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Perspective

Are Mendel's Data Reliable? The Perspective of a Pea Geneticist

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Abstract

Mendel's data exhibit remarkable agreement to the ratios he predicted. In this article, alternative explanations for this close agreement (that inheritance in pea does not conform to the standard statistical model, that data were omitted, that ambiguous data were categorized to better match predicted ratios, and that some data were deliberately falsified) are tested using approaches that are designed to distinguish between these alternatives. The possibility that garden pea (*Pisum sativum* L.) naturally produces segregation ratios more closely matching Mendelian expectations than predicted by statistical models is rejected. Instead the opposite is found to be the case, making Mendel's results even more remarkable. Considerable evidence is introduced that Mendel omitted some of his experimental results, but this alternative cannot adequately explain the low average deviation from expectations that is characteristic of the segregation data he presented. An underlying bias in Mendel's data favoring the predicted ratio is present, but my analysis could not clearly determine whether the bias was caused by misclassifying ambiguous phenotypes or deliberate falsification of the results. A number of Mendel's statements are argued to be unrealistic in terms of practical pea genetics, suggesting that his text does not represent a strictly accurate description of his experimental methods. Mendel's article is probably best regarded as his attempt to present his model in a simple and convincing format with a minimum of additional details that might obscure his message.

Subject areas: Quantitative genetics and Mendelian inheritance; Genomics and gene mapping
Key words: experimental bias, history of genetics, segregation analysis

It has been 150 years since Gregor Mendel published a brief article presenting compelling evidence for the then novel concept that individual heritable units control specific traits. Mendel's ideas have now become the basis of diploid transmission genetics, and as genetics has developed into a field central to all the biological sciences the precepts expounded by Mendel have been recognized as "laws of inheritance." Mendel's reputation has also grown considerably, and most introductory genetics textbooks refer to him as the "father of genetics."

Some science historians have argued that he really does not deserve this title as his article emphasized the behavior of plant hybrids and he never fully described the 2-allele genetic system that we are familiar with today (Corcos and Monaghan 1990; Monaghan and Corcos 1990). However, his stated purpose was "to deduce the law according to which they (the polymorphic traits) appear in the successive generations." Certainly, even if Mendel did not use the term "inheritance," there can be little doubt that he was interested in how traits were passed on from one generation to the next. A more serious charge was raised by Fisher (1936), who after a careful statistical evaluation of Mendel's data concluded that "the data of most, if not all, of the experiments have been falsified so as to agree closely with Mendel's expectations." The close agreement between Mendel's results and the predicted ratios actually was first raised by Weldon (1902), Weldon's concerns being recently described in detail by Radick (2015).

Interest in Fisher's analysis blossomed into a series of articles around the centennial celebration of Mendel's work, attracting the attention of such prominent geneticists as Sturtevant (1965), Wright (1966), and Dobzhansky (1967). Much of the debate regarding the quality of Mendel's data has been reviewed relatively recently (Fairbanks and Rytting 2001), and a collection of relevant articles published as a book to "end the Mendel-Fisher controversy," (Franklin 2008). It is not the purpose of the current manuscript to review the debate again but rather to introduce the perspective of a pea geneticist, which has been surprisingly absent from previous articles, and to submit Mendel's data to specific additional analyses.

An Overview of the Claims Against Mendel

In his statistical analysis of Mendel's experimental data, Fisher (1936) criticized Mendel for using the wrong expected ratio in his testing of the 2:1 predicted segregation ratio for F_3 families from F_2 plants possessing the dominant phenotype. Fisher argued that if Mendel planted only 10 seeds per family the actual expected ratio would be 1.8874:1.1126 due to sampling error (Fisher 1936). As Mendel's observed data corresponded more closely to the 2:1 ratio, Fisher felt that this discrepancy was particularly strong evidence that Mendel misstated his results to better fit his model.

Others have suggested that it is more likely that Mendel planted more seed from each F_2 plant but included only 10 in the data he reported (Wright 1966; Orel and Hartl 1994; Fairbanks and Rytting 2001). Such an alteration in experimental design would resolve the discrepancy between Mendel's results and theory for the F_2 dominant phenotype tests. The issue rests on whether Mendel's statement "ten seeds of each were cultivated" is to be taken literally or more loosely, the latter option reflecting what may have typically been done in order to ensure the availability of 10 plants to phenotype. Normally, in a scientific article, a strict interpretation of the text would be appropriate, and Fisher insisted on this interpretation. However, we will see that a number of statements Mendel makes are inaccurate, tending to be broad generalizations rather than precise descriptions, indicating that Mendel's writing was not as rigorous as Fisher would have desired.

Most of the data that Mendel presented in his 1866 article are summarized in Table 1. The format is similar to that of Fisher (1936) except that I include χ^2 and *P* values rather than simple χ values. Furthermore, the data are not subdivided into units that maximize the degrees of freedom in the results but rather are presented by trait in order to facilitate comparisons with data generated on that same trait by other researchers. Because of the debate mentioned above regarding the number of seeds actually planted by Mendel for his testing the 2:1 ratio, I have omitted these data.

Table 1. Segregation data presented in Mendel (1866)

Phenotype			Expected ratio	χ^2 (1 df)[a]	*P*[a]
Dominant	Recessive	Total			
Seed coat color (locus *A*)					
705	224	929	3:1	0.391	0.5318
473	166	639	3:1	0.326	0.568
85	81	166	1:1	0.096	0.7567
Average				**0.271**	**0.6188**
Plant height (locus *Le*)					
787	277	1064	3:1	0.607	0.4359
87	79	166	1:1	0.386	0.5344
Average				**0.496**	**0.4852**
Pod color (locus *Gp*)					
428	152	580	3:1	0.45	0.5023
Seed shape (locus *R*)					
5474	1850	7324	3:1	0.263	0.6081
423	133	556	3:1	0.345	0.557
480	159	639	3:1	0.005	0.9436
43	47	90	1:1	0.178	0.6731
57	53	110	1:1	0.145	0.7034
44	43	87	1:1	0.011	0.9165
49	49	98	1:1	0	1
372	193	565	2:1	0.176	0.6748
Average				**0.14**	**0.7596**
Cotyledon color (locus *I*)					
6022	2001	8023	3:1	0.015	0.9025
416	140	556	3:1	0.01	0.9203
489	150	639	3:1	0.795	0.3726
45	45	90	1:1	0	1
58	52	110	1:1	0.327	0.5674
47	40	87	1:1	0.563	0.4531
46	52	98	1:1	0.367	0.5446
353	166	519	2:01	0.425	0.5145
Average				**0.313**	**0.6594**
Flower distribution on stem (locus *Fa*)					
651	207	858	3:1	0.35	0.5541
Pod shape (locus *V*)					
882	299	1181	3:1	0.064	0.8003

[a]Numbers in bold represent average values of c^2 and *P* for each trait.

As is evident from Table 1, Mendel's data agree very well with the expected ratios. All the χ^2 values are considerably below the 3.84 standard cut-off for rejecting the null hypothesis with 1 degree of freedom. Indeed, of the 24 data sets presented, none gives a χ^2 value that would be expected less than 1 of every 3 determinations. Taking each trait separately, the segregation ratios for the 3 traits with only one entry each (pod color, pod shape, and stem fasciation) do not appear to be questionable on their own. Both pod color and stem fasciation have moderate χ^2 and *P* values, and although the segregation ratio for pod shape is relatively close to expected, it certainly can be considered a reasonable outcome of 1 experiment or the combination of several progeny all segregating for this trait. The data for stem height segregation also appear normal, generating a very reasonable average χ^2 value for the 2 determinations. Only when all the data are taken together, and particularly when those data on seed characters (seed coat color, seed shape, and cotyledon color) are included, do the results begin to arouse suspicion with their consistently low χ^2 and high *P* values (average *P* for the seed traits are 0.62, 0.76, and 0.66, respectively) (Table 1).

Fisher's original analysis of these data is more compelling than the summary presented in Table 1 due to the much greater number of degrees of freedom he generated by further subdividing the segregation data as well as the inclusion of the F_3 data establishing the 2:1 ratio. However, I suspect Fisher would still question the close agreement between observed and predicted ratios, particularly those for the seed characters. As mentioned above, the purpose of this article is not to reiterate the statistical arguments for treating Mendel's data as suspect. Rather, I am more interested in investigating why the results are so close and am willing to accept that Mendel's results, as Weldon first pointed out, are "surprisingly close to the expected ratios."

Possible Reasons for Mendel's Results Being "Too Good"

Beyond the possibility that Mendel fabricated at least some of his data, there are several alternative hypotheses, listed below, that have been suggested by Sturtevant (1965) as well as by others. In the following 4 sections I will examine each of the alternatives, using data from a considerable number of studies in pea published between 1920 and 2001 to test the plausibility of each of the alternatives.

Alternatives

1) Some mechanism in pea influences the segregation ratio of characters so that the statistical model Fisher used is not valid for Mendel's data.
2) Data deviating significantly from the expected ratios were omitted.
3) There may have been a tendency to score individuals with ambiguous phenotypes in such a way as to match the expected ratios.
4) Some of the data may have been falsified by assistants who were trying to match the expected ratios.

Is Meiotic Segregation Somehow Different in Pea So That Typical Statistical Models Are Not Valid?

As unlikely as this possibility may seem, it has been given some attention in the past and it also provides an opportunity to introduce aspects of pea biology that are directly relevant to segregation data in this species. It was postulated by Thoday (1966) that pollen tetrad formation in pea could proceed in such a way that in a heterozygous plant pollen grains possessing alternate alleles were somehow grouped so that the process of pollination was not a random sampling of pollen grains but directed to enforce a consistent 1:2:1 combination of progeny. Although it is doubtful that Thoday or others seriously supported this hypothesis, it has been tested in several ways as the correlated pollen model (Seidenfeld 1998) or tetrad-pollen model (Fairbanks and Schaalje 2007) and rejected as a possibility.

Another method of testing the general possibility that pea gives more consistent segregation ratios than predicted by statistical models is to examine the segregation data in pea published by other researchers. Johannsen (1926) compared Mendel's F_2 results on cotyledon color segregation with those of 7 subsequent researchers who had also reported results on segregation for this same gene either during or after the "rediscovery" of Mendel's laws (Table 2). The results of the 7 post-Mendel determinations were similar to those of Mendel in that none gave a significant deviation from the expected 3:1 ratio. However, these later results displayed a slightly larger average χ^2 and a greater variance (Table 2) and were accepted by both Johannsen (1926) and Sturtevant (1965) (who cited Johannsen's comparison while discussing Fisher's criticism of Mendel's data) as being consistent with statistical theory.

One limitation to the studies listed by Johanssen is that all were done to directly test the hypothesis that traits give a 3:1 segregation ratio in pea. Thus, all the investigators could be accused of having a bias similar to that suspected of Mendel: expecting the hypothesis to be true and classifying ambiguous phenotypes in a way that best fit the hypothesis. Each of these studies was testing predicted segregation ratios, yet only that by Bateson and Kilby (1905) included a classification category of "dubious" phenotypes. Even before Mendel performed his studies it was known that green peas could be "bleached" by sunlight to appear yellow and yellow peas could remain green if the maturation process was disturbed (Mendel 1866), yet the cited investigations generally forced all observations into the 2 expected categories. We will see that the classification of questionable phenotypes probably was an important source of bias in Mendel's work, and all the studies cited by Johannsen except for Bateson and Kilby, could be said to suffer the same drawback.

To address this limitation, I have assembled additional data reported in the literature by a number of pea researchers who published later than those Johannsen cited (Table 3 and Supplementary Table S1). The difference between the data sets listed by Johannsen and those in Table 3 and Supplementary Table S1 is that the latter contain only data that were part of linkage studies. In such studies, the investigator is not as interested in testing segregation ratios as in classifying the segregating traits accurately so that linkage between traits can be identified. The data were selected to include only those traits also investigated by Mendel and involve population sizes comparable with those Mendel used (population sizes less than 100 were not included). The reason for assembling the linkage data into 2 tables is that many crosses within what is currently recognized as *Pisum sativum* L. display distorted segregation (Kosterin and Bogdanova 2015 and discussion below). Mendel screened his crosses for high fertility. The data presented in Table 3 represent my attempt

Table 2. F_2 segregation data from several early 20th century geneticists testing pea cotyledon color for conformance to a 3:1 ratio

Source	Dominant	Recessive	χ^2	*P*
Correns (1900)	1394	453	0.221	0.638
Tschermak (1900)	3580	1190	0.007	0.933
Hurst (1904)	1310	445	0.119	0.73
Bateson and Kilby (1905)	11902	3903	0.786	0.375
Lock (1905)	1438	514	1.841	0.174
Darbishire (1909)	109060	36186	0.578	0.447
Johannsen (1926)	19195	6553	2.787	0.095

Table 3. Segregation data for Mendel's 7 traits from linkage studies in the literature

Reference	Phenotype		Expected ratio	χ^{2a}	P^a
	Dominant	Recessive			
	Locus A (seed coat color)				
Marx (1984)	251	83	3:1	0.004	0.9496
Marx (1984)	179	71	3:1	1.54	0.2144
Marx (1987b)	167	61	3:1	0.374	0.5407
Swiecicki and Wolko (1987)	148	46	3:1	0.172	0.6785
Czerwinska (1988)	301	88	3:1	1.173	0.2788
Swiecicki (1989b)	98	26	3:1	1.08	0.2998
Kosterin and Rozov (1993)	83	40	3:1	3.71	0.0541
Weller (1997)	268	96	3:1	0.366	0.545
Gorel' et al. (2000)	87	29	3:1	0	1
Kovalenko and Ezhova (1992)	655	223	3:1	0.074	0.785
Lamprecht (1942)	340	103	3:1	0.723	0.3951
Lamprecht (1942)	350	99	3:1	2.085	0.1487
Lamprecht (1961)	730	202	3:1	5.499	0.019
Lamprecht (1961)	279	86	3:1	0.403	0.5257
Lamprecht (1961)	3942	1368	3:1	1.647	0.1993
Lamprecht (1961)	539	169	3:1	0.482	0.4875
Lamprecht (1961)	540	189	3:1	0.333	0.5637
Lamprecht (1961)	2510	873	3:1	1.171	0.2793
Lamprecht (1961)	5341	1748	3:1	0.442	0.506
Hammarlund (1927)	254	78	3:1	0.402	0.5263
Hammarlund (1927)	228	87	3:1	1.152	0.2831
Hammarlund (1927)	204	74	3:1	0.388	0.5331
Rasmusson (1927)	599	187	3:1	0.612	0.4339
Rasmusson (1927)	153	52	3:1	0.015	0.9037
Rasmusson (1927)	245	78	3:1	0.125	0.7238
Rasmusson (1927)	205	51	3:1	3.521	0.0606
Rasmusson (1927)	354	97	3:1	2.933	0.0868
Rasmusson (1927)	759	253	3:1	0	1
Rasmusson (1927)	547	154	3:1	3.436	0.0638
Sverdrup (1927)	3859	1234	3:1	1.613	0.204
Average				**1.18**	**0.443**
	Locus Le (stem height)				
Muehlbauer (1987)	92	25	3:1	0.823	0.3642
Trifu (1987)	276	80	3:1	1.213	0.2706
Trifu (1987)	130	44	3:1	0.008	0.9302
Lamprecht (1942)	332	111	3:1	0.0007	0.978
Lamprecht (1961)	784	251	3:1	0.31	0.578
Lamprecht (1961)	417	143	3:1	0.086	0.7697
Lamprecht (1961)	781	260	3:1	<0.0001	0.9857
Lamprecht (1961)	317	98	3:1	0.425	0.5145
Lamprecht (1961)	1803	562	3:1	1.929	0.1648
Lamprecht (1961)	1468	462	3:1	1.161	0.2812
Lamprecht (1961)	1556	493	3:1	0.965	0.326
Lamprecht (1961)	24 343	8176	3:1	0.351	0.5536
Lamprecht (1961)	817	245	3:1	2.11	0.1463
Lamprecht (1961)	1050	344	3:1	0.077	0.7807
Rasmusson (1927)	597	189	3:1	0.382	0.5367
Rasmusson (1927)	361	132	3:1	0.828	0.3628
Rasmusson (1927)	298	100	3:1	0.003	0.9538
Rasmusson (1927)	111	31	3:1	0.761	0.3832
Rasmusson (1927)	347	104	3:1	0.905	0.3413
Rasmusson (1927)	759	253	3:1	0	1
Rasmusson (1934)	82	89	1:1	0.287	0.5924
Rasmusson (1934)	124	132	1:1	0.25	0.6171
Rasmusson (1934)	115	135	1:1	1.6	0.2059
Sverdrup (1927)	3256	1089	3:1	0.009	0.9232
Average				**0.604**	**0.565**
	Locus *Gp* (pod color)				
Marx (1969)	255	97	3:1	1.227	0.2679
Marx (1971)	320	98	3:1	0.539	0.4628

Table 3. *Continued*

Reference	Phenotype		Expected ratio	χ^{2a}	P^a
	Dominant	Recessive			
Marx (1972)	359	113	3:1	0.282	0.5951
Marx (1983)	283	98	3:1	0.106	0.7449
Wellensiek (1971)	747	293	3:1	5.585	0.0181
Statham and Murfet (1974a)	108	36	3:1	0	1
Statham and Murfet (1974b)	52	59	1:1	0.441	0.5064
Ezhova and Gostimski (1984)	350	95	3:1	3.165	0.0752
Swiecicki (1985a)	173	61	3:1	0.142	0.7059
Swiecicki (1985b)	339	116	3:1	0.059	0.8075
Swiecicki (1987b)	371	103	3:1	2.7	0.1001
Trifu (1987)	135	51	3:1	0.581	0.4461
Trifu (1987)	135	44	3:1	0.017	0.897
Swiecicki (1988)	374	104	3:1	2.681	0.1061
Swiecicki (1989a)	319	107	3:1	0.003	0.9554
Murfet (1990)	97	31	3:1	0.042	0.8383
Swiecicki (1990)	303	72	3:1	6.73	0.0095
Sidorova and Uzhintseva (1995)	254	95	3:1	0.918	0.338
Rozov et al. (1997)	94	28	3:1	0.273	0.6021
Lamprecht (1957)	260	67	3:1	3.548	0.0596
Lamprecht (1942)	339	110	3:1	0.06	0.8063
Lamprecht (1961)	1003	355	3:1	0.944	0.3314
Lamprecht (1961)	958	335	3:1	0.569	0.4505
Lamprecht (1961)	3704	1213	3:1	0.286	0.5925
Lamprecht (1961)	389	101	3:1	5.031	0.0249
Lamprecht (1961)	1068	336	3:1	0.855	0.3552
Lamprecht (1961)	2707	933	3:1	0.775	0.3786
Lamprecht (1961)	1808	566	3:1	1.699	0.1924
Lamprecht (1961)	477	126	3:1	5.418	0.0191
Hammarlund (1927)	252	80	3:1	0.145	0.7038
Hammarlund (1927)	230	85	3:1	0.661	0.4161
Hammarlund (1927)	205	73	3:1	0.235	0.6278
Sverdrup (1927)	2588	796	3:1	3.94	0.0471
Average				**1.5**	**0.4388**
	Locus *R* (seed shape)				
Marx (1986)	181	65	3:1	0.266	0.6063
Marx (1986)	89	27	3:1	0.18	0.668
Marx (1986)	315	110	3:1	0.176	0.6744
Marx (1986)	184	55	3:1	0.503	0.478
Marx (1987a)	614	205	3:1	0.0004	0.9839
Marx (1987b)	176	74	3:1	2.821	0.093
Marx (1987b)	168	64	3:1	0.828	0.363
Swiecicki (1987a)	187	35	3:1	10.1	0.0015
Swiecicki (1989c)	333	123	3:1	0.947	0.3304
Swiecicki (1990)	251	65	3:1	3.31	0.0689
Murfet (1990)	93	35	3:1	0.375	0.5403
Smirnova (1990)	149	47	3:1	0.109	0.7415
Rozov et al. (1993)	208	65	3:1	0.206	0.6496
Swiecicki (1998)	514	160	3:1	0.572	0.4496
Swiecicki (1998)	119	55	3:1	4.05	0.0441
Swiecicki (1998)	326	98	3:1	0.805	0.3696
Gorel' and Berdnikov (2001)	139	51	3:1	0.344	0.55576
Lamprecht (1961)	7575	2359	3:1	8.322	0.0039
Lamprecht (1961)	2004	676	3:1	0.072	0.789
Lamprecht (1961)	837	292	3:1	0.448	0.5028
Lamprecht (1961)	813	262	3:1	0.226	0.6345
Rasmusson (1927)	580	206	3:1	0.612	0.4339
Rasmusson (1927)	165	40	3:1	3.293	0.0696
Rasmusson (1927)	391	102	3:1	4.885	0.0271
Rasmusson (1927)	810	202	3:1	13.708	0.0002
Rasmusson (1927)	545	156	3:1	2.819	0.0931
Sverdrup (1927)	3006	986	3:1	0.192	0.6609
Sverdrup (1927)	431	406	1:01	0.747	0.3875
Average				**2.18**	**0.3997**

Table 3. *Continued*

Reference	Phenotype		Expected ratio	χ^{2a}	P^a
	Dominant	Recessive			
	Locus *I* (cotyledon color)				
Snoad (1971)	1188	379	3:1	0.553	0.457
Kielpinski (1982)	864	281	3:1	0.128	0.7201
Marx (1984)	183	64	3:1	0.109	0.7409
Marx (1984)	133	46	3:1	0.047	0.8292
Marx (1984)	114	28	3:1	2.113	0.1461
Kovalenko and Ezhova (1992)	674	206	3:1	1.188	0.2758
Lamprecht (1942)	327	116	3:1	0.332	0.5646
Lamprecht (1961)	325	120	3:1	0.918	0.3381
Lamprecht (1961)	307	111	3:1	0.539	0.4628
Lamprecht (1961)	3034	878	3:1	13.633	0.0002
Rasmusson (1927)	595	191	3:1	0.205	0.6505
Rasmusson (1927)	392	101	3:1	5.356	0.0207
Rasmusson (1927)	113	40	3:1	0.107	0.7439
Sverdrup (1927)	3778	1252	3:1	0.032	0.8579
Sverdrup (1927)	713	699	1:01	0.139	0.7095
				1.69	**0.5012**
	Locus *Fa* (position of flowers on stem)				
Marx (1987c)	359	120	3:1	0.001	0.979
Muehlbauer (1987)	103	14	3:1	10.6	0.0011
Lamprecht (1961)	433	114	3:1	5.046	0.0247
Lamprecht (1961)	344	86	3:1	5.733	0.0166
Lamprecht (1961)	682	210	3:1	1.01	0.3148
Sverdrup (1927)	2369	701	3:1	7.683	0.0056
Average				**5.01**	**0.2236**
	Locus V (pod shape)				
Rasmusson (1927)	151	54	3:1	0.197	0.6574
Rasmusson (1927)	343	108	3:1	0.267	0.6055
Rasmusson (1927)	603	183	3:1	1.237	0.2661
Lamprecht (1961)	2005	690	3:1	0.523	0.4697
Lamprecht (1961)	485	114	3:1	11.38	0.0007
Lamprecht (1961)	755	218	3:1	3.495	0.0616
Average				**2.85**	**0.3435**

[a]Numbers in bold represent average values of c^2 and *P* for each trait.

to provide a comparable screen, eliminating data sets that are greatly distorted ($P < 0.0001$) or publications that have a high level of distorted data sets (e.g., Winge 1936). However, for completeness these data sets are presented in Supplementary Table S1.

Table 3 presents 30 linkage segregation data sets for *A* (testa and flower color), 24 for *Le* (stem height), 33 for *Gp* (pod color), 28 for *R* (seed shape), 15 for *I* (cotyledon color), 6 for *Fa* (flower distribution on stem), and 6 for *V* (pod shape). Within these 142 sets, 18 show a significant ($P < 0.05$) deviation from the predicted ratio, approximately 2.5 times the expected number. When Mendel's results are compared to those in Table 3 important differences become evident. For each of the 7 traits, the χ^2 or average χ^2 for Mendel's data is less than the corresponding value for the trait in the linkage studies, in several instances by a factor of 10 or more. Including data sets from Supplementary Table S1 only increases the differences between the linkage data and those of Mendel. To summarize, rather than indicating that pea segregation data is likely to conform more closely to expected ratios, the result from the linkage studies suggests the opposite.

The distribution of *P* values for the 3 data sets (Mendel's data, those Johannsen cited, and those from Table 3) is compared in Figure 1. In such a graph, the expected frequency is equal for all units along the *x* axis. The distribution of the studies cited by Johannsen appears to fit this prediction, although the sample size is too small to provide a significant test. Neither the data of Mendel nor those of the linkage studies provide a good fit to the predicted distribution. Mendel's data display a truncated distribution, with no results with a *P* value less than 0.35 (Figure 1). It should be noted that in a similar analysis of Mendel's segregation data, Fairbanks and Rytting (2001) also found an uneven distribution of *P* values with a strong bias in the $P > 0.9$ category, although because they included the tests of the 2:1 ratio there were 2 cases in which the *P* value was below 0.35. In contrast, the selected data from linkage studies has a relatively flat distribution except for the lowest *P* values, with $P < 0.05$ containing over twice as many data sets as predicted. Thus, even after elimination of results that might be attributed to wider crosses than Mendel used, the data from linkage studies do not support the alternative currently being discussed—segregation ratios produced in pea do not tend to give higher *P* values than would be predicted by standard statistical models. The truncated distribution that is observed for *P* values on Mendel's data does not reflect what is typically found in pea.

Did Mendel Repeat Experiments That Deviated Significantly from the Expected Ratios or Select Only Those Results for Publication that Strongly Supported His Model?

Fisher (1936) discounted this alternative because of the limited garden space Mendel had available to grow his plants, making it

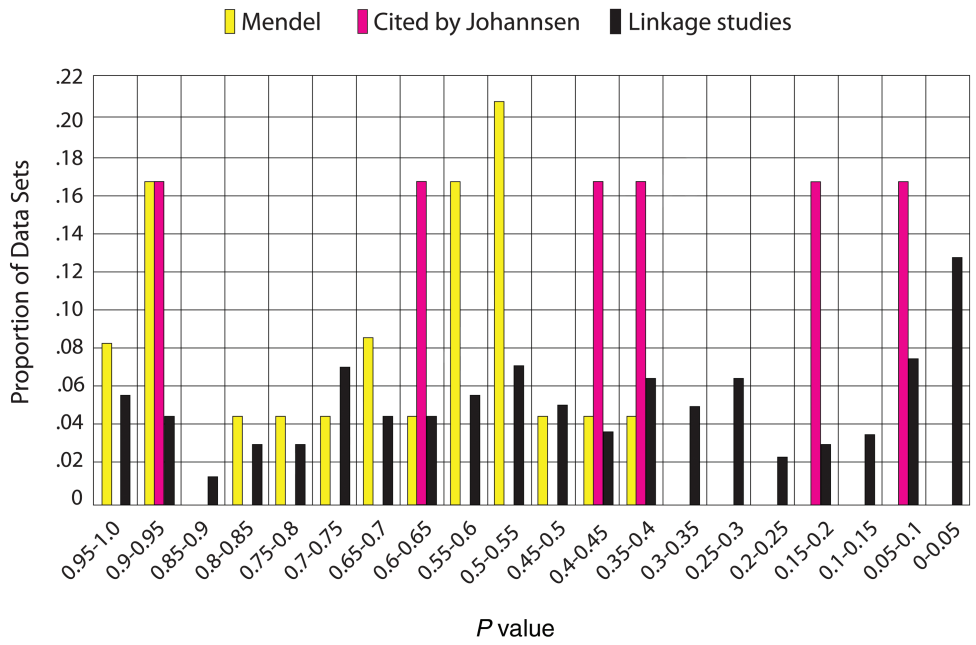

Figure 1. Distribution of *P* values calculated for Mendel's data (bars with black outline), for those studies cited by Johanssen (gray bars), and for the studies listed in Table 3 (black bars). The units on the vertical axis are the proportion of data sets in the respective *P* value range for the specified source of data. For Mendel's data, $n = 24$; for Johanssen's data, $n = 6$; for the linkage data, $n = 142$.

unlikely that Mendel could have grown many more plants than he mentioned in his manuscript. Novitski (1995) performed a detailed analysis on the 5 experiments Mendel describes in his section on "The Reproductive Cells of the Hybrids," and concluded that it would be nearly impossible for Mendel to obtain such consistent data even if he performed all 5 experiments in triplicate and selected the best replication for each experiment. Hence, based on space availability and statistical arguments, it does not appear that Mendel could have grown a sufficient number of populations to select only those that would provide the particularly low variance and close agreement to his model).

It is doubtful that in his studies Mendel encountered as much segregation distortion as is present in Table 3 and Supplementary Table S1, but he should have observed some. He selected 22 lines for his crossing studies, and described them as being from 4 different species (*P. sativum*, *Pisum quadratum*, *Pisum saccharatum*, and *Pisum umbellatum*). The exact lines Mendel used in his crosses are unknown, but almost certainly all the "species" Mendel worked with would now be classified as being from the same subspecies, *P. sativum* ssp. *sativum* (Maxted and Ambrose 2001). Even within this subspecies there exist lines that when crossed will produce F_2 progeny with distorted segregation ratios (Kosterin and Bogdanova 2015). Mendel stated that he only selected crosses with "no marked disturbance in their fertility in the successive generations," but, he also noted that "Weakly plants always afford uncertain results, because even in the first generation of hybrids, *and still more so in the subsequent one* (my emphasis), many of the offspring either entirely fail to flower or only form a few and inferior seeds." Here, Mendel may be describing the reduced vigor of the F_2 generation that is often observed in wider crosses in plants (Taylor and Ingvarsson 2003). This possibility is further supported by the fact that in his analysis of hybrids segregating for several factors, Mendel observed that 2.5% (14 out of 556) and 7% (48 out of 687) of the seed from the F_1 did not produce fertile plants in the dihybrid and trihybrid experiments, respectively (Mendel, 1866). Thus, particularly in his bi- and trifactorial crosses, Mendel probably crossed lines with relatively divergent genetic backgrounds, comparable to many of the crosses used to produce the data in Table 3.

The conclusion relevant to the current discussion is that although Mendel screened his hybrids and discarded those showing a significant loss of fertility, he still encountered some F_2 populations that gave weak plants. He probably eliminated some F_2 populations that displayed a considerable fraction of weak plants, but he did not have time or space to eliminate a significant proportion of his populations. Thus, even in his relatively limited number of analyses, Mendel should have observed some distorted sets. Similar to the close agreement between observed and expected ratios noted by Weldon and Fisher, the lack of any statistically significant deviation in Mendel's data from the expected ratios is exceptional rather than typical for pea.

Of particular interest are Mendel's data for the distribution of flowers along the stem (controlled by the locus *Fa*). The data in Table 3 reveal that for over half the mapping experiments cited the segregation at this locus was distorted. The explanation lies not just in the genetic background of the crosses used but also in the determination that the recessive allele is not 100% penetrant in many crosses (Swiecicki 2001). In the crosses giving distorted segregation at this locus in Table 3, all give an excess of the wild-type phenotype, consistent with incomplete penetrance of the mutant phenotype.

Mendel examined over 1000 F_2 individuals for this trait, which probably reflects the progeny from at least 30 hybrid plants. Undoubtedly, the line(s) he used as the mutant parent was highly penetrant for the trait. However, once Mendel crossed the trait into a mixture of genetic backgrounds, it is doubtful that the trait would always exhibit high penetrance. Nor would we expect an "averaging out" of the deviations from expected, as all deviations would be expected to favor the wild type. For fasciated stem it seems most likely that Mendel obtained his data from only 1 or 2 crosses that

gave excellent penetrance of the trait. If so, there should have been data from other crosses involving *Fa* that displayed skewed ratios that were not included in his article; otherwise he could not have concluded that this trait assorted independently from all others.

As Mendel acknowledges directly in his manuscript that wide variation could occur in observed segregation ratios, there appears no reason for him to eliminate the relatively few cases that failed to support his hypothesis. Yet the absence of wild-type bias at *Fa* and the general lack segregation distortion in Mendel's other data strongly suggests that some data were ignored. His method of presenting the bulk of his data (combining data from several crosses into 1 segregation set, such as for pod color, pod shape, and fasciation) would allow him to selectively exclude certain data sets from a segregating population while including others.

Just how thoroughly data need to be presented in a manuscript is somewhat subjective, as is evident to anyone who has gone through preparation and review of a scientific manuscript. In Mendel's case, the critical questions focus on whether such omissions affected the interpretation of the results and why he felt compelled to exclude such data. Based on the 13% occurrence of distorted segregation ratios in Table 3 and Mendel's statement that he selected his hybrids for high fertility, we might expect that he excluded some 10% of his results, perhaps the equivalent of 2 or 3 crosses. Such selection of data could have eliminated divergent segregation sets and allowed Mendel to slightly reduce the overall variance in his data. However, it would not be sufficient to bring into doubt his general conclusions, and it is doubtful that just elimination of data could explain the absence of segregation results with *P* values less than 0.35. As will be discussed later, it is likely that Mendel simply eliminated highly divergent results because he did not want to confuse his audience with experimental details that detracted from the demonstration of his model.

Is There Evidence That Individuals with Ambiguous Phenotypes may have been Classified in Such a Way to Provide a Better Fit with Expected Ratios?

This alternative was suggested by both Fisher (1936) and Sturtevant (1955), but a test of this hypothesis has yet to be performed. To undertake such a test we need to know more about the phenotypes Mendel was trying to classify in order to establish which traits might produce such uncertain or intermediate phenotypes.

The exceptional property of pea that made it so valuable to Mendel was its suite of polymorphic morphological characters that turned out to be primarily controlled by single loci in the germplasm he used. Mendel was careful to choose characters that he felt were "constant and easily and certainly recognizable" and makes the rather uncompromising statement that "Transitional forms were not observed in any experiment" ("Übergangsformen wurden bei keinem Versuche beobachtet"). He further indicated that several additional polymorphic traits were not used in his studies because they did not "permit of a sharp and certain separation, since the difference is of a 'more or less' nature."

Although he acknowledged in several instances that certain of the characters he chose to study were occasionally difficult to evaluate accurately ("ambiguous" phenotypes could occasionally be observed) he eventually makes the statement "… jedoch sind bei einiger Übung im Sortiren Fehler leicht zu vermeiden" (… but, with a little practice in sorting, errors are easily avoided). Thus, near the very start of his manuscript Mendel dismisses the possibility that errors in classification of phenotypes occurred. He does not mention further problems with phenotypes and when he presents his experimental data he does not indicate encountering ambiguous phenotypes or discarding data that he thought might be suspect. Notably, in his description of the dihybrid and trihybrid crosses where he details the number of seeds that did not germinate and the number of plants that failed to reproduce, there is no mention of plants expressing uncertain phenotypes. The reader must accept that all plants were completely and accurately classified. However, in my own experience, and I believe for many other individuals who have analyzed these traits, the phenotypes of several of the traits are not always clearly discernible despite considerable familiarity with their variation. Indeed, Weldon appears to have been concerned about this same question in his discussion of Mendel's results (Radick, 2015).

Three of Mendel's traits, stem height, testa color, and pod color, should be very easy to classify not only because of the clarity of the difference in the primary character but also because each of these are associated with other characters. Tall plants also have longer internodes and often have longer peduncles and tendrils. Mendel's "colorless" seed coats are caused by a mutation in a gene regulating the phenylpropanoid pathway (Hellens et al. 2010) so that the plants generating these seeds cannot synthesize anthocyanin pigments and their flowers are white. Indeed, scoring segregation of this gene is usually performed by classifying flower color rather than seed coat color. The yellow pod character produces an upper stem, peduncles, and pedicels with a yellowish tinge. In addition, the yellow pods typically have thinner pod walls. Mendel mentioned many of these associated traits and presumably could have used them to confirm instances where there may have been some doubt about the primary character.

The other 4 characters can produce what I will call "ambiguous" phenotypes in many crosses or nonideal environments. In his own description of "form of the seed" Mendel uses "round or roundish" versus "angular wrinkled," the "roundish" wording giving some subjectivity to the classification, as poorly developing round seeds often have some wrinkles or dents. A much more detailed description of the variation in seed shape can be found in Khvostova (1975). An excellent method of discriminating between round and wrinkled peas is to examine the shape the starch granules in the cells of the cotyledons. This feature was used by several of the researchers cited by Johannsen but was unknown at the time Mendel did his studies. Hence, Mendel's classification was based primarily on the shape of the seed, with all its environmental dependence. A similar situation exists for cotyledon color, a trait that Mendel also mentioned could be misclassified as a result of bleaching of green cotyledons or a failure to mature properly, although Mendel did not know of the genes affecting green pigments in the seed coat that can also obscure the yellow/green cotyledon color difference (Lamprecht 1959; Ubayasena et al. 2011; Weeden et al. 2016).

Pod shape and flower distribution on the stem are 2 additional traits that tend to be difficult to score in certain crosses, although these were not mentioned specifically by Mendel as problematic. The edible podded character results from a reduction of schlerenchyma in the pod wall. This reduction can be produced by either of 2 unlinked mutations, *p* or *v*, the pattern of the reduction of the schlerenchyma being different in the 2 mutations (Rasmusson 1927). From Mendel's description of the mutant having "constrictions between the seeds" and his confidence in classifying the observed phenotypes, the gene almost certainly was *v* rather than *p*. Due to its slightly greater amount of schlerenchyma, the pod wall in the latter mutation does not always collapse between seeds and is often harder to distinguish from the wild type (Rasmusson 1927). Yet even Rasmusson, who worked extensively with *v*, did not appear to be

able to consistently score the phenotype in various genetic backgrounds, determining linkage frequencies between *V* and *Le* ranging from 5 to 15 cM (Rasmusson 1927). The 2 loci are close together at one end of pea linkage group III, and the variance in the linkage intensities determined by Rasmusson probably reflects more the difficulty in classifying pod phenotype than a variation in recombination frequency.

As has been mentioned above, the phenotype and penetrance of the fasciated stem mutation varies in different genetic backgrounds. We are faced with the possibility that either he selected 1 cross that gave him good fertility and an excellent segregation ratio at *Fa* or much of the data is fabricated. I feel there is sufficient concern about the *Fa* data that I have omitted them from the following analyses.

The critical aspect of the issue for the purposes of this article is that we can now group Mendel's traits into 2 categories: those (seed color, stem height, and pod color) with very little tendency to generate ambiguous phenotypes and those (seed shape, cotyledon color, and pod shape) that at least have the potential to do so. If there were a tendency to classify dubious individuals in a way to fit the expected ratio, segregation ratios for these traits should fit the expected ratio more closely than the data obtained for traits with unambiguous phenotypes.

Two approaches were used to evaluate this possibility. In Table 4, the data sets for ambiguous and nonambiguous traits obtained by Mendel and in the linkage studies are each divided into 2 bins, those with $P < 0.5$ and those with $P > 0.5$. In 2 cases where $P = 0.50$ half a dataset was assigned to each bin. Theoretically, the number of data sets in each bin pair should be equal. Chi-square analysis based on the predicted 1:1 ratio reveals that only for the case of Mendel's data for the ambiguous traits does the observed ratio deviate significantly ($P = 0.0018$). As the data sets are correlated (the same plants are used for the 3 ambiguous traits, the Bonferroni correction should be used, reducing the critical *P* value 3-fold (e.g., $P_{critical} = 0.05/3 = 0.017$). However, the *P* value for Mendel's ambiguous traits is still a factor of 10 below this revised $P_{critical}$ (Table 4).

The Mann–Whitney *U* test (Mann and Whitney 1947) was also employed to compare the range of *P* values in ambiguous and nonambiguous traits. For the data from the linkage studies there was no significant difference in *P* value distributions between the 2 categories. However, for Mendel's data the difference was significant, albeit barely so ($U = 25$, critical *U* for significance = 26). Thus, both approaches indicate that a confounding influence was acting when seed shape, pod shape, and cotyledon color were being classified. The most straightforward explanation is that the investigator, whether it was Mendel or an associate, being faced with having to classify ambiguous phenotypes did so with a consideration to what was predicted by the model.

Could a Portion of the Data Been Collected by Someone Else Who in an Attempt to Please Mendel Deliberately Altered the Data to Better Fit the Expected Outcome?

The possibility of an assistant deliberately altering the data to appease Mendel has been mentioned in the literature several times. Novitski (1995) argued against this alternative because Mendel's early data did not differ much from the later, and supposedly Mendel did not know what to expect before beginning his experiments. However, Fisher believed that Mendel had developed his model before starting any experiments, and thus his expectations would have been known to assistants before much data were collected.

As was pointed out earlier, the data collected on seed traits gave particularly low χ^2 values, and because they constitute over half of the data sets collected by Mendel they become the primary source of the high correlation between observed and expected ratios. It is plausible that Mendel assigned the classification of seed phenotypes to others while handling the vegetative characters (stem height, pod color, pod shape, and flower distribution) himself. If such were the case, the modification of the seed trait data to better fit the model being tested would be a competing explanation to the "ambiguous data" hypothesis discussed in the previous section.

Seed coat color is the key trait to allow a test between the "ambiguous phenotype" and the "fabricated data" alternatives because this trait would be scored with other seed traits but in contrast to the

Table 4. Comparison of *P* value distributions derived from the segregation of Mendel and those of the linkage studies cited in Table 3

Trait	Mendel's data		Linkage data	
	No. of sets with $P < 0.5$	No. of sets with $P > 0.5$	No. of sets with $P < 0.5$	No. of sets with $P > 0.5$
Unambiguous traits				
Seed coat color	0	3	16	14
Stem height	1	1	10	14
Pod color	0.5[a]	0.5[a]	19	14
Total (unambiguous traits)	1.5	4.5	45	42
Chi square[b] and P[c] (based on 1:1 expected ratio for $P < 0.5$: $P > 0.5$)	$\chi^2 = 1.50$ (n.s.)		$\chi^2 = 0.29$ (n.s.)	
Ambiguous traits				
Seed shape	0	8	16.5[a]	11.5[a]
Cotyledon color	2	6	7	8
Pod shape	0	1	4	2
Total (ambiguous traits)	2	15	27.5	21.5
Chi square[b] and P[c]	$\chi^2 = 9.94$ ($P = 0.0018$)		$\chi^2 = 0.73$ (n.s.)	

n.s., not significant.

[a]Those data giving a $P = 0.50$ were treated as half a set with $P < 0.5$ and half a set with $P > 0.5$.

[b]Based on 1:1 expected ratio for $P < 0.5$:$P > 0.5$.

[c]One degree of freedom.

other 2 seed traits is not likely to generate intermediate phenotypes. For Mendel's results to support the "fabricated data" alternative the *P* values for seed coat segregation should be distorted in the same manner as those for seed shape and cotyledon color and these as a group should differ significantly from the *P* values of the other traits. Rearranging the grouping in Table 4 so that seed coat color is grouped with seed shape and cotyledon color and concomitantly grouping pod shape with stem height and pod color again gives only 1 of the 3 groups with a significant deviation: that containing Mendel's data for the seed traits. The calculated χ^2 value is slightly larger for this grouping (11.4) than for the ambiguous/nonambiguous grouping, but the number of data sets being compared is so low that the difference in the 2 values is not significant. A Mann–Whitney *U* test could not performed because the total of stem height + pod shape + pod color data sets is too small for an accurate estimate of *U*. However, based on the chi-square analysis, the deliberate falsification alternative is still consistent with the data.

Why Mendel Did Not Observe Linkage

The issue of why Mendel did not observe linkage has been discussed by several previous authors (Dunn 1965; Blixt 1975; Novitski and Blixt 1979; Fairbanks and Rytting 2001; Franklin 2008). I resurrect this subject again for 2 reasons. First, all the previous discussions of this subject were based on the incorrect linkage map for pea published by Blixt (1972), and second, the determination that Mendel should have observed linkage at least between 2 traits speaks to the issue of whether Mendel's text can be taken literally.

As early as 1984, the mapping of molecular markers gave results inconsistent with the map of Blixt (Weeden and Marx 1984, 1987). A joint effort among pea geneticists to determine the standard arrangement of loci in pea led to the publication of a "consensus linkage map" (Weeden et al. 1998), which differed from that of Blixt (1972) for 6 of the 7 linkage groups, including the incorporation of a totally new linkage group that had been poorly marked with classical mutants. Thus, the discussions by Blixt (1975), Novitski and Blixt (1979) and, surprisingly, even Fairbanks and Rytting (2001) and Franklin (2008) require slight revisions in order to be consistent with the accepted linkage map for pea. The corrected map places cotyledon color locus (*I*) near one end of linkage group I (LG I), the only one of Mendel's genes on this linkage group. Similarly, the seed coat color locus (*A*) is alone on LG II and the fasciated stem locus (*Fa*) alone on LG IV. However, the loci controlling seed shape (*R*) and pod color (*Gp*) are both on the same chromosome (LG V) and the remaining 2 loci controlling stem height (*Le*) and pod shape (*V*) are both on LG III.

The distance between *R* and *Gp* is relatively large and the recombination value between the 2 loci can often exceed 40%. Mendel did not include in his article the actual data for joint segregation between the seed shape and pod color characters, but it is likely that in the limited populations he examined, he failed to observe a significant deviation from independent assortment between these 2 traits. The same cannot be said for a test of independent assortment between *Le* and *V*. These loci display a recombination frequency of approximately 5 cM (Rasmusson 1927; Weeden NF, unpublished data). If Mendel had these 2 traits co-segregating in a population, as he implied in his statement "It is demonstrated at the same time that the relation of each pair of different characters in hybrid union is independent of the other differences in the 2 original parental stocks," then he did not carefully examine his results.

Further information on Mendel's work with this pair of traits can be obtained from his second letter to Carl Nägeli (Stern and Sherwood 1966, p. 62). In this letter, Mendel mentions a cross between a tall line with constricted pods and a dwarf line with "arched" pods, confirming that he had examined progeny from a cross in which stem height and pod shape co-segregated. In this cross, the 2 recessive mutations are in repulsion, so that the primary deviation from random assortment would be the lack of the double mutant phenotype (dwarf, constricted pods). Assuming Mendel obtained only 2–3 hybrid seeds from the original cross, the F_2 population probably would be only 40–120 individuals, and only 3–8 double recessives would have been expected based on Mendel's model (0–1 are expected based on the linkage value). Mendel may have dismissed the lack of the double mutant in the F_2 to sampling error. However, as he had taken at least some of the progeny to the F_4 he should have noted the persistent low frequency of the double recessive phenotype.

Discussion

Based on a large number of statistical analyses as well as the review of several well-known geneticists, there can be little doubt that the data Mendel presented in 1866 corresponded much more closely to the predictions of his model than could be reasonably expected by chance. In the present article, I used Mendel's original data, segregation data generated in pea by others, and a general knowledge about the biology of this organism to search for evidence supporting or rejecting alternative explanations for this bias.

The suggestion that pea for some reason naturally generates segregation ratios that adhere much more strictly to the 3:1, 1:1, 2:1, and 1:2:1 ratios tested by Mendel was dealt with fairly simply by examining the segregation ratios obtained by more recent geneticists when studying the same traits that Mendel analyzed. Rather than greater conformity to the expected ratios, this later work displayed a slightly greater tendency for pea to produce distorted segregation ratios than predicted by models. The possibility of the tetrad-pollen model as an explanation was discounted through work by Fairbanks and Schaalje (2007). Hence, the alternative listed by Sturtevant (1965) could not explain any of the bias in Mendel's data.

The remaining 3 alternatives all appear to have some merit. The second alternative, that Mendel selected the data he presented in his article, is highly likely. The lack of any segregation data deviating significantly from the expected ratio, the absence of significant deviation for the distribution of flowers on the stem, and the peculiar method of presenting the segregation data (as summaries rather than as individual crosses) all suggest that some data were not presented. However, even had Mendel been willing to (or permitted to) present all of his data, particularly data sets that deviated significantly from expected ratios, these would have been limited in number and would not have impacted his primary conclusions. In addition, this hypothesis does not effectively address the absence of data sets with χ^2 values between 0.8 and 3.84. Mendel did not have sufficient space or time to perform an extensive enough analysis (presumably repeating each experiment numerous times) for him to select only those data sets with χ^2 values less than 0.8.

Either or both alternative 3 and 4 could explain much of the bias present in Mendel's data. The seed shape trait is the most offending character with regard to having a close match between observed and predicted segregation ratios (Table 1), and it is both a trait capable of producing ambiguous phenotypes and one for which the

classification of phenotypes could have been delegated to an assistant. The limited number of data sets available for seed coat color trait prevents a clear discrimination between these 2 alternatives. All 3 data sets have *P* values above 0.5, but the probability of this result (0.125) is still reasonable.

If we attribute much of the tight fit between observed and predicted ratios for seed shape, cotyledon color, and pod shape to a bias classification of ambiguous phenotypes, we still have several inconsistencies in Mendel's experiments to explain. Fisher's concern regarding the testing of the 2:1 ratio in the F_3 remains an issue that seems to be best resolved by claiming that Mendel planted more seed per F_2 plant or more F_3 families than he stated. The relatively low average χ^2 and variance Mendel observed for the traits giving unambiguous phenotypes, the absence of any data sets displaying distorted segregation, and the normal segregation for fasciated stem I can only ascribe to omission of some of his data or his being extremely lucky. Finally, Mendel's apparent need to force all observed phenotypes into alternate categories, and his failure to adequately test joint segregation between all traits (leading to his erroneous conclusion that they all assorted independently) appear to be a result of his confidence that his model was correct, making unnecessary the careful testing of these 2 assumptions. One can only conclude that Mendel's research does not reflect the approach of a circumspect researcher exploring the possibility of a novel hypothesis but rather of one who has developed a brilliant model and wants to rigorously demonstrate its properties to an unenthusiastic audience.

One of the most intriguing aspects of Mendel's model is that it was not immediately tested by other researchers in other organisms. Mendel's style of writing is clear to the point of being pedantic, and except for the terminology used would make excellent reading for an introductory genetics course. Nor can one argue that the concepts being introduced or the methods being used were so sophisticated as to be beyond the understanding of the typical biologist at that time. Instead, we are forced to conclude that the scientific community in the latter half of the 19th century was simply not prepared to incorporate Mendel's finding into the current body of knowledge. Mendel probably encountered many uncomprehending colleagues over the years he developed and tested his model, resulting in his being convinced that his presentation needed to be as simple as possible. He may have felt that to carefully detail many of his experimental procedures would merely complicate concepts that he was already finding extremely difficult to communicate.

As Fisher (1936) originally postulated, Mendel was attempting to prove a hypothesis and "his experimental programme becomes intelligible as a carefully planned demonstration of his conclusions." Such a goal would provide a rationale for his insistence that that he could accurately score each plant, because recognition of dubious phenotypes would only complicate his analysis. The same rationale would explain his elimination of segregation data that deviated significantly from his predicted ratios. Finally, in his model all traits assorted independently; there was no reason to expect that they would not, and thus there was no need to rigorously analyze the joint segregation ratios of each pair of traits.

Mendel's genius was his ability to assemble a plausible model for the transmission of certain traits in pea hybrids and test the predictions of the model with a logic and tenacity that few of his colleagues could match. Based on later studies in pea, Mendel appears to have been very lucky in not encountering problems with segregation distortion. Whether Mendel should be placed on a pedestal as the founder of experimental genetics is probably still a moot point. It is not time to "end the controversy" but to acknowledge that none of us is an unbiased observer, and it is only as a community that science becomes self-correcting.

Supplementary Material

Supplementary material can be found at http://www.jhered.oxfordjournals.org/.

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