CHAPTER IV

THE DETERMINATION OF DOMINANCE; HETEROZYGOUS CHARACTERS AND THEIR FIXATION; ATAVISM OR REVISION

WE have noticed that when a black guinea-pig of pure race is mated with a white one, only black offspring are produced; and that when rough-coated guinea-pigs are mated with smooth-coated ones, only rough-coated young are produced; and that when short-haired guinea-pigs are mated with long-haired ones, only short-haired young are produced. The character which in each case is seen in the young we call dominant, that which is unseen we call recessive. Thus black is dominant over *white, rough coat over smooth coat, and short* coat over long coat.

A question which has given much concern to students of heredity is this, — upon what does dominance depend? Why should black dominate white rather than the reverse?

In poultry, indeed, the relations are often reversed, white dominating black. Why is this? Several attempted explanations have been made, but none of them is thoroughly satisfactory. The one which has found widest acceptance is this: In the dominant individual something is present which is wanting in the recessive. Thus, in the black guinea-pig *there is present some ferment-like body* or some ingredient of black which is wanting in the albino. Accordingly, the black guinea-pig forms pigment, a thing which the albino can do only feebly or not at all. The distinctive *something* of the black parent therefore dominates a corresponding *nothing* of the white parent. White fowls, on the other hand, are not albinos. They have pigmented eyes. Accordingly they do not lack the power to form pigment, owing to the absence of some necessary ferment or pigment ingredient.

White guinea-pigs occur which are in a way comparable with white fowls. They look exactly like albinos, except that their eyes are black, whereas the eyes of the albino are pink. If such a black-eyed white guinea-pig is crossed with an albino of the sort shown in Fig. 15, the young produced will be black all over. Now this result shows that the black-eyed white animal *possesses* what is lacking in the albino as compared with the all-black animal. It would seem, therefore, that it lacks something different from what the albino lacks, and that a cross of the two supplies *both lacks*, the albino supplying what is wanting in the black-eyed white, and *vice versa.* Accordingly, wholly black offspring result from the crossing of the two white races.

But the case of white poultry is different from this, since white poultry lack *nothing* that is necessary to produce the complete black plumage. For when white fowls crossed with black ones produce *white* offspring, if these offspring are then bred with each other, they produce both white offspring and black ones in the ratio 3 to 1. White fowls, therefore, *are* able to produce the black condition. This ability is in the white individual held in abeyance, it is not exercised. Why, we do not know. Some suppose it to be held in check by an additional unit-character, an inhibiting factor, but we have no direct evidence that such a factor exists. All that we are warranted in saying at the present time is that black and white in poultry represent *different* conditions of pigmentation, alternative to each other in heredity. In crosses of the two, white is ordinarily dominant over black, but in crosses between certain strains of white and black poultry this relationship is reversed, as Bateson has shown.

In still other cases, a cross of white with black fowls produces offspring which resemble neither parent closely, but which are in reality intermediate. They are known as blue or Andalusian fowls. They manifest a dilute condition of black, such as one might obtain by mixing lampblack with flour; they are in reality a fine mosaic of black with white. Such a condition has thus far been obtained only from a cross of black fowls with a peculiar strain of impure sooty whites. This strain undoubtedly contains the mosaic pattern but without sufficient black pigment to make it plainly visible. A cross with a black race makes it visible. No one, however, has succeeded in "*fixing*" a blue race, that is, in obtaining a strain which would breed true.

When two blue individuals are bred together they produce black, blue, and white offspring in the ratio 1 : 2 : 1. The blacks are homozygous, B B; the whites also are homozygous, W W, but the blues are invariably heterozygous, B W. Blue accordingly in this case is called a *heterozygous* character, one which is due to the presence in one zygote of two unlike unit-characters, which invariably segregate from each other at the genesis of gametes, but which jointly produce a different appearance from what either produces by itself. If a strain of Andalusian fowls should ever be secured which would breed true, it would have to come about by the association of black with white in a *non-segregating* relationship, so that *both* would be transmitted in the same gamete. That is, one would have to secure in the same gamete with white enough black pigment to bring out the latent mosaic pattern, and further, one would have to secure a homozygous race of fowls which formed such gametes.

Success would be most likely to attend the experiment if one selected always the sootiest whites obtained from blue parents, for blue results, as we have seen, from the association of *more black* with the white and in the pattern borne already by the white race.

A much-debated case of inheritance which involves this principle of unfixable heterozygous characters occurs among fancy mice, in the variety known as yellow. A wonderful series of color varieties exists among mice kept as pets, equalling or perhaps surpassing that known in the case of any other mammal. All these varieties appear to be derivatives of the common house-mouse, with which they cross readily. All are capable of explanation as unit-character variations from the condition of the house-mouse. Among all these varieties yellow is most peculiar in its behavior. In crosses it is dominant over all others, yet is itself absolutely unfixable.

If certain strains of yellow mice are crossed with black ones, the offspring produced are of two sorts equally numerous, yellow and black. From this result alone it is impossible to say which is the dominant character, but breeding tests of the offspring show that yellow is the dominant character. For the black offspring bred together produce only black offspring, but the yellows bred together produce both yellow offspring and black ones. The curious feature of the case is that when yellows are bred with each other no pure yellows, that is, homozygous ones, are obtained. Hundreds of yellow individuals have been tested, but the invariable result has been that they are found to be heterozygous; that is, they transmit yellow in *half* their gametes, but some other color in the remaining gametes — it may be black, or it may be brown, or it may be gray. The black, brown, or gray animals obtained by mating yellow with yellow mice never produce yellow offspring if mated with each other. This shows that they are genuine recessives and do not contain the yellow character, which is dominant.

Now ordinary heterozygous dominants, when mated with each other, produce three dominant individuals to one recessive. Accordingly we should expect yellow mice, if, as stated, they are invariably heterozygous, to produce three yellow offspring to one of a different color, but curiously enough they do not. They produce *two* yellows (instead of the expected three) to every one of a different color. About the ratio there can be no reasonable doubt. It has been determined with great accuracy by my pupil, Mr. C. C. Little, who finds that in a total of over twelve hundred young produced by yellow parents almost exactly two-thirds are yellow. Instead of the regular Mendelian ratio 3 : 1, we have then in this case the peculiar ratio 2 : 1, and this requires explanation. The explanation of this ratio is to be found in the same circumstance as is the total absence of *pure* yellows. Pure yellow zygotes are indeed formed, but they perish for some unaccountable reason. For a yellow individual forms gametes of two sorts with equal frequency, viz. yellow and non-yellow (let us say black). For, if yellow individuals are mated with black ones, half the offspring are black, half yellow, as already stated.

If now yellow individuals are mated with each other we expect three sorts of young to be produced numerically, as 1 : 2 : 1, viz. 1 Y Y, 2 Y B, and 1 B B. But since observation shows that only *two* combinations are formed which contain yellow to one not containing yellow, and since further all yellows which survive are found to be heterozygous (Y B), it must be that the expected Y Y individual either is not produced or straightway perishes. As to which of these two contingencies happens we also have experimental evidence. Mr. Little finds that yellow mice when mated to black ones produce larger litters of young than when they are mated to yellow ones. The average-sized litter contains something like 5.5 young when the mate is a black animal, but only 4.7 when it is a yellow animal. It is evident, then, that about one young one out of a litter perishes when both parents are yellow, and this undoubtedly is the missing yellow-yellow zygote. The yellows which are left are heterozygous yellow-black zygotes, and they are to those that perish as 2 : 1. They are also to the non-yellow zygotes as 2 : 1, the ratio observed also among the surviving young of yellow by yellow parents.

This interpretation of the 2 : 1 ratio observed in this case is strongly supported by a similar case among plants, in which the evidence is even more complete. A so-called "golden" variety of snapdragon, one in which the foliage was yellow variegated with green, was found by the German botanist, Baur, to be unfixable, producing when self-pollinated fully green plants as well as golden ones, in the ratio 2 golden : 1 green. The green plants were found to breed true, that is, to be recessives, while the golden ones were invariably found to be heterozygous. Baur found, however, by germinating seeds of golden plants very carefully, that there were produced in addition to green plants and golden ones a few feeble seedlings entirely yellow, not variegated with green, as the golden plants are. These, for lack of assimilating organs (green chlorophyl), straightway perished. Clearly they were the missing pure yellow zygotes.

Some Mendelian characters, while not themselves heterozygous and so unfixable, are nevertheless produced only when two independently inherited factors are present together. A character of this sort does not itself conform with the simple Mendelian laws of inheritance, but its factors do. Herein lies the explanation of atavism or reversion, and the process by which reversionary characters may be fixed.

Atavism or reversion to an ancestral condition is a phenomenon to which Darwin repeatedly called attention. He realized that it is a phenomenon which general theories of heredity must account for. He supposed that the environment was chiefly responsible for the reappearance in a species of a lost ancestral condition, but that in certain cases the mere act of crossing may reawaken slumbering ancestral traits. Thus he noticed that when rabbits of various sorts are turned loose in a warren together, they tend to revert to the gray-coated condition of wild rabbits. And when pigeons are crossed in captivity they frequently revert to the plumage condition of the wild rock pigeon, *Columba livia.* In plants, too, Darwin recognized that crossing is a frequent cause of reversion. The explanation which he gave was the best that the knowledge of his time afforded, but it leaves much to be desired. This lack, however, has been completely supplied by the Mendelian principles. An illustration or two may now be cited.

When pure-bred black guinea-pigs are mated with red ones, only black offspring are as a rule obtained. The hairs of the offspring do indeed contain some red pigment, but the black pigment is so much darker that it largely obscures the red. In other words, black behaves as an ordinary Mendelian dominant. In the next generation black and red segregate in ordinary Mendelian fashion, and the young produced are in the usual proportions, three black to one red, or 1 : 1 in back-crosses of the heterozygous black with red. All black races behave alike in crosses with the same red individual, but among red animals individual differences exist. Some, *instead of behaving like* Mendelian recessives, produce in crosses with a black race a third apparently new condition, but in reality a very old one, the agouti type of coat found in all wild guinea-pigs, as well as in wild rats, mice, squirrels, and other rodents. In this type of coat reddish yellow pigment alone is found in a conspicuous band near the tip of each hair, while the rest of the hair bears black pigment. The result is a brownish or grayish ticked or grizzled coat, *inconspicuous, and hence protective in many* natural situations.

Some red individuals produce the reversion in half of their young by black mates, some in all, and others, as we have seen, in none, this last condition being the commonest of the three. It is evident that the reversion is due to the introduction of a third factor, additional to simple red and simple black. It is evident further that this new third factor, which we will call A (agouti), has been introduced through the red parent, and that as regards this factor, A, some individuals are homozygous (AA) in character, others are heterozygous (transmit it in half their gametes only), while others lack it altogether. Further observations show that it is independent in its inheritance of both black and red; it is in fact an independent Mendelian character, which can become visible only in the presence of both black and red, because it is a mosaic of those two pigments. If the F_1 agouti individuals are bred together they produce in the next generation (F_2) three sorts of young, viz. agouti, black, and red, which are numerically as 9 : 3 : 4. This evidently is a modification of the dihybrid Mendelian ratio 9 : 3 : 3 : 1, resulting from the fact that the last two classes are superficially alike. They are red animals with and without the agouti factor respectively; but this agouti factor is invisible in the absence of black, so that both sorts of reds look alike. Together they number four in sixteen of the F_2 offspring.

Fig. 35 is intended to show how the independent factors behave in heredity. The black parent contributes the factor B, the red parent, R and A, so that the zygote, or new individual, contains the three factors necessary to the production of agouti. When the new individual forms gametes (sex-cells), these will be of four different kinds, for A is independent of B and of R and may pass out with either one in the reduction division which sepa-

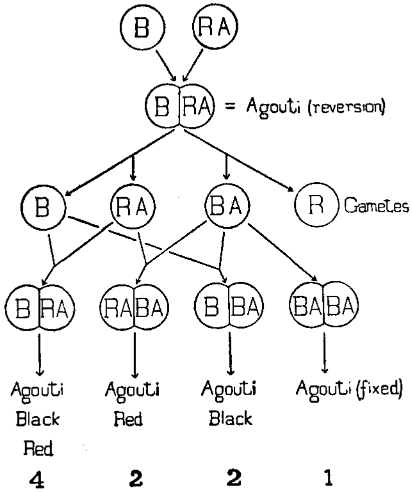

FIG. 35. — Diagram to show the gametic combination and recombinations which occur in the production and fixation of an atavistic coat-character in guinea-pigs.

Row 1 shows the character of the gametes formed by the parents crossed; row 2 shows the character of the F_1 agouti individuals resulting from the cross; row 3 shows the two different sorts of gametic splittings which may occur in the production of gametes by the F_1 agoutis, and how four different kinds of gametes result; row 4 shows how among such gametes four different kinds of unions may occur that will produce agouti young. The BA·BA combination, it will be understood, could result only from the union of a BA gamete with another gamete of like constitution. Below each of the four combinations is indicated the kinds of young which an animal of that sort would produce if mated with an animal like itself. The numerals show the expected relative frequencies of the four sorts of combinations.

rates B from R. That division accordingly may occur either so as to form gametes B and R A respectively, or what is equally probable, so as to produce gametes B A and R. Observation confirms this interpretation, for it is found that the reversionary agoutis do not breed true, but produce young of the three sorts, agouti, black, and red, as expected. We expect black individuals from unions of B with B, or of B with R; we expect red individuals from unions of R with R or with R A, and from unions of R A with R A; we expect agoutis to be produced by any gametic union which brings together the three factors B, R, and A. There are six chances in sixteen for the occurrence of such a union, when the reversionary agoutis are bred together. In fact, however, agoutis are produced much oftener. Approximately nine out of sixteen of the young have been found to be agoutis. The unexpected excess of agoutis in our experiments was fully explained when these second-generation agoutis were tested individually. It was then found that they are of four sorts as regards breeding capacity. The first sort produces the three kinds of young, agouti, black, and red; the second sort produces only agouti young and red young; the third sort produces only agouti young and black young. The fourth sort produces only agouti young, i. e. represents the fully fixed agouti type, the completely recovered wild type.

In the chart (Fig. 35) are indicated certain gametic unions which would lead to the production of these four classes of agoutis. The probable frequencies of their occurrence on the basis of chance are 4 : 2 : 2 : 1.

Experiment made it clear that R as an independent gametic factor is not necessary to the production of the agouti character, as was at first thought to be the case, but that any gametic union which includes both B and A will produce an agouti individual whether R is or is not present. Yet a microscopic examination of the agouti hair shows that red pigment is present in a distinct band near the hair-tip. As a matter of fact all black individuals, even when they breed true, probably form some red pigment along with the black, but its presence is overlooked when the more opaque black is distributed throughout the whole length of the hair. When, however, black is excluded from the hair-tip, the red then becomes visible as the agouti marking; elsewhere the hair appears black. Red, then, we may assume, is always present with black in sufficient quantities to produce the agouti marking if the factor A is present (absence of black from the hair-tip). This explains why blacks never give the reversion in any sort of cross, but it is always brought about through the agency of the red parent. If a black individual contained the factor A, it would no longer be a black individual, but an agouti one.

The existence of a third factor, A, in cases of reversion in coat-character among rodents was long overlooked merely because it does not represent a distinct pigment or set of pigments, but consists in a particular kind of pigment distribution on the individual hairs. The agouti hair is due to a definite cycle of activity of the hair follicle in forming its pigments, — first black, then red, then black; the wholly black hair is due to a continuous process of pigment formation without alternation in the character of the pigments produced.

In rabbits as well as in guinea-pigs reversion to the original wild type, in this case gray, may be obtained by crossing a black animal with a yellow one. In guinea-pigs the yellow (or red) animal which will yield this result cannot be distinguished in appearance from one which will not; but in rabbits the yellow animal which will give reversion has a white belly and tail, while the one which will not give reversion is not so distinguished.

We now know what is implied in the fixation of a heterozygous character obtained by crossing. When A and B are crossed we obtain a third condition, C. C is due either to the simple coexistence of A with B, or to the coexistence with them of a third factor introduced with one or the other. In either case fixation will consist in getting into the *gamete* all the factors necessary to the production of C. In the first supposed case the *zygote* is A·B and the resultant is equivalent to C. Fixation will consist in getting a zygote of the formula AB · AB. In the second supposed case the zygote produced is either A·CB or AC·B; fixation will consist in obtaining a zygote ACB·ACB; every gamete formed will then contain the three factors A, C, and B.

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