

The ommatidium of the dorsal eye of *Cloeon* as a specialization for photoreisomerization

BY G. A. HORRIDGE, F.R.S.

*Department of Neurobiology, Australian National University,
Box 475, P.O., Canberra, A.C.T. 2601*

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[Plates 1-5]

The turbanate dorsal eyes of *Cloeon* have thin biconvex corneal facets, large crystalline cones, and long retinula cells which cross the clear zone. There is no large-scale movement of screening pigment upon adaptation. The combination of anatomical features suggests that the eye operates with high visual acuity because the corneal lens is focused on the tip of the cone, from which light is guided by the retinula cell column across the clear zone. By this means the eye could function near the diffraction limit. The suggestion that the main visual path is by light guides has some experimental support from examination of embedded slices of the eye, but leaves no function for the clear zone, as there is negligible movement of pigment upon light adaptation.

A clue to the function of the clear zone is provided by the unique appearance of a distal collection of rhabdom microvilli which are formed by all seven retinula cells around the tip of the crystalline cone. This distal rhabdom necessarily acts as a filter for light which crosses the clear zone. It is suggested that this light is utilized in the photoregeneration of the visual pigment *after* the effective visible wavelengths have been reduced. Filtering at this level could prevent unfocused regenerative rays, which cross the clear zone, from interfering with the angular sensitivity of the receptors. In other clear zone eyes, screening pigment around the cone tip could similarly serve a double function by acting as the aperture of the light guide and at the same time transmitting photoregenerative rays which cross the clear zone outside the light guides.

INTRODUCTION

In several quite separate groups of mayflies the compound eyes of the male have a specialized dorsal part which can cover the whole of the dorsal region of the head. These are sometimes called 'turbanate' eyes. In contrast, the eyes of the female are small and simple, resembling the lateral part of the eye of the male. The significance of the enlarged dorsal eye is not certain. The sexes dance in swarms at dawn or dusk, rarely in bright sunlight and the obvious presumption is that the male sees the swarm and catches the female visually on the background of the clear sky. As in many insects which are active in dim light, the dorsal part of the

eye has a wide clear-zone between the crystalline cones and the receptor layer (Zimmer 1897). This arrangement has for many years been interpreted as indicating that a superposition image is formed on the receptor layer by an afocal combination of lenses in the cornea and crystalline cone (Exner 1891). That theory certainly applies to some types of eyes with clear zones, but not necessarily to all. Clear zone eyes prove to be diverse (Horridge 1975*a*) and each must be examined on its merits. The first step is to redescribe the anatomy, because the pioneer work of Zimmer, and the redescription of Streble (1960) by light microscopy, are no longer adequate as an anatomical basis for the study of the peculiar dorsal eye of this group of mayflies.

From the outset it should be made clear that although this type of ommatidium found in *Cloeon* may be typical of Baetoidea, a completely different type of mayfly ommatidium occurs in the enlarged dorsal eyes of male *Atelophlebia* (Leptophlebioidae), of which preliminary notes have already appeared (Meyer-Rochow 1971; Horridge 1975*b*).

METHODS

Larvae of the locally common species of *Cloeon* were collected in streams near Canberra and, for convenience, reared to adults in the laboratory. There are problems in identifying the common Canberra species of *Cloeon*, and possibly more than one species is involved. However, it seems unlikely that the eye structure will be diverse in a genus which is so homogeneous that species identification is a major difficulty. Pieces of the eye were cut in the primary fixative at pH 7.35 at room temperature, and left overnight at 4 °C. They were then rinsed in buffer and postfixed in 2% OsO₄ in buffer for 2 h at room temperature. The primary fixative was 2% paraformaldehyde and 2.5% glutaraldehyde in Millonig's buffer, which consisted of 83 ml of 2.25% sodium monobasic phosphate and 17 ml of 2.52% NaOH solution. Some material was also satisfactorily fixed in this fixative to which had been added 1.2 g of D-glucose and 1 ml of 1% CaCl₂ per 100 ml. These fixatives were the most satisfactory that could be found over a period of five years, during which numerous standard e.m. fixation methods were tried in succession, season after season. After treatment in the osmic buffer, the tissue was washed in buffer, dehydrated in an ethanol series, embedded in Araldite, cut with a diamond knife and picked up on Formvar-coated grids. Staining was with uranyl acetate in methanol for 30 min followed by lead citrate for 12 min according to the formula of Venable & Coggeshall (1965).

RESULTS

Anatomy

The general plan of the ommatidium, with sections at various levels, and a key to the locations of the electron micrographs, is set out in figure 1.

The cornea is thin and composed of numerous layers (figure 2*a*, plate 1). As discovered by Bouligand (1965) and described in terms of molecular architecture

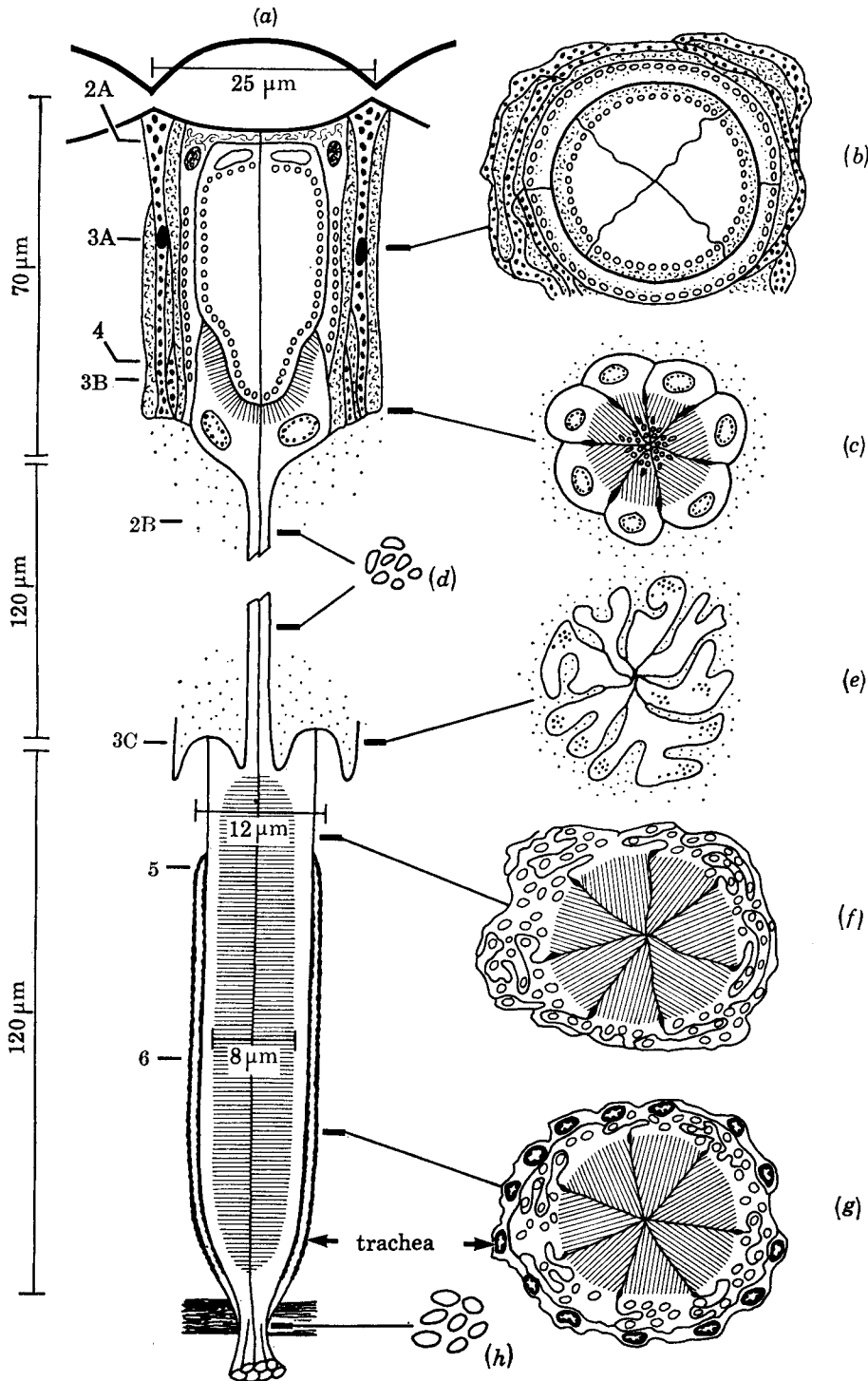


FIGURE 1. The ommatidium of *Cloeon* dorsal eye. (a) In longitudinal section. (b-g) Transverse sections at the levels indicated. The arabic numbers on the left show the figure numbers of the electron micrographs taken at these levels. (b) Crystalline cone; (c) distal rhabdom; (d) retinula cell columns; (e) broadening of retinula cells proximal to the clear zone; (f, g) proximal rhabdom; (h) seven retinula cell axons at basement membrane.

by Neville (1967), the layers are caused by the spiral arrangement of the chitin micelles. The appearance of the layers and the distance between them is exactly as in insects which secrete their cornea slowly, although in *Cloeon* the imago cuticle follows that of the subimago by less than a day. The diameter of the facets is 18–20 μm ; the radius of curvature of the corneal facet surface is $20 \pm 2 \mu\text{m}$ and the length of the cone 60 μm . Therefore if the refractive index, is similar to that for other cornea material (1.5 ± 0.05) a first inverted image must be formed inside the cone near the tip.

Two principal pigment cells surround the crystalline cone (figure 1; figure 3a, plate 2). There is only one pair of these: their nuclei lie beneath the cornea: the cell bodies are in contact with the cornea. The cytoplasm of these two cells fills the space between the cornea and crystalline cone. No trace has been found of other cells that can be related to the corneagenous cells of Crustacea. An early controversy on this topic (Hesse 1901) has been settled in favour of the view that the two principal pigment cells of the insect ommatidium are equivalent to the two corneagenous cells of crustaceans (Paulus 1972, p. 43) and no examples have both. The ommatidium of *Cloeon* fits this scheme.

The principal pigment cells are notably clear and watery immediately around the cone, as if to generate a sharp discontinuity of refractive index. In this layer, and against the cone cells, there are scattered microtubules lying separately in the clear cytoplasm. Numerous mitochondria and pigment grains are pressed against the outer margin of the principal pigment cells (figure 3a). The pigment grains are smaller, less numerous and less electron-opaque than those of the accessory pigment cells. This is unusual, because in compound eyes of most insects, where the principal pigment cells form a screen around the cone and often limit the aperture at the cone tip, they are filled with electron-dense pigment grains that are larger than those of the accessory pigment cells.

The accessory pigment cells are small, short, and for much of their length isolated from each other by an extracellular matrix (figure 3a), which has not been found in other insect eyes. Their pigment grains under the electron microscope are the most electron-dense in the eye but even so are less dense than those commonly found in insects (see figure 2a, plate 1). Their nuclei are small in transverse section and mainly at one level (figure 1a). Extension of these cells reach to the cornea in the angles between the biconvex lenses (figure 2a). They extend proximally only as far as the level of the rhabdom around the cone tip.

DESCRIPTION OF PLATE 1

FIGURE 2. Optical components. (a) Longitudinal section in the angle between two lenses of the cornea, showing the pigment-containing accessory cells (a.p.c.) and clear cytoplasm of the principal pigment cell (p.p.c.) around the cone. (b) Transverse section of the seven elements of the retinula cell column in their natural spacing on the non-cellular background of the fluid which fills the clear zone. (c) Light micrograph of a thick Araldite section cut across the clear zone showing that individual retinula cells can act independently of each other as light guides. (Photograph by Dr W. Ribi.)

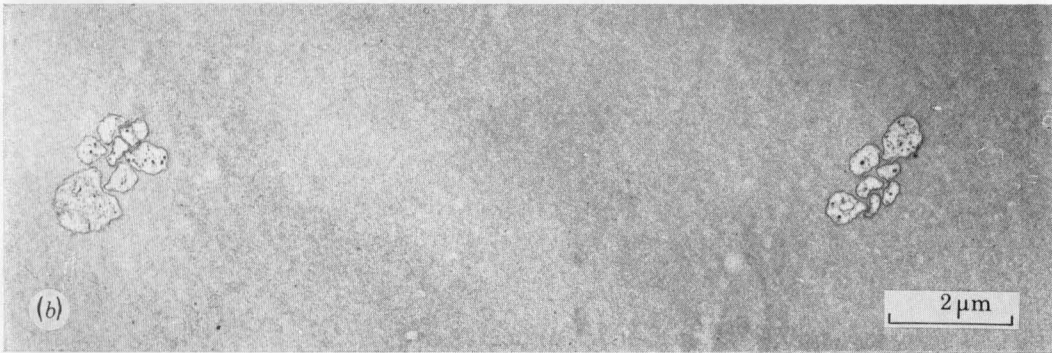
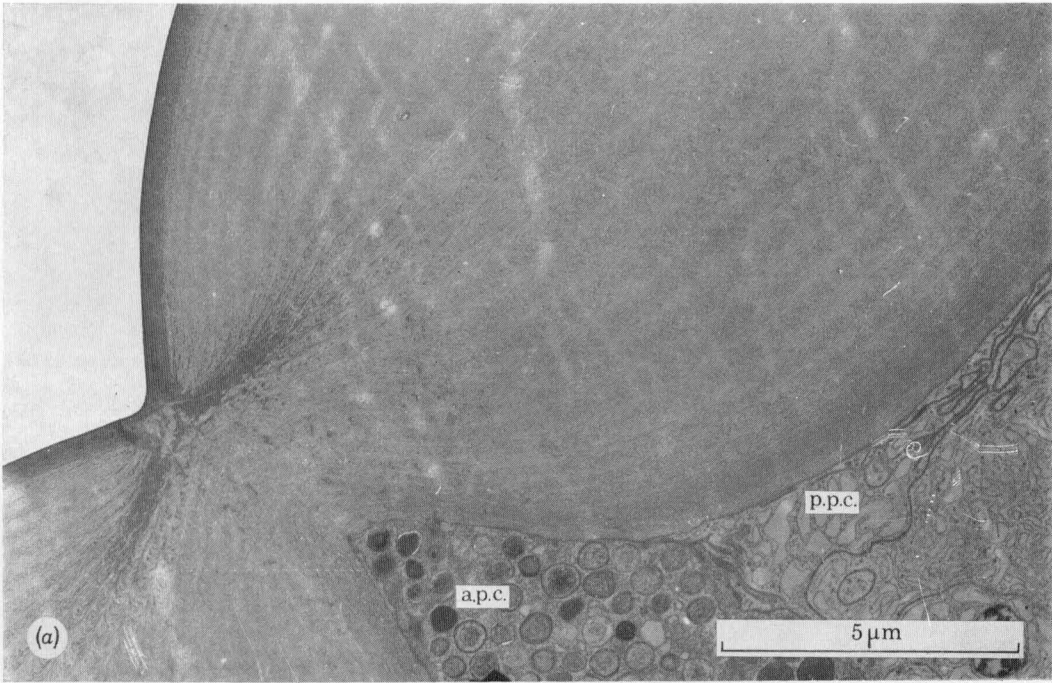


FIGURE 2. For description see opposite.

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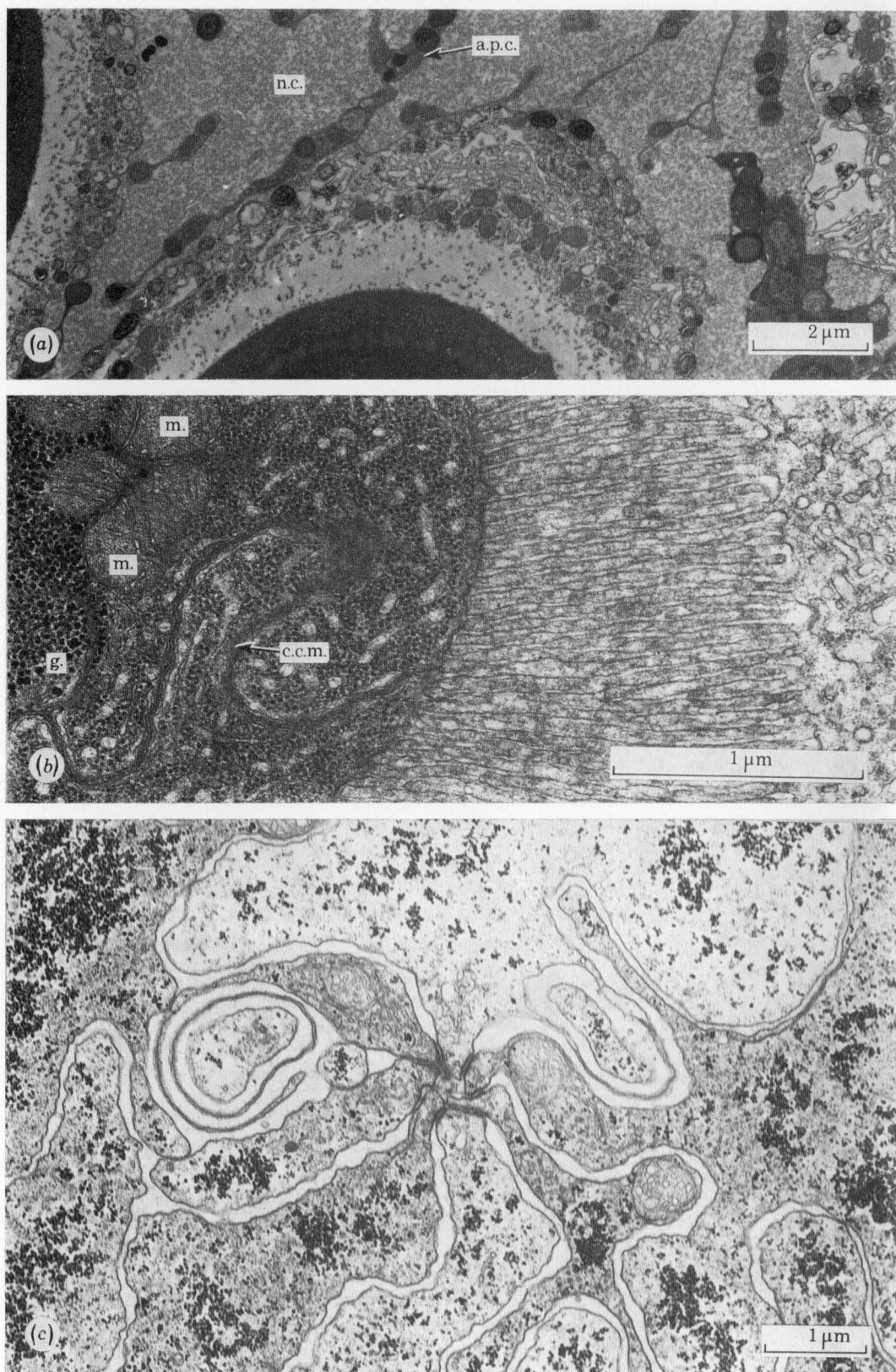


FIGURE 3. For description see opposite.

As shown by light microscopy this pigment layer forms an effective lateral barrier for visible light between the ommatidia at this level, a point which makes all the more significant the unusual anatomy at the cone tip.

The crystalline cone is more complex than in most insects. The entire central region is crowded with granules, shown on the extreme left of figure 3*b*. Similar granules have been inferred to be glycogen in the bee (Perrelet 1970), and occur in the whole central region of the cone in many insects. Around this granular core is a coat formed by a single layer of mitochondria. These are faintly seen in figure 3*a* and four of them occur in figure 3*b*. Outside this is a layer of curious endoplasmic reticulum in the form of tubular membranes, smaller than mitochondria and larger than microtubules, separated by granules which are smaller and less dense than those in the centre of the cone. The tubes are seen mainly in cross-section in figure 3*b*, but their elongated shape can be seen in the centre of figure 4, plate 3. A study of this region suggests that these worm-like bodies are a specialized form of endoplasmic reticulum that is synthetically active in the formation of the granules that fill the cone.

The four cells of the cone meet at a boundary which is seen as a sinuous line in sections (figure 3*b*). Between the membranes of the cone cells is a layer which appears dark in sections, as if there is a thin sheet of material between the cell membranes. Towards its tip the cone narrows suddenly as shown in figure 1*a* and from this point to the tip it is surrounded by rhabdomeres of all seven retinula cells (figure 4). At this level the cone is so narrow that the layers of its internal coating displace the granular core, leaving only the mitochondria and endoplasmic reticulum. Principal and accessory pigment cells do not extend proximally beyond this level even in bright light (figure 1*a*).

The most remarkable feature of this eye, which distinguishes it from all compound eyes so far described, is the rhabdom formed around the tip of the cone by the distal ends of the seven retinula cells (figures 1*a*, 3*b*, 4). As shown by successive sections from the same block, this distal rhabdom has a three dimensional radial structure so that light passing through its centre is parallel to the microvilli. The shape shown in figure 1*a* can be seen in longitudinal sections. Therefore, if coloured this rhabdom must act as a graded filter. The seven retinula cells have their nuclei around the tip of the cone at this level. Their long narrow cell bodies reach across the clear zone (figures 1, 2*b*) as previously described by Streble (1960). Where they

DESCRIPTION OF PLATE 2

FIGURE 3. (*a*) Non-cellular material (n.c.) surrounding the accessory pigment cells (a.p.c.) in the region between the cones, in cross-section at the level of the accessory pigment cell nuclei. (*b*) On the left are the densely packed components of the tip of the crystalline cone; on the right is the distal rhabdomere of a retinula cell. g, Granules resembling glycogen; m, mitochondria; c.e.m., membrane between two of the four cone cells. (*c*) Transverse section just grazing the proximal edge of the clear zone, showing the retinula cell column as it runs into the layer of proximal rhabdoms.

meet the cone cell membrane, outside the rhabdomere region, the retinula cells form thickened membranes that resemble desmosomes, but along the line where each retinula cell meets its neighbours at the limit of its rhabdomere there is the typical elongated narrow desmosome (d. in figure 4) that occurs like a seam between retinula cells at the boundary of the rhabdomeres in all insect eyes. No physiological conclusions about electrical coupling between retinula cells can be drawn from the presence of these desmosomes, as they occur in all compound eyes irrespective of the degree of electrical coupling where that has been measured. A notable feature is the paucity of mitochondria in the retinula cells at this distal level (figure 4).

Below the cone the seven retinula cells stretch across a clear zone which is $150 \pm 10 \mu\text{m}$ in width, forming a highly refractile bundle that is so loose that the individual cells are not in contact in many of the sections (figure 2*b*).

Where the retinula cells touch each other in this region they form desmosomes at some places, but never a fused column as in moths, night-flying beetles and other neuropteroid insects with clear zone eyes.

Another unique feature of this eye is that the fluid matrix of the clear zone is continuous with the intercellular space and therefore with the haemocoel. In other insect orders the clear zone is always entirely occupied by pigment-free regions of accessory pigment cells, often with a migration of pigment grains within the cells on adaptation to light. In *Cloeon*, however, it is evident that screening pigment cannot spread in the same way across the clear zone because it is not cellular. This fluid-filled space penetrates between the accessory pigment cells (figure 3*a*) and for a short distance between the loose folds of the retinula cells where they begin to form the rhabdom columns on the proximal edge of the clear zone (figure 3*c*).

At the proximal side of the clear zone is the main receptor layer, formed by columns of rhabdoms. Each rhabdom column, $130 \pm 10 \mu\text{m}$ in length, is formed by the proximal rhabdomeres of all seven retinula cells of the ommatidium. The microvilli are parallel within each rhabdomere and orientated approximately radially. The desmosomes where the retinula cells meet each other at the boundary of the rhabdomeres (d. in figure 5, plate 4), continue around the end of the rhabdom column to the base of the retinula cell column (figures 1*e*, 3*c*). The distal parts of the rhabdom columns are not surrounded by sheaths of pigment grains or tracheae (figure 5). This feature affects the optics of the eye in that there is no structure which can isolate the rhabdomes of adjacent ommatidia optically. The rhabdom itself is not surrounded by a palisade or low density region of the endoplasmic reticulum which could improve the performance of the rhabdom as a light guide and increase its optical isolation. Instead, the cytoplasm around the rhabdom is crowded with membranes and mitochondria (figure 5) which presumably increase the refractive index around the rhabdoms. Therefore rays within a small critical angle may be held within the rhabdom but rays at larger angles to the axis must pass through the rhabdom and out the other side. The retinula cell membranes are



FIGURE 4. Transverse section near the bottom of the crystalline cone, showing the components of the cone and the distal rhabdomeres. d., Desmosomes.

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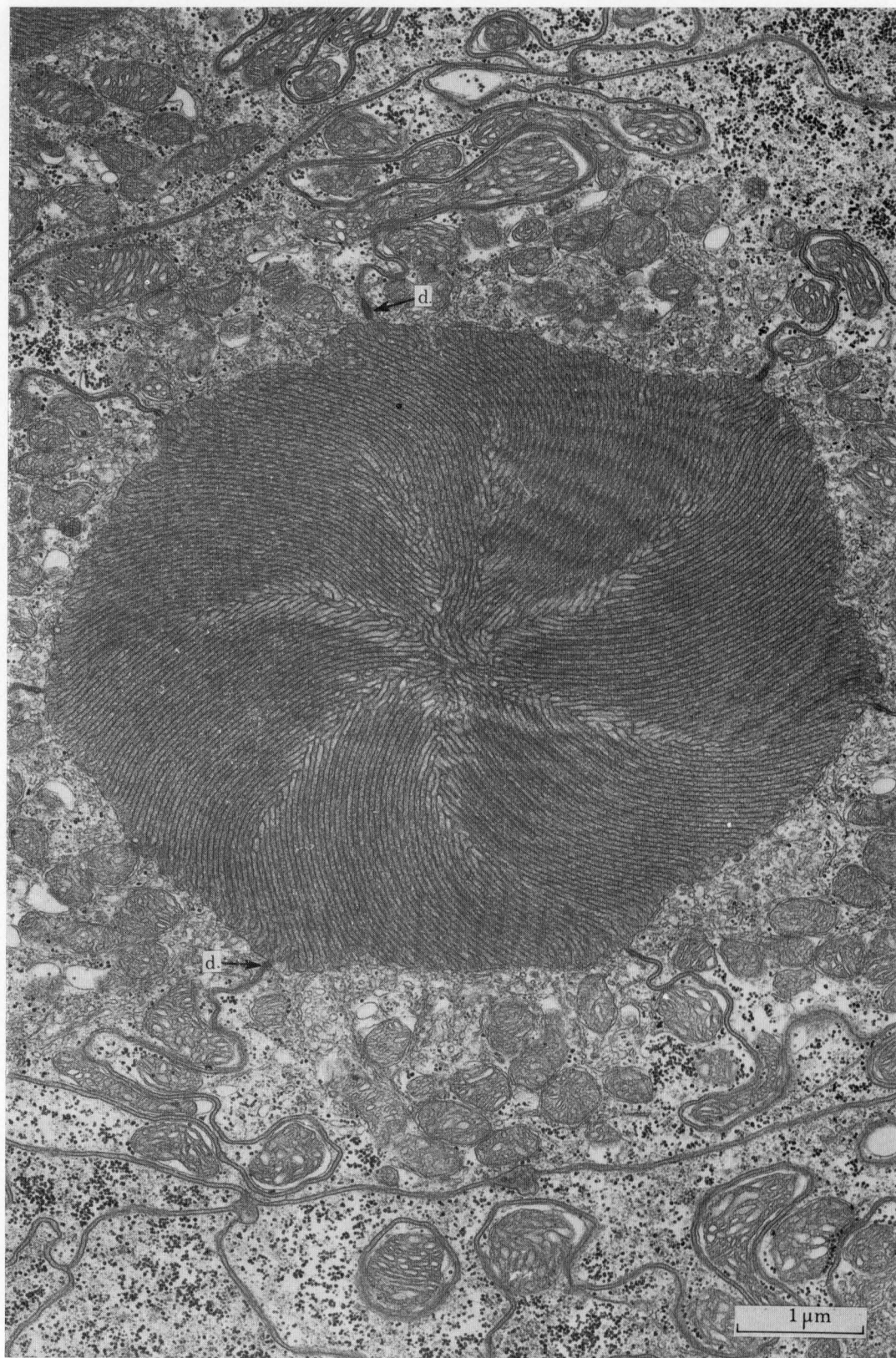


FIGURE 5. Transverse section through the proximal rhabdom, peripheral to the trachea showing the seven sections, and the seven desmosomes (d.) where the retinula cells meet at the boundary between cytoplasm and rhabdom.

highly convoluted throughout this region of the eye but the significance of this detail is not apparent. No pigment cells can be found at this level or through most of the rhabdom column region. Between this layer and the cones the retinula cells are the only cells seen in transverse sections. The retinula cell cytoplasm is characterized by clumps of granular material (figures 3c, 5).

On the proximal part of the rhabdom columns the retinula cells are surrounded by a loose ring of rather small tracheae (figure 1g; figure 6a, plate 5). These are far apart, not flattened or specialized by having large numbers of parallel plates as in many Lepidoptera, and therefore cannot be regarded as optically significant. For this reason alone it seems doubtful whether *Cloeon* could utilize a superposition image even if one were thrown on the proximal surface of the rhabdom layer, because the layer is 120 μm deep and not adapted to preserve the separate elements in an image cast by oblique rays. Before this can be shown, however, optical examination of the isolated rhabdom layer of *Cloeon* is necessary.

The retinula axons pass out of the eye through the basement membrane in groups of seven. Between the bases of the rhabdoms and the basement membrane there is a layer about 10 μm thick in which the retinula cells are filled with large pigment grains as they narrow to form axons. This pigment moves a few micrometres distally in the light and proximally in the dark, as Streble (1960) reports. In the same region there is an obvious ring of 12–16 tracheae round each axon bundle. Each trachea appears to have its own cell body and nucleus at this level, incorporated in the glia of the axon bundle. A large glial cell nucleus is associated with each axon bundle below the basement membrane. No other cells, branches of retinula cells or axon terminals of other neurons have been found in the retina.

The retinula cell columns as light guides

The living eye is extremely fluid, difficult to cut, and so far has proved impossible to examine optically. No doubt this difficulty is caused by the non-cellular fluid nature of the clear zone. Therefore the retinula cell columns were examined embedded in Araldite. This procedure is not entirely satisfactory because the refractive index of the column is altered by extraction of the salts and lipids, and the ratio of refractive index between its inside and outside is altered by the loading of both with the resin. However, the embedded retinula cell columns have the appropriate dimensions and sufficient residual protein to act as light pipes, as shown in figure 2c, plate 1. As they do this after some of their components have been washed out, and with the refractive index differential reduced by the resin, they are likely to act as light guides in the living eye. The retinula cell columns are described by Streble (1960) as highly refractile threads 1 μm thick. In the mayfly *Atelophlebia*, which also has large dorsal eyes in the male, the crystalline cone is almost homogeneous, so that with only the single lens formed by the thin cornea of each ommatidium, the eye does not have the optical components necessary to form a superposition image.

In *Cloeon* there is no migration of pigment across the clear zone and no evidence

of any change on dark adaptation. The relative intensities of light held in the retinula cell column as a light guide and light freely crossing the clear zone are not under control by pigment, so that the eye is necessarily adapted to a rather narrow intensity range. The retinula cell columns therefore do not have the function of carrying the light through a pigment screen which forms in the clear zone when the eye is light-adapted, as in typically the situation in fireflies and most beetles and moths that fly in dim light. One must infer that the retinula cell columns conduct a significant fraction of the total light when not surrounded by pigment. Perhaps more significant, the light-guides provide the only obvious mechanism whereby vision can be sharp, and the capture by males of females in flight suggests that sharp vision in dim light is at a premium in these animals. If vision functions via the light guides, then the problem is to find a selective advantage for the clear zone, for the eye would function just as well if the rhabdoms started at the cone tips.

DISCUSSION

The layer of rhabdom around the tip of the cone is a feature in the *Cloeon* ommatidium new to the structure of compound eyes. This structure suggests a significance of filtered unfocused light in clear zone eyes.

The enormously enlarged dorsal eyes of *Cloeon* appear to assist the male to find the flight swarm and to catch the female in flight. Insects with enlarged *dorsal eyes* always seem to use them to catch small objects against the sky. To do this most effectively the eye must have a spectral sensitivity to match the background and an angular sensitivity as narrow as possible. There are two possible ways in which an eye with a clear zone can have high angular sensitivity: either parallel axial rays must be accurately focused upon the distal end of the light guides in the clear zone, or else there must be a second lens which focuses a second image exactly on the distal ends of the rhabdom and, the latter must be optically isolated from each other. The anatomy favours the first of these alternatives. For a review of the diverse types of compound eyes, and the background of this argument, see the review by Horridge (1975*a*).

If we infer, as the anatomy suggests, that *Cloeon* sees by the rays passing down the light guides, we have to explain how it is an improvement upon an apposition eye. To function against a dim blue background the eye would need maximum

DESCRIPTION OF PLATE 5

FIGURE 6. Trachea and mitochondria around the rhabdom columns in relation to the optical isolation of ommatidia. (a) Transverse section through the lower part of a rhabdom column showing it to be surrounded by numerous mitochondria and a single layer of small unspecialized trachea. (b) The same region in LS between two rhabdoms which are unusually close together. There are none of the typical specializations which could ensure the optical isolation of ommatidia at this level.

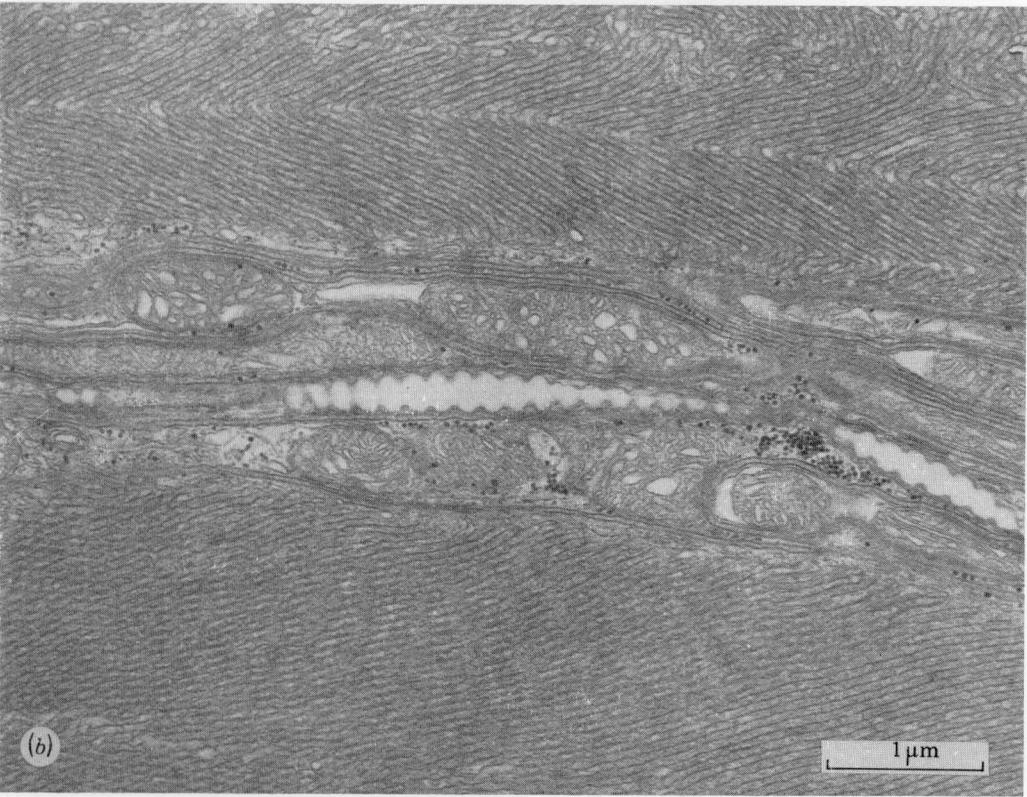
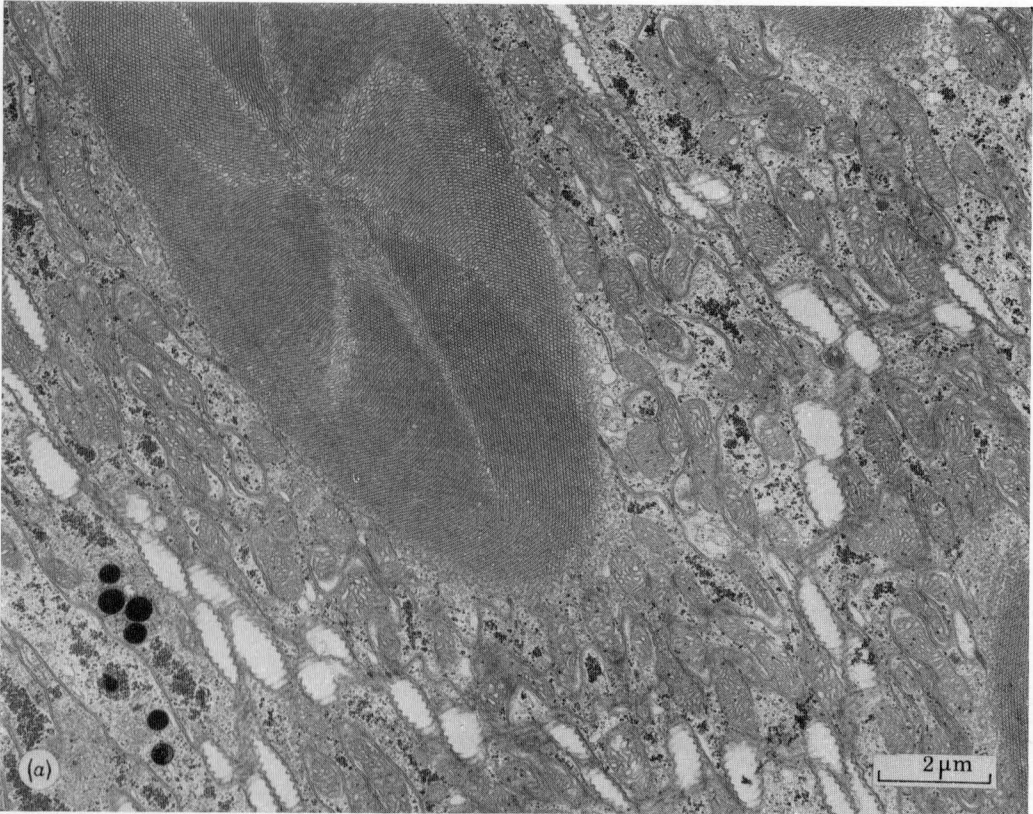


FIGURE 6. For description see opposite.

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sensitivity at the short wavelength end of the spectrum. Insects have available a mechanism which increases sensitivity by photogeneration of the visual pigment rhodopsin from its photoproduct metarhodopsin (Hamdorf, Paulsen & Schwemer 1973). For blue and u.v.-sensitive pigments, absorption of longer wavelengths increases the sensitivity and signal/noise ratio by increasing the percentage of visual pigment in the rhodopsin form. Although this non-seeing function of the long wavelengths has been demonstrated for several years, no optical mechanism have yet been found for making best use of them in clear zone eyes with least interference to the seeing mechanisms.

The anatomy of the *Cloeon* ommatidium makes sense on the theory that parallel axial rays are focused exactly on the distal end of the light guides, so that a narrow field of view results. Rays from other angles falling outside this small target comprise most of the light falling on the eye, and this light is available for photoregeneration if it can be prevented from interfering with the acuity of vision. The off-axis light is necessarily filtered as it passes through the distal rhabdom. *The most appropriate filter around the cones to remove those rays that would be seen by the effective visual pigment is either the same rhodopsin as in the proximal rhabdoms, or a screening pigment with the same absorption spectrum (figure 7).* In the present case, at the cone tip, the distal rhabdom has its microvilli *along the axis*, so that here it will have least absorbance if we assume that the visual pigment dipoles are in the plane of the membranes. Further requirements of this theory are that (a) the distal rhabdomere should be ineffective as a receptor, so that it cannot broaden the effective visual field of each retinula cell, and (b) the distal pigment should be of the appropriate density to act as a filter. Less obviously, the distal pigments must be stable to light, and not change to a colour specific equilibrium with metarhodopsin, as this would nullify its effect on the main rhabdom layer. Finally, this type of eye combining acuity and sensitivity, is not compatible with colour vision over a wide range of wavelengths.

The distal filter need not be a rhabdom, but could equally well be a distinct screening pigment. Also the photoregenerative light does not need to be focused. A wide clear zone with long light guides then makes possible (a) sensitivity to a wide range of intensity because a long sleeve of attenuating pigment can reduce the effectiveness the light guides as the eye becomes light-adapted and (b) a high acuity path for visual light in each light guide, while suitably filtered photoregenerative rays are free to cross the clear zone (figure 7).

This theory explains many previously inexplicable details of clear zone eyes of some Lepidoptera, Trichoptera, Neuroptera and Ephemeroptera, especially those like *Cloeon* or *Chrysopa* which have red or yellow eyes. A number of these have retinula cell columns or crystalline tracts and pigment in the appropriate situation, as in figure 8a. For example, looking again at the ommatidium of *Ephestia*, we find that in the dark-adapted eye (figure 8b) a separate retinula cell pigment stands across the light path for rays crossing the clear zone in the dark-adapted eye, while a central thread of rhabdomere carries axial light directly to the proximal

rhabdom. The same pigment acts as an attenuator for the visual pathway in the light-adapted eye (figure 8c), a function which again requires an absorption peak near that of the visual pigment. Measurements of the angular distribution of the back-scattered light in the eyeshine of *Ephesia* showed that it could not be a well-focused superposition eye (Horridge 1972). However, some of this back-scattered light, as well as the rays utilized by Kunze (1972) in pigment-free eyes of mutant *Ephesia*, could have been *photoregenerative* light in a wild-type eye, and therefore not relevant to the optics of seeing.

Similarly, the typical neuropteran type of clear zone eye, found in Neuroptera, Trichoptera, and many moths and beetles, has an arrangement of screening pigment which could function as described above. In the dark-adapted eye (figure 8a, e) there is a thin layer of pigment of the principal pigment cell remaining near the cone tip. Often this is red or yellow, not black. The same pigment cell, with

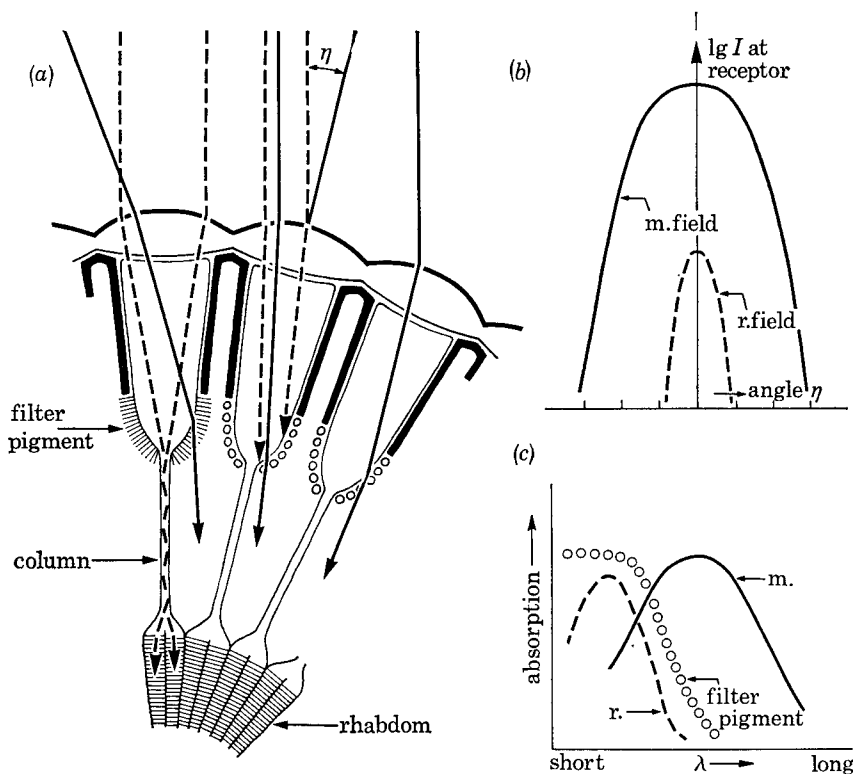


FIGURE 7. (a) Diagram illustrating the theory outlined in this paper. High acuity at short wavelengths depends on the focus upon the distal end of the light guide, while sensitivity depends upon longer wavelengths which regenerate rhodopsin from metarhodopsin (solid rays). The essential component is the disc of pigment at the cone tip, which prevents entry of the unfocused short wavelengths. (b) Possible relation between the field sizes for the rhodopsin and metarhodopsin systems, showing that most of the pigment will be in the rhodopsin form. (c) The required absorption curves of the screening pigment (○) in relation to those of the rhodopsin (dashed line) and metarhodopsin (solid line).

pigment grains that are different from those of the accessory pigment cells, acts as an attenuator round the cone extension in the light-adapted state.

Current theories have left untouched the importance of the exact morphological position of a screening pigment in relation to its colour. Photoregeneration of rhodopsin as a way of increasing sensitivity of moth eyes has been discussed by Carlson & Philipson (1972) and measured by Hoglund, Hamdorf & Rosner (1973) but without reference to the exact optical rôle of the screening pigments.

The eye of the owlfly *Ascalaphus* has two principal pigment cells which surround

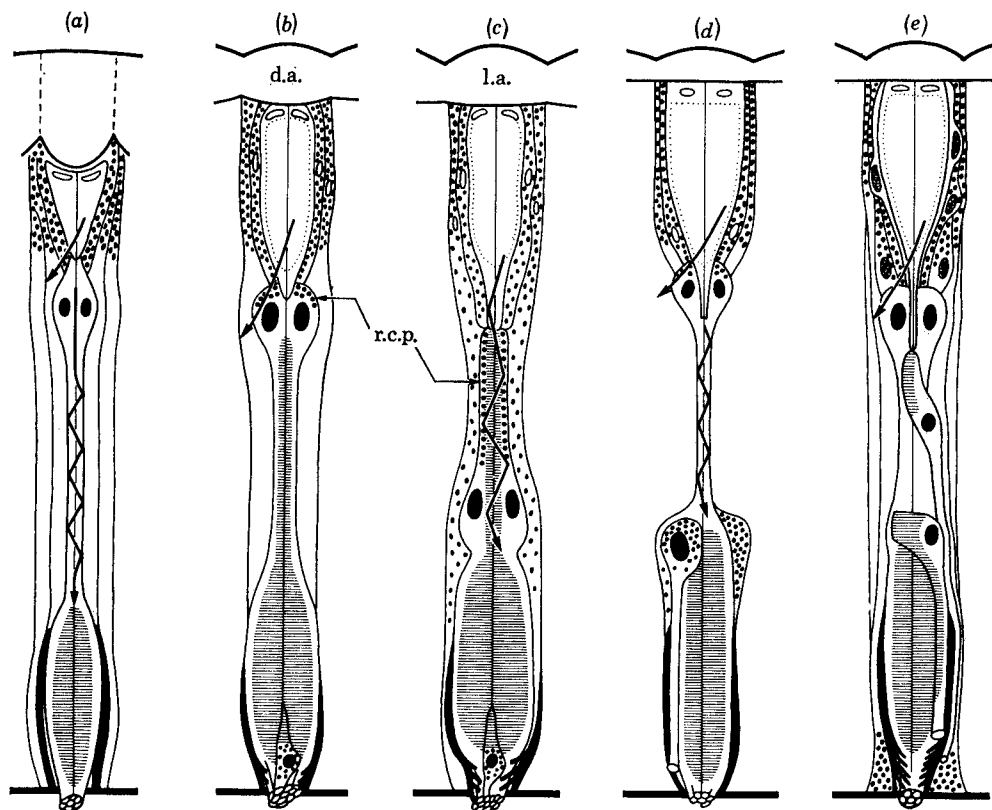


FIGURE 8. Clear zone eyes suggesting the significance of screening pigment in allowing photoregenerative oblique rays to pass through the side of the cone tip. In each of these eyes the anatomy suggests that part of the light is carried in a light guide across the clear zone, whereas direct observation shows that other rays freely cross the clear zone. Observed light paths are figured as rays with arrows. Retinula cells are distinguished by nuclei drawn black. (a) *Reptsimus* (Coleoptera) almost dark-adapted (Horridge & Giddings 1971). (b) *Ephestia* (Lepidoptera) dark-adapted. Note the position of the retinula cell pigment, r.c.p. (Horridge 1972). (c) *Ephestia* light-adapted, with retinula cell pigment now acting as an attenuator of the visual pathway (Horridge 1972). (d) *Atelophlebia* (Ephemeroptera), dorsal turbanate eye, with fixed pigment position and no pigment cells in the clear zone (unpublished observation). (e) *Chrysopa* (Neuroptera) almost dark-adapted, with rhabdomeres of retinula cells 7 and 8 in positions that suggest an even more complex optical system (unpublished observation).

the end of a retinula cell column that is only about 2 μm in diameter. The pigment in these cells is yellow, with peak absorption near 400 nm. Stimulating light (within the u.v. range) can enter the deeper parts of the ommatidium only through this narrow aperture, whereas light of longer wavelength that is effective in photo-reisomerization, enters through a much larger effective aperture (Langer 1975). The u.v. optics of the owl eye have not yet been described but the situation looks similar to that discussed here.

In Lepidoptera the pigment grains have almost flat absorption curves from 300 to 700 nm in *Heliconius* (Langer & Struwe 1972) and in several moths (Hoglund, Langer, Struwe & Thorell 1970), but these all have colour vision. In several insects there is a correlation between the absorption peaks of screening pigments and the spectral sensitivity of the receptors they screen (Strother & Casella 1972). More particularly, peripheral screening pigments are yellow whereas deeper ones are red. Some Australian skipper butterflies, with superposition eyes, notably of the genus *Chaetecneme* Felder, have eyes that are yellow or red from the screening pigment forming the iris around each cone. The unfocused long-wavelength rays that pass this screen are presumably photoregenerative. A similar function for the red pigments of *Drosophila* apposition eyes has been recently suggested by Stark (1975).

The theory set out here also provides a route for evolving clear zone eyes without the difficulty inherent in Exner's superposition theory, that the clear zone and dioptric structure need to be well-developed before they begin to confer an advantage. As long as there is a light guide crossing it, the clear zone can widen progressively and so increase the available photoregenerative light, even when there is no focusing mechanism at all (Horridge, Ninham & Diesendorf 1972).

To conclude, some examples of compound eyes have features which suggest that they enjoy the best of both worlds, by having a high acuity which depends on the first image being focused on the end of the light guide, and an improved sensitivity that depends on photoregenerative light, focused, however poorly, across the clear zone.

I am indebted to Miss Ida Henderson for her painstaking technical assistance.

Note added in proof, 5 January 1976. Strong support for the theory outlined comes from the further finding that in the dorsal eye of the mayfly *Atelophlebia* the pigment around the cone tip is yellow. Also, as shown by the e.g., the dorsal eye is sensitive only to ultraviolet light, which is relatively the most abundant wavelength (in terms of photons) in the scattered light of the evening sky.

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