THE GENETICS OF FORE AND HINDWING COLOUR IN CROSSES BETWEEN Danaus chrysippus FROM AUSTRALIA AND FROM SIERRA LEONE (DANAIDAE)

C. A. Clarke, P. M. Sheppard and A. G. Smith
Nuffield Unit of Medical Genetics, University of Liverpool, England

Unlike most warningly colored species, the butterfly Danaus chrysippus (L.) is known to be polymorphic in large parts of its range. Before one can understand the reason for this it is necessary to determine the genetic control of the forms. Recently we obtained a stock of D. chrysippus from Sydney, NSW and another from Sierra Leone. This paper gives preliminary results obtained by crossing the two races.

MATERIALS AND METHODS

The material from Australia, which was sent to us as living butterflies by post, was monomorphic and typical f. chrysippus of the race D. c. petilea (Fig. 1a). The ground colour of these butterflies is tawny orange tending to nutbrown towards the costal margin of the forewing. The hindwing upperside is bordered by black, sometimes with a vestige of white spotting close to the hindwing border. The apical third of the forewing upperside is black, with a variable subapical bar of white spots.

The specimens from Sierra Leone, f. alcippus, differed from the Australian ones in that the ground colour was more orange and most of the hindwing was covered by a patch of white scaling (Fig. 1b, c). The pale areas of the forewings were of two types—those with a narrow costal border of nutbrown pigmentation similar to the Australian butterflies (Fig. 1b) and others in which the nutbrown extended over most of the forewing (Fig. 1c). There was not enough orange on the hindwing to determine whether its hue differed in the two Sierra Leone forms.

Hybrids between the two races were obtained by allowing the males
Fig. 1. Parental and F₁ phenotypes: (a) f. chrysippus, Australia; (b) f. alcippus, tawny, Sierra Leone; (c) f. alcippus, nutbrown, Sierra Leone; (d) F₁, tawny; (e) F₁, nutbrown.

of one subspecies and the females of the other to fly freely in two heated greenhouses. Mating took place spontaneously and the females laid on a foodplant of the genus Asclepias. Unfortunately in these circumstances we were unable to keep the broods separate. The F₁ when they emerged were allowed to mate and F₂ generations were readily produced, but here again we did not keep the broods separate.
Fig. 2. F₁ phenotypes: (a) *f. chrysippus*-like, tawny; (b) *f. chrysippus*-like, nutbrown; (c) F₁-like, tawny; (d) F₁-like, nutbrown; (e) *f. alcippus*-like, tawny; (f) *f. alcippus*-like, nutbrown.
In the F₁ we obtained two distinct types of progeny with respect to the ground colour of the fore and hind wings. In one the ground colour of the forewings was nutbrown and the hindwings, although slightly paler in hue, had scales which also tended towards being nutbrown (Fig. 1e). In the other the ground colour was tawny to tawny orange, the nutbrown pigmentation being confined to an area close to the costal border of the forewings (Fig. 1d). Over the hindwings of both forms there was also a scattering of white scales which was variable in extent, being undetectable in some specimens but quite obvious in others. Of 12 butterflies with a tawny ground colour 6 had no detectable white scaling whereas of 11 nutbrown individuals only 2 lacked it. The reciprocal F₁s gave comparable results.

Both types of F₁ gave rise to F₂s. Among these were nutbrown individuals (Fig. 2b, d, f) and those of the tawny phenotype (Fig. 2a, c, e). There was a range of hindwing phenotypes from the Australian form without white (Fig. 1a) through intermediate forms up to a degree of white scaling found in the more extreme F₁s. With difficulty these could be divided into the parental and F₁ types, but the distinction was not clear (Fig. 2a, b, c, d). In addition, there was a phenotype with a white patch on the hindwing similar to that found in the Sierra Leone grandparents (Fig. 2e, f) (f. alcippus). The extent of the white was variable but quite distinct from that in the other insects. Both the nutbrown and the tawny phenotypes were to be found among the offspring with the white hindwings and those lacking it (Table 1).

**Discussion**

Since both in the F₁ and F₂ generations the broods were not kept separate, we do not know the phenotype (tawny or nutbrown) of the Sierra Leone parents. However we do know that the Australian stock was monomorphic for the tawny phenotype, consequently the nutbrown form must be dominant since it segregated in a clear cut manner in the F₁.

**Table 1. Phenotypes in the F₂.**

<table>
<thead>
<tr>
<th>Ground colour</th>
<th>No white</th>
<th>A little white (F₁-like)</th>
<th>White</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nutbrown</td>
<td>15</td>
<td>21</td>
<td>14</td>
</tr>
<tr>
<td>Tawny</td>
<td>58</td>
<td>15</td>
<td>20</td>
</tr>
</tbody>
</table>

**Results**

In the F₁ we obtained two distinct types of progeny with respect to the ground colour of the fore and hind wings. In one the ground colour of the forewings was nutbrown and the hindwings, although slightly paler in hue, had scales which also tended towards being nutbrown (Fig. 1e). In the other the ground colour was tawny to tawny orange, the nutbrown pigmentation being confined to an area close to the costal border of the forewings (Fig. 1d). Over the hindwings of both forms there was also a scattering of white scales which was variable in extent, being undetectable in some specimens but quite obvious in others. Of 12 butterflies with a tawny ground colour 6 had no detectable white scaling whereas of 11 nutbrown individuals only 2 lacked it. The reciprocal F₁s gave comparable results.

Both types of F₁ gave rise to F₂s. Among these were nutbrown individuals (Fig. 2b, d, f) and those of the tawny phenotype (Fig. 2a, c, e). There was a range of hindwing phenotypes from the Australian form without white (Fig. 1a) through intermediate forms up to a degree of white scaling found in the more extreme F₁s. With difficulty these could be divided into the parental and F₁ types, but the distinction was not clear (Fig. 2a, b, c, d). In addition, there was a phenotype with a white patch on the hindwing similar to that found in the Sierra Leone grandparents (Fig. 2e, f) (f. alcippus). The extent of the white was variable but quite distinct from that in the other insects. Both the nutbrown and the tawny phenotypes were to be found among the offspring with the white hindwings and those lacking it (Table 1).
Because the two stocks were both monomorphic with respect to the hindwing pattern we can say that white patch on the hindwing is partially recessive and completely so in some individuals. Thus in both the F₁ and F₂ butterflies white scaling was detectable in a higher proportion of the nutbrown phenotype than in the tawny one (p < 0.001). In fact, the ratios in the F₁ and F₂ suggest that the dominance is absent in most individuals with the nutbrown phenotype but not in those with the tawny ground colour. This difference may be due to the easier detection of a few white scales on the darker background.

The presence or absence of the white patch (as distinct from white scaling) on the hindwing segregated in a clear cut manner and in a good approximation to a 3:1 ratio in the F₂ (Table 1). Thus we can conclude that the presence or absence of the white patch on the hindwing is controlled by a single gene, the heterozygote being variable in expression.

Since the broods were not reared separately one cannot usefully examine the ratio of the nutbrown phenotype to the tawny one in the F₂. However, one can examine the data for evidence of linkage. We know that the nutbrown form and the white hindwing patch must both have been derived from Sierra Leone, and therefore in the presence of linkage the two loci would be in repulsion.

An examination of the ratio of white hindwing patch to its absence amongst the F₂ nutbrown individuals provides no good evidence for a departure from the expected 3:1 ratio (non-white to white hindwings) on the assumption of no linkage. Furthermore, if there had been close linkage there should have been an excess of the nutbrown phenotype amongst the white hindwinged individuals.

**Summary**

In the cross between *D. chrysippus* material from Australia and that from Sierra Leone, it was shown that the white hindwing area of *f. alcippus* is recessive, or nearly so, to the tawny hindwing of *f. chrysippus*, and the character is controlled in the main by a single locus.

In our Sierra Leone material there were two shades of brown on the forewings, tawny and nutbrown. The matings showed that the nutbrown coloration is dominant and extends on to the hindwing in the hybrids. It also appears to be controlled by a single locus. Segregation of the characters in the F₂ does not suggest close linkage between the two loci concerned.