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Bristle patterns and compartment boundaries in the tarsi of *Drosophila*

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SUMMARY

We describe cell lineage of the tarsus of wild-type *Drosophila*. Large *Minute*$^+$ clones were made to map the position of the antero-posterior compartment boundary in all three tarsi. The tarsus is mirror symmetric, but the compartment boundary does not coincide with the mirror plane. This boundary runs along the dorsal and the ventral rows of bristles which are immediately posterior to the mirror plane; elements in these rows being made by both anterior and posterior polyclones. The provenance of bristles and bracts suggests that the bristle cells move into their final positions. The homoeotic mutation *engrailed* affects only the posterior compartments of all three tarsi. The mutations *bithorax* and *postbithorax* affect only the anterior and posterior compartments of the third legs, respectively, transforming them into homologous compartments of the second leg. These results support the selector gene model of development (Garcia-Bellido, 1975) and emphasize that collaboration between polyclones is important in pattern formation.

INTRODUCTION

A compartment (Garcia-Bellido, Ripoll & Morata, 1973, 1976) is a specific region of the insect which is formed by a polyclone – all the descendants of a small group of founder cells (Crick & Lawrence, 1975). The boundary separating one compartment from another is precisely positioned: for example, the mesothoracic segment of *Drosophila* is subdivided into anterior and posterior compartments and the boundary bisects the wing running just anterior to vein IV (Garcia-Bellido *et al.* 1973, 1976). This boundary extends to the thorax and down the mesothoracic leg, dividing it longitudinally into anterior and posterior regions (Steiner, 1976). The position of the compartment boundary has been defined in the wing, the thorax and most of the leg, but not in the tarsus. Here we report an analysis of the cell lineage of the tarsus in which we find, unexpectedly, that both anterior and posterior polyclones can form common elements in the same bristle row. This illustrates that patterns can result from inter-

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actions between polyclones. The provenance of bristles and bracts in this row suggests that the bristle-forming cells *move* as the row develops.

The tarsus of the second leg is mirror symmetric, but the compartment boundary does not coincide with the mirror plane. This same boundary delimits the area affected by the homoeotic mutation *engrailed*, while in the third leg *bithorax* and *postbithorax* affect the anterior and posterior compartments respectively – results which support the selector gene model of development (Garcia-Bellido, 1975).

MATERIAL AND METHODS

We used the standard methods of clonal analysis (Becker, 1957; Bryant & Schneiderman, 1969; Garcia-Bellido & Merriam, 1971*a*) and the *Minute* technique (Morata & Ripoll, 1975). The tarsus is normally rather yellowish in colour, which makes the mutant *yellow* less useful as a marker. This problem is overcome when yellow clones are looked for in an *ebony* background. After dehydration in absolute alcohol the legs were mounted directly in a new mountant devised by Gary Struhl and John Sulston (dried canada balsam dissolved in a clearing agent, methyl salicylate). Standard methods of egg collection (the time is given as hours after egg laying, h AEL) and irradiation were used (see Lawrence & Morata, 1977). The genotypes (see Lindsley & Grell, 1968) used are listed with each section. Clones were classified as anterior or posterior on the basis of their position in the tarsus and in the proximal leg segments (Steiner, 1976).

RESULTS

Cell lineage of the tarsus of the second leg

(i) *The* Minute *technique*

[Flies were $M(1)o\ ^{Sp}/y\ wf^{36a}$ and irradiated with 1000 R at 3 ± 1, 36 ± 12 and 60 ± 12 h AEL.]

In the second leg all the tarsal segments are mirror symmetric, there being four well-defined rows of bristles in each half; the claws and associated structures are also symmetrically arranged. In this study we have concentrated particularly on two rows of bristles, the anterior and posterior ventral rows (rows 1 and 8 of Hannah-Alava, 1958) which flank the mirror plane on the ventral face (see Figs. 1, 2).

Large clones were made during the embryonic and larval period and these were always either anterior or posterior. Posterior clones extended up to the posterior ventral row (Fig. 1b) and marked bristles and bracts in it. None (0/31) of the clones completely filled this row and none crossed to the anterior ventral row, even to the extent of a *single bristle* or *bract* (Fig. 1b). Anterior clones could completely mark the anterior ventral row, including every bristle and bract; such clones usually extended to the posterior ventral row although they never filled it (Fig. 1a). Of 22 clones studied in detail, 17 crossed the mirror

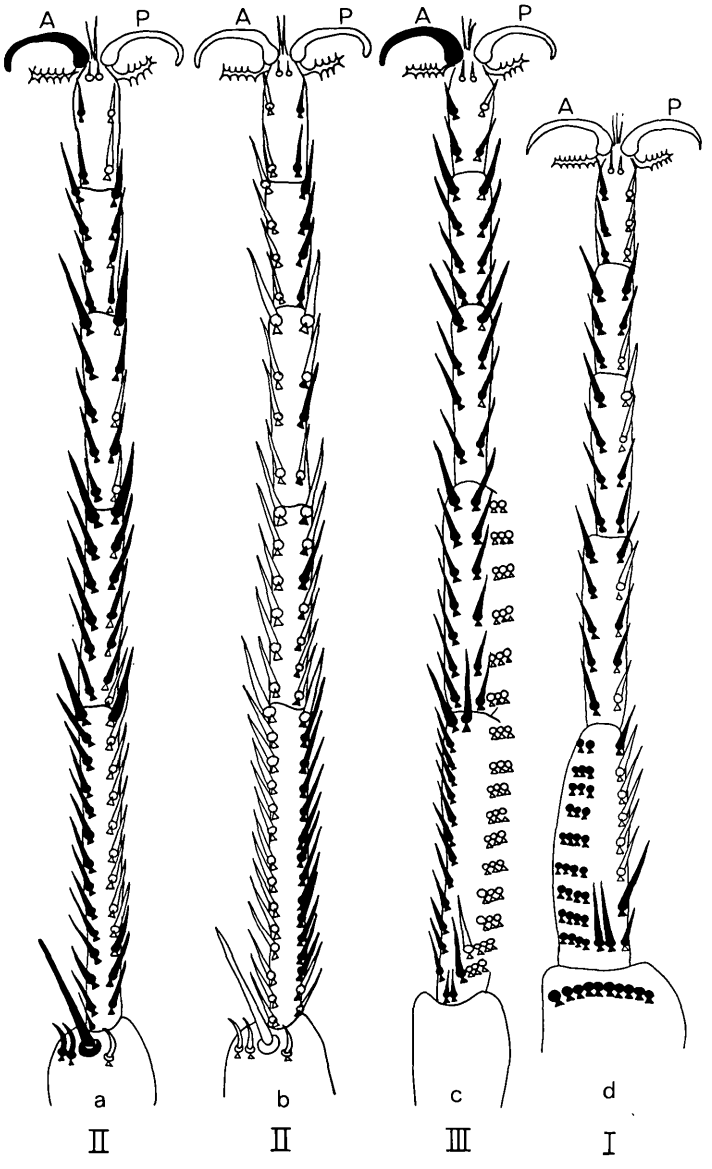

Fig. 1. The ventral face of tarsi bearing *Minute*$^{+}$ clones; those bristles and bracts marked with *yellow* and *forked*^{36a} are shown in black (*forked* phenotype is not drawn). For convenience, all legs are drawn with anterior to the left. The two main bristle rows are shown; they are the anterior (A) ventral row and the posterior (P) ventral row. Transverse rows are indicated but the bristle shaft is not shown. (a) Anterior clone on second leg. (b) Posterior clone on second leg. (c) Anterior clone on third leg. (d) Anterior clone on first leg.

plane and marked bristles in the posterior ventral row. Anterior clones also crossed the dorsal midline of the tarsus, while posterior ones respected it. Accordingly, one anterior clone could mark bristles in six of the eight bristle rows on the tarsus (see Fig. 2b), while a posterior clone could not extend to more than 4/8.

To investigate the provenance of bristles and bracts in the posterior ventral row one would ideally need tarsi in which all the cells of either one or the other compartment were genetically marked. Large *Minute*$^+$ clones often almost fill a compartment (Garcia-Bellido *et al.* 1973). Fourteen large anterior and 14 large posterior clones were chosen and together these clones marked 369 bristles of the posterior ventral rows in the 28 legs. If these clones had completely filled their respective compartments then the total number of bristles in 14 posterior ventral rows would have been marked; as there are about 30 bristles in each posterior ventral row this would have been some 420 bristles. As these 28 clones filled nearly 90% (369/420) of the row bristles they were used to investigate the provenance of bristles and bracts. The 14 large anterior clones marked 156 bristles and 82 bracts in the posterior ventral row, while the 14 posterior clones marked 213 bristles and 272 bracts in the same row. Clearly, the posterior ventral row is made by the two polyclones together, although there is a greater contribution by the posterior cells. Scrutiny of the clones (for example, Fig. 1a, b) shows there is variation in the origin of particular bristles and bracts. Although the elements of the posterior ventral row cannot be divided into two sets, one always being made by the anterior, and one by the posterior polyclone there is some consistency in the formation of the row, for example, the central bristles in the basitarsus are only rarely made by anterior cells, while the bristles at each end are frequently anterior (e.g. Fig. 1b).

Anterior clones marked more bristles than bracts in the posterior ventral row [156 bristles:82 bracts]; which shows that the bristles are more likely to be formed by anterior cells than bracts. If this is so then posterior clones should mark more bracts than bristles, which they do [213 bristles:272 bracts]. We can conclude that, on average, the bristles of the posterior ventral row have a more anterior origin than the bracts.

(ii) *Conventional clonal analysis*

[Flies were $y/+$ and irradiated with 1000 R at 36 ± 12 h AEL.]

There was the possibility that *Minute*$^+$ clones, growing disproportionately in a *Minute* background, might not behave normally with respect to bristle pattern. We therefore made clones that were marked only with *yellow*, which we can assume to be a gratuitous marker. A large number of second legs (640) were studied and 13 clones that marked the anterior or posterior ventral rows were found in the tarsi. All these clones, although small, were subsets of the larger clones studied earlier. For example, some clones were confined to the posterior ventral row and were presumably posterior (they marked more bracts

than bristles, Fig. 2b), others crossed between the two rows (Fig. 2a, c, d) and behaved like small parts of the anterior *Minute*$^+$ clones. We can conclude that the *Minute*$^+$ clones express the normal cell lineage of the tarsus.

Cell lineage of the first and third leg

[Flies were $M(1)o^{Sp}/y\ wf^{36a}$ and irradiated with 1000 R at 3 ± 1, 36 ± 12 and 60 ± 12 h AEL.]

In the first and third legs *Minute*$^+$ clones in the tarsal segments II, III, IV and V behaved as in the second leg in all respects listed above (Fig. 1c, d). These segments have anterior and posterior ventral rows although, in addition, there are transverse rows present in segment II (Fig. 1c).

In the *basitarsus* of the first leg of females the anterior ventral row is missing, instead there are transverse rows (Fig. 1d). These bristles can be completely marked by anterior clones which, as in the second leg, can cross to the posterior ventral row (Fig. 1d). Posterior clones in the basitarsus also mark the posterior ventral row but not the anterior transverse rows.

In the basitarsus of the third leg transverse rows are present and the posterior ventral row is missing – there is a large gap in the medial region (Fig. 1c). Anterior clones behave as in the second leg, they fill the anterior ventral row and cross to some bristles which are more medial. They do not extend across the gap to the transverse rows proper (Fig. 1c). Posterior clones can completely fill the transverse rows.

In summary. In all three thoracic legs the compartment boundary coincides approximately with the posterior ventral and dorsal rows, and not with the mirror plane. The posterior ventral row is made by both anterior and posterior polyclones, but anterior cells contribute more bristles than bracts to it.

Selector genes and tarsal pattern

(i) engrailed

We have examined tarsi of flies mutant for *engrailed* and wild-type flies bearing *engrailed Minute*$^+$ clones. We find that *engrailed* clones in the anterior compartment of the second tarsus behave like wild-type clones and do not affect the pattern. However, posterior clones form numbers of extra bristles (compare Fig. 3a and b). In the first tarsus of *engrailed* flies there are extra bristles in the posterior compartment of males and females, although they do not form clear transverse rows. In males there is an additional sex comb in the posterior compartment (Tokunaga, 1961). In the third tarsus there are extra transverse rows in the posterior compartment, they have more bristles but are less well-ordered than in wildtype. There are no effects on the anterior compartments of either leg.

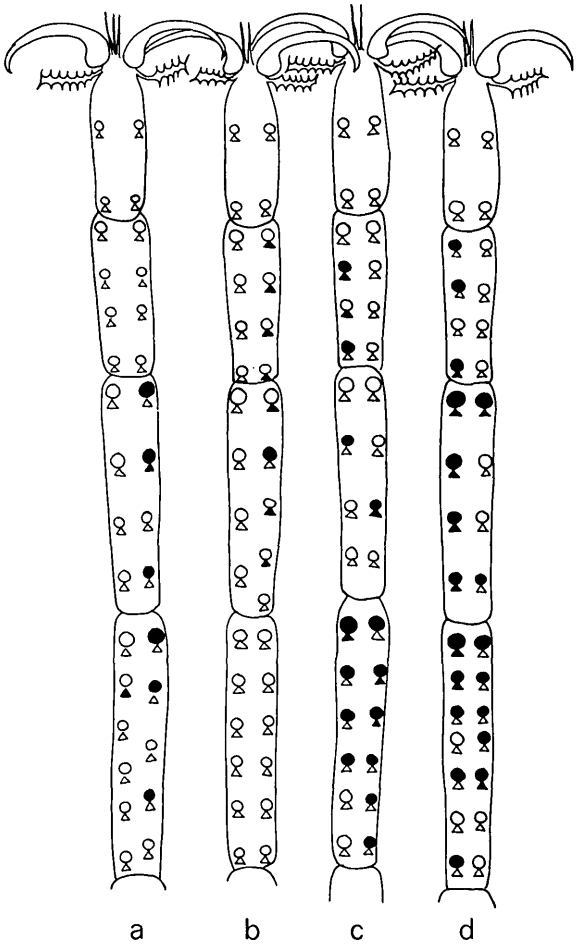

Fig. 2. Clones on the ventral face of the second leg (*Minute*$^+$ in a *Minute*$^+$ background), only the anterior and posterior ventral rows are shown. Anterior is on the left in each leg. Marked bristles and bracts are filled. (a) Anterior clone which marks only one bract in the anterior ventral row but six bristles and a bract in the posterior ventral row. (b) Posterior clone confined to the posterior ventral row (seven bracts, one bristle). (c) and (d) Anterior clones extending to both rows and marking more bristles than bracts in the posterior ventral row.

(ii) bithorax *and* postbithorax

We have looked at these mutants in the tarsi of third legs. In legs mutant for *postbithorax*, the transverse rows of the basitarsus and second tarsal segment disappear and are replaced by four rows of bristles characteristic of the posterior second leg, including a posterior ventral row. The same phenotype is found in legs carrying large posterior clones of *postbithorax* (Fig. 3d). Smaller clones behave autonomously; they do not contribute to the transverse rows, although transverse rows are formed by wild-type cells outside the clone (Fig. 4a).

In the tarsi of third legs mutant for *bithorax* (bx^3/Ubx^{130}) the anterior ventral

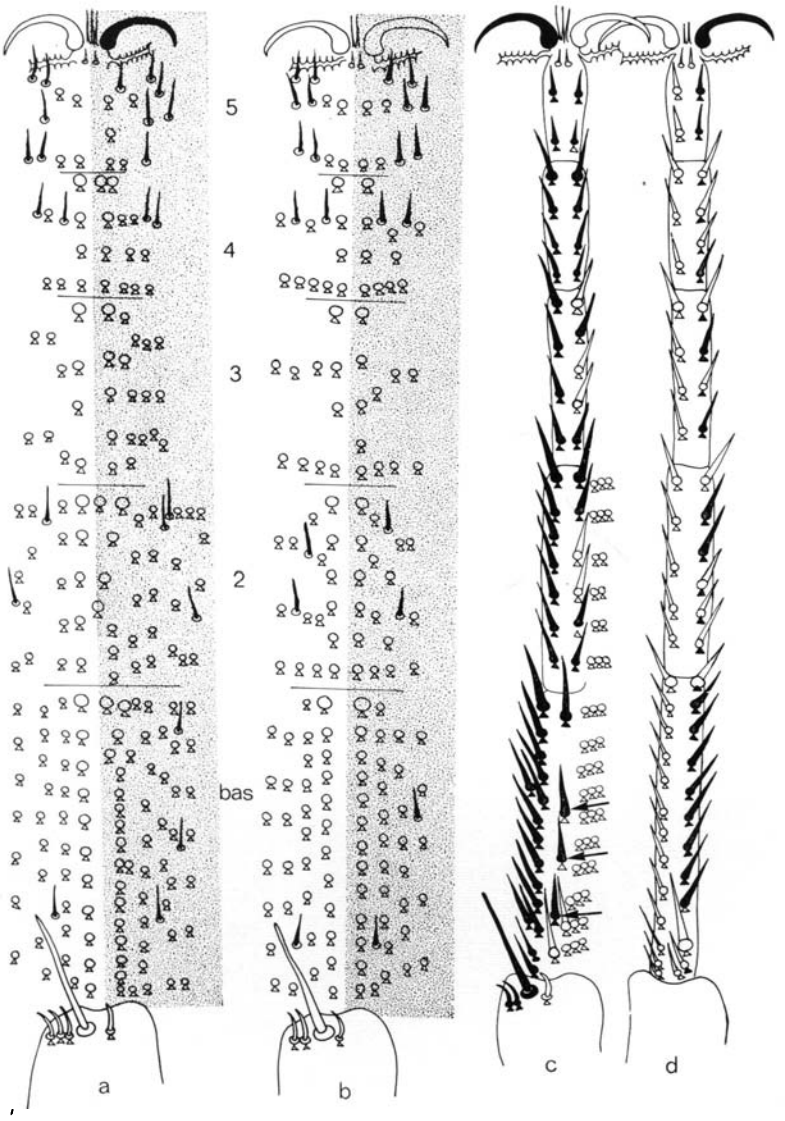

Fig. 3. The effect of homoeotic mutants. (a) A large *engrailed* clone in the posterior compartment of a second tarsus. The fly was *DfM(2)c*^{33a}*/stw en* and irradiated at 3 ± 0·5 h AEL with 1000 R. Although it was clear that the posterior region (shaded) was mainly *straw* and therefore *engrailed* it was not possible to unambiguously score some bristles and bracts. Note the numerous extra bristles in the posterior region (n = 128) compared with the anterior region (n = 86). We did not measure the size of the posterior compartment. (b) Normal second tarsus showing every bristle. In this example there are 86 bristles in the anterior half and 92 in the posterior half (shaded). The basitarsus (*bas*) and the four other tarsal segments are indicated (2–5). (c) A *bithorax* clone in the anterior compartment of a third leg; genotype of fly was *M(1)o*^{Sp}*Dp115, bx*$^{+}$*pbx*$^{+}$*/y f*^{36a}; *Df89E1-2, bx*$^{-}$*pbx*$^{-}$*/Ubx*^{130} and irradiated with 1000 R at 36 ± 12 h AEL. Marked bristles are shown in black. In the basitarsus three adventitious bristles are formed by the clone (arrows). (d) A *postbithorax* clone in the posterior compartment of a third leg, genotype and irradiation as in Fig. 3(c). Marked bristles are shown in black, compare with Fig. 1c and note the appearance of a posterior ventral row in the basitarsus.

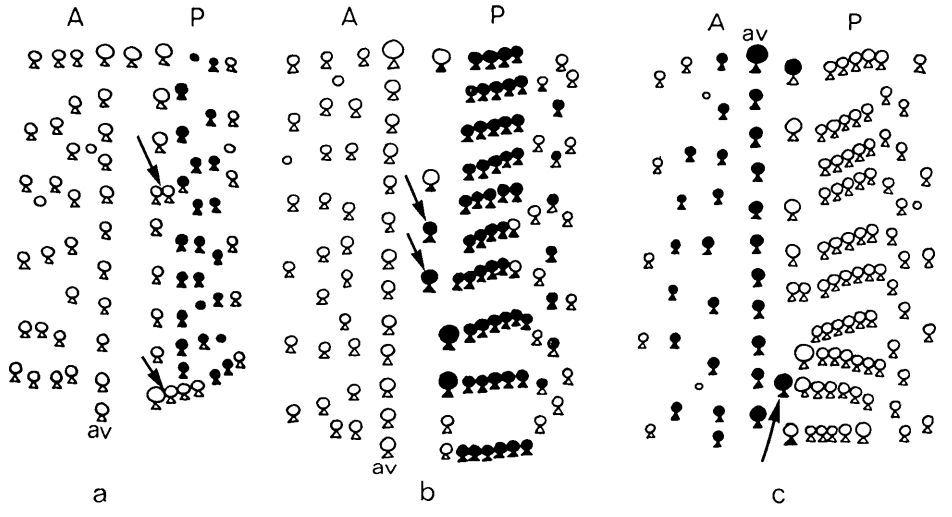

Fig. 4. The basitarsus and second tarsal segments of metathoracic legs. (a) A posterior *postbithorax* clone (genotype and irradiation as in Fig. 3c, d). Note that transverse rows are not formed by marked bristles, while immediately adjacent to the clone wildtype cells form partial transverse rows (arrows). (b) and (c) The cell lineage of metathoracic tarsi of *bithorax* flies; genotype was $M(1)o^{Sp}/yf^{36a}$; bx^3/Ubx^{130} and irradiated at 36 ± 12 h AEL with 1000 R. (b) Posterior clone labelling two adventitious bristles. (c) Anterior clone marking one adventitious bristle.

row bristles are similar to those found in the second leg. In the basitarsus the posterior transverse rows are unaffected, but in the gap there are always some 'adventitious' bristles which form a partial posterior ventral row. This row is sometimes almost complete, but usually consists of three to eight bristles. Similar bristles are almost never found in the gap in normal or Ubx^{130} third legs. The cell lineage of *bithorax* flies was studied to determine the polyclonal origin of this 'adventitious' row. We found that both anterior and posterior polyclones formed bristles and bracts in the row (Fig. 4b, c), so that in this respect it behaved like a typical posterior ventral row of a second leg.

We also made fast-growing clones of cells that were mutant for *bithorax* in a wild-type background. A typical anterior clone is illustrated in Fig. 3a. Note that the transverse rows are not marked and that all the adventitious bristles are of anterior origin – although their bracts can come from either anterior or posterior polyclones. Seven large anterior clones which made one or more 'adventitious' bristles were examined. In every case all the 'adventitious' bristles ($n = 20$) were marked, although only half the bracts belonged to the clones (10/20). Some posterior clones filled the transverse rows completely, but none of these made any 'adventitious' bristles ($n = 11$).

DISCUSSION

Cell lineage of the wild-type tarsus

Clonal analysis of the tarsus of the second leg has shown that although the pattern is mirror symmetric the compartment boundary does not coincide with the mirror plane. This example illustrates that formation of some patterns can be independent of compartments; the tarsal cylinder decorated with the mirror symmetric bristle rows conceals an underlying asymmetry of the two polyclones which construct it (Fig. 6).

Two bristle rows each contain elements formed by both anterior and posterior polyclones and there is variation in the provenance of specific bristles and bracts. The same observation has been made independently by Held (personal communication) who has also shown that in the other rows of the tarsus there is relative movement by the bristle forming cells. A similar situation has been described in the antenna, where two bristles, identifiable by their size and position, can be made either by the anterior or by the posterior polyclone (Morata & Lawrence, 1978, 1979).

The posterior ventral row was studied in detail; anterior cells form twice as many bristles as bracts in the row; while, because every bristle has a bract, posterior cells necessarily form more bracts than bristles. If the variable origin of bracts and bristles were simply due to an irregular compartment boundary along a straight presumptive bristle row, one would expect bracts and bristles to be of anterior origin equally often. The results show that, on average, the bracts have a more posterior origin than the bristles. As bracts and bristles are finally positioned in a straight row which is parallel to the antero-posterior axis it follows that there must be *relative movement* of the cells forming them. The bracts are formed from nearby epidermal cells which are induced by the bristle-forming cells (Tobler, 1966; Tobler, Rothenbuhler & Nöthiger, 1973) so it is most likely they develop later than the bristle forming cells, and *in situ*. We therefore envisage the bristle rows forming as shown in Fig. 5.

It is clear from Fig. 5 that the polyclonal origin of the cells plays little part in the process; the area competent to form the bristle rows is determined according to the pattern of the limb as a whole. This situation can be contrasted with the anterior wing margin. Here the asymmetric triple row is formed by the dorsal polyclone always and only forming the two dorsal rows, while the ventral polyclone forms the ventral row (Bryant, 1970; Garcia-Bellido & Merriam, 1971*a*). It would appear that in the wing, unlike the tarsus, pattern elements form as a consequence of the juxtaposition of two polyclones (Santamaria & Garcia-Bellido, 1975).

The idea that cells forming organules can move is not new: in the formation of the sex comb a group of cells is thought to rotate (Tokunaga, 1962) and in the abdomen marked bristles are frequently found separated from a patch of epidermal cells of the same clone (Garcia-Bellido & Merriam, 1971*b*). In the

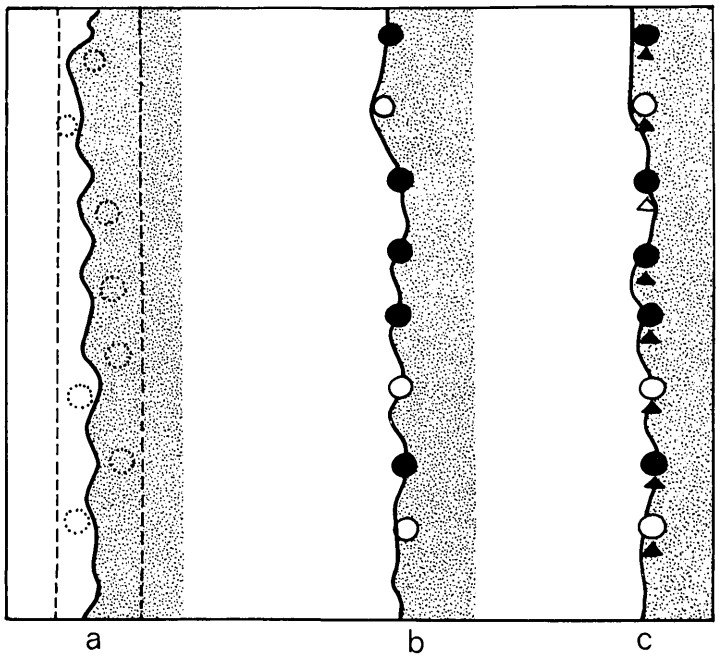

Fig. 5. Model for development of the posterior ventral row of bristles and bracts. The shaded area marks cells of the posterior polyclone. The two lines define the area from which the bristle cells can be taken – they presumably develop from normal epidermal cells by a spacing mechanism (Wigglesworth, 1940; Lawrence, 1969), followed by differential divisions (Wigglesworth, 1953; Lawrence, 1966). In (b) the bristle precursors have moved into a line, and in (c) the bracts have been induced. The compartment border is essentially straight but at this scale individual cell boundaries would impose a local wiggle, the border has therefore been drawn to resemble a antero-posterior boundary on the wing.

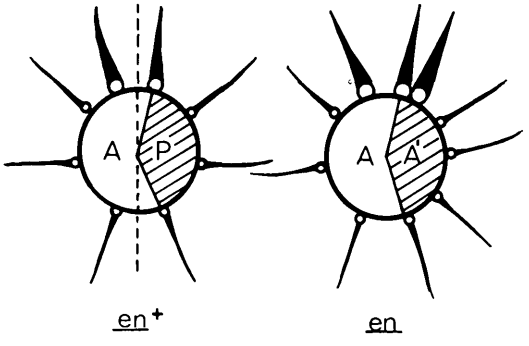

Fig. 6. Diagrammatic cross section of tarsal segment in *engrailed*$^{+}$ and *engrailed* tarsi. Extra bristles develop in the posterior part of the *engrailed* tarsus.

triple row of the wing small clones become split into separate regions suggesting that the bristle-forming cells shuffle into position (Garcia-Bellido & Merriam, 1971*a*; unpublished observations). Moreover, during development of hairs in *Oncopeltus* (Lawrence, 1966) poorly arranged cells have been seen to form into precisely oriented rows. Local cell movement seems therefore to be a general mechanism of pattern formation in insects.

The role of selector genes

Selector genes are one class of homoeotic genes. Their products are continuously required for the development of a polyclone so that without them development is switched to another pathway (Lewis, 1963; Garcia-Bellido, 1975; Morata & Lawrence, 1977). We have studied three mutations in selector genes to see their effect on tarsal pattern.

The gene *engrailed* is thought to determine the posterior developmental pathway in at least the three thoracic segments (Garcia-Bellido & Santamaria, 1972; Morata & Lawrence, 1975; Lawrence & Morata, 1976) and the eye–antennal segment (Morata & Lawrence, 1978). The first leg of *engrailed* flies has been described in detail (Brasted, 1941; Tokunaga, 1961) while some effect was noted on the posterior part of the third leg (Garcia-Bellido & Santamaria, 1972). No effect on the second leg had been reported, but one would be predicted on the selector gene model. Accordingly we have studied the mirror symmetric tarsus of the second leg. As in the wing, and as expected, *engrailed* does not alter the anterior compartment. However, when the posterior compartment is mutant for *engrailed* numerous extra bristles are formed. The wild-type posterior compartment is smaller and contains fewer bristles (Fig. 6), so if it were to be transformed into an anterior compartment one would expect extra bristles, as is observed (Figs. 3, 6).

In the metathoracic segment the anterior compartment depends on the *bithorax* selector gene, and the posterior on *postbithorax*. Without these genes the anterior and posterior polyclones of the metathorax develop into the corresponding compartments of the mesothorax (Lewis, 1963; Garcia-Bellido, 1975; Morata & Garcia-Bellido, 1976).

In the tarsus the mutation *postbithorax* behaves as expected, the transverse bristle rows characteristic of the posterior compartment of the third segment are eliminated and replaced with ordinary rows of bristles. In *postbithorax* clones the transverse rows are removed autonomously, clones were seen to contribute bracts but not bristles to the transverse rows, suggesting that transverse row bristles are exclusively part of the 'repertoire' of the posterior metathoracic polyclone. In the case of *bithorax*, where the anterior metathoracic compartment becomes mesothoracic, the picture is complicated by the partial development of a posterior ventral row – a row which is missing in normal third legs. These 'adventitious' bristles would be readily explicable if they came exclusively from the anterior polyclone (which, in second legs, contributes to a posterior ventral

row). This is indeed the case when large $bx^3/-$ clones are induced in a wild-type background (Fig. 3c). However, cell lineage analysis of bx^3/Ubx^{130} legs shows that some are formed by the posterior polyclone. This could be due to slight *pbx* phenotype (Ubx^{130} is deficient for *pbx*, and bx^3 has some polarity effect on pbx^+, Lewis, 1963).

CONCLUSION

These experiments cast some light on the relationship between compartments and pattern. Some elements of the pattern belong to the repertoire of a specific compartment; for example, the sex comb teeth are only made by male cells belonging to the anterior first leg. These structures can be made in other places on the fly but only when they have the same genetic address as male, anterior first leg. They can be found in the posterior compartment of the first leg when it is mutant for *engrailed* (Tokunaga, 1961) or in the anterior compartment of second and third legs when mutant for *Polycomb* (Lindsley & Grell, 1968). *engrailed* partially transforms posterior into anterior, *Polycomb* second and third legs into first. Sex combs cannot be formed by female cells even when there are only a few such cells in the area where the sex comb teeth normally form (Tokunaga, 1962). Another example is those transverse rows which characterize posterior third legs and are locally removed by clones of *pbx* cells. The formation of such elements is cell autonomous, depending only on the genotype of the responding cells (see Stern, 1968).

The *arrangement* of pattern elements which one or more compartments have in common may involve co-operation between different polyclones. In the tarsus, a prepattern is established without regard to the compartment boundary and the bristle-forming cells taken indiscriminately from the two polyclones. Similarly, in the wing, the first cross vein extends smoothly over the antero-posterior boundary. These are further illustrations that compartment boundaries are no barrier to intercellular communication and co-operation (Lawrence, 1975) even though these boundaries may coincide with the limits of gradients of positional information (Crick & Lawrence, 1975).

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REFERENCES

BECKER, H. J. (1957). Über Röntgenmosaik-flecken und Defektmutationen am Auge von *Drosophila* und die Entwicklungsphysiologie des Auges. *Z. indukt. Vererb. Lehre.* **88**, 333–373.

BRASTED, A. (1941). An analysis of the expression of the mutant '*engrailed*' in *Drosophila melanogaster*. *Genetics* **26**, 347–373.

BRYANT, P. J. (1970). Cell lineage relationships in the imaginal wing disc of *Drosophila melanogaster*. *Devl Biol.* **22**, 389–411.

BRYANT, P. J. & SCHNEIDERMAN, H. A. (1969). Cell lineage, growth and determination in the imaginal leg discs of *Drosophila melanogaster*. *Devl Biol.* **20**, 263–290.

CRICK, F. H. C. & LAWRENCE, P. A. (1975). Compartments and polyclones in insect development. *Science, N.Y.* **189**, 340–347.

GARCIA-BELLIDO, A. (1975). Genetic control of wing disc development in *Drosophila*. In '*Cell Patterning*'. *Ciba Foundation Symposium* **29**, 161–182.

GARCIA-BELLIDO, A. & MERRIAM, J. (1971*a*). Parameters of the wing imaginal disc development of *Drosophila melanogaster*. *Devl Biol.* **24**, 61–87.

GARCIA-BELLIDO, A. & MERRIAM, J. (1971*b*). Clonal parameters of tergite development in *Drosophila*. *Devl Biol.* **26**, 264–276.

GARCIA-BELLIDO, A., RIPOLL, P. & MORATA, G. (1973). Developmental compartmentalization of the wing disk of *Drosophila*. *Nature, New Biol.* **245**, 251–253.

GARCIA-BELLIDO, A., RIPOLL, P. & MORATA, G. (1976). Developmental compartmentalization in the dorsal mesothoracic disc of *Drosophila*. *Devl Biol.* **48**, 132–147.

GARCIA-BELLIDO, A. & SANTAMARIA, P. (1972). Developmental analysis of the wing disc in the mutant *engrailed* of *Drosophila melanogaster*. *Genetics* **72**, 87–104.

HANNAH-ALAVA, A. (1958). Morphology and chaetotaxy of the legs of *Drosophila melanogaster*. *J. Morph.* **103**, 281–310.

LAWRENCE, P. A. (1966). Development and determination of hairs and bristles in the milkweed bug (*Oncopeltus fasciatus*) (Lygaeidae, Hemiptera). *J. Cell Sci.* **1**, 475–498.

LAWRENCE, P. A. (1969). Polarity and patterns in the postembryonic development of insects. *Adv. Insect Physiol.* **7**, 197–266.

LAWRENCE, P. A. (1975). The structure and properties of a compartment border: the intersegmental boundary in *Oncopeltus*. In '*Cell Patterning*'. *Ciba Foundation Symposium* **29**, 373–382.

LAWRENCE, P. A. & MORATA, G. (1976). Compartments in the wing of *Drosophila*: a study of the *engrailed* gene. *Devl Biol.* **50**, 321–337.

LAWRENCE, P. A. & MORATA, G. (1977). The early development of mesothoracic compartments in *Drosophila*. *Devl Biol.* **56**, 40–51.

LEWIS, E. B. (1963). Genes and developmental pathways. *Amer. Zool.* **3**, 33–56.

LINDSLEY, D. L. & GRELL, E. L. (1968). Genetic variations of *Drosophila melanogaster*. *Carnegie Inst. Wash. Publ.*, No. 627.

MORATA, G. & GARCIA-BELLIDO, A. (1976). Developmental analysis of some mutants of the bithorax system of *Drosophila*. *Wilhelm Roux' Arch. Devl Biol.* **179**, 125–143.

MORATA, G. & LAWRENCE, P. A. (1975). Control of compartment development by the *engrailed* gene of *Drosophila*. *Nature, Lond.* **255**, 614–617.

MORATA, G. & LAWRENCE, P. A. (1977). Homoeotic genes, compartments and cell determination in *Drosophila*. *Nature, Lond.* **265**, 211–216.

MORATA, G. & LAWRENCE, P. A. (1978). Anterior and posterior compartments in the head of *Drosophila*. *Nature, Lond.* **274**, 473–474.

MORATA, G. & LAWRENCE, P. A. (1979). Development of the eye–antenna imaginal disc of *Drosophila*. *Devl Biol.* (in the Press).

MORATA, G. & RIPOLL, P. (1975). *Minutes*: mutants autonomously affecting cell division rate in *Drosophila*. *Devl Biol.* **42**, 211–221.

SANTAMARIA, P. & GARCIA-BELLIDO, A. (1975). Developmental analysis of two wing scalloping mutants ct^6 and Bx^J of *Drosophila melanogaster*. *Wilhelm Roux' Arch. Devl Biol.* **178**, 233–245.

STEINER, E. (1976). Establishment of compartments in the developing leg imaginal discs of *Drosophila melanogaster*. *Wilhelm Roux' Arch. Devl Biol.* **180**, 9–30.

STERN, C. (1968). *Genetic Mosaics and Other Essays*. Cambridge Mass.: Harvard University Press.

TOBLER, H. (1966). Zellspezifische Determination und Beziehung zwischen Proliferation und Transdetermination in Bein- und Flügelprimordien von *Drosophila melanogaster*. *J. Embryol. exp. Morph.* **16**, 609–633.

TOBLER, H., ROTHENBUHLER, V. & NÖTHIGER, R. (1973). A study of the differentiation of bracts in *Drosophila melanogaster* using two mutations H^2 and sv^{de}. *Experientia* **29**, 370–371.

TOKUNAGA, C. (1961). The differentiation of a secondary sex comb under the influence of the gene *engrailed* in *Drosophila melanogaster*. *Genetics* **46**, 157–176.

TOKUNAGA, C. (1962). Cell lineage and differentiation on the male foreleg of *Drosophila melanogaster*. *Devl Biol.* **4**, 489–516.

WIGGLESWORTH, V. B. (1940). Local and general factors in the development of 'pattern' in *Rhodnius prolixus* (Hemiptera). *J. exp. Biol.* **17**, 180–200.

WIGGLESWORTH, V. B. (1953). The origin of the sensory neurones in an insect, *Rhodnius prolixus*. *Q. Jl microsc. Sci.* **94**, 93–112.

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