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Recruitment of Epidermal Cells by the Developing Eye of *Oncopeltus* (Hemiptera)

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Summary. Oncopeltus eyes grow by recruiting epidermal cells which become transformed into ommatidial components. We show by grafting experiments using a genetic label, that head epidermal cells from adults can also be recruited by growing larval eyes. However, prothoracic cells sort out from the head epidermis and do not become incorporated into the eye. A previous claim for successful transformation of cockroach thoracic cells into eye is discussed.

Grafting experiments on a mosquito (White, 1961), a cockroach (Hyde, 1972) and a Hemipteran, *Oncopeltus* (Shelton and Lawrence, 1974) have shown that the insect eye grows by recruitment; epidermal cells being progressively transformed into new ommatidia at the anterior border of the eye. Similarly, in *Drosophila* a front passes from posterior to anterior across the developing eye and is associated with mitoses and determination of ommatidia (literature reviewed in Meinertzhagen, 1974).

This note is concerned with the nature of the recruitment process. We ask the question: can cells which are not presumptive eye be recruited and transformed into normal ommatidia? For the cockroach *Periplaneta* the answer is already claimed; Hyde succeeded in grafting a piece of prothorax from a *pearl* donor (white eye) into the eye of a *lavender* host (pink eye); the *pearl* tissue subsequently developed into apparently normal eye. This is such a striking claim that we attempted to extend it to *Oncopeltus.*

In a previous study (Shelton and Lawrence, 1974) small grafts from near to the eye were exchanged between white-eyed (*wb*; *re*) and red-eyed (wb^+; re^+) (Lawrence, 1970) 3rd-stage larvae and it was found that regularly these grafts became incorporated into the host eye. We now report the result of transplanting pieces of wild-type prothorax to the anterior margin of the eye in *Oncopeltus* (50 operations; 27 moulted to adults of which 12 bore graft tissue in the head, 0 had genetically mosaic eyes). In order to optimise the chance of incorporation, 3rd-stage larval tissue was used for the grafts onto 3rd stage hosts. Although many (34) of the grafts survived the first moult they behaved peculiarly. The young 4th-stage larvae typically bore a graft very close to the eye; but the graft was always circular in outline. At the next moult the graft was frequently rejected, but if it survived the amount of contact between head and prothoracic tissues was further reduced, the graft becoming vesicular and only attached to the host by a narrow neck. In only 12 cases did the graft survive the moult to the adult; in no case did any of the grafted cells become incorporated into the host eye.

The graft always secreted cuticle that was characteristic for the region of prothorax that it had been taken from.

In a further series of experiments, again designed to test the capacity of cells whose presumptive fate was *not* eye, we grafted pieces of *adult* head epidermis from near to the eye, to a site anterior to the eye of 3rd and 4th-stage larvae. The grafted epidermis frequently became incorporated into the developing eye (26 operations; 19 moulted to adult of which 13 bore patches of graft tissue in the head, 9 had genetically mosaic eyes) giving rise to apparently normal ommatidia. Fig. 1 shows one such eye in surface view, and Fig. 2 and 3 another sectioned across the host-graft border at the level of the retinula cells. Both host and graft ommatidia appear perfectly normal, and as in those cases where larval tissues are used as a graft (Shelton and Lawrence, 1974) the border between pigmented and unpigmented cells runs through ommatidia, suggesting that the cells entering any particular ommatidium are not necessarily related by lineage. The grafted epidermis would have undergone cell division during wound healing, moulting and probably during recruitment.

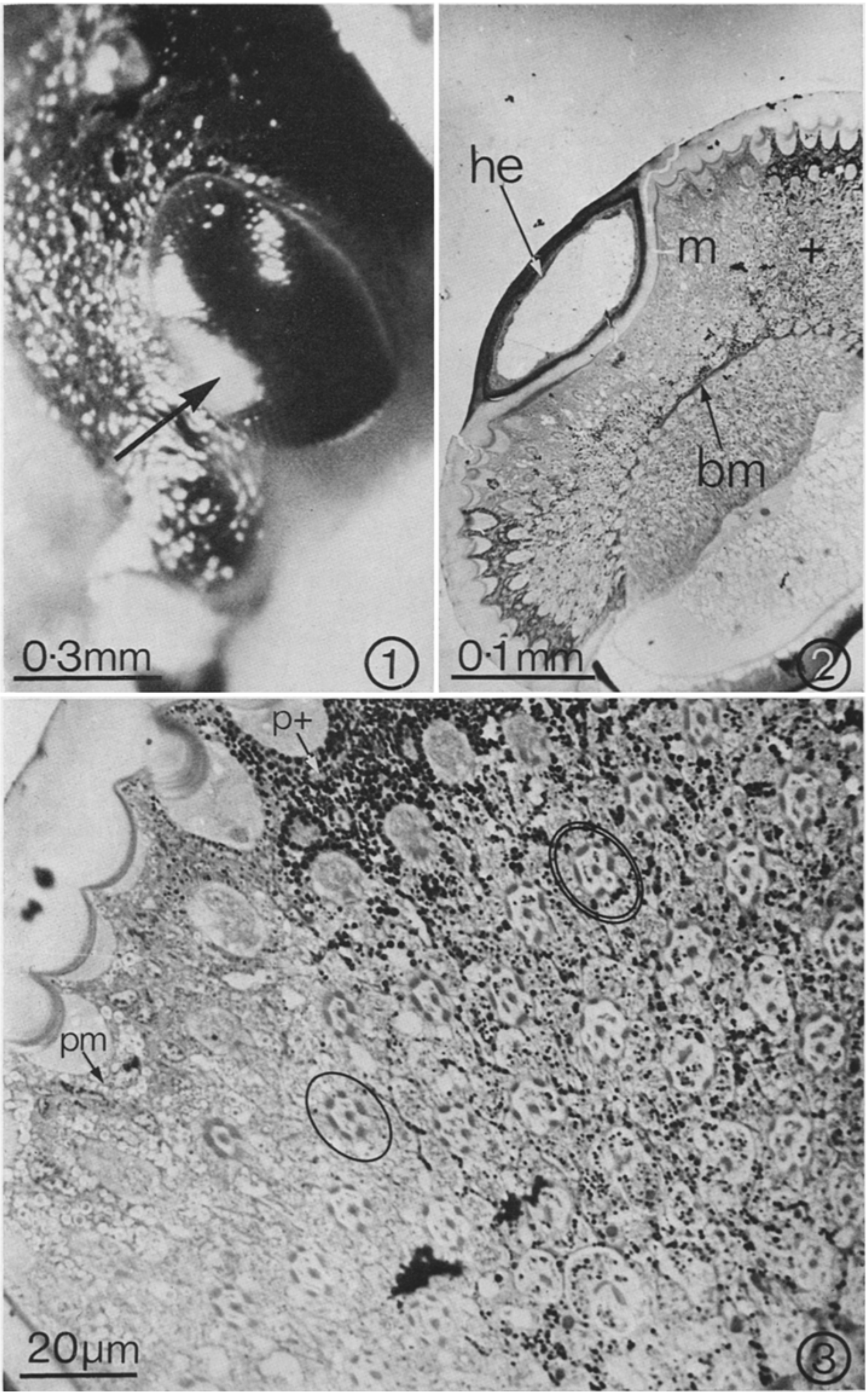
Discussion

We have shown that, when placed near to the eye of a larval host, adult head epidermal cells can become transformed into normal ommatidia. Since these cells have progressed through the whole of development without becoming eye, they are, by definition, cells whose prospective fate was not eye. It follows that the area of larval head epidermis capable of generating ommatidia is larger than that which actually does so. This does not mean that any cell can form eye; Mouze's (1974) pictures suggest that dragonfly head epidermis, taken from an area distant from the eye, did not become ommatidia. Hyde (1972) claimed that prothoracic tissue could be transformed into ommatidia, but her case is not unequivocal, since the argument depends only on pigmentation and not on a cytological examination. She used the mutants *pearl* (white eye) and *lavender* (purple eye). By means of other grafting experiments she showed that the expression of *lavender* is autonomous, but that *lavender* cells can donate something to neighbouring *pearl* cells which results in that tissue forming wild-type pigments

Fig. 1. The result of grafting a piece of adult *wb*; *re* tissue near to the eye of a 3rd-stage larval host (wb^+; re^+). The eye of the adult host contains a sector of *wb*; *re* tissue (arrow)

Fig. 2. A 1 μ section of another mosaic eye. The eye was fixed in Karnovsky's fixative embedded in araldite and stained in toluidine blue (Shelton and Lawrence, 1974). The wild-type (+) and mutant (*m*) ommatidia can be clearly distinguished. *h.e.* head epidermis, *b.m.* basement membrane

Fig. 3. Detail of Fig. 2. Note primary pigment cell of wild type (p^+) and mutant (*pm*) and normal arrangement of rhabdomeres in both wild-type (double ellipse) and mutant (single ellipse)


0·3mm
1
he
m
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(black eye). Hyde demonstrated that when a piece of *pearl* prothorax is transplanted into the eye of a *lavender* host it developed some wild-type pigmentation near to the anterior margin (her Fig. H, p. 373). She also transplanted a piece of *lavender* eye into the prothorax of a *pearl* host; wild-type eye pigments apparently developed in the surrounding host tissue (her Fig. D, p. 372). Since she states "There is no synthesis of these pigments until the cells become eye cells" it would seem to follow that the *pearl* prothoracic tissue has been transformed into ommatidia. However, the apparent absence of pigment in normal epidermal cells still allows for the possibility that, when placed close to *lavender* cells after an operation, *pearl* cells might make some pigment without differentiating into normal ommatidia. Examination of sections would probably settle the matter.

The failure of thoracic cells to become recruited in *Oncopeltus* may be partially due to the sorting out that occurs. Sorting out also happens when cells from two different imaginal discs of *Drosophila* are mixed following dissociation (Nöthiger, 1964) or when, following a change in genotype, a cell in one disc acquires the characteristics of another, and gives rise to a clone which subsequently becomes vesiculated and separates off from its untransformed surroundings (Morata and Garcia-Bellido, in preparation).

Most organs in insects can be considered to develop by means of intercellular systems (such as gradients, Lawrence, 1973) which may lead to the determination of subsets of cells (such as compartments, Garcia-Bellido, Ripoll and Morata, 1973). The determined state is then propagated through cell heredity and may become further refined as a result of subsequent cell interaction. Thus, in development, the fate of any cell depends mostly on its determined state and its present position. The developing eye of *Periplaneta* or *Oncopeltus* seems to be a partial exception to this generalisation, for whether a head epidermal cell continues to give rise to head cuticle with its associated bristles, or instead develops into ommatidial components, appears to depend more on its proximity to an inductive eye margin, than on its own ancestry.

Whether we have demonstrated another case of "reversal of metamorphosis" (Wigglesworth, 1940; Willis, 1974) is a moot point. Certainly it is a characteristic of larval, but not of adult eye, to grow by recruiting head epidermal cells; we have shown that the larval eye can also recruit adult epidermal cells. We do not know whether cell division is a necessary component in this process.

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