FEATURE ARTICLE

Still Learning from Gregor Mendel after 200 Years

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Abstract

Although unrecognized for his scientific achievements during his life, Gregor Mendel pioneered our modern understanding of the gene, work that shaped the field of genetics and advances in biology and medicine. The field that he set in motion 200 years ago lies at the center of current ethical debates about the future of humanity, the limits of science, and how best to employ our knowledge for betterment of the human condition. Mendel's personal life also offers lessons, especially for those of us engaged in teaching future generations.

Key Words: *Mendel; history of medicine; history of science; genetics; Darwin; philosophy of science.*

○ Heredity

I am the family face;
Flesh perishes, I live on,
Projecting trait and trace
Through time to times anon,
And leaping from place to place
Over oblivion.

The years-heired feature that can
In curve and voice and eye
Despise the human span
Of durance—that is I;
The eternal thing in man,
That heeds no call to die.

—Thomas Hardy, 1917

○ Introduction

In this strikingly prescient poem, the famous English author Thomas Hardy elegantly articulated the central elements of a profound mystery—what is the mechanism of heredity? What explains why a daughter looks like her mother or a son's gesture so uncannily echoes that of his long-dead father? How does such information "leap" from one generation to another, heeding no "call to die"? Shortly before Hardy penned these lines, the scientific work of Gregor Mendel, a previously obscure Augustinian priest, was rediscovered, propelling him to posthumous fame and providing an answer to this age-old mystery.

This July 20, we celebrate Mendel's 200th birthday (Mendel Museum, 2021). Although unrecognized for his scientific achievements during his life, Mendel pioneered the modern conception of the gene, anticipating the field of genetics and the astounding advances in biology and medicine that we are now witnessing. Recognizing these advances and Mendel's unsung genius would be reason enough to celebrate his birth. But we can still learn from Gregor Mendel. For genetics now lies at the center of thorny ethical debates about the future of humanity, the limits of science, and how (or whether) to employ our knowledge for betterment of the human condition. And on a more personal note, Mendel's life—his struggles, anxieties, and hopes (both requited and unrequited)—offer us lessons that may be less grand but are perhaps more intimately applicable to our own lives, especially for those of us engaged in teaching future generations.

> *"Mendel's results pointed to a radically different notion—that the units of inheritance persisted unchanged in a 'particulate' manner and could reappear, unchanged, in subsequent generations."*

○ A Brief Biographical Sketch

Johann Mendel (who only later took the name of Gregor upon entering the priesthood) was born to a modest farming family in the small agricultural village of Heinzendorf (now Hynčice in the Czech Republic). His father, Anton, like many farmers, was interested in the creation of hybrids to improve the qualities of fruit trees, presaging Gregor's

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own lifelong fascination with hybridization. Mendel's mother, Rosine, was a devoted mother who, like his sisters, doted on the young man. A few central themes emerge from Mendel's early life—a keen intellect, a disinclination toward farming, and periods of incapacity that saw him bedridden for months at a time (Henig, 2001). For those who wish for more detail about Mendel's life, see the biographies by Robin Marantz Henig, *The Monk in the Garden* (2001), and Simon Mawer, *Gregor Mendel: Planting the Seeds of Genetics* (2005).

Mendel's intellect was recognized and fostered by his parents, who, although of limited means, managed to send him to a "gymnasium," or secondary school, in the nearby city of Troppau (now Opava, in the Czech Republic). Before graduating at the age of 17, he abruptly returned home, taking to his bed for months. From our vantage point, it seems almost certain that Mendel was suffering from what would be the first of several episodes of severe clinical depression. Ironically, given his scientific legacy, it is possible that Mendel inherited from his melancholic father a predisposition to depression, a condition now known to have a strong genetic component (Mullins & Lewis, 2017). Possible genetic predisposition aside, the 17-year-old was also under considerable stress as, due to his family's meager resources, it was necessary for him to support himself while maintaining academic standing. Moreover, as the eldest son Gregor was expected to take over the family farm, a prospect that held no appeal for him. Ultimately, he spent four months in bed, cared for by his mother and 10-year-old sister, Theresia, who encouraged him during what must have been a difficult time for the entire family. Consistent with current knowledge about clinical depression, which often lifts after several months, Mendel reentered the gymnasium and graduated in 1840.

In the fall of 1840 Mendel enrolled in the Philosophical Institute of the University of Olomouc, meant as a stepping-stone to students aspiring to a university education. Young Gregor supported himself by tutoring, but as a German speaker, he struggled to attract students in this Czech-speaking city. In 1841, hungry and feeling defeated, he fled home and again was bedridden for a year. It was difficult for him to see a way forward—dreams of an academic life seemed unreachable, he still faced expectations that he would take over the family farm, and he was likely crippled with feelings of inadequacy and anxiety. However, once again his family rallied round. His older sister and her husband agreed to take over the farm, relieving Mendel of this daunting obligation, and his 12-year-old sister, Theresia, loaned Gregor her dowry to finance his studies. It is difficult for us today to appreciate the magnitude of Theresia's generosity since her life's prospects were directly tied to her ability to marry well. Putting her future at risk to help her 19-year-old brother, incapacitated by what must have seemed a perplexing malady, was an act of immense love and selflessness (Historical Figures, 2018). Mendel never forgot her generosity; he and Theresia maintained a loving relationship throughout his life, and later he helped to support her children, two of whom became physicians.

Bolstered by his family's support, Mendel returned to Olomouc to complete his studies in philosophy and physics. However, his road remained challenging, and by 1843 it became clear that even with Theresia's dowry he simply could not afford university. Would his and his family's struggles be in vain? At this critical juncture his physics professor, Friedrich Franz, made a life-changing suggestion to Mendel (Hasan, 2004). Franz, a priest, pointed out that the Augustinian Order of the Catholic Church placed great value on intellectual pursuits and that the priesthood could offer Mendel a viable path to a life of learning, research, and teaching. Thus, at the age of 21 Mendel traveled to Brno (now in the Czech Republic) and entered the Abbey of St. Thomas to begin training as a priest.

Although Mendel found a degree of stability in the monastery and a mentor in Abbot Cyril Napp, his path remained difficult. After five years of study Mendel was ordained a priest in 1847—only to realize that he was wracked with anxiety when called upon to perform his official duties, especially giving last rights or comforting the sick. Once again it seems that Mendel was plunged into debilitating depression, this time being rescued by Abbot Napp, who realized that while Mendel was decidedly not "priest material," he was an excellent teacher. Napp petitioned the bishop to allow Mendel to become a teacher of Greek, math, and physics to local high school students, fulfilling an obligation of the Augustinian Order and providing a viable way forward for Mendel.

Mendel proved to be a popular teacher, and his success compelled him to seek full teaching certification in 1850 (Richter, 2015). However, Mendel suffered from devastating test anxiety; he performed poorly in the written certification exam and disastrously in the oral component. The examiners failed him but, recognizing his passion and earnestness, suggested he obtain further schooling at the University of Vienna. After Abbot Napp successfully pleaded with the bishop for dispensation, Mendel began classes at the age of 29, fulfilling his long-standing dream of attending university.

Mendel's two years at university were tremendously formative. He studied under Christian Doppler (of the Doppler effect); Andreas Von Ettingshausen, who provided Mendel with a rigorous mathematical education; and Franz Unger, a botanist who introduced Mendel to his own experiments in which he had used the garden pea (!) as a model to study the transmission of hereditary traits. Thus, equipped with rigorous training in subjects that in retrospect can only be seen as stunningly fortuitous, the 31-year-old monk headed back to St. Thomas where he began breeding mice to investigate coat-color transmission. However, Mendel's bishop was aghast that one of his priests would engage in research involving sex and forbade this line of research. So, in 1854 Mendel switched his research to the garden pea, demonstrating his sly sense of humor along the way by remarking, "You see, the bishop did not understand that plants also have sex" (Henig, 2001).

○ Mendel's Research

Although the transmission of traits from parents to offspring was well know, the mechanisms involved were utterly mysterious in the 19th century. This profound mystery, coupled with its obvious practical importance in agriculture, made it an appealing focus of study for an ambitious young scientist. While others had studied trait transmission in plants, Mendel employed several previously neglected strategies. Critically, he spent two years ensuring that his parental stocks "bred true" for the traits he would investigate (in today's parlance, ensuring that they were homozygous for the traits of interest) (Edelson, 1999). Another innovation was his focus on seven specific traits of *Pisum sativum* (including flower color and seed shape) that turned out to assort independently during meiosis (being, as we now understand, distant from one another in the *P. sativum* genome). Although it is often assumed that Mendel was "lucky" in the traits he chose to study, it is more likely that his choices were practical and insightful. During the years he was establishing breeding stocks, he likely noted which traits gave the most consistent results and thus focused on those. The classical view of the scientific method often posits a simplistic notion

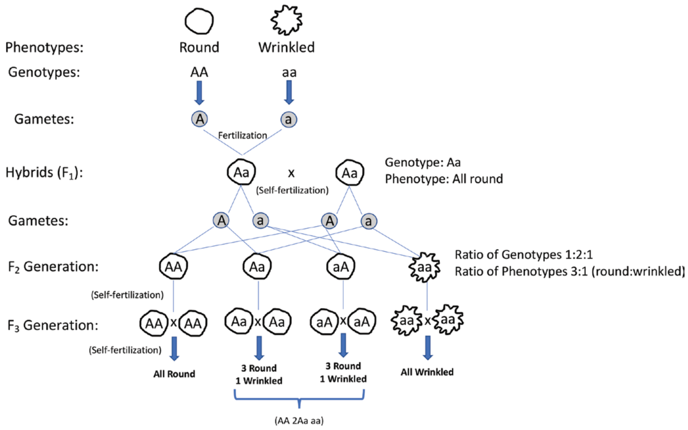

Figure 1. An example of Mendel's first experiment in the transmission of seed shape, in *Pisum sativum*. After painstaking work to ensure that his parental stocks "bred true," he crossed plants that each produced only round or only wrinkled (a trait also known as angular) seeds to yield the "F_1" generation. All peas in the F_1 generation were round—the wrinkled trait had "disappeared." However, in the 7324 peas of the next "F_2" generation, while the majority (5474) were round, 1850 of the F_2 peas were wrinkled—the trait that had been in the grandparental generation suddenly reappeared, with a ratio of three round to one wrinkled pea. The underlying "element" encoding the wrinkled trait had not vanished at all but had only been somehow "hidden" while in the F_1 generation. It should be noted that accusations by statistician Ronald Fisher in 1936 that Mendel was guilty of falsifying his data have not been upheld by subsequent investigation: reproduction of Mendel's experiments and reanalysis of Fisher's accusations conclusively demonstrate no bias (Monaghan & Corcos, 1985; Novitski, 2004; Hartl & Fairbanks, 2007).

that observation leads to hypotheses in that rigid order. However, scientists typically pursue observations and hypotheses in a synergistic manner, formulating hypotheses while simultaneously searching for observations that support (or disprove) them. Thus, Mendel was likely formulating the hypothesis of independent segregation while feeling his way forward in his research, thereby influencing the traits he would ultimately choose to study.

Mendel spent nine years crossing and examining some 300,000 peas, observing multiple traits and analyzing what it all meant (Henig, 2001). At that time the leading view of heredity was the notion of "blending inheritance"—that progeny are a mixture of parental traits. However, Mendel's results pointed to a radically different notion—that the units of inheritance persisted unchanged in a "particulate" manner and could reappear, unchanged, in subsequent generations.

Mendel's patience and keen mathematical mind led him to formulate his now-famous laws of inheritance. Today we would summarize them as follows:

1. Each inherited trait is governed by an underlying element (gene), which can exist in alternate forms (alleles) that lead to different visible traits (phenotypes).
2. Genes for different traits are inherited independently of one another.
3. Each individual plant or animal possesses two sets of genes, one set inherited from each parent.
4. Genes remain unaltered from generation to generation.
5. Alleles of genes can be dominant or recessive; a recessive trait will be displayed only if an individual inherits two recessive alleles.

Mendel could only anticipate our modern understanding of the gene, simply recognizing that his "elements" were somehow responsible for the traits that were ultimately manifested. Although major modifications of Mendel's laws would occur with the description of, for example, mutations and genetic linkage, Mendel's insights continue to undergird our understanding of heredity. It is for good reason that even today, from middle school to medical school, we teach Mendelian genetics to describe the transmission of traits and diseases that are dictated by single genes.

Mendel's subsequent studies of other species (including beans, snapdragons, and maize) generally confirmed his conclusions, leading him to remark that "the law of development discovered for ***Pisum*** applies also to the hybrids of other plants" (Henig, 2001). But while Mendel recognized the general applicability of his conclusions, the rest of the world failed to. He presented his work to the Natural History Society of Brno in 1865 and sent 40 reprints of his paper to preeminent scientists of the day (Mendel, 1866). Sadly, the only scientist who didn't ignore his results at the time, Carl Nägeli, failed to understand them.

While Mendel evinced interest in the natural world to the end of his days, by 1868 his biological research ended. In that year his beloved Abbot Napp died and Mendel was elected as the next abbot of St. Thomas, effectively ending his research career due to new responsibilities. Mendel famously enjoyed the splendid food of St. Thomas, and his obvious weight gain over the years, coupled with his failing eyesight and deteriorating kidney

Parallel Currents of Thought in 19th Century Science

Mendel may have been influenced considerably by the work of contemporaries in physics and chemistry who were then establishing the first atomic theories, research the monk would have been well aware of due to his university studies. The finding of whole-number ratios in both atomic weights and the combinatorial chemical properties of elements were critical clues to the structure of matter (Scientific Odyssey, 2015). In a parallel manner, Mendel recognized that his finding of a whole-number ratio of round to wrinkled peas in the F_2 generation strongly hinted at fundamental "rules" underlying the mechanism of inheritance. Further hinting at the influence of those investigating the structure of matter on Mendel was his choice of the German word for "element" to describe his genetic factors. Just as chemists were discovering that the elements of the periodic table remained unaltered throughout chemical reactions, appearing in different forms depending only on their combinations, Mendel's "elements" were likewise not destroyed or altered when passing from generation to generation, simply revealing different properties when combined in various ways. Alas, we will likely never know details of Mendel's reasoning since his personal papers were burned by the abbot who succeeded him upon his death (Carlson, 2004).

function, indicates that it was likely that he suffered from uncontrolled Type II diabetes. He died of renal failure on January 6, 1884, at the age of 61.

○ Lessons from Mendel

Delayed Recognition

As is common knowledge (and perhaps part of Mendel's allure—after all, who hasn't felt unappreciated?), Mendel received no contemporary recognition for the formulation of laws that would explain an age-old mystery of life and undergird a new science. Indeed, it would be almost 40 years after his original publication that his work was rediscovered.

What explains the decades in which Mendel's work was neglected? One likely explanation is that Mendel's work represented a "premature" scientific discovery (Stent, 1972), a discovery that cannot be contextualized in terms of contemporary understanding and is simply ahead of its time. Other examples of such "premature" discoveries include Copernicus's heliocentric model of the universe and Oswald Avery's identification of DNA as the genetic material. Premature discoveries are typically neglected (at best) or ridiculed (at worst) by contemporaries, until further developments make them comprehensible and they finally enter the scientific mainstream. As Mendel was arguably the first biologist to pursue rigorous mathematical analysis of data, his contemporaries were woefully ill-equipped to appreciate his statistical arguments and thus ignored them. Also contributing to the obscurity of his work, Mendel was a monk living outside the scientific establishment, without ample time to devote to his research and its promotion due to teaching and administrative responsibilities. Finally, Mendel was not inclined to self-promotion, being a shy man immersed in a religious community that frowned upon vanity. Taking all this into consideration, it may be less a wonder that Mendel's work was ignored than that he ultimately received credit for it.

We can learn clear lessons from the historic neglect of Mendel's work. We must make conscious efforts to be open to new ideas, even when they don't comport with our preconceived notions. We need to be receptive to novel cross-disciplinary approaches (such as Mendel's application of mathematics to biology). And critically we must disregard humble origins of an idea and judge it on its merits. In our modern world of pre-prints, peer review, and the internet, one might think that the playing field is level—but science is not yet free of bias, hostility toward novel notions, class considerations, or a tendency to look askance at outsiders with new ideas.

Mendel & Darwin

The delay in appreciating Mendel's work leads to a compelling historical "what if" scenario: imagining a meeting of Charles Darwin and Gregor Mendel. These contemporaries had much in common—both were scientifically curious, both were seeking basic laws that would explain fundamental scientific mysteries and, unbeknownst to Darwin, the work of Mendel solved many problems that plagued Darwin's theory of evolution by natural selection.

Darwin's theory is the bedrock upon which all biology is founded. But during Darwin's life, ignorance regarding the mechanism of inheritance was a profound impediment to the theory's acceptance. The current prevailing notion of blending inheritance was incompatible with Darwin's theory since in this model new, advantageous traits would be quickly diluted and lost from a population. Darwin's theory required a particulate mechanism of inheritance, in which the factors that control traits persist through generations—precisely what Mendel demonstrated to be the case a mere six years after *The Origin of Species* was published.

Mendel's copy of *The Origin of Species* is heavily annotated with marginal notes that show he understood the strong support his work lent to Darwin's theory (Evans, 2021). And it was not for lack of trying by Mendel that his ideas were unappreciated by Darwin: Mendel sent Darwin a copy of his paper—where it appears to have remained unread in Darwin's library. We know this because at that time many books and manuscripts needed to be cut open at the top and sides to be read. Sadly, Darwin's copy of Mendel's paper was found uncut, indicating that it had never been opened. Had Darwin or one of his supporters been capable of appreciating Mendel's work, many contemporary objections to evolutionary theory would have been swept aside and the "modern synthesis" combining genetics and evolution may have occurred earlier (Lorenzano, 2011). Again, Mendel's work was "premature"—Darwin and his contemporaries were not inclined toward mathematical analysis and were simply ill-equipped to see that his work offered a central pillar of support to the theory of evolution.

Finally, from a personal standpoint, it seems a pity that Darwin and Mendel never met. Beyond their mutual scientific and professional interests, they were both humble, friendly, and curious men. I suspect they would have enjoyed one another's company greatly.

Heeding Science

The field of genetics has improved the human condition in countless ways, from agricultural to medical advances. However, the aftermath of Mendel's rediscovery also tells a cautionary tale. Trofim Lysenko, who directed the USSR's Institute of Genetics in the 1940s, decided that Mendel's laws were antithetical to Communist ideology, formulating his own (evidence-free) theory of "environmentally acquired inheritance." His ideologically motivated attacks on science, backed by the power of a totalitarian state, led to the persecution, imprisonment, and even death of dissenting scientists. More broadly, this embrace of state-sponsored pseudoscience led to the implementation of devastating agricultural practices responsible for famines that killed millions of Soviet citizens (Kean, 2017). Extension of these ignorant but ideologically "correct" notions to China in 1958 led, in part, to the Great Chinese Famine of 1959–62.

Mendel's chilly reception by those blinded by ideology is highly relevant today. The world's response to the COVID pandemic reminds us that science and evidence matter. When a society abandons reliance on fact and ideology eclipses evidence, we court disaster. One need look no further than today's efforts by some to deny overwhelming evidence of human-induced climate change because scientific reality threatens their political beliefs and business interests. We engage in willful ignorance at our own peril.

Genetics in Medicine—Promise and Peril

It is remarkable how quickly after the rediscovery of Mendel's work in 1900 that it was found to apply not just to garden peas but to humans when, in 1902, Archibald Garrod observed that transmission of the human disease alkaptonuria conformed to Mendelian laws (Prasad & Galbraith, 2005). In the ensuing century medical geneticists described over 7000 diseases that are caused by changes in a single gene and therefore demonstrate Mendelian transmission (OMIM). Going beyond single-gene disorders, we now recognize that almost every human disease has at least some genetic component, usually from the contribution of variants in numerous genes, each with a small effect.

In the 1940s Avery and coworkers demonstrated that the chemical at the heart of Mendel's "elements" was DNA (ironically another example of a premature scientific discovery) (Avery, 1944). In 1953 Watson and Crick elucidated DNA's double helical structure, relying significantly on the research of Rosalind Franklin (who, like Mendel, did not receive sufficient credit during her lifetime) (Watson & Crick, 1953).

A century after the rediscovery of Mendel's work, the international effort to sequence the human genome was declared complete (International Human Genome Sequencing Consortium, 2001), and today the tools of molecular genetics are routinely used to investigate every malady to which humans are subject.

Genetics has been particularly successful in the realm of public health. Every child on earth born in a developed country undergoes newborn screening, through which countless lives have been improved or saved; soon we will likely see similar, routine genetic analysis of adults to identify those at high risk of severe but preventable disease (Evans et al., 2013). Genome-scale sequencing of individual patients has become a powerful diagnostic tool, and we now stand poised on an era in which we will routinely manipulate Mendel's elements through gene therapy to treat a host of devastating diseases (Dunbar et al., 2018).

Mendel would have been deeply gratified to see the benefits to human health that were anticipated by work he carried out in his monastery garden with the humble garden pea. However, this gentle monk might also caution us that uncritical application of knowledge can be a double-edged sword as our burgeoning ability to manipulate the human genome presents difficult ethical dilemmas. Most might agree that the ability to genetically tweak an individual to eradicate a serious disease such as sickle cell anemia is desirable. But what about parents who wish to have a baby who is taller, smarter—or lighter skinned? From Nazi Germany to the US, we witnessed chilling abuses of human rights during the eugenics era, which began distressingly quickly after the rediscovery of Mendel's work (Bashford, 2010). How much more room for misapplication and outright evil is now afforded by our growing power over the human genome? This is not to argue that we should eschew research designed to better understand our world. But humans have a long history of (ab)using scientific knowledge, and Mendel might well caution us to tread carefully as our increasing knowledge gives us the power to change the genetics of individuals, future generations, and ultimately our species itself.

Mendel—Student and Teacher

Mendel played many roles throughout his life, including priest, abbot, brother, and scientific researcher. But of all his roles, few were as prominent as those of student and teacher. Just as Mendel's research remains relevant today, his life as a student and teacher holds invaluable lessons for us.

As a student, Mendel was influenced repeatedly by teachers and mentors who helped him overcome overwhelming obstacles. His professor Friedrich Franz stepped in during one such crisis, guiding Mendel toward the monastery and enabling an academic life otherwise unobtainable for this young man of limited means. Likewise, the supportive Abbot Napp recognized both Mendel's weaknesses and strengths, seeing that while Mendel was a poor priest, he was an excellent teacher, helping find a path that coincided with his talents rather than trying to force him into a preconceived role for which he was ill-suited.

When Mendel twice failed to obtain full teaching certification, the very same panel of examiners who unanimously failed him paved the way for study at the University of Vienna, transforming failure into an opportunity that would change Mendel's life—and the history of science. At university, Mendel's mentors profoundly influenced his subsequent research career by emphasizing combinatorial mathematics and the use of the garden pea as a model organism.

Mendel's crippling test anxiety, which on multiple occasions threatened to derail his future, serves as a lesson to those of us who are charged with assessing and mentoring students. While rigorous assessment is critical to education, blind adherence to testing formats that ignore individual variation seem destined to throw otherwise promising students on the academic scrap heap. Mendel's examiners recognized that he had earnest passion and they worked to foster his potential. They saw Mendel as an individual worthy of another chance, helping him find a way forward that coincided with his strengths rather than focusing on his limitations. It is highly unlikely that his teachers suspected that his work could change the course of science—it is impossible for anyone to see that clearly into the future. Rather, a teacher's role is not necessarily to identify genius but to foster each student in ways that harness and promote their strengths. By doing so we may indeed occasionally (sometimes unknowingly) foster genius—but regardless we will routinely improve individual lives and propel human knowledge forward.

Mendel's financial struggles are highly relevant today as we cope with a higher educational system that is increasingly out of reach to those with limited means. Mendel was brilliant and hard-working. But he was also lucky to have a generous family who sacrificed to provide for his education and a monastic path that enabled him to earn a university degree. How many other students throughout history who might have advanced human knowledge were thwarted because they couldn't afford schooling? We are attracted to the story of the genius who overcomes great odds. But even genius cannot blossom without help. We do ourselves and society a grave disservice if we do not facilitate accessible, quality education for all.

Finally, Mendel's lifelong struggles with depression and anxiety are both poignant and instructive. The unstinting support provided to the young man by family and compassionate teachers is remarkable, especially in an era when mental health struggles were often seen as moral failings rather than medical disorders. That Mendel was not stigmatized—but rather encouraged and loved—allowed him to rise above these profound obstacles and not only contribute great things to the world but also find a path in life that allowed for personal satisfaction and a measure of happiness. Interestingly, the same can be said of Charles Darwin, who struggled with anxiety throughout his life and yet, with the support of friends, mentors, and a loving family, would also go on to greatness. We now live in a world that recognizes mental health as a medical condition (with treatments undreamt of in the days of Mendel and Darwin), but all too often continue to stigmatize those suffering from these cruel diseases. It is vital that we recognize when our students are suffering and offer them assistance and kindness to allow them to rise above such challenges.

○ Conclusion

As we celebrate Gregor Mendel's birthday, we may see his life in somewhat tragic terms because his work was unrecognized by contemporaries. However, that would be doing him a disservice. His was a full life with loving family, friends, fulfilling work, and the joys derived from a life of learning. What more can one really ask from this world? Gustav von Niessl, a contemporary and friend of Mendel's who lived to see his posthumous fame, reported that during his years of anonymity Mendel was fond of telling his friends, "My time will come" (Henig, 2001). Whether this appealing anecdote is true or not, it is instructive to examine lines from a poem Mendel wrote as an adolescent:

May the might of destiny grant me
The supreme ecstasy of earthly joy,
The highest goal of earthly ecstasy,
That of seeing, when I arise from the tomb,
My art thriving peacefully
Among those who are to come after me.

This poem is usually interpreted to illustrate Mendel's longing for (what was ultimately to be unrequited) fame. However, I am struck that at the root of his adolescent fantasy there was a more mature aspiration—not a shallow version of worldly fame but ultimately a hope that he might contribute something of value to this world. Indeed, his poem seems to eerily presage just the sort of posthumous recognition that would be his.

Surely if Mendel were able to glimpse our world and how his work has blossomed, he would be joyous indeed.

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