

### Cover illustration: How many eyes do you need?

Found throughout North America, the carpenter bee (*Xylocopa micans*) is a member of the order Hymenoptera, and resembles the ubiquitous bumblebee, but has distinct ecological differences. *X. micans* is often considered a pest because it bores into wooden structures to nest, but it rarely damages the structure. Although this species serves a minor function as a pollinator, it is not as good as other hymenopteran species because this bee often bites through the base of the flower instead of sipping through the opening. If the bee chooses this method of feeding, it is not dusted with pollen. It drains the flower of its nectar, damages the flower, and does not distribute pollen to the next flower. Other ecological differences exist although these are relatively minor. For example, the males of this species fare better than some other hymenopterans since they overwinter with the female. Pity the poor male of the common bumblebee who mates with the female and then dies in the autumn.

These bees are not aggressive and rarely sting. The female lays single eggs in separate chambers, and the eggs are relatively few in number.

Their compound eyes, as seen on the cover photograph, reveal the clever solutions evolution has developed to solve the problems of maximising visual acuity in small creatures. Unfortunately, this solution, which utilises a compound eye, has also restricted the maximum size the insect can realise.

Determined by the position of the photoreceptors, compound eyes are found in at least two basic forms, apposition and superposition. Superposition eyes allow for an image two to three orders brighter than the apposition eyes. Additionally, the variety of superposition compound eyes is stunning, for evolution has continued to vary the optical anatomy, thus creating most unusual and imaginative structures with telescopic features, reflection optics, and combinations. Ocular pass filters including pigmented corneas, intracellular filters, and other unusual adaptations have also evolved much like those in the vertebrate eye. These compound eyes are usually constructed of individual units called ommatidia. These ommatidia do not vary greatly in size, ranging from 15–40  $\mu\text{m}$ , although their number can vary from 4000 to more than 25 000. The number and angle of units vary depending upon ecological habits, as you might expect. These numerous ommatidia create a mosaic of an upright image because each individual unit is stimulated by light of a slightly different incident angle. To understand the resolution of such an eye, one must appreciate the ommatidial angle. This concept reveals the angular extent of the visual field subtended by the combined ommatidia. Each ommatidium is set at a slightly different angle and, much like a digital camera with individual pixels, each ommatidium adds its separate view to the combined visual field. The number of ommatidia in combination with the angle of each determines the quality of the “grain” of the image. Of course, as the number of ommatidia increases, and the angle of separation decreases, the discrimination of the image increases. The trade-off for this increased image quality, at least in apposition eyes, is the loss of individual photon capture, and hence overall sensitivity. Although the individual angle has not been calculated in this species of bee, a closely related species has an angle that varies approximately  $1^\circ$  per ommatidial unit and thus sets the lower limit of resolution. The numerous interesting aspects of these compound eyes cannot be entirely explored in these paragraphs, so these issues will be revisited with other covers.

*X. micans* has an apposition eye divided into many ommatidia as can be seen on the top portion of the front cover. Each ommatidium measures approximately 25  $\mu\text{m}$  and can

probably resolve objects no smaller than those that subtend an angle of  $1^\circ$  or more (a human can probably resolve 100 times this in satisfactory conditions). In an apposition eye, each photoreceptor cluster will have its own optical system and will have a single spatial sample as an individual ommatidium. This allows for resolution at, or very near to, the optical limits of diffraction, and provides the best resolution for a compound eye. This apposition eye, on the other hand, will be restricted in sensitivity and the animal confined to daylight hours. Additionally, pigment is found between the individual crystalline cones, and is housed in the primary pigment cells distal to the photoreceptors. This pigment allows the insect to isolate the ommatidium optically in order to maintain image quality. Although the dark ommachrome pigment is similar to melanin, the pigment molecule is different. The visual pigments of these insects include pigments to respond to stimulation by short wavelengths including blue, violet, and ultraviolet. Interestingly, these pigments are bi-stable, meaning that a photon will convert this pigment to a thermostable metarhodopsin, which then can be converted back to rhodopsin by the absorption of another photon.

The less studied invertebrate photoreception system is seen in the bottom portion of the photograph. The three dome-like structures on the dorsal aspect of the head of this insect (with the geniculate antenna to the left corner of the photograph) are called ocelli. They are surrounded by hair-like structures that combine to create a gravity detection mechanism. This system, known as the Ishay organ, with the input from the ocelli, is probably responsible for navigation and gravity detection.

Ocelli are known as “simple eyes”. Despite the word “simple”, these structures still hold their secrets since we only superficially understand them. The three ocelli (and no one knows why their number can vary from one to three, or perhaps more) can distinguish light and dark and probably polarised light. In other related species, the ocelli seem to coordinate with the ommatidia to enhance or inhibit their function. There is evidence that these “simple eyes” are used for navigation, photoperiodicity, circadian rhythm, and shade detection. Evolutionarily, these organs are very old and probably began as successors to the primitive eyespots. In one species, *Triatoma infestans*, the ocelli have been observed to have an elongated “pupil” that is surrounded by a ring of reddish-brown pigment, which would correspond to the “iris”. Although this does not change shape with light stimuli, it does seem to change size with ecdysis (moulting of cuticular layer), as the corneal lens grows beneath the cuticular layer.

Our understanding of these ocelli is rapidly increasing as new tools are applied to the investigation. In a related wasp, *Vespa orientalis*, investigators have confirmed that an ocellus is composed of multiple units, each called an ocellon. This structure includes two reticular cells and a common rhabdom at the distal aspect of the reticular cells and a focusing element called a corneogenic cell to direct light toward the rhabdom. Surrounding the base of these elements, there is a canalicular system, which enables the insect to sense radial acceleration much like vertebrate semicircular canals (Rosenzweig *et al*, *Physiol Chem Phys Med NMR* 1998; 30:S241–69). It is this combination organ that probably senses gravity, and participates in navigation as mentioned. And we thought that the miniaturisation of computer products was fantastic.—IVAN R SCHWAB, MD, UC Davis Department of Ophthalmology, 4860 Y Street, Suite 2400, Sacramento, CA 95817, USA ([irschwab@ucdavis.edu](mailto:irschwab@ucdavis.edu))



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