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Visual Organization and Spectral Sensitivity of Larval Eyes in the Moth *Trabala vishnou* Lefebur (Lepidoptera: Lasiocampidae)

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Jin-Tun Lin, Pi-Chi Hwang and Li-Chu Tung (2002) Visual organization and spectral sensitivity of larval eyes in the moth *Trabala vishnou* Lefebur (Lepidoptera: Lasiocampidae). *Zoological Studies* **41**(4): 366-375. The caterpillar of the moth, *Trabala vishnou* Lefebur, has 6 stemmata on each side of its head. The diameter of the lens of each stemma varies. However, the basic structure of a stemma is similar to an ommatidium of a compound eye. Each stemma has a corneal lens, corneagenous cells, a crystalline cone, and retinular cells. The 7 retinular cells in each stemma are organized in 2 tiers, distal and proximal. Stemmata II and V both have 4 distal and 3 proximal retinular cells, while the other stemmata have 3 distal and 4 proximal cells in each stemma. The distal rhabdom is star-shaped radially around the central axis of the stemma, and the proximal one is irregular. The proximal part of each retinular cell narrows forming an axon. The 42 axons from the ipsilateral stemmata join together to form an optic nerve which directly enters into the brain. Axons I-IV project anterodorsally to the optic neuropile of the brain, while axons V and VI project posteroventrally. From the spectral sensitivities of stemmata, it is evident that stemmata I-IV have UV, blue, and green receptors, whereas stemmata V and VI have only blue and green units without UV receptors. http://www.sinica.edu.tw/zool/zoolstud/41.4/366.pdf

Key words: Lepidoptera, *Trabala vishnou* Lefebur, Stemmata, Spectral sensitivity.

Most adult insects and hemimetabolous larvae have compound eyes composed of many ommatidia, each of which usually contains 7-9 retinular cells (Menzel 1975). On the other hand, most holometabolous larvae have special eyes called stemmata (also termed lateral ocelli by many workers) (Toh and Iwasaki 1982, Toh and Sagara 1982, Toh and Tateda 1991). Since caterpillars lack compound eyes, the stemmata are the only light-sensitive organs. The stemmatal system is much simpler than compound eyes, but performs the same role in terms of behavior for larval stages. However, published reports provide a rather limited knowledge of the stemmatal system. Furthermore, there have been only a few studies on the projection of retinular axons to the brain and the spectral sensitivities of caterpillar eyes (Toh and Sagara 1982, Ichikawa and Tateda 1984).

The aims of present study were to determine the structure and spectral sensitivity of the stemmata in the larva of the moth *Trabala vishnou* Lefebur. Projections of the retinular axons to the brain and the retinular organization of the stemmatal system were determined and are discussed herein. It is hoped that the results of this study will provide a foundation for future developments in electrophysiological studies of visual functions.

MATERIALS AND METHODS

Insects

Caterpillars of the moth, *Trabala vishnou* Lefebur, were collected on the campus of National Taiwan Normal University and reared in a laboratory with fresh maple leaves. Caterpillars were maintained at 22±2°C in a 12h light-12h dark photoperiod regime. The final (5th) instar larvae,

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2-3d postecdysis, were used for all experiments.

Light microscopy

For light microscopic observations, the part of head with 6 stemmata was dissected out and fixed in 2% glutaraldehyde buffered in 0.1 M cacodylate at pH 7.4. Following a brief washing in fresh buffer solution, tissues were post-fixed in 1% OsO_4 in the same buffer, dehydrated through graded ethanol solutions and embedded in paraffin (Lin et al. 1992, Tsai et al. 1995). The 10-15-μm-thick paraffin sections were stained with eosin and hematoxylin.

Cobalt injection

To determine the course of the stemmatal tract, retinular axons were injected with cobalt and followed in the brain. After anesthetization at low temperature, caterpillars were immobilized with beewax on a plastic platform. The lens of each stemma was removed. A piece of cotton soaked in 0.2 M cobalt chloride was placed over each stemma for several hours at a temperature below 20°C to permit the spread of cobalt ions throughout the retinular axons. Brains were subsequently isolated and transferred to a petri dish containing fresh saline (NaCl 4, KCl 40, $MgCl_2$ 18, $CaCl_2$ 3, [mM]; glucose 150 g; pH 6.5 with 2.5 mM KH_2PO_4-$KHCO_3$). A few droplets of ammonium sulfide were added to the saline. The cobalt-injected retinular axons became black for a few moments. For whole-mount observation, brains were fixed in Carnoy's solution and dehydrated through graded ethanol, cleared in methyl salicylate, and then embedded in Canada balsam (Chang et al. 1994).

Spectral sensitivity

For the electrophysiological study, a caterpillar was anesthetized at low temperature and immobilized using wax to secure the body to a stand. The head was rigidly fixed by placing staples over the neck. A tiny piece of cuticle on the head near the targeted stemma was cut away with a sharp razor blade making a window to expose the photoreceptors. The hole was immediately sealed with a drop of paraffin oil to prevent moisture loss. Single retinular potentials were recorded by glass pipette microelectrodes (50-100 MΩ) filled with 2.5 M KCl (Lin 1993, Lin and Wu 1996). An indifferent electrode of tungsten wire was placed in the thorax. After successful penetration of a single retinular cell, each stemma was separately illuminated with a white test light of a constant intensity to determine the visual axis. Then the stemma was exposed to a monochromatic test light. The wavelength of light was changed from 300 to 700 nm in 10-nm steps. The spectral sensitivity was determined by the stimulus intensity required to produce a constant criterion response at each wavelength. More-detailed descriptions of the experimental techniques for determining the spectral sensitivities of insect photoreceptors are provided in previous papers (Wu and Hsu 1989, Lin and Wu 1992, Lin 1993).

RESULTS

Anatomy

A larva of the moth, *Trabala vishnou*, has 6 pairs of stemmata on its head, arranged roughly in a semicircle. When the stemmata are observed in a live larva under a dissecting microscope, all appear uniformly light brown.

For convenience, the most-dorsal stemma is referred to as stemma I, and the remainder are numbered II-VI in a clockwise direction on the right side and counterclockwise on the left side from the front. Five of these, numbered I-V, are arranged in a nearly semicircular pattern; the remaining one, numbered VI, sits apart from the semicircle near the base of the short antenna (Fig. 1a). The distance between neighboring stemmata and the diameter of the corneal lens increase as the larva grows. Since the head and body of larvae are continually growing, the absolute size of a stemma is difficult to estimate. Therefore, growth changes were not examined in our study. A 5th instar larva's body is 77 mm long; the diameters of the corneal lens of stemmata III and IV are 160-200 μ, and those of stemmata V and VI are 100-140 μ. The size of the corneal lens in stemmata I and II is between those of stemmata III and VI. Stemmata I-IV are usually close together and separated from stemmata V-VI. Stemma VI is conspicuously separated from the others, and may be difficult to observe because it is very low and relatively small (Fig. 1b).

The dioptric apparatus of an each stemma is composed of a corneal lens and a crystalline cone in series (Fig. 2a). The corneal lens of stemmata I-V is cylindrical, and that of stemma VI is biconvex (Figs. 1a, 2a). The crystalline cone is situated just beneath the lens. Each crystalline cone is formed

by 3 cone cells of equal size (Fig. 2b). An elongated retinula sits beneath the crystalline cone. The rhabdom of a stemma is oriented around the central axis of the retinula and is surrounded by retinular cells (Fig. 2c, d).

Each stemma consists of 7 retinular cells which are arranged into 2 tiers of distal and proximal cells. The diameters of both retinular cells and the rhabdomere in the distal part are much larger than those in the proximal part (Fig. 2e, f). There are 3 distal cells and 4 proximal cells (this type is called a 3-4 pattern stemma) in stemmata I, III, IV, and VI. On the other hand, stemmata II and V consist of 4 distal and 3 proximal retinular cells (this type is called a 4-3 pattern stemma) (Figs. 2-4). The retinular cells are ensheathed by an envelope of 3 corneagenous cells, each of which shares almost 1/3 of the space in the distal part of the stemma (Fig. 2c, d).

Since the arrangement of the retinular 3-4 pattern is nearly identical for stemmata I, III, IV, and VI, for these stemmata, we only describe the structure of stemma III, the largest of the 6 stemmata. The retina of stemma III can be divided into 2 layers: 3 distal cells and 4 proximal cells according to the position of their rhabdomeres within the rhabdom (Figs. 2d, 2e, 3). Three rhabdomeres of the distal cells form the distal part of the rhabdom, whereas the 4 proximal cells form the proximal rhabdom. In longitudinal section, the distal rhabdom appears wedge-shaped, tapering toward the proximal rhabdom, which has a columnar shape. It is approximately 15 to 25 μ wide at its distal end and 1/2 this width at the proximal end. Rhabdomeres of distal cells gradually disappear in the upper part of the proximal rhabdom. The nuclei of all retinular cells are localized under the rhabdomic layer. In cross-section, the distal rhabdoms are arranged in a radial shape along the axis of the stemmata. The 3 distal cells are also arranged radially around the central axis. Although the 4 proximal cells are also located around the axis, the cellular pattern of the rhabdomeric region differs from that of the distal cells. The arrangement of proximal cells is irregular. However, the proximal rhabdom is composed of 4 rhabdomeres in a shape like the letter "C" (Figs. 2e, 3).

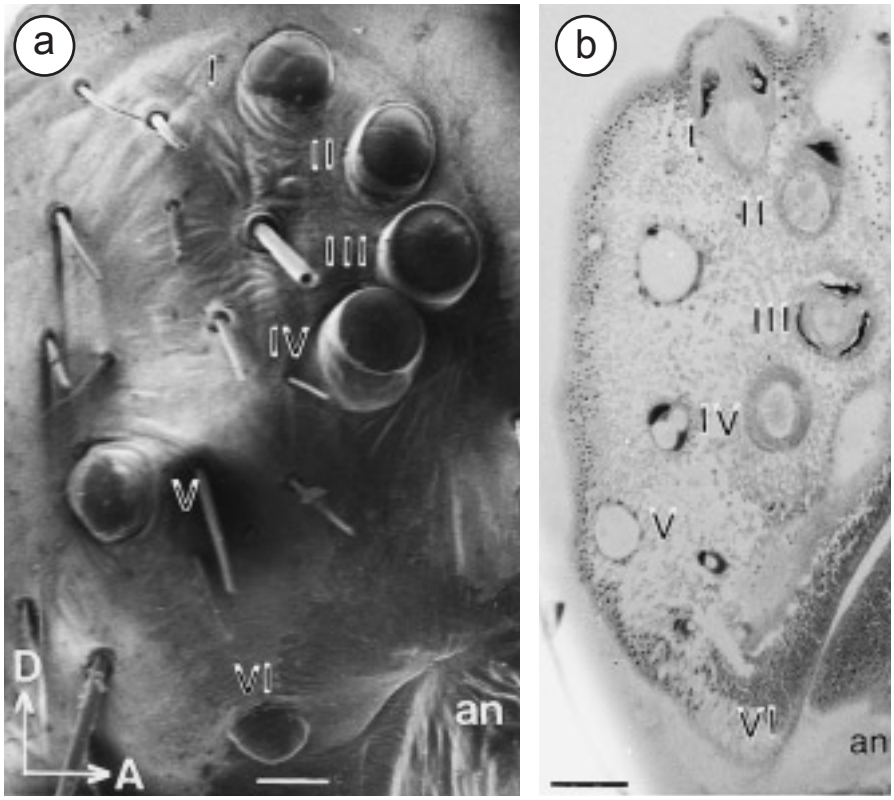

Fig. 1. Scanning electron microscopy (a) and light microscopy (b) of the right lateral aspect of the head of a 5th instar larva showing the arrangement of the 6 stemmata (I-VI). Arrows indicate the dorsal (D) and anterior (A) directions, respectively. an: antenna. Scale bar = 100 μ.

Based on the cellular organization of the retinula, stemmata II and V belong to the 4-3 pattern group in which 4 retinular cells form the distal part and 3 form the proximal part of the retinula. We describe stemma V as follows (Fig. 4). The 4 distal rhabdomeres also surround the central axis.

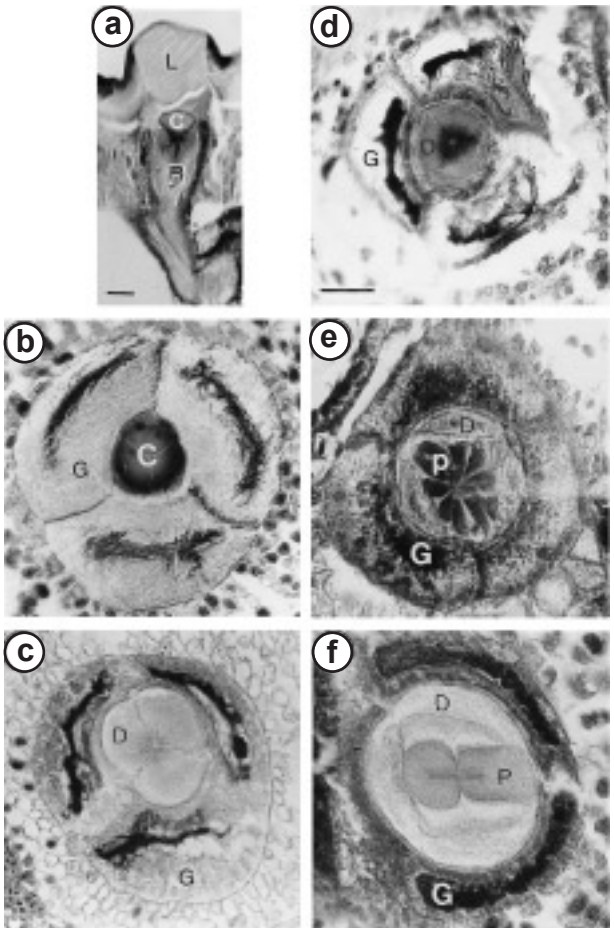

Fig. 2. Light microscopy of the stemmata. (a) A longitudinal section through stemma III. L: corneal lens; C: crystalline cone; R: retinular cells. (b) Cross-section through the mid-portion of the crystalline cone from stemma III. The crystalline cone (C) consists of 3 cone cells surrounded by 3 corneagenous cells (G). (c) Cross-section through the distal part of stemma III. Three distal cells (D) possess radial rhabdoms. (d) Cross-section through the lower level of the distal part of stemma III. A radial rhabdom consists of 3 rhabdomeres of distal cells (D). (e) Cross-section through the transient region between distal cells (D) and proximal cells (P) from stemma III. Four proximal cells, possessing "C"-shaped rhabdoms, are surrounded by 3 distal cells which are enveloped by 3 corneagenous cells. (f) Cross-section through the transient region between distal cells and proximal cells from stemma V. Three proximal cells (P), possessing "I"-shaped rhabdoms, are surrounded by 4 distal cells (D) which are enveloped by 3 corneagenous cells (G). Scale bar = 50 μ.

Beneath the crystalline cone is a rhabdom consisting of the large rhabdomeres of the 4 distal cells. In cross-section the rhabdomeres of the 4 retinular cells fuse centrally to form a star-shaped rhabdom. The basic structures of reticular cells are similar to those of stemma III. Likewise, the rhabdomeres of the 3 proximal retinular cells are fused centrally to form a characteristically "I"-shaped or "X"-shaped rhabdom (Figs. 2f, 4).

The rhabdoms of all stemmata terminate some 60 μm above the basement membrane. Each retinular cell extends proximally as a slender axon through the basement membrane. The 7 axons from each stemma come together to form a short bundle of nerves. These nerves are all wrapped in glial cells which are continuous with the enveloping cells of the stemmata. All 6 of these from the ipsilateral stemmata join together to form an optic nerve (stemmatal tract) which is about 2 mm long before it enters the brain (Fig. 5).

Visual organization

In order to visualize the pattern of the stemmatal projection, the course of the stemmatal tract was followed in whole-mount preparations of cobalt-injected specimens. In specimens in which cobalt was injected into 1 stemma, only a single bundle was densely stained (Fig. 5a), whereas in specimens in which cobalt was injected into all 6 stemmata, six bundles were apparent in the stemmatal tract (Fig. 5b). The stemmatal tract ascends dorsally along the surface of the brain. After traveling dorsally for about 300 μ along the surface of the brain, the stemmatal tract turns toward the interior of the brain. The bundles swell about 100 μ below the surface of the brain. The swelling may represent neuropiles. However, a few thin fibers do extend more deeply beyond the swellings (Fig. 5c).

The caterpillar of *Trabala vishnou* like most lepidopterans has 6 stemmata on each side of its head. Each stemma contains 7 retinular cells. The proximal part of each stemma narrows to a bundle containing 7 axons, and the bundle from each of the 6 stemmata join together to form a single optic nerve, 0.1 mm in diameter and 2 mm in length, which projects directly into the brain. Therefore, each optic nerve is composed of 42 axons of all retinular cells (Fig. 5d). Cobalt filling of single stemma confirmed that each group of 7 retinular axons is isolated from the others. Stemmata I-IV project to the anterior optic neuropile (in the lamina of the brain), while stemmata

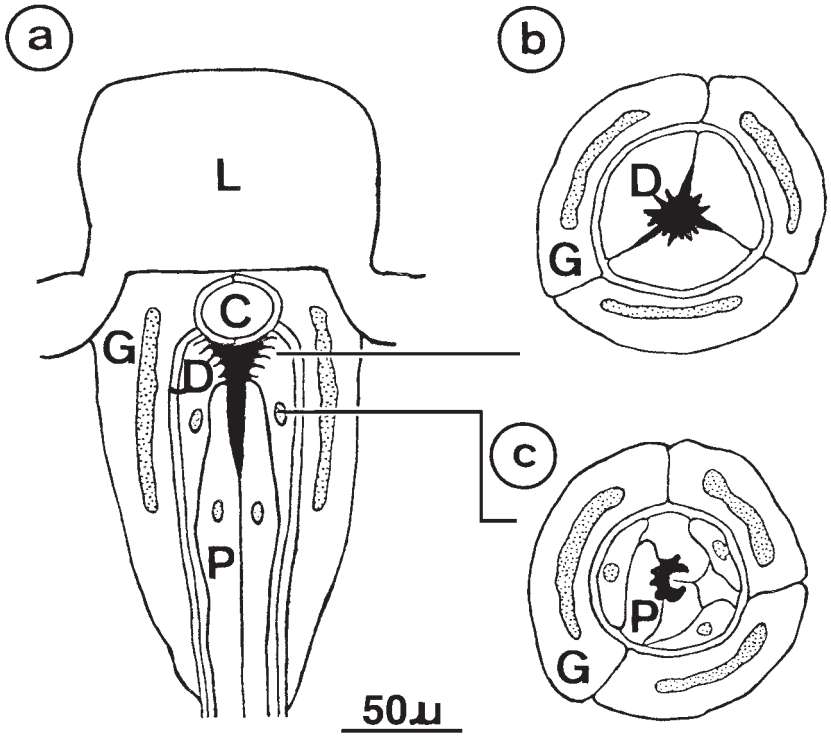

Fig. 3. Diagrams of stemma III. Longitudinal sections (a) and cross-sections through the distal (b) and proximal retinular layers (c). Stemma III has 3 distal and 4 proximal retinular cells. L: corneal lens; C: crystalline lens; G: corneagenous cells; D: distal retinular cells; P: proximal retinular cells. Black areas indicate rhabdoms.

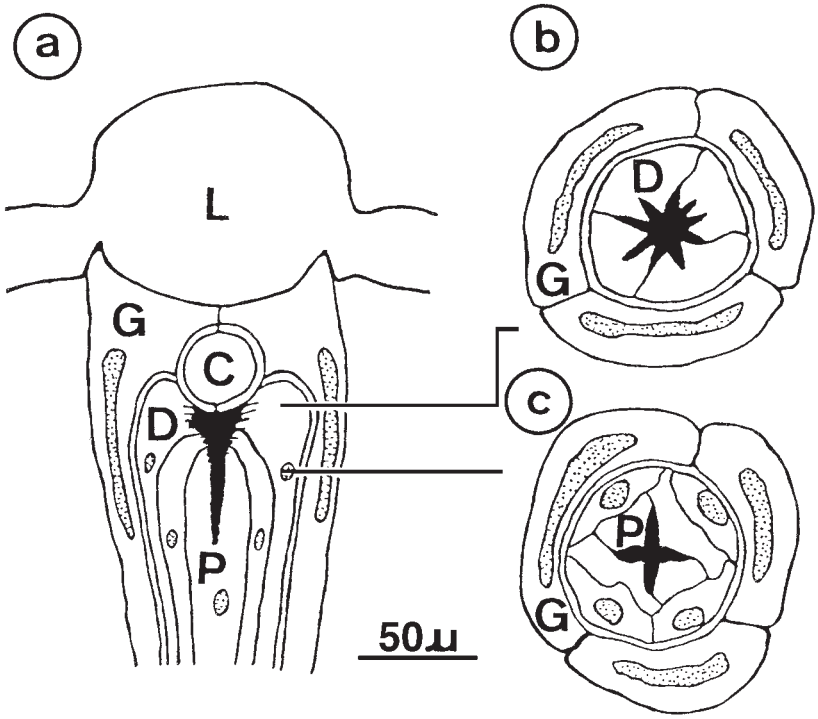

Fig. 4. Diagrams of stemma V. Longitudinal section (a) and cross-sections through the distal (b) and proximal retinular layers (c). Stemma V has 4 distal (D) and 3 proximal (P) retinular cells. L: corneal lens; C: crystalline lens; G: corneagenous cells; D: distal retinular cells; P: proximal retinular cells. Black areas indicate rhabdoms.

V-VI project to the posterior one (Fig. 6). It is obvious from these results that the optic nerve of the 6 stemmata, in contrast to the situation in the dorsal ocelli, does directly enter the brain (Chang et al. 1994).

Spectral sensitivity

The spectral sensitivity of retinular cells in the stemmata was investigated by recording the intracellular potentials of a single receptor. After a microelectrode was introduced into the retinula cell, the resting membrane potentials detected were between -30 and -50 mV, to occasionally -60 mV. The maximal depolarization response of a retinula cell was obtained under illumination with "white light" (containing all wavelengths). With flashes of very low intensity (3.5 log units below the maximum intensity of the stimulus light) small bumps of up to 2 mV above noise level were observed topping the depolarization. These miniature potentials are interpreted as quantum bumps like those reported by Ichikawa and Tateda (1980) for caterpillars of the swallowtail butterfly *Papilio xuthus*. Increasing the light intensity of the stimulus makes the quantum bumps disappear, but gives rise to an initial peak, and after the stimulus is turned off, an delayed return of the response to the level of the resting potential occurs.

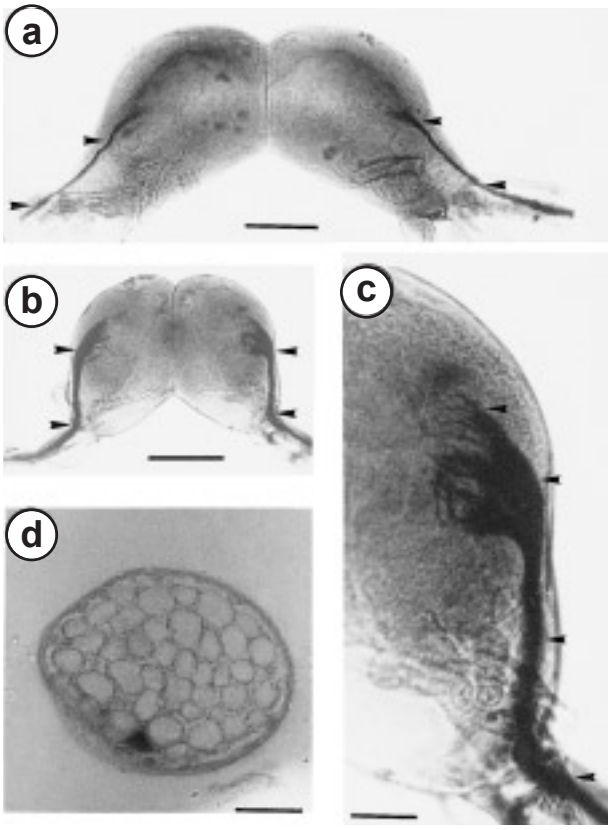

Fig. 5. Whole-mount preparation of the brain with cobalt chloride injected through retinular axons (arrowheads), through 1 stemma (a) and through 6 stemmata (b) in both sides. (c) High magnification of the right hemisphere of the brain with 6 bundles (2 out of focus) of cobalt chloride-injected retinular axons (arrowheads). (d) Cross-section of the optic nerve (stemmatal tract). Forty-two axons of 6 stemmata are enveloped by the sheath. Scale bar = 50 μ.

The intracellular responses recorded from 5th larval instars are typical retinular cell receptor potentials with an initial peak when the stimulus is switched on and a sustained depolarization plateau during continued illumination (Fig. 7). All measurements were made on the initial peak, which did not overshoot the 0 membrane potential and which had a rise time of about 3 ms.

The inset in figure 7 shows a typical potential response of an insect photoreceptor. It can be divided into 3 phases: rapid depolarization, plateau, and repolarization. The peak height of the rapid depolarization phase varies, depending on the intensity of the flash. It also depends on whether the flash was focused on the targeted receptor or not. Results show that when the light stimuli was exactly aligned with the tested receptor's visual axis, the maximal amplitude of the receptor potential (V_{max}) was between 25 and 30 mV. Therefore, in subsequent experiments, only cells with a V_{max} greater than the 25 mV were accepted for data collection.

The spectral sensitivity of a single retinular cell was defined as the relative number of quanta needed to elicit a constant response. Initially, the responses of retinular cells (V) to various light intensities expressed in log units (log I) were plotted. The responses of tested receptors to various light wavelengths (at the same intensity) were normalized to the maximal response and plotted as a spectral sensitivity curve. An example of the intracellular recording for the amplitude of the same intensity to different wavelengths across the spectrum is presented in figure 7. In this study, we show that stemmata I-IV have 3 types of receptors: UV (λ_{max} about 360 nm), blue (λ_{max} about 440 nm), and green (λ_{max} about 530 nm) receptors (Fig. 8a). On the other hand, stemmata V and VI have only 2 types of receptors: blue (λ_{max} at 430 nm) and green (λ_{max} at 540 nm) units, but lacking a UV receptor (Fig. 8b). All spectral sensitivity curves agree well with those predicted by

Dartnall's nomogram (Darthnall 1953) for visual pigments with their λ_{max} values.

DISCUSSION

Stemmata can be classified into 2 types depending on the cellular organization in a stemma. One is the lens eye type which is similar to the dorsal ocellus, consisting of numerous retinular cells under a large corneal lens (e.g., neuropterans and most coleopterans). The other is the ommatidium type which is similar to an ommatidium of the compound eye, comprising several retinular cells beneath a small corneal lens (Toh and Sagara 1982, Toh and Tateda 1991). The stemmata of *Trabala vishnou* are structurally identical to the ommatidium of the compound eye. The dioptric apparatus consists of a corneal lens and an underlying crystalline cone formed by 3 cone cells. Seven elongated retinular cells occur around a central axis. However, an obvious difference from the ommatidium is the absence of a neuropile within the stemma. The retinular axons of *T. vishnou* do not end in the stemma, but continue as the stemmatal tract into the brain, where they form a synapse with 2nd-order neurons to form the optic neuropile. This also contrasts with the dorsal ocellus (Chang et al. 1994) in which a neuropile occurs within the posterior region of the ocellus (Mizunami 1994 1995).

The visual organization of lepidopteran stemmata has been investigated in *Isia isabella* (Dethier 1942 1943), *Pieris barassicae* (Barrer 1969), and *Papilio xuthus* (Ichikawa and Tateda 1980). Dethier (1942 1943) pointed out that in *Pieris* every stemma has 7 retinular cells: 3 distal and 4 proximal cells. However, differences in the organization of photoreceptors among the stemmata have not been reported. In the present study, we found that in the 6 stemmata of *T. vishnou* there are 4 stemmata with the 3-4 type pattern and 2 stemmata with the 4-3 type pattern. These results coincide with observations of the cellular pattern of the lateral ocelli in the swallowtail butterfly, *Papilio xuthus* (Ichikawa and Tateda 1980), but

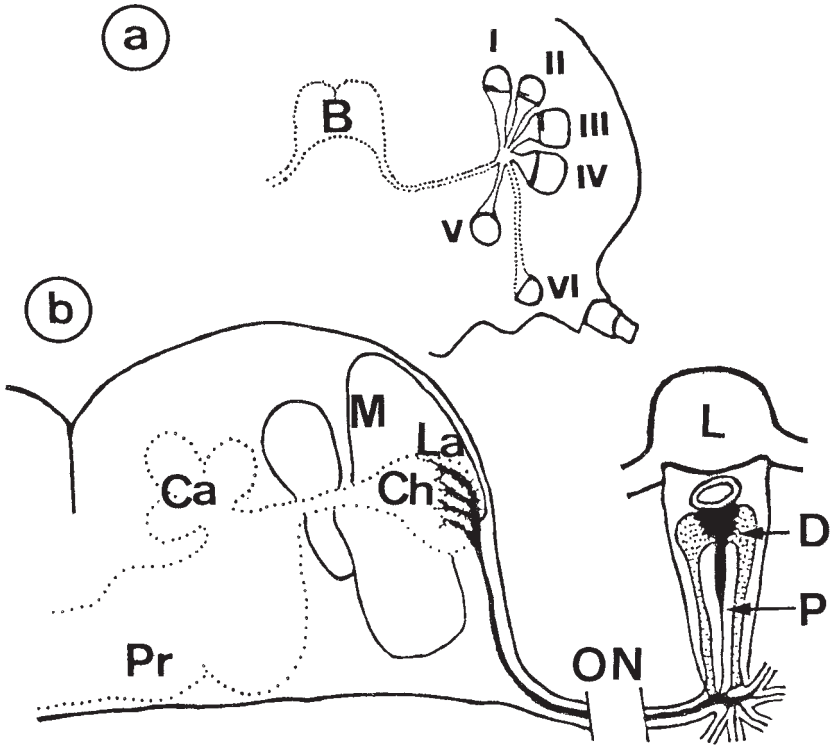

Fig. 6. Semischematic diagrams of the visual organization of a larva of *Trabala vishnou*. (a) Right lateral aspect of the brain and a larval eye to illustrate the arrangement of the 6 stemmata (I-VI), stemmatal tracts and brain (B). Stemmata are connected to the brain (B) by an optic nerve (ON). (b) Simple structure of a stemma. Each stemma has a retinula under a corneal lens (L). The retinula consists of 7 retinular cells arranged into 2 tiers, distal (D) and proximal (P). The optic nerve (ON) from the 6 stemmata project to the lamina (La) forming an optic neuropile. Ch: chiasma; M: medulla; Ca: calyx; Pr: protocerebrum.

differ from those in the noctuid moth *Mamestra brassicae* (Ichikawa and Tateda 1982).

Photoreceptors in insect compound eyes are generally classified into 3 receptor types: UV, blue, and green (Menzel 1975). Our results indicate that the spectral receptor types in *T. vishnou* stemmata approximately fit these 3 types. Four of the 6 stemmata in *T. vishnou* have 3 types of color photoreceptors, whereas 2 stemmata have only blue and green receptors without the UV type. Stemmata I-IV with trichromatic color vision are close together and arranged in a semicircle near the dorsal part of the head. On the contrary, stemmata V and VI are separated from the semicircle near the ventral side of head and are equipped with dichromatic color vision without UV receptors. It is reasonable to consider that these 2 types of stemmata may have functional differences in vision because it is more likely to receive UV light from the dorsal side than the ventral side of the head. Electrophysiological and behavioral studies indicated that most insects, such as ants, use UV receptors to detect polarized light. In addition, lepidopteran larvae can use polarized light of the sky to maintain their orientation (Wellington et al. 1951). Our results indicate that all stemmata containing UV receptors found in *T. vishnou* are localized on the dorsal side of the head.

The ability for wavelength discrimination by lepidopteran larvae has been suggested by inborn

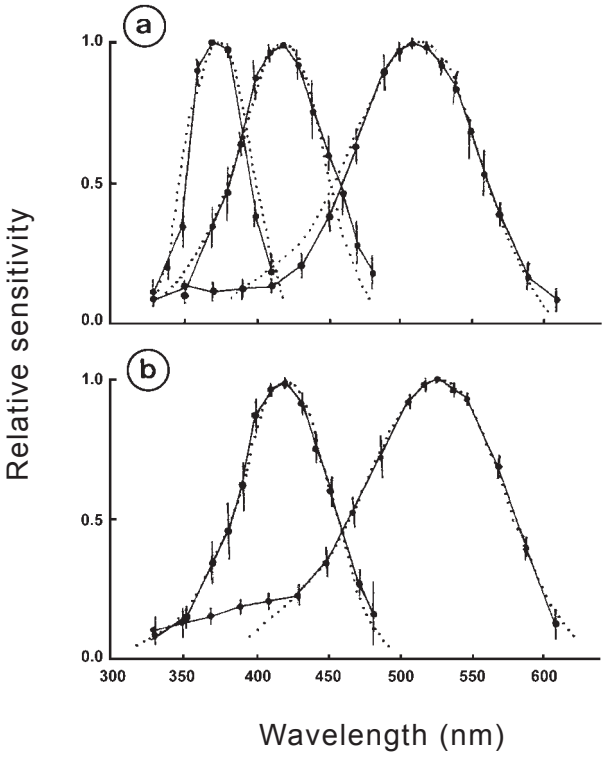

Fig. 8. Spectral sensitivity curves of photoreceptors obtained from dark-adapted stemmata III (a) with 3 types of receptors and V (b) with only 2 types of receptors. Dashed curves are Dartnall's nomogram (Dartnall 1953) reference of ideal visual pigments. Vertical bars are standard deviations.

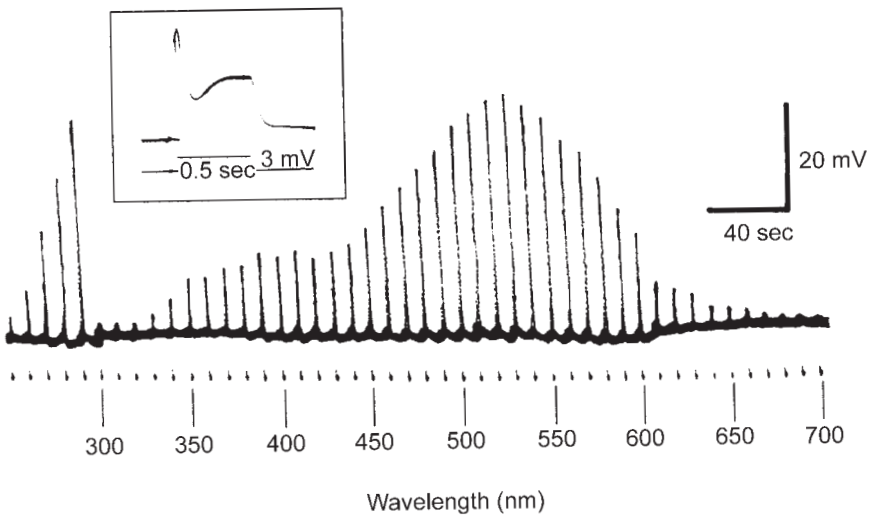

Fig. 7. Intracellular recording of spectral responses of a green receptor found in larval eyes. Ordinate: electrical responses (mV) of photoreceptor to flashes at different wavelengths of the same intensity. Abscissa: calibration and wavelengths of the flashes. For the first 5 responses from left to right, the light intensity is given in log units of increasing order: -3.5, -2.5, -1.5, -1.0, and 0. The response was recorded with slow spectral scanning from 300 to 700 nm, then from 700 to 300 nm (not shown), in 10-nm intervals. Inset: high-speed recording of a typical response of a retinular cell to a flash of maximal light intensity at 530 nm.

behavioral reactions to colored objects or to chromatic light (Kitabatake et al. 1983). The close similarity in basic structures of the visual systems between larvae with stemmata and adults with compound eyes (Wu et al. 1985, Yang et al. 1998) makes the larval visual system a simple model of insect color vision. Therefore, investigations of the larval system may reveal basic or general aspects of neural integration mechanisms of visual signals in insects.

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青枯葉蛾幼蟲視神經系統之結構與光譜感度

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青枯葉蛾 (*Trabala vishnou* Lefebur) 的幼蟲在頭部兩側各有六個單眼，每個單眼的大小不同，而基本結構類似小眼，具角膜晶體、角膜生成細胞、圓錐晶體和視細胞等構造。每個單眼均由七個視細胞組成，依其位置歸為遠端和近端兩類，然而排列方式分為兩型：單眼II和V具四個遠端視細胞配三個近端視細胞；其他單眼具三個遠端視細胞配四個近端視細胞。遠端視細胞的桿狀體位於中央，輻射狀排列成星形；近端視細胞桿狀體的排列不規則。各視細胞的基部形成軸突伸出，同側單眼的42條軸突聚成一束單眼視神經，直接投射到腦部視神經叢的特定位置，單眼I-IV投射於前背側，V和VI則較近後腹側。由光譜感度得知單眼I-IV含紫外光、藍光和綠光受器，而V和VI只有藍光和綠光兩種受器，沒有紫外光受器。

關鍵詞：鱗翅目，青枯葉蛾，側單眼，光譜感度。

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