CHAPTER 2

MENDEL

Gregor Johann Mendel was born in 1822 in the village of Heinzendorf in northern Moravia—then a part of Austria, now in Czechoslovakia, near the Polish border. The area had long been populated by people of German and Czech ancestry, living side by side and presumably intermarrying. Mendel's native tongue was the peculiar Silesian dialect of German; in later life he had to learn to speak Czech. He came of peasant stock, and only by persistence and hard work was he able to get a start in education. In 1843 he was admitted as a novice at the Augustinian monastery at Brünn; four years later he became a priest. He took an examination for a teaching certificate in natural science and failed (1850). It has been suggested that the examining board was biased because he was a priest or because his scientific views were unorthodox; the plain fact seems to be that he was inadequately prepared. In order to remedy this, he spent four terms, between 1851 and 1853, at the University of Vienna, where he studied physics, chemistry, mathematics, zoology, entomology, botany, and paleontology. In the first term he took work in experimental physics under the famous Doppler and was for a time, an "assistant demonstrator" in physics. He also had courses with Ettinghausen, a mathematician and physicist, and with Redtenbacher, an organic chemist—both productive research men. We may surmise that this background led to his use of quantitative and experimental methods in biological work. Another of his professors at Vienna, Unger in botany, was also an outstanding figure. Unger was one of the important men in the development of the cell theory; he had demonstrated the antherozoids of mosses and correctly interpreted them as the male generative cells, and he had shown (in opposition to Schleiden) that the meristematic cells of higher plants arise by division. In 1855 Unger published a book on the anatomy and physiology of plants that is rated by Sachs as the best of its time; in this book he made the first suggestion that the fluid content of animal cells and that of plant cells are essentially similar. Mendel was thus in contact with at least two first-rate research scientists, and evidence of their influences upon him shows in his major paper.

Mendel returned to Brünn after the summer term of 1853 at Vienna. At a meeting of the Vienna Zoological-Botanical Society in April, 1854, his teacher Kollar read a letter from him, in which he discussed the pea weevil (*Bruchus pisi*). In the summer of 1854, Mendel grew thirty-four strains of peas; he tested them for constancy in 1855. In 1856 he began the series of experiments that led to his paper, which was read to the Brünn Society for Natural History in 1865 and was published in their proceedings in 1866. Before discussing this paper and its consequences, it will be well to describe some later events in Mendel's life.

He was interested in honeybees and was an active member of the local beekeepers' society. He attempted to cross strains of bees, apparently without success. It has been suggested by Whiting and by Zirkle that he probably knew of the work of Dzierzon on bees, and that Dzierzon's description of segregation in the drone offspring of the hybrid queen may have given Mendel the clue that led to his studies of peas. He is also known to have kept mice, and Iltis and others have suggested that he may have first worked out his results with them, but hesitated, as a priest, to publish on mammalian genetics. These suggestions both seem unlikely to me; there seems no reason to doubt Mendel's own statement: "Experience of artificial fertilization, such as is effected with ornamental plants in order to obtain new variations in color, has led to the experiments which will here be discussed." Perhaps the selection of peas as his experimental material was due in part to Gärtners's account of the work of Knight on peas.

Mendel was also interested in meteorology. At least as early as 1859, he was the Brünn correspondent for Austrian regional reports, and he continued to make daily records of rainfall, temperature, humidity, and barometric pressure to the end of his life. He also kept records of sunspots and of the level of ground water as measured by the height of the water in the monastery well. In 1870 a tornado passed over the monastery, and Mendel published a detailed account of it in the *Proceedings of the Brünn Society*. He noted that the spiral motion was clockwise, whereas the usual direction is counterclockwise. He gave many details, and attempted a physical interpretation. This paper was stillborn, as was his earlier one on peas, published in the same journal. According to Iltis, a catalogue issued in 1917 lists 258 tornadoes observed in Europe but does not include Mendel's account.

In 1868 Mendel was elected abbot of the Brünn monastery. This led to administrative duties and, beginning in 1875, to a controversy with the government on taxation of monastery property. It appears that he continued his meteorological and horticultural observations, but his productive scientific work was finished about 1871. He died January 6, 1884.

Mendel sent a copy of his major paper to Nägeli, together with a letter in which he stated that he was continuing his experiments, using Hieracium, Cirsium, and Geum. Nägeli was professor of botany at Munich and a major figure of his time in biology. He was also interested in heredity and was actively working on it. He completely failed to appreciate Mendel's work and made some rather pointless criticisms of it in his reply to Mendel's letter. He did not refer to it in his publications. He was greatly interested in Hieracium, however, which fact led to a correspondence with Mendel. Nägeli's letters have been lost, but he kept some of Mendel's letters to him. Found among his papers, these were published by Correns in 1905 (I have used the translation in *The Birth of Genetics,* issued in 1950 as a supplement to Volume 35 of *Genetics).* There are ten of these letters, written between 1866 and 1873, and they give a picture of Mendel's biological work during the period. Because of Nägeli's interest, much of the account has to do with Hieracium, the subject of Mendel's only other published paper in genetics (published in 1870 in the *Proceedings of the Brünn Society* for 1869; a translation may be found in Bateson's *Mendel's Principles,* 1909).

The work on Hieracium must have been a great disappointment to Mendel. He obtained several hybrids by dint of much hard work, and all of them bred true. It is now known that this occurs because the seeds are usually produced by apomixis, that is, they are purely maternal in origin and arise without the intervention of meiosis or fertilization (Raunkiär 1903, Ostenfeld 1904). In other words, this was the worst possible choice of material for the study of segregation and recombination—for reasons that could not be guessed at the time.

It appears from Mendel's letters to Nägeli that he was very actively engaged in genetic studies on several other kinds of plants through 1870. His experiments (previously mentioned) with single pollen grains of Mirabilis were repeated in two different years with the same result. He reports studies on Mirabilis, maize, and stocks. Of these three he says "Their hybrids behave exactly like those of Pisum." The character studied in stocks was hairiness; with respect to flower color in this plant, he says the experiments had lasted six years and were being continued—this in 1870. He had grown 1500 specimens for the purpose in that year; his difficulty arose from the mutiplicity of shades that were hard to separate.

In Mirabilis he had seen and understood the intermediate color of a heterozygote and had made the appropriate tests to establish this interpretation. He also mentioned experiments with several other plants—Aquilegia, Linaria, Ipomoea, Cheiranthus, Tropaeolum, and Lychnis.

The picture that emerges is of a man very actively and effectively experimenting, aware of the importance of his discovery, and testing and extending it on a wide variety of forms. None of these results were published; it is difficult to suppose that his work would have been so completely ignored if he had presented this confirmatory evidence, even though it was not enough to convince Nägeli.

This, in outline, is the man. I have tried to give an account of him in order to form a basis for judging his paper—how it came about that he did the work, and what one is to think in view of the analysis by Fisher that will be discussed. A fuller account of Mendel will be found in the biography by Iltis.

There are a number of new procedures in Mendel's work. He himself said in the paper, ". . . among all the numerous experiments made [by his predecessors], not one has been carried out to such an extent and in such a way as to make it possible to determine the number of different forms under which the offspring of hybrids appear, or to arrange these forms with certainty according to their separate generations, or definitely to ascertain their statistical relations." One may agree with Bateson's comment on this passage: "It is to the clear conception of these three primary necessities that the whole success of Mendel's work is due. So far as I know this conception was absolutely new in his day."

This was his experimental approach, but it was effective because he also developed a simple interpretation of the ratios that he obtained and then carried out direct and convincing experiments to test this hypothesis. The paper must be read to be appreciated. As has often been observed, it is difficult to see how the experiments could have been carried out more efficiently than they were.

As Fisher (1936) puts it, it is as though Mendel knew the answer before he started, and was producing a demonstration. Fisher has attempted to reconstruct the experiments as carried out year by year, knowing the garden space available and the number of years involved.* He concludes

* Fisher's dates are wrong. He gives them as 1857 to 1864, but it is clear from Mendel's letters to Nägeli that the final year was 1863. Fisher includes the two years of preliminary testing in the eight years that Mendel says the experiments lasted. I have interpreted the statement to mean that these two years preceded the eight years of actual experiments—an interpretation also given by Yule (1902). Fisher's interpretation may be right, but if Yule and I are right there are two more years available and Fisher's year-by-year reconstruction needs revision. It may also be pointed out that Mendel

that the crosses were carried out in the order in which they are described. He also points out several other aspects of the work that seem significant. For example, in testing F_2 individuals to distinguish homozygous dominants from heterozygotes, Mendel must have had a much larger number of seeds illustrating the 3 : 1 ratio than those recorded in F_2; but he did not report these numbers (if he even troubled to count them). Evidently he felt that larger numbers were of no importance.

The most serious matter discussed by Fisher is that Mendel's ratios are consistently closer to expectation than sampling theory would lead one to expect. For yellow vs. green seeds, his F_2 numbers were 6022 : 2001—a deviation of 5 (from 3 : 1), whereas a deviation of 26 or more would be expected in half of a large number of trials, each including 8023 seeds. Fisher shows that this same extremely close fit runs through all Mendel's data. He calculates that, taking the whole series, the chance of getting as close a fit to expectation is only .00007, that is, in only 1 trial of 14,000 would one expect so close an agreement with expectation.

If this were all, one might not be too disturbed, for it is possible to question the logic of the argument that a fit is too close to expectation. If I report that I tossed 1000 coins and got exactly 500 heads and 500 tails, a statistician will raise his eyebrows, though this is the most probable exactly specified result. If I report 480 heads and 520 tails, the statistician will say that is about what one would expect—though this result is less probable than the 500 : 500 one. He will arrive at this by adding the probabilities for all results between 480 : 520 and 520 : 480, whereas for the exact agreement he will consider only the probability of 500 : 500 itself. If now I report that I tossed 1000 coins ten times, and got 500 : 500 every time, our statistician will surely conclude that I am lying, though this is the most probable result thus exactly specified. The argument comes perilously close to saying that no such experiment can be carried out, since every single exactly specified result has a vanishingly small probability of occurring.

In the present case, however, it appears that in one series of experi-

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probably used some time and garden space in the later years of this period to carry out the experiments with beans and hawkweeds and with the several other plants referred to in the letters to Nägeli.

Fisher also quotes extensively from a paper by Nägeli (1865), and concludes that "it is difficult to suppose that these remarks were not intended to discourage Mendel personally, without drawing attention to his researches." But this paper of Nägeli's was published before Mendel's—clearly before Nägeli could have known anything about Mendel's work!

ments Mendel got an equally close fit to a *wrong* expectation. He tested his F_2 plants that showed dominant characters to see which were homozygous and which were heterozygous, since his scheme required that these occur in the ratio of 1 : 2. For the seed characters (yellow vs. green, round vs. wrinkled), it was necessary only to plant the F_2 seed and observe the seeds the resulting plants produced when allowed to self-pollinate. For the other characters, it was necessary to plant the F_3 seeds and see what kinds of plants they produced. For this purpose, Mendel planted 10 seeds from each tested F_2 dominant. If the tested plant was heterozygous, one-fourth of its offspring would show the recessive. Fisher points out that there is an uncertainty here that was not taken into account by Mendel. For a plant that is heterozygous, the chance that any one offspring will not be a homozygous recessive is .75. The chance that none of 10 will be a homozygous recessive therefore is $(.75)^{10} = .0563$. That is to say, by this test between 5 and 6 percent of the actual heterozygotes will be classified as homozygotes. Fisher shows that Mendel's results are very close to the 2 : 1 ratio expected without this correction and are not in close agreement with the corrected expectation of 1.8874 to 1.1126—in fact as poor an agreement (with the corrected expectation) as Mendel recorded would be expected to occur rather less often than once in 2000 tries.

The argument that a fit to expectation is not close enough is not subject to the criticisms that were levelled earlier against the argument that a fit is too close. There are, however, some further aspects that need discussion. The critical passage in Mendel's paper reads: "Für jeden einzelnen von den nachfolgenden Versuchen wurden 100 Pflanzen ausgewählt, welche in der ersten [second, by current terminology] Generation das dominierende Merkmal besassen, und um die Bedeutung desselben zu prüfen, von jeder 10 Samen angebaut." Fisher is right if only 10 seeds were planted from each tested F_2 dominant. If the experiment included at least 10 seeds but often more than 10, then the correction to the 2 : 1 expectation will be less, and Fisher's most telling point will be weakened. The statement by Mendel seems unequivocal, but the possibility remains that he may have used more than 10 seeds in some or many tests.

There is a possible slight error in Fisher's expectations. In the pea flower, the anthers are closely apposed to the style, and if a plant is allowed to self-pollinate it may be expected that, as a rule, one anther will break at one point. The pollen grains near the break will then be first on the stigma and will be the ones that function. Under these conditions, it may be that the functioning pollen will not be a random sample but will represent all or most of the grains from one or a few pollen-mother-cells. This does not seem likely to be an important factor, since there are so few seeds per flower; but in the limiting case it could result in the sampling error (from a self-pollinated heterozygote) being limited to the eggs alone. Calculations based on this improbable limiting assumption indicate that Fisher's general conclusions would still hold good; but the point remains that in any such analysis one needs to examine the assumptions very carefully, to make sure there may not be some alternative explanation.

Mendel's experiments have been repeated by many investigators, and the question arises: have they also reported unexpectedly close agreement with expectation? For the F_2 ratio for yellow vs. green seeds, the data from several sources have been tabulated by Johannsen, and the statistical calculations have been carried out by him, with the results shown in Table 1.

TABLE 1. F_2 RESULTS, PEA CROSSES

Source	Yellow	Green	Total	Dev. from 3 in 4	Prob. Error	Dev. ÷ P.E.
Mendel, 1866	6,022	2,001	8,023	+ .0024	± .0130	.18
Correns, 1900	1,394	453	1,847	+ .0189	± .0272	.70
Tschermak, 1900	3,580	1,190	4,770	+ .0021	± .0169	.12
Hurst, 1904	1,310	445	1,775	– .0142	± .0279	.51
Bateson, 1905	11,902	3,903	15,806	+ .0123	± .0093	1.32
Lock, 1905	1,438	514	1,952	– .0533	± .0264	2.04
Darbishire, 1909	109,060	36,186	145,246	+ .0035	± .0030	1.16
Winge, 1924	19,195	6,553	25,748	– .0180	± .0125	1.44
Total	153,902	51,245	205,147	+ .0008	± .0038	.21

SOURCE: Johannsen, 1926.

Evidently this is in good agreement with expectation. It would be expected that the values in the last column would be more than 1.00 in half of the series, less than 1.00 in half—which happens to be just what is observed. One observer, Tschermak, achieved an even closer approach to 3 : 1 than did Mendel. Of the eight observers, five (including Mendel) obtained a small excess of dominants, three got a small deficiency. The poorest fit (that of Lock) would be expected to occur in about 1 out of 6 tries, and it did occur in 1 of 8 series. The over-all impression is that the agreement with expectation is neither too good nor too poor.

In summary, then, Fisher's analysis of Mendel's data must stand essentially as he stated it. There remains the question of how the data came to be as they are. There are at least three possibilities:

1. There may have been an unconscious tendency to classify somewhat doubtful individuals in such a way as to fit the expectation.
2. There may have been some families that seemed aberrant, and that were omitted as being probably due to experimental error.
3. Some of the counts may have been made for him by students or assistants who were aware of his expectations, and wanted to please him.

None of these alternatives is wholly satisfactory, since they seem out of character, as judged by the whole tone of the paper.

Perhaps the best answer—with which I think Fisher would have agreed—is that, after all, Mendel was right!