

Fine structure and optical features of the compound eyes of adult female *Ceratosolen gravelyi* (Hymenoptera: Agaonidae)

Hua Xie ¹, Yan Shi ², Shouxian Zhang ¹, Yonghui Zhu ¹, Subo Shao ¹, Yuan Zhang ¹, Pei Yang ^{3,*}, Zongbo Li ¹ **and** *

- ¹ Key Laboratory of Forest Disaster Warning and Control in Yunnan Province, Southwest Forestry University, Kunming 650224, China; hxie21527@outlook.com (H.X.); zsxdy@outlook.com (S.Z.); zyhsun11@outlook.com (Y.Z.); shaosub01122@outlook.com (S.S.); yuanyzhang@swfu.edu.cn (Y.Z.); lizb@swfu.edu.cn (Z.L.)
- ² Institute of Management Cadres, State Forestry and grassland Administration, Beijing, 102600, China; mdf-shiyan@sohu.com (Y.S.)
- ³ College of Traditional Chinese Medicine, Yunnan University of Chinese Medicine, Kunming 650500, China; 521yangpei@163.com (P.Y.)
- * Correspondence: 521yangpei@163.com (P.Y.); lizb@swfu.edu.cn (Z.L.)

Simple Summary: Fig wasps and fig trees depend on each other to survive, and wasps locate their host trees with their sense of smells. However, the role that vision plays in locating host trees remains unclear. Here, we examined the eye structure of female *Ceratosolen gravelyi* wasps (which only pollinate *Ficus semicordata*) using light/scanning/transmission electron microscopy. Their oval-shaped eyes have 228–263 tiny eye units (ommatidia). Each unit has a clear lens, a four-part light-focusing structure, and light-sensing cells wrapped in pigment cells. The neurons (retinula cells) form a light-catching rod (rhabdom) with nine cells per unit. Eight photoreceptors (R1–R8) form the rhabdom from the cone base to the ommatidial core, and a ninth cell peripherally replaces R8 in the apical third of the rhabdom. Various optical measurements revealed that their eyes collect light efficiently. These features are consistent with their daytime activity, suggesting that their eyes process visual cues when approaching figs. This indicates that vision likely works with smell and touch to guide wasps to the right trees. Our findings thus enhance our understanding of how senses work together to mediate fig-wasp interactions.

Abstract: Pollinating fig wasps (Agaonidae) engage in an obligate mutualism with *Ficus* species, which is mediated by host-specific chemical cues. However, the role of visual perception in host recognition remains poorly understood, particularly because of a lack of structural studies of their compound eyes. We investigated the ocular morphology of female *Ceratosolen gravelyi*, the exclusive pollinator of *Ficus semicordata*, using light/scanning/transmission electron microscopy. The oval apposition-type eyes contain 228–263 ommatidia per eye, which are asymmetrically distributed between the left and right eyes. Each ommatidium comprises a biconvex corneal lens overlying a tetrapartite eucone crystalline cone with interlaced proximal cone cells. Pigment cells encapsulate each ommatidium, and a few pigment granules are present in pigment and retinula cells. Nine retinula cells comprise a unit, with eight photoreceptors (R1–R8) forming the rhabdom from the cone base to the ommatidial core; a ninth cell peripherally replaces R8 in the apical third of the rhabdom. Optical metrics, including F-number (1.1°), acceptance angle (10.0°), and ommatidial sensitivity (0.26 $\mu\text{m}^2/\text{sr}$), indicate diurnal activity in bright environments. These adaptations suggest that their eyes are critical for processing visual cues during host interactions, which improves our understanding of multimodal sensory integration in fig–wasp mutualisms.

Academic Editor: Firstname Last-name

Received: date

Revised: date

Accepted: date

Published: date

Citation: To be added by editorial staff during production.

Copyright: © 2025 by the authors. Submitted for possible open access publication under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

Keywords: Agaonidae; vision; ultrastructure; TEM; apposition eye; fused rhabdom

1. Introduction

Insect compound eyes, which comprise numerous repeating units called ommatidia, exhibit marked structural and functional diversity across species [1–3]. The number of ommatidia varies drastically among species, from 29,247 in Odonata [4] and 16,000 in carpenter bees [5] to 800 in *Drosophila* [6] and a few dozen in miniature feather-winged beetles [7] and parasitoid wasps [8,9]. In extreme cases, such as parasitic lice (Phthiraptera), fleas (Siphonaptera), female scale insects (Hemiptera), and permanently subterranean species (e.g., termites, cave crickets and beetles), eyes are severely reduced or absent [1,10]. Variation is also observed within species (e.g., among *Apis* spp.) and even across different eye regions in a single individual [11]; for example, the eyes of *Megaphragma viggianii* feature three distinct zones: dorsal rim ommatidia (specialized for polarized light detection), transitional ommatidia, and regular ommatidia [9]. Each ommatidium comprises a corneal lens, crystalline cone, light-sensitive rhabdom, and pigment cells, which work together to focus light, convert it into neural signals, and prevent optical crosstalk. Ommatidial elements further vary between species: facet diameters range from 180 μm (*Titanus giganteus*) [12] to 5.8 μm (*Trichogramma evanescens*) [13], rhabdomere lengths range from 400 μm (*Apis* drones) [14] to 24.29 μm (*T. evanescens*) [13], and pigment granule shapes range from spherical (normal) to ellipsoidal (miniature) [8,9,15]. This variation regulates light intake of the ommatidia, which directly affects both the spatial resolution and light sensitivity of the compound eye's mosaic vision [16,17]. Compound eyes can be classified into three major types according to their design, apposition, optical superposition, and neural superposition eyes [1], which are each adapted to specific ecological needs; these different types of compound eyes provide insects with a broad visual field and acute motion detection and allow them to perform their activities under diverse light conditions [16,18].

In Hymenoptera, the apposition eye, characterized by the absence of a clear zone between the facet lens and retina, operates as an independent optical unit, detecting only light that enters through its lens. This structure is typical of diurnal species, including most wasps, bees, and ants [3,6,14,18–21]. However, some nocturnal Hymenoptera, such as the sweat bee *Megalopta genalis* (Halictidae) [22] and formicine ants *Myrmecia* spp. (Formicidae) [20], have retained this eye type despite their nocturnal activity. This contrasts with nocturnal moths, which have evolved superposition or neural superposition eyes for enhanced photon capture and improved sensitivity in low-light conditions [23–25]. Across Hymenoptera, compound eyes also show marked structural modifications: diurnal species feature tightly packed ommatidia for sharp vision [5,26], whereas ommatidial spacing is increased in crepuscular forms such as *Xylocopa carpenter* to promote light-gathering [21,27]. Specialized adaptations are observed in parasitic wasps (*Trichogramma* spp.), which have reduced interommatidial angles to increase the width of the visual fields to help them locate host eggs [8,13,15], and facultatively nocturnal wasps *Vespa* spp., which have larger facet lenses and widened rhabdoms with a longer focal length to facilitate flight in dim light [28,29]. These diverse modifications reflect flexible evolutionary adaptations to each species' unique lifestyle, behavioral ecology, and the constraints of their specific optical environments [3,30].

Pollinating fig wasps (Agaonidae), which are minute parasitic Hymenopterans, engage in obligate mutualisms with *Ficus* species (Moraceae), and each host fig relies on one, or rather often, several congeneric agaonid wasp species for pollination [31–33]. This symbiosis centers on the syconia (figs), an urn-shaped enclosed inflorescence progressing through five developmental stages: (A) pre-female, (B) receptive, (C) interfloral, (D) male,

and (E) postfloral. The ostiole, a bract-sealed entry portal at the syconium apex, opens exclusively during stage B to admit mated female wasps carrying pollen. These wasps simultaneously pollinate female flowers and oviposit in select ovaries of the female flowers, where their larvae develop obligately. After some weeks, their offspring become adults. Winged females possess fully developed antennae and compound eyes and are capable of dispersing to new host figs, while flightless males retain vestigial sensory organs and are confined to natal syconia over their lifetime [34,35]. Pollinating wasps were mainly thought to be attracted specifically by species-specific volatile cues from stage B figs [35–39]. However, our empirical observations have reveal novel phototactic behavior, including positive phototaxis towards ambient light sources (e.g., window-proximal regions), chromatic discrimination capacity among colored traps (yellow > green > white), and stage-specific visual preference for daytime oviposition (Stage B > A/C/D syconia). More importantly, genomic analysis of two *Ceratosolen* species (*C. solmsi* and *C. marchali*) [40,41] has shown that their trichromatic vision is mediated by three photoreceptors peaking at 340 nm (UV), 430 nm (blue), and 535 nm (green), which is consistent with ancestral hymenopteran spectral sensitivity patterns [42]. These findings indicate that the validity of chemo-centric models of fig–wasp communication should be re-evaluated and that the role of vision in the fig–wasp mutualism might be underappreciated, especially for short-range discrimination in heterogeneous microhabitats [43]. Studies of the structural specialization of compound eyes, including ommatidial densities, optimized interommatidial angles, and rhabdom dimensions, are needed to clarify multimodal signaling integration (e.g., chemical, visual, tactile) in this conserved mutualism.

Here, we employed light microscopy (LM), scanning electron microscopy (SEM), and transmission electron microscopy (TEM) to characterize the ocular morphology and ultrastructural adaptations of adult females *Ceratosolen gravelyi*, the obligate pollinator of the functionally dioecious *Ficus semicordata*. Furthermore, we quantitatively analyzed key optical features and performed comparative optometric measurements of three-minute parasitoids, *Trichogramma evanescens* [13,44], *Anaphes flavipes* [15], and *Megaphragma viggianii* [2,8,9,15]. We also discussed the general functions of small compound eyes and their evolutionary trade-offs between visual acuity and body size.

2. Materials and Methods

2.1. Wasp community in *Ficus semicordata* and sample preparations

Ficus semicordata, a functionally dioecious species, maintains an obligatory mutualism with its exclusive pollinator *Ceratosolen gravelyi*, which serves as a host of four non-pollinating wasps from Sycophaginae (*Sycophaga cunia*) and Pteromalidae (*Philotrypesis dunia*, *Apocrypta* sp., and *Sycoscapter trifennensis*). The reproductive cycle is initiated when *C. gravelyi* locates receptive trees and enters male figs for offspring development and female figs for pollination. Following this pioneer species, *P. dunia*, *S. cunia*, *Apocrypta* sp., and *S. trifennensis*, which are usually sympatric, sequentially oviposit into figs at progressive developmental stages over ca. 30 days (Figure 1). All offspring reach sexual maturity simultaneously by developmental stage D, and their oviposition schedules are staggered. Adult females of all five species exhibit fully developed wings, eyes and coordinated emergence, but males have reduced eyes, atrophied antennae, and an apterous morphology and usually perish within the fig cavity.

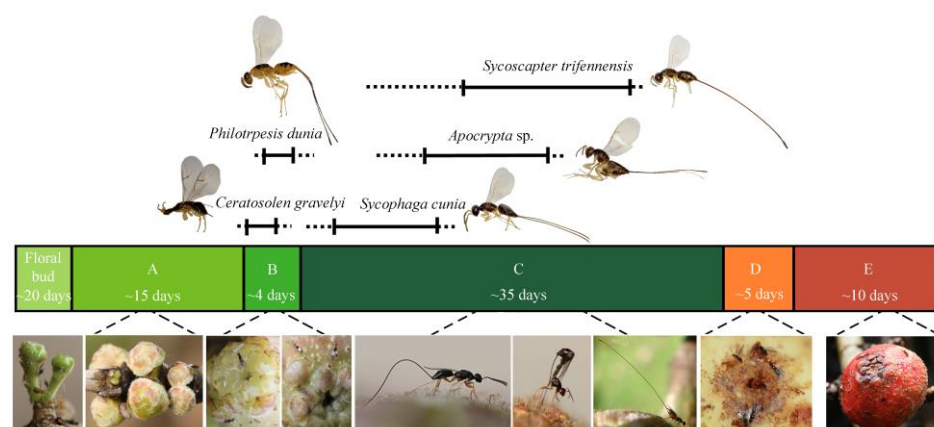


Figure 1. Oviposition patterns of five parasitoid wasp species across five developmental stages (A–E) of *Ficus semicordata* figs. Solid lines represent oviposition timing for the top 50% of individuals in each species, while dotted lines indicate the oviposition activity of the remaining individuals. Top inset panels display morphological differences among the five wasp species, and bottom inset panels illustrate both fig morphological development across stages and species-specific oviposition behaviors corresponding to different fig stages.

We collected newly matured stage D figs of *Ficus semicordata* (male wasps emerge from galls while females remain within the galls) from Xishuangbanna Tropical Botanical Garden, Yunnan, China (21°41'N, 101°25'E). Figs were enclosed in nylon mesh bags to permit natural wasp emergence. Newly emerged individuals were anesthetized at -20°C for 20 minutes. For ultrastructural observations, samples were divided into two groups: 1) intact wasps fixed in 2% glutaraldehyde for SEM, and 2) decapitated specimens immersed in a mixed fixative solution (2.5% glutaraldehyde, 4% paraformaldehyde, 0.1 mol/L phosphate-buffered saline) for TEM. All samples were maintained at 4°C for 3 days.

2.2. Scanning electron microscopy (SEM)

Following ultrasonic cleaning, 20 selected female specimens underwent sequential dehydration using a graded ethanol series (50%, 75%, 80%, and 95% for 10 min each and absolute alcohol for 20 min twice). The specimens were then subjected to critical point drying using a Quorum K850 dryer (Ashford, Kent, UK). The dried samples were mounted on SEM stubs according to their right and left eye orientations and sputter-coated with a gold film for 30 seconds using a Cressington 108 coater (Chalk Hill, Watford, UK) to enhance electrical conductivity. Final imaging was performed using a Zeiss Sigma300 field emission scanning electron microscope (Jena, Germany) operating at an acceleration voltage of 20 kV.

2.3. Transmission electron microscopy (TEM)

Following fixation, the heads were rinsed three times in phosphate-buffered saline (PBS; 0.1 M, pH 7.2) for 7 min per wash and postfixed with 1% osmium tetroxide (OsO₄) in PBS at 4°C for 2 hours. Subsequently, the samples were washed three times with double-distilled water (ddH₂O) (7 minutes for each wash), followed by dehydration with a graded ethanol series (as previously described) and 5 min in acetone. The specimens were then embedded in Epon 812 resin and polymerized at 60°C for 48 hours. After post-polymerization, uniform serial sections were prepared using a Leica EM UC7 ultramicrotome, including semithin sections (800 nm thickness) and ultrathin sections (60 nm thickness). Ultrathin sections were mounted on copper grids, dual-stained with 2% uranyl acetate and lead citrate, and examined using a JEM-1400 Plus transmission electron microscope (JEOL Ltd., Tokyo, Japan) operating at 80 kV.

2.4. Facet number, size and distribution

Following Ribi, et al. [45], facet counts and dimensions of female *C. gravelyi* eyes were estimated by applying a thin layer of colorless nail polish to the head region. After natural drying, the corneal replicas were carefully detached and flattened on microscope slides using micro-scalpel incisions. The replicas were secured under coverslips and imaged with a Zeiss SteREO Discovery V20 light microscope (Göttingen, Germany) at a standardized magnification. Facet numbers and diameters were measured for five individuals, with one representative replica selected for detailed spatial mapping of the facet distribution and surface area using a custom R script (Version 4.4.1, <https://cran.r-project.org/>).

2.5. Optometric measurements and analyses

All morphological analyses were performed using Image J software Version 1.53 (National Institutes of Health, Bethesda, MD, USA). SEM micrographs were utilized to quantify dorsal-ventral (height) and antero-posterior (width) ocular dimensions as well as the diameters of facets and ocelli. Total ommatidial counts per eye (right vs. left) were determined from corneal replicas. For TEM analyses, longitudinal sections provided measurements of ommatidial length, corneal thickness, cone length, rhabdom length, and corneal facet dimensions; transverse sections enabled quantification of rhabdom diameter (distal and proximal regions), microvilli diameter, and morphological characteristics (shape and size) of pigment granules in primary pigment cells (PPCs), secondary pigment cells (SPCs), and retinula cells [13,15]. The radius of eye curvature was calculated at the maximum eye width using a circular measurement tool over the eye surface in the image analysis software. Rhabdom diameter measurements were conducted at both distal and proximal rhabdom extremities [13]. SEM micrographs of blade-sectioned specimens further contributed to assessments of PPC and SPC morphology and dimensions. At least five female *C. gravelyi* eyes per treatment were examined in all SEM and TEM analyses.

To evaluate the optical characteristics of female *C. gravelyi* eyes, seven key parameters were derived from anatomical measurements: focal length (f), image focal length (f'), F-number, Airy disk half-width (ΔQ_1), interommatidial angle ($\Delta\theta$), acceptance angle (ΔQ_{rh}), and optical sensitivity (S_w). These parameters were calculated as follows:

The focal length (f) and image focal length (f') were computed using the formulae $f = n/P_1$ and $f' = n'/P_1$, where $n = 1$ (air refractive index) and $n' = 1.348$ (image space refractive index). P_1 was determined by $(n_1 - n)/r_1$, with $n_1 = 1.452$ representing lens power and r_1 denoting the distance from the inner corneal lens curvature center to the rhabdom tip [15,46]. The F-number, quantifying light-gathering efficiency, was defined as the ratio of the focal length to maximum facet diameter (A): f/A .

For optical resolution assessment, the Airy disk half-width ΔQ_1 was calculated as λ/A , where $\lambda = 0.5 \mu\text{m}$ (green light wavelength). The interommatidial angle $\Delta\theta$, which reflects the spatial resolution, was derived from $\Delta\theta = A/R$. The eye radius (R) was estimated using the geometric relationship $R = (s^2/4 + h^2)/(2h)$, where s represents the eye segment length and the eye height.

The acceptance angle ΔQ_{rh} , indicating the light acceptance capacity, was determined by the ratio of the rhabdom distal diameter to the focal length. Finally, optical sensitivity S_w was calculated using the formula $S_w = (\pi/4)^2 A^2 (d/f)^2 (kl/(2.3+kl))$, which incorporates the maximum facet diameter (A), rhabdom diameter (d), focal length (f), rhabdom length (l), and absorption coefficient of invertebrates ($k = 0.0067 \mu\text{m}^{-1}$) [16,47].

3. Results

3.1. General morphology of the eye

In female *C. gravellyi*, a pair of convex reddish compound eyes is symmetrically positioned on the lateral head (Figure 2A–B). These oval-shaped eyes measure 137.8–164.7 μm in dorsoventral length (eye height) and 188.0 - 210.5 μm in anteroposterior length (eye width) (N=20), and they contain 228–263 ommatidia with facet diameters (corner-to-corner distance) ranging from 9.3 to 13.5 μm (Figure 2C; Table 1). Central facets display a typical hexagonal geometry and are regularly arranged, while peripheral facets progressively transition from pentagonal lattices to strongly curved cuticular structures, which are particularly pronounced at the eye margins (Figure 2D). The largest facets were observed in the anteroventral region, and the smallest facets were observed in the posteroventral zone (Figure 3). The corneal surface features smooth interommatidial spaces averaging 0.66 μm in width, with 13–19 interommatidial hairs (6.5–21.6 μm long, 1.0–1.7 μm thick) that are predominantly localized in the mid-inferior ocular region (Figure 2C–D). Notably, ommatidial counts exhibit bilateral asymmetry within individuals (e.g., left eyes: 248, 247, 228; right eyes: 262, 263, 256, respectively), and SEM analysis indicated that this stems from variation in spatial constraints during ommatidial differentiation (Figure 3). Additionally, three ocelli are dorsoposteriorly positioned; a circular median ocellus (35.0 μm diameter) is flanked by two elongate lateral ocelli (33.2 μm diameter) (Figure 2B; Table 1).

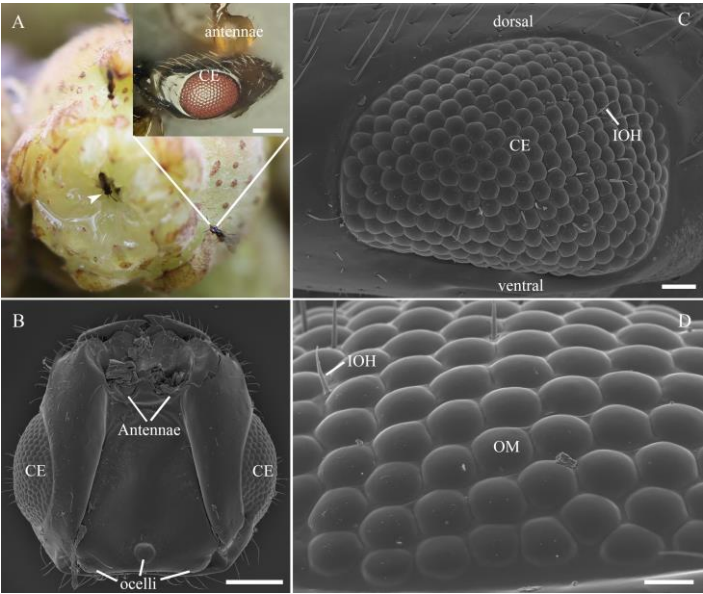


Figure 2. External morphological features of the compound eyes in female *C. gravellyi*. (A) Females exhibit a distinct and reddish-colored compound eye (top right); entry point of female wasps into the fig through the apical ostiole (arrowhead). (B) A pair of convex eyes are positioned symmetrically on the lateral sides of the head. (C) The eyes display an overall oval shape, with sparse interommatidial hairs (IOH) irregularly distributed across the surface. (D) External details of the ommatidia (OM) show the smooth, curved facets characteristic of the dorsal rim area. Scale bar: A, B and inset = 100 μm ; C=20 μm ; D=10 μm .

Table 1. Histological and optical parameters of the compound eyes in female *C. gravellyi*. Data are shown as mean $\pm$ standard deviation. * indicates the largest diameter and pigment granules are oval.

Structural elements	Parameters	Unit	N	Average	Range (min – max)
Compound eyes	eye height	μm	20	147.6 $\pm$ 5.9	137.8–164.7
	eye width	μm	20	201.3 $\pm$ 6.0	188.0–210.5
	facet number	-	11	247 $\pm$ 14	228–263
	eye radius	μm	3	90.4 $\pm$ 5.9	86.4–97.4

Ommatidia	facet diameter	μm	150	11.8 ± 0.7	9.3–13.7
	length	μm	30	54.3 ± 6.8	46.8–59.9
	interommatidial angle	deg	30	9.3 ± 0.9	7.7–12.5
Cornea	outer lens radius	μm	20	7.1 ± 0.6	5.6–8.3
	inner lens radius	μm	20	8.7 ± 0.9	7.7–10.8
	maximum thickness	μm	50	5.7 ± 0.8	4.1–7.9
	number of chitin layers	-	20	9.0 ± 1.0	8–10
Crystalline cone	length	μm	50	12.7 ± 2.3	9.3–18.4
	distal diameter	μm	50	8.9 ± 1.2	6.4–11.3
Pigment granule	PPC diameter *	μm	150	0.62 ± 0.11	0.4–1.0
	SPC diameter *	μm	150	0.57 ± 0.12	0.3–0.8
Rhabdom	length	μm	20	35.7 ± 4.3	29.1–43.9
	distal diameter	μm	20	2.4 ± 0.2	2.0–2.8
	proximal diameter	μm	12	0.69 ± 0.1	0.5–0.9
	microvillus diameter	nm	150	57.2 ± 7.5	41.1–81.6
	PG diameter *	μm	150	0.47 ± 0.10	0.2–0.7
Interommatidial hairs	number	-	20	15 ± 2	13–19
	length	μm	30	13.0 ± 3.9	6.5–21.6
	basal diameter	μm	30	1.4 ± 0.2	1.0–1.7
Basal matrix	thickness	nm	20	198.9 ± 63.3	128–354
Ocellus	diameter	μm	15	35.0 and 33.2	25.5–42.8

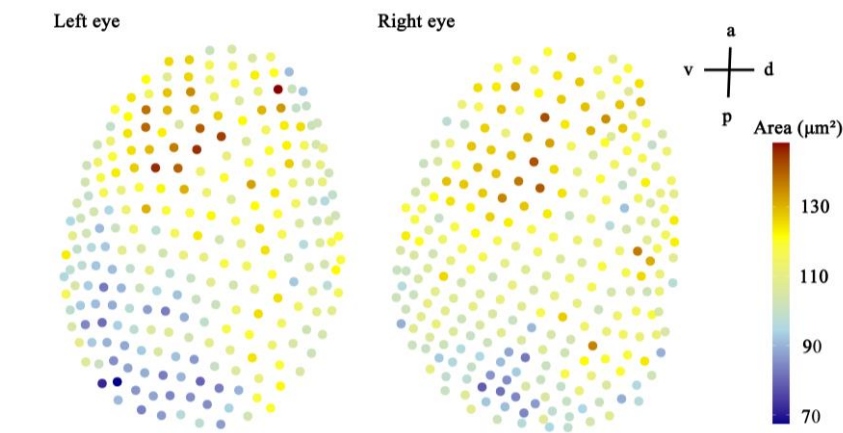


Figure 3. Facet size and distribution pattern in a female *C. gravellyi*, with anatomical orientation indicated in the top-right corner (a, anterior; p, posterior; v, ventral; d, dorsal).

3.2. Fine structural organization of the eye

Each ommatidium comprises two elements: the distal dioptric apparatus and the proximal photoreceptive retinula. The dioptric apparatus includes a biconvex, multi-layered cornea and a tetrapartite crystalline cone, both of which are surrounded by primary and secondary pigment cells. The photoreceptive retinula contains light-sensitive retinula cells and screening pigment cells. All retinula cells converge to form a fused, cone-shaped rhabdom, which is distally connected to the crystalline cone. Figure 4 represents semischematic illustrations of the ommatidium structure in female *C. gravellyi*. The average length of an ommatidium is $54.3 \pm 4.3 \mu\text{m}$ (Figures 4; 5A), and the interommatidial angle between adjacent ommatidia measures 9.3° . In general, the rhabdoms appear uniformly arranged across the eye; however, occasional irregularly shaped rhabdoms are observed in peripheral regions (Figure 5B).

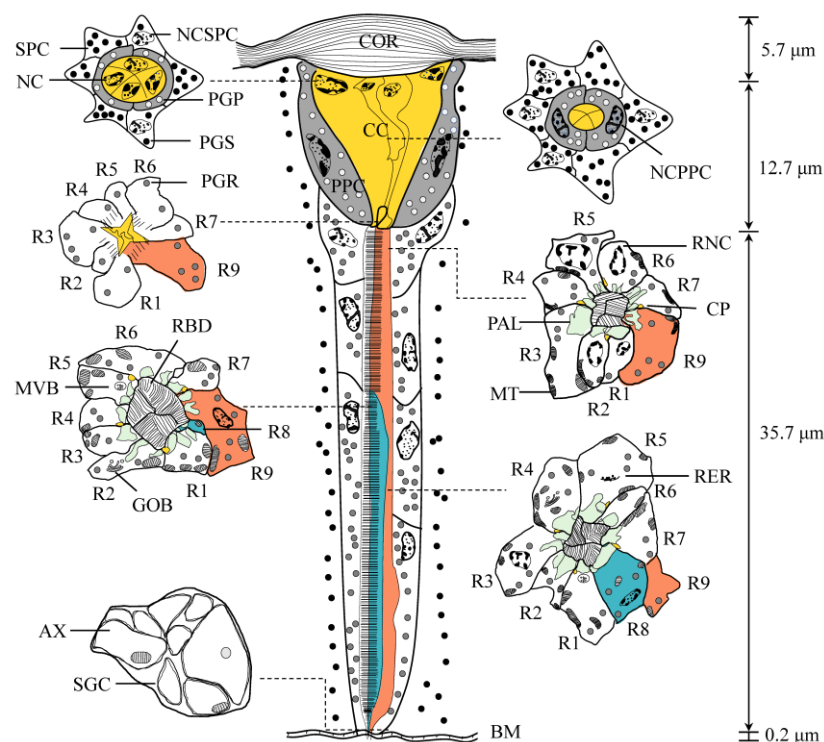


Figure 4. Semischematic illustrations of a single ommatidium from female *C. gravelyi*, showing longitudinal (middle) and corresponding transverse sections (dashed lines). Key structures and abbreviations: Ax, axon; BM, basal matrix; CC, cone cell (yellow); COR, cornea; GOB, Golgi body; PGP, PGS and PGR, pigment granule present in primary/secondary pigment cell and retinula cell, respectively; MT, mitochondria; MVB, multivesicular bodies; NC, nucleus; PAL, palisade (green); PPC, primary pigment cell (gray); R1-9, retinula cell numbers 1–8, the labeled cyan and orange regions represent the position of retinula cell 8 and 9, respectively; RBD, rhabdom; RER, rough endoplasmic reticulum; RNC, retinula cell nucleus; SGC, sheaf of glial cell; SPC, secondary pigment cell. The labelled colors and abbreviations are consistent in the following micrographs.

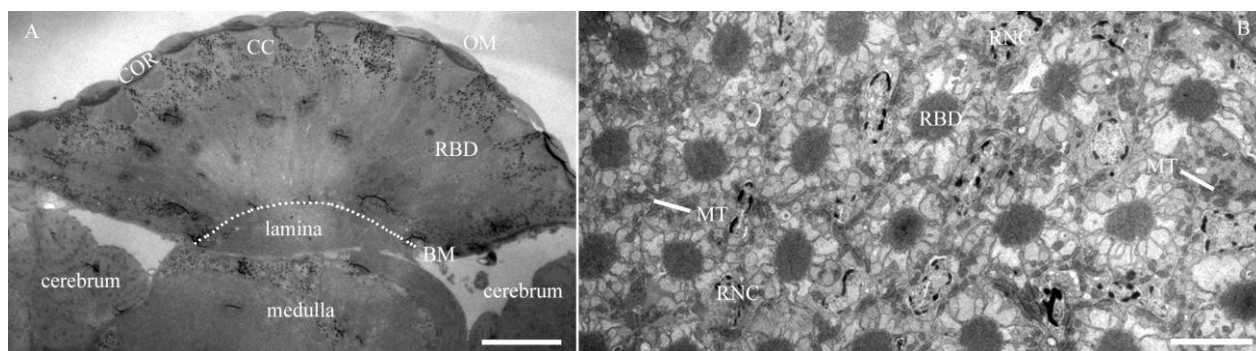


Figure 5. An overview of the compound eyes in female *C. gravelyi*. (A) Longitudinal section of the eye in the anterior-right plane, with the cerebrum positioned adjacent to the eye. (B) Transverse section of the eye in the distal region, displaying rhabdom and associated cellular components. Scale bar: A= 20 μ m; B=5 μ m.

3.2.1. Dioptric apparatus

The transparent, biconvex corneal lens features a smooth external surface with outer and inner radii of curvature measuring 7.1 μm and 8.7 μm (Table 1), respectively. Each corneal facet has a central thickness of approximately 5.7 μm and comprises approximately 9 horizontally stacked microfibrils that progressively thicken from the distal to proximal regions (Figures 6A, 7A). Corneal thickness is minimal in the interommatidial

areas. Immediately beneath the cornea lies the subcorneal layer, which reaches a maximum thickness of 0.38 μm . This layer contains fibrous structures originating from the proximal corneal region and extends to the crystalline cone through subcircular pores (Figure 6B). These fibers display a loose, randomly oriented arrangement without any discernible pattern (Figure 7A).

The eucone-type crystalline cone measures 12.7 μm in average length and 8.9 μm in maximum width and comprises four cone cells (also termed Semper cells). Each cone cell contains a large nucleus positioned in its distalmost region, although no other organelles were observed (Figure 7A Inset, 7B–C). The cone matrix is densely packed with ribosomes and particles less than 2 nm in diameter, likely glycogens (Figures 6B; 7D). In the longitudinal section, the cone exhibits a tapered morphology that gradually narrows proximally before transitioning into a slender crystalline tract (Figure 7B). Within this tract, the cone cell processes interweave with each other (Figure 7D). The crystalline tract, which is approximately 5.20 μm in width and 2.51 μm in length, directly connects to the rhabdom's distal end. Cone cell projections extend to the rhabdom and terminate at the basal matrix.

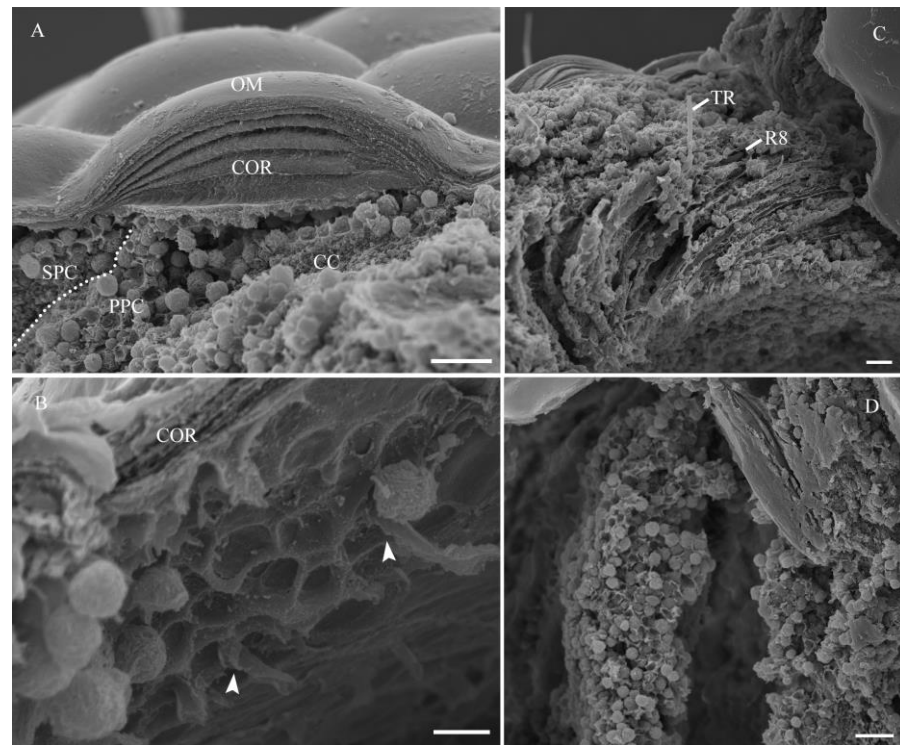


Figure 6. Ultrastructure of the compound eyes in female *C. gravellyi*. (A) Longitudinal fracture of an ommatidia, showing spherical pigment granules beneath the multilayered cornea. The dotted line demarcates the boundary between primary and secondary pigment cells. (B) High-magnification image of the proximal corneal lamella, showing multiple microfibrils (arrowheads) extending from subcircular pores. (C) Longitudinal fracture through the photoreceptor region, displaying the tightly packed, banded rhabdom structure. The termination of retinula cell 8 (R8) and injected tracheoles (TR) are observed. (D) Detailed morphology of the banded rhabdom, surrounded by numerous pigment granules. Scale bar: A, C, and D = 2 μm ; B = 500 nm.

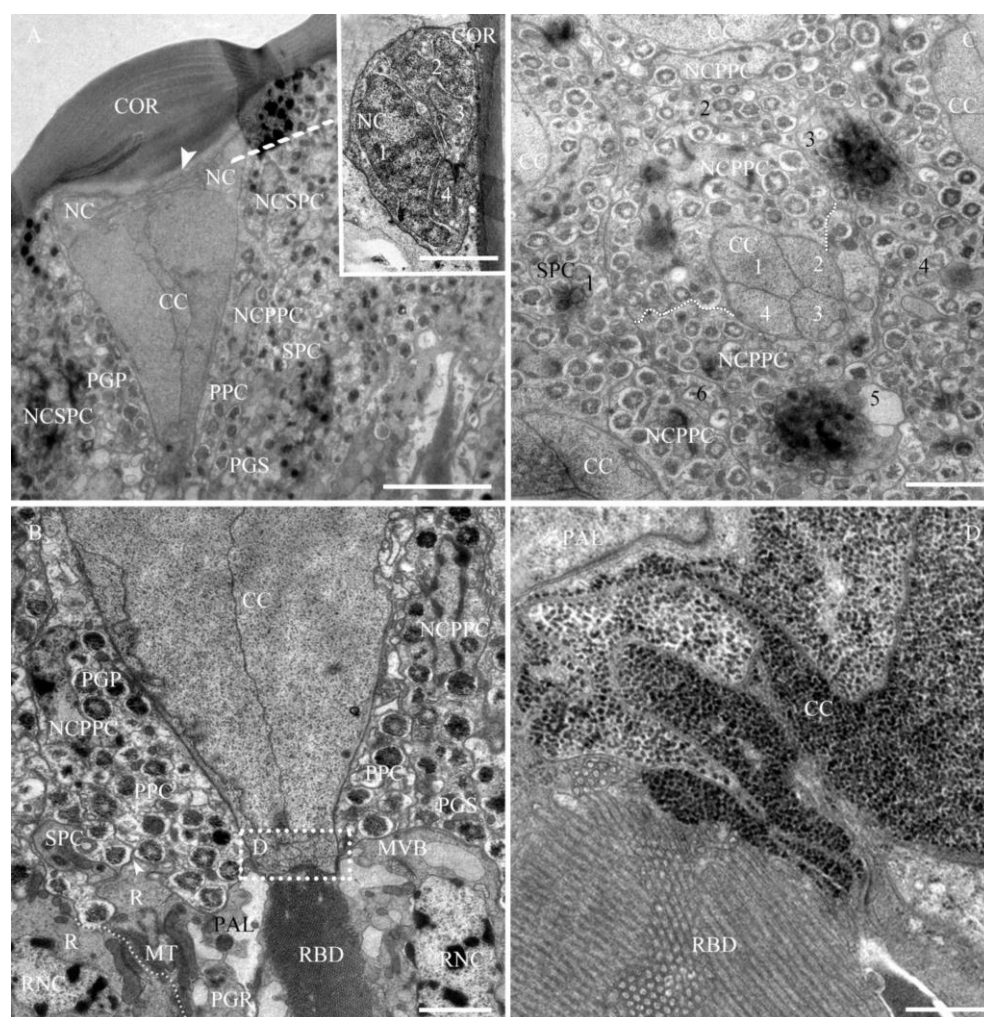


Figure 7. Ultrastructure of the dioptric apparatus in the compound eye of female *C. gravellyi*. (A) Longitudinal section through the complete dioptric apparatus. Inset: corresponding transverse section along the dashed line. The arrowhead indicates a subcorneal layer positioned between the corneal lens and crystalline cone. (B) Longitudinal section of the cone cell's proximal region, showing structural details. (C) Transverse section through the distal third of the cone cell. Cone cells (CC) and associated pigment cells (PPC and SPC) are numbered clockwise for orientation. (D) High-magnification image of the cone-rhabdom junction, revealing an interlaced connective morphology. The dotted lines demarcate the boundary between adjacent organelles. Scale bar: A and C = 5 μm; A inset & B = 2 μm; D=500 nm.

3.2.2. Pigment cells

Primary pigment cells (PPCs), also known as pigmented corneagenous cells, are consistently present in pairs in each ommatidium. They symmetrically envelop both the crystalline cone and the crystalline tract, and their proximal ends contact the distal tips of the retinula cells (Figure 7A–C). The nucleus of each PPC is a large, ellipsoidal structure positioned between the cornea and the proximal end of the crystalline cone. It connects to the innermost subcorneal layer via hemidesmosomes. The cytoplasm of PPCs contains numerous spherical pigment granules, which exhibit high electron density and measure approximately 0.62 μm in diameter (Figures 6A–B; 7A–C). Proximally, the PPCs form a sheath around the crystalline cone and extend narrow, pigment-free projections a few micrometers into the spaces between the retinula cells near the rhabdom (Figure 7D). The PPCs of adjacent ommatidia are closely apposed to each other, but they leave gaps elsewhere to accommodate secondary pigment cells (SPCs) (Figure 7A–C).

SPCs comprise six cells positioned in the spaces between the distal third of the PPC of adjacent ommatidia and the cornea (Figures 6A; 7A–C). These cells are restricted to this region and do not extend to the basal matrix; thus, they cannot be classified as interommatidial pigment cells. In the cone region, SPCs are relatively narrow but broaden between the crystalline tract and the distal tip of the rhabdom, tapering again as they extend proximally. Their nuclei exhibit highly condensed chromatin and measure 3.4 μm in transverse section, and they are located at the base of the crystalline cone. The cytoplasm of SPC contains numerous spherical, electron-dense pigment granules, with the largest reaching 0.57 μm in diameter. No other cell organelles were observed within the cytoplasm of SPCs (Figure 7C).

3.2.3. Retinula cells and rhabdom

The rhabdom, measuring approximately 35.7 μm in length, spans from the proximal end of the crystalline cone to just above the basement membrane (Figure 4). In longitudinal sections of *C. gravelyi* eyes, the nuclei of retinula cells are distributed along nearly the entire length of the retinula cells, from the distal rhabdom region to the lower third, rather than being confined to one plane (Figure 8A–B). Notably, no retinula cell nuclei, tracheoles, or basal pigment cells were observed in the area immediately above the basement membrane. Furthermore, in any given transverse plane, the nuclei of two adjacent retinula cells from neighboring ommatidia are rarely positioned at the same level (Figures 4; 8E–J). This alternating nuclear arrangement within a single ommatidium and between neighboring ommatidia allows for more efficient use of the limited space.

In the distalmost region of the ommatidium, where the rhabdom attains its maximum diameter (averaging 2.4 μm), up to three retinula cell nuclei may occupy a horizontal plane (Figures 5B, 7B, 8E). Proximally, as the ommatidial radius decreases, the number of nuclei per transverse plane and horizontal plane progressively diminishes. The centrally fused rhabdom of *C. gravelyi* is formed by eight regular retinula cells along its entire length. However, consistent with the observation of nine axons per bundle (Figures 8B, 9A–C), a ninth retinula cell (R9, referred to as an irregular retinula cell) emerges in the distal two-thirds of the rhabdom. This R9 displaces R8 and contributes a small rhabdomere primarily to the proximal rhabdom region (Figure 8B). The microvilli of rhabdomeres exhibit a stereotypic orthogonal arrangement: each pair of neighboring retinula cells aligns their microvilli perpendicular to one another (Figure 8C), creating a banded pattern in longitudinal sections. Individual microvilli measure approximately 57.2 nm in diameter. Four cone cell projections extend proximally alongside the retinula cells, separating these retinula cell pairs and reaching down to the basement membrane (Figure 8E–J).

The rhabdom is encircled by cisternae of smooth endoplasmic reticulum (ER), which is collectively termed the perirhabdomeric or palisade ER (Figures 4; 7B; 8C). The structure of this specialized ER system varies depending on the light adaptation states. During dark adaptation, the palisade ER significantly expands. Conversely, under light-adapted conditions, its development becomes constrained to a pigment-free annular zone measuring 0.4–0.9 μm in width surrounding the rhabdom. Retinular cell pigment granules, averaging 0.47 μm in longitudinal diameter are spatially associated with these ER structures, and their density is highest near the perirhabdomeric cisternae (Figures 6C–D; 7B; 8E–J). Analysis of longitudinal sections revealed that these pigment granules are preferentially aligned along two axes: 1) parallel to the elongated ER cisternae, and 2) oriented with the ommatidial longitudinal axis, as illustrated in Figure 9A. This dual orientation pattern suggests coordinated structural organization between the ER system and pigment distribution within the retinula cells.

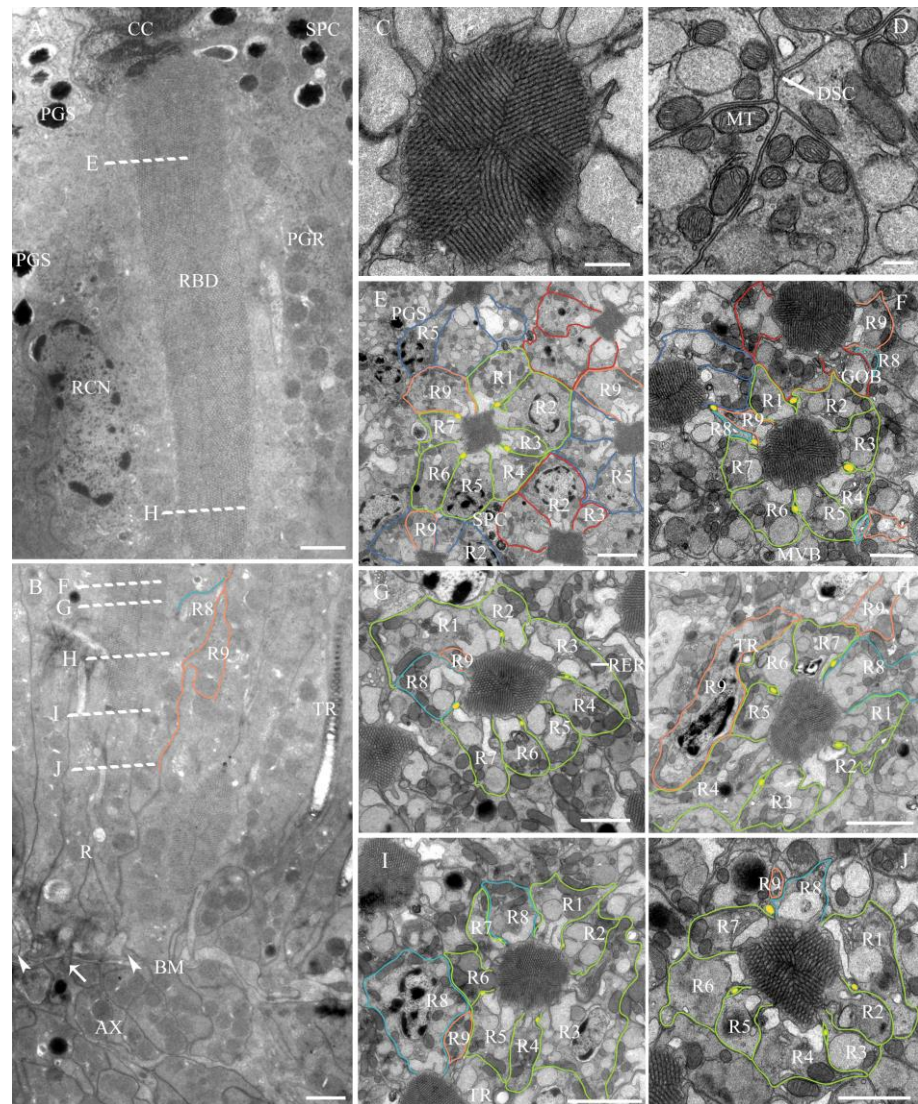


Figure 8. Ultrastructure of retinula cells and rhabdom in the compound eye of female *C. gravelyi*. (A) Longitudinal section through the distal third of the rhabdom. (B) Longitudinal section of the proximal two-thirds of the rhabdom, demonstrating the overlapping region between retinula cells 8 and 9. The cone cell projection (arrowhead) and axon (arrow) penetrating the basal matrix are indicated. (C) Transverse section of the rhabdom showing vertically oriented microvilli. (D) Retinula cell adhesive junctions, featuring desmosomes (DSC) and mitochondria clustered near the cell membrane. (E–I) Serial transverse sections of the rhabdom at levels corresponding to the dashed lines in A and B. Retinula cells surrounding the central rhabdom are color-coded (red and blue). Scale bar: A, F and J = 1 μ m; B, E, G, H and I = 2 μ m; C = 500 nm; D = 200 nm.

The numbering of retinula cells is determined by the presence of an irregular R9. These cells are sequentially numbered from 1 to 8 in the direction of the adjacent cone cell projection, independent of their right or left positioning (Figure 8E–J). R9 occupies the upper third of the rhabdom, displacing R8 to the ommatidial periphery. This positional shift causes three adjacent rhabdomeres to have an identical microvillar alignment, thus forming a rhabdomeric triplet (Figures 5B; 8F). Notably, single retinula cells with a uniform microvillar orientation can also separate opposing triplets, and their microvilli are positioned between two such structures. Furthermore, intermediate configurations are observed, in which triplet arrangements are mixed with orthogonal duplets that have paired rhabdomeres with perpendicular microvillar orientations.

Further proximally, all retinula cells progressively taper along the rhabdom and transition into axons approximately 1 μm above the basal matrix (Figure 8A–B, E–J). Therein, retinula cells R4, R3, and R7 undergo early volumetric reduction, whereas the opposing cells R2 and R6 maintain their full length, extending from the distal to proximal extremities of the rhabdom. These latter cells (R2, R6) are consequently the longest retinula cells in the ommatidium. Additionally, cells R1 and R5 are positioned diametrically opposite from each other within the ommatidium, yet share identical microvillar orientations. Cell R9 follows this sequence and has a similar axonal transformation. Near the proximal terminus of the rhabdom, R2 and R6 enlarge roughly and contain a few pigment granules. Ultimately, the axons of all retinula cells, including those of the atypical R9, converge into discrete bundles of nine fibers that traverse the basal matrix (Figures 8B; 9A–C).

3.2.4. Basal matrix

The basal matrix, measuring approximately 198.9 nm in thickness, forms a critical boundary layer between the retina and lamina, demarcating the optical compartment from the neuropil (Figures 5A, 8B, 9B). This matrix is perforated by regularly spaced circular apertures that permit the passage of ommatidial axon bundles, which are each ensheathed by glial cells. Each bundle contains nine fibers: two centrally positioned large-diameter fibers flanked by three smaller fibers on each lateral side, with an additional small fiber occupying the central axis of the bundle (Figures 9B–C). Pigment granules and mitochondria are present in some axons. Additionally, the interommatidial space in the basal matrix allows tracheoles to project distally into the optical region (Figures 8B; 9A). The region directly beneath the basal matrix houses large nuclei and electron-dense pigment granules, which potentially has screening functions.

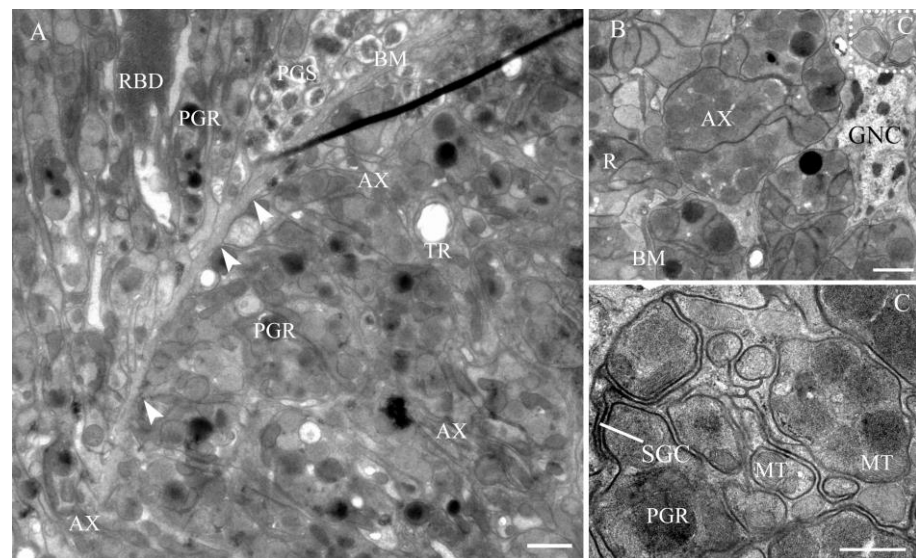


Figure 9. Ultrastructure of the basal matrix in the compound eye of female *C. gravelyi*. (A) Oblique section through the proximal-most retinula cell terminals, demonstrating axonal penetration of the basal matrix via ommatidial cartridges (arrowhead). (B) Transverse section of axon bundles enveloped by glial cell sheaths (SGC), each containing a prominent glial nucleus (GNC). (C) High magnification image of a single axon bundle from panel B, showing ultrastructural details. Scale bars: A and B = 1 μm ; C = 500 nm.

3.3. Optical properties

Following the methodology described in Section 2.4, seven key optical parameters of female *C. gravelyi* eyes are summarized in Table 2. Calculations using lens curvatures (P1: 0.064 μm^{-1} ; P2: 0.012 μm^{-1} ; P3: -0.003 μm^{-1}) and a total lens power (Pl) of 0.073 yielded a

focal length of 13.7 μm and an image focal length of 18.5 μm (See Table S1 in supplementary materials). These results indicate that lens power is predominantly governed by the outer surface curvature (P1), with the calculated focal plane positioned near the distal tip of the rhabdom. The F-number, derived from the focal length and facet diameter measurements, was determined to be 1.1 for *C. gravelyi*, which is lower than values reported for *T. evanescens* and *A. flavipes*, but marginally higher than that of *M. mymaripenne* (Table 2). Further analysis revealed an acceptance angle ΔQ_{rh} of 10.0° and a half-width blur circle (ΔQ_i) of 2.4°. Notably, the optical sensitivity (S_w) reached 0.26 $\mu\text{m}^2/\text{sr}$, substantially exceeding values observed in the three comparative parasitoid wasp species.

Table 2. Optical parameters of female *C. gravelyi* were calculated from direct eye measurements, and comparative data for three parasitoid wasp species were obtained from previously published studies by Makarova et al. (2015) [15] and Fischer et al. (2011) [13].

Parameters	<i>C. gravelyi</i>	<i>M. mymaripenne</i>	<i>T. evanescens</i>	<i>A. flavipes</i>
Body size (mm)	2.74	0.2	0.3–0.4	0.45
f (μm)	13.7	6.2	8.9	10.7
f' (μm)	18.5	8.4	12.0	14.4
F-number	1.1	0.8	1.4	1.3
ΔQ_{rh} (°)	10.0	22.2	8.1	4.8
ΔQ_i (°)	2.4	3.5	4.5	3.5
S_w ($\mu\text{m}^2/\text{sr}$)	0.26	0.23	0.06	0.04

4. Discussion

Comprehensive morphological analyses of hymenopteran compound eyes have been performed for taxa in numerous common families such as Apoidea, Vespidae, and Halictidae [2,5,14,27,45,48]. However, ultrastructural research on parasitoid wasps is scarce [2]; the lack of studies on parasitoid wasps is particularly significant given their estimated global diversity of approximately 500,000 to 1,000,000 species [49]. The compound eyes of only three species, *M. mymaripenne* [8,9,15], *T. evanescens* [13,44], and *A. flavipes* [15], have been analyzed to date. Our findings provide novel insights into the ultrastructure of the compound eyes of an additional parasitoid species, which enhances our comparative understanding of vision within this ecologically significant group.

4.1. External structural features of compound eyes among parasitoid species

The compound eye of *C. gravelyi* has an oblong and narrow shape, and the antero-posterior length (eye width: 201.3 μm) exceeds the dorsoventral length (eye height: 147.6 μm) (Figure 2C; Table 1). This morphological pattern is consistent with observations reported for parasitoid wasps exceeding 0.3 mm in total body size [2,13,15,44], but is in contrasts to the ocular dimensions of the smallest known thrips egg parasitoid, *M. viggianii*, which displays a short and wide eye [2,9,15]. Insects often show allometry between eye size and body size, which is associated with spatial constraints on eye growth. This correlation is evident during postembryonic development [1,2,50] and is affected by environmental factors, biological traits, and diurnal activity rhythms [47], as well as sex [13,15,34]. A recent large-scale analysis of insect compound eyes by Makarova et al. (2022) [2] revealed allometric relationships between ommatidial traits and body size: Ommatidia number $y=56.89x^{1.46}$ and Ommatidia diameter $y=9.84x^{0.36}$. Notably, *C. gravelyi* (body size >1.5 mm), which is morphometrically similar to small hymenopterans in Makarova's dataset, has eye dimensions and facet diameters comparable to other fig wasps, which corroborates these scaling patterns. However, critical gaps remain in parasitoid wasp research. Makarova's segmented regression analysis highlights this discontinuity and

reveals divergent scaling slopes between wasps at over 1.5 mm and those below 1.5 mm [2]. Additionally, insects within the 2–5 mm body size range exhibit specialized adaptations [1,24,51], which further emphasizes the need for systematic morphological investigations of parasitoid wasps varying in size.

In apposition eyes, both facet diameter and lens curvature influence sensitivity and spatial resolution [16], yet facet diameter cannot be reduced indefinitely. Makarova et al. (2022) [2] demonstrated 4- to 30-fold variation in facet diameters across insects of varying sizes, ranging from large to the smallest known species. However, parasitoid wasps exhibit minimal interspecific variation in this trait. For instance, *C. gravelyi* (body length 2.74 mm) in this study has a facet diameter of 11.8 μm , whereas miniaturized parasitoid species (body length <0.4 mm) such as *T. evanescens* [13,44], *M. viggianii* [9,15], *A. flavipes* [15], and *Kikiki huna* [52] show facet diameters of 6.39 μm (female), 8.1 μm , 8.1 μm , and 7.65 μm (SEM-measured), respectively. These measurements reveal facet diameters far below theoretical limits, even in extreme cases of miniaturization such as *M. viggianii* [9]. In general, the eyes of parasitoid wasps are often notably convex, which is a structural constraint resulting from their reduced radius of curvature. This morphology, exemplified by the curved facets in the dorsal rim area of *C. gravelyi* (Figure 2D), likely enhances the visual field by expanding angular sensitivity, even under severe miniaturization [2,24].

4.2. Internal structural features of compound eyes among parasitoid species

The cellular organization of ommatidia in hymenopterans is generally highly conserved across insects varying in body size and compound eye morphology and comprises two primary pigment cells, six secondary pigment cells, four cone cells, and nine retinula cells [1,3,5,9,13,15,19,44,45,47]. The reduction in body size necessitates a corresponding decrease in eye dimensions because of the constraints of smaller head capsules, exemplified by the extreme miniaturization observed in parasitoid wasps such as *M. viggianii* [9]. However, the complete abandonment of photoreception is evolutionarily unfavorable, as even certain cavernicolous species retain light-detection capabilities to facilitate habitat selection and thus enhance survival [1,53]. To accommodate conserved cell numbers or specialized cell types under spatial constraints, these minute parasitoid wasps have evolved compensatory modifications in other structural components.

4.2.1. Dioptric apparatus

In nearly all parasitoid wasps, the corneal lens exhibits a smooth external surface characterized by distinct outer and inner radii of curvature [13,15]. A reduction in the outer corneal radius of curvature is correlated with an increased radius of curvature across the ommatidial surface, producing more convex facets. Through calculations using the lens formula (Section 2.5), we demonstrate that lens power is primarily determined by the anterior lens surface, and the outer facet radius is the critical factor for achieving short focal lengths (f). This optical requirement is physiologically essential for miniature species, where optimization of the focal length is evolutionarily constrained [50]. In *C. gravelyi*, the outer radius of curvature slightly exceeds half the diameter of the facet (Table 1). To further shorten the focal lengths, additional reductions in the curvature radius would necessitate a proportional decrease in facet diameter. However, this imposes functional trade-offs given that smaller facets exacerbate light diffraction and reduce interommatidial angles, thereby diminishing ommatidial sensitivity. Notably, the examined eyes circumvent diffraction limitations, as the blur circle width remains smaller than the rhabdom's acceptance angle. Furthermore, gradual variation in facet size from the eye's center to periphery (Figure 3) may reflect adaptive modifications to enhance light-capture efficiency during navigations [17,47].

A well-developed subcorneal layer is consistently observed in each ommatidium of *C. gravelyi* (Figure 7A). However, this structure is absent in previously studied parasitoid wasps [13,15] but ubiquitously present in nonparasitic hymenopterans [20,47]. Phylogenetic comparisons further reveal its convergent evolution in nocturnal Lepidoptera, including *Macrosoma* sp. [54] and *Grapholita molesta* [25]. The maximum thickness of this layer within individual ommatidia is inversely related to the ambient light intensity [25]. This supports the hypothesis that the subcorneal layer functions as a photomechanical adaptation for low-light vision, particularly critical for crepuscular behaviors such as dawn dispersal in fig wasps emerging from natal figs [55].

The eucone crystalline cone of *C. gravelyi*, formed by four cone cells, measures approximately 12.7 μm in length, which is significantly longer than those of smaller parasitoid wasps such as *A. flavipes* (10.0 μm) [15], *T. evanescens* (7.88 μm) [13], and *M. mymaripenne* (5.3 μm) [15]. However, these dimensions are not allometrically correlated with body size compared with crystalline cones in other hymenopterans [2,5,47]. The nuclei of the crystalline cone are positioned at the distalmost region, and interconnected cone cell processes interweave with each other to maximize spatial efficiency; this is a ubiquitous morphological adaptation among miniaturized parasitoid wasp species, which is associated with evolutionary constraints imposed by extreme body size reduction [9,44].

4.2.2. Pigment cells and pigment granules

Pigment cells in hymenopteran eyes are categorized into two types: primary pigment cells (PPCs) and secondary pigment cells (SPCs). PPCs (typically two are present across taxa) are positioned subjacent to the cornea and envelop the crystalline cones. In contrast, the number of SPCs encircling the PPCs varies within Hymenoptera. In miniaturized parasitoid wasps, SPCs terminate proximally at the level of the crystalline cone and lack distal extensions [7,9,13,15,44]. According to descriptions of two egg parasitoids, *T. evanescens* ommatidia contain 5 [44] or 6 SPCs [13], whereas *M. viggianii* contains 24 SPCs across 29 ommatidia [9]. Spatial reconstructions by Makarova et al. (2025) [9] further delineate regional specialization; central ommatidial rows are encircled by four SPCs, and peripheral rows are only in contact with two or three. Our findings confirm that *C. gravelyi* possesses six SPCs per ommatidium (Figure 7C), which is consistent with observations in *T. evanescens* [13]. However, a comprehensive 3D reconstruction of *C. gravelyi* is needed in light of discrepancies between the 2D and 3D ultrastructural datasets in *T. evanescens*. The observed reduction in SPC counts across parasitoid species is strongly correlated with ocular miniaturization, suggesting that this trait represents an evolutionary compromise associated with spatial constraints in parasitoid wasp visual systems [2,9,44].

Morphological studies revealed variation in pigment granule dimensions between parasitoid wasps and other hymenopterans. First, pigment granule diameter in miniature parasitoid wasps, such as *C. gravelyi* examined here (Figures 6A, C; 7A–C), did not significantly diverge from that observed in larger hymenopteran species. This is supported by 3D reconstructions of pigment-containing cells in *T. evanescens* [44] and *M. viggianii* [9], which indicate that granule volume/diameter is consistent with typical measurements for large hymenopterans. By contrast, adaptive modifications in granule morphology and spatial organization are observed in miniature parasitoid wasps. Unlike the spherical granules characteristic of larger hymenopterans [2,14,17,22,48], their photoreceptor cells contain ellipsoidal granules [9,13,15,44]. These granules are aligned parallel to the ommatidial axis, creating a dense light-blocking structure that compensates for limited cellular space [13,15]. Furthermore, analogous granule patterning has been observed in miniature Coleoptera [7] and Lepidoptera [24]. Finally, retinula cells have a markedly higher pigment granule packing density per cell, with 13, 5, and 4–5 observed in *M. mymaripenne*, *A.*

flavipes, *C. gravelyi*, which might reflect evolutionary adaptations for overcoming spatial limitations in miniature parasitoid wasps [15].

4.2.3. Retinula cells and rhabdom

The ommatidia of *C. gravelyi* exhibit a distal rhabdom structure featuring four paired rhabdomeric units directly connected to the crystalline cone (Figures 4; 5A; 7A; 8A), a characteristic apposition eye configuration shared with larger hymenopterans such as ants and bees [14,19–21]. While nine retinula cells are typical in hymenopterans, the ninth cell is initiated more proximally in *C. gravelyi*, as well as in the miniature parasitoids *M. mymaripenne*, *T. evanescens*, and *A. flavipes*, which likely stem from their shortened rhabdoms compared with those of the intertidal ants *Polyrhachis sokolova* [47] and *A. mellifera* drones [14]. Furthermore, these spatial modifications, including the contribution of the retinula cell to rhabdom formation, are conserved across hymenopterans, which reflects evolutionary stability in compound eye organization in pterygote insects. Nevertheless, miniaturization drives specific structural adaptations, and this has led to divergence in various characteristics of hymenopterans relative to the ancestral states of their common ancestors [2,13,15,18,48]. In *C. gravelyi*, the irregular rhabdom shapes resemble those documented in the dorsal rim area of *Megalopta genalis* [22] and *M. viggianii* [9]. However, in this pollinating fig wasp and the trichogrammatid wasp *T. evanescens*, irregular rhabdoms occur diffusely across the eye and are not regionally restricted [13]. The prevalence of such irregular morphologies reflects selective pressures to maintain high visual acuity under spatial limitations, which likely permit structural variation without compromising optical performance [2,13].

As documented in Fischer et al. (2011) [13] and Makarova et al. (2015, 2025) [9,15], miniature parasitoids exhibit a comparable distal rhabdom extension. These parasitoids possess shortened rhabdoms, with a distally expanded and proximally tapered morphology (Figure 5A). Theoretically, increased distal rhabdom diameter enhances total rhabdom volume and also alters its optical properties: structures $<2\ \mu\text{m}$ function as waveguides, whereas those $>2\ \mu\text{m}$ operate as lightguides [16,19]. For instance, distal rhabdom diameters in *C. gravelyi* and *M. mymaripenne* measure $2.4\ \mu\text{m}$, exceeding the $2\ \mu\text{m}$ threshold, while those in *T. evanescens* ($1.67\ \mu\text{m}$) and *A. flavipes* ($1.4\ \mu\text{m}$) are less than the $2\ \mu\text{m}$ threshold. Regardless of their rhabdomeric configuration as waveguides or lightguides, the palisade ER structures (Figures 4, 8E–J) observed across these parasitoid species mediate critical transitions between dark and light adaptation states. This mechanism likely enhances the photon capture efficiency of apposition eyes, which optimizes visual performance across varying light intensities [46].

A prominent structural feature observed across all studied parasitoid species, including *C. gravelyi*, *M. mymaripenne*, *T. evanescens*, and *A. flavipes*, is the interlocking arrangement of retinula cells between neighboring ommatidia, characterized by staggered nuclear positioning at the vertical levels [9,13,15]. This spatial configuration optimizes tissue packing efficiency, minimizing wasted space both within individual ommatidia and across adjacent units. Furthermore, volumetric constraints drive size reductions or the loss of non-critical organelles in retinula cells, including nuclei, mitochondria, and ER, and such adaptations enhance spatial economy in extreme cases of ocular miniaturization in parasitoids [2]. Furthermore, in the four aforementioned parasitoid species, retinula cell nuclei occupy nearly the entire length of the cell, excluding the extremely constricted proximal region. Spatial constraints imposed by shortened ommatidia and increased rhabdom diameters in the smallest species *M. mymaripenne* ($<0.3\ \text{mm}$ body size) drive partial nuclear displacement into inter-ommatidial spaces between primary pigment cells. This nuclear redistribution, unlike the conserved ommatidial proportions observed in

other three larger parasitoids (>0.3 mm), reflects a compensatory adaptation to maintain the functional demands of the photoreceptor under extreme miniaturization [7,9,13,15].

Data from Makarova et al. (2022) [2] reveal that the mean microvilli diameter in microinsects measures 60 ± 10 nm, which is consistent with values observed in larger insects [14,22]. In this study, *C. gravelyi* exhibits a microvilli diameter of 57.2 nm (Table 1), which is consistent with values in other miniature parasitoids such as *M. mymaripenne* (57.4 nm), *T. evanescens* (62.2 nm), and *A. flavipes* (72.9 nm) [15]. No significant interspecific variation was observed among these parasitoids. In contrast to crustaceans, where microvilli diameter varies during postembryonic development or with light/dark adaptation [1], the dimensional stability of insect microvilli is high. This non-scalable trait likely stems from biophysical constraints governed by the dimensions of photopigment molecules, which ensure the absorption efficiency of light across different body sizes [2,8,13].

4.3. Optical features among parasitoid species

Theoretical analyses demonstrate that optimizing compound eye functionality in a given species requires coordinated adjustments among three core components: the dioptric apparatus, photoreceptive rhabdom, and essential organelles, which are shaped by ecological demands [16,30,50]. Increase in rhabdom diameters to improve light capture of an apposition eye in dim environments, as observed in species such as *C. gravelyi* (10° acceptance angle; body >2 mm) and *M. mymaripenne* (22.2° ; body size <2 mm) (Table 2), reduce organelle space and necessitate shorter lengths of the dioptric apparatus. Although shortened focal lengths coupled with broad rhabdoms increase acceptance angles, there are trade-offs in these adaptations. For example, the light sensitivity of *C. gravelyi* is 2.6 times higher than that of *A. mellifera* ($0.1 \mu\text{m}^2/\text{sr}$) because of its enlarged rhabdom [22], whereas smaller parasitoids such as *A. flavipes* ($0.04 \mu\text{m}^2/\text{sr}$) and *T. evanescens* ($0.06 \mu\text{m}^2/\text{sr}$) display only half the sensitivity of *A. mellifera* [13,15]. Comparative analyses of acceptance angles across hymenopterans, including an Australian intertidal ant ($\Delta\rho_{\text{rh}} = 4.45^\circ$ day; 8.48° night), honeybees ($\Delta\rho_{\text{rh}} = 1.7$), diurnal halictid bees ($\Delta\rho_{\text{rh}} = 1.6$), yellow sand wasps ($\Delta\rho_{\text{rh}} = 0.41$), and parasitoids listed in Table 2, reveal inherent limitations in increasing acceptance angles [16,22,47]. However, since visual resolution becomes irrelevant without sufficient photon capture to form detectable signals [2,19], the relative importance of sensitivity is higher than that of other parameters in miniature compound eyes. This pattern is exemplified by eyeless cave-dwelling *Leptonetela* spiders, in which photon detection is prioritized over structural complexity [53]. Relatively speaking, the need to adapt rhabdom acceptance angles through facet diameter enlargement explains the non-allometric reduction in ommatidial count, which is similar to the trend observed in larger species where facet number decreases approximately linearly with body size [2,3,5,23,24,30]. Thus, reduced body size primarily results in fewer facets per compound eye. However, the minimum lens size is constrained by diffraction limits [16]. A viable strategy involves maintaining an optimized number of smaller facets to maintain visual resolution. For instance, the larger species *C. gravelyi* in this study possesses twice as many ommatidia as *T. evanescens* [13] and 8.5 times more than *M. mymaripenne* [15], which reflects the size-dependent scaling of ommatidial density and maintains visual resolution under physical constraints.

According to the V-parameter analysis of rhabdom diameter versus wavelength in *T. evanescens* [13], female *C. gravelyi* exhibit trichromatic light sensitivity, which overlaps with *T. evanescens* in both the second- and third-order modes. This suggests enhanced sensitivity in blue, violet, and ultraviolet wavelengths (<500 nm, <400 nm, and far UV, respectively), with these spectral ranges dominating light absorption within their rhabdoms [16,46,56]. These findings are consistent with phototactic behavior and genomic studies of two *Ceratosolen* species [40,41]; *C. gravelyi* demonstrates high light sensitivity

compared with *M. mymaripenne*, *T. evanescens*, and *A. flavipes* (Table 2), which likely stems from V-parameter optimization for trichromatic vision. Eye structure variation in parasitoids is often associated with ecological factors, although spatial constraints on head morphology may also limit eye size. Given their need for precise host fig detection and oviposition, *C. gravelyi* females exhibit minimal nocturnal activity and lack specialized adaptations for low-light vision; instead, they exhibit diurnal activity and rely on eyes adapted to high light sensitivities [18,55,57]. Moreover, their asymmetric ommatidial distribution (Figure 3), similar to that in *Temnothorax albipennis* ants, may facilitate behavioral lateralization [58]. Conversely, species with small eyes, low ommatidial counts, and reduced internal optical parameters are not inherently limited in their visual capabilities. For instance, the ant *Leptothorax albipennis*, which possesses only 60 ommatidia, effectively navigates using visual landmarks [59]. Similarly, female fig wasps such as *C. gravelyi* may rely more heavily on olfactory and chemical signals for host localization. Nevertheless, neural adaptations, including multimodal sensory integration pathways similar to those in *Drosophila* [43], can offset restricted visual input, allowing even species with sparse ommatidia to perform intricate behaviors [9,43,59,60]. This highlights how compensatory mechanisms in neural processing can decouple visual task performance from strict anatomical constraints.

5. Conclusions

We investigated the fine structural and optical characteristics of the compound eyes in adult female *C. gravelyi*, the exclusive pollinator of *F. semicordata*, using light, scanning, transmission electron microscopy. The apposition compound eyes of *C. gravelyi* contain 228–263 ommatidia per eye, with an asymmetric distribution between the left and right eyes. Each ommatidium comprises a biconvex corneal lens covering a tetrapartite eucone crystalline cone, formed by interlaced proximal cone cells. Pigment cells surround each ommatidium, and a few pigment granules are localized in pigment cells and retinula cells. Nine retinula cells constitute each unit: eight photoreceptors (R1–R8) collectively form the rhabdom from the cone base to the ommatidial core, while a ninth cell replaces R8 in the apical third of the rhabdom. Optical calculations indicate that the eyes of *C. gravelyi* predominantly show trichromatic light sensitivity and are optimized for diurnal activity in bright diurnal environments. The findings advance our understanding of multimodal sensory integration (e.g., combining visual, olfactory, and chemical signals) in the fig–wasp mutualism and highlight how a specialized eye morphology supports ecological niche specialization.

Supplementary Materials: The following supporting information can be downloaded at: www.mdpi.com/xxx/s1, Table S1: Optical parameters of female *C. gravelyi* and three other parasitoid wasp species.

Author Contributions: Conceptualization, P.Y. and Z.L.; methodology, H.X., P.Y. and Z.L.; software, H.X., P.Y. and Z.L.; validation, P.Y. and Z.L.; formal analysis, H.X., Y.S., S.Z., Y.Z., S.S., Y.Z., P.Y. and Z.L.; investigation, H.X., S.Z., Y.Z., S.S. and Y.Z.; data curation, H.X., Y.S., S.Z., Y.Z., S.S., Y.Z., P.Y. and Z.L.; writing—original draft preparation, H.X., P.Y. and Z.L.; writing—review and editing, P.Y. and Z.L.; visualization, H.X., Y.S., P.Y. and Z.L.; supervision, P.Y. and Z.L.; funding acquisition, Z.Y., P.Y. and Z.L.. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the National Natural Science Foundation of China (32260719, 32160296, and 31760107), Young Top-Notch Talent of Yunnan Outstanding Talent Program (YNWR-QNBJ-2018-131, YNWR-QNBJ-2019-123, and

XDYCNRC-2022-0207), Yunnan Fundamental Research Projects (202401AT070265 and 202401BD070001-111, and the First Class Forestry Academic Subject in Yunnan Province (523003).

Data Availability Statement: The data presented in this study are available upon request from the corresponding authors.

Acknowledgments: We thanks Zhi-Jia Gu, Kunming Institute of Botany, Chinese Academy of Sciences (CAS), and Ying-Qi Guo, Kunming Institute of Zoology, CAS for technological assistance with the electron microscopy. We thank Yanqiong Peng's Laboratory, Xishuangbanna Tropical Botanical Garden, CAS, for collectind fig wasps.

Conflicts of Interest: The authors declare no conflicts of interest.

References

- Meyer-Rochow, V.B. Compound eyes of insects and crustaceans: Some examples that show there is still a lot of work left to be done. *Insect Sci.* **2015**, *22*, 461–481, doi:10.1111/1744-7917.12117.
- Makarova, A.A.; Diakova, A.A.; Chaika, S.Y.; Polilov, A.A. Scaling of the sense organs of insects. 1. Introduction. Compound eyes. *Entomol. Rev.* **2022**, *102*, 161–181, doi:10.1134/S0013873822020026.
- Kittelman, M.; McGregor, A.P. Looking across the gap: Understanding the evolution of eyes and vision among insects. *BioEssays* **2024**, *46*, 2300240, doi:10.1002/bies.202300240.
- Sherk, T.E. Development of the compound eyes of dragonflies (odonata). III. Adult compound eyes. *J. Exp. Zool.* **1978**, *203*, 61–79, doi:10.1002/jez.1402030107.
- Jander, U.; Jander, R. Allometry and resolution of bee eyes (Apoidea). *Arthropod Struct. Dev.* **2002**, *30*, 179–193, doi:10.1016/S1467-8039(01)00035-4.
- Perl, C.D.; Niven, J.E. Differential scaling within an insect compound eye. *Biol. Lett.* **2016**, *12*, 20160042, doi:10.1098/rsbl.2016.0042.
- Makarova, A.A.; Meyer-Rochow, V.B.; Polilov, A.A. Morphology and scaling of compound eyes in the smallest beetles (Coleoptera: Ptiliidae). *Arthropod Struct. Dev.* **2019**, *48*, 83–97, doi:10.1016/j.asd.2019.01.001.
- Chua, N.J.; Makarova, A.A.; Gunn, P.; Villani, S.; Cohen, B.; Thasin, M.; Wu, J.; Shefter, D.; Pang, S.; Xu, C.S.; et al. A complete reconstruction of the early visual system of an adult insect. *Curr. Biol.* **2023**, *33*, 4611–4623.e4614, doi:10.1016/j.cub.2023.09.021.
- Makarova, A.A.; Chua, N.J.; Diakova, A.V.; Desyatirskina, I.A.; Gunn, P.; Pang, S.; Xu, C.S.; Hess, H.; Chklovskii, D.B.; Polilov, A.A. The first complete 3D reconstruction and morphofunctional mapping of an insect eye. *eLife* **2025**, *14*, RP103247, doi:10.7554/elife.103247.1.
- Howarth, F.G. Ecology of cave arthropods. *Annu. Rev. Entomol.* **1983**, *28*, 365–389, doi:10.1146/annurev.en.28.010183.002053.
- Buffry, A.D.; Curra, J.P.; Franke-Gerth, F.A.; Palavalli-Nettimi, R.; Bodey, A.J.; Rau, C.; Samadi, N.; Gstöhl, S.J.; Schlepütz, C.M.; McGregor, A.P.; et al. Evolution of compound eye morphology underlies differences in vision between closely related *Drosophila* species. *BMC Biol.* **2024**, *22*, 67, doi:10.1186/s12915-024-01864-7.
- Dvořáček, J.; Sehadová, H.; Weyda, F.; Tomčala, A.; Hejníková, M.; Kodrík, D. First comprehensive study of a giant among the insects, *Titanus giganteus*: Basic facts from its biochemistry, physiology, and anatomy. *Insects* **2020**, *11*, 120, doi:10.3390/insects11020120.
- Fischer, S.; Müller, C.H.G.; Meyer-Rochow, V.B. How small can small be: The compound eye of the parasitoid wasp *Trichogramma evanescens* (Westwood, 1833) (Hymenoptera, Hexapoda), an insect of 0.3- to 0.4-mm total body size. *Vis. Neurosci.* **2011**, *28*, 295–308, doi:10.1017/S0952523810000192.
- Perrelet, A. The fine structure of the retina of the honey bee drone. *Z. Zellforsch. mikrosk. Anat* **1970**, *108*, 530–562, doi:10.1007/BF00339658.
- Makarova, A.; Polilov, A.; Fischer, S. Comparative morphological analysis of compound eye miniaturization in minute Hymenoptera. *Arthropod Struct. Dev.* **2015**, *44*, 21–32, doi:10.1016/j.asd.2014.11.001.
- Land, M.F. Visual acuity in insects. *Annu. Rev. Entomol.* **1997**, *42*, 147–177, doi:10.1146/annurev.ento.42.1.147.
- Gutiérrez, D.; Rigosi, E.; Nagloo, N.; O'Carroll, D.; Warrant, E.J. Spatial resolution and optical sensitivity in the compound eyes of two common European wasps, *Vespula germanica* and *Vespula vulgaris*. *J. Exp. Biol.* **2024**, *227*, doi:10.1242/jeb.246670.
- Freas, C.A.; Spetch, M.L. Varieties of visual navigation in insects. *Anim. Cogn.* **2023**, *26*, 319–342, doi:10.1007/s10071-022-01720-7.
- Warrant, E.J.; Kelber, A.; Gislén, A.; Greiner, B.; Ribi, W.; Wcislo, W.T. Nocturnal vision and landmark orientation in a tropical halictid bee. *Curr. Biol.* **2004**, *14*, 1309–1318, doi:10.1016/j.cub.2004.07.057.
- Narendra, A.; Greiner, B.; Ribi, W.A.; Zeil, J. Light and dark adaptation mechanisms in the compound eyes of Myrmecia ants that occupy discrete temporal niches. *J. Exp. Biol.* **2016**, *219*, 2435–2442, doi:10.1242/jeb.142018.

21. Araújo, P.; de Almeida Caetano, C.; Schlindwein, C.; Alves-Dos-Santos, I.; Mota, T. Body size and the architecture of the visual system in crepuscular and diurnal bees. *Biol. J. Linn. Soc.* **2023**, *138*, 328–340, doi:10.1093/biolinnean/blac154. 770
22. Greiner, B.; Cronin, T.W.; Ribi, W.A.; Wcislo, W.T.; Warrant, E.J. Anatomical and physiological evidence for polarisation vision in the nocturnal bee *Megalopta genalis*. *J. Comp. Physiol. A* **2007**, *193*, 591–600, doi:10.1007/s00359-007-0214-1. 771
23. Yagi, N.; Koyama, N. *The compound eye of Lepidoptera: approach from organic evolution*; Shinkyo Press: Tokyo, 1963. 772
24. Fischer, S.; Meyer-Rochow, V.B.; Müller, C.H.G. Compound eye miniaturization in Lepidoptera: a comparative morphological analysis. *Acta Zool.* **2014**, *95*, 438–464, doi:10.1111/azo.12041. 773
25. Yang, X.; Ran, H.; Jiang, Y.; Lu, Z.; Wei, G.; Li, J. Fine structure of the compound eyes of the crepuscular moth *Grapholita molesta* (Busck 1916) (Lepidoptera: Tortricidae). *Front. Physiol.* **2024**, *15*, 1343702, doi:10.3389/fphys.2024.1343702. 774
26. Taylor, G.J.; Tichit, P.; Schmidt, M.D.; Bodey, A.J.; Rau, C.; Baird, E. Bumblebee visual allometry results in locally improved resolution and globally improved sensitivity. *eLife* **2019**, *8*, e40613, doi:10.7554/eLife.40613. 775
27. Jones, B.M.; Seymoure, B.M.; Comi, T.J.; Loew, E.R. Species and sex differences in eye morphometry and visual responsivity of two crepuscular sweat bee species (*Megalopta* spp., Hymenoptera: Halictidae). *Biol. J. Linn. Soc.* **2020**, *130*, 533–544, doi:10.1093/biolinnean/blaa064. 776
28. Kelber, A.; Jonsson, F.; Wallén, R.; Warrant, E.; Kornfeldt, T.; Baird, E. Hornets can fly at night without obvious adaptations of eyes and ocelli. *PLoS ONE* **2011**, *6*, e21892, doi:10.1371/journal.pone.0021892. 777
29. Spiewok, S.; Schmolz, E. Changes in temperature and light alter the flight speed of hornets (*Vespa crabro* L.). *Physiological and Biochemical Zoology* **2006**, *79*, 188–193, doi:10.1086/498181. 778
30. Pichaud, F.; Casares, F. Shaping an optical dome: The size and shape of the insect compound eye. *Semin. Cell Dev. Biol.* **2022**, *130*, 37–44, doi:10.1016/j.semcdb.2021.11.002. 779
31. Cook, J.M.; Rasplus, J.-Y. Mutualists with attitude: coevolving fig wasps and figs. *Trends Ecol. Evol.* **2003**, *18*, 241–248, doi:10.1016/s0169-5347(03)00062-4. 780
32. Su, Z.-H.; Sasaki, A.; Kusumi, J.; Chou, P.-A.; Tzeng, H.-Y.; Li, H.-Q.; Yu, H. Pollinator sharing, copollination, and speciation by host shifting among six closely related dioecious fig species. *Commun. Biol.* **2022**, *5*, 284, doi:10.1038/s42003-022-03223-0. 781
33. Bain, A.; Borges, R.M.; Chevallier, M.H.; Vignes, H.; Kobmoo, N.; Peng, Y.Q.; Cruaud, A.; Rasplus, J.Y.; Kjellberg, F.; Hossaert-Mckey, M. Geographic structuring into vicariant species-pairs in a wide-ranging, high-dispersal plant–insect mutualism: the case of *Ficus racemosa* and its pollinating wasps. *Evol. Ecol.* **2016**, *30*, 663–684, doi:10.1007/s10682-016-9836-5. 782
34. Kjellberg, F.; Jousset, E.; Hossaert-Mckey, M.; Rasplus, J.Y. Biology, ecology, and evolution of fig-pollinating wasps (Chalcidoidea, Agaonidae). In *Biology, ecology and evolution of gall-inducing arthropods*, Raman, A., Schaefer, C.W., Withers, T.M., Eds.; Science Publishers, Inc.: Enfield, New Hampshire, and Plymouth, 2005; Volume 1-2, pp. 539–572. 783
35. Krishnan, S.; Karpe, S.D.; Kumar, H.; Nongbri, L.B.; Venkateswaran, V.; Sowdhamini, R.; Grosse-Wilde, E.; Hansson, B.S.; Borges, R.M. Sensing volatiles throughout the body: geographic- and tissue-specific olfactory receptor expression in the fig wasp. *Insect Sci.* **2025**, *n/a*, doi:10.1111/1744-7917.13441. 784
36. Ware, A.B.; Kaye, P.T.; Compton, S.G.; Noort, S. Fig volatiles: Their role in attracting pollinators and maintaining pollinator specificity. *Plant Syst. Evol.* **1993**, *186*, 147–156, doi:10.1007/bf00940794. 785
37. Grison-Pigé, L.; Hossaert-Mckey, M.; Greeff, J.M.; Bessiere, J.-M. Fig volatile compounds—a first comparative study. *Phytochemistry* **2002**, *61*, 61–71, doi:10.1016/S0031-9422(02)00213-3. 786
38. Borges, R.M. On the air: Broadcasting and reception of volatile messages in brood-site pollination mutualisms. In *Deciphering Chemical Language of Plant Communication*, Blande, J.D., Glinwood, R., Eds.; Springer International Publishing: Cham, 2016; pp. 227–255. 787
39. Hossaert-Mckey, M.; Soler, C.; Schatz, B.; Proffit, M. Floral scents: their roles in nursery pollination mutualisms. *Chemoecology* **2010**, *20*, 75–88, doi:10.1007/s00049-010-0043-5. 788
40. Xiao, J.-H.; Yue, Z.; Jia, L.-Y.; Yang, X.-H.; Niu, L.-H.; Wang, Z.; Zhang, P.; Sun, B.-F.; He, S.-M.; Li, Z.; et al. Obligate mutualism within a host drives the extreme specialization of a fig wasp genome. *Genome Biol.* **2013**, *14*, R141. 789
41. Miao, B. Research on the species divergence and behavior of pollinators associated with *Ficus hispida*. University of Chinese Academy of Science, Beijing, 2024. 790
42. van der Kooij, C.J.; Stavenga, D.G.; Arikawa, K.; Belušić, G.; Kelber, A. Evolution of insect color vision: From spectral sensitivity to visual ecology. *Annu. Rev. Entomol.* **2021**, *66*, 435–461, doi:10.1146/annurev-ento-061720-071644. 791
43. Ohyama, T.; Schneider-Mizell, C.M.; Fetter, R.D.; Aleman, J.V.; Franconville, R.; Rivera-Alba, M.; Mensh, B.D.; Branson, K.M.; Simpson, J.H.; Truman, J.W.; et al. A multilevel multimodal circuit enhances action selection in *Drosophila*. *Nature* **2015**, *520*, 633–639, doi:10.1038/nature14297. 792
44. Fischer, S.; Lu, Z.; Meinertzhagen, I.A. Three-dimensional ultrastructural organization of the ommatidium of the minute parasitoid wasp *Trichogramma evanescens*. *Arthropod Struct. Dev.* **2019**, *48*, 35–48, doi:10.1016/j.asd.2018.12.003. 793
45. Ribi, W.; Engels, E.; Engels, W. Sex and caste specific eye structures in stingless bees and honey bees (Hymenoptera: Trigoniidae, Apidae). *Entomol. Gen.* **1989**, *14*, 233–242, doi:10.1127/entom.gen/14/1989/233. 794
46. Stavenga, D.G. Angular and spectral sensitivity of fly photoreceptors. II. Dependence on facet lens F-number and rhabdome type in *Drosophila*. *J. Comp. Physiol. A* **2003**, *189*, 189–202, doi:10.1007/s00359-003-0390-6. 795
47. Narendra, A.; Alkaladi, A.; Raderschall, C.A.; Robson, S.K.A.; Ribi, W.A. Compound eye adaptations for diurnal and nocturnal lifestyle in the intertidal ant, *Polyrhachis sokolova*. *PLoS ONE* **2013**, *8*, e76015, doi:10.1371/journal.pone.0076015. 796

48. Aepli, F.; Labhart, T.; Meyer, E.P. Structural specializations of the cornea and retina at the dorsal rim of the compound eye in hymenopteran insects. *Cell Tissue Res.* **1985**, *239*, 19–24, doi:10.1007/BF00214897. 829–830
49. Burke, G.R.; Sharanowski, B.J. Parasitoid wasps. *Curr. Biol.* **2024**, *34*, R483–R488, doi:10.1016/j.cub.2024.03.038. 831
50. Barlow, H.B. The size of ommatidia in apposition eyes. *J. Exp. Biol.* **1952**, *29*, 667–674. 832
51. Fischer, S.; Meyer-Rochow, V.B.; Müller, C.H.G. Challenging limits: Ultrastructure and size-related functional constraints of the compound eye of *Stigmella microtheriella* (Lepidoptera: Nepticulidae). *J. Morphol.* **2012**, *273*, 1064–1078, doi:10.1002/jmor.20045. 833–835
52. Huber, J.T.; Noyes, J. A new genus and species of fairyfly, *Tinkerbella nana* (Hymenoptera, Mymaridae), with comments on its sister genus *Kikiki*, and discussion on small size limits in arthropods. *J. Hymenoptera Res.* **2013**, *32*, 17–44, doi:10.3897/jhr.32.4663. 836–838
53. Wang, K.; Wang, J.; Liang, B.; Chang, J.; Zhu, Y.; Chen, J.; Agnarsson, I.; Li, D.; Peng, Y.; Liu, J. Eyeless cave-dwelling *Lep-tonetela* spiders still rely on light. *Sci. Adv.* **2023**, *9*, ead0348, doi:10.1126/sciadv.ad0348. 839–840
54. Yack, J.E.; Johnson, S.E.; Brown, S.G.; Warrant, E.J. The eyes of *Macrosoma* sp. (Lepidoptera: Hedyloidea): A nocturnal butterfly with superposition optics. *Arthropod Struct. Dev.* **2007**, *36*, 11–22, doi:10.1016/j.asd.2006.07.001. 841–842
55. Harrison, R.D.; Rasplus, J.-Y. Dispersal of fig pollinators in Asian tropical rain forests. *J. Trop. Ecol.* **2006**, *22*, 631–639, doi:10.1017/S0266467406003488. 843–844
56. Snyder, A.W. Physics of vision in compound eyes. In *Comparative Physiology and Evolution of Vision in Invertebrates: A: Invertebrate Photoreceptors*, Autrum, H., Ed.; Springer Berlin Heidelberg: Berlin, Heidelberg, 1979; 225–313. 845–846
57. Schwarz, S.; Narendra, A.; Zeil, J. The properties of the visual system in the Australian desert ant *Melophorus bagoti*. *Arthropod Struct. Dev.* **2011**, *40*, 128–134, doi:10.1016/j.asd.2010.10.003. 847–848
58. Hunt, E.R.; Dornan, C.; Sendova-Franks, A.B.; Franks, N.R. Asymmetric ommatidia count and behavioural lateralization in the ant *Temnothorax albipennis*. *Sci. Rep.* **2018**, *8*, 5825, doi:10.1038/s41598-018-23652-4. 849–850
59. McLeman, M.A.; Pratt, S.C.; Franks, N.R. Navigation using visual landmarks by the ant *Leptothorax albipennis*. *Insectes Soc.* **2002**, *49*, 203–208, doi:10.1007/s00040-002-8302-2. 851–852
60. Dahake, A.; Stöckl, A.L.; Foster, J.J.; Sane, S.P.; Kelber, A. The roles of vision and antennal mechanoreception in hawkmoth flight control. *eLife* **2018**, *7*, e37606, doi:10.7554/eLife.37606. 853–854

Disclaimer/Publisher’s Note: The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content. 855–857