The Dorsal Eye of *Cloëon dipterum* (Ephemeroptera) (A Light- and Electronmicroscopical Study)

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Cloëon dipterum, Superposition Eye, Apical and Basal *Rhabdomes*

The superposition eye of *Cloëon dipterum* is a clear zone type of compound eye. The central ommatidia have two rhabdomes, at different levels, a small apical and a main basal one. The number of basal rhabdomes is greater than the number of dioptric apparatuses. This and the role of the retinula cell processes is discussed with regard to superposition or light-guide theory.

The male of *Cloëon dipterum* has two types of compound eyes, a dorsal "turban-shaped" superposition eye and a lateral apposition eye [1–3]. The dorsal eye of the male provides an example of a typical "clear zone" eye, well known from studies of superposition eyes of insects that are active in dim light.

The dioptric apparatus of each ommatidia consists of a biconvex-layered lens (diameter 20–24 µm, thickness 17 µm) and a non-homogeneous cone formed by four cone cells surrounded by two principal pigment cells and several smaller accessory pigment cells, the latter filled with many pigment granules (Fig. 1). In the light-adapted eye* no crystalline tracts *i.e.* no extensions of the four cone cells towards the receptors are visible. Instead, the seven retinula cells with distal nuclei, situated directly beneath the tip of the cone, form a tract ca. 1.0–1.5 µm in diameter across the clear zone of ca. 130–150 µm in width (Fig. 1). These retinula cell processes are connected by terminal bars, contain mitochondria and glycogen but no pigment granules. The tracts of seven cell processes are isolated from each other by a homogenous mass that earlier authors have called haemolymph [2, 3]. During the transformation from subimago to imago the haemolymph is secreted and separates the dioptric apparatus from the basal receptor. In the nuclear region the seven retinula cells form a fused rhabdom. This apical rhabdom is composed of seven rhabdomeres resulting in a calyx-like structure directly beneath the crystalline cone cells (Fig. 1).

On the proximal side of the clear zone the retinula cells enlarge again to a diameter of ca. 7–8 µm and form the main basal fused rhabdomes, which are 150 µm long and spindle-shaped. The surrounding cytoplasm contains many mitochondria; the cytoplasm of the distal part of the basal retinula cell is vesiculated and filled with granular material;

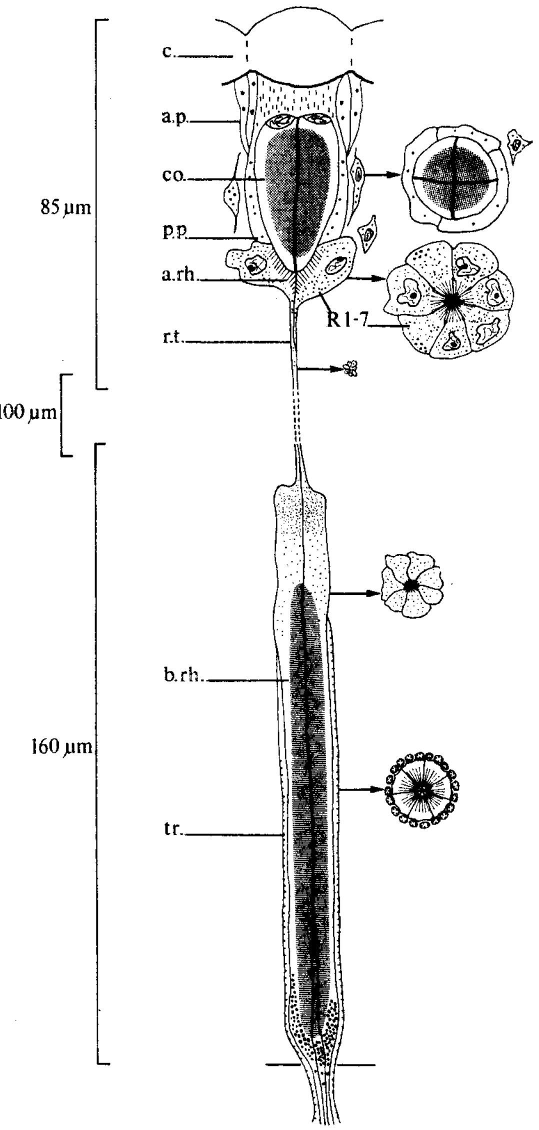

Fig. 1. Diagram of the light-adapted ommatidium of the superposition eye of *Cloëon dipterum* (male) with transvers sections at different levels; c., cornea; a.p., accessory pigment cells; c.o., crystalline cone formed by four cone cells; p.p., principal pigment cells; a.rh., apical rhabdom formed by seven retinula cells (R 1-7); r.t., retinula cell tract; b.rh., basal rhabdom; tr., tracheal tapetum.

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* Animals adapted with normal daylight were fixed in Karnovsky's glutaraldehyde-formaldehyde, postfixed with OsO_4, dehydrated in ethanol and embedded in Araldite.

in the proximal part near the basement membrane the retinula cells contain pigment granules (Fig. 1). The basal ommatidia are separated from each other by a tracheal tapetum that probably functions as a reflector of the incident light[4]. At the base of the retina the retinula cell fibres pass in bundles of seven through the basement membrane. A basal eighth retinula cell, found in other superposition eyes, is not evident here.

In most superposition eyes the clear zone exists during dark adaptation[4–6], while in the light-adapted state screening pigments isolates the individual ommotidia. This is not the case in *Cloëon dipterum*: in the light-adapted eye the granules of accessory pigment cells lie between the cones and separate exclusively the apical rhabdomes. Further, it is surprising that the rhabdomeres, arranged at two different levels, belong to the same retinula cells. The functional mechanism of this tiered retina (*e. g.* how images are generated) cannot be resolved by morphological techniques alone.

Another interesting point is the fact that in the lateral ommatidia the retinula cells do not extend to the apical dioptric apparatus but end proximally from the cornea in the lateral part of the eye. Hence the number of basal rhabdomes counted in an equatorial horizontal row exceeds the number of dioptric apparatuses by a factor of two. Further, it can be assumed that all basal rhabdomes are functionally intact since all of them – even the lateral ones – are connected 1:1 to lamina cartridges and medulla columns[7]. On the basis of these findings it seems highly suggestive that images on the receptor layer are generated mainly by classical superposition[1] rather than light guide mechanisms, as recently postulated[6], since only the central rhabdomes have retinula cell processes which could function as light guides.

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