CHAPTER IV

MENDEL'S SECOND LAW—THE INDEPENDENT ASSORTMENT OF THE GENES

MENDEL proved that when races differ from each *other in two pairs of characters, each pair considered* by itself alone gives the 3:1 ratio, and the inheritance of one pair is independent of that of the other. If a tall race of peas with colored flowers is crossed to a short race with white flowers the offspring show the two dominant characters, *i.e.,* they are tall and have colored flowers. If these are inbred they produce tall and short offspring (F_2) in a ratio of 3:1, and these same individuals, if reclassified for pigment, are colored or white in the ratio of 3:1. For example, the ideal for 12 tall peas would be 9 colored and 3 white; and for 4 short peas there would be 3 colored and 1 white. Expressed in a diagram we have:

12 tall	4 short
9 colored : 3 white	3 colored : 1 white

The preceding way of stating the results deals *directly with the facts. The explanation of these results,* based on the segregation of the members of the two independent pairs of factors, is as follows: If we call the gene for tallness by the same name as the character itself, viz., tall, and the gene for shortness by the name of this character, viz., short, and similarly for the other pair of characters, viz., color *versus* white, then when crossed the hybrid has two pairs of allelomorphs,

$$\frac{\text{tall}}{\text{short}} \quad \frac{\text{color}}{\text{white}}$$

If at the maturation (whether of egg or sperm) tall and color go to one cell, then short and white go to the other cell; but if one of the pairs is turned, so to speak, the other way, thus

$$\frac{\text{short}}{\text{tall}} \quad \frac{\text{color}}{\text{white}}$$

so that short and color go to one cell, then tall and white go to the other. Four classes of germ-cells are expected in F_1, namely,

tall color, tall white, short color, short white.

Chance meeting of any one of these four kinds of pollen grains with any one of the same four kinds of eggs will give the sixteen recombination classes shown in the following table:

Eggs	tall color	tall white	short color	short white
Sperm tall color	tall color tall color	tall white tall color	short color tall color	short white tall color
tall white	tall color tall white	tall white tall white	short color tall white	short white tall white
short color	tall color short color	tall white short color	short color short color	short white short color
short white	tall color short white	tall white short white	short color short white	short white short white

The four kinds of eggs are written above and the four kinds of sperm are written to the left. There are 16 possible combinations. Since tall and color are dominant the recombinations give: 9 tall color, 3 tall white, 3 short color, 1 short white. In this table the genes have the same name as the character for which they stand, and these names are written out in full, but it is generally more convenient to use symbols for the genes in order to save space and time. It is customary to represent the members of a pair by the same letter, as Mendel himself did, and to represent the dominant member by the capital letter, the recessive member by a small letter. Thus if $A=$ tall and $a=$ short; and $B=$ color and $b=$ white, the recombination square becomes:

Eggs	*AB*	*Ab*	*aB*	*ab*
Sperm *AB*	*AB* *AB*	*Ab* *AB*	*aB* *AB*	*ab* *AB*
Ab	*AB* *Ab*	*Ab* *Ab*	*aB* *Ab*	*ab* *Ab*
aB	*AB* *aB*	*Ab* *aB*	*aB* *aB*	*ab* *aB*
ab	*AB* *ab*	*Ab* *ab*	*aB* *ab*	*ab* *ab*

Instead of using arbitrary letters for the characters as above, it has been found more convenient to use a mnemonic system in which the first letter of one of the members of each pair becomes the symbol. The two members of such a pair are then distinguished from each other by using a capital letter for one and a corresponding small letter for the other. For example, we might let $t=$ short, $T=$ tall, $c=$ white, $C=$ color. In this case the capital letter represents the dominant character, and the small letter represents the *loss* of that character, as seen in the recessive type. But besides prejudging the question as to what kind of a change took place in the germ-plasm to change a dominant to a recessive by assuming that it is due to a loss, this system is unsatisfactory in cases where many modifications of the same organ exist (such as the 40 eye colors of the vinegar fly), and where new ones are being found. For example, if the symbol R (red) is used for the dominant wild eye color, small r would stand for any one of 40 mutant eye colors, and when several of these occur in the same experiment there would be no way of telling for which one the small letter stood. Some other system becomes imperative in such cases,[1] and the most consistent seems to be to use a small letter for the mutant gene in question (or when unknown for the recessive gene), and the corresponding capital letter for its allelomorph (usually the wild type). Thus, $s =$ short, $S =$ tall, $w =$ white, $W =$ color. The recombination square for the same characters treated above is then:

Eggs	*SW*	*Sw*	*sW*	*sw*
Sperm *SW*	*SW* *SW*	*Sw* *SW*	*sW* *SW*	*sw* *SW*
Sw	*SW* *Sw*	*Sw* *Sw*	*sW* *Sw*	*sw* *Sw*
sW	*SW* *sW*	*Sw* *sW*	*sW* *sW*	*sw* *sW*
sw	*SW* *sw*	*Sw* *sw*	*sW* *sw*	*sw* *sw*

Since the large letters simply represent the wild type of each particular character it may sometimes simplify the formulæ to omit them, or since this may lead to confusion in making up pairs of genes, some convention for wild type, such as N (normal), T (type), or the + sign, or a dash, or a dot may be used. Such short-hand methods are followed by many workers, but it is not necessary to advance the claims of any one of them here. If, for

[1] An even more serious objection to the system is explained in "The Mechanism of Mendelian Heredity," pages 233–235.

example, the normal, meaning the wild type in each factor pair, is represented by N, the foregoing table becomes:

Eggs	NN	Nw	sN	sw
Sperm NN	NN NN	Nw NN	sN NN	sw NN
Nw	NN Nw	Nw Nw	sN Nw	sw Nw
sN	NN sN	Nw sN	sN sN	sw sN
sw	NN sw	Nw sw	sN sw	sw sw

In the preceding illustration one grand-parent (P_1) was assumed to have had both dominant characters (tall and colored), while the other grand-parent had both recessives (short and white). Obviously the grand-parents might have happened to be made up differently—one might have been tall and white, the other short and colored. The F_1 plants (Ss, Ww) would have been the same in either case, and so would the F_2 results. In other words, for the principle of assortment it should make no difference from which parent the characters have come. This is illustrated in the following cross (Fig. 29), in which a wingless vestigial (recessive) *Drosophila* male having the wild-type color (dominant) is bred to long-winged (dominant) female with ebony (recessive) body color. The F_1 flies have long wings and wild type body color. Inbred, they give 9 long wild type color, 3 long ebony, 3 vestigial wild type color, and 1 vestigial ebony. In the diagram the gene for vestigial is represented by v, and its allelomorph for long wings by V; the gene for ebony by e, its allelomorph for wild type color by E. The germ-cells of the two P_1 flies are therefore vE and Ve. Each contains the wild-type allelomorph of the recessive mutant gene in the other parent. The

F_1 fly has the formula *vVeE*. Independent assortment of the two pairs of factors

$$\frac{v}{V}\ \frac{E}{e}$$

gives four kinds of germ-cells both in males and females, thus:

vE Ve VE ve

Any one of the four kinds of egg may be fertilized by any one of the same four kinds of sperm giving the same result as in the case of the peas, viz., four kinds of F_2 individuals in the ratios of 9:3:3:1. In practical tests the occurrence of or the possession of a race with both recessives in it is highly desirable for use in making a back-cross to P_1 (instead of inbreeding F_1's), because the numerical results obtained by back-crossing furnish, for a smaller number of individuals, more significant data. For example, if a tall pea with colored flowers is crossed to a short pea with white flowers, and the F_1 individuals (*SsWw*) are back-crossed to short white peas (*sw*), the expected ratio will be 1:1:1:1, because the four kinds of gametes in F_1 (*SW, Sw, sW, sw*) will then reveal themselves in the offspring, since the double recessive individual (*sw*) used for back-crossing (having only recessive gametes) will not "cover up" any of the factors coming from the F_1 hybrid. For instance. as shown in our type example, the F_1 gametes are *SW, Sw, sW, sw*. The only kind of gamete produced by the double recessive, short white, is *sw*. When this meets each of the above gametes only four kinds of combinations are possible, *viz., SWsw, Swsw, sWsw, swsw;* and these zygotes, containing only the same dominants as the F_1 gametes, will reveal what the kinds of gametes were. In practice an approximation to a 1:1:1:1 ratio is much more likely to be evident than an approximation to a 9:3:3:1 in which only one double recessive individual out

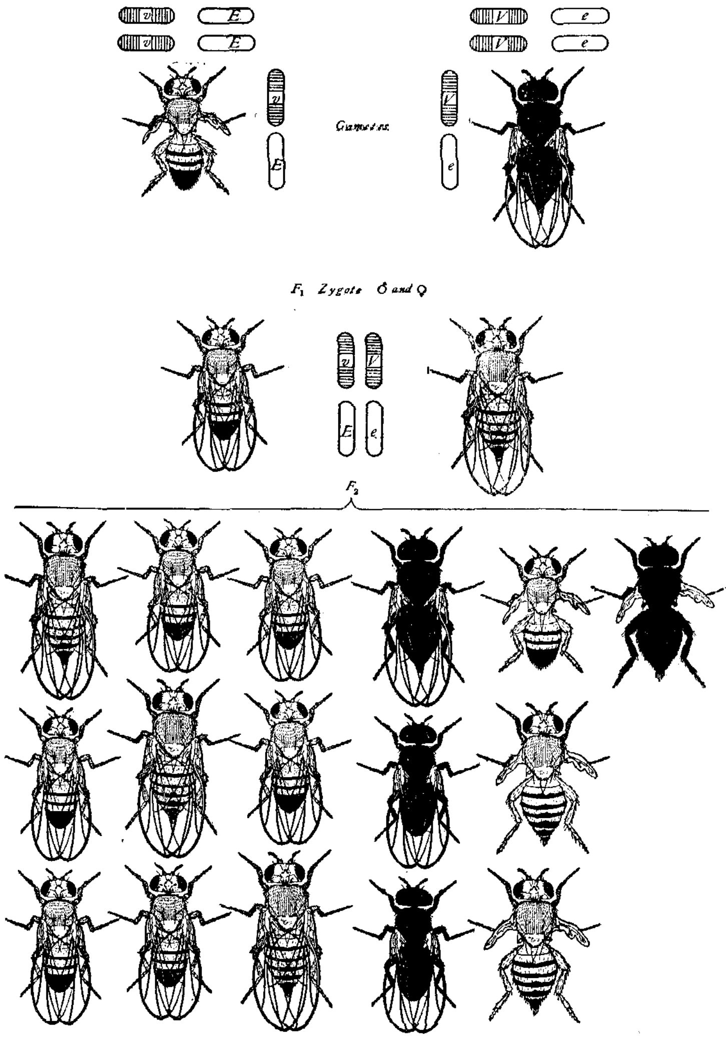

FIG. 29.—Cross between wingless and ebony vinegar fly.

of 16 individuals is expected. Whenever possible, therefore, the back-cross experiment is preferable to the inbred F_1 cross.

In animals and in plants with separate sexes it has been found that both F_1 males and F_1 females give when back-crossed, identically the same results, showing that free assortment takes place in both sexes.

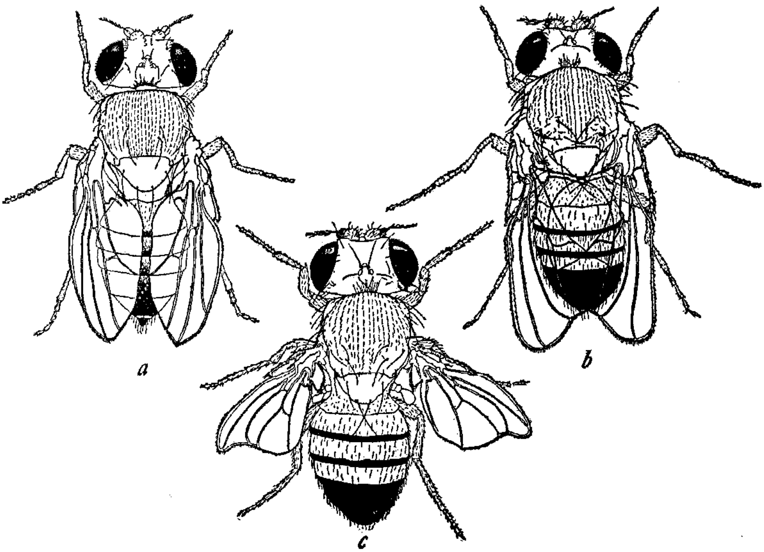

FIG. 30.—Miniature wing, *a;* and dumpy, *b;* and minature dumpy, *c.*

There is a corollary to the cross involving two pairs of factors that is interesting, because it gives an explanation of the phenomena of atavism. The wild vinegar fly, *Drosophila melanogaster* (Fig. 4), has long wings. It gave rise, through mutation, to a race with miniature (*mm*) wings (Fig. 30, *a*), and also to another race with short wings (Fig. 30, *b*) called "dumpy" (*dd*). If a female miniature (*mmDD*) is crossed to a dumpy male (*MMdd*), all the offspring (*MmDd*) have long wings like those of the wild fly. The miniature fly carries the dominant (*DD*) wild-type allelomorph of the dumpy gene, and the dumpy carries the dominant (*MM*) wild-type allelomorph of the miniature gene. Since the hybrid contains the two wild-type genes (*DM*) it "reverts" to the long-winged fly. The proof that two pairs of factors are involved is found by inbreeding an F_1 male and female, which give 9 long, 3 miniature, 3 dumpy, and 1 miniature dumpy (Fig. 30, *c*) fly.

There are certain modifications of the two-pair ratio that arise sometimes when different factors produce a like effect on the same organ. Such cases have sometimes been treated as special cases, and rather peculiar interpretations given to them on the basis that the situation is unusual. In reality they are only interesting cases of Mendelian behavior, the results obscured to some degree by superficial character relations. The absence of color, albinism, is, perhaps, the most familiar example of this sort. There are certain recessive factors that when homozygous interfere in some unknown way with the development of color. Albinos of the ordinary house mouse are white because they are homozygous for the albino factor, although they may be pure for all other factors that are essential for color. If a certain kind of albino mouse is crossed to a pure black mouse the offspring will be gray because black (*bb*), being recessive to its wild-type allelomorph (*BB*), brought in by the albino, disappears; and white (*ww*) being recessive to its wild type allelomorph for color (*WW*), brought in by the black, also disappears, so that the color of the resulting animal, gray, is due to the hybrid having recovered all the factors that give this color. The two factor-pairs involved are black (*b*) and its normal allelomorph ($B=$ gray), and white (*w*) and its normal allelomorph ($W=$color). The F_2 results, put into the recombination square, are as follows:

Sperm \ Eggs	*BW*	*Bw*	*bW*	*bw*
BW	*BW* *BW* gray	*Bw* *BW* gray	*bW* *BW* gray	*bw* *BW* gray
Bw	*BW* *Bw* gray	*Bw* *Bw* white	*bW* *Bw* gray	*bw* *Bw* white
bW	*BW* *bW* gray	*Bw* *bW* gray	*bW* *bW* black	*bw* *bW* black
bw	*BW* *bw* gray	*Bw* *bw* white	*bW* *bw* black	*bw* *bw* white

The resulting ratio is 9 grays, 3 blacks, and 4 whites. The last two terms of the 9 : 3 : 3 : 1 ratio are here united in one class (4 whites) because when homozygous for absence of color the individual is white, regardless as to whether the other color-producing factors make for the wild type of coloration or for some mutant color.

Another interesting two-pair case involves varieties of the combs of domesticated breeds of fowls. There is a dominant type called "Rose" (Fig. 31, *c*), which, bred to single (wild type, Fig. 31, *a*), gives Rose in F_1, and 3 Rose to 1 Single in F_2. Another dominant type called "Pea" (Fig. 31, *b*) likewise gives Pea in F_1 and 3 Peas to 1 Single Comb in F_2. But when Rose is bred to Pea there is not produced the wild type, as one might have anticipated, but a comb called "Walnut" (Fig. 31, *d*), that differs from both parental types. The character is due to the combined action of both dominants. If two F_1 birds with Walnut combs are bred to each other they give 9 Walnut, 3 Pea, 3 Rose, 1 Single comb. This ratio shows that two factors are involved, and that the Walnut comb appears in all birds carrying both the Rose and the Pea genes. The Single comb is the double recessive form.

If the single comb be supposed to be the wild type, then Pea and Rose represent dominant mutant types

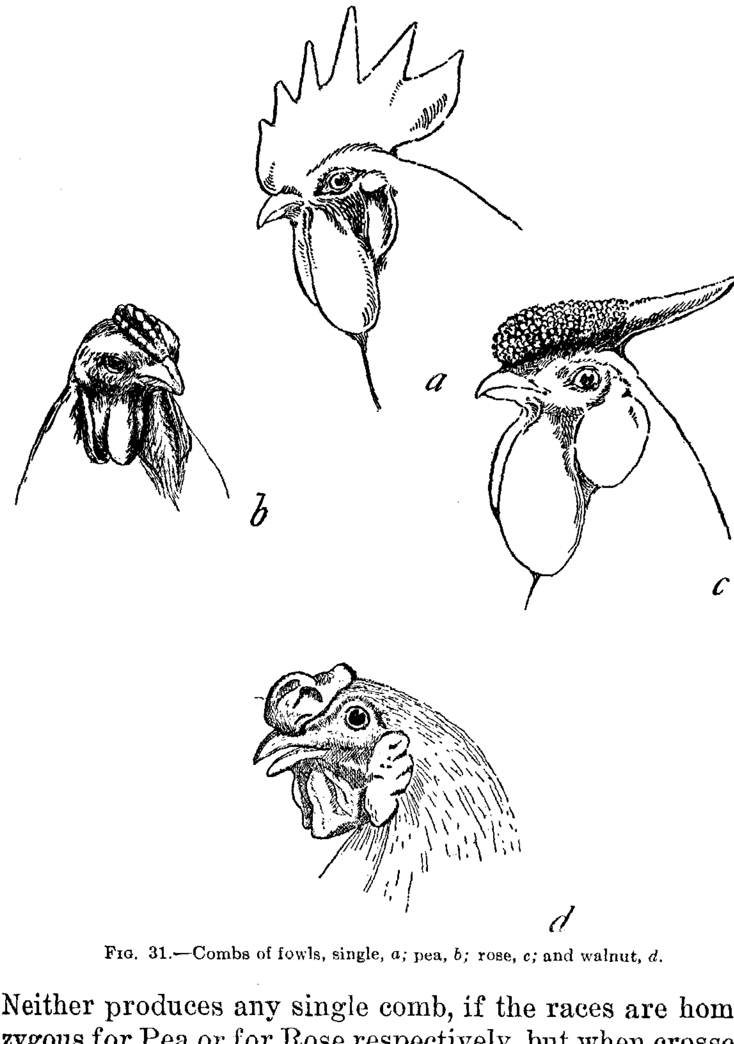

FIG. 31.—Combs of fowls, single, *a*; pea, *b*; rose, *c*; and walnut, *d*.

Neither produces any single comb, if the races are homozygous for Pea or for Rose respectively, but when crossed, the Pea comb brings in the normal recessive allelomorph of Rose, and the Rose comb the normal recessive allelomorph of Pea: but the result is not an atavistic normal comb, but a Walnut produced by the action of both dominants that are here the mutant characters.

An important class of factors that are known as diluters or intensifiers are often met with in genetic work. For instance, a black mouse pure for a certain "diluting" factor has a "blue" color (just as a black mouse pure for albino factors is white). Such a blue mouse crossed to black gives F_1 black mice, and in F_2 three blacks to one blue. A two-factor cross results when a blue mouse is bred to a "chocolate" (=black cinnamon) mouse. *The F_1 will be black, the F_2 will be 9 black, 3 blue,* 3 chocolate, 1 "silver-fawn" (dilute black cinnamon). In this case, the same factor that changes black to blue also changes chocolate to silver-fawn. If the diluter had been a specific one affecting black only, then F_2 from the above cross would have been 9 black, 3 blue, 4 chocolate. Such a case is found in the vinegar fly, in which the diluter affects only a recessive factor—eosin. This specific diluter for eosin is called "whiting." It gives the following results: A red-eyed female homozygous for whiting is indistinguishable from the ordinary wild type. If a female of this kind is crossed to an eosin male the offspring (F_1) are red eyed. If they are inbred they give 12 red-eyed flies, 3 eosin, 1 eosin-whiting which is colorless.

Another modification of the 9:3:3:1 ratio appears when the last three classes are superficially alike. For example, Bateson and Punnett crossed two white flowering varieties of sweet peas. The F_1 had purple flowers, which, inbred, gave 9 purple and 7 whites. Here there are two different recessive factors which in homozygous condition give white, *ww* and *aa;* each has a normal dominant allelomorph in the other white, *AA* and *WW*. The two white parents are then *wwAA* and *aaWW*. The F_1 individuals are *WwAa,* and the four gametes are *WA, Wa, wA, wa.* The table below gives the sixteen recombinations of these gametes:

Eggs	*WA*	*Wa*	*wA*	*wa*
Sperm *WA*	*WA* *WA* purple	*Wa* *WA* purple	*wA* *WA* purple	*wa* *WA* purple
Wa	*WA* *Wa* purple	*Wa* *Wa* white	*wA* *Wa* purple	*wa* *Wa* white
wA	*WA* *wA* purple	*Wa* *wA* purple	*wA* *wA* white	*wa* *wA* white
wa	*WA* *wa* purple	*Wa* *wa* white	*wA* *wa* white	*wa* *wa* white

Any individual that has both recessives *ww* or *aa* is white. There are 7 such classes to 9 that carry both *A* and *W.* Lastly, a 15:1 modification of the 9:3:3:1 ratio is obtained when an individual homozygous for both pairs of recessive genes gives a different result from any other combination. Thus, Shull found when *Bursa pastoris,* with triangular capsules, is crossed to one with round capsules, the latter appears in F_2 only once in 16 times.

Assortment of Three Factors

When three independent factor-pairs are present the numerical expectation can be directly derived from the 9:3:3:1 ratio in the same way that the latter was derived from the 3:1 ratio. Thus:

3		1		One pair of factors.
9	3	3	1	Two pairs of factors.
27:9	9:3	9:3	3:1	Three pairs of factors.

Each F_2 class of the two-factor case (9:3:3:1) will contain a three-to-one ratio for the third factor-pair. Thus, in the 9 class there will be 3 dominants of the third factor to one recessive (27:9). So for each 3 class: each contains the third factor in the ratio of 3:1. So also for the 1 class. The total result therefore is:

$$27:9:9:9:3:3:3:1$$

In actual practice the three-factor cases are almost never used. Other methods are employed to detect the factors present, so that these three-factor ratios have a theoretical rather than a practical value. In cases where multiple factors are suspected, some of them may be only modifiers of some one of the other more conspicuous characters and in such cases special methods of procedure will recommend themselves.