The pattern of campaniform sensilla on the wing and haltere of *Drosophila melanogaster* and several of its homeotic mutants

By ERIC S. COLE and JOHN PALKA

From the Department of Zoology, University of Washington, Seattle

**SUMMARY**

A detailed mapping and description of campaniform sensilla on the wing and haltere of *Drosophila melanogaster* is provided. Six types of sensilla are distinguished. Similarities in the pattern of their distribution on the dorsal and ventral surfaces of each appendage, as well as between the wing and haltere, are apparent. These data are used to assess the quality of homeotic transformation in several mutants of the bithorax complex in which the halteres are transformed into wings. Flies homozygous for *abxbx3pbx* produce a complete inventory of wing sensilla on the homeotic appendage. In *abx, bx3* and *bx3 pbx* homozygotes the transformation of haltere into wing is incomplete, and each mutant shows characteristic fields of haltere and wing sensilla. It appears that specific regions of the anterior haltere compartment require different combinations of mutant alleles to produce a distinct homeotic transformation. Furthermore, the *pbx* mutation appears to influence expression of the *bx3* mutation within the anterior compartment.

**INTRODUCTION**

Genes of the bithorax complex (BX-C) of *Drosophila melanogaster* are involved in the commitment of larval and imaginal tissues to specific developmental pathways. Garcia-Bellido (1975) has suggested that specific genes of the bithorax complex are active in particular segments and compartments. Lewis (1963, 1978, 1981) has developed a model which proposes that individual genes of the BX-C produce substances which act within a given segment to change its developmental identity from a mesothoracic ground state towards a more posterior state such as metathorax or abdomen. He suggests (Lewis, 1951) that the developmental programmes of metathoracic and abdominal segments have evolved from an ancestral mesothoracic programme so that the absence of appendages on the abdominal segments, and the presence of halteres rather than wings on the metathorax, represent evolutionarily acquired variations upon the mesothoracic theme under the genetic control of the BX-C. Most mutations in

1 *Authors' address*: Department of Zoology, University of Washington, Seattle, Washington 98195, U.S.A.
the BX–C result in a reversion of the phenotype to the mesothoracic ground state.

In the present study we have examined three mutants of the BX–C: anterior-bithorax (abx), bithorax (bx$^3$) and postbithorax (pbx). All demonstrate a transformation of metathoracic to mesothoracic structures, and in particular of haltere to wing (Lewis, 1981). The mutant abx produces a highly variable transformation of the anterior haltere towards anterior wing; bx$^3$ generates a more consistent but nevertheless incomplete transformation of anterior haltere to anterior wing (cf. Adler, 1978); and pbx demonstrates a transformation of posterior haltere to posterior wing. The combination bx$^3$pbx produces a four-winged fly by transforming both the anterior and posterior compartments of the haltere into wing tissue, but with significant imperfections. When abx is combined with the bx$^3$pbx genotype, a near-perfect second pair of wings is produced. Thus, it appears that the wild-type genes abx$^+$, bx$^+$ and pbx$^+$ all introduce meta-thoracic variations upon the basic mesothoracic developmental theme. Mutations at these loci prevent the variations from being expressed, thereby revealing the mesothoracic programme within the third thoracic segment.

We describe here in detail the quality of segmental transformation brought about by these BX–C mutations at the level of structural resolution afforded by the scanning electron microscope (SEM). In particular, we focus upon sensory structures called campaniform sensilla, because they provide cuticular markers of wing and haltere identity permitting an assessment of the quality of homeotic transformation.

A campaniform sensillum is composed of cuticular and hypodermal elements and a primary sensory neuron. The cuticle of these organs forms a socket and a dome to which the fan-shaped sensory dendrite attaches (e.g. Chevalier, 1969). Their morphology and orientation make them selectively sensitive to cuticular deformation along particular lines of mechanical stress (Pringle, 1957).

The distribution and morphology of campaniform sensilla on the wings and halteres of flies have been described by many authors. Weinland (1890) and Pflugstaedt (1912) give extensive reviews of the early literature concerning sensilla on the halteres of flies, as well as offering detailed descriptions at the light microscopic level. Zacwilichowsky describes in a series of papers (e.g. 1930, 1934) the distribution and innervation of sensilla on a variety of insect wings and halteres. More recently, Bryant (1978), working at the light microscopic level, and Hodgkin & Bryant (1978), using scanning electron microscopy, have provided the most comprehensive survey of wing and haltere sensilla in D. melanogaster.

In all of the work previous to our own, the sensilla have been grouped into identified fields exclusively on the basis of local clustering. Upon detailed examination with the SEM, however, it becomes apparent that sensilla of different fields have distinct morphological characteristics. Furthermore, some of the previously defined fields prove to be composed of smaller subpopulations
of sensilla differing in morphology. The number of sensilla types is limited, and it has been possible to map and characterize all of the campaniform sensilla of the wing and haltere in Drosophila according to three morphological criteria.

We describe the wild-type distribution of sensilla and discuss the significance of pattern symmetries between dorsal and ventral surfaces of the wing and haltere, as well as segmental homologies between the two appendages. We then apply this survey of specific wing and haltere pattern elements to assess the quality of transformation brought about by the abx, bx* and pbx mutations of the BX-C, singly and in combination.
Fig. 2. Schematic map of the haltere sensilla. (A) The dorsal surface: Met.Pap. = the metathoracic papillae. d.Scab. = sensilla of the dorsal scabellum. d.Ped. = sensilla of the dorsal pedicellus. (B) The ventral surface: v.Scab. = sensilla of the ventral scabellum. v.Ped. = sensilla of the ventral pedicellus. Scale = 100 μm.

MATERIALS AND METHODS

Wild-type flies were of the Sevelen stock provided by G. Schubiger, Department of Zoology, University of Washington. Mutant phenotypes of abx, bx\(^3\), and bx\(^3\)px were obtained from inter se crosses of abx/+, sdb\(^3\)bx\(^3\)e\(^11\)/+ and sdb\(^3\)bx\(^3\)px e\(^11\)/+ respectively. The yield of homozygous flies from these crosses was far greater than from the original abx/TM1, sdb\(^3\)bx\(^3\)e\(^11\)/TM1 or sdb\(^3\)bx\(^3\)px e\(^11\)/TM1 stocks. The abx bx\(^3\)px phenotypes were selected from the abx bx\(^3\)px/ Ubx\(^{std}\) stock. All mutants were obtained from E. B. Lewis, Division of Biology, California Institute of Technology. Flies were raised at 25 °C on a standard Drosophila medium provided by L. Sandler, Department of Genetics, University of Washington.

Adult flies were anasthetized with CO\(_2\) and placed immediately in amyl acetate for one hour to several days for dehydration. They were then partially dissected and mounted for SEM. This simplified procedure preserved the three-
Campaniform sensilla in wild-type and homeotic Drosophila

dimensional structure of the cuticle at least as well as conventional fixation, dehydration and critical-point-drying procedures. Specimens were coated with a gold/palladium alloy for three min at 15 A in a Hummer Sputter-Coater, and examined on a JEOL JSM-U3 microscope. More than twenty wild-type specimens and six or more specimens of each mutant were examined.

In all the mutant genotypes, the sensilla on the normal, mesothoracic wings were indistinguishable from those of wild-type individuals. Thus, there was no indication that the marker mutations sbd^2 and e^{11} had any effect on our structural analysis.

RESULTS

The system of sensilla nomenclature presented here has been modified from that used by Bryant (1978). The distribution of sensilla on the dorsal and ventral surfaces of the proximal wing is shown in Fig. 1, that of the haltere appears in Fig. 2.

A 'field' is defined as a population of sensilla sharing a common morphological type, distinct from that of neighbouring sensilla and spatially isolated from other sensilla having the same morphology. Single sensilla are not considered fields in themselves, but are treated individually or in association with neighbouring fields. The large campaniform sensilla are described only briefly and other sensilla, such as the bristle sensilla of the anterior wing margin, have been described elsewhere (Palka, Lawrence & Hart, 1979).

While examining and characterizing the sensilla of the wing and haltere, it became evident that differences among sensilla could be attributed to three general characteristics. Sensilla were either circular or elliptical in outline, either high or low in profile, and either socketed or socketless. Based upon these three criteria we identified six sensilla types on the wing and haltere (Fig. 3). The dimensions of sensilla from the various wing and haltere fields are given in Table 1.

The dorsal wing surface

The most proximal field of sensilla appears on the anterior notal wing process (Fig. 1). This field, the ANWP sensilla, consists of two type-5 sensilla and a single type-1 sensillum (Fig. 3). These are arranged in a fused linear array.

The medial face of the tegula bears eighteen type-5 sensilla comprising the Teg. field (Figs. 1, 3 and 4E). Fourteen of these form a compact central population composed of elliptical sensilla oriented with their major axes perpendicular to the proximodistal axis of the wing. Two larger sensilla of the same type are situated anterior to this central population and are oriented orthogonally to the others, with their long axes parallel to the proximal–distal axis of the wing. Finally, two larger type-5 sensilla flank the central population and are also oriented parallel to the wing axis.

Leaving the wing hinge and proceeding to the wing blade proper, we find five
Fig. 3. The morphological types of small campaniform sensilla and their locations. Details in text.
Campaniform sensilla in wild-type and homeotic Drosophila

Table 1. Sensilla dimensions. Elliptical sensilla were measured along their long axes from the outer perimeter of their sockets. The diameter of circular sensilla was measured from the outer perimeter of their sockets, if present, or from the outer perimeter of their domes if the socket was absent.

<table>
<thead>
<tr>
<th>Sensilla field</th>
<th>Sensilla dimensions (μm)</th>
<th>Morphology</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANWP</td>
<td>6.0</td>
<td>Type 5, Type 1</td>
</tr>
<tr>
<td>Teg. sensilla peripheral to main field</td>
<td>5.0</td>
<td>Type 5</td>
</tr>
<tr>
<td>Teg. main field</td>
<td>3.5</td>
<td>Type 5</td>
</tr>
<tr>
<td>d.Rad.A</td>
<td>3.5-4.5</td>
<td>Type 2</td>
</tr>
<tr>
<td>d.Rad.B</td>
<td>2.5-3.0</td>
<td>Type 6</td>
</tr>
<tr>
<td>d.Rad.C</td>
<td>2.5-3.5</td>
<td>Type 4</td>
</tr>
<tr>
<td>d.Rad.D</td>
<td>4.5</td>
<td>Type 1</td>
</tr>
<tr>
<td>d.Rad.E</td>
<td>5.0-5.5</td>
<td>Type 3</td>
</tr>
<tr>
<td>d.HCV</td>
<td>8.0</td>
<td>Type L.C.*</td>
</tr>
<tr>
<td>GSR</td>
<td>9.0</td>
<td>Type L.C.*</td>
</tr>
<tr>
<td>v.Rad.A</td>
<td>2.5-3.5</td>
<td>Type 6</td>
</tr>
<tr>
<td>v.Rad.B</td>
<td>2.5-3.5</td>
<td>Type 1</td>
</tr>
<tr>
<td>v.Rad.C</td>
<td>4.5</td>
<td>Type 3</td>
</tr>
<tr>
<td>v.HCV</td>
<td>6.5</td>
<td>Type L.C.*</td>
</tr>
<tr>
<td>Met.Pap.</td>
<td>5.0</td>
<td>Type 5</td>
</tr>
<tr>
<td>d.Scab.</td>
<td>2.5-4.0</td>
<td>Type 2</td>
</tr>
<tr>
<td>d.Ped.</td>
<td>3.0-4.0</td>
<td>Type 5</td>
</tr>
<tr>
<td>v.Scab.</td>
<td>4.0</td>
<td>Type 5</td>
</tr>
<tr>
<td>v.Ped.</td>
<td>3.5-4.0</td>
<td>Type 5</td>
</tr>
</tbody>
</table>

* L.C. — large campaniform type (see Palka et al. 1979 for description).

major fields of small campaniform sensilla located on the dorsal radial vein (Fig. 1). This vein probably represents the fusion during evolution of at least two separate veins, the radial 1 vein and the subcostal vein. From descriptions of other insect wings (e.g. Comstock, 1915; Pringle, 1957), it appears likely that both the radial 1 and subcostal veins originally bore separate fields of sensilla which became juxtaposed as the veins fused. For simplicity, we refer to this vein complex as the radius and call the five dorsal sensilla fields d.Rad.A–d.Rad.E. Furthermore, we refer to the three portions of the radius, divided from one another by incomplete transverse septa, as the proximal, medial and distal radius (Fig. 1).

The first three fields of sensilla are situated on the proximal radius. Field d.Rad.A consists of four type-2 sensilla arranged in a row and increasing in diameter distally (Figs. 1, 4B). Field d.Rad.B consists of seven type-6 sensilla distributed in a round patch (Figs. 1, 4A). The d.Rad.C field contains approximately seventeen type-4 sensilla. These appear to be sunken into depressions in the surrounding cuticle rather than surrounded by an elevated socket (Fig. 4D).
Fig. 4. Sensilla types of the wing. (A) Type-1 sensilla (v.Rad.B). Scale = 1.7 μm. (B) Type-2 sensilla (d.Rad.A). Scale = 2.4 μm. (C) Type-3 sensilla (v.Rad.C). Scale = 5.0 μm. (D) Type-4 sensilla (d.Rad.C). Scale = 1.7 μm. (E) Type-5 sensilla. (Teg.) Scale = 3.3 μm. (F) Type-6 sensilla (v.Rad.A). Scale = 2.5 μm.
Campaniform sensilla in wild-type and homeotic Drosophila

Two fields of sensilla, d.Rad.D and E (Fig. 1) are situated on the medial radius. Field D contains four type-1 sensilla situated on the anterior face of the medial radius; they often bear a tiny peak in their dome cuticle. Field E consists of eight type-3 sensilla arranged linearly.

On the distal radius there are two isolated sensilla: the dorsal humeral cross-vein sensillum (d.HCV), and the giant sensillum of the radius (GSR), so named because of its massive sensory neuron (Palka et al. 1979). The dHCV sensillum is situated at the base of the humeral cross-vein (Fig. 1). It is a circular, high-profile sensillum with a socket which is prominent on one side but becomes indistinct on the other. The GSR sensillum, situated on the posterior face of the distal radius (Fig. 1), is typical of all of the large campaniform sensilla. It is circular, with a high profile and a distinct discontinuity between dome and socket.

Two large campaniform sensilla occur on the first longitudinal vein near the tip of the costa. These have been called the twin sensilla of the margin, TSM (Palka et al. 1979). Another large campaniform sensillum is located on the anterior cross-vein, the ACV sensillum, and three others (sometimes four) occur along the third longitudinal vein, d.L.III 1–4. Their morphology is indistinguishable from that of the GSR (see Palka et al. 1979).

The ventral wing surface

The ventral wing bears three distinct fields of sensilla on the radius, v.Rad.A–v.Rad.C (Fig. 1), and two isolated sensilla, v.HCV and v.L.III. Field A of the ventral radius is composed of four or five type-6 sensilla, often arranged in a diamond pattern, on the proximal segment of the radius (Fig. 4F). Field B is composed of three type-1 sensilla on the border of the proximal and medial radius. The cuticle of their domes is often peaked. Field C consists of five type-3 sensilla arranged linearly along the medial radius (Fig. 4C).

The two isolated sensilla, v.HCV and v.L.III, are situated on the humeral cross-vein (Fig. 1) and on the third longitudinal wing-vein respectively. The v.HCV sensillum bears a socket which is tightly fused to the dome and diminishes on one side. The v.L.III sensillum is similar in form to the large campaniform sensilla of the dorsal wing surface.

Sensilla of the haltere

The haltere is divided into three sections, the scabellum, the pedicellus and the capitellum (Fig. 2). The scabellum is believed to correspond to the proximal radius region of the wing. The pedicellus includes areas comparable to the medial and distal regions of the radius up to and including the GSR, and the capitellum corresponds to the wing-blade distal to the GSR (Morata, 1975; Bownes & Seiler, 1977).

Five distinct fields of small campaniform sensilla appear on the haltere (Fig. 2): the dorsal metathoracic papillae, the dorsal and ventral fields of the scabellum, and the dorsal and ventral fields of the pedicellus. The metathoracic papillae
Fig. 5. Sensilla of the haltere. (A) The metathoracic papillae, type 5. Scale = 3·3 μm. (B) Dorsal scabellar sensilla, type 2. Arrow indicates flanking sensillum (see Fig. 7D). Scale = 6·7 μm. (C) Dorsal pedicellar sensilla, fused type 5. Arrow indicates flanking sensillum. Scale = 6·7 μm. (D) Flanking sensillum of the dorsal scabellum, type 5 (Dorsal Hicks' papilla, see text). Scale = 1·7 μm. (E) Ventral scabellar sensilla, type 5. Scale = 1·9 μm. (F) Ventral pedicellar sensilla, fused type 5. Scale = 8·3 μm.
Campaniform sensilla in wild-type and homeotic Drosophila

Table 2. Summary of the varying degrees of homeotic transformation expressed in different regions of the metathoracic appendage. ‘Wing’ indicates a nearly perfect wing phenotype for a given sensilla field, ‘Haltere’ indicates the persistence of haltere-like sensilla. More complete details are provided in more complex cases.

<table>
<thead>
<tr>
<th>Sensilla field</th>
<th>abx</th>
<th>bx³ pbx</th>
<th>bx³ pbx</th>
<th>bx³</th>
<th>abx</th>
</tr>
</thead>
<tbody>
<tr>
<td>ANWP Teg.</td>
<td>Wing</td>
<td>Wing</td>
<td>Wing</td>
<td>Wing</td>
<td>Haltere</td>
</tr>
<tr>
<td>d.Rad.A</td>
<td>Wing</td>
<td>Wing</td>
<td>Wing</td>
<td>Wing</td>
<td>Wing</td>
</tr>
<tr>
<td>d.Rad.B</td>
<td>Wing</td>
<td>Wing</td>
<td></td>
<td>Wing, with occasional supernumerary type 2.</td>
<td>Variable</td>
</tr>
<tr>
<td>d.Rad.C</td>
<td>Wing</td>
<td>Wing, distal sensilla bear sockets</td>
<td>Wing, distal sensilla appear</td>
<td>Variable</td>
<td></td>
</tr>
<tr>
<td>d.Rad.D</td>
<td>Wing</td>
<td>Haltere, fused type-5 sensilla appear</td>
<td>Haltere, indeterminate sensilla appear</td>
<td>Variable</td>
<td></td>
</tr>
<tr>
<td>d.Rad.E distal, dorsal radius</td>
<td>Wing</td>
<td>Wing</td>
<td>Wing, Haltere, GSR is present</td>
<td>Wing,  Haltere, GSR is present</td>
<td>Variable</td>
</tr>
<tr>
<td>v.Rad.A.</td>
<td>Wing</td>
<td>Wing</td>
<td>Wing</td>
<td>Wing</td>
<td>Wing</td>
</tr>
<tr>
<td>v.Rad.B</td>
<td>Wing</td>
<td>Wing, haltere, sensilla absent</td>
<td>Wing, sensilla sometimes present</td>
<td>Wing</td>
<td></td>
</tr>
<tr>
<td>v.Rad.C distal, ventral radius</td>
<td>Wing</td>
<td>Haltere</td>
<td>Haltere</td>
<td>Haltere</td>
<td>Variable</td>
</tr>
</tbody>
</table>

(Fig. 5A) are two type-5 sensilla, fused by the cuticle of their sockets. The dorsal scabellum bears a field of approximately 42 type-2 sensilla arranged in six longitudinal rows. Their diameters increase distally in each row (Fig. 5B). This field of sensilla is flanked by a single type-5 sensillum on the anterior margin, which we regard as representing the dorsal Hicks papillae (Weinland, 1890) of other fly species (Fig. 5B and D, arrow). The dorsal pedicellar field bears about 43 sensilla arranged in ten transverse rows (Fig. 5C). We interpret these as type-5 sensilla whose sockets are fused to one another, as is seen in the ANWP and metathoracic papillae. This interpretation is consistent with the observation that supernumerary haltere sensilla found on homeotic appendages (see below) are often clearly of type-5 morphology and appear in varying states of fusion. One or two unfused type-5 sensilla flank the major sensilla field on the anterior margin (Fig. 5C, arrow); these are similar to the ‘unbestimmte Papillen’ described by Weinland (1980).

The ventral scabellum bears five type-5 sensilla arranged in a diamond pattern (Fig. 5E). The sensilla of the ventral pedicellar field are virtually identical to those of the dorsal pedicellus (Fig. 5F). There are about 46 type-5 sensilla...
arranged in ten transverse rows, each sensillum fused to its neighbour by the prominent socket cuticle. We have not detected any solitary sensilla flanking this field.

This completes the survey of wild-type sensilla on the wing and haltere. The pattern described above is consistent from specimen to specimen, except for subtle differences in the size and sometimes number of sensilla in a given field.

**Sensilla of the Bithorax mutants**

Figure 6 shows scanning electron micrographs of sensilla found on the homeotic appendages of flies homozygous for the mutant genotypes $bx^3$, $bx^3pbx$ and $abx$. Two regions in particular, the proximal and medial radius of these homeotic appendages, are illustrated because they show the full range of mutant phenotypes we have observed. Sensilla of the $abxbx^3pbx$ mutants are not shown since they were indistinguishable from those of the wild-type flies.

$abxbx^3pbx$. The homeotic appendage is occasionally somewhat smaller than the normal wing, but almost always bears the full wild-type complement of wing sensilla. Each field is situated in the appropriate location and is composed of sensilla with the appropriate morphology. The only noticeable difference between the sensilla fields of the homeotic appendage and those of the wild-type wing is an occasional decrease in the number of sensilla in fields d.Rad.B and d.Rad.C, and very rarely the presence of one or a few supernumerary sensilla of the haltere pedicellar type.

$bx^3$. In mutants homozygous for the genotype $sbd^2bx^3e^{11}$ only the anterior compartment of the homeotic appendage is transformed into wing tissue. The phenotype is somewhat variable. The appendage is often misshapen and the sensilla fields can be difficult to locate amongst the folds of cuticle so that our sample size for this genotype is the smallest. In $bx^3$ flies the proximal-most sensilla fields are the most perfectly transformed whereas the more distal fields more often remain haltere like.

Fig. 7. Homeotic transformation of the mutant appendages. Unmarked areas represent regions of strong homeotic transformation bearing well-defined wing structures. Stippled areas represent regions of imperfectly formed wing structures. Single-hatched regions represent imperfect haltere regions and double-hatched areas possess well-defined haltere structures.

On the dorsal surface, the ANWP and Teg. sensilla characteristic of wings always appear normal. On the dorsal radius, field d.Rad.A occasionally shows supernumerary type-2 sensilla (Fig. 6A, arrows). The d.Rad.B field often contains fewer than the normal seven sensilla, but these always have the appropriate morphology. The d.Rad.C sensilla are also reduced in number, and the distalmost sensilla possess rudimentary sockets rather than smooth depressions.

Sensilla on the medial radius show more pronounced deviations from the wing pattern. Field D is composed of aberrant type-5 sensilla not representative of either wing or haltere (Fig. 6D, arrow). The neighbouring d.Rad.E sensilla appear wing-like though crowded (Fig. 6D, arrow). The distal radius possesses the normal dHCV and GSR sensilla, surrounded by supernumerary sensilla of varying numbers and morphology.

Of the four cases where we could examine the proximal-ventral surface, the
Campaniform sensilla in wild-type and homeotic Drosophila

Fig. 8. Pattern symmetries and segmental homologies. (A) Symmetries between sensilla fields of the dorsal and ventral wing surfaces. (B) Symmetries between the dorsal and ventral haltere surfaces. (C) Homologies between dorsal wing and dorsal haltere sensilla fields. (D) Homologies between ventral wing and haltere sensilla fields.

v.Rad.A sensilla showed normal wing morphology though a fifth sensillum appeared in two of the four cases, a situation which is rare in the normal, mesothoracic wing. The v.Rad.B sensilla were present in three of the bx^3 mutants, showing the normal wing pattern and morphology. They were entirely absent in the fourth bx^3 mutant examined. The v.Rad.C field was present in two out of five cases and in the other three cases was largely replaced by fused, pedicellar-type sensilla extending out over the more distal regions of the ventral radius.

bx^3pbx. The homeotic appendage of flies homozygous for sbd^3bx^3pbx^e^11 is smaller than the wild-type wing; the cuticle is often folded and the veins can be obscure. As in bx^3 homozygotes, the ANWP and Tegula fields appear identical to those of the normal wing. The three fields of the proximal radius, d.Rad.A–C, seem perfectly wing like with one subtle exception – the most distal sensilla of d.Rad.C, which normally are socketless, show a slight elevation in the surrounding cuticle (Fig. 6B, arrows). Thus the homeotic transformation in this region is more complete than in bx^3/bx^3 flies.

On the medial radius, fields d.Rad.D and d.Rad.E show different degrees of homeotic transformation, as we have also seen above in the case of bx^3 homozygotes. Field E is composed predominantly of type-3 sensilla such as would
Table 3. *The apparent dependence of specific sensilla fields on the activity of the wild-type alleles, abx* and bx*, for the expression of the haltere phenotype*

<table>
<thead>
<tr>
<th></th>
<th>Case 1</th>
<th>Case 2</th>
<th>Case 3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>abx+</td>
<td>bx+</td>
<td></td>
</tr>
<tr>
<td>+</td>
<td>Absent</td>
<td>Absent</td>
<td>Absent</td>
</tr>
<tr>
<td>−</td>
<td>Present</td>
<td>Absent</td>
<td>Present</td>
</tr>
<tr>
<td>+</td>
<td>Present</td>
<td>Absent</td>
<td>Present</td>
</tr>
<tr>
<td>−</td>
<td>Present</td>
<td>Present</td>
<td>Present</td>
</tr>
</tbody>
</table>

be seen here on the normal wing. Field D, however, contains sensilla resembling, though not identical to, the pedicellar sensilla of the haltere (Fig. 6E).

The distal radius shows normal dHCV and GSR sensilla, but in addition bears a cluster of supernumerary sensilla. These supernumerary sensilla are highly variable in morphology, ranging from circular, low-profile type-3 sensilla to elliptical, high-profile type-5 sensilla fused by their socket cuticle and resembling the pedicellar sensilla of the haltere.

On the ventral radius, field A is consistently wing-like except for a more frequent occurrence of a fifth sensillum in the cluster. The field B sensilla are often absent, while in place of the field C sensilla is found an extensive field of fused pedicellar-type sensilla which extend over the distal radius.

*abx*. There is a great deal of variability among flies homozygous for the abx mutation. The anterior compartment can be largely unaffected, bearing only a few bristles of the wing triple row upon an otherwise normal haltere, or it may have the form of a well-developed anterior wing bearing the normal wing pattern of sensilla fields.

Unlike bx3 mutants, abx flies most often show a pair of metathoracic papillae characteristic of the normal haltere, and only occasionally the three ANWP sensilla found on the wing. The tegula sensilla are always present, even in the most haltere-like specimens. The proximal radius shows great variability. Many individuals show a perfect dorsal scabellar field with no wing sensilla. Some individuals show the normal wing sensilla pattern interrupted by all or part of the dorsal scabellar field (Fig. 6C).

The medial and distal radius also show much variability. In some cases normal wing fields d.Rad.D and d.Rad.E are formed as well as the GSR. However, in most cases these fields are interrupted or entirely replaced by a dorsal haltere field of pedicellar sensilla (Fig. 6F).

On the ventral side of the appendage the v.Rad.A field usually appears wing-like. The v.Rad.B sensilla are usually absent and the v.Rad.C sensilla are entirely replaced by a field of haltere sensilla.
Campaniform sensilla in wild-type and homeotic Drosophila

A summary of the sensilla found on each of the mutants examined is given in Table 2, and Fig. 7 indicates the regions of weak or strong homeotic transformation.

**DISCUSSION**

We have assembled a detailed description of the pattern and diversity of small campaniform sensilla on the wing and haltere of *Drosophila melanogaster*. Using this inventory of wild-type sensilla as a standard, we have assessed the quality of homeotic transformation effected by each of the following homozygous mutant combinations in the BX-C: \( abx^3 pbx, bx^3 pbx, bx^3 \) and \( abx \).

**Theme and variations in sensilla structure**

As we sought criteria for identifying sensilla, it became apparent that sensilla from different fields can be classified on the basis of three major distinctions other than overall size. They differ in the prominence of their sockets; the prominence of their domes; and their overall shape, circular or elliptical. These characteristics could well be the result of simple variations in the synthetic activity of the socket- and dome-forming cells (the tormogen and trichogen respectively).

It has been suggested that campaniform sensilla are evolutionary homologues of bristle sensilla (Snodgrass, 1935). Evidence supporting this suggestion comes from mutants such as *Hairy wing*, in which campaniform sensilla may be replaced by bristles or intermediate structures (Lees, 1942). If this is a true homology, we may conceive of an ancestral developmental programme responsible for the morphogenesis of the entire spectrum of bristles and campaniform sensilla found on the wing and haltere.

**Dorsal–ventral pattern symmetries**

Sensilla fields in similar locations on the dorsal and ventral surfaces of the wing frequently bear a close resemblance to one another. We have termed these similarities pattern symmetries. They are apparent, for example, between sensilla fields B, D and E of the dorsal radius and sensilla fields A, B and C of the ventral radius respectively (Fig. 8A). Even more striking similarities exist in the haltere. The dorsal and ventral pedicellar fields, for example, are virtually identical (Fig. 8B).

Another pattern symmetry becomes apparent in the light of comparative studies. The sensilla of the ventral scabellum have been named the ventral Hicks papillae in the older literature, and a cluster of similar sensilla on the dorsal surface, flanking the main dorsal scabellar field on the anterior side, have been called the dorsal Hicks papillae (e.g. Weinland, 1890). Scanning electron microscopy shows that in *Musca* these sensilla have the morphology of our type-5 sensilla (Smith, 1969). In *Drosophila* we find that the ventral scabellar field is likewise composed of type-5 sensilla, as is the single distinct sensillum flanking
the dorsal scabellar field on the anterior side (Fig. 5B, D). Thus, we propose that this single dorsal sensillum and the ventral field of the haltere represent the remnant of yet another pattern symmetry.

As in the case of sensilla types described above, and segmental homologies below, these pattern symmetries suggest the presence of common developmental mechanisms.

Segmental homologies

It has long been recognized that the haltere is homologous to the wing (e.g. Weinland, 1980; Zacwilichowski, 1934). It is pleasing, therefore, to find this homology apparent even at the level of resolution afforded by the SEM (Fig. 8C and D). For example, the sensilla of the ANWP field of the wing closely resemble the two metathoracic papillae of the haltere (Fig. 8C), both being composed of fused, type-5 sensilla. The d.Rad.A sensilla of the wing and the dorsal scabellar sensilla of the haltere are likewise similar to one another. Both fields possess type-2 sensilla arranged in longitudinal rows, and increasing in diameter distally (Fig. 8C). Their similarity is emphasized in homeotic appendages where intermediate numbers of rows are found (Figs. 6A, and C).

Similarly, the ventral radius bears a field of sensilla which is almost identical to that found on the ventral scabellum (Fig. 8D). The v.Rad.A sensilla are elliptical, low-profile sensilla bearing sockets (type 6). There are four and occasionally five sensilla in this field, arranged in a diamond pattern. The ventral scabellum bears five elliptical high-profile sensilla with sockets which share the same size range and pattern of distribution. In fact, it is only the difference in dome prominence which makes this field distinguishable from that of the wing.

Though there are no sensilla on the normal wing which resemble the fused pedicellar sensilla of the haltere, the homeotic appendage often bears pedicellar-like sensilla in the wing regions which correspond in position to the pedicellus of the haltere, strengthening the sense of positional homology emerging from this work. Similar observations have been made in the mutant Contrabithorax (Cbx), in which the wings are at least partially transformed into halteres (Morata, 1975), in the mutant trithorax (trx) which shows a patchy transformation of many segments towards mesothorax (Ingham & Whittle, 1981), and in ether phenocopies showing haltere to wing transformations (Bownes & Seiler, 1977).

The homeotic mutants

Table 2 and Fig. 7 summarize the apparent wing or haltere identity of sensilla in all the mutant phenotypes we have examined. Some general inferences are suggested by these data: (1) The presence of the mutation pbx influences the expression of bx in the anterior compartment. (2) The segmental identity of particular regions of the anterior compartment appears to be under the control of either the abx or bx gene functions or both.
Campaniform sensilla in wild-type and homeotic Drosophila

Anterior effects of pbx. Though it has been held that pbx mutations do not affect the anterior compartment of the metathorax, and indeed flies homozygous for the pbx mutation show no wing sensilla in the anterior compartment (unpublished observations), we have found evidence suggesting that the pbx mutation exerts a subtle, yet distinct influence upon the homeotic expression of bx3 (Table 2, Fig. 7). Regions which demonstrate imperfect wing expression in the bx3 homeotic appendage, such as fields A and B of the dorsal radius, produce strong wing expression in the bx3pbx double mutant. Regions which display imperfect haltere expression in the bx3 homeotic appendage, such as fields d.Rad.D and v.Rad.B, often produce distinct haltere characteristics in bx3pbx. It would seem, therefore, that the pbx mutation exaggerates tendencies in bx3 expression: imperfectly transformed regions (stippled in Fig. 7) become more wing-like in appearance (unshaded), while haltere-like regions (single-hatched) display even stronger metathoracic expression (cross-hatched). A somewhat similar situation was observed by Palka et al. (1979) in the axonal projections of sensilla into the CNS of bx3/Ubx13Q and bx3bpz/Ubx130 mutants. The mechanism by which this (quite possibly indirect) effect of pbx is produced has not been examined.

Interactions of abx+ and bx+. The genes abx+ and bx+ both influence the development of the anterior compartment of the metathorax (Lewis, 1981). Some of the complexity of their cooperative control is seen in our material.

Consider first the tegula of the wing (Table 3, Case 1). This structure bears a large, complex field of sensilla in the normal wing, but a homologous field has not been recognized in the haltere. Among individuals mutant for either abx or bx3 alone, the tegula and its sensilla appear fully formed on the metathoracic appendage. This implies that both wild-type genes, abx+ and bx+, must be active in order to suppress tegula expression, and that the loss of activity of either one permits mesothoracic expression in this particular region.

By contrast, consider the d.Rad.D field and the distal radius (Table 3, Case 2). These are cases in which the activity of either abx+ or bx+ is sufficient to generate haltere expression even in the absence of the other. In bx3 flies the sensilla of d.Rad.D appear to be a mixture of haltere pedicellar sensilla and sensilla of indeterminate morphology, and none possess the morphology expected of wing sensilla in this location. The addition of the pbx mutation enhances the haltere characteristics of this field, as described earlier. Yet when abx is added to this set of mutations, and animals homozygous for abxbx3pbx are examined, the indeterminate and haltere sensilla are eliminated and replaced by perfect wing sensilla. In other words, only when both the abx+ and bx+ loci are mutant does this region revert to a wing morphology.

A similar situation prevails in the distal radius. In bx3 animals we find the GSR of the dorsal wing accompanied by clusters of haltere and indeterminate sensilla. Supernumerary haltere sensilla also appear on the distal, ventral radius. In bx3pbx individuals these supernumerary sensilla appear even more halter-
like, as they do in most abx individuals. However, when the abx mutation is combined with bx^3 and pbx, all haltere sensilla are eliminated. Hence, both bx and abx loci must be mutant in order to consistently prevent haltere expression, and either wild-type gene alone can generate haltere expression in these regions.

Finally, there are regions of tissue which appear to be under the preferential control of one or the other of these two genes, abx^+ and bx^+ (Table 3, Case 3). For example, the ANWP sensilla appear wing like on the homeotic appendage of all mutants carrying the bx^3 mutation in their genotype, but in abx mutants this field most often remains haltere like as the metathoracic papillae. Hence, metathoracic expression in this region of tissue appears to be controlled more by the bx^+ locus than by the abx^+ locus.

Any inferences to be made from examinations of these mutant phenotypes must be tempered by the fact that we have almost certainly not dealt with null alleles, and by the observation of Morata & Kerridge (1980) that different mutant alleles at the bx locus alone can have their strongest effects in different areas of the metathoracic anterior compartment. Nevertheless, our observations suggest a possible subdivision of the anterior compartment into regions of gene influence which do not coincide with the subcompartments (dorsal–ventral, proximal–distal) defined by clonal restrictions (Garcia-Bellido, Ripoll & Morata, 1973, 1976), and at least an indirect influence of the pbx mutation upon the expression of bx^3 in the anterior compartment.

This work was supported by an NSF graduate fellowship (E. S. C.) and NSF Grant no. BNS-7914111 (J. P.). We are grateful to Professor E. B. Lewis for supplying us with stocks, to M. Schubiger for many extended and illuminating discussions, to M. Schubiger and C. Miles for their careful examination of the manuscript and finally to R. Ellison and S. Hart for their invaluable assistance in the preparation of the figures.

REFERENCES


Campaniform sensilla in wild-type and homeotic Drosophila


(Received 11 January 1982, revised 14 April 1982)