

Ocellar optics in nocturnal and diurnal bees and wasps

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Abstract

Nocturnal bees, wasps and ants have considerably larger ocelli than their diurnal relatives, suggesting an active role in vision at night. In a first step to understanding what this role might be, the morphology and physiological optics of ocelli were investigated in three tropical rainforest species – the nocturnal sweat bee *Megalopta genalis*, the nocturnal paper wasp *Apoica pallens* and the diurnal paper wasp *Polistes occidentalis* – using hanging-drop techniques and standard histological methods. Ocellar image quality, in addition to lens focal length and back focal distance, was determined in all three species. During flight, the ocellar receptive fields of both nocturnal species are centred very dorsally, possibly in order to maximise sensitivity to the narrow dorsal field of light that enters through gaps in the rainforest canopy. Since all ocelli investigated had a slightly oval shape, images were found to be astigmatic: images formed by the major axis of the ocellus were located further from the proximal surface of the lens than images formed by the minor axis. Despite being astigmatic, images formed at either focal plane were reasonably sharp in all ocelli investigated. When compared to the position of the retina below the lens, measurements of back focal distance reveal that the ocelli of *Megalopta* are highly underfocused and unable to resolve spatial detail. This together with their very large and tightly packed rhabdoms suggests a role in making sensitive measurements of ambient light intensity. In contrast, the ocelli of the two wasps form images near the proximal boundary of the retina, suggesting the potential for modest resolving power. In light of these results, possible roles for ocelli in nocturnal bees and wasps are discussed, including the hypothesis that they might be involved in nocturnal homing and navigation, using two main cues: the spatial pattern of bright patches of daylight visible through the rainforest canopy, and compass information obtained from polarised skylight (from the setting sun or the moon) that penetrates these patches.

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1. Introduction

Bees and wasps are highly visual insects that rely on their compound eyes for a variety of behavioural tasks, including the discrimination of flower shape and colour, the identification of prey, the extraction of compass information from polarised skylight, the recognition of learned terrestrial landmarks, and the stabilisation and control of flight using information derived from the optical flow field. Nearly all species of bees and wasps execute these tasks exclusively in bright daylight. However, in the world's tropical rainforests several

species provide notable exceptions to this rule. Due to the pressures of predation and competition for limited food resources, some groups of bees and wasps have evolved a nocturnal lifestyle (Cockerell, 1923; Richards, 1978; Roubik, 1992; Wcislo et al., 2004). Remarkably, despite experiencing light levels 100 million times dimmer than their day-active relatives, these species are still able to forage and orient using visual cues (Warrant et al., 2004).

All hymenopteran insects – both diurnal and nocturnal – possess apposition compound eyes, an eye design that is better suited to vision in bright light. Apposition eyes are found in most day-active insects, including flies, butterflies and dragonflies, but their poor sensitivity to light makes them rare in nocturnal insects with demanding visual requirements. Such nocturnal insects typically have considerably more sensitive

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superposition compound eyes. The apposition eyes of the nocturnal sweat bee *Megalopta genalis*, an insect capable of learning visual landmarks at starlight intensities, have thus generated considerable interest. However, despite being 30 times more sensitive to light than those of diurnal bees (Greiner et al., 2004a; Warrant et al., 2004), *Megalopta*'s apposition eyes are still insufficiently sensitive on their own to explain the bee's impressive nocturnal visual abilities. Recent work has shown that nocturnal vision in *Megalopta* can be explained if neural summation of visual signals in space and time occurs at a higher level in the visual system, a hypothesis that is supported by anatomical and theoretical evidence (Greiner et al., 2004b, 2005; Theobald et al., 2006).

In addition to the compound eyes, many insects – including bees and wasps – possess two or three conspicuous ocelli on the dorsal surface of the head between the eyes. Ocelli are single-lens eyes of the camera type, and their exact role is still a matter of conjecture. They most likely have different roles in different insects, and there is now good evidence that they support a variety of behavioural tasks including flight stabilisation, navigation and orientation, absolute intensity measurement and neurosecretion (for reviews see Goodman, 1981; Wehner, 1987; Mizunami, 1994). The properties of ocelli are well suited to these tasks. Compared to the compound eyes the ocellar pathways are fast, with large neurons and few synapses, ensuring that information from the ocelli can reach thoracic motor centres rapidly (Guy et al., 1979). This high temporal resolution is, however, in stark contrast to their spatial resolution. Optical measurements of back focal distance in a variety of insects (Homann, 1924) – particularly in flies (Cornwell, 1955; Schuppe and Hengstenberg, 1993) and locusts (Parry, 1947; Cornwell, 1955; Wilson, 1975) – have all indicated that the plane of best focus of the ocellar lens lies a considerable distance behind the retina. This under-focusing ensures that the photoreceptors receive a very blurry image. Moreover, ocelli typically have a slightly oval shape that can cause astigmatism, degrading the image even further (Schuppe and Hengstenberg, 1993) – images focused by the long (major) axis of an oval ocellus are likely to be located further from the back surface of the lens than images focused by the short (minor) axis. Even if a perfectly crisp image could be focused on the distal photoreceptor tips, the wiring of the retina would still prevent good spatial resolution. Firstly, the arrangement of photoreceptors in the ocellar retina is typically disorganised, and not arranged in the tight sampling matrix that might be expected for high spatial resolution. Secondly, the outputs of these photoreceptors are then summed within large groups by second-order L-neurons – in the extreme case of cockroaches, for instance, over 10 000 photoreceptors synapse onto just four L-neurons (Toh and Tateda, 1991), effectively reducing the visual space sampled by the ocellus to just four image pixels.

Thus, most ocelli so far studied are coarse, fast and sensitive organs of vision, well suited for rapidly signalling changes in light intensity but not for resolving fine spatial detail. These properties – in combination with their broad partially-overlapping visual fields covering the forward horizon and the dome

of the sky (Wilson, 1975) – make them ideal for detecting the changes of light intensity that would be experienced when insects change pitch or roll during flight, a task now considered to be their most common function. However, as Mizunami (1993, 1995) rightly points out, the structure and wiring of ocellar systems is so varied within the insects, that many other roles are likely. A case in point is the recently described median ocellus of dragonflies (Stange et al., 2002; van Kleef et al., 2005; Berry et al., in press). Optical and electrophysiological measurements have shown that these ocelli are capable of resolving the sharp boundary between sky and land, rather than simply the brightening and darkening associated with sequentially viewing one after the other. The optics of the median ocellar lens provides an image that has good spatial resolution in the vertical direction (Stange et al., 2002), and this resolution is preserved by both the photoreceptors (van Kleef et al., 2005) and the second-order L-cells to which they connect (Berry et al., in press). These features allow an accurate one-dimensional analysis of the horizon over a wide angular azimuth, and this may be used for fine control of flight attitude.

What role might the ocelli play in a nocturnal bee or wasp that flies in a cluttered rainforest environment where the horizon is obscured? Kerfoot (1967) has shown that the ocelli of nocturnal bees are larger than those of crepuscular bees, and that these in turn are larger than those of diurnal bees, suggesting that ocelli may play an important role in dim light. Indeed, the ocelli of bumblebees allow them to navigate using polarised skylight at dusk when terrestrial landmarks have become too dim for the compound eyes to recognise (Wellington, 1974). Can the ocelli of a nocturnal bee or wasp help to stabilise flight in a cluttered rainforest at night, or to aid in navigation? A first step in answering this question is to study the imaging properties of their ocelli. Are they capable of spatial resolution, like the median ocellus of the dragonfly? Or are they simply highly sensitive light detectors? The goal of the present paper is to answer these questions by studying the large ocelli of the nocturnal sweat bee *M. genalis* (Halictidae) and the nocturnal paper wasp *Apoica pallens* (Vespidae). Both species are active at night in the tangled tropical rainforest, and both have demanding visual behaviours, including homing. As a comparison, the ocelli of a close diurnal relative to *Apoica* – the day-active tropical paper wasp *Polistes occidentalis* (Vespidae) – will also be studied.

2. Materials and methods

2.1. Animals

All wasps and bees used in this study were collected on Barro Colorado Island in the Panama Canal (a tropical rainforest field station of the Smithsonian Tropical Research Institute, Panama City). Nocturnal polistine paper wasps (*A. pallens*) and halictid bees (*M. genalis*) were collected at night in the rainforest on white sheets illuminated by ultraviolet-enriched light. The diurnal halictid bee shown in Fig. 2 was kindly

loaned to us by Dr. David Roubik (Smithsonian Tropical Research Institute), who tentatively identified the species as *Au-gochloropsis* (*Paraugochloropsis*) cf. *Fuscognatha*. Diurnal paper wasps (*P. occidentalis*) were collected from nests built under the eaves of research buildings on the island.

2.2. Histology

Light microscopy, and transmission and scanning electron microscopy, were performed using standard methods. Whole eyes were placed for 2 h at 4 °C in standard fixative (2.5% glutaraldehyde and 2% paraformaldehyde in phosphate buffer (pH 7.2)). Following a buffer rinse, eyes were then added to 2% OsO₄ for 1 h. Dehydration was performed in an alcohol series and eyes were embedded in Araldite. Ultrathin sections for electron microscopy were stained with lead citrate and uranyl acetate. Thin (3.5 µm) sections for light microscopy were stained with toluidine blue. Rhabdom cross-sectional areas were calculated from light and electron microscope sections using NIH Image.

2.3. Determination of ocellar receptive field centres

The small end was cut from a plastic pipette tip leaving an opening large enough for a bee or wasp head to protrude through. The insect was fixed in position by gluing the mouthparts to the tube with dental wax, and this preparation was then mounted at the centre of curvature of a Leitz goniometer. The goniometer was placed onto the foot-plate of an Askania macroscope. The insect was then manipulated so that the long axis of the eye edge was parallel to the plane of the stage. The head was further manipulated so that (1) the origin of the three goniometer axes was in the centre of the head, and (2) the three goniometer axes were lined up with the dorsal–ventral (yaw), anterior–posterior (roll), and left–right (pitch) axes, respectively, of the insect’s head. With the stage horizontal, the head then looked vertically upwards into the objective of the macroscope, and when observed in this position, the head was oriented exactly anteriorly (from the animal’s point of view). The goniometer allowed us to tilt the stage (and thus the head) in defined angular steps of latitude and longitude, with latitude = 0° and longitude = 0° defined as the anterior orientation described above (“A_p” in Fig. 5A). Dorsal (“D_p”) corresponds to a latitude of +90° and lateral (“L_p”) to a latitude of 0° and a longitude of ±90°.

To illuminate the eyes we introduced a half-silvered mirror, angled at 45°, just beneath the objective of the macroscope. Collimated white light (from a halogen source) was directed laterally to the mirror so that the eyes were illuminated and viewed along the same axis (“orthodromic illumination”). A bright spot of light – the reflection of the white halogen source – was then visible on the surface of the ocellus. To determine ocellar receptive field centres, the goniometer stage was tilted both in longitude and latitude until the reflected spot was judged to be at the absolute centre of the ocellus. The

coordinate of latitude and longitude required to do this was taken as the ocellar receptive field centre.

2.4. Optical measurements of ocellar image quality

The back focal distances and focal lengths of ocellar lenses were measured using a modification of Homann’s (1924) hanging-drop method. A small piece of cuticle containing either a lateral or median ocellus was carefully dissected from the head capsule, placed in a petri dish of saline and lightly cleaned from tissue and pigment using a small paintbrush. It was then placed external side outwards in a tiny drop of physiological saline (refractive index = 1.34) that was placed on the centre of a microscope cover slip. An o-ring was waxed to a conventional microscope glass, after which the upper surface of the o-ring was lightly greased with Vaseline. The cover slip was then turned upside down and placed onto the greased o-ring, thus creating an air-tight chamber containing the saline drop and its downward pointing ocellus. The microscope slide was mounted on the stage of a conventional light microscope (Leica) with condenser removed. Objects of known size (typically patterns of dark stripes on translucent tracing paper) were placed on the foot of the microscope, over the lamp aperture. Images of these objects were focused by the ocellus within the saline drop. These images were then viewed with the 40× objective, and photographed with a digital camera fitted to the microscope.

The focal length f of each ocellus was calculated according to the following equation:

$$f = s_o \frac{\lambda_i}{\lambda_o}, \quad (1)$$

where s_o is the distance between the striped object and the ocellus (127 mm), λ_o is the spatial wavelength of the striped pattern (the distance between the centre of one stripe and the centre of the next: 4.53 mm) and λ_i is the spatial wavelength of the image of the striped pattern (mm).

The optical back focal distance – the distance from the back of the ocellar lens to the plane of best focus – was measured by first focusing upon small particles of debris attached to the back of the lens. The back focal distance was determined by focussing upwards until the best image of the striped object was obtained. The change in focus (in micrometres) was measured using a micrometer gauge attached to the microscope stage. This procedure was repeated at least 10 times and the values averaged. This mean value was corrected for the refractive index of the saline by multiplication by 1.34.

Images collected from wasp and bee ocelli were found to be astigmatic: images focused by the long (major) axis of the oval ocellus were found to be located further from the back surface of the lens than images focused by the short (minor) axis. Back focal distances were calculated for both image planes by using patterns whose stripes were either perpendicular (far image plane) or parallel (near image plane) to the long axis of the ocellus.

3. Results

3.1. External ocellar morphology and location

All bees and wasps have three ocelli on the dorsal head capsule between the eyes (Figs. 1–4). The ocelli of all species have a slightly oval shape (Table 1), although the median ocellus of *Apoica* is almost round (Fig. 3C, Table 1). The ocelli of nocturnal species appear to bulge prominently from the dorsal surface of the head (Figs. 1 and 3), whereas those of diurnal species are less conspicuous (Figs. 2 and 4). As previously described, nocturnal species have larger ocelli (Figs. 1 and 3) than diurnal species (Figs. 2 and 4), suggesting an active role in dim light. As a percentage of head diameter, the ocelli of nocturnal *Apoica* (Fig. 3) and *Megalopta* (Fig. 1) are about twice the size (12–14%) of those of diurnal *Polistes* (Fig. 4) and *Augochloropsis* (Fig. 2) (6–8%).

The median ocellus of an immobilised specimen of the nocturnal bee *Megalopta* has the centre of its receptive field centred frontally, about 10° above anterior on the equator of the eye (“A_p” in Fig. 5A), where “anterior” is defined as the direction perpendicular to the physical long axis of the head and compound eyes (see *Materials and methods*). The co-ordinate of the median ocellus receptive field centre (latitude, longitude) is thus [+10°, 0°]. The two lateral ocelli have receptive fields centred 50° above the equator, and 60° laterally on either side (coordinates [+50°, +60°] and [+50°, –60°]). Immobilised specimens of *Apoica* reveal a distinctly more dorsal placement of the ocelli (Fig. 5A), with receptive field centres located at [+25°, 0°], [+60°, +100°] and [+60°, –100°] for the median and two lateral ocelli, respectively.

Immobilised specimens, however, are unable to reveal the true orientations of the ocelli in a flying animal – if the head is tilted upwards or downwards during flight, the receptive field centres shown in Fig. 5A will likewise be tilted. To account for this possibility, film sequences of flying *Megalopta* were analysed (Kelber, unpublished data), and head angles relative to true horizontal (“A_t” in Fig. 5B) were calculated for a number of bees. In free flight *Megalopta* tilts its head upwards by 52°, meaning that its ocelli have a considerably more dorsal orientation than indicated in Fig. 5A (see Fig. 5B). This substantial head tilt during flight is typical of many bees (Kelber, unpublished data). Even though we did not have the opportunity to film *Apoica* in free flight, inspections of photographs of two species of wasps in flight – *Sceliphron caementarium* (Sphecidae) and *Polistes metricus* (Vespidae) – reveal a considerably lower upward head tilt: 9.3° and 11.4°, respectively (Dalton, 1975). If we assume that *Apoica* employs a similar head tilt during flight (say 10°), then the receptive field centres of its two lateral ocelli have a very similar dorsal location to those of the lateral ocelli in flying *Megalopta* (Fig. 5B): around 50° above the horizon, and somewhat posterior (longitudes of ca. ±120°). Interestingly, the receptive field centre of the median ocellus in *Apoica* is almost 30° more anterior than the receptive field centre of the median ocellus in *Megalopta* (Fig. 5B).

3.2. Internal ocellar morphology

The median ocellar lens in all three species overlies a retina of photoreceptors (Fig. 6). In the two nocturnal species, the distal retinal surface is positioned close to the proximal surface of the lens, and in *Megalopta* these are directly in contact (Fig. 6B). In *Apoica* the distal retinal surface is concentric with the proximal surface of the lens, with these surfaces being separated by an approximately 35 µm depth of corneal cells (Fig. 6A). In the diurnal wasp *Polistes*, the retina is not concentric with the proximal lens surface (Fig. 6C). Unlike *Polistes*, neither *Megalopta* nor *Apoica* possesses screening pigments in the retina, an adaptation likely to improve light capture at night and thus sensitivity.

In cross-section, the rhabdoms of the retina do not form an orderly matrix, but form an array that is somewhat disorganised. Rhabdoms in all species are highly elongated, and constructed from the rhabdomeres of two retinula cells whose dominant microvillar directions are practically parallel to each other (Fig. 7). The rhabdoms of the nocturnal bee *Megalopta* are the largest of three species studied (17.5 × 1.3 µm; Table 1), followed by the rhabdoms of the nocturnal wasp *Apoica* (5.9 × 0.6 µm) and the diurnal wasp *Polistes* (4.6 × 0.6 µm). The large rhabdoms of *Megalopta* are clearly an adaptation for improved sensitivity at night, and the interesting observation that the equally nocturnal *Apoica* has small rhabdoms suggests that some of their sensitivity may have been offered in favour of spatial resolution. This conclusion is reinforced by calculations of the occupation ratio of rhabdoms in the retina (the percentage cross-sectional area of rhabdoms within a unit cross-sectional area of retina). The occupation ratios of the wasps *Apoica* and *Polistes* are quite small (9.5% and 6.1%, respectively; Table 1). Even though *Apoica* is nocturnal, its rhabdom occupation ratio is only slightly larger than that of its diurnal relative. In contrast, the nocturnal bee *Megalopta* has a rhabdom occupation ratio over three times greater (33.6%; Table 1).

3.3. The optical properties of ocelli

Images formed behind the lenses of the ocelli in all three species were astigmatic (Fig. 8, Table 1): images formed by the major axes of the oval ocelli (b, d, f in Fig. 8) were located further from the proximal surface of the lens than images formed by the minor axes (a, c, e in Fig. 8). Despite being astigmatic, images formed at either focal plane were reasonably sharp in all ocelli investigated.

Ocellar focal lengths f were determined for each of the two astigmatic focal planes: f_{maj} (for the ocellar major axis) and f_{min} (for the ocellar minor axis). Their values in the lateral and median ocelli do not differ significantly in any of the three species (Table 1). Values of f_{maj} for all ocelli are in the range 510–690 µm in *Megalopta*, 430–460 µm in *Apoica* and 180–220 µm in *Polistes*. Corresponding values of f_{min} are 370–600 µm, 300–420 µm and 150–200 µm, respectively. Significant variations in measured focal lengths for median or lateral ocelli were found in *Megalopta*, but the variation was in most cases not as great in the two wasps (Table 1),

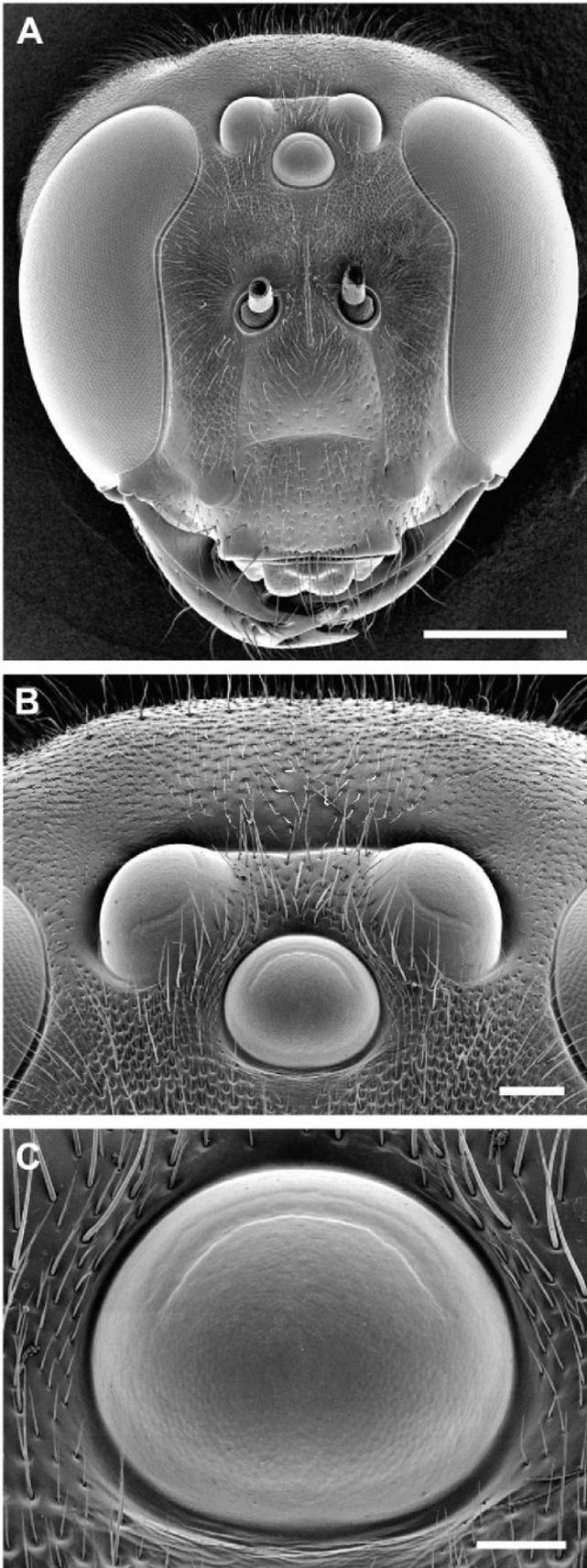


Fig. 1. The ocelli of the nocturnal halictid bee *Megalopta genalis*, showing their position on the head (A) and their arrangement as a group (B). (C) The median ocellus. Scales: 1 mm (A), 200 μ m (B) and 100 μ m (C).

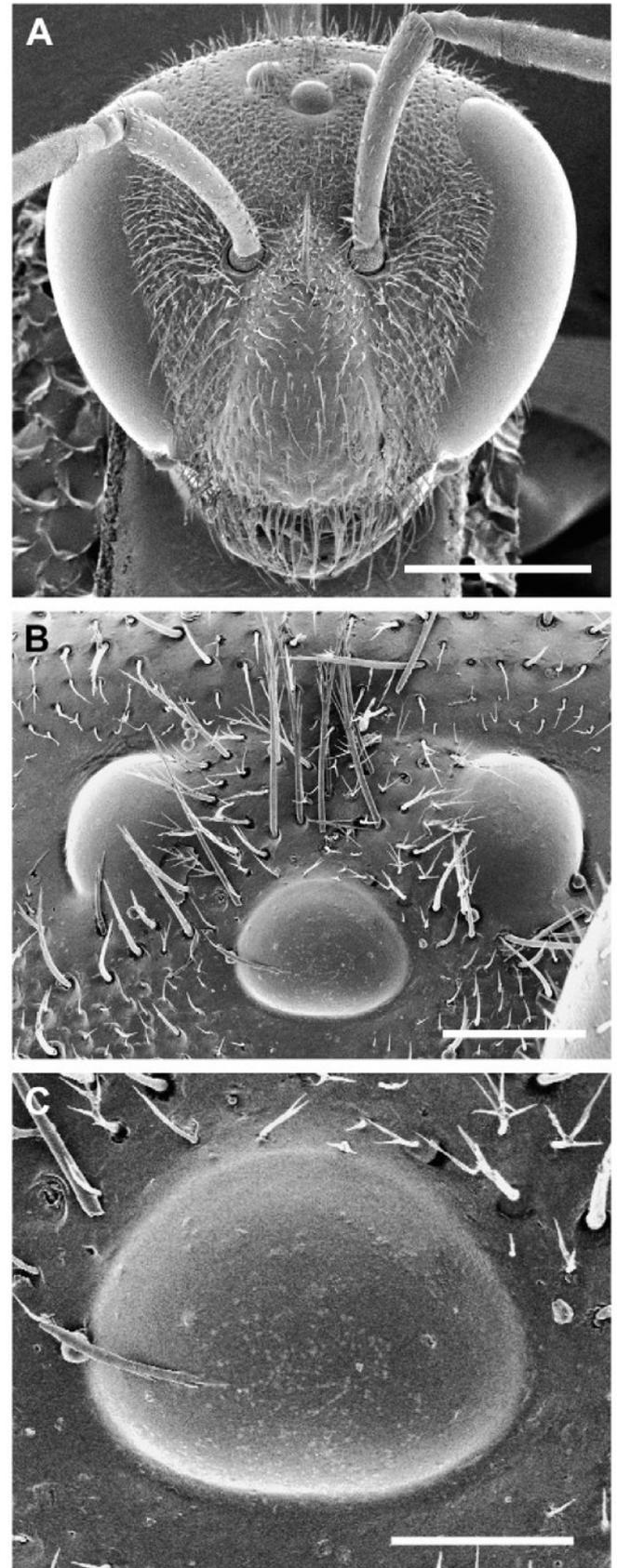


Fig. 2. The ocelli of the diurnal halictid bee *Augochloropsis* (*Paraugochloropsis*) cf. *Fuscognatha*. Descriptions and scales as for Fig. 1.

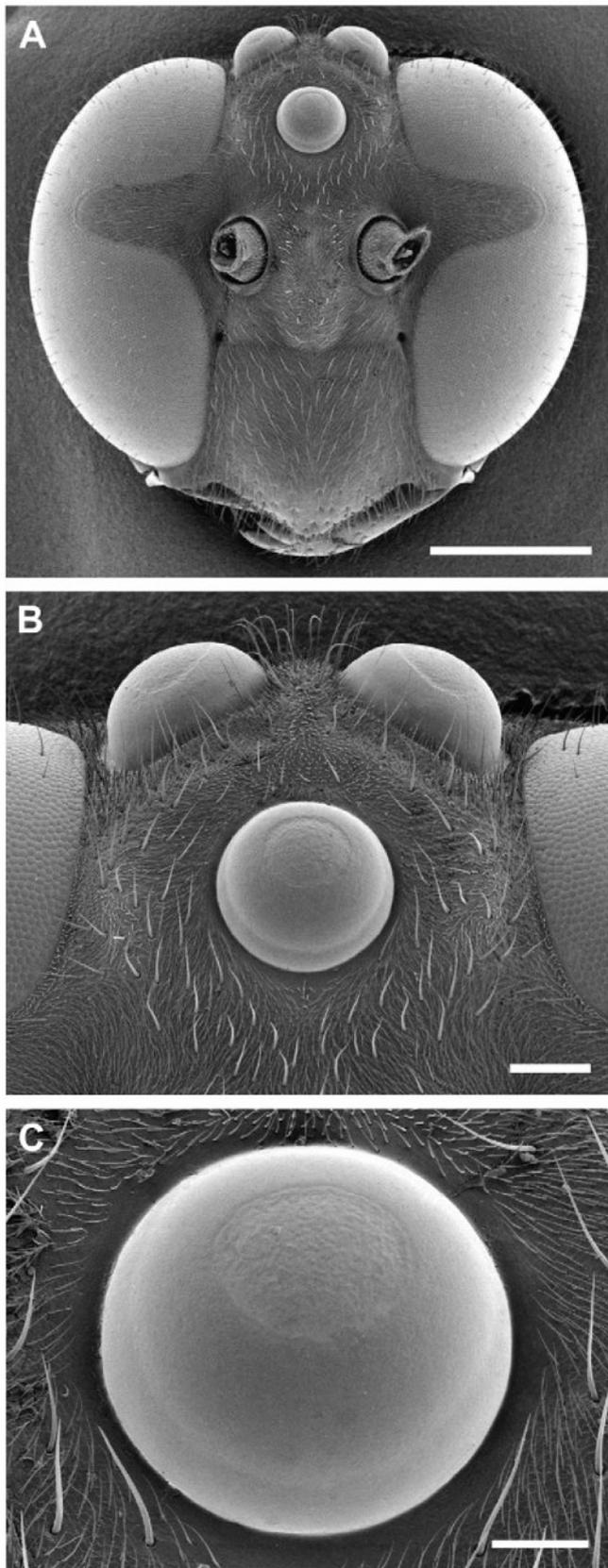


Fig. 3. The ocelli of the nocturnal paper wasp *Apoica pallens*. Descriptions and scales as for Fig. 1.

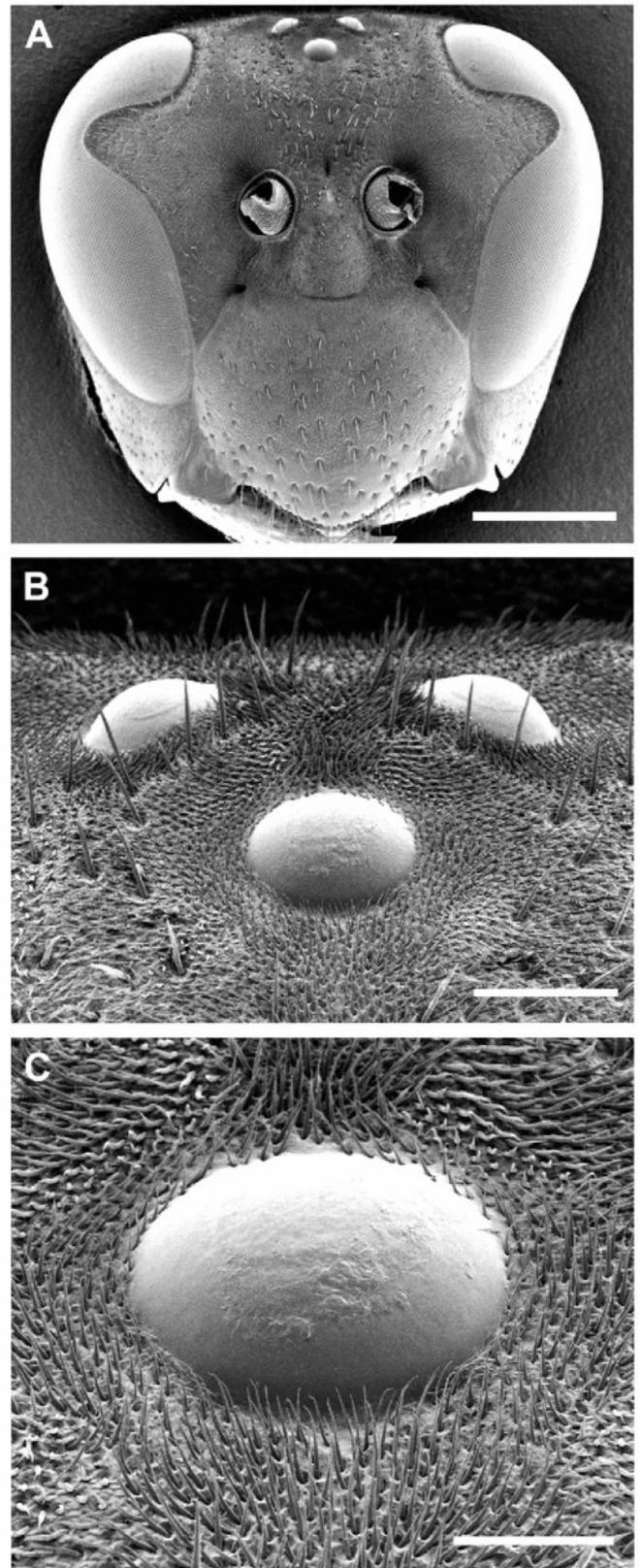


Fig. 4. The ocelli of the diurnal paper wasp *Polistes occidentalis*. Descriptions and scales as for Fig. 1.

Table 1
Optical and anatomical dimensions in the lateral and median ocelli

Parameter	<i>Megalopta</i>		<i>Apoica</i>		<i>Polistes</i>	
	Median (3)	Lateral (5)	Median (3)	Lateral (2)	Median (2)	Lateral (2)
Φ_{\min}	410 ± 60	398 ± 63	416 ± 16	414	216 ± 12	161 ± 18
Φ_{maj}	471 ± 40	457 ± 66	427 ± 9	486	273 ± 8	218 ± 21
$\Phi_{\text{maj}}/\Phi_{\text{head}}$	0.120	0.117	0.122	0.139	0.070	0.056
f_{\min}	427 ± 59	500 ± 106	357 ± 63	331 ± 4	168 ± 13	185 ± 15
f_{maj}	644	599 ± 88	436	450 ± 8	213 ± 9	190 ± 8
l_{\min}	409 ± 14	447 ± 140	162 ± 14	184 ± 7	100 ± 8	120 ± 11
l_{maj}	565	548 ± 108	190	304 ± 25	170 ± 19	185 ± 15
d_{\min}	1.3 ± 0.1	—	0.6 ± 0.1	—	0.6 ± 0.1	—
d_{\max}	17.5 ± 1.0	—	5.9 ± 2.1	—	4.6 ± 0.8	—
OR %	33.6	—	9.5	—	6.1	—

All dimensions are given in μm . Φ_{\min} = minor diameter of the elliptical ocellus; Φ_{maj} = major diameter of the elliptical ocellus; Φ_{head} = frontal diameter of the head (between lateral edges of eyes); f_{\min} = near focal length (for objects focused by the minor axis of the ocellus); f_{maj} = far focal length (for objects focused by the major axis of the ocellus); l_{\min} = distance between the near focal point and the rear side of the lens; l_{maj} = distance between the far focal point and the rear side of the lens; d_{\min} = minimum cross-sectional diameter of the rod-shaped rhabdom; d_{\max} = maximum cross-sectional diameter of the rod-shaped rhabdom. OR% = occupancy ratio of rhabdoms in the retina (percentage cross-sectional area of rhabdoms within a unit cross-sectional area of retina). Variations (\pm) in measured rhabdom diameters are shown as standard deviations. For all other dimensions, the measurement variation represents the maximum deviation from the mean value. Numbers in brackets indicate the number of animals investigated.

implying that the optical properties of the ocelli are more uniform across individual wasps than across individual bees.

The optical back focal distance l – the distance from the back of the ocellar lens to the plane of best focus – was determined for both focal planes (l_{maj} and l_{\min}). Their values in the lateral and median ocelli do not differ significantly in any of the three species, with the exception of l_{maj} in *Apoica* (Table 1). Values of l_{maj} for all ocelli are in the range 450–650 μm in *Megalopta*, 150–200 μm in *Polistes* and around 190 μm (median) and 300 μm (lateral) in *Apoica*. Corresponding ranges of l_{\min} are 310–590 μm , 100–130 μm and 150–190 μm , respectively. Again, significantly greater variation in measured values for median or lateral ocelli was found in *Megalopta*.

In order to achieve the highest possible spatial resolution, the plane of best focus of the ocellus should lie on or in the retina. To determine whether this is the situation in the bees and wasps studied here, the average back focal distances l_{maj} and l_{\min} , were used to construct light paths that could be superimposed on schematic representations of median ocelli from each of the three species (Fig. 8). These schematic ocelli were traced from the anatomical sections shown in Fig. 6. In *Megalopta*, the planes of best focus (l_{\min} and l_{maj}) are located considerably below the retina (Fig. 8A), at distances of 350 μm and 510 μm , respectively (a and b in Fig. 8A). In *Apoica*, the equivalent planes of best focus are located just below the retina (Fig. 8B), at distances of 10 μm and 40 μm , respectively (c and d in Fig. 8B). Finally, in *Polistes*, the focal plane of the minor ocellar axis (l_{\min}) lies within the retina (Fig. 8C), while that of the major axis (l_{maj}) lies just 35 μm below (e and f in Fig. 8C). These results show that the median ocelli of *Megalopta* are distinctly astigmatic and profoundly underfocused. Their spatial resolution is therefore quite poor, and likely limits the ocellus to sensing changes in general illumination level. In surprising contrast are the median ocelli of the two wasps. Images suffer comparatively less from

astigmatism, and are focused in or just below the retina, opening the possibility for roles that require some degree of spatial resolution.

4. Discussion

A striking characteristic of nocturnal bees and wasps is their enormous ocelli, a feature that did not escape early hymenopterists (Cockerell, 1923; Bischoff, 1927; Rau, 1933). Long before the first experimental studies of ocellar function were undertaken, these enlarged ocelli were assumed to be the main organs of vision in nocturnal Hymenoptera, with the compound eyes being merely used for daylight vision (Rau, 1933). Whilst we now know that the compound eyes are certainly used for nocturnal orientation in bees (Warrant et al., 2004), and probably also in wasps (Greiner, 2006), the enlarged ocelli of nocturnal hymenopterans still suggest they play an important role in vision at night. Exactly what role (or roles) is still a matter of conjecture, but the results presented here offer several hypotheses for future investigation.

4.1. Nocturnal and diurnal ocelli

Overwhelming evidence from bees (Kerfoot, 1967; Kelber et al., 2006) and ants (Moser et al., 2004) shows a strong correlation between ocellar size and the light intensity at peak activity: species active in dimmer light have larger ocelli. The ocellar sizes of the nocturnal and diurnal bees and wasps presented in this paper are in accordance with this correlation (Fig. 9), with the ocelli of nocturnal species reaching almost half a millimetre in diameter. The largest ocelli encountered in hymenopterans are those of giant nocturnal Indian carpenter bees of the genus *Xylocopa*. These are twice the diameter of the nocturnal ocelli reported here (Kelber and Warrant, unpublished data), no doubt due to *Xylocopa*'s larger body size and its need to fly at even dimmer light levels.

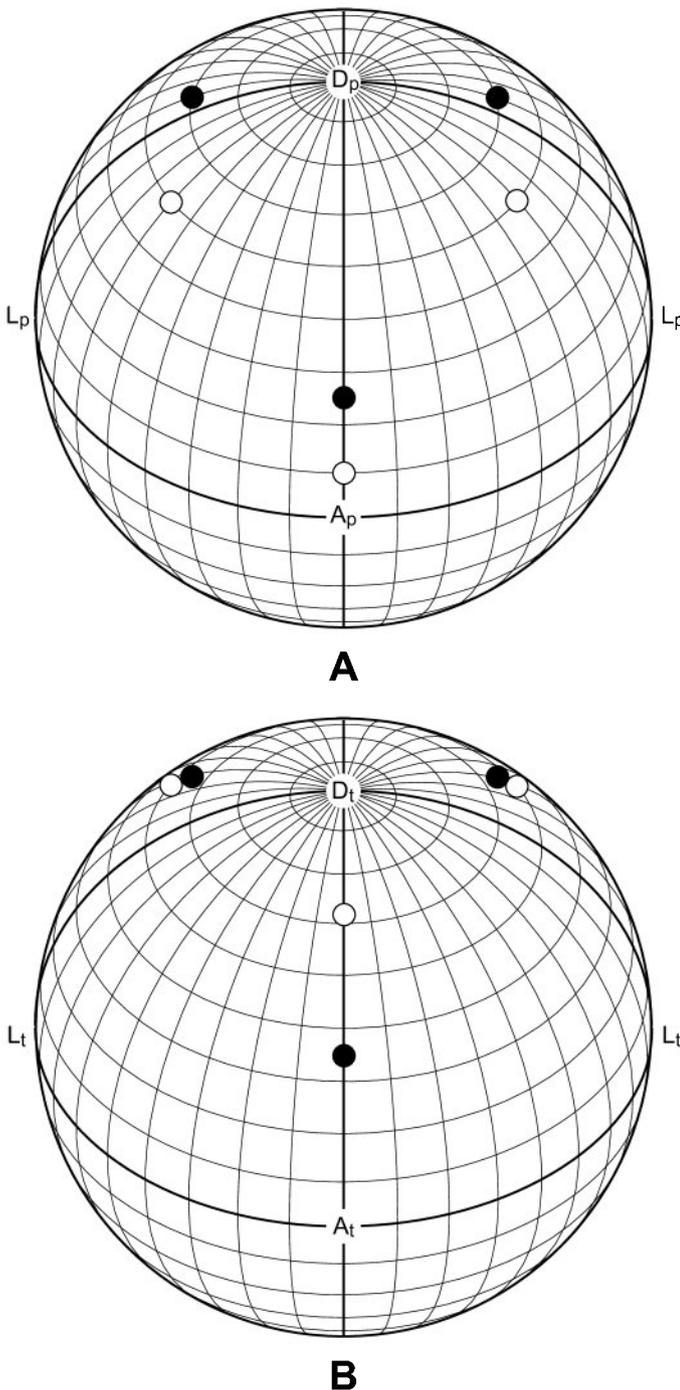


Fig. 5. Ocular receptive field centres in the nocturnal halictid bee *Megalopta genalis* (open circles) and the nocturnal paper wasp *Apoica pallens* (filled circles) plotted on a sphere representing the three-dimensional space around the animal. (A) The receptive field centres specified by their physical locations on the heads of immobilised specimens, relative to the morphological anterior direction, A_p . A_p is defined as the direction perpendicular to the physical long axis of the head and compound eyes, D_p is dorsal relative to A_p , and L_p is lateral ($\pm 90^\circ$ longitude from A_p). (B) The receptive field centres specified by their locations during free flight when the head is tilted upwards by 52° in *Megalopta* (Kelber, unpublished data) and probably around 10° in *Apoica* (based on head tilt in other wasps: see Dalton, 1975). A_t is true anterior (i.e. a horizontal direction), D_t is true dorsal, and L_t is lateral ($\pm 90^\circ$ longitude from A_t).

In addition to their size, the ocelli of nocturnal *Apoica* and *Megalopta* share another common feature: during flight, their ocelli view the same region of visual space (Fig. 5). Their lateral ocelli are positioned to view the dorsal visual field, while their median ocelli receive information from the dorsal–frontal visual field. Electroretinographic (Schuppe and Hengstenberg, 1993) and optical (Cornwell, 1955) measurements of ocellar visual field size in blowflies reveal a similar dorsal and dorsal–frontal coverage during flight. These measurements also reveal that blowfly ocelli have a significant dorsal-posterior field of view, a feature also likely in the ocelli of *Apoica* and *Megalopta* during flight. This dominance of the dorsal visual world is not found in all insects. The visual fields of the ocelli of dragonflies and locusts are much more frontal (Wilson, 1975; Stange et al., 2002), and in the case of the median ocellus of dragonflies, are shaped for narrowly sampling the forward horizon (Stange et al., 2002). These differences in visual field location further support the idea that ocelli may be used for different purposes in different insects.

Despite their similar size and visual fields, the ocelli of *Apoica* and *Megalopta* also differ in two significant ways. Firstly, the ocellar rhabdoms of *Megalopta* are much larger than those of *Apoica*, and occupy a much larger fraction of the cross-sectional area of the retina (Table 1), suggesting the potential to capture considerably more light at night. Strangely, the retina of *Apoica* is more similar to that of its day-active relative *Polistes*, both in terms of rhabdom size and occupation ratio (Table 1). Secondly, the ocelli of *Megalopta* are profoundly underfocused, producing a significantly astigmatic image several hundred micrometres below the retina (Fig. 8A), which suggests that they are little more than highly sensitive detectors of changes in overall mean light level. In contrast, the images formed by the ocelli of *Apoica* are considerably less astigmatic, with planes of best focus at the proximal edge of the retina (Fig. 8B). The same is true in the diurnal *Polistes* (Fig. 8C), again revealing an unexpected similarity between the two wasps.

The fact that the ocelli of wasps form images at the proximal edge of the retina allows the possibility of crude spatial resolution, an ability that until recently was assumed impossible for ocelli. However, in an impressive series of studies, Stange and colleagues have recently shown that the elliptical median ocellus of dragonflies – which also focuses astigmatic images in the retina – is capable of resolving the horizon during flight (Stange et al., 2002; van Kleef et al., 2005; Berry et al., in press). Even though the ocellar image is coarsely resolved in the horizontal (azimuthal) plane, in the vertical (elevation) plane the image is resolved considerably better. These spatial properties are preserved by both the photoreceptors (van Kleef et al., 2005) and the second-order L-neurons (Berry et al., in press), allowing the dragonfly median ocellus to function as an efficient detector of the position of the one-dimensional horizontal boundary between sky and earth.

The ocelli of *Apoica* are much less elliptical than the median ocellus of dragonflies, and images in both astigmatic focal planes are relatively undistorted (Fig. 8B). If some

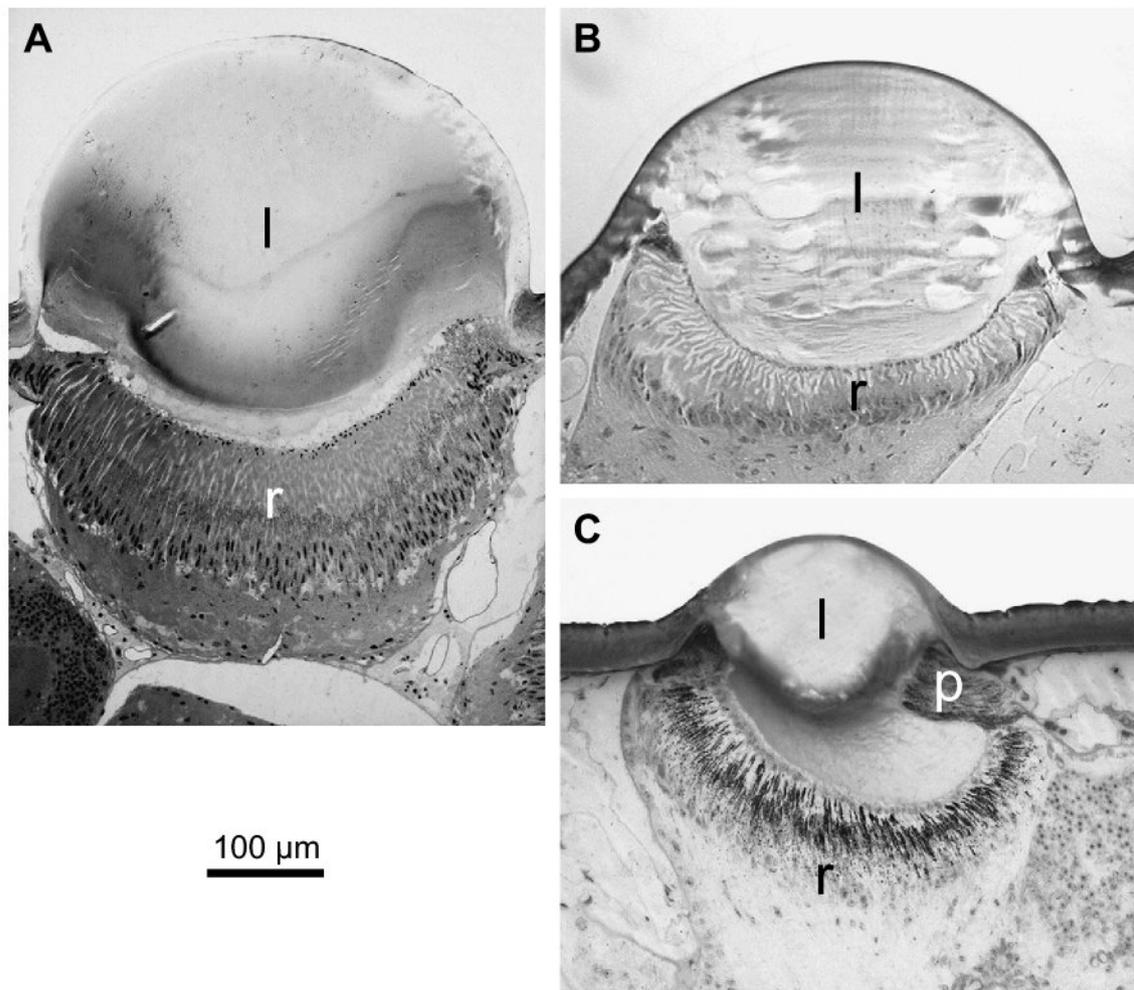


Fig. 6. Longitudinal light microscope sections of median ocelli in the nocturnal paper wasp *Apoica pallens* (A), the nocturnal halictid bee *Megalopta genalis* (B), and the diurnal paper wasp *Polistes occidentalis* (C). l = lens, r = retina, p = screening pigment granules. Scale for all parts: 100 µm.

spatial information from the image is preserved in the photoreceptors and the L-neurons, then it will be preserved equally well in all directions, and not just in the horizontal direction as in dragonflies. The photoreceptors of *Apoica* are relatively small and widely separated (Table 1), as they are in dragonflies and the diurnal *Polistes* (Table 1), an unexpected finding in a nocturnal insect concerned with maximising sensitivity, where large and tightly packed rhabdoms would be more the norm (as in *Megalopta*: Fig. 7). Small and widely separated rhabdoms are typical adaptations for maximising resolution by reducing the effects of optical cross-talk resulting from a wide cone of rays penetrating the retina (Warrant and McIntyre, 1991). All these features suggest that the large ocelli of *Apoica* could function as sensitive detectors of nocturnal light whilst maintaining a modest spatial resolving power. This of course assumes that this spatial resolution is preserved by the L-neurons (as in dragonflies). In stark contrast are the ocelli of *Megalopta*, which are clearly more sensitive to light than those of *Apoica*, but are only capable of detecting light intensity changes integrated over their entire receptive field, just like most other ocelli so far described.

4.2. Possible roles for nocturnal ocelli in rainforest habitats

Thus, despite living in identical habitats and having similar lifestyles, *Apoica* and *Megalopta* possess quite dissimilar ocelli, suggesting different roles in the nocturnal rainforest. What roles might these be?

Many roles have now been postulated for insect ocelli (reviewed in Mizunami, 1994). Chief among these is a role in controlling flight attitude in many species of flying insects. The upwards direction (towards the sky) is always associated with brighter light levels, and a simple mechanism to maintain level flight would be to continuously measure the dorsal light intensity relative to a separate measurement in the ventral (ground) direction, a task well suited to the ocelli (Hesse, 1908). In many flying insects, such as locusts (Wilson, 1975; Stange et al., 2002), the receptive fields of the three ocelli collectively view the horizon. During flight, rotations around the body axis (roll) are coded by changes in image brightness experienced by the lateral ocelli, while changes in body axis inclination (pitch)

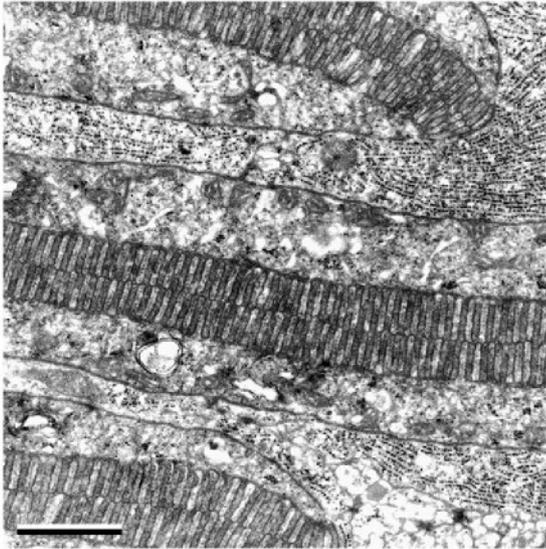


Fig. 7. An electron microscope transverse section through the ocellar rhabdoms of the nocturnal halictid bee *Megalopta genalis*. Scale: 1 μm .

are instead coded by the median ocellus. The combined pattern of light intensity changes detected by the three ocelli can thus be used to monitor the position of the horizon relative to the body axis and to steer flight. Extra precision and flight stability can be obtained if the median ocellus is adapted to accurately view the horizon (as we saw earlier in dragonflies: Stange et al., 2002; van Kleef et al., 2005; Berry et al., in press), but in most insects poor spatial resolution is probably preferred since it blurs out confounding details, such as bushes and clouds, that might penetrate the horizon.

However, unlike the open visual world of a field or pond seen by locusts and dragonflies, the rainforest understorey is a cluttered habitat with no clearly visible horizon. Patches of sky, visible through gaps in the canopy, provide the brightest stimuli, and this is also true even on a moonless night. These patches occupy a restricted field of view centred dorsally — outside this region the world is very much dimmer. Ocelli adapted for localising the horizon — like those of locusts and dragonflies — would thus be useless in a rainforest. Changes in pitch, for instance, would remain undetected because the visual field of the median ocellus would always view the dim understorey. Interestingly, the ocelli of both *Apoica* and *Megalopta* are directed very dorsally during flight — even their median ocelli (Fig. 5B) — and this may allow them to maintain level flight at night by detecting changes in intensity that arise relative to this restricted illumination field. Thus a role in nocturnal flight control cannot be ruled out in either species. A word of caution, however, should be added. The blowfly *Calliphora* also has dorsally directed ocelli with little or no horizontal field of view. Experimental manipulations of the brightness experienced by the median and one lateral ocellus elicited minimal steering responses, suggesting that their dorsally directed ocelli are not used in flight control (Schuppe and Hengstenberg, 1993).

In many insects the ocelli appear to control the exact timing of daily activity by accurately measuring the ambient

light intensity, a task for which they are well adapted due to their excellent sensitivity. The initiation and cessation of daily activity frequently occurs at a particular threshold light intensity (Schricker, 1965; Dreisig, 1980; Warrant et al., 2004; Kelber et al., 2006), and both bees (Schricker, 1965; Gould, 1975) and moths (Eaton et al., 1983; Sprint and Eaton, 1987) use their ocelli to measure this intensity. If the ocelli are occluded, the timing of activity is significantly altered (Eaton et al., 1983; Sprint and Eaton, 1987; Wunderer and de Kramer, 1989). Prior to emerging from its nest to forage in the morning and the evening, the nocturnal bee *Megalopta* crawls out towards the nest entrance and waits. When light levels have risen (morning) or fallen (evening) to precisely the right intensity, *Megalopta* emerges to forage (Warrant et al., 2004; Kelber et al., 2006). The nocturnal wasp *Apoica* also departs its nest at a specific time in the evening — in fact, hundreds of wasps depart *en masse* — and this too is almost certainly dependent on the light level (Hunt et al., 1995; Nascimento and Tannure-Nascimento, 2005). Although experimental evidence is lacking, the ocelli could play an important role in the timing of foraging in *Apoica* and *Megalopta*.

4.3. A nocturnal ocellus-based navigation system?

A final and intriguing possibility is that the ocelli form part of a sophisticated nocturnal navigation system used during foraging. Both *Apoica* and *Megalopta* are active nocturnal foragers: *Apoica* collects arthropod prey (Hunt et al., 1995) and pollen (von Schremmer, 1972), and *Megalopta* collects pollen (Wcislo et al., 2004). *Megalopta* leaves the nest for periods of up to 30 min, within about an hour after sunset and about an hour before sunrise when light levels are as low as 10^{-4} cd/m^2 (Fig. 9; Warrant et al., 2004; Kelber et al., 2006). Hunt et al. (1995) found that *Apoica* forages during the first 4 h of the evening when the moon is new or small. Just before dawn there is another small peak of activity, but these were observed to be wasps returning to the nest (possibly because it was too dark to find their way home any earlier: Hunt et al., 1995). As the moon waxes, *Apoica* begins to forage all night (Hunt et al., 1995; Nascimento and Tannure-Nascimento, 2005). Foraging in both species requires individuals to “home”, that is, to find their way back to the nest at night, a task that is far from trivial in a dark rainforest. *Megalopta* is capable of learning visual landmarks around the nest entrance at night (Warrant et al., 2004), and is presumably capable of doing the same thing along the foraging route. Many insects, including bees, use such terrestrial landmarks for homing (review: Collett et al., 2003).

Two other navigational cues are also available. The most obvious is the characteristic pattern of bright patches of sky visible through the canopy. For a human observer standing in a dark rainforest at night this is the *only* visible landmark! Its complexity — due to the overlapping silhouettes of tens of thousands of small leaves and branches — is however overwhelming, and it is difficult for a human observer to see any order or pattern. However, if seen through the poor spatial

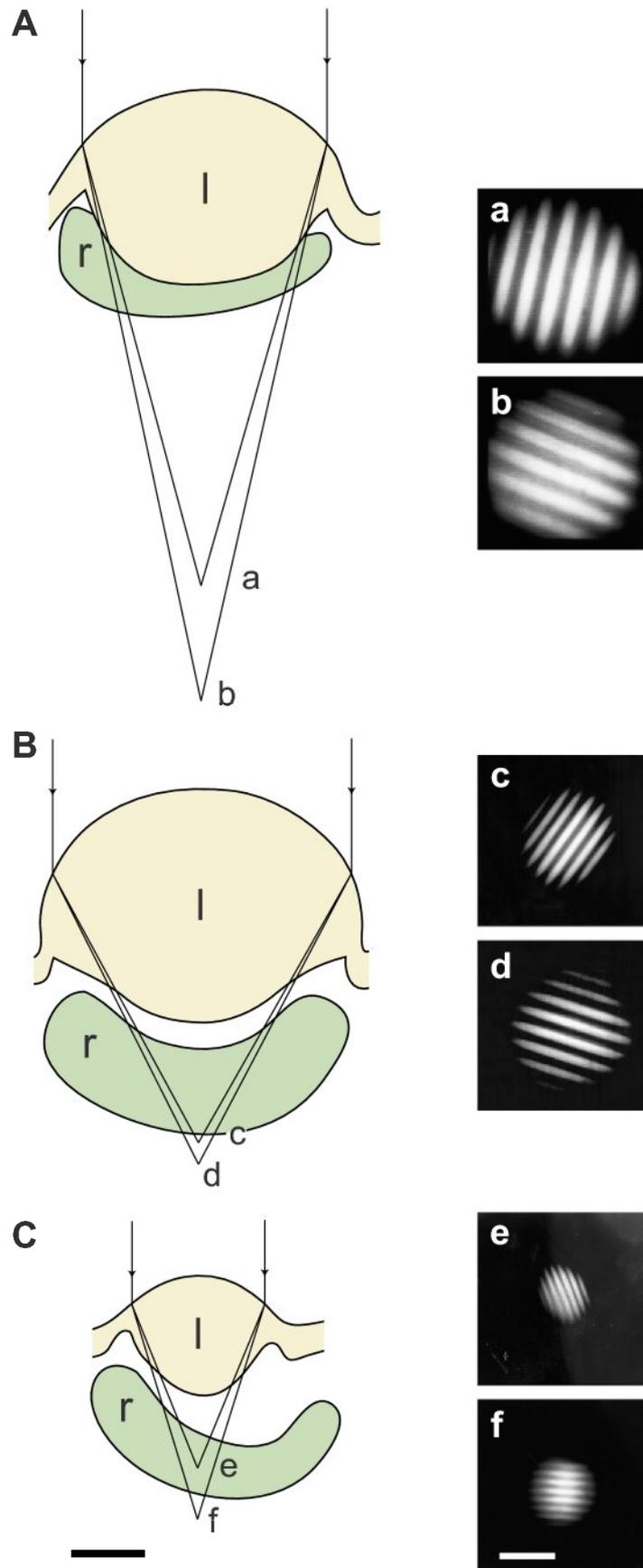


Fig. 8. The optical properties of median ocelli in the nocturnal halictid bee *Megalopta genalis* (A), the nocturnal paper wasp *Apoica pallens* (B), and the diurnal paper wasp *Polistes occidentalis* (C). Schematic ocelli were traced from the anatomical sections shown in Fig. 6. Ray diagrams for each species show the positions of the astigmatic focal planes for the major (b, d, f) and minor (a, c, e) axes of the oval ocellus, and corresponding images of a square-wave striped grating. l = lens, r = retina. Scales A–C: 100 μm ; a–f: 50 μm .

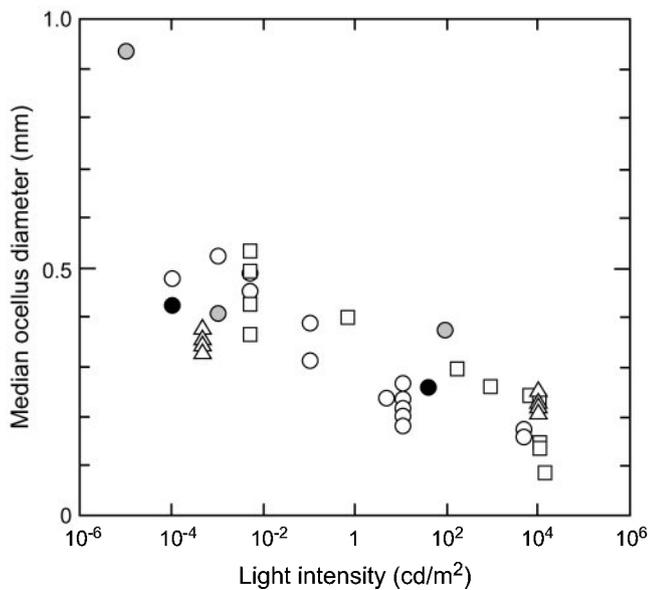


Fig. 9. The major diameter of the median ocellus (Φ_{maj}) as a function of the minimum light intensity at which a hymenopteran species is active. Open squares: data for bees from Kerfoot (1967); open circles: data for bees from Kelber et al. (2006); grey circles: three Indian species of carpenter bees (*Xylocopa*: Warrant and Kelber, unpublished data); black circles: wasps *Apoica* and *Polistes*, this study; open triangles: leaf-cutting ants (Moser et al., 2004). Light levels were either measured (*Xylocopa*), taken from the papers above, or estimated from the known flight activity pattern and light intensities measured in the respective light habitats: $5\text{--}10 \times 10^3 \text{ cd/m}^2$ for species flying in bright daylight under the open sky, $10\text{--}50 \text{ cd/m}^2$ for species flying during daytime in a Panamanian rainforest, 0.005 cd/m^2 for species flying on moonlit nights under an open sky, and $0.0005\text{--}0.001 \text{ cd/m}^2$ for crepuscular species flying in a Panamanian rainforest.

resolution of an ocellus or compound eye, this complexity disappears and the pattern becomes much more obvious (Warrant and Åström, in preparation). If, in addition, the pattern is sufficiently different at different places in the rainforest, this would allow its use as a landmark for an insect flying or walking beneath it. Indeed, in a very impressive study, Hölldobler (1980) discovered that an African ponerine ant navigates to and from its nest using the rainforest canopy pattern as a visual landmark. The ocelli of *Megalopta* are probably too poorly resolved to discern the canopy pattern, but those of *Apoica* may have sufficient resolution to accomplish it. In either species the dorsal region of the compound eyes may also have sufficient resolution and sensitivity to do the job.

The canopy patches also contain the second cue — polarised skylight, either due to the setting sun, or formed around the moon, a cue used by other crepuscular and nocturnal insects for navigation (Dacke et al., 2003, 2004a,b). During the hour directly after sunset or before sunrise, the sun's pattern of skylight polarisation is very simple, with the dominant direction of polarisation identical in all parts of the sky, and oriented roughly north–south (Cronin et al., 2006). The degree of polarisation is also very high (Cronin et al., 2006). Thus, in addition to its characteristic pattern, the patches of sky visible through the canopy after dusk and before dawn are each rich in a single direction of highly aligned polarised light. The two cues together — a spatial pattern of canopy

landmarks and a single directional compass cue defined by the plane of polarised skylight — might be sufficient to allow homing in nocturnal bees and wasps. This would require that the ocelli and/or the compound eyes are sensitive to polarised light. The dorsal areas of compound eyes in many insects have long been known to contain photoreceptors sensitive to polarised light (Wehner and Labhart, 2006). Indeed, even *Megalopta* has such a “dorsal rim” area, and the cells located there have enormous rhabdoms and are highly polarisation sensitive (Greiner et al., in preparation). Much less is known about the polarisation sensitivities of ocelli. Mote and Wehner (1980) discovered that the ocellar photoreceptors of the diurnal desert ant *Cataglyphis* are highly sensitive to polarised light. In a later study, it was found that after foraging these ants are able to find their way back to the nest using the ocelli alone, implying that the ocelli are capable of analysing the pattern of skylight polarisation (Fent and Wehner, 1985). Bumblebees also use their ocelli to analyse polarised skylight for homing (Wellington, 1974), even allowing them to find their way home later in the dusk when landmarks are no longer visible to the compound eyes.

Could the ocelli of *Apoica* and *Megalopta* be used to extract compass information from the dominant direction of polarised light present in the sky at dusk and dawn? Certainly the structure of the ocellar photoreceptors suggests that they have the potential for high sensitivity to polarised light (Fig. 7). Each rhabdom is elongated and constructed of two rhabdomeres, one from each of two retinula cells, and their microvilli are more or less aligned in a single direction. Further investigations of the retinal morphology and physiology are required to determine with certainty whether the ocelli are capable of analysing polarised light.

Thus, of the two nocturnal species studied here, only the ocelli of *Apoica* have sufficient resolving power to potentially discern the pattern of sky patches visible through the canopy. *Megalopta* would be forced to rely on their compound eyes for this task. The ocelli of both species, on the other hand, could potentially have sufficient sensitivity to detect and analyse polarised light and thereby to determine a compass bearing for navigation. Whether these and other nocturnal insects use the rainforest canopy — and the polarised light that it transmits — for navigation and homing remains a tantalising and interesting field for future research.

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