

## Eye morphology and optics of the double-eyed mysid *Euchaetomera typica*

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### Abstract

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The structure and optics of the mesopelagic double-eyed mysid crustacean *Euchaetomera typica* Sars, 1884 are described for the first time. The lateral eye is a typical refracting superposition eye with a wide field of view ( $172^\circ$ ) and low resolution (interommatidial angle of  $7.3^\circ$ ). The antero-dorsal part of the eye is elongated due to the extension of the clear zone. This dorsal eye has a restricted field of view ( $33^\circ$ ) but much higher resolution ( $1.5^\circ$ ). The dorsal eye also uses refracting superposition optics, although the optical array is unusual as many of the peripheral ommatidia lack crystalline cones. The centre of curvature of the cornea is in front of the flattened rhabdom layer whereas the axes of the crystalline cones are centred on a point about twice as deep as the rhabdom layer. This results in a well-focused eye, free of spherical aberration. There is a remarkable similarity in eye structure between this species and some mesopelagic double-eyed euphausiid crustaceans.

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## Introduction

The eyes of mesopelagic animals often show asymmetry as a result of adaptations to the unique distribution of light in the oceans. As a result of the selective absorption and scattering of photons, light is attenuated logarithmically with depth and is highly directional. This results in a dim light environment in which the upwelling irradiance is around 0.5% of the downwelling irradiance (Denton 1990).

The eyes of mesopelagic fish (Locket 1977; Lythgoe 1979), cephalopod molluscs (Chun 1910; Matsui *et al.* 1988) and various crustacean taxa (Land *et al.* 1979, 1989; Gaten *et al.* 1992) have been shown, in some species, to be modified in the dorso-ventral axis, apparently in response to the light distribution. Modifications described in crustacean eyes range from internal variations in the rhabdom layer (Gaten *et al.* 1992) and tapetum (Shelton *et al.* 1992; Johnson *et al.* 2000) in decapods, to the development of double-eyed species of euphausiids (Land *et al.* 1979) and hyperiid amphipods (Land 1989).

The order Mysida includes around 120 genera of shrimplike crustaceans including shallow-, mid- and deep-water species. Their eyes are generally of the refracting

superposition type (Nilsson *et al.* 1986), although there are considerable structural variations depending on the depth from which the animals are obtained. Shallow-water species, such as *Praunus flexuosus* and *Neomysis integer*, have stalked, spherical eyes (Hallberg 1977), although in the case of *Dioptrymysis paucispinosa* this is augmented by an acute zone that operates on the principle of the simple eye (Nilsson and Modlin 1994). Some mesopelagic genera, such as *Euchaetomera* and *Euchaetomeropsis* (Murano 1977), have double eyes, whilst deep-water species have eyes of various shapes, usually with reduced or absent optics (Zharkova 1970; Elofsson and Hallberg 1977).

This paper describes the structure and optics of the double eye of *Euchaetomera typica* Sars, 1884 in the context of previous work on the apparently similar double eyes of some euphausiids (Land *et al.* 1979). A closely related species, *Brutomysis vogtii* (*Euchaetomera tenuis*), was illustrated in Chun (1896) but there has been no further examination since then of double-eyed mysids.

## Results

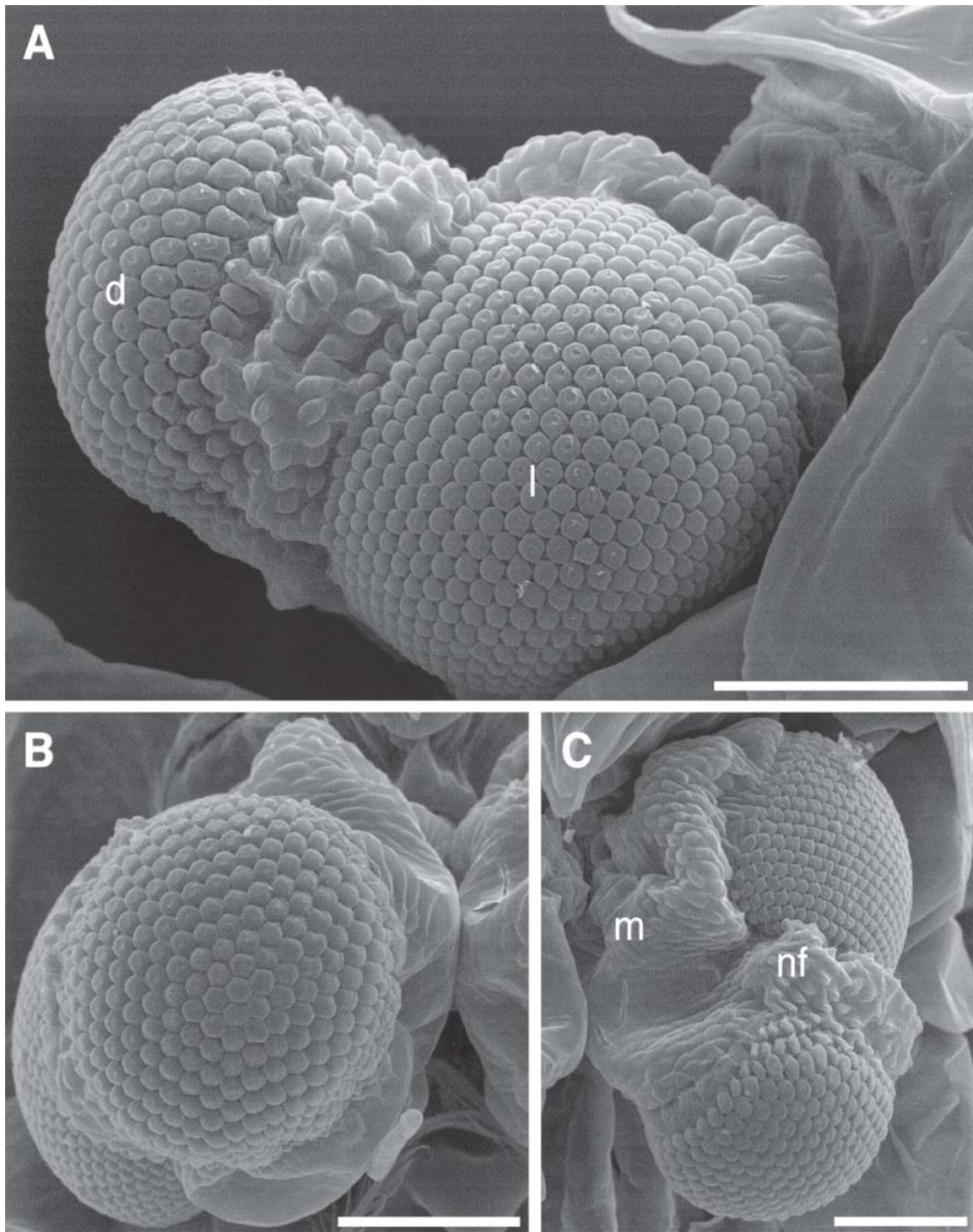
### *External appearance*

The eye of *Euchaetomera typica* (Fig. 1A) consists of two parts, a lateral eye and a dorsal, or anterior, eye (Fig. 1B). The eye is borne on a short eyestalk and the dorsal eye is angled upwards at 30° to 50° in fixed specimens. In live specimens observed immediately after capture the eyes were capable of rotation through almost 90° from a directly forward view to directly upwards. The lateral eye is hemispherical with a diameter of around 400 µm and is covered with about 500 circular facets arranged in a hexagonal pattern. The facets have a mean diameter of 21.3 µm (SD 0.73 µm).

The dorsal eye projects from the antero-dorsal region of the lateral eye and takes the form of a short cylinder with a diameter of around 350 µm with a hemispherical distal end. The facets (around 175 in number) are similar in appearance to those of the lateral eye, but are around 50% larger in surface area (diameter 26.6 µm, SD 0.48 µm). The two parts of the eye are separated by what appears to be a region of modified facets. On the lateral face the rows of modified facets can be clearly seen although they do not have the appearance of functional facets (Fig. 1A). On the medial face, the modified facets are less clear and there seems to be a mixture of corneal facets and eyestalk cuticle (Fig. 1C).

### *Internal appearance of the lateral eye*

When sectioned, the lateral eye has the typical appearance of a spherically symmetrical superposition eye, with a distal crystalline cone cell layer separated by a clear zone from the proximal rhabdom layer (Fig. 2A). The cornea is convex externally and does not vary much in thickness (2–3 µm). Beneath the cornea each ommatidium has two corneagenous cells whose thin nuclei lie towards the periphery of the cells. In the centre of the ommatidium, the four crystalline cone cells taper distally to join the centre of the facet (Fig. 2B). The crystalline cones are bullet-shaped, tapering proximally with a distinct waist just over half way down (Fig. 2B). They are circular in cross-section and are each



**Fig. 1**—Scanning electron micrographs of the eyes of *Euchaetomera typica*. —**A**. Lateral view of the left eye showing the dorsal eye (d) extending upwards from the spherical lateral eye (l). —**B**. Distal end of the dorsal eye showing hexagonal packing of the facets. —**C**. Dorsal view of both parts of the eye, showing the non-functional facets (nf) separating lateral and dorsal eyes. The medial face of the eye (m) consists of modified facets and eyestalk cuticle. Scale bars for all figures = 200  $\mu$ m.

secreted by two of the crystalline cone cells. The cones do not stain evenly, but are stained more densely towards their periphery (Fig. 2B). Distal pigment cells are found between the cones. They contain dark shielding pigment that extends from the distal end of the cone to a point about three-quarters of the way down (Fig. 2B). The clear zone is filled with retinula cells that extend from the crystalline cones down to the basement membrane. The retinula cell nuclei are located just proximal to the crystalline cones (Fig. 2B). The rhabdoms are square in cross-section with a width of approximately 11.5  $\mu\text{m}$  at the distal end, tapering proximally. They are around 25  $\mu\text{m}$  long, flattened distally and have a more rounded proximal end. They have the layered appearance often found in crustacean rhabdoms due to the interlocking rhabdomeres contributed by the retinula cells. The rhabdoms contain up to 20 alternating layers. The retinula cells contain proximal shielding pigment that extends from below the basement membrane to above the rhabdoms, indicating that the eyes were light adapted. There was no indication of gross light-induced damage to the rhabdoms. The retinula cell axons contain shielding pigment and extend through the basement membrane to the lamina, the first of the three neuropiles (Fig. 2A). At the junction between the two eye types the lamina appears to form separate lobes for the lateral and dorsal eyes (Fig. 2D).

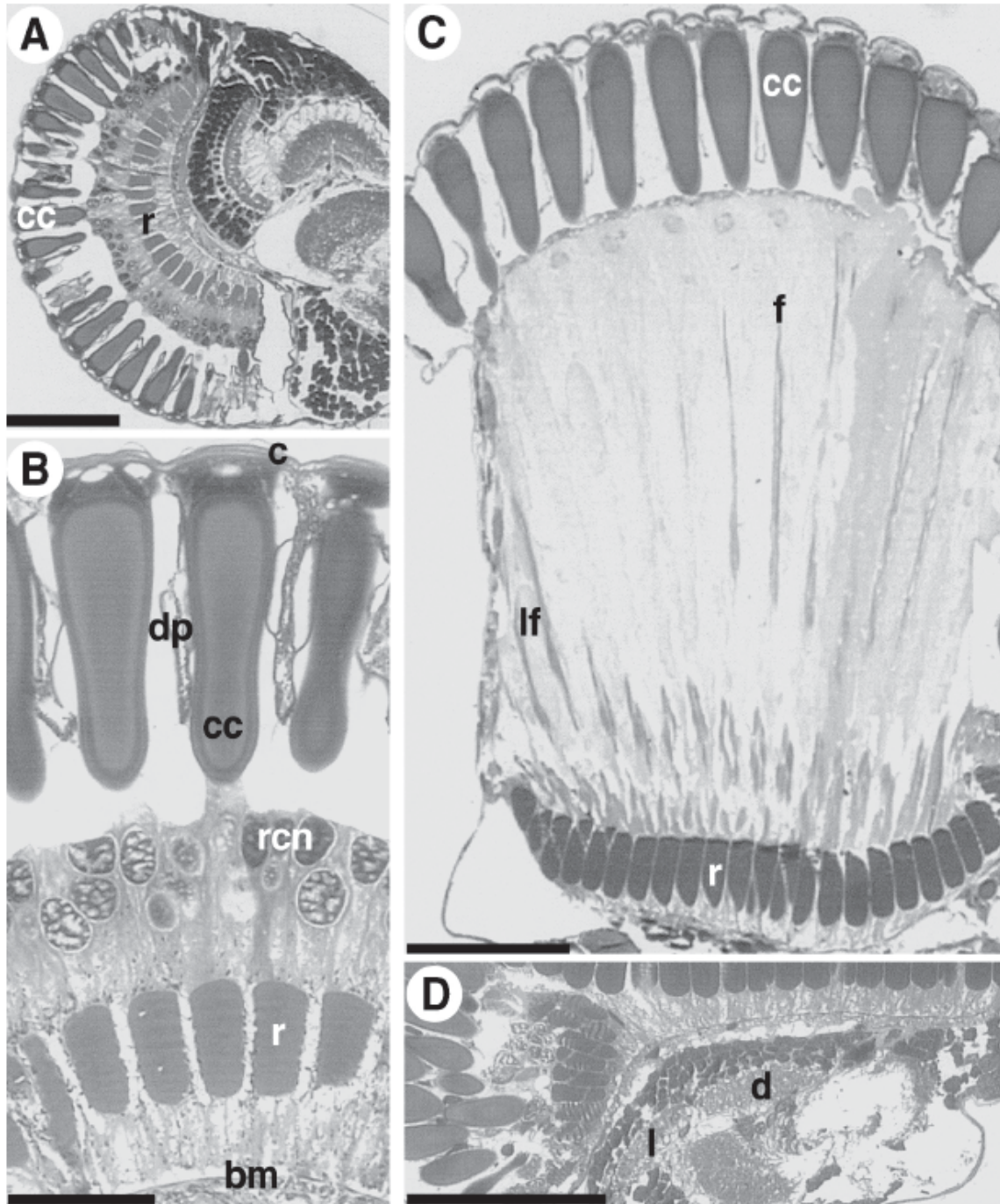
#### *Internal appearance of the dorsal eye*

Although the radii of curvature of the surfaces of the two eyes are similar, the dorsal eye is much more elongate than the lateral eye (Fig. 2C). The cornea, corneagenous cells and crystalline cone cells (Fig. 3A,B) are similar to those seen in the lateral eye. However, the crystalline cones are more elongate and tapered proximally (Fig. 3A). They are formed by two cone cells and adjacent cones are separated along much of their length by distal pigment cells (Fig. 3C). The proximal ends of the cones project through a dense layer of shielding pigment (Fig. 3D). The clear zone contains the cell bodies of the retinula cells and a contiguous layer of retinula cell nuclei is present at the distal margin of the clear zone. These are mostly of similar appearance, but one cell per ommatidium has a larger nucleus that is displaced proximally from this layer (Fig. 3A,D).

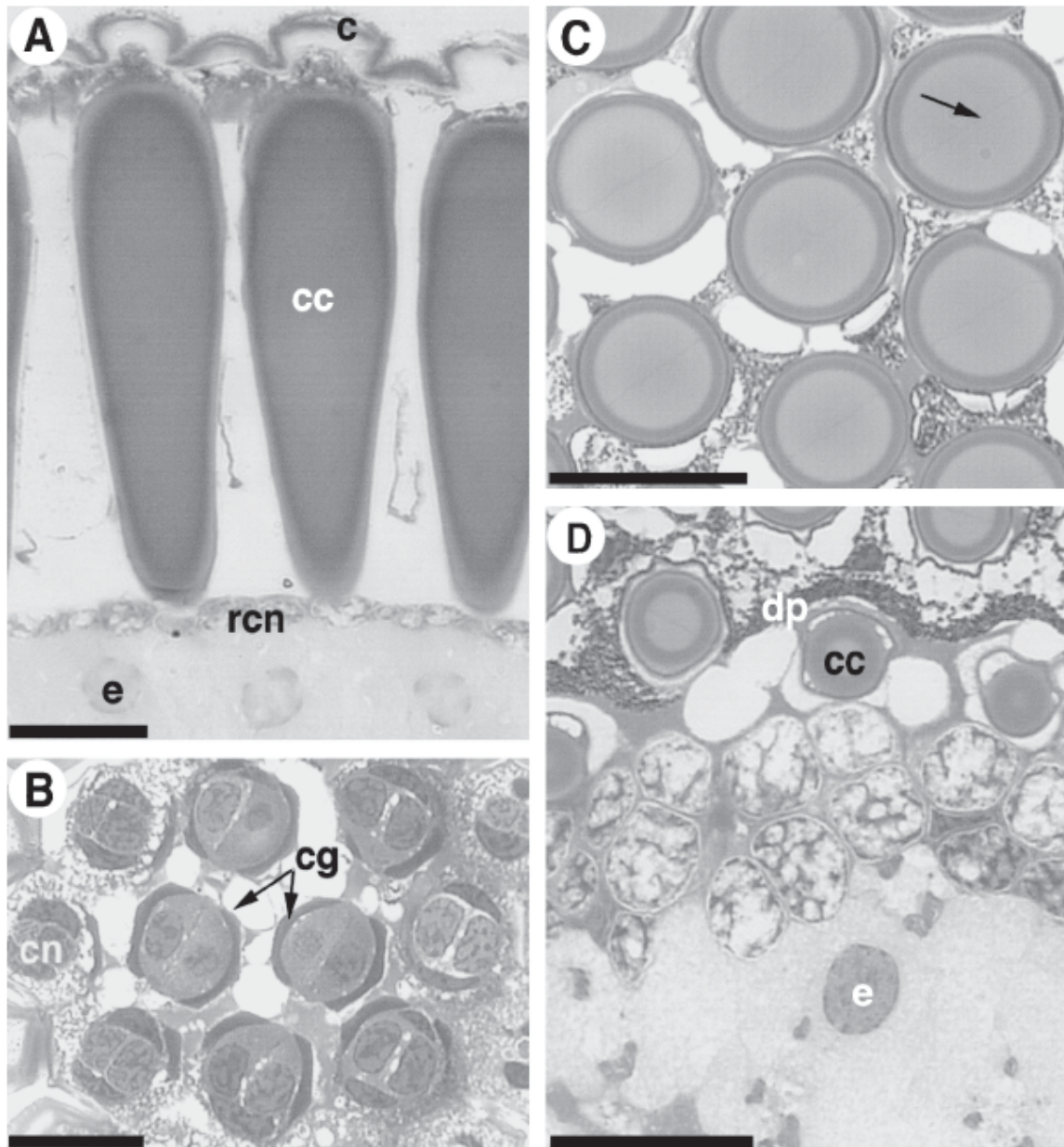
Distally the retinula cell cytoplasm appears to have few cellular inclusions (Fig. 4A). More proximally the cytoplasm is filled with intracellular membranes (Figs 2C, 4B). Associated with each ommatidium there are also 'filaments' extending across the full length of the clear zone (Figs 2C, 4A), which appear to be membranous rather than of more solid structure. Distally there are three 'filaments' and more proximally there are four. The appearance of the fourth may correspond to the disappearance of the distal eccentric retinula cell nucleus, suggesting that at least one of these threads may correspond to the proximal extension of this retinula cell. In contrast to the situation in the lateral eye, the dorsal eye does not have equal numbers of cones and rhabdoms. A typical section through the centre of the eye (Fig. 2C) shows 12 cones and around 22 rhabdoms. The central rhabdoms are clearly connected to the cones by retinula cell membranes, whereas the retinula cells forming the more peripheral rhabdoms have their nuclei along the sides of the eye as described below.

The dioptric apparatus is modified along the sides of the dorsal eye. The facets on the lateral part of the dorsal eye (Fig. 4D) still cover recognizable corneagenous cells and



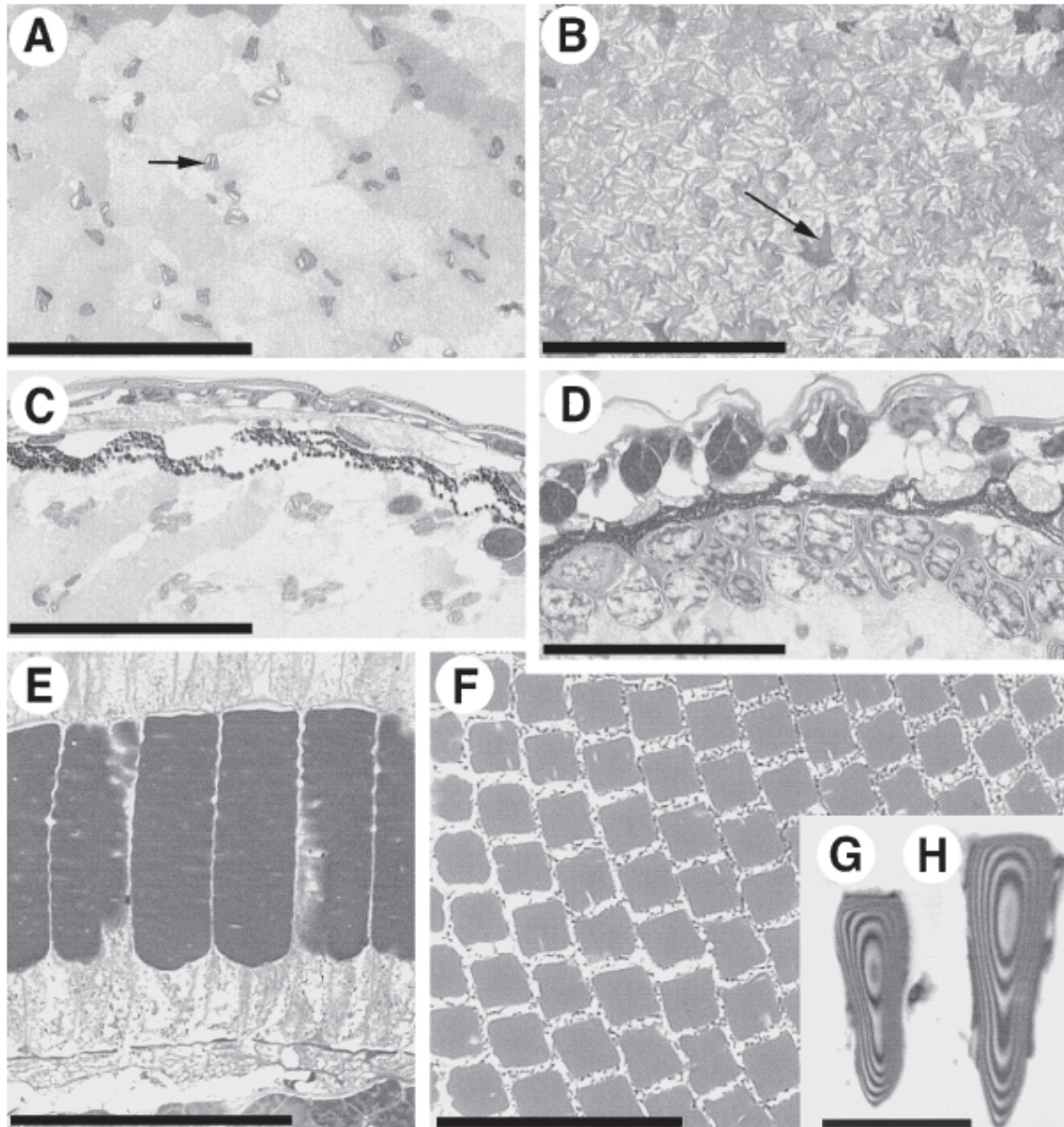


**Fig. 2**—Light micrographs of semithin sections through the eye of *Euchaetomera typica*. —**A**. Horizontal section through the lateral eye showing the distal crystalline cone layer (cc) and the proximal rhabdom layer (r) separated by a clear zone. Scale bar = 100  $\mu$ m. —**B**. Ommatidia from the lateral eye showing the thin cornea (c) and the crystalline cones (cc). Distal pigment cells (dp) are found between the cones. The retinula cells have distal nuclei (rcn) and extend from the bases of the cones down to the basement membrane (bm). Scale bar = 30  $\mu$ m. —**C**. Longitudinal section through the dorsal eye showing the hemispherical crystalline cone layer and flat rhabdom layer. Membranous filaments (f) connect the central rhabdoms to the crystalline cones whereas those from the other rhabdoms (lf) project to the sides of the eye. Scale bar = 100  $\mu$ m. —**D**. Section taken through the junction of the two rhabdom layers showing the separation of the lamina into lateral (l) and dorsal (d) parts. Scale bar = 100  $\mu$ m.



**Fig. 3**—Light micrographs of the dorsal eye of *Euchaetomera typica*. —**A**. Longitudinal section through the dioptic apparatus, showing the thin cornea (c) and the variable staining within the crystalline cone (cc). Below the cones, a contiguous layer of retinula cell nuclei (rcn) can be seen with a single, more proximal, eccentric nucleus (e) in each ommatidium. —**B**. Transverse section through the distal part of several ommatidia showing the four cone cell nuclei (cn) and the more peripheral corneagenous cell nuclei (cg). —**C**. Transverse section through the mid cone region. Note that the cones are bipartite (arrow) and that they stain more densely towards the margin of the cone. Distal shielding pigment cells are present between the cones. —**D**. This oblique section through the distal clear zone shows the dense pigment shield (dp) through which the proximal tips of the cones (cc) project. The layer of retinula cell nuclei and an eccentric nucleus (e) can also be seen. Scale bars for all figures = 50  $\mu$ m.





**Fig. 4**—**A**. Transverse section through the distal part of the clear zone showing the absence of stainable material, with the exception of three or four columns of membranes (arrow) in each ommatidium. —**B**. At the proximal end of the clear zone, the membranes are more apparent and particularly dense projections close to the distal end of the rhabdom (arrow) can be seen. —**C**. The clear zone is separated from the cuticle on the medial side of the dorsal eye by a dense pigment screen. —**D**. On the lateral side, the nuclei of corneagenous cells and crystalline cone cells are seen overlying the pigment shield. —**E**. Longitudinal section through the rhabdoms showing the parallel sides and layered appearance. Shielding pigment is present all around the rhabdoms and below the basement membrane. —**F**. Transverse section through the rhabdom layer showing the square rhabdoms and dense shielding pigment. —**G**, **H**. Interference micrographs of isolated crystalline cones from the lateral and dorsal eyes, respectively. Scale bar for all figures = 50  $\mu\text{m}$ .

cone cells. Beneath these are a dense layer of shielding pigment and a continuous layer of retinula cell nuclei, but no crystalline cones. On the medial face of the dorsal eye, a layer of epidermal cells and a layer of shielding pigment separate the clear zone from the cuticle (Fig. 4C).

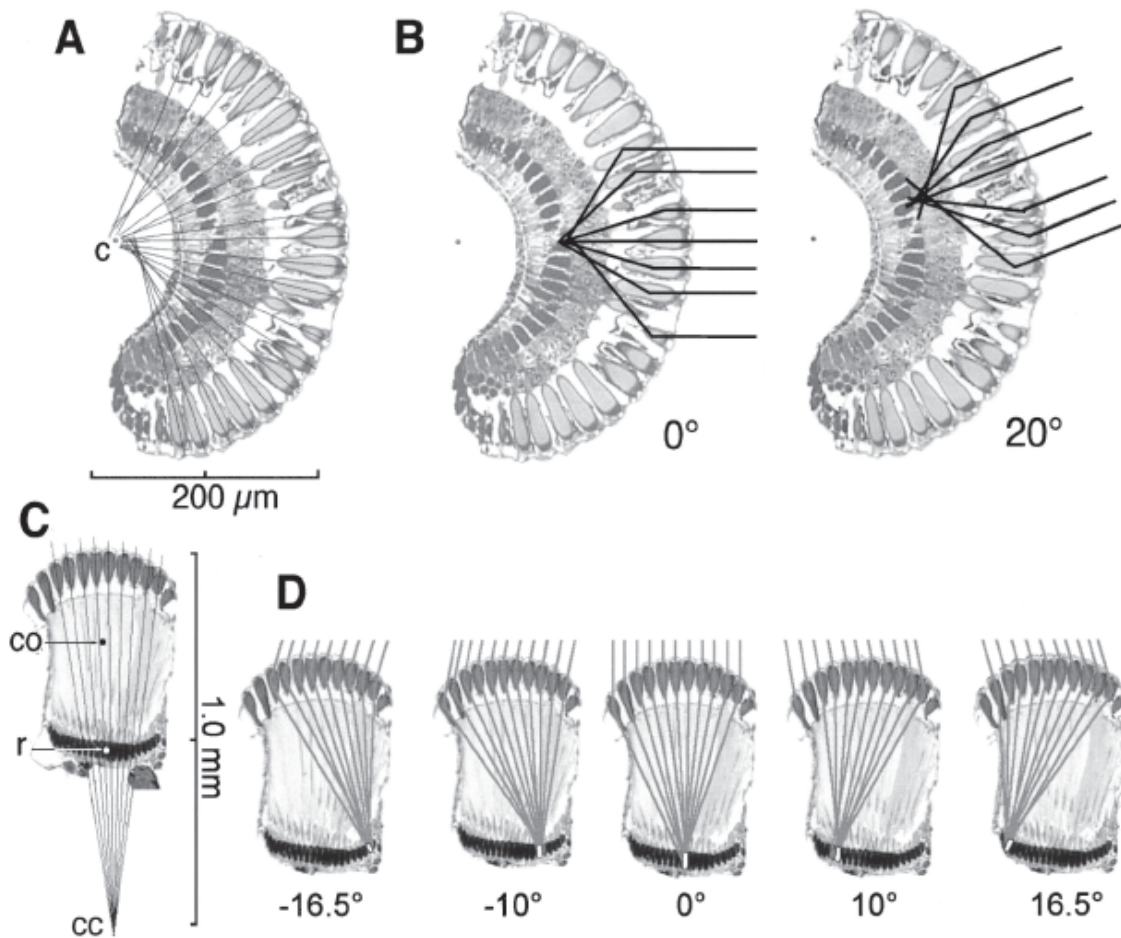
The rhabdoms are parallel-sided, flattened distally and rounded proximally (Fig. 4E). They are square in crosssection (Fig. 4F) with a width of approximately 14  $\mu\text{m}$  and a length of around 45  $\mu\text{m}$ . Each rhabdom consists of up to 36 alternating layers of microvilli. The rhabdom layer is flat centrally, but tends to be concave towards the edge of the eye (Fig. 2C). Proximal shielding pigment is present in the retinula cells from the distal end of the rhabdom down to below the basement membrane.

### *Optics*

Although differing in size, the crystalline cones of both eyes show a similar distribution of interference fringes when viewed using interference microscopy (Fig. 4G,H). No attempt was made to calculate the refractive index profiles of these cones due to the extended period of fixation. They do, however, show the typical appearance of cones taken from eyes that use refracting superposition optics (see Nilsson 1990). In view of this, and the fact that no mysid has yet been described that does not use these optics, the ray paths for each eye type were drawn assuming that refracting superposition would occur. All rays entering ommatidia axially are transmitted directly to the rhabdom. Off-axis rays are redirected due to the continually varying refractive index within the crystalline cone in such a way that the angle of incidence (with respect to the ommatidial axis) is equal to the angle at which the ray leaves the cone. As it is not possible to plot the precise course of the rays through the crystalline cones the ray paths are superimposed onto micrographs of sections through the eye with this change in direction occurring in the middle of the cone (Fig. 5).

The cornea of the lateral eye has a radius of curvature of around 200  $\mu\text{m}$  with most of the crystalline cones centred around the same point (Fig. 5A). Parallel rays incident on the eye are refracted within the crystalline cones so that superposition occurs within the rhabdom layer (Fig. 5B). Spherical aberration is caused by the most peripheral cones contributing to the image. The field of view, calculated as the angle subtended by the retina at the centre of curvature of the cones, is  $172^\circ$  in the horizontal plane. As a result of this, the animal has all round vision except where its own body obscures the view posteriorly. The interommatidial angle, which ultimately limits the resolution of the eye, is  $7.3^\circ$ . The dorsal eye does not show the same spherical symmetry. Although the radius of curvature of the cornea is 250  $\mu\text{m}$ , the cones are centred on a point approximately 1000  $\mu\text{m}$  from the cornea, around twice the distance between the centre of the cones and the centre of the rhabdom layer (Fig. 5C). The angle subtended by the retina at the centre of curvature is  $33^\circ$ . Parallel rays of light axial to the central ommatidium are focused onto the target rhabdom with very little overlap onto adjacent rhabdoms. When the light is moved off-axis, the image continues to be well focused up to the limit of the field of view when the light is  $16.5^\circ$  off-axis (Fig. 5D).





**Fig. 5**—**A.** Lateral eye showing the crystalline cone axes. These are centred on the same point (c) as the eye surface and the rhabdom layer. —**B.** Parallel rays incident on the eye are focused onto the axial rhabdom. Some spherical aberration is caused by the most peripheral rays contributing to the image. —**C.** In the dorsal eye the point on which the crystalline cone axes are centred (cc) is much deeper than the centre of curvature of the cornea (co). The rhabdom layer (r) is roughly half way between the former point and the cornea. —**D.** Parallel incident rays are focused without aberration up to the limit of the field of view.

## Discussion

The structure of the lateral eye of *Euchaetomera typica* follows the pattern seen in mysids from shallow water (Hallberg 1977; Nilsson *et al.* 1986; Richter 1999). The dioptric apparatus consists of a thin convex corneal facet secreted by two corneagenous cells and a bullet-shaped crystalline cone secreted by two crystalline cone cells (the two accessory cone cells do not contribute to cone formation). The remainder of the ommatidium is occupied primarily by seven retinula cells which have distal nuclei and which contribute layers of microvilli to form a rhabdom. The pigment shield is formed by distal pigment cells between the cones and by proximal pigment within the retinula cells. No evidence was found for the presence of an epirhabdom as reported from several species (e.g. *Praunus flexuosus*, Hallberg 1977; *Neomysis integer*, Richter 1999), although a more

densely staining region around the distal ends of the rhabdoms of the dorsal eye was observed. This bears some resemblance to structures seen at the distal ends of the rhabdoms in the eyes of the euphausiid *Thysanopoda tricuspidata* (Meyer-Rochow and Walsh 1978). An eighth retinula cell has been recorded from some mysids (*P. flexuosus*, *Siriella norvegica*, *Mysidopsis gibbosa*, Hallberg 1977) although not from others (Hallberg 1977; Richter 1999). Only seven retinula cells could be seen in *E. typica* although an eccentric retinula cell nucleus could be seen in each ommatidium of the dorsal eye. Such eccentric nuclei are often typical of the eighth retinula cell.

There was no evidence for the presence of proximal reflecting pigment cells. Tapeta have been recorded from several species of mysid from shallow water (Hallberg 1977), but they occur inconsistently in those from deeper water. In species of *Amblyops* tapeta are absent (Elofsson and Hallberg 1977) whereas they are found in the genera *Gnathophausia* and *Boreomysis* (unpublished observations). The absence of reflecting pigment cells may seem counterintuitive as a tapetum (which increases sensitivity by effectively doubling the length of the rhabdom) would be of use to the animal in the photon-limited mesopelagic environment. It has been shown that in decapods, eyeshine brightness is reduced in situations where reflected light might compromise the camouflage of the animal (Shelton *et al.* 1992, 2000). It may be that tapeta have been abandoned in some deep-water mysids in order to maintain an effective camouflage.

The dorsal eye contains all of the cell types seen in the lateral eye, but considerable elongation of the ommatidia is seen. Although the crystalline cones and the rhabdoms are slightly longer than in the lateral eye the increase in length is due chiefly to the elongation of the retinula cell bodies within the clear zone. Several species of deep-water mysids have been shown to possess modified eyes (Zharkova 1970; Elofsson and Hallberg 1977), usually resulting in the loss of dioptric apparatus. The only reported instances where the dioptric apparatus has been retained within an elongated eye are *Brutomysis vogtii* (synonymous with *Euchaetomera tenuis*) and *Arachnomysis leuckartii* (Chun 1896). The other notable feature of the dorsal eye is the reduction in the number of crystalline cones. In most compound eyes, each ommatidium contains one crystalline cone and one rhabdom, whereas in the dorsal eye of *E. typica* this is only true of the central ommatidia. In the more peripheral ommatidia the cone is lost and the retinula cell columns in the clear zone project to the redundant facets along the side of the eye. Loss of crystalline cones has been reported from the compound eyes of the larval euphausiid *Thysanopoda tricuspidata* (see Land 1981) and from part of the eye of the mysid *Dioptrromysis paucispinosa* (Nilsson and Modlin 1994). The loss of crystalline cones allows the resultant acute zone to have a higher density of rhabdoms without the accompanying increase in diffraction caused by smaller facets (Nilsson and Modlin 1994).

The presence of a clear zone and bullet-shaped crystalline cones indicate that both lateral and dorsal eyes are probably using refracting superposition optics (Exner 1891). The lateral eye is spherically symmetrical with a large field of view (172°) in contrast to the elongate dorsal eye with a field of view of only 33°. The appearance of the double eyes is remarkably similar to that seen in some euphausiid eyes. The anatomy of these eyes was described in detail by Chun (1896) and the optics were later investigated by Land *et al.*

(1979). The interommatidial angle, which ultimately limits the resolution of which the eye is capable, is around  $7.3^\circ$  in the lateral eye, whereas in the dorsal eye the value is around  $1.5^\circ$ . If the dorsal eye were modified solely to increase resolution, the rhabdoms would be expected to be narrower. This is not the case in *E. typica* where the lateral rhabdoms are  $11.5\text{ }\mu\text{m}$  wide, compared with  $14\text{ }\mu\text{m}$  in the dorsal eye. This is similar to the situation in euphausiid double eyes, in which the upper eye usually has wider rhabdoms than the lower eye (Land *et al.* 1979). In mesopelagic crustaceans the upper eyes are predominantly used for the detection of silhouettes against the residual downwelling light, whereas the lower eyes are mainly used for the detection of bioluminescence (Land 2000). The dorsal eye appears to be adapted to increase resolution, but wide rhabdoms are still necessary to catch sufficient photons to be able to make use of the higher resolving power.

One other significant difference between the two regions of the eye is in the reduction of spherical aberration. The lateral eye, like all spherically symmetrical eyes, suffers a reduction in sharpness because the more peripheral rays contributing to the superposition image are focused more distally than the axial rays. Land *et al.* (1979) showed that a model euphausiid eye with a longer focal length, restricted field of view and a flat rhabdom layer did not suffer from spherical aberration. They found that the upper eyes of some double-eyed euphausiids conformed to their model eye in three ways. The eyes are spherical, with the centre of curvature close to, or in front of, the rhabdom layer; the crystalline cones are centred on a point around twice as deep as the rhabdom layer; the rhabdom layer is flat or slightly curved (Land *et al.* 1979). It is apparent that the dorsal eye of *E. typica* conforms to all of these criteria and should therefore be free of spherical aberration.

In all respects, the double eyes of *E. typica* are remarkably similar to those of some deep-water euphausiids in the possession of lateral eyes with a wide field of view and low resolution and a dorsal eye with a narrow field of view and high resolution. Although this could be due entirely to convergent evolution, it may equally lend weight to the views expressed by several authors (Fincham 1980; Land 1981; Richter 1999) that, on the basis of eye structure and optics, the mysids and euphausiids are more closely related than is suggested by current classifications.

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