

Three unexpected cases of refracting superposition eyes in crustaceans

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Summary. Compound eyes of the decapod shrimp *Gennadas*, the hermit crab *Dardanus*, and the syncarid crustacean *Anaspides* are studied histologically and with optical experiments. The results demonstrate that these three crustaceans all have refracting superposition eyes. The conclusion is based on the following observations:

1. There is a wide clear-zone, which allows for a superposition image to be formed.
2. Dark-adapted eyes display a large eye-glow, and the ommatidia are not optically isolated.
3. The crystalline cones have the shape typical for refracting superposition eyes, and they contain the required lens-cylinder gradient of refractive index.

Euphausiids and mysids were previously thought to be the only crustaceans with refracting superposition eyes, whereas the species investigated here were assumed to have reflecting superposition eyes (decapod shrimps) or apposition eyes (hermit crabs and syncarids). The present findings increase more than twofold the number of crustacean groups that are known to have developed refracting superposition optics. It also provides insight into the evolutionary mechanisms that may have led to the development of this type of imaging optics.

Key words: Compound eye – Optics – Crustacea – Evolution

Introduction

The compound eyes of arthropods appear in many different optical designs. The classical and functionally most important division is between apposition and superposition eyes. Within these two main classes are several distinct types, each with its own characteristic way of producing an image on the retinal mosaic (see Land 1981; Nilsson 1989). Although there is generally no principal difference in the representation of the outside world on the receptor mosaic, the way sampling is accomplished optically varies so much that it is tempting to

consider eye type as a conservative feature. The three types of superposition eye provide an illuminating example. The refracting superposition eye relies on graded index optics, and the principle of a Keplerian telescope, to achieve a cooperation of many ommatidia in producing a common retinal image (Exner 1891). Reflecting superposition eyes achieve the same goal by sets of orthogonally arranged plane mirrors, generally without the need of any refracting structures (Vogt 1975). The recently discovered parabolic superposition eye (Nilsson 1988) produces a superimposed image by the combined action of ordinary lenses, cylindrical lenses, parabolic mirrors, and light guides. All types of superposition eye – refracting, reflecting and parabolic – share the same fundamental advantage of a bright superimposed image. But since the three means of achieving this image are conceptually different, it seems that they must have been invented independently. It is difficult, however, to see how any of the superposition eye types can evolve smoothly from an apposition eye. This makes it seem that evolutionary changes of optical design should be rare events, making eye type a consistent characteristic of major taxonomic groups.

The aim of this paper is not to confirm the above view, but instead to show how easy it is to underestimate the competence of evolution. I here present three intriguing cases of crustaceans with apparently the ‘wrong’ type of eye. The three cases are (i), the decapod shrimp genus *Gennadas*; (ii), the hermit crab genus *Dardanus*; and (iii), the syncarid genus *Anaspides*. Quite unexpectedly, these animals all have well developed refracting superposition eyes. It was generally assumed that mysids and euphausiids are the only crustaceans with refracting superposition eyes (Land and Burton 1979; Nilsson et al. 1983), whereas decapod shrimps, crayfish and squat lobsters all were believed to have reflecting superposition eyes (Land 1981). It has further been assumed that all other crustaceans, apart from a few decapods with parabolic superposition, possess apposition eyes. The new findings presented in this paper more than double the number of crustacean groups that are known

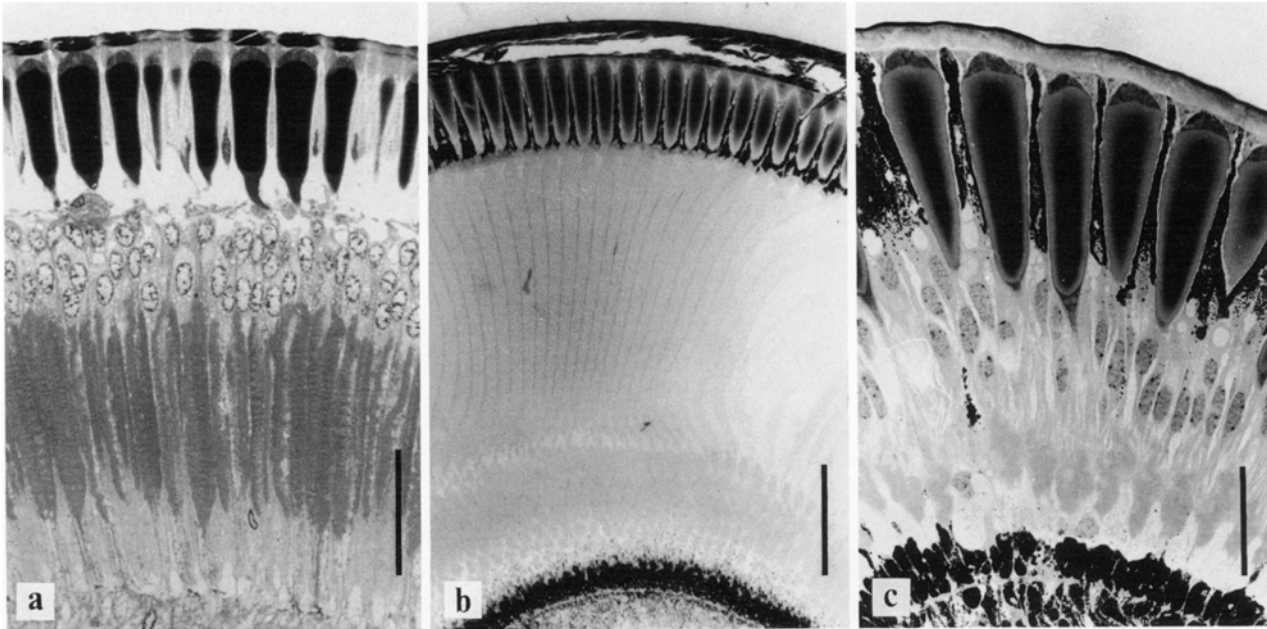


Fig. 1 a–c. Light micrographs of longitudinal semithin sections through the eyes of **a** *Gennadas*, **b** *Dardanus*, and **c** *Anaspides*. Compare Fig. 2 for identification of structures. In *Gennadas* (**a**) the clear zone is entirely collapsed, a histological artifact which appeared in all material of this species and of *Benthesicymus* and *Bentheogennema*. The presence of a clear zone in *Gennadas* is demonstrated in Fig. 3. The sections of *Dardanus* (**b**) and *Anaspides* (**c**) are from dark-adapted animals. Scale bars: **a** 50 μm , **b** 150 μm , **c** 50 μm

to have evolved refracting superposition eyes, and it poses intriguing questions concerning the evolutionary paths that may lead to this highly sophisticated type of eye.

Material and methods

Animals. Decapod shrimps, *Gennadas brevisrostris*, *Benthesicymus bartletti* and *Bentheogennema* sp. were collected during the RRS Discovery cruise 168 to the North-African region of the Atlantic. Animals were brought up in good condition by a midwater net with a closing cod-end. Catches containing these shrimps were mainly from depths between 400 and 1000 m. Experiments requiring live animals were carried out on board.

Two species of hermit crab, *Dardanus megistos* and *Dardanus logopodes* were caught during night-dives around Lizard Island, Great Barrier Reef, Australia. The animals were kept in water tanks at the Lizard Island Research Station, and used for experiments at noon or midnight depending on whether light- or dark-adapted eyes were required. The handling of dark-adapted animals was greatly facilitated by the fact that they remained dark adapted when brought into light if the temperature was kept below 10 °C.

Anaspideaceans (Syncarida) of one species, *Anaspides tasmaniae*, were collected in small ponds in the vicinity of Mt Wellington, Tasmania. Experiments were performed at the Department of Zoology, University of Tasmania, Hobart. Light and dark adapted animals were used at noon and midnight, respectively.

Histology. For light- and electron microscopy the following basic fixative was used: 2.5% glutaraldehyde and 3% paraformaldehyde

in 150 mM Na-cacodylate buffer (pH 7.2). For the decapod shrimps and hermit crabs, 10% sucrose was added, whereas for *Anaspides*, this amount was reduced to 3%. Fixation times were between 1 and 2 h. Following a buffer rinse, the excised eyes were treated for 1 h in 1% OsO_4 . Dehydration was performed in an alcohol series and embedding in Araldite. For light microscopy, semithin sections (1–3 μm) were stained with methylene blue and azure blue. Ultrathin sections for electron microscopy were stained with lead citrate and uranyl acetate.

Ophthalmoscopy. Intact eyes of live animals were observed through a simple ophthalmoscopic setup, based on a compound microscope with an epi-illumination attachment. The illumination beam path was arranged such that one adjustable diaphragm was in focus at the eye's surface and another at infinity. The two diaphragms allowed full control of both the area and angle of illumination. In most experiments a few ommatidia were illuminated with a near parallel beam and the resulting eye-glow was recorded on Kodak Tri-X film.

Interference microscopy. Intact crystalline cones were isolated by tearing an eye apart with fine needles in a drop of physiological saline. Depending on species, this was performed on fresh (*Dardanus*, *Anaspides*) or briefly fixed (*Gennadas*) eyes. Preparations were completed with a coverslip and observed in a Jamin-Lebedeff type interference microscope. The pattern of interference fringes was photographed using monochromatic light ($\lambda = 500 \text{ nm}$) and a background compensation of zero. Refractive index gradients were calculated according to Nilsson et al. (1983).

Interference microscopy was also performed on cross-sections of crystalline cones, cut from lightly fixed material at $-12 \text{ }^\circ\text{C}$ on a cryotome. The section thickness (4–8 μm) was measured on occasional cone slices that stood on their side in the preparation. For refractive index measurements the phase shift was determined either by counting fringes or by use of an Ehringhaus compensator (Nilsson and Odselius 1981).

Results

All the decapod shrimps investigated in this paper (see Material and methods) were found to have nearly identical eyes. The same is true for the two species of hermit

crab – only a general difference in eye size could be noted. To simplify presentation of the results, the following deals mainly with three representative species on which the bulk of investigations were performed. These species are: the decapod shrimp *Gennadas brevisrostris*, the hermit crab *Dardanus megistos* and the syncarid *Anaspides tasmaniae*. In the following, they will be referred to by the genus only.

Structure of the eyes

All the species share the common feature of a well developed clear-zone between crystalline cones and rhabdoms

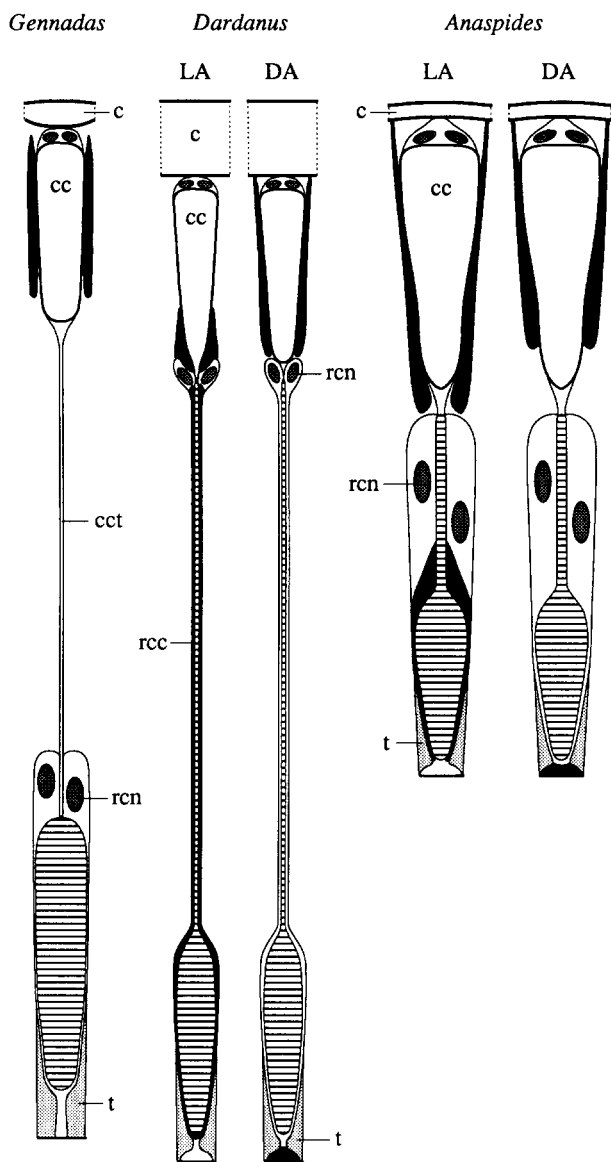


Fig. 2. Semischematic diagrams of ommatidial structure in *Gennadas*, *Dardanus* and *Anaspides*. In the two latter species changes occur between light-adapted (LA) and dark-adapted (DA) states. Rhabdoms are indicated by striped patterns and dark screening pigment by solid black. Abbreviations: *c* cornea, *cc* crystalline cone, *cct* crystalline cone thread, *rcn* retinula cell nuclei, *rcc* retinula cell column, *t* tapetum

(Fig. 1). In *Dardanus* and *Anaspides* the clear zone is invaded by screening pigment during light adaptation (see Fig. 2), whereas *Gennadas* displays no anatomical changes in response to light exposure. The general construction of the eyes and especially the shape of the crystalline cones gives the impression of a refracting superposition type of eye in all three species. Table 1 gives a summary of important structural and optical features of the three eyes.

The corneas of *Dardanus* and *Gennadas* incorporate corneal lenses. Observations of isolated fresh pieces of cornea show that the lenses are rather weak in *Gennadas* but powerful in *Dardanus*. The absence of facet curvature in *Dardanus* implies that, in this species, the focal power comes from a refractive index gradient within the thick cornea. In *Anaspides* the cornea is thin and without optical function.

Table 1. Structural and optical parameters of the eyes of *Gennadas brevisrostris*, *Dardanus megistos*, and *Anaspides tasmaniae*. Measurements refer to the centre of the eye. In each species, all measurements are made on a single eye, which was first studied fresh, to measure interommatidial angle and glow size, before it was prepared for histology

	<i>Gennadas</i>	<i>Dardanus</i>	<i>Anaspides</i>
Corneal thickness (μm)	5	45	7
Crystalline cone length (μm)	60	125	105
Clear-zone depth (μm)	180	400	60
Proximal rhabdom length (μm)	115	155	50
Facet diameter (μm)	18	36	34
Diameter of eye glow (mm)	0.42	1.22	0.31
Radius of eye (mm)	0.55	1.25	0.35
F-number (half radius/glow diameter)	0.63	0.51	0.56
Interommatidial angle (degrees)	2	1.8	6

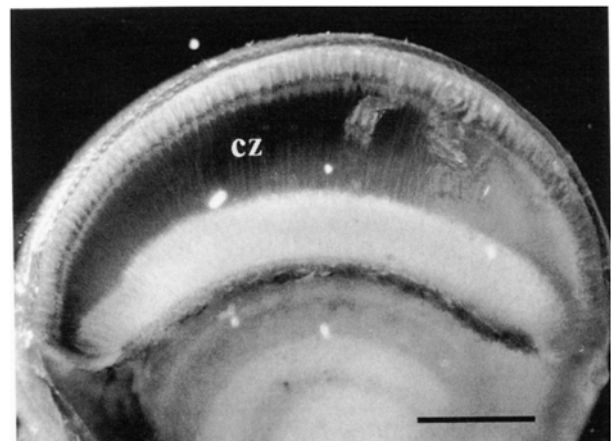


Fig. 3. A hemisected fresh eye of *Gennadas*, showing the clear zone (cz) traversed by thread-like extensions of the crystalline cones. The thick bright layer is the retina. Scale bar: 200 μm

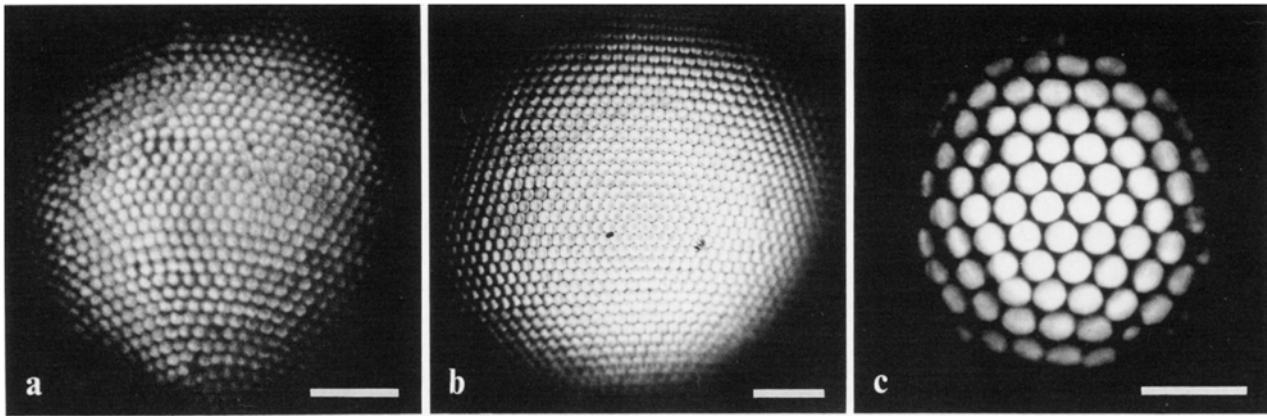


Fig. 4a–c. Eye glow seen with orthodromic illumination in **a** *Gennadas*, **b** *Dardanus*, and **c** *Anaspides*. Crossed polarizer and analyser were used to eliminate corneal glare. Only a few ommatidia in the centre of the glow were illuminated. *Dardanus* (**b**) and *Anaspides* (**c**) were dark adapted prior to this experiment. Scale bars: **a** 100 μm , **b** 200 μm , **c** 100 μm

All three species have four cone cells, but in *Anaspides* only two of these take part in the formation of the crystalline cone. In *Gennadas* the proximal tip of each crystalline cone continues, through the entire clear-zone, as a pulled out thread, 1–2 μm in diameter. In histological sections of *Gennadas* the clear zone is often collapsed (Fig. 1a), presumably because there are no supporting structures apart from the thin cone-threads. This artifact led Meyer-Rochow and Walsh (1977) to erroneously conclude that *Gennadas* has no clear zone. The true nature of the clear zone is best revealed by hemisecting a fresh eye as in Fig. 3. In such a preparation the watery clear-zone and the cone threads are obvious. In *Dardanus* the clear zone is traversed by dense and narrow (4 μm) columns of the retinula cells, which form a thin additional rhabdom extending through the entire clear-zone. This rhabdom is partially degenerated and the whole column appears mainly to be a lightguide for axial light. The clear zone of *Anaspides* is entirely occupied by the retinula cells, also in this animal forming an additional narrow (3 μm) rhabdom which spans the depth of the clear-zone.

The position of retinula cell nuclei differs in the three species: in *Gennadas* they are found in the proximal part of the clear zone, in *Anaspides* they more or less fill the clear zone, and in *Dardanus* they lie distally just beneath the cones.

As would be expected if the eyes are of superposition type, the region proximal to the clear zone, in all three species, is occupied by wide voluminous rhabdoms. In cross-section these rhabdoms are star-shaped with 3 or 4 arms in *Gennadas* and *Anaspides*, whereas they are round in *Dardanus*. The three species all have reflecting tapeta of white pigment cells surrounding the most proximal part of the rhabdoms (see Fig. 2).

Eye glow

The most direct way of confirming that a compound eye is of superposition type is to demonstrate the absence of optical isolation between neighbouring ommatidia. This is most elegantly done if the eye has a reflecting tapetum at its base: illuminating a few ommatidia from the direction of observation will result in a large patch of glowing ommatidia in a superposition eye, whereas only the illuminated ommatidia will shine back if it is an apposition eye.

Fortunately, *Gennadas*, *Dardanus* and *Anaspides* all possess well developed tapeta and they display the large eye-glow characteristic of superposition eyes (Fig. 4). The eyes of *Dardanus* and *Anaspides*, however, display massive pigment migrations upon light adaptation (see previous section), and not unexpectedly the glow in these species disappears when they become light adapted. Stopping down the illumination to a single ommatidium does not affect the size of the glow in any of the three species, indicating the presence of some kind of superposition optics. The demonstration is further reinforced by the fact that the appearance and position of the glow is independent of which of the glowing ommatidia are receiving the light, as long as the angle of illumination is kept constant. The F-numbers (focal length/pupil diameter) of the eyes are all slightly above 0.5 (Table 1), which are typical values for superposition eyes adapted for dim conditions (Land et al. 1979; Land 1984a).

Optics of the crystalline cone

Next we determine the type of superposition optics employed by these eyes. The principal difference between the three known types of superposition optics lies in the design of the crystalline cone. As judged from the shape of the cones of all the species in this investigation, the eyes should be of the refracting superposition type. This assumption can be confirmed if the cones are shown to contain a powerful refractive index gradient with highest optical density along the central axis and decreasing towards the periphery. But if the superposition optics is of the reflecting or parabolic type, the crystalline cones should be either square and homogeneous

in cross section or circular in cross section with an internal cylindrical lens (Nilsson 1988).

An interference microscope was used to determine the distribution of refractive index in the cones. The interference patterns in the intact cones are seen in Fig. 5a–c, and although there are differences, the general appearance is similar to the cones in other documented cases of refracting superposition eyes. Using the computer iteration technique of Nilsson et al. (1983), the interference fringes of the intact cones were used to calculate the refractive index profile from centre to periphery. The results of these calculations is presented in Fig. 6, and, as expected, they all show the smooth, near parabolic profile gradient characteristic of refracting superposition optics. The cones of *Dardanus* and *Anaspides* are of similar size, but the gradient is much weaker in *Dardanus*, presumably because the cornea here acts as a powerful lens.

The presence of a typical refracting superposition gradient can be demonstrated in a more direct way as illustrated in Fig. 5d–f. Here, cross-sections (4–8 μm) are cut from frozen tissue and viewed in the interference microscope. Since the sections are parallel-sided, the ob-

served fringes result solely from variations in refractive index across the cone.

Electron microscopic cross-sections of the cones reveal the density gradients (Fig. 7) that are responsible for the graded distribution of refractive index. Such density gradients are typical for crystalline cones with graded index optics, and thus constitute an alternative demonstration of a lens cylinder in the crystalline cones.

Discussion

The demonstration of refracting superposition eyes in some decapod shrimps, some hermit crabs, and one anaspideacean are all quite unexpected. Decapod shrimps were believed generally to have reflecting superposition optics (Land 1984b), and hermit crabs were thought to have simple apposition optics (Land 1984b), although some were recently (Nilsson 1988) shown to possess the new parabolic type of superposition eyes (see Table 2). Anaspideacea belong to the Syncarida which are considered as primitive malacostracans, and thus assumed to have only apposition eyes.

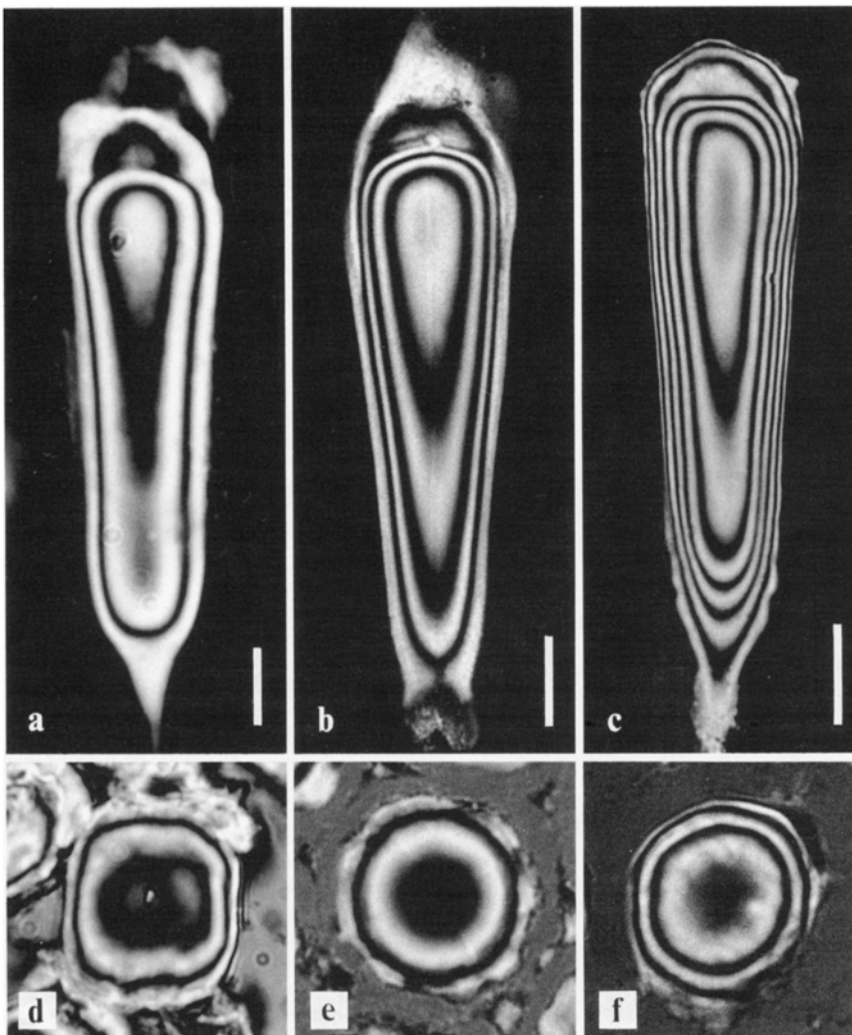


Fig. 5a–c. Interference micrographs of intact isolated crystalline cones of **a** *Gennadas*, **b** *Dardanus*, and **c** *Anaspides*. Scale bars: **a** 10 μm , **b** 20 μm , **c** 20 μm . **d–e** Cryotome cross-sections of crystalline cones from **d** *Gennadas*, **e** *Dardanus*, and **f** *Anaspides*. Since the surfaces of the sections are parallel, the interference fringes result solely from variations in refractive index across the cones. Note the somewhat squarish shape of the *Gennadas* cone (**d**)

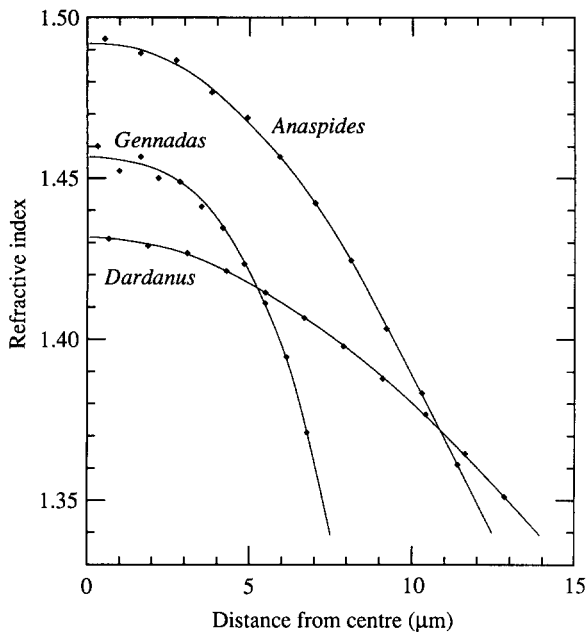


Fig. 6. Refractive index profiles perpendicular to the optical axis. The values are calculated from the interference patterns of intact crystalline cones (see Nilsson et al. 1983). All three profiles are taken from a position approximately midway along the cone. In neither of the species do these profiles hit the position of maximal axial value: in *Gennadas* and *Dardanus* the highest axial values were found in more distal profiles, whereas in *Anaspides* more proximal profiles showed the highest refractive indices

The first question we must ask is: why did these animals develop such complicated optics? Comparing apposition and superposition optics in general, it is clear that, if the eye is not to be used strictly in very bright conditions, then a superposition eye is a good choice, because of its superior light gathering capacity (see Land

1981; Nilsson 1989). Comparing the three known types of superposition optics, it seems that refracting superposition is the mechanism which involves the least aberrations (Nilsson 1988, 1989). In both reflecting and parabolic superposition eyes there are some rays that are not handled correctly. It would thus seem that there are reasons for a great many arthropods to evolve refracting superposition optics in their compound eyes. We may now turn the question around and ask why not all arthropods, which are active under at least partially dim conditions, possess refracting superposition eyes. This question probably does not have a single simple answer, but an important part must be that this type of eye does not evolve easily from any of the other known types. For a transformation to happen, it requires that there is a continuous succession of negligible small improvements spanning the entire range from one type to the other. This crucial requirement probably fails much more often than it is fulfilled. The lack of existing intermediates supports this view, as does the difficulty of finding hypothetical ones. Only two cases of possible paths from apposition to refracting superposition are known: (i) the afocal apposition optics of diurnal butterflies leads naturally to refracting superposition which is present in the related and predominantly nocturnal moths (Nilsson et al. 1988); (ii) the transparent apposition eyes of planktonic larval euphausiids provide a functional connection to the superposition eyes of the adult shrimps (Nilsson 1983). In both the above cases evolutionary obstacles have been circumvented by a change in life style.

The present material does not suffice to fully sort out the corresponding evolutionary paths that led to the refracting superposition eye of *Gennadas*, *Dardanus*, and *Anaspides*. But as a first step, it may be possible

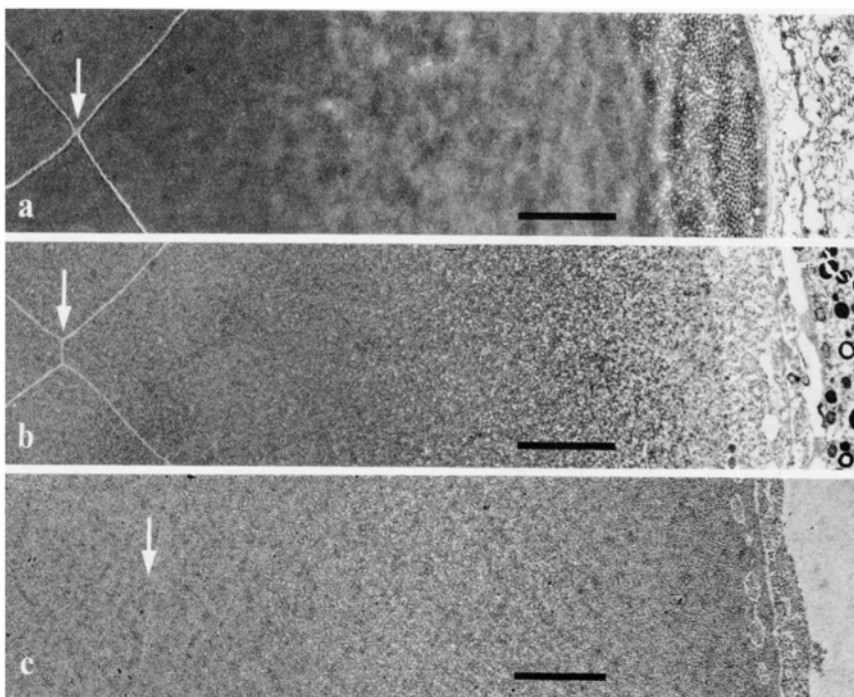


Fig. 7a-c. Electron micrographs demonstrating a density gradient, from centre to periphery, in cross-sections of the crystalline cones of **a** *Gennadas*, **b** *Dardanus* and **c** *Anaspides*. The gradient in *Anaspides* is less obvious, and appears more like a gradual transition from one granular matrix to another. Note that the blue staining used for light microscopy in Fig. 1 reveals a gradient in *Anaspides* and *Dardanus*, but surprisingly not in *Gennadas*. The approximate centres of the cones is indicated by arrows; the periphery is to the right. Scale bars: **a** 1 μm , **b** 2 μm , **c** 2 μm

to get some idea of what eye type preceded the present one.

Gennadas, *Benthescymus* and *Bentheogennema* are taxonomically close and they differ from decapod shrimps in general (see Table 2) by having refracting instead of reflecting superposition optics. It is interesting to note that in all the above genera, and especially in *Benthescymus*, more than one third of the eye has square packing of the ommatidia and many of the crystalline cones are somewhat squarish in cross-section (Fig. 5d). Since square cones and square packing are the key characteristics of reflecting superposition eyes, it seems likely that these were the precursors of the present refracting superposition eyes. We thus face indications of a transformation from reflecting to refracting superposition optics. The fact that all other decapod shrimps have the reflecting type of optics is a strong support to this hypothesis, but it is less clear how it can have happened. No functional intermediates between reflecting and refracting optics are yet known, but I stress 'yet' since the comparative knowledge of reflecting superposition optics is still very limited. *Gennadas*, *Benthescymus* and *Bentheogennema* are all deep water inhabitants and the gain in performance by a change from reflecting to refracting optics is hard to appreciate under these circumstances. Such a transformation may have been possible if a species with the reflecting type of optics moved into very dark habitats during evolution, and then returned to a slightly brighter habitat. If, during such a process, the intensity became too low for spatial vision to be useful, the sophisticated optics in the crystalline cone – i.e. multilayer mirrors and 90° corners – may have been lost early. Upon return to brighter habitats, functional optics could be recovered either by reinventing reflectors or by inventing the graded index optics of a lens cylinder. If the species did the latter, then the transformation from reflecting to refracting optics would have been completed. The remarkably small facets and small interommatidial angles (Table 1) may fit into this scheme: if extremely low intensities in the animal's evolutionary history have led to a coarse resolution by extensive pooling of signals from adjacent ommatidia, then this may still persist so that the array of ommatidia no longer correlates to visual resolution.

The case of refracting superposition optics in the hermit crab genus *Dardanus* is more involved. Hermit crabs belong to the anomuran decapods, which already before were known to possess a great variety of eye types (Table 2). Among the Anomura, the squat lobsters (Galatheididae) have reflecting superposition eyes (Land 1984b; see also Kampa 1963; Bursley 1975), some pagurid hermit crabs have the parabolic type of superposition eyes (Nilsson 1988), and most of the smaller hermit crabs (both Paguridae and Diogenidae) have apposition eyes (Nilsson 1989).

The anatomy of the eye of *Dardanus* presents a few possible clues to their origin. The cornea has powerful lenses, the clear zone is traversed by dense threads connecting cones to rhabdoms, and the cones display a change in shape upon light/dark-adaptation (Fig. 2). All

Table 2. Summary of the distribution of eye types in the major groups of crustaceans

	Apposition	Refracting superposition	Reflecting superposition	Parabolic superposition
Branchiopoda	X			
Ostracoda	X			
Maxillopoda	X			
Anaspideacea		new		
Amphipoda	X			
Isopoda	X			
Mysidacea		X		
Euphausiacea	X (larvae)	X		
Decapoda: Natantia	X (larvae)	new	X	
Decapoda: Macrura	X (larvae)		X	
Decapoda: Anomura	X	new	X	X
Decapoda: Brachyura	X			X
Stomatopoda	X			

these features are characteristic of the parabolic superposition eyes of other hermit crabs and some brachyuran crabs (Nilsson, unpublished). The *Dardanus* species are nocturnal or crepuscular inhabitants of shallow coastal waters, and the intensities in which these animals are active may be sufficiently high to make useful the potentially more aberration-free imaging of the refracting design compared to that of the parabolic design. There is thus a possible motive for a change from parabolic to refracting superposition optics. If this change has actually taken place, then there must be a way to gradually improve parabolic superposition optics so that the end product becomes a refracting superposition eye. A plausible possibility would be that the step-index cylindrical lens inside the crystalline cone of a parabolic superposition eye (see Nilsson 1988) is gradually turned into a graded index cylindrical lens, which actually is an accurate description of the cone optics in a refracting superposition eye. Such a development would eliminate the aberrations of peripheral rays in the cylindrical lens (Nilsson 1989), and the parabolic mirrors would become superfluous.

The finding of refracting superposition eyes in *Anaspides* is perhaps less peculiar. The eyes of syncarids have received very little attention, and they have simply been assumed to be of apposition type. Anaspideaceans are the only syncarids with compound eyes, and the few recent species are typically what can be called 'living fossils'. It is therefore understandable if it appeared legitimate to substitute 'apposition type' for 'unknown eye type'. *Anaspides tasmaniae* lives in shallow fresh-water ponds in Tasmania and they seem to be active both day

and night. A refracting superposition eye, which through light adaptation can turn into apposition, is thus an ideal choice for these animals. Unfortunately, the eye's anatomy does not offer any obvious clues to the origin of its present optical design. Likewise, the phylogenetically isolated position of the Anaspideacea does not leave much basis for hypotheses of eye-optics evolution, and the only hope seems to be in the yet unknown ontogeny of the eye.

Only two groups of crustaceans – the mysids and the euphausiids – were previously known to possess refracting superposition eyes. With the present findings of this eye type in *Gennadas*, *Dardanus* and *Anaspides* the number now adds-up to five. It seems that refracting superposition eyes must have evolved independently numerous times in the Crustacea, and there also appear to be several different ways of deriving this type of eye.

The evolution of eye types can provide much information about the animal's evolutionary history (see Nilsson 1983, 1989; Nilsson et al. 1986, 1988). But the evolutionary hypotheses presented in this discussion are necessarily speculative, since there are still large gaps in our knowledge about crustacean compound eyes. Nevertheless, it is obvious that the optical type of compound eye is not a reliably conservative character and thus unsuitable as a taxonomic tool.

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