JOURNAL OF MORPHOLOGY 205:243–253 (1990)

# The Ultrastructure of the Compound Eye of *Munida rugosa* (Crustacea: Anomura) and Pigment Migration During Light and Dark Adaptation

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*ABSTRACT* The galatheid squat lobster, *Munida rugosa*, has compound eyes of the reflecting superposition type in which a distal cone cell layer and a proximal rhabdom layer are separated by an extensive clear zone. The eye is shown to have certain unique features. In all other reflecting superposition eyes, the clear zone is traversed by crystalline tracts formed by the cone cells. In *M. rugosa* a thin distal rhabdom thread, formed by the eighth retinula cell, connects the cones to the proximal fusiform rhabdoms. The cytoplasm of the other retinula cells also crosses the clear zone in a complex pattern. Fully light-adapted ommatidia are optically isolated by limited migrations of distal shielding pigments. A reflecting pigment multilayer lines each cone to facilitate the formation of a superposition image. This also shows a light-induced change which may limit the acceptance angle of the eye during light adaptation.

The ultrastructure of the compound eye has been described for many crustacean taxa including Branchiura (Hallberg, '82), Mysidacea (Hallberg, '77), Isopoda (Edwards, '69), Amphipoda (Ball, '77), Penaeidae (Meyer-Rochow and Walsh, '77), Palaemonidae (Doughtie and Rao, '84), Astacidea (Krebs, '72), Palinura (Meyer-Rochow and Tiang, '84), and Brachyura (Arikawa et al., '87). However, anatomical accounts of the structure of the galatheid eye have been few in number and confined to light microscopic observations (Pike, '47; Kampa, '63; Bursey, '75; Fincham, '88).

The affiliation of various groups of Crustacea in the infra-order Anomura has been questioned (Fincham, '80; Land, '81) on account of the disparity in the types of compound eyes found within this taxon. The Galatheidae possess a square-facetted superposition eye (Kampa, '63) as found in long-bodied decapods. Such eyes consist of a distal cone cell layer and a proximal retinula cell layer separated by an extensive clear zone. Other anomuran families, however, were thought to have apposition eyes typical of the brachyuran crabs (Fincham, '80). This led both Fincham ('80) and Land ('81) to conclude that the Anomura may not be a coherent taxon and that the galatheids should perhaps be classified with the long-bodied decapods. However, the work of Nilsson ('83) has shown that larval decapods have eyes that are preadapted for superposition optics, suggesting that reflecting superposition eyes may have evolved more than once. Various anomurans, including the hermit crabs (Paguridae), have now been shown to possess eyes which use a previously undescribed type of optics, termed parabolic superposition eyes (Nilsson, '88).

In all previous investigations of galatheid eye structure, the presence of retinula cell cytoplasm in the clear zone has been reported, variously described as surrounding a rhabdom (Pike, '47), a hyaline filament (*Pleuroncodes planipes*, Kampa, '63), or a tract (*Munida irrasa*, Bursey, '75). The following account of the eye of a squat lobster, *Munida rugosa*, describes for the first time the ultrastructure of the galatheid retina and resolves the question of the arrangement of the retinula cells in the clear zone. The anatomical changes occurring during light and dark adaptation are also described.

## MATERIALS AND METHODS

*Munida rugosa* is a squat lobster found in the vicinity of rocky ground from Greenland to Morocco at depths ranging from low water springs down to more than 1,250 m (Howard, '81). Fifty adult *M. rugosa* were obtained, mostly at night, from Upper Loch Torridon, West Scotland using baited creels at depths of 30 to 40 m. Some eyes were fixed immediately in a mixture of glutaraldehyde and formaldehyde (Karnovsky,

'65) for 2 to 4 hours with the eyestalks split to ensure penetration of the fixative. Other animals were transported to Leicester and maintained in circulating seawater under controlled illumination (12 hour dark: 12 hour light) at 10°C (see Shelton et al., '85). These were fixed as described above following 6 hour light or dark adaptation. Light adaptation was carried out under white light at approximately 2.5 $\mu$mol $m^{-2}s^{-1}$ (1 $\mu$mol = $6.023 \times 10^{-17}$ photons).

The state of adaptation of the eye was determined by observing the eyeshine (Kunze, '79). To photograph the eyeshine, dark-adapted *Munida rugosa* were restrained in seawater and illuminated via a half-silvered mirror mounted below the objective lens of a Zeiss Tessovar photomacroscope (Carl Zeiss, Oberkochen, W. Germany). Animals were handled under red light (between 600 and 800 nm) and eyeshine was photographed at regular intervals after switching on a white light giving a photon flux at the eye of approximately 1 $\mu$mol $m^{-2}s^{-1}$.

Eyes were dissected into small pieces and postfixed in 1% $OsO_4$ in phosphate buffer for 1 to 2 hours, dehydrated through acetone and embedded in Spurr resin. Serial semithin (1.0 $\mu$m) sections were prepared by use of a Huxley ultramicrotome (Cambridge Instruments Ltd., Cambridge, England) and glass knives and stained with 1% toluidine blue in 1% borax. At intervals during the preparation of each series, ultrathin (c.0.1 $\mu$m) sections were cut using a diamond knife, picked up on pyroxylin film, and mounted on 2 × 0.5 mm slot grids. These were stained in uranyl acetate and lead citrate and observed on a Jeol 100CX electron microscope (Jeol Ltd., Colindale, London, England). All measurements were calculated from the resulting micrographs which were usually taken from two to five animals.

## RESULTS

The eye is slightly flattened dorso-ventrally (antero-posterior axis 3.5 to 5.0 mm, dorso-ventral 2.0 to 3.5 mm) and includes over 10,000 ommatidia. Square facets (approximately 50 $\mu$m wide) cover most of the surface of the cornea, although hexagonally packed facets are seen along the eye margin. In the fully light-adapted eye, a small luminous pseudopupil is present, surrounded by a square black pseudopupil (Fig. 1A). Following dark adaptation, a large area of brilliant eyeshine can be seen (Fig. 1B). In eyes of intermediate adaptational state, the brightness of the eyeshine is reduced except for the central few facets (Fig. 1C). In longitudinal section, the eye is semicircular with the radius of curvature of the basement membrane (at the proximal limit of the ommatidia) being approximately equal to half that of the cornea.

The arrangement of cells within the ommatidium is shown semi-schematically in Figure 2. The ommatidia are typically 1 to 1.2 mm long in an eye 4 mm in length. The ommatidium is limited distally by the cornea (30 to 35 $\mu$m thick) with square facets defining the positions of the underlying ommatidia. Each corneal facet is secreted by a pair of corneagenous cells, triangular in cross section, which have their nuclei located distally and peripherally (Fig. 2b). The cytoplasm extends proximally to ensheath the crystalline cones and tracts. The four cone cells in each ommatidium are closely adjoined throughout their length and each contains an internally secreted crystalline cone (cc), square in cross section (Fig. 2d). The cones are surrounded by a thin layer of smooth endoplasmic reticulum (SER). Above the nuclei the cone cells taper distally to join the cornea in the centre of the facet, passing between the corneagenous cells (Fig. 2a,b). The cone cells taper proximally at an angle of 6 to 7°. This taper continues along the proximal part of the cone cell, the crystalline tract (ct). The crystalline cones and tracts occupy approximately 250 $\mu$m of a typical 1,000 $\mu$m long ommatidium (measured from cornea to basement membrane).

The cones are separated distally by cells (Fig. 3) containing small nuclei and spherical granules (0.3 $\mu$m in diameter) having the typical appearance of crustacean reflecting pigment granules. Each distal reflecting pigment cell appears to extend across several adjacent ommatidia. Two distal pigment cells (dpc) containing shielding pigment surround each crystalline cone with one cell lining two sides of a cone. The shielding pigment granules are 0.35 $\mu$m in diameter throughout most of the cell, although smaller granules (0.22 $\mu$m) are present at the distal extremity. In the dark-adapted eye these cells reach to the proximal end of the crystalline cone, but during light adaptation they extend well down the crystalline tract (Fig. 2a). The distal pigment cell nuclei are situated between the corners of four adjacent cones (Fig. 2d) and it is down this space that the cells migrate during light adaptation. The distal pigment cells also contain cylindrical organelles which line the mid-cone region as a multilayer separated from the cone cell by the cytoplasmic extension of the corneagenous cell (Fig. 4A). The multilayer consists of three or four layers of organelles 0.15 to 0.22 $\mu$m in diameter and 0.3 $\mu$m long. The layers are 0.20 to 0.25 $\mu$m apart, separated by cytoplasm and SER. In light-adapted eyes the multilayer is frequently distorted, apparently by expansion of the cister-

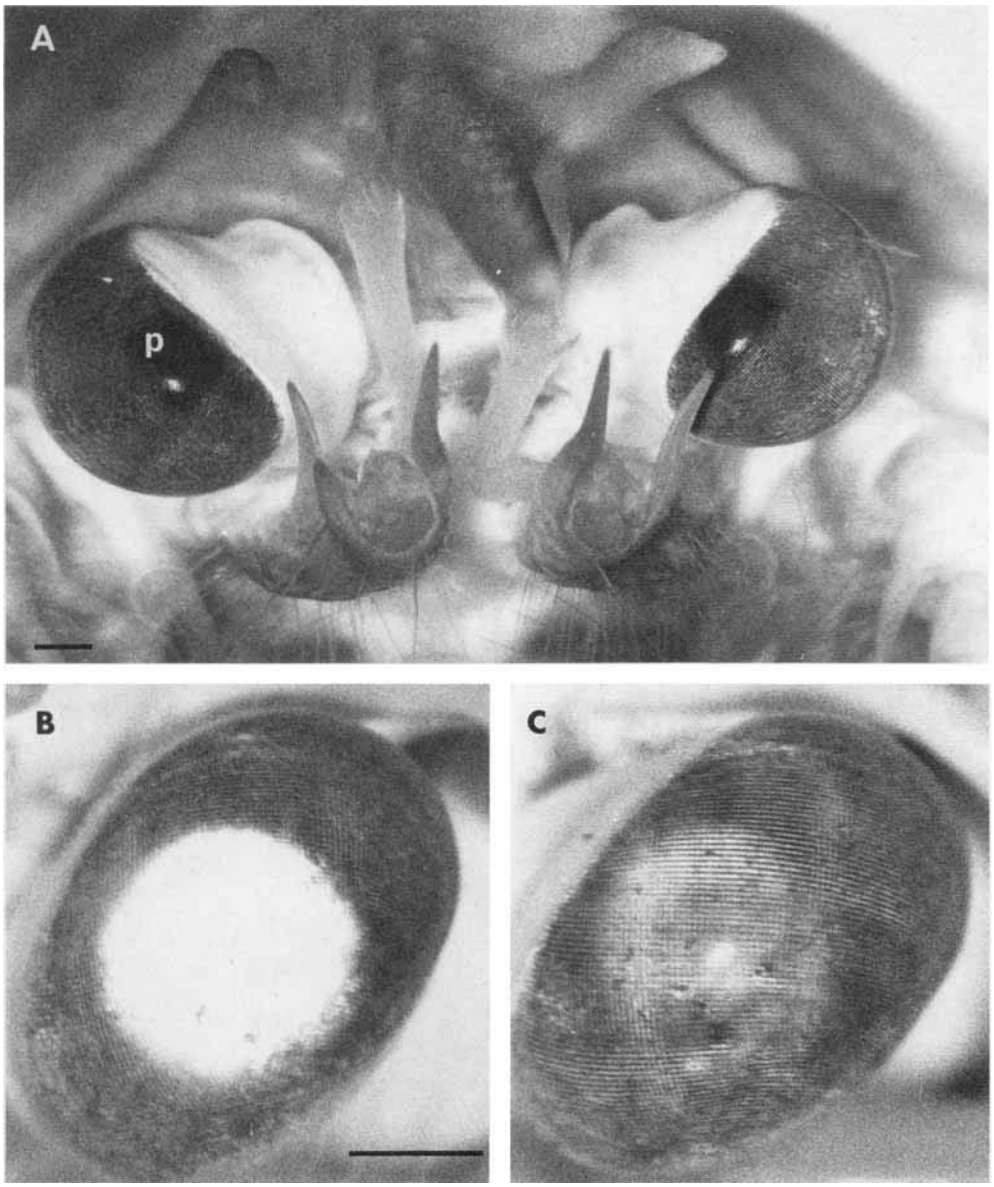


Fig. 1. External appearance of the eyes of live *Munida rugosa*. **A:** Anterior view of a light-adapted individual showing the square black pseudopupil (p). **B:** Lateral view of a dark-adapted eye showing eyeshine. **C:** After 1 hour adaptation to light the brightness of the eyeshine is reduced over most of the area of the eye, although a small luminous pseudopupil remains centrally. Scale bar = 1 mm.

nae of the SER in the cone cells, distal pigment cells and corneagenous cell extensions (Fig. 4B).

Proximal to the cone cell layer is the clear zone, some 500 $\mu$m wide, which is traversed by ribbons of retinula cell cytoplasm. There are eight retinula cells in each ommatidium, six with distal nuclei (R1 to 6) and two with proximal nuclei (R7,8). A narrow distal rhabdom thread abuts the proximal end of the crystalline tract (Fig. 5A) and crosses the clear zone (Fig. 5B). The four parts of the crystalline tract separate (Fig. 6A) and lie adjacent to each corner of the rhabdom thread (Fig. 6B). Proximally, they are reduced in diameter and are found between the

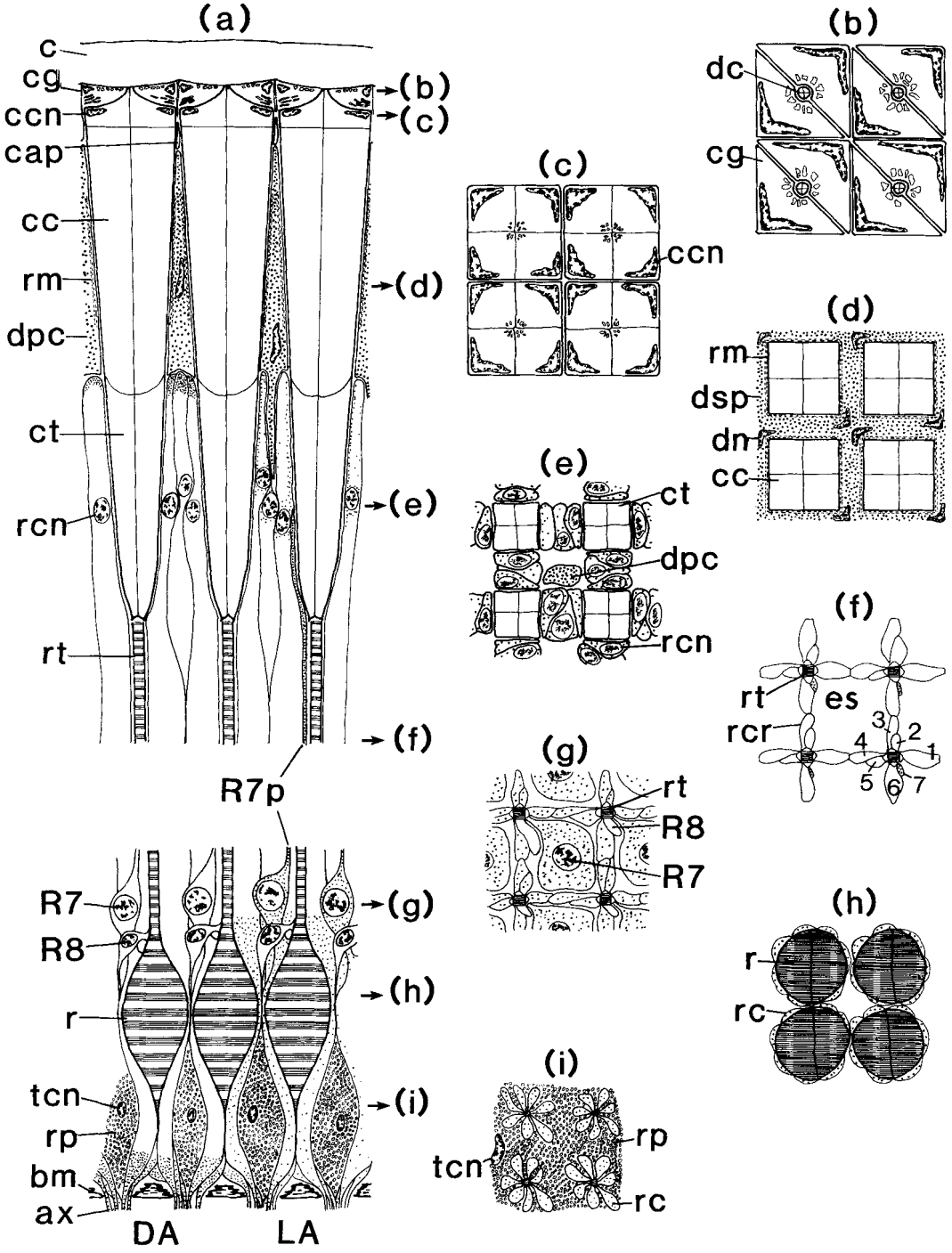
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Figure 2

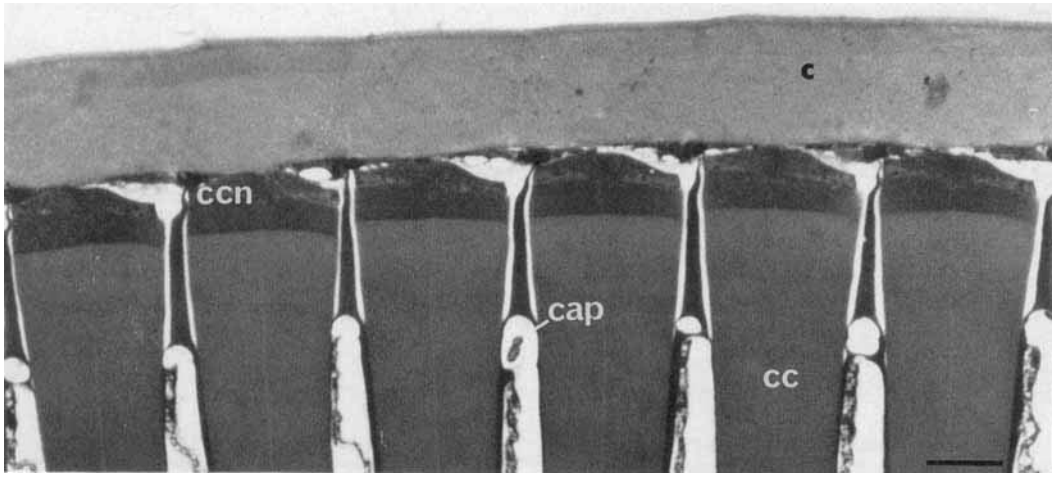


Fig. 3. This toluidine blue stained semithin section shows the cornea (c), the distal region of the cone cell containing the nucleus (ccn), and the crystalline cone (cc). The distal reflecting pigment cells (cap) are located between the distal parts of the crystalline cones. Scale bar = 20 μm.

retinula cells, some distance from the thread. The rhabdom thread is roughly square in cross section, 4 to 5 μm wide, and each side of the thread is associated with a lobe of the eighth retinula cell (R8) (Figs. 2f,g, 6A–C). The lobes of R8 are packed with SER cisternae (Fig. 6C) and contribute alternate layers of orthogonally orientated microvilli to the rhabdom thread. Adjacent rhabdom threads are joined by a ribbon formed of three retinula cell processes. A region of extracellular material, square in cross section, is enclosed by four such ribbons together with a rhabdom thread at each corner (Figs. 2f, 5B).

Two of the retinula cell processes in each ribbon are associated with one thread and one with the next (Fig. 2f). The retinula cells may be numbered conventionally (Parker 1897; Shaw and Stowe, '82) by designating the cell flanked by two cone cell processes as R1 and numbering the remainder clockwise or anticlockwise depending on the eye (or region of the eye) from which the section was taken. In a section from a dorsal ommatidium of the right eye of *Munida rugosa*, the retinula cells are numbered anticlockwise from R1 (Fig. 5B), whereas ventral ommatidia are numbered clockwise. R1 lies to one side of the rhabdom thread, R2 and R3 adjoin the next, and R4 and R5 the third. Associated with R6 on the fourth side of the rhabdom thread is the distal process of the seventh retinula cell (R7) which extends distally to the level of the crystalline tract. The cell bodies of R1 to R6 are located distal to the clear zone in such a way that three retinula cell somata separate the sides of two adjacent crystalline tracts (Figs. 2e, 5A). The cell bodies are packed with mitochondria and contain screening pigment granules (0.3 μm in diameter) which are located at the distal extremity of the cell when the eye is dark adapted (Fig. 2a). During light adaptation, this pigment migrates centripetally to surround the nucleus and to line the edges of the crystalline tract (Fig. 5A).

In the proximal region of the clear zone, the cytoplasm of R7 fills the area between the rhabdom threads (Fig. 2g). The nucleus of R7 is always located posterior to the rhabdom thread with which the cell is associated. Abundant screening pigment is present in R7; this is located around the level of the basement membrane in the dark-adapted eye but migrates along the distal processes of R7 during light adaptation to form thin columns of pigment crossing the clear zone (Fig. 5B) and filling the space

Fig. 2. **a**: Semischematic diagram of light- (LA) and dark- (DA) adapted ommatidia in longitudinal section from the eye of *Munida rugosa*. The distance from the cornea to the basement membrane is typically 1,000 μm although most of the clear zone (c.400 μm) has been omitted. ax, retinula cell axon; bm, basement membrane; c, cornea; cap, distal reflecting pigment cell; cc, crystalline cone; ccn, cone cell nucleus; cg, corneagenous cell; ct, crystalline tract; dpc, distal pigment cell; r, rhabdom; rcn, retinula cell nucleus of cells R1–R6; rm, reflecting multilayer; rp, reflecting pigment; rt, rhabdom thread; R7, retinula cell 7; R7p, distal process of R7; R8, retinula cell 8; tcn, tapetal cell nucleus. **b–i**: Transverse sections of four ommatidia from a light-adapted right eye taken at the levels shown on Figure 2a). dc, distal cone cell processes; dn, distal pigment cell nucleus; dsp, distal shielding pigment; es, extracellular space; rc, retinula cell; rcr, retinula cell ribbon; 1–7, retinula cells of one ommatidium numbered conventionally.

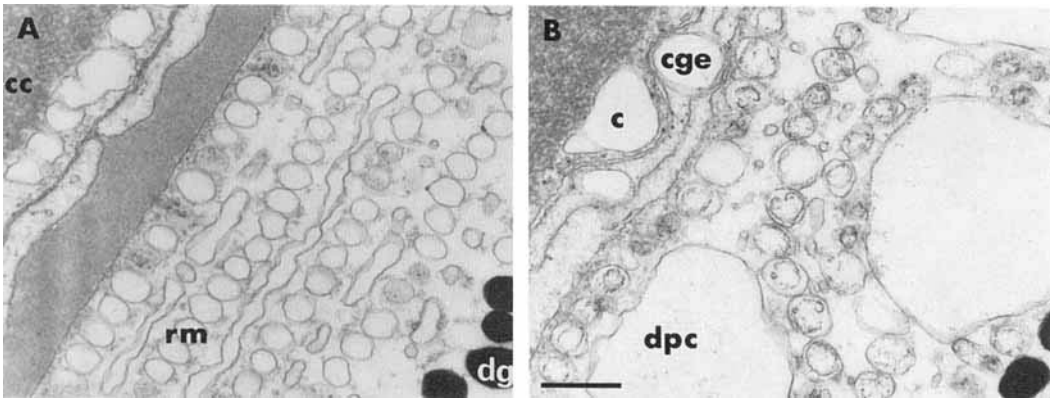


Fig. 4. **A:** Transverse section of a distal pigment cell in the dark-adapted state with its screening pigment (dg) and the multilayer of reflecting pigment granules (rm) lining the sides of a cone (cc). **B:** When light adapted, the pigment multilayer is distorted by expansion of cisternae of the endoplasmic reticulum in the cone cell (c), in the corneagenous cell extension (cge), and in the distal pigment cell (dpc). Scale bar = 0.5 μm.

between the corners of adjacent crystalline tracts below the distal pigment cells.

Below the level of the R7 cell body, the rhabdom thread becomes more rounded in cross section. The lobe of R8 adjacent to R7 becomes dominant (Fig. 2g) and forms the cell body from which an axon extends proximally. The other three lobes of R8 diminish and the rhabdom is surrounded by cytoplasmic lobes of the other seven retinula cells. The cytoplasm of R8 appears to be free of screening pigment throughout its length. The remaining retinula cells (R1 to R7) together form a banded, fusiform rhabdom, approximately 100 μm long, which extends to within 50 μm of the basement membrane. Alternating layers of orthogonally orientated microvilli are contributed by the retinula cells in a fashion typical of decapod eyes. Longitudinal sections show that the diameters of the microvilli in the rhabdom thread (Fig. 7A) and in the rhabdom (Fig. 7B) are similar (0.05 to 0.07 μm). In the rhabdom thread the layers are thinner (usually five to eight rows of microvilli) and more loosely packed (Fig. 7A). The rhabdoms appear banded, due to the layering of the microvilli, although the eyes of some animals caught during daylight showed evidence of disruption typical of light-induced damage (Shelton et al., '85; Gaten, '88). The proximal shielding pigment found in the retinula cells R1 to R6 is located around the basement membrane in dark-adapted eyes, thus exposing the tapetum. In the light-adapted eye, the proximal pigment rises to the level of the proximal nuclei (R7, R8), completely shielding the rhabdom layer (Fig. 2a).

The proximal third of the rhabdom is surrounded by reflecting pigment cells forming an extensive tapetum (Fig. 2a). These cells contain a small nucleus just below the proximal end of the rhabdom and masses of reflecting granules (0.4 μm in diameter) which do not migrate during light adaptation (Fig. 8A). Reflecting pigment granules, similar to those found in the tapetum, are present below the basement membrane, but it is not clear whether these are associated with the tapetal cells. Proximal to the rhabdom, the retinula cells appear in transverse section as a seven-lobed rosette (Figs. 2i, 8A). Throughout the length of the ommatidium, neighbouring retinula cells are joined by belt desmosomes (Fig. 8A). The retinula cells of each ommatidium separate below the rhabdom and form axons which pass through three or four neighbouring holes in the basement membrane (Fig. 8B). These axons form bundles of fibres which cross a haemocoelic sinus before entering the lamina ganglionaris. The cone cell processes, having crossed the clear zone, pass between the tapetal and retinula cells before terminating at the basement membrane. The basement membrane (Fig. 8B) consists of a collagenous sheet of material fenestrated in a regular fashion. It is modified beneath each rhabdom, forming a layered stack.

## DISCUSSION

The *Munida rugosa* eye is of the same general pattern as that of other known galatheid eyes (Pike, '47; Kampa, '63; Bursey, '75; Fincham, '88). Its ultrastructure has not been described before and presents a number of unusual features. It is apparently of the reflecting superposition type (Vogt, '75; Land, '76) found in long-bodied decapod crustaceans, although in these

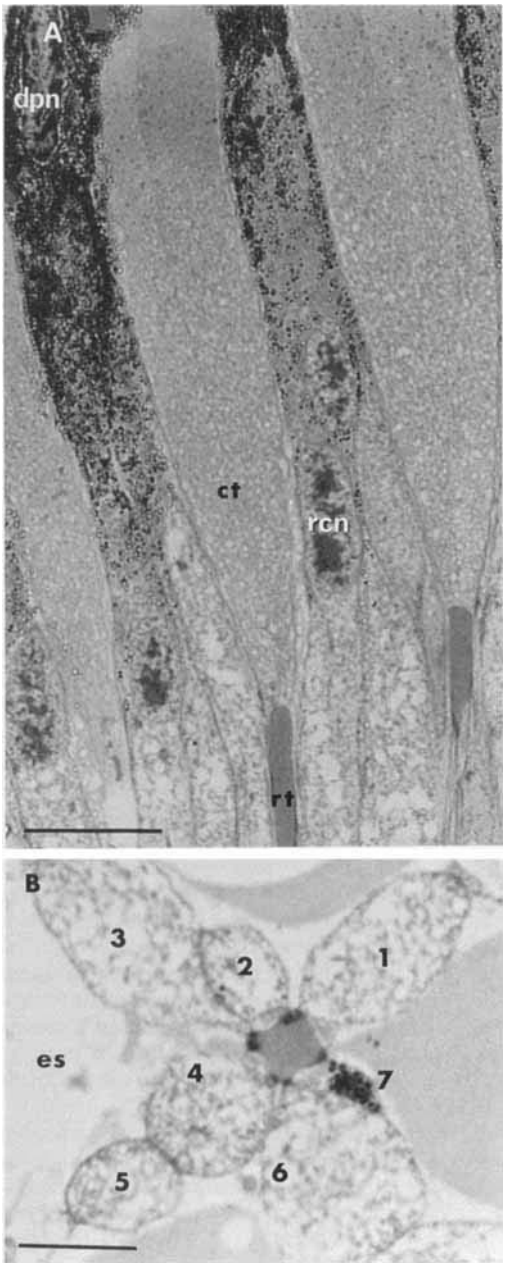


Fig. 5. **A:** Light micrograph showing the junction between the crystalline tract (ct) and the distal rhabdom thread (rt). In this light-adapted eye, the distal shielding pigment of the retinula cells surrounds the nuclei (rcn) and lines the edge of the tract. The distal pigment cell has migrated proximally and its nucleus (dpn) is seen between the crystalline tracts. Scale bar = 20 $\mu$m. **B:** The conventional system of numbering the retinula cells (1–7) is shown in this semithin section from the middle of the clear zone in the dorsal half of a right eye. The presence of screening pigment in R7 shows that this section is from a light-adapted eye. A large extracellular space (es) is present between the retinula cell ribbons. Scale bar = 10 $\mu$m.

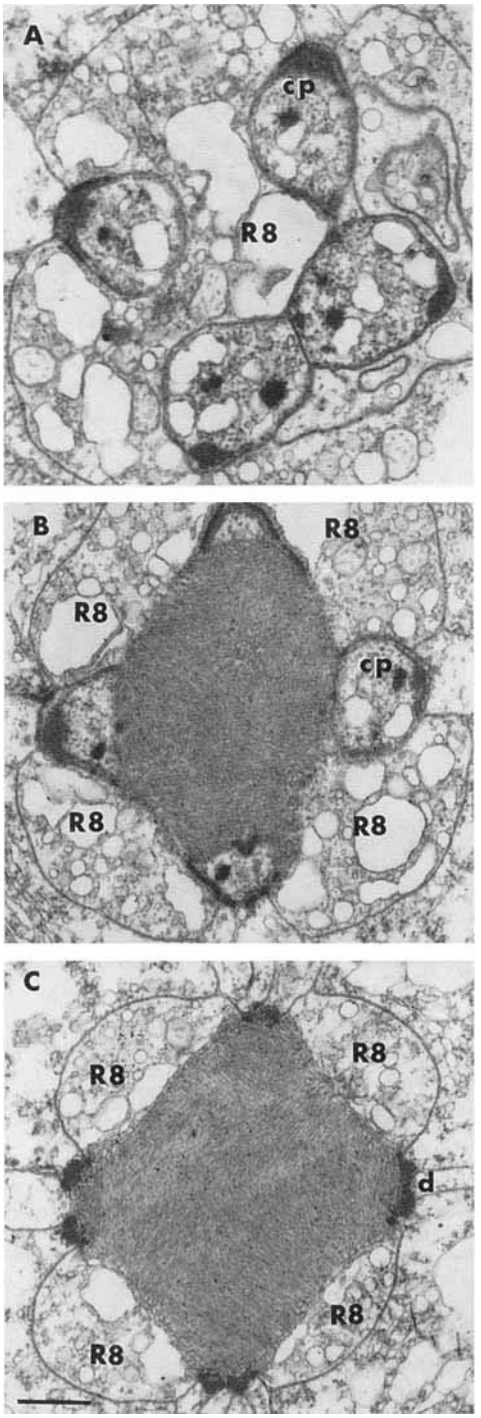


Fig. 6. **A:** This electron micrograph shows a transverse section through the base of the crystalline tract at a level where the four cone processes (cp) separate. At this level R8 has not separated into four lobes. **B:** More proximally four separate lobes of R8 are associated with the sides of the thread whilst the cone cell processes (cp) are located at the corners. **C:** This electron micrograph of the rhabdom thread in the mid clear zone shows the electron-lucent lobes of R8 along each side. The retinula cells are joined at the corners by belt desmosomes. (d). Scale bar = 1 $\mu$m.

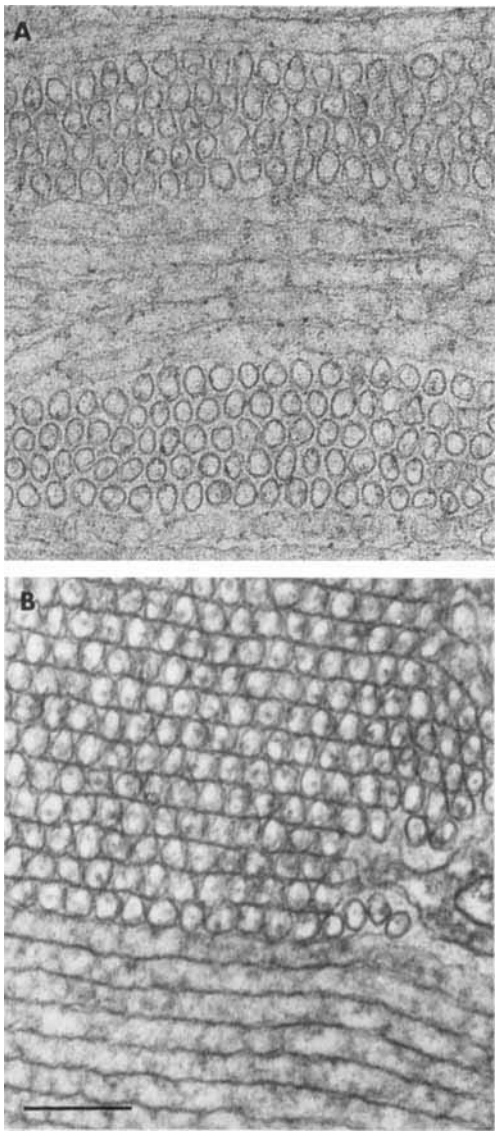


Fig. 7. **A:** Electron micrograph of a distal rhabdom thread in longitudinal section showing the orthogonal layering of microvilli. **B:** A similar micrograph of the proximal rhabdom shows that the microvilli are of a similar diameter to those in the rhabdom thread. They are, however, packed more closely and in wider layers. Scale bar = 0.2 μm.

eyes the clear zone is traversed by crystalline tracts. In contrast, the crystalline tracts in *M. rugosa* are short and the clear zone is crossed by retinula cell cytoplasm and thin rhabdom threads, together with cytoplasmic processes of the cone cells. The presence of rhabdom threads which cross the clear zone has not been reported in any other reflecting superposition eye, although a similar arrangement exists in the refracting superposition eye of the moth *Ephestia* sp. (Horridge and Giddings, '71). A short, thin distal rhabdom is also seen in the rock lobsters, *Panulirus longipes* (Meyer-Rochow, '75) and *Jasus edwardsii* (Meyer-Rochow and Tiang, '84), although it does not cross the clear zone. In all of these cases the distal thread is formed by all of the retinula cells, whereas in *M. rugosa* the thread is formed only by the eighth retinula cell. This is in contrast to the situation in most decapods and mysids, where R8 normally contributes only a small portion of the distal tip of the rhabdom (Shaw and Stowe, '82). Authors of previous descriptions of galatheid eyes (Pike, '47; Kampa, '63; Bursey, '75; Fincham, '88) have been unsure of the origin of the distal thread. They also report the presence of only seven retinula cells. It is clear from the current account that *M. rugosa* has eight retinula cells, in common with most decapods, and that it is the eighth retinula cell that forms the distal rhabdom thread.

In their orthogonal layering and microvillar dimensions, the distal rhabdom threads are very similar to the proximal rhabdoms; on the basis of anatomical evidence there is no reason to doubt that they are able to function as photoreceptors. However, as the rhabdom thread is not in the superposition image plane and is formed by the eighth retinula cell alone, the effect of the rhabdom threads on sensitivity and image quality is difficult to predict. When the eye is light adapted, most light will be axial and this will be retained within the rhabdom thread by its light guide properties. The dense packing of microvilli results in a high internal refractive index, whereas the surrounding lobes of R8 are largely vesiculated and will be of low refractive index. This will probably result in the propagation of paraxial light along the thread by total internal reflection (Miller, '79).

Reflecting pigment granules occur in several regions of the *Munida rugosa* eye, although the reflecting pigment is extremely labile and frequently lost during normal processing (Piekos, '86). The distal reflecting pigment cell, the tapetum below the rhabdoms, and a diffuse layer of uncertain origin subjacent to the basement membrane all contain populations of non-migratory granules. The latter may be continuous with the tapetum, although no connections were observed. The layers of cylindrical organelles in the distal pigment cells of *M. rugosa* almost certainly form a reflective surface that operates on the principle of thin film interference (Land, '72). The appearance of the reflecting multilayer changes during light adaptation in a way that

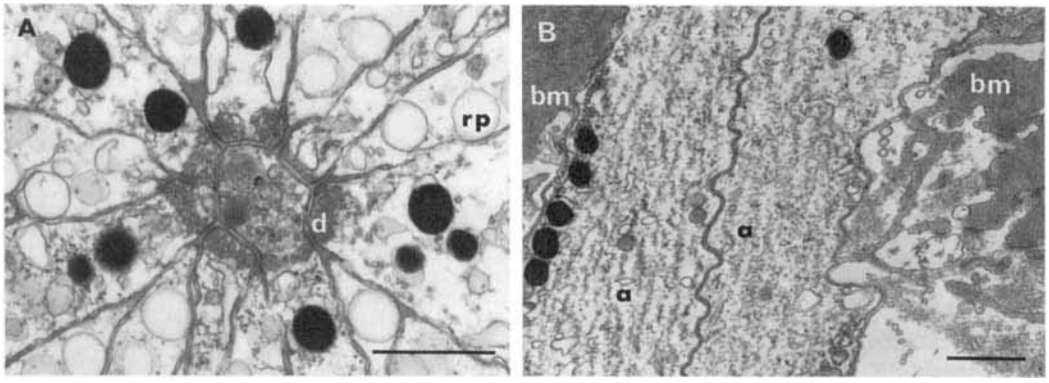


Fig. 8. Electron micrographs of the proximal part of an ommatidium. **A:** A transverse section just below the level of the rhabdom shows the seven retinula cells joined by desmosomes (d). Tapetal cells containing reflecting pigment granules (rp) are seen separating the retinula cells. Scale bar = 1 μm. **B:** Longitudinal section showing axons (a) passing through the basement membrane (bm). Scale bar = 1 μm.

may reduce the effective aperture of the eye. When dark adapted, the reflecting organelles are aligned in three or four rows of parallel and equally spaced layers, conforming to the "ideal" multilayer necessary for reflection by thin film interference (Land, '72). However, when light adapted, the multilayer is disrupted by the expansion of cisternae of the endoplasmic reticulum in cone cells, and corneagenous cell extensions. Focussing would then have to depend on total internal reflection at the cone boundary because the disorganized multilayer would no longer reflect efficiently. Accordingly, the effective aperture of the eye would be significantly reduced (Land, '80). Light-induced changes in endoplasmic reticulum cisternae have been reported in the pallisade surrounding the rhabdoms of several species of arthropods with apposition eyes (e.g., *Locusta migratoria,* Horridge and Barnard, '65; *Limulus* sp., Miller and Cawthon, '74); and in the retinula cells of crayfish (Frixione et al., '79; Tsutsumi et al., '81; Frixione and Porter, '86). In the distal pigment cells of *Palaemonetes pugio* (Doughtie and Rao, '84), the reflecting multilayer is completely disrupted during the photomechanical movements of the distal pigment cells. The corneagenous cell sheath is also distended and vesiculated during light adaptation in this species (Doughtie and Rao, '84). In *M. rugosa,* the disruption of the multilayer was not always observed and may only occur when the light levels are sufficiently high to initiate movement of the distal pigment cells.

During light adaptation, the various populations of screening pigment granules migrate to reduce the effective aperture of the eye and to protect the rhabdoms from excess light. The distal pigment cell undergoes photomechanical centripetal migration between the corners of four adjacent crystalline tracts. Similar migration of distal pigment occurs in the eye of *Panulirus longipes* (Meyer-Rochow, '75). The pigment cell does not line the sides of the tract as shown for *Pleuroncodes planipes* (Kampa, '63); it appears likely that this is the retinula cell screening pigment. The presence of screening pigment at the distal extremity of the dark-adapted retinula cells has not been reported before. In *Munida rugosa,* this pigment undergoes a proximal migration during light adaptation to surround the nuclei of cells R1 to R6 and to line the sides of the crystalline tracts. Here it acts as a screen and also raises the refractive index in the retinula cell cytoplasm bordering the tract. As the total internal reflection of light here depends on a low refractive index outside the tract, the presence of pigment granules close to the membrane would allow light rays to pass into the retinula cells. Here it will be scattered and absorbed by the screening pigment, so reducing the intensity of the propagated beam (Miller, '79).

The proximal screening pigment of the retinula cells shows extensive centrifugal migration with light adaptation. That of cells R1 to R6 moves from the basement membrane level to the top of the fusiform rhabdom; that of R7 crosses the clear zone as a thin column as recorded for other galatheids (Pike, '47). The brilliant eyeshine seen in dark-adapted eyes is reduced to a very small patch in light-adapted eyes. Although the movement of the proximal pigment to cover the tapetum causes a reduction in eyeshine brightness, it is thought that the movements of distal pigment and R7 proximal pigment reduce

the diameter of the eyeshine, resulting essentially in the optical isolation of individual ommatidia. In other reflecting superposition eyes, optical isolation of ommatidia is brought about by extensive migration of the distal pigment into the clear zone (e.g., *Cherax destructor*, Bryceson and McIntyre, '83). In the *Munida rugosa* eye it appears to be necessary for the distal pigment to migrate only the length of the comparatively short crystalline tract to effect optical isolation. The clear zone, which occupies more than half the depth of the ommatidia, thus remains free of pigment when light adapted except for thin columns of pigment from R7.

The eye of *Munida rugosa*, with its extensive clear zone and brilliant eyeshine, is undoubtedly a superposition eye when dark adapted. However, following light adaptation, the optical isolation of the ommatidia and the situation of the retinal elements in proximity to the cones suggest that apposition optics are being used. It appears that the galatheid eye functions by a mixture of reflecting superposition optics when dark-adapted and light-guide apposition optics when light adapted.

## ACKNOWLEDGMENTS

I would like to thank Dr. P.M.J. Shelton for helpful comments during the course of this work and in the preparation of this manuscript, C.J. Chapman (Department Agriculture and Fisheries for Scotland) for catching and supplying the animals, and Mrs. E.M. Roberts (Leicester University Electron Microscope Suite) for greatly improving my EM technique. This work was supported in part by NERC grant number GR3/5564.

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