

CHAPTER IV

THE DETERMINATION OF DOMINANCE; HETEROZYG-
GOUS CHARACTERS AND THEIR FIXATION; ATA-
VISM 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

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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

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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

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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

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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 fur-

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ther, 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 domi-

nant 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.

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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 ob-

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served 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 chlorophyll), straightway perished. Clearly they were the missing pure yellow zygotes.

Some Mendelian characters, while not themselves heterozygous and so unfixable, are never-

theless 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

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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

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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

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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-

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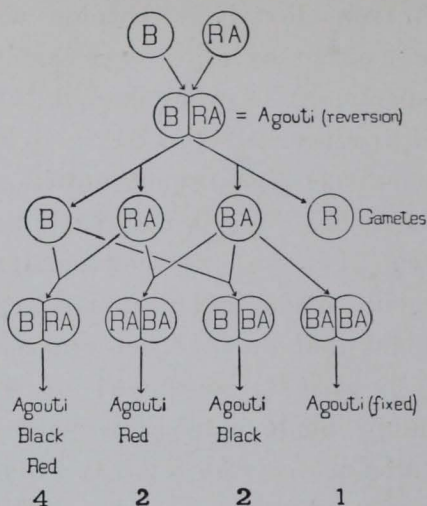


FIG. 35. — Diagram to show the gametic combination and recombinations which occur in the production and fixation of an atavistic coat-character in guinea-pigs.

Row 1 shows the character of the gametes formed by the parents crossed; row 2 shows the character of the F₁ 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 F₁ 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.

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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

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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

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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

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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 $A \cdot B$ and the resultant is equivalent to C. Fixation will consist in getting a zygote of the formula $AB \cdot AB$. In the second supposed

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case the zygote produced is either $A \cdot CB$ or $AC \cdot B$; fixation will consist in obtaining a zygote $ACB \cdot ACB$; every gamete formed will then contain the three factors A , C , and B .

BIBLIOGRAPHY

BATESON, W.

1909. "Mendel's Principles of Heredity," 393 pp., illustrated. University Press, Cambridge; also G. P. Putnam's Sons, N. Y. [Contains translation of Mendel's original papers.]

BAUR, E.

1907. "Untersuchungen über die Erbliehkeitsverhältnisse einer nur in Bastardform lebensfähigen Sippe von *Antirrhinum majus*." *Ber. d. Deutsch Bot. Gesellsch.*, 25, p. 442.

CASTLE, W. E.

1907. "On a Case of Reversion Induced by Cross-Breeding and its Fixation." *Science, N. S.*, 25, pp. 151-153.
1907. "The Production and Fixation of New Breeds." *Proc. Amer. Breeders' Ass'n*, 3, pp. 34-41.

CASTLE, W. E. and LITTLE, C. C.

1910. "On a Modified Mendelian Ratio Among Yellow Mice." *Science, N. S.*, 32, pp. 868-870.

CUÉNOT, L.

1908. "Sur quelques anomalies apparentes des proportions Mendéliennes." *Arch. Zoöl. Exper.* (4), Notes et Revue, p. vii.

DAVENPORT, C. B.

1906. "Inheritance in Poultry." *Carnegie Institution of Washington, Publication No. 52*, 104 pp., 17 pl.
1909. "Inheritance of Characteristics in Domestic Fowl." *Carnegie Institution of Washington, Publication No. 121*, 100 pp., 12 pl.

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.

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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:

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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 pro-

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duce 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

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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

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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,

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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

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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

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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

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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

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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.

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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 sci-

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entific 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

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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.

CHAPTER VI

EVOLUTION OF NEW RACES BY VARIATIONS IN THE POTENCY OF CHARACTERS

IN the last chapter we discussed the color variations of mammals, and we concluded that these result largely from the loss or modification of some half-dozen independent Mendelian unit-characters. As to the material basis of these unit-characters some interesting evidence has recently been collected by Riddle. Melanin pigment has been for some time known to be formed by oxidation. A variety of organic compounds may undergo oxidation into melanin pigments ranging in intensity from light yellow to black; the greater the oxidation, the darker the product. But it is not certain, as assumed by Riddle, that the chemical *method* of oxidation is the same in all cases or that the substance to be oxidized is the same. The results obtained from breeding experiments

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show that the capacity to form pigment of all sorts may be lost by a single variation, which we have called loss of the color factor, C. We do not know whether it consists in the loss of a substance capable of oxidation, or of the power to take some indispensable first step in the process of oxidation, perhaps due to loss of an enzyme; but we do know that when this particular variation has occurred, the power to produce other than albino individuals cannot be recovered by any known means except a cross with colored animals. We know also that the capacity to form specific kinds of pigment (yellow, brown, or black) is independent of the general color-factor, C, for albinos may transmit those specific powers without themselves being able to form any kind of pigment at all, i. e. without possessing C. Any animal which forms pigment of one of the higher grades has the capacity apparently to form pigment also of the lower grades. Thus a black animal can form also brown and yellow pigment granules. Brown (chocolate) animals, however, lack the capacity to form black pigment. The oxidation, it would seem, can in

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this case be carried no further than the brown stage, because of the lack of some oxidizing agency necessary to the last stage in pigment production. The production of yellow is probably a first or early step in the oxidation process preliminary to the production of brown or black, yet all yellow animals, so far as known, are able to take the further steps; they retain the capacity to form either brown or black pigment to some extent, if only in the eye.

The variations thus far described are what De Vries has called retrogressive, i. e. due to loss or modification. A much rarer sort of variation has been called by De Vries progressive, i. e. due to gain, acquisition of some character not before possessed by the race. I can call to mind very few cases which certainly fall in this category. One which it would seem must belong here is the rough or rosetted condition of the hair in guinea-pigs, a variation similar in nature to the reversed plumage of birds, seen, for example, in the Jacobin pigeon. The rough coat of guinea-pigs is surely not an ancestral condition, yet it behaves as a

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dominant character in crosses. It can scarcely be explained by loss; the only alternative is to consider it an acquisition, unless we choose to consider it a modification of the normal condition.

Aside from the sorts of variations already discussed, which consisted either in the loss or modification of existing unit-characters or in the gain of new ones, we must also recognize, as a cause of permanent and heritable variation, changes in the *potency* of unit-characters, i. e. their tendency to dominate in crosses.

When a gamete containing a particular unit-character unites with a gamete not containing it, the zygote formed will ordinarily show the character in question fully developed. This result following Mendel's terminology we call dominance. But dominance is frequently imperfect and may even be reversed. The zygote in which a character is doubly represented frequently develops the character more fully than the zygote in which it is represented but once. If a black guinea-pig is crossed with a yellow one the offspring are black, but oftentimes of a slightly yellowish shade. Likewise if black

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is crossed with brown, the crossbreds are apt to develop in their coats more brown pigment granules than do homozygous or pure blacks. Nevertheless, we have no reason to question the entire purity of the gametes, both dominant and recessive, formed by such cross-bred black animals. It is the dominance, not the segregation, which is imperfect.

In other cases still the dominance may be entirely reversed in character, owing to variation in the potency of a unit-character. Thus in most rodents the gray or agouti pattern-factor of the hair, *A*, is dominant. A cross of black with homozygous gray, in rats, mice, or rabbits, produces only gray offspring, which in F_2 produce three grays to one black. But the so-called black rat, *Mus rattus*, a species distinct from the one which has given rise to the varieties kept in captivity, behaves in a different way, as shown by Morgan ('09). When crossed with its gray variety, the roof rat, *Mus alexandrinus*, it produces only black offspring, and in F_2 , three blacks to one gray. If we suppose the gray coat in this case to be due to the same factor as in other rodents,

we must assign to it a different potency, or power of dominance, so that it produces a visible effect only when doubly represented in the zygote.

In guinea-pigs, rabbits, and mice we have seen that the presence together in the same zygote of two factors, A and B, in any combination whatever, produces the gray or agouti coat. The two factors are A, the agouti or gray marking of the hair, and B, black pigment in the fur. If A is lacking, the coat is black; if B is lacking, it is brown, cinnamon, or yellow. If both are lacking, it is either brown or yellow. But if both are present, the wild or agouti type is produced. So far as the production of the agouti coat is concerned, it makes no difference whether either factor is singly or doubly represented in the zygote. Each factor has potency enough to produce the full effect either in a single or in a double dose. Accordingly, as we noticed in an earlier chapter, we can distinguish by their breeding capacity, though not by their looks, four types of agouti guinea-pigs or gray rabbits, viz.:

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1. A A B B, which breeds true, since it forms gametes all A B;
2. A B B, which produces agouti young and black ones in the ratio 3 : 1, since it forms gametes A B and B;
3. A A B, which produces agouti young and yellow ones in the ratio 3 : 1, since it forms gametes A B and A;
4. A B, which produces agouti, black, and yellow young in the ratio 9 : 3 : 4. For the gametes formed by this sort are of four kinds, A B, A, B, and neither A nor B.

Now in rats we have no evidence that the factor B has ever been lost, a matter to which we shall presently return; but the agouti factor is apparently frequently wanting in ordinary rats, which are then black. For ordinary rats, then, the known combinations of A and B seem to be three, viz.:

A A B B = the pure gray (wild type);
A B B = heterozygous gray, which produces offspring 3 gray : 1 black. This type is obtained by crossing black with wild gray;
B B = pure black.

Now in *Mus rattus*, as we have seen, the middle or heterozygous type is *black*, not gray

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in appearance, but it produces both the gray and the black types. So the same gametic formulæ will account for both sets of facts, if we suppose merely that the *potency* of A is different in the two cases. In ordinary rats (*Mus norvegicus*) A produces the gray coat in a single dose; but in *Mus rattus* its potency is less, two doses are required to produce the gray coat. I am unable to frame any hypothesis other than this which will account for the reversal of dominance in one case as compared with the other.

Yellow color in mammals affords another illustration of this same thing,—reversal of dominance. Black and brown are in most mammals dominant over yellow in crosses, but in mice the reverse is true. The differential factor between black and yellow, if it is the same in mice as in other rodents, must be in one case potent enough to show itself if singly represented in the zygote, whereas in the other case it produces no visible effect unless doubly represented in the zygote. Yellow certainly seems to be a retrogressive variation from gray, black, or brown. The pigment granules

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remain in a *lower* oxidation stage in yellow than in black or brown. We suppose that in the yellow animal something is wanting which makes that further oxidation possible. This hypothesis would fully account for the observed recessive nature of yellow in the case of all mammals except mice. But here the capacity to form black or brown pigment is regularly present in the yellow individual but is held in check. We may suppose, therefore, that the differential factor, that which converts yellow into brown or black, must in this case be *doubly* represented in the zygote in order to produce brown or black fur, whereas in most mammals a single dose is effective. Accordingly, if the unmodified black or brown factor is represented only *once* in the zygote, and the yellow modification is represented once, the latter will show, since the former is singly ineffective. The animal accordingly is a heterozygous yellow, capable of producing also black or brown offspring. But mice are peculiar in that they cannot exist in the doubly deficient condition of a pure yellow zygote, consequently *all* yellow mice are heterozygous dominants,

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whereas other yellow mammals are homozygous recessives.

In connection with this same case may possibly be found the explanation of the complete absence of the yellow variation in rats. In nearly all mammals kept in captivity yellow as well as black varieties occur; this is true of horses, cattle, swine, dogs, cats, rabbits, guinea-pigs, and mice. In rats, however, a yellow variety is unknown. We know that rats are able to form yellow pigment, for all wild rats do form yellow pigment in their agouti fur, yet singularly enough no *all-yellow* rat has ever been observed, so far as we have any record, either wild or in captivity. A rat of this sort would command a high price at the hands of any fancier. Suppose the variation did occur in a single gamete. If, as in most mammals, it behaved as a recessive in crosses, it would not become visible, and might be carried along for untold generations without ever becoming visible unless two yellow gametes met. But if, as in mice, the yellow-yellow combination when formed quickly perished, then the character might never become visible. So the yellow

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variation may have occurred many times in rats, as it has in so many other mammals, but failed to become visible simply because it has the same potency as in most mammals, but is subject to the same *physiological limitations* as in mice, so that it cannot exist in a homozygous state. In that case the only evidence of its existence in a race would lie in a slightly diminished fecundity under inbreeding, as is found to be the case in yellow mice.

Such sharply contrasted variations in the potency of characters as we have been discussing are evidently of prime importance in evolution, making all the difference between a dominant and a recessive condition of a character, or between the occurrence and the permanent suppression of a particular variation. The character which is potent enough to show itself in a single dose will behave as a dominant character in crosses. We might call it *unipotent*. That which must be present in a double dose to produce a visible result will behave as a recessive character in crosses. We might call it *semi-potent*. It is not impossible that the *same character* may as regards domi-

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nance behave in different ways under different circumstances, at one time dominating completely, at another only feebly, and at other times not at all.

Undoubtedly the chief condition affecting dominance is the nature of the gamete with which a union is made in fertilization. In 1905 (*Carnegie Inst. Publ. No. 23*) I described a case in which a particular guinea-pig (male 2002, shown in Fig. 32) having a rough or rosetted coat gave a varying result in crosses. In crosses with most smooth animals his rough character dominated completely (see Fig. 24, which shows a son of the male 2002 by a smooth mother), but with one particular smooth animal the dominance was very imperfect in all the young (Fig. 36), while with a second it was imperfect in half the young. The conclusion was drawn that gametes vary in potency, and that parents, too, differ as regards the potency of the gametes which they produce, some individuals producing gametes all of which are relatively potent, others producing gametes only half of which are potent, while still others produce gametes none of which are potent.

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Relative potency would, therefore, seem to be a character inherited in Mendelian fashion.¹

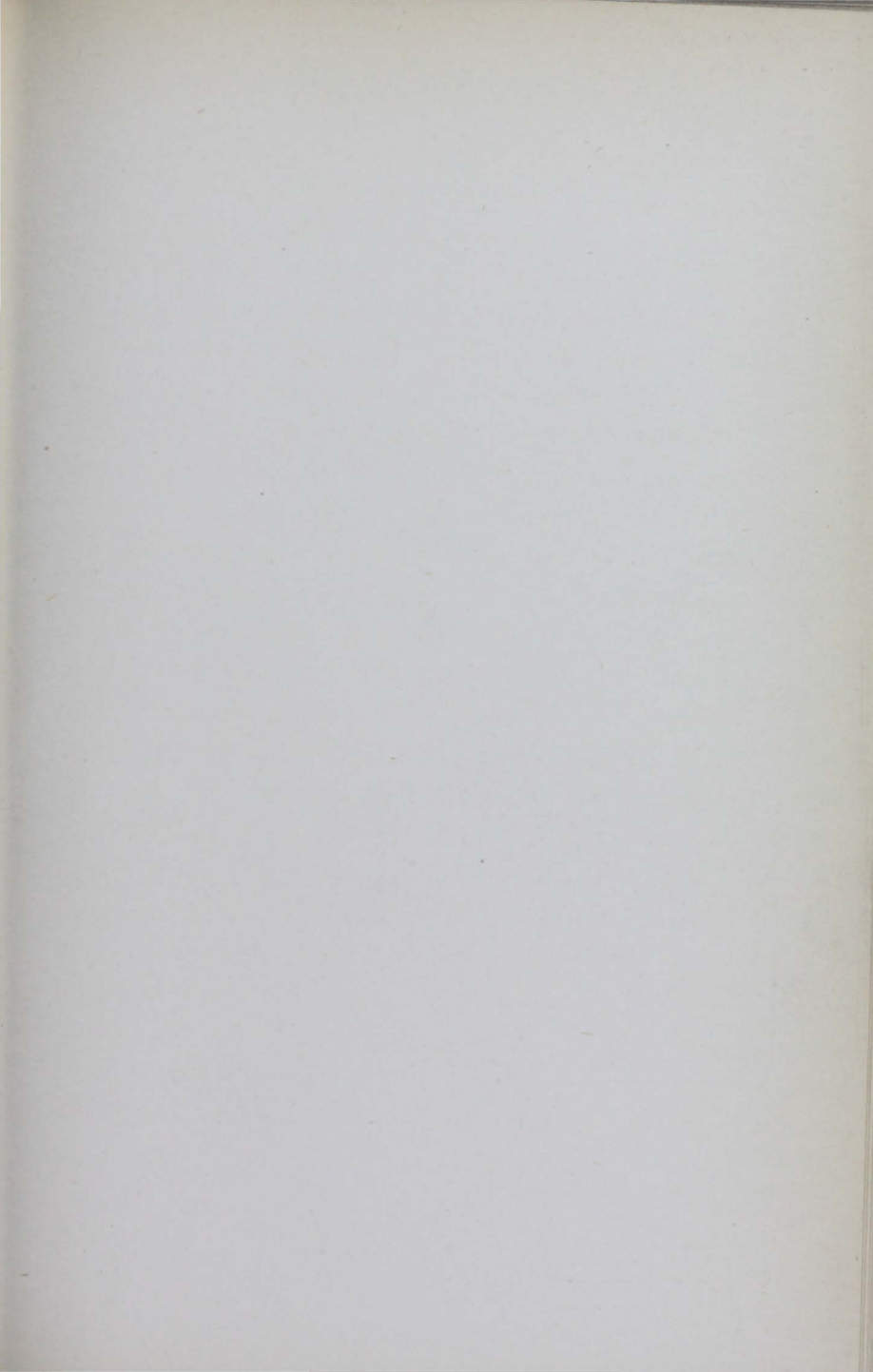
Observations of Coutagne on silk-moths may be cited in support of this idea. Coutagne made crosses between races of silk-moths differing in cocoon color, viz. between a race which spun yellow cocoons and another one which spun white cocoons. He found that *some* of the F_1 offspring spun yellow cocoons, others white ones. The F_1 yellow cocooned animals when bred together produced F_2 progeny which spun some yellow, others white cocoons, the two sorts being as 3:1. In other words, yellow in such cases behaved consistently as a *dominant* character. And the white-cocooned F_1 moths produced in F_2 cocoons of both colors, but in this case the white cocoons were to the yellow ones as 3:1. In other words, when yellow behaved as a dominant in F_1 it behaved as a dominant also in F_2 ; and the same was true of white. Each retained throughout the two generations the *relative potency* with which

¹ It is of course possible to interpret such a case as due to the separate inheritance of a factor which inhibits the development of the character, but it is doubtful whether this line of explanation can be successfully applied to cases presently to be described.

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it started. C. B. Davenport has also produced much evidence favoring the idea of varying potency of characters in recent papers based on his extensive studies on poultry.

The case which I described in 1905 was one in which unusual potency seemed to inhere in the gametes of a recessive individual, — one which apparently did not possess the character whose dominance was affected. But there occur also cases in which the varying gametic potency is associated directly with the character affected. One such I was able to describe in 1906, — that of an extra toe in guinea-pigs. It was found while building up a polydactylous race by selection and crossing it with other races that individuals varied in the potency which the character had in their gametes. In general the better developed the character was in an individual the more strongly was it transmitted, i. e. the larger was the proportion of polydactylous individuals produced in crosses. In no case, however, was this a recognizable Mendelian proportion, though both dominance and segregation seemed to be taking place. Variation in potency was, however, unmistak-



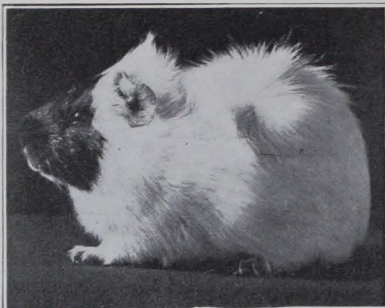


FIG 36

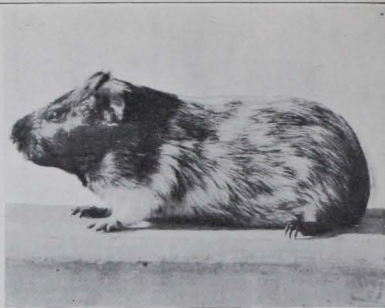


FIG 37

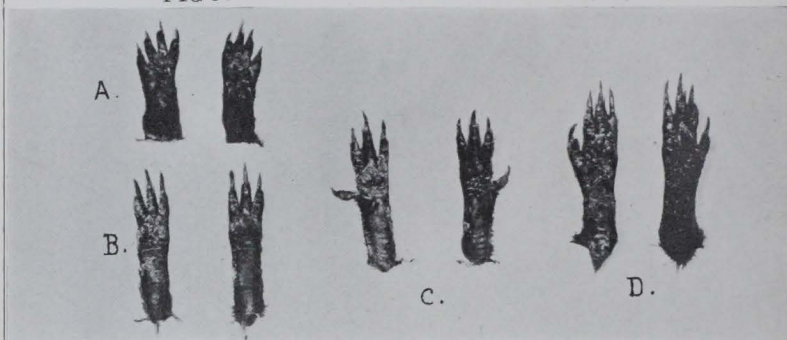


FIG 38

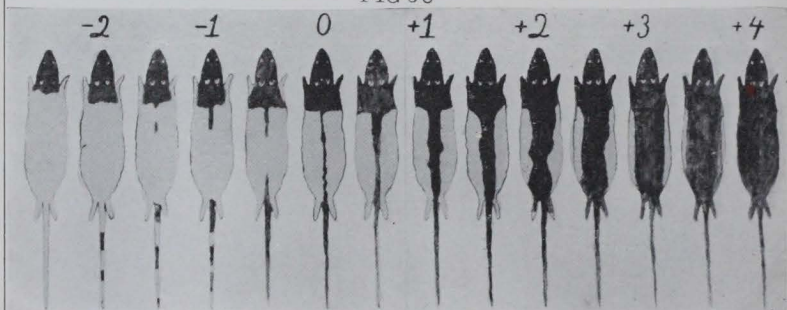


FIG 39

FIG. 36. — An imperfectly rough guinea-pig. Produced by mating the guinea-pig, shown in Fig. 32, with a particular smooth animal; female, 2005.

FIG. 37. — A silvered guinea-pig. One in whose coat occur white hairs interspersed with pigmented ones. The amount of the silvering has been greatly increased by selection.

FIG. 38. — A. Front feet of an ordinary guinea-pig. B. Its hind feet. D. Hind feet of a race four-toed on all the feet. C. Ordinary condition of the hind feet of young obtained by crossing B with D.

FIG. 39. — Diagram showing variation in the color-pattern of hooded rats.

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able and was transmitted from generation to generation.¹ See Fig. 36.

It is an important question whether potency is a property of the unit-character or of the gamete, i. e. whether it affects all the characters transmitted by a gamete or only a particular one. Practical breeders as a rule favor the idea of gametic rather than of unit-character potency, but this is probably due to a failure to discriminate between the two. They designate as "prepotent" an individual supposed to impress *all* its characters upon the offspring, but it is very doubtful whether such individuals exist. It is easy to mistake for an animal potent in *all* respects one which is potent in one or two important respects only, especially if the observer is unaware, as every one has been until quite recently, that one character is independent of another in transmission.

Conditions other than the character of the gametes themselves may determine the extent

¹ An alternative explanation is possible, viz. that the development of the fourth toe depends upon the inheritance of several independent factors, and that the more of these there are present, the better will the structure be developed. The correctness of such an interpretation must be tested by further investigations.

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to which a character develops in the zygote, i. e. the completeness or incompleteness of its dominance in a particular case. For example, in salamanders, which apparently, like mammals, form skin-pigments of different sorts, such as yellow, brown, and black, Tornier has found that by feeding one may control the proportions in which chromatophores of the several sorts are formed in the skin. Abundant feeding causes preponderance of pigment of one sort, scanty feeding causes preponderance of pigment of another sort. Here external conditions determine the degree of development of characters. In other cases internal conditions may exercise a controlling influence. Thus in cattle the capacity to develop horns is a semi-potent unit-character, behaving as a recessive in crosses, heterozygotes developing only "scurs," that is, mere thickenings of the skin, or else no trace of horns at all. In sheep, moreover, horns are more strongly developed in males than in females, the presence of the male sex-gland in the body, or rather probably some substance given off into the blood from the sex-gland, favoring growth of the horns.

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In merino sheep the male has well-developed horns but the female is hornless; yet if the male is castrated early in life no horns are formed.

When a breed of sheep horned in both sexes, such as the Dorset, is crossed with one hornless in both sexes, such as the Shropshire, horns are borne by the male but not by the female offspring. Both sexes, however, are heterozygous in horns, as is shown by their breeding capacity. For in F_2 occur both horned and hornless individuals in both sexes. The hornless males and the horned females prove to be homozygous, but the horned males and the hornless females may be either heterozygous or homozygous. Accordingly the character, horns, behaves consistently as a dominant character in one sex, but as a recessive in the other. Further, the presence of the male sex-gland in the heterozygote raises the potency of the character, horns, from semi-potent to uni-potent, as the result of castration shows.

It is impossible to be certain that in a hornless race the character horns has been wholly lost. It may merely have fallen so low in potency that under ordinary conditions it pro-

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duces no visible structures. The occasional occurrence of an imperfectly horned animal as a sport within a hornless race need not, then, occasion surprise. It would be a variation of the same sort as the extra toe in guinea-pigs (see Fig. 38), which, from a single sport, was built up by selection into a well-established race within a very few generations. This character, seemingly lost from the germ-plasm for an indefinite period, had perhaps merely fallen so low in potency that it no longer produced the fourth toe on the hind foot, though this was still present on the front foot. In the variant observed, the first polydactylus guinea-pig of my stock, the toe was imperfectly developed on one hind foot, doubtless as the result of an unusually potent condition of the character in one of the gametes which produced the individual. This manifestation of the character, though feeble, was sufficient to afford a guide for selection of those individuals which formed the most potent gametes, and so a polydactylous race was formed by selection and inbreeding.

Great as has been the contribution of Mendelian principles to our knowledge of heredity,

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they do not reduce the whole art of breeding to the production of new combinations of unit characters through crossing. Selection is required also, not merely among different combinations of unit-characters, but also among individuals representing the same combinations selection is required of those possessing the desired characters in *greatest potency*. The further rôle of selection in evolution we shall need to consider in a subsequent chapter.

BIBLIOGRAPHY

CASTLE, W. E., and LITTLE, C. C.

1909. "The Peculiar Inheritance of Pink Eyes Among Colored Mice." *Science, N. S.*, 30, pp. 312-314.

COUTAGNE, G.

1902. "Recherches expérimentales sur l'hérédité chez les vers-a-soie." *Bull. Sci.*, 37, pp. 1-194, 9 pl.

MORGAN, T. H.

1909. "Breeding Experiments with Rats." *American Naturalist*, 43, pp. 182-185.

DE VRIES, H.

1901-03. "Die Mutationstheorie." Leipzig, Veit and Co.

See also the Bibliographies to Chapters III., IV., and V.

CHAPTER VII

CAN MENDELIAN UNIT-CHARACTERS BE MODIFIED BY SELECTION?

IF, as suggested in the last chapter, the potency of a character in crosses may be modified by selection, why may not the character itself be modified by selection, or are not the two things perhaps identical, viz. modification of the potency of a character and modification of the character itself? Darwin firmly believed that the characters of organisms can be modified by selection, and he made this the foundation stone of his theory of evolution. De Vries and Johannsen, however, have taught us a different doctrine, maintaining that selection is able to affect characters in superficial and transitory ways only, that the slight variations in characters which we see everywhere among organisms have no evolutionary significance or permanent value; that they come and

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go like the wavelets on the ocean beach, but have no more relation to evolution than the waves have to the tides. The brilliancy of the Mutation theory of De Vries, coupled with his great service to biology in rediscovering the Mendelian laws, has somewhat dazzled our eyes and led us, I think, to accept too readily his views concerning the efficacy of selection also. Ten years' continuous work in selection convinces me that much can be accomplished by this means quite apart from the process of mutation. The work of De Vries himself argues strongly in favor of this idea. To be sure, his interpretation of it is adverse to selection, and has seemed to most of us at times overwhelmingly convincing; but from his interpretation we may fairly appeal to the record of the work itself, and with this compare the record of our own work.

One of the most extensive selection experiments conducted by De Vries was made on the common buttercup, *Ranunculus bulbosus*, which occurs as a weed in pastures and meadows in this country as well as in Europe. It has, as is known, regular 5-petaled flowers. An ex-

amination of 717 flowers in the field made by De Vries in 1887 showed the rather frequent occurrence of 6 and 7 petaled flowers also, the average number of petals in the entire collection being 5.13. De Vries set himself the task to see if the proportion of many petaled flowers could be increased or the number of petals to a flower be further increased. In both these respects he succeeded surprisingly well. As a result of five successive selections the average number of petals was raised from 5.6 to 8.6, the upper limit of variation from 8 to 31, and the mode (or commonest condition) from 5 to 9. Singularly enough De Vries concludes, in accordance with general ideas which he had adopted, that selection had in this case done practically all that it could accomplish, that further selection, while it might advance the average somewhat farther, would have no permanent effect in modifying the type. This belief seems to have rested on considerations such as these. De Vries had found, as had others, that variations which are heritable have their origin in the germ-cells only. He recognized that the tendency to produce double

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flowers in the buttercup is a heritable variation and supposed it to be a unit-character, and so to conform with Mendel's law.

Now, if the tendency to produce double flowers were a simple Mendelian character it could exist in only three conditions, — that of a recessive, that of a homozygous dominant, or that of a heterozygous dominant. But recessives and homozygous dominants are pure, that is, they form only one type of gamete, and selection therefore from among their progeny could produce no new type. As regards the heterozygous dominant type, this would itself be unfixable, and selection could accomplish nothing permanent except by isolating a homozygous type. But such types should all be in evidence within two generations; therefore, if a completely and permanently double type had not been discovered within the five generations covered by the experiment, such a type was not to be expected at all from the material in hand, unless either a wholly new unit-character were introduced or an existing one were profoundly modified. De Vries considers changes of both these sorts possible.

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He calls them *mutations*, and regards them as the *sole means* of evolutionary progress. But it is a peculiarity of his mutation theory that it regards only *large* changes in unit-characters as having any permanency, namely, such changes as mean a practical making over of the character. To borrow a figure from Bateson, just as the gas carbon monoxide, CO , may change into a very different gas, — carbon dioxide, CO_2 , — by taking up a single atom of oxygen, but can make no less extensive change, since oxygen atoms do not split; so, according to De Vries, a unit-character may not change unless it changes profoundly. Various circumstances may modify the degree of its expression, but these are without permanent effect, since the character itself remains unchanged.

But there are both *a priori* and experimental grounds for questioning the correctness of De Vries' conclusions. It is known that the chemical compounds within the germ-cells are not so simple in composition as CO and CO_2 . They are very complex substances, made up, it is thought, of very many atoms, often hun-

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dreds in a single molecule. If so, it is quite possible that an atom or two might be transposed in position within the molecule without wholly altering its chemical nature, and that thus slight changes in the germ-plasm might result, which, however, would be as permanent as more profound changes.

The argument of De Vries against any permanent effect of selection in modifying unit-characters has been greatly strengthened by the subsequent work of Johannsen and Jennings. Johannsen has found that if one selects from a handful of ordinary beans the largest seeds and the smallest seeds, and plants these separately, the former will produce beans of larger average size than the latter. Selection here has effect.

But if the selection is made, not from a general field crop of beans, but from those beans borne on one and the same homozygous mother plant, then the progeny of the selected large seed will be no larger than that of the selected small seed. Selection here is without effect.

The different result in the two cases may be explained, according to Johannsen, on

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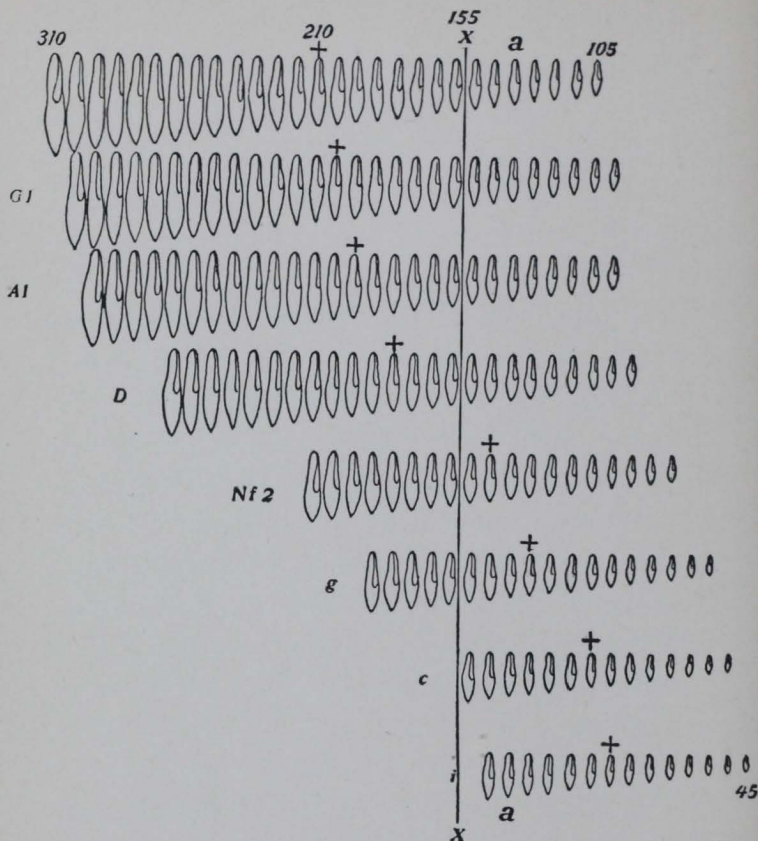


FIG. 40. — Diagram showing the variations in size of eight different races of paramecium. Each horizontal row represents a race derived from a single parent individual. The individual showing the mean size in each race is indicated by a cross placed above it. The mean of the entire lot is shown at X—X. The numbers show the measurements in microns. (After Jennings.)

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the principle of the "pure line." The progeny of a single self-fertilized homozygous bean plant constitute a pure line. They are all alike, so far as the hereditary transmission of size is concerned, for they are all derived from like gametes. The differences in size which occur among them are due to differences in nutrition, not to germinal differences, and they are not transmitted. But in a mixed population of beans, such as is represented by a field crop, differences of size occur which are due to heredity as well as those which are due to the environment. In the case of the former, selection naturally has effect; in the case of the latter, it does not.

Jennings has obtained similar results in his studies of paramecium,—a one-celled animal which multiplies asexually by dividing into two similar parts. It lives in stagnant water and may be reared in great numbers in a hay-infusion, for it multiplies with great rapidity, dividing two or three times within twenty-four hours. The variations in size which occur in paramecium are shown in Fig. 40.

When from an ordinary culture of parame-

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cium Jennings selects the largest and the smallest individuals respectively, he finds that the descendants of the one lot will be of larger size than the other. This looks like an effect of selection upon racial size. But if selection is made not within a mixed population but among the descendants of a single individual, it is found that the descendants of large individuals are of no greater average size than those of small individuals.

The explanation of this fact is to be found in the existence of what Johannsen has called pure lines. Jennings has been able to isolate eight distinct pure lines of paramecium differing in average size, as shown in Fig. 40. The range of variation in size within one of these races is great, but if one selects extremely large or extremely small individuals within the same pure line, i. e. among the asexually produced descendants of the same animal, no change in the average size of the race is brought about.

A very different result is obtained, however, if one mixes together several pure lines and then selects from the mixed race on the basis of size.

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The larger animals then produce larger average offspring and *vice versa*. An examination of Fig. 40 will show why. Animals of the same absolute size are there placed in the same vertical row. If, now, one selects from the mixed population only the largest individuals, he will naturally secure representatives of only two or three pure lines, viz. of those lines which are characterized by the largest average size, and which, therefore, will produce large average offspring. If on the other hand he selects extremely small individuals, he will secure representatives of only the smallest races, which naturally will produce small offspring, so that selection seems to be effective in modifying racial size, but in reality it does this by sorting out the elementary constituents of the race.

It is impossible to deny the soundness of the reasoning of Johannsen and Jennings. It is perfectly clear that the effects of selection *should* be more immediate and much greater in the case of a mixed race than in that of a pure line, but is it certain, as assumed by them, that selection is *wholly* without effect in

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the case of a pure line? We know the effects should be *less*, but are they *nil*? Concerning this matter we are perhaps justified in awaiting further evidence. For in the case of beans and of paramecium alike size is subject to very great variation through the influence of nutrition. Variations due to this cause are naturally not inherited, since the germ-cells are not affected by them, but only the body. But is it not possible that along with the striking size differences due to nutrition there may occur also slight size differences due to germinal variation within the pure line, that is owing to variations in the potency of the same unit-character or combination of unit-characters? To be sure, Johannsen and Jennings have not observed these, but this does not prove their non-existence. Others may yet be able to do so; indeed one case is already on record in which such observations have been made in the case of a small crustacean (or water-flea), *Daphnia*.

Daphnia is a small transparent animal, about the size of a pin-head, which occurs in enormous numbers in fresh-water lakes and pools,

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forming a large part of the food supply of fresh-water fishes. It multiplies chiefly by the production of unfertilized eggs, — those which undergo no reduction and which develop without fertilization into an individual like the parent. The germinal composition, therefore, of all descendants produced in this way by the same mother should be identical, unless germinal composition can be modified in other ways than by reduction and recombination of unit-characters. Now the German zoölogist, Woltereck, has shown that, among the offspring developed from the unfertilized eggs of the same mother *Daphnia*, variations do occur which are heritable, so that if one selects extreme variants he obtains a modified race. Systematic zoölogists recognize as a generic distinction between *Daphnia* and *Hyalodaphnia* absence from the latter of the rudimentary eye found in *Daphnia*. Woltereck observed that in a pure line of *Hyalodaphnia* the rudimentary eye, usually wanting, may occur in individual cases. He found further that it occurred in varying degrees of development, which ranged all the way from a group of

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pigmented cells outside the brain, through stages in which cells were present without pigment, and others in which pigment was visible within the brain but no cells outside it were developed, and finally to those in which all traces of the eye had vanished, cells and pigment alike. By selection in three successive generations of the mother having the rudimentary eye best developed offspring were obtained, 90 % of which had the pigmented eye, and which would therefore pass for animals of a wholly different genus. The degree of development of the organ in the last generation was also greater than in the previous generations. Here within a pure line produced by parthenogenesis selection served to augment both the degree of development of an organ and the frequency of its occurrence within the race, a result precisely parallel to that which I obtained some years ago by selection in the case of a rudimentary fourth toe in the guinea-pig. The experiment with *Daphnia* is not open to the objection that may be offered to the guinea-pig experiment, that it is possibly a result of gametic segregation and recombina-

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tion, for in *Daphnia* the reproduction was exclusively by unreduced and unfertilized eggs.

The rudimentary eye of *Daphnia* is an organ the development of which, so far as observed, is wholly independent of environmental influence; but the case is different with another structure of *Daphnia*, upon which also Woltereck made observations, namely, a projection or spine borne on the head of the animal. This is not a constant structure, but is sometimes present, sometimes wanting altogether, in the same pure line. In extreme cases it forms a great angular extension of the head forward. To a considerable extent its development is subject to control through the temperature of the surrounding water, but independently of such influence the degree of its development varies and is heritable. Although in general, just as in the experiments of Johannsen and Jennings, selection of animals with the best-developed spine did not increase the degree of development of the organ or the frequency of its occurrence, yet in individual cases such increase was observed, so that the structure occurred in over 50 % of the offspring. In

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such cases, then, it would seem that along with the cases due to environmental influence occurred others due to germinal variation. Although selection of the former would not influence the race permanently, there is every reason to think that the latter would so influence it, and did in the experiment.

Accordingly the results of Johannsen and Jennings on the one hand, and of Woltereck on the other, are not necessarily in opposition to each other. Woltereck's conclusions agree with those of Johannsen and Jennings so far as concerns the great bulk of the variations, those caused by external influences. All agree that they are not inherited. Woltereck, however, observes also, what the others have failed to observe, that along with the non-inherited variations occur other similar but less numerous ones which are inherited.

My own observations are entirely in harmony with those of Woltereck. Like him, I find that selection may modify characters. In several cases I have observed characters at first feebly manifested gradually improve under selection until they became established racial

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traits. Thus the extra toe of polydactylous guinea-pigs made its appearance as a poorly developed fourth toe on the left foot only. Only 6 % of the offspring of this animal by normal unrelated mothers were polydactylous, but among his offspring were some with better developed fourth toes than the father possessed. Such individuals were selected throughout five successive generations, at the end of which time a good four-toed race had been established. It was found in general that those animals which had best-developed fourth toes transmitted the character most strongly in crosses with unrelated normal animals. The percentage of polydactylous individuals produced in such crosses varied all the way from 0 to 100 %. By selection this percentage was increased, as was also the degree of development of the fourth toe in crosses.

Another character which made its appearance among our guinea-pigs, at first feebly expressed, was a silvering of the colored fur, due to interspersing of white hairs with the colored ones (see Fig. 37). The first individuals observed to have this character bore

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white hairs on the under surface of the body only. By inbreeding, a homozygous strain of the silvered animals was soon obtained, one in

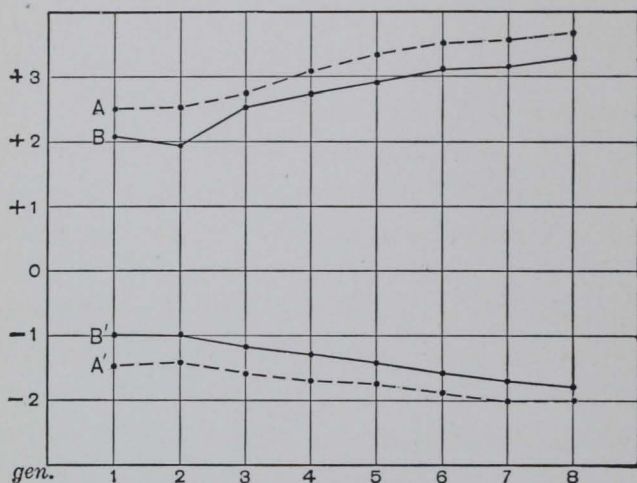


FIG. 41. — Chart showing effects of selection in eight successive generations upon the color-pattern of hooded rats. *A*, average condition of the selected parents in the *plus* series; *B*, average condition of their offspring. *A'*, average condition of the selected parents in the *minus* series; *B'*, average condition of their offspring.

which all the offspring were silvered to a greater or less extent. Selection was now directed toward two ends, — (1) to secure animals which were free from spots of red or white, a condition which was present in the

original stock, and (2) to secure extensive and uniform silvering on a black background. In both these objects good progress has been made. We have animals which are silvered all over the body except on a part of the head, and the percentage of such well-silvered individuals is relatively high.

But the most extensive selection experiment which I have personally observed is one in which I have been assisted by Dr. John C. Phillips (see Figs. 39 and 41). Selection in this case has been directed toward a modification of the color pattern of hooded rats, — a pattern which is known to behave as a recessive Mendelian character in crosses with either the self (totally pigmented) condition or the so-called Irish (white-bellied) condition found in some other rats. The extreme range of variation among our hooded rats at the outset of this experiment is indicated by the grades — 2 and + 3 of Fig. 39. Selection was now made of the extreme variates in either direction and these were bred separately. Two series of animals were thus established, — one of narrow striped animals, *minus* series; the

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other of wide striped, *plus* series. In each generation the most extreme individuals were selected as parents; in the narrow series, those with narrowest stripe; in the wide series, those with widest stripe.

TABLE I

Results of Selection for Modification of the Color-pattern of Hooded Rats.

	GENERA- TION.	AVERAGE GRADE, PARENTS.	AVERAGE GRADE, OFFSPRING.	NUMBER OF OFF- SPRING.
Plus series.	1	2.50	2.05	150
	2	2.51	1.92	471
	3	2.73	2.51	341
	4	3.09	2.72	444
	5	3.33	2.90	610
	6	3.51	3.09	834
	7	3.53	3.14	874
	8	3.65	3.30	91
				<hr/> 3,815
Minus series.	1	1.46	1.00	55
	2	1.41	1.07	132
	3	1.56	1.18	195
	4	1.69	1.28	329
	5	1.73	1.41	701
	6	1.86	1.56	1252
	7	2.00	1.70	1544
	8	2.03	1.78	713
				<hr/> 4,921

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The result of the selection is shown graphically in Fig. 41 (compare Table I). The offspring in the narrow series became with each generation narrower; those in the wide series became with each generation wider, with a single exception. In generation two the wide stock was enlarged by the addition of a new strain of animals. This caused a temporary falling off in the average grade of the young, the two series overlapping for that generation. No new stock was at any other time introduced in either series, the two remaining distinct at all times except in generation two. It will be observed that a change in the average grade of the parents is attended by a corresponding change in the average grade of the offspring. The amount of variability of the offspring is not materially affected by the selection, but the average about which variation occurs is steadily changed, as are also the limits of the range of variation.

The interesting feature of this experiment is the production, as a result of selection, of wholly new grades; in the narrow series, of animals having less pigment than any known type

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other than the albino; in the wide series, of animals so extensively pigmented that they would readily pass for the "Irish type," which has white on the belly only, but which is known to be in crosses a Mendelian alternative to the hooded type. By selection we have practically obliterated the gap which originally separated these types, though selected animals still give regression toward the respective types from which they came. But this regression grows less with each successive selection and ultimately should vanish, if the story told by these statistics is to be trusted. As yet there is no indication that a limit to the effects of selection has been reached.

From the evidence in hand we conclude that Darwin was right in assigning great importance to selection in evolution; that progress results not merely from sorting out particular combinations of large and striking unit-characters, but also from the selection of slight differences in the potentiality of gametes representing the same unit-character combinations. It is possible to ascribe such differences to little units additional to the recognized larger ones, but

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if such little units exist, they are indeed very little as well as numerous, and by adding to the effect of the larger ones they produce what amounts to modification of them.

BIBLIOGRAPHY

CASTLE, W. E.

1906. "The Origin of a Polydactylous Race of Guinea-pigs." *Carnegie Institution of Washington, Publication No. 49*, pp. 17-29.

JENNINGS, H. S.

1909. "Heredity and Variation in the Simplest Organisms." *The American Naturalist*, 43, pp. 321-337.

JOHANNSEN, W.

1909. "Elemente der exakten Erblchkeitslehre." G. Fisher, Jena, 516 pp.

DE VRIES, H.

(See Bibliography to Chapter VI.)

WOLTERECK, R.

1909. "Weitere experimentelle Untersuchungen über Artveränderungen, speciell über das Wesen quantitativer Artunterschiede bei Daphniden." *Verh. Deutsch. Zool. Gesellsch.*, pp. 110-172.