

## Cell lineage of the *Drosophila* abdomen: the epidermis, oenocytes and ventral muscles

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### SUMMARY

We use a new cell marker to study cell lineage of the epidermis, oenocytes and ventral muscles in the *Drosophila* abdomen. We find that while the epidermal cells and the oenocytes share common precursors until late in development, the muscles derive from a separate lineage. Marked clones in the muscles, but not in the epidermis and oenocytes, can occasionally extend between neighbouring segments, supporting a previous hypothesis that mesoderm cells may not be determined as to segment.

### INTRODUCTION

Every segment of the adult *Drosophila* abdomen consists of an epidermal polyclone (Szabad, Schüpbach & Wieschaus, 1979; Lawrence, 1981*a*). Associated with each segment there is a band of oenocytes, two strips of fat body and a specific pattern of superficial muscles (Robertson, 1936; Koch, 1945; Miller, 1950). The adult epidermis develops from cells which, although integrated into the larval epidermis (Pearson, 1972), remain small. In each hemisegment these cells or 'histoblasts' are gathered into three nests and their development has been well described by both direct observation (Madhavan & Schneiderman, 1977; Madhavan & Madhavan, 1980) and by clonal analysis (Garcia-Bellido & Merriam, 1971; Guerra, Postlethwait & Schneiderman, 1973; Lawrence, Green & Johnston, 1978).

The lineage relationship between the histoblasts and the non-epidermal tissues is unclear. Robertson (1936) and Koch (1945) suggested that the epidermis, oenocytes and fat body arise from these histoblasts, but could not establish a lineage relationship between them. Ferrus & Kankel (1981), using mitotic recombination and a cell marker, presented some evidence that clones extend between all three cell types. The lineage relationship between the precursors of abdominal muscles and histoblasts is unknown (Perez, 1910; Crossley, 1965, 1978). In this paper we use a new cell marker to study the cell lineage of the epidermis, oenocytes and muscles; we find that while the ventral epidermis

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and oenocytes of each segment do derive from a common cell pool, the muscles have a separate origin. We were unable to study the cell lineage of the fat body.

#### MATERIALS AND METHODS

To mark clones of cells we used the cuticular cell markers *straw*, (see Lindsley & Grell, 1968 for all genetic nomenclature, except when other references are given), *pawn* (Garcia-Bellido & Dapena, 1974) and *yellow*. The oenocytes and muscles were marked with the cell-autonomous marker *sdh*<sup>8</sup>, an allele which gives clones of cells with altered activity for succinate dehydrogenase (Lawrence, 1981*b*). Staining solutions were made up as described in Lawrence (1981*b*). For muscles, whole abdomens were heated in Ringer solution at 52° for 10 min, washed in buffer in ice for 30 min, and dissected free of gut and fat body. These pieces were then stained for 5–6 h, washed in water, dehydrated in absolute alcohol, cleared in methyl salicylate and mounted in Euparal or Struhl's mountant (see Struhl, 1981). For the epidermal cells and oenocytes the optimum heating temperature was 47–48 °C: other steps were as for muscles. We failed to find suitable conditions for studying cell lineage of the fat body.

Embryos and larvae of the following genotypes were irradiated and 1-week-old females were studied because they are larger and easier to dissect than males.

genotype 1 *cn sdh*<sup>8</sup> *bw/cn bw M(2)c*<sup>33a</sup>

genotype 2 *stw pwn sdh*<sup>8</sup> *bw/cn bw M(2)c*<sup>33a</sup>

genotype 3 *stw pwn en*<sup>IO</sup> *sdh*<sup>8</sup> *bw/M(2)c*<sup>33a</sup> (*en*<sup>IO</sup> is a lethal allele at the *engrailed* locus (Kornberg, 1981*a*) made and kindly provided by Christiane Nüsslein-Volhard and Eric Wieschaus – see their paper, 1980)

genotype 4 *y/Dfsc*<sup>S2</sup>, *y*; *cn sdh*<sup>8</sup> *bw/M(2)S7 Dpsc*<sup>S2</sup>, *y*<sup>+</sup>

Irradiations were performed at 3.5 ± 0.7 h after egg laying (h AEL), 48 ± 4 h AEL and 60 ± 12 h AEL.

#### Recognizing muscle clones

In the thoracic muscles, *Minute*<sup>+</sup> clones growing in a *Minute*<sup>+</sup> background are not seen, while clones of the same genotype, which grow excessively in a *Minute* background, are (Lawrence, 1982). We believe this is because a fibre which contains even a few *sdh*<sup>+</sup> nuclei is indistinguishable from entirely *sdh*<sup>+</sup> fibres. The probability of a single fibre being entirely *sdh* and therefore recognized, will depend mainly on the growth rate of the *sdh* clone (which will increase the probability), and the degree of intermingling (which will reduce it). In the abdominal muscles of irradiated insects unstained patches were rarely seen and frequently extended to only a few fibres. In order to recognize the clones and distinguish them from artefacts, such as general leaching of stain, two criteria were used: the individual muscle fibres must be entirely unstained

while associated nerve fibres should be stained. Neighbouring muscle fibres, oenocytes and fat body must be stained. When these criteria were applied to the dorsal muscles of the tergites the few unstained patches failed to meet them. Consequently, results on only the ventral abdomen are reported. Evidence that ventral clones scored by these criteria are genuine comes from the results; their frequency depends on X-ray dose (Table 2). Muscle clones were most easily detected under polarized light when the birefringence of unstained fibres was conspicuous.

#### *Recognizing clones in the oenocytes*

Oenocytes often stain capriciously: clones were only registered when the unstained cells were adjacent to and formed a sharp contrast with, stained cells. Again, neighbouring muscles and fat body must be stained. To ascertain whether cuticle clones extended to oenocytes, patches of mutant bristles were sometimes detected under the dissecting microscope and those abdomens stained and mounted.

### RESULTS

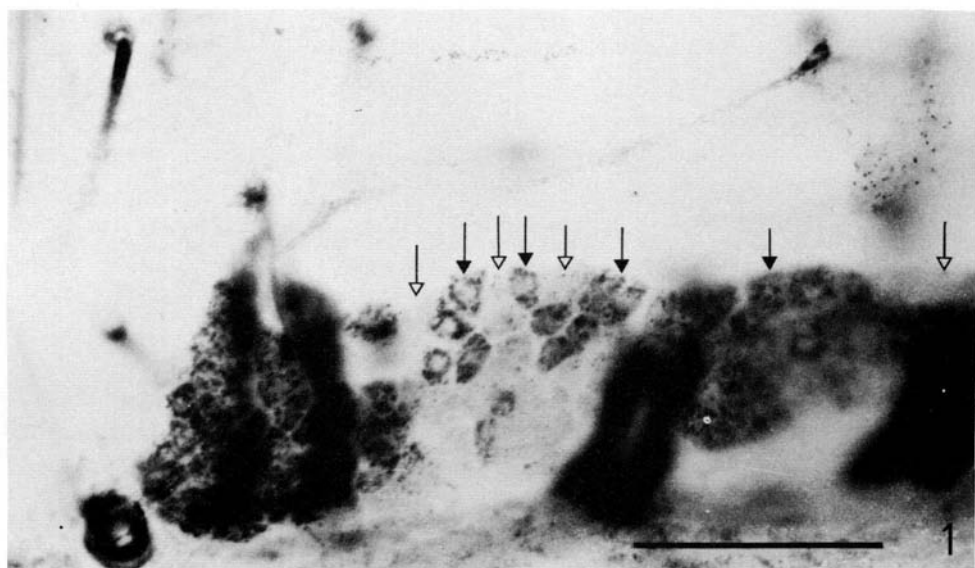
#### *Clones in the epidermis and oenocytes*

Clones in the epidermal cells were either marked directly with *sdh* and seen after staining or indirectly with cuticle markers that affected the bristles and trichomes (*yellow*, *straw*, *pawn*). Epidermal *stw pwn sdh*<sup>8</sup> *M(2)c*<sup>+</sup> clones were as expected, the *stw pwn* trichomes in the cuticle being coextensive with the unstained epidermal cells beneath. Frequently, *stw*<sup>+</sup> *pwn*<sup>+</sup> bristles entered the epidermal territory, and *stw pwn* bristles were found at some distance from their parent clone (Garcia-Bellido & Merriam, 1971).

Clones in the oenocytes were also unevenly shaped, and usually marked  $\frac{1}{3}$ – $\frac{1}{2}$  of all the oenocytes in the hemisegment (Fig. 1). Many oenocyte clones also marked bristles in the same hemisegment; this was true both dorsally and ventrally, and up to at least 96 h of development (Table 1). The histoblasts are therefore the precursors of both oenocytes and epidermal cells. The bristles probably derive from anterior compartments of the abdominal segments (Kornberg, 1981*b*). As marked clones frequently extended from the bristles to oenocytes, the oenocytes are probably also anterior, which is consistent with the position where oenocytes arise (Madhavan & Madhavan, 1980), and with our observation that clones of oenocytes that are homozygous for a lethal allele of *engrailed* (genotype no. 3) are normal.

#### *Clones in the ventral musculature*

Each sternite has a group of longitudinal muscle fibres, one on each side of the midline. In addition, in abdominal segment II there are two pairs of fine oblique fibres. In abdominal segment I there are several extra muscles which link the abdomen to the thorax (Fig. 2). The pattern is a little variable and

Table 1. *Oenocytes and epidermis share a common primordium*

Genotype of clone (see methods)	Age at irradiation (h AEL)	Dose (rads)	Location	No. of bristle clones	No. extending to oenocytes	Pure oenocyte clones*
No. 4. <i>y, sdh</i>	4 ± 2	500	Dorsal	17	10/17	0
No. 4. <i>y, sdh</i>	60 ± 12	1500	Dorsal	24	13/24	0
No. 3. <i>stw pwn en<sup>10</sup> sdh</i>	60 ± 12	1500	Dorsal	36	27/36	6
No. 3. <i>stw pwn en<sup>10</sup> sdh</i>	60 ± 12	1500	Ventral	10	2/10	0
No. 4. <i>y, sdh</i>	96 ± 4	1500	Dorsal	21	5/21	4

\* These oenocyte clones were found in other hemisegments of those abdomens carrying bristle clones. Abdominal segments II–VI were usually scoreable.

occasionally lateral bundles are found. The pleura is covered with a thin sheet of mediolaterally oriented fibres.

Clones have only been detected in the longitudinal bundles; usually only some of the fibres were unstained (Figs. 3, 4), but sometimes the entire bundle belonging to a hemisegment was unstained (Figs. 5, 6). Clones, with one exception, did not cross the midline and could not be discerned at all in the pleural muscles. In four cases several fibres in adjacent segments on the same side were marked (Fig. 7). As the clone frequency per abdomen is very low (Table 2), and there are 10 hemisegments being screened per abdomen, these cases cannot have been due to independent events. Note that two of these cases were found after irradiation during the larval period (Table 2).

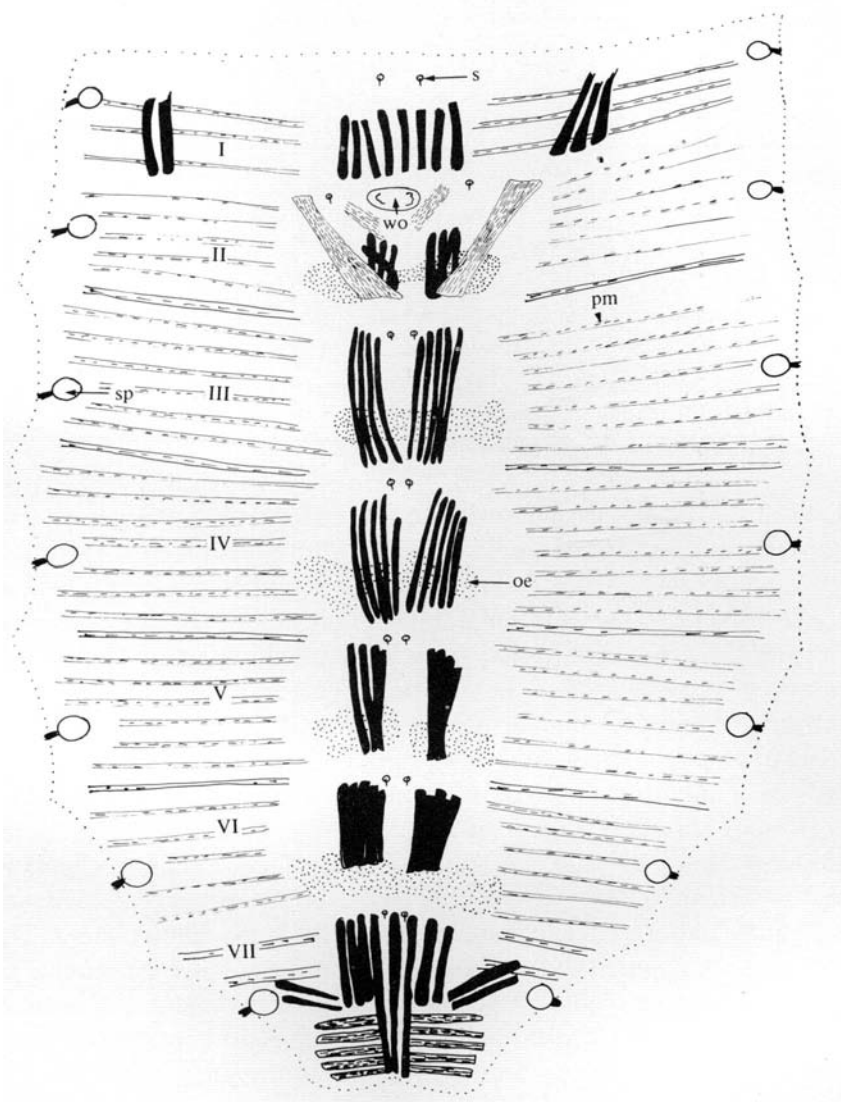


Fig. 2. Diagram of the dissected ventral abdomen of a female. Each segment (numbered I–VI) bears a pair of sensilla (*s*) and spiracles (*sp*), a patch of oenocytes (*oe*), and some longitudinal muscles (black bands). In the second segment, in addition to the longitudinal muscles, there are two pairs of fine muscles and a cuticular Wheeler's organ (*wo*). Each spiracle bears a closing muscle and the pleura is covered with a fine sheet of mediolateral muscle fibres (*pm*).

Table 2. *Clones in the ventral abdomens (segments II–VI)*

Genotype	Age at irradiation	Dose (rads)	No. of abdomens	No. of muscle clones (1 segment)	No. of muscle clones (2 segment)	No. of cuticle clones*
No. 1. <i>sdh</i>	$3.5 \pm 0.7$	750	1744	15	2	NS
No. 1. <i>sdh</i>	$48 \pm 4$	1500	477	23	2	NS
No. 2. <i>stw pwn sdh</i>	$48 \pm 4$	1500	514	22	0	76
No. 3. <i>stw pwn en<sup>10</sup> sdh</i>	$60 \pm 12$	1500	27†	3	0	21
No. 4. <i>y, sdh</i>	$60 \pm 12$	1500	280	8	0	30

\* All bristle clones counted in the ventral abdomens screened (sternites II–VI) for genotypes no. 2, 3 and 4. NS = not scored.

† These 27 abdomens were selected because cuticle clones were detected (sometimes in error) under the dissecting microscope.

Table 2 shows that, even allowing for the different X-ray doses, the frequency of muscle clones rises between blastoderm ( $3.5 \pm 0.7$  h AEL) and the late first stage larva ( $48 \pm 4$  h AEL): following irradiation at blastoderm the frequency is about 1/1000 hemisegments while following irradiation in the first larval stage, with twice the X-ray dose, it rises to *ca.* 1/200 hemisegments. This might suggest an approximate doubling in the number of precursor cells between blastoderm and the first stage larva but, as there are several important unknowns (the effects of X-rays on cell number at the two different stages, the possibility that many events of somatic recombination go undetected because of myoblast fusion), this estimate should be taken with caution.

In genotypes 2, 3 and 4, 127 cuticle clones and 33 muscle clones were detected in 821 abdomens; in only one case (simply explained as a chance event) did a cuticle and a muscle clone coincide in the same hemisegment. This result shows that the muscles and *anterior* epidermis do not share common precursor cells in the larva (the posterior compartments of the abdominal segments were not studied since they cannot be easily marked, Kornberg, 1981 *b*).

The three muscle clones presumed to be homozygous for a lethal allele of *engrailed* (genotype no. 3, Table 2) were normal in appearance. This is similar to the result in the thorax which is discussed in Lawrence (1982).

#### DISCUSSION

We describe the cell lineage of three abdominal tissues of adult *Drosophila*: the epidermis, the oenocytes and the ventral muscles. Epidermal and oenocyte clones are confined to individual hemisegments while muscle clones can extend between two hemisegments. The epidermis and oenocytes derive from common precursor cells, but the muscles have a separate lineage.

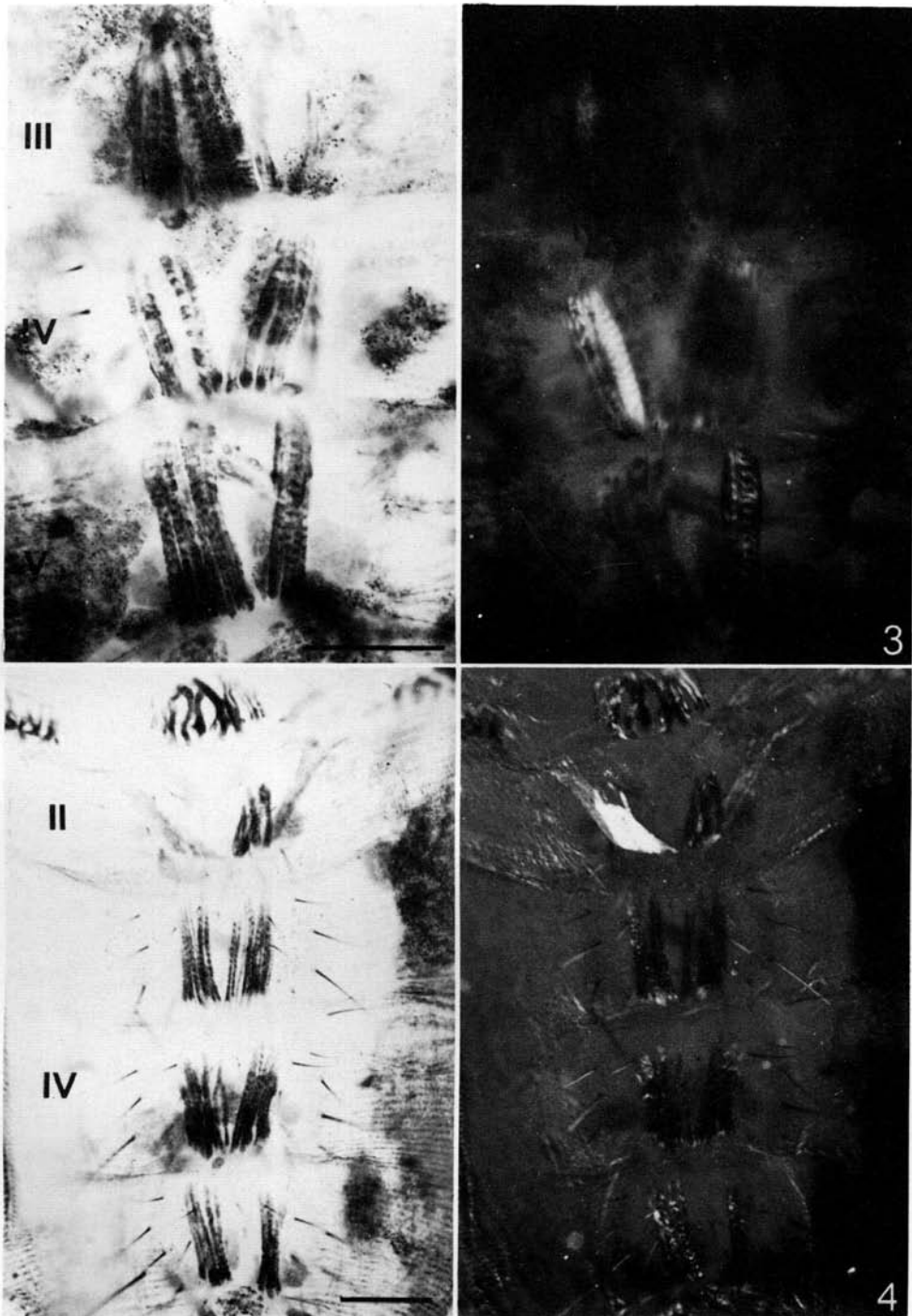
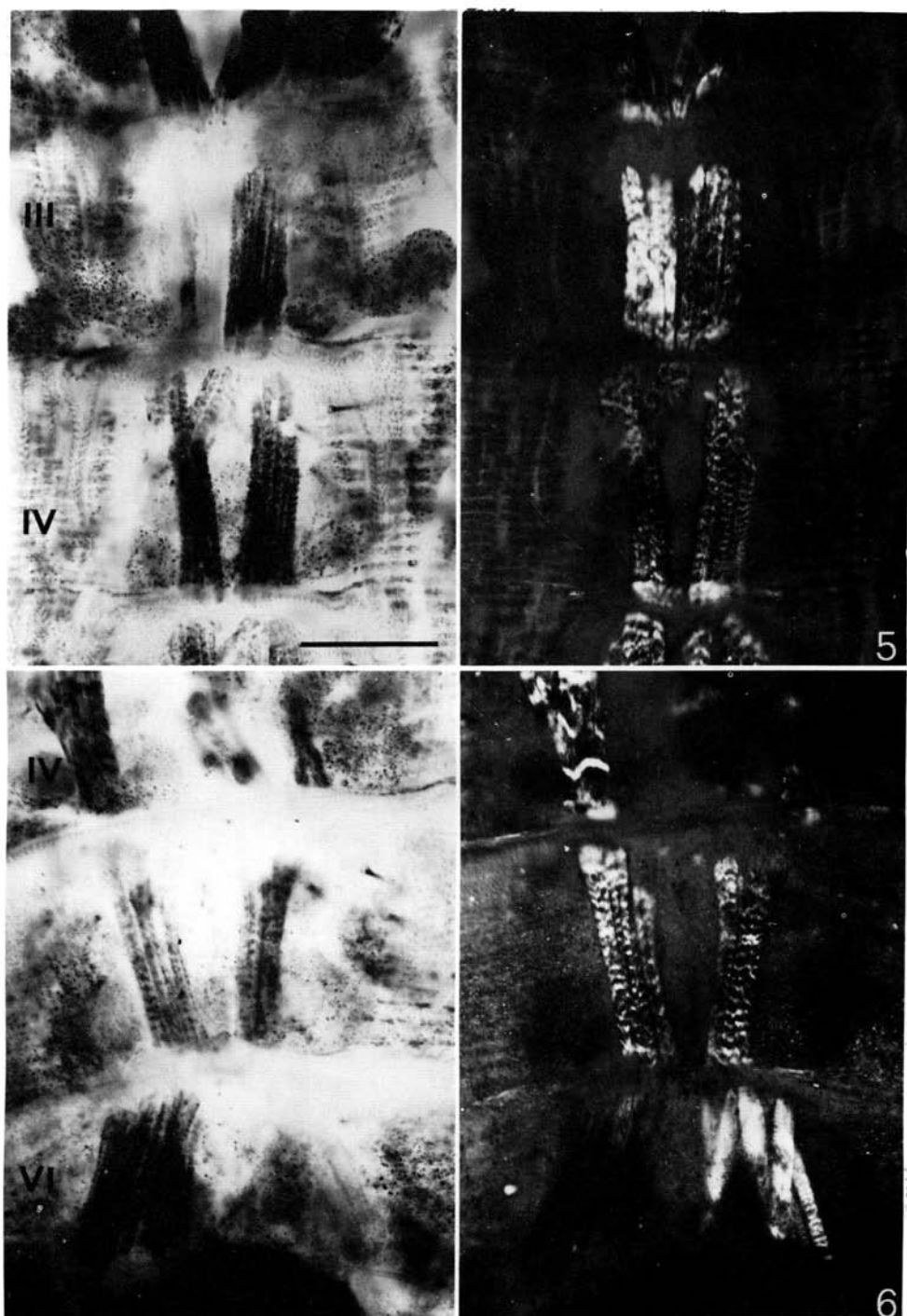


Fig. 3, 4. Ventral abdominal muscles: pairs of bright field (left) and polarized light photographs (right). The *sdh*<sup>8</sup> muscle fibres are almost invisible in bright field but are birefringent under polarized light.

Fig. 3 shows a single marked fibre. Bar = 100  $\mu$ m,  $\times$  215.

Fig. 4 shows a group of marked fibres in segment II.



Figs. 5, 6. Ventral abdominal muscles: pairs of bright field (left) and polarized light photographs. The *sdh*<sup>8</sup> muscle fibres are almost invisible in bright field, but are birefringent under polarized light. Bar = 100  $\mu$ m,  $\times$  215.

Fig. 5 shows a case where the ventral fibres on one side of segment III are marked, while Fig. 6 shows a case where all the fibres on one side of segment VI are *sdh*<sup>8</sup>.



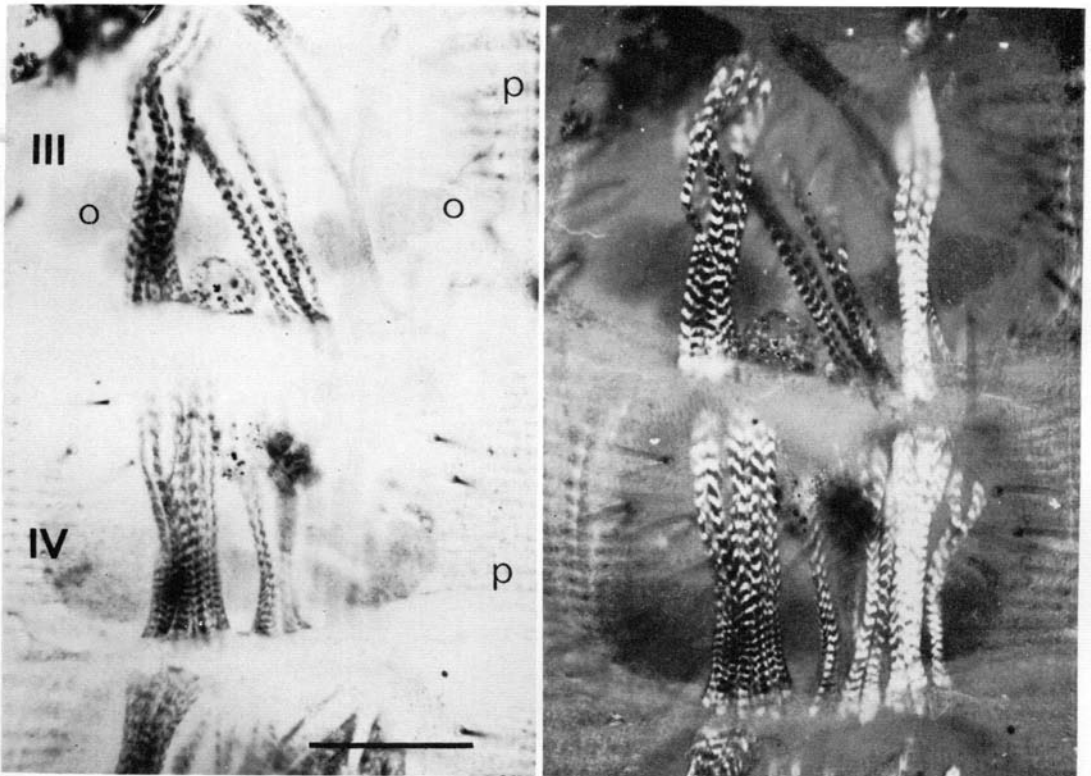


Fig. 7. Ventral abdominal muscles: a pair of bright field (left) and polarized light photographs. The *sdh*<sup>8</sup> muscle fibres are almost invisible in bright field, but are birefringent under polarized light. Bar = 100  $\mu$ m,  $\times 215$ . This muscle clone extends between segments III and IV on one side. Note even staining of oenocytes (*o*) and pleural muscles (*p*).

The epidermal cells of each hemisegment arise from the three nests of abdominal histoblasts, one ventrally and two dorsally located, as well as from the spiracular anlagen (Robertson, 1936; Santamaria & Garcia-Bellido, 1972; Roseland & Schneiderman, 1979; Madhavan & Madhavan, 1980). Early in the pupal period, oenocytes can be seen in close association with the histoblasts (Koch, 1945; Madhavan & Madhavan, 1980) and they probably arise by differentiative cell divisions from the epidermal cells (as in hemimetabolous insects, Wigglesworth, 1933). In a prior and independent study, using the mutation *Pgd* (W. J. Young, see Kankel & Hall, 1976) Ferrus & Kankel (1981) also showed that a large proportion of clones in the cuticle marked oenocytes.

Marked cells have been detected in the ventral muscles, where individual fibres were scored as *sdh* if they completely lacked stain. Some of these clones were small, which suggests that some went undetected. Nevertheless, their frequency can be used to give a minimal estimate of the number of precursor cells. In Table 2 (genotype no. 2) ventral muscle and ventral bristle clones were counted

in one set of abdomens, and there were three to four times as many cuticle clones. Since there are 10–14 ventral abdominal histoblasts which produce the sternite and the pleural cuticle (Madhavan & Schneiderman, 1977; Lawrence *et al.* 1978) the number of muscle precursors for each hemisegment of the ventral abdomen in the larva should be four or more. It is not known where these cells are; there are some small cells near the histoblasts (Madhavan & Schneiderman, 1977) which could be the muscle precursors and groups of small cells are also seen near the muscles of the body wall in the mature larva (Perez, 1910; our observations).

Following blastoderm irradiation, and allowing for different X-ray doses, the frequency of clones was about half that following larval irradiation. This suggests that the presumptive adult myoblasts divide about once in the embryo. In the thorax, muscle clone frequencies are remarkably similar to those in the abdomen: a frequency of 2 clones/1000 dorsal hemisegments was recorded in the thorax following irradiation with 750 R at the blastoderm stage (Lawrence, 1982) compared to 1/1000 ventral hemisegments in the abdomen (Table 2). Probably therefore, at the blastoderm stage, similar numbers of adult muscle precursors are found in the segments of the thorax and abdomen. In the thorax (Lawrence, 1982), as in the abdomen, these precursors divide one to two times before the end of the first instar. These findings support the hypothesis that at segmentation every metameric unit is similar, diversification coming only later in development (Lohs-Schardin, Cremer & Nüsslein-Volhard, 1979; Lawrence & Morata, 1979).

Ventral muscle and epidermis of the anterior compartments of the abdominal segments do not have common precursor cells, at least in the larva. This is the clear conclusion based on 160 ventral muscle and cuticle clones in about 9800 half segments (genotypes nos. 2, 3, 4, Table 2) when there was only one case where a muscle and a cuticle clone was found in the same hemisegment. Since there is only about one division between the blastoderm stage and the larva, both in the epidermis (Szabad *et al.* 1979) and in the muscle, it is likely that the muscle and epidermal precursors are always separate (as is probably the case in the thorax, Lawrence, 1982; Ferrus & Kankel, 1981). This is in accord with the allocation of abdominal muscle precursors to the mesoderm (Perez, 1910; Poulson, 1950).

Four muscle clones extended between two neighbouring segments, two of these being induced in the larval stage. While this could perhaps be an artefact produced by the high X-ray dose and consequent cell death we think that it is not. In descriptions of abdominal muscle development (Perez, 1910; Crossley, 1965) the impression given is one of free, or almost free, myoblasts which can wander. If this is an accurate impression, then, even if separate primordia were established by segmentation of the embryo, their descendant myoblasts could mingle later on in the pupa. This interpretation is supported by an experiment: if myoblasts from the wing disc are released into the abdomen, they can con-

tribute to the ventral and dorsal abdominal muscles (Lawrence & Brower, 1982). If free myoblasts can contribute to form the normal muscle pattern of any segment, what determines the different patterns of muscles that are found in the different segments? The answer appears to be the ectoderm, with which the myoblasts are associated (Bock, 1942; see Lawrence, 1982, for discussion). Unlike the myoblasts, the epidermal cells of each segment never mix with those of other segments (Lawrence, 1973, 1981*a*).

We have not been able to study the fat body, which, in the embryo at least, is classified as mesoderm (Johannsen & Butt, 1941; Poulson, 1950). However, Ferrus & Kankel (1981) find many epidermal clones which extend to the oenocytes and the fat body. There is room for some doubt because, as they point out, the autonomy of the marker they used is not completely established. If confirmed, their results would show that at least part of the adult fat body is ectodermal.

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