

THE HEREDITY OF SOME SPOT ABERRATIONS
IN *LYCÆNA PHLÆAS* AND *L. HYPOPHLÆAS*

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In Europe and to some extent in North America several aberrant forms of the common Copper butterflies, *Lycæna phlæas* L. and *L. hypophlæas* Bdv., have been reported. In this paper a few of the more important studies on spot aberrations and one significant investigation of another form will be reviewed and the results of one of our own rearing experiments will be presented.

The forms herein discussed fall into three categories. The first concerns the copper-colored band on the outer margin of the hindwing. In occasional specimens this band is replaced by black, and such aberrations have been named "obsoleta". From the data presented by HOLMES (1943) on *L. phlæas*, it is clear that the presence of this copper band is controlled by an autosomal gene which is dominant to its "obsoleta" allele.

The aberration in the second category has been termed "octomaculata". As is characteristic of the two species (or subspecies) under discussion, there are two rows of black spots basal to the copper band on the upperside of the hindwing which are indefinite in number and often indistinct. In "octomaculata" usually three to four black spots in each row are joined by more or less distinct blue scaling. In the same paper in which "obsoleta" was discussed, HOLMES also presented interesting data concerning "octomaculata". In short, his findings indicate that at least one pair of autosomal genes is responsible for this effect. Moreover, the allele for blue spotting appears to show intermediate dominance to the allele for lack of blue spotting, since the offspring of a strongly blue-spotted female \times a normal male were "all with four dull blue spots on each hindwing." In the F_2 HOLMES obtained 129 specimens arbitrarily arranged from strong (42) to weak (87) blue spotting, plus 16 normal specimens. Although the Chi-squared test applied to his results indicates that the blue spotting is more likely controlled by two pairs of autosomal genes than by one pair, neither interpretation can yet be definitely accepted. In both explanations, the greatest deviation from the expected ratio is in the number of normal forms obtained. This fact itself suggests that some uncontrolled selective agent may have been operating to alter the ratios in the conditions under which the experiment was carried out. That natural selection can operate on these forms was indicated in JACOBS' (1920) observations of the proportion of blue-spotted to "normal" *L. phlæas* in two close but ecologically distinct areas. In a marshy area, he found that 80.7% (117 out of 145) of the specimens were blue-spotted, whereas in a dry meadow only 13.8% (54 out of 392) were blue-spotted. It is thus apparent that further investigation of "octomaculata" could produce some interesting results, especially if both European and American forms were to be considered.

The third and final category to be discussed in this paper includes several of the aberrations which affect the black spots on the wings of these two species (or subspecies) of butterflies. SMITH (1946) has conveniently classified these aberrations into four groups. The first two involve (1) a reduction (*i.e.*, proportional reduction) and (2) an increase (*i.e.*, proportional increase) in the size of the black spots. It is probable that these first two groups are influenced by environmental factors, especially temperature. This is indicated in the work of LEECH (1893), MERRIFIELD (1893a, 1893b), and WEISMANN (1895) on *L. phlæas*, which showed that spring specimens and adults reared from pupæ kept at low temperatures have smaller black spots than those of the summer brood or those from pupæ kept at high temperatures. SMITH's third and fourth groups include those aberrations in which (3) the spots elongate inwards towards the base of the wing and (4) those in which the spots elongate outwards towards the outer margin of the wing. A typical example of inward elongation is the aberration "fasciata", described by STRECKER (1878). The extent of this inward elongation is extremely variable, a fact noted by SCUDDER (1899) and easily seen in looking over a good series of specimens. KLOTS (1951) and BROWER (1952) noted that this form is more common in some areas and in some years than others. This is substantiated by our own observations in New Jersey and Connecticut.

An example of outward elongation is found in the aberration "fulvus". SMITH pointed out that this outward elongation is much rarer than the inward elongation. The paucity of the former in collections supports SMITH's statement.

In addition to these four groups, a variable number of anterior and/or posterior elongations of the black spots occurs in some individuals, especially on the underside of the wings, and we would therefore like to add this group to SMITH's classification. Examples of these aberrations can be seen among the specimens of *L. hypophlæas* in the collection of Mr. OTTO BUCHHOLZ of Roselle Park, New Jersey.

SMITH emphasized "the lack of affinities" among butterflies showing these elongated spot aberrations and illustrated the same in a good plate. By "lack of affinities" he meant, for example, that elongation of the spots on the upperside of the forewing or hindwing may or may not be paralleled on the underside. Our own experience indicates that it is impossible to predict the condition of the spots on the underside of the wings by observing those above and *vice versa*. SOUTH's (1893) observation also implied this, as did that of SABINE (1893), and SCUDDER wrote that "... the suffusion shows no preference for the upper or under surface of the wings or for one pair of wings" (p. 1351).

Finally, a sixth aberration which we feel should be added to SMITH's classification (causally distinct from his first class) is "obliterata". In this variety, the extra-mesial spots on the upper and under sides of the forewing are lost or greatly reduced, and in some cases the discal spots are also gone.

It is our belief that these last four groups of aberrations — inward elongation, outward elongation, anterior and posterior elongation, and loss of spots — are primarily genetically produced, whereas the proportional increase and decrease in the size of the spots is largely environmentally controlled. The extreme variability in the extent of inward and outward and anterior and posterior elongation of the black spots and the noted lack of affinities suggest either modifying genes or environmental influence, or both. Evidence which we believe tends to support the hypothesis that "obliterata" and "fasciata", at least, are genetically governed will now be considered.

In 1899, SCUDDER mentioned a specimen of *L. hypophlaeas* which was more or less typically "obliterata" on the upperside but tended to be more like "fasciata" on the underside. This led SCUDDER to believe that these two forms were "closely connected". The following observations may help to elucidate SCUDDER's statement and suggest the possibility of genetic relationship between these two forms.

On 8 September 1953, two "fasciata" males, one "fasciata" female, and one worn "obliterata" female were taken in a field bordering the Great Swamp in Green Village, New Jersey. The "obliterata" female was brought back to the laboratory and induced to oviposit on *Rumex acetosella* L. (Sheep Sorrel). From the four eggs obtained, two individuals were reared to the pupal stage. Subsequently one male and one female emerged, neither of which was the normal form nor the maternal "obliterata" form. Both were the "fasciata" form. Our attempts to cross the F_1 may or may not have proved successful, but the female laid no eggs, thus terminating the experiment, which had been carried out under uncontrolled conditions.

A thorough genetic analysis of these findings is impossible without further data; however, the data obtained do suggest several possibilities, all of which could be tested by simple breeding experiments. For example, one interpretation is that "obliterata" and "fasciata" are controlled by two independent autosomal genes, each recessive to its allele for the normal color pattern. If this were the case, then the parent female would have been homozygous "obliterata" and heterozygous "fasciata", while her unobserved mate could have been either heterozygous or homozygous "fasciata", carrying one or two of the dominant wild-type alleles of "obliterata". Another explanation is that "obliterata" is controlled by a recessive sex-linked gene and "fasciata" by a recessive autosomal gene as in the first example.

However, one important but negative fact is evident. A comparison of these forms and normal individuals shows that the three types appear as three successive steps in extent of black spotting, with "obliterata" spotted to the least extent, "fasciata" spotted to the greatest extent, and the "normal" condition appearing intermediate between the two extremes. In the absence of breeding evidence it could have been hypothesized that a single pair of genes controls the three forms, with (ff) being "fasciata", (Ff) being "normal", and (FF) being "obliterata". The prevalence of the hypothesized normal (Ff) genotype in nature could then be explained by heterosis for the heterozygote and sublethality for both homozygotes. This possibility is eliminated

by our small F_1 brood, since an (FF) female could not produce (ff) offspring, regardless of the genotype of her unknown mate.

DISCUSSION

Very similar aberrations have been observed in other Coppers in addition to *L. phlæas* and *L. hypophlæas*. SMITH (1946) figures *L. dispar rutilus* var. "radiata", which shows outward spot elongation. In the BUCHHOLZ collection a striking aberrant male *L. epixanthe* Bdv. & Lec. from the cranberry bogs at Pakim Pond, New Jersey (23 June 1951), exhibits inward spot elongation on the underside of the forewings. In fact these aberrations are not limited to the Coppers but are also found in their near relatives, the Blues. According to SEITZ (1909), "As regards individual variability most species [*i.e.*, of Blues] are liable to modifications in the ocelli of the underside; these ocelli may be absent or reduced or enlarged, or their number may have increased; they may be ovate, elongate, or prolonged to form rays, or even confluent with one another. These modifications, which have all been found in nearly every species . . . certainly occur in all the species . . ." (p. 299). For other examples and illustrations of some of these forms, see also Geldart (1875), de Laussure (1914), Verity (1941), and Smith (1946).

If the American Coppers are considered alone, it is seen that the "obliterata"-like characteristics are usual in the males of several species, whereas the females of these same species normally tend towards the "fasciata" condition (*e.g.*, *Tharsalea arota* Bdv., *T. virginensis* Edw., *Lycæna gorgon* Bdv., *L. thoe* Guér., etc.). It is therefore possible that the aberrations which we have considered genetic in nature were important factors in the evolution of the different species. The results of further breeding experiments to ascertain the genetic nature of the aberrations, hybridizing of the different species to clarify further the nature of the spot inheritance, and the determination of relative frequencies of aberrations in several populations of each of the species would be of much interest.

SUMMARY

1. The present paper is concerned primarily with blue and black spot aberrations in *Lycæna phlæas* and *L. hypophlæas*.

2. A hypothesis is set forth in which the black spot "aberrations" are classified into two groups: those environmentally produced and those genetically controlled.

3. An analysis of a rearing experiment on *L. hypophlæas* suggests but does not prove the nature of the genetic control of "obliterata" (loss of black spots) and "fasciata" (inward elongation of black spots). However, balanced polymorphism involving these two forms and the normal form as controlled by a single pair of alleles is ruled out.

4. The occurrence of the black spot aberrations in Coppers and Blues in general is noted, and the importance of these aberrations in the evolution of the species of American Coppers is suggested.

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AN APPARENT HYBRID *LIMENITIS* FROM ARIZONA

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The year 1952 was a very good one for the three species of *Limenitis* found in the Verde Valley of central Arizona. The three species occupy for the most part separate habitats. *L. archippus obsoleta* Edwards is found at the lowest elevations, 3,000 ft. and less, among the Cottonwoods and Willows along the Verde River, and is never found far from this habitat. *L. astyanax arizonensis* Edwards is also found along the Verde River, but its chief habitat