

CHAPTER II

MENDEL'S FIRST LAW—SEGREGATION OF THE GENES

MENDEL succeeded in discovering the principle of segregation because he simplified the conditions of his experiments so that he had to deal with one process at a time. Others before him had failed because they worked with too complex a situation. In each case Mendel picked out for study a pair of contrasted characters of a kind that were sharply distinguishable from each other whenever they appeared. He chose plants that normally self-fertilize and are little liable to accidental cross-fertilization, which made it possible easily to obtain in the second generation numbers large enough to give significant results. To Mendel's foresight in arranging the conditions of his work, as much as to his astuteness in interpreting the data, is due his remarkable success.

Mendel used varieties of the common edible garden pea (*Pisum sativum*). Many of these varieties (races) differ from each other in a particular character. Some races are tall, others short; some have green peas (seeds in the pods), others have yellow peas; some of these seeds have a smooth surface, others are wrinkled; some of the pods are hard, others are soft. One of the crosses made by Mendel will serve as an illustration of his work (Fig. 1).

Pollen from a race of tall peas was put artificially on the stigma of a plant of a short race, whose own stamens, and therewith the pollen, had been previously removed. The hybrid plants that came from the seed were tall. These hybrids were allowed to self-fertilize and their seeds collected. Some of the seeds produced tall plants,

PHYSICAL BASIS OF HEREDITY

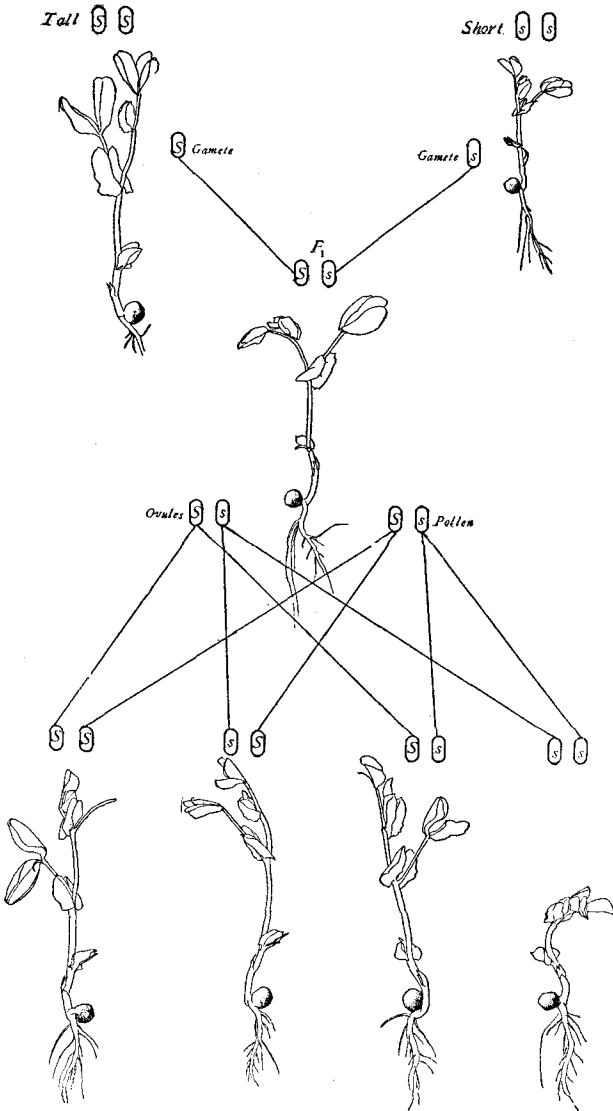
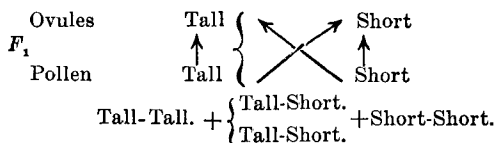


FIG. 1.—Cross between a tall and a short race of garden peas. The *F*₁ generation is tall. In the second generation, *F*₂, there are three tall to one short. (*P*₁, *F*₁ and *F*₂ were reared from peas supplied by Dr. O. E. White.)

others produced short plants; in the ratio of 3 tall to 1 short. In other words, the contrasted characters of the grandparents reappeared in the grandchildren in the ratio of 3 to 1. The experiment was carried through one more generation, which was necessary in order to get data for finding out what had been taking place. The short peas were allowed to fertilize themselves. They produced only short peas. The tall peas were also allowed to fertilize themselves. One-third of the tall peas produced only tall offspring; two-thirds produced both tall and short offspring in the ratio of 3:1, as had the first generation hybrids. Evidently then the grandchildren had been of three kinds, one kind was pure for shortness, others were hybrids, and the remaining kind was pure for tallness. These kinds appeared in the proportion of 1:2:1.

Some factor or factors in the original tall peas must cause the peas of that race to be always tall, and some factor in the original short peas must cause them to be short. The short factor may be represented by s , and the long factor by S . When crossed, the fertilized egg should contain both factors (sS), and since the hybrids coming from this egg were tall, it is evident that tall must *dominate* over short. Now if the two factors (sS) present in the hybrid should separate (*i.e.*, "segregate") when its ovules and its pollen-grains are formed, half of the eggs would contain the factor that represents the short peas (s), and half of the eggs the factor that represents tall peas (S); also half of the pollen grains would contain the factor that represents the short peas (s), and half of them would contain the factor that represents the tall peas (S). Chance meeting between egg-cells and pollen-cells (one ovule being always fertilized by one pollen grain), would, on the average, give one fertilized egg containing two factors for short (ss); to two fertilized eggs that contain one of each kind of factor (sS); to one that contains two

factors for tall (SS). The chance combination just given may be represented graphically as follows:



In the actual experiment that Mendel carried out, plants of the tall race measured from 6 to 7 feet, and those of the short plants three-quarters to one foot and a half. The F_1 plants were as tall as, or even taller than the tall parent. When these F_1 's were self-fertilized, the seeds (either from the same plant or from a random collection of seeds from different F_1 plants) produced 787 long plants and 277 short plants—a ratio of 2.84 to 1.

As a fair sample of each plant, ten seeds were taken from each of 100 tall plants of this second (or F_2) generation. Out of the 100 plants so tested, 28 plants produced only tall plants, while 72 of them produced some tall and some short offspring. This means that 28 plants were pure (homozygous) tall, whilst 72 were hybrid like the F_1 plants. Taking, then, all F_2 plants together, the results show $\frac{1}{4}$ were short, $\frac{2}{4}$ were hybrid, and $\frac{1}{4}$ were tall, *i.e.*, they stand in a ratio of 1 : 2 : 1.

This relation is illustrated in the scheme below, based on what 16 F_2 plants might give. Twelve would be tall to 4 short. If the tall plants are tested, they are found to consist of 4 pure tall (SS) and 8 hybrid tall (sS). Altogether, then, there are 4 tall to 8 hybrid tall to 4 short, *i.e.*, there are three kinds of F_2 peas in the ratio of 1 : 2 : 1.

$$\begin{array}{ccc}
 \underbrace{12 \text{ tall}} & + & \underbrace{4 \text{ short}} \\
 \underbrace{4SS + 8sS} & + & \underbrace{4ss} \\
 \underbrace{1 \quad 2} & & \underbrace{1}
 \end{array}$$

The process of disjunction, or separation of the members of a pair of factors, is known technically as *segregation*. While we sometimes also speak of the segrega-

tion of the characters themselves, it seems better, I think, to avoid as far as possible this application of the word. The factor for tall and the factor for short are said to be allelomorphic to each other. The parents are generally designated by P_1 ; the first hybrid generation is known as the first filial generation, or briefly F_1 . The next generation, derived from F_1 is called F_2 , etc. When one member of the pair of contrasted characters appears in F_1 to the exclusion of the other it is said to be dominant, the eclipsed character is said to be recessive. The hybrid itself is said to be heterozygous, meaning that it contains one factor or gene of each kind, while an individual containing both genes of the same sort is said to be homozygous for the genes involved. Mendel did not emphasize the idea that even in pure races each character is also represented, as a rule, by a pair of factors or genes that segregate in the formation of the germ-cells in the same way as do the pair of contrasted genes in the heterozygotes, but at the present time this idea is accepted by all geneticists. It was at least implied on Mendel's view that the two pure classes in F_2 (SS and ss), formed by the recombination of two like genes, are identical with the two grandparental races (P_1).

A crucial test of the correctness of the assumption that segregation of the members of a pair of elements takes place in the germ-cells of the hybrid, consists in back-crossing the hybrid (F_1) to one of the parent stock, viz., to the not dominant stock, here the short pea. Since short is recessive to tall, it will not influence the height of the offspring when a tall and a short factor are brought together. Such a cross should show whether the germ-cells of the hybrid are, as postulated, of two sorts, and whether equal numbers of each sort are produced. Mendel made such tests, and obtained equal numbers of two kinds of offspring.

Mendel obtained results like these with tall *versus* short peas for other pairs of characters, such as fasciated *versus* normal stems, hard *versus* soft pod, yellow *versus*

green pods, gray *versus* white-skinned peas, yellow *versus* green cotyledons (seen through the skin of the seed), and round *versus* wrinkled seeds (determined by the nature of the cotyledons within the seed coat).

The 3:1, F_2 , ratio characteristic for a single pair of characters is the expectation based on the chance meeting of either one of two kinds of eggs with either one of two kinds of pollen grains. In actual numbers this ratio is, of course, not always exactly realized, but only approximately. For the seven pairs of characters that Mendel examined, the F_2 ratios were as follows:

		Dominants	Recessives	No's. per 4
Form of seed.....	7,324	5,474	1,850	2.99 : 1.01
Color of cotyledons.....	8,023	6,022	2,001	3.00 : 1.00
Color of seed coats.....	929	705	224	3.04 : 0.96
Form of pod.....	1,181	882	299	2.99 : 1.01
Color of pod.....	580	428	152	2.95 : 1.05
Position of flowers.....	858	651	207	3.03 : 0.97
Length of stem.....	1,064	787	277	2.92 : 1.08
Totals.....	19,959	14,949	5,010	2.996 : 1.004

The following collective data for the inheritance of color of the cotyledons of garden peas show that the approximation to a 3 to 1 for the recessive character is very close:

	Yellow	Green	Total	No's. per 4	Probable errors
Mendel.....	6,022	2,001	8,023	3.002 : 0.998	±0.0130
Correns.....	1,394	453	1,847	3.019 : 0.981	±0.0272
Tschermak.....	3,580	1,190	4,770	3.002 : 0.998	±0.0169
Hurst.....	1,310	445	1,755	2.986 : 1.014	±0.0279
Bateson.....	11,903	3,903	15,806	3.012 : 0.988	±0.0093
Lock.....	1,438	514	1,952	2.947 : 1.053	±0.0264
Darbishire.....	109,060	36,186	145,246	3.004 : 0.996	±0.0030
Darbyshire.....	1,089	354	1,443	3.019 : 0.981	±0.0308
White.....	1,647	543	2,190	3.008 : 0.992	±0.0250
Correns.....	1,012	344	1,356	2.985 : 1.015	±0.0319
Tschermak.....	3,000	959	3,959	3.031 : 0.969	±0.0186
Lock.....	3,082	1,008	4,090	3.014 : 0.986	±0.0183
Darbishire.....	222	1,856	7,518	3.013 : 0.987	±0.0135
Correns.....	2,405	70	295	3.051 : 0.949	±0.2151
Lock.....	50	850	3,250	2.954 : 1.046	±0.0205
Totals.....	218,425	50,676	203,500	3.004 : 0.996	±0.0026

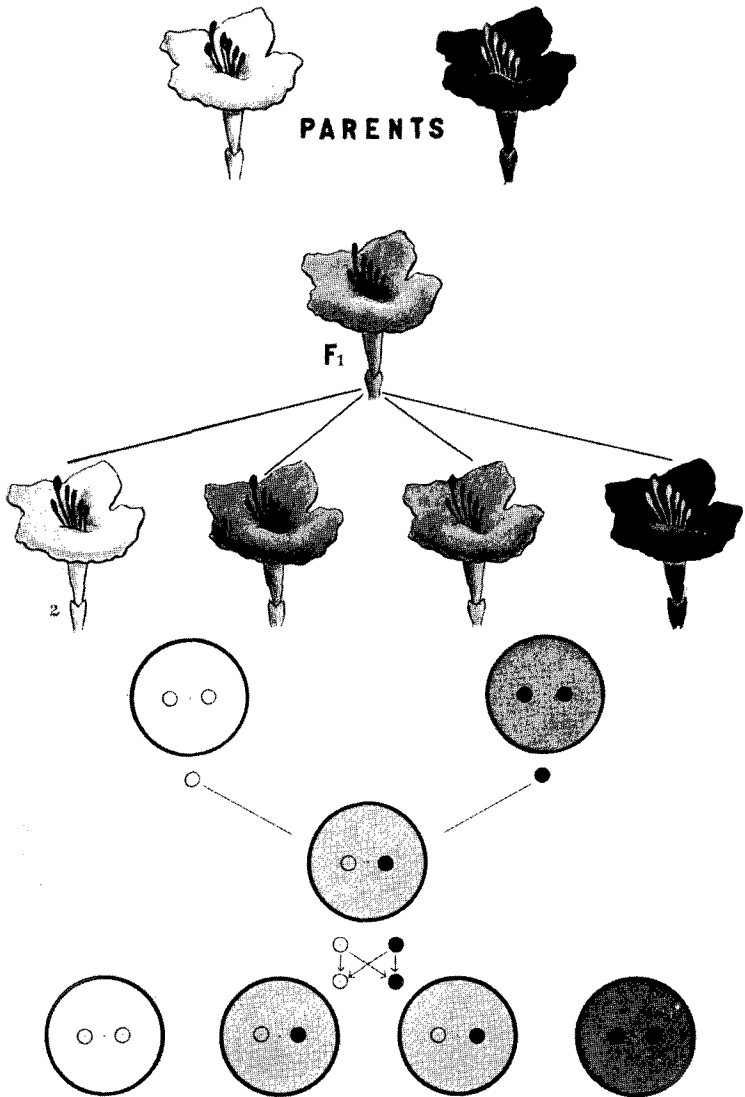


FIG. 2.—Cross between white and red flowered four-o'clocks (*Mirabilis jalapa*). In the lower part of the diagram the large circles represent somatic conditions, the included small circles the genes that are involved.

That Mendel's principles apply to animals was first made out by Bateson and by Cuénot in 1902. Since then many characters both in domesticated and in wild animals and plants have been studied, and there can be no question of the wide application of Mendel's discovery.

During the years immediately following the re-discovery of Mendel's principles (1900) much attention was paid to the phenomena of dominance and recessiveness. This was due, no doubt, to the striking fact that the hybrid sometimes resembles only one parent in some particular trait, whereas the older observations, where many characters were generally involved in the cross, seemed to have shown that hybrids are intermediate in regard to their parents. We now know, however, that although there are cases in which the dominance is as complete as in those described by Mendel, yet in a very large number of forms the hybrid is intermediate between the parents, even when only a single pair of characters is involved. A few examples will serve to illustrate these relations.

The common garden four o'clock, *Mirabilis jalapa*, has a white-flowered and a red-flowered variety (Fig. 2). When crossed, the hybrid has a pink flower, which may be said to be intermediate in color between white and red. Here neither color can strictly be said to dominate. When the hybrid (F_1) is self-fertilized the offspring (F_2) are in the proportion of one white, to two pink, to one red-flowered plant. The F_2 reds and the F_2 whites breed true; the pinks when self-fertilized give white, pink and red in the proportion of 1:2:1. In a case of this kind the color of the F_2 plants reveals the nature of the three classes present, so that it is not necessary to test them out, as was the case in the F_2 generations of Mendel's peas, where the F_2 tall were found in this way to be of two sorts. The F_2 results with the four o'clock also show that the segregation of the genes is clean, for the F_2 whites never produce in subsequent generations anything

but white descendants, and the F_2 reds never anything but red descendants.

In this case the color of the F_1 flowers is obviously somewhere between red and white. In so far as the F_1 flower is colored, it may be said that red is dominant; in which case the red and the pink F_2 classes ($1 + 2 = 3$) are to be counted together as contrasted with the white, giving a 3:1 ratio. On the other hand, if one chose to emphasize the fact that the F_1 pink flower is not red, but affected by the white-producing element in its make-up, then not red, but white, might be said to be the dominating character; in which case the white and the pink F_2 classes ($1 + 2 = 3$) would be counted together as contrasted with the red giving an inverse 3:1 ratio. It appears then largely a matter of choice as to what is to be called dominance (see below). The essential fact of segregation is not affected by the decision, and it is this that is fundamentally important.

Another example of failure of complete dominance is shown in the race of Andalusian fowls. In this race there are blue, splashed-white, and black birds; the blue birds going under the name of Andalusians. When splashed-white is mated to black, all the offspring (F_1) are blue (Fig. 3); when these blues are bred together they give 1 splashed-white : 2 blues : 1 black. Evidently the blue birds are the heterozygous type. Their feathers show under the microscope less black pigment, somewhat differently distributed from that in the black birds. The intermediate blue color is due in this case to the less dense distribution of the pigment in the heterozygote. Lippincott, who has recently examined this cross in greater detail than heretofore, states that the colored areas or splashes in the white males are either blue or blackish according to the part of the body on which they occur, and that this corresponds with the distribution of the color on the Andalusian, for while the latter is said to be blue, this applies

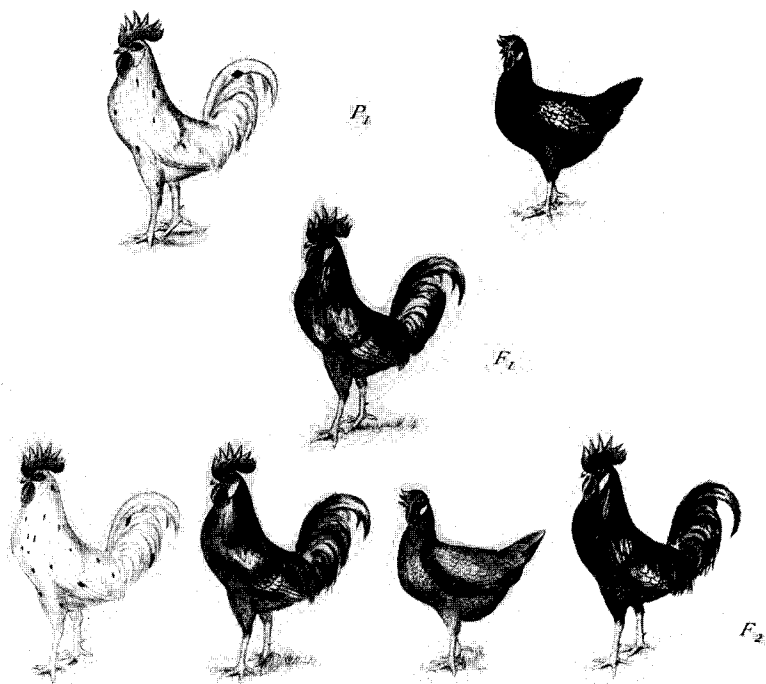


FIG. 3.—Cross between splashed-white and black, giving in F_1 Andalusian, and in F_2 one splashed-white, two Andalusian, and one black.

strictly only to the hen and to the lower parts of the body in the cock whose upper surface is very dark blue or even black.

In this case neither black nor white can be said to be dominant. The blue brought in as splashes by the splashed-white might indeed be regarded as dominant over the black of the other (black) parent, but if so, then the uniform distribution of the blue must be determined by dominance of the allelomorphic gene brought in by the black parent. Each parent then would contribute at the same time a dominant and a recessive effect, each the product of one member of the same pair of allelomorphs.

There are other cases in which the hybrid is intermediate in color, and, in addition, its range of variation is so large that the extremes overlap one or even both of the two parental types. For example: In the vinegar fly, *Drosophila melanogaster*, there is a race with ebony wings and another race with sooty wings. When such flies are crossed to each other, the wings of the F_1 fly are intermediate in color, ranging from wings like those of sooty to wings as black as ebony. When the F_1 flies are inbred they give rise to a series that at one extreme has gray wings and at the other black wings. Separation into three classes is difficult or impossible. Here it may appear that the two original characters have completely blended in F_1 and in F_2 , but that there are in reality three classes of flies in F_2 can be demonstrated by suitable tests. If, for instance, we pick out a sufficient number of F_2 males to give a fair sample of the population, and mate each male first to an ebony female of pure stock, and then to a female of sooty stock, we shall find that one-quarter of the males mated to ebony give only ebony, one-quarter mated to sooty give only sooty, while the remaining two-quarters give, both in the back-cross to sooty, and in that to ebony, a wider ranging group, which is darker on the whole when mated to ebony, and lighter when mated to

sooty. These and other tests show that in the F_1 hybrid segregation of the same kind as in the preceding cases has taken place, but the results are obscured by the wide variability of the hybrid flies. In other words, evidence can be obtained that the segregation of the genes has been clean cut, even although this is obscured by the character of the heterozygous flies.

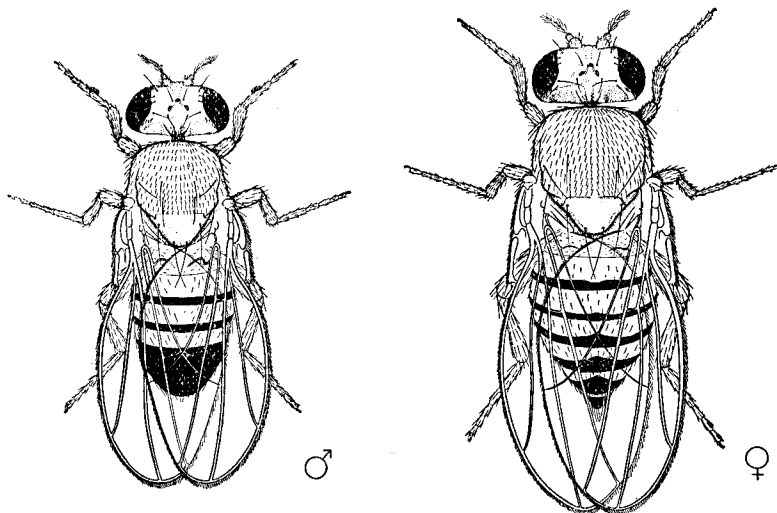


FIG. 4.—Male and female vinegar fly (*Drosophila melanogaster*).

In the preceding illustrations the character difference between the two races is supposed to show itself in the same environment. It has been found in a few other cases that the dominance of one character over the other may depend on the environment. For example, in the normal vinegar fly the black bands of the abdomen show great regularity (Fig. 4), but in a mutant race called "abnormal abdomen" (Fig. 5) the bands may be irregularly broken up, or even absent. In cultures with abundance of fresh food and moisture, all the individuals have very irregular bands, but as the culture gets old, and the

food and moisture become less and less, the bands become more and more regular until at last the flies are indistinguishable from normal flies. If a cross is made between a female with abnormal bands and a wild male, the offspring that first hatch under favorable conditions are all very abnormal. Here abnormal completely dominates normal bands. But as the culture dries up, the hybrid offspring become more and more normal, until finally they are all normal. At this time it might be said that normal dominates abnormal. Both statements are correct, if we add that in one environment abnormal banding dominates,

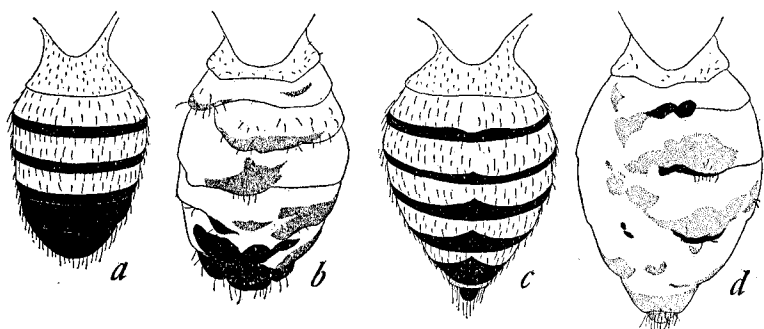


FIG. 5.—Normal and abnormal abdomen of *D. melanogaster*.

in another environment normal banding dominates. The genetic behavior of the pairs of genes is the same here as in all other cases of Mendelian behavior, but this is revealed only when the environment is one in which the abnormal gene produces one effect, the normal a different one. That the gene is not itself affected by the environment can be shown very simply. If a female from the abnormal stock be picked out, at a time when the stock has only normal bands, and crossed to a wild male, the offspring will all be as "abnormal" as when the mother herself is abnormal, provided the food and moisture conditions are of the right kind. The late hatched normal flies of abnormal stock may be bred from for several

generations, but as soon as a generation hatches under favorable conditions they are as abnormal as though all their ancestors had been of this sort. Thus it is evident that no fundamental importance is to be attached to dominance of characters. On the other hand, it is equally obvious that it would be entirely unwarranted to suppose that incompleteness of dominance is due to failure of segregation of the genes that stand for the characters.

While the problem of segregation can be studied to greatest advantage where the characters of a pair are sharply separated, yet even where the pair does not possess this advantage, the cleanness of the segregation process can be just as definitely, though more laboriously, demonstrated.

In cases where there is an overlap between the heterozygous type and one of the parental types it may, simply as a matter of convenience, be advantageous to call that character that gives the more continuous F_2 group the dominant, thus leaving the smaller more sharply defined group as the recessive. For example, the F_2 group from black by wild-type *Drosophila* may be represented by such a scheme (Fig. 6) as the following:

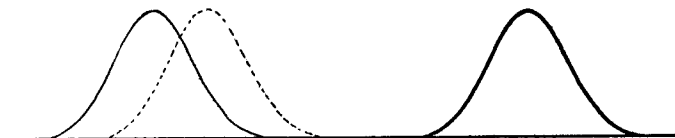


FIG. 6.—Relation of black body color to wild type as shown by the classes of F_2 flies. The heavy outline includes the mutant class, the lighter line the wild type, and the dotted line the heterozygous class.

Here the heterozygous flies are typically intermediates, but their variability overlaps that of the wild type to such an extent that separation of the intermediate from the wild type is practically impossible. On the other hand, there is no difficulty in making a complete separation between the heterozygous class and the homozygous black.

Black is accordingly treated as a recessive in nearly all experiments.

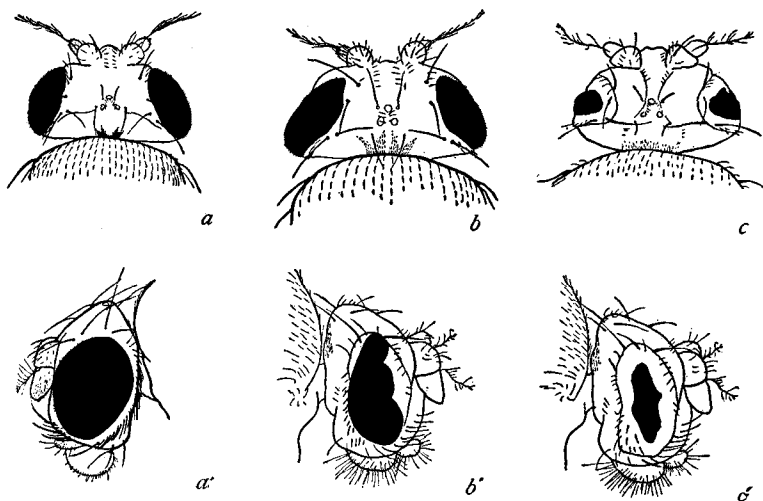


FIG. 7.—Normal eye, *a*, *a'*, heterozygous eye *b*, *b'*, and bar eye *c*, *c'*, of the vinegar fly.

A mutant eye shape of *Drosophila*, called “bar” (Fig. 7, *c*) has an intermediate hybrid type (Fig. 7, *b*). The F_2 group may be represented (Fig. 8) in the following scheme :



FIG. 8.—Relation of bar eye to normal eye, as shown by the F_2 classes.

In this case the hybrid, intermediate type, overlaps the bar type, so that in F_2 these two latter types give a nearly continuous class. At the other end of the F_2 series, the round eyed normal (or wild) type can be distinguished without difficulty from either of the other classes. Bar is therefore normally treated as a dominant.

The case of *Mirabilis*, or of the Andalusian fowl, might be represented (Fig. 9) in the following scheme:



FIG. 9.—Relation of Andalusian to splashed white and to black as shown by classes of F_2 birds.

Here all three types are fully separable, in which case either homozygote might be considered the dominant.

Finally, to return to the case of the tall and short peas, the following scheme (Fig. 10) represents the F_2

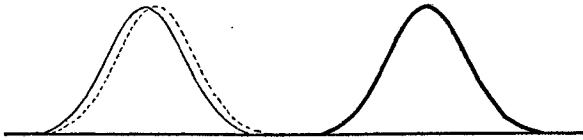


FIG. 10.—Relation of tall to short peas as shown by F_2 classes.

group: Here the tall and the heterozygous group are alike, and inseparable by ordinary inspection, even at the extreme end of their variation curves, and short is “completely” recessive.

In cases in which the environment enters more obviously into the result (as in “abnormal abdomen,” Fig. 5), the following scheme (Fig. 11) represents the relation:

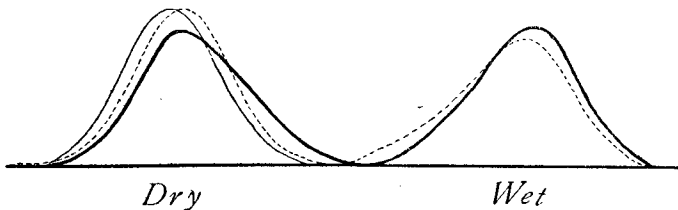


FIG. 11.—Relation of normal to abnormal abdomen as shown by classes of F_2 flies. “Dry” signifies conditions that make for normal; wet for abnormal.

In this case both the heterozygous and the parental “abnormal” type may show “normal” abdomen like the

wild type. The abnormal type is treated as the dominant although only when the conditions are favorable to its appearance is the hereditary phenomenon seen. In another case (duplicate legs) only the homozygous form may show the duplications (in a special environment). The following scheme (Fig. 12) represents this relation, reduplication of legs being treated as a recessive:



FIG. 12.—Relation of normal to duplicate legs.

There are still other relations that affect the dominance of characters. For example, there may be internal factors, which when present, determine that a character shall be dominant over its allelomorph, or recessive to it. In this connection might be mentioned what has been called "reversal of dominance." An example from Davenport will illustrate what is meant. In a certain strain of fowls there is a tendency for the toes to be united by a web at the base. Crossed to birds with normal feet, no birds with united toes (syndactyls) appeared in F_1 . The F_1 birds inbred gave in F_2 only about 10 per cent. of syndactyl birds. It would appear that the latter character is recessive, and that the recessive type overlaps largely the dominant heterozygous type.

Davenport interpreted, however, the syndactyl as the dominant type, because "two syndactyls may give normals, but no *true* normals give syndactyls." In other words, he defines the dominant type as the one that can carry the other type, because he says dominance is due to presence of factors, recessiveness to absence. "Now dominance may fail to develop but recessiveness never can do so." For this reason two syndactyls may give

normals, because a dominant character may fail to develop, even though its factors be present. Since normal feet never give syndactyls, the normal type must be recessive. But Davenport's definition of a recessive type as one that never shows in the heterozygous condition is in my opinion based on an arbitrary distinction of what is the *cause* of dominance and recessiveness. The evidence may, I think, be better interpreted as indicated in the same diagram as that for abnormal abdomen (Fig. 11) in that part marked "dry," in which the syndactyl condition would be represented as recessive (heavy line). In the hybrid the character is usually seen only in a few individuals, *i.e.*, it is intermediate, overlapping both parent types. While this case shows that it is often only a convention as to which type is called the dominant and which the recessive, I can see no special reason why in these cases of syndactylism the usual convention may not be followed which recognizes the small F_2 class as the recessive.

Mendelism rests on the theory of a clean separation of the members of each pair of factors (genes). In every heterozygote the factor for the dominant and that for the recessive are supposed to come into relation to each other and then to separate at the ripening of the germ-cells. If we think of the two genes coming together and afterwards separating, it would seem that a favorable situation might exist for the two to become mixed, and one "contaminate" the other. If any extensive process of this kind occurred the Mendelian phenomena would be so irregular and erratic that they would have little interest. But even those who are inclined to appeal to contamination as an exceptional phenomenon, grant that clean separation of the genes is the rule. The best critical evidence against contamination is in cases in which for many successive generations breeding has taken place from heterozygous forms only (which creates a favorable situation for contamination to take place were it possible). No influence of contamination has been found in such cases.

Marshall and Muller kept flies heterozygous for three recessive mutant factor for about seventy-five generations, and at the end of that time found that these factors had not been weakened in any way as a result of juxtaposition

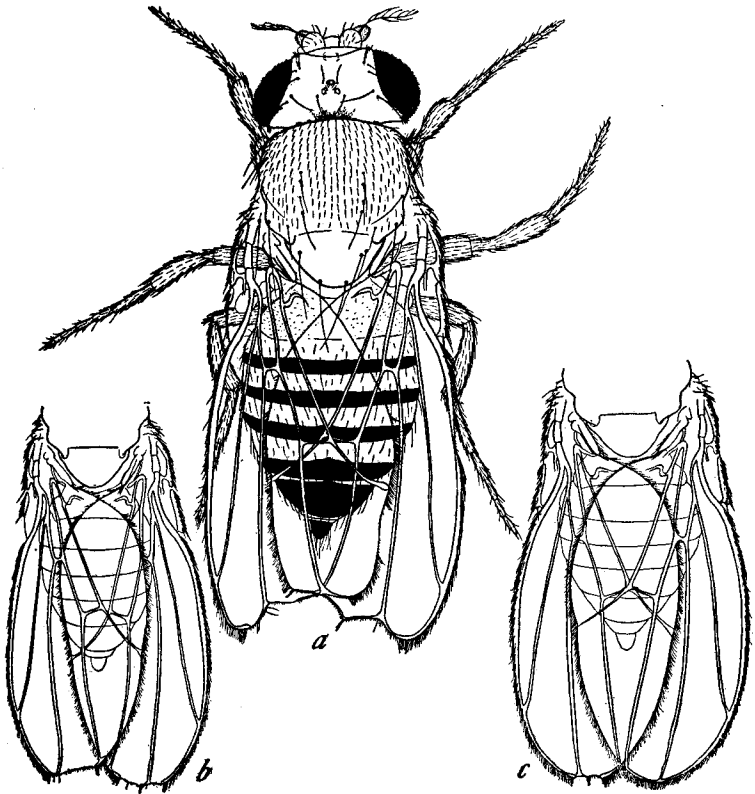


FIG. 13.—Notch wings in the vinegar fly, extreme condition, *a*; average condition, *b*; nearly normal condition, *c*.

with their normal dominant allelomorphs. I have kept a stock of notch-winged flies under selection for twenty-five generations. Notch (Fig. 13) is a character varying in the direction of normal wings (Fig. 13, *c*); in every generation of notch, many notch flies have normal wings. The character is dominant, and exists only in heterozy-

gous condition, since a fly homozygous for notch dies. The race is therefore necessarily maintained in a heterozygous state. In each generation females that were genetically notch, but had normal wings, were selected and bred to normal males. The selection was away from notch (*i.e.*, toward normal). After a time more than half of the notch flies had normal wings. The effect produced proved to be due not to a change in the notch gene through contamination, but to modifying genes; for at the end of the selection the original notch could be recovered at any time by removing the influence of the modifying factor.

It has been sometimes stated, usually by the opponents of Mendel's theory, or by advocates of doctrines of evolution that appeared to be compromised by the Mendelian conception of "unit factors," that Mendelism deals only with such superficial characters as the color of flowers or the hair color of mammals. This statement contains an element of truth in so far as it covers most of the kinds of characters that students of heredity find most convenient to study; but it contains an entirely false inference as to the limitations of Mendelism. The issue involved is this: changes in superficial characters are not so likely to affect the ability of the organism to survive as are changes in essential organs; hence they are the best kind of hereditary characters for study. But there is no evidence that such superficial characters are inherited in a different way from "fundamental" characters, and there is evidence to the contrary. A common class of characters showing perfect Mendelian behavior are so-called lethals that destroy the individual when in homozygous condition. There can be no question as to the fundamental importance of such factors. Between these extreme cases and the superficial shades of eye color, for example, all possible gradations of structure, physiological and pathological, are known. The only possible question that might be seriously raised is whether these characters are all losses or deficiencies, while progres-

sive advances may belong to a different category. This may be a serious question for the evolutionist, but has nothing to do with the problem that concerns us here.

In recent years an entirely unexpected and important discovery in regard to segregating pairs of genes (allelomorphs) has been made. In an ever-increasing number of cases it has been found that there may be more than two distinct characters that act as allelomorphs to each other. For example, in mice, yellow, sable, black, white-bellied gray, and gray-bellied gray (wild type) are allelomorphs, *i.e.*, any two may be present (as a pair) in an individual, but never more than two. In *Drosophila* the eye colors white, eosin, cherry, blood, tinged, buff, milk, ivory, coral and the normal allelomorph form a series of multiple allelomorphs. In the grouse locust, *Paratettix*, there are nine types that may be allelomorphic, all of which exist in the wild state (Nabours). In *Drosophila*, again, there are as many as twelve other series of allelomorphs known at present; in rats there is a small allelomorphic series, also two in guinea pigs and two in rabbits. In plants there are a few cases known, especially in corn. In all these series it is the same organ that is mainly affected by the different allelomorphs, which seems "natural," but was not necessarily to have been expected. The chief interest of these series is that they appear to demonstrate that the normal (wild type) allelomorph, and its mutant mates need not be due to presence and absence, but rather represent modifications of the same unit in the hereditary material; for, taken literally, only one absence is thinkable, and yet in *Drosophila* there are eight such "absences" in one series.

As has been stated, Mendel did not make it clear that there exists in the normal animal or plant the same duality that comes to light when a hybrid is produced; nevertheless this condition is implied, at least, in his paper, and has been taken for granted in practically all of the modern work on heredity. The demonstration that such

is the case is, however, not a simple matter. It could not have been made by Mendel or in the earlier days after the rediscovery of Mendelism (1900). An attempt to furnish this demonstration is given in Chapter XX. Assuming the demonstration to be satisfactory, we reach the highly important conclusion that segregation is not something peculiar to hybrids, but something most readily demonstrated by means of hybrids, and that in all probability the germ-plasm is at first made up of pairs of elements, but at the ripening of the germ-cells these elements (genes) separate, one member of each pair going to one daughter cell, the other member to the other cell. The mechanism by means of which such a process might take place had been known for several years before its relation to Mendel's principles of segregation was realized. This mechanism is to be found in the conjugation and reduction processes that take place in the maturation of egg- and sperm-cell. An account of this process is given in the next chapter.