

The Optical Geometry of Euphausiid Eyes

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Summary. 1. Euphausiid eyes have all the features of classical refracting superposition eyes. The crystalline cones, which resemble those of moths very closely, are hard, circular in cross section and hexagonally packed. They are thus unlike the optical elements of macruran decapods with reflecting superposition optics, which are soft and square in section.

2. The clear zone always has a thickness of about half the local radius of curvature of the eye, when the centre of curvature is defined as the point of intersection of the axes of the cones. This zone appears to contain only the clear cytoplasm of the receptor cells, and there are no structures that could be considered to be light-guides.

3. It is shown that the crystalline cones have the property of bending incident light across their axes, so that it emerges into the clear zone at an angle equal and opposite to the angle of incidence at the eye surface. This is a necessary condition for superposition image formation.

4. Many deep-water euphausiids have double eyes, usually with a region of enlarged facets pointing upwards and covering a narrow angle, and a downward pointing region covering a wider angle. The upper eye often has a peculiar geometry, with the eye surface centred on a point in the receptor layer, but the long axes of the cones centred on a point twice as deep in the eye. It is shown that this condition produces a superposition image with no axial spherical aberration.

5. A consequence of this arrangement is that the focal plane is flat, not curved as in spherical-eyed forms, and this explains why the retina has a flattened appearance in the upper but usually not the lower eyes.

6. Unlike the eyes of both moths and macruran decapods, euphausiid eyes do not show eye-shine. The rhabdoms are relatively short and wide, and are not shielded by reflecting pigment.

Introduction

The Euphausiacea is a family of shrimp-like crustaceans that inhabit the mid- and deep-water regions of the sea. They are related to the true shrimps and prawns (Decapoda: Macrura) but are usually regarded as more primitive because they lack the specialised thoracic appendages of the decapods. Their eyes are generally large, often double with separate dorsally and ventrally directed regions, and have the general structure of classical superposition compound eyes. That is to say they have a peripheral array of crystalline cones, and a wide clear zone between the crystalline cones and the receptors. Their anatomy was described in the early studies of Chun (1896), and more recently by Kampa (1965) who confirmed Chun's main findings.

The principal reason for the present study is the recent discovery that the eyes of the macruran decapods do *not* employ the refracting superposition mechanism that Exner (1891) devised to account for image formation in nocturnal insects. Instead of the highly refractile 'afocal' crystalline cones found in moths (Cleary et al., 1977; Horridge et al., 1977), both shrimps and crayfish have 'cones' that are square-sided, have a low refractive index, and are silvered over part of their length with a multilayer mirror (Vogt, 1975, 1977; Land, 1976). This array of radially arranged mirrors produces an image of the superposition type (Fig. 1), but by reflection not refraction. Because of their phylogenetic proximity to the Macrura, the Euphausiacea might well be expected to use this same method of image formation. However, existing anatomical studies suggest that this is probably not the case: euphausiid crystalline cones appear to be circular in cross section, not square, and their packing is along hexagonal not orthogonal rows. Both of these features should preclude the reflecting kinds of optical system. This paper sets out to reassess the evidence for and against the three

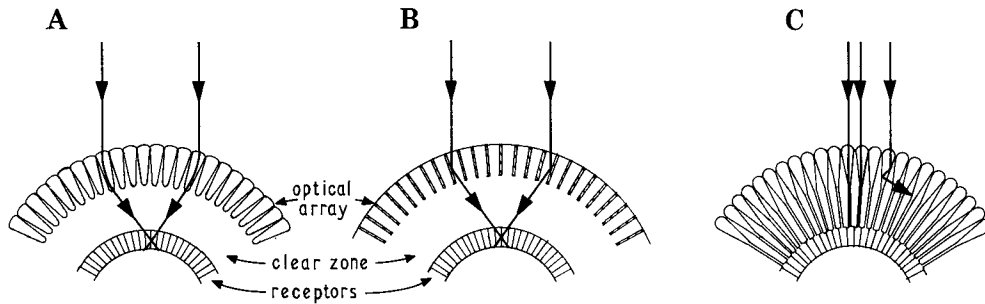


Fig. 1A–C. Candidate mechanisms for image formation in euphausiids. **A** Classical superposition mechanism. Rays focussed by lens cylinders in crystalline cones. Proposed by Chun (1896) endorsing Exner (1891). **B** Reflecting superposition mechanism with multilayer mirrors replacing the refracting cones. Shown to exist in macruran decapods by Vogt (1975) and Land (1976). **C** Light-guide mechanism, with threads crossing the clear zone conducting axial light and excluding off-axis rays. Proposed by Kampa (1965) for euphausiids, and known to exist in some amphipod crustacea (Ball, 1977)

contending hypotheses of how euphausiid eyes work; these are the refracting lens-cylinder mechanism of Exner, some variant of the reflecting arrangement found in the Macrura, or the third possibility proposed by Kampa (1965) that these are really apposition eyes with light guides traversing the clear zone, and joining each crystalline cone to a corresponding rhabdom (Fig. 1). In fact all the evidence, direct and indirect, indicates that these are classical refracting superposition eyes (Fig. 1A).

The double-eyes of the deep-sea euphausiids (Fig. 3) raise special problems. Are the images separate or do they overlap? Are the two eye parts differently specialised in their resolving power or sensitivity? And most intriguingly, why are the two parts of the eyes differently shaped, with the lower eye having typically a concentric structure, but the upper eye an elongated form with the crystalline cones not always aligned at right angles to the eye surface? It turns out that the odd shape of the upper eyes can be explained quite simply: this is the geometrically correct way of constructing a superposition eye with a relatively narrow field of view.

Materials and Methods

Most of the animals were obtained during a recent (summer 1976) cruise of the R.R.S. Discovery in the North Atlantic, from trawls

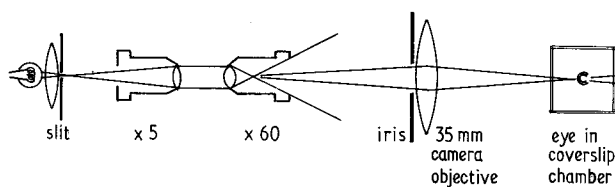


Fig. 2. Arrangement for producing a narrow intense beam of light to illuminate hemisected eyes (Fig. 5)

at depths from 200 to 1,000 m. *Meganyctiphanes norvegica* were supplied by the Glasgow University marine station at Millport, Scotland. For histology, eyes were fixed either in 5% formaldehyde in sea-water or in aqueous Bouin's fluid. They were dehydrated and embedded in araldite, sectioned at 1 or 2 μm with a glass knife and stained with toluidine blue or polychrome stain.

To demonstrate the optical paths in the eye (Fig. 5) requires a narrow but intense beam of light, and this was produced by the device shown in Fig. 2. A microscope lamp bulb illuminates a slit through a field lens which directs the light into a reducing telescope made by mounting two microscope objectives ($\times 5$ and $\times 60$) front to front. The reduced image is projected into a sea-water chamber using a 35 mm photographic lens, and the eye is situated at the final focussed image of the slit. The width of the beam is controlled by the slit width, and its taper by the iris of the projection lens. The chamber containing the eye is made from 4 microscope coverslips, and the sea-water in it has a small quantity of fluorescein added to make the light path visible. Formaldehyde-fixed eyes were used, and these were carefully hemisected with a razor blade.

The measurements on which Table 1 is based come partly from the plates of histological sections in Chun (1896) and Kampa (1965) and partly from new material. In the latter most measurements, the radii of curvature in particular, were made on photographs of formalin fixed, hemisected eyes rather than on histological preparations. This not only avoids problems of shrinkage and distortion, but it is also much easier to see when a cut is properly centred.

A taxonomic comment: "Macrura" is used here to cover all the long-bodied decapods, all of which have reflecting superposition eyes. More recent systems split this group between the Natantia and Reptantia (swimming and crawling) or the suborders Dendrobranchiata and Pleocyemata. The older terminology is kept here partly for convenience and partly because it does coincide well with eye-type.

Results

General Features of Euphausiid Eyes

The original descriptions of these eyes by Chun (1896) were so good that no authors since have had any important amendments to make to them. Kampa (1965) confirmed most of Chun's anatomical findings (while disagreeing with his optical conclusions) and

Meyer-Rochow and Walsh (1978) have added some ultrastructural detail for a spherical-eyed species *Thysanopoda tricuspidata*. Their paper should be consulted for a full review of the anatomical literature. In this section we simply outline the known facts as a background to a discussion of the optical system.

Whatever their shape, euphausiid eyes all contain the same component parts. On the outside is a cornea which consists of several layers of thin parallel-sided cuticle. The cuticle over each crystalline cone is raised into a lens-like dome, so that the whole cornea has a hexagonally faceted appearance. It is unlikely, however, that the cornea itself contributes at all to the

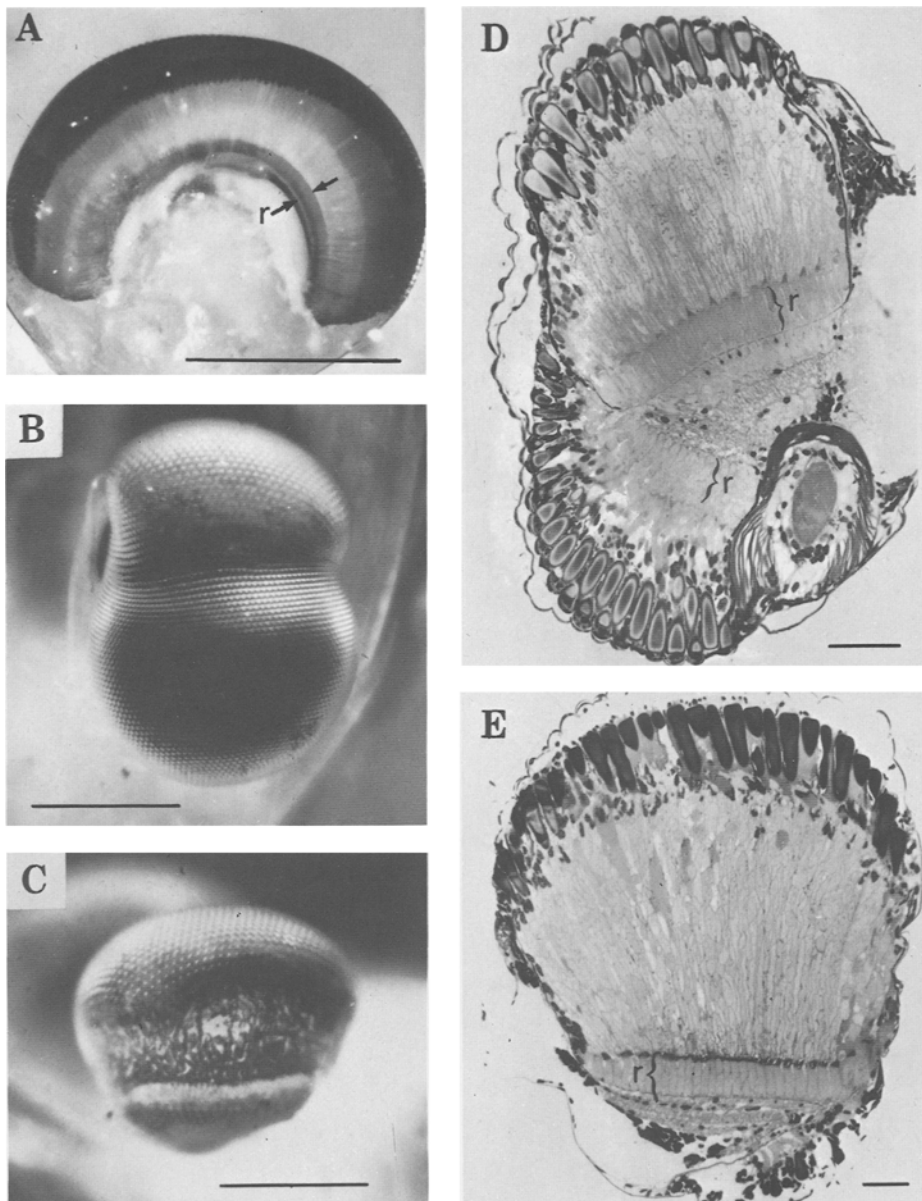


Fig. 3A–E. Gross structure of euphausiid eyes. **A** Spherical-eyed form, *Meganyctiphanes norvegica*, fixed and hemisected. *r*: rhabdom layer. **B** Double-eyed form, *Nematoscelis megalops*, from the live animal. Eye seen from the side with anterior to the right. **C** Eye of *Nematobranchion boopis* in which the lower eye is almost absent. Living animal, seen from the side with anterior to the left. Scale bars on **A–C**: 1 mm. **D** Transverse section through the double eye of *Nematoscelis atlantica*, showing crystalline cones, clear zones and rhabdom layers (*r*). The structure at lower right is a downward-pointing photophore. Receptor nuclei lie beneath the cones. **E** Transverse section of *Nematobranchion boopis* eye. Note that the crystalline cones point to a centre much deeper than the retina, but that the eye surface is centred near or in front of the retina. Scale bars on **D** and **E**: 100 μm . Both are 1 μm epoxy resin sections, stained with toluidine blue

eye's optics because there is no refractive index difference between the two parallel faces of each facet. In some of the double-eyed forms there are often corneal facets with no cones beneath them, especially on the flanks of the upper eye (Fig. 3, and Chun (1896) Fig. 4). Presumably they are functionless developmental relics.

Beneath the cornea lies the array of crystalline cones. Each is a bullet-shaped structure (Fig. 4), almost flat-ended distally where it is widest, tapering proximally to a sharply parabolic point. The cones are often slightly "waisted" about half way along their length. The resemblance between euphausiid cones and those of moths is uncanny (Fig. 4), and it is hard to escape the conviction that this shape reflects a common optical design principle, though exactly what that is (even if it is conceded that both are lens cylinders) is not clear at present. The cones are separated from each other by screening pigment, but only for the distal $\frac{2}{3}$ of their length; as other authors have found (see Meyer-Rochow and Walsh, 1978) the proximal tips are always free of pigment.

In spherical-eyed species the cones are of nearly uniform size (maximum dimensions $115 \mu\text{m}$ by $39 \mu\text{m}$ in *Meganyctiphanes norvegicus*), but in double-eyed forms they may have very different dimensions in the upper and lower eyes, and even between different regions particularly in the upper eye. Table 1 illustrates some of these differences.

Between the cones and the rhabdoms lies a clear zone composed principally of the cell bodies of the receptor cells that make up each rhabdom. These cells have their nuclei distally, near the crystalline cones (Fig. 3), and in transverse sections the cells can be seen as rosettes of 7 membrane profiles, with little or no structural specialisation (Fig. 4). Like Meyer-Rochow and Walsh (1978), and in contrast to Kampa (1965), we have been unable to find any "hyaline threads" or other structures that could be interpreted as light-guides (see Discussion). There seem to be no good reasons for thinking that in life the clear zone is other than transparent and optically homogeneous.

The rhabdoms in spherical-eyed forms occupy a near-hemisphere located about half a radius out from

Table 1. Dimensions of euphausiid eyes

Species	Source eye	Radius of curvature of		$\frac{b}{a}$	Focal length μm	Field of view degrees	Maximum dimension of		
		Eye surface (a) μm	Cone axes (b) μm				Crystalline cones μm	Rhabdoms μm	
Spherical-eyed forms									
<i>Meganyctiphanes norvegica</i>	L	750	750	1.0	340	235°	115 × 39	63 × 17	
<i>Nyctiphanes simplex</i>	K	430	470	1.1	244	—	—	—	
<i>Euphausia pacifica</i>	K	520	515	0.99	276	—	—	—	
Double-eyed forms									
<i>Nematoscelis tenella</i> (= <i>mantis</i>)	C	upper	415	890	2.1	390	70°	90 × 37	75 × 20
		lower	440	420	0.95	180	245°	80 × 33	75 × 14
<i>N. microps</i> (= <i>rostrata</i>)	C	upper	120	365	3.0	205	45°	55 × 20	35 × 9
		lower	160	170	1.1	85	125°	45 × 23	35 × 10
<i>N. atlantica</i> (<i>juvenile</i>)	L	upper	240	580	2.4	190	90°	100 × 35	60 × 15
		lower	260	300	1.2	75	130°	85 × 30	55 × 12
<i>Stylocheiron longicorne</i> (= <i>mastigophorum</i>)	C	upper	235	825	3.5	235	83°	165 × 55	80 × 20
		lower	280	290	1.0	135	130°	60 × 23	50 × 12
<i>S. maximum</i>	L	upper	677	1880	2.8	940	51°	160 × 45	50 × 20
		lower	808	808	1.0	376	120°	130 × 40	50 × 17
<i>Nematobranchion boopis</i>	L	upper	865	2189	2.5	1229	48°	200 × 65	90 × 25
		lower	—	rudimentary —	—	—	—	75 × 35	60 × 20

Notes

1. Sources. C: Chun (1896); K: Kampa (1965); L: Land, Burton & Meyer-Rochow (this study)
2. A ratio b/a of around 1 implies spherical symmetry (Fig. 7A). b/a greater than 2 implies the condition in Fig. 7B
3. Focal length and field of view are as defined in Fig. 10. The fields of view are only approximate since they depend very heavily on the planes of the sections used

the centre of the eye. They are banded structures composed of layers of microvilli contributed by the 7 receptors, and with alternating orientations (Meyer-Rochow and Walsh, 1978). The rhabdom dimensions do not vary much between species (Table 1) and those of *M. norvegica* (63 μm long by 17 μm wide) are fairly typical. In cross section they are square, and form a brickwork-like pavement, with very little space between one rhabdom and the next. There does not appear to be much pigment in this region of either an absorbing or reflecting kind (this is particularly odd, since in both Lepidoptera and in macruran decapods – both of which have superposition eyes – the rhabdoms are optically isolated from each other by one or both types of pigment). This point may require more fresh material for clarification. Distal to each rhabdom is a densely-staining structure that extends a short distance into the clear-zone, and which Meyer-

Rochow and Walsh (1978) refer to as a rhabdom-lens. In some accounts it appears pointed and in others domed. It probably does have an optical function, and various possibilities are discussed by Meyer-Rochow and Walsh (1978), but quite what this is still obscure. These authors also describe a cup-shaped structure behind each rhabdom which they designate as a reflector. There is certainly something there, but it appears not to have the laminated structure one would expect of a reflector (see Land, 1972). Further, if there were reflectors behind the rhabdoms one would expect to see “eye-shine” when a fresh eye is viewed from the direction of the incident light (just as in some moths and macruran Crustacea, see Kunze, 1972). One of us (M.F.L.) has looked hard for this in living eyes, but not found it, and the inevitable conclusion seems to be that there is no reflecting material either behind the rhabdoms or around them.

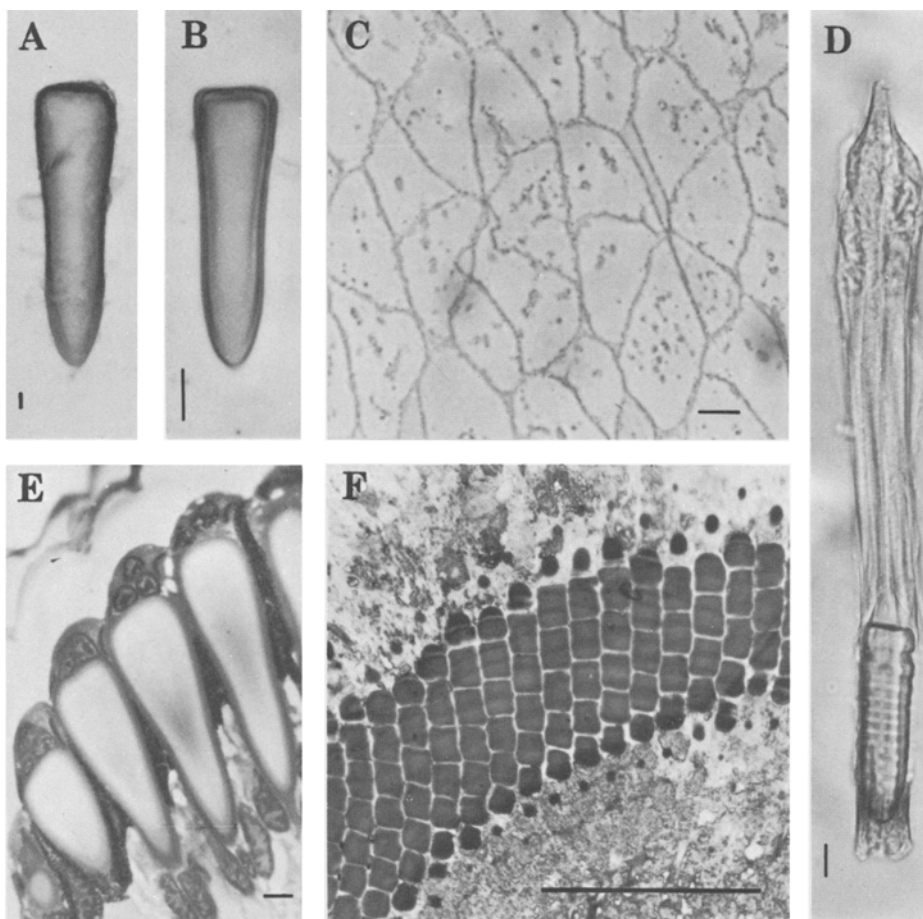


Fig. 4A–F. Structural details. **A** and **B** Intact crystalline cones from a euphausiid (*Nematobranchion boopis*) and a moth (*Noctua pronuba*), respectively. **C** Tangential section through the clear zone of *N. boopis*, showing membrane profiles of two groups of 7 receptors and absence of light-guide-like structures. **D** Dissection of one rhabdom from *Meganyctiphanes norvegica* (fixed but unstained) showing banded appearances and the distally situated cell bodies. **E** Cone region of *Nematoscelis atlantica* showing screening pigment not extending to proximal tips of cones. **F** Oblique tangential section through rhabdom layer of *Euphausia gibboides* showing square packing. Scales on **A–E**, 10 μm , and on **F**, 100 μm . **C**, **E** and **F** are 1 μm epoxy resin sections stained with toluidine blue or polychrome stain

The peculiarities of the geometry of the double eyes of some euphausiids are discussed in a later section.

A Demonstration of Superposition Image Formation

When a narrow (ca. 30 μm diameter) light beam is directed just below the cut surface of a fixed hemisected eye of *Meganctiphanes norvegicus* it is possible to see the initial path of the refracted ray as it emerges from the cone layer (Fig. 5). It is visible because the material of the clear zone, after fixation, scatters an adequate amount of light. For the same reason, however, the light beam only manages to penetrate through about half the depth of the clear zone, so that the point at which the rays intersect the rhabdom layer cannot be clearly made out. Nevertheless, by moving the light beam across the surface of the eye, and photographing the refracted beams for several positions of the incident beam, the position of the focus for parallel light entering the eye can be built up by extrapolation of the visible portions of the emergent beams. The result is illustrated in Fig. 6A, which shows that within the limits of the accuracy of the extrapolation all rays meet at a point in or close to the rhabdom layer, as would indeed be expected. It does seem, however, that the outermost rays of the total bundle intersect each other slightly in front of the rhabdom layer, and in front of the point of intersection of the more axial rays. This is a consistent observation, and as we shall see it is what one would expect if the cones redirect light across their axes as though they were mirrors; that

is, the angle between the incident ray and the cone axis is the same as that between the emergent ray and the cone axis.

Refraction by the Crystalline Cones

The important optical properties of the crystalline cones can be defined in terms of the relationship between the angle that an incident beam makes with the cone axis (α) and the angle between the same axis and the refracted beam (β). This relationship is shown in Fig. 6B, and it is apparent that rays entering the cones are deviated by an angle nearly equal to twice the angle they first encountered with the cone axis. I.e., $\beta \simeq \alpha$, or the total bending ($\alpha + \beta$) is about 2α , for all values of α up to roughly 30° which seems to be the highest angle a cone will accept. Above this no emergent ray is visible. The parallel demonstration, for a skipper butterfly, is given by Horridge et al. (1972). In both cases the relation between α and β is closely approximated by a straight line with a slope of one: rays are bent in the cones through twice the incident angle.

A consideration of the refractive powers of the front and rear surfaces of the cones leads to the conclusion that surface refraction alone cannot explain this degree of ray-bending, and that it is necessary to invoke lens-cylinder properties in the cones themselves. The conditions for this kind of refraction were specified by Exner (1891). He concluded that the refractive index of the cones must decrease from the centre outwards, and the exact form of the required refractive index gradient was determined by Fletcher et al. in 1954. Exner called this type of optical struc-

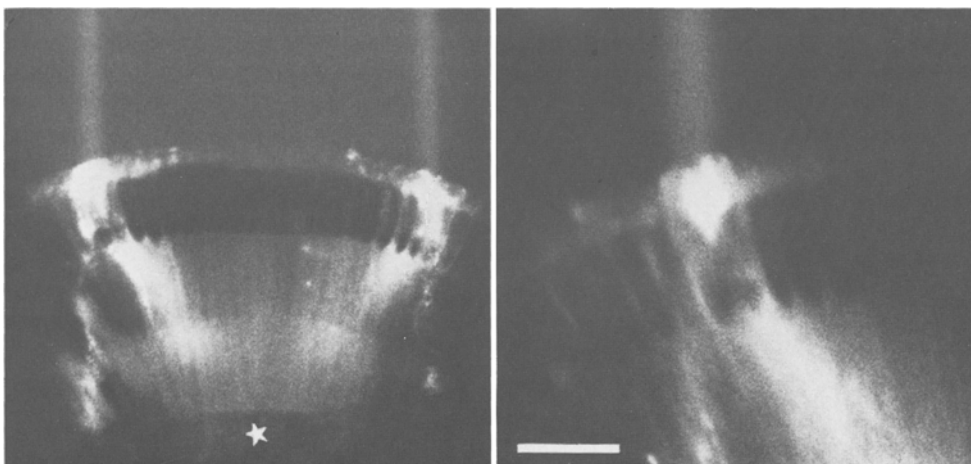


Fig. 5. Light paths of rays refracted by the cone layer of *Meganctiphanes norvegica*. Left: double exposure. The refracted rays are converging to a point in the rhabdom layer (*). Right: refraction by one or two cones showing that the incident ray is bent across the axis of the cones. Scale 100 μm . Both photographs were made on formalin-fixed, hemisected eyes. Incident beam made visible with fluorescein, refracted beam is light scattered out from the fixed tissue and is therefore wider and less sharp than it would be in a living eye. The apparent continuation of the incident beams is simply the intersection of the slit-like beam with the cut surface, and is irrelevant. Both photographs $\frac{1}{2}$ h exposure on Ilford HP5 film

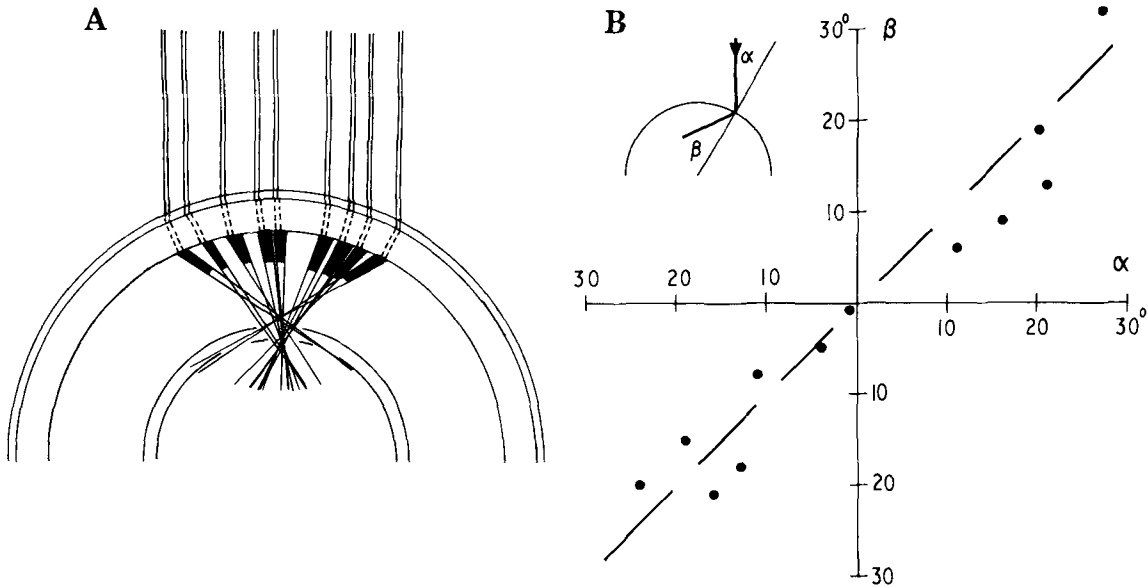


Fig. 6. **A** Reconstruction of initial refracted light paths from 9 photographs like those shown in Fig. 5. Visible portions are shown solid black, and these have been extrapolated to their focus, which lies in the rhabdom layer. **B** Relation between incident angle (α) and refracted angle (β) using data from **A** and 3 other photographs. Dashed line implies that $\alpha = \beta$. Calculated regression line actually has a slope of 0.91, and a standard error of 0.08. 95% confidence limits for the slope are 0.74 and 1.08

ture a “lens-cylinder”, and all that the present study has done is to reconfirm the necessity of Exner’s conjecture; the cones must act as lens-cylinders. That this is so is actually more obvious here than in moths because, with water on the external face the cones have no cornea/air interface that might contribute to the ray-bending properties of the structure as a whole. It is worth noting that Chun had accepted the lens cylinder explanation in 1896.

The Aperture of the Superposition Pupil

The largest angle β at which it is possible to observe rays leaving the crystalline cones in the direction of the image is about 30°. When the whole eye is illuminated from a point source the cone of light seen converging to a focus through the clear zone has an angular width of 100°. This should be equal to $2 \times 2\alpha$, giving a value for α of about 25°. The limiting value of α and β is thus somewhere between 25 and 30°. Translated into the amount of eye surface that collects light onto a single image point, this means that the effective aperture has a diameter of about half the diameter of the whole eye ($\alpha = 30^\circ$) as seen from the direction of illumination.

Another way of putting this is that the *F-number* of the eye, in photographer’s terms, is 0.5, which is impressive since the lowest *F-number* currently available in man-made lenses is about 0.9. The image in euphausiid eyes should be brighter than that of the best camera lens by a factor of $0.9^2/0.5^2$, or about

3.2. The *F-number* of the human eye with a fully open pupil is about 2, meaning that our image is dimmer than that of a euphausiid viewing the same scene by a factor of 16.

The Spherical Aberration of Superposition Eyes

Superposition eyes which cover a large field of view – a substantial part of the 360° around them – are necessarily spherically symmetrical. This is because any departure from spherical symmetry in one part of the eye, in the interests of improved resolution, will distort or degrade the image elsewhere. Thus we find that the “wide-angle” eyes of coastal euphausiids

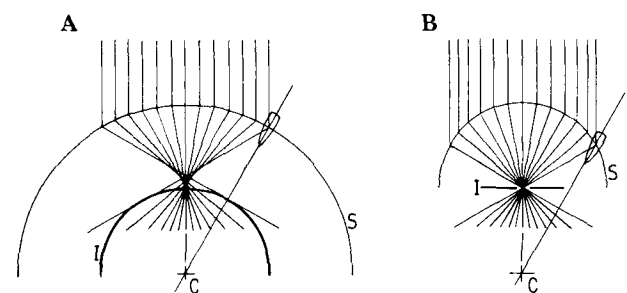


Fig. 7. **A** Construction showing extent of aberration in a spherically symmetrical superposition eye in which each cone behaves as an “ideal superposition element” ($\alpha = \beta$ for all values of α). **B** Construction showing that this aberration is removed if the eye surface is centred on the image point but the axes of the cones themselves are centred at twice that depth. *S*: surface containing crystalline cones; *C*: centre towards which all cone axes point; *I*: image surface

like *M. norvegica* (Fig. 3) are almost perfectly spherical, with the cornea, the rhabdom layer and the axes of the crystalline cones all sharing a common centre of curvature. There is an important disadvantage to this spherical arrangement, and that is that if the crystalline cones behave as “ideal superposition elements” (which can be arbitrarily defined as optical structures for which $\alpha = \beta$, for all values of α) the image will not be sharp, but will suffer from a defect very similar to the spherical aberration of an ordinary spherical lens (Fig. 7A). Light from a distant source making large angles (20–30°) with the axes of the crystalline cones will not be refracted to the axial focus, but to a point somewhat in front of it, and the result will be that the “focus” is a circle of confusion many rhabdoms wide situated well in front of the focal point for rays parallel to the crystalline cone axes (Fig. 7A).

Can Superposition Eyes Form Perfect Images?

Where an eye is required to produce an image over only a small sector of the surroundings it does not have to be spherically symmetrical, and one might expect that the various surfaces (cornea, cones and receptors) might be arranged in such a way as to minimise or eliminate the optical defects imposed by the constraint of spherical symmetry. Clearly, the upper eyes of deep-sea euphausiids are not spherically symmetrical (Fig. 3), and the interesting question is whether the differences in geometry that they show can be interpreted as useful, in the sense that they improve the quality of the image.

An obvious starting point is to ask whether the crystalline cones producing the defective image in Fig. 7A can be shifted around in some way so that the refracted rays are all imaged at the same point. For example, if the outermost crystalline cones in Fig. 7A were brought down slightly their refracted rays could be made to intersect the other rays at the axial focus. It turns out that there is a simple solution to the problem, which is that the axes of the cones should remain directed towards a centre of curvature lying twice as deep as the receptor layer (C: Fig. 7B and 8A) but that the centre of curvature of the layer containing the cones should lie *in the receptor layer itself*, rather than at C as in the spherically symmetrical eyes. The proof of this is given in Fig. 8A. A ray APX passes axially through a cone, and is not deviated. A second ray BQ is drawn parallel to it, and this is refracted by the cone at Q along QX . From the definition of an “ideal superposition element” the angles $S\hat{Q}B$ and $X\hat{Q}C$ must be equal. However, the angles $S\hat{Q}B$ and $Q\hat{C}X$ are also equal,

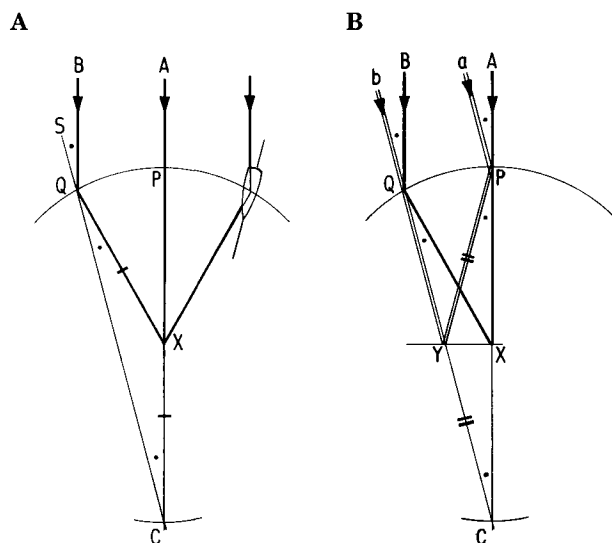


Fig. 8. A Proof that the geometry of Fig. 7B produces perfect imagery at X (see text). B Demonstration of the fact that off-axis rays (a, b) form images in a flat plane through X (see text)

because BQ is parallel to AC , and hence angles $X\hat{Q}C$ and $X\hat{C}Q$ are equal. Triangle XQC is thus isosceles, and QX equals XC . Thus all points like Q must be equidistant from X , which means that they must all lie on a circle of radius XC centred on X .

This arrangement thus produces an aberration-free image at X . It is not the only possible configuration that will do this – in principle the cones could be arranged on a surface of almost any shape provided each is angled appropriately. It is, however, probably the simplest in that this is the only arrangement in which the cone axes have a common centre of curvature, which is possibly important developmentally. More important perhaps, this is the configuration that one actually observes (Fig. 3).

The Shape of the Image Surface

Having established that perfect superposition imagery is possible for *one* point (X) in image space, we can then ask whether other points in the image region receive a good image as well, and if so, what is the appropriate configuration for the receiving layer? The answer to the first question appears to be a qualified yes, and to the second that the receiving layer should be flat, not spherical as in Fig. 7A. Fig. 8B shows how this result is arrived at. Rays from A and B are imaged at X as before. A ray bQ directed towards C passes straight along the axis of the cone at Q without deviation, but a ray aP parallel to it is refracted at P and intersects bQC at Y . Angles $a\hat{P}A$ and $b\hat{Q}B$ are equal because AP

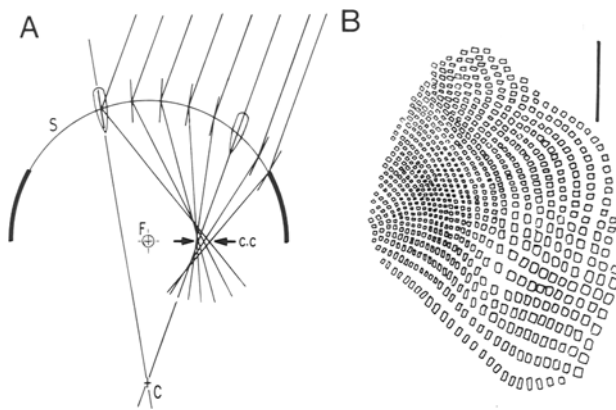


Fig. 9. **A** Off-axis imagery is not perfect in an eye of the type shown in Fig. 7B, but the best image still lies on or near a plane through *F*, the aberration-free focus and centre of curvature of the cone-containing surface (*S*). In this construction, which resembles an upper eye, the cone-containing surface subtends 60° at the centre of curvature of the cone axes (*C*) and it is assumed that the maximum value of α and β (Fig. 6) is 30° . *c.c.* is the circle of least confusion for rays inclined at 20° to the axis of symmetry of the eye. **B** Complete section through the retina of the upper eye of *Stylocheiron longicorne* (= *mastigophorum* Chun). From Chun (1896). Note the differences in receptor separation. Scale bar: 100 μm approx.

is parallel to BQ and aP to bQ , and if P and Q are “ideal superposition elements” then the angles XPY and XQY will also be equal. Also, from the previous argument, XQY is equal to XCY , so that XPY and XCY are equal and PYC is an isosceles triangle. PY and YC are thus equal, which means that the locus of all image points like Y is a straight line (or flat plane in a 3-dimensional structure) aligned at right angles to the axis PC .

If one draws in other image-forming rays, in addition to PY and QY , it becomes clear that they do not all intersect exactly at Y , and that off-axis image formation is not perfect (as it is at X). However, the interesting thing about the circles of confusion that are generated by complete ray-tracing is that they are all still centred about the straight line XY . The best image surface thus is flat, although resolution is perfect only on the axis of symmetry of the eye (Fig. 9A).

Conclusions: The Design of an Aberration-Free Superposition Eye

The outcome of the preceding arguments is an eye whose form is like that shown in Fig. 7B, and the major “design features” are (1) that the surface containing the crystalline cones is a sphere centred near the centre of the receptor layer; (2) that the axes of the cones are directed to a point (C) lying twice

as deep as the receptor layer; and (3) that the receptor surface is flat, rather than concentric either with the eye surface or with axes of the crystalline cones. The total field of view of an eye constructed in this way cannot exceed an absolute maximum of 90° , and in reality probably a lot less, so it is not usable as an “all-round” eye. Several similar eyes could, of course, be combined.

The Form of the Upper Eyes of Double-Eyed Euphausiids

The structure of the upper eyes of some of the deep-water euphausiids does conform remarkably well to the design outlined in the preceding section. Figure 3 shows (1) that the eye surface is approximately spherical, and is centred near, or even in front of the receptor layer; (2) that the crystalline cones themselves – especially those near the periphery of the eye – are not aligned at right angles to the eye surface, but instead have their axes pointing towards a much deeper part of the eye. The point of convergence of the cone axes is approximately twice as deep as the receptor layer (Table 1, a and b); and (3) the receptor layer is either flat, as in *Nematobranchion boopis*, or only slightly curved in some other species. This is in striking contrast to the configuration in the spherically symmetrical types and also in the lower eyes of double-eyed forms where the retina is usually concentric with the corneal surface. The points (1–3) above are clear not only from this study (Fig. 3) but also from the plates of Chun (1896) and Kampa (1965).

The correspondence between these features and those outlined for the “ideal” eye suggests very strongly that these eyes have evolved to provide excellent resolution over a relatively narrow, dorsally directed field of view. There are, however, differences in detail between real eyes and the model eye shown in Fig. 7B that suggest that this idealisation is not the complete story. The surfaces of the upper eyes are not always exactly spherical; the eyes shown in Fig. 3B and C, for example, are somewhat elliptical in profile. In *Nematobranchion boopis* the eye is also asymmetrical, with a stronger curvature transversely than sagittally. Furthermore it is not always clear that the cone axes point towards a single point twice as deep as the receptor layer, but rather intersect in a broader region centred around such a point.

The divergences from the scheme in Fig. 7B are minor, but they do suggest that there may be additional subtleties in the way the cones are arranged. One possibility is that these are concerned with improving the quality of the image over a larger area

than would be provided by the model eye, which only has better resolution than the spherically symmetrical type over an angle of about 10° . However, there is an indication from one of Chun's figures that in one species at least (*Stylocheiron longicorne*) there is a "fovea" in which the receptors are more closely packed ($5\ \mu\text{m}$) than they are around it ($15\ \mu\text{m}$) and this is indirect evidence that the field of view is not of uniform quality, just as in the model eye (Fig. 9B). Alternatively, if the cones departed substantially from the "ideal" condition (i.e., $\beta \neq \alpha$) this too would introduce non-spherical distortions into the arrangement required for perfect image formation.

We feel that the hypothesis outlined in Figs. 7 and 8 is as close an approximation to the true situation as we can make at present, and that a comprehensive examination of all the possible ways of improving the quality of superposition images is a study beyond the scope of this paper.

Discussion

Superposition Optics

The evidence given here wholly supports the belief that euphausiid eyes employ classical (refracting) superposition optics, as Chun (1896) originally proposed. The crystalline cones bend light in precisely the manner required by Exner's theory (1891), and there is no evidence of any structures crossing the "clear zone" that could reasonably be expected to function as light guides. The latter point is rather important, since at least some insect eyes probably function in a "dual-mode" kind of way (see Horridge, 1975) with superposition optics in the dark, but an approximation to apposition optics in the light-adapted state, the change being brought about by the radial migration of pigment in the clear-zone cutting off the more oblique rays. It has often been inferred, though never we believe adequately demonstrated, that in the latter state the remaining light passes from crystalline cone to rhabdom down some form of light guide. This kind of argument cannot be applied to euphausiid eyes because they appear to have no equivalent adaptation mechanism. It can reasonably be supposed that all published figures of these eyes are from animals exposed to the light after capture, and yet not one illustration shows opaque pigment even reaching the proximal tips of the crystalline cones. Euphausiids are for the most part deep-sea animals, and probably no adaptation mechanism is necessary as the light is always dim. In any event, for an eye without a "longitudinal pupil" mechanism of adaptation, light-guides or other inhomogeneities in the clear zone would not only be redundant, they would actually spoil the quality of the superposition image.

However, Kampa (1965), certainly saw structures that she interpreted as light-guides in histological material, although she comments that they were only about $1\ \mu\text{m}$ wide [in animals that really do have light-guides, like the amphipod *Phronima* (Ball, 1977) these are much wider, $10\ \mu\text{m}$ or more]. Probably what she saw were the cell membranes of the receptors, whose nuclei are situated distally in the clear zone. Especially where several membranes join in the centre of each rosette of cells (Fig. 4) there is inevitably a local concentration of material that would stand out in sections, but there is no reason at all to suppose that this conducts light. It should perhaps be remembered that in the 1960's belief in Exner's superposition theory was in a temporary decline: for example Kuiper (1962) had rejected the superposition principle for decapod crustacean eyes on the grounds that the required refractive index variations were not present (he was right, but mirrors later came to the rescue) and had cast doubt on the existence of "lens-cylinder" optics in insects (this was resolved by Seitz in 1969). There was thus a need to find alternatives to superposition optics at that time, and the only other candidate seemed to be a light-guide theory. In fact Kampa (1965) in her conclusions gives an interesting insight into the poor esteem in which the superposition theory was then held. Of the lobster eye: "The image formed is of the superposition type, informing the animal that light conditions may be changing but giving it no discrete picture of the objects within its field of vision". And of euphausiids: "On these grounds, then, the euphausiid eye, like that of galatheids, can be credited with the capacity for apposition-type vision and mosaic-image formation, and can be elevated to the category of having good image formation amongst crustacea". Fortunately, there are no longer good reasons for believing either that lens cylinders do not exist, or that superposition images are inherently poor.

The final piece of indirect but strong evidence in support of the superposition mechanism in euphausiid eyes comes from a consideration of the shape of the upper eyes of double-eyed forms. As outlined in the Results, this makes perfect sense as an arrangement for improving the quality of the superposition image over a narrow angle, but no sense at all on any other basis. This unexpected explanatory power of the superposition principle is a further test of the correctness of the principle itself.

The Optical Meaning of the Shapes of Double Eyes

The shapes of the eyes of mid-water euphausiids vary greatly between species, so much so that they are

important taxonomic characteristics. Different species live at different depths, and hence light conditions, and they may well also require vision for different purposes. (The double-eyed species tend to be carnivorous and the round-eyed species filter-feeders, though this is not a hard and fast rule: Dr. A. Baker, personal communication.) It would be valuable, therefore, to try to establish some rules for interpreting eye structure in terms of visual parameters that may have some meaning in the lives of the animals.

The view proposed and, hopefully, demonstrated in this paper is that these eyes obey the rules of classical superposition optics. This means that, like ordinary lens eyes, it is possible to derive a number of useful properties just from their geometry and dimensions. The three most important are (i) the minimum resolvable angle; (ii) the field of view; and (iii) the absolute sensitivity (Fig. 10).

All three properties depend on a knowledge of the focal length of the eye (f), and it is not immediately clear, in a superposition eye, what this is. In a lens eye the appropriate measurement is the 1st focal length, or posterior nodal distance. That is, the distance from the nodal point, through which all rays pass undeviated by the optics, to the image surface. In a superposition eye the nodal point is at the centre of curvature of the eye as determined by the point of intersection of the cone axes (Fig. 10); and the focal length is the distance out from the centre of curvature to the image plane. In an eye of the euphausiid type, where each optical element rotates rays across its axis (like a mirror: angle $\beta \approx$ angle α in Fig. 6B) the focal length will also be equal to the distance in from the centres of the crystalline cones to the image surface. For practical purposes it doesn't matter which measure is taken, but the easier one to obtain, histologically, is the distance from the centres of the crystalline cones to the centre of the rhabdom layer – which we assume that natural selection has put in the appropriate place to receive the image! With the focal length defined, the calculation of minimum resolvable angle, field of view and absolute sensitivity can be performed as for any other eye, using the data in Table 1.

A convenient way of defining resolution is by the angle ($\Delta\phi$) subtended at the nodal point (and hence in outside space) by the centre-to-centre separation of adjacent receptors (Fig. 10). If the receptor separation is d , then

$$\Delta\phi = \frac{d}{f}(\text{rad}) \quad \text{or} \quad 57.3 \frac{d}{f}(\text{deg}).$$

A pattern of stripes will not be resolvable, however good the optics of the eye, if one period of the stripe pattern subtends an angle greater than $2\Delta\phi$ (see

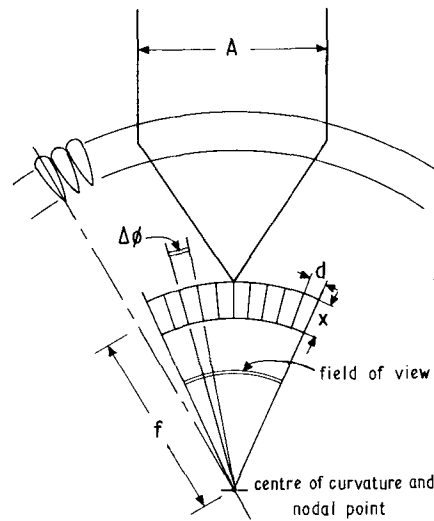


Fig. 10. Definitions of symbols used in the Discussion

Kirschfeld, 1976), so this anatomical constraint imposes a real limit to an animal's ability to separate visual targets. In *M. norvegica*, a typical spherical-eyed form, f is $340 \mu\text{m}$ and d is $17 \mu\text{m}$, so that $\Delta\phi$ is about 2.9° . In the double-eyed species *S. maximum*, $\Delta\phi$ for the lower eye is similar (2.6°), but for the upper eye it is very much smaller (1.2°). This doubling of resolution is due entirely to the greater focal length of the upper eyes, and seems to be typical of other double-eyed species. They should be able to see finer detail upwards.

The field of view is the angle the retina subtends at the nodal point. In *M. norvegica* this is about 235° . In the lower eye of *S. maximum* it is about 120° [although in some species like *Nematoscelis tenella* (= *mantis*), figured by Chun (1896) the lower field is clearly much larger: about 245°]. The field of the upper eye of *S. maximum*, however, is quite small, about 51° . In *Nematobranchion boopis*, which effectively only has an upper eye, the field is similar in size, about 48° . It is a fair generalisation to say that the lower eyes have wide fields and low resolution, and the upper eyes narrow fields but higher resolution (Table 1).

The sensitivity of an eye is harder to assess, but it is in principle possible to determine, for a given background luminance, how many photons per second single receptors will absorb, and it is this that limits the eye's ability to resolve well in dim light. Sensitivity depends on the light collecting power of the optical system, which as in photography is given by the reciprocal of the square of the *F-number*, i.e. $(A/f)^2$, where A in a superposition eye is the diameter of the whole patch of eye surface that contributes to the image at a single retinal point. It also depends

on the cross sectional area of the receptors, and on their length, as it is the latter that determines the proportion of incident photons that are absorbed. The full expression relating photons absorbed per receptor to photons emitted by a unit area of an extended source is:

$$S = \left(\frac{\pi}{4}\right)^2 \left(\frac{A}{f}\right)^2 d^2 (1 - e^{-kx})$$

where A is the aperture diameter, f the focal length, d the receptor diameter, x the receptor length, and k is the natural extinction coefficient of the photopigment in the receptors. A full derivation is given in Land (1979), but the principles are well explained by Kirschfeld (1974).

Of the various terms in this equation, the relative aperture (A/f) and receptor width (d) are much the same as they are in the reflecting superposition eyes of macrurans (Land, 1976). The rhabdom length (x), however, is rather shorter, with a typical value around 60 μm compared with 100 μm in the mesopelagic shrimp *Oplophorus*, and as much as 240 μm in the lobster *Homarus* (Bruno et al., 1977). If a euphausiid rhabdom had the same pigment density as a lobster rhabdom ($k=0.0067$; Bruno et al., 1977) it would only absorb about 33% of the light reaching its distal end. If each rhabdom had a reflective backing (as is the case in the Macrura) this would nearly double the effective length, but the present evidence is against this suggestion. There is thus a real problem: either euphausiids waste 67% of the light reaching their eyes, in a situation where photons are scarce, or they must have rhabdoms whose pigment density is much higher than in the macrurans. Whether or not the short rhabdoms of euphausiid eyes make them less efficient at exploiting the available light remains to be seen.

One of the most interesting groups, in terms of eye structure, are the *Stylocheiron* species. The upper eyes of some of these double-eyed forms are greatly reduced, not in length but in the number of facets and area of eye surface. In four species for which information is available, *S. suhmii* has only 3 crystalline cones per row and lives at a daytime depth of 0–50 m, *S. affine* has 4–8 cones per row and lives at 40–140 m, *S. longicorne* has 7–19 cones per row and lives at 100–380 m, and *S. elongatum*, with 13–16 cones per row and a clearly wider upper eye surface, lives between 180 and 420 m. The eye data are from Brinton (1975), and depth data from Baker (1970). This relationship between upward-pointing eye surface and depth strongly suggests that the surface living species simply reduce the light reaching the retina by having fewer cones, and thus a smaller aperture (A) contributing light to the image. This seems a

clumsy and inflexible way of reducing eye aperture, compared with the kind of radial pigment migration mechanism of light adjustment found in lepidopteran insects and most macruran crustacea, but for animals that have evolved to live in different stratified light environments it probably makes just as much sense as having an adjustable pupil. There is no reason why the reduced size of the effective aperture in these species should have any effect on either resolution or field of view of the eye, but further anatomical studies could easily clarify this.

Eye Structure and Phylogeny

The difference between the structures of macruran eyes with reflecting superposition optics (Fig. 1 B) and those of the Euphausiacea with refracting optics (Fig. 1 A) is so profound that it is difficult to believe that the two groups are at all closely related. The square-sided multilayer-coated cones of the Macrura, and the perfected lens-cylinder cones of the euphausiids are different in ways that would require a great number of coordinated modifications if one were to evolve into the other. Taxonomically, therefore, the principle of optical design employed must be a very "conservative" characteristic, and a reliable indication of a group's origins.

For reasons given in detail in Vogt's paper (1977) reflecting superposition eyes *must* have square facets, basically because a square "corner reflector" will reflect light so that the incident and doubly reflected rays lie in the same plane, whereas hexagonal reflectors do not have this property, and cannot form images. On the other hand, hexagons are the naturally most compact way of packing structures that do not have to be square. What this means is that if an eye has square facets it is almost certainly of the

Table 2. Probable optical mechanisms in some malacostracan crustacea

	Corneal geometry	Clear zone	Optical mechanism
Mysidacea	Hexagonal	Present	Refr. Sup.
Euphausiacea	Hexagonal	Present	Refr. Sup.
Macrura	Square	Present	Refl. Sup.
Anomura			
Galatheids	Square	Present	Refl. Sup.
Eupagurids	Hexagonal	Absent	App.
Brachyura	Hexagonal	Absent	App.

Refr. Sup. = Refracting (classical) superposition
 Refl. Sup. = reflecting superposition
 App. = apposition

reflecting type, and if hexagonal, of the refracting type. Some rare exceptions do employ light-guide mechanisms (like the amphipods *Phronima* (Ball, 1977) and *Streetsia* (Meyer-Rochow, 1978), and these too have hexagonal or sometimes pentagonal packing) but they are so peculiar that there is no problem in separating them from the superposition types of eyes. Table 2 summarises the distribution of square and hexagonally faceted eyes amongst some of the higher crustacean groups with a claim to relatedness.

There are several surprises. Only two groups have square facets, the Macrura and the galatheids (squat lobsters) (Fig. 11). Interestingly the other group usually classed with the galatheids, the eupagurids (hermit crabs), have hexagonal facets and it might be wise for taxonomists to have another look to see whether the sub-order Anomura should be re-examined. Perhaps the galatheids should be grouped with the Macrura and the eupagurids with the true crabs (Brachyura) which have apposition eyes. The older classification of the euphausiids with the mysids (the

“Schizopoda”) finds some support here in that both have a very similar eye-structure – hexagonal packing (Fig. 11 B), similar crystalline cones, a wide clear zone and a similar rhabdom structure. Chun (1896) actually figures a double-eyed mysid (*Brutomysis vogtii* Ch.) which has exactly the same geometry as the double-eyed euphausiids, described in his paper and here. This could of course be parallel evolution (euphausiids are not related to moths, in spite of Fig. 4!) but again the mysid-euphausiid relationship could stand more examination. One thing is certain: there is no way that the euphausiids can be regarded as close relatives of the macruran shrimps that in many ways they so closely resemble.

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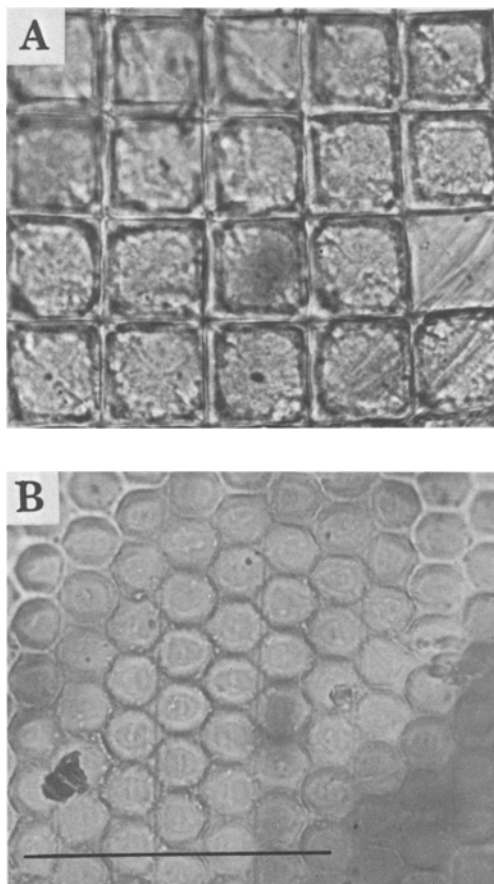


Fig. 11 A and B. Corneas, **A:** of a squat-lobster (*Galathea squamifera*) and **B:** of a mysid (*Praunus inermis*). Same scale on both; bar 100 μ m

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