Cover illustration

Low-vision device

Diffraction depends on the size, and limits the performance of an eye. As creatures become smaller, visual mechanisms become more challenging if sight is to be one of the primary sensory modalities, especially if the intended prey is yet smaller. Hence, a small creature risks sensory disability simply by being small, particularly if it is a predator. Resourceful solutions, however, have been found and perfected.

Mysid shrimp are a family of small decapods, each species generally being no longer than 5–15 mm. There cannot be much of an eye in such a creature. All shrimp have compound eyes, and the larger, long-bodied decapods have reflecting superposition eyes (*Br J Ophthalmol*, November 2006). However, *Dioptrromysis paucispinosa*, one of the smallest of the mysid shrimp at 5 mm in length, has refracting superposition eyes similar to those of moths (*Br J Ophthalmol*, September 2003). This particular species of mysid shrimp has another eye within the primary eye, as its generic name would suggest, providing two different ocular forms in the same eye. Moreover, this second eye is truly special.

Many mysid shrimp are shallow-water creatures, remaining motionless on the floor of warm coral reefs where they live. They feed on detritus and smaller living creatures. Generally, although they themselves are predators, these species are prey for other larger predators. To be a predator, then, requires vision at least good enough to sight its prey. As mysid shrimp themselves are often prey, they need a wide visual field and high sensitivity. These requirements are demanding for a creature that has an eye approximately 0.4 mm in size.

Compound eyes are defined in two general groups, apposition and superposition. Most diurnal insects, such as houseflies, have apposition eyes. These are perfectly adequate for such insects, as they are active in bright light. In apposition eyes, each facet lens represents a single point of light to the brain. To achieve better acuity in these eyes, the ommatidia must be smaller and more compact to create more individual points. This arrangement, however, is limited by diffraction, and the size of the ommatidia can be only so small. Nevertheless, some

Dioptrromysis from above. © Dan-E Nilsson.

species, such as the mantis shrimp (*Br J Ophthalmol*, February 2003) have zones of smaller, more compact ommatidia for more acute vision analogous to a visual streak in vertebrates or an infula in birds (*Br J Ophthalmol*, August 2000). Superposition compound eyes, however, are different optically as there is more space between the refracting elements and the rhabdoms, creating an upright image from each ommatidium (*Br J Ophthalmol*, November 2006). Narrowing the ommatidia in a superposition eye will not improve the acuity, but narrowing the rhabdoms and enlarging the optical elements, such as the lens, will. *D paucispinosa* has done just that to the optical and physical limits of its size.¹

Viewing these shrimp head-on would show a compound eye seemingly similar to other arthropods with multiple ommatidia. But, a closer inspection shows an unusual nipple-like projection from the lateral aspect (white arrows on upper cover image). Viewing the animal from behind is positively eerie, with what appears to be a backward-looking eye (black arrows on lower cover image). This appears to be an eye because of the black spots in the centre, called the pseudopupils. A pseudopupil is a feature that has elements absorbing all the incoming light and not reflecting any back, looking right at you, if you will.

The frontal view shows what is actually a refracting superposition compound eye, much like those found in moths, but the posterior structure is quite different and most extraordinary. The projection that appears to be “looking directly at you” is indeed a lens, and is combined with the necessary rhabdoms (photoreceptors) present deeper within the eye to create a simple eye. Simple eyes are generally a

lens with photoreceptive elements located behind it, somewhat akin to a camera-style eye, but without its complexity. Generally, simple eyes are just that—simple—and do not generally provide good spatial vision.

This simple eye, however, is different. It has evolved from the superposition eye that accompanies it and has a resolution comparable to insects 10 times its size. The more conventional compound eye, or normal eye, has better sensitivity, but poorer acuity. This simple eye has evolved to allow the creature to maximise its acuity for such a small eye because its rhabdoms are light guides at the lower limit of size, and are, at that size, diffraction limited. Apparently, this animal has reached the physical optical limits with this eye to achieve the absolute best vision in such a small package.

Why, then, would this evolutionary wonder point such an eye backwards? Actually, it does not, despite its appearance. When needed, *D paucispinosa* will rotate the eyestalks 130° to bring this “acute-zone” simple eye into the frontal position for direct viewing. It is as if it has added a low-vision device—like a pair of binoculars—to its primary visual system. It can swing these acute-zone eyes into proper position in approximately ≤ 0.16 s. Furthermore, there is binocular overlap of approximately 15° with the contralateral eye, creating binocularity, and there is probably stereopsis, although this is not confirmed.

In essence, *Dioptrromysis* shrimp have a simple eye within a compound eye, the simple eye functioning much like binoculars would function as a low-vision device.

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Photographs by Dan-E Nilsson.

REFERENCE

- 1 Nilsson D-E, Modlin RF. A mysid shrimp carrying a pair of binoculars. *J Exp Biol* 1994;189:213.