THE DUTCH RABBIT—CASTLE, PEASE AND PUNNETT.

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As a test case involving the explanation of a series shewing apparently continuous variation the Dutch rabbit has of late years superseded the much discussed hooded rat. Since it is most desirable that clear ideas should prevail as to the nature and interpretation of this case I need offer no excuse for the following comments upon Professor Castle's discursive criticism of Mr Pease and myself, which appears in the same number of this journal. Fortunately my comments can be brief, because, as will appear below, Professor Castle has provided critical data for a decision between our rival explanations. But before considering these data it may be as well, in view of the continual modifications of Professor Castle's interpretation, if I attempt to outline what at present appears to be its residual form.

We are to suppose the existence of three principal factors **Du**, $\mathbf{du_d}$ and $\mathbf{du_w}$ belonging to a series of multiple allelomorphs and corresponding to the pattern types, Self-colour, Dark Dutch and White Dutch respectively. An animal of the constitution **DuDu** is always self-coloured, but Dark Dutch ($\mathbf{du_d du_d}$) and White Dutch ($\mathbf{du_w du_w}$) show a very wide range of variation. The former range from grades 1–7[1], that is from almost self down to the typical Dutch of the fancy; the latter may be anything from grade 2 down to grade 18, that is from a rabbit which is almost self-coloured to one that is almost white. Between the more heavily pigmented White Dutch and the Dark Dutch of similar grades there is, however, a difference. In the former the white "blaze" is usually wider, and they may often show *heterochromia iridis*, which is never the case in Dark Dutch. The cause of this immense range of variation was originally assigned by Professor Castle to what he termed "residual heredity," aided by some mysterious process of "mutual modification." He has now come round to the view that in order to account for this variation we need only invoke modifying factors in the ordinary sense of the geneticist. But he seems to have made no attempt either to analyse or to define these factors. Yet they may bring about

[1] See Pl. I of Castle's *Studies of Heredity in Rabbits, Rats and Mice*, Washington, 1919, which is also reproduced on p. 190 of the present issue of this *Journal*.

an enormous difference in the appearance of a rabbit, for a White Dutch ($\mathbf{du_w du_w}$) of Professor Castle may be in appearance almost self-coloured (grade 2)[1], or almost white (grade 18) according to its make up in respect of these postulated modifying factors. I may say at once that I have no quarrel with the hypothesis of such modifying factors. Indeed Mr Pease and I may fairly claim to have identified certainly two of them (**S** and **T** of our paper), and probably a third (**N**). Apart from the fact that we have given a reasoned experimental analysis of these factors which Professor Castle is content to leave in a confused jumble, the essential difference between our interpretations is that whereas he invokes a series of three multiple allelomorphs (**Du**, $\mathbf{du_d}$, $\mathbf{du_w}$) to account for what may be termed the major pattern differences, we have found that the facts are covered by the simpler hypothesis of a single factor (**P**). On our view the **PP** animal, in the absence of any of the modifying factors, is what Professor Castle would term Dark Dutch, and the addition of modifying factors brings about an increase in the pigmentation until, in the presence of **N**, **S** and **T**, the animal becomes self-coloured. The self-coloured condition is merely the end term reached when a sufficient number of modifying factors, known from independent analysis, are added to the **PP** animal. On Professor Castle's view the true-breeding self-coloured rabbit is a thing *sui generis*, containing a factor (**Du**) which is not to be found in either Dark Dutch or White Dutch. An animal of the constitution **DuDu** is a self-coloured animal, whatever its condition in respect of modifying factors: an animal heterozygous for **Du** may sometimes be self-coloured, but more frequently shows some white—from which we must infer that every self-coloured animal must have been formed by at least one gamete containing the **Du** factor.

At this point we may turn to an experiment of Professor Castle's to which I particularly drew his attention in 1920, and of which the significance appears even yet to have escaped him. I refer to the cross between Dark Dutch and Tan Dutch (Castle, 1919, pp. 13–15), which on his multiple allelomorph hypothesis is of the nature $\mathbf{du_d du_d} \times \mathbf{du_w du_w}$[2]. Castle found that the F_1 animals from this cross were on the average darker than either parent, some of them being even self-coloured. A large F_2 generation of 275 animals was bred, showing a range over grades 0–11

[1] Viz. when it is of the form that Castle previously termed "Tan Dutch."

[2] For Castle has been driven to admit definitely that his "Tan Dutch" is fundamentally a White Dutch with certain modifying factors (cf. p. 195 of the present number of this *Journal*).

on Castle's scale; but the most striking feature was that out of these 275 F_2 animals no less than 89, or nearly 30 per cent., *were self-coloured.*

This experiment makes it perfectly clear that animals containing only Castle's $\mathbf{du_d}$ allelomorph can be self-coloured, provided that they contain the proper independent modifying factors. Moreover if such self-coloured animals were homozygous for $\mathbf{du_d}$ as well as for the modifying factors in question, there is every expectation that they would breed true to self-colour. For my own part I feel not the least doubt that in this experiment Castle has achieved what he declares to be impossible[1], and has effected the synthesis of the self-coloured animal from the cross between animals belonging to his Dark and White Dutch classes. As I pointed out years ago this result is just what we should be led to expect on our hypothesis.

In the light of all this, what is the pertinence of Castle's **Du** factor? Clearly it is an entirely unnecessary assumption unless one is afflicted by the desire to drag in at all costs an interpretation in terms of multiple allelomorphs. The simplest explanation is surely the best. If, as we have already done, Professor Castle will identify his $\mathbf{du_d}$ factor with our **P**, and his $\mathbf{du_w}$ with our **p**, at the same time consigning his **Du** factor into the limbo of the unwanted, he will then have effected the reconciliation after which he would appear to pine. By doing so, too, he will find the simple way out of the linkage problem that he so triumphantly propounds to us. Self-coloured and Dark Dutch both show linkage with the short hair—Angora pair because both self-coloured and Dark Dutch contain the identical factor **P**. If **S** represents the factor for short hair, then it is a case of linkage between **P** and **S**, and that is all there is to it.

[1] Cf. p. 194 of the present number of this *Journal.*