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Mendel in the Modern Classroom

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Abstract Mendel is an icon in the history of genetics and part of our common culture and modern biology instruction. The aim of this paper is to summarize the place of Mendel in the modern biology classroom. In the present article we will identify key issues that make Mendel relevant in the classroom today. First, we recount some of the historical controversies that have relevance to modern curricular design, such as Fisher's (Ann Sci 1:115–137, 1936/2008) claim that Mendel's data were too good to be true. We also address questions about Mendel's status as the father of genetics as well as questions about the sequencing of Mendel's work in genetics instruction in relation to modern molecular genetics and evolution. Next, we present a systematic set of examples of research based approaches to the use of Mendel in the modern classroom along with criticisms of these designs and questions about the historical accuracy of the story of Mendel as presented in the typical classroom. Finally, we identify gaps in our understanding in need of further study and present a selected set of resources that, along with the references cited, should be valuable to science educators interested in further study of the story of Mendel.

Abbatical Coat of Arms of Gregor Mendel.
http://www1.villanova.edu/villanova/vpaa/mendelmedal/aboutmendel/experiments.html

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1 Mendel and Mendelism: Myth and Reality in the History of Genetics

Mendel is an icon in the history of genetics and part of our common culture and history together with Galileo, Newton, Lavoisier, Darwin, and others. According to Moore, "Gregor Mendel (1822–1884) ranks second only to Charles Darwin on most biologists' scale of hero worship" (2001, p. 13). Nevertheless, the veracity of a number of aspects of the Mendel story has been questioned. Perhaps the best known of these is the Mendel-Fisher controversy. In 1936 the British statistician and biologist R.A. Fisher analyzed Mendel's data and concluded that they were "too good to be true" (Fisher 1936/2008). Fisher concluded that Mendel "knew very surely what to expect, and designed them [the reported experiments] as a demonstration for others rather than for his own enlightenment" (Fisher 1936/2008, p. 135). Essentially, Fisher was questioning whether Mendel's descriptions of his experiments were fictitious because it was statistically impossible to obtain the results that Mendel reported.

As with Mendel's work, Fisher's allegations slipped into oblivion and were overlooked until 1964, the centennial of Mendel's original paper (Franklin 2008; Orel 1996). At that time Zirkle again asked if "Father Mendel had fudged his results a little" (1964, p. 66). Thereafter at least 50 papers, letters, and discussions have been published about the Mendel-Fisher controversy (Franklin 2008), and a few of these articles have addressed the educational issues involved.

Daniel Fairbanks (2008) summarized the main questions about Mendel's work from Fisher's original claims and others that have been proposed as follows:

1. Are Mendel's data too good to be true?
2. Is Mendel's description of his experiments fictitious?
3. Did Mendel detect but not mention linkage?
4. Did Mendel support or oppose Darwin?
5. Did Mendel articulate the laws of inheritance attributed to him?

The first two issues are related to the original Mendel-Fisher controversy and are still being debated. Hartl and Fairbanks concluded: "Fisher's allegation of deliberate falsification can finally be put to rest, because on closer analysis it has been proven to be unsupported by convincing evidence" (2007, p. 979). In contrast, Franklin concluded: "The issue of the 'too good to be true' aspect of Mendel's data found by Fisher still stands, however. No one has yet raised any valid criticism of Fisher's analysis" (2008, p. 68). Hence the controversy remains unresolved.

We have found no report of use of the Mendel-Fisher controversy in the introductory genetics classroom, but, time permitting, instructors may find it useful. First, some students will find the history interesting. Second, the controversy also seems to be an interesting way to address the issues of linkage and synteny (see below).[1] Perhaps most valuable, the work of Fisher is a good teaching example of the importance of publication of detailed research methods employed and the value of re-examination of the study, its methods, and its findings by other scientists. The Fisher work could be considered without dissecting the statistics involved, further enhancing its utility for this purpose. Discussing the Fisher controversy would not, of course, require the teacher to actually take a position on the veracity of Mendel's claims, but the fact that the controversy remains unresolved for many scientists provides a teaching example for another nature-of-science issue, namely that

[1] Two genes are "syntenous" when they are located on the same chromosome. They are "linked" if they are located close enough to tend to be inherited together (i.e., they separate <50 % of the time during meiosis).

such controversies do exist, i.e., that science is not merely a set of "facts" to be memorized.

A more recent but related controversy stemming from the 1960s is whether Mendel detected linkage or not. In simple terms, Dunn (1965) and others after him have argued that it was unlikely that Mendel happened to study seven characteristics which just happened to be on the seven separate chromosomes (i.e., seven different linkage groups) of *Pisum*. If two of the characteristics he chose to study were determined by genes that were close together on a single chromosome (were "linked"), they would not have assorted independently during meiosis. Crosses in such cases would not have produced the expected 3:1 ratios. To Mendel, who knew nothing of linkage and the yet-to-be-proposed chromosomal theory of inheritance, such data would have confounded his findings. The implication is that Mendel ignored or purposely omitted reporting crosses between such traits to keep his model of independent assortment intact (Dunn 1965; Fairbanks 2008).

Today we know, in fact, that the seven factors Mendel studied are in six different linkage groups. The stem length (tall/short) and pod form (inflated/constricted) genes (known today as *V*/v and *LE*/le) are indeed linked, 12.6 cM apart in linkage group III (Reid and Ross 2011). Corcos and Monaghan (1985) explain that perhaps Mendel did not encounter aberrant ratios impacted by linkage (and thus inconsistent with independent assortment) because he did not count the number of individuals in the four F_2 classes of the necessary dihybrid and trihybrid crosses. Mendel noted that he reported conducting dihybrid and trihybrid crosses not documented in his papers but that "all gave *approximately* the same results" (italics added by Corcos and Monaghan). They take the word "approximately" to mean that Mendel did indeed not count the offspring in each of the F_2 classes. Reid and Ross (2011) later proposed that Mendel may not have counted these progeny because "he may have checked only to find that all four combinations of the characters occurred" (p. 7), presumably because he was focused on the production of hybrids more than on support of a new law of independent assortment (in keeping with Kampourakis 2013). At least among his reported di- and trihybrid crosses, Mendel did not cross stem length and pod form, the only pair of genes he reported studying that were in the same linkage group and <50 cM apart (Corcos and Monaghan 1985).

Both sets of authors add that luck "appears" to be or "was definitely" involved as well. We find these arguments intriguing and reasonable but less than convincing, especially given the meticulous care with which Mendel counted and recorded the offspring of his experiments.

The question of why the data Mendel published all conform to the now-standard ratios, of how he could have studied so many traits and not have encountered an instance of anomalous data that we today would know as evidence of linkage, is potentially interesting for students. How could we know whether Mendel selected for publication the data from some crosses and ignored others? What is the likelihood? Such questions provide a potentially stimulating context in which students could see the need for understanding linkage and synteny and the difference between the two. Delving more deeply into this issue would, of course, require knowledge of rudimentary statistical analysis such as the Chi square statistic. Few teachers and even fewer students likely have that knowledge or the interest in mathematics that would impel that further study, but some individuals will find the challenge to be exciting.

The last two of Fairbank's issues concern what Mendel left unsaid and events that happened long after his death in 1884. As to Mendel's relation to Darwin's theory of evolution, Bateson (1909) suggested that one of the incentives for Mendel's work was his disagreement with Darwin's ideas. Today we know that this scenario was not possible

given that Mendel first obtained a copy of *On the Origin of Species by Means of Natural Selection* in 1863, by which time his work had been completed (Galton 2009). There is little doubt, however, that Mendel had in fact read Darwin's book by the time he presented his paper in 1865 because historians have discovered Mendel's copy of Darwin's tome in which there are notes in Mendel's hand that relate to his own experiments (Fairbanks and Rytting 2001). Based on these notes, as well as the four written references to Darwin in Mendel's *Hieracium* paper from 1870, Fairbanks and Rytting conclude that: "we find no strong evidence that Mendel either strongly supported or opposed Darwin" (p. 298).

Another tenacious myth in Mendelian history is that Darwin had an uncut (and thus unopened) copy of Mendel's paper lying on his desk. This myth likely confuses Mendel's paper with a book Darwin owned, *Die Pflanzen-Mischlinge* by Focke (1881), which referred to Mendel, the pages of which were indeed uncut in Darwin's copy (Fairbanks 2008). The central idea of the myth is the missed opportunity—perhaps if Darwin had only read Mendel's paper he would have been able to connect the theory of evolution to the theory of heredity. This is an unlikely scenario as well because recent scholarship has shown that Darwin was indeed likely to have known about Mendel through secondary sources. Bizzo and El-Hani (2009) claim that Darwin's notes (in a book by Hoffmann) that refer to Mendel likely suggest not only that Darwin was aware of Mendel's work but furthermore that this knowledge did not make Darwin change his mind about his pangenesis[2] theory of inheritance. In addition, Darwin was known to have frequently been in contact with Hoffmann and Nägeli, two brilliant plant researchers who both knew Mendel's work well (Vorzimmer 1968; Olby and Gautrey 1968), although not even Hoffmann or Nägeli recognized any contradiction between Darwin's and Mendel's work.[3] Bizzo and El-Hani (2009) argue that these facts strongly suggest that Darwin was so "stuck" in his own pangenesis framework that he was not able to solve the problem of how heredity is involved in evolution, even if he had read Mendel's paper—a suggestion with which Olby concurs (2009).

The last of Fairbanks' issues concerns a more recent debate about whether or not Mendel explicitly articulated the laws of inheritance attributed to him (Olby 1979), or more broadly, should Mendel be credited as the father of genetics, as the author of what modern geneticists call Mendelism?[4] Callender (1988) and Monaghan and Corcos (1990) claim that Mendel did not express the laws of segregation and independent assortment and thus that the honor should be given to the turn-of-the-century geneticists who rediscovered his work, especially Correns. In science education this claim has been promoted by Allchin (2003) and more recently by Kampourakis (2013). Kampourakis argued that Mendel was not part of the community of researchers that tried to develop theories of heredity under an evolutionary perspective but rather worked in the research tradition of hybridists. According to Kampourakis, Mendel was seeking a theory of hybrid development, not a

[2] Pangenesis is the idea that small particles which Darwin called *gemmules* are formed by cells in the body and that they diffuse and aggregate in the reproductive organs to determine the observable features in the offspring (Bizzo 1999; Bizzo and El-Hani 2009).

[3] See also Schlater (2006) and Galton (2009).

[4] We consider Mendelism as the simplistic view of inheritance derived from Mendel's work as the understanding of his work evolved within the corpus of genetics research in the early Twentieth Century. This is the view that traits are determined solely by genetics (determinism—to be discussed below), that inheritance is determined by particles, i.e., "factors" (what we today call genes) that assort independently during reproduction and are tandemly ordered (as "beads on a string"), and that most traits are binary ("normal" vs. "abnormal") and determined in a simple ("Mendelian") dominant or recessive pattern (with a few simple exceptions such as sex linkage).

theory of heredity, and that is why both he and his contemporaries failed to see the implications of his results.

Both Falk and Sarkar (1991) and Fairbanks and colleagues (Fairbanks and Rytting 2001; Westerlund and Fairbanks 2004) argue for the opposing view. Fairbanks (2008) argues that the following sentence from Mendel's famous paper essentially presents the law of segregation:

> It is only possible for the differentiating elements to liberate themselves from the enforced union when the fertilizing cells are developed. In the formation of these cells all existing elements participate in an entirely free and equal arrangement, by which it is only the differentiating ones which mutually separate themselves. (Mendel 1866/2008; p. 111)

Similarly, Fairbanks argues that the law of independent assortment is to be found in the following: "The behavior of each pair of differentiating characters in hybrid union is independent of the other differences between the two original plants" (Mendel 1866/2008, p. 111).

At the center of this problem is the issue of gene function, how to relate the gene to its end product(s)—genotype and phenotype. This is one of the central questions genetics has struggled with since its inception. The controversy discussed above about whether Mendel can appropriately be considered to be the founder of what we know as Mendelism today, in fact, revolves around whether or not Mendel understood the difference between a trait and its underlying determinant (the gene). In the *Versuche* paper Mendel drifted between description of this phenomenon by the terms *merkmale (*feature) and *elemente* (elements). According to Allchin (2003), Monaghan and Corcos (1990), and Olby (1985), this inaccuracy suggests an inadequate understanding of the separation between the two meanings. Others have noted, however, that Mendel used the term *merkmale* to refer to both the outward traits and the underlying determiners of heredity only in the earlier sections of his paper. In the concluding remarks of his paper where he explains his findings in more theoretical terms he used the term *elemente* for the first time, which then appears another nine times, always referring to the underlying elements (Westerlund and Fairbanks 2004). Sadler (1983) notes as well, that Mendel referred to individuals as carrying the "potential" for a trait. Mendel's terminology for describing a trait and its determining "factor" (gene) is, nevertheless, undeniably vague. Thus, how well Mendel himself understood this fundamental precept remains surprisingly open to question.

Perhaps Olby (1985) put the issue most accurately:

> If we absolutely defined a Mendelian as one who subscribes explicitly to the existence of a finite number of hereditary elements which in the simplest case is two hereditary traits only one of which may enter one germ cell, then okay Mendel was clearly no Mendelian. On the other hand if by Mendelian we mean one who treats hereditary transmission in terms of independent character pairs and the statistical relationships of hybrid progeny as approximations to the combinatorial series, then Mendel was a Mendelian. (p. 254)

The question for a genetics educator is then the same one as asked by Hartl and Orel (1992): Does Mendel "deserve…credit for Mendelism"? Which story of Mendel should we bring into the classroom? Both Allchin (2003) and Kampourakis (2011) claim that textbooks and genetics instruction in general depict a false story and that "Mendel has been recreated historically to fill a monumental, heroic image" (Allchin 2003, p. 333). Moore (2001) summarizes the issue as follows:

> Many aspects of the 'rediscovery story' of Mendel's paper are inaccurate. Mendel's original paper announced no major findings; it was known and acknowledged as 'typical' science for its day. When it was 'rediscovered,' Mendel's paper became famous as a result of a priority dispute between de

> Vries and Correns. This dispute prompted researchers to reinterpret and *read importance into* Mendel's paper (p. 21; emphasis added).

As noted above, Fairbanks (2008) and many if not most geneticists and genetics educators still view Mendel and his discoveries as the origin of genetics. Fairbanks argues that "most of the questions about these controversies can be resolved on the basis of botanical, historical, and statistical evidence often overlooked by Mendel's critics" (Fairbanks 2008, p. 310). On the other hand, Allchin (2003, 2012) has presented sound arguments in support of claims that Mendel's work has been grossly oversimplified and that the model we present not only incorrectly describes what occurred but also leads to student misconceptions. Allchin (2012) demonstrates, for example, that the inheritance of seed shape (smooth vs. wrinkled), perhaps the best known example of Mendel's work and the source of the "law of dominance", can be understood at the molecular level as a case of what would today be called "incomplete" or "partial dominance." The gene involved codes for starch-branching enzyme 1 (SBE1) which converts simple sugars into large starch molecules; homozygous mutant seeds which lack the normal enzyme cannot produce the starch molecules and thus do not absorb as much water due to osmotic pressure (and taste sweeter) and are more prone to be "wrinkled" when dried. Heterozygotes (Ww), however, produce an amount of starch that is intermediate between the two homozygotes. Bateson (1902, 1909), Correns (1900), Tschermak (1900), and even Mendel himself (1866/1966), recognized this phenomenon in various *Pisum* traits.

Today we know that dominance is in fact not the norm but the exception to the rule. Most heterozygotes do indeed show intermediate phenotypes, largely because the one functional allele in heterozygotes typically produces half the normal amount of the gene product which typically has at least a modest effect on the phenotype. This fact does not auger against valuing Mendel's work, however. As Allchin (2012) points out, dominance is not needed to understand segregation (the "law of independent assortment"), which is the more important concept in Mendelian genetics. Allchin even argues cogently that segregation might be more easily understood in the case of intermediate heterozygotes than in cases of complete dominance. The problem, however, is that textbooks and teachers present dominance as the rule and not the exception, resulting in an important misconception about inheritance.

Allchin (2012) also notes that most traits are not binary; multiple alleles are not the exception as we often lead our students to believe. The norm is that a gene has multiple alleles, not just two. Today, in fact, we know that the SBE1 gene that impacts starch content in *Pisum* producing either smooth or wrinkled seeds has many different alleles (differing DNA sequences producing different amino acids in the resulting protein) (Bhattacharyya et al. 1990) and that *Pisum* seed starch content is affected by no less than five different genetic loci. Therefore, the inheritance of seed shape in Mendel's peas not only shows intermediate phenotype in heterozygotes (incomplete dominance)—not simple dominance but also multiple alleles—not just two, and polygenic determination—not determination by a single gene.

Is it then more accurate to present Mendel as making a crucial contribution to the understanding of heredity but presenting Mendelism as only the simplified initial model of inheritance? Perhaps. Is it appropriate to continue to present Mendelism as the primary way our students understand inheritance? Probably not (see Section 3 below). One way to address the issue might be to make use of this debate in the classroom. Present the history; include not one side of the story in the classroom, but both. This approach would consume instructional time but has the advantage of highlighting the tentativeness of science.

In reality, the myth of the Mendel story is likely to persist in society and in the culture of science, as evidenced particularly in student textbooks. Some issues in the history and philosophy of science are simply never resolved. Whether or not to address the issue in the classroom is a matter of the teacher's concern for historical accuracy as well as the extent to which the goals of the course focus on the nature of science.

Next, we turn to questions about the proper place of Mendel within the genetics curriculum alluded to above. Exactly what role should Mendel and his laws play in the standard genetics curriculum today? Should Mendelian genetics still be the core of contemporary genetics or merely a historical decoration in the introduction? Where should this content appear in the standard introductory genetics curriculum?

2 Mendel in the Genetics Curriculum

In the last few decades the relatively new field of genetics has developed rapidly, including most recently findings of the Human Genome and ENCODE Projects and the emergence of the study of genomics (Zwart 2008). One might then ask whether Mendelian genetics, a field of knowledge that is some one hundred years old, is and should remain as a part of the modern genetics curriculum. Has the time come to set aside the teaching of the outdated (or at least supplanted) Mendelian model to allow time for addressing the ever increasing complexities of modern genetics?

Dougherty et al. (2011) found that Mendelian genetics, such as the principles of segregation and independent assortment, is one of the most frequently addressed genetics topics emphasized in the US state standards. In a survey of the genetic content in US introductory biology courses for non-science majors Hott et al. (2002) found that Mendelian genetics was the most emphasized of all genetic topics. Instructors in this study also rated Mendelian concepts as one of the most important to teach. Hott et al. (2002) also found that Mendelian transmission genetics was the first or second most addressed genetic topic in textbooks for these courses.

Similarly, international studies of high school biology textbooks used in many countries (including European, North and South American countries and Australia) found that 21–27 % of the explanatory models of gene function presented were based on Mendelian genetics; all classical genetics models combined accounted for almost half of the content (Gericke and Hagberg 2010a, b; Gericke et al. 2012; Santos et al. 2012). Given these data, along with the widely recognized role of textbooks in determining the content presented in the classroom (DiGisi and Wilett 1995; Moody 2000), it is clear that biology teachers worldwide dedicate much of their instructional time to Mendelian genetics. Mendelian genetics is still a very prominent part of contemporary genetics education. Mendelian explanations are a cornerstone in the classroom, and most teachers find it an important topic to teach.

Sjøberg (1998) argues that the selection of content to teach in science education could be based on one or more of four arguments: *economy*, i.e. knowledge should be made profitable for the individual who should learn about content needed for his or her future profession; *utility*, i.e. knowledge should be usable in the everyday life of the citizen; *democracy*, i.e. knowledge should be acquired as a base for participatory democratic decision making; and *culture*, i.e. knowledge is an important part of human culture and is therefore important for every citizen to know about. In vocational and professional education the economy argument is preeminent, in compulsory schooling the latter three

would be valid, and in higher education for non-science majors the cultural argument would stand at the forefront.

How then does Mendel fit into this framework? In most cases, Mendel should be an important part of the genetics curriculum due to the fact that Mendelian genetics is so pervasive in modern culture. Science shapes our understanding of the world, and Mendel's work is a cornerstone in the history of our understanding of inheritance among living things, including ourselves. Could a person who has no knowledge of Mendel be considered an educated person in modern society? We think not. Given that the twentieth century has been called the "Century of the Gene" (Keller 2009), some knowledge of Mendel who first proposed a particulate model of inheritance, seems to be an essential requirement of science literacy today. However as recognized throughout this paper, this view does not preclude us from questioning the extent to which Mendelian genetics should be addressed within the curriculum and how Mendelian genetics should be presented in textbooks and classrooms.

The utility and democracy arguments might also widely apply if only for those relatively rare situations where understanding Mendelian genetics is useful for interpreting genetic phenomena or taking an informed political position about a genetic phenomenon (e.g., universal genome sequencing or genetically modified foods). The economy argument is probably less applicable to universal education but is undeniably central to training professionals in medicine, biotechnology, agriculture, etc.

We argue elsewhere (Smith and Gericke) that there are also likely utilitarian values in teaching about Mendel, including the motivational arguments for a historical approach such as that developed by Clough (2011), Clough et al. (2010) described below. In brief, our own argument is that Mendel's work may have heuristic value as a simplified model of genetics. We believe it is likely that understanding Mendelian explanations of *Pisum* inheritance (e.g., simple dominance) which are clearly atypical cases may make it easier to understand more complex but also more typical genetic phenomena (e.g., polygenics and multifactorial inheritance).

Presenting simplified models as a way of scaffolding student understanding upon which to build more complex and accurate understandings is a common pedagogical technique in the sciences, from the Bohr model of the atom to frictionless planes, to the Central Dogma of Biology. The effectiveness of instruction based on such use of Mendelian genetics as a model of inheritance compared to other approaches remains to be experimentally tested but is clearly called for.

In light of recent trends in genetics research, especially genomics, perhaps the most crucial and widespread instructional mistake based on simplistic views is the tendency toward genetic determinism—the idea that the genes solely determine physical characteristics or behaviors rather than in combination with other factors. The new field of genomics highlights the importance of the entire context of the genetic material, i.e., the non-coding regions, the cytoplasm and its constituents, the transcription and translation machinery, levels of control above the DNA, etc. Genomics therefore views genes, not as the sole determinants of each characteristic of the organism, but as only one of the vital components of the process leading to the phenotype.

We consider genetic determinism to be a central aspect of Mendelism, the view of inheritance as promulgated by Mendel and early twentieth century geneticists, as well as interpreted (erroneously or not) by geneticists, textbooks, and teachers from that time to the present. And as can be seen in the literature, the simplified Mendelian view in which genes are the sole determiners of phenotypic characteristics, is the most common conception of genetics among students at all levels (e.g. Duncan and Reiser 2007; Lewis

et al. 2000; Lewis and Kattmann 2004; Marbach-Ad 2001; Shaw et al. 2008; Smith and Williams 2007; Venville and Treagust 1998). Mendelism is a form of reductionism in the sense that everything of importance in inheritance is reduced to the gene and its DNA sequence (Hull 2002). There is simply a gene (more appropriately an "allele") for each phenotype—a "gene FOR hemophilia", for blue eyes, for cystic fibrosis, for albinism, etc. Many people who have learned only the Mendelism view of heredity, therefore, mistakenly believe for example that the genetic material contains a form of "the eye color gene" that codes for a blue pigment in the iris. They do not understand that there is a complex biochemistry involved in the production of the color of the pupils of the human eye, involving many genes, enzymatic reactions, and pigments.[5] The allele "for blue eyes", of course, does not "produce" or "determine" blue eyes; this phenotype is simply the result of the absence of the normal DNA sequence, leading to absence of pigment in the iris.

Determinism is clearly tied up with the understanding of phenotype and genotype—of the trait and the potential for the trait discussed above. Neither Mendel nor his re-discoverers understood the nature of the "factor" that determined pea traits, but his peas behaved as if these factors were of particulate nature (Gericke and Hagberg 2007; Mayr 1982). However, geneticists of this era disagreed about whether genes are material entities (a realist view) or hypothetical constructs (an instrumentalist view). The instrumentalist view takes the gene not necessarily as a real object but as a tool that is useful, as for example in the analysis of pedigrees (as did Mendel). As early as 1889, Weismann took a realist view that "the nuclear *substance*" (italics added) determines heredity (1889, p. 167). Johannsen, who coined the terms *gene* in 1909, did not take a position on the material nature of the gene but instead talked about "something" (*etwas*) found in the gametes and the zygote that determines heredity, but

> No hypothesis about the nature of this 'something' should thereby be constructed or supported…The genotype is something which we reach by inference, though we nevertheless dare to hold it as a real entity' (Johannsen 1909, p. 124).[6] [7]

Morgan manipulated genes "as if" they were material units, even though he made it clear in his Nobel Prize lecture that in his practice, "it does not make the slightest difference whether the gene is a hypothetical unit or whether the gene is a material particle" (Morgan 1933, p. 315). Goldschmidt, a contemporary of Muller, held a diametrically opposed instrumentalist "holistic" view of genes as "unproved, additional systems of units" (1954; p. 704)[8]

Later on, the view of geneticists shifted toward a more realist, materialist gene. The X-ray mutagenesis work of Muller convinced him that "genes exist as ultra-microscopic particles" (1922, p. 32). This view would perhaps reach its zenith with the discovery of the structure of DNA (Watson and Crick 1953).

The determinism that arises from Mendelism and its relationship to realism/instrumentalism and molecular definitions of the gene are perhaps best understood by dividing the single concept of gene into two sub-concepts, Gene-P and Gene-D, as proposed by Moss (c.f., 2001, 2003). Gene-P "is defined by its relationship to a phenotype…When

[5] Very early on, Johannsen (1923) recognized the shortcomings of such Mendelism.

[6] Both English translations taken from Falk (1986, p. 140).

[7] Falk (1986) refers to this view as "instrumental reductionism" (p. 141).

[8] The very public argument between Goldschmidt and the genetic materialists, especially Muller, is an interesting part of genetic history. For more on this topic, see Falk 1986.

one speaks of a gene in the sense of Gene-P, one simple speaks *as if* it [alone] causes the phenotype… Gene-P is defined strictly on the basis of its *instrumental* utility in predicting a phenotypic outcome" (Moss 2001, pp. 87–88; emphasis added). In contrast, Gene-D "is defined by its molecular sequence. A Gene-D is a developmental resource (hence the "D") which in itself is indeterminate with respect to phenotype" (Moss 2001, p. 88).

Using these terms, the Mendelian gene is best described more as a Gene-P, as for example the Gene-P for blue eyes or for cystic fibrosis (CF). In contrast, the molecular understanding of the gene is more a Gene-D. The Gene-D for cystic fibrosis is a chloride-ion conductance channel template sequence (Moss 2001). Gene-P language is more useful for certain tasks such as pedigree analysis, but Gene-D is more useful for tasks such as identifying multiple genes involved in normal functioning (one of the roughly 30,000 genes involved in normal pulmonary functioning in the case of CF) (Moss 2001).

Other arguments have been made, as well, for the incommensurability of the Mendelian and the molecular gene, focusing largely on the complexity and variety in the structure and function of various instances of the latter. Fogle (1990), for example, notes that the Mendelian gene concept simply cannot account for such complexities as overlapping DNA regions coding structural molecules that are "overlapping on opposite or like strands, nested, and even physically split", genes with or without introns, nucleotide sequences that can be both coding and non-coding, alternative splicing that can produce multiple polypeptides, multifunctional proteins, frame-shifting that results in two different polypeptides from the same sequence, etc. "The list seems endless…The simple [Mendelian] gene, then lacks coherent meaning at the molecular level." (Fogle 1990, pp. 366–367).

> The importation of a classical unit concept into molecular genetics, more than just being ambiguous, so oversimplifies genetic architecture than almost any statement about the structure of the gene is doomed to a litany of exceptions" (Fogle 1990, p. 369).

The Mendelian gene is therefore inconsistent with this more modern, molecular understanding of the gene, and therefore it is not possible to reduce the Mendelian gene into the molecular gene. These two opposing views are each valuable, but which is most appropriate, or even which is being tacitly employed at a given time, can only be determined by the context. Geneticists implicitly understand these vagaries, but the danger is in the potential to cause student misunderstanding.

In this light, genetic determinism can be seen as a case of understanding the gene as only a Gene-P. When Mendelism is taught as the sole mechanism of inheritance or when Mendelian genetics is implicitly or explicitly reduced to molecular genetics, the learner is led toward an inappropriate deterministic understanding of genetics (Gericke et al. 2012). The conflation of the Mendelian and molecular gene concepts has been reported to be a common instructional phenomenon (Sarkar 2002), especially in biology textbooks from many countries (Gericke et al. 2012). Other recent studies (Gericke et al. 2013) suggest that high school biology students typically embrace deterministic explanations and spontaneously and inappropriately apply Mendelian concepts to molecular genetics (Gericke and Wahlberg 2013). Such determinism has been reported as a problem in classroom instruction (Castéra et al. 2008) and as the source of many student conceptual difficulties and public misunderstandings (Lanie et al. 2004).

Although it is not our purpose in this article to judge the relative merits of the arguments for and against the inclusion of Mendel in modern genetics instruction, based largely on cultural/historical and pedagogical utility grounds, there appears to be merit in continuing to teach about Mendel and his work. Given its pervasiveness in the standard genetics

curriculum, including textbooks and standards documents, it would indeed be challenging to remove Mendel. We acknowledge, however, that the question of the relative importance and value of this instruction compared to modern genetic concepts and technologies remains open. Comparison studies of different approaches that consider the effect on genetics learning of including or omitting Mendel are clearly called for, although the cultural value of Mendelian instruction will remain as an issue for philosophical argument. Also, the differing reasons for teaching Mendelian genetics noted above should lead to differing approaches to genetic instruction, which should be tested as well.

Assuming that Mendelian genetics is retained in the curriculum, the question of the proper sequencing of Mendel compared to other content has also been raised. Introductory genetics instruction has typically begun with Mendel's laws, but some authors have recently questioned whether this is the most effective placement (Dougherty 2009). Redfield (2012) suggests beginning with teaching gene function before inheritance patterns in an a-historical manner. The rationale for this sequence is that students otherwise will learn inheritance patterns by heart without understanding the underlying processes (Redfield 2012). Burian (2013) advocates in the opposite direction in favor for a historical teaching approach (discussed in more detail below) that connects conceptual understanding with the understanding of the history and philosophy of genetics, pointing out the importance of including the discovery process of science in genetic instruction to promote conceptual understanding.

The relation between Darwin and Mendel discussed earlier may be relevant to the debate about whether evolution should be taught prior to genetics or if genetics should be taught first in order to give students a genetic tool to facilitate evolution understanding. Bizzo and El-Hani (2009) argue that the claim that understanding genetics is necessary to understanding evolution is "wrong from an historical and an epistemological perspective" (Bizzo and El-Hani 2009, p. 113), although they do not claim that the opposite sequence is more effective. Noting that Darwin held "a 'right' model of evolution while having a 'wrong' model for heredity" (p. 113), their primary argument is that evolution should be taught more extensively throughout the introductory biology curriculum and that "curriculum design that takes Genetics as a requisite to Evolution can be of no help in the proper development of student understanding of biological evolution" (p. 113). If evolution is taught before genetics, this ordering provides students with the more appropriate "image of science… including some that proved to be wrong" (p. 113). The question of the most effective sequencing awaits empirical testing.

In the following section we will identify traditional and innovative uses of the Mendel story and Mendel's work in the classroom.

3 Uses of Mendel in the Modern Classroom

Telling the story of Mendel has been a common practice for decades for both biology and genetics textbooks and for biology teachers at both the secondary and postsecondary levels. This telling typically begins with a brief summary of Mendel's life and service as a monk, followed by discussion of his experiments, leading to "Mendel's Laws". The apparent purpose of telling this story is to present the field of Mendelian genetics (i.e., the inheritance of uncomplicated two-allele traits) via a simple storyline that is relatively accessible to learners who have little or no knowledge of genetics. The primary purpose, therefore, is to enhance the learning of the genetics content. Gericke and Hagberg (2007), Gericke and Smith (in press), and Smith and Adkison (2010) provide helpful summaries of the

historical content that is likely appropriate for introductory courses that focus on gains in genetics content understanding.

Although it is rarely mentioned explicitly, the likely principal aim of most instructional use of Mendel's story and work is to enhance student understanding of the basic rules ("laws") of genetics, i.e., to make these concepts accessible in a logical way. A recent example of such work is the Henson et al. (2012) development of a "Socratic tutorial", "Mendel's Factors and Muller's Mutations", which is available in print format and (soon to be) online (http://beSocratic.clemson.edu). The tutorial first asks students "to reflect on what Mendel knew about his factors in physical or molecular terms" (p. 3). The purpose of this tutorial is to provide students with a "coherent, robust, and generalized framework" for understanding mutations.

The more human side of the Mendel story (service as a monk, repeated failure of his science teacher certification exams, later service as an abbot, etc.) is likely included in instruction to enhance student motivation and to "humanize" science (Matthews 1994), i.e., to help students view science as a human endeavor, not just performed by nerds and geniuses in ivory towers. To our knowledge the studies of the effectiveness of this approach (vs. a presentation of the laws of inheritance without the story) in achieving these two purposes has not been reported, at least within the past two decades.

Another aim of instruction based on presentation of the Mendel story has traditionally been to enhance problem-solving. Most introductory instruction in genetics includes sets of practice problems (monohybrid, dihybrid, sex-linked, etc.). The goal here is to ensure in-depth understanding of Mendelian inheritance by requiring students to be able to apply their understanding to specific contexts In addition to understanding, some (now quite dated) genetics education research aimed to enhance specific (and sometimes more general) problem-solving skills (c.f., Smith 1988; Smith and Good 1984).

In the early 1990s James Stewart and his graduate students at the University of Wisconsin (c.f., Johnson and Stewart 2002) developed and tested a radically different, "science-in-the-making" approach to teaching Mendelian genetics at the 12th-grade (high school) level. In this approach, students work in small teams, deal with realistic problems (in the context of a computer simulation called the Genetics Construction Kit—GCK), collect and analyze data, and present to and are critiqued by their peers. Students produce genotype-level models to explain the phenotypic data that they generate; anomalous data require rounds of model revision. Students begin the course by reading an "abridged version" of Mendel's original paper, followed by meeting Gregor Mendel himself (in the person of a graduate student acting the part), who explains his basic model of simple dominance. Students investigate the use of this model and their subsequent revisions of it to explain their GCK-generated inheritance data.

According to Johnson and Stewart (2002), a primary purpose of this instructional design is to produce "greater model-revising, problem-solving success" (p. 464). The focus on the use, evaluation, and revisions of models, identification of anomalous data, etc. along with discussion of "student scientists" suggests that the instruction aims not only at developing genetic understanding and skill manipulating genotypic data to solve problems but also at developing skills that can be transferred to other scientific questions. This approach also seems to foreshadow the more prominent trend in the following decade of designing science instruction, including genetics, whose primary aims are to enhance student understanding of both genetics content and the nature of science (NOS). This work has often employed the history of science such as the story of Mendel as a primary pedagogical approach.

The best example of this research is the NSF-funded "Story behind the Science" project of Michael Clough and his collaborators at the University of Iowa. The Clough group has developed a set of thirty short stories about a wide range of science topics. The stories "address the development of fundamental science ideas (using the words of scientists) with embedded comments and questions that explicitly draw students' attention to key NOS ideas" (Clough 2011, p. 713). The project recognizes the common deficit in epistemological training and understanding among teachers, as well as the common teacher concern that NOS and historical instruction will detract from the time available for content instruction. The stories are carefully constructed in light of current understandings of effective instruction and are designed to avoid recognized narrative elements that can interfere with accurately portraying NOS (monumentality, idealization, affective drama, explanatory and justificatory narrative—Allchin 2003).

The Clough and colleagues instructional design employs "learner-centered teaching", focuses on common misconceptions and conceptual changes, seeks to "humanize" science, is interdisciplinary, and promotes interest in science, science careers, and life-long science learning. The short stories include not only the story of Mendel, but such diverse stories as black holes, dark matter, Neptune, Darwin, global warming, and continental drift. The Clough et al. version of the Mendel story is appealing and loaded with historical detail and humanizing familiarity with the man and his work. The NOS focus is on creativity and discovery in his experiments and his thinking.[9]

To date, the Clough design has been employed with success in introductory biology classes at the postsecondary level. Qualitative and quantitative analyses revealed that this use of historical short stories was associated with "meaningful positive impacts on students' understanding of the NOS, interest in science careers, and interest in science content" (Clough et al. 2010, p. 11).

Two other approaches to teaching genetics with a focus on NOS, history, and the story of Mendel have been reported. In Lonsbury and Ellis' (2002) design, the instruction included lectures, small group work, and the theories of Hippocrates, Aristotle, Bacon, Descartes and Mendel. Compared to controls who received "normal" instruction, students in the intervention group made statistically greater gains in NOS understanding as measured by the Nature of Scientific Knowledge Scale (Rubba 1977). There was no statistically significant difference between the two groups on a genetics content test, evidencing that the intervention did not detract from student content learning.

Westerlund and Fairbanks (2010) proposed a design for teaching NOS using the original Mendel paper, though not the larger historical story, in a postsecondary genetics course. The instructors "include explicit nature of science instruction … during the lecture on Gregor Mendel … by discussing selected passages from Mendel's … paper" (p. 298). Explicit parallels are drawn between six specific characteristics of science and six aspects of Mendel's work. For example, "Mendel's decision to allow the F_2 offspring to self-fertilize and to apply mathematics to his theory" is recognized as an example of the characterization of science as originating "from imaginative and creative processes" (p. 301). Although this approach has not to our knowledge been evaluated, it merits further study.

Allchin (2012) raises concerns about the Westerlund and Fairbanks approach, however, as presenting an inappropriate ("positivistic" and "distorting") view not only of Mendel's conclusions (discussed above) but also of the characterization of his approach as the quintessential example of the nature of science (or "the scientific method"). Based on Di

[9] The stories and support materials are freely available on the Internet at: http://www.storybehindthescience.org. [Accessed June 10, 2013].

Trocchio's (1991) analysis of Mendel's work, Allchin argues that Mendel himself noted that he excluded from study those traits that "do not permit of a sharp and certain separation" (i.e., excluded all but the clearly binary traits) (Mendel 1866/2008, §2). Mendel also noted that his findings applied only to "those differentiating characters which admit of easy and certain recognition" (i.e., not to the majority of traits we know today) (§ 8). Allchin argues that Mendel's work (at least his initial studies) could therefore be more accurately described as "a strategy of blind search and selection." As Allchin notes that Mendel did not design "a simple confirm/reject test" (2012, p. 9). The conclusion that follows is that textbooks and teachers typically present a "simplified, stereotypical, and misleading" description of Mendel, inheritance, and the nature of science.

Burian (2013) has proposed an approach related to that of Westerlund and Fairbanks that "aims to teach the processes of discovery, correction, and validation…[using] four major episodes from Mendel's paper to the beginning of World War II" (p. 1). Like the approaches above, Burian's design focuses on providing students with "an understanding of science" (p. 2). The Mendel story is used to focus on the importance of cultural changes and the changes in the standards of scientific work (e.g., technological advances) on acceptance of theories and the development of science. Although this design has not been experimentally tested and, as Burian recognizes, he is a philosopher and historian of genetics and does not teach introductory genetics courses, this approach seems worthy of consideration in future genetics curriculum research and development.

> Based on his rather opposing view of the Mendel story, Allchin (2012) proposes a different strategy for effective genetics instruction. First, teach inheritance "without the additional, complicating factor of dominance." Second, "adopt the language and notation" of multiple alleles without dominance. Third, "teach phenotypic expression…as part of development (molecular genetics), not inheritance…[highlighting] the complete pathway from gene to trait(s)" (Burian 2012, p. 7).

Reid and Ross (2011) have also proposed an interesting genetics course based almost entirely on our modern understandings of Mendel's seven characters. Modern molecular characterization of these *Pisum* genes has revealed, not only their locations and even their sequences in four cases,[10] but also the mechanisms leading to the effects of each, which present a wide range of phenomena including a transition mutation in an intron splice donor site leading to a frameshift and a premature stop codon (white flowers) (Hellens et al. 2010); the insertion of a transposon in a structural gene (round seeds); a single base deletion resulting in a truncated protein with no enzymatic activity (stem length); a basic helix-loop-helix transcription factor (purple flower color allele); insertion, incorrect splicing, or transcriptional defects (in the three possible cotyledon color alleles Mendel might have employed) (Armstead et al. 2007; Offner 2011; Sato et al. 2007); among others. Determination of these mechanisms has also involved a wide range of modern genetic techniques such as cloning, heterologous screening, synteny, mapping, candidate gene analysis, and allelic diversity. This seems to be a pedagogical design worthy of experimental testing, but it seems likely that a course focusing on human traits along with traits in other familiar organisms as needed, would be more interesting and thus motivating for most students.

As these examples demonstrate, several studies that employ the story of Mendel and his work have been reported in the last decade or so, but the number of science educators interested in designing and testing innovative and effective approaches to this material is

[10] The exact location of the pod color gene (green/yellow/*GP/gp*) is not known but is assumed to be in linkage group V.

quite limited. Published consideration of the most effective way to sequence Mendelism with the ensuing genetic theory and research has been even more limited.

4 Suggestions for a Teaching Approach Including Mendel

In light of the preceding discussions of philosophical issues, pedagogical pitfalls, and creative instructional approaches, the question of how one might continue to teach about Mendel and his work is challenging. Therefore, based on our own work and extensive genetic teaching experience, we provide here some modest suggestions that we hope teachers and curriculum developers will find helpful.

We acknowledge that there are possibly many different approaches to genetics instruction that could be effective. The ideas presented below are but one set of potentially fruitful ideas that might be useful. These proposals are based on research on model-based instruction (c.f., Jackson et al. 2008), use of analogies in instruction (Glynn et al. 1995), and conceptual change pedagogy (Johnson et al. 1990; Limon and Mason 2002), and are designed as part of a combined majors/non-majors university course in introductory biology. The primary goals of the course are content understanding, cultural/historical knowledge, and motivation toward biology, the study of biology, and biology careers. The central guiding approach to teaching about Mendel's work is historical, explicitly presenting the Mendelian explanations of heredity as a simplified model as described above.

Such genetics instruction should include the following:

1. Mendelian concepts should be explicitly identified as a simplified model that is accurate for only a limited number of special cases of inheritance.
2. It should be presented as only a tool for understanding, a scaffold on which to build a more complete understanding of genetics through later learning.
3. Genetics educators should know which misconceptions their students hold, how strongly they are held, and how these ideas differ from current scientific explanations.
4. Teachers should present so-called "discrepant events", i.e., manipulations, demonstrations, observations, and/or discussions that ask students to make predictions and explain their predictions in cases where misconceptions are likely to lead to predictions and conclusions that are at odds with what is observed or otherwise known. The genetics educator might, for example, ask if there is a gene (or allele) for tallness in humans or a gene (or allele) for sickle cell anemia. Likewise, students might be given a case of non-Mendelian inheritance to explain (the specific phenomena involved depending on the level of instruction but including at least polygenic and multifactorial inheritance). The case might involve, for example, two siblings known to carry the same allele for a genetic disorder such as albinism but the phenotypes are not identical, perhaps presenting the students with photographs of the pupils of the sibs' eyes of different blue hues. Students should then discuss how the Mendelian model fits the case and how it is an inadequate explanation.
5. Students should be given cases or problems in which to employ both Mendelian and more modern genetic explanations so as to identify for themselves the value and utility of post-Mendelian explanations (e.g., determining the mode of inheritance of a simple Mendelian trait by pedigree vs. a non-Mendelian trait) (e.g., PKU vs. Charcot Marie Tooth syndrome).

6. Students should be given ample opportunities to discuss their observations, predictions, explanations, and understandings in small groups and then in class discussion with the teacher.
7. The teacher helps the students see the deficiencies of their prior understandings (in this case determinism) and to consolidate their new understandings (in this case the effect of environmental influences).
8. At this point the teacher introduces the standard scientific terminology used to describe the observed phenomena within the framework of modern molecular genetics (in this case multi-factorial inheritance, penetrance, expressivity, etc., depending on the level of instruction).
9. To further consolidate understanding the teacher then provides a challenge case(s) and asks students to make predictions and generate explanations. In this activity, the challenge case(s) might be variability in genetically identical sibs for any of several alleles such as retinoblastoma or, preferably, the example of a case currently in the news (e.g., Jennifer Lopez and BRCA) or other case of personal interest to the students.
10. We also recommend that teachers take advantage of the many excellent opportunities for improving student understanding of the NOS that are provided by including Mendel, his story, his work, his findings, and the role of his work in twentieth and twenty first century genetics.

Of course, however Mendel's work is taught, it is crucial for the instructor to understand its status as only a simplified model, not the current model of inheritance or the ultimate goal of instruction, and to avoid its various misrepresentations and simplistic views that make it inconsistent with modern genetics noted above. We take the primary pitfalls to be: (1) genetic determinism, (2) promulgation of common myths, and (3) failure to address common misconceptions.

Genetic determinism might best be addressed in two ways: careful use of language and explicit recognition of the fallacy. Teachers must become ever more aware of their use of genetic and related vernacular language, of how the one is easily conflated with the other leading to student confusion, and of student use of that language. Regarding determinism, examples of this troublesome language noted above include "X is the gene for Y" and "X determines Y." Other examples would include any references to the genes (and DNA) as the sole source of the phenotype, e.g., DNA as "the book of life" or "what makes us who we are." In simplest terms, teachers must eschew such language that implies simple causation, a difficult challenge indeed given that deterministic language has become a central part of "gene talk" in today's media (Keller 2009).

Taking a cue from the NOS-instruction literature, determinism might also be effectively discouraged by explicit instruction, i.e., we suggest that introductory genetics instruction should point out the shortcomings of deterministic understandings of inheritance. Such instruction would make it clear that phenotype is the product, not only of the genetic material, but also of environmental effects at all levels, epigenetic effects, etc. Instruction might also include discussion of examples that give clear evidence of the shortcomings of deterministic language; teachers might, for example, discuss the use of language such as "the gene for blue eyes" or "for PKU". Examples of environmental effects could be as simple as discussing height in humans, perhaps with comparison to this trait in peas and even in achondroplastic dwarfs.

There are many historical myths about Mendel, some of which have been detailed above. Corcos and Monaghan (1985) point to a number of other simple myths that should

be corrected both among teachers and students, myths that are often acquired in earlier genetics instruction. These include the following:

> (1) Mendel's laws as we teach them are found in his writings…*They are not*; (2) Mendel thought that one character was always dominant to another…*He did not*; (3) He discovered the now famous "Mendelian" ratio, 9:3:3:1…*He does not mention such a ratio;* and (4) His data showed that the seven pairs of characters he worked with were inherited independently…*Mendel cites the data of only two experiments involving only three of the seven traits*" (p. 233).

The last of these myths has been discussed above. For further explanation of the other myths, see Corcos and Monaghan (1985). As with the issues we discussed earlier, these issues are largely a matter of historical fact and interpretation. We think students may find these widespread but erroneous ideas to be fascinating. We also propose these myths can likely be corrected by explicit verbal instruction, pointing as before to the importance of the teacher's personal understanding of genetics and to the accuracy of what is presented in the classroom.

More importantly, we believe, is the common myth that Mendel was a heroic figure who worked in isolation to generate novel understandings that were light years ahead of his time. Allchin (2003) has cautioned about the way teachers often lionize and romanticize our scientific heroes. The stories developed by Clough and colleagues (Clough 2011; Clough et al. 2010) provide a good example of how to avoid this instructional pitfall. This myth is most important to address properly because of the mistaken view of science that it presents. Although Mendel was a sole investigator to a degree that rarely if ever exists today, he was not working in isolation (c.f., Henig 2000)

Third, students often hold more deep-seated genetic misunderstandings, sometimes called misconceptions or naïve misunderstandings. These might include the idea that all alleles exhibit simple Mendelian dominance, that traits are always determined by changes in a single gene, that phenotype is determined solely by the genetic material, that dominance equates with adaptive fitness, etc. (For an excellent summary documenting such misconceptions, see American Association for the Advancement of Science 2013).

5 Summary and Conclusions

Mendel has an extensive presence in the modern introductory biology classroom worldwide. There are apparently sound cultural/historical and pedagogical arguments for teaching about Mendel's life and work, whether in the majors or non-majors classroom. There are, however, pitfalls, misconceptions, and various learning difficulties that can arise to impact this learning, including in particular the issue of determinism in view of the recent rise of the field of genomics. Solutions to many of these problems or even proposals for how to approach them remain largely either unidentified or untested and are much needed.

A primary contribution of this paper is the presentation of the first systematic set of example approaches that make use of Mendel and his work and the Mendelian narrative. We have identified examples of innovative approaches that focus on enhancing student learning of genetics content, humanizing and making the content more relevant, enhancing problem-solving skills, and enhancing learning about the nature of science. We assume that there are other undocumented approaches at various educational levels and others that we did not identify in our search of the literature as well.

This review suggests that effective use of Mendel in the classroom is a topic ripe for science education research, especially for addressing the issue of the proper place of Mendelism in the introductory genetics curriculum. The view of Mendel and his work typically presented in today's textbooks and classrooms is clearly a simplification at best and misleading or false at worst. Nevertheless, there is clearly value in presenting simplified models early in a learning progression. The question of how textbook writers and classroom teachers can present a more historically accurate view of Mendel while also capitalizing on the value of the simplified model needs immediate study. In particular, the work of Allchin in this regard should be carefully considered. Another crucial issue that sorely needs to be addressed is the question of how best to teach the foundational concept of the gene in introductory genetics classes given that the concept is currently in such a state of disarray and constant flux. We also find it remarkable that few if any studies have considered how teachers might make good use of the rediscovery of Mendel (i.e. Moore 2001) or of the controversies surrounding his work (e.g. Allchin 2003, 2012; Fairbanks 2008), both of which would appear to be excellent source material for teaching the nature of science.

We owe much to this man who helped to lay the foundation for the relatively young but burgeoning field of genetics. The field is growing rapidly and basic precepts and approaches are changing just as rapidly, such that even the definition of the term *gene* is in a jumbled state of flux. Thus, teachers and even textbooks likely have outdated understandings of some concepts in the field. There is clearly a need for science education researchers and curriculum developers not only to develop and document the most effective instructional approaches and materials but also to develop innovative ways to promote the more rapid development of such materials and access to up-to-date understandings.

6 Additional Selected Resources for Educators

6.1 Books

Carlson, E. A. (2004). *Mendel's legacy: The origin of classical genetics*. New York: Cold Spring Harbor Laboratory Press.

Henig, R. M. (2001). *The monk in the garden: The lost and found genius of Gregor Mendel, the father of genetics*. New York: Houghton Mifflin Company.

Olby, R. (1985). *Origins of Mendelism*, 2nd ed. Chicago IL: University of Chicago Press.

Stern, C., & Sherwood, E. (Eds.) (1966). *The origin of genetics: A Mendel source book*. San Francisco: W. H. Freeman

6.2 Papers

Comptes Rendus de l'Académie des Sciences—Series III—Sciences de la Vie. Volume 323, Issue 12 (2000). Includes:

On the internal dynamics of Mendelian genetics
Richard M. Burian* C. R. Acad. Sci. Paris, *Sciences de la vie*/Life Sciences 323 (2000) 1127–1137 © 2000 *Académie des sciences/Éditions scientifiques et médicales Elsevier SAS. Tous droits reserves* S0764446900012488/FLA

6.3 Web Pages

MendelWeb (mendelweb.org) (Includes teacher materials)

Electronic Scholarly Publishing (esp.org) An extensive collection of original papers related to classical genetics, including

Mendel, Gregor. 1866. Versuche über Plflanzenhybriden. *Verhandlungen des naturforschenden Vereines in Brünn, Bd. IV für das Jahr 1865*, Abhandlungen, 3–47.

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