germany was still fragmented into many separate kingdoms and principalities), the Habsburg Empire[6] was one of the "great powers" of Europe, militarily and politically.

Its rulers were shocked, however, in 1740, when the much-smaller Kingdom of Prussia attacked and captured their northern province of Silesia, their most highly industrialized province, with its textile factories and iron and coal mines. The loss was an economic blow as well as a military embarrassment. The young empress, Maria Theresa (ruled 1740–1780), spent over twenty years trying to get Silesia back, fighting the War of the Austrian Succession (1740–48) and the Seven-Years' War (1756–63) against Prussia and a changing constellation of allies. She never did reclaim it, but held on only to a sliver, where the Mendel family happened to live, and which became part of Moravia, administratively.

Maria Theresa's efforts to compete with Prussia and maintain the status of the empire as a great power were not exclusively military and diplomatic in nature. She, and especially her son Joseph II (ruled 1780–90, but co-regent with his mother from 1765 on), also modernized and centralized their administration. They applied the eighteenth-century ideals of "enlightened absolutism," a political and economic theory that emphasized efficiency and rational organization, and they instituted reforms that aimed to weaken the competing, decentralized, redundant, and inefficient feudal powers, such as the noble landlords, high church officials, and religious orders. Some of these Theresian-Josephine reforms were to have direct effects on Mendel's life and career: partially emancipating the serfs, modernizing agricultural practices, making primary and secondary education more widely available, encouraging the study of the natural sciences, and forcing the monasteries to be of service to the Empire and the economy.

6. After 1804 also called the Austrian Empire; after 1867, Austria-Hungary.

## Mendel's Early Life and Schooling

Mendel's father, Anton Mendel, was a peasant in a little village called Heinzendorf (Czech: Hynčice).[7] The family was ethnically German, and the region majority-German as well.

Anton Mendel took a special interest in cultivating and grafting fruit trees, and taught young Mendel to do it, too. He was encouraged in this by the local countess, an enlightened ruler in the Josephine tradition, who made an effort to promote scientific agriculture in her territory. She imported and distributed fruit trees, and had natural science taught at village schools.

Our scientist was born Johann Mendel on July 22, 1822, the second of three children. (He took the name Gregor as an adult, upon entering the monastery.) Only limited schooling was available nearby, but because he was considered exceptional, the priests who taught the village children arranged for him to continue his education in town, and helped him talk his parents into it. They had little means of financing his studies, and they would miss the help of their only boy on the farm, for peasants like Anton Mendel had been only partially emancipated. He owned his own farm, but still had to work three days a week for the countess, an obligation known as the *Robot*.[8]

In 1834, at the age of thirteen, Mendel began attending *Gymnasium* (the academically oriented secondary school that opened the door to university education and the elite professions) some twenty-five miles away. His parents could only afford room and half board, and he had to tutor slower, but wealthier pupils to earn his lunch money. Mendel got along like that until 1838, when his father was crushed in a logging accident, while performing his *Robot*. He survived, but never recovered fully, had trouble maintaining the farm, and could not support his son at school as before. Mendel in the meantime had earned a teaching certificate that qualified him as a private tutor and was able to eke out a living at school, but at times, the pressure of school and work and worries about his family became too much for him. He suffered some kind of breakdown in 1839 and returned home for several months to recuperate. Several more of these breakdowns are recorded, both during and after his schooling, but no precise medical information about them is available.

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7. Biographical details are from: Hugo Iltis, *The Life of Mendel* (New York: W. W. Norton, 1932); and Vítězslav Orel, *Gregor Mendel: The First Geneticist*, trans. Stephen Finn (Oxford and New York: Oxford University Press, 1996).

8. From the Slavic "*robota,*" meaning the corvée or, figuratively, "drudgery"; the word has entered the English language, by way of Czech science fiction, to mean an artificial human.

In 1840, Mendel completed *Gymnasium* and moved on to Olmütz (Czech: Olomouc) in southern Moravia for a two-year course of university-level study (all that was offered; there was no full-fledged university in Moravia). Because of another breakdown and an extended stay on the farm, it took him three years to finish at Olmütz, after which he decided not to continue his struggle to get a university degree. Instead, he followed his family's wishes and the advice of his Olmütz professors (one of whom was a monk himself), and took holy orders. Against stiff competition, he was accepted into the Augustinian order, at the monastery of St. Thomas, in Brünn, in 1843. There he received training in theology and was prepared for the priesthood. He was ordained in 1847.

The monastery offered Mendel not only some much-needed security, but also an intellectual community and an opportunity to do good works and improve the lives of Moravians through education and applied science. The monastery had been influenced by the Josephine reforms, which had eliminated the more contemplative (or uncooperative) monastic orders and confiscated their property. The surviving ones had to be active and productive in worldly affairs.

The monks of Brünn served as highly qualified instructors at several *Gymnasien* as well as at Olmütz. Some were experts in scientific agriculture, managed the monastery's extensive landholdings, and made an effort to share their knowledge with farmers and businesses in the region. Several, among them the abbot, were interested in pure science, too, and they had experimental gardens, a herbarium, a mineralogical collection, meteorological instruments, and a big, up-to-date library. In short, Mendel found himself in learned company, who thought the study of nature was important and useful for their work and their community. It was, admittedly, not a major European research center, but the isolation of the monastery should not be exaggerated, either. Had Mendel been seeking an opportunity to get involved in scientific research, he could hardly have made a more practical choice.

## Mendel's Nineteenth-Century Sources (1): Plant- and Animal Breeding

The work of the monks and the economic interests of the monastery and the surrounding community were tied to a large extent to agriculture and its improvement, and Mendel clearly was motivated to keep the practical goals of his research in sight. His work promised to explain, among other things, how traits combined and interacted in plant hybrids, and it suggested ways of rationalizing hybridization methods to produce desired combinations of traits at will.[9]

An important line of research into Mendel's agricultural connections has focused on the theory and practice of animal breeding, particularly sheep breeding. Vítězslav Orel and Roger Wood have sought out the writings of sheep breeders who were active in Brünn and vicinity from the 1810s through the 1830s and have analyzed their methods and their conceptions of heredity. The Moravians, like many breeders throughout Europe, built upon the work of British breeder Robert Bakewell (1725–95) and others, who had explored ways of making breeding more systematic and scientific. They analyzed the animal into checklists of simple characteristics, measured those characteristics objectively and quantitatively, and devised procedures for comparing, selecting, and inbreeding the animals.

In Brünn, there were also significant discussions of theoretical matters, and it was asserted that heredity must be a law-abiding and predictable process, amenable to scientific study. The breeders there inquired into the effects of inbreeding and outcrossing, and into the stability of varieties. Why did inbred varieties not always breed true? What made them revert to their ancestral condition or become more average? When two varieties were crossed, what determined whether maternal or paternal characteristics would predominate in the offspring? Did it depend on the inner constitution or organization of the parent, or on environmental conditions?[10]

Since Mendel only arrived in Brünn in the 1840s, when sheep breeding was in decline there and few of the older breeders were still around, it is difficult to document a direct influence of their methods and ideas on Mendel's later work. Nonetheless, it seems safe to assume that Mendel was aware of the earlier Moravian ideas and practices, either through his abbot, who had been

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9. For a concise overview of Mendel's life, work, and legacy, emphasizing the interconnections with agriculture, see: Garland E. Allen, "Mendel and Modern Genetics: The Legacy for Today," *Endeavour* 27, no. 2 (2003): 63–68.

10. Vítězslav Orel and Roger J. Wood, "Empirical Genetic Laws Published in Brno before Mendel was Born," *Journal of Heredity* 89 (1998): 79–82; Roger J. Wood and Vítězslav Orel, "Scientific Breeding in Central Europe During the Early Nineteenth Century: Background to Mendel's Later Work," *Journal of the History of Biology* 38, no. 2 (2005): 239–272; Roger J. Wood, "The Sheep Breeders' View of Heredity Before and After 1800," in Müller-Wille and Rheinberger, *Heredity Produced*; Roger J. Wood and Vítězslav Orel, *Genetic Prehistory in Selective Breeding: A Prelude to Mendel* (Oxford: Oxford University Press, 2001).

a practical breeder himself, from the published breeding literature, or from younger plant- and animal breeders who were active, along with Mendel, in the Brünn scientific society.

And there are several important things that Mendel does seem likely to have learned from the old sheep breeders and from his own efforts at plant breeding. First and foremost was the "breeder's gaze," the ability to look at the animal and analyze the overall impression into individual characteristics—the "points of the breed," or, much later, the "unit characters" of the geneticist. The kinds of questions the breeders had asked also recurred in Mendel's work: when does one trait from one parent get inherited in preference to a contrasting trait from the other parent? How can a breeder reliably get desirable traits from two different strains to combine in a hybrid? Also of great importance was the conviction that heredity would turn out to be a predictable and repeatable process, amenable to scientific study and the formulation of general laws.

## Teaching Career and University Studies

For most of his early years at the monastery, Mendel was assigned to teach at the local *Gymnasium*. He taught Latin and Greek, German literature, math, and science, and was found to be very good at it. The abbot sent him to Vienna in 1850 to take the licensing examinations, which were very demanding and dragged on for several weeks. Although Mendel barely passed the written parts, and failed the orals, at least one Viennese professor thought he had some potential and advised the abbot to send him to the University for further training, which he did, for two years (1851–3).

Much had changed in the educational system since Mendel had left it for monastic life, several of the changes resulting from the Revolutions of 1848. Politically, the Revolutions are considered failures. In Austria, the Habsburgs beat them down and emerged more powerful than before, but some reform efforts did ensue. One of them was to modernize the universities and build them into research centers, an effort that also placed new pressures on secondary education to better prepare students for the reformed universities. That is what created the sudden demand at the *Gymnasien* for teachers like Mendel. Meanwhile, at the university level, Vienna had recruited a number of prominent researchers, and Mendel had the opportunity to take courses with some of the best-known scientists of his day, including the physicist Christian Doppler (1803–53) and the botanist Franz Unger (1800–70).

## Mendel's Nineteenth-Century Sources (2): Franz Unger and Academic Botany in Vienna

Mendel's university studies provide historians several more ways of linking him to nineteenth-century scientific thought and methodology. Much has been made of his physics, math, and meteorology coursework as the sources of his quantitative thinking, his conception of a scientific law, and the value he ascribed to experimentation. His exposure to issues in biology, especially pre-Darwinian evolutionary thought, have also been noted.[11]

The old view of Mendel as an outsider in biology, along with the unsafe assumption that biologists were unfamiliar with quantitative and experimental methods, has led most authors to focus on physics, math, and meteorology as the important academic influences from Vienna. But I am much more impressed by Mendel's apparent debts to his botany professor Franz Unger, whose multi-facetted research program covered everything from cell theory to microscopic plant anatomy and plant pathology, and to plant biogeography, paleobotany and evolutionary theory.

Central to Unger's approach was the assumption that there were special forces at work in living creatures that made them grow, develop, reproduce, and evolve, and that these forces obeyed quantifiable laws. In his paleobotanical work, for instance, Unger counted fossil species in different geological periods, broke the counts down by taxonomic group, calculated the ratios between the groups, and traced how the ratios shifted over time. That enabled him to show, quantitatively, that the flora of the earliest period was dominated by algae; that there followed an age of ferns; then horsetails and club mosses; conifers; and finally flowering plants. To him, the pattern of changing ratios indicated that a quantifiable law of nature was at work, a law of evolution or

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11. Robert C. Olby, *Origins of Mendelism*, 2nd ed. (Chicago: University of Chicago Press, 1985), ch. 5; Vítězslav Orel, "Mendel and New Scientific Ideas at the Vienna University," *Folia Mendeliana Musei Moraviae Brno* 7 (1972): 27–36; Franz Weiling, "J. G. Mendels Wiener Studienaufenthalt 1851–1853," *Sudhoffs Archiv für Geschichte der Medizin und der Naturwissenschaften* 51 (1966): 260–266; Franz Weiling, "J. G. Mendel als Statistiker und Biometriker: Sowie die Quellen seiner statistischen Kenntnisse," in *Biometrische Vorträge*, Deutsche Region der Internationalen Biometrischen Gesellschaft, 15. Biometrischen Kolloquium (Hannover, 1968); Franz Weiling, "Das Wiener Universitätsstudium 1851–1853 des Entdeckers der Vererbungsregeln Johann Gregor Mendel," *Folia Mendeliana Musei Moraviae Brno* 21 (1986): 9–40.

development. (Unger used the same word—"*Entwicklung*"—for all kinds of progressive, organic change, whether in paleontology or embryology.)[12]

Classifying and counting plants, calculating ratios, and searching for numerical relationships and laws were not peculiar to Unger, but were common practices in mid-nineteenth-century botany and zoology, particularly in the study of the geographic distribution of species.[13] As we shall see, Mendel classified and counted plants in a similar way, drew conclusions from the resulting ratios, and used the language of *Entwicklung* to describe the changes in the ratios over successive generations. It was a novel application of the method, but it is hardly surprising to find a student of Unger's using it, and it can hardly have been incomprehensible to the botanists of the day. This use of counts and ratios in deriving laws of change marks Mendel as a member of yet another nineteenth-century intellectual community.

## Scientific Research in Brünn

Mendel never did pass his exams and earn proper teaching credentials, but that was apparently because of one of his breakdowns during his last try in 1856, which caused him to give up before finishing the written portion. But back home in Brünn, there were no doubts about either his teaching ability or his knowledge of math and science. During the post-1848 reform period, the *Gymnasium* employed quite a few unlicensed adjuncts, and they had no trouble keeping Mendel on until he was elected abbot in 1868.

12. Sander Gliboff, "Evolution, Revolution, and Reform in Vienna: Franz Unger's Ideas on Descent and their Post-1848 Reception," *Journal of the History of Biology* 31, no. 2 (1998): 179–209; Sander Gliboff, "Gregor Mendel and the Laws of Evolution," *History of Science* 37 (1999): 217–235; Sander Gliboff, "Franz Unger and Developing Concepts of *Entwicklung*," in *Einheit in der Vielfalt: Franz Ungers (1800–1870) Naturforschung im internationalen Kontext*, ed. Marianne Klemun (Göttingen: Vienna University Press of V & R Unipress, 2015).

13. Janet Browne, *The Secular Ark: Studies in the History of Biogeography* (New Haven and London: Yale University Press, 1983); Susan Faye Cannon, "Humboldtian Science," in *Science in Culture: The Early Victorian Period* (New York: Science History Publications, 1978); Sander Gliboff, "H. G. Bronn and the History of Nature," *Journal of the History of Biology* 40 (2007): 259–294; Malcolm Nicolson, "Alexander von Humboldt, Humboldtian Science and the Origins of the Study of Vegetation," *History of Science* 25 (1987): 167–194.

In the years after his return to Brünn in 1853, Mendel appears to have engaged in many and varied scientific activities in his spare time. He was a co-founder and active member of the Brünn scientific society. He ran a weather station at the monastery and wrote about weather forecasting and the possibilities for communicating weather reports by semaphore and telegraph. He studied sunspots. He analyzed epidemiological data for correlations with changes in the water table. He tried his hand at beekeeping and became one of the very first to breed bees systematically. He was a chess player and inventor of chess problems. And, of course, he continued his gardening and plant breeding, with special interests in ornamental plants (he bred prizewinning fuchsias), fruit trees, and the peas and beans with which he did his famous experimental crosses. He began his published experiments with the peas in 1856, right after his last attempt at the licensing exams in Vienna.

## Mendel's Nineteenth-Century Sources (3): The Hybridizing Tradition

In the published article on those "Experiments in Plant Hybridization" Mendel himself suggests some additional nineteenth-century (or earlier) sources and inspirations for his research. Most prominently, he cites the scholarly literature on plant hybridization, particularly the work of Joseph Gottlieb Koelreuter (1733–1806) and Carl Friedrich Gaertner (1772—1850). Several authors, most notably Robert Olby, have looked into these pre-Mendelian hybridizers, and have seen Mendel as using their methods and following up some of their open questions, especially concerning the nature and stability of plant species and of hybrids, the possibility of species transformation, whether—and how—plants reproduce sexually, and the relative importance of the pollen and the germ- or egg cell in determining the appearance of the offspring.[14]

Although Mendel does not discuss him explicitly, the great taxonomist Linnaeus (1707–1778) also had taken an interest in plant hybridization as a mechanism by which new species could be produced from old, for example, if hybrids were stable and remained distinct from the parent stocks. So it would

14. Olby, *Origins of Mendelism*, ch. 1; Herbert F. Roberts, *Plant Hybridization before Mendel* (Princeton: Princeton University Press, 1929); Conway Zirkle, *The Beginnings of Plant Hybridization* (Philadelphia: University of Pennsylvania Press, 1935); for a sharp contrast between Mendel the hybridizer and the twentieth-century view of Mendel the geneticist, see also Augustine Brannigan, "The Reification of Mendel," *Social Studies of Science* 9 (1979): 423–454.

seem that Mendel, at least indirectly, was addressing questions about evolution and classification that had been quite central in European science since the eighteenth century.[15]

### The Hybridization Paper

Mendel's published account of his experiments systematically addresses each of his communities and audiences: "Artificial pollinations, done with ornamental plants with the aim of producing new color variations, occasioned the experiments to be discussed here."[16] So begins the famous paper, with a reference to practical breeding—maybe his own experience cross-pollinating fuchsias—as a resource and motivation for the research.

Immediately after this overture to the breeders, Mendel engages the Unger-style biogeographers, developmentalists, and evolutionists, with their interests in formulating laws of organic change (*Entwicklung*):

> The conspicuous regularity with which the same hybrid forms always reappeared, as long as the pollination occurred between the same strains, provided the motivation for further experiments, whose task it was to follow the development [*Entwicklung*] of the hybrids in their descendants.[17]

As has also been noted by Floyd Monaghan and Alain Corcos, Mendel writes repeatedly about developmental laws and the changing composition of the entire experimental population as he lets the hybrids and their offspring self-pollinate for six generations. This is not quite the approach of a modern geneticist, who

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15. L. A. Callender, "Gregor Mendel: An Opponent of Descent with Modification," *History of Science* 26 (1988): 41–75; Staffan Müller-Wille and Vítězslav Orel, "From Linnean Species to Mendelian Factors: Elements of Hybridism, 1751–1870," *Annals of Science* 64 (2007): 171–215; Pablo Lorenzano, "What Would Have Happened if Darwin Had Known Mendel (or Mendel's Work)?" *History and Philosophy of the Life Sciences* 33 (2011): 3–48. On Mendel's place in a broader European intellectual context: Margaret Campbell, "Mendel's Theory: Its Context and Plausibility," *Centaurus* 26 (1982): 38–69.

16. Gregor Mendel, *Versuche über Pflanzenhybriden* (Weinheim: H. R. Engelmann, 1960), facsimile of the original paper from *Verhandlungen des naturforschenden Vereines in Brünn* 4 (1866): 3–47, on 3 (= section 1 of the MendelWeb version). Translations are my own.

17. Ibid., 3 (= section 1 on MendelWeb).

would focus instead on the mechanisms of transmission from one pair of parents to its offspring.[18]

But Mendel is still not finished introducing his paper and drawing his communities and audiences together. The second paragraph is devoted to the academic plant hybridizers, such as Gaertner and Koelreuter. Those authors are on the right track, Mendel finds, yet have not quite been able to satisfy the demand for "a generally valid law for the formation and development [*Entwicklung*] of the hybrids,"[19] that is, the kind of law that Unger would want him to look for.

Mendel weaves these approaches together. With his breeder's gaze, he analyzes the pea plant into individual characteristics of interest, and chooses pairs of parental plants that contrast in each, for example, having green or yellow as the pea color, round or wrinkled as the pea shape, or dwarf or tall as the plant height.[20] But unlike the breeder, his goal is not so much to improve these features or create new combinations of them, but rather to ask general questions about their interactions and changing ratios. Like the academic plant hybridizers, he wants to know about the nature of hybrids, the extent to which each of a pair of contrasting parental characteristics gets expressed, and what rules determine whether hybrid characteristics persist over multiple generations. Will, for example, yellow and green blend to an intermediate color? Interact somehow to produce something wildly different? No, he observes that one trait wins out consistently over the other, and defines "dominance" and "recessiveness" of traits accordingly.[21]

Next, Mendel pursues the developmental/evolutionary question by letting the hybrids and their offspring propagate by self-pollination, and by classifying and counting the progeny. He observes the recessive trait reappearing in predictable ratios for six generations before he stops the experiments. He can then provide a formula that predicts the composition of the experimental population after any number of generations of self-pollination following a cross. This fulfills Franz Unger's ideal of a developmental law.[22]

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18. Floyd Monaghan and Alain Corcos, "Mendel, the Empiricist," *Journal of Heredity* 76, no. 1 (1985): 49–54.

19. Mendel, *Versuche über Pflanzenhybriden*, 3 (= section 1 on MendelWeb).

20. Ibid., 5–7 (= section 2 on MendelWeb).

21. Ibid., 10–12 (= section 4 on MendelWeb).

22. Ibid., 12–18 (= sections 5–7 on MendelWeb).

Finally, and very tentatively, Mendel also provides something destined to catch the eye of the twentieth-century geneticist. He hypothesizes that there are physical differences in the pollen- and germ cells that correspond to the differing parental characteristics,[23] and begins to speak of material "elements"[24] that segregate into the reproductive cells and come together in new pairings after fertilization. He is exceedingly cautious and vague about what these elements might be, physically, but it would be enough to inspire later conceptions of the "gene" as a hereditary unit, locatable on a chromosome.[25]

Also of great importance to the early geneticists were the ideas that these elements occurred in pairs, one from each parent, and that the entire plant could be analyzed into individual characteristics, each governed by such a pair of elements. The geneticists also adopted and expanded upon the rules of dominance and recessiveness and looked for other kinds of interactions between genes. They took over the rules of "segregation" and "independent assortment," which governed the way in which the individual elements (later "genes") were divvied up into the pollen- (or sperm-) and egg-cells, to be paired up in new ways after fertilization. And they soon made the connection between these rules and the movements of chromosomes during cell division, and modified Mendel's rules by allowing for linkage of multiple genes on the same chromosome. More generally, they prized Mendel's paper for its use of experimentation, its quantitative approach, its search for mechanisms, and its emphasis on making and testing precise predictions.

## Conclusions

Mendel did indeed have much to say to the early geneticists, and he gave them good reason to claim him posthumously as a founder and a long-lost insider, but he was hardly such a tragic and isolated figure as some have imagined. He was a successful breeder, teacher, monk, and abbot, and a member of multiple communities and intellectual traditions.

To be sure, the image of the isolated genius was never universally accepted among geneticists. Thomas Hunt Morgan, for example, one of the founders of

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23. Mendel, *Versuche über Pflanzenhybriden*, 24–32 (= section 9 on MendelWeb).

24. Ibid., 41–42 (= section 11 on MendelWeb).

25. Olby rightly has cautioned against reading the modern gene concept back into Mendel's paper: Robert C. Olby, "Mendel No Mendelian?" *History of Science* 17 (1979): 53–72.

classical *Drosophila* genetics, was pretty sure that "The genial abbot's work was not entirely heaven-born, but had a background of one hundred years of substantial progress that made it possible for his genius to develop to its full measure."[26]

Writing at the time of the Mendel centennial of 1965, geneticist L.C. Dunn, too, complained of "the aura of isolation which has clung" to Mendel and how "Even some biologists of today tend to think of him as though he had been a visitor from outer space whose brief transit through European Science was unobserved at the time."[27] But they both had only limited means of correcting the picture and putting Mendel into context. Morgan referred to the literature on plant hybridization for pre-Mendelian hints about dominance and segregation. Dunn was able to add a bit more, by pointing to some of Mendel's more worldly activities and connections to local scientific societies, but even he had to admit that "[Mendel] does seem rather an outsider in European botany."[28]

It has taken much longer for historians to piece together the more complete picture that is symbolized nicely by Figure 2, the group portrait that was the source of Figure 1. It shows Mendel not only in his most important community, but also choosing to hold a fuchsia as his attribute, thus connecting himself to the plant breeders as well as the monastery.

As a plant breeder, he was an heir to a local tradition of practical breeding that had already developed methods of delimiting and analyzing individual traits and had begun to investigate theoretical questions about heredity as early as the 1820s. He could hardly have done his research at all, were it not for his membership in the Abbey of St. Thomas in Brünn and the transformations of monastic life brought about by enlightened absolutism and the Josephine reforms. Mendel's order fulfilled its obligations to the state in part by promoting science, especially scientific agriculture, and by sending out experts like Mendel to teach in the schools. Further, the monastery enabled him to go to Vienna, for exposure to new ideas and methods from several fields of scholarship, such

26. Thomas Hunt Morgan, "The Rise of Genetics," *Science* 76, nos. 1969–1970 (1932): 261–267 & 285–288, on 263.

27. L. C. Dunn, "Mendel, His Work, and His Place in History," in "Commemoration of the Publication of Gregor Mendel's Pioneer Experiments in Genetics," *Proceedings of the American Philosophical Society* 109, no. 4 (1965): 189–198, on 191.

28. Ibid.

Figure 2: Mendel in context (standing, second from right), among his brethren in Brünn. They are all trying to strike distinctive poses, and Mendel has chosen to hold a fuchsia and associate himself with his breeding work on ornamental plants.

as experimental physics and especially quantitative botany and biogeography. And either his studies or his own reading led him to cutting-edge questions about the nature of hybridization and its role in evolution.

In Mendel's Moravia, the lines between pure and applied science, religious and scientific institutions, and professional scientists and amateur naturalists were not drawn as sharply as in the twentieth century. Neither were the fields of heredity, development, and evolution as strongly demarcated. Mendel could participate in various fields, communities, and institutions. Perhaps he was a modern geneticist, too, in some sense, but that would not make him an outsider everywhere else. On the contrary, it would underscore his multi-sidedness.

With the many sides of Mendel in mind, we can see how his celebrated paper on hybridization addressed the interests of contemporary breeders, plant hybridizers, Mendel's teachers in Vienna, brothers at the monastery, and colleagues at the Brünn Society, while also engaging with themes of the international scholarly literature. Contemporaries would easily have seen where Mendel was getting his ideas and methods from, and where he wanted to go with his laws and hypothetical elements, but did not yet have much reason to see the implications as truly groundbreaking. The breeders, especially, would have known of too many cases that did not follow Mendel's laws, as would Mendel himself. In fact, his paper freely discusses counterexamples such as hybrids that breed true instead of segregating out into dominants and recessives in the proper ratios.[29]

Instead of an "outsider" or a "boundary crosser," Mendel is better described as a synthesizer of multiple approaches, one whose synthesis has been mistaken for an abrupt origin *de novo*. Early twentieth-century geneticists, eager to distinguish their new field from older lines of research, overemphasized the novelty and exaggerated the divisions between the first geneticist and his contemporaries. As genetics became a discipline and defined its boundaries, it drew Mendel in, while banishing the breeders, monks, Linnaeans, and old-fashioned hybridizers to the outside and obscuring their presence in the historical picture.

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29. Mendel followed up the pea work with one more project on plant hybridization, and that one focuses on just such a counterexample, the hawkweeds: Gregor Mendel, "Ueber einige aus künstlicher Befruchtung gewonnenen Hieraciumbastarde" (1869), in *Versuche über Pflanzenhybriden: Zwei Abhandlungen (1865 und 1869)*, ed. Erich Tschermak (Leipzig: Wilhelm Engelmann, 1901). It is also clear from his surviving letters to the botanist Carl von Naegeli—his only known scientific correspondent—that there were questions about the generalizability of his laws: see Carl Correns, "Gregor Mendels Briefe an Carl Nägeli, 1866–1873: Ein Nachtrag zu den veröffentlichten Bastardierungsversuchen Mendels," in *Gesammelte Abhandlungen zur Vererbungswissenschaft aus periodischen Schriften, 1899–1924* (Berlin: Julius Springer, 1924).

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