

## ANATOMY OF THE REGIONAL DIFFERENCES IN THE EYE OF THE MANTIS *CIULFINA*

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### SUMMARY

1. In the compound eye of *Ciulfina* (Mantidae) there are large regional differences in interommatidial angle as measured optically from the pseudo-pupil. Notably there is an acute zone which looks backwards as well as one looking forwards. There are correlated regional differences in the dimensions of the ommatidia.

2. The following anatomical features which influence the optical performance have been measured in different parts of the eye:

- (a) The facet diameter is greater where the interommatidial angle is smaller. This could influence resolving power, but calculation shows that facet size does not exert a dominant effect on the visual fields of the receptors.
- (b) The rhabdom tip diameter, which theoretically has a strong influence on the size of visual fields, is narrower in eye regions where the interommatidial angle is smaller.
- (c) The cone length, from which the focal length can be estimated, is greater where the interommatidial angle is smaller.

3. Estimation of the amount of light reaching the rhabdom suggests that different parts of the eye have similar sensitivity to a point source of light, but differ by a factor of at least 10 in sensitivity to an extended source.

4. There is anatomical evidence that in the acute zone the sensitivity has been sacrificed for the sake of resolution.

5. Maps of the theoretical minimum fields of the photoreceptors, plotted in their positions on the eye in angular coordinates, suggest that there are too few ommatidia for the eye as a whole to reconstruct all the visual detail that the individual receptors can resolve.

6. The conclusion from (3) and (4), together with some behavioural evidence, suggests that the eye structure must make possible the resolution of small movements of contrasting edges and of small dark contrasting objects but there is less emphasis on the total reconstruction of fine patterns because the interommatidial angle is greater than the estimate of the acceptance angle.

### INTRODUCTION

Many insects have on their eyes one or more *acute zones*, which are defined as regions where the interommatidial angles are smaller than elsewhere and consequently where there is the finest sampling of the visual world. Earlier such a zone in a

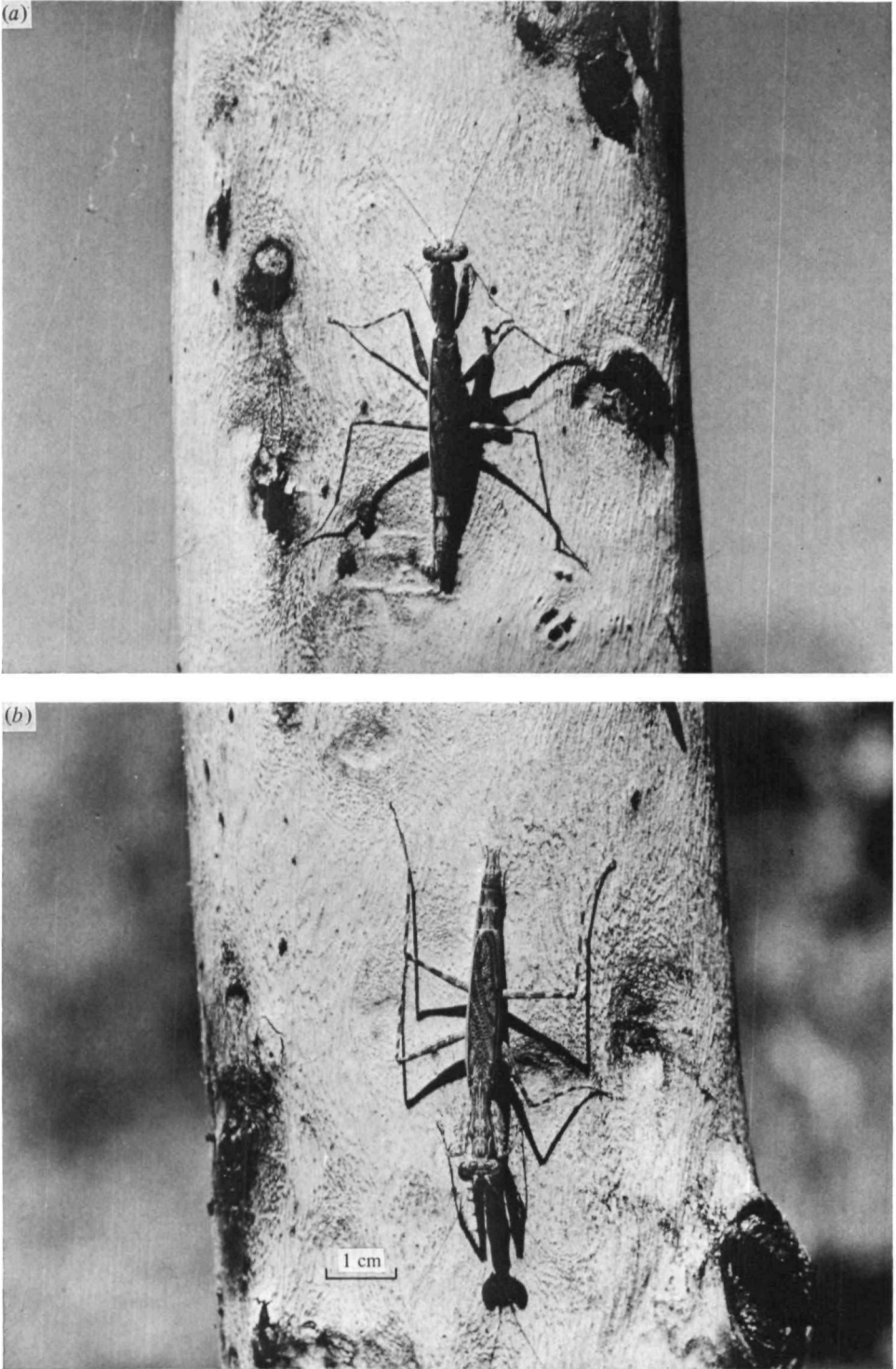


Fig. 1. *Ciulfina* in its two preferred positions in a vertical twig.  
(a) Facing upwards; (b) facing downwards.



## THEORY

*Eye dimensions which govern the optics*

The ommatidium of *Ciulfina* is different from others previously described in that the cornea is thin, the corneal facets have hardly any curvature on either side, and both cornea and crystalline cone are not obviously inhomogeneous. The principal refracting surface appears to be the front surface of the crystalline cone (see Fig. 5). In *Ciulfina* the front surface of the crystalline cone is almost hemispherical, and thereby quite unlike the cones in most apposition eyes with corneal lenses, where the front surface of the cone is approximately flat or pressed against the inner surface of the cornea. The functional significance of this arrangement will be clarified when the structure of the eye as a whole is described.

The combination of theory and anatomical measurements in this paper originates from the fact that two angles determine the sampling performance of a regular hexagonal array of photoreceptors. One of these angles, between the optical axes of adjacent ommatidia, called the interommatidial angle  $\Delta\phi$ , can be measured from the position of the pseudopupil when the eye is viewed from different angles. The other is the angular width of the visual field of individual photoreceptors, called the acceptance angle  $\Delta\rho$ , which can be calculated from the physical dimensions of the optical components of the ommatidium. The relation between the interommatidial angle and the acceptance angle is a measure of the overlap of the adjacent visual fields of receptors. The smaller the interommatidial angle, the finer is the pattern that can be reconstituted by the eye. The smaller the acceptance angle, the finer the pattern of stripes that will just cause sufficient modulation (relative to that caused by wide stripes) to make a threshold stimulus at the rhabdoms.

The two factors of significance for the calculation of the theoretical field width of individual receptors are the aperture and the receptor size. The angular width  $\Delta\alpha$  of the Airy disc, subtended at the posterior nodal point, defined as in Fig. 2*a*, is the diffraction component. The anatomical component is the angular width  $\Delta\sigma$  of the rhabdom, also subtended at the posterior nodal point, as in Fig. 2*b*. These two components interact together to yield the field of angular width  $\Delta\rho$  of the individual retinula cells which contribute to the rhabdom.

The width of the Airy disc  $\Delta\alpha$  is defined as the angular width at the 50% *intensity* contour: the width of the receptive field  $\Delta\rho$  is defined as the angular width at the contour of 50% *sensitivity*. Sensitivity in this context is defined as the reciprocal of the number of effective photons per unit time required to give a constant response. The posterior nodal point is defined as the point through which rays pass when their path inside the eye is parallel to their path outside the eye (see the dashed ray in Fig. 2*a*). By making use of the posterior nodal point it is possible to compare the field width  $\Delta\rho$ , which is an angle measured outside the eye, with the two angles  $\Delta\alpha$  and  $\Delta\sigma$  which generate it from inside the eye.

From the elementary theory of the refracting power  $P$  of a thin lens with different media on the two sides, the positions of the nodal point and the focus may be calculated as follows (Southall, 1933). Assuming that the ommatidium is focused, the position of the posterior nodal point relative to the rhabdom tip is given by:

$$f = n_0/P \mu\text{m}, \quad (1)$$

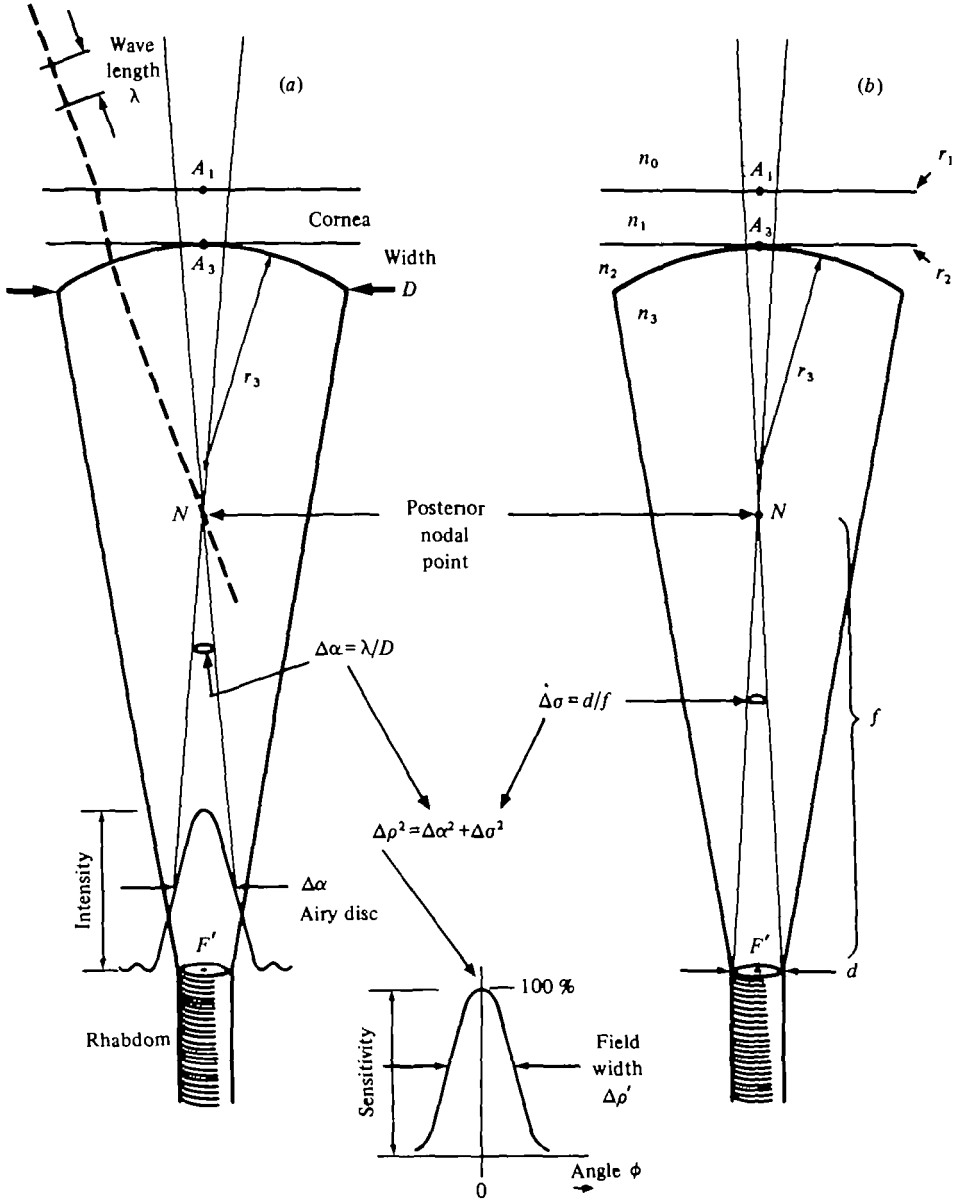


Fig. 2. Optics and symbols employed. The lens is assumed to be near the convex front surface of the crystalline cone with the focal plane at the tip of the rhabdom. The Airy disc subtends an angle  $\Delta\alpha$  rad at the posterior nodal point ( $N$ ), which lies proximal to the centre of curvature of the single refracting surface and at a distance  $f$  from the focal plane. (a) The angular width of the Airy disc at 50% intensity, subtended at the posterior nodal point, is  $\lambda/D$ , the diffraction component. (b) The angular subtense of the rhabdom at the posterior nodal point is  $d/f$ , the anatomical component. As indicated, these two components interact to form the field of width  $\Delta\rho'$  at 50% sensitivity.

where  $f$  is  $NF'$  in Fig. 2a;  $n_0$  is the refractive index outside the eye (usually air,  $n = 1$ ) and  $P$  is the power of the lens combination in dioptres  $\times 10^{-6}$ .

The distance from the focus at  $F'$  to the front surface of the cornea, at  $A_1$  in Fig. 2a, is given approximately by

$$A_1F' = n_3/P, \quad (2)$$

where  $n_3$  is the refractive index of the cone. Therefore, from (1) and (2) the ratio:

$$F'N/A_1F' = n_0/n_3 = 1/n_3 \quad \text{for an eye in air.} \quad (3)$$

This ratio, from which the position of the nodal point can be found, is independent of the cone length, or of the combination of curved surfaces, as may be readily tested using sample calculations with the formulae for thick lenses (Southall, 1933). Although equations (1) and (2) are approximations for a thin lens when  $AF'$  is measured from  $A_3$  rather than from  $A_1$ , the ratio in equation (3) still turns out to be a good approximation, even when the thickness of the lens is not negligible, as long as measurements are made from  $A_1$ . This has been checked by numerous calculations for typical insect eyes and will be the topic of a further publication.

The field sizes are estimated as follows. With symbols as in Fig. 2a, from diffraction theory, the distribution of intensity in the Airy disc has an angular width  $\Delta\alpha$  at the 50% level of intensity, subtended at the PNP, given by

$$\Delta\alpha = \lambda/D \text{ rad.} \quad (4)$$

The acceptance function of the rhabdom for light is the angular subtense of the rhabdom tip as seen in the outside world, and therefore also subtended at the PNP (Fig. 2b). Therefore

$$\Delta\sigma = d/f \text{ rad.} \quad (5)$$

Following Snyder (1977), the theoretical angular width of the angular sensitivity curve at its 50% sensitivity contour,  $\Delta\rho'$  (called the acceptance angle or field width) is approximated by

$$(\Delta\rho')^2 = (\lambda/D)^2 + (d/f)^2. \quad (6)$$

Equation (6) is the convolution between two Gaussian functions, treating the Airy disc and the angular subtense of the rhabdom both as Gaussian functions, with widths measured at their 50% contour. From equation (6) it is clear that the theoretical field width  $\Delta\rho'$  is always greater than either the diffraction component measured by  $\Delta\alpha$  or the anatomical component measured by  $\Delta\sigma$ . When these two components are equal then  $\Delta\rho'$  is greater than either by a factor  $\sqrt{2}$ . When they are unequal, the acceptance angle  $\Delta\rho'$  is a little larger than the larger of the two. Therefore if the rhabdom is large relative to the Airy disc it will determine the field size, but if the rhabdom is relatively small, the field is determined by the aperture  $D$ .

To estimate  $\Delta\rho'$  by equation (6), measurements must therefore be made of  $D$ ,  $d$  and  $f$ , in each part of the eye. Ideally, the theoretical  $\Delta\rho'$  can then be compared with the value of  $\Delta\rho$  measured by intracellular recording as done by Horridge, Mimura & Hardie (1976). In fact no measurements of  $\Delta\rho$  have yet been published from insects with large regional differences in the parameters in equation (6). However, from unpublished work of Rossel (1978) on mantid retinula cells and of Hardie (1978) on

several species of flies, we know that equation (6) gives a good prediction of the experimentally determined acceptance angles. Meanwhile in *Ciulfina* the calculated values of  $\Delta\rho'$  must suffice for comparison with the interommatidial angle  $\Delta\phi$ , to see whether the separation of theoretical minimum fields is constant or how it changes with the other parameters of the eye.

### *Intensity at the receptors*

The amount of light caught by the eye that is useful in vision is the primary factor which governs the lower intensity limit at which various insects, or the different parts of the eye, can see. An estimate of the photon flux ( $I_d$ ) falling on the distal end of the rhabdom from a diffusely luminous source large enough to fill the field of view of a single receptor can be calculated from the angular subtense of the rhabdom tip as seen in the outside world, multiplied by the area of the aperture through which the tip catches light:

$$I_d = 0.89kI_0 d^2 D^2 / f^2 = 0.89kI_0 d^2 / F^2, \quad (7)$$

where  $I_d$  is the mean number of photons per second per rhabdom and  $I_0$  is the mean number of photons per second per square  $\mu\text{m}$  of facet per steradian of field for diffuse light falling on the eye surface. The factor 0.89 arises from the integration of that part of the diffuse light falling on the facet which is included in the acceptance function of the rhabdom, assuming the latter to be gaussian in shape. If correlations with receptor sensitivity measured in other ways are to be made it must be remembered that there are small losses by absorption in the optics and not all photons caught in the rhabdom are effective stimuli. For photons at peak sensitivity, however, the factor  $k$  for a mantid is probably comparable to that in the locust, where Lillywhite (1977) recently found a value of  $0.59 \pm 0.19$  s.d. total effective photon captures per ommatidium per incident photon on the facet (for axial light, which is not quite the same, see below).

To estimate how  $I_d$  varies in different parts of the eye for a constant stimulus situation, we again need the anatomical measurements of  $d$ ,  $D$  and  $f$  in equation (7). The focal ratio  $F$  is  $f/D$ , so that equation (7) is also the formula which tells us that the sensitivity of a camera, which takes pictures of extended objects, is proportional to the area of single grains on the film divided by the square of the focal ratio.

The photon flux caught from a point source on axis is also readily estimated from the anatomical data. When the rhabdom has a diameter sufficient for it to accept the full width of the Airy disc, all the light from a point source is caught. The illumination of the rhabdom tip from a point source is then

$$I_p = I_A k \pi D^2 / 4 = I_A k' D^2, \quad (8)$$

where  $I_A$  is the mean number of photons per square  $\mu\text{m}$  of facet per second of axial light,  $D$  is the diameter of the facet aperture, and  $k$  as in equation (7).

When the diameter ( $d$ ) of the rhabdom is less than the full width of the Airy disc, not all the light in the disc is caught, even when the point source is on the optical axis. The amount of light caught by the rhabdom is approximately proportional to the ratio of the rhabdom diameter to the Airy disc diameter. This may be demonstrated by plotting the exact relation from tables of the circle coverage function for the circular

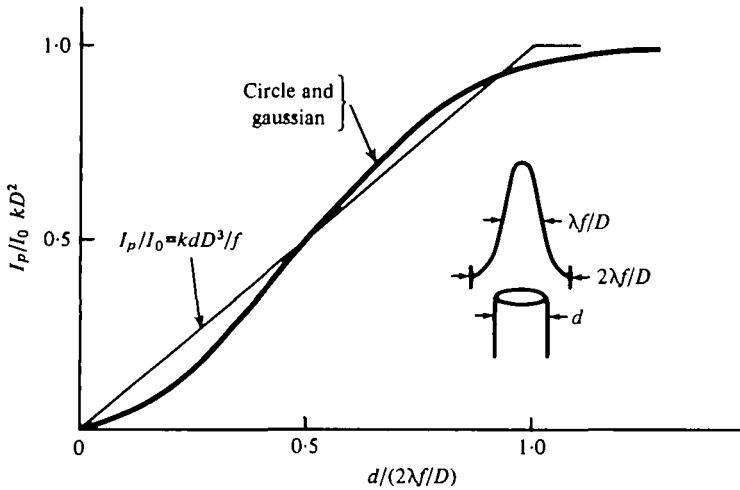


Fig. 3. The fraction of the total light in the Airy disc which is caught by the circular end of the rhabdom, assuming that the Airy disc is approximated by a Gaussian distribution and that geometrical optics apply. The ordinate is the intensity at the rhabdom per unit area of the aperture, and the abscissa is the width of the rhabdom relative to the full width of the Airy disc. The straight line is the approximation employed.

normal distribution (Horridge, Mimura & Hardie, 1976). The curve deviates little from a straight line up to  $d = 2\lambda f/D$  (Fig. 3). Approximately therefore

$$I_p = I_0 k' D^2 \cdot d/(2\lambda f/D) = I_0 k' D^3/f \quad \text{when } \lambda = 0.5 \mu\text{m}. \quad (9)$$

To plot  $I_p$ , first we calculate  $x = dD/f$ . If  $x$  is greater than unity then  $I_p = I_0 k' D^2$ ; if  $x$  is less than unity, then  $I_p = I_0 k' dD^2$ , as plotted for different parts of the eye in Fig. 14, taking  $k'$  as constant for all parts of the eye.

The optical radius ( $R$ ) of the eye is defined as the distance from the aperture to the point in the eye where optical axes of neighbouring ommatidia cross. Therefore

$$R = D/\Delta\phi. \quad (10)$$

The optical radius is the effective local size of the eye. As will be shown, the optical radius  $R$  cannot be guessed from the external curvature of the eye surface because ommatidia are usually not at right angles to the tangent at that point on the cornea. In fact, where the cornea is anatomically flattest the eye turns out to have the smallest optical radius. Parts of the eye with greater optical radius, like larger eyes, have better resolution and they catch more light than small eyes.

*The eye parameter  $D\Delta\phi$*

The facet diameter and the interommatidial angle can both be measured from outside the eye, and their product  $D\Delta\phi$ , defined as the eye parameter, has been related as follows to the intensity of light at which the eye normally operates (Snyder, 1977). The theory assumes that the eye as a whole is able to reconstruct the patterns which individual ommatidia can resolve. As a result of diffraction at the lens, stripes with a repeat pattern which subtends at the eye an angle of less than  $\lambda/D$  radians cannot cause modulation of light at the receptors, even if the rhabdom tip were of negligible



width. The modulation caused by finer patterns of regular stripes fail to pass the optics. Therefore, supposing conditions of high illumination, there is no point in the interommatidial angle being smaller than the angle subtended by a single black or a single white stripe. Under those circumstances the adjacent receptors are able to distinguish the alternate black and white regions of the pattern. When  $\lambda/D = 2\Delta\phi$ , therefore, the spatial resolution of the eye is just adequate to reconstruct all regular striped patterns that will pass the lens. At this point, rearranging, we have  $D\Delta\phi = \frac{1}{2}\lambda = 0.25 \mu\text{m}$  when  $\lambda = 0.5 \mu\text{m}$ .

At lower ambient intensities, however, more modulation is required, and to achieve that the threshold stripe period must now be greater than  $\lambda/D$  radians. In eyes which customarily operate at low intensities  $\Delta\phi$  is therefore greater than is suggested by the diameter of the facets, and the facets themselves may be enlarged simply to catch more light. Therefore their product  $D\Delta\phi$  is greater than  $0.25 \mu\text{m}$  by a factor which depends on the intensity at which the eye normally functions. Theoretical values of  $D\Delta\phi$  as a function of intensity are given by Snyder (1977).

Maps of the compound eye plotted as in figures 9 and 10 shown below have circles representing the minimum possible fields. The circles have their centres separated by the angle  $\Delta\phi$  and they have a diameter of  $\lambda/D$  radians, so that the spacing of the circles relative to each other gives a measure of  $D\Delta\phi$  at every point. The maps are therefore *maps of the eye parameter*. For example, when the circles touch, their diameter  $\lambda/D$  equals the separation of their centres  $\Delta\phi$ , so that  $D\Delta\phi = 0.5 \mu\text{m}$ . For the eye parameter to be  $0.25 \mu\text{m}$  the circles must overlap so that each circle runs through the centre of its neighbour. If the circles are separated by a distance equal to their diameter then  $\Delta\phi = 2\lambda/D$  and  $D\Delta\phi = 1$ . From this we see that the eye parameter  $D\Delta\phi$  is one quarter of the *ratio of the spatial resolution of the eye as a whole to the spatial resolving power of its individual ommatidia*. The eye parameter can be read off from each region of the eye map for any row of visual axes in any direction on the eye surface.

### *Anatomy*

#### *The cornea*

From the outside of the eye one sees regular hexagonal facets but the eye surface is glassy smooth. In the scanning electron microscope it is difficult to see facets no matter how the eye is prepared. In sections of the cornea, both of its surfaces are almost flat. Moreover the cornea is thin for such a large eye, ranging from 33–34  $\mu\text{m}$  at the front of the eye to 19–20  $\mu\text{m}$  at the side. Histologically, there are no obvious zones in the cornea when examined in thick or thin sections.

#### *The cone*

The crystalline cones range in length from 340  $\mu\text{m}$  at the front of the eye to 140  $\mu\text{m}$  at the side, and they reach 240  $\mu\text{m}$  at the back of the eye (Figs. 4, 5). An unpublished survey by the authors shows that this wide range of cone length is more marked than in most other insect eyes. The longer cones are always broader, reaching 50  $\mu\text{m}$  maximum diameter at the front of the eye but only 30  $\mu\text{m}$  at the side. The novel feature of the crystalline cone is its distal surface, which is smoothly convex, forming almost half of a sphere that almost touches the cornea. When the axis of the cone is

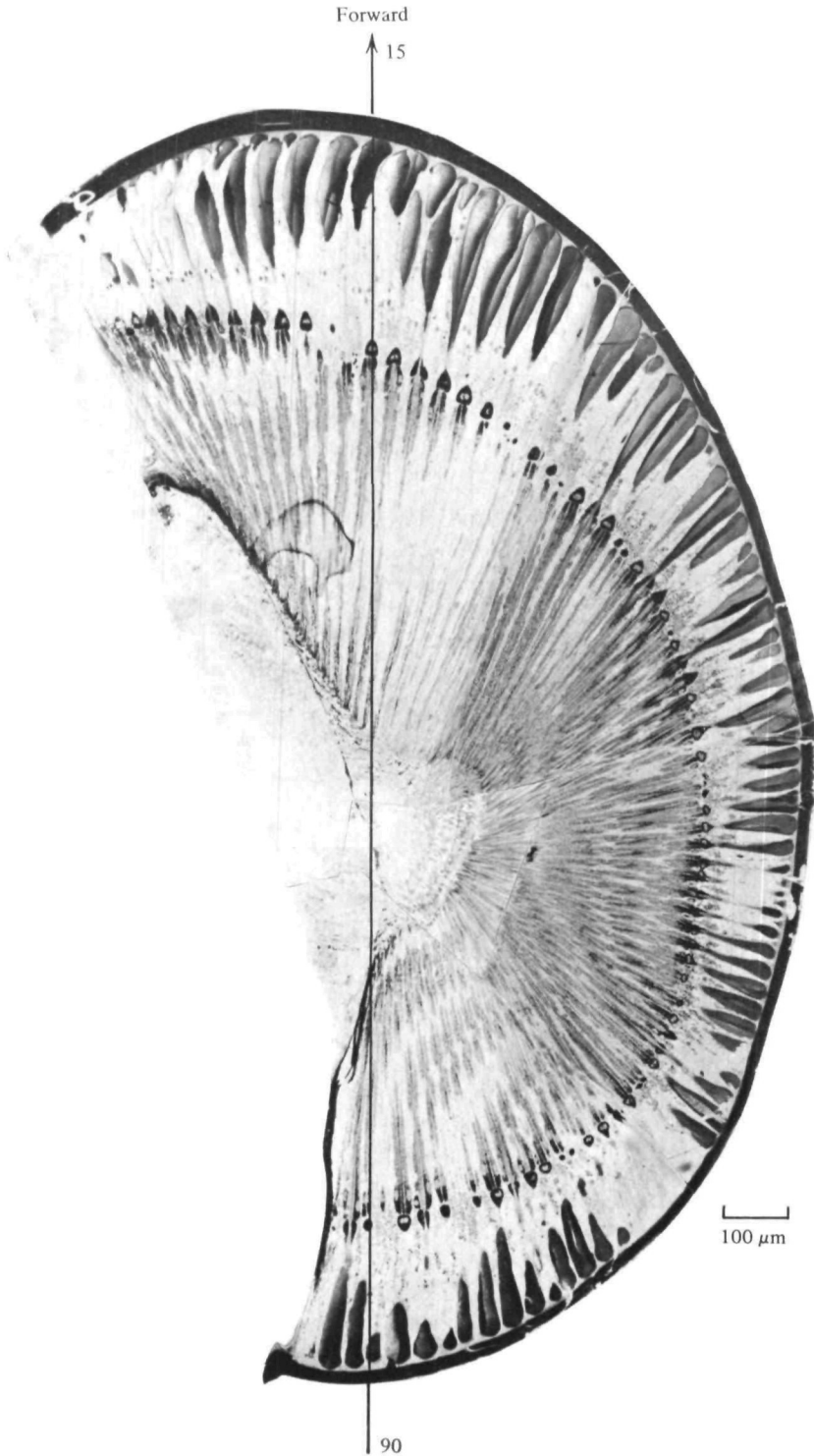


Fig. 4. Montage of longitudinal sections through the eye in the horizontal plane, i.e. along the centre of the black band in Fig. 8. The morphological axes of the cones are tilted relative to the eye surface, except at the forward and rear view acute zones and at  $90^\circ$  to these (see Fig. 15).

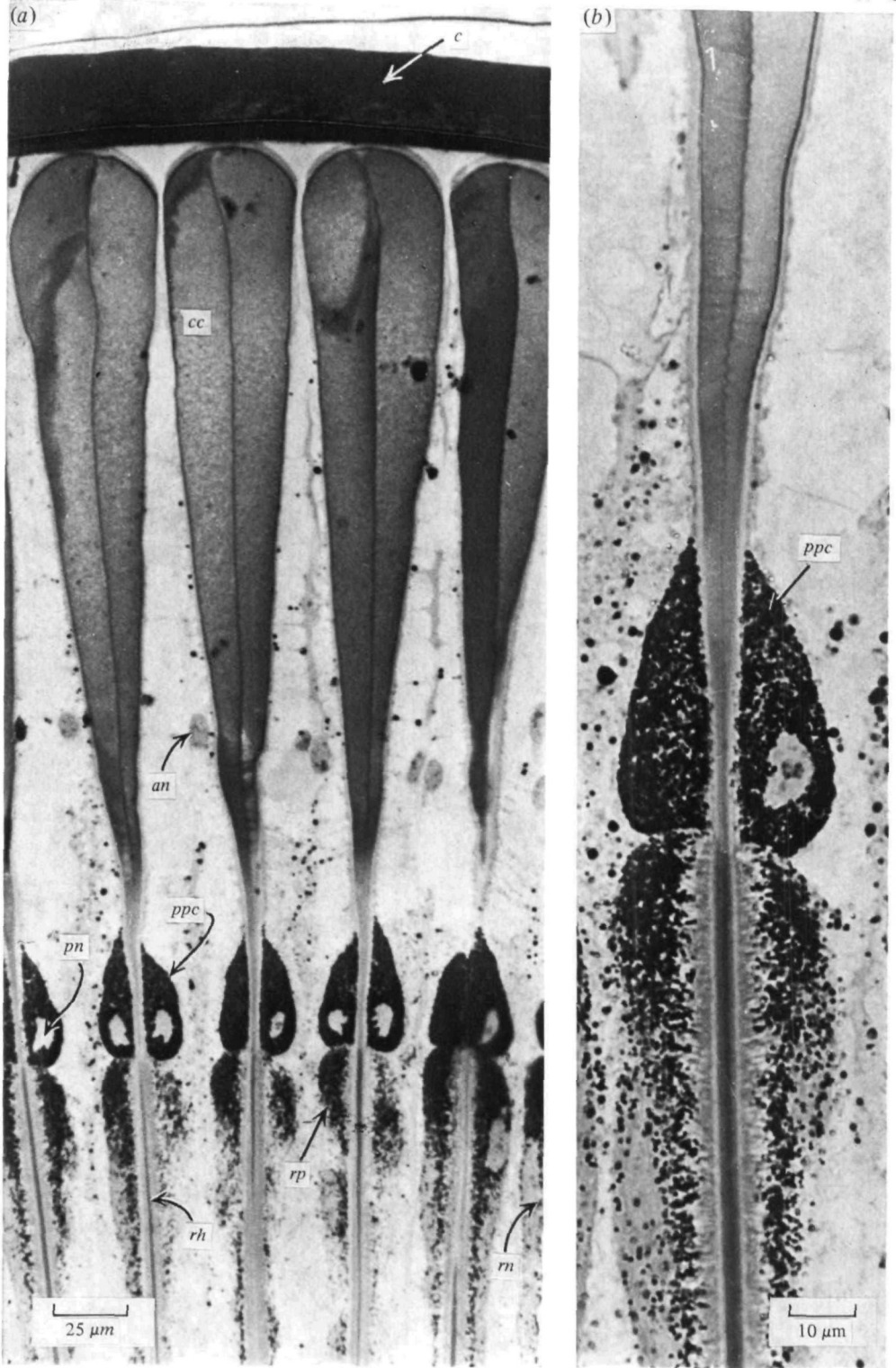


Fig. 5. Light micrographs. (a) The forward-looking acute zone. (b) At higher power through the critical region at the tip of the cone, to show the dense central fibre in the cone and its continuation to the rhabdom, which is also surrounded by a less dense cylindrical region. The principal pigment cells are almost solid with pigment; the retinula cells also contain pigment grains at their peripheral ends. *an*, Accessory pigment cell nucleus; *c*, cornea; *cc*, crystalline cone; *ppc*, principal pigment cell; *pn*, nucleus of principal pigment cell; *rh*, rhabdom; *rp*, retinula cell pigment; *rn*, retinula cell nucleus.

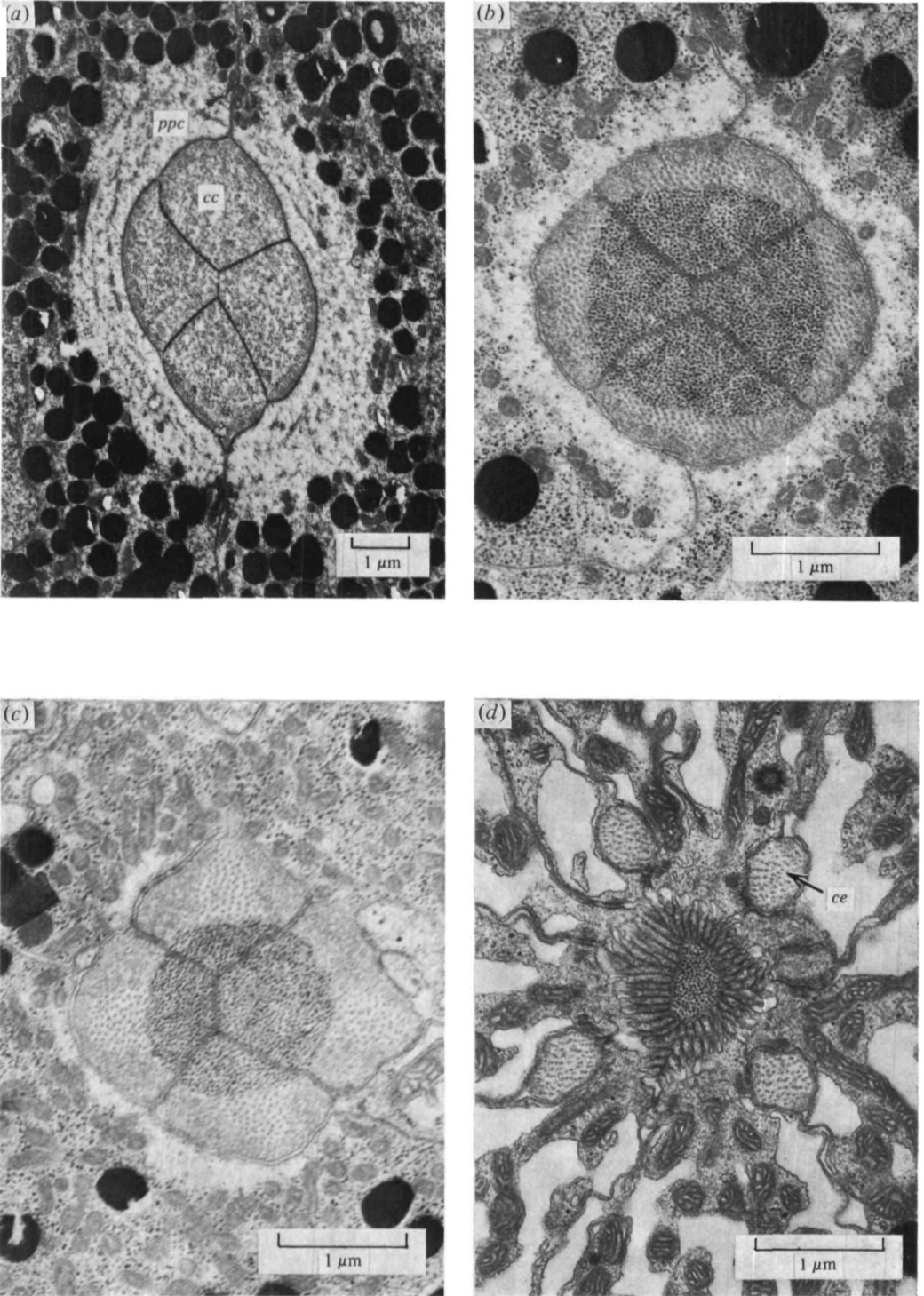


Fig. 6. Electron micrographs working down in a series of sections through the narrow part of the cone in a light-adapted eye. (a) Where the cone is 3-4  $\mu\text{m}$  wide it is surrounded by a clear region of the two principal cells. (b) Where the cone is 2-3  $\mu\text{m}$  wide it has a central core of dense granules, and is still surrounded by the light zone in the two surrounding principal pigment cells. (c) At a lower level the cone is quite closely surrounded by mitochondria, immediately adjacent to the retinula cells. (d) The cone forms five arms which enclose the end of the rhabdom. *cc*, crystalline cone; *ce*, extension of cone cell; *ppc*, principal pigment cell.

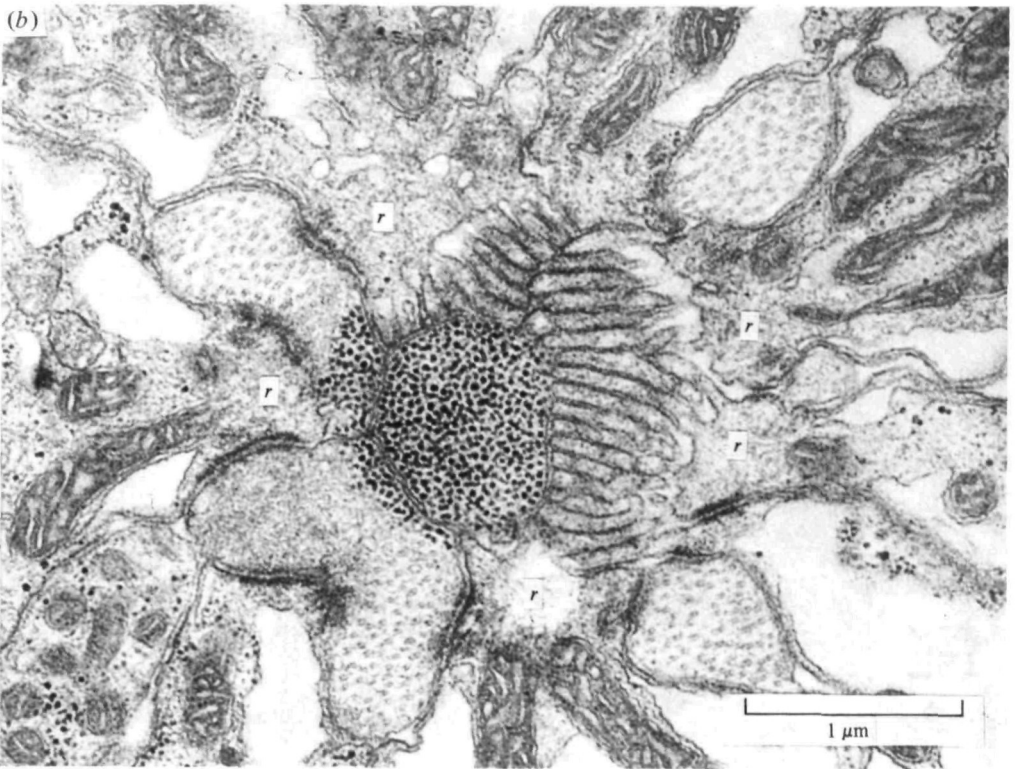
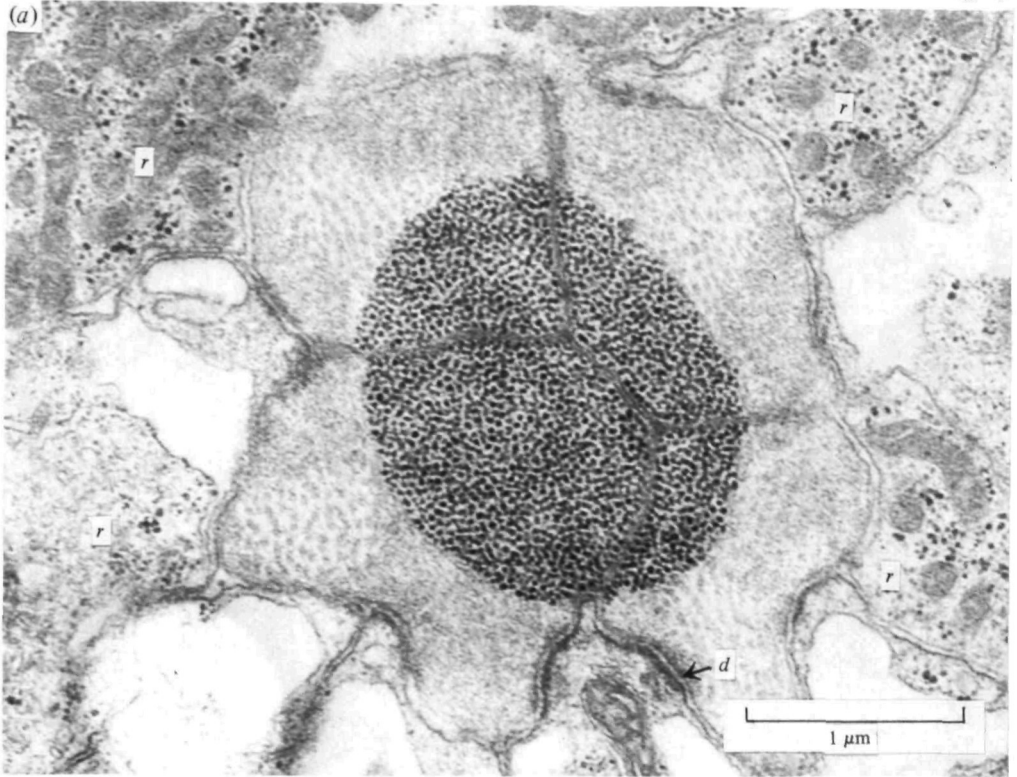


Fig. 7. Electron micrographs of the critical region at higher power (a) just distal to the rhabdom (b) where the rhabdom first appears in sections. Note the desmosomes where cone cells meet the retinula cells and the dense core of the cone. *d*, desmosome; *r*, retinula cell.

tilted relative to the radius at that point on the eye, the same smoothly rounded surface almost touches the cornea.

Between the cones are relatively empty spaces consisting of accessory pigment cells with some sparse pigment grains (Fig. 5).

The crystalline cone in histological and electron microscope sections is obviously made of material that is richer in protein than the surrounding tissue, and this curved outer surface of the cone is the most obvious structure which could act as a lens. Measurements of the refractive index of the cone, as part of an analysis of the optics (McIntyre, 1978), show that the index is close to 1.4. There are other optical components in the cornea, and possibly a small effect from radial inhomogeneities of the crystalline cone. Calculation from the formulae for a thick lens shows that the distal surface of the cone contributes about half of the power to make a focus at the cone tip. This does not affect equations (1-3) because the lens power originates near the corneal surface.

### *The cone tip*

The cone consists of four equal cells, which taper gradually to a long narrow tip that passes between the two densely pigmented principal pigment cells (Fig. 5). The narrow neck is clearly divided, as seen in the electron microscope, into a central region which is uniformly filled with small granules that appear to be glycogen, and an outer zone 0.2-0.5  $\mu\text{m}$  wide which is the clear cytoplasm of the cone cells. The outer zone of low density contains microtubules that are orientated along the cone's axis, occasional mitochondria and some endoplasmic reticulum. Outside this zone, separated by the cell membranes, is the cytoplasm of the two principal pigment cells which in this region is even less dense as seen in the electron microscope (Fig. 6a). The pigment grains of the pigment cells are always separated by a gap of at least 0.5  $\mu\text{m}$  from the cone by this zone or sleeve of apparent low density (Fig. 6b), which suggests that the narrow neck of the cone acts as a light guide. The nearest pigment grains to the cone cells are 0.3-0.5  $\mu\text{m}$  in diameter and densely crowded at the outer limits of their cells. The pigment cells always lie between the cone cells and the retinula cells, which are recognized by their smaller pigment grains in sections at the level of the cone tip (Figs. 6d, 7b). If the neck of the cone acts as a light guide, then the optical width in the focal plane, which determines the field size as in equation (6) is not the diameter of the rhabdom but the effective diameter of this light guide. Throughout the eye, however, the width of the cone neck is always closely related to the width of the rhabdom, which unlike the cone neck, is an object of clearly defined width, and so it is the rhabdom which has been measured.

Close to its tip the central region of the cone becomes a relatively dense central rod of granules; the less-dense zone of cone cell cytoplasm is now more crowded than before with microtubules in the surrounding pigment cells. The outermost and least dense zone continues as before (Fig. 7a). In a series of sections the rhabdom suddenly appears at this point, and it clearly lies directly beneath the end of the column of granules in the cone (Figs. 6d, 7b). The top of the rhabdom is approximately flat. Several anatomical features appear simultaneously at this point. The four cone cells, crowded with microtubules, separate and surround the tip of the rhabdom (Fig. 7) as

in the locust (Horridge (1966); figs. 3 and 5). In *Ciulfina* one of the cone cells always splits into two, making five cone cell extensions in all, as also now reported in the locust (Wilson, private communication; contra Horridge, 1966, where four were reported). These cone-cell extensions narrow rapidly to less than  $1\ \mu\text{m}$  diameter around the rhabdom tip, then at a few microns below the cone tip they become ribbons only  $0.2\text{--}0.3\ \mu\text{m}$  thick; they are therefore too narrow to act as light guides beyond the cone tip.

The other anatomical feature is that the retinula cells, which are recognized in sections by their small dense mitochondria, small pigment grains and abundance of organelles, form large densely staining desmosomes where they meet the cone cells. Presumably this is one of the places where the retina is held together mechanically.

Immediately below the cone tip are 8 retinula cells, of which 6, in 3 pairs, contribute to a rhabdom with its cross-section divided into three regions, with microvilli pointing at angles of approximately  $120^\circ$  to each other. Measurements of rhabdom diameter were taken only in the region where the rhabdom tip was recognizable by these features. A few microns below the cone tip the rhabdom divides further, adding an additional region of differently orientated microvilli which are contributed by one of the two remaining retinula cells that had no microvilli against the cone tip.

The retinula cells have numerous vacuoles at the endoplasmic reticulum, called 'palisade' in the locust (Horridge & Barnard, 1965). Beginning at the cone tip this sleeve of vacuoles forms a wide sheath of apparently low refractive index that separates the rhabdom from the pigment-loaded cytoplasm of the retinula cells. Sections through the retinula cells are recognized as being near the cone tip when the cone cell extensions are close to the rhabdom (Fig. 6*d*).

#### *Pseudopupils and interommatidial angles*

##### *Mapping the eye by the pseudopupil*

Mantid eyes show a small sharp pseudopupil, which is the black spot that is always directed towards an observer who looks at the eye (Fig. 8). The pseudopupil of *Ciulfina* is obscured along the horizontal line around the eye by a band of dense black pigment, but this does not prevent the mapping of the pseudopupil which can be seen as an even blacker area, and which remains visible when the corneal surface is defocused.

The head is mounted in a goniometer stage, facets are marked with particles of chalk dust blown on the eye, and the eye is photographed at intervals of  $10^\circ$ , or  $5^\circ$  in the acute zones. The direction of the optical axis of an ommatidium in space is given by the direction of the observer when the ommatidium is in the centre of the pseudopupil. The pseudopupil is larger when seen in the centre of the acute zone than when seen elsewhere on the eye (Fig. 8*b*).

To make a map in angular coordinates from a set of photographs it is first necessary to map the facets along a zone around the eye by tracing them from successive photographs on to one piece of paper. Because the eye is rounded, this mapping of facets can be accurate only along particular lines across the surface of the eye, shown as dashed lines in the eye maps. Upon the map of the facets made in linear coordinates one then marks the position of the pseudopupil centre for each angle of observation. Lines

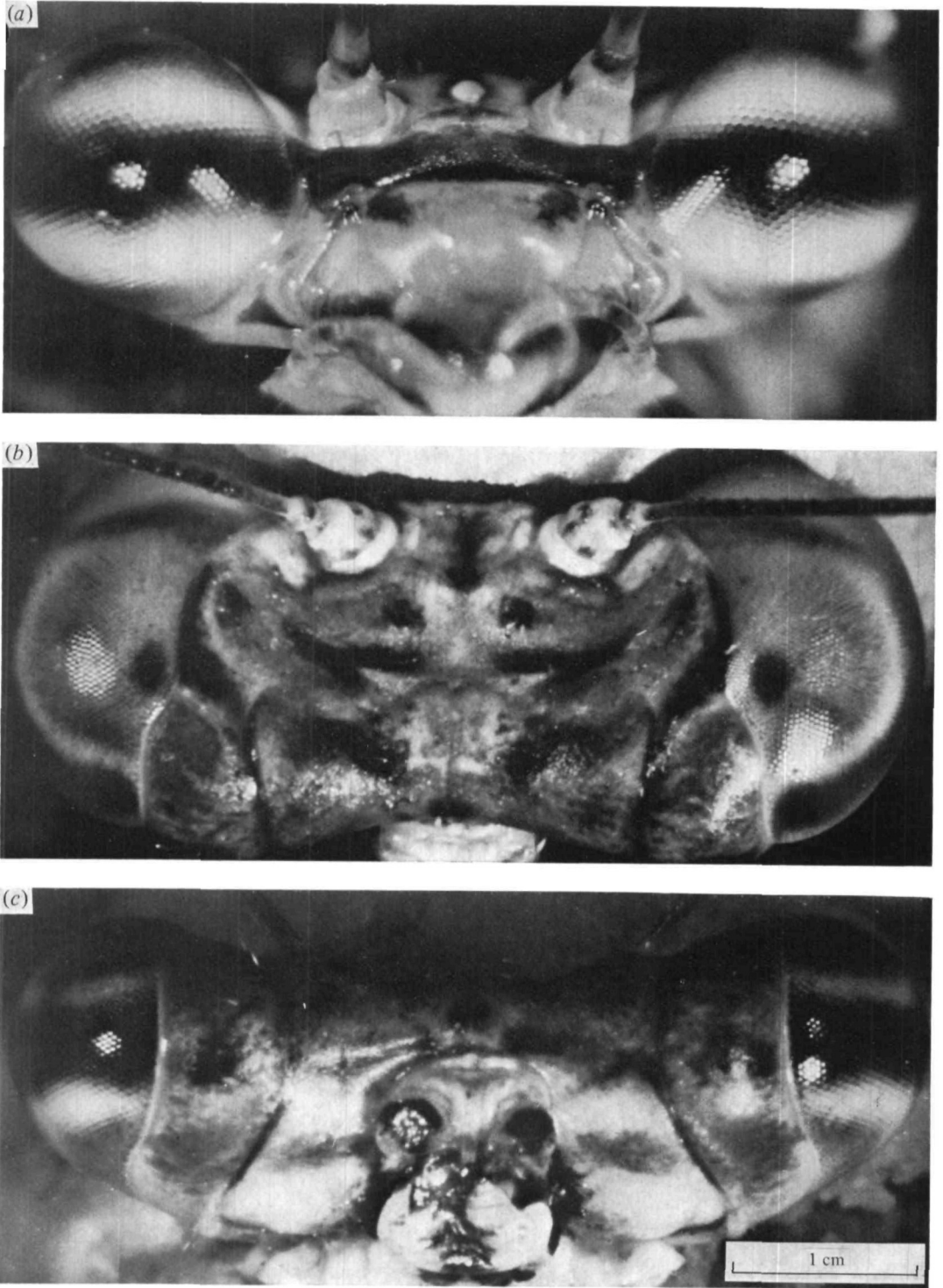


Fig. 8. Different orientations of the head of *Ciulfina* showing the pseudopupils (a) seen from directly in front (b) from above, at an angle of  $60^\circ$  to the forward-looking acute zone front, (c) from directly behind.





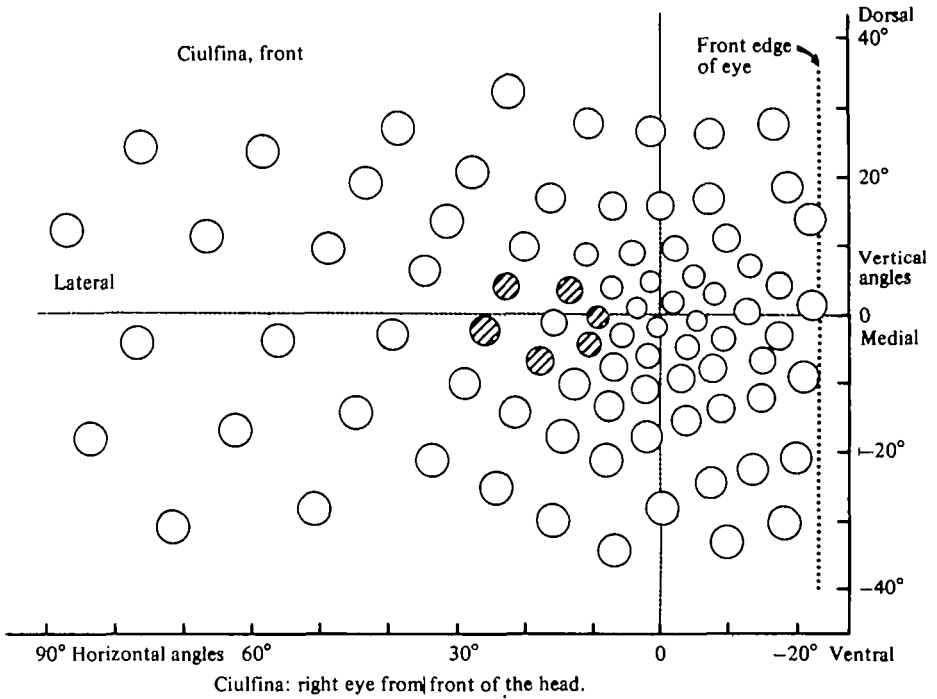


Fig. 9. Map of the forward-looking part of the right eye in angular coordinates. The centre of each circle represents the direction in space of the optical axis of every fifth ommatidium, and the diameter of each circle is the width ( $5\lambda/D$  radians) of its theoretically minimum field at 50% sensitivity (magnified 5 times). The separation of circles gives a measure of the eye parameter at each point. At the acute zone the fields are narrower and also closer together.

joining pseudopupil positions for all angles in one plane are called isopupil lines (Maldonado & Barrós-Pita, 1970). Next, the positions of the optical axes in space are drawn for every fifth ommatidium on a new map which is drawn in angular coordinates. These directions of the optical axes are the centres of the circles in the eye maps in Figs. 9 and 10. The diameter of each circle is the theoretical minimum width of the field of the ommatidium with its axis looking in that direction,  $\Delta\alpha$  in equation (4). Actually the circles in the diagrams in this paper have a diameter of  $5\lambda/D$  and the angle between their centres is  $5\Delta\phi$  so that field overlaps or separations can be seen on a map of a convenient number of circles. Maps plotted by this method in angular coordinates therefore show the relation between the theoretical optimum resolving power of each ommatidium ( $\lambda/D$ ) and the spatial resolution of the eye as a whole. Calculated field widths ( $\Delta\rho'$ ) from equation (6) are always wider than their theoretical minimum ( $\Delta\alpha$ ) on account of the finite diameter of the rhabdom. The measured values of the acceptance angle of retinula cells ( $\Delta\rho$ ) are likely to be larger still for a variety of reasons including imperfections of the lens.

The maps show the angular extent of the acute zone and the way it differs from the rest of the eye. *Ciulfina* is distinguished by having a rear-view acute zone, which has not been previously described in any insect and which does not occur in the mantids *Orthodera*, *Tenodera* and *Archimantis*. This rear-view acute zone, close by the hind-edge of the eye, looks directly backwards at  $180^\circ$  from the forward-looking acute zone.

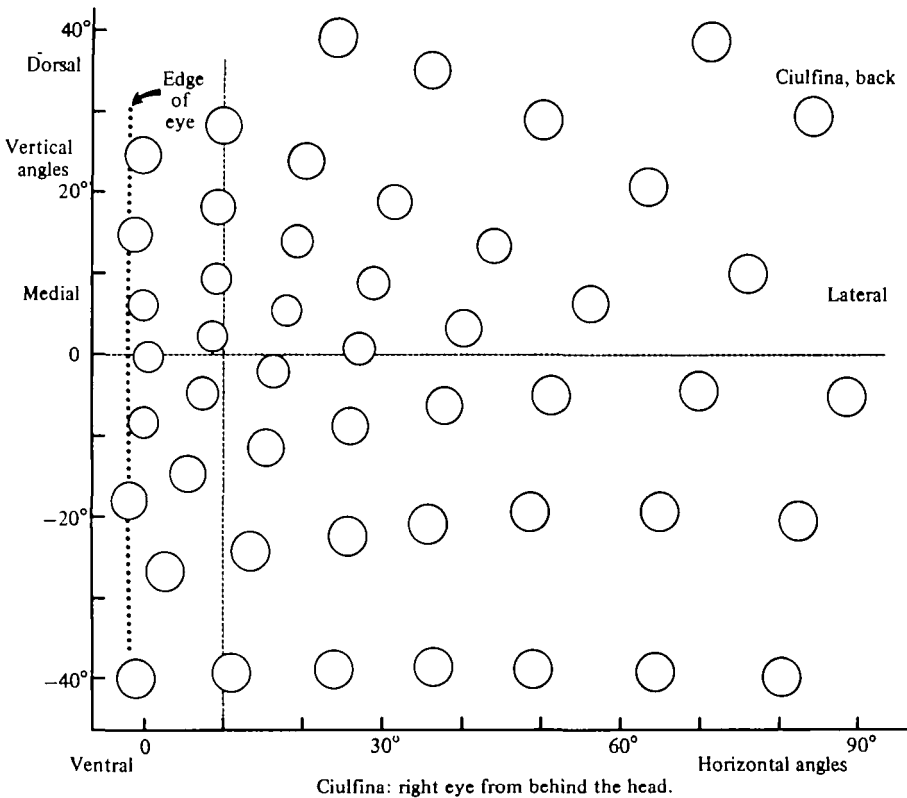


Fig. 10. Map of the rear-view part of the right eye in angular coordinates and continuation of Fig. 9. The centre of each circle represents the direction of the optical axis of every fifth ommatidium and the diameter of each circle is the minimum theoretical field width at 50% sensitivity (magnified 5 times). The map was developed along the dashed lines, where it is free from projection errors.

The rear-view zone is less differentiated from the rest of the eye than the one looking forward. Both acute zones are formed by local increase in facet size and local reduction in the interommatidial angle, but these two gradients do not compensate for each other in that their product  $D\Delta\phi$  is smallest at the centre of the acute zone. This can be seen in the maps because the circles are relatively closer together at the acute zones, particularly in the forward looking one.

The maps also show that the theoretical minimum fields of individual ommatidia are well separated in angular coordinates, implying that these eyes have far fewer facets than one might expect from the resolving power of each, if the function of the eye is to pick the maximum amount of detail from its surroundings. Except at the centre of the forward acute zone, the eye parameter ranges from 1 to 3, which sets a problem that is considered in the Discussion.

The eye maps also show several other features. First, lines of visual axes on mantid eyes never run horizontally across either the front, side or back of the eye (Fig. 9, 10). Maps in angular coordinates show that a straight row of facets is usually in reality a curved row of visual axes. Thirdly, where the pseudopupil is circular, there is a regular hexagonal pattern of circles on the eye map, in that  $\Delta\phi$  is similar in the different

directions across the eye. Where the pseudopupil is vertically elongated, however, the circles form a vertically elongated pattern with smaller vertical  $\Delta\phi$  than horizontal  $\Delta\phi$ , as shown by the shaded circles in Fig. 9. Because the lines of visual axes are drawn together to form an acute zone, their pattern cannot be regularly hexagonal, i.e. interommatidial angles cannot be equal in different directions at one place on the eye, except at the centre of the acute zone or far from it. This may be seen intuitively by perusal of Fig. 9.

#### *Regional anatomical differences*

A horizontal section through both forward and rear-view acute zones shows qualitatively all the main features (Fig. 4). Crystalline cones are longest and broadest in the forward-looking acute zone, not so large in the rear-view acute zone, and smallest in the part of the eye looking to the side. Rhabdoms are longer where cones are larger. Although there are consistent gradients in the inclinations of the axes of the cone to the cornea, at all points on the eye the axis of the cone is exactly in line with its rhabdom. Most of the pigment grains in the eye are concentrated in the narrow zone where the tips of the cones join the rhabdoms.

A theory of insect vision based on the idea that as much detail as possible is discriminated must assume that the eye is crowded with as many ommatidia as is compatible with the dimensions of individual ommatidia. Therefore we might look for those anatomical features where crowding is obviously the limiting factor. Significantly, the only place where the ommatidia appear to be crowded in mantid eyes is at the optical aperture, where the widest parts of the cones almost touch. At other levels there is no indication from the anatomy that the retinula cells, the rhabdom or the supporting cells are squeezed for lack of space. In all other large diurnal insects we find the same significant situation. In contrast, in a clear zone eye like those of the firefly or most moths, the rhabdom region is where there is maximum crowding, in agreement with the idea that the nocturnal eye is adapted for maximum sensitivity in the dark-adapted state, with a large grain size at the receptor layer (see equation 7). In *Ciulfina* the premium for space in the eye is clearly at the optical aperture of each ommatidium and therefore brings about a compromise between the number of ommatidia and the aperture of each.

The anatomical features which fix the width of each visual field are shown in Fig. 2. The vital region for the formation of the visual fields is the transition from the cone tip to the rhabdom (Fig. 5). The narrow neck of the cone, still composed of four cells (Fig. 6), runs between the dense black principal pigment cells, which form a layer across the eye. The sharp transition from the cone to the rhabdom defines the cone length in each part of the eye. Neighbouring ommatidia have the transition at exactly the same level. The fine structure revealed by electron-microscopy shows an accumulation of granules along the axis of the cone near its tip (Fig. 7a), a contact with many desmosomes between the cone cells and the retinula cells (Fig. 7b), and the continuation of the extensions of the cone cells around the rhabdom. Clearly the cone cells are strongly bonded to the retinula cells. What actually fixes the cone length during growth, and therefore the focus, is, however, quite unknown. The general impression is of a highly specialized optical system.

Away from the acute zones one finds regions where the anatomical axes of the

ommatidia are tilted at an angle of up to  $30^\circ$  to the normal cornea. The optical significance of this is discussed below. In these regions the curvature at the broad end of the cone is not symmetrical about its anatomical axis; instead the curvature tends to be symmetrical about a line drawn at right angles to the cornea.

Despite careful examination by interference microscopy (McIntyre, 1978) no evidence has appeared that the crystalline cone has any special focusing system that is dependent upon gradients of refractive index. As a lens, therefore, the cone is presumably a single curved surface. In the narrow region near its tip, the axis of the crystalline cone is clearly denser than the superficial layer of this neck. In sections one can see a dense core, but closer examination reveals that the whole cone has an outside layer  $1-2 \mu\text{m}$  thick of low density. There appears to be a thread down the centre of the narrow neck of the cone because one sees the continuation of the superficial low-density and the central high-density layers in this region, whereas the intermediate zone is squeezed out of existence where the cone passes between the pigment cells. This central thread of high density in the neck of the cone is narrower than the rhabdom into which it leads. It undoubtedly plays an important part in the establishment of the waveguide conditions which continue the path of the light down the rhabdom, but as yet we do not know how to calculate its effect on the width of the visual fields. We assume that the width of the rhabdom is matched optically to the effective width of the cone neck, which would be the most effective anatomical arrangement, and we take the width as that of the rhabdom. As mentioned in the Discussion, the neck of the cone must have an effect on the width of the visual field. The model set out in Fig. 2 is not the whole story but it is the best model at present available until the control of field width is investigated in greater detail.

#### *Anatomical measurements of optical significance*

Measurements of the ommatidial aperture ( $D$ ), cone length ( $l$ ) and rhabdom diameter ( $d$ ), given in Fig. 11, are the primary anatomical features which enter into equation (1)–(4). From these measurements the widths of the fields and the sensitivities of different ommatidia can be estimated from equation (5)–(10). Regional differences in rhabdom lengths are also given in Fig. 11. These must influence sensitivity to a small extent, but are not included in the present calculations.

The apertures and the cone lengths are greater in the acute zones, but inside the eye the rear-view acute zone is not so differentiated anatomically as the forward-looking one.

The new feature, not previously described for an eye, is that the diameters of the rhabdom tips are less in the acute zones than in the lateral part of the eye (Fig. 11). In fact, the rhabdom diameter turns out to be the inverse of the cone length as one plots these measurements round the eye. At first sight it may be surprising that all the cells and other components of the ommatidium are physically larger in the acute zones except the diameter of the rhabdom tip, which is smaller. If the potentially greater resolution made possible by a larger aperture is to be realized, however, the rhabdom will have to subtend a smaller angle at the posterior nodal point. The two ways to achieve smaller fields in the acute zone, by narrower rhabdom and by greater focal length, are both found in *Ciulfina* eye.

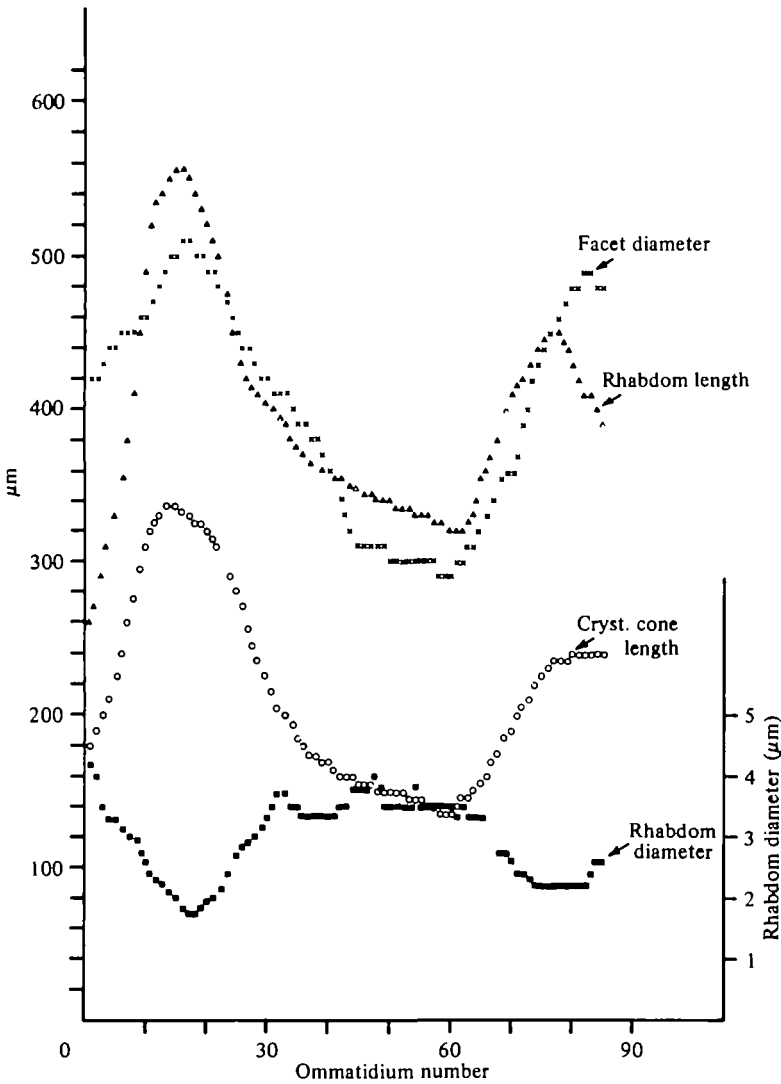


Fig. 11. Measurements of optical significance taken from the sections of the eye in the plane shown in Fig. 4. The facet diameter, the rhabdom length, the cone length and the rhabdom diameter all vary consistently across the eye. Where the other dimensions are large the rhabdom diameter is small.

*Calculated regional differences*

From the primary data in Fig. 11 one can calculate by equations (4) to (10) a number of properties of the eye that must be related to function (Fig. 12). The focal length  $f$  is calculated from equation (3) with  $n_3 = 1.4$ . The width of the Airy disc  $\Delta\alpha$ , calculated from equation (4), is least in the acute zones but does not vary much across the eye because  $D$  does not vary much. The angular subtense  $\Delta\sigma$  of the rhabdom tip as seen in the outside world is given by equation (5). The theoretical acceptance angle  $\Delta p'$  (the calculated angular sensitivity) is generated by the motion of the Airy disc

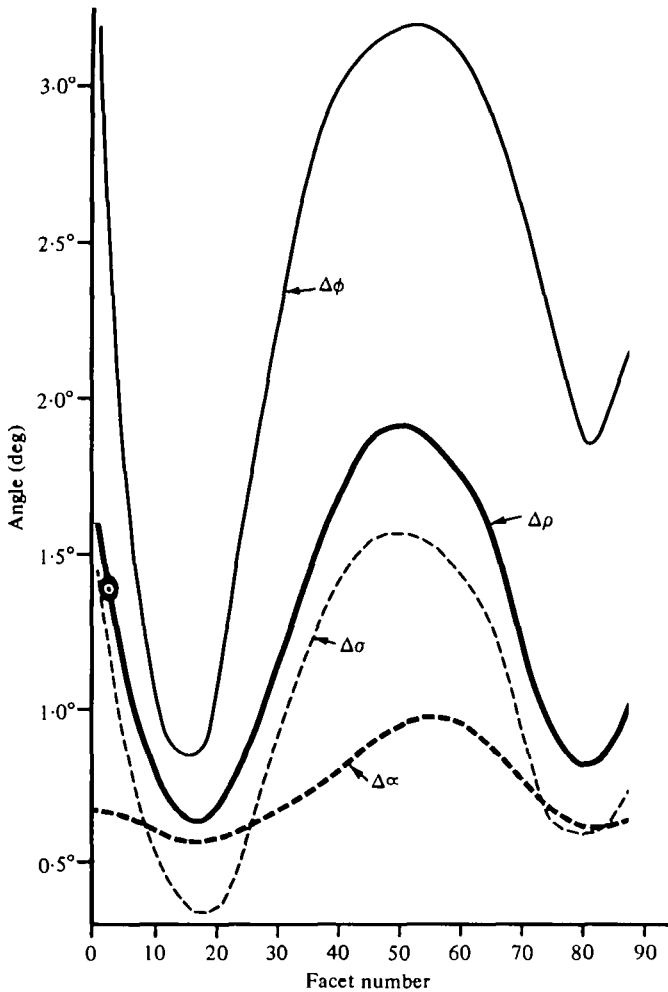


Fig. 12. The theoretical acceptance angle  $\Delta\rho'$  in different parts of the eye, calculated with its two components  $\Delta\alpha$  from diffraction and  $\Delta\sigma$  from anatomy, by use of equation (6). The regional differences in the field sizes are less than those of the interommatidial angle  $\Delta\phi$ , which is about twice as large as the acceptance angle. Note that, except in the acute zone, the theoretical acceptance angle  $\Delta\rho'$  is dominated by the anatomical component  $\Delta\sigma$ . In the acute zone the rhabdom is narrower than the Airy disc.

across the rhabdom tip, as in equation (6). The full resolution available in the Airy disc is realized only when the rhabdom is narrow compared to the disc, but some light in the Airy disc is then not caught, and sensitivity is reduced (Fig. 3). In fact, for a point source and a circular rhabdom tip, only 50% of the light in the Airy disc is caught when  $\Delta\alpha = \lambda/D = \Delta\sigma = d/f$ , assuming geometrical optics, where  $d$  is the full diameter of the rhabdom (Horridge *et al.* 1976). If, on the other hand, the cross-section of the rhabdom tip for light is taken to be a Gaussian function of width  $d$  at the 50% contour, then when  $\Delta\alpha = \lambda/D = \Delta\sigma = d/f$ , all of the light in the Airy disc should be caught by the rhabdom. This convention, introduced by Snyder (1977) in the calculations of the theoretical values of the eye parameter for different intensities, allows a readier calculation of theoretical fields by equation (3) but at present it is not known whether

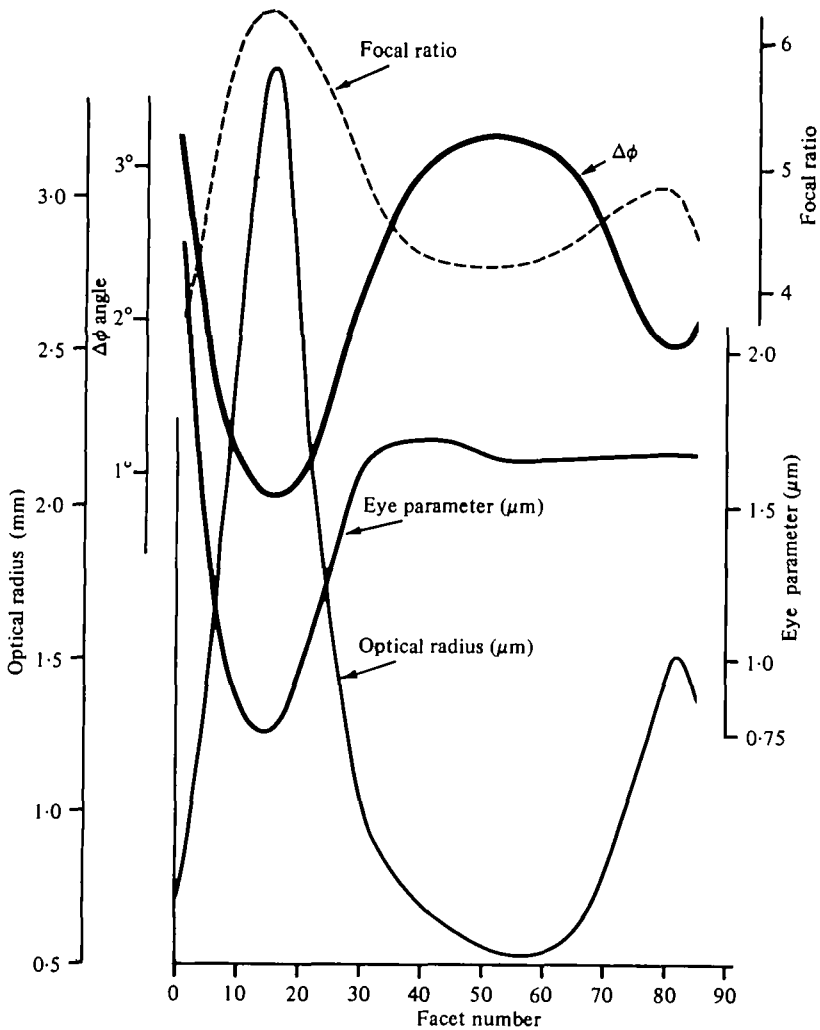


Fig. 13. The focal ratio, the eye parameter  $D\Delta\phi$ , and the optical radius at each part of the eye, calculated from the data in Fig. 11.

it is in fact the best treatment of the optical situation described above and outlined in Fig. 2.

Measurements of anatomical detail show three points of interest (Fig. 12). First, in the forward-looking acute zone the angle subtended by the rhabdom is *smaller* than that subtended by the Airy disc. Therefore focused light is rejected in a way that improves the resolving power at the expense of sensitivity. Secondly, the absolute values of these angles are remarkably small, so that the lens must have a precise anatomical shape to realize the resolution available. Thirdly, outside the acute zones the rhabdom is larger than it need be to catch the light in the Airy disc. Therefore this part of the eye shows anatomical signs of increased sensitivity at the expense of resolution.

Four other parameters have been calculated for every fifth ommatidium in Fig. 13.



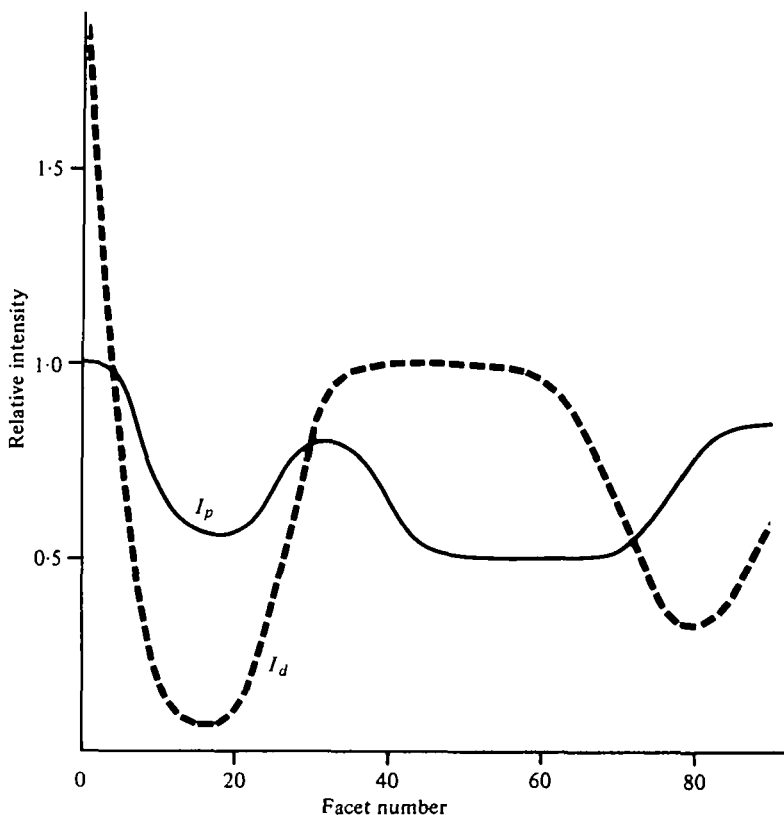


Fig. 14. The relative amounts of light caught by the rhabdom in the different parts of the eye,  $I_p$  from a point source and  $I_d$  from a diffuse source, calculated from the data in Fig. 11 by use of equations (7) and (9).

First, the optical radius ( $R = D/\Delta\phi$ ) is greatest at the acute zones, and least in the area looking sideways, being mainly dominated by differences in the interommatidial angle because  $D$  changes little. The optical radius is the most differentiated feature of the acute zone. Secondly, the eye parameter ( $D\Delta\phi$ ) is about 1.7 over much of the eye but falling to 0.7 at the centre of the forward-looking acute zone. It will be recalled that for a compound eye which normally resolves stationary objects in bright light with maximum resolution, current theory predicts that the eye parameter  $D\Delta\phi$  should be about 0.3 (Snyder, 1977) and that an eye region with  $D\Delta\phi$  of 1.7 should be adapted to vision at an intensity of one hundred thousandth of sunlight. Clearly these predictions are not fulfilled in the case of this mantid (or any other mantid so far examined).

The ratio of the calculated field size to the interommatidial angle ( $\Delta\rho/\Delta\phi$ ) is also predictable from theory. In *Ciulfina* this ratio is near 0.5 across the whole eye, which according to Snyder (1977) suggests a nocturnal eye. Some species of mantids are certainly active at night although our experience with mantids in captivity is that they require bright light to enable them to feed. Certainly, in Arnhem Land in August 1977, *Ciulfina* was twice seen feeding at night. Rossel (1978) has found that the acceptance angle of retinula cells is widened in the dark-adapted eye by some as yet unidentified mechanism. Despite these signs of effectiveness in dim light, however,

mantids still appear to be diurnal animals which depend on visual discrimination for most of their food. According to the theory of Snyder (1977) the large value of  $D\Delta\phi$  also shows that mantids are nocturnal but in fact the small size of the rhabdom and the small experimentally measured light-adapted acceptance angles (Rossel, unpublished) do not correlate with the large values of facet diameter and interommatidial angle in the way predicted for a nocturnal insect.

Sensitivity can also be estimated from the anatomical data. The effectiveness of the rhabdom tip as a light trap in different regions of the eye is calculated from equation (7) for diffuse light ( $I_a$ ) and for point sources ( $I_p$ ) and plotted in Fig. 14. As the aperture  $D$  varies little, we see that  $I_a$  and  $I_p$  are governed by the cone length and the rhabdom diameter, which in the acute zone both reduce sensitivity to a diffuse source to such an extent that in the most sensitive region at the side of the eye,  $I_a$  should be ten times as great as in the centre of the forward-looking acute zone. On the other hand, the calculated values of  $I_p$  show that the sensitivity towards a point source should be approximately constant in all parts of the eye. As this is the result that Rossel (1978) finds experimentally in the mantid *Tenodera*, we again provide support for the outline of the optics in Fig. 2. The eyes of *Ciulfina* and *Tenodera* are apparently so arranged that the different parts of the eye are similarly sensitive to point sources or very small contrasting objects, and are not equally sensitive to objects which fill the fields of the receptors. As will be found in the Discussion, this provides further evidence that the eyes of mantids do not agree with the basic premises in the recent theory of Snyder (1977).

#### *The physical basis of the acute zone*

In an eye like our own, with a single lens and a cup-shaped retina, an acute zone is formed by crowding together receptors that are usually narrower than elsewhere on the eye, so that reduced field sizes are compatible with increased density of sampling per unit solid angle. The situation is quite different in a compound eye, where increasing the resolving power of individual ommatidia depends on increasing the facet size, which inevitably reduces the number of facets on the eye, other things being equal.

In a compound eye, increasing the facet size and at the same time reducing the interommatidial angle might be done by a local increase in the anatomical radius of the eye, i.e. a flatter cornea. This arrangement, however, does not allow the smooth continuity of the facet lines on the eye surface, and it is a feature of all acute zones in insects and crustaceans that the facet lines are more perfect in the acute zones than elsewhere (Horridge, 1977*a, b*, 1978). There is, however, a way of constructing a perfect acute zone.

#### *Fitting the optical axes to the anatomy*

If the horizontal section through the eye is constructed from sections like those in Fig. 4, but illustrating the cones as if a horizontal row of them existed, one can add the optical axes outside the eye from the pseudopupil measurements of every fifth ommatidium (Fig. 15). The optical axes inside the eye are given by the morphological axes of the crystalline cones. By drawing in the normals to the corneal surface (dashed lines in Fig. 15) one can see that rays have been bent through angles up to at least  $20^\circ$  at the corneal surface and that approximately they obey Snell's law.

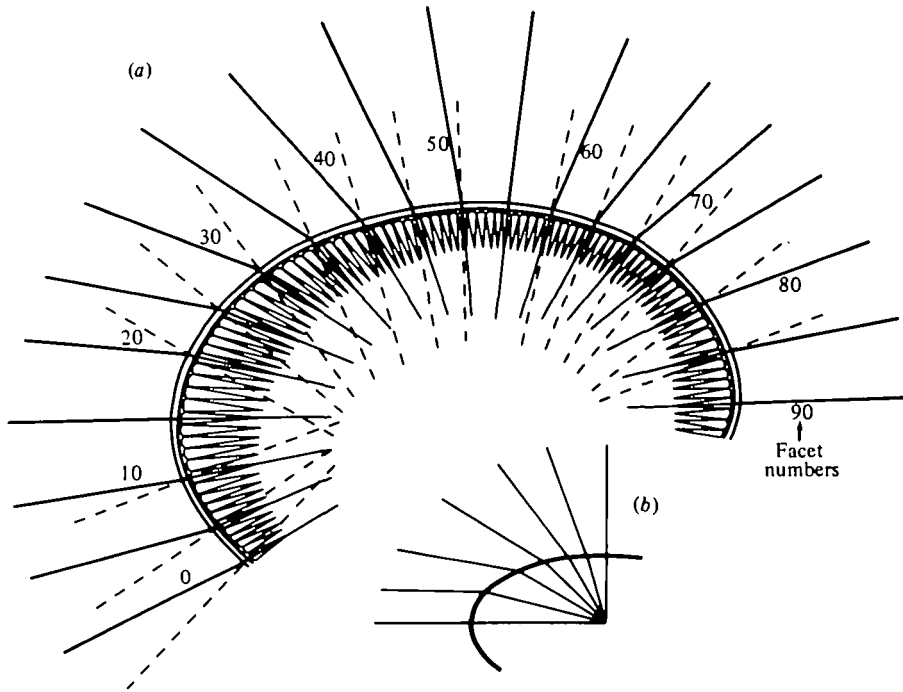


Fig. 15. The structure of the eye and its acute zones. (a) The shape of the eye in horizontal section and the positions of the cones drawn to scale have been taken from sections like that in Fig. 4. The optical axes from the pseudopupil measurements have then been superimposed, with ray paths inside the eye drawn as the anatomical axes of the ommatidia. The normals to the eye surface (dashed lines) show that each ray approximately obeys Snell's law at the eye surface and therefore it is the inclination of the crystalline cone to the surface which is largely responsible for the relative crowding of axes in the acute zones. (b) For comparison, rays emanating from the centre of an ellipsoid of refractive index 1.5 have a similar pattern.

The acute zone in *Ciulfina* is formed by tilting the anatomical axes of the ommatidia relative to the cornea. By that device the facet sizes can be larger and at the same place the interommatidial angles are smaller in the acute zone, but the local improvement is at the expense of other parts of the eye.

Drawing the rays upon the diagram of the eye, as in Fig. 15, also shows that the gathering together of the rays at the acute zone is partly a result of the elliptical shape of the eye. Where the outside of the eye is relatively flat, at the side of the eye, is where the axes of the cones are tilted progressively further from each other inside the eye and this is where the interommatidial angle, measured outside the eye, is greatest. When the axes inside are drawn to its centre, even a simple ellipsoid of glass generates the same kind of acute zone (Fig. 15b). Now it becomes apparent that the ellipsoidal shape allows for larger facets in the acute zone *without crowding out any facet rows*, because the eye *bulges* where the facets are larger.

#### *Optical radius and anatomical radius*

If the optical axes outside the eye are continued into the eye until they meet their neighbours we see that the eye has no single optical centre (Fig. 16). The optical radius ( $R$ ) is defined as the distance from the aperture to the point where neighbouri

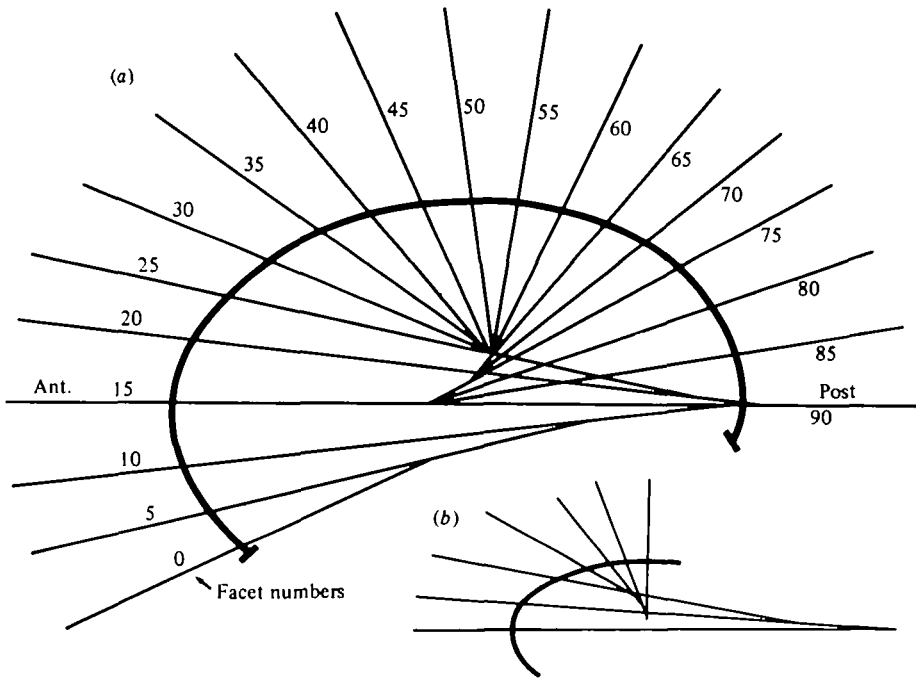


Fig. 16. The optical axes seen from outside the eye are continued into the eye until they meet, showing the large range in optical radius ( $D/\Delta\phi$ ) which is a measure of the effective local size of the eye.

optical axes meet, and is therefore given by  $R = D/\Delta\phi$  with  $\Delta\phi$  in radians. Values of  $R$  are given in Fig. 13; those in Fig. 16 are averaged over each group of five facets and therefore the extremes at the acute zones have been smoothed out. However, we see that the optical centre of the front part of the eye is just outside the back of the eye. These illustrations show that if some parts of the eye have smaller interommatidial angles than they would in a uniform eye, other parts have to compensate by having larger angles. The inset, Fig. 16(b), shows that the simple ellipsoid in Fig. 15(b) behaves in exactly the same way. The region of the eye where the cornea has the greatest anatomical curvature is the region where it is optically relatively flat, and the region at the side, where the cornea is anatomically flat is the region where the eye has the sharpest optical curvature.

*Posture in relation to light*

The characteristic habit of *Ciulfina* is to face along the trunk or branch on which it rests, and to feed on any small insects which approach, commonly on ants. The likely directions of a visual stimulus are therefore directly forwards or backwards along the branch. This fits very well with the possession of a rear-view as well as a forward-looking acute zone. Other mantids, which spend most of their time among foliage, have only the forward-looking one.

On collecting trips in Queensland and in the Northern Territory, the position in which *Ciulfina* was found on vertical branches was noted for more than 100 individuals.

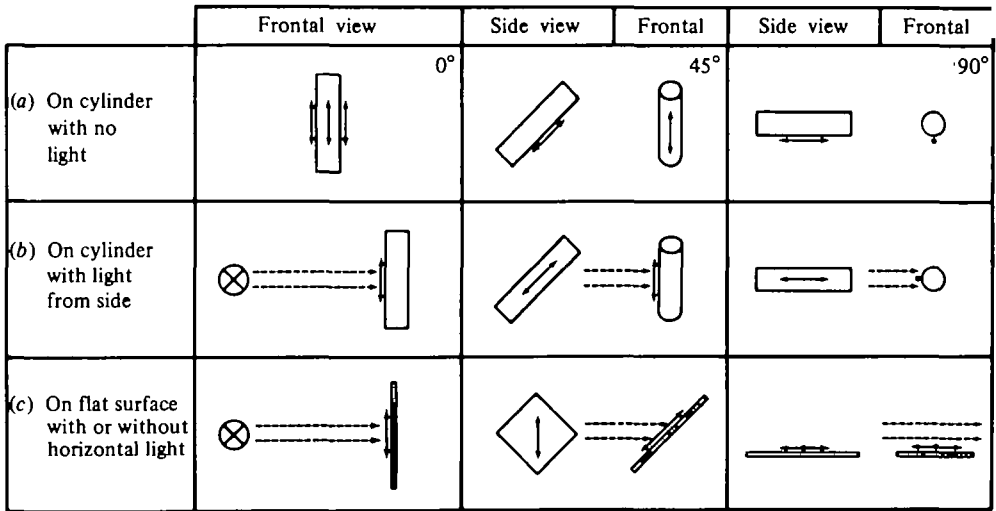


Fig. 17. The orientation taken up by *Ciulfina* when allowed to stand freely. (a) The animal always points along a cylindrical surface in the dark. (b) It prefers any light to be dorsal to it. (c) On a flat vertical or tilted surface it always rests with head pointing straight up or straight down. On a horizontal flat surface it faces in any direction relative to the light.

Half of the animals faced upwards, the other half downwards. On the other hand, animals often revealed an individual preference in the direction in which they were found, either in normal daylight, or when artificially illuminated from above.

Observations have been made in the laboratory in an effort to discover the function of the rear view acute zone. In the dark, animals resting on a twig always orient along the length of the twig, whatever the orientation of the twig (Fig. 17a). With the twig at an angle or horizontal in the dark, *Ciulfina* always rests along the twig on its underside.

When illuminated from the side, animals resting on a twig always orientate along the length of the twig, whatever the orientation of the twig, and if they are able to do so they take up a position with the light shining on their dorsal side (Fig. 17b). The direction of the light overrides gravity in this case. When illuminated from the side, but on a flat surface, *Ciulfina* always orientates facing directly uphill or downhill, however the light is arranged relative to the surface. When the flat surface is horizontal it points in any direction relative to the light (Fig. 17c). These results show the very strong tendency to orientate along a twig, or facing up or down. These are the directions from which other animals, predators or prey, are likely to approach. Under certain circumstances, however, light can exert an effect.

#### DISCUSSION

Several points may now be raised which have not recently been discussed for any compound eye. They stem primarily from the relation between the anatomical measurements and the optics of the eye, but the ramifications are diverse.

*Regional differences in rhabdom diameter*

Not only do regional differences clearly occur, they are large and they lie in the range where they must have an effect on the field size and on the amount of light caught. The regional differences in rhabdom diameter show that there is something equivalent to the different sizes of grains in film. The agreement of the measured values of the acceptance angle in mantids with the value calculated from equation (6) (Rossel unpublished) shows that the lens is focused on the rhabdom. The domination of the resolution and of the sensitivity towards extended sources by the rhabdom diameter, and not by the aperture, is seen by comparison of the curves of  $\Delta\rho'$  and  $I_a$  in Figs. 12–14 with the data in Fig. 11 from which they originate. The form of equation (6) is such that whichever is the larger of the two components,  $\Delta\alpha$  and  $\Delta\sigma$ , dominates the field size and therefore the acuity of the retinula cells. The aperture is the dominating factor only in the acute zone.

The differences in rhabdom diameter are greater than they would be if inversely proportional to the facet diameter, as predicted by equation (2). The rhabdoms in the centre of the acute zone are narrower than the Airy disc but elsewhere on the eye they are wider, which only serves to emphasize once again that in the acute zone sensitivity has been sacrificed for the sake of resolving power of individual ommatidia. According to calculation from equation (9), for ommatidia at the centre of the acute zone, less than half of the light from a point source on axis is caught by the rhabdom, and this is only partially compensated by the larger facets (Fig. 14), but the rhabdoms are also longer in the acute zones.

*Behavioural indications of eye function*

There are several details in the published work on the function of the eye of mantids which suggest that the eye primarily sees jitter of small objects rather than patterns, and that it does not reconstruct areas that are large enough to fill several visual fields. The most effective stimulus in eliciting a strike is a small object the size of a fly which must move in a jerky way and should have moving legs and wings (Rilling, Mittelstaedt & Roeder, 1959). Mantids stare fixedly for a long time before they strike at prey, and they are inhibited if presented with numerous prey simultaneously. The narrower a visual field the smaller are the dark contrasting objects it can resolve, but to detect an object which moves jerkily, over a relatively long period of time, does not require as many sampling stations as for the perception of all the pattern that individual ommatidia can resolve. At present, with our limited knowledge of the behavioural thresholds, the relatively wide separation of very narrow fields is to be understood as a specialization for seeing very small dark contrasting objects which move relative to the head. Tests with dragonflies, for example, show that in field tests they respond to black targets subtending only 5 min of arc or more at the eye (Mokrushov, 1970). An eye specialized to do this would have fewer but larger facets than an eye of the same size that is specialized to see a maximum range of stripe widths. At present we have no model to describe the optimum separation of axes in an eye which looks for small moving objects because the optimum depends on the angular extent of the expected movement.

The 'fovea' of a mantid was defined by Maldonado & Barrós-Pita (1970) as the region necessary for a successful strike at a fly, as demonstrated by covering different

parts of the eye with opaque paint. This fovea is not the region of largest facets or smallest interommatidial angle, but is the surrounding annular region. This finding remained a puzzle until Collett & Land (1975) made the suggestion that the annulus corresponds to the edges of a prey of typical size centred at the strike distance. This result implies that the mantis is *centring the direction of the head* by the total silhouette of the fly and then estimating the object distance from the actual locations of the facets looking at the edge of the fly. Again, this suggests that the mantis is more interested in the movement and direction of edges rather than in the reconstitution of either large areas or small patterns.

#### *Anatomical basis of the acute zone*

The acute zone is formed partly by the tilting of the ommatidial axes to the line at right angles to the cornea, but that is not the whole story because the cornea is not uniformly curved. The interesting feature that emerges from a study of *Ciulfina* eye is that the cornea at the acute zone is physically more curved than at the side of the eye, but optically the eye is flattest at the acute zone in the sense that the optical radius is there greatest (Fig. 16). The bulging front of the eye serves to contain the longer cones of the acute zone and also to accommodate the larger facets. The organization of the eye depends on the tilt of the ommatidial axes, as in Fig. 15, but this may have been possible only because in the mantid eye the cornea is flat and the distal end of the crystalline cone is smoothly curved. If the power of the lens had depended on the convexity of the facet outer surface, as it does to a large extent in most orders of insects, it is possible that the acute zone of the mantid eye could not have evolved.

#### *Function of the iris at the tip of the cone*

By the theory presented here, the width of the field is dependent on the angular width of the rhabdom, or of the neck of the cone, subtended in the outside world. There is therefore a conflict with an earlier theory in which the increase in acceptance angle on dark-adaptation, confirmed by Wilson (1975), was supposed to be due to changes in refractive index around the rhabdom (Horridge, 1966). The point is that the action of the rhabdom as a light guide is after the stage at which the acceptance angle is decided. We must therefore look for another mechanism which can act in equation (6). The neck of the cone is the obvious place. Radial pigment movement at this point, as described in the dragonfly (Horridge, 1969) could reduce the effective width from that of the whole cone neck to that of just the central thread (Fig. 6*b, c*). Such a mechanism would explain the dense central core of the cone (Fig. 7*a*) and also the increase in size of the pseudopupil on dark-adaptation, but further work is needed to prove that this is in fact the mechanism.

#### *Separation of the fields*

A large interommatidial angle, relative to the field width, is characteristic of mantid eyes, and *Ciulfina* is no exception. Even at the centre of the acute zone the fields do not overlap (Fig. 9). It is not possible that the large values of  $D\Delta\phi$  indicate a crepuscular eye as would be inferred from the only extant theory (Synder, 1977), because the rhabdoms are narrow. Some other factor is at work, but the only suggestion so far is

that the mantids depend for some reason on a large overlap of the sectors covered in common by the forward-looking and upward-looking regions of the two eyes, and therefore the density of sampling stations over the eye as a whole is less than in other insects (Horridge, 1977*b*). The difficulty is that the mechanism that lies behind this correlation between eye parameter and binocular overlap has not been found.

#### *Light-catching power of eye regions*

Measurements from the anatomy lead to the conclusion that the ability of the eye to catch light is not equal in different parts of the eye when diffuse sources are considered. On the other hand, the different regions are better matched in ability to catch light from a point source. This prediction has already been confirmed experimentally by Rossel (1978) in the mantis *Tenodera*. Several conclusions can be drawn.

The theory of insect vision outlined by Snyder (1977) depends on several assumptions that are not validated by experimental work. Primarily the theory assumes that all parts of the area seen by the eye are sampled simultaneously. Secondly, it is assumed that extended objects are seen as such, or at least there is spatial summation of some kind such that larger objects are more readily seen because they emit more photons *in toto*. In contrast to this, experimental work suggests that the important feature is the flicker caused by the movement of edges, not by bands of different *width*, across the eye. Much insect visual behaviour depends on the directions of contrasting edges relative to the eye, and there are several examples where objects subtending less than the interommatidial angle have a strong influence according to their angular size (reviewed by Horridge, 1978). Possibly eye tremor is significant. One series of experiments which set out to test whether the edges or the areas are seen in a regular striped pattern (by the crab *Carcinus*) showed that some individuals behave as if they see mainly the edges (Horridge, 1966). Such experiments could be extended now with more insight.

There are strong indications therefore from the measurements on *Ciulfina* that the mantid eye is optimized for seeing objects which are effectively black dots. Possibly the eye has evolved so that it sees only the highest spatial frequency components of sharply contrasting edges. To do this it would need small fields and high sensitivity, and would therefore have to sacrifice coverage, having only a limited eye size. If eye tremor compensates for lack of coverage we must question whether the animal has information, other than visual, about its own eye tremor.

#### CONCLUSION

In this paper an attempt is made to measure the appropriate anatomical features of a compound eye that are relevant to the understanding of its function. To a large extent, however, the function must be understood before the appropriate measurements can be made. The measurements have been published as soon as the theory seemed secure. Similarly, when an engineer examines the structure of a bridge he makes the appropriate measurements that allow an estimate of its performance. A bridge, however, 'works' mainly in one way, and within one discipline. When four engineers, specializing in optics, strength of materials, electrical control systems and moving mechanical parts, examine an object of complex function like a giant telescope or an



aeroplane they make measurements appropriate to the particular part of the function that they consider most relevant. In the case of biological structure, even one so specialized as an eye, we do not know what is the full range of its significance *to the animal*, and therefore the measurements we make are relevant to the mechanisms of action that are already demonstrated.

## REFERENCES

- COLLETT, T. S. & LAND, M. F. (1975). Visual control of flight behaviour in the hoverfly *Syrirta pipiens* L. *J. comp. Physiol.* **99**, 1-66.
- HARDIE, R. (1978). Unpublished measurements on dipteran retinula cells.
- HORRIDGE, G. A. (1966). The retina of the locust. In *The Functional Organisation of the Compound Eye* (ed. C. G. Bernhard), pp. 513-541. Oxford: Pergamon Press.
- HORRIDGE, G. A. (1969). Unit studies of the retina of dragonflies. *Z. vergl. Physiol.* **62**, 1-37.
- HORRIDGE, G. A. (1977*a*). The compound eye of insects. *Sci. Am.* **237** (July), 108-120.
- HORRIDGE, G. A. (1977*b*). Insects which turn and look. *Endeavour*, N.S. **1** (1), 7-17.
- HORRIDGE, G. A. (1978). A different kind of vision. The compound eye. In *Handbook of Perception*. vol. 9 (ed. E. Carterette and M. Friedman). Academic Press.
- HORRIDGE, G. A. & BARNARD, P. B. T. (1965). Movement of palisade in locust retinula cells when illuminated. *Q. Jl microsc. Sci.* **106**, 131-135.
- HORRIDGE, G. A., MIMURA, K. & HARDIE, R. C. (1976). Fly photoreceptors. III. Angular sensitivity as a function of wavelength and the limits of resolution. *Proc. Roy. Soc. Lond. B* **194**, 151-177.
- LILLYWHITE, P. G. (1977). Single photon signals and transduction in an insect eye. *J. comp. Physiol.* **122**, 189-200.
- MCINTYRE, P. (1978). Unpublished measurements on mantid crystalline cones.
- MALDONADO, H. & BARRÓS PITA, J. C. (1970). A fovea in the praying mantis eye. I. Estimation of the catching distance. *Z. vergl. Physiol.* **65**, 58-78.
- MOKRUSHOV, P. A. (1972). Visual stimuli in the behaviour of dragonflies. I. Hunting and settling. *Libellula quadrimaculata* L. *Vestnik Zoologia. Kiev.* no. 4, pp. 46-51.
- RIBI, W. A. (1976). The first optic ganglion of the bee. II. Topographical relationships of the monopolar cells within and between cartridges. *Cell Tiss. Res.* **171**, 359-373.
- RILLING, S., MITTELSTAEDT, H. & ROEDER, K. D. (1959). Prey recognition in the praying mantis. *Behaviour* **14**, 164-184.
- ROSSEL, S. (1978). Regional differences in photoreceptor performance in the eye of the praying mantis. *J. comp. Physiol.* (in the press).
- SOUTHALL, J. P. C. (1933). *Mirrors, Prisms and Lenses*, 3rd ed. New York: Macmillan.
- SNYDER, A. W. (1977). Acuity of compound eyes: physical limitations and design. *J. comp. Phys.* **116**, 161-182.
- WILSON, M. (1975). Angular sensitivity of light- and dark-adapted locust retinula cells. *J. comp. Physiol.* **97**, 313-328.

*Note added in proof.* A further seasons' work recording from retinula cells of *Ciulfina* intracellularly, by Ljerka Marcelja, reveals a *dark-adapted* value of  $\Delta\rho = 0.85^\circ$  near the centre of the anterior acute zone, and up to  $2.9^\circ$  at the side of the eye near facet 50 (Fig. 12), but with similar absolute sensitivity to a point source ( $0.4^\circ$ ) at the peak wavelength (548 nm).