Gregor Mendel and "Myth-Conceptions"

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In a recent article, in *Science Education*, entitled "Scientific Myth-Conceptions" (Allchin, 2003), the author aptly criticized "popular histories of science that romanticize scientists, inflate the drama of their discoveries and cast scientists and the process of science in monumental proportion" (p. 329). The first example cited of such romanticism is Gregor Mendel. However, there is also tendency among some historians, such as Monaghan and Corcos (1990) and Di Trocchio (1991), to disparage Mendel's contributions with claims that contradict his original writings (Orel, 1996; Orel & Hartl, 1994; Fairbanks & Rytting, 2001). Such is also the case with the depiction of Gregor Mendel in Allchin's article.

Following the lead of Monaghan and Corcos (1990), the article credits Mendel's principle of independent assortment not to him but to geneticists who worked several years after the rediscovery of his work. It states: "in his classic 1865[1] paper, Mendel did not explicitly formulate a 'Second Law,' the principle of independent assortment," and "geneticists did not distinguish 'Mendel's' 1st and 2nd laws until several years after the revival of his work when they encountered anomalous ratios in the offspring" (Allchin, 2003, p. 332). These assertions concerning Mendel's Second Law are easily refuted. Although Monaghan and Corcos (1990) claimed that Mendel did not articulate the principle of independent assortment, other authors, among them Di Trocchio (1991), Orel (1996), and Fairbanks and Rytting (2001), pointed out that Mendel clearly stated the principle of independent

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[1] Although Mendel presented his paper verbally in 1865, it was published in 1866.

assortment in a passage that Olby (1979) called the "climax" of Mendel's paper (Mendel, 1866). After summarizing the results of his dihybrid and trihybrid experiments, Mendel concluded the section with his interpretation, stating,

> *the behavior of each pair of differing traits in a hybrid association is independent of all other differences in the two parental plants*. (Stern & Sherwood, 1966,[2] p. 22, italics in the original)

Mendel repeats this conclusion in almost these same words later in his paper when discussing his theory derived from experimentation. Modern textbooks typically define Mendel's principle of independent assortment in terms of chromosomes, genes, and alleles. Given the fact that chromosomes had yet to be discovered and that the terms *gene* and *allele* had not been coined in Mendel's day, one could hardly formulate a more lucid description of independent assortment than Mendel's. Moreover, geneticists clearly distinguished segregation and independent assortment from the very beginning of the rediscovery of Mendelian principles in 1900, not several years later. Correns (1900), near the end of his classic paper, explained the principle of independent assortment, quoting the same passage from Mendel's paper that we quoted above, and distinguished it from the principle of segregation.

The article erroneously concluded: "Ironically, then, while Mendel's 2nd law bears Mendel's name, he himself did not state it. Accounts credit Mendel with more than he did" (Allchin, 2003, p. 332). In fact, Mendel did formulate the principle of independent assortment and has been rightfully credited for it since the rediscovery in 1900.

The article further asserts that Mendel:

> did not distinguish clearly between traits and material units of heredity—today's phenotype/genotype distinction, at the heart of Mendelian genetics. Nor did Mendel see his 'elementes' [sic][3] (today's genes) as occurring in pairs in each organism. Mendel's notation clearly shows, that an A × A cross yielded A + 2Aa + a: the homozygous form was "A" and not a diploid "AA" (Olby, 1985). Mendel, it seems, was not quite "Mendelian." Again Mendel gets undue credit. (p. 332)

The assertion that Mendel did not clearly distinguish between traits and material units of heredity, which has been voiced by some historians (Monaghan & Corcos, 1990; Olby, 1979, 1985), derives to some degree from Mendel's use of the term *Merkmale* (characters) to refer to both the outward traits and the underlying determiners of heredity in the earlier sections of his paper. However, in the concluding remarks of his paper (section 11), Mendel explains his findings in purely theoretical terms and uses the term *Elemente* (elements) for the first time. This term appears 10 times in 4 consecutive paragraphs, always in reference to underlying hereditary elements.

Furthermore, that Mendel himself understood the difference between genotype and phenotype can hardly be disputed. In several places in his paper, he first presents phenotypic classes, then breaks them down into genotypic classes. For example, when reporting his dihybrid experiment for seed shape and color, he presents the numbers of individuals in the four phenotypic classes in the F_2 generation, giving them only phenotypic designations

[2] All passages we quote from Mendel's paper are from Eva Sherwood's English translation in Stern and Sherwood (1966).

[3] The spelling of "elementes" in this quotation is confusing. It is either a misspelling of the English word *elements*, or a misspelling of, and failure to capitalize, the German word *Elemente*, which is the plural of *Element*.

(such as "round and yellow"). He then breaks these down into the nine possible genotypic classes (as determined by the F_3 progeny) using symbols to represent their respective genotypes (such as *AaB* to represent an individual heterozygous for *A* and *a* and homozygous for *B*).

The article's assertion that Mendel did not perceive elements as paired is misleading because the technical accuracy of this statement rests entirely on the qualifying phase "in each organism," which the article did not explain. In fact, Mendel clearly perceived differing hereditary elements as being paired in heterozygotes, as is evident in the following passage:

> One could perhaps assume that in those hybrids [heterozygotes] whose offspring are *variable* a compromise takes place between the differing elements of the germinal and pollen cell great enough to permit the formation of a cell that becomes the basis for the hybrid, but that this balance between antagonistic elements is only temporary and does not extend beyond the lifetime of the hybrid plant. Since no changes in its characteristics can be noticed throughout the vegetative period, we must further conclude that the differing elements succeed in escaping from the enforced association only at the stage at which the reproductive cells develop. In the formation of these cells, all elements present participate in completely free and uniform fashion, and only those that differ separate from each other. In this manner the production of as many kinds of germinal and pollen cells would be possible as there are combinations of potentially formative elements. (Stern & Sherwood, 1966, pp. 42–43, italics in the original)

As Fairbanks and Rytting (2001) noted, Mendel's reference to "potentially formative elements [*bildungsfähigen Elemente*]" can hardly mean anything but inherited determiners of traits carried within the pollen and egg cells (what we now call alleles). His reference to "enforced association (*erzwungenen Verbindung*)" of these elements demonstrates his understanding that the different alleles (*A* and *a*) are paired in heterozygotes (*Aa*). He further visualized the elements as being paired until they separate from one another when "the reproductive cells develop," a phenomenon we now refer to as the segregation of paired alleles during meiosis, or Mendel's principle of segregation.

However, in Mendel's understanding, the *A* and *a* elements were not paired and did not segregate in homozygotes, but were paired and did segregate in heterozygotes, hence his depiction of homozygotes as *A* and *a*, instead of *AA* and *aa* (Fairbanks & Rytting, 2001; Hartl & Orel, 1992). Nothing in Mendel's results could have led him to conclude otherwise; he observed segregation only in the offspring of heterozygotes. Not until the twentieth-century discovery that genes are located on chromosomes, and that homologous chromosomes pair during meiosis, was it shown that pairing and segregation of alleles apply equally to homozygotes and heterozygotes. Mendel could not have known this. However his explanation of pairing and segregation in the offspring of heterozygotes is correct and he certainly merits credit for the experimental design, observation, and insight that led him to this interpretation.

Further, there is an error (p. 332) in the depiction of Mendel's notation. Mendel did not depict his crosses with a multiplication sign ($\times$) but even if he had, the cross $A \times A$, produces only *A* offspring, not $A + Aa + a$. The cross should be depicted as $A \times a$, which yields all hybrid *Aa* offspring in the first (F_1) generation. When self-fertilized, the *Aa* hybrid produces, as Mendel described it, $A + 2Aa + a$.

Also, the article criticized Mendel's experimental design:

> Everyone knows how Mendel examined seven character pairs in peas: tall–dwarf, smooth–wrinkled, green–yellow, etc. Mendel actually investigated 22 (Di Trocchio, 1991). He set

> aside the ones whose results were too confusing. Yet stories have long paraded the image of a perfect a priori experimental design. Textbooks seemed eager to boast of Mendel's insight, even when there was no evidence of it. (p. 332)

This quotation reveals confusion of the number of traits (i.e. "character pairs") Mendel studied with the number of pea varieties he selected for hybridization. Mendel obtained 34 varieties from seed dealers and from them selected 22 to study. As Mendel stated in his paper:

> From several seed dealers a total of 34 more or less distinct varieties of peas were procured and subjected to two years of testing. . . . Twenty-two of these varieties were selected for fertilization and planted annually throughout the entire experimental period. (Stern & Sherwood, 1966, p. 4)

Mendel selected 22 varieties of pea plants to investigate, *not* 22 character pairs as indicated in the article, an error that cannot be attributed to Di Trocchio (1991). Mendel listed the traits that differed among these 22 varieties as, "differences in length and color of stem; in size and shape of leaves; in position, color, and size of flowers; in length of flower stalks; in color, shape, and size of pods; in shape and size of the seeds; and in coloration of seed coats and albumen" (Stern & Sherwood, 1966, p. 5). The number of differing traits in this list is 15, of which Mendel chose 7 to study. He excluded the others, not because they were "too confusing" but because (in his words),

> Some of the traits listed do not permit a definite and sharp separation, since the difference rests on a "more or less" which is often difficult to define. Such traits were not usable for individual experiments; these had to be limited to characteristics which stand out clearly and decisively in the plants. (Stern & Sherwood, 1966, pp. 5–6)

In other words, Mendel excluded some traits from study because they were quantitative (traits that display continuous variation). He chose to focus on qualitative traits (those that display discontinuous variation) permitting him to clearly distinguish contrasting phenotypes. Mendel's decision to exclude quantitative traits from his experiments was appropriate. During the first decade of the twentieth century, some biologists considered quantitative traits to be much more important than qualitative traits in nature (indeed natural variation is more often continuous than discontinuous). They dismissed Mendelian principles as applying exclusively to qualitative traits, a notion that geneticists have long since abandoned. Mendel, however, had no such illusions, as he indicated in the following passage:

> The complete agreement shown by all characteristics tested probably permits and justifies the assumption that the same behavior can be attributed also to the traits which show less distinctly in the plants, and could therefore not be included in the individual experiments. (Stern & Sherwood, 1966, p. 23)

This passage contradicts yet another assertion made in the article: "For Mendel, his law applied only to 'those differentiating characters, which admit of easy and certain recognition' (section 8). Other characters followed another, different rule or law" (Allchin, 2003, p. 332). There is no evidence from Mendel's paper to support the allegation that he perceived his "law" as applying only to distinct, qualitative characters with a simple dominant/recessive form of inheritance or that he set aside the results of experiments because he found them too confusing. Instead, there is ample evidence of Mendel's insight in choosing seven qualitative characters for experimentation and concluding that the principles of inheritance governing these characters likewise applied to other, less-distinctive characters.

Allchin's article (2003) correctly dispels the notion that Mendel was the first to observe dominance and considered it to be universal. Indeed, Mendel reported observation of intermediate forms in hybrids and was well aware that other researchers had previously observed both dominance and intermediacy in hybrids, citing the works of Kölreuter, Gärtner, Herbert, Lecoq, and Wichura. In fact, seven years before Mendel's paper was published, Darwin compared dominance and intermediacy in *Origin of Species* in a passage that Mendel marked in his personal copy of Darwin's book (Fairbanks & Rytting, 2001).

In summary, we agree with Allchin that scientific myths "distort history and foster unwarranted stereotypes about the nature of science." Indeed, heroic depictions of Mendel often detract from his real contributions, but so do claims that discredit them. Orel (1996) divides historical accounts of Mendel into two periods: "the period of Mendel's glorification, which coincided with genetics becoming pre-eminent among the biological sciences, and the period of Mendel's diminution, reflecting the general iconoclasm and hero-bashing of more recent times" (p. 179). When it comes to Mendel, the pendulum, it seems, swings widely in both directions. Secondary sources disagree about Mendel's understanding and contributions. Ultimately, however, the best source of what Mendel did and understood is what Mendel wrote.

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