

A new functional interpretation of the visual system of male scale insects (Coccida, Homoptera)

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Summary. In a flight position with vertical body axis, both the 'dorsolateral' and the characteristic 'ventral' lens eyes of male coccid insects are arranged in a horizontal ring around the head. The interpretation that they mainly serve for stabilizing the flight position with regard to the horizon can explain the extraordinary structural features known for these eyes.

Key words. Coccida; vision; ocelli; flight.

Scale insects are a group of homopteran insects where the females in the adult stage are sessile and wingless. Most of them reproduce parthenogenetically. Male coccids, if present at all, are much smaller than the females. They are fragile and, lacking functional mouthparts, they cannot feed and only live for a few hours. In most families the males are capable of flight, but usually only the forewings are developed. Most male scale insects have long waxen abdominal appendices to stabilize flight position. In a number of families (e.g. Pseudococcidae, Eriococcidae) the heads of the tiny males have a strangely comical look, they bear a pair of ventral ocelli situated at a position where insects usually have their mouthparts (fig., a), and two dorsolateral ocelli where most insects have compound eyes (fig., b).

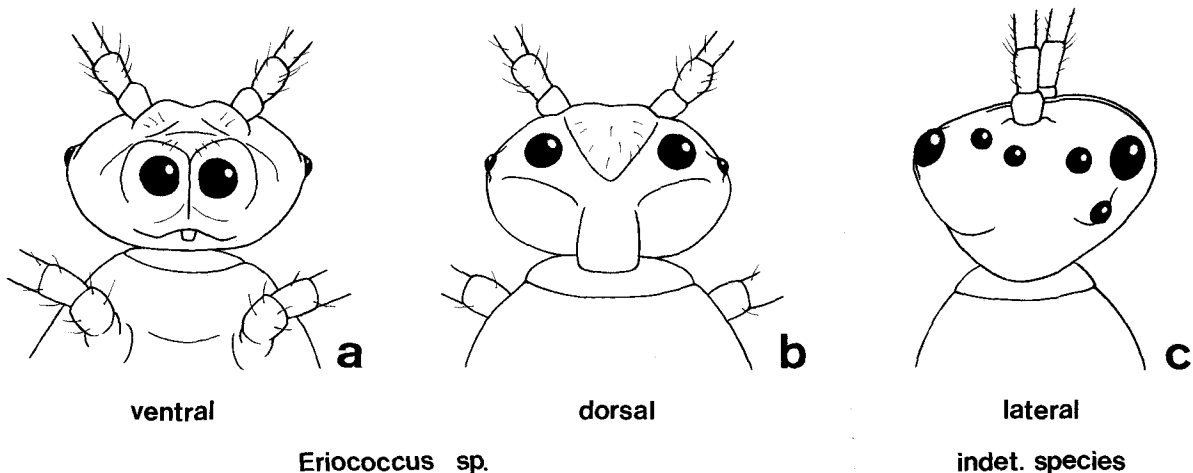
In a description of a detailed anatomical investigation of these bizarre simple eyes² it was hypothesized that the 'ventrally' looking ocelli were used to locate landing sites on vegetation where the sedentary receptive females emit sex pheromones. Several outstanding morphological features (corneal nipples, shallow receptor configuration, lack of screening pigments, disc-like membrane arrangement instead of tubular microvilli) were interpreted as adaptations in an extremely small eye to combine relatively high photon capture with reasonable resolving power². These interpretations were based on the assumption that light was focussed on the receptor layer.

In the light of recent investigations on the structure and function of insect ocelli³⁻⁵ this functional interpretation of the arrangement and the anatomy of the male coccid visual system has to be reevaluated. These investigators have found that the ocelli of locusts, dragonflies and hoverflies are involved in horizontal course stabilization during flight. Any change around the roll

and pitch axes is immediately monitored by comparison of inputs from the three ocelli. Artificially changing the orientation of the horizon or even reducing the light intensity on one side of a tethered flying locust elicits correcting steering motions⁵. In addition, it has been established that the retina of the locust ocellus does not receive a focussed image^{3,6}. If pattern recognition is not required in a visual system, sensitivity can be enhanced by having the rhabdoms out of focus. The assumption of a focussed fish-eye lens for *Eriococcus*² resulted in an estimated F-number (calculated from the ratio between the estimated focal length and the lens diameter) of only 0.55, which was an exceptionally low value for an arthropod eye. Assuming an unfocussed eye for *Eriococcus* would allow for a higher F-number. Furthermore, screening pigments are not necessary in an unfocussed retina.

With these ideas in mind, and observing that male coccids, like other tiny insects such as very small hymenoptera and diptera, are hovering or 'swimming' in flight, with their body axis almost vertical, the 'ventral' ocelli are in fact looking straight ahead. If shown in upright position (fig.) it is evident that in the Australian *Eriococcus* sp. all four ocelli (or even six, including the two small, probably vestigial, ocelli) are looking more or less horizontally. In another Australian coccid (fig., c) a ring of twelve ocelli can be seen.

It thus seems reasonable to assume that the 'ventral' and 'dorsal' ocelli in male scale insects in natural flight position form a ring of unfocussed, more or less horizontally looking eyes. Their main function would be to monitor changes in the position of the body axis with regard to the horizon.



a and b Anterior ('ventral') and posterior ('dorsal') view of the head of an Australian male coccid of a yet undescribed species in the genus *Eriococcus*.

c Drawings from SEM photographs. c Lateral view of the head of an unidentified Australian male scale insect.

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