# An Apposition-Like Compound Eye With A Layered Rhabdom in the Small Diving Beetle Agabus japonicus (Coleoptera, Dytiscidae)

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*ABSTRACT* The fine structure of the compound eyes of the adult diving beetle Agabus japonicus is described with light, scanning, and transmission electron microscopy. The eye of A. japonicus is mango-shaped and consists of about 985 ommatidia. Each ommatidium is composed of a corneal facet lens, an eucone type of crystalline cone, a fused layered rhabdom with a basal rhabdomere, seven retinula cells (including six distal cells and one basal cell), two primary pigment cells and an undetermined number of secondary pigment cells that are restricted to the distalmost region of the eye. A clearzone, separating dioptric apparatus from photoreceptive structures, is not developed and the eye thus resembles an apposition eye. The cross-sectional areas of the rhabdoms are relatively large indicative of enhanced lightsensitivity. The distal and central region of the rhabdom is layered with interdigitating microvilli suggesting polarization sensitivity. According to the features mentioned above, we suggest that 1) the eye, seemingly of the apposition type, occurs in a taxon for which the clear-zone (superposition) eye is characteristic; 2) the eye possesses adaptations to function in a dim-light environment; 3) the eye may be sensitive to underwater polarized light or linearly water-reflected polarized light. J. Morphol. 275:1273-1283, 2014. © 2014 Wiley Periodicals, Inc.

KEY WORDS: diving beetle; *Agabus japonicus*; compound eye; layered rhabdom; polarization sensitivity

#### **INTRODUCTION**

Ever since Exner's (1891) comparative study of arthropod photoreceptors, apposition and superposition compound eyes have been distinguished. With a pigment-free clear zone separating the dioptric apparatus from the retinal layers, the superposition eye is generally more sensitive to light than the apposition eye (Land and Fernald, 1992; Warrant and McIntyre, 1993), provided that the eye is not too small (Meyer-Rochow and Gál, 2004). Although exceptions exist (see below), most diurnally active insects possess apposition eyes, while most nocturnal insects and insects occurring in light-poor habitats have superposition eyes (Goldsmith and Bernard, 1974; Horridge, 1975). Some notable exceptions are a) a few day-active insects that possess superposition eyes including moths of the hesperid genera *Cephonodes* and *Macroglossum* (Eguchi, 1982; Warrant et al., 1999), skipper butterflies (Horridge et al., 1972), and a few other diurnal insects (Warrant, 2001) or those that have evolved modifications to superposition (Fischer et al., 2013) and b) a few nocturnal insects equipped with apposition eyes such as the tropical sweat bee *Megalopta genalis* that navigates and forages at night (Greiner et al., 2004).

Up till now, nearly all the eyes of diving beetles of the family Dytiscidae (Coleoptera) studied were shown to possess superposition eyes (Horridge, 1969; Horridge et al., 1970; Meyer-Rochow, 1973; Sbita et al., 2007). Species of the genera *Cybister* and *Dytiscus*, large diving beetles with body lengths of 20 mm or more, dominated these earlier investigations. However, little is known about the eyes of diving beetles belonging to other genera like *Agabus*, which is the largest genus of Dytiscidae (with over 150 known species) and even less is known of the eyes of the smallest diving beetles. Thus, a detailed study of the compound eyes of smaller diving beetles seemed valuable.

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Many aquatic insects (including some diving beetles), capable of flight, detect water surfaces on account of their polarized light reflection (Schwind, 1991; Horváth and Varjú, 2004; Stowasser and Buschbeck, 2012). Some aquatic insects also use polarization sensitivity to detect prey, as has been observed in the larvae of the sunburst diving beetle Thermonectus marmoratus (Stecher et al., 2010). The ability of insects to detect the polarized light depends on (Horváth and Varjú, 2004; Wehner and Labhart, 2006; Roberts et al., 2011) alignment and orientation of the microvilli located in the rhabdoms of each ommatidium into two perpendicularly arranged sets (Waterman, 1981; Rossel, 1989; Eguchi, 1999; Horváth and Varjú, 2004). In diving beetles, the eyes of both Cybister and Dytiscus meet the characteristics in the proximal region of their rhabdoms (Horridge et al., 1970; Meyer-Rochow, 1973) and are thus thought to be sensitive to polarization.

Agabus japonicus Sharp (Coleoptera, Dytiscidae) is a small (body lengths of 10 mm or less), brown, dytiscid predator widely distributed in Japan, Korea, and China (Nilsson and Kholin, 1994). Adults of this species are active during the day, but they occasionally fly in the evening to disperse and find new habitats. Female adults deposit their eggs in the stems of underwater plants. Eggs hatch in late spring or early summer and larvae form a cell in damp soil near the water; adults return to the water after emerging in late August (Larson et al., 2000; Saijo, 2001).

The present article provides morphological and ultrastructural information about the compound eyes of the diving beetle *A. japonicus* and gives a discussion on the possible polarization sensitivity and other potential functions of the eye.

#### MATERIALS AND METHODS

Adult Agabus japonicus Sharp (1873) were collected by hand from shallow ponds in the Beijing Botanical Garden, Beijing, China during the day and kept in a bucket of freshwater under a 16L: 8D photoperiod at 25°C. Three specimens were prepared around 1,200 h in the light-adapted state for observation by transmission electron microscopy.

After removal from the head, the ventral part of the eye was cutoff with dissecting scissors and immediately fixed in 2.5% glutaraldehyde, buffered in 0.1 mol  $l^{-1}$  cacodylate buffer (pH 7.4), for at least 24 h. The specimens were postfixed in 1%  $OsO_4$ , also buffered in 0.1 mol  $l^{-1}$  cacodylate buffer (pH 7.4) for 1 h. The samples were then rinsed three times in the same buffer and dehydrated in a graded series of ethanol. Specimens were passed through different acetone/Epon mixtures (3:1, 1:1, 1:3, pure Epon), embedded in pure Epon (Serva, Heidelberg, Germany), and hardened at a temperature of 60°C for 3 d. Semithin sections for light microscopy (from cornea to basement membrane) were cut on an ultramicrotome (Leica EM UC6+FC6, Wetzlar, Germany) with a glass knife and stained with a 0.5% aqueous solution of toluidine blue. Serial ultrathin sections (~65 nm) were cut on an ultramicrotome (Leica EM UC6+FC6, Wetzlar, Germany) with a 45° diamond knife (Diatome, Bienne, Switzerland) and picked up on uncoated 200mesh copper grids. The ultrathin sections were then stained with 2% aqueous uranyl acetate for 15 min and Reynolds' lead citrate for 5 min and observed under a Spirit transmission electron microscope (FEI Tecnai Spirit, Hillsboro), operated at a voltage of 100 kV.

For observations by scanning electron microscopy, heads of five adult specimens were dehydrated in an alcohol series, critical point dried with liquid carbon dioxide (Leica EM CPD300, Leica Microsystems, Wetzlar, Germany), and sputter-coated with gold (Leica EM SCD050, Leica Microsystems, Wetzlar, Germany). The specimens were finally observed under a FEI Quanta 450 scanning electron microscope (FEI, Hillsboro), operated at 15 kV. Body sizes of *A. japonicus* were measured with a vernier caliper and other measurements in the text were taken and analyzed with the Image-Pro Plus 6.0 software (Media Cybernetics, Silver Spring, USA).

### RESULTS

#### **General Structural Organization**

A. japonicus possesses a prominent mangoshaped compound eye on each side of its head (Fig. 1A). Each eye consists of 985.11  $\pm$  46.83 facets. Those located close to the periphery region of the eye are pentagonal and rectangular (Fig. 1D) and account for 1/4 of the total number of facets. Remaining facets are typically hexagonal (Fig. 1C). Center-to-center distances of adjacent hexagonal facets measure  $24.03 \pm 2.05 \ \mu\text{m}$ , while marginal rectangular facets have dimensions of  $22.39 \pm 1.57 \ \mu\text{m} \times 18.53 \pm 1.71 \ \mu\text{m}$ . Facet surfaces are smooth and devoid of interfacetal hairs or corneal nipples (Fig. 1B).

Ommatidial length near the center of the eye is  $\sim 178 \ \mu m$ , but it decreases to  $\sim 150 \ \mu m$  toward the dorsal margin of the eye (Fig. 2A). Each ommatidium consists of two distinct structures: the dioptric apparatus, made up of a corneal facet lens and a crystalline cone, and the photoreceptive structure, consisting of seven retinula cells and their rhabdomeres (Figs. 2C and 3). A clear-zone, separating the dioptric apparatus from the photoreceptive structure, is not developed and the eye thus resembles an apposition eye.

A large number of darkly stained screening pigment granules exists near the cuticular ridge of the eye. These screening pigment granules measure 0.5–1.6  $\mu$ m in diameter and form a ~3- $\mu$ m thick barrier (Fig. 2I). The barrier, which presumably functions as a light-shield, is next to the cuticular ridge on one side and the ommatidium structures on the other side.

#### **Dioptric Apparatus**

The cornea is a plano-convex lens (Fig. 2C) and the inner radius of curvature is  $9.05 \pm 0.59 \ \mu\text{m}$ . Corneal thickness varied greatly from the thinner dorsal side to the thicker ventral side of the eye. The ventral cornea  $(45.31 \pm 2.21 \ \mu\text{m})$  is at least 1.5 times thicker than the dorsal cornea  $(30.49 \pm 1.13 \ \mu\text{m})$ . In longitudinal sections, the corneae appear cylindrical in shape and adjacent corneae are fused to one another except for the most distal



Fig. 1. *Agabus japonicus*, surface appearance of the compound eye. **A.** Scanning electron micrograph of the head, showing the location of the two compound eyes. Scale bar: 500 μm. **B.** Scanning electron micrograph of the right compound eye, showing its mango shape. Scale bar: 100 μm. **C.** Scanning electron micrograph of the hexagonal facets. Scale bar: 10 μm. **D.** Scanning electron micrograph of the marginal rectangular facets. Scale bar: 10 μm.

and strongly curved ends (Fig. 2A,C). In transverse sections, corneae appear laminated and strongly curved (Fig. 4A,B), an optical artifact known since Bouligand (1965).

Under the corneal lens lies a bullet-shaped crystalline cone (Fig. 2C). It measures  $34.03 \pm 2.10 \ \mu m$ in length and  $11.74 \pm 0.82$  µm in diameter at its distal end. The cone, which is of the eucone type, is made up of four cone cells with each cone cell occupying a quarter of the cone (Figs. 2E, 3, and 4C). Distally, cone cells are in direct physical contact with the cornea with which they form the dioptric apparatus of the ommatidium and proximally they end just above the rhabdom. In longitudinal sections, the cone exhibits a slight threadlike elongation that connects with the most distal tip of the rhabdom (Figs. 2C and 3). In transverse sections, the cone displays a circular outline and exhibits its quadripartite nature of four equal segments (Figs. 2B,E and 4C). The nuclei of the cone

cells, which are spherical and measure  ${\sim}3.8~\mu m$  in diameter, pack themselves in the cytoplasm between the cornea and the cone (Figs. 3 and 4B).

Two primary pigment cells (ppc) surround the four cone cells (Figs. 2C and 4C). The cytoplasm of ppc is filled with screening pigment granules measuring  $1.26 \pm 0.25 \ \mu m$  in diameter. The huge ellipsoidal nuclei of the ppc (Fig. 2F), measuring over 7.0  $\mu m \times 2.5 \ \mu m$  along their major axes, are present near the proximal region of the cone.

A difficult-to-determine number of secondary pigment cells (spc), probably 12 in each ommatidium, envelop the ppcs, and thus occupy the interommatidial spaces between the adjacent ommatidia (Fig. 4B,C). With a diameter of  $0.40 \pm 0.04 \mu$ m, the screening pigment granules of spc are significantly smaller than those of the ppc (Fig. 4C). Instead of passing alongside the length of the retinula cells, the secondary pigment cells are confined to the peripheral region of the cone



Fig. 2. Agabus japonicus, light micrographs of the anatomical organization of the eye. A. Longitudinal section through the central region of the eye in the dorsoventral plane, showing retinula of a few ommatida. Scale bar: 100  $\mu$ m. B. Transverse section through the cornea and cone layers. cc, crystalline cone; co, cornea. Scale bar: 100  $\mu$ m. C. Longitudinal section of three ommatidia. cc, crystalline cone; ce, cone extension; co, cornea; ppcn, nucleus of primary pigment cell; rcn, nucleus of retinula cell; rh, rhabdom; ax, axon; bm, basement membrane. Scale bar: 10  $\mu$ m. D-H. Transverse sections through one ommatidium at different levels: cornea (co), crystalline cone (cc), primary pigment cell (ppc), nucleus of retinula cell (rcn), axon bundle (ax). Scale bar: 5  $\mu$ m. I. Longitudinal section through the contact area between the eye and the surrounding tissue. Arrow shows ~3  $\mu$ m thick barrier made up of a large number of screening pigment granules. Scale bar: 10  $\mu$ m.

and reach from the proximal end of the cornea to the distalmost region of the rhabdom.

#### **Photoreceptive Structure**

The rhabdom is located just beneath the cone. It measures over 90  $\mu$ m in length and occupies 2/3 of

Journal of Morphology

the whole ommatidium (Fig. 2C). Each ommatidium contains seven retinula cells. Six of them pass through the whole length of the ommatidium giving rise to a fused layered rhabdom, while the seventh retinula cell only appears in the proximal region of the ommatidium, forming a basal rhabdomere (Fig. 3). As mentioned above, the



Fig. 3. Agabus japonicus, semischematic drawing representing ommatidial organization in longitudinal view and cross-sections at different levels. At the level of section **a**, crystalline cone (cc) is surrounded by two ppcs which are enveloped by some secondary pigment cells (spc). At the level of sections **b**, the rhabdom formed by the rhabdomeres of retinula cell R2/5 pair shows an elliptical outline and the microvilli are oriented in the same direction. At level **c**, the rhabdom is formed by the rhabdomeres of R1/6 pair and R3/4 pair. Microvilli are oriented perpendicular to the microvilli of level **c**. At level **d**, the basal retinula cell (R7) appears and forms a proximal rhabdomere (prh) with a circular outline. Other six retinula cell extensions surround the basal cell. Level **e** shows seven retinula cell extensions that are filled with darkly stained screening pigment granules. ax, axon; bcn, nucleus of basal cell nucleus; bm, basement membrane; cc, crystalline cone; ce, cone extension; ccn, nucleus of cone cell; ccr, cone cell root; pg, screening pigment granule; ppc, primary pigment cell; ppcn, nucleus of primary pigment cell; prh, proximal rhabdomere; rcn, nucleus of retinula cell; rh, rhabdom; spc, secondary pigment cell; spcn, nucleus of secondary pigment cell. Scale bar: 50  $\mu$ m.

secondary pigment cells are not detectable throughout the rhabdom layer.

The ommatidium exhibits bilateral symmetry in transverse sections (Fig. 5A–D). The long axis of rhabdom cross-sections represents the axis of symmetry. The four cone cell roots, squeezing between the retinula cells, can be distinguished (Fig. 5A–D). Based on the positions of the cone cell roots and the numbering system used by Friedrich et al. (1996, 2011) and Melzer et al. (1997), the basal cell is referred as R7, while the remaining retinula cells are referred as R1/6, R2/5, and R3/4 pairs (Fig. 5A–D).

In the distalmost region of the rhabdom, nuclei (rcn) of R1/6, R2/5, and R3/4 pairs are present (Fig. 2C). These nuclei measure  $\sim$ 4.5 µm in length

and  ${\sim}1.7~\mu{\rm m}$  in diameter. Retinula cells contain numerous electron-opaque pigment granules which are measured  $0.73\pm0.20~\mu{\rm m}$  in diameter. Retinula cells also contain various cytoplasmic organelles such as mitochondria, endoplasmic reticulum, and multivesicular bodies, etc. Mitochondria are 0.47–0.85  $\mu{\rm m}$  in size. The multivesicular bodies are at least 1.5 times larger than the mitochondria.

The distal and central region of the rhabdom is layered (Fig. 3). Microvilli are regularly aligned in a given direction for one layer and in a perpendicular direction for adjacent layers (Fig. 3). Rhabdom is formed by rhabdomeres of the R2/5 pair of retinula cells in one layer (Fig. 5A,B) and is formed by rhabdomeres of the R1/6 and R3/4 pairs



Fig. 4. Agabus japonicus, transmission electron micrographs through the distal region of the eye. **A.** Laminated cornea (co) and nucleus of cone cell (ccn). Scale bar: 5 µm. **B.** Cornea (co), crystalline cone (cc), nucleus of cone cell (ccn), primary pigment cell (ppc), and secondary pigment cell (spc). Scale bar: 5 µm. **C.** Crystalline cone (cc) as well as its surrounding two primary pigment cells (ppc) and secondary pigment cells (spc). Screening pigment granules (pg) of ppc are noticeably bigger than those of spc. Scale bar: 5 µm. **D.** Transverse section of the proximal region of the crystalline cone (cc), primary pigment cell nucleus (ppcn) and its large pigment granules (pg). Scale bar: 2 µm.

of retinula cells in the adjacent layer (Fig. 5C,D). In each layer, the cross section of rhabdom shows an elliptical outline (Fig. 5B,D) with the major axis up to 8  $\mu$ m and the minor axis up to 6  $\mu$ m. The lengths of the microvilli vary greatly from rhabdom to rhabdom, depending on where the microvilli are present, but the diameter of the microvilli changes little and measures 0.10 ± 0.01  $\mu$ m (Fig. 6A).

In the proximal region of the rhabdom, the basal rhabdomere of the seventh (basal) retinula cell

appears in the center shortly above the basement membrane (Fig. 6B). Basal rhabdomere is short (only a few micrometers) and shows a circular cross section (Figs. 3 and 6B). Although microvilli are of the same diameter as those of the distal and central rhabdom, they are less aligned and their orientation is irregular. The nucleus of the basal cell appears closely above the basement membrane and is not in the distal region of the rhabdom as are the nuclei of the other six retinula cells (Fig. 6C). The basal cell contains numerous pigment



Fig. 5. Agabus japonicus, transmission electron micrographs through different levels of the distal and central rhabdom. A, B. Transverse sections through one layer of the rhabdom. In this layer, the rhabdom is contributed by the rhabdomeres of R2/5 pair of the retinula cells. Arrows show the four cone cell roots that appear between the retinula cells. Scale bar: 1  $\mu$ m. C, D. Transverse section through another layer of the rhabdom. At this level, the rhabdom is contributed by the rhabdomeres of the R1/6 and R3/4 pairs of the retinula cells. Arrows show the four cone cell roots that appear between the retinula cells. Scale bar: C = 2  $\mu$ m, D = 1  $\mu$ m.

granules in its cytoplasm (Fig. 6D). All retinula cells of each ommatidium penetrate the basement membrane as axons.

## DISCUSSION Apposition-Like Type Compound Eye in A. japonicus

Previous work on eyes of the dytiscid beetle species reported superposition eyes (Horridge, 1969; Horridge et al., 1970; Meyer-Rochow, 1973; Sbita et al., 2007). The present study, however, shows that the eye in A. *japonicus* is an eucone compound eye with a fused rhabdom that appears to represent the apposition type. This type of compound eye is universal in most diurnal insects, but rarely exists in nocturnal insects or insects living in a dim underwater environment; it is not typical of dytiscid beetles. With special optics (Exner, 1891; Land, 1981), a superposition eye improves photon catch (Nilsson, 1989), but the mechanism requires eyes of a certain size (Meyer-Rochow and Gál, 2004). Compound eyes have to strike a balance between high absolute sensitivity (often

1279



Fig. 6. Transmission electron micrographs through proximal region of the rhabdom. **A.** Extremely aligned microvilli of the distal and central rhabdom. Mitochondria (mt) and pigment granules (pg) appear within the cytoplasm of the retinula cells. Scale bar: 0.5  $\mu$ m. **B.** Transverse section through the basal rhabdomere (brh) which displays a circular outline. Scale bar: 2  $\mu$ m. **C.** More proximally, the basal rhabdom disappears and the nucleus of the basal retinula cell (bcn) characterized by its darkly stained chromatin is found in the center. A lot of pigment granules (pg) can be seen around the bcn. Scale bar: 2  $\mu$ m. **D.** Basal retinula cell extension is centered by other six retinula cells. Scale bar: 2  $\mu$ m.

associated in large compound eyes with superposition) and high resolving power (a feature of apposition compound eyes and possible also in tiny eyes of superposition heritage: cf., Fischer et al., 2010, 2012).

A. japonicus is a beetle with a phylogenetic heritage of a superposition eye. Adults of the species are predaceous and spend most of their lives underwater. Even when they expose their abdomens to the air, their head (including their eyes) remains underwater (Larson et al., 2000). Under these conditions *A. japonicus* definitely need lightsensitive eyes to survive in the dim, lightimpoverished environment of weedy ponds. But the beetle also is an active predator feeding on larvae of other insects, amphibians, and even small fishes. Therefore, it does not seem disadvantageous to modify the light-sensitive superposition eye into what resembles an apposition eye. Its diurnal activity matches this modification and appears to follow evolutionary consequences of size reductions in superposition eyes generally and a shift to more diurnal activities in a species with an intermediate eye type as explained in detail by Fischer et al. (2013).

# Eye Adaptions for Dim-Light Environment in A. japonicus

Light sensitivity of an apposition type of compound eye is determined by the size of the eye, the diameter of the aperture, and the diameter of receptor. According to Kirschfeld (1974), light sensitivity can be calculated by sensitivity =  $(\pi/4)^2 D^2$  $\Delta \rho^2 P_{\rm abs}$ , where *D* represents the facet diameter in insects,  $\Delta \rho$  is the angle of the outside space over which a receptor accepts light (increasing rhabdom size will increase  $\Delta \rho$ ), and  $P_{\rm abs}$  is the proportion of the light entering a receptor that is absorbed. To interpret the equation in details, readers may refer to Land (2004).

The size, shape, and surface properties of the compound eye in *A. japonicus* limit the sensitivity to light, but the mango-shaped eyes, occupying 1/3 of the beetle's head, provide a reasonably large visual field for this insect (Fig. 1A,B).

Facet diameters of the eye of A. japonicus, measuring  $24.03 \pm 2.05 \,\mu\text{m}$ , are rather small when compared with the 30 µm reported for those of Cybister and Dytiscus by Horridge (1969) and Meyer-Rochow (1973). However, what matters most is the rhabdom cross-sectional area. With a cross-sectional area over 40  $\mu$ m<sup>2</sup> in *A. japonicus*, it is even larger than that of the superposition eye of the diving beetle Dytiscus marginalis, for which Horridge et al. (1970) gave a value of nearly 30 µm<sup>2</sup>. Compared with other apposition eye-bearing insects, the rhabdom of A. *japonicus* is 3–4 times wider than that of the honeybee Apis mellifera (Greiner et al., 2004), 5-6 times wider than the butterfly Aglais urticae (Kolb, 1985), and 2–3 times wider than the dragonfly Sympetrum striolatum (Meyer and Labhart, 1993). This represents an adaptation clearly for a dim-light environment and inherited from the superposition eye typical of dytiscid beetles.

Another adaptation seen in small eyes as a consequence of the enlargement of the rhabdoms and avoidance of light losses through unwanted absorption is the absence of secondary pigment cells in the retinal layer (Fischer et al., 2010). Although only the light-adapted stage was investigated in this work, the presence of the short crystalline cone thread in *A. japonicus* further indicates the relationship of this seemingly apposition type of eye to the superposition eye of an ancestor (cf. discussion in Fischer et al., 2012, 2013).

In most compound eyes, eight sensory cells contribute to the formation of the rhabdom (Paulus, 1979). So, why are there only six contributing cells in the main rhabdom layer of *A. japonicus*? The amount of available photons to each one of them may not be high enough to generate a conductible electrical signal, but with only six retinula cells (i.e., 17% of the light entering the rhabdomeres vs. 12.5% in rhabdoms composed of eight cells), the share of photons that each one receives is increased and may well be sufficient to generate a conductible response. The original number of sensory cells per ommatidium may have evolutionarily been reduced in combination with an enlargement of rhabdom diameter, as also demonstrated by Hallberg et al. (1980) for the deep-sea amphipods *Eurythenes gryllus* (40  $\mu$ m) and *Orchomenopsis obtusa* (20–40  $\mu$ m) or by Meyer-Rochow (1981) for the benthic *Orchomene* sp. compare to *O. rossi* (~40–50  $\mu$ m).

# Layered Rhabdom and Polarization Sensitivity

The rhabdom in the compound eyes of *A. japonicus* is layered with interdigitating microvilli. This layered rhabdom, known as crustacean-like rhabdom, is thought to be characteristic of crustacean species (Wolken, 1971). However, it has also been found in the compound eyes of some insect groups, such as Thysanura, Coleoptera, and Lepidoptera (Meyer-Rochow, 1971, 1972; Home, 1976).

Based on detailed calculations, Snyder (1973) found that layered rhabdom possesses high absolute sensitivity, as well as high polarization sensitivity, that provide an adaptive advantage for aquatic animals living in underwater environments. Most crustacean species use this high underwater polarization sensitivity to enhance contrast, maintain their body position, and navigate in migration and orientation (see review by Meyer-Rochow, 2001). As an aquatic insect species, the compound eyes of *A. japonicus* with layered rhabdom may perform the same functions as in crustacean species.

A number of insects living underwater or living on moist substrates use linearly polarized-light reflected from flat water surfaces as a clue to find water bodies, such as the backswimmer Notonecta glauca (Schwind, 1985), mayflies (Kriska et al., 1998, 2007, 2009; Málnás et al., 2011), dragonflies (Wildermuth, 1998; Horváth et al., 1998, 2007; Bernáth et al., 2002), and many other aquatic insects (Schwind, 1991; Csabai et al., 2006; Kriska et al., 2006, 2008). A. japonicus also have to find water bodies; larvae usually form a cell in the soil of the shore and return to water as adults. Adults occasionally fly to a new habitat when the former one becomes uninhabitable or dries up (Larson et al., 2000; Saijo, 2001). Hence, the possibility that A. *japonicus* may use reflected polarized light to detect water bodies should be considered.

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- Journal of Morphology

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