Reference: *Biol. Bull.* **175:** 144–153. (August, 1988)

Electrophysiological and Histological Observations on the Eye of Adult, Female *Diastylis rathkei* (Crustacea, Malacostraca, Cumacea)

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Abstract. The approximately 200 μm wide eye of *Diastylis rathkei* consists of two closely apposed eye halves with four lenticular complexes measuring 40 μm in diameter in each. Each lenticular complex consists of a lens rich in 30 nm electron-opaque glycogen-like particles made up of smaller (5–6 nm) subunits, and a rhabdom comprising regularly aligned microvilli. The retinula cell somata, which are in a proximal location, are linked with the distally placed rhabdom via approximately 10 μm thick, cellular strands. The strands are surrounded by cells crowded with reflecting organelles of *ca.* 0.8 μm in diameter.

Dark/light adaptational changes affect the position of uniformly spherical organelles measuring 0.4–0.5 μm in diameter and presumed to contain carotenoids, the overall size of the rhabdom, and the diameter of individual microvilli. The latter measure 75 nm in the light-adapted state and 90–120 nm in the dark-adapted state. There is ultrastructural evidence (swollen and abundant endoplasmic reticulum and widely distributed glycogen-like particles) that, under light-adapted conditions, the retinula cells are in a phase of intense metabolic activity.

A multilamellar structure, similar in appearance to that found in the organ of Bellonci of other crustaceans, but also resembling a trophospongium, was noticed in close proximity to the eye within the optic lobe. Extracellular electrophysiological recordings obtained with NaCl-filled glass electrodes consisted of a cornea-negative potential change and reached a maximum amplitude of nearly 400 μV to 300 ms flashes of white light.

Superimposed spectral response curves from eight different animals, based on a criterion amplitude of 50 μV, were nearly congruent in shape and displayed one single sensitivity peak to light of 512–549 nm in wavelength. Intensity/response curves obtained to light of 472, 549, and 628 nm wavelengths and the single spectral sensitivity peak strongly suggest that only one type of excitatory visual pigment is involved in the visual process of *D. rathkei.*

It is concluded that in spite of its tiny size, the eye of *D. rathkei* could be useful in the coordination of reproduction and synchronization of vertical migrations.

Received 2 February 1988; accepted 31 May 1988.

Introduction

Cumaceans are an order of peracaridan crustaceans traditionally placed near the Isopoda (Siewing, 1956; Fryer, 1967). Certain species of Cumacea, including *Diastylis rathkei,* regularly occur in the plankton, sometimes hundreds of meters above the seabottom (Fricke, 1931; Forsman, 1938). It is thought that the males, which have considerably larger eyes than the females (Zimmer, 1941), seek the latter in the open water at night during the mating season (Forsman, 1938).

At certain times of the year, these small crustaceans can be very abundant (1214/m^2: Kaestner, 1959) and represent an important component of the diet of various species of fishes; yet virtually all we know about the cumacean photoreceptor goes back almost 60 years to a study of *D. rathkei* by Fricke (1931), who asserted that the cumacean eye was a degenerated compound eye. Though in some species of cumaceans, *e.g., Nannastacus euxinicus,* two clearly separated, lateral eyes are present (Bacescu, 1951), this view was challenged by Mayrat (1981), who claimed the cumacean eye was a dorsal ocellus. Arguments for and against either opinion were sum-

marized by Meyer-Rochow (1988) and supplemented with ultrastructural observations on the larval eye of *D. rathkei*. However, a detailed examination of the structure and function of the eyes of the adults is still lacking. Since male and female *D. rathkei* differ in their behavior to a light source (Forsman, 1938; Zimmer, 1941) and the short-lived males are much less common than the females, this paper is concerned with one form only: the female sex.

Materials and Methods

Collection and maintenance of organisms

In early April, live, adult specimens of the cumacean *Diastylis rathkei* were dredged from the sandy bottom of the Baltic Sea southwest off the Danish island of Langeland in approximately 40 m depth. The animals, all females, were taken to the Zoological Institute of the University of Kiel and kept in brackish water aquaria. Within a week, during which time histological preparations of the *D. rathkei* eye were being made, 10 individuals in a 2 liter thermos bottle were taken by one of us (V. B. Meyer-Rochow) to Finland in an airplane and subsequently housed at Tvärminne Zoological Station at 6°C in total darkness. Individuals were picked at random for both anatomical and physiological observations.

Histology

Eyes of daytime specimens as well as night specimens were carefully extirpated under a dissecting microscope at 10:00 h and 24:00 h, respectively. A paraformaldehyde/glutaraldehyde mixture of 7.4 pH, buffered in Millonig's phosphate and adjusted with 3 g d-glucose/100 ml for reasons of osmolarity matching Baltic Sea water, served as the initial fixative, in which the eyes stayed for about 40 h. They were then washed in buffer and post-fixed for 1.5 h in 2% osmiumtetroxide using the same buffer. The specimens were then embedded in Spurr's medium.

One μm sections were stained with toluidine-blue for light microscopy. Gold or silver sections were stained with uranyl acetate and lead citrate for electron microscopy. Four light-adapted and two dark-adapted specimens were examined.

Electrophysiology

Experimental procedures closely followed those reported by Lindström and Meyer-Rochow (1987). During preparation, using infra-red image converters mounted on a Wild-5 stereo-microscope, each animal was illuminated by light that had passed through two Kodak Wratten 87 gelatin filters and a heat filter. These were inserted in the ray path of white light coming from a 15 W microscope lamp. The incident light leaving the 3 mm wide tip of a light guide perpendicular to the eye, was centered around the hole through which the recording electrode was lowered some 40–50 μm into the eye. The light spot made by the stimulating light flash covered the entire eye. The light output had been calculated in absolute units ($qu \cdot cm^{-2} \cdot s^{-1}$) by an Airam UVM-8LX luxmeter calibrated by Airam Laboratories for a wavelength of 564 nm (Donner and Lindström, 1980). Based on these readings, we estimate the quantal amount of the flashes of light on the eye to elicit a response to have been 3.4×10^{10} $qu \cdot cm^{-2} \cdot s^{-1}$. Measurements of light levels in the field at the site of capture are unavailable, but Lindström and Nilsson (1983) mention summer and autumn figures of 10^{12} and 10^{9} $qu \cdot cm^{-2} \cdot s^{-1}$, respectively, for a depth of 100 m at "Norwegian northern latitudes." The stimulus time was usually set at 300 ms.

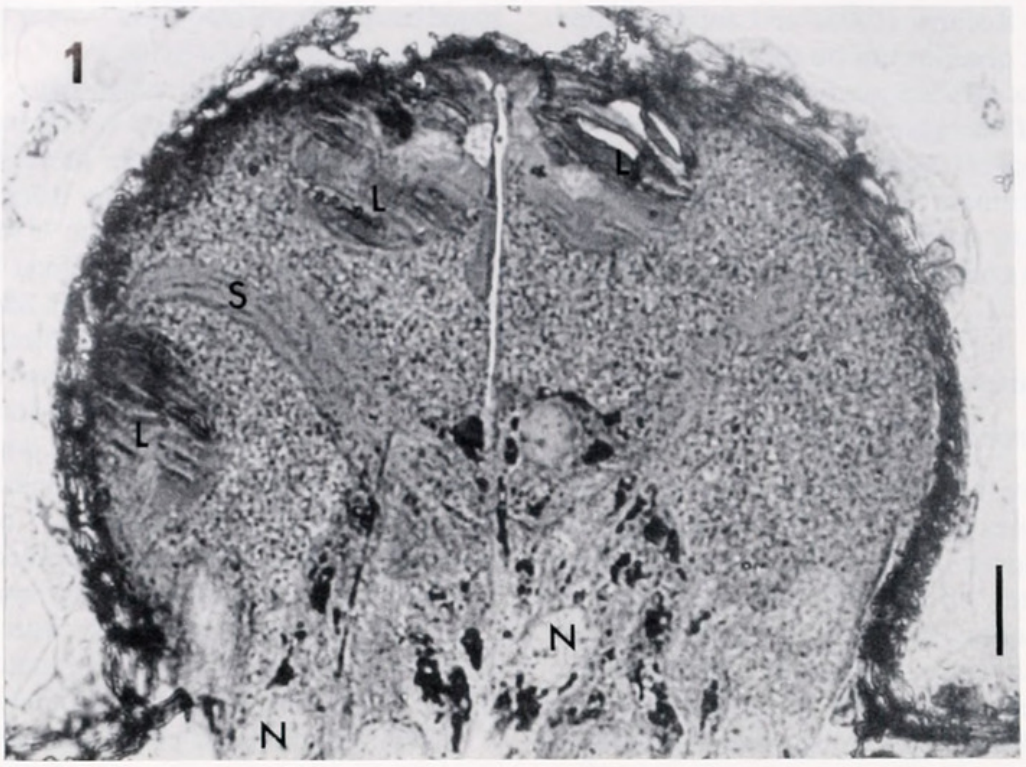
Tips of glass electrodes drawn with an Ealing microelectrode puller were cut off to an outer diameter of approx. 10 μm. The measuring electrode was filled with a 1 *M* NaCl solution and connected to a Tektronix 5031 dual beam storage oscilloscope. Setting-up procedures averaged no longer than 5–10 minutes. Thereafter the test animals were given 30 minutes of total darkness to recuperate from the operation. In the spectral sensitivity studies a criterion response of 50 uV was employed. All recordings were made in the AC-setting.

Results

Histology

Gross anatomy. The eye consists of two symmetrical eye halves on a common forward-projecting ocellar lobe, separated from each other along the midline by a 1 μm wide gap (Fig. 1). There are four bright red retinal complexes in each eye half, but facets or corneal lenses are not developed. The integument covering the eye is transparent and uniformly 5 μm thick. Distally, each retinal complex possesses a lenticular structure (diameter approx. 40 μm) and is in intimate contact with the microvilli of a rhabdom that is produced by retinula cells. The large nuclei (Fig. 2) of these cells are located some 100–150 μm more proximally near the center of the dome-shaped eye.

Cytoplasmic strands of approx. 10 μm diameter swerve in an arc through a massively developed layer of reflecting material and connect retinula cell bodies and rhabdom (Fig. 1). The rhabdom/lens interface is characterized by unclear cell boundaries that give the impression that the two form a functional unit (Figs. 3, 4). The lens component of each such complex, contrary to Fricke (1931), appears to contain more than one nucleus (Fig. 3). Apart from the large, chromatin-rich nuclei on the proximal or lateral sides of the lens, each lens is made



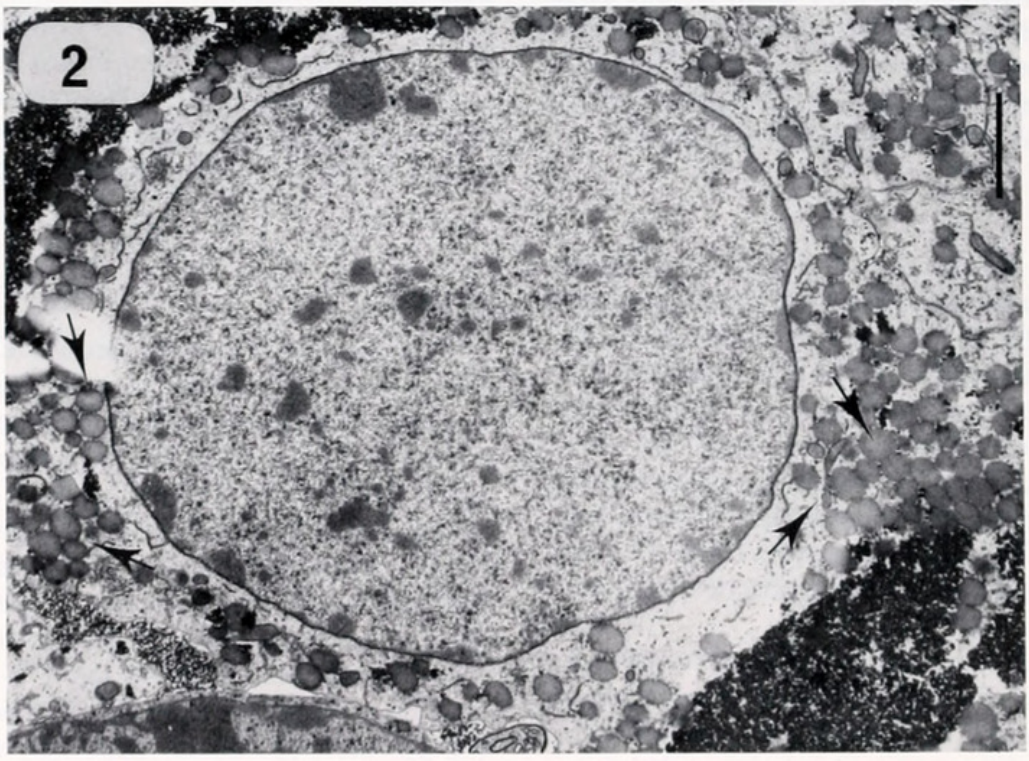


Figure 1. Light micrograph of horizontal section through the eye of an adult female. The symmetrical eye halves joined along the midline are apparent and lenticular complexes (L), retinula cell strands (S), and nuclei (N) are clearly visible. Scale = 20 μm.

Figure 2. Electron micrograph of proximally located retinula cell nucleus with surrounding clusters of electron-opaque glycogen particles and presumed carotinoid bodies (arrows). Scale = 2 μm.

up of a dense aggregation of electron-opaque particles, measuring 30 nm in diameter (Figs. 3, 4). These particles are composed of 40–50 smaller subunits of approx. 6 nm in size (Fig. 5).

Cumacean retinula cells contain uniformly shaped 0.4–0.5 μm large, spherical organelles (Fig. 3). These are identical in appearance and location with bodies identified as carotinoid grains in the crustacean chromatophore (Elofsson and Hallberg, 1973). They are thought to be present in the photoreceptive cells of other peraca-

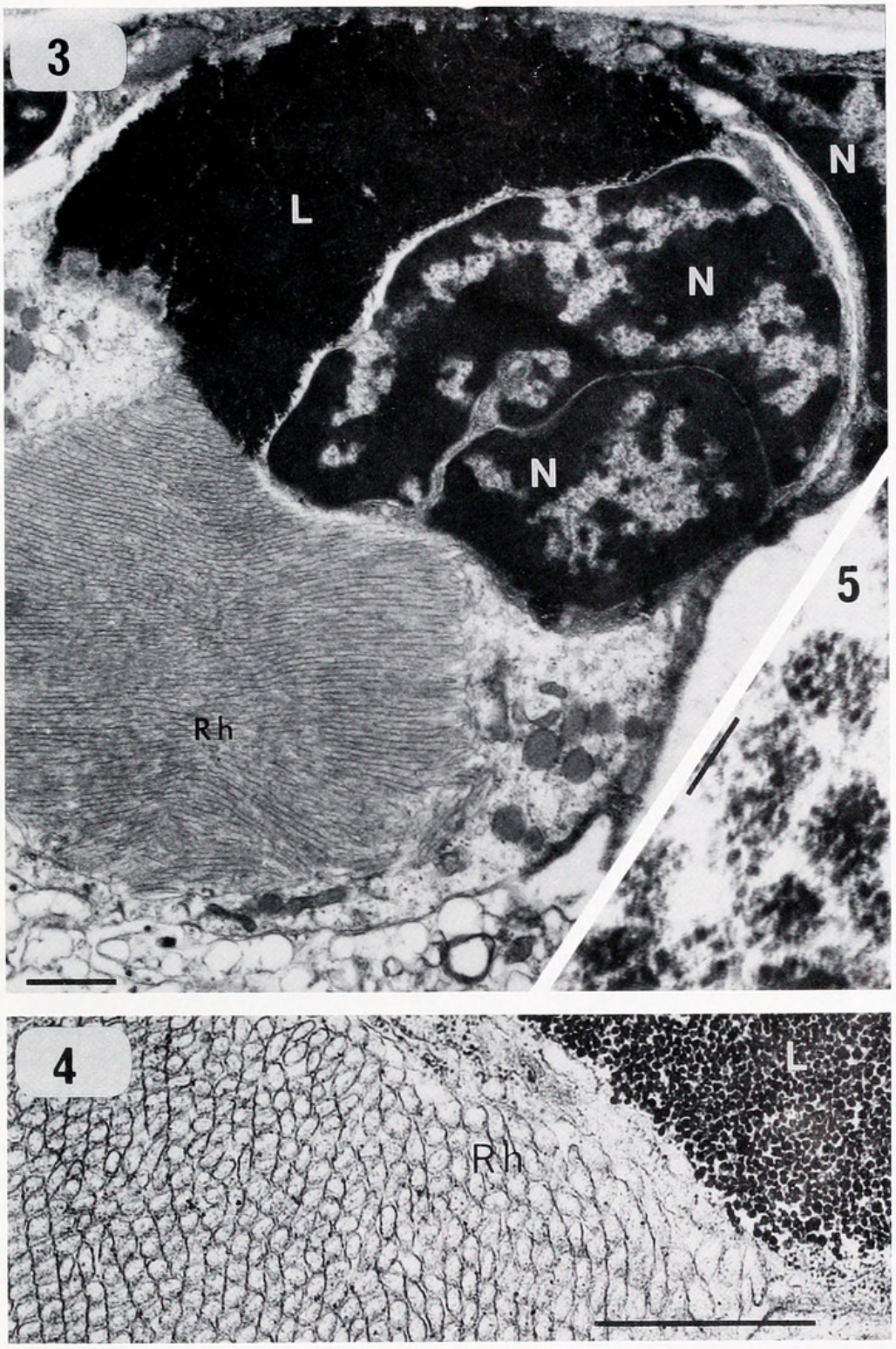


Figure 3. Oblique section through single lenticular complex (L), showing dense aggregations of glycogen-like particles and nuclei (N) as well as the regular alignment of microvilli in the distal portion of the rhabdom (Rh). Scale = 1 μm.

Figure 4. The borderline between lens (L) and rhabdom (Rh) is fuzzy, which should facilitate cell/cell interactions. Scale = 1 μm.

Figure 5. Each glycogen-like granule consists of a variable number of minute (approx. 5–6 nm), spherical subunits. Scale = 30 nm.

rids (*e.g.*, Amphipoda: Michel and Anders, 1954; Hallberg *et al.*, 1980; Meyer-Rochow, 1985; Mysidacea: Hallberg, 1977; Isopoda: Nilsson, 1983). Dark, ommochrome-containing screening pigment granules or melanosomes do not apparently exist in the eye of *D. rathkei,* but reflecting organelles do. The interstitial cells that surround

the retinula cells and isolate individual retinulae (Fig. 6), are crowded with reflecting vesicles of 0.7–0.8 μm in diameter which, on occasions, contained a protein skeleton.

A 14 μm long, multitubular structure was seen in the optic ganglion. This could be mistaken for a rhabdom (Fig. 7) or part of the organ of Bellonci' (Renaud-Mornant *et al.*, 1977). However, because of its proximity to glial cells, it probably represents a trophospongium (Scharrer, 1964; Eguchi and Meyer-Rochow, 1983). No further observations on it or the higher visual centers were made.

Dark/light adaptational changes. Fricke (1931) observed that the yellow pigment inside the retinula cells of *Cuma rathkei* was not stationary but had the ability to migrate towards or away (= up and down) from the lenticular apparatus. A dark-adapted eye, in which most of the carotenoid pigment is withdrawn and only the whitish reflecting organelles remain, changes within 4 minutes into the light-adapted condition upon exposure to daylight (Fricke, 1931). Ultrastructurally, at night the eye (Fig. 9) had considerably more voluminous rhabdoms than during the day (Fig. 8) and the diameters of the individual microvilli in the "night eye" were significantly enlarged over those of the "day eye" (*i.e.*, 0.09–0.125 μm *versus* 0.075 μm). A centrally placed cytoskeletal rod was also more obvious within the dark-adapted microvilli. An actual change in shape of the microvillar transverse profile upon dark and light adaptation, as claimed by Yoshida and Kaga (1983), was not seen.

The border between rhabdom and cytoplasm in the light adapted eye, however, gave the impression of greater jaggedness in comparison to the dark adapted condition. Also there were consistently more tiny ribosome-like dark particles and Golgi bodies in the cytoplasm of the light adapted eye (Fig. 8), and the endoplasmic reticulum was more obvious and more widely distributed. Longitudinally arranged microtubules, along which glycogen-like particles from storage areas near the proximally located retinula cell nuclei could possibly be transported and carotenoid pigment bodies could slide, were identified in both the dark and light adapted eyes (see discussion on transport mechanisms in the crustacean cell: Frixione *et al.*, 1979; Rao and Fingerman, 1983). However, large, empty cisternae and a lack of multi-vesicular and Golgi bodies were predominantly confined to the dark adapted cells. No obvious difference with regard to rise and abundance of mitochondria between dark and light adapted states was seen, but occasionally tiny vesicles (50 nm diameter) budded off the cristae in light adapted mitochondria.

Electrophysiology

Results were obtained from eight of ten animals tested. Responses were generally small and rarely reached the maximum amplitude of 360 μV, recorded in one animal to the highest available flash of white light. The ERGs were typical cornea-negative responses of the slow type with little or no positive component (Fig. 10) similar to the responses of the isopod *Porcellio loewis* (Benguerrah and Carricaburu, 1976).

The spectral response curves (Fig. 11) had but one smooth sensitivity peak in the vicinity of 512–549 nm. Responses to long ultraviolet radiation were down by one sensitivity log unit from the maximum, whereas to light of wavelengths greater than 600 nm the drop was even steeper. The curves of the 8 successfully tested animals were remarkably congruent and fitted a Dartnell nomogramme of a rhodopsin visual pigment with λ_{max} at 530 nm.

Intensity/response curves to light flashes of 472 nm, 549 nm, and 628 nm were, of course, horizontally shifted and had different maximal amplitudes. They shared more or less the same slope over the linear part of the curve with only the 628 nm curve being slightly less steep (Fig. 12). The fact that there was not even an obvious difference to the V/logI curve obtained by using flashes of white light is interpreted as evidence that there is only a single excitatory visual pigment present in the photoreceptor of *D. rathkei* and that the ERG-recordings correctly reflect the eyes' spectral capacity in the scotopic state.

Discussion

There is nothing about the overall anatomy or ultrastructure of the eye of *D. rathkei* that would preclude it from being functional photoreceptors. Absolute sensitivity is high and spectral sensitivity appears to match the downwelling spectrum of the prevalent light. In fact, the presence of internal lenses of a diameter close to 40 μm and a rhabdom only 20 μm away from the center of the lens would result in an F-number of only 0.5, indicative of considerable light-gathering power in each lenticular complex. We know little about the optical quality or properties of the lens, or whether a radial gradient of refractive index exists as, for example, in the eye of the aquatic beetle *Cybister* (Meyer-Rochow, 1973), that could produce a focus in the distal end of the rhabdom. However, even if the lenticular refractive index only "*liegt etwas uber dem des Seewassers*" (Fricke, 1931), each retinular complex in the eye of *D. rathkei* obtains a further boost in photon-capture from the all-abundant reflecting organelles.

Similarities in lenticular ultrastructure between *D. rathkei* and other arthropods exist. The tiny, compact clusters of electron-opaque particles making up the bulk of the lens or crystalline cones have repeatedly been claimed to represent glycogen material (Perrelet, 1970; Eakin and Kuda, 1971; Elofsson and Odselius, 1975).

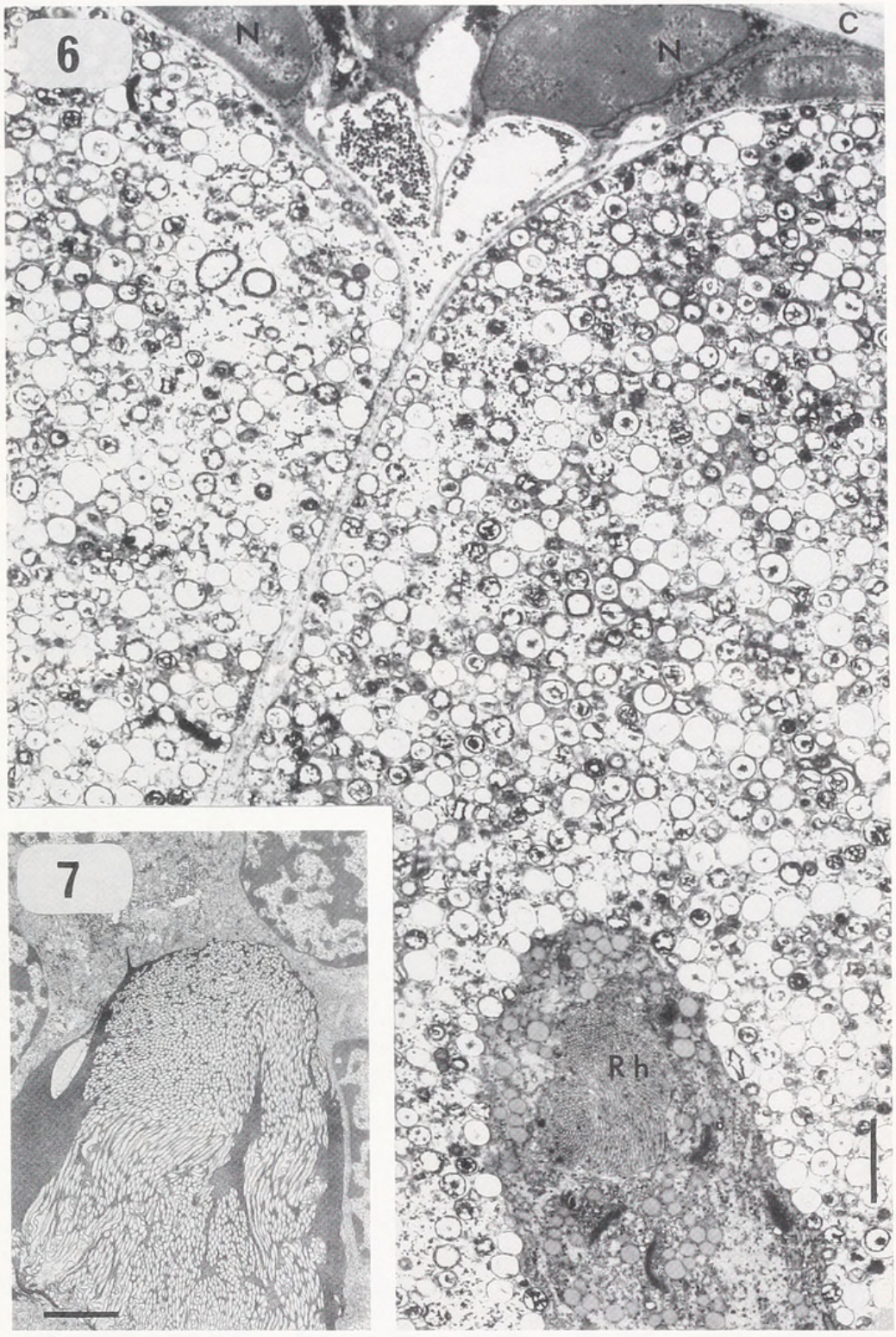


Figure 6. Inward-projecting narrow elongations of hypodermal cells (N), under the cuticle (C), separate the two eye halves, whose major components are cells that are crowded with circular vesicles which are thought to be reflecting in nature, to isolate individual retinular (Rh) complexes, and thus to improve photon capture. Scale = 2 μm.

Figure 7. A short distance behind the eye, this multi-tubular structure, at first glance resembling a rhabdom and probably identical to what Ståhl (1938) interpreted as the "X-organ" in the eye-bladder of *D. rathkei*, was located. Scale = 2 μm.

The granular fine structure in the center of the crystalline cone in the eye of the mantis *Ciulfina* resembles that of the *D. rathkei* lens, but Horridge and Duelli (1979) state that "the crystalline cone in histological and electron microscope sections is obviously made of material that is richer in protein than the surrounding tissue." Be this as it may, there seems little controversy about the chemical nature of the intracellular 'islands' of granular inclusions

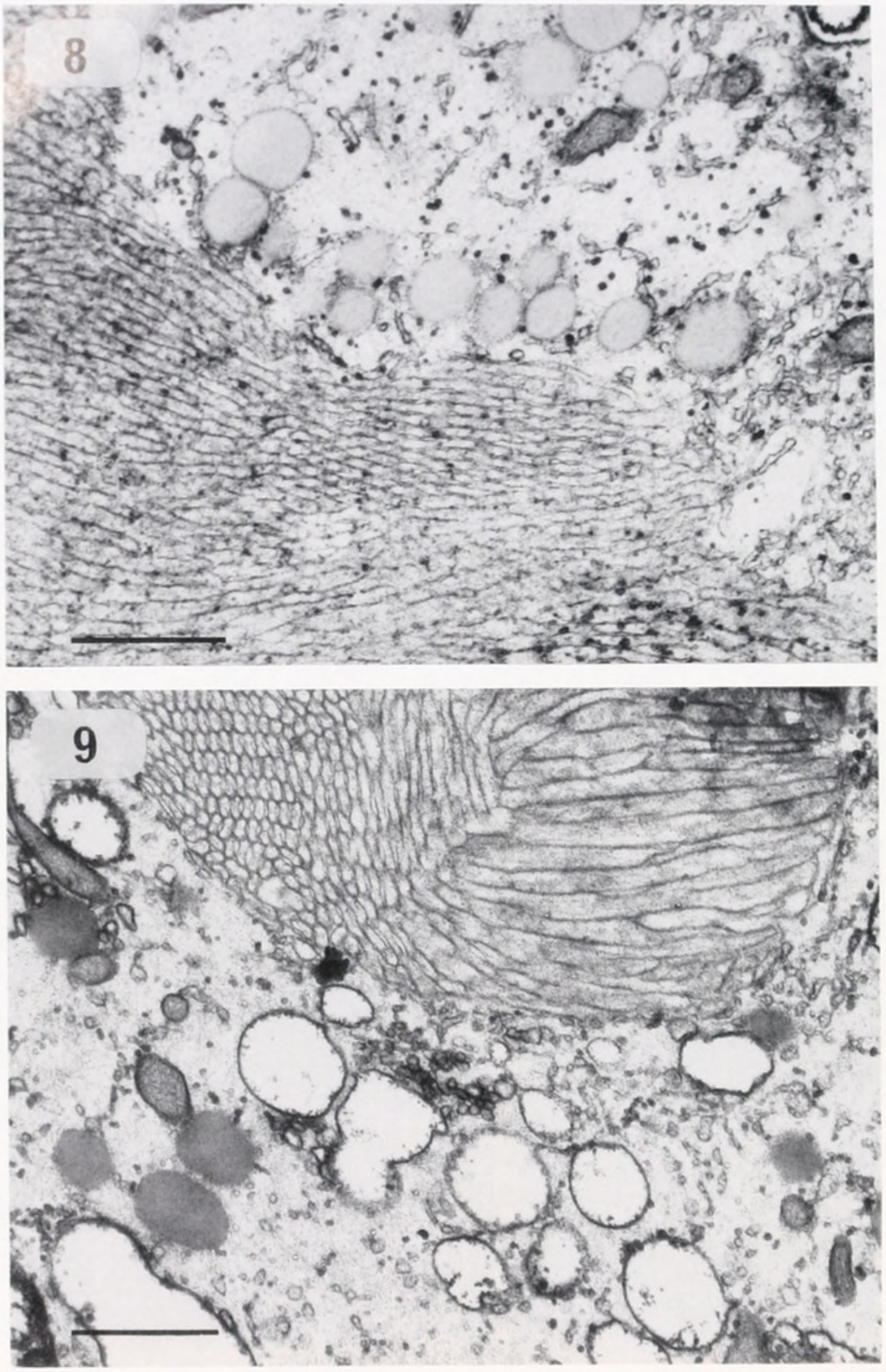


Figure 8. In the light adapted condition the total rhabdom volume is reduced, carotenoid organelles migrate towards the rhabdom edge, and microvilli are 75 nm in diameter. Scale = 1 μm.

Figure 9. In the dark adapted eye the rhabdom volume is enlarged, electron-empty cisternae instead of carotenoid bodies are more numerous around the edge of the rhabdom, and microvillus diameters have become noticeably wider and more variable. Scale = 1 μm.

near the retinula cell nuclei, for they are identical to those reported from the eye of the tick *Amblyomma americanum* (Ill and Cromroy, 1977) and intracerebral ocelli of several species of isopods, in which specific glycogen tests revealed their true character (Martin, 1976). The great abundance of tiny black particles in virtually the

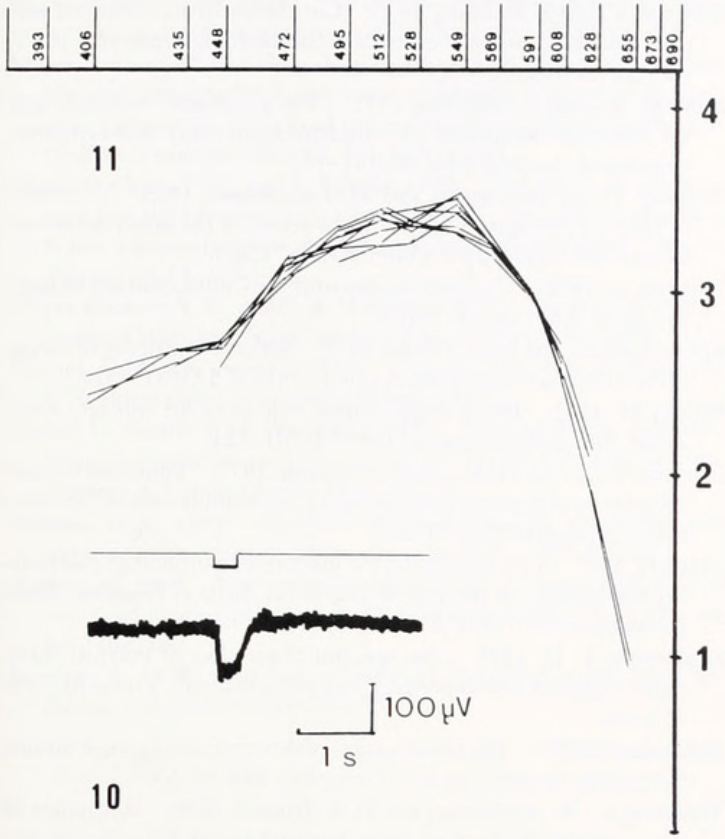


Figure 10. The extracellularly recorded ERG responses are cornea-negative potential changes with little or no positive component.

Figure 11. The superimposed spectral response curves of eight animals based on a criterion response of 50 μV, clearly demonstrate a single sensitivity peak in the range of 512–549 nm wavelengths.

entire retinula cell plasma of the light-adapted eye suggests the involvement of glycogen as an energy source during the energy consuming process of light perception (Hamdorf and Kaschef, 1964; Evequoz *et al.*, 1983). The hypertrophied nature of the endoplasmic reticulum is consistant with, and probably signifies, intense visual pigment synthesis.

The unquestionable increase in microvillus diameter during dark adaptation is somewhat surprising as this would offset the possible gain in sensitivity made by an overall enlargement of rhabdom volume. However, increases in microvillus diameters of a similar magnitude under dark conditions have been reported (Nässel and Waterman, 1979) in the crab *Grapsus grapsus,* in *Gryllus bimaculatus* (Hoff, 1985), and can also be calculated from electron micrographs on the eye of the brine shrimp *Artemia salina* (Hertel, 1980). They are also in agreement with observations by Yoshida and Kaga (1983) if we assume that their "dumbbell-shaped" microvilli in the light-adapted condition actually represented an oblique section through two rows of microvilli. Yoshida and Kaga (1983) state that in the cumacean *Dimorphostylis asiatica* the change from the 30–50 nm wider dark adapted to the narrower light adapted microvillar ultrastructure is completed in 10 minutes at 130 lux illumination, but that it requires 3 times longer in reverse. Although not specifically tested in *D. rathkei,* this time course would agree with pigment granule displacements in arthropods that display such dark/light adaptational changes (Meyer-Rochow and Horridge, 1975; Frixione *et al.*, 1979; Hallberg *et al.*, 1980).

The reasons as well as the trigger for *D. rathkei* to occur more frequently in the plankton at certain times of the year (Valentin, pers. comm.) are not fully understood. However, in agreement with crustacean larvae with adults living lower intertidally (Forward and Cronin, 1979), the spectral response curves in *D. rathkei* lack a strong UV-component and resemble those of the barnacle *Balanus amphitrite* (Stratten and Ogden, 1971). According to Stratten and Ogden (1971) an increase in the slope of the response/intensity function points to increased light adaptation. It also narrows the spectral response curve if only a single photopigment is present. This means then that in addition to the filtering properties of the cuticle and lens, the self-screening of the rhabdom and the transmission characteristics of the screening pigments (see also discussions in Goldsmith, 1978, and Meyer-Rochow and Eguchi, 1984), the changing environmental light intensity, not only between day and night, but also between different seasons, must affect the shape of the spectral response curve. That seasons, time of day, and temperature affect the shape of the spectral response curves in various species of crustaceans, has indeed been shown (Nosaki, 1969; Meyer-Rochow and Eguchi, 1984; Hariyama *et al.*, 1986).

The eye of *D. rathkei,* at least when dark adapted, seems useless as an analyzer of color or as an image-

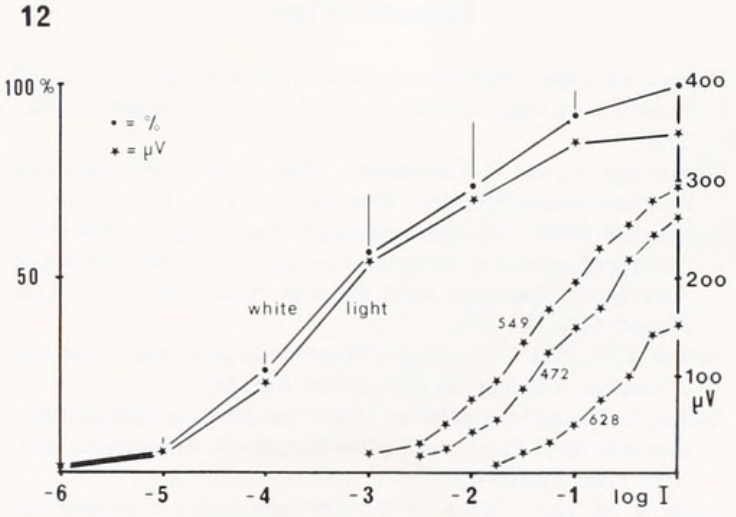


Figure 12. Normalised intensity/response curves (dotted) and responses in μV (ordinate on the right) to flashes of white light and light of 472, 549, and 628 nm wavelength. The slopes of the V/logI functions are identical apart from that of the 628 nm curve which is slightly less steep.

forming photoreceptor. However, it is quite capable of registering small changes in the quantity and quality of environmental light. Thus it must be of some use to the animal, even though the latter spends most of its life buried in the sand (Kaestner, 1959). Segerstråle (1970) invoked photoreception and not the perception of environmental temperature *per se* as the principal agent involved in the coordination of reproduction in the Baltic Sea amphipod *Pontoporeia affinis*. *P. affinis* eyes are also tiny and consist of no more than 30–40 facets (Donner, 1971). Our study of the eye of *D. rathkei* suggests that photoreceptive properties and changes of the latter, perhaps in conjunction with the seasonal fluctuation of consumed carotenoids (Czeczuga, 1980), could be equally important in Cumacea. One could speculate that they are involved in coordinating vertical migrations and synchronising mating activities.

Acknowledgments

The authors thank the Alexander von Humboldt Foundation (Bonn, West Germany) and the Finnish Academy of Sciences for the support rendered towards this project in Germany and Finland, respectively. Further, V. B. Meyer-Rochow acknowledges the help of Dr. Stephan (University of Kiel, W. Germany) and the crew of research cutter "Alkor" in catching the animals, and he is indebted to the Meat Industry Research Institute of New Zealand for making available electron microscope facilities. Finally V. B. Meyer-Rochow expresses his gratitude to Professor Dr. W. Noodt and the staff of the Zoological Museum (University of Kiel) for their fine hospitality.

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