CHAPTER 4

THE REDISCOVERY

To Bateson and to de Vries, the logical approach to the study of heredity seemed to be the study of variation, which was then to be followed by the study of the transmission of variations. As the event showed, the effective approach was the reverse of this, since the origin of variability could begin to be analyzed only after the nature of segregation and recombination was understood.

By the end of the century both men felt that the time had come to begin a serious study of the inheritance of discontinuous variations. In 1899 Bateson published an analysis of what was needed, which is remarkable, among other things, for the statement "If the parents differ in several characters, the offspring must be examined statistically, and marshalled, as it is called, in respect to each of those characters separately." Here was, clearly, a man whose mind was ready to appreciate the Mendelian approach.

The story of the finding of Mendel's paper and of the confirming of his results in 1900 has often been told—perhaps most fully by Roberts (1929).

Mendel had forty reprints of his paper. He sent copies to Nägeli and to Kerner, professors of botany at Munich and at Innsbrück, respectively, and both interested in plant hybrids. It is not known what happened to the other thirty-eight copies; after Kerner's death, his copy was found in his library with the pages uncut.* As was pointed out earlier, Nägeli did reply but did not appreciate the work or refer to it in print. The journal was perhaps rather obscure, but the Brünn Society had a considerable exchange list, and its *Proceedings* were sent to more than 120 libraries. According to Bateson, there were at least two copies in London. Only

* As will appear below, a third reprint was in the library of the Dutch botanist Beijerinck. I have received, through the kindness of Dr. H. Gloor and Dr. F. Bianchi, a photostat of the cover and first page of this reprint; there is no indication of how or when Beijerinck acquired it, or to whom Mendel sent it.

four printed references to the paper before 1900 are known, however, other than a listing in the *Royal Society Catalogue* of scientific papers. Hoffmann (1869) published an account of experiments with beans, in which Mendel's paper is referred to without any indication of its nature. Focke (1881) published a rather extensive account of the literature of plant hybridization, in which he referred to Mendel's paper under the heading "Pisum." He failed to appreciate or even to understand the work, but he did state that Mendel "believed that he found constant numerical relationships between the types"—a statement that ultimately led to the paper being found, as will be discussed.

The third reference was by L. H. Bailey (1895), who copied Focke's statement without having himself seen Mendel's paper; this was the source that led de Vries to Mendel, according to one account. Finally, Mendel was listed, without comment, as a plant hybridizer by Romanes in the ninth edition of the *Encyclopaedia Britannica* (1881–1895)—evidently again following Focke.

Hugo de Vries (1848–1935) was born in Holland. His university training was largely in Germany, where he studied plant physiology with Sachs. In 1871 he became a lecturer at the University of Amsterdam and, from 1881 until his retirement, was a professor there. His early work was on local floras, the microorganisms in water supplies, and the turgor of plant cells. In the latter field, he carried out a beautiful series of quantitative studies of the effects of the concentrations of various salts on plasmolysis. These results were of importance in the development (by Arrhenius and van't Hoff) of the ionic theory of the osmotic properties of solutions of electrolytes. His *Intracellular Pangenesis* (1889) has been described in Chapter 3; his work on mutation will be discussed in Chapters 10 and 11.

De Vries published three papers on Mendelism in 1900, one of which has, for the most part, been overlooked. The first was read by G. Bonnier before the Paris Academy of Sciences on March 26 and was published in the Academy's *Comptes Rendus.* A reprint of this paper was received by Correns on April 21. Another paper by de Vries is dated "Amsterdam, March 19, 1900," and was published in the *Revue général de botanique,* which was edited by Bonnier. It seems likely, then, that these two French manuscripts were sent to Bonnier at the same time. The third paper, in German, was received by the editor of the journal *(Berichte der deutschen botanischen Gesellschaft)* in Berlin on March 14 and was published April 25. These dates are of some interest because the brief note in the *Comptes Rendus,* the first to be published, does not mention Mendel, though it uses some of his terminology. The *Revue général* paper is the one that is rarely cited. It is longer and does mention Mendel—though only on the last page, where is also an added footnote referring to the *Berichte* paper and to the papers by Correns and by Tschermak, which did not appear until May (apparently this paper was published in July). The reference to Mendel on this page may be translated as follows: "This law is not new. It was stated more than thirty years ago, for a particular case (the garden pea). Gregor Mendel formulated it in a memoir entitled *'Versuche über Pflanzenhybriden'* in the *Proceedings of the Brünn Society*. Mendel has there shown the results not only for monohybrids but also for dihybrids.

"This memoir, very beautiful for its time, has been misunderstood and then forgotten."

In the *Berichte* paper, the second to be published but evidently the first to be submitted, there is much the same material as in the longer French one, but Mendel is mentioned in several places in the text and is given full credit for his discovery.

In a letter received and published by Roberts, de Vries later stated that he had worked out the Mendelian scheme for himself, and was then led to Mendel's paper by reading Bailey's copy of Focke's reference. In 1954, nineteen years after the death of de Vries, his student and successor Stomps reported that de Vries had told him that he learned of Mendel's work through receiving a reprint of the 1866 paper from Beijerinck, with a letter saying that he might be interested in it. This reprint is still in the Amsterdam laboratory, as has been stated.

There is a persistent and widespread story to the effect that de Vries at first intended to suppress any reference to Mendel and changed his mind only when he found that Correns (or Tschermak) was going to refer to him. This is based on the failure to refer to Mendel in the *Comptes Rendus* paper, the first to be published—and, one may add, also in the *Revue général* paper until the last page that was, at least in part, added some months later. This view can be maintained only if it is supposed that the *Berichte* paper was extensively altered in proof—a suggestion that gets some support from the fact that nine of the twenty-two *errata* listed at the end of the volume concern just the pages that would have had to be altered. These *errata* are rather minor, but they do make one wonder if the printer was confused by extensive alterations in the proofs.

A careful comparison of the available dates, however, makes it seem impossible that such changes could have been a result of a letter from Correns after he had seen the *Comptes Rendus* paper, and very unlikely also that a letter from Tschermak could have been involved. Both of these men have stated (Roberts) that they learned that de Vries had the interpretation when they received reprints of this paper from him.

It remains possible, though, that de Vries did come to realize that Correns knew and appreciated Mendel's paper, from the reference in the January, 1900 paper on xenia (to be discussed). This conclusion cannot be accepted as established but seems to be the simplest interpretation of the puzzling facts.

In these three papers de Vries recorded a series of quite different genera of plants that had given the 3 : 1 ratio, and, in several of them, he had also seen the 1 : 1 ratio on crossing the F_1 to the recessive. There was, therefore, no question that the scheme was generally applicable. De Vries concluded that it probably held for all discontinuous variations.

Carl Correns (1864–1933) was a student of Nägeli and of the plant physiologist Pfeffer, who, like de Vries, was a student of Sachs. Correns studied the anatomy and the life cycle of mosses and also became interested in the origin of the endosperm. This tissue in the seeds of higher plants was long supposed to be of purely maternal origin, but it was often observed—especially in maize—that the nature of the endosperm was influenced by the pollen. Correns set out to study this phenomenon (called xenia by Focke). He reached the conclusion that the endosperm was in fact derived from the "double fertilization" that had just been described by Nawaschin in lilies. A preliminary account of these results appeared *(Berichte deutsch. botan. Gesellsch.* January 25, 1900), the manuscript having been received December 22, 1899. The same conclusion was also reached by de Vries in 1899.

In the last paragraph of this paper, Correns pointed out that the superficially similar phenomenon in the case of green and yellow peas was due to color in the cotyledons, that is, in true embryonic tissue "as already correctly pointed out by Darwin and by Mendel." This was the first printed indication that anyone had understood any part of Mendel's work.

In connection with this study, Correns grew hybrids of maize and of peas through several generations, and arrived at the interpretation (that is, the Mendelian one) in 1899. This caused him to read Mendel's paper, because he found Focke's statement that Mendel believed he had found "constant numerical relationships." Correns (in a letter quoted by Roberts) compared his own and Mendel's solution of the problem: ". . . through all that in the meantime had been discovered and thought (I think above all of Weismann), the intellectual labor of finding out the laws anew for oneself was so lightened that it stands far behind the work of Mendel."

Correns reported in detail on his work with peas, in a paper that appeared in May 1900, after he had seen de Vries' account. He fully confirmed Mendel* and said that he had observed the same kind of results with maize; these results were published in full in 1901. He disagreed with de Vries in that he thought there were cases that did not conform to the Mendelian scheme. The only one described in any detail, having to do with the color of the seed coat in peas, seems to have involved the carrying of a dominant gene for color pattern in a plant which also had a recesssive that prevented all color, with the result that the F_1 did not resemble either parent. This type of situation later became familiar but seemed then to contradict the Mendelian scheme.

Erich von Tschermak (1871–1962) was a grandson of Fenzl, under whom Mendel studied systematic botany and microscopy at Vienna. Tschermak was trained at Halle, where he received his doctorate in 1895. His interests were in practical plant breeding, and this led to studies (at Ghent and Vienna) on the effects of crossing and inbreeding on vegetative vigor, following the work of Darwin. In this connection he made crosses of peas and raised F_2, noting the 3 : 1 ratios and also the 1 : 1 on back-crossing to the recessive parent. He later wrote (to Roberts) that he had realized the significance of this result before he found Mendel's paper (through the reference by Focke), but since he had reared only two generations when he published his accounts, he cannot have known that the recessives bred true or that there were two classes of individuals in F_2 that had the dominant character. He published two papers on the subject in 1900. Of these, the first is much less clearly indicative of a real understanding of the situation than is the second, which was written after he had seen the de Vries and Correns papers in the *Berichte*.

William Bateson (1861–1926) was trained as a zoologist at Cambridge. He was influenced by Sedgwick, by F. Balfour, and by his contemporary, Weldon. The summers of 1883 and 1884 were spent at Hampton, Virginia, and Beaufort, North Carolina, studying the embryology of Balanoglossus under W. K. Brooks. Bateson has recorded that it was Brooks who gave him the idea that heredity is a subject worth studying for itself. In passing, it may be remembered that Brooks also influenced the history of genetics through the fact that both E. B. Wilson and T. H. Morgan were trained by him.

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* This confirmation included extensive tests over several generations, showing that extracted homozygotes bred true. This was perhaps the one of Mendel's observations that was hardest to accept at the time. We know that Nägeli balked at it, and that as late as 1910, Morgan tried to explain it away.

Bateson's *Materials for the Study of Variation* (1894) and his outline of what was needed in the study of heredity (1899) have been discussed in Chapter 3 and earlier in this chapter. In May, 1900, he read a paper before the Royal Horticultural Society in London, in which he described the work of Mendel and its confirmation by de Vries. According to Mrs. Bateson (1928), he first learned of Mendel's work on a train, while going from Cambridge to London to deliver this paper, and was so impressed by it that he immediately incorporated it into his lecture.

Bateson at once became the most active proponent of the new approach and developed a very active group of workers at Cambridge, including, in the early years of this century, Saunders, Punnett, Durham, Marryatt, and others. Mendelian studies were actively pursued in Germany by Correns, in Austria by Tschermak, in France by Cuénot, and in the United States by Castle and Davenport. These workers and others soon built up a great mass of data and laid the foundations for later developments.

There were two immediate problems: How widespread are the Mendelian phenomena, and what is the interpretation of the so-called compound characters? Another question, that now seems less important, concerned the generality of the phenomenon of dominance.

Mendel's work established his principles for peas and beans; they were confirmed for peas by Correns and by Tschermak. In his 1900 papers, de Vries showed that the principles applied to about a dozen widely different genera of seed plants, including one monocotyledon (maize, which Correns confirmed). There was thus clear evidence for the general applicability to angiosperms. Correns suggested in 1901 that the principles applied to animals, citing a number of experiments from the earlier literature that appeared to be Mendelian. That the principles do apply to animals was definitely shown in 1902, independently by Cuénot (mice) and by Bateson (fowl). It was therefore concluded that the same general scheme must apply to all higher animals and plants; the later applications to invertebrates and to lower plants were, when they were made, interesting chiefly because they offered means of studying new kinds of problems.

The other important question during the early development was that of the nature of "compound characters"—or, as we should now say, cases where more than one pair of genes affect the same character.

Mendel reported a cross with beans, using as parents a strain with white flowers and one with colored flowers. F_1 was colored, but the cross was between quite different species, and these F_1 plants were only slightly fertile. Mendel obtained a total of 31 F_2 plants, of which only one had white flowers. He suggested, tentatively, that there were two independent dominant genes, A_1 and A_2 either of which alone would give colored flowers. The expectation in F_2 would then be 15 colored : 1 white; but because of the small number of plants available he did not urge this interpretation. In 1902, Bateson criticized this suggestion, since he felt that A_1 and A_2 would be expected to behave as alleles; that is to say, he was still thinking in terms of a single gene for each visible character. A similar point of view is found in the 1900 paper by Correns, as has been pointed out, in his argument that the Mendelian principles could not be general; the same view later led Cuénot to lay no emphasis on his demonstration of multiple alleles (see Chapter 8).

Several examples of a related sort soon turned up—first in the case of flower color in the sweet pea, where a cross of two whites gave colored flowers in F_1, and in F_2, 9 colored : 7 white (Bateson and Punnett). Tests of individual F_2 plants showed that this occurred because color development requires the presence of both of two independent dominants. The F_2 ratio is 9 : 3 : 3 : 1, with the last three classes indistinguishable, rather than the first three, as in Mendel's beans. With this cleared up (by Bateson and Punnett), it was not difficult to interpret the 9 : 3 : 4 cases that were soon found.

The case of combs in fowl was puzzling at first. Here the familiar "rose" comb was soon shown to be dominant to single, and "pea" was also shown to be dominant to single. When rose was crossed to pea, a new type, called "walnut," appeared; this did not seem to be, structurally, a combination of rose and pea. The relations became clear when it was found that the F_2 ratio is 9 walnut : 3 rose : 3 pea : 1 single (again by Bateson and Punnett)—for Mendel had already shown that this ratio meant that two independent pairs of genes were segregating.

The occasional occurrences of cases in which the heterozygote is intermediate, that is, strict dominance is absent, was indicated by Correns in a footnote added to his 1900 paper in proof. This had been seen and understood, with the appropriate tests carried out, in Mirabilis by Mendel, according to his letters to Nägeli, and is implied in his account of flowering time in peas in the 1866 paper. The Mirabilis case and that of the Andalusian fowl became clear very early in the period after 1900, and as a result, the phenomenon of dominance was recognized as of only secondary importance.

New terminology was needed. Many of the now-familiar terms were introduced by Bateson—such as *genetics,* for the subject itself, and *zygote,* for the individual that develops from the fertilized egg, as well as for the fertilized egg itself (which was the older usage). *Homozygote,* *heterozygote,* and the adjectives derived from them followed. Mendel had spoken of the hybrids and the first generation from them; Bateson suggested that these be designated "F_1" and "F_2," respectively—to stand for first and second filial generations.* The term *allelomorph* (later, especially in the United States, shortened to *allele)* also dates from Bateson's early work. Mendel usually used the word *Merkmal* for what we now term *gene,* and this was translated as *character,* often appearing as *unit character*; Bateson usually used the word *factor.* It was somewhat later (1909) that Johannsen introduced the word *gene*.

* The confusion existing may be illustrated further by the fact that Haacke (Chapter 3) considered the parental generation as the first and referred to what we now call "F_1" and "F_2" as the second and third generations, respectively.