Structure and functional implications of visual systems in non-marine ostracods: a review

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All non-marine ostracod species belong to the order Podocopida. They usually possess a simple optical system composed of three eyecups called naupliar eye. Phylogenetic data and morphological characteristics support the homology of naupliar eyes between ostracods and other crustacean groups. The photoreceptive system is formed by several specialised cells and can be approximated by a lens-mirror optical apparatus. In some cases, a transparent area of the calcitic carapace can form an additional lens. The visual stimuli are processed by the protocerebrum, possibly via monoaminergic neurons. The presence or absence of one or more specialised cells influence the function of the eyes, and, most likely, their evolution or loss are associated with the adaptation to different habitats. Podocopid ostracods may express long-wavelength sensitive rhabdomeric opsins and may possess nonvisual opsins. The few ethological experiments so far conducted demonstrate that non-marine ostracods might be capable of associative learning when trained with light or specific light wavelengths. This work will provide an overview of what is known and what remains to be further investigated about vision and how light cues affect the behaviour in non-marine ostracods.

1. Photoreceptive system in podocopid ostracods: naupliar eye

Fig. 1 - A. Historic drawing by Walter Klie (unpublished), showing the naupliar eye of a *Cypridopsis elongata* specimen. B. Light microscopic image of the right body side of a *Tanycypris alfonsi* (Nagler, Geist & Matzke-Karasz, 2014); arrow pointing to naupliar eye. C. Antero-dorsal view of a *Eucypris virens* specimen with valves removed, and view on naupliar eye in situ. Scale bar for B, C: 100 µm.

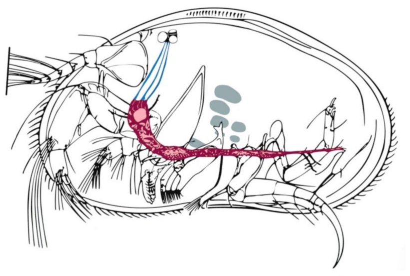


Fig. 2 - Lateral view of fused naupliar eye of *Cypridopsis vidua*. In blue, three nerves connecting the eye to the protocerebrum. In red, the ventral nerve chord. After Kesling 1951.

The naupliar eye is positioned anterodorsally and connected through optic nerves to the anterio-median area of the protocerebrum (Elofsson 1966, 2006).

When illuminated, the **naupliar eye is iridescent** and appears as a glowing spot.

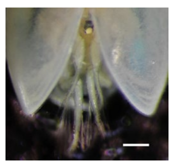
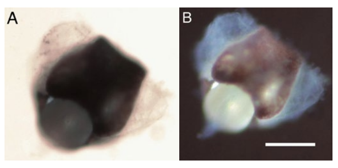


Fig. 3 - Anterior-dorsal view of *Australocypris robusta* De Decker, 1974. Scale bar: 250 µm.

Fig. 4 - Naupliar eye of *Australocypris robusta* in transmission light microscope, using (A) inbuilt lighting from above and (B) and external lateral light. Scale bar: 100 µm.



2. General morphology of naupliar eyes in podocopid ostracods

Comprised of **three eyecups,** that can be either fused together or separated, possibly composed of specialized cells and an additional lens (Elofsson 1966, 2006).

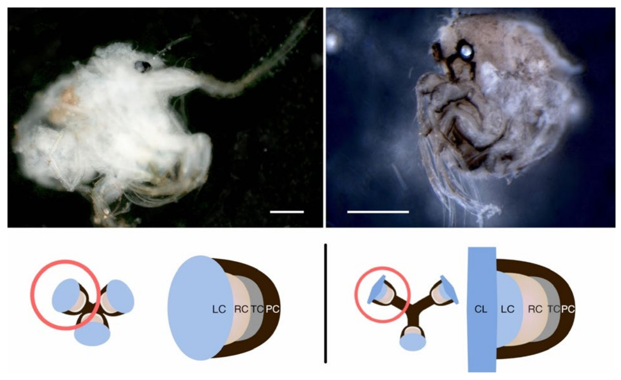


Fig. 5 - Upper panel: lateral views of *Eucypris virens* (left) and *Newnhamia fenestrata* King, 1855 (subfamily Notodromadinae) (right), valves removed. Scale bar: 250 µm. Lower panel: sketches of a fused eye (left) as in *E. virens* and a separated eye (right) as in *N. fenestrata*.

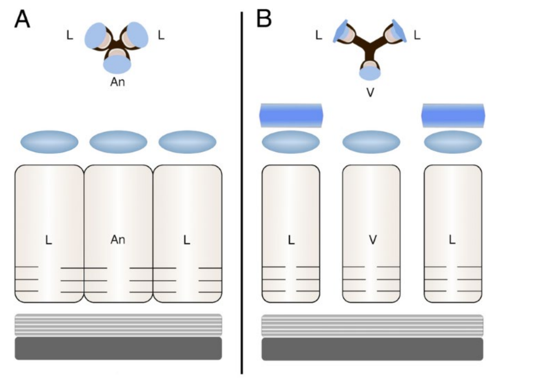


Fig. 6 - Scheme of podocopid naupliar eyes. A. fused eyecups; B. separated eyecups. Vertical rectangular boxes are the eyecups, the striped horizontal bars are the tapetum and the dark bars at the bottom are the pigments cells. Lens cells are the light blue ellipses, the cuticular lenses are the dark blue rectangles (L=lateral, An=anterior, V=ventral).

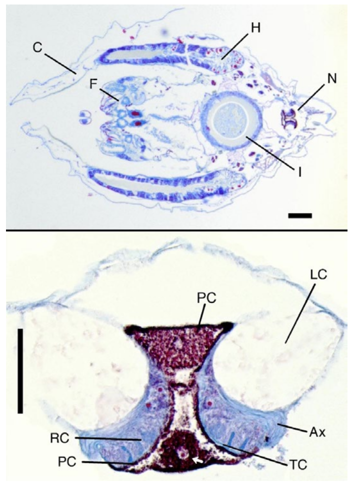


Fig. 7 - Histological section of *Eucypris virens*. A. Section in frontal body plane (dividing dorsal from ventral), near dorsum. Naupliar eye (N), other organs (C,F,H,I). B. Frontal section through the naupliar eye below the anterior eye cup, cutting the axons (Ax). Scale bar: 100 µm for A, 5 µm for B.

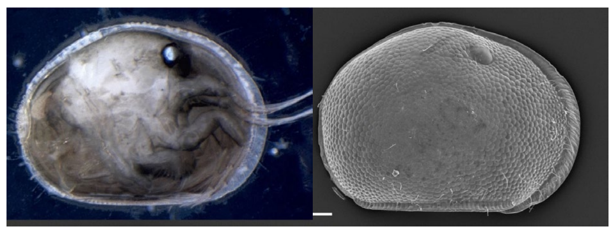


Fig. 8 - *Newnhamia fenestrata*. Left part: valve removed, with the (separate, right) lateral naupliar eye cup clearly visible. Right part: right valve, with calcified cuticular lens located directly above the area of the right naupliar eye cup. Scale bar: 100 µm.

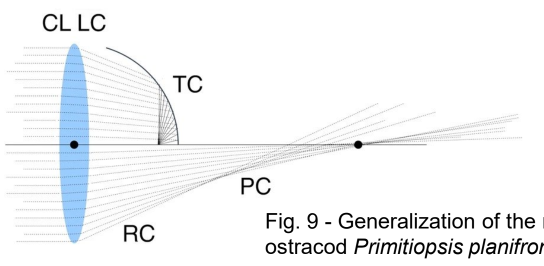
- **Pigment Cells (PC)** shield photoreceptors from light intensity
- **Tapetal Cells (TC)** reflect and focus light onto sensory cells
- **Retinal Cells (RC)** go from a number of 6 to 40 (Elofsson 2006)
- **Lens Cells (LC)** enhance light sensitivity via light diffusion
- **Cuticular lenses (CL)** refractive index 1.62-1.64—present if eyecups are separated

Sexual dimorphism exists in cuticular lens shapes in species of the genus *Notodromas* (Bonaduce & Danielopol 1988).

At least **six different subtypes** can be distinguished by considering the presence or absence of specialized cells and their morphology (Tanaka 2005).

	Eyecups	Position	Lens cells	Cuticular lens	Reported for non-marine species
Eye type 1	Fused	Naupliar eye separated from the carapace	No	No	No
Eye type 2	Fused	Naupliar eye near the carapace	Yes/No	No	*Cypria exsculpta* Fischer, 1855, *Cypris herricki* Turner, 1892, *Cypris pubera* O.F. Müller, 1776, *Cypris* sp., *Herpetocypris reptans* Baird, 1835
Eye type 3	Separated	Lateral eye connected with the carapace	No	Meniscus	No
Eye type 4	Separated	Lateral eye connected with the carapace	Yes/No	Biconvex	*Notodromas monacha* (O.F. Müller, 1776)
Eye type 5	Separated	Lateral eye tightly connected with the carapace, ocular pit observed from inside	No	Biconvex	No
Eye type 6	Separated	Lateral eye connected with the carapace, ocular sinus observed from inside	No	Aplanat-like	No

3. Physics of the podocopid naupliar eyes



The naupliar eyes operate as a **mirror-lens system**. The retina first receives the unfocused light passing through the lens and then the focused rays are collected by the mirror.

Fig. 9 - Generalization of the naupliar eye optics based on ray tracing applied to the naupliar eye of the Silurian ostracod *Primitiopsis planifrons* (Jones, 1887), from Tanaka et al. (2009).

-Thin lens and mirror system model (Myers & Kontrovitz 1988).

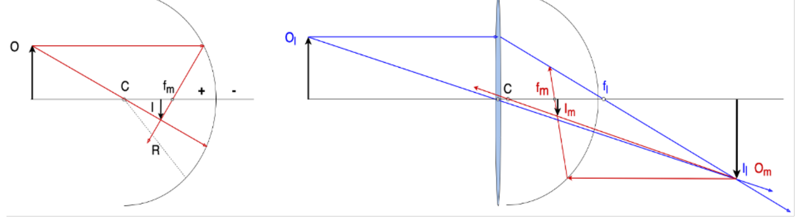


Fig. 9 - Schematic representation of hemispherical mirror optics (left), and lens-mirror optics (right). In blue color the lens optics, in red, that of the mirror. O: object; I: image; C: center of the mirror; R: radius of the mirror; f: focal lengths.

-Thick lens and mirror model: F-numbers for the podocopid naupliar eye is 0.25-0.50 (Myers & Kontrovitz 1988). The measured value for *Notodromas monacha* is 0.27 (Andersson & Nilsson 1981).

-Computational model: light-gathering is affected by the cuticular lens (Tanaka 2006).

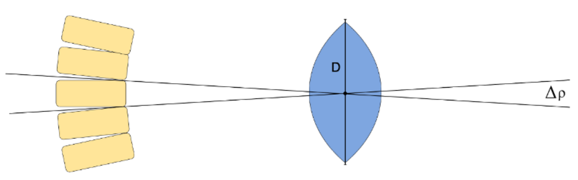


Fig.10 - Schematic representation of the angle for which the receptors absorb light.

Spatial resolution increases with the decrease of the light-acceptance angle for receptors. In *Notodromas monacha* this angle is 0,17 rad for the lateral cups and 0,35 rad for the ventral one (Andersson & Nilsson 1981)—for deep-sea isopod *Cirolana* sp. it is 0,78 rad and for copepod *Labidocera* sp. it is 0,06 rad.

Podocopid ostracods may possess stereoscopic vision (Andersson & Nilsson 1981).

4. Visual stimuli transduction in podocopid ostracods

Visual-Opsins: *Heterocypris* transcripts seem to express only long-wavelengths sensitive rhabdomeric opsins (Henze & Oakley 2015; Palecanda et al. 2022).

Non-Visual Opsins: they are likely involved in circadian rhythms and other physiological processes. In transcripts of *Heterocypris incongruens* were found three non-visual opsins (Palecanda et al. 2022).

Central Nervous System and Visual Processing: in *Heterocypris incongruens*, fluorophores from biogenic monoamines emitted weakly in the naupliar eyes and strongly in the neuropile. More complex fluorescent patterns were observed in the deutocerebrum and tritocerebrum (Aramant & Elofsson 1976).

5. Photoreception and learning in non-marine ostracods

-***Cyclocypris forbesi*** shows a preference for dark environments and navigates light-guided mazes to avoid light (Applewhite & Morowitz 1966).

-***Cypris* spp.** shows preference for UV-B light illuminated chambers (Barcelo & Calkins 1979).

-***Heterocypris incongruens*** shows phototactic behaviors to specific light colors associated with food or stressors (Romano et al. 2022).

-***Cyclocypris forbesi*** closes its valves when illuminated by a light color previously associated with negative stimuli (Applewhite & Morowitz 1966).

Ostracods may display a complex interplay of senses to detect environmental stimuli. Further research is needed to gain broader insights into the evolutionary adaptations of photoreception in podocopid ostracods.

For more information on the topic:
Bellavere, E., Matzke-Karasz, R., Romano, D., & Rossetti, G. (2024). Structure and functional implications of photoreceptive systems in non-marine ostracods: a review. *Hydrobiologia*, 851: 4051–4075.

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