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DIURNAL CHANGES IN STRUCTURE AND FUNCTION OF THE COMPOUND EYE OF *LIGIA EXOTICA* (CRUSTACEA, ISOPODA)

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SUMMARY

The ultrastructure of the retinula cells of *Ligia exotica* changes diurnally and in response to light/dark adaptation. At the low phase of electroretinogram (ERG) amplitude (at noon), the arrangement of microvilli is ordered and the rhabdom is of the open type. An irregular arrangement of microvilli appears at the high phase of ERG amplitude (at midnight), when the rhabdom is of the closed type. The pigment granules disperse at midnight and assemble at noon. A centrally positioned, spike-producing eccentric cell is present in each ommatidium.

Spectral response curves based on ERG measurements have two maxima, one to light of 383 nm wavelength, the other at around 520 nm. These two peaks represent the two classes of receptor cells identified by intracellular recordings. The ERG responses to light of 383 nm and 520 nm wavelengths display a diurnal rhythmicity, being high at night and low during the day. However, the responses to green light are more strongly affected than those to ultraviolet light. Consequently, the eye displays a relatively higher ultraviolet-sensitivity during the day, whereas at night sensitivity to green light is increased.

This behaviour, which persists in continuous darkness, suggests that an endogenous mechanism is involved in bringing about the observed diurnal morphological and physiological changes in the compound eye of *Ligia exotica*.

INTRODUCTION

In terms of exploitation of different habitats and food resources, Isopoda represent the most successful group of living crustaceans (Kaestner, 1970). The available

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literature on isopod eyes (recently reviewed by Meyer-Rochow, 1982) suggests that they have varied and complex vision.

The eyes of *Ligia oceanica* have been the subject of a morphological study by Edwards (1969) and those of *L. occidentalis* have been tested electrophysiologically by Ruck & Jahn (1954). The eyes of *Ligia exotica* seemed worth a separate combined structural and functional study for three main reasons. First, *Ligia exotica* displays a very characteristic body colour change, which was studied in detail by Enami (1944). This author found that body pigments expand during the day and contract at night. Second, Tuurala, Lehtinen & Nyholm (1966) and Tuurala & Lehtinen (1967, 1971) have shown in a series of papers that in the eye of the isopod *Oniscus asellus* absence as well as presence of light affects rhabdom and retinula organization and also the position of the screening pigments. Nemanic (1975) extended these studies to *Porcellio scaber*. Third, the question as to whether screening pigments in compound eyes of crustaceans move under the influence of hormones (Fingerman, Nagabushanam & Philpott, 1962; Kleinholz, 1966) or display direct reactivity to light (Aréchiga, 1977; Olivo & Chrismer, 1980) has recently been studied by Frixione, Aréchiga & Tsutsumi (1979) and Frixione & Aréchiga (1981), who investigated the roles of different ions in pigment migration, and Meyer-Rochow & Tiang (1979, 1982) and Meyer-Rochow (1982), who tested the effects of temperature on pigment migration in eyes of Antarctic amphipods and isopods.

Pigment migrations can have a profound effect on such visual parameters as sensitivity and acuity (Aréchiga & Wiersma, 1969; Walcott, 1974) and spectral response (Leggett, 1979; Stowe, 1980) and are sometimes under the influence of a circadian rhythm (see reviews by Ninnemann, 1979; Autrum, 1981). A considerable part of our study has centred on the problem of how constant light or dark conditions affect the diurnal rhythm of structure and function of the eyes of *Ligia exotica*.

MATERIALS AND METHODS

Adult female and male specimens (approx. 4–5 cm) of *Ligia exotica* were obtained from beaches of Arasaki, Chojagasaki (Miura Peninsula, Kanagawa Pref.) and Ushimado (Okayama Pref.).

Morphology

The compound eyes were dissected out in prefixative, consisting of 2% paraformaldehyde, 2% glutaraldehyde in 0·1 mol l^{-1} sodium cacodylate solution (pH 7·2). When dark-adapted eyes had to be studied, they were located in total darkness by touch, removed in total darkness with a razor blade and prefixed in darkness for 2 h at room temperature. Tissues were then rinsed in the buffer solution and postfixed for 2 h with 1% OsO_4 in the same buffer. Fixed tissues were dehydrated through a graded series of ethanol solutions, transferred to propylene oxide and embedded in TAAB embedding resin or Epon 812.

For transmission electron microscopy, sections were cut with a Porter-Blum MT-2B microtome and picked up with formvar-coated 75- or 100-mesh copper grids.

They were double-stained with 1 % uranyl acetate and 0·1 % lead citrate solution for 20 min and 30 min, respectively. Observations were made with a Hitachi-H500 electron microscope or with a JEOL JEM 100B electron microscope.

For scanning electron microscopy, specimens were fixed with 2·5 % glutaraldehyde in the same buffer, dehydrated through a graded series of ethanol solutions, dried with a critical point apparatus (Hitachi HCP-1) and coated with gold (Eico ion coater IB-3). Observations were made with a Hitachi S-310 electron microscope.

Physiology

Preparation of specimens for extracellular (ERG) recordings

When the responses of the intact eye in the intact animal were to be studied, the thorax and the posterior half of the head were fixed with wax (resin : paraffin = 1 : 1).

Animals were placed in a small Petri dish filled with saline. The uropods were kept damp during the course of these experiments. Animals so mounted survived for a week. A tungsten electrode was introduced just below the cornea by a micromanipulator.

Preparation of specimens for intracellular recordings

The whole animal, with the exception of the legs and antennae, was fixed firmly with wax/resin mixture. A small triangular hole, equivalent to 3–5 facets, was made in the dorsal part of the cornea using a fresh chip of a razor blade, in order to facilitate the electrode insertion.

Recording procedure

Responses were measured with a pre-amplifier (Nihon Koden MVZ-8) and a Nihon Koden VC-10 dual-beam oscilloscope with Nihon Koden AVH-10 high-gain amplifier. Permanent records were obtained with a Watanabe pen-recorder (Watanabe Instrument Corp. Type WTR-281). Temperature was maintained at 20–23 °C during the course of the recordings.

Apparatus for delivering stimuli

A Nikon (d.c.) power supply (DSB-501 N/2) was used to run a 500-W xenon arc lamp (Ushio Inc., Type UXL-451-0). Quartz lenses produced a parallel beam of light which passed through a heat absorption filter, and one of a set of 16 narrow-band interference colour filters (Vacuum Optics Corp., Japan IF-S) scanning a range of 330 to 660 nm. With the aid of a quartz neutral density filter (optical wedge), these monochromatic lights were adjusted so that they contained an equal number of photons. At all wavelengths the maximum intensity available at the eye was $9{\cdot}0\times10^{13}$ quanta $cm^{-2}s^{-1}$, a value which corresponds to about the brightness of a dull day. The quartz light guide led the stimulating light into a Faraday cage and to the preparation; stray light was prevented from exciting the eye by enclosing the light beam in felt. The light-emitting end of the light guide was attached to a perimeter

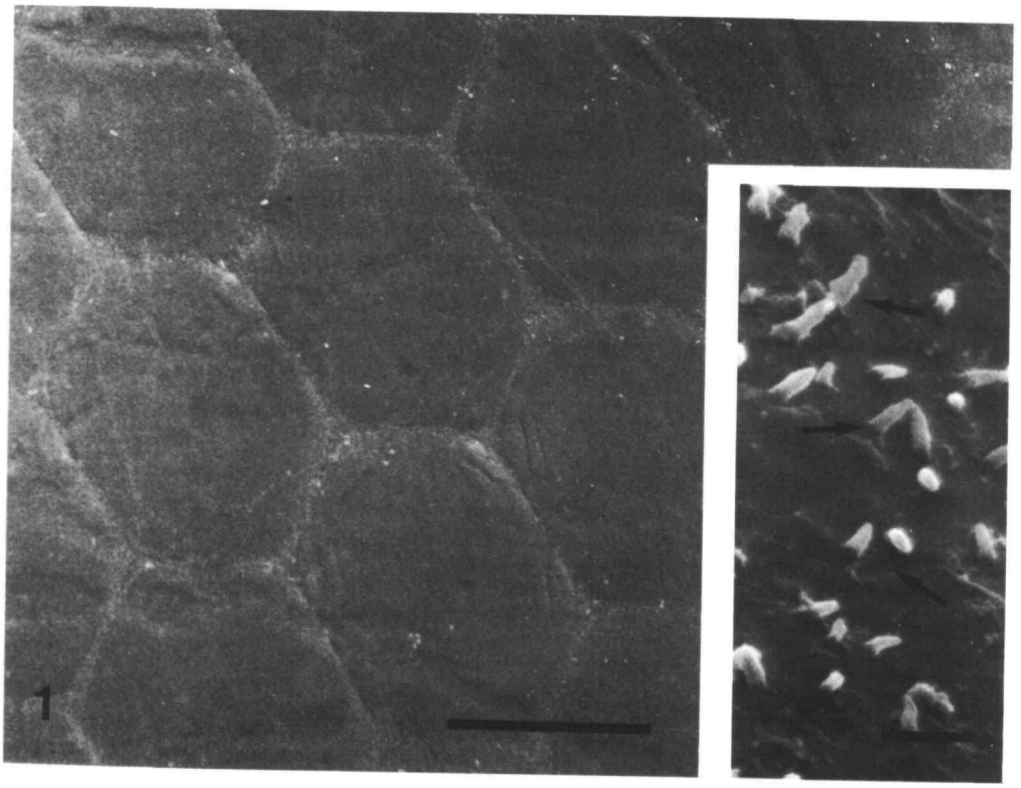


Fig. 1. Scanning electron micrograph of the outer surface of the cornea. The ommatidia form a hexagonal lattice. The corneae possess an array of fine nipples. Scale bar, 50 μm. The inset shows these nipples under higher magnification (arrows). Scale bar, 0·5 μm.

device and held 5 cm from the eye of the specimen. A photodiode which was used to monitor these operations revealed no significant ripples.

RESULTS

Morphology and anatomy

General features

The eyes of *Ligia exotica* are compound and sessile, occupying almost the entire lateral region of the head. From the outside the eyes are uniformly black with no obvious morphological differences between dorsal and ventral halves (but see Discussion).

The dioptric apparatus

The structural units of the compound eye are the ommatidia, which form a hexagonal lattice. The ommatidial centre-to-centre distances are about 60 μm.

Externally the convex cornea possesses an array of fine nipples (Fig. 1), not unlike those reported from a few other peracaridan crustacean (Dahl, 1951) and moth eyes (Gemne, 1971). Corneal nipples in *Ligia* measure 0·1 μm round their base and are

approx. 0·5 μm high. The density of the nipples at the facetal region is about 1·5 μm^{-1}. They are particularly dense (= 7 μm^{-1}) in the interfacetal regions.

The cornea itself is approx. 20 μm thick and multilayered, but it is not known whether the layers are related to the age of the animal (Neville, 1967) or whether they change with time of day as in the eye of the insect *Chrysopa* (Horridge & Henderson, 1976). The inner surface of the cornea is uneven and only rather flat corneal cones are developed.

The crystalline cones, which lie directly below the cornea, are the products of four cells. In the dorsal regions of the eye the crystalline cones measure approx. 100 μm in length and their maximum diameter is 35 μm. In agreement with Peabody (1939) and Nilsson (1978), who reported rudimentary crystalline cone cells in the eyes of adult shallow-water asellotes, we found that two of them were considerably bigger than the other two (Fig. 2). When sectioned transversely, the cones show up as a bipartite structure with circular outline and spongy-vesicular contents. They show a strong affinity to toluidine blue and stain very easily.

The 'suture' between the two large hemispheres of the cones is always parallel to the long axis of the ommatidium and to the direction of the microvilli of retinula cells R1 and R4,R5. The exact number of distal pigment cells is difficult to determine,

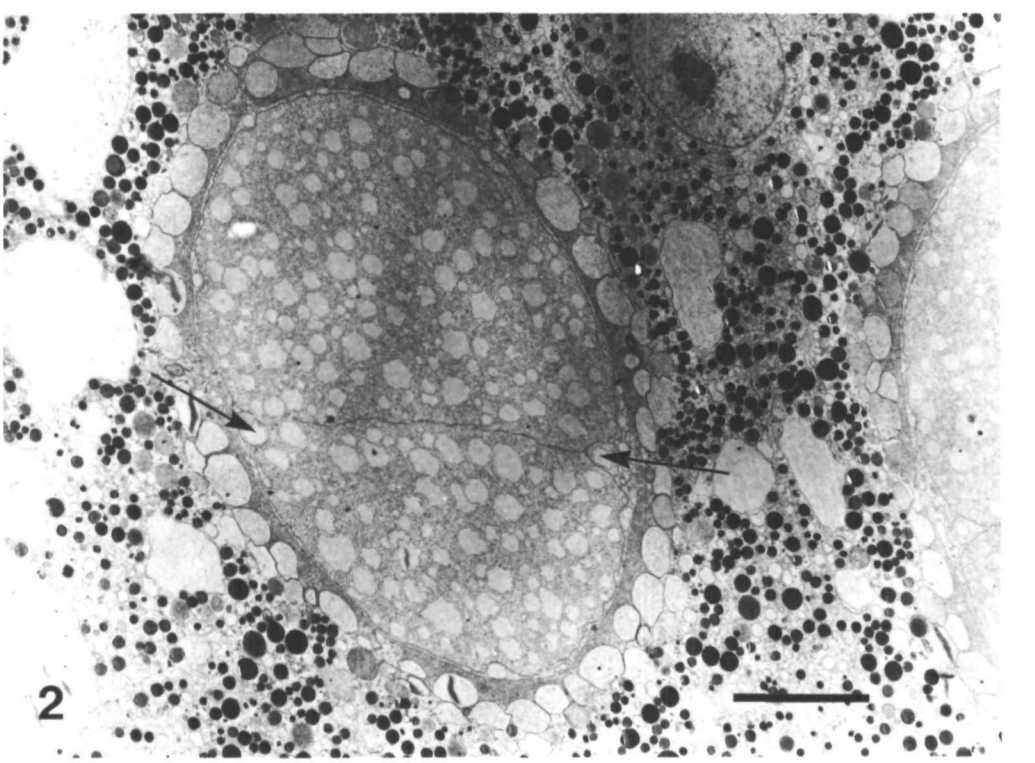


Fig. 2. Transmission electron micrograph of a transverse section through crystalline cone cells. There are four crystalline cone cells. Two of them are bigger than the other two cells (indicated by arrows). Scale bar, 10 μm.

though judging from the number of their nuclei at least six surround each cone. Their pigment granules, which do not migrate significantly following dark/light adaptation, have diameters of 0·1–1·2 μm and their cytoplasm regularly contains vacuoles of 1–3 μm in diameter.

Retinula cells and rhabdom

In both dorsal and ventral regions of the eye there are, in each ommatidium, seven retinula cells (R1–7) with rhabdomeres (Fig. 3). In addition, an eighth cell (R8) without a rhabdomere is present. This cell occupies a central position and possesses a dendrite that extends into the area of the rhabdom where it is surrounded by the rhabdomeres of retinula cells R1–7 (Fig. 3). In *Limulus* a cell, occupying an identical position, is called the 'eccentric cell'. This cell reacts to flashes of light with spike discharges, and since spikes were recorded by us from any region of the retina of *Ligia*, we are convinced R8 is a distally placed second-order neurone like the eccentric cell in *Limulus*.

In the dorsal eye region, retinula cells R1–7 are about 100 μm long and measure 25 μm in diameter (= radial width). The corresponding figures for the equivalent cells of the ventral eye region are 120 μm and 30 μm, respectively. The centrally pointed rhabdomeres consist of numerous parallel microvilli. Retinula cells R4 and R5 are somewhat smaller than the others. The microvilli of their rhabdomeres run parallel. On some occasions an additional retinula cell, flanked by R4 and R5, was found to contribute to the rhabdom. Its microvilli were always aligned with those of R4 and R5 and its cytoplasm was characteristically electron-empty.

Lengths and widths of all microvilli (R1–7) vary with time of day and their location within the retinula. Distally, the rhabdoms are of the fused type and reach the cone. Approximately 7 μm below the cone, the rhabdomeres are pushed apart by the distal end of the dendrite of R8 in the centre of the rhabdom so that in transverse sections the rhabdom appears ring-like (Fig. 3). Still further proximally, the rhabdom takes on the appearance of an open rhabdom during the day, but remains more or less ringlike at night (see below). The spherical nuclei of the retinula cells are found in the vicinity of the basement membrane.

Each ommatidium has seven interstitial cells. Both interstitial, as well as retinula, cells, but the latter in particular, vary in size depending on dark/light adaptation and diurnal rhythm.

Retinula cells R1–7 of both dorsal and ventral ommatidia contain numerous pigment granules. Somewhat lower pigment granule densities than in the other retinula cells are found in R4 and R5. The screening pigments are probably ommin and xanthommatins (Bouthier, 1981).

Organelles such as mitochondria, Golgi apparatus, multivesicular bodies, lamellated bodies, coated vesicles, rough and smooth endoplasmic reticulum are frequently seen in the cytoplasm of all retinula cells, though their relative abundance depends on both state of adaptation, as in *Libinia* (Eguchi & Waterman, 1967), and time of day (Toh & Waterman, 1982).

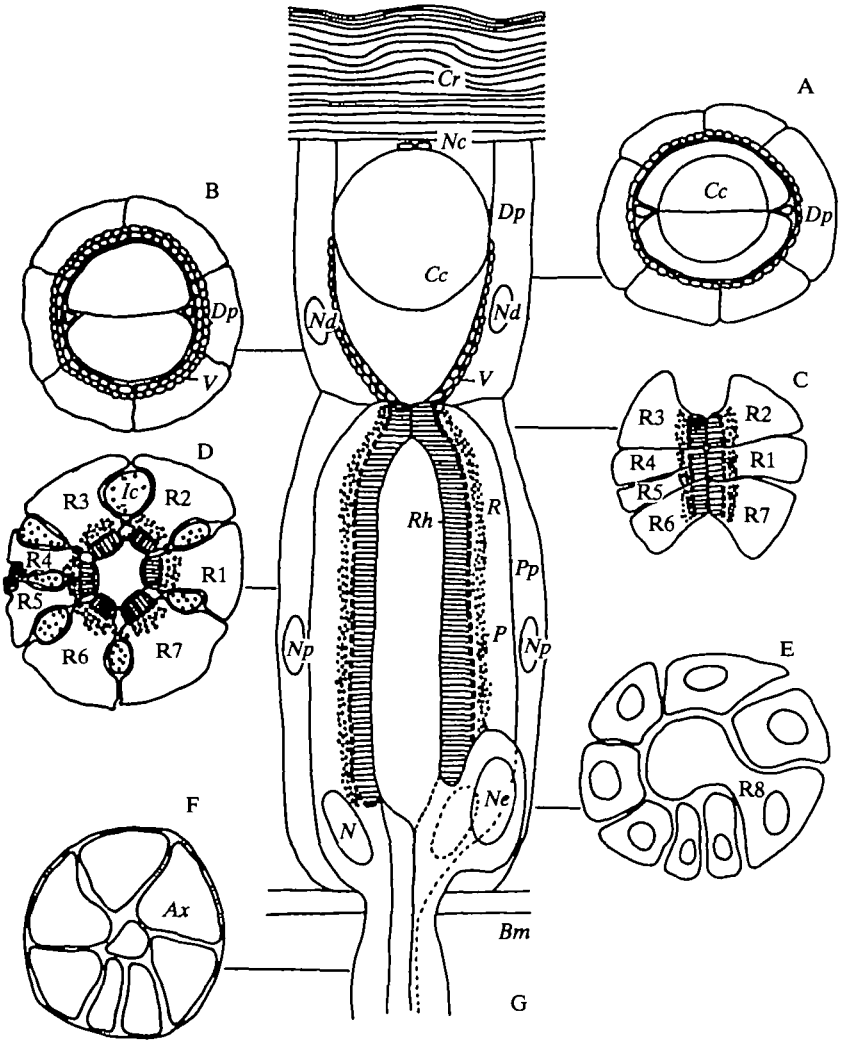


Fig. 3. Semi-schematic drawings depicting longitudinal (G) and transverse (A–F) sections of a light-adapted ommatidium. Black dots near the rhabdom show the position of pigment granules under the light-adapted condition. Abbreviations used: *Cr*, cornea; *Cc*, crystalline cone; *Nc*, nucleus of corneagenous cell; *Dp*, distal pigment cell; *Nd*, nucleus of the distal pigment cell; *V*, vacuoles; *Rh*, rhabdom; *R*, retinula cell; *P*, screening pigments of the retinula cell; *Pp*, proximal pigment cell; *Np*, nucleus of the proximal pigment cell; *N*, nucleus of retinula cell; *Ne*, nucleus of the eccentric cell; *Bm*, basement membrane; *Ic*, interstitial cell; *Ax*, axon. Retinula cells are labelled R1–7; R8 is the eccentric cell. Electron micrographs Figs 6, 7, 9, 10, 11 were taken of transversely sectioned ommatidia at the level of the pigment cell nuclei, marked *Np* in this diagram.

The retinula cells are held together by desmosomes, which are always well developed at the base of two neighbouring rhabdomeres. The connection between R4 and R5 seems particularly close, for fine strands of cytoplasm were often found extending from one cell to the other, almost locking the two neighbours together

(Fig. 4). As in *Oniscus asellus* (Tuurala *et al.* 1966) and *Astacilla longicornis* (Nilsson & Elofsson, 1978), an extracellular palisade was present.

Axons

In contrast to the situation in *Ligia oceanica* (Edwards, 1969), there is little evidence of glial encapsulation of retinula cell axons in *Ligia exotica*. The axons in *Ligia exotica* contain pigment granules (Fig. 5), but to what extent they participate in photomechanical migrations was not studied. As usual in arthropod nervous tissue, the axons themselves were filled with neurotubules of approx. 20–30 nm diameter.

Normal diurnal changes in eye structure (Figs 6, 7)

Only dorsally located ommatidia of about 70 animals were investigated in detail for this aspect of the research. Shape and size of the rhabdom were found to vary more with time of day than with dark/light adaptation at the same time of the day.

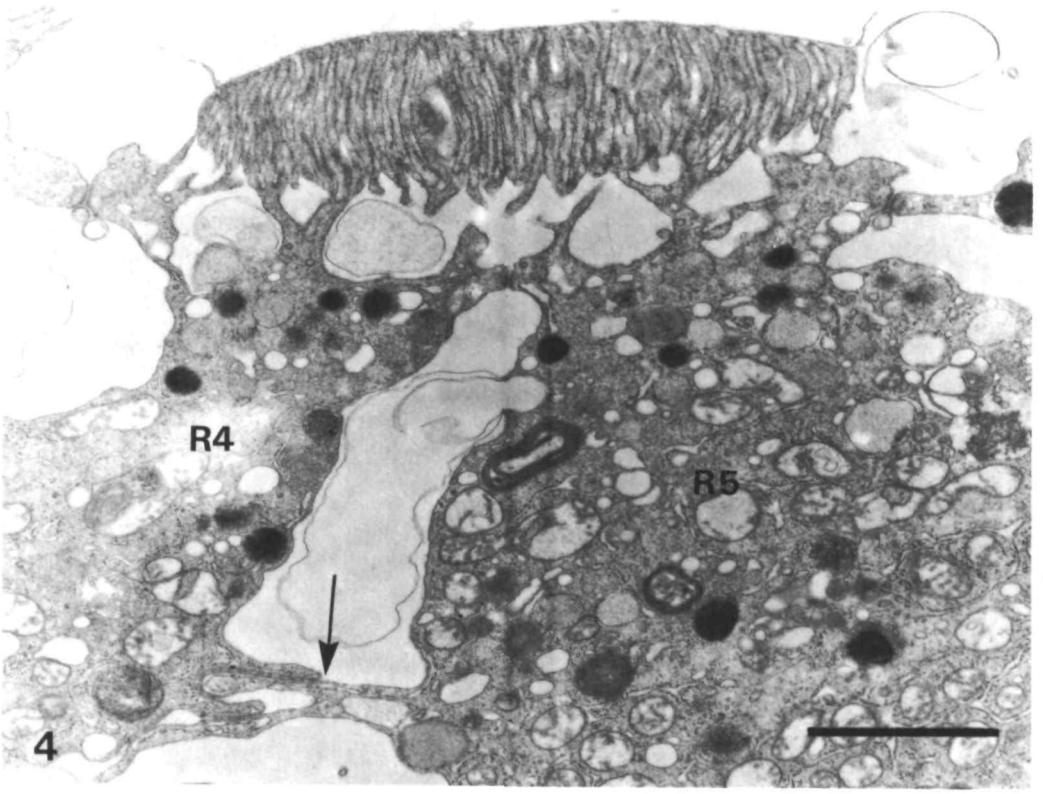


Fig. 4. In this transmission electron micrograph (taken at mid-rhabdom level, see Fig. 3), fine branches extending from the two retinula cells 4 and 5, which form one single rhabdomere, are seen interdigitating (arrow). Scale bar, 2 μm.

Under normal conditions in the animal's natural environment, rhabdom microvilli are irregular at midnight (Fig. 6). It is interesting to note that Nemanic (1975), studying dark/light adaptation in the eye of *Porcellio scaber*, found that only 15 min after the onset of dark adaptation some disruption of the orderly array of rhabdom microvilli occurred. At 00.00 h the rhabdomeres are in contact with one another in *Ligia exotica* so that over its entire length the rhabdom looks as if it belonged to the closed type (Fig. 6). At noon (12.00 h) the arrangement of the microvilli is regular and the rhabdom, partly as a consequence of its smaller size, is of the open type (Fig. 7).

The ommatidial rhabdom occupation area during the night (30 %) is more than twice that seen during the day (14 %) (Fig. 12). At midnight, as in *Leptograpsus* (Stowe, 1982), doublet endoplasmic reticulum (ER) is present in the cytoplasmic bridges across the palisade, but pigment granules are dispersed. At noon, pigment granules assemble closely around the rhabdom.

Structural changes despite constant photic conditions

The rhabdom of one of five animals fixed at 00.00 h, but kept in continuous light of $3{\cdot}0\times10^{13}$ quanta $cm^{-2}s^{-1}$ for 84 h, is shown in Fig. 8. The microvillus arrangement of the distal region of the rhabdom is irregular, quite like that of a normal night eye at 00.00 h The pigment granules are not in a fully light-adapted position, but they are not fully dark-adapted either. (One is reminded of the situation in *Palaemonetes*, where diurnal rhythm and adaptational phenomena also interact; Webb & Brown, 1953).

Quite a different organization is shown by a section through the eye of a representative animal fixed at noon (12.00 h), but kept for 72 h in continuous light of $3{\cdot}0\times10^{13}$ quanta $cm^{-2}s^{-1}$ (Fig. 9). This time rhabdomeres are compact and the arrangement of the microvilli is orderly. Screening pigment granules have aggregated at the rhabdom edge, especially in cells R1–3, R6 and R7.

The formation of numerous vacuoles in the retinula cell cytoplasm is independent of the time of day and seems solely related to the amount of light the animal is exposed to. In a series of experiments the reverse condition, namely continuous darkness, was studied. In spite of the absence of light for 3 days (Figs 10, 11), the screening pigment granules disperse at night and the arrangement of the microvilli, with the exception of rhabdomere R4 and/or R5, shows a pattern similar to that obtained under normal, natural conditions at midnight (cf. Fig. 6). At 03.00 h the microvillus organization of all rhabdomeres was irregular, irrespective of whether the animal had been exposed to continuous light or darkness. At noon (12.00 h), microvilli, once again, are ordered and the rhabdom is of the open type (Fig. 11). The ommatidial rhabdom occupation area during the night is almost identical to that seen during the subjective night, while during the day it agrees almost completely with that of the subjective day (Fig. 12). Pigment granules of all retinula cells, with the exception of R4 and R5, have migrated to within 3 μm of the edge of the rhabdom.

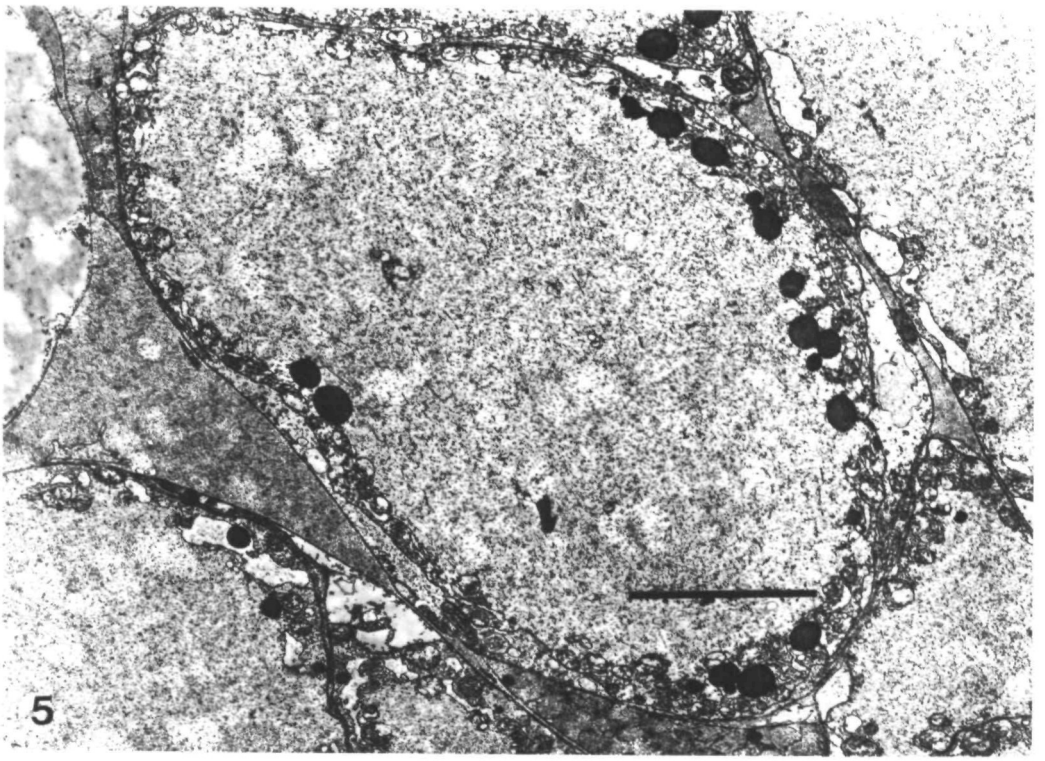


Fig. 5. This transmission electron micrograph reveals that the axon below the basement membrane (see Fig. 3) contains pigment granules. Scale bar, 5 μm.

From a few sections through the ventral halves of day and night eyes, we may be justified in extending our observations to the ventral halves of the eye but emphasize that the ventral regions of the eye were not scrutinized to the same degree as the dorsal halves.

Physiology

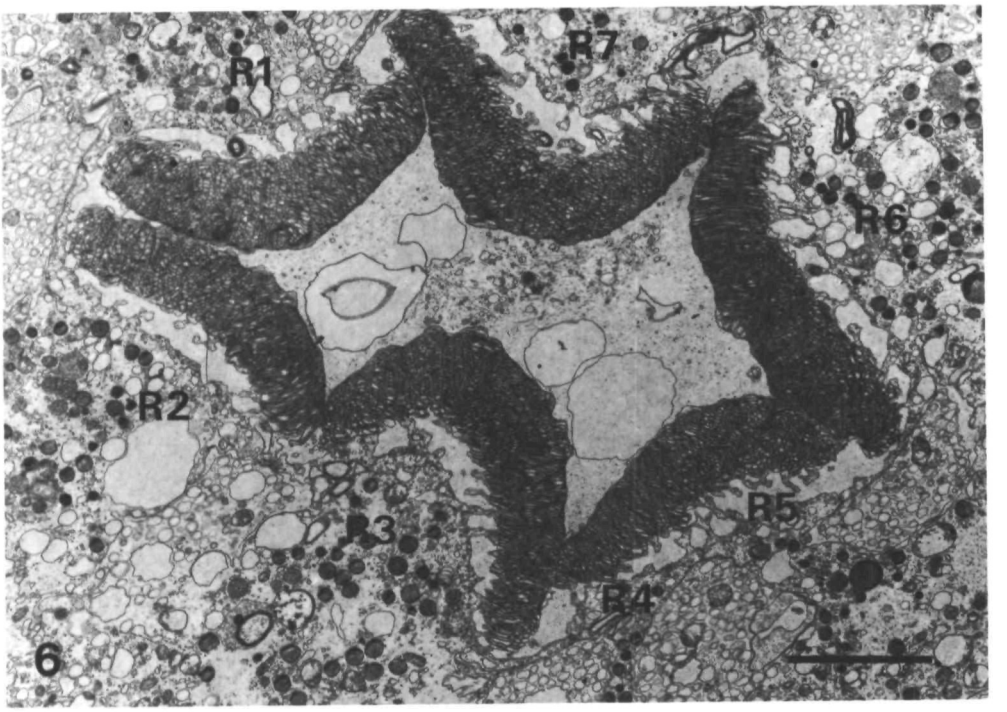
General observations

The waveform of the electroretinogram (ERG) of the eye of *Ligia exotica* is a cornea-negative monophasic response, followed by a sustained phase during stimulation with a flash of light. According to Autrum (1958), this kind of response belongs to the slow type of compound eye responses. For analyses (see below) only the 'on'-transient component was measured.

Figs 6, 7. Transmission electron micrographs of rhabdom cross sections of specimens directly from the natural environment. R1–R7, retinula cells. Scale bars, 5 μm.

Fig. 6. At midnight (00.00 h), the arrangement of the microvilli is irregular and the rhabdomeres are in contact with each other. Screening pigment grains are dispersed.

Fig. 7. At noon (12.00 h), the arrangement of the microvilli is ordered and the rhabdom is of the open type. Screening pigment grains have approached the edge of the rhabdom.


R1
R7
R6
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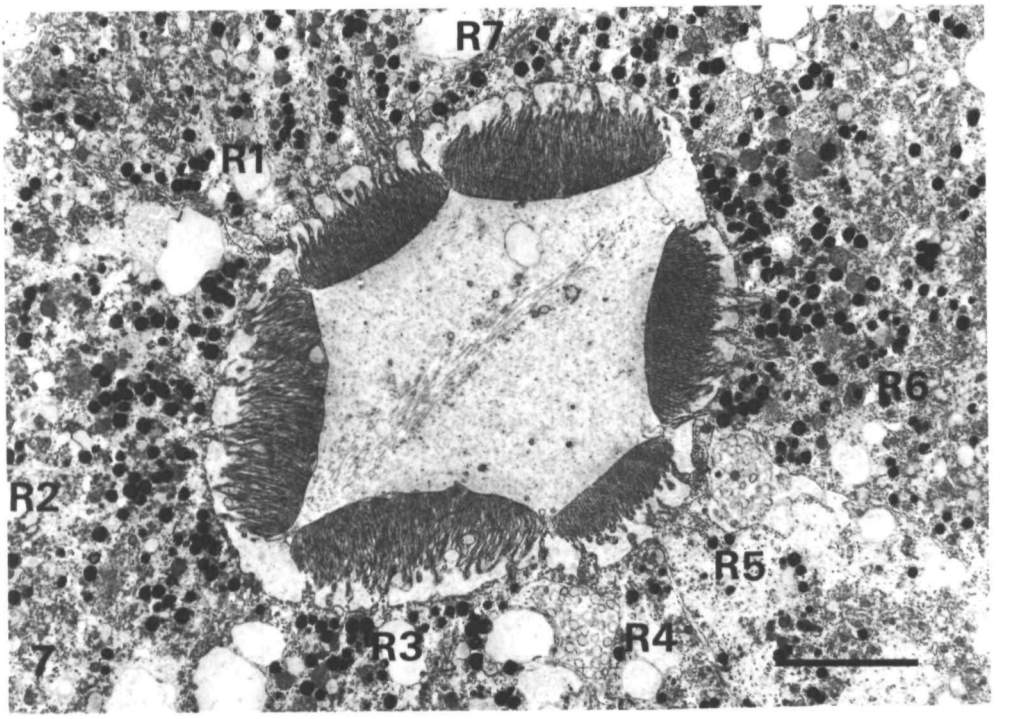
R7
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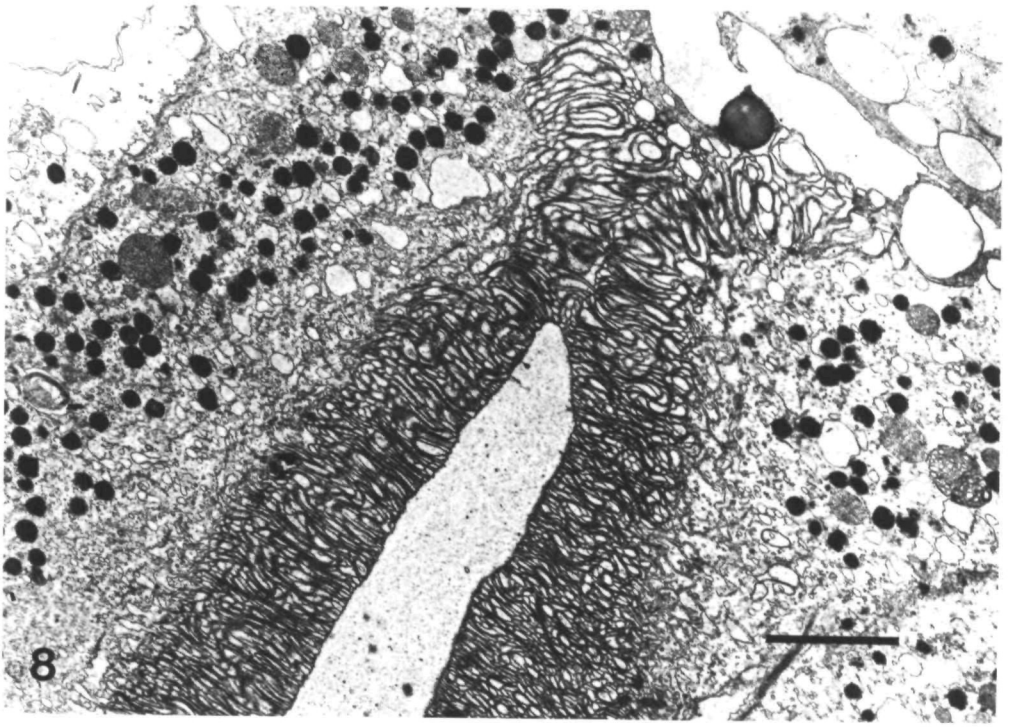
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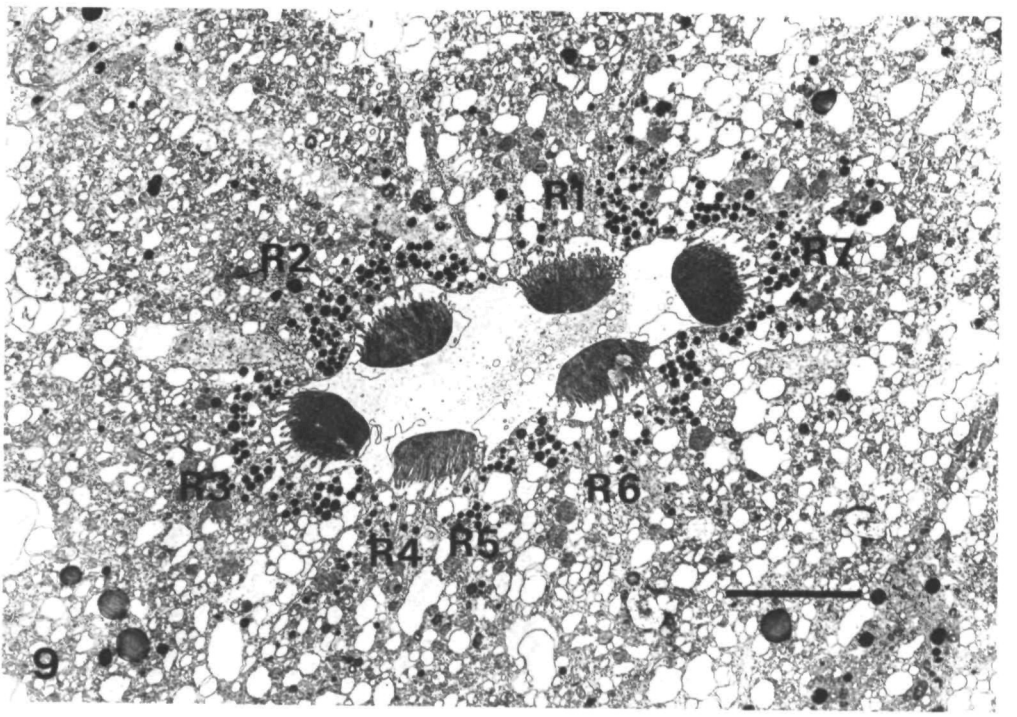

R1
R2
R7
R3
R6
R4
R5
9

Intracellular recordings with glass microelectrodes showed that the retinula cells had resting potentials of approx. −40 mV. Intracellular responses to light were graded depolarizations that reacted sensitively to flashes of different brightness.

Spectral sensitivity

Of 60 penetrated cells of the dorsal eye region, 58 were identified as green receptors with a peak response at 530 nm (Fig. 13). Only two cells represented ultraviolet receptors, with peak responses at 330 nm (Fig. 14). When the light stimulus intervals were less than 30 s, the spectral response curves of green cells, whether recorded intracellularly or by ERG, differed slightly from one another depending on whether the scan across the visual spectrum was carried out from shorter to longer wavelengths or in the opposite direction. The former displayed a major peak at 500 nm, the latter at 540 nm. These phenomena may have been caused by transient light adaptation during the course of the experiment. No shift of spectral response peaks was observed when light stimulus intervals of 1 min or longer were used.

Diurnal changes in the spectral response curve

Some crustaceans display shifts of their peak spectral sensitivity upon illumination or light adaptation (Leggett, 1979; Stowe, 1980; Meyer-Rochow & Tiang, 1984), but whether under natural conditions such spectral sensitivity changes accompany day/night vision and are possibly under the influence of an internal clock – whether, in other words, they are rhythmic phenomena – has hitherto received little attention. To be able to record responses from the eye of the same animal for at least 24 h, intracellular recordings had to be replaced with continuous ERG recordings.

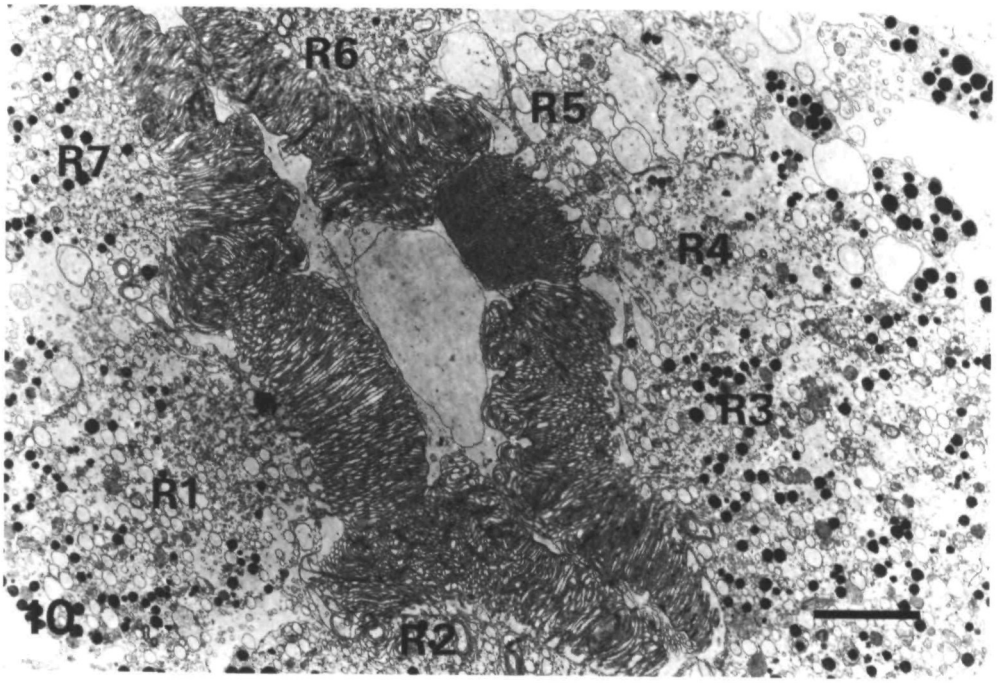
As soon as the animals were located in the dark experimental room (just after sunset), the tungsten electrode was inserted just below the cornea under the illumination of dim red light. Recordings were carried out from 09.00 h the next morning until noon the following day in such a way that one spectral response scan from shorter to longer wavelengths was carried out every 3 h. 500-ms flashes of equal photon content were used and the interflash interval between the different wavelengths tested was exactly 1 min. Five animals were examined in this way and all gave similar results.

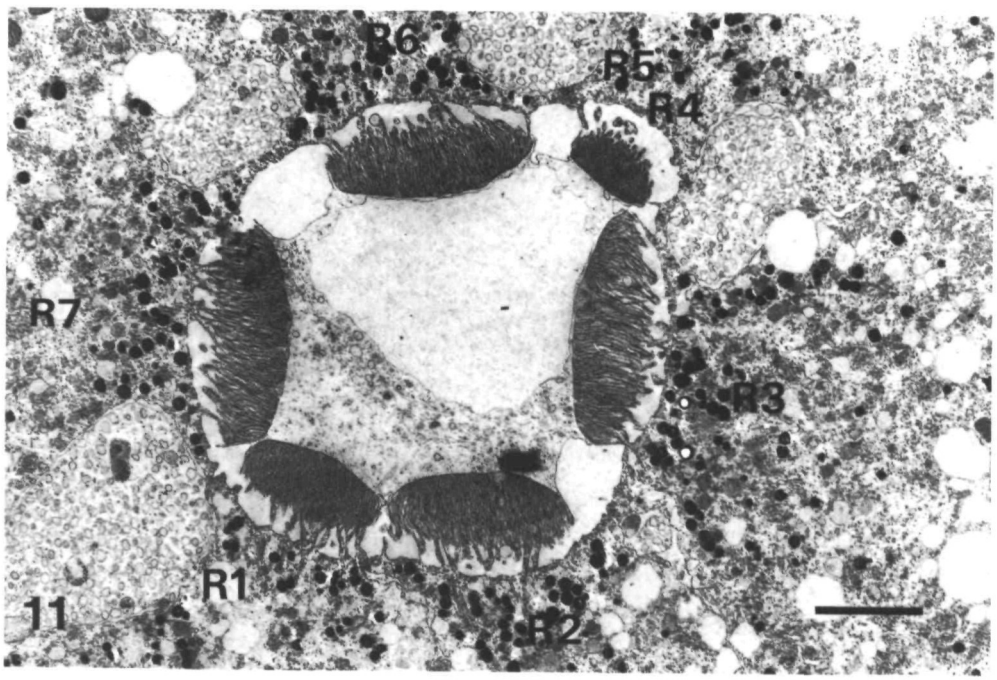
Spectral response curves based on ERG measurements have two distinct maxima, one to light of 383 nm wavelength, the other at around 520 nm. Depending on the time of day, the responses to the green light (520 nm) changed significantly, but those to ultraviolet light were less affected (Figs 15, 16). The Fisher–Behrens test was used to show that the changes represented real changes (confidence level for

Figs 8, 9. Transmission electron micrographs of specimens which were kept in continuous light.

Fig. 8. At midnight (00.00 h), the microvillar arrangement of the distal part of the rhabdom is irregular. Scale bar, 3 μm.

Fig. 9. At noon (12.00 h), the rhabdomeres are very compact and the arrangement of the microvilli is ordered. R1–R7, retinula cells. Scale bar, 5 μm.





Figs 10, 11. Transmission electron micrographs of specimens kept in continuous darkness. R1–R7, retinula cells. Scale bars, 5 μm.

Fig. 10. At midnight, with the exception of one rhabdomere, the arrangement of the microvilli is irregular and resembles the pattern seen in eyes of animals kept under natural conditions.

Fig. 11. At noon, the arrangement of the microvilli is ordered.

00.00:12.00 h curves = 99 %) and not simply random fluctuations. During the day, *Ligia*'s sensitivity to ultraviolet light is relatively higher than at night, but the reverse holds true for green light.

Having established this fact, we recorded the responses of five different animals each hour for 24 h to 500-ms flashes of only two wavelengths, namely ultraviolet (383 nm) and green (520 nm) light of equal photon content ($9{\cdot}0\times10^{13}$ quanta cm^{-2} s^{-1}). Although ERG amplitudes increased with both wavelengths in the evening and decreased in the morning, it was the response to *green* light that displayed a considerably greater sensitivity loss in the morning (Fig. 16). This result suggests that the observed variation is indeed diurnal and probably parallels the anatomical circadian changes described above.

DISCUSSION

Behavioural and morphological considerations

Ligia exotica is a terrestrial, diurnally active arthropod that is abundant along the Japanese seashore on boulders and rocky platforms. It crawls around in bright sunlight and reacts visually to the approach of an object. On being disturbed it runs swiftly away or seeks refuge in a dark crevice, from where it reappears when the threat is over. Its body colour (dark in the day; pale during the night) varies rhythmically, not unlike that of *Ligia oceanica*, for which Smith (1938) has shown that the illumination of dorsal ommatidia is responsible for initiating the discharge of

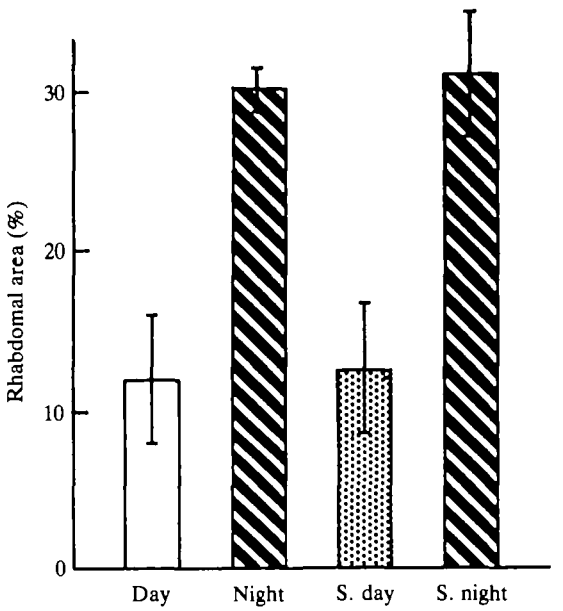


Fig. 12. The ommatidial rhabdom occupation area, expressed in percentage on the ordinate, varies considerably between day and night. These cyclic fluctuations continue even under conditions of constant darkness (subjective day; subjective night). The bars indicate standard deviation based on measurements from 70 eyes.

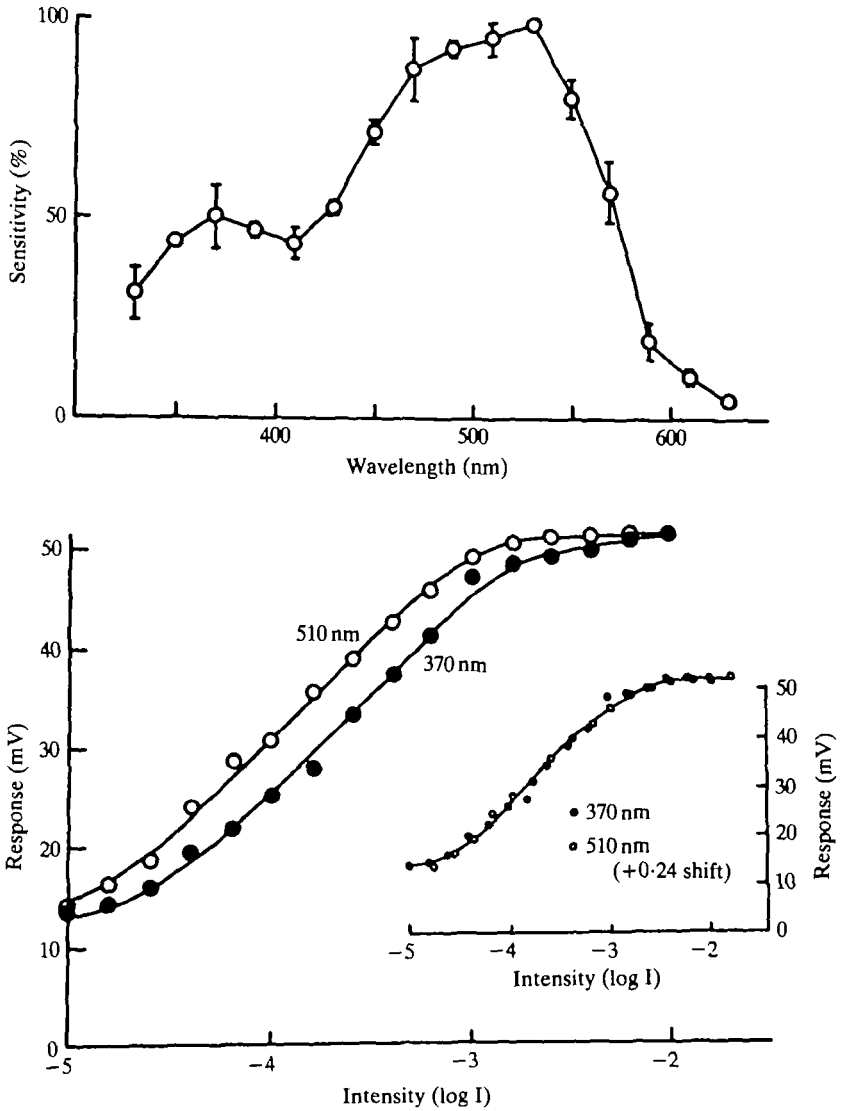


Fig. 13. Spectral sensitivity curves and V/log I curves of green-sensitive cells. There are slight differences in the two V/log I curves obtained with monochromatic lights of 520 nm and 370 nm, but the curve shift amounts to only 0·24 log intensity and the two curves are of identical shapes (see inset). Vertical bars indicate ±1 S.E.M.

a hormone that evokes melanophore expansion, whereas the ventral areas of the same eye pick up light scattered from the immediate surroundings and are thus responsible for initiating the discharge of a hormone that evokes melanophore contraction.

Compound eyes in which dorsal and ventral halves carry out different tasks are not restricted to *Ligia*. Insect species, in which dorsal facets vary considerably from ventral ones, are known (see review by Wehner, 1981) and amongst crustaceans, Euphausiaceae (Chun, 1896; Land, Burton & Meyer-Rochow, 1979) and Amphipoda (Ball, 1977) include species with sometimes grotesquely asymmetrical

eyes. The only isopod known to have completely divided dorsal and ventral eye regions is *Glyptonotus antarcticus* (Meyer-Rochow, 1982), a valviferan isopod and, therefore, phylogenetically not too distantly related to *Ligia*. However, Meyer-Rochow (1982) points out that mere physical separation of dorsal and ventral eye regions is unlikely to produce eyes of different physiological properties, unless dorsal and ventral ommatidia exhibit structural dissimilarities.

The open rhabdom

The dorsal half of the eye in *Ligia* has a rhabdom which is open over most of its length during the day. This finding agrees with those of Edwards (1969) on *Ligia oceanica* and Beddard (1888) on *Aega* sp., although the latter, a light microscope investigation, requires confirmation by electron microscopy. In insects, open rhabdoms, especially those of flies (Eckert, 1973), are regarded as an adaptation for

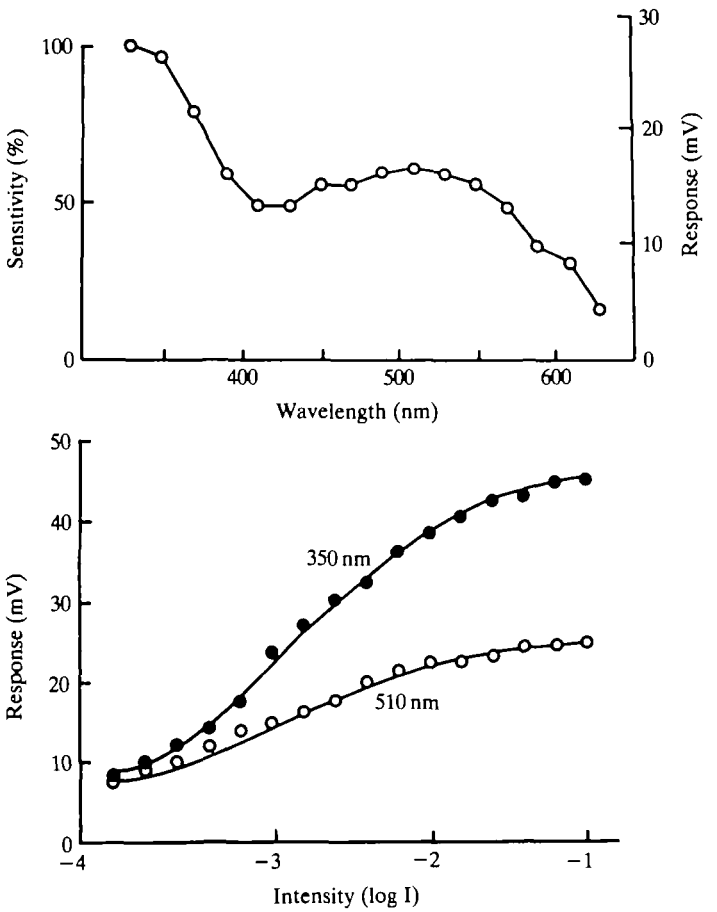


Fig. 14. Spectral sensitivity curves and V/log I curves of ultraviolet-sensitive cells. One V/log I curve was obtained to light of 510 nm, and the other was the result of 350 nm stimulation. There is apparently a difference in their slopes (statistical confidence level 99 %).

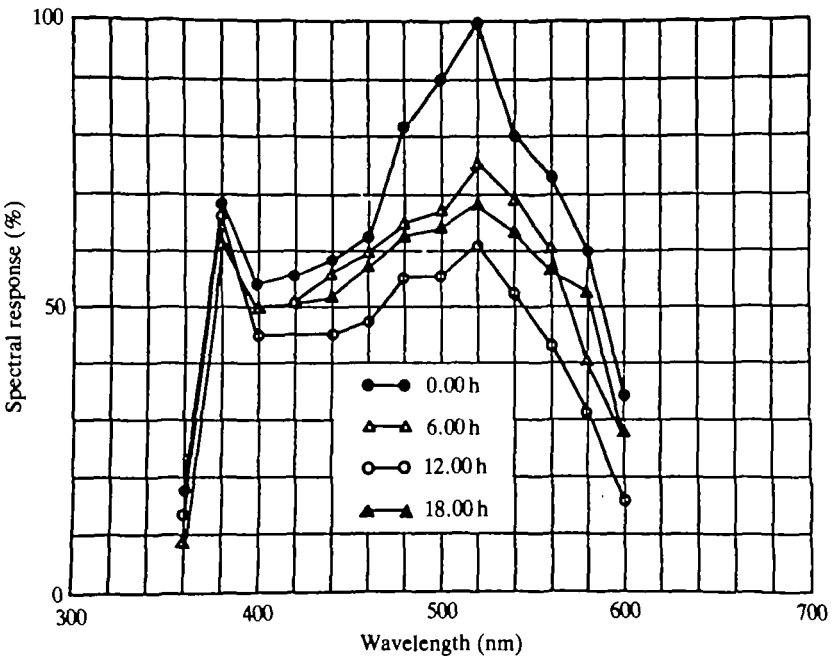


Fig. 15. The mean spectral response curves (see text) in relation to time of day. These curves, each one based on recordings from five different animals, have two distinct maxima (one at 383 nm, the other at 520 nm).

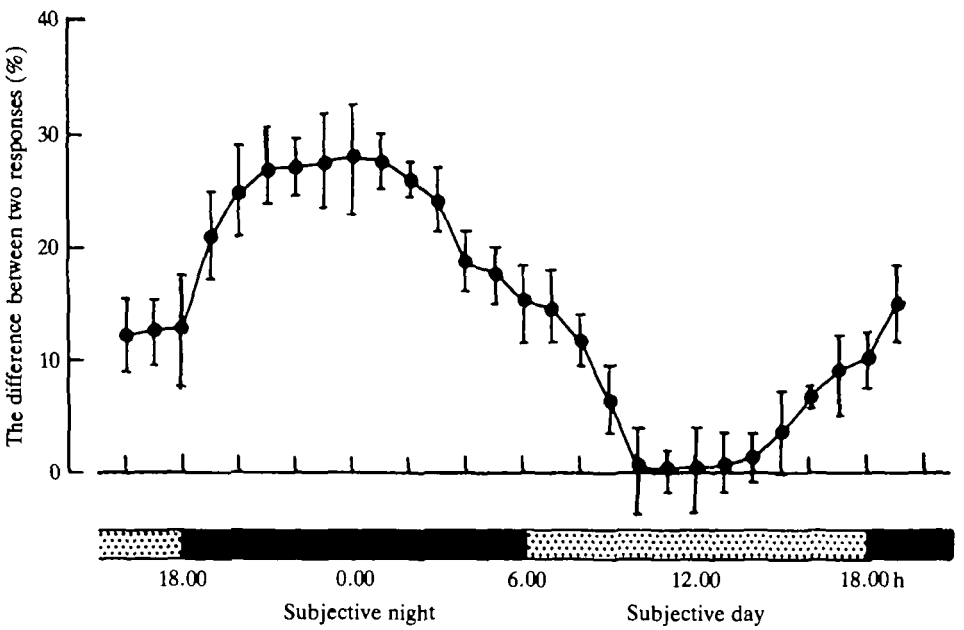


Fig. 16. Both ultraviolet and green peaks display sensitivity changes between night and day even in continuous darkness. However, it is evident that green peaks are considerably more strongly affected than ultraviolet peaks when the differences between green and ultraviolet maxima of recordings from five animals are plotted against time of day. Vertical bars indicate ±1 S.E.M.

vision in bright but not low light conditions. However, an open rhabdom need not be static, for, as in the eye of *Ligia exotica*, increases of rhabdom volumes following dark adaptation have been reported from the open rhabdoms of the mosquito *Aedes* (White & Lord, 1975), the glowworm fly *Arachnocampa* (Meyer-Rochow & Waldvogel, 1979) and a tipulid cranefly (Williams, 1980). An open rhabdom in a decapod shrimp, inhabiting a constantly dimly lit environment, was recently reported by Meyer-Rochow & Juberthie-Jupeau (1984).

The retinomotor phenomenon in *Ligia exotica* resembles that of many insects, in which a reduction of the acceptance angle during the day and an increase of absolute sensitivity at the expense of acuity at night have been reported (Tunstall & Horridge, 1967; Walcott, 1971*a*,*b*; Butler & Horridge, 1973; Meyer-Rochow, 1974*a*,*b*). We can, therefore, expect the structural differences between the eyes of *Ligia* during the day and the night to affect this animal's acuity and sensitivity in a similar way (T. Hariyama, in preparation).

Functional implications: spectral sensitivity

Sensitivities to flashes of ultraviolet as well as green light increased at night and decreased during the day parallel to the ultrastructural changes described earlier in this paper. However, the finding that not only does the absolute sensitivity fluctuate, but also that the ratio – the 'balance' – between ultraviolet and green sensitivity fluctuates rhythmically with time of day is a new aspect requiring detailed discussion.

Using the ERG method, Goldsmith & Fernández (1968) have measured the spectral sensitivity of the eye of the isopod *Porcellio scaber*. They found two sensitivity peaks (the main one at 515 nm; a secondary one at 350 nm) but concluded from experiments in which animals were exposed to red light that only a single visual pigment with an α-absorption band in the blue-green and a minor β-band in the near ultraviolet was present. In *Ligia*, intracellular recordings have unquestionably shown that at least two classes of receptor cells are present in the retina: ultraviolet cells with a λ_{max} of 330 nm and green cells with a λ_{max} of around 530 nm.

Leggett (1979), working with the portunid crab *Scylla*, demonstrated that considerable differences occurred between the spectral sensitivity curves of light-adapted and dark-adapted cells. Bearing in mind that microspectrophotometrical data from related portunids exhibited only one visual pigment (Goldsmith & Bruno, 1973), the most probable explanation of Leggett's observation seemed that changes in the spectral sensitivity accompanying light adaptation were caused by the introduction into the ray path of spectrally selective filters of some kind (Leggett, 1979). In *Leptograpsus*, Stowe (1980) reported that during the first 2–5 min of light adaptation, peak sensitivities shifted dramatically to shorter wavelengths, so that the principal peak came to lie between 360 and 440 nm and the secondary peak at 500–537 nm. Over 30–40 min of bright light adaptation, the relative sizes of the two peaks changed steadily, the one representing responses to shorter wavelengths becoming less and less pronounced.

Shifts in the relative heights of two spectral sensitivity peaks in dark-adapted night eyes and light-adapted day eyes were observed by Eccles, Tiang & Meyer-Rochow

(1983) in *Paranephrops planifrons*. Meyer-Rochow & Tiang (1984), in agreement with observations on *Leptograpsus* (Stowe, 1980) and *Ligia* (this paper), reported that sensitivity scans from shorter to longer wavelengths did not produce identical spectral sensitivity curves. The differences were thought to be caused by the self-screening properties of photopigments and their photoproducts in the rhabdom column (Goldsmith, 1978). Aware of these phenomena, Stowe (1980) studied spectral response curves from dark-adapted receptors of the eye of *Leptograpsus* during the day and during the night, but failed to find significant differences, although a diurnal rhythm, also shown to operate in the eye of the related *Grapsus* (Nässel & Waterman, 1979), causes changes in rhabdom volume and pigment migrations that are, in principle, not unlike those of *Ligia exotica*.

Spectral sensitivity and pigment screening

In *Ligia*, spectral sensitivity curves from dark-adapted animals tested during the night differ from those of dark-adapted animals studied during the day. What causes this change? Circadian oscillations of absolute sensitivity have been reported repeatedly from a variety of arthropod eyes. For example, Aréchiga & Wiersma (1969) and Larimer & Smith (1980) have shown that the ERG amplitude rhythm in the intact eye of crayfish continued to oscillate in constant darkness, a process related to circadian migrations of the screening pigment (Aréchiga, Fuentes & Barrera, 1973). In *Ligia* it is easy to see how the combination of increased rhabdom volume and withdrawal of screening pigment grains, both little affected by ambient light levels because they are driven by an internal clock, could account for the increase of the responses at night. But why are the responses to green light more strongly affected than those related to ultraviolet?

By measuring the ERGs of two dark-adapted lepidopteran species (*Hydroecia fucosa* and *Conistra vaccinii*), Mikkola (1972) found that the sensitivity to shorter wavelengths was considerably higher at night than during the day. Biologically, this does not seem to make much sense since there is very little natural ultraviolet radiation at night (Munz & McFarland, 1977). Mikkola suggested that this difference corresponded to the effect on the ERG that was caused by the total removal of screening pigments from the distal region of the retinula in moths (Höglund & Struwe, 1970). It is true that in *Ligia*, too, screening pigment granules move under the influence of an internal clock and that they therefore act as filters owing to their own spectral absorbance characteristics.

Goldsmith (1965) has convincingly argued that the so-called red receptor in flies was largely due to the fact that screening pigment granules absorb relatively less light towards the red end of the spectrum. Screening pigments of insect and crustacean eyes are rather flat across the spectral range of 350–550 nm and mostly consist of ommin and xanthommin compounds (Langer, 1975; Struwe, Hallberg & Elofsson, 1975; Bouthier, 1981). If they are withdrawn, responses in all spectral cell types should increase at the same rate, but in *Ligia exotica* the *green* peak is more strongly affected than the ultraviolet peak. There could be at least three reasons for this.

Visual pigments. Sensitivity is related to photopigment concentration (Hamdorf, 1971), and since there is relatively more rhabdom volume available at night, an increase in green photopigment at night exceeding that of ultraviolet pigment would cause a shift in the balance of the two receptor sensitivities in favour of the green peak.

Screening pigments. In the eye of *Ligia*, grains of screening pigment may not absorb uniformly across the visual spectrum. Though it is unlikely that they would display a leakage solely in the ultraviolet, pigment granules with such a property would cause a greater increase in sensitivity in the green if they were withdrawn at night.

Anatomical and physiological differences between green and ultraviolet cells. Ultraviolet cells could be considerably smaller than green cells and they might contain relatively fewer screening pigment grains than green cells. Assuming that all screening pigment grains, i.e. those of both receptor cell types, follow a circadian rhythm, but that there are more granules shielding the green cells, then *their* withdrawal must have a greater effect on the sensitivity of the latter than on that of the ultraviolet cells.

It was recently shown by Hariyama & Tsukahara (1985) that green cells are indeed more numerous and larger than ultraviolet cells and that at least one of the smaller pair of retinula cells R4 and R5 (both possessing a smaller amount of screening pigment granules than the green cells) is an ultraviolet receptor.

Acuity and diurnal rhythm of screening pigments

By behavioural experiments, de Bruin & Crisp (1957) showed that sensitivity increases associated with a deterioration of the acceptance angle occurred in those species exhibiting pigment migrations, but not in species in which no obvious pigment migrations took place. For this reason we expect acceptance angles in green cells of *Ligia exotica* to display greater diurnal changes than in ultraviolet cells – after all, there is considerably less screening pigment in the latter. Dark/light adaptation and rhythmicity have been reviewed by Autrum (1981) and it is clear that rhythmicity, where it occurs, complicates the picture of adaptational phenomena, which are influenced, but not completely suppressed, by rhythmicity (Webb & Brown, 1953; Rossel, 1979).

The effects of rhythmic pigment migrations on absolute sensitivity and acceptance angles have been studied rather extensively (see review by Autrum, 1981), but the control mechanism, the site of the 'internal clock', is still unknown. Pigment migrations can be controlled by the visual cells themselves (*Musca*: Eichenbaum & Goldsmith, 1968; Kirschfeld & Franceschini, 1969), or migrations occur in continuous darkness, but not under constant illumination (*Gammarus*: Ali & Steele, 1961; *Anoplognathus*: Meyer-Rochow & Horridge, 1975) or the movements of the pigments entirely obey a diurnal rhythm (*Limulus*: Barlow & Chamberlain, 1980; *Ligia*: this paper).

According to the definition, here given in an abbreviated form, by Ninnemann (1979), diurnal rhythms have in common that (1) they are triggered or synchronized

by an external *Zeitgeber*, (2) the rhythms follow a 24-h pattern and continue to 'free-run' under constant darkness or constant dim light for at least 2–3 days, and (3) circadian rhythms are temperature-compensated. In crustaceans in which eyestalk ablation alters or suppresses circadian rhythmicity, there is good evidence that the location of the pacemaking oscillator lies in the eyestalks with the eyes as photoreceptors coupled to them (Kalmus, 1938*a*,*b*). However, persistent circadian locomotor rhythms in eyestalkless *Grecarcinus lateralis* and *Procambarus clarkii* have been reported by Bliss (1962) and Page & Larimer (1972), respectively.

In the crayfish, neither the compound eyes nor the caudal photoreceptors are necessary for entraining the rhythm (Page & Larimer, 1976), and in *Limulus* Chamberlain & Barlow (1979) demonstrated that efferent activity from a clock located in the brain adapts the eye for optimal function at very low light levels. Recently discovered intracerebral ocelli in isopods (Martin, 1976*a*,*b*) may be involved in setting the rhythm in *Ligia exotica*, since Hariyama, Yoshida, Eguchi & Meyer-Rochow (1982) were able to show by means of extracellular recordings that these ocelli respond to light. However, intracerebral photoreceptors need not necessarily be required, since Jacklet (1969) has shown that the isolated eye of *Aplysia* maintains its rhythm and Prichard & Lickey (1981) concluded that the intracerebral photoreceptors, identified by Block & Smith (1973), 'do not instruct the eye about the magnitude of the reset. Instead, they activate or modulate circadian functions that are latent in the eye itself'.

Is this the situation in *Ligia* also? We do not know, but we believe that *Ligia*, with its circadian body colour changes and its pronounced rhythmic changes in eye ultrastructure and function, is an ideal candidate for future research into oscillating processes.

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