CHAPTER II

TYPES OF MENDELIAN HEREDITY

Experience has shown that Mendelian inheritance applies to all sorts of characters, structural, physiological, pathological, and psychological; to characters peculiar to the egg, to the young, and even to old age; to length of life; to fundamental taxonomic characters as well as to "superficial" characters; and to characters intimately concerned in maintaining the life of the individual, as well as to characters which apparently do not influence survival. Some of these different types and their mode of inheritance will be briefly described, but since the general principles involved are more important than the kind of character that is affected, the results will be treated under general headings.

Dominance and Recessiveness

The four-o'clock (Mirabilis jalapa) has a white and a red-flowered variety. If these are crossed the hybrid is pink in color. The pink hybrid inbred (self-fertilized in this case) gives in the next generation (F_2) one red, to two pink, to one white (Fig. 14). Owing to the intermediate color of the hybrid (or heterozygote) it is impossible to say that either color dominates the other. The factor for red and the factor for white both affect the plant in which they occur. In this and in similar cases the F_2 ratio of 1 : 2 : 1 is obtained, because it is possible to distinguish the pure red and the pure white from the heterozygous plants.

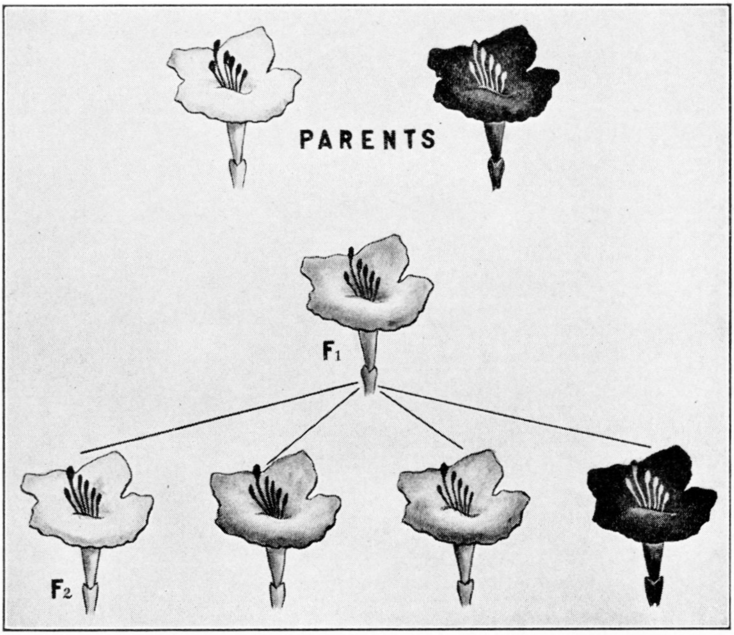

FIG. 14.—Diagram to illustrate the cross between a red and a white flowered Mirabilis jalapa (4 o'clock), which produces a pink, intermediate heterozygote.

The Andalusian fowl is a similar case. When certain races of black are bred to certain races or kinds of "white" the hybrid is slate "blue" in color. These blue birds, called Andalusians, when inbred, give one black to two blue to one white. Blue is the heterozygous condition; it is not possible to produce a pure breeding race of Andalusians, for the combination that produced an Andalusian falls apart in the germ cells of the Andalusian birds. The bird is blue because the pigment is not spread evenly over the feather but is restricted to small but black specks.

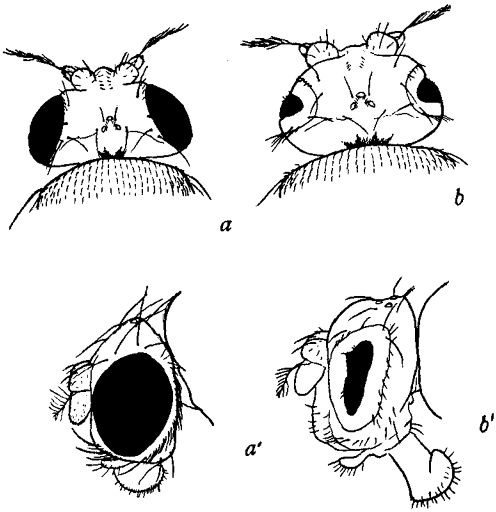

FIG. 15.—Normal (*a*, *a′*) and bar eye (*b*, *b′*) of Drosophila; shown in side view, and as seen from above.

The Andalusian blue is a mosaic of black and white, and not at all a dilute black.

A good example of an intermediate hybrid is found when the mutant fly with bar eye (Fig. 15) is bred to a wild fly. The daughters have bar eyes that are not as narrow as those of the pure bar stock. The range of variation is great, however, for some of the hybrids have eyes that are nearly as round as the normal, and in others the eye is nearly as narrow a bar as that of pure stock. In the male, which has one factor for bar eye, the eye is as narrow as in the pure (*i.e.*, homozygous) female with two factors. The intermediate condition in the female which is hybrid (heterozygous) for this factor is hence not explained by the lesser effect of the single factor, but is probably due to the competing influence of the other allelomorph. Of course it might be contended that since in the male there is a different chromosome complex (XABCD YABCD) from that in the female (XABCD-XABCD) it is this difference in other factors that causes the heterozygous female to have a wider eye than the male; but this argument is rendered improbable here, when we recall that in only one out of many cases of sex linked inheritance, in which the heterozygous female is intermediate, is the male different from the homozygous female.

In other cases the influence of one of the parents of the cross may be so slight as to escape detection on ordinary observation, and may require special measurements for demonstration. When flies with miniature wings (Fig. 16) are mated to wild flies, the daughters have long wings, which Lutz has shown to be a little shorter in proportion to the length of the legs than are the wings of wild females; but the difference is so slight that it could not have been detected without biometrical methods.

Finally, we must consider the class of cases in which complete dominance has been described. All the cases given by Mendel in peas were supposed to fall under this heading: yellow dominates green, round dominates wrinkled, etc.

Whether a character is completely dominant or not appears to be a matter of no special significance. In fact the failure of many characters to show complete dominance raises a doubt as to whether there is such

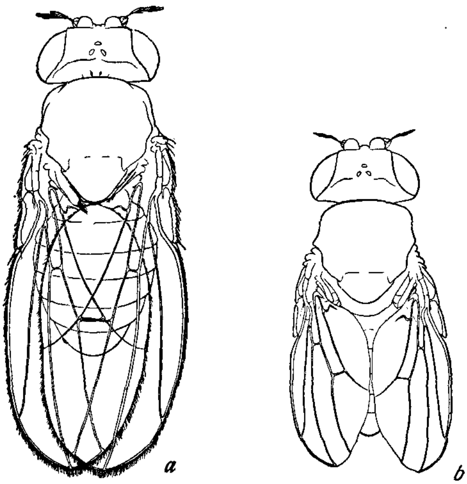

FIG. 16.—*a*, Long wing (wild type) of Drosophila; *b*, miniature wing. (*a* and *b* are not drawn to scale.)

a condition as complete dominance. Some cases approach so nearly to that condition that special tests may be required to show that the hybrid is affected by the recessive factor. For instance, in flies the factor for white eyes seems to produce no effect when white is bred to red. The F_1 reds are indistinguishable from pure reds. But by weakening the red by adding recessive factors other than white, the influence of white can be demonstrated, as Morgan and Bridges have shown. Therefore although the effect of the white factor can not be detected in the single combination with red, it is reasonable to suppose that some effect is really present. Similarly, conditions were found in which the effect of heterozygosis for eosin, vermilion, or pink could be demonstrated. While the question is one of only subsidiary importance, yet in the separation of classes it is often useful to be able to distinguish the pure from the hybrid form; but whether this can or can not be done in any given case does not affect the fundamental principle of segregation which is the essential feature of Mendel's discovery.

Manifold Effects of Single Factors

It is customary to speak of a particular character as the product of a single factor, as though the factor affected only a particular color, or structure, or part of the organism. But everyone familiar at first hand with Mendelian inheritance knows that the so-called unit character is only the most obvious or most significant product of the postulated factor. Most students of Mendelian heredity will freely grant that the effects of a factor may be far-reaching and manifold. A few examples may make this plain.

In Drosophila there is a mutant stock called "club," in which the wing pads fail to unfold (Fig. 17) in about 20 per cent. of the flies. In the majority of club flies the wings expand fully, and are like those of the wild fly. Owing to this fact, that not all the flies even in a pure stock of club show this character, it was difficult to study the inheritance of the supposed factor that sometimes inhibits the unfolding of the wing pads. Nevertheless, it was possible even with this handicap to show that the character depended on a sex linked recessive factor. Later

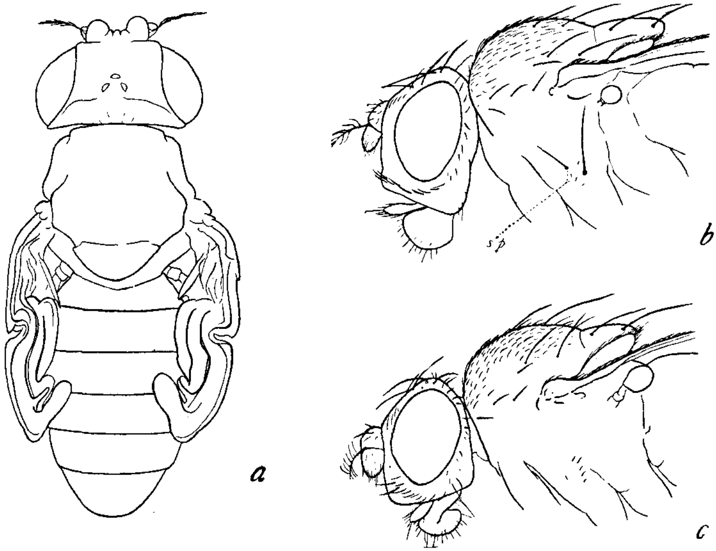

FIG. 17.—Club wing (to left). The absence of the spines on the side of the thorax in "club" is shown in *c*, and the normal condition is shown in *b*.

the discovery was made that a particular pair of spines always present on the side of the thorax of the wild flies, is absent from the club flies, irrespective of whether the wings do or do not unfold (Fig. 17, *c*). This constant feature of the mutant made its study quite simple. Another pair of spines, those upon the rear margin of the scutellum, point constantly in an abnormal direction in club stock. The head of club flies is often flattened, the eyes are smaller, and the thorax and abdomen are somewhat distorted. Here we have an example of a single germinal difference, the factor for club, producing several distinct effects,

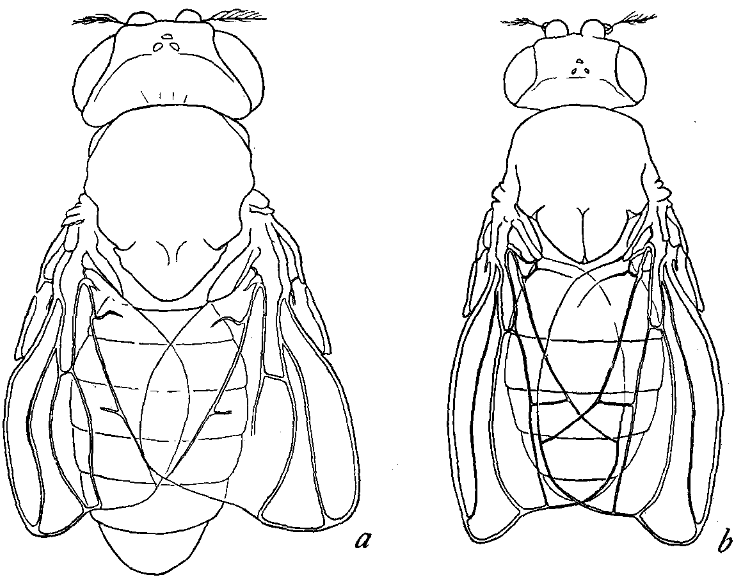

FIG. 18.—Rudimentary wing (to left), and truncate wing (to right).

some of which are constant features of the stock, while others are occasional or variable.

Another and similar example is found in the rudimentary winged flies (Fig. 18, *a*). The wing is usually shorter than the abdomen, but may be longer and even approach the normal wing in length and shape. The last pair of legs are often thicker and shorter. If many larvæ are present, or the food conditions poor, the larvæ of rudimentary flies can not stand the competition and die off, and in consequence the rudimentary class is smaller than expected. The males are fertile, but the females are almost entirely sterile, although rarely one of them may lay a few eggs and some of these hatch. The infertility is probably due to absence or rareness of mature eggs in the ovaries. There are also other effects than these four mentioned, all of which are produced by the same factor, and, no doubt, were our knowledge complete, we should find in all mutants many differences in addition to the ones picked out for study and called "unit characters." DeVries' definition of mutation entirely covers this relation; in fact, it even goes further and implies that a single difference may affect the entire organization. Perhaps this does occur, but practically the number of differences that can be *observed* between a wild and a mutant stock derived from it, is limited. The attack that is sometimes made on the unit character hypothesis fails in its intention the moment it is understood that a single factor (difference) has generally not one but many effects. Most workers in Mendelian heredity are fully conversant with these facts. This attack on the unit character conception is usually made by those not familiar with the actual situation and who take the expression unit character too literally. It may be conceded that the expression has at times been abused even by some of Mendel's followers.

Similar Effects Produced by Different Factors

There are many cases in which characters that are superficially alike are the product of different factors. White color that characterizes so many domesticated races of plants and animals is a case in point. There are two pure breeding races of white flowered sweet peas. When crossed, they produce colored flowers. When the F_1 offspring are inbred the F_2 generation consists of 9 reds to 7 whites. This 9:7 ratio is a special case of the 9:3:3:1, in which the last three classes are superficially alike. The explanation here is that there are two kinds of recessive whites that have originated independently. On the chromosome hypothesis one white is due to mutation in one chromosome and the other white to mutation in another chromosome. When the races are crossed, each race supplies that chromosome which contains the normal factor of the white of the other race. In the F_2 generation any plant that contains at least one of the normal chromosomes of both pairs will not be white. There will be nine such cases. Any plant that contains both of the white-producing chromosomes of either pair will be white. There will be seven such cases.

There are also two pure races of white fowls that, when crossed, give colored birds. Each white behaves as a recessive to color. For instance, the white silky crossed to a white dorking gives colored birds. These inbred give 9 colored to 7 white birds.

There is a third kind of white race of poultry, namely, white Leghorn, in which white is dominant. Crossed to colored birds the offspring are white (with often a few colored feathers, which indicates that dominance is not complete).

In the silkworm also a dominant white and a recessive white factor have been found. The genetic results are comparable in all respects to those in the fowl.

There are also cases of blacks or melanic types, that have different factorial bases. There are three black races of Drosophila—called sable, black, and ebony—that belong respectively to the first, second, and third groups. These are much alike, but close scrutiny reveals slight differences. Any two crossed together give gray F_1 flies.

There are three pink eye colors in Drosophila, one whose locus is in the third chromosome (*pink*), and two sex linked eye colors which are so similar that no certain difference between them can be observed.

Not only pigment but also structural characters may parallel each other in a remarkable manner. For example, in Drosophila the mutant stocks "bow" (sex linked) and "arc" (II chromosome) have wings that curve evenly downward over the abdomen. There are also two kinds of flies whose wings turn up sharply near the ends. These stocks are "jaunty" (second chromosome) and "jaunty I," which is sex linked. Two types, called "fringed" (II chromosome) and "spread" (III chromosome), are characterized by thin textured wings held out nearly at right angles to the body. In the case of rudimentary and truncate (Fig. 18) the wings are so similar that without breeding tests one of them might easily be taken for the other. Finally, "facet" and "rough" both have the ommatidia of the eye disarranged very much in the same way.

Modification of the Effects of Factors

I. By Environmental Influences

It is a commonplace that the environment is essential for the development of any trait, and that traits may differ according to the environment in which they develop. In most cases different genetic types produce different results in any ordinary environment. The environment, being common to the two, may therefore in such cases be ignored, or rather taken for granted. There are other cases, however, in which a particular genetic type appears different from another one only in a special environment. Where this environment is not the normal one, its discovery is an essential element of the experiment.

One of the best cases is that given by Baur. The red primrose (Primula sinensis rubra) reared at a temperature of 30°–35° C. (with moisture and shade) has pure white flowers, but the same plants reared at 15°–20° have red flowers. If the white-bearing plants are brought into a cooler place, the flowers that are already in bloom remain white, but those that develop later in the cooler temperature are red. There is another race of primula (Primula sinensis alba) that always has white flowers, even at 20°. Strictly speaking, we should say, not as we generally do for brevity's sake, that the difference between the two races is that one has white, the other red flowers, but we should say rather that P. rubra reacts at 20° by producing red, at 30° by forming white flowers; P. alba, on the other hand, reacts both at 20° and at 30° by producing white flowers. The constant difference between these races is not in their color, but in the possibility of producing specific colors at certain temperatures.

This is the point of view, of course, that must also be taken for cases in which differences exist in all the usual environments; for, here also, it is the different possibilities of reaction that are inherited. Brevity warrants us in speaking of particular characters as inherited, rather than the specific possibility of reaction that gave these characters; but no one need be misled by the shorter expression.

Two similar cases of the influence of the environment have been found in Drosophila. There is a mutant stock known as abnormal abdomen in which the normal black bands of the abdomen are broken and irregular or even entirely absent (Fig. 19). In flies reared on moist food the abnormality is extreme; but even in the same culture the flies that continue to hatch become less and less abnormal as the culture becomes more dry and the food scarce, until finally the flies that emerge later can not be told from normal flies. If the culture is kept well fed the change does not occur, but if the flies are reared on dry food they are normal from the beginning. The character is a sex linked dominant, as shown by the following crosses. When an abnormal male is bred to a normal (wild) female, the daughters are abnormal (if the

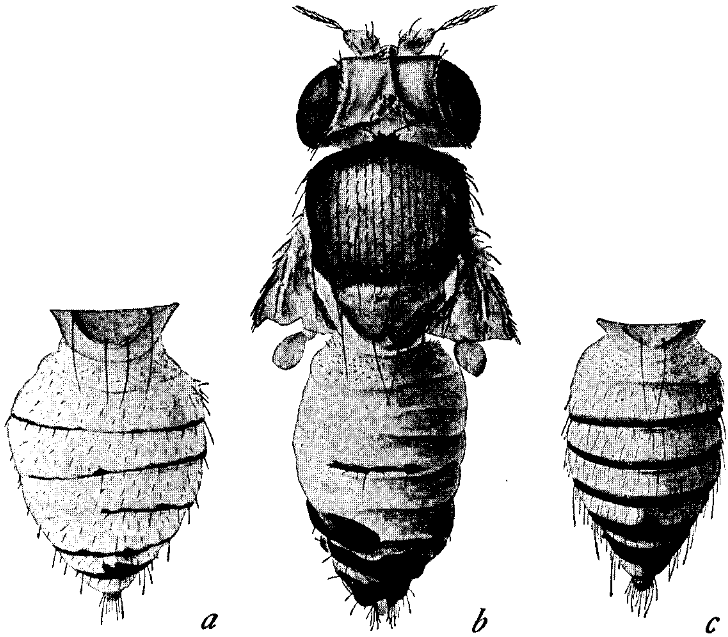

FIG. 19.—Mutant type called Abnormal Abdomen of Drosophila ampelophila (the wings have been cut off); *a* is female; *b*, male; *c*, female that approaches the normal type.

food is moist), but all the sons are normal. If the medium is dry, however, both the daughters and the sons alike are normal. But these normal F_1 daughters will produce the expected abnormal offspring if the conditions are suitable, and these offspring are just as abnormal as though the female had herself been abnormal. The reciprocal cross, viz., abnormal females by normal males, gives abnormal sons and daughters, if the food is suitable, but normal if the food is dry, etc. In both cases the F_2 gives the expectation for a sex-linked dominant factor if the medium is suited to bring out the abnormal character, and the result is entirely obscured if the food is dry. Here, at will, we can demonstrate a regular Mendelian ratio by control of the environment, and conversely, we can conceal completely what is taking place by substituting another environment. That the same genetic process is going on in both cases can be demonstrated by suitable tests.

A case similar in principle occurs in a mutant stock of Drosophila that produces supernumerary legs. This stock was observed in winter to produce a considerable percentage of flies with supernumerary legs, but few or none in summer, especially in warm weather. Miss Hoge, who has studied this stock, finds that when the flies are kept in an ice chest at a temperature about 10° C. a high percentage of flies with supernumerary legs occurs. Sometimes several legs or parts of a leg are doubled, or the doubling may occur twice in the same leg. The general rule that Bateson pointed out for duplicated legs in other insects appears to hold here, viz., the adjacent parts are mirror images of each other.

In the cold the duplicate leg gives a regular Mendelian result; but at normal temperature the duplication is a rare event and its mode of inheritance obscured. In a hot climate there would be no evidence that such a factor was being regularly transmitted. But if the type moved into a cold region it would show duplication in many of the legs.

II. By Developmental Influences

"Age," too, is in a sense an environmental condition, which influences the development of characters. Thus a white flower may change to purple as the plant gets older, or the flaxen hair of a child may turn to brown when he becomes a man. But, as in the case of other "environmental" conditions, age may not have the same effect on individuals with different factors; in this way it comes about that animals or plants which differ by certain factors may show a difference in character only at certain ages, or may not show the same difference at all ages. In Drosophila, flies with the factor for pink eyes are easily distinguishable from those with the factor for purple eyes, when the flies are young, but as they grow older, the eyes of both races assume a dark purplish shade, and become practically indistinguishable from each other. Conversely, old flies with the factor for black are usually easy to separate from those having the normal "gray" factor, but the newly hatched flies, in which the black pigment is not yet fully developed, are separated with greater difficulty.

These cases in which a factor-difference has a visible effect only at a certain age are in no fundamental respect different from cases like that of the Drosophila with reduplicated legs, where a factor difference has a visible effect only under special external circumstances.

A number of cases of Mendelian inheritance are known in which only the larvæ, and not the adults, are affected. Tower has described crosses in which the beetle Leptinotarsa signaticollis was crossed with L. undecimlineata (Fig. 20, *A*, *B*). In the first stage (*C*), the larvæ of these two beetles are exactly alike, but in the second stage, the larvæ of L. undecimlineata are white and the larvæ of L. signaticollis are yellow; and in the third stage the undecimlineata larvæ are still white without stripes, while the others have well-developed tergal stripes (*B*). When these species are crossed under certain external conditions the F_1 larvæ are yellow and, later, striped. The beetles that come from them are intermediate. Inbred, these beetles give three larvæ of the yellow type to one of the white type.

There is extensive evidence from cytology, experimental embryology, and regeneration, to show that all the different cells of the body receive the same hereditary factors. We must suppose, then, that the Mendelian factors are not sorted out, each to its appropriate cell, so that factors for color go only to pigment cells, factors for wing-shape to cells of the wings, etc., but that differentiation is due to the cumulative effect of regional differences in the egg and embryo, reacting with a complex factorial background that is the same in every cell. These regional peculiarities of different parts of the egg and embryo, may, like the age of the individual, also be considered as influences external to the hereditary factors which affect the development of characters. And not only

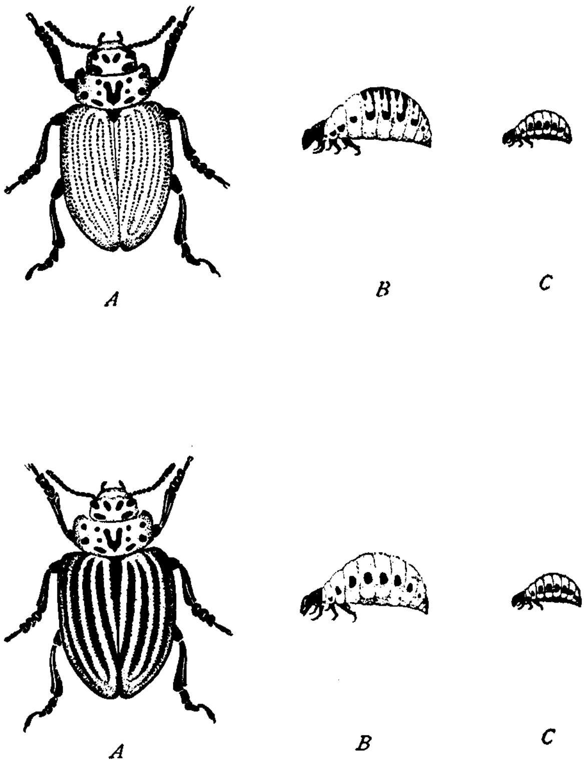

FIG. 20.—Leptinotarsa signaticollis (above), and L. undecimlineata (below), with their full grown (*B*) and second stage (*C*) larvæ to the right of each. (After Tower.)

do regional peculiarities influence characters, but special regions are usually required for a given factor difference to manifest itself, just as certain temperatures or ages may be necessary. Thus when we speak of factors for eyes or for legs, we really mean factor-differences which can produce effects only in the eye, the leg, or other regions of the body. In other cases the expression of a factor-difference may not be limited to one region but may produce a different effect in different regions; for example, a gray white-bellied mouse, which differs from the yellow mouse by only a single factor, is lighter than yellow on the under side, but darker on the upper side.

III. By the Influence of Other Factors

Analogous also is the fact that certain factor-differences produce a visible effect only when they are in company with a particular complex of other hereditary factors. Thus, a fly with the factors for vermilion eyes can not be distinguished from one with the factors for pink eyes if both contain, in addition, the factors for white eyes, for the factors for white allow no other color to develop. Again, it is obvious that without the factors necessary for the development of a given character, no factors merely determining special modifications of that character can have any effect. In other cases, the effect of a given factor may not be entirely suppressed, but greatly changed, if certain other factors in the hereditary complex are changed. Thus, in flies which already have the factor for vermilion eyes, the factor for purple eyes produces an eye still lighter than vermilion, but in flies containing the normal allelomorph of the factor for vermilion, the factor for purple produces an eye decidedly darker than normal. Such cases of interaction of factors, in which the effect of one factor is altered by the action of another factor, are very numerous.

IV. Conclusion

It would have been indeed strange if Mendelian factor-differences had not been found that require special conditions—environmental, developmental, or factorial—in order to produce a given effect, or any effect at all. For Mendelian factors may cause or influence all sorts of characters—that is, any or all kinds of developmental or physiological reactions; and many of these reactions are known to be affected by age, temperature, region of the body, and so forth. The facts given above are in no possible sense subversive to Mendelian principles. On the contrary they illustrate to great advantage the previously given interpretation of all hereditary characters—namely, that every character is the realized result of the reaction of hereditary factors with each other and with their environment. Failure to understand this viewpoint has led to some futile criticism by the opponents of the modern Mendelian interpretation in terms of unit factors. This criticism is as pointless as it would be to criticize the atomic theory on the ground that oxygen does not, under all conditions, and in all its compounds, give rise to substances with the same properties.

The validity of the unit factor conception rests upon the fact that whenever (as often happens) all other conditions, external and internal, that modify characters remain constant, clear-cut ratios are obtained which can be explained only as due to segregation, in definite ways, of particular hereditary factors that perpetuate themselves unchanged from generation to generation. The validity of the factorial hypothesis may also be proved under circumstances not so well controlled, however. In cases where, on the factorial hypothesis, a certain factor is expected to be present in an individual, then, even if the individual fails to develop the character commonly taken as indicative of the factor, the actual presence of the factor may be demonstrated by breeding tests. For if, in subsequent generations, circumstances—genetic or environmental—are provided, like those in which the character previously appeared, it will again show itself. Flies of the race with abnormal abdomen, if raised in a dry bottle, appear perfectly normal, but the presence within them of the factor for abnormal may be demonstrated by rearing their offspring in a wet bottle. Again, the factor for pink eyes may be carried by a race with white eyes, and although pink does not show in the white-eyed race, its presence there may then be demonstrated by crosses of these flies with flies that are not white. Cases like these could be multiplied over and over again.