

# One-winged *Drosophila subobscura*: a phenotype with an obscure genetic basis

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## ABSTRACT

A line of one-winged *Drosophila subobscura* was studied. The absent wing is substituted by a bulky structure with macro and microchaetes, showing a thoracic appearance. Genetic crosses showed that there is no way to select for the trait by simple crossing. The number of one-winged flies in the various generations was always low. In one case a wingless fly was also obtained. The trait presents an unknown genetic pattern.

## INTRODUCTION

There is only one lethal balanced strain known for *Drosophila subobscura*: *Va/Ba* developed by Sperlich *et al.* (1977). Individuals with only one wing appear in this strain, although with low frequency (Mestres and Busquets, 1991; Orengo and Mestres, 1993). The absent wing is replaced by a bulky structure with a thoracic appearance, which presents a variable number of macro- and microchaetes. This trait could be a homeotic substitution. In a previous study (Orengo and Mestres, 1993) this trait appeared to be heritable and controlled by at least three genes.

The *Va/Ba* strain carries the dominant gene *Va* (*Varicose*: irregular thickenings at the junctions of the wing veins and short irregular side branches to the veins). It is lethal in homozygous condition. This chromosome carries two X-ray-induced overlapping inversions (VIII + 210), and the natural arrangement (3 + 4). The other O chromosome of the strain presents a standard arrangement and carries the dominant gene *Ba* (*Bare*). The number of macrochaetes, and occasionally microchaetes, is variably reduced, but the bristle sockets are always present. It is lethal in homozygous condition.

The aim of the present study was to obtain a pure-breeding strain of one-winged flies and to analyze the hereditary pattern.

## MATERIAL AND METHODS

Two different sets of genetic crosses were carried out in order to obtain a pure-breeding strain of one-winged flies. In both cases the parental individuals belonged to lethal chromosomal lines heterokaryotypic for the *Va* balancer chromosome (Mestres *et al.*, 1990, 1995). One-winged flies seldom arose in these lines, but if crosses were carried out among different lines the frequency increased. In the first set of genetic crosses it was possible to reach the F<sub>3</sub> generation and in the second set the F<sub>5</sub>.

To examine the phenotype of the trait a one-winged *D. subobscura* fly was treated with acetone (70 and 100%) and dried with CO<sub>2</sub>. After that the sample was overlaid with gold (about 20 nm) and observed with a scanning electron microscope (S.E.M.) model Hitachi S 4000 (Figure 1).

## RESULTS

A bulky structure with macro and microchaetes that appears in place of the wing was clearly visible in the thoracic region (Figure 2).

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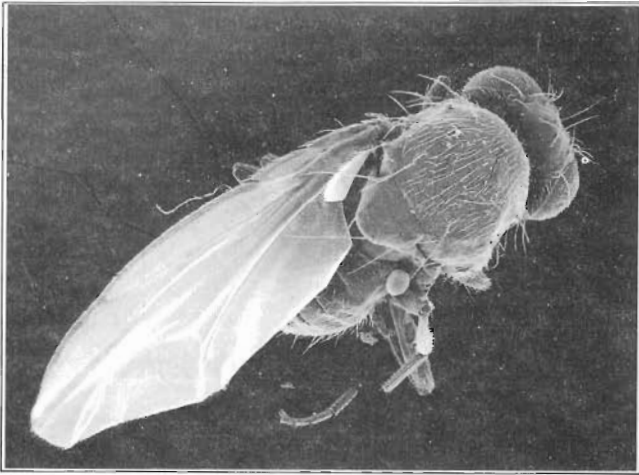


Figure 1 - General aspect of a one-winged *Drosophila subobscura* fly. It is possible to observe the bulky structure that appears in the place of the wing. X20.

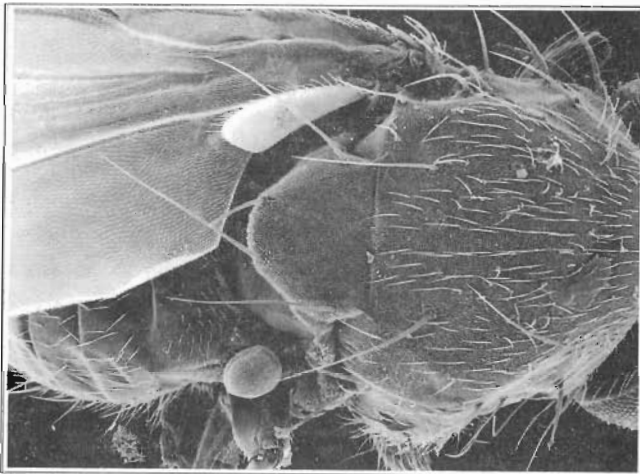


Figure 2 - Detail of the thorax of the same fly presented in Figure 1. The magnification allows comparison of both sides of the thorax. X45.

In the first set of crosses (Figure 3) the parental individuals were one male and a virgin female, both with only one wing. Both came from different lethal chromosomal lines. The  $F_1$  was homogeneous and normal.  $F_1$  individuals were used as parents for the  $F_2$  generation. In this generation, out of 198 flies three (one male and two females) were one-winged (1.5%) and one female without either wing was also obtained (0.5%). This is the first time that this phenotype has been reported. As in the case of one-winged flies, both absent wings were replaced by bulky structures with a thoracic appearance. In order to analyze the next generation the one-winged male was crossed in an individual vial with the wingless female. The offspring of this cross was composed of 147 normal and two (one male and one female) one-winged flies (1.3%). The one-winged male of the  $F_2$  was also crossed in another vial with one of the one-winged females of the  $F_2$ . All 64 flies of the offspring were normal.

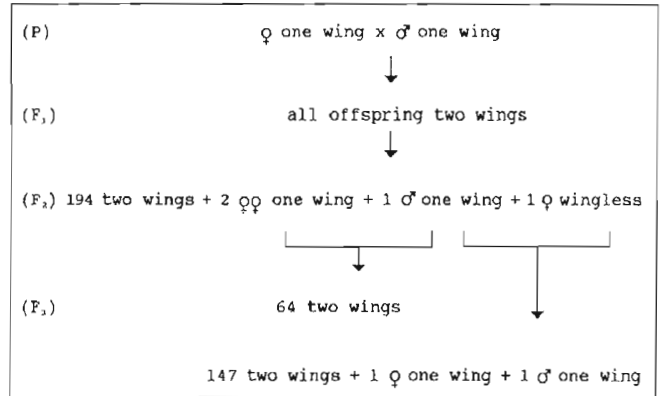


Figure 3 - Schematic diagram of the first set of crosses.

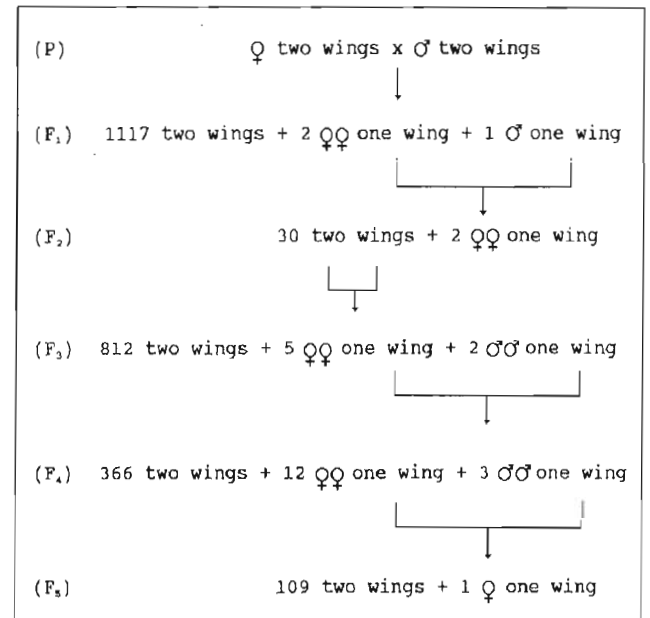


Figure 4 - Schematic diagram of the second set of crosses.

In the second set of crosses (Figure 4) the parental individuals presented a normal phenotype and were from two different lethal chromosomal lines. They were heterokaryotypic for the *Va*/lethal chromosome. Out of 1120 offspring flies three (one male and two females) were one-winged (0.27%). These one-winged flies were used to obtain the  $F_2$  generation. In this generation, out of 32 flies two (both females) presented only one wing and died soon. Thus, in order to obtain the  $F_3$  generation normal flies of the  $F_2$  were used as parents. In the  $F_3$ , out of 819 individuals seven (two males and five females) were one-winged flies (0.86%). These one-winged flies were selected as progenitors of the next generation (in this genetic cross some females may not have been virgin). In the  $F_4$ , out of 381 individuals 15 (three males and 12 females) presented only one wing (3.9%). Of these one-winged individuals two males and two females were selected as parents for the next generation. In the  $F_5$ , out of 110 flies only one (a female) was one-winged.

When the offspring of the two sets of genetic crosses in all generations are analyzed together, 25 (75.6%) were female and eight (24.2%) male. The difference is significant (Normal (0.1) statistic value = 2.954,  $P = 0.00157$ ).

## DISCUSSION

One-winged flies can arise in the *Va/Ba* strain or in genetic crosses between wild and *Va/Ba* individuals. The trait also appears in lethal chromosomal lines maintained with the *Va* chromosome or when crossing between these lines. All one-winged flies descend direct or indirectly from the *Va/Ba* strain. Thus, we can assume that the hereditary factors that control the trait come from this balancer strain, as reported earlier (Mestres and Busquets, 1991; Orengo and Mestres, 1993). The absent wing is always replaced by a thoracic structure of variable size.

In both crossing sets carried out the frequency of one-winged individuals in successive generations presented little variation. One-winged flies appeared in each generation, but at low frequencies. Thus, it seems that little response is obtained when the trait is selected. However, as a result of these crosses the new phenotype with both wings absent was detected for the first time. This could indicate that the expression of this trait was increased by the crosses. On the other hand, if the observed frequencies of one-winged flies are analyzed in the different generations it is difficult to understand the genetic pattern that controls the trait. For instance, in the first set of genetic crosses the  $F_2$  one-winged flies seem to be present in trihybrid proportions (observed frequency of 0.0202 and an expected value of  $1/64 = 0.0156$ ). The fly without wings also seems to be present in a tetrahybrid proportion (observed frequency of 0.0051 and an expected value of  $1/256 = 0.0039$ ). These results are difficult to understand when we look at the phenotypes of the parental and  $F_1$  generations. Furthermore, both sets of genetic crosses ended in extinction. The female-based sex-ratio detected in one-winged flies is also interesting.

Probable a number of interacting genes are involved, and environmental effects cannot be ruled out. Maybe a transposable element could be involved.

The low penetrance of the trait could be due to "epistatic stability". A system of epigenetic interactions may compensate or "buffer" some of the mutations and thus stabilize the phenotype with respect to these mutations (Wagner, 1996).

## ACKNOWLEDGMENTS

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## RESUMO

Estudou-se uma linhagem de *Drosophila subobscura* com apenas uma asa. A asa ausente é substituída por uma estrutura maciça com macro e microquetas, com aspecto de estrutura torácica. Cruzamentos genéticos mostram que não é possível selecionar o caráter por cruzamento simples. O número de moscas com uma asa nas várias gerações foi sempre baixo. Em um caso, uma mosca sem asa foi também obtida. O caráter tem um padrão genético desconhecido.

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