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Fine structure of the anterior median eyes of the funnel-web spider *Agelena labyrinthica* (Araneae: Agelenidae)

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ABSTRACT

Only few electron microscopic studies exist on the structure of the main eyes (anterior median eyes, AME) of web spiders. The present paper provides details on the anatomy of the AME in the funnel-web spider *Agelena labyrinthica*. The retina consists of two separate regions with differently arranged photoreceptor cells. Its central part has sensory cells with rhabdomeres on 2, 3, or 4 sides, whereas those of the ventral retina have only two rhabdomeres on opposite sides. In addition, the rhabdomeres of the ventral retina are arranged in a specific way: Whereas in the most ventral part they form long tangential rows, those towards the center are detached and are arranged radially. All sensory cells are wrapped by unpigmented pigment cell processes. In agelenid spiders the axons of the sensory cells exit from the middle of the cell body; their fine structure and course through the eye cup is described in detail. In the central part of the retina efferent nerve fibres were found forming synapses along the distal region of the receptor cells. A muscle is attached laterally to each eye cup that allows mainly rotational movements of the eyes. The optical performance (image resolution) of these main eyes with relatively few visual cells is discussed.

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1. Introduction

Spider eyes have been studied with the light microscope for a long time (Grenacher, 1879; Bertkau, 1886; Hentschel, 1899; Widmann, 1907, 1908; Scheuring, 1914; Land, 1969a; Homann, 1928, 1971; Dacke et al., 2001), but there exist only few investigations using electron microscopy. Those deal mostly with the eyes of lycosids and salticids (Bacetti and Bedini, 1964; Melamed and Trujillo-Cenoz, 1966; Eakin and Brandenburger, 1971; Kovoor et al., 1993); only two publications describe the morphology of web spider eyes (Schröer, 1974; Uehara et al., 1977). One focused on the question, of whether the structure of the retina could meet the requirements for perception and analysis of polarised light (Schröer, 1974), however, it contained only limited information on the fine structure of the main eyes and will be supplemented by the present study.

The visual performance of an eye depends largely on the particular morphological design of its retina. If we compare the fine structure of anterior median eyes (AME) of hunting spiders (e.g. lycosids and salticids) with those of the web spider *Agelena labyrinthica*, we notice large differences not only in the dimensions of their lenses but also in the number of photoreceptor cells. Ground spiders hunting for prey can rely on the high resolution of the perceived images. By contrast, the main eyes of the funnel-web spider *Agelena* possess a relatively wide-meshed photoreceptor mosaic with relatively few receptor cells. Therefore, *Agelena* has to rely mainly on vibrations of its web for locating the position of a prey. The spider sits in the funnel entrance, but probably receives only coarse images of its prey. Instead, prey is detected by its vibrations or changes of tension in the sheet web (Bartels, 1929; Baltzer, 1930; Holzapfel, 1933, 1934). Nevertheless, *Agelena* has a remarkable ability to analyse the natural polarisation pattern of the sky with its main eyes and uses it as a compass for orientation (Görner, 1958). Due to the limited resolution of AME, visual cues are of little importance in prey-capture, except when a prey is right in front of the spider. The present study of the main eyes in *Agelena* provides the morphological basis for subsequent physiological investigations that could explain how polarization patterns allow *Agelena* to orient itself on its web.

2. Materials and methods

A. labyrinthica was anesthetised with CO_2 and injected with ice-cold cacodylate-buffered 2.5% glutaraldehyde (pH 7.3)

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through a small hole in the posterior carapace to optimise the penetration of the fixative. The front part of the carapace was cut off under bright light (to provide natural adaptation conditions); then rinsed in buffer and post-fixed in 1% osmium tetroxide (in cacodylate- or veronal acetate buffer). After dehydration in ethanol and propylene oxide specimens were flat embedded in Epon 812 to ensure proper orientation during sectioning. Thin sections were obtained with a Reichert-Ultratom, using glass knives. After staining with uranyl acetate and lead citrate sections were studied either in a Zeiss EM9A or EMS-2 transmission electron microscope.

3. Results

3.1. General

The AM eyes of *Agelena* are situated medially between the anterior and posterior lateral eyes (Fig. 1a). Their semi-circular protruding lenses are slightly larger than those of the six secondary eyes. Horizontal sections show a marked deviation (~45° of the optic axes between the tightly joined eye-cups (Fig. 1b). Furthermore, they are tilted by 45° with respect to the horizontal plane (Fig. 1a).

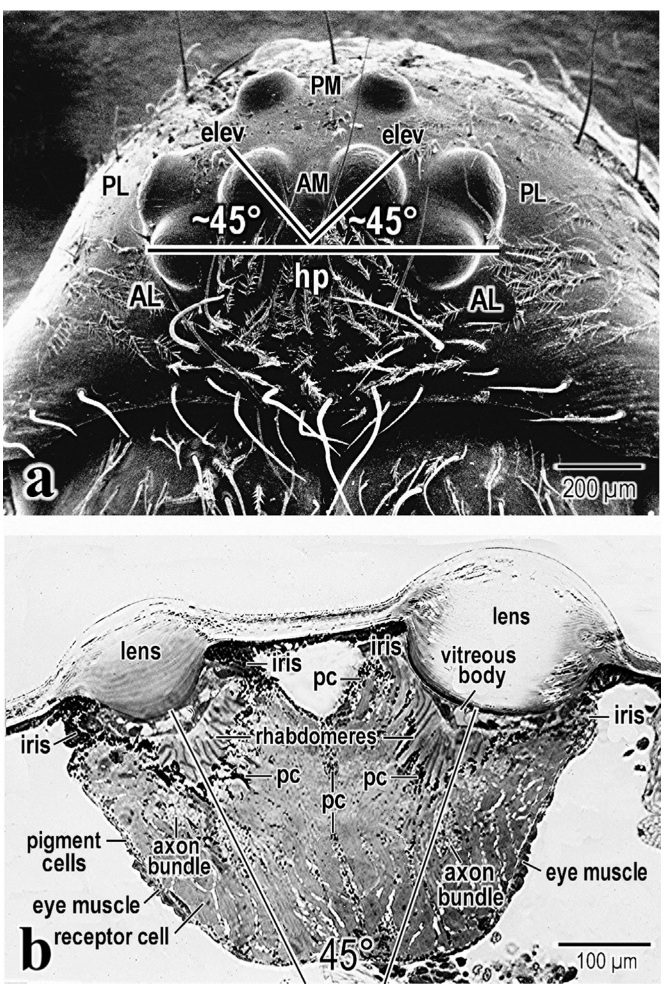

Fig. 1. Eye arrangement of the anterior median eyes of *Agelena labyrinthica*. (a) Frontal view: **AL** – anterior lateral eyes, **AM** – anterior median eyes, ***elev*** – elevation of the AM eyes, ***hp*** – horizontal plane, **PL** – posterior lateral eyes, **PM** – posterior median eyes; **(b)** oblique horizontal section, divergence angle between the optical axes; the eye cups are fused along their midline; ***pc*** – pigment cells.

Below the cuticular lens lie the vitreous cells (also referred to as *cone cells:* Eakin and Brandenburger, 1971); they are enclosed by a cup of pigment cells. The retina follows under a thin layer of unpigmented pigment cell processes and consists of slim photoreceptor cells (Fig. 2). The light absorbing rhabdomeres extend on the distal sides of each visual cell. The axons of adjacent sensory cells meet near the middle of the eye cup. The resulting axon bundles form the optic nerve which leaves the eye cup on its upper posterior part (Fig. 2). A delicate muscle inserts on the lateral side of each eye cup which is firmly attached to the basal membrane of pigment cells (Fig. 2); this membrane forms the exterior sheath of the eye cup.

3.2. Dioptric elements

3.2.1. Lens

The nearly spherical lens of an AME measures approx. 200 µm in diameter (adult female). Thin sections of the cornea show a granular stratification running parallel to the surface. The outermost layer exhibits a fine dentation (Fig. 2, inset) that is due to narrow grooves in the corneal epicuticle (*Foelix*, pers. comm.).

3.2.2. Vitreous body

The vitreous body consists of 100–120 cone cells which form a single layer between the lens and a layer of pigment cell processes which together provide the distance for correct focussing. At the periphery of the eye cup pigment cells, densely packed with pigment granules, serve as a light-proof coating (Fig. 2) and act as an aperture (pseudo-iris).

Vitreous cells are between 15 and 20 µm in diameter (Fig. 3a), their length varies between 15 and 40 µm, depending on their location in the eye cup; they attain their maximum length near the central axis of the eye. The middle and distal segment of the vitreous cells contain fine granular material without any organelles; the large basal nuclei (up to 15 µm diameter) are closely surrounded by an endoplasmatic reticulum (Fig. 3c). In longitudinal sections the nuclei of the vitreous cells appear like a chain of pearls (Figs. 2 and 4). Mitochondria and other organelles are sparse throughout these cells. The vitreous body sits on a 0.3 µm wide basal membrane also referred to as *preretinal membrane* (Figs. 2 and 3) which is surrounded by unpigmented extensions of further proximal lying pigment cells; hemidesmosomes attach the layer of vitreous cells to the preretinal membrane (Fig. 3d).

The AME have different visual fields due to the elevation of the optic axes above the horizontal plane (Fig. 1a), combined with a divergence angle between both eye cups (Fig. 1b). This certainly enlarges the frontal field of vision significantly.

3.3. Retina

3.3.1. General

The photoreceptor cells lie below the vitreous body. Figs. 2 and 4 show a part of the overall 220 to 240 receptor cells which make up the entire retina. The angle between adjacent receptor cells varies from 8° to 12°. About 120 receptor cells lie around the optical axis (*central retina*, Fig. 6c). Further receptor cells are located more ventrally, forming an easily identifiable part of the retina due to the different arrangement of the cells' rhabdomeres (*ventral retina*, Figs. 6a, 12a and 13a). The rhabdomeres are of different length: those of the central retina measure up to 70 µm, while those in the ventral part are shorter (45–55 µm) (Fig. 5).

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