
Lee R. Berger

Nautilus from the side.


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Head of an Eastern diamond-back rattlesnake with one of two distinctive cranial pits.


Robert S. Simmons

Fluted giant clam

The Eye in the Spiral: Animals with Pinhole Visual Systems

Stephen R. Wilk

Most organisms have evolved precise, camera-like visual systems that allow them to easily find food and escape danger. But a few still rely on lensless eyes with crude pinhole optics. Why?

Evolutionary biologists have postulated that the visual systems of most animals began as light-sensitive patches of cells. These areas eventually became further specialized and were enclosed as simple pinhole structures. Finally, over time, pinhole optics were displaced by more sophisticated visual systems that included lenses, which can concentrate more light and produce detailed images. Following this developmental sequence, vertebrates and cephalopods independently evolved eyes with the same general structure as one another, including a cornea, iris, lens and retina within a spherical capsule.

Compared to lens-based optics, pinhole visual systems are inefficient: If the eye has a small hole, its sensitivity is very low; however, if the hole is enlarged to admit more light, the eye's imaging quality becomes poor. Thus, pinhole eyes lost out evolutionarily to the modern camera-type eye, which combines a good light-gathering ability with high-quality imaging.

Seeing heat and shadows

Yet the pinhole eye persists, in three different cases. One of these is the "pits" of pit viper snakes (*Crotalinae*) and some pythons (*Boidae*). These pit organs occur in addition to standard eyes; they are deep indentations between their eye and nostril on either side of their face, with a somewhat restricted entrance (whose size is much larger than one would like to call a "pinhole") and a floor lined with infrared-sensitive cells. Because of the large aperture, pit organs allow a snake to "see" blurry images of radiant heat. This is very useful feature for a creature that hunts for warm-blooded prey, especially when combined with ordinary light-sensitive vision.

The second organism with pinhole structures is *Tridacna maxima*, the giant clam, which has several hundred dark eyespots around the border of its mantle. Each 500-μm-diameter eye has a 90-μm-diameter aperture. Based on the animal's response in experiments, and on the optics of the eye, researchers have determined that the clam's eyes have a resolution of about 20°.

In this instance, the pinhole structure actually confers a biological advantage to the clam, which closes its shell in response to dimming light (a defensive reaction that occurs when predators such as birds and fish cast a shadow overhead). Due to its relative insensitivity, the eyes

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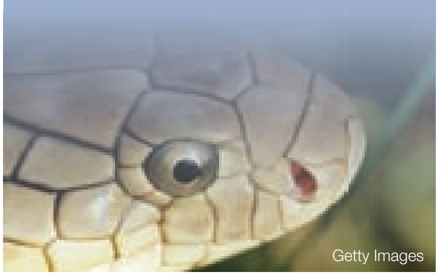

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act as a behavioral filter, keeping the clam from constantly opening and closing its shell, as it would do if it had a more developed visual system.

The pinhole structure provides just the right level of sensitivity. A less developed eye wouldn't serve the clam well. According to Michael F. Land, who has studied the clam's eyes at length, the pinhole system allows the clam more time to react than would be possible if its eye had mere shadow sensitivity (i.e., only light-sensitive patches), enabling the clam to retract its sensitive mantle before a predator can approach.

Thus, the clam's pinhole eyes seem like a "Goldilocks" solution to its environment: They are sensitive enough to allow the animal to protect itself when danger looms, but not so sensitive that it responds to every stimulus.

The mysterious nautilus

The third case of the pinhole eye is found in a distant relative of the octopus—which is surprising given that octopus eyes are often described as similar to those of humans. Two simple, lensless eyes are found in the most unusual of the cephalopods, the one with the spiral shell that has inspired submarine christeners and exercise machines: the chambered nautilus.

The nautilus is part of a group of marine mollusks known as the nautiloids, which developed during the Cambrian period and are now mostly extinct—except for the chambered nautilus. Today, the nautilus is restricted to the Southwestern Pacific. It is a nocturnal creature with an active and unusual optical sense.

Its eyes consist of two elongated ovals, each about 10 mm long × 15 mm wide. The distance from pupil to retina measures about 9 mm, and the pupil is an ellipse measuring, on average, about 2 mm high × 1 mm wide. There is neither lens nor cornea in the eye, and the pupil is simply an opening to the outside, so the interior of the eye is filled with seawater. There is a trough running vertically downward from the pupil, which is lined with cilia that can propel water. Biologists have speculated that these hairs provide a current of water across the pupil that keeps it free of debris.

In 1983, W.R.A. Muntz and U. Raj made models of nautilus eyes with different pupil sizes and used them to photograph standard eye charts. With the smallest pupils (1 mm high × 0.4 mm wide), horizontal features could be clearly discerned, but vertical features were nearly blurred out by the larger pupil dimension. For larger pupil sizes (2 × 1 and 2.8 × 1.7), structural details were almost lost along both directions, although the locations of the objects were nevertheless very evident.

The nautilus use their vision to orient themselves, both horizontally and with regard to their surroundings. To test this, Muntz and Raj placed the animal in a tank surrounded by drums with regularly spaced stripes; in one case, the stripes subtended angles of 22.5° and 11.25°, while in another they subtended angles of 5.5° and 2°. When the researchers rotated the drums, the nautilus rotated to follow the stripes, but only when they subtended the larger angles. This experimental evidence accords well with the visual acuity of about 5° that Muntz and Raj had calculated based on the eye model.

One would expect that the retina of the nautilus, like that of the giant clam, would have a primitive system of sensing cells to match its coarse optical resolution, but the density of receptors is actually comparable to that of other cephalopods that can resolve objects with 17 minutes of separation.

Thus, the visual system of the nautilus is something of an enigma. The animal has crude pinhole resolution that is better for horizontal than vertical objects, yet it also has a densely packed retina. It lives in a low-light environment, but can apparently compete with creatures that have more highly developed eyes with better light-gathering capability. Muntz and Raj estimate that comparable eyes with lenses would gather two orders of magnitude more light.

Moreover, despite the fact that vision is clearly important for the organism—it has demonstrated the ability to learn based upon vision—its optical system seems extremely primitive. In fact, early researchers, finding no lenses in the nautilus, were concerned that they had misplaced the lenses in the process of preserving their specimens.

What is the reason behind the nautilus's visual system? Do they hunt for bioluminescent prey? (Muntz and Raj raise the possibility, but point out objections as well.) Can their brains process the information from the blurred images passing over the dense receptors and deconvolve to obtain high-resolution information? Are the features remnants of an earlier complexity that has somehow resisted genetic drift? This beautiful, 500-million-year-old creature holds many secrets.

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