

ON THE PATTERN OF THE DUTCH RABBIT, A DISCUSSION OF THE RESULTS OF PUNNETT AND PEASE.

BY W. E. CASTLE.

(With Two Text-figures.)

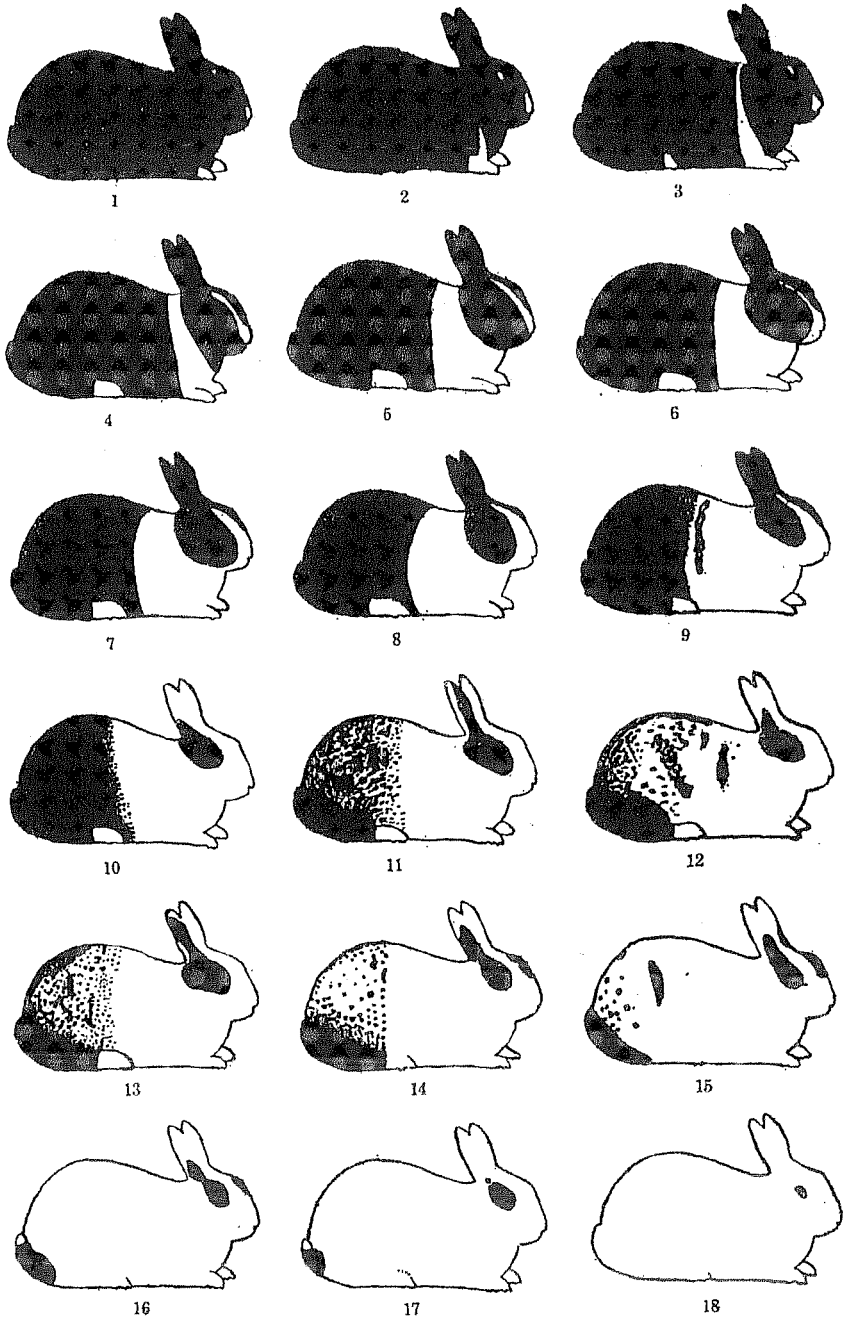
GENETIC studies of the Dutch rabbit have been made by a number of investigators, more particularly in recent years by Professor Punnett and myself. Our findings as to fact agree in a remarkable way but our interpretations are quite divergent, at least they seem so to a reader of the recent paper of Punnett and Pease¹. In reality they are not so far apart as they seem.

In 1919 I advanced the view that variation in the Dutch pattern (which is extraordinarily great) was due to two agencies, (1) variation in the Dutch gene itself, which assumes several allelomorphic forms, and (2) the modifying action of genes other than the Dutch gene proper, "residual heredity" as I then designated it. Punnett (1920) attacked the first of these conclusions vigorously in a review of my paper published in this *Journal*, and Punnett and Pease continue irreconcilable to the idea of multiple allelomorphs in the case of Dutch pattern, though meantime Punnett has adopted it in the case of the Japanese rabbit².

Punnett offered as a substitute for the idea of allelomorphic conditions of a single Dutch gene, an explanation which would make Dutch pattern dependent on the combined action of three independent genes, *P*, *S*, and *T*. Punnett and Pease now find it convenient to invoke the existence of a fourth "definite" Dutch factor, *N*, in addition to certain supposed modifying factors, *X* and *Y*.

It would seem to be a very easy matter to reach a decision between rival hypotheses, one of which called for monohybrid inheritance ratios, the other for trihybrid or tetrahybrid ratios. In reality Punnett and Pease have not made the direct experiment of crossing their supposed multiple recessive variety (White Dutch) with the supposed multiple dominant (self). It may be of interest therefore to inquire what the results of such a cross are and whether they suggest a tetrahybrid or a monohybrid segregation among the gametes formed by F_1 individuals.

¹ *Journal of Genetics*, Vol. xv. p. 375, July, 1925. ² *Ibid.* Vol. xiv. August, 1924.



Grades 1-18 of Dutch rabbits.

Fig. 1.

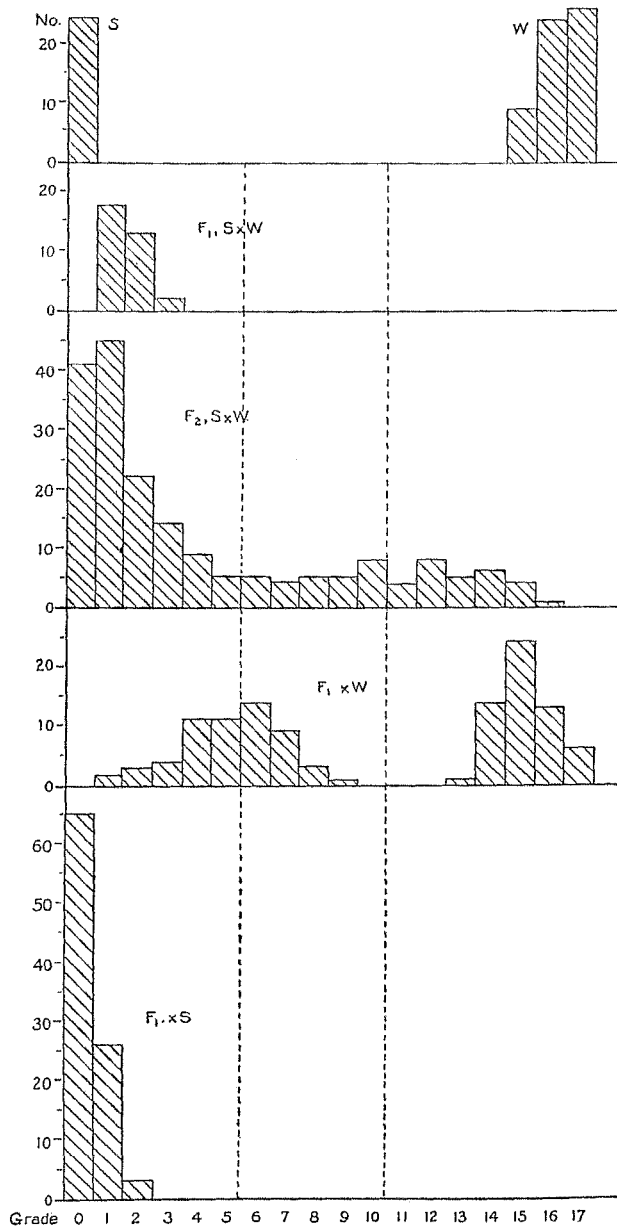


Fig. 2.

This cross I made several years ago and reported on its results in considerable detail in 1919. The results are presented graphically in Fig. 2, in terms of the grades shown in Fig. 1. The range of variation in the race of White Dutch (W) used in making the cross, is shown in the top row of Fig. 2 as from grade 15 to 17, while the self race (S) was true breeding (grade 0). The grade of the F_1 young is shown immediately below ($F_1, S \times W$), ranging from grade 1 to 3. The F_2 generation ranged from grade 0 to grade 16. The back-cross with the white race ($F_1 \times W$) is particularly instructive. It shows two (and only two) distinct, monomodal groups, containing 58 individuals each. It would be difficult to imagine a clearer demonstration of unifactorial segregation. I so interpreted it in 1919 and so interpret it now. The hypothesis of Punnett and Pease, on the other hand, suggests a difference of four major factors between self and White Dutch, the former being $N P S T$, the latter $n p s t$. It is difficult to see how a four-factor hypothesis can be reconciled with the obvious 1 : 1 segregation of the back-cross to the White Dutch parental variety. Nevertheless Punnett did, in 1920, attempt to fit a three-factor scheme to these very figures. Doubtless with a sufficient number of subsidiary hypotheses, making certain factors inactive when their presence would otherwise be troublesome, the fitting can be done as well with four factors as with three.

If, in crossing White Dutch with self in the foregoing experiment, one uses Dutch individuals which have long hair (Angora) and self individuals which have short hair, the F_1 young all have short hair, Angora being a recessive character. When the back-cross is then made with the Dutch Angora race, approximately half the young are short-haired and half long-haired, obviously a unifactorial segregation for the Angora character as well as for the Dutch. But the long-haired segregates are mostly White Dutch, as the long-haired were exclusively in the P_1 generation, and the short-haired segregates are mostly like the F_1 generation in grade. In a particular experiment of this sort, which will be reported in greater detail elsewhere, there were produced 123 back-cross young grouped as follows:

$S W$ group (like F_1 in grade)	$W W$ group (like White Dutch)
54 short-haired	11 short-haired
9 Angora	49 Angora
<hr style="width: 50%; margin-left: 0;"/>	<hr style="width: 50%; margin-left: 0;"/>
Totals 63	60

There is unmistakable linkage here between White Dutch and Angora, and between self and short hair. An idea of the strength of the linkage may be gained by comparing the size of the *crossover* or recombination

classes with that of the *non-crossover* or original combination classes. The recombination classes number 9 and 11, the original combination classes number 54 and 49. In this experiment and others of a similar nature, a total of 1213 back-cross young has been produced, of which 173 only are recombinations or crossovers. The percentage of crossovers is accordingly 14.26 ± 0.96 . On the chromosome theory, this means that the Angora gene lies in the same chromosome as the White Dutch gene at a distance of about 14 units (morgans) from it.

When by similar methods an investigation is made of the linkage relation of Angora to Dutch in a race which I have called Dark Dutch, and which corresponds closely to what Punnett and Pease call Deep Dutch, it is found that here also linkage exists between Angora and Dutch. In 1919 I reported that White Dutch and Dark Dutch are allelomorphs. The fact that both show linkage with Angora supports this conclusion. Punnett and Pease now report that White Dutch and Deep Dutch contain different allelomorphs of the same Dutch factor, P , which is in their view the chief or basal factor for Dutch, the only one which, unaided by other factors, can produce a Dutch pattern. This is in complete accord with my findings in the case of White and Dark Dutch. We are agreed, then, that the Dutch factor proper (P) occurs in two different allelomorphous forms in two different true-breeding races of rabbits, White and Dark (Deep). I assume further that self contains a third allelomorph, and am able to show that it has the same linkage relation to Angora that the Dutch allelomorphs proper have. If Punnett and Pease were to admit that a *third* allelomorph of P exists in self races, they would be fully committed to a multiple allelomorph hypothesis. Therefore they do not call this *tertium quid* a variant of P , but N , and assume that it is independent of P , although they have admittedly never studied the character or its linkage relations.

They do present, however, strong indirect evidence that a third allelomorph of P exists in self races. By crossing two Dutch races (Typical and Deep), each of which in their view carried a different allelomorph of P , and had no other character in common, they expected to synthesize a self rabbit. This they were unable to do, although an F_2 generation of 551 individuals was produced, among which their hypothesis called for 9 selfs. Further, an F_3 generation was produced from selected F_2 animals. Here the expectation for the production of self individuals was considerably higher, but none appeared among 120 young. This result makes it seem improbable that a self rabbit can be produced which contains two doses of either or both allelomorphs of P

which they recognize, for their experiment should have yielded every possible combination of all other associated factors. Self accordingly would seem to require a *different* allelomorph of P than those which characterize Dutch races.

Now if we suppose two Dutch races to contain different allelomorphs of Dutch, and self to contain a third, there is no reason to expect that by crossing the two we should obtain the third (self), any more than by crossing Chinchilla with Polish rabbits, we should expect to get grays, which contain a third allelomorph of the colour factor.

Nor is it possible by crossing White Dutch with self to segregate in F_2 a Dark (Deep) race. One may obtain a *modified* White race, such as the Typical race of Punnett and Pease, and possibly my Tan race, but these are very different from a Dark (Deep) race, as Punnett and Pease correctly observe. Two striking differences are found between the two Dutch allelomorphs. (1) White Dutch and its modifications have much white in the head and frequently have an iris which on its front face is either completely white or white in segments (heterochromia iridis, Punnett). (2) There is a tendency in White Dutch and its modifications to develop numerous fine white spots in the pigmented areas posterior to the belt. Neither of these characteristics is found in Dark (Deep) Dutch, as is agreed both by Punnett and Pease and by myself.

The second conclusion reached in my 1919 and 1920 papers, the existence of modifying factors which make the Dutch pattern darker or lighter than it would otherwise be, has always been entirely acceptable to Punnett. He indeed holds in substance that this is the whole explanation of the variation in the Dutch pattern, aside from the now admitted allelomorphism of P with p . His factors S and T , and the N , X and Y of Punnett and Pease, are nothing but names for supposed modifying factors. No evidence has been presented to show that apart from a Dutch factor proper (P or p) any number of the supposed subsidiary or modifying factors would be able to produce a Dutch pattern.

The extent to which such modifiers may affect the appearance of White Dutch, Dark (Deep) Dutch, and the heterozygote between them is shown in Fig. 2 of Punnett and Pease, p. 378. My own observations are entirely in harmony with theirs as to the large extent of such modifications and their apparent genetic independence of the Dutch factor proper. In my 1919 paper I repeatedly called attention to the fact that parents of high grade regularly produce offspring of higher grade than do lower grade parents of the same genetic constitution as regards the Dutch factor proper.

In consequence of this fact, selection is effective in modifying patterns of the rabbit or of other mammals, as I have long insisted, much to the disgust of supporters of the pure line and pure gamete hypotheses, to whom the idea of "contamination" or "modifiability" is highly distasteful. It is gratifying to receive confirmation in such observations as Punnett and Pease report for their males R 204 and T 35b.

The "Typical Dutch" of Punnett and Pease is by their account only a "modified" White Dutch, since it contains the same Dutch factor proper, p , as characterizes White, and differs only in the modifying factors, S and T . I assent to their explanation except as to the number of supposed modifying factors. I see no reason for assigning the total effect to two factors rather than twelve or twenty. But I do consider it likely that the modifications observed are due to genetic factors independent of the Dutch factor proper, the modifying genes accordingly being located in chromosomes other than that which contains the Angora gene.

Punnett and Pease are in error if they think that their Typical Dutch is the same genetically as the exhibition type of Dutch with which I have worked. The latter corresponds rather with their Mock Dutch, being like it heterozygous for two types of Dutch, White and Dark (Deep).

As to the "Tan Dutch" of my 1919 paper, I am inclined to think, in agreement with the view of Punnett and Pease, that, like their Typical Dutch, it was only a modified White Dutch, containing the same Dutch factor proper and with only modifiers to make its appearance different. For (1) I have found in studies of the last five years that White Dutch extracted from a cross with self may range much lower in grade than it was observed to do in my 1919 studies, extending in fact into the range of Tan Dutch. (2) Even in my 1919 paper it was shown that Tan extracted from a cross with Dark may extend into the lower part of the range of White. (3) After a cross between Dark and Tan, Dark (extracted) was found to be darker and Tan whiter than before the cross. This is in harmony with the view that before the cross Dark contained the *same modifiers* as White, but Tan contained a different series of darkening modifiers. The cross tended to lift some of these darkeners from Tan and add them to Dark. (4) The cross between Tan and White, like the cross between Typical and White of Punnett and Pease, lifted darkeners from Tan and added them to White, bringing the two closer together in grade (mutual modification of my 1919 paper). (5) Tan and White Dutch are similar in appearance, when not very different in grade. Compare Figs. 19 and 21 (Castle, 1919). The head is predominantly white and the iris frequently white. Also, as the belt widens, there is a tendency for the

region behind the belt to be invaded with fine spots of white. (6) Tan originated as a recessive extracted from a self race, whence it emerged in a darkened form, made so by modifiers derived from the self race. White Dutch also is darkened (lowered in grade) by a cross with a self race, as Fig. 2 shows.

In conclusion, I would qualify the multiple allelomorph hypothesis of my 1919 and 1920 papers in only one respect. I am no longer inclined to regard Tan Dutch as containing a fourth Dutch allelomorph; more probably it contained the same allelomorph as White Dutch, associated with modifiers (darkeners) derived from its self ancestors. Unfortunately the race is now extinct so no renewed investigation can be made of its genetic constitution. The other three allelomorphs are in my own stock of rabbits still, and can be obtained quickly by anyone who will take the trouble to cross exhibition Dutch with any true-breeding self race, the exhibition Dutch containing regularly two allelomorphs, and self a third.