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THE PRODUCTION AND FIXATION OF NEW BREEDS.

By W. E. CASTLE, *Assistant Professor of Zoology, Harvard University, Cambridge, Mass.*

The art of animal breeding has been practiced by man since the earliest dawn of civilization. In many cases its products attained centuries ago a degree of excellence which we can scarcely hope to surpass, as in the horses of Arabia and the poultry of China. Of course, these and other breeds have since been modified in useful directions and are capable of further useful modifications; but for the needs of the time and place where bred, the horses and the poultry of centuries ago were probably not inferior to our own. In creating new breeds of domesticated animals, we are merely adapting to new and special conditions very ancient and excellent breeds. This is a work of the highest importance, and I have no desire to minimize it. But while we contemplate with satisfaction present attainments and prospects, let us not forget our debt to the past for taking wild species into domestication and moulding them to meet man's needs. To those unchronicled pioneer breeders we owe entirely the material with which we work.

We stand at the beginning of a new era in which breeding will pass from the condition of an art into that of a science. The difference will be that we shall know the reasons for our procedure, whereas the breeder of the past did not. We shall continue to produce breeds just as he produced them, but we shall know how we produce them, a thing of which he was largely ignorant. His work was largely haphazard; ours will be orderly. He experimented until he got what was wanted or until he found his ideal unattainable; we shall produce what we want, and knowing what is attainable will not attempt the impossible. He progressed indirectly, awaiting the caprice of chance; we shall go straight to the goal, knowing the way beforehand.

No finer swords, perhaps, were ever made than those which the Saracens produced six centuries ago at Damascus and Toledo, but to produce steel of the many varieties now in use, and in the quantities required by the diversified industries of to-day would have been a task beyond the powers of the Saracen either to accomplish or to imagine. Scientific knowledge of metallurgy has brought about the change; no less revolutionary does the application of scientific knowledge to the art of animal breeding promise to be.

The first great advance made toward such a knowledge was taken by Gregor Mendel when he discovered the principle of unit characters in heredity, the principle, namely, that the various physical and physiological characteristics of individuals are transmitted in heredity as distinct units. An individual is nothing but the sum total of these unit characters, which it receives from its parents and hands on to its children. The ordinary individual has two parents and, for each unit character, it receives a contribution from either parent. When

the contributions made by the two parents are similar in character or when they unite to form a blend in the offspring, we are apt to overlook their separate existence. It is easiest to demonstrate the existence of units when a different contribution is made by either parent and when the inheritance is alternative between the two parental contributions. It was in this category of cases that Mendel's discovery of the principle of unit characters was made.

The practice of breeders had long accorded with the principle of unit characters, because that practice gave desired results. Now came a wholly unpractical man of science, a recluse, but a man who could give a reason, and that reason (the principle of unit characters) marks the first and greatest step yet taken in the transformation of breeding from an art to a science. Breeders knew that crossing of dissimilar parents induced variation; from variations so induced selection might be made of such variations as were desirable and these might be fixed by inbreeding. Further than this the analysis of the matter had not been carried. We now know, thanks to Mendel, that the variation following crossing is due largely to the production of new combinations of unit characters. Thus, in rats, to take an illustration from my own experience, coat pigmentation and coat pattern are distinct unit characters separately heritable. A cross between parents unlike in both particulars makes the matter entirely plain, leading to the production in offspring of the second generation of all the possible combinations of the units in question. A wild self-gray rat mated with a tame black hooded¹ one produces offspring all with the wild color and wild color pattern (though usually slightly modified); but when these young are bred together, there are produced in the next generation, four sorts of young representing the following combinations:

- (1) Wild color and wild pattern.
- (2) Tame color and wild pattern.
- (3) Wild color and tame pattern.
- (4) Tame color and tame pattern.

By selection, any or all of these combinations may now be fixed. The empirical breeder's idea that fixation of a new variation can be secured only by inbreeding, we now see, rested on a misconception. It is not the relatedness of parents which results in fixation, but the fact that they represent like combinations of characters. We might cross one pair of rats in Massachusetts and another one in California, and bringing the hybrids together in pairs secure complete fixation of the new varieties produced without ever pairing relatives. Here we get from the principle of unit characters a practical suggestion worth remembering, which allows fixation of characters without inbreeding.

Not all characters give alternative inheritance; in the case of some a blend (or condition intermediate between that of the two parents)

¹A "hooded" rat is white all over except on the head and shoulders and along a median dorsal back-stripe, in which regions it bears either black or gray pigmentation.

results from a cross. This seems to be true in mammals as regards general size, dimensions of the skull and long bones, of the tail, and of the ears. A variation produced as a blend needs no fixation. It breeds true from the start, as I pointed out at our meeting two years ago in the case of ear-length of rabbits. In the case of blending characters no less than in that of alternative ones, the principle of unit characters holds good. Hair color, hair length, and coat pattern, are in rabbits independent unit characters, which can be combined in any desired way in conformity with the laws of alternative heredity. Ear length is another unit, distinct from all three hair characters and capable of combination in any desired way with them, but harder to manipulate simultaneously because of its blending nature. I pointed out at our meeting two years ago a method of fixing simultaneously characters which blend and those which do not.

Perhaps the most important extension which has been made of Mendel's law consists in the demonstration (chiefly by Tschermak, Cuénot, and Bateson) that certain characters are produced only when two or more separately heritable factors are present together. Such a character does not conform with the simple Mendelian laws of inheritance, but its factors do. Herein lies the key to the explanation of so-called heterozygous characters and to the practical process of their fixation. This same principle serves to explain also atavism or reversion, and the process by which reversionary characters may be fixed.

When purebred 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. All black races behave alike in crosses with the same red individual, but among red animals individual differences exist. Some, instead of behaving like Mendelian recessives, produce in crosses with a black race a third apparently new condition, but in reality a very old one, the agouti type of coat found in all wild guinea-pigs, as well as in wild rats, mice, squirrels and other rodents. In this type of coat, red 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 (*A-A*) in character, others are heterozygous (transmit it in half their gametes only), while others lack it altogether. Further observations show that it is independent

in its inheritance of both black and red; it is in fact an independent Mendelian character, which can become visible only in the presence of both black and red, because it is a mosaic of those two pigments.

The chart (Fig. 1) 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 separates B from R .

FIG. 1.—Diagram showing how the three independent characters, B (black), R (red), and A (agouti), are transmitted in the production and fixation of an agouti race. A circle represents a reproductive cell (gamete); gametes united in pairs form zygotes (new individuals). The first horizontal row shows the kinds of gametes which unite to produce the reversion (second row). In the third row, are shown the four kinds of gametes formed by the reversionary individual; and, in the fourth row, the four kinds of agouti individuals produced by different combinations of those gametes. Below are indicated their expected numerical proportions and the kinds of young which they will respectively produce in crosses with red individuals (R).

That division accordingly may occur either so as to form gametes B and RA respectively, or what is equally probable so as to produce gametes BA 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 RA , and from unions of RA with RA ; we expect agoutis to be produced by any gametic union which brings together the three factors B , R , and A . There are 4 chances in 16 for the occurrence of such a union, when the reversionary agoutis are bred together. In fact, however, agoutis are produced much oftener. Approximately 9 out of 16 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 three sorts as regards breeding capacity. The first sort produces the three kinds of young, agouti, red, and black: the second sort produces only agouti young and red young; and the third sort produces only agouti young and black young. A fourth sort, known to exist but not yet obtained in these experiments, will produce only agouti young, *i. e.*, will represent the fully fixed agouti type.

In the chart (Fig. 1) I have 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. Only a few animals of this generation have yet been fully tested, but it is clear that the class indicated at the left in the chart is as expected the largest, and the class indicated at the right (not yet obtained) will be the smallest.

FIG. 2.—Diagram illustrating the nature of heterozygous characters and the mode of their fixation. For explanations, see text.

These experiments make it clear that *R* as an independent gametic factor is not necessary to the production of the agouti character, but that any gametic union which includes both *B* and *A* will produce an agouti individual. Yet a microscopic examination of the agouti hair shows that red pigment is present in a distinct band near the hair-tip. As a matter of fact all black individuals, even when they breed true, probably form some red pigment along with the black, but its presence is overlooked when the more opaque black is distributed throughout the whole length of the hair. When, however, black is excluded from the hair-tip, the red then becomes visible as the agouti marking, elsewhere the hair appears black. Red, then, we may assume, is always present with black in sufficient quantities to produce the agouti marking if the factor *A* is present (absence of black from the hair-tip). This explains why blacks never give the reversion in any sort of cross, but it is always brought about through the agency of the *red* parent. If a black individual contained the factor *A*, it would not be a black individual, but an agouti one.

The existence of a third factor, *A*, in cases of reversion in coat-character among rodents has been heretofore overlooked merely because it does not represent a distinct pigment or set of pigments, but consists in a particular kind of pigment distribution on the individual hairs. The agouti hair is due to a definite cycle of activity of the hair follicle in forming its pigments, first black, then red, then black; the wholly black hair is due to a continuous process of pigment formation without alternation in the character of the pigments produced. The relation between agouti and black is precisely the same as that between short hair and long hair, due likewise to differences in follicle activity, as I have elsewhere shown, but inherited quite independently.

FIG. 3.—Diagram showing how the characters B (black) and R (red) are transmitted in the production and fixation of a brindle race from a self-black and a self-red one.

of hair pigmentation. Short hair is the result of a determinate growth cycle; the hair grows so long and then stops growing; long or angora hair is the result of indeterminate activity on the part of the hair follicle; the hair keeps growing so long as its follicle is alive.

We are now able to give a rational explanation of the origin of the various color varieties of rodents. The wild cavy transmits in all its gametes the three factors *A*, *B*, and *R*. By accident (mutation) a gamete has been formed which lacked *A*. When two such gametes come together the result was a black individual, and this individual would breed true. Here is the explanation of our occasional black squirrels, porcupines, and the like. If by a further mutation *B* is lost, leaving *R* alone, a red race is produced which will breed true and will not give reversion on crossing with blacks. Such are ordinary red guinea-pigs.

But if mutation is directly from the wild or agouti condition, ABR , by loss of B , leaving AR , then there is produced a red not different from ordinary reds in appearance, but which will give reversion in crosses with black.

The albino (or wholly white) mutation, which is frequently found in wild as well as in tame rodents, is not due, as might be supposed, to simultaneous loss of the three factors A , B , and R , for albinos can be shown to possess some one, some two, and some all three of these factors. They have, according to Cuénot, lost a certain other factor necessary for the production of pigment of any kind, an activating or ferment-like factor.

It has been observed that one mutation is often followed by another. DeVries in his "Mutationstheorie" speaks repeatedly of periods of mutation. We can begin to see the significance of this; given one mutation, we can produce others. Suppose, for example, that we possess agouti and ordinary red varieties only and desire black, we are not compelled to await a mutation to produce it; we can cross red with agouti and obtain black in the second generation. This is not hypothesis merely; its correctness has already been in part demonstrated. Thus, in one experiment, there was employed an agouti of the formula $AB-AR$ (which gave only reds and agoutis in crosses with red), but the agoutis so produced when mated in the same way as the parent gave blacks as well as reds and agoutis, for they were of the formula $AB-R$. From such animals homozygous blacks ($B-B$) are readily obtained.

To produce a red variety from agoutis and blacks alone would not be so easy; it would be necessary either to await a mutation or to work by the slow process of selection from continuous variations in the intensity of blacks under cross-breeding with agoutis. In mice and rabbits as well as in guinea-pigs, red (or yellow) varieties are well-known, but in rats yellow has never been obtained separate from black, though black and agouti varieties are common, both wild and in captivity.

We now know what the fixation of a heterozygous character implies. When A and B are crossed, we obtain C . C is due either simply to co-existence of A with B , or to the co-existence 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 which produce C . On the first hypothesis, the zygote is $A-B$ (Fig. 2), and the resultant is equivalent to C . Fixation will consist in getting a zygote of the formula $AB-AB$; every gamete formed will then bear the equivalent of C , viz. AB . On the second hypothesis, the zygote is either $AC-B$ or $A-CB$, (Fig. 2); fixation will consist in obtaining a zygote $ACB-ACB$; every gamete formed will then contain the three factors A , C , and B . This latter case is illustrated in the production of fixed agoutis from a cross of black with red, as already explained (Fig. 1).

The first mentioned case is well illustrated in the production of homozygous (*i. e.*, fixed) brindles from crossing of black with red

(Fig. 3). A single cross of black with red (when not attended by reversion, *i. e.*, when the factor *A* is not present) produces commonly black individuals of a reddish hue, as already stated. These individuals form gametes of the two sorts, *B* and *R*. Repeated crossing, however, is apt to produce blacks which bear patches of red hair interspersed with the black. Such animals we may call brindles. Breeding these together we may obtain (1) brindles which produce brindles and blacks (*B-BR*, Fig. 3); (2) those which produce brindles and reds (*R-BR*, Fig. 3); and (3) brindles which breed true, *i. e.*, are fixed (*BR-BR*, Fig. 3). The fixation is really due (1) to contamination of black with red, so that gametes containing black contain also fragments of red along with the black; and (2) to the formation of a zygote out of such contaminated gametes.

To recapitulate, where Mendelian (or alternative) inheritance is involved, new characters are produced by cross breeding in one of two ways: First, a new character may be produced by the becoming visible of an element previously invisible in one of the parents; or second, the characters brought together by the cross may form a mosaic different from either parental condition by itself. Fixation of the new character will consist in either case in securing gametes which separately contain all the factors necessary for the production of the new character.

The question now arises: How long will it take to secure fixation? To this we may reply: All will depend upon how the new character has been produced; if by bringing together factors previously separated (as in the agouti reversion), complete fixation may be secured in two generations. If, however, the new character is a mosaic of alternative conditions (as of self-red and self-black) fixation will probably require much longer; one cannot in advance say how long. In this case, gametic contamination is involved, the production, out of a $B + R$ zygote, of *B* gametes containing fragments of *R*, or of *R* gametes containing fragments of *B*, instead of the theoretical pure *B* and pure *R* gametes. We cannot say in advance how soon this contamination will occur. All we can say is that the more sharply alternative the inheritance and the more complete the dominance in a first cross, the less likely is contamination to occur, for experience shows that where dominance is most perfect, segregation is most complete. Gametic contamination is non-Mendelian, it borders on *blending* inheritance, and will occur most speedily when the inheritance deviates most from the Mendelian type. When the inheritance is completely blending no fixation at all of the hybrid character is required; it is already fixed.

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