

A NOTE ON THE INHERITANCE OF EGG-COLOUR IN THE SILKWORM

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IN a recent publication on "Maternal Inheritance" Uda¹ has shown that the inheritance of the egg-colours slate (normal) and brown, in *Bombyx mori*, hitherto supposed to be determined maternally, is subject to several complications. Our knowledge of the inheritance of silkworm egg-colours, before the publication of Uda's paper, had been derived from the work of the late Professor K. Toyama². In this paper the reader is given clearly to understand that as regards the normal slaty and the brown colours of the eggs the inheritance is purely maternal and that batches mixed in colour do not occur³. But this conclusion neither agrees with Uda's statements, nor with the details given in Toyama's papers of his own breeding experiments. This ambiguity, and doubtless also the complications of the case, have led to diverse misconceptions that have now been introduced into text-books, and the object of this note is to endeavour to clear up these mistaken conclusions.

One complication, introduced both into Toyama's and Uda's experiments, is the use of divoltine and multivoltine races. In such races the eggs laid by the spring brood generally do not develop dark pigment in the serosa. Occasionally, however, some of these eggs develop pigment, and the pigmented eggs usually do not hatch till the following spring. In the investigation of egg-colour these breeds are a complication, though the fact itself may not bear on the question of the relations between different egg-colours.

Besides the slate and brown pigments, Toyama worked with blue and crimson. He states that all these pigments are deposited in the serosa, a layer produced by the fertilised embryo, whereas other egg-colours, such as whitish-grey, or yellow and white of newly-laid eggs, are due to the shell or yolk, and are purely maternal in origin. Toyama concludes that all the pigments deposited in the serosa are inherited—as is the whitish-grey—maternally, with the exception of crimson which Mendelises normally. Inspection of Toyama's tables, in which are set out the

¹ *Genetics*, VIII. 1923, p. 322.

² *Journ. Gen.* II. 1912, p. 351.

³ See especially *ibid.*, II. pp. 400 and 402.

details of his breeding experiments, shows that this is true in respect of the relations between slate and blue, and slate and crimson, respectively. In the slate and blue experiments no mixed broods occur, and the eggs of separate broods are all slate if the mother carries the dominant factor for slate, or all blue if she is a homozygous recessive. On the other hand, in the slate and crimson experiment, mixed broods occur, slate and crimson eggs of each mixed brood being in the ratio of 3 slate : 1 crimson ; and, further, reciprocal crosses between pure forms give F_1 eggs all slate. Turning to the slate and brown experiment, we find mixed broods are recorded in considerable numbers, and these are noted by Toyama (p. 355). Moreover, these mixed broods were laid both by moths descended from brown-egg families and by moths descended from slate-egg families. These facts appear inconsistent. How Toyama proposed to reconcile the mixed broods with his representation of the inheritance is not clear. He speaks of an intended discussion of this subject, but postpones it. Unfortunately he made no crosses between pure slate and brown varieties, but worked with an impure race.

Starting with pure breeds Uda found that slate ♀ and brown ♂ gave slaty F_1 eggs, but the reciprocal cross gave brown F_1 eggs, the colour in both cases being exactly as in the pure breeds. F_2 eggs, laid by F_1 females of either type mated with F_1 males of either type, consisted of slaty and brown eggs in the ratio 3 : 1, but the brown eggs were slightly darker than those of the pure brown breed. Both the F_1 types were crossed reciprocally with slaty males and females, and gave only slaty broods. Pure brown females crossed with either F_1 type, whether slaty or brown, laid brown eggs, but the reciprocal cross, *i.e.* F_1 females of either type, fertilised by brown males, laid eggs mixed slaty and brown, in the ratio of 1 : 1.

The extensive series of experiments made by Uda leave no doubt that the facts are as described, and that we have here a peculiar combination of Mendelian inheritance and maternal influence. Two exceptions to simple Mendelian behaviour are to be observed. First, that the homozygous (recessive) brown female, however fertilised, lays typical brown eggs ; and secondly, that the brown eggs in mixed broods, *i.e.* those derived from heterozygous parents, are darker than the pure brown, and apparently assume an intermediate colour between normal and brown (Uda, p. 333). Thus the somatic influence of the homozygous brown mother maintains the eggs brown, fertilisation by male cells bearing the dominant slaty factor being powerless to change this colour. But the somatic influence of the heterozygous mother is such, that though egg-

colour is mainly determined by the factorial constitution of the embryo, the brown eggs are darkened.

To sum up. The three egg-colours, blue, brown, and crimson, are all recessive to slate, and, in relation to that colour, blue is determined by the mother, crimson by the factorial constitution of the embryo, and brown by the mother when she is homozygous, but mainly by the factorial constitution of the embryo when she is heterozygous.

We have no further exact knowledge of the genetic relations between the slate, blue, brown, and crimson colours, though Toyama says that the order of dominance is probably that in which they are here set out. That a knowledge of these relations would throw light on the meaning of the facts is probable. The four egg-colours are shown in Toyama's coloured plate, and their appearance leads one to suspect that slate, blue, and brown are nearly related, and that possibly the differences may be quantitative: *i.e.* they may be multiple allelomorphs. Until further information is available, no satisfactory discussion of the facts is possible.