The Eyes of Mesopelagic Crustaceans

III. *Thysanopoda tricuspidata* (Euphausiacea)*

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Summary. The compound eyes of the mesopelagic euphausiid *Thysanopoda tricuspidata* were investigated by light-, scanning-, and transmission electron microscopy. The eyes are spherical and have a diameter that corresponds to 1/6 of the carapace length. The hexagonal facets have strongly curved outer surfaces. Although there are four crystalline cone cells, only two participate in the formation of the cone, which is 90–120 μm long and appears to have a radial gradient of refractive index. The clear zone, separating dioptric structures and retinula, is only 90–120 μm wide. In it lie the very large oval nuclei of the seven retinula cells. Directly in front of the 70 μm long and 15 μm thick rhabdom a lens-like structure of 12 μm diameter is developed. This structure, known in only a very few arthropods, seems to be present in all species of Euphausiacea studied to date. It is believed that the rhabdom lens improves near-field vision and absolute light sensitivity. Rod-shaped pigment grains and mitochondria of the tubular type are found in the plasma of retinula cells. The position of the proximal screening pigment as well as the microvillar organization in the rhabdodom are indicative of light-adapted material. The orthogonal alignment of rhabdovilli suggests polarization sensitivity. Behind each rhabdom there is a cup-shaped homogeneous structure of unknown, but possibly optical function. Finally, the structure and the function of the euphysiid eye are reviewed and the functional implications of individual components are discussed.

Key words: Compound eyes – Arthropod vision – Deep-sea crustaceans – Ultrastructure – *Thysanopoda tricuspidata* (Euphausiacea).

The first two papers in this series on the eyes of mesopelagic crustaceans dealt with the photoreceptors of the penaeid shrimp *Gennadas* sp. and the amphipod *Streetsia*
challengeri (Meyer-Rochow and Walsh, 1977; Meyer-Rochow, 1978). In this paper we examine the spherical eye of the euphausiid Thysanopoda tricuspidata.

Eyes and their anatomy vary greatly within the 90 species of the malacostracan family Euphausiacea (Kaestner, 1970). Location, size and shape of the eyes are important taxonomic criteria, and attempts to correlate eye morphology with habitat and depth distribution have been made (Kampa et al., 1963). With the exception of Bentheuphausia amblyops, which lacks both eyes and photophores, all euphausiids possess eyes and light organs. The eyes, which may be spherical or bilobed, are almost always well developed and large, and according to Mauchline and Fisher (1969) there are several species "in which the diameter of the widest part of the eye is about one sixth of the length of the body, the eyes of these species thus being among the largest in the stalk-eyed Crustacea".

Chun (1896) prepared the first in-depth study of the anatomy of the euphausiid eye. This paper is still the most outstanding example of histological work on euphausiid photoreceptors; his results are quoted and his excellent drawings are still reproduced today. Chun, who compared his results with those of Grenacher (1879), pointed out that in contrast to the crystalline cones of decapod compound eyes (four cone cells for each ommatidium) the ommatidial cone in Euphausiacea consisted of only two major cone cells; he also mentioned the 'Achsenfaden', a fine filament that connected the proximal end of the cone with the distal end of the rhabdom in the euphausiid eye, but not in decapods. Chun did, however, demonstrate convincingly that the differences between the decapod and euphausiid eye were of a minor nature and that, in principle, the gross anatomy of the compound eyes of these two crustacean groups was very similar.

Future investigations by Hanström (1928) on optic lobes and brains of euphausiids and mysids confirmed Chun's view, but Hanström, furthermore, showed that affinities to Leptostraca and Stomatopoda existed as well. (An ultrastructural investigation of the eye of a stomatopod was recently published by Schönenberger, 1977). A review of Euphausiacea by Zimmer (1956), apart from being a thorough and comprehensive piece of work, added little to what was already known about sense organs and the nervous system of this group. Kampa (1965) in her re-evaluation of the euphausiid eye confirms most of the earlier observations and emphasizes the similarity between the eyes of euphausiids and galatheids. She does, however, disagree with Chun's interpretation of the rhabdom architecture as columns of plates, and believes, in agreement with Vaissière (1961), who examined the rhabdom of an unidentified euphausiid, that the rhabdom is a 'spiral' (Kampa, 1965). In the same year Elofsson (1965) published ultrastructural results on frontal organs and nauplius eyes of nine species of euphausiids representing eight genera. He found that rhabdoms were developed in all cases and that each eye consisted of nine cells arranged in three groups of three, separated from each other by clusters of screening pigment.

More recently a detailed review on euphausiids by Mauchline and Fisher (1969) provides particularly useful information on the biochemistry of vision in these crustaceans, but does not contain any reference to ultrastructural work on the euphausiid compound eye. Because mysid shrimps are often regarded as the closest decapod relatives of the Euphausiacea (and in fact the two families until less than half a century ago were commonly combined into one group known as