

BREEDING  
AND THE  
MENDELIAN DISCOVERY

A. D. DARBISHIRE.

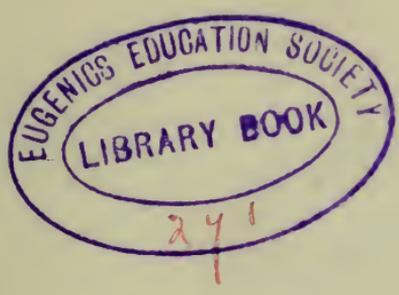




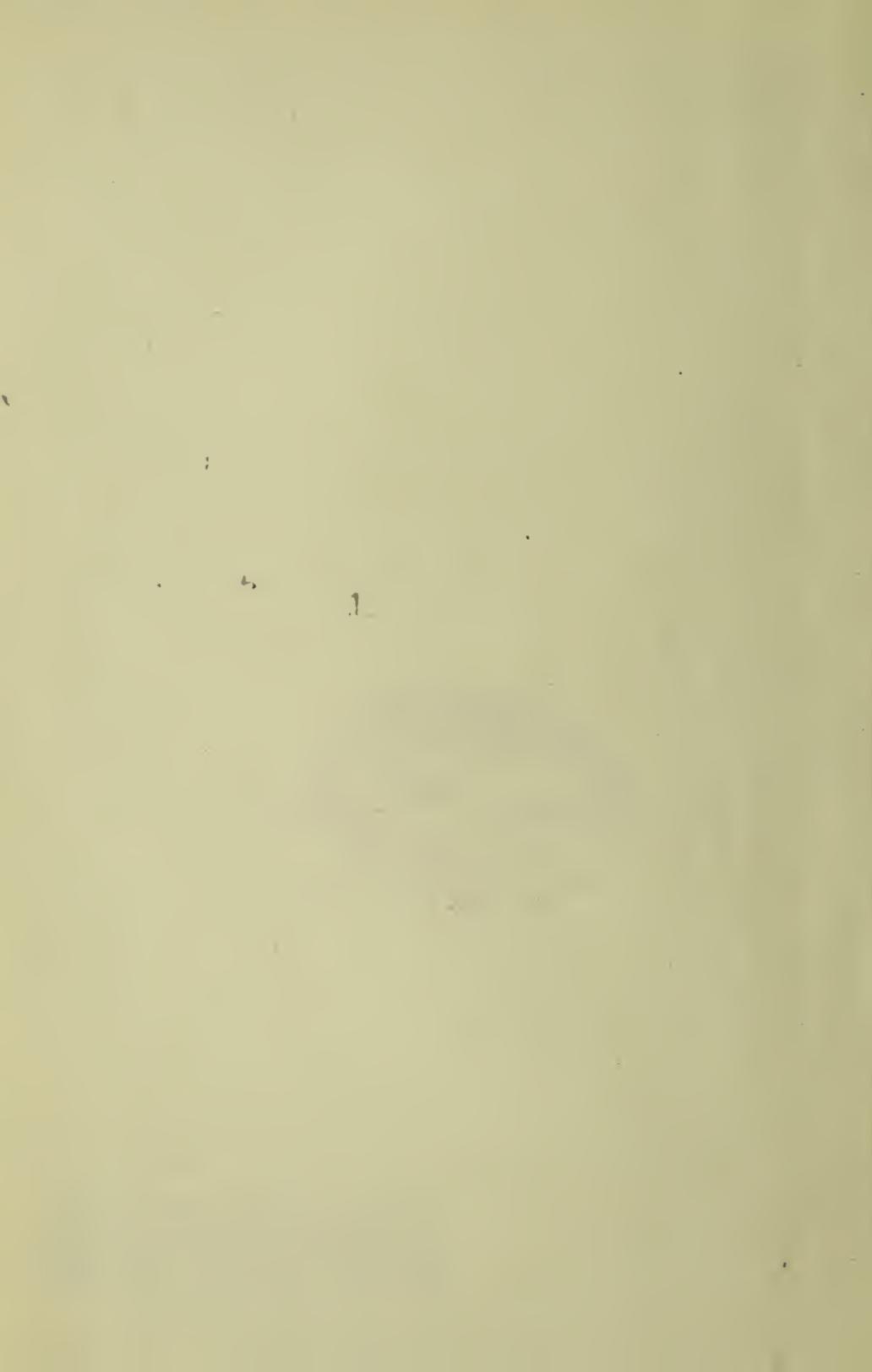
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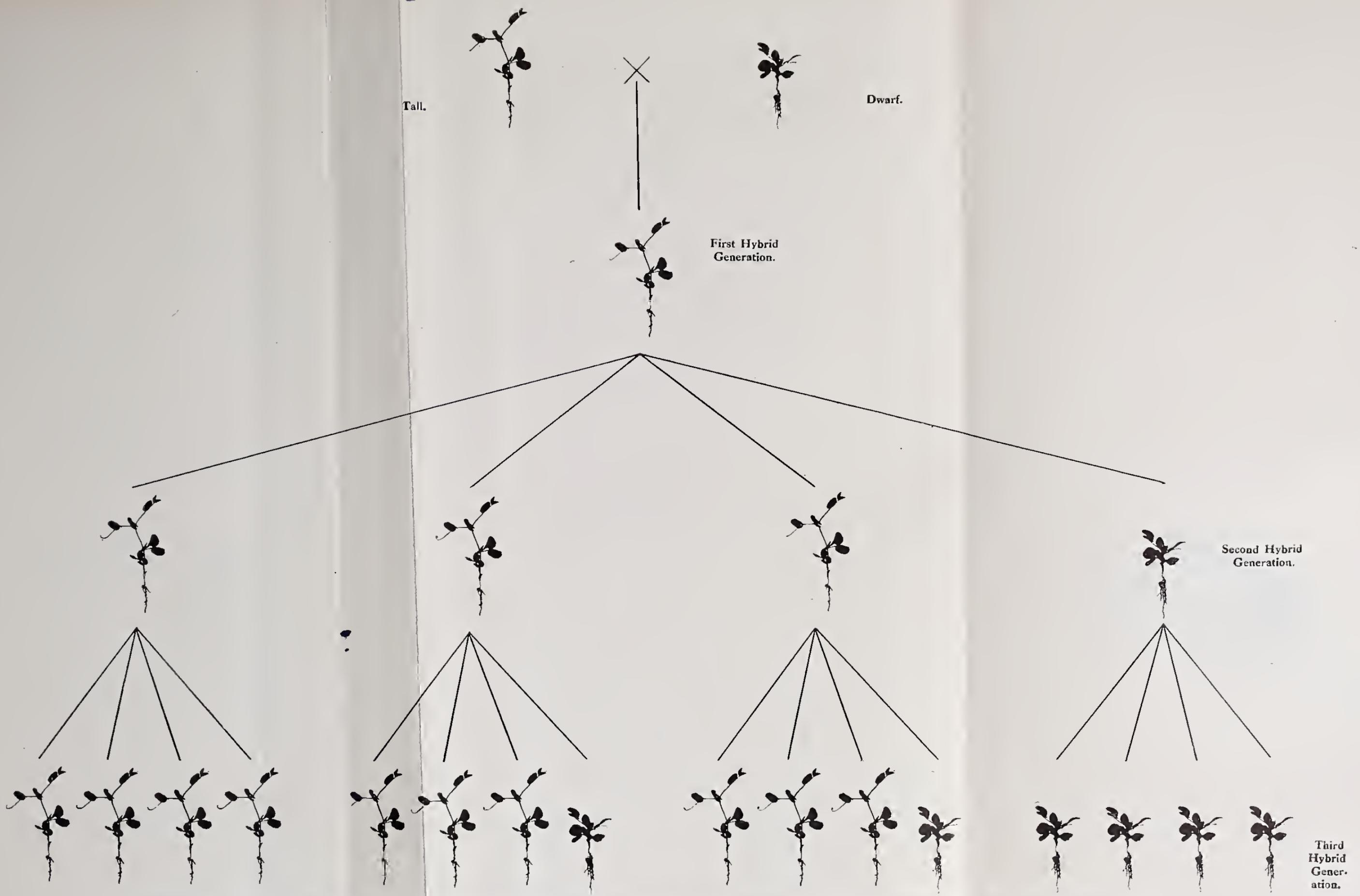


DIAGRAM TO ILLUSTRATE THE MENDELIAN INHERITANCE OF TALLNESS AND DWARFNESS IN THE CULINARY PEA

# BREEDING

AND

## THE MENDELIAN DISCOVERY

BY

A. D. DARBISHIRE, M.A.

Demonstrator of Zoology, and Lecturer on Genetics at the University of  
Edinburgh, and late Demonstrator of Zoology and Lecturer  
on Heredity at the Imperial College of Science  
and Technology, South Kensington

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## PREFACE

THIS book deals, as its title indicates, with the facts discovered by Mendel, and with the bearing of these facts, and of the theory put forward to explain them, on the science of heredity and the practice of breeding. It is intended to serve merely as an introduction to the subject. My conception of the most serviceable form of such an introduction has not been to place before the reader a sketch which takes in the whole range of discovery and speculation in this sphere of inquiry, but, rather, to open the door to an intimate familiarity with a few instances of the Mendelian phenomenon, and especially with those studied by Mendel himself. To this end I have given a fuller account of the phenomena observed by Mendel than has yet appeared in popular form: the seven pairs of characters studied by him are all figured for the first time; and other results of his are illustrated by photographs from specimens which I have bred myself. But, in case the reader takes up the position, with which I heartily sympathise, of refusing to be satisfied with anything short of actually seeing the things which Mendel discovered, I have given full instructions as to how such an

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experiment as Mendel's is carried out, together with the addresses of the seedsmen from whom peas bearing one or more of the fourteen characters studied by Mendel can be procured.

But although I regard a thorough knowledge of the Mendelian discovery as the proper foundation on which the attempt to breed, in the light of it, should be based, I have not limited myself to an attempt to impart this knowledge. I have also indicated the more important lessons which the practical breeder can learn from this discovery, and dealt with some of the more interesting biological questions which it raises, or helps to answer.

My endeavour, throughout, has been to eliminate from my picture of the things described everything with which these things have been invested by the human imagination; in other words, to make my picture not the finished work of the post-impressionist, but the untouched proof of the photographer. And I hope that, in this way, I may do something, in my own sphere of interest, to counteract the prevalent tendency of that which is written, on any topic, to bear but a remote relation to what can actually be observed. This remoteness of words from actuality is especially characteristic of much of the literature on the subject of heredity which has accumulated during recent years. The rational imagination, in its

## PREFACE

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flights in this sphere, has left the ground of facts below, and attained to altitudes which put the feats of airmen in the shade. I am not arguing that it is desirable that those writers to whom the ground is distasteful should cease to fly, but merely pointing out that, inasmuch as so much energy is at present devoted to enterprise of this kind, there is room for a book that will enable anyone to look closely at some of the facts which, though they constitute the ground over which a great deal of recent discussion has raged, are seldom known at first hand by those who witness, or even in some cases by those who take part in, these battles of the air.

My thanks are due, and are readily tendered to Professor de Vries for having taken the photographs which constitute Figs. 1 to 5 inclusive expressly for this book; and to the trustees of the British Museum for permission to photograph the case of my mice which is reproduced in Plate II.

I should claim more credit than is properly mine if I did not acknowledge the help which I have received in the actual carrying out of the breeding experiments to which such value as this book may possess is in great part due. In connection with the breeding experiments with mice, now concluded, my thanks are especially due to Mr. Charles Biddolph

for much help which he very generously gave me. The task of harvesting and recording the peas, on the scale on which the experiment is now carried on, is made possible, and pleasant, by the assistance of Mr. Frank Sherlock ; whilst the fullness of the harvest itself is due to the energy and skill of my gardener, Mr. George Reeves.

#### NOTE TO SECOND EDITION

THE issue of a Second Edition gives me opportunity to correct a few mistakes due to my own inadvertence. For discovering and pointing out to me these mistakes I am especially grateful to my cousin, Dr. O. V. Darbishire, and to my friend Mr. C. F. Meade.

A. D. D.

Go plow in the stubble, for now is the season  
for sowing of fitchis, of beanes, and of peason  
Sowe runcibals timelie, and all that be gray,  
but sowe not the white till S. Gregeries day.

Sow peason and beanes in the wane of the moone  
who soweth them sooner, he soweth too soone  
That they with the planet may rest and arise,  
and flourish with bearing most plentifulwise.

Both peason and beanes sowe afore ye doo plow,  
the sooner ye harrow, the better for yow.  
White peason so good for the purse and the pot:  
let them be well used else well doo ye not.

Stick plenty of bows among runcibal pease  
to climber thereon, and to branch at their ease,  
So dooing more tender and greater they wer,  
if peacock and turkey leave jobbing their ber.

*From Thomas Tusser's "FIVE HUNDRED POINTS OF GOOD HUSBANDRIE."*

*[Edition of 1580 collated with those of 1573 and 1577.]*



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# BREEDING :

AND

## THE MENDELIAN DISCOVERY

### CHAPTER I

#### BREEDING AND HEREDITY

THE practical breeder and the student of heredity both deal with the same natural process, but for very different reasons. The breeder's object is to maintain or increase the value of the animals and plants which minister to the needs or please the fancy of mankind. The student of heredity aims at finding out how the characters of animals and plants are handed on from generation to generation. The breeder is not concerned with the interpretation of what he achieves; he does not care how the characters of his stock are handed on from generation to generation, so long as the changes which he effects tend in the direction of an improvement. The student of heredity, on the other hand, is not concerned with the application of what he finds out; he does not care whether the characters of his material are tending in the direction of an improvement, so long as he finds out how they are handed on from generation to generation. But there cannot, I think, be any doubt that both the practical breeder and the

student of heredity would profit much by a knowledge of the methods employed and the results obtained by the other. It is a question which of the two would gain most: the man of science by the knowledge of the facts relating both to the successes and the failures of the breeder; or the breeder by an acquaintance with the principles elucidated, and the precision of the records kept and the methods employed by the man of science. It is desirable that the student of heredity should, for the sake of his science, become interested in breeding. It is desirable that the breeder should, for the sake of his art, become interested in heredity. And, in general, it is desirable that each should recognise that he has much to learn from the other; for though, as we have seen, the objects of their work are different, the problem which they are both investigating is the same.

My object in writing this book is to place within reach of the practical breeder some of the things found out by the scientific student of heredity, which are likely to be of service to him.

The methods of the breeder are two. They are, as a matter of fact, nearly always used in conjunction, and not separately; but they are nevertheless essentially distinct. They are selection and crossing. Pure selection, operating on material which is not the immediate result of a cross, modifies the form of an animal or plant, and leaves it different from what it was when the selection began; something has been added or taken away; something

created or destroyed. The primary object of crossing is to combine within one strain two desirable qualities existing in distinct strains. But an apparent result of crossing is very often a much more rapid production of something new than is brought about by selection (*see* Plate II.). The novelty in such a case, however, is an illusion, and due to the recombination of characters which have been long hidden and long separated. Selection, then, creates something new; crossing merely recombines characters which already exist. Very little—it may almost be said that nothing—is known of the causes which determine the origin of new characters, either in the domesticated state or in a state of nature. At any rate, there is not enough known to base a scientific practice of breeding upon. But the art of breeding by the recombination of already existing characters—and it is a question whether in its ultimate analysis this may not be all that the breeder can do—has been brought to a point of extreme precision by the discovery made by Mendel in 1865. And the object of this book is to make perfectly clear what that discovery was, and how it affects the practice of breeding. The manner of origin of new forms will be dealt with because a knowledge of Prof. de Vries' observations on this process is necessary to an appreciation of the significance of Mendel's discovery.

Ever since 1859, when Darwin effected the general acceptance of the doctrine of evolution, it has been believed that new forms have originated by the accumulation of the almost imperceptible differ-

ences between individuals, whether this has been brought about by the stress of circumstance or the skill of the breeder. In other words, the material upon which selection, both natural and artificial, has been supposed to operate has been assumed to be these imperceptible differences, the occurrence of which is referred to as the phenomenon of continuous variation.

This belief was attacked by Mr. Bateson in his "Materials for the Study of Variation" in 1894, and was severely shaken by the publication of Prof. de Vries' "Mutationstheorie" in 1901. The belief embodied in both these works is that evolution has not proceeded by the accumulation of the differences presented by continuous variation, but by the differences which are furnished from time to time by what is called "discontinuous variation" by Mr. Bateson, and "mutation" by Prof. de Vries.

The point at issue between the Selectionist, who holds that evolution has been brought about by the selection of continuous variations, and the Mutationist, is this. It is admitted that species, as we see them, constitute a discontinuous series; they are, with rare exceptions, distinct from and do not merge into the species most closely allied to them. The question is whether, when one species arises from another, the new species arises at one bound, i.e. in one generation, or whether it only comes into existence after all the imperceptibly small gradations, between it and the old species from which it sprang, have been traversed over the



FIG. 1.—*CENOTHERA LAMARCKIANA*



course of many generations. According to the former view, species cannot be said to *arise* by selection. If, when they have once arisen, they have defects which hamper them in the struggle for existence, where this occurs, they will doubtless drop out. But this does not constitute *origin* by selection. According to the latter view, on the other hand, the character of the new species is only attained by the traversing of the gradational stages between it and the parent one; and inasmuch as it may be supposed that these gradational forms would not have left offspring if they had any defects which prevented them doing so, it may be said that the new species arises by a process of natural selection.

The view that species have originated by mutation is based on Prof. de Vries' observations on the Evening Primrose (*Oenothera Lamarckiana*) (Fig. .1). Working with this form, he was able to witness, for the first time, the actual process of the origin of new species.

For some time he had been searching in the neighbourhood of Amsterdam for plants which were giving off new forms; but as he failed to find any he concluded that they were all in an immutable condition. At last he found a plant which appeared to be in a mutable state. This was *Oenothera Lamarckiana*. It was growing in a disused potato field near Hilversum, in Holland. This plant had escaped into the field from a bed in a park close by, where some annuals were grown every year. The *Oenotheras* were thickest at the corner of the field

where they had invaded it; and at this spot they formed a dense thicket of vigorous plants as high as a man. From this point outwards the plants became sparser, and the extreme edge of the area which they covered was occupied by an advance guard of seedlings and young rosettes.

Two new species were found in the field—*Ænothera lævifolia*, characterised by its smooth, as opposed to crumpled, leaves and by its narrow petals, which do not overlap one another as do those of *O. Lamarckiana*; and *O. brevistylis*, characterised by the shortness of its style, which is so short that, when the flower is first looked into, it looks as if there were no style or stigma.

Seed was collected from the plants in the potato field at Hilversum and sown in the Botanic Garden at Amsterdam; and rosettes—i.e. plants in their first year, which have not yet developed a stem—were also transplanted there. In this way there arose a series of pedigree cultures in which a number of other new species originated. Of these I will only refer to those which are figured in this book.

*Ænothera gigas* is the rarest and the finest of the new species which has arisen in the Garden at Amsterdam. It has only appeared three times; and it is in every respect more vigorous and more heavily built than its parent *O. Lamarckiana*.

The flowering spike is shown in Fig. 2; and its fruits, alongside those of *O. Lamarckiana*, in Fig. 3. The following characteristics of *O. gigas* can be made out from these figures. Its leaves are broader; its



FIG. 2.—*OENOTHERA GIGAS*





FIG. 3.—*ÆNOTHERA*  
*LAMARCKIANA*

*Æ. GIGAS*



fruits shorter but stouter ; its stem thicker ; and its petals broader, and consequently its buds fatter, than those of the parent species. The top of the stem is densely clothed with foliage ; and its appearance forms a striking contrast to the naked look of the top of the stem of *O. Lamarckiana*. This feature is due to the greater breadth of the leaves, to the fact that they are bent downwards, and to the shortness of the internodes, especially at the extreme top of the stem (see Fig. 3) in *O. gigas*.

Its first appearance was as follows. In 1895 there was a crop of about 14,000 plants, constituting the fourth generation of the *Lamarckiana* culture. All the mutational forms had been transplanted from the crop, and most of the plants of *O. Lamarckiana* had been thrown away. In the beginning of August about 1,000 of these plants were in flower, but many were still in the rosette stage. Thirty-two of the strongest of these rosettes were selected and planted out ; they flowered in the July and August of the following year. One of them attracted Prof. de Vries' attention by its thick stem, and by its large cup-shaped flowers. On August 10 all of its flowers were picked off, both the open and the withered ones, and the whole top of the plant enclosed in a paper bag to ensure self-fertilisation. It set a quantity of good seed. This plant was the parent of the new species *O. gigas*. Its ancestors, for at least three generations back, were ordinary *O. Lamarckiana*. The numbers of seed-bearing plants in these three generations were successively only nine, six, and ten,

and the characters of *O. gigas* are so striking that if one of these twenty-five plants had been a *gigas* it could not have been overlooked, as the seed-bearing plants were under continual and close observation.

The self-fertilised seeds of the original *gigas* were sown in 1897. They produced somewhat over 450 plants. All of them were exactly like their parent, with one exception, to be mentioned later; and they constitute a type distinct, from the very outset, from *O. Lamarckiana*. They bred true on their first appearance, and have continued to do so ever since.

*Oenothera rubrinervis*, which, unlike *O. gigas*, is one of the commonest of the new species which arose from *O. Lamarckiana*, is characterised, as its name implies, by the possession of bright red veins on the leaves and broad red stripes on the calyx and fruit. The flowering spike is shown in Fig. 4. The leaves are narrower than those of *Lamarckiana*; but perhaps the most remarkable feature of this new species is the brittleness of the stem. If the stem of the flowering plant is hit, it breaks in two or three places with perfectly smooth surfaces of fracture. The cause of this brittleness is the extremely slight development of the bast fibres in the vascular bundles, in the stem. In all other respects *rubrinervis* is a healthy species, and it is the only one of the new species which produces as much pollen and seed as the parent species.

*O. rubrinervis* arose from *O. Lamarckiana* sixty-six times in all, and not only did it always possess



FIG. 4.—*ÆNOTHERA RUBRINERVIS*  
(Slightly Enlarged.)



the same set of characters—the red colouring, the brittleness, the narrow leaves—but none of these characters ever appeared separately. It also, like *O. gigas*, produces offspring, all of which are indistinguishable from itself.

*Ænothera nanella*.—This is the dwarf *Ænothera*. A whole plant is shown in Fig. 5. It does not attain to half the stature of the parent form. It arose 158 times during the whole course of the experiments, during which some 50,000 plants were raised, i.e. it appeared in a ratio of about 3 per cent. It also, like the other two new species already mentioned, came perfectly true to seed directly it had arisen.

*O. nanella* is distinguished from the other new species which I have described, first in the fact that it differs from its parent species by only one salient feature—dwarfness; and secondly in the fact that this characteristic is commonly found in other genera of plants, as for instance the pea (see Fig. 6), to mention one of a large number of plants which present this peculiarity. Professor de Vries has proposed to give the name “varietal” to characters like dwarfness, which are widely distributed throughout the vegetable kingdom, to distinguish them from specific characters which, according to him, do not recur in this way. Varieties are forms characterised by the possession of varietal characters, and species are forms characterised by specific characters thus defined. For instance, the complex of characters possessed by *O. gigas* or by *O. rubrinervis* do not occur

elsewhere in the vegetable kingdom, and these two forms are regarded as true species; whilst the character of *O. nanella*, which is regarded as a variety, not only occurs in the pea and in other plants, but also amongst the new forms which have arisen from *O. Lamarckiana*. In fact the single exception referred to amongst the 450 plants raised from the first *O. gigas* was a plant which had all the characters of *O. gigas*, but possessed the dwarf habit of *O. nanella*, and should be designated *O. gigas-nanella*.

Professor de Vries has drawn this further extremely important distinction between specific and varietal characters. Specific characters, according to him, blend in inheritance; whilst varietal ones behave in Mendelian fashion when crossed. Indeed, he makes the behaviour of a particular character when crossed the test whether it is a varietal or a specific one. Professor de Vries has made a number of crosses between *O. gigas* and other species of *Ænothera*. For instance, *O. gigas*, crossed with *O. Lamarckiana*, gives rise to forms which are a blend between their two parents, and moreover breed true to this intermediate character. The conclusion to which he comes in the paper in which he describes these results is stated as follows by him: "In all these respects, and in others as well, *O. gigas* behaves as a true species when crossed, and not as a variety, as *O. nanella* does when crossed with the same forms." There are certain complications in the case of *O. nanella*, but these need not detain us now. Full details can be found in the paper referred



FIG. 5.—*CENOTHERA NANELLA*



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to below \* by those who wish to follow the matter further. Having thus indicated the mode of origin and possible nature of characters which are inherited in Mendelian fashion, we may now proceed to a consideration of the Mendelian phenomenon itself.

\* "Berichte der Deutschen Botanischen Gesellschaft." Jahrgang 1908. Band XXXIA, Heft 10.

## CHAPTER II

### THE MENDELIAN PHENOMENA OF INHERITANCE ; THE RESULT OF CROSSING TALL WITH DWARF PEAS

MENDEL published his results in the journal of a local scientific society in Brünn, in Austria, in 1865; but his paper remained unnoticed\* until the year 1900, when attention was directed to it almost simultaneously by Correns, Tschermak and de Vries, the former two of whom had repeated some of Mendel's experiments, and were thus able to attest the accuracy of his observations. I shall deal in Chapter XII. with the circumstances in which Mendel's discovery was made, and with the probable causes which led to its being forgotten for so long; and shall pass on now to a description of the Mendelian phenomena themselves.

The reader is probably familiar with two kinds of the edible pea (*Pisum sativum*), the tall and the dwarf. The tall peas grow to any height from three to six, or even eight, feet, and need to be supported with sticks; the dwarf peas do not rise more than a foot or two above the level of the ground, and need not be staked.

The difference between a tall and a dwarf pea is

\* With the single exception of a reference in Focke's *Pflanzenmischlinge*, 1881.



FIG. 6.—SEEDLING OF TALL PEA      SEEDLING OF DWARF PEA

The seeds were sown at the same time.



not the same as the difference between a tall and a dwarf man. In a human dwarf everything is on a smaller scale than in the normal man. But a dwarf pea is not simply a miniature edition, as it were, of a tall one: it differs from a tall pea in one single characteristic, the length of the internodes, i.e. the sections of the stem between two nodes, or joints, where the leaves are given off. This is shown in Fig. 6, which represents a seedling of a tall, and a seedling of a dwarf pea sown on the same day. The number of nodes between the seed and the point of insertion of the two leaves which are face to face and enclose the growing point of the stem, is the same in both cases, namely five. They can all be clearly seen in the tall seedling, but the lowest one in the dwarf is difficult to make out on account of the shadow. The shortness of the dwarf pea is thus seen to be due solely to the shortness of its internodes.

If seed is saved from a dwarf plant it will give rise, when sown, to dwarf plants only; and seed saved from tall plants will only produce tall plants. In other words, both tall and dwarf peas, when left to themselves, breed true.

It is desirable to state here that the pea is normally self-fertilised. The male and female organs and products are both present in every flower; and what happens when a plant is "left to itself" is that the female products (or egg-cells) of a single flower are fertilised by the male products (the pollen grains) of the same flower. When one kind, such as tall, is crossed with another kind, such as dwarf, the pollen

grains are transferred from the flowers of a tall plant to a particular part of the female organ of a dwarf plant, or vice versa. The details of this process will be described in Chapter X. The main point which I wish to be noted here is that the pea is always self-fertilised unless it is artificially cross-fertilised by the agency of man.

We have seen that dwarf plants, when left to themselves, set seed which produces dwarf plants only; and that tall similarly breed true.

We will now consider the result of crossing a tall with a dwarf.

The plants which result from a cross between a tall and a dwarf are always tall. These tall are no shorter than their pure tall parents; in fact, as a rule, they are a little taller, because, like most hybrids, they are very vigorous. They constitute the first hybrid generation.

These hybrid tall are allowed to self-fertilise. If the seed saved from them is sown, about three-quarters of the plants produced are tall, and about a quarter are dwarf. That is to say, in every four plants, three are tall and one is dwarf, on the average. This average result is shown in the genealogical table which forms the frontispiece, where it will also be seen that this generation—namely, the one which consists of three tall and one dwarf in every four—is called the second hybrid generation.

Let us now consider the result of sowing the seed saved from the plants composing the second hybrid generation. These plants, like those of the first

## THE MENDELIAN PHENOMENA 15

hybrid generation, are allowed to self-fertilise. The seed set by the dwarfs produces only dwarfs. This is what we should expect, if we look at the tall and dwarfs in the genealogical table from the point of view of their stability in breeding, that is to say according as to whether they produce their own kind only, or both kinds, namely tall and dwarf. If we look back through the pedigree of the dwarfs of the second hybrid generation, we do not come to a dwarf until we reach the pure dwarf parent of the cross. This pure dwarf, as we know, breeds true. We might, therefore, expect that the dwarfs will breed true when they reappear in the second hybrid generation. And we see that they do.

Before we consider the offspring of the tall in the second hybrid generation, let us look back in their pedigree and see if we can form any idea as to what their offspring will be. In the case of the dwarfs of the second hybrid generation we had to go back two generations, namely, to the parents of the cross, before we met with an ancestor bearing the dwarf character. But in the case of the tall we have only to go back one generation—to the first hybrid generation—to find a tall. But this hybrid, although it resembles the pure tall externally, differs from it in its breeding properties. The pure tall produces only tall; from the point of view of its breeding properties, it is stable. But the hybrid tall produces both tall and dwarfs, in the proportion of three tall to one dwarf in every four; it is unstable. That is to say, if we look back through

the ancestry of the second hybrid generation, we find only one kind of dwarf—a pure, true-breeding or stable kind; but we find two kinds of tall, a pure stable kind which produces tall offspring only, and a hybrid or unstable one which produces both tall and dwarf.

What, then, is the nature of the three tall of the second hybrid generation? There are three possibilities. They may be all pure; or all hybrid; or, lastly, some of them may be hybrid and some pure. This latter is actually the case. Two of the three are hybrid, and produce tall and dwarf in the ratio of three tall to one dwarf in every four. The remaining tall is pure, and produces only tall.

In the genealogical table we have supposed that each plant of the second hybrid generation produces only four offspring, because this enables us to put the average proportions of tall and dwarf amongst these offspring most conveniently in diagrammatic form. The pure tall which produces only tall is seen at the extreme left of the second hybrid generation. In the middle are the two hybrid tall, each producing three tall and one dwarf on the average; and at the extreme right is the dwarf, which produces only dwarf.

Let us now glance at the actual proportions observed by Mendel himself. He does not say how many plants of the first hybrid generation he raised; he only states that he made thirty-seven crosses between tall and dwarf. We do not, therefore, know how many of these were successful. His second

## THE MENDELIAN PHENOMENA 17

hybrid generation consisted of 1,064 plants, of which 787 were tall, and 277 were dwarf, a very close approximation to a ratio of 3 to 1.

Ten seeds from each plant of a hundred only of these 787 tall were sown. Twenty-eight of these produced tall; seventy-two produced both tall and dwarf. This result departs considerably from the expected one. Let us examine it more closely. Of the three tall in the second hybrid generation, two should produce tall and dwarf in the proportion of 3 to 1; one should produce tall only. This is one way of expressing the average result. Another way is to say that two-thirds of the tall in the second hybrid generation produce tall and dwarf in the ratio of 3 to 1; and one-third tall only. Of a hundred tall in the second hybrid generation we should, therefore, expect sixty-six or sixty-seven to produce tall and dwarf in the ratio of 3 to 1, and thirty-four or thirty-three to produce only tall, if the general statement I have made as to these ratios is true. It will, therefore, be seen that amongst the hundred tall of the second hybrid generation which Mendel tested, the number of pure tall was too low (twenty-eight as against thirty-four or thirty-three), and the number of hybrid tall too high (seventy-two as against sixty-six or sixty-seven). This brings us up against a very important question, namely, how close a fit between the so-called Mendelian expectation and the actual result must we expect? The general rule is that the greater the numbers of individuals dealt with, in the experiment,

the closer will the actual result approximate to the Mendelian expectation. This is a very important question, which will be dealt with later.

In the course of the description of the Mendelian phenomenon, which is diagrammatically represented in the frontispiece, it was said that certain of the results were what we should have expected them to be if we looked at the whole pedigree from a certain point of view, namely, that of stability in breeding. They are what they would be expected to be by anyone who had no knowledge of the Mendelian phenomenon, and who looked at them from the point of view of stability. For instance, the true breeding of the dwarfs in the second hybrid generation was in harmony with the fact that only *one* kind of dwarf, a pure breeding one, occurred in the ancestry of the cross. And, similarly, the fact that there are *two* kinds of tall, a hybrid and a pure, in the second hybrid generation, is in harmony with the fact that there are two kinds of tall, a hybrid and a pure, in this ancestry.

But, beyond this, most of the results we have described differ widely from what current notions of heredity would lead us to expect them to be. In the first place the general expectation, as to the result of crossing a tall with a dwarf would probably have been that the resultant hybrid would have been intermediate in height between its two parents. But the individuals composing the first hybrid generation are all tall, as we have already seen. Intermediates between tall and dwarf have never been

## THE MENDELIAN PHENOMENA 19

observed to occur in the first hybrid generation, nor do they occur in any subsequent generation derived from the cross. It is perhaps not surprising that the dwarf which disappears altogether in the first hybrid generation should reappear in the second. And although we have said that the true breeding of the dwarf when it does reappear is roughly what we should expect from one point of view, there is a point of view from which it is the very opposite of what we should expect. The fact of the dwarfs in the second hybrid generation breeding true means that they are entirely free from the taint of tallness in spite of the fact that both of their parents and half of the rest of their ancestors were tall. A dwarf occurring in the second hybrid generation—an "extracted" dwarf as it is called—is as pure a dwarf as the pure parental dwarf with which the cross was made, not only in its external characteristics, but also, what is more remarkable, in its breeding properties. The true breeding of one-third of the tall in the second hybrid generation is not quite such a remarkable fact, because in this case their parents at least bore the tall character; but it is remarkable that these tall should exhibit no trace of the dwarf character of half the grand-parental generation and of half the ancestry behind that point.

When we come to consider the fourth and further hybrid generations we shall find that the results come to differ still more widely from what current notions of heredity would lead us to expect them to be.

Suffice it for the present that the actual results, so far as we have considered them, of crossing a tall with a dwarf pea stand out in unexpected simplicity and orderliness against the vague and, as we have seen, often contradictory expectations based on the notions of heredity which were current when Mendel's results were discovered.



FIG. 7.—TOP OF NORMAL STEM OF THE CULINARY PEA



## CHAPTER III

### THE INHERITANCE OF FOUR OTHER CHARACTERS OF THE CULINARY PEA STUDIED BY MENDEL

MENDEL also made crosses between peas which differed from one another in other characters than those of tallness or dwarfness.

Another character with which he dealt was the position of the flowers on the stem. These either arise, in the ordinary way, from the whole length of the stem, above the point, on the stem, where they begin; or they are all bunched together at the top. Fig. 7 shows the former, ordinary, arrangement of the flowers, which is characteristic of all the varieties of peas commonly grown for the kitchen. Fig. 8 shows the latter, in which they are bunched together at the top. The photographs were taken late in the year, so that pods are shown instead of flowers.

I have described these two types of pea in terms of the position of their flowers. But the difference between the two lies deeper than this. In a normal stem the flowers are given off at successive nodes up the stem. The node at which the first one is given off varies greatly in the different kinds of peas. But the essential point is that, in the normal stem, the nodes follow one another at fairly regular intervals; the actual distance between them depending usually

on whether the plant is tall or dwarf, that is to say, on whether the internode is long or short.

If a normal growing stem is examined, from the ground upwards, it will be found that the nodes succeed one another in this regular way, and that the arrangement of the flowers which arise from the nodes is correspondingly regular.

But if a plant on which the flowers are bunched together at the top is examined from the ground upwards, it will be found that, about three quarters of the way up the plant, there are two nodes where there should be only one; so that at this point there are two leaves, and sometimes two flower-stalks, where there should be only one of each. Beyond this point, as we proceed upwards, abnormal nodes of this kind follow one another in rapid succession until we reach the top of the plant, from which the flower-stalks arise in such profusion that they form a sort of crown of flowers. The name "fasciated" is given to this kind of stem; and in the pea, at any rate, the fasciation seems to be due to the loss, by the plant, of something which brings about the production of nodes at regular intervals, as in the normal stem.

The fasciated pea was known in this country in the sixteenth century, when it was described by Gerarde in his "Herbal," published in 1597.\* He calls it "*Pisum umbellatum* (Tufted or Scottish Pease)," and says that these peas "carry their

\* For directing my attention to this and further references to different kinds of peas I am much indebted to a very interesting paper by Mr. N. N. Sherwood, on "Garden Peas" in the *Journal of the Royal Horticultural Society* Vol. XXII., Part 3, 1898.

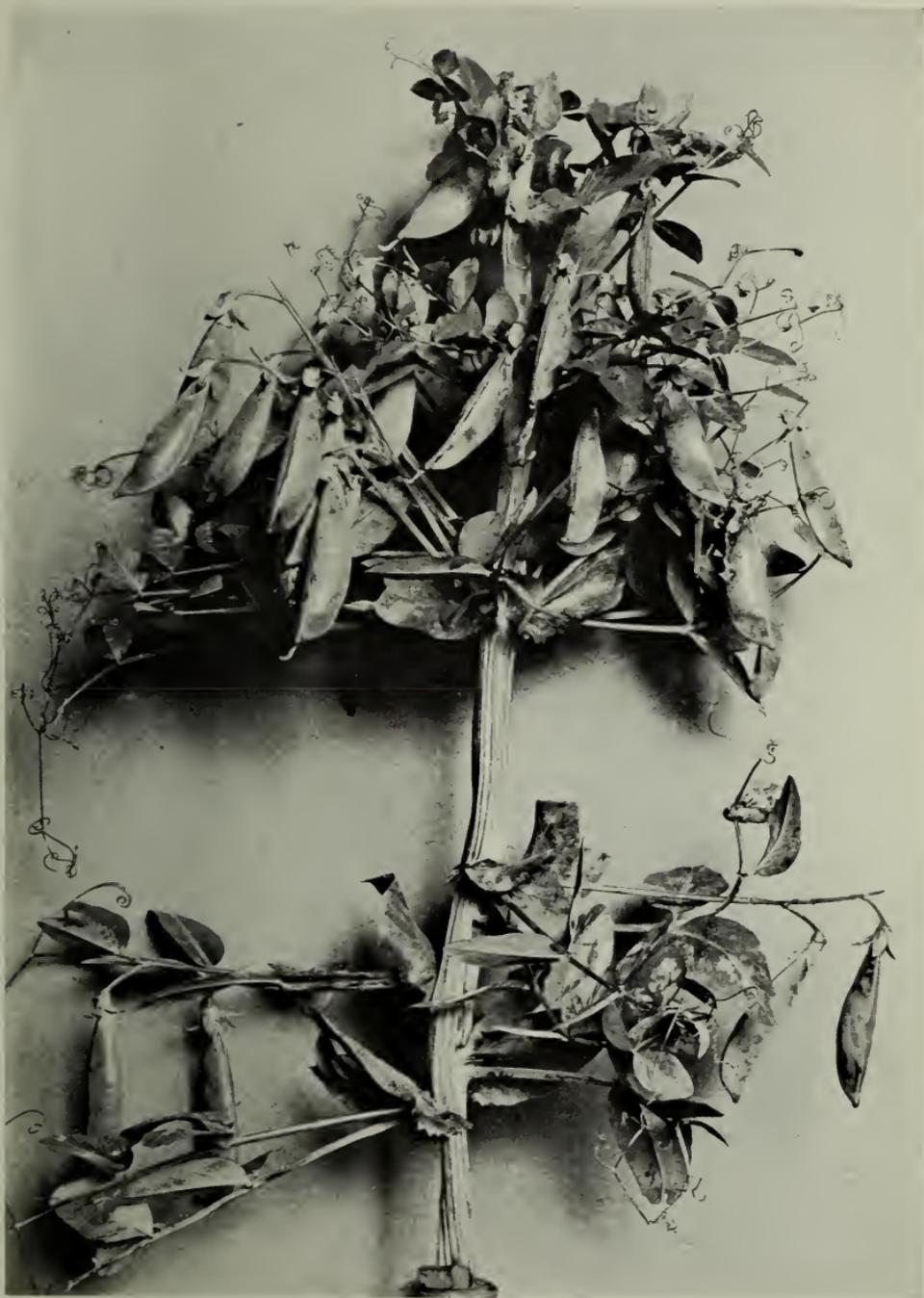


FIG. 8.—TOP OF FASCIATED STEM OF CULINARY PEA



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fruit on the top of the branches, and they are esteemed and taken for Scottish Peason, which is not very common." The fasciated variety now exists under the name Mummy Pea. What this name means I do not know. Many people imagine that these peas are found in Egyptian tombs.

Mendel crossed a variety characterised by a fasciated stem, with a variety the stem of which was normal; and found that the stem of the resultant hybrid was normal.\* The second hybrid generation consisted of 651 normal, and 207 fasciated plants. Only a hundred of these 651 normal plants were tested to see if they were pure or hybrid normals. Ten seeds of each of the hundred were sown, as in the case of the tall and dwarf character. The offspring of thirty-three of the hundred were normal without exception. Of the offspring of the remaining sixty-seven, on the other hand, some were normal and some fasciated in the case of every plant—as close an approximation to the expected Mendelian ratio as can be obtained. In other words, of every three normals in the second hybrid generation two on the average were hybrid and one was pure.

We have so far dealt with characters of the stem of the plant; first, with the differences in the length of the internodes which produce tall and dwarf stems, and then with the differences in the arrangement of

\* Particulars as to how to procure varieties which exhibit the characters studied by Mendel are given on page 158.

the nodes which produce normal and fasciated stems. We shall now deal with characters of the pods ; first with differences in texture, and then with differences in colour.

The third character, with which Mendel experimented, which we shall consider is therefore the shape or, more strictly, the texture of the pod. The pods of all the varieties of culinary pea commonly grown possess a tough, parchment-like lining, which makes the immature pod inedible and the axis of the ripe pod straight (in the sense that a horse's back is straight), and its surface even, as shown in the right-hand pair of pods in Fig. 9. For brevity in reference, this type of pod may be called "hard." There is also a variety of pea, the pods of which lack this tough lining, the absence of which renders it possible for the immature pods to be eaten—and very good they are. They are called sugar peas in England and Germany, and the variety is described as *sans parchemin* in France. The absence of this parchment-like lining has a very noticeable effect on the shape of the pod throughout its development. The main axis of the pod, unsupported by this tough tissue, becomes much bent and contorted, and the two flanks of the pod collapse on to the seeds, so that the contour of the seeds can be clearly seen on the outside of the pod, and the surface of the ripe pod is generally uneven, as is well shown in the left-hand pair of pods in Fig. 9. We may conveniently refer to this type of pod as "soft."



Two "Soft" Pods.

Two "Hard" Pods.

FIG. 9.—MENDELIAN CHARACTERS IN THE TEXTURE OF THE POD



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The hard- and soft-podded varieties were also known to Gerarde. He recognised "Some with tough skins or membranes on the cods, and others have none at all, whose cods are to be eaten with the Peason, when they are young, as those of Kidney Beans."

Mendel crossed these two forms and found that the hybrid resulting from a cross between a hard- and a soft-podded pea was hard-podded. It has since been found that the pod of the hybrid is never so hard as that of the hard-podded parent. But this point requires further investigation, and need not concern us here. The second hybrid generation raised by Mendel from these hybrids consisted of 882 plants with hard pods and 299 plants with soft pods. A hundred of the hard-podded plants were tested by sowing ten seeds of each of them. Twenty-nine of them produced hard-podded plants only; seventy-one produced families in which both hard-podded and soft-podded plants occurred—a tolerably close approximation to the Mendelian expectation (twenty-nine instead of thirty-three or thirty-four, and seventy-one instead of sixty-seven or sixty-six).

The fourth characteristic of the pea with which Mendel dealt was, as I have already said, the colour of the unripe pod. This is, of course, usually green, and, in ordinary kinds, the green only disappears as the pod becomes dry and ripe. But there is a variety of the culinary pea in which the pod goes

yellow *before* it ripens. This change in colour is not the same as that which ripening pods undergo ; or, if it is, it is the same change shifted back in development, because it takes place long before the pods begin to dry and ripen. This turning yellow, whilst the plant is still juicy and growing, affects the stem and, afterwards, the leaves, as well as the pods ; and if seed of yellow-podded and ordinary green-podded plants are sown together the numbers of the two kinds of plants can be counted more conveniently by the stems than by the pods, so pronounced is the difference between the colour of the green and that of the yellow stems. In Fig. 10 there is seen, to the left, part of a plant of the yellow-podded variety ; and, to the right, a specimen of the ordinary green-podded kind. In the yellow-podded specimen, the pods themselves have gone yellow, but the leaves are still green ; the contrast between the pale colour of the pod and the deeper colour of the leaf is clearly shown. The pod looks as if it were made of yellow wax ; and the analogous yellow-podded dwarf bean is sometimes called the wax-pod bean.

Mendel crossed a green-podded with a yellow-podded variety of pea, and found that the offspring were green-podded. The second hybrid generation consisted of 428 plants with green pods and 152 with yellow ones. A hundred of the green-podded plants were tested, and forty of them gave rise to green-podded plants only, and sixty to both green- and yellow-podded ones.



The Yellow-podded Variety.

The ordinary Green-podded Variety.

FIG. 10.—MENDELIAN CHARACTERS IN THE COLOUR OF THE POD IN THE CULINARY PEA



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We now leave the characters of the pods and pass on to the colour of the seed coats, which is the last of the characters dealt with by Mendel which we shall consider at present. The two colours that Mendel worked with were white and "grey"—or, more strictly speaking, a grey-green that becomes brown with age. They were recognised in the sixteenth century by Thomas Tusser, who refers to them in his remarks on February in his "Hundred Points of Good Husbandrie," which is printed on p. iii of this book.

"Sowe runcival\* timelie and all that be gray,  
but sowe not the white till S. Gregories day."

The white seed-coat is characteristic of the majority of peas commonly grown in the kitchen-garden. A plant that has white seed-coats always has white flowers. The grey colour of the seed-coat is characteristic of many but by no means of all field peas. In addition to the plain grey of the seeds there is very often a greater or lesser amount of purple colour in the form of minute spots distributed uniformly over the seed-coat. This purple colour is left out of account in considering the result of crossing white with grey. A plant with a grey seed-coat always has purple flowers.

A grey-skinned pea is shown in Fig. 11. This particular race, which was given to me by Mr. R. H. Lock, does not exhibit the purple spots. An ordinary white-skinned culinary pea is illustrated in Fig. 12.

\* A kind of pea, figured by Gerarde.

I have shown the peas in the pods, in order to emphasise the fact that all the seed-coats on a plant are the same—all grey on the plant in Fig. 11, and all white on the plant in Fig. 12. This is a very important point to bear in mind.

The hybrid produced by crossing a white-skinned pea with a grey-skinned one was found by Mendel to be grey. The second hybrid generation consisted of 705 grey-skinned plants, and 224 white-skinned ones. A hundred of the former were tested, and thirty-six gave grey-skinned ones only; the remaining sixty-four gave both grey-skinned and white-skinned plants.

Let us now take a retrospective glance at the five characters of the pea, the manner of inheritance of which has just been described.

Let them be considered first from the point of view of the time at which they appear in the life-history of the plant. The difference between tall and dwarf appears in the very young seedling long before it needs to be supported with a stick. The difference between normal and fasciated cannot be detected until the plant has grown to some height and needs the support of a stick; but it can be seen before the appearance of the flower buds. The difference between hard and soft pods cannot, of course, be detected until after the flower is "over" and the pod has begun to develop, but it can be seen very soon after the pod projects beyond the withered petals, and long before the peas begin to fill out the



FIG. 11.—“GREY” PEA



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pod. It is not, however, until this stage in the development of the pod is reached that the difference between the yellow and the green pod can be observed. And, lastly, the colour of the seed-coat cannot be seen, because it is not developed, until the pod, containing it, is ripe and dry.

It will be noted that in the above recapitulation the five characters have been placed in the order in which we have considered them in detail, and also in the order in which they appear on the plant.

There remain two characters of the pea dealt with by Mendel; but they will be taken out of their order. They are the earliest of all to appear; so early, indeed, that they can be seen before the seed is planted—i.e. as soon as it is taken out of the pod. It will be remembered that the earliest character which we have yet considered (the distinction between tallness and dwarfness) was visible in the young seedlings. The two characters still to be dealt with belong to the first two leaves of the plant which remain in the seed, and never come above the ground. These first two leaves, or cotyledons, are so important economically, because they contain the food-material (starch and sugar) which renders the pea valuable as food, and the characters in respect of which they differ have played so prominent a part in establishing the reality of the Mendelian phenomenon, and in testing the theories put forward to explain it, that a special chapter will be devoted to their consideration.

Let us now take a general survey of the five

instances of the Mendelian phenomenon with which we have dealt, and note the points which they exhibit in common. In each of the five instances the characters were considered in pairs—tall and dwarf, normal and fasciated, and so on. The justification for this is that in every case the two characters of a pair always appertain to the same part of the plant—to the stem, or pod, or seed-coats. And not only so, but to the same feature of a particular part of the plant. Thus tallness of stem and softness of pod do not constitute a pair, because they relate to different parts of the plant. Nor even do tallness of stem and fasciation of stem constitute a pair, because, though both relate to the stem, one relates to the length of the internode and the other to the arrangement of the nodes. Thus the two characters which constitute a pair appertain to the same feature of a particular part of the plant.

A further characteristic of the two members of a pair is that when an individual bearing one of them is mated with an individual bearing the other, the resulting hybrid usually bears one of the pair of characters to the complete exclusion of the other. In the case of tallness and dwarfness, for instance, the hybrid exhibits no trace of the dwarf character; but in the case of hardness and softness of pods, the pod of the hybrid is a little softer than that of its hard-podded parent. That character of a pair which completely or partially excludes the other of the pair, in the hybrid, is called the Dominant member of the pair; the other character is called the Recessive



FIG. 12.—“WHITE” PEA



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one because it recedes, as it were, for one generation, but reappears in the next.

The dominant and recessive members of the five pairs of characters which we have dealt with are shown in the following table :—

	<i>Feature of the Plant affected by the two characters of the Pair.</i>	<i>Dominant Member of Pair.</i>	<i>Recessive Member of Pair.</i>
1st pair	Length of internode	Long (producing tallness)	Short (producing dwarfness)
2nd „	Arrangement of nodes	Normal	Abnormal (producing fasciation)
3rd „	Texture of pod	Hard	Soft
4th „	Colour of unripe pod	Green	Yellow
5th „	Colour of ripe seed-coat	Grey	White

The Mendelian phenomenon (*see* the Frontispiece) can now be described in general terms.

The result of crossing an individual bearing a dominant character with one bearing a recessive character are hybrids bearing the dominant character. These constitute the first hybrid generation. The second hybrid generation consists both of individuals\* bearing the dominant character and of individuals† bearing the recessive character, in the ratio of three dominants to one recessive in every four, on the average. Of these dominants one is a pure dominant, and will produce only dominants. The

\* Sometimes called dominants for brevity.

† Sometimes called recessives for brevity.

other two are hybrids, and will produce dominants and recessives in the proportion three to one, just as the hybrids of the first hybrid generation did.

We see, therefore, that when the recessive reappears in the second hybrid generation (an extracted recessive, as it is then called), we may count on its being pure, and be confident that it will breed true; but we cannot tell whether the dominants which occur in the second hybrid generation are pure dominants or hybrids until we have bred from them. This can be done in the case of self-fertilising plants by allowing self-fertilisation to take place and by sowing the seed thus set. If dominants only are produced, it is pure; if dominants and recessives, it is hybrid. But there is another way which is much more suitable in the case of animals, in which the sexes are separate. It has been found that if a hybrid of the first hybrid generation is mated with a recessive, half of the offspring are hybrids (bearing the dominant character, of course), and half are recessives.





FIG. 13.—ANDALUSIAN FOWLS

(Reproduced from Wright's "Book of Poultry.")

## CHAPTER IV

### GENERAL CHARACTERISTICS OF THE MENDELIAN PHENOMENON ILLUSTRATED BY THE CASE OF THE ANDALUSIAN FOWL AND THE INHERITANCE OF EYE-COLOUR IN MAN

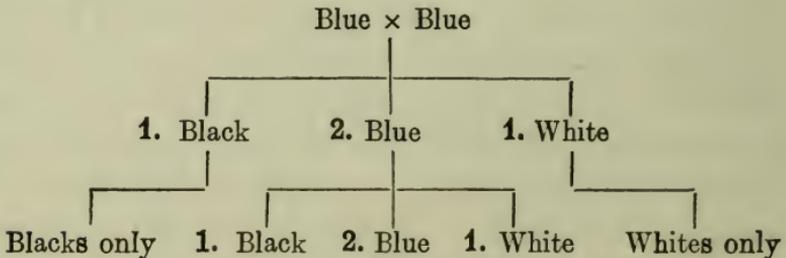
I PROPOSE to give now some further instances of the Mendelian hereditary phenomenon to illustrate some of its general characteristics. One of the most striking instances of the Mendelian phenomenon is that which is exhibited by the breeding properties of the Andalusian fowl. In perhaps no other case is the contrast between what actually occurs and what we expect to happen, seen in bolder relief.

The blue Andalusian fowl owes its popularity with the public, and its interest to the student of heredity, to its colour. This is a slaty blue-grey.

If two birds of this strain are mated, it will be found that they do not breed true. Besides the blue birds which hatch out, there will also be a certain number of blacks, and of whites with occasional black points, hereafter to be referred to simply as "whites." If the blues thus produced are mated together, blacks and "whites" will again appear amongst their offspring, and no amount of breeding from the blues alone will rid them of the

black and white blood which will crop out at every generation, although blue birds only are mated every time.

I gave an account of the above facts in an article on Mendelian principles which I wrote for the *Country Home*. An acquaintance, who kept fowls, read the article, and said to me that though the article as a whole was very interesting, what I had said about Andalusian fowls was, of course, untrue. "It stands to reason," she said, "that if you continue to breed from the Andalusians alone you will ultimately fix the strain. It is common sense." Let us see what actually happens. When blue Andalusians are mated together, birds of three types of colour are produced in the following proportions: one black, two blue Andalusians, and one white in every four birds, on the average. The blacks are found to breed true; so are the whites. The Andalusians when mated together again produce these three types in the same proportions. The result may be expressed in the form of a genealogical table, as follows:—



It is impossible to look at this table without suspecting that the blue Andalusian is a hybrid, like

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the hybrid tall pea, and that the two forms which correspond to the pure tall and pure dwarf in the peas are the black and white birds respectively. Or, rather, this case more closely resembles that of the texture of the pods in the pea where, it will be remembered, the result of crossing a hard-podded with a soft-podded pea was a pea whose pods were intermediate in texture—between those of its two parents, but closer to those of the former.

Be this as it may, the result of crossing a black and a white is a blue Andalusian, and blue birds obtained in this way, when mated together, produce a generation of fowls consisting of about one black, two blues, and one white in every four.

The Mendelian phenomenon exhibited by these fowls may be set forth in the form of a genealogical table (Fig. 14) corresponding to that representing the result of crossing a tall with a dwarf pea. A comparison between the table of the fowls and that of the peas brings out one important point of difference between them. In the case of the peas, the hybrid tall, whether it occurs in the first or second hybrid generation, only differs from the pure tall by its breeding properties and not by any outward characteristics of its own—or, more strictly, not by any characteristics of its own so far as we know at present. It is not improbable that accurate measurement may reveal a difference. For the present, however, at any rate, the hybrid tall and pure tall are identical so far as we know them, except in their breeding properties. In other words, the tall

character behaves as a simple dominant when it meets the dwarf character, in a cross.

But the case exhibited by the Andalusian fowl is different. The so-called blue colour of this bird may, or may not, be described as an intermediate between the black and white of the fowls which produce it when they are crossed; but, at any rate, it is different from either of them, and the important point to note is that the hybrid, whether of the first or second or third hybrid generation, is distinguished from both of the parents of the cross, not only by its breeding properties, but by easily observable external characteristics.

The reader will probably admit the reasonableness of referring to the black fowl as the dominant, and the white as the recessive, although the black is not absolutely dominant over the white in the result of the cross. It is expedient to use these terms in this case, because it is convenient to have a general term to apply to the characters of the two forms crossed. It is also legitimate to use them because the difference between the result of crossing the black and the white fowl and the result of crossing the tall and dwarf pea is only one of degree. In the case of the pea, tallness is completely dominant over dwarf; in the case of the fowl blackness may be said to be only partially dominant over whiteness. Moreover, it may be that the appearance of complete dominance is merely due to the fact that we are as yet unable to detect the difference between the hybrid and the dominant in the case of stature in peas. This is no

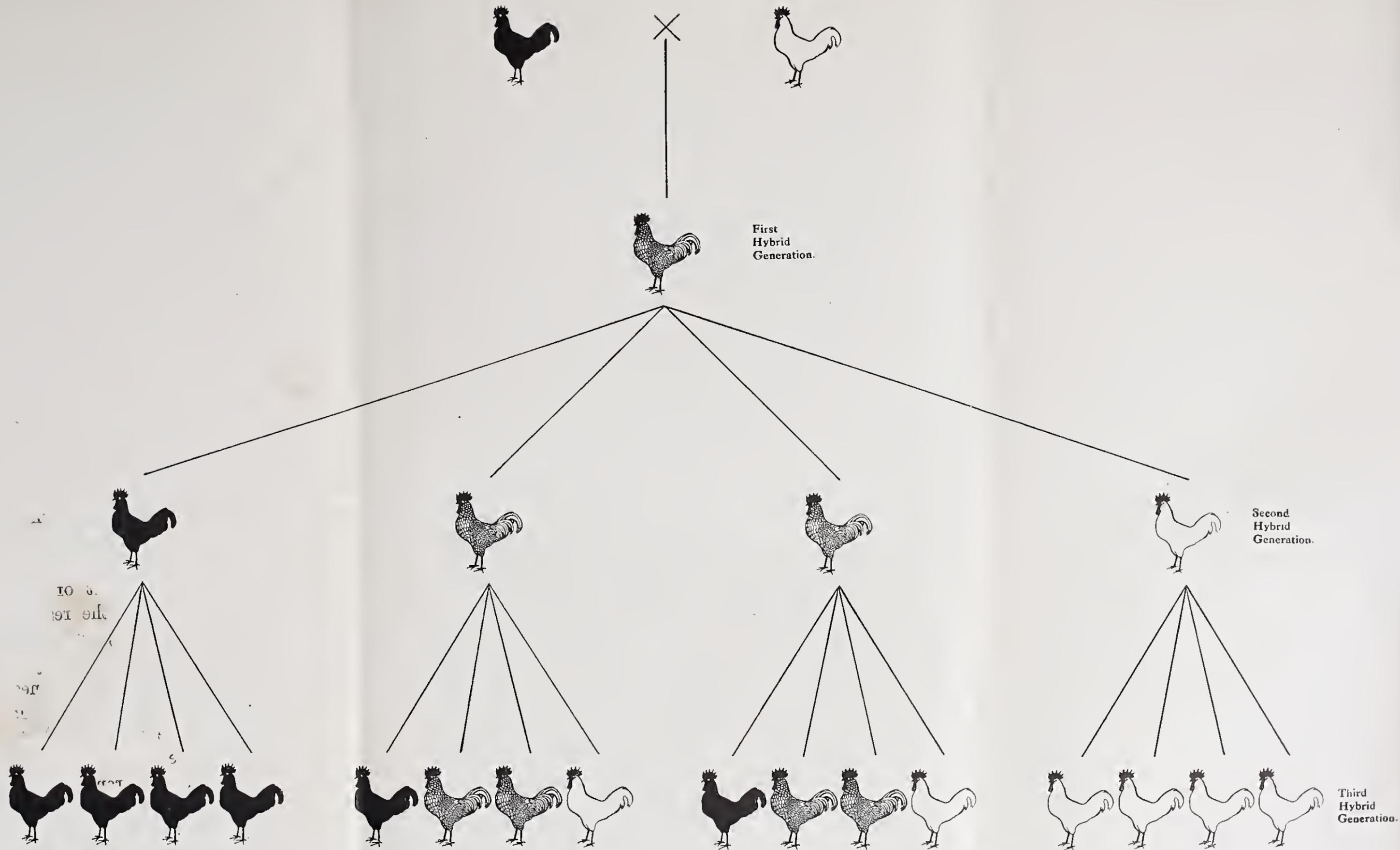


FIG. 14.—DIAGRAM TO ILLUSTRATE THE MENDELIAN INHERITANCE OF COLOUR IN THE ANDALUSIAN FOWL



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The prophecy; for a difference between the hybrid and the dominant parent has recently been detected by the aid of the microscope in a stock instance of simple dominance—roundness and wrinkledness in peas. This will be described in detail in Chapter IX.

If, therefore, we compare the two genealogical tables (Frontispiece and Fig. 14), we see that the Mendelian phenomena, as exhibited by these two cases, are perfectly analogous. The only difference between the two is that in one case (that of the peas) the completeness of dominance of one character makes it impossible to distinguish between dominants and hybrids, so that the second hybrid generation appears at first sight to consist of three individuals bearing the dominant character, and one bearing the recessive in every four, on the average; and it is not until we breed from these apparent dominants that we discover that one of the three is a pure dominant and the other two are hybrids. In fact, it is only when we have raised the third hybrid generation that we discover that the second hybrid generation consists of one pure dominant, two hybrids, and one recessive in every four.

But in the case of the fowls, where the dominance of black over white is incomplete, or, at any rate, where the hybrid bears a colour which is peculiar to itself, the real constitution of the second hybrid generation (one pure dominant, two hybrids, and one recessive) is apparent directly the individuals composing it have been raised.

If the Frontispiece and the Andalusian pedigree

are folded out and compared it will be seen that the two are fundamentally the same, and correspond with one another individual for individual. The point in which they differ is an unessential feature of the Mendelian phenomenon—namely, the matter of dominance. The fact that the dominant and hybrid tall appear to us identical is probably no more than a measure of the crudeness of the means which have hitherto been adopted to distinguish between them—observation by the naked eye.

The point in which the two tables agree is the essential feature in Mendelian inheritance, and consists in the orderly reappearance of the characters of the two varieties crossed, amongst the progeny of the cross, in definite numerical ratios and in a state as pure as that in which they existed in the two parental varieties before the cross was made. The term Segregation is commonly used to denote this splitting out of the parental characters amongst the offspring of hybrids.

We may obtain some idea of the value of a knowledge of the Mendelian phenomenon to the practical breeder by comparing the fate of a would-be breeder of Andalusians who possessed this knowledge with that of one who did not. The breeder who had not heard of the Mendelian discovery, or had heard of it and had rejected it as contrary to common sense, would continue to breed from his Andalusians from generation to generation in the hope that ultimately he would eradicate the black and also the white taint. But he would never obtain more than 50 per cent.

## CASE OF THE ANDALUSIAN FOWL 39

Andalusians amongst his chickens, and he would not be able to sell the blacks and whites, which would make up the remaining 50 per cent., at anything like the price which the Andalusians fetch. Mr. Sturges, in his "Poultry Manual," states (p. 244) that these so-called mismarked chicks are usually killed at an early age or sold as wasters.

The breeder familiar with the Mendelian phenomenon would never mate Andalusians together, but keep a small stock of blacks and whites, and always pair black cocks with white hens, or vice versa. In this way he would be relieved of the expense of rearing, and the trouble of getting rid of the black and the white wasters; and would be certain of raising 100 per cent. Andalusians, all of which he would sell at good prices.

The case of the Andalusian fowl places the whole question of the fixation of varieties in an entirely new light.

Breeders have long been familiar with certain varieties which were tolerably easily fixed, and with others which seemed to withstand every effort of the breeder to fix their qualities. The Andalusian fowl has for long been a flagrant example of such an unfixable variety. For fifty years it has been bred, and it comes true to type no more now than when the attempt to fix it began. The reason is simply that the Andalusian is a hybrid: the particular blue colour, which characterises it, is peculiar to and only manifested by the hybrid bird, whether this be produced by the union of such hybrids or

by the union of a black and a white. Mr. Sturges, indeed, seems to incline to the view that the Andalusian actually arose from such a cross. There is no doubt that the Andalusian is a very near relation of the Black Spanish, and that both of them came from Spain about the middle of the nineteenth century. In 1846 a Mr. Barber imported black and also white fowls from Spain ; and Mr. Sturges suggests (" Poultry Manual," p. 437) that " these may have been the foundation of the Andalusian. This," he continues, " is borne out by a further note : Another gentleman says : ' I have a few chickens out from Mr. Barber's Andalusian hens (called Andalusian because they came from thence), some of which seem to be the true old Black Spanish, and some a grizzly white . . . some of these are of a blue or grey or slaty colour.' "

Here we catch a glimpse of the Mendelian phenomenon being unfolded before the eyes of a man who cannot have apprehended its significance, and before Mendel had begun his experiments. Such glimpses are comforting to those who, like myself, have a horror that this kind of orderliness in natural processes is not seen or, at any rate, not so easily seen until we have been led by some portent, like Mendel's discovery, to expect to see it.

#### HUMAN EYE COLOUR

In the case of the Andalusian fowl we considered an instance of the Mendelian phenomenon in which the hybrid bears a character peculiar to itself—the blue colour we have described.



**FIG. 15.—VERTICAL SECTION OF HUMAN EYE OF  
SIMPLEX TYPE**

Bulging out to the left is the tough transparent cornea. At the points where this joins the main wall of the eye there are two projections, each bordered on their sides remote from the cornea by a dark line; this is the iris seen in section. The space between the free ends of the projections corresponds to the pupil of the eye. The large oval body behind the iris is the lens. The branching projections just above and below the lens and the long ones farther to the right do not concern us.



The character which I propose to consider now resembles the case of stature in peas, in that the hybrid does not differ externally, so far as we can see, from the pure dominant. It is also of especial interest because it is one of the few Mendelian characters which have been discovered in man.

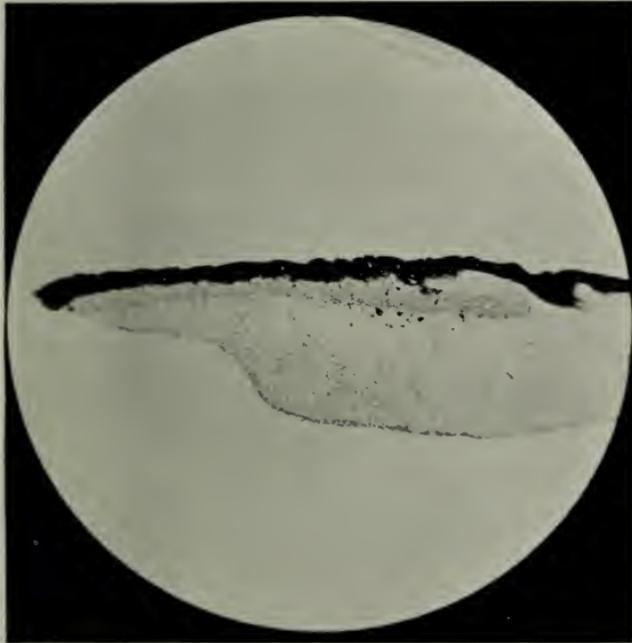
When we speak of the colour of the human eye, we are speaking only of the colour of a particular part of it namely the iris, which is the only part of the eye the colour of which varies to any great extent. There is, of course, an almost infinite variety in the colour of the eye; but the various types of colour can be grouped into two large classes according as to whether there is brown pigment on the outer surface of the iris or not. When the whole of this surface, which is the one that we see when we look at the eye, is covered with brown pigment, the eye is brown; and when there is no such brown pigment on the outer surface of the iris the eye is generally blue. The word duplex has been coined to denote those eyes in which there is some brown pigment in front of the iris; and simplex to denote those eyes in which there is none.\* Speaking generally, duplex eyes are brown, and simplex are blue. But as the two classes, duplex and simplex, include the whole range of human eye colour it is evident that duplex does not simply mean brown and simplex blue,

\* These terms were introduced by Mr. C. C. Hurst, who was the first to discover, investigate and record the Mendelian inheritance of eye colour in man.

because they also include the green, the grey, and the hazel eyes.

A duplex eye is, as we have said, any eye in which there is brown pigment in front of the iris. This brown pigment exists on the top of the fibrous tissue of the iris which appears blue; so that if we could dissolve away the brown pigment from a dark brown eye the blue would appear underneath. There is every degree in the amount of this brown pigment. If there is very little indeed, it usually exists as a thin ring round the pupil, all the rest of the iris being blue. This has been called a ring-duplex, and if there is a mere trace of the brown pigment, a duplex eye of this kind would doubtless often pass as a "grey" or even "blue" eye. If there is more of the brown pigment, a "hazel" eye is very often the result. In another form of duplex eye the brown pigment is distributed in patches over the blue ground colour which can be seen between the patches; "hazel" eyes are also often the result of this arrangement. When there is a very thin uniform layer of brown pigment, the colour of this (a sort of yellow ochre) blends with the blue of the background, which can be seen through, and a "green" eye is the result. And, finally, there are the self-coloured duplex eyes in which the brown pigment is spread uniformly over, and completely concealing, the blue background, giving the various intensities of brown eye, according to its abundance.

A simplex eye is one in which there is no brown pigment on the anterior surface of the iris. All the



**FIG. 16.—SECTION OF IRIS OF SIMPLEX EYE**

This is the uppermost end of the lower projection in Fig. 15. The thick black layer to the extreme right of the section is the layer of deep purple pigment (called the uvea) which is deposited in the posterior face of the iris, i.e. that which is not exposed to the light. No pigment is seen on the anterior face of the iris, i.e. that which is exposed to the light. The name Simplex is given to this type of iris because it possesses only one layer of pigment.—that which forms the uvea.



**FIG. 17.—SECTION OF IRIS OF DUPLIX EYE**

This section is of an exactly similar part of an eye to that shown in Fig. 16, but the eye was of the Duplex type. The uvea has unfortunately become broken away from the posterior face of the eye; in its natural position it lies close up against the iris, as shown in the figure of the Simplex eye.

The important thing to notice in this section is the dark layer of (brown) pigment on the anterior face of the iris. The name Duplex is given to this type of iris because it possesses two layers of pigment; the brown in front, and the purple, in the uvea, behind.



clear blue and grey eyes are of this class. The colour of simplex eyes is not due to the colour of the fibrous tissue of the iris itself, which consists of muscle fibres, nerves, blood-vessels, and so forth, but to a layer of dark purple pigment behind the iris, called the *uvea*. In the new-born infant the fibrous tissue of the iris is very delicate and transparent, so that most of the colour of the uvea can be seen through it: that is why the eye of the new-born infant is dark blue. A clear blue eye is due to the delicacy of the fibrous tissue of the iris, which permits the colour of the uvea to shine through. A pale blue or grey eye is due to the coarseness or "stringiness" of the fibrous tissue, which prevents most of the colour of the uvea from being seen. Evidence that the colour of very pale blue and of grey eyes is due to the colour of the uvea which can filter through the fibrous tissue in front of it, and not to the colour of the fibrous tissue itself, is afforded by the fact that in albinos in whom the uvea is colourless the iris appears pink, this colour being given by the blood in the fibrous tissue. The various colours of simplex eyes, namely, the different intensities of blue and grey eyes and the intermediates between these two colours, are therefore due to differences in the texture of the fibrous portion of the iris, which allow different amounts of the colour of the purple uvea behind to filter through.

A simplex eye, therefore, is one in which there is only one layer of pigment, the purple of the uvea; a duplex eye is one in which there are two layers of

pigment, the purple of the uvea behind the iris and a varying amount of brown pigment in front of it.

If the reader prefers the use of familiar terms duplex may be spoken of as brown and simplex as blue, and in nine cases out of ten the application of these common words will be correct; but it must be remembered that there are some eyes which would be described as blue in common parlance, but which really fall into the duplex class because they possess a trace of brown pigment.

The result of a union between a person with a pure duplex eye and one with a simplex eye is a child with a duplex eye. Duplex, therefore, is dominant and simplex is recessive. The generation produced by the union of such hybrid duplexes, as we may call them, consists of three duplex and one simplex in every four. These simplexes breed true, i.e. produce offspring with simplex eyes only, when mated with their like. Of the three duplexes, one, the pure dominant, will, if mated with another of the same kind produce pure duplexes only. The other two duplexes are hybrid, and when mated with similar hybrid duplexes will produce duplexes and simplexes in the ratio of three to one. The reader may make a scheme of the mode of inheritance of human eye-colour by substituting duplex for tall, and simplex for dwarf in the frontispiece.

At the beginning of the last paragraph I spoke of "the result of a union between . . . a *pure duplex eye* . . ." By "pure" I do not mean anything which

relates to the colour of the eye. I mean pure from the point of view of its breeding properties, as opposed to hybrid, in order to distinguish it from the latter. But the question will present itself to the reader: How is a pure duplex to be distinguished from a hybrid one? The answer has been briefly given at the conclusion of the third chapter. It was there stated that the simplest way, in the case of animals, to distinguish between the pure dominant and the hybrid bearing the dominant character was to mate the individual in question with one bearing the recessive character. The reason that it is simpler to find out whether an individual is hybrid or pure by mating it with a recessive, than by mating it with another hybrid (which was the means adopted in the case of the peas) is that there is no means of finding a hybrid to mate it with, other than by breeding one for the purpose by mating a dominant with a recessive—for this purpose it does not matter whether “the dominant” is pure or hybrid. And even if a hybrid could be found, if the individual to be tested happened to be a pure dominant, the result of mating it with a hybrid would be equal numbers of pure dominants and hybrids, all of which would be alike; that is to say, it would be the same result, so far as we could see from the characters of the individuals themselves, as that of mating two pure dominants, which would, of course, be nothing but pure dominants.

The difficulty of distinguishing between pure dominants and hybrids has not presented itself

before, because in the peas where self-fertilisation always takes place, when it is not artificially prevented, like always mates with like, so that there is no chance of a hybrid mating with a dominant; and because in the case of the Andalusian fowl, the hybrid differed from the dominant (which we called the black type for convenience, and not without justification) in visible characteristics. This difficulty presents itself not only in the case of human eye colour, but in all cases in which self-fertilisation does not occur, and the hybrid is externally indistinguishable from the dominant parent. The practical solution of the difficulty is to mate the individual in question with one bearing the recessive character. If all the offspring bear the dominant character, it was a pure dominant; if half bear the dominant and half the recessive, it was a hybrid. Another reason why it is better to test the nature of an individual bearing the dominant character by mating it with a recessive, than by mating it with a hybrid, is that if the individual tested is a hybrid it will only produce one recessive in every *four* in the latter case, but will produce one in every *two* in the former. And where only a small total number of offspring can be raised this is obviously an advantage.

I have discussed this at some length, because it is a question which is very likely to crop up in practice and because I wish to lay emphasis on a general property of the hybrid, namely, that when hybrids are mated with recessives they produce hybrids and recessives in equal numbers, and when mated with domi-

nants they produce dominants and hybrids in equal numbers. Thus, if our tall peas of the first hybrid generation had been crossed with dwarfs they would have produced tall and dwarfs in equal numbers; and if Andalusian fowls had been mated with the whites they would have produced equal numbers of Andalusians and whites. And if hybrid tall had been crossed with pure tall, equal numbers of these two kinds of tall would be produced; and if Andalusian fowls were mated with the blacks equal numbers of black and Andalusians would have been the result. It is desirable to know this property of hybrids, because if one does not, the existence of families composed of both blue-eyed and brown-eyed children, one of the parents of whom was blue-eyed whilst the other was brown-eyed, does not seem reconcilable at first with the statement that the result of mating duplex (or brown) with simplex (or blue) is invariably duplex. There is, of course, no contradiction, as the reader will now readily see; in such cases the duplex parent has evidently been a hybrid duplex.

Moreover, this type of mating—hybrid by dominant, or hybrid by recessive—plays an important part in the Mendelian theory of sex, and in the theory of the origin of Mendelian characters.

Before quitting the subject of the inheritance of eye-colour in man, it may be useful to set forth the breeding properties of simplex, and of pure and hybrid duplex eyes, in a few short general statements.

The nature and result of the union between two persons, both with duplex eyes, may be any one of the three following kinds :—

- A. Pure duplex by pure duplex, giving all pure duplex.
- B. Pure duplex by hybrid duplex, giving these two kinds in equal numbers.
- C. Hybrid duplex by hybrid duplex, giving 25 per cent. pure duplex, 50 per cent. hybrid duplex, and 25 per cent. simplex.

Unions between duplex and simplex can only be of two kinds :—

- D. Pure duplex by simplex, giving all hybrid duplex.
- E. Hybrid duplex by simplex, giving hybrid duplexes, and simplexes, in equal numbers.

Unions between two simplexes can only be of one kind, inasmuch as there is only one kind of simplex, the pure.

The above statements are true of the three kinds, simplex, pure duplex, and hybrid duplex, whatever may have been their origin. Thus, if a simplex occurring in the second hybrid generation mates with another simplex of like extraction he or she will produce nothing but simplexes as assuredly as will two individuals both with simplex eyes who have descended from, say, two generations of simplex ancestry. Or, to express this in general terms, the offspring of a man and a woman both possessing blue

eyes, but both descended from (of course, hybrid) duplex parents on both sides in both cases, will possess blue eyes as certainly as if their four grandparents all had blue eyes. The offspring of the union of two persons with simplex eyes, whatever their ancestry is, will never have brown eyes. At any rate, no exceptions to this rule have yet been observed and recorded.

## CHAPTER V

### THE INHERITANCE OF THE CHARACTERS OF THE SEED IN THE CULINARY PEA

WE have so far dealt with only five of the seven characters of the pea experimented with by Mendel; and the reader may remember that they were dealt with in the order in which they appeared on the plant: the first was the stature of the plant, whether tall or dwarf; the last was the colour of the ripe "seed," whether "grey" or "white."

Suppose that it is spring, and that you have just sown the seed to produce the second hybrid generation from a cross involving any of the five pairs of characters already dealt with. If the pair of characters is tallness and dwarfness, you will be able to count the numbers of tall and dwarfs as soon as the young plants are a few inches high, that is to say, early in May; but it will be necessary to wait till the plant is ripe and dry, that is to say, till the middle of August at the earliest,\* before the number of white-seeded and grey-seeded plants can be counted. And the numbers of plants with the three characters intervening in the date of their appearance between these two extremes can be counted at intervening dates.

\* Except when there is a drought like that of the summer of 1911.

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The two characters, to be dealt with now, appear earlier than the earliest of the five which we have so far considered, namely stature. But these two characters appear by the heading of the chapter to be characters of "the seed"; yet I have just said that the difference between grey-seeded and white-seeded plants was the *latest* to appear. How can characters of "the seed" be both the earliest and the latest to appear? What is the meaning of this apparent contradiction? There is no contradiction, and we can understand how a character of "the seed" can be both the earliest and latest to appear when we understand what a seed is.

Suppose that you decide to repeat Mendel's experiments with peas, and to cross tall with dwarfs; suppose that you decide to breed tall and dwarfs separately for five generations to make sure that they breed true to their characters before you cross them; and suppose, further, that you buy some seed of a tall variety and some of a dwarf, and sow it; the plants raised may be described as belonging to the *first generation* of the five that you propose to breed. Now, consider one of the seeds produced by one of these plants. Only the seed-coat—the thin, outer skin of the seed—is a part of this plant of the first generation; all that is inside this seed-coat is the embryo plant of the next, or second, generation, together with its first two relatively enormous "leaves." If the seed is soaked and dissected the two hemispherical "leaves," or cotyledons as they are called, are seen to fill up

almost the entire space within the seed-coat; and, lodged between them—and, of course, attached to them—are seen the little shoot and root, which are all there is, as yet, of the embryo plant.

These two cotyledons (which are the hemispheres which constitute “split peas”) are supposed by some botanists to represent leaves which have become greatly modified in accordance with their having taken on a function not usually performed by leaves, namely, that of acting as a storehouse of food material for the young plant. Unlike ordinary leaves, these cotyledons do not come above the ground when the seed germinates. In the case of many plants, however (as, for instance, the sunflower), in which the cotyledons are less specialised as storehouses of food material, they do come above the ground; and, although in the latter case they behave physiologically like ordinary leaves, they nearly always differ in shape from the other leaves of the plant.

The whole of this store of food material is laid down in the first two leaves (or cotyledons) of the embryo plant before the embryo pea-plant has become detached from its parent. In other words, the food material in the first two leaves of our plant of the *second* generation is being laid down whilst that plant is undergoing its early development within the seed-coat, which, as we have said, is a part of our plant of the *first* generation, just as the embryo of a mammal is nourished in the womb. In fact, the womb with its contained

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embryo is roughly comparable to the seed: the womb is a part of the mother, the embryo is the next generation. The seed-coat is a part of the parent-plant, the embryo with its two cotyledons is the next generation.

Mendel experimented with two pairs of characters of these cotyledons: one pair related to their colour, which was either yellow or green; the other to their shape, which was either round or wrinkled. Let us consider the colour first.

In the title to this chapter I have spoken of its contents as being concerned with the characters of "the seed." But, now that I have explained that a seed is a composite structure, i.e. that the seed-coat is a part of the parent plant, and that everything inside this seed-coat is the embryo of the next generation, it is necessary when we speak of the characters of "the seed" to make it perfectly clear whether we are referring to the seed-coat which belongs to one generation or to the cotyledons which belong to the next. Let it be clearly understood, therefore, that the character with which we are now dealing is the colour of the cotyledons, and not of the seed-coat.

Mendel crossed a plant the first two leaves or cotyledons of which were yellow, with a plant the cotyledons of which were green. The result was a plant the cotyledons or first two leaves of which were yellow.

This description of the cross made by Mendel may sound unnecessarily explicit. But it is not so.

The bald statement that he crossed a yellow pea with a green pea leaves one completely in the dark as to the true nature of the character dealt with ; and even the statement that he crossed a yellow-seeded with a green-seeded pea does not make it clear whether by yellow-seeded (for instance) is meant a pea-plant grown from a yellow seed, or a pea-plant which produces yellow seeds. What *should* be meant by " a yellow pea " or " a yellow-seeded pea " is a pea-plant grown from a yellow seed, because it is the yellow colour of its first two leaves or cotyledons, seen through the enveloping seed-coat, which is the character with which we are concerned ; and also because, as we shall see later on, a plant grown from a yellow seed does not necessarily produce yellow seeds.

When a tall is crossed with a dwarf pea the result cannot be seen until the seed resulting from the cross is sown. But the result of crossing a yellow-seeded pea (as defined above) with a green-seeded pea can be seen directly the pod, which has developed from the flower on which the cross was made, is opened. Let me briefly describe here how such a cross is made. A detailed account is given on pp. 146-152. To make a cross between a tall and a dwarf, pollen is taken from a flower of a tall pea and placed upon the pistil in the flower of a dwarf, or vice versa. We will consider the former case. A label is tied round the stalk of the flower of the dwarf plant which has received the pollen from the tall. In due course, the petals wither ; and, if all is well, the pod

grows from within the withered petals. When the pod is dry and ripe, which is not likely to be much earlier than the beginning of August, it is opened, the seeds are taken out, and sown in the following spring. All the seeds will produce tall plants, tallness being dominant over dwarfness. The result would have been the same if the flower of a tall plant had been pollinated with pollen from the flower of a dwarf one. The point is that the result of a cross made, say, in the summer of 1910 is not seen until the *spring* of 1911 in the cases of tallness and dwarfness. And the result of a cross between a grey-seeded pea (or, more strictly, a pea-plant which produces grey seed-coats) and a white-seeded pea (i.e. a pea-plant which produces white seed-coats) made in the summer of 1910 will not be seen till the *autumn* of 1911.

But if, in the summer of 1910, pollen is taken from the flower of a plant, the first two leaves or cotyledons of which were yellow, and placed on the pistil of the flower of a plant which had green cotyledons, the result of the cross is seen when the pod which develops from the latter flower is opened. For instead of the pod containing "green seeds" (as all the other pods of the plant will, if no other crosses have been made on the plant), it will contain yellow ones, because the first two leaves of the plants of the first hybrid generation will be yellow, inasmuch as yellowness in the cotyledons is dominant over greenness. That is to say, whilst the result of a cross made in the summer of 1910 between a

tall and a dwarf will not be seen till the spring of 1911, the result of a cross made on the same day between a plant which had yellow cotyledons and one which had green, will be seen in the autumn of the same year, namely 1910.

Before we proceed to describe the reappearance of the parental characters in the second hybrid generation, let us pause to consider the Mendelian phenomenon manifested by the colour of the cotyledons, and compare it with the other instances of it with which we have dealt up to the present.

So far as we know, yellowness is a simple dominant to greenness, in the case of the cotyledons in *Pisum*, just as tallness is to dwarfness. That is to say, no difference between the pure yellow and the hybrid yellow has so far been detected; but it does not seem to me unlikely that a difference between them may be revealed by spectral analysis.

It is curious that yellow is dominant over green in the case of the cotyledons, in view of the fact that in the case of the pods green is dominant over yellow, according to Mendel's account.

We will now follow up the results of the supposed cross that was made in the summer of 1910. As a matter of fact, I did make many such crosses during that summer.

In our supposed cross a flower of a plant raised from a green seed was pollinated in the summer of 1910 from a flower of a plant raised from a yellow seed; and in the autumn of the same year the result

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was seen as soon as the pod which developed from the flower of the former plant was opened. The seeds in it, instead of being green like those on all the other pods on the plant, were yellow; or, more accurately stated, the cotyledons within the seed-coats in this pod were yellow, instead of green as they would be in all the other pods. Stated in the most general, but also the most simple and the most correct, terms, the result which we have hitherto observed is that when a plant whose first two "leaves" are yellow is crossed with a plant whose first two "leaves" are green the result is a plant whose first two "leaves" are yellow. Such a "plant" constitutes the first hybrid generation, and though the fact that it bears the dominant character can be observed in the year in which the cross was made, the "plant" does not, of course, become mature until sown in the following year, 1911.

The yellow peas in the pod which developed from the flower on which the cross between the yellow-seeded and the green-seeded variety had been made, would be taken from the pod in the autumn of the same year in which the cross was made (1910), and sown in the following spring. Let us suppose there were five seeds in the pod, and that five plants were produced from them during the summer of 1911.

These five plants, growing in 1911, belong, as already indicated, to the first hybrid generation produced by crossing, in 1910, a yellow-seeded (as defined above) with a green-seeded pea; just as the tall plants growing in 1911 belonged to the first

hybrid generation produced by crossing, in 1910, a tall with a dwarf pea. The only difference between the two cases is that the character of the first hybrid generation can be seen before the seed to produce plants of the first hybrid generation is sown, in the case of the colour of the cotyledons; but cannot be seen until after the plants of the first hybrid generation have grown a few inches, in the case of the stature of the plant.

It will be remembered that the colour of the first two "leaves," or cotyledons, of the plants of the *first* hybrid generation could be seen in the pods of one of the parent plants in the same year in which the cross was made. Similarly, the colours of the cotyledons of the plants of the *second* hybrid generation can be seen in the pods borne by the plants of the first hybrid generation; that is to say, in the case of the cross made in 1910, in the autumn of 1911.

In Plate I. are shown the results of crossing a green-seeded with a yellow-seeded pea, as far as the second hybrid generation which we are now considering. Above, to the left, are seen a group of ten peas, the cotyledons in which are green; on the right a group of six peas containing yellow cotyledons. The skin of the vividly yellow pea to the top left of this group has been removed in order to show the colour of the cotyledons themselves. These two groups represent the parents of the cross. The group of three yellow peas in the middle, below, contain the cotyledons of the first hybrid generation.



PLATE I.—MENDELIAN INHERITANCE OF THE COLOUR OF THE SEED IN THE CULINARY PEA

(Top left) Green Parent.

(Top right) Yellow Parent.

(Three Peas in middle line) First Hybrid Generation.

(In the pods) Second Hybrid Generation.



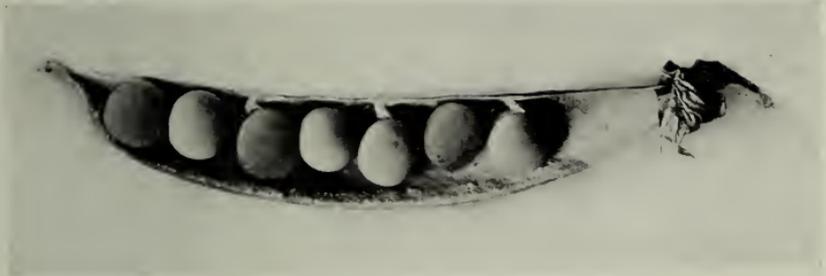
And in the two pods are seen the cotyledons of the second hybrid generation; the skins of the two peas to the extreme left of the upper pod have been removed in order to show the yellow and the green of the cotyledons of the second hybrid generation in juxtaposition to one another. In the two pods shown there are eleven yellow and four green—as close an approximation to a ratio of three yellow to one green as can obtain amongst fifteen seeds.

The colours of “the seeds” borne on a plant of the first hybrid generation which has been produced by a cross between a yellow-seeded and green-seeded pea are simply the colours of the first two “leaves” or cotyledons of the plants of the second hybrid generation.

I have endeavoured to illustrate this—and, incidentally also, the general fact with which the reader is now familiar, that the colours of “the seeds” (whether yellow or green), borne by a plant, are the colours of the first two leaves of its children—by taking a photograph, reproduced in Fig. 18, of a pod containing the cotyledons of the second hybrid generation; then sowing the seeds in a row in the order in which they were in the pod, and photographing the seedlings thus raised (Fig. 19). This illustration shows, I think, sufficiently clearly that the characters, yellowness and greenness, of cotyledons are characters which appear at a very early stage in the development of the plant, so early in fact that they can be seen in the seed (if the seed-coat be transparent) before they are sown to produce the

plant. Indeed, not only *can* the colour of the cotyledons be seen before the seed is sown, it *must* be seen then, or not at all, inasmuch as it cannot be seen for long after the seed has begun to germinate, because as the growing plant absorbs the food-material in the cotyledons, their colour fades. But it could still be clearly seen in the seedlings represented in Fig. 19.

Stated in general terms, therefore, the second hybrid generation consists of three plants with yellow cotyledons, and one with green, in every four. In practice this result is seen in the existence of yellow and green peas in the ratio of three to one in the pods of a plant of the first hybrid generation. In our imaginary cross made in the summer of 1910 the numbers of these yellow and green seeds could be counted in the autumn of 1911. These seeds would be sown in the spring of 1912. It would be found that the green seeds produced plants on which all the seeds were green; that one of every three yellow seeds would produce a plant on which the seeds were all yellow, and that the remaining two yellows would produce plants which would bear yellow and green seeds in the ratio of about three to one. Stated in more general terms, this means that of every four plants (on the average) of the second hybrid generation: one (recessive) plant with green first two "leaves" gives rise solely to plants like itself when it is allowed to self-fertilise; two (hybrid) plants with yellow first two leaves will produce plants with yellow, and plants with green first two leaves, in the



G Y G Y Y G Y

**FIG. 18.—THE SEVEN SEEDS WHICH GAVE RISE TO THE SEVEN SEEDLINGS IN FIG. 19, IN THEIR NATURAL POSITIONS IN THE POD**

*Colours of the seeds. G Green ; Y Yellow.*





FIG. 19.—THE SEVEN SEEDLINGS RAISED FROM THE SEVEN SEEDS SHOWN IN THE  
 POD IN FIG. 18

*Colours of the cotyledons of the seedlings. G Green; Y Yellow.*



## INHERITED SEED-CHARACTERS 61

ratio of three to one ; and one (dominant) plant with yellow first two leaves will give rise solely to plants like itself. The mode of inheritance of the colour (whether yellow or green) of the first two "leaves," or cotyledons, of the plants is therefore precisely analogous to that of the stature (whether tall or dwarf) of the plant. And if the reader wishes to see the inheritance of the colour of the cotyledons set forth in diagrammatic form, all that is necessary is to substitute yellow for tall and green for dwarf in the frontispiece.

But in order that the way in which this result appears on the plants themselves may be understood, I give, on the next page, an actual instance of the total numbers of yellow and green "seeds" constituting the second hybrid generation ; and also of the total numbers of yellow and green "seeds" constituting the third hybrid generation.

The crosses were made by me in 1905 ; the second hybrid generation (which I give here) was recorded in the autumn of 1906 ; and the third hybrid generation was recorded in the autumn of 1907. By "plant number" is simply meant the number by which a particular plant was named in the records of my experiments. In the first column to the left of the Table are given the number of yellow and green seeds constituting the second hybrid generation. It will be seen that every one of the twenty-six plants bears both yellow and green seeds ; in other words, every plant, of the first hybrid generation, produces, after self-fertilisa-

## BREEDING

Plants Bearing Cotyledons of the Second Hybrid Generation			Plants Bearing Cotyledons of the Third Hybrid Generation																	
Plant Number	No. of Yellow Seeds	No. of Green Seeds	Plant Number	No. of Yellow Seeds	No. of Green Seeds	Plant Number	No. of Yellow Seeds	No. of Green Seeds	Plant Number	No. of Yellow Seeds	No. of Green Seeds	Plant Number	No. of Yellow Seeds	No. of Green Seeds	Plant Number	No. of Yellow Seeds	No. of Green Seeds	Plant Number	No. of Yellow Seeds	No. of Green Seeds
1	23	5	1-1	136	35	1-2	49	15	1-3	96	26	1-4	53		1-5	47	22	8-6	58	7
2	27	14	2-1	60		2-2	8	4	2-3	30		2-4	46	21	2-5	30	6	10-6	63	13
3	38	11	3-1	77	26	3-2	118		3-3	54	13	3-4	56	14	3-5	100	39	14-5	35	14
4	20	12	4-1	50		4-2	203		4-3	150		4-4	169	68				15-6	119	15
5	51	14	5-1	286		5-2	83	36	5-3	451		5-4	321		6-5	97	31	16-6	92	15
6	37	8	6-1	32	13	6-2	35	8	6-3	24	10	6-4	99		7-5	53	61	18-6	14	3
7	68	14	7-1	59	15	7-2	134		7-3	57	28	7-4	47	5	8-5	61	14	19-6	106	
8	82	28	8-1	61	22	8-2	60	12	8-3	97	34	8-4	9	5	9-5	62	14			
9	50	19	9-1	21	6	9-2	48	18	9-3	99	39	9-4	69	24	10-5	65	20			
10	20	5	10-1	53	21	10-2	31	8	10-3	72	22	10-4	20	5	11-5	69				
11	44	16	11-1	90	28	11-2	50	11	11-3	51	11	11-4	49	18	12-5	92				
12	42	15	12-1	42	11	12-2	53	17	12-3	85		12-4	47	19	13-5	38	15			
13	36	13	13-1	36	21	13-2	94	16	13-3	33	8	13-4	89		14-5	17	2			
14	66	20	14-1	33	12	14-2	48	18	14-3	41	18	14-4	62	20	15-5	55	20			
15	54	11	15-1	34	11	15-2	72	26	15-3	44	15	15-4	129	28	16-5	62	14			
16	32	11	16-1	69		16-2	36	15	16-3	33	33	16-4	65	28	17-5	29	15			
17	32	5	17-1	17		17-2	34	10	17-3	96	48	17-4	29	11	18-5	27	18			
18	29	13	18-1	15	6	18-2	22		18-3	11	9	18-4	60	12	19-5	39	18			
19	24	9	19-1	109		19-2	127		19-3	77	22	19-4	37	18						
20	33	7	20-1	96	41	20-2	117		20-3	94	23	20-4	138	51						
21	16	5	21-1	30	13	21-2	86	26	21-3	101	27	21-4	102		22-5	59	21			
22	13	4	22-1	139	42	22-2	28	11	22-3	36	8	22-4	72	18	23-5	64	22			
23	81	23	23-1	92	22	23-2	19	10	23-3	65	18	23-4	47	18	24-5	20	3			
24	85	30	24-1	110		24-2	64	13	24-3	107		24-4	30		25-5	14	7			
25	39	19	25-1	118	30	25-2	37	9	25-3	49		25-4	31	14	26-5	125				
26	47	24	26-1	33	9	26-2	57	11	26-3	40	17	26-4	97							

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tion, a family consisting in every case of plants with yellow, and plants with green first two leaves.

To return to common parlance. Either five or six of the yellow seeds constituting the second hybrid generation were sown, and the colours of the seeds (containing the third hybrid generation) borne on the plants raised are given on the same line in the Table, to the right of the record of the seeds of the second hybrid generation. Thus, five of the yellow seeds borne on plant No. 1 were sown and gave rise to five plants numbered 1·1, 1·2, 1·3, 1·4 and 1·5, all of which happened to produce both yellow and green seeds. In other words, all of the yellow-seed leaved plantlets contained within the seeds sown, were hybrids. But of the five yellow seeds of Plant No. 2 that were sown, two—namely, those which produced plants numbered 2·1 and 2·3 contained pure dominant plantlets because the plants raised from them produced only yellow seeds. The important point to notice is that *every* grown plant of the first hybrid generation produces both yellow and green seeds containing the second hybrid generation in embryo (*see* the first column in the Table); i.e. segregation or reappearance of the parental characteristics occurs in every family in the second hybrid generation. On the other hand, some of the grown plants of the second hybrid generation—namely, the hybrid ones—produce both yellow and green seeds (containing the third hybrid generation in embryo), whilst others, the pure dominants, produce yellow seeds only.

If the green seeds containing the cotyledons of the second hybrid generation had been sown they would produce greens only; but as I did not test the true breeding of these so-called "extracted" greens in this particular experiment, the fact that they breed true is not illustrated in the Table on p. 62.

Fig. 20 shows the distribution of yellow and green seeds borne by Plant No. 12, which was selected at random. Yellow seeds are indicated by ● and green ones by ○. It will be seen that no order can be detected in the distribution of the seeds of the two colours.

This diagram brings home to one's mind the fact that the colours of the seeds of a plant, when we mean the colours of the contained cotyledons, are the colours of the offspring (or, rather, of the first two leaves of the offspring) of that plant; whilst the colour of the seed-coats of the seeds borne by a plant is the colour of a part of the plant itself, just as the colour of the pods is, or the colour of the stem. That is why the colours of the seed-coats (whether grey or white) of the seeds borne by a plant are always the same (*see* Fig. 11 or 12), and why the colours of the cotyledons of the seeds borne by a plant need not be always the same (*see* Plate I., facing p. 58). And the apparent paradox that "the seed" presents a pair of characters (grey and white) which are the latest to appear in the life history of the plant, and another pair (yellow and green), which are the earliest to appear, is explained by the fact that



FIG. 20.—DIAGRAM TO ILLUSTRATE THE DISTRIBUTION OF YELLOW AND GREEN SEEDS IN PLANT No. 12 IN TABLE ON PAGE 62

(Yellow Peas are indicated by full black; green ones by outlines.)



## INHERITED SEED-CHARACTERS 65

the seed-coats (which may be grey or white) are not developed till the plant is mature, whilst the cotyledons (which may be yellow or green) are among the first parts of the plant to be developed.

I have been at pains to make this point clear, partly because I am concerned to bring the actual facts discovered by Mendel home to the reader, and partly because the cotyledon characters of *Pisum* are the most valuable that I know for illustrating the Mendelian phenomenon and for testing the truth of general statements made with regard to it. For it must be plain already that one of the features by which the Mendelian phenomenon may be recognised, when it occurs in a breeding experiment, is the definiteness of the ratios in which the parental characters reappear or segregate in the second hybrid generation. It is therefore desirable, in critical experiments of this kind, to use material which will furnish the maximum number of individuals at a minimum expense, and in a minimum space. That end is attained by selecting characters, to experiment with, which appear as early as possible in the life history of the animal or plant which bears them, and this condition is better fulfilled by the characters of the cotyledons of *Pisum* than by any other that I know. A plot of land fifteen yards square will bear 100,000 seeds.

The actual numbers which Mendel himself obtained in his experiments with the colour of the cotyledons are as follows: He made fifty-eight crosses on ten plants; and found the yellow colour of the cotyledon

to be dominant over the green in every case. The second hybrid generation was distributed over 258 plants, and consisted of 6,022 yellows and 2,001 greens; a very close approximation to the three-to-one ratio. Mendel gives the distribution of yellow and green seeds on ten plants in his paper; it was as follows:—

	Y.	G.		Y.	G.	
1.	25	11		6.	20	6
2.	32	7		7.	32	13
3.	14	5		8.	44	9
4.	70	27		9.	50	14
5.	24	13		10.	44	18

Of the total number of individuals (i.e. seeds) which composed the second hybrid generation (namely,  $6022 + 2001 = 8023$ ) only 519 yellow-cotyledoned ones were tested: 166 produced yellows only, i.e. were pure dominant yellows; 353 produced yellows and greens in the ratio of three to one, i.e. were hybrid yellows. In other words, 519 of 8023 seeds (which contained the second hybrid generation) were sown, 166 gave rise to plants which produced yellow seeds only, 353 gave rise to plants which produced yellow seeds and green seeds in the ratio of three to one.

We will now proceed to a consideration of the mode of inheritance of the shape of the cotyledons in *Pisum*. The pair of characters in this case is round (which is dominant) and wrinkled (which is

recessive). The inheritance of these characters is precisely analogous to that of the colour of the cotyledons; and a diagrammatic representation of it may be made by substituting round for tall and wrinkled for dwarf in the Frontispiece.

The shape of the seed (whether round or wrinkled) is determined by the cotyledons, and not by the seed-coats; we may therefore say that the pair of characters is roundness of the first two leaves of the plants and wrinkledness of these structures. The shape of the cotyledons, therefore, is just as valuable a character, for the reasons stated above, as their colour, to experiment with for the purpose of testing general statements with regard to the Mendelian phenomenon. But over and above this it possesses an interest which the colour of the cotyledons does not. In the first place, the distinction between round and wrinkled peas is one of great economic importance, the nature of which will be fully discussed later; and in the second place, it is possible in the case of this character to see below the surface, as it were, of the Mendelian phenomenon, and thus to obtain a truer view of the essential nature of this process. But at present we are concerned with the phenomena as they present themselves to the senses unaided by the microscope and the scales. Fig. 21 represents the result of crossing of round-seeded with wrinkled-seeded pea. The round cotyledons of the first hybrid generation do not differ, so far as the unaided eye can see, from those of the round parent.

Mendel himself made sixty crosses between round-seeded and wrinkled-seeded varieties on fifteen plants. The second hybrid generation consisted of 7,324 seeds, of which 5,474 were "round or roundish," and 1,850 were wrinkled; 565 of the rounds were tested; 193 gave rounds only, 372 rounds and wrinkled in the ratio of three to one.

The seven pairs of characters of the culinary pea experimented with by Mendel have now been dealt with. In all of them the mode of inheritance is essentially the same. Two organisms differing in respect of a single pair of characters produce, when mated, a hybrid, which manifests the so-called "dominant" member of that pair to the more or less complete exclusion of the recessive one. Dominance, however, is an unessential feature of Mendelian inheritance. Mendel himself stated that one member of each of his seven pairs was completely dominant over the other of that pair. But it is now known that, in the case of the texture of the pod, the hybrid between the hard and the soft bears pods of intermediate texture. And we shall see later that, in the case of the very first pair of characters in Mendel's list, the round cotyledons of the hybrid produced by crossing a round with a wrinkled-seeded pea are only superficially indistinguishable from those of the pure round; and that a fundamental difference between them can easily be demonstrated.

The essential feature of the Mendelian phenomenon is that which the mode of inheritance of the seven pairs

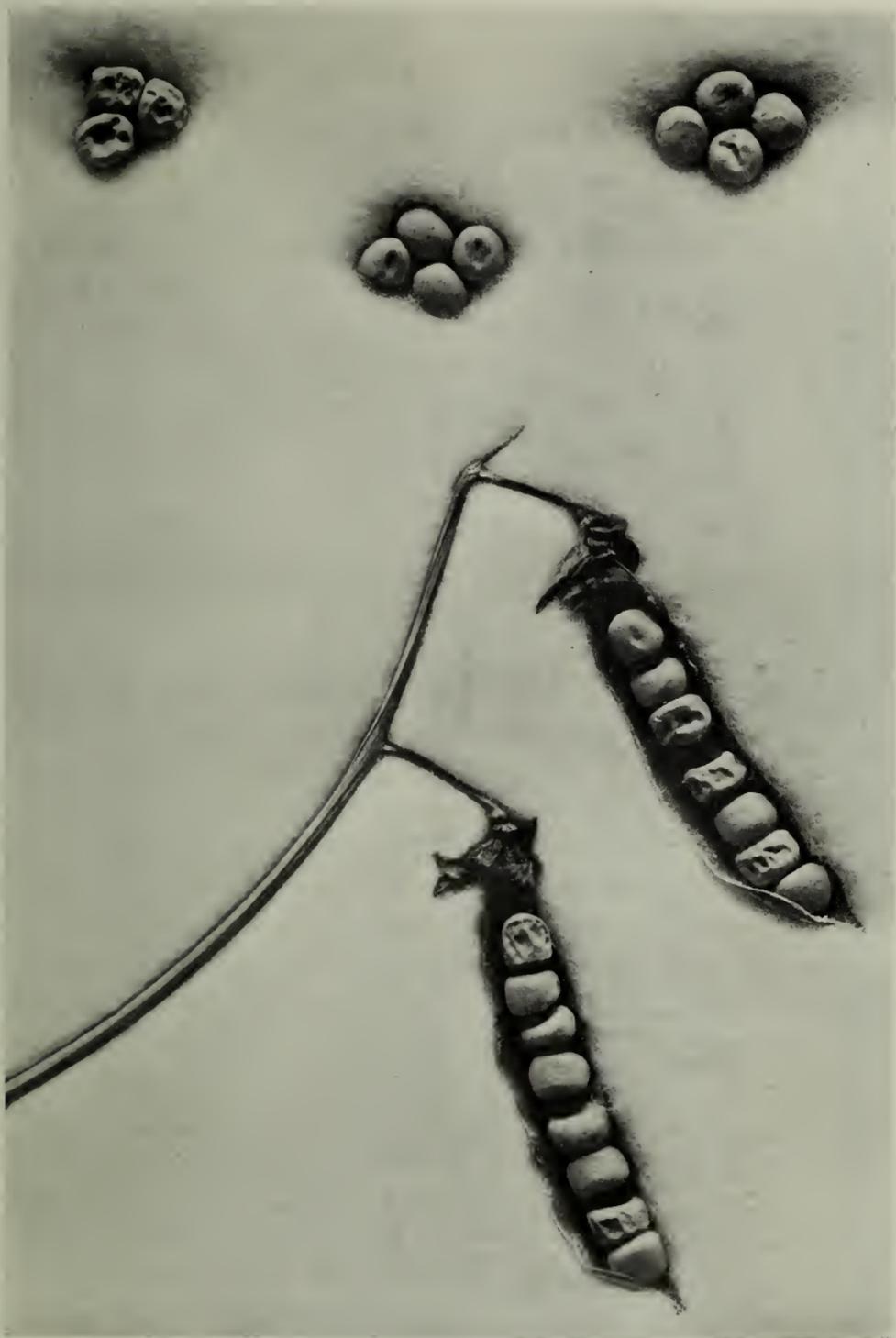


FIG. 21. - MENDELIAN INHERITANCE OF THE SHAPE OF THE SEED IN THE CULINARY PEA

(Top left) Wrinkled Parent.

(Top right) Round Parent.

(Four Peas in middle line) First Hybrid Generation.

(In the pods) Second Hybrid Generation.



of characters dealt with by Mendel, and that of the colour of the Andalusian fowl and the human eye, possess in common, i.e. that in which the genealogical table of the tall and dwarf peas and that of the Andalusian fowl agree, namely the orderly reappearance of the characters of the parents of the hybrid, and of the hybrid itself, in the second hybrid generation in definite numerical proportions.

There is another characteristic of the Mendelian phenomenon which can only be said to be an essential one in the sense that it follows from Mendel's theory\* to account for the composition of the second hybrid-generation. This characteristic is the repetition, in each successive hybrid generation, of the ratios obtaining in the second. The second, and all subsequent hybrid generations, should all have exactly the same composition as one another, if this characteristic is found to be an invariable feature of Mendelian crosses. Let it be clearly understood what this means. It means that, for however many generations hybrid yellow peas are bred from, they will produce pure yellows and hybrid yellows and pure greens in the ratio of 25 : 50 : 25 per cent. What is most remarkable in this generalisation, because most at variance with current notions of heredity, is the idea that although the parent of each successive hybrid generation is as yellow as a yellow of a pure strain, there will be produced an average number of green, namely, 25 per cent., which will not

\* See Chapter XI.

diminish as the generation in question becomes more remote from the green parent of the cross. In other words, it is a remarkable thing that a yellow of the tenth hybrid generation, with nine generations consisting solely of yellows behind it, should contain as many greens as the second hybrid generation, which has only one such generation behind it. There is no possibility, here, of eradicating the green by breeding only from the yellow; unless pure yellows are bred from. The evidence, as yet available, as to the ratios of recessives, in the case both of cotyledon colour and shape, has been collected by Mr. Lock in his useful paper, "The Present State of Knowledge of Heredity in *Pisum*,"\* and is as follows. The name of the investigator is given in the case of each separate result:—

*Cotyledon Shape*

<i>Hybrid Generation</i>	<i>Observer</i>	<i>Round</i>	<i>Wrinkled</i>	<i>Percentage of Wrinkled</i>
Second . .	Mendel	5,474	1,850	25.2
	Tschermak	884	288	24.6
	Bateson	10,793	3,542	24.8
	Hurst	1,335	420	23.9
	Lock	620	197	24.1
Third . .	Tschermak	2,087	661	24.0
	Lock	769	259	25.2
Fourth . .	Lock	2,328	812	25.8

\* *Annals of the Royal Botanic Gardens, Peradeniya, Vol. IV., Pt. iii.*

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## *Cotyledon Colour*

<i>Hybrid Generation</i>	<i>Observer</i>	<i>Yellow</i>	<i>Green</i>	<i>Percentage of Green</i>
Second . .	Mendel	6,022	2,001	24.9
	Correns	1,394	453	24.5
	Tschermak	3,580	1,190	24.9
	Bateson	11,903	3,903	24.7
	Hurst	1,310	445	25.4
	Lock	1,438	514	26.2
Third . .	Correns	1,012	344	25.5
	Tschermak	3,000	959	24.2
	Lock	3,082	1,008	24.6
Fourth . .	Correns	225	70	23.7
	Lock	2,400	850	26.1

These figures show how closely the ratios of recessives observed by different investigators approximate to 25 per cent.; but they also show that beyond the fourth hybrid generation we have no evidence for saying that this ratio is repeated in the case of these two characters of the cotyledons in *Pisum*.

## CHAPTER VI

### THROWING BACK, OR REVERSION

IN the crosses which have hitherto been dealt with, the result of mating two individuals which differed in respect of a particular characteristic has been a hybrid which has resembled one of the parents so closely as to be indistinguishable from it; or it has been intermediate between them, as in the texture of the pod in peas, and the colour of the feathers in the fowl. We shall now proceed to cases in which the hybrid differs from either parent, but is not intermediate between them. Into this class fall those cases in which the result of mating two varieties is the production of the features of the wild ancestral form from which the two varieties are supposed to have descended. A very characteristic instance of such a result is afforded by the result of crossing the ordinary albino mouse with the so-called Japanese waltzing mouse. These two varieties differ from one another in respect of their colour, and in respect of their customary movements; the one walking and running normally, the other exhibiting the so-called waltzing movements which are indicated by its name. We are concerned at present solely with the colour of the two forms; the question of the mode of progression must be banished from the reader's

mind until it comes to be considered separately. The colour of the two varieties crossed will be first briefly considered.

The common albino mouse (Plate II., No. 1) has a pure white coat; there is no pigment in it at all. The tail, hands, feet and ears are very pale pink, and the eyes are a deep pink, the colour of these organs being due to the blood in them.

The Japanese waltzing mouse, with which I have experimented, is coloured exactly like the albino except that it possesses patches of fawn-yellow fur on its shoulders and haunches. That is to say, it is a fawn-and-white piebald with pink eyes (Plate II., No. 2). The extent of these patches of fawn-yellow fur varies very little from individual to individual in this variety.

A hybrid produced by mating these two varieties is shown at No. 3. The coat is a dark grizzly grey, hardly distinguishable from that of the house mouse; and the eyes are jet black. The tail may be either deeply pigmented over its whole extent or, as in the specimen shown, the dark pigment may not extend over the whole of it. The hybrid shown at No. 3 is the usual result of mating mice Nos. 1 and 2. I have, however, observed rare exceptions to it, but these are usually attributable to the impurity of the albino stock used, and need not detain us now. It makes no difference to the result whether the albino is the male and the fawn-and-white mouse the female parent, or the albino is the female and the fawn-and-white the male.

The result, then, of crossing a pure albino mouse with a fawn-and-white, pink-eyed (waltzing) mouse is a mouse which differs very little from the common house-mouse. As a matter of fact, it is usually paler beneath than the house mouse is ; and the wild race which it most resembles exists in St. Kilda, an island far out in the Atlantic, to the west of Scotland. Be this as it may, the result is a typical instance of reversion on crossing. These reversionary mice constitute the first hybrid generation.

When these hybrids are mated together they produce a generation (the second hybrid generation) which consists of a variety of forms which can be classified in three groups (A, B, and C), which correspond roughly to the albino, the fawn-and-white, pink-eyed (waltzing) mouse, and the hybrid. Let us examine them more closely in conjunction with the figures of them on Plate II. For the present, mice Nos. 4, 6 and 10 will be left out of account, and attention will only be paid to those individuals in each group which are below the label indicating the group.

Mice included in Group A correspond exactly to one of the parental forms, namely the albino ; there is, therefore, only one mouse (below the label) in Group A. These mice are indistinguishable from the pure albino mouse.

Mice included in Group B correspond to the reversionary forms which constitute the first hybrid generation ; but the correspondence between analogous types in the two generations is much less

### COMMON ALBINO MOUSE

This mouse has pure white skin and pink eyes, and walks and runs normally.



①

### JAPANESE WALTZING MOUSE

Its colouring is the same as that of the Albino except for the patches of yellow on the neck and haunches. Its eyes are pink, as in the Albino. It exhibits the waltzing movements described in the text.



②

The result of mating the two varieties of mice shown above (Nos. 1 and 2) is the Hybrid shown immediately below (No. 3).



③

This Hybrid (No. 3) is very like the common House Mouse. With rare exceptions it has a dark grey coat, and it always has jet black eyes. It does not waltz.

The result of mating two such Hybrids is the generation shown below. Considered with regard to its colour this generation is made up of three types of coloration—Albinos (Group A), dark-coloured mice with black eyes (B), and pale-coloured mice with pink eyes (C). Considered with regard to its movements this generation is made up of waltzers and animals which progress normally. Both normal and waltzing mice occur in each of the colour groups as shown.



④

Group A



⑤



⑥

Group B



⑦



⑧

Group C



⑨



⑩



⑪



⑫



⑬

Mice in this group (A) when mated together invariably breed true.

Mice in this group (B) when mated together produce the same three colour types (groups A, B and C), as a rule.

Mice in this group (C) breed true with very rare exceptions (about 2 per cent. Albinos are produced).



⑭

Waltzers are omitted from this row of specimens.



⑮



⑯



⑰



⑱



⑲



⑳



㉑

PLATE II.—MENDELIAN INHERITANCE IN MICE

The case of specimens, of which this is a direct photograph, was presented by the Author to the Natural History Museum, South Kensington, and is reproduced here by kind permission of the Director



exact than in the case of the albinos. In the first place the colour may be grey or black ; in the second place there may be patches, of greater or less extent, of white fur, as well as the grey or black in the coat ; various degrees of piebaldness being thus produced. There may therefore be, roughly, four kinds of mice in Group B : mice which have a completely grey coat ; (No. 7)—self-coloured greys as they are called ; self-coloured blacks (No. 8) ; piebald greys (No. 9) ; and piebald blacks which are not figured. Amongst the piebalds there may be every gradation between a mouse which, but for the possession of a few white hairs (on the forehead usually), would be a self-coloured mouse, to one which has no more than a small patch of grey or black, which is usually near the ears. The extreme form of piebald in this direction is a white mouse with black eyes ; but this type has never occurred in my experiments. There are also differences in the intensities of the grey and black, so that the number of possible different types of coloration in the second hybrid generation is very great indeed. All the members of Group B, however, possess the following characters in common : (a) black eyes ; and (b) a greater or less amount of a dark colour, either black or grey, in the coat.

Mice included in Group C correspond to the fawn-and-white (waltzing) pink-eyed mice. But here, again, the correspondence is not exact. For just as in Group B, which corresponds roughly to the first hybrid generation, there were blacks as well as greys,

so in Group C, which corresponds roughly to the fawn-and-white mice (No. 2), there are "lilacs" as well as fawns. The parallel, indeed, between the two cases is very close, for the fawn colour may be regarded as a dilute grey; and the lilacs as a dilute black. "Lilac" was the name I first gave to these mice, and I have adhered to it, but "pale lavender" more accurately conveys the exact colour. Then, again, as in Group B, there may be "sels" as well as piebalds. But whilst in Group B the piebald was the new appearance, in Group C the "self" is. In other words, in the case of the dark colours (grey and black) the "self" appears first in the first hybrid generation, and the piebald does not appear till the second; but in the case of the paler colours (fawn and lilac) the fawn exists first in a piebald form in one of the parents of the cross, and does not appear as a "self" until the second hybrid generation.

There may, therefore, be—as in Group B—four kinds of mice in Group C: self-coloured fawns (No. 11), self-coloured lilacs (not figured), piebald fawns (No. 12), and piebald lilacs (No. 13, which has a white face).

The second hybrid generation is made up of the representatives of the three Groups, A, B and C, in the ratio of about 25 per cent. A, 50 per cent. B, and 25 per cent. C, or, roughly, one of A, two of B, and one of C in every four, on the average. These ratios obviously do not obtain in every litter, even if only because the number of young in a litter is not necessarily a multiple of four; in fact, in none of the twenty litters, selected at random and shown

on the following page, did the exact ratio occur. The total numbers obtained in my experiment were : Group A, 137 ; Group B, 287 ; Group C, 134.

Now let us consider the breeding properties of the mice representative of the three groups, A, B, and C. The albinos (Group A) breed true without exception. With rare exceptions, the mice in Group B again produce representatives of Groups A (No. 15), B (Nos. 16 and 17), and C (Nos. 18 and 19), when they are mated together ; the exceptions referred to do not produce albinos or fawns, but only mice with black eyes and dark coats—that is to say, they breed true to the characters of Group B. The mice in Group C, with very rare exceptions indeed, breed true to the characters of their group.

The breeding properties of the various colour types within the three Groups, A, B, C, are as follows, so far as my published records permit me to judge : Black by black do not give grey ; but grey by grey may give black, as also may grey by black. Lilac by lilac do not give fawn ; but fawn by fawn have not yet given lilac, nor have lilac by fawn. Self-colour by self-colour occasionally give piebalds, but piebald by piebald do not give “sels,” and piebald by “sels” give both piebalds and “sels.” It is desirable now to pause and to consider the phenomenon represented on Plate II. as a whole.

The parallel between this phenomenon and that exhibited by, for instance, tallness and dwarfness in the pea, or by the colour of the Andalusian fowl, is at once obvious. Albinism may be called the

TABLE SHOWING THE COLOUR-CHARACTERS OF THE  
MICE IN TWENTY LITTERS OF THE SECOND  
HYBRID GENERATION

<i>Litter No.</i>	<i>Group A (albinos)</i>	<i>Group B (Dark-coloured mice with black eyes)</i>	<i>Group C (Pale-coloured mice with pink eyes)</i>	<i>Total</i>
1	none.	grey, grey, grey, black.	piebald fawn, piebald fawn.	6
2	albino, albino.	piebald grey, piebald grey.	fawn.	5
3	albino, albino.	piebald grey, piebald grey, grey, black.	none.	6
4	albino.	grey, grey, grey, piebald grey.	piebald fawn.	6
5	none.	grey, grey, black.	fawn, piebald fawn.	5
6	none.	grey, grey, grey, grey, piebald black.	fawn, lilac.	7
7	albino, albino, albino, albino.	grey, piebald grey.	none.	6
8	albino, albino.	grey, grey.	none.	4
9	albino.	grey, grey, piebald grey, black.	none.	5
10	none.	grey, grey.	fawn, fawn, fawn.	5
11	none.	grey, piebald grey, piebald grey.	piebald fawn, piebald fawn.	5
12	albino, albino	grey, piebald grey.	piebald lilac.	5
13	albino.	grey, grey, grey, grey.	fawn.	6
14	albino.	grey, piebald grey.	fawn, fawn, fawn.	6
15	albino.	grey, grey, grey, grey.	piebald fawn.	6
16	albino.	grey, grey, grey, piebald grey, piebald grey, piebald black.	piebald fawn.	8
17	none.	grey, grey, piebald grey.	lilac.	4
18	albino, albino.	piebald grey, piebald grey.	fawn, lilac, piebald lilac.	7
19	albino, albino.	grey, grey, grey.	fawn.	6
20	albino.	grey, black.	fawn, fawn, piebald fawn.	6

The mode of progression of the mice, whether waltzing or normal, is left out of account in this Table.

recessive character, the "fawn-and-white" type of coloration may be called the dominant; although it may be argued that, in a sense, it is just as recessive as albinism inasmuch as it disappears from the first hybrid generation as much as albinism does; but it is convenient to speak of it as the dominant character, and it is justifiable if we state the case by saying that in the cross shown on Plate II. "some colour" is dominant over "no colour"; further, if the white Andalusian is regarded as the recessive it is legitimate to regard the white mouse as recessive, and, if this is done, the fawn-and-white falls into its place as the dominant.

In all three cases—the pea, the fowl, and the mouse—the two characters (of the two parents respectively) reappear in the second hybrid generation of which they each make up 25 per cent.; the remaining 50 per cent. being composed of individuals resembling the hybrids of the first hybrid generation in all three cases. The parental characters, when they have reappeared in the second hybrid generation, breed true without exception in the case of the so-called "extracted" recessive; and, with the extremely rare exceptions afforded by the mice in Group C, they also breed true in the case of the "extracted" dominant. And in all three cases the hybrids of the second hybrid generation again produce the dominants, hybrids and recessives with the exceptions afforded by the true-breeding mice in Group B.

We are thus again brought round to the conclusion

that the character borne by the hybrid is not essential to the Mendelian phenomenon; in the three cases which we are considering the hybrid has been either (*a*) indistinguishable from one parent, or (*b*) intermediate between the two, or (*c*) it has borne the character of the remote ancestral form of both. What is common to all three cases is the reappearance in the second hybrid generation of the "dominant" parental character, the hybrid character (when different from this) and the "recessive" parental character in the ratios of 25 per cent., 50 per cent. and 25 per cent. respectively—a phenomenon to which the term segregation has been applied.

The fact that the hybrid frequently bears characters which are peculiar to itself, and the occurrence of segregation, are the two features of the results of crossing which lead to the production of novelties; and they correspond, in the main, to two distinct practical methods. In the first of these methods the novelty is obtained in the first hybrid generation by virtue of the fact that the hybrid bears characters peculiar to itself. The hybrid in these cases is usually not reversionary, but intermediate between the two parents, as in the case of the Andalusian fowl, and that of the roan colour in cattle, which is produced by crossing red with white, and which, when mated with roan, gives 25 per cent. red, 50 per cent. roan, and 25 per cent. white. The novelty which arises in this way is unstable.

In the second of these practical methods the novelty is not obtained till the second hybrid genera-

tion, the first hybrid generation consisting usually of reversionary forms. In this class of cross nothing must be expected from the immediate result of the cross. Nothing, for instance, could be more disappointing to the mouse fancier than the result of crossing the albino with the Japanese waltzing mouse—namely, an animal scarcely distinguishable from one that could be caught in a trap, any day, in the pantry. Yet I know no more beautiful colour in an animal than that of the “lilacs” which are produced in small numbers by mating these hybrids of the first generation together. I am given to understand that this colour is new to the “fancy,” but I do not know if there is a class for it at the shows.

It is very important to keep these two ways in which novelties are obtained by crossing, distinct in the mind. In the “first generation method,” as it may be called, an unstable new form is the immediate result of the cross; and to obtain it again it is better to repeat the cross than to breed these hybrids together, partly because by this means 100 per cent. of the offspring are of the desired kind (as opposed to the 50 per cent. produced by mating the first crosses together); and partly because of the greater vigour of first crosses. In the “second generation method,” as it may be called, a stable new form is obtained in the second hybrid generation; the hybrid, which is usually reversionary, is useless in itself, and merely serves as a sort of mill which will turn out any desired quantity of the new forms.

The two methods are like the two chief methods

of photography—the method of Daguerre and the method of Fox-Talbot, who invented the negative. By Daguerre's method a positive image was produced on a silvered surface, and the picture could not be copied except by an elaborate process of electrotypy. A new daguerreotype could only be reproduced by exposing a fresh plate. The negative, like the reversionary hybrid, is useless in itself; but it revolutionised photography. Daguerre's might be called the one-generation method, and Fox-Talbot's the two-generation method of photography. A breeder who threw away his first crosses because they did not possess the character he was working for, would be as foolish as a photographer who threw away his negatives because the light parts in the objects appeared dark, and the dark light, in them.

First crosses are, however, not always bred because they possess new characteristics, but because they very often possess greater vigour than either of the parents crossed. This is another reason why it is better to raise those hybrids which possess characteristics peculiar to themselves, such as roan cattle, by repeating the cross than by breeding roan cattle *inter se*. I do not know, and it does not much matter, whether the excessive vigour of the first cross is to be considered as a phenomenon of reversion, but it is a fact that, in the case of my mice, reversion to the ancestral condition in regard to disposition is just as invariable a result of the cross as the reversion in regard to colour. The difference between the disposition of the hybrid and that of the

albino is as great as that between the colour of the two.

Though I did not make pets of my albinos, they were perfectly tame, and would very seldom attempt to escape from the cage when it was opened. But the greatest caution had to be exercised when a cage containing first crosses was opened, for if care is not taken the mouse will spring from the nest directly the lid is lifted, and be lost. I lost one or two mice in this way before I learnt this characteristic of the first crosses. But even if the mouse does not escape, the wildness of its disposition is manifested in the frenzied way in which it darts about the cage when it is subjected to treatment (such as mating up, or the separation of the males from the females in a family when they become adult) under which the albino behaves with perfect tameness. The excessive vigour of the first cross is manifested also in the glossy condition of its coat, which I have always noticed to be much sleeker than that of any of the other mice—its parents or its offspring—in my experiments.

The phenomenon of the inheritance of colour in these mice has now been described; and the application of the knowledge of this and the other results which we have discussed, has been briefly referred to. The luxuriant "condition" of the hybrid has been illustrated, and this reference to a physiological character leads naturally on to the consideration of another character in respect of which the two parent

forms differ—namely, the nature of their customary movements.

It is not necessary, I think, to describe the walking and running movements of the common white mouse. Moreover, it would be difficult to give a description of its demeanour which would be generally true, because the habits of the individual mouse is determined to a very great extent by the treatment to which it has been subjected. For instance, the habits of one of my mice, more than a thousand of which were kept in a room whilst the breeding experiment was in progress, would be very different from that of the ewe lamb of the schoolboy. The characters which “tame” mice possess in common are sufficiently familiar to the reader. They can run straight away if free to do so. But the so-called waltzing mouse cannot.

The actual waltzing itself, which gives the breed its name, does not, of course, resemble waltzing, and is not executed on the hind legs only. A better name, which is sometimes given it, is “spinning.” The animal runs round and round in a small circle, the diameter of which is about half the length of the animal’s body excluding the tail, at so great a pace that the mouse becomes a blur. No. 2 on Plate II. represents a waltzing mouse in the act of waltzing, with great faithfulness. This excellent representation of the waltzing habit is due to the skill of Mr. Gerrard, of Camden Town, who kept some of the waltzing mice under observation for a considerable time before stuffing them. An individual mouse does not

always spin in the same direction, but sometimes with the hands of the clock, and at other times in the contrary direction. A "waltzing" mouse is not, however, always spinning. It spins at night, as a rule, and sleeps during the day when it is not being fed. But it can always be recognised as a "waltzer," even if it is not spinning, so long as it is awake, by the following characteristics: first, an apparently complete lack of control over the movements of its head, which is thrust up and down and moved rapidly from side to side in a peculiar manner which cannot be forgotten, but is not easily described; secondly, by a curious habit which it has, when placed in a large open space, such as the floor, of backing very vigorously as if it were on a slow-moving avalanche, and moving its head, which is kept near the floor, rapidly from side to side. Not only can the adult "waltzer" be recognised as such when it is not waltzing, but the young can also be recognised before they can waltz, because they can hardly keep on their four legs. The waltzer is characterised by great delicacy and stupidity. The death-rate is higher amongst them than amongst ordinary tame mice; they often fall out of the cage when the door is opened, and are greatly inferior to the albino, for instance, in the care of the brood. They seem to be deafer than ordinary mice; at any rate, they take fright much less readily at a small noise than an ordinary mouse does. For instance, if a noise is made with the tongue and teeth whilst a waltzer is at food, he will not, as the albino probably,

and the hybrid certainly, will, scuttle back into the hind part of the cage, if this is divided off by a partition. The waltzer differs from the ordinary tame mouse in the matter of disposition as much in one direction as the wild mouse or the hybrid does in the other. An albino, if set free, can run away, but does not; a hybrid or wild mouse, if set free, can run away and does; but a "waltzer" cannot escape; it cannot keep up a run in direct line for long, and soon lapses into spinning.

The cause of the spinning is supposed to be an abnormality in certain organs in close connection with the internal part of the ear. There are three of these semicircular canals, as they are called, in connection with each ear in the normal vertebrate animal, one horizontal and two vertical for each ear, and they are said to be concerned in the normal animal in maintaining the balance of the body. It was formerly stated that the waltzing mouse lacked the horizontal canal in connection with each ear; but this statement has been proved to be incorrect by the application of a new method of preparing the semicircular canals and of preserving them in their natural state. All six canals are present. But a deficiency in the nerve supply of the semicircular canals is said to have been discovered; and the waltzing habit may be due to this. At any rate, it seems to be generally agreed that this phenomenon of waltzing is determined by some abnormality in the organs which are responsible for preserving the balance of the animal. A physiologist once expressed

to me his conception of the causation of the waltzing habit in the statement that it is due to the absence of the power of becoming giddy. The unpleasant sensations which would soon stop a normal mouse from spinning round are not felt by the waltzing mouse, and what ultimately brings the bout of spinning to an end is not nausea, but exhaustion.

Let us, now, turn to the inheritance of the waltzing character. When two waltzing mice are mated together the offspring produced are all waltzers. The character breeds true.

When a waltzing mouse is mated with a mouse with normal movement, as in my own cross represented on Plate II., the hybrid produced never exhibits the waltzing movements. This, at any rate, has invariably been the case in the hundreds of hybrids raised by Dr. von Guaita and by myself. The waltzing character is, therefore, recessive and normality of progression is dominant. Being a recessive character, waltzing should reappear in the second hybrid generation in one individual in every four. It does reappear in the second hybrid generation, but not in a quarter of the individuals; there were 97 out of 555, which is less than a fifth. But I do not think that this proportion should lead us to the conclusion that waltzing does not behave as a Mendelian character in inheritance, because I believe that the reason that the number of waltzers falls short of the expected ratio is simply that waltzers are more delicate constitutionally than normal mice; and that relatively more waltzers

die before the age at which the characters of the litters are noted, than normal ones do. But to return to the actual reappearance of the waltzing character in the second hybrid generation. The waltzing of the "extracted" waltzers, as the individuals of this generation which manifest this character are called, does not differ from that of individuals of the pure race, except that in occasional individuals it seems to be accentuated.

The waltzing character, when it reappears in the second hybrid generation, is not confined to mice coloured like the pure waltzer, No. 2; that is to say, it does not only occur amongst the mice of Group C, but amongst those of Group A and B also. Waltzing representatives of each of the three groups are shown at No. 4, No. 6 and No. 10. We are now in view of a new and very important subject. Hitherto we have been considering the relation to one another of two characters which stand to one another in the relation of dominant and recessive—i.e. characters which constitute a single pair, and affect the same organ or feature of the plant or animal. We now come in view of the question: What is the relation between members of distinct pairs of characters—i.e. characters of distinct features of the animal or plant—for instance, the colour of a mouse and its mode of progression? The answer in this case is very simple. There is no relation. The colour of a mouse and the nature of its movements, i.e. whether normal or "waltzing," are inherited entirely independently of one another. The

pure race of waltzers breed true to their colour and "waltzing"; but in the second hybrid generation produced from a cross between a waltzing mouse and an albino, there is no association between colour and the waltzing character. The waltzing character is distributed at random over the three colour-groups, A, B and C—i.e. without any preference to any particular colour-group, as can be seen on page 91 and Plate II. The numerical proportions in which the various combinations of colour and mode of progression occur will not be considered in detail now; suffice it to say that rather less than a quarter of the mice in each colour-group, A, B and C, are waltzers. Our attention may now be turned to points of theoretical and practical interest in the results displayed on Plate II.

To consider the facts from their theoretical side first; it is seen that the fact of the independent inheritance of the colour and mode of progression, which could not be detected by observing the results of breeding from the pure waltzing race for an unlimited number of generations, is at once revealed (in the second hybrid generation, to be precise) by the simple experiment of crossing two mice which differ in their colour and the mode of their progression. The practical interest of such facts is too obvious to need insisting upon. The number of new varieties in the second hybrid generation is considerable; and some of them may be counted upon to breed true. The re-combination of characters possessed by the two parents of the cross may be considered first.

The albino waltzer (No. 4) possesses the recessive character, waltzing, of one parent, and the recessive character, albinism, of the other parent, and as both these characters breed true when they reappear in the second hybrid generation, the new albino waltzer will be a constant variety from the first. The colouring of the pure waltzer and the normal progression of the albino are combined in mouse No. 12. Mice in which the waltzing character is associated with one of the colours or arrangements of colour not existing in either of the two parents of the cross constitute a further set of new forms. The most beautiful of these is undoubtedly the lilac waltzer (a specimen of which I have not figured), and the most curious of them is the form shown at No. 6, a mouse in which the coloration of the first hybrid generation is associated with the waltzing character—a house-mouse that cannot run away. Whether it was a constant variety or not would depend upon whether, when mated with its like, it bred true to its colour or not; for it would be certain to breed true to the waltzing character if mated with a mouse like it. But as the majority of the mice in Group B produce, again, representatives of Groups A, B and C, it is impossible that a constant race of mice like No. 6 could be raised, except after long waiting for two mice, of opposite sexes, both of which breed true to grey coat and black eye.

In this chapter I have set forth an example of reversion on crossing, and the result of breeding from these reversionary hybrids. The inheritance of colour

TABLE SHOWING THE DISTRIBUTION OF THE WALTZING CHARACTER OVER THE TWENTY LITTERS EXHIBITED ON PAGE 78

Litter No.	Group A (albinos)	Group B (Dark-coloured mice with black eyes)	Group C (Pale-coloured mice with pink eyes)	Total of normal mice	Total of waltzing mice
1	none.	grey, grey, grey, black.	piebald fawn, pie- bald fawn.	6	none.
2	albino, albino.	piebald grey, pie- bald grey :W.	fawn.	4	1
3	albino :W, albino :W.	piebald grey, pie- bald grey, grey, black :W.	none.	3	3
4	albino :W	grey, grey, grey, piebald grey.	piebald fawn.	5	1
5	none.	grey, grey, black.	fawn :W, piebald fawn.	4	1
6	none.	grey, grey, grey, grey, piebald black.	fawn, lilac.	7	none.
7	albino :W. albino, albino, albino.	grey, piebald grey	none.	5	1
8	albino, albino.	grey, grey.	none.	4	none.
9	albino.	grey, grey, piebald grey, black.	none.	5	none.
10	none.	grey, grey :W.	fawn, fawn, fawn.	4	1
11	none.	grey :W, piebald grey :W, pie- bald grey :W.	piebald fawn :W, piebald fawn :W.	none.	5
12	albino, albino.	grey, piebald grey.	piebald lilac :W.	5	1
13	albino.	grey, grey, grey, grey.	fawn.	6	none.
14	albino.	grey :W, piebald grey.	fawn :W, fawn, fawn	4	2
15	albino.	grey, grey, grey, grey.	piebald fawn.	6	none.
16	albino.	grey, grey, grey, piebald grey, piebald grey, piebald black.	piebald fawn.	8	none.
17	none.	grey, grey :W, pie- bald grey :W.	lilac.	2	2
18	albino :W, albino :W.	piebald grey, pie- bald grey.	fawn, lilac, pie- bald lilac.	5	2
19	albino, albino.	grey, grey, grey.	fawn.	6	none.
20	albino.	grey, black :W.	fawn, fawn, pie- bald fawn.	5	1

W printed after the name of the colour of a mouse in the above Table indicates that the mouse was a waltzer. All the other mice were normal in their mode of progression.

in the mice represented on Plate II. runs on the same lines as that of, for instance, tallness and dwarfness in peas, and colour in the Andalusian fowls. All these three instances agree in the production of "dominants," "hybrids," and "recessives" in the second hybrid generation in the proportion 1 : 2 : 1 in every four, and differ in the character of the hybrid which, in the case of stature in the peas was indistinguishable from one parent, in the case of colour in the fowls was intermediate between that of the two parents, and in that of colour in the mice, constituted a reversion to the ancestral type of coloration. The mice, further, afforded an instance of a cross in which two pairs of independently inherited characters were involved. A closer consideration of such cases will form the subject of the next chapter, and the line of argument to be followed now will lead us back again to the phenomenon of reversion, and show how, at any rate, some cases of it may be explained in the light of Mendelian phenomena.

## CHAPTER VII

### THE RELATION BETWEEN CHARACTERS BELONGING TO DISTINCT PAIRS

THE reader is already familiar with the relation between two characters of the same pair, such as yellowness and greenness of the cotyledons; that is to say, with the results which follow when an individual bearing one character of a pair (yellow) is crossed with one bearing the other member of the same pair (green). The question to be dealt with now is the relation between members of distinct pairs of characters, such as yellowness of cotyledons, belonging to one pair of characters, and roundness or wrinkledness belonging to another pair. A proper understanding of this relation is of great practical value, because it enables the breeder to effect the combination of desirable characteristics existing in distinct strains with great swiftness and precision.

The nature of this relation will at once become apparent when the result of a cross between two individuals which differ from one another in respect of characters which belong to two pairs of characters has been described. For this purpose I shall describe the result of a cross between a pea with wrinkled yellow cotyledons, and a pea with round green ones. Let the exact nature of this cross be clearly under-

stood before the result of it is described. Plate I. represents the result of a cross between two races of peas which differ in the *colour* of their cotyledons. The two races crossed only differed in respect of a single characteristic—colour. Both the parent forms happened to be round. Fig. 21 represents the result of a cross between two races of peas which differ only in the *form* of their cotyledons. Both the parent forms happened to be yellow—but this is not shown in the figure. In the cross about to be described the parent forms differ in respect of both the colour and the form of their cotyledons; that is to say, the results shown separately in Plate I. and Fig. 21 are shown together. There is nothing new in the case we are about to deal with: it is merely two cases which have already been considered separately, in separate crosses, considered together in one cross. Indeed, every detail of the result of the cross between the yellow wrinkled and the green round can be predicted from the knowledge which we now possess of the result of crossing a yellow with a green, and a round with a wrinkled. Yellow is dominant to green and round dominant to wrinkled; the result, therefore, of crossing a yellow wrinkled with a green round is a yellow round. This is shown in Plate III.; the yellow wrinkled race is represented by a group of six peas to the (top) left of the picture, the green round one by a group of eight peas to the (top) right. The first hybrid generation is represented by five yellow round peas between and a little below the parent forms.



PLATE III.—THE RESULT OF CROSSING A YELLOW WRINKLED  
WITH A GREEN ROUND PEA

(Top left) Yellow Wrinkled Parent.

(Top right) Green Round Parent.

(Five Peas in middle line) First Hybrid Generation.

(In the pods) Second Hybrid Generation.



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A cross between a yellow round and a green wrinkled would have involved the same two pairs of characters. The hybrid would have been, as in the case I have shown, yellow round ; that is to say, exactly like one of its parents. The second hybrid generation would have been the same in the two cases. The difference between the two cases, of course, lies in the distribution of the characters over the parent forms ; in other words, in the case I have figured, each parent has a dominant member of one pair and a recessive member of the other pair. But when a yellow round is crossed with a green wrinkled the former has both the dominant members and the latter both the recessive ones. That is why in this case the result of the cross is identical with one of the parents. I have, however, described a cross between two individuals, each of which bears a dominant and each a recessive character, for a definite reason, to illustrate the fact that the dominance or recessiveness of a character is not a result of constitutional vigour or weakness of the animal or plant that bears it, but is a property peculiar to that particular character. A cross between a round and a wrinkled does not show this ; nor does a cross between a yellow and a green ; nor even does a cross between a yellow round and a green wrinkled. In all these cases the hybrid is like one of its parents, and we have no means of knowing that its character is not determined by the superior vigour of that parent. But directly we have seen the result of a cross between two forms, each of which possesses a dominant

character, we perceive that dominance attaches not to the individual but to the character. Some individuals in certain animals, such as horses, are said to possess the power of impressing their characteristics on their offspring whenever they are mated, which, in the case of stallions, is pretty often. Whatever be the nature of this power, which is called prepotency, it is clear that it has nothing to do with dominance. Prepotency is an attribute of individuals, and capricious in its appearance. Dominance is an invariable attribute of particular characteristics. In the case before us there is no question of a certain individual impressing its characters on its offspring. The hybrid takes one of its characters, yellow, wholly from one parent, and another, round, from the other.

We are thus brought in view of one of the conclusions to which experimental breeding has led, namely, the conception that living things are made up of a number of characters which arise separately and are transmitted separately. Whatever may be the value of this suggestion as a help to the understanding of evolution, there is no doubt as to its value as a guide in the practice of breeding.

The second hybrid generation produced by the self-pollination of the yellow round hybrids referred to above must now be considered. Briefly, this generation consists of individuals presenting all the four possible combinations of yellow, round, green and wrinkled; namely (9) yellow round, (3) yellow wrinkled, (3) green round, and (1) green wrinkled, in the proportions indicated by the figures in brackets

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prefixed to them. This proportion is a very important one; it is, therefore, desirable to make this point perfectly clear. In the second hybrid generation resulting from a cross between a yellow wrinkled and a green round pea there will be:

9 Yellow round, 3 Yellow wrinkled, 3 Green round,  
and 1 Green wrinkled

in every sixteen peas, on the average.

It will at once be seen that the peas bearing two dominant characters are in the majority: there are nine out of sixteen. Next come peas with a dominant and a recessive character, which may be either yellow and wrinkled or green and round. Of each of these combinations, there are three in the sixteen. Last of all, in point of number, come those peas both of the characters of which are recessive, namely the green wrinkled ones; of these there is only one in every sixteen.

This 9 : 3 : 3 : 1 proportion follows from the co-existence of two 3 : 1 ratios in the second hybrid generation produced by a single cross, in the following way. The two pairs of characters, yellow and green, and round and wrinkled, are distributed in their proportions of three to one, at random, over the individuals composing the second hybrid generation. What is meant by "at random" is that the shape of the cotyledons is not affected, one way or the other, by their colour, or their colour by their shape. It would be an even chance that a round pea were a yellow or green, or that a yellow one were a round

or wrinkled, if yellows and greens, and rounds and wrinkleds occurred in equal numbers. But there are three yellows to one green in every four, and three rounds to one wrinkled in every four. And the proportions in which each of the four combinations occur is arrived at by multiplying together the ratios in which each of the characters in a combination occur separately:—

Yellow and round	.	.	.	$3 \times 3 = 9$
Yellow and wrinkled	.	.	.	$3 \times 1 = 3$
Green and round	.	.	.	$1 \times 3 = 3$
Green and wrinkled	.	.	.	$1 \times 1 = 1$

A glance at Plate III. will show the kind of approximation to the 9 : 3 : 3 : 1 ratio which is obtained in a small number; there are thirty-eight seeds altogether, and the various combinations of characters occur in the following proportions:—

18 Yellow round, 7 Yellow wrinkled, 12 Green round, and  
1 Green wrinkled

That is to say, there are too many green rounds and too few green wrinkleds; but deviations of this magnitude in so small a sample are of no significance.

So far the visible characters of the plants—i.e. of the cotyledons of the young plants seen through the seed-coats—have alone been considered. The distinction between pure and hybrid individuals bearing the dominant character has been left out of account. It must now be considered. The simplest case is that of the green wrinkled; every one of these, appearing in the second hybrid generation, will

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breed true, inasmuch as both of its characters are recessive.

The green rounds breed true to their recessive character (greenness), but may or may not breed true to their dominant one, roundness. There are, therefore, two kinds of green rounds—a kind that breeds true to both of its characters and produces green rounds only, and a kind that breeds true to colour but not to shape, and produces green rounds and wrinkleds. Amongst every three green rounds there will be one of the former and two of the latter kind, on the average.

The yellow wrinkled are in like case. They breed true to their recessive character (wrinkledness), but may or may not breed true to their dominant one (yellowness). There are, therefore, two kinds of yellow wrinkled, a kind that breeds true to both of its characters and produces yellow wrinkleds only, and a kind that breeds true to shape but not to colour, and produces yellow and green wrinkleds. Amongst every three yellow wrinkleds there will be one of the former kind and two of the latter, on the average.

There are four kinds of yellow rounds: (1) A kind that breeds true to both of its characters and produces yellow rounds only; of which kind there is one in every nine on the average. (2) A kind that breeds true to colour and not to shape and produces yellow rounds and wrinkleds; of which kind there are two in every nine. (3) A kind that breeds true to shape but not to colour, and produces yellow and green rounds; of

which kind there are also two in every nine. And, lastly, (4) a kind that does not breed true to, but is hybrid in respect of, both its characters, and produces all four kinds—yellow round, yellow wrinkled, green round, and green wrinkled. Of this kind there are four in every nine on the average. On the opposite page are given the actual characters of the seeds of ten plants which were all raised from the yellow round seeds of a hybrid generation, such as that which we have considered; it will be seen that there are two instances of the first kind (Plants Nos. 5 and 8), one of the second (Plant No. 7), two of the third (Plants Nos. 1 and 4), and five of the fourth kind (Plants Nos. 2, 3, 6, 9 and 10). Of course it does not always happen that, in a sowing of ten seeds, representatives of each of the four kinds occur. Nor, when they do occur, amongst ten plants is there likely to be a close approximation to the ratio given above. The composition of the second hybrid generation we are considering may, therefore, be summarised as follows:—

1. Yellow round—

(i) Pure to colour and shape . . .	1
(ii) Pure to colour but not to shape . . .	2
(iii) Pure to shape but not to colour . . .	2
(iv) Hybrid in both respects . . .	4
	<hr/>
	9

2. Yellow wrinkled—

(i) Pure to colour and shape . . .	1
(ii) Pure to shape but not to colour . . .	2
	<hr/>
	3

Table to show the distribution of yellow round, yellow wrinkled, green round, and green wrinkled seeds, containing cotyledons of the third hybrid generation, on ten plants (1 to 10) of the second hybrid generation. From actual specimens.

The numbers in each horizontal row, under each plant, relate to the seeds in individual pods. Thus, there were sixteen pods on the first plant, eleven in the second, and so on. The first pod on the first plant contained eight seeds, the second six, the third five, and so on.

1				2				3				4				5			
YR	YW	GR	CW																
4		4		2		4	1	3	1	1		6		1		6			
5		1		6		1		3	1	2		1				5			
5				3	3			3	2	1		5		1		7			
4		1		5				1	1	1	1	4		2		6			
3				6		2		4	2		1	4		2		6			
1		1		3	2	1		6		1	1	3		3		6			
2		3		1	2	1			1	4		6		1		6			
5				5	1			1	1	1	1	5		1		6			
3		2		3	1			4	2	1		4		2		5			
2				2	1	1		4	2			3		2		6			
1		3		1	1			1	1			4		1		4			
3		1						2	1	2		2		1		3			
3		1						1	1	1		3		2		2			
2		3						1	1	1		2		1		3			
3								2	1	2	1	2		1		2			
3		1						1	1	2	1	2		1		2			
								2				4		1		2			
												3				3			
												3				2			
												2		1		1			
												1		3					
												2		2					
												2		1					
												2		1					
49		21		37	11	10	1	39	17	16	4	73		30		74			

6				7				8				9				10			
YR	YW	GR	CW																
1	1			5	2			6				3		2		1		3	1
	4	1	1	5	1			5				3		1		3		1	
5	1	1		3	2			7				1	1			2	1	1	
2	1	2		6	1			8				3		2		3	1	1	1
2	3	2		3	1			6				3	1			4	1	1	
4	2	2		2	1			7				3	1		1	2			
3	1	1		3				6				3		2		2	1	1	1
3			1	4				6				3			1	3			
4		1		4				5				4				2	1		1
4	1		1	4	3			5				3		1		3	1		1
3			1	2	2			6				4				1			
1				2				4				3				1			
4	1			5				3				4							
2	1	2		2				4				3							
1	1	2		5	1			4				4							
				4				3				3							
2		1		1	4			5				4							
2		1		3	2			3				4							
				5				3				3							
				3	1			5				3							
				1	2							3							
				3	2							5							
43	18	16	4	78	25			86				26	3	8	2	23	7	7	6

3. Green round —		
(i) Pure to colour and shape	. .	1
(ii) Pure to colour but not to shape	. .	2
		3
4. Green wrinkled—		
Pure to colour and shape	. .	1

It will be observed that there is only one pure breeding representative of each of the four categories yellow round, yellow wrinkled, green round, and green wrinkled.

The ratios in the above may be arrived at by multiplying together the ratios in which the particular characters which make up each combination occur separately, having regard to the question whether the character is in a pure or hybrid state. Thus, when a yellow is crossed with a green the second hybrid generation is composed as follows: 1 pure yellow, 2 hybrid yellow, 1 green, in every four; and the second hybrid generation from a cross between a round and a wrinkled has the following composition: 1 pure round, 2 hybrid round, 1 wrinkled, in every four, on the average. The combination of these six classes will, therefore, occur in the following ratios:—

[1. Yellow round]—

Pure yellow and pure round	. .	$1 \times 1 = 1$
Pure yellow and hybrid round	. .	$1 \times 2 = 2$
Hybrid yellow and pure round	. .	$2 \times 1 = 2$
Hybrid yellow and hybrid round	. .	$2 \times 2 = 4$
		9

## CHARACTERS OF DISTINCT PAIRS 103

[2. Yellow wrinkled]—

Pure yellow and wrinkled.	.	1 × 1 = 1
Hybrid yellow and wrinkled	.	2 × 1 = 2

—3

[3. Green round]—

Green and pure round	.	1 × 1 = 1
Green and hybrid round	.	1 × 2 = 2

—3

[4. Green wrinkled]—

Green and wrinkled .	.	1 × 1 = 1
----------------------	---	-----------

—1

The epithet “pure” is omitted before the recessive character in the above table to lay stress on the fact that the recessive character is always pure.

To consider for a moment the practical application of the facts which have now been set forth, it will be seen that there are four combinations of characters in this second hybrid generation, two of which are different from the parent forms started with, namely, the green wrinkled and the yellow round. Of these four combinations only one type—that which possesses two recessive characters, the green wrinkled—can be counted on to breed true, straight away. We have to wait no longer in this instance than the second hybrid generation for a constant new variety. In the case of the other three combinations, it is necessary to wait till the next generation before we can be certain of getting a constant type. For directly we find a plant (bearing a fairly large number of seeds)

which produces only yellow rounds, or only yellow wrinkleds, or only green rounds, we can be sure that it is pure in respect of both colour and shape, and will continue so. And it may be laid down as a general rule that the permanent combination of two recessive characters may be effected in the second hybrid generation, but that the permanent combination of a recessive and a dominant character (belonging, of course, to distinct pairs), or of two dominant characters, cannot be effected till the third hybrid generation. It is curious that the great majority of the best culinary peas are green wrinkled. But this fact is probably not merely due to the facility with which these two characters can be combined; for though there is no advantage, from the culinary point of view, in the green over the yellow, the advantage of the wrinkled over the round will be seen to be very great.

An instance of the value a familiarity with this 9 : 3 : 3 : 1 ratio, as a help to understanding otherwise unintelligible results of cross-breeding, will now be given. One of the characteristics which distinguish the various breeds of poultry is the form of the comb. The commonest type of comb, and that possessed by the wild ancestor of our domestic poultry, is known as the single comb, which is represented in Fig. 22. The comb is flat from side to side, and its free edge is marked by deep indentations. Another type of comb, which characterises the Wyandottes, is shown in Fig. 23, and is known as the "rose" comb. It is



FIG. 22.—SINGLE COMB  
(Black Leghorn.)



FIG. 23.—ROSE COMB  
(Partridge Wyandotte.)

*Photographs by the kindness of the Rev. T. W. Sturges.*



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squat, and its surface is marked, all over, by many convolutions. A third type (Fig. 24), known as the "pea" comb, occurs in the Sumatra game, for instance, and may be said to consist of three low ridges, a median and two lateral ones. A fourth type of comb, known as the walnut comb, and only occurring in the Malays, is shown in Fig. 25. It consists of a globular excrescence not unlike a walnut.

If a fowl with a "pea" comb is mated with one bearing a "rose" comb the resulting hybrids have "walnut" combs. When these hybrids are mated together, the generation produced has the following remarkable composition: 9 "walnut," 3 "rose," 3 "pea," : 1 "single." No "single," it will be remembered, was put into the cross. What is the origin of the single comb in this second hybrid generation, and what are the two pairs of characters responsible for this 9:3:3:1 ratio are questions which naturally present themselves.

The result of crossing the yellow wrinkled with the green round pea gives the clue. It will be remembered that in that instance both the dominant characters occurred together in the individuals which appeared in the proportion of nine in the sixteen; and that the dominant characters occurred separately in the two lots of individuals which appeared in the ratio of three in the sixteen, i.e. the yellow in the yellow wrinkled, and the round in the green round. In this case, therefore, we should suppose that the two dominant characters are "rose" and "pea." What the recessive characters corresponding to them

are will be indicated shortly. For the present, let us observe the result of their union. It will be at once noted that we cannot, as in the case of the peas, observe the co-existence of the two characters "rose" and "pea" in the hybrid. But this should give no cause for surprise. In the case of the peas, one pair of characters relates to colour and the other to shape; so, not only is it natural to expect to see them separately in the hybrid, it is impossible to imagine how they could become merged. But in the case of the fowls' combs, both the characters relate to shape, and it is therefore hard to conceive how, when they both exist in the same comb, they can escape blending, or at any rate producing a shape which is different from either, and in which neither can be recognised separately.

The "walnut" character is, therefore, due to the co-existence in the same comb of the "pea" and "rose" types. The "single" comb, which makes up one-sixteenth of the second hybrid generation we are considering, is the result of the absence of the two characters "pea" and "rose." The case is entirely analogous to that of the peas: the yellow rounds have two dominant characters; so has the "walnut," namely, "pea" and "rose"; the yellow wrinkled has one dominant character and one recessive; so has the "pea," namely presence of the "pea" character, and absence of the "rose"—if the "rose" were present the comb would be "walnut." The green round also has one dominant character and one recessive; so has the "rose,"



FIG. 24.—PEA COMB  
(Sumatra Game.)



FIG. 25.—WALNUT COMB  
(Malay.)

*Photographs by the kindness of the Rev. T. W. Sturges.*



## CHARACTERS OF DISTINCT PAIRS 107

namely presence of "rose" and absence of "pea"; the green wrinkled has two recessive characters, so has the "single"—absence of both "pea" and "rose." And the proportions in which these analogous things occur in the second hybrid generation are the same, thus :—

9 "Walnut"	3 "Pea."	3 "Rose."	1 "Single."
[="Pea" and "Rose"]		[=absence of both "Pea" and "Rose"]	
9 Yellow round, 3 yellow wrinkled, 3 green round, 1 green wrinkled.			

It will be remembered that it was said earlier in this chapter that the same results would have followed if, instead of crossing a yellow wrinkled with a green round pea, a yellow round were crossed with a green wrinkled. The two crosses only differ in the fact that in the former each parent has a dominant character, whilst in the latter both dominant characters exist in one parent. The cross we have described in the case of the fowl's comb, namely "pea" by "rose," is analogous to the one displayed in Plate III., namely, yellow wrinkled by green round. In both cases each parent has a dominant character. The cross in the case of the combs, analogous to that between yellow round and green wrinkled, is a cross between "walnut" (possessing, or consisting of, two dominant characters, "pea" and "rose") and "single." Here, as in the case of the peas, precisely the same results follow in the second hybrid generation, namely 9 "walnut," 3 "rose," 3 "pea," and 1 "single." The appearance, in the

second hybrid generation, of two entirely new characters—the “rose” and “pea” combs—which were not present in either of the parents or in the first hybrid would have been unintelligible to the experimenter who was not familiar with the 9 : 3 : 3 : 1 ratio, and with the proof, which this ratio affords, that we are dealing with a cross between two forms which differ in respect of two pairs of characters.

The reader will have noticed that a new conception of the nature of the Mendelian pair of characters has been invoked to explain the phenomena of inheritance presented by the characters of the fowl's comb. Mendel's own results led to the conclusion that characters which were inherited in Mendelian fashion were associated together in pairs, such that one member of a pair was dominant and the other recessive. No indication was given of any features which were peculiar to dominant characters—that is to say, no clue was given by which a dominant character could be known or suspected to be dominant before the result of mating it with a recessive one was known. The two members of a pair possessed this feature in common, that they were not merely drawn at haphazard from the characters of the plant, but both pertained to the same part of the organisation of the plant. Thus, yellow and wrinkled do not constitute a pair, but yellow and green. The two members of a pair only differ from one another by

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the fact that when two individuals, each of which possesses one of them, are mated, a hybrid is produced in which one of them, which is called the dominant, exists to the more or less complete exclusion of the other.

This is the general conclusion, as to the relation between the two characters of a pair, which was derived from a consideration of Mendel's own experiments with peas. Now, it will be seen that from the breeder's point of view it is very desirable to possess some sign by which a dominant character may be known before the crosses are made; also one is naturally curious to know what it is that makes one character of a pair dominant and the other recessive. A conception of the nature of dominant, in contradistinction to recessive, characters has already been hinted at in the explanation which was given of the result of crossing a fowl with a "pea" comb with one with a "rose" comb. The two pairs of characters involved in that cross were supposed to be the character of the comb known as "pea" (dominant) and the *absence* of that character (recessive); and the character of the comb known as "rose" (dominant) and the *absence* of that character (recessive). In both cases the presence of a particular character constituted the dominant member of the pair, and the absence of that character the recessive member. The dominant character is due to the presence of something—the recessive to the absence of that something. It is not easy at present to see how this conception may be applied to the pairs of

characters we have already considered, such as yellow and green, round and wrinkled ; and before I attempt to show how it can be applied to them I will describe a cross involving two pairs of characters to which its application is obvious.

This cross is between two kinds of peas (*Pisum*) which differ in the colour and arrangement of the pigment in their seed-coats. In one of them there is a rich brown mottling of anastomosing brown lines on a paler background ; this is characteristic of the so-called "maple," or "partridge," peas which can be had of any corn chandler. The brown mottling is only visible on close inspection ; in the mass the peas appear brown. A specimen of a pea with a "maple" seed-coat is shown, magnified, in Fig. 26. The seed-coat of the other variety, with which the "maple" is crossed, is marked with a great number of minute purple spots on a background, which is pale greenish grey in the newly ripe pea, but becomes dark brown with age. Certain garden peas, such as the French sugar pea, exhibits this type of coloration. A pea with this greyish seed-coat always has purple flowers, whether there are purple spots on the seed-coat or not. Further, the grey may exist in the seed-coat without purple spots, but the purple spots are not known to occur on seed-coats which are not grey. This fact does not concern us now, but is of great importance in the theory of reversion, which will be set forth later. For the sake of brevity, the type of seed-coat which has purple spots on a grey background will be referred to as

"Maple."

"Purple-spotted maple."

"Purple spot."



"Purple-spotted maple."

"Maple."

"Purple spot."

Pea showing absence of both "maple" and "purple spot."

FIG. 26.—THE RESULT OF CROSSING MAPLE AND PURPLE-SPOTTED SEED-COAT IN *PISUM*



## CHARACTERS OF DISTINCT PAIRS III

“purple spot” simply. A specimen is shown in Fig. 26.

When peas bearing these two varieties of seed-coat are crossed, there results a hybrid, the seed-coat of which exhibits both the “maple” and the “purple spot” character, which is seen below and between the two parent forms in Fig. 26. This result is rather surprising, because it might have been supposed that “maple” and “purple spot” were the dominant and recessive members of a single pair of characters from the fact that they were stated to characterise one and the same part of the plant, namely, the seed-coat. It will be remembered that one feature of characters which constituted a Mendelian pair of characters was said to be the fact that they pertained to the same part of the organisation of the animal or plant which bore them; and it might be supposed that the converse was true, namely, that two characters which pertained to a particular part of the plant, *ipso facto*, constituted a pair of Mendelian characters. But the fact that both “maple” and “purple spot” are simultaneously present in the hybrid shows that these two characters do not constitute a pair, but are members of distinct pairs. The generalisation, however, in regard to the common location of the two members of a pair of characters, and the converse of this generalisation are saved by the fact that there are two layers in the seed-coat of the pea, an outer and an inner, and that the pigment to which the “mapling” is due is lodged in one of them and the pigment which

gives rise to the purple spots is situate in the other.

The second hybrid generation produced by the self-fertilisation of the hybrids just described shows at once what the pairs of characters involved in this cross are. It consists of nine plants, the seed-coats of which bear both "maple" and "purple spot," three with "maple" seed-coats only, three with "purple spot" only, and one with neither "maple" nor "purple spot," but a pale homogeneous grey coat, amongst every sixteen plants, on the average. The cases of a 9 : 3 : 3 : 1 ratio in the second hybrid generation, which have already been described, at once show what the two pairs of characters are. In these cases, it will be remembered, the individuals which occur in the ratio of nine possess two dominant characters; the two lots, which occur in the ratio of three, possess respectively the dominant member of one pair and the recessive of the other; whilst the individuals, which occur in the ratio of one, possess the recessive members of both pairs. The two pairs of characters in the instance under consideration are, therefore, "maple" (dominant) and the absence of "maple" (recessive); and "purple spot" (dominant) and the absence of "purple spot" (recessive). Cases such as this have given rise to the theory that one (the dominant) of the two characters, which make a pair, consists in the presence of something, and that the other (the recessive) consists in the absence of that something. The theory has been called the Presence and Absence hypothesis. The reader who

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is reminded of logical exercises, and suspects that this theory, like other products of the imagination, may bear but a very distant relation to actuality, may discover that his suspicion is happily—to a large extent, at any rate—without foundation by making the cross which I have described, if he has a few square yards of ground at his disposal; when he will obtain about once in every sixteen plants, in the second hybrid generation, a plant bearing peas in the seed-coats of which the two absences of “maple” and “purple spot” are combined—peas which can be seen and handled.

We have dealt in this chapter with pairs of characters which are inherited in complete independence of one another, i.e. with cases in which characters belonging to one pair are unaffected by characters belonging to another, and have come in view of a simple theory of the nature of dominant and recessive characters. The further consideration of this theory will be dropped for the present, to be resumed in the chapter after next. In the next chapter we shall deal with cases in which characters, belonging to one pair, are very profoundly affected by characters belonging to another pair.

## CHAPTER VIII

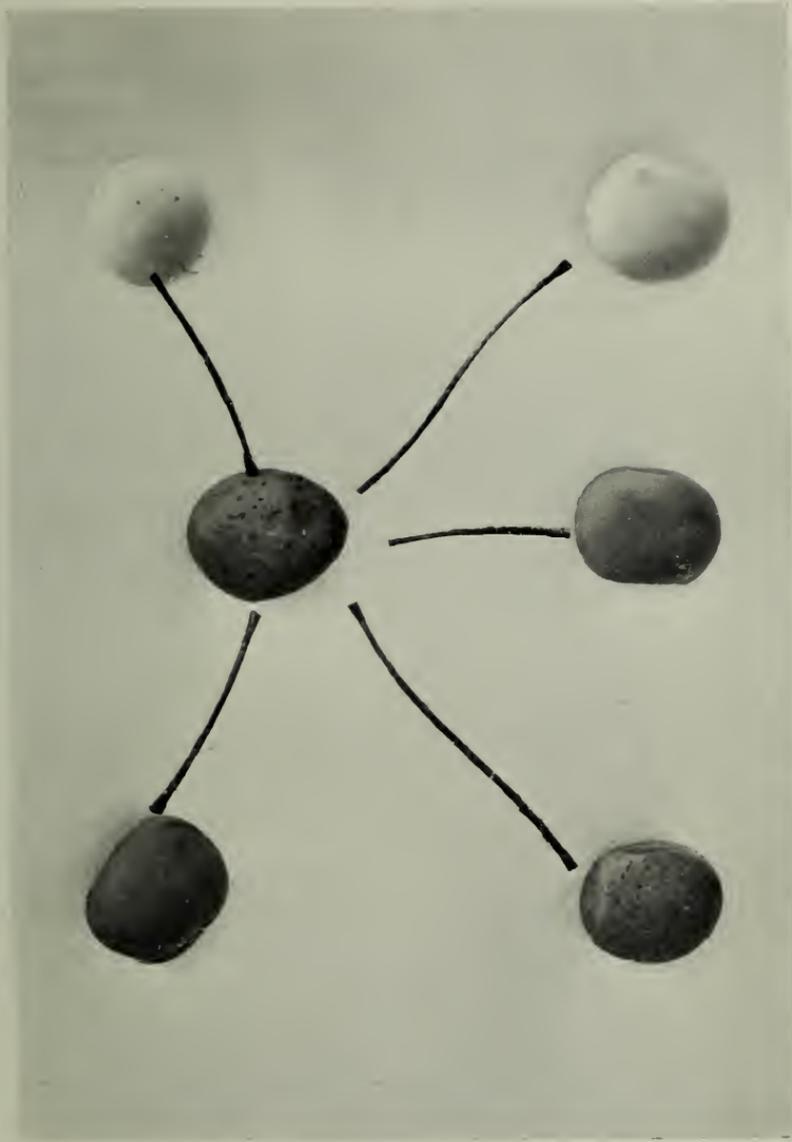
### THE INTERPRETATION OF REVERSION

FOR instances of reversion which may be explained in the light of Mendelian facts of inheritance we can again draw on the characters of *Pisum*. One of the characters with which Mendel experimented was the colour of the seed-coat, which was either grey (dominant) or white (recessive). The grey seed-coat might, or might not, be marked with the purple spots which contributed to the subject matter of the last chapter. We are now concerned with the grey seed-coat which is stated to be destitute of the purple spot. As a matter of fact, purple spots are present, but they are very faint and scarcely discernible. So that the difference between the two kinds of greys is not that one has, and the other has not, purple spots, but that one has pronounced purple spots (which have already been seen in one of the parents of the cross described in the last chapter, Fig. 26) and the other scarcely discernible ones (which cannot be seen in the pea to the top left of Fig. 27). The latter will be referred to simply as grey to avoid circumlocution; the former as grey with purple spot. We are now concerned with the spotless grey (Fig. 27, top left), and with the pure white, which is shown at the top right of Fig. 27. When

"Grey."

"Grey with purple spots."

"White."



"Grey with purple spots."

"Grey."

"White."

FIG. 27.—THE RESULT OF CROSSING GREY WITH WHITE SEED-COAT IN *PISUM*



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peas characterised by these two types of seed-coat are crossed, the resultant hybrid may either have a seed-coat like the grey parent or it exhibits the full purple spotting. This latter result is shown in Fig. 27, the hybrid grey seed-coat with purple spots being seen below and between the two parent forms. The hybrid here possesses a character, the purple spotting, which is absent from both parent forms, but exists in the wild pea found in Palestine and elsewhere, which probably corresponds more closely than any other to the wild ancestral form from which our cultivated peas have descended. The reappearance, therefore, of this purple spotting as the result of a cross between two forms, neither of which possesses it, constitutes a typical instance of reversion or throwing back.

The second hybrid generation, produced by the self-fertilisation of these reversionary hybrids, consists of peas with purple-spotted grey seed-coats, peas with grey seed-coats, and peas with white seed-coats, in the ratio of 9 purple-spotted grey, 3 grey, and 4 white. This is an entirely new proportion, the meaning of which is not at first sight obvious. The theory which has been put forward to explain it is as follows: It is supposed that two pairs of characters are involved in this cross: they are "grey" and "absence of grey"; and "purple spot" and "absence of purple spot"—exactly as in the instance described at the end of the last chapter, "maple" and its absence, and "purple spot" and its absence. But in the instance now under con-

sideration the results are supposed to be complicated by the fact that one of the characters of one pair is affected by a character belonging to the other pair. It is supposed that the character "purple spot" can only exist in a pea which has a grey seed-coat. In other words, the character "purple spot" cannot be manifested unless the character "grey" is also present. But the character "grey" can be manifested in the absence of the "purple spot." If there was not this connection between the characters of two distinct pairs we should expect the composition of the second hybrid generation to be analogous to that which we have seen to follow from other instances in which two pairs of characters are involved. We should expect it to consist of 9 grey with purple spot (two dominant characters), 3 grey, but without purple spot (one dominant and one recessive character), 3 purple-spotted, but without greyness of seed-coat (one dominant and one recessive character), and one white, i.e. without purple spot or greyness (two recessive characters): an ordinary 9:3:3:1 proportion. This is what we should expect if we did *not* suppose that purple spot and greyness of seed-coat were connected in the manner stated above, viz. the impossibility of the manifestation of purple spot in the absence of grey; and the possibility of the manifestation of grey in the absence of purple spot. Now, let us see how this supposition affects the 9:3:3:1 ratio. The second 3 represents three plants the seed-coats of which would exhibit purple spots on a white seed-coat on the supposition

## INTERPRETATION OF REVERSION 117

that purple spot was not dependent on the simultaneous presence of grey for its manifestation. But on the supposition that the purple spotting cannot exist in the absence of grey, the seed-coats of these three plants will be simply *white*, and, therefore, indistinguishable from the single *white* plant occurring at the end of the series, in the ratio of one in the whole sixteen. The first 3 in the series will not be affected by this supposition, because grey can exist in the absence of purple spot; nor will the 9, because both characters are present. The second hybrid generation will, therefore, consist, according to this theory, of nine plants the seed-coats of which are grey with purple spot, three grey and four white. And this, it will be remembered, is the result which was actually obtained. Of course, the fact that the theory harmonises with the facts does not prove that the theory is true. Its truth can only be tested by finding out whether all the consequences which follow from it actually occur.

But assuming that it is true—and I, for one, believe that it approximates fairly closely to the truth—it brings us within reach of an explanation of one of the phenomena with which the breeder is most familiar, namely, that of reversion, or throwing back. Reversion on crossing, in such cases as those which we have been considering, is due, according to this theory, to the reunion in one individual of two characters, the simultaneous presence of both of which is necessary for the existence of the ancestral character. In the instance discussed above, the

purple spotting of the wild ancestor of our culinary peas depends on the co-existence in one individual of two characters, the purple spotting itself and a grey seed-coat. At some period, probably after the pea had been domesticated, these two characters became separated; how, we cannot do more than guess. And the reappearance of the ancestral character on crossing is due to the union of two individuals one of which has one, and the other has the other, of the two characters necessary for the production of the ancestral character.

Another instance of reversion is afforded by the colour of the flower of the culinary pea. The three colours known are shown on Plate IV. On the right is shown the commonest type, the pure white flower; on the left is what may be called the pink flower; the flower is not however, as a matter of fact, equally pink over its whole extent, the outer single petal, the "standard," is nearly white, and the paired inner ones, the "wings," are salmon pink, the keel, enclosed by the "wings," is white with green veins.

Between these two flowers, and above them, is the so-called *purple* flower, which approximates most closely in its colour to that of the wild ancestor of garden peas. The standard is a pale purple in which the blue is in excess of the red; the wings are a dense purple in which the red preponderates over the blue.

When a pink-flowered variety is crossed with a white-flowered one, the result is a purple-flowered plant. The pink and the white flowers on Plate IV.



PLATE IV.—MENDELIAN INHERITANCE OF THE COLOUR OF THE FLOWER IN THE CULINARY PEA

Two flowers of a plant  
of a pink-flowered race.

Two flowers of a plant produced by  
crossing the pink with the white.

Two flowers of a plant  
of a white-flowered race.



## INTERPRETATION OF REVERSION 119

are from plants belonging to pure pink-flowered and pure white-flowered races respectively; and the purple flower is from a plant of the first hybrid generation produced by crossing these two races.

These purple-flowered hybrids produce, when self-fertilised, a second hybrid generation which consists of purple-flowered, pink-flowered, and white-flowered plants in the ratio of 9 : 3 : 4 respectively. The explanation of this case is precisely similar to that suggested to account for the result of crossing a grey- with a white-seed-coated pea. But it was not so obvious in the present case, for a reason which will be given shortly. The two pairs of characters in this case are supposed to be "blue" and "absence of blue," and "pink" and "absence of pink"; but the blue, like the purple spot, cannot be manifested in the absence of the pink; so that the composition of the second hybrid generation which, if the blue could be manifested in the absence of pink, would be—

9 Pink and Blue	. . .	[= Purple]
3 Pink and not Blue	. . .	[= Pink]
3 Blue and not Pink	. . .	[= Blue]
1 not Blue and not Pink	. . .	[= White]

is, as a matter of fact—

9 Pink and Blue	. . .	[= Purple] i.e. 9 Purple
3 Pink and not Blue	. . .	[= Pink] i.e. 3 Pink
3 Blue and not Pink	. . .	[= White] } i.e. 4 White
1 not Blue and not Pink	. . .	[= White] }

The type of second hybrid generation which has been met with twice in this chapter deserves further

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consideration. It may be expressed in general terms in the following scheme :—

[Parents]	Pale form	×	Colourless form
[First Hybrid Generation]	Dark form		
[Second Hybrid Generation]	3	Pale form	
	9	Dark form	
	4	Colourless form	

The three categories are written in this order, 3 : 9 : 4, instead of 9 : 3 : 4 for a reason which will shortly appear. The manner in which the two cases which we have considered fit into this scheme is as follows :—

*Seed-coat Colour*

[Parents]	Grey	×	White
[First Hybrid Gen.]	Grey with purple spots		
[Second Hybrid Gen.]	3	Grey	
	9	Grey with purple spots	
	4	White	

*Flower Colour*

[Parents]	Pink	×	White
[First Hybrid Gen.]	Purple		
[Second Hybrid Gen.]	3	Pink	
	9	Purple	
	4	White	

It will also be apparent, on reflection, that the phenomena of the inheritance of colour observed in the mice fits into the same scheme :—

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[Parents]            Fawn and white ×        White  
                           with pink eyes    |    with pink eyes

[First Hybrid Gen.]        Grey with black eyes

[Second Hybrid Gen.] 1 Fawn or lilac, with pink eyes  
                                   2 Grey or black, with black eyes  
                                   1 White with pink eyes

The attempt to fit this last case into the scheme brings out another point—the similarity of the proportion 1 : 2 : 1 to that of 3 : 9 : 4. This similarity should, however, be merely accidental, because the 3 : 9 : 4 (or 9 : 3 : 4) is supposed to follow from the 9 : 3 : 3 : 1 ratio, and its connection with the 1 : 2 : 1 ratio is thus very remote and devious. For my own part, I am inclined to think that the resemblance is not accidental. I find it difficult, for instance, to regard the fact that in both the 3 : 9 : 4 and the 1 : 2 : 1 the colourless forms occur in the proportion of 25 per cent. of the generation as a mere fluke, and entirely without significance. But I do not think that it is profitable to discuss this matter until more cases of second hybrid generations, in which these ratios are said to occur, have been bred on a scale large enough to satisfy statisticians that they really do occur.

For instance, in the case of the mice, it is possible that the ratio in that case is 3 : 9 : 4 and not 1 : 2 : 1. And the question which of the two it is has still to be decided.

Moreover, in this chapter I have been merely concerned to point out that certain cases of reversion

can be easily described in terms of Mendelian hereditary processes.

The reader should be familiar by now with the manner of inheritance of Mendelian pairs of characters in the result of crossings in which only one such pair is involved, and in crossings in which two such pairs are involved; and with those cases in which the members of one pair of characters exert no effect on members of another pair, i.e. in which cases there is a 9 : 3 : 3 : 1 ratio in the second hybrid generation; and also with those cases in which a member of one pair of characters depends for its manifestation on the presence of a member of another pair, in which cases there is a 9 : 3 : 4 ratio in the second hybrid generation.

Our review of the main phenomena of Mendelian inheritance is now concluded. Most of the illustrative cases are such as can be bred by the reader if he has the curiosity to do so. A full description of the conduct of a breeding experiment, together with the names of the varieties which exhibit the characters referred to, will be found in Chapter X.

We now pass on to the subject alluded to at the end of the last chapter, namely, the nature of the Mendelian pair of characters. This question is of the greatest interest to the practical breeder and to the investigator. But we are as yet very far from a satisfactory answer to it. The work of the practical breeder would be greatly simplified by the possession of some simple rule which would tell him before he

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made his crosses which characters would behave as dominants and which as recessives. To the biologist, some conception of the nature of the Mendelian pair of characters is a necessary preliminary to any attempt to estimate the true significance of the Mendelian phenomena.

## CHAPTER IX

### THE NATURE OF THE MENDELIAN PAIR OF CHARACTERS

A QUESTION which naturally and frequently presents itself to the mind is: "What is it that makes one character dominant over another when they meet in a cross?" A common answer to this question is that the dominant character is strong and the recessive one is weak; but this is too vague a notion to be of the nature of an explanation; moreover, it is, in fact, little more than a restatement of the difficulty involved in the question.

Before proceeding to the two theories which appear to be worthy of consideration, I think it is desirable to warn the reader against an idea, which has found its way into print, that there is some connection between selection and dominance; that a dominant character is the result of a long process of selective breeding. There is no ground whatsoever for such an idea, and it is difficult to imagine how it can have arisen.

Two theories of the nature of the Mendelian pair of characters, and of the cause of dominance in particular, have obtained wide credence. One of them has already been exploded, the other is still supported by a considerable party of adherents.

The first of these is the idea that the oldest of

the two members of a pair of characters is the dominant. When, for instance, one of the members of a pair of characters is that borne by the species in which the character occurs in its wild state, and the other only occurs in a state of domestication, it would be supposed, according to this theory, that the "wild" character, being the older, would be the dominant, and the "domesticated" one, being the more recent, would be the recessive. In mice, for instance, the grey of the house mouse would be expected to be—and is—dominant over the white of the albino. Now, there are a great number of cases which support this theory. For instance, the dominant members of the pairs of characters presented by the cotyledons in *Pisum*—yellow and round—both occur in the wild specimens of the wild *Pisum* which have been examined. There are, however, a number of cases in which this theory breaks down entirely. For instance, the single comb in the domestic fowl, which is known to be the form of the comb in the wild ancestral stock of the jungle, is recessive to the "rose" and to the "pea" comb. The absence of a tail in rumpless breeds of fowl is dominant to the ordinary tailed condition which characterises the majority of domestic breeds, and, of course, the wild representatives of the species. So this theory falls to the ground.

We see, therefore, that though many characters of wild species are dominant to their domesticated counterparts, the fact that certain of them are not dominant suggests that, in those cases where they

are, dominance is not simply due to the fact that the character in question belongs to the wild species; and that some other cause must be sought for.

This is suggested by the second theory. The reader will remember that, in order to explain the result of crossing a pea with a maple seed-coat with a pea with a purple-spotted one, we invented the theory that, in this case, the pair of characters did not really consist of two characters, like yellow and green, but of a particular character, maple, as the dominant member, and the mere absence of this character as the recessive member of the pair. And the impression may have been given that this theory was only invoked to explain an outstanding case. So far from this being the case, this theory, which is called the Presence and Absence hypothesis, is now being applied to all the other Mendelian characters. In many cases the fitness of this application is at once obvious. In the case of eye-colour in man, for instance, the duplex character which is dominant, is due to the presence of the brown pigment, and the recessive character, simplex, is due to the absence of this pigment. Stated in its most general terms, this theory is that the dominant character is due to the presence of something, and the corresponding recessive character is due to the absence of that something. It will be perceived that this conception of the constitution of the Mendelian pair of characters differs profoundly from that which we should naturally derive from a contemplation of, for instance, the seven pairs of characters studied by Mendel. In all these seven

cases the recessive character appears to be as much due to the presence of something as the dominant one—greenness as much as yellowness, wrinkledness as much as roundness, and so on; and it appears that in these seven cases we really are dealing with seven genuine pairs of two equally real characters, and that in no case is one of the characters merely the absence of its counterpart. But we shall see that not only can the presence and absence hypothesis be made to apply to these cases, but that it probably throws much light on the real nature of these characters.

The application of this theory to the characters of the cotyledons does not consist merely in the statement that wrinkledness is simply the absence of roundness. That would be a mere juggling with words. The application of this theory consists in the statement that wrinkledness is due to the absence of that which determines roundness. And this raises the question: What is it that determines roundness? To answer this question it is necessary to consider the part played by the cotyledons in the economy of the plant. They are, as the reader is probably aware, storehouses of food material on which the young plant depends almost exclusively from the moment at which germination begins until the young plant has attained a height of about six inches.

This food material is, of course, laid down in the cotyledons whilst the seed is still in the pod. It first appears in the form of a sugary solution, and as the seed matures, this sugar is gradually converted

into starch. This starch is in the form of grains which, in the case of the round pea, may be best described as potato-shaped. They are shown in Fig. 28. These grains can easily be seen, in the following way: A dry round pea is soaked in water for twenty-four hours; a thin slice is then cut off with a razor, the cut surface of the pea is then wetted with a drop of water, and scraped. The whitish fluid scraped off will be found to consist almost entirely of these starch grains, when examined through the microscope.

If the starch grains of a wrinkled pea (Fig. 29) are examined in the same way they will be found to present a very different appearance from those of the round pea, for whilst the latter are entire, the former are compound; their substance is subdivided by radiating strands of a refringent yellow matter. Moreover, whilst the grains of a round pea are distinctly elongate, those of a wrinkled one are roughly circular, if we neglect the indentations caused by the radiating strands.

It is evident, then, that the starch is in a different state in the round pea from that in which it occurs in the wrinkled. The probable nature of this difference is indicated by the following experiment: If a round pea is weighed, and then soaked in water for twenty-four hours, and then weighed again, the weight of water absorbed can be determined. If this weight is then expressed as a fraction of the weight of the dry pea, a certain figure, which I have called the "absorptive capacity," is obtained. The

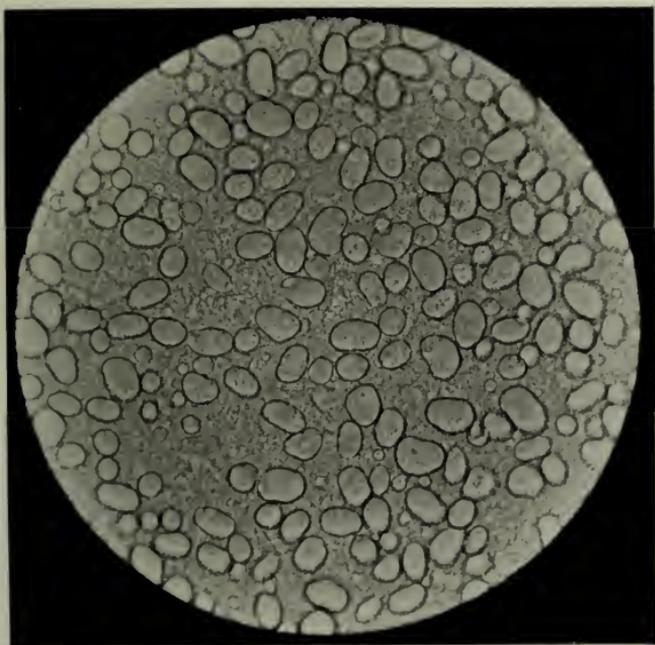


FIG. 28.—STARCH GRAINS OF ROUND PEA  
Magnified about 300 times.

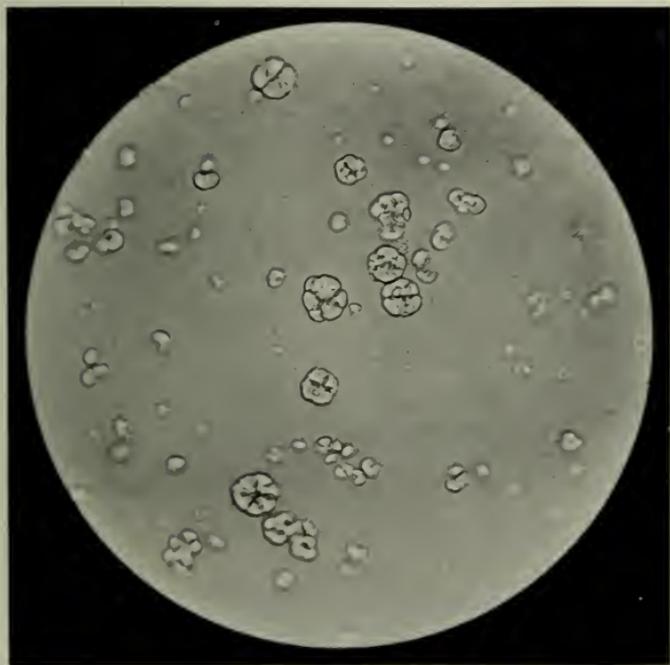


FIG. 29.—STARCH GRAINS OF WRINKLED PEA  
Magnified about 300 times.



amount of water absorbed by a round pea in twenty-four hours is about 80 per cent. of its weight when dry. In other words its absorptive capacity is 80. It does not absorb its own weight of water in twenty-four hours. A wrinkled pea, on the other hand, absorbs more than its own weight of water in twenty-four hours. Its absorptive capacity is about 120.

The cause of this difference is probably that, in the case of the wrinkled pea, the whole of the sugar is not converted into starch. In fact, the wrinkling itself, which takes place during the ripening of the seed, is probably due to this incomplete conversion of the sugar into starch. All peas, wrinkled as well as round, are round before they are dry; that is, in the state in which they are eaten. Cooks think that all peas are round. It is only gardeners, who sow or harvest the dry seed, who know the distinction between round and wrinkled. Wrinkled peas wrinkle because more water escapes from them than from round peas; and more water escapes from them because water can escape from a sugary solution more easily than it can from the grains of starch. The water is, so to speak, locked up in the solid starch grain much more securely than it is in a solution of sugar.

It is not possible—at any rate it would be very difficult—to measure the relative amounts of water given off by round and by wrinkled peas during the process of ripening. But what can be done is to measure the converse of this process, namely, the relative amounts of water taken up by round and wrinkled

peas when they germinate; for, inasmuch as round and wrinkled peas are equally round before they lose their water, and are equally round when they have taken it up again, we have some ground for assuming that each kind takes up as much when it germinates as it loses when it ripens. The fact, therefore, that a wrinkled pea takes up more water than a round one does, when it germinates, may be taken to mean that it loses more than a round one does when it ripens.

The theory that less of the sugar in the wrinkled pea is converted into starch is supported by the well-known fact that wrinkled peas are sweeter than round ones, and also by the fact that all the favourite eating peas on the market are wrinkled ones.

We are now in a position to give tentative answers to the questions: What is it that determines roundness? and, What is it that determines wrinkledness? and then to indicate the way in which the presence and absence hypothesis applies to this pair of characters.

In a round pea, it would seem that all the sugar is converted into starch; in a wrinkled one, only part of it is; and the wrinkling is primarily due to the escape of the water from the solution of sugar left over after ripening; and, consequently, in the last resort, due to the *absence* of that which completes the conversion of the sugar into starch or, at any rate, to an insufficiency in the quantity of that substance, whatever it is. The round pea has the full dose—to use Mr. Bateson's phrase—of this

substance; the wrinkled pea an insufficient dose. Something is absent from the wrinkled pea which is present to the full in the round.

It will be gathered from the above that the object of our inquiries is not merely to analyse an organism into its component characters and to leave the matter there, but to push deeper and obtain some insight into the fundamental nature of these characters. The reader will do well to lay it to heart that in the case of the pair of characters, roundness and wrinkledness, which Mendel placed first on his list of the seven with which he experimented, we are at present only on the threshold of an investigation of the true nature of the characters themselves.

The application of the presence and absence hypothesis to the other pair of cotyledon characters will now be considered. The two characters which meet the eye are yellow and green. But the matter is not so simple as this. Mr. Bunyard has shown that there is a yellow and a green pigment *both* in the yellow *and* in the green cotyledon. When both are present at the same time, as in the ripe but still moist pea, the green masks the yellow. All peas, both yellow and green varieties, are green when they are eaten. Just as cooks think that all peas are round, so they think that all peas are green. It is only gardeners who sow and harvest them who know the distinction between yellow and green.

The ripe but still moist cotyledons of both yellow- and green-seeded varieties are, therefore, green. The yellow kind become yellow as they ripen; the green

do not change colour during this process. The yellowing of the former is brought about by the gradual fading and disappearance of the green pigment, which thus leaves the yellow pigment (which is present in both kinds) exposed. The successive stages in the fading of the green can be easily observed. The simultaneous presence of both green and yellow pigment in yellow and in green peas has also been demonstrated.

To sum up, green-seeded varieties contain two pigments in their cotyledons, a yellow and a green; neither of them fade during the process of ripening, and, inasmuch as the green masks the yellow, the ripe seed is green. Yellow-seeded varieties also contain the same two pigments, but the green fades during the process of ripening; so that the ripe seed is yellow. This fading of the green pigment in the yellow pea is supposed to be brought about by the *presence* of some substance which is *absent* from the green pea.

It is not possible to indicate the manner in which this presence and absence hypothesis applies to the remaining of the seven characters dealt with by Mendel, except, of course, in those cases in which its application is obvious—for instance, to the colour of the seed-coats, which may be grey or white. It would be easy to say that normality of stem was due to the presence, and fasciation to the absence, of some factor controlling the normal succession of nodes in the stem; but this is doing no more than re-stating the problem in other terms. And until

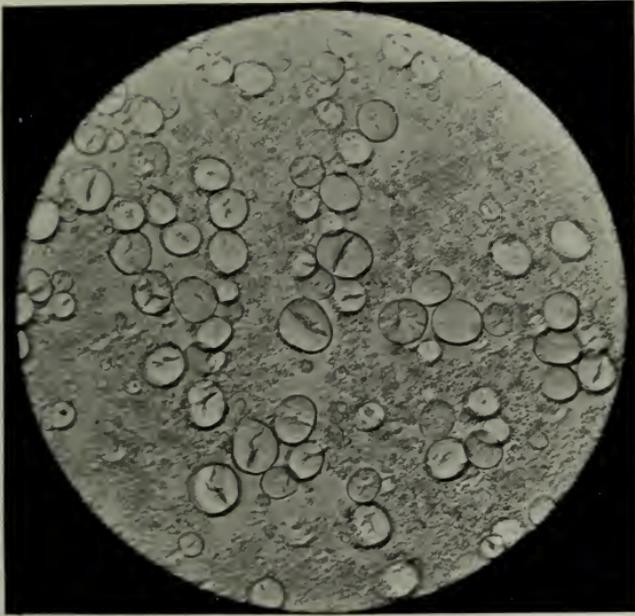
an exhaustive inquiry into the causes determining the nature of these two characters—normality and fasciation—has been carried out it is absurd to attempt to interpret them by means of any theory whatsoever. With regard to tallness and dwarfness, a start has been made by Mr. Keeble, who has shown that tallness depends on two characters, length and (rather curiously) thickness of internode; dwarfness depends on the absence of both of these qualities. Peas which possess only one of them fall into the category known as half-dwarf.

Before we leave Mendel's seven characters it will be well to pay some attention to a question which can be most conveniently discussed here, though it may seem that none of the questions so far dealt with in this chapter are worth discussing until it has been answered—and in the affirmative, too. The question is, Is there such a thing as dominance? Does one character hold the stage in the first hybrid generation to the complete exclusion of its partner? If an affirmative answer cannot be given to these questions, what reason is there in discussing the causes determining dominance, a thing whose reality has not yet been established? But in the present case it is desirable to present a consistent scheme of the whole set of phenomena, and then to consider to what extent it is justified. Let us take the first pair of characters, cotyledon shape. If we content ourselves, as the impressionist does, with the mere impression produced on the unaided eye, the answer to the question in regard to the existence of dominance

is an unqualified affirmative. A round is crossed with a wrinkled, and the hybrid is a round, indistinguishable from the pure parent round. But if we refuse to be content with this impressionist aspect, and set about to find out as much as possible about the true nature of wrinkledness and roundness, both in the pure and in the hybrid rounds, we shall find that the matter is not by any means so simple.

The starch grains of pure round and wrinkled peas have already been dealt with. Those of the round are elongate and entire, those of the wrinkled are circular and compound, the number of component pieces varying between 2 and 8, the commonest number being 6.

The starch grains of the cotyledons of the first hybrid generation are shown in Fig. 30. They constitute about as complete a blend between the two parental types as can be imagined. In the first place the grains are intermediate in shape; this has been demonstrated by measurements. They are also intermediate in compoundness, in two ways; in what may be called the distribution of compoundness, some of the hybrid grains being compound and some of them single; and, secondly, in what may be called the degree of compoundness of those grains which are compound; the number of component pieces in the hybrid is intermediate between the number in the starch grains of the wrinkled pea and entirety, as we may name the feature presented by the grains of round peas. The number of component pieces in those hybrid grains which are compound varies



**FIG. 30.—STARCH GRAINS OF A CROSS  
BETWEEN A ROUND AND A WRINKLED  
PEA**

Magnified about 300 times.



between 2 and 4, and the commonest number, based on a large number of counts, is 3.

It is only to the superficial observer that dominance is complete in this instance, the first character dealt with by Mendel. The microscope at once reveals the fact that the pure and hybrid rounds, though externally indistinguishable, are in fact of radically different constitutions. This fact is also revealed by a determination of the absorptive capacities of the pure parental and hybrid rounds. It will be remembered that the absorptive capacity of the wrinkled pea was stated to be about 120, and that of the pure round 80. The absorptive capacity of the hybrid round is almost exactly intermediate between the two.

The hybrid round, therefore, is seen to resemble the pure only in the fact of being round, and to differ in what must be regarded as more fundamental properties; and it is probable that with further inquiry the number of cases in which simple dominance occurs, i.e. where the hybrid is identical with the dominants, will be greatly reduced.

The following considerations are suggested by the facts set forth in this chapter. In the experimental study of heredity, it is not sufficient to find that round and wrinkled, or any other characters, constitute a Mendelian pair, and are inherited in Mendelian fashion. Some attempt must be made to get behind the appearance of roundness, for instance, and to find out what roundness really consists in. If no such attempt is made the fact

that the result of a cross between a round and a wrinkled is *apparently* a round identical with the round parent, but is in reality a blend between the round and wrinkled, is entirely missed. The vulgar reluctance to be clear in the mind as to the things which are represented by words used has not been without its effect on the complexion of the Mendelian doctrine as expounded by the less considerable of its adherents. When a character has been found to behave in Mendelian fashion in inheritance, it is considered that the nature of the character and its mode of inheritance have been determined; and that any further investigation of the matter is superfluous. In this way a great many instances of characters which apparently behave in a Mendelian way in inheritance have been accumulated. But as to the essential nature of the characters themselves we are still ignorant. It is probable that, when the seven pairs of characters investigated by Mendel have been thoroughly worked out, the terms now used to designate these characters will have no more than the most remote application to them, and that, for the purpose of accurately representing the essential nature of these characters, they will be wholly valueless.

It is here that the value of a theory like the presence and absence hypothesis comes in. This hypothesis leads to the investigation of the nature of the characters themselves. This is its chief value. If it does not do this, if it is used merely to restate already known facts in new terms, it is

useless. But if it stimulates an investigation of the nature of characters described as Mendelian, it is justified.

How far the truth of this hypothesis is borne out by the available evidence is an entirely different question, which will now be discussed. There is a large number of pairs of characters to which this theory obviously applies. There are also a number of cases, like cotyledon shape and colour, which this theory correctly describes, though the manner of application is not at first sight easy to see. But there is also a considerable number of cases which constitute obstacles in the way of its general application. For instance, there are certain cases where apparently the same character is dominant in one animal, or plant, and recessive in another. For instance, the possession of horns is dominant in sheep, but recessive in cattle, to the hornless condition; white in pigs appears to be dominant to black, but recessive to it in sheep; and, lastly, the dissection of the margin of the leaf is dominant to the entire condition of the edge in the nettle, and recessive to it in *Chelidonium*. It is doubtful in this last case whether the condition of entirety is of the same nature in the two cases; but the possession of horns in cattle and sheep certainly would seem to be.

Then there is a further set of cases, in which the dominant character seems to consist in the *absence* of something and the recessive in the *presence* of that something. For instance, the possession of

five heavily pigmented, brown bands in the snail of the hedgerows (*Helix hortensis*) is *recessive* to the pale yellow, entirely bandless condition. Again, it is not, at present, easy to see how the fact, discovered by Mr. Biffen, that susceptibility to the attacks of "rust" in wheat is dominant to immunity from such attacks can be brought in line with this hypothesis. In the case of the snails, it must be supposed that the possession of bands is due to the absence of something which is present in the pale yellow snail and prevents them appearing. In the case of the wheat it must be supposed that resistance is due to the presence of some anti-toxin, and susceptibility to the presence of some substance which prevents the formation of the anti-toxin. With further inquiry the scope of this hypothesis can be better estimated; at present its chief service is that it stimulates this inquiry.

Another point raised by this Presence and Absence hypothesis can be brought out by comparing it with Prof. de Vries's conception of the Mendelian pair. This theory, as stated in the first chapter, is that specific characters blend on crossing; but that varietal ones exhibit Mendelian phenomena. The reason for this is that the specific characters are new creations, isolated and without partners, whilst varietal characters are the result of the transference of an already existing character from one state to another, as, for instance, from the patent to the latent, or vice versa. Thus when one organism is crossed with another from which it differs in the

possession of a specific character, this specific character meets nothing in the other organism corresponding to it, and the result is a permanent blend. Such crosses are called unisexual. But if one organism is crossed with another from which it differs in the possession of a varietal character, the particular character in a patent state in one organism meets the same character in a latent state, in the other organism, and the result may or may not be a blend, but is invariably segregation. These crosses are called bisexual, or balanced crosses, the latter of which is a much better term. Prof. de Vries's theory of the nature of the Mendelian pair differs from the presence and absence hypothesis in that, according to him, the pair consists of a character in an active or patent state (dominant) and the same character in a latent state (recessive); whilst according to the other theory the dominant member of a pair of characters consists in the presence of something and the recessive in the complete absence, not the latency, of that something. It is premature to hold the scales between these two before a much greater body of evidence bearing on the question is available. The investigation designed to furnish this evidence must start from a perception of an essential difference between the two theories; the most important of these, in my opinion, is the difference, according to the two theories, between the constitution of the recessives. According to the one theory, the recessive is the dominant character in a latent state; according to the other, it is the absence of

the dominant character. Now, in the latter theory the recessive character is nothing; there is no difference, according to it, between the absence of fasciation and the absence of greyness of seed-coat—a point which deserves careful consideration. And one way of attacking the question of the relative truth of the two theories is to find out if the recessive members of, say, Mendel's seven characters are identical, or if they do not each manifest something corresponding to their dominant counterpart.

## CHAPTER X

### THE CARRYING OUT OF A BREEDING EXPERIMENT WITH A PLANT

I HAVE two objects in view in dealing with this matter: first, to render the reader familiar with the means by which the facts which have already been related have been determined, and in particular to give directions for the repetition of the actual crosses made by Mendel; and, secondly, to lead up to an exposition of Mendel's theory, through a familiarity with the germ cells themselves, acquired by actually handling them.

I think it may be said that in the case of no other branch of science can results of such interest be obtained at so small a cost. The experiments by means of which the high-water mark of modern chemistry has been reached, such as—to take an instance at random—the determination of the properties of radium, are so expensive that there are few who can command the means to perform them, and they are practically outside the reach of the great mass of teachers of chemistry altogether. But in the case of that branch of biology which, rightly or wrongly, has attracted a share of interest which is comparable with that attracted by radium in chemistry, the case is very different. The obser-

vations made by Mendel can be repeated by anyone who has, or can obtain the use of, a few square yards of ground; the expenses in addition to this are trifling, and amount to no more than the few shillings which will buy the seeds and the pea-sticks. And anyone who has a kitchen garden, and room to spare in it, can contribute new results of great value with very little extra outlay.

The following directions are based on six years' experience in my own garden.

It is desirable that the ground in which peas are to be grown should be deeply dug in the autumn before the spring in which the seeds are to be sown. My own ground was dug two spits deep, and an ample quantity of farmyard dung incorporated with the bottom and with the top spit. If the land is at all clayey, it should be well limed; but if it is coarse, open and sandy, chalk should be used instead of lime. During the digging a sharp eye should be kept open for wireworms (the larvæ of the skipjack beetle); for if many of these are left in the ground they will play havoc amongst the seedlings in the spring. It is well to remind those who are not familiar with wireworms that they are very tough, and that it is therefore necessary to pull them in two, to make certain that they are destroyed.

The first week in March is the earliest date at which it is advisable to sow the seed; for even when seed is sown at this time the seedlings do not begin to break through the ground until the beginning of April. The chief enemies of the swollen seeds, before

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the seedlings have shown above ground, are mice; and these vermin must be destroyed once and for all, with a stern hand. When the seedlings have begun to unfold their leaves they are by no means free from enemies, either above or below ground. But the subterranean enemies are now no longer mice, but wireworms. The signs of the attack of one of these on a plant are unmistakable. The leaves of a seedling which has been making vigorous growth will one day be seen to flag and droop; if the soil round the underground part of the stem is examined, a wireworm will in nine cases out of ten be found there. The enemies above ground are birds, and these are best guarded against by nets hung loosely over the rows on low sticks. Having now dealt with the enemies of the peas during their earlier stages, we may revert to the actual sowing of the seed.

The seed should be sown in drills, which should be drawn with an ordinary hoe. Adjacent drills in the case of tall peas should never be closer than six feet asunder. What may be gained in an increase in the number of plants by planting the rows closer will be lost in a decrease in the quality and quantity of the seed produced by the plants, and in a lowering of the health of the plants themselves. I can most heartily endorse the opinions on this matter expressed in that most excellent of all books on gardening, William Cobbett's "English Gardener," published in 1838.

The seed should be sown between two and three

inches deep in the ground. The distance of the seeds apart depends on whether it is desired to produce as large a number of plants as possible in a given space, or as large a number of seeds as possible per plant. In the former case, it is not advisable to place the seeds nearer than three inches apart in the drill, but two rows may be sown in one drill, three inches apart from each other, in such a way that a seed of one row is opposite an interval in the other row. If seeds are sown thicker than this, I find that there is a danger of weaker plants being fatally overshadowed by their better-favoured fellows, or, at any rate, of their being prevented from flowering or setting seed. In the case in which it is desired to obtain as many seeds as possible per plant, the seeds may be sown at least nine inches apart in a single row in the drill. Whether, if the seeds were sown one foot apart, the plants would be able to avail themselves of the additional soil-space and light, and bear more seeds than plants grown nine inches apart, I do not know. But that plants grown nine inches apart set a vastly greater quantity of seed than plants grown three inches apart I know as the result of experiment.

It is desirable to cover the patch of ground, on which the peas are growing, with netting before the time when the pods have swollen to the size at which they are usually gathered for the table. The unripe peas at this stage constitute an irresistible temptation to birds, especially to jays and hawfinches, which can do a great deal of damage in a very short time. And

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I have sometimes lost nearly half my harvest through not netting the peas in time. The netting is effected by hanging ordinary strawberry nets over a framework consisting of stout ashen poles standing eight feet out of the ground, and long, slender horizontal ones of the same material, nailed to the tops of them. Slender poles are better than laths (which I have tried) for this purpose, as the nets can be slipped over them easily, whilst they catch on the laths. The small birds which can get through the mesh of a strawberry net do little, if any, harm.

If the poles are a good eight feet out of the ground and the net is not permitted to sag between the cross-pieces, the presence of a net does not interfere with the giving of such attention as the plants require during the summer. This attention is of two kinds: one which is always necessary, hoeing and weeding; another which may or may not be required, cross-fertilisation.

It is desirable that the ground immediately round the plants should be kept free of weeds by the hand, say, once a fortnight, and that the six feet between adjacent rows be kept free of weeds, and its surface broken by the hoe, especially two or three days after heavy rain so as to prevent the surface from caking and the water in the soil from evaporating. The Dutch hoe is best for this purpose, because with this tool it is not necessary to walk over the part which has been hoed, during the process itself.

The cross-fertilising can easily be done by any one with nimble fingers.

The pea carries its reproductive organs in its flowers ; and the brightness of the flowers is supposed to serve as an attraction to insects whose services are required to transfer the fertilising element from one flower to another. Whether the pea-flower ever required these services, I cannot say. But it is certain that it does not do so now ; for the pea is normally self-fertilised. It may be necessary to remind the reader that the reproductive organs of both sexes are present in one and the same flower in the pea, as in the majority of flowering plants. The male cells are contained in the nine yellow bodies, called *anthers*, borne on long, delicate stalks, inside the flower ; the anther together with its stalk is called the *stamen*. The female cells are contained in the rod-like structure called the *ovary*, which has a curved and tufted tip called the *pistil*. If a newly but fully opened flower of a pea be plucked and examined, it will be found to consist of the following parts : Five green "petals" encircling the flower and appearing to be continuous with the flower stalk, called *sepals* : a single, erect petal, known as the *standard* ; a pair of petals, facing one another, more or less, the *wings* ; and inside the wings a single, boat-shaped, and much stiffer and greener structure with a projecting keel, which gives this part its name, the *carina*. Inside the carina are the anthers, and, surrounded by the anthers, the pistil. If the flower is fully open, the anthers will be ripe ; that is, they will have burst and discharged their pollen grains. Each pollen grain contains a male reproductive cell. The pollen

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appears to the naked eye as a fine yellow dust, but the individual grains composing it can easily be seen by the aid of a small hand lens.

If the ovary be slit by a vertical incision, it will appear to be—what, indeed, it actually is—the future pod in miniature. It is almost exactly like the ripe pod full of peas; everything is there, but in miniature; the whole pod is not longer than one-third of an inch. Inside each of the miniature peas is a minute cell, the female reproductive cell, or egg, or ovule.

Before such an egg can develop it must unite with or, in other words, be fertilised by a male reproductive cell. In the case of a great many plants there are special arrangements by which the eggs are always fertilised by pollen from another flower, the pollen being transferred by the agency of the wind, or by that of insects. This is what is known as cross-fertilisation. But in the pea, and in many other plants as well, the ovules in a particular flower are fertilised by the pollen from the same flower. This is known as self-fertilisation. But the essential process in the two cases is the same: it is the union of a male with a female reproductive cell. In all cases of biparental reproduction, which is all we are concerned with in this book, both in plants and in animals, fertilisation consists essentially in this union of a male with a female reproductive cell, and until this union has taken place the development of the egg into the future plant or animal cannot proceed.

The pea, as has been already stated, is self-fertilised. Fertilisation occurs before the flower has opened. The fact that a flower is open is a certain sign that fertilisation has taken place. Fertilisation occurs in the following manner: At a stage in the development of the flower, shown in Fig. 31, i.e. long before the flower has opened, in



Fig. 31.—Stage in the development of the flower when fertilisation occurs.

fact whilst its petals, the only one of which to be seen at this period is the folded standard, are still of a greenish colour, the anthers burst and the pollen grains escape into the space enclosed between the two halves of the carina. In the centre of this space lies the pistil, so that it at once becomes surrounded with an immense number of pollen grains. The male reproductive cells in the pollen grains reach the ovules in the following way. Some pollen grains stick to the free end of the pistil, and each one of them sends out a structure, known as the pollen tube, which grows like a root into the tissue of the pistil and travels down it until it reaches one of the ovules. This pollen tube contains the male reproductive cell, and when this has fused with an ovule, the ovule proceeds to develop.

When, therefore, it is desired to make a cross between two kinds of peas, it is necessary to select a flower, on the plant which is to function as the female parent, of such an age that the anthers have not

## EXPERIMENT WITH A PLANT 149

yet burst in it (i.e. a little younger than the one shown in Fig. 31), that is to say, of such an age that the ovules in it have not yet been fertilised. The reader is recommended to discover the external appearance of the latest stage in the growth of the flower at which the anthers usually burst, by picking, say, ten stages in the development of the flower, ranging from a bud in which the petals do not extend beyond the sepals, to the nearly open flower. The stage, in the development of the flower, at which the pollen is set free will be found to be much earlier than was expected. A flower, at a stage of development preceding this, must be selected to function as what we may, for convenience sake, call the female parent, or female flower.

Having described the appearance of the flower suitable to function as female parent, we can proceed to a description of the method by means of which one variety may be crossed with another. A very simple set of implements is required for this—(1) a pair of fine forceps; (2) a pair of fine scissors; (3) a glass tube, or wide-mouthed bottle with cork stopper, to contain methylated spirit. A hand lens is also a desirable addition but is not a necessity.

Having selected the flower of the right age to function as female plant, the first thing is to make certain that it has not already fertilised itself, by seeing that the anthers have not yet burst (with a hand lens if available); the next thing to do is to make it impossible for the flower to be self-fertilised, and

this is done by cutting out the anthers. The reader will doubtless evolve the details of his own method of procedure in carrying out cross-pollination. For myself, I have found that a simple way of getting at the parts to be manipulated is to hold back the standard and wings, and to make a transverse tear right across one half the carina near its base, and then bend the whole of the carina in front of the tear to one side, so that the anthers and stigma project free from the part of the carina, in front of the tear. The stamens are then easily removed by nipping them off with the forceps. The forceps should then be dipped in the spirit to sterilise them, in case the anthers may have been accidentally burst during these manipulations.

The flower is now ready to receive the pollen of the flower which is to function as male parent. This should have been selected before the female flower was operated on in the manner just described, so that it may be at hand as soon as the female flower is ready.

The age of the flower to function as male parent should be older, but not much older than that which acted as female. The reason for this is not that an older flower would not contain enough pollen, but that it might contain too much; I mean pollen which does not belong to it, brought to it by bees. For though the bees who visit the pea flowers, once they are fully open, do not effect cross-pollination, because self-pollination has already taken place, they may bring to the flower some pollen from another

## EXPERIMENT WITH A PLANT 151

flower. It is, therefore, not wise to use as pollen-bearer a flower which has opened.

Having selected a bud of a suitable age, the plan I adopt is to pluck it from the plant on which it is growing, to pull off the sepals, the standard and the wings, and to snip a piece about the size of a large pin's head from the extreme tip of the carina with the scissors. This flower may, for convenience, be called the "male flower." After this operation the scissors should be dipped in the methylated spirit, so as to kill any pollen grains that may be sticking to them, and so avoid mixing them with the pollen of the next flower similarly operated on.

The female flower should now be held between the thumb and finger of the left hand, and its pistil thrust through the entrance in the tip of the carina of the "male flower" made by snipping off its tip, into the mass of pollen which is just inside, if the anthers have burst. There is no difficulty in telling whether they have or not. If they have, the pistil when withdrawn will be seen to be yellow with pollen; if they have not, it will bear no trace of pollen; which means that too young a bud was taken; in which case it must be thrown away, and an older one procured.

When the pistil of the flower which is to function as female parent has been thoroughly covered with pollen, the part of the carina in front of the tear made across it, which was slipped aside to set the pistil and anthers free, may be put back in its natural position so that it encloses the pistil; the wings

which have been folded back during the manipulation are allowed to revert to their natural position, one on either side of the carina, and the standard also allowed to return to the position natural to it in a bud of this age, shown in Fig. 31.

A bud treated in this way grows, opens, and blossoms, then withers and dies, in exactly the same way as a bud which has not been interfered with. But the course of its subsequent history, as traced in the characters of its progeny, has been profoundly altered by what has been done.

We are brought very close up against the mystery of heredity when the extreme narrowness of the channel through which the characters of organisms have to find their way between each generation is forced upon our attention, as it is by actually making a cross between, say, a tall and a dwarf. From the flower of a dwarf pea will grow out a pod containing seeds all of which will be dwarf. But if such a flower is deprived of its stamens and its pistil covered with the pollen from a tall pea, all of its offspring will be tall peas. We are thus firmly held, without any possibility of escape, and forced to recognise the fact that the character of the tall pea is contained in each one of the pollen grains, themselves scarcely visible, as individual grains, to the naked eye. This is how the problem of heredity presents itself to the mind to-day: How are the characters of the organism represented in the germ cells which produce it? The solution of this problem



Magnified about 50 times.



Magnified about 160 times.

FIG. 32.—POLLEN GRAINS OF THE  
CULINARY PEA



## EXPERIMENT WITH A PLANT 153

put forward by Mendel will be dealt with in the next chapter.

When the petals of the pollinated flower have been folded into their place a label should be tied round the stalk of the flower by means of an 8-shaped loop, one half of which encircles the flower stalk, and the other the main stem. A number, corresponding to a number in a record of all the necessary details with regard to the cross, should then be written on the label. A label bearing the same number, preceded by "f. of" (meaning "father of"), should be tied in the same manner round the stalk of the flower which furnished the pollen with which the cross was made. And nothing further need be done to it until the autumn when the pod is hard and dry (*see* Fig. 33), when the seeds can be taken out of it and put into a packet with the number on the label tied round the flower in the summer, written on it. In order to render the possibility of error as remote as possible, it is well to cut off the label and put it into the packet with the seeds.

It is convenient to describe here a system of keeping the records of my experiments which I have found to work very well. I have two classes of numbers from 1 onwards in each year—"mating numbers" and "sowing numbers." "Mating numbers," which are written on the labels tied round the crossed flowers, and on those tied round the plant which furnished the pollen, are distinguished by the year in which the cross is made; for instance, the first cross I shall make this year, 1911, will be 11.1, and

the hundredth 11.100. But it is not necessary to write the prefix indicating the year on the labels themselves, because the only crosses harvested in a given year are crosses made in that year; this prefix must, however, of course be written on the packet in which the seeds are kept, because the packets may be kept for many years. "Sowing numbers," which are written on the pegs marking where peas are sown, are distinguished by capital letters, A standing for the first year of the experiment, B for the second, and so on. But here, as in the case of the "mating number," it is not necessary to write the prefix indicating the year on the pegs, because all the pegs in the ground in any given year relate to seeds sown in that year; this prefix must, however, as in the case of the mating prefix, of course, be written on the packets in which the harvested seeds are kept.

I strongly recommend anyone undertaking breeding experiments not to use note books, but loose sheets of squared paper. The year, in full, should be written or, still better, stamped on one of the top corners of every sheet.

With regard, now, to the harvesting of the peas. A plant should be pulled up, as a general rule, when all its pods, save the uppermost one or two, are hard and dry. The stem should be pulled off as far below the level of the ground as the unaided fingers can get; it is necessary to do this because stems sometimes branch very near the ground, and the two divisions of one plant might easily be harvested as two plants if the precaution which I have advised



**FIG. 33.—TO ILLUSTRATE METHOD OF LABELLING MALE AND FEMALE PARENTS OF CROSS**



## EXPERIMENT WITH A PLANT 155

is not taken. It is not advisable to dig up the whole root of the plant, partly because it is a superfluous and inconvenient cumbrance in the subsequent dealings with the plant, and partly because the roots do good to the soil if left in it, by contributing to its humus and to its supply of nitrogen-fixing bacteria.

All the plants related to by one peg should be pulled up at once and tied together near the roots with a coarse open twine which will not cut or break the stems. The piece of twine should first be tied round the peg (notched on either side so that the twine does not slip) relating to the plants tied up. If these bundles consist of about ten plants, ten such bundles should be tied together to form a "secondary bundle." The terms "peg" to signify a bundle of peas tied up with a single peg, and "bundle" to signify a secondary bundle as just defined, have come into everyday use between myself and the assistant who helps me with harvesting. The bundles should be hung up so that the tops of the plants hang downwards in any place where they are likely to dry, and are secure from the depredations of birds, rats or mice. The likelihood of their drying properly depends partly on the dryness of the air of the shed or room they are hung in, and partly on whether they were harvested during a drought or at any rate in sunshine; or in rain or damp. It is hardly necessary to say that, if it can possibly be avoided, plants should not be harvested during wet or damp weather. I did this one year, and the recollection of the unpleasantness of handling mouldy pods, and of the

destruction of a great part of the crop by the germination of the seeds in the pods and their subsequent drying, is not likely to allow me to make the same mistake again.

To keep the plants secure from the attack of birds they must be hung up indoors. To keep them secure from rats and mice is a more difficult matter. The plan I have found to answer this purpose is to suspend the bundles on stout wire stretched from one wall of a disused stable to the other, taking care that the bundles do not touch the walls or any other object from which rats or mice could get at them.

For hanging the bundles on to the wire I have found a form of picture-hanger so useful that a better thing for the purpose could not have been invented. This is the brass picture-hanger which has a broad hook at one end from which the picture is suspended, and is itself nailed to the wall by three nails which pass through three holes, one in each of the three subdivisions of its trifoliate base. In the use to which I put it, the hanger is hung the other way up; it hangs from the wire by the hook, and a loop from the twine suspending the bundle is passed over the two lateral subdivisions of its base.

If the weather is hot, the peas will probably be dry enough in ten days' time for the business of recording to be started. But it is well to give them time to become thoroughly dry; say a fortnight or three weeks.

A word as to the patch of ground on which the

## EXPERIMENT WITH A PLANT 157

peas have been grown. When the last bundle has been taken in, it is my practice to dig and well manure the ground as soon as possible, and to plant it at once with vetches, to be dug in, in January, as a green manure. For sowing the vetch, the ground is left fairly rough, and shallow drills, one foot apart, are drawn across it; the seed is sown broadcast, and the ground is then nicely raked over with a fine rake. If the weather has been favourable it should be possible to finish the harvesting and get the vetches planted by the end of August; and, of course, the earlier they can be got in the better, for the more growth will they have made when the time comes to dig them in. Besides acting as a valuable green manure, the vetches serve other useful ends. To a certain extent they keep weeds down by smothering them; and, by keeping the frost out of the ground they render it possible to begin tilling the ground at an earlier date in the year. In January of this year, 1911, a frost, which had left a piece of ground, adjoining the patch in which the vetches were, so hard that it was impossible to work it with a spade or a fork, had not touched the ground in which the vetches grew. This was perfectly soft and open, and the vetches were dug in with the greatest ease.

My practice is not to use this patch again for peas before two years have elapsed.

The reader who wishes to repeat Mendel's observations will require to know the names of those varieties which bear the various characters dealt

with by Mendel. I give this information in the following Table :—

<i>Character concerned</i>	<i>Dominant Member of Pair</i>	<i>Name of Variety</i>	<i>Recessive Member of Pair</i>	<i>Name of Variety</i>
Shape of Cotyledon	Round	<i>Express</i>	Wrinkled	<i>Laxton's Alpha</i>
Colour of Cotyledon	Yellow	<i>Sangster's No. 1</i>	Green	<i>Express</i>
Colour of Seed-coat	Grey	<i>Grey Field Pea</i>	White	<i>Sangster's No. 1</i>
Texture of Pod	Hard	<i>Grey Field Pea</i>	Soft	<i>French Sugar Pea</i> (Messrs. Suttons)
Colour of Pod	Green	<i>Sangster's No. 1</i>	Yellow	<i>Gold von Blocksberg</i> (Haage und Schmidt, Erfurt, Germany)
Distribution of flowers on stem	Normal	<i>Sangster's No. 1</i>	Fasciated	<i>Mummy Pea</i> (Henry Eckford, Wem, Shropshire)
Stature	Tall	<i>Carter's Quite Content</i>	Dwarf	<i>William Hurst</i>

The varieties for which no source is specified in this Table can be supplied by, or obtained through, any established seedsman. Some care must be taken with the Grey Field Pea. The term "grey" is

## EXPERIMENT WITH A PLANT 159

sometimes used among seedsmen in so wide a sense as to signify peas with a maple seed-coat. The strain which I have used were given me by Mr. R. H. Lock. In the case of all the pairs of characters excepting that relating to the distribution of flowers on the stem, the two varieties named differ from one another only in respect of the two characters which they are stated in the Table to bear.

The simplest way of obtaining a result to illustrate the ratio obtained when two pairs of characters are involved (*see* Plate III.) is to cross a yellow wrinkled variety with a green round one. A good yellow wrinkled one to use is *British Queen*, and a good green round *Express*.

The best way of exhibiting the results of crosses involving characters either of the seed-coat or of the cotyledon is to mount them in cotton wool in glass-topped cardboard boxes about three-quarters of an inch deep. Figs. 11, 12, 21, 26, and 27, and Plates I. and III. are direct photographs from specimens mounted in this way. The method is as follows: Plenty of cotton wool is laid in the box; half of each of the pods is cut off at the base, and the peas attached to it are gummed into the other half. The specimen is now laid on the cotton wool and the lid put in its place and kept there with seccotine. The whole process requires patient and careful manipulation.

## CHAPTER XI

### MENDEL'S EXPLANATION OF HIS RESULTS

IN this chapter we pass from the description of facts as to which men with unimpaired sense of sight are all agreed, to the consideration of hypotheses about which men whose judgment estimated by the usual standards is sound are widely at variance. At this point, therefore, we bid farewell to the broad daylight of observation, and enter the dark and treacherous alleys of inference. Before we take this step, it is well to reflect on the nature of the errand on which we are engaged.

A theory commonly held as to the nature of the explanation of a sequence of events is that explanation consists in the discovery of the principles underlying and determining this sequence. The essence of this theory is that explanation consists in seeing below what is observed, and finding out how it is worked; and this probing downwards is regarded as one step of a grand downward journey of exploration, the goal of which is the discovery of the causes of all phenomena. Those who hold this theory of the nature of explanation believe that each downward step is one stage nearer to the truth below—a day's march nearer home.

Now, if this view of the matter were the true

one it would follow that the deeper we probed, that is, the nearer we got to the underlying truth, the more closely we should agree. The very reverse of this is, however, the case. The further we leave the crust of phenomena behind, and the more we approach fundamentals, the more are we at variance with one another. The extent to which we agree with one another is not directly, but inversely, proportional to the depth to which we probe. And when we reach the most fundamental questions of all, such as the theory of the relation between spirit and matter, so far from finding unanimity, we find the profoundest and widest gulf of disagreement.

True it is, that when we try to explain the things which reach us through our senses, we leave the crust of indisputable phenomena behind. But we do not leave it behind, above us, by burrowing beneath it; we leave it behind in the other direction by retreating into the recesses of our own minds. And the further we retreat into these recesses, the more does our explanation become an expression of our own mind, and the less relation does it bear to anything in the world outside. That is why the "deeper" we probe the more violently do we disagree with one another. It is only so long as we stick to the crust that we agree.

We may regard the facts described by Mendel as established. The theory which he put forward to explain them is probably a very close approximation

to the true one. And it is given here partly for its general biological interest, and partly because it is true up to such a point that it is possible, by means of it, to predict the results of all the simpler types of matings which the practical breeder is likely to want to make.

In the previous chapter we were confronted with the fact that there must be something in the male reproductive cell, or germ cell, as it is called, contained in the pollen grain taken from a flower on a tall plant, which made the offspring of a dwarf plant fertilised by this pollen, develop into a tall plant. Mendel's theory is that every germ cell, whether male or female, of a tall plant contains something representing the character tallness. It is not known what this something is, so it does not matter what it is called. The term that has come into general use is "factor." The germ cells of tall peas are, therefore, said to contain the factor for tallness. Similarly the germ cells of a dwarf pea contain the factor for dwarfness. So that when a tall pea is self-fertilised, a male germ cell containing the factor for tallness unites with a female germ cell also containing the factor for tallness, and the result of this double dose of tallness in the fertilised ovule is that it develops into a tall pea. Similarly, when a dwarf pea is self-fertilised a male germ cell containing the factor for dwarfness unites with a female germ cell also containing this factor, with the result that a dwarf pea is produced. In both cases, it will be noted, two doses of the same factor are necessary for the pro-

duction of the character represented by that factor in the germ cell.

Now, what happens when a germ cell bearing the factor for tallness unites with a germ cell bearing the factor for dwarfness? We know the answer to this question. A tall pea is produced. The fertilised egg contains in this case, as in the others, two factors; but one is the factor for dwarfness, and the other that for tallness. But the latter seems to dominate completely over the former, and allows it no share in determining the stature of the plant; for the hybrid tall pea which is produced is indistinguishable from its pure tall parent, except that it possesses the exceptional vigour which is characteristic of hybrids, and is often a little taller than its pure tall parent. It should be noted that the result of crossing "female dwarf" with "male tall" is the same as that of crossing "male dwarf" with "female tall." In technical parlance, the reciprocal crosses are identical. We have now to consider the condition in which these factors exist in the germ cells produced by the hybrid tall. And in so doing we get to the kernel of Mendel's theory. It might be expected that one kind of factor occurred in all the germ cells, and that this factor represented a mixture between tallness and dwarfness; or it might be concluded from the fact that the hybrid itself was tall that all its germ cells contained the factor for tallness, and that the dwarf factor had been eliminated altogether. Neither of these views were held by Mendel. He supposed that half of the germ cells, produced by the hybrid, contained the

tall factor, and the other half the dwarf factor ; the tall factor has not been adulterated with dwarfness by its union with a dwarf factor, nor the dwarf by the tall. The two kinds of factors occurring in equal numbers amongst the germ cells of the hybrid are as pure, in respect of the character they represent, as the same two factors existing in the germ cells of the parental tall and dwarfs, according to the theory.

Assuming this to be true, what result would be expected to follow from the self-fertilisation of such a hybrid ? Let us be perfectly clear, before we attempt to answer this question, as to what we are considering. On the one hand there are all the ovules in all the flowers on a plant, amounting, if the plant has been given plenty of room to grow, to anything between two and five hundred ovules ; half of these ovules are supposed to contain tall factors, and the remaining half, dwarf factors. On the other hand, there are all the pollen grains on the plant. The numbers of these must be immense, and I know of no estimate of their number in a single flower ; nor is the matter of any importance for our purpose. Suffice it that the number of them is vast. Half of these pollen grains are supposed to contain tall factors and the remaining half dwarf factors. I shall speak of pollen grains as synonymous with the male germ cell, to avoid circumlocution. What is the result of the fertilisation of these few hundred ovules by the few hundred pollen grains necessary for the purpose ? Let us consider first the ovules with the tall factor. They have an equal chance of being fertilised by a

pollen grain with a tall factor as by a pollen grain with a dwarf factor; that is to say, the following unions will be, approximately, equally frequent:—

Tall factor (borne by ovule)	×	Tall factor (borne by pollen grain)
Tall factor (borne by ovule)	×	Dwarf factor (borne by pollen grain)

Now let us consider the ovules with the dwarf factors. These again have an equal chance of being fertilised by a pollen grain with a tall factor as by one with a dwarf factor; that is, the following unions will be, approximately, equally frequent:—

Dwarf factor (borne by ovule)	×	Tall factor (borne by pollen grain)
Dwarf factor (borne by ovule)	×	Dwarf factor (borne by pollen grain)

All the ovules have now been accounted for, and it will be seen that the result is four kinds of unions of germ cells, when these unions are classified according to the factors contained in the two germ cells uniting in each case. Moreover, these four kinds of union are, on the average, equally frequent. They may now be written in one list, with their frequency written after them in percentage:—

Tall-Tall	.	.	.	.	25 per cent.
Tall-Dwarf	.	.	.	.	25 „
Dwarf-Tall	.	.	.	.	25 „
Dwarf-Dwarf	.	.	.	.	25 „

These are the kinds of unions of germ cells classified

according to the factors in the two cells uniting in each case. We have now to consider what will be the nature of the plants which develop from these fertilised ovules. Let us deal, first, with the first and last on the list. It may be supposed that the *Tall-Tall* type will develop into a pure tall, and that the *Dwarf-Dwarf* will produce a dwarf, inasmuch as this was the theory of the reproduction of tall and dwarfs with which we started. Anyhow, we shall see how this supposition fits the facts.

Now, with regard to the second and third types of union on the list. It should be remembered that the character written first in each pair is that borne by the ovule, and the character written second that borne by the pollen grain. The *Tall-Dwarf* couple, therefore, was produced by pollinating a pistil on a tall plant with pollen from a dwarf; and the *Dwarf-Tall* couple by pollinating a pistil on a dwarf plant by pollen from a tall. Now, we know that in the case of this character reciprocal crosses are identical; that is to say, that the result of both of these crosses is a hybrid tall plant. We are, therefore, now in a position to say what will be the average result of the random union of a large number of ovules, 50 per cent. of which bear the factor for tallness and the other 50 per cent. the factor for dwarfness, with a similar number of pollen grains containing similar factors in the same proportions. By "random" I mean that germ cells bearing a particular factor do not show a preference for germ cells bearing a particular factor, whether similar or dissimilar.

# MENDEL'S EXPLANATION 167

TABLE TO ILLUSTRATE MENDEL'S EXPLANATION OF  
SEGREGATION IN THE 1:2:1 RATIO.

<i>Types of fertilised ovules</i>	<i>Percentage of frequency.</i>	<i>Nature of Plants into which they will develop</i>	<i>Percentage of frequency.</i>
Tall-Tall . . .	25	Pure Tall . . .	25
Tall-Dwarf . . .	25	} Hybrid Tall . . .	50
Dwarf-Tall . . .	25		
Dwarf-Dwarf . . .	25	Pure Dwarf . . .	25

It will at once be seen that the proportions in which the three kinds of plant—pure tall, hybrid tall and pure dwarf—would be expected to occur on the basis of this theory is exactly that in which they do occur.

The fact that the theory is in perfect accord with the facts which it attempts to explain is not, of course, proof that the theory is true; no one would invent a theory which did not fit the facts. This is, however, not the place to discuss the question how nearly true it is, for we are concerned now with Mendel's theory as stated by him, and not with the question whether it is true or not, which will be dealt with in a later chapter.

It was stated, categorically, above that the four kinds of unions of germ cells occurred with equal frequency. The truth of this statement can be tested in the following way: Two people each take a coin, and they both toss it at the same time. This act is repeated, say, a thousand times, and the result

written down each time. The result of any given pair of throws may, of course, be one of three things : head-head, head-tail, and tail-tail. And the total result of a thousand throws will not be very far from 250 head-heads, 500 head-tails, and 250 tail-tails.

In this illustration the matter of sex has been left out, so that the equal frequency of the four types of unions of germ cells seen in the first column of the Table on p. 167 has not been illustrated. This can easily be done. One of the persons who tosses the coins may be designated the "male," and the other the "female." If the sex of the tosser be taken into account and recorded, it will be found that the four following events will occur equally frequently. Male will be denoted by the symbol ♂, and female by the symbol ♀:—

Head tossed by ♂	and	Head tossed by ♀
Head tossed by ♂	and	Tail tossed by ♀
Tail tossed by ♂	and	Head tossed by ♀
Tail tossed by ♂	and	Tail tossed by ♀

Before we leave this illustration of the manner in which the Mendelian ratio 1 : 2 : 1 is brought about, a matter of great theoretical and practical importance must be dealt with.

This ratio 1 : 2 : 1 in the second hybrid generation, which is the essential and diagnostic feature of Mendelian inheritance, is brought about by the random union of male germ cells (50 per cent. of which contain the factor for the dominant, and 50

per cent. the factor for the recessive character) with female germ cells containing the same factors in the same proportions. The union, be it noted, is random; it is what is called a chance result. And inasmuch as it may be—nay, must be—important to know, for practical or theoretical purposes, whether a particular ratio under investigation is a Mendelian one or not, a familiarity with certain attributes of chance is the barest necessity to the student of heredity.

Two things may be meant by the statement that a thing happens by chance, according as to whether reference is being made to the result of a single event, or to the total result of a large number of such events; according, for instance, as to whether we are referring to the result of tossing a penny or to the result of, say, ten thousand such tosses. Nothing, of course, is more uncertain than the result of a single throw, yet certain features of the result of a very large number of throws can be predicted with great accuracy. We are not concerned here with the first signification of the statement that a thing happens by chance, with the result of tossing a single penny once; and we can, therefore, proceed directly to a consideration of those features of chance which bear on the causes which determine the Mendelian ratios.

As a familiar instance of an aggregate chance result the result of tossing a penny a number of times may be considered. It is stated that the result of tossing a penny an infinite number of times is an

equal number of heads and tails, but as the truth of this statement can never be tested, it does not concern us. It is also stated that the nearer the number of tosses approaches infinity the closer will be the approximation to equality of the number of heads and tails thrown. This can be tested, and concerns us here very deeply; but before we deal with its significance a minor feature of it, which is sometimes forgotten, may be pointed out. As the number of times a penny is tossed becomes larger and larger, the absolute difference between the number of heads and of tails becomes larger and larger; but, on the other hand, the ratio of the two approximates more closely to the ratio 50% : 50%. Thus at 10 throws there might be 6 heads and 4 tails, an absolute difference of 2; but at 100 there might be 54 heads and 46 tails, an absolute difference of 8; yet the latter is a closer approximation to 50 per cent. heads 50 per cent. tails than the former. To sum up, the essential feature of the aggregate result is that the approximation to the expected result becomes closer as the number of trials becomes greater.

Now, since the Mendelian ratio is the result of the union of germ cells which unite without regard to the factors which they contain, that is to say, by chance, it is evident that this essential feature will also characterise the Mendelian ratio. That is to say, a very close approximation to the 25 per cent. of recessives (which is the ratio which can be tested on the largest scale) is not to be expected in a small number such as that of the peas in a pod, or

the children of a human family, any more than three heads and three tails are to be expected whenever a penny is tossed six times. The statement that the recessives appear in the ratio of 25 per cent. to the whole second hybrid generation stands the experimental test well, when it is tested on a large scale. In the case of the colour of the cotyledons in the pea, I raised a generation of 139,837 individuals; the ratio in which the greens occurred was 24.88 per cent. The point I wish to insist on here is that when small numbers of individuals are being dealt with small deviations from the expected number do not indicate that the Mendelian theory does not apply to that case, any more than a close approximation is proof that it does. For instance, if a brown-eyed couple marry, the fact that their first four children are brown-eyed does not prove that both parents are pure-bred brown. The next child might be blue-eyed, which would show that both the parents were hybrid brown. Nor would the production by a brown-eyed woman of three brown-eyed and one blue-eyed child prove that the father was, like the mother, a hybrid duplex; he might be a simplex, and the family would, in that case, be exhibiting such an approximation to 50 per cent. duplex : 50 per cent. simplex as might be expected in so small a number.

Having dealt with this question, we may now return to the Mendelian theory itself.

There is a way of illustrating the result of the random union of the germ cells, which is in some

respects better than the tossing of coins. It is done with counters. Equal numbers of red and white ones are required. Only one pair of characters is being taken into consideration in the case to be illustrated. The female germ cells, half of which bear the dominant member of a pair of factors whilst the other half bear the recessive member, are represented by a collection of 100 red counters (representing the factor for the dominant character) and 100 white (representing the factor for the recessive character). The male germ cells, containing similar factors in the same proportions, are represented by a precisely similar collection of red and white counters.

Three columns are now ruled on a large sheet of paper, to receive the three kinds of couples of counters which can be drawn from these two collections. These three kinds are, of course, red-red, red-white, and white-white. A counter is now drawn at random from one collection, and another counter from the other, and the pair is placed in the column prescribed for it on the paper, according as to whether it is red-red (RR), red-white (RW), or white-white (WW). Another pair is drawn in the same way until, say, a hundred pairs have been placed on the paper. It will be found that the numbers of the three kinds of pairs approximate to the ratio 25 per cent. RR, 50 per cent. RW, 25 per cent. WW.

The illustrative value of this device may be greatly increased by making it a rule, when a red and a white are drawn together, to put the red on the

top of the white when the pair is placed in its column on the paper. This is supposed to represent the dominance of red over white; and if the pairs of counters are placed on the paper so carefully that the lower counter is in each case concealed, the conclusion derived from a superficial glance at the paper with the counters on it, will be that reds and whites occur in the proportion of 75 per cent. and 25 per cent. respectively. Closer inspection of these apparent reds will reveal the fact that, of these seventy-five, fifty consist of a red and of a white counter, and correspond to the hybrid individuals bearing the dominant character; and the remaining twenty-five consist of two reds, and correspond to the individuals which both bear, and breed true to, the dominant character.

This device brings home vividly to the spectator the reason, according to the Mendelian theory, why the recessive which appears in the second hybrid generation, the extracted recessive as it is called, breeds as true to the particular character under consideration as the recessive with which the cross was made. The extracted recessive breeds true for precisely the same reason as the pure one does; it is the result of the union of like germ cells, or, to speak more fully and accurately, of germ cells containing factors for like characters. The factor for dwarfness, for instance, contained in the ovule of a hybrid tall pea is identical with such a factor borne by a pure dwarf pea; and when two such factors borne by the hybrid tall unite and result in the

production of a dwarf, the dwarf character is no more tainted with tallness than a white counter becomes pink by lying in a heap with red ones.

The cause of the pure breeding of the 25 per cent. tall appearing in the second hybrid generation, namely, the union of two germ cells containing similar character-factors, is also well demonstrated by means of these counters. So, also, is the fact that the remaining 50 per cent. of the tall are hybrids, and, moreover, that these hybrids of the second hybrid generation will produce a third hybrid generation exactly similar to that produced by the hybrids of the first hybrid generation, for the reason that the contents of the germ cells of both these hybrids (of the second and first hybrid generation) are identical.

It is furthermore plain why, according to Mendel's theory, this segregation of characters in these proportions should continue as long as the seeds of hybrid plants are sown. A hybrid, whether it occurs in the first or the fiftieth hybrid generation, will produce germ cells half of which contain the dominant, and the remaining half the recessive character; and the generations produced by them will, consequently, have the same composition. But we must guard against the error of assuming that Mendel's theory is true, and of then dogmatically stating, from the standpoint of this assumed basis, that the segregation in these ratios will be continued for all time. If the theory is true they will. Let us, then, turn the tables; and test its truth by finding out if they do.

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The most convenient way of representing the supposed causes of Mendelian segregation on paper is to use the four-square table. Along the top of the table are written the two kinds of factors that occur in equal numbers amongst the male germ cells of the hybrid, namely, the tall, for which the letter T is written, and the dwarf, for which D is written. The same is written along the left of the table, but the T and D here refer to the factors in the female germ cells.

		♂	
		T	D
♀	T	TT	TD
	D	DT	DD

Two squares alongside one another are called a row. Two squares superimposed on one another are called a column. The T above the whole square relates to the column below it, and the D, to the right, to the column below it. Similarly the T and D at the left of the table relate to the rows to the right of them. In the square formed by the intersection of a row with a column is written the result of the union of the factor at the head of the column with the factor at the left of the row. This Table is merely another way of stating what has already been

set forth on p. 165. But it is introduced here to pave the way for the sixteen-square Table which is indispensable for explaining the 9 : 3 : 3 : 1 ratio.

There are certain general terms and formulæ introduced by Mr. Bateson which have come into general use. They may now be briefly indicated.

The letter D is used to signify the dominant character, and R the recessive, and consequently the hybrid is spoken of as DR, the pure dominant as DD, and the recessive as RR. It will be noted that the single letters D and R are stated to signify characters, whilst the organisms bearing these characters are represented by two figures, DR, DD, RR, etc. This latter fact is an expression of a part of the Mendelian theory according to which the organism is a double structure. Indeed, it may almost be said that this is not a theory but a fact. Every organism with which we are concerned in this book is formed by the union of two germ cells. And the simplest evidence of this duplicity is that the number of chromosomes in the cells of an animal or plant is twice that of the number in each of the two germ cells which united to produce it.

A single word for a germ cell is wanted. This is supplied in *gamete*.\* A more urgent need is a single word for the result of the union of two gametes, the animal or plant into which it develops. For this, the word *zygote*† has been coined.

In the illustration above, the single counter

\* From the Greek *γάμέω*, marry.

† From the Greek *ζυγόν*, a yoke.

represented the gamete, and the pair the zygote. The single letters at the top of the four-square Table represented gametes, and the pairs in the squares zygotes.

This Table may now be written in a generalised form in which D and R represent dominant and recessive characters in general. Thus :—

		♂	
		D	R
♀	D	DD	DR
	R	RD	RR

Another form of such a Table, in which the capital and small sizes of the same letter are used instead of D and R to represent the dominant and recessive characters of a pair, should be referred to here, because it is necessary to use this form of notation in the general form of the sixteen-square Table, which is used to represent the union of gametes of hybrids between forms differing in respect of two pairs of characters. This form of the Table is given on the next page.

An inspection of this Table, or a casting back of the memory to the counters, will reveal the fact that there are two kinds of zygotes. One is the result

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of the union of gametes bearing *similar* character-factors, and is called a *homozygote*, the adjectival form of which is *homozygous*: of this there are two kinds, DD and RR. The other kind of zygote is

		♂ gametes	
		A	a
♀ gametes	A	AA	Aa
	a	aA	aa

the result of the union of gametes bearing dissimilar character-factors, and is called a *heterozygote*, the adjectival form of which is *heterozygous*: of this there is only one kind, DR.

The heterozygote may either bear the character of its dominant parent, as in stature in peas; or it may possess a character peculiar to itself and inseparable from the heterozygous condition, as in the case of the Andalusian fowl. In such a case it is useless to attempt to fix the hybrid character. A similar case amongst cattle is red-roan, which is a heterozygote between red and white.

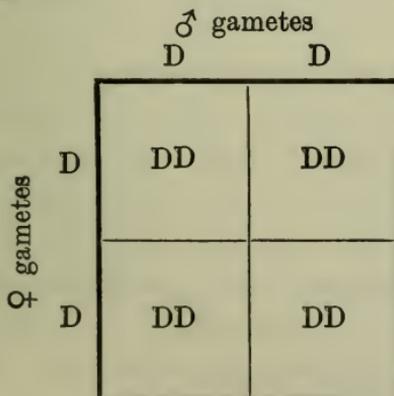
It now remains to consider the results of the different types of matings which may be made between the three types of zygotes, DD, DR, and RR. It is hardly necessary to point out how impor-

# MENDEL'S EXPLANATION 179

tant a finger-end familiarity with such results is, both to the student of heredity and to the practical breeder. It will be convenient, first, to display them in tabular form, so as to obtain a general view of them, and to see which have already been dealt with, and which remain to be considered.

	<i>Zygotes mated</i>		<i>Nature and relative numbers, in percentage, of zygotes resulting from preceding union</i>		
			DD	DR	RR
1	DD	DD	100		
2	RR	RR			100
3	DD	RR		100	
4	DR	DR	25	50	25
5	DR	DD	50	50	
6	DR	RR		50	50

The first four of these types of mating have already been considered. No. 1 represents the true-breeding of pure dominants, according to the following scheme:—



No. 2 represents the true-breeding of pure recessives, according to a precisely analogous scheme in which R is substituted for D. No. 3 represents the crossing of DD with RR, according to this scheme:—

		♂ gametes				♂ gametes		
		D	D			R	R	
♀ gametes	R	DR	DR	or	♀ gametes	D	DR	DR
	O+	DR	DR			O+	D	DR

and No. 4 represents the mating together of these hybrids, which has already been represented in this scheme on p. 177. Nos. 5 and 6 have not yet been dealt with, and are very important for more reasons than one.

One feature which these two types of mating possess in common is so simple that even when it is noticed at all it is usually passed over with a few words. Yet this feature has, in my opinion, a very important bearing. Although these two types of mating are usually considered last, as a not very important corollary to the Mendelian theory, they possess this feature in common, that of all the six matings, in the above Table, in which the forms mated differ from one another (i.e. in all except 1 and 2) they are the only two in which the two parental

forms are reproduced in the next generation in equal numbers. In No. 3, one parental form, the recessive, is not reproduced at all. In No. 4, where the two parents, the hybrids, are similar, they only account for a half of the next generation, the remaining half being made up of the grand-parental dominants and recessives in equal numbers.

This extremely simple feature of matings, Nos. 5 and 6, is also characteristic of the inheritance of sexual characters; the result of the union of a male with a female is the production of equal numbers of males and females on the average. And this fact, which the founders of the Mendelian theory have, until recently, neglected, has become the corner-stone of the Mendelian theory of the inheritance of sex, and will also, in my opinion, play a very important part in elucidating the origin of the Mendelian mode of inheritance.

These two types of mating may now be dealt with separately. No. 5 is represented on the four-square Table as follows:—

		♂ gametes	
		D	R
♀ gametes	D	DD	DR
	D	DD	DR

This type of mating is not one of any practical value, but its existence should be borne in mind, because superficially the results of it are indistinguishable from the result of mating two dominants (DD and DD) in those cases in which the character of the hybrid is the same as that of the dominant; and if this fact is not borne in mind the false conclusion might be drawn from the results of breeding, that a dominant character had become fixed when it really had not. Take, for instance, the duplex eye in man; the result of mating a hybrid duplex with a pure one is, as far as we can see from the immediate result of the mating, the same as that of mating two pures, namely, the production of nothing but duplexes; the fact that half of them are heterozygous, or hybrid, and half homozygous, or pure, can only be determined by subsequent breeding. And so long as DR is mated with DD, and for however many generations, the apparent result will be the same as mating DD with DD. What, then, it may be asked, does it matter whether DD is mated with DR or with DD, if the result is the same? The answer is that it does not matter provided that the union of DR  $\times$  DD can be ensured, but as this is a laborious matter (involving as it does the testing of both forms before they are mated) the union DR  $\times$  DR is sure to occur sooner or later; and then the fat is in the fire, and a quarter of the generation produced consists of recessives.

Mating of type No. 6 is represented in the four-square Table on the next page.

		♂ gametes	
		D	R
♀ gametes	R	DR	RR
	R	DR	RR

This type of mating is of great practical value because it is the one by means of which the question whether an animal or plant bearing the dominant character is heterozygous or homozygous can be most expeditiously decided. This question could, it is true, be answered by mating the individual in question with another hybrid, if a hybrid of the first generation were at hand (a hybrid of the second generation can only be known to be such by testing it, and that is what we are trying to do); and even if this were available an inconveniently large number of offspring would have to be produced before there were sufficient grounds (derived from this test) for believing that the individual tested was not a hybrid. Directly a recessive is produced by mating a particular individual, which may be called A for brevity, with a hybrid, it is certain that A is a hybrid; but the production of a family of six containing no recessives does not by any means prove that A is a dominant; the next child might be a recessive. But the probability of A being a dominant becomes

less and less as the size of a family containing no recessive increases.

By far the most convenient way, as stated at the beginning of the last paragraph, of testing the zygotic constitution (that is, of determining whether it is heterozygous or homozygous) of an individual bearing the dominant character is to mate it with a recessive. There are two advantages of this over any other way; the first and most practically important is that an individual bearing the recessive character can only be one thing, RR, in contradistinction to one bearing the dominant character, which can, of course, be DD or DR; so that the recessive can be used at once, without any preliminary time-wasting testing which is necessary to determine the constitution of an individual bearing the dominant character. The recessive wears its gametic constitution on its sleeve, and no further credentials are required. The second advantage of testing by mating with a recessive is that the result of mating a hybrid with a recessive is the production of twice as many recessives as are produced by the union of two hybrids, 50 per cent. as against 25 per cent.; and consequently twice as great a likelihood of the form tested throwing a recessive, if it is a hybrid, as there would be if it were mated with a hybrid.

My hybrid mice of the first hybrid generation were mated with albinos, not to test their hybridity, for that was obviously not in question, but to test the truth of the statement that hybrids mated with

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recessives produced hybrids and recessives in equal numbers. The actual numbers produced by mating hybrids and albinos were 378 hybrids and 368 albinos. The following list of families, which were the first ten raised, will give some idea of the distribution of recessives over the families. The largest family in the whole experiment in which no recessives occurred was one which consisted of six hybrids.

PARENTS		OFFSPRING	
<i>Female</i>	<i>Male</i>	<i>Hybrids</i>	<i>Albinos</i>
Albino	piebald grey	4 grey	None
Albino	piebald grey	1 grey, 2 piebald greys, 1 piebald black	5
Albino	piebald grey	6 greys	4
Albino	grey	2 greys, 1 black	2
Albino	grey	4 greys	1
Albino	grey	2 greys	2
Albino	piebald grey	1 black	5
Piebald grey	albino	1 piebald grey, 2 blacks	2
Grey	albino	1 grey, 1 black	1
Grey	albino	2 piebald blacks	4

## CHAPTER XII

### THE ANTECEDENTS AND FATE OF MENDEL'S DISCOVERY

IT may not be without interest to consider here how it came about that Mendel's discovery, made in 1865, remained unknown until 1900, and to emphasise the fact that what constitutes a great discovery is not the mere unfolding of a sequence of events before the eyes of an observer, but the appreciation of the significance, or perhaps the invention of a significance, or the reading of a meaning into, this sequence by the observer.

To deal first with the first question. The problem of heredity, i.e. the question how the resemblance between one generation and the next is brought about, as it presented itself to biologists interested in the matter at the time when Mendel worked, was to determine how the characters of the parent got into the germ-cells which produced the next generation. It was natural that the problem should present itself in this way; that the inquirer should start with the grown parent, and wonder how its characters could be compressed into the minute germ, subsequently to emerge and expand and develop into the next generation. For, compared with the grown

body of the parent, the germ was a recent discovery. It was natural, therefore, that the fixed starting-point in the inquirer's mind should be the body, and that the problem of heredity should present itself to him as the task of finding out how its characters could get into the germ-cells which (so he had recently discovered) it produced, and which give rise to the next generation.

There can be no doubt that that was the way in which the problem presented itself to Darwin's mind. His theory of Pangenesis is an answer to the question, How do the characters of the parent get into the germ-cells which it produces? He imagined that this was brought about by every cell of the body giving off a particle which somehow reached the germ-cells, so that each germ-cell contained a representative particle from every cell of the body which housed it. This theory would account not only for the inheritance of so-called inborn characters, but also for so-called acquired ones; because if a dog had its tail cut off, the tail would not be represented in the germ-cells of the dog unless the particles had left the tail before it had been amputated. Pangenesis died, not because Galton's experiments designed to test it had a negative result, but because Weismann's writings effected a swinging round of biological opinion, through 180 degrees, to a statement of the problem of heredity which was the diametric opposite to that which had prevailed hitherto. The doctrine preached by Weismann was that to start with the body and inquire

how its characters got into the germ was to view the sequence from the wrong end; the proper starting-point was the germ, and the real question was not "How do the characters of the organism get into the germ-cells *which it produces?*" but "How are the characters of an organism represented in the germ cell *which produces it?*" Or, as Samuel Butler has it, the proper statement of the relation between successive generations is not to say that a hen produces another hen through the medium of an egg; but to say that a hen is merely an egg's way of producing another egg. According to Weismann, the problem how the characters of the body get into the germ-cells which it encloses is as unreal as the problem which puzzled one of our kings—how does the apple get into the dumpling? The answer in both cases is the same. The apple does not get into the dumpling. The characters of the parent do not get into the germ-cells which they enclose. The apple and the germ-cells were there first. The germ-cells are merely part of an unbroken line of germ plasm which under certain circumstances, usually the fusion of two of its constituent germ-cells, froths up and produces a great excrescence, the body of the next generation, and continues its existence in this body. The germ plasm, according to this view, is immortal; the excrescence, the body, is mortal. The germ plasm only comes to an end along a particular line when the body containing it dies without leaving offspring. The animal does not, as it appears to do, give rise to germ-cells when it reaches maturity; the germ-cells

are not formed afresh by each generation. When the fertilised egg divides, some cells are at once set apart to become the germ-cells of the organism into which this fertilised egg develops. It is the body which is formed afresh at each generation: the germ plasm has existed since the dawn of life. The reader will, of course, understand that this is not a statement of fact, but a presentation of the Weismannian doctrine.

The relation between Mendelian theory and this doctrine may be considered from two points of view. In the first place, a general acceptance of Weismann's way of stating the problem of heredity was necessary before the significance of Mendel's observation could be understood. In the second place, Mendel's discovery was a confirmation and amplification of Weismann's thesis.

These two points will be dealt with separately. The publication of Mendel's paper in 1865 was the throwing of pearls before swine. The problem of heredity, as it presented itself to those who were interested in the matter at that time, was, as I have already stated, to explain how the characters of an organism got into the germ-cells which it produced. To Mendel, on the other hand, the problem was so obviously the converse of this—namely, the question how the characters of an organism are represented in the germ-cells which produce it, that he did not stop to discuss the matter. Mendel was so sure that this was the correct statement of the problem that he made no defence of it, and proceeded at once to

account for his results on the assumption of its correctness. He knew it so well that he did not know he knew it. But those who read Mendel's papers were still labouring to find out how the characters of an organism got into the germ-cells which it produced. The result was that no point was seen in Mendel's theory, and it quickly lapsed into the oblivion from which it was not rescued till 1900.

It is not as if Mendel were out of touch with the recognised representatives of biological orthodoxy. He was in correspondence with Carl Nägeli, to whose criticisms Charles Darwin paid more attention than to those of any other of his critics. This correspondence has been published by Prof. Correns. It includes a patient attempt by Mendel to make clear to Nägeli those points which the latter had not understood in Mendel's paper. Not only did he do this; he also sent packets of peas resulting from his experiments to Nägeli, in the assurance that if he (Nägeli) grew them he could not fail to perceive the significance of the results which he (Mendel) had obtained. But so deeply was Nägeli imbued with his view of heredity that Mendel's explanations, and his seeds as well, were as water on a duck's back. "These" says Mr. Bateson,\* referring to Mendel's letters and his illustrative specimens, "must have utterly failed to arouse his (Nägeli's) interest, for when in 1884, the year of Mendel's death, he published his great treatise on heredity, no reference was made to Mendel or his work. That this neglect was due to want of com-

\* "Mendel's Principles of Heredity," p. 55.

prehension is evident from a passage where he describes an experiment or observation on cats which, as it happens, gave a simple Mendelian result. The Angora character (recessive) disappeared in a cross with a certain common cat whose hair character is, as we now know, dominant. The crossbreeds were mated together, and the Angora character reappeared in one individual among a litter of common cats. This typically Mendelian fact was thus actually under Nägeli's own observation, but from the discussion which he devotes to the occurrence it is clear that Mendel's work must have wholly passed from his memory, having probably been dismissed as something too fanciful for serious consideration."

Mendel's theory could not be grafted on to contemporary biological opinion: the cross was too wide, to borrow Butler's simile. But, grafted on to the biological opinion prepared by Weismann, it flourished like a green bay tree; and its immense value was at once recognised.

To regard, now, the relation between Mendel's and Weismann's work from the second-mentioned point of view.\* In the first place, Mendel's results support Weismann's doctrine, because the only theory which can as yet account for these results leaves the characters of the soma or body entirely out of account and relates solely to the contents of the germ cells which produce the generation whose character has to be explained. On no other theory but Weismann's would an extracted green pea of the fifth

\* Second paragraph on p. 189.

hybrid generation be identical in appearance and in its breeding properties with a green of a pure strain. Yet these two are identical, as will be shown on p. 236. Both Mendel's and Weismann's are "germinal" theories of inheritance. Mendel's a particular, and Weismann's a general one, on the basis of which Mendel's is erected. And Weismann's general doctrine receives strong support from the fact that the predictions based on Mendel's theory are fulfilled.

Mendelian inquiry does more than afford evidence of the truth of Weismann's general theory; it fills in the details of the general theory of heredity outlined in charcoal by Weismann. As has already been said, Weismann was the first to point out that the problem of heredity was to find out how the characters of an organism were represented in the germ-cells which produced it. Weismann showed what the question was. Mendelian inquiry is slowly building up an answer to it. And already, in the ten years which have elapsed since Mendel's papers were discovered, a rich store of information relating to the manner in which characters are represented in the germ-cells has been accumulated. I have endeavoured thus briefly to indicate what I conceive to be the real nature of the respective parts played by Mendel and Weismann in building up our modern conception of heredity, because it is often complained that credit which is due to Mendel is given to Weismann, and that ideas which are described as Mendelian were really introduced by Weismann.

I will proceed now to a short description of a hybridisation experiment identical with one of Mendel's which was begun in 1820, two years before Mendel's birth. The work was done by John Goss in the garden shown in Fig. 34, in the village of Hatherleigh, in Devonshire, which is eight miles from the northern border of Dartmoor. The results of the experiment were published in the "Horticultural Transactions" in 1822, in a paper which is reproduced on pp. 199-202.

As will be seen from his third paragraph, he proceeded as directed in Chapter X., except that he applied the pollen (of the dwarf pea) on the following day. He obtained three pods of hybrid seed. In the sentence beginning "In the following spring . . ."\* the phenomenon of dominance is described, and in the next sentence the phenomenon of segregation. But Goss went farther than this. Not only did he witness the phenomenon of dominance and of segregation; he also observed the true-breeding of recessives. "Last spring I separated all the blue peas from the white, and sowed each colour in separate rows, and I now find that *the blue produce only blue. . .*"†

But, as the words which follow show, Goss failed to discover that some of the plants bore only yellow seeds, and some both yellow and green. The reason for this, I have little doubt, is that Goss did not

\* Bottom of p. 199.

† In the colours of peas "blue" is synonymous with green, and "white" with yellow.

record his plants separately, plant by plant, after they had been pulled up and dried; but looked at a pod here and there as they stood in the ground, or shelled the whole lot from the dried bundles without regard to the individuality of the plants from which the seeds came.

That Goss did not examine the plants separately after they had been pulled up is evident from the fact that he never speaks of plants, but only of pods; that when he does deal with things separately, as in the case of the green and yellow seeds of the second hybrid generation, he says so. This conclusion is also supported by the fact that Goss was not seeking for an interpretation of the phenomenon he was dealing with, but was trying to raise a new vegetable. "*The edible qualities of this pea I have not tried, having but few.*"

How it came about that Goss, with the phenomena ready to his hand, failed to make the discovery which is now associated with Mendel's name is a question which naturally presents itself. In the first place, it is, of course, more true in Goss's case than it is in Mendel's that biological opinion was not ready to receive a theory such as Mendel's, which lies on the surface of properly recorded results of such an experiment as Goss made. If Mendel failed to graft his theory on to current biological theory, such an attempt made by Goss would have been doomed to failure from the outset. Nevertheless Mendel did what Goss did not do; he extracted something from or projected something into his observations which



FIG. 34.—JOHN GOSS'S GARDEN; WHERE HE MADE HIS CROSSES IN 1820



though at the time it fell on deaf ears, was at once recognised as of immense value when it was again brought forth and exhibited before a generation of biologists which had been prepared by Weismann. Why did Goss fail to do this? The answer is manifold. In the first place, he was not seeking for an interpretation of his results. And, in the case of interpretations, he who does not seek will not find; he may not find what he is seeking; but if he does not seek at all he will find nothing at all. Another reason why Goss failed to make Mendel's discovery is that he did not record the proportion in which his types recurred in the second hybrid generation. But this is scarcely remarkable in view of the fact that not only did he not know that it was a second hybrid generation: he did not know that it was a generation. He says (last paragraph, p. 200): "Should this new variety of pea neither possess superior merit nor be deemed singular in its bicoloured produce . . ." From this it is evident that he perfectly naturally regarded the coloured parts of the seeds borne by a pea plant as its fruit, and did not know, what he could not be expected to know, that they were the cotyledons of the next generation. The recording of the numbers was an essential preliminary to the suggestion of the theory put forward by Mendel; and in my opinion the great future advances in this line of work will be made by paying close attention to numerical ratios, and testing them with statistical formulæ. Another reason why Goss failed where Mendel succeeded is that he did not record the off-

spring of each plant separately. And the reason for this was, as before, that he did not know that "the seeds" were the offspring of a plant. Mendel, who of course knew this, laid the foundations of the modern analytical method in the investigation of heredity, because he perceived the importance of tracing the offspring of each individual separately, and of keeping the records of an experiment in such a way that the ancestry and progeny of every individual concerned may be looked up from them. Much has been talked of the essential antagonism between those methods which deal with individuals in the mass and the Mendelian or analytical method. But I have been unable to find that any such antagonism exists. The analytical method is the only one by which hereditary processes can be unravelled; whilst the significance of the numerical results of these analytical experiments can only be estimated by statistical formulæ. Both methods appear to me to be indispensable.

Goss failed where Mendel succeeded. But the lessons of failure are not less illuminating than those of success, and the lives of those who fail not less valuable or interesting than the lives of those who succeed. Be this as it may, I was unable to resist the temptation to satisfy my curiosity as to the life of a man who, at any rate, spent part of his time in work which has occupied much of my own. I owe the following facts and the photograph of Goss's garden to the kindness of the Rev. J. W. Banks, vicar of Hatherleigh, Devonshire.

John Goss was born in Hatherleigh and baptized on June 27, 1787. He is next heard of as a lad who cleaned boots and did other odd jobs in the Rectory at Iddesleigh, where the Rector took a number of pupils. One of these became interested in Goss and helped to educate him with a view to his entering the Church. But Goss had "scruples," and he became an usher in a school. He was an active and inventive man. He made an orrery, i.e. a model of the solar system, a reading-book for teaching the aged poor to read, and a calculating machine. What a pity he did not conduct his hybridisation experiments on so large a scale that the services of this machine were required !

At the age of 26 he married, under romantic circumstances. A lady came one day to Hatherleigh to visit an old servant, and created a sensation in this out-of-the-way village by driving up to her door in a post-chaise. On getting out of her carriage she stumbled and would have fallen but for the timely intervention of a young man, who stepped forward and saved her. This was John Goss. He was sent for to be thanked for his services. They were married on March 6th, 1813. His wife was twenty-nine years older than he was. At their marriage he was 26, and she was 55. It was during his married life that he made the crosses with peas (in 1820) and sent his note of them to the Royal Horticultural Society (1822). It may be that the carrying out of this experiment was made possible by a leisure which he owed to his wife. He speaks of

“living retired” in the country. It seems that his horticultural work was successful, for he received a prize (purse with gold) for his work from a horticultural society. His wife died, aged 65, on January 19th, 1823, and he went to live at Okehampton, where he died on May 31, 1833, at the age of 46, leaving his money to establish libraries in Hatherleigh and Okehampton.

There is a sentence,\* part of which has already been quoted, in Goss's letter to the Horticultural Society which possesses a curiously prophetic significance: “Should this new variety of pea neither possess superior merit nor be deemed singular in its bicoloured produce, yet there is, I conceive, something in its history that will emit a ray of physiological light . . .” Little can he have guessed how bright a ray was destined to be emitted by this singular pea with its bicoloured produce.

\* Last paragraph of p. 200.

The exception to the dominance of yellow over green related in the “Note by the Secretary” on p. 201 is apparent only. Mr. Bateson has discovered that the Imperials have a thick green *seed-coat*, which prevents the cotyledons of the first hybrid generation being seen. Messrs. Sutton's *King Edward* has a similar opaque green seed-coat, which prevents the colour of the enclosed cotyledons from being seen.

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XXVII. *On the Variation in the Colour of Peas, occasioned by Cross Impregnation. In a Letter to the Secretary. By Mr. JOHN GOSS.*

Read October 15, 1822.

SIR,

LIVING retired in the country, and having a taste for gardening, I have been for some years past endeavouring to raise new varieties of vegetables. A gentleman in the neighbourhood, seeing some of the fruits of my labours, put into my hands the *Transactions* of your Society: this was like the rising sun after the dawn, and I was enabled to see, not only how to do my work better, but that some things which occupied my attention had by others been already accomplished.

I have raised some *new varieties of Peas*, and as one of these appears to be at least a singular production, and finding very little on this subject in your volumes, I am tempted to give you a description of it, accompanied with a few observations.

In the summer of 1820, I deprived some blossoms of the *Prolific blue* of their stamina, and the next day applied the pollen of a *dwarf Pea*, and of which impregnation I obtained three pods of seeds.\* In the following spring, when these

\* I have not been able to ascertain with certainty the names by which the two parent Peas are usually known by gardeners and seedsmen; but I believe that the *Prolific Pea*, which was the female parent of the new variety, is the *Blue Prussian*, and the *dwarf Pea* which was its male parent, the *Dwarf Spanish*.

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were opened, in order to sow the seed, I found, to my great surprise, that the colour of the Peas, instead of being a deep blue, like their female parent, was of a yellowish white, like the male. Towards the end of the summer I was equally surprised to find that these white seeds had produced some pods with all blue, some with all white, and many with both blue and white Peas in the same pod.

Last spring, I separated all the blue Peas from the white, and sowed each colour in separate rows; and I now find that the blue produce only blue, while the white seeds yield some pods with all white, and some with both blue and white Peas intermixed.

The edible qualities of this Pea I have not tried, having but few. It grows two or two feet and a half high, and attains maturity about the same time with its blue parent, which it much resembles, and unfolds a large, deep green rich foliage, superior to any I have seen. It seems to require a greater depth and richness of soil than other sorts, or than I have given it.

Should this new variety of Pea neither possess superior merit, nor be deemed singular in its bi-coloured produce, yet there is, I conceive, something in its history that will emit a ray of physiological light, or at least militate against an opinion held by Mr. SALISBURY, who, in his remarks on the anomaly of the Peach and Nectarines growing on the same branch, says,\* "I have not a doubt of the important consequences which ensue, when the stigma of one plant imbibes pollen belonging to another, but these are only manifested in the succeeding generation."

\* Horticultural Society's Transactions, Vol. I. page 105.

*Facsimile from the Horticultural Society's Transactions.*

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That this is incorrect, is not here "determined by a more able physiologist," but by the above statement—by the above fact; for the effect was strikingly evident in the seed, which was changed by the impregnation from a deep blue to a yellowish white. And if the seed undergoes such a change, why may not the fruit? It is more than probable that it does; but, the change not being so conspicuous as the difference between blue and white, it has escaped observation. Perhaps the most effectual way to unravel the mystery of the anomaly, would be to impregnate a considerable number of Peach blossoms with the pollen of the Nectarine, and to examine minutely if any change succeeded in the fruit.

If this communication should be thought worthy to appear in your *Transactions*, I trust Mr. SALISBURY will excuse an humble attempt to reflect a little light on an obscure part of a science in which he himself is so luminous.

I am, Sir,

Yours respectfully,

JOHN GOSS.

Hatherleigh, Devonshire,

October 5, 1822

*Note by the Secretary.*

Previous to the receipt of the above communication, one on the same subject was transmitted by ALEXANDER SETON, Esq. and read at the Meeting of the Society on the 20th of August, 1822. Mr. SETON had happened to make a similar experiment, by impregnating the flowers of the *Dwarf Imperial*, a well known green variety of the Pea, with the pollen of a white free growing variety. Of the flowers so treated one

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only produced a pod, and it contained four Peas, which did not differ in appearance from the others of the female parent. It thus appears from the different results in this stage of the experiments made by Mr. GOSS and Mr. SETON, that the appearance of the fruit in the first instance is sometimes affected by extraneous impregnation, and sometimes not; the impregnation being effectual, as it was proved to have been, by the progeny in both of these instances, and it seems desirable that this interesting point, on which so much difference of opinion has arisen,\* partly from observation, and partly from analogical reasoning, should be subjected to further experiment.

The plants which grew from the four Peas obtained by Mr. SETON, seemed to partake of the nature of both parents, being taller and more diffuse than the Dwarf Imperial, and less so than the male white parent; but the pods resembled those of the former, being short, and having but few Peas in each. On their ripening it was found that instead of their containing Peas like those of either parent, or of an appearance between the two, almost every one of them had some Peas of the full green colour of the Dwarf Imperial, and others of the whitish colour of that with which it had been impregnated mixed indiscriminately and in undefined numbers; they were all completely either of one colour or the other, none of them having an intermediate tint, as Mr. SETON had expected. The representation of one of the pods in Plate IX. Fig. 1. conveys a very perfect idea of its appearance.

\* See observations on the accidental intermixture of character in certain fruits, at page 63 of the present Volume.

## CHAPTER XIII

### THEORY TO ACCOUNT FOR THE RESULTS WHICH FOLLOW A CROSS INVOLVING TWO PAIRS OF CHARACTERS

THE theory enunciated in Chapter XI., to account for the fact of segregation and the ratio in which the segregated characters occur has more an *indirect* practical value than a direct one. Its value in practice is the lesson which it teaches rather than the immediate practical effects which it is capable of achieving. This lesson is that any attempt to predict the result of a given mating must be based on a knowledge of the character-factors contained in the germ cells of the individuals mated, and not merely on the visible characters of these individuals themselves. The scientific control of breeding must depend on a knowledge of characters as represented in the germ cells ; no amount of familiarity with the mere external features of the animals or plants dealt with will assist towards this control, except, of course, in so far as these external features afford a clue as to the contents of the germ cells within. The chief value, then, of the theory enunciated in the last chapter lies in the support which it affords to those new principles of breeding which look for guidance to the germ, and reject the indications of the body or soma, and are based partly on Mendel's

theory already described, and partly on de Vries' work, referred to in Chapter I. These new principles of breeding, together with an account of an experiment carried out to test their truth, will form the subject of Chapter XV.

But whilst the value of the theory enunciated in the last chapter is of this indirect nature, the theory to be described in this, which is merely an extension of the first-named, is of immediate practical value, inasmuch as a familiarity with it greatly increases the facility with which one of the most important methods of the breeder, the combination, in one strain, of characters existing in distinct strains, can be carried out.

The two methods of the breeder are, first, the method of selection, which alters and improves the characters of breeds; and, secondly, the method of hybridisation which merely effects the recombination of characters which are not themselves altered. And it may be said that the theory to account for the results which follow a cross involving a single pair of characters, described in the last chapter, throws an indirect light on the first of these methods; whilst the theory to account for the results which follow a cross involving two pairs of characters, to be described in this chapter, directly facilitates the second of these methods.

These preliminary remarks are intended to indicate, roughly, the application of the theory which has been, and that which is about to be, dealt with. Both of them, of course, have other applications as

well, but these remarks will, it is hoped, help to effect a preliminary orientation of the novice.

With a view to explaining the theory to account for results which follow a cross involving two pairs of characters, I propose to select as an instance of such a cross the classical one investigated by Mendel, namely, the result of crossing a yellow wrinkled with a green round pea shown in Plate III.

A single-square Table is sufficient for the representation of the union of gametes which occurs in making the cross; though a four-square one might have been used as on p. 175. Y is written for the factor for yellow, G for green, R for round, and W for wrinkled. The Table is filled up as follows:—

	♂ gametes YW		♂ gametes GR
♀ gametes	GR YG.RW	or	YW YG.RW
♀			♀

This may be simply written as follows:—

$$YW \times GR = YG.RW$$

It will be seen that each gamete is represented by two letters, and not one, as in the case of the cross between two forms differing in respect of one pair of characters; and each zygote by four, and not two, as in the other case. This is a simple indication of the fact that the two forms crossed differ in respect of two pairs of characters instead of one.

Our next duty is to predict the result of mating these hybrids from a knowledge of the contents of their germ cells. The first step towards this end is to determine the number of possible combinations of any two of the characters, yellow, green, round and wrinkled, except such combinations as involve the association in one gamete of the two characters of a pair; that is to say, except YG and RW. Also there cannot, of course, be gametes with the formula YY, GG, RR, or WW: it is only zygotes, which are of double structure, that can contain two of the same factor. With these exceptions the number of possible combinations of the characters Y, G, R and W are YR, YW, GR, GW. All that we have to do, therefore, to predict the result of mating the yellow-round hybrids together is to determine the number and relative frequency of the possible combinations of these four types of gametes. And this is mostly simply done by means of a sixteen-square Table. The formulæ for the four types of ♂ gamete are written along the top, and four similar formulæ for the ♀ gametes on the left side of the Table on the opposite page.

Here, again, four horizontal squares are referred to as a row, and four squares superimposed vertically, as a column.

Let us now see what the various kinds of zygotes formed by the union of the four kinds of gametes are, and write the formulæ for each in the square formed by the intersection of the column relating to the male gamete concerned, the formula of which is written at its top, with the row relating to the

female gamete concerned, the formula of which is written at its end. Let us begin with the left-hand square of the top row. This is a union between a ♂ YR gamete and a ♀ YR gamete; and the result, YY.RR, is obviously a yellow round which is homozygous both for yellowness and for roundness; in other words, both in colour and shape. All the zygotes on the top row are yellow rounds. The second, YY.RW, is, like the first, homozygous for colour, but is heterozygous for shape. The third, YG.RR, on the other hand, is heterozygous for colour but homozygous for shape. Whilst the fourth and last, YG.RW, is heterozygous for both colour and shape.

		♂ gametes			
		YR	YW	GR	GW
♀ gametes	YR	YY.RR 1	YY.RW 2	YG.RR 3	YG.RW 4
	YW	YY.RW 5	YY.WW 6	YG.RW 7	YG.WW 8
	GR	YG.RR 9	YG.RW 10	GG.RR 11	GG.RW 12
	GW	YG.RW 3	YG.WW 14	GG.RW 15	GG.WW 16

To proceed now to the second row. The first zygote in it, to the left, is a yellow round, YY.RW, homozygous for colour but heterozygous for shape. The second, YY.WW, is a yellow wrinkled, homozygous for colour and, of course, homozygous for shape, inasmuch as wrinkledness is recessive. The third is another yellow round, heterozygous for both colour and shape; whilst the fourth and last, YG.WW, is another yellow wrinkled, this time heterozygous for colour.

The first zygote in the third row, YG.RR, is a yellow round, heterozygous for colour and homozygous for shape. The second, YG.RW, is also a yellow round, but heterozygous in both respects. The third, GG.RR, is a green round, homozygous, of course, for colour, green being recessive; whilst the fourth and last, GG.RW, is a green round like the last, but heterozygous for shape.

The first zygote in the last row, YG.RW, is a yellow round, heterozygous in both respects. The second, YG.WW, is a yellow wrinkled, heterozygous for colour only. The third, a green round, GG.RW, heterozygous for shape only; whilst the last is a green wrinkled, homozygous for both of its characters, both of them being recessive.

This Table is now written again on p. 209 with the visible characters of the zygotes, instead of their formulæ.

It will be seen from this Table that there are nine yellow round, three yellow wrinkled, three green round, and one green wrinkled zygotes,

which is the actual ratio in which these types occur in the second hybrid generation from this cross.

It may also be noted that the yellow rounds occupy the top row, the left column, and the squares

	YR	YW	GR	GW
YR	Yellow Round 1	Yellow Round 2	Yellow Round 3	Yellow Round 4
YW	Yellow Round 5	<b>Yellow Wrinkled</b> 6	Yellow Round 7	<b>Yellow Wrinkled</b> 8
GR	Yellow Round 9	Yellow Round 10	<i>Green Round</i> 11	<i>Green Round</i> 12
GW	Yellow Round 13	<b>Yellow Wrinkled</b> 14	<i>Green Round</i> 15	<b>GREEN WRINKLED</b> 16

along a diagonal crossing the whole Table from the right top to the left bottom corner; and that representatives of each of the four types, YR, YW, GR, GW, occur in the squares lying on the other diagonal of the square, namely, that crossing it from the top left to the bottom right-hand corner.

Much more can, however, be made out from the

Table in which the zygotic formulæ are written; for instance, in regard to this last point, the Table on p. 209 only gives half the truth; it only shows that a representative of each of the four externally distinguishable types occurs along the top-left to bottom-right diagonal; the whole truth, as revealed by the Table on p. 208, being that these four representatives are the only representatives of these four forms which are homozygous in respect both of colour and of shape. A glance at the gametic formulæ at the ends of the columns and rows which intersect to form these squares at once gives the reason. These are the squares formed by the intersection of columns and rows with the same gametic formulæ at their ends.

Another point brought out by this Table is that the zygotes lying in the squares on the diagonal passing from the top right to the bottom left corner of the Table, contain the four yellow rounds which are heterozygous in respect both of colour and of shape.

It will also be seen that the four kinds of zygotes in a row to the right of a given gametic formula are the same, and follow one another in the same order (reading from above below in the column, and from left to right in the row) as those in the column under the same gametic formula. In the YR column and row, the squares 1, 2, 3, 4 are the same as 1, 5, 9, 13. In the YW, 5, 6, 7, 8 are the same as 2, 6, 10, 14. In the GR, 9, 10, 11, 12 are the same as 3, 7, 11, 15. And, lastly, in the GW, 13, 14, 15, 16 are the same as 4, 8, 12, 16.

A familiarity with the simple properties of such

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a sixteen-square table as this is indispensable both to the student of heredity and to the practical breeder.

Now, with regard to the breeding properties of various zygotic types exhibited on this Table. These may be most conveniently exhibited in tabular form :—

<i>Number of externally distinguishable forms</i>	<i>Zygotically different types</i>	<i>Number</i>	<i>Breeding properties, when allowed to self-fertilise</i>
YR	(1) YY.RR	1	Produces yellow rounds only
	(2) YY.RW	2	Produces yellows, about 75 per cent. of which are round, and the rest wrinkled
	(3) YG.RR	2	Produces rounds, about 75 per cent. of which are yellow, and the rest green
	(4) YG.RW	4	Produces YR, YW, GR and GW in the ratio 9 : 3 : 3 : 1
		<u>9</u>	
3 YW	(5) YY.WW	1	Produces yellow wrinkleds only
	(6) YG.WW	2	Produces wrinkleds, about 75 per cent. of which are yellow, the rest green
		<u>3</u>	
3 GR	(7) GG.RR	1	Produces green rounds only
	(8) GG.RW	2	Produces greens, about 75 per cent. of which are round, the rest wrinkled
		<u>3</u>	
1 GW	(9) GG.WW	1	Produces green wrinkleds only
		<u>1</u>	

I have recognised all these nine zygotic types in my own breeding experiments.

It will be remembered that the cross which gave this variety of forms was between a yellow wrinkled and a green round. Two new types have arisen in the second hybrid generation—the yellow round and the green wrinkled. The latter may be counted upon to, and actually does, breed true at once; and it only takes one generation longer to fix the yellow round. All that is necessary, to do this, is to sow the YR seeds, the cotyledons of which constitute the second hybrid generation, so that the plants raised have plenty of room, and then, when they are ripe, to look for a plant all of the seeds of which are yellow round. There should be one such plant amongst every nine of the YR of the second hybrid generation, and its seeds, when sown, will produce nothing but yellow rounds.

If, instead of crossing a yellow wrinkled with a green round, a cross had been made between a yellow round and a green wrinkled, the same series of forms would have been produced in the second hybrid generation, and in the same proportions; but the two new forms in it, in this case, would have been the yellow wrinkled and the green round. The isolation of both these forms in a pure state takes the same time as that of the yellow round described above. The yellow wrinkled seeds, the cotyledons of which constitute the second hybrid generation, are sown. All the seeds on the plants produced will be wrinkled, but in two out of every three plants they

will be yellow and green in the ratio of three to one ; on the remaining plant they will be yellow wrinkled only. These, when sown, will produce nothing but yellow wrinkled. Similarly with the isolation of the green rounds. The green rounds in the second hybrid generation are sown ; two out of every three plants produced will bear round as well as wrinkled green, the remaining plant will produce green rounds only. These, when sown, will do likewise.

It is not, in my opinion, necessary to give any further instances of the application of this sixteen-square Table to practical problems. What the breeder wants is a working familiarity with this Table. If the reader understands it properly and has cases which can be dealt with by its help, there will be no difficulty in applying it to them. It is convenient for this purpose to have this Table in a general form, as on p. 214. "A" and "a" stand for the dominant and recessive members of one pair ; "B" and "b" for those of another pair.

There is one point in regard to the criticism of Mendelian theory which may be emphasised here. The fact that the 9 : 3 : 3 : 1 ratio can be deduced from a theory of the gametic contents of the germ cells of the hybrid does not prove that theory to be true, because not only can the 9 : 3 : 3 : 1 ratio be shown to follow from the mere combination of two 3 : 1 ratios, but the existence, and frequency of occurrence, of the nine zygotic types described on p. 211 follows from the combination of two 1 : 2 : 1 ratios, as explained on p. 100. My point is this :

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It is not permissible for the Mendelian to argue in this way, "I start with my theory to account for the phenomenon of segregation in the 1 : 2 : 1 ratio ; from this I derive the 9 : 3 : 3 : 1 ratio ; from this, in its turn, I derive the 9 : 3 : 4 ; and so on. I am like a con-

		♂ gametes			
		AB	Ab	aB	ab
♀ gametes	AB	AA.BB	AA.Bb	Aa.BB	Aa.Bb
	Ab	AA.Bb	AA.bb	Aa.Bb	Aa.bb
	aB	Aa.BB	Aa.Bb	aa.BB	aa.Bb
	ab	Aa.Bb	Aa.bb	aa.Bb	aa.bb

jurer who balances successive objects one on the top of the other. Surely if the first object were insecure, the whole series would totter. Surely there could be no better evidence of the truth of the theory which constitutes the foundation than the fact that the successive predictions based on it, and then on one another, are fulfilled." The answer to this is that the fulfilment of the successive predictions would

certainly support the theory in question if this theory were the foundation on which they were based. But it is not. The basis on which these two types of segregation, in the ratio  $9:3:3:1$  and  $9:3:4$ , rest is the phenomenon of segregation in the ratio  $1:2:1$ , and not the theory by which it is sought to explain this phenomenon. And the fact that the predictions made from this basis are fulfilled is only evidence of the reality of this basis, i.e. of the occurrence of the  $1:2:1$  ratio (about which, however, there is no doubt), and it throws no light on the theory put forward to account for this basis.

I propose to deal now with the general biological conclusions which have been derived from the theoretical considerations set forth in this chapter.

It will have been observed that we have dealt with the interpretation of the mode of inheritance of only two pairs of characters; and, moreover, that these two pairs of characters were entirely independent of one another in their transmission. But it is obvious that a very much larger number of characters is concerned every time fertilisation takes place; and it is a fact that distinct characters are not always transmitted independently. Let us deal with the general question of the number of characters first, and with their relation to one another, whether independent or otherwise, afterwards.

In the opinion of those who accept Mendel's theory as foreshadowing, if not as, in its present state, actually constituting a valid theory of heredity in general, the number of characters con-

cerned every time fertilisation takes place is certainly very large; it is nothing less than the sum total of the characters of the organism in question. According to this generalised Mendelian theory, the organism is made up of a number of characters which are called unit-characters, because they are transmitted as independent units in inheritance. These unit-characters were, in the early days of Mendelian speculation, considered to be associated in pairs, but as explained in Chapter IX., the pair is now regarded as consisting in the presence of a particular character as its dominant member, and the absence of this character as its recessive member. But this is a secondary feature of the theory. The essence of it is that the organism is built up of an obviously immense number of separately transmissible unit-characters, the number, limits, and nature of which can be determined by experimental breeding. With regard to the soundness of this theory, all we know at present is that it applies to the relatively small number of characters which have been dealt with in Mendelian studies. This knowledge is sufficient to justify its application to practical problems, if there is reason to believe that the inheritance of the hereditary characters under consideration is of, or approximates to, the Mendelian type. But this knowledge is not as yet by any means sufficient to warrant even the hope that the future problems of heredity will be solved by its aid. I am, however, merely concerned here in enunciating this theory, and not in estimating its truth.

There remains one section of the theory to be dealt with. This relates to what has been called gametic purity. By this is meant the idea that the distribution of unit-characters amongst the germ-cells is discontinuous; in other words that a germ cell either contains the factor for a particular unit-character or it does not; there is no intermediate condition, no half-way house. It is not possible for a germ cell to contain a mixture of yellowness and greenness; that was why YG was not a permissible combination of letters amongst the formulæ of the gametes outside the sixteen-square Table. Also, it is not possible for a germ-cell to have more or less of a particular character; it has either got it or it has not. That was why GG was not a permissible formula for a gamete. For a zygote it is, of course.

There has been a good deal of misunderstanding as to what is meant by gametic purity, and consequently a good deal of unintentionally irrelevant criticism of Mendelian theory. Let me indicate what the precise significance of the Mendelian teaching on this point is. One of the most practically important of the corollaries which follow from this doctrine of gametic purity is that the extracted dominants or recessives of the second hybrid generation *are identical in respect of a particular character* with their pure dominant or recessive grandparents which were mated to make the cross. The form which this sometimes takes in the mouths of objectors is, "The extracted recessive or dominants *are identical* with the pure dominant and recessive grandparents,

etc.” Now this is demonstrably untrue, and no one familiar with Mendelian phenomena ever made such a statement. Pure and extracted forms are only supposed to be identical *in respect of particular character or characters*.

For instance, the albinos which appeared in the second hybrid generation of my experiment, though to all appearances identical with the pure albinos, proved themselves, when mated with waltzers, to be very different from them in their breeding properties. For amongst the offspring of extracted albinos mated with waltzers there appeared pink-eyed and even albino mice, forms which are never produced when pure albinos are mated with waltzers; and this fact was hailed by objectors to the Mendelian theory as a conclusive proof of the falsity of the doctrine of the purity of the gamete. “We have met you on your own ground,” they declared, “and have defeated you. Here were two albinos which ought, according to your theory, to be identical. We tested the contents of their germ cells according to your teaching, and we have demonstrated that they are fundamentally different.”

But a familiarity with the Mendelian account of reversion, to be given in the next chapter, will at once explain how such a result could occur and be in perfect accord with Mendelian theory as now held. There were, in all probability, amongst the albinos in my second hybrid generation three zygotic types corresponding to the three zygotic types of white-flowered peas in the second hybrid generation

of the experiment illustrated on Plate IV., and interpreted on p. 226.

I mention these facts and their possible interpretation merely to show the reader that results which, in the mind of a casual observer, may appear to be incompatible with the doctrine of gametic purity do not in fact bear on it one way or the other.

In this chapter attention has been paid to two pairs of characters in which neither of the characters of one pair exert any effect on either of those of the other. The theory to be enunciated in the next chapter is based on the fact that the dominant member of one pair exerts a very profound effect on the dominant member of another pair; it is a necessary condition of its visible existence.

## CHAPTER XIV

### THE THEORY OF REVERSION

THE Mendelian theory by which it is sought to explain the phenomenon of reversion will be dealt with in this chapter. By way of illustration, the result of crossing a white-seeded with a grey-seeded pea, and that of crossing a white-flowered with a pink-flowered variety of pea will be taken (see Fig. 27 and Plate IV.).

The two pairs of characters in the colour of the seed-coat with which we are concerned here are purple-spot (P) and absence of purple-spot (p), and grey (G) and absence of grey (g). According to the theory, the character P has this remarkable property, that the zygote which contains it cannot manifest the purple-spot unless the character G be present also. The formulæ for the gametes of the white-coated and grey-coated pea crossed are, for the grey-skinned, Gp, namely, presence of grey and absence of purple-spot; and for the white-skinned, gP, namely, absence of grey and presence of purple-spot, which, however, cannot be manifested in the absence of the grey-coat. Suppose the white-coated were used as the female parent, the union of the gametes and its result would be represented as follows:—

$$\begin{array}{rcccl} \text{Gametes of white} & & \text{Gametes of grey} & & \\ \text{seed-coated } \text{♀ parent} & & \text{seed-coated } \text{♂ parent} & & \text{Zygote produced} \\ gP & \times & Gp & = & GgPp. \end{array}$$

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The purple-spot appears in the zygote produced because the factor for grey-coat and purple-spot co-exist in this zygote. The reason of its absence from either parent will be seen from their zygotic formulæ; the grey-coated is GGpp, i.e. grey but no purple-spot; the white is ggPP, i.e. purple-spot but no grey.

Germ-cells of four kinds, according to the character-factors which they contain, would be produced by the hybrid, namely GP, Gp, gP, gp, and the number and kinds of zygotes produced by their random union can be discovered, as in the case of the 9 : 3 : 3 : 1 ratio, by plotting their possible combinations on a sixteen-square Table. This Table conforms precisely to the general type given on p. 214.

		♂ gametes			
		GP	Gp	gP	gp
♀ gametes	GP	GGPP 1	GGPp 2	GgPP 3	GgPp 4
	Gp	GGPp 5	GGpp 6	GgPp 7	Ggpp 8
	gP	GgPP 9	GgPp 10	ggPP 11	ggPp 12
	gp	GgPp 13	Ggpp 14	ggPp 15	ggpp 16

## BREEDING

The external appearance of these four zygotic types is given in the subjoined Table :—

Purple-spotted Grey 1	Purple-spotted Grey 2	Purple-spotted Grey 3	Purple-spotted Grey 4
Purple-spotted Grey 5	<b>Grey</b> 6	Purple-spotted Grey 7	<b>Grey</b> 8
Purple-spotted Grey 9	Purple-spotted Grey 10	WHITE 11	WHITE 12
Purple-spotted Grey 13	<b>Grey</b> 14	WHITE 15	WHITE 16

From this it will be seen that there are nine purple-spotted greys, three greys and four whites. This Table is precisely analogous to that for cotyledon colour and shape. The purple-spotted grey characters correspond to "yellow round" in that, in both of them, two dominant characters are present in the same zygote, either in the homozygous or heterozygous condition. The greys correspond to the yellow-wrinkled because they possess only one dominant character, namely grey (in the DR or DD condition); and one recessive, absence of purple-spot.

The three whites—and here we come to the really interesting part of the sixteen-square Table illustrating the union of gametes of reversionary hybrids—the three whites in squares 11, 12 and 15 correspond to the green rounds, and bear the same relation to the greys as the green rounds bore to the yellow wrinkleds; that is to say, they possess the recessive factor for the character in respect of which the grey was dominant, namely, absence of grey; and they possess the dominant factor for the character in respect of which the grey was recessive, namely, purple-spot, which, however, is not seen in the seed-coat because this is white and not grey—the presence of grey, as already explained, being a necessary condition for the manifestation of the purple-spot. The white in the corner (in square 16) corresponds to the green wrinkleds, possessing, as it does, two recessive characters; and it differs from the other whites in that it is a pure white, i.e. it does not possess the factor for purple-spot as the three other whites do.

The parallelism between the Tables giving the 9:3:4 ratio and that giving the 9:3:3:1 is complete in every particular. For instance, in the former, as in the latter, the four zygotes homozygous in respect of both their characters lie along a diagonal passing across the Table from the top-left to the bottom-right corner, whilst the four zygotes heterozygous in both their characters (all purple-spotted greys in this Table, as all yellow rounds in the other) lie along the other diagonal.

The theory put forward to explain the results of crossing a pink-flowered with a white-flowered pea will now be briefly set forth on the same lines. This case is given as well, because, for practical purposes, it is more convenient than the seed-coats; in the first place, the characters, pertaining as they do to the flowers, form more suitable objects for demonstration in the garden than the seed-coat characters; though these are very useful as permanent exhibits. In the second place, for the purposes of experimentation, characters of the flower are much more convenient than those of the seed-coat, because in the case of the former the character of the individuals being mated can be seen at the time the cross is being made—indeed, it cannot but be seen; whilst in the case of the seed-coat characters the actual characters of the plants mated cannot be determined until they are dry and ripe, except indirectly and imperfectly by the known fact that a white flower is associated with a white seed-coat, and a purple one with a grey *or* purple-spotted grey seed-coat.

The instances of flower colour and of seed-coat colour also follow one another in a natural sequence, inasmuch as the interpretation of the former is made more readily intelligible by a familiarity with the theory which is put forward to explain the latter. For in the case of the flower colour it is unlikely that the theory that the purple was due to the simultaneous presence of two colour factors (namely, blue and pink) belonging to distinct pairs, would have suggested itself if the similarity of the composition of the

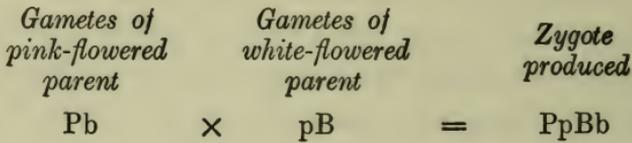
second hybrid generations in the two cases (9 purple, 3 pink, and 4 white in flower colour, and 9 purple-spotted grey, 3 grey, and 4 white in seed-coat) had not given the clue. In the case of the seed-coat this interpretation is relatively obvious, inasmuch as the two dominant characters, the purple-spot and the grey background, can be seen as distinct and separate things when present in the same zygote; whereas in the case of flower colour the one is superimposed on the other, the blue on the pink, or vice versa, in such a way as to afford no indication that the resultant blend is compounded of two distinct things.

The two pairs of factors involved in this case are blue (B) and absence of blue (b), and pink (P) and absence of pink (p). Blue bears the same relation to pink as purple-spot does to grey—namely, that the blue factor is unable to manifest itself in the absence of pink. It can only come into being in a zygote in which pink also exists, so that blue never appears as such, because it can only exist in the presence of pink, and the two together make purple. But pink can exist in the absence of blue, just as grey can exist in the absence of purple-spot.

If blue were not dependent on the presence of pink for its development, the second hybrid generation, the types composing which are shown in Plate IV, would have been 9 purple, 3 pink, 3 blue, and 1 white. Also the cross would have been between a pink and blue, or between a purple and white.

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But to return to the case as it is. The union of the gametes of the pink and white parents of the cross may be represented as follows:—



The union of the gametes produced by this hybrid would be represented as follows:—

		♂ gametes			
		PB	Pb	pB	pb
♀ gametes	PB	PPBB 1	PPBb 2	PpBB 3	PpBb 4
	Pb	PPBb 5	PPbb 6	PpBb 7	Ppbb 8
	pB	PpBB 9	PpBb 10	ppBB 11	ppBb 12
	pb	PpBb 13	Ppbb 14	ppBb 15	ppbb 16

The external appearance of the sixteen zygotes shown in this Table is given on page 228.

The relation between the constituent factors and the resulting external appearance can be more readily perceived by comparing the Table on p. 229 with that on p. 228.

The factor for *pink* is written ○

The factor for *absence of pink* ◐

The factor for *blue* ●

The factor for *absence of blue* ◑

In this Table, as in that representing gametic unions in seed-coat colour, the four whites occupy the four bottom right-hand squares. The three whites in the squares 11, 12 and 15 carry the factor for blue, as the Table on p. 229 shows. There are two types of them. One of them, No. 11, is homozygous for the blue factor; the other two, Nos. 12 and 15, are heterozygous for the blue factor. The only white carrying no blue is the one in square 16. That is to say, there are three zygotic types of whites altogether.

Now, it must not be supposed that the correspondence between the theory, as set forth on this Table, with the actual result which it was invented to explain, is proof that the theory is true. It cannot be denied that the expectation based on this theory is the occurrence of four white, three pink, and nine purple-flowered plants amongst every sixteen, on the average, in the second hybrid generation. Nor can it be denied that these three things occur in these proportions. But a great deal more than this is wanted before the truth of the theory can be admitted. The three zygotic types of white, for instance, must be shown

to exist. In this case the theory is in advance of our knowledge; it is not yet known whether these three types do exist. But this can be easily determined by mating all the whites which occur in such a second hybrid generation with pure pinks. Let

1 Purple	2 Purple	3 Purple	4 Purple
5 Purple	6 <b>Pink</b>	7 Purple	8 <b>Pink</b>
9 Purple	10 Purple	11 WHITE	12 WHITE
13 Purple	14 <b>Pink</b>	15 WHITE	16 WHITE

us see what will be the result of mating the three types of white with pure pinks the formula of which would be PPbb.

The single white homozygous for blue with the formula ppBB (No. 11)\* will be considered first. The union is of this type. The pink produces only one kind of gamete, Pb, and the white also produces only one kind, pB; the result of their

\* See Table on p. 226 or p. 229.

union is, therefore, always heterozygous purples.  
Thus :—

$$pB \times Pb = PpBb$$

The two whites heterozygous for blueness, Nos. 12 and 15, with formula  $pPbB$ , will produce two kinds

		♂ gametes							
		○ ●	○ ☾	☾ ●	☾ ☾				
♀ gametes	○ ●	○ ○ ● ● 1	○ ○ ● ☾ 2	○ ☾ ● ● 3	○ ☾ ● ☾ 4				
	○ ☾	○ ○ ● ☾ 5	○ ○ ☾ ☾ 6	○ ☾ ● ☾ 7	○ ☾ ☾ ☾ 8				
	☾ ●	○ ☾ ● ● 9	○ ☾ ● ☾ 10	☾ ☾ ● ● 11	☾ ☾ ● ☾ 12				
	☾ ☾	○ ☾ ● ☾ 13	○ ☾ ☾ ☾ 14	☾ ☾ ● ☾ 15	☾ ☾ ☾ ☾ 16				

of gametes,  $pB$  and  $pB$ , so the result of mating them with pink can be most conveniently foretold by means of the four-square table on p. 230, the external characters of the four zygotes produced being shown in the Table alongside.

The result of this union is, therefore, equal numbers of purples and pinks.

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		Gametes of Pink			
		Pb	Pb		
Gametes of White	pB	PpBb	PpBb	Purple	Purple
	pb	Ppbb	Ppbb	Pink	Pink

The last remaining white, No. 16, which produces one kind of gamete only (pb), carries no blue at all, so that when mated with pink it will produce no purples, but only pinks. Thus:—

$$pb \times Pb = Ppbb$$

The total result of mating these three zygotic types of white-flowered peas of the second hybrid generation with pure pinks may be represented in tabular form, thus:—

White Parent	Pink Parent	Percentage of Purples produced	Percentage of Pinks produced
ppBB	PPbb	100	
}	ppBb	50	50
	ppBb	50	50
	ppbb	PPbb	

That is to say, equal numbers of purples and pinks will be produced on the average, if a large number of crosses are made; and, if the theory expressed in

the sixteen-square Table on p. 226 be true, they must be distributed as shown in the last two columns of the foregoing Table. Nothing short of the carrying out of an experiment of this kind on a large scale will suffice to prove the truth of the Mendelian theory of reversion in this case.

Assuming that it will stand this test—and I have reasons for believing that it will—we see that we have here a consistent theory of reversion for the first time. Reversion, according to this theory, is due to the meeting in one zygote of the two factors necessary for the production of the ancestral character. These factors had, presumably, at some period become separated and lodged the one in one and the other in the other of the two strains which, when they are mated, produce the reversionary hybrids. In the case of flower colour in *Pisum* it is not difficult to make a suggestion as to how this occurred. The wild *Pisum*, of which I have grown plants from seed kindly given me by Mr. Arthur Sutton, has a purple flower. But this is not a heterozygous purple but homozygous (i.e. of the formula PPBB), because it breeds true to purpleness and never produces pinks and whites. Where, then, did the pink come from? This question may be answered by making only one assumption, which is amply warranted by the frequency of analogous instances of the same occurrence throughout the vegetable kingdom. This assumption is that a white-flowered variety of the pea arose by mutation from the purple-flowered by the sudden and simultaneous loss of both

of the factors necessary for the production of purple. It would have the formula ppbb. If mated with the pure purple it would give heterozygous purples, PpBb; and if these were then self-fertilised and set seed, they would produce purples, *pink*s, and white. Another possibility, and perhaps a more probable one, is that the homozygous purple suddenly mutated to the heterozygous condition; the self-fertilised seed of such a plant would produce whites, purples and *pink*s. In this case it is not necessary to assume, first, that a new form appeared by mutation from the purple, and then was crossed back with it. This question, however, of the origin of Mendelian characters will be dealt with in Chapter XVII. All that I am concerned with now is the idea that the two factors necessary for the production of purple in the power of *Pisum* did become separate at some period, and one of them (P) lodged in a pink-flowered strain, and the other (B) in a white-flowered one, and that the reappearance of this purple as the result of a cross is due to the re-union of these two factors in the zygote resulting from a cross between the two strains mentioned.

## CHAPTER XV

### SOME NEW PRINCIPLES OF BREEDING BASED ON MENDEL'S THEORY

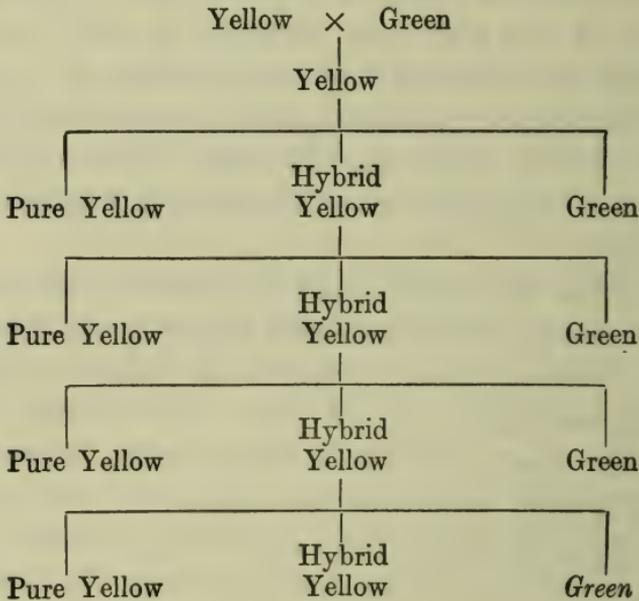
How the theory of heredity of the future will differ from that of the past can, perhaps, be most easily made clear by describing an experiment as to the result of which the expectation based on the Mendelian theory and that based on the older notions which it is likely to supplant are diametrically opposed to one another.

The reader will not need to be reminded that the result of crossing a yellow-seeded with a green-seeded pea is a yellow, which produces a second hybrid generation consisting of 75 per cent. yellow and 25 per cent. green. There is this proviso, however, that this is only known to be true when the green and yellow, with which the cross is made, belong to pure green and pure yellow strains. But this should make no difference according to the Mendelian theory: a yellow, provided its zygotic formula is YY, and a green, provided its zygotic formula is GG, should, whatever their ancestry, give rise to yellows which will produce 75 per cent. yellows and 25 per cent. greens, when self-fertilised. The expectation based on the Mendelian theory is in violent opposition to what the old notions of heredity would lead us to

## BREEDING

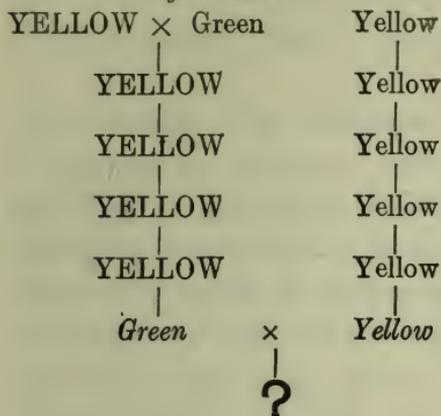
expect, for according to these notions the ancestry of two individuals mated, play a very large part in determining the result of the mating.

The cross made was this. Instead of mating a pure yellow cotyledoned strain with a pure green one, I mated it with an extracted green of the fifth hybrid generation; that is to say, with the green printed in italics in the following pedigree:—

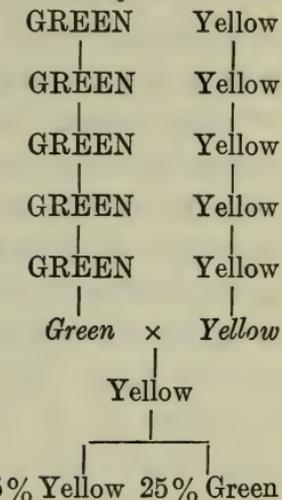


This green was mated with a pure yellow and, according to the Mendelian theory, the result of the union should be the same as that of a mating between a pure yellow and a pure green. Before considering the actual result, it will be well to look at the ancestries of these two kinds of mating set forth, side by side, in the form of pedigrees:—

*Ancestry of cross between pure yellow and extracted green of the Fifth hybrid generation*



*Ancestry of cross between pure yellow and pure green*



When the two parents of a generation are alike, their character is only written once. The two forms crossed in each case are printed in italics. The ancestors in respect of which their pedigrees differ are printed in capital letters.

The result of the type of mating at the right is well known, and is written there to emphasise the fact that the result of the mating to the left is not known.

Anyone unfamiliar with Mendelian phenomena, and with only these two pedigrees to go upon, would unhesitatingly declare that the result of the two matings would not be the same. He would predict with some confidence that, the result of the mating to the right being what it is stated to be, the result of the mating to the left will differ from it in showing a much lower percentage of greens in the second hybrid generation. "I cannot but believe," he would argue, "that the great weight of yellow

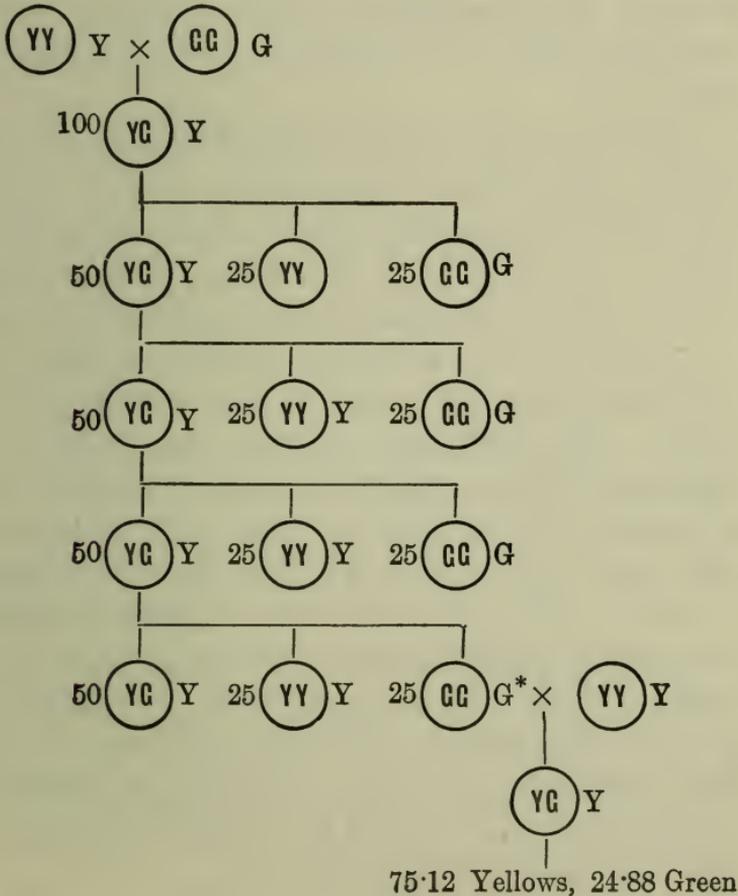
ancestry behind the green in this case will make itself felt by increasing the proportion of yellows and diminishing that of greens in the second hybrid generation produced."

The actual result is entirely in accord with Mendelian expectation. Our interest, of course, is focused on the second hybrid generation. The first is yellow, as in the normal cross. The ratio of greens in the second hybrid generation is 24.88 per cent., as close an approximation as is ever obtained to 25 per cent. This ratio, 24.88 per cent., is based on what is, I believe, the largest second hybrid generation that has been observed. It consisted of 139,837 individuals (in this case, of course, seeds), the actual number of yellow ones being 105,045, and of greens 34,792.

To anyone brought up solely on Mendelian principles—and it is possible that this book may, some day, fall into the hands of such an one—this result will not seem in the least unexpected. But I would remind the reader that this is written at a time when the number of people who have derived their notions of heredity solely from teaching given in post-Mendelian times (namely, since 1900) is very small, and that I myself derived my ideas of heredity from teachers who held exactly the same views on heredity as those expressed in the last paragraph but one.

The conformity of the result with Mendelian expectation is seen directly we pay attention, not to the somatic characters of the individuals in the pedigrees on the preceding page, but to the contents

of their germ-cells. The ancestry of the extracted green, marked with an asterisk, is given below in a pedigree which includes the collateral ancestors, and displays the zygotic constitution, and consequently the germinal contents, of all the ancestors. Outside the circles, which represent zygotes, are printed to the right the somatic characters of the individuals, whether yellow (Y) or green (G); outside the circles, to the left, the ratios in which they occur; and inside the circles their zygotic formulæ:—



Only the ratio of the greens to the yellows is inserted in the bottom line of the pedigree, because the constitution of the yellows has not been determined. Nor does it concern us here.

The result of this experiment, therefore, shows that, if we confine our attention to one pair of characters at a time, the attempt to predict the result of a given union must be based on a knowledge of the factors representing these characters in the germ-cells of the two individuals mated, and that the only knowledge of the characters of their ancestors which is required is such as is necessary to discover what these factors are.

Besides supporting this general thesis, the result of this experiment tests another corollary of equal practical interest which follows from the Mendelian theory. It tests the truth of the assertion that an "extracted" individual in any generation is as pure in respect of the character which it bears as an individual in a pure strain characterised by this feature. For instance, it tests the truth of the statement that an extracted green in the fifth hybrid generation is identical in respect of its greenness with a pure green, and it proves that this statement is correct. Not only is the colour of such an extracted green apparently identical with a green of a pure strain, but its breeding properties are identical, as shown by the result of mating it with a pure yellow. This conclusion is merely, however, an instance of the special application of the general conclusion set forth in the last paragraph.

There are two points of view from which this conclusion may be regarded—the general biological one and the strictly utilitarian one. If we regard it from the former point of view, we have to ask ourselves whether we are prepared to believe that the activities of the soma play no part in determining the structure of the soma in subsequent generations. For my own part, I am by no means prepared to state that I believe any such thing. In the first place it is extremely doubtful whether any more than a few hundred characters, the vast majority of which exist only in a state of domestication, are inherited in Mendelian fashion; and, in the second place, we have to remember that the changes to which evolution is due have either been imperceptibly small or, if not small, have been separated by immense numbers of generations, and that, in either case, they have extended over such prodigious periods of time that it is improbable that any observations likely to throw any light on their nature will be made in the number of centuries during which public opinion will remain stable enough to continue these observations on the same lines, and still less in the number of years during which a single man can devote his attention to them.

If on the other hand the conclusion, stated at the end of the last paragraph but two, be regarded from the utilitarian point of view, comfort may be derived from the reflection that most of the characters of animals and plants which are of economic importance seem to be inherited in Mendelian fashion; and

also from the fact that the equipment and time at the disposal of the biologist, though at present absolutely inadequate for the purpose of grappling with evolution as a whole, are probably sufficient for the task of effecting such improvements in domesticated races of animals and plants as may be required.

This being the case, our next step is to deal more fully with the application of Mendelian principles to the practice of breeding. I have already insisted on what, in my opinion, is the most important service which Mendel's work has done for the science of heredity, namely, the establishment of the principle that the contents of the germ-cells, and not the outward characteristics of the animals and plants dealt with, must be our guide in breeding.

This principle can as yet only be applied when the inheritance of the characters, which are being bred for, fits, or may be expected to fit, into some recognised scheme of heredity, such as the Mendelian. If the mode of inheritance of the character in question is demonstrably not Mendelian, and does not correspond to any of the types recognised by de Vries in the vegetable kingdom, it must be carefully described and, if possible, interpreted; though the latter is not important. What is urgently needed is an accurate description of the various ways in which the characters of domesticated animals and plants are inherited. It will be time enough to interpret them when our knowledge of them is a great deal more perfect than it is at present. For instance, there is one question of the greatest importance to

the breeder on which the present available information is very scanty. It is the simple question of the inheritance of bulk. In the pea, for instance, there is a race with a seed as large as that of *Victoria Marrow*, and also a race with a seed half its size, as in some of the continental field peas. Now these two characterisers, "large" and "small," do not constitute the two members of a Mendelian pair; the cross between them is a blend, and so far as data at present available show, segregation does not occur when the hybrids are self-fertilised. If one of these "small" races possessed, as one of them happens to do, an economically valuable character, and if it is desired to combine this character with "large" size in a single strain, this would be an easy matter if "large" and "small" constituted the members of a Mendelian pair. But as—or let us say, supposing—they are not, we cannot proceed to effect this combination until the mode of inheritance of these two characters has been determined. The most important point to discover in such an inquiry would be to determine which, if any, of the types in the second hybrid generation bred true. This generation might consist of a complete series of gradations between a "small" identical with the pure "small" at one end, and a "large" identical with a pure "large" at the other end; and it might possibly be that these two extremes of the series bred true, that the blends in the middle of the series never did, and that the forms intermediate between the blends and the extremes bred true in some individuals and not in

others. This is the kind of thing which would have to be found out.

But if the characters bred for are inherited in a Mendelian manner, there is no difficulty as to how to proceed in practice, and, moreover, no question but that the only guide which will conduct the breeder to the end which he wishes to achieve is a knowledge of the character-factors concerned, in the germ-cells of the animals or plants under consideration. For instance, it is clear that in the case of the blue colour in Andalusian fowls, or the red-roan in cattle, the attempt, based on the confinement of one's attention to outward bodily characteristics alone, to raise a pure breed possessing these colours, by only mating animals which exhibited them, is doomed to failure. True, the Mendelian cannot tell the breeder how to raise a strain which will breed true to these colours; but he can tell him how to raise 100 per cent. in each generation where the breeder, acting on the principles which he had learnt from his ancestors, only succeeded in raising 50 per cent.

With regard, now, to this principle of conducting breeding on the basis of a knowledge of the contents of the germ-cells. It may be asked, "How are we to determine the nature of these contents?" The answer in most cases is "By breeding from the individuals themselves; to determine what are the characters in respect of which they are homozygous and what those in respect of which they are heterozygous." Indeed, the difference between modern and old-fashioned principles of breeding may be sum-

marised in the statement that whilst the old-fashioned breeder looked for guidance to the pedigree of the animals and plants he was breeding, the modern one looks to their gametes; the former looks to their ancestry, and the latter to their offspring; the former looks backwards, the latter forwards. A criticism which may be made of the modern method is that it amounts to nothing more than predicting what will happen by finding out what does happen. But this is not, in fact, a fair criticism. In the antithesis in the last paragraph ancestry was opposed to offspring and not to posterity—to one generation only and not to many. The breeder, according to the old principles, required a knowledge of the parents and of as many of the ancestors as possible, and based his prediction on this knowledge without going beyond it. The breeder, according to the new principles, only requires a knowledge of the offspring, and he only needs this as an indication of the germinal contents of their parents; he *does* go beyond the characters of the offspring to the germinal contents of their parents, and bases his prediction on this, and not on the characters themselves.

We have now to deal with another part of the Mendelian doctrine, and with its application to practice. This is the idea that the organism is built up of independently heritable unit-characters. I do not propose to consider here the question how far it is likely that this conception will be found to be applicable to all the characteristics of organisms. That is a question to which, it seems to me, it is not

profitable to attempt to supply an answer until information with regard to a much larger number of characters of wild animals and plants than we know about at present is available. But that this conception does apply to a very large number of the characters of domesticated races is sufficient for the practical breeder. The general realisation of the fact that the unit which has to be handled in experimental breeding is not the individual animal or plant, but the independently heritable unit-character, marks the beginning of a new epoch in the history of the practice of breeding. Once it is clearly understood that dominance and recessiveness attach to characters and not to individuals, one serious obstacle to progress has been removed. And, in my opinion, the most important advance which is rendered possible by the removal of this obstacle will be effected by a systematic inquiry into the nature and mutual relationships of the characters, whether Mendelian or not, which go to make up the organism. By "nature" I mean whether they conform to the Mendelian or to some scheme (which must then become the subject of investigation) in the manner of their inheritance; and by "mutual relationships" I mean whether they are transmitted independently of other characters in inheritance or in association, and, if so, how close the association is. This phenomenon of the association of character is a very important one in practice, and may be illustrated by characters of the culinary pea. The colour and shape of the cotyledons are, as the reader knows,

absolutely independent of one another. A pea which is yellow is not for that reason any more or less likely to be round. At the other end of the series there are two such characters as the purpleness of the flower and the purpleness of the axil, the angle where the flower-stalk joins the main stem. These two characters cannot be separated by hybridising; it is impossible to breed a purple-flowered pea with a green axil, or a purple-axilled one with a white flower. The two characters are apparently indissolubly connected. The comment may be made, on this, that they are not two characters, but one. And my answer to this is that I have no objection to expressing the fact that two characters are indissolubly associated by calling them one character, except that it is better to refer to two apparently indissociable characters which we can conceive of as being separated, or desire to be separated, as two characters, partly because it may turn out that they are separable by as yet undiscovered methods, and partly because by naming them one character we renounce the attempt to separate them.

Between these two extremes of association there are intermediate forms. A great deal of work has been done in the hope of interpreting the various types of association on Mendelian lines. These, however, do not concern us here, and it will suffice to describe a single instance of two characters belonging to distinct pairs which are imperfectly associated together. One of these characters is purpleness of flower in the culinary pea; the other is the occurrence

of the first flower at a relatively high node on the plant, which is the chief condition determining lateness. The allelomorph to purpleness in the flower is white, and the allelomorph\* to highness of node of first flower is lowness. In the second hybrid generation, raised from a hybrid produced by crossing a "high" purple with a "low" white, there is evidently a strong tendency for purple to be associated with "high" and white with "low." With a very low percentage of exceptions, all the purples are "high" and all the white "low"; but there are just a few "lows" amongst the purples, and a few "highs" amongst the whites, which show that the two characters are not associated so closely as, for instance, purpleness of flower and purpleness of axil.

In conclusion it may be said that the urgent need of the present is an exhaustive enquiry, undertaken by independent observers, into the mode of inheritance of the characters of domesticated animals and plants. It will be time enough to systematise this knowledge when there is more of it.

\* I.e., the other character of the same pair.

## CHAPTER XVI

### THE INHERITANCE OF SEX

IN the previous chapter the manner in which the practice of breeding will probably be modified by the dissemination of the main conclusion which flows from Mendel's work was indicated. In the present chapter a theme of mere academic interest will engage our attention, namely, the application of Mendelian principles to the question whether there is a fundamental and constitutional—to be absolutely precise, a zygotie—difference between the sexes.

One of the most recent, and certainly the most interesting, of the applications of Mendelian principles consists in the attempt to interpret the phenomena of sex by means of these principles. But before this theory is described it is necessary to present certain cases in which the normal course of Mendelian inheritance is disturbed by the interference of sex.

A horned breed of sheep—the Dorset Horned—in which the horns are well developed in both sexes, was crossed\* with a hornless race, such as the Suffolks, both sexes in which are hornless. The result was that all male lambs of the first hybrid generation developed

\* Note on the "Inheritance of Horns and Face Colour in Sheep."—*Journ. Agric. Sci.*, vol. i., pt. 3, p. 364.

horns, whilst the female remained hornless. The result of reciprocal crosses was identical. It looks as if the horned character were dominant in males, but recessive in females. But this view is shown to express the truth imperfectly by the appearance in the second hybrid generation of horned ewes and hornless rams. The explanation of these phenomena, so far as it is an explanation, is found to be that a ram is horned both when he is heterozygous (DR) and homozygous (DD) for the horned character, whilst a ewe is horned only when she is homozygous for it. That is why all the ewes in the first hybrid generation were hornless. In other words, a ram will develop horns with only one dose of the horned character, which is present in the heterozygous condition of that character; but a ewe needs the two doses which are only present in the homozygous condition of that character. There appears to be something in the constitution of the female which inhibits the development, in this case, of the horned character when this is only present in the diluted heterozygous condition. This phenomenon is known as sex-limited inheritance, because the course of descent of a character is affected by the sex of the individuals which bear it.

Another instance of it is afforded by the phenomena of colour-blindness in man. This peculiarity occurs both in men and women, but is very rare amongst the latter. Colour-blind men may transmit the peculiarity to their sons, but very rarely do so to their daughters. These unaffected daughters may,

however, transmit it to their sons. In a word, men cannot transmit the peculiarity without having it, whilst women can. The mode of transmission and the interference of sex would appear to be exactly the same as in the case of the horned character in sheep. A woman is only colour-blind when she is homozygous for the character; a man is colour-blind both when he is homozygous and when heterozygous for it. The normal women who transmit it are heterozygous for it. If this theory is true all the sons of colour-blind women should be affected, because even if she is mated to a normal male all her offspring will be heterozygous for the peculiarity, and that is sufficient to make her male offspring develop it. Records in the possession of Mr. Bateson show that the seventeen sons (who lived to be tested) of seven colour-blind women were all colour-blind. The bearing of these facts of sex-limited inheritance on the Mendelian theory of sex will shortly appear.

Another familiar instance of the results of sex-limited inheritance is afforded by the difference between the male and female offspring resulting from a cross between a black and an orange cat. The general rule would appear to be that the male offspring are orange, whilst the female are tortoiseshell. This is why male tortoiseshells are practically unknown, and why the females occur sporadically, inasmuch as it is not possible to raise a race of tortoiseshells because there are no toms to mate the cats with.

The idea that sex was a Mendelian character

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was first suggested by Professor Castle.\* According to Professor Castle, sex was represented by a factor in the germ-cells exactly as a Mendelian character is. (The factor for maleness will be written ♂, and that for femaleness ♀.) He supposed that both male and female were heterozygous for sex, i.e. both were of the zygotic formula ♂♀. He accounted for the equality in the numbers of the sexes by supposing that, in about half the zygotes, maleness was dominant, and in the other half femaleness was dominant. He also supposed that, when these heterozygotes mated, the unions between like gametes were infertile, because it was his theory that each sex had the formula ♂♀, and it was therefore necessary to explain the non-existence of the zygotes ♂♂ and ♀♀ which, according to the ordinary Mendelian scheme, would result from the union of ♂♀ and ♂♀, thus:—

		Gametes of male	
		♂	♀
Gametes of female	♂	♂♂	♂♀
	♀	♀♂	♀♀

It will be seen that this theory involves two serious assumptions; first, the alternativens of dominance

\* Castle, W. E. "The Heredity of Sex." *Bull. Mus. Comp. Zool. Harvard*, 903. Vol. xl., No. 4.

in the two characters in the heterozygote, to account for the approximate equality in the numbers of the sexes; and, secondly, the sterility of unions between gametes bearing like characters.

Castle's form of the theory has now been superseded by a much simpler one which is due to Mr. Geoffrey Smith. It was briefly referred to in the remarks on p. 181, relating to the possible kinds of union between any two of the zygotic forms, DD, DR and DD, where it was seen that there are only two kinds of union in which the parental types are reproduced in equal numbers, namely,  $DR \times RR$ , and  $DR \times DD$ . Of these two the former is the only one in which the two parental types differ from one another in all cases; that is to say,  $RR$  is always different from  $DR$  in outward appearance, whilst  $DD$  is indistinguishable from  $DR$  except in those cases, like the Andalusian fowl, in which the  $DR$  zygote has a character peculiar to itself. Inasmuch, therefore, as the male differs by external characteristics from the female, and inasmuch as the result of their union is usually the production of males and females in approximately equal numbers, it is natural that the suggestion that one sex was of constitution  $DR$  and the other of constitution  $RR$  should be made.

The theory is this: Femaleness and maleness constitute the two characters of a Mendelian pair. Femaleness is dominant; that is to say, femaleness is due to the presence of a factor the mere absence of which constitutes maleness. But femaleness never occurs in the homozygous condition ♀♀ ( $DD$ ), but

always in the heterozygous ♀♂ (DR), whilst maleness occurs in the homozygous (recessive) condition ♂♂ (RR).

Only one instance of the kind of evidence, based on Mendelian investigations, by which this theory is supported will be given here.

The common currant moth (*Abraxas grossulariata*) has a variety *lacticolor*, which is characterised by the fact that the black spots on its wings, though they resemble those of the parent species in distribution, are very much smaller. This variety is only known as a female.

A series of crossings between the parent species and its variety were made by Mr. Doncaster and Mr. Raynor, and gave the following remarkable results :—

1. *Lacticolor* ♀ × *grossulariata* ♂ gave in F1\* ♂s and ♀s all *grossulariata*.
2. F1 *grossulariata* ♀ × F1 *grossulariata* ♂ gave *grossulariata* ♂s and ♀s, and *lacticolor* ♀s; no ♂s of *lacticolor* appeared.
3. *Lacticolor* ♀ × F1 *grossulariata* ♂ gave all four kinds, *grossulariata* ♂s and ♀s and *lacticolor* ♂s and ♀s. The *lacticolor* males were the first males of the variety that had ever been seen.
4. Perhaps the most curious result of all. F1 *grossulariata* ♀ × *lacticolor* ♂ gave equal numbers of *lacticolor* ♂s and *grossulariata* ♀s.

Mr. Doncaster attempted to account for this remarkable series of results by adopting Professor Castle's idea that both sexes were heterozygous; and he elaborated a consistent explanation of his results.

\* A symbol, introduced by Mr. Bateson, to denote the first hybrid generation.

His theory involves five distinct assumptions, which will not be gone into here because a much simpler explanation, suggested by Mr. Bateson and now accepted by Mr. Doncaster, has obtained general credence. Mr. Bateson's theory involves two assumptions, which are as follows, in his own words:—

1. "That the female is heterozygous in sex, femaleness being dominant, and the male a homozygous recessive (see pp. 251-2).

2. "That when in F1 the two dominant characters femaleness and the *grossulariata* factor co-exist, there is spurious allelomorphism or repulsion between them, such that each gamete takes one or other of these factors, not both."\*

A word in explanation of spurious allelomorphism. True allelomorphism expresses the relation between the dominant and recessive members of the same pair—yellow with green, or round with wrinkled. Spurious allelomorphism is a relation between factors belonging to distinct pairs which gives the appearance of their belonging to the same pair. If a relation of this kind, similar to that which exists between the two dominant characters, femaleness and the *grossulariata* character, were to exist between the two dominant characters, yellow and round, in the heterozygote produced by crossing a yellow wrinkled with a green round, yellow would repel round, so that they could not both exist in the same gamete, just as in true allelomorphism yellow and green cannot exist in the same gamete; yellow could only exist in the

\* "Mendel's Principles of Heredity," p. 175.

same gamete with wrinkled, and a relation of spurious allelomorphism would thus be established between these two characters.

The explanations of the results of the four kinds of mating made by Doncaster would then be represented by the following schemes. The dominant and recessive member of the pair of characters relating to colour, namely *grossulariata* and *lacticolor*, are written D and R respectively; and the dominant and recessive members of the pair of characters relating to sex are written ♀ and ♂ respectively. The gametes are written outside the square, the zygotes inside the squares, and underneath the zygotic formulæ the actual character and sex of the zygote:—

1. *Lacticolor* ♀ × *grossulariata* ♂ produces 50 per cent. ♂s and 50 per cent. ♀s, all *grossulariata*. Thus:—

		Lact. ♀	
		R♀	R♂
F1 <i>Gross.</i> ♂	D♂	DR♀♂ <i>gross.</i> ♀	DR♂♂ <i>gross.</i> ♂
	D♂	DR♀♂ <i>gross.</i> ♀	DR♂♂ <i>gross.</i> ♂

2. F1 *grossulariata* ♀ × F1 *grossulariata* ♂ produces 50 per cent. *gross.* ♂, 25 per cent. *gross.* ♀, and 25 per cent. *lact.* ♀:—

		F1 <i>Gross.</i> ♀	
		D♂	R♀
F1 <i>Gross.</i> ♂	D♂	DD♂♂ <i>gross.</i> ♂	DR♀♂ <i>gross.</i> ♀
	R♂	DR♂♂ <i>gross.</i> ♂	RR♀♂ <i>lact.</i> ♀

3. *Lacticolor* ♀ × F1 *grossulariata* ♂ gives 25 per cent. *gross.* ♀, 25 per cent. *gross.* ♂, 25 per cent. *lact.* ♀, and 25 per cent. *lact.* ♂:—

		<i>Lact.</i> ♀	
		R♀	R♂
F1 <i>Gross.</i> ♂	D♂	DR♀♂ <i>gross.</i> ♀	DR♂♂ <i>gross.</i> ♂
	R♂	RR♀♂ <i>lact.</i> ♀	RR♂♂ <i>lact.</i> ♂

4. F1 *grossulariata* ♀ × *lacticolor* ♂ produces 50 per cent. *gross.* ♂ and 50 per cent. *lact.* ♀:—

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		F1 <i>Gross.</i> ♀	
		D♂	R♀
Lact. ♂	R♂	DR♂♂ <i>gross.</i> ♂	RR♀♂ <i>lact.</i> ♀
	R♂	DR♂♂ <i>gross.</i> ♂	RR♀♂ <i>lact.</i> ♀

Doncaster has since found that the result of crossing pure wild *grossulariata* ♀ with ♂ *lacticolor* is precisely the same as that of mating No. 4 on p. 252; that is, as the result of crossing F1 *grossulariata* with ♂ *lacticolor*. This proves that the wild *grossulariata* female is heterozygous in regard to this character, half her germ-cells bearing the *grossulariata* factor, the other half the *lacticolor* factor.

Here, then, is an instance in which the simplest interpretation of the phenomena is the supposition that the female is heterozygous for sex, femaleness being the dominant character, whilst the male is pure recessive. The value of this case as evidence for the theory that the female is a hybrid in respect of sex and the male is pure recessive does not merely lie in the fact that this is the simplest way of accounting for the facts; for this is also the simplest way of accounting for the fact that males and females are produced in equal numbers in the human species,

and this circumstance would be slender evidence for the truth of this theory. The peculiar interest and value as evidence of cases like that of the currant moth lies in the fact that in them the character of sex has, as it were, become entangled with and entered into permanent relations with a varietal colour-character, the consequences of which insignificant little event has been to withdraw the veil which has all this time hidden the real difference between the sexes from our view.

Bearing in mind the presence and absence hypothesis of the nature of the two characters of a Mendelian pair, it will be observed that, according to the theory we are considering, the female who is heterozygous for sex is characterised by the *presence* of the factor in virtue of which she is female, whilst the male lacks this factor altogether. Even the female, being a hybrid, has only one dose of this factor, whatever it is. The male is male in virtue of the fact that he has none at all. Half of the germ cells of the female contain this factor; the other half lack it. All the germ-cells of the male lack it.

Now this factor, which is present in the female alone, has been identified with the thing which checks the development of certain characters which attain to their full development in the male, in cases of sex limited inheritance. In the case of the horns in sheep there is something in the female hybrid resulting from a cross between a horned and hornless individual which inhibits the development of horns, which attain

their normal size in the male hybrids from the same cross. And this inhibiting something is, as I have said, identified with the dominant factor which is present in the zygotic constitution of the female and absent from that of the male. Those of my readers who are familiar with Otto Weininger's theory, expounded in his "Sex and Character," of the difference between the two sexes will detect a very close parallel between it and the Mendelian view.

Evidence derived from widely different and absolutely independent lines of inquiry tends to support the Mendelian theory. But there is a qualification. The various lines of evidence point to the conclusion that one sex is hybrid and the other pure; but they do not all point to the same sex as being hybrid and pure respectively.

Let us examine them separately. We will deal first with the only one, of those I propose to consider, which, like the Mendelian theory, points to the female as the hybrid. This is contained in a book entitled "The Causation of Sex," by Dr. R. Dawson, which appeared recently. The theory, however, was first enunciated at the Obstetrical Society in 1900, so that there is no possibility of the author having heard of the Mendelian theory of sex, even if the fact that he does not refer to it were not sufficient evidence of this. Dr. Dawson thinks that the male plays no part in determining sex in the human species, that his germ-cells are all indifferent in respect of sex; the female, on the other hand, gives rise to two kinds of

ova, one kind which, when fertilised, will give rise to males, and another which, when fertilised, will give rise to females. The former, the male-producing, arise in the right ovary, and the latter, the female-producing, in the left ovary. So that about equal numbers of the two kinds are given off. When a woman is once mature, an ovum is produced alternately from each ovary, one at a time, at each ovulatory period; a male-producing one from the right ovary; next month a female-producing one from the left; next, a male from the right; then a female from the left again, and so on. So that when a woman has had one child under such circumstances that the date of the ovulatory period at which the egg, from which the child developed, was extruded from the ovary can be calculated, the sexes of any future children required may be arranged. The evidence adduced for the allocation of the male- and female-producing ova to the right and left ovaries respectively cannot yet be considered to have proved the point; nor is the point necessary for our purpose. What is of intense interest is the fact that clinical observations conducted in complete ignorance of Mendelian speculation should have led to the enunciation of a theory of sex which is practically identical with the Mendelian one. The two theories, at any rate, have these points in common. According to both, one sex, the female, produces two kinds of germs, male-producing and female-producing, in equal numbers, whilst the male only produces germ-cells of one kind. The sex, therefore, is determined by the female. Dr. Dawson's

theory and the Mendelian one are, of course, expressed in different terms, but in their essential features they are identical. And, I think, it is very difficult to regard this circumstance as a mere coincidence. It is not likely that either of them is closely in touch with actuality, but that up to a certain point they agree is an indication that a clue has been found.

We have now to deal with pieces of evidence, very different from one another and from those already considered, which strongly support the view that one sex is a hybrid, or, to use a word of wider signification, bipotential, and the other pure, or unipotential, but point to the *female* as pure, or unipotential and the male as hybrid or bipotential.

The first of these indications is derived from Mr. Geoffrey Smith's observations on crabs in the Bay of Naples. The female of this species of crab is characterised by the breadth of her abdomen and the presence, on it, of long filamentous appendages to which the eggs are attached when they are laid, and by the delicacy of her pincer-claws. The male is characterised by the narrowness of his abdomen, the possession of a pair of hard copulatory appendages instead of a number of flexible filamentous ones, and by the much greater size and strength of his pincer-claws.

This crab is occasionally infected by a parasite, called *Sacculina*, which is also a crustacean, though it would never be recognised as such, for it hangs, like a full wallet, from the body of its host, whilst inside it consists of a ramifying system of fibrils which

extend root-like throughout the body. The parasite may kill the crab; if it fails to do this, and the crab recovers, the effects which it produces are sufficiently profound. The internal root-like part attacks the genital organs and destroys them. If the crab recovers the genital organs are regenerated. What is remarkable about the case is that the effect differs according to the sex of the crab affected. If it is a female that was affected very little effect beyond such a slight diminution in the size of her filamentous limbs as could be attributed to the shock of the infection and strain of recovery is observed when she has recovered.

But if it was a male that was affected, the changes brought about are very much more profound, and of a very remarkable nature. They consist not only in the assumption by the male of the external features, already described, which distinguish the female, but in the actual development by him, in the place of the destroyed testis, of a genital organ which contains eggs. The pincers of the male lose their robustness and become reduced to the size characteristic of the female. So do the copulatory appendages. This change might, however, be ascribed to shock and general debility consequent on it; but the other two changes which occur cannot be so interpreted. Not only does the abdomen lose the pointed shape characteristic of the male, but it actually develops the long filamentous swimmerets characteristic of the female.

In a word, this parasite is capable of making a male crab undergo a series of changes which, in bad

cases, may end in its becoming a female; but it is incapable of making the female undergo even the smallest change in the direction of becoming a male.

The general conclusion derived from these facts is that the male contains within his organisation the potentiality of both sexes, only one of which—the male—is manifested under ordinary circumstances; though under the exceptional ones just described it may be suppressed and the female given the opportunity of appearing; whilst the female contains only the potentiality of that sex to which she ostensibly belongs. This conclusion, stated in Mendelian terms, is that the male is a heterozygote, and the female a homozygote, which agrees with the Mendelian theory of the constitution of the sexes in so far as it asserts that one of them is heterozygous and the other homozygous, and differs from it in that it makes the *male* heterozygous and the *female* homozygous.

In the case of the next piece of evidence bearing on the constitution of the sexes we come to very close quarters with the processes which determine sex, and the course of heredity in general—to the germ-cells themselves. The weakness in Mendel's theory to account for his simplest results is that the existence of factors in the gametes is no more than an assumption. The assertion that they exist rests on an *a priori* basis. They have never been seen. In the case to be considered now, the statement that one sex is heterozygous for sex, and that half of its germ-cells carry a thing which determines a particular

sex and the other half do not, is based on the existence in half of the germ-cells of things which can actually be seen.

It has been discovered that in certain insects half the spermatozoa contain a supernumerary, or, as it is called, accessory, chromosome. This chromosome is not merely an additional one, but it behaves differently from the other chromosomes in the division of the cells. In the insect *Anasa*, for instance, a form allied to the Bug, the number of chromosomes in one half of the spermatozoa is nine; in the other half ten; the number in all the eggs is ten. The result of the union between a spermatozoon with nine chromosomes and an egg (with ten) is a male; and of the union between a spermatozoon with ten and an egg (with ten) is a female. This is known to be the case because the number of chromosomes in the somatic cells of males is nineteen; whilst that in the somatic cells of females is twenty.

If a case such as this is described in Mendelian terms, the male, half of whose germ-cells contain an element which the other half lack, must be regarded as heterozygous (DR), whilst the female, all of whose germ-cells are alike in respect of this element, must be regarded as homozygous, but inasmuch as all her germ-cells are alike in the *possession* of an element she must be regarded as a *dominant* homozygote, namely DD, not RR.

It will be noted that the general conclusion as to the nature of the difference between the sexes based on the behaviour of the accessory chromosome is

almost identical with that based on the changes effected by the parasites in the crabs. In both cases the male is bipotential and the female unipotential. This is all the more remarkable when the profoundly different nature of the phenomena from which the conclusions are derived, in the two cases, is borne in mind.

It would be unprofitable in the present stage of inquiry, when every inference ought to be regarded as *sub judice*, to attempt to base a verdict on such conflicting and insufficient evidence as that which is at present obtainable. For the present it will be sufficient to sum up the evidence which has been considered.

All four sets of evidence examined point to the conclusion that one sex is bipotential and the other unipotential. The first two, the clinical and the Mendelian, point to the female as the heterozygote. The last two point to the male as the heterozygote. In estimating the relative value of the evidence in these two sets of evidence it should be borne in mind that in the case of the Mendelian and the clinical, the conclusion is only reached by a long and devious argumentative route; it is as if the secret of the constitution of the sexes were at the end of a winding passage, and the glimpse we get of it by the Mendelian and clinical methods is such a one as we might get by the adjustment of mirrors in the passage so as to see the far end of it. The conclusion is liable to be falsified in proportion to the number of distinct steps (where error may creep in) in the argument by which

it is reached; just as the image of the end of the passage will be distorted in proportion to the number of mirrors it has to be reflected in on its way to the eye. In the case of the effects produced by the parasites in the crabs and in that of the accessory chromosome, we are, as it were, much farther along the passage, at much closer quarters with the actual constitution of the sexes, and can look directly in. Compare the crabs with the currant moth; in the former actual sexual changes can be observed; in the latter we could learn nothing about the nature of sex at all if the sex-character had not become entangled in the gamete with a varietal character of pigmentation. Compare the long chain of argument, some of the links of which are not very strong, which leads to the conclusion that a woman produces equal numbers of female- and male-producing ova with the demonstrable fact that in certain insects half the spermatozoa contain an element which the other half lack.

A comparison between the conclusion based on the Mendelian and cytological evidence in connection with that derived from the crabs is profitable because it may help to divest the problem of certain pre-conceptions which, in my opinion, tend to obscure its real nature.

The difficulty created by the fact that the Mendelian evidence points to the male as the homozygote and the cytological to the female may be cleared up in one of two ways: It may be proved that the Mendelian indication or (less likely) the cytological

one is wrong; or it may be that one sex is heterozygous in one species and another in another. But there is another point in which the conclusions derived from these two sources differ. According to the Mendelian conclusion the homozygous sex, which happens to be the male, is a *recessive* homozygote (RR), whilst according to the cytological the homozygous sex, which happens to be the female, all of whose germ-cells possess the "extra" chromosome possessed by only half of the spermatozoon, is a *dominant* homozygote (DD). Now, if the Mendelian theory, and especially the presence and absence hypothesis, means anything at all, both these conclusions cannot be true. DD contains two "doses" of the sex factor; RR contains none. They differ more from one another than a male from a female, as interpreted by Mendelian theory. DR differs from RR only by one "dose." It *may* be that the homozygous sex is DD in some cases, and RR in others. But this *impasse* may be due to the initial error of founding a theory of sex, as the Mendelian theory of it has been founded, on a basis of material particles. And it may be that the antithesis is really not between heterozygous and homozygous, i.e. between the presence and absence of particles, but, as the case of the crabs seems to indicate, between an unstable condition and a stable one.

## CHAPTER XVII

### THE ORIGIN OF THE MENDELIAN MODE OF INHERITANCE

It is a very important matter to determine whether, as some hold, Mendelian heredity is a fundamental process the true understanding of which will render all other phases of heredity intelligible, or whether, as others believe, it is an anomalous phase of heredity which is restricted to a small group of characters belonging chiefly to domesticated animals and plants. For if the latter is the case, the investigation of Mendelian phenomena can throw no light on the problem of the relation between successive generations of organisms, nor help to elucidate the nature of the processes to which evolution is due. The chief exponent of the view that Mendelian inheritance is merely an anomalous phase of heredity is Dr. Archdall Reid, whose views on this subject are expressed in his recent book, "The Laws of Heredity," to which the reader is referred for a full exposition of this view. Perhaps the simplest way of expressing this view is to say that, according to it, we have begun to read the series of phenomena and of hypotheses, which extends from the first to the sixteenth chapter in this book, at the wrong end. We have taken the simple Mendelian phenomenon as the starting-point, and have finished up by interpreting the inheritance and nature of sex in the light of it; whereas, according

to Dr. Reid and his adherents, the mode of inheritance by which sexual characters are transmitted is the real starting-point, and Mendelian phenomena are anomalous occurrences caused by certain varietal characters taking to be inherited by the sexual mode of transmission, and occupying a mere cul-de-sac in the stream of evolution. "It has been suggested," says Dr. Reid, "that the inheritance of sexual characters is Mendelian; we shall be nearer the truth if we say that the inheritance of Mendelian characters is sexual." By this he simply means that the sexual and not the Mendelian mode of inheritance is the phenomenon in the light of which the other must be interpreted. According to his view both sexes are bipotential, each sex contains the opposite one, *in potentia*; this he calls alternative latency and potency; there is no such thing as alternative inheritance, which is the distribution of characters to the germ-cells in such a way that one germ-cell may receive a character in its entirety and another not at all. The illusion of alternative inheritance is created by the occurrence in about half the individuals, of a species, of a particular sex in a patent and the other sex in a latent state; and, in the other half, of the same sex in a latent, but the other sex in a patent state. This view resembles that of Castle in that, according to it, both sexes have the same constitution—that is, they contain the potentiality of both sexes—and only differ from one another in the matter of which sex happens to be uppermost, or patent.

Now, the indications that one sex, to state it in the broadest terms, is bipotential and the other unipotential is based on minute evidence of a strictly *a posteriori* nature, whilst the conclusion that both sexes are bipotential is based on evidence which its author claims to be "massive," and reached by the *a priori* ladder, which he believes to be trustworthy. For my own part, the minute weighs more heavily with me than the massive. At any rate, I propose to regard it as more probable that one sex is bipotential and the other unipotential than that both are bipotential. And in any case, this is a secondary point at issue. The essential one is: Which came first, the Mendelian or sexual mode of inheritance? And by the sexual mode I mean, now, the theory that one sex is bipotential and the other unipotential, and not Dr. Reid's alternative latency and potency. The Mendelian may here interpose that I am holding his brief. I am, in the sense that I am prepared to accept an interpretation of sex on the basis of the Mendelian one. But I also incline to the view that the sexual preceded the Mendelian mode in so far as it seems to me likely that the mode of inheritance from which both are differentiations was, in the first place, only used (if the expression may be allowed) by sexual characters, and was of the type  $DR \times RR$ , or, more generally, heterozygote  $\times$  homozygote, or  $xy \times xx$ ; and that all the phenomena which we regard as characteristically Mendelian—the existence of pure dominants and recessives, the uniformity of first hybrid generations, the segregation in the ratio

## BREEDING

1 : 2 : 1 in the second hybrid generation, and so on— are, as it were, a secondary display set off by certain varietal characters becoming inherited by the sexual mode described in this paragraph. The heterozygote, together with the ordinary (or homozygous) type ( $xy + xx$ ) first came into existence in connection with the inheritance of sexual characters. And it will readily be admitted that an extremely simple way of bringing about the production of the two sexes in equal numbers would be the institution of one sex (A), half of whose germ-cells contained the factors for one sex, whilst the other half contained those for the other; and of another sex (B) all of whose germ-cells were indifferentiated as regards sex.

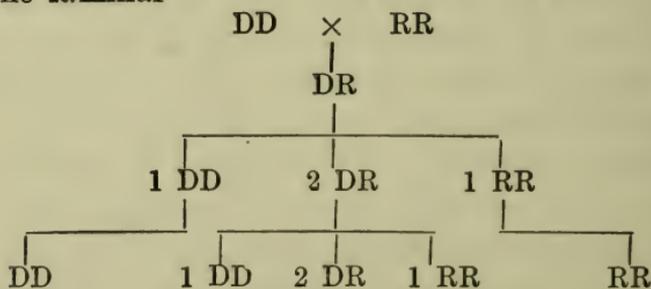
The original mode of inheritance, of which the Mendelian is a later development, and which has possibly persisted without much modification as the sexual mode, may, therefore, be expressed in the formula—

$$DR \times RR = 50 \% DR + 50 \% RR$$

Or, more generally—

$$xy \times xx = 50 \% xy + 50 \% xx$$

The familiar



is a secondary development, and only appeared when

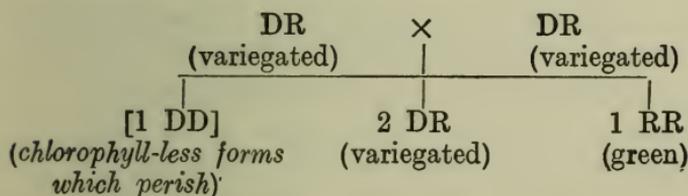
non-sexual characters came to be inherited by the above-outlined sexual mode of inheritance. So long as the only character which existed in the DR condition was one of the sexes, the DR condition could never unite with anything but the RR condition, which was that in which the other sex existed. If that of the ♀ was the bipotential one, only one kind of mating could take place, DR (♀) × RR (♂). But directly a non-sexual character acquired the bipotential condition the fat was in the fire. It became possible for the DR condition to mate with the DR condition, and this led to the origin of the pure dominant and recessive types, DD and RR, which, as being perfectly constant, would be greedily seized on by the breeder so soon as such types came under his intelligent observation. And the existence of these two pure types, DD and RR, suggested themselves as suitable material for hybridisation experiments, probably hundreds of years after they were isolated, to Mendel, who tabulated the results of his crosses and discovered the phenomenon (illustrated on the frontispiece of this book) which we are apt to regard as so fundamental. Mendelian segregation in the ratio 1:2:1 only became possible when it became possible for a DR to mate with a DR; and this only became possible when the DR condition ceased to be the exclusive attribute of, say, femaleness, and became an attribute of, say, yellowness. Mendelian segregation in the ratio 1:2:1 could never take place *before* this event, because a DR could not mate with a DR, both being females; but once it

had happened, the way for Mendelian segregation was made clear by the possibility of a union between two DRs. A female cannot mate with a female; but a yellow can mate with a yellow.

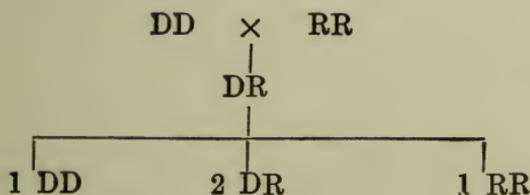
The only alternative to this view of the origin of the Mendelian phenomena is the supposition that the first types to originate were the pure dominant and recessive homozygous forms. Now, apart from the fact that this is rendered improbable by the probability of the common origin of the Mendelian and sexual modes of inheritance from a mode which most closely resembles, even if it differs from, the sexual one, it can be shown that at least in one case this cannot have been the way in which these phenomena arose. And it is well to remember that the question we have to ask ourselves when we are considering the value of evidence for a particular theory is not: how many facts are consistent with it? but: is there a single one which is inconsistent with it? The statements of forty of the friends of the Irishman who was accused of shooting his landlord, to the effect that they had not seen him doing it, were consistent with his statement that he had not done it. But he was hanged, because the fact that one man had seen him do it was not consistent with his statement.

One of the varieties of the Snapdragon, which ordinarily has green leaves, is a form with much yellower, variegated, leaves; this variety is spoken of as *aurea* (golden). The inheritance of these characters has been investigated by Dr. Baur. He found that the greens bred true but that the varie-

gateds, when self-fertilised, produced altogether 573 variegated and 286 green. Now this is a ratio of *two to one*, instead of the *three to one* which would be expected in an ordinary case of segregation. It looks like a 1 : 2 : 1 ratio shorn of one of its ones. This is what, in fact, it actually is. Dr. Baur examined the seedlings raised from the seeds of a variegated plant very shortly after the germination of the seeds, and found 77 green, 160 variegated, and 51 seedlings which were almost white and entirely destitute of green. These latter possess no chlorophyll, and consequently die. They evidently represent the homozygous condition of the character, the heterozygous condition of which is the variegated form. This case, therefore, may be represented thus, assuming that the green is recessive :—



This particular case of the Mendelian phenomenon can, therefore, never have originated in the union of pure dominant and recessive homozygous forms, DD and RR, thus :—



because the dominant form does not exist—or, rather, gets no nearer maturity than the seedling stage.

The general trend of the evidence seems to be that the Mendelian mode of inheritance originated from—or, at any rate, in close connection with—that by which sexual characters are inherited. At any rate, the similarity between the two modes is very close.

## GLOSSARY

**Allelomorph**, a member of a Mendelian pair of characters. The adjectival form allelomorphic is useful, because by its employment the statement that the character "round" bears that relation to the character "wrinkled" which the two characters of a Mendelian pair bear to one another, can be condensed into the statement that round is allelomorphic to wrinkled.

**Bisexual crosses**, according to Prof. de Vries, are those between two individuals each of which bears a particular character, one of them possessing it in a latent and the other in a patent state. Compare with "unisexual."

**Chromosome**, a term applied to certain minute bodies, in the kernel or nucleus of the animal and vegetable cell, which appear at definite periods in the division of the cell, are constant in number for each species of animal or plant, and are characterised by the fact that they stain very deeply with certain dyes. The number of chromosomes in a germ cell is half the number of them in a body cell of a given plant or animal.

**Cotyledon**, a term applied to the first leaf or leaves of the plant. One group of plants, of which the wheat is an example, is characterised by the possession of only one; they are called *monocotyledons*. Another group, of which the pea is an example, has two; these plants are called *dicotyledons*.

DD (*See* Homozygote).

DR (*See* Heterozygote).

**Dominant characters** are those borne by the first generation

from a cross between two individuals possessing respectively the two characters of a Mendelian pair.

**Duplex eyes** are those which have a layer of brown pigment in front of the iris (*See Iris*).

“**Extracted**” is the term applied to the individuals, in the second hybrid generation from a cross, which resemble the parent forms that were mated to make the cross. An “**extracted**” green is a green which appears in the second or a subsequent hybrid generation from a cross between a yellow and a green pea.

**F<sub>1</sub>**, a symbol, introduced by Mr. Bateson, as an abbreviation for the first hybrid generation.

**F<sub>2</sub>**, a symbol for the second hybrid generation.

**F<sub>3</sub>**, a symbol for the third hybrid generation. And so on.

**Factor**, a name for the thing in a germ cell which makes that germ cell develop a particular character, such as tallness as opposed to dwarfness.

**Fasciated plants** are those in which the nodes do not, as in the normal plant, succeed one another regularly up the stem, but occur in profusion at the top.

**Gamete**, a name for the reproductive cell, whether male or female, in both animals and plants.

**Germ cell**, the equivalent of Gamete.

**Heterozygote**, a zygote (q.v.) resulting from the union of two gametes bearing *dissimilar* factors—one a dominant, the other a recessive one. DR is the symbol for heterozygote.

**Homozygote**, a zygote (q.v.) resulting from the union of two gametes bearing *similar* factors, which may be either both dominant, producing a dominant homozygote or DD, or both recessive, producing a recessive homozygote or RR.

**Internode**, the section of the stem of a plant between two nodes.

- Iris**, the coloured part of the human eye surrounding the pupil.
- Mutation**, the origin of species by discontinuous variation (*See* Variation, discontinuous).
- Prepotency**, the property said to be possessed by certain individuals, especially amongst stallions, of transmitting their qualities to their offspring, whatever female they are mated with.
- Pure**, a term applied to those individuals which when mated together produce, exclusively, individuals indistinguishable from themselves.
- Recessive characters** are those which, in a cross between individuals the two characters of each of which bear one of the same Mendelian pair, entirely disappear in the first hybrid generation.
- Reversion**, the production, on crossing, of a supposed remote ancestor of the two forms crossed.
- Segregation**, the reappearance in definite ratios, in the second hybrid generation, of the characters of two forms crossed; and of the first hybrid generation (where this differs from the dominant character).
- Soma**, the body, as opposed to the germ cells.
- Somatic**, of, or pertaining to, the body as opposed to the germ cells.
- Unisexual crosses**, according to Prof. de Vries, are those between two individuals, one of which bears a particular character entirely lacking in the other (*See* Bisexual).
- Variation**, the production by animals and plants of those differences the accumulation of which is supposed to have resulted in the various forms of living things. *Continuous variation* is the name given to the occurrence of such differences as always exist in any sample of a given species. These variations are not supposed to be transmitted to the next generation. *Discontinuous variation* is the term applied to the

differences which are said to be exhibited after long intervals of time by all species of living things. Instances of such differences occurring in the Evening Primrose (*Enothera Lamarckiana*) are given in Chapter I. These differences are transmitted to the next generation when two individuals bearing them are mated.

**Zygote**, the result of the union of two gametes (*See Gamete*).

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