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INVITED SPECIAL PAPER

MENDELIAN CONTROVERSIES: A BOTANICAL AND HISTORICAL REVIEW[1]

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Gregor Mendel was a 19th century priest and botanist who developed the fundamental laws of inheritance. The year 2000 marked a century since the rediscovery of those laws and the beginning of genetics. Although Mendel is now recognized as the founder of genetics, significant controversy ensued about his work throughout the 20th century. In this paper, we review five of the most contentious issues by looking at the historical record through the lens of current botanical science: (1) Are Mendel's data too good to be true? (2) Is Mendel's description of his experiments fictitious? (3) Did Mendel articulate the laws of inheritance attributed to him? (4) Did Mendel detect but not mention linkage? (5) Did Mendel support or oppose Darwin?

A synthesis of botanical and historical evidence supports our conclusions: Mendel did not fabricate his data, his description of his experiments is literal, he articulated the laws of inheritance attributed to him insofar as was possible given the information he had, he did not detect linkage, and he neither strongly supported nor opposed Darwin.

Key words: Darwin; fabrication of data; fictitious experiments; laws of inheritance; linkage; Mendel.

The science of genetics traces its origin to Gregor Mendel's classic experiments with the garden pea (*Pisum sativum* L.) and common bean (*Phaseolus vulgaris* L.). Mendel presented his findings to the Brünn Natural History Society in two lectures in the spring of 1865 and then published the lectures in the following year as a single paper under the title ''Versuche über Pflanzen-Hybriden'' (Experiments on Plant Hybrids), hereafter referred to as ''Versuche'' (Mendel, 1866). ''Versuche'' contains data from eight years of experimentation, statistical analysis of those data, and mathematical models of the fundamental laws of inheritance. Although his paper would eventually become the foundation for the science of genetics, Mendel did not live to see that day. He died in relative obscurity in 1884, 16 years before his work became widely known. This is not to say that ''Versuche'' was entirely ignored: it was cited at least 15 times between 1865 and 1899 (Olby, 1985). However, no one recognized its relevance to the science of inheritance until 1900 when three European botanists, Hugo de Vries, Carl Correns, and Erich von Tschermak, independently observed the same phenomena and arrived at the same interpretation as Mendel. In the first years of the 20th century, genetics established itself as a core discipline in biology and Mendel's work finally began to receive widespread recognition.

The year 2000 marks a century since the discovery of Mendel's work and the birth of genetics. During that century, Mendel's name became indispensable to science. The fundamental laws of inheritance are now known as Mendel's laws, and the science on which they are based is called Mendelian genetics. However, because Mendel's importance was unrecognized during his lifetime, little original information about his scientific work was preserved. Most unfortunately, his scientific records were apparently burned around the time of his death (Olby, 1985; Orel, 1996).

In part because of the paucity of original documents, controversy plagued discussions of Mendel's work throughout the 20th century. Some authors praise Mendel as a brilliant scientist whose work was ahead of its time, others are critical of his methods, and a few claim he was a fraud. There is substantial disagreement about his objectives, the accuracy of his presentation, the statistical validity of his data, and the relationship of his work to evolutionary theories of his day. In the following pages we address five of the most contentiously debated issues by looking at the historical record through the lens of current botanical science: (1) Are Mendel's data too good to be true? (2) Is Mendel's description of his experiments fictitious? (3) Did Mendel articulate the laws of inheritance attributed to him? (4) Did Mendel detect but not mention linkage? (5) Did Mendel support or oppose Darwin?

We begin with a brief overview of Mendel's data. When quoting Mendel's paper in English, we use Sherwood's English translation (Stern and Sherwood, 1966) as is customary for authors who write about Mendel's work in English. We refer to the original German when necessary.

A BRIEF REVIEW OF MENDEL'S DATA

Mendel chose *Pisum* for his work after preliminary experiments with several plant species and an examination of botanical literature on plant hybridization, particularly C. F. Gärtner's (1849) *Versuche und Beobachtungen über die Bastarderzeugung im Pflanzenreiche* (Experiments and Observations on Hybrid Production in the Plant Kingdom). For his hybridization experiments, Mendel selected 22 pea varieties that he had confirmed through two years of testing to be true-breeding. He reported data from hybridization experiments on seven traits that differed among the varieties. In the following list of these traits, we include some information that is not in Mendel's paper but is pertinent for our later discussions, such as the modern designations of the genes Mendel studied and the chromosomes on which they reside:

1. Seed shape. In mature seeds, the dominant phenotype is a smooth or slightly indented round seed, and the recessive phenotype is a wrinkled angular seed. The varieties with wrinkled angular seeds were classified

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at the time as *Pisum quadratum.* The gene Mendel studied that governs this trait is *r* on chromosome 7.

2. Cotyledon color. In mature seeds, the dominant phenotype is yellow cotyledon color, and the recessive phenotype is green cotyledon color. The gene Mendel studied that governs this trait is *i* on chromosome 1.
3. Seed coat color. The dominant phenotype is a colored-opaque seed coat, and the recessive phenotype is a colorless-transparent seed coat. The gene Mendel studied that governs this trait is *a* on chromosome 1. Mendel noted that in his experiments, variation for seed coat color was always associated with variations for flower color and axillary pigmentation. He always found colored seed coats, colored flowers, and anthocyanin pigmentation at the axils of the stipules on the same plants, and colorless seed coats, white flowers, with no axillary pigmentation on the same plants in both parents and progeny. This complete association of phenotypes that Mendel observed was a case of pleiotropy, which Mendel observed because he studied alleles of the *a* gene. Pea researchers in the early 1900s reported epistatic interactions of these traits in a few experiments with other genes (White, 1917). However, variation for seed-coat color, flower color, and axillary pigmentation in most pea varieties is due to variation for alleles of the *a* gene, and consequently the pleiotropic association of these three traits is complete in most experiments.
4. Pod shape. The dominant phenotype is inflated pods, due to a parchment layer inside the pod, and the recessive phenotype is constricted pods, due to the absence of the parchment layer. The constricted-pod varieties were classified at the time as *Pisum saccharatum*, currently known as edible-pod sugar peas. The gene Mendel studied that governs this trait is either *v* on chromosome 4 or *p* on chromosome 6.
5. Pod color. The dominant phenotype is green unripe pods with green venation in the leaves, and the recessive phenotype is yellow unripe pods with yellow venation in the leaves. The gene Mendel studied that governs this trait is *gp* on chromosome 5.
6. Flower position. The dominant phenotype is flowers borne at upper axillary positions along the plant, and the recessive phenotype is terminal flowers with stem fasciation near the plant apex. Varieties with terminal flowers were classified at the time as *Pisum umbellatum.* The gene Mendel studied that governs this trait is *fa* on chromosome 4.
7. Stem length. The dominant phenotype is a long stem between the internodes, causing a tall plant, and the recessive phenotype is short internodes, causing a dwarf plant. Some of Mendel's varieties had semi-dwarf phenotypes; however, he conducted experiments on stem length only with tall and dwarf parents. The gene Mendel studied that governs this trait is *le* on chromosome 4.

The first two of these traits are considered seed traits because they are observed in the seed cotyledons, which consist of embryonic tissue. Because each seed embryo is genetically a different individual, seed-trait phenotypes may differ among the seeds on a single heterozygous plant. The remaining five traits are considered plant traits because they are observed in whole plants. The seed coat consists of maternal rather than embryonic tissue, so its phenotype is the same on every seed coat of a single plant. Thus, it is considered a plant trait along with its pleiotropic counterparts, flower color and axillary pigmentation.

The data from ''Versuche'' are summarized in Table 1. Mendel reported the results of the F_1 and F_2 generations of seven monohybrid experiments, one for each trait, and observed near 3 : 1 phenotypic ratios in the F_2 generation of each experiment (Experiments 1–7 in Table 1). He allowed some of the F_2 plants with the dominant phenotype to self-pollinate and obtained F_3 progeny from which he determined the genotypes of those F_2 plants. In each case, the ratio of homozygotes to heterozygotes among the F_2 individuals was close to 2 : 1 (Experiments 8–15 in Table 1).

He then conducted dihybrid or trihybrid experiments for all combinations of the traits but reported data for only one dihybrid experiment (for seed shape and cotyledon color; Experiments 16a and 16b in Table 1) and one trihybrid experiment (for seed shape, cotyledon color, and seed coat color; Experiment 17 in Table 1). In both experiments, he planted the F_2 seeds and allowed the F_2 plants to self-fertilize, then determined the genotypes of the F_2 individuals from the phenotypes of their F_3 progeny. The phenotypic and genotypic ratios for both the dihybrid and trihybrid experiments were consistent with the laws of segregation and independent assortment.

He also conducted a series of testcrosses and reported data for four dihybrid testcrosses for seed shape and cotyledon color and one dihybrid testcross for flower color and stem length (Experiments 18–22 in Table 1). In the dihybrid testcrosses for seed shape and cotyledon color, he hybridized F_1 plants that were doubly heterozygous with the homozygous parental genotypes in all four possible combinations of reciprocal crosses. He carried each experiment through the number of generations required to determine the genotypes of the testcross progeny. In all four experiments, he observed near 1 : 1 : 1 : 1 ratios in the testcross progeny. He also observed a near 1 : 1 : 1 : 1 ratio in the progeny of the dihybrid testcross for flower color and stem length.

Mendel reported general non-numeric results for several experiments with the common bean (*Phaseolus vulgaris*) and stated that in most cases the results were similar to those obtained with *Pisum.* He also reported the numeric results of one preliminary experiment for flower color in *Phaseolus.* He hybridized a variety that had colored flowers with one that had white flowers, and in the F_2 generation he observed 30 plants with colored flowers and one with white flowers. He interpreted these results as adhering to either a 15 : 1 ratio for two factors, or a 63 : 1 ratio for three factors.

Having reviewed Mendel's data, we now address five of the most important controversies about his work.

ARE MENDEL'S DATA TOO GOOD TO BE TRUE?

In 1902, two years after Mendel's work was rediscovered, W. F. R. Weldon suspected that Mendel's results were very close to expected values and tested this suspicion with Pearson's newly developed χ^2 test. He concluded that Mendel's observed ratios were astonishingly close to his expectations (Weldon, 1902). Weldon's analysis created a brief controversy and was quickly forgotten (Mangello, 1998). The next statistician to question the proximity of Mendel's results to expected values was Ronald A. Fisher (1936) who published a now-famous paper in which he closely examined Mendel's paper and reconstructed the thought process of the experiments. Fisher's analysis is careful and thorough and reveals his admiration for Mendel's work. However, his paper is best known for its conclusion, the same one that Weldon had arrived at 32 years earlier, that Mendel's results were consistently so close to expected ratios that the validity of those results must be questioned. Fisher's work spawned a series of papers dealing with this issue. Citations of these papers can be found in several reviews (Edwards, 1986; Piegorsch, 1986; Di Trocchio, 1991; Weiling, 1991; Nissani, 1994; Orel, 1996). Unfortunately, all this effort has failed to yield a definitive solution: according to Nissani (1994, p. 182), ''the subject remains every bit as controversial today as it was in 1936.''

Like Weldon's analysis, Fisher's was based on consistently low χ^2 values produced when he subjected Mendel's data to χ^2 tests. We present the χ^2 values and their associated probabilities with the appropriate degrees of freedom for each of Mendel's independent *Pisum* experiments in Table 2. As Edwards (1986) noted, about half of all independent experiments should yield χ^2 values with probabilities <0.5 and half with probabilities >0.5. Of Mendel's 22 experiments, only two yield χ^2 values with probabilities <0.5 and six yield χ^2 values with probabilities >0.90, indicative of the bias toward expectation in Mendel's data (Table 2).

As Fisher (1936) and several subsequent authors (Sturtevant, 1965; Edwards, 1986) have pointed out, Mendel's data are most suspicious where they closely approach an incorrect

TABLE 1. A summary of Mendel's experiments on *Pisum* hybrids.

Experiments	Results								Expected ratio
F$_2$ Generation of Monohybrid Experiments									
1. Seed shape[a]	Round	5474	Angular	1850					3:1
2. Cotyledon color[a]	Yellow	6022	Green	2001					3:1
3. Seed coat color	Colored	705	White	224					3:1
4. Pod shape	Inflated	882	Constricted	299					3:1
5. Pod color	Green	428	Yellow	152					3:1
6. Flower position	Axial	651	Terminal	207					3:1
7. Stem length	Long	787	Short	277					3:1
Totals	Dominant	14 949	Recessive	5010					3:1
F$_3$ Progeny Tests of F$_2$ Individuals from Monohybrid Experiments									
8. Seed shape	Heterozygous	372	Homozygous	193					2:1
9. Cotyledon color	Heterozygous	353	Homozygous	166					2:1
Totals for seed traits	Heterozygous	725	Homozygous	359					2:1
10. Seed coat color	Heterozygous	64	Homozygous	36					2:1
11. Pod shape	Heterozygous	71	Homozygous	29					2:1
12. Pod color	Heterozygous	60	Homozygous	40					2:1
13. Flower position	Heterozygous	67	Homozygous	33					2:1
14. Stem length	Heterozygous	72	Homozygous	28					2:1
15. Pod color (repeat)	Heterozygous	65	Homozygous	35					2:1
Totals for plant traits	Heterozygous	399	Homozygous	201					2:1
F$_2$ Generation of Dihybrid Experiment for Seed Shape (*A*, *a*) and Cotyledon Color (*B*, *b*)									
16a. Phenotypic	Round, yellow	315	Angular, yellow	101					
	Round, green	108	Angular, green	32					9:3:3:1
16b. Genotypic[b]	*AB*	38	*Abb*	65					
	AaB	60	*AaBb*	138					
	aB	28	*aBb*	68					
	Ab	35	*AaB*	67					
	ab	30							1:2:1:2:4:2:1:2:1
F$_2$ Generation of Trihybrid Experiment Seed Shape (*A*, *a*), Cotyledon Color (*B*, *b*), and Seed Coat Color (*C*, *c*)									
	ABC	8	*ABCc*	22	*ABbCc*	45			
	ABc	14	*AbCc*	17	*aBbCc*	36			
	AbC	9	*aBCc*	25	*AaBCc*	38			
	Abc	11	*abCc*	20	*AabCc*	40			
	aBC	8	*ABbC*	15	*AaBbC*	49			
	aBc	10	*ABbc*	18	*AaBbc*	48			
	abC	10	*aBbC*	19					
	abc	7	*aBbc*	24	*AaBbCc*	78			
			AaBC	14					
			AaBc	18					
			AabC	20					
17. Genotypic[b]			*Aabc*	14					
									1:2:1:2:4:2:1:2:1:2:4:2:4:8:4:2:4:2:1:2:1:2:4:2:1:2:1
Progeny Genotypes[b] of Reciprocal Dihybrid Testcross Experiments for Seed Shape (*A*, *a*) and Cotyledon Color (*B*, *b*), (Female Parent Listed First)									
18. *AaBb* × *AB*	*AB*	20	*ABb*	23	*AaB*	25	*AaBb*	22	1:1:1:1
19. *AB* × *AaBb*	*AB*	25	*ABb*	19	*AaB*	22	*AaBb*	21	1:1:1:1
20. *AaBb* × *ab*	*AaBb*	31	*Aab*	26	*aBb*	27	*ab*	26	1:1:1:1
21. *ab* × *AaBb*	*AaBb*	24	*Aab*	25	*aBb*	22	*ab*	27	1:1:1:1
Progeny Genotypes[b] of Dihybrid Testcross Experiments for Flower Color (*A*, *a*) and Stem Length (*B*, *b*), (Female Parent Listed First)									
22. *Aab* × *aBb*	*AaBb*	47	*Aab*	40	*aBb*	38	*ab*	41	1:1:1:1

[a] Mendel also reported data for ten individual plants from each of these experiments to illustrate the variation among plants. Because these data are a subset of Experiments 1 and 2, we have not included the data for individual plants in this table.

[b] Throughout this table, we have used Mendel's genotypic designations, which are *A* = homozygous for *A*, *Aa* = heterozygous for *A*, and *a*, *a* = homozygous for *a*, etc. Experiments 16a and 16b carry the same number because the data are from the same plants. The total number of individuals in Experiment 16b is less than in Experiment 16a because some F$_3$ seeds failed to germinate and others produced plants that failed to bear seeds.

expected ratio. After presenting the F$_2$ segregation ratios of his seven monohybrid experiments, Mendel proposed that two-thirds of the F$_2$ individuals with the dominant phenotype should be hybrids (heterozygotes) and the remaining third should be constant (homozygotes) for the trait in question, giving a ratio of 2 : 1. To test this hypothesis, he allowed F$_2$ plants with the dominant phenotypes to self-fertilize, then observed the phenotypic traits of the F$_3$ progeny. For the seed traits, cotyledon color and seed shape, this was a relatively easy task because the cotyledons of the seeds on the F$_2$ plants displayed the F$_3$ phenotypes at maturity, so there was no need for him to grow F$_3$ plants to score these traits. The five plant traits presented some difficulty because the F$_3$ phenotypes could only be scored in the F$_3$ plants. Because of limited gar-

TABLE 2. Results of chi-square tests for Mendel's *Pisum sativum* experiments.

Experiment from Table 1	Degrees of freedom	χ^2	Probability
1.	1	0.1314	0.7169
2.	1	0.0075	0.9310
3.	1	0.1954	0.6584
4.	1	0.0318	0.8586
5.	1	0.2253	0.6350
6.	1	0.1748	0.6759
7.	1	0.3033	0.5818
8.	1	0.1735	0.6771
9.	1	0.4249	0.5145
10.	1	0.3200	0.5716
11.	1	0.8450	0.3580
12.	1	2.0000	0.1573
13.	1	0.0050	0.9436
14.	1	1.2800	0.2579
15.	1	0.1250	0.7237
16a.	3	0.4700	0.9254
16b.	8	2.8110	0.9457
17.	26	15.3224	0.9511
18.	3	0.5778	0.9015
19.	3	0.8621	0.8346
20.	3	0.6182	0.8923
21.	3	0.5306	0.9121
22.	3	1.0843	0.7809

den space, Mendel chose 100 F_2 plants with the dominant phenotype for each of the five traits and grew ten F_3 descendents from each of these plants. If all ten F_3 descendents had the dominant phenotype, he classified the F_2 plant as constant (homozygous); if the F_3 descendents had both dominant and recessive phenotypes, he classified the F_2 plant as hybrid (heterozygous). One of the experiments (for pod color) yielded results that Mendel felt were too far from the predicted ratio of 2 : 1, so he repeated the experiment and obtained results that were more acceptable to him. By the conclusion of this set of six experiments (Experiments 10–15 in Tables 1 and 2), Mendel had scored the progeny of 600 F_2 plants, 399 classified as heterozygotes, and 201 classified as homozygotes, a ratio that was extremely close to his predicted 2 : 1 ratio.

Fisher (1936) explained that although the predicted ratio of 2 : 1 is genotypically correct, Mendel should have misclassified some heterozygotes as homozygotes:

> *In connection with these tests of homozygosity by examining ten offspring formed by self fertilization, it is disconcerting to find that the proportion of plants misclassified by this test is not inappreciable. If each offspring has an independent probability, .75, of displaying the dominant character, the probability that all ten will do so is* $.75^{10}$*, or 0.0563. Consequently, between 5 and 6 percent of the heterozygous parents will be classified as homozygotes, and the expected ratio of segregating to nonsegregating families is not 2 : 1, but 1.8874 : 1.1126, or approximately 377.5 : 222.5 out of 600. Now among the 600 plants tested by Mendel 201 were classified as homozygous and 399 as heterozygous. Although these numbers agree extremely closely with his expectation of 200 : 400, yet, when allowance is made for the limited size of the test progenies, the deviation is one to be taken seriously. . . . We might suppose that sampling errors in this case caused a deviation in the right direction, and of almost exactly the right magnitude, to compensate for the error in theory. A deviation as fortunate as Mendel's is to be expected once in twenty-nine trials.*
>
> —Fisher (1936, pp. 125–126)

Later in his paper, Fisher cited these experiments once again as evidence that Mendel's data were questionable:

> *A serious and almost inexplicable discrepancy has, however, appeared, in that in one series of results the numbers observed agree excellently with the two to one ratio, which Mendel himself expected, but differ significantly from what should have been expected had his theory been corrected to allow for the small size of his test progenies. To suppose that Mendel recognized this theoretical complication, and adjusted the frequencies supposedly observed to allow for it, would be to contravene the weight of evidence supplied in detail by his paper as a whole. Although no explanation can be expected to be satisfactory, it remains a possibility, among others that Mendel was deceived by some assistant who knew all too well what was expected. This possibility is supported by independent evidence that the data of most, if not all, of the experiments have been falsified so as to agree closely with Mendel's expectations.*
>
> —Fisher (1936, p. 132)

The last sentence (or part of it) is the most frequently quoted passage from Fisher's paper and is often quoted out of context. Fisher did not accuse Mendel of fraud, nor did he claim that Mendel's description of his experiments was fictitious, as later historians were to do. Nonetheless, he suspected that an assistant manipulated the data and he was most disturbed by the fact that Mendel's data in the F_2 progeny tests were biased toward a 2 : 1 ratio rather than the ratio expected when the presumed effect of Mendel's misclassification is taken into account.

A χ^2 test of Mendel's observed values of 399 and 201 and Fisher's expected values of 377.5 and 222.5 yields a χ^2 value of 3.3020 with one degree of freedom, which is not statistically significant because its probability is 0.0692. However, the probability derived from a χ^2 test is the probability of a deviation as great as or greater than the observed deviation in either direction from the expected value. Fisher's calculation of a probability of one in 29 that Mendel would observe the deviation he did assumes a deviation of both the magnitude *and in the direction* he observed. This halves the probability to 0.0346, which corresponds closely to one in 29 trials.

Fisher (1936) stated his assumption that the probability of 0.75 for each individual displaying the dominant phenotype required independence. Weiling (1986, 1989) argued that Mendel sampled ten seeds per plant without replacement in the F_3 progeny tests, and that the sampling, therefore, was not independent. He assumed that the average pea plant in Mendel's experiments had 30 seeds per plant, 23 of which had the dominant phenotype ($0.75 \times 30 = 22.5$, rounded to 23). Based on this assumption, Weiling determined that the average probability of misclassification was $23/30 \times 22/29 \times 21/28 \times 20/27 \times 19/26 \times 18/25 \times 17/24 \times 16/23 \times 15/22 \times 14/21 = 0.0381$, instead of 0.0563 as determined by Fisher.

However, although Weiling's estimate is correct for a plant with 30 seeds, 23 of which have the dominant phenotype, it cannot be used to estimate the average probability of misclassification for a population of plants. For any particular number of seeds per plant, the average probability of misclassification must be determined as the sum of the probabilities of misclassification for all possible combinations weighted by the expected frequencies of those combinations according to the binomial distribution. When this is done, the average probability of misclassification is consistently 0.0563. In other words, if Mendel's data are from random seed samples collected from a binomially distributed population, Fisher's estimate of 0.0563 as the probability of misclassification is correct, even when the effect of sampling seeds without replacement is taken into account.

Because Mendel provided data for each of the six experiments with 100 F_3 plants, we can partition the χ^2 test to examine each experiment individually, then calculate a series of χ^2 values which can then be summed and the probability determined with six degrees of freedom. Fisher (1936) partitioned these experiments in his calculation of the χ^2 values in Table 5 of his paper, but did not partition them when he concluded that "[a] deviation as fortunate as Mendel's is to be expected once in twenty-nine trials." As Piegorsch (1983) pointed out, when χ^2 values are calculated with Fisher's expectations after correction for misclassification and partitioning of the six experiments, the summed χ^2 value is 7.6582 with a corresponding probability of 0.2642 with six degrees of freedom. When this probability is halved to 0.1321, it corresponds to a probability of about one in 7.6 trials, which is not statistically significant and much less serious than that implied by Fisher's estimate of one in 29 trials.

The proximity of Mendel's F_3 progeny data to an incorrect expectation is not as questionable as it might seem when viewed in a botanical context. Fisher's analysis is based on the assumption that Mendel scored exactly ten F_3 progeny from every F_2 plant in his experiments for plant traits. However, had Mendel sown exactly ten F_3 seeds from each F_2 plant, he would have scored fewer than ten F_3 progeny in some cases because of losses due to germination failure, and his misclassification of heterozygotes as homozygotes would have been even greater than that proposed by Fisher. For example, in experiments with nine plants, Mendel would have misclassified on average 7.51% of the heterozygotes as homozygotes ($0.75^9 = 0.0751$). On the other hand, Mendel probably sowed more than ten seeds in a space to be occupied by ten plants, then thinned the seedlings to ten to ensure that there were ten F_3 progeny from each F_2 plant. Indeed, Mendel's description of his method, "*von jeder 10 Samen angebaut*" is most appropriately translated as "10 seeds were cultivated," rather than "10 seeds were sown."

Had Mendel sown more than ten seeds from each F_2 plant, then he could have scored two of the plant traits in seedlings before thinning. Differences in stem length, as Mendel noted in his paper, can be easily scored in seedlings a few days after germination. Also, as Mendel further noted in his paper, variation for seed-coat color was perfectly correlated with variation for axillary pigmentation in his experiments. Mendel could score F_3 plants for the presence or absence of axillary pigmentation as early as two to three weeks after germination and identify the phenotypes for flower color and seed-coat color that the plants would attain if grown to the flowering stage or to maturity. Indeed, almost half of the deviation from Fisher's expectations in Mendel's F_2 progeny tests comes from these two experiments, in which the 136 heterozygotes reported by Mendel exceed Fisher's expectation by ten plants (nine from the experiment for stem length). If the results of these two experiments are excluded, χ^2 values for Fisher's expectations are not statistically significant for either summed data ($\chi^2 = 1.3795$, 1 df, $P = 0.2402$) or partitioned data ($\chi^2 = 4.0687$, 4 df, $P = 0.3968$).

Fisher raised the same concern about Mendel's trihybrid experiment (Experiment 17 in Table 1). In the trihybrid experiment, Mendel determined the genotypes for all three traits (seed shape, cotyledon color, and seed-coat color) of each F_2 individual in the F_3 progeny. He could determine the seed-shape and cotyledon-color genotypes directly from the F_3 seeds on the F_2 plants (although he had to remove at least part of the opaque seed coats from the seeds on plants with colored seed coats to determine cotyledon color). However, to determine the F_2 genotypes for seed coat color he had to grow F_3 plants. Fisher (1936) speculated that Mendel must have grown ten F_3 progeny from each F_2 plant with colored seed coats, as in the F_3 progeny tests for seed-coat color (Experiment 10 in Tables 1 and 2). However, Mendel's description of his method is vague; he simply referred to it as "further investigations [*Weiteren Untersuchungen*]." Had Mendel scored exactly ten F_3 progeny from each F_2 plant with colored seed coats, the bias in his data toward an incorrect expectation is even greater than in the monohybrid F_3 progeny tests when the summed data are used ($\chi^2 = 4.9617$, 1 df, $P = 0.0259$). When halved, the probability corresponds to about one in 77 trials.

To explain the bias in the trihybrid experiment, Orel and Hartl (1994, p. 460) suggested that "if Mendel had cultivated 12 seeds per plant rather than 10, then $\chi^2 = 3.0$, for which $P > 0.05$ and the insinuation of data tampering evaporates." Fisher (1936, p. 129) recognized this possibility, stating in reference to the trihybrid experiment that "if we could suppose that larger progenies, say fifteen plants, were grown on this occasion, the greater part of the discrepancy would be removed. However, even using families of 10 plants the number required is more than Mendel had assigned to any previous experiment." Fisher's concern in this passage is Mendel's lack of garden space for growing the large number of plants required for this experiment (4730 F_3 plants if he grew ten F_3 plants from each F_2 plant that had colored seed coats).

Hennig (2000) raised an additional concern about this experiment, questioning why Mendel chose seed-coat color as the third trait for analysis in a trihybrid experiment. It created more work for Mendel than the other traits plant traits because for many of the seeds he had to remove part of the seed coats to score seed color. Also, "he would know about the first two components of his trihybrid cross (pea shape and color) more than nine months before he found out about the third" (Hennig, 2000, p. 127).

However, we can dismiss Fisher's concern about lack of garden space and Hennig's concern about a nine-month delay in scoring when we consider that Mendel could distinguish the plants in question for presence or absence of axillary pigmentation as seedlings. Because this trait can be scored in seedlings, it is an excellent choice for the third trait in the trihybrid experiment because it creates at most a three-week delay between data collection for the first two traits and the third. Garden space is not as critical because many seedlings can be grown in the space occupied by a single mature plant. Mendel probably harvested the F_3 seeds for this experiment in July or early August. Had he planted the seeds in the garden soon after harvest, he could have scored the seedlings for axillary pigmentation within three weeks, long before cold weather affected the plants. Alternatively, Mendel had a 27.5 × 4.5 m greenhouse available to him (Orel, 1996) and he could have grown as many as 15–20 seedlings per pot for scoring in the greenhouse during the fall and winter months. If he had allotted one pot for the F_3 seedlings from each F_2 plant, he had more than ample space in the greenhouse for the 473 pots required for this experiment.

When these statistical and botanical aspects of Mendel's F_3 progeny tests are considered, there is no reason for us to question his results from these experiments. However, we must still account for the bias that is evident when the data for all of the experiments that he reported are compared as a whole (Table 2). After Fisher, numerous authors have sought reasonable explanations for the bias in Mendel's data that do not imply fraud, but most cannot withstand botanical or historical scrutiny.

Wright (1966) and Beadle (1967) proposed that Mendel might have unconsciously misclassified individuals with questionable phenotypes to favor his expectations. From a botanical point of view, this explanation can account for only a negligible degree of bias. The five plant traits display very distinct phenotypes in multiple positions within each plant so that each plant's phenotype can be readily identified without error. The two seed traits, seed shape and cotyledon color, however, are potentially subject to misclassification of phenotypes. Round seeds often have indentations that under certain circumstances might lead an untrained researcher to misclassify a round seed as being wrinkled. Also, some seeds whose genotype should confer a round-seed phenotype do not fully develop in the pod and may appear wrinkled. However, such seeds have irregular wrinkles, and Mendel used for his seed-shape experiments varieties with seeds that have regular angular wrinkles (in Mendel's words, *kantig runzlig Samen*). Angular wrinkled seeds have a cube-shaped phenotype and for this reason were classified as *Pisum quadratum* in Mendel's day. Under these circumstances, the number of seeds that Mendel misclassified for seed-shape phentotypes was probably negligible.

The trait most likely to be misclassified is cotyledon color because it is subject to some degree of environmental variation. Green seeds may turn yellow when mature plants are left unharvested too long in the sun. Yellow seeds may appear green if they are harvested before reaching full maturity. Mature pea seeds of some varieties may have segments of green and yellow coloration in the cotyledons. Mendel was aware that misclassification of seed color was possible: ''in individual seeds of some plants green coloration of the albumin is less developed and can be easily overlooked.'' However, he dismissed the possibility of misclassification of cotyledon color, stating in reference to this trait that ''with a little practice in sorting, however, mistakes are easy to avoid'' (Stern and Sherwood, 1966, p. 12).

Also, because of his experimental design, Mendel only could have misclassified cotyledon color and seed shape in a limited number of individuals. For some of the F_2 individuals in his monohybrid experiments and for all individuals in his dihybrid and trihybrid experiments, Mendel identified not only the phenotypes, but also the genotypes of individual seeds through examination of their self-fertilized progeny. This procedure would have allowed him to correct any initial phenotypic misclassifications for individuals whose genotype had been determined.

Olby (1985) and Beadle (1967) suggested that Mendel might have stopped counting individuals when the numbers were close to the ratios he expected. However, as Campbell (1985) and Orel (1996) pointed out, Mendel explicitly denied this practice when he wrote near the beginning of his paper, ''To discover the relationships of hybrid forms to each other and to their parental types it seems necessary to observe *without exception all* members of the series of offspring in each generation'' (Stern and Sherwood, 1966, p. 4).

Despite this statement Olby (1985) claimed that the data for Mendel's seed shape experiment indicate that he indeed did not count all of the individuals in this experiment:

> *If Mendel stopped recording his seeds before he had exhausted the material, one would expect that his totals would be less than that of an average crop for the population of mother plants grown. This is so. Mendel stated that fully ripe pods contained between 6 and 9 seeds. If we take 6 as the average number, in order to make an allowance for unripe pods, then the 7,324 seeds which Mendel harvested from 253 plants would have come from 1046 pods, thus giving 4 to 5 pods per plant.*
>
> —Olby (1985, p. 211)

Olby considered this estimate of pods per plant to be too small, implying that Mendel did not count all of the seeds in this experiment. Di Trocchio (1991) raised a similar concern:

> *From a calculation made by Margaret Campbell* [1976], *it appears that Mendel obtained an average of 28 to 37 seeds per plant. . . . If the pea plant actually produced so few seeds, this vegetable would be a rarity in the markets! Instead, we know that each plant produces on average more than 60 pods, and Mendel himself informs us that his plants produced pods that contained an average of 6–9 seeds; he would therefore have obtained at least 400–500 seeds from every plant.*
>
> —Di Trocchio (1991, p. 504)

If all the information provided by Mendel on numbers of seeds per plant is taken into account, the average number of seeds per plant is close to 30 (16 590 seeds divided by 550 plants = 30.16 seeds per plant from the monohybrid, dihybrid, and trihybrid experiments for seed shape and cotyledon color). Is 30 seeds per plant too low for 19th century pea cultivation? Fisher (1936, p. 123) addressed this question and quoted Dr. J. Rasmussen, a pea geneticist, who wrote to Fisher: ''About 30 good seeds per plant is, under Mendel's conditions (dry climate, early ripening, and attacks of *Bruchus pisi*) by no means a low number.''

Olby's and Di Trocchio's estimates that the average number of seeds per pod in Mendel's experiments is six to nine are based a passage in ''Versuche'':

> *In these two experiments* [Experiments 1 and 2 in Table 1] *each pod usually yielded both kinds of seed. In well-developed pods that contained on the average, six to nine seeds, all seeds were fairly often round (Experiment 1) or all yellow (Experiment 2); on the other hand, no more than 5 angular or 5 green ones were ever observed in one pod.*
>
> —Stern and Sherwood (1966, p. 11)

According to Mendel, the average number of seeds per pod was not six to nine for all pods, but rather for ‘‘well-developed pods [*gut ausbebildeten Hülsen*].’’ His point in this passage was not to give the average number of seeds per pod in all of his experiments, but to illustrate variation for phenotypic ratios within well-developed pods that have a relatively large number of seeds. The average number of seeds per pod in all of Mendel's experiments was probably between three and four, which results in an average number of about seven to ten pods per plant.

We searched for a significant body of data collected during the 19th century on numbers of seeds per pod, pods per plant, and seeds per plant in *Pisum sativum.* The earliest data we found were from a field test of 24 garden-pea varieties conducted at the New York Agricultural Experiment Station in Geneva, New York during 1888 (Curtis, 1889). The average number of seeds per pod was 4.47, the average number of pods per plant 10.82, and the average number of seeds per plant 47.18, averages that are only slightly higher than those Mendel observed. This confirms Rasmussen's claim. Of the 24 varieties tested, four produced averages of less than 30 seeds per plant. Therefore, although Olby's and Di Trocchio's skepticism about the average number of seeds per plant in Mendel's data might be valid for modern pea varieties grown under conditions of high fertility, the number of seeds per plant reported by Mendel cannot be considered unreasonably low for pea varieties grown in the 19th century.

Another explanation of the bias in Mendel's data is botanical. Sturtevant (1965), Thoday (1966), and Weiling (1989, 1991) proposed that because pollen grains are produced in tetrads that consist of the four products of a meiotic event, and because the mature pollen grains from a tetrad may remain juxtaposed following dehiscence, there is a possibility that ovules in a self-pollinated pea flower may be fertilized by two or more pollen grains from the same tetrad. This model has often been called the ‘‘urn model’’ because it is analogous to a person sampling items without replacement from an urn. If such an event is common in pea fertilization, it could bias genetic data away from binomial distributions and toward mean ratios. Beadle (1967) determined that such an effect is insufficient to explain the bias in Mendel's data. There is currently no empirical evidence to support the urn model in *Pisum,* but it is one that can be empirically tested because it should produce a significant deviation from a binomial distribution for phenotypes of individual seeds from the same pod (or plants grown from those seeds). We have initiated the necessary experiments but do not yet have the results.

We believe that the most likely explanation of the bias in Mendel's data is also the simplest. If Mendel selected for presentation a subset of his experiments that best represented his theories, χ^2 analyses of those experiments should display a bias. His paper contains multiple references to experiments for which he did not report numerical data, particularly di- and trihybrid experiments. For example, he conducted dihyrid or trihybrid experiments for all combinations of the seven characters he studied. However, he reported data for only one dihybrid and one trihybrid experiment. In his words: ‘‘Several more experiments were carried out with a smaller number of experimental plants in which the remaining traits were combined by twos or threes in hybrid fashion; all gave approximately equal results’’ (Stern and Sherwood, 1966, p. 22). He also conducted dihybrid testcross experiments with all seven traits but reported only those for seed shape and cotyledon color, and flower color and stem length: ‘‘Experiments [dihybrid testcrosses] on a small scale were also made on the traits of *pod shape, pod color*, and *flower position,* and the results obtained were in full agreement: all combinations possible through union of the different traits appeared when expected and in nearly equal numbers’’ (Stern and Sherwood, 1966, p. 29). In his second letter to Nägeli (Stern and Sherwood, 1966), Mendel described a true-breeding genotype that he obtained in 1859 (the fourth year of his experiments) from a tetrahybrid experiment for cotyledon color, seed coat color, pod shape, and stem length. He did not report the results of this or any other tetrahybrid experiment in his paper. He described in the concluding remarks of his paper a pentahybrid reciprocal backcross experiment carried through several generations, but he only reported a few selected data from this experiment. He also reported in his paper that he conducted experiments on the timing of flowering, peduncle length, and brownish-red pod color but he likewise did not report the data for these experiments.

Mendel made it very clear that the data reported in his paper are from a subset of experiments that he conducted. In Mendel's second letter to Nägeli, he referred to his paper as ‘‘the unchanged reprint of the draft of the lecture mentioned; thus the brevity of the exposition, as is essential for a public lecture’’ (Stern and Sherwood, 1966, p. 61). Had he included all of his data, the paper would have been much longer. Mendel's choice to present data from a subset of his experiments created a bias that was detected only when 20th century scientists subjected his data to statistical analysis.

Several authors have been quick to label Mendel as a fraud on the basis of Fisher's analysis. As examples, Orel (1996) cited articles by Doyle (1968, ‘‘Too many small χ^2's or hanky-panky in the monastery?’’) and Gardner (1977, ‘‘Great fakes of science’’), and a book by Broad and Wade (1983, *Betrayers of the Truth*). Orel (1996, p. 207) then stated, ‘‘These selected examples show how great scientific achievements can be discredited by dilettantes who claim a combination of two incompatibles: the rigorousness of a meticulous scientist, and falsification of the results.’’ We conclude that, although the bias in Mendel's experiments is evident, there are reasonable statistical and botanical explanations for the bias, and insufficient evidence to indicate that Mendel or anyone else falsified the data.

IS MENDEL'S DESCRIPTION OF HIS EXPERIMENTS FICTITIOUS?

Some authors claim that although the data in Mendel's paper may be accurate, his description of the experiments is fictitious. This assertion stems mostly from suppositions about his monohybrid experiments. A monohybrid experiment is one in which two homozygous individuals that differ from each other in only one trait are hybridized. The F_1 progeny are called monohybrids and are heterozygous for only one of the genes under study.

After reporting the results of his monohybrid experiments on each of the seven traits, Mendel wrote, ‘‘In the experiments discussed above, plants were used which differed in only one essential trait [*wesentliches Merkmal*]’’ (Stern and Sherwood, 1966, p. 17). Several authors doubt Mendel's claim and argue that he did not conduct true monohybrid experiments. The first to do so was William Bateson, the most ardent defender of Mendelism in the first decade of the 20th century. In a footnote to the Royal Horticultural Society's English translation of Mendel's paper, Bateson (1913) referred to Mendel's claim:

> *This statement of Mendel's in light of present knowledge is open to some misconception. Though his work makes it evident that such varieties may exist, it is very unlikely that Mendel could have had seven pairs of varieties such that the members of each pair differed from each other in only one considerable character* (wesentliches Merkmal).
>
> —Bateson (1913, p. 350)

In the introduction to his paper, Fisher (1936) quoted Bateson's statement that Mendel's experiments might be fictitious and proposed that a reconstruction of Mendel's experiments might determine whether or not they were. After a detailed analysis and proposed reconstruction of the experiments, Fisher concluded that ''there can, I believe, be no doubt whatever that his report is to be taken entirely literally, and that his experiments were carried out in just the way and in much the order that they are recounted'' (p. 132).

Half a century later, Corcos and Monaghan (1984) resurrected Bateson's claim and held it to be of ''considerable importance.'' They entitled their paper ''Mendel had no 'true' monohybrids'' and concluded that Mendel's '' 'monohybrid' experiments were performed with varieties [that differed] in several traits but that in each offering he concentrated his attention on only one'' (p. 499).

Such claims that Mendel's experiments were fictitious have little foundation when viewed from a botanical perspective. Taken in the context of Mendel's paper, we must interpret his statement that ''plants were used which differed in only one essential trait'' as meaning that each pair of parental varieties used for the monohybrid experiments differed from each other in only one of the seven traits he studied. Much of the confusion on this issue arises from the fact that *Pisum sativum* is a domesticated species and among the many cultivated varieties there are several different phenotypes. Bateson's claim, which other authors have accepted (Corcos and Monaghan, 1984; Di Trocchio, 1991; Bishop, 1996), is based on the notion that the pea varieties available to Mendel were so highly varied that he could not have paired his pea varieties to create seven monohybrid experiments.

Contrary to this claim, the nature of variation in pea varieties (both old and modern) facilitates, rather than prevents, the construction of monohybrid experiments. Pea varieties fall into three general categories: garden varieties (also called shelling varieties), field varieties, and sugar varieties. Most garden varieties have white seed coats (also white flowers and no axillary pigmentation), inflated pods, green pods, and axillary flowers; they vary for seed shape, cotyledon color, and stem length. White seed coats are desirable for garden varieties because colored seed coats can discolor the cooked peas. Inflated pods are desirable because they facilitate shelling unripe peas from the pod. Because garden varieties typically do not vary for seed-coat color, pod shape, pod color, and flower position, Mendel could easily design monohybrid experiments among them for seed shape, cotyledon color, and stem length. Garden varieties with all possible combinations of the differing phenotypes for these three traits were readily available in Mendel's day and still are available among modern commercial garden varieties. Field varieties were used mostly as fodder in Mendel's day and they typically display the dominant phenotypes for all seven traits. Many sugar varieties also display the dominant phenotypes for all traits except pod shape. Thus, Mendel's monohybrid experiment for pod shape may have included a field variety and a sugar variety as parents. There are several possibilities for Mendel's monohybrid experiment for seed-coat color. He could have hybridized a field variety with a garden variety that differed only for seed-coat color. Also, sugar varieties with white seed coats were available in his day, so he could have used two sugar varieties that differed only for seed-coat color. Varieties with terminal flowers have always been rare novelties. The most readily available terminal-flowered variety in the 19th century was called the Mummy Pea and it is probably the variety that Mendel used. White (1917) described two Mummy varieties, one with white flowers and one with colored flowers. The colored-flower variety was the one probably available to Mendel, and this variety differs from most field varieties only in flower position. Thus Mendel could have easily designed a monohybrid experiment for flower position. Most pea varieties have green pods. However a few garden and sugar varieties, called gold varieties, have yellow pods. Mendel could have matched any one of the gold varieties with another garden or sugar variety in a monohybrid experiment. A mathematical minimum of eight varieties is required for seven monohybrid experiments. We conclude that Mendel could have easily designed and conducted seven monohybrid experiments with 22 varieties at his disposal.

Di Trocchio (1991) accepted the argument of Bateson (1913) and Corcos and Monaghan (1984) that Mendel's experiments were fictitious. He then took the argument a step further, claiming that instead of conducting monohybrid experiments, Mendel must have hybridized the 22 varieties in all possible combinations, then disaggregated the data into fictitious mono-, di-, and trihybrid experiments in his presentation, for the sake of simplicity. Bishop (1996) used Di Trocchio's (1991) proposed reconstruction of Mendel's experiments as evidence that Mendel began his experiments in 1861 and conducted them over a period of four years. Mendel stated in ''Versuche'' that he conducted his experiments over a period of eight years, and he clarified the dates as 1856–1863 in his second letter to Nägeli (Stern and Sherwood, 1966). Bishop argued that the dates in Mendel's second letter to Nägeli must have been wrong and that Mendel wrote them because the letter was ''obviously a defensive response to the latter's [Nägeli's] criticism'' (Bishop, 1996, p. 206). Bishop's claim that Mendel's experiments as reported in his paper were fictitious was part of an attempt to demonstrate that they were inspired by his reading Darwin's (1859) *On the Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life* (hereafter referred to as the *Origin*). Bishop surmised that Mendel was inspired by Darwin's work in 1861 (when Mendel may have first heard of Darwin's theory of natural selection in a lecture) and that he thereafter began his experiments to counter Darwin's theory and promote the theory of special creation.

Di Trocchio's (1991) and Bishop's (1996) claim that Mendel hybridized his 22 varieties in all possible combinations runs counter to the experimental design that Mendel described and the logic on which it is based. Mendel first tested each trait individually in monohybrid experiments, then subsequently combined traits in twos and threes to determine whether the patterns of inheritance were independent. When he began his monohybrid experiments, he probably did not know whether or not the inheritance of one trait influenced the inheritance of another. Monohybrid experiments were essential to his experimental design if he intended to study the inheritance of a particular trait in the absence of any possible confounding influences from other differing traits. Once he had determined that the inheritance of each trait in isolation followed the same pattern, he could then study the patterns of inheritance for combinations of two or more traits. Taken literally, Mendel's account describes a well-conceived experimental design that would not have been difficult for him to perform.

DID MENDEL ARTICULATE THE LAWS OF INHERITANCE ATTRIBUTED TO HIM?

The two laws of inheritance most often attributed to Mendel are segregation and independent assortment. The law of segregation, stated in modern terms, is the idea that during meiosis two alleles of a single locus, one inherited from each parent, pair with each other, and then segregate from one another into the germ cells so that each germ cell carries only one allele of that locus. Segregation in heterozygous individuals produces in equal proportions two different types of gametes, each with one of the two alleles. The law of independent assortment, stated in modern terms, is the idea that the segregation of alleles of a single locus has no influence on the segregation of alleles at another locus. The result is completely random and uniform combinations of alleles of different loci in the self-fertilized progeny of dihybrid (or multihybrid) individuals.

Several authors question Mendel's articulation of these laws. Olby (1985) attributed segregation of character elements (not necessarily what we now perceive as alleles) to Mendel:

> *The whole theory rests on one inference which no one else had the thought of making. It was simply the prediction of the number of different forms that would result from the random fertilisation of two kinds of ''egg cells'' by two kinds of pollen grains. Naudin had postulated the segregation of specific essences in the formation of germ cells; Mendel postulated the segregation of character elements.*
>
> —Olby (1985, p. 101)

However, although Olby attributes the laws of inheritance to Mendel, he also concluded that ''the laws of inheritance were only of concern to him [Mendel] in so far as they bore on his analysis of the evolutionary role of hybrids,'' and that ''Mendel did not have the conception of pairs of factors or elements determining his pairs of contrasted characters'' (Olby, 1979, p. 67). (Monaghan and Corcos (1990, p. 268) fully rejected the idea that Mendel articulated the laws of segregation and independent assortment, stating that ''he [Mendel] did not explain his results by employing invisible particulate determiners, paired or otherwise,'' and that ''the traditional Mendelian laws of segregation and independent assortment are not given in the paper.'' They also concluded that ''the first Mendelian law, the law of segregation is not present anywhere in Mendel's paper. That it cannot be found has been said many times by quite a few writers'' (p. 287). Callender (1988, pp. 41–42) called it ''the myth of 'Mendel's Law of Segregation'; a law not to be found in either of Mendel's papers, nor in his scientific correspondence, nor in any statement that can be unambiguously attributed to him.'' Monaghan and Corcos (1990, 1993) claimed that two of Mendel's rediscoverers, DeVries (1900) and Correns (1900), were the first to articulate the law of segregation and that Thomas Hunt Morgan (1913) was the first to articulate the law of independent assortment.

The claim that Mendel did not articulate or perceive the law of segregation in his interpretation of his experiment is based in part on the difficulty that modern readers have finding in Mendel's paper statements that resemble the current concept of segregation. Genetic terms, such as *allele, locus,* and *chromosome*, had not been coined in Mendel's day, nor was the cellular process of meiosis understood. Therefore, we must look for statements in Mendel's paper indicating that he perceived paired hereditary factors that segregate from one another during the formation of germ cells.

As pointed out by Olby (1985), Hartl and Orel (1992), Orel and Hartl (1994), Weiling (1994), and Fairbanks and Andersen (1999), Mendel referred to segregation of hereditary elements several times in his paper. We (along with Olby, 1985) believe that the clearest statement is in the concluding remarks of ''Versuche'':

> *One could perhaps assume that in those hybrids 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 and Sherwood (1966, p. 42–43)

Those who search for statements on segregation in Mendel's paper often overlook this paragraph, probably because it is near the end of the paper embedded in a discussion in which Mendel attempted to reconcile his observations of predictable variation in the offspring of hybrids with those of other hybridists who reported that some hybrids breed true. Also, some reprints of English translations of Mendel's paper omit the part of his paper that includes this paragraph (for example, see Peters, 1959). This paragraph, however, is a remarkably lucid summary of the law of segregation. Mendel's reference to ''potentially formative elements [*bildungsfähigen Elemente*]'' implies the existence of invisible particulate determinants of inherited traits. We might well view the term ''element [*Element*],'' which Mendel used five times in this passage, as the equivalent of the modern term ''allele.'' This view is reinforced by Hennig's (2000) observation that Mendel used the German term *Element* only ten times in his paper, all near the end of the paper in reference to the plant's genotype. Mendel's reference to the ''enforced association [*erzwungenen Verbindung*]'' of differing elements indicates that he perceived the differing elements as being paired in hybrids (heterozygotes). His statement that differing elements ''separate from each other [*sich gegenseitig ausschliessen*]'' shows a clear understanding of segregation that is similar to the modern view. He also correctly recognized that segregation takes place ''only at the stage at which the reproductive cells develop'' (i.e., during meiosis).

This paragraph, however, reveals one aspect of Mendel's perception that differs from the modern concept of segregation. According to the modern concept, alleles at a single locus, whether different as in heterozygotes or the same as in homozygotes, segregate from one another during meiosis. The above passage suggests that Mendel perceived segregation as an anomaly restricted to hybrids (heterozygotes). He called the differing elements ''antagonistic elements [*widerstrebenden Elemente*]'' whose association in the hybrid is a ''compromise [*Vermittlung*],'' and wrote that ''only those elements that differ separate from one another,'' statements that, rephrased in modern terms, suggest that only those alleles in the heterozygous condition, and not those in the homozygous condition, are paired and segregate from one another.

In the paragraph that precedes the one we cited, Mendel explained his understanding of this concept:

> *When the reproductive cells are of the same kind and like the primordial cell of the mother* [i.e., a homozygous cell], *development of the new individual is governed by the same law that is valid for the mother plant. When a germinal cell is successfully combined with a* dissimilar *pollen cell we have to assume that a compromise takes place between those elements of both cells that cause their differences. The resulting mediating cell* [heterozygous cell] *becomes the basis of the hybrid organism whose development must necessarily proceed in accord with a law different from that of the two parental type.*
>
> —Stern and Sherwood (1966, p. 42)

Mendel's apparent perception of segregation as a phenomenon restricted to heterozygotes sheds light on another aspect of his paper. Although Mendel represented heterozygotes with a two-letter designation (*Aa*), as modern geneticists usually represent them, he consistently represented homozygotes with a single letter (*A* or *a*), rather than the two letters (*AA* or *aa*) used today. For example, Mendel represented the genotypic ratio of the F_2 generation of a monohybrid experiment as $A + 2Aa + a$, instead of $AA + 2Aa + aa$. According to the passage above, Mendel may have concluded that like elements (alleles) do not pair with one another and do not segregate in plants that are not hybrids (i.e., are not heterozygotes), and that therefore a single letter was an accurate way to represent such plants. Hartl and Orel (1992, p. 250) defended Mendel's understanding of segregation, reminding us that Mendel was not aware of chromosomes, and when the law of segregation is stated only in terms of different alleles, rather than in terms of chromosomes, ''Mendel's view of segregation occurring only in the heterozygotes (i.e., with different alleles) could easily be defended as being completely consistent even with the modern use of the term.''

Although many authors have overlooked the passage we cited above, in which Mendel described the law of segregation, few have missed the following often-quoted statement of independent assortment, which Olby (1979) called the climax of Mendel's paper. This statement appears immediately after Mendel's presentation of his di- and trihybrid experiments:

> *In addition, several more experiments were carried out with a smaller number of experimental plants in which the remaining traits were combined by twos and threes in hybrid fashion; all gave approximately equal results. Therefore there can be no doubt that for all traits included in the experiment, this statement is valid:* The progeny of hybrids in which several essentially different traits are united represent the terms of a combination series in which the series for each pair of differing traits are combined. *This also shows at the same time that* the behavior of each pair of differing traits in a hybrid association is independent of all other differences in the two parental plants.
>
> —Stern and Sherwood (1966, p. 22)

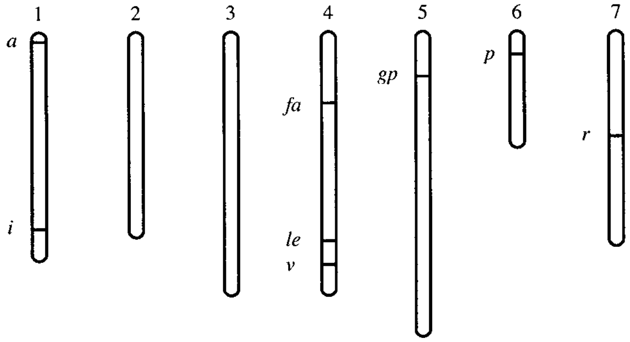

Fig. 1. Chromosomal locations of the genes that Mendel studied.

Mendel's liberal use of italics in this passage (reverse italics in our quotation) indicates that he wished to emphasize his conclusion of the independent inheritance of different traits.

DID MENDEL DETECT BUT NOT MENTION LINKAGE?

Linkage is defined as a significant deviation from independent assortment due to proximity of genes on the same chromosome. In his statement on independent assortment quoted above, Mendel concluded that for all of the traits he studied ''the behavior of each pair of differing traits in a hybrid association is independent of all other differences in the two parental plants'' (Stern and Sherwood, 1966, p. 22). Scientists have often been intrigued by the notion that Mendel studied seven traits in a species that has a haploid number of seven chromosomes, implying that Mendel discovered one gene on each of the seven chromosomes, and for this reason he observed independent assortment. According to some accounts, had he chosen to study just one more trait he would have detected linkage. Dunn (1965), under the assumption that Mendel studied one gene on each of the seven chromosomes, calculated the probability of doing so as $6/7 \times 5/7 \times 4/7 \times 3/7 \times 2/7 \times 1/7 = 0.0061$ (<1%), again calling Mendel's experimental results into question.

However, based on genetic maps of pea chromosomes, Nilsson (1951), Lamprecht (1968), Blixt (1975), and Novitski and Blixt (1979) showed that Mendel did not study one gene per chromosome. Instead, he studied two genes on chromosome 1 (*a* and *i*), no genes on chromosomes 2 and 3, either two genes (*fa* and *le*) or three genes (*fa, le,* and *v*) on chromosome 4, one gene (*gp*) on chromosome 5, possibly one gene (*p*) on chromosome 6, and one gene (*r*) on chromosome 7 (Fig. 1). The gene in doubt is the one that governs pod shape. Recessive alleles of the *v* gene on chromosome 4 and the *p* gene on chromosome 6 both confer constricted (unparchmented) pods when homozygous, and it is not known which of the two Mendel studied.

The idea that two genes on the same chromosome are necessarily linked is a common misconception. Genes on the same chromosome are said to be syntenic but are linked only if they are so close to one another that the frequency of crossovers between them is significantly less than the frequency of recombination for independent assortment. The genetic map distance at which linkage cannot be detected depends on the type of experimental population, the number of individuals in the experimental population, the degree of undetected double crossovers, and several other factors. In most testcross experiments (the most reliable type of linkage experiment), linkage often cannot be distinguished from independent assortment for genes located more than ~60 cM (centiMorgans) apart unless researchers use large numbers of progeny and a mapping function that is appropriate for the species under study. The two genes that Mendel studied on chromosome 1, *i*, which governs seed color, and *a*, which governs flower color, are 204 cM apart, so distant that they assort independently. The same is true for two of the genes that Mendel studied on chromosome 4; *fa*, which governs flower position, and *le*, which governs stem length, are 121 cM apart.

Given the traits he studied, Mendel would not have detected linkage if he studied the *p* gene, which governs pod shape, on chromosome 6. He could have observed one case of linkage if he studied the *v* gene, which also governs pod shape. The *v* gene is located 12 cM from the *le* gene on chromosome 4. Novitski and Blixt (1979) compared the arguments favoring the *p* gene with those favoring the *v* gene for Mendel's studies and concluded that either scenario was possible. Because the varieties that Mendel used are not known, the question as to which of these two genes he studied is not likely to be resolved.

However, let's suppose that Mendel did study the *v* gene and thus had the opportunity to observe linkage. As Novitski and Blixt (1979) pointed out, Lamprecht (1968) reported that observed recombination between *le* and *v* may vary from 2.6 to 38.5% and that, according to Lamprecht (1941), the mutation rate for *v* may be as high as 40%. Had either or both of these values been on the higher side in Mendel's experiments, he would not have detected linkage for the *v* and *le* genes.

Also, Mendel conducted his experiments with F_2 progeny, which are not as reliable for detection of linkage as are testcross progeny. Although Mendel did not report data for his experiment with stem length and pod shape, we are fortunate that he described such an experiment in his second letter to Nägeli. The experiment was a tetrahybrid experiment in which one parental variety had green cotyledons, white seed coats, inflated pods, and short stems, and the other had yellow cotyledons, colored seed coats, constricted pods, and long stems. Mendel obtained a true-breeding F_3 plant in 1859, the fourth year of his experiments, that had yellow cotyledons, white seed coats, inflated pods, and long stems. Thus, the dominant alleles for pod shape and stem length, if they were linked, were in repulsion conformation in the F_1 generation and were recombined into coupling conformation in the true-breeding descendent that Mendel described.

Linkage for loci that are 12 cM apart in repulsion conformation may escape detection in an F_2 population because recombination frequencies differ by only 5.89% from those for independent assortment (Fairbanks and Andersen, 1999). If, as Mendel stated, he examined a small number of individuals in this experiment and he observed at least one recombinant type (the true-breeding descendent mentioned in his letter to Nägeli), he probably did not detect linkage, if indeed the genes he studied were linked.

Di Trocchio (1991, p. 506) raised another question about linkage and from it drew an unusual conclusion to support his case that Mendel's experiments were fictitious: "we must determine why Mendel did not perform other hybridization experiments with an eighth, ninth, or tenth character in order to test the general validity of his law. This is a particularly intriguing question since we know that crosses with a number of characters higher than seven would quite surely have shown linkage." Di Trocchio concluded that "Mendel did find linkage, but he discarded it as senseless in order to concentrate on the only evident regularity—namely, 3:1 ratio. In doing so he thus chose, from among all the characters he experimented on, the famous seven non linked traits" (p. 511).

For us to evaluate such claims, it is useful to determine how Mendel chose the traits he studied. Did he choose them because their inheritance obeyed the laws he wished to illustrate (as Di Trocchio claimed), or did he choose them for other reasons? One way to answer this question is to examine which traits other pea hybridists who had no knowledge of Mendel's work chose to study. Roberts (1929) reviewed the work of plant hybridists who published their results before Mendel and described the traits that they studied. Among the hybridists before Mendel are several who studied pea. Knight (1799, 1823) studied seed coat color and described the phenomenon of dominance. Goss (1824) studied cotyledon color and described dominance, as well as segregation, although in purely qualitative terms. Seton (1824) studied stem length and cotyledon color. Gärtner (1849) reviewed Knight's work with seed coat color, and described his own work in *Pisum* with stem length, flower color, cotyledon color, and seed shape. Mendel studied Gärtner's (1849) book on plant hybridization in detail before and during his experiments, as he indicated in his first letter to Nägeli and as evidenced by his 17 references to it in "Versuche." Thus, he was familiar with both Knight's and Gärtner's pea hybridization experiments. We examined Mendel's copy of Gärtner's book and found numerous marginalia throughout it. On the page facing the back cover are Mendel's handwritten notes about traits in *Pisum*, which, as translated by Olby (1985) read:

> Pisum arvense: *flowers solitary, wings red.*
> Pisum arvense et sativum: *pods almost cylindrical, in* Pisum umbellatum *Mill. [terminal-flowered varieties] cylindrical and straight; in* saccharatum *Host. [sugar varieties] Straight, ensiform, constricted on both sides. (var.* flexuosum *Willd. sickle-shaped, seeds small, angular); in Pisum quadratum Mill. [wrinkled-angular seeded varieties] straight, ensiform, not constricted, seeds pressed tightly together. In* Pisum sativum *and* arvense *the bases of the stipules rounded and denticulate-crenate, stipules cordate. In* saccharatum *and* quadratum, *stipules obliquely incised, pods pressed flat. In* sativium, saccharatum *and* umbellatum, *seeds round.*
>
> —Olby (1985, pp. 212–213)

Mendel studied all four traits that previous hybridists had studied, seed shape, cotyledon color, stem length, and seed-coat color (also flower color). His handwritten note mentions flower color, pod shape, and seed shape, and flower position is implied in the note by his mentioning *P. umbellatum.*

The following comment from Mendel's paper about the monohybrid experiments reveals information about the order of his monohybrid experiments: ''Experiments 1 and 2 [seed shape and cotyledon color] have by now been carried through six generations, 3 and 7 [seed coat color and stem length] through five, and 4, 5, and 6 [pod shape, pod color, and flower position] through four'' (Stern and Sherwood, 1966, pp. 15–16). The generation for seed traits can be scored one growing season earlier than that for plant traits, so Mendel must have initiated the monohybrid experiments for seed shape, cotyledon color, seed coat color, and stem length (the same traits that Gärtner studied) in the first year of his hybridization experiments, and the monohybrid experiments for the three remaining plant traits in the following year.

The four traits studied by previous hybridists were the same four traits that Mendel used in his first year of hybridization. The remaining three traits, pod shape, pod color, and flower position, were not among those studied by previous hybridists, and Mendel initiated experiments on them during the following year. This reconstruction argues against Di Trocchio's (1991, p. 508) assertion: ''It is likely, in fact, that he [Mendel] planned his hybridization experiments following the checkerboard method. A checkerboard of 22 × 22 squares represents all of the crosses.'' Several other items in Mendel's paper also argue against Di Trocchio's assertion. According to statements in Mendel's paper, the varieties he used as parents for his monohybrid experiments for seed color did not include varieties with colored seed coats (because the opaque colored seed coats prevent observation of cotyledon color), and those he used for his monohybrid experiments for stem length did not include those with intermediate stem lengths.

The type of analysis that Mendel conducted relies on traits that display discontinuous variation, as does detection of linkage. The traits that Mendel chose to study are among only a few that varied in a discontinuous fashion among commercially available 19th century varieties. Mendel's varieties certainly differed in more than the seven traits on which he reported data. However, most of the other traits display continuous variation and are governed by multiple genes and environmental influences and cannot be easily analyzed in a simple Mendelian fashion. Mendel listed a number of these traits in his paper, then stated that he could not clearly analyze such traits: ''However, 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 and Sherwood, 1966, pp. 5–6).

Mendel's choice of traits apparently was based first on those studied by his predecessors and second on those that had distinct discontinuous phenotypic differences that permitted conclusive analysis. Because of the locations of the genes that governed such traits and the design of his experiments, it is unlikely that he could have detected linkage. There is no botanical or historical evidence to support the claim that Mendel observed and then disregarded linkage.

DID MENDEL SUPPORT OR OPPOSE DARWIN?

We addressed the four previous controversies in botanical contexts. This final controversy is purely historical, but it is widely debated by the same authors who address botanical issues and they have related their conclusions on botanical issues to this issue. Thus, we also are compelled to include it. Mendel and Darwin were contemporaries and both addressed evolutionary questions in their work. Twice in ''Versuche'' Mendel used the term ''*Entwicklungsgeschichte,*'' which in the English translations of ''Versuche'' is rendered as ''evolution'' or ''evolutionary history.'' One of the passages with this term appears near the beginning of ''Versuche'' where Mendel referred to his experiments as ''the one correct way of finally reaching the solution to a question whose significance for the evolutionary history [*Entwicklungs-Geschichte*] of organic forms must not be underestimated'' (Stern and Sherwood, 1966, p. 2).

Thus, Mendel was clearly interested in evolution and he considered his experiments as relevant to an understanding of evolution. At the time Mendel wrote his paper, the *Origin* was well known and evolution through natural selection was a popular topic for discussion in scientific societies. Alexander Makowsky, who was a student at the same school as Mendel and was among his closest friends, presented a lecture that favorably treated Darwin's theory of natural selection to the Brünn Natural History Society the month before Mendel presented the first of two installments of his article to the Society (Makowsky, 1866).

Although there is no evidence that Darwin knew of Mendel's work, there is ample evidence that Mendel read some of Darwin's writings and that those writings may have influenced his work. Efforts to elucidate the Mendel–Darwin connection have been underway for nearly a century (for examples, see Bateson, 1913; Iltis, 1924; Fisher, 1936; Olby, 1985; Callender, 1988; Bishop, 1996; Orel, 1996).

In spite of much research, there is no consensus about Mendel's views on Darwinism. The numerous articles and commentaries on this topic begin with a comment in a letter to William Bateson written in 1902 by Mendel's nephew, Ferdinand Schindler, who stated, ''He [Mendel] read with great interest Darwin's work in German translation, and admired his genius, though he did not agree with all of the principles of this immortal natural philosopher'' (Orel, 1996, p. 188). Bateson (1913, p. 329) wrote, ''With the views of Darwin which at that time were coming into prominence Mendel did not find himself in full agreement.'' Fisher (1936, p. 118) believed that Mendel understood his laws to ''form a necessary basis for the understanding of the evolutionary process'' and that ''had he [Mendel] considered that his results were in any degree antagonistic to the theory of selection it would have been easy for him to say this also.'' Sapp (1990) determined that Fisher's 1936 paper was the turning point for the ''modern synthesis'' of Mendelism and Darwinism. In the mid-1960s, when a large number of articles were published at the centennial of Mendel's paper, most authors viewed Mendel as a supporter of Darwinism. By contrast, Olby (1979, 1985) studied the historical context of evolutionary thought during Mendel's day and determined that Darwin's ''views on the role of hybridization in evolution were very far removed from Mendel's'' (Olby, 1979, p. 67). Callender (1988) and Bishop (1996) expressed the most extreme views of Darwin's influence on Mendel. Callender (p. 72) claimed that ''Mendelism came into being historically as a sophisticated form of the doctrine of Special Creation'' and that it ''stood in open conflict with the Darwinian conception of evolution as descent with modification by means of Natural Selection.'' Bishop (p. 212) proposed that ‘‘Mendel’s sole objective in writing his *Pisum* paper, published in 1866, was to contribute to the evolution controversy that had been raging since the publication of Darwin’s the *Origin of Species* in 1859,’’ and that ‘‘Mendel was in favor of the orthodox doctrine of special creation.’’ After a detailed review of the literature on Mendel’s perception of evolution, Orel (1996, p. 198) determined that ‘‘Mendel came across Darwin’s theory as his *Pisum* experiments were drawing to a close. From his notes and from indirect evidence one can suppose that he did not see any conflict between this theory and his own.’’

The extreme disagreement among scholars about Mendel’s view of Darwin’s writings is probably because Mendel wrote very little about Darwin, and thus most claims are suppositions about what Mendel must have thought about Darwin. In his surviving writings, Mendel’s overtly referred to Darwin only four times, all in 1870, four years after the publication of ‘‘Versuche.’’ One reference is in Mendel’s (1870) *Hieracium* paper and three are in his eighth and ninth letters to Nägeli (Stern and Sherwood, 1966). All four references are brief and reveal neither strong support of nor opposition to Darwin’s theories.

Because Mendel’s major contribution to the science of genetics was ‘‘Versuche,’’ we will focus on how Darwin may have influenced Mendel before the 1866 publication of ‘‘Versuche.’’ Of Darwin’s writings, only the *Origin* was available to him before 1866. Several authors have noted that Mendel’s personal copy of the *Origin* contains marginalia (Iltis, 1924; Moore, 1963; Voipio, 1987; Hartl and Orel, 1992; Bishop, 1996; Orel, 1996). Mendel purchased a copy of the second German edition, published in 1863, which was translated from the third English edition (Darwin, 1861). This copy contains Mendel’s marginalia and is in the collection of the Mendelianum Museum Moraviae in Brno.

When Mendel began his classic experiments with pea in 1856, none of Darwin’s works were available for him to read. According to Orel (1971, 1996), Mendel probably first heard of Darwin in September 1861 during a lecture. He might have read the *Origin* during the latter part of 1862 or early 1863 when the Brünn Natural History Society acquired a copy of the German translation of the first English edition (Darwin, 1859). The 1863 publication date of Mendel’s personal copy of the *Origin* coincides with the last year of his experiments with peas. Therefore, the *Origin* had no effect on the design or conduct of those experiments, although it may have influenced Mendel’s interpretation of those experiments in ‘‘Versuche.’’ Orel (1996), de Beer (1964), Fisher (1936), and Bateson (1913) concluded that Darwin’s influence on Mendel, primarily from the *Origin*, is evident in ‘‘Versuche.’’ Our comparison of Mendel’s marginalia in the *Origin* with passages in ‘‘Versuche’’ supports this view.

Mendel’s complete marginalia in the *Origin* have not been published, although Orel (1996) discussed a few of them. The appendix to this paper contains full German and English texts of the complete marginalia along with our commentary and can be accessed electronically at http://ajbsupp.botany.org/v88/fairbanks.html. When quoting from the English version of the *Origin* in both this manuscript and the appendix we use the third edition text (Darwin, 1861) because this is the English edition from which Mendel’s German copy was translated.

The marginalia consist of passages marked in pencil and two very brief notes in script. The marks are either single or double vertical lines in the margins next to passages that Mendel apparently found interesting. Mendel marked passages on only 18 pages. The marked passages are clustered into two groups. Eight of them are in Chapters 1–4 (five in Chapter 2 ‘‘Variation Under Nature’’), and ten of them are in Chapters 8 and 9 (eight in Chapter 8 ‘‘Hybridism’’).

The marginalia include only two notes in script that can be attributed to Mendel. One of them is the series of numbers ‘‘1·6·7·13·16·48·52·57·62·63·76·78·80’’ written inside the back cover of the book. These may be page numbers, but our examination of the corresponding pages suggests that the numbers do not refer to pages in the *Origin* (see the Appendix). The other note in script is on page 1 and reads ‘‘pag 302.’’ The term ‘‘pag’’ probably is an abbreviation of the Latin word *pagina* for page. On page 302 is a passage that Mendel marked with double lines. In the original English it reads: ‘‘The slight degree of variability in hybrids from the first cross or in the first generation, in contrast with their extreme variability in the succeeding generations, is a curious fact and deserves attention’’ (Darwin, 1861, p. 296).

Apparently, Mendel found this to be the most interesting of the passages he marked. It is the only passage he cited by page number and is one of only two passages marked with double lines. Mendel’s observations of uniformity in the F_1 generation and predictable variability in the F_2 generation and his theoretical explanations for these phenomena form one of the key points of his paper. According to Orel (1996, p. 193), ‘‘Here Mendel must have felt some gratification in the thought that his theory was soon to explain this curious fact.’’

Of interest is Darwin’s explanation, which immediately follows this passage and is partially included within Mendel’s mark. Darwin’s explanation of the uniformity of hybrids in the F_1 generation and the variability of their F_2 offspring differs substantially from Mendel’s in that Darwin places the cause on altered reproductive systems rather than constant inherited traits:

> *For it bears on and corroborates the view which I have taken on the cause of ordinary variability; namely, that it is due to the reproductive system being eminently sensitive to any change in the conditions of life, being thus often rendered either impotent or at least incapable of its proper function of producing offspring identical with the parent-form. Now hybrids in the first generation are descended from species (excluding those long cultivated) which have not had their reproductive systems in any way affected, and they are not variable; but hybrids themselves have their reproductive systems seriously affected, and their descendants are highly variable.*
>
> —Darwin (1861, p. 296)

This is one of many passages in the *Origin* in which Darwin uses the phrase ‘‘conditions of life,’’ which in Mendel’s German edition of the *Origin* is translated as *Lebens-Bedingungun.* Mendel marked three passages in the *Origin* with this phrase (pages 17, 295, and 302 in his German edition; see the Appendix). The most important is the first marked passage in Mendel’s copy of the *Origin*:

> *It seems pretty clear that organic beings must be exposed during several generations to the new conditions of life to cause any appreciable amount of variation; and that when the organization has once begun to vary, it generally continues to vary for many generations.*
>
> —Darwin (1861, p. 7)

This passage appears in the opening remarks of Chapter 1, ''Variation Under Domestication,'' in which Darwin (1861, p. 7) suggested that the higher degree of variations in domesticated species compared to their wild counterparts is due to the ''domestic productions having been raised under conditions of life not so uniform as, and somewhat different from, those to which the parent-species have been exposed under nature.'' Mendel's view of this subject differed from Darwin's. From ''Versuche'':

> *Granted willingly that cultivation favors the formation of new varieties and that by the hand of man many an alteration has been preserved which would have perished in nature, but nothing justifies the assumption that the tendency to form varieties is so extraordinarily increased that species soon lose all stability and their progeny diverge into an infinite number of variable forms. If the change in living conditions* [Lebensbedingungun] *were the sole cause of variability one would expect that those cultivated plants that have been grown through centuries under almost identical conditions should have regained stability. This is known not to be the case, for it is precisely among them that not only the most different but also the most variable forms are found.*
>
> —Stern and Sherwood (1966, p. 37)

Commenting on this passage, Fisher (1936, p. 134) wrote: ''The reflection of Darwin's thought is unmistakable, and Mendel's comment is extremely pertinent, though it seems to have been overlooked. He may at this time have read the *Origin,* but the point under discussion may equally have reached his notice at second hand.'' Indeed, Mendel probably had read the *Origin* at the time he presented ''Versuche.'' This passage from ''Versuche'' seems to be a direct response to the passage he marked on page 17 of the *Origin.* In it Mendel contradicted Darwin's claim that changing conditions of life were the cause of variation in domesticated species.

In spite of all that has been written about Mendel's views of Darwinism, Mendel's marginalia in the *Origin* and his written comments in ''Versuche'' are the best indicators of his opinion of Darwin's writings when he wrote ''Versuche.'' Surprisingly, although many authors have addressed Darwin's influence on Mendel, only Orel (1996) used the content of Mendel's marginalia in the *Origin* as a source for his conclusions.

Several writers have claimed that Mendel marked *many* passages in the *Origin* and thus was very interested in and familiar with Darwin's writings (Iltis, 1924; Moore, 1963; Voipo, 1987; Bishop, 1996). In fact, Mendel's marginalia in his copy of the *Origin* are sparse; as mentioned above, the marked passages are found on only 18 pages. Mendel, however, was not one to avoid marking his books. His marginalia are abundant in his copies of Gärtner's (1849) book and Darwin's (1868) the *Variation of Animals and Plants Under Domestication,* which, however, was published two years after ''Versuche'' and thus had no influence on it.

Mendel never mentioned Darwin in ''Versuche,'' although he mildly contradicted some of the points that Darwin made in the *Origin* and supported a few others (see our commentary in the Appendix). Mendel also did not mention special creation or deity in ''Versuche,'' even though such a practice was not unusual in his day, especially for a priest. Instead, his paper is a highly focused and objective treatment of his work and its relationship to the work of other plant hybridists. It is devoid of polemics, sweeping conclusions, or speculations about theories that his experiments did not directly address.

Mendel's apparent reserved rather than intense interest in the *Origin* may be due to his well-known concern for detail. Even though Gärtner's descriptions of experiments in plant hybridization are far more detailed than the information Darwin provided in the *Origin,* Mendel lamented in his first letter to Nägeli:

> *The results which Gärtner obtained in his experiments are known to me; I have repeated his work and have reexamined it carefully to find, if possible, an agreement with those laws of development which I found to be true for my experimental plant. However, try as I would, I was unable to follow his experiments completely, not in a single case! It is very regrettable that this worthy man did not publish a detailed description of his individual experiments, and that he did not diagnose his hybrid types sufficiently, especially those resulting from like fertilizations.*
>
> —Stern and Sherwood (1966, p. 57)

Darwin wrote that the *Origin* was merely a ''brief sketch'' and an ''abstract,'' and has far less detail on plant hybrids than Gärtner's (1849) book. Also, regarding the information he presented on plant hybridization in the *Origin,* Darwin (1861, p. 277) wrote: ''The following rules and conclusions are chiefly drawn up from Gärtner's admirable work on the hybridisation of plants.'' Therefore, most of the information on plant hybridization in the *Origin* was a summary of detailed information that Mendel had already studied.

Perhaps Mendel's apparent lack of engagement with Darwin can shed some light on an old question. Historians have searched in vain for evidence that Darwin knew of Mendel's work, that Mendel contacted Darwin, or that Mendel sent a reprint of his paper to Darwin. According to Iltis (1924), Darwin's son examined his father's belongings and found no copies of Mendel's publications. As Olby (1985) pointed out, Darwin had a copy of Focke's (1881) *Die Pflanzen-Mischlinge* containing references to Mendel including summaries of Mendel's work with *Pisum* and *Phaseolus,* although the pages with the summaries were uncut and therefore unread. Mendel visited London in July and August of 1862, when his *Pisum* experiments were nearly completed, but there is no evidence that he attempted to contact Darwin, who in any case was not in London at the time (Orel, 1996).

Perhaps one of the most obvious reasons that Mendel did not attempt to contact Darwin is the language barrier; Mendel did not speak English, according to Orel (1996). However, apart from the language barrier, the answer may also lie in the nature of Darwin's writings. Although the passages Mendel marked in the *Origin* briefly address phenomena that he observed experimentally, the book had little in the way of detailed results and explanations that would have been useful to him. Mendel may not have contacted Darwin because, under the circumstances, there was little to gain in doing so.

In response to the question that heads this section, we find no evidence that Mendel either strongly supported or opposed Darwin when he wrote ''Versuche.''

CONCLUSION

Although Mendel's paper is considered a classic in the history of biology, it generated much controversy throughout the century that elapsed since the rediscovery of Mendelian laws in 1900. Scholars disagree about Mendel's integrity in his presentation, his articulation of the fundamental laws of inheritance, his experimental design, his motives for conducting his experiments, and his conclusions. Our review of Mendel's work in a botanical and historical context leads us to agree with Fisher (1936, p. 132) that Mendel's ''report is to be taken entirely literally, and that his experiments were carried out in just the way and in much the order that they are recounted.'' There is no credible evidence to indicate that Mendel was inaccurate or dishonest in his description of his experiments or his presentation of data. The main questions about his results can be resolved by an appeal to botanical principles and historical evidence.

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