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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 imagos 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 (Leptophlebiidae) 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.

COMPOUND EYES

In mature nymphs the compound eyes are usually moderately large and located laterally or dorsally near the posterio-lateral margin of the head. Most mayfly adults exhibit sexual dimorphism, the eyes of the male being large and close together, while those of the female are smaller and further apart. In some species, however, such as in the families Caenidae and Tricorythidae, 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 orange. Those of Baetis fuscatus are orange while the lower portions of their eyes are blackish-green.

Many eyes are very dark, almost black as in some Australian Siphlonuridae. Certain mayflies also have green or turquoise eyes, such as Ecdyonurus dispar. In contrast, Ephemerella excrucians has bright yellow eyes, while those of Baetisca rogersi are greyish yellow.

The degree of development of the turbinate eyes is not always constant for a given species and polymorphism in the turbinate eyes of Baetidae has been the source of synonymies. Müller-Liebenau (1970) has shown that in eastern Europe the turbinate 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 ommatidia. 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 population. However, Lyman (1943) reported that individual males imagos of Stenonema changed the colour of their eyes in accordance 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 simply 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 vision at low light intensities. In certain species eye colour may also be a function of the age of the male imago (J. Fon-

taine, 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 nymphal instar to the fully developed imago. Probably the most detailed investigation is that by Rawlinson (1939) on Ecdyonurus venosus in which she distinguished 17 nymphal stages. In the first instar the visual organs are situated at the margin of the head, the compoud 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

of 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 Brittain 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 (Leptophlebiidae) 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 Mc Lean 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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