# 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
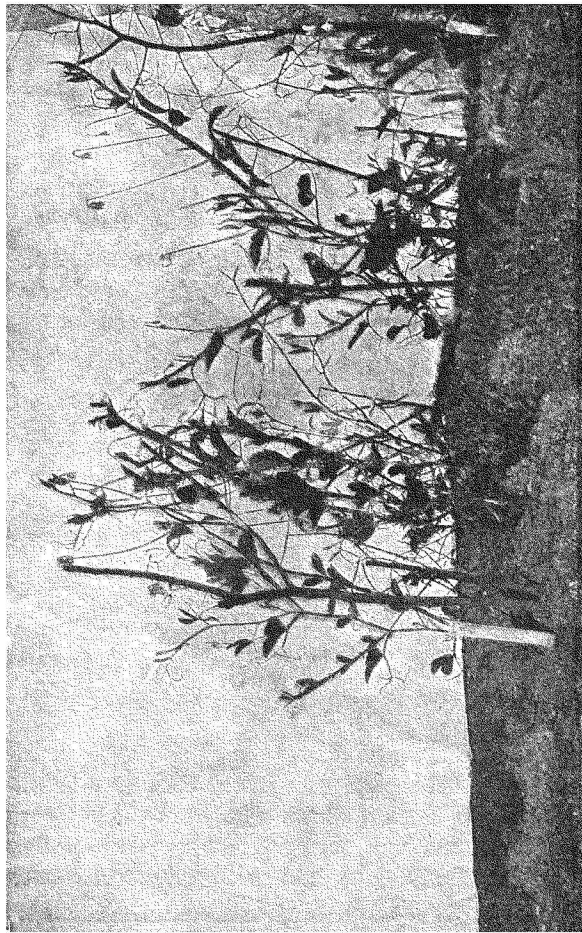
3 Dwarfs   5 Talls

Fig. 7. Eight plants in the second (F_2) generation from the cross tall sweet-pea × dwarf (Cupid). The five talls and three dwarfs came from one pod of seed. (From Bateson.)

dominant tallness, he called 'recessive.   More recent
work has indicated that a dominant character pos-
sesses 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 '$2Tt$' in F_2 will be explained immediately.)

Original parents		$T \times t$		
F_1		Tt		
F_2	TT	$2Tt$		tt
F_3	TT	TT $2Tt$ tt		tt
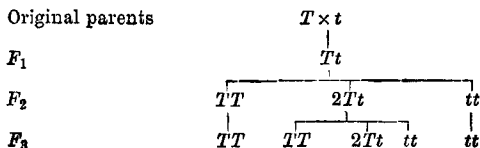
It is thus clear that among the offspring of the F_1
(hybrid) generation, some (tt) have eliminated the
tall factor altogether and show no difference from
their short ancestors; others (TT) have nothing but
the tall factor and thus breed true to tallness; and
a third group, which Mendel found was twice as
numerous as either of the others (therefore marked
$2Tt$), 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, con-

taining 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 forma-
tion 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 $1TT$, $2Tt$, $1tt$; 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 alter-
native characters which segregate in the gametes, as
described, are called allelomorphs.   When an indi-
vidual 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

F_1 Zygotes

Gametes of F_1

F_2 Zygotes
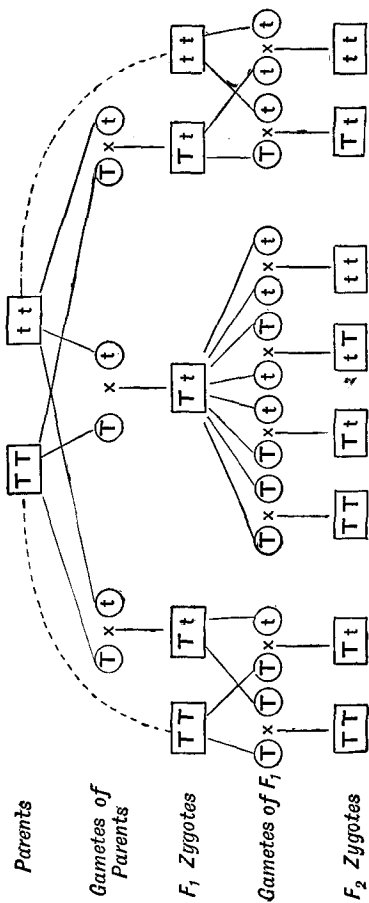
of allelomorph of a pair it is a 'homozygote,' e.g. individuals of composition TT and tt are 'homozygous' for tallness and shortness respectively. As will be seen immediately, it is possible for an individual to be heterozygous for one pair of allelomorphs and homozygous for another. The essence of Mendel's 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 com-
binations 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

into one race of wheat the characters previously found in different varieties.

The chief reason that breeders of plants and animals believe that the race is permanently contaminated by crossing different breeds is that commonly two breeds differ in several or many pairs of characters. If two pairs of allelomorphic
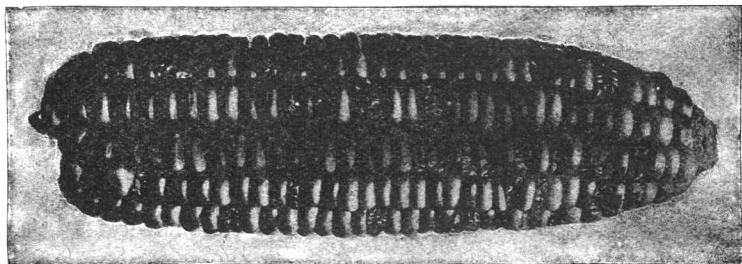

Fig. 8. A cob of Maize borne by an F_1 plant from the cross smooth (starchy) seed × wrinkled (sugary) seed, fertilised with its own pollen, showing about three smooth (dominant) to one wrinkled (recessive) seeds on the same cob. (From Bateson.)

characters are combined in the heterozygote, we have seen that only one in sixteen of its offspring is homozygous for any particular combination; if three characters, one in 64, if four characters, one in 256, so that it is clear that Mendel's method of considering distinct characters separately must be followed, if

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 horn-less 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,
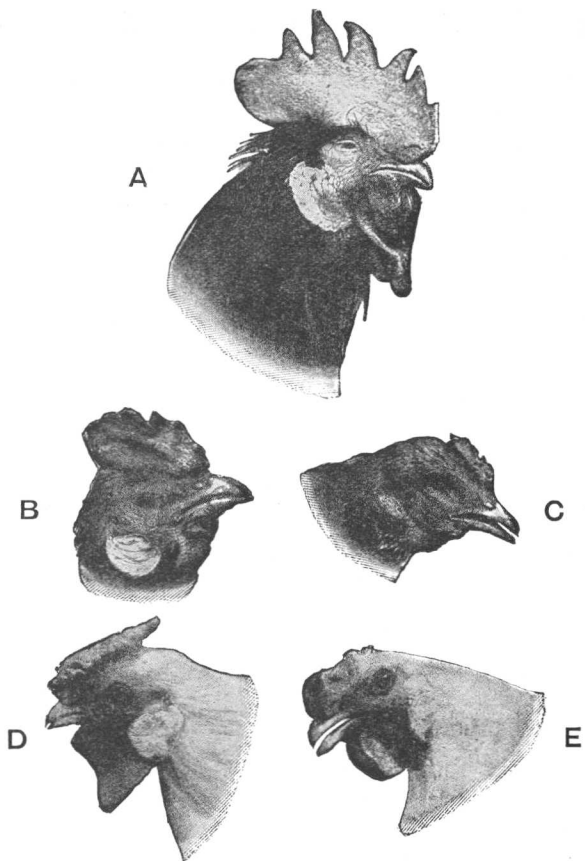
Fig. 9. Types of combs in Fowls. A. Single Comb (cock). B. Pea Comb (cock). C. Pea Comb (hen). D. Rose Comb (cock). E. Walnut Comb (young cock). (From Bateson.)

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 genera-

tions 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.