CHAPTER V

MENDELIAN HEREDITY

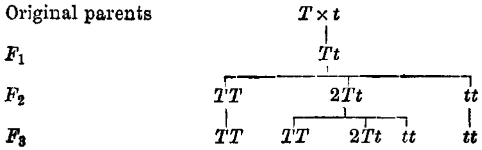
In the last chapter the distinction has more than once been referred to between the statistical rules of inheritance discovered by observing great numbers of cases taken together, and the physiological laws which determine the actual manner of transmission in individual cases. The province of the present chapter is to indicate the methods by which one at least of these physiological laws has been investigated, and the results to which such work has led. In studying this part of the subject it is necessary to consider, at least in the first place, characters which vary and are inherited discontinuously, so that they may be sharply marked into distinct categories. The foundation of the study was laid by Johann Gregor Mendel, a monk of the monastery of Brünn in Bohemia. His most important paper was published in 1866 [2], but perhaps owing to the fact that the biological world was then occupied almost solely with the discussion of the 'Origin of Species,' his work attracted no attention at the time, and only became celebrated on its rediscovery in 1900. One cannot avoid speculating on the possible effects on biological thought, had the experiments and conclusions of his now famous contemporary ever come to the knowledge of Darwin.

The method which led Mendel to his great discovery was to experiment with plants exhibiting discontinuous characters, and to consider each character separately. Previous workers in the same field had made many laborious experiments in crossing different races of plants or animals [7], but had always regarded the individual as the unit, and hence arose the belief that mongrels or hybrids were usually intermediate between the parents, resembling one in some features, the other in others, but with no regular rule; and further, that when hybrids were bred together the offspring were often almost infinitely variable, extending in a series from some closely approaching one original parent through a diversity of intermediate or new forms to others like the second parent. So grew up the belief that the crossing of distinct races or breeds is a potent cause of variability, which, however, except when 'reversion on crossing' took place, seemed to fall under no ascertainable law.

Mendel's most important experiments were made with races of the edible pea, which he grew in the garden of his monastery. He found in peas several characters which vary and are inherited discontinuously, and he crossed together races which differed in one or more of such characters, but in the offspring and later generations he considered the distribution of each character by itself, quite apart from the other characters of the plant. As an example we may take the character height or tallness. Certain varieties of peas grow stems some six feet in height, others are short and do not exceed about two feet. The heights fluctuate about a mode, but the smallest individuals of one race (grown under proper conditions) are taller than the largest of the other, and each race breeds true. Similar tall and short races exist in the sweet-pea (fig. 7), the short race being called 'Cupid' sweet-peas. When the two races are crossed—and reciprocal crosses give identical results—the offspring are not intermediate but all are tall, perhaps taller than the tall parents. When now these hybrid talls are self-fertilised, among the plants produced some are tall and others short, but again none are intermediate. Mendel regarded the tallness or shortness as distinct alternative characters, and since tallness alone appears in the first cross, he spoke of it as 'dominant,' and the shortness, which disappeared when crossed with the

dominant tallness, he called 'recessive. More recent work has indicated that a dominant character possesses some factor which is absent in its recessive alternative; in the present example the stem has the power of continued growth which is absent in the short pea. Dominance and recessiveness may thus be regarded as presence and absence respectively of the factor in question; but since the presence or absence of the factor may often give rise to the appearance of an alternative pair of characters, such a pair have been named by Bateson a pair of 'allelomorphs.' When a tall pea is crossed with a short, the factor tallness is introduced from the tall parent, and thus all the offspring are tall. These are called the first filial generation, or more shortly the generation F_1. When these hybrid (F_1) talls are self-fertilised, their offspring (second filial or F_2 generation) consist of talls and shorts. Now it has been seen that if the factor tallness is present it makes itself visible, and therefore the short peas in F_2 should contain no tall factor. And in fact when self-fertilised, or fertilised with the original short stock, they give only short offspring for as many generations as the experiment has been carried to. The tall factor has thus apparently been completely eliminated from these short peas.

Further, Mendel found that among the talls in the F_2 generation, some breed true to tallness when self-fertilised, while others again give a mixture of talls and shorts. The whole result may be clearer in symbolic form. If *T* stands for the tall factor, *t* for its absence (shortness), the following results appear. (The '2*Tt*' in F_2 will be explained immediately.)

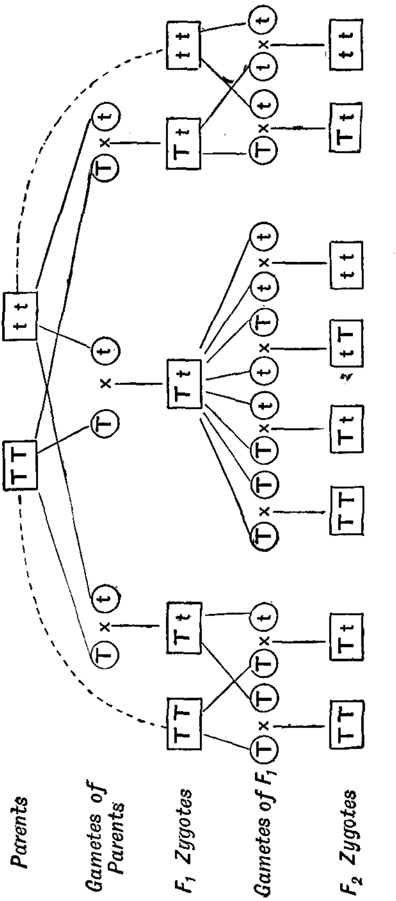


It is thus clear that among the offspring of the F_1 (hybrid) generation, some (*tt*) have eliminated the tall factor altogether and show no difference from their short ancestors; others (*TT*) have nothing but the tall factor and thus breed true to tallness; and a third group, which Mendel found was twice as numerous as either of the others (therefore marked 2*Tt*), proved, by giving mixed offspring when selfed, that it is hybrid like its F_1 parent.

The explanation offered by Mendel of these facts was as follows. The original tall plant produces germ-cells ('gametes') bearing tallness; the short plant produces gametes bearing shortness (absence of tallness). The F_1 (hybrid) thus contains both conditions; its cells, resulting from the union of two gametes, may be regarded as double structures, containing a double set of determinants for the various characters of the plant, one determinant of each pair being derived from the male parent, the other from the female. An individual produced by union of two germ-cells (gametes) and having this double character is called a 'zygote.' The F_1 zygote thus contains a determinant for tallness derived from one parent, and a corresponding determinant in which the tall factor is absent derived from the second parent. Now Mendel's hypothesis to account for the observed facts was that although the zygote produced by union of tall-bearing and short-bearing gametes contains both factors, yet when this hybrid zygote gives rise to gametes, it produces some bearing tallness and others bearing shortness, but none bearing both determinants; i.e. that the alternative characters segregate from each other in the formation of the gametes, and that gametes bearing one or other of the two conditions are formed in equal numbers. Since large numbers of gametes of each kind are formed, and since they meet indiscriminately in fertilisation, a tall will equally often meet a tall or a short, and a short will equally often meet a tall and a short, and the combinations will thus be in the ratio of $1TT$, $1Tt$, $1tT$, $1tt$, or $1TT$, $2Tt$, $1tt$. If this hypothesis is true, it can be tested by fertilising the F_1 hybrid zygote with the pure parental types; the F_1 zygote produces equal numbers of T and t gametes, the pure short race produces only *t*, so the offspring of the hybrid and the original short should give equal numbers of hybrid talls and pure shorts. Similarly the hybrid zygote crossed with the pure tall should give equal numbers of pure talls (*TT*) and hybrid talls (*Tt*). Mendel found that this expectation was in fact verified by experiment. The whole series may be made clearer by a diagram (p. 60), in which the zygotes are represented by squares, the gametes by circles.

The middle part of this diagram represents the production of the F_1 zygote and its offspring when self-fertilised, producing equal numbers of *T* and *t* gametes (four of each being represented) and thus giving offspring in the ratio of 1*TT*, 2*Tt*, 1*tt*; the sides of the diagram represent the results of crossing back the F_1 zygote with the parental types *TT* and *tt*.

At this point it is necessary to explain certain convenient technical terms introduced by Bateson. It has already been mentioned that a pair of alternative characters which segregate in the gametes, as described, are called allelomorphs. When an individual is produced by two gametes bearing different allelomorphs, so that it contains both members of a pair, it is called a 'heterozygote,' or is said to be 'heterozygous' in respect of the character considered, e.g., an individual of constitution *Tt* is heterozygous in respect of tallness. If it contains only one kind


Parents
Gametes of Parents
F₁ Zygotes
Gametes of F₁
F₂ Zygotes
TT
tt
T
t
Tt
TT
Tt
tT
tt

of allelomorph of a pair it is a 'homozygote,' e.g. individuals of composition *TT* and *tt* are 'homozygous' for tallness and shortness respectively. As will be seen immediately, it is possible for an individual to be heterozygous for one pair of allelomorphs and homozygous for another. The essence of Mendel's theory is that owing to the segregation of allelomorphs from each other in the production of the gametes of a heterozygote, the homozygous offspring, when self-fertilised or mated with others of like constitution, breed true to the character in question irrespective of their ancestry. As far as observation can show, the homozygous individuals *TT* and *tt* in the generation F_2 breed as true to tallness or shortness as did their pure-bred grandparents, in spite of the fact that they are the offspring of a cross.

Hitherto the original parents have been considered as differing from each other in only one pair of alternative characters (allelomorphs), but Mendel found that in the pea there were several such pairs of characters. For example, some races of peas have purple flowers, others white; these behave quite similarly to tallness and shortness. The purple flower contains a factor lacking in the white; when therefore purple is crossed with white, the purple colour is dominant and the heterozygote (F_1 hybrid) is purple. Such a heterozygous purple if self-fertilised yields 75 per cent. of purple offspring and 25 per cent.

of white; the whites and one in every three of the purples so produced are 'extracted' homozygotes, being pure for whiteness or purpleness respectively, and therefore breeding true, while the remaining purples are heterozygous and when 'selfed' will give both colours among their offspring.

If now a tall purple-flowered pea is crossed with a short white-flowered, the heterozygous offspring will be tall with purple flowers, for both these characters are dominant. In the production of their gametes (pollen-cells and egg-cells) segregation will take place between tallness and shortness, and between purpleness and whiteness, but as these pairs of characters are totally independent of one another they may be associated in any combination as long as both members of a pair do not occur in the same gamete. Gametes will thus be produced of four kinds; if P represents purple, p its absence (white); T tallness and t its absence (shortness), the gametes produced by an individual heterozygous in both characters will be PT, pT, Pt, pt, with equal numbers of each. Since these will meet one another at random in fertilisation, the F_2 generation will consist of individuals (zygotes) made up of all possible combinations of these four types of gametes, viz. in the proportion of $4PpTt$, $2PpTT$, $2PPTt$, $1PPTT$; $2Pptt$, $1PPtt$; $2ppTt$, $1ppTT$; $1pptt$.

Since purple is dominant over white and tall over short, the first four types of zygote, which all contain both P and T, will be purple talls; the next two containing P but no T will be purple short; the two containing T but not P will be tall white, and the last with neither P nor T will be short white. The F_2 offspring will thus *appear* in the ratio of 9 purple tall, 3 purple short, 3 white tall, 1 white short. Further, of the first group one will be homozygous in both characters ($PPTT$), four homozygous in one and heterozygous in the other ($2PPTt$, $2PpTT$) and four heterozygous in both ($PpTt$). Of the remainder, one in each class will be homozygous in both characters, and the others heterozygous in one, the homozygous (pure) types being $PPtt$, $ppTT$ and $pptt$.

It is clear then that by crossing two races which differ in two allelomorphic characters, and self-fertilising (or mating together) the crossed individuals, in the F_2 generation a definite proportion of *new* pure combinations are produced. In the above example, by crossing tall purple with short white, in the second generation not only these types are produced, but also short purple and tall white, and by selecting the pure (homozygous) individuals pure races of these new types are immediately established. We thus obtain a new conception of organic characters, as factors which can be replaced by alternative characters without otherwise altering the constitution of the organism. The process is comparable with a chemical reaction, where one element may replace another in a compound; for example, by mixing silver nitrate with sodium chloride, silver chloride and sodium nitrate are produced. Or a grosser analogy may be taken from bricks in a wall; a red brick may be removed and replaced by a blue or a yellow one without altering the rest of the wall, and similarly in pea-plants by the process described white flowers may be replaced by purple, or yellow seed by green. After the fact of the segregation of allelomorphic characters in the production of the germ-cells of a heterozygote, the most striking result of Mendelian investigation is this discovery of the independence of characters belonging to different pairs.

That these results are not of merely academic interest is shown by the work of Prof. Biffen on wheat. Some valuable wheats are liable to the attacks of a fungus giving rise to the disease called 'rust,' other less valuable races are immune. Biffen has found that by crossing the two races together, fertilising the hybrids (F_1) among themselves, and selecting the homozygous plants in the F_2 generation, wheat can be produced which combines the valuable features of one race with the immunity to rust of the other, and so a new and most useful variety of wheat is produced. This is only one out of many examples that could be given of the possibility of combining

any rules are to be arrived at for the distribution of characters among the offspring of hybrids.

Before proceeding to consider some of the further applications of Mendelian inheritance, a few examples will be given of characters in animals and plants which are found to be inherited according to this law.

In plants, flower-colour, seed-colour (due to either seed-coat or the contained embryo); production of starch or sugar in seeds (maize, see fig. 8 in which both forms of seed are shown on the same cob); hairiness or smoothness (stocks, Lychnis, etc.); 'bearded' or 'beardless' ears (wheat); 'palm-leaf' or 'fern-leaf' (Primula); long or short styles ('pin-eye' and 'thrum-eye' of Primula); pollen-shape, and also fertility or sterility of anthers (sweet-pea). Many other examples could be given; it should be noted that several of these normally occur in nature, e.g. the two flower-types of the primrose.

In animals, coloured coat and albino (many mammals); and many other colour-characters in mammals and birds; normal and long or 'Angora' hair in rabbit, guinea-pig, etc. (some doubt as to completeness of segregation); comb-characters in fowls; leg-feathering in pigeons; horned and hornless condition (sheep and cattle); colour-characters in moths, beetles, and snails. In man, several abnormal conditions, and presence or absence of brown pigment in the iris of the eye.

As in plants, several of these cases are not in any way connected with domestication, and the wide diversity of species and characters in which Mendelian inheritance has been discovered shows that the phenomena are not rare or exceptional, but universally *distributed*.

It has been mentioned that of a pair of allelomorphic characters, one is regarded as containing some factor absent from the other, and it may be well to give an example of the kind of evidence that leads to this conclusion. In fowls there are three chief forms of comb; 'single' with a median serrated ridge, 'rose' with a broad upper surface covered with papillae, and 'pea' with a shape consisting essentially of three parallel low ridges. Rose and pea each behave as dominants to single, but when rose is crossed with pea a fourth type, 'walnut' results, which in the adult is swollen and dimpled, and, in the young at least, is crossed by a transverse band of bristles. In the Malay breed such 'walnut' combs breed true, but when made by crossing 'rose' by 'pea,' and mated together, the resulting chicks appear in the ratio of 9 walnut, 3 rose, 3 pea, 1 *single*. The appearance of singles in the F_2 generation from pure rose by pure pea is explained by the 'presence and absence' hypothesis. Rose (R) and pea (P) are each allelomorphic with their absence (r, p). A rose-combed bird is thus Rp, and a pea-combed rP,

and the walnut combs produced by crossing them have constitution *RrPp*. They produce four kinds of germ-cells, *RP*, *Rp*, *rP*, *rp*, giving the normal ratio in F_2 of 9 birds containing *R* and *P*, 3 with *R* and *p*, 3 with *r* and *P*, 1 *rp*. This *rp*, containing neither rose nor pea is *single*, which may be regarded as the normal comb with no other factor superposed upon it.

In conclusion, one further fact should be noted. Although the members of an allelomorphic pair differ from each other in that one contains a factor lacking in the other, and this present factor is commonly dominant over its absence, yet a number of cases are known in which the introduction of a factor from one parent only is not sufficient to cause its full development in the heterozygote. The crossed offspring are then different from both the parental types, and are commonly intermediate between them. But when such heterozygous forms are mated together or self-fertilised, both the homozygous parental types are produced in addition to the heterozygous form, as in the offspring of a heterozygous tall pea there occur homozygous talls and shorts in addition to heterozygous talls. The classical example of this condition is the blue Andalusian fowl. This breed cannot be bred true; when blues are paired together about half the chickens are blues and the remainder evenly divided between blacks and dirty-whites. By many generations of selection breeders have tried without success to eliminate these black and white 'wasters,' but it remained for Bateson and Punnett to show that if a black and a white are paired together, only blues are produced. The two homozygotes are black and white respectively; when these are paired together the single black factor introduced from one parent is insufficient to cause the crossed chicks to be full black, and a dilute black or 'blue' results. Such incomplete dominance, in which a single factor introduced from one parent is insufficient to bring about the same effect in the heterozygote that is produced by the 'double dose' present in the homozygote, has been observed in a number of cases, some of which must be referred to later.