THE STRUCTURE, FUNCTION AND DEVELOPMENT OF THE EYES IN THE EPHEMEROPTERA

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Abstract. In relation to their life history and especially to their short adult life, mayflies /Ephemeroptera/ have very variable eyes. They range from the hardly visible structures in small nymphs to the large prominent, and often strikingly coloured, turbinate eyes of the male imagoes of certain species. The development of both the external structures and the internal innovation of the visual centres is discussed in relation to the influence of internal and external factors. Recent studies concerning the mechanism of vision in mayflies are also reviewed with respect to nymphal and adult ecology and behaviour. There is a need for an integration of structural, physiological and ecological aspects of vision.

Morphology, vision, effects of light, behaviour, ecology

In relation to their environment, the relatively low number of species and their short aerial life, mayflies show an astonishing diversity in eye structures and colouration (Verrier 1956). In the very young aquatic nymphs the eyes are hardly distinguishable. However, the striking eyes present in the males of many species have long attracted the attention of naturalists and scientists, and even by 1839 Westwood had described the sexual dimorphism of the eyes in adult mayflies. The visual centres in mayflies are composed of two components, the ocelli and the compound eyes.

OCELLI

The ocelli are often positioned at the extremities of a more or less flat triangle; the anterior ocellus is often smal-
ler than the other two. However, in Nathanella (Leptophlebi-
idae) their shapes are also very different; the median ocellus
being small and round, whereas the two lateral ocelli are large
and half-moon shaped (Peters and Edmunds 1970). In male adults
the ocelli are often elevated and close together, while in the
female they are hardly elevated and well separated. They are
usually black at their base. None of the ocelli possess a lens,
but each one has its own nerve innovation.

COMPUND EYES

In mature nymphs the compound eyes are usually moderately
large and located laterally or dorsally near the posterio-late-
ral margin of the head. Most mayfly adults exhibit sexual di-
morphism, the eyes of the male being large and close together,
while those of the female are smaller and further apart. In so-
me species, however, such as in the families Caenidae and Tri-
corythidae, the eyes of both sexes are usually small and wide
apart. The eyes of the male may be either uniformly coloured
or the upper part may be of a different colour. In the Baetidae
and some Leptophlebiidae the upper facets may be raised on a
stalk, the so-called turbinate eyes. The eyes of the female are
generally uniform in colour and facet size. The colour of the
males eyes can vary widely, although often a shade of red or or-
ange. Those of *Baetis fuscatus* are orange while the lower port-
tions of their eyes are blackish-green.

Many eyes are very dark, almost black as in some Australi-
an Siphlonuridae. Certain mayflies also have green or turquoise
eyes, such as *Ecadyonus dispar*. In contrast, *Ephemerella ex-
crucians* has bright yellow eyes, while those of *Baetisca roger-
si* are greyish yellow.

The degree of development of the turbinate eyes is not al-
ways constant for a given species and polymorphism in the tur-
binate eyes of Baetidae has been the source of synomynies. Müll-
er-Liebenau (1970) has shown that in eastern Europe the turbi-
nate eyes of the male *Baetis melanonyx* are tall, cylindrical
and with few ommatidia, while in western Europe the eyes are
shorter, more usual in shape and with a greater number of omma-
tidia. Intermediates occur in southern Europe. A similar form
of polymorphism has been reported in African Cloeon (Gillies,
1978) and North American Potamanthus (Lord and Meier 1977). Eye
colour will obviously vary somewhat within a single species po-
pulation. However, Lyman (1943) reported that individual males
imagos of *Stenonema* changed the colour of their eyes in accord-
ance with light intensity. In bright daylight their eyes were
pale bluish-grey, but changed to a very dark bluish-black in
the evening. Lyman was able to change their eye colour by sim-
lply changing light intensity! This phenomenon was restricted to
the male imagos, and Lyman suggested that the colour changes
were due to the migration of pigment facilitating improved vi-
sion at low light intensities. In certain species eye colour
may also be a function of the age of the male imago (J. Fon-
tain, pers. comm.) or may differ in fresh and preserved specimens.

THE FOSSIL RECORD

Certain fossil adult mayflies from the Cretaceous had equivalent eyes to those of most present-day mayflies. Male mayflies from the Cretaceous of Siberia (Tshernova 1971) and the Oligocene Baltic amber (Demoulin 1968) all had large distinctive eyes. However, not all fossil mayflies had such large eyes, and Triplosoba pulchella, the earliest known fossil mayfly, appears to have had relatively small, laterally-placed eyes, although one should be cautious in drawing definitive conclusion from a single male imago (Demoulin 1956). It appears, however, that the present variation in eye morphology within the Ephemeroptera has existed since the Cretaceous.

DEVELOPMENT OF THE EYES

There are few studies which follow eye development in detail from the first nympha1 instar to the fully developed imago. Probably the most detailed investigation is that by Rawlinson (1939) on Ecdyonurus venosus in which she distinguished 17 nympha1 stages. In the first instar the visual organs are situated at the margin of the head, the compound eyes do not show facets and they are only slightly larger than the ocelli. In subsequent stages the compound eyes gradually increase in size and become triangular in shape. By stage 9 the facets become distinct and in subsequent stages the compound eyes of the males gradually approach each other, whereas those of the female are widely separated. Both internal and external factors appear to govern eye development in mayflies. Rawlinson (1939) suggested that the seasonal abundance of sessile algae affected differentiation in E. venosus. Also internally protocerebral secretions reach a surprising intensity. In older nymphs it is possible to detect these secretions overloading the brain and migrating into the endocrine glands (corpora cardiaca and corpora allata) and the blood (Arvy and Gabe 1952, 1953a, 1953b). It would be interesting to determine how such neurosecretion varies in the mayflies in species in which we know their external morphological development in detail. There is likely to be a correlation between stimulation by neurosecretion at certain stages and the growth and differentiation of the eyes.

THE INNOVATION OF THE VISUAL CENTRES

The optical centres, both the ocelli and the compound eyes, are well supplied with nerves in the mature nymphs and adults (e.g. Wisely 1965, Strenger 1970, Soldán 1979, Schönmann 1981). The optical ganglia behind the eyes are large, especially in the males and together with the eyes themselves constitute a complex that is larger than the cerebral ganglion or brain. There is a close connection between the development
cf the eyes and sexual development in the mayflies. The extraordinary development of the eyes in the male is associated with hyperactivity of the gonads. Castration of the male would most likely hinder differentiation of the visual centres. Evidence for this is provided by the fact that when sexual development is abnormal, as in gynandromorphism, ocular morphology is modified (Soldán and Landa 1981). A good example of this is the gynandromorph of *Baetis fuscatus* in which both genitalia and optical centres are modified as a result of mermithid parasitism.

**EYE FUNCTION**

The prominence of the visual centres in the mayflies, especially in the males, indicates their major importance at some stages in their life. In small nymphs the ocelli and compound eyes are insignificant and they probably have little functional importance. In larger, more mature nymphs the visual centres assume a much greater morphological prominence.

In contrast to the recent detailed studies of the mechanism of vision in adult mayflies, little similar modern work has been carried out on nymphs. Most, although not all, mayfly nymphs appear to be negatively phototactic (Wodsedalek 1911, Elliott 1968, Pescador and Peters 1974, Nagell 1977). However, in certain environmental situations, such as lack of oxygen, this may be reversed (Nagell 1977, Brittain and Nagell 1981). In *Baetis harrisoni* the visual centres have been shown to play a role in maintaining dorso-ventral orientation and microhabitat choice (Hughes 1966a, b). It was postulated that the dorsal light response is initiated by the ocelli and maintained tropotactically by the compound eyes.

Newkirk (1981) has recently suggested that light intensity governs metamorphosis in mayfly nymphs and that the ocelli are the receptors involved in this process. He draws support for this hypothesis from the fact that, in contrast to the ocelli, especially the ventral ocellus, the compound eyes are scarcely developed in the initial nymphal instars.

Visual acuity does not appear to be high in mayfly nymphs, perhaps not surprising in view of the fact that they are predominantly night active organisms apart from the period immediately prior to emergence (Harker 1953, Elliott 1968, Solem 1973). Extremely high visual acuity would be required if sight were to be important at such low light intensities. Peckarsky (1980) has recently shown that predator avoidance in mayfly nymphs takes place through chemical and tactile rather than visual stimuli and the presence of mechanoreceptors has recently been confirmed in mayfly nymphs (Corcum and Clifford 1981). Also vision is clearly unlikely to be important for burrowing species of mayflies. We do not know whether predatory mayflies hunt largely by tactile cues as has been shown for stoneflies (Sjöström 1983).

On account of the primitive nature of the order and their
distinct sexual dimorphism mayflies have attracted the attention of workers investigating the structure and function of arthropod visual centres. The enlarged turbinate eyes of the males appear to assist them in finding the flight swarm and in catching the female in flight (see Britain 1982). Insects with enlarged dorsal eyes always seem to use them to catch small objects against the sky (Horridge 1976). To do this most effectively the eyes must have a spectral sensitivity to match the background. Horridge and McLean (1978) have recently discovered that turbinate eyes of Atalophlebia (Leptophebiidae) are sensitive to ultra-violet which becomes a significant part of the light spectrum for organisms which see objects against the twilight sky. This sensitivity to ultra-violet in mayflies may not only assist in finding a mate in the crepuscular swarms that characterize many, especially temperate, mayflies, but also enable them to avoid predators that may not have such visual sensitivity. There is still discussion as to the precise mechanism of light transmission and image production in mayfly eyes (see Wolburg-Buchholz 1976, 1977; Horridge and McLean 1978). It is interesting to note that the adults of the families such as the Caenidae and the Tricorythidae, that show little sexual dimorphism, have evolved very short adult lives, often less than two hours (Edmunds and Edmunds 1980). This does not appear to have any direct connection with the time of swarming, however, as even within the same genus one may have both morning and evening swarming species, although it may be connected with light intensities at these periods of the day. It is interesting to note that the African caenid genera Caenopsella and Afrocaenis are remarkable not only for the large eyes of the male, but for the daytime swarming of the imagos (Gillies 1977, 1982). Detailed studies within a single species of the morphology, sensitivity and image formation of the visual centres coupled with an investigation of the timing of adult swarming and adult behaviour are likely to be especially fruitful. It is probable that the diversity in the eyes of mayflies is also expressed in an equivalent way in their behavioural ecology.

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EYES IN EPHEMEROPTERA

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