J. Embryol. exp. Morph. Vol. 32, 2, pp. 337–353, 1974
Printed in Great Britain

Structure and development of ommatidia in *Oncopeltus fasciatus*

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SUMMARY

The structure and development of ommatidia has been examined in *Oncopeltus fasciatus* (Lygaeidae). Each ommatidium is composed of 18 cells comprising four crystalline cone cells, two primary pigment cells, four secondary pigment cells and eight retinula cells. Ommatidia are of the apposition type and the retinula cells are arranged on the open rhabdomere plan.

During the five larval stages the retina grows anteriorly to provide a 12-fold increase in numbers of ommatidia. Grafts of presumptive eye epidermis show that the proliferating anterior border of the developing retina is an area of epidermal cell recruitment rather than a special budding zone.

Mosaic retinae were formed by grafting epidermis from near the eye of wild-type donors into the corresponding region of mutant hosts. Ommatidia which developed at the borders of the graft contained mixtures of wild-type and mutant cells in variable and unpredictable combinations. Similar mosaic structures were seen in retinae generated by irradiation at early stages of development. The suggestion that each ommatidium is clonally derived from a single epidermal stem cell is thus disproved.

The frequent occurrence of mosaic ommatidia containing only one cell of a different genotype from the rest suggests that the formation of ommatidial clusters follows the main proliferative phase of eye growth. We conclude that cell determination within ommatidia is not connected with lineage but is dependant upon cell position within the developing ommatidium.

INTRODUCTION

The component cells of insect sensory bristles are clonally derived. A single epidermal cell transforms into a bristle mother cell and undergoes a precise sequence of differential divisions to generate the socket, shaft, nerve and neurilemma cells (Wigglesworth, 1953; Peters, 1965; Lawrence, 1966). Ommatidia, which also develop from the epidermis, consist of a fixed number of component cells which are even more precisely arranged than bristle-forming cells. It was thought that an ommatidium developed in a similar way to a bristle and was clonally derived from a single stem cell (Bernard, 1937; Kühn,

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1965). Histological sections of the ant *Formicina* were interpreted in this fashion (Bernard, 1937) but the proposed lineage was never confirmed experimentally.

The eye develops in an unusual way; in hemimetabolous insects the retina grows throughout larval development by addition of new ommatidia to the anterior margin. The process is best established for the cockroach, *Periplaneta* (Hyde, 1972), but it is likely that eye growth follows a similar pattern in other species. The advancing edge of the retina recruits cells from the surrounding epidermis which subsequently undergo mitosis to provide a pool of cells from which the ommatidia differentiate. The same process probably occurs in holometabola; White (1961) has shown that in *Culex* the adult eye develops by recruiting epidermal cells.

We have studied experimentally produced mosaics of *Oncopeltus*. Small pieces of red epidermis from near to the eye of red-eyed donors were grafted onto white-eyed second and third instar hosts. During subsequent retinal growth the donor tissue was incorporated into the host eye and could be distinguished by the colour of the pigment cells and the structure of the retinula cells. We found that ommatidia in the centre of the graft were entirely composed of donor cells, but many of those at the margins contained cells of both host and donor phenotype in a variety of combinations. Mosaic ommatidia were also found at the border of clones of ommatidia with defective pigmentation induced by X-ray treatment. We conclude that in *Oncopeltus* the cells forming each ommatidium are normally derived from several unrelated cells and that the determination of retinula and primary pigment cells depends not on lineage, but instead on cellular interaction. Initial reports for *Drosophila* (Hanson, Ready & Benzer, 1972; Benzer, 1973) indicate a similar pattern of ommatidial development.

MATERIAL AND METHODS

Oncopeltus fasciatus were maintained on a diet of milkweed seeds and water at 29 ± 1 °C (16 h light, 8 h dark). The following stocks (Lawrence, 1970*a*) were used for grafting: wild-type (which have red-brown eyes) and a white-eyed double mutant stock $\left(\frac{wb}{wb}\,\frac{re}{re}\right)$. Clones of ommatidia with pigmentation defects were generated in a red-eyed stock $\left(\frac{wb}{wb^{+}}\,\frac{re}{re^{+}}\right)$ by irradiation of eggs aged 21–43 h with 400 R (220 kV at 15 mA, 1 mm aluminium filter, distance of 5 cm; rate of 500 R/min, R = $2{\cdot}58 \times 10^{-4}$ C/kg). The genetic basis of clone production is not understood (Lawrence, 1973).

The wild-type stock was used for studying basic eye structure. The operations were performed on newly moulted second- and third-stage larvae. After anaesthesis in water, a small area of epidermis anterior to the eye was removed

from a white-eyed host and replaced by a matching area from a wild-type donor.

For light- and electron-microscope studies whole eyes were fixed for 2–24 h in phosphate buffered osmium tetroxide, pH 7·2–7·4 (Millonig, 1964). The tissues were dehydrated in ethanol and embedded in Araldite after passing through propylene oxide. The sections for electron microscopy were mounted on Formvar-coated grids and stained with uranyl acetate and lead citrate.

Care was taken to maintain the correct orientation of the graft during the transfer. Of a total of 34 operations seven gave adult eyes with an appreciable area of grafted tissue incorporated into the eye. In the present study we examined 239 ommatidia in the vicinity of a graft on the left eye of an adult *Oncopeltus*.

Serial sections (1 μm thick) of the retina containing the graft were prepared using a Huxley Ultramicrotome. The sections were collected singly and mounted in order on glass slides. They were stained with 1 % aqueous toluidine blue in a borax/boric acid buffer (Trump, Smuckler & Benditt, 1961). A series of approximately 100 sections was necessary to trace retinal structure from the cornea to the basement membrane. They were photographed using an oil-immersion objective and the pictures were arranged in order. Ommatidia in the vicinity of the graft were given arbitrary numbers and they were examined at a number of levels. In deciding the phenotypes of cells in mosaic ommatidia reference was made to the original slides and each cell was examined in several different sections.

RESULTS

Gross morphology of the retina

The compound eyes of *Oncopeltus* form bulbous hemispherical projections on the lateral regions of the head. They occupy a relatively small area and the dorso-ventral axis, which is the longest, measures about 0·6 mm in the adult. The external surface is marked by a regular pattern of hexagonal corneal facets. Each has a diameter of about 15 μm and is formed by an underlying ommatidium. In a fully developed eye there are just over 700 facets.

The structure of a single ommatidium is illustrated in Fig. 1, additional details are provided in subsequent figures. The ommatidium is conveniently divided into three functionally distinct regions; the dioptric apparatus, the pigment cells and the retinula cells. In the following account they are described in that order.

The dioptric apparatus

The dioptric apparatus occupies up to half the length of the ommatidium and is composed of the cuticular cornea and the underlying crystalline cone. Its supposed function is to direct light rays on to the underlying photoreceptive layer. The crystalline cone is composed of four cone cells, CC_1–CC_4, which are remarkable for the uniformity of their cytoplasm (Fig. 2). There is an

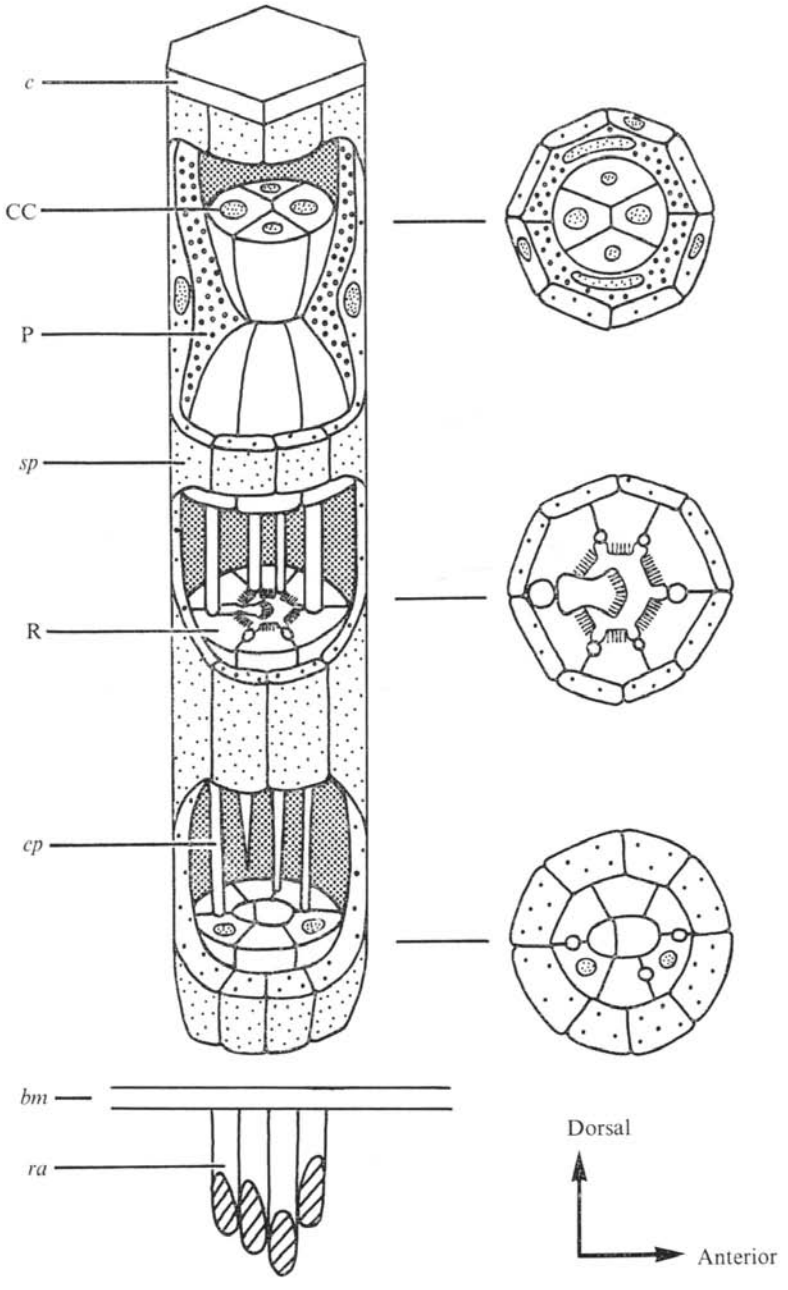


FIGURE 1

A diagrammatic cutaway view showing the arrangement of cells within a single ommatidium. The appearance of the structure in transverse sections is shown at various levels on the right. *bm*, basement membrane; *c*, cornea; CC, crystalline cone; *cp*, cone cell process; P, primary pigment cell; R, retinula cell; *ra*, retinula cell axon; *sp*, secondary pigment cell.

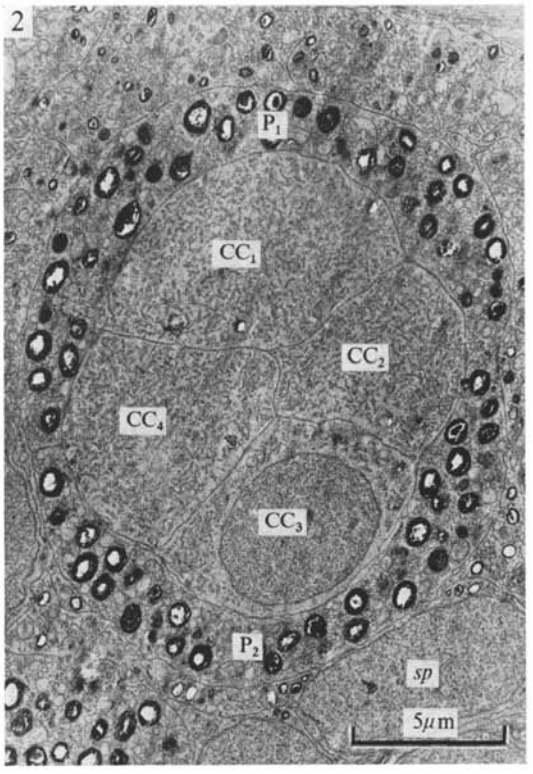
almost total lack of organelles apart from a mass of small cisternae of smooth endoplasmic reticulum. The nuclei are spherical and are centrally located within each cell. Transverse sections reveal a predictable symmetry in the arrangement of cells within the crystalline cone. Six cytoplasmic processes extend proximally from the cone cells into the retinula cell layer. They pass between the retinula cells and are attached to them by junctions of the zonula adherens type. Similar junctions are visible between adjacent retinula cells (Fig. 6). The cone cell processes terminate at or just above the basement membrane. Their function is unknown but it has been suggested that they have a structural role (Horridge, 1966).

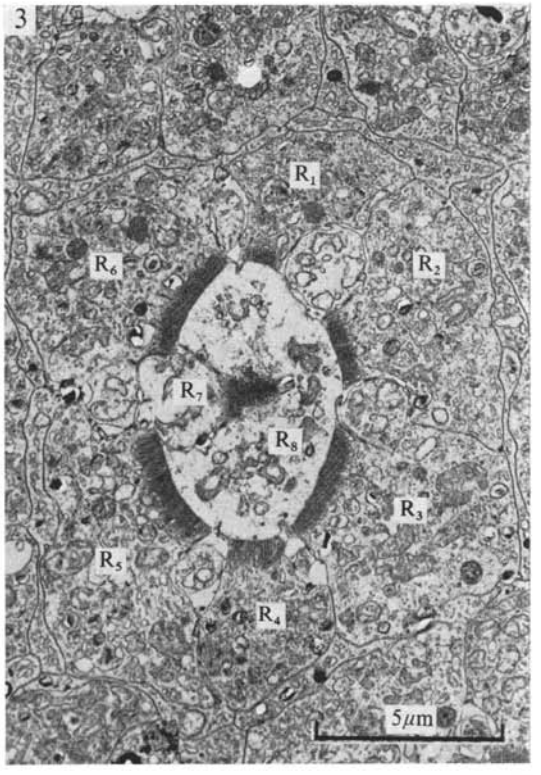
The pigment cells

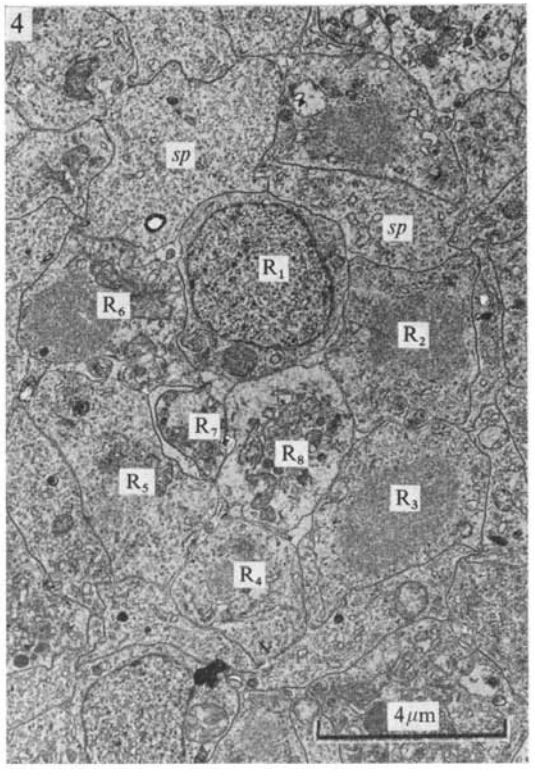
Two primary pigment cells, one dorsal, P_1, and the other ventral, P_2, surround the crystalline cone and the distal extremities of the retinula cells (Fig. 2). They contain sausage-shaped nuclei and the cytoplasm is packed with pigment granules which measure up to 0·7 μm in diameter. Secondary pigment cells fill the spaces between adjacent ommatidia. They extend from the cornea to the basement membrane and effectively isolate each ommatidium from the others. The arrangement of secondary pigment cells is somewhat variable, but on average each ommatidium is surrounded by eight of these cells. However, because they are shared by adjacent ommatidia, there are only four times as many secondary pigment cells as there are ommatidia. Pigment granules are fairly sparsely distributed throughout the cytoplasm and are noticeably smaller (0·4 μm) than the granules in the primary pigment cells. The nuclei of the primary pigment cells are spherical and are situated distally at the level of the crystalline cone.

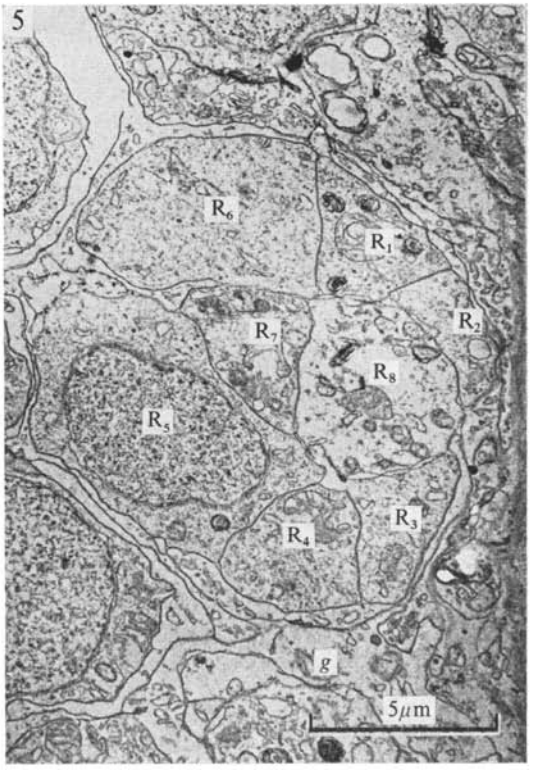
The retinula cells

There are eight retinula cells in each ommatidium forming a column about 13 μm in diameter and 40 μm long. They lie directly beneath the cone cells and extend proximally to the basement membrane. Six relatively large retinula cells, numbered R1–R6, surround a smaller central pair designated R7 and R8 (Fig. 3). The ommatidium is of the open rhabdomere type, the rhabdomeres of the peripheral cells being quite separate from one another. Those of R7 and R8 are fused to form a single central rhabdom which is often arrow-shaped in cross-section and points anteriorly (Fig. 6). The rhabdomeres form the most distinctive feature of the retinula cells and are composed of numerous microvilli between 0·35 μm and 0·7 μm long and approximately 50 nm in diameter. Four of the peripheral retinula cells have rhabdomeres of similar cross-sectional area, those of R1 and R4 are considerably smaller. The retinula cell cytoplasm contains the usual organelles and scattered pigment granules of approximately the same dimensions as those found in secondary pigment cells. The retinula cell nuclei are unusual in their location. In most insects they are situated above


2
P1
CC1
CC2
CC4
CC3
P2
sp
5μm


3
R1
R6
R2
R7
R8
R3
R5
R4
5μm


4
sp
sp
R1
R6
R2
R7
R8
R5
R3
R4
4μm


5
R6
R1
R2
R7
R8
R5
R3
R4
g
5μm

the level of the basement membrane in the proximal part of the retinula cell. In *Oncopeltus* a few are found at this level (Fig. 4), but at least half of them occur below the basement membrane, some as much as 50 μm along the retinula cell axons. Immediately beneath the basement membrane the retinula cell axons are grouped into bundles of eight each enclosed in a glial sheath (Fig. 5).

Thus there are four cell types in the retina, cone cells, primary pigment cells, secondary pigment cells, and retinula cells with a total of 18 cells per ommatidium.

Post-embryonic growth of the retina

The total number of corneal facets at each of the five larval stages was counted in different specimens using photographs of whole retinae, giving the following results: 58, 149, 320, 474 and 593. In the adult the corresponding count was 713. Thus, from the first nymphal stage to the adult there is an approximately 12-fold increase in the total number of ommatidia. The increase arises from the continual addition of new ommatidia to the anterior margin of the eye throughout the nymphal period. In our experiments wild-type epidermis was grafted immediately anterior to the retina of second- and third-stage mutant hosts. In those cases where a successful graft was made sufficiently close to the eye, transplanted tissue became incorporated into the retina. Ommatidia derived from the graft were distinguishable by their red pigmentation in an otherwise white eye (Fig. 7). This experiment shows that epidermal cells of extra-retinal origin are recruited into the eye during growth. In the cockroach, grafts of epidermis from the prothorax can be recruited into the retina (Hyde, 1972).

Dissection of the retina using a mosaic

According to Bernard's (1937) hypothesis each ommatidium is derived from a single stem cell. If this were true of *Oncopeltus* no single ommatidium could contain cells of both genotypes. In our genetic mosaics two cellular markers

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FIGURES 2–5

Fig. 2. A transverse section through the distal region of an ommatidium showing dorsal (P_1) and ventral (P_2) primary pigment cells. They surround the four crystalline cone cells (CC_1–CC_4). Secondary pigment cells (*sp*) separate adjacent ommatidia.

Fig. 3. A transverse section of an ommatidium at the level of the retinula cells showing the open rhabdomere arrangement and the numbering of cells R_1–R_8. The same field is shown at higher magnification in Fig. 6.

Fig. 4. A transverse section of an ommatidium proximal to the rhabdomeres showing a retinula cell nucleus in cell R_1 and the surrounding secondary pigment cells (*sp*).

Fig. 5. A section through a bundle of retinula cell axons proximal to the basement membrane. One cell (R_5) contains a retinula cell nucleus. The axon bundle is enveloped by glial elements (*g*).

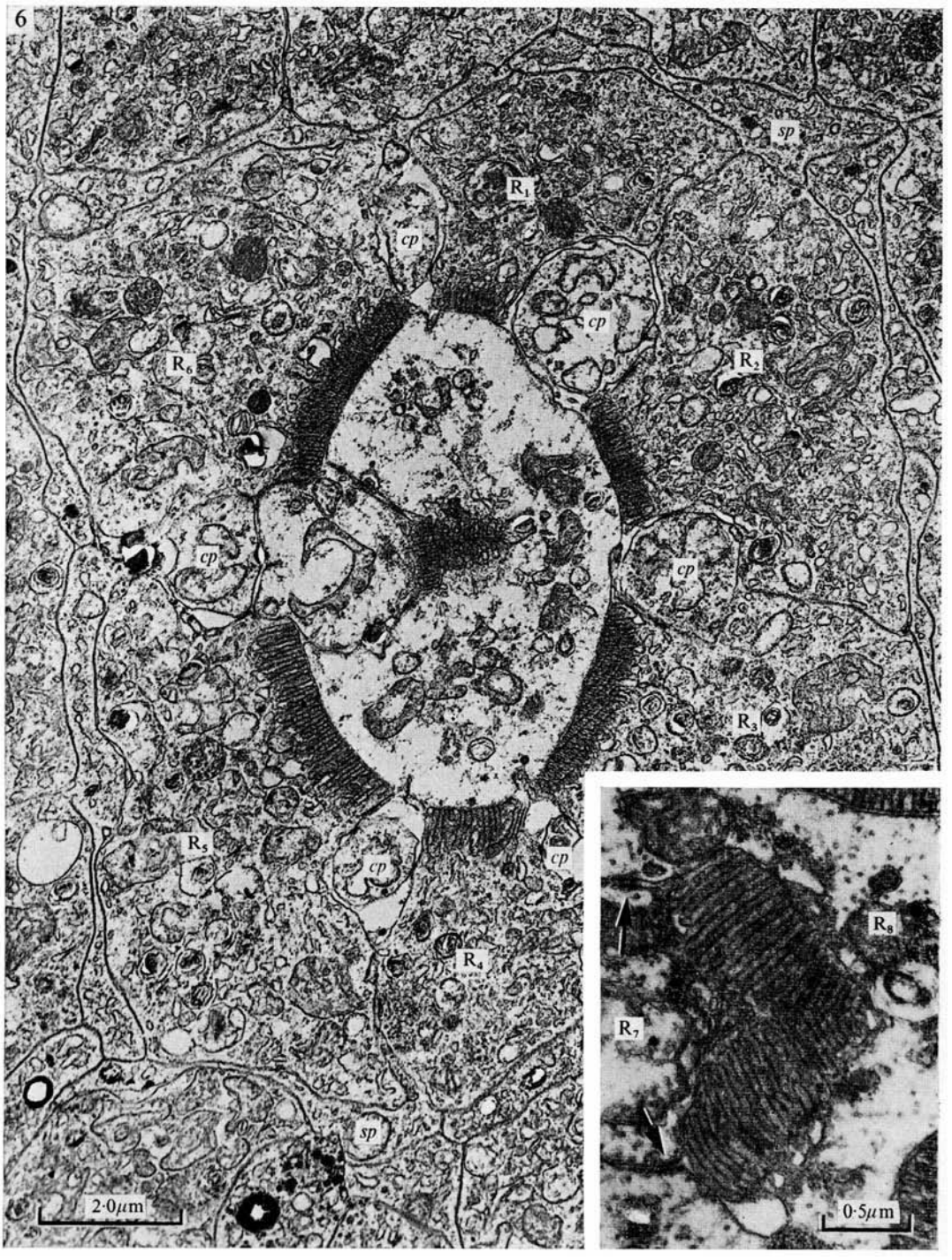


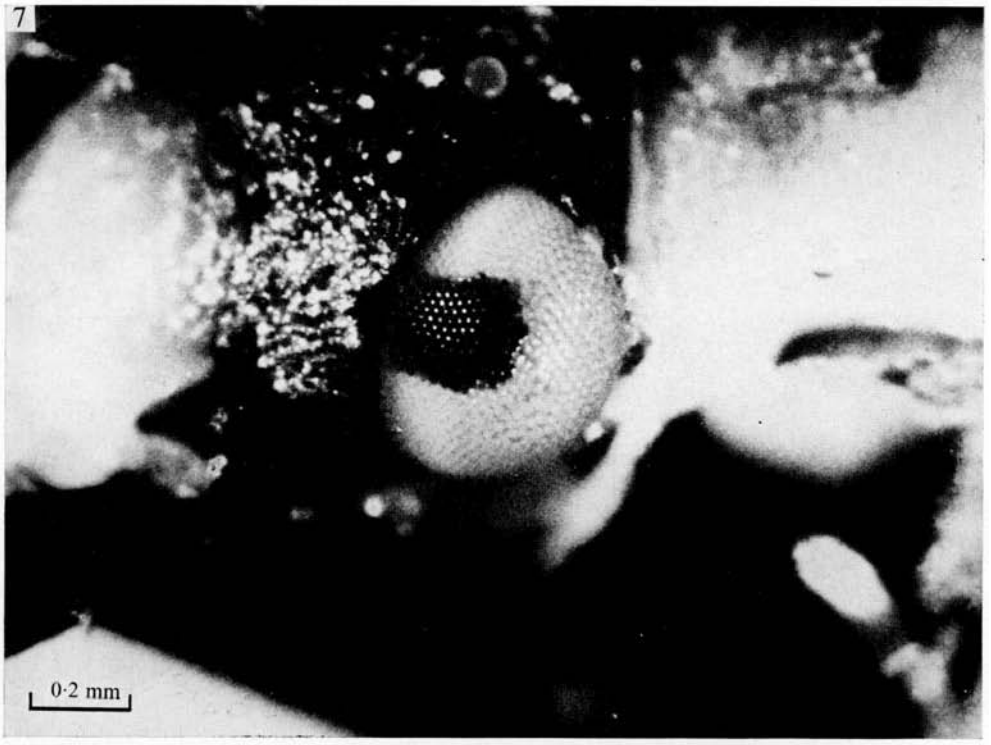
FIGURE 6

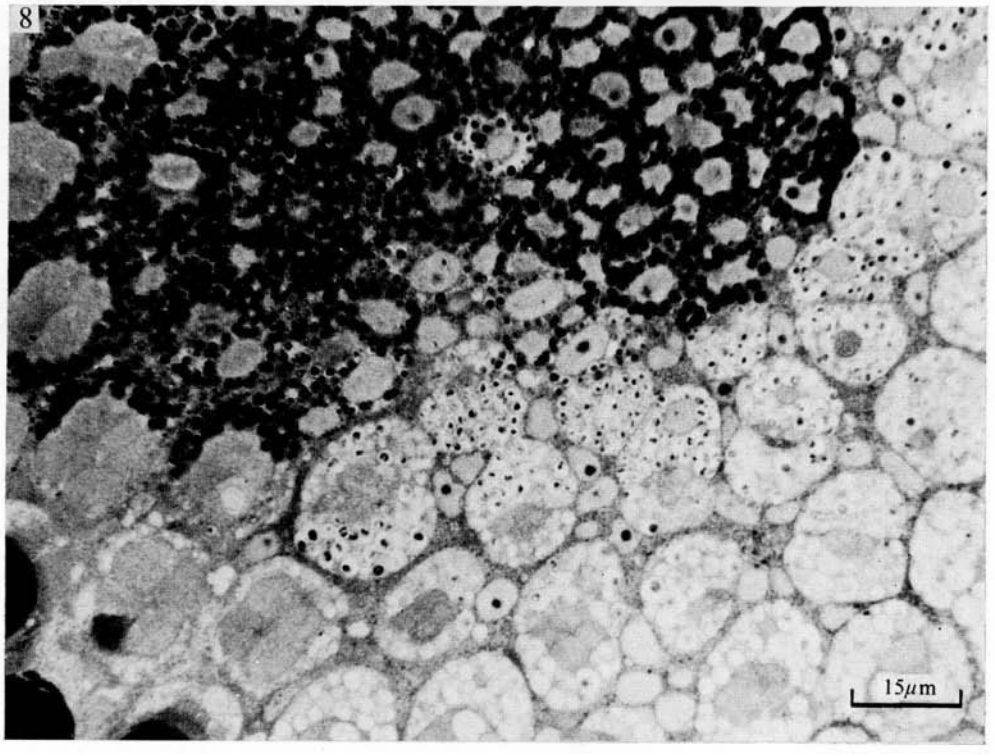
The distal region of the retinula cells shown in transverse section. The rhabdomeres of cells R_1–R_6 are separate from one another while those of cells R_7 and R_8 are fused. Cone cell processes (*cp*) pass between adjacent outer retinula cells. The column of retinula cells is surrounded by secondary pigment cells (*sp*) which it shares with adjacent ommatidia. The inset shows the rhabdomeres of cells R_7 and R_8 in transverse section at a more proximal level where they have an arrow-shaped configuration. Junctions of the zonula adherens type are visible between cells R_7 and R_8 (arrows).

distinguish wild-type from mutant ommatidial cells. First, red pigment granules are abundant in the primary pigment cells of the wild-type but are absent in the mutant. Secondly, the wild-type and double-mutant retinae show differences in rhabdomere thickness. It is somewhat variable between different animals, but in the retina chosen for study the double-mutant rhabdomeres were approximately double the cross-sectional area of those in the wild-type. These differences were consistent in the two parts of the retina. The retinula cell marker is completely autonomous and adjacent retinula cells with different genotypes are clearly distinguishable on the basis of rhabdomere thickness (Figs. 9–11). However, towards the distal extremity of the retinula cells the rhabdomeres of the peripheral cells R_1–R_6 converge towards the centre. At this level transverse sections through the ommatidium cut the rhabdomeres obliquely. Consequently there is an apparent increase in rhabdomere thickness distally. In assessing cell phenotype we were careful to avoid this region. In the case of the pigment cell marker there is some spread of pigment into mutant cells from adjacent wild-type cells (Fig. 8). Nevertheless, since the quantity of pigment spread is small it is easy to distinguish the two phenotypes.

The retina chosen for the analysis is illustrated in Fig. 7. It was oriented so that most ommatidia in the vicinity of the graft were cut transversely, and was serially sectioned at 1 μm thickness. In all 239 ommatidia were examined to determine the genotypes of their two primary pigment cells and retinula cells R_1–R_6. Retinula cells R_7 and R_8 were not considered because their rhabdomeres were fused and too small to permit unequivocal identification. The results are summarized in Fig. 11 and representative microscope fields are shown in Figs. 12 and 13. Ommatidia fell into four broad categories: those in which all eight cells were of the same genotype, either mutant or wild-type; those containing cells of both genotypes; and those which were defective in some way. The latter were localized along the posterior border of the graft, and because these would have been the first to develop after the operation we assume that the damage was caused by wounding. They were characterized by the absence of at least one of the six retinula cells being considered; the primary pigment cells developed normally. Such deficiencies made the numbering of the remaining retinula cells unreliable and we did not attempt to score them. We also ignored ommatidia at the edges of the area when their profiles in section were too oblique for certain identification of retinula cell genotypes.

Of the 239 ommatidia, 41 contained cells of both genotypes. In four cases both primary pigment cells were of one genotype and all the retinula cells were of the other. The presence of such ommatidia demonstrates that there is no direct correlation between the lineages of the cells at the two levels. On 16 occasions the two primary pigment cells within the same ommatidium were of different genotypes, showing that each primary pigment cell can be derived independently of its partner. Inspection of ommatidia containing


7
0·2 mm


8
15μm

separately derived pigment cells confirms the observation that the retinula cell lineage is in no way correlated with that of the pigment cells. At the retinula cell level, lineage is similarly unpredictable. Many different combinations were observed in a total of 27 ommatidia containing both mutant and wild-type retinula cells. Such variability is consistent with the view that retinula cell determination is independent of lineage.

From 418 adult eyes screened after irradiation of eggs aged between 21 and 43 h eight retinae were found to contain clones of ommatidia of a different colour from background. These eyes were fixed and stained, and found to be normal in structure apart from the alteration in pigmentation associated with the clone. In no cases were the retinula cells of the clone different from those of the surrounding retina. However, the primary pigment cells lacked the red pigment and frequently ommatidia were mosaic for these cells.

DISCUSSION

The compound eye of *Oncopeltus* (Lygaeidae) is a typical apposition eye and its anatomy closely resembles that found in other Hemiptera. Each ommatidium contains eight retinula cells arranged on the open rhabdomere plan. Two of these are centrally placed and contribute towards a single fused rhabdomere, six larger cells surround the central pair and their rhabdomeres are separate. Eight retinula cells are also described in *Lethocerus* (Belastomatidae) (Walcott, 1971), but in *Notonecta* (Notonectidae) only one central retinula cell has been observed (Lüdtke, 1953).

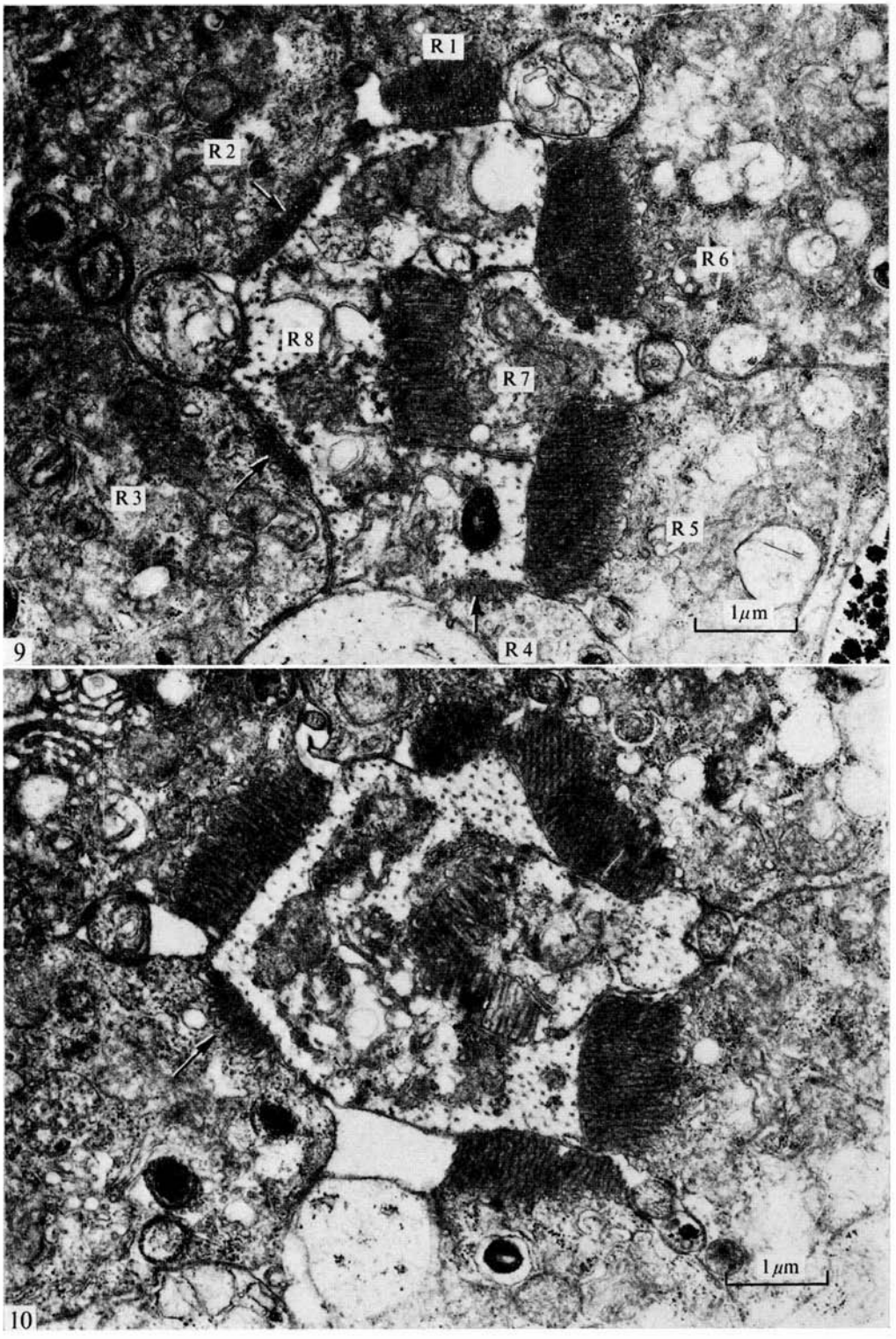
The ommatidia are noticeable for their internal symmetry about the antero-posterior axis. This contrasts with the distinctive asymmetrical pattern of rhabdomeres in Diptera, where the retina is divisible into dorsal and ventral halves so that on either side of an equator the rhabdomere patterns are mirror images. There is no visible equator in *Oncopeltus*.

The literature on the post-embryonic growth of insect eyes is extensive, largely descriptive and is reviewed elsewhere (Bodenstein, 1953; Meinertzhagen, 1973). In *Oncopeltus* there is a 12-fold increase in numbers of ommatidia during the nymphal stages.

FIGURES 7 AND 8

Fig. 7. A photograph of a mutant host retina containing a graft of wild-type pigmented tissue. This particular retina was used in our investigation of cell lineage.

Fig. 8. A section through the retina of a mosaic eye showing the donor/host border at the level of the primary pigment cells. Pigment granules are normally absent in the mutant but in mosaic retinae there is some spread of pigment across the margins of the graft from the wild-type retina. However, the amount of pigment spread is small and it is always possible to distinguish primary pigment cell phenotypes at the margins.



FIGURES 9 AND 10

Transverse sections of genetically mosaic ommatidia near host-graft border (not the same eye as shown in Fig. 7). Note that in Fig. 9, three of the rhabdomeres R1–R6 are wild-type (arrows), the others being mutant.(*wb*/*wb*, *re*/*re*). In Fig. 10 the ommatidium has only one wild-type rhabdomere (arrow).

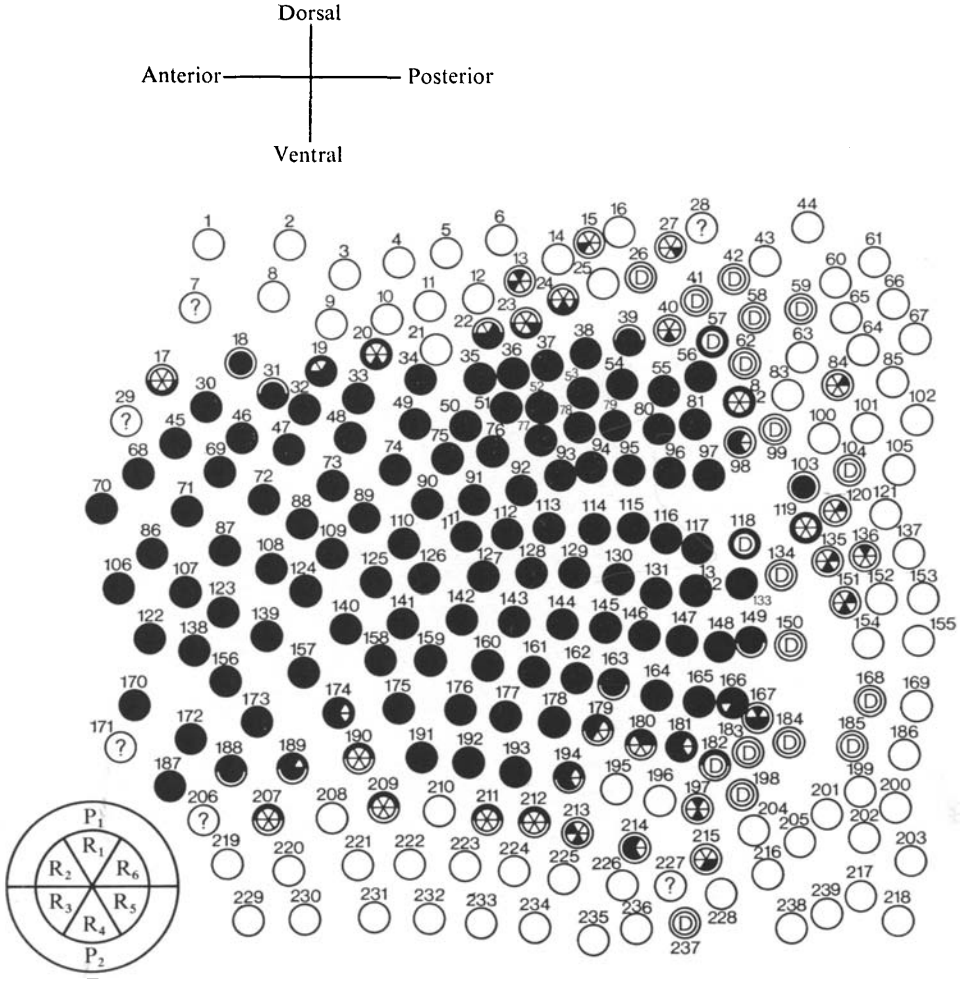


Fig. 11. A schematic map showing phenotypes of retinula cells R1–R6 and primary pigment cells P_1 and P_2 in the mosaic retina chosen for study. Wild-type cells are black and mutant cells are white. Four classes of ommatidia are visible: those where all the cells are of the same phenotype (e.g. 1 and 30), those containing cells of both phenotypes (e.g. 17 and 22), those which were defective (e.g. 57), and those sectioned too obliquely for analysis (e.g. 171). The numbering of ommatidia is entirely arbitrary.

We confirm the results of grafting experiments with mutants of *Culex* (White, 1961, 1963) and *Periplaneta* (Hyde, 1972) which indicate that the proliferating anterior border of the eye is an area of recruitment rather than a budding zone as proposed by Bodenstein (1953).

In our grafts we found some spread of pigment from the graft into the host at the margins of the transplant. Presumably, either pigment itself, or more probably some precursor molecule, can diffuse in small quantities from

15μm
214
213
212
211
210
197
195
196
194
193
192
191
182
180
181
179
178
177
176
165
164
163
162
161
160
159

13

15μm
214
213
212
197
196
195
194
193
182
180
181
179
178
177
165
164
163
162
161

12

one cell to another. In *Periplaneta* Hyde (1972) has demonstrated metabolic co-operation between the cells of two mutants (*pearl* and *lavender*) which results in the eventual spread of normal amounts of wild-type pigmentation in the *pearl* tissue. These observations and ours show that significant intercellular exchange of molecules can occur.

Our principal result concerns the non-clonal origin of cells within a single ommatidium. This has been shown in genetic mosaics generated in two ways, by grafting and by X-irradiation. Since Bernard's (1937) descriptive study of eye growth in *Formicina* it has been assumed that each ommatidium is derived from a cluster of cells formed by determinative divisions of a single stem cell (Kühn, 1965; Weber 1966). The occurrence of ommatidia containing cells of mixed lineages in mosaic retinae shows that this is certainly not the case for *Oncopeltus*. Similar work on *Drosophila* has recently shown that the ommatidia are not clonally derived (Hanson *et al.* 1972; Benzer, 1973). In *Oncopeltus* the variability of cell lineages in mosaic ommatidia rules out the possibility that particular classes of retinal cells are clonally derived. We are forced to conclude that cell determination within ommatidia is in no way connected with their lineage. Ommatidia which contain only one scorable cell of a different genotype from the remainder are quite frequent (e.g. nos. 40 and 166 in Fig. 11). This cell occupies no particular locus; possibly therefore most mitoses have been completed prior to the formation of ommatidial clusters. We do not know when determination occurs, but the fate of the cells must be decided depending on the position they occupy in the developing ommatidium.

In insect pattern formation there are other examples where one cell will induce the development of other cell types in clonally unrelated tissue nearby. One clear example is the development of a bract near to certain types of *Drosophila* bristle (Peyer & Hadorn, 1966; Tobler, Rothenbühler & Nöthiger, 1973). Marcus (1962) showed that in *Galleria* grafting of small groups of segment margin cells into the main part of the segment (see Lawrence, 1970*b*) induced the host cells to form different types of scales and other structures

FIGURES 12 AND 13

Fig. 12. Selected field at the level of the primary pigment cells showing part of the donor/host border in the retina chosen for study. The numbering of ommatidia corresponds to that in Fig. 11. In some ommatidia the dorsal primary pigment cell is of the wild-type and the ventral cell is mutant (e.g. 179, 180, 182, 194 and 212).

Fig. 13. This micrograph shows a corresponding field at a more proximal level. The wild-type retinula cells have rhabdomeres of approximately half the cross-sectional area of those in mutant cells. Some ommatidia contain both classes of retinula cell (e.g. 179, 180, 181, 194 and 213), some contain either only wild-type cells (e.g. 161 and 178) or only mutant cells (e.g. 210 and 211). The micrograph also demonstrates the necessity for examination of retinula cell phenotypes at several levels. 214 contains retinula cells of both phenotypes but at this level, which is close to the distal extremities, rhabdomere thicknesses are indistinguishable (see text). Fixation damage is responsible for the clear areas.

whose polarity was also dependent on the orientation of the graft (Piepho & Marcus, 1957). The component cells of ommatidia are very precisely arranged in a polarized group and it may be of general interest that an interactive mechanism, rather than a lineage mechanism, can achieve sufficient precision.

We thank Sheila Green and Carol Orme for extensive help in preparing the electron micrographs and Graeme Mitchison for help with the MS. The work was supported in part by a Science Research Council grant to P. M. J. Shelton.

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(*Received 14 December 1973*)