NOTES AND COMMENTS

EVIDENCE FOR AUTOSOMAL MEIOTIC DRIVE IN THE BUTTERFLY *DANAUS CHRYSIPPUS* L.

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1. INTRODUCTION

Danaus chrysippus (Danaidae) in East Africa is highly polymorphic for colour, the genetic control of which resides at three loci. The *B* locus has two alleles, *B* giving a nutbrown ground colour and *bb* orange on both fore and hindwings. The *C* locus determines forewing pattern: there are two alleles, *C* giving a wing uniformly coloured except for a black margin (form *dorippus*) and *cc* a large black apical area traversed by a row of white subapical spots (form *aegyptius* = form *chrysippus* of my earlier papers). Heterozygotes (*Cc*) are basically *dorippus* but are often phenotypically distinct in showing the " *aegyptius* " subapical spots on the underside of the forewing. The *B* and *C* loci are closely linked (Smith, 1975*a*). The *A* locus has a recessive allele *a* the homozygous possessor of which has a large white patch on the hindwing (form *alcippus* when combined with the *aegyptius* forewing and form *albinus* with the *dorippus* forewing). The *A* locus probably assorts independently from the *B* and *C* loci (Clarke, Sheppard and Smith, 1973; Smith, 1975*a*).

All-female broods commonly occur in *D. chrysippus*. These probably result when a Y-linked gene *D* causes meiotic drive for the Y chromosome so that it always enters the secondary öocyte at the first meiotic division in the female. Females from all-female broods usually themselves produce all-female broods but a switch to bisexual broods can occur and seems to depend on the acquisition of a dominant autosomal suppressor gene *S* from the maternal male grandparent. The *S* locus is probably closely linked with the *C* locus (Smith, 1975*b*).

2. RESULTS

In the course of breeding an all-female line through seven generations, three broods, all from females of known colour genotype, reared in the laboratory and mated only once, gave F1 segregations which defy a normal interpretation (table 1). Although in each case wild males had to be used, their genotype for colour was either clear from inspection (broods 60 and 72) or could be deduced from the progeny (brood 70).

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TABLE 1

Details of the broods of D. chrysippus *discussed in the text*

Brood no.	Source, phenotype and genotype of ♀ parent	Source, phenotype and genotype of ♂ parent	Forewing phenotype of offspring			
			brown *dorippus*	brown *aegyptius*	orange *dorippus*	orange *aegyptius*
54[1]	Brown *alcippus* (wild) Bc/Bc	Orange *aegyptius* (wild) (bc/bc)	0	7	0	0
60[2]	Brown *aegyptius* (54) Bc/bc	Orange *dorippus* (wild)[3] bC/bc	0	0	2	3
69	Orange *aegyptius* (68) bc/bc	Brown *dorippus* (wild)[4] Bc/bC	0	14	12	0
70	Brown *aegyptius* (69) Bc/bc	Brown *dorippus* (wild)[4] Bc/bC	0	14	10	0
72	Brown *aegyptius* (69) Bc/bc	Orange *dorippus* (wild)[3] bC/bc	0	0	10	13

Notes. (1) This brood alone segregated for sex, the other four being all-female. The phenotype and genotype of the male parent are inferred from its offspring and grand-offspring. (2) Brood 60 also segregated at the *A* locus, giving a single *alcippus* (aa). (3) Males known to be heterozygous at the *C* locus on phenotypic grounds. (4) Males known to be heterozygous at the *B* and *C* loci from their progeny.

In broods 60 and 72 the expected segregation for forewing phenotypes is:

$$bC/bc \; ♂ \qquad \times \qquad Bc/bc \; ♀$$
$$\text{orange } dorippus \qquad | \qquad \text{brown } aegyptius$$

bC/Bc	bC/bc	Bc/bc	bc/bc
brown *dorippus*	orange *dorippus*	brown *aegyptius*	orange *aegyptius*
1 :	1 :	1 :	1

The absence of both brown phenotypes is significant in brood 60 (P = 0·031) (one-tail test) and highly significant in brood 72 (P < 0·001).

The expectation for brood 70 with the male parent in repulsion and no crossing over is:

$$Bc/bC \; ♂ \qquad \times \qquad Bc/bc \; ♀$$
$$\text{brown } dorippus \qquad | \qquad \text{brown } aegyptius$$

Bc/Bc	Bc/bc	Bc/bC	bC/bc
brown *aegyptius*	brown *aegyptius*	brown *dorippus*	orange *dorippus*
2	: 1	:	1

Brown *dorippus* is missing and the segregation departs significantly from expectation ($\chi_{(2)} = 9·0$; P < 0·02). The possibility that the male parent is in coupling is ruled out by the presence of orange *dorippus* and the absence of both orange *aegyptius* and brown *dorippus* from the progeny.

In all three broods the aberrant segregation is explained if the *Bc* chromosome of the female parent fails to enter the secondary öocyte due to meiotic

drive, leading to an expectation for only two phenotypes instead of three (brood 70) or four (broods 60 and 72). None of the broods shows a significant departure from a 1 : 1 expectation on this hypothesis.

3. CONCLUDING REMARKS

My hypothesis regarding the genetic control of sex ratio (Smith, 1975b) requires the presence of a dominant autosomal gene S if bisexual broods are to be obtained in the presence of the Y-linked gene D. In segregations at the C locus, Ss XYD females may give semi-bisexual broods such as broods 26, 29 and 51 (Smith, *op. cit.*), segregating for sex in one morph (*dorippus*) and all-female in the other (*aegyptius*) whereas ss XYD females always give all-female broods. Given that this model is correct (and I have indicated that others are possible), the C and S loci are linked, usually in coupling. At the time of writing five broods have been obtained in which one parent was a double heterozygote and are, therefore, valid for linkage estimation. There were two probable recombinants (*aegyptius* males) in 60 offspring. Although this result indicates close linkage, the estimated cross-over value of 3·3 per cent must be treated with caution as at least two types of cross are involved (backcross for both loci, or backcross for one and F2 for the other) and the linkage phase of two male grandparents is unknown. (In segregations at the S locus, the male parent has no influence on his own immediate offspring.) The B and C loci are also closely linked (Smith, 1975a). In 18 broods in which one parent was doubly heterozygous, only three detectable recombinants have occurred in 322 offspring (broods 1-95). The cross-over value based on all types of cross (single and double backcrosses and dihybrid crosses between repulsion phases, coupling phases or one parent of each type) is probably about 1·9 per cent. Unfortunately, as the linkage phase of wild parents is often unknown and double backcrosses, which are the most informative, hard to obtain, it is difficult to estimate linkage with precision and to provide standard errors. Progeny tests on wild caught heterozygotes show that repulsion phase chromosomes are commoner than those in coupling (16 cases out of 18 to give a clear result). Therefore, the commonest chromosomes in the population are expected to be bCS and Bcs (the order not determined).

As all three broods discussed here were both all-female and gave distorted segregations for colour, it must be supposed that meiotic drive was operating simultaneously on the sex chromosomes and the BCS autosomes. This interpretation has the interesting implication that the two homologous pairs do not always assort independently. The female parent in each case had the genotype Bcs/bcs XYD as the presence of S would have resulted in some male segregants: that all were heterozygous at the B locus is known from their ancestry. However, it has not escaped my attention that in brown *dorippus* females of genotype bCS/Bcs XYD, which are probably very common at Dar es Salaam (Smith, in prep.), meiotic drive for bCS eggs or, in other words, removal of the Bcs chromosomes to the first polar body as suggested for the broods under consideration, would lead to the elimination of all-female broods in the next generation as only two types of egg would form, bCS X and bCS YD, both of which carry the driving Y suppressor. Sex ratios could, therefore, oscillate if selection alternately favoured females having the two types of meiotic drive. If the frequency of the autosomal drive gene is ever

sufficiently high in the field (and this is unknown), its presence could lead to an increase of gene S and its linked colour genes, giving an explanation for the observed increase of orange *dorippus* following a rising sex ratio (Smith, 1975*b* and in prep.). The meiotic drive appears to act specifically on the B locus as all the female parents of broods 60, 70 and 72 are homozygous recessives at the C and S loci. It is clear that drive for Y, leading to excess of females, could only occur in the presence of s and that drive for b (orange) would reduce the frequency of s and, therefore, of females. If we postulate seasonally alternating selection for the two wing colours, it follows that selection for brown (B-) would give rise to female dominance and selection for orange (bb) restore the sex ratio to normality. The evidence from field sampling tends to support this hypothesis: brown *aegyptius* and brown *dorippus* are most frequent during the rains when the sex ratio is usually low, whereas orange *dorippus* is dominant in the dry season when sex ratios are normal (Smith, in prep.).

The data to hand give no firm indication how the autosomal drive mechanism might be either activated or suppressed. However, a Y-autosome translocation, as considered by Clarke, Sheppard and Scali (1975) for *Hypolimnas bolina* L., could establish linkage between the *BCS* loci and the D locus providing the autosomal drive suggested for broods 60, 70 and 72 without postulating further mutations for either drive or its suppression. The results from broods 54 and 60, which provided all the female parents, do not rule out this possibility. An alternative explanation is to propose affinity (Mitchie, 1953; Wallace, 1953) between the centromeres of the sex chromosomes and the *BCS* autosomes giving quasi-linkage for sex ratio and colour segregation. Although this could explain the present results it is unlikely that it would provide a satisfactory mechanism underlying the seasonal fluctuations of both sex and morph ratio found in the field. If my hypothesis regarding the role of the autosomal drive mechanism in the population genetics of *D. chrysippus* is correct, then one would expect a negative feedback relationship between the two drive mechanisms. Drive for Y would give the excess of females concomitant with population growth and drive for *bCS* the return to normal sex ratio appropriate for a population which has reached the carrying capacity of the habitat.

4. REFERENCES

CLARKE, SIR CYRIL, SHEPPARD, P. M., AND SCALI, V. 1975. All-female broods in the butterfly *Hypolimnas bolina* (L.). *Proc. R. Soc. Lond. B, 189*, 29-37.

CLARKE, C. A., SHEPPARD, P. M., AND SMITH, A. G. 1973. The genetics of fore and hindwing colour in crosses between *Danaus chrysippus* from Australia and from Sierra Leone (Danaidae). *J. Lep. Soc., 27*, 73-77.

MITCHIE, D. 1953. Affinity: a new genetic phenomenon in the house mouse. *Nature, 171*, 26-27.

SMITH, D. A. S. 1975*a*. Genetics of some polymorphic forms of the African butterfly *Danaus chrysippus* L. (Lepidoptera: Danaidae). *Ent. scand., 6*, 134-144.

SMITH, D. A. S. 1975*b*. All-female broods in the polymorphic butterfly *Danaus chrysippus* L. and their ecological significance. *Heredity, 34*, 363-371.

WALLACE, M. E. 1953. Affinity: evidence from within laboratory stocks. *Nature, 171*, 27-28.