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

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

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

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

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.:

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

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

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,

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

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-

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.

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.

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-

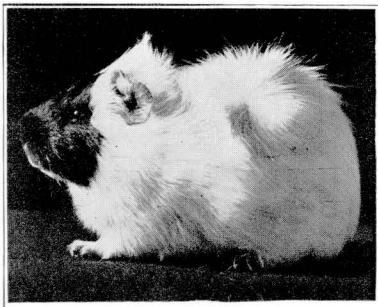

FIG 36

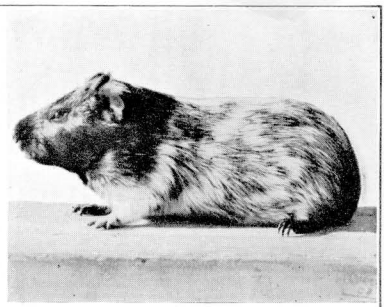

FIG 37

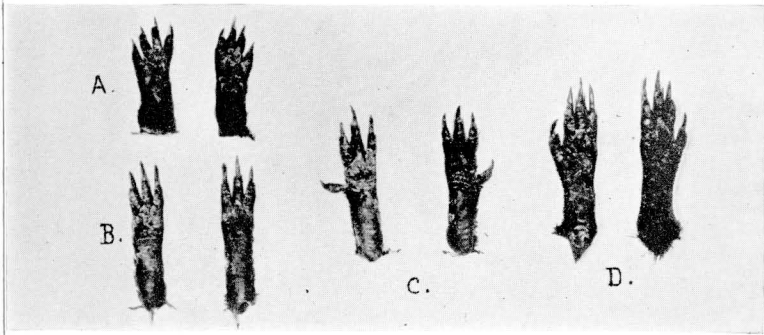

FIG 38

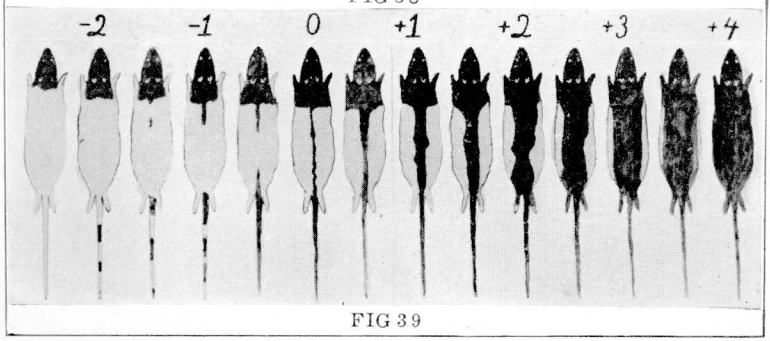

FIG 39

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.

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.

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.

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 unipotent, 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-

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,

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.

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