MENDELISM

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PREFACE

LIKE the writing of contemporary history, the treatment of contemporary discovery can at best be attended with but limited success. The exigencies of human existence almost always preclude the possibility of a great advance in scientific thought being based upon more than a few classes of facts. As fresh facts are brought to light, as the theory is tested by experience, the first rough draft is often greatly modified. That which is newly discovered must be brought into relation with what was already known. Only the slow operation of time is able to sift the essential from the merely incidental, and to point out the track which leads to further knowledge.

A short and popular essay can do little more than concern itself with the particular discovery of which it treats. Many points of interest involving unsolved problems must be omitted. For those, however, who wish to learn more of these matters, a few recent references may be given. A full account of most of the experiments alluded to, together with many others, will be found in the Reports to the Evolution Committee of the Royal Society for the years 1902 and 1905. In the same publications will be found also references to nearly all the papers hitherto published on the subject, including the important contributions of Correns and of Tschermak. The question of variation with reference to the formation of species is treated of at some length by de Vries in his "Species and Varieties, their Origin by Mutation" (Chicago and London, 1905). Lastly, an appreciation of Mendel's work, together with a translation of his papers, is given in Bateson's book on "Mendel's Principles of Heredity" (Cambridge, 1902).

R. C. P.

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Mendelism

It is the fortune of some great discoveries in natural knowledge to appear with the good will and acclamation of all. So it has been with gravitation and radio-activity. It is the lot of others to stir up immediate animosity, causing men to judge of them rather through their passions than by their reason. More especially is this so where the religious beliefs and prejudices of mankind are concerned, as instance Galileo and Darwin. In either case the issue of the forward step is, from the first, clear to all according to their degree. But it may at times happen that a discovery of the first magnitude excites but little interest or comment. For the meaning of it is not at once apparent. Such has been the fortune of Gregor Mendel's great discovery in heredity, of which the story forms one of

Introductory.

the most romantic chapters in the history of science. It is the aim of the following pages to give a brief account of Mendel's work with its more recent developments, and to touch upon some of the general consequences that flow from his experiments.

Biographical.

Gregor Mendel was born in 1822 of Austro-Silesian peasants. When twenty-one years of age he entered a religious foundation at Brünn, and a few years later was ordained priest. Subsequently he studied the natural sciences for several years in Vienna (1851—53). He became interested in the problems of hybridisation, and on his return to the cloister of Brünn, commenced his classic experiments on the eating pea—*Pisum sativum*. The results appeared as a paper in the Proceedings of the Natural History Society of Brünn, under the title "Experiments in Plant Hybridisation." Besides this paper Mendel contributed very little to biological literature. Nevertheless, we now know that he devoted much of his time to similar work on other plants. In a series of letters to Carl Nägeli, the botanist, he gives an account of his pea experiments, and also of others dealing with *Lychnis*, thistles, etc. Nägeli, however, like the rest of his contemporaries who knew of Mendel's work, was unable to appreciate the magnitude of the discovery. Perhaps Darwin alone could have valued Mendel's little pamphlet at its proper worth, and into his hands unfortunately it never fell.

The Abbot of Brünn, for such he afterwards became, was a man of wide and varied interests. Besides his experiments on plants he is known to have carried out others on bees, though the record of them would appear to have been lost. Meteorology was a hobby with him, and he contributed numerous observations on the subject to the Brünn Natural History Society. He was also greatly interested in sun-spots, and was for a time the manager of a bank. By the members of his cloister he was greatly liked and respected, though perhaps not altogether understood. *He died of Bright's disease in 1884* at the age of 61.

Early neglect of Mendel's work.

For five-and-thirty years Mendel's work *remained unknown. It had appeared at an un*favourable moment. Six years previously Darwin's views on the origin of species had been given to the world, and men of science were beginning eagerly to explore the new fields which he opened up. Hybridisers there had been before Darwin, but for lack of a central clue their results appeared as an inconclusive and disappointing tangle. Yet it *was this very clue that Mendel's work supplied.* With the advent of the "Origin of Species" men regarded as settled the question which *the hybridisers had striven to answer,* and directed their energies into other and more promising channels. Of late years doubts have been cast upon the all-sufficiency of natural selection in the production of new *species. A revival of interest in these matters* on the part of a few biologists led, in 1900, to the re-discovery of the principles of heredity which Mendel had clearly enunciated nearly forty years before. To gain an idea of the scope of these principles one cannot do better than turn to Mendel's own account of his experiments.

Mendel's experiments.

In the selection of a plant for experiment Mendel recognised that two conditions must be fulfilled. In the first place the plant must possess differentiating characters, and, secondly, the hybrids must be protected from the influence of foreign pollen during the flowering period. In *Pisum sativum* Mendel found an almost ideal plant to work with. The separate flowers are self-fertilising, whilst complications from insect-interference are practically non-existent. As is well known, there are numerous varieties of the eating-pea exhibiting characters to which they breed true. In some varieties the seed colour (due to that of the albumen of the cotyledons) is yellow, whilst in others it is green. In some varieties the seeds are round and smooth when ripe; in others they are wrinkled. Some peas have purple, others have pure white flowers. Some peas again, *when grown under ordinary conditions*, attain to a height of 6 to 7 feet, whilst others are dwarfs which do not exceed 1½ to 2 feet. Mendel selected a certain number of such differentiating characters, and investigated their inheritance *separately for each character.* Thus in one series of experiments he concentrated his attention on the heights of the plants. *Crosses were made between tall and dwarf varieties which previous experience had shewn to come true to type with regard to these characters. It mattered not which was the pollen-producing and which the seed-bearing plant. In every case the result was the same. Tall plants resulted from the cross. For this reason Mendel applied the terms **dominant** and **recessive** to the tall

* See note at end, p. 61.

and dwarf habits respectively. The next step was to collect the seeds thus formed and to sow *them in the following year.* When this was done it was found that both tall and dwarf plants appeared in the offspring. Each individual was either tall or dwarf, and no intermediate appeared. Thus in one series of experiments Mendel obtained 1064 plants, of which 787 were tall and 277 were dwarfs. That is to say, the tall plants were almost three times as numerous as the dwarfs. In other words, the dominant and recessive characters occur in the second generation of hybrids (F_2*) in the proportion of 3 : 1.

In the following year the seeds of this generation (F_2) were sown as before. From the seeds of the dwarfs came only dwarfs,

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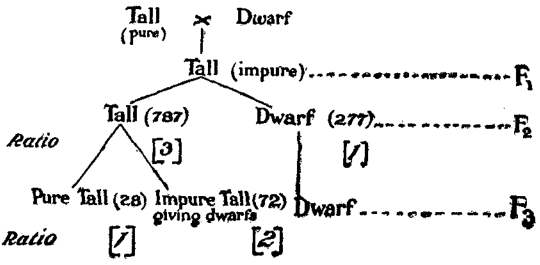
* For convenience it is customary to denote the hybrids arising from a first cross by the letter F_1 (= 1st filial generation). The successive generations arising from this F_1 generation are denoted by the letters F_2, F_3, ..., etc. The parents of the F_1 generation are called P_1 (= 1st parental generation), the grandparents P_2, and so on.

i.e., the recessive character bred true. The tall plants, however, were not all of the same nature. Some of them produced seed which gave rise to tall plants only. Others, again, formed seed from which sprang both talls and dwarfs in the proportion of 3:1. The tall plants of the F_2 generation were of two kinds, viz., those which carried only the tall character, and those which carried both the tall and the dwarf characters. The former we may for the present call pure, and the latter impure dominants. Thus in one experiment plants were raised from the seeds of 100 tall plants of the F_2 generation. Of these 100 plants, 28 produced seed giving tall plants only, whilst 72 yielded seed which gave rise to both talls and dwarfs. Hence, of the 100 tall plants tested in the F_2 generation, 28 must have been pure for the tall character, whilst 72 must have been carrying the dwarf as well as the tall character. The former numbers, 28 and 72, do not make a very exact approximation to the ratio 1:2.

The numbers, however, are small, and the proportion is greatly affected by a slight deficiency on either side. From a much larger number of similar cases (between one and two thousand) Mendel found the ratio 1 : 2 borne out almost exactly. The dominants therefore which come in the F_2 generation are of two kinds—pure and impure. On the other hand, the dwarf recessives always breed true in whatever generation they appear. We may conveniently summarise the result of the experiments up to this stage in the following short table.



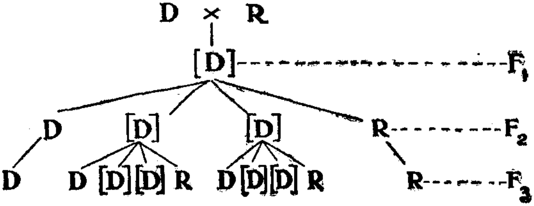
By breeding subsequent generations Mendel shewed that the pure dominants and recessives always bred true, resembling in this way the original parents. The impure dominants, on the other hand, always gave dominants and recessives in the constant proportion of 3 : 1. Since the pure dominants are only half as numerous as the impure dominants, it follows that the impure dominant, on being *selfed, produces as offspring pure dominants, impure dominants, and recessives in the proportion of 1 : 2 : 1. And this held good for all impure dominants, no matter *in what generation they were bred.* We have considered the case of one pair of characters only, but Mendel shewed that the rule holds good for all the various pairs of differentiating characters studied by him. Wherever there occurs a pair of differentiating characters, of which one is dominant to the other, three possibilities exist. There are recessives which always breed true to the recessive character. There are dominants

* See note at end, p. 61.

which breed true to the dominant character, and are therefore pure. And thirdly there are dominants which may be called impure, and which on self-fertilisation (or in-breeding where the sexes are separate) give both dominant and recessive forms in the fixed proportion of three of the former to one of the latter.

General results of the experiments.

We are in a position now to make a general scheme to shew the result of crossing individuals which each bear one of a pair of differentiating characters. If we denote the pure dominant by *D*, the impure dominant (which cannot be distinguished in appearance from the last) by [*D*], and the recessive by *R*, we may construct the following scheme of inheritance.



Such a scheme brings out clearly the points already referred to. When two pure strains, each possessing one of a pair of differentiating characters, are crossed together, the resulting hybrids (F_1) all *resemble the dominant parent. When selfed or bred among themselves they give offspring (F_2), of which one quarter bear the recessive and three quarters the dominant character. Of the latter, however, only a third are pure dominants, giving, when selfed, offspring in which the dominant character alone appears. The remaining two-thirds are impure dominants, which on selfing behave as the original F_1 hybrids, and yield pure dominants, impure dominants, and recessives in the proportions 1 : 2 : 1. And this is true of all impure dominants, no matter in which generation they occur. Both the "extracted" pure dominants and the "extracted" reces-

* The statement that the hybrid of the first generation cannot be distinguished from the dominant parent holds good for peas and many other forms of life, but, as will appear later (p. 28), it is not universally true.

sives, which are formed in any generation after a cross, breed true to the types of the original parents used in that cross.

Mendel himself verified this principle of dominance for several characters in *Pisum*, finding round seeds dominant over wrinkled, coloured seed coats over white seed coats, yellow seed albumen over green albumen, etc. Within the last few years the validity of the principle has been extended to numerous differentiating characters, both structural and physiological, in animals as well as plants. To mention but a few cases; the coloured coat of mice and rabbits is dominant over the unpigmented or "albino" coat; the long "Angora" fur found in some rabbits is recessive to the normal short fur; the "rose" comb which occurs in certain breeds of poultry, such as Hamburghs and Wyandottes, behaves as a simple dominant towards the high-serrated "single" comb characteristic of Leghorns, Andalusians, and others.

Experiments subsequent to Mendel. (*a*) on Animals

Owing to the numbers in which they can be produced, and the ease with which they can be controlled, plants lend themselves more readily than animals to investigations of this nature. Of the many characters already investigated a few only can be mentioned here. In wheat and barley the beardless have been shewn to be dominant over the bearded forms. The dwarf or "Cupid" variety of sweet pea, but a few inches in height, behaves as a recessive to the normal form. In maize the yellow-seeded variety is dominant over the white, and the so-called "sugar" seed is recessive to the "starch" seed. Among plants possessing coloured and white varieties of flowers it has been shewn, in such species as have been investigated (*e.g.* *Datura*, stocks, sweet peas, etc.), that the white forms are recessive to the coloured. The hybrid resulting from the crossing of a white with a coloured form is always coloured, though its actual colour is not necessarily that of the coloured parent.

(*b*) **on Plants.**

Thus a picotee sweet pea crossed with a white gives, not picotee, but purple.

Waltzing Mice

The characters hitherto dwelt upon are concerned either with colour or with what may be termed normal structural features. Leaving these we may turn for a moment to consider two most interesting cases, in which one of the pair of differentiating characters is in a markedly abnormal condition. Of the many breeds of fancy mice the Japanese "waltzer" is one of the most distinct, and derives its name from a curious habit of vigorously circling round, sometimes for hours together, as if intent upon its own evasive tail. It has been shewn that these mice suffer from a malformation of the labyrinth of the ear, and it is of the greatest interest to find that this condition behaves as a single recessive to the normal state.

The second case alluded to occurs in the sweet pea. Sometimes there may be seen a few plants in a row, which, though to all appearance healthy and vigorous, set little or no seed. The reason is at once apparent when a flower is pulled to pieces. The anthers are sterile, containing only a little degenerate pollen, and the flower is consequently incapable of the normal self-fertilisation which obtains among these plants. Such few pods as are formed presumably owe their origin to insect-agency, for the female parts of the flower are perfectly normal, and readily set seed when pollinated from another plant. The F_1 hybrids so formed are all normal, shewing that the fertile anther is dominant to the sterile. In the next generation (F_2) plants with sterile anthers reappear approximately in the proportion of 1 : 3 of the fertile, which is in accordance with expectation. This case of the sterile sweet pea is of great interest from its bearing on the problem of sex. Looked at from this standpoint we have here a unisexual form, a female, which has suddenly arisen from the normal hermaphrodite form

Sterile Sweet Peas.

by functional suppression of the male organs. It strongly suggests that in cases where the sexes are separate this condition may have suddenly arisen from the hermaphrodite one. The story of sex, however, is too long and too complex for us to enter upon in this connection.

The characters we have just considered, though highly abnormal, are yet essentially structural. The Mendelian principles of heredity have, however, been demonstrated in the case of other characters of a less tangible nature. It has been shewn, for instance, that the earlier ripening habit of Polish wheat is recessive to the later ripening habit of Rivett wheat. A still more interesting case occurs in the same species of plant. Certain forms of wheat are highly susceptible to the attacks of a fungus which causes "rust," whilst others are immune. It has recently been shewn that immunity in this instance behaves as a recessive to the non-immune condition.

Resistance to Disease.

When an *immune* and a non-immune strain are crossed together the resulting hybrids are all susceptible to "rust." On *self-fertilisation* such hybrids produce seed from which appear dominant "rusty" and recessive immune plants in the expected ratio of 3 : 1. From this simple experiment the phrase "resistance to disease" has acquired a more precise significance, and the wide field of research here opened up in this connection promises results of the utmost practical as well as theoretical importance. To the question, "Who can bring a clean thing out of an unclean?" we are beginning to find an answer, nor is the answer the same as that once given by Job.

Theoretical Deductions.

So far we have been concerned with the phenomenon of dominance as enunciated by Mendel and borne out by subsequent experiments. We must now consider the theoretical results which Mendel deduced from his facts. It is a matter of common knowledge that in the majority of animals and plants the genesis of a new individual is the result of a sexual process, the essential feature of which consists in the union of a female cell, the egg or ovule, with a more minute male cell, the spermatozoon or pollen grain. Such cells, both male and female, are termed **gametes**, and the cell formed by the fusion of a male with a female gamete is spoken of as a **zygote**. This unicellular zygote, by a process of repeated nuclear division ultimately gives rise to the adult animal (or plant as the case may be) with its contained germ-cells. The germ-cells, at first immature, subsequently ripen to form the gametes, thus completing the life-cycle. Since the gametes form the link connecting successive adult generations, the characters peculiar to the latter must be represented in the constitution of the former. In the case of a tall pea some at least of the gametes formed, both male and female, must carry the tall character; for from an impure tall three-quarters of the offspring are tall. And if the strain of tall peas is shewn by experiment to be pure for that character, all the gametes must be carrying that character, and that alone. The union of two gametes in this case will result in a zygote having the tall character, to the formation of which each gamete has equally contributed. Such a zygote is known as a **homozygote**, and when it comes to form gametes these will all be similar as regards the character under consideration. A zygote formed by the union of two dissimilar gametes, *e.g.* in the case of peas, where one bears the tall and the other the dwarf character, is termed a **heterozygote.** The heterozygote frequently exhibits the form of the pure dominant, from which it can only be distinguished by the test of breeding. That the recessive character is likewise carried is shewn by the fact that when such heterozygotes are bred *inter se*, one quarter of the offspring produced are recessive. It is only in this way that we can distinguish between the pure tall pea and the tall which bears the

Homozygotes and Heterozygotes.

dwarf characters—between the pure "rose" comb and the "rose" comb which carries also the "single" comb. There are cases, however, in which the heterozygote does not resemble the dominant, but has a character peculiar to itself. Reference will be made to such cases later on.

Unit characters

These facts led Mendel to the conception of pairs of unit characters, of which either can be carried by any one gamete to the exclusion of the other. A fundamental property of the gamete is that it can bear either one such a pair of characters, though not both. But the heterozygote is formed by the union of two dissimilar gametes, and consequently the cells of the individual into which it grows must contain both characters.* To reconcile these statements it must

* The subjoined scheme may render it easier to follow the idea given above. Two gametes, of which one bears the dominant, and the other the recessive, character, unite to form a zygote which is at first, of course, unicellular. This divides up into numerous cells, of which some form the

be supposed that at some cell division in the formation of gametes a primitive germ cell divides into two dissimilar portions. Instead of the dominant and recessive constituents passing in combination to the two daughter-cells, the whole of the dominant goes into one of these, and the whole of the recessive into the other. From this it follows that every gamete contains one only of such a pair of characters, *i.e.*, it is *pure* for that character. In other words, a simple heterozygote, such

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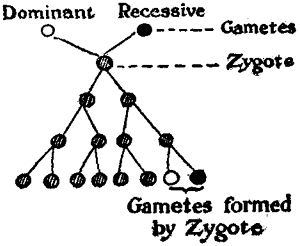
various tissues of the body and others the primitive germ-cells. All may be supposed to bear both the dominant and recessive characters. When the gametes are formed from the primitive germ-cells, the dominant and recessive portions split away from one another. Hence each gamete carries either the dominant or the recessive character, and that alone. In other words, the gametes are pure with respect to the character which they carry.



as we are considering, *produces gametes of two kinds and produces them in equal numbers.* The characters are said to **segregate** in the gametes. In this conception lies the simple explanation of the facts, that from the inbred heterozygote comes dominants and recessives in the proportion of 3 : 1, and that only one dominant in three is pure, the other two being heterozygotes.

The Principle of Gametic segregation.

To revert to the case of the pea. Each heterozygote flower is producing equal numbers of ovules bearing the tall and the dwarf characters—let us say 2*n* of each. These are fertilised by a mass of pollen, of which half the grains bear the tall and half the dwarf character. Each tall-bearing ovule therefore has an equal chance of being fertilised by a tall or by a dwarf-bearing pollen grain. Consequently, of the zygotes formed by the 2*n* tall-bearing ovules, *n* will be fertilised by tall-bearing and *n* by dwarf-bearing pollen grains, *i.e.*, there will be formed *n* tall homozygotes and n heterozygotes in which the tall character dominates. Similarly, the $2n$ ovules bearing the dwarf character will form n homozygotes carrying the dwarf recessive, and n heterozygotes with the tall character dominating. Therefore, from the $4n$ ovules and the unlimited number of pollen grains from which we started, there will be formed n homozygotes bearing only the recessive dwarf character, n homozygotes bearing only the dominant tall character, and $2n$ heterozygotes similar to the parent plants, the last bearing both characters, but outwardly indistinguishable from the pure dominants. And this theoretical deduction accords with the actual experimental facts.

A convenient system of notation is to denote the heterozygote by the letters *DR*, thus signifying that it gives off equal numbers of gametes bearing the dominant and recessive characters. On the same system the pure dominant and the pure recessive are represented by the terms *DD* and *RR* respectively. So far we have considered only the results obtained by inbreeding the heterozygotes. The theory of gametic purity can be further tested by deducing from it the results which should follow from crossing the heterozygote with either of the homozygotes, and seeing how far such theoretical results accord with those obtained by experiment. When the heterozygote, *DR*, is crossed with the recessive, *RR*, each dominant and each recessive gamete arising from the former can unite only with a recessive gamete formed by the latter. Consequently we should look for the production of equal numbers of zygotes of the constitution *DR* and *RR*. This is what actually happens on crossing a fowl having a single comb (*RR*) with one having a heterozygous "rose" comb (*DR*). Half the offspring are pure recessives and the other half are dominants which may be all proved to carry the "single" character, *i.e.*, are heterozygotes. Similarly, when the hete-

Homozygote bred with Heterozygote.

rozygote *DR* is crossed with the pure dominant form, *DD*, we should from theory expect all the offspring to be dominant in form, and one half of them to be pure dominant. Here again experiment has borne out theory. The generalisation known as the principle of gametic segregation may be regarded as firmly established on the phenomena exhibited by plants and animals when strains are crossed which possess pairs of differentiating characters. Whether the principle applies universally or not can only be answered by subsequent experiment.

Limitations of the Phenomenon of Dominance.

We have already seen that the heterozygote frequently resembles the dominant homozygote so closely that the two cannot be distinguished by inspection alone. This is by no means always the case. It sometimes happens that the heterozygote, whilst bearing a general resemblance to the dominant, differs from it sufficiently to enable us to tell the two apart. The white Leghorn breed of poultry is characterised by its pure white plumage. In this case white plumage is dominant to coloured, but the dominance is not quite perfect. When a white and a brown Leghorn are crossed together all the resulting offspring are white, but almost invariably have a few coloured feathers. The presence of these "ticks" is the outward and visible sign of the heterozygous nature of the bird on which they occur. Such birds give off equal numbers of gametes bearing the white and coloured characters. This is easily tested by breeding them together. It is found that from such matings one quarter of the offspring are coloured recessives, whilst the remainder are pure white, or white with a few ticks. The heterozygote resembles the dominant form much more closely than it does the recessive. Though we may speak of dominance in such a case, it is necessary to remember the dominance is not quite perfect. This, however, makes no difference to the essential feature of Mendel's discovery, which of course is the segregation of the dominant and recessive characters in the gametes.

The case of the Andalusian fowl.

In addition to cases where the heterozygote differs slightly from the dominant homozygote, there are others in which it is quite distinct from either parent, and exhibits characters peculiar to itself. The blue Andalusian fowl offers a very pretty instance of this. Breeders have long recognised the impossibility of obtaining a pure strain of this variety. No matter how carefully the blues are selected they always throw "wasters" of two sorts, some pure black and others of a peculiar white, with black splashes. Careful breeding shews that on the average one half of the offspring from a pen of blue Andalusians come blue, one quarter black, and one quarter white. These proportions at once suggest that the blues are heterozygotes. For we have already seen that the breeding of heterozygotes together results in one half of the total offspring coming heterozygotes.

If this is so, it follows that the blacks and splashed whites are by nature homozygous, and consequently ought to breed true. Experiment has shewn that such is actually the case. Further, we should be led to expect heterozygous offspring from a union of the two different homozygotes. Here again the experimental result accords with the theory. When splashed white and black are bred together all the offspring without exception are blue. Paradoxical as it may sound, the mating together of the black and the white "wasters" gives a proportion of blue Andalusians twice as great as does the mating of blue with blue.* The black and the white splashed are really the pure breeds; the "pure" blue Andalusian is, and from its

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* The following scheme, which may be compared with that on p. 11, will perhaps serve to render the above account easier to follow. The theory of course supposes that the blues are giving off white-bearing and black-bearing gametes in equal numbers, there being no such thing as a blue-bearing gamete. In the cross blue × blue the ♀ is producing

nature ever must be, a mongrel. From our point of view it is of interest as a case

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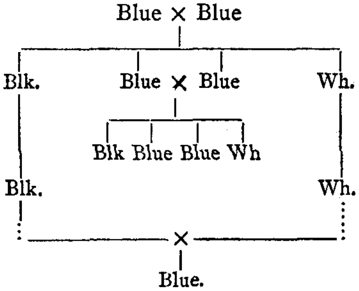
equal numbers (n) of "white" and "black" eggs—the ♂ equal numbers of "white" and "black" sperms. A "white" egg therefore has an equal chance of being fertilised by a "white" or a "black" sperm. When "white" meets "white" the result is "white," and when "black" meets "black" the result is "black." But when "white" meets "black" the result is blue. Hence n white eggs result in $\frac{n}{2}$ white and $\frac{n}{2}$ blue zygotes. Similarly n "black" eggs give rise to $\frac{n}{2}$ black and $\frac{n}{2}$ blue zygotes. Therefore if the blue ♀ produce $2n$ eggs to the blue ♂, $\frac{n}{2}$ of these will result in black zygotes, $\frac{n}{2}$ in white zygotes, and $2\ \frac{n}{2}$ in blue zygotes. In other words the black, white, and blue birds produced must be numerically in the proportion of 1 : 1 : 2. And this is the proportion found by experiment.



where the appearance of the heterozygote is quite unlike that of either of the homozygotes from whose union it springs. Yet, though there is no dominant and no recessive here, the essential feature of gametic purity could not be shewn more clearly.

Primulas.

In the vegetable world a case in some ways similar is to be found among the primulas. The familiar form of this plant, *Primula sinensis*, is characterised by its short main axis, from which the flower stalks all arise very close together. As these are all of much the same length, the flowers come to form a dense cluster or umbel in the centre of the plant. The crinkle-edged petals are wide and overlap one another, so that the outline of the flower is approximately circular. The range of colour in the blooms is of course considerable, but in this connection is immaterial. Now there exists also a variety known as the Star primula (*P. stellata*), which in habit is quite distinct from *P. sinensis.** The main axis is tall, and the flower stalks come off in circular tiers from nodes which are several inches apart. The number of flower stalks given off from each node gradually diminishes towards the apex of the plant. In a well-grown specimen there are about four tiers of flower stalks. The individual petals scarcely overlap. Their edges are not crinkled, and a deep notch in each gives to the flower the characteristic five-rayed star appearance from which it gets its name. When these two varieties are crossed, the resulting heterozygote is more or less intermediate between them in habit and flower shape. From its constancy of form, and its unlikeness to either parent, it has received the name *pyramidalis*. But *pyramidalis*, in spite of its constancy of form, would appear to be no more a pure race than is the blue Andalu-

* A good idea of the appearance of these two forms may be got from Sutton's catalogue for the current year. For the opportunity of examining *P. pyramidalis*, the writer is indebted to the kindness of Mr. Leonard Sutton.

sian fowl. When self-fertilised it gives off again the two parent forms, the proportions of *sinensis*, *stellata*, and *pyramidalis* being, as might be expected, 1 : 1 : 2. It is the property of *pyramidalis* to throw *stellata* and *sinensis*, just as the blue Andalusian must always produce some blacks and some whites. These examples are sufficient to shew that the phenomenon of dominance occurs only in certain cases. Nevertheless, whether the heterozygote exhibit dominance or not, it always produces in equal numbers gametes like those of the two parent forms from which it has arisen. The law of gametic segregation, the essence of Mendel's discovery, holds good whether the phenomenon of dominance be found or not.

Simple and Compound Allelomorphs.

Hitherto we have been dealing with pairs of differentiating characters capable of replacing one another. To such unit characters the term **simple allelomorph** has been applied. Certain characters, however, cannot be regarded as simple allelomorphs. There are many which on inbreeding behave as simple allelomorphs, but which when crossed give rise to complex results. In such cases we are probably dealing with characters built up of several components, of which each singly may be capable of acting on isolation as a simple allelomorph, or of combining with others to form **compound allelomorphs** of different composition.

The Combs of Fowls.

Certain phenomena shewn by the crossing of fowls with different types of comb would seem, in the light of our present knowledge, to be most readily explicable on the hypothesis of compound allelomorphs. Attention has already been drawn to two forms of comb found in different breeds of poultry, viz. to the high serrated "single" comb characteristic of the Mediterranean races, such as the Leghorns and Andalusians, and to the flattened papillated "rose" comb with its posterior pike that occurs in Wyandottes, White Dorkings, and others. As was mentioned above, the single and rose comb behave towards each other as simple recessive and dominant. A third type of comb is characteristic of the Indian Game fowl. This, the so-called "pea" comb, is a rather low structure, possessing three well-marked ridges, of which the median is somewhat higher than the two lateral ones. Towards the single comb it behaves as a simple dominant. When, however, the rose and pea combs are crossed together, as for example by mating a White Dorking with an Indian Game, an entirely new form of comb results. This is a broad flattened and somewhat corrugated structure, exhibiting neither the pike nor working of a rose comb nor the three ridges of a pea. From its resemblance in shape to the half of a walnut it may be called the "walnut" comb. It occurs normally in a certain breed of fowls—the Malays. One of its peculiarities is that from certain portions of it grow out small bristle-like hairs. They occur on the posterior part of it, and often form a band running right across the comb at the junction of its posterior third with the remainder. The junction is usually marked also by a distinct transverse groove. The peculiar feathering of the comb is a feature not found in any of the other three types of comb mentioned above. It might have been expected, from analogy with other cases, that the heterozygotes from the Indian game × White Dorking cross would produce gametes bearing the rose and the pea characters in equal numbers, and that the result of breeding the hybrids together would be the production of rose, pea, and walnut combs in the proportion of 1 : 1 : 2. Such, however, is not the case. When bred together these heterozygotes *produce all four types of comb*, walnuts, roses, peas, and singles appearing in definite proportions.* The explanation lies in the fact

* The proportion of walnuts, roses, peas, and singles produced from this mating is as 9 : 3 : 3 : 1. All the walnuts will not be of the same constitution, and this applies also to the peas and roses. As the case is of considerable importance to

that the heterozygotes are giving off equal numbers of gametes of four kinds corresponding to the four types of comb.

This view has been confirmed by crossing such heterozygous walnuts with a single. Since the single is recessive to the other three, and since the single has an equal chance in such a cross of meeting either of the four different comb characters, we should

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those interested in these matters, it may be worth a brief digression to see how the above proportion comes about. We know from experiment that each sex is producing equal numbers of gametes corresponding to the four types of comb. Let us suppose that the ♀ produces 16 ova, of which 4 carry the walnut, 4 the rose, 4 the pea, and 4 the single character. Each of the 4 walnut bearing ova will have an equal chance of being fertilised by a spermatozoon bearing any one of the 4 characters. Consequently one will unite with a walnut-bearing spermatozoon to give a homozygous walnut $\left(\frac{w}{w}\right)$; another will unite with a rose-bearing spermatozoon to give a heterozygous walnut $\left(\frac{w}{r}\right)$; another will unite with a pea to give a heterozygous walnut $\left(\frac{w}{p}\right)$; and the last will be fertilised by a single-bearing spermatozoon, forming a zygote which produces all four types of gamete (*wrps*). As this expect one quarter of the resulting offspring to exhibit walnut, rose, pea, and single respectively. And experiment has shewn that among more than 1000 chickens produced from a number of such matings the four

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process holds good for each of the four ova bearing the other comb characters, our 16 ova will form zygotes as follows :—

From 4*w* ova

$$\frac{w}{w} + \frac{w}{r} + \frac{w}{p} + wrps$$

From 4*r* ova

$$\frac{w}{r} + wrps + \frac{r}{r} + \frac{r}{s}$$

From 4*p* ova

$$\frac{w}{p} + wrps + \frac{p}{p} + \frac{p}{s}$$

From 4*s* ova

$$wrps + \frac{r}{s} + \frac{p}{s} + \frac{s}{s}$$

$$\text{Total } \underbrace{\frac{w}{w} + 2\frac{w}{r} + 2\frac{w}{p} + 4wrps}_{9 \text{ walnut}} + \underbrace{\frac{r}{r} + 2\frac{r}{s}}_{3 \text{ rose}} + \underbrace{\frac{p}{p} + 2\frac{p}{s}}_{3 \text{ pea}} + \underbrace{\frac{s}{s}}_{1 \text{ single.}}$$

From such a mating are produced in all nine different kinds of zygotes as judged by the criterion of gametic output. All these forms of zygote have been met with in experiment over and over again, and, with one possible exception, no other form of zygote has up till now occurred from the many various matings which have been worked out.

types of comb appear in approximately equal numbers. Such then is the nature of the birds bearing the walnut comb which are produced by the mating of rose with pea. It is, however, obvious that from the union of two such walnut combs some birds will result which also possess the walnut comb, but differ in the gametes which they produce. The walnut-bearing ova of the hen have an equal chance of being fertilised by a spermatozoon bearing the character of any one of the four types of comb. Walnut may meet walnut, or it may meet rose or pea or single. Experiment shews that there are certainly four kinds of walnuts of different gametic constitution answering to these four possibilities. From the union of walnut-bearing gametes arises a homozygote whose gametes are all walnut-bearing. When walnut meets rose or pea there is formed a *heterozygote* in which the walnut comb is dominant, and which gives off in equal numbers gametes bearing the walnut character, and either the rose or pea, as the case may be. Lastly, when walnut meets single there is formed a zygote which gives off an equal number of gametes bearing all the four characters. The combination of walnut with single results in the production of a zygote whose gametic behaviour is, as far as we can see, precisely similar to that of the zygote produced by the union of rose and pea. There are four kinds of zygote bearing the walnut comb, indistinguishable hitherto in external appearance, but differing in the nature of their gametic output.

Such is, in brief, the story of the walnut comb, of which the essential features are as follows: The walnut character is represented in the gamete by a compound allelomorph. This is shewn by the fact that it may be synthesized from pure rose and pure pea. It behaves as a dominant to rose, pea, and single combs. In a zygote formed by the union of walnut with rose or pea the walnut character is stable, and such heterozygotes form an equal number of gametes bearing the walnut, and either the rose or the pea allelomorphs. In other words, the compound allelomorph is stable in the presence of certain presumed simple allelomorphs. When, however, the zygote is formed by the union of walnut with single, the compound allelomorph would appear to undergo partial disintegration with the formation of walnut, rose, pea, and single allelomorphs in equal proportions. The zygote formed by the union of walnut with single is, so far as we at present know, precisely similar to that produced by the meeting of rose and pea. Further generalisation on the subject of compound allelomorphs would be unprofitable until more cases have been studied as fully. The instance of the walnut comb has been gone into at some length, because it suggests that much which at present seems enigmatic in inheritance may be due to the formation of compound allelomorphs, whose nature and behaviour can only be unravelled by accurate and detailed analysis.

Before leaving the subject we may touch briefly upon another complex case. Of the white sweet peas which go by the name of 'Emily Henderson,' there are at least two strains outwardly indistinguishable except for the shape of their pollen grains. These are round in the one instance and oblong in the other. Experiment has shewn that each strain comes true to colour under normal conditions of self-fertilisation. It has also been shewn that the white sweet pea, when crossed with a colour variety, behaves as a recessive. When, however, the two strains of whites are crossed with one another, the offspring are not white but purple. Such purples on self-fertilisation produce three other colour varieties in addition to purple, viz., picotees, pink bicolors, and tinged whites. Sometimes the picotees and tinged whites are absent. The purples of this generation on being selfed do not all give the same result. Some produce the five-colour classes again. Some give purples, pink bicolors and whites.

Sweet peas.

Others again give purples, picotees, and whites, and so on. Up to the present at least eight different kinds of purples have been shewn to exist in the F_2 generation, though they cannot be distinguished from one another until a further generation (F_3) has been bred from them. For our present purpose the important point is that one of these eight kinds produces only purples on being selfed. From the union of the two whites there has been formed by synthesis a pure purple sweet pea. It is not unnatural to regard this as a case analogous to the synthesis of the walnut comb from the rose and the pea. Whether it is so, and whether the hypothesis of compound allelomorphs holds good here also, one cannot at present say. The case of the sweet pea is one of greater complexity, and until the experiments now in progress have been carried on somewhat longer no definite answer can be given. At present it affords an excellent example of the more complicated type of problem with which the student of heredity is called upon to deal.

Such then are the facts elicited by Mendel and others, and such is the interpretation put upon them. Does all this, it may be asked, affect our conceptions of the nature and origin of living forms? The answer must be in the affirmative. Of the fact of evolution we are certain. Of the workings of natural selection we have no doubt. But with regard to the nature of the variations upon which selection works there is much diversity of opinion. The discoveries associated with Mendel's name have introduced no fresh view here. Nevertheless, they must greatly influence our conception of the part played by the different forms of variation in the evolutionary process. To see why this is so will necessitate a brief historical digression. More than half-a-century ago Darwin recognised that the problem of the origin of species is inseparably bound up with the nature of

Mendel and current biological conceptions.

variation. The evolution of fresh species depends upon the action of natural selection on the variations that occur in living forms. Individuals of a species, which from their variations are more adapted to *their environment, survive in the struggle for* existence ; individuals less adapted are placed at a disadvantage, and tend to perish in the competition with their more favoured kin. The survivors leave offspring, of which some shew the favoured variation in a rather greater, some in a rather less, degree. Natural selec*tion sifts out the former as the parents of the* next generation. And so for generation after generation. The process is a cumulative one. By the action of natural selection small variations are gradually worked up into a specific difference and finally fixed. Natural selection is, as it were, the guiding hand that is continually exerting a steady pressure upon the species, and the species, from its inherent variability, is a plastic thing, ever responding

Variation and Natural Selection.

to the touch of natural selection. It is true that Darwin recognised that large variations may *suddenly arise complete from the first,* and he instances, among others, the cases of the large-crested Polish fowls, and of the familiar short-legged Ancon ram. But he was disinclined to attach much importance to such *variations* in the production of species, holding that from the rarity of their occurrence they would rapidly become swamped by intercrossing with the normal form. He considered that it was by the action of natural selection on small continuous variations that species had been and were being built up. This idea, supported by the wealth of facts marshalled together by Darwin, dominated thought for forty years. Here and there a dissentient voice was heard, but it was not until ten years ago that Bateson drew attention to the frequency of Discon*tinuity in variation, and suggested that such* saltatory variations may have played an important part in the production of species.

More recently the Dutch botanist, Hugo de Vries, has emphasised this point of view. He considers that the term 'variation' has been used to include several distinct phenomena. There are variations which arise suddenly, and are discontinuous. These de Vries calls **mutations.** They are sharply divided from the stock whence they took their origin, and their inheritance is discontinuous. The mutation may be dominant to the original form, as for example the rose comb in fowls, which doubtless arose from the single. Or the mutation may be the recessive form, as in the Cupid variety of the sweet pea. The magnitude of the mutation may be great and striking, or it may be comparatively small. But whatever its size, its inheritance would seem to be according to the law of gametic segregation.

Mutations.

Another form of variability recognised by de Vries is found among the instances which he terms ever-sporting varieties.* The com-

* A free translation of the original terms "Halb-rassen" and "Mittel-rassen."

mon snapdragon, *Antirhinum majus*, is a case in point. There exists a variety of this flower in which the yellow ground colour is relieved by red stripes. This striped variety apparently cannot be fixed. Among the plants raised from its seed there occurs a certain proportion, generally small, which produces red flowers. By selection it is possible to get a strain of snapdragons whose seed gives rise to over 90 per cent. of striped. Similarly, by selection of the red-flowered plants, a strain may be produced which gives about 80 per cent. of red, the rest being striped. In neither case did de Vries succeed in getting a pure strain either of striped or of red. These ever-sporting varieties are undoubtedly complex in their nature, but as far as one can judge from his account, de Vries' experiments do not preclude the possibility of the existence of pure strains of striped and unstriped forms. It seems not unlikely that when attention is more closely concentrated on the progeny of

Ever-sporting varieties.

individual plants, a strain of reds may be produced which throws no striped, and possibly also a strain of striped which throws no reds. Segregation implies gametic purity, and before we can deny the presence of this phenomenon in the flower-colour of the snapdragon, further experimental work is necessary.

Fluctuating Variations.

Lastly, we must recognise with de Vries the type of variation which he has termed fluctuating. The occurrence of such fluctuations is universal. To say that no two individuals of a species are exactly alike is to reiterate a truism. The tall pea is a distinct race, and the dwarf pea is another. It is probable that the dwarf pea arose suddenly as a mutation from the tall. Having once arisen, it breeds true to the dwarf character. It is the property of a mutation to do so. But the dwarfs are not all of precisely the same height. Some are rather taller, and some rather shorter than the normal. The dwarf mutation is subject to fluctuating variations which are probably due to the environment peculiar to each individual. A little more manure in its particular patch of soil, fewer surrounding weeds, greater freedom from the attacks of pests,—these and many other factors may have contributed to the increased height of a plant as compared with its neighbours. But the fluctuating variations due to these causes are, so far as we know, not inherited. No horticulturist of experience would propose to produce from the dwarf pea a permanently taller race by a process of manuring. There is little doubt but that the seeds from the richly manured and those from the normally grown plant would, when raised under similar conditions, each produce a row of plants indistinguishable in point of size. Nevertheless, the view is generally accepted that careful selection of fluctuating variations will eventually lead to the improvement of a stock. At first sight this might appear to contradict what has been written above. Probably the truth is, that under the head of fluctuating variations we are dealing with distinct phenomena. Doubtless some of the so-called fluctuations are in reality small mutations, whilst others are due to environmental influence. The difficulty of distinguishing between the two is very great. The simultaneous existence of small mutations and large fluctuations leads to the disguising of the former by the latter. Only careful and laborious analysis will avail us here, and such analysis is precisely what is at present lacking. The position is roughly as follows. Of the inheritance of mutations there is no doubt. Of the transmission of fluctuations there is no very strong evidence. It is therefore reasonable to regard the mutation as the main, if not the only basis of evolution. And the great service which Mendel has rendered to this branch of philosophy is the demonstration of the fact, that the mutation when once it has arisen is not likely to be swamped by inbreeding with the normal form, provided that it is not injurious to the species. We now recognise discontinuity in inheritance as well as in variation. The new character which arises as a mutation has its representative in the gamete. Once it has arisen selection alone can eliminate it. Mendel's discovery then has led us to materially alter our ideas of the evolutionary process. The small fluctuating variations are not the material on which selection works. Such fluctuations are often due to conditions of the environment, to nutrition, correlation of organs, and the like. There is no indisputable evidence that they can be worked up and fixed as a specific character. Tall peas fluctuate considerably in height, but no gradual process of selecting the shortest will ever result in a permanent race of dwarfs. It is conceivable that the soil may be so doctored as to retard their growth so that they come to mimic, as it were, the dwarfs. But remove the special conditions and their true nature will be manifest. A cursory examination of horticultural literature must convince anyone, that it is by selection of mutations, often very small, that the gardener improves his varieties. Evolution takes place through the action of selection on these mutations. Where there are no mutations there can be no evolution. How and why these mutations arise is the great outstanding problem of biology. It is enough here to emphasise their existence, and to see how the recognition of them must modify current ideas. Thus our conception of the individual becomes that of an aggregation of unit characters which may be entirely independent of one another. In the individual pea for instance, there is a size-character, a flower-colour-character, a pod-character, a seed-colour character, and so on. But different strains of peas exhibit different characters. The flowers may be white in one, purple in another. For each character, therefore, there exists within the species a category containing one or more characters—a category of flower-colour-characters, a category of height-characters, etc. Each

The conception of the individual.

individual pea exhibits one character from each category, and the characters of each such category are, as it were, of equal value and interchangeable. A pea plant may have purple flowers, or it may have white flowers, but never both purple and white. In the simplest cases the individual exhibits outwardly a single character from each category proper to the species; which of such characters it shews depends upon its breeding.

But the individual is also a bearer of gametes, and the nature of these gametes cannot always be decided from the external appearance of an individual exhibiting dominance. The plant arising from a yellow pea seed may bear only yellow seeds, or it may bear both yellow and green in definite proportions. In such cases breeding is the sole test of the nature of the gametes carried. Nevertheless, certain alternatives only are possible. The number of these depends upon the complexity of the characters dealt with, and can be determined by careful analysis.

When this has been effected we may proceed to synthesis.

The position of the biologist of to-day is much the same as that of the chemist a century ago, when Dalton enunciated the law of constant proportions. In either case the keynote has been Discontinuity—discontinuity of the atom, *and the discontinuity of* the variations in living forms. With a clear perception of this principle, and after a long and laborious period of analysis, the imposing superstructure of modern chemistry has been raised upon the foundation of the atom; not otherwise may it be with biology; though here perforce the analytical process must be lengthier, both from the more complex nature of the material, and from the greater time involved in experiments on living forms. For, unlike the chemist, the biologist is trammelled by the times and seasons. Nevertheless, the achievements of the last few years are such as to warrant us in looking forward hopefully to the time when our progress in the knowledge of the living may bear comparison not unworthily with the science of the things that are without life.

Meanwhile a few words on the general aspects of the conceptions that have arisen from Mendel's discovery may not be out of place in this connection. Economically their influence must be very great. Since the principles of heredity form the very basis of the breeder's operations, anything which throws new light on these hitherto obscure matters must largely influence an important industry. From the little that has already been found out the breeder is enabled to proceed with some degree of certainty. Till now his methods have been almost entirely empirical, and in great measure wasteful. He has bred together those that seemed likely to produce what he required. From their numerous offspring he has selected those few that seemed to come nearest to what he wanted. The rest, and these the great ma-

Economic aspects of the discovery.

jority, must be rejected. Many be called, but few chosen. True, the end aimed at, fixation, is eventually attained. But its accomplishment entails much unnecessary waste by the way. Mendel's discovery must react strongly upon these methods. As soon as he recognises the definiteness of his problems, as soon as he realises the conception of unit characters and their mode of inheritance, the breeder will reach his end more swiftly and more surely, with greater economy of time and of material. Few individuals comparatively will suffice for his preliminary process of analysis, and when this has been done he may pass to greater numbers with a feeling of certainty as to the result. He will now know with what he is dealing. The possession of a transmissible character, desirable or otherwise, is no longer a question merely of degree. Either the individual has it, or has it not. Either it is represented in his gametes, or it is not. Once its presence or absence has been determined by analysis the line can be definitely drawn. The breeder may proceed to build up synthetically, character by character, the plant or animal which he requires. His chief limitations will be those imposed by Nature upon the variations of living forms. These he will learn from simple observation and experiment, thereby saving time and labour in futile attempts to achieve the impossible. For he will have read the riddle of the blue Andalusian fowl.

Conclusion.

In conclusion, a few words upon another aspect of Mendel's discovery. How the discovery arose from the accurate analysis of a simple instance we have already seen. How the principle of gametic segregation applies to numerous cases in plants and animals has been pointed out. That it must apply to man also—that most complex of living forms—there is little reason to doubt. If there is aught in these matters the time is coming when they must be taken into account by those whose business is with the ruling and advising of their fellow-men, whose wish is to leave the world a little less aimless than they found it, who desire not to "promiscuously swim down the turbid stream and make up the grand confusion." Most of us are agreed that the circumstances of modern life are susceptible of change and of improvement. That end we seek to attain by better teaching and better sanitation. And in this direction we have made a start by concentrating attention upon the lower strata of society. Speaking broadly, our present policy aims at raising the standard of the less fit, at attempting to bring them closer by such means to those who are richer in natural endowment. Has such a line of endeavour any hope of permanent success? Or is it based upon a misconception of the nature of living things? Some there are doubtless already who question whether the general policy pursued with regard to the lowest classes of the nation is a sound policy, who are troubled with the suspicion that hygiene and education are fleeting palliatives at best, which, in postponing, but augment the difficulties they profess to solve. To them the facts of heredity may speak with no uncertain voice. Education is to man what manure is to the pea. The educated are in themselves the better for it, but their experience will alter not one jot the irrevocable nature of their offspring. Permanent progress is a question of breeding rather than of pedagogics; a matter of gametes, not of training. As our knowledge of heredity clears and the mists of superstition are dispelled, there grows upon us with an ever increasing and relentless force the conviction that the creature is not made but born.

NOTE

As some readers may possibly care to repeat Mendel's experiments for themselves, a few words on the methods used in crossing may not be superfluous. The flower of the pea with its standard, wings, and median keel is too familiar to need description. Like most flowers it is hermaphrodite. Both male and female organs occur on the same flower, and are covered by the keel. The anthers, ten in number, are arranged in a circle round the pistil. As soon as they are ripe they burst and shed their pollen on the style. The pollen tubes then penetrate the stigma, pass down the style, and eventually reach the ovules in the lower part of the pistil. Fertilisation occurs here. Each ovule which is reached by a pollen tube swells up and becomes a seed. At the same time the fused carpels enclosing the ovules enlarge to form the pod. When this, the normal mode of fertilisation takes place, the flower is said to be **selfed.**

In crossing it is necessary to emasculate a flower on the plant chosen to be the female parent. For this purpose a young flower must be taken in which the anthers have not yet burst. The keel is depressed, and the stamens bearing the anthers are removed at their base by a pair of fine forceps. It will probably be found necessary to tear the keel slightly in order to do this. The pistil is then covered up again with the keel, and the flower is enclosed in a bag of waxed paper until the following day. The stigma is then again exposed and dusted with ripe pollen from a flower of the plant selected as the male parent. This done, the keel is replaced, and the flower again enclosed in its bag, to protect it from the possible attentions of insects until it has set seed. The bag may be removed in about a week after fertilisation. It is perhaps hardly necessary to add, that strict biological cleanliness must be exercised during the fertilising operations. This is readily attained by sterilising fingers and forceps with a little strong spirit before each operation, thereby ensuring the death of any foreign pollen grains which may be present.

The above method applies also to sweet peas, with these slight modifications. As the anthers ripen relatively sooner in this species, emasculation must be performed at a rather earlier stage. It is generally safe to choose a bud about three parts grown. The interval between emasculation and fertilisation must be rather longer. Two to three days is generally sufficient. Further, the sweet pea is visited by the leaf-cutter bee, *Megachile*, which, unlike the honey bee, is able to depress the keel and gather pollen. If the presence of this insect is suspected, it is desirable to guard against the risk of admixture of foreign pollen by selecting for pollinating purposes a flower which has not quite opened. If the standard is not erected it is unlikely to have been visited by *Megachile*. Lastly, it not infrequently happens that the little beetle *Meligethes* is found inside the keel. Such flowers should be rejected for crossing purposes.

J. PALMER, PRINTER, CAMBRIDGE.