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The Eyes of Mesopelagic Crustaceans

II. *Streetsia challengeri* (Amphipoda)*

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Summary. In *Streetsia challengeri* left and right eyes have fused and become a single cylindrical photoreceptor, which occupies the basal half of a forward directed head projection. This unusual compound eye consists of approximately 2500 ommatidia, which are arranged in such a way that the animal has almost circumferential vision, but cannot look ahead or behind. It is thought that the eye operates on light-guide principles, and that the crystalline cones are the major dioptric component. Ommatidia in anterior-posterior rows show a greater overlap of visual fields than dorso-ventrally arranged ommatidia. Cone layer and retinula are separated by a 4 μm thick screen-membrane, which contains tiny pigment granules of 0.15 μm diameter. Cells of unknown function and origin, containing unusual multitubular organelles, are regularly found near the proximal ends of the crystalline cone threads. The twisted rhabdoms measure 18–20 μm in diameter, and consist of microvilli 0.05 μm in width, which belong to five retinula cells and which show no trace of disintegration. The position of interommatidial screening pigment, the density of retinula cell vesicles and inclusions, and the narrowness of the perirhabdomal space all suggest that the eyes have been light-adapted at the time of fixation for electron microscopy. The retinula cell nuclei lie on the proximal side of the heavily pigmented basement membrane. A tapetum or basal retinula cells are not developed. It is concluded that the eye optimally combines acuity with sensitivity, and that for distance estimation parallax may be important.

Key words: Arthropod vision – Deep-sea crustaceans – *Streetsia* (Amphipoda) – Eye ultrastructure.

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Zusammenfassung. In *Streetsia challengeri* sind linkes und rechtes Auge zu einem einzigen zylindrischen Auge zusammengewachsen, das die basale Hälfte eines nach vorn weisenden 'Kopfhorns' bildet. Dieses ungewöhnliche Komplexauge besteht aus ca. 2500 Ommatidien, die auf Grund ihrer besonderen Anordnung dem Tier zwar ein Sehfeld von 360° verleihen, es ihm aber nicht ermöglichen, nach vorn oder nach hinten zu sehen. Es wird vermutet, daß das Auge nach Lichtleiterprinzipien arbeitet, und daß die Kristallkegel die Hauptelemente des dioptrischen Apparates sind. Kristallkegel und Retinula werden voneinander durch eine 4 µm dicke Schicht getrennt, die aus winzigen Pigmentgrana von 0.15 µm Durchmesser besteht. Benachbarte Ommatidien in anterio-posteriorer Richtung zeigen eine größere Überlappung des Sehfeldes als dorso-ventral benachbarte Ommatidien. Zellen unbekannter Herkunft und Funktion mit ungewöhnlichen multitubulären Organellen wurden regelmäßig nahe der Kristallkegelenden gefunden. Die schraubigen Rhabdome haben einen Durchmesser von 18–20 µm; ihre Mikrovilli messen 0.05 µm im Querschnitt. Mikrovilli gehören 5 Retinulazellen an und zeigen keinerlei Anzeichen von Disintegration trotz Helladaptation. Letztere manifestiert sich in der Position der interommatidialen Pigmentkörner, der geringen Weite des perirhabdomalen Zwischenraumes und der Dichte vesikulärer und anderer intrazellulärer Körper in den Retinulazellen. Retinula-Zellkerne befinden sich auf der proximalen Seite der stark pigmentierten Basalmembran. Ein Tapetum oder basale Retinulazellen sind nicht entwickelt. Es wird gefolgert, daß das Auge Sehschärfe und Empfindlichkeit optimal vereinigt, und daß es zur Entfernungsmessung u.a. das Phänomen der Parallaxis verwendet.

Introduction

In a previous paper, Meyer-Rochow and Walsh (1977) described the eye of the mesopelagic decapod *Gennadas* sp. and compared its microanatomy with that of nocturnal species inhabiting shallow water. The subject of this paper is the eye of the mesopelagic amphipod *Streetsia challengeri.*

Amphipods like *Hyperia, Phronima, Thaumatops,* and *Lycaea* are frequently recovered in mesopelagic hauls and must, therefore, be regarded as a significant faunal element in waters of 100–1000 m. *Streetsia,* a cosmopolitan genus which has been recorded from 20 to 3000 m (Fage, 1960) is less often caught than the other pelagic amphipods mentioned above, and appears to lead a rather more solitary life than many other deep-sea crustaceans.

The enormous enlargement of the eyes of many hyperid amphipods, e.g. *Phronima, Thaumatops, Lycaea,* is a familiar feature to all students of zoology, and has prompted many early microscopists to investigate the anatomy of some of these photoreceptors. Gerstaecker (1884) in "Bronn's Klassen und Ordnungen des Thier-Reichs" summarized accurately what was known about the amphipod eye up to this time and surprisingly little information, obtained by light microscopy, has been added since (Carrière, 1885; Schatz, 1929; Hanström, 1933; Debaisieux, 1944).

The discovery of sun-moon compass orientation in the beach hopper *Talitrus* (Pardi and Papi, 1953; Papi and Pardi, 1953) revived interest in amphipod eyes, but

shifted the emphasis towards functional aspects of amphipod vision. However, with the advent of the electron microscope detailed studies of hitherto unknown ultrastructure became possible, and a renewed interest in the fine structure of amphipod photoreceptors was predictable. Ball (1977) has recently carried out an electron microscopic study of the eye of *Phronima*. Meyer-Rochow is presently investigating other amphipod species.

To date no electron microscopic study of the eye of *Streetsia* has been published, but and earlier light microscopic investigation by Hanström (1933) exists. It was thought worthwhile to re-investigate the eye of *Streetsia* by electron microscopy and to supplement the findings of Hanström.

Materials and Methods

According to Fage (1960), four species of *Streetsia* occur in the Indo-Malayan region. Three specimens which were collected from different night-hauls in April and May, 1975 near the Banda Islands (Indonesia) were identified as *Streetsia challengeri*. Fage (1960) states that "cette espèce ne semble pas former d'essaims nombreux" and that specimens with body lengths of around 30 mm are predominantly caught in the deeper water below 200 m. Specimens, which were brought up from approximately 500 m and which were all 30 mm in length, were sorted in a cold-room under illumination of ordinary incandescent desk lamps. Eyes were taken from two individuals. The third was needed for morphological measurements and was preserved undamaged.

The eyes were left for 4 h in a fixative which consisted of a 2.5% glutaraldehyde/2.0% paraformaldehyde mixture buffered with Millonig's phosphate and brought to a 0.4 M sugar solution with the appropriate amount of glucose added. The eyes were then transferred to buffer for 2 days, and then postfixed in a 2% buffered solution of OsO_4. Acetone dehydration was followed by embedding in normal Spurr's medium and hardening for 2 days at 65° C. One µm sections, cut on a Reichert OM U2, were stained with toluidine blue. Ultrathin sections, double-stained with uranyl acetate and lead citrate, were observed with a Philips EM200 electron microscope operated at a voltage of 80 kV.

Results

1. General Features

Streetsiae possess large, single compound eyes, which have evolved from two (left and right) lateral photoreceptors. The cylindrical, collar-like eye occupies the basal half of a forward-directed head projection. This structure, which in a 3 cm animal measures 1.4 cm in length, gives *Streetsia* a unicorn-like appearance or, the use a more modern comparison, a "concorde"-look. The anterior, ommatidia-free half of the 'head-projection' resembles an ocular style (examined in ocypodid crabs by v. Hagen, 1970) and may function as one. It also bears the antennules, the neurons of which pass between the two retinal eye halves and through a gap in the lamina (Hanström, 1933). (An excellent colour photograph of *Streetsia* and its unusual head is found on page 124 of the book "Deep Oceans", edited by Herring and Clarke, 1971.)

The eye of *Streetsia* consist of approximately 2500 ommatidia, but individual facets, in other words externally distinguishable corneae, are not developed. At its posterior base the eye measures about 2 mm in diameter. Near its rostral end the diameter in cross section is 1 mm. The almost totally transparent eye, therefore,

represents a cut-off cone, lying on its side. Running along the ventral side of the eye, a narrow red structure can be seen beneath the overlying transparent tissue. This represents the retinula and associated components.

Dorsally, the two halves of the eye fuse, but along the mid-ventral line a kind of suture remains, which lies in a shallow groove. With the exception of this narrow ventral line the entire 30 mm^2 area of the cylindrical eye appears to be capable of receiving light. *Streetsia* possesses a visual field of 360° in a plane which lies perpendicular to its body axis. Vision is circumferential, and the animal does not seem to be able to see ahead, unless during forward-swimming its head is tilted downward. Ommatidia are arranged on circles around the long axis of the head projection. The longest ommatidia (Approximately 1.9 mm) occur near the dorsal mid-line of the eye; the shortest ommatidia are found towards the ventral and anterior region of the eye.

An interommatidial angle is difficult to measure in the eye of *Streetsia*, because the ommatidia are almost always curved. The straightest ommatidia are present in an approximately 3 mm wide band near the dorsal side of the eye. Here, the interommatidial angle between ommatidia lying on the same circle perpendicular to the long axis of the head projection is 5–6°. Angles between adjacent ommatidia in an anterior-posterior direction approach one degree or more only at the anterior and posterior ends of the eye; otherwise, and this holds true for the greatest part of the eye, anterior-posterior ommatidia lie more or less parallel and their interommatidial angle does not exceed a fifth of a degree.

2. Cornea and Crystalline Cone

The 5 μm thick cornea is not compartmentalised into facets and appears to consists of normal crustacean cuticle. A 6 μm thick hypodermal layer of flat, presumably corneagenous, cells is developed just below the cornea (Fig. 1A). The nuclei of these cells are clearly visible under the light microscope, and it appears that the cells in this layer are distributed independently of the number of ommatidia below them. On an average, one and a half hypodermal cells per ommatidium were counted. The hypodermis is typically developed as a monolayer of cells, but occasionally two cells, one below the other, are seen. Whether this is an indication of any pre- or post-moult changes or normal cell turnover and renewal remains to be elucidated.

As in the eyes of other amphipods, the crystalline cone is made up of two cells. These cells are in contact with the hypodermis by a 4–5 μm thick, weakly convex protoplasmic cap, which contains the two nuclei (Fig. 1A). The crystalline cone itself is a bipartite structure and consists of material which appears completely featureless in both light and electron microscopic examinations (Fig. 1B, C). It is readily stained with toluidine blue, but because of its high refractability even in unstained 1 μm thick sections, it stands out distinctly. Serial cross sections have revealed that at its distal end the crystalline cone possesses its widest diameter (up to 40 μm), and that the two halves of the cone are usually oriented in such a way that one half points in an anterior and the other in a posterior direction. The two halves are separated from each other over most of their lengths by a gap of at least 0.5 μm.

The crystalline cone tapers down progressively towards the rhabdom until it has

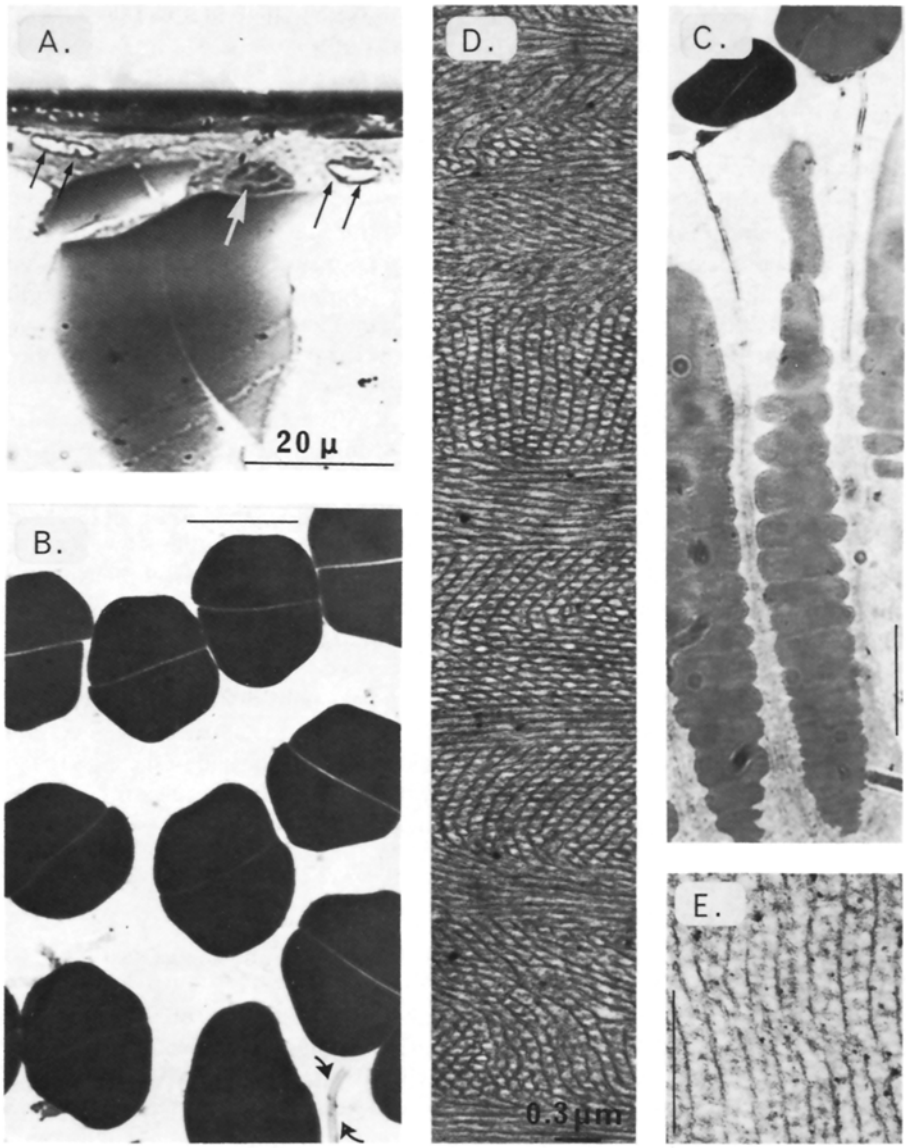

Fig. 1. A Section through cornea and crystalline cone, showing nuclei of corneagenous cells (black arrows) and cone cells (white arrow). **B** Transverse section through bipartite cones. No cell borders are discernible in the interconal space, which is of a clear and transparent nature. For ultrastructure of worm-shaped cells (arrows) see Figure 3B. (Scale as in Fig. 1A). **C** Longitudinal section through crystalline cones and rhabdoms. A 3–4 µm thin layer of dark screening pigment separates the retinula from the clear zone. (Scale as in Fig. 1A). **D** Longitudinally sectioned rhabdoms show alternating transverse and longitudinally cut microvilli. There is evidence that the rhabdom is twisted. **E** Individual microvilli measure approximately 50 nm in diameter and often show fine strands or discs of cytoplasmic material within them. (Scale as in Fig. 1D)

reached a diameter which is of roughly equal size to that of the rhabdom in transverse section. Longitudinal sections through entire cones are never completely straight. The longest cones (approximately 1.6 mm) are found near the dorsal region, the shortest occur on the ventral side. With regard to the surrounding tissue, Hanström (1933) has described crystalline cones ".... in dem faserigen Gewebe liegend, das den Rest der Bildungszellen der Kegel darstellt", but in our material neither cell borders directly associated with the cones, nor interconal cell membranes were seen. As both Hanström's and our material seemed equally-well fixed, it appears that either different species were examined, or there are indeed individual differences within the same species. Banda specimens were large and from relatively deep water, and it seems possible that in older animals the cone cell borders disappear and the cells become surrounded by a clear watery substance alone.

At the proximal tip of the cones, just outside the retinula cell layer, peculiar strands of 2–3 μm diameter were regularly found (Fig. 1 B). These unusual structures enveloped the bases of adjacent cones in a random fashion. The strands were definitely cellular in origin, and nuclei were sometimes seen light microscopically. Because of their complicated interconal location, however, the total length of these narrow cells could not be determined. Electron microscopically, each cell was seen to contain brick-shaped organelles which consisted of parallel tubules (Fig. 3 B). These measured 15–20 nm in diameter and had a length of at least 1.5 μm. Structures of this sort, which could be highly modified fibres of smooth muscle, an unusual type of mitochondria, para-crystalline material or membrane specialization, have apparently not been described previously. A certain likeness, however, exists with the 'multitubular bodies' described in the cockroach ocellus by Weber and Renner (1976) and with photogenic granules reported in *Linophryne* light organs (Hansen and Herring, 1977).

3. Retinula Cells and Rhabdom

As in other amphipods the sensory portion of the ommatidium, the retinula, consists of five large retinula cells (Fig. 2A). Towards the clear zone the retinulae are shielded by a 3–4 μm thick layer of accessory pigment cells, which contain tiny pigment granules of a rather uniform diameter of 0.15 μm (Fig. 3 B, inset). Other accessory pigment cells occupy the interstitial spaces between inter- and intra-ommatidial retinula cells (Fig. 2A, B). Often the gaps between retinula cells are only one pigment granule wide, giving the minute pigment granules in transverse section the appearance of pearls on a string, completely filling the available space.

Distally, only the cone cell processes penetrate the black layer of screening pigment. The rhabdom, which is the product of five centrally-fused rhabdomeres, abuts on the proximal end of the cone. The rhabdoms, like the crystalline cones, are not straight but curved, and their largest diameters are found distally. In spite of the banded appearance of the rhabdom in longitudinal section, the microvilli do not seem to be arranged in alternating orthogonal layers (Fig. 1 D). Instead, the rhabdom appears to be twisted. Rhabdom microvilli range from 0.04 μm to 0.07 μm in diameter, but with an average diameter of 0.05 μm; *Streetsia* microvilli are

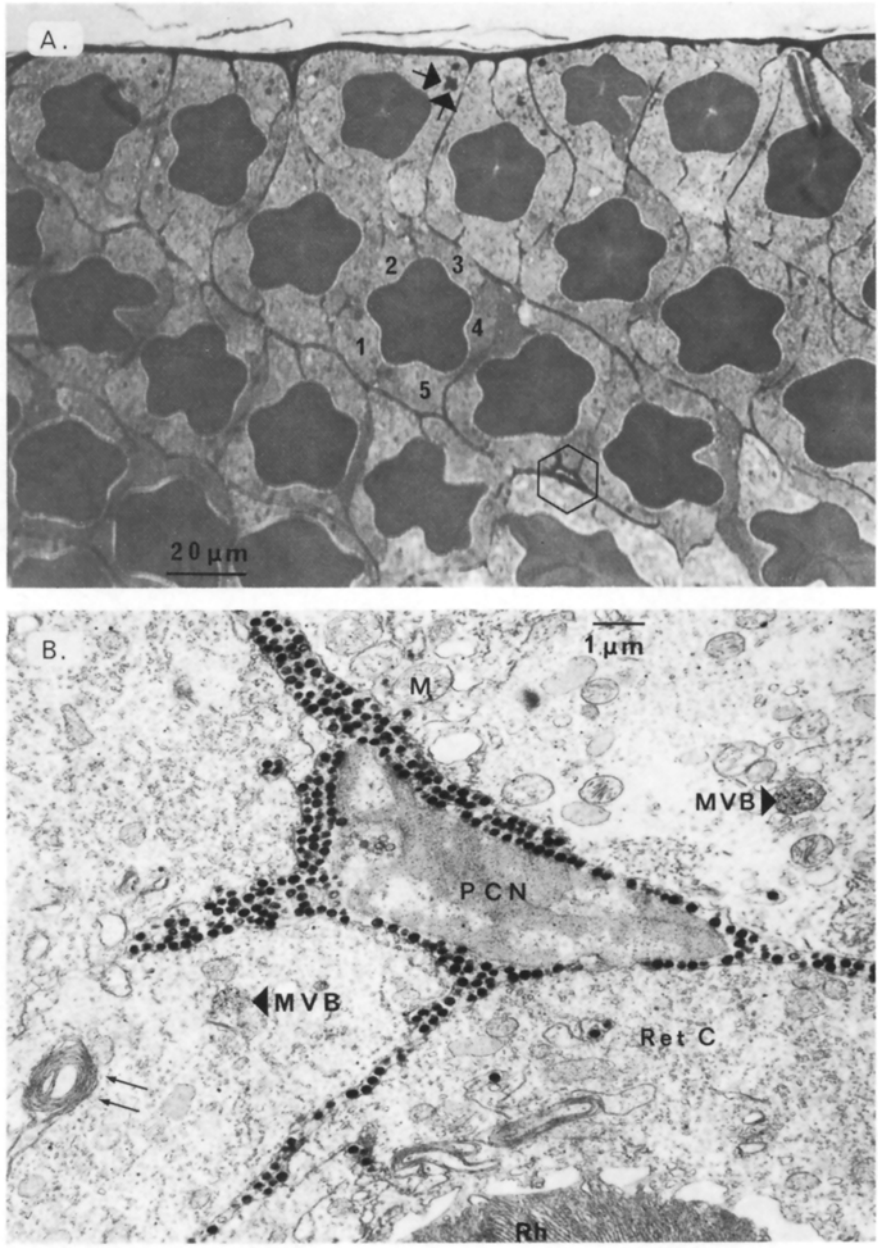

Fig. 2. A Each large pentagonal central rhabdom is surrounded by a narrow space of perirhabdomal vacuoles, which belong to five retinula cells. Pigment cells (framed area) and their tiny pigment granules (0.1–0.2 µm) are located in the interommatidial spaces. The fibrous cells at the top are identical to those shown in Figures 1 B and 3 B. **B** Pigment cells, nuclei of which (*PCN*) are easily recognisable because of their position, send out curtain-like folds which occupy the narrow gaps between retinula cells of one or more ommatidia. The retinula cells (*Ret C*) contain numerous cell organelles and inclusions. Most numerous are small vesicles, multivesicular bodies with (*MVB*) and without enveloping membranes, dense core vesicles, mitochondria (*M*), folded membrane convolutions (arrows) and clusters of lipid droplets (not depicted in this electron micrograph but marked by arrows in Fig. 2A). The rhabdom (*Rh*), which is surrounded by an electron transparent ring of perirhabdomal space, is in contact with retinula cell plasma via cytoplasmic bridges

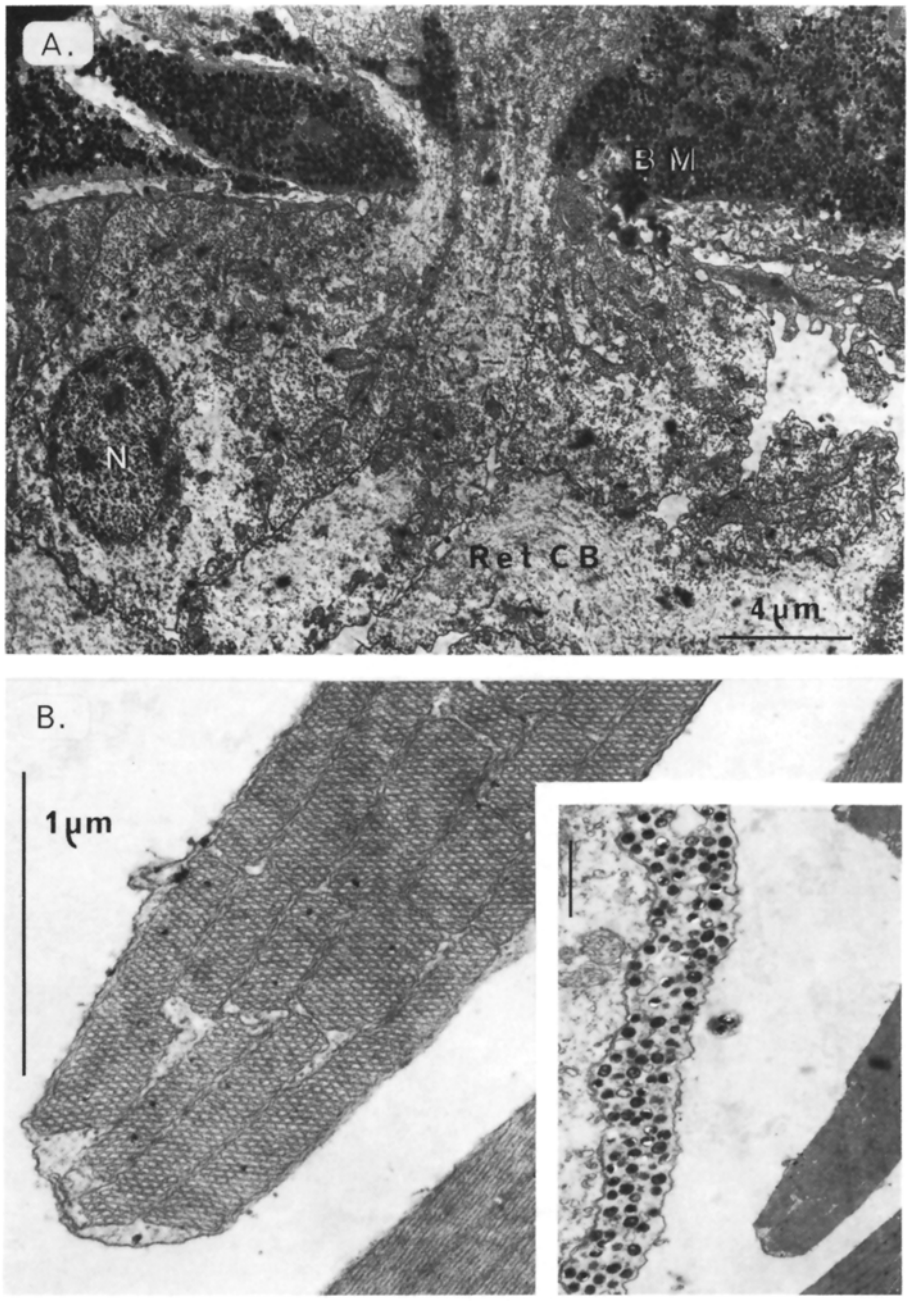

Fig. 3. A Retinula cell bodies (*Ret CB*), containing the nuclei, are found below the basement membrane (on the proximal side of the retinula). There are five retinula cells per ommatidium, which penetrate the 4 µm thick layer of basement membrane (*BM*) and screening pigment. **B** The *inset* shows the area from which the high magnification electron micrograph was taken. Near the pigment granules of the outer limiting membrane unusual worm-shaped cells surround the tips of some crystalline cones (compare with Fig. 1 B). These cells contain an unknown type of organelle, which appears to consist of packages of regularly-stacked tubules. Function and origin of neither the cell nor its organelles are known

unusually narrow. Some high magnification electron micrographs reveal bridges within the microvilli, resembling the rungs of a ladder (Fig. 1E). Whether such connections between the membranes represent artifacts, perhaps caused by a deeper layer of microvilli which is also included in the depth of the section and in which the parallel microvilli are displaced by a certain angle from the microvilli of the top layer (because of rhabdom twist), is not known.

All rhabdoms are surrounded by an electron transparent space, measuring on an average 0.6 µm in width, which appears in transverse sections light microscopically as a narrow white seam, associated with every rhabdom (Fig. 2A). As in *Squilla,* where the rhabdoms are surrounded by a similar clear space (Schönenberger, 1977), the retinula cell cytoplasm is in contact with the rhabdom via numerous 0.2–1 µm wide cytoplasmic bridges crossing the perirhabdomal space (Fig. 2B). The retinula cells themselves are crowded with many organelles and inclusions. The largest of these are groups of three to five lipid droplets, each measuring 0.1–0,2 µm in diameter, which commonly occur near the proximal end of the retinula. Most numerous, however, are vesicles, which measure approximately 80 nm in diameter. Multivesicular bodies, often containing a few dense core vesicles, folded membranous structures such as "onion bodies", and mitochondria are also plentiful (Fig. 2B) The great abundance of all these subcellular components, together with the distal position of the screening pigment granules in the accessory pigment cells, indicates that the eyes of *Streetsia* were in a state of light or semi-light adaptation when fixed for electron microscopy. This is to be expected when considering that the animals were sorted under normal room illumination.

It is difficult to give accurate figures on rhabdom lengths. Firstly, these vary in different parts of the eye and secondly rhabdoms and retinula cells are curved (Fig. 1C). An average rhabdom from the basal half of the eye is 150 µm long and 18 µm wide (diagonals taken at mid-rhabdom level).It ends about 15 µm above the basement membrane. The latter would be a rather insignificant layer of less than 1 µm thickness, were it not for numerous accessory pigment cells, which "reinforce" the basement membrane and convert it into a 4 µm thick black screen (Fig. 3A). The cells that make up this secondary basement membrane ("Grenzmembran" in Hanström's account of the eye of *Streetsia*) are densely filled with pigment granules of 0.15 µm diameter.

Groups of five retinula cells penetrate this screen, but they do not immediately change into thin axons. On the contrary, they enlarge, for as in *Echinogammarus* (Debaisieux, 1944), the retinula cell nuclei are located below the basement membrane. Finally, the retinula cell projections become axons, which run along the ventral side of the eye in a posterior direction towards the lamina, where they make synaptic contacts with second order neurons.

Discussion

The gross structure of the eye of *Streetsia challengeri* appears similar to that of the eyes of other amphipods (Grenacher, 1879; Gerstaecker, 1884; Carrière, 1885; Schatz, 1929; Debaisieux, 1944): external facets are not developed; the crystalline

cone consists of two cells, and retinula cells, numbering five per ommatidium, give rise to a centrally-fused rhabdom.

Hanström (1933) pointed out that the eyes of the family of oxycephalid amphipods, to which *Streetsia* belongs, differ from the photoreceptors of other amphipods in three points: (a) complete lack of pigment cells between cones, (b) presence of a special membrane around the entire retinula, and (c) filiform shape of crystalline cones. Although these may seem minor points, they are of important functional consequences. Considered together with the information given in this paper on the ultrastructural organisation, they provide the basis for the following discussion on the possible function of the unusual eye of *Streetsia.*

In *Streetsia* the crystalline cones are longer than in other amphipod eyes and they are thought to act as light guides. The cones are surrounded by a clear material, which is of extraordinary light and electron transparency, and presumably possesses a refractive index which is significantly lower than that of the cones. If one accepts a refractive index of $n_{co}=1.5$ for the cone (a figure commonly found in facets of other crustaceans: Carricaburu, 1968), and a refractive index of $n_{cl}=1.35$ for that of the clear surrounding, the angle ε, at which total internal reflection ceases to exist within the cone, is 65° (calculated from $\sin \varepsilon = n_{cl}/n_{co}$).

Because of their shape, size and optical properties, the cones must be able to collect a considerable amount of light – clearly an adaptation to the conditions of low environmental brightness. Interommatidial angles vary with regard to the x- and y-plane, which means that the visual fields of individual ommatidia show a greater overlap in an anterior/posterior direction than in the dorsal/ventral plane. This may be of significance if the animal is to judge horizontal or vertical movement of an object. There can be no question that the cones alone are the major dioptric component in the eye of *Streetsia*, for the cornea is merely a flat, undifferentiated, transparent layer. The main function of the cornea seems to be a protective one. Since adjacent crystalline cones are not separated by curtains of pigment, isolation has to be distance and optical means alone. This suggests once more that light guide properties of the long, curved cones are likely to be involved.

Both rhabdom and cone have wide diameters and are relatively long; *i.e.*, they show features which are usually interpreted as adaptations to increase absolute sensitivity. The region between cornea and rhabdom layer is devoid of pigment and only occupied by crystalline cones and clear interconal substance. Therefore, superficially the eye of *Streetsia* resembles that of many nocturnal insects, e.g. scarabaeid beetles (Meyer-Rochow, 1977b), in which large rhabdoms and extensive clear zones interact to produce photoreceptors which have improved their sensitivity at the expense of acuity. The eye of *Streetsia,* however, seems to function quite differently. Because of the pigmented layer which is interposed between dioptric apparatus and retinula, individual rhabdoms can only receive light from crystalline cones directly above them. This could affect spatial resolution, and it appears that in spite of increased absolute sensitivity due to the enlargement of the entire eye in general and crystalline cones in particular, acuity is largely retained, because of the light guide properties of both rhabdoms and cones, and the pigmented screen separating the two layers. The eye of *Streetsia* is likely to operate on principles which were originally suggested by Döving and Miller (1969) for moth clear zone eyes, but which have not yet been convincingly demonstrated to exist in

insects. The optical isolation of individual rhabdoms is continued in the retinula: a 0.5 µm wide perirhabdomal space surrounds each rhabdom, the latter lies in the centre of voluminous retinula cells, and narrow screening pigment cells occupy interommatidial gaps. The functional consequences of such facet-separating pigments on optomotor response and retinal action potential were in fact studied in *Drosophila* mutants by Hengstenberg and Götz (1967).

Gennadas (Meyer-Rochow and Walsh, 1977) also possesses long and wide rhabdoms, but the latter are not isolated by pigment, cytoplasm of perirhabdomal vacuoles as in *Streetsia,* but form an almost continuous layer of visual membranes. This indicates that acuity, for a particle feeder like *Gennadas,* is less important than for the predatory *Streetsia.* Through evolution and selective pressure increased sensitivity has been accomplished in the eye of *Streetsia* but without concomitant loss in acuity. However, the questions of colour perception, polarisation sensitivity, and distance estimation – parameters which must also be of importance for an organism that hunts in almost total darkness – remain to be explained.

Recently, it has been suggested by Laughlin et al. (1975) that a correlation between colour sensitivity and diameter of rhabdom microvilli exists in insects (see also discussion in Meyer-Rochow, 1977a). Ultraviolet receptors, it is thought, possess microvilli which have smaller diameters than those of blue receptors, which in turn possess smaller diameters than those of green receptors. Based on this hypothesis, *Streetsia* with its very small microvilli ought to be maximally sensitive to light of 450 nm, which is the blue-violet portion of the spectrum. According to Denton and Warren (1957) this is almost exactly the wavelength which penetrates deepest into sea-water. But unfortunately, even though this coincidence makes good sense biologically, it does not prove the hypothesis, for other deep-sea crustaceans such as *Gennadas* (Meyer-Rochow and Walsh, 1977) and *Euphausia* (Meyer-Rochow and Walsh, in preparation) do not possess the same small diameter microvilli as *Streetsia,* but rather possess microvilli which on the average measure 75 nm in cross section. Whether retinula cells with different colour sensitivities are developed in the eye of *Streetsia* is unknown. If they do occur, they at least show no structural differences in either fine structure of microvilli or retinula cell cytoplasm, under the conditions of adaptation and fixation procedures used in the present study.

Many crustaceans have been shown to be sensitive to the plane of polarisation. It was thought that this ability was related to the orthogonal orientation of microvilli in a 'banded' rhabdom (Shaw, 1969; Waterman et al., 1969), and that a rhabdom had to be straight, not twisted, in order to detect the e-vector. Since the intrinsic (*i.e.* photopigment orientation-dependent) birefringence component dominates in invertebrate photoreceptors (Israelachvilli et al., 1976), a decrease in the diameter of the microvillus is expected to cause a greater alignment of visual molecules in the microvillous membrane. Hence, slender, unidirectionally oriented thin microvilli favour polarisation sensitivity. On the other hand, according to Shaw (1969), a unit length of rhabdom is more efficient as a light gatherer if it contains microvilli oriented in more than one direction. It seems that, as in the case of acuity and sensitivity, polarisation and high absolute light sensitivity are incompatible.

Recently, however, it was demonstrated by Wehner et al. (1975) that both

twisted and non-twisted rhabdoms can exhibit polarisation sensitivity, if rhabdom parameters such as birefringence, dichroism and rhabdom length are considered (Kirschfeld and Snyder, 1975). It was not examined whether in *Streetsia* two mirror-imaged types of twisted rhabdoms existed (as in the bee, see Wehner et al., 1975), but if it can be shown experimentally that the long rhabdoms in this amphipod, in which twists of up to $20°/\mu m^{-1}$ were measured, combine high absolute sensitivity with e-vector discrimination, it is believed that the latter could be used by *Streetsia* for navigational purposes, and prey or predator detection (*i.e.* increase of background contrast).

Supposing that dark/light adaptational changes in the eye of *Streetsia* follow a similar pattern to those reported from other crustacean photoreceptors (pigment migrations: Kleinholz, 1936; de Bruin and Crisp, 1957; density of vesicles in retinula cell plasma: Eguchi and Waterman, 1967), the eyes examined in this investigation must be regarded as light-adapted. The perirhabdomal vacuole-system is reduced; inter-rhabdomal screening pigments occupy a more distal position; and retinula cell cytoplasm is crowded with vesicles, lamellar and multivesicular bodies as well as other inclusions. Since it has not been possible to study dark-adapted eyes, the structure of the latter remains speculation at this stage.

A very important visual parameter for predatory animals is distance estimation. This is generally thought to depend on binocular vision and widely separated eyes. However, the predacious *Streetsia* does not have separated, stalked eyes. Instead, the two eyes have become almost fused and form a cylindrical photoreceptor which is located at the base of a rostral projection in front of the head. Because of this arrangement one is tempted to compare the eye of *Streetsia* with a 360° inner-surface-scanner (Langford, 1963). Citing Wallace (1959), who showed that the estimation of distance in the jump of a grasshopper does not require both eyes, Horridge (1977) suggests that many insects estimate distance by parallax while they are in motion. A predatory, pelagic animal such as *Streetsia* is constantly in motion (either sinking or actively swimming), and may make use of parallax in conjunction with luminosity differences to estimate distance. However, as long as we do not have more behavioural or cybernetic data on this species, any interpretation as to how it analyses its environment remains guesswork.

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