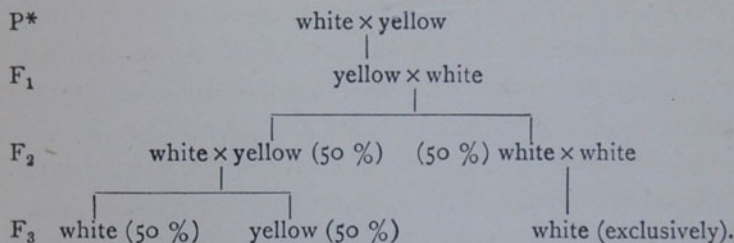


Half the grains, then, of the parentage (*white* × *yellow*) × *white* are pure white in colour, and not to be distinguished from grains of the parentage *white* × *white* even after an extensive examination of their offspring, which is the most rigorous test we are able to apply.

The yellow grains born upon the same hybrid plants (F_2)* had clearly each of them one white parent—namely, the plant from which the white pollen was derived. On sowing these yellow grains and once more pollinating by pure white, a precisely similar result was observed to that obtained in the preceding generation—that is to say, these plants, derived from yellow grains, produced once more 50 per cent. of white grains and 50 per cent. of yellow. We are, therefore, led to suppose that the yellow grains born upon the hybrid plants are of precisely the same nature as the original yellow hybrid grains (*white* × *yellow*), since their behaviour when pollinated from the same white strain is identical. We may express the result so far obtained in the form of the following diagram :



* The following shorthand expressions are adopted to denote the different generations in cross-breeding experiments: P is the generation of the original parents; F₁ is the first generation of offspring—the cross-bred seeds and the plants to which they give rise. To the F₂ generation belong the seeds produced upon the F₁ plants, and the plants to which they give rise, and so on.

The pollen of the F_1 plants (*i.e.*, those plants which were derived from the yellow cross-bred grains)—when applied to the female flowers of the same pure white strain of maize, caused in like manner the appearance of white and yellow grains in equal numbers. This result is equally well expressed by the above diagram on simply regarding the yellow in F_1 as the male parent (pollen-parent) instead of as the female parent (seed-parent) of F_2 .

What is, then, the meaning of these results? The case is really very simple. The germ-cells (ova and pollen-nuclei) of the cross-bred plants (*white* \times *yellow*) must be potentially either pure white or pure yellow, with no blending of these characters. Further, the two kinds (yellow and white) of male germ-cells or pollen-nuclei must arise in equal numbers, and the same must be true of the female germ-cells or ova. By this supposition only can the observed facts be explained. If the supposition is true, then, when the cross-bred plant (F_1) is crossed again with the pure white form, its white germ-cells give rise to white grains which are of the nature (*white* \times *white*), and are therefore pure. Its yellow germ-cells give rise to yellow grains which are of the nature (*yellow* \times *white*). And, since the number of yellow- and white-bearing germ-cells is equal, the number of yellow and of white grains produced in this way is approximately the same. The yellow grains are of the same composition as the original cross-bred grains obtained by crossing pure white with pure yellow, and we have seen that they behave in exactly the same way on further cross-

breeding. This conclusion is at least so far firmly established that no alternative hypothesis has been put forward which will explain the facts.

We have next to consider what will be the result of crossing our cross-bred plants with one another instead of with the pure white form. The following possibilities present themselves :

A yellow female gamete may pair with a yellow male gamete.						
" " " " " "	white					
A white " " " " "	yellow					
" " " " " "	white					

All these combinations are equally likely to occur, because in each plant there are the same number of yellow and white female gametes as well as of yellow and white male gametes. In the long-run, therefore, each of the above pairings will be found to have taken place in an equal number of cases. The grains which we shall obtain, then, will be yellow and white in colour, and the two kinds will occur in the following proportions : 1 pure white ; 2 white \times yellow or yellow \times white, which, as we have already seen, will be yellow in appearance ; and 1 pure yellow. Altogether, we shall expect a ratio of 3 yellow grains to 1 white.

In an actual experiment the following result was obtained :

Yellow grains	16,592,	or	74.5	per cent.
White	"	5,681,	"	25.5

—that is to say, a ratio of 2.9 yellow to 1 white.

The expression $1A : 2Aa : 1a$, in which A represents the dominant character (yellow) and a the recessive character (white), may be spoken of as a Mendelian

formula. It indicates the proportion in which the two pure types and their hybrid brethren will appear, on breeding together the offspring of a simple or *mono-hybrid* cross—*i.e.*, one in which attention is paid to the behaviour of a single pair of characters only,

So far we have been dealing with a pair of characters consisting in the presence and absence respectively of a particular pigment. Precisely similar results are to be obtained in the case of a pair of *structural* characters. The endosperm, or reserve substance, of certain varieties of Indian corn shows a smooth surface, and contains an essentially starchy reserve material, whilst in other races the surface of the endosperm is wrinkled and the reserve product is of a sugary nature. This sugary endosperm is characteristic of the kinds of corn largely used in the United States of America as a table vegetable.

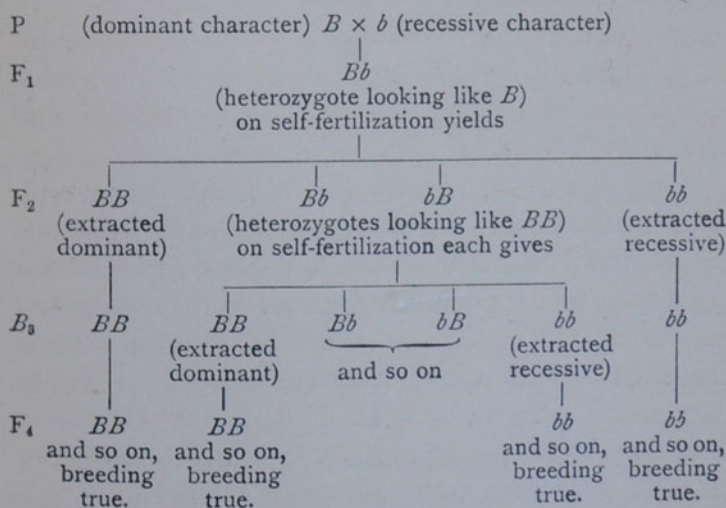
On crossing together a variety with smooth starchy grains and one with wrinkled sugary grains, the grains immediately resulting are smooth and starchy, no matter whether the starchy strain is used as the seed-parent or as the pollen-parent—that is to say, the starchy character is dominant, a dominant character being one which appears in F_1 to the complete or almost complete exclusion of the corresponding character exhibited by the other parent, which is spoken of as recessive. In the present case the sugary character is recessive.

The further behaviour of the cross between smooth and wrinkled is precisely the same as that of yellow

crossed with white. Thus, if the hybrid plants are bred together or self-fertilized, the resulting cobs will exhibit a proportion of three smooth grains to one wrinkled grain. In an actual example there were obtained 5,310 smooth grains and 1,765 wrinkled, or 75.06 per cent. of the former and 24.94 per cent. of the latter.

In a further generation the wrinkled grains breed true. On the average one out of every three smooth grains does the like. The remaining two smooth grains are of hybrid nature, and on self-fertilization yield again the same proportion of three smooth to one wrinkled. Such hybrid grains and the plants into which they develop are spoken of as *heterozygotes*.

Thus, if we write *B* for smooth and *b* for wrinkled, the following scheme will express the result of crossing together plants which bear these characters, and afterwards self-fertilizing the offspring obtained :



So far we have seen that both a pair of structural characters and a pair of colour characters can 'Mendelize,' according to the phrase coined by the Germans—that is to say, the germinal representatives of such pairs of characters remain perfectly distinct in the hybrid plant, and separate completely at the formation of its gametes, in such a way that an equal number of gametes arises containing either character.

The members of a pair of characters which behave in this way on crossing are called *allelomorphs*. When a pair of gametes fuse together in the process of fertilization the resulting cell is known as a *zygote*. A zygote formed by the conjunction of two like gametes is called a *homozygote*. When the gametes contain opposite members of a pair of allelomorphs the result is called a *heterozygote*. The same terms may also be applied to the adult multicellular organisms into which these fertilized egg-cells develop.

We have still to consider what happens when parents are crossed which differ in more than one pair of allelomorphs. The actual result is as follows :

Suppose a smooth yellow type of maize to be crossed with a wrinkled white variety, both smoothness and yellowness being dominant. The grains produced in F_1 are therefore yellow and smooth. Let the F_1 plants, arising from the smooth yellow heterozygote grains, be crossed with the wrinkled white parent, which is recessive in respect of both these characters. In this way the true nature of every germ cell produced by the heterozygote will be able to manifest

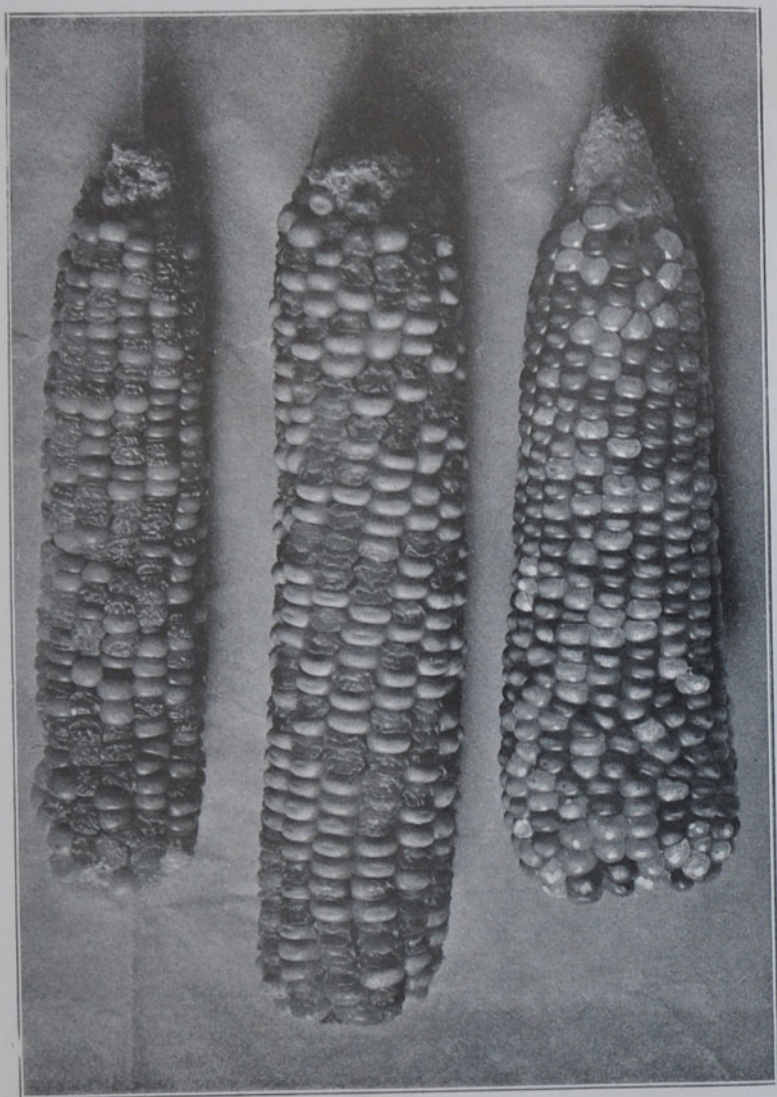


FIG. 14.—MENDELIAN PROPORTIONS IN MAIZE.

Cobs born by heterozygote plants pollinated with the recessive, showing equality of smooth and wrinkled and of coloured and white grains.

[To face p. 175.]

itself in the visible character of the grain produced from it.

The following result was actually obtained in this way :

Smooth yellow grains	2,869,	or 25.3	per cent.
Smooth white grains	2,933,	or 25.7	"
Wrinkled yellow grains	2,798,	or 24.5	"
Wrinkled white grains	2,803,	or 24.5	"

Thus we see that a nearly equal number of the germ cells of the double heterozygote bears each of the four possible combinations of characters—that is to say, it is an even chance whether a particular gamete, which bears the allelomorph yellowness, bears also smoothness or wrinkledness. In other words, the two pairs of allelomorphs segregate in entire independence the one of the other. It is particularly to be noticed that we arrive in this way at two perfectly new combinations of characters, which were not shown by the original parent strains. We have synthesized two new sorts of maize with smooth white and wrinkled yellow grains respectively. In a precisely similar way, if the cross is made between strains of which the grains are respectively smooth white and wrinkled yellow, we should obtain in F_2 the new combinations smooth yellow and wrinkled white.

The result obtained on self-fertilizing the hybrid plant is somewhat more complicated.

If we write A for yellowness, a for whiteness, B for smoothness, and b for wrinkledness as before, $AB \times ab$ gives the heterozygote $ABab$. Equal numbers of the germ cells of the heterozygote will be of the compositions AB , Ab , aB , and ab .

All the following zygotic combinations are, then, equally likely :

ABAB ABAb ABaB ABab

AbAB AbAb AbaB Abab

aBAB aBAb aBaB aBab

abAB abAb abaB abab

Altogether there are sixteen combinations. The result can be expressed more shortly in the form $(A + 2Aa + a)(B + 2Bb + b)$,* which will be found to give the above terms when expanded. Thus the combination of the Mendelian formulæ for F_2 when each of the pairs of allelomorphs is considered separately, gives us the formula for the two pairs of allelomorphs considered simultaneously.

The same result may also be written in the form :

$$\left. \begin{array}{l} 4 A \\ 8 Aa \\ 4 a \end{array} \right\} \text{ combined with } \left\{ \begin{array}{lll} 1 B & 2 Bb & 1 b \\ 2 B & 4 Bb & 2 b \\ 1 B & 2 Bb & 1 b \end{array} \right.$$

or

$$\begin{array}{lll} AB & 2 ABb & Ab \\ 2 Aab & 4 AaBb & 2 Aab \\ aB & 2 aBb & ab^* \end{array}$$

* It is customary to condense these expressions as far as possible by never repeating the same letter more than once in each term. Thus, A stands for AA , B for BB , and so on. On expansion, *i.e.*, multiplying together the contents of the two brackets, $A \times B$ gives $ABAB$, $A \times Bb$ gives $ABAb$, and so on for all the other terms of the expression.

Let us consider the external appearance of these various types in the particular example before us.

Nine of the above sixteen terms include A and B , and are therefore smooth yellow in appearance. (We need not stop to consider whether a or b or both are present in addition, since these are recessive.)

Three terms include A and b , B being absent. These, therefore, appear wrinkled yellow.

Three include a and B , A being absent. These, therefore, appear smooth white.

One contains a and b only, and is, therefore, wrinkled white.

With regard to internal constitution :

The nine individuals of appearance AB include the following types :

One pure, $ABAB$, breeding true to the smooth yellow type on self-fertilization.

Two $ABAb$, heterozygous in respect of the pair $B-b$, but pure yellow.

Two $ABaB$, heterozygous in respect of $A-a$, but pure smooth.

Four $ABab$, heterozygous in respect of both pairs of characters.

The three individuals of appearance Ab include the following types :

One pure, $AbAb$, breeding true to the (new) wrinkled yellow type.

Two $Abab$, giving both wrinkled yellow and wrinkled white.

The three individuals of appearance aB include the following types :

One pure, $aBaB$, breeding true to the (new) smooth white type.

Two $aBab$, giving both smooth white and wrinkled white.

The remaining individual is ab in appearance and $abab$ in constitution, and breeds true to the wrinkled white type.

The expected behaviour of all these different types can be followed out by the aid of suitable breeding experiments, and not only has this been done in the case of the cross which we have been considering, but precisely similar phenomena have been shown to be taking place for a large number of other characters in many different species of plants and in a good many animals as well.

We are now in a position to state the important proposition known as Mendel's law, which is to the following effect :

The gametes of a heterozygote bear the pure parental allelomorphs completely separated from one another, and the numerical distribution of the separate allelomorphs in the gametes is such that all possible combinations of them are present in approximately equal numbers. (Note that it is impossible for more than one member of the same pair of allelomorphs to occur together in the same gamete.)

This is the essence of the great discovery made by Gregor Mendel, Abbot of Brunn, and published by him in the Transactions of the Brunn Natural History Society in 1866. By some extraordinary chance Mendel's paper was entirely lost sight of until the

same facts were independently rediscovered in 1899 by de Vries working in Holland, by Correns in Germany, and by Tschermak in Austria.

Gregor Johann Mendel was born on July 22, 1822, at Heinzendorf, near Odrau, in Austrian Silesia. In 1843 he entered as a novice the Augustine Convent at Altbrunn, and was ordained priest in 1847.

Mendel was a teacher of natural science in the Brunn Realschule from 1853 to 1868, when he was appointed Abbot of his monastery. During this time he was largely occupied with experiments in cross-breeding a great variety of plants, and some idea of his activity in this line of scientific work is to be gathered from a perusal of his letters to the German biologist Nägeli, a correspondence which has recently been published by Professor Correns. Mendel himself only published the result of his work with peas, and that of a few of his experiments with *Hieracium*.

After 1873 the cares associated with the position of Abbot of Brunn appear to have prevented further biological work. His death took place in 1884, two years after that of Charles Darwin, to whom Mendel was thirteen years junior.

Mendel's own experiments—that is to say, the chief ones published by him—were made with peas, a kind of plants which were found to be remarkably well suited to this kind of work. Seven pairs of characters in these plants were found to behave in precisely the same manner as those characters of the maize-plant which have already been described, and in all of them the phenomenon of dominance also

appeared. The characters dealt with by Mendel were as follows, the dominant member of the pair being in each case placed first :

Smooth seeds, and wrinkled seeds.

Yellow, and green reserve material—*i.e.*, cotyledons.

Deeply coloured (grey), and nearly colourless testas or seed-coats.

Inflated or stiff, and wrinkled or soft pods.

Green, and yellow pods.

Flowers scattered up the stem, and flowers in a terminal bunch or umbel.

Tall, and dwarf stems.

As the result of these experiments Mendel came to the conclusion with which his name is now closely associated—that the male and female germ-cells of hybrid plants contain each of them one or the other member only of any pair of differentiating characters exhibited by the parents, and that each member of such a pair of characters is represented in an equal number of germ-cells of both sexes. Furthermore, separate pairs of differentiating characters (allelomorphs) conform to this law in complete independence of one another.

Although in Mendel's own experiments one member of each pair of differentiating characters was always dominant, dominance is by no means an universal phenomenon when different varieties of plants are crossed together. In a considerable number of instances the heterozygote is found to exhibit an appearance which is more or less intermediate between the types of character shown by the parents. It may be

almost exactly intermediate, or the appearance of the cross-bred form may be nearer to that of one parent than to that of the other. Dominance is clearly only an extreme case of this latter phenomenon. The term 'dominance' is applied to those cases in which the appearance of the hybrid offspring is so near to that of one parent as to be no longer clearly distinguishable from it.

In other cases, still of a simple Mendelian nature, the appearance of the heterozygote may be quite different from that of either parent homozygote. An excellent example which is almost certainly of this nature is afforded by the Andalusian fowls studied by Messrs. Bateson and Punnett. And this will also serve as our first illustration of the application of these principles to animals as well as to plants. The facts of the case are as follows :

The 'blue' type of Andalusian appears to be a heterozygote form which has never been got to breed true. When a pair of these birds are mated together only about half their offspring are like themselves, the remainder being entirely different. Half these remaining 'wasters' are black, and half are nearly white, showing only a few black 'splashes.' If, now, a pair of the black wasters are mated together, they breed perfectly true, yielding only black offspring like themselves. Similarly the splashed whites mated together give rise to splashed white, and nothing else. Both these forms, then, the black and the splashed white, are clearly pure homozygotes. On mating a black and a splashed white together, black-bearing

gametes and white-bearing gametes will meet together in fertilization. In every case in which this form of mating was carried out the resulting chicks were invariably blue.

The gametes of the blue type of Andalusians, then, according to our supposition, do not bear the blue character at all. Half of them contain the black and half of them the splashed white allelomorph. Such gametes, meeting by chance when a pair of blue Andalusians are mated together, give rise to the zygotes—one black-black, two black-white, one white-white—the black-whites being, of course, blue in appearance as before.

Now, we may put this explanation to the test by a very simple experiment—namely, by mating the supposed heterozygote blues with the black and with the splashed white types respectively. Both these forms of mating were examined by Bateson and Punnett, and the results were as follows: It was found that blues crossed with blacks gave rise to equal numbers of blue and of black offspring, whilst when blues were crossed with splashed whites there appeared blue and splashed white chicks in equal numbers. And by a repetition of the process it could be shown that the blues so obtained were heterozygotes as before. Here, then, we have clear evidence that equal numbers of the germ-cells produced by the blue birds bear the pure black allelomorph and the pure splashed white allelomorph respectively, since half the offspring obtained on mating the blue birds with black are black, and half the offspring obtained on mating them with

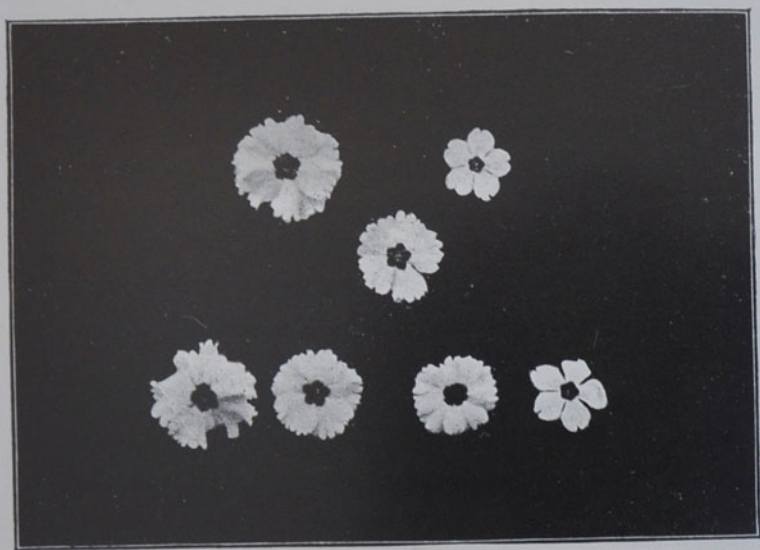
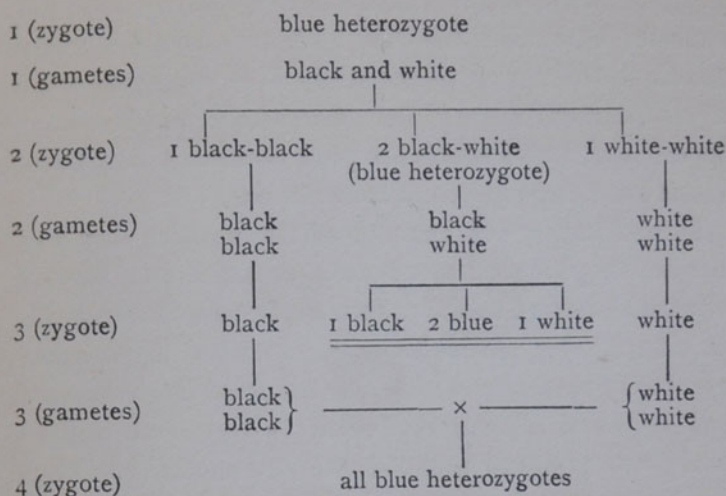


FIG. 15.—PRIMULA SINENSIS CROSSED WITH *P. STELLATA*.

Above, the parents. In the middle, the heterozygote offspring—*P. pyramidalis*. Below, the result of self-pollinating *P. pyramidalis*: 1. *P. sinensis*: 2. *P. pyramidalis*: 1. *P. stellata*.

[To face p. 183.]

splashed white are splashed white. The following scheme of inheritance illustrates the phenomena described :



A case which is closely similar to that of the Andalusian fowl is afforded by the cross between *Primula sinensis* and *Primula stellata*.

P. sinensis crossed with *P. stellata* gives rise to a type which is different from either parent, being in some respects intermediate between the two. The hybrid is so distinct that a special name has been given to it, and the new type is known as *P. pyramidalis*. So far it has been found impossible to obtain a strain of *P. pyramidalis* which will breed true. On self-fertilization the offspring are found to show the types of *P. sinensis*, *P. pyramidalis*, and *P. stellata* in the ratio of 1 : 2 : 1.

Cases like the above illustrate the essential part of

Mendel's law even better than those in which dominance is present, the characteristic proportion of one of each homozygote type to two of the heterozygote being at once recognisable in such a case without the necessity for further breeding; whereas, in cases where there is dominance, further study is necessary in order to distinguish, among the individuals of dominant appearance, those which are pure dominant and those which are heterozygous in constitution.

In concluding our account of the simpler forms of Mendelian phenomena we may consider one further point with regard to the nature of the two allelomorphs making up any particular pair. In what is probably a majority of the cases hitherto examined the dominant and recessive allelomorph seem to represent respectively the presence and absence of something. Thus the dominance of colour to absence of colour, or whiteness, is a very frequent phenomenon. And in some of the more complex cases to be described in the next chapter we shall find the presence and absence of a particular factor very often behaving as a pair of Mendelian allelomorphs. The question arises as to how far this conception should be extended. It seems, for instance, somewhat far-fetched to speak of dwarfness as being simply determined by the absence of the factor for tallness, though it is not impossible that this may be the correct way of looking at the facts. Be this as it may, it is to be remembered that a Mendelian pair often represents the presence and absence respectively of a particular feature.

CHAPTER VIII

MENDELISM (*continued*)

MENDEL'S law, as stated in the preceding chapter, has already been found to hold good in a very large number of cases—cases in which all kinds of characters are concerned, belonging to many different species of animals and plants. In certain instances, however, complications arise, and these may be treated of in two main sections.

The first kind of complication arises from the phenomenon known as *coupling*. The essence of this phenomenon consists in the existence of some kind of affinity occurring in the same individual between allelomorphs which belong to distinct pairs. In consequence of such an affinity exceptions are found to the rule that separate pairs of allelomorphs segregate independently.

The closeness of the connection between the characters concerned shows a series of gradations in different cases. In the simplest cases of all, what are loosely spoken of as separate characters are found on closer examination to be only different aspects of one and the same characteristic feature. These cases, then, offer no real exception to the rule, for only one pair of allelomorphs is actually concerned. As an example, we

may take the case of the wrinkled sugary type of maize already contrasted with the smooth starchy variety. The essential difference between the two kinds depends upon the fact that in the former the reserve product laid down in the endosperm is different, being largely of a sugary nature instead of being starchy. With this circumstance is associated the presence of a larger proportion of water in the unripe grain. And the result of this is that, when the grain dries, its surface falls into folds. The sugary nature of the grains also causes them to take on a more hyaline or semi-transparent appearance than the grains of the starchy variety. All these characters, if they can be so called, behave on crossing as a single Mendelian allelomorph, and are doubtless represented in the germ cells by a single substantive representative.

A simple example of what may probably be regarded as a real case of coupling is afforded by certain colour characters exhibited by pea-plants. In these plants coloured flowers, a red or purple colouration in the axils of the leaves, and a marked pigmentation of the testas, or seed-coats, are always associated together on the same plants; so that, if we find a plant which has green leaf axils, we may be sure that its flowers will be white, and the testas of its seeds only slightly pigmented. On crossing plants bearing coloured axils, coloured flowers, and pigmented testas, on the one hand, with plants bearing green axils, white flowers, and unpigmented seed-coats, on the other, the two sets of characters are found to behave as a simple pair of allelomorphs, and the simultaneous appearance of

colour in these different situations doubtless depends upon the presence of a particular pigment in the plant which exhibits it. Nevertheless, we can scarcely fail to look upon these three separate manifestations of the pigment as representing distinct characters, and this being so, we suppose their germinal representatives to be coupled together in such a way that they remain associated at the time when, during the formation of the germ-cells of the heterozygote, other allelomorphs become independently segregated.

And this way of looking at the facts is further justified by the behaviour of the characters in question in another species of plant. For in the sweet pea it is possible for the coupling between these characters to be broken down, so that a plant which exhibits green leaf axils may, under certain circumstances, bear coloured flowers. In such a plant the leaf-axil-colour and the flower-colour must clearly be represented by independent allelomorphs.

In other cases, again, there may be coupling between characters which have no obvious relation to one another at all. In illustration we may take the case of a cross between two strains of peas, one of which had white flowers and opened its buds several days earlier than the second, the blossoms of which were purple.

The F_1 plants (with purple blossoms) came into flower at a period intermediate between those of the parents. In F_2 506 plants were grown successfully. Some of these flowered as early as the white parent, and others as late as the purple parent; but the majority of the plants ranged between these two extremes, so that it

was impossible to rank the individuals into definite classes in respect of so indefinite a character as time of flowering. On making a perfectly arbitrary division, however, it was found that 175 purple and 104 white plants were in flower on a certain day, and that 208 purple and 19 white plants did not open their buds until afterwards. There is, therefore, clearly some coupling between the presence of white blossoms and early flowering on the one hand, and between lateness and purple flowers on the other. Two characters more diverse than colour of the flowers and time of flowering could at first sight scarcely be imagined.

The second class of complications that we have to deal with—although the term complication may be to a certain extent justified in connection with it—does not involve any exception to Mendel's law of segregation. The phenomenon of so-called *reversion on crossing* has long been familiar to biologists. Its meaning, however, was totally obscure, and even the Mendelian was at first unable to offer any explanation. The phenomenon consists in the appearance, in the offspring of a cross, of a character which was not visibly present in either parent, and in many cases this character can properly be regarded as ancestral—it is a character which has been lost by both parents in the course of their divergent evolution from a common primitive form. Now, these cases differ entirely from those of the appearance of a heterozygote form on crossing, such as are due to the combined action of the two parental allelomorphs in the cross-bred offspring,

because in true cases of reversion a certain proportion of the reversionary individuals of F_2 are found to breed true, which a simple heterozygote will never do.

It has been found that the essential part of this phenomenon of reversion on crossing consists in the existence in the parents of certain hereditary factors—allelomorphs, in fact—which, although by themselves invisible, yet, when combined in cross-breeding with certain other allelomorphs, belonging to independent pairs, lead to the appearance of new visible characters.

The term reversion cannot properly be applied to these phenomena as a class, because, in the first place, characters may arise in this way which cannot be regarded as ancestral, and, secondly, because reversions may take place in other ways; for example, the reappearance of a simple recessive character would legitimately be ranked among reversions. The best general name for the class of phenomena we are about to describe is perhaps *latency of characters*, or *cryptomerism*, the latter being the term employed by Tschermak, who was the first to describe these phenomena in connection with Mendelian ratios.

In the simpler cases an invisible or *latent* factor derived from one parent, on becoming associated with a different factor born by the other parent, and already visibly represented among the external features of this second parent, makes itself apparent among the visible characteristics of the heterozygote. In such a case the characteristic appearance exhibited by the heterozygote may subsequently become permanent, owing

to the building up of a type which is a homozygote in respect of both the necessary factors.

This may be made clearer by a definite illustration.

A pea-plant characterized by the presence of a greyish or brownish testa to its seeds (grey) was crossed with a plant having nearly colourless testas (white). The testas of the F_1 plants were marked with bright purple dots on a grey ground (purple). These hybrid plants were self-pollinated, and in F_2 the three types appeared in the following proportions: 9 purple, 3 grey, 4 white. What is the meaning of this ratio? In order to complete the ordinary expectation for a simple Mendelian case in which two pairs of allelomorphs are concerned (di-hybridism) we must write down the following expression:

$$9 \left\{ \begin{array}{l} \text{purple} \\ \text{grey} \end{array} \right\} : 3 \left\{ \begin{array}{l} \text{no purple} \\ \text{grey} \end{array} \right\} : 3 \left\{ \begin{array}{l} \text{purple} \\ \text{no grey} \end{array} \right\} : 1 \left\{ \begin{array}{l} \text{no purple} \\ \text{no grey} \end{array} \right\}$$

But it would seem that the purple character cannot appear when the grey colour, or some factor constantly associated with this colour, is absent, as is the case in the original white parent from which the factor for purple spots was derived. Consequently, the three $\left\{ \begin{array}{l} \text{purple} \\ \text{no grey} \end{array} \right\}$ plants are indistinguishable from the $\left\{ \begin{array}{l} \text{no purple} \\ \text{no grey} \end{array} \right\}$ plants or whites, and we thus arrive at the result which was described as being the one actually obtained—namely, 9 purple : 3 grey : 4 white.

In other respects this example is precisely like the case of two pairs of allelomorphs described on p. 176.

We may write A for presence of grey pigment, a for absence of grey pigment, B for presence of purple, and b for its absence. Then the original cross was of the form $Ab \times aB$, from which $AaBb$ resulted in F_1 . And the visible characters of the types which appeared in F_2 would be represented by $9AB + 3Ab + (3aB + 1ab)$. On referring to the account given on p. 176 it will be seen that one in nine of the purple plants is of the constitution $ABAB$, and may be expected to breed true.

A precisely similar result may be obtained in F_2 in cases where there is no reversion in F_1 . In the following example a white pea, which did not contain the latent purple factor, was crossed with a 'maple-seeded' pea. The characteristic feature of maple is a marbling of brown spots on a grey ground colour. In F_1 the marbling was dominant, and the seeds resembled the maple parent.

In F_2 there appeared 9 maple : 3 grey : 4 white—*i.e.*, the same ratio as in the previous case, this time without reversion. This ratio is brought about by the simple combinations of two pairs of allelomorphs $A-a$, and $C-c$, C being unable to manifest itself unless A is present in the same zygote. As a matter of fact, in this particular case C does sometimes just manage to appear in the absence of A , the result being a white seed with a sort of faint 'ghost' of a maple marking.

When a strain bearing both maple marking and purple spots is crossed with a white in which neither of these factors is latent, we can easily calculate the

ratio to be expected in F_2 by using the formula $(A + 2Aa + a) (B + 2Bb + b) (C + 2Cc + c)$. The result works out as follows (writing m for maple, p for purple, and g for grey): $27mpg$, $9mg$, $9pg$, $3g$, $(9mp, 3m, 3p, 1w)$. Since g is absent from all the members of the series enclosed in the bracket, these appear white, or nearly so, the total number of whites being thus 16. And the numbers obtained in an actual experiment accorded closely with the expected ratio 27 : 9 : 9 : 3 : 16.

Among the sixteen whites, some will be bearing the factors for m and p , others that for p only, others that for m only, whilst one in sixteen will contain neither of these factors. Until such invisible differences between the different white plants are actually proved to be present the whole account so far given will remain more or less hypothetical. The proof is obtainable by crossing the different whites with a pure grey strain. The grey factor being thus introduced, the whites which contain a p or an m factor will exhibit the same in their offspring. A number of the whites obtained in F_2 and in later generations were actually crossed with the same grey-seeded plant. Some of the offspring showed both the maple and the purple character, others the maple without the purple, others the purple without the maple, and others, again, showed neither; the seeds of these last being exactly like those of the grey parent owing to simple dominance of the grey allelomorph over white.

Another example of the same kind of phenomenon may be taken from the work of the French zoologist Cuénot. In the present instance the experimental

crosses were made with animals—namely, mice. As the result of his experiments Cuénot framed the hypothesis that in mice the colours yellow (*J*), grey (*G*), and black (*N*) can only make their appearance when the zygote containing them contains also a perfectly independent colour-producing factor (*C*), which is allelomorphic to, and dominant over, the albino factor (*A*). (According to the notation which we have previously adopted, this last pair of factors would be more properly written *C* and *c*.)

According to Cuénot's scheme all albino mice (white mice with pink eyes) contain some colour in a latent condition. The different individuals with which experiments were made were found to be capable of representation by the following 'formulae' of heredity :

Homozygotes, *AG* ; *AN* ; *AJ*.

Heterozygotes, *AG . AN* ; *AG . AJ* ; *AN . AJ*.

In the visible expression of these colours when *C* is present, yellow was found to be dominant over grey and over black, and grey was dominant over black. In the formation of the gametes the various factors concerned follow Mendel's law precisely. There is, however, one curious point to be noticed, if Cuénot's interpretation is really correct. We have in this case three alternative characters instead of a simple pair of allelomorphs. On referring to the list of different kinds of individuals given above, it will be seen that homozygotes contain only one of these alternative characters, whilst a heterozygote contains two. It is not possible for a single individual to contain all three

characters at once. A pair of individuals may, however, between them carry all the possible colour allelomorphs. Cuénot gives the following example, being one of three possible methods by which all the three colours, yellow, grey, and black, as well as the albino character, can appear among the offspring of a single pair of animals :

Parents :	<i>AG</i> (albino) <i>AN</i> (albino)	<i>CN</i> (black) <i>AJ</i> (albino)																		
F_1	<i>AG . AN</i>	<i>CN . AJ</i>																		
Gametes	$\overbrace{\quad \quad \quad}^{AG \quad \quad AN}$	$\overbrace{\quad \quad \quad \quad \quad}^{CN \quad AJ \quad CJ \quad AN}$																		
F_2	<table style="margin-left: auto; margin-right: auto;"> <tr> <td style="padding-right: 10px;"><i>AG . CN</i></td> <td style="padding-right: 10px;">grey</td> <td rowspan="6" style="font-size: 3em; vertical-align: middle; padding: 0 10px;">}</td> <td rowspan="6" style="vertical-align: middle;">4 albinos</td> </tr> <tr> <td><i>AN . CN</i></td> <td>black</td> </tr> <tr> <td><i>AG . AJ</i></td> <td rowspan="4" style="font-size: 2em; vertical-align: middle;">} albinos</td> <td rowspan="6" style="vertical-align: middle;">2 yellow</td> </tr> <tr> <td><i>AG . AN</i></td> </tr> <tr> <td><i>AN . AJ</i></td> </tr> <tr> <td><i>AN . AN</i></td> </tr> <tr> <td><i>CJ . AG</i></td> <td rowspan="2" style="font-size: 2em; vertical-align: middle;">} yellow</td> <td rowspan="6" style="vertical-align: middle;">1 black</td> </tr> <tr> <td><i>CJ . AN</i></td> </tr> </table>	<i>AG . CN</i>	grey	}	4 albinos	<i>AN . CN</i>	black	<i>AG . AJ</i>	} albinos	2 yellow	<i>AG . AN</i>	<i>AN . AJ</i>	<i>AN . AN</i>	<i>CJ . AG</i>	} yellow	1 black	<i>CJ . AN</i>	<table style="margin-left: auto; margin-right: auto;"> <tr> <td style="font-size: 3em; vertical-align: middle;">}</td> <td style="vertical-align: middle;">1 grey</td> </tr> </table>	}	1 grey
<i>AG . CN</i>	grey	}	4 albinos																	
<i>AN . CN</i>	black																			
<i>AG . AJ</i>	} albinos					2 yellow														
<i>AG . AN</i>																				
<i>AN . AJ</i>																				
<i>AN . AN</i>																				
<i>CJ . AG</i>	} yellow	1 black																		
<i>CJ . AN</i>																				
}	1 grey																			

The actual numbers of offspring which were obtained in F_2 from this cross were as follows : 81 albinos, 34 yellow, 20 black, 16 grey ; the expected proportion being—76 : 38 : 19 : 19.

By the process of crossing followed by selection of those families in which a uniform series of young appeared in F_3 , Cuénot was able to extract without difficulty pure homozygous races of blacks *CN . CN*, and of greys *CG . CG*, as well as the corresponding albino races *AN . AN*, and *AG . AG*. But in the case of the yellow a curious and unexpected phenomenon appeared, and one which, if Cuénot's explanation of it

proves to be well established, is likely to be of great theoretical interest.

When $CJ \cdot CG$ (or $CJ \cdot CN$) is crossed with CG (or CN), since yellow is dominant, equal numbers of yellow and of grey (or black) offspring are to be expected, and in various crosses of this nature Cuénot actually obtained 177 yellows and 178 blacks or greys. Hence we may deduce that the heterozygote yellow was giving off the expected proportion of gametes bearing the yellow character (*i.e.*, 50 per cent.).

When such heterozygous yellows are bred together the expected result would be as follows :

$$CJ \cdot CG \times CJ \cdot CG = \underbrace{CJ \cdot CJ + 2 CJ \cdot CG}_{3 \text{ yellow}} + CG \cdot CG \quad 1 \text{ grey}$$

Eighty-one yellow mice were actually obtained in this way. Among them some twenty-seven would naturally be expected to be pure dominant, and to give yellow only when crossed with black or grey individuals. To Cuénot's astonishment, he found on making the necessary crosses that every one of these eighty-one yellows gave some black or grey among its offspring; not one of them was a pure homozygous yellow.

The only way in which this result can be explained at present is by supposing that there is some obstacle to the fertilization of one yellow-bearing gamete by another gamete of the same kind. The combinations $CJ \times CG$ and $CG \times CG$ take place, it would seem, readily enough, but there is some mutual repulsion between CJ and CJ which prevents their union. We

shall find later on that there is some evidence derived from an entirely different class of facts which seems to support the idea that a selective fertilization of this kind really does take place in certain cases. The phenomenon is nevertheless so remarkable that we may have some hesitation in accepting it without further evidence. In the meantime it must be recorded as a distinctly exceptional case, though not, be it noted, as an exception to Mendel's law. The gametes obey the law, as was shown by crossing yellow with non-yellow, and it is only in their manner of combination that a complication has been introduced.

We have still to describe a case in which two latent factors, one derived from each parent, give rise, by their simultaneous presence in the zygote produced, to the appearance of an entirely new character. The following example is the first one of the kind to be completely elucidated, and is one of those studied by Messrs. Bateson and Punnett and Miss Saunders.

The white-flowered variety of sweet-pea known as Emily Henderson was found to exist in two forms, only to be distinguished from one another by the shape of the pollen grains which they produced. In one of the two the shape of the pollen is elliptical (long pollen), in the other it is approximately spherical (round pollen). Sweet-peas normally undergo self-pollination, so that the two types naturally remain distinct. Let us see what happened when the long- and the round-pollined forms were crossed together.

The cross-bred plants (F_1) had coloured flowers—flowers of the old-fashioned purple type known to

florists as Purple Invincible, which is characterized by a purple standard and blue wings. The pollen produced by these plants was of the long type. Thus as regards the shape of the pollen grains there was simple dominance. But the union of two white-flowered types has given rise to a series of plants all possessing a definite colour character—purple with blue wings. This character is very probably the same as that exhibited by the common ancestor of all our cultivated sweet-peas. Here, then, we seem to have a clear case of reversion to the ancestral type on crossing. We shall find that the Mendelian principles will enable us to arrive at a clear conception of the mechanism of this process.

The cross-bred plants were self-pollinated, and in F_2 the following types made their appearance in approximately the proportions given :

Purple Invincible	81	}	or	{	3	}	3	}	9
Picotee	27								
Painted Lady	27	}	or	{	3	}	1		
Tinged white	9								
White...	112							7	

Painted Lady is a well-known colour type which is characterized by the presence of a red standard and white wings. Picotée and tinged white are also forms well known to the sweet-pea fancy. They appear to be diluted forms of the purple and Painted Lady types respectively, their appearance depending upon the presence of a definite diluting factor in addition to the

factor for the colour in question, or perhaps more properly upon the absence of the proper strengthening factor which converts Picotee into purple, and tinged white into Painted Lady.

The following explanation of the result so far described has now been well established by further experiment. In the first place, we may consider all the coloured forms together as a single group opposed to white. It is now clear that the coloured type of F_1 is due to the meeting together of two factors, one of them born by one white parent and the other by the second, and it is necessary for both these factors to be simultaneously present in order that any colour may make its appearance. We may call these two factors C and R , denoting the absence of either by c and r respectively. By the simple Mendelian behaviour of these two pairs of factors $C-c$ and $R-r$, the ratio of nine coloured plants to seven white appearing in F_2 is readily explicable, and the way in which this happens is shown in the diagram on the opposite page.

To explain the presence of the four different types of coloured plants which make their appearance in F_2 , two further pairs of allelomorphs are called in. The dominant member (B) of one of these, when present in combination with C and R , produces the purple or Picotee colour (blue), whilst its absence (b) in presence of C and R is accompanied by the appearance of the red colours—Painted Lady and tinged white.

Purple Invincible and Painted Lady are regarded as intensified forms of Picotee and tinged white respectively. The presence of the second factor (T) is attended

by the development of the full colours purple and Painted Lady; its absence (*t*) causes the appearance of the diluted forms Picotee and tinged white.

B and *T* may be present when either *C* or *R* or both are absent; the resulting plant has then white flowers. And it is interesting to notice that the ultimate recessive white, containing *c r b t*, occurs only once among 256 individuals of F_2 . The whole apparently complex system

	CR	cR	Cr	cr
CR	CR CR	cR CR	Cr CR	cr CR
cR	CR cR	<div style="display: flex; justify-content: space-around;"> cR cR </div>	Cr cR	<div style="display: flex; justify-content: space-around;"> cr cR </div>
Cr	CR Cr	cR Cr	<div style="display: flex; justify-content: space-around;"> Cr Cr </div>	<div style="display: flex; justify-content: space-around;"> cr Cr </div>
cr	CR cr	<div style="display: flex; justify-content: space-around;"> cR cr </div>	<div style="display: flex; justify-content: space-around;"> Cr cr </div>	<div style="display: flex; justify-content: space-around;"> cr cr </div>

FIG 16.

The shaded squares represent coloured plants, the blank squares white plants.

of floral colours is thus explained by the simple Mendelian behaviour of four separate pairs of allelomorphs.

Bateson and his collaborators have, therefore, provided a complete account of the phenomenon of reversion on crossing, an account which has already been demonstrated to hold good in other instances besides that of the sweet-pea. The facts are expressed in the following manner by their discoverers. "Reversion" is thus seen to be a simple and orderly phenomenon due to the meeting of factors belonging to distinct

though complementary allelomorphic pairs, which at some moment in the phylogeny of the varieties have each lost their complement.*

We may now proceed to pass in rapid review a selection of the more remarkable instances of Mendelian inheritance which have been so far demonstrated.

The ease with which characteristics of colour can be distinguished and defined has naturally led to a good deal of attention being paid to the phenomena of their inheritance. In this way many cases of simple dominance have been discovered in plants and in animals, as well as several examples of reversion in F_1 , followed in both cases by a Mendelian segregation of characters.

Thus the colours of many flowers afford perfectly simple phenomena, whilst other cases, like the sweet-peas and the closely similar case of stocks studied by Miss Saunders, have required long and arduous experiment for their elucidation. No case of this kind hitherto examined has been definitely proved to be non-Mendelian.

Colour characters which follow Mendel's law have been observed in mice, rats, rabbits, guinea-pigs, pigeons, fowls, cats, and so on. In butterflies and other insects, and even in snails, similar phenomena have been described. The study of the larger domestic animals awaits for the present the proper endowment of these researches. When this takes place the inheritance of far more important characters than colour will be adequately studied to the great profit of all who are concerned in the breeding industry.

* Proceedings of the Royal Society, B. vol. 77, p. 238.

Hurst has already shown from an examination of the stud book that the bay and brown colours of thoroughbred horses are Mendelian dominants to chestnut.

Other characters of the most diverse kinds are also similarly inherited. We have already referred to structural characters in maize and in peas. Stature is a character which is definitely inherited in many plants. Among more subtle characters a similar mode of transmission has been found in the case of differences in chemical composition, and in that of immunity from and susceptibility to the attacks of certain diseases. The thrum-eyed condition of the primrose has been shown by Bateson and Gregory to be a Mendelian dominant to the pin-eyed condition, so that we have here the solution, so far as solution is possible, of a biological problem to which Darwin devoted the greater part of a volume.

A study of numerous pedigrees has enabled Bateson to show that there is great probability that in the case of the human race certain congenital diseases are simply transmitted from parent to offspring in accordance with Mendel's law.

How far the influence of the Mendelian principles may extend we do not yet know. But it is certain that very few, if any, cases have so far been discovered in which differentiating characters do not behave in this way when the types which exhibit them are crossed together. Experiments have now been made upon a great variety of plants and animals, involving a considerable diversity of kinds of characters. Nevertheless

it is scarcely possible to cite a case in which it is definitely and certainly known that Mendel's law, subject to the modifications already described, does not hold good. Cases of various kinds are, indeed, recorded, but these records are derived from experiments either carried out before the bearings of the Mendelian phenomena were at all fully appreciated, or—and this is the most frequent case—without any knowledge at all of Mendel's discovery.

Thus a considerable number of cases were formerly described in which the first cross or heterozygote of F_1 bred true instead of segregating in F_2 . There is some doubt whether any case of this kind will really stand criticism; Millardet's case, for example, which was described at the end of the last chapter but one, has never been confirmed. It is quite certain that among all the numerous crosses studied during the last six years no example of the kind has been substantiated. The most recent cases to be described of a first cross breeding true are those of de Vries, and at these we are bound to pause, because de Vries is surpassed by no recent observer in weight of authority. Nevertheless, de Vries' cases are of so complex a kind that we have some hesitation in accepting them without further study. For the rest, this is one of the problems which remain for the future to deal with.

We may now turn for a brief space to some of the cases in which we have as yet no certain knowledge of the manner in which inheritance proceeds.

The most obvious extension of Mendel's law to processes where it cannot be directly shown to hold

good is to suppose that the same rule applies to cases of normal fertilization as to hybrid fertilizations. We should then picture the former process as taking place in somewhat the following way. Every visible character of the individual which can be separately distinguished, and which on cross-breeding would be inherited on ordinary Mendelian lines, must be represented in the gametes by a definite factor of some kind, possibly by a definite substance or combination of substances. The pair of parental factors for a particular character would combine on fertilization, and at the formation of the gametes in the offspring its members would separate as perfectly definite entities, to recombine when these gametes meet once more with their corresponding mates. Such a definite segregation of characters taking place within a pure strain would be very difficult of absolute demonstration, but it is hard to avoid the conclusion that this is a true deduction from the facts observed when cross-breeding takes place. Such a segregation would formerly have been thought a very small assumption in comparison with that of the segregation of pairs of allelomorphs of which no trace is externally visible, and yet the latter assumption has now been shown to be perfectly well established.

This idea of unit characters, capable of being inherited independently of one another, is one of the most important conceptions which has ever been introduced into the science of biology, and the introduction of it has followed as the direct result of Mendel's work. It is a conception which has led to a complete change in

our ideas of heredity, since we no longer look upon the individual as a unit, but find ourselves compelled to study separately the independent characters of which the individual is built up. The idea of the individual as a living mosaic—an idea put forward long ago by Naudin with only a partial realization of its significance—has thus returned to us. In this connection a curious problem presents itself. What would be left if we could imagine all the separable characters of a living creature as having been taken away? Would there, or would there not, be any residuum? Upon this knotty point there is a disagreement among authorities, and so we may be content to leave it, since the question is hardly one which is capable of a practical solution.

A phenomenon to which it is scarcely doubtful that Mendelian principles will ultimately be found to apply, although as yet the precise proof is wanting, is that of sex. In the male and female sexes of the majority of animals we have a very clear example of a pair of definite differentiating characters. And the fact that in the majority of forms the two sexes make their appearance in nearly equal numbers, may be thought to point clearly to the conclusion that the separation of the sexes depends upon some quite simple gametic process. Light has recently been thrown upon this question from the side of the study of the minute structure of the gametes, and we shall defer the further discussion of the problem to the chapter which deals with microscopic phenomena within the cell.

A proper understanding of Mendel's law enables us

to escape certain theoretical difficulties which have long been prominent in the minds of students of evolution. Many evolutionists were accustomed to argue that a new form suddenly arising in the midst of an old-established species could not give rise to a new and permanent variety or elementary species, because it would immediately be 'swamped' by intercrossing with the parent species from which it was derived. If, however, the character distinguishing the new type is allelomorphic to the corresponding character, or absence of a character, shown by the parent form, this difficulty disappears. For suppose as an extreme case that the new type arises as a single individual only, which is therefore compelled to mate with a member of the original species. If the new character is recessive it will disappear in the immediate offspring of this cross. But half the germ-cells produced by the cross-bred form will bear the new character pure and undiluted. If any of these cross-breds mate together the new type will appear in a quarter of their offspring. Even if all of them mate with members of the original type, half the offspring of such matings will be heterozygous, and sooner or later the heterozygotes will be sure to mate with one another, and give rise once more to the novel type of individuals. If the new form has any structural or other advantage over the old species, the former will tend to survive at the expense of the parent type, and it may survive if it is only equally well fitted for the battle of life. In the case of dominance of the new form the same process will take place, only it will be apparently

more rapid in the early stages because the cross-breds will themselves exhibit the new character. In this case, even if the new type has a very marked advantage over the parent form, the process of completely supplanting the latter will be delayed, because the old type of character can survive concealed in heterozygote individuals.

Let us pause for a moment to sum up the novel ideas which have so far been presented in this and the preceding chapter.

We found in the first place that from the point of view of heredity we must look upon an animal or a plant as a composite being, made up of a great number of unit characters, each capable of separate description, and all inherited independently of one another.

When a pair of nearly-related animals or plants are mated together, when, in fact, like is bred with like, and with still greater certainty in cases of self-fertilization such as are not uncommon among plants, every unit character born by one gamete finds a corresponding mate among the characters born by the second gamete. It naturally follows that a series of characters similar to those of the parent or parents make their appearance in the offspring.

When a pair of individuals belonging to distinct varieties or races are mated together, the result is the same in the case of the majority of characters exhibited by each of them. For separate varieties of the same species differ from one another in a small number of units only, and organisms which differ in more than a

few unit characters refuse altogether to unite for the production of offspring. From the study of the precise behaviour of those characters in which a pair of parental organisms differ, a flood of light has been thrown upon the phenomena of inheritance.

We find, as a rule, that opposed to every differentiating unit character of one parent there exists a corresponding but different character in the other parent. One parent may have smooth seeds and the other wrinkled seeds, for example. Very frequently the corresponding feature consists in the absence—or failure to appear—of a particular character, as, for instance, when the non-development of pigment leads to the appearance of white flowers.

We can now realize how necessary it is, in order to avoid hopeless confusion, to follow the behaviour of each pair of characters in the offspring separately.

The result of the meeting between the two opposed characters of the same pair we saw to be different in different cases. There may arise in the offspring (1) the appearance of a simple blend of the two parental characters. Or (2) one character may be more or less dominant over the other. Or (3) the combination of the two parental characters in the offspring may give rise to an appearance quite different from that of either of them, very much in the same way as in chemistry oxygen and hydrogen when combined give rise to water. Or (4) we may get further complications in which unsuspected characters, present in an invisible condition in one or both parents, take a part, often giving rise to the appearance of a supposed reversion.

The most important phenomenon of all, however, is that which is found to occur at the formation of the germ cells of the heterozygote plant or animal. Whatever the appearance of the hybrid form may have been, at this stage in its history the determining factors for each member of the pair of parental allelomorphs reappear in their entirety in certain cells which by their division give rise to the gametes, and at one of the divisions in question the parental characters (in a potential condition) separate completely from one another, so that half the gametes bear one allelomorph and half of them the other. In cases where more than one pair of allelomorphs has taken part in the cross, the members of each pair are found, as a rule, to undergo this process of segregation quite independently of all the other pairs.

Whether this process of Mendelian segregation is a universal one, we cannot tell at present, but we do know that it is of very widespread occurrence. Nor do we know whether a similar process takes place at the gamete-formation of homozygotes, though it seems scarcely possible to suppose otherwise.

We have seen enough to enable us to recognise very clearly the vital importance of an understanding of the constitution of the gametes in all questions of heredity. There must exist in the gametes, in an uncombined condition, those units which by their combination in zygotic organisms lead to the appearance of the characters which we can recognise. But we have seen that, owing to the appearance of dominance and other kindred phenomena, the visible external

characters of an organism are not a complete guide to the nature of its gametes. It is only by careful breeding that we can distinguish the heterozygote from the pure dominant form—to take the simplest possible example of this difficulty. For this reason it has now become the chief business of the student of heredity to determine by experiment what combinations of allelomorphs are present in the gametes of the individuals with which he is working.

The behaviour of these allelomorphs has now been disentangled in many cases of very considerable complexity; and all such cases as have been so far examined in detail have proved explicable in terms of a larger or smaller number of allelomorphic pairs, all of which obey Mendel's law—with the single exception of those cases in which coupling between the allelomorphs of different pairs introduces a slight further complication. Although it is perhaps scarcely probable that Mendel's law will ultimately prove universal in its application, nevertheless the few exceptions recorded by competent observers still require further examination before they can be accepted as invalidating the law in any single instance.

The question naturally arises as to how far the Mendelian rule of inheritance agrees with or contradicts those estimations of hereditary values which have been arrived at by the labours of the biometricians.

So long ago as 1902 Mr. G. Udny Yule endeavoured with some apparent success to reconcile the Mendelian results with those of biometry. Progress has been

rapid during the last four years, and what we have now before us is rather the question of reconciling the biometrical conclusions with the firmly-established facts of Mendelian inheritance. Quite recently Mr. Yule seems to have succeeded in performing this service for science, although the comments of other biometrical students upon his work have still to be awaited.

In 1902 Yule considered the case of a pair of simple Mendelian characters, A and a , exhibited in a mixed population breeding together at random, in such a way that the total number of germ cells bearing A and a respectively might be regarded as equal in any generation. In such a case it will always be an even chance whether a recessive parent will produce a dominant or a recessive child, because the chance of its gamete (a) mating with A or a is the same. A knowledge of the ancestry of the recessive parent makes no difference to the result. Consequently the case of the pure recessive does not fall in with any possible theory of ancestral heredity.

But on turning to the dominant parent, the case is found to be different. For such an one may be either a pure dominant homozygote giving off A -gametes only, or it may be a heterozygote giving off equal numbers of A - and a -gametes. Yule shows that if both the parents of the A individual exhibited the character A , the proportionate number of its offspring which may on the average be expected to show the A character is greater than would have been the case if one of its parents exhibited the character a . And in a similar

way a knowledge of the characters shown by the grandparents adds something to the certainty of the prediction as to the proportionate numbers of offspring of the two kinds which are to be expected, when the average of a number of cases is taken according to the usual statistical method.

Yule therefore regarded the case of the dominant character as showing conformity with the law of ancestral heredity, according to his own statement of that generalization, which was to the following effect: The law that '*the mean character of the offspring can be calculated with the more exactness, the more extensive our knowledge of the corresponding characters of the ancestry*,'* may be termed the law of ancestral heredity.*

It may be remarked in passing that Yule's distinction of the problems of genetics into those of intra-racial heredity and those of hybridization cannot now be regarded as holding good, unless the term hybridization is to be extended to many cases—*e.g.*, that of the inheritance of coat colour in thoroughbred horses, which would have been classed unhesitatingly as instances of heredity by all biometricians in 1902. Bateson's instinct did not fail him when he divided these problems into those of continuity and those of discontinuity respectively, although at the present time the realm of continuous variation and inheritance is being steadily encroached upon owing to the analysis of complex characters into definite constituents.

In 1904 Karl Pearson struck a blow at the prospect of conformity between biometrical and Mendelian

* 'New Phytologist,' vol. i., p. 202.

results in his memoir, 'On a Generalized Theory of Alternative Inheritance, with special reference to Mendel's Laws.' Pearson's treatment of the subject involved advanced mathematical reasoning, and we can, therefore, only give a brief summary of his main results. Pearson proposes special terms for the A and the a elements respectively of a couplet or pair of allelomorphs. He proposes to call the A element a *protogene*, and the a element an *allogene*, and he thus distinguishes between the two sorts of homozygotes by calling AA a *protozygote* and aa an *allozygote*.

Pearson considered the case of a population breeding together at random, in which a single measurable character, such as stature, is determined by the combined action of an indefinite number of pairs of allelomorphs, and he proceeded to work out the value of parental correlation which was to be expected under these circumstances. This value he found to be exactly one-third, a value which happens to be identical with Galton's original determination of parental correlation from his statistics of human stature. A considerable number of determinations of parental correlation have, however, since been made in the case of all kinds of characters. The values show considerable variation, but the average which they indicate is much nearer to 0.5 than to 0.33. Pearson therefore concluded that in none of these cases could anything resembling Mendelian inheritance be taking place, and that the latter is, in fact, the exception rather than the rule.

Mendelians, aware of the certainty of their own

results, and being convinced that these facts must have a very wide application, were thereupon driven reluctantly to the conclusion that something was seriously wrong with the methods adopted by biometricians for determining the coefficients of correlation. It seems, however, that this conclusion may have been arrived at with undue haste.

In August of the present year (1906) Mr. Yule read before the International Congress of Hybridization assembled in London a very interesting paper on 'The Theory of Inheritance of Quantitative Compound Characters on the basis of Mendel's Laws.' Though some difficulty was then experienced in following his argument by an audience unaccustomed to statistical methods, Yule's conclusion is really very simple.

Yule points out that the only character dealt with in Pearson's memoir is the number of protogenic or allogenic couplets present in the individual, and it is the proportionate number of these couplets present in the parent and in the offspring respectively which is taken as determining the value of the correlation coefficient. Consequently Pearson's treatment of the subject does not justify his statement that the Mendelian theory gives a rigid value for the coefficients of parental correlation for all races and characters—a conclusion which he regards as fatal to this theory, because the coefficients for different characters and races, as found statistically, show considerable individual differences, and seem to cluster round a value considerably higher than that indicated by his elaboration of the theory of

the pure gamete. Yule thereupon discusses a somewhat more general case, and considers the inheritance of a length made up of a number of distinct segments, each of which is determined by an independent pair of allelomorphs. Supposing each segment to take the length a , b , or c , according as the corresponding protozygote, heterozygote, or allozygote is present, Yule arrives at an equation from which the correlation between parent and offspring may be found. From that equation the following results are deducible :

If there is dominance—*i.e.*, if $a = b$, or $b = c$, the correlation coefficient is the same as that found by Pearson—*i.e.*, one-third.

But if the heterozygote always gives rise to a length exactly intermediate between those due to the respective homozygotes, the correlation is found to be one-half.

Cases of partial dominance will give an intermediate value. Consequently, according to the degree of imperfection of dominance, and without assuming any other disturbing circumstances, values of parental correlation varying from 0.33 to 0.5 are to be expected on the Mendelian theory of inheritance when applied to populations. These figures are calculated on the supposition that there is random mating of the parents, but if there were a tendency for like to mate with like the correlation values would become still higher. Yule therefore concludes that 'there is therefore no difficulty in accounting for a coefficient of 0.5 on the theory of segregation, but such a value probably indicates an absence of the somatic phenomenon of

dominance. In the case of characters like stature, span, etc., in man this does not seem very improbable.'

It is impossible to bring the present chapter to a conclusion without some reference to the practical aspects of the Mendelian discovery. The progress of experimental research in this field during the last half-dozen years has been so rapid, that there is little ground for astonishment in the fact that only a small proportion of those to whom the discovery of the Mendelian method is of the very highest importance from a commercial point of view have yet arrived at any serious appreciation of it. The improvement of the breeds of cultivated plants and domestic animals is a subject of vital importance to the whole human race, quite apart from the question of the commercial profit which it represents for those whose business it is to be directly concerned with the process—the actual plant- and animal-breeders themselves.

Hitherto the methods of amelioration which have been adopted have depended largely upon guess-work, or at the best upon the result of practical experience. We are now within sight of the day when a complete system of precise scientific methods will have been elaborated. The time required for the development and application of these methods must chiefly depend upon the apathy or enterprise of those in whose hands rests the means of subsidizing this kind of work, for without proper resources the progress of any such study must of necessity be slower than it would be

if properly-equipped establishments were at the disposal of duely-trained experimenters receiving an adequate remuneration.

The practical application of Mendelism cannot be better illustrated than by an account of Mr. R. H. Biffen's work upon the improvement of cereals, particularly of wheat—work which exhibits an extraordinary contrast in point of scientific exactness with everything of the kind which has been previously undertaken. This contrast was remarkably displayed at one of the morning sessions of the recent International Congress on Hybridization and Plant Breeding, held under the auspices of the Royal Horticultural Society. On that occasion a series of communications upon the subject of cereals culminated in an admirable account given by Mr. Biffen of the way in which the problems of their improvement have been overcome at the experimental farm of the Cambridge University Department of Agriculture. And it was a gratifying sign of better times to observe the enthusiastic interest with which practical men greeted his communication.

As a preliminary measure Biffen has worked out the inheritance of a number of comparatively simple characters, many of which have little practical importance. But the fact of their strictly Mendelian behaviour showed the possibility of readily obtaining any desired combination of them, and at the same time rendered it highly probable that characters of a more practical value to the farmer would prove similarly amenable to the breeder's art.

Thus Biffen found that the following pairs of

characters, among others, exhibited simple Mendelian phenomena, the one placed first being in each case the dominant :

Beardless ears.	Bearded ears.
Keeled glumes.	Round glumes.
Felted glumes.	Glabrous glumes.
Red chaff.	White chaff.
Red grain.	White grain.
Thick and hollow stem.	Thin and solid stem.

And so on. In other cases, again, the F_1 generation showed a character intermediate between those of the parents, and in F_2 there appeared a ratio corresponding to $A : 2Aa : a$.

Thus when Polish wheat (early) was crossed with Rivet wheat (late), the time of ripening of the F_1 generation was intermediate between those of the parents. In F_2 , 103 early, 210 intermediate, and 100 late plants, were counted. Time of ripening is, moreover, clearly a character which may be of considerable practical importance.

In further illustration of what can be done from a commercial point of view, we will consider the case of two other characters only—rust immunity and ‘strength.’

There is a quality of wheat grains known as *strength* which is essential for the production of a flour such as can be baked into the kind of loaf which is at present the only one saleable in England. This quality unfortunately happens to be wanting in all the strains of wheat which it has hitherto been possible to grow at a profit in this country. For this reason imported American and Canadian hard wheats, which possess

this quality of strength, are worth in England some shillings a quarter more than home-grown wheats.

When such strong American varieties are grown in this country the majority of them are rapidly found to lose this quality, and to become after a short time as 'weak' as ordinary English wheats. Some of them do, however, retain their strength, and after several seasons—in one case fourteen—show no signs of deterioration. An example of a wheat of this latter type is afforded by Red Fife, which is the basis of the mixed wheat known commercially as Manitoba Hard, the latter consisting, as a matter of fact, of a mixture of several different varieties. Unfortunately these permanently hard wheats do not yield so large a crop as the commonly cultivated English varieties, and so their higher price does not make up for the smaller number of bushels per acre obtained when they are grown.

Biffen therefore set to work upon the problem of combining hardness or strength with the power of yielding a good crop, and with the other desirable qualities characteristic of the home-grown varieties. With this end in view Manitoba Hard was crossed with a typical English wheat—Rough Chaff.

The F_1 plants produced grains all of which were fully as hard as those of the Manitoba variety.

These grains were sown, and it was found that some of the resulting plants produced strong grains and others weak ones, and that the former were to the latter very nearly in the numerical ratio of 3:1. Actually they were as 152:48 in a sample of 200 taken at random.

In order to obtain confirmation of this most important result, Mr. Biffen sent samples of the grains born by the F_2 plants to a well-known authority on milling wheats, requesting his judgment upon them, but without telling him their manner of origin. The answer was even more satisfactory than could possibly have been anticipated. Certain of the samples were stated by the expert to belong to the variety Red Fife, which is the name of the particular strain of Manitoba Hard originally made use of in the experiments, whilst others were assigned to a definite strain of ordinary weak English wheat. The segregation of these characters was, therefore, complete, strength being a Mendelian dominant to weakness.

In the next generation certain of the dominant plants, as was to be expected, bred true, and amongst them were individuals which combined with strength of grain the other desirable qualities of the second parent. The problem has, therefore, been completely solved, and there can be little doubt that when these new types are brought into general cultivation the profit obtainable from the growing of wheat in this country will be increased by several shillings to the acre of crop grown.

We may next turn to an even more important achievement. In many countries the annual loss of crop due to the attacks of yellow rust, *Puccinia glumarum*, amounts on a moderate estimate to a considerable number of millions of pounds sterling. Certain strains of wheat exist, indeed, which are more

or less completely immune to the ravages of this fungus, but these are usually wanting in other qualities which are indispensable to the farmer. If it should be found that immunity to rust is a simple Mendelian allelomorph, it would be possible to combine this quality with any other useful character which obeyed the same law of inheritance—as several useful characters have already been shown to do. At one time it must have been thought that a similar method of inheritance of the character rust-immunity was too excellent a boon to be reasonably hoped for.

Among a great number of strains of wheat grown on the Cambridge experimental farm, several types showed marked differences in the degree of their immunity from, or susceptibility to, the attacks of *Puccinia glumarum*. Among them Mr. Biffen found one which was apparently quite immune, and, though grown in the midst of numbers of rusted plants, itself never showed a trace of infection. Of another type, known as Michigan bronze, no single individual ever escaped the rust, and so badly were the plants of this strain diseased that very few ripe grains could ever be obtained from them.

Biffen crossed these two types together. In the first generation every plant without exception was badly rusted, but fortunately a considerable number of ripe grains was obtained, and these were sown to produce the second generation. When the plants of this generation had grown up it was observed that among a majority of badly-rusted plants certain individuals stood out fresh and green, being entirely

free from infection. On examination it was found that every plant could be placed in one or other of two categories—either it was badly rusted or it was entirely free from rust; and the numbers of the two kinds of plants were as follows: 1,609 infected, 523 immune.

It is clear, then, that immunity and susceptibility to the attacks of yellow rust behave as a simple pair of Mendelian characters, immunity being recessive. And it is, therefore, possible to obtain by crossing, in three generations, a pure rust-free strain containing any other desired quality which is similarly capable of definite inheritance.

CHAPTER IX

RECENT CYTOLOGY

EVERY living creature may be regarded as being built up of a number of structural units which are known as cells. In the case of some of the simplest animals and plants, indeed, the whole body of the organism is composed of a single cell—a small mass of living protoplasm, containing, as a rule, only one nucleus. But in all the higher animals and plants the adult body is made up of a great number of such cells living in intimate association with one another.

The living material of which the cell is composed is known as *protoplasm*. Protoplasm is a highly complicated and unsteady combination of substances, amongst the constituents of which the chemical elements, carbon, oxygen, hydrogen, nitrogen, and sulphur, play the chief parts. Its consistency is slimy and semifluid.

Concerning the nucleus—the most essential and characteristic of cell organs—more will have to be said later on. Other important organs of cells are a wall or membrane which externally surrounds them, one or more vacuoles or cavities containing a watery fluid, or sometimes a gas, and a certain number of more solid

bodies or *plastids*. Certain plastids present in the majority of plants are of particular importance as containing the green substance chlorophyll, which plays an essential part in the fixation of carbon from the atmosphere.

Amongst unicellular organisms—the creatures already mentioned as being made up of a single cell only—those which contain chlorophyll and are provided with a firm cell wall, built up of a material known as cellulose, are usually regarded as simple plants; whilst those in which chlorophyll and a cell wall are absent are looked upon as simple types of animals. Similarly slight differences distinguish the cells which build up the fabric of the higher plants from those of which the bodies of the more complicated animals are composed, so that in almost all essential points an account of the behaviour of the cells of the members of one kingdom will apply equally well to those of the other. After a few further preliminary remarks we shall, therefore, for the sake of simplicity, speak of a generalized type of cell, the behaviour of which, except in points of detail, will resemble that of the actual cells of plants or animals indifferently. But in order to convey a more definite idea of an unicellular animal to those who are unfamiliar with the now flourishing science of Protozoology, we may refer briefly to the well-known form *Amæba*, which will serve as an excellent type of an animal consisting of a single free-living cell.

This little creature consists of a mass of protoplasm enclosing a nucleus which is more or less centrally

situated and approximately spherical in form. The protoplasm is divided into an outer hyaline and an inner granular portion, the former being limited externally by a very delicate membrane. The shape of the animal is irregular, and, moreover, undergoes gradual alteration owing to the characteristic amœboid movements. These consist in a slow protrusion and withdrawal of processes of the body, enabling the animal to change its position by a kind of flowing movement, and also to engulf its food, which consists of various

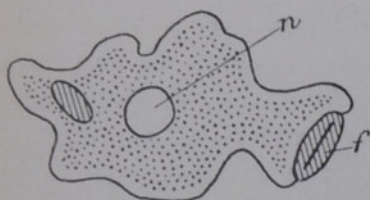


FIG. 17.—AMŒBA.

n, Nucleus; *f*, food particle.

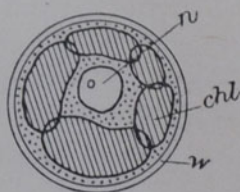


FIG. 18.—PLEUROCOCCUS.

n, Nucleus; *w*, cell-wall; *chl*, chloroplast.

minute organic particles, by the simple process of flowing around it.

In contrast with *Amœba* the unicellular plant *Pleurococcus* is motionless, and is surrounded by a firm wall of cellulose. In addition to a central nucleus, the plant contains, embedded in its peripheral protoplasm, several plastids which bear the chlorophyll concerned in the assimilation of carbon from the gases of the atmosphere. This chlorophyll lends a green colour to the whole contents of the cell, and in its natural habitat the plant is quite conspicuous. The green powdery substance often to be seen on the bark of trees,

especially on the side turned to the north, and in similar shady situations, consists, as a rule, of great numbers of minute *Pleurococcus* plants, although the size of a single specimen may be represented by a diameter of little more than the two-thousandth part of an inch.

We are more particularly concerned, however, with the higher animals and plants, the bodies of which are built up of a great number of separate cells. Some of these cells may be modified in various ways, but they all conform, at least in the youthful condition, to types not far removed from those of *Amœba* and *Pleurococcus* respectively. Certain parts of these higher organisms, indeed, such as the bones of vertebrate animals and the wood of trees, do not consist solely of living cells, but are composed to a great extent of dead material excreted or built up by the activity of living cells. These latter have, then, either ceased to live, or they may continue to exist in the interstices of the hard skeletal framework.

New cells come into existence in only one way—namely, by a process of division which takes place in a pre-existing cell. In comparatively rare cases a cell may give off a small bud which forthwith develops into a new cell like the old one. In such a case we may speak of the cell which gives off the bud as the mother-cell, and of the cell into which the bud develops as the daughter-cell. But by far the most frequent method of cell-reproduction, and the only one which is characteristic of the higher animals and plants, takes place by the equal division of an old cell into two

new ones. In this case, it is only by a stretch of language that we can speak of parent- and daughter-cells, for the individuality of the pre-existing cell is completely lost, and two fresh individualities have now taken its place.

Since all the cells of the animal or plant body arise by the bipartition of pre-existing cells, it is clear that if we follow these processes far enough back, in the case of any individual organism, we may arrive at a period at which only one cell was present. And under ordinary circumstances this is actually the case. Every individual among the higher animals and plants, arising by the ordinary sexual method, existed at the earliest stage of its embryonic history in the form of a single cell, the fertilized ovum. And the first obvious process in the development or embryology of the young organism consisted in the division of this primitive cell into two new cells. Each of these new cells then divided again in like manner, and the multiplication of cells continued until all the innumerable cells which build up the organs of the adult body had finally come into existence. When growth is completed cell-divisions continue more slowly, producing new cells to make good the wear and tear of the bodily tissues.

As the number of cells increased, their relation to one another in space was constantly changing. Different cells, too, became modified in different ways; for instance, the cells on the outside of the young embryo took on a different form from those within, in accordance with the different conditions to which they were exposed, and a host of other changes took

place too numerous for us to follow in detail. Thus the complicated structure of the adult organism was gradually arrived at by a process of development in which cell-multiplication played a most prominent and essential part.

We have next to inquire what is the method of origin of the original embryonic cell—the fertilized ovum—from which the new animal or plant develops.

As is indeed implied by the expression ‘fertilized ovum,’ this cell arises by the fusion together of two independent cells, such fusion constituting the process of fertilization or impregnation. One of the cells which took part in the fusion was derived from one parent organism, and bore the distinguishing characteristics of the cells which composed that parent—or at least some part of those characteristics—whilst the other was in like manner derived from the second parent.

It is to be observed that this fusion together of a pair of cells, derived (in the case we are considering—namely, that of ordinary biparental reproduction) from two separate individuals, results in the formation of a complete new individuality, which arises definitely at that point of time at which the fusion of the two conjugating cells takes place. In this way the cells of the offspring are seen to be of double origin, and it is found that traits and characters derived from both the father and the mother can co-exist in them side by side.

The cells which take part in the above-mentioned fusion are known as *gametes*, or *germ-cells*—male and

female respectively, according to the sex of the parent from which each is derived. In animals the female gamete is known as the *ovum*, and the male as the *spermatozoon*, and the product of their fusion, as already said, is called the fertilized ovum. Germ-cells of a similar kind arise in a slightly different way in plants. The germ-cells are produced in special parts of the organism known as the generative organs, which in flowering plants are represented by the pistils and stamens.

A more convenient expression for the fertilized ovum is that of *zygote*, a term which we have previously encountered in the shape of the homo- and heterozygotes of the Mendelian. By an expansion of meaning the term *zygote* is also used to express the whole organism which ultimately arises from the product of fusion of a pair of gametes, and by this use the importance of the gamete, as opposed to the zygotic organism as a whole, is brought into due prominence.

We find, then, that the succession of generations in the higher animals and plants, according to the common use of this expression, depends upon the succession of a much larger number of cell-generations. By repeated divisions, each giving rise to a new generation of cells, the fertilized ovum gradually develops into the adult organism. By the division of certain members of the later generations of cells which compose this organism the gametes are produced. By the conjugation of a pair of gametes a *zygote* of the second generation arises, and the same processes are continually repeated.

Each of the cells hitherto referred to possesses a single nucleus, which is usually a more or less spherical body occupying a central position within the cell. Nuclei, like the cells which contain them, arise only by the division of pre-existing nuclei. Thus the history of the nuclei is in every way similar to the history of the cells, of which they constitute so important a part. In fertilization the nuclei of the conjugating cells or gametes fuse together to form the single nucleus of the fertilized ovum, and every division of this cell, as well as of its cell-progeny, is preceded by a division of the nucleus into two similar portions.

We may forthwith concentrate our attention upon the nucleus as being that part of the cell which is of primary importance from the point of view of heredity, for it is now generally recognised that the nucleus is the part of the cell in which hereditary features are in some way carried. And we may next consider a little more closely the structure of the nucleus as seen under high powers of the microscope.

In what is somewhat improperly called its resting condition—a condition which is characteristic of nuclei at all times when they are not actually undergoing division, or preparing for that process—the nucleus may be seen to be bounded by a more or less definite *nuclear membrane*. The internal structure of such a nucleus is described as reticular—that is to say, at least two different substances are differentiated within the nucleus, one of them forming a reticulated meshwork, the interspaces of which are occupied by the other (Fig. 19).

In entering into a detailed description of the changes which take place in the finer structure of the nucleus, it must be clearly understood that the more minute features alluded to are only to be seen with any degree of definiteness in dead cells which have been killed practically instantaneously by the action of some powerful chemical poison. Under suitable conditions it is believed that treatment of this kind fixes the constituent parts of the nucleus in very nearly the same relative positions as they occupied in life at the moment immediately preceding the death of the cell. The tissues containing the cells to be examined are then usually cut into very thin sections, and other chemicals are applied to them, the result of this treatment being to stain different parts of the nucleus of different colours and with different degrees of intensity. It is to the behaviour of the structures thus made visible that our description applies, since it is impossible to follow these changes in actually living cells except to a very imperfect extent. It may be pointed out, however, that we have every reason for believing that the differential effect produced by the processes of fixing and staining only serves to render more clearly visible real differences which actually existed during the life of the cell, and some indications of many of these differences have even been actually seen in living cells under exceptionally favourable conditions.

The nucleus, when treated in the manner described, is seen to be built up of a network of branching fibrils, the meshes of which enclose a comparatively clear and hyaline substance. The fibrils of the network are made

up of a material of comparatively weak staining capacity; embedded in this substance are numerous granules of a very intensely staining material which is known as *chromatin*. There are strong reasons for believing that the chromatin of the nucleus is of special importance from the point of view of the mechanism of heredity. This reticular structure of the nucleus is indicated in a diagrammatic fashion in Fig. 19.

Further light is thrown upon the detailed structure of the nucleus by the changes which become visible during the process of nuclear division. This process, which is known as *mitosis*, we must now proceed to describe.

In the description of mitosis which follows, the account of this process has been somewhat generalized and simplified, and Figs. 19 to 26, which illustrate the phenomena, are purely diagrammatic. It is hoped that the most important features of this complicated process may be in this way rendered comprehensible; and although in different organisms considerable variations in the details of the process are to be met with, yet in their general features all ordinary mitoses in animals and plants are believed to conform to the essential type of our description.

The first change in the appearance of the nucleus which indicates that a division is about to take place consists in a rearrangement of the chromatin network, which now takes on the appearance of a tangled thread (Fig. 20). The outwardly-directed loops of this skein often correspond to the separate portions

into which the thread eventually breaks up. The thread gradually grows shorter and thicker, and presently becomes divided into a number of pieces which are known as *chromosomes*. In the chromosomes the shortening and thickening process is continued until these bodies arrive finally at the form of stumpy rods, each of which often becomes bent into

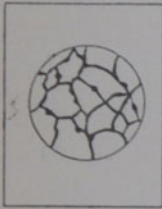


FIG. 19.

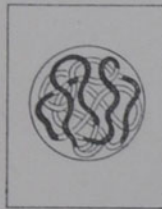


FIG. 20.



FIG. 21.

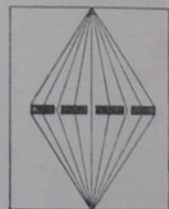


FIG. 22.

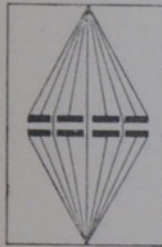


FIG. 23.



FIG. 24.

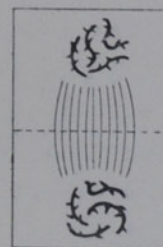


FIG. 25.

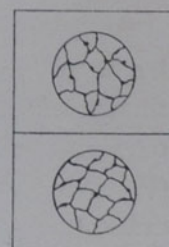


FIG. 26.

the form of a horseshoe. Meanwhile the nuclear membrane breaks down, so that the hyaline substance of the nucleus becomes continuous with that of the cell body surrounding it. A fresh phenomenon now becomes visible. A spindle-shaped arrangement makes its appearance consisting of a number of minute fibrils which connect together two points—the poles of the spindle—situated at opposite ends of the cell. The

chromosomes now change their position so that they come to lie in the plane of the equator of the spindle, and about this time, but sometimes earlier, each chromosome splits longitudinally into two equal portions (Figs. 22, 23). This splitting in the case of each chromosome takes place in the equatorial plane of the spindle, so that one member of each pair of daughter chromosomes faces towards one pole of the spindle, and the second towards the other pole. The members of each pair of daughter chromosomes now begin to move away from one another towards the two poles of the spindle, and as they do so the first indication of a dividing wall between the two new cells begins to make its appearance in the equatorial plane.

Arriving at the poles, the daughter chromosomes begin to elongate, and to put out processes which finally meet and fuse with those of their neighbours to form the chromatin reticulum of the new nuclei (Fig. 25). Surrounding each new nucleus, thus developing at either pole of the now rapidly disappearing spindle, a new nuclear membrane makes its appearance; the dividing wall in the position of the equator of the spindle develops into a complete partition (at least in the case of plants, in which, however, a number of minute passages are left penetrating the cell wall and preserving the communication between the protoplasmic contents of the separate cells); and the division into two new cells is thus completed (Fig. 26). Each new cell is provided with a nucleus into which has entered precisely its fair

share of the chromatin which was present in the parent nucleus.

A great deal of evidence has recently accumulated to show that chromosomes are very definite and important organs. In the first place, the number of chromosomes which make their appearance at each cell division is the same in all the cells of any given creature, and this numerical constancy further extends to the cells of all the members of a particular species, though in members of allied species the number of chromosomes may be different. In widely separated species the number of chromosomes varies considerably; thus from 2 to 200 have been counted in the case of various different members of the animal and vegetable kingdoms. One of the commonest numbers found is twelve, and this number occurs in a considerable variety of different animals and plants.

Next it has been shown that the chromosomes which arise at the beginning of a nuclear division are identical with those daughter chromosomes of the preceding division which originally entered into the nucleus now about to divide. An example of the kind of evidence upon which this conclusion is based may next be given.

Figs. 27, 28, and 29 show the three possible arrangements of the four chromosomes which are found in the cells of the worm-like animal *Ascaris*, as seen from the direction of the pole of the spindle in the dividing nucleus. Of these arrangements, that shown in Fig. 29 is much the least common. Now in this particular case the chromosomes, when they first make

their appearance immediately before the process of division, are found with their extremities situated in little pockets or bulgings of the nuclear membrane, so that their exact position is very definitely marked; and the arrangement of the chromosomes may be any one of those already indicated. Boveri observed that



FIG. 27.

FIG. 28.

FIG. 29.

in the case of two neighbouring cells which had originated by the division of the same mother-cell, the chromosomes made their appearance in both cases in the uncommon position of Fig. 29. Figs. 30 and 31 indicate their actual arrangement. The conclusion to be drawn from this observation is that the same

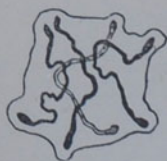


FIG. 30.



FIG. 31.

chromosomes have preserved their individuality right through the resting stage of the nucleus, to reappear in the same position at the outset of a new phase of division.

It is believed, then, that the same stages which the chromosomes passed through at the close of one

nuclear division, giving rise to the nuclear reticulum in the daughter nucleus, are repeated in the reverse order at the outset of the next division; the same processes are withdrawn into the same chromosomes, and these shorten into structures identical with those which passed into the nucleus at its first formation, except that they have increased in bulk during the interval.

Boveri, in fact, concludes that the separate chromosomes are to be looked upon as distinct individuals—almost as separate simple organisms—which preserve their individuality throughout the history of the cell, and reproduce themselves, just as cells and nuclei do, by a process of bipartition. As far as the chromosomes themselves are concerned, their typical or resting form is that of the short simple rods seen in mitosis. The branched anastomosing character seen during the stage of the nuclear reticulum is associated with the active co-operation of the chromosomes in the physiological processes going forward within the nucleus. For this reason the term 'resting stage' applied to this condition of the nucleus is a particularly inappropriate one.

Boveri illustrates the amount of credence which he would attach to this theory of the individual persistence of the chromosomes throughout the resting condition of the nucleus, by means of the following analogy: 'We make water from oxygen and hydrogen, and from this water we can obtain oxygen and hydrogen again in the same proportions. Just in the same way as the chemist on the evidence of these facts regards

water as containing oxygen and hydrogen, although the properties of these substances are completely in abeyance, so I believe it to be with equally good reason that our theory regards the individual chromosomes as being preserved in the resting nucleus.*

Since Boveri expressed this opinion Rosenberg has produced further evidence of an equally convincing kind. He finds that in the case of certain plants the chromosomes do not pass over into a continuous reticulum during the resting condition of the nucleus, but remain separate, so that the same number of chromatic bodies can be counted during this stage as during the actual process of mitosis.

Boveri has also produced evidence to show that different chromosomes play different parts in the economy of the organism. For example, when different chromosomes were artificially removed from the nucleus of an embryonic cell by taking advantage of certain abnormal methods of division, the embryos which arose from these cells developed to different extents and in different abnormal ways.

This result is of particular interest, because it gives full corroboration to the suspicion, previously entertained, that the chromosomes are specially concerned with hereditary processes—with the building up of particular parts of the developing organism into shapes which resemble those of the corresponding parts displayed by other members of the same species; and it seems further to show that particular chromosomes

* Dr. T. Boveri, 'Ergebnisse über die Konstitution der Chromatischen Substanz des Zellkerns,' p. 22.

may be specially concerned in the development of particular parts.

Sutton has recently shown that the different chromosomes contained in the same nucleus of a particular animal may be of different shapes and sizes, so that each is individually recognisable. It was thus possible to demonstrate that an identically similar set of chromosomes appeared at each of several successive cell divisions. In this way additional evidence is afforded of the individual persistence of the chromosomes and of their separate identity.

We have already pointed out how, in the process of fertilization, the two conjugating germ-cells, as well as the nuclei which they contain, become completely fused together to form a single cell containing only one nucleus. It might have been expected that the separate chromosomes contained in the conjugating nuclei would also fuse together in pairs during this process, but this is not the case. The paternal and maternal chromosomes remain separate, so that the nucleus of the zygote contains twice as many chromosomes as does that of either of the gametes by the fusion of which it arose. This double number of chromosomes reappears at every cell division during the embryonic history of the zygote, and thus the fact is accounted for that the number of chromosomes in a somatic nucleus is always even.* Thus we see that the chromosomes derived from the two parents are present side by side in the nuclei of the offspring, and reproduce themselves by bipartition at every nuclear division which takes place

* See, however, p. 253 for an exceptional case.

in the zygote. In this way every somatic nucleus of the latter contains a double set of chromosomes, half of them being descended from the chromosomes introduced by one parent, whilst the other half came from the second parent.

There is reason to believe that the set of chromosomes derived from one parent is complete in itself, containing everything necessary for the development of a normal individual. Indeed, in some cases of parthenogenesis (development of the unfertilized egg), egg cells have been known to develop which contained only a single set of chromosomes. Boveri proved very prettily that the paternal set of chromosomes is equally adequate for complete development. By dint of violent shaking Boveri contrived to remove the nucleus from the egg-cells of a sea-urchin, and he afterwards allowed a sperm-nucleus to enter the enucleated egg, which presently developed into a complete embryo. Thus it was shown that the paternal as well as the maternal set of chromosomes is sufficient by itself to determine the proper production of all the organs of the embryo. But Boveri also showed that if any chromosome of the paternal (or maternal) set were wanting in such a case, normal development of the embryo could no longer take place. Let it once more be emphasized that the somatic cells of an ordinary organism contain a double complement of essential nuclear material.

Since the gametes contain only half as many chromosomes as the somatic cells, and since the number of chromosomes present in the latter is constant for each

species, it follows that either during the formation of the gametes, or at some one or other of the cell divisions leading up to their formation, there must occur a reduction in the number of chromosomes to one-half of their former number. In the case of the higher animals this reduction takes place during the two cell divisions which directly lead up to the formation of the gametes themselves. In plants, on the other hand, the reduction takes place during the formation of those cells which are known as *spores*. From these, after a certain number of intervening cell generations, the gametes take their origin. These intervening cell divisions in plants are characterized in every case by the appearance of the reduced number of chromosomes. In the higher plants, in fact, a generation is, as it were, interposed between the reducing division and the actual formation of the gametes. For the spores are themselves unicellular reproductive bodies like the gametes, but differ from the latter in the fact that they develop without undergoing conjugation, and give rise to a larger or smaller mass of tissue consisting of cells with the reduced number of chromosomes. From the fact that the cells of this gamete-bearing generation contain half as many chromosomes as those of the spore-bearing generation with which it alternates, the generation produced from the spores has been spoken of as the x -generation in contrast with the ordinary, or $2x$ -, generation. In animals the x -generation is reduced to a single generation of cells only, which is represented by the gametes themselves.

We must next proceed to examine the actual

method by which the reduction in the number of the chromosomes is brought about.

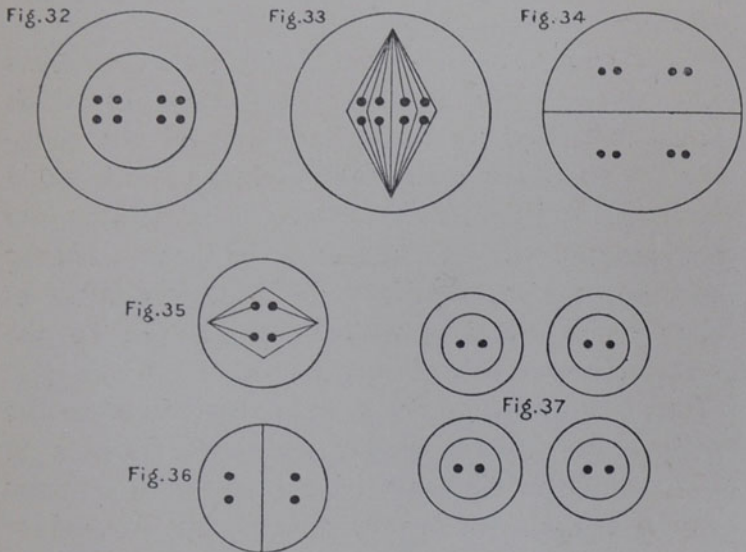
The simplest type of the process of reduction of the chromosomes takes place at the formation of the male germ-cells, or spermatozoa, of animals. For the sake of clearness we shall consider the case of an animal in which the somatic cells contain four chromosomes only, and in which the reduced number characteristic of the gametes is therefore two.

The reduction in number of the chromosomes takes place during two successive cell divisions which immediately lead up to the formation of the germ-cells. A particular mother-cell divides twice in rapid succession, and the four cells thus arising develop into spermatozoa without further subdivision. During these two nuclear divisions the somatic number of chromosomes becomes halved, giving rise to the number characteristic of the gametes.

Immediately before the first of these divisions the chromosomes become closely associated together in pairs, and in certain cases it has been shown that one member of each pair is very probably the descendant of a chromosome derived from the male parent, whilst the other member of the pair is the descendant of the corresponding maternal chromosome.

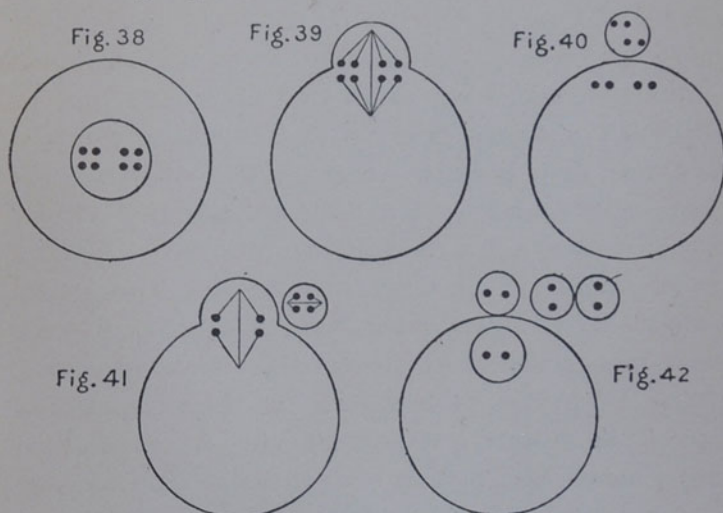
This association of the chromosomes in pairs may be so close, and may take place so early, that when these bodies are first visibly differentiated only half the usual number of them is to be seen. But in these cases, too, it is reasonable to believe that each of the chromosomes actually visible consists of a maternal

and a paternal member fused together. Each of the visible chromatic bodies next divides into four parts, the set of four deeply staining bodies being known as a *tetrad*. Thus when there are four somatic chromosomes the number of tetrads appearing will be two (Fig. 32). A mitosis now takes place, during which there is no further division of chromosomes, but half of each



tetrad passes to either pole of the nuclear spindle, so that each daughter nucleus comes to contain two half-tetrads, each consisting of a pair of deeply-staining bodies (Fig. 34). This division is not followed by the production of a resting nucleus, for before any nuclear reticulum is formed, and while the half-tetrads still retain their definite appearance, the daughter nuclei divide again. At this second division in each nucleus

the separate members of each of the two half-tetrads pass to opposite poles (Figs. 35, 36). In the nucleus of each of the four cells which thus arise there is, therefore, present one quarter of each of the four chromosomes which originally appeared—one member, that is to say, of each tetrad (Fig. 37). Each of the cells of which we have thus traced the origin develops directly into a single spermatozoon.



The method of development, or maturation, of the ova, or egg-cells, of animals is in all essential respects similar to the process by which the spermatozoa arise. It differs, however, in the fact that of the four cells which result from the corresponding divisions, one is very large and constitutes the ovum, whilst the other three are very minute, and are apparently of no further importance. In the accompanying diagrams (Figs. 40 to 42), the smaller cells, or polar bodies, have been

enormously exaggerated relatively to the size of the ovum itself.

The original tetrad is believed in all cases, and has been actually observed in a few cases, to arise by a separation of the two fused chromosomes, followed by a division of each of these bodies into two. In cases where the chromosomes retain their rod-like appearance throughout these changes there would seem to be some doubt as to whether the first of the divisions giving rise to the 'tetrad' is transverse or longitudinal in direction, and it is possible that the process may be different in different cases. But it is generally agreed that the first division separates the two original chromosomes, and that at the first of the two nuclear divisions which ensue the members of a pair of parental chromosomes pass into separate nuclei. The second division, on the other hand, like an ordinary mitosis, separates halves of chromosomes. This agreement among authorities is explained by the circumstance that those observers who have seen a longitudinal first division believe that the parental chromosomes conjugated side by side, whilst those who describe a transverse division describe also an end-to-end conjugation of the chromosomes.

The first of these two ideas is the one illustrated in the accompanying diagram (Fig. 43), representing the behaviour of a single pair of parental chromosomes during the two nuclear divisions which give rise to four sperm cells. The chromosome derived from one parent is shaded, whilst the other is left blank.

Thus the first of the two gamete-producing divisions

differs from all other mitoses in the fact that in it an actual separation of whole chromosomes takes place; it is a qualitative and not only a quantitative division. It is to this mitosis that the term *reducing division* is properly applied.

We have to notice that at one stage of the process now described the chromosomes derived from the two parents are in a close state of fusion. It would seem as if the actual conjugation of chromosomes, which failed to take place when the conjugating gametes and their nuclei fused together in the formation of the zygote, was only delayed, and now occurs hundreds or

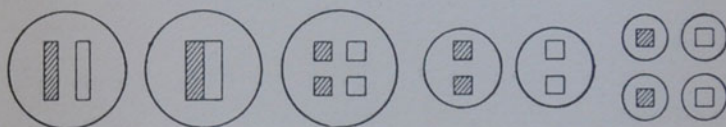


FIG. 43.

thousands of cell generations after the actual process of fertilization, and immediately before the production of those cells which are to give rise to the new individual.

It may be pointed out that, although the chromosomes which emerge from this fusion seem to be identical with those which entered into it, yet it is difficult to believe that they have not undergone some change, or exercised some mutual influence upon one another. If no such influence has been exerted, it is difficult to imagine any possible reason for the process of fusion taking place at all.

In the higher plants a similar reducing division

takes place at the formation of the spores, which arise in sets of four, each set corresponding to a group of four spermatozoa, or to the ovum and the three polar bodies of an animal. In the case of flowering plants the nuclei contained in the spores make a few further divisions, at each of which the reduced number of chromosomes is to be observed, and one or more of the cells thus finally produced take on the character of germ-cells. The spores are of two kinds, large and small, the latter being the pollen grains. The larger spores give rise to female gametes and the smaller to male, and fertilization takes place in the ordinary manner by a fusion between the nuclei of these germ-cells.

We have seen so far that the number of chromosomes contained in the somatic nuclei of a given species is always the same, and is always even. We have also seen that this number is made up of two separate sets derived respectively from the two parents, and that the members of the two sets preserve their separate individuality right through the long series of nuclear divisions which take place during the development of the individual zygote. A fusion of chromosomes of paternal and maternal origin respectively takes place only in the direct line of ancestry of the germ-cells which are destined to give rise to new members of the species. This process of fusion takes place in animals immediately before the formation of the actual germ-cells, but in plants a larger or smaller number of cell generations earlier. After fusion the paternal and maternal chromosomes apparently separate, and the

nuclear division which ensues differs from all other mitoses in the fact that instead of merely dissevering halves of chromosomes, the actual somatic chromosomes separate and become distributed equally between the resulting nuclei, so that in these nuclei, and in the germ nuclei which arise by their division, the number of chromosomes is reduced to half the somatic number. When fertilization takes place the somatic number of chromosomes is restored by the union of nuclei, each of which contains half that number.

Is it possible to throw any further light upon the meaning of these facts regarding the behaviour of the minute constituent parts of organisms?

Let us return to Mendel's experimental discovery, of which an account was given in the last two chapters, and let us consider the case of a cross between parents which differ in respect of two pairs of allelomorphs. Expressing these pairs as $A-a$ and $B-b$, Mendel showed that the germ-cells of the cross-bred or heterozygote bear in equal numbers the combinations AB , Ab , aB , and ab . Now, it seems clear from this behaviour that the allelomorphs must be represented in the cells of the organism by some kind of definite particles, which remain distinct from one another throughout all the cell divisions of the body, since we know that at the formation of the germ-cells these characters are capable of becoming completely segregated. Let us, then, trace the behaviour of the allelomorphs in a diagrammatic way, regarding each as a distinct particle. These particles we may distinguish by certain letters. A and a are the allelomorphs of one pair,

B and b those of the other, and we will suppose that one of the parents exhibits the characters A and b and the other the characters a and B (Fig. 44). Then, in the zygote resulting from fertilization, A , a , B , and b will all be present.

Since all the cells, at least in the direct line of ancestry of the gametes, must contain every allelomorph, it will be necessary for the particle representing each allelomorph always to divide into two before a cell division takes place, for only in this way can something corresponding to each allelomorph pass into each of the two cells produced by the division. And a similar process will be repeated at each somatic mitosis (Fig. 44). At the formation of the germ-cells, however, or at some preceding cell division, the two members of each pair of allelomorphs must become separated from one another in such a way that the particles originally derived from different parents pass over into different cells. When two pairs of allelomorphs are concerned, this process of separation can take place in either of the two ways shown in Fig. 45. And the experimental evidence shows that the two methods occur with equal frequency in the formation of the germ-cells of the same heterozygote.

Anyone who has succeeded in following the above account of the behaviour of the supposed particles representing Mendelian allelomorphs in the cells of a hybrid organism, on comparing it with the preceding description of the behaviour of chromosomes in the somatic and reducing divisions respectively, can scarcely fail to be struck by the extraordinary simi-

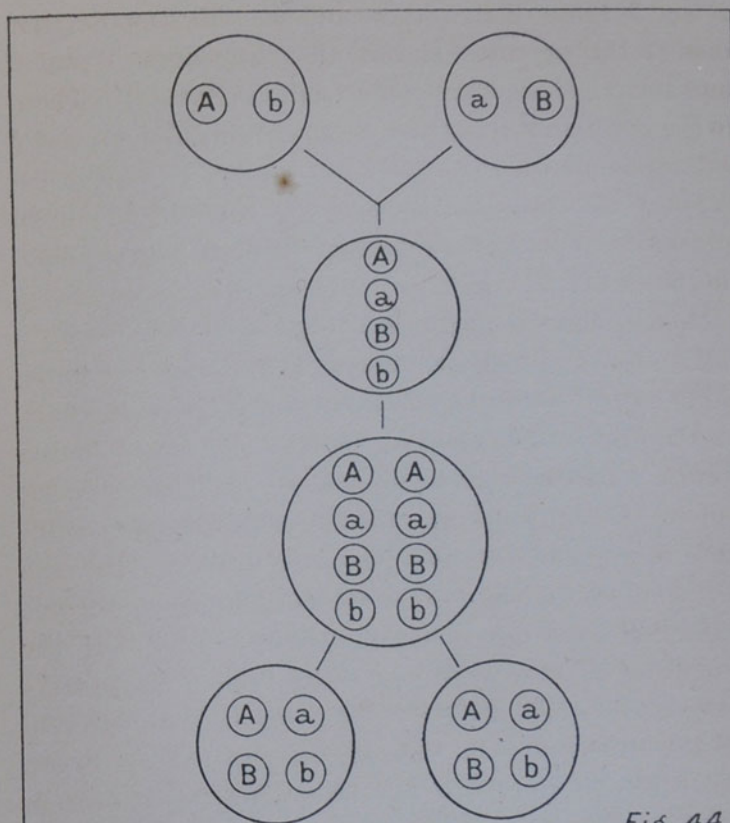


Fig. 44.

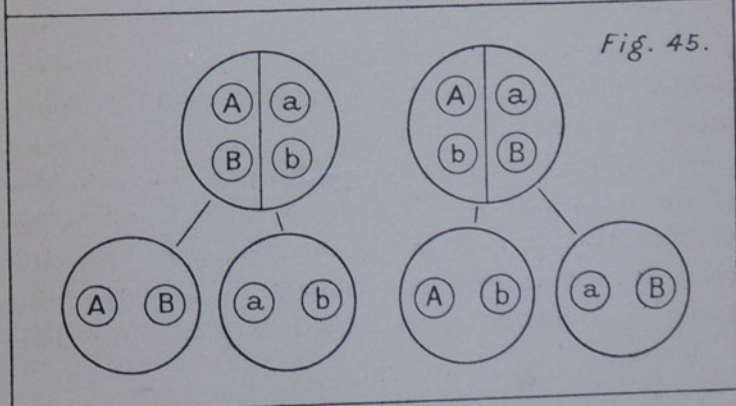


Fig. 45.

larity between the two processes. It seems quite clear that there must be some real connection between the behaviour of chromosomes as seen microscopically on the one hand, and the behaviour of allelomorphic characters as deduced from the results of experiment on the other ; and that the evidence derived from these two forms of study is bound to be of considerable mutual benefit.

At first sight it might be thought that the chromosomes are the actual bearers of Mendelian characters, in the sense that each chromosome represents a single allelomorph ; and, indeed, there is no fundamental difference between the behaviour of chromosomes and that of our supposed character-bearing particles. But there is, at least in some cases, a fatal objection to this belief in the fact that in certain plants the number of separate allelomorphic pairs which may be born by a hybrid is greater than the reduced number of chromosomes which the germ-cells of this hybrid contain. For instance, in the case of the pea the reduced number of chromosomes is seven, and Mendel himself described the behaviour of seven independent pairs of allelomorphs in peas. Recent study has revealed the presence of at least four additional pairs of allelomorphs in these plants, all of which are probably equally independent of one another.

We must, therefore, seek a different explanation, and de Vries has recently suggested one which up to the present time appears the most likely to represent the true account of the phenomena. De Vries' explanation is associated with the finer structure of the

chromosomes themselves, a subject upon which we have not hitherto entered. Under high powers of the microscope, and after very careful preparation, it is possible to observe that each chromosome contains a number of separate darkly-staining granules which are known as *chromomeres*. When the pairs of parental chromosomes fuse together previous to the reducing division, the chromomeres which they contain appear to meet together in corresponding pairs. The members of each pair fuse together completely, afterwards separating as the chromosomes separate.



FIG. 46.

De Vries supposes the Mendelian allelomorphs to be contained in the chromomeres, and that when these granules fuse together an exchange of allelomorphs takes place between the chromosomes. This exchange proceeds in such a way that when the chromosomes separate after fusion, it is a matter of simple chance whether a particular allelomorph has remained in the chromomere which originally contained it, or has passed over into the other member of the pair. Thus, in a sufficient number of cases we should get all possible chance distributions of allelomorphs between the two chromosomes, except that, of course, the two members of the same pair of allelomorphs would never coexist in the same chromosome. Since the two chromosomes of a pair pass into different germ-

cells, precisely that chance distribution of allelomorphs which is required on the Mendelian theory would thus be arrived at.

De Vries' explanation throws light on one phenomenon which is not accounted for on the supposition that each chromosome represents a separate allelomorph. In the diagrams previously given of the behaviour of Mendelian characters within the cells we have given no indication of a conjugation in pairs previous to the reducing division. Such a process of fusion is, however, one of the most marked phenomena in the behaviour of the chromosomes at the parallel stage of their existence. On the chromosome-allelomorph view, the phenomenon of mitosis as bringing about an equal division of hereditary particles between the cells, and the process of reduction in the number of the chromosomes, are both accounted for, but there is no explanation of the fusion between the pairs of chromosomes. On de Vries' view, however, this process is necessary in order to bring about the necessary redistribution of allelomorphs between the chromosomes, and so between the germ-cells into which the latter pass.

In cases where the phenomenon of correlation or coupling has been observed we must suppose that there is some mechanism which causes the representative particles of the respective characters concerned to remain in company during the process by which the other allelomorphs are being reassorted between the chromosomes. Of this process of coupling the cytologists have not yet been able to observe any visible

indication in the behaviour of the chromosomes, any more than they can really see the redistribution of the supposed factors carried by the chromomeres. But apart from this it must be allowed that the facts of experiment and of microscopic observation fit in with one another in a remarkable way, and that the Mendelian theory throws considerable light on the minute features of cell anatomy.

The possibility still remains that in certain cases particular characters may be associated with particular chromosomes as a whole, and we shall next proceed to describe what actually seems to be an example of this sort.

The case we have to describe is directly concerned with one of the most interesting and elusive of biological problems—namely, the problem of the heredity of sex. Prof. E. B. Wilson has recently investigated the behaviour of the chromosomes in the somatic cells and in the germ-cells of a particular species of insect known as *Protenor belfragi*. The case afforded by this animal is remarkable, inasmuch as the somatic cells in the male, and only in the male, contain an odd number of chromosomes. An irregularity is accordingly introduced into the process of fusion of the chromosomes in pairs, which, as already described, always precedes the formation of the germ-cells with their reduced number of chromosomes. In the case of the male *Protenor* all the chromosomes fuse in pairs except one, which is, of necessity, left over. This odd chromosome is described as the *heterotropic* chromosome. The female *Protenor* has one more

chromosome in its somatic cells than the male, thus making up an even number—that is to say, in the female the pair to the odd chromosome of the male is present, so that there are two heterotropic chromosomes, or *idiochromosomes*. These fuse and separate in the reducing division, which thus proceeds in the normal manner in this sex. In the male, on the other hand, when the reducing division occurs, the heterotropic chromosome passes complete into one of the resulting cells. In the second gamete-producing division, every chromosome present having divided into two, the products of this division pass into different gametes. These latter divisions are of two kinds, since in one of them the heterotropic chromosome takes part, whilst in the other it is wanting; consequently, two out of the four spermatozoa eventually produced contain the heterotropic chromosome and two do not. (Only one spermatozoon of each kind is shown in Fig. 47.) Thus there is a differentiation of the spermatozoa into two different kinds, and one of these kinds contains a chromosome less than the other. On the other hand, every egg (as well as every polar body) contains an idiochromosome.

In fertilization some of the eggs become impregnated by spermatozoa containing the heterotropic chromosome. Such eggs invariably develop into females having a pair of idiochromosomes in each somatic cell. Other eggs are fertilized by spermatozoa lacking the heterotropic chromosome, and these become males, their somatic cells containing only the single heterotropic chromosome derived from the egg. The ac-

companying diagram illustrates the behaviour of the chromosomes during these processes. The heterotropic chromosomes are represented as black, whilst the remaining chromosomes are left white, and for the sake of simplicity only two pairs of the latter are indicated in the somatic cells.

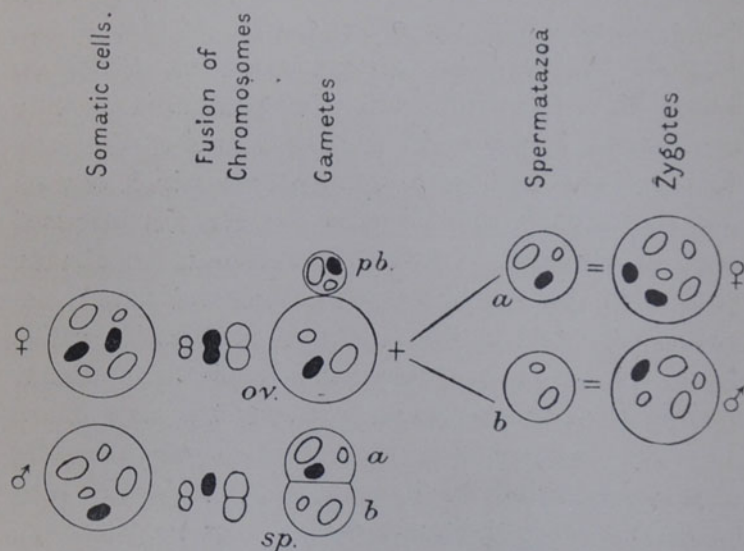


Fig. 47.

ov, ovum ; *pb*, polar body ; *sp*, spermatozoa (*a* and *b* the two kinds).

When the above facts are taken into consideration it is scarcely possible to doubt that there is a causal relationship between the characteristics of the female sex and the presence of two heterotropic chromosomes, and that a similar connection exists between maleness and the presence of only one. Let us trace this relationship a little further.

The facts clearly prove, in the first place, that the unpaired heterotropic chromosome alternates between the two sexes in alternate generations, passing from the male to the female in the production of females, and from the female to the male in the production of males (see the diagram).

Assuming that these particular chromosomes are really concerned in the determination of sex, Wilson suggests the following interpretation on Mendelian lines. Since the heterotropic chromosome is the only one present in the male, it must represent the male determinant. But, since spermatozoa which contain this chromosome produce only females, the maternal mate of the male heterotropic chromosome, already present in the egg, must be a dominant female determinant. And in the process of fertilization which gives rise to males the heterotropic chromosome derived from the egg must represent the male determinant. Two different sorts of eggs are therefore produced—presumably in equal numbers—which contain the male and female determinant respectively; the former are fertilized only by spermatozoa lacking the heterotropic chromosome and *vice versâ*. The combinations which arise in this way may be represented as $(m)f$ and m .

A selective process of fertilization is therefore a *sine quâ non* for this explanation—it must be impossible for a spermatozoon bearing the male determinant to fertilize an egg in which a male determinant is already present—in other words, only eggs containing the female determinant can be fertilized by sperms which

contain a heterotropic chromosome. At first sight this necessary supposition of a selective fertilization presented itself to Wilson as a serious difficulty. He points out, however, that the experiments of Cuénot with yellow mice* afford perfectly independent evidence of the actual occurrence of a selective fertilization of this kind in a particular species of animal (and similarly Wilson's observations lend a welcome confirmation to Cuénot's conclusions from his experiments).

In mice Cuénot found that on crossing together heterozygous yellows $CYCG \times CYCG$, he obtained no pure dominant yellows— $CYCY$ —such as were to be expected; and this in spite of the fact that $CYCG \times CGCG$ gave equal numbers of yellows and greys (showing that the $CYCG$ individuals were giving off equal numbers of yellow- and of grey-bearing gametes). Cuénot explained his unusual result by supposing that yellow-bearing spermatozoa unite only with grey-bearing eggs, and *vice versa*. On this explanation, one might at first sight expect to get a proportion of two yellows to one grey instead of nearly three to one, which was the ratio actually observed, since the fertilization yellow by yellow fails altogether. But Wilson points out that, since spermatozoa are in great numerical excess as compared with eggs, it will be possible for all the Y -bearing eggs to be fertilized by G -bearing spermatozoa, as well as half the G -bearing eggs by Y -bearing spermatozoa, thus bringing the proportion of yellows to greys more or less nearly up to three to one.

* See p. 195.

In another species of insect closely allied to *Protenor* the somatic cells of the male, like those of the female, contain each a pair of idiochromosomes; but in the male one member of the pair is much larger than the other, whilst in the female they are of equal size. The behaviour of the larger member of the unequal pair of chromosomes, in the various nuclear processes which occur during the life-history, is precisely like that of the single heterotropic chromosome of *Protenor*. It is still possible to regard this chromosome as representing a recessive male determinant, and to suppose that the process of sex determination is precisely similar in the two cases. On this supposition, the smaller idiochromosome is regarded as being without function so far as sex is concerned.

In a third insect belonging to the same natural group both male and female sexes bear alike a pair of idiochromosomes of equal size. Here, again, it is possible to apply the same theory of sex determination by simply disregarding one of the idiochromosomes of the male as unimportant. We may suppose, in fact, that one of these chromosomes corresponds to the smaller idiochromosome of the preceding case, and that it takes no essential part in these phenomena. The fact that this chromosome takes no active part in these processes may, indeed, have led to its reduction in the second of the three species, and to its final disappearance in the first.

Thus, by dint of a good deal of speculation, Wilson has arrived at a possible Mendelian description of the phenomenon of sex in a species in which the chromo-

somes of male and female are alike ; and it is a description which has its basis in actual phenomena observed in two other related animals.

Other explanations of the sex phenomena of *Protenor* and its allies may, as Wilson points out, be possible ; but if Cuénot's result meets with confirmation from other observers, the one given above will certainly take the rank of a very probable hypothesis. In any case these observations of Wilson's mark a considerable advance along the road towards a complete interpretation of the problem of sex determination. One thing, at any rate, seems certain, and that is that the male or female character is already fully determined in the fertilized egg, so that no subsequent action of the environment can have any influence upon the sex of the offspring. This definite determination of sex in the very earliest stage of the zygote follows of necessity from any Mendelian view of the phenomenon, and the evidence afforded by *Protenor* points very clearly in the same direction.

By way of further illustrating the far-reaching importance of the information which has been rendered available by the combined use of experimental and cytological methods, we may here briefly criticise the celebrated theory of inheritance put forward by Weismann in 1892 under the name of the 'Germ Plasm Theory.' Some notice of this theory, which might otherwise have been permitted to go the way of similar valuable provisional hypotheses, is rendered almost necessary by the circumstance of its having been

recently revived in a prominent manner in the English translation of Weismann's book, 'The Evolution Theory.' In this book, published in 1904, the bearing of the Mendelian evidence upon the subject of inheritance is practically ignored; although, in the face of the definite experimental information now rendered available, the younger biologists, at least, are beginning to realize that the circumstantial evidence, formerly so much relied upon, will in future constitute a much less prominent feature in these discussions.

Weismann's theory of inheritance, and the Theory of Ancestral Heredity in its original form, are based upon a common assumption, which is now shown by Mendel's discovery to have been unfounded. This is the assumption that all ancestors of the same degree—*e.g.*, grandparents—make a substantially equal contribution to the hereditary qualities of the offspring. Mendel has shown that in the case of particular hereditary characteristics this is not the case.

But if we venture to criticise Weismann's conception in the light of more recent knowledge, it must not be forgotten that biology, and especially modern cytology, owes a great debt to Weismann. To Weismann is due the conception of the isolation of the germ-cells from somatic influences, a view which is in complete accordance with the Mendelian view of the inheritance of definite characters. And it was Weismann who first emphasized the belief that the chromosomes represent those parts of the nucleus which are specially concerned in the processes of heredity. These conceptions—which, indeed, constitute an essential part of his own

theory of heredity—have stood the test of time in an admirable manner.

Let us turn our attention, then, for a short space to the Germ Plasm Theory of inheritance. On Weismann's theory, as in most other theories of heredity from the time of Darwin and Nägeli downwards, the separate parts of the living organism are supposed to be represented by separate material particles in the germ-cells. These representative particles are known as *determinants*. A complete set of determinants in which every part of the organism is thus represented constitutes an *id*. So far Weismann's hypothesis is in close agreement with the idea of representative particles which we are driven to adopt by the facts of Mendelian inheritance, except that, following de Vries, we should speak of separate characters rather than parts as being thus represented ; for there seems to be no doubt that the same character-determinant can affect the development of a number of different parts. But at the next step the Mendelian parts company with Weismann. The latter assumes that the cells of an organism contain a large number of *ids*, or complete sets of determinants, half of the total number being derived from either parent, and that, although at the reducing division which precedes the formation of the gametes the total number of *ids* is reduced to half of what it was in the somatic cells, still, several *ids* derived from each parent are present in every germ-cell.

Thus the reduced number of chromosomes in the germ-cells is regarded as containing all the primary

constituents of both parents. And it is an essential point in Weismann's theory that he regards a given germ-cell as containing a considerable number of *ids* derived from its ancestors, all near ancestors being thus represented.

But Mendel's experiments and others of the same kind show, in the case of a great number of different characters, that although every essential character is represented in every germ-cell, yet each Mendelian character is represented by a paternal or a maternal determinant only, and not by both. Thus, not only are all immediate ancestors not represented in the germ-cells in respect of any particular character, but only one of the parents is so represented—to the complete exclusion, so far as we can tell, of the other parent. In fact, we are led to believe that the germ-cells contain one set of determinants only—a single *id*—whilst the somatic cells contain two *ids* only. The Mendelian theory is thus seen to be considerably simpler than the germ plasm theory, which it replaces. At the same time it must not be forgotten that many of the conceptions used in the Mendelian expression of the facts are borrowed from Weismann's theory, and that but for Weismann's work it would have been impossible for us to have got so far in the co-ordination of the facts derived from experiment and microscopic observation respectively.

The preceding sketch may serve to show how Mendel's observations have been found to throw light upon many of the facts of cytology the meaning of which was previously obscure ; and how it affords at the same time

a criterion by which may be tested the truth of theories based upon the interpretation of minute phenomena only made visible by the highest powers of the microscope. The disinterment of Mendel's discovery took place only six years ago; and the rapid manner in which the facts of cytology have been found to fall into line with Mendelian conceptions augurs well for the future progress of discovery in these fields.

CHAPTER X

CONCLUDING CHAPTER

IN the preceding chapters a considerable variety of topics has been dealt with, and in spite of the fact that all are more or less intimately connected with the study of organic evolution, the nearly historical order in which the subject-matter has been in great part presented has inevitably rendered the treatment a little disjointed.

The method we have so far adopted serves to illustrate the state of transition in which our studies stand, and which it is our first object to assist in hastening to a close—the transition between the speculative philosophy of evolution and the exact science of genetics.

Future treatises on genetics will make a fair beginning with the law of Mendel, and will then deal with the application of this law in detail; and in this concluding chapter we may adopt the same method, and proceed to show how Mendel's discovery affords the connecting-link between the various divergent branches which we have already sketched in outline.

The central generalization, then, around which the subjects considered in the preceding pages are found

naturally to group themselves is afforded by the law of inheritance discovered by the Abbé Mendel about the year 1865. This discovery has rendered possible that rapid advance of the science of genetics, or the study of the hereditary phenomena of organisms, which has taken place during the first few years of the twentieth century. There can be no sort of doubt that Mendel's brief paper is the most important contribution of its size which has ever been made to biological science. Little apology is therefore needed for formulating once again the law based by Professor Correns upon the conclusions which this paper contains.

Mendel's law relates to the inheritance of certain definite characters, which have since been called allelomorphs. It is a distinctive feature of allelomorphic characters that they are found to group themselves naturally into pairs of more or less antagonistic qualities. In many cases the pair is represented by the presence and absence respectively of a certain definite feature. The two allelomorphs of a pair may be conveniently written as A and a .

We have seen that the cells of zygotic organisms—organisms, that is to say, which have arisen by the process of sexual reproduction—contain a double complement of hereditary qualities. Such cells may contain A and A , a and a , or A and a . The forms AA and aa are described as homozygotes, the form Aa as a heterozygote. In the simpler cases we are enabled to study the behaviour of such a single pair of allelomorphs by itself, without reference to any other features which the animals or plants under consideration may

display. The demonstration that there exist definite and separable unit characters of this kind is the first great debt that science owes to Mendel.

Up to the present our certain knowledge of the Mendelian behaviour of unit characters has been confined to cases of cross-breeding. In the simplest case which we have to consider, two homozygote forms, AA and aa , are crossed together.

The external character or visible appearance of the heterozygote Aa , produced in this manner, differs in different cases. In the commonest case A represents the dominant allelomorph, and in this case the appearance of the heterozygote Aa is practically indistinguishable from that of the homozygote AA . In other cases the heterozygote Aa is different in appearance from either homozygote AA or aa . Sometimes Aa is intermediate between AA and aa , in other cases it is to all appearances totally distinct from either.

So much for the external appearance of homozygote and heterozygote forms. In the production of the gametes, or germ-cells, we arrive once more at the simplest possible form of hereditary constitution, for we believe each feature in the body to be represented in the germ-cells by a single determining factor only. Still confining our attention to the representatives of a single pair of allelomorphs, we find that all the germ-cells of a homozygote contain only A or only a , as the case may be. But in the case of the germ-cells derived from a heterozygote, A and a are represented in an equal number of the gametes produced by the same individual. And the separation between the two

allelomorphs is found in almost all cases to be perfectly complete.

This complete segregation of the two allelomorphs in equal numbers of the germ-cells of a heterozygote constitutes the first and most important section of the generalization known as Mendel's law.

The second part of the law refers to the fact that, as a general rule, separate pairs of allelomorphs segregate quite independently of one another. To this rule a few exceptions have been recorded in cases where apparently distinct pairs of determining factors behave in segregation like a single pair of allelomorphs. In such cases we regard the members of the distinct pairs of allelomorphs as being coupled together, although no serious attempt has yet been made to picture the way in which this coupling comes about. In other cases, again, the coupling seems to be only partial. These phenomena are not yet by any means completely understood.

The fact that in the great majority of cases separate pairs of allelomorphs segregate independently of one another leads to the possibility of new combinations of the parental characters being formed in the germ-cells of the cross-bred individuals; in fact, this must always happen when the parent types differ in more than one pair of segregable characters. When two similar germ-cells, each bearing the same new combination of allelomorphs, meet together in fertilization, the result is a new zygotic combination which is a pure type in respect of the characters concerned, and henceforth breeds true. Thus if $AB . AB$ is crossed with $ab . ab$

the heterozygote $AB . ab$ produces in equal numbers the germ-cells $AB, Ab, aB,$ and ab . Among the combinations of these germ-cells which are represented by the various offspring of the heterozygote there must appear $Ab . Ab$ and $aB . aB$ —novel types which are pure in constitution, and which may form the starting-points for new strains or races.

Upon this fact depends the enormous importance of Mendel's law in the breeding of new and useful types of animals and plants. When it is remembered that in wheat, for example, resistance and non-resistance to the attacks of disease, earliness and lateness of ripening, good and bad milling quality, are all pairs of Mendelian allelomorphs, and that it is now possible to take a different example of these qualities from each of three different strains, and to combine them together in a single new variety with perfect certainty and in four generations, it does not require much imagination to foresee that every department of the animal and plant breeding industries must sooner or later benefit enormously from Mendel's discovery.

So far we have only been dealing with the very simplest of Mendelian phenomena, leading to the arithmetical addition and subtraction of definite visible characters. Other kinds of allelomorphs also exist which undergo a similar process of segregation during gamete formation, following Mendel's law in a perfect manner; but which may remain entirely invisible and unsuspected so long as certain other allelomorphs, belonging to quite distinct pairs, are excluded from the zygotes in which these invisible factors are concealed. When

this other complementary allelomorph is introduced, however, by crossing with an individual which contains it, the feature previously hidden becomes visible, giving rise to the phenomenon which has long been familiar under the name of reversion on crossing. The demonstration of these invisible factors, and of the fact that they also obey Mendel's law with perfect regularity, is surely one of the most remarkable discoveries which have ever been made in the whole history of biology. This, again, is a piece of knowledge which may be of the very greatest importance, not only to breeders of bright flowers, some of which are already known to exhibit the phenomenon described, but also in all classes of breeding work where similar facts doubtless await discovery.

To the man of science, however, the practical aspect of these achievements will be of little account in comparison with the importance of their application to the advance of human knowledge in that most fascinating of scientific studies—biology. Let us, then, turn to consider the way in which Mendel's discovery affects other branches of biological science.

We have so recently had occasion to point to the remarkable coalition between Mendelism and cytology that little more need be said here upon the subject. Mendel's theory has, indeed, thrown a flood of light upon the meaning of the microscopic phenomena exhibited by the minute constituent parts of the cells of living organisms, phenomena the meaning of which could only be vaguely guessed at previously to the introduction of the new method.

The intimate connection between Mendelism and cytology rests to a large extent upon the close parallel which exists between the behaviour of allelomorphous characters on the one hand and that of chromosomes on the other.

In the germ-cells of the higher animals the allelomorphs of the Mendelian become segregated, being reunited in fertilization, and, as a consequence, the cells of the zygote contain twice as many of these factors as do the gametes or germ-cells themselves.

Similarly, in the cell processes upon which the vital functions of the higher animals are founded, the number of chromosomes characteristic of somatic or zygotic cells becomes halved at the formation of the gametes, the double number being restored by the association of chromosomes derived from two separate gametes in the process of fertilization. We have said that in the higher animals the gametes are sometimes spoken of as constituting an ' x ' generation, which alternates with the ' $2x$ ' generation represented by the zygote. We may justify the use of these expressions by a brief comparative statement of the facts relating to the two so-called generations which recur in the life-history of certain families of plants. In doing so we shall begin our account with the most primitive and simplest forms, and then pass on to other types which are regarded as standing on higher planes of evolution.

What are probably some of the most primitive members of the vegetable kingdom belong to the class of the green algæ. This group includes a great

number of comparatively lowly organisms, the majority of which dwell submerged beneath the surface of fresh or salt water. In such members of the green algæ as have so far been examined from this point of view, it would appear that the $2x$ -generation is exclusively represented by the single cell which arises as the actual product of conjugation between a pair of gametes. Reduction takes place in the actual zygotic cell, so that each of the products of this cell's division shows once more the reduced number of chromosomes. Thus the great bulk—the vegetative mass—of the species is constituted by the x -generation, and the $2x$ -generation is composed of a single cell only—a state of things which is exactly the reverse of what is to be seen in the higher animals.

In the vegetable kingdom evolution seems to have been accompanied by a gradual increase of the $2x$ -generation, and a corresponding reduction of the x -generation in point of importance. Between the two extremes afforded by the algæ on the one hand, and the flowering plants on the other, we can trace a series of intermediate stages represented by types in which many other features also must be regarded as standing on intermediate planes of organization.

As an example of an intermediate condition of this kind, we may take the case of the ferns.

The fern plant, as commonly understood, represents the $2x$ -generation. The method by which the life-history of the fern plant is continued is by the formation of unicellular reproductive bodies which are known as spores. The formation of the spores takes

place in sets of four, and their production is preceded by a reducing division, so that each spore nucleus contains half as many chromosomes as the nuclei of the fern-plant—the spores, in fact, represent the initiation of the x generation.

Spores take no part in any process of conjugation. They at once germinate and enter on an embryonic development of their own, giving rise to a considerable mass of cells, all of which contain the reduced number of chromosomes. Thus in the case of the fern we have a small but well-developed x -generation alternating with a much larger $2x$ -generation. The mass of cellular tissue making up the x -generation has been named the *prothallus*.

Certain cells of the prothallus develop, without change in the number of their chromosomes, into the gametes. These are differentiated in the usual way into male and female—ova and spermatozoids respectively.

Fertilization of the ovum by the spermatozoid gives rise to a zygote in which the double number of chromosomes is restored. In this way the $2x$ -generation or fern plant is initiated, and by the usual processes of cell multiplication and differentiation this body becomes completed, developing its characteristic fronds and so forth. Thus in the ferns the $2x$ -generation has arrived at a high degree of development, and represents the chief bulk of the plant. The x -generation, however, still embodies a considerable mass of cells.

Turning to the higher plants, among which we may include those which produce typical flowers with

stamens or with pistils, or more usually with both, we find that the x -generation has become still further reduced, so that it no longer occupies an independent phase of the life-history, but has come to be entirely dependent upon the $2x$ -generation for its support.

A plant which bears both stamens and pistils gives rise to spores of two kinds, differing greatly in size. The smaller spores are represented by the pollen-grains, and in these, after one or two cell divisions, unaccompanied by growth, the one or two male gametes are produced. The small association of cells arising in this way is all that is left of the x -generation on the male side.

The nucleus of the larger spore also divides a few times, and one of the final products of division becomes the ovum. Spore and ovum, as well as the few intervening cells, bear the reduced number of chromosomes. The x -generation thus represented is never set free, but remains enclosed in the tissues of the $2x$ -generation right up to the time of fertilization. In the process of fertilization the double number of chromosomes characteristic of the $2x$ -generation is once more arrived at.

We can look upon the $2x$ -generation of the higher plants as being formed by an expansion of the fertilized ovum. The zygote, instead of comprising a single cell only, by dint of delaying the reducing division, has come to consist of a great mass of cells, all the nuclei of which contain the double number of chromosomes. This fact is also our excuse for applying the same term of zygote to the cell produced by the conjugation of

gametes, as well as to the mass of cells to which the zygote (in the strictest sense) eventually gives rise. In the simplest forms, such as the green algæ, the cell- and nuclear-fusion constituting conjugation are immediately followed by fusion of the chromosomes, an event which we have seen to be the first step towards a reduction in the number of these bodies. In the higher plants, by delaying this fusion of chromosomes until many cell generations later than the fusion of the nuclei, the advantages associated with the possession of a double nucleus have been obtained for a large and complicated mass of cells. And this mass has gradually advanced in organization and relative importance, until ultimately the x -generation has been reduced almost to the vanishing point.

The sex-phenomena of the higher animals can most readily be brought into line with those of the higher plants if we consider that in animals the spore and the gamete are identical; the x -generation is here condensed into the smallest possible limits—namely, those of a single cell.

A female animal produces ova, and a male produces spermatozoa. Similarly, we may regard as a female plant one which produces only the larger variety of spores from which ova arise; and we may regard as a male plant one which produces only pollen. It is much more usual to find a flowering plant bearing both pistils and stamens, and producing both large and small spores. Such an organism is described as hermaphrodite—bearing both sexes. Among animals examples of hermaphrodite species are also not infrequent,

and here, just as in the case of plants, whole families may display this method of reproduction.

We see, then, that the course of evolution in the vegetable kingdom would appear to have been accompanied by a gradual increase in the $2x$ -generation at the expense of the x -generation. Starting with lowly aquatic organisms, and passing upwards through the mosses and ferns to the flowering plants, we find a steady diminution in the x -generation, whilst the vegetative labour of the plant is taken over by the $2x$ -generation. It is, therefore, proper to suppose that organisms in which the main stage in the life-history is of double origin, and bears a double complement of hereditary factors, have some advantage over organisms in which this is not the case. We cannot, of course, be certain as to the exact nature of this advantage, but we may point out that it is only in the former kind of organisms that the operation of Mendel's law can lead to the production of new combinations of parental characters in the body which represents the main stage of the life-history; and that this circumstance may possibly lead to a greater power of adaptability to external circumstances.

Perhaps the most interesting application of the information afforded by Mendel's discovery is shown in its bearing upon the question of discontinuity in the origin of species. The fact of the definite and discontinuous inheritance of the differentiating features which distinguish cultivated varieties from one another would point very plainly to a belief that such differences had arisen in a definite and discontinuous manner, even if

we did not actually know from direct evidence that the origin of new races under cultivation is usually sudden and complete.

It is not necessary to repeat Darwin's demonstration of the close analogy between the origin of varieties under cultivation and the origin of species in Nature. It is more to the purpose to point out that Mendel's law has already been shown to hold good in the case of many differences which have certainly not arisen under cultivation, and that we have, moreover, sure knowledge of the definite and spontaneous origin of some natural species.

Here we arrive at a point at which the evidence is not yet by any means complete. We do not know whether all or even many specific differences obey Mendel's law on crossing, and a sharp limit is put to our researches in this direction by the fact that so many natural hybrids are sterile. Still less do we know from direct evidence whether the majority of natural species have arisen discontinuously, although there is much circumstantial evidence which points to the conclusion that this must have been the case.

Clearly this discontinuous method of variation is likely to repay some further discussion. That such mutation, or definite variation, is a phenomenon of the germ-cells follows from the fact that every germ-cell normally bears the complete specific character. Bateson has shown that we must regard mutation as consisting in the production of new kinds of gametes, which differ from those normally characteristic of the species. Such a change is most readily pictured by

imagining an asymmetrical nuclear division taking place immediately before the formation of the germ-cells, and this would lead us to expect a mutating species to give rise to more than one new kind of offspring at the same time. Such was actually the case with the *Œnothera Lamarckiana* studied by de Vries; and this observation stands as the most complete piece of evidence of a mutating species so far known to us. We may be assured, then, that the complete potential nature of new types as well as of old ones is already laid down in the germ-cells previous to fertilization. As Bateson puts it : ' For the first time in the history of evolutionary thought Mendel's discovery enables us to form some picture of the process which results in genetic variation. It is simply the segregation of a new kind of gamete, bearing one or more characters distinct from those of the type. We can answer one of the oldest questions in philosophy. In terms of the ancient riddle, we may reply that the owl's egg existed before the owl; or, if we hesitate about the owl, we may be sure about the bantam.'*

Let us consider a little more closely the evidence of mutation afforded by de Vries' studies of *Œnothera Lamarckiana*. Semi-wild specimens of this species, when transplanted and carefully observed, were found to yield nearly 3 per cent. of seedlings which differed definitely from their parent, and among these *mutants* some fifteen distinct new sorts were described. Some of the new species equalled or even surpassed the parent

* British Association, Cambridge, 1904. Address to the Zoological Section, p. 14.

O. Lamarckiana in vigour and prolific habit, and two of them actually became established side by side with the parent type without man's assistance.

It is unfortunate from the point of view of de Vries' interpretation of this case that the behaviour of *O. Lamarckiana* should suggest in some respects, as Bateson has pointed out, the phenomena of hybridization. It must be observed in support of de Vries' view that the species appears to exhibit the same phenomenon in other localities, and, further, that it has not been possible to make any suggestion as to the second species with which the pure *Lamarckiana* might be supposed to have been crossed.

From one point of view, as de Vries has himself pointed out, mutation in *Oenothera* is clearly a phenomenon of hybrids, and this circumstance of itself introduces considerable complications into the story.

We saw just now that there is every reason for the conviction that mutation takes place in the germ-cells, and not in the zygote after fertilization. Since the number of mutants given off under the most favourable circumstances did not exceed 3 per cent. of the total offspring, the enormous majority of mutated germ-cells (on de Vries' view) must unite with germ-cells bearing the ordinary specific character. Consequently, the new types which appear will in most cases have originated in the form of a cross between a mutated germ-cell and an ordinary germ-cell. And since this is not the final limit to the possible complications of the case, we can easily recognise that the complete inter-

pretation of the behaviour of *Oenothera Lamarckiana* is not by any means an easy matter.

As enunciated by de Vries, the theory of mutation amounts to a very complete and definite hypothesis. A large part of this author's suggestions are, however, almost purely speculative, and for this reason we have treated the whole at somewhat less length than it perhaps deserves. Some of de Vries' speculations are, indeed, more picturesque than convincing.

Thus, de Vries regards the number of unit characters—each of which has arisen by a single mutation—to be quite limited, even in the highest organisms. Three or four thousand such characters, he thinks, may go to build up the hereditary endowment of the most complicated species. He further supposes a period of mutation to recur about once in 4,000 years. Four thousand multiplied by 4,000 gives 16,000,000—the number of years required to evolve the lords of creation from a 'primordial protoplasmic atomic globule.' And he points out that this estimate is well within the limits of geological time as allowed by the physicist. In this way de Vries believes that his mutation theory removes a difficulty which besets the selection hypothesis—the difficulty, namely, of insufficient time. The selectionist may reasonably reply that the amount of change necessary to produce in 4,000 years, by the gradual method, a difference equal to that represented by a single unit character, might very well be quite imperceptible in a single generation.

We may summarize our present conclusions as to

the discontinuous nature of species in the following manner: A great number of specific characters are, without doubt, definite; they are inherited as definite entities, and there can be no question that their first coming into existence was a definite event. Every year tends to increase the range of characters to which the conception of discontinuity has to be applied.

Certain groups of characters do, however, seem to exhibit the phenomena of continuity. Let us endeavour to arrive at some closer idea as to the nature of these characters.

A study of continuous variations very quickly leads to the conclusion that the variable features are those which are especially liable to modification during the lifetime of the individual, owing to the action of external circumstances. Such quantitative features of size and shape and number of parts are particularly plastic in the case of plants.

The habit, or general form and appearance, of a plant is a feature very characteristic of individual species. The presence of a dwarf or of a tall habit does, indeed, constitute a frequent distinction between different strains of garden plants, and the inheritance of these characters in many cases follows Mendel's law. But leaving aside this particular example, the inheritance of habit is very little understood; although habit is a feature which is very liable to considerable fluctuations. Habit seems, in fact, usually to afford an example of continuous variability.

The habit of some species of plants when grown under alpine conditions on mountain summits is so

different from that of the same species when growing in the plains, that inexperienced persons might readily suppose two such forms to belong to as many distinct species. At intermediate levels the habit is more or less intermediate. Bonniér made the experiment of dividing individual plants into two portions, planting one part at a high elevation and the other near the level of the sea. In a few years the plant grown on the mountain had taken on the full alpine habit, whilst that grown on the plain retained the ordinary appearance of the species. In this way very considerable differences in habit were shown to be directly dependent on external conditions.

In some few cases the environment determines the production of perfectly definite and discontinuous features. The water ranunculus, when growing submerged beneath the surface of a pond, produces leaves the blades of which are cut up into a great number of fine thread-like segments. As soon as the top of the plant reaches the surface of the water those leaf rudiments which are just commencing their existence proceed to develop in a totally different fashion. The leaves to which they give rise possess a wide and undivided blade, which floats upon the surface of the water. The two sorts of leaves are as utterly different in appearance as it is possible for leaves to be. Yet the effect of external conditions upon the young leaf-rudiment determines which of the two kinds is to appear.

In this instance we see a discontinuous change in conditions—the change from water to air as a sur-

rounding medium—giving rise to a discontinuous change in structure. Such cases are, however, comparatively rare. Much more usually the changes in external conditions are continuous, as changes of altitude, moisture, or chemical composition of the soil, and so on; and the changes induced by them in the plant are similarly of a continuous kind.

In most animals changes in external circumstances have a much smaller influence on the form and structure of the individual than is the case with plants. In animals considerable modifications are, however, brought about by exercise and the use of different parts, as Lamarck long ago observed. But these modifying factors usually affect all the members of a single species in nearly the same manner. Nevertheless, some part of the differences between individuals in respect of strength and of proportion, and possibly also of stature, is undoubtedly associated with differences of training and nutrition, as the example of the human race is sufficient to show. Professor Cope has pointed out how the proper development of such structures as the joints of vertebrates depends to a very large extent upon exercise; and the effect of disuse may be practically tested by anyone whom accident obliges to keep a knee or other joint immovable for any length of time. The so-called play in which the young of many animals indulge—for example, lambs and kittens—must have a great influence upon the perfection of their locomotory functions.

We can now see more clearly the reason for that great instability of vegetative type which sessile

animals, like plants, exhibit. No necessity for definite and co-ordinated movements involving their whole structure forces the development of these animals along certain definite paths. External circumstance is, therefore, free to mould them into a host of slightly different shapes. And thus the great variability of the species of corals, for instance, is doubtless determined to a large extent by the influence of different environmental conditions.

Strictly speaking, the term variability ought not to be applied to modifications of this description. It will, perhaps, be most convenient, however, to distinguish true variations—having their origin in differences among the germ-cells—as *genetic variations*, contrasting them with the *acquired variations* which arise during the development of individuals.

Enough has now been said to show that it is a very difficult matter to distinguish in the case of continuous variations between those which are genetic and those which are acquired.

It is easy to understand how acquired variations come to be continuous, and to obey the law of normal variability. We saw that the normal distribution of characters was induced by the random operation of a multitude of small causes. During the development of the individual a great number of different external influences come into play, leading to slight modifications of every part, now in one direction, now in another. This being so, we may be quite sure that a large proportion of the normal variability which any species exhibits is acquired.

Now we saw that there seems to be good evidence that normal or continuous variations are inherited. Logic does not, however, permit us to make the step: Acquired variations are continuous variations; continuous variations are inherited; therefore acquired variations are inherited. It seems, indeed, to be this fallacy which has led to the long-continued belief in the inheritance of acquired characters as an important factor in organic evolution, in spite of so many arguments to the contrary.

Formal disproof of this proposition is very difficult, and in the meantime the confusion between continuous acquired variations and continuous genetic variations, which is always present in practice, constitutes a very serious drawback to the biometric method of research. At present Johannsen's explanation of these phenomena seems to afford so much the simplest solution that we may once more repeat his statement of the case, though with the proviso that the proof of his hypothesis is still to be awaited.

Johannsen looks upon a population which, as a whole, exhibits continuous or normal variability, as being capable of analysis into a number of pure lines. In a single pure line genetic variability is sensibly absent. The members of such a pure line exhibit, however, very considerable acquired variability, so that in this way each line shows a normal variability of its own. And the range of this variability may greatly exceed the limits which separate two pure lines from one another. The result is to give a completely blurred picture when all the lines are looked at simul-

taneously. And thus the normal variability of the population as a whole is brought about by the combination of these two separate factors.

This statement applies to the case of an organism in which self-fertilization is the general rule, so that in this way the separate lines are kept distinct. Where cross-fertilization takes place between the members of different pure lines the case becomes enormously complicated, and this is much the most frequent instance which we have actually to deal with. It has been suggested that the members of different lines when crossed together may display Mendelian phenomena, but the existence of so large a proportion of acquired variability renders the problem of analyzing the result almost insuperable. We have seen, however, that the numerical results obtained by the biometricians do not appear to be inconsistent with the existence of Mendelian inheritance in populations.

We find, then, that the questions of inheritance of acquired characters and of evolution by the aid of continuous genetic variations are not yet absolutely settled. But the evidence seems to be such that for all practical purposes the former factor at least may be disregarded. Meanwhile the number of cases in which discontinuity of inheritance can be shown to hold good is constantly increasing, and the analysis of some cases of supposed continuous variation into discontinuous Mendelian factors has already been made. It may be safely concluded that a very large part, if not the whole, of evolution has taken place by the discontinuous method.

New little species—Jordan's species—arise, then, from time to time, each at a single step, from pre-existing species. Upon the material thus supplied natural selection operates; the weaker go to the wall, the stronger survive. This is also, in all probability, the way in which adaptations have arisen. Creatures which came into existence displaying a particular new structure, which happened to be fitted for a particular new function or suited to a particular niche in Nature, survived and flourished exceedingly. Those in which undesirable organs appeared perished and were no more seen. To take Aristotle's example. If a man were to be born with molars in front and incisors at the back of his jaw he would die—at least, in the days before dentistry. Having his teeth in the positions in which they actually stand (although not for this reason only), he survives and rules the world.

After all, the difference between the point of view thus briefly indicated, and that of Darwin as expressed in the 'Origin of Species,' is only one of detail—of detail as to the particular sort of variations by which evolution chiefly proceeds. Darwin's analogy between the origin of species in Nature and the origin of races under cultivation may be repeated with emphasis, although Huxley's famous criticism, to the effect that races which are sterile together have not arisen in cultivation, is not yet completely answered. But this renders the discontinuous origin of such sterility only the more likely; and when we recall the Mendelian behaviour of such characters as long and short style in the primrose, or sterility of the anthers in the sweet-

pea, the solution of the problem does not seem very far to seek.

Let us see how the principles of which an outline has now been given affect the human race itself. The question of improving the human stock in this country has lately excited a good deal of attention. But without a scientific knowledge of the factors upon which improvement and degeneration depend the discussion is not likely to be of much profit, and in such a case misdirected energy may be even worse than apathy. Without venturing to make any very positive suggestions, it may at least be pointed out that our present practice in these matters is in almost every case the very worst possible.

Professor Karl Pearson has lately shown how the low birth-rate of the professional and middle classes—the classes amongst which the intelligence of the nation is to a large extent segregated—leads to the recruiting of these classes from amongst the lower and less intelligent strata of society. In other words, a steady breeding out of intelligence is taking place. Recognising that intelligence is an important factor in national greatness, we proceed to remedy this defect by endeavouring to reduce the infant mortality among the less desirable classes, and by offering every inducement to the production of large families by the said lower strata of society; indeed, we propose to remove from them all responsibility for the production of children, and to feed and house the latter as we already educate them (save the mark!) at the expense of the State.

The principles of heredity teach us that education and training, however beneficial they may be to individuals, have no material effect upon the stock itself. If they have any effect at all, this is undoubtedly unimportant in comparison with the effect which would be produced by the selection of individuals which exhibit desirable qualities. The demand for a higher birth-rate ought to apply strictly to desirables. Instead of this the cry is for education and physical training, processes which can have no permanent beneficial effect upon the race.

One writer who holds to some extent the attention of the intelligent public has recognised the true state of affairs—I mean Mr. Bernard Shaw. Unfortunately the public does not take Mr. Bernard Shaw seriously, wherein, when I recall Mr. Shaw's published views on such topics as vivisection and the medical profession, the said public has my sympathy. Nevertheless I know of no better expression of the moral to be drawn from the science of genetics than that which is embodied in the following passage :

‘ I do not know whether you have any illusions left on the subject of education, progress, and so forth. I have none. Any pamphleteer can show the way to better things, but when there is no will there is no way. My nurse was fond of remarking that you cannot make a silk purse out of a sow's ear, and the more I see of the efforts of our churches and universities and literary sages to raise the mass above its own level, the more convinced I am that my nurse was right. Progress can do nothing but make the most of us all as we are,

and that most would clearly not be enough even if those who are already raised out of the lowest abysses would allow the others a chance. The bubble of heredity has been pricked, the certainty that acquirements are negligible as elements in practical heredity has demolished the hopes of the educationists as well as the terrors of the degeneracy-mongers, and we now know that there is no hereditary "governing class" any more than a hereditary hooliganism. We must either breed political capacity or be ruined by democracy, which was forced on us by the failure of the older alternatives. Yet if despotism failed only for want of a capable benevolent despot, what chance has democracy, which requires a whole population of capable voters—that is, of political critics who, if they cannot govern in person for lack of spare energy or specific talent for administration, can at least recognise and appreciate capacity and benevolence in others, and so govern through capably benevolent representatives? Where are such voters to be found to-day? Nowhere. Promiscuous breeding has produced a weakness of character that is too timid to face the full stringency of a thoroughly competitive struggle for existence, and too lazy and petty to organize the commonwealth co-operatively. Being cowards, we defeat natural selection under cover of philanthropy; being sluggards, we neglect artificial selection under cover of delicacy and morality.*

Mr. Shaw recognises, however, that our knowledge is at present insufficient to prescribe for the breeding

* 'Man and Superman,' p. xxiii.

of a 'Superman,' even if we were able to come to any agreement as to what qualities are the most desirable. Nevertheless it is along the lines which we have endeavoured to indicate that such knowledge must be sought in the future.

GLOSSARY

[Many technical terms not included in this glossary are printed in italics on their first appearance in the body of the book, and their meaning is then defined. Such definitions may be discovered on a reference to the index.]

ADAPTATION.—A teleological explanation of the correspondence often shown between the structure and habits of a particular creature and the environment in which the creature lives.

ALBINO.—An animal or plant characterized by the absence of colouring matter from its external tissues.

ALGÆ.—A group of plants, mostly aquatic and of relatively simple organization.

ANTHER.—The upper part of a stamen, containing the pollen.

ATOM.—The smallest part of a chemical element which can exist as such.

AXIL.—The angle enclosed between the base or stalk of a leaf and the stem upon which the leaf is borne.

BINOMIAL NOMENCLATURE.—The application of a double name to an animal or plant, the first name being that of the genus, the second that of the species.

BIOLOGY.—The science of the phenomena of life.

BIOMETRY.—The application of statistical methods to biological problems.

BOTANY.—The scientific study of plants.

CALYX.—The outermost whorl of floral leaves, which in the bud usually encloses the other organs of the flower.

CHARACTER.—In heredity, a single definable attribute.

CLASS.—One of the larger subdivisions of the animal kingdom—*e.g.*, mammals, birds.

COMPOSITÆ.—A family of plants, including the daisy, chrysanthemum, and many others.

CONJUGATION.—The process of fusion of a pair of gametes.

COROLLA.—The second envelope of a flower, consisting of petals—leaf-like organs—usually brightly coloured.

CORPUSCLE.—A very minute particle.

CYTOLOGY.—The scientific study of the minute constituent parts of organisms by the aid of the microscope.

DENUDATION.—The wearing away of the earth's surface by the action of rain, rivers, etc.

DIFFERENTIATION.—The separation or discrimination of parts which were previously more or less united and uniform.

EMBRYO.—A young plant or animal—usually one which is still contained in the seed or the womb.

EMBRYOLOGY.—The history of the development of young plants or animals from the egg.

ENVIRONMENT.—Natural surroundings.

EVOLUTION.—See p. 21.

FAMILY.—A group of allied genera, as the family of apes (*Anthropoidæ*), the buttercup family (*Ranunculaceæ*).

FAUNA.—The sum total of animals inhabiting a particular region.

FERTILIZATION.—The union of male and female reproductive cells or gametes.

FLORETS.—The separate flowers of a crowded inflorescence.

GAMETES.—Sexual cells which unite in conjugation or fertilization.

GENUS.—A group of allied species.

GEOLOGY.—The study of the earth's crust.

GEOMETRIC RATE OF INCREASE.—Progress consisting in successive multiplications of the preceding number, instead of simply in additions to it.

GERM-CELLS.—See GAMETES.

HERBALIST.—One who collects and studies herbs.

HEREDITY.—The transference of similar characters from one generation of organisms to another, a process effected by means of the germ-cells or gametes.

IGNEOUS.—Produced in connection with great heat.

INBREEDING.—The mating together of near relatives for a number of generations.

LARVA.—The young of an insect after it has emerged from the egg—*e.g.*, a caterpillar.

MANTIDAE.—A group of predatory insects.

MAXILLARY.—Connected with the mouth parts.

MORPHOLOGY.—The study of form and structure.

MUTATION.—The sudden origin of a new species at a single step.

ORGANISM.—A living creature.

ORNITHOLOGIST.—A student of birds.

OVARY.—In animals the organ which produces ova. In plants the organ which contains the ovules.

OVUM.—The female gamete.

OVULE.—The structure surrounding the spore which gives rise to the female gamete or ovum in the higher plants.

PETAL.—One of the (usually) coloured leaves composing the corolla.

PETALOID.—Resembling the corolla, usually in the circumstance of being coloured.

PHYSIOLOGY.—The study of the functions of organisms.

PIN-EYED.—Having the stigma on a level with the throat of the corolla, and the anthers lower down, enclosed within the tube.

PISTIL.—The central organ of a flower, which contains the ovules, and ultimately becomes the fruit, or the chief part of it.

POLLEN.—Those spores of the flowering plants which produce the male gametes.

POLLINATION.—The transference of pollen to the stigma of a plant.

PRIMARY, SECONDARY, AND TERTIARY EPOCHS.—The three great divisions of geological time during which the known fossiliferous strata were deposited.

RADICAL LEAVES.—Leaves arising immediately from the root-stock in the form of a rosette.

REVERSION.—The reappearance in the offspring of a character proper to a more or less remote ancestor, and not exhibited by the immediate parents.

ROTIFERS.—A kind of minute aquatic animals.

SEGMENT.—One of a series of more or less similar transverse divisions.

SESSILE.—Fixed and stationary, but (in the strict sense) without a stalk.

SOMATIC.—Belonging to the body of a zygote.

SPECIES, LINNÆAN.—A group of organisms of closely similar appearance.

SPECIES, JORDAN'S.—A group of organisms believed to have arisen by a mutation. (Jordan himself did not, however, suppose so.)

SPORT.—A marked mutation—often one occurring under domestication.

STAMENS.—The organs of a flower which bear the pollen.

STANDARD.—The large, upright petal at the back of such a flower as that of the sweet-pea.

STIGMA.—The uppermost part of the pistil, upon which the pollen is received.

STRATUM.—A layer.

STYLE.—A stalk connecting the stigma with the ovary—part of the pistil.

TESTA.—The skin or coat covering a seed.

THRUM-EYED.—Having the anthers situated at the throat of the corolla, and the stigma lower down, enclosed in the tube.

TUBE.—The basal tubular portion of a corolla in which the separate petals are closely fused together, as is the case with that of the primrose.

UNICELLULAR.—Consisting of a single cell.

VARIATION, CONTINUOUS.—See Chapter IV.

VARIATION, DISCONTINUOUS.—See Chapter V.

WINGS.—The lateral petals of a pea-flower.

ZOOLOGY.—The scientific study of animals.

ZYGOTE.—The organism produced by the fusion of a pair of gametes.

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