Pattern and polarity of sclerites in adult abdominal segments of *Calliphora erythrocephala* (Diptera): anlage rotation experiments

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SUMMARY

The anlagen of imaginal histoblasts in the abdominal segments of *Calliphora* (higher Diptera) present an interesting problem, which bears on recent concepts employed in the consideration of spatial patterning in insects. They differ from imaginal discs with respect to larval organization and activity, and in the absence of the progressive pattern of genetic determination during the larval period, characteristic of imaginal discs. How is the adult pattern in the abdominal segments determined?

The experiments presented here seek to clarify the spatial parameters involved in control of adult pattern and polarity in the adult segment. A series of 180° rotations of hypodermal grafts bearing the anlagen singly, or in combination, or of larval intersegmental hypodermis, indicate that polarity is determined within the anlagen, through interaction with local larval epidermis either before or during histoblast migration. The nature of the sclerites, too, is primarily carried by the anlagen rather than determined by intersegmental information.

The whole question of 'determination of polarity' is set out more carefully than hitherto in the light of (a) observations of the movement of epidermal cells in other systems in response to disturbance of pattern, and (b) the obvious vectorial nature of the phenomenon, which cannot be a genetic matter, but one of cell axes and of the relation of cells to segment/organism.

The demonstration that (i) hemitergite and hemisternite are primarily determined by the anlagen themselves, and not by larval intersegmental membranes; and (ii) evidence indicates an influence of epidermal cells of the larva on the differentiation (as well as polarity) of imaginal histoblasts, leads to the conclusion that neither of two models considered will account for the establishment of the adult abdominal pattern among the histoblasts at metamorphosis. These models are (a) of a segmental gradient, set by the intersegmental boundaries of the previous instar, to which imaginal cells respond by interpretation of positional information; and (b) of progressive compartmentalization of pattern within the anlagen, without reference to epidermal context.

INTRODUCTION

Two basic aspects of the spatial problem in developmental biology may be considered separately as (i) the establishment of developmental fields, with parameters of 'positional information'; and (ii) the cellular determination of pattern within such a field. Work on epidermal patterns in insects has principally focused these two aspects in two separate experimental systems: the epidermal
segment in hemimetabolous insects which exemplifies gradient properties of polarity and pattern (Lawrence, 1970); and the imaginal discs of higher dipterous flies which show the progressive genetic determination of pattern, and its segregation during larval development (Bryant, 1974; Garcia-Bellido, 1975).

In the abdominal segments of higher Diptera, the adult pattern of sclerites and pleurum is differentiated by imaginal histoblasts which replace the larval cells at metamorphosis (as in the thorax and genital region) but which are not organized during the larval instars as imaginal discs. In *Calliphora* the abdominal histoblasts comprise three pairs of anlagen in each of the first seven segments (Bautz, 1971), and during larval life they are actively secreting epidermal cells (Pearson, 1972). The same three pairs of anlagen are seen in *Drosophila* larvae (Pearson, unpublished) where clonal analysis of pattern formation by the presumptive tergite histoblasts indicates that the adult abdominal pattern, unlike that of head, thorax and genitalia, is not determined before pupariation (Garcia-Bellido & Merriam, 1971; Guerra, Postlethwait & Schneiderman, 1973). It should be possible to explore the origin of the adult pattern in abdominal segments by experimental manipulation of spatial parameters in the puparial stage.

In this study, the following questions are asked: are the local patterns – of tergite, pleurum, and sternite – and polarity in the adult abdominal segment determined within the anlagen during metamorphosis? or is the pattern of each hemisegment determined with reference to hemisegmental spatial parameters, perhaps to positional information (as in the gradient model) deriving from the intersegmental boundaries? (Lawrence, 1966).

**MATERIALS AND METHODS**

Third instar larvae of *Calliphora erythrocephala* were operated between 4 and 8 h after pupariation. All operations were performed on the fourth left (4L) hemisegment of the abdomen. After washing in alcohol, square or rectangular fragments of hypodermis were cut with a razor edge and the isolated region either rotated through 180° or transplanted according to the experimental design described below and in Fig. 1. Wounds were covered by wax of 39 °C melting point and the animals kept at 25 °C until examination of the emergent fly, or late pharate adults when chaetal polarity is most clearly seen.

**RESULTS**

*Control experiments*

(1) *Rotation of dorsal larval epidermis without anlagen*

Following 180° rotation of a 1 mm square of dorsal larval hypodermis in twelve animals, three adults showed perfectly normal fourth abdominal tergites and nine normal hemitergites but slight irregularity in the mid-dorsal fusion of the contralateral hemitergites. In all, the polarity of tergal chaetae was normal.
Fig. 1. A scheme of the experiments a to h. (a) Expt. a: 180° rotation of a hypodermal square containing the D anlage. (b) Expt. b: 180° rotation of D + PD anlagen together. (c) Expt. c: 180° rotation of the V anlage. (d) Expt. d: 180° rotation of hypodermal fragment containing both D and V anlage leads to translocation as well as rotation of anlagen. (e) Expt. e is similar; the hypodermal rotation contains all three anlagen. (f) Expt. f: 180° rotation of a strip of intersegmental hypoderm. (g) Expt. g: rotation of the intersegmental hypoderm between segments 3 and 4 together with the D anlage of segment 4. (h) Expt. h: an exchange of the anlagen D and V without rotation.

(2) Dorsal anlagen excised and replaced in normal orientation

Following the excision and replacement of both dorsal (D + PD) anlagen (see Fig. 1) in a hypodermal square in 16 animals, two died after operation. In all other cases (14) a hemitergite was differentiated with normal orientation of chaetae. The following slight abnormalities were seen:

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<tr>
<th>Abnormality</th>
<th>Frequency</th>
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<tr>
<td>100% normal</td>
<td>2</td>
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<tr>
<td>Macrochaetae missing</td>
<td>4</td>
</tr>
<tr>
<td>Reduced hemitergite</td>
<td>2</td>
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<tr>
<td>Failure to join contralateral hemisegment</td>
<td>4</td>
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Experimental operations

In the following experiments mortality after operation varied from 0% to 70% in any batch operated together. This variation showed little correlation with type of operation, nor with the kind of subsequent result. Survival appears to depend critically on the successful healing of wounds with the wax protection (39° melting point) at a suitable temperature.

The scheme of these experiments is shown in Fig. 1.

Experiment a. Rotation of the dorsal (D) anlage through 180°

Following 180° rotation of a small square of hypodermis which includes the D (but not PD) anlage, the D anlage is reversed in both dorso-ventral and antero-posterior axes. After metamorphosis the following results were scored in the 4L hemisegment of late pharate adults. No other segment was affected.

Of 53 operated animals 35 survived metamorphosis. More than half of these had regulated for normal tergite differentiation with normal microchaete polarity; but in all cases macrochaetes failed to form. Where there was reversal of microchaete polarity it concerned the more dorsal part of the hemitergite rather than the ventrolateral margin (Fig. 4). Irregularities in chaete polarity were as follows:

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<tr>
<td>Normal</td>
<td>18</td>
</tr>
<tr>
<td>Some reversal</td>
<td>6</td>
</tr>
<tr>
<td>Area of dense disoriented chaetae</td>
<td>4</td>
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In another seven cases a peristigmatal marginal region of hemitergite only was formed, in which polarity was normal.

Tergite size and morphology were also affected by the rotation. In addition to the seven where no dorsal hemitergite was formed, but only a peristigmatal sclerite, another 15 adults showed hemitergite reduction in antero-posterior width, and irregular shape, often with an indeterminate boundary between scleral and non-sclerotized cuticle. However, 13 experimental adults showed no morphological abnormality other than absence of 4L hemitergal macrochaetae. Sternites were all normal.

Experiment b. Rotation of the two dorsal (D + PD) anlagen together

Of 37 operated animals, 29 survived of which only two were normal with respect to 4L hemitergite morphology and polarity. Again, sternites were all normal.

In this experiment there was complete reversal of polarity in the dorsal two-thirds of the hemitergite in ten cases; and in another six cases there was partial reversal with areas of reversed chaetae, or a disturbed pattern of polarity, comparable to the effect in some cases of D anlage rotation. The hemitergite was
Fig. 2. Experiment c: the result of a V anlage rotation, in which polarity has regulated. In this case the 4L hemisternal structure is displaced and enlarged (with many chaetae) to form almost a ventral extension of the tergite (arrow). × 15.

Fig. 3. Experiment c: more typical result, with regulation of polarity, and lateral displacement of hemisternite (arrow). (The preparation is photographed from the inside of the cuticle; hence the contralateral image of the disturbance, cf. Fig. 2.) × 15.

Fig. 4. The 4L hemitergite following 180° rotation of the D anlage (expt. a); in this case polarity of chaetae has not properly regulated. Although there is reversal in the posterior half of the dorsal hemitergite, however, polarity in the lateral region associated with the spiracle (sp) is normal. × 25.
frequently larger than normal in the case of reversal, and in two the morphology was grossly abnormal.

A further 11 animals showed more or less reduction of the dorsal region of the hemitergite, with thin scleral cuticle and occasionally failing to join the contralateral hemitergite in the dorsal midline. In only one of these was there sign of reversal and, in most, very few chaetae formed.

*Experiment c. Rotation of the ventral (V) anlage through 180°*

Of 31 animals operated, 20 survived through metamorphosis. In two of these the rotated graft apparently died since there was no 4L hemisternal structure at all. One showed a hemisternite with reversed chaetae, but in the other 17 polarity of the sternal chaetae was normal. In most of these 17, 4L hemisternite morphology was irregular, and the hemisternite itself displaced from the ventral midline (Figs. 2, 3). In a few, this hemisternal sclerite was attached to the ventrolateral margin of the tergite (Fig. 2). Otherwise the hemitergite was always normal.

*Experiment d. Rotation of the D + V anlagen through 180°*

A large part of the 4L hemisegment including both D and V anlagen was rotated through 180° (see Fig. 1) so that, after operation, a reversed D anlage is found in the ventral position and a reversed V anlage in the dorsal position. In this experiment, the anlagen did not regulate to their new orientation, nor to their new position in the segment. They behaved autonomously to give upside down, reversed hemiclernetes in abnormal position (Fig. 6).

Of 20 animals operated, 11 survived. All 11 showed a small reversed hemitergite in ventral position. As well as polarity of chaetae, morphology is clearly

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**Figures 5-9**

Fig. 5. Another non-regulating hemitergite from expt. a (D anlage rotation). In this case all but the most antero-dorsal corner of the dorsal hemitergite is reversed, but as in all these cases, there is normal chaetal polarity below the spiracle (sp). ×15.

Fig. 6. Expt. d: the rotation of D + V anlagen together, giving a dorsally placed, reversed hemisternite (4s) and a ventral, compressed and reversed hemitergite (4t). Further dorsally (x), there is no sclerite. Magnfn. ×15.

Fig. 7. Expt. d: rotation of D + V anlagen together, as in Fig. 6. However, in this animal, there is a dorsal hemitergal region (x) above the rotation graft margin. ×15.

Fig. 8. Expt. d: in this case, the chaetae of the dorsal hemitergal region beyond the rotated graft show some reversal of polarity (x) (cf. Fig. 7, where polarity in this region is dorsal, or antero-dorsal). ×15.

Fig. 9. Expt. h: following exchange of anlagen D and V, hemitergite (4t) and hemisternite (4s) in the adult are reversed in position. Since there has been no rotation of the anlagen, polarity is normal, and the small hemitergal region formed dorsal to the grafted V anlage is also of normal polarity (cf. Figs. 7, 8). ×15.
Rotation of histoblasts in Calliphora
reversed. The hemisternal structure is a small scleral plate in the dorsolateral region of the hemisegment, with reversed chaetae in five cases, and uncertain (disorganized) polarity in another two; while in four animals there was no hemisternite.

A curious feature of these experimental flies, in six cases, was the tergal region which formed dorsal to the margin of the graft: that is, in the unrotated hypodermis. Polarity in this region (Figs. 7, 8) is abnormal; either with partial reversal (Fig. 8) or chaetae directed mainly dorsally (as in Fig. 7). In the other five adults there was no scleral structure dorsal to the graft margin (as in Fig. 6).

Experiment e. Rotation of the D + PD + V anlagen together

In order to test whether the normally differentiating dorsal hemietergite region formed in the previous experiment is the product of an undisturbed PD anlage, a further six larvae were operated so that the rotated graft contained all three anlagen.

Of these six, one died; in another no hemitergite was formed. In all five survivors, however, a dorsally displaced and clearly reversed hemisternite was formed. In each of these five animals, the hemisegmental area dorsal to the graft showed scleral cutical with chaetae of dorsal (2) or antero-dorsal (3) orientation (as in Fig. 7).

Experiment f. Rotation of the intersegmental membrane

In 12 animals, a long intersegmental strip between hemisegments 3L and 4L was rotated through 180° in the puparial stage. Only five of these survived metamorphosis. In four cases morphology and chaetal polarity was normal; the only visible defect being the absence of marginal macrochaetae. In one case however there was some local chaetal reversal in the anterior part of the 4L hemitergite. (It is possible that in this graft a part of the 4D anlage was mistakenly rotated with the intersegmental membrane. Certainly, the result was the same as that following rotation of a part of the intersegmental membrane plus the D anlage together, as in expt. g below.)

Experiment g. Rotation of the intersegmental hypodermis with the D anlage

A square of hypodermis containing both intersegmental membrane and the D anlage was rotated through 180° so that, after operation, the 4D anlage is rotated and situated in the intersegmental region between hemisegments 3L and 4L, and is now anterior to the adjacent intersegmental membrane (see Fig. 1).

Of eight animals operated, six survived to give fairly similar results: all showed reversal of chaetal polarity in the dorsal two-thirds part of the 4L hemitergite. In one, however, only posterior chaetae were reversed, and in another only the anterior chaetae; but in four cases all the chaetae of the dorsal two-thirds hemitergite were reversed. In the marginal ventrolateral hemitergite, which in all six cases appeared morphologically almost separate, chaetal polarity was normal.
Experiment h. Exchange of dorsal (D) and ventral (V) anlagen without rotation

In this experiment, involving a double graft, mortality was severe. In 20 animals, 6 h after pupariation, a square of hypodermis containing the D anlage was exchanged without rotation for a similar square containing the V anlage of the same hemisegment.

Of the five surviving adults, four showed a small ventrolateral hemitergite with normal polarity (Fig. 9); three of them also with a more dorsal hemisternite (as in Fig. 9). In one case there was no hemisternite; and in a fifth adult a ventrolateral hemitergite was continuous with a dorsal tergal area above the D anlage graft. As in the case of experiments d and e where dorsal and ventral anlagen are rotated together, all five adults showed a tergal differentiation of the hypodermis dorsal to the D anlage graft, and in this experiment chaetal polarity was in each case normal (Fig. 9).

DISCUSSION

A constant abnormality following operation, even in controls where a graft is replaced unrotated, is the failure of macrochaete differentiation. Microchaetes form, however, wherever there is a sclerite formed, and serve as markers of polarity in the underlying hypodermis.

In a study of the determination of adult epidermal polarity at metamorphosis in Calliphora abdominal segments, Bautz, Pihan & Stephan (1973) rotated together both the dorsal anlagen (D + PD) in the 6 h puparium, and found in 84 % cases reversed polarity in the tergal chaetae. They concluded that 6 h after pupariation the polarity of tergal chaetae is determined. In the sternite, since ventral anlage rotation led to chaetal reversal in only 17 % cases, they concluded polarity was more labile at the time of operation: in 25 % cases chaetal orientation was the same as the host hypodermis. In the present study, while the results of experiments a, b and c may be compared with those of Bautz et al. (1973), the matter is shown by further experiments to be rather more complex than their interpretation allows.

(i) Reversal and regulation of polarity

In the tergite, 180° rotation of the D anlage in the puparial larva leads consistently to reversal of adult chaetal polarity only when (i) the graft is large and/or (ii) encompasses both D + PD anlagen (as in expt. b) or D + V anlagen (as in expt. d).

In expt. a, where only the D anlage was rotated, 50 % survivors showed normal chaetal polarity. In most of these (38 %) tergite size and morphology was also normal. In 20 % survivors local areas of chaetal reversal show failure of the graft to regulate, and in another 12 % dense disordered chaete occur in the graft region. In expt. b however, when D + PD anlagen are rotated together (as in the
experiment of Bautz et al. (1973)), all but the ventrolateral margin of the hemitergite – which is formed by imaginal cells from the spiracle anlage (Bhaskaran, 1973) – is reversed in 34% cases. There is considerable reversal in another 20%; but only in two cases (7%) is there a normal hemitergite with normally oriented chaetae. In expt. d, when D + V anlagen are rotated as one graft, both hemitergite and hemisternite differentiate autonomously to give morphologically recognizable sclerites in reversed dorso-ventral position and with reversed polarity (Fig. 6). Now in this latter operation the PD anlage is not affected (see Fig. 1), so that the difference of result between D rotation alone (expt. a) and other experiments in which tergal polarity is not regulated can only be plausibly correlated with the size of the rotated graft, and not with the presence of any other specific anlage – either the PD or the V anlage. Thus, in expt. g, when the D anlage is rotated with intersegmental hypodermis, hemitergal polarity of chaetae is reversed even though the rotation of intersegmental hypodermis alone has no effect: the graft is simply larger than in expt. a.

It would be a logical step to demonstrate this conclusion experimentally by rotating a single anlage in progressively larger grafts. Unfortunately, as can be seen by reference to Fig. 1, it is not possible to rotate either the D or V anlage alone in a significantly larger graft without either incorporating material from another anlage, intersegmental membrane, or contralateral hemisegment, or displacement of the anlage position.

(ii) Determination of polarity

In the classical work on imaginal discs of higher flies, determination is shown to occur in populations of cells, progressively, and involves simple genetic switch mechanisms (Garcia-Bellido, 1975). The property of polarity, however, cannot be referred to a genetic switch since polarity is a vectorial differentiation within the cell. ‘Determination of polarity’ is not determination in the usual genetic, autonomous sense; rather, polarity implies co-ordinates beyond the cell itself which give the vectorial sense which is manifest as polarity.

The present experiments do not decide whether or not the polarity of imaginal cells is determined at the time of operation. For example, consider polarity determination in the imaginal cells in relation to their movements; where either A, this determination occurs before; or B, after the rotation.

(i) In the former case A we expect the rotation to result in reversed polarity, without regulation. (ii) In case B – the case of determination after rotation – if some overall segmental parameter directs the determination of cell polarity in a virgin adult segment after the migration of the histoblasts, then we would expect complete regulation of polarity following anlage rotations. If, for example, the larval intersegmental boundaries direct polarity determination in the imaginal cells, then the disposition of histoblast anlagen should not be relevant.

If, however, in case B some larval epidermal parameter is important in determining the polarity of histoblasts before they spread out from the anlagen,
then the question of polarity regulation depends entirely on whether such information persists in the locally rotated epidermis up to the time of determination, or whether it quickly conforms to the rest of larval segmental polarity.

The dependence of the present results on the size of grafts does indicate some influence of local larval epidermis on imaginal determination of polarity. We cannot conclude, however, that cellular polarity is not yet determined at the time of rotation. Indeed, the question of polarity determination cannot be referred to the histoblasts alone because, even if histoblasts determine a cellular axis of polarity in relation to vectorial properties of the field before the rotation, it is nevertheless possible that this relation may be re-established by cell movement, and thus to regulate the pattern of polarity in the adult segment. (Such cellular movements have been demonstrated following rotation grafts in the segmental epidermis of hemimetabolous insects, giving rise to patterns of cuticular structure in subsequent moult which were thought previously to reflect changes in the patterned determination of cells (Bohn, 1974; Lawrence, 1974; Nübler-Jung, 1974).) We cannot tell by rotation experiments whether cells are themselves polarized at a particular stage, but only whether the vectorial relations between cells and segment are irrevocably established before or after operation; and in the present context, this is what is meant by ‘determination of polarity’. Since there is regulation of polarity in the adult segment following some experimental rotations, polarity is clearly not determined, in this sense, at the time of rotation.

(iii) The rules of polarity regulation following anlage rotations

(i) Anlage rotation can be regulated in small grafts. Polarity is not yet finally determined at the third larval puparial stage.

(ii) In a larger graft, rotations are not regulated. There is a decisive difference in this respect between small and large grafts containing anlagen.

(iii) Rotations of intersegmental membrane (expt. 1) or of other larval epidermis which does not involve anlagen (control expt. 1) has no effect on adult polarity.

The results presented demonstrate that vectorial information which determines polarity in the adult segment cannot derive from larval intersegmental boundaries. Not only is there no effect following reversal of intersegmental membrane; when D + V anlagen are rotated together in a hypodermal graft a reversed hemisegmental pattern and polarity result although there has been no disturbance of the intersegmental membrane. The extrinsic vectorial information which polarizes the imaginal anlagen is rotated in such a large graft and remains rotated up to the time of imaginal polarity determination. This information therefore resides in the hypodermis local to the anlagen, and not in intersegmental boundary conditions (cf. Sobels, 1952).

It is unlikely that this information resides in the cuticle, since it is difficult to see how regulation could then occur in any instance. If the information is
provided by local epidermis, in small grafts it alters to conform with the overall segment before imaginal determination. It seems that this information is communicable from cell to cell in the larval epidermis; that it is capable of regulating in these cells according to some overall directional parameter; and that this regulation either spreads from the margin of the graft, or involves a mass effect such that in a large graft the anlage is polarized in accord with rotated directional information.

It appears that polarity is finally determined at the time of histoblast migration. Polarity is not determined over the segment as a whole, but affects anlagen independently. D anlage reversal never affects sternal polarity. More interestingly, following reversal of the D anlage, polarity is usually normal in the spiracular region (Figs. 4, 5).

There is, however, evidence of interaction with larval epidermal polarity during migration in expt. d where in spite of reversal of a very large part of the hemisegmental pattern and its polarity, nevertheless, in the dorsal tergal region the unrotated larval epidermis clearly exerts an influence on the final polarity in this region (Fig. 8). This effect is as of a compromise: either between reversed histoblast polarity and normally polarized larval epidermis which they are invading; or between a reversed polarizing influence spreading from the graft, and normal host epidermis before the migration of histoblasts. The result (Fig. 8) should be compared with the effective control of expt. h (Fig. 9) where anlagen, although translocated, are not rotated.

(iv) Spatial control of the scleral pattern in the adult abdominal segment

The result of expt. d shows how not only polarity but also the pattern of sclerites in the segment is also determined without reference to larval inter-segmental boundaries. This is demonstrated in Figs. 6–8. A similar conclusion was reached through a study of the relation between larval and adult abnormalities in abdominal segmentation in *Calliphora* (Pearson, 1974); there is no support for the contention of Sobels (1952) that ‘the larval segmental borders constitute the determinative pattern which governs the differentiation of hypodermal histoblasts to form normal tergites’.

Are anlagen always sclerite-specific? It may be asked whether the result of expt. d, like polarity, depends upon the size of the rotated graft; and whether in a translocation of these anlagen in a smaller graft the resultant pattern of adult sclerites might conform to normal. Expt. h, however, shows clearly that even in small grafts, a V anlage gives rise to hemisternite, and a D anlage to hemitergite, regardless of reversed dorso-ventral position in the hemisegment (Fig. 9). Unlike polarity, we find here no evidence that a local influence of the larval epidermis determines the scleral fate of anlagen after the third instar. There is, however, the curious result in experiments d, e, and h (where the positions of D and V anlage are reversed) of a dorsal tergite region where the hypodermis was not rotated, beyond the dorsal margin of the graft. Tergal
Rotation of histoblasts in Calliphora

cuticle is differentiated here apparently regardless of anlage derivation of its imaginal histoblasts, since these cells, at least in expt. e, must derive from a V anlage. (When anlagen of a hemisegment are extirpated, there is no scleral regulation from the contralateral hemisegment.) It seems that the larval epidermis can decisively influence patterned scleral differentiation, even though the primary determinants of sclerite pattern are carried within the anlagen themselves. Further, we may conclude that this determinative influence is exerted after migration, since histoblasts ventral to the graft margin, in the rotated hypoderm, behave as though in a ventral position; it is only as they cross the graft margin that their imaginal determination becomes a tergal one.

CONCLUSION

These experiments show that the pattern of scleral elements and polarity in the imaginal abdominal segments of Calliphora are not determined by reference to pre-existing intersegmental boundary properties.

Imaginal polarity is determined under influence from surrounding (local) larval epidermis. Following the disturbance of a rotated graft, these cues in the larval epidermis can apparently regulate to conform with overall segmental polarity. Thus, in small grafts, polarity in the imaginal pattern is normal. In large grafts, however, either a mass effect maintains a reversed polarity in the graft despite an opposite polarity of the host epidermis; or else there is a gradual spread inward from the graft margin of the regulating reversion which may or may not reach the anlage by the time of imaginal determination. There is evidence that polarity of larval epidermis may still influence imaginal polarity during histoblast migration.

On the one hand, it is already known that imaginal pattern in abdominal segments in higher flies is not genetically determined during the larval period (Garcia-Bellido & Merriam, 1971) in the progressive manner shown by imaginal discs of head, thorax and genitalia (Garcia-Bellido, 1975). On the other hand, it is shown here that the abdominal segmental pattern of sclerites is not determined in the manner of the segmental patterns of hemimetabolous insects, by reference to intersegmental boundaries in the previous instar. The primary determinants of scleral pattern, at the end of larval life, appear to reside in the anlagen themselves, yet the scleral pattern in experimental cases appears, at least in the dorsal tergal region, to be the result of larval epidermal/histoblast interaction.

The importance of this conclusion is to suggest that, at the cellular level, imaginal pattern is not determined in an anlage autonomous way. The development of the adult abdomen cannot be referred to 'compartments' which have been shown to segregate genetically, and progressively, in imaginal discs (Garcia-Bellido, 1975). Consequently, perhaps, imaginal discs should not be taken as a direct model for the solution of all the developmental problems posed by organisms, nor even the adult form of higher dipterous flies.
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REFERENCES


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