CHAPTER VIII

MENDELIAN INHERITANCE WITHOUT DOMINANCE, "BLENDING" INHERITANCE

WE shall now discuss a seemingly different type of inheritance from that discovered by Mendel, — one in which the offspring are a true intermediate or *blend* between the parents, and in which the occurrence of segregation has not in all cases been certainly established.

Differences in size between parents have been found to behave in this blending fashion. Rabbits are apparently favorable material in which to study size inheritance, for some races are fully twice as large as others. If a large rabbit is crossed with a small one the young are of intermediate size, and the F_2 offspring show no such segregation into large, small, and intermediate individuals as a simple Mendelian system would demand. For this reason size has been de-

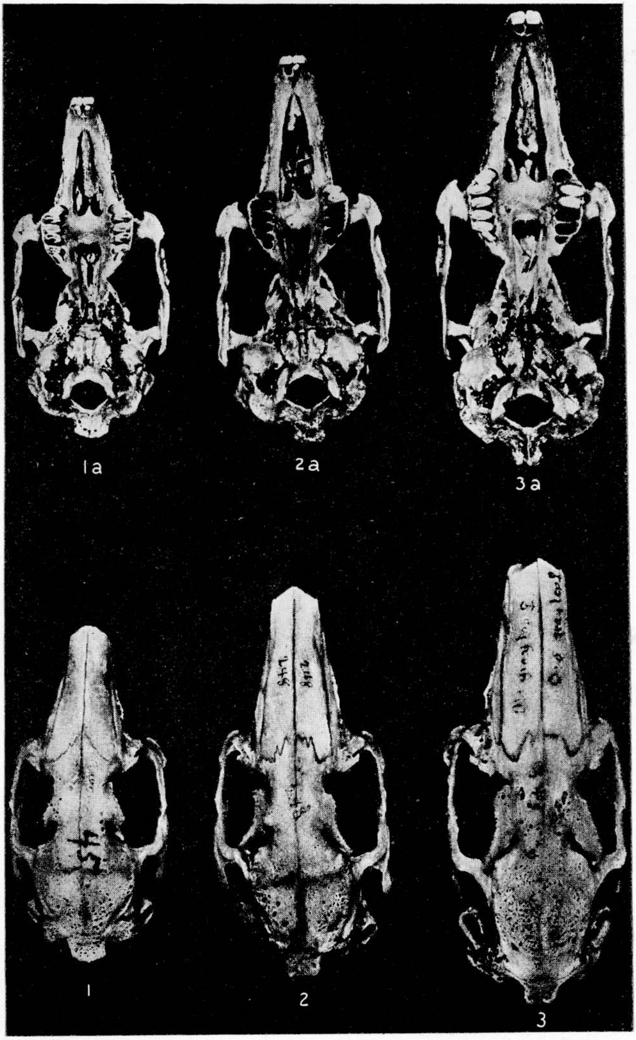

Fig. 42.—Skulls of three rabbits. Father (1 and 1*a*), mother (3 and 3*a*), and son (2 and 2*a*).

scribed as a non-Mendelian, non-segregating type of inheritance, but recent discoveries place this interpretation in doubt. Let us first consider what are the observed facts and afterward the interpretation.

Fig. 42 shows the skulls of three rabbits,—of the father at the left, of the mother at the right, and that of the son between. Notice the fully intermediate or blended character of the son's skull as regards both absolute dimensions and proportions. The intermediate character was possessed also by the next generation of offspring. Now this same cross, while producing a blend in size and ear-length, was yielding dominance and segregation of coat-characters. Fig. 43 shows a picture of the rabbit with the small skull in the cross just described. He was an albino and his fur was long. The mother, which had the large skull, was *a sooty-yellow rabbit, with short fur and* long ears (see Fig. 44). The son is shown in Fig. 45. His fur was black and short, the albinism and long fur of his father having become recessive in the cross in accordance with Mendel's law. The pigmentation is also intensified in the son, black having been received through the albino parent as a latent factor, which became fully active in the son. The excluded albinism, recessive in the son and his brothers and sisters, all seven of which were similar in character, reappeared among the grandchildren, as, for example, in the one shown in Fig. 46, which was short-haired. Other F_2 offspring were long-haired, some of them being albinos, others being pigmented. But the size and ear-length of the son were intermediate between the sizes and ear-lengths of his parents, and this intermediate character persisted without apparent segregation among the F_2 offspring. The animals in the pictures are unfortunately not all shown on the same scale, but the relative ear-lengths are sufficiently clear.

A Mendelian interpretation of blending inheritance, illustrated in the inheritance of skull-size and ear-length among rabbits, has been suggested by my colleague Dr. East, and by others, an interpretation in which Mendelian dominance is indeed wanting but segregation nevertheless occurs, yet not of a simple kind, involving one or two segregating factors, but involving several such factors. Before entering into this explanation it will be necessary to discuss a further extension of Mendelian principles recently made.

Some modified Mendelian ratios of particular interest have lately been obtained by the Swedish plant-breeder, Nilsson-Ehle (1909, Lunds Universitets Arsskrift) in crossing varieties of wheat of different color. When a variety having brown chaff is crossed with one which has white chaff, the hybrid plants are regularly brown in F_1 and 3 brown : 1 white in F_2, but a particular variety of brown-chaffed wheat gave a different result. In 15 different crosses it gave uniformly a close approximation to the ratio 15 : 1 instead of 3 : 1. The totals are sufficiently large to leave no doubt of this. They are 1410 brown to 94 white, exactly 15 : 1. This is clearly a dihybrid Mendelian ratio, and Nilsson-Ehle interprets it to mean that there exist in this case two independent factors, each of which is able by itself to produce the brown coloration, though no qualitative difference can be detected between them.

A still more remarkable case was observed in crosses between varieties of wheat of different grain-color. Red crossed with white gave ordinarily all red in F_1 and 3 red to 1 white in F_2, but a certain native Swedish sort gave only red (several hundred seeds) in F_2. This result was so surprising that one cross which had yielded 78 grains of wheat in F_2 was followed into F_3, with the following result:

50	plants	gave	only red seed;		expected	37
5	"	"	approximately	63 R: 1 W;	"	8
15	"	"	"	15 R: 1 W;	"	12
8	"	"	"	3 R: 1 W;	"	6
0	"	"		*all* white;	"	1

The interpretation given by Nilsson-Ehle is this. The red variety used in this cross bears three independent factors, each of which by itself is able to produce the red character. Their joint action is not different in kind from their action separately, though possibly quantitatively greater. The F_2 generation should contain 1 white seed in 64. It happens that none were obtained in this generation. The next generation should contain in a total of 64 individuals, the sorts actually observed as

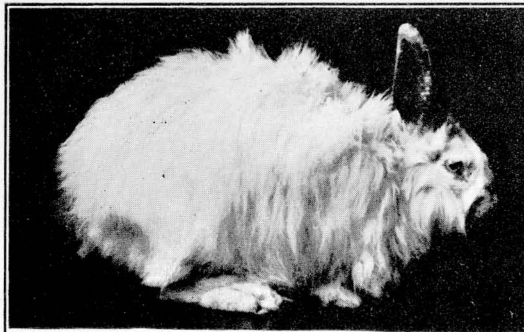
FIG. 43

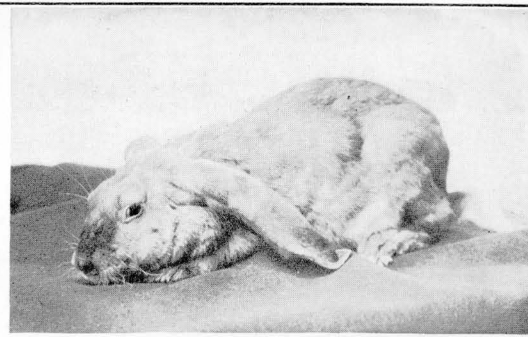
FIG. 44

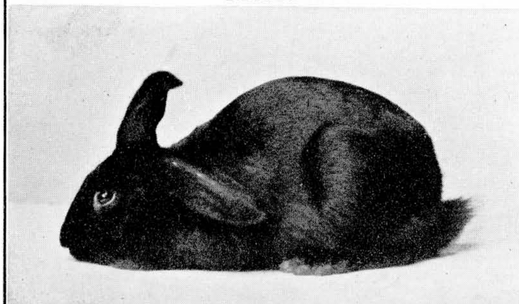
FIG. 45

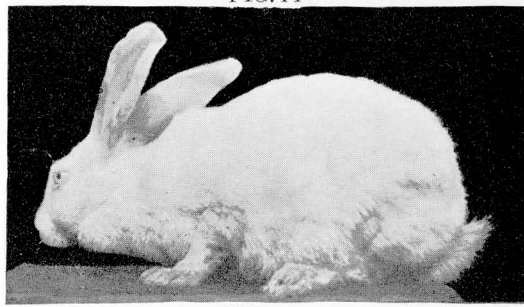
FIG. 46

FIG. 43. — A long-haired, albino rabbit, having erect ears. His skull is shown in Fig. 42 (1 and 1*a*).

FIG. 44. — A short-haired, sooty yellow rabbit, having lop ears. Her skull is shown in Fig. 42 (3 and 3*a*).

FIG. 45. — A short-haired, black rabbit, son of the rabbits shown in Figs. 43 and 44. Notice the intermediate ear length. His skull is shown in Fig. 42 (2 and 2*a*).

FIG. 46. — An F_2 descendant of the rabbits shown in Figs. 44 and 45.

well as a sort which would produce only white seed, the progeny namely of the expected white seed of F_2, but as that was not obtained, the all-white plant of F_3 could not be obtained either. The expected proportions of the several classes in F_3 are given for comparison with those actually obtained. The agreement between expected and observed is so good as to make it seem highly probable that Nilsson-Ehle's explanation is correct. Corroborative evidence in the case of maize has been obtained by Dr. E. M. East (Am. Naturalist, Feb., 1910).

This work introduces us to a new principle which may have important theoretical consequences. If a character ordinarily represented by a single unit in the germ-plasm may become represented by two or more such units identical in character, then we may expect it to dominate more persistently in crosses, fewer recessives being formed in F_2 and subsequent generations. Further, if duplication of a unit tends to increase its intensity, as seems probable, then we have in this process a possible explanation of quantitative variation in characters which are non-Mendelian, or at any rate do not conform with a simple Mendelian system. Consider, for example, the matter of size and skeletal proportions in rabbits. It is perfectly clear from the experiments described that in such cases no dominance occurs, and also that no segregation of a simple Mendelian character takes place, but it is not certain that the observed facts may not be explained by the combined action of several similar but independent factors, the new principle which Nilsson-Ehle has brought to our attention. Let us apply such a hypothesis to the case in hand.

Suppose a cross be made involving ear-lengths of approximately 4 and 8 inches respectively, as in one of the crosses made. The F_1 young are found to have ears about 6 inches long, the mean of the parental conditions, and the F_2 young vary about the same mean condition. If a single Mendelian unit-character made the difference between a 4 inch and an 8 inch ear, the F_2 young should be of three classes as follows:

Classes	4 in.	6 in.	8 in.
Frequencies	1	2	1

(Compare Fig. 47, bottom left.) The grandparental conditions should in this case reappear

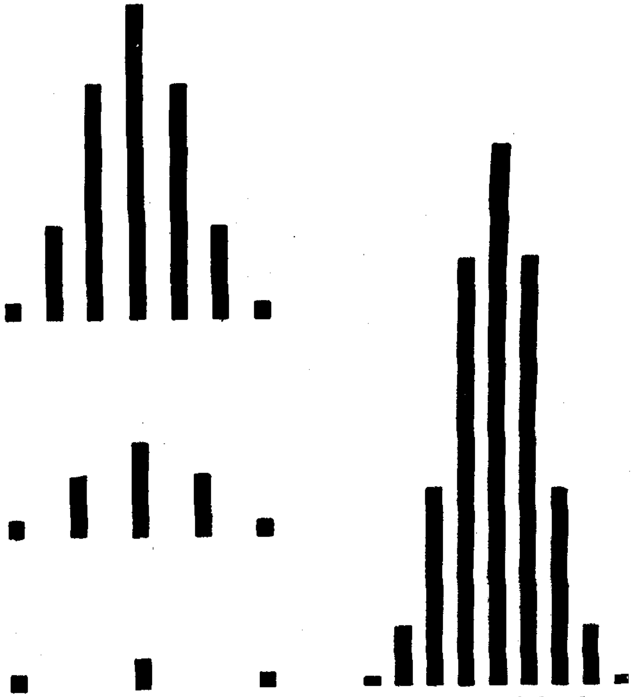

FIG. 47. — Diagrams to show the number and size of the classes of individuals to be expected from a cross involving Mendelian segregation without dominance. One Mendelian unit involved, bottom left; two units, middle left; three units, top left; four units, right.

in half the young. This clearly does not occur in the rabbit experiment. But if two unit-characters were involved, F_1 would be unchanged, all 6 inches, yet the F_2 classes would be more numerous, viz., 4, 5, 6, 7, and 8 inches, and their relative frequencies as shown by the height of the columns in Fig. 47, middle left, 1, 4, 6, 4, 1. The grandparental states would now reappear in 1/8 of the F_2 young, while 3/8 would be intermediate. It is certain, however, that in rabbits the grandparental conditions, if they reappear at all, do not reappear with any such frequency as this.

If three independent size-factors were involved in the cross, the F_1 individuals should all fall in the same middle group, as before, viz. 6 inches, but the F_2 classes should number *seven*, and their relative frequencies would be as shown in Fig. 47, top left. For 4 independent size-factors, the F_2 classes would be more numerous still, viz., 9 (Fig. 47, right), and the extreme ear-size of either grandparent would be expected to reappear in only one out of 256 offspring, while considerably more than half of them would fall within the closely intermediate classes included between 5½ and 6½ inches, the three middle classes of the diagram.

With six size-characters, the extreme size of a grandparent would reappear no oftener than once in 4000 times, while with a dozen such independent characters it would recur only once in some 17,000,000 times. It would be remarkable if under such conditions the extreme size were ever recovered from an ordinary cross.

There is one means by which we can determine with certainty whether in a particular case of seemingly blending inheritance segregation does or does not occur, namely, by comparing the variability of the F_1 and the F_2 generations. If segregation does not occur, F_2 should be no more variable than F_1, whereas if segregation does occur, F_2 should be more variable. For, in a segregating system, the F_1 individuals should all fall in a middle, intermediate group, but the F_2 individuals should be distributed also in classes more remote from a strictly intermediate position, that is, they should be more variable. But, in a non-segregating system, F_1 and F_2 individuals alike should fall in the same intermediate group, that is, they should have the same variability.

The matter should be easy of determination by observation of considerable numbers of F_1 and F_2 offspring. Investigations are now in progress to test this matter.

My colleague, Dr. East, has found clear evidence that, in maize, size-characters, although they give a blending result in F_1, nevertheless give segregation in F_2. The character to be considered relates to length of ear in corn. A single illustration will suffice. The variation in two pure varieties is shown in the two upper rows of Fig. 48. The " Length " of each class is given in centimetres, its frequency just below at " No. Var.," abbreviation for number of variates. The variation in the F_1 offspring obtained by crossing the two pure varieties is shown in the third row, and that of the F_2 offspring in the lowest row. Note that the variability in the F_1 generation is not increased; its range is intermediate between the range in the parental varieties. In the F_2 generation, however, the variability is so increased that it includes almost the entire range of both parental varieties, together with the intervening region.

In the light of this evidence it is clear that

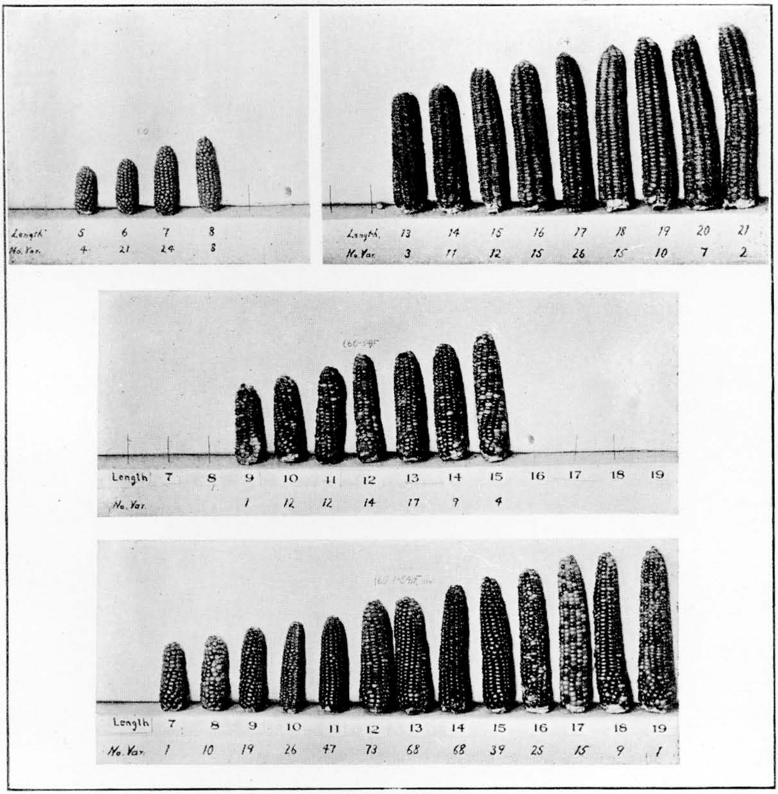

FIG. 48. — Photographs to show variation in ear length of two varieties of maize (upper row), of their F_1 offspring (second row), and of their F_2 offspring (third row). (After East.)

in maize, seemingly blending is really segregating inheritance, but with entire absence of dominance, and it seems probable that the same will be found to be true among rabbits and other mammals; failure to observe it hitherto is probably due to the fact that the factors concerned are numerous. For the greater the number of factors concerned, the more nearly will the result obtained approximate a complete and permanent blend. As the number of factors approaches infinity, the result will become identical with a permanent blend.

Theoretically it is important to know whether segregating units are involved in inheritance which we call blending; practically it does not matter much, since if these units are only as numerous as six or eight it will be practically impossible to undo the effects of a cross and to recover again the conditions obtaining previous to the cross. The great majority of the offspring both in the first and in subsequent generations following the cross will be strictly intermediate between the conditions crossed whether several units, an infinite number of units, or no units at all are involved.

A practical question of some importance is how to manipulate simultaneously blending (or seemingly blending) and Mendelian inheritance. This must be by a system of line-breeding in *alternate* generations, not in successive generations. To test the practicability of this matter I several years ago set myself the task of combining in one race the large size of some lop-eared, yellow rabbits which I had, with the albino character of some small white rabbits of common race. A first cross produced gray rabbits of intermediate size, but no white ones. On inbreeding the gray animals, there were obtained in F_2 white young of intermediate size. These were now crossed again with the original yellow stock, and again colored young were obtained, but now with 3/4 of the desired increase in size. These bred *inter se* again produced albinos, this time of the 3/4 size. A third cross with the original large stock brought the size up to 7/8 of that desired, and combined it in F_2 with the desired albinism. Having satisfied myself of the correctness of the method, the experiment was now discontinued. By further crosses, especially with a fresh lop-eared stock, to avoid ill-effects of inbreeding, the size could have been still further increased, with judicious selection doubtless up to the extreme size of colored lop-eared rabbits.

The general conclusion to be drawn is that in attempting to combine in one race by cross-breeding characters which exist separately in different races, one should first inquire very carefully how each character, in which the races differ, behaves in transmission, for on the answer to this question should depend the mode of procedure to be chosen.

If simple Mendelian characters only are concerned, nothing is required but to cross the two races and select from the second generation offspring the desired combination. If blending characters only are concerned and F_1 yields the desired blend, this is secure without further procedure, except possibly selection to reduce its variability; but if the desired blend is not yet secured, further back-crossing with one race or the other may be necessary. If, finally, both blending and Mendelian characters are simultaneously involved in a cross, then the method of combined line-breeding and selection in alternate generations, already described, should be adopted.

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