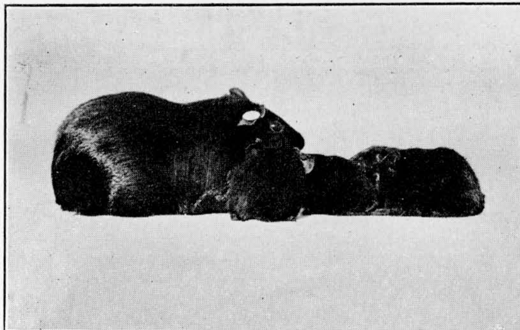
CHAPTER III

MENDEL'S LAW OF HEREDITY

GREGOR JOHANN MENDEL was a teacher of the physical and natural sciences in a monastic school at Brünn, Austria, in the second half of the last century. He was, therefore, a contemporary of Darwin, but unknown to him as to nearly all the great naturalists of the period. Although not famous in his lifetime, it is clear to us that he possessed an analytical mind of the first order, which enabled him to plan and carry through successfully the most original and instructive series of studies in heredity ever executed. The material which he used was simple. It consisted of garden-peas, which he raised in the garden of the monastery. The conclusions which he reached were likewise simple. He summed them up, the results of eight years of arduous work, in a brief paper published in the proceedings of the local scientific society. There they remained unheeded for thirty-four years, until their author had long been dead. Meantime biological science had made steady progress. It reached the position Mendel had attained in advance of his time, and Mendel's law was rediscovered simultaneously in 1900 by De Vries in Holland, by Correns in Germany, and by Tschermark in Austria. It gratifies our sense of poetic justice that to-day the rediscovered law bears the name, not of any one or of all of its brilliant rediscoverers, but of the all-but-forgotten Mendel.

The essential features of this law can best be explained in connection with some illustrations, which I choose for convenience from my own experiments. If a black guinea-pig of pure race (Fig. 14) be mated with a white one (Fig. 15), the offspring will, as explained on page 10, all be black; none will be white. To use Mendel's terminology, the black character dominates in the cross, while white recedes from view. The black character is, therefore, called the *dominant* character; white, the *recessive* character.



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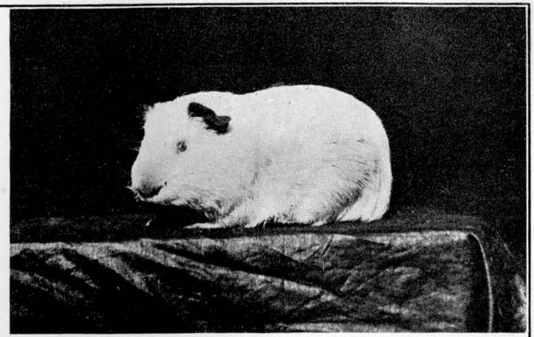

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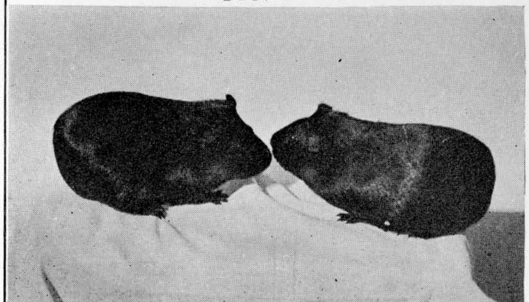

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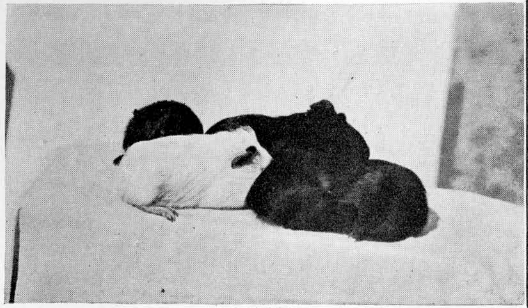


FIG.17.

FIG. 14. — A black, female guinea-pig, and her young.

FIG. 15. — An albino male guinea-pig, father of black young like those shown in Fig. 14.

FIG. 16. — Two of the grown-up young of a black and of an albino guinea-pig. Compare Figs. 14 and 15.

FIG. 17. — A group of four young, produced by the animals shown in Fig. 16.

But, if now two of the cross-bred black individuals (Fig. 16) be mated with each other, the recessive white character reappears on the average in one in four of the offspring (Fig.

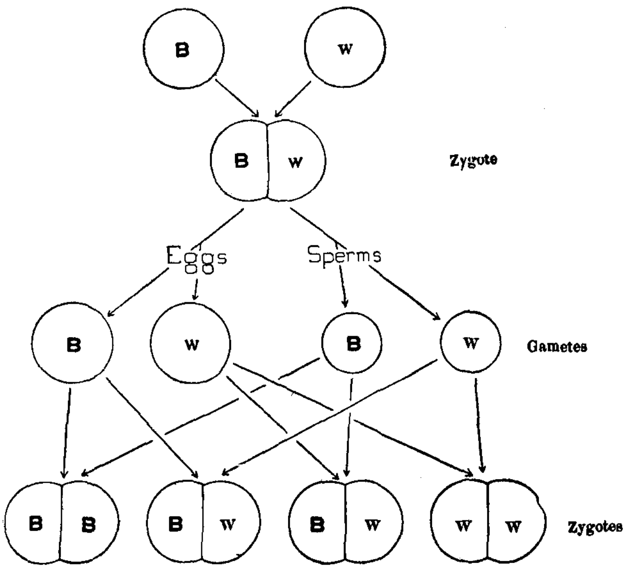


FIG. 18. — Diagram to explain the result shown in Fig. 17.

17). Its reappearance in that particular proportion of the offspring may be explained as follows (see Fig. 18): The gametes which united in the original cross were, one black, the other white in character. Both characters were then asociated together in the offspring; but black from its nature dominated, because white in this case is due merely to the lack of some constituent supplied by the black gamete. But when the cross-bred black individuals on becoming adult form gametes, the black and the white characters separate from each other and pass into different cells, since, as we have seen, gametes are simplex. Accordingly, the eggs formed by a female cross-bred black are half of them black, half of them white in character, and the same is true of the sperms formed by a male cross-bred black. The combinations of egg and sperm which would naturally be produced in fertilization are accordingly 1 B B : 2 B W : 1 W W, or three combinations containing black to one containing only white, which is the ratio of black to white offspring observed in the experiment.

Now the white individual may be expected to transmit only the white character, never the black, because it does not contain that character. Experiment shows this to be true. White guinea-pigs mated with each other produce only white offspring. But the black in-

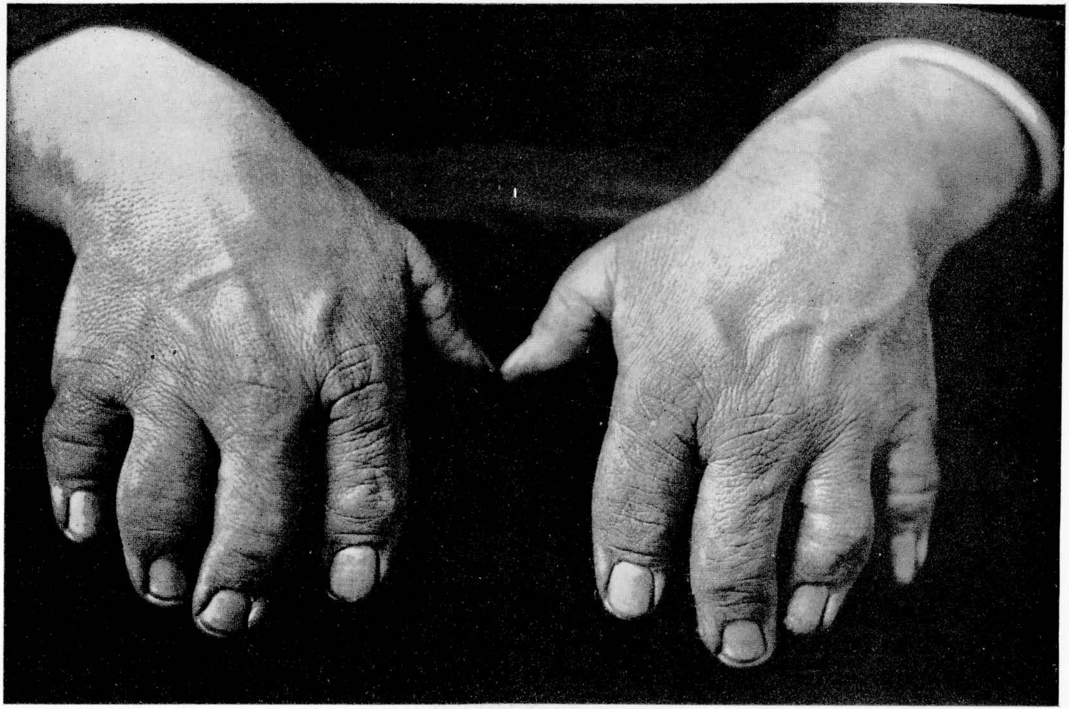


FIG. 19. — A shortened condition of the skeleton, particularly of the fingers, as here shown, is a dominant character in heredity. (After Farabee.)

dividuals of this generation are of two sorts, — B B and B W in character. The B B individual is *pure*, so far as its breeding capacity is concerned. It can form only black (B) gametes. But the B W individuals may be expected to breed exactly like the cross-bred blacks of the previous generation, forming gametes, half of which will carry B, half W. Experiment justifies both these expectations. The test may readily be made by *mating the black animals one by one with white ones.* The pure (or B B) black individual will produce only black offspring, whereas those not pure, but B W in character, will produce cffspring half of which on the average will be black, the other half white. These two kinds of dominant individuals obtained in the second generation from a cross we may for convenience call homozygous and heterozygous, following the convenient terminology of Bateson. A homozygous individual is one in which *like* characters are joined together, as B with B; a heterozygous individual is one in which *unlike* characters are joined together, as B with W. It goes without saying that recessive individuals are always homozygous, as W W for example. For they do not contain the dominant character, otherwise they would show it.

It will be observed that in the cross of black with white guinea-pigs black and white behave as units distinct and indestructible, which may meet in fertilization but separate again at the formation of gametes. Mendel's law as illustrated in this cross includes three principles: (1) The existence of *unit-characters*, (2) *dominance*, in cases where the parents differ in a unit-character, and (3) *segregation* of the units contributed by the respective parents, this segregation being found among the gametes formed by the offspring.

The principles of dominance and segregation apply to the inheritance of many characteristics in animals and plants. Thus in guinea-pigs a rough or rosetted coat (Figs. 23 and 24) is dominant over the ordinary smooth coat. If a pure rough individual is crossed with a smooth one, all the offspring are rough; but in the next generation smooth coat reappears in one fourth of the offspring, as a rule. Again, in guinea-pigs and rabbits a long or angora condition of the

Fig. 20. — Radiograph of a hand similar to those shown in Fig. 19. Notice the short, two-jointed fingers. (After Farabee.)

fur is recessive in crosses with normal short hair. All the immediate offspring of such a cross are short-haired, but in the next generation long hair reappears in approximately one fourth of the offspring.

In cattle, the polled or hornless condition is dominant over the normal horned condition; in man, two-jointed fingers and toes (Figs. 19 and 20) are dominant over normal three-jointed ones. This is clear from an interesting pedigree given by Farabee of the inheritance of the abnormality in a Pennsylvania family (see Fig. 21). In no case was an abnormal member of the family known to have married any but an unrelated normal individual. It will be seen that approximately half the offspring throughout the four generations of offspring shown in the table were of the abnormal sort, — short-bodied and with short fingers and toes.

In each of the cases thus far considered a single unit-character is concerned. Crosses in such cases involve no necessary change in the race, but only the continuance within it of two sharply alternative conditions. But the result is quite different when parents are crossed

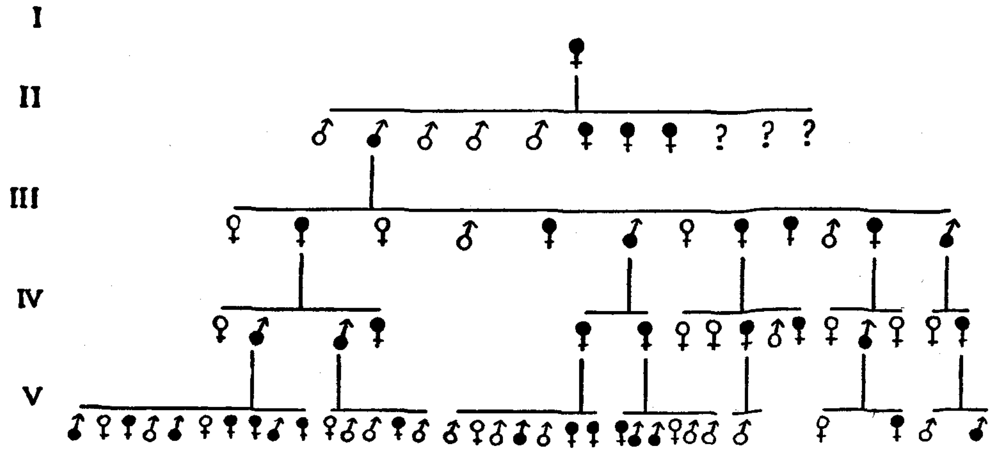


FIG. 21. — Diagram showing the descent, through five generations, of the condition shown in Figs. 19 and 20. Black symbols indicate affected individuals.

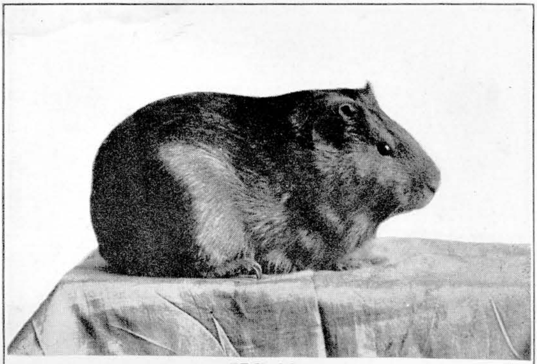
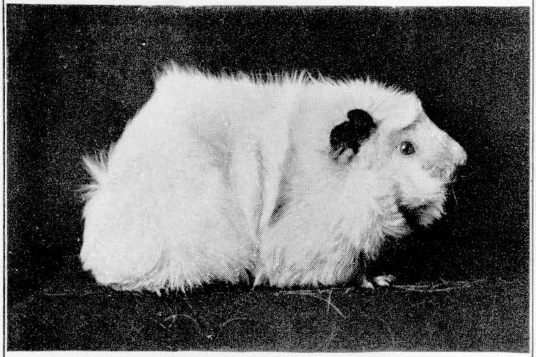


FIG. 22.



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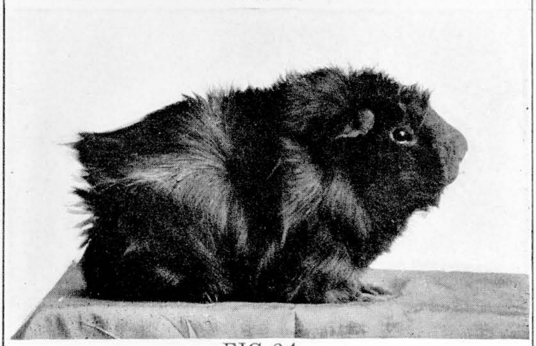


FIG. 24.

FIG. 22. — A smooth, dark guinea-pig.

FIG. 23. — A rough, white guinea-pig.

FIG. 24. — A dark, rough guinea-pig. The new combination of characters obtained when animals are mated *like those shown in* Figs. 22 and 23.

which differ simultaneously in two or more independent unit-characters. Crossing them becomes an active agency for the production of new varieties.

In discussing the crosses now to be described it will be convenient to refer to the various generations in more precise terms, as Bateson has done. The generation of the animals originally crossed will be called the parental generation (P); the subsequent generations will be called filial generations, viz. the first filial generation (F_1), second filial (F_2), and so on.

When guinea-pigs are crossed of pure races which differ simultaneously in two unit-characters, the F_1 offspring are all alike, but the F_2 offspring are of four sorts. Thus, when a smooth dark animal (Fig. 22) is crossed with a rough white one (Fig. 23) the F_1 offspring are all rough and dark (Fig. 24), manifesting the two dominant unit-characters, — dark coat derived from one parent, rough coat derived from the other. But the F_2 offspring are of four sorts, viz. (1) smooth and dark, like one grandparent, (2) rough and white, like the other grandparent, (3) rough and dark, like the F_1 generation, and (4) smooth and white, a new variety (Fig. 25). It will be seen that the pigmentation of the coat has no relation to its smoothness. The dark animals are either rough or smooth, and so are the white ones. Pigmentation of the coat is evidently a unit-character independent of hair-direction, and as new combinations of these two units the cross has produced two new varieties, — the rough dark and the smooth white.

Again, hair-length is a unit-character independent of hair-color. For if a short-haired dark animal (either self or spotted, Fig. 26) be crossed with a long-haired albino (Fig. 27), the F_1 offspring are all short-haired and dark (Fig. 28); but the F_2 offspring are of four sorts, viz. (1) dark and short-haired, like one grandparent, (2) white and long-haired, like the other, (3) dark and long-haired, a new combination (Fig. 29), and (4) white and short-haired, a second new combination (compare Fig. 25).

Now the four sorts of individuals obtained from such a cross as this will not be equally numerous. As we noticed in connection with

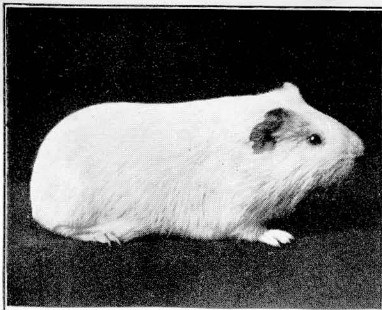


FIG. 25.

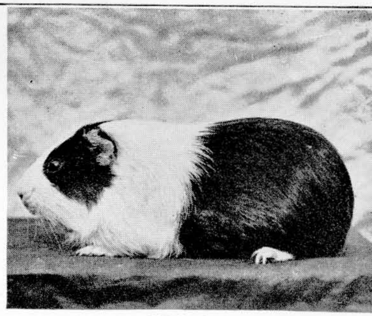
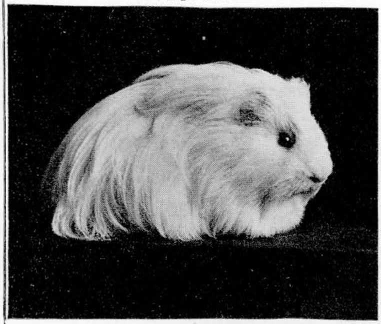


FIG. 26.



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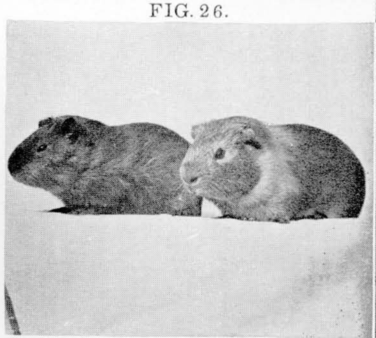

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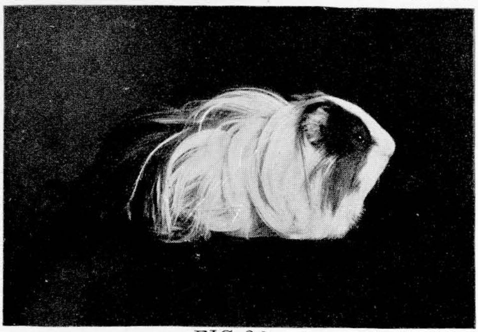

FIG. 29.

FIG. 25. — A smooth, white guinea-pig. A second new combination of characters, but obtained first among the *grandchildren* of such animals as are shown in Figs. 22 and 23.

FIG. 26. — A short-haired, pigmented guinea-pig. ("Dutch-marked" with white.)

FIG. 27. — A long-haired, albino guinea-pig.

FIG. 28. — Offspring produced by animals of the sorts shown in Figs. 26 and 27. One shows the "Dutch-marked" pattern as a belt of pale yellow; the other does not. Both are short-haired and pigmented (not albinos).

FIG. 29. — A long-haired, pigmented guinea-pig, "Dutch-marked" with white. Its parents were like the animals shown in Fig. 28; its grandparents like those shown in Figs. 26 and 27.

the black-white cross, dominant individuals are to the corresponding recessives as three to one. Therefore, we shall expect the short-haired in-

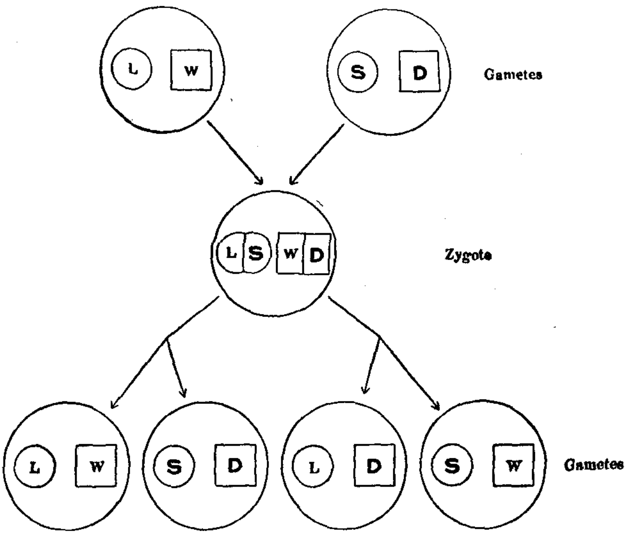

FIG. 30. — Diagram to explain the result of a cross between the sorts of guinea-pigs shown in Figs. 26 and 27. L stands for long hair, S for short hair, D for dark hair, and W for white hair. Dominant characters are indicated by heavy type.

dividuals in F_2 to be three times as numerous as the long-haired ones, and dark ones to be three times as numerous as white ones. Further, individuals which are *both* short-haired and dark should be 3×3 or 9 times as numerous as those which are not. The expected proportions of the four classes of F_2 offspring are accordingly 9 : 3 : 3 : 1, a proportion which is closely approximated in actual experience. The Mendelian theory of independent unit-characters accounts for this result fully. No other hypothesis has as yet been suggested which can account for it.

Suppose that each unit has a different material basis in the gamete. Let us represent the material basis of hair-length by a circle, that of hair-color by a square, then combinations and recombinations arise as shown in Fig. 30. The composition of the gametes furnished by the parents is shown in the first line of the figure; that of an F_1 individual (or zygote), in the second line; that of the gametes formed by the F_1 individual in the third line. L meets S and W meets D in fertilization to form an F_1 individual double and also heterozygous as regards hair length and hair color, but these units segregate again as the gametes of the F_1 individuals are formed, and it is a matter of chance whether or not they are associated as originally, L with W and S with D, or in a new relationship, L with D and S with W. Hence we expect the F_1 individuals to form four kinds of gametes all equally numerous, — L W, S D, L D, and S W. By chance unions of these in pairs nine kinds of combinations become possible, and their chance frequencies will be as shown in Fig. 31. Four of these combinations, including nine individuals, will show the two dominant characters, short and dark; two classes, including three individuals, will show one dominant and one recessive character, viz. dark and long; two more classes, including three individuals, will show the other dominant and the other recessive character, viz. short and white; and lastly, one class, including a single individual, will show the two recessive characters, long and white. The four *apparent* classes, or, as Johannsen calls them, *phenotypes*, will accordingly be as 9 : 3 : 3 : 1. This is called the normal Mendelian ratio for a dihybrid cross, — that is, a cross involving two unit-character differences.

One individual in each of these four classes will, if mated with an individual like itself, breed true, for it is homozygous, containing only like units. The double recessive class, long white, of course contains *only* homozygous individuals, but in each class which shows a dominant unit, heterozygous individuals outnumber homozygous ones, as 2 : 1 or 8 : 1. Now the breeder who by means of crosses has pro-

Short Dark.	Long Dark.	Short White.	Long White.
1 S D. S D	1 L D. L D	1 S W. S W	1 L W. L W
2 S D. L D	2 L D. L W	2 S W. L W	
2 S D. S W			
4 S D. L W			
9	3	3	1

FIG. 31. — Diagram showing the kinds and relative frequencies of the young to be expected in F_2 from the crossing of animals shown in Figs. 26 and 27.

duced a new type of animal wishes, of course, to " fix " it, — that is, to obtain it in a condition which will breed true. He must, therefore, obtain homozygous individuals. If he is dealing with a combination which contains only recessive characters, this will be easy enough, for such combinations are invariably homozygous. His task will become increasingly difficult the more dominant characters there are included in the combination which he desires to fix.

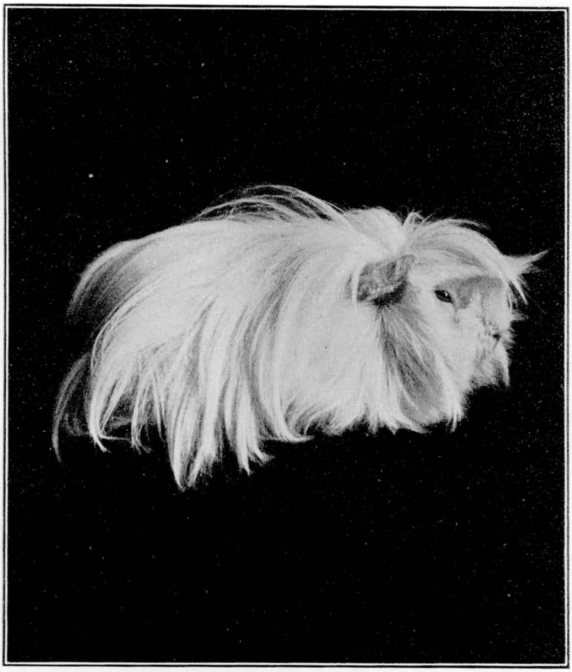

FIG. 32. — A long-haired, rough albino guinea-pig; male, 2002.

The most direct method for him to follow is to test by suitable matings the unit-character constitution of each individual which shows the desired combination of characters, and to reject all which are not homozygous. In this way a pure race may be built up from individuals proved to be pure. Such a method, however, though sure, is slow in cases where the desired combination includes two or more dominant unit-characters, for it involves the application of a breeding test to many dominant individuals, most of which must then be rejected. It is therefore often better in practice to breed *from all individuals which show the desired* combination, and eliminate from their offspring merely such individuals as do not show that combination. The race will thus be only gradually purified, but a large stock of it can be built up much more quickly.

We may next discuss a cross in which three unit-character differences exist between the parents, instead of two. If guinea-pigs are crossed which differ simultaneously in three unit-characters, color, length, and direction of the hair, a still larger number of phenotypes is obtained in F_2, namely, eight. A cross between a short-haired, dark, smooth guinea-pig (compare Fig. 22) and one which was long-haired, white, and rough (Fig. 32) produced offspring in F_1 which were short-haired, dark, and rough (compare Fig. 24), these being the three dominant characters, two derived from one parent, one from the other. The F_2 offspring were of eight distinct types, two like the respective grandparents, one like the F_1 individuals (parents), and the other five new, shown in Fig. 33. They are short white rough, short white smooth, long white smooth, long dark rough, and long dark smooth. The largest of the eight apparent classes (phenotypes) was the one which manifested the three dominant characters, short, dark, and rough, which had been the exclusive F_1 type; the smallest class was the one which manifested the three recessive characters, long, white, and smooth. Theoretically these two classes should be to each other as 27 : 1. Of the twenty-seven triple-dominants, twenty-six should be heterozygous.

A comparison of this case with the one just previously described shows what an increas-

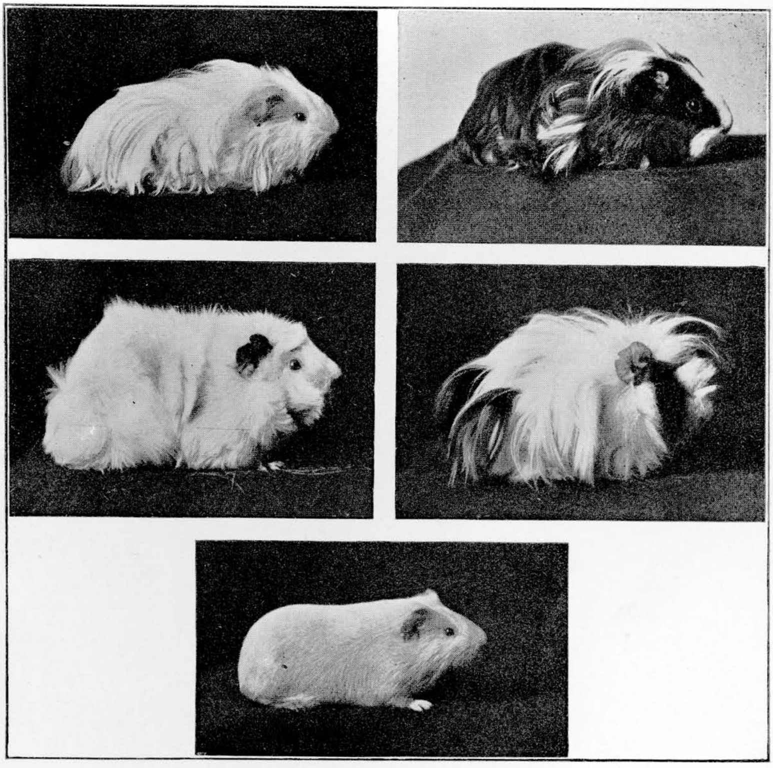

FIG. 33. — Five new combinations of unit-characters obtained in generation F_2, by crossing the animal shown in Fig. 32 with animals like that shown in Fig. 22.

ingly difficult thing it is to fix types obtained by crossing, if the number of dominant characters

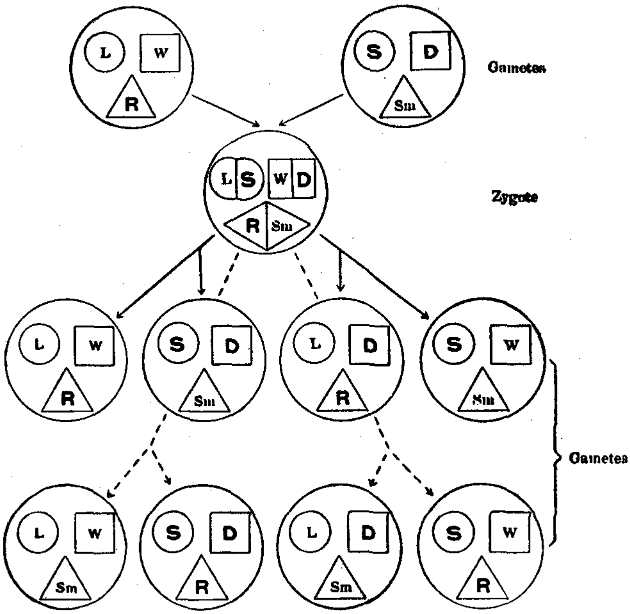

FIG. 34. — Diagram to show the gametic combinations and segregations involved in a cross between guinea-pigs differing in three unit-characters. L stands for long hair, S for short hair, W for white hair, and D for dark hair; R for rough, and Sm for smooth coat. Compare Figs. 22 and 32.

in the selected type increases. On the theory of unit-characters the gametic combinations and segregations involved in this cross are as shown in Fig. 34. The nature of the gametes formed by the parents crossed is shown in the first row; the composition of the F_1 individuals, immediately below. In the two lower rows are shown four different sorts of gametic splittings which may occur in the F_1 individuals, producing thus eight different kinds of gametes. If, in reality, the F_1 individuals form eight kinds of gametes, all equally numerous, and chance unions in pairs occur among them, there should be produced eight corresponding sorts of individuals numerically as 27 : 9 : 9 : 9 : 3 : 3 : 3 : 1. In a total of 64 individuals there should be on the average one pure individual in each of the eight different classes. The class numerically 27 in 64 manifests three dominant characters; those which are numerically 9 in 64 manifest two dominant characters; those which are numerically 3 in 64 manifest one dominant character. Among each of these there will be on the average one pure individual, but the class which contains 1 individual in 64 is a pure recessive, for it contains no dominant character. This combination, then, requires no fixation. It will breed true from the start.

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