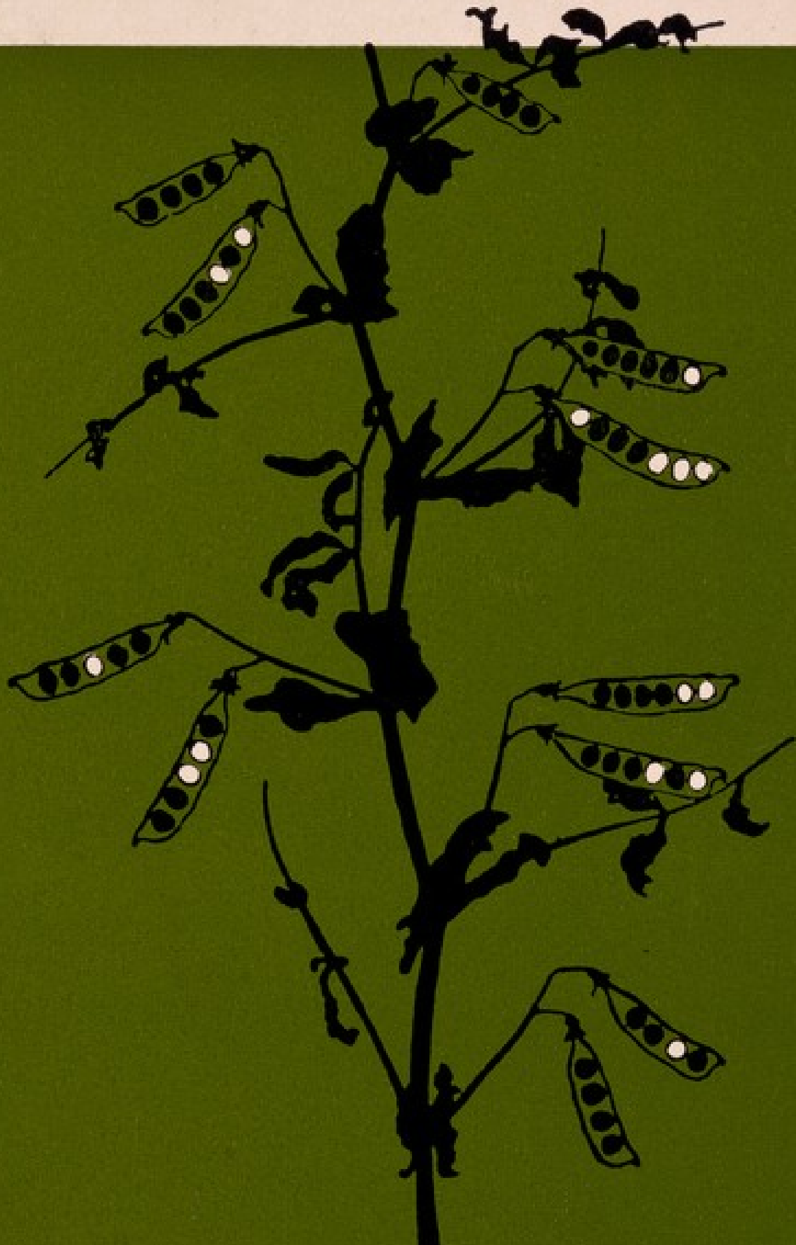
experiments in PLANT HYBRIDISATION

GREGOR MENDEL



INTRODUCTION BY R.A.FISHER

Mendel's paper *Experiments in Plant Hybridisation,* recording his discovery of the laws of inheritance using the garden pea, is famous as the foundation of Genetics. A feature of this centennial reprint of the English translation is the inclusion of the previously unpublished introduction and marginal notes prepared by the late Sir Ronald Fisher, Sc.D., F.R.S., in 1955 when Professor of Genetics in the University of Cambridge. The penetrating comments contained in these pages and in Fisher's 1936 article 'Has Mendel's work been rediscovered?', also reprinted, mark out this collection as one of particular significance for Genetics and the History and Philosophy of Science.

Although Mendel's work has received much publicity since its rediscovery in 1900, following 35 years of neglect, it has usually been examined only superficially and not critically as in these pages. Here is the remarkable statistical evidence indicating that "the data of most, if not all, of the experiments have been falsified so as to agree closely with Mendel's expectations". Here also are Fisher's suggestions that Mendel was perhaps deceived by an assistant who "knew too well what was expected" and that the experimental programme described was probably a carefully planned demonstration of the factorial scheme which Mendel had discovered earlier. Further light is thrown on these suggestions in this book and attention is drawn to other important aspects of Mendel's work which have hitherto passed unnoticed.

An outline of the more important events in Mendel's life is given in a reprinted biographical note by W. Bateson.

(See back flap)

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EXPERIMENTS IN PLANT HYBRIDISATION

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Experiments in Plant Hybridisation

GREGOR MENDEL

Mendel's original paper in English translation
with Commentary and Assessment
by the late

SIR RONALD A. FISHER
M.A., Sc.D., F.R.S.

together with a reprint of
W. Bateson's Biographical Notice of Mendel

Edited by
J. H. BENNETT

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Editor's Preface

In 1955, Sir Ronald Fisher wrote an introduction and commentary for an English translation of Mendel's paper, "Versuche über Pflanzenhybriden". This was done at the request of the editor of a projected series of publications on source papers in the structure of science. But this series did not come to fruition and Fisher's manuscript has remained unpublished until now. Fortunately, Fisher's literary executors and Oliver & Boyd Ltd readily agreed that the opportunity should not be lost of publishing a translation of Mendel's paper together with this material for the Mendel centenary. In addition, it seemed appropriate to include both an outline of the more important events in Mendel's life, by reprinting the biographical notice from W. Bateson's book *Mendel's Principles of Heredity*, and Fisher's article, "Has Mendel's work been rediscovered?" (*Annals of Science* **1**, 115-137, 1936). It was this characteristically searching and stimulating examination of Mendel's paper which established Fisher's position as leading commentator on Mendel's work.

Fisher's article of 1936 contains two remarkable findings:

(i) statistical tests applied to Mendel's data show that the very close agreement between his observed and expected series is most unlikely to have arisen by chance;

(ii) there is a large discrepancy in one series of results where the observations agree closely with the 2:1 ratio, which Mendel expected, but differ significantly from the expectations corrected so as to allow for the small size of the test families.

To account for the rather sensational evidence that "the data of most, if not all, of the experiments have been falsified so as to agree closely with Mendel's expectations", Fisher suggested that Mendel was possibly deceived by an assistant "who knew too well what was expected" and that the experimental programme was probably a carefully planned demonstration of the factorial scheme which Mendel had discovered earlier.

It is of interest that H. Iltis in his *Life of Mendel* (translated from the German, Allen & Unwin, 1932, p. 209) writes:

> "I had several opportunities of talking about Mendel with an old man named Josef Maresch, the monastery gardener who died only a few years ago. Unfortunately Maresch was of bibulous inclinations (Mendel, we gather, had rather a poor opinion of the man), and this failing had played havoc with his memory. He told me that he had some of Mendel's notebooks, but was never able to produce them, and no one could find them among his belongings after his death."

On page 105 of the same work, there occurs the following passage:

> "We know from the reports of Hornisch and Nowotny that Mendel used to breed mice in his rooms, grey mice as well as white mice, crossing these varieties. We may plausibly suppose that during these experiments, undertaken perhaps more 'for the fun of the thing' than for any profoundly conceived scientific purpose, the phenomena of dominance and separation forced themselves upon his notice. Mendel himself tells us nothing about this matter, making no reference whatever to his experiments on mice."

Fisher was evidently not familiar with Iltis' biography of Mendel when he wrote the 1936 paper. The German edition of Iltis' work is indeed listed in the bibliography to Fisher's paper but the only reference to it occurs in a footnote* (*p. 76*) written after the paper was completed and apparently supplied by the late Dr J. Rasmussen. Furthermore, if Fisher had been familiar with Iltis' work, it is hardly possible that he would have overlooked the reference (p. 108) to Mendel's letter to von Nageli in which 1856-63 is stated as the period of the experimental work with peas, whereas Fisher (1936) writes (*p. 66*), "if he first grew his experimental peas in 1857, he could then be reporting on eight seasons' work. . . . On this basis, parts of the experiment can be definitely dated".

The circumstances in which Fisher came to make his examination of Mendel's results are of some interest. In a

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* Page references in italics refer to the present publication.

letter to Dr Douglas McKie, one of the Editors of the *Annals of Science*, on 8th January 1936, Fisher writes:

> "I am sending enclosed a copy of my paper on Mendel which I wrote in the Christmas holidays, after getting your letter. I started writing the paper with a strong impression that innumerable people who referred to the rediscovery of Mendel's work as the foundation of modern (genetical) knowledge had paid very little attention to the paper itself, and were not aware that it presents some rather remarkable problems. I had not expected to find the strong evidence which has appeared that the data had been cooked. This makes my paper far more sensational than ever I had intended, and adds another mystery to those that have been puzzling me, some of which I think I had made some progress with. As it stands, my title is now more ironical than I had intended it to be, but I cannot help it if circumstances proceed to emphasise so strongly my main point, that Mendel's own work, in spite of the immense publicity it has received, has only been examined superficially, and that the re-discoverers of 1900 were just as incapable as the non-discoverers of 1870 of assimilating from it any idea other than those which they were already prepared to accept.
>
> "I suppose the real mystery is how science manages to make any progress at all."

For P.S.A?

Fisher's *Introduction* and *Marginal Comments* (Chapters 1 and 3 of this present book) naturally reflect the findings of the 1936 paper but it is of interest to note what, after twenty years, he has added to that account. We see that, in particular, he lays emphasis on the importance of the role of combinatorial mathematics in Mendel's work and he draws attention to the fundamental difference between Mendel's demonstration of what might be called the combinatorial independence of the separate characters and the tests required to show whether or not there is independent assortment.

That Mendel's paper warrants reprinting and so amply repays careful study one hundred years or more after it was written is perhaps sufficient testimony to the outstanding and lasting merit of Mendel's work. With Fisher's analysis and commentary added, there is an abundance of intellectual excitement and still some mystery associated with this fundamental advance in scientific thought. Amongst the many papers which now exist describing basic advances in genetical knowledge, none stands out more than these as essential reading for a proper understanding of the foundations of Genetics. In the History of Science—to which, as Fisher often remarked, more attention should be paid, especially by biologists—this material must have a very special place. Invaluable as a demonstration of the importance of statistics in genetical experimentation, these papers also help us to appreciate how in the twentieth century and in Fisher's hands, Mendel's factorial scheme provided the stimulus for the development of factorial and other experimental designs of still wider consequence. For all readers, the careful study of this material which is needed for its true understanding offers a splendid exercise in critical thinking and evaluation.

As editor, I am greatly indebted to Miss Denise Ryan for her generous assistance in checking the translation of Mendel's paper with the original, to Dr Jean Mayo for her helpful suggestions on the presentation of this material, and to the publishers and editors of the *Annals of Science* for permission to reproduce the article contained in Chapter 4.

J. H. BENNETT

22nd November, 1964.
Department of Genetics,
University of Adelaide.

All royalties from this publication are being given to the University of Adelaide for Fisher Memorial Scholarships, etc., in Genetics.

Contents

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INTRODUCTORY NOTES ON MENDEL'S PAPER

Ronald A. Fisher

Mendel's celebrated paper on inheritance in the garden pea was read at two successive meetings, 8th February and 8th March 1865, of the Brünn [now Brno] Natural History Society, and was published in the following year in the Proceedings of that Society for 1865. Although Mendel's material was thus laid rather fully before a not undistinguished provincial society, and although the publication was doubtless made available to the leading Academies of Europe (Bateson verified that copies were received in London by the Royal and by the Linnaean Society), it must be supposed that it did not come under the eyes of any scientist capable of appreciating its importance, for it attracted little contemporary notice, and required to be "rediscovered" with some sensational circumstances in 1900, when three European botanists, de Vries in Holland, Correns in Germany, and Tschermak in Austria, had all discovered its existence. It had at this time the triple aspect of a confirmation, an anticipation, and an interpretation of their own researches. Almost instantly, or at least so quickly that it is difficult to discern the order of events, it was recognised that Mendel's discovery was applicable not only to plants, but also to inheritance in animals, including Man, for human pedigrees existed eminently susceptible to a Mendelian explanation.

In 1900, therefore, it was natural that scientific attention should be concentrated on a discovery of blazing importance. This was the interpretation of the phenomena of heredity, bafflingly complex as these had appeared to be, in terms of the *transmission* unchanged from generation to generation of relatively permanent units, for which Johannsen later suggested the convenient name of "genes". It is true that much work was still needed to show how widely this simple concept would be successful; with quantitative characters, for example, or with microorganisms widely different in their reproductive processes from the higher plants and animals at first investigated. The facts available in 1900 were at least sufficient to establish Mendel's contribution as one of the greatest experimental advances in the history of biology. The minority who could not adjust their ideas, only demonstrated in the ensuing controversies how great a revolution in biological thought was in progress.

For the twentieth century, therefore, in order to understand Mendel's paper, it is necessary to set aside very much that to us is obvious. We must come with a fresh mind to such questions as; What was Mendel's purpose in the series of experiments he sets forth ? Or, what, at their conclusion, did he think he had demonstrated ? Of the phenomena he had discovered how confident was he that they extended beyond the genus *Pisum* ? If he was tempted by the notion of generalisation, were his hopes shattered by his experience with *Hieracium*, in which, in the absence of true sexual reproduction he was unable to demonstrate the Mendelian phenomena ?

The eight years which he tells us his researches had occupied, are known from his letters to have extended from 1856 to 1863. Mendel had, therefore, more than a year for the preparation of his report, which was evidently a work of studious care. When he started, the evolution of organisms by progressive modification was not a burning question. In 1865 it was the central preoccupation of the biological world. It is therefore misleading to say, as Bateson does (*p. 90*) "with the views of Darwin, which at that time were coming into prominence, Mendel did not find himself in full agreement, and he embarked on his experiments . . ." as though Mendel's primary aim was to enter into the evolutionary controversy. It is improbable indeed that he had even heard of Darwin at the beginning of his work. When he came to write it up, the situation in this respect was greatly changed, and it is interesting to note the references to evolution in his paper. In the first of these he expresses the modest confidence that an understanding of inheritance had an important contribution to make towards the understanding of evolution; a process which he appears to accept quite simply as factual. Towards the close of his paper he makes a contribution, showing quite a deep understanding, in which without emphasis he shows that his views on inheritance would remove one of the difficulties which Darwin, with characteristic candour, had himself discussed. As an amateur, and a newcomer to biological research he felt perhaps that it would be unbecoming for him to drop more that this light hint.

If we read his introduction literally we do not find him expressing the purpose of solving a great problem or reporting a resounding discovery. He represents his work rather as a contribution to the *methodology* of research into plant inheritance. He had studied the earlier writers and tells us just in what three respects he thinks their work should be improved upon. If proper care were given, he suggests, to the distinction between generations, to the identification of genotypes, and, to this end, to the frequency ratios exhibited by their progeny, when based on an adequate statistical enumeration, studies in the inheritance of other organisms would yield an understanding of the hereditary process as clear as that which he here exhibits for the varieties of the garden pea. There is no hint of a tendency to premature generalisation, but an unmistakable emphasis on the question of method.

"The friendly decision of the reader" to which he appeals on this fundamental issue, was, it cannot be doubted, to be aided by his unmistakable success in explaining the phenomena he had demonstrated in *Pisum*. This, however, is very different from asking the reader to extend to other organisms the operative rules, or the notation which he had found effective in his own studies. In Mendel's view it would seem that the laws of inheritance in other plants were to be elucidated one by one by the application of the same painstaking and thorough method of which his work with *Pisum* had exhibited an example.

The two concluding sections of the paper, namely "Experiments with hybrids of other species of plants" and "Concluding remarks" are of interest in that while reaffirming his methodological principle, Mendel points out that the type of inheritance discovered in *Pisum* receives some confirmation in the preliminary and incomplete trials he had made with *Phaseolus*, and that some steps can be taken to reinterpret some of the published results of Kölreuter and Gärtner on the same principles. The sections are especially interesting in revealing Mendel's clear realisation that, especially with wide crosses, a large number of genetic factors may be expected to segregate, and that these, so far as the analogy of *Pisum* is to be relied on, must yield an enormous number of different genotypes, so that the comparatively small number of individuals that can be bred will be quite insufficient to include them all, and still less to exhibit the true proportions of their occurrence. In this respect Mendel's thought is in advance of genetic opinion in the earlier decades of the twentieth century, in which there are many examples of two- or three-factor hypotheses being set up on no stronger basis than an approximately continuous distribution of second generation hybrids, and for which only a minority of geneticists were sufficiently thorough to attempt to demonstrate, by further tests, the real existence of the diverse genotypes postulated by their theories.

The fact that Mendel was principally concerned to justify a method of investigation, and not primarily to exhibit particular results, is at least a partial explanation of another group of peculiarities of his paper, which might flow from the fact that he is reporting a carefully planned demonstration, rather than the protocol of the first observations which led to the formation of his ideas. The simplicity of his plan, and the adequacy of the numbers of the first crosses reported, are indications that he knew in advance very much what he intended to do, and what he ought to expect. He constantly omits reference to the confirmation of his first conclusions, which the later generations and other experiments reported must have supplied in abundance. Only once is he led to repeat a test. He seems never to be unsure of the sufficiency of the first evidence reported, even when it is not really so strong as might be wished, as in reporting on the independence in inheritance of his seven factors. He is acting as it were on principle, and without the opportunism with which research workers usually seek vigilantly for supplementary information.

In the bifactorial and trifactorial experiments reported in the eighth section, the only new *experimental* evidence Mendel was supplying was that on the genetic or statistical independence of the two or three factors used. Mendel's interest in these experiments was not, however, instigated by this question of statistical independence, for he seems scarcely to have considered the possibility of linked inheritance. His interest, as his exposition shows, lay in the purely mathematical or combinatorial properties of the set of genotypes made possible by two or three factors. The independence he was concerned to demonstrate was, so far as the distinction can be made, closer to a logical than to a statistical independence. His summary statement on this section is in fact (*p. 27*)

> "Thereby is simultaneously given the practical proof *that the constant characters which appear in the several varieties of a group of plants may be obtained in all the associations which are possible according to the laws of combination, by means of repeated artificial fertilisation.*"

This stress on combinatorial mathematics, which has been almost constantly overlooked by commentators, very well deserves the attention of all who teach the subject; for it is common experience that young workers are at first quite unprepared even for the task of enumerating the genotypes to be expected when several factors are segregating, and this is an obvious first step towards exploring the possibilities of a cross. More recently, indeed, in the exploration of the complexities to be expected in tetrasomic and hexasomic inheritance, combinatorial mathematics, of by no means an elementary character, has provided the only possible means of clarification.

Mendel's summary statement is also to be read as a hint to plant breeders. Practical plant improvement in this century might be described as an extensive commentary on this text.

With the understanding that Mendel's interest in the simultaneous segregation of characters was not concerned with the exclusion of linkage, several statements become intelligible.

> "In addition, further experiments were made with a smaller number of experimental plants in which the remaining characters by twos and threes were united as hybrids; all yielded approximately the same results" (*p. 27*).

If there had been serious tests of statistical independence, they would have to have been as large as the two trials reported, the latter of which obviously strained Mendel's resources to the utmost. In reality they must on the contrary have been small trials merely to check that all recombinant phenotypes were produced; as such they are quite compatible with the fact that two of the seven factors which Mendel had declared to be independent, have in later tests been shown to be linked.*

It is noticeable too that of the two tests reported on gametic ratios the first involves simultaneous segregation, and, therefore, so far as it goes, tests the possibility of linkage between the two seed characters. The second, between two plant characters, involves segregation of one factor in the pollen, and of the other in the ovules of the parents, and therefore involves no test of linkage at all. Mendel calls no attention to this difference, and, for him, it must be supposed that they were equivalent demonstrations.

The History of Science has suffered greatly from the use by teachers of second-hand material, and the consequent obliteration of the circumstances and the intellectual atmosphere in which the great discoveries of the past were made. A first-hand study is always instructive, and often, as in this case, full of surprises.

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* H. Lamprecht, who has made an extensive study of linkage relations in *Pisum*, advises me that the seven genes used by Mendel are, in present gene symbolism, 1. R; 2. I; 3. A; 4. V; 5. Gp; 6. Fa; 7. Le (cf. Mendel's list of character differences (*p. 11*)) and that these are located in linkage groups I-VII as follows:

I. A-I	V. Gp
IV. Fa-Le-V	VII. R

Only Le and V show linkage, the recombination frequency being about 13 per cent (cf. H. Lamprecht (1961): Die Genenkarte von *Pisum* bei normaler Struktur der Chromosomen, *Agric. Hortique Genetica*, 19, 360-401).—J.H.B.

2

EXPERIMENTS IN PLANT HYBRIDISATION

Gregor Mendel

1. *INTRODUCTORY REMARKS*

Experience of artificial fertilisation, such as is effected with ornamental plants in order to obtain new variations in colour, has led to the experiments which will here be discussed. The striking regularity with which the same hybrid forms always reappeared whenever fertilisation took place between the same species induced further experiments to be undertaken, the object of which was to follow up the developments of the hybrids in their progeny.

Editor's Note. Mendel's paper, "Versuche über Pflanzenhybriden", was read at meetings of the Brunn Natural History Society on 8th February and 8th March 1865, and was published in the *Verhandlungen des Naturforschenden Vereins in Brünn*, 4, 1865, which appeared in 1866. An English translation was made by the Royal Horticultural Society of London and published in volume 26 of the Society's Journal in 1901. It is the modified version of this translation as given by W. Bateson in his book, *Mendel's Principles of Heredity* (C.U.P., 1909) that is reprinted here. The footnotes and changes due to Bateson are shown within square brackets whilst the few small changes introduced with this reprinting are enclosed within double square brackets. Attention should perhaps be drawn to one of these changes. Some confusion has arisen in the past from the use of the same word " trial " for Mendel's preliminary two-year tests and for his later experimental breeding work. Here, "trial" is used to translate "Probe" with which Mendel describes his tests with the 34 varieties of peas in 1854-55; "Versuch" and "Experiment", which Mendel uses in referring to the rest of his programme, are translated throughout as "experiment".

As suggested by Fisher in his *Marginal Comments*, the sections of Mendel's paper have been numbered from 1 to 11 for ease of reference.

To this object numerous careful observers, such as Kölreuter, Gärtner, Herbert, Lecoq, Wichura and others, have devoted a part of their lives with inexhaustible perseverance. Gärtner especially in his work "Die Bastarderzeugung im Pflanzenreiche" [The Production of Hybrids in the Vegetable Kingdom], has recorded very valuable observations; and quite recently Wichura published the results of some profound investigations into the hybrids of the Willow. That, so far, no generally applicable law governing the formation and development of hybrids has been successfully formulated can hardly be wondered at by anyone who is acquainted with the extent of the task, and can appreciate the difficulties with which experiments of this class have to contend. A final decision can only be arrived at when we shall have before us the results of detailed experiments made on plants belonging to the most diverse orders.

Those who survey the work done in this department will arrive at the conviction that among all the numerous experiments made, 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.*

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.

The paper now presented records the results of such a detailed experiment. This experiment was practically confined to a small plant group, and is now, after eight years' pursuit, concluded in all essentials. Whether the plan upon which the separate experiments were conducted and carried out was the best suited to attain the desired end is left to the friendly decision of the reader.

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* [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.]

2. SELECTION OF THE EXPERIMENTAL PLANTS

The value and utility of any experiment are determined by the fitness of the material to the purpose for which it is used, and thus in the case before us it cannot be immaterial what plants are subjected to experiment and in what manner such experiments are conducted.

The selection of the plant group which shall serve for experiments of this kind must be made with all possible care if it be desired to avoid from the outset every risk of questionable results.

The experimental plants must necessarily—

1. Possess constant differentiating characters.
2. The hybrids of such plants must, during the flowering period, be protected from the influence of all foreign pollen, or be easily capable of such protection.

The hybrids and their offspring should suffer no marked disturbance in their fertility in the successive generations.

Accidental impregnation by foreign pollen, if it occurred during the experiments and were not recognised, would lead to entirely erroneous conclusions. Reduced fertility or entire sterility of certain forms, such as occurs in the offspring of many hybrids, would render the experiments very difficult or entirely frustrate them. In order to discover the relations in which the hybrid forms stand towards each other and also towards their progenitors it appears to be necessary that all members of the series developed in each successive generation should be, *without exception*, subjected to observation.

At the very outset special attention was devoted to the *Leguminosae* on account of their peculiar floral structure. Experiments which were made with several members of this family led to the result that the genus *Pisum* was found to possess the necessary qualifications.

Some thoroughly distinct forms of this genus possess characters which are constant, and easily and certainly recognisable, and when their hybrids are mutually crossed they yield perfectly fertile progeny. Furthermore, a disturbance through foreign pollen cannot easily occur, since the fertilising organs are closely packed inside the keel and the anthers burst within the bud, so that the stigma becomes covered with pollen even before the flower opens. This circumstance is of especial importance. As additional advantages worth mentioning, there may be cited the easy culture of these plants in the open ground and in pots, and also their relatively short period of growth. Artificial fertilisation is certainly a somewhat elaborate process, but nearly always succeeds. For this purpose the bud is opened before it is perfectly developed, the keel is removed, and each stamen carefully extracted by means of forceps, after which the stigma can at once be dusted over with the foreign pollen.

In all, thirty-four more or less distinct varieties of Peas were obtained from several seedsmen and subjected to a two years' trial. In the case of one variety there were noticed, among a larger ⟦considerable⟧ number of plants all alike, a few forms which were markedly different. These, however, did not vary in the following year, and agreed entirely with another variety obtained from the same seedsman; the seeds were therefore doubtless merely accidentally mixed. All the other varieties yielded perfectly constant and similar offspring; at any rate, no essential difference was observed during ⟦the⟧ two trial years. For fertilisation twenty-two of these were selected and cultivated during the whole period of the experiments. They remained constant without any exception.

Their systematic classification is difficult and uncertain. If we adopt the strictest definition of a species, according to which only those individuals belong to a species which under precisely the same circumstances display precisely similar characters, no two of these varieties could be referred to one species. According to the opinion of experts, however, the majority belong to the species *Pisum sativum*; while the rest are regarded and classed, some as sub-species of *P. sativum*, and some as independent species, such as *P. quadratum*, *P. saccharatum*, and *P. umbellatum*. The positions, however, which may be assigned to them in a classificatory system are quite immaterial for the purposes of the experiments in question. It has so far been found to be just as impossible to draw a sharp line between the hybrids of species and varieties as between species and varieties themselves.

3. *DIVISION AND ARRANGEMENT OF THE EXPERIMENTS*

If two plants which differ constantly in one or several characters be crossed, numerous experiments have demonstrated that the common characters are transmitted unchanged to the hybrids and their progeny; but each pair of differentiating characters, on the other hand, unite in the hybrid to form a new character, which in the progeny of the hybrid is usually variable. The object of the experiment was to observe these variations in the case of each pair of differentiating characters, and to deduce the law according to which they appear in the successive generations. The experiment resolves itself therefore into just as many separate experiments as there are constantly differentiating characters presented in the experimental plants.

The various forms of Peas selected for crossing showed differences in the length and colour of the stem; in the size and form of the leaves; in the position, colour, and size of the flowers; in the length of the flower stalk; in the colour, form, and size of the pods; in the form and size of the seeds; and in the colour of the seed-coats and of the albumen [cotyledons]. Some of the characters noted do not permit of a sharp and certain separation, since the difference is of a "more or less" nature, which is often difficult to define. Such characters could not be utilised for the separate experiments; these could only be applied to characters which stand out clearly and definitely in the plants. Lastly, the result must show whether they, in their entirety, observe a regular behaviour in their hybrid unions, and whether from these facts any conclusion can be come to regarding those characters which possess a subordinate significance in the type.

The characters which were selected for experiment relate:

1. To the *difference in the form of the ripe seeds*. These are either round or roundish, the depressions, if any, occur on the surface, being always only shallow; or they are irregularly angular and deeply wrinkled (*P. quadratum*).

2. To the *difference in the colour of the seed albumen* [endosperm].* The albumen of the ripe seeds is either pale yellow,

* [Mendel uses the terms "albumen" and "endosperm" somewhat loosely to denote the cotyledons, containing food-material, within the seed.]

bright yellow and orange coloured, or it possesses a more or less intense green tint. This difference of colour is easily seen in the seeds as [= if] their coats are transparent.

3. To the *difference in the colour of the seed-coat*. This is either white, with which character white flowers are constantly correlated; or it is grey, grey-brown, leather-brown, with or without violet spotting, in which case the colour of the standards is violet, that of the wings purple, and the stem in the axils of the leaves is of a reddish tint. The grey seed-coats become dark brown in boiling water.

4. To the *difference in the form of the ripe pods*. These are either simply inflated, not contracted in places; or they are deeply constricted between the seeds and more or less wrinkled (*P. saccharatum*).

5. To the *difference in the colour of the unripe pods*. They are either light to dark green, or vividly yellow, in which colouring the stalks, leaf-veins, and calyx participate.*

6. To the *difference in the position of the flowers*. They are either axial, that is, distributed along the main stem; or they are terminal, that is, bunched at the top of the stem and arranged almost in a false umbel; in this case the upper part of the stem is more or less widened in section (*P. umbellatum*).†

7. To the *difference in the length of the stem*. The length of the stem is very various in some forms; it is, however, a constant character for each, in so far that healthy plants, grown in the same soil, are only subject to unimportant variations in this character.

In experiments with this character, in order to be able to discriminate with certainty, the long axis of 6 to 7 ft. was always crossed with the short one of $\frac{3}{4}$ ft. to $1\frac{1}{2}$ ft.

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* One species possesses a beautifully brownish-red coloured pod, which when ripening turns to violet and blue. Trials with this character were only begun last year. [Of these further experiments it seems no account was published. Correns has since worked with such a variety.]

† [This is often called the Mummy Pea. It shows slight fasciation. The form I know has white standard and salmon-red wings.]

Each two of the differentiating characters enumerated above were united by cross-fertilisation. There were made for the

1st trial ⟦experiment⟧	60 fertilisations	on	15 plants.
2nd ,,	58 ,,	,,	10 ,,
3rd ,,	35 ,,	,,	10 ,,
4th ,,	40 ,,	,,	10 ,,
5th ,,	23 ,,	,,	5 ,,
6th ,,	34 ,,	,,	10 ,,
7th ,,	37 ,,	,,	10 ,,

From a larger ⟦considerable⟧ number of plants of the same variety only the most vigorous were chosen for fertilisation. Weakly plants always afford uncertain results, because even in the first generation of hybrids, and still more so in the subsequent ones, many of the offspring either entirely fail to flower or only form a few and inferior seeds.

Furthermore, in all the experiments reciprocal crossings were effected in such a way that each of the two varieties which in one set of fertilisations served as seed-bearer in the other set was used as the pollen plant.

The plants were grown in garden beds, a few also in pots, and were maintained in their natural upright position by means of sticks, branches of trees, and strings stretched between. For each experiment a number of pot plants were placed during the blooming period in a greenhouse, to serve as control plants for the main experiment in the open as regards possible disturbance by insects. Among the insects * which visit Peas the beetle *Bruchus pisi* might be detrimental to the experiments should it appear in numbers. The female of this species is known to lay the eggs in the flower, and in so doing opens the keel; upon the tarsi of one specimen, which was caught in a flower, some pollen grains could clearly be seen under a lens. Mention must also be made of a circumstance which possibly might lead to the introduction of foreign pollen. It occurs, for instance, in some rare cases that certain parts of an otherwise quite normally developed flower wither, resulting in a partial exposure of the fertilising organs. A

* [It is somewhat surprising that no mention is made of Thrips, which swarm in Pea flowers. I had come to the conclusion that this is a real source of error and I see Laxton held the same opinion.]

defective development of the keel has also been observed, owing to which the stigma and anthers remained partially uncovered.* It also sometimes happens that the pollen does not reach full perfection. In this event there occurs a gradual lengthening of the pistil during the blooming period, until the stigmatic tip protrudes at the point of the keel. This remarkable appearance has also been observed in hybrids of *Phaseolus* and *Lathyrus*.

The risk of false impregnation by foreign pollen is, however, a very slight one with *Pisum*, and is quite incapable of disturbing the general result. Among more than 10,000 plants which were carefully examined there were only a very few cases where an indubitable false impregnation had occurred. Since in the greenhouse such a case was never remarked, it may well be supposed that *Bruchus pisi*, and possibly also the described abnormalities in the floral structure, were to blame.

4. [F_1] *THE FORMS OF THE HYBRIDS*†

Experiments which in previous years were made with ornamental plants have already afforded evidence that the hybrids, as a rule, are not exactly intermediate between the parental species. With some of the more striking characters, those, for instance, which relate to the form and size of the leaves, the pubescence of the several parts, etc., the intermediate, indeed, is nearly always to be seen; in other cases, however, one of the two parental characters is so preponderant that it is difficult, or quite impossible, to detect the other in the hybrid.

This is precisely the case with the Pea hybrids. In the case of each of the seven crosses the hybrid-character resembles ‡ that of one of the parental forms so closely that the other either escapes observation completely or cannot be detected with certainty. This circumstance is of great importance in

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* [This also happens in Sweet Peas.]

† [Mendel throughout speaks of his cross-bred Peas as "hybrids", a term which many restrict to the offspring of two distinct *species*. He, as he explains, held this to be only a question of degree.]

‡ [Note that Mendel, with true penetration, avoids speaking of the hybrid-character as "transmitted" by either parent, thus escaping the error pervading the older views of heredity.]

the determination and classification of the forms under which the offspring of the hybrids appear. Henceforth in this paper those characters which are transmitted entire, or almost unchanged in the hybridisation, and therefore in themselves constitute the characters of the hybrid, are termed the *dominant*, and those which become latent in the process *recessive*. The expression "recessive" has been chosen because the characters thereby designated withdraw or entirely disappear in the hybrids, but nevertheless reappear unchanged in their progeny, as will be demonstrated later on.

It was furthermore shown by the whole of the experiments that it is perfectly immaterial whether the dominant character belongs to the seed plant or to the pollen plant; the form of the hybrid remains identical in both cases. This interesting fact was also emphasised by Gärtner, with the remark that even the most practised expert is not in a position to determine in a hybrid which of the two parental species was the seed or the pollen plant.*

Of the differentiating characters which were used in the experiments the following are dominant:

1. The round or roundish form of the seed with or without shallow depressions.

2. The yellow colouring of the seed albumen [cotyledons].

3. The grey, grey-brown, or leather-brown colour of the seed-coat, in association with violet-red blossoms and reddish spots in the leaf axils.

4. The simply inflated form of the pod.

5. The green colouring of the unripe pod in association with the same colour in the stems, the leaf-veins and the calyx.

6. The distribution of the flowers along the stem.

7. The greater length of stem.

With regard to this last character it must be stated that the longer of the two parental stems is usually exceeded by the hybrid, a fact which is possibly only attributable to the greater luxuriance which appears in all parts of plants when stems of very different length are crossed. Thus, for instance, in repeated

* [Gärtner, p. 223.]

experiments, stems of 1 ft. and 6 ft. in length yielded without exception hybrids which varied in length between 6 ft. and $7\frac{1}{2}$ ft.

The hybrid seeds in the experiments with seed-coat are often more spotted, and the spots sometimes coalesce into small bluish-violet patches. The spotting also frequently appears even when it is absent as a parental character.*

The hybrid forms of the seed-shape and of the albumen [colour] are developed immediately after the artificial fertilisation by the mere influence of the foreign pollen. They can, therefore, be observed even in the first year of experiment, whilst all the other characters naturally only appear in the following year in such plants as have been raised from the crossed seed.

5. [F_2] *THE FIRST GENERATION* [*BRED*] *FROM THE HYBRIDS*

In this generation there reappear, together with the dominant characters, also the recessive ones with their peculiarities fully developed, and this occurs in the definitely expressed average proportion of three to one, so that among each four plants of this generation three display the dominant character and one the recessive. This relates without exception to all the characters which were investigated in the experiments. The angular wrinkled form of the seed, the green colour of the albumen, the white colour of the seed-coats and the flowers, the constrictions of the pods, the yellow colour of the unripe pod, of the stalk, of the calyx, and of the leaf venation, the umbel-like form of the inflorescence, and the dwarfed stem, all reappear in the numerical proportion given, without any essential alteration. *Transitional forms were not observed in any experiment.*

Since the hybrids resulting from reciprocal crosses are formed alike and present no appreciable difference in their subsequent development, consequently the results [of the reciprocal crosses] can be reckoned together in each experiment. The relative numbers which were obtained for each pair of differentiating characters are as follows:

Expt. 1. Form of seed.—From 253 hybrids 7324 seeds

* [This refers to the coats of the seeds borne by F_1 plants.]

were obtained in the second trial ⟦experimental⟧ year. Among them were 5474 round or roundish ones and 1850 angular wrinkled ones. Therefrom the ratio 2·96 to 1 is deduced.

Expt. 2. Colour of albumen.—258 plants yielded 8023 seeds, 6022 yellow, and 2001 green; their ratio, therefore, is as 3·01 to 1.

In these two experiments each pod yielded usually both kinds of seed. In well-developed pods which contained on the average six to nine seeds, it often happened that all the seeds were round (Expt. 1) or all yellow (Expt. 2); on the other hand there were never observed more than five wrinkled or five green ones in one pod. It appears to make no difference whether the pods are developed early or later in the hybrid or whether they spring from the main axis or from a lateral one. In some few plants only a few seeds developed in the first formed pods, and these possessed exclusively one of the two characters, but in the subsequently developed pods the normal proportions were maintained nevertheless.

As in separate pods, so did the distribution of the characters vary in separate plants. By way of illustration the first ten individuals from both series of experiments may serve.

	Experiment 1		Experiment 2	
	Form of Seed		Colour of Albumen	
Plants	Round	Angular	Yellow	Green
1	45	12	25	11
2	27	8	32	7
3	24	7	14	5
4	19	10	70	27
5	32	11	24	13
6	26	6	20	6
7	88	24	32	13
8	22	10	44	9
9	28	6	50	14
10	25	7	44	18

As extremes in the distribution of the two seed characters in one plant, there were observed in Expt. 1 an instance of 43 round and only 2 angular, and another of 14 round and 15 angular seeds. In Expt. 2 there was a case of 32 yellow and only 1 green seed, but also one of 20 yellow and 19 green.

These two experiments are important for the determination of the average ratios, because with a smaller number of experimental plants they show that very considerable fluctuations may occur. In counting the seeds, also, especially in Expt. 2, some care is requisite, since in some of the seeds of many plants the green colour of the albumen is less developed, and at first may be easily overlooked. The cause of this partial disappearance of the green colouring has no connection with the hybrid-character of the plants, as it likewise occurs in the parental variety. This peculiarity [bleaching] is also confined to the individual and is not inherited by the offspring. In luxuriant plants this appearance was frequently noted. Seeds which are damaged by insects during their development often vary in colour and form, but with a little practice in sorting, errors are easily avoided. It is almost superfluous to mention that the pods must remain on the plants until they are thoroughly ripened and have become dried, since it is only then that the shape and colour of the seed are fully developed.

Expt. 3. Colour of the seed-coats.—Among 929 plants, 705 bore violet-red flowers and grey-brown seed-coats; 224 had white flowers and white seed-coats, giving the proportion 3·15 to 1.

Expt. 4. Form of pods.—Of 1181 plants 882 had them simply inflated, and in 299 they were constricted. Resulting ratio, 2·95 to 1.

Expt. 5. Colour of the unripe pods.—The number of trial ⟦experimental⟧ plants was 580, of which 428 had green pods and 152 yellow ones. Consequently these stand in the ratio 2·82 to 1.

Expt. 6. Position of flowers.—Among 858 cases 651 had inflorescences axial and 207 terminal. Ratio, 3·14 to 1.

Expt. 7. Length of stem.—Out of 1064 plants, in 787 cases the stem was long, and in 277 short. Hence a mutual ratio of 2·84 to 1. In this experiment the dwarfed plants were carefully lifted and transferred to a special bed. This precaution was necessary, as otherwise they would have perished through being overgrown by their tall relatives. Even in their quite young state they can be easily picked out by their compact growth and thick dark-green foliage.*

If now the results of the whole of the experiments be brought together, there is found, as between the number of forms with the dominant and recessive characters, an average ratio of 2·98 to 1, or 3 to 1.

The dominant character can have here a *double signification*—viz. that of a parental character, or a hybrid-character.† In which of the two significations it appears in each separate case can only be determined by the following generation. As a parental character it must pass over unchanged to the whole of the offspring; as a hybrid-character, on the other hand, it must maintain the same behaviour as in the first generation [F_2].

6. [F_3] *THE SECOND GENERATION* [*BRED*] *FROM THE HYBRIDS*

Those forms which in the first generation [F_2] exhibit the recessive character do not further vary in the second generation [F_3] as regards this character; they remain constant in their offspring.

It is otherwise with those which possess the dominant character in the first generation [bred from the hybrids]. Of these *two*-thirds yield offspring which display the dominant and recessive characters in the proportion of 3 to 1, and thereby show exactly the same ratio as the hybrid forms, while only *one*-third remains with the dominant character constant.

The separate experiments yielded the following results:

Expt. 1. Among 565 plants which were raised from round seeds of the first generation, 193 yielded round seeds only, and remained therefore constant in this character; 372, however, gave both round and wrinkled seeds, in the proportion of 3 to 1. The number of the hybrids, therefore, as compared with the constants is 1·93 to 1.

* [This is true also of the dwarf or "Cupid" Sweet Peas.]

† [This paragraph presents the view of the hybrid-character as something incidental to the hybrid, and not "transmitted" to it—a true and fundamental conception here expressed probably for the first time.]

Expt. 2. Of 519 plants which were raised from seeds whose albumen was of yellow colour in the first generation, 166 yielded exclusively yellow, while 353 yielded yellow and green seeds in the proportion of 3 to 1. There resulted, therefore, a division into hybrid and constant forms in the proportion of 2·13 to 1.

For each separate trial ⟦experiment⟧ in the following experiments 100 plants were selected which displayed the dominant character in the first generation, and in order to ascertain the significance of this, ten seeds of each were cultivated.

Expt. 3. The offspring of 36 plants yielded exclusively grey-brown seed-coats, while of the offspring of 64 plants some had grey-brown and some had white.

Expt. 4. The offspring of 29 plants had only simply inflated pods; of the offspring of 71, on the other hand, some had inflated and some constricted.

Expt. 5. The offspring of 40 plants had only green pods; of the offspring of 60 plants some had green, some yellow ones.

Expt. 6. The offspring of 33 plants had only axial flowers; of the offspring of 67, on the other hand, some had axial and some terminal flowers.

Expt. 7. The offspring of 28 plants inherited the long axis, and those of 72 plants some the long and some the short axis.

In each of these experiments a certain number of the plants came constant with the dominant character. For the determination of the proportion in which the separation of the forms with the constantly persistent character results, the two first experiments are of especial importance, since in these a larger ⟦considerable⟧ number of plants can be compared. The ratios 1·93 to 1 and 2·13 to 1 gave together almost exactly the average ratio of 2 to 1. The sixth experiment gave a quite concordant result; in the others the ratio varies more or less, as was only to be expected in view of the smaller number of 100 trial ⟦experimental⟧ plants. Experiment 5, which shows the greatest departure, was repeated, and then in lieu of the ratio of 60 and 40, that of 65 and 35 resulted. *The average ratio of 2 to 1 appears,* *therefore, as fixed with certainty.* It is therefore demonstrated that, of those forms which possess the dominant character in the first generation, two-thirds have the hybrid-character, while one-third remains constant with the dominant character.

The ratio of 3 to 1, in accordance with which the distribution of the dominant and recessive characters results in the first generation, resolves itself therefore in all experiments into the ratio of 2 : 1 : 1 if the dominant character be differentiated according to its significance as a hybrid-character or as a parental one. Since the members of the first generation [F_2] spring directly from the seed of the hybrids [F_1], *it is now clear that the hybrids form seeds having one or other of the two differentiating characters, and of these one-half develop again the hybrid form, while the other half yield plants which remain constant and receive the dominant or the recessive characters [respectively] in equal numbers.*

7. *THE SUBSEQUENT GENERATIONS [BRED] FROM THE HYBRIDS*

The proportions in which the descendants of the hybrids develop and split up in the first and second generations presumably hold good for all subsequent progeny. Experiments 1 and 2 have already been carried through six generations, 3 and 7 through five, and 4, 5, and 6 through four, these experiments being continued from the third generation with a small number of plants, and no departure from the rule has been perceptible. The offspring of the hybrids separated in each generation in the ratio of 2 : 1 : 1 into hybrids and constant forms.

If A be taken as denoting one of the two constant characters, for instance the dominant, a, the recessive, and Aa the hybrid form in which both are conjoined, the expression

$$A+2Aa+a$$

shows the terms in the series for the progeny of the hybrids of two differentiating characters.

The observation made by Gärtner, Kölreuter, and others, that hybrids are inclined to revert to the parental forms, is also confirmed by the experiments described. It is seen that the number of the hybrids which arise from one fertilisation, as compared with the number of forms which become constant, and their progeny from generation to generation, is continually diminishing, but that nevertheless they could not entirely disappear. If an average equality of fertility in all plants in all generations be assumed, and if, furthermore, each hybrid forms seed of which one-half yields hybrids again, while the other half is constant to both characters in equal proportions, the ratio of numbers for the offspring in each generation is seen by the following summary, in which *A* and *a* denote again the two parental characters, and *Aa* the hybrid forms. For brevity's sake it may be assumed that each plant in each generation furnishes only 4 seeds.

Generation	*A*	*Aa*	*a*	Ratios *A* : *Aa* : *a*
1	1	2	1	1 : 2 : 1
2	6	4	6	3 : 2 : 3
3	28	8	28	7 : 2 : 7
4	120	16	120	15 : 2 : 15
5	496	32	496	31 : 2 : 31
n				2^n-1 : 2 : 2^n-1

In the tenth generation, for instance, $2^n - 1 = 1023$. There result, therefore, in each 2048 plants which arise in this generation 1023 with the constant dominant character, 1023 with the recessive character, and only two hybrids.

8. *THE OFFSPRING OF HYBRIDS IN WHICH SEVERAL DIFFERENTIATING CHARACTERS ARE ASSOCIATED*

In the experiments above described plants were used which differed only in one essential character.* The next task consisted in ascertaining whether the law of development

* [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 (*wesentliches Merkmal*). The point is probably of little theoretical or practical consequence, but a rather heavy stress is thrown on "*wesentlich*".]

discovered in these applied to each pair of differentiating characters when several diverse characters are united in the hybrid by crossing. As regards the form of the hybrids in these cases, the experiments showed throughout that this invariably more nearly approaches to that one of the two parental plants which possesses the greater number of dominant characters. If, for instance, the seed plant has a short stem, terminal white flowers, and simply inflated pods; the pollen plant, on the other hand, a long stem, violet-red flowers distributed along the stem, and constricted pods; the hybrid resembles the seed parent only in the form of the pod; in the other characters it agrees with the pollen parent. Should one of the two parental types possess only dominant characters, then the hybrid is scarcely or not at all distinguishable from it.

Two experiments were made with a considerable number of plants. In the first experiment the parental plants differed in the form of the seed and in the colour of the albumen; in the second in the form of the seed, in the colour of the albumen, and in the colour of the seed-coats. Experiments with seed characters give the result in the simplest and most certain way.

In order to facilitate study of the data in these experiments, the different characters of the seed plant will be indicated by *A*, *B*, *C*, those of the pollen plant by *a*, *b*, *c*, and the hybrid forms of the characters by *Aa*, *Bb*, and *Cc*.

Expt. 1.—	*AB*, seed parents;	*ab*, pollen parents;
	A, form round;	*a*, form wrinkled;
	B, albumen yellow;	*b*, albumen green.

The fertilised seeds appeared round and yellow like those of the seed parents. The plants raised therefrom yielded seeds of four sorts, which frequently presented themselves in one pod. In all, 556 seeds were yielded by 15 plants, and of these there were:

315 round and yellow,
101 wrinkled and yellow,
108 round and green,
32 wrinkled and green.

All were sown the following year. Eleven of the round yellow seeds did not yield plants, and three plants did not form seeds. Among the rest:

38 had round yellow seeds	*AB*
65 round yellow and green seeds	*ABb*
60 round yellow and wrinkled yellow seeds .	*AaB*
138 round yellow and green, wrinkled yellow and green seeds	*AaBb*

From the wrinkled yellow seeds 96 resulting plants bore seed, of which:

28 had only wrinkled yellow seeds	*aB*
68 wrinkled yellow and green seeds	*aBb*.

From 108 round green seeds 102 resulting plants fruited, of which:

35 had only round green seeds	*Ab*
67 round and wrinkled green seeds	*Aab*.

The wrinkled green seeds yielded 30 plants which bore seeds all of like character; they remained constant *ab*.

The offspring of the hybrids appeared therefore under nine different forms, some of them in very unequal numbers. When these are collected and co-ordinated we find:

38	plants	with the	sign	*AB*
35	,,	,,	,,	*Ab*
28	,,	,,	,,	*aB*
30	,,	,,	,,	*ab*
65	,,	,,	,,	*ABb*
68	,,	,,	,,	*aBb*
60	,,	,,	,,	*AaB*
67	,,	,,	,,	*Aab*
138	,,	,,	,,	*AaBb*.

The whole of the forms may be classed into three essentially different groups. The first includes those with the signs *AB*, *Ab*, *aB*, and *ab*: they possess only constant characters and do not vary again in the next generation ⟦following generations⟧. Each of these forms is represented on the average thirty-three times. The second group includes the signs *ABb*, *aBb*, *AaB*, *Aab*:

these are constant in one character and hybrid in another, and vary in the next generation only as regards the hybrid-character. Each of these appears on an average sixty-five times. The form *AaBb* occurs 138 times: it is hybrid in both characters, and behaves exactly as do the hybrids from which it is derived.

If the numbers in which the forms belonging to these classes appear be compared, the ratios of 1, 2, 4 are unmistakably evident. The numbers 33, 65, 138 present very fair approximations to the ratio numbers of 33, 66, 132.

The developmental series consists, therefore, of nine classes, of which four appear therein always once and are constant in both characters; the forms *AB*, *ab*, resemble the parental forms, the two others present combinations between the conjoined characters *A*, *a*, *B*, *b*, which combinations are likewise possibly constant. Four classes appear always twice, and are constant in one character and hybrid in the other. One class appears four times, and is hybrid in both characters. Consequently the offspring of the hybrids, if two kinds of differentiating characters are combined therein, are represented by the expression

$$AB+Ab+aB+ab+2ABb+2aBb+2AaB+2Aab+4AaBb.$$

This expression is indisputably a combination series in which the two expressions for the characters *A* and *a*, *B* and *b* are combined. We arrive at the full number of the classes of the series by the combination of the expressions:

$$A+2Aa+a$$
$$B+2Bb+b.$$

Expt. 2.

ABC, seed parents;	*abc*, pollen parents;
A, form round;	*a*, form wrinkled;
B, albumen yellow;	*b*, albumen green;
C, seed-coat grey-brown;	*c*, seed-coat white.

This experiment was made in precisely the same way as the previous one. Among all the experiments it demanded the most time and trouble. From 24 hybrids 687 seeds were obtained in all : these were all either spotted, grey-brown or grey-green, round or wrinkled.* From these in the following year 639 plants fruited, and as further investigation showed, there were among them :

8	plants	*ABC*	22	plants	*ABCc*	45	plants	*ABbCc*
14	,,	*ABc*	17	,,	*AbCc*	36	,,	*aBbCc*
9	,,	*AbC*	25	,,	*aBCc*	38	,,	*AaBCc*
11	,,	*Abc*	20	,,	*abCc*	40	,,	*AabCc*
8	,,	*aBC*	15	,,	*ABbC*	49	,,	*AaBbC*
10	,,	*aBc*	18	,,	*ABbc*	48	,,	*AaBbc*
10	,,	*abC*	19	,,	*aBbC*			
7	,,	*abc*	24	,,	*aBbc*			
			14	,,	*AaBC*	78	,,	*AaBbCc*
			18	,,	*AaBc*			
			20	,,	*AabC*			
			16	,,	*Aabc*			

The whole expression contains 27 terms. Of these 8 are constant in all characters, and each appears on the average 10 times; 12 are constant in two characters, and hybrid in the third; each appears on the average 19 times; 6 are constant in one character and hybrid in the other two; each appears on the average 43 times. One form appears 78 times and is hybrid in all of the characters. The ratios 10, 19, 43, 78 agree so closely with the ratios 10, 20, 40, 80, or 1, 2, 4, 8, that this last undoubtedly represents the true value.

The development of the hybrids when the original parents differ in three characters results therefore according to the following expression:

$$ABC + ABc + AbC + Abc + aBC + aBc + abC + abc + 2ABCc + 2AbCc + 2aBCc + 2abCc + 2ABbC + 2ABbc + 2aBbC + 2aBbc + 2AaBC + 2AaBc + 2AabC + 2Aabc + 4ABbCc + 4aBbCc + 4AaBCc + 4AabCc + 4AaBbC + 4AaBbc + 8AaBbCc.$$

Here also is involved a combination series in which the

* [Note that Mendel does not state the cotyledon-colour of the first crosses in this case; for as the coats were thick, it could not have been seen without opening or peeling the seeds.]

expressions for the characters A and a, B and b, C and c, are united. The expressions

$$A + 2Aa + a$$
$$B + 2Bb + b$$
$$C + 2Cc + c$$

give all the classes of the series. The constant combinations which occur therein agree with all combinations which are possible between the characters A, B, C, a, b, c; two thereof, ABC and abc, resemble the two original parental stocks.

In addition, further experiments were made with a smaller number of experimental plants in which the remaining characters by twos and threes were united as hybrids: all yielded approximately the same results. There is therefore no doubt that for the whole of the characters involved in the experiments the principle applies that *the offspring of the hybrids in which several essentially different characters are combined exhibit the terms of a series of combinations, in which the developmental series for each pair of differentiating characters are united.* It is demonstrated at the same time that *the relation of each pair of different characters in hybrid union is independent of the other differences in the two original parental stocks.*

If n represent the number of the differentiating characters in the two original stocks, 3^n gives the number of terms of the combination series, 4^n the number of individuals which belong to the series, and 2^n the number of unions which remain constant. The series therefore contains, if the original stocks differ in four characters, $3^4 = 81$ classes, $4^4 = 256$ individuals, and $2^4 = 16$ constant forms: or, which is the same, among each 256 offspring of the hybrids there are 81 different combinations, 16 of which are constant.

All constant combinations which in Peas are possible by the combination of the said seven differentiating characters were actually obtained by repeated crossing. Their number is given by $2^7 = 128$. Thereby is simultaneously given the practical proof *that the constant characters which appear in the several varieties of a group of plants may be obtained in all the associations which are possible according to the* [*mathematical*] *laws of combination, by means of repeated artificial fertilisation.*

As regards the flowering time of the hybrids, the experiments are not yet concluded. It can, however, already be stated that the time stands almost exactly between those of the seed and pollen parents, and that the constitution ⟦development⟧ of the hybrids with respect to this character probably follows the rule ascertained in the case of the other characters. The forms which are selected for experiments of this class must have a difference of at least twenty days from the middle flowering period of one to that of the other; furthermore, the seeds when sown must all be placed at the same depth in the earth, so that they may germinate simultaneously. Also, during the whole flowering period, the more important variations in temperature must be taken into account, and the partial hastening or delaying of the flowering which may result therefrom. It is clear that this experiment presents many difficulties to be overcome and necessitates great attention.

If we endeavour to collate in a brief form the results arrived at, we find that those differentiating characters, which admit of easy and certain recognition in the experimental plants, all behave exactly alike in their hybrid associations. The offspring of the hybrids of each pair of differentiating characters are, one-half, hybrid again, while the other half are constant in equal proportions having the characters of the seed and pollen parents respectively. If several differentiating characters are combined by cross-fertilisation in a hybrid, the resulting offspring form the terms of a combination series in which the combination ⟦developmental⟧ series for each pair of differentiating characters are united.

The uniformity of behaviour shown by the whole of the characters submitted to experiment permits, and fully justifies, the acceptance of the principle that a similar relation exists in the other characters which appear less sharply defined in plants, and therefore could not be included in the separate experiments. An experiment with peduncles of different lengths gave on the whole a fairly satisfactory result, although the differentiation and serial arrangement of the forms could not be effected with that certainty which is indispensable for correct experiment.

9. THE REPRODUCTIVE CELLS OF THE HYBRIDS

The results of the previously described experiments led to further experiments, the results of which appear fitted to afford some conclusions as regards the composition of the egg and pollen cells of hybrids. An important clue is afforded in *Pisum* by the circumstance that among the progeny of the hybrids constant forms appear, and that this occurs, too, in respect of all combinations of the associated characters. So far as experience goes, we find it in every case confirmed that constant progeny can only be formed when the egg cells and the fertilising pollen are of like character, so that both are provided with the material for creating quite similar individuals, as is the case with the normal fertilisation of pure species. We must therefore regard it as certain that exactly similar factors must be at work also in the production of the constant forms in the hybrid plants. Since the various constant forms are produced in *one* plant, or even in *one* flower of a plant, the conclusion appears logical that in the ovaries of the hybrids there are formed as many sorts of egg cells, and in the anthers as many sorts of pollen cells, as there are possible constant combination forms, and that these egg and pollen cells agree in their internal composition with those of the separate forms.

In point of fact it is possible to demonstrate theoretically that this hypothesis would fully suffice to account for the development of the hybrids in the separate generations, if we might at the same time assume that the various kinds of egg and pollen cells were formed in the hybrids on the average in equal numbers.*

In order to bring these assumptions to an experimental proof, the following experiments were designed. Two forms which were constantly different in the form of the seed and the colour of the albumen were united by fertilisation.

If the differentiating characters are again indicated as A, B, a, b, we have :

AB, seed parent;	ab, pollen parent;
A, form round;	a, form wrinkled;
B, albumen yellow;	b, albumen green.

* [This and the preceding paragraph contain the essence of the Mendelian principles of heredity.]

The artificially fertilised seeds were sown together with several seeds of both original stocks, and the most vigorous examples were chosen for the reciprocal crossing. There were fertilised :

1. The hybrids with the pollen of *AB*.
2. The hybrids „ „ *ab*.
3. *AB* „ „ the hybrids.
4. *ab* „ „ the hybrids.

For each of these four experiments the whole of the flowers on three plants were fertilised. If the above theory be correct, there must be developed on the hybrids egg and pollen cells of the forms *AB*, *Ab*, *aB*, *ab*, and there would be combined:

1. The egg cells *AB*, *Ab*, *aB*, *ab* with the pollen cells *AB*.
2. The egg cells *AB*, *Ab*, *aB*, *ab* with the pollen cells *ab*.
3. The egg cells *AB* with the pollen cells *AB*, *Ab*, *aB*, *ab*.
4. The egg cells *ab* with the pollen cells *AB*, *Ab*, *aB*, *ab*.

From each of these experiments there could then result only the following forms :

1. *AB*, *ABb*, *AaB*, *AaBb*.
2. *AaBb*, *Aab*, *aBb*, *ab*.
3. *AB*, *ABb*, *AaB*, *AaBb*.
4. *AaBb*, *Aab*, *aBb*, *ab*.

If, furthermore, the several forms of the egg and pollen cells of the hybrids were produced on an average in equal numbers, then in each experiment the said four combinations should stand in the same ratio to each other. A perfect agreement in the numerical relations was, however, not to be expected since in each fertilisation, even in normal cases, some egg cells remain undeveloped or subsequently die, and many even of the well-formed seeds fail to germinate when sown. The above assumption is also limited in so far that while it demands the formation of an equal number of the various sorts of egg and pollen cells, it does not require that this should apply to each separate hybrid with mathematical exactness.

The first and second experiments had primarily the object of proving the composition of the hybrid egg cells, while the third and fourth experiments were to decide that of the pollen cells.* As is shown by the above demonstration the first and third experiments and the second and fourth experiments should produce precisely the same combinations, and even in the second year the result should be partially visible in the form and colour of the artificially fertilised seed. In the first and third experiments the dominant characters of form and colour, A and B, appear in each union, and are also partly constant and partly in hybrid union with the recessive characters a and b, for which reason they must impress their peculiarity upon the whole of the seeds. All seeds should therefore appear round and yellow, if the theory be justified. In the second and fourth experiments, on the other hand, one union is hybrid in form and in colour, and consequently the seeds are round and yellow; another is hybrid in form, but constant in the recessive character of colour, whence the seeds are round and green; the third is constant in the recessive character of form but hybrid in colour, consequently the seeds are wrinkled and yellow; the fourth is constant in both recessive characters, so that the seeds are wrinkled and green. In both these experiments there were consequently four sorts of seed to be expected—viz. round and yellow, round and green, wrinkled and yellow, wrinkled and green.

The crop fulfilled these expectations perfectly. There were obtained in the

1st Experiment, 98 exclusively round yellow seeds;
3rd „ 94 „ „ „ „ .

In the 2nd Experiment, 31 round and yellow, 26 round and green, 27 wrinkled and yellow, 26 wrinkled and green seeds.

In the 4th Experiment, 24 round and yellow, 25 round and green, 22 wrinkled and yellow, 27 wrinkled and green seeds.

* [To prove, namely, that both were similarly differentiated, and not one or other only.]

There could scarcely be now any doubt of the success of the experiment; the next generation must afford the final proof. From the seed sown there resulted for the first experiment 90 plants, and for the third 87 plants which fruited: these yielded for the

1st Exp.	3rd Exp.		
20	25	round yellow seeds	*AB*
23	19	round yellow and green seeds . . .	*ABb*
25	22	round and wrinkled yellow seeds . .	*AaB*
22	21	round and wrinkled green and yellow seeds	*AaBb*

In the second and fourth experiments the round and yellow seeds yielded plants with round and wrinkled yellow and green seeds, *AaBb*.

From the round green seeds plants resulted with round and wrinkled green seeds, *Aab*.

The wrinkled yellow seeds gave plants with wrinkled yellow and green seeds, *aBb*.

From the wrinkled green seeds plants were raised which yielded again only wrinkled and green seeds, *ab*.

Although in these two experiments likewise some seeds did not germinate, the figures arrived at already in the previous year were not affected thereby, since each kind of seed gave plants which, as regards their seed, were like each other and different from the others. There resulted therefore from the

2nd. Exp.	4th. Exp.			
31	24	plants of the form		*AaBb*
26	25	,,	,,	*Aab*
27	22	,,	,,	*aBb*
26	27	,,	,,	*ab*

In all the experiments, therefore, there appeared all the forms which the proposed theory demands, and they came in nearly equal numbers.

In a further experiment the characters of flower-colour and length of stem were experimented upon, and selection was so made that in the third year of the experiment each character ought to appear in half of all the plants if the above theory were correct. *A*, *B*, *a*, *b* serve again as indicating the various characters.

A, violet-red flowers;	*a*, white flowers;
B, axis long;	*b*, axis short.

The form *Ab* was fertilised with *ab*, which produced the hybrid *Aab*. Furthermore, *aB* was also fertilised with *ab*, whence the hybrid *aBb*. In the second year, for further fertilisation, the hybrid *Aab* was used as seed parent, and hybrid *aBb* as pollen parent.

Seed parent, *Aab*;	Pollen parent, *aBb*;
Possible egg cells, *Ab*, *ab*;	Pollen cells, *aB*, *ab*.

From the fertilisation between the possible egg and pollen cells four combinations should result, viz.:

$$AaBb + aBb + Aab + ab.$$

From this it is perceived that, according to the above theory, in the third year of the experiment out of all the plants

half should have violet-red flowers (*Aa*),	Classes	1, 3,
,, ,, ,, white flowers (*a*)	,,	2, 4,
,, ,, ,, a long axis (*Bb*)	,,	1, 2,
,, ,, ,, a short axis (*b*)	,,	3, 4.

From 45 fertilisations of the second year 187 seeds resulted, of which only 166 reached the flowering stage in the third year. Among these the separate classes appeared in the numbers following:

Class	Colour of flower	Stem	
1	violet-red	long	47 times
2	white	long	40 ,,
3	violet-red	short	38 ,,
4	white	short	41 ,,

There subsequently ⟦consequently⟧ appeared

the violet-red flower-colour	(*Aa*)	in 85 plants,
the white flower-colour	(*a*)	in 81 plants,
the long stem	(*Bb*)	in 87 plants,
the short stem	(*b*)	in 79 plants.

The theory adduced is therefore satisfactorily confirmed in this experiment also.

For the characters of form of pod, colour of pod, and position of flowers, experiments were also made on a small scale and results obtained in perfect agreement. All combinations, which were possible through the union of the differentiating characters duly appeared, and in nearly equal numbers.

Experimentally, therefore, the theory is confirmed that *the pea hybrids form egg and pollen cells which, in their constitution, represent in equal numbers all constant forms which result from the combination of the characters united in fertilisation.*

The difference of the forms among the progeny of the hybrids, as well as the respective ratios of the numbers in which they are observed, find a sufficient explanation in the principle above deduced. The simplest case is afforded by the developmental series of each pair of differentiating characters. This series is represented by the expression $A+2Aa+a$, in which A and a signify the forms with constant differentiating characters, and Aa the hybrid form of both. It includes in three different classes four individuals. In the formation of these, pollen and egg cells of the form A and a take part on the average equally in the fertilisation; hence each form [occurs] twice, since four individuals are formed. There participate consequently in the fertilisation

the pollen cells $A+A+a+a$,
the egg cells $A+A+a+a$.

It remains, therefore, purely a matter of chance which of the two sorts of pollen will become united with each separate egg cell. According, however, to the law of probability, it will always happen, on the average of many cases, that each pollen form A and a will unite equally often with each egg cell form A and a, consequently one of the two pollen cells A in the fertilisation will meet with the egg cell A and the other with an egg cell a, and so likewise one pollen cell a will unite with an egg cell A, and the other with egg cell a.

$$
\begin{tikzcd}
\text{Pollen cells} & A \arrow[d] & A \arrow[dr] & a \arrow[dl] & a \arrow[d] \\
\text{Egg cells} & A & A & a & a
\end{tikzcd}
$$

The result of the fertilisation may be made clear by putting the signs for the conjoined egg and pollen cells in the form of fractions, those for the pollen cells above and those for the egg cells below the line. We then have

$$\frac{A}{A}+\frac{A}{a}+\frac{a}{A}+\frac{a}{a}.$$

In the first and fourth term the egg and pollen cells are of like kind, consequently the product of their union must be constant, viz. A and a; in the second and third, on the other hand, there again results a union of the two differentiating characters of the stocks, consequently the forms resulting from these fertilisations are identical with those of the hybrid from which they sprang. *There occurs accordingly a repeated hybridisation.* This explains the striking fact that the hybrids are able to produce, besides the two parental forms, offspring which are like themselves; $\frac{A}{a}$ and $\frac{a}{A}$ both give the same union Aa, since, as already remarked above, it makes no difference in the result of fertilisation to which of the two characters the pollen or egg cells belong. We may write then

$$\frac{A}{A}+\frac{A}{a}+\frac{a}{A}+\frac{a}{a}=A+2Aa+a.$$

This represents the average result of the self-fertilisation of the hybrids when two differentiating characters are united in them. In individual flowers and in individual plants, however, the ratios in which the forms of the series are produced may suffer not inconsiderable fluctuations.* Apart from the fact that the numbers in which both sorts of egg cells occur in the seed vessels can only be regarded as equal on the average, it remains purely a matter of chance which of the two sorts of pollen may fertilise each separate egg cell. For this reason the separate values must necessarily be subject to fluctuations, and there are even extreme cases possible, as were described

* [Whether segregation by such units is more than purely fortuitous may perhaps be determined by seriation.]

earlier in connection with the experiments on the form of the seed and the colour of the albumen. The true ratios of the numbers can only be ascertained by an average deduced from the sum of as many single values as possible; the greater the number the more are merely chance effects eliminated.

The developmental series for hybrids in which two kinds of differentiating characters are united contains among sixteen individuals nine different forms, viz.:

$$AB+Ab+aB+ab+2ABb+2aBb+2AaB+2Aab+4AaBb.$$

Between the differentiating characters of the original stocks *Aa* and *Bb* four constant combinations are possible, and consequently the hybrids produce the corresponding four forms of egg and pollen cells *AB*, *Ab*, *aB*, *ab*, and each of these will on the average figure four times in the fertilisation, since sixteen individuals are included in the series. Therefore the participators in the fertilisation are

Pollen cells $AB+AB+AB+AB+Ab+Ab+Ab+Ab+aB$
$+aB+aB+aB+ab+ab+ab+ab.$

Egg cells $AB+AB+AB+AB+Ab+Ab+Ab+Ab+aB$
$+aB+aB+aB+ab+ab+ab+ab.$

In the process of fertilisation each pollen form unites on an average equally often with each egg cell form, so that each of the four pollen cells *AB* unites once with one of the forms of egg cell *AB*, *Ab*, *aB*, *ab*. In precisely the same way the rest of the pollen cells of the forms *Ab*, *aB*, *ab* unite with all the other egg cells. We obtain therefore

$$\frac{AB}{AB}+\frac{AB}{Ab}+\frac{AB}{aB}+\frac{AB}{ab}+\frac{Ab}{AB}+\frac{Ab}{Ab}+\frac{Ab}{aB}+\frac{Ab}{ab}$$
$$+\frac{aB}{AB}+\frac{aB}{Ab}+\frac{aB}{aB}+\frac{aB}{ab}+\frac{ab}{AB}+\frac{ab}{Ab}+\frac{ab}{aB}+\frac{ab}{ab},$$

or

$$AB + ABb + AaB + AaBb + ABb + Ab + AaBb + Aab$$
$$+ AaB + AaBb + aB + aBb + AaBb + Aab + aBb + ab$$
$$= AB + Ab + aB + ab + 2ABb + 2aBb + 2AaB + 2Aab$$
$$+ 4AaBb.$$

* [In the original the sign of equality (=) is here represented by +, evidently a misprint.]

In precisely similar fashion is the developmental series of hybrids exhibited when three kinds of differentiating characters are conjoined in them. The hybrids form eight various kinds of egg and pollen cells—*ABC*, *ABc*, *AbC*, *Abc*, *aBC*, *aBc*, *abC*, *abc*—and each pollen form unites itself again on the average once with each form of egg cell.

The law of combination of different characters which governs the development of the hybrids finds therefore its foundation and explanation in the principle enunciated, that the hybrids produce egg cells and pollen cells which in equal numbers represent all constant forms which result from the combinations of the characters brought together in fertilisation.

10. *EXPERIMENTS WITH HYBRIDS OF OTHER SPECIES OF PLANTS*

It must be the object of further experiments to ascertain whether the law of development discovered for *Pisum* applies also to the hybrids of other plants. To this end several experiments were recently commenced. Two minor experiments with species of *Phaseolus* have been completed, and may be here mentioned.

An experiment with *Phaseolus vulgaris* and *Phaseolus nanus* gave results in perfect agreement. *Ph. nanus* had together with the dwarf axis, simply inflated, green pods. *Ph. vulgaris* had, on the other hand, an axis 10 ft. to 12 ft. high, and yellow-coloured pods, constricted when ripe. The ratios of the numbers in which the different forms appeared in the separate generations were the same as with *Pisum*. Also the development of the constant combinations resulted according to the law of simple combination of characters, exactly as in the case of *Pisum*. There were obtained

Constant combinations	Axis	Colour of the unripe pods	Form of the ripe pods
1	long	green	inflated
2	,,	,,	constricted
3	,,	yellow	inflated
4	,,	,,	constricted
5	short	green	inflated
6	,,	,,	constricted
7	,,	yellow	inflated
8	,,	,,	constricted

The green colour of the pod, the inflated forms, and the long axis were, as in *Pisum*, dominant characters.

Another experiment with two very different species of *Phaseolus* had only a partial result. *Phaseolus nanus*, L., served as seed parent, a perfectly constant species, with white flowers in short racemes and small white seeds in straight, inflated, smooth pods; as pollen parent was used *Ph. multiflorus*, W., with tall winding stem, purple-red flowers in very long racemes, rough, sickle-shaped crooked pods, and large seeds which bore black flecks and splashes on a peach-blood-red ground.

The hybrids had the greatest similarity to the pollen parent, but the flowers appeared less intensely coloured. Their fertility was very limited; from seventeen plants, which together developed many hundreds of flowers, only forty-nine seeds in all were obtained. These were of medium size, and were flecked and splashed similarly to those of *Ph. multiflorus*, while the ground colour was not materially different. The next year forty-four plants were raised from these seeds, of which only thirty-one reached the flowering stage. The characters of *Ph. nanus*, which had been altogether latent in the hybrids, reappeared in various combinations; their ratio, however, with relation to the dominant plants was necessarily very fluctuating owing to the small number of trial plants. With certain characters, as in those of the axis and the form of pod, it was, however, as in the case of *Pisum*, almost exactly 1 : 3.

Insignificant as the results of this experiment may be as regards the determination of the relative numbers in which the various forms appeared, it presents, on the other hand, the phenomenon of a remarkable change of colour in the flowers and seed of the hybrids. In *Pisum* it is known that the characters of the flower- and seed-colour present themselves unchanged in the first and further generations, and that the offspring of the hybrids display exclusively the one or the other of the characters of the original stocks. It is otherwise in the experiment we are considering. The white flowers and the seed-colour of *Ph. nanus* appeared, it is true, at once in the first generation [*from* the hybrids] in one fairly fertile example, but the remaining thirty plants developed flower-colours which were of various grades of purple-red to pale violet. The colouring of the seed-coat was no less varied than that of the flowers. No plant could rank as fully fertile; many produced no fruit at all; others only yielded fruits from the flowers last produced, which did not ripen. From fifteen plants only were well-developed seeds obtained. The greatest disposition to infertility was seen in the forms with preponderantly red flowers, since out of sixteen of these only four yielded ripe seed. Three of these had a similar seed pattern to *Ph. multiflorus*, but with a more or less pale ground colour; the fourth plant yielded only one seed of plain brown tint. The forms with preponderantly violet-coloured flowers had dark brown, black-brown, and quite black seeds.

The experiment was continued through two more generations under similar unfavourable circumstances, since even among the offspring of fairly fertile plants there came again some which were less fertile or even quite sterile. Other flower- and seed-colours than those cited did not subsequently present themselves. The forms which in the first generation [bred from the hybrids] contained one or more of the recessive characters remained, as regards these, constant without exception. Also of those plants which possessed violet flowers and brown or black seed, some did not vary again in these respects in the next generation⟦s⟧; the majority, however, yielded, together with offspring exactly like themselves, some which displayed white flowers and white seed-coats. The red flowering plants remained so slightly fertile that nothing can be said with certainty as regards their further development.

Despite the many disturbing factors with which the observations had to contend, it is nevertheless seen by this experiment that the development of the hybrids, with regard to those characters which concern the form of the plants, follows the same laws as in *Pisum*. With regard to the colour characters, it certainly appears difficult to perceive a substantial agreement. Apart from the fact that from the union of a white and a purple-red colouring a whole series of colours results [in F_2], from purple to pale violet and white, the circumstance is a striking one that among thirty-one flowering plants only one received the recessive character of the white colour, while in *Pisum* this occurs on the average in every fourth plant.

Even these enigmatical results, however, might probably be explained by the law governing *Pisum* if we might assume that the colour of the flowers and seeds of *Ph. multiflorus* is a combination of two or more entirely independent colours, which individually act like any other constant character in the plant. If the flower-colour A were a combination of the individual characters A_1+A_2+... which produce the total impression of a purple coloration, then by fertilisation with the differentiating character, white colour, a, there would be produced the hybrid unions A_1a+A_2a+... and so would it be with the corresponding colouring of the seed-coats.* According to the above assumption, each of these hybrid colour unions would be independent, and would consequently develop quite independently from the others. It is then easily seen that from the combination of the separate developmental series a complete colour-series must result. If, for instance, $A = A_1+A_2$, then the hybrids A_1a and A_2a form the developmental series—

$$A_1+2A_1a+a$$
$$A_2+2A_2a+a.$$

The members of this series can enter into nine different combinations, and each of these denotes another colour—

1 A_1A_2	2 A_1aA_2	1 A_2a
2 A_1A_2a	4 A_1aA_2a	2 A_2aa
1 A_1a	2 A_1aa	1 aa.

The figures prescribed for the separate combinations also indicate how many plants with the corresponding colouring belong to the series. Since the total is sixteen, the whole of the colours are on the average distributed over each sixteen plants, but, as the series itself indicates, in unequal proportions.

Should the colour development really happen in this way, we could offer an explanation of the case above described, viz. that the white flowers and seed-coat colour only appeared

* [As it fails to take account of factors introduced by the albino this representation is imperfect. It is however interesting to know that Mendel realised the fact of the existence of compound characters, and that the rarity of the white recessives was a consequence of this resolution.]

once among thirty-one plants of the first generation. This colouring appears only once in the series, and could therefore also only be developed once in the average in each sixteen, and with three colour characters only once even in sixty-four plants.

It must, nevertheless, not be forgotten that the explanation here attempted is based on a mere hypothesis, only supported by the very imperfect result of the experiment just described. It would, however, be well worth while to follow up the development of colour in hybrids by similar experiments, since it is probable that in this way we might learn the significance of the extraordinary variety in the colouring of our ornamental flowers.

So far, little at present is known with certainty beyond the fact that the colour of the flowers in most ornamental plants is an extremely variable character. The opinion has often been expressed that the stability of the species is greatly disturbed or entirely upset by cultivation, and consequently there is an inclination to regard the development of cultivated forms as a matter of chance devoid of rules; the colouring of ornamental plants is indeed usually cited as an example of great instability. It is, however, not clear why the simple transference into garden soil should result in such a thorough and persistent revolution in the plant organism. No one will seriously maintain that in the open country the development of plants is ruled by other laws than in the garden bed. Here, as there, changes of type must take place if the conditions of life be altered, and the species possesses the capacity of fitting itself to its new environment. It is willingly granted that by cultivation the origination of new varieties is favoured, and that by man'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 we 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 since it is precisely under such circumstances that not only the most varied but also the most variable forms are found. It is only the *Leguminosae*, like *Pisum*, *Phaseolus*,* *Lens*, whose organs of fertilisation are protected by the keel, which constitute a noteworthy exception. Even here there have arisen numerous varieties during a cultural period of more than 1000 years under most various conditions; these maintain, however, under unchanging environments a stability as great as that of species growing wild.

It is more than probable that as regards the variability of cultivated plants there exists a factor which so far has received little attention. Various experiments force us to the conclusion that our cultivated plants, with few exceptions, are *members of various hybrid series*, whose further development in conformity with law is varied and interrupted by frequent crossings *inter se*. The circumstance must not be overlooked that cultivated plants are mostly grown in great numbers and close together, affording the most favourable conditions for reciprocal fertilisation between the varieties present and the species itself. The probability of this is supported by the fact that among the great array of variable forms solitary examples are always found, which in one character or another remain constant, if only foreign influence be carefully excluded. These forms behave precisely as do those which are known to be members of the compound hybrid series. Also with the most susceptible of all characters, that of colour, it cannot escape the careful observer that in the separate forms the inclination to vary is displayed in very different degrees. Among plants which arise from *one* spontaneous fertilisation there are often some whose offspring vary widely in the constitution and arrangement of the colours, while that of others shows little deviation, and among a greater number solitary examples occur which transmit the colour of the flowers unchanged to their offspring. The cultivated species of *Dianthus* afford an instructive example of this. A white-flowered example of *Dianthus caryophyllus*, which itself was derived from a white-flowered variety, was shut up during its blooming period in a

* [*Phaseolus* nevertheless is insect-fertilised.]

greenhouse; the numerous seeds obtained therefrom yielded plants entirely white-flowered like itself. A similar result was obtained from a sub-species, with red flowers somewhat flushed with violet, and one with flowers white, striped with red. Many others, on the other hand, which were similarly protected, yielded progeny which were more or less variously coloured and marked.

Whoever studies the coloration which results in ornamental plants from similar fertilisation can hardly escape the conviction that here also the development follows a definite law which possibly finds its expression *in the combination of several independent colour characters.*

11. *CONCLUDING REMARKS*

It can hardly fail to be of interest to compare the observations made regarding *Pisum* with the results arrived at by the two authorities in this branch of knowledge, Kölreuter and Gärtner, in their investigations. According to the opinion of both, the hybrids in outward appearance present either a form intermediate between the original species, or they closely resemble either the one or the other type, and sometimes can hardly be discriminated from it. From their seeds usually arise, if the fertilisation was effected by their own pollen, various forms which differ from the normal type. As a rule, the majority of individuals obtained by one fertilisation maintain the hybrid form, while some few others come more like the seed parent, and one or other individual approaches the pollen parent. This, however, is not the case with all hybrids without exception. Sometimes the offspring have more nearly approached, some the one and some the other of the two original stocks, or they all incline more to one or the other side; while in other cases *they remain perfectly like the hybrid* and continue constant in their offspring. The hybrids of varieties behave like hybrids of species, but they possess greater variability of form and a more pronounced tendency to revert to the original types.

With regard to the form of the hybrids and their development, as a rule an agreement with the observations made in

Pisum is unmistakable. It is otherwise with the exceptional cases cited. Gärtner confesses even that the exact determination whether a form bears a greater resemblance to one or to the other of the two original species often involved great difficulty, so much depending upon the subjective point of view of the observer. Another circumstance could, however, contribute to render the results fluctuating and uncertain, despite the most careful observation and differentiation. For the experiments, plants were mostly used which rank as good species and are differentiated by a large number of characters. In addition to the sharply defined characters, where it is a question of greater or less similarity, those characters must also be taken into account which are often difficult to define in words, but yet suffice, as every plant specialist knows, to give the forms a peculiar appearance. If it be accepted that the development of hybrids follows the law which is valid for *Pisum*, the series in each separate experiment must contain very many forms, since the number of the terms, as is known, increases with the number of the differentiating characters as the powers of three. With a relatively small number of experimental plants the result therefore could only be approximately right, and in single cases might fluctuate considerably. If, for instance, the two original stocks differ in seven characters, and 100-200 plants were raised from the seeds of their hybrids to determine the grade of relationship of the offspring, we can easily see how uncertain the decision must become since for seven differentiating characters the combination ⟦developmental⟧ series contains 16,384 individuals under 2187 various forms; now one and then another relationship could assert its predominance, just according as chance presented this or that form to the observer in a majority of cases.

If, furthermore, there appear among the differentiating characters at the same time *dominant* characters, which are transmitted entire or nearly unchanged to the hybrids, then in the terms of the developmental series that one of the two original parents which possesses the majority of dominant characters must always be predominant. In the experiment described relative to *Pisum*, in which three kinds of differentiating characters were concerned, all the dominant characters belonged to the seed parent. Although the terms of the series in their internal composition approach both original parents equally, yet in this experiment the type of the seed parent obtained so great a preponderance that out of each sixty-four plants of the first generation fifty-four exactly resembled it, or only differed in one character. It is seen how rash it must be under such circumstances to draw from the external resemblances of hybrids conclusions as to their internal nature.

Gärtner mentions that in those cases where the development was regular among the offspring of the hybrids the two original species were not reproduced, but only a few individuals which approached them. With very extended developmental series it could not in fact be otherwise. For seven differentiating characters, for instance, among more than 16,000 individuals—offspring of the hybrids—each of the two original species would occur only once. It is therefore hardly possible that these should appear at all among a small number of experimental plants; with some probability, however, we might reckon upon the appearance in the series of a few forms which approach them.

We meet with an *essential difference* in those hybrids which remain constant in their progeny and propagate themselves as truly as the pure species. According to Gärtner, to this class belong the *remarkably fertile hybrids Aquilegia atropurpurea canadensis*, *Lavatera pseudolbia thuringiaca*, *Geum urbano-rivale*, and some *Dianthus* hybrids; and, according to Wichura, the hybrids of the Willow family. For the history of the evolution of plants this circumstance is of special importance, since constant hybrids acquire the status of new species. The correctness of the facts is guaranteed by eminent observers, and cannot be doubted. Gärtner had an opportunity of following up *Dianthus Armeria deltoides* to the tenth generation, since it regularly propagated itself in the garden.

With *Pisum* it was shown by experiment that the hybrids form egg and pollen cells of *different* kinds, and that herein lies the reason of the variability of their offspring. In other hybrids, likewise, whose offspring behave similarly we may assume a like cause; for those, on the other hand, which remain constant the assumption appears justifiable that their reproductive cells are all alike and agree with the foundation-cell [fertilised ovum] of the hybrid. In the opinion of renowned physiologists, for the purpose of propagation one pollen cell and one egg cell unite in Phanerogams * into a single cell, which is capable by assimilation and formation of new cells to become an independent organism. This development follows a constant law, which is founded on the material composition and arrangement of the elements which meet in the cell in a vivifying union. If the reproductive cells be of the same kind and agree with the foundation cell [fertilised ovum] of the mother plant, then the development of the new individual will follow the same law which rules the mother plant. If it chance that an egg cell unites with a *dissimilar* pollen cell, we must then assume that between those elements of both cells, which determine opposite characters some sort of compromise is effected. The resulting compound cell becomes the foundation of the hybrid organism the development of which necessarily follows a different scheme from that obtaining in each of the two original species. If the compromise be taken to be a complete one, in the sense, namely, that the hybrid embryo is formed from two similar cells, in which the differences are *entirely and permanently accommodated* together, the further result follows that the hybrids, like any other stable plant species, reproduce themselves truly in their offspring. The reproductive cells which are formed in their seed vessels and anthers are of one kind, and agree with the fundamental compound cell [fertilised ovum].

With regard to those hybrids whose progeny is *variable* we may perhaps assume that between the differentiating elements of the egg and pollen cells there also occurs a compromise, in so far that the formation of a cell as foundation of

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* 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 fertilisation 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 so far have in no wise confirmed. An evident proof of the complete union of the contents of both cells 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 or which the pollen parent.

the hybrid becomes possible; but, nevertheless, the arrangement between the conflicting elements is only temporary and does not endure throughout the life of the hybrid plant. Since in the habit of the plant no changes are perceptible during the whole period of vegetation, we must further assume that it is only possible for the differentiating elements to liberate themselves from the enforced union when the fertilising cells are developed. In the formation of these cells all existing elements participate in an entirely free and equal arrangement, by which it is only the differentiating ones which mutually separate themselves. In this way the production would be rendered possible of as many sorts of egg and pollen cells as there are combinations possible of the formative elements.

The attribution attempted here of the essential difference in the development of hybrids to *a permanent or temporary union* of the differing cell elements can, of course, only claim the value of an hypothesis for which the lack of definite data offers a wide scope. Some justification of the opinion expressed lies in the evidence afforded by *Pisum* that the behaviour of each pair of differentiating characters in hybrid union is independent of the other differences between the two original plants, and, further, that the hybrid produces just so many kinds of egg and pollen cells as there are possible constant combination forms. The differentiating characters of two plants can finally, however, only depend upon differences in the composition and grouping of the elements which exist in the foundation-cells [fertilised ova] of the same in vital interaction.*

Even the validity of the law formulated for *Pisum* requires still to be confirmed, and a repetition of the more important experiments is consequently much to be desired, that, for instance, relating to the composition of the hybrid fertilising cells. A differential [element] may easily escape the single observer,† which although at the outset may appear to be unimportant, may yet accumulate to such an extent that it must not be ignored in the total result. Whether the variable hybrids of other plant species observe an entire agreement must also be

* ["Welche inden Grundzellen derselben in lebendiger Wechselwirkung stehen."]

† ["Dem einzelnen Beobachter kann leicht ein Differenziale entgehen."]

first decided experimentally. In the meantime we may assume that in material points an essential difference can scarcely occur, since the unity in the developmental plan of organic life is beyond question.

In conclusion, the experiments carried out by Kölreuter, Gärtner, and others with respect to *the transformation of one species into another by artificial fertilisation* merit special mention. Particular importance has been attached to these experiments, and Gärtner reckons them among "the most difficult of all in hybridisation".

If a species *A* is to be transformed into a species *B*, both must be united by fertilisation and the resulting hybrids then be fertilised with the pollen of *B*; then, out of the various offspring resulting, that form would be selected which stood in nearest relation to *B* and once more be fertilised with *B* pollen, and so continuously until finally a form is arrived at which is like *B* and constant in its progeny. By this process the species *A* would change into the species *B*. Gärtner alone has effected thirty such experiments with plants of genera *Aquilegia*, *Dianthus*, *Geum*, *Lavatera*, *Lychnis*, *Malva*, *Nicotiana*, and *Oencthera*. The period of transformation was not alike for all species. While with some a triple fertilisation sufficed, with others this had to be repeated five or six times, and even in the same species fluctuations were observed in various experiments. Gärtner ascribes this difference to the circumstance that "the specific [*typische*] power by which a species, during reproduction, effects the change and transformation of the maternal type varies considerably in different plants, and that, consequently, the periods within which the one species is changed into the other must also vary, as also the number of generations, so that the transformation in some species is perfected in more, and in others in fewer generations". Further, the same observer remarks "that in these transformation experiments a good deal depends upon which type and which individual be chosen for further transformation".

If it may be assumed that in these experiments the constitution of the forms resulted in a similar way to that of *Pisum*, the entire process of transformation would find a fairly simple explanation. The hybrid forms as many kinds of egg cells as there are constant combinations possible of the characters conjoined therein, and one of these is always of the same kind as that of the fertilising pollen cells. Consequently there always exists the possibility with all such experiments that even from the second fertilisation there may result a constant form identical with that of the pollen parent. Whether this really be obtained depends in each separate case upon the number of the experimental plants, as well as upon the number of differentiating characters which are united by the fertilisation. Let us, for instance, assume that the plants selected for experiment differed in three characters, and the species *ABC* is to be transformed into the other species *abc* by repeated fertilisation with the pollen of the latter; the hybrids resulting from the first cross form eight different kinds of egg cells, viz.:

$$ABC,\ ABc,\ AbC,\ aBC,\ Abc,\ aBc,\ abC,\ abc.$$

These in the second year of experiment are united again with the pollen cells *abc*, and we obtain the series

$$AaBbCc + AaBbc + AabCc + aBbCc + Aabc + aBbc + abCc + abc.$$

Since the form *abc* occurs once in the series of eight terms, it is consequently little likely that it would be missing among the experimental plants, even were these raised in a smaller number, and the transformation would be perfected already by a second fertilisation. If by chance it did not appear, then the fertilisation must be repeated with one of those forms nearest akin, *Aabc*, *aBbc*, *abCc*. It is perceived that such an experiment must extend the farther *the smaller the number of experimental plants and the larger the number of differentiating characters* in the two original species; and that, furthermore, in the same species there can easily occur a delay of one or even of two generations such as Gärtner observed. The transformation of widely divergent species could generally only be completed in five or six years of experiment, since the number of different egg cells which are formed in the hybrid increases as the powers of two with the number of differentiating characters.

Gärtner found by repeated experiments that the respective period of transformation varies in many species, so that frequently a species *A* can be transformed into a species *B* a generation sooner than can species B into species A. He deduces therefrom that Kölreuter's opinion can hardly be maintained that "the two natures in hybrids are perfectly in equilibrium". It appears, however, that Kölreuter does not merit this criticism, but that Gärtner rather has overlooked a material point, to which he himself elsewhere draws attention, viz. that "it depends which individual is chosen for further transformation". Experiments which in this connection were carried out with two species of *Pisum* demonstrated that as regards the choice of the fittest individuals for the purpose of further fertilisation it may make a great difference which of two species is transformed into the other. The two experimental plants differed in five characters, while at the same time those of species A were all dominant and those of species B all recessive. For mutual transformation A was fertilised with pollen of B, and B with pollen of A, and this was repeated with both hybrids the following year. With the first experiment $\frac{B}{A}$ there were eighty-seven plants available in the third year of experiment for selection of the individuals for further crossing, and these were of the possible thirty-two forms; with the second experiment $\frac{A}{B}$ seventy-three plants resulted, which *agreed throughout perfectly in habit with the pollen parent*; in their internal composition, however, they must have been just as varied as the forms in the other experiment. A definite selection was consequently only possible with the first experiment; with the second the selection had to be made at random, merely. Of the latter only a portion of the flowers were crossed with the A pollen, the others were left to fertilise themselves. Among each five plants which were selected in both experiments for fertilisation there agreed, as the following year's culture showed, with the pollen parent:

1st Experiment	2nd Experiment	
2 plants	—	in all characters
3 ,,	—	,, 4 ,,
—	2 plants	,, 3 ,,
—	2 ,,	,, 2 ,,
—	1 plant	,, 1 character

In the first experiment, therefore, the transformation was completed; in the second, which was not continued further, two more fertilisations would probably have been required.

Although the case may not frequently occur in which the dominant characters belong exclusively to one or the other of the original parent plants, it will always make a difference which of the two possesses the majority of dominants. If the pollen parent has the majority, then the selection of forms for further crossing will afford a less degree of certainty than in the reverse case, which must imply a delay in the period of transformation, provided that the experiment is only considered as completed when a form is arrived at which not only exactly resembles the pollen plant in form, but also remains as constant in its progeny.

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 beyond 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.

Among the experimental species there were cultivated plants, such as *Aquilegia atropurpurea* and *canadensis*, *Dianthus caryophyllus*, *chinensis*, and *japonicus*, *Nicotiana rustica* and *paniculata*, and hybrids between these species lost none of their stability after four or five generations.

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* ["Es sieht" in the original is clearly a misprint for "Er sieht".]

3

MARGINAL COMMENTS ON MENDEL'S PAPER

Ronald A. Fisher

Mendel does not number the sections of his paper. For convenience of reference I have therefore numbered them from 1 to 11. On Section 1 "Introductory remarks" I have already commented sufficiently. It must have been written after he had had time to review and summarise the complete extent of these eight years' trials.

In Section 3 "Division and arrangement of the experiments" Mendel does not give a comprehensive classification, nor does he say in which years the different cultures were grown. It would appear that in the second year, 1857, crossings were made of the two seed characters and of two of the plant characters, involving the recessives *dwarf* and *white flowers*, and that the three other plant characters were first crossed in the following year, 1858. For the seed characters therefore he could observe the hybrid character, or in other words dominance, in 1857, the 3 : 1 ratio of F_2 in 1858, and the 1 : 2 : 1 genotypic ratio in 1859. For *dwarf* and *white flowers* dominance would not be observable until 1858, the 3 : 1 ratio in 1859 and the genotypic classification in 1860. The three other plant characters would follow in all respects one year later. The repeated test with yellow pods was presumably in 1862. This first series of tests must therefore have spread over seven of the eight experimental years, and have overlapped the two other series of tests reported.

The bifactorial and trifactorial experiments are dealt with in Section 8. The latter of these must have taken four years and involved more plants than any other trial. It may well have occupied the whole of the available space in 1863.

The exceedingly important tests of gametic ratios, reported last (Section 9) involved only a few plants, and may well have been completed in 1862.

For the first series Mendel's plan emerges in Sections 3 to 6, where the results are rearranged according to the generations of each cross. In summary they are of the form

(i)		$AA = aa$		Initial cross
(ii)		Aa		F_1 exhibiting dominance
(iii)	$\frac{1}{4}\,AA$	$\frac{1}{2}\,Aa$	$\frac{1}{4}\,aa$	F_2, phenotypic 3 : 1 ratio
	True breeding	Segregating		F_3 demonstrating 1 : 2 : 1 genotypic ratio in F_2

For the two seed characters it was only necessary to grow the plants from dominant F_2 seeds, for the seeds on these would distinguish the true breeding homozygotes from the segregating heterozygotes.

For the plant characters a different procedure was necessary, and that adopted by Mendel, as stated in Section 6, was to choose one hundred plants out of the several hundred available showing the dominant character, and to grow ten plants in the following year from the seeds from each of these. Thus with a total progeny of 1000, it seemed possible to establish the genotype of 100 chosen F_2 plants. There is a difficulty about this scheme, which was not discussed by Mendel, and which he may have overlooked. The probability of 10 seeds chosen at random from a heterozygote all carrying the dominant character is not altogether negligible. In fact, $(\frac{3}{4})^{10}$ is rather more than 5 per cent. So that instead of expecting one non-segregating to two segregating progenies, Mendel ought to have expected the ratio of 1·1126 to 1·8874, out of three F_2 plants tested. Out of the 600 progenies tested in all Mendel should not have expected 200 non-segregating, but about 223. He actually records 201.

There is no easy way out of the difficulty. The same discrepancy must have occurred with the 473 test progenies needed to complete the trifactorial experiment; and an examination of the general level of agreement between Mendel's expectations and his reported results shows that it is closer than would be expected in the best of several thousand repetitions. The data have evidently been sophisticated systematically, and after examining various possibilities, I have no doubt that Mendel was deceived by a gardening assistant, who knew too well what his principal expected from each trial made.

At many points it is clear that Mendel expected much closer agreement than the laws of chance would ordinarily allow. In Section 6 he mentions that, when, expecting 2 : 1, he found 60 segregating to 40 non-segregating progenies for yellow pods, he repeated the trial, and at the second test obtained 65 to 35. The original discrepancy was not, however, a significant one, on the numbers used. The measure of discrepancy, χ^2, was only 2·00 for one degree of freedom, so that on a critical test he had no reason to feel dissatisfied. Whether the labour of growing 1000 additional plants provided a motive for making sure that he would be satisfied at the second trial, it is impossible to know.

The first bodies of data available for comparison with theory were the 3 : 1 tests with the two seed characters available probably in 1858. Each of these was based on the total seeds borne by over 250 plants, 7324 seeds in one case, and 8023 in the other (Section 5). With these large numbers a close approximation to the theoretical ratio was to be expected, and was in fact recorded. This may have misled Mendel into expecting an almost equally close agreement in later comparisons where the counts were much smaller. The five series on gametic ratios (Section 9) have very small numbers, i.e.

20	25	31	24	47
23	19	26	25	40
25	22	27	22	38
22	21	26	27	41
90	87	110	98	166

In each of these the four frequencies observed have equal expectations, and in every case they are strikingly more nearly equal than should be expected. Counts of about 500 might be expected to give as close an agreement as these.

It is remarkable how much of the material, which Mendel must have bred, has not been reported, either in confirmation, or for comparison with what he has given. The two seed character counts showing 3 : 1 ratios, were of 7324 and 8023 seeds respectively in 1858. In the following year the numbers of seeds are not given, but the product of 372 seed parents in one case and 353 in the other were ascertained to be from heterozygous parents. Eleven or twelve thousand more seeds, of each kind, from this source alone, must have been available to check the first results.

Since Mendel tells us that each cross was made reciprocally, so that the transmissible elements which entered in one case through the ovules, came in the other case through the pollen, and *vice versa*, it is surprising that he does not, in these F_2 seed counts, separate these reciprocal classes, so as to demonstrate that the reciprocal hybrids were alike, not only in appearance, but in their breeding behaviour.

In the seed characters it was evidently Mendel's intention to obtain the phenotypic 3 : 1 ratio from about 1000 plants. In the case of "yellow pods" there were in the first year only 580 available; in the following year however there were 600 plants from segregating families, and at a later repetition 650 more. Even though the plan had not been completed, no use was made of the supplementary material. In scoring the progenies of ten note must have been made of the occurrence of recessive plants. Presumably the number of these was noted for each progeny. It is a curious fact if these numbers were never added up. Moreover a report of the numbers of progenies scoring 1, 2, 3, ... recessives would have been instructive, especially to any worker anxious to follow Mendel's method with other plants. Presumably such an enumeration would have shown that of those progenies recognised as showing segregation, about one-fifth had been so classified by reason of one recessive member only. This would have revealed cause for some anxiety as to the possibility that some families from heterozygotes had been by chance overlooked altogether. Indeed Mendel might have been led to recommend 15 as a safer number than 10, for each progeny.

In Section 7 Mendel's notation first appears. When he writes

$$A+2Aa+a$$

modern writers would prefer

$$AA+2Aa+aa$$

or

$$A_2+2Aa+a_2$$

using the abbreviation familiar in chemical symbolism, with which modern genetical notation is entirely analogous. Mendel's is the kind of notation developed in symbolic logic; his are not properly mathematical symbols, but may be regarded as contractions of such.

Section 7 is also remarkable for the table showing the progressive effects of inbreeding by self-fertilisation in the simplest case in which inbreeding may be practised, namely with a self-fertile disomic hermaphrodite.

Of the experiments reported in Section 8 the bifactorial experiment with the two seed-characters required only 15 doubly heterozygous plants in the second year, and the survivors from 556 seeds in the third year. It was a light experiment compared with the trifactorial experiment in which flower-colour is added as a third factor. This required 24 plants in the second year, 639 in the third and 4730 in the fourth, for the heterozygote *Cc* could only be distinguished from the homozygote *CC* by a test progeny, and even if only ten seeds were used from each, the large number of 4730 would be required. Perhaps he used less, but this would increase the number of segregating progenies not detected, whereas the number of homozygotes reported is only 152, which is less than one-third of the number tested. It is most likely therefore that Mendel's procedure was the same as that which he had previously explained, and that his results were in some way biased in the same direction.

The greater part of the section is devoted to an elaborate exposition of the combinatorial situation produced by the segregation of three factors. This aspect of genetics is usually ignored in text-books but Mendel's experience as a teacher is surely in accordance with all who have tried to explain genetical ideas, namely that the combinatorial situation needs to be explained quite elaborately. In much more recent times I believe the genetics of the Rhesus blood group factor in Man would have been much more quickly elucidated had serological geneticists had just such an instructional course as is given in Section 8.

Logically the experiments of Section 9 are of immense importance; in time and ground space, however, these form a very trifling part of Mendel's programme. As they are reported last they may have been an afterthought.

As explained in the introductory notes (*p. 6*) the first four tests, derived from a cross of the two seed-characters, involved simultaneous segregation in a double heterozygote, and could serve to test statistical independence of these factors separately in ovules and in pollen. The demonstration of the segregation in the gametes separately was of central interest. The approximate statistical independence of the two factors, which would strike a modern reader as the main point of the experiment, was evidently not so to Mendel, for in the following experiment with plant characters what he reports is not a linkage mating at all, but one of the kind called preparation matings, for the reason that they constitute a necessary stage in the preparation, when these are wanted, of double heterozygotes in repulsion. It is striking that it was not these double heterozygotes, of which 47 were reported, that were used to test the gametic ratios.

In this Section again Mendel's interest is shown in the combinatorial situation involved.

In Section 10 Mendel uses the incomplete and qualitative results reported for *Phaseolus* as a basis for some constructive or speculative thinking. On *p. 41* occurs the only contribution offered in this paper to the discussions arising from the theory of evolution:

> "It is willingly granted that by cultivation the origination of new varieties is favoured, and that by man'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 we 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, since it is precisely under such circumstances that not only the most varied but also the most variable forms are found."

There may well be several passages in various writings of C. Darwin capable of inspiring this reflection. The most obvious is one on the first page of Chapter I of the *Origin of Species*. (I quote from the second edition, 1860):

"There is also, I think, some probability in the view propounded by Andrew Knight, that this variability may be partly connected with excess of food. It seems pretty clear that organic beings must be exposed during several generations to the new conditions of life to cause any appreciable amount of variation; and that when the organisation has once begun to vary, it generally continues to vary for many generations. No case is on record of a variable being ceasing to be variable under cultivation. Our oldest cultivated plants, such as wheat, still often yield new varieties: our oldest domesticated animals are still capable of rapid improvement or modification."

The nature of the argument in Darwin's mind, and the relevance of Mendel's comment appear more clearly from a corresponding passage in Darwin's 1844 essay which was largely embodied in the paper to the Linnaean Society of 1858:

"When plants are transported from high-lands, forests, marshes, heaths, into our gardens and greenhouses, there must be a considerable change of food, but it would be hard to prove that there was in every case an excess of the kind proper to the plant. If it be an excess of food, compared with that which the being obtained in its natural state, the effects continue for an improbably long time; during how many ages has wheat been cultivated, and cattle and sheep reclaimed, and we cannot suppose their *amount* of food has gone on increasing, nevertheless these are amongst the most variable of our domestic productions."

On the blending theory of inheritance Darwin was right to infer that new variations, however caused, would speedily die away, and that the variability of cultivated plants had continued on this view for "an improbably long time". For Mendel, thinking in terms of particulate inheritance, this difficulty would seem very unreasonable. The conditions of cultivation do not need to originate the variations, but only to conserve them.

4

HAS MENDEL'S WORK BEEN REDISCOVERED?*

Ronald A. Fisher

I. 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

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Editor's Note. As indicated in the Preface (*p. v*), all of the years given in Fisher's (1936) reconstruction of the timing of Mendel's experimental programme must be reduced by one. These modified datings were adopted by Fisher in his *Marginal Comments*. They are also used in this printing of his 1936 paper.

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 proceedings 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

* The page numbers given for the English translation of Mendel's paper here refer to its appearance in the present book.

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 hybridisation 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 recognised, 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. 90*):

> "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 Linnaean 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 recognises 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. 8*):

> "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. 51*):

> "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 beyond 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. 22*):

> "In the experiments above described 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 of little theoretical or practical consequence, but a rather heavy stress is laid on *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 of 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 fore-knowledge 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. 22*) "The next task consisted in ascertaining . . .", and the opening sentence of the ninth section (*p. 29*) "The results of the previously described experiments 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. 8*):

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

Mendel's paper was presented on the 8th February 1865; if he first grew his experimental peas in 1856* 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. 10*):

> "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† (1857) 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. 21*) to have shown segregation for six years, which must be 1858-63, the two named plant characters for five (1859-63), 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 (1858).

In 1857 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-fertilised seeds borne by the same plants. From the cross round by wrinkled, sufficient seed was sown to raise 253 plants in 1858, 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 1858, but we are only told the numbers of plants raised from their seed in 1859, and these do not exceed what could have been bred from forty plants of each kind. In

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* This was given as 1857 in the original reconstruction; cf. Preface (*p. vi*).—J.H.B.

† This refers not to the second year of the trial mentioned in the previous paragraph but to the second year of the experiments.—J.H.B.

any case, ground for some 600 to 1000 cross-bred plants must have been needed in 1858, and it may be noted that in this year the number of self-fertilised 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 1856, 1857, and 1858.

The heterozygous plants grown in 1858 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 1858 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 1858 results, he had convinced

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* Here Fisher seems to have mistaken the two-years' trial completed in 1855 for the first two years of the experiments (1856-7). The number of self-fertilised lines was reduced from 34 to 22 (i.e. by 12 rather than 16).—J.H.B.

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. 17*). 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 two 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.*

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* 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

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. 46*):

> "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 both cells 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 or which the pollen parent."

If, in 1858, any doubt as to the equivalence of the contributions of the two parents had entered Mendel's mind, he would

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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 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."

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 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 1859 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 (1859) 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 1857 Mendel must in this year have raised perhaps 250 heterozygous plants from each of the three crosses started in 1858. His cultures were therefore probably increased this year by about 3000 plants.

In 1860 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 1859 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 were 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 1858 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 1861 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, show 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 1862, gave 65 : 35, as near to expectation as could be desired. Although in 1860 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-fertilisation, it is disconcerting to find that the proportion of plants misclassified by this test is not inappreciable. If each offspring has an independent probability, 0·75, of displaying the dominant character, the probability that all ten will do so is $(0{\cdot}75)^{10}$, or 0·0563. 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 0·9437. 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 1859 and 1860. Apart from the continuation of heterozygous series they account for only 3000 in 1861 and for 1000 in 1862. The pollinations for his second series of experiments were, therefore, probably carried out in 1860. 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 1859, it is difficult to place it earlier. The bifactorial experiment took a year less, and might have been started in 1859, since the ripened seeds of 1858 had established the 3 : 1 ratios of the two factors. I shall suppose that both were initiated in 1860, and that the same is true of the important but smaller experiments devoted to determining the gametic ratios.

To 1861, 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 1862, 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 1862 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.

	AA	*Aa*	*aa*	Total
BB . .	38	60	28	126
Bb . .	65	138	68	271
bb . .	35	67	30	132
Total .	138	265	126	529

TABLE I.—*Classification of plants grown in the bifactorial experiment.*

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 1861, which gave 639 offspring in 1862. 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 1863. Of this experiment Mendel says (*p. 25*):

> "Among all the experiments it 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 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

	CC				*Cc*				*cc*				Total			
	AA	*Aa*	*aa*	Total	*AA*	*Aa*	*aa*	Total	*AA*	*Aa*	*aa*	Total	*AA*	*Aa*	*aa*	Total
BB	8	14	8	30	22	38	25	85	14	18	10	42	44	70	43	157
Bb	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

TABLE II.—*Classification of plants grown in the trifactorial experiment.*

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 473 together, must have been grown on in 1863. In addition to abundant new unifactorial data the additional bifactorial data supplied by the experiments are 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 1863. 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 *Aa* and *Bb*, 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).

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-fertilised 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 1862 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-fertilisation. 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.* 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.

	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

TABLE III.—*Comparison of numbers reported with uncorrected and corrected expectations.*

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 trifactorial experiment there was no selection, for all plants

* 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.

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 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 nine 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 1863.

To 1862 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 1862 we have:

	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

TABLE IV.—*Measure of deviation expected and observed in 1862.*

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.

		Expectation		χ^2		Probability of exceeding deviations observed
3 : 1 ratios	Seed-characters	2		0·2779		
	Plant characters	5		1·8610		
			7		2·1389	·95
2 : 1 ratios	Seed-characters	2		0·5983		
	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

TABLE V.—*Deviations expected and observed in all experiments.*

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 1862 give only 7·1872, a value which would be exceeded about 12 times in 13 trials.

What I have inferred respecting the extent of Mendel's cultures is summarised 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 1861 and 1862 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 1863 was probably the fullest of all.

	1856	1857	1858	1859	1860	1861	1862	1863
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

TABLE VI.—*Approximate numbers of plants grown in different years.**

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

* If we take account of the point raised in the footnote on *p. 67*, the total of 2280 plants in 1856 and 1857 would be reduced to 2040.—J.H.B.

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 recognised 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-four 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.* *Next*, it appears that Mendel regarded the numerical

* 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."

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 1858 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 this 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 realised 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, and 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 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 realised 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. 41*):

> "It is willingly granted that by cultivation the origination of new varieties is favoured, and that by man'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 we 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 Linnaean 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 on 15th December 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 hybridisation would in recent times have made more progress, if many observers, instead of beginning

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* Attention should perhaps be drawn here to the following passage from a talk which Fisher gave at a Darwin Centennial Symposium held in Canberra in 1958. (An abbreviated version of this talk was printed in *Aust. J. Science* (1959) **22**, 16-17.)—J.H.B.

> "To the series of accidents which prevented the appreciation of Mendel's work, one more must therefore be added. The two men above all others to whom Mendel's discovery would have been all-important, August Weismann and Francis Galton, both lived indeed to hear of the discovery, thirty-five years later, in the eighth or ninth decades of their lives. Even when in 1900 attention was called to Mendel's paper and it was widely reprinted and translated, the sense of his own allusions to evolution theory was overlooked, and neither Weismann nor Galton came to know how fully these forgotten researches justified the point of view for which each in his own way had fought."

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

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* In 1865 von Nägeli was very likely unaware of Mendel's work. Mendel's first letter to him is dated 31st December 1866.—J.H.B.

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 recognisable 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 summarising. 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 and pretentious 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 recognise 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 hybridisation 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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* [cf. Preface *p. vi* for reference to English translation—J. H. B.]

5

BIOGRAPHICAL NOTICE OF MENDEL*

William Bateson

Gregor Johann Mendel was born on 22nd July 1822, at Heinzendorf bei Odrau, in the "Kuhland" district of Austrian Silesia. His father was a small peasant proprietor, being the first of the family to raise himself to that degree, and he held his land by a kind of socage, performing "Robot" (agricultural labour) for the lord.

The name Mendel suggests a Jewish origin, but it is practically certain that the suggestion is incorrect. The family appears in the Church Register of the seventeenth century—the earlier ones were burnt by the Hussites—usually under the name M*a*ndel, whereas it was not till the reign of Joseph II (1765-1790) that the Jews in Austria assumed definite surnames. At the time of the Thirty Years' War, Kuhland was a protestant district, and several of Mendel's ancestors were of that persuasion. His four grandparents were all of the local Heinzendorf stock, which may be described as a German colony surrounded by a Slavonic population. It is recorded of his father that he took special interest in fruit-culture, initiating his son at an early age into the methods of grafting. Mendel's maternal uncle, Anton Schwirtlich, was evidently a man of intellectual tastes, which is shown by the fact that he started private classes for the children of Heinzendorf who could not walk so far as the neighbouring village, for in Heinzendorf itself there was at that time no regular school. Mendel was thus able to say with some pride that he came from an educational family.

On the death of Schwirtlich a government-school was established which Mendel attended as a young boy. His

* Reprinted from W. Bateson, *Mendel's Principles of Heredity*, Camb. Univ. Press, 1909, pp. 309-316.

talent was noticed and encouraged by the master. At this time also two older boys who had gone away to the school at Leipnik fell in with Mendel during their holidays, and excited his ambition, with the result that he asked his parents to let him study, and eventually he too was sent to Leipnik at 11 years old, though this involved considerable sacrifice on the part of the family. Here he distinguished himself so much that it was decided to continue his education at the gymnasium at Troppau, a course which finished with a year at Olmütz. The parental resources were severely taxed by such expenses, and Mendel was only enabled to complete his course through the generosity of a younger sister, who voluntarily contributed a part of her dowry for this purpose. In after years he repaid her advance many times over, himself providing the education of her three sons, his nephews.

At Troppau one of the teachers was an Augustinian, and it is surmised that perhaps his description of the scholarly tranquillity of the cloister may have turned Mendel's thoughts towards a monastic life. However that may have been, when his time at the gymnasium was ended he became a candidate for admission to the Augustinian house of St Thomas in Brünn, an institution generally spoken of as the Königskloster. His application was successful, and he was elected with a view to his taking part in the educational work which then devolved on this institution. On admission he took the name of Gregor "in religion", Johann being his baptismal name. In 1847 he was ordained a priest.

At the expense of the cloister he was sent in 1851 to the University of Vienna, where he remained till 1853, studying mathematics, physics, and natural sciences.* Returning to Brünn he became a teacher, especially of physics, in the Realschule. He appears to have taken great pleasure in teaching and to have been extraordinarily successful in interesting his pupils in their work. He continued this occupation till 1868, when he was elected Abbot, or more strictly, Prälat of the Königskloster.

* To this period belong two notes which he published in the *Verh. zool. bot. Verein, Wien,* on *Scopolia margaritalis* (1853, III. p. 116) and *Bruchus pisi* (*ibid.* 1854, IV. p. 27). In these papers he speaks of himself as a pupil of Kollar.

The experiments which have made his name famous throughout the world were carried on in the large garden of the cloister. From the time of his novitiate he began experimental work, introducing various plants into the garden and watching their behaviour under treatment. He was fond of showing these cultures to his friends. Dr von Niessl relates how on one occasion he was taken to see *Ficaria calthaefolia* and *Ficaria ranunculoides* (two forms now regarded as varieties of *Ranunculus Ficaria*) which had for some years been cultivated side by side without manifesting any noticeable change. Mendel jokingly said: "This much I *do* see, that nature cannot get on further with species-making in *this* way. There must be something more behind."

With the views of Darwin which at that time were 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 results were communicated to the Brünn Society in 1865 and published in 1866, but they passed unheeded. The subsequent paper on *Hieracium* appeared in 1869, meeting a similar fate.

During his period of scientific work Mendel, as we now know, was engaged on a great variety of cognate researches. In his letters to Nägeli there are allusions to some of these subjects, but unhappily few statements of results. His largest undertaking besides the work on *Pisum* was an investigation of the heredity of bees. He had 50 hives under observation. He collected queens of all attainable races, European, Egyptian, and American, and effected numerous crosses between these races, though it is known that he had many failures. Attempts were made to induce the queens to mate in his room, which he netted in with gauze for the purpose, but it was too small or too dark, and these efforts were unsuccessful. We would give much to know what results he obtained. In view of their genetic peculiarities a knowledge of heredity in bees would manifestly be of great value. The notes which he is known to have made on these experiments cannot be found, and it is supposed by some that in the depression which he suffered before his death they were destroyed.

In 1905 I had the pleasure of visiting the Königskloster, hoping that some trace of the missing books might be discovered. I was most courteously received by the present Prälat and the brethren of the cloister. My thanks are due in particular to Dr Janetschek for the assistance he gave me. It is to him that I owe the photographs of Mendel given in this volume. I saw the hives which had been used standing in their places, but the note-books are gone.* A rich harvest of discovery awaits those who may successfully repeat the work.

With his appointment as Prälat his researches may be said to have ended. To Nägeli he wrote that he hoped that after an interval his elevation might enable him to find better opportunities for study, but it was not to be. In 1872 the Government passed a law imposing special taxes on the property of religious houses. This enactment Mendel conceived to be unjust and he decided to resist, claiming that all citizens should be equal in law, and that if these taxes were imposed on one class of institution they should be imposed on all. He thus took up a position which in England we should call that of a "Passive Resister". At first several monasteries stood out with Königskloster, but gradually they conformed, Mendel alone remaining firm. The quarrel involved him in protracted trouble and litigation. High emissaries are said to have visited him proposing a compromise, and even offering honours in case of submission. Old friends and acquaintances tried to influence him, but it was all in vain. He attended neither to cajolement nor menace. The property of the house was eventually distrained upon, but he did not give in. He became also involved in the racial controversies which are often rife in this part of Austria, and it is only too certain that the last ten years of his life were passed in disappointment and bitterness. From being a cheerful, friendly man he became suspicious and misanthropic. During this period he fell into ill-health, contracting a chronic nephritis, of which he died on 6th January 1884.

As to the propriety of his action in the great quarrel with the Government I have no means of forming an opinion. It

* On chance of finding something, I obtained a file of the local bee-journal of Brünn, but beyond the fact that Mendel was a Vice-President of the *Verein*, whose organ it is, I could discover in it nothing relating to him.

is nevertheless interesting to know that a few years after his death the tax was removed without debate or dispute.

For many years he attended closely to meteorology and published his records annually in the Brünn *Abhandlungen*. He also took a great interest in sunspots, making such observations on them as he could by simple means,* drawing them and recording the frequency of their occurrence. He was among those who incline to the view that there is a connection between the appearance of spots on the sun and meteorological events on the earth. His notes on this subject are also lost. He served a term as President of the Naturforscher Verein in Brünn. That he was credited with good faculties for business is shown by the fact that he was chosen to be Chairman of the Moravian Hypotheken-Bank in that city. He is said also to have attained considerable skill as a chess-player, and he composed a good many problems which however were not published. This faculty reappears in one of his nephews.

His handwriting is remarkable for its extreme neatness, every letter being formed with meticulous precision.

In Heinzendorf, his native village, he is remembered as having been the organiser of a fire-brigade. When he eventually became famous, the erection of a new fire-station was used as an opportunity of commemorating him, and a memorial tablet was placed over the building in his honour.

The types of the great discoverers are most various. To the naturalist the fact is full of meaning. The wild, uncertain, rapid flash of genius, the scattered, half-focussed daylight of generalisation, the steady, slowly-perfected ray of penetrative analysis, are all lights in which truth may be seen. Mendel's faculty was of the latter order. From the fragmentary evidence before us we can in all probability form a fairly true notion of the man, with his clear head, strong interest in practical affairs, obstinate determination, and power of pursuing an abstract idea.

The total neglect of his work is known to have been a serious disappointment to him, as well it might. He is reported to have had confidence that sooner or later it would be noticed,

* He used one of Fritsch's "brachytelescopes".

and to have been in the habit of saying "Meine Zeit wird schon kommen!" This episode in the history of science is not a very pleasant one to contemplate. There are of course many similar examples, but there must be few in which the discovery so long neglected was at once so significant, so simple, and withal so easy to verify. The scientific world may comfort itself with the thought that in this case it sinned through inadvertence. With the exception of Nägeli perhaps none of the leading naturalists ever saw the paper on peas. We would like to know whether Mendel made any other attempt to interest his contemporaries in his discovery. Probably having tried Nägeli and failed, he gave up further efforts.

So far as I have discovered there was, up to 1900, only one reference to Mendel's observations in scientific literature,* namely that of Focke, *Pflanzenmischlinge*, 1881, p. 109, where it is simply stated that Mendel's numerous experiments on *Pisum* gave results similar to those obtained by Knight, but that he believed he had found constant numerical ratios among the types produced by hybridisation. In the same work a similar brief reference is made to the paper on *Hieracium*. For these references we may now be grateful since it was through them that the papers were rediscovered.

The fact that the Brünn journal is rather scarce does not in itself explain why the work was not noticed. Such a circumstance has seldom long delayed general recognition. The cause is unquestionably to be found in that neglect of the experimental study of the problem of Species which supervened on the general acceptance of the Darwinian doctrines. The problem of Species, as Kölreuter, Gärtner, Naudin, Wichura, and the other hybridists conceived it, attracted thenceforth no workers. The question, it was imagined, had been answered and the debate ended. No one felt much interest in the matter. A host of other lines of work were suddenly opened up, and in 1865 the more original investigators naturally found those new methods of research more attractive that the tedious observations of the hybridisers, whose inquiries were supposed, moreover, to have led to no definite result.

* The *Hieracium* paper is referred to by Peter, *Engler's bot. Jahrb.* Bde. v and vi, 1884, but only in its systematic bearings.

Nevertheless the total neglect of such a discovery is not easy to account for. Those who are acquainted with the literature of this branch of inquiry will know that the French Academy offered a prize in 1861 to be awarded in 1862 on the subject "*Étudier les Hybrides végétaux au point de vue de leur fécondité et de la perpétuité de leurs caractères*". This subject was doubtless chosen with reference to the experiments of Godron of Nancy and Naudin, then of Paris. Both these naturalists competed, and the accounts of the work of Godron on *Datura* and of Naudin on a number of species were published in the years 1864 and 1865 respectively. Both, especially the latter, are works of high consequence in the history of the science of heredity. In the latter paper Naudin clearly enunciated what we shall henceforth know as the Mendelian conception of the dissociation of characters of cross-breds in the formation of the germ-cells, though apparently he never developed this conception.

In the year 1864, George Bentham, then President of the Linnaean Society, took these treatises as the subject of his address to the Anniversary meeting on 24th May, Naudin's work being known to him from an abstract, the full paper having not yet appeared. Referring to the hypothesis of dissociation which he fully described, he said that it appeared to be new and well supported, but required much more confirmation before it could be held as proven (*J. Linn. Soc. Bot.* VIII. *Proc.* p. 14).

In 1865, the year of Mendel's communication to the Brünn Society, appeared Wichura's famous treatise on his experiments with *Salix* to which Mendel refers. There are passages in this memoir which come very near Mendel's principles, but it is evident from the plan of his experiments that Mendel had conceived the whole of his ideas before that date.

In 1868 appeared the first edition of Darwin's *Animals and Plants*, marking the very zenith of these studies, and thenceforth the decline in the experimental investigation of Evolution and the problem of Species has been steady. With the rediscovery and confirmation of Mendel's work by de Vries, Correns and Tschermak in 1900 a new era begins.

That Mendel's work, appearing as it did at a moment when several naturalists of the first rank were still occupied with these problems, should have passed wholly unnoticed, will always remain inexplicable, the more so as the Brünn Society exchanged its publications with most of the Academies of Europe, including both the Royal and Linnaean Societies.

Naudin's views were well known to Darwin and are discussed in *Animals and Plants* (ed. 1885, II. p. 23); but, put forward as they were without full proof, they could not command universal credence. Darwin took the objection that Naudin's ideas were not incompatible with cases of reversion, though as we now know, such cases are perfectly consistent with the phenomenon of segregation. Gärtner, too, had adopted opposite views; and Wichura, working with cases of another order, had proved the fact that some hybrids breed true. Consequently it is not to be wondered at that Darwin was sceptical. Moreover, the Mendelian idea of the "hybrid-character", or heterozygous form, was unknown to him, a conception without which the hypothesis of dissociation of characters is quite imperfect.

Had Mendel's work come into the hands of Darwin, it is not too much to say that the history of the development of evolutionary philosophy would have been very different from that which we have witnessed.

". . . 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 recognise 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 hybridisation 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."—R. A. Fisher.