

# The Fine Structure of the Compound Eyes of Shallow-Water Asellotes, *Jaera albifrons* Leach and *Asellus aquaticus* L. (Crustacea: Isopoda)

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## Abstract

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Both species have small sessile compound eyes. The dioptric apparatus of *J. albifrons* consists of a biconvex lens and a pyriform crystalline cone, the latter formed by two principal and two accessory cone cells. *A. aquaticus* has a reduced lens and a round cone formed by two to four principal cone cells with two to no accessory cone cells. Distal pigment cells and pigmented reticular cells lie between the ommatidia in *J. albifrons*. *A. aquaticus* has only the pigmented reticular cells. Both species have a fused, continuous (unbanded) rhabdom formed by eight reticular cells (R1—8), one of which (R8) is situated distally. The reticular cells R1—7 form, in *J. albifrons*, a cylinder-shaped middle portion with three microvillar directions (60° apart) and a proximal star-shaped portion. The entire rhabdom of *A. aquaticus* is star-shaped. Distal pigment-cell processes and basal cells form the fenestrated membrane in *J. albifrons* and “eye-cup cells” in *A. aquaticus*.

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## Introduction

A great variation in the organization of the isopod retinae has been shown by previous light-microscopic studies (e.g. Parker 1891, Hesse 1901, Debaisieux 1944) and by a few electron-microscopic investigations (*Oniscus*, Tuurala et al. 1966, Tuurala and Lehtinen 1967, *Ligia*, Edwards 1969, *Porcellio*, Nemanic 1975).

Only a few physiological investigations of the isopod eye have been conducted: electroretinogram (ERG) measurements of the spectral sensitivity of *Porcellio scaber* (Goldsmith and Fernandex 1968) and an analysis of the ERG components in *Ligia oceanica* (Ruck and Jahn 1954) and in *Ligia italica*, *Porcellio loewis* and *Arma-*

*dillo officinalis* (Benguerrah and Carricaburu 1976).

All of these above-cited investigations indicate that the isopod compound eye and visual properties offer an interesting and valuable object for study. The group as such is taxonomically distinct within the Peracarida, yet it shows successful adaptation to a wide variety of ecological niches, including terrestrial, semi-aquatic and aquatic (deep-sea as well as shallow-water) environments. One would expect to find within such a group adaptationally derived variations based on a common eye type.

The present ultrastructural study of the isopods *Jaera albifrons* and *Asellus aquaticus* is part of an investigation attempting to disclose the mor-

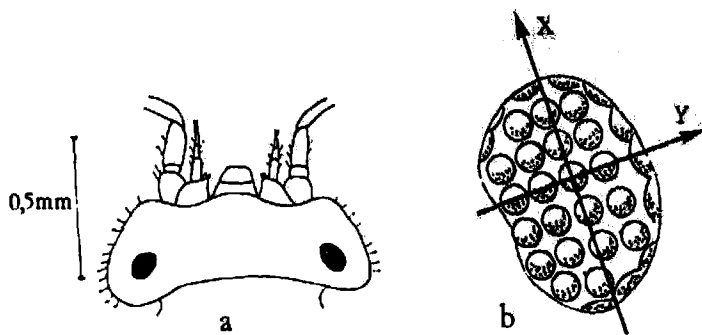


Fig. 1. a) Schematic drawing of the dorsal side of the head of *Jaera albifrons*. b) Enlargement of the right eye, which has orthogonal ommatidial rows. X and Y are eye co-ordinates.

phological variation of the isopod compound eye and its bearing on the phylogeny and functional properties of the eye. The present study describes in detail the eye of aquatic isopod species hitherto neglected (no aquatic isopods have previously been studied ultrastructurally).

## Material and Methods

Adult *Jaera albifrons* Leach were obtained locally in Öresund Channel and adult *Asellus aquaticus* L. were caught in ponds in the town of Lund. The specimens were fixed after being adapted to daylight conditions. For scanning electron microscopy, they were washed in seawater and freshwater, respectively, together with ultrasonic treatment for 5 sec. Fixation was performed according to Karnovsky (1965) at 4°C for 4 hours (pH 7.3). The specimens were then washed in sodium-cacodylate buffer and taken through a graded series of alcohol. Ultimately, they were left in xylol for 24 hours and then air dried. The preparations were gold-platinum coated and examined with a Cambridge Stereoscan Mk II electron microscope.

For transmission electron microscopy, half or whole heads were prefixed for 4 hours at 4°C in paraformaldehyde-glutaraldehyde (Karnovsky 1965) buffered with sodium cacodylate (pH 7.3). Postfixation was carried out for 2 hours in 2% OsO<sub>4</sub> with the same buffer. Dehydration was performed in an alcohol series, block-staining in 1% PTA and 0.5% UA and embedding in Vestopal W. Ultrathin sections were cut with glass knives. They were placed on formvar-coated grids and examined with Philips EM 300 and Zeiss EM 10 electron microscopes. The latter, equipped with a goniometer, was used to obtain better membrane resolution in critical areas. For light microscopy, 2 μm sections were cut, mounted on glass, and stained with azure-methyl (Richardson et al. 1960).

## Results

### *Jaera albifrons*

#### General Description

The compound eyes of *J. albifrons* are small (0.15 × 0.20 mm), sessile, dome-shaped and slightly oval in cross section; they are situated on top of the head, with the round corneal facets oriented upwards (Fig. 1). Each eye consists of about 25 ommatidia. The packing of the ommatidia is orthogonal with four to five rows along the long axis of the eye (x-axis) and six to seven rows in the other axis (y-axis, Fig. 1b). The x-axis makes an angle of 20° with the median line of the animal (Fig. 1a). A peripheral distortion in the packing of the ommatidia is caused by the oval shape of the eye. The corneal facets are covered with small processes (Figs. 3, 5, 7). No accessory sensory sensilla or cilia are associated with the eyes.

#### Ommatidia

Basically, the single ommatidium is composed of a dioptric apparatus, a receptor cell unit (the retina) and shielding pigment cells (Fig. 2). The dioptric apparatus consists of a biconvex cuticular lens, 23 μm in diameter, and a crystalline cone with a distal and proximal diameter of 15 μm and 7 μm. Distal pigment cells lie between adjacent ommatidia. Eight reticular cells contribute to the formation of a rhabdom. The rhabdom is 18 μm long and 10 μm in diameter. The ommatidia are delimited proximally by a fenestrated membrane (definition according to Peabody 1939) below which most of the reticular cell nuclei are situated (R1—7). An exception is the growth zone where the reticular cell nuclei are above the fenestrated membrane. The axons run to the lamina ganglionaris. The entire eye is very compact and is a typical apposition eye (Figs. 2, 4).

#### Dioptric Apparatus

The cuticular lens is formed by two corneagenous cells with large elongated nuclei (Figs. 3, 8). Profuse, rough endoplasmic reticulum is characteristic of the cytoplasm of the corneagenous cell (Fig. 3). Its abundance might be due to the time in the molt cycle (Nemanic 1975). The biconvex lens is thick, 26 μm in the centre and 5 μm at the edges. Alternating dense and clear endocuticular lamellae constitute most of the lens. There are a

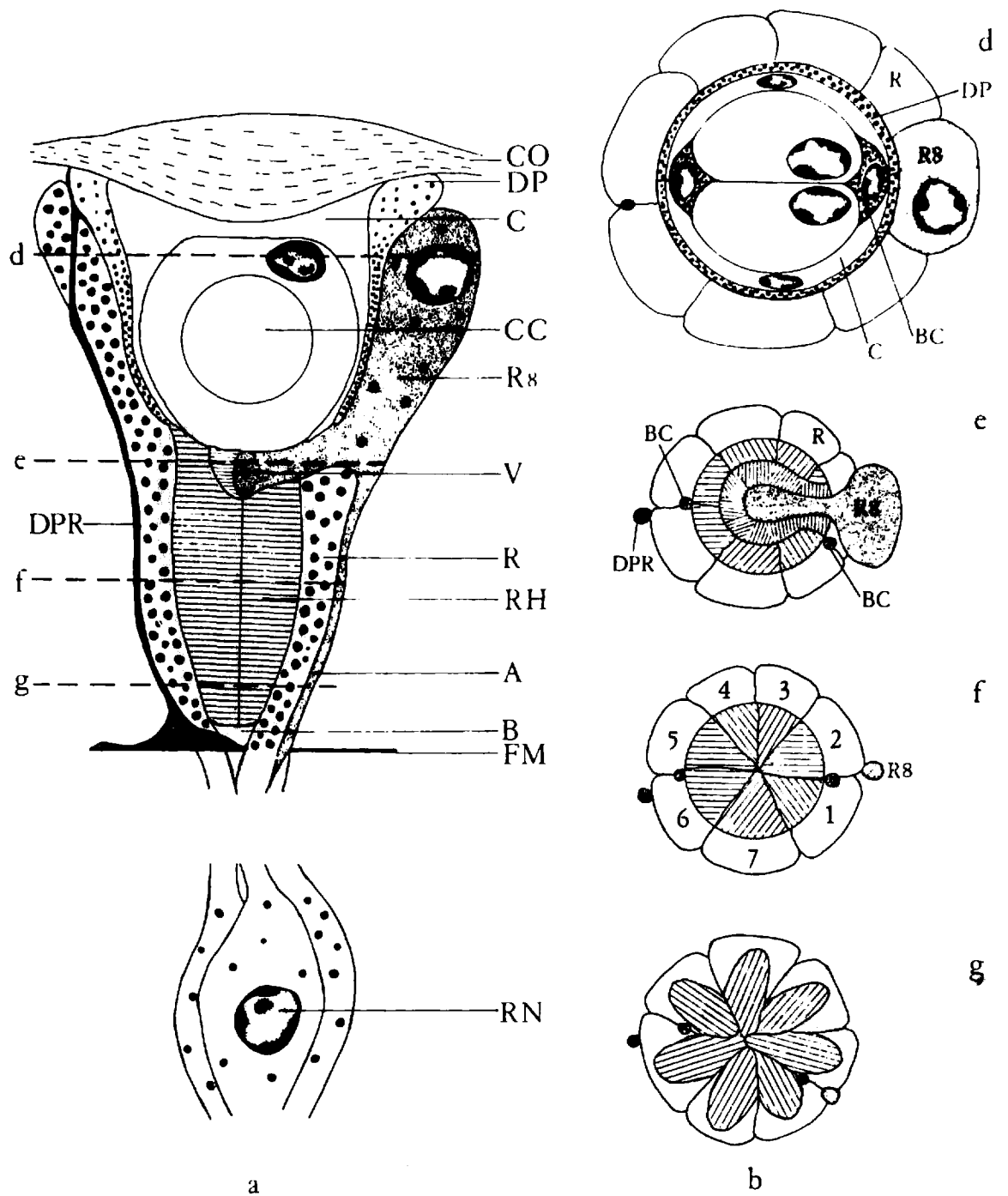
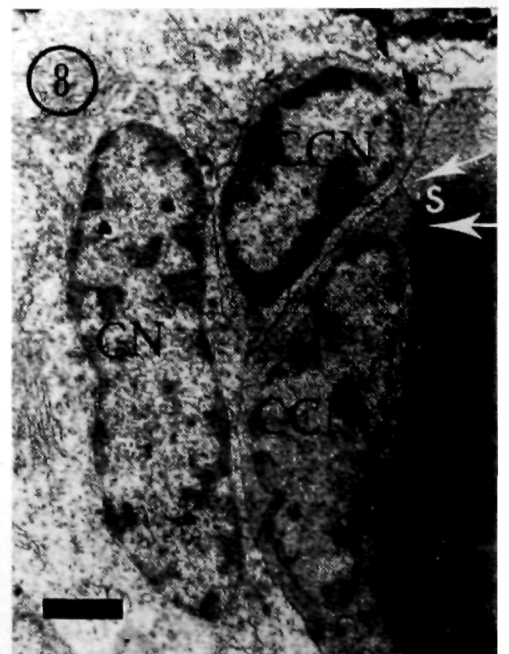
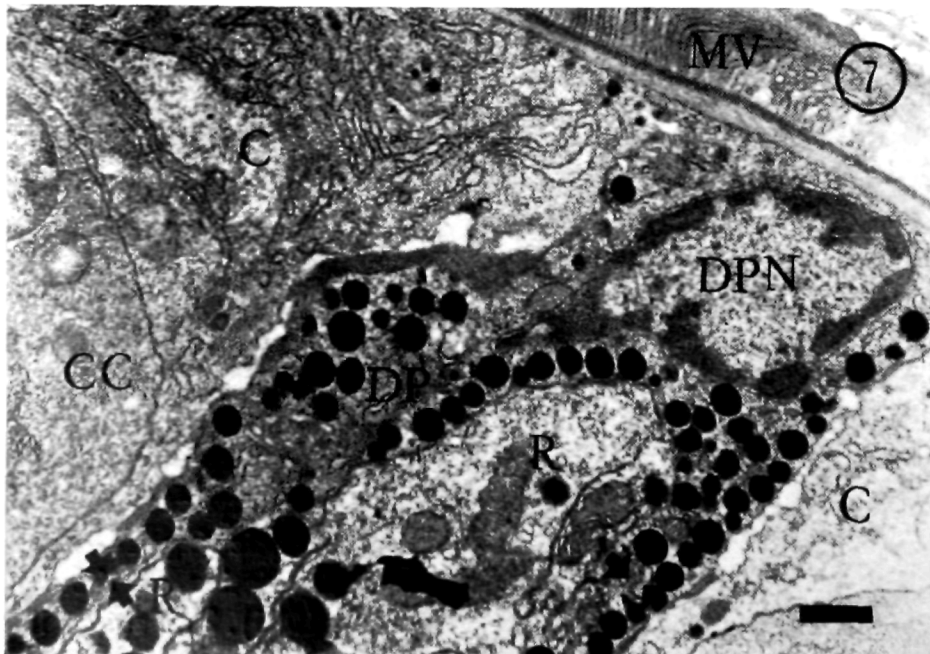
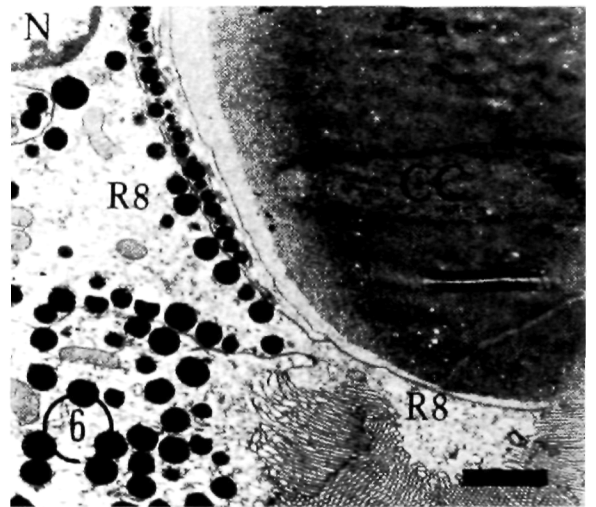
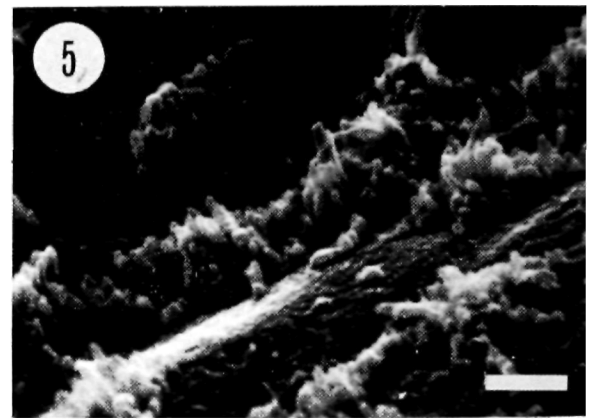
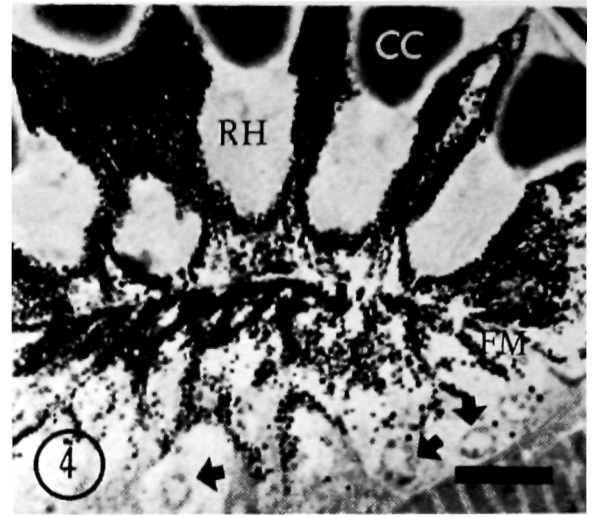
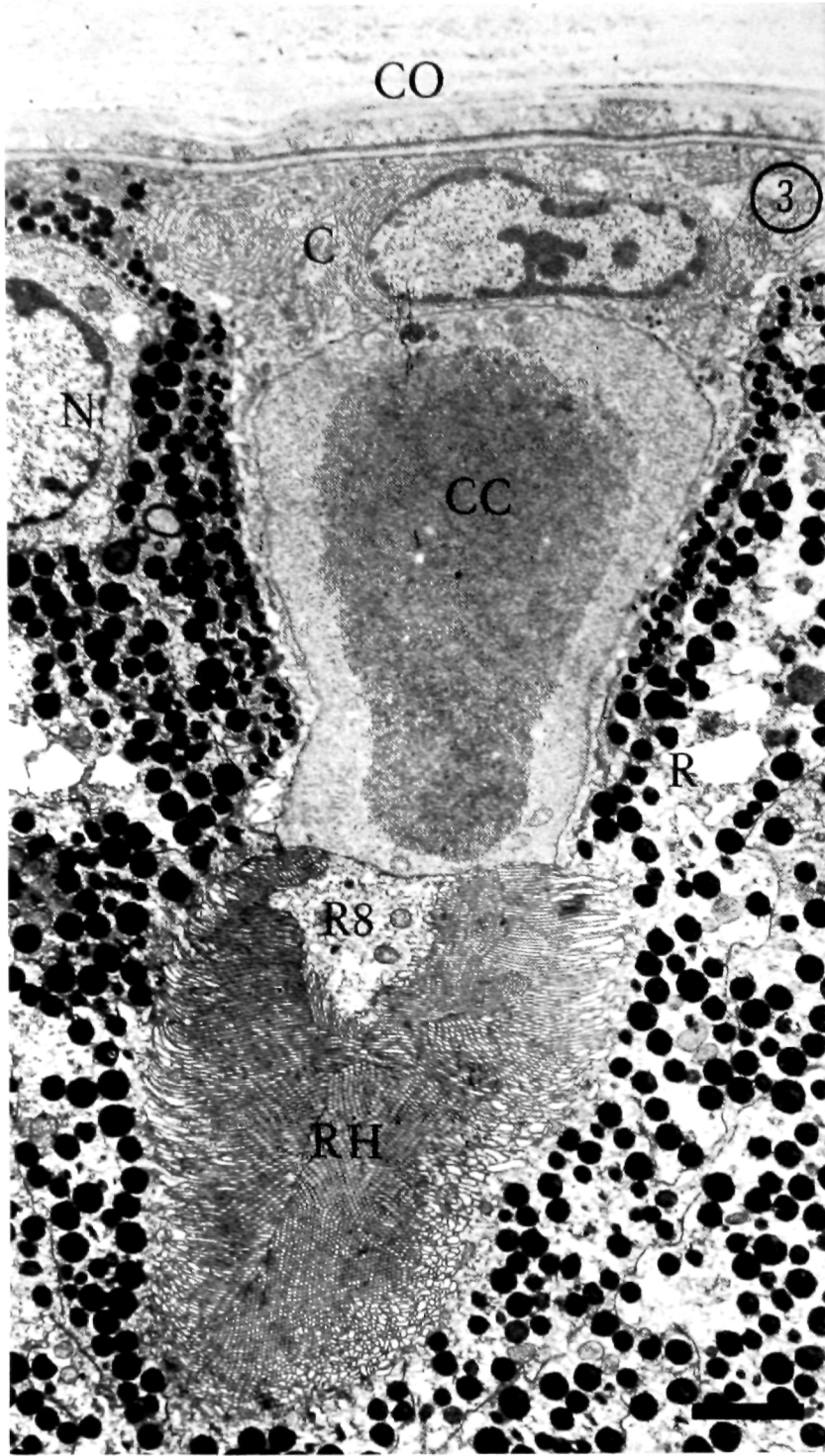


Fig. 2. a) Schematic drawing, longitudinally bisected, of an ommatidium of *Jaera albifrons*. b) Cross sections of an ommatidium at levels indicated in a). A axon of R8, B end-foot of an accessory cone cell, BC accessory cone cell, C corneagenous cell, CC crystalline cone, CO corneagenous lens, DP distal pigment cell, DPR distal pigment cell process, FM fenestrated membrane, R retinular cell, R8 retinular cell No. 8, RH rhabdom, RN retinular cell nucleus, V rhabdomere of R8, 1—8 retinular cells.

thin epicuticle, an exocuticle and an endocuticle (Fig. 3). The protrusions (length  $1 \mu\text{m}$ ) from the cuticular surface are arranged in bush-like clusters on the lens surface (Figs. 3, 5, 7). However, these processes are also found on the dorsal body cuticle, and both the old and the new cuticle of a molting animal have them (Figs. 3, 7).

The crystalline cone is pyriform with the broadest and flattest end distally. It is formed mainly by two cone cells. Two more cells are situated opposite each other on the suture line between the main crystalline cone cells (on the x-axis, Figs. 2, 8, 18). The latter cells are referred to as accessory cone cells.

The morphology of the amorphous core and that of the peripheral cytoplasmic ring of the cone do not differ from the description of those of *Porcellio scaber* (Nemanic 1975). The suture line of the cytoplasmic ring between the two principal



cone halves has a characteristic appearance, which looks like a zipper with the teeth pointing outwards (Fig. 17a). A similar appearance of cone sutures is described from decapods (Roach 1976).

One process from each of the two principal cone cells is interposed between the reticular cells, but these elongations terminate 4  $\mu\text{m}$  below the cone (Fig. 10). The two accessory cone cells, on the other hand, send two extensions to the fenestrated membrane, where they end (Figs. 9—13, 18). These extensions are easily recognized along their course because of their constant position between R1 and R2 and between R5 and R6. They exhibit a large content of microtubules (Fig. 18a). Just above the fenestrated membrane, they attach to the widened end-feet of the distal pigment cells (see below) and interdigitate (Fig. 13).

### Retina

The reticular cells (R1—7) have a high content of pigment granules, presumably ommochrome (Elofsson and Hallberg 1973), with an average diameter of 0.7  $\mu\text{m}$ . Elongated mitochondria, Golgi apparatus, multivesicular bodies, rough and smooth endoplasmic reticulum, microtubules, free ribosomes and vacuoles are frequent within the reticular cell cytoplasm (Figs. 9—14). Subrhabdomeric cisternae of extracellular origin are present, although poorly developed (Figs. 10, 11). This could be an effect of daylight conditions (Horridge and Barnard 1965, Horridge 1966,

Tuurala et al. 1966, Tuurala and Lehtinen 1967). An extracellular palisade has also been shown in *Oniscus asellus* (Tuurala et al. 1966) and in the isopod *Astacilla longicornis*, where it is very prominent (Nilsson and Elofsson 1978). A well-developed palisade similar to the one in *A. longicornis* is also present in the amphipod *Phronima* (Ball 1977). Most of the round nuclei of R1—7 are situated below the fenestrated membrane (Fig. 4). Only those in the medial periphery of the eye have a position above it. The reticular cells also send protrusions towards the cornea. Thus, the pigment granules of the reticular cells will add to the distal pigment cell layer and will effectively screen off nearby ommatidia from one another (Figs. 2, 3, 7, 17). The reticular cells are connected by zonula adherens, positioned close to the rhabdomeres.

R8 is easily recognized by its electron transparency and the presence of large vacuoles (Fig. 9). As a general rule, the preservation of the cytoplasm in the cell soma of R8 is poor compared with R1—7. Pigment granules are similar to those found in R1—7, but are less frequent. Elongated mitochondria (1.4  $\mu\text{m}$  long, 0.4  $\mu\text{m}$  in diam.) are mostly found in the cell body. The nucleus is situated at the level of the distal part of the crystalline cone, thereby differing from R1—7. The axon, with its microtubules, has a constant position between R1 and R2 (Figs. 2, 10, 12, 13).

Seven reticular cells (R1—7) contribute to the main part of the fused rhabdom (Figs. 2, 11, 12). Distally, the rhabdom is formed by R1—7 and the eighth reticular cell (R8, Figs. 2, 10). A cross section of the main part of the rhabdom is oval (Fig. 11). The most proximal part, however, has a stellate appearance (Fig. 12). The seven rhabdomeres are the same size (Fig. 11). The microvilli have a diameter of 60 nm. All rhabdomeres meet centrally. The main part of the rhabdom has microvilli oriented in three directions, 60° from one another.

The individual rhabdomeres can be placed in three groups with respect to the different microvillar orientations as follows: R1 and R4; R3 and R7; and R2, R5 and R6; with each group sharing the same microvillar orientation (Figs. 2f, 11). In the stelliform proximal part of the rhabdom, the microvillar orientations have changed to a radial arrangement with approximately the same angles between each rhabdomere (Figs. 2g, 12).

The appearance of the R8 rhabdomere is that of a microvilli-coated club pushed down centrally within the distal portion of the main rhabdom

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Figs. 3—8. *Jaera albifrons*. The figure labels are the same as in Fig. 2.

Fig. 3. Longitudinal section, peripherally cut, of an ommatidium. *N* nucleus of R8. Scale 2  $\mu\text{m}$ .

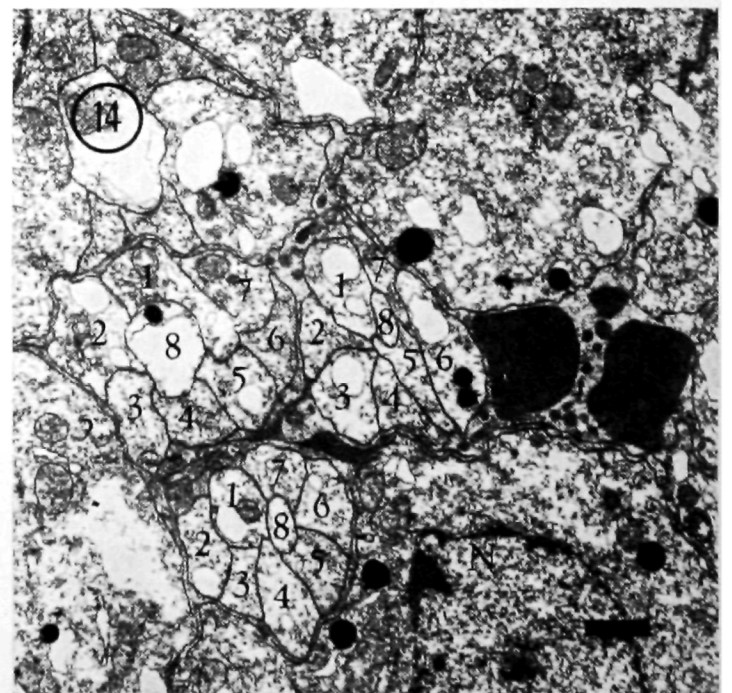
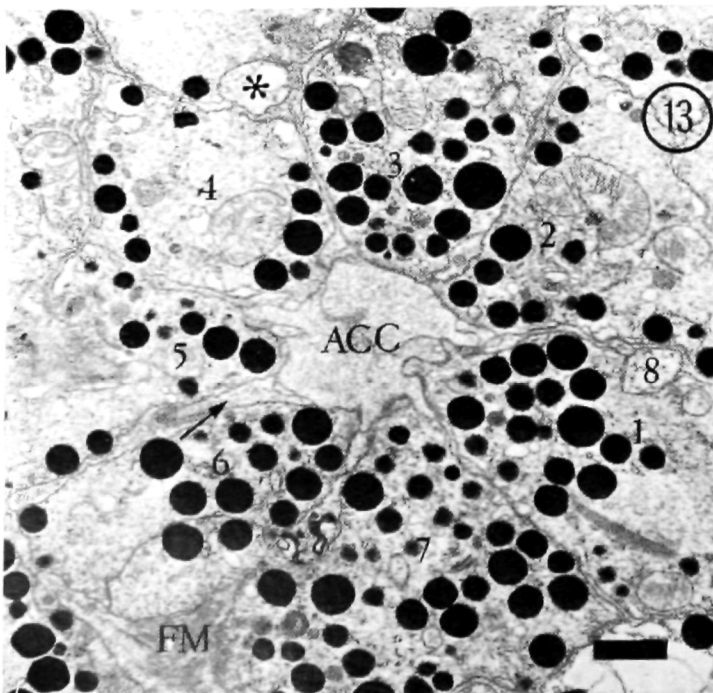
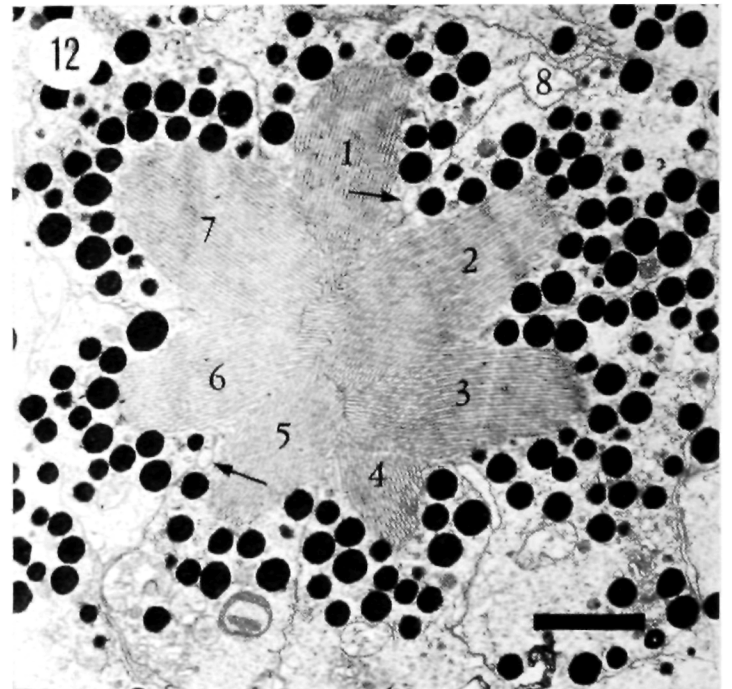
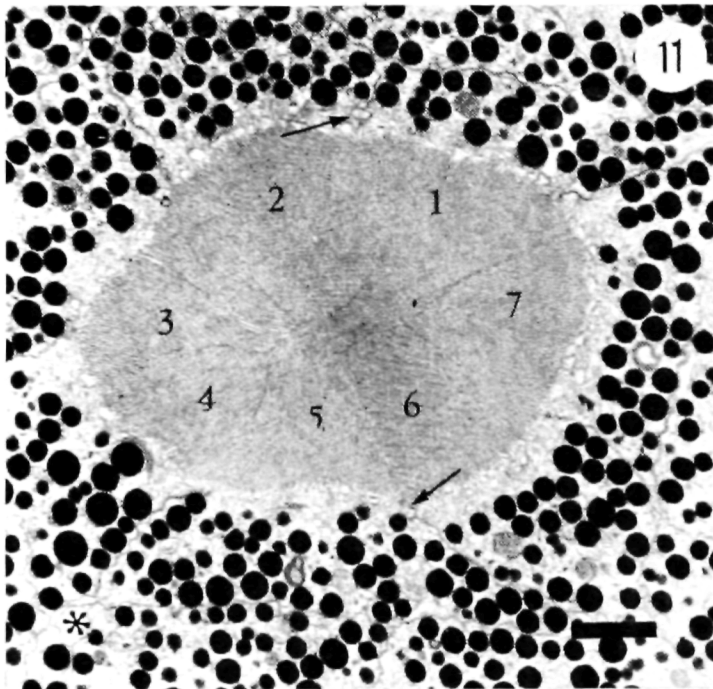
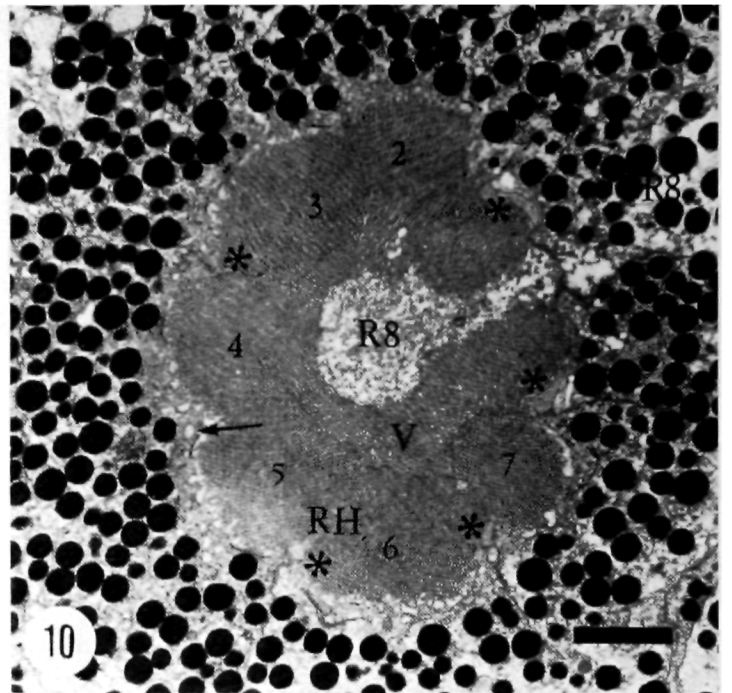
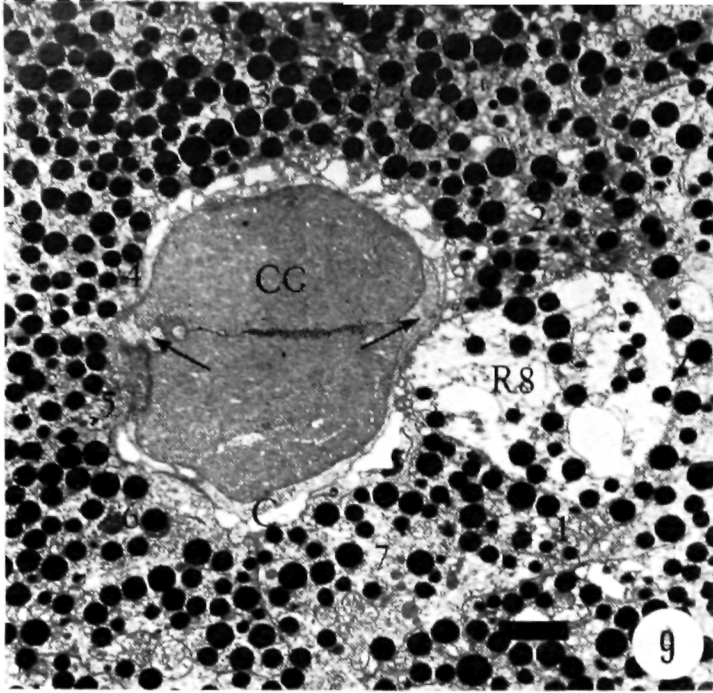
Fig. 4. Light-microscopic longitudinal section of ommatidia. Arrows reticular cell nuclei below the *FM*. Scale 10  $\mu\text{m}$ .

Fig. 5. Side view of the bush-like processes on the cuticular lens surface (SEM). Scale 1  $\mu\text{m}$ .

Fig. 6. Longitudinal section of the distal part of an ommatidium. Note the entry of R8 and its rhabdomere just below the *CC*. *N* nucleus of R8. Scale 1.5  $\mu\text{m}$ .

Fig. 7. Longitudinal section of the distal part of an ommatidium. *DPN* distal pigment cell nucleus, *MV* microvilli on the new cuticle in a molting animal. Scale 1  $\mu\text{m}$ .

Fig. 8. Oblique cross section of an ommatidium showing nuclei belonging to the dioptric apparatus. *ACCN* accessory cone cell, *CN* corneagenous cell, *CCN* crystalline cone cell, *S* and arrows suture line between the two principal cone cell halves. Scale 1  $\mu\text{m}$ .



(Figs. 2a, e, 3, 6, 10). The diameter of the club is  $6\ \mu\text{m}$ . The microvilli,  $2\ \mu\text{m}$  long and  $60\ \text{nm}$  thick, project radially (Fig. 10). They do not interdigitate with the rest of the rhabdom as in the eccentric cell of *Limulus polyphemus* (Lasansky 1967, Fahrenbach 1969). The surface of the club facing the crystalline cone does not have any microvilli. The entry of the R8 rhabdomere is between R1 and R2 (Figs. 2e, 10). The axon of R8 emerges from the cell body at the level of the proximal part of the crystalline cone. The diameter of the axon is approximately  $0.7\ \mu\text{m}$ . It runs outside the ommatidium, and the position can fluctuate somewhat, but is always close to R1 and R2 (Figs. 2e—g, 10, 12).

Two rhabdom types are present. They differ from each other with respect to the position of R1 and R2 if a symmetry line is drawn between the accessory cone-cell elongations (x-axis, Fig. 15). From each ommatidium, a bundle with eight profiles penetrates the fenestrated membrane (Fig. 14). These bundles are dendrites, i.e. distal extensions of the reticular cells bearing the rhabdomeres. The bundles are grouped into larger units, but the characteristics of the individual bundles of eight are maintained (Fig. 14). The

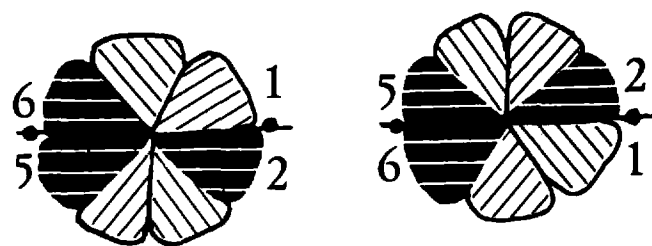


Fig. 15. Two rhabdom types, which are mirror images of each other. A symmetry line runs through the accessory cone cell elongations (black dots between R1, R2 and R5, R6). Black rhabdomeres have microvilli oriented along the symmetry line (x-axis of the eye).

extracellular space between the dendrites and the reticular cell bodies (below the fenestrated membrane) is filled with ground substance and processes from glial cells (Figs. 14, 20).

#### Screening Pigments

The ommatidia are isolated from one another by black screening pigments. These are suggested to be ommochrome in isopods (Elofsson and Hallberg 1973) and are present in two cell types—the distal pigment cells and the reticular cells—within the ommatidium.

The small electron-dense nuclei of the distal pigment cells are situated just below the cornea (Fig. 3). The cell body of these cells envelop the crystalline cone in a thin layer outside that of the corneagenous cells (Figs. 2a, 7, 17). Each distal pigment cell, present between the ommatidia, covers two crystalline cone halves belonging to two adjacent ommatidia (Fig. 16), thereby

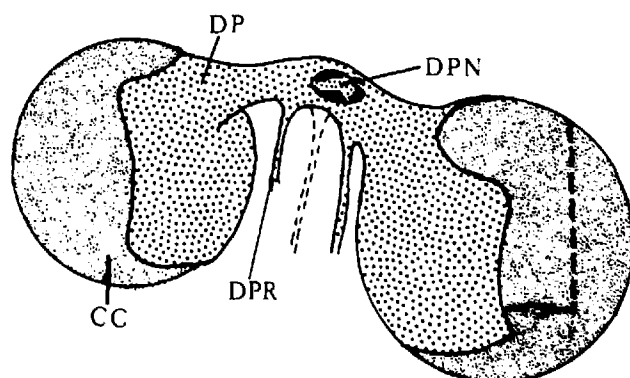


Fig. 16. The spatial arrangement of the distal pigment cell (DP). One cell encapsulates two crystalline cone cell halves belonging to two neighbouring ommatidia. Several extensions, distal pigment cell roots (DPR), emerge from the soma and terminate at the fenestrated membrane. CC crystalline cone, DPN distal pigment cell nucleus.

Figs. 9—14. *Jaera albifrons*. The figure labels are the same as in Fig. 2. Series of cross sections (partly oblique) from different ommatidia beginning from the proximal region of the crystalline cone and ending in the reticular cell dendrites below the fenestrated membrane.

Fig. 9. The proximal part of the crystalline cone. Note the electron-lucent cytoplasm of R8. Arrows accessory cone cells. Scale  $2\ \mu\text{m}$ .

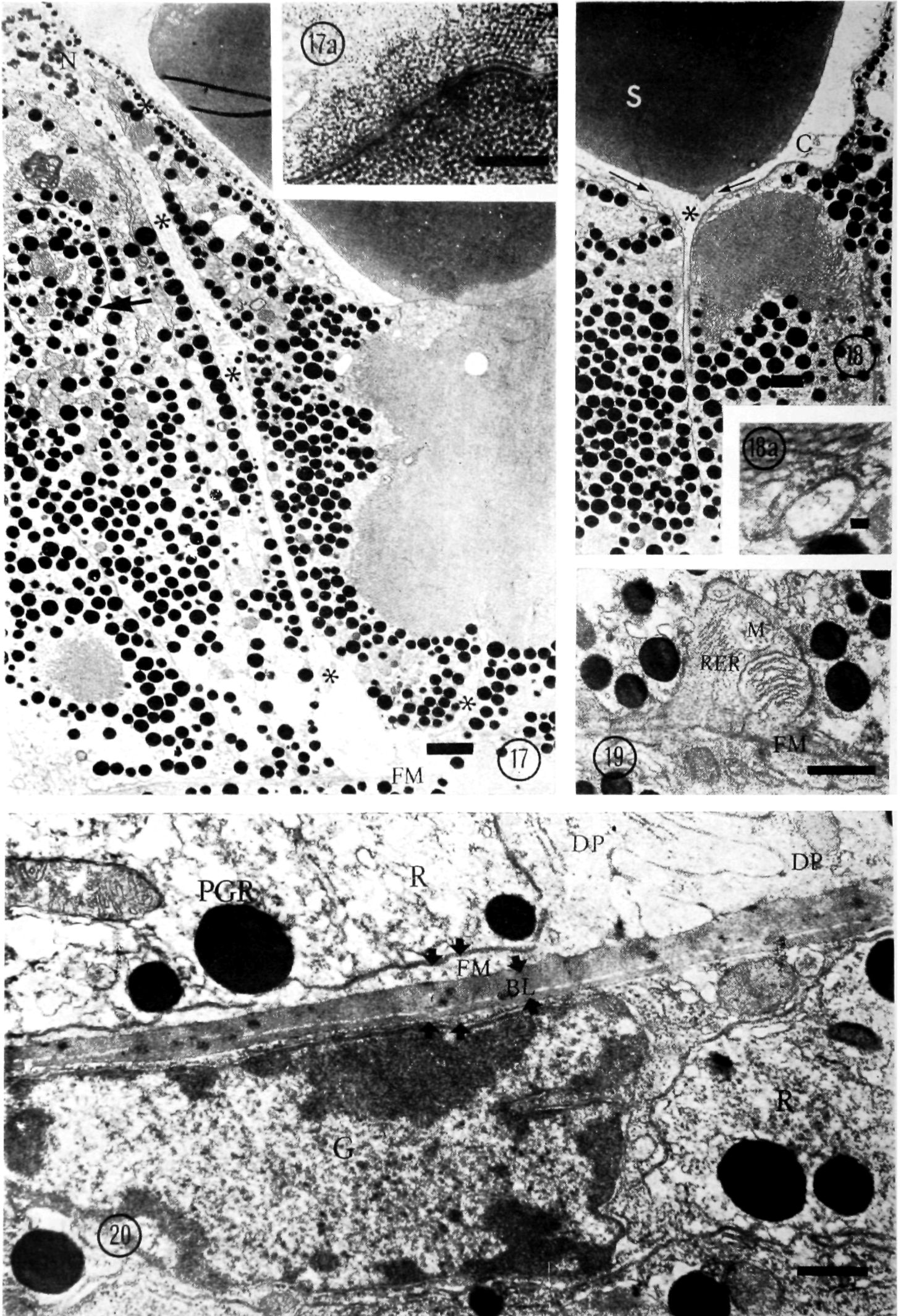
Fig. 10. The distal part of the rhabdom (R1—8) with the microvilli-coated "club" of R8 pushed down centrally within the main rhabdom. Asterisk residues of crystalline cone cells; arrows accessory cone cell root. Scale  $2\ \mu\text{m}$ .

Fig. 11. Main portion of the rhabdom (R1—7). Arrow accessory cone cell root, asterisk R8 axon belonging to a nearby ommatidium. Scale  $2\ \mu\text{m}$ .

Fig. 12. The most proximal part of the rhabdom, star-shaped in cross section. Note the R8 axon between R1 and R2. Arrow accessory cone cell root. Scale  $2\ \mu\text{m}$ .

Fig. 13. Cross section immediately below the rhabdom. Asterisk R8 axon belonging to nearby ommatidium, ACC widened accessory cone cell processes, arrow distal pigment cell process. Scale  $2\ \mu\text{m}$ .

Fig. 14. Bundles of dendrites (arbitrary numbering) below the fenestrated membrane. Each bundle of eight belong to one ommatidium. Gr ground substance, N reticular cell nucleus. Scale  $1\ \mu\text{m}$ .





differing from, e.g. *Idothea baltica* and *I. metallica* (Peabody 1939), where two distal pigment cells are shared by three ommatidia.

The largest diameter of the pigment granules is  $0.3 \mu\text{m}$ , being only half of that of the reticular cells. The granules are often in one tightly packed layer. A small unpigmented area is found at the proximal part of the cone (Figs. 3, 9). Several sparsely pigmented extensions extend to the fenestrated membrane (see below).

#### Fenestrated Membrane

Two cell types, the accessory cone cells and the distal pigment cells, send extensions to the fenestrated membrane. The extensions from the distal pigment cells flatten out and terminate as end-feet (Figs. 2a, 17, 20). These have a high content of rough endoplasmic reticulum; mitochondria are present (Fig. 19). The accessory cone cells also terminate at the fenestrated membrane and attach to the end-feet. The latter together with proximally situated basal cells (Fig. 20) form a cellular and an acellular part of the membrane. The acellular basal lamina is  $0.3 \mu\text{m}$  thick and is composed of parallel rows of fibrillar material (Fig. 20). The fenestrated membrane is thus composed of three components, the basal lamina, the cellular extensions from the distal pigment cells and the proximal cellular portion from the basal cells. The last-mentioned also forms a mesh-

work of thin cytoplasmic strings between the reticular cells below the fenestrated membrane. The basement membrane proper, which is laid down during embryogenesis, forms the eye-cup (Peabody 1939).

#### *Asellus aquaticus*

##### General Description

The compound eye of a living specimen of *A. aquaticus* looks like a cluster of four small black pinheads on the lateral margin of the head segment. In a SEM preparation (Fig. 22) the eye is but a little bulb on the cuticular surface. The four ommatidia in each eye have strongly divergent optical axes, all pointing upwards (Fig. 23). The cornea is  $10 \mu\text{m}$  thick and the round crystalline cone is  $30 \mu\text{m}$  in diameter. Eight reticular cells form the rhabdom, which is  $35 \mu\text{m}$  long and  $30 \times 18 \mu\text{m}$  wide. The eye is surrounded by an eye capsule formed by special cells. These cells also form the fenestrated membrane. The eye capsule is surrounded by a haemocoel.

##### Dioptric Apparatus

The thin transparent cornea has a very faint convexity on the inner surface and it is formed by an unidentified number of corneagenous (hypodermal) cells that have large oval nuclei (diam.  $4 \mu\text{m}$ , Fig. 21). The cytoplasmic properties and the composition of the cuticular lens are similar to those of *Jaera albifrons*. Folds from the corneagenous cells form a thin ( $0.7 \mu\text{m}$ ) envelope around the crystalline cone. No processes on the cuticular surface are present.

Of the four round crystalline cones, two are formed by two principal crystalline cone cells plus two accessory cone cells, and the other two are formed by three principal cone cells plus one accessory cone cell and four principal cone cells. This is in agreement with the light-microscopic investigation by de Lattin (1939, Fig. 23). The accessory cone cells have a tiny, easily overlooked, nucleus and very little cytoplasm. The cytoplasmic properties and the composition of the cone do not differ from those of *J. albifrons* and *Porcellio scaber* (Nemanic 1975). At the base of the cone a thin enfolding from the "eye-cup cells" (see below) replaces the envelope of the corneagenous cells (Fig. 21). No cone cell processes have been found.

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Figs. 17—20. *Jaera albifrons*. The figure labels are the same as in Fig. 2.

Fig. 17. Longitudinal section of an ommatidium showing distal pigment cell processes (*asterisks*). One process encapsulates the cone and one terminates as an end-foot and contributes to the formation of the fenestrated membrane. *Arrow* another distal pigment cell process. Scale  $2 \mu\text{m}$ . a) Detail of crystalline cone substructure and suture line. Scale  $0.5 \mu\text{m}$ .

Fig. 18. Accessory cone cell process (*asterisk*) emerging from the crystalline cone and continuing proximally. *Arrow* cell border between accessory cone cell and corneagenous cell, *S* suture line. Scale  $1 \mu\text{m}$ . a) Cross section of accessory cone cell root with prominent microtubules. Scale  $0.1 \mu\text{m}$ .

Fig. 19. End-foot of distal pigment cell process. Abundance of rough endoplasmic reticulum (*RER*) and mitochondria (*M*). Scale  $1 \mu\text{m}$ .

Fig. 20. Distal pigment cell processes flatten out as end-feet and form the fenestrated membrane together with a basal cell (*G*). *PGR* reticular cell pigment granule, *BL* basal lamina. Scale  $0.5 \mu\text{m}$ .

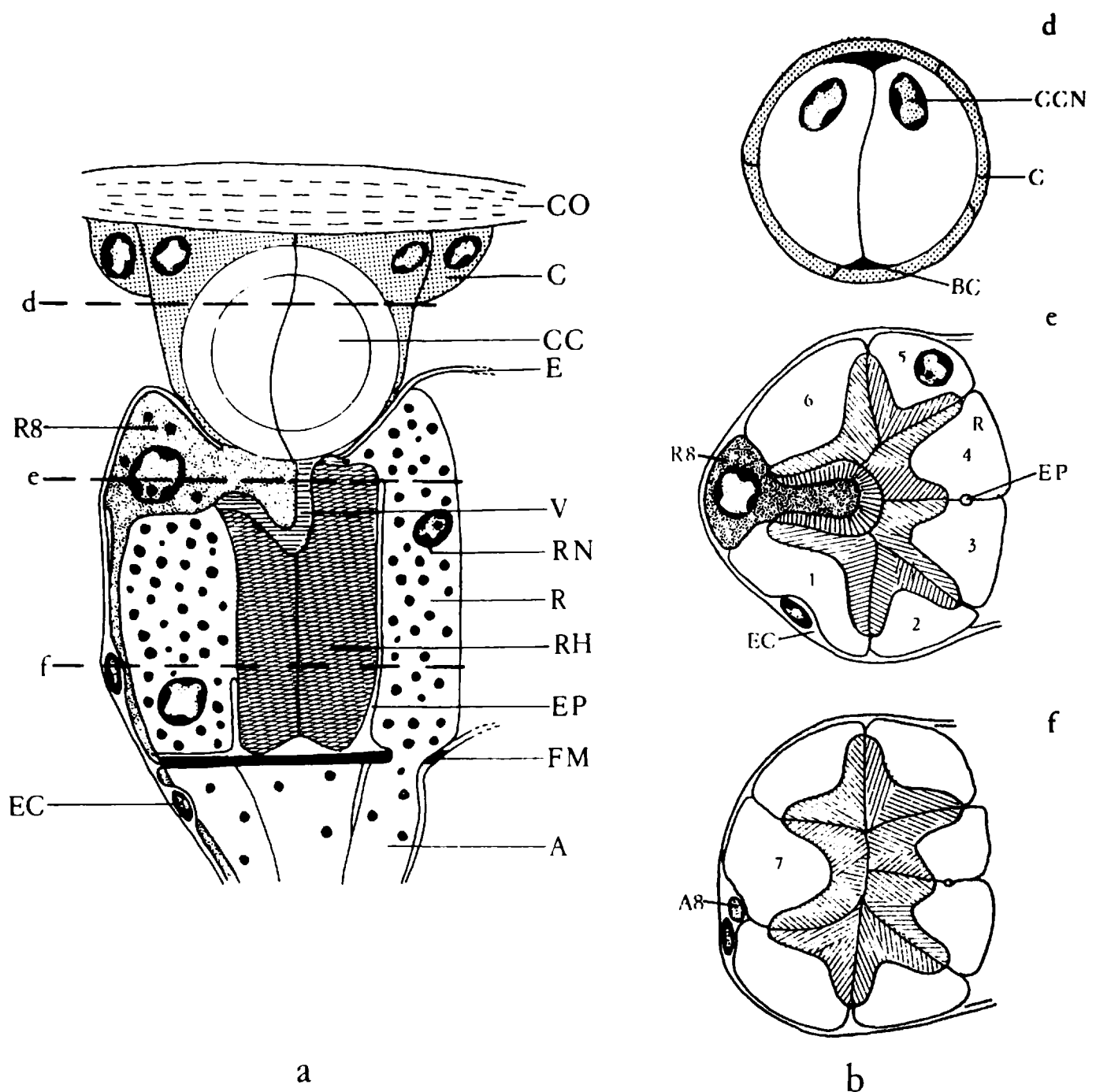


Fig. 21. a) Schematic drawing, longitudinally bisected, of an ommatidium of *Asellus aquaticus*. b) Cross sections of an ommatidium at levels indicated in a). *A* axon of a retinular cell, *A8* axon of R8, *BC* accessory cone cell, *C* corneagenous cell, *CC* crystalline cone cell, *CCN* crystalline cone cell nucleus, *E* eye-cup, *EC* "eye-cup cell", *EP* "eye-cup cell" process, *FM* fenestrated membrane, *R* retinular cell, *R8* retinular cell No. 8, *RH* rhabdom, *RN* retinular cell nucleus, *V* rhabdomere of R8, *1–8* retinular cells.

#### Retina

The cytoplasmic organelles of R1–7 do not differ from those described in *J. albifrons*. The soma of R8 in *A. aquaticus* (situated between R1 and R7) shows a better preservation of the cytoplasm,

being less electron-transparent than in *J. albifrons*. However, its cytoplasm is more electron-lucent than that of R1–7. The number and variety of organelles in R8 of *A. aquaticus* do not differ from those of R1–7 except by having fewer pigment granules. The round retinular cell nuclei of R1–7 are situated peripherally in the receptor cell soma, and they are arbitrarily distributed at different levels above the fenestrated membrane, thereby differing from the situation in *J. albifrons*. The nucleus of R8 is apical. The extracellular palisade is very poorly developed.

The retinular cells form a cup-shaped depression in which the crystalline cone rests. The large number of pigment granules in the retinular cells

are the only screening pigment between contiguous ommatidia (Fig. 21). The axons of R1—7, below the fenestrated membrane, are filled with a very electron-dense cytoplasm, many mitochondria, and a few pigment granules are present (Fig. 28). The R8 axon, situated outside R1 and R7, has an electron-lucent cytoplasm. A tight web of "eye-cup cell" processes and glial processes envelop the axons indiscriminately (Figs. 24, 28).

\* The fused rhabdom of *A. aquaticus* is formed by eight reticular cells (R1—8), and R8 is similar to the one in *J. albifrons*. The rhabdom is star-shaped in transverse sections throughout its length. The microvilli of each reticular cell (R1—7) are situated on a keel-like protrusion from the cell side facing the other reticular cells (Figs. 21, 26, 27). This is in contrast to other isopods' rhabdomeres (Tuurala et al. 1966, Nemanic 1975) in stellate rhabdoms where the microvilli are situated in a trough along the side of the cell.

Rhabdomeres Nos. 1, 2, 5 and 6 are of equal intermediate size. Nos. 3 and 4 are small and No. 7 is large. The microvilli are 60 nm thick and opposing microvilli meet end to end. The extracellular space between the microvilli is highly osmophilic, and each microvillus has a thin filament (Fig. 26, inset). No continuation of the filament into the cell soma is seen as in *Astacilla longicornis* (Nilsson and Elofsson 1978). Each rhabdomeric "ray" in the irregular star-shaped rhabdom is the fusion of microvilli from two adjacent reticular cells (Figs. 21, 27), and these converge towards each other at a certain angle. Similar rhabdomeres with convergent microvilli are present in *Oniscus asellus* (Tuurala et al. 1966) and *Porcellio scaber* (Nemanic 1975), but in these species each "ray" consists of microvilli from one reticular cell. No absolute angle between the microvilli in such a "ray" has been measured in *A. aquaticus* because the angle may be influenced by light and dark adaptations as has been shown in *Oniscus asellus* (Tuurala and Lehtinen 1967) and *Porcellio scaber* (Nemanic 1975).

#### *Eye-Cup and Fenestrated Membrane*

An unidentified number of cells, here designated "eye-cup cells", with triangular nuclei (in cross section), are situated in the periphery of the eye. They envelop the entire eye, form the fenestrated membrane and part of the glial encapsulation of the axons (Figs. 21, 24, 28). Additional processes from these cells are radially inserted as septa

between the reticular cells (Fig. 24), and they extend to the crystalline cone.

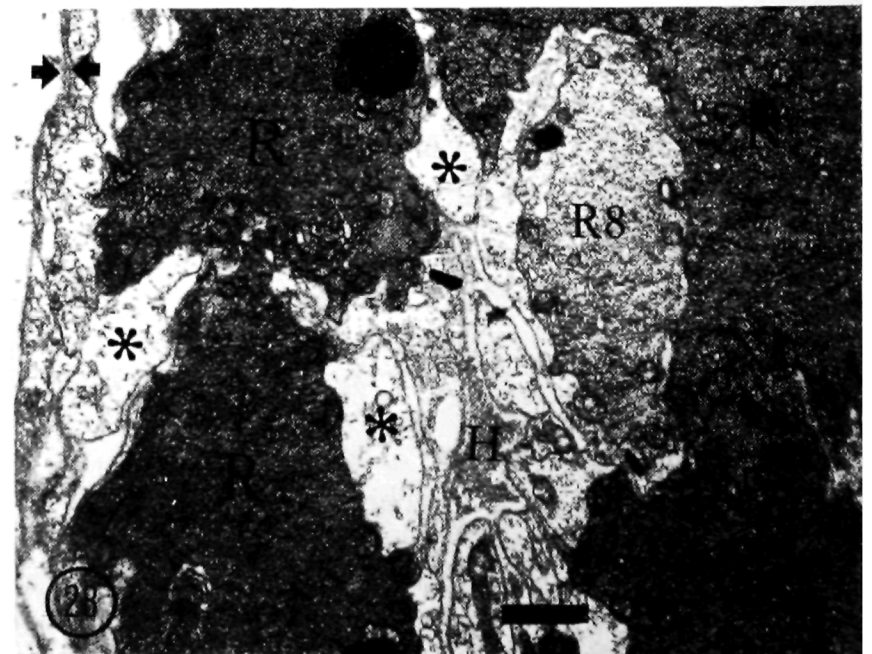
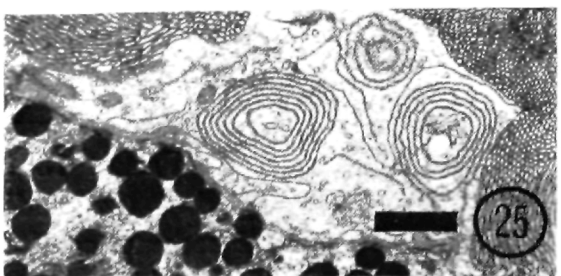
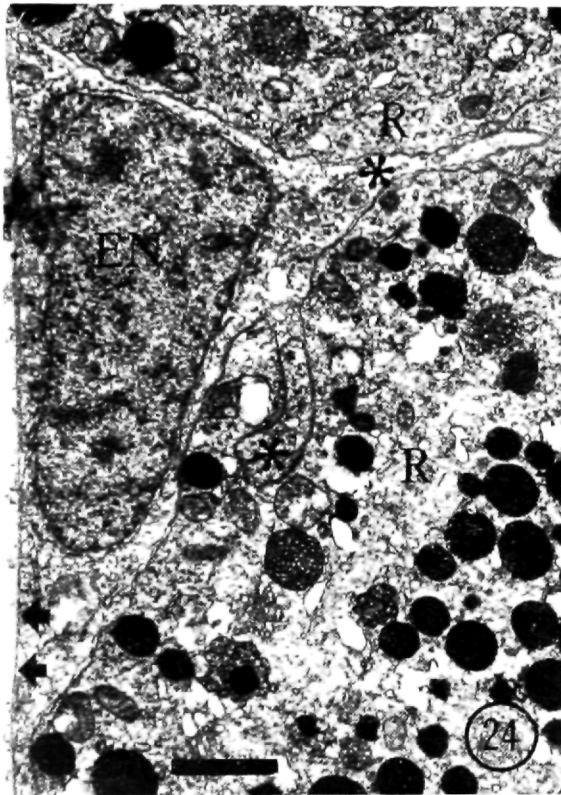
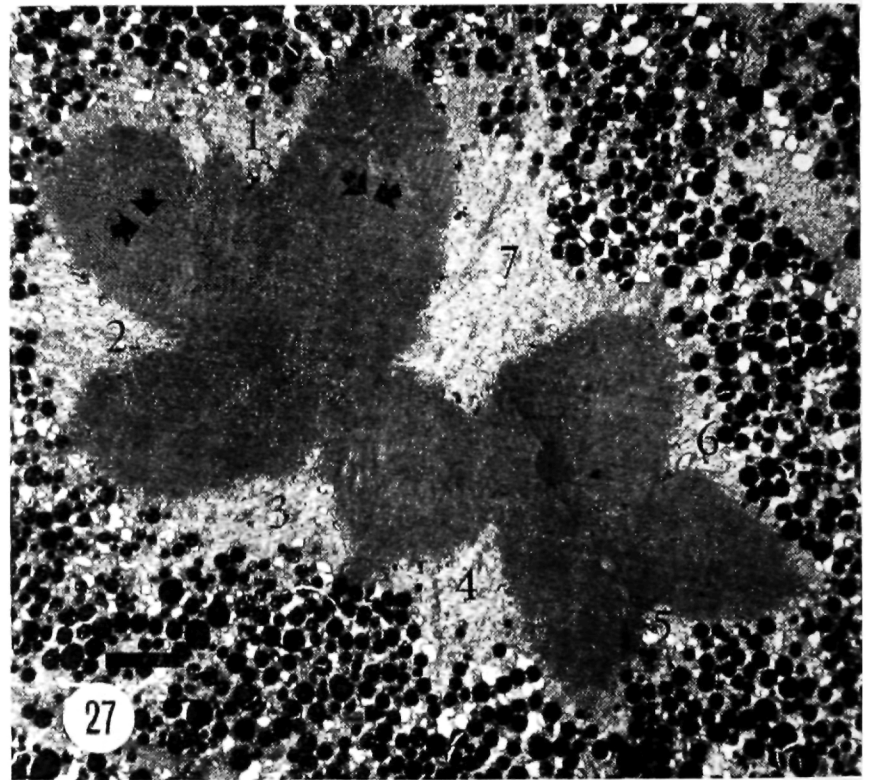
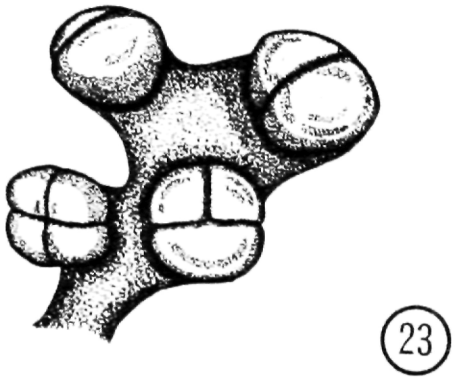
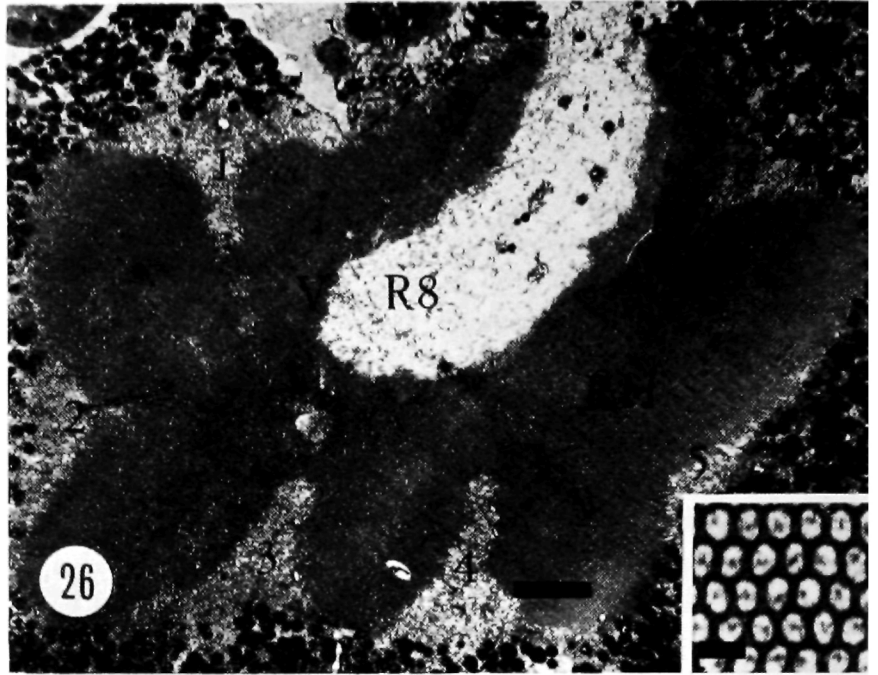
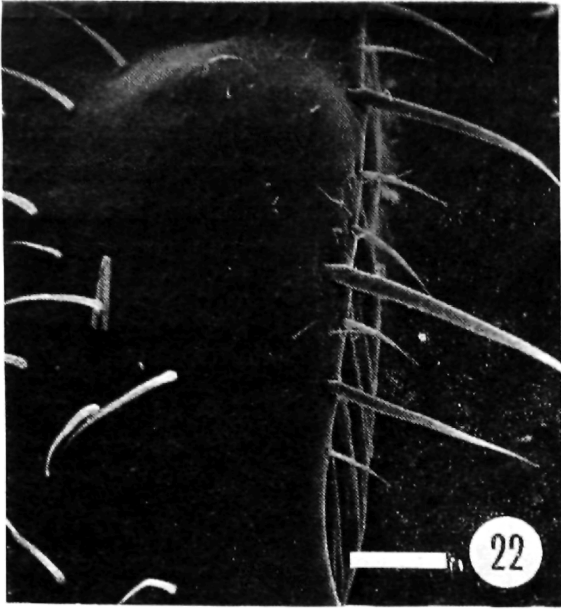
The fenestrated membrane in *A. aquaticus* is formed by an acellular (basal) lamina and a cellular part, both originating from the "eye-cup cells". At the base of each rhabdom the cellular part has conspicuous concentric rings of rough endoplasmic reticulum (Fig. 25). Although the composition of the fenestrated membrane of *J. albifrons* is somewhat more complicated than in *A. aquaticus*, the basal cell type of the former seems to be the homologue to the "eye-cup cells" of the latter. Basal cells contributing to a fenestrated membrane are also found in amphipods (Hallberg and Nilsson, unpubl.). A basal cell type found in tanaids is also thought to be homologous to those in isopods and amphipods (Andersson et al. 1978). The envelope around the eye, the eye capsule, is formed by interdigitating cellular processes and an acellular lamina both originating in the "eye-cup cells" (Fig. 24).

#### Discussion

The compound eyes of *Jaera albifrons* and *Asellus aquaticus* manifest similarities and differences between each other and also between other isopods investigated. Both first-mentioned species have eyes that show the characteristic gross morphology of apposition eyes (definition according to Exner 1891). In finer detail the cornea, crystalline cone, retina and fenestrated membrane display differences in the two species.

The biconvex lens of *J. albifrons* is formed by two corneagenous cells and the poorly differentiated cornea of *A. aquaticus* is formed by an unidentified larger number of corneagenous (hypodermal) cells. Two corneagenous cells in *J. albifrons* accord well with other investigated isopods (Sye 1887, Parker 1891, Hesse 1901, Debaisieux 1944). The poorly differentiated cornea of *A. aquaticus* is present in the trichoniscid isopods (de Lattin 1939) and also in tanaids (Andersson et al. 1978). An undifferentiated cornea is present in amphipods (Debaisieux 1944), cumaceans (Friche 1931) and in anostracans (Debaisieux 1944) that have been investigated to date.

Isopod crystalline cones are generally believed to be formed by two cone cells (Parker 1891, Debaisieux 1944). The finding that two rudimentary accessory cone cells are present together with the two principal ones in *J. albifrons* and



also in *Idothea baltica* and *I. viridis* and in *Astacilla longicornis* (Nilsson, unpubl.) show that the old statements of two cone cells are no longer valid. Also the finding that the cones of *A. aquaticus* may have up to four developed cone cells (De Lattin 1939) and accessory cone cells confirm this. In *Oniscus asellus*, Debaisieux (1944) observed two additional nuclei near the cone, but the nature of these nuclei was not fully understood. It is suggested here that these nuclei belong to accessory cone cells. In the electron microscopic investigation of *Ligia oceanica* (Edwards 1969) and of *Porcellio scaber* (Nemanic 1975), accessory cone cells might have been overlooked. In *Porcellio scaber* (Nemanic 1975, Fig. 5) one cell and a corresponding nucleus can be interpreted as the accessory cone cell.

Four cone cells are present in decapods (Debaisieux 1944) and now this number is also established in isopods (although they are most often rudimentary). Mysids (Hallberg 1977), cuphasids (Zimmer and Gruner 1956), tanaids (Andersson et al. 1978) and amphipods (Ball 1977, Hallberg and Nilsson, unpubl.) also possess two accessory cone cells. A different number of cone cells are present in cladocerans (5, Parker 1891) and in anostracans (3—5, Debaisieux

1944). The accumulated data suggest that the number, viz. four crystalline cone cells in isopods, is in agreement with that of the Malacostraca Crustacea and that this number is a general building plan of the crystalline cone of this group.

The fused continuous (unbanded) rhabdoms of *J. albifrons* and of *A. aquaticus* have eight receptor cells, and R8 is aberrant and bears a rhabdomere. The main differences in rhabdom morphology between the two species lie in the formation of the rhabdomeres and in the microvillar orientations. In *J. albifrons* the medial part of the rhabdom has three microvillar orientations, differing by 60° from each other. In the proximal part the rhabdomeres twist slightly and become radially projected, which confers a star-shaped appearance in a transverse section. *A. aquaticus*, on the other hand, has a fully star-shaped rhabdom throughout its length. The stellate appearance of rhabdoms is well known from terrestrial isopods (*Oniscus asellus*, Debaisieux 1944, Tuurala et al. 1966, *Porcellio scaber*, Grenacher 1879, Nemanic 1975) and has also been previously described in *A. aquaticus* (Parker 1891, de Lattin 1939) and in *J. albifrons* (Sye 1887).

The rhabdom of the littoral isopod *Ligia oceanica* (Edwards 1969) exhibits still another variation in that the distal portion of the rhabdom is fused and the proximal part is open, i.e. the rhabdomeres are separated. Partly open rhabdoms are also found in the suborder Flabellifera (Beddard 1888, Parker 1891, Hesse 1901). Different microvillar orientations are also present in the distal and proximal parts of the rhabdom in *Ligia oceanica* (Edwards 1969). A noteworthy exception to these common rhabdom types in isopods is the presence of a layered (banded) rhabdom in *Astacilla longicornis* (Nilsson and Elofsson 1978). The layered rhabdom has been described from a variety of malacostracan crustaceans (for references, see Elofsson 1976) and in some insects (Meyer-Rochow 1971, 1972, Home 1976).

The presence of an aberrant eighth receptor cell is a common feature among crustaceans. R8 is of special interest partly because of its varied structural appearance in different animals and partly because of its unknown function. So far, the only general statement that can be made is that of its apical position (except for *Ligia oceanica*, Edwards 1969). In both *J. albifrons* and *A. aquaticus*, R8 has a similar appearance and the contribution of the rhabdomere in rela-

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Figs. 22—28. *Asellus aquaticus*. The figure labels are the same as in Fig. 21.

Fig. 22. Scanning electron micrograph of the right eye. Scale 50  $\mu\text{m}$ .

Fig. 23. Schematic drawing of the right compound eye with the cornea dissected and the eye-cup disclosed. Note the variable number of crystalline cone cells. The eye is surrounded by a haemocoel. (Drawn freely after de Lattin 1939.)

Fig. 24. "Eye-cup cell" with processes (asterisks). Arrows delimiting membrane of the eye-cup. Scale 1  $\mu\text{m}$ .

Fig. 25. Widened "eye-cup cell" processes at the base of the rhabdom. Note the prominent concentric rings of rough endoplasmic reticulum. Scale 1  $\mu\text{m}$ .

Fig. 26. Cross section of the rhabdom at a distal position. Note the entry of R8 on top of the rhabdom. Scale 3  $\mu\text{m}$ . Inset: transverse section of rhabdomeric microvilli with central filaments and heavily osmophilic extracellular space. Scale 0.1  $\mu\text{m}$ .

Fig. 27. Cross section of the rhabdom in medial and proximal positions. Scale 3  $\mu\text{m}$ .

Fig. 28. Oblique section of reticular cell axons. Note the heavily osmophilic cytoplasm of R1—7 and the electron-lucent cytoplasm of R8. The axons are encapsulated in "eye-cup cell" processes and glia (asterisks). Haemocoel is present (H). Arrows delimiting membrane of the eye-cup. Scale 1  $\mu\text{m}$ .

tion to the rhabdom size is the same. *Porcellio scaber*, which also has an R8 rhabdomere with microvilli projecting radially, has a coated process with microvilli that runs centrally throughout the length of the rhabdom (Nemanic 1975). In this respect it is similar to the eccentric cell of *Limulus polyphemus* (Fachenbach 1969). R8 of *Ligia oceanica* is basal and has no rhabdomere (Edwards 1969).

In non-isopod crustaceans, R8 differs both in the morphology of the soma and in the rhabdomere. A four-lobed R8 with orthogonally oriented microvilli has been described in *Grapsus grapsus* (Eguchi and Waterman 1973) and in *Panulirus longipes* (Meyer-Rochow 1975) or with horizontally oriented microvilli in *Praunus flexuosus* (Mayrat 1962) and *Pacifastacus leniusculus* (Nässel 1976) and in several mysids (Hallberg 1977). A four-lobed R8 with disrupted microvilli is present in *Ocypode cursor* and *O. saratan* (Kunze 1967, Kunze and Boscheck 1968). Still another kind of aberrant cell is the sixth reticular cell of *Artemia salina*, which contributes to the rhabdom on different levels (Elofsson and Odselius 1975).

The present investigation has revealed that within a seemingly homogeneous eye type differences appear in fine structure. The functional importance of the detailed structure of photoreceptors has been shown by several recent investigations (Bernhard 1966, Wehner 1972, Snyder et al. 1973, Horridge 1975). The rhabdom may serve as an example of variation within the isopods. This photopigment-bearing part can be either partly open or fused, and in the latter case the rhabdoms are layered or continuous. Fused continuous rhabdoms have many different shapes when observed in cross section. The functional implications of these rhabdom types are discussed by Snyder et al. (1973).

The rhabdoms of the valviferans, *Astacilla longicornis* (Nilsson and Elofsson (1978) and *Idothea baltica* (Nilsson, unpublished), differ markedly from the asellot type described here by being a fused layered type. In the same way, the rhabdom of the suborder Flabellifera differs from the previous two (Beddard 1888, Parker 1891, Nilsson unpubl.). The rhabdom of the large suborder Oniscoidea has quite a variable appearance and a common type can presently not be established. This indicates, on the one hand, that the different suborders can each have their own common construction of the eye and, on the other hand, that the variation within a group might conceal this pattern.

Any attempt to unravel the adaptional forces acting on the isopod eye has as an inescapable prerequisite a thorough analysis of the structural plan upon which the eyes are built. Because differences are found within closely related taxa or even species, a broader investigation is needed comprising animals from a variety of ecological niches.

### Summary

1. A bush-like arrangement of processes is present on the eye surface and on the dorsal body cuticle of *Jaera albifrons*.
2. The cornea is well differentiated in *J. albifrons* and poorly so in *Asellus aquaticus*.
3. In *J. albifrons* two accessory crystalline cone cells are found in addition to the two principal ones. *A. aquaticus* has two, three or four developed cone cells or complementary accessory ones for a total of four cone cells in each cone.
4. Both *J. albifrons* and *A. aquaticus* have a fused continuous rhabdom formed by eight reticular cells in which the eighth one is aberrant.
5. The rhabdom of *J. albifrons* is oval in the distal and medial part and star-shaped in the proximal part when observed in cross section.
6. The entire rhabdom of *A. aquaticus* is irregularly star-shaped.
7. In both species the distally situated R8 rhabdomere has radially oriented microvilli. An axon emerges from the cell soma in the distal position and runs outside along the rhabdom.
8. The fenestrated membrane in *J. albifrons* is formed by distal pigment cell processes and basal (glial) cells and in *A. aquaticus* by "eye-cup cells", here considered to be homologues to the basal cells.
9. In *J. albifrons* screening pigments are present in the reticular cells and distal pigment cells. *A. aquaticus* lacks distal pigment cells.

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