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OBSERVATIONS ON THE COMPOUND EYES OF THE DEEP-SEA OSTRACOD *MACROCYPRIDINA CASTANEA*

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Summary

Macrocypridina lives at depths of 800 m, where residual daylight is very weak. It has a pair of mobile apposition compound eyes with large lenses, wide rhabdoms and high acceptance angles, all of which contribute to a calculated sensitivity comparable with the superposition eyes of deep-water decapod crustaceans. The axes of the 27 ommatidia in each eye are not uniformly distributed in space, with a modest acute zone in the anteroventral region. Here the interommatidial angles are about 6°, compared with 20° at the rear of the eye.

The eyes make two kinds of spontaneous movements: large slow rotations of up to 50° around a transverse axis, and a superimposed 2 Hz tremor with an amplitude of 5°.

Introduction

Clear ocean water attenuates blue light by a factor of 10 for every 70 m, and other wavelengths more strongly (Jerlov, 1968). Thus, at a depth of 700 m, at which *Macrocypridina* is commonly encountered, the intensity of penetrating sunlight is about 10^{10} times lower than at the surface. If the surface is sunlit, then this level corresponds approximately to the human absolute threshold for vision. Nevertheless, in these dim conditions, vision remains a major sense for many animals. The changes in the camera-type eyes of vertebrates and cephalopods with increasing depth are well-documented (e.g. Marshall, 1954; Locket, 1978). The ways that compound eyes achieve increased sensitivity are less well understood. Most deep-water arthropods have superposition eyes, based on lenses in the euphausiids and mirrors in the decapod shrimps (see Land, 1984). The superposition design with its wide effective pupil and large receptors is intrinsically more sensitive than the more usual apposition type of compound eye. Nevertheless, a few deep-sea arthropods (some isopods, hyperiid amphipods and ostracods) have retained apposition eyes, and it is interesting to determine how this type of eye has been 'stretched' to deal with very dim conditions. Some information is available for a deep-sea isopod, *Cirolana* (Nilsson and Nilsson, 1981) and for the

Key words: eye, eye-movement, ostracod, deep-sea.

hyperiid amphipods *Phronima* and *Cystisoma* (Land, 1981*a*, 1989). This paper provides an unusual example from a third group, the myodocopid ostracods.

The ability of an eye to resolve under different light conditions can be estimated with reasonable accuracy from a knowledge of its anatomy (Kirschfeld, 1974; Snyder, 1979; Land, 1984). In an apposition compound eye the features that contribute most to the sensitivity are the facet diameter (D) and the rhabdom acceptance angle ($\Delta\rho$). Other things being equal, the square of their product $(D\Delta\rho)^2$ determines the number of photons each rhabdom receives from a scene of given luminance. In contrast, under bright conditions the resolution of an eye is determined by the inter-ommatidial angle ($\Delta\phi$). There are thus a number of measures by which the performance of eyes can be compared that do not require knowledge of either electrophysiological characteristics or behaviour. *Macrocypridina* eyes have several features that suggest very high sensitivity – most obviously enormous facets – and here we try to assemble the evidence that will make possible comparisons with the eyes of animals from similar dark environments and from much brighter ones.

In spite of the depth from which they were brought to the surface, specimens of *Macrocypridina* were often in good condition. They swam actively and, to our surprise, made quite complicated spontaneous eye movements. These were studied by video recording and frame-by-frame analysis. We believe that these are the only eye movements known from an ostracod, and they invite comparison with the well-described eye movements of cladocerans such as *Daphnia* (Frost, 1975) and *Polyphemus* (Young and Taylor, 1987).

Materials and methods

Macrocypridina castanea are unmistakeable 'chocolate drop' ostracods with shells about 7 mm long. They were obtained during Cruise 168 of the RRS *Discovery*, at a depth of about 800 m in the vicinity of 20 °N 20 °W in the N. Atlantic. The net used (8 m^2 rectangular mid-water trawl) could be opened and closed at preselected depth by an acoustic signal. The animals were kept in cooled sea water until used for histology or filming, and they usually remained active for several hours.

For histological work, eyes were excised into cold (4 °C) fixative with the following composition: 2.5 % glutaraldehyde; 3 % paraformaldehyde; 3 % sucrose and 10 mmol l^{-1} EGTA in 150 mmol l^{-1} sodium cacodylate buffer. After 2 h the eyes were rinsed in buffer and postfixed for 1 h in OsO_4 before they were transferred to buffer solution and stored at 4 °C for 3 weeks. Dehydration was performed in an alcohol series followed by embedding in Araldite. Semi-thin sections (1–2 μm) for light microscopy were cut on a glass knife and stained with Toluidine Blue. For electron microscopy (Jeol 1200 EX) ultrathin sections were cut on a diamond knife and stained with lead citrate and uranyl acetate.

Video films of eye movements were made using a portable camera (Sanyo VC 500) attached to a dissecting microscope, and a video recorder with single-fram

facilities (Sanyo VTC7100). The animals were in water at about 20°C, considerably higher than the 5–10°C of the water at 800 m depth.

Results

External structure and fields of view

The paired eyes are situated dorsally, slightly anterior to the centre of the animal (Fig. 1). They are cylindrical structures 1.3 mm long and 0.7 mm in diameter. In life the long axis is inclined top-forwards at an angle of about 45° to the longitudinal axis of the body (taken as the longest diameter of the carapace), and the top is also tilted inwards towards the midline by about 25°. In front of the

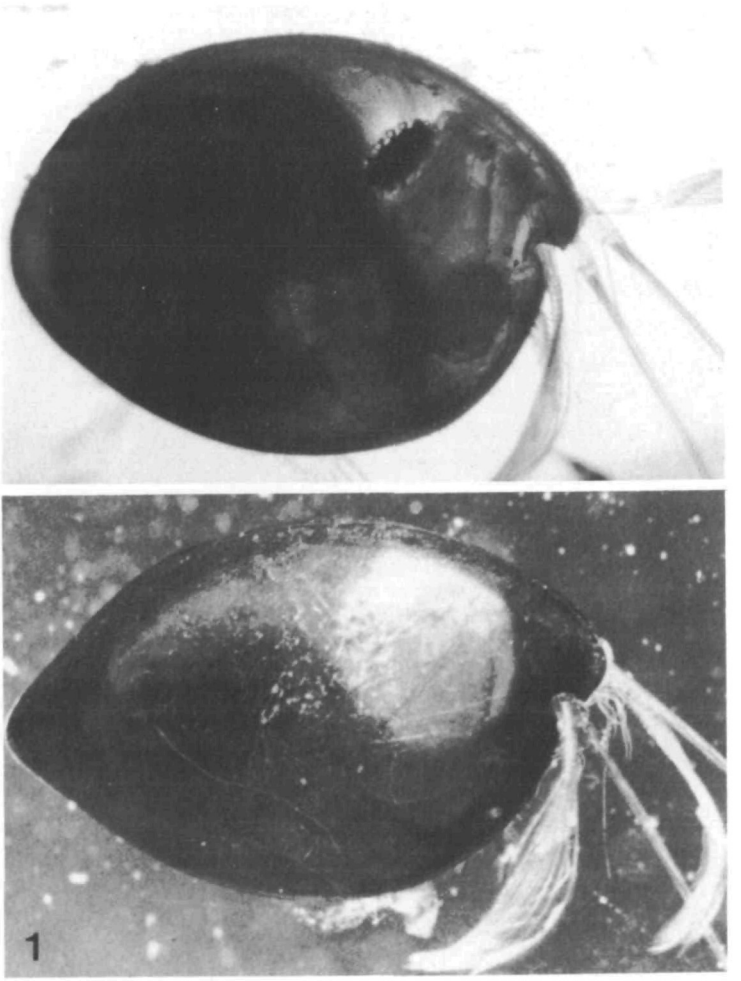

Fig. 1. Living *Macrocypridina castanea* viewed in transmitted light (above) showing the position of the eye, and reflected light (below) showing the position of the window. The length of the major axis of the shells is 7 mm.

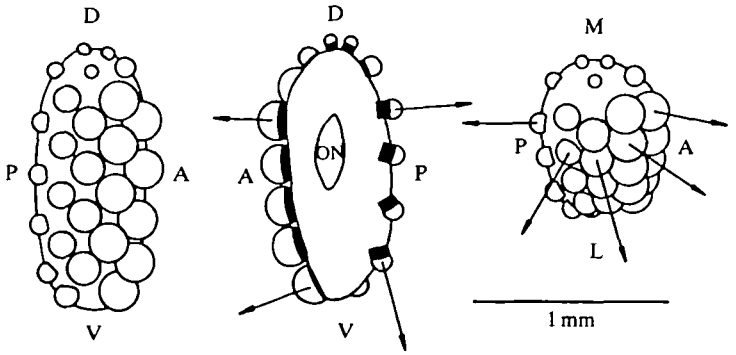

Fig. 2. Drawings of the right eye from lateral, medial and dorsal aspects (left to right) showing the sizes and locations of the lenses. Arrows indicate the long axes of the lenses and hence the approximate directions of view of the ommatidia. A, anterior; P, posterior; D, dorsal; M, medial; ON, optic nerve stump.

eye and extending somewhat ventrally there is a clear circular region in the otherwise brown-pigmented carapace, and this is undoubtedly a window for the eye to see through (Fig. 1). Each eye contains 27 ommatidia in five rows in an approximately hexagonal lattice which covers only the lateral face of the eye (Fig. 2). The eyes from three individuals all showed the same pattern. The eyes are not symmetrical; the anterior two rows of lenses are much the largest (220 μm) and the posterior lenses the smallest (120 μm). The five most dorsal lenses are all small and belong less clearly to the ommatidial rows that make up the rest of the eye.

The directions of the axes of individual ommatidia were estimated from the axes of the pear-shaped lenses and the pigmented collars around their bases. Although this method is only accurate to a few degrees, it is clear that there are large differences in the inter-ommatidial angles ($\Delta\phi$) in different regions of the eye. They are smallest anteriorly (about 6°) and greatest at the rear (about 20°). Fig. 3 shows how the ommatidial axes of the right eye map onto a sphere around the animal, when the eye is in the 'rest' position. There is a definite concentration of axes, and hence greater resolution, in the anteroventral part of the field, with fair coverage of the dorsal hemisphere, and almost none in the posteroventral region. The direction of this 'acute zone', and the position of the window in the carapace, anteroventral to the eye, both suggest that this is the most important direction for vision. It is likely that in the sea this region points upwards, since this is the direction of the residual daylight and, if that is the case, the swimming orientation of the animal would be as shown in the lower inset of Fig. 3.

Some information is available for the eyes of two other species of myodocopid ostracods, *Cypridina norvegica* from a depth of about 400 m and *Philomedes globosa* which lives in the surface waters down to 50 m (Andersson, 1979). In both species the eyes are generally similar to those of *Macrocypridina* but much smaller, less than 300 μm long, and the lenses are also smaller: 55 μm in diameter in male *Cypridina* and 20 μm in male *Philomedes*. In both species there are only three rows

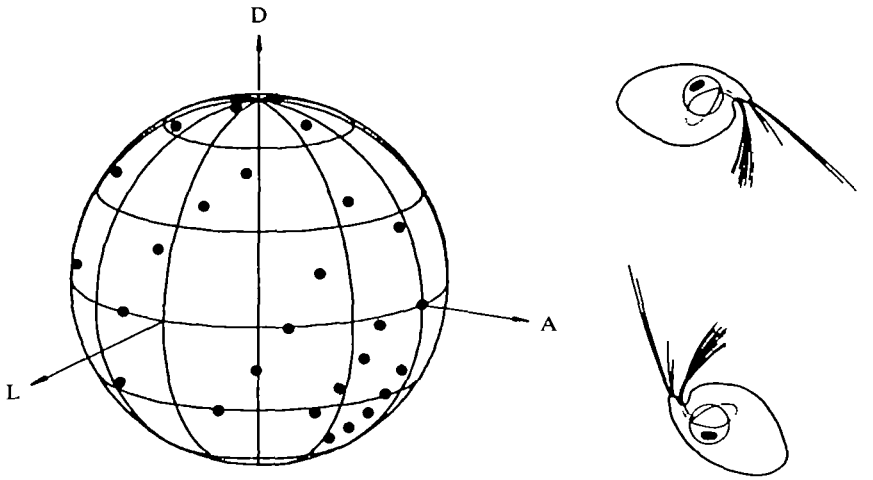

Fig. 3. Projection of the axes of the 27 ommatidia of the right eye onto a sphere around the animal. A, D and L are the anterior, dorsal and lateral directions, assuming the animal's long axis is horizontal (inset upper right). If the animal's direction of best vision (indicated by the acute zone and the clear window) is towards the surface, the swimming attitude would be as shown at the lower right.

of ommatidia, but the total number is 16 in *Cypridina* and 35 in *Philomedes*. There is no indication of the kind of anteroposterior asymmetry seen in *Macrocypridina*.

Internal structure

The entire eye is contained in a thin hypodermal envelope consisting of a cuticular sheath and a single layer of cells. The envelope is only loosely attached to the eye and there is no correlation between the arrangement of ommatidia and hypodermal cells. The cellular composition of the ommatidia is simple and not unlike that of other ostracod compound eyes (see Andersson, 1979).

There is only one class of pigment cell. These lie distally, contain a dark pigment (Figs 4 and 5) and occupy the space between the crystalline cones: one cell in each corner between three cones. The same type of pigment cell also screens the back of the eye where there are no ommatidia. The pigmentation gives the impression of a dark shell around the eye, penetrated only by the crystalline cones.

The shape of the cones depends on their size; the smaller cones are nearly spherical, whereas the larger ones are pear-shaped (Fig. 4). As judged by the staining density in both light and electron microscopy, the cones contain a refractive index gradient. In the smaller ommatidia this gradient constitutes the entire cone, but in the larger ommatidia the gradient is confined to a well-defined body, a lens, inside each cone (Fig. 4). The crystalline cone is composed of two cells, each forming one half. Their nuclei are found basally in the eye, below the rhabdom, and are connected to the cone by thin cytoplasmic threads which lie embedded between folds of the rhabdom (Fig. 5).

Each ommatidium contains six retinula cells contributing equally to a very wide

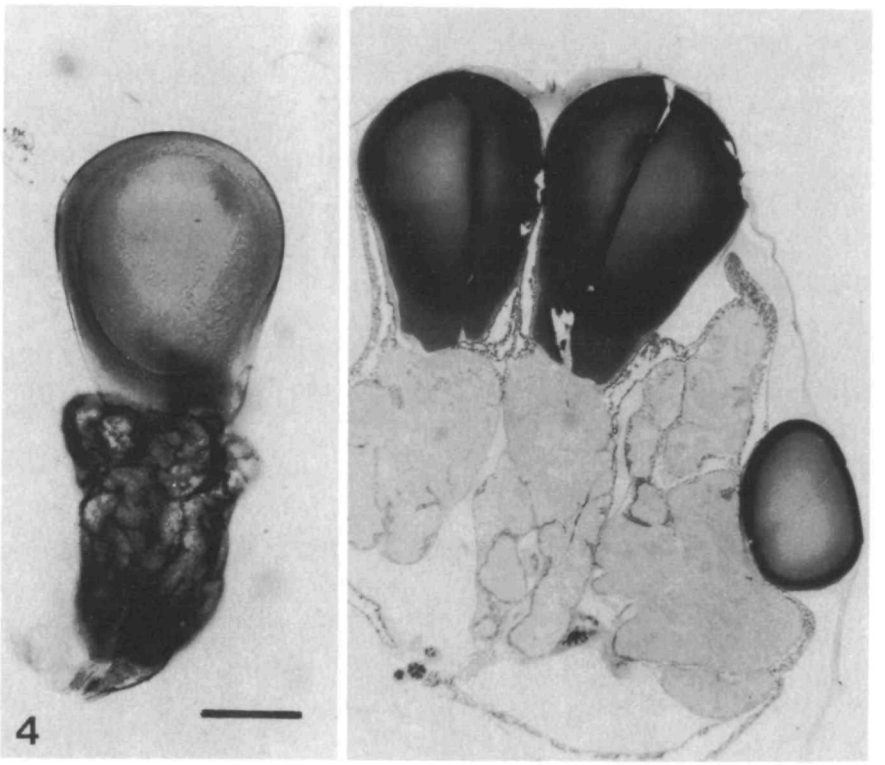

Fig. 4. Ommatidia in the eye of *Macrocypridina*. Left: isolated ommatidium under Nomarski optics. Note the well-defined lens within the crystalline cone. Right: semi-thin section cut across the longitudinal axis of the eye. Two ommatidia with large crystalline cones and narrow fields of view are seen, together with one ommatidium with a small cone and wide field of view. The section shows the lobed and irregular shape of the rhabdoms, the pigmentation in the outer parts of the retinula cells, and the pigment cell layer around the entire eye. Scale bar, 100 μm.

and short rhabdom. The enormous size of the rhabdoms allows only a thin peripheral layer of ordinary cytoplasm in the retinula cells (Fig. 5). This peripheral layer contains tiny, dark pigment granules which probably prevent any light passing between ommatidia. The rhabdom is irregularly arranged into lobes, sometimes partially separated by folds of the peripheral pigmented layer (Fig. 4). It even seems that in some cases these folds would shade parts of the rhabdom and thus impair the sensitivity. Another unusual feature of the *Macrocypridina* eye is that some retinula cell nuclei are displaced down the axon, giving the impression of a bipolar sensory cell (Fig. 5).

The fields of view of individual ommatidia were estimated from semi-thin sections. The refractive index gradient in the crystalline cones is the only lens in the ommatidium and, since this lens is nearly concentric and the eye is in water, the nodal point must be very close to the centre of the gradient. The field of view is then the angle that the pigment aperture between cone and rhabdom subtends at

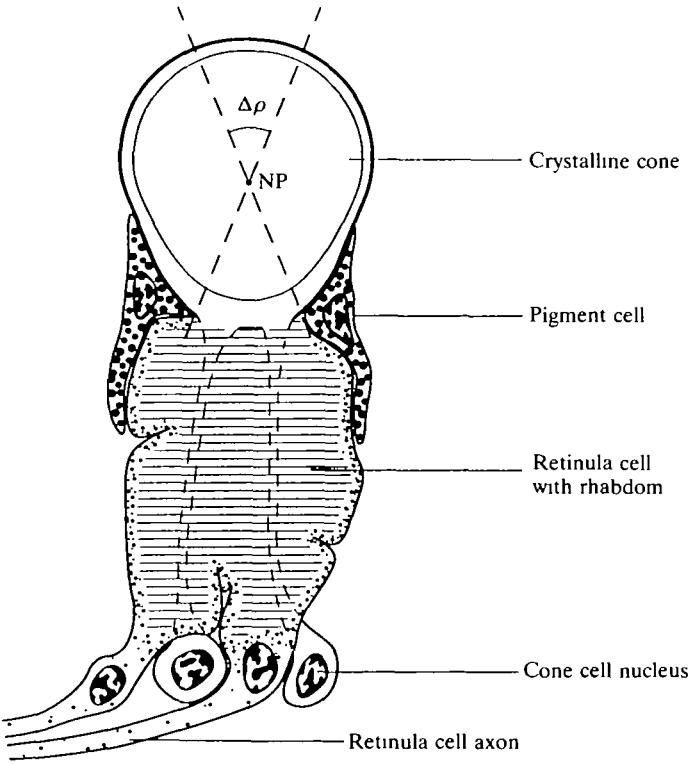

Fig. 5. Semi-schematic diagram of an ommatidium. The principle used to estimate the rhabdom's field of view ($\Delta\rho$) is indicated by the lines through the nodal point (NP).

the nodal point (Fig. 5). This type of estimate is reasonably accurate, and is not dependent on the actual focal length of the lens. Measurements made on several sections cut in different planes revealed a large variation depending on the size of the crystalline cones. The largest cones typically gave acceptance angles ($\Delta\rho$) of 15–20° and the smallest cones 50–60°. These follow the same pattern as the inter-ommatidial angles ($\Delta\phi$), but are about three times longer. These estimates of acceptance angle may be slightly larger than the real physiological values, because the most skew rays travel shorter distances through the rhabdom, but this is certainly not a large enough effect to explain the discrepancy between the $\Delta\phi$ and $\Delta\rho$ values.

Eye movements

The eyes show considerable movement in the pitch plane, rotation occurring around a transverse axis through the optic nerve (Figs 2 and 6). Some of the movement is 'accidental' in that when the second antennae are withdrawn the muscles actually make contact with the eyes and knock them into a more dorsoventral orientation. However, not all movements are passive and, when the antennae are extended and out of contact with the eyes, bursts of spontaneous

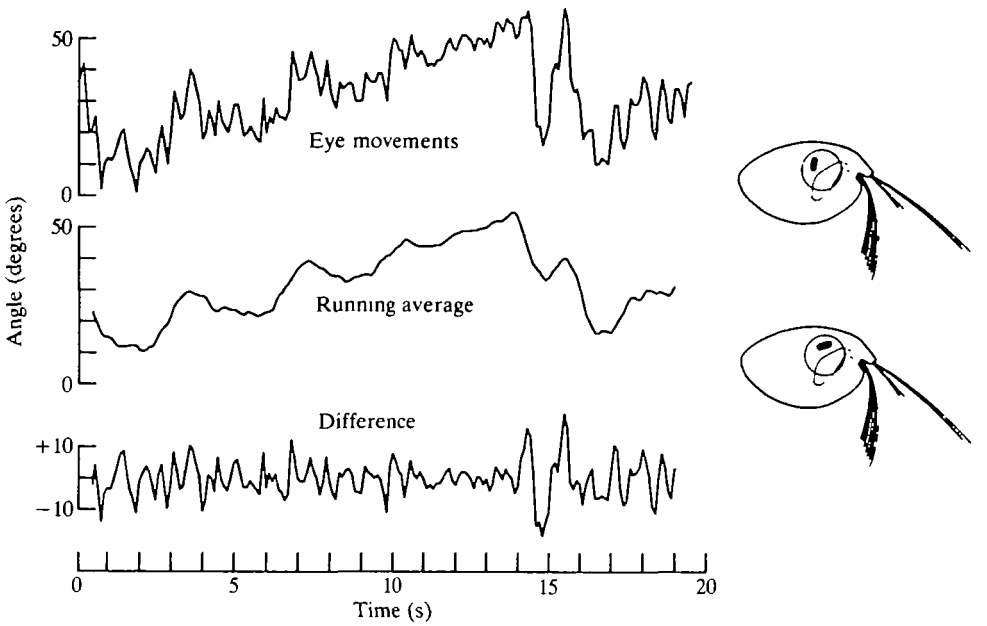

Fig. 6. Eye movements. Top: movements in the pitching plane recorded by analysing video films at 0.1 s intervals. Upward movement of trace indicates a top-backward movement. The extreme positions of the eye are shown on the right. Centre: slow components extracted by making a running average of the top record taking the half-second on either side of each time sample. Bottom: the 'tremor' component obtained by subtracting the middle from the top record. The large disturbance around second 15 is caused by a movement of the second antenna.

activity can be seen. An analysis of a video recording of such a burst is given in Fig. 6. The upper figure shows the full sequence, in which the eye moves through about 50°, rotating top-backwards in the sagittal (pitch) plane. After 14 s there is a large movement caused by retraction of the antennae, followed by resumption of spontaneous movements. The 'spikiness' of the record is not due to measurement error, which is only about 1°. There is a real 'tremor' component, with a frequency of about 2 Hz and an amplitude of about 5°, superimposed on a series of slower movements of larger amplitude. In Fig. 6 these components have been separated by taking a running average of the data (averaging period 1 s), and then taking the difference between this and the original record. The former shows the slow movements and the latter the tremor.

Discussion

Adaptations of apposition eyes to dim conditions

In poor light the ability of an eye to detect local differences in the brightness of the environment – to see, in other words – is determined by the rate at which single receptors, or rhabdoms, absorb photons. The reason is simply that larger photo

numbers provide better statistical samples (see Pirenne, 1967). The photon flux absorbed depends on the brightness of the image (related to the F-number, f/A where f is the focal length and A the aperture diameter), the diameter d of the receptor, its length x and absorption coefficient k. We can define the eye's sensitivity S, by means of equation 1 (see Land, 1981*a*). This gives the number of photons absorbed per receptor when the eye views an extended source emitting 1 photon per steradian per μm^2, if the dimensions of the eye structures are given in μm.

$$S = (\pi/4)^2 \times (A/f)^2 \times d^2 \times (1 - e^{-kx}) . \quad (1)$$

In a compound eye d/f is geometrically the same as the rhabdom acceptance angle $\Delta\rho$, so S becomes:

$$S = (\pi/4)^2 \times A^2 \times \Delta\rho^2 \times (1 - e^{-kx}) . \quad (2)$$

Other things being equal, if one eye has a value of S 100 times greater than another, the first will be able to perform the same visual tasks at a light intensity 100 times lower than the second. Thus for deep-sea eyes we may expect very high values for S. In earlier surveys (Land, 1981*a*, 1984) some deep-sea crustaceans with superposition eyes were shown to have values of S in the hundreds or thousands (when A is in μm and $\Delta\rho$ in radians) compared with values around 1 for diurnal terrestrial eyes, and between 10 and 100 for crepuscular eyes. There was an evident match between environment and eye design.

Data for *Macrocypridina* and some comparable species are given in Table 1. It is

Table 1. *Optical dimensions of ommatidia in* Macrocypridina *and some other arthropods*

Species	A (μm)	$\Delta\phi$ (degrees)	$\Delta\rho$ (degrees)	d (μm)	x (μm)	S (μm^2)
Macrocypridina[1]						
Largest	220	6	15	200	350	1849
Smallest	120	20	50	200	200	4994
Cirolana[2]	150	15	45	100	100	4181
Phronima[3]						
Largest	135	0.44	3.5	10	350	38
Smallest	100	10	15	20	50	120
Limulus[4]						
Light-adapted	200	6	6	17	150	172
Dark-adapted	200	6	13	60	115	683
Leptograpsus[5]						
Light-adapted	45	1.5	2	5	170	1.0
Dark-adapted	45	1.5	3.5	9	170	3.2

References: 1, this paper; 2, Nilsson and Nilsson, 1981; 3, Land, 1981*b*; 4, Barlow *et al.* 1980; 5, Stowe, 1980.

Definitions of symbols are in the text. S is obtained from equation 2, using a value for k of .0067 μm^{-1}.

clear that values for S are very high, and similar to the deep-water isopod *Cirolana* studied by Nilsson and Nilsson (1981) which also has an apposition eye. Both are comparable with that of the reflecting superposition eye of the deep-sea shrimp *Oplophorus* where S is 3300. These high values contrast with the diurnal shore crab *Leptograpsus* where S is only about 1 in the light-adapted eye. Both *Macrocypridina* and *Cirolana* owe their extraordinary sensitivity to a combination of very large facets (A) and large acceptance angles ($\Delta\rho$). *Limulus*, which lives in fairly shallow water but is nocturnal in its habits, has S values not far short of those of the deep-water crustaceans.

The large acceptance and inter-ommatidial angles found in both *Macrocypridina* and *Cirolana* carry the penalty of poor resolution, since grating-like objects will not be resolved if they have periods less than $\Delta\rho$ or $2\Delta\phi$. The eye of neither species achieves good resolution as well as high sensitivity, although there is a weak anterior acute zone in *Macrocypridina*. This contrasts with the situation in the deep-water amphipod *Phronima*, which is also encountered down to about 800 m. Here the value of S is high compared with that of *Leptograpsus*, but not nearly as high as in *Macrocypridina*. However, in the dorsal eyes of *Phronima* the inter-ommatidial angles are very small indeed, less than 0.5°, and this appears to be an adaptation to a predatory life style in which the function of the eye is to detect small objects that are slightly darker than the background provided by the sea surface (Land, 1981*b*, 1989). The key feature here is the devotion of a very large amount of eye surface to a very small visual angle. In *Macrocypridina* there is really no possibility that the eyes could be used in this way. Even if the animal could detect a target that subtended the smallest inter-ommatidial angle, this would still mean that it would only be able to detect an object as large as itself at a distance of 10 body lengths, or about 7 cm. This does not exclude a role for the eyes in the detection of living targets, but certainly means that they cannot detect prey at any distance.

Another comparison can be made between *Macrocypridina* and the freshwater cladocerans *Daphnia* and *Polyphemus*. The former is a suspension feeder and uses its eye principally to maintain body orientation and position in the water column (Young, 1981), whereas the latter is a predator and uses its eye to track prey (Young and Taylor, 1987, 1988). In *Daphnia* there are only 22 ommatidia, there is no acute zone, and the $\Delta\phi$ is nearly 60°. However, in *Polyphemus* there are 130 ommatidia, and in the centre of the pronounced acute zone $\Delta\phi$ is only 2° (Nilsson and Odselius, 1982). *Macrocypridina*, with a total of 54 ommatidia and a minimum value for $\Delta\phi$ of 6° in the acute zone, is thus intermediate, in terms of resolution. Again this does not exclude a role for the eyes in predation, but does not support it either.

Apposition vs *superposition eyes in dim light*

It is often stated that superposition optics are a better solution to the problems of dim-light vision than apposition optics, and yet both *Macrocypridina* and *Cirolana* have apposition eyes with sensitivities (S) comparable with the most

sensitive superposition eyes. Is there some other way that these eyes are less effective than a superposition equivalent? In particular, would eyes of the two types with the same size and sensitivity have the same resolution? To answer this, like must be compared with like, and this is not straightforward because the design principle of a single superposition eye does not allow the range of values of $\Delta\phi$ and $\Delta\rho$ found in *Macrocypridina*. A fair comparison would be with a double superposition eye, like those found in many mid-water euphausiids (Land *et al.* 1979). If the *Macrocypridina* eye is thought of as consisting of two roughly spherical halves each with a diameter of 0.7 mm, representing the higher and lower resolution regions, then a comparison can be made between these and two model part-spherical superposition eyes with *S*-values of 1851 and 5031, respectively (see Table 1).

The first eye, representing the acute zone, need only have a narrow field, like the dorsal part of a divided euphausiid eye. In this case the eye radius could be the full 0.7 mm, and allowing 350 μm for the rhabdom length, the distance (f) from cornea to image would also be 350 μm. The F-number (f/A') for a superposition eye can be as low as 0.5 (*Oplophorus*, Land, 1976), giving an effective pupil diameter (A') of 700 μm, the full width of the eye and clearly the largest possible. Compared with the largest cone diameter of 220 μm in *Macrocypridina*, the pupil diameter of the model eye is 3.2 times larger, and from equation 2 this means that the angular field of view ($\Delta\rho$) of each receptor can be 3.2 times smaller without reducing the *S*-value of 1851. Keeping the ratio of $\Delta\rho$: $\Delta\phi$ the same in the model as in *Macrocypridina*, the angular receptor separation $\Delta\phi$ can also be 3.2 times smaller, and the spatial resolution better by the same factor. The other part of the eye, with a larger field, must be modelled as a spherical superposition eye with a radius of 350 μm, and an image formed at half this depth from the cornea, i.e. 175 μm. With an F-number of 0.5 the effective aperture would be 350 μm, which is 2.9 times larger than the small (120 μm) posterior cones of *Macrocypridina* (Fig. 2). By the same logic as for the first eye, this means that the resolution can be 2.9 times greater without loss of sensitivity.

Degradation of the image quality of dim-light superposition eyes, which is often caused by optical aberrations (Bryceson and McIntyre, 1983; Land *et al.* 1979; McIntyre and Caveney, 1985), does not invalidate this particular comparison. These defects will tend to make the acceptance angle $\Delta\rho$ large in relation to $\Delta\phi$; but in *Macrocypridina* the ratio of $\Delta\rho$: $\Delta\phi$ of about 3:1 is itself already high. This ratio is similar to that estimated for the meal-moth *Ephestia*, which results from image aberrations (Cleary *et al.* 1977), and also to the ratio measured electrophysiologically in dark-adapted crayfish by Bryceson and McIntyre (1983). We conclude that, if *Macrocypridina* had a divided superposition eye with the same size, sensitivity and $\Delta\rho$: $\Delta\phi$ ratio as its actual apposition eye, the resolution would improve by a factor of three.

Roles of eye movements

It is interesting to compare the eye movements of *Macrocypridina* with those of

Daphnia, since both are somewhat similar bivalved crustaceans with small movable eyes. Frost (1975) distinguished four types of movement in *Daphnia*: (i) a high-frequency tremor of 3–4° at 16 Hz, (ii) a slower rhythmic scanning of 5–6° at 4 Hz, (iii) large spontaneous 'saccades', and (iv) optokinetic nystagmus driven by a rotating pattern. Young (1981) also found a 4 Hz, 7° movement, which he described as a tremor, and noted that a number of other cladocerans had a tremor of similar frequency and amplitude. It looks as though *Macrocypridina* shows a tremor analogous to the 4 Hz tremor of *Daphnia* although a little slower (Fig. 6), plus some other movements perhaps like the saccades described by Frost. We made no study here of stabilizing (optokinetic) movements, nor of possible tracking movements like those seen in *Polyphemus* (Young and Taylor, 1987). Our observations lend support to the idea that low-amplitude tremor is important in the operation of the compound eyes of lower crustaceans, but they do not tell us what its function is.

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