29 Square facets in a hexagonal world

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Square facets have previously been reported to occur in the upper portion of male compound eyes in Atalophlebia. *This is the only detailed study of square facets in Insecta. It is now known that square facets characterize the Atalophlebiinae (Leptophlebiidae: Ephemeroptera), while hexagonal facets characterize the Leptophlebiinae. The phylogenetic significance of this discovery is discussed.*

Introduction

Among Arthropoda, adult compound eyes consist of a large number of hexagonal facets and each facet or lens represents the outer portion of a single eye element or ommatidium. In males of Insecta, the upper facets sometimes are much larger than the lower and occasionally, as in Ephemeroptera, the male eyes are divided into separate dorsal and ventral or lateral portions.

Hexagonal facets occur among all insect orders that have compound eyes and these facets are known in all groups within the Arthropoda with the exception of some higher Crustacea. Land (1980) noted that the compound eyes of crabs (Brachyura) and hermit-crabs (Anomura) have square facets. However, the larval stages of these two groups have hexagonally faceted eyes; in *Palaemonetes*, the facets square off as the shrimp approaches maturity — about molt 15 (Land 1980).

Structure and Function of Square-faceted Eyes

Meyer-Rochow (1971) and Horridge and McLean (1978) reported square-faceted eyes among Insecta in their anatomical and functional studies of the dorsal compound eyes of three unidentified species of the Australian mayfly genus *Atalophlebia*. Although square-faceted eyes have been known for Atalophlebiinae for many years (e.g., Gillies 1951; Edmunds 1963; Peters and Edmunds 1970), their taxonomic uniqueness was not recognized until Dr. Land discussed the

evolution of eyes with the junior author; the first published phylogenetic use of square eyes occurred in discussion of the *Terpides*-group genera (Savage 1986).

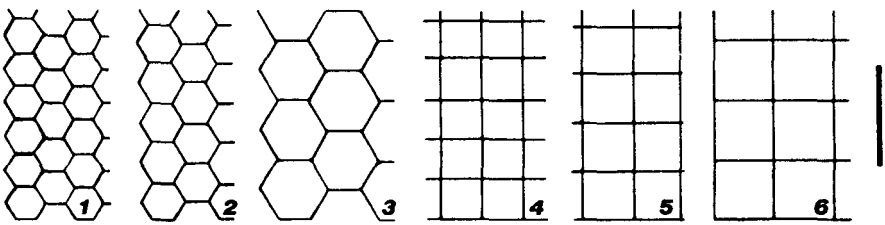
Unlike the square eyes of Crustacea, these were not reflecting superposition eyes (Horridge and McLean 1978). The square facets in the dorsal eyes of *Atalophlebia* were sensitive only to ultraviolet (u.v.) light; the outer surface of the cornea was strongly convex and coated with fine nipples, "suggesting a strong selection pressure to catch every possible photon" (Horridge and McLean 1978). Earlier, Horridge (1976) had studied the ommatidium of *Cloeon* sp. from Australia, a member of the Baetidae with large, dorsal male eyes consisting of hexagonal facets. In contrast to *Atalophlebia*, dorsal eyes of *Cloeon* are rather flat (Horridge et al. 1982).

Horridge et al. (1982) experimentally studied the dorsal male eyes of one species of *Atalophlebia*, and found that each facet individually perceives u.v. light. They suggested that u.v. vision enabled the males to see the females against the background of the sky more effectively during nuptial flight. If so, they suggested, female wings should absorb u.v. light, but their experiments showed that the female wings of many insects (including *Atalophlebia*) did not absorb u.v. light, nor was there any difference between male and female wings (Horridge et al. 1982).

Based on many years of field experience the original hypotheses of Horridge and McLean (1978) and Horridge et al. (1982) are probably correct, and the lack of difference between male and female wings is not a cause for concern. After all, in species of mayflies that form "typical" mayfly swarms, including Leptophlebiidae, the swarms are made up of males (Brodsky 1973). There are other types of swarm behaviour in mayflies, but males that engage in other behaviours do not have eyes divided in the same way as the first group (Brodsky 1973). In typical swarms males orient individually to a marker but somehow see other males in order to maintain their position within the swarm (Brodsky 1973; Savolainen 1978). The flickering motions of wings of other males, and females, may be enhanced by perception of a narrow range of wavelengths, particularly shorter wavelengths that are more easily bent as they pass through a wing membrane. To this add the other arguments of Horridge and McLean (1978) concerning visual discrimination and background illumination, and it is possible that mayflies see more clearly, distinctly and strongly the same shimmer of wings that human observers see. There is some doubt that males actually recognize females of a species in these swarms, and in some cases females also orient towards markers (Savolainen 1978). In cases of swarming mayflies studied, males attempt to mate with anything moving through the swarm, including other males, other mayflies, other insects and decoys (Fremling 1960).

The work of Horridge and his colleagues, most of it on atypical square-faceted *Atalophlebia* spp., provides a foundation for other studies on mayfly vision. At present we cannot compare the functional properties of square eyes with those

Figures 1-6. Relative shape and size of dorsal male eyes (1-3. Leptophlebiinae; 4-6. Atalophlebiinae): 1. *Habrophlebia (Hesperaphlebia) vibrans* Needham; 2. *Leptophlebia nebulosa* (Walker); 3. *Habrophlebiodes* sp. from Malaysia; 4. *Meridialaris laminata* (Ulmer); 5. *Penaphlebia* (s.s.) *chilensis* (Eaton), 6. *Miroculis* (s.s.) *rossi* Edmunds. Scale bar at right = 0.050 mm.



hexagonal eyes. We can, however, address the subject of square eyes in insect phylogeny, as proposed by Land (1980).

Phylogenetic Significance of Square-faceted Eyes

Eyes with square facets are not known for other orders of insects. We studied representative genera from every family of Ephemeroptera and all described genera of Leptophlebiidae. Although dorsal male eyes of most Ephemeroptera are differentiated into a lower and upper portion (sometimes only by colour of the facets), square facets were found only in the Leptophlebiidae.

Peters (1980) divided the Leptophlebiidae into two subfamilies, Leptophlebiinae and Atalophlebiinae. The Leptophlebiinae are represented by eight genera restricted to the Northern Hemisphere, and the Atalophlebiinae are composed of many primitive to highly specialized phyletic lineages throughout the world. The dorsal male eyes of all genera of Leptophlebiinae studied have hexagonal facets (Figs. 1-3); the ventral (lateral) male eyes and female eyes also consist entirely of hexagonal facets. The dorsal male eyes of all but one genus of the Atalophlebiinae have square facets (Fig. 4-6). The exception is *Fulleta* from the area of Lake Tanganyika in

Africa. In *Fulleta* the dorsal portion of the male eyes appears to be missing and the entire compound eye consists of the ventral (lateral) eyes with hexagonal facets, as in female Atalophlebiinae. Ventral (lateral) eyes of all male Atalophlebiinae consist of hexagonal facets as do female compound eyes.

We studied the developing compound eyes in a series of both immature and mature nymphs of several South American and Australian species of the Atalophlebiinae. In all cases the developing dorsal male eyes were square-faceted. Therefore, this paper records the first example in Arthropoda of male dorsal eyes being square-faceted in both the immature and adult stages.

Based on the phylogenetic study by Peters (1980) on the two extant subfamilies of the Leptophlebiidae, facet shape of male dorsal eyes can be included in the character state analysis (Table 1 of Peters 1980). Hexagonal facets in the dorsal male eyes of the Leptophlebiinae are the ancestral state, and square facets of Atalophlebiinae are derived.

Within the Atalophlebiinae, the dorsal male eyes are extremely variable. Often the dorsal and ventral portions are almost entirely contiguous and the dorsal portion contains many hundreds of square facets. In several phyletic lineages, the dorsal portion can be on a short to long stalk and the number of square facets greatly reduced. Examples have been noted for *Isca* (Gillies 1951), for *Megaglena* (Peters and Edmunds 1970) and for *Miroculis* (Edmunds 1963). In these genera the dorsal portion is on a relatively long stalk with no more than 11 or 12 facets in a row; Savage and Peters (1983) discussed stalk length and facet size in *Miroculis*. Within the genus the dorsal portion can be stalked (derived) or unstalked (ancestral) and the facet number can be reduced (derived) or not reduced (ancestral). It is interesting that species of Atalophlebiinae with stalked dorsal eyes are found only in tropical environments.

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