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HAS MENDEL'S WORK BEEN REDISCOVERED?

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1. THE POLEMIC USE OF THE REDISCOVERY.

THE tale of Mendel's discovery of the laws of inheritance, and of the sensational rediscovery of his work thirty-four years after its publication and sixteen after Mendel's death, has become traditional in the teaching of biology. A careful scrutiny can but strengthen the truth in such a tradition, and may serve to free it from such accretions as prejudice or hasty judgment may have woven into the story. Few statements are so free from these errors as that which I quote from H. F. Roberts' valuable book *Plant Hybridisation before Mendel* (p. 286):

> "The year 1900 marks the beginning of the modern period in the study of heredity. Despite the fact that there had been some development of the idea that a living organism is an aggregation of characters in the form of units of some description, there had been no attempts to ascertain by experiment, how such supposed units might behave in the offspring of a cross. In the year above mentioned the papers of Gregor Mendel came to light, being quoted almost simultaneously in the scientific contributions of three European botanists, De Vries in Holland, Correns in Germany, and Von Tschermak in Austria. Of Mendel's two papers, the important one in this connection, entitled 'Experiments in Plant Hybridization', was read at the meetings of the Natural History Society of Brünn in Bohemia (Czecho-Slovakia) at the sessions of February 8 and March 8, 1865. This paper had passed entirely unnoticed by the scientific circles of Europe, although it appeared in 1866 in the Transactions of the Society. From its publication until 1900, Mendel's paper appears to have been completely overlooked, except for the citations in Focke's 'Pflanzenmischlinge', and the single citation of Hoffmann, elsewhere referred to."

When the History of Science is taken seriously the number of enquiries which such a story suggests is somewhat formidable. We want to know first : What did Mendel discover ? How did he discover it ? And what did he think he had discovered? Next, what was the relevance of his discoveries to the science of his time, and what was its reaction to them ? In the case of Mendel these last questions must be duplicated, for we are concerned not only with the period following the reading of his principal paper in 1865, but with that following the widespread publicity it received in 1900. This will be considered first.

Seeing how often it is taken for granted that all clouds were cleared away at the rediscovery in 1900, it is singularly difficult to ascertain exactly how Mendel's experiments were conducted and, indeed, what experiments he carried out. We have, of course, his paper, principally devoted to garden peas, entitled "Versuche über Pflanzenhybriden", printed in the transactions of the Natural History Society of Brünn, in Bohemia, in 1866, and reprinted in 1910. In 1901 it was also twice reprinted, in *Flora,* and in Ostwald's *Klassiker der exakten Wissenschaften* (No. 121). A valuable English translation, prepared for the Royal Horticultural Society, was published in 1901, and reprinted with modifications by Bateson on several occasions. I shall refer to its appearance in Bateson's book *Mendel's Principles of Heredity* (Cambridge, 1909).

It cannot be denied that Bateson's interest in the rediscovery was that of a zealous partisan. We must ascribe to him two elements in the legend which seem to have no other foundation : (1) The belief that Darwin's influence was responsible for the neglect of Mendel's work, and of all experimentation with similar aims ; and (2) the belief that Mendel was hostile to Darwin's theories, and fancied that his work controverted them. On the first point we may note a paragraph from Bateson's preface (p. 2) :

> "While the experimental study of the species problem was in full activity the Darwinian writings appeared. Evolution, from being an unsupported hypothesis, was at length shown to be so plainly deducible from ordinary experience that the reality of the process was no longer doubtful. With the triumph of the evolutionary idea curiosity as to the significance of specific differences was satisfied. The *Origin* was published in 1859. During the following decade, while the new views were on trial, the experimental breeders continued their work, but before 1870 the field was practically abandoned."

It should be noted that Bateson here identifies experimental breeding with the hybridization of species. He ignores the fact that Mendel's advance over his predecessors was due to crossing closely allied varieties, not different species, which, as Mendel actually recognized, would differ in a large number of different factors. It is a consequence of Darwin's doctrine that the nature of the hereditary differences between species can be elucidated by studying heredity in crosses within species. So far were the new evolutionary ideas from discouraging experimental breeding that Darwin, himself, apart from other work, devoted eleven years prior to 1876 to the great series of experiments of which his book on *The Effects of Cross- and Self-fertilisation in the Vegetable Kingdom* is a report. Had his example been followed there would have been no such lull as succeeded his death. Like Mendel's experiments a few years earlier they seemed to lead to nothing more at the time. To-day, in the light of genetic analysis, we can go further towards appreciating their significance.

Bateson's eagerness to exploit Mendel's discovery in his feud with the theory of Natural Selection shows itself again in his misrepresentation of Mendel's own views. Although he was in fact not among those responsible for the rediscovery, his advocacy created so strong an impression that he is still sometimes so described. In the biographical notice which Bateson prefixes to his reprint of Mendel's papers he writes (p. 311):

> "With the views of Darwin which were at that time coming into prominence Mendel did not find himself in full agreement, and he embarked on his experiments with peas, which as we know he continued for eight years."

The suggestion that Mendel was prompted by disagreement with Darwin's views to undertake his experiments is easily disproved. Mendel's experiments cannot have commenced later than 1857. Darwin's views on evolution were known only to a few friends prior to the papers which he communicated, jointly with Wallace, to the Linnean Society in 1858. That Mendel had heard of Darwin, as a geologist or an explorer, at the time his experiments with peas were commenced is, indeed, possible. More probably he knew nothing of Darwin's existence, and certainly nothing of the theory of Natural Selection, at this date. When, in 1865, Mendel reported his experiments, the situation had doubtless changed. Mendel now recognizes that the study of inheritance has a special importance in relation to evolutionary theory. He alludes to the subject, in his introductory remarks, in words which suggest not doubts, but rather a simple acceptance of the theory of evolution (p. 318):

> "It requires indeed some courage to undertake a labour of such far-reaching extent; this appears, however, to be the only right way by which we can finally reach the solution of a question the importance of which cannot be overestimated in connection with the history of the evolution of organic forms."

In this paper the only other mention of evolution occurs in the concluding remarks, in which the results and opinions of Gärtner are discussed. It will be seen that Mendel expressly dissociates himself from Gärtner's opposition to evolution, pointing out on the other hand that Gärtner's own results are easily explained by the Mendelian theory of factors (p. 361) :

> " Gärtner by the results of these transformation experiments was led to oppose the opinion of those naturalists who dispute the stability of plant species and believe in a continuous evolution of vegetation. He perceives in the complete transformation of one species into another an indubitable proof that species are fixed within limits which they cannot change. Although this opinion cannot be unconditionally accepted we find on the other hand in Gärtner's experiments a noteworthy confirmation of that supposition regarding variability of cultivated plants which has already been expressed."

It is seen from these, the only two allusions to evolution in Mendel's paper, that he did not regard his work as a direct contribution to that subject. What he does claim for the laws of inheritance he established is that they make sense of many of the results of the hybridists, and that they form a necessary basis for the understanding of the evolutionary process. On this point he shows himself fully aware of the importance of what he had done. Had he considered that his results were in any degree antagonistic to the theory of selection it would have been easy for him to say this also.

2. Should Mendel be taken Literally ?

Bateson raised a point of great interest as to the conduct of Mendel's experiments in a footnote to a passage in the translation he used. After describing his first seven experiments Mendel opens his eighth (unnumbered) section with the words (p. 332) :

> " In the experiments described above plants were used which differed only in one essential character " (*wesentliches Merkmal*).

Bateson notes :—

> " This statement of Mendel's in the light of present knowledge is open to some misconception. Though his work makes it evident that such varieties may exist, it is very unlikely that Mendel could have had seven pairs of varieties such that the members of each pair differed from each other in *only* one considerable character. The point is probably one of little theoretical or practical consequence, but a rather heavy stress is laid on the word *wesentlich*."

Most practical experimenters will feel the weight of this difficulty. Unless Mendel had known in advance of the separate inheritance of the characters he was studying he could scarcely have used seven such pairs oı varieties. More probably, perhaps, he would have used fewer varieties, say four or five, and crossed these in all, six or ten, possible ways. In any case, we should expect that some or all of the crosses would have involved more than one contrasted pair of characters. Each progeny would then have segregated in more than one factor, and the question arises as to what Mendel did with these additional data. Two courses seem possible :

(i) He might, for each cross, have chosen arbitrarily one factor, for which that particular cross was regarded as an experiment, and ignored segregation in other factors.

(ii) He might have scored each progeny in all the factors segregating, assembled the data for each factor from the different crosses in which it was involved, and reported the results for each factor as a single experiment.

The first course seems incredibly wasteful of data. This objection is not so strong as it might seem, since it can be shown that Mendel left uncounted, or at least unpublished, far more material than appears in his paper. He evidently felt no anxiety lest his counts should be regarded as insufficient to prove his theory. But, apart from being wasteful, to have adopted this course would seem to imply as much foreknowledge of the outcome as if he had deliberately chosen unifactorial crosses. It would seem in any case an extremely arbitrary course to take.

The second course is in effect what most modern geneticists would do, unless they were discussing either the linkage or the interaction of more than one factor. Mendel nowhere gives summaries of the aggregate frequencies from different experiments, and this would be intelligible if the " experiments " reported in the paper were fictitious, being in reality themselves such summaries. Mendel's paper is, as has been frequently noted, a model in respect of the order and lucidity with which the successive relevant facts are presented, and such orderly presentation would be much facilitated had the author felt himself at liberty to ignore the particular crosses and years to which the plants contributing to any special result might belong. Mendel was an experienced and successful teacher, and might well have adopted a style of presentation suitable for the lecture-room without feeling under any obligation to complicate his story by unessential details. The style of didactic presentation, with its conventional simplifications, represents, as is well known, a tradition far more ancient among scientific writers than the more literal narratives in which experiments are now habitually presented. Models of the former would certainly be more readily accessible to Mendel than of the latter.

The great objection to the view suggested by Bateson's hint, that

Mendel's " experiments " are fictitious, and that his paper is a didactic exposition embodying his accumulated data, lies in the words which Mendel himself used in introducing the successive steps of his account, *e. g.*, at the beginning of the eighth section (p. 332) " The next task consisted in ascertaining . . . . ", and the opening sentence of the ninth section (p. 338) " The results of the experiments previously described led to further experiments ". It is true that the different experiments described are not numbered in a single series ; those described in any one section are numbered afresh 1, 2, 3, ... , so that these numbers were certainly assigned when the account was written ; also we are never told in what year different plants were grown ; yet, if Mendel is not to be taken literally, when he implies that one set of data was available when the next experiment was planned, he is taking, as *redacteur*, excessive and unnecessary liberties with the facts. Moreover, the style throughout suggests that he expects to be taken entirely literally ; if his facts have suffered much manipulation the style of his report must be judged disingenuous. Consequently, unless real contradictions are encountered in reconstructing his experiments from his paper, regarded as a literal account, this view must be preferred to all alternatives, even though it implies that Mendel had a good understanding of the factorial system, and the frequency ratios which constitute his laws of inheritance, before he carried out the experiments reported in his first and chief paper. Such a reconstruction is attempted in the next section.

3. An Attempted Reconstruction.

A framework for dating the experiments is afforded by the statement (p. 318) :

> " This experiment was practically confined to a small plant group, and is now, after eight years, concluded in all essentials."

Mendel's paper was presented on the 8th of February, 1865 ; if he first grew his experimental peas in 1857 he could then be reporting on eight seasons' work. His monastery had sent him for two years to the University at Vienna, where he had studied mathematics, physics, and biology. He returned and took up teaching duties in the Technical High School in 1853 ; he may then have undertaken work in the monastery garden for three years before starting his investigation of peas.

On this basis parts of the experiment can be definitely dated (p. 320) :

> " In all thirty-four more or less distinct varieties of peas were obtained from several seedsmen and subjected to a two-years' trial . . . For fertilization twenty-two of these were selected and cultivated during the whole period of the experiments."

It was evidently in the second trial year (1858) that the first cross-pollinations were made, namely, crosses for the two seed-characters *wrinkled* and *green*, and the two plant characters *white flowers* and *dwarf*. Of these the two first are said (p. 331) to have shown segregation for six years, which must be 1859–64, the two named plant characters for five (1860–64), while the three other plant characters used by Mendel, *constricted pods*, *yellow pods*, and *terminal flowers*, for which only four segregating generations are mentioned, may have been first crossed a year later (1859).

In 1858 the recessiveness of the two seed characters must have appeared in the ripe seeds from the flowers cross-pollinated, for these would be round (or yellow) irrespective of the shape (or colour) of the self-fertilized seeds borne by the same plants. From the cross round by wrinkled sufficient seed was sown to raise 253 plants in 1859, while from the cross yellow by green 258 plants were raised. It is not improbable that about 250 plants heterozygous for each of the other two factors were also grown in 1859, but we are only told the numbers of plants raised from their seed in 1860, and these do not exceed what could have been bred from forty plants of each kind. In any case, ground for some 600 to 1000 cross-bred plants must have been needed in 1859, and it may be noted that in this year the number of self-fertilized lines was reduced from 38 to 22, releasing probably the ground occupied by sixteen rows. The area of the experiments may well have been the same in the three years 1857, 1858, and 1859.

The heterozygous plants grown in 1859 from white-flowered parents, and those from dwarf parents, must have established the recessiveness of these characters, and so confirmed the fact of dominance in reciprocal crosses observed with the seed-characters in the previous year. In 1859 too, when the pods were ripe, seeds on plants heterozygous for *wrinkled* and *green* showed segregation in 3 : 1 ratios. For wrinkled seeds 253 plants gave 7324 seeds, an average of 29 to a plant. 5474 were round and 1850 wrinkled. The deviation from the expected 3 : 1 is less than its standard error of random sampling. For green seeds 258 plants gave 8023 seeds, an average of 31 to a plant. 6022 were yellow and 2001 green. The agreement with expectation is here even closer. Mendel does not test the significance of the deviation, but states the ratios as 2·96 : 1 and 3·01 : 1, without giving any probable error. The yield per plant seems low. Possibly only four or five pods on each plant were left to ripen, the remainder being consumed green ; it is possible again that little room was allowed for each plant.

The discovery, or demonstration, whichever it may have been, of the 3 : 1 ratio was evidently the critical point in Mendel's researches. The importance of the work was demonstrated, if not to Mendel himself, at least to his associates, and, in the following years, the area of the experimental site must have been greatly enlarged. Perhaps for the same reason, in this year also three new crosses were initiated, using the factors for *constricted pods*, *yellow pods*, and *terminal flowers*.

That Mendel was satisfied with the two approximate ratios so far obtained would be intelligible if, either previously or immediately upon reviewing the 1859 results, he had convinced himself as to their explanation, and framed the entire Mendelian theory of genetic factors and gametic segregation. His confidence and lack of scepticism shows itself in three distinct ways.

(*a*) He has numerous opportunities in subsequent years of testing on a large scale whether or not the ratios really remained constant from year to year. If he made any such verification he does not record the data.

(*b*) The test of significance of deviations from expectation in a binomial series had been familiar to mathematicians at least since the middle of the eighteenth century. Mendel's mathematical studies in Vienna may have given little attention to the theory of probability; but we know that he was engaged in other researches of a statistical character, in meteorology, and in connection with sun-spots, so that it is scarcely conceivable, had the matter caused him any anxiety, that he knew of no book or friend that would enable him to examine objectively whether or not the observed deviations from expectation conformed with the laws of chance. He goes so far as to give "by way of illustration" the classification of the seeds from "the first ten individuals" of each of these two series (p. 327). In both cases the variations are no larger than the deviations to be expected, but Mendel does not say so. The average numbers of seeds from these two samples are above those for the whole series, being 44 against 29 in the first case and 48 against 31 in the second. Indeed, only three of the twenty plants give less than the average number for its experiment. Possibly some poor-yielding plants were rejected when the list was made up, in which case Mendel's statement, though it may be entirely honest, cannot be entirely literal. Possibly, again, the first ten plants had happened in each case to have been grown in more favourable conditions than the majority of the rest [1].

[1] I am obliged to Dr. J. Rasmussen, who has extensive experience of genetical work with *Pisum*, for the following explanation of Mendel's probable method of selection:

> "It is my impression that the classification was made throughout on dry plants in Winter. That is to say, that Mendel harvested his plants in Autumn, probably tied them up plot by plot, and for scoring loosened up the bunch of plants and picked out from it one plant after another. This is the method which first presents itself in work of this kind; it is also the method I am accustomed to use. The fact is that, working in this way, one will unconsciously choose the best plant first. This happens

Mendel also gives examples of extreme deviations in both directions from each series. These extreme cases, again, cannot be judged more extreme than would be expected among samples of about 250 plants, but Mendel gives no grounds for this opinion, and, indeed, does not express it.

(*c*) The third point on which Mendel seems more incurious than we could imagine him being, were he not already satisfied, is in not comparing the outcome of reciprocal crosses. He alludes to the point at issue in a footnote to his concluding remarks (p. 355) :

> " In *Pisum* it is placed beyond doubt that for the formation of the new embryo a perfect union of the elements of both reproductive cells must take place. How could we otherwise explain that among the offspring of the hybrids both original types reappear in equal numbers and with all their peculiarities ? If the influence of the egg-cell upon the pollen-cell were only external, if it fulfilled the rôle of a nurse only, then the result of each artificial fertilization could be no other than that the developed hybrid should exactly resemble the pollen parent, or at any rate do so very closely. This the experiments have in nowise confirmed. An evident proof of the complete union of the contents of the two gametes is afforded by the experience gained on all sides that it is immaterial, as regards the form of the hybrid, which of the original species is the seed parent and which the pollen parent."

If, in 1859, any doubt as to the equivalence of the contributions of the two parents had entered Mendel's mind, he would surely have made a separate enumeration of the seeds borne by the two types of heterozygous plants derived from reciprocal pollinations. Their equivalence as regards dominance had been indicated in the previous year. Their equivalence in genic content Mendel seems early to have felt very sure of.

In 1930, as a result of a study of the development of Darwin's ideas, I pointed out that the modern genetical system, apart from such special features as dominance and linkage, could have been inferred by any abstract thinker in the middle of the nineteenth century if he were led to postulate that inheritance was particulate, that the germinal material was structural, and that the contributions of the two parents were equivalent. I had at that time no suspicion that Mendel had arrived at his discovery in this way. From an examination of Mendel's work

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to me, whether I do the work myself or have other people picking out the plants from the bunch."

In respect to the average yield Dr. Rasmussen also says :

> " About 30 good seeds per plant is, under Mendel's conditions (dry climate, early ripening, and attacks of *Bruchus pisi*) by no means a low number. It seems to me, indeed, rather a good one, and I feel convinced that Mendel classified all the seeds from these plants."

it now appears not improbable that he did so and that his ready assumption of the equivalence of the gametes was a potent factor in leading him to his theory. In this way his experimental programme becomes intelligible as a carefully planned demonstration of his conclusions.

In 1860 the obstacles to the extension of his experimental programme had been overcome. In this year the two experiments with seed characters were completed by demonstrating that the 3 : 1 ratios observed in the previous year were genetically 1 : 2 : 1 ratios. In addition to an unknown number of wrinkled seeds, which came true for this character, 565 plants were raised from round seeds, of which 193 yielded round seeds only, while 372 behaved like their parents. Although at least a couple of pods from each of these 372 plants must have been allowed to ripen, the seed numbers are not reported and, perhaps, were not counted. In the second experiment some green seeds were sown, which duly gave green seeds only, while of 519 plants raised from yellow seeds 166 yielded yellow only and 353 were heterozygous. Again, no seed counts are reported from the 353 heterozygous plants. The ratios in both cases show deviations from the expected 2 : 1 ratio of less than their standard errors. This pair of experiments occupied the space of something more than 1084 plants. They were continued with smaller numbers for the next four years, but no further counts are given.

For the two plant characters *white flowers* and *dwarf*, which in this year (1860) first showed segregation, provision was made on a larger scale. Of 929 plants 224 bore white flowers, while of 1064 plants 277 were dwarfed. In both cases the deviation is less than the standard error of random sampling. In addition to making provision for over 3000 plants from the crosses made in 1858 Mendel must in this year have raised perhaps 250 heterozygous plants from each of the three crosses started in 1859. His cultures were therefore probably increased this year by about 3000 plants.

In 1861 provision was made for 1000 plants each for completing the experiments with the first two plant characters, these being families of 10 plants each from a hundred of the 1860 crop, chosen as showing the dominant characters, coloured flowers, and tall stems respectively. The families from 36 plants had only coloured flowers, while those from 64 contained one or more white-flowered plants. The proportionate numbers among the 640 plants of these families was apparently not counted. Again, the families from 28 plants were exclusively tall, while 72 showed segregation of dwarfs. We are not told what was the frequency of dwarfs among these 720 plants. In neither case does the ratio depart significantly from the 2 : 1 ratio expected, although in the second case the deviation does exceed the standard deviation of random sampling.

In this year also the three crosses of plant characters started in 1859 required provision for nearly 1000 plants each. Of 1181 plants counted 299 had constricted pods, of 580 plants 152 had yellow pods, and of 858 plants 207 had terminal inflorescences. The deviation is below the standard in every case. Apart from progenies grown from recessive plants, these experiments account in all for 4619 plants. The total was thus probably greater than in the previous year, but the increase was not great.

So far as this, the first series of experiments, is concerned, there only remained in 1862 to provide for 3000 plants to establish the 2 : 1 ratios among the progenies of plants segregating for constricted pods, yellow pods, and terminal flowers. Out of a hundred parents tested there were respectively 29, 40, and 33 homozygous. Of these the first and third conform well with expectation. In the second case the observed frequencies, 40 homozygous to 60 heterozygous, shows a relatively large, but not a significant, deviation. It is remarkable as the only case in the record in which Mendel was moved to verify a ratio by repeating the trial. A second series of a hundred progenies, presumably grown in 1863, gave 65 : 35, as near to expectation as could be desired. Although in 1861 only 580 plants had been available to display the 3 : 1 ratio for yellow pods, and in these two trials respectively 600 and 650 more must have appeared, they do not seem to have been counted, and are not reported in the paper.

In connection with these tests of homozygosity by examining ten offspring formed by self-fertilization, it is disconcerting to find that the proportion of plants misclassified by this test is not inappreciable. If each offspring has an independent probability, 75, of displaying the dominant character, the probability that all ten will do so is $(\cdot 75)^{10}$, or ·0563. Consequently, between 5 and 6 per cent. of the heterozygous parents will be classified as homozygotes, and the expected ratio of segregating to non-segregating families is not 2 : 1 but 1·8874 : 1·1126, or approximately 377·5 : 222·5 out of 600. Now among the 600 plants tested by Mendel 201 were classified as homozygous and 399 as heterozygous. Although these numbers agree extremely closely with his expectation of 200 : 400, yet, when allowance is made for the limited size of the test progenies, the deviation is one to be taken seriously. It seems extremely improbable that Mendel made any such allowance, or that the numbers he records as segregating are "corrected" values, rounded off to the nearest integer, obtained by dividing the numbers observed to segregate by ·9437. We might suppose that sampling errors in this case caused a deviation in the right direction, and of almost exactly the right magnitude, to compensate for the error in theory. A deviation as fortunate as Mendel's is to be expected once in twenty-nine trials. Unfortunately the same thing occurs again with the trifactorial data.

These seven experiments of the first series require, as we have seen, a total of four or five thousand plants in the years 1860 and 1861. Apart from the continuation of heterozygous series they account for only 3000 in 1862 and for 1000 in 1863. The pollinations for his second series of experiments were, therefore, probably carried out in 1861. The large trifactorial experiment could not indeed have been finished had it started later, and, as the factor for white flowers first showed segregation in 1860, it is difficult to place it earlier. The bifactorial experiment took a year less, and might have been started in 1860, since the ripened seeds of 1859 had established the 3 : 1 ratios of the two factors. I shall suppose that both were initiated in 1861, and that the same is true of the important but smaller experiments devoted to determining the gametic ratios.

To 1862, then, are ascribed the fifteen doubly heterozygous plants of the bifactorial experiment, of which the 556 seeds displayed the first 9 : 3 : 3 : 1 ratio reported. All these were sown in 1863, even the thirty-two wrinkled-green seeds, which suggests that in this year space was abundant. (It was, indeed, in this same year that we have supposed Mendel to depart from his usual practice, and repeat the determination of a frequency ratio, at the expense of growing 1000 additional plants. Even with these additions the summary (Table VI) shows 1863 as less crowded than most of the other years.) The plants from these seeds, classified by the seeds they bore, exhibited independent segregation of the two factors. Mendel's classification of the 529 plants which came to maturity is shown in Table I.

TABLE I.—*Classification of Plants grown in the Bifactorial Experiment.*

	AA.	A*a*.	*aa*.	Total.
BB	38	60	28	126
B*b*	65	138	68	271
bb	35	67	30	132
Total	138	265	126	529

The numbers are close to expectation at all points, but they are not very large. In relation to possible linkage, for example, they may be regarded as excluding, at the 5 per cent. level of significance, recombination fractions less than 44·9 per cent., which is not very strong negative evidence ; yet on this point also Mendel evidently felt that further data would be superfluous, for he certainly could have obtained many more for the counting. The 138 plants, for example, recorded in the table above as being doubly heterozygous, doubtless bore over 4000 seeds segregating in the 9 : 3 : 3 : 1 ratio, and, even if the bulk of the crop were needed when green, at least ten seeds from each plant must have been allowed to ripen in order to classify the plant on which they grew.

The trifactorial experiment required 24 hybrid plants grown in 1862, which gave 639 offspring in 1863. In order to distinguish heterozygotes from homozygotes among the plants with coloured flowers progenies from at least 473 of these must have been grown. If, as in other cases, Mendel used a progeny of ten plants for such discrimination the experiment must have needed 4730 plants in 1864. Of this experiment Mendel says (p. 335) :

> "Among all the experiments this demanded the most time and trouble ",

and the extent of the third filial generation explains this remark. It was evidently on the completion of this extensive work that Mendel felt that

TABLE II.—*Classification of Plants grown in the Trifactorial Experiment.*

	CC.				C*c*.				*cc*.				Total.			
	AA.	A*a*.	*aa*.	Total.	AA.	A*a*.	*aa*.	Total.	AA.	A*a*.	*aa*.	Total.	AA.	A*a*.	*aa*.	Total.
BB...	8	14	8	30	22	38	25	85	14	18	10	42	44	70	43	157
B*b* ...	15	49	19	83	45	78	36	159	18	48	24	90	78	175	79	332
bb....	9	20	10	39	17	40	20	77	11	16	7	34	37	76	37	150
Total .	32	83	37	152	84	156	81	321	43	82	41	166	159	321	159	639

his researches were ripe for publication. It may have constituted the whole of his experimental work with peas in the last year before his paper was read. Even so, probably this year saw more experimental plants than were grown in any previous year. Since the factor for coloured flowers used in this experiment obscures the cotyledon-colour of unopened seeds, not all of the vast number of seeds borne by these three generations was easily available to supplement the bifactorial and trifactorial data reported, yet even what was easily available must have been much more extensive than any data which Mendel published. Mendel's trifactorial classification of the 639 plants of the second generation is shown in Table II, which follows Mendel's notation, in which *a* stands for *wrinkled* seeds, *b* for *green* seeds, and *c* for *white flowers*.

In order to discriminate CC from Cc plants progenies from these, which are seen to number 463 together, must have been grown on in 1864. In addition to abundant new unifactorial data the additional bifactorial data supplied by the experiments is seen to be large. 175 of the plants were heterozygous for both of the two seed characters, and, if 30 seeds from each had been classified, these would have given 5250 seeds, nearly ten times as many as the 556 reported from the bifactorial experiment. The classification of these plants as double heterozygotes must indeed have required that about half this number of seeds from each plant were examined. In the following year also nine-sixteenths of the progeny of 127 F_2 plants, or about 815 F_3 plants, must have borne seeds segregating in the 9 : 3 : 3 : 1 ratio, so that a further 24,000 seeds could have been so classified in 1864. Evidently, however, Mendel felt that the complete classification of 529 plants in the bifactorial experiment was sufficient; he does not even add, for the simultaneous segregation of A*a* and B*b*, the 639 plants completely classified in the trifactorial experiment, which suffice to raise the recombination fraction significantly higher than 46·56 per cent. (from 44·9 per cent.).

TABLE III.—*Comparison of Numbers reported with Uncorrected and Corrected Expectations.*

	Number of plants tested.	Number of non-segregating progenies observed.	Number expected.		Deviation.	
			Without correction.	Corrected.	Without correction.	Corrected.
1st group of experiments.	600	201	200·0	222·5	+1·0	−21·5
Trifactorial experiment .	473	152	157·7	175·4	−5·7	−23·4
Total	1073	353	357·7	397·9	−4·7	−44·9

In the case of the 600 plants tested for homozygosity in the first group of experiments Mendel states his practice to have been to sow ten seeds from each self-fertilized plant. In the case of the 473 plants with coloured flowers from the trifactorial cross he does not restate his procedure. It was presumably the same as before. As before, however, it leads to the difficulty that between 5 and 6 per cent. of heterozygous plants so tested would give only coloured progeny, so that the expected ratio of those showing segregation to those not showing it is really lower than 2 : 1, while Mendel's reported observations agree with the uncorrected theory.

The comparisons are shown in Table III. A total deviation of the magnitude observed, and in the right direction, is only to be expected once in 444 trials; there is therefore here a serious discrepancy.

If we could believe that Mendel changed his previous practice, and in 1863 went to the great labour of back-crossing the 473 doubtful plants, the data could be explained, for in such progenies misclassification would be only about one-fiftieth part as frequent as in progenies by self-fertilization. Equally, if we could suppose that larger progenies, say fifteen plants, were grown on this occasion, the greater part of the discrepancy would be removed. However, even using families of 10 plants the number required is more than Mendel had assigned to any previous experiment, and there is no reason for thinking that he ever grew so many as 7000 experimental plants in one year, apart from his routine tests [2]. Such explanations, moreover, could not explain the discrepancy observed in the first group of experiments, in which the procedure is specified, without the occurrence of a coincidence of considerable improbability.

An explanation of a different type is that the selection of plants for testing favoured the heterozygotes. In the first series of experiments the selection might have been made in the garden, or, if the whole crop was harvested, on the dry plants. In either case the larger plants might have been unconsciously preferred. It is also not impossible that, in some crosses at least, the heterozygotes may have been on the average larger than sister homozygotes. The difficulties to accepting such an explanation as complete are three. (i) In the tri-factorial experiment there was no selection, for all plants grown must have been tested. The results here do not, however, differ in the postulated direction from those of the first series. On the contrary, they show an even larger discrepancy. (ii) It is improbable that the supposed compensating selection of heterozygotes should have been equally effective in the case of five different factors. (iii) The total compensation for all five factors (21·5 plants) must be supposed to be greater than would be needed (16·8 plants) if families of 11 had been grown, and less than would be needed (30·0) if 9 only had been grown, though nearly exactly right for the actual number 10 of F_3 plants in each progeny (22·5).

The possibility that the data for the trifactorial experiment do not represent objective counts, but are the product of some process of sophistication, is not incapable of being tested. Fictitious data can seldom survive a careful scrutiny, and, since most men underestimate the frequency of large deviations arising by chance, such data may be

[2] The area available is given by Iltis as only 7 m. by 35 m. Dr. Rasmussen estimates that he might have grown 4000–5000 plants in this area.

expected generally to agree more closely with expectation than genuine data would. The twenty-seven classes in the trifactorial experiment supply twenty-six degrees of freedom for the calculation of χ^2. The value obtained is 15·3224, decidedly less than its average value for genuine data, 26, though this value by itself might occur once in twenty genuine trials.

This total may be subdivided in various ways; one relevant subdivision is to separate the nine degrees of freedom created by the discrimination of homozygous and heterozygous plants with coloured flowers from the remaining seventeen degrees of freedom based on discriminations made presumably in the previous year. To the total the 9 supply 6·3850, leaving only 8·9374 for the remaining 17. If anything, therefore, the subnormality in the deviations from expectation is more pronounced among the seventeen degrees of freedom than among the nine. If there has been sophistication there is no reason to think that it was confined to the final classification made in 1864.

To 1863 belong probably the bifactorial experiment and the five comparisons, each of four equal expected frequencies, supplied by the experiments on gametic ratios. The bifactorial experiment, having nine classes, supplies eight degrees of freedom for comparison, and gives a χ^2 of only 2·8110—almost as low as the 95 per cent. point. The fifteen degrees of freedom of gametic ratios supply only 3·6730, which is beyond the 99 per cent. point. In the same year also should be included the verified 2 : 1 ratio for yellow pods, giving 0·125 for one degree of freedom.

Putting together the comparisons available for 1863 we have :—

TABLE IV.—*Measure of Deviation Expected and Observed in* 1863.

	Expectation.	χ^2 observed.
Trifactorial experiment	17	8·9374
Bifactorial experiment	8	2·8110
Gametic ratios	15	3·6730
Repeated 2 : 1 test	1	0·1250
Total	41	15·5464

The discrepancy is strongly significant, and so low a value could scarcely occur by chance once in 2000 trials. There can be no doubt that the data from the later years of the experiment have been biased strongly in the direction of agreement with expectation.

One natural cause of bias of this kind is the tendency to give the theory the benefit of doubt when objects such as seeds, which may be deformed or discoloured by a variety of causes, are being classified. Such an explanation, however, gives no assistance in the case of the tests of gametic ratios and of other tests based on the classification of whole plants. For completeness it may be as well to give in a single table the χ^2 values for all the experiments recorded.

TABLE V.—*Deviations Expected and Observed in all Experiments.*

	Expectation.		χ^2.		Probability of exceeding deviations observed.
3 : 1 ratios — Seed characters ...	2		0·2779		
3 : 1 ratios — Plant characters ...	5		1·8610		
		7		2·1389	·95
2 : 1 ratios — Seed characters ...	2		0·5983		
2 : 1 ratios — Plant characters ...	6		4·5750		
		8		5·1733	·74
Bifactorial experiment		8		2·8110	·94
Gametic ratios		15		3·6730	·9987
Trifactorial experiment		26		15·3224	·95
Total		64		29·1186	·99987
Illustrations of plant variation ..		20		12·4870	·90
Total		84		41·6056	·99993

The bias seems to pervade the whole of the data, apart, possibly, from the illustrations of plant variation. Even the 14 degrees of freedom available before 1863 give only 7·1872, a value which would be exceeded about 12 times in 13 trials.

TABLE VI.—*Approximate Numbers of Plants grown in different Years.*

	1857.	1858.	1859.	1860.	1861.	1862.	1863.	1864.
Stock lines .	2280	2280	1320	1320	1320	1320	1320	1320
1st group ..	—	—	1011	3927	4719	3200	1350	350
2nd group .	—	—	—	—	—	65	1719	4730
Total ..	2280	2280	2331	5247	6039	4585	4389	6400

What I have inferred respecting the extent of Mendel's cultures is summarized by years in Table VI. I have arbitrarily allowed sixty plants for each of the stock lines and fifty for each segregating line which was continued with smaller numbers after the completion of the main experiments. I have included also in 1862 and 1863 the two small experiments devoted to the demonstration of gametic ratios. Some of the totals for years may be correct to the nearest hundred, but I do not expect all to be so. I feel justified in concluding only that the experiment was greatly enlarged after the first three years and that, with only ten plants to a family, the year 1864 was probably the fullest of all.

4. The Nature of Mendel's Discovery.

The reconstruction has been undertaken in order to test the plausibility of the view that Mendel's statements as to the course and procedure of his experimentation are to be taken as an entirely literal account, or whether, on the other hand, there is evidence that data have been assembled from various sources, or the same data rediscussed from different standpoints in different sections of his account. There can, I believe, now be no doubt whatever that his report is to be taken entirely literally, and that his experiments were carried out in just the way and much in the order that they are recounted. The detailed reconstruction of his programme on this assumption leads to no discrepancy whatever. A serious and almost inexplicable discrepancy has, however, appeared, in that in one series of results the numbers observed agree excellently with the two to one ratio, which Mendel himself expected, but differ significantly from what should have been expected had his theory been corrected to allow for the small size of his test progenies. To suppose that Mendel recognized this theoretical complication, and adjusted the frequencies supposedly observed to allow for it, would be to contravene the weight of the evidence supplied in detail by his paper as a whole. Although no explanation can be expected to be satisfactory, it remains a possibility among others that Mendel was deceived by some assistant who knew too well what was expected. This possibility is supported by independent evidence that the data of most, if not all, of the experiments have been falsified so as to agree closely with Mendel's expectations.

The importance of the conclusion, if it is well established, that Mendel's statements are to be taken literally, lies in the inferences which flow from this view. *First*, that prior to the reported experiments Mendel was sufficiently aware of the independent inheritance of seven factors in peas to have chosen seven pairs of varieties, each pair differing only in a single factor. If it be thought that out of thirty-eight varieties he could not by deliberate choice have found the material for seven such crosses, it should be remembered also that at this stage he was choosing not only the varieties but, perhaps, also the factors to use in his experiment, and that he may have known of other factors in peas in addition to those with which his experiments are concerned, which, however, could not have been introduced without bringing in an undesirable complication [3]. *Next*, it appears that Mendel regarded the numerical frequency ratios, in which the laws of inheritance expressed themselves, simply as a ready method of demonstrating the truth of his factorial system, and that he was never much concerned to demonstrate either their exactitude or their consistency. It may be that the seed counts of 1859 were a revelation to him of the precision with which his system worked, and could be demonstrated ; they may also possibly have given him an exaggerated impression of the precision with which the theoretical ratios should be verified, but from that moment it is clear, from the form his experiments took, that he knew very surely what to expect, and designed them as a demonstration for others rather than for his own enlightenment. That the hereditary contribution of the two parents might be unequal he did not seriously consider, although his first experiments provided splendid evidence on this important question, which it does not occur to him to present. It seems also not to have occurred to him that the inheritance of different factors might not be wholly independent. He asserts independence for all his factors, but gives evidence for only three of them, and for these much less than he might have given. A feature such as linkage would have been a complication extraneous to his theory, as he conceived it, which he would only have taken seriously had the observations forced it under his notice.

The theoretical consequences of his system he had thought out thoroughly, and in his respect his thought is considerably in advance of that of the first generation of geneticists which followed his rediscovery. He pointed out that n factors would give rise to 3^n different genotypes, of which 2^n would be capable of breeding true. He realized that even in intra-specific crosses n would be sufficiently great for these to be very large numbers, and that even more factors must be involved when crosses are made between different species, when minor in addition to major differences are considered. This understanding of the consequences of the factorial system contrasts sharply with many of the speculations

[3] It is particularly gratifying that this conclusion is supported by Dr. Rasmussen, basing his opinion upon existing types of garden peas, and on the development of these types since Mendel's time. He writes :—

> "From the most probable assortment of varieties available to Mendel there would be no difficulty whatever in making unifactorial crosses in all characters. Indeed, the assortment at hand seems to have been much better fitted for such crosses than for other combinations."

of the earlier geneticists, such as that new species might be formed by the mutation of a single factor, or that the mimetic groups, found among butterflies and other insects, might be explained by the paucity of the genetic factors controlling the pattern and coloration of the wings. In these respects it has taken nearly a generation to rediscover Mendel's point of view.

Mendel seems also to have realized that the factorial system resolved one of the chief difficulties felt and discussed by Darwin, namely that, if the wide variation observable in cultivated plants were caused by the changed conditions and increased nourishment experienced on being brought into cultivation, then this cause of variation must continue to act, as Darwin had written, " for an improbably long time ", since anciently cultivated species are not less but rather more variable than others. With segregating, heritable factors, on the other hand, the variability is easily explained by the preservation in culture of variants which, apart from man, would have been eliminated by natural selection. This, indeed, seems to have been Mendel's view (p. 351):

> " It will be willingly granted that by cultivation the origination of new varieties is favoured, and that by men's labour many varieties are acquired which, under natural conditions, would be lost; but nothing justifies the assumption that the tendency to the formation of varieties is so extraordinarily increased that the species speedily lose all stability, and their offspring diverge into an endless series of extremely variable forms. Were the change in the conditions the sole cause of variability you might expect that those cultivated plants which are grown for centuries under almost identical conditions would again attain constancy. That, as is well known, is not the case, . . . "

The reflection of Darwin's thought is unmistakable, and Mendel's comment is extremely pertinent, though it seems to have been overlooked. He may at this time have read the *Origin*, but the point under discussion may equally have reached his notice at second hand.

5. The Contemporary Reaction to Mendel's Work.

The peculiarities of Mendel's work, to which attention has been called in the previous sections, seem to contribute nothing towards explaining why his paper was so generally overlooked. The journal in which it was published was not a very obscure one, and seems to have been widely distributed. In London, according to Bateson, it was received by the Royal Society and by the Linnean Society. The paper itself is not obscure or difficult to understand; on the contrary, the new ideas are explained most simply, and amply illustrated by the experimental results. In view of the parallel failure of the biological world to appreciate and follow up Darwin's experiments, it is difficult to suppose that, had Mendel's paper been more widely read, there would have been many mentally prepared to appreciate its significance. Some there certainly were ; and, had the new facts and methods come to the knowledge of Francis Galton, the experimental analysis of heredity might well have been established twenty-five years earlier than it was in fact ; but minds equally receptive were certainly rare.

Among German biologists the one with whom Mendel is known to have corresponded is von Nägeli. From his writings it is apparent either that Mendel's researches made no impression on his mind or that he was anxious to warn students against paying attention to them. In a paper published December 15, 1865, only ten months after the delivery of Mendel's paper on peas, and before its appearance in print, he seems to reprove observers who venture to think for themselves and to plan their own experiments instead of using the results of Gärtner and Kölreuter (p. 190) :

> " The knowledge of hybridization would in recent times have made more progress, if many observers, instead of beginning anew, had made use of the results of the two first-named German investigators, who applied the labour of their lives to the solution of this problem."

In the beginning of his paper Mendel had, with modest confidence, contrasted his method of procedure with that of these two distinguished predecessors. In his final discussion, also, he reinterprets the results of Gärtner in terms of the factorial system, showing that Gärtner's observations agreed with Mendel's theory, while dissenting from Gärtner's opinion that they were opposed to the theory of evolution.

In spite of his correspondence von Nägeli does not refer to Mendel's recent paper, and the following passage seems designed positively to ignore it (p. 231) :

> " Variability of the hybrids, that is to say, the diversity of forms which belong to the same generation, and their behaviour on propagation once or many times by self fertilization, form two points in the study of hybridization which are still least ascertained, and which appear to be the least subject to strict rules."

Mendel had claimed to have established precisely such strict rules. Another passage in the same paper seems designed directly to contradict Mendel's claims as to the dominance and independence of genetic factors (p. 222) :

> " The characters of the parental forms are, as a rule, so transmitted that, in each individual hybrid both influences make themselves felt. It is not that one character is transmitted, as it were, unchanged from the one parent, a second unchanged from the other ; but there occurs an interpenetration of the paternal and the maternal character, and a union between their characters."

It is difficult to suppose that these remarks were not intended to discourage Mendel personally, without drawing attention to his researches.

No such dishonourable intention can be ascribed to W. O. Focke, who, in his *Pflanzenmischlinge*, makes no less than fifteen references to Mendel. As in the case of other voluminous compilers, most of these references, though doubtless relevant to the different topics Focke had in mind, ignore the point of Mendel's work. The nearest Focke comes to giving any idea of what Mendel had done is found in the following sentence. This may stand as a good example of the limitations of even the best intentioned compilers of comprehensive treatises (p. 110) :

> " Mendel's numerous crossings gave results which were quite similar to those of Knight, but Mendel believed that he found constant numerical relationships between the types of the crosses."

The fatigued tone of the opening remark would scarcely arouse the curiosity of any reader, and in all he has to say Focke's vagueness and caution have eliminated every point of scientific interest. Could any reader guess that the " constant numerical relationships " were the universal and concrete ratios of 1 : 1 and 3 : 1, or even that Focke was speaking of the frequency ratios of a limited number of recognizable genotypes ?

It is not an accident that Focke was vague. In this case, as perhaps in others, he had not troubled to understand the work he was summarizing. Mendel's discovery of dominance and the great use he had made of seed characters had escaped him altogether. His comment continues :

> " In general, the seeds produced through a hybrid pollination preserve also, with peas, exactly the colour which belongs to the mother plant, even when from these seeds themselves plants proceed, which entirely resemble the father plant, and which then also bring forth the seeds of the latter."

H. F. Roberts makes an instructive comment on Focke's book :

> "A careful study of Focke's report brings into interesting relief the reason for his having failed to appraise the Mendel paper at its present value. In the first place, Focke was especially interested in the works of those who produced more extended contributions. The work of Kölreuter, Gärtner, Wichura and Wiegmann, whose works were much more voluminous in the field which they occupied, receive appropriate consideration, as do also Naudin's and Godron's prize contributions; but Mendel's paper evidently appeared to Focke simply in the guise of one of the numerous, apparently similar, contributions to the knowledge of the results of crossing within some single group . . . It was supposedly not at all conceivable that the laws of hybrid breeding could be compassed within a series of experiments upon a single plant."

Roberts ends his comment on a note of appreciation :

> "The details of his (Focke's) data are laborious, exact, well-classified and scientifically arranged, comprising 79 families of dicotyledons, 13 families of monocotyledons, 2 families of gymnosperms, 2 of pteridophytes, one of the musci and one of the algæ."

It is very well to be reminded that the high qualities catalogued in the sentence last quoted are yet compatible with the learned author having overlooked, in his chosen field, experimental researches conclusive in their results, faultlessly lucid in presentation, and vital to the understanding not of one problem of current interest, but of many.

The peculiar incident in the history of biological thought, which it has been the purpose of this study to elucidate, is not without at least one moral—namely, that there is no substitute for a careful, or even meticulous, examination of all original papers purporting to establish new facts. Mendel's contemporaries may be blamed for failing to recognize his discovery, perhaps through resting too great a confidence on comprehensive compilations. It is equally clear, however, that since 1900, in spite of the immense publicity it has received, his work has not often been examined with sufficient care to prevent its many extraordinary features being overlooked, and the opinions of its author being misrepresented. Each generation, perhaps, found in Mendel's paper only what it expected to find ; in the first period a repetition of the hybridization results commonly reported, in the second a discovery in inheritance supposedly difficult to reconcile with continuous evolution. Each generation, therefore, ignored what did not confirm its own expectations. Only a succession of publications, the progressive building up of a *corpus* of scientific work, and the continuous iteration of all new opinions seem sufficient to bring a new discovery into general recognition.

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