



The development and evolution of the eyes of vent shrimps (Decapoda: Bresiliidae)

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Introduction

The question of how the thoracic organ of *Rimicaris exoculata* Williams & Rona, 1986 has evolved from the compound eyes of ancestral deep-sea shrimps is unresolved. Shrimp compound eyes generally consist of a hemispherical array of ommatidia on the end of an eyestalk. The eyestalk usually contains the optic neuropiles (the lamina, medulla externa and medulla interna) in an optic tract that projects to the region of the brain known as the lateral protocerebrum. It is not immediately apparent how this arrangement could have evolved into that found in vent shrimps such as *Rimicaris exoculata* in which the large thoracic organ underlies the dorsal carapace, and from which axons project to the back of the protocerebrum (O'Neill et al., 1995).

Methods

Using the limited range of developmental stages available we examined eye development in vent shrimps to see if this elucidates the problem. Late embryos removed from the pleopods of *Mirocaris fortunata* (Martin & Christiansen, 1995) were studied to show the general arrangement of the larval eye. Three types of post-larval eye in shrimps obtained during 1995 by trawling above vent sites on the Mid-Atlantic Ridge (Herring, this volume) were examined. The identity of these post-larvae has been determined by DNA analysis (Dixon et al., this volume). "Type A" post-larvae include morphologically indistinguishable individuals of all three genera of common vent shrimps (*Rimicaris*, *Chorocaris* and *Alvinocaris*). The second type *Alvinocaris* consists of *Alvinocaris markensis* Williams, 1988 post-larvae, whilst the third type "*Chorocaris*" includes post-larvae of both *Rimicaris* and *Chorocaris*. In

addition, a few post-settlement juvenile *Rimicaris exoculata*, obtained by submersible from Atlantic vent sites, were examined.

Results

Sections through the late embryonic eyes of *Mirocaris fortunata* show that the zoeal eye is generally similar to those of most other decapod larvae. There is a gradient of ommatidial development from undifferentiated cells at the anterior margin of the developing eye to comparatively well-developed ommatidia posteriorly. The optic ganglia are located below the basement membrane in the area that will eventually form the eyestalk. Electron microscopical examination shows that the ommatidia are typical of apposition eyes, with a thin rhabdom (formed by 8 retinula cells) surmounted by a crystalline cone. The retinula cell axons project through the basement membrane to the lamina ganglion. These specimens suggest that the early larval stages are planktonic.

The "Type A" post-larvae were caught at depths of between 2000 and 3000 m, presumably as they were returning to the vent sites (Gaten et al., 1998). These post-larvae have reduced stalked eyes projecting forwards at an angle to the head with the ommatidia confined to the lateral and anterior parts of the eyestalk. The medial face of each eyestalk bears what appears to be a sensory papilla. In longitudinal sections through the eyestalk (Fig. 1A), crystalline cones are still found in the lateral parts of the eye, although the anterior ommatidia consist mainly of hypertrophied rhabdoms. Much of the eyestalk is taken up with lipid globules and neuropile. Transverse sections show that the lamina ganglion is displaced ventro-laterally in the eyestalk by the hypertrophied neuropile of the lateral

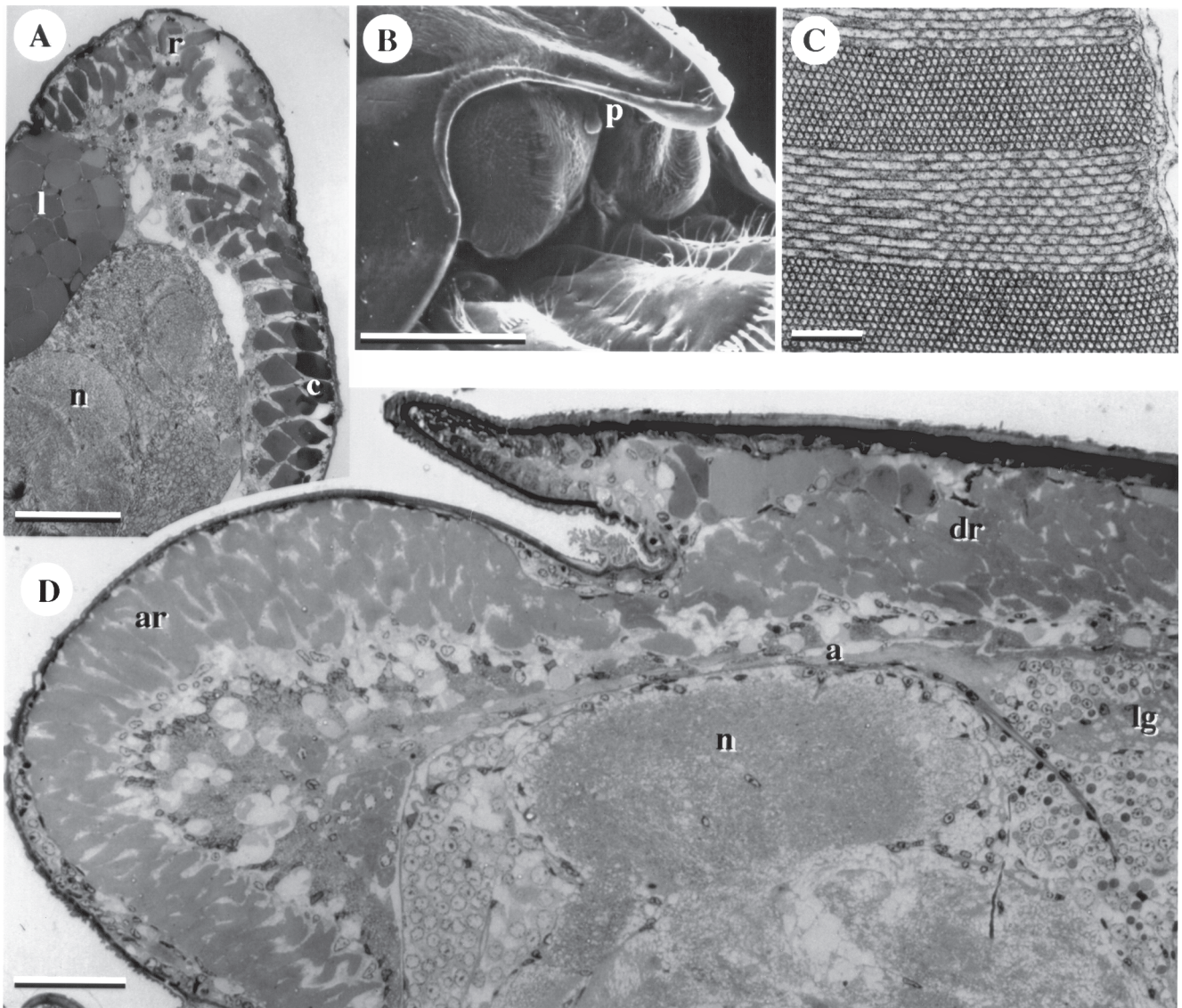


Figure 1. A) Longitudinal section through the eyestalk of a “Type A” post-larva, showing hypertrophied rhabdoms (r) anteriorly and the presence of crystalline cones (c) laterally. The eyestalk contains lipid (l) and the neuropile of the lateral protocerebrum (n). B) Scanning electron micrograph of the anterior end of a “Chorocaris” post-larva showing the sensory papilla (p) on the medial face of the eyestalk. C) An electron micrograph showing the orthogonally-oriented layers of microvilli in the rhabdom of an “Alvinocaris” post-larva. D) Sagittal section of a “Chorocaris” post-larva showing the unbroken layer of rhabdoms in the anterior (ar) and dorsal (dr) eyes. The tract of retinula cell axons (a) passes around the lateral protocerebrum (n) and projects to the lamina (lg). Scale bars: A = 200 μ m; B = 500 μ m; C = 0.5 μ m; D = 100 μ m.

protocerebrum. As a result the retinula cell axons are routed around the protocerebral neuropile before projecting to the lamina.

Both the *Alvinocaris* and “Chorocaris” post-larvae have markedly reduced eyestalks, lack external facets and have sensory papillae on the cornea (Fig. 1B). *Alvinocaris* has a longer rostrum whereas “Chorocaris” has a thoracic organ, seen as a white area beneath the dorsal carapace in the living animal (Herring & Dixon, 1998).

In *Alvinocaris* post-larvae, horizontal sections through the eye show that the rhabdoms are mostly directed anteriorly with a small interommatidial angle. There is no dioptric apparatus so the eyes are not capable of forming a focused image. They are probably capable of some directional sensitivity as a result of the separation of rhabdoms by regions of cytoplasm of low refractive index. The rhabdoms in these light-protected specimens were in good condition and show the layered microvilli typical of

decapod eyes (Fig. 1C). All published micrographs of the rhabdoms of adult vent shrimps show disruption and vesiculation of the microvilli. Such damage is typical of light-induced rhabdom breakdown which might be expected after exposure to the searchlights of the submersible. Equally, however, the damage could be a result of extended exposure to hot vent fluid. It is clearly necessary to obtain adult specimens adequately protected from high light levels to resolve this question.

In a sagittal section through the eye and brain of a "*Chorocaris*" type post-larva the morphology of the eye

and the protocerebrum can be seen (Fig. 1D). The anterior eye contains an extensive array of rhabdoms which can be traced in a contiguous layer backwards beneath the thoracic carapace where they form the dorsal eye, demonstrating that the two regions of the eye share a common origin. Behind the eye, the neuropile of the lateral protocerebrum predominates, with the retinula cell axons forming a layer distal to the basement membrane, routed around the hypertrophied lateral protocerebrum as a discrete optic tract. Posterior to the lateral protocerebrum the optic tract projects to the optic neuropiles.

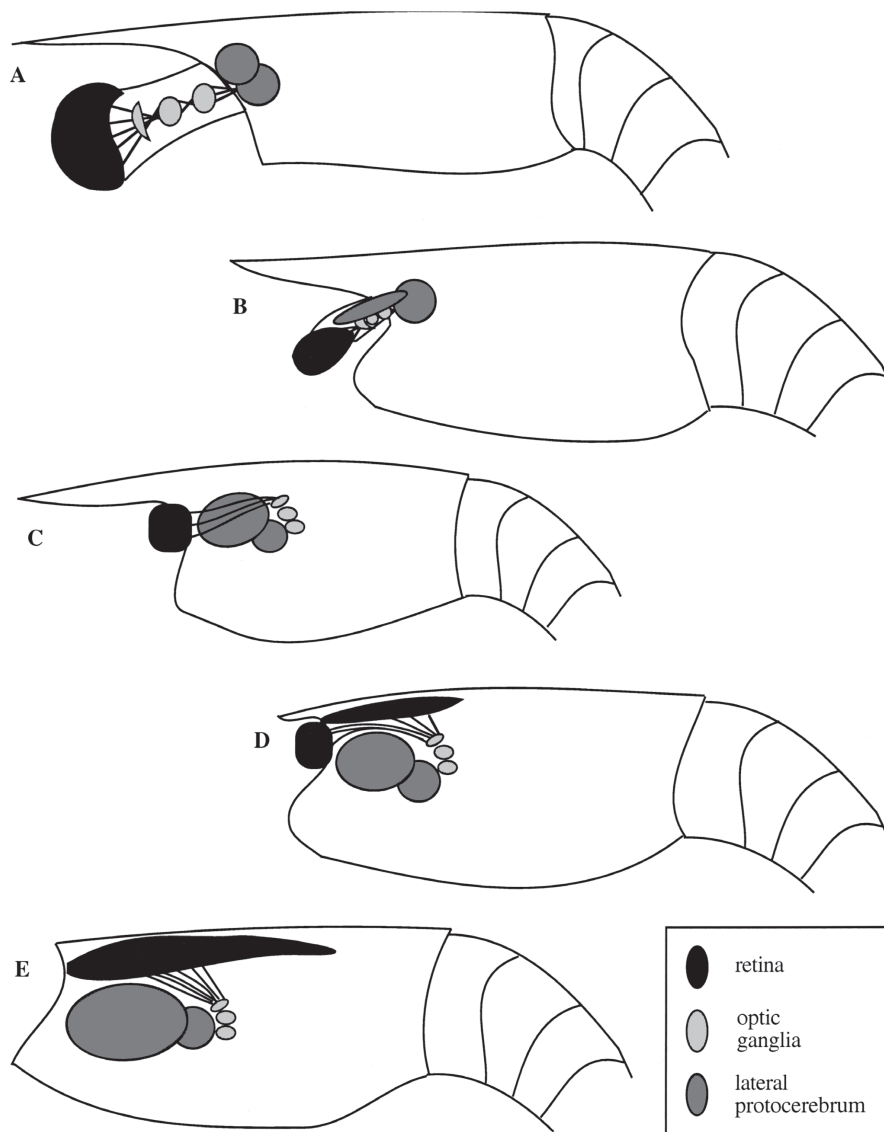


Figure 2. Schematic diagram showing the evolution of the dorsal eye of *Rimicaris* from the stalked compound eye of an ancestral deep-sea shrimp. A) in oplophorid shrimps the optic ganglia occupy most of the eyestalk. B) in this stage, based on "Type A" post-larvae, the eyestalk is reduced and the optic ganglia are displaced by the enlargement of the lateral protocerebrum. C) with the loss of the eyestalk and posterior displacement of the optic ganglia, "*Alvinocaris*" adults are preadapted for the evolution of a dorsal eye. D) this occurs in "*Chorocaris*" adults by addition of ommatidia to the dorsal eye. E) the anterior eye is further reduced in *Rimicaris*.

The development of the optical system of *Rimicaris exoculata* is completed after settlement at the vent site by enlargement of the thoracic organ and the progressive reduction in the anterior eyes during which the separate smooth corneas of the eyes are replaced by a single ocular plate.

Discussion

This ontogenetic sequence is far from complete due to the lack of developmental stages. However, we can use the information described here to suggest an evolutionary pathway from the stalked compound eye of an ancestral deep-sea shrimp (Fig. 2A) to the thoracic eye of the vent shrimp. The sequence begins with the intrusion of the lateral protocerebrum into the eyestalk (as seen in "Type A" individuals). This results in the optic ganglia being displaced ventro-laterally, with the retinula cell axons routed around the lateral protocerebral neuropile to the lamina (Fig. 2B). In the next stage (as seen in *Alvinocaris markensis*) the eyestalk is dramatically reduced in size and the optic ganglia are further displaced posteriorly. As a result of this, the tissues of the eye are contiguous with those of the cephalothorax and the optic tract passes posteriorly to the optic ganglia (Fig. 2C). Hence, this stage is preadapted for the formation of the thoracic eye, the axons of which can readily join the optic tract.

The thoracic eye is formed in "*Chorocaris*" merely by the addition of ommatidia posterior to the eye and the addition of axons to the optic tract (Fig. 2D). The sequence

is completed in *Rimicaris* by the further reduction of the anterior eye and growth of the thoracic eye (Fig. 2E).

This suggests that the evolution of the thoracic eye is driven by the reduction in the length of the eyestalk and the hypertrophy of the lateral protocerebral neuropile as the shrimps rely more on chemosensory than visually-guided behaviour. However, it must be emphasized that the anterior and thoracic eyes of vent shrimps are functional and not degenerate. They appear to be uniquely adapted for the location of, and the orientation towards, a dim light source.

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