

Effect of the *Wingless* (wg^1) Mutation on Wing and Haltere Development in *Drosophila melanogaster*

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Genetic and developmental studies of *wingless* (wg^1), a new second chromosome recessive mutation in *Drosophila melanogaster*, have shown that it affects not only wing and haltere development (giving rise to wingless and/or halterless flies), but also results in various abnormalities of the mesothorax. The larvae destined to develop into wingless and/or halterless flies possessed underdeveloped mesothoracic and/or metathoracic imaginal discs.

INTRODUCTION

A mutation affecting wing and haltere development in *Drosophila* (*wingless*, wg^1) was reported by Sharma (1973). The *wingless* condition was governed by a recessive gene (Table 1) that mapped on the left arm of the second chromosome at a distance of about 18 map units to the left of the *black* body colour (*b*) gene. The progeny of *wingless* flies always consisted of wingless, one winged and "two winged" flies in approximately 2:2:1 ratio (Table 2). Further, the progeny of one winged \times one winged and "two winged" \times "two winged" flies (isolated from the progeny of *wingless* flies) also segregated into all the three phenotypes. This segregation pattern suggests that wg^1 is a gene with incomplete penetrance and variable expressivity. Attempts at stabilizing the *wingless* condition as a homogeneous population have not been successful. Selection for five generations for the three phenotypes still yielded individuals that threw out segregants. However, it has been observed that the proportion of the *wingless* phenotype during the five cycles of selection has been advanced to about 70% in comparison with around 40% in the base population of the original stock (Table 3).

The wg^1 mutation also has an associated effect on haltere development. There is no consistent correlation, however, between failure of wing and haltere development, since flies with all combinations of wing

and haltere number were present in the progeny of *wingless*, one winged and "two winged" parents.

Besides the *wingless* and/or halterless condition, the flies also showed various abnormalities of the mesothorax, which gave clues to the mode of operation of the wg^1 gene and suggested that it operates early during development. The mesothoracic abnormalities observed in our studies were found to be associated in general with the suppression of wing development on one or both sides. The prominent abnormalities included irregular arrangement of hairs, partial to complete absence of mesothoracic bristles, absence or deformation of scutellum (Fig. 1), unequal development of the two mesothoracic portions with partial to complete fusion (Fig. 2), and hemithoracic flies (Fig. 3).

Third instar larvae destined to develop into *wingless* and/or halterless flies possessed underdeveloped mesothoracic and/or metathoracic imaginal discs (Figs. 4-6). In a large number of abnormal mesothoracic discs studied, while the anterior region (the mesothorax-forming region) was normal, the posterior region that gives rise to the wing had not developed (Fig. 6). It would appear that, despite developmental autonomy of meso- and metathoracic discs, some stages in their differentiation are under common control, since the wg^1 mutation has effects on both.

Hadorn and Buck (1962), Garcia-Bellido

TABLE 1

F₂ SEGREGATION DATA OF THE CROSSES INVOLVING WINGLESS, ONE WINGED, AND "TWO WINGED" FEMALES TO Or-k MALES

S. No.	Cross	F ₁	F ₂ segregation				
			Ork-k	wg ¹			X ² ^b
				Two winged ^a	One winged	Wingless	
1	Wingless × Or-k	Normal	707	47	81	95	0.95
2	One winged × Or-k	Normal	648	39	77	78	2.04
3	Two winged × Or-k	Normal	506	33	47	66	2.36

^a Since "two winged" (wg¹) flies are indistinguishable from Or-k, their frequency was calculated on the basis of their occurrence in a wingless × wingless cross (see Table 2), which is approximately half of the number of wingless flies.

^b Calculated X² value is not significant at 5% probability.

TABLE 2

BREEDING BEHAVIOUR OF WINGLESS, ONE WINGED, AND "TWO WINGED" FLIES

Cross	Total flies	Wingless (%)	One winged (%)	"Two winged" (%)
Wingless × wingless	890	42.7	40.6	16.7
One winged × one winged	801	38.5	41.3	20.1
"Two winged" × "Two winged"	645	40.3	42.9	16.6

TABLE 3

BREEDING BEHAVIOUR OF WINGLESS AND WINGED FLIES SELECTED FROM THE PROGENY OF wg¹ FEMALES TO WILD TYPE MALES AFTER FIFTH BACK-CROSS

Cross	Total flies	Wingless (%)	One winged (%)	"Two winged" (%)
Wingless × wingless	1257	79.6	19.5	0.9
One winged × one winged	478	75.6	19.2	5.1

(1966), and Garcia-Bellido *et al.* (1973) have shown that a fully developed mesothoracic disc differentiates into anterior and posterior regions from which the mesothorax and wing originate. Each region consists of a mosaic of morphogenetic fields wherein all the cells are determined and fixed in their prospective significance. From an analysis of cell lineage relationships, using X-ray induced somatic crossing-over at specific states of development, Bryant (1970) has concluded that in the embryo, presumptive wing disc cells are not determined as between wing and mesonotum. The determination takes place at a later stage of development. One plausible

explanation for the results reported here could be that the wg¹ gene acts at the level of initial cell determination in the embryo and prevents invagination of meso- and metathoracic disc initials. This would result in hemithoracic flies, as is observed in the present study. Flies that lack mesothorax completely will probably be nonviable and therefore are not recovered in the progeny. If the process of invagination escapes wg¹ action, inhibitory action of this gene could later prevent or alter the differentiation of the discs into various morphogenetic fields. This would result in a wide array of abnormalities of the types observed in the present study.



FIG. 1. Showing irregular arrangements of hairs, complete absence of prominent mesothoracic bristles, and deformed scutellum.

FIG. 2. Unequal development and partial fusion of two mesothoracic portions.

FIG. 3. Hemithoracic fly. Prominent mesothoracic bristles and scutellum are missing.

FIG. 4. Fully mature imaginal discs for meso- and metathorax and third pair of legs from a third-instar larva.

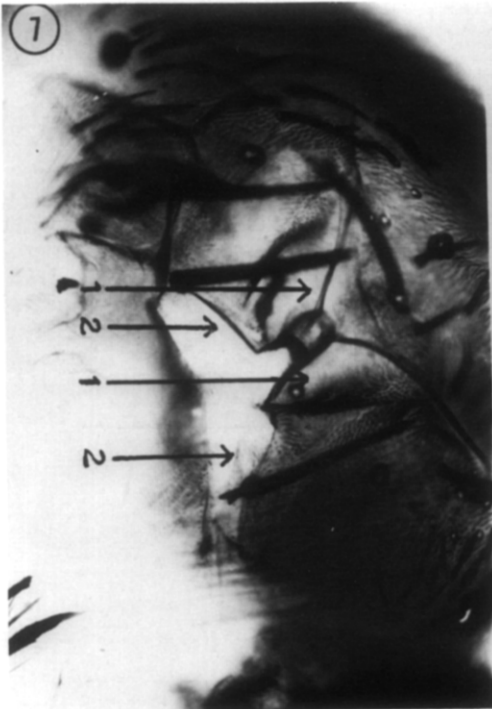
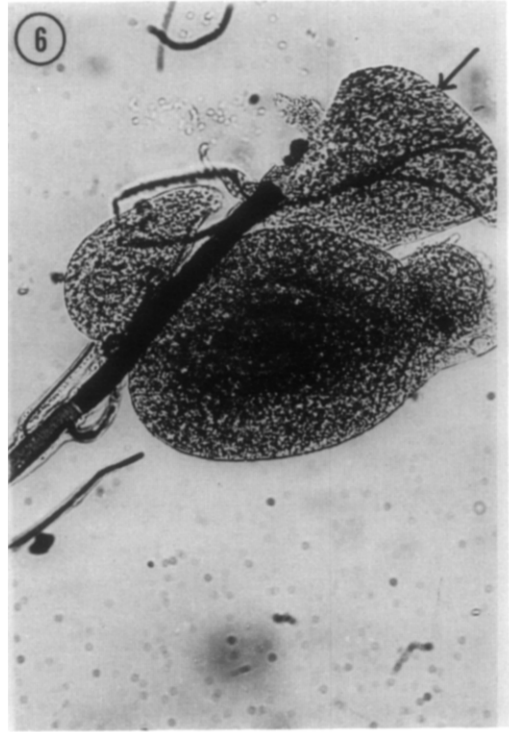


FIG. 5. Underdeveloped metathoracic disc (arrow) from a third instar larva.

FIG. 6. Underdeveloped meso- and metathoracic discs from a third-instar larva. Note (arrow) the undifferentiated presumptive wing region in the mesothoracic disc.

FIG. 7. Mirror image duplication of notopleurite region (1) and notopleural suture (2).

FIG. 8. Showing wingless fly with normal halteres. On both sides of normal scutellum, duplicated scutellumlike structures can be seen (arrow).

An alternative interpretation for the observed wingless condition coupled with the various mesothoracic abnormalities could be that although the invagination and determination of the cells in the wing disc follows a normal course, at a later stage of development and much before the maturation of disc, the *wg*¹ gene causes degeneration of the presumptive wing area as has been shown to be the case for *vestigial* (Fristrom, 1969). This would lead to mirror-image duplication of at least some of the thoracic regions, as is evidenced from our observations that parts of the scutum and notopleural suture as well as notopleural bristles (Fig. 7) and scutellum (Fig. 8) are duplicated. Duplication of structures in the form of mirror images has been explained on the basis of a gradient in developmental capacity in the imaginal disc (Bryant, 1971). Cells at a higher level of the gradient could regenerate the missing parts while cells at lower gradient levels will only duplicate. Bryant (1974, 75) showed that certain segments of the wing disc, when allowed to grow in the abdominal cavity of the adult and then to metamorphose by transplantation into third instar larvae, could regenerate the entire disc. Others could only duplicate producing a mirror image duplication. The mesothoracic region of the wing disc, or a part of it, was shown to undergo only duplication and to be devoid of regenerative capacity, indicating it to be at a lower level in the gradient in developmental capacity.

If the primary effect of *wg*¹ is to cause

degeneration of the presumptive wing region of the imaginal disc, then the known tendency of the presumptive thorax to undergo duplication can account for the ultimate effects of this mutation on the phenotype.

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