COVER ILLUSTRATION

The best of a bad situation

Evolution is a meandering process that works by chance, error, and success using unfathomable lengths of geological time to produce the astonishing adaptations we see on earth. But, evolution is not a conscious process that would design according to set principles of biology, physics, or mathematics. As creatures evolve to fill empty niches, the aimless process of evolution cannot simply revert to an older model or start from scratch, but must proceed with the tools currently at hand. Bees prove the test.

Diurnal bees are principal pollinators for our robust and diverse angiosperm community (flowering plants). Although controversial, current evidence points to the emergence of the angiosperms in the late Jurassic or early Cretaceous periods, perhaps 150 million years ago. Since a food source rarely goes unexploited, these early flowering plants probably evolved in concert with their pollinators.

Eventually some angiosperms became nocturnal, and, as that would provide an opportunity, their pollinators would have co-evolved into the night. So, the diurnal pollinators of the early angiosperms had vision that was adapted for the torrent of photons of full daylight. Even now, most bees are strictly diurnal and visually do not tolerate even the limits of crepuscular light. So, what happened?

Nocturnal angiosperms would have provided a new and beneficial niche for any pollinator that would accompany them into darkness. After all, many predators and parasites attack diurnal bees, and a nocturnal life would eliminate the potential of predation by many of them. Moreover, there would be less competition for the food source since nocturnal birds are not interested in pollen or nectar, although some bats and moths would be. Additionally, nocturnal blooming angiosperms may have a higher protein and nectar content with anthesis (release of pollen/nectar) providing richer provender to any pollinator such as a bee. But, there is a catch.

Illustrated on the cover, *Megalopta genalis* is one such bee and the extent to which evolution has proceeded illustrates the power of this random process when it is combined with the pressure

Upper two images compare facets of megalopta and a diurnal bee (*Apis*) and lower two images compare rhabdoms of the same two. Scale bar = 25 μ m.

of competition and unimaginable spans of time.

Bees are a derived monophyletic group that probably arose in the mid to late Cretaceous period following the arrival of the angiosperms. The family of sweat bees containing this animal probably evolved in the late Cretaceous or early Palaeocene periods. Little fossil evidence exists to document when *Megalopta* evolved, but the best evidence suggests that this nocturnal bee preceded the fruit bats (*BJO* cover, November 2005), and may have helped usher in these species by permitting nocturnal angiosperms. The best amber evidence would suggest the Miocene (24 million years ago), although that is surprisingly late in the geological timescale, although it could have been earlier.

By the Miocene, though, bees were resolutely diurnal and had apposition compound eyes (*BJO* cover, March 2001) well tuned to that enterprise. Apposition compound eyes are not well suited to nocturnal activities, and those invertebrates that are crepuscular or nocturnal long ago evolved a different form of compound eye, known as the superposition compound eye (*BJO* covers, September 2001; September 2003; September 2004). Bees were too far along the ocular evolutionary path to return to these strategies.

M. genalis, then, had to enter a scotopic world with an ill suited eye. To permit this, evolution squeezed a surprising performance from this apposition compound eye. This social, Central American sweat bee can find the 6 mm entrance to its home in a hollowed out

stick and forage in the rainforest understorey at light levels equivalent to starlight. Humans would be blind to these objects at these light levels.

To accomplish this, *M. genalis* has several unique adaptations. The compound eye is composed of individual facets called ommatidia. The aperture of each ommatidium in this nocturnal bee is nearly double the diameter of the ommatidium in diurnal bees without changing the total number of facets (see fig, this page). This makes the eye considerably larger, thus giving the bee its generic name. The cells within each ommatidium, called rhabdoms, analogous to individual photoreceptors in our eye, are four times larger and somewhat longer than those found in diurnal bees (fig) (Warrant *et al*, *Curr Biol* 2004;14:1309–18). Using a camera analogy, the aperture is bigger and the shutter speed is slower, but this isn't enough to complete this task.

This neurological marvel uses spatial and perhaps a bit of temporal summation. Through an ingenious system of neuronal wiring at the level of the first order interneurons, the bee probably combines the input of many ommatidia to increase the receptive field. This is spatial summation (Greiner *et al*, *Cell Tiss Res* 2004;318:429–37) Temporal summation is also suspected but, as yet, its exact nature has not been unravelled.

These adaptations do degrade the image quality, and temporal summation, if it exists, will slow the recognition of movement. But it is better for this tropical *Halictid* bee to see a slower and coarser world than to see nothing at all.

This remarkable little bee survives in a world with light intensities that are 8 log units dimmer than those found in daytime, but it has not had the possibility to resort to the more conventional techniques seen in moths, nocturnal beetles or benthic arthropods of the ocean. In essence, evolution has, quite by accident, made the best of a bad situation.

I R Schwab,

University of California Davis, 4860 Y Street,
Suite 2400, Sacramento, CA 95817, USA;
irschwab@ucdavis.edu

E J Warrant,

University of Lund, Sweden

Cover image by Michael Pfaff and image on this page by Birgit Greiner.