# The Crustacean Eye: Dark/ Light Adaptation, Polarization Sensitivity, Flicker Fusion Frequency, and Photoreceptor Damage

[REVIEW]

# The Crustacean Eye: Dark/ Light Adaptation, Polarization Sensitivity, Flicker Fusion Frequency, and Photoreceptor Damage

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**ABSTRACT**—Compound eyes, nauplius eyes, frontal organs, intracerebral ocelli, and caudal photoreceptors are the main light and darkness detectors in crustaceans, but they need not be present all at once in an individual and in some crustaceans no photoreceptors whatsoever are known. Compound eye designs reflect on their functions and have evolved to allow the eye to operate optimally under a variety of environmental conditions. Dark-light-adaptational changes manifest themselves in pigment granule translocations, cell movements, and optical adjustments which fine-tune an eye's performance to rapid and unpredictable fluctuations in ambient light intensities as well as to the slower and predictable light level changes associated with day and night oscillations. Recycling of photoreceptive membrane and light-induced membrane collapse are superficially similar events that involve the transduction cascade, intracellular calcium, and membrane fatty acid composition, but which differ in aetiology and longterm consequence. Responses to intermittant illumination and linearly polarized light evoke in the eye of many crustaceans characteristic responses that appear to be attuned to each species' special needs. How the visual responses are processed more centrally and to what extent a crustacean makes behavioural use of e-vector discrimination and flickering lights are questions, however, that still have not been satisfactorily answered for the vast majority of all crustacean species. The degree of light-induced photoreceptor damage depends on a large number of variables, but once manifest, it tends to be progressive and irreversible. Concomittant temperature stress aggravates the situation and there is evidence that free radicals and lipid hydroperoxides are involved.

**Key words**: vision, eye, photoreceptor, Crustacea, adaptation

## INTRODUCTION

Despite numerous thorough investigations important gaps still exist in our understanding of how exactly crustaceans detect light, process visual information, and adjust their photoreceptors to the changing ambient thermal and photic conditions caused (a) by shifts in cloud cover and/or the animal's entry into shaded or illuminated areas and (b) by the regular exposure to a daily dark/light rhythm (Meyer-Rochow, 1999a).

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This paper is dedicated to my good friend Dr. Yukitomo Morita, formerly Professor of Physiolgy at Hamamatsu University, Medical School, who passed away on September 27th, 2001.

Another area of crustacean vision in which our understanding is still incomplete concerns polarization sensitivity and the perception of flickering lights. This review provides an introductory survey of crustacean photoreceptors before addressing some of the above issues in more detail. It will end with a brief discussion on light-induced photoreceptor damage in the crustacean eye.

**Crustacean Photoreceptors**

Amongst the crustaceans, a variety of structures may be involved in the perception of light. The most conspicuous and best-studied organs are the compound eyes (Fig. 1a). They reach their highest degree of sophistication in the stomatopod (Cronin, *et al.*, 1994), euphausiid (Land, 1981), and decapod crustaceans (Herring and Roe, 1988), but are absent from
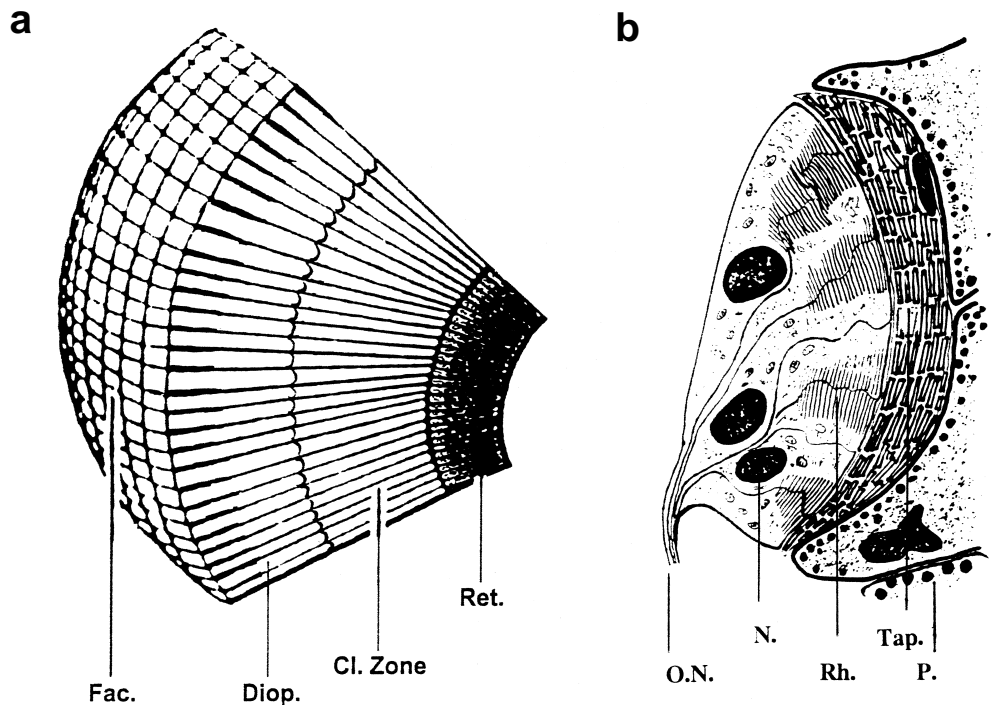
**a** **b**



**Fig. 1.** (a): Sector of crayfish compound eye with facets (Fac.) to the left and major internal layers, i.e. dioptric structures (Diop.), clear-zone (Cl. Zone), and retina (Ret.), visible in the longitudinal section (parallel to the ommatidial axes). Scale=0.1 mm. (b): Section through nauplius eye of the Antarctic ostracode *Acetabulastoma* sp., showing optic nerve (O.N.), photoreceptor cell nuclei (N.), visual membranes (Rh.), crystalline tapetum (Tap.), and screening pigment grains (P.). The direction of the light is from the left. Scale=1 μm.

the Copepoda, Mystacocarida, Cephalocarida, and some smaller groups with very few species (see further below). In Cirripedia they still occur in the last larval stage and amongst the Ostracoda they are known from the Myodocopa.

Another kind of crustacean photoreceptor (Fig. 1b) are the nauplius eyes (Elofsson, 1965; 1966), which are usually present in the earliest larval stages, but may persist throughout adulthood (except in Leptostraca, Mysidacea, Cumacea, Isopoda, and Amphipoda). In some crustacean taxa (e.g., Copepoda, Mystacocarida, Cephalocarida, and Cirripedia) they represent the only photoreceptors. For ultrastructural details see, for example, Fahrenbach (1964), Dudley (1969), Ong (1970) and Meyer-Rochow (1999b).

The frontal organs, present in a large number of crustaceans, are clearly photoreceptors that are usually not homologous with the nauplius eye and which form the third category of crustacean light detectors (Elofsson, 1965, 1966). Examinations of individual cases are required before any statement concerning a specific frontal organ's ontogeny can be given and homology with the nauplius eye, or perhaps intracerebral ocelli (see below), can even be suggested. Incidentally, the term 'median eye', sometimes found in the literature to describe either nauplius eyes or frontal organs, is ambiguous and, henceforth, had better be avoided.

The fourth type of photoreceptive structure in crustacea is represented by the intra-cerebral ocelli, which are usually not visible from the outside of an intact animal and occur in the brain as clusters (or cluster) of a few photoreceptive

cells (Martin, 1976; Sandeman *et al.*, 1990; Martin *et al.*, 1995; Frelon-Raimond *et al.*, 2001). The tail (or caudal) photoreceptor, known from the sixth abdominal ganglion of some decapods, forms the fifth and last group of light and darkness detectors in crustacea (reviewed in Wilkens, 1988).

In certain crustacean taxa eyes occur that cannot be immediately and easily categorized and assigned to, for instance, the compound eyes or the nauplius eyes; yet they probably represent modified, but already known types of eyes rather than completely new classes of photoreceptor structures. Included in this group of "aberrant" or "non-typical" eyes are the single-lens eyes of the ampelisid amphipods (Hallberg *et al.*, 1980), the "accessory eyes" of shrimps (Itaya, 1976; Ugolini and Borgioli, 1993), the unusual eyes of cumacea (Meyer-Rochow, 1989) and the facet- as well as cone-less eyes of hydrothermal vent shrimps (O'Neill *et al.*, 1995; Lakin *et al.*, 1997). All four kinds of eye are interpreted, by most researchers, as modified compound eyes. Equally unusual and somewhat difficult to classify phylogenetically as well as physiologically are the single-lens nauplius eyes of certain copepods, e.g. *Copilia*, *Corycaeus*, and *Sapphirina* (Vaissière, 1961; Elofsson, 1969) whose retinas have been likened in function by Gregory *et al.* (1964) to the electron beam and screen of the television tube.

This brief introductory survey of photoreceptors in the crustacea does not rule out the possibility that other sense organs might also possess some sensitivity to light (crustacean integumental chromatophores and the 'organ of Bellonci'

come to mind) or that as yet undiscovered light-sensors might exist (cf. Edwards, 1984). All the crustacean taxa considered to consist of individuals that have not evolved any eyes whatsoever (e.g., Remipedia, Thermosbaenacea, Spelaeogriphacea, Mictacea), ought to be re-examined just like some other so-called "eyeless" cave species (e.g., mysids, amphipoda, isopoda, shrimps, and crabs) in view of the fact that (a) not all photoreceptors are compound or nauplius eyes and (b) retinula cells can exist under the cuticle even when externally no eye can be seen (an example from the insects would be the eyeless grylloblattid *Galloisiana nipponensis*: Nagashima, 1990, an example from the decapods *Typhlatya garciai*: Meyer-Rochow and Juberthie-Jupeau, 1983).

With the exception of the nauplius eye of the adult barnacle, for which considerable physiological data exist (Stuart, 1983), and excluding the compound eye, which will be dealt with in more detail further below, very little is known about adaptational processes in any of the other kinds of photoreceptors or the extent to which they influence each other (e.g., the caudal photoreceptor's role in phase-shifting ERG-amplitude in juvenile crayfish: Bernal-Moreno *et al.*, 1996). Changes in sensitivity thresholds have been documented in several extraocular photoreceptors by electrophysiological methods (Wilkens, 1988; Sandeman *et al.*, 1990) and apparently light-induced structural and behavioural changes can occur in nauplius eyes, if not frontal organs as well (Debaisieux, 1944; Meyer-Rochow and Keskinen, unpublished). Whether, however, also intracerebral ocelli respond structurally and not only functionally (Hariyama *et al.*, 1982) to variations in ambient light intensity and, as with the compound eye, undergo regular cyclic daily changes regarding volume of photoreceptive membranes and variety and density of cell organelles, are still open questions.

## Crustacean Compound Eye: Basic Structure

The overall uniformity of the crustacean compound eye and its similarity in basic design with the compound eyes of xiphosuran chelicerates (e.g., *Limulus*) and insects had been noticed more than a hundred years ago (Exner, 1891). Melzer *et al.* (1997) give reasons and summarize arguments for a common evolutionary origin of the insect and crustacean ommatidium. A typical crustacean compound eye (for instance, Figs. 1a, 2a) consists of a number of similar anatomical units known as ommatidia, which are covered on the outside by a faceted, transparent, and multilayered cornea. The cornea is secreted by two corneagenous cells per ommatidium and forms, together with usually four cone cells, the dioptric apparatus of the eye. On the proximal side of the cone cells lies a group of retinula cells (frequently eight, but depending on the taxon also seven, six, or even five) with membrane specializations termed rhabdomeres which are the light-receptive elements of the ommatidium and contain the photopigment. Axons from the retinula cells penetrate the basement membrane in distinct bundles and terminate in the lamina from where second-order neurons link up with cells of the medulla. A variety of distal and proximal screening pigment cells

(Hallberg and Elofsson, 1989) completes the basic structure of the crustacean compound eye. An eye conforming to the anatomy thus outlined, would be called an "apposition eye" and can be considered to represent the original archaic principle of the compound eye (Richter, 1999).

One modification of this basic arrangement is so characteristic that it has led to the establishment of a separate type of crustacean compound eye: an eye which can easily be distinguished from the apposition eye by the presence of a clear-zone, i.e., a region devoid of pigment (at least under dark-adapted conditions) between dioptric and receptor layers (Fig.2b). The clear-zone may be formed by the elongated proximal ends of the cone cells or some narrow distal projections of the retinula cells. It was originally thought that amongst the crustaceans, clear-zone eyes occurred only in some malacostraca (e.g., Euphausiaceae, Mysidaceae, and Decapoda) and that this anatomical design was an adaptation to improve vision in dimly lit environments through superposition either by refraction or reflection (Land, 1981; Cronin, 1986). However, additional designs and mechanisms have been described in recent years (Cronin, 1986; Nilsson, 1989). Also, some species with this kind of eye (e.g., the hermit crab *Dardanus* and the syncarid *Anaspides tasmaniae*) were discovered in groups not previously expected to harbour species operating with superposition (Nilsson, 1990). It could also be shown that some apposition eyes can be as sensitive as superposition eyes (Land and Nilsson, 1990) or possess long and narrow cones which act as light-guides (Meyer-Rochow, 1978; Land, 1981b). Additional and more detailed information on functional differences between apposition and superposition eyes can be obtained in a recent publication by Warrant (1999).

Both apposition (Hallberg *et al.*, 1980; Schiff *et al.*, 1986; Cronin *et al.*, 1994) and superposition eyes (Elofsson and Hallberg, 1977; Hiller-Adams and Case, 1988; Gaten *et al.*, 1992; Richter, 1999) probably as an evolutionary consequence of environmental pressures, may display further structural and functional modifications. Forms, for instance, that flourish in extreme environments (mesopelagic and deep-sea crustaceans, and species adapted to a life underground or in caves) frequently exhibit morphologies that differ from the basic design (Meyer-Rochow and Nilsson, 1999). Within the genetic confines of the taxon such changes may affect primarily the optical components of the crustacean compound eye, the retina, or both. With regard to the eye's optics, for example, reflecting, refracting, and parabolic superposition eyes as well as apposition eyes with and without light guides and with and without screening or tapetal structures are now known (Nilsson, 1989). On the retinal side, long and thin, short and fat, solid or multilobed as well as fused or open rhabdoms may occur (Elofsson, 1976) and the nuclei of the retinula cells may be positioned above or below the basement membrane of the eye (Debaisieux, 1944). Yet, despite the variations in design, all compound eyes that display dark/light adaptational changes, exhibit these changes for the same purpose, namely to optimize the function of the eye under particular photic con-
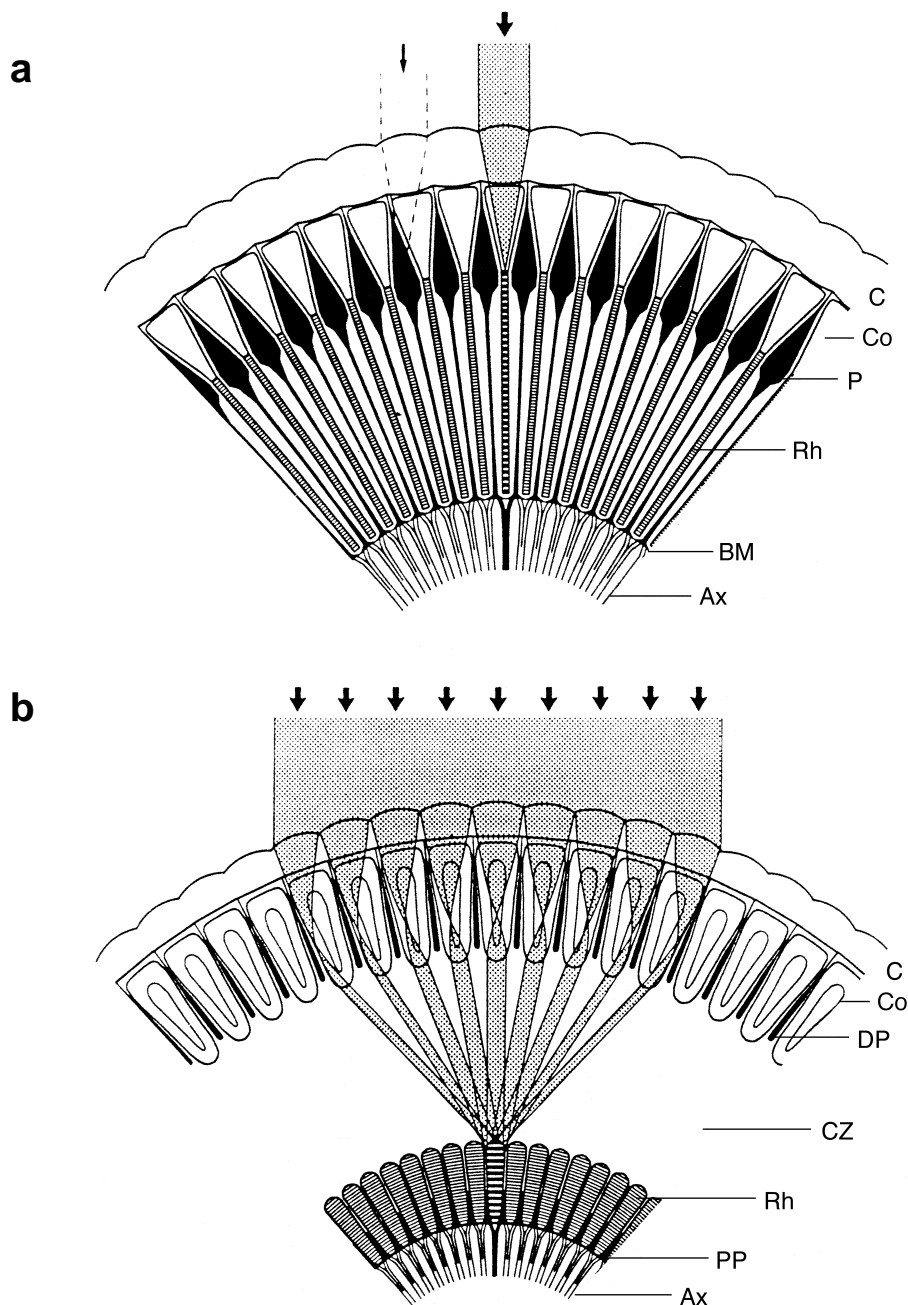
**Fig. 2.** (after Hardie 1988 and Nilsson 1989). (a): Pathway of the light and structural elements in a model crustacean apposition compound eye (C=cornea, Co=cones, P=screening pigment, Rh=rhabdoms, BM=basement membrane, Ax=axons). (b): Pathway of the light and structural organization of a model crustacean superposition compound eye (C=cornea, Co=crystalline cones, DP=distal screening pigment, CZ=clear zone, Rh=rhabdoms, PP=proximal screeining pigment, Ax=axons).

ditions. Photomechanical changes may affect the positions and shapes of whole cells, the amounts and distributions of organelles, and the chemical compositions of membranes, photopigments and intracellular messengers (cf. Meyer-Rochow, 1999a) so that firstly, the crustacean's requirements for light sensitivity and acuity are met and secondly, the constituent cells of the eye derive maximum protection against potentially damaging radiation.

Although specific environmental adaptations have been described from the compound eyes of a large number of spe-

cies covering all the major taxa and it has been possible to formulate generalizations (see below), the crustacean compound eye can undergo changes within an animal's life span: in some species the eyes turn from apposition into superposition eyes as the animal grows (Meyer-Rochow, 1975; Hafner *et al.*, 1982a; Nilsson *et al.*, 1986), microvillar dimensions can change (Meyer-Rochow and Reid, 1996), and in others the eyes may develop an extremely high degree of asymmetry as, for instance, in some mesopelagic species with totally different dorsal and lateral ommatidia (Land *et al.*, 1979; Land,
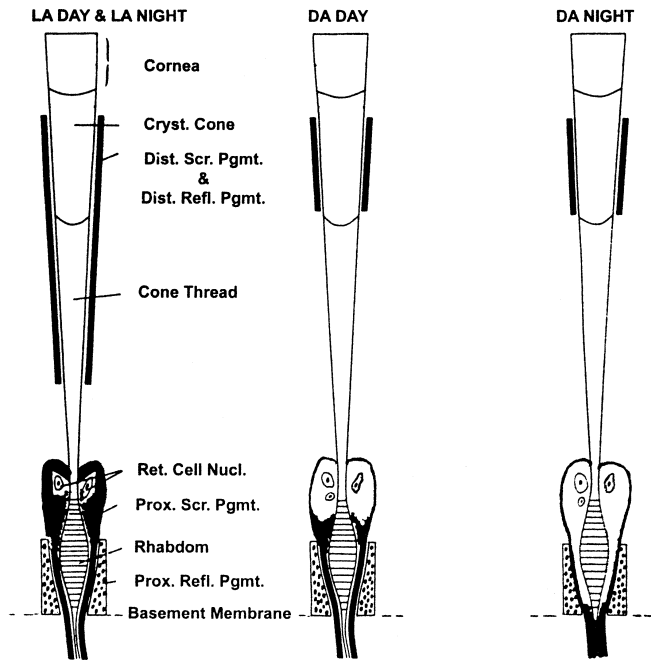
1981a; Gaten *et al.*, 1992). What is more, new findings have shown that regional differences are present in the eyes of many crustaceans and not just those adapted to extreme environments (Odselius and Nilsson, 1983; Tokarski and Hafner, 1984; Cronin *et al.*, 1992; Zeil and Zanker, 1997), highlighting the need for additional research into how the various regions of a compound eye behave (and perhaps influence each other) and how, more generally, post-embryonic eye differentiation occurs (cf., Meyer-Rochow *et al.*, 1990; Ziedins and Meyer-Rochow, 1990; Hafner and Tokarski, 1998, 2001).

A further complicating factor in qualitative and quantitative studies of eyes and vision in crustaceans is that structural (Fig. 3), and functional (Fig. 4), responses of the eye depend on the time of day as well as on the previous photic exposure history of an individual. For example, the well-documented



**Fig. 3.** (after Bryceson and McIntyre 1983). Schematic illustration of the anatomy of an ommatidium of the crayfish *Cherax destructor* under three conditions of adaptation (LA=light adapted, DA=dark adapted). The small retinula cell R8 has been omitted for the sake of clarity.
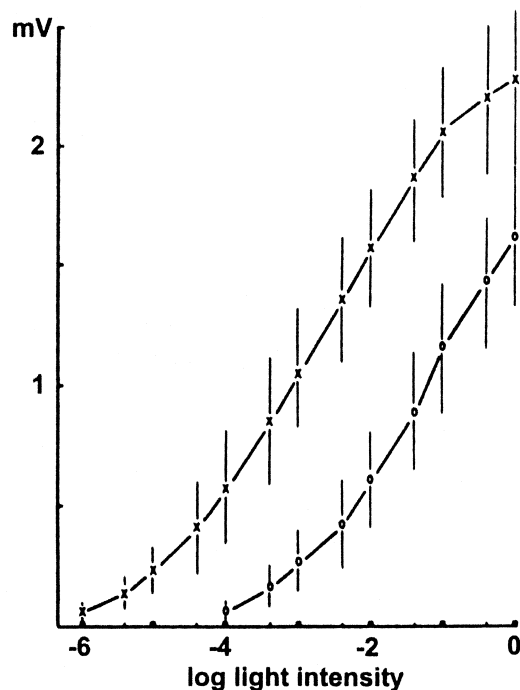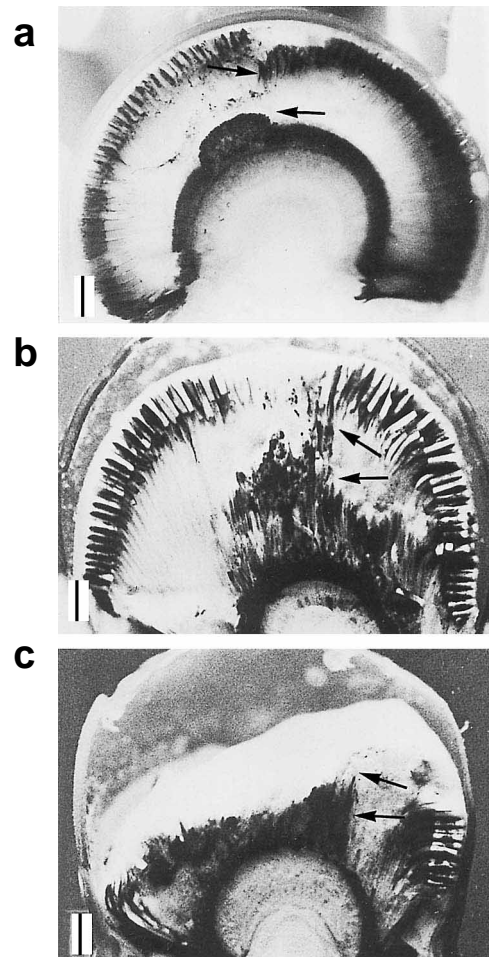


**Fig. 4.** (after Meyer-Rochow and Tiang 1984). Stimulus/response curves (standard deviations indicated) based on ERG-recordings from the eyes of 10 rock lobsters (*Jasus edwardsii*) at night (left curve) and during the day (right curve). At night the eyes are at least 100 times more sensitive.



**Fig. 5.** (after Meyer-Rochow and Tiang 1984). (a): Bisected eye of rock lobster kept under normal 12h dark/light conditions, but exposed to white light of approx. 60000 lux from a xenon arc lamp for ca. 3 sec one week previously. Damage to cones and retina (arrows) is evident. (b): Bisected eye of rock lobster kept under normal conditions for two months, but prior to that exposed to sunlight for 420 min accumulated over a period of 7 days. Increased damage to dioptric structures and retina is obvious. (c): Bisected eye of rock lobster kept under normal conditions for almost 3 months, but with exposures to sunlight of 240 min on day 1, 240 min on day 2, 30 min on day 35, and 150 min on day 48. The damage to the eye is severe. Scale=0.5 mm.

long-term damaging effect of bright light on the structural integrity and performance of the lobster compound eye (Fig. 5) is very much dependent on the depth, i.e., the ambient light intensity and the adaptational state to which the animals had been adjusted prior to the experimental exposure (Gaten, 1988; Gaten *et al.*, 1990), a conclusion earlier reached also by Lindström and Nilsson (1984) on the basis of observations on light-induced photoreceptor damage and recovery in the oppossum shrimp *Mysis relicta*. Furthermore, photoreceptor membrane recycling, a diurnally modulated phenomenon, can result in very different profiles of rhabdoms and retinula cells at different times of day (see below).

## DARK/LIGHT ADAPTATIONAL CHANGES: CAUSES AND EFFECTS

Excellent descriptions of photomechanical changes affecting the crustacean compound eye and their underlying possible causes can be found in Autrum's (1981) review, which, furthermore, provides very useful definitions for the various kinds of sensitivity (e.g., absolute-, increment-, detection-, range-, and polarization sensitivity) and also deals with membrane dynamics during adaptations. An updated view on compound eye pigment and cell migrations as well as other micro-anatomical changes upon dark/light adaptation has recently been published by Meyer-Rochow (1999a). This review will, therefore, focus on new and perhaps little-known aspects of adaptation.

Although any component of the crustacean compound eye can be affected by dark/light adaptational changes (Meyer-Rochow, 1999a), the two most obvious involve (a) the position of the screening pigment granules (Fig. 6) and (b) the position, size, and shape of the rhabdom (Figs. 7, 8). The main purpose of these and other adjustments is to allow more
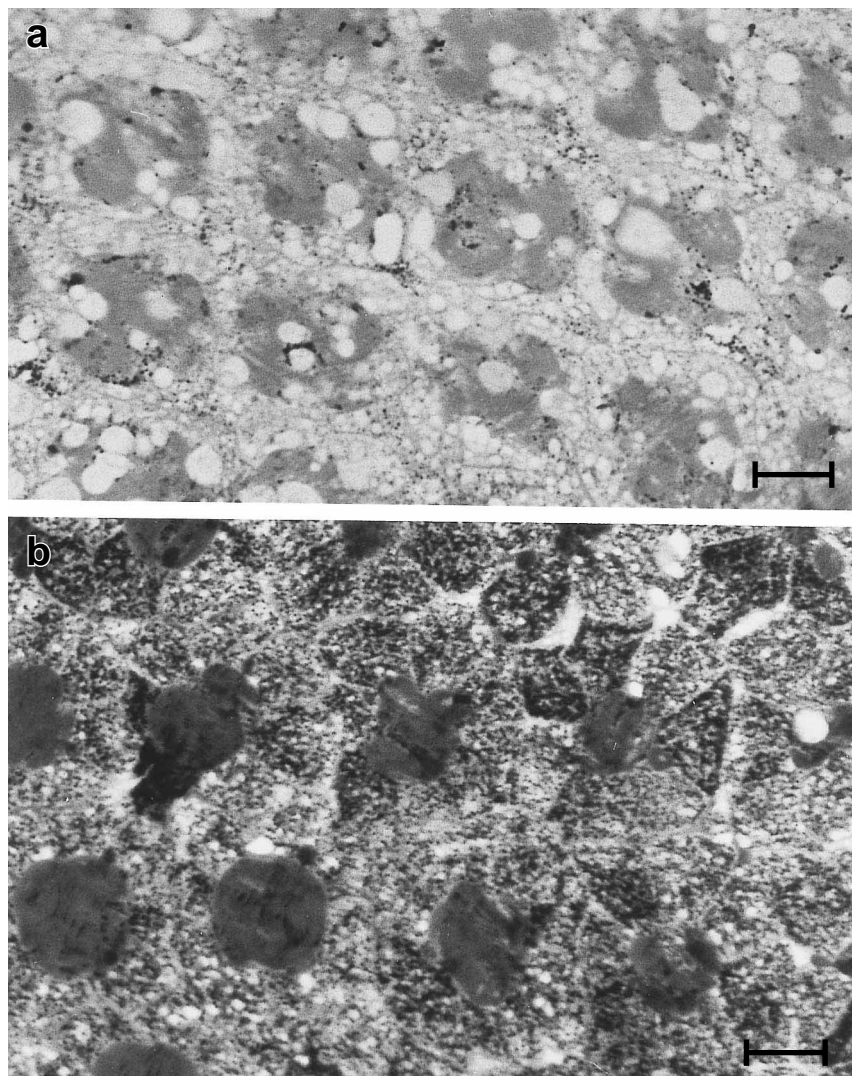


**Fig. 6.** (a): Cross section through retina of crayfish *Procambarus clarkii*, kept for 3 weeks in total darkness at 10°C; dark screening pigment granules are almost totally absent. Scale=10 μm. (b): Cross section through retina of crayfish *Procambarus clarkii*, kept for 3 weeks in the light at 10°C; dark screening pigment granules are abundant and insulate adjacent rhabdoms. Scale=10 μm.
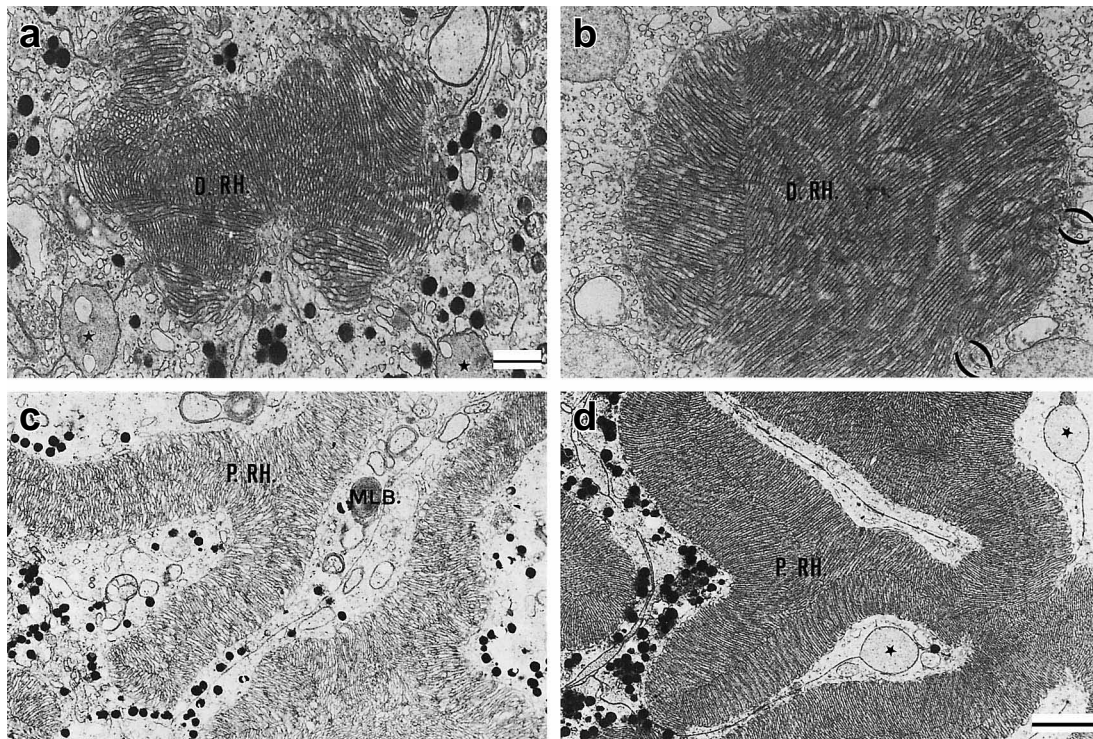
**Fig. 7.** (after Meyer-Rochow and Tiang 1984). (a) and (b): Cross sections through light- and dark-adapted distal rhabdoms of the rock lobster *Jasus edwardsii*, showing difference in screening pigment distribution, rhabdom size and shape. Scale=1 μm. (c) and (d): Cross sections through part of light- and dark-adapted proximal rhabdoms of the rock lobster *Jasus edwardsii*, showing difference in screening pigment distribution, microvillar sizes and shapes. Scale=2 μm. Cone cell processes are denoted by asterisks.
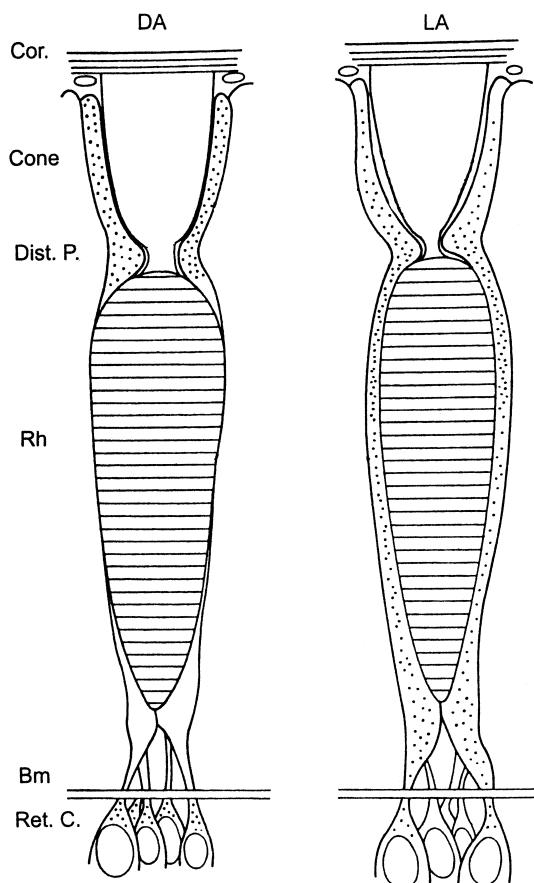


light under dim conditions to enter the eye in order to improve the 'photon-capture-rate' through interceptions by the molecules of the photopigment (Struwe *et al*., 1975; Frixione *et al*., 1979; Land, 1981; Hallberg and Elofsson, 1989; Meyer-Rochow *et al*., 1990). This explains why at night in many species of crustaceans the apertures of the dioptric apparatus are frequently enlarged and screening pigments are withdrawn to regions outside the path of the light within the eye (Fig. 9), why often a reflecting tapetum at the back of the retina or around the retinula cells becomes exposed (Fig. 10), and why the rhabdom volume may dramatically increase (Fig.11). In cases where adaptational changes of these kinds occur, there is usually a trade-of between sensitivity and acuity: one gains, the other loses. The gap between the two can be considerable as in the crayfish *Cherax* (Walcott, 1974) or it may be rather small as in *Ligia exotica* (Hariyama *et al*., 2001).

Photomechanical changes involving screening pigments (both distal and proximal) can be observed in the living animal (Fig. 12) by examining its eye-glow (Arechiga *et al*., 1973; Frixione *et al*., 1979) or pseudopupil (Cronin, 1992). In species with "glowing eyes", the animal is given a second chance to make use of the light that on its inward direction has first

**Fig. 8.** (after Meyer-Rochow and Tiang 1979). Diagrammatic representation of dark (DA) and light adaptational (LA) changes in the eye of the Antarctic amphipod *Orchomene plebs* (Cor.=cornea, Dist. P.=distal pigment, Rh.=rhabdom, Bm=basement membrane, Ret.C.=retinula cell bodies).
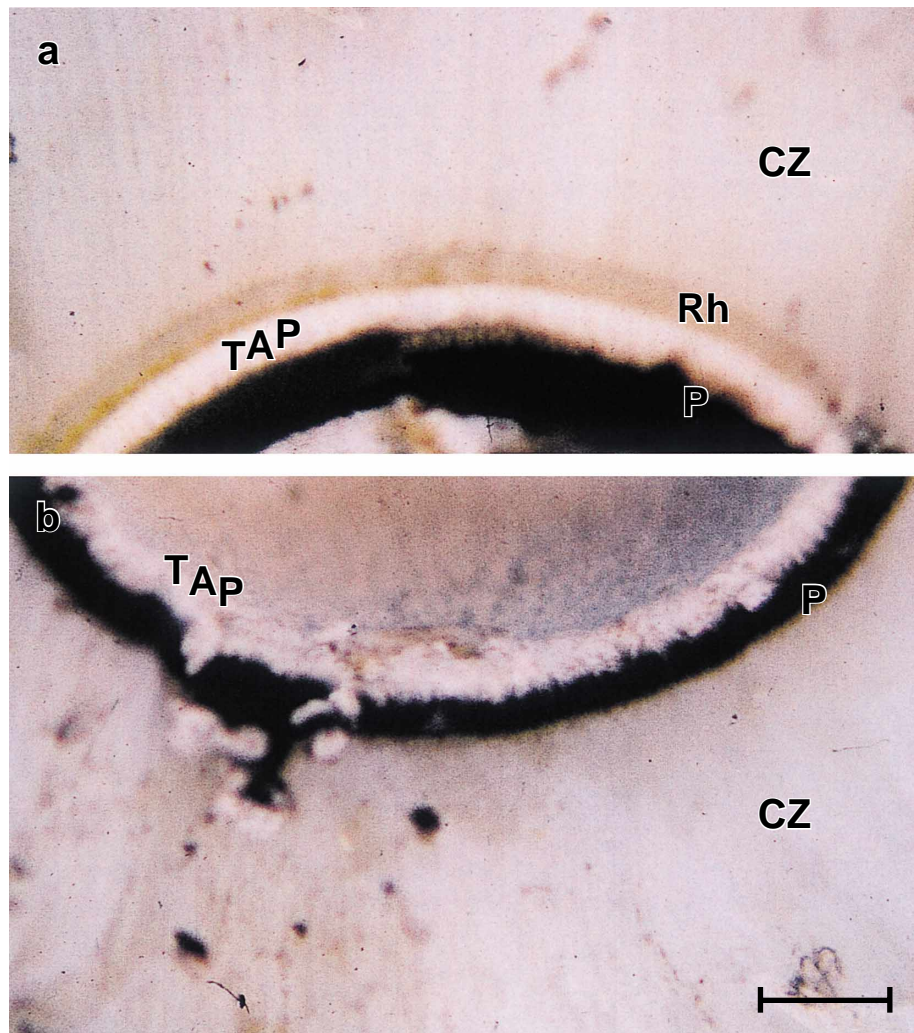
**Fig. 9.** Bisected, unfixed eye of *Jasus edwardsii* at night (a) and during the day (b), showing clear zone (CZ) and migration of screening pigments (P) to either below or above the reflecting layer (Tap) and the photoreceptive elements of the retina (Rh). Scale=0.1 mm.

passed through the retina without being absorbed and then has undergone reflection at the tapetum behind the retina, reversing its path and directing it through the retina for a second time. Ommatidial 'sleeves' of reflecting granules or a zone of lower refractive index (frequently referred to as 'palisade') are also often involved in the enhancement of the rhabdom's photon capture efficiency. The screening pigment granules inside the receptor cell may move toward or away from the edge of the rhabdom (=radial migration), thereby altering the diameter of the pseudopupil (Cronin, 1992). Many of the known screening pigment translocations and changes in cell shape position upon adaptation can be generated at any time of day. However, exposing a crustacean to a light at night, for example, may produce additional adaptational changes that differ significantly from those seen during the day (Henkes, 1952; Bryceson and McIntyre, 1983; Meyer-Rochow *et al.*, 2001). The same holds true for dark adaptation (Fig. 3). In insects (Nilsson *et al.*, 1989), pupil control mechanisms vary between apposition (control over screening pigment position entirely retinal) and superposition eyes (independent distal

and retinal control); in crustaceans, although less well-studied than insects, the situation seems to be somewhat more complicated with pigmentory effectors responding directly to the light (Frixione *et al.*, 1979), but also to neurohormones (see below).

There is, first of all, usually a difference in the speed with which light and dark adaptations proceed (light adaptation is generally faster and often requires no more than a few minutes, whereas total dark adaptation can take hours: Meyer-Rochow, 1999a). Pigment granules involved in longitudinal migrations may cover a distance of up to 200 μm in 7–8 minutes, but after an initial fast translocation, pigment grains slow down progressively (Hallberg *et al.*, 1980). Therefore, a value of 0.38 μm/sec for granule translocations in the crayfish given by Frixione *et al.*, (1979) has to be an average. Radial pigment migrations may be as fast (King and Cronin, 1994), but cover shorter distances. Different cytoskeletal structures seem involved in radial and longitudinal pigment translocations (King and Cronin, 1993). Irrespective of time of day, the influence of light tends to supersede all other influences and can push the proximal pigment of the dark-adapted crayfish
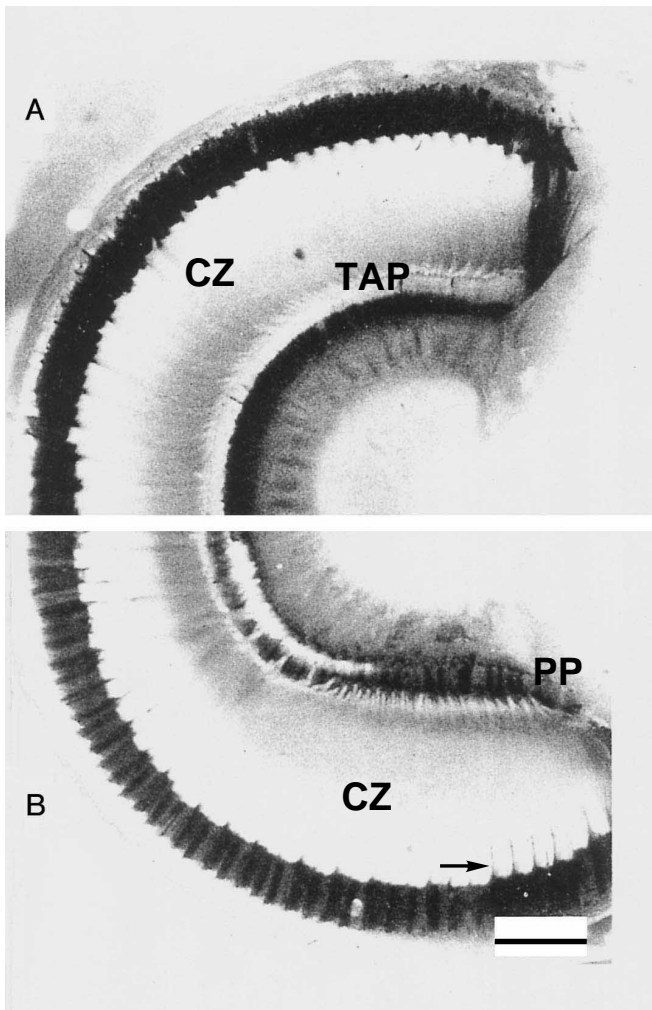
eye more rapidly into the light adapted position than it can the distal pigment. According to Bryceson (1986), the reverse holds true for dark adaptation. That the daily changes in morphology do not depend on the geographic latitude was shown in studies by Rosenberg and Langer (2001) with four species of *Ocypode*.

Much work (e.g. DeBruin and Crisp, 1957; Bryceson and McIntyre, 1983; Shelton *et al.*, 1986) has been devoted to elucidate circadian effects on the responsiveness of distal, proximal, and reflecting pigments (Fig. 13), and considerable excitement was generated in the 70s and 80s after the discovery was made that photoreceptor turnover processes are diurnally modulated (Nässel and Waterman, 1979; Stowe, 1980; Toh and Waterman, 1982). Numerous intracellular changes, associated with rhabdom degradation (Hafner *et al.*, 1982b) and up to 20 fold differences in rhabdom volume between day and night conditions were recorded in some species (Nässel and Waterman, 1979). It is possible that the circadian changes in the detectability of the microvillar actin core-filaments, reported by Hevers and Stieve (1995) for the crayfish *Orconectes limosus*, are related to the recent finding that in the crab *Hemigrapsus sanguineus* vesicles containing opsin are increasing in number in the retinula cell bodies towards dusk (Matsushita *et al.,* 1999). The same vesicles are then thought to be incorporated into the rhabdom, thus caus-
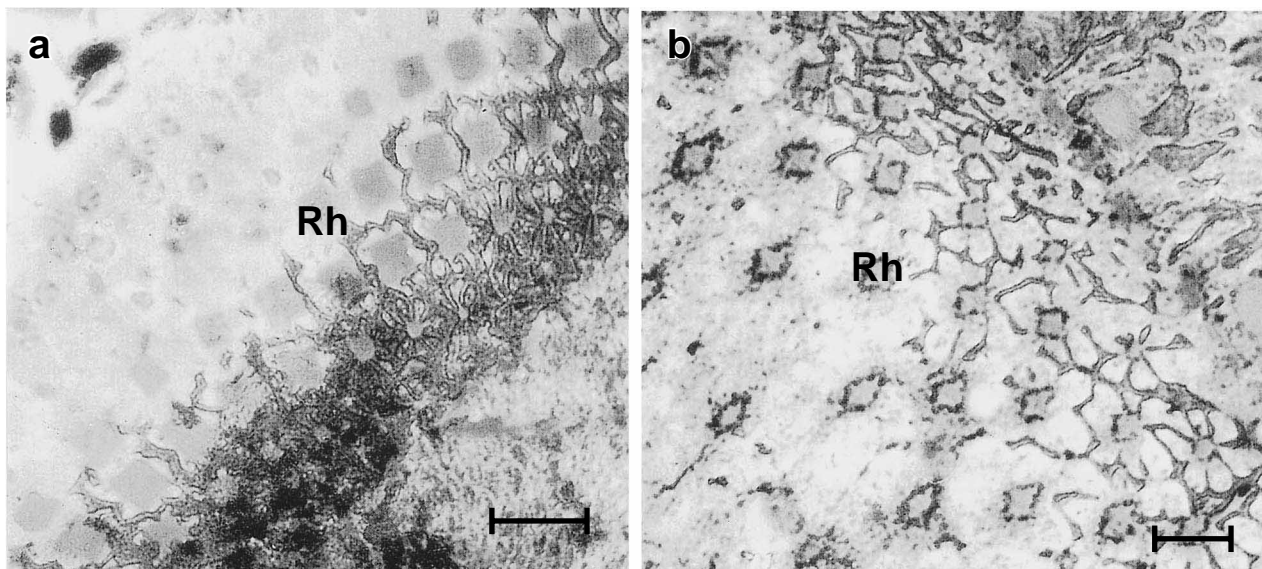


**Fig. 11.**  Transverse section of the eye of the shrimp *Macrobrachium heterochirus*, fixed instantaneously (a) at night, showing rhabdom enlargement (Rh) and (b) during the day, showing diminution of rhabdom. Scale=50 μm.
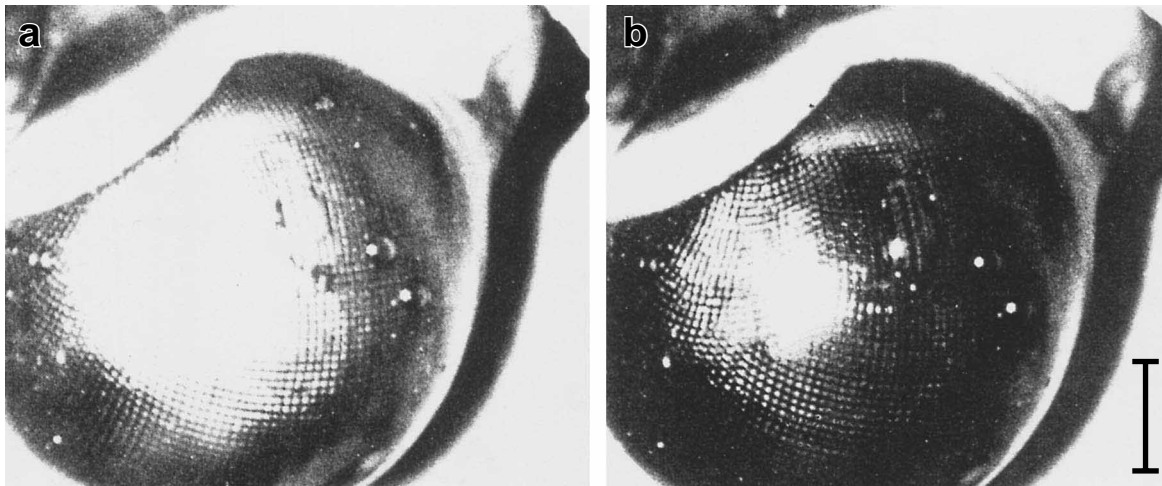
**Fig. 12.** Eyeglow of the eye of a dark adapted rock lobster (a) immediately and (b) 8 minutes after the first photographic flash of light. Scale=1.5 mm.
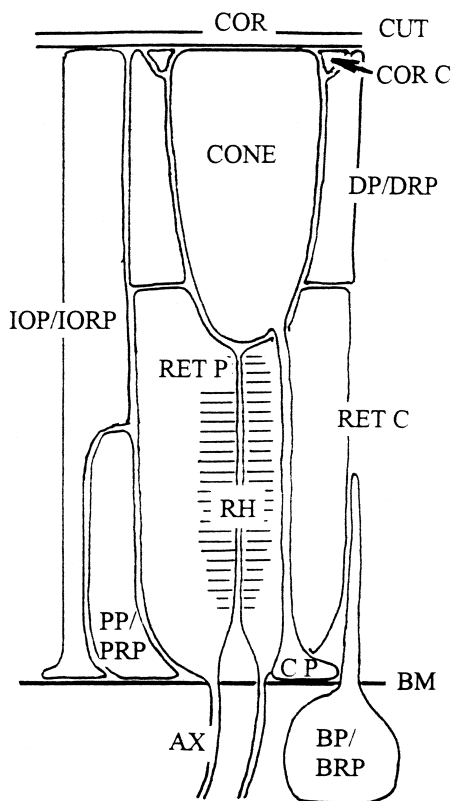


**Fig. 13.** Ommatidial pigment shield (after Hallberg and Elofsson 1989), COR=cornea, CUT=cuticle, COR C=corneagenous cells, DP/DRP=distal screening pigment/distal reflecting pigment cells, IOP/IORP=interommatidial screening pigment/interommatidial reflecting pigment cells, RET C=retinula cell, RET P=retinula cell pigment, RH=rhabdom, PP/PRP=proximal screening pigment/proximal reflecting pigment, CP=cone cell process, BM=basement membrane, BP/BRP=basal screening pigment/basal reflecting pigment, AX=axon.

ing its well-documented nocturnal enlargement (Arikawa *et al.*, 1987). However, membrane recycling and adaptational phenomena are two separate issues and despite progress, some fundamental questions remain unanswered. How, for example, do different species cope, on the one hand, with the need for an immediate readiness to respond to changes in ambient light levels and, on the other, with the requirement to prepare the eye for the predictable and recurring cyclic luminosity oscillations between day and night? There is evidence that proximal retinal screening pigments, at least in crayfish, operate independently from distal screening pigments and that the latter obey a biphasic movement pattern (Frixione and Perez-Olvera, 1991).

Humoral control has been implicated in some screening pigment displacements, especially those affecting the distal pigments (Kulkarni and Fingerman, 1987; Nordtug and Krekling, 1989) and ERG-amplitudes in the crayfish *Orconectes* were shown to rise and fall in response to certain neuropeptides: for example RPCH (=red pigment-concentrating hormone) increased, PDH (=pigment dispersing hormone) decreased ERG-amplitudes (Gaus and Stieve, 1992). A host of chemicals, some like colchicine affecting microtubules (e.g., Schraermeyer, 1992), others like oxygen and $CO_2$ being involved in respiration and metabolism (Henkes 1952; Fanjul-Moles *et al.*, 1998) or, like $Ca^{2+}$, $Na^+$, $K^+$, etc. (Frixione and Arechiga, 1981), being part of the excitation cascade and the generation of the bioelectrical response, are known to interfere with adaptational processes. Ambient temperature (Meyer-Rochow and Tiang, 1979, 1982; King and Cronin, 1994) and pH (Delpiano *et al.*, 1992; Coles et al. 1996) also apparently have a role to play, but an efferent control system, passing signals from brain to eye as in *Limulus* (Kier and Chamberlain, 1990; Chamberlain, 1998) has never been convincingly demonstrated to occur in the crustacea. This, despite the fact that Nagano (1986) was able to show that serotonin, now known to be present in the crustacean brain (Sandemann *et al.*, 1995) and in fibres of the vicinity of photoreceptor axons (Arechiga *et al.*, 1990), affected the circadian changes in pseudopupil size, presumably via its action on the sinus gland.

Moreno-Saenz *et al.* (1987), furthermore, demonstrated

an effect of serotonin, which is the precursor of melatonin, on the size of the crayfish ERG and Meyer-Rochow (unpublished), through radioimmunological surveys, explored melatonin concentrations of severed eyes in dark and light adapted *Astacus* crayfish and the isopod *Saduria entomon*. In some preliminary tests, melatonin levels in the heads of immature, juvenile isopods were elevated when compared with those of adult, light- adapted day animals (Meyer-Rochow, unpublished), and occasionally dark- and light-adapted mature individuals also possessed different melatonin concentrations. Yet, in fully-grown crayfish no statistically significant differences in melatonin levels of eyes of dark- and light-adapted animals were ever noticed. On the other hand, towards winter crayfish eye melatonin concentrations, generally, tended to increase and a seasonal effect, therefore, cannot be ruled out. Since Withyachumnarnkul *et al.* (1995) were also unable to detect significant day/night fluctuations in melatonin levels in the optic lobes of the shrimp *Penaeus monodon*, most likely a single melatonin/serotonin-based control system of adaptational events in the crustacean eye does not exist and, just like different eye anatomies have evolved to meet different environmental challenges, different adaptational control mechanisms may have evolved. It is interesting in this context to note that deep-sea species frequently do not display any obvious photomechanical responses to light whatsoever (e.g. *Gennadas* sp.: Nilsson, 1990) and apparently lack membrane cycling (Chamberlain, 1998).

Turning our attention now back to those species that do display photomechanical adjustments, what do the structural changes really mean in terms of function? Behavioural observations on animals under different photic conditions have given us some answers (DeBruin and Crisp, 1957), as have biochemical (Barnes and Goldsmith, 1977; Kong and Goldsmith, 1977) and electrophysiological studies (Arechiga *et al.*, 1973; Walcott, 1974; Meyer-Rochow and Tiang, 1984; Bryceson and McIntyre, 1983; Bryceson, 1986; Lindström *et al.*, 1988). There is no doubt that fully dark adapted animals possess eyes of greater absolute sensitivity to light than specimens with light-adapted eyes, i.e. animals kept in the light and/or studied during the day (Fig. 4). There is also no question that in most cases in which photomechanical changes occur, acuity (=degree of resolution) improves at the expense of sensitivity as the eye becomes light adapted. This is reflected in a narrower acceptance angle during the day and/or upon light adaptation (Bryceson and McIntyre, 1983). Juvenile individuals with eyes differing from those of the adults in structure and function frequently also display movement patterns and behaviours that are different (Meyer-Rochow, 1975; Hines *et al.*, 1995). Likewise, individuals in which significant changes in eye organization accompany the daily light cycle, display very different behaviours at night and during the hours of daylight. It was noticed that rock lobsters with imbalanced visual inputs due to unilateral light adaptation or damage to the eye acquired a lop-sided stance (Meyer-Rochow and Tiang, 1984) and that bilaterally-blinded individuals instead of remaining concealed during the day, tended to expose themselves far more frequently than normal individuals (Meyer-Rochow, 1988). Electrophysiologically a correlation between ERG and locomotor activity was shown by Fuentes-Pardo and Inclan-Rubio (1981) for the crayfish. However, a consensus on whether the adaptational state in one eye of a crustacean influences that of the other (Barrera-Mera and Berdeja-Garcia, 1979) or whether the two eyes operate independently of each other (Meyer-Rochow, 1982) may not be possible, as more than one control system could exist.

All kinds of known superposition eyes are generally interpreted as an attempt by Nature to come up with a compromise between the demands for optimal sensitivity and optimal acuity. There are, however, apposition eyes that possess identical sensitivities to eyes that operate on the superposition principle, but the latter do outperform the former by a factor of three with regard to resolution (Land and Nilsson, 1990). Theoretically, in addition to the various possible optical improvements of vision under dim conditions, crustacea that make large vertical migrations could improve photon capture by widening the spectral sensitivity window as they get closer to the surface and by 'narrowing' it to wavelengths that are maximally transmitted to greater depths as they swim downward. Shifts in spectral sensitivity as a consequence of the migrations of screening pigment granules in the day- and night-eye have been reported from the isopod *Ligia exotica* by Hariyama *et al.* (1986) as well as the crayfish *Procambarus* (Fanjul-Moles and Fuentes-Pardo, 1988) and may be more common than is presently realized.

Additional and apparently much greater gains could be achieved by neural means: neighbouring visual channels could be summed (=spatial summation) or be allowed increased periods (=temporal summation) over which they could count "a sample of photons" (Warrant, 1999). But while visual processing at higher level has been studied relatively well in some insects (Strausfeld, 1989), crustacean compound eye research despite some excellent studies in relation to polarization sensitivity by, to name but a few, Legget (1976), Glantz and Bartels (1984), and Wang-Bennett and Glantz (1987), has lagged somewhat behind in this respect. Circadian anatomical changes affecting lamina cells have not been described yet from any crustacean eye, but are known to occur in, for example, the fly (Pyza and Meinertzhagen, 1995). Cyclic variations in ERG amplitude of several crustacean eyes have, however, been well documented (e.g., Arechiga *et al.*, 1973; Barrera-Mera and Abaster, 1978; Meyer-Rochow and Tiang, 1984) and now lead us to examine the events that occur right at the onset of photoreception and culminate in a signal being sent from the receptor cell to the brain.

## THE PHOTOTRANSDUCTION CASCADE

The chain of events starts with the photopigment molecules (they are visible on freeze-fracture electron micrographs as intramembraneous ca. 10 nm particles that most likely represent aggregates of 4 molecules: Eguchi *et al.*, 1989) in the microvilli of the crustacean rhabdom (Eguchi and Waterman,
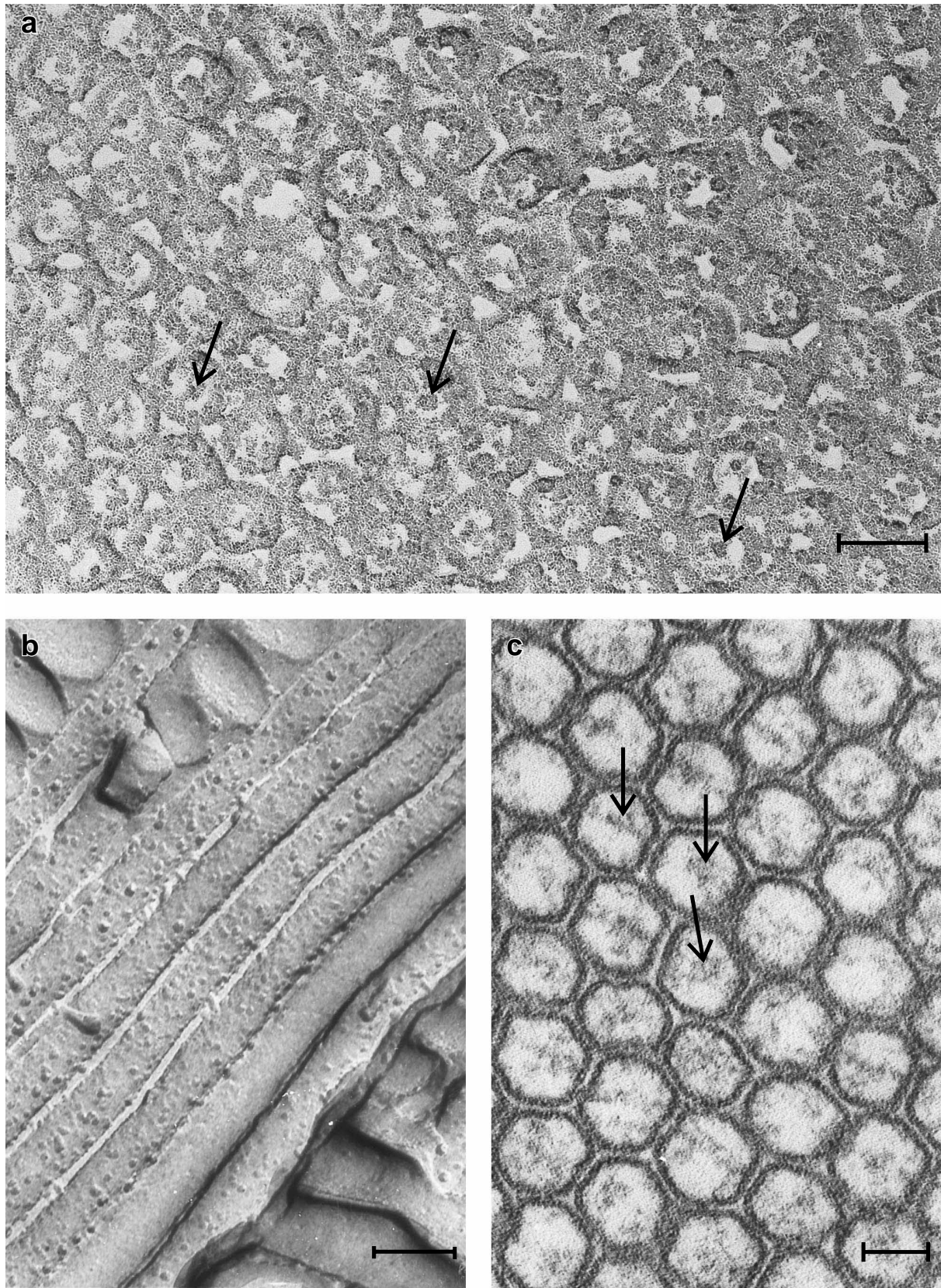
**Fig. 14.** (a): Deep-etched crayfish rhabdom, showing microvilli in transverse section and core filaments (arrows). Scale=0.1 μm. (Courtesy of E.Eguchi). (b): Freeze-fractured crayfish rhabdom, showing photopigment molecules in microvillar membranes. Scale=0.1 μm (after Meyer-Rochow and Eguchi 1984). (c): High power electron micrograph of transversely sectioned microvilli from the dark adapted crayfish eye, showing core filament (arrows). Scale=50 nm.

1976; Meyer-Rochow and Eguchi, 1984). The microvilli are hollow, fingerlike tubes of usually 60-80 nm in diameter and variable length that are oriented perpendicular to the light path. Their membranes, apart from the photopigment, contain a variety of phospholipids as well as very fine fibrilar links to the core-filament (identified as actin: Hafner *et al.*, 1992; Hevers and Stieve 1995) in the centre of each microvillus (Fig. 14).

The spaces between the microvilli, which are connected to one another by glycoproteins, leave little room for extracellular lacunae. Retinal (vitamin A1) is the major chromophore in the crustacean eye, but 3-dehydroretinal (porphyropsin) can also be present (Suzuki and Eguchi, 1987; Zeiger and Goldsmith, 1993). Through the action of a single photon the chromophore changes from the 11-*cis* to the all-*trans* molecular configuration. The resulting conformational change of the apoprotein (the opsin) to the photoactivated state can cause G-proteins to initiate the downstream phototransduction cascade. Perhaps better studied in the insect eye (Suzuki, 1999), but probably not very different in the crustacean photoreceptor, the ensuing process sees photoactivated metarhodopsin activate phospholipase-C to hydrolyze phosphatidylinositol 1,4-biphosphate, producing phosphatidylinositol triphosphate (IP3) and diacylglycerol (DG). $Ca^{2+}$-ions are then liberated (most likely from intracellular stores) by IP3, consequently exerting their influence on calcium-release-activated channel proteins. A comprehensive review on the role of calcium in the phototransduction cascade of *Limulus* has recently been published by Dorlöchter and Stieve (1997).

Since G-proteins, known to become released in the crayfish retina by photo-regeneration (Terakita *et al.*, 1993), appear to play a pivotal role in the phototransduction cascade

they have also come under considerable scrutiny. One G-protein, known as Gq(alpha), was localized in the rhabdoms of dark-adapted crayfish as the membrane-bound form, but as the soluble form in the cytoplasm following light adaptation. What this means is that the amount of Gq that can be activated by rhodopsin is light-modulated and, at least *in vitro*, regulated by the fatty-acid modification of Gq(alpha) (Terakita *et al.*, 1996). Clearly this has ramifications for the integrity of the microvillus since the often reported light-dependent reduction of rhabdom diameters in the crustacean eye is probably affected by light-activated phospholipases (Trowell *et al.*, 1991). When the phospholipase inhibitor manoalide was applied to the retina of the crab *Leptograpsus variegatus*, the rhabdoms failed to exhibit the light-dependent reductions in diameter (Blest and Stowe, 1997). G-proteins, therefore, not only play a role in the phototransduction cascade, but also influence amount and structural integrity of the visual membranes.

Very recently the concept that cation-selective channels in the compound eye might be regulated by polyunsaturated fatty acids (PUFA) has been introduced (Chyb *et al.*, 1999; Kiselyov and Muallem, 1999) and this concept may be applicable to the crayfish retina. When, as shown for example in Fig. 15, crayfish eyes are exposed to bright light, they react with marked decreases in phosphatidylcholine and PUFA-levels, but, when exposed in the presence of phospholipase-A2 inhibitors, like DMDA or manoalide, no such decreases occur (Kashiwagi *et al.*, 1999). PUFA-mediated effects of light other than changes in membrane fluidity alone (e.g., intracellular Ca-concentration) may, therefore, be involved in photic damage (Meyer-Rochow, 2000).
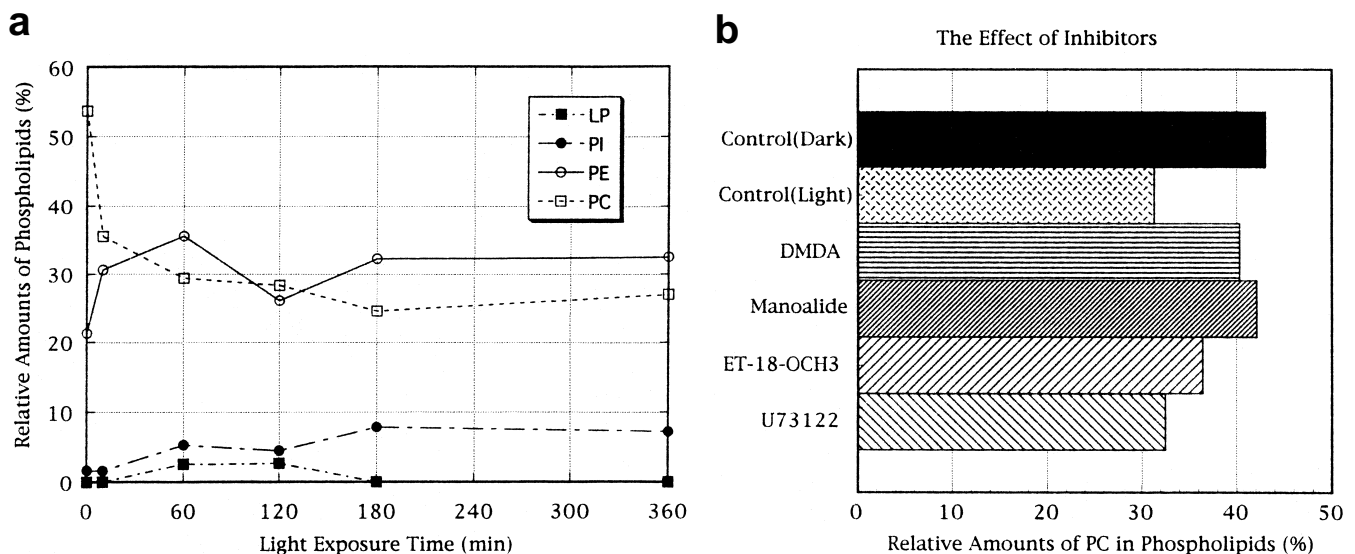


**Fig. 15.** (a): Changes in the retinal lipids of the eye of the crayfish *Procambarus clarkii* following exposure to light of approx. 5000 lux. Phosphatidylcholine amounts decrease sharply (after Kashiwagi *et al.* 1997). (b): Effect of phospholipase inhibators on phosphatidylcholine changes in the retina of the crayfish *Procambarus clarkii*, following exposure to light of approx. 5000 lux. Manoalide and DMDA prevent the light-induced decrease of PC in the light (after Kashiwagi *et al.*, 2000).

## INTERMITTANT ILLUMINATION AND FLICKER FUSION FREQUENCY

The overwhelming majority of all crustacean species live in the water. Those not concealed and close to the surface are almost constantly exposed to wave-induced flicker frequencies, which are most intense and far-reaching when the sun is at its zenith during midday and least obvious at night during new moon. In clear tropical seas at least down to 5 m from the surface the power spectrum of flickers from downwelling light was dominated (i.e., >50%) by frequencies below 15 Hz, but even at 5 m some power was present above 50 Hz (McFarland and Loew, 1983). The boundary frequencies for 50% of the total power spectrum amounted to 14.5 Hz, 6 Hz, and 4 Hz for depths of 0.25 m, 2.5 m, and 4.5 m, respectively (McFarland and Loew, 1983). As waves can also produce fluctuating patterns of spatial frequencies underwater, it has been suggested by the same authors that body markings like reticulations and gratings, common in surface water fishes, have been an evolutionary consequence of the sunlight-wave interactions. It would be interesting to examine to what extent that argument is applicable to crustaceans and crustacean vision.

It would certainly seem plausible that eyes of crustaceans subjected to these naturally-generated underwater flickers should possess temporal characteristics that match the flicker rates created by the surface waves. Given the fact that crustaceans are not known to produce flickering light signals themselves by blinking or to be able to rapidly switch on and off their photoreceptor cells (as had once been suggested for *Limulus*: Fuortes and Hodgkin, 1964), the crustacean eye has to cope with the rapid successions of light and dark inherent to flickers in other ways. With regard to the structural organization of the eye, flickering lights usually lead to light adaptation and, if excessive, to photoreceptor damage (see below).

As a measure of the eye's physiological performance in the presence of flickers, i.e. its temporal resolution, the so-called 'flicker fusion frequency' (defined as the critical frequency at which discrete individual responses to a flickering stimulus become fused to a continuous response), has proved useful. The signals to generate flickers in connection with electrophysiological recordings can be of two kinds: (a) the periods between low and bright phases of the oscillations are of equal duration and, by necessity, become shorter as the frequency of the flickers increases or (b) the flash of light used as the stimulus is very brief, e.g. 1 ms, and remains of the same duration as the number of flashes per second delivered to the eye is increased. Most commonly the first kind of stimulation is used. Both depend on the eye's, or better, the visual cell's ability to 'recover' and to reach an excitable state each time again the bright phases of the flickers are followed by a light-trough.

From the small amount of data available (Table 1), the following generalizations seem possible: in comparison with insects (and especially flying species: Nakagawa and Eguchi, 1994), crustaceans with the exception of some semi-terres-

**Table 1.** Flicker fusion frequencies (FFFs) of the eyes of some crustacean species

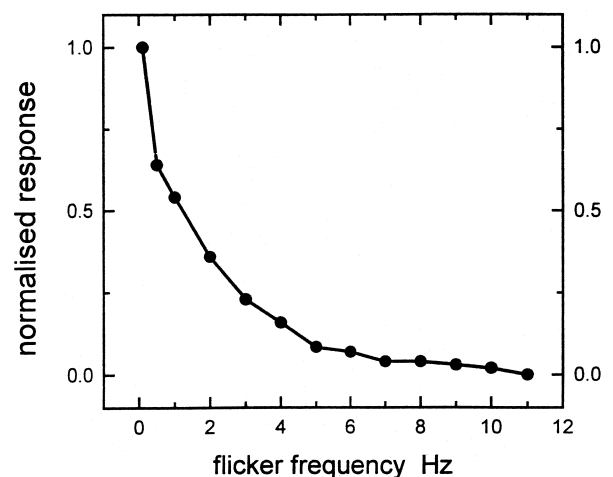| Animal | Hz | Reference |
|---|---|---|
| *Jasus edwardsii* | 50–60 | Meyer-Rochow and Tiang 1984 |
| *Cambarus & Pagurus* | 50–56 | *Waterman 1961* |
| *Nematobrachion flexipes* | 44 | Frank 1999 |
| *Oplophorus gracilirostris* | 31 | *Frank 1999* |
| *Sergia filictum* | 25 | Frank 1999 |
| *Systellaspis debilis* | 20 | Frank 1999 |
| *Ligia occidentalis* | 120 | Ruck and Jahn 1954 |
| *Glyptonotus antarcticus* | 10–12 | Meyer-Rochow and Laughlin 1997 |



**Fig. 16.** Flicker fusion frequency to flashes of white light in the Antarctic isopod *Glyptonotus antarcticus* (after Meyer-Rochow and Laughlin 1997).

trial species like *Ligia*, which does not avoid bright sunshine, possess much lower FFFs (Table 1). As with insects, however, FFF values increase as the intensity of the flashes used in the flickering lights increases. Whether the exceptionally low FFF of the Antarctic isopod *Glyptonotus antarcticus* (Fig. 16) has something to do with the subzero temperatures of the water in which the animal lives (Meyer-Rochow and Laughlin, 1997) or is a reflection of the fact that flickering lights are of no importance in that animal's habitat, remains an open question for the time being.

## POLARIZATION SENSITIVITY

Many crustaceans possess eyes with photoreceptor cells that respond to linearly polarized light. Depending on whether the e-vector of the polarized light excites the photopigment maximally or minimally, up to an at least tenfold sensitivity difference may be recorded intracellularly from a retinula cell under these two situations (Shaw, 1969). A crustacean, which turns its body or rotates its eyes in a polarized photic environment must therefore experience changes in ambient luminosity that cannot be too unlike fluctuations in absolute or spectral light intensities. Indeed, selective adaptations of those retinula cells maximally sensitive to a given e-vector should result

in pigment distributions and other signs typical of receptor cells exposed to bright light.

While Waterman's (1981) review of polarization sensitivity is still timely and relevant especially with regard to the crustacean compound eye, considerable progress has been made in elucidating the physical details, the degree and direction of linear polarization, the "transmissivity and the shape of the refraction-polarization oval" of underwater polarization patterns (Horvath and Varju, 1995). To what extent the bright eye-glow seen in many dark adapted crustacean eyes is polarized remains to be measured. The molecular basis of crustacean polarization sensitivity has been revisited by Eguchi (1999), who reiterates, and provides further evidence, for the view that the orthogonal orientation of microvilli in separate retinula cells is the anatomical manifestation of e-vector discrimination. In other words, twisted crustacean rhabdoms (Meyer-Rochow, 1978) and retinula cells with multidirectional microvilli (e.g., retinula cell R8 in *Libinia* and other decapods: Eguchi and Waterman, 1967) cannot adequately convey information on the e-vector to the optic ganglia, whereas layered (or 'banded') rhabdoms, in which perpendicularly oriented plates of microvilli belonging to different cell groups apparently terminate as two separate channels in the lamina (Nässel and Waterman, 1977), can. Thus, ultrastructural analyses of crustacean rhabdoms may be used to make predictions on whether or not a given crustacean eye has the potential of being polarization sensitive. On the basis of retinal symmetries and microvillar directions, the compound eyes of mantis shrimps (Stomatopoda) ought to possess the most complicated polarization vision of any crustacean (Marshall *et al.*, 1991).

In the crayfish eye, neurons of the lamina exhibit polarization sensitivities that are not directionally sensitive to e-vector rotations and are generally comparable to those of the receptor cells (Glantz and Bartels, 1984). However, medullary neurons of both the crab (Leggett, 1976) and the crayfish eye (Glantz, 1996, 2001) possess neurons that are highly sensitive to a rotating polarizer. It has been postulated by Glantz (1996) that this may be of importance to the animal in its natural environment as it has to respond to changing e-vectors due to rotations of the head, and that the tangential neurons responsible for the response may exploit the local variations in the e-vector to enhance motion detection at low contrasts. Other functions suggested by a variety of investigators over the years for underwater polarization sensitivity include contrast enhancement, maintenance of body position, navigational aid in (vertical) migration and orientation (Goddard and Forward, 1991). In the cephalopod *Sepia officinalis*, moreover, polarization vision plays a role in intraspecific communication (Shashar *et al.*, 1996), but for crustaceans a similar role has yet to be demonstrated.

## PHOTORECEPTOR DAMAGE

Obviously, crustacean photoreceptors can be damaged in a variety of ways. There is mechanical damage, perhaps due to (a) physical (wave action, water currents, collisions with inanimate objects, etc.) or (b) biological effects (attacks by predators, disease, incomplete moulting, etc.) and there is damage that is due to radiation (ionic, photic, thermal). This section will not deal with damage of a mechanical origin, but will focus instead on the other causes of damage. Crustaceans with one eye or both eyes painted or blinded (Fraenkel and Gunn, 1960) provide us with information on the role(s) the eyes play in the intact, undamaged animal. It has become clear that visually impaired crustaceans frequently display abnormal reactions (Meyer-Rochow and Tiang, 1984; Attramadal *et al.*, 1985; Meyer-Rochow, 1988).

Light-induced photoreceptor damage (Fig. 17) in crustaceans results in suppressed visual sensitivity and has recently been reviewed (Meyer-Rochow, 1994). Unlike regular light-adaptation, which tends to result in a parallel shift of the V/log I curve so that brighter lights are required to produce the same receptor potential of the eye or receptor cell, damage manifests itself in a flattening of the V/log I curve, i.e., in a reduction of the slope of the V/log I relationship (Fig. 18). Like the less well-studied damage caused by prolonged darkness (reviewed by Eguchi, 1986), light-induced damage is undoubtedly multifactorial. The effects of ionizing radiation and X-rays, known to damage the vertebrate photoreceptor (e.g., Brunst, 1967), have not yet been examined in the crustacean eye. What we do know about light-induced damage in the crustacean eye deals almost entirely with the receptor cells and the rhabdom; much less is known about the effects of bright light on the dioptric structures cornea and crystalline cone (Meyer-Rochow, 1981; Meyer-Rochow and Tiang, 1984: Gaten, 1988). A total lack of information exists in relation to the question of whether and how the damage seen in the retinula cells affects the second-order neurons.

Obviously, what constitutes light-induced damage has to be distinguishable from normal light-induced adaptations as well as membrane shedding and re-cycling, and that is not always easy (cf. Figs. 7 and 17). Another good example comes from the eye of the amphipod *Pontoporeia affinis* (Rosenberg and Langer, 1995). Taking, for instance microvillar diameter and ultrastructure, there are many reports of crustacean eyes that exhibit wider microvilli (Meyer-Rochow, 1999a) and fragmentation, or even loss, of the core filament during the day (Hevers and Stieve, 1995). An increase in free cellular $Ca^{2+}$ has been linked to this lability of core filament architecture (Blest *et al.*, 1982), but greater calcium concentrations are an inevitable consequence of photoreception in arthropods, generally (Dorlöchter and Stieve, 1997). Whether or not the retinula cell runs into problems and begins to destroy the photoreceptive membranes and, thereafter, itself (in that order: Meyer-Rochow and Järvilehto, 1997), depends on a variety of factors.

Clearly, photopigment concentration in the visual membranes and amount of opsin precursors in the cytoplasm are important, but so are G-proteins and lipid composition of the membranes. In fact, since it could be shown that, in Antarctica, crustacean eyes, containing predominantly long-chain polyunsaturated fatty acids (Meyer-Rochow and Pyle, 1980),
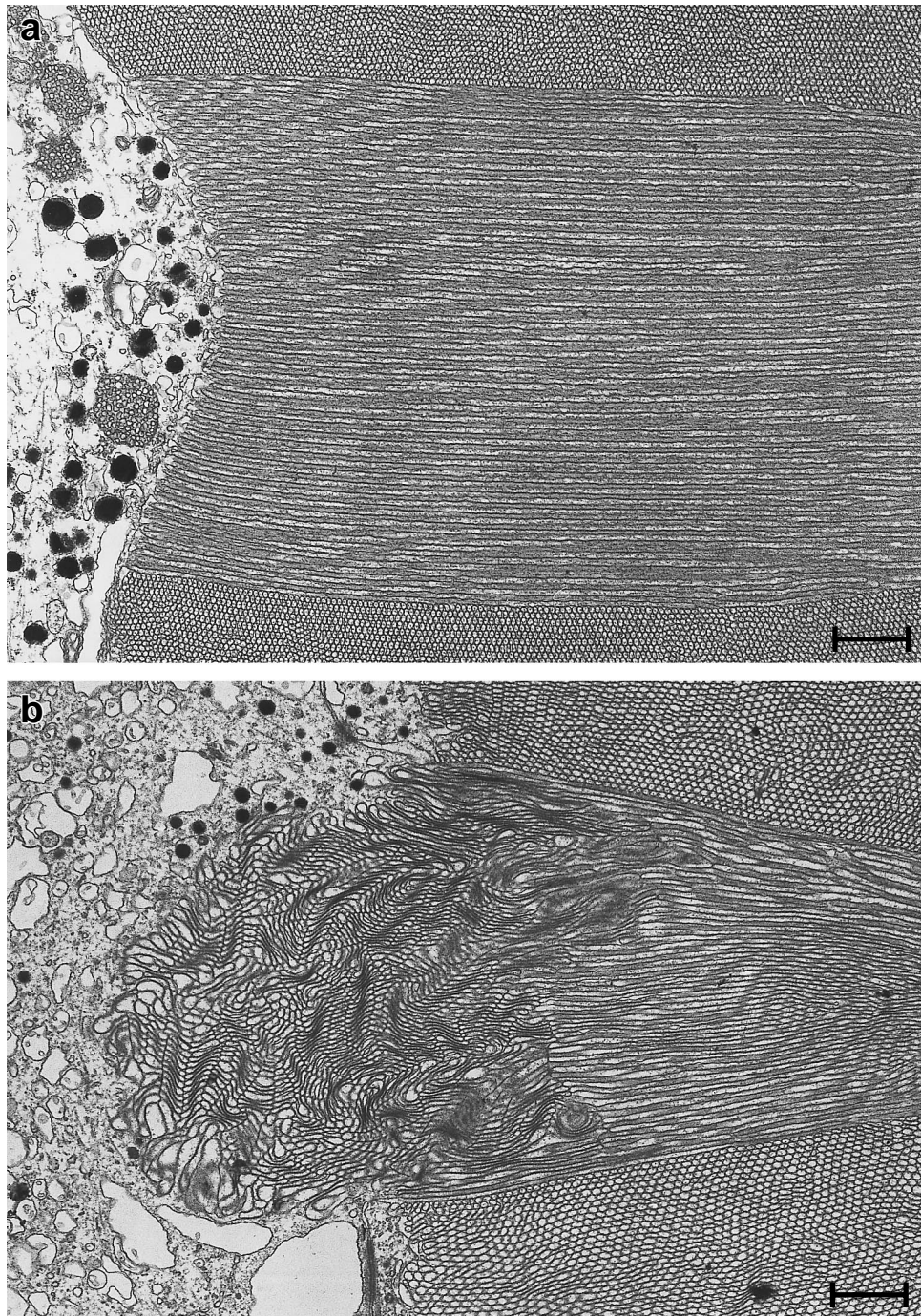
**Fig. 17.** Longitudinal section through normal (undamaged) rhabdom of the crayfish eye (a) and rhabdom that displays obvious light-induced membrane damage (b). Scale=1 μm (courtesy of E. Eguchi).

were easily damageable by elevated temperature (Meyer-Rochow and Tiang, 1979; Meyer-Rochow, 1982), research was initiated to investigate the role lipids played in membrane maintenance. Differences in retinal lipid compositions were found in crayfish that came from high-latitude and medium-latitude environments (Meyer-Rochow et al., 1999a), providing further evidence for the view that ambient light levels and temperature influence membrane biochemistry. Elevated temperature alone can adversely affect membrane ultrastruc-

ture (Meyer-Rochow and Eguchi, 1984), but the most severe membrane disintegrations (Fig. 19) occur as a result of a combined bright light/elevated temperature assault (Lindström et al., 1988; Kashiwagi et al., 1997).

Thermal and photic stress cause an increase in fatty acid 18:0 and decreases in acids 16:1, 20:1, and 22:6 (Kashiwagi et al., 1997), but that alone is insufficient to cause visible membrane damage. The latter is likely to occur when dormant lipoxygenases, present in all animal cells, get activated (Hölzel
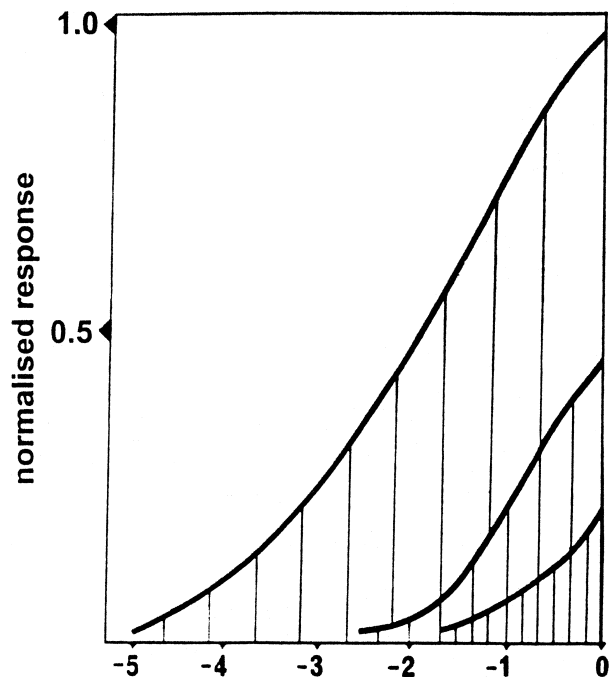
**Fig. 18.** Diagram showing differences between response/stimulus intensity curves of eyes from rock lobsters at night (curve on the left), during the day (curve in the centre), and following an exposure of 1 hr to sunlight (curve on the right).

and Spiteller, 1995). They oxidize unsaturated membrane fatty acids, a process that does not as tacitly assumed involve only arachidonic acid, but also others (Hölzel and Spiteller, 1995). The oxidized fatty acids are then decomposed to chemically highly reactive species that further interfere with cellular organelles and their functions, leading to additional damage. The discovery of peroxidase activity (Fig. 20), e.g. in secondary lysosomes that degrade photosensory membrane (Schraermeyer and Stieve, 1991), fits this scenario, but a reported midday rhabdom enlargement paralleled by a decrease in multivesicular bodies (Piekos, 1989) seems difficult to reconcile with it and suggests that multivesicular body production and rhabdom diminution "are not causally related in the manner predicted by the lysosome-related-body hypothesis of rhabdom cycling". However, membrane damage due to excessive light is likely to result in a disruption of normal membrane cycling and, therefore, may follow a different path.

Bright illumination of the retina can lead to the production of singlet oxygen and this can lead to membrane damage involving oxidation of either proteins or lipids or both, ultimately increasing fluidity of the membrane (Delmelle, 1977). Increases in the amount of peroxidated retinal fatty acids following an exposure to light in crayfish kept in the dark prior to irradiation were, indeed, recorded, but not until at least 2 hours after the exposure (Kashiwagi et al., 1997). This is consistent with the electron microscopical findings and means that sensitivity loss (very rapid) and membrane damage (delayed) are linked, but separate phenomena (Lindström et al., 1988). The key question is "What activates the dormant lipoxygenases?". Hölzel
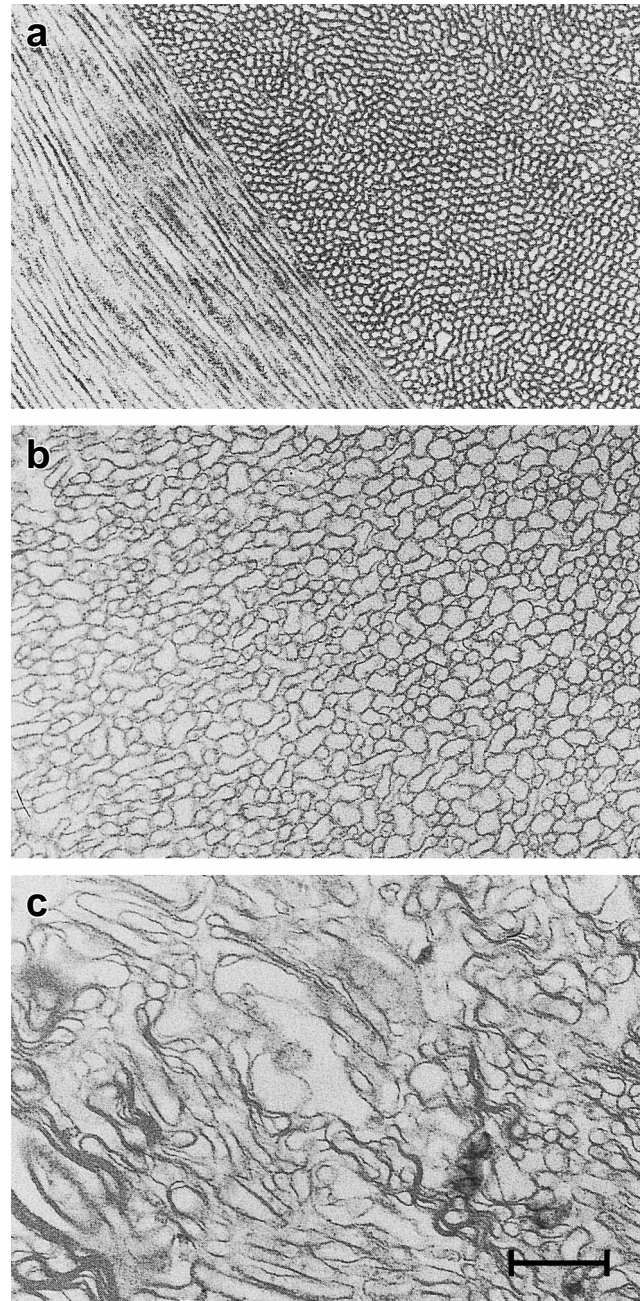


**Fig. 19.** (after Lindström et al. 1988). (a): Normal microvilli of the rhabdom of the opossum shrimp *Mysis relicta*, kept at 4°C. (b): Swollen microvilli of an individual of *M. relicta*, exposed to white light of 4000 lux for one hr, but subsequently kept in darkness for 5 days at 4°C. (c): Microvilli of *M. relicta* individual, kept in darkness and water at 14°C for 5 days, following an exposure to white light of 4000 lux for one hour. The damage exceeds that of (b). Scale (a,b,c)=0.5 μm.

and Spiteller (1995) list a variety of diseases in humans that qualify, diseases that have in common a tendency to weaken or injure cell membranes. Heat, in particular, is singled out as a potent liberator of the dormant lipoxygenases. Could, therefore, screening pigment granules, closely approaching the rhabdom in order to protect it against excessive radiation, aggravate the situation by absorbing light and slowly dissipat-
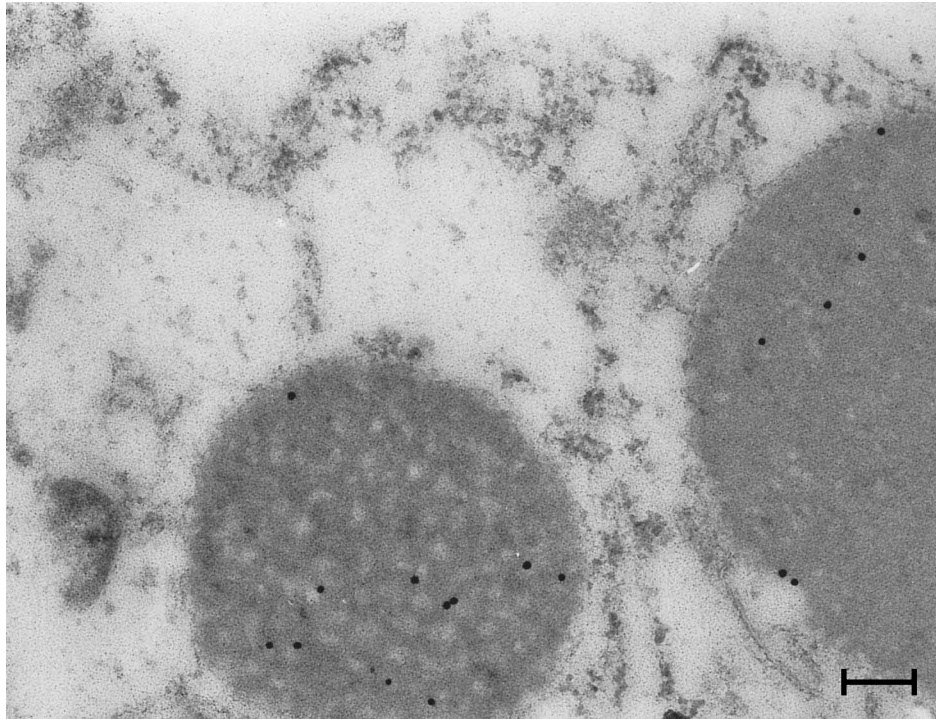
**Fig. 20.** Immuno-gold-labelled active peroxisomes in the retinula cells of the eye of the crab *Ucides* sp. Scale=0.17 µm (courtesy Silvana Allodi and Ahmed Yagi).



**Fig. 21.** (after Meyer-Rochow *et al.*, 1999 b) Proximal rhabdomeres of crayfish (a) exposed for 3 days to 5000 lux bright, white flashes of light, flickering at a rate of 3 Hz, exhibit considerbable damage, but the same treatment has virtually no effect on the microvilli of the distal rhabdomere R8 (b). Scale (a,b)=1 µm.

ing the gained energy as heat?

This is supported by the recent discovery by Meyer-Rochow *et al.* (1999b) that, in the crayfish retina, the eighth, distally placed retinula cell R8 (which has the rhabdomere most at risk due to it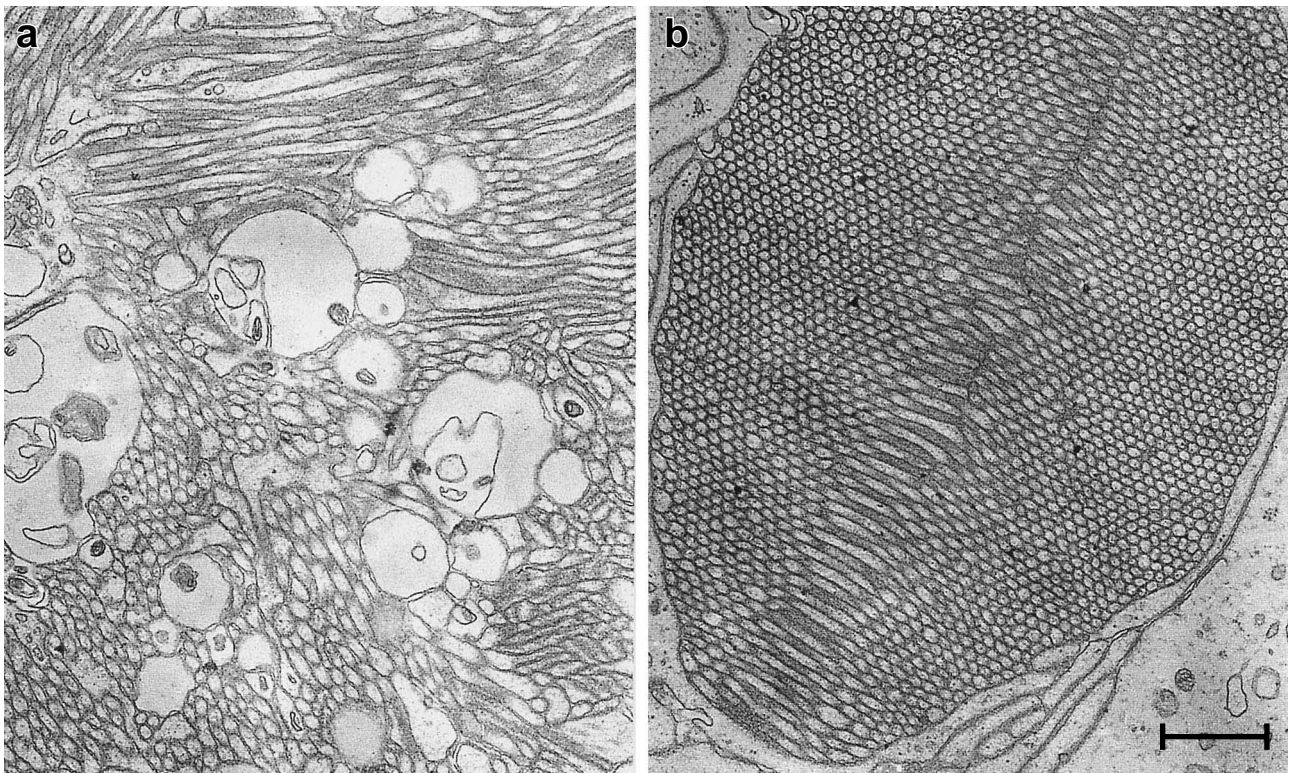s position) escapes damage and remains totally normal, while proximal rhabdomeres become almost unrecognizable due to the light-induced degradation (Fig. 21). Significantly, R8 is also the only retinula cell without screening pigment granules. However, other explanations cannot be ruled out and R8 membranes may be chemically different, contain another visual pigment, or are synthesized in a cell that does not operate on the same metabolic principle as the other retinula cells. Observations by Hafner *et al.* (1982) on white-eyed, pigmentless crayfish that also exhibit more damage in the proximal than in the distal rhabdom point into the same direction. Perhaps the total volume of visual mebrane in R8 is so small that it never gets in danger of receiving excessive amounts of damaging radiation. Membrane damage is a complex problem and in some species may continue in darkness after a brief, but very intense exposure (Shelton *et al.*, 1985), more or less ruling out any prolonged heat effects. Damage is often more pronounced following exposure to shorter wavelengths (Meyer-Rochow and Tiang, 1984; Rapp and Smith, 1992), and can depend on the pre-exposure state of eye-adaptation (Nilsson and Lindström, 1983; Lindström *et al.*, 1988), on population differences regarding tolerance to light (Meyer-Rochow and Lindström, 1998), depth at which the animals were caught (Gaten *et al.*, 1990), dietary history (Tschugunoff, 1913), perhaps season (Suzuki *et al.*, 1985), and time of day at which the exposure is carried out.

In conclusion, we have to admit that we have yet to establish whether or not the various manifestations of light- (and perhaps temperature-) induced damages to receptor cells and dioptric elements have a common origin. Regular adaptational phenomena such as pigment translocations and cell kinetics complicate the picture further and the occurrence of diurnally modulated membrane recycling makes it almost impossible to examine one effect in isolation from the others. Tissue cultures and lines of selected cell types from the crustacean eye could help, but in the absence of such material, the use of specific mutants is one promising avenue, the selection of species lacking, for instance, membrane recycling or dioptric elements like hydrothermal vent shrimps, is another.

### ACKNOWLEDGMENTS

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