CHAPTER V

EVOLUTION OF NEW RACES BY LOSS OR GAIN OF CHARACTERS

OUR knowledge of Mendelian phenomena is most complete in the case of color-inheritance. We find that the flower-colors of plants and the coat-colors of mammals are alike complex, and that what seem at first sight simple results may really depend on several independent factors acting conjointly. By analysis of such complex cases we are able to gain some idea of what the probable course of evolution has been in the production of the color varieties found among cultivated plants and domesticated animals.

Thus among rodents (mice, rabbits, guinea-pigs) the coat is grayish, consisting of black, brown, and yellow pigments mingled together on the same individual hair in a pattern of greater or less complexity.

The simplest variation from this ancestral type of coloration is albinism, a wholly unpigmented condition in which the eyes are pink. This is due to the loss of the capacity to form pigment. Albinism is recessive in crosses. We explain it by assuming that something necessary for color production is wanting in the albino, and call that something the color-factor C, without necessarily making any assumption as to its nature. Another common variation is the loss of the pattern-factor of the individual hair, the agouti or A factor. An account of the discovery of this factor was given in the last chapter. In consequence of the loss of this factor the pigments become mingled together without order, and the result is a uniform black, the denser pigment hiding the others.

A third variation is the loss of the capacity to form *black* pigment (factor B), only brown and yellow pigments being left. Thus arise brown and cinnamon varieties. Through these three independent loss-variations there arise eight different color-varieties as follows:

Gray (or agouti)	= C B Br A;	Cinnamon	= C Br A
Black	= C B Br;	Brown	= C Br
Albino (1)	= B Br A;	Albino (3)	= Br A
Albino (2)	= B Br;	Albino (4)	= Br

Proof of the correctness of this interpretation may be obtained from crosses. Suppose the four kinds of albinos described be crossed with the same colored variety, brown; albino 1 will produce gray offspring, albino 2 will produce black ones, albino 3 will produce cinnamon ones, and albino 4 will produce brown ones. The cross with albino 1 brings together all the four factors entering into the production of gray, viz. C, B, Br, and A, hence the young are gray. The cross with albino 2 brings together the factors C, B, and Br only. The result is black. The cross with albino 3 brings together the factors C, Br, and A; result, a cinnamon animal. The cross with albino 4 brings together no factors except C and Br; result, a brown animal.

Thus far we have considered merely variations which arise by loss of one or more of the three unit-characters, A, B, and C. We may now consider variations which arise by modification without loss of these same factors.

Yellow varieties owe their origin to a reduction in the amount of black or brown pigment in the fur, and to a corresponding increase in the amount of yellow. In some yellow animals, such as the sooty yellow rabbit, black and brown pigments are not wholly lacking in the fur, but are only greatly reduced in amount. They always persist in the eye. In other yellow animals, mice for example, the black or brown pigments are wholly absent from the fur, and they may also be greatly reduced in amount in the eye, as in the variety known as pink-eyed yellow, but in no yellow animal, so far as I am aware, is the production of black and of brown pigments wholly suppressed.

In any mammal which possesses yellow varieties we can produce by suitable crosses as many different varieties of yellows as there are of gray, black, cinnamon, and brown varieties combined. For example, in mice, yellow individuals of which, as was shown in the last chapter, are invariably heterozygous and produce some other variety than yellow, even when mated with yellows, we can recognize the following varieties distinct in breeding capacity, though all looking very similar.

1. Yellows which produce yellow young and gray ones;
2. Yellows which produce yellow young and black ones;
3. Yellows which produce yellow young and cinnamons;
4. Yellows which produce yellow young and brown ones.

Albino varieties occur which correspond with each of these yellow varieties, viz. (1) albinos which if crossed with brown will produce yellow young and gray ones; (2) albinos which crossed with brown produce yellow young and black ones; (3) albinos which crossed with brown produce yellow young and cinnamon ones; and (4) albinos which crossed with brown produce yellow young and brown ones. Such albinos, of course, differ from the corresponding yellow varieties merely by the general color factor C, which the albino lacks. If this is added by a cross, they produce the same visible result as the corresponding yellow variety in the same cross.

In addition to the modification which produces yellow varieties, we can recognize several other modified conditions of the unit-characters A, B, C, and Br, which modifications produce whole series of color varieties. For a modified condition of a single unit-character is capable of producing as many new varieties as there are possible combinations of the modified character with other unit characters.

One who attends a poultry-show cannot fail to be impressed with the great number of color varieties among poultry. Let him first observe these among fowls of common size, and if he then visits the bantam section he will find them all duplicated in miniature among the bantams. If a new color variety is brought out, it is only a short time until it finds its place among the bantams as well as among fowls of common size. The dwarf size of the bantam is clearly due to a modified condition of one or more unit-characters capable of combinations with as many different kinds of coloration as occur among poultry. The various combinations are of course brought about by crossing, and two generations suffice theoretically for securing them.

In mice, if one possessed only the albino variety last described, — the one which corresponds with the brown-eyed yellow variety, — he could easily produce within six months every one of the various color varieties which have been mentioned. *All he would have to do* would be to catch some wild mice and cross these with his albinos. The immediate offspring produced by the cross might seem unpromising; they would either be gray, exactly like wild mice, or else yellow. But if our breeder possessed the faith to breed a second generation from these animals, he would be rewarded by seeing all the color varieties which I have described put in an appearance, viz. yellows with black eyes, and yellows with brown eyes, blacks, browns, cinnamons, and grays, and albinos corresponding in character with each colored variety except for the lack of the color-factor C.

It may be of interest to consider how some additional color varieties of mice have arisen, for of all mammals bred in captivity the mouse is probably richest in color varieties. In one series of these the capacity to form black or brown pigments is greatly weakened, so that the coat is less heavily pigmented and the eye is *almost* wholly unpigmented, and looks pink, due to the red color of the blood in the eye. This series we may call the pink-eyed series. All the common color varieties occur in a pink-eyed as well as in a dark-eyed series. Thus there are pink-eyed grays, pink-eyed blacks, pink-eyed cinnamons, pink-eyed browns, and pink-eyed yellows, as well as albinos which transmit the pink-eyed condition in crosses.

Given a single pink-eyed individual in any one of these varieties, all the others may be produced from it by suitable crosses. Thus a pink-eyed gray crossed with brown produces in F_1 reversion to the condition of the wild house-mouse, but in F_2 (that is, among the grandchildren) occur eight varieties,—four dark-eyed and four pink-eyed. Gray, black, cinnamon, and brown occur, both in dark-eyed and in pink-eyed individuals, the latter being also far lighter in color than the dark-eyed varieties. The pink-eyed condition is therefore in mice a unit-character modification of the pigmentation, independent of any of the pigment factors previously mentioned, since it can be transferred by crosses from association with one of these to association with another. It may also be transmitted equally well through colored and through albino individuals, *though it produces a visible effect* only in colored individuals.

Another unit-character modification of the pigmentation seen in mice produces a series of dilute or pale pigmented varieties, but different in character from the pink-eyed series, since their eyes may be dark, not pink. The pale modification of gray is known to fanciers as "*blue-gray,*" *that of black is known* as "blue," and that of brown is known as "silver fawn." The pale quality is interchangeable between black, brown, and yellow pigmentation, so that if one has a pale gray variety he may by crosses obtain also pale black, pale cinnamon, pale brown, and pale yellow varieties. Or if one starts with pale yellow, he may by crosses with a perfectly wild mouse obtain also pale gray, pale black, pale cinnamon, and pale brown varieties, all within two generations from the cross.

Now the pale modification is distinct from the pink-eyed modification, and independent of it in transmission. Accordingly, it is possible to have the two modifications combined in the same race. Thus arises a series of pale pink-eyed grays, blacks, cinnamons, browns, and yellows. Since paleness is in crosses recessive to intense pigmentation, and pink eyes are recessive to dark ones, it follows that a variety which is both pale and pink-eyed will breed true to those characteristics without fixation.

The lightest colored of the pale pink-eyed varieties develop very little pigment indeed, yet the modifications to which they are due are wholly different in nature from the albino variation, as a very simple experiment will show. Cross together an albino of variety (1), page 74, — which is a snow-white animal with pink eyes, — and a pale pink-eyed, brown animal, whose coat is pale straw color, and whose eyes, like those of the albino, are pink. Although both parents are pink-eyed, and one develops no pigment whatever in its fur, while the other develops very little, nevertheless the offspring *are as dark as the darkest wild mice, eyes,* fur, and all. They look just like common house-mice. This result shows that the albino variation is something very different in nature from the modifications found in the pink-eyed brown parent, since each parent contains those constituents of the wild gray coat which the other parent lacks.

I can think of no more instructive laboratory experiment illustrative of Mendelian inheritance than to follow through two generations the cross just described, and to analyze critically the results obtained. One who does this can never be sceptical about the value of crossing as an agency in the production of new varieties. For in the second generation from the cross he will obtain (1) ordinary gray, black, cinnamon, and brown varieties; (2) *pale* gray, black, cinnamon, and brown varieties; (3) *pink-eyed* gray, black, cinnamon, and brown varieties; (4) *pink-eyed and pale* gray, black, cinnamon, and brown varieties; and lastly, albinos, which, if he has the patience to test them one by one, will prove to be of sixteen different homozygous kinds, to say nothing of the much more numerous heterozygous sorts.

No mention has thus far been made of spotted races, in which a unit-character modification has occurred which results in a distribution of pigment to part of the coat only, the remainder being unpigmented. Although this modification apparently regulates the distribution of *pigment over the body, it is independent of the* general color factor C, since it is transmitted through albinos, which by hypothesis lack C.

Spotting is also independent of all the other unit-character modifications which have been described. Consequently we have in mice four different series of spotted varieties, — the intense spotted, the dilute spotted, the intense pink-eyed spotted, and the dilute pink-eyed spotted. In each of these series are gray, black, cinnamon, brown, and yellow individuals, making a total of twenty spotted sorts, all of which may be obtained from crossing a single pair of properly selected parents, such, for example, as an albino and a wild house-mouse of the kind every barn contains.

The color variations of guinea-pigs are similar to those of mice; the same series of unit-character changes has produced them with one exception. The pink-eyed modification is wanting in guinea-pigs. We are therefore limited here to the intense series, the pale series, the intense spotted series, and the pale spotted series. In each of these occur gray (or agouti) individuals, black ones, cinnamon ones, and brown ones.

The parallelism between the color variations in guinea-pigs and in mice received an interesting demonstration in a particular case. The brown pigmented series in mice has been known for some time, but in guinea-pigs the brown variety is of comparatively recent origin, and the cinnamon variety was wholly unknown until some three years ago. After an analysis had been made in terms of unit-characters of the color varieties of the mouse, it became clear that if the color variation of guinea-pigs followed a like course, a then unknown variety of guinea-pig, cinnamon, should be capable of production by crossing an agouti animal with a brown one. In 1907 a statement of the scientific expectation in the case was published, and a few months later I had the satisfaction of announcing its fulfillment in the second generation (F_2) from the cross in question.

The experiment progressed as follows: The parents were an agouti and a black, their F_1 offspring were agoutis in character; but the F_2 offspring were of four sorts, — *agouti, black, cinnamon,* and *brown. The cross thus produced* two varieties new to the experiment, viz. black and cinnamon, the latter being a variety at that time new among guinea-pigs.

The subsequent behavior, too, of the newly produced cinnamon variety is in harmony with expectation based on Mendelian principles. The cinnamon variety has not produced agouti or black individuals, which from the formulæ it will be seen it may not be expected to produce, since it lacks the factor B. But it has in some cases produced brown individuals, as it clearly could in case both parents to a mating were heterozygous (single) in factor A.

On the whole the evidence seems very clear that the numerous color varieties of animals kept in captivity arise chiefly from loss or modification of Mendelian unit-characters. Loss of a unit-character might easily come about by an irregular cell-division in which the material basis of a character failed to split, as normally. The consequence would be that the character in question would be transmitted by one only of the two cell-products produced. The cell lacking a character might be the starting-point of a race lacking the character, as of a black race, derived from a gray one. On the other hand a modified condition of a unit-character might possibly result from *unequal* division of the material basis of a character, so that one of the cell-products would transmit the character in weakened intensity, the other in increased intensity.

BIBLIOGRAPHY

CASTLE, W. E.
1907. "Color Varieties of the Rabbit and of Other Rodents: Their Origin and Inheritance." *Science, N. S.*, 26, pp. 287–291.
1908. "A New Color Variety of the Guinea-pig." *Science, N. S.*, 28, pp. 250–252.
1909. "Studies of Inheritance in Rabbits." *Carnegie Institution of Washington, Publication No. 114*, 70 pp., 4 pl.