

Consequences of Extreme Miniaturization: The Ultrastructure of the Compound Eyes of a 0.65 mm Long “Three-Eyed” Gall Midge (Diptera; Cecidomyiidae)

Folgen einer extremen Miniaturisierung:
die Ultrastruktur des Facettenauges einer 0,65 mm langen
„dreiäugigen“ Gallmücke (Diptera; Cecidomyiidae)

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Summary: Cecidomyiid midges of the genera *Trisopsis* and *Lestodiplosis* possess three compound eyes. The single dorsal compound eye of our only 0.65 mm long cecidomyiid specimen contained 90 ommatidia and represented the fusion product of left and right dorsal moieties jointly covering an area at the top of the head of 7000 μm^2 . Each of the two latero-ventral compound eyes on either side of the head consisted of approximately 35 ommatidia that did not differ anatomically from those of the dorsal eye (with the exception of the interommatidial angles, which measured 10-12° and were thus much smaller than those of the dorsal eye). The retinal layers of both the dorsal and the two lateral eyes were extraordinarily thin, only measuring approximately 12 μm , but all ommatidia were capped by 8 μm thick and 8-10 μm wide corneal lenses with a dense and regular coverage of 160 nm high corneal nipples. Despite being a species of the order Diptera, for which open rhabdoms with non-connected rhabdomeres are characteristic, our tiny cecidomyiid possessed the fused type of rhabdom. The microvilli were of usual width for insect eyes, i.e. 65 nm in diameter. It is postulated that despite the reduction in body and eye size, microvilli could not be scaled down and rhabdomeres, too, had already reached their functional cross sectional limit of 1.5-2.0 μm in Diptera the size of *Drosophila*. A further reduction would have rendered the rhabdom ineffective as a waveguide. As the tiny insect was a swift flyer and on the basis of the eye's anatomy it is discussed what the insect could possibly see with its tiny eyes.

Keywords: Scaling, apposition eye, open rhabdom, insects, vision, photoreception

Zusammenfassung: Cecidomyiiden der Gattungen *Trisopsis* und *Lestodiplosis* besitzen drei Facettenaugen. Das unpaare dorsale Auge einer nur 0,65 mm langen Cecidomyiide mit 90 Ommatidien stellt das Fusionsprodukt der dorsalen Hälften der Augen auf beiden Seiten des Kopfes dar und bedeckt eine Fläche von 7000 μm^2 . Jedes der latero-ventralen Facettenaugen besteht aus 35 Ommatidien, die sich anatomisch nicht von denen des Dorsal Auges unterscheiden (außer dass ihre Interommatidialwinkel mit 10-12° viel schmäler als die des Dorsal Auges sind). In beiden Fällen sind die Retinae nur 12 μm dick, aber alle Ommatidien besitzen 8 μm dicke corneale Linsen mit Durchmessern von 8-10 μm und einer dichten Beschichtung mit 160 nm hohen „Nippeln“. Trotz ihrer Zugehörigkeit zur Ordnung der Diptera, deren Charakteristika sogenannte „offene Rhabdome“ sind, besitzt unsere winzige Cecidomyiide ein geschlossenes Rhabdom mit den für Insektenaugen typischen 65 nm Mikrovillositäten. Es ist anzunehmen, dass eine Reduktion der Mikrovilli und Rhabdomere trotz Habitus- und Augenminiaturisierung nicht stattfinden können, weil mit einem Durchmesser von 1,5-2,0 μm der Rhabdomere ein Grenzwert schon für Dipteren wie *Drosophila* erreicht wurde; dünnere Rhabdome können nicht als Lichtleiter fungieren. Der schnelle Flug des kleinen Insekts macht ein Sehvermögen wahrscheinlich; auf Basis der anatomischen Daten wird diskutiert, wozu die Augen dieses Insekts visuell in der Lage sein sollten.

Schlüsselwörter: Reduktion, Appositionsauge, offenes Rhabdom, Insekten, visuelle Wahrnehmung, Photorezeption

1. Introduction

It is certainly not very common to publish a scientific article based on a single specimen representing a species that cannot be identified. However, there are cases in which this can be justified and is acceptable. And this is one of them.

Miniaturization in insects has intrigued researchers for a long time, but it has only recently begun to be approached seriously (POLILOV 2016) and, as MINELLI & FUSCO (2019) so aptly pointed out, miniaturization has led to “design innovations that allow evolutionary change to evade the limits posed by scaling laws”. With regard to compound eyes of insects, BARLOW (1952) concluded that there had to be a lower limit of functional miniaturization and that ommatidial diameters smaller than about 8-10 μm should not be expected to occur. Although he was wrong about this in relation to ommatidial or facet sizes, because some as small as 6 μm have been reported by MAKAROVA et al. (2019) for the smallest ptiliid beetles and by FISCHER et al. (2011) for the tiny wasp *Trichogramma evanescens*, he was certainly correct in a more general sense with regard to his comment of a size limit of miniaturized structures imposed by functional (and I might add physical or stereochemical) constraints.

Individual ommatidia of an insect's compound eye are anatomically surprisingly uniform (HARZSCH & HAFNER 2006; ANONYMOUS 2019) and are basically always composed of a) the dioptric system (i.e. the cuticular corneal facet with a group of four cone cells underneath), and b) the proximally placed retina, which comprises ommatidial clusters of a number of photoreceptive cells (frequently, but not necessarily, eight and termed retinula cells: WERNET et al. 2015) that possess a fringe of fingerlike, narrow processes known as microvilli. The latter contain the photopigment and collectively give rise to the axial

rhabdom. To complete this basic design of a compound eye, dark ommochrome-type screening pigment granules are present in special pigment as well as the retinula cells and serve to shield neighbouring ommatidia to prevent unwanted “leakage” of light from one ommatidium to another and to protect cells and their organelles from being damaged by dangerously high levels of photic radiation. Variations of this basic design do occur and have to be seen as evolutionary consequences of a taxon's life style and activity maximum, sexual dimorphism and environment (GOKAN & MEYER-ROCHOW 2000; MEYER-ROCHOW 2008). The major distinction between superposition eyes (common in nocturnal species of, for example, Neuroptera, Trichoptera, Lepidoptera and Coleoptera) and apposition eyes (present in predominantly diurnal species, in which dioptric apparatus and retinula cells are not separated by a wide clear-zone devoid of screening pigments as in the superposition design) was first described by EXNER in 1891 and is still accepted today. However, the overall anatomical organization of both of these compound eye types conforms to the basic design description given above.

Based on ultrastructural investigations of the rhabdoms of various very small species of insects (MEYER-ROCHOW & REID 1996; HONKANEN & MEYER-ROCHOW 2009; FISCHER et al. 2011, 2012a,b, 2014; MAKAROVA et al. 2015, 2019), it was noticeable that the rhabdom's individual microvilli housing the photopigments were not correspondingly reduced and appeared to be of a rather ubiquitous 55-75 nm diameter irrespective of the insect's body size. This held true even for the microvilli in the eyes of very small collembolans (PAULUS 1972; MEYER-ROCHOW et al. 2005). A similar situation appear to be the diameters of the compound eye's screening pigment granules, for they usually range between 0.3 and 1 μm in diameter and very much smaller ones simply do not occur. This does, of course, pose the question why

these structural elements of a compound eye cannot become further scaled down, even in eyes with severely reduced facet sizes, ommatidial diameters and even to some extent the nuclei (although with regard to the latter, positional adjustments within the ommatidium have been reported to offset the impossibility of infinite reduction: FISCHER et al. 2011).

Rhabdoms, being the structures that capture the impinging photons and start the cascade of photoreception, are of particular interest and there certainly is a trend of bigger insects possessing wider and more voluminous rhabdoms than smaller species. The limit of a rhabdom's diameter is governed by its functional properties: as a structure to operate like a lightguide, its diameter cannot be considerably smaller than about 2 μm (SNYDER 1979; WARRANT & MCINTYRE 1993), because otherwise part of the propagated light has to travel outside the waveguide. This would explain why almost all of the miniature moths (HONKANEN & MEYER-ROCHOW 2009; FISCHER et al. 2012a,b 2014), miniature beetles (MAKAROVA et al. 2019) and even the tiniest of wasps like *Megaphragma mymaripenne* of a body size of 0.2 mm (MAKAROVA et al. 2015) possessed rhabdoms with diameters not smaller than 2 μm . There are, however, exceptions: the tiny wasps *Trichogramma evanescens* (FISCHER et al. 2009) and *Anaphes flavipes* (MAKAROVA et al. 2015), both less than 0.5 mm long, were reported to possess rhabdom diameters of 1.67 and 1.4 μm , respectively.

It was suggested by MEYER-ROCHOW (2015) in this context that perhaps the most interesting rhabdoms to be examined in view of functional miniaturizations would be those of minute dipteran species. The reason being that a characteristic feature of Diptera were their so-called open rhabdoms that embryologically develop from fused rhabdoms (WOLFF & READY 1993; READY 2002; MEYER-ROCHOW & YANG 2004; MAHATO et al. 2018). In these kinds of rhabdom the mi-

crovillar fringes of the retinula cells do not in the adult come centrally together to form a columnar axial waveguide structure in the centre of the ommatidium, but remain separated from each other (as so-called rhabdomeres) by gaps of inter-rhabdomeral spaces. In the typical dipteran rhabdom, exemplified by that of the eye of *Drosophila* but equally apparent so also in much larger species, six rhabdomeres form an open ring surrounding the two rhabdomeres of retinula cells 7 and 8 arranged in a tandem formation with rhabdomere 7 above that of number 8 in the centre (cf. MEYER-ROCHOW & WALDVOGEL 1979). Open rhabdoms such as these owing to complex interactions between groups of seven neighbouring ommatidia (KIRSCHFELD 1967; HORRIDGE & MEINERTZHAGEN 1970) are believed to be particularly good at reacting to movement, but what is interesting in view of miniaturization is that the diameters of the individual rhabdomeres are already close to the limit of 2 μm , below which they should not be able to function as waveguides (SNYDER 1979; WARRANT & MCINTYRE 1993). Therefore, the pressing question was what the retinulae and rhabdomeres of the tiniest dipterans would look like, given that even large Diptera contain in their compound eyes photoreceptive elements that would lose their ability to effectively propagate light if these photoreceptive elements were to be scaled down and reduced to below 2 μm in diameter. Fused rhabdoms are present in many aerobically competent and large insects like Odonata and Hymenoptera, but being “stuck” with the open rhabdom design characteristic of Diptera generally should pose a real dilemma to the smallest of the dipteran species as rhabdomere sizes had reached their lower functional size limit already in the larger dipteran species. The smallest known fly measures a mere 0.4 mm in body length (BROWN 2012), but it has reduced eyes, and therefore our cecidomyiid (this paper) will be the smallest dipteran that has had its eyes examined.

2. Material and methods

The senior author of this paper, working on his laptop at midnight on the Japanese Pacific island of Hachijojima during the summer of 2018, noticed a tiny insect repeatedly flying against the bright screen of his computer. When a first attempt to capture the fast flying mini-insect failed, the room light was switched off in the hope that the little critter would settle on the computer screen once again. That did happen indeed and ultimately a small glass tube, handily placed on the desk for exactly these kinds of unexpected event, was placed over the small insect. The moment it had entered the tube a sheet of paper was pushed between computer screen and glass tube, which was then capped and put into the freezer for some minutes to kill the insect. The dead insect was briefly examined under a stereomicroscope and identified not as a small wasp (as initially assumed) but a dipteran species, which on account of its extremely rapid and directional flying modus made total sense.

Then, still during the same night, the small dipteran was put into pre-fixative solution, which was always kept for such events in the fridge (for chemical details see further below). The glass tube with the insect was then posted to the co-author of the paper at Hamamatsu Medical University, where the insect was photographed and further processing took place. Unfortunately because of the distance and flight connections between Hachijojima Island and Hamamatsu on the mainland it took about three days before the specimen reached Hamamatsu and the first close-up photographs could be taken and further processing could commence.

On the basis of these photos the cecidomyiid specialist Dr. MATHIAS JASCHHOF concluded that in all likelihood the insect represented a member of either the genus *Trisopsis* or *Lestodiplosis*, both of which known to contain “three-eyed” species of around

1 mm body lengths or smaller. Our individual measured (outstretched and with the 0.08 mm long head slightly pushed forward and severed from the remaining thorax) 0.76 mm (head plus rest of the body), but the live and intact animal would more likely have had a total body length of 0.65 mm or even smaller, which would make it one of the smallest species of the genera mentioned above. Since cecidomyiid flies generally and *Trisopsis* and *Lestodiplosis* species in particular are for a non-expert not always easy to sex and to differentiate at generic level (JASCHHOF, personal communication), but both genders are known to possess the fused dorsal eyes and separate latero-ventral eyes, we have reason to assume that there would not have been significant differences between the eyes of males and females. Japanese experts to whom photos of the insect were shown could not identify the species and thought it likely that it represented a new species, but that more specimens would be required to confirm this. What is known, however, is that species of the genera *Trisopsis* and *Lestodiplosis* possess carnivorous larvae that feed on collembolans, mites and other microarthropods (REGUZZI & CHIAPPINI 2013).

For the ultrastructural examination of the insect's eyes the specimen was prefixed in a 2% glutaraldehyde/2% paraformaldehyde mixture in 0.1M cacodylate buffer (pH 7.2) for three days (but kept in the refrigerator only for the first night). The protocol that followed was essentially the same that had been used by MEYER-ROCHOW & YAMAHAMA (2017) before. The specimen was rinsed three times in cacodylate buffer, then post-fixed for 2 h in 1% in OsO_4 in cacodylate buffer, dehydrated in a graded series of ethanol, passed through propylene oxide twice for 15 min and finally embedded in Epon via five steps of propylene oxide/Epon concentrations. Polymerization occurred over 2 days at 60 °C. Ultrathin sections for electron microscopy were cut with a dia-

mond knife on a Leica UC-7 ultramicrotome and deposited on one-hole, formvar-coated copper mesh grids. Double-staining with uranyl acetate for 5 min and lead citrate for 3 min completed the protocol before the sections were observed at a voltage of 100 kV under a Jeol 1400plus transmission electron microscope.

3. Results

The defining feature of our cecidomyiid is its head with its three compound eyes (Fig. 1 a-e). Unlike the vast majority of Diptera, which possess a single compound eye on either side of the head, albeit with an equator running through it between dorsal and ventrally located ommatidia, our cecidomyiid's compound eyes have split into two physically separate components: a) the dorsal ones have turned into a single dorsal compound eye of approximately 90 ommatidia due to the fusion of the left and right compound eye moieties that together cover an area of at least 7,000 μm^2 , and b) the latero-ventral components that collectively cover an area

of around 6000 μm^2 on either side of the head and are separated by a facet-free gap from the dorsal eye of at least 0.025 μm . The latero-ventral compound eyes consist of approximately 35 ommatidia each.

Facet sizes, shapes and the diameters of the corneal lenses vary little between latero-ventral (Fig. 2a) and dorsal facets (Fig. 3a, b). corneal lenses possess an outer surface diameter of close to 10 μm , but on account of their mushroom-like shapes approximately 3 μm below the corneal apices the diameters of their columnar region only measure 8 μm . Thus, each lens basically resembles a 8 μm thick bi-convex lens with a somewhat wider top (= distal) than bottom (proximal) surface. The corneal lenses are not closely fitting together and gaps a few microns wide separate neighbouring facets from each other that are seemingly rising above the eye's inter-ommatidial cuticle around them. The surfaces and even the sides of the lenses are covered by very regularly spaced corneal nipples, 160 nm in height and 75 nm in width, separated by nipple-to-nipple tip distances of approximately 200 nm between them. This holds true

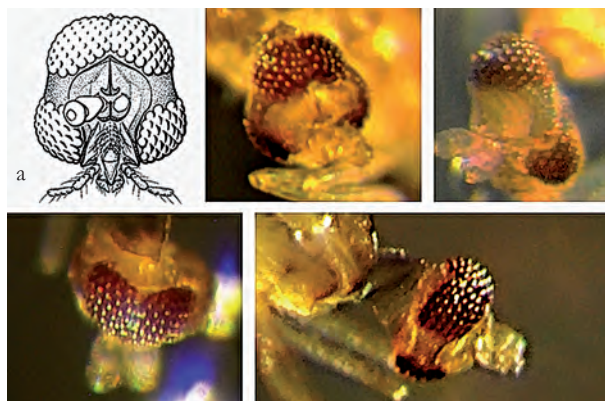


Fig. 1: a Drawing of the head of a male *Trisopsis* sp. (after GAGNÉ 1981), showing the two latero-ventral compound eyes (one on either side of the head) and the single dorsal compound eye as a fusion product of left and right eyes. b-e Close-up photographs of the head of this paper's cecidomyiid viewed from various angles.

Abb. 1: a Kopf einer männlichen *Trisopsis* sp.-Gallmücke (Zeichnung nach GAGNÉ 1981) mit den beiden latero-ventralen Facettenaugen und dem aus der Fusion des linken and rechten Auges hervorgegangenen unpaaren dorsalen Facettenauge. b-e Nahaufnahmen aus verschiedenen Richtungen vom Kopf der in dieser Arbeit untersuchten Cecidomyiide.

for the latero-ventral (Fig. 2b) as well as dorsal ommatidia (Fig. 3c,d). The striations seen in longitudinally sectioned lenses are evidence of growth layers and concavely aligned with respect to the cornea's outer convexly curved surface (Fig. 2d).

Ommatidial lengths from outer corneal surface to basement membrane vary only between 18–20 μm for the latero-ventral eyes (Fig. 2a) and 16–18 μm for the dorsal eye (Fig. 3a). In some places with respect to both kinds of eye, half of the ommatidium's length is occupied by the bulky corneal lens, restricting the retina to a relatively shallow layer of not more than approximately 12 μm wide. The dorsal eye with a radius of curvature of 0.5 mm for the eye as a whole (and not its constituent individual ommatidia) is considerably more strongly curved than the lateral eyes are and the respective interommatidial angles of 30° and 11° are a reflection of this. Just beneath the lens' proximal cuticle a thin cytoplasmic circumferential 'collar' is visible (Fig. 1a, 3b) that appears to represent a distal extension of the primary pigment cells that are usually present in all compound eyes in this region of the compound eye. Another regular component of the ommatidial architecture are cone cells, four in number, that usually supplement the cornea as dioptric elements on the former's proximal side. Cone cell nuclei are present also in our material (Fig. 1d, but there is no hint of any crystalline cone or cluster of the four cone cells. It appears as if the rhabdoms of individual ommatidia are being pushed as close as possible to the underside of the corneal lenses with any ever so thin or even no cytoplasmic layer at all interposed between corneal lens and microvilli of the rhabdom (Fig. 2d).

No inter-rhabdomeral spaces are present and each rhabdom represents a centrally-fused structure of about 2.5 μm in diameter. The bulk of the rhabdom is formed by the rhabdomeres of six retinula cells, but a seventh and eighth most proximally located

retinula cell may contribute some microvilli to the rhabdom (Fig. 3e) just above the basement membrane, i.e. a thin layer of pigmented cells with perforations for the retinula cells' axons on the proximal side of the retinal layer. Given that the retinal layer is so narrow, the retinula cell nuclei, measuring approximately 2 μm in diameter, have to be accommodated in the 10–12 μm long retinula cells. Some nuclei can be identified in the distal retinula cell cytoplasm (Fig. 2c), but others and most likely those of retinula cells 7 and 8 are mainly positioned below the rhabdom on the proximal side of the retina (Fig. 3e). Microvilli of an approximate diameter of 65 nm are identifiable in the rhabdoms, but special arrangements or preferred directions are not discernable. Their rather loose organization suggests that they might have sustained some light-induced stress and the position of the retinula cells' screening pigments, too, indicates that the eyes must have become light-adapted (MEYER-ROCHOW 1999) during the insect's repeated attempts to fly into the bright computer screen.

Screening pigment granules, stained black, are surprisingly abundant in the shallow retinae of the dorsal and the two lateral eyes. Although their shapes vary and those in retinula cells may generally be of the smaller kind and often elongated, reaching lengths of up to 0.8 μm , the most spherical and largest granules with a maximum diameter of 0.8 μm were present close to the corneal lenses of the lateral eyes. Most likely they belonged to the two primary pigment cells common in all compound eyes. A narrow band of screening pigment containing cells was present immediately above the basement membrane (Fig. 2a, 3b) seemingly shielding the tissue on the proximal side of the membrane against radiation.

4. Discussion

The presence of a head of barely 0.1 mm in height and width and even less in depth

(anterior-posterior extent) with three clusters of facets arranged as two latero-ventral and one dorsal compound eye (and thereby occupying a considerable area of the head's surface) suggests that photoreception has to have a function in the life of this tiny insect. The fact, moreover, that it flew around at night, was attracted to the bright light of a computer screen and on several occasions evaded capture shows that it can see, uses its eyes and is apparently nocturnal. Whether other “three-eyed” cecidomyiids of the genera *Trisopsis* and *Leptodiplosis* are also predominantly nocturnal and attracted to bright surfaces is unfortunately not known, although an unidentified species of *Trisopsis* studied by REGUZZI & CHIAPPINI (2013) has been reported to be captured in large numbers with light traps.

The fact that our cecidomyiid was an agile, fast-flying miniature insect is noteworthy as it has long been held that small insects often have feathery or oar-like wings (KUE-THE 1975) to fly with and mate in a viscous medium (CROMPTON et al., 2003). It seems that small fast-flying insects employ a wing-flapping and drag system “to generate the weight-supporting vertical force” (CHENG & MAO, 2018). To fly without an adequate visual capability simply wouldn't make sense, which suggests that the three compound eyes of our cecidomyiid are necessary and important sensors in the life of this insect when airborne.

The observed facet sizes agree with the functional limit of a diameter of around 10 μm as predicted by BARLOW (1952), but there are two features that make the ommatidial corneae stand out. Firstly, the corneae are extraordinarily thick for an eye with a retina only about 12 μm thick and one is reminded of the telescopic lenses commonly seen in the eyes of mesopelagic fishes, species that exist in the twilight zone of the oceans (MARSHALL 1971). It almost seems as if the very thick corneae in the eye of our tiny cecidomyiid specimen represent omma-

tidial telescopic lenses that have replaced the functional unit of cornea plus cone, an arrangement that is standard in the eyes of larger insects. The concave bands visible across longitudinally sectioned corneae are artefactual growth layers of the corneal cuticle described in detail by BOULIGAND (1965). Although on anatomical evidence alone it is therefore not possible to conclude that a radial refractive index with higher central and lower peripheral values occurs in the cornea to increase the angle over which light can be channelled into the ommatidium, it is nevertheless conceivable that there is such a gradient, for radial refractive index gradients in the dioptric structures have been reported from some compound eyes as early as 1886 by EXNER and were later confirmed by several others using interference microscopy (e.g., SEITZ 1969; MEYER-ROCHOW 1973).

Many of the corneal lenses appear mushroom shaped with a convexly curved umbrella and straight, approximately 8 μm wide, “stems”. These shapes could possibly be fixation artefacts indicative of some shrinkage and suggesting that the corneal lenses would not have consisted of hard cuticular material. On the other hand the unusual shapes of the corneal lenses are so common and uniform in both dorsal and lateral eyes, featuring an inner peripheral darker staining shell just below the cuticular surface that could function as a stabilizer, so that the observed mushroom-like shapes might represent a genuine adaptation to increase the amount of light capable of entering the ommatidium.

Secondly, there are well developed and regularly spaced corneal nipples on the corneal surfaces of both lateral eyes and the dorsal compound eye. Although these nipples with a height of 160 nm seem very slightly less efficient as a broadband anti-reflection device to enable more light to enter the eye by reducing the reflected component than what DEWAN et al. (2012) have concluded with regard to an optimal height of the

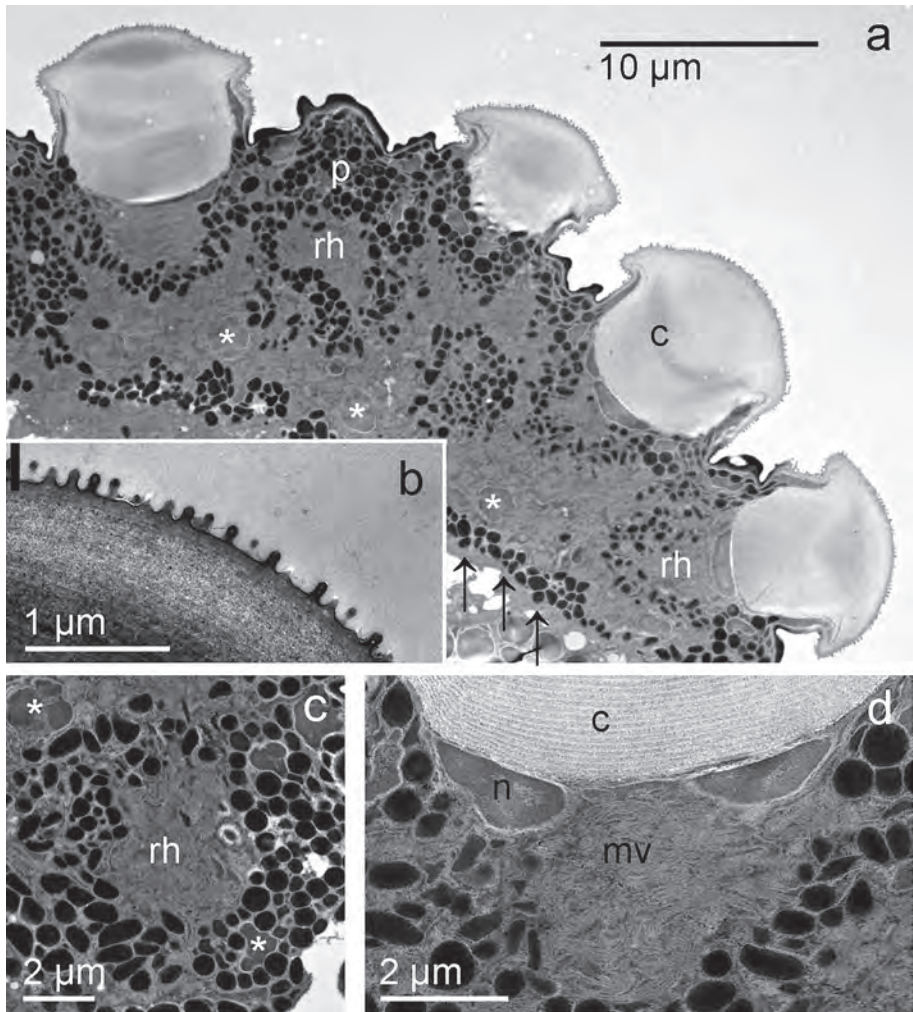


Fig. 2: Transmission electron micrographs of sections through this paper's cecidomyiid's lateral eyes. **a** Longitudinal section through the left lateral eye with corneal lens (C), rhabdom (Rh), screening pigment granules (P) and retinula cell nuclei (white asterisks) clearly visible. The arrows point to the basement membrane. **b** Corneal nipples on the surface of the corneal lens longitudinally sectioned. **c** Group of six retinula cells with fused rhabdomeres forming a centrally placed, axial rhabdom (Rh) surrounded by electron-opaque retinula cell screening pigment granules. White asterisks denote retinula cell nuclei. **d** Two flat nuclei of cone cells (N) beneath the corneal lens (C) are noticeable and the rhabdom's microvilli (mv) can be seen in close contact with the underside of the corneal lens.

Fig. 2: Elektronenmikroskopische Fotos von Schnitten der latero-ventralen Augen der in dieser Arbeit untersuchten Cecidomyiide. **a** Längsschnitt durch das linke lateral-ventrale Auge, die corneale Linse (C), Rhabdome (Rh), Schirmpigmentgrana (P) und Retinulazellkerne (weiße Sternchen) zeigend. **b** Corneale, als Nippels bezeichnete Oberflächenstrukturen im Längsschnitt. **c** Gruppen von 6 Retinulazellen mit geschlossenem zentralem Rhabdom, umgeben von elektronendichten Pigmentgranula der Retinulazellen. Weiße Sternchen weisen auf die Retinulazellkerne hin. **d** Zwei flache Zellkerne der Kristallkegelzellen (N) sind unterhalb der Cornea (C) ebenso erkennbar wie die Mikrovilli (mv) des Rhabdoms auf der Unterseite der Cornea.

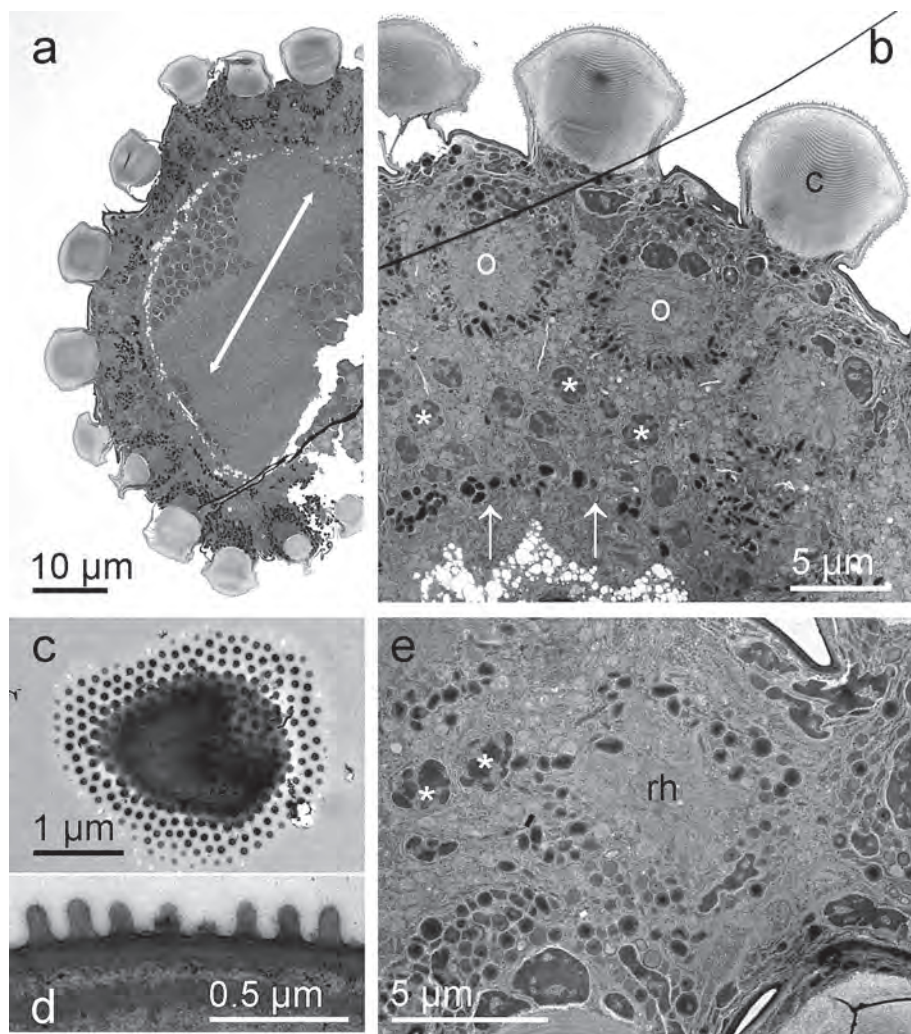


Fig. 3: Transmission electron micrographs of sections through this paper's cecidomyiid's dorsal eye. **a** Longitudinal section through the area of left and right compound eyes' fusion (double arrow) at the apex of the head. **b** Oblique section through the distal retinal region with corneal lenses (C) and transversely cut rhabdoms (white circles) as well as retinula cell nuclei (white asterisks) clearly visible. The white arrows point to a layer of screening pigment just above the basement membrane. **c** Transversely cut corneal nipples. Note the constant nipple diameters and inter-nipple distances. **d** Longitudinally-sectioned corneal nipples and outermost epicuticular layer of the corneal lens identifiable. **e** Transversely-sectioned fused rhabdom (Rh) formed at this level by seven retinula cells with some nuclei visible (white asterisks).
Fig. 3: Elektronenmikroskopische Fotos von Schnitten des dorsalen Auges unserer Cecidomyiide. **a** Längsschnitt durch die Region der linken und rechten Augenteile, die an der Spitze des Kopfes zusammenstoßen. **b** Schrägschnitt durch die distale Augenregion mit Corneallinse (C) und Rhabdomen (weiße Kreise) sowie Retinulazellkernen (weiße Sternchen). Die Pfeile weisen auf die Basalmembran hin. **c** Querschnitt durch die cornealen Nippel: Bemerkenswert sind der konstante Durchmesser letzterer sowie deren einheitlicher Abstand zueinander. **d** Längsschnitt durch die cornealen Nippel und die darunter liegende Epikutikula. **e** Querschnitt durch das geschlossene Rhabdom (Rh), welches auf dieser Schnittebene von 7 Retinulazellen gebildet wird. Retinulazellkerne sind durch weiße Sternchen gekennzeichnet.

nipples of 200 nm, those of our cecidomyiid nonetheless can be expected to increase the amount of light admitted into the eye, especially light of shorter wavelengths like the ultraviolet radiation of the spectrum. The fact that these nipples also occur on the sides and not just the upper surface of the corneal lens is difficult to explain, but if the nipples favour admission of UV-wavelengths and given Diptera generally are known to be UV-sensitive, it would make sense to cover as large a surface of the cornea as possible with these nipples. In any case, the absence of a tracheal tapetum behind the retina suggests that the prevention of ghost images created by light bouncing off the tapetal mirror, an idea championed by MILLER (1979) for the corneal nipples of the eyes of moths, could not have been the reason for the nipples on the corneal surfaces and sides of our cecidomyiid.

Although some flat cone cells are apparently present with their nuclei being clearly visible below the cornea, the peripheral position of these cells and their small sizes allows the light-sensitive rhabdom to contact the underside of the corneal centre with only a very thin, if at all, cytoplasmic layer of cone cells separating the rhabdom from the cornea. A situation such as this has been described for the first time by MEYER-ROCHOW (1975) to occur in the eye of a minute *Corylophodes* beetle, a species not exceeding a body length of 0.9 mm. Although not accompanied by any illustrations the latter study by MEYER-ROCHOW (1975) was the first ever in which the eyes of any insect species smaller than 1 mm body length were examined by transmission electron microscopy. With a distance from the inner surface of the cornea to the basement membrane of just 10–12 μm in the eye of our cecidomyiid, there simply is not a great deal of space to accommodate cone cells above the retinula cells with their rhabdoms. In order to create the necessary space the head would have had to be of a bigger size. As the retinal

layer of all three eyes in our cecidomyiid is already very thin (compared with that of larger species) any further shortening of an ommatidial rhabdom's length to create space for cone cells would, in turn, have the consequence of an even more severely compressed rhabdom, fewer microvilli (as the latter cannot apparently be made much smaller than about 50 nm in diameter), and therefore less photopigment overall and of ultimately reduced visual sensitivity.

To escape from this dilemma in the face of needing to possess photoreceptive structures capable of capturing sufficient photons to see by, small dipterans, burdened by the evolutionary heritage of an open rhabdom, had to modify their rhabdoms. A typical and efficient adaptation, seen also in the eye of the small Antarctic wingless midge *Belgica antarctica* (MEYER-ROCHOW & REID 1996) and other dipterans having to see in conditions of low light levels (MEYER-ROCHOW & WALDVOGEL 1979; LAND & HORWOOD 2005), is to bring the open rhabdomeres closer together, especially their distal tips, and to create a rhabdom in which the six outer rhabdomeres form a fused ring (see also WIJNGAARD & STAVENGA 1975 on discussing optical crosstalk between neighbouring rhabdomeres in such a situation). When the two central rhabdomeres of retinula cells 7 and 8 also join in and the inter-rhabdomeral space that separates the outer from the central rhabdomeres disappears, a rhabdom not unlike that of species of other insect orders like those, for example, of Hymenoptera, Orthoptera, Plecoptera and many others results.

Reversals of evolution according to Dollo's law (DOLLO 1893) are not possible, but atavisms, on the other hand, representing a re-awakening of suppressed genetic information do occur and have been linked with evolutionary change (TOMIC & MEYER-ROCHOW 2011). It would seem as if the cecidomyiid had reverted to an ancestral retinal structure by halting the increasing vacuolization that culminates in the spaces that separate indi-

vidual rhabdomeres from each other in the open dipteran rhabdom (MEYER-ROCHOW & YANG 2004). Joint rhabdomeres forming a fused rhabdom of a diameter greater than 2 μm would allow the rhabdom to function as a waveguide structure and to be able to interact with more photons under poor light conditions than an open rhabdom is capable of. That the eye reverted to the fused rhabdom of largely diurnally active insects is not surprising as also the more efficient superposition eye with its clear-zone and particular dioptric and light perceiving structures is thought to have evolved from a fused rhabdom-bearing ancestor as well (MEINERTZHAGEN 1991; MAHATO et al. 2018).

Pigment granules are highly conservative organelles in the compound eyes of insects and it is therefore not totally surprising to find that some granules in the eye of our tiny cecidomyiid measured up to 0.8 μm in diameter, although diameters of around 0.3-0.5 μm were most commonly encountered. As sections of spherical pigment granules need not necessarily go through the centre of these granules, recording smaller diameters can be misleading as they could represent slivers off the bigger grains. The eyes of the live insect were dark and the amount of screening pigments in the compound eyes is considerable. Obviously the eye is in need to shield vulnerable structural elements to prevent them from getting damaged and it uses ommatidial pigment sleeves to insulate neighbouring ommatidia. The layer of screening pigments along the basal lamina would reduce light not captured by the rhabdom; light that could penetrate deeper into the eye, reach and damage brain cells, something that seemingly should not occur.

What can our tiny cecidomyiid possibly see with its small compound eyes? A look at the eyes of other, much larger Diptera shows us firstly that body size rather than mere allometry, at least for *Chrysomyia megacephala*, explains activity in low light (SMITH et al.

2015) and secondly that a feature to possess separate dorsal and ventral compound eye moieties with mirror image internal organization exists in many species and that an equator separates the dorsal from the ventral ommatidia (MEINERTZHAGEN 1972; WOLFF & READY 1993; AGI et al. 2014). The two regions may display different coloration, possess facets of unequal sizes and in a few cases have evolved into physically divided compound eyes (COLLESS & MCALPINE 1991). However, while in the larger dipteran species facets located on the dorsal surface of the eye were usually bigger than those located more ventrally (STAVENGA et al. 1990), size differences between dorsal and lateral eyes were either absent or too small in our cecidomyiid to be noticed.

In larger species of flies the region of the eye with the biggest facets faces the sky. Almost certainly this leads to greater absolute sensitivity to light, but not necessarily to a higher resolution, the latter depending on smaller acceptance and interommatidial angles. With relatively large interommatidial angles and their thick and convexly bulging corneal lenses, the fused single dorsal compound eye of our cecidomyiid can be expected to possess a visual sensitivity that helps the insect to distinguish objects of different luminosity, especially when we consider that during the flight the head is slanted downward and the dorsal eye points forward. The latero-ventral eyes with lenses of similar dimensions to those of the dorsal eye are also likely to be mainly involved in detecting luminosity changes as their acuity cannot possibly allow them to see any great details even if their interommatidial angles are half as wide as those of the dorsal eye. Both dorsal and latero-ventral compound eyes, however, may possess high flicker fusion frequencies (FFF) as it has been shown that aerobically competent species possess higher FFFs than slow flying or wingless insects (CAMPAN et al. 1965). Stereoscopic vision, on the other hand, would require a

pair of eyes physically separated from each other, but with overlapping visual fields. As this is not the case in our cecidomyiid, it would therefore rule out the single dorsal compound eye as a device to estimate distance (unless parallax were involved: WALLACE 1959; HORRIDGE 1977b) and most likely the latero-ventral eyes as well, since their visual overlap is minimal and possible only in a downward direction. Although interommatidial angles of the latero-ventral eyes are half as wide (or even narrower still) than those of the dorsal eye, acuity can be expected to be extremely poor and probably similar to that of the eyes of the 2 mm long psocopteran *Psyllipsocus ramburi* (MEYER-ROCHOW & MISHRA 2007), although somewhat better than that of the dorsal eye. Equations, given in LAND (1981), like those for the F-number of an optical system exist ($F = f/D$, where f is the focal length of the system and D the diameter of the lens), and an examination of visual axes in apposition eyes (HORRIDGE 1978) allows one to estimate the brightness that the system delivers. The resolution can be calculated according to $R = r/D_{om}$, where r = local optical radius and D_{om} is the functional diameter of the corresponding ommatidium and the eye parameter 'p' is the product of D_{om} and $\Delta\Phi$, where $\Delta\Phi$ is expressed as the product of D_{om} and r_{rad} . The angle over which a rhabdom can effectively capture light ($\Delta\Omega$) is accessible by this equation: $\Delta\Omega = D_{rh}/f$ where D_{rh} is the diameter of the rhabdom and f the focal length. However, without reliable data for the corneal lens' and other eye tissue's refractive index distribution, it is difficult to come up with an accurate estimate for the focal plane let alone focal point. The thick and possibly optically not totally homogeneous corneal lens of our cecidomyiid fly complicates matters further. What can, however, give us at least a rough estimate of the F number and the eye parameter, is to assume that the focal point should not be too far behind (or in front of) the rhabdom

layer. Whether the corneal lenses of the eye of our cecidomyiid can achieve this is guesswork, but if this did occur and the focal point were to lie somewhere within the retinal layer, then the eye could operate with an F number of close to 1 and thereby make maximum use of the available dim light at night. The corresponding eye parameter according to HORRIDGE (1977a, b) would be 5 for the dorsal eye and approximately 2.5 for the latero-ventral eyes, highlighting the extraordinary sensitivity of the dorsal facets and a value for the latero-ventral eyes that corresponds to that suggested for the eyes of glowworm flies by MEYER-ROCHOW & WALDVOGEL (1979).

A very different kind of eye miniaturization has been reported from that of the male strepsipteran insect *Xenos peckii*. Although endowed, as is common in insects generally, with green and UV sensitive receptors (JAMES et al. 2016), the eyes of this tiny flyer do not consist of conventional compound eye ommatidia as described in the introduction of this paper, but possess eyelets with individual retinas of about 100 receptor cells. Spatial vision can be improved by this method if the brain can combine and make sense of the different small images that are created by the projections onto each eyelet's retina (BUSCHBECK et al. 1999). For the time being this small strepsipteran insect represents the only species that has evolved a different imaging system from that employed by other insects. Yet, it demonstrates that a study of tiny insect eyes can still surprise the vision researcher – and lead to possible technological innovations (KEUM et al. 2018).

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