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The effect of lethal mutations and deletions within the bithorax complex upon the identity of caudal metameres in the *Drosophila* embryo

J. R. S. WHITTLE, S. Y. K. TIONG AND C. E. SUNKEL*
School of Biological Sciences, University of Sussex, Falmer, Brighton, Sussex BN1 9QG, UK

SUMMARY

Mutations and deletions of the *abdA* and *AbdB* functions in the bithorax complex of *Drosophila melanogaster* have been examined for their effect upon the hypodermal derivatives of the caudal segments of the embryo, employing light- and scanning electron microscopy. No cuticular structures located posterior to the denticle belt of abdominal segment 8 are affected in $abdA^-$ embryos. Embryos of $AbdB^-$ genotype no longer have six of the seven pairs of sense organs present in this region, lack posterior spiracles but instead have sclerotized cuticle and sense organs typical of the head region and a rudimentary extra ventral denticle belt. The anal pads, tuft and sense organ 1 do not require BX-C functions for their specification. We discuss the provenance of these cuticular structures and the domain of function of elements within the bithorax complex in terms of parasegmental metameric units.

INTRODUCTION

Cell lineage restrictions that form compartments occur soon after cellular blastoderm and metameric units become visible by 4·5 h after the start of embryogenesis in *Drosophila*. Differential expression of selector genes between compartments within each metameric unit causes these anterior and posterior polyclones to elaborate particular and different larval or imaginal structures (Garcia-Bellido, 1975). Martinez-Arias & Lawrence (1985) have recently provided arguments and evidence that a functional unit other than the segment, namely the parasegment (each one comprising a posterior compartment and its immediately caudal anterior compartment) is an important component or 'unit of construction' during metameric segmentation. In the light of these arguments, we have extended the observations on the segmental limits of homoeotic transformation produced by mutations within the bithorax complex.

The bithorax complex (BX-C) (Lewis, 1978; Lawrence & Morata, 1983) is one of two major selector gene complexes essential for the determination of segment

* Present address: Eukaryotic Molecular Genetics Research Group, Department of Biochemistry, Imperial College, London SW7 2AZ, UK.

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and compartment identity over a large domain of the embryo, extending caudally from the anterior–posterior border in thoracic segment 2. In embryos lacking the entire BX-C, the head and first thoracic segment develop normally whereas more posterior segments are transformed so that their anterior compartment is T2 type and the posterior compartment T1 (together equivalent to the normal derivatives of parasegment 4; Lewis, 1978; Struhl, 1984 and T. Sato & R. Denell, personal communication). These effects extend caudally at least as far as segment A8, but the precise posterior limit of the BX-C domain has remained vague. This paper reports the results of examination of embryos and larvae carrying new mutations and deletions within the BX-C which help to resolve the relationship between caudal metameric units and BX-C function.

MATERIALS AND METHODS

Stocks

The wild-type stock used was Oregon-R. The BX-C deletions *Df(3R)P115 Df(3R)P9* and *Df(3R)Ubx*^{109} are described in Lewis (1978). All the *abdA* and *AbdB* alleles were induced in our laboratory (Tiong, Bone & Whittle, 1985). *Df(3R)SX1* is a gamma-irradiation-induced deletion in a *multiple wing hairs*, *red*, *ebony* chromosome of *abdA*, *AbdB* and four lethal complementation groups to the right of *AbdB*.

Embryo preparations for scanning electron microscopy

Egg collections were made over 2 h at 25 °C and timed to obtain wild-type embryos at particular stages. Embryos from lethal genotypes were incubated for 30 h before being dechorionated and devitellinized by hand, and placed in boiling water for 10 s prior to fixation. Subsequent steps followed were as in Hayes, Sato & Denell (1984). Observation and photography were carried out on a Joel 100C electron microscope with an ASID-4D scanning attachment at 20 kV, using FP4-120 film.

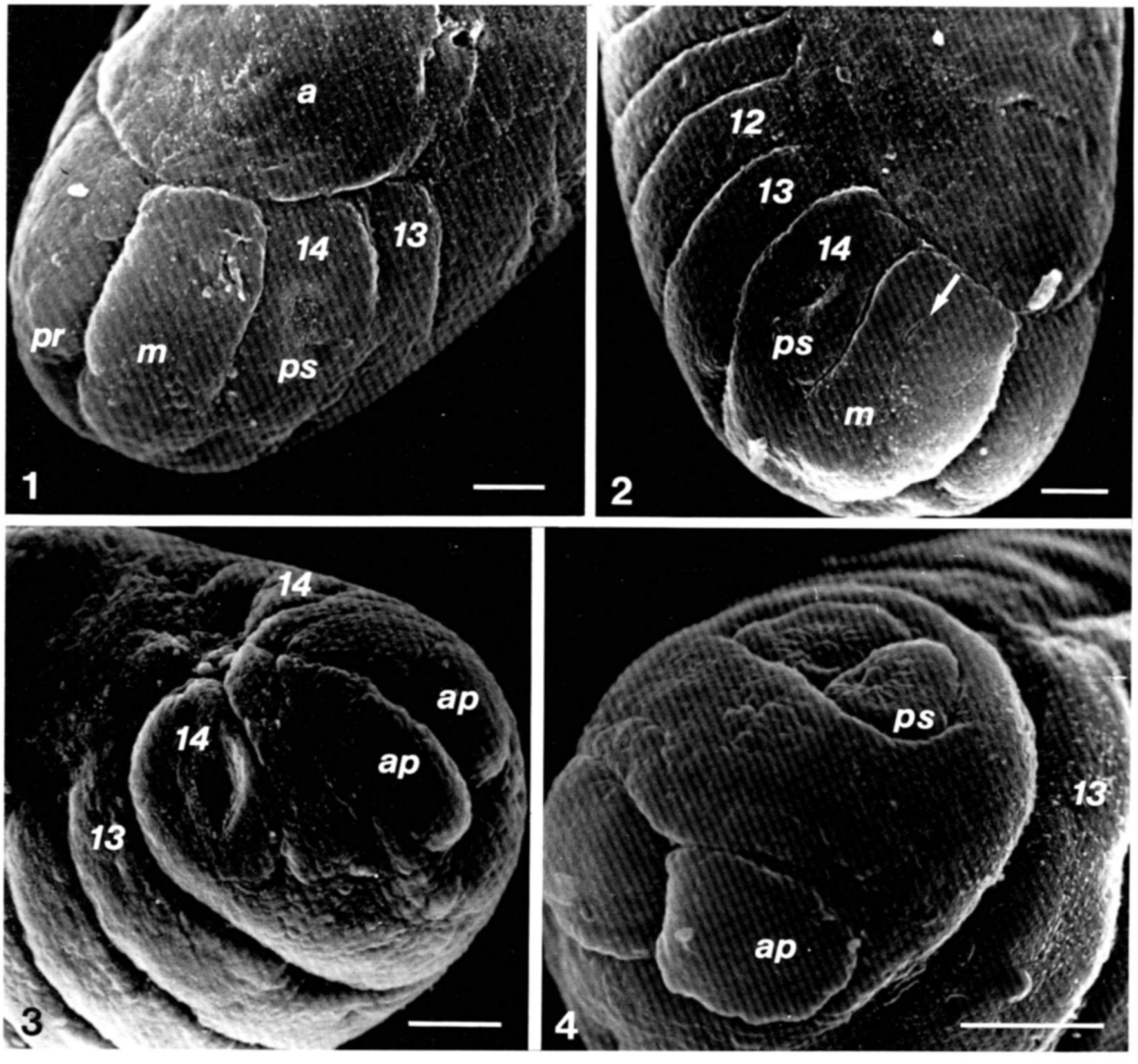
Embryo preparations for light microscopy

Egg collections were incubated for 30 h at 25 °C before being dechorionated and devitellinized and mounted following the method of Van de Meer (1977). Phase-contrast photomicrographs were taken on Kodak Technical Pan film.

RESULTS

The appearance and location of caudal surface structures in wild-type embryos

In the abdomen, more anterior metameric units are morphologically distinct by the germ-band-extension stage but the infoldings distinguishing terminal structures only become resolvable during later stages of germ-band shortening at about 9–10 h after egg deposition. The infoldings at this early stage can be interpreted as parasegmental borders (Martinez-Arias & Lawrence, 1985). The posterior spiracles appear within the penultimate metameric unit, which is parasegment 14 (Fig. 1). A short time later it is possible to discern a transient dorsal infolding within the cell group posterior to parasegment 14 (Fig. 2). The anal pads become well defined by this time within the most caudal cell group (Fig. 2), and the



Figs 1–4. Scanning electron micrographs of the posterior aspect of wild-type embryos. Bar, 20 μm.

Fig. 1. Dorsolateral view at germ-band shortening. Posterior to parasegment 14 (*14*) within which cells are forming the posterior spiracles (*ps*), there is only one further metameric unit, (*m*). *pr*, proctodeum; *a*, the amnioserosa.

Fig. 2. At a later stage in germ-band shortening, an infolding (arrow) divides into two parts the cell group (*m*) posterior to parasegment 14 which contains the posterior spiracle (*ps*).

Fig. 3. Dorsal view at dorsal closure showing left and right derivatives of parasegment 14 (*14*) moving together. The cells forming the anal plates (*ap*) are part of the terminal metamere.

Fig. 4. Lateral aspect during late dorsal closure. The infolding between cells within the posterior metameric unit has disappeared and no morphological discontinuity separates parasegment 14 from the more terminal structures.

proctodeal opening forms the ventral border between parasegment 14 and the terminal metameric unit (Fig. 3). The dorsal sides of parasegment 14 move closer to each other at the dorsal midline during dorsal closure (Fig. 3). The dorsal infoldings posterior to parasegment 14 and the dorsal midline furrow then disappear (Fig. 4).

By the end of embryogenesis the larval hypodermal cells have synthesized cuticular structures. There are eight ventral abdominal denticle belts of which the eighth is rectilinear and only separated from the anal plates by a narrow bald area posterior to this belt. We have identified seven pairs of sense organs which we have numbered 1 to 7 following the classification of Denell & Frederick (1983) (Fig. 5). These sense organs are of three morphological types, either peg shaped (Fig. 6), hair shaped (Fig. 7) or form a joint hair and peg unit (Fig. 11). They are distributed spatially in the following way. Sense organs 5 and 6 are found dorsolaterally within the spinule-covered area at the same point on the long axis of the embryo as the 8th abdominal denticle belt. The peg sense organ 5 is anterior (Fig. 6), and hair sense organ 6 is located more dorsally (Fig. 7). Peg sense organ 7, very similar to 5, lies within the prominent darker spinules at the dorsal base of the posterior spiracles.

Morphogenetic movements take the terminal metameric unit so that its posterior edge abuts the ventral 8th abdominal denticle belt, a ventral derivative of parasegment 14 (Turner & Mahowald, 1979). Considering this terminal unit as if in its initial orientation at the tip of the embryo, immediately posterior to the posterior spiracles and dorsal spinule belt, we find sense organs 4 (peg), 3 (peg, Figs 5, 9) and 2 (hair, Figs 5, 10). More posterior to these are the pair of sense organs (numbered 1, a joint hair and peg, Fig. 11), each on a protuberance flanking a central group of denticles (Lohs-Schardin, Cremer & Nüsslein-Volhard, 1973) and the tuft (Figs 17, 18, 20), which is shown at a slightly earlier stage in Fig. 8. The most posterior structures which we have noted are the anal pads (Figs 5, 8, 15).

In their dorsal aspect, all thoracic and abdominal segments carry spinules. In the prothorax, spinules cover only the anterior 30% of the segment, but the area covered increases in more posterior segments so that in abdominal segment 6 and those more caudal, spinules completely cover the dorsal surface (Table 1). Dorsally, thoracic segments each have a pair of pits, which are not found in abdominal segments.

Caudal larval structures in embryos lacking the BX-C

In embryos homozygous for the deletion *Df(3R)P9* or the deletion *Df(3R)P115* both of which lack the entire BX-C, each of the anterior-most seven denticle belts in the abdominal region resemble that of a normal second thoracic segment (Lewis, 1978). These segments each have a Keilin's organ and ventral pits, both of which are thoracic structures. The 8th abdominal denticle belt is intermediate between that of a wild-type prothoracic and metathoracic segment. Neither

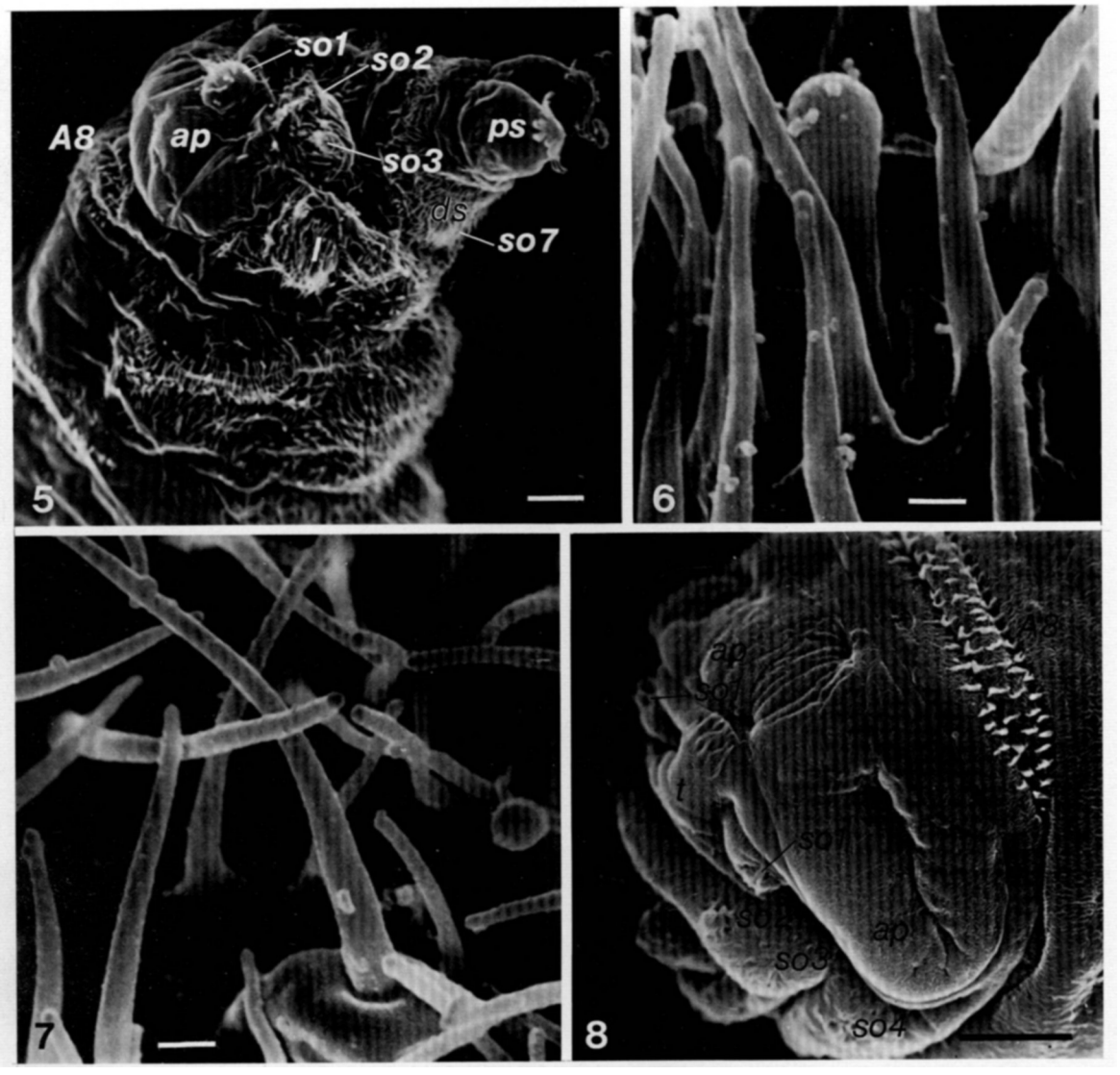


Fig. 5. Lateral view of posterior of a wild-type first instar larva indicating the relative location of sense organs and other morphological markers. *A8*, ventral denticle belt of *A8*; *ap*, anal plate; *so* (numbered), sense organs; *ps*, posterior spiracles; *ds*, spinules at dorsal base of posterior spiracles; *l*, lateral spinule patch containing sense organs 5 and 6. Bar, 20 μm.

Fig. 6. Peg sense organ 5. Bar, 1 μm.

Fig. 7. Hair sense organ 6. Bar, 1 μm.

Fig. 8. Wild-type embryo in ventral aspect showing the relative locations of sense organs 1, 2, 3 and 4 (*so1–4*) as they form. *ap*, anal plate; *t*, tuft of ventral denticles; *A8*, denticle belt of abdominal segment 8. Bar, 20 μm.

posterior spiracles nor sense organs 5, 6 and 7, normally in the vicinity, are in evidence.

There is a prominent metameric unit posterior to segment 8 in BX-C$^-$ embryos, which has resulted in a separation of the 8th abdominal denticle belt from the anal

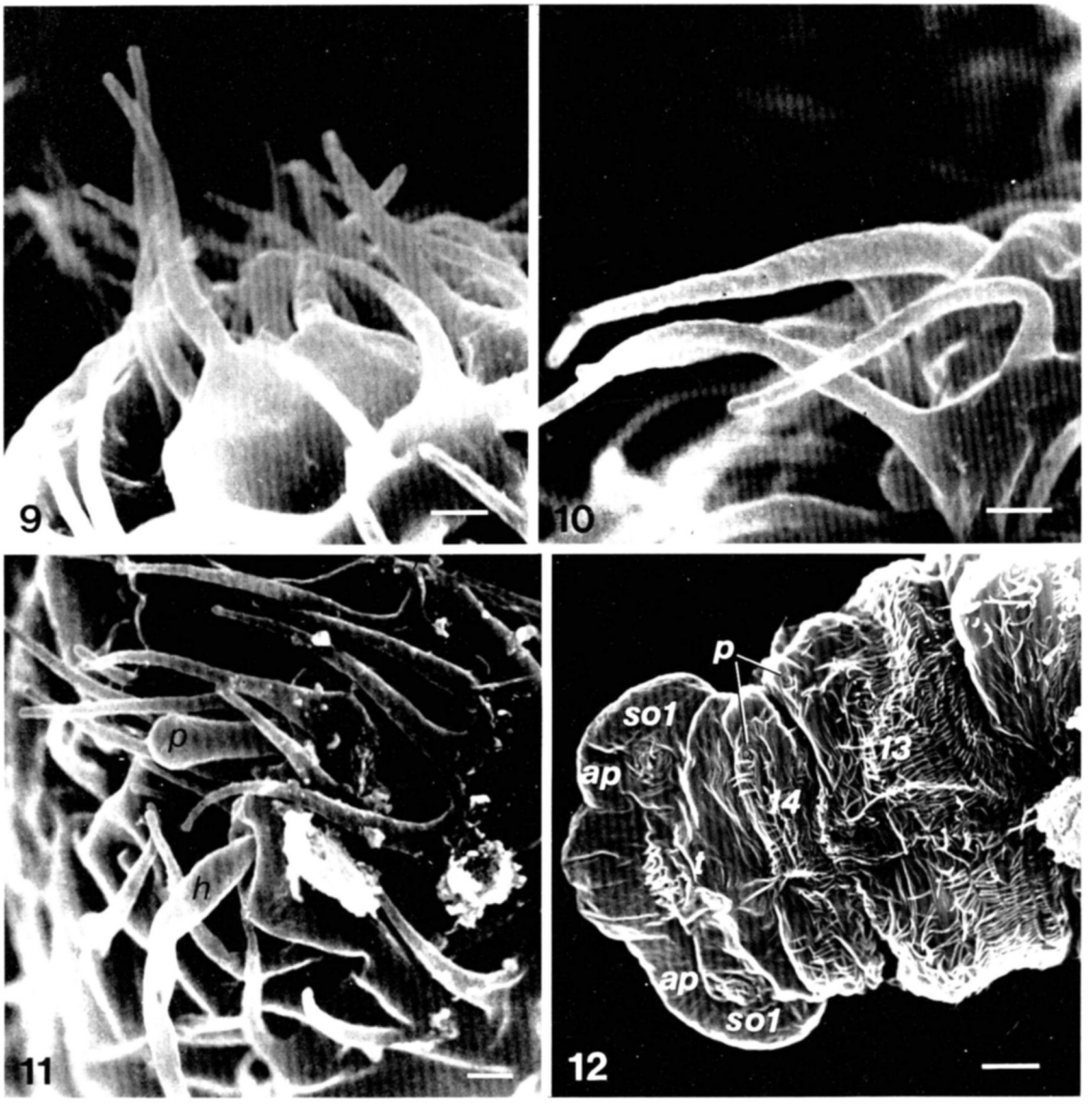


Fig. 9. Peg sense organ 3, surrounded by a group of spinules. Bar, 1 μm.

Fig. 10. Hair sense organ 2. Bar, 1 μm.

Fig. 11. Sense organ 1, containing both a peg (*p*) and a hair (*h*) element. Bar, 1 μm.

Fig. 12. Dorsal posterior aspect of a homozygous *Df(3R) P9* embryo. Parasegments 13 and 14 carry spinules characteristic of thoracic segments 1 or 2 and thoracic structures, pits (*p*). The tuft (*t*), sense organ 1 (*so1*) and the anal plate (*ap*) remain. Bar, 20 μm.

pads ventrally. Dorsally the spinules only cover the anterior part of this segmental unit, more like the situation in a normal prothoracic segment (Table 1). Laterally, this segment which we call A9, now carries dorsal pits (Fig. 12), characteristic of thoracic segments. Embryos of this genotype do not have sense organs 2, 3 or 4. Only the anal plates, sense organ 1 and the midline tuft of denticles are unchanged.

Caudal larval structures affected by abdA *mutations and deletions*

In the genotype $abdA^{S1}$/BX-C^{-}, the denticle belts in A2 to A8 are transformed in overall dimensions and row number to an appearance intermediate between those normally found in A1 and A8, and the denticles are all oriented posteriorly (Fig. 13) resembling the orientation in a wild-type A1 segment. Monohairs of Keilin's organ appear frequently though not invariably in the bald area of the ventral cuticle in segments A1 to A7 (Sanchez-Herrero, Vernos, Marco & Morata, 1985; Tiong *et al.* 1985; Fig. 13) but we never find them posterior to the A8 denticle belt.

The genotype $Df(3R)SX1/Df(3R)Ubx^{109}$ represents a null mutation of *abdA*. No structures posterior to the altered denticle belt in A8 are changed; the posterior spiracles, Filzkörper and the full complement of sense organs 1 to 7 are present (Fig. 14), and the distribution of dorsal spinules surrounding sense organ 7 is unchanged. The ventral denticle belt of A8 remains closely apposed to the anal plates (Fig. 14).

Caudal larval structures affected by AbdB *mutations*

The twelve *AbdB* alleles recovered in our laboratory fall into several classes with respect to their effects on structures within abdominal segment 8 and more posterior structures although all share the common feature that the denticle belts from abdominal segment 5 to 7 are more trapezoid than in wild-type embryos and hence resemble the belt in A4.

$AbdB^{S1}$/BX-C^{-} embryos also have a trapezoidal denticle belt ventrally in A8 resembling that of a wild-type A3 or A4 segment (Sanchez-Herrero *et al.* 1985;

Table 1. *Area of dorsal cuticle free of spinules in thoracic and abdominal segments*

Genotype		T1	T2	T3	A1	A2	A3	A4	A5	A6	A7	A8	A9
Wild-type	%	70*	40	38	36	20	15	19	14	0	0	0	—
	S.D.	2	6	4·3	5·5	4·6	3·2	3·3	2·4	0	0	0	—
BX-C^{-}	%	73	56	53	52	49	53	50	51	53	53	53	51
	S.D.	6·2	4·6	2	2·5	3·8	7·3	2·9	4·8	2·4	6·3	8·5	7

Each figure is based on measurements from ten embryos.

* The area free of spinules is expressed as a percentage of the total area of the segment in dorsal aspect, measured using a *camera lucida*.

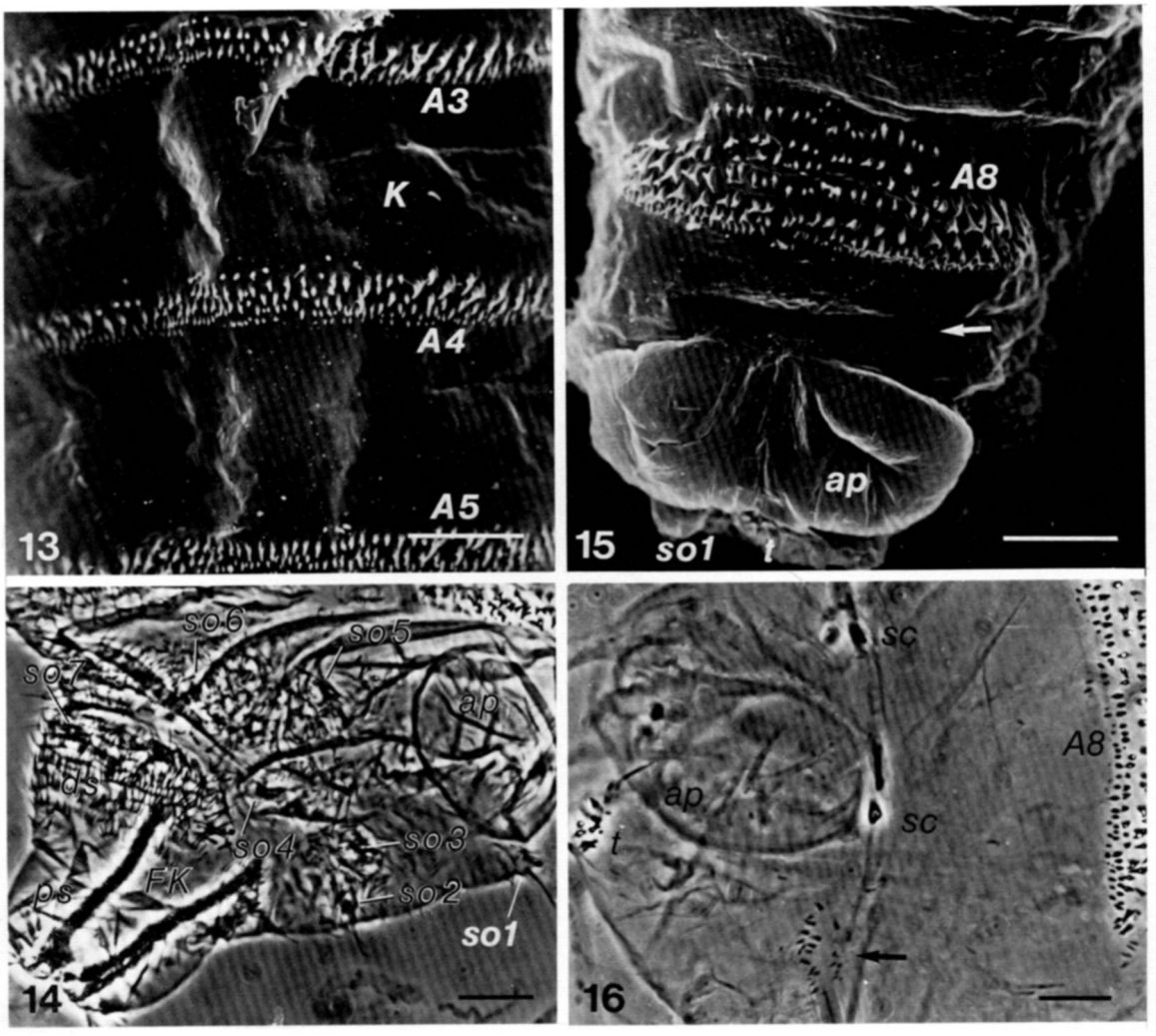


Fig. 13. Ventral denticle belts of $abdA^{S1}$/BX-C^{-} in abdominal segments 3, 4 and 5 (*A3–5*). Segment 3 has a monohair of Keilin's organ (*K*). Bar, 40 μm.

Fig. 14. Light micrograph of an embryo of genotype $Df(3R)SX1/Df(3R)Ubx^{109}$. Sense organs 1 to 7, the posterior spiracles (*ps*), Filzkörper (*FK*), anal plates (*ap*) and dorsal spinules (*ds*) are all unchanged. Bar, 14 μm.

Fig. 15. Ventral caudal aspect of an $AbdB^{S1}$/BX-C^{-} embryo. Denticle belt A8 is trapezoidal in outline and is separated from the anal plates by a bald area (arrow). Bar, 30 μm.

Fig. 16. A homozygote for $AbdB^{S3}$ showing an extra rudimentary band of denticles (arrow) formed ventrally posterior to those of A8. *ap*, anal plate; *sc*, sclerotized cuticle; *t*, tuft. Bar, 18 μm.

Tiong *et al.* 1985), an enlarged bald region posterior to the denticle belt (Fig. 15) and lack sense organs 5, 6 and 7 but still carry sense organs 1, 2, 3 and 4. The posterior spiracles are absent or very poorly formed and the dorsal spinules normally at their base have gone.

AbdB^{S3} homozygotes do not show such a strong anteriorly directed transformation of the denticle belt in A8, sometimes lack sense organs 5, 6 and 7, but show two small extra groups of fine denticles just anterior to the anal plates (Fig. 16) and an extra band of spinules dorsally posterior to those of A8 but distinct from those normally found at the base of the posterior spiracles, which themselves are absent.

AbdB^{S4}/BX-C^{-} embryos lack sense organs 2 to 7 and the posterior spiracles, have an obvious trapezoidal denticle belt in A8, an enlarged bald area separating this belt from the anal plates, and a vestige of an extra ventral denticle belt as in *AbdB*^{S3} homozygotes. Dorsally there is an extra area of spinules posterior to those in A8 with spinules at its anterior edge characteristic of the anterior edge of other abdominal segment spinule patches (Fig. 17), and there is now a lateral hair at the edge of this patch (Fig. 17). In addition this genotype carries two new pairs of sense organs close to the position where sense organs 2 and 3 normally appear and has an area of sclerotized cuticle, neither feature normally being found in the caudal region of wild-type embryos (Fig. 18). The sclerotized cuticle is internal and lies posterior to A8 and has the same refractile appearance as the cephalopharyngeal skeleton. The pairs of ectopic sense organs (Fig. 19) lie laterally at the position where sense organs 2 and 3 normally appear and resemble components of the maxillary sense organ. Sense organs 2 to 7 are never present.

The larval phenotype of the simultaneous deletion of abdA *and* AbdB

The genotype *Df(3R)SX1/Df(3R)P9* lacks *abdA* and *AbdB*, and in larvae of this genotype the A8 denticle belt resembles that in *abdA*$^{-}$ larvae (Fig. 20) but posterior to it is a broad naked band of cuticle typical of the *AbdB*^{S4} mutant. Sense organs 2 to 7 are absent in all individuals, but the tuft of denticles, the anal pads and sense organ 1 are unaffected. We also find sclerotized cuticle and the two pairs of ectopic sense organs in the region but the small extra vestiges of ventral denticle belts found in enbryos carrying *AbdB* alleles are not present in this double mutant combination.

DISCUSSION

The intention in this study has been to relate morphological features of the posterior tip of the *Drosophila* embryo to the metameric units present, and in turn to describe and relate the morphological changes seen in *abdA*$^{-}$ and *AbdB*$^{-}$ embryos to the wild-type and BX-C^{-} phenotypes. Following Martinez-Arias & Lawrence (1985), we have taken the infoldings or grooves seen at early germband-extension stage to define the borders of parasegmental metameric units, and find posterior to parasegment 14 a clear terminal unit which shows a transient morphological separation into two groups of cells during germ band shortening (Fig. 2). The posterior spiracle clearly arises within parasegment 14 (Figs 2, 3) and may derive from cells in both compartments of this parasegment (see also

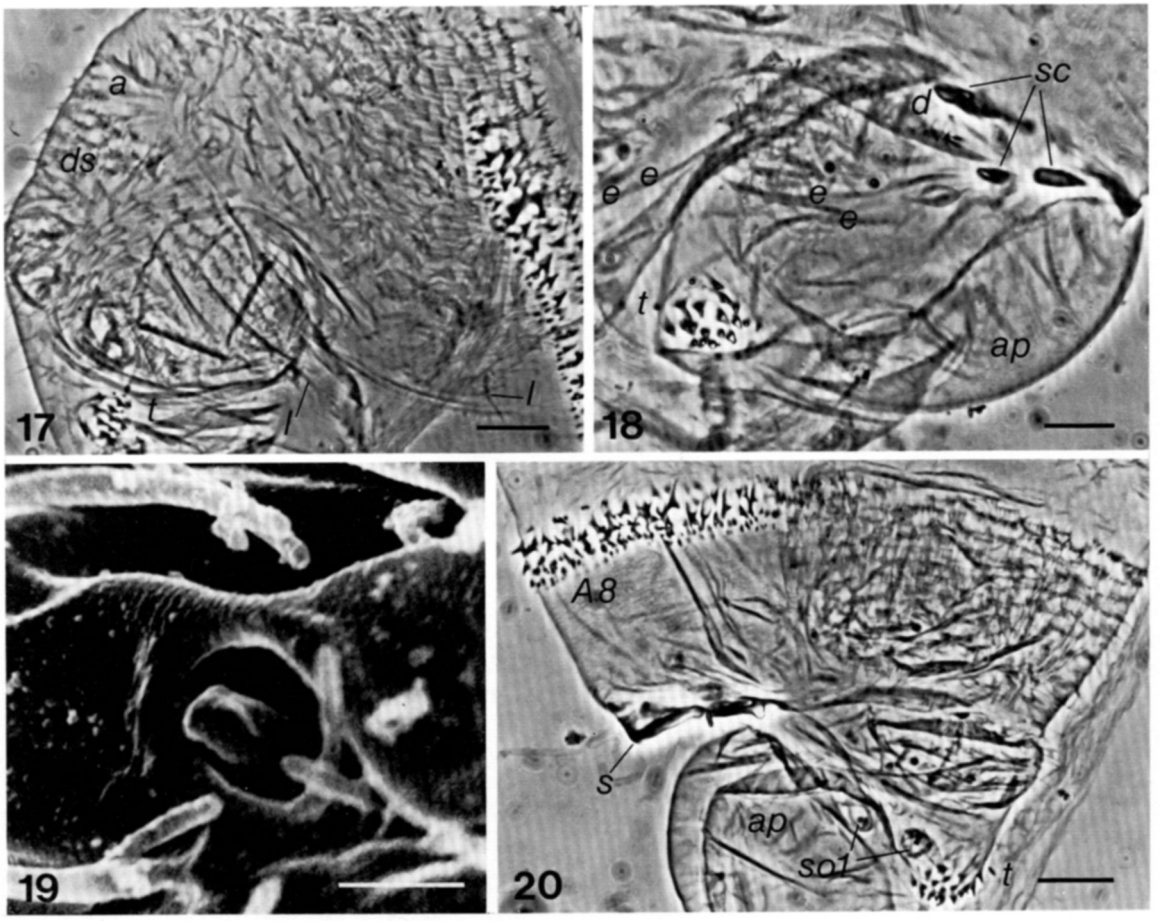


Fig. 17. An $AbdB^{S4}$/BX-C^{-} embryo showing an extra dorsal spinule patch (*ds*) with characteristic anterior-edge spinules (*a*) posterior to the normal spinule patch. Each of these two dorsal spinule patches carries a lateral hair (*l*). Bar, 18 μm.

Fig. 18. An $AbdB^{S4}$/BX-C^{-} embryo showing the location of the extra denticle belt (*d*) (out of focus), internal sclerotized cuticle (*sc*) and two pairs of ectopic sense organs (*e*). Bar, 18 μm.

Fig. 19. Scanning electron micrograph of an ectopic sense organ in $AbdB^{S4}$/BX-C^{-}. Bar, 1 μm.

Fig. 20. Posterior tip of an embryo of genotype *Df(3R)SX1/Df(3R)P9*. The denticle belt of A8 is narrow, all denticles are oriented posteriorly and there is a bald area posterior to it. Refractile sclerotized cuticle (*s*) lies beneath the anterior edge of the anal plate (*ap*). Sense organ 1 and the tuft of denticles (*t*) are present. Bar, 18 μm.

Martinez-Arias & Lawrence, 1985). We are confident from SEM observations that the tuft of denticles and the anal pads derive from the cell group posterior to parasegment 14, but are not able definitively to assign the seven sense organs to individual segmental units (cf. Turner & Mahowald, 1979; Denell & Frederick, 1983) on the basis of embryological evidence available to us, and consider that this will require a high-resolution ablation or fate-mapping study. Relative proximity

of cuticular structures on the embryo surface is insufficient alone as a basis for reconstruction of cell lineage. Nevertheless we do make the separate suggestion later that, based on the detailed phenotype of the BX-C mutants, it is reasonable to divide the surface cuticular markers into several groups which identify *functionally* separate cell groups during early embryogenesis.

The posterior limit to the domain of function of *abdA* appears to be parasegment 13, whereas that for *AbdB* includes parasegment 14. In embryos carrying mutations ($abdA^{S1}$/BX-C$^-$) or deletions of *abdA* ($Df(3R)SX1/Df(3R)Ubx^{109}$) only the ventral denticle belt in A8 and the distribution of dorsal spinules in A8 change. All seven pairs of sense organs and the posterior spiracles remain unchanged, showing that cells that form these structures do not require the *abdA* function. The trihair structure of the Keilin's organ is a thoracic structure (Keilin, 1915) to which two hairs are contributed by the anterior compartment and one from the posterior compartment (Struhl, 1984). Although monohairs appear in abdominal segments A1 to A7 in *abdA* hemizygotes, we have never seen them posterior to the denticle belt in A8 and propose that the region of A8 untransformed in $abdA^-$ embryos is the posterior compartment, although we have no direct cell lineage evidence. This corroborates the finding of T. Sato & R. Denell (personal communication). Because the transformation in $abdA^-$ embryos is effectively a reiterated parasegment 6 in place of the structures normally seen in parasegments 7 to 13, and yet leaves unchanged all seven pairs of posterior sense organs, these sense organs must be produced by cells posterior to the anterior compartment of A8. Our findings support the conclusion drawn from several approaches, including the definition of the spatial limits of transcription, that the domains of the *Ubx* and *abdA* units of the BX-C are parasegmental (Hayes *et al.*1984; Struhl, 1984; and references in Martinez-Arias & Lawrence, 1985).

All the *AbdB* alleles we have examined form one lethal complementation group and the majority cause anteriorly directed transformation of the denticle belts of A6, 7 and 8 and some also affect A5, but when judged by the most caudal structures they affect, they cannot be ranked as a simple allelic series with increasing monotonic effects within this array of segments. The lack of structures of clear posterior provenance in A4 and A5 make the definition of the anterior limit of transformation difficult. $AbdB^{S1}$ transforms the denticle belt in A8 towards the trapezoid pattern of a more anterior abdominal segment, deletes sense organs 5, 6 and 7 but leaves sense organs 1 to 4 untouched. $AbdB^{S3}$ produces a rudimentary extra denticle belt posterior to A8, deletes sense organs 5, 6 and 7 but has a less obvious effect upon the A8 belt and produces an extra dorsal spinule band. $AbdB^{S4}$ mutant embryos have an A8 denticle belt like that in $abdA^{S1}$, and an extra belt like $AbdB^{S3}$ but in addition lack sense organs 2 to 7 inclusive. This genotype has an extra dorsal group of spinules of pattern and composition similar to those in A8. All three *AbdB* alleles examined eliminate or severely reduce the posterior spiracles (within parasegment 14) but differ in the intensity of their effects upon the A8 denticle belt (parasegment 13). The *AbdB* unit is not required for the formation of anal plates, sense organ 1 or the tuft. Indeed the phenotype of

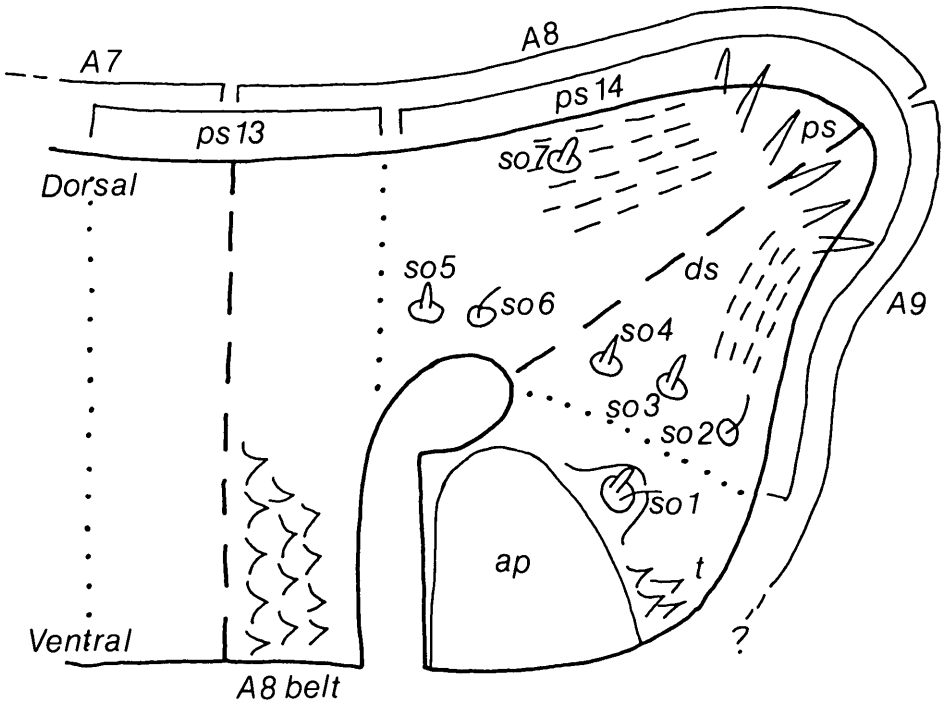


Fig. 21. Schematic representation of the relative location of caudal structures on the surface of a first instar larva. Dashed lines are segment borders, dotted lines are compartment borders. Abbreviations as in previous figures. The compartmental locations of sense organs 1 to 7 are tentative (see Discussion for details).

BX-C$^-$ embryos confirms that this gene complex is not required at all for these structures. The phenotypic variability between *AbdB* alleles divides the seven pairs of sense organs into three groups, (1) (2, 3 and 4) and (5, 6 and 7). The first group is not affected at all, the last group is invariably deleted (confirmed by Sato & Denell, personal communication) and the middle group is only removed by *AbdB*^{S4}, the allele that produces the largest inventory of changes. We have recovered several *AbdB* alleles identical to each of the three alleles described and therefore regard these phenotypic classes as significant. This raises the possibility that particular *AbdB* alleles have lesions in different one or more *iab* functions (Lewis, 1978) each having a role restricted to particular parasegments (Tiong & Whittle, in preparation). Sense organs 5, 6 and 7 and the posterior spiracles (the latter deriving from cells both sides of the segment border between A8 and A9) can be removed independently of sense organs 2, 3 and 4 (*AbdB*^{S1}). If the area affected by each *AbdB* allele is a spatially coherent area on the longitudinal axis of the embryo, then it follows that sense organs 2, 3 and 4 would derive from cells in A9 and not A8.

Fig. 21 is a diagrammatic representation of the distribution of the surface cuticular structures we have examined in relation to caudal metameric and

compartmental units. The most caudal ventral denticle belt has been well established to be anterior A8 in provenance by many authors, the posterior spiracle comes from within parasegment 14 at the A/P border, and the anal pads derive from the metameric unit caudal to parasegment 14. From our observations and the arguments given earlier, we would predict that sense organs 5, 6 and 7 will derive from the posterior compartment of A8 (within parasegment 14) that sense organs 2, 3 and 4 will be found to derive from the anterior compartment of A9 (within parasegment 14), and that sense organ 1 and the tuft of denticles will derive from cells posterior to parasegment 14. Presently we have no independent way to investigate whether there are functional subdivisions within the terminal metameric unit. Therefore it is not yet possible to say whether the *AbdB* unit has a domain defined at its anterior or posterior extent by parasegmental or segmental borders.

The phenotype of the simultaneous removal of *abdA* and *AbdB* reveals an interaction between these two elements. A rudimentary extra denticle belt appears in $AbdB^{S4}$ mutants (Fig. 16) but is absent from the $abdA^{-}AbdB^{-}$ phenotype, and may therefore represent an ectopic effect of $abdA^{+}$ seen only in the absence of $AbdB^{+}$.

The domain of function of *AbdB* described here raises an interesting question about the regulation of the BX-C, and the compartment in which it is maximally expressed. Both *Polycomb* (*Pc*) and *extra sex combs* (*esc*) have been described as negative regulators of the BX-C (Lewis, 1978; Struhl, 1981). The phenotypes of putative null mutations in these two genes are therefore thought to represent complete derepression of the BX-C. This phenotype is, in both mutants, a reiterated series of metameres each resembling a wild-type A8, particularly with respect to the type of ventral denticle belt formed. The ninth abdominal metameric unit in esc^{-} embryos clearly has a rectilinear denticle belt (Struhl, 1981). Moreover, Pc^{3}/Pc^{3} embryos also have poorly formed posterior spiracles in each of the reiterated segments (Duncan & Lewis, 1982). We have assigned the A8 denticle belt to parasegment 13 and the posterior spiracle to parasegment 14, so the derepression phenotypes of Pc^{-} and esc^{-} appear to be a reiterated A8 segmental unit and not a parasegmental unit. This is surprisingly at variance with the observations by a number of authors, including ourselves, that the limits of function of the *Ubx* and *abdA* units of the BX-C are parasegmental borders. However, the BX-C derepression phenotype may be regarded as closest to a reiterated parasegment 13 in which the anterior compartment has *Ubx*, *abdA* and *AbdB* at 'maximal' expression as in the most caudal compartment that requires all three units (A8a), and the posterior compartment is that of parasegment 13 modified by the *AbdB* function 'elevated' to the level customary in a wild-type posterior compartment of A8. Alternatively, the explanation may lie in the atypical behaviour of other selector genes controlled by *Pc* and *esc* (Struhl, 1983; Sato, Hayes & Denell, 1985), or interactions between BX-C and other selector genes (Harding, Wedeen, McGinnis & Levine, 1985).

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