Zoomorphologie 94, 279–306 (1980)

Zoomorphologie

Classification of Amphipod Compound Eyes – the Fine Structure of the Ommatidial Units (Crustacea, Amphipoda)*

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Summary. The ultrastructure of the compound eyes of 13 amphipod species has been investigated. An amphipod type of compound eye can be characterized by the constellation and consistency of a number of morphological features, most of which are also found in other compound eyes. The amphipod eye falls into four sub-categories (types). The ampeliscid type has a tripartite aberrant lens eye; the lysianassid type has a reduced or no dioptric apparatus and a hypertrophied rhabdom; the hyperid type possesses a large number of ommatidial units with long crystalline cones and dark instead of reflecting accessory pigment; and finally, the gammarid type can be interpreted as a generalized amphipod type. The lysianassid type is adapted to low light intensities and demonstrates convergent development with the compound eyes of other deep-sea crustaceans. The ampeliscid type is more similar to the gammarid type. The type characterization of the amphipod compound eye might well serve as a basis and incentive for functional studies also revealing adaptational mechanisms.

A. Introduction

The amphipods are one of the most successful crustacean groups. During their evolution, they have managed to populate the seas from shallow waters to abyssal depths and also to invade freshwater and terrestrial habitats. Consequently, this wide ecological range has required the amphipods, as such, to adapt to great environmental variation. Thus, adaptational forces act upon the structural elements so that an optimal function is attained. The study of

* This paper is dedicated to Professor Erik Dahl on his 65th birthday and retirement from the Chair of Structural Zoology, Department of Zoology, University of Lund

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*** The investigation has been supported by grants from the Swedish Natural Science Research Council (Grants 2760-009 and 009-43). Our thanks are due to the staffs of the marine biological stations in Espegrend (Norway) and Kristineberg (Sweden) and of the research vessel "Jean Charcot", Brest, France. The skilled technical assistance of Mrs. Rita Wallén and Miss Maria Walles is gratefully acknowledged

0340-6725/80/0094/0279/$05.60

the effects of these adaptational forces can only be conducted by a thorough investigation of recent species, that is, specifically of the structure of sensory organs used by the animals, e.g., to perceive their milieu in different habitats. The eye serves as a good example because light perception is relatively well defined structurally and functionally. Light microscopic investigations (Parker, 1891; Woltereck, 1909; Strauss, 1926; Hanström, 1933; Debaisieux, 1944) and more recent electron microscopic studies (Ercolini, 1965; Donner, 1971; Ball, 1977; Meyer-Rochow, 1978) indicate a variation in the structure of the amphipod eyes. The present investigation was undertaken to provide a basis for subsequent discussions of (1) variations and variable parts of the compound eyes, (2) correlation between eye structure and habitat, and (3) the interaction between evolutionary and adaptational forces in the structural development of the compound eye. Prerequisites for these discussions are comprehensive material and the use of the electron microscope. Thus, the investigation of a large number of species provides a firm basis for generalizations, and knowledge of the fine structure is likewise essential to elicit the functional capabilities of the eyes.

B. Material and Methods

Studies were made on the species listed below. Most localities are to be found along the west coast of Sweden. Exceptions are the Bay of Biscay, west of France, and the Raune fiord, south of Bergen, Norway. Information about depth range has been obtained from Stephensen (1928) and Schellenberg (1927).

	Bathymetric range	Localities
Gammaridea		
Corophiidae		
Ericthonius difformis	0–200 m	Kristineberg, 0.2 m. On *Zostera*
Gammaridae		
Gammarus pulex	limnic	Freshwater brooks outside Lund
Orchestia gammarellus	terrestrial	Kristineberg, wrack
Ampeliscidae		
Ampelisca gibba	50–2,300 m	Koster fiord, 120 m
Haploops tubicola	15–1,100 m	Öresund, 40 m
Lysianassidae		
Eurythenes gryllus	0–5,000 m	Bay of Biscay, 2,000 m
Orchomenopsis obtusa	150–750 m	Koster fiord, 170 m
Tmetonyx cicada	0–2,000 m	Raune fiord, Bergen 100 m
Hyperiidea		
Hyperia galba	0–2,000 m	Kristineberg. On *Aurelia*
Parathemisto abyssorum	0–3,000 m	Väderöarna, 170 m
Parathemisto compressa	0–? m	Koster fiord, 180 m
Caprellidea		
Caprella loveni	littoral	Kristineberg, 5 m
Caprella monocera	littoral	Kristineberg, 5 m

Cut heads were fixed according to Karnovsky (1965) for 4 h at 4° C and postfixed in 2% OsO_4 for 2 h at room temperature, both fixatives in 0.2 M cacodylate buffered to pH 7.2. Dehydration was performed in an alcohol series, block-staining in 0.5% uranyl acetate/ 1% phosphotungstic acid and embedding in Vestopal w. For light microscopy, sections (1–2 μm) were stained according to Richardson et al. (1960) and those for electron microscopy were poststained in uranyl acetate (1% in 75% ethanol) and examined in a Zeiss EM 10 or in a Philips EM 300.

C. Results

The compound eyes of Amphipoda are sessile. One pair of eyes is the rule, but Ampeliscidae has two or three pairs.

A general comment is made below on two features peculiar to the compound eyes of amphipods. The amphipod eyes are situated beneath an undifferentiated cuticle (except in the Ampeliscidae) formed by a hypodermal layer proximally delimited by a basal lamina. This layer consists of interdigitating cells with elongated nuclei and electron-dense cytoplasm. The thickness of the cell layer varies between 16 and 3 μm in different species, and that of the basal lamina can be up to 0.25 μm. The amphipods are unique in having a fully developed hypodermis and basal lamina between the cuticle and the ommatidia in otherwise well-developed eyes (Figs. 2 and 12). Around the margins of the compound eves the basal lamina splits into two sheets, one being the above-mentioned, the other enveloping proximally the whole eye. The ommatidia thus give the impression of being detached from the hypodermis and having sunk into the head cavity, however, not deeper than into the enlarged basal lamina (Fig. 1).

Another feature characteristic of all amphipods (except the Ampeliscidae) is the so-called fenestrated membrane (BM1 of Ball, 1977) (Fig. 7). This divides the compound eye in half: the distal half houses the crystalline cone, the distal region of the retinular cells with the rhabdom, and the accessory pigment cells, and the proximal half contains the nuclear part of the retinular cells and the glial cells (Fig. 1). The fenestrated membrane is formed by the glial cells. These appear as cytoplasmic sheets part of which enclose the retinular cells and part form an intricately interwoven tangential layer that together with the basal lamina, secreted by the glial cells, constitutes the fenestrated membrane. Thus, the fenestrated membrane can comprise both cellular and acellular constituents (Fig. 4). Proximally, the glial cells, together with the basal lamina, may form the so-called eye capsule (BM2 of Ball, 1977). This basal lamina also is probably secreted by the glial cells, but it may also contain parts of the basal lamina of the hypodermis with which it is continuous (see above). The fenestrated membrane and the eye capsule are differentially developed in the types and species described below and the degree of development will be discussed.

There is a regional difference within the compound eye, and the ommatidia in the central area are longer than those in the periphery. Sizes given in the descriptions are for the central ommatidia.

I. The Gammarid Type

The following species are included in this category: *Gammarus pulex, Orchestia gammarellus, Ericthonius difformis* (Gammaridea); *Caprella loveni* and *Caprella monocera* (Caprellidea).

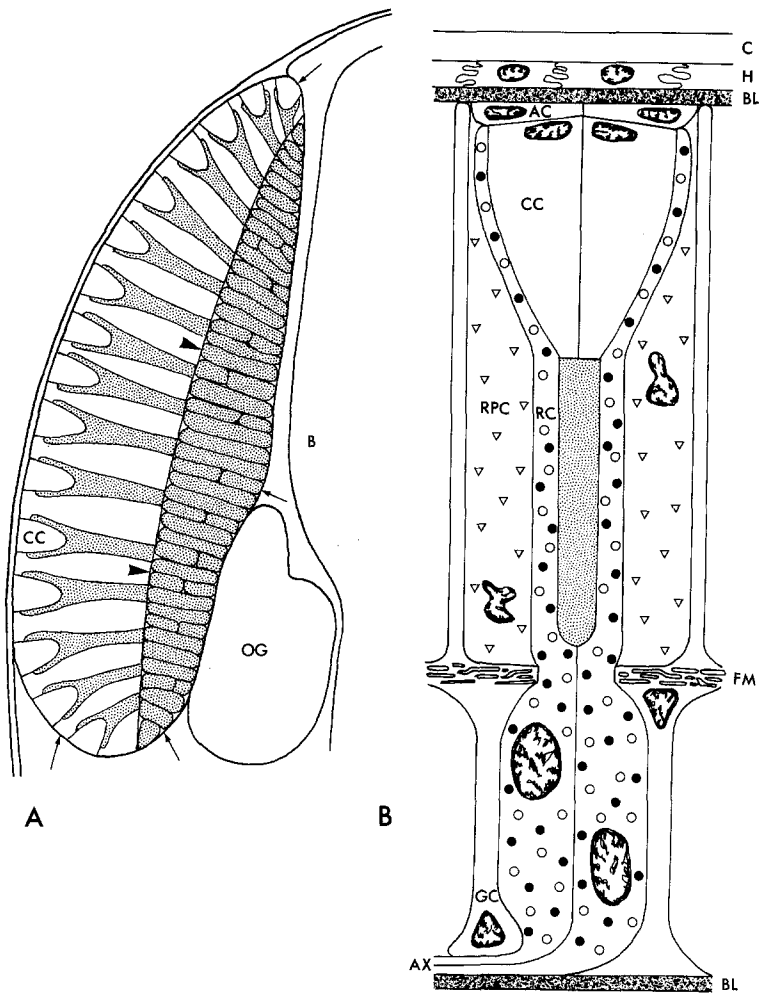
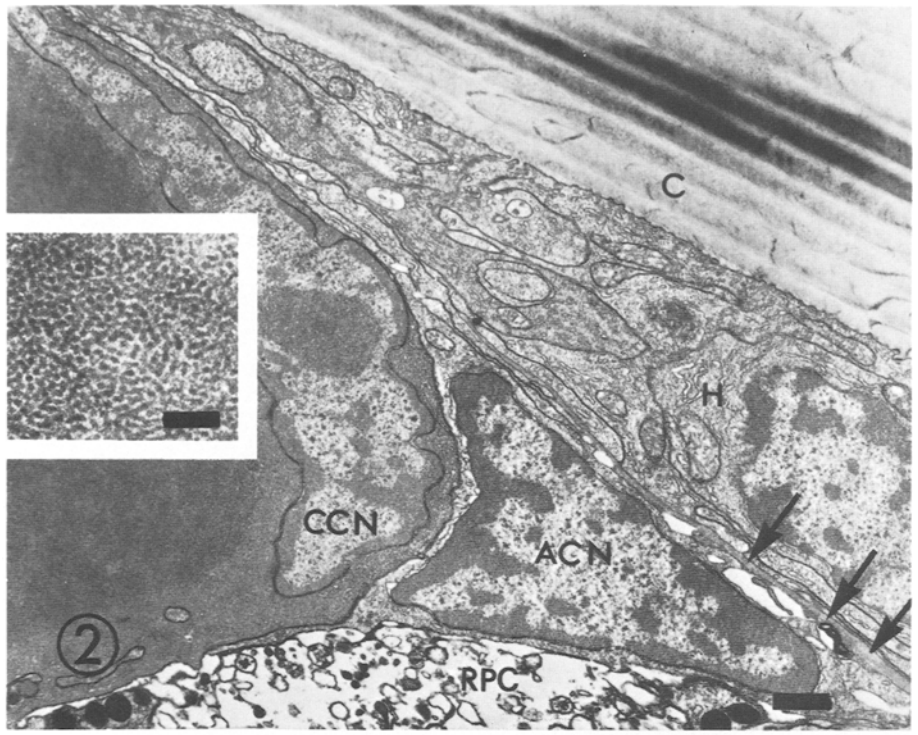


Fig. 1. **A** Schematic presentation of a transverse section through the head of *Gammarus pulex*. The retinular cells are stippled. The arrows point to the basal lamina that delimits the eye: *Arrowheads,* fenestrated membrane; (*OG*) optic ganglia; (*CC*) crystalline cone; (*B*) brain **B** Schematic drawing of the ommatidium of *Gammarus pulex*. The rhabdom is stippled, and the red, dark, and reflecting pigments are represented by *open circles, filled circles* and *open triangles,* respectively: (*AC*) accessory cone cell; (*AX*) axon; (*BL*) basal lamina; (*C*) cuticle; (*CC*) cone cell; (*FM*) fenestrated membrane; (*GC*) glial cell; (*H*) hypodermal layer; (*RC*) retinular cell; (*RPC*) reflecting pigment cell

Fig. 2. Longitudinal section of dioptric elements in *Gammarus pulex:* (*ACN*) nucleus of accessory cone cell; (*C*) cuticle; (*CCN*) nucleus of cone cell; (*H*) hypodermal layer; (*RPC*) reflecting pigment cell. *Arrows* point to the basal lamina. Scale: 1 μm. Inset: Glycogenlike particles in the crystalline cone in *Orchestia gamarellus*. Scale: 0.25 μm

Fig. 3. Distal glial process (*GP*) terminating at the distally situated basal lamina (*BL*) in *Gammarus pulex*. (*AC*) accessory cone cell. *Arrows* point to microtubules in the glial process. Scale: 0.5 μm

Fig. 4. Fenestrated membrane (*FM*) in *Gammarus pulex* appearing like an interwoven tangential layer of cellular sheets and basal lamina (*BL*). A distal glial process (*GP*) is emerging from the membrane. (*RPC*) reflecting pigment cell. *Asterisks:* Two kinds of retinular cell pigment granules. Scale: 1 μm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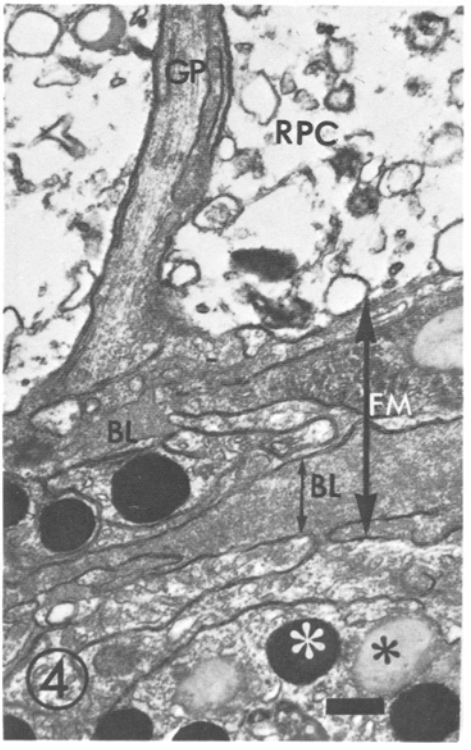
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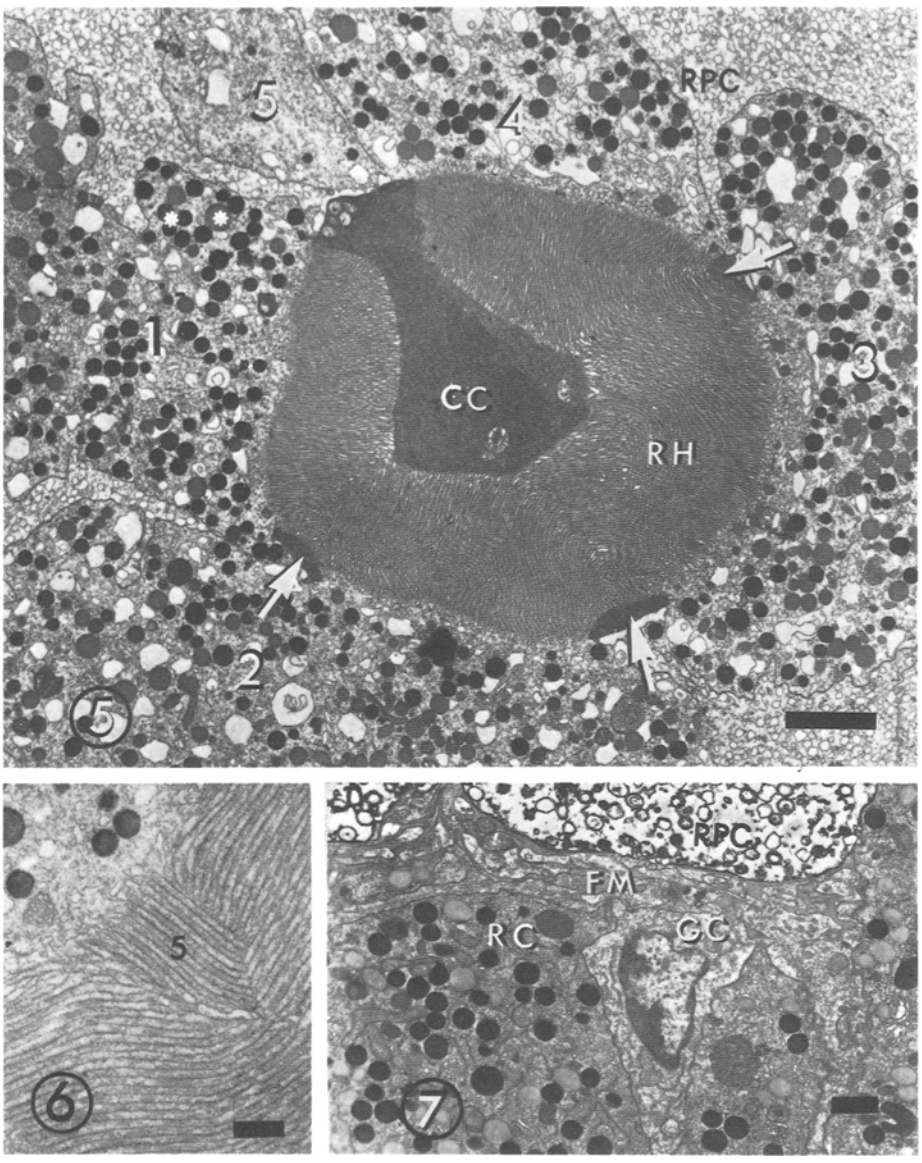


Fig. 5. Cross section, most distally, of the rhabdom (*RH*) in *Gammarus pulex*. Four regular retinular cells (*1–4*), with microvilli orthogonally directed, and one aberrant fifth cell (*5*) comprise the rhabdom: (*CC*) cone cell; (*RPC*) reflecting pigment cell. *Arrows*, residues of a crystalline cone. Scale: 3 μm

Fig. 6. Cross section of the aberrant fifth rhabdomere (*5*) of *Gammarus pulex*. Scale: 0.5 μm

Fig. 7. Longitudinal section of the fenestrated membrane (*FM*) and a glial cell soma (*GC*), the latter contributes to the formation of the membrane in *Gammarus pulex:* (*RC*) retinular cell; (*RPC*) reflecting pigment cell. Scale: 1 μm

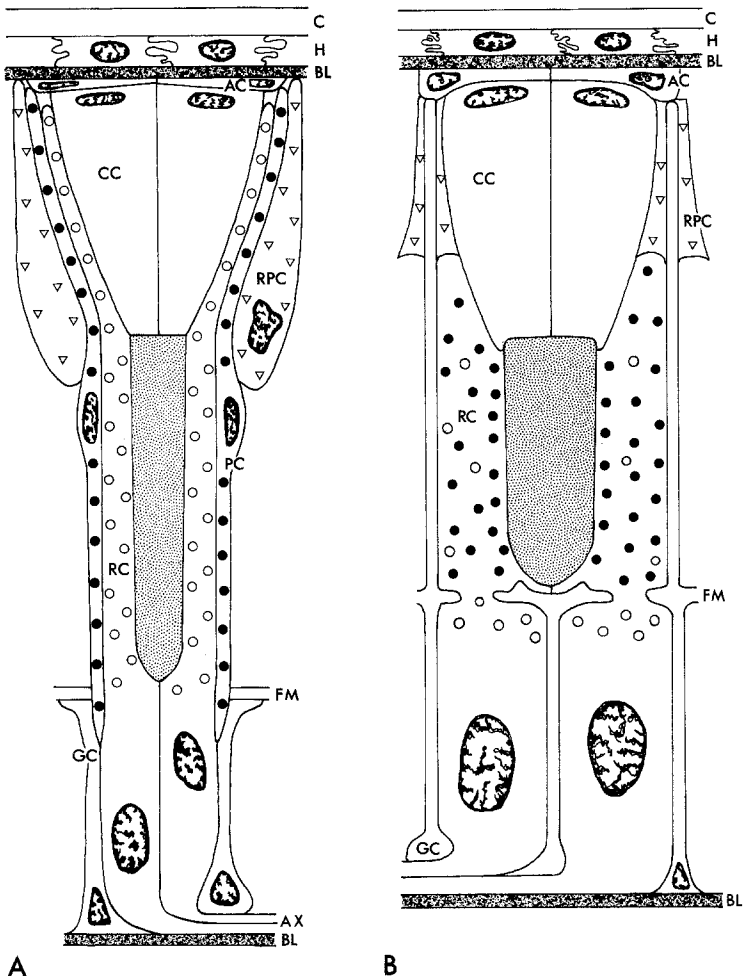
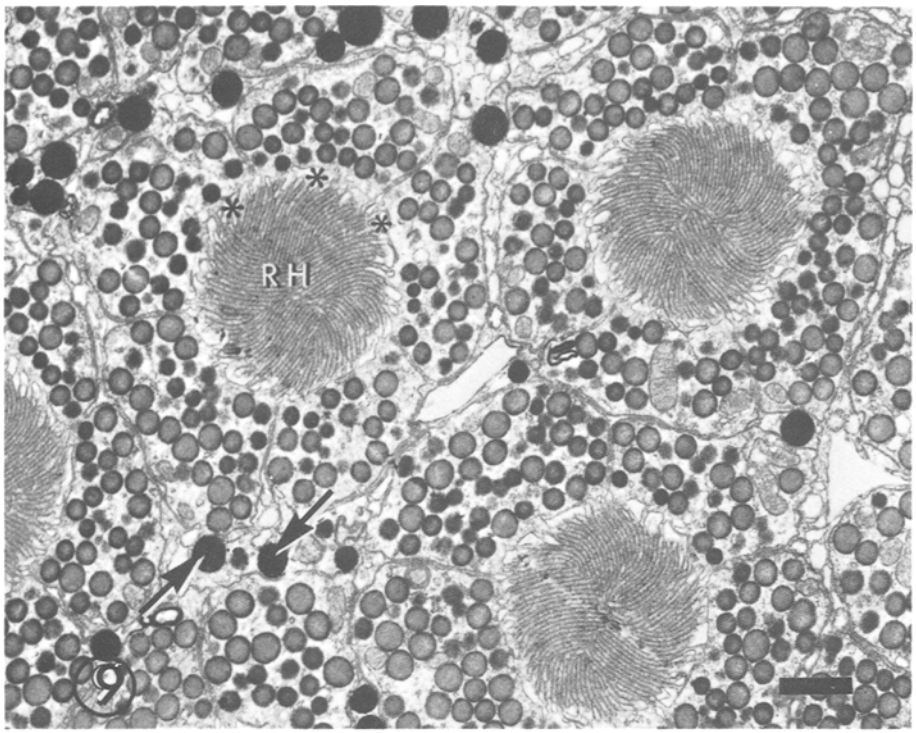


Fig. 8A and B. Schematic drawings of the ommatidia of: **A** *Ericthonius difformis* and **B** *Caprella loveni.* The rhabdom is stippled, and the red, dark and reflecting pigments are represented by *open circles, filled circles* and *open triangles,* respectively: (*AC*) accessory cone cell; (*AX*) axon; (*BL*) basal lamina; (*C*) cuticle; (*CC*) cone cell; (*FM*) fenestrated membrane; (*GC*) glial cell; (*H*) hypodermal cell; (*RC*) retinular cell; (*RPC*) reflecting pigment cell

1. Gammarus pulex (Linné, 1758) (Fig. 1)

a) Dioptric Elements. The hypodermis (4 μm) secretes a lensless cuticle (7 μm). The pyriform crystalline cone (diameter 20 μm and length 30 μm) is formed by two main cone cells; and in addition two accessory cone cells are present, but they take no part in the formation of the cone. The nuclei of both cell types are situated distally and away from the suture line of the cone, those of the accessory cells having the most distal and peripheral position (Fig. 2). The cone itself has the same morphological appearance as in a variety of crusta-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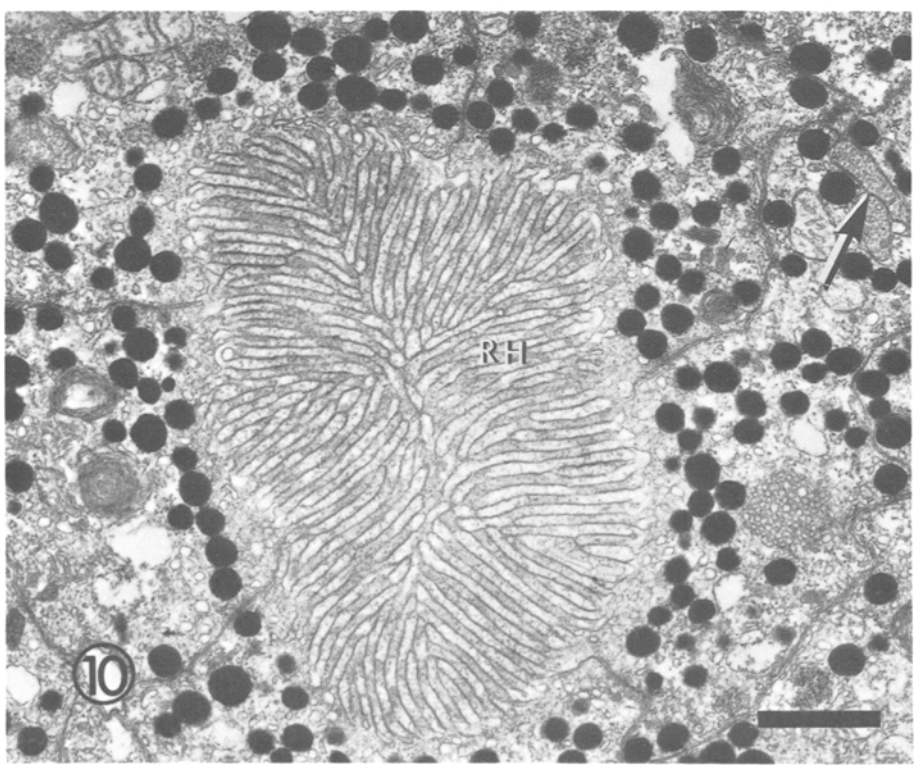
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ceans (see Elofsson and Odselius, 1975), i.e., a central amorphous core that stains intensely and an outer cytoplasmic envelope with rough endoplasmic reticulum and mitochondria. In the boundary zone, between the cytoplasm and the central core, glycogen-like particles are present. This is also the case in *Orchestia* (Fig. 2, inset). Accessory cone-cell cytoplasm extends laterally toward neighboring cones and makes contact. Thus, a thin contiguous cytoplasmic layer is present proximal to the basal lamina of the hypodermis. The retinular cells are closely attached to and envelop the cone.

b) Retinular Cells and Rhabdom. In cross section the five retinular cells are radially arranged. Pigment granules of two kinds are evenly distributed in the retinular cell cytoplasm (Figs. 4 and 5). One type, mean diameter 0.45 μm, is electron-dense, whereas the other type, mean diameter 0.55 μm, is more electron-translucent. Because of their morphological characteristics, the dark and light granules are thought to contain ommochromes and carotenoids, respectively (Elofsson and Hallberg, 1973). The retinular cells are connected by intermediate junctions close to the rhabdom. The retinular cells penetrate the fenestrated membrane and the nuclei are situated proximal to this (Fig. 1 B).

The five retinular cells (R1–5) form a fused continuous rhabdom (for rhabdom definitions, see Elofsson, 1976) that in a cross section is roughly quadrate distally (Fig. 5) and slightly stellate (four-rayed) proximally. The stellate shape is caused by a gentle bulging of the retinular cell cytoplasm into the rhabdom. Distally, the side of the rhabdom quadrate is 15 μm, decreasing successively to zero at the base of the rhabdom. The length of the rhabdom is 30 μm and it terminates 2 μm above the fenestrated membrane. The triangular rhabdomeres of R1–4 are of equal size, and the microvillar orientation of the pair R1 and R3 is orthogonal to the pair R2 and R4 (Fig. 5). The smaller R5 has its microvilli oriented 45° to R1–4 (Fig. 6). The area of the fifth rhabdomere is about 3–4% of the total cross sectional area of the rhabdom.

c) Non-Retinular Screening Pigments. Screening pigments are present between the ommatidia above the fenestrated membrane (Fig. 1 B). These cells contain reflecting pigment granules that appear as empty vesicles and have a diameter of 0.4 μm (Figs. 4 and 7). Each ommatidium is surrounded by five screening pigment cells, but these cells are also shared by adjacent ommatidia; thus, the number is less than five per ommatidium. The nuclei of the screening pigment cells are often extensively lobed and are situated at different levels above the fenestrated membrane.

d) Glial Cells and Fenestrated Membrane. Glial cell nuclei are situated at two different levels: close to the eye capsule, and, to a lesser extent, just beneath

Fig. 9. Cross section of rhabdoms (*RH*) in *Ericthonius difformis*. *Asterisks*, extracellular palisade. *Arrows*, pigment granules of accessory pigment. Scale: 1 μm

Fig. 10. Cross section of the rhabdom (*RH*) in *Caprella loveni*. *Arrow*, distal glial cell process. Scale: 1μm

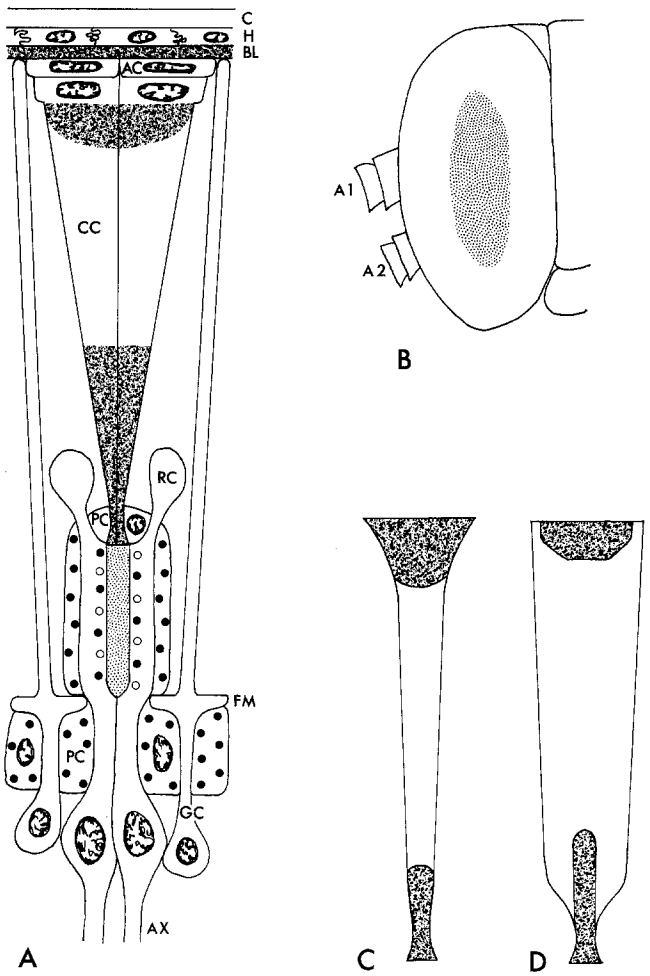


Fig. 11. **A** Schematic presentation of the ommatidium of *Hyperia galba*. The rhabdom is stippled, and the red and dark pigments are represented by *open* and *filled circles*, respectively. The denser zones of the crystalline cone are shown in a stippled pattern: (*AC*) accessory cone cell; (*AC*) axon; (*BL*) basal lamina; (*C*) cuticle; (*CC*) cone cell; (*FM*) fenestrated membrane; (*GC*) glial cell; (*H*) hypodermal layer; (*PC*) pigment cell; (*RC*) retinular cell. **B** The head of *Hyperia galba*. The externally visible pigments of the retina are represented by the stippled area: (*A1*) first antenna; (*A2*) second antenna. **C and D** The crystalline cones of *Parathemisto compressa* and *P. abyssorum*, respectively. Denser zones of the cones are indicated by stippling

the fenestrated membrane (Fig. 1 B). The latter is about 1 μm thick, and in sections the cytoplasm of the glial cells and the basal lamina resemble sandwiched lamellae. Distal to the fenestrated membrane, the glial cells form microtubuli-filled slender processes (approx. 1 μm thick) that ascend between the ommatidia (Fig. 4). Distally, these processes make contact with the accessory cone cells, and terminate at this level (Figs. 1 b and 3). The distribution of the glial processes is irregular, but on the average there is one process for each ommatidium.

Proximally, the glial cells form sheets that, together with the basal lamina, form the eye capsule.

The compound eye of *Orchestia gammarellus* is almost identical to that of *Gammarus*, differing only in details.

2. *Ericthonius difformis* (Milne-Edwards, 1830) (Fig. 8A)

The ruby-red compound eyes in this species are housed in protrusions from the anterior part of the head. There are about 50 ommatidia in each eye. Smaller, as well as somewhat more pronounced, variations of the *Gammarus* type occur.

a) Dioptric Elements. The crystalline cone is rather elongated, the distal and proximal diameters being 8 and 2.5 µm, respectively, and the length 20 µm.

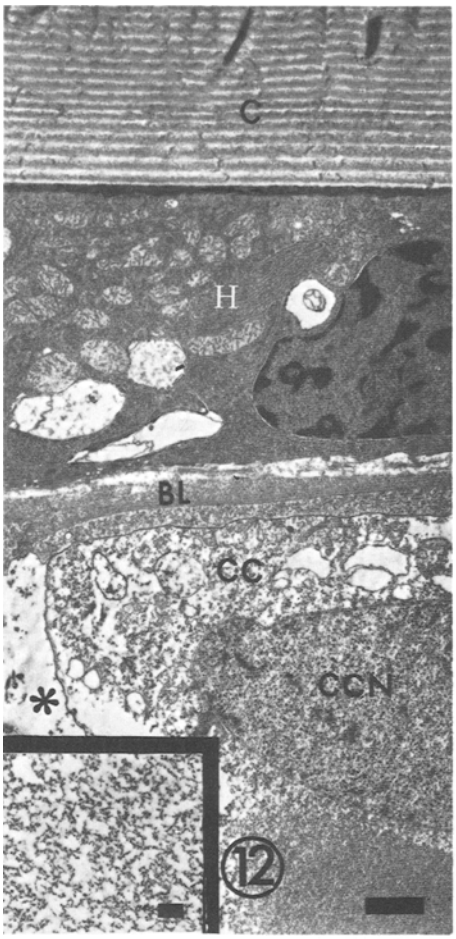
b) Retinular Cells and Rhabdom. The five retinular cells extend all the way to the distal parts of the cone and contain pigment granules (0.4 µm), probably consisting of carotenoids that are uniformly distributed in the cells above the fenestrated membrane (Fig. 9). These pigments probably evoke the red eye colour. The rhabdom is circular in a transverse section, being about 16 µm and 2.5 µm in diameter. Surrounding the rhabdom is an extracellular palisade. The retinular cells and their rhabdomeres are equally large. And, lastly, the radially arranged microvilli display a peculiar whorl-like pattern similar to that found in *Hyperia* (see below) (Fig. 9).

c) Non-Retinular Screening Pigments. The compound eyes of *Ericthonius* have, apart from the pigment present in the retinular cells, two kinds of pigment cells. Reflecting pigment cells are present in the distal part of the eye extending from the accessory cone cells to the distal part of the rhabdom (Fig. 8A). The pigment granules in these cells are preserved as vesicles with a mean diameter of 0.3 µm. The second type of screening pigment is dark and the cells contain electron-dense granules (diameter 0.6 µm). They are situated between the distal parts of the ommatidia down to the level just below the fenestrated membrane (Figs. 8A, 9). These cells do not surround the ommatidia but form slender processes between them, and thus do not obscure the red colour of the eye (Fig. 9). The nuclei are situated at the level of the distal part of the rhabdom.

d) Glial Cells and Fenestrated Membrane. The membrane is feebly developed in this species (0.5 µm) and the glial cells do not form any distal processes in the eye.

3. *Caprella loveni* Boeck, 1870 (Fig. 8B) and *C. monocera* G.O. Sars, 1895

The small ruby-red eyes of *Caprella loveni* (about 60–70 ommatidia) and *C. monocera* (approx. 100 ommatidia) are situated laterally on the head. Only small differences exist between the eyes of these two species, as well as those of *Gammarus*.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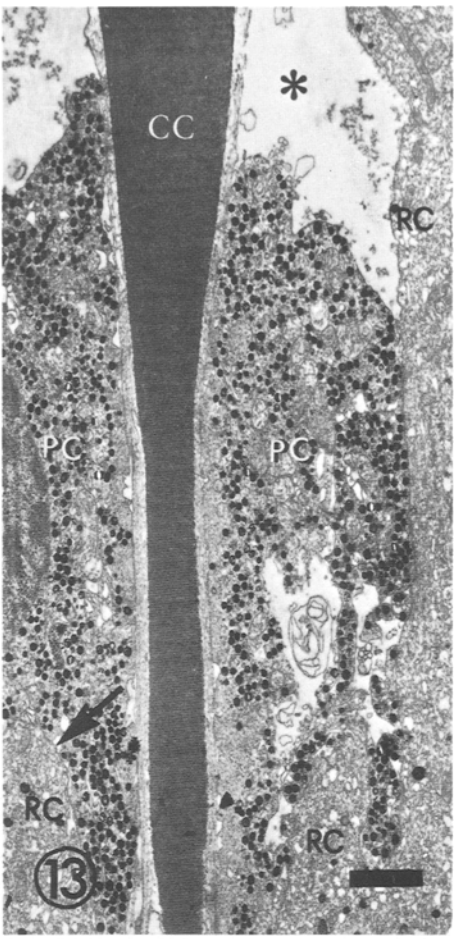
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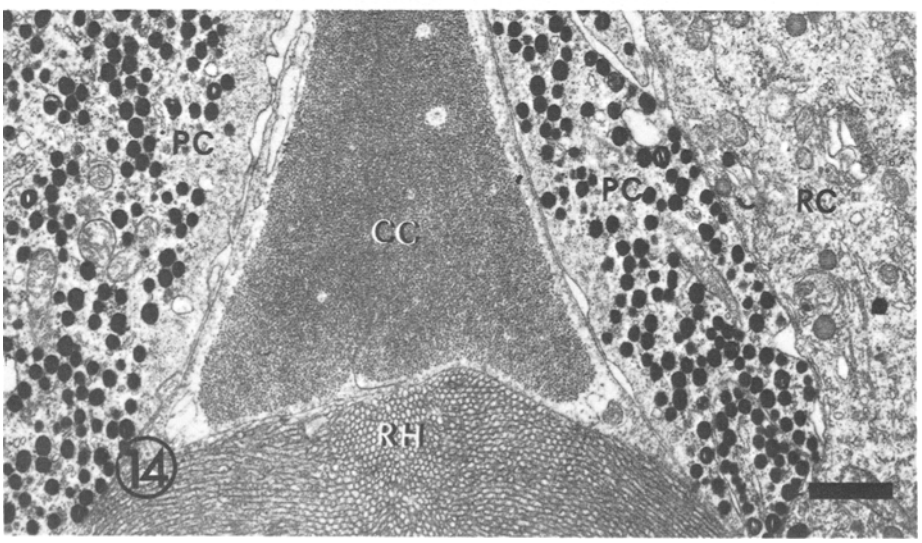
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a) Dioptric Elements. The pyriform cone of *C. loveni* is compact with a distal diam. of 12 μm and a proximal diam. of 4 μm and a length of 15 μm. The cone of *C. monocera* is more elongated (distal diam. 25 μm, proximal 4 μm, length 40–50 μm). The most proximal tip of the cone of *C. loveni* forms a depression into which the rhabdom fits tightly. The nuclei of the accessory cone cells are situated above the nuclei of the main cone cells.

b) Retinular Cells and Rhabdom. Five retinular cells with uniform rhabdomeres form a fused continuous rhabdom with radially arranged microvilli. The rhabdom of *C. loveni* is oval or almost rectangular in shape (average diam. 6.4 μm, length 15 μm) (Fig. 10), whereas the rhabdom of *C. monocera* is round to oval in a cross section (diam. 4 μm, length 25 μm). An extracellular palisade is present in both species–weakly developed in *C. loveni* and more prominent in *C. monocera* (width about 0.6 μm). The retinular cells contain a large number of pigment granules of two kinds: small electron-dense and large electron-translucent. In *C. loveni* the small ones have a mean diameter of 0.1 μm, and in *C. monocera* they are 0.4 μm. The larger granules have a mean diam. of 0.7 μm and 1.0 μm, respectively. The dense granules are dispersed throughout the retinular cell cytoplasm, but are more abundant close to the rhabdom. The electron-translucent granules are sparsely distributed in the retinular cells above the fenestrated membrane, but below this they are more concentrated, resulting in a heavily pigmented basal layer 3–5 μm thick in *C. loveni* and 18–20 μm thick in *C. monocera*. The electron-dense and electron-translucent granules have the ultrastructural characteristics of ommochromes and carotenoids, respectively. In addition, a large number of granules occur that have a varied electron density and size (0.3–1.0 μm). The soma region of the retinular cells is unpigmented and is characterized in these species by a very large number of mitochondria, free ribosomal or glycogen-type granules, as well as a dense rough endoplasmic reticulum.

c) Non-Retinular Screening Pigment. Only one type of pigment cell is present between the crystalline cones of the ommatidia. The cells contain a large number of empty vacuoles indicating an eluted content as in reflecting pigment.

d) Glial Cells and Fenestrated Membrane. The continuations of the processes above the fenestrated membrane are branched in contrast to the single processes of *Gammarus*.

Fig. 12. Longitudinal section of dioptric elements in *Hyperia galba:* (*BL*) basal lamina; (*C*) cuticle; (*CC*) crystalline cone; (*CCN*) nucleus of crystalline cone cell; (*H*) hypodermal layer; *Asterisk,* extracellular space. Scale: 2 μm. *Inset:* the undifferentiated cone cytoplasm of the medial part of the cone in *Parathemisto abyssorum.* Scale: 1 μm

Fig. 13. Longitudinal section of the proximal crystalline cone (*CC*) in *Hyperia galba.* Note the slender cone shape, the distal accessory pigment screen (*PC*) and the retinular cell continuation (*RC*) above the pigment layer. *Arrow,* cell-membrane border between the accessory pigment cell and the retinular cell. *Asterisk,* extracellular space. Scale: 2 μm

Fig. 14. The swollen proximal cone tip (*CC*) abutting the rhabdom (*RH*) in *Hyperia galba:* (*PC*) pigment cell; (*RC*) retinular cell. Scale: 1 μm

II. The Hyperid Type

In the hyperid species the eyes are extremely well developed, the numerous ommatidia occupying almost the entire head. The compound eyes of *Streetsia* and of *Phronima*, although the latter are bilobed, are similar in most essential features to those of the three species investigated here (Meyer-Rochow, 1978; Ball, 1977).

1. Hyperia galba (Montagu, 1813) (Fig. 11 A and B)

The ommatidia in this species are very long, 600 μm. In live animals most of the eye appears as a clear space. Deep in the middle of the head, however, there is a dark spot representing the pigments of the retina (Fig. 11 B).

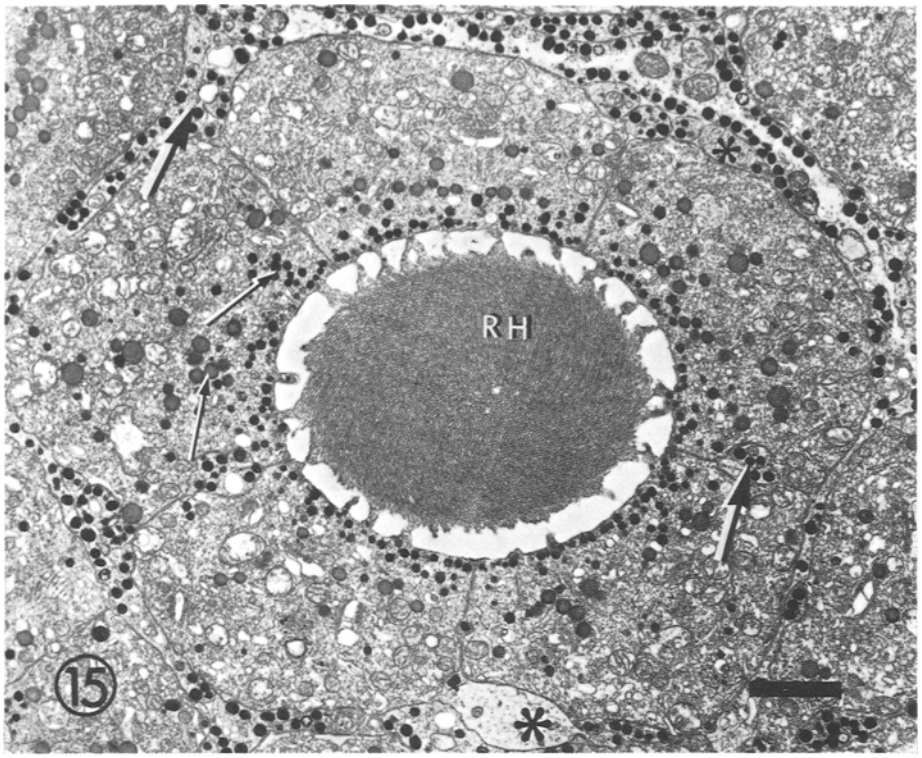
a) Dioptric Elements. The distal part of the cone is fairly thick, tapering proximally to just above its most proximal part, where it has its smallest diam. (4 μm) (Figs. 11 A and 13). The most proximal part, abutting the rhabdom, is broader, having a diam. of 10 μm (Fig. 14). There are very pronounced density gradients within the cone; the distal and proximal parts of the cytoplasm are dense and have a granular content. The periphery and middle parts of the cone have an almost structureless cytoplasmic matrix (Fig. 12).

b) Retinular Cells and Rhabdom. The five retinular cells form a rhabdom with a circular outline in a transverse section. It is 135 μm long and 10 μm in diam. (distally only 5 μm). The rhabdom is surrounded by a conspicuous extracellular palisade 0.7 μm in width, bridged by thin (0.2–0.4 μm) cytoplasmic sheets. The microvilli of the rhabdom have the same peculiar appearance as in *Ericthonius*, i.e., they form a whorl-like figure in cross sections (Fig. 15). The retinular cells penetrate the distal screening pigment layer and can be seen here in sections as rounded islets outside the pigment cells (Figs. 11 A and 13). The retinular cells contain electron-dense and electron-translucent pigment granules. The electron-dense granules (0.25 μm) are present mainly around the rhabdom; the electron-translucent ones (0.5 μm) are more dispersed in the cells, but above the fenestrated membrane (Fig. 15). A third type of granule is infrequently found (see also *Parathemisto*) that is also found in *Phronima* (Ball, 1977).

c) Non-Retinular Screening Pigments. There are a distal and a proximal population of cells containing dark pigment granules. The distal layer surrounds the

Fig. 15. Cross section of the spiralled rhabdom (*RH*) in *Hyperia galba*. Note the prominent palisade: *large arrows*, accessory pigment cell; *Small arrows*, two kinds of retinular cell pigment granules: *asterisk*, glial cell processes. Scale: 2 μm

Fig. 16. Cross section of the spiralled rhabdom (*RH*) in *Parathemisto abyssorum*. Scale: 1 μm. *Inset:* enlargement of the extracellular palisade (*asterisk*). *Arrow*, a third type of retinular cell pigment granule (for the other two types see Fig. 15). Scale: 0.5 μm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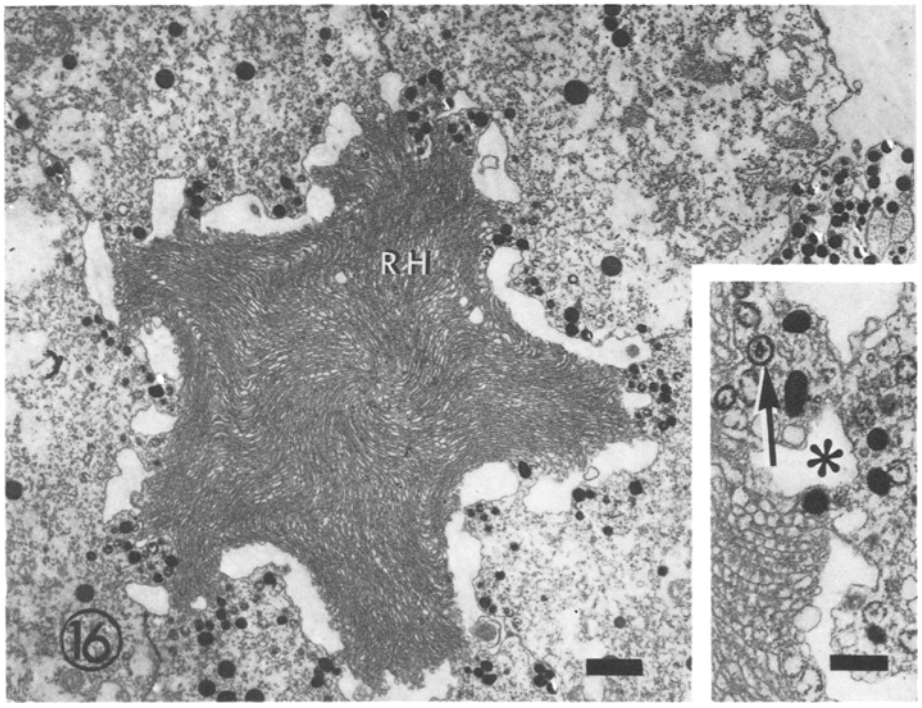
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distal parts of the rhabdom down to the fenestrated membrane (Figs. 11A and 13). The pigment cells are wedged between the retinular cells extending to the intermediate junction delimiting the palisade (Fig. 15). The proximal screening layer is situated mainly below the fenestrated membrane extending about 20 μm proximally. The pigment granules in both cell types are similar and have a diam. of 0.4 μm. The eyes of *Phronima* (Ball, 1977) seem to have only one dark pigment cell type that is similar in position to the distal layer in *Hyperia*. Further, an enigmatic pigment-like cell type occurs distally in the *Phronima* eye with a position analogous to the retinular cell islets in *Hyperia*.

d) Glial Cells and Fenestrated Membrane. Centrally, the fenestrated membrane is more homogeneous and mainly built up by cellular elements of the glial cells. Peripherally, the extracellular material predominates.

5. Parathemisto abyssorum Boeck, 1870 and *P. compressa* (Goes, 1865)

The eyes are similar to those of *Hyperia*, the main differences being the shape of the dioptric elements and the rhabdom.

a) Dioptric Elements. The crystalline cones of *P. abyssorum* (Fig. 11D) and *P. compressa* (Fig. 11C) are long, about 830 μm and 360 μm, respectively. The cones of the former species have a distal diam. of 65 μm and then taper slightly, having a diameter of 50 μm all along their lengths except along the most proximal parts. The cone of the latter species has a distal diam. of 75 μm that tapers to 50 μm in the first 40 μm and then rapidly decreases to about 25 μm. However, the diameter of the cones in both species is only 8–10 μm where they abut the rhabdom. The most proximal tip of the cone is slightly widened as in *Hyperia*. The crystalline cones of *P. abyssorum* are closely packed all along their lengths, but in *P. compressa* they are, just as in *Hyperia*, separated by a conspicuous extracellular space (Figs. 12 and 13).

b) Retinular Cells and Rhabdom. The rhabdom is stellate in a transverse section and is formed by five fused rhabdomeres (Fig. 16). The main part of the rhabdom has a diam. of 20 μm. The distal diam. is 8 μm that corresponds to the proximal cone diameter. The microvilli are radially arranged, but they display the same peculiar pattern as in *Ericthonius* and *Hyperia*, appearing as an anticlockwise turning of the microvilli. A conspicuous extracellular palisade, 1 μm wide, is present with a few broad cytoplasmic bridges. Pigment granules of the electron-dense type (0.2 μm) cross the bridges and occur at the margin of the rhabdom (daylight adapted eyes). A third type of granule (0.2 μm) is frequently found close to the rhabdom, and these are partly filled by electron-dense material (Fig. 16, inset).

III. The Ampeliscid Type

Earlier investigations have shown that the ampeliscids possess more than one pair of compound eyes (Strauss, 1926; Svensson, 1933). In the present species *Haploops tubicola* and *Ampelisca gibba*, there are three pairs of eyes, dorsofrontal, dorsocaudal, and ventrofrontal (Fig. 17A). In *Haploops* the dorsofrontal

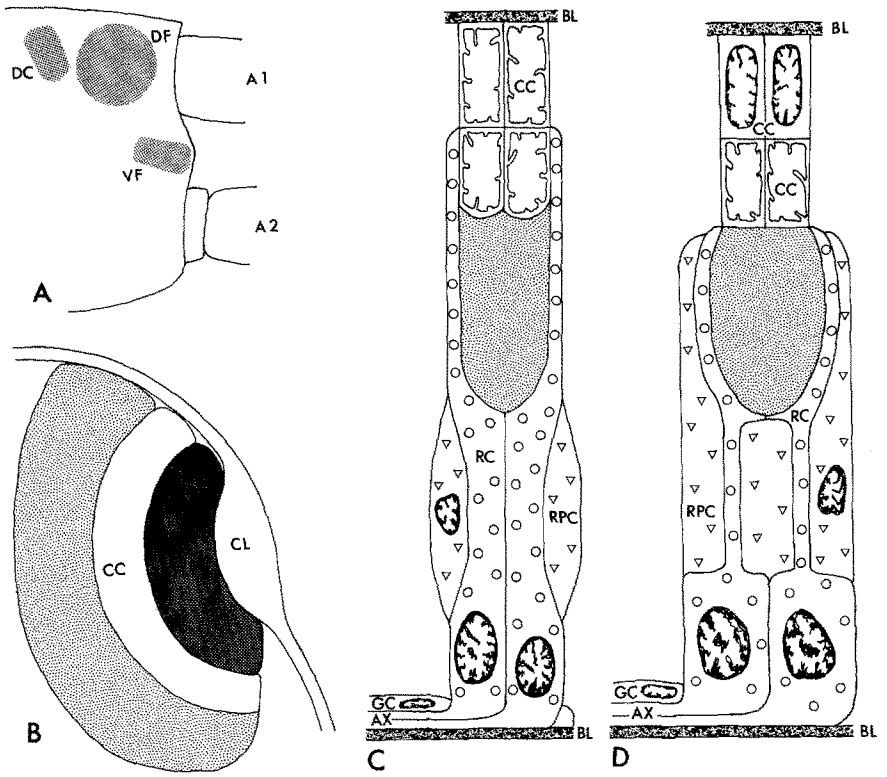


Fig. 17. A Lateral view of the head of *Haploops tubicola*. The positions of the three eyes are indicated by stippling: (*A1*) first antenna; (*A2*) second antenna; (*DC*) dorsocaudal eye; (*DF*) dorsofrontal eye; (*VF*) ventrofrontal eye. **B** The arrangement of the dorsofrontal eye of *Haploops tubicola*. The cuticular lens (*CL*) is situated above the vitreous body (*dark stippling*), cone cell layer (*CC*) and retinal layer (*light stippling*). **C and D** Schematic drawings of the ommatidia of *Haploops tubicola* and *Ampelisca gibba*, respectively. The rhabdoms are stippled, and the red and reflecting pigments are represented by *open circles* and *open triangles*, respectively (*AX*) axon. (*BL*) basal lamina. (*CC*) cone cells. (*GC*) glial cell. (*RC*) retinular cell. (*RPC*) reflecting pigment cell

pair is more developed than the other two pairs; in *Ampelisca* the dorsofrontal and ventrofrontal are equally well developed and the dorsocaudal pair is strongly reduced. The dioptric arrangement of these compound eyes is unique in crustaceans, as only one well-developed corneal lens is present and it is shared by the whole retina (Fig. 17B). In this respect the eyes are similar to the camera eye found in vertebrates and certain molluscs. Another peculiar feature, related to the lens arrangement, is that all the ommatidia converge toward the lens in contrast to other crustaceans, where the ommatidia diverge toward the cuticular facets. In *Haploops* the angle of convergence is greater in the dorsofrontal eyes than in the other two pairs of eyes.

1. Haploops tubicola (Lilljeborg, 1855) (Fig. 17C)

The red eyes have a more or less elaborate refractive apparatus, the dorsocaudal pair being situated beneath an undifferentiated cuticle and the ventrofrontal

pair beneath one cuticular lens. The dorsofrontal pair possesses both a cuticular lens and beneath it a so-called vitreous body (Svensson, 1933), another structure unique to ampeliscid compound eyes. Apart from the arrangement of the refractive elements, the three pairs of compound eyes are similarly constructed.

a) Dioptric Elements. The cuticle overlying the eyes forms a biconvex lens with a diam. of 115 μm and a maximal thickness of 90 μm. The vitreous body situated beneath the cuticular lens is kidney-shaped with its concave side facing outwards, fitting the cuticular lens (Fig. 17B). It is 170 μm in diam. and 60 μm thick. The vitreous body is extracellular and consists of an electron-dense granular substance (Fig. 18). It is formed by surrounding cells, which contain an extensive rough endoplasmic reticulum. The arrangement of the crystalline cone cells is unusual; the main cone cells and the accessory cone cells are equally well developed, but do not form a regular crystalline cone. They are piled two on top of the other two (Fig. 17C). All the cone cells have large nuclei, which comprise about 90% of the total cell volume. The nuclear matrix is homogeneous, lacking heterochromatin (Fig. 18), and there are no traces of deposited granular material in the cytoplasm.

b) Retinular Cells and Rhabdom. Distally, the five retinular cells envelop the proximal cone cells. The retinular cells contain moderately electron-dense pigment granules (0.4 μm) that are evenly dispersed in the cytoplasm (Fig. 19). The rhabdomeres are equally large and form a 50 μm-long rhabdom with a diam. of 8 μm. The rhabdomeric microvilli are radially arranged. The elongated nuclei of the retinular cells are situated close to the basal lamina (Fig. 20).

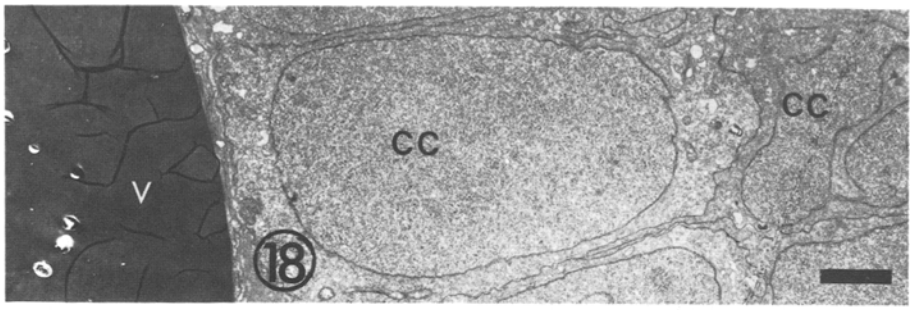
c) Non-Retinular Screening Pigment. The rhabdom region of the ommatidia is surrounded by reflecting pigment cells. The pigment granules (0.6 μm) have a characteristic appearance with an outer membrane inside which occasionally an electron-dense substance is radially arranged (Fig. 19, inset).

d) Glial Cells and Fenestrated Membrane. A fenestrated membrane and an eye capsule are lacking in the eyes of *Haploops tubicola*. The entire eye is delimited by a basal lamina that is formed by glial cells distal to the lamina (Fig. 20). These cells are probably homologous with the glial cells, in the same position, of other amphipod compound eyes.

Fig. 18. Longitudinal section of the vitreous body (*V*) and parts of the crystalline cones (*CC*) in *Haploops tubicola*. Note the large cone cell nuclei lacking heterochromatin. Scale: 3 μm

Fig. 19. Cross section of the rhabdom (*RH*) in *Haploops tubicola*. The presence of a nucleus (*N*) at this position is due to a peripheral section of the eye: (*RPC*) reflecting pigment cell; *Arrow*, pigment granule of the retinular cell. Scale: 1 μm. *Inset:* reflecting pigment granules containing a protein skeleton. Scale: 0.5 μm

Fig. 20. Longitudinal section of the eye-capsule membrane (*BL*) situated between one pair of compound eyes (eyes lie close together) in *Haploops tubicola*. Retinular cell axons (*AX*) run close to the membrane. (*N*) nucleus of retinular cell. Scale: 3 μm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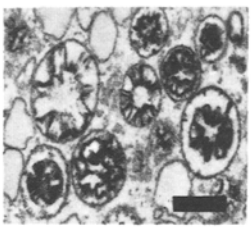

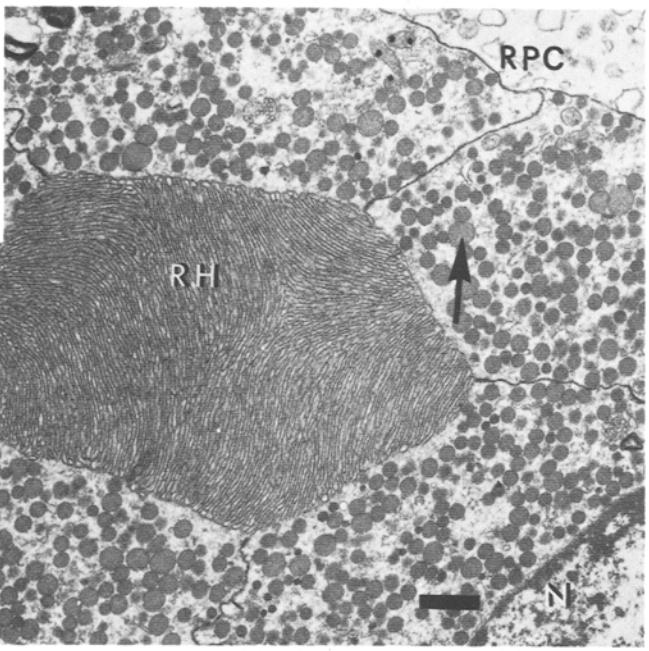
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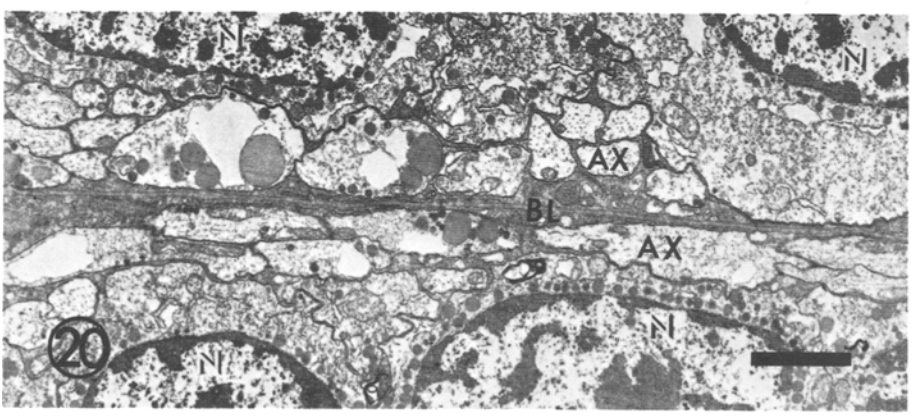
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2. Ampelisca gibba G.O. Sars, 1882 (Fig. 17D)

a) Dioptric Elements. The cuticular lens of the dorsofrontal and ventrofrontal eyes is 50 µm in diam. Centrally, it is 25 µm thick and peripherally 6 µm. The inner convexity is greater than the outer. The dorsocaudal eye has no lens. A vitreous body is lacking in *Ampelisca,* but a large fluid-filled space is present where the vitreous body is situated in *Haploops.* This space is delimited by a basal lamina.

b) Retinular Cells and Rhabdom. Five retinular cells form the rhabdom, and they surround it with 1–2 µm thin cytoplasmic sheets densely stacked with electron-dense pigment granules (0.65 µm). Proximal to the rhabdom, the retinular cells appear as slender processes (2 µm) penetrating the massive reflecting pigment layer and do not broaden until the nuclear region. In the dorsofrontal and ventrofrontal eyes the 45 µm rhabdom is barrel-shaped, the diameter being 14 µm in the middle and 10 µm at the ends.

c) Non-Retinular Screening Pigment. A more than 20 µm thick layer of reflecting screening pigment cells surrounds the rhabdoms and continues proximally. The granules are similar to those of *Haploops.*

IV. The Lysianassid Type

As has been shown by Strauss (1926), the morphology of the ommatidia of deep-sea amphipods differs from that of littoral species. Generally, the dioptric elements are more or less reduced and the rhabdoms are hypertrophied. Of the three species investigated, two, namely *Tmetonyx cicada* and *Orchomenopsis obtusa,* have a moderate structural adaptation to low light intensities. In *Eurythenes gryllus* these processes have proceeded further, resulting in a greatly transformed eye.

1. Tmetonyx cicada (O. Fabricius, 1780) (Fig. 21A)

The ruby-red eyes of this species occupy an L-shaped area on the sides of the head.

a) Dioptric Elements. The cornea of *T. cicada* is the thickest (48 µm) of the species investigated. The cones are cylindrical and roughly rounded in cross section. The diam. is about 40–50 µm and the length 50–60 µm. The main cone cell nuclei are situated distally and are remarkably elongated (40 µm) and encompass half the cone. Three distinct zones of the cone are observed in cross section: a dark central amorphous core (35 µm in diam.); a dark middle zone (7 µm thick) that is well developed with large granules marginally arranged in layers; and finally a lighter outer cytoplasmic zone (4 µm thick). The cones are surrounded by retinular cells.

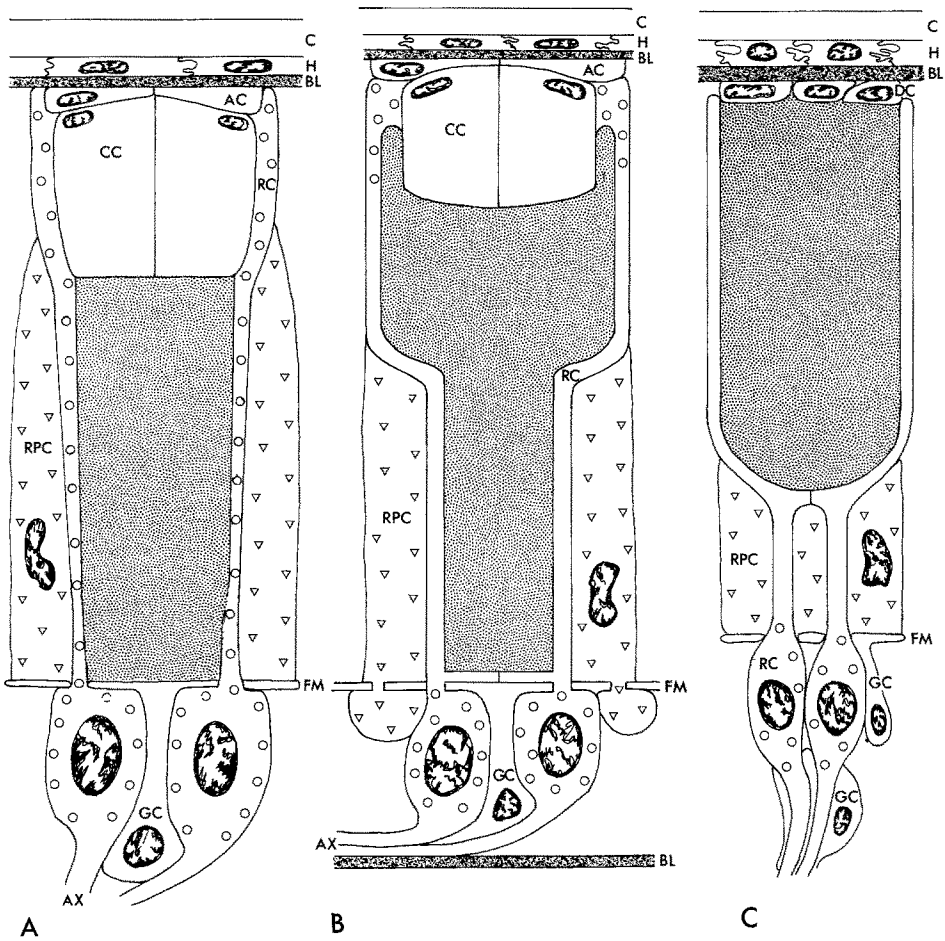


Fig. 21 A–C. Schematic drawings of lysianassid eyes: **A** *Tmetonyx cicada.* **B** *Orchomenopsis obtusa.* **C** *Eurythenes gryllus.* Rhabdom is shown stippled. The red and reflecting pigments are represented by *open circles* and *open triangles,* respectively: (*AC*) accessory cone cell; (*AX*) axon. (*BL*) basal laminal; (*C*) cuticle; (*CC*) cone cell; (*DC*) distal cell; (*FM*) fenestrated membrane; (*GC*) glial cell; (*H*) hypodermal layer; (*RC*) retinular cell; (*RPC*) reflecting pigment cell

b) Retinular Cells and Rhabdom. The five retinular cells extend to the hypodermis. They are very thin (0.2–1.0 μm) and are filled with electron-dense pigment granules (0.25 μm) (Fig. 22). These are distributed in a monolayer peripherally in the nuclear region. A number of moderately electron-dense granules (0.7 μm) and a large number of mitochondria are found in the expanded region of the retinular cells. The mitochondria are practically absent in the rhabdom region. The retinular cells below the fenestrated membrane are filled with irregularly shaped vacuoles (1.3 μm) that appear empty (Fig. 22, inset). The fused continuous rhabdom is round to rectangular distally, and medially and proximally it is four or five-rayed (Fig. 22). The diam. is about 20–25 μm, and the entire rhabdom is 100 μm long. The microvilli have small dilatations and are

irregularly arranged. The rays of the adjacent rhabdoms fit into one another, and only narrow interspaces filled with reflecting pigment are present.

c) Non-Retinular Screening Pigment. Reflecting pigment (granular diam. about 0.25 μm) forms a tapetal layer around the rhabdom (Fig. 22). Extensions from the reflecting pigment cells extend halfway up on the sides of the crystalline cones.

d) Glial Cells and Fenestrated Membrane. The fenestrated membrane is poorly developed, and only a thin (0.2–0.7 μm) basal lamina is present distal to the retinular cell bodies. The basal lamina is formed by glial cells that intermingle between the retinular cell somas. No distal extensions are present. The glial cells encapsulate the axons, but take no part in the formation of the eye capsule.

2. Orchomenopsis obtusa G.O. Sars, 1895 (Fig. 21 B)

a) Dioptric Elements. In the central region of the eye the crystalline cones are more or less spherical with a diam. of 40 μm Toward the periphery of the eye, the cones are progressively compressed and assume the shape of a biconvex lens with a maximal thickness of 10 μm. The zonation of the crystalline cone is similar to that of *Tmetonyx*.

b) Retinular Cells and Rhabdom. The five retinular cells of the light – red eye are similar to those of *Tmetonyx*, the electron-dense pigment granules, however, being 0.55 μm and the electron-translucent 0.4 μm. The five-rayed rhabdoms (Fig. 23) are broad distally (40 μm) and extend at least halfway up the sides of the crystalline cones (40 μm). Proximal to the cones, the rhabdom narrows and has a diam. of 25–30 μm (length 60 μm).

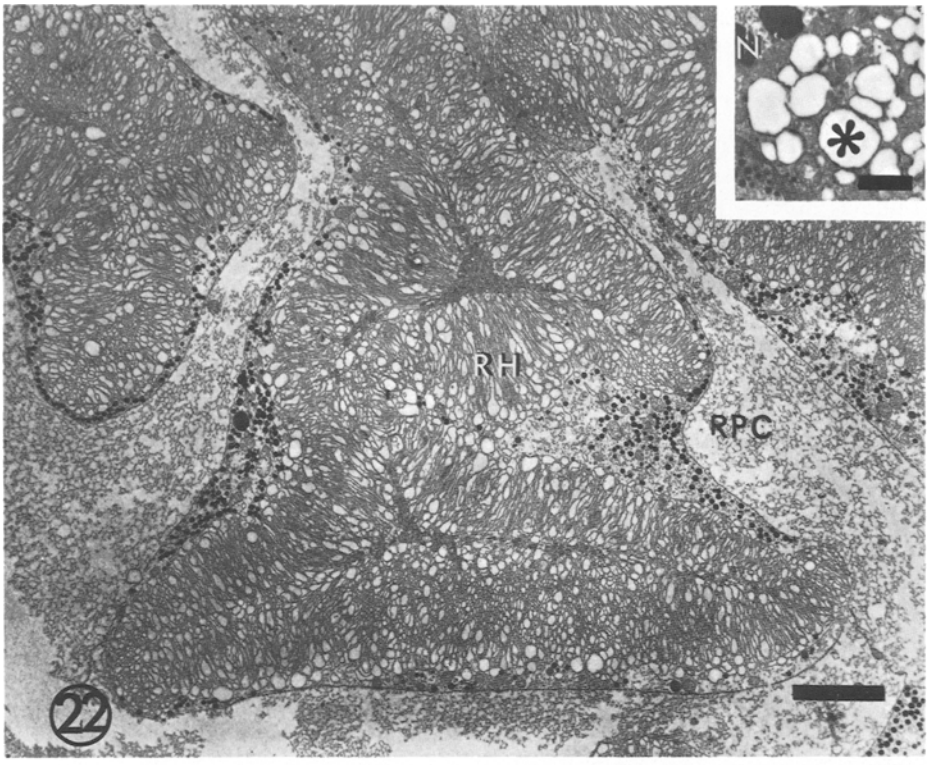
3. Eurythenes gryllus (Lichtenstein, 1822) (Fig. 21 C)

The yellowish eyes in this species occupy a large area of the head, extending from the dorsal to the ventral side as an irregular band. The ommatidia are large, the length being about 225 μm from the cuticle to the eye capsule.

Fig. 22. Cross section of the rhabdom (*RH*) in *Tmetonyx cicada*. Note hypertrophied rhabdom, thin sheets of retinular cell cytoplasm and large amount of reflecting pigment (*RPC*). Scale: 5 μm. *Inset:* irregularly shaped vacuoles in the cytoplasm of the retinular cell soma (*Asterisk*): (*N*) nucleus of retinular cell. Scale: 2 μm

Fig. 23. Cross section of the rhabdom (*RH*) in *Orchomenopsis obtusa*. Note hypertrophied rhabdom, thin sheets of retinular cell cytoplasm and large amount of reflecting pigment (*RPC*). Scale: 5 μm

Fig. 24. Cross section of the rhabdom in *Eurythenes gryllus*. Note the hypertrophied rhabdom (*RH*), thin sheets of retinular cell cytoplasm (*arrow*), the reflecting pigment (*RPC*), and the absence of retinular cell pigment granules. Scale: 5 μm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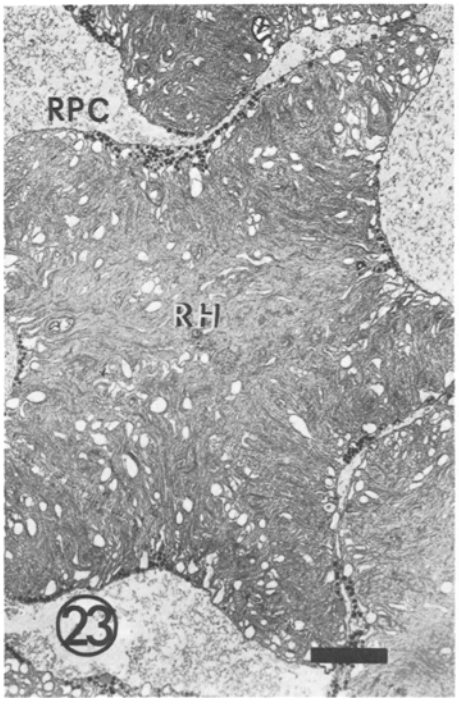
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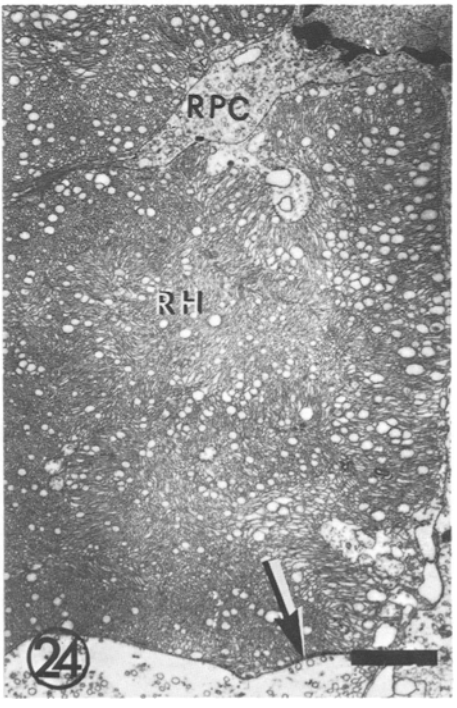
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a) Dioptric Elements. There are no traces of the crystalline cone, except for some flattened cells distal to the rhabdom that probably represent the remnants of the cone cells. These cells contain very little cytoplasm around the nuclei.

b) Retinular Cells and Rhabdom. The five retinular cells appear as thin sheets of cytoplasm surrounding the rhabdom (Fig. 24). Below the rhabdom they continue as narrow processes wedged between the reflecting pigment cells. There are pigment granules (0.4 μm) in the nuclear region of the cytoplasm, proximal to the fenestrated membrane, resembling carotenoid-bearing granules. The rhabdoms are large and in a transverse section have a rectangular outline with a side of about 40 μm and a length of approximately 100 μm. The microvilli of the rhabdom are arranged in a twisted pattern. They originate from thin lamellae of the retinular cells that project into the rhabdom. The lamellae are coiled around one another, and no regular microvillar orientation exists.

c) Non-Retinular Screening Pigments. Cells containing reflecting pigment granules are present between the basal parts of the ommatidia and the fenestrated membrane. The granules appear as empty vesicles (0.4 μm).

d) Glial Cells and Fenestrated Membrane. The glial cells are present around the nuclear part of the retinular cells and form thin sheets around them. Distally, the glial cells form a feebly developed fenestrated membrane. There are no distal processes from the glial cells.

D. Discussion

The present survey of the compound eyes of a fairly large number of amphipod species belonging to different taxa reveals a common pattern that can be designated as the amphipod type of compound eye. This is not characterized by a number of unique features because many of the structures are found elsewhere among crustaceans, but instead by the constellation and consistency of a considerable number of morphological features. These will be briefly reviewed below.

It is notable in the amphipod eye that all ommatidia are separated from the cuticle by a well-developed hypodermal layer including the basal lamina. Thus, the compound eye conveys the impression of being more detached from the hypodermis than in other compound eyes, where there is a much more intimate connection between the ommatidia and the cuticle. This may also have a bearing upon the fact that cuticular lenses are lacking in amphipods except for the aberrant eyes of the ampeliscid type.

The dioptric apparatus thus consists only of the crystalline cone, which in all well-developed eyes is formed by two main cells. In addition two accessory cone cells are present that do not participate in the formation of the cone. The sensory cells are always five. Often they are equally well developed, although differences between them can occur. They form together a fused continuous rhabdom that in some species is isolated by an extracellular palisade. These retinular cells consistently have nuclei proximally in the eye. A very common

characteristic is the presence of two different types of pigment granules in the cytoplasm indicating two different pigments in one cell. Finally, the amphipod compound eye has a peculiar double membrane sealing it from the rest of the body. This is formed by thin glial cells situated around the nuclear part of the retinular cells. These cells also assume a transverse direction distal and proximal to the nuclear region, thus enchambering this part of the retinular cells. The glial cells secrete a basal lamina. Distally, this and the cellular components of the glial cells form the so-called fenestrated membrane (or basement membrane 1; Ball, 1977), whereas proximally it is called the eye capsule (or basement membrane 2; Ball, 1977). The basal lamina of the latter structure merges with the hypodermal basal lamina marginally in the eye.

Within this common type, we can distinguish four subtypes in the present material. Naturally, a larger sample might produce more subtypes or confirm the types already classified. The size of the task has also imposed other limitations. The descriptions, for example, pertaining to central ommatidia, and regional differences in the compound eye have not been considered except in a few instances.

The most conspicuous is the ampeliscid type, where the compound eye has been divided into three separate units, each with a common dioptric apparatus. However, the ampeliscid *Ampelisca rubella* obviously has a 'conventional' compound eye with several facets (Della Valle, 1893; Strauss, 1926). The lysianassid type is recognized by the more or less complete reduction of the dioptric apparatus and the hypertrophy of the rhabdom. The hyperid type diverges from the others by the vastly exaggerated size of the dioptric apparatus and the enormous development of the eye that occupies most of the head. The gammarid type. finally, is, in a way, characterized negatively by its lack of conspicuous features. It comes close to some sort of a common type that has no phylogenetic implications so far.

Viewing the ommatidium as such and the variations it undergoes in the different types, it seems as if the retinular cells and rhabdom are subjected to the least variation in number and gross structure, whereas the dioptric apparatus and the pigment equipment are more prone to change.

The pigment equipment of the amphipod eye is situated in the retinular cells and in the accessory pigment cells. It was remarked above that the retinular cells contain two different types of pigment granules. One, being smaller (0.1–0.65 μm) and electron-dense, could represent ommochrome pigments; and the other, being larger (0.4–1.0 μm) and electron-translucent, could consist of carotenoids (Elofsson and Hallberg, 1973). This conforms well with the observations of Michel and Anders (1954), who found both ommochromes and carotenoids in the eyes of *Gammarus pulex*. Further, the carotenoids were the first to appear in the developing eye and they were later followed and masked by the ommochromes. This is observed externally as a shift from red to black eyes. In those instances (*Tmetonyx, Haploops*) where a red compound eye still exists in the adult stage, this might be due to the fact that the ommochromes have failed to develop. It is possible to find a correlation with the depth distribution and colour of the pigment shield, because below a certain water depth where the red component of the spectrum is absent the red pigment will function

as a black pigment. The most common non-retinular pigment is a reflecting pigment that is usually found around the retinular cells above the fenestrated membrane. It is absent only in the hyperid type. Only in a few genera, *Ericthonius* and *Hyperia,* another type of accessory cell occurs containing dark pigment. In *Ericthonius* both reflecting and dark pigment exist together, for which reason a homology between the two seems excluded. Hence, although a certain common pigment pattern is found, there is a variation in position and abundance of granules.

The number of retinular cells is very stable and only in a few instances (*Gammarus* and *Orchestia*) a hint of an aberrant retinular cell occurs, which is often found in crustacean ommatidia (Kunze, 1967; Edwards, 1969; Nemanic, 1975; Eguchi and Waterman, 1966; Meyer-Rochow, 1975; Nilsson, 1978; Hallberg, 1977; Elofsson and Odselius, 1975; Nässel, 1976). The only variation seen is the overall shape of the fused continuous rhabdom, which can appear cylindrical, fusiform, or cylindrical with ridges (starshaped in cross section). The significance of this is unknown.

If the subtypes of compound amphipod eyes are analysed with regard to habitat, one group, the lysianassid type, is fairly well understood as an adaptation to its habitat. The lysianassid species investigated are deep-sea animals: *Tmetonyx* and *Orchomenopsis* live in deep fiords and *Eurythenes* is a true deep-sea species. There is also a clear trend among the species toward a reduction of the dioptric apparatus, which is completed in *Eurythenes.* In addition to this the rhabdom hypertrophies; this, the retinular cells accomplish by forming a cylinder in which folds from the walls enlarge the surface from which microvilli project. This gives a greater light-gathering power. At the same time the microvilli lose their regular orientation compared with, e.g., the gammarid type of rhabdom. Because of the polar arrangement of the pigment molecules (Laughlin et al., 1975) along the microvilli, an irregular pattern contributes to a reduced masking and a greater ability to perceive unpolarized light. Summing up, the ommatidium with these arrangements adapts to low light intensities. Also, in this instance, a development from the gammarid or hyperid types is easy to understand. In this connection deep-sea mysids offer a good comparison. It was found that some fiord and deep-sea mysids (Elofsson and Hallberg, 1977) adapted to low light intensities, lose the dioptric apparatus and form a hypertrophied rhabdom. Were it not the fact that the mysid rhabdom was formed by seven retinular cells arranged in two layers, the amphipod and mysid eyes would have been difficult to distinguish. This illustrates the convergence problem: convergent development imposed by the habitat in certain situations can lead to organs very similar in appearance, but resulting from bidirectional selective forces.

The hyperid species are planktonic forms, and some species are temporarily or permanently associated with other organisms: *Hyperia* is often found in scyphozoans, and *Phronima* inhabits empty tunicate barrels (Wimpenny, 1966). The species we investigated have a large vertical distribution (see Material and Methods), and are thus subjected to variable light intensities. In *Phronima* the large number of ommatidia, the elongated crystalline cones and pigment constellation have been interpreted by Ball (1977) as morphological adaptations

resulting in an increased sensitivity and spatial resolution. When considering the organization of the structural elements, it is also easy to envisage a trend leading to or from the eyes of the gammarid type.

The majority of the ampeliscids are 'true deep-water forms' (Sars, 1895). This group comprises benthic forms; some species (among them *Haploops*) live in self-constructed tubes (Stephensen, 1928). The structure of the eyes is, however, difficult to understand as an adaptation to the deep sea. According to Strauss (1926) the arrangement of the ommatidial units and the possession of large lenses enhance the field of view that would enable the animals to perceive predators and make a fast retreat. The development of this type parallels that of the other types and appears as an experiment with the optics of the compound eye.

The gammarid type involves species of very different habitat, and also in this instance a correlation between eye type and habitat is difficult. One is tempted to speculate that this is an eye capable of coping with many kinds of surroundings, but the structural analysis attempted here is ahead of functional considerations, and consequently any such statement would be premature. The distinctions made between types can, however, serve as a basis for closer functional analyses which could begin with a generalized type, perhaps represented by the gammarid and proceed with adaptive forces acting on this type.

A phylogenetic approach is, of course, implicit in the above discussion of compound eyes within the Amphipoda. One might speculate that the gammarid type is an original type from which all others have evolved, even the aberrant ampeliscid type where the species *Ampelisca rubella,* as an exception, evidently retains the 'original' type. However, a more detailed discussion of these problems must be based on a more extensive study in which functional considerations have been thoroughly evaluated.

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Received October 27, 1979