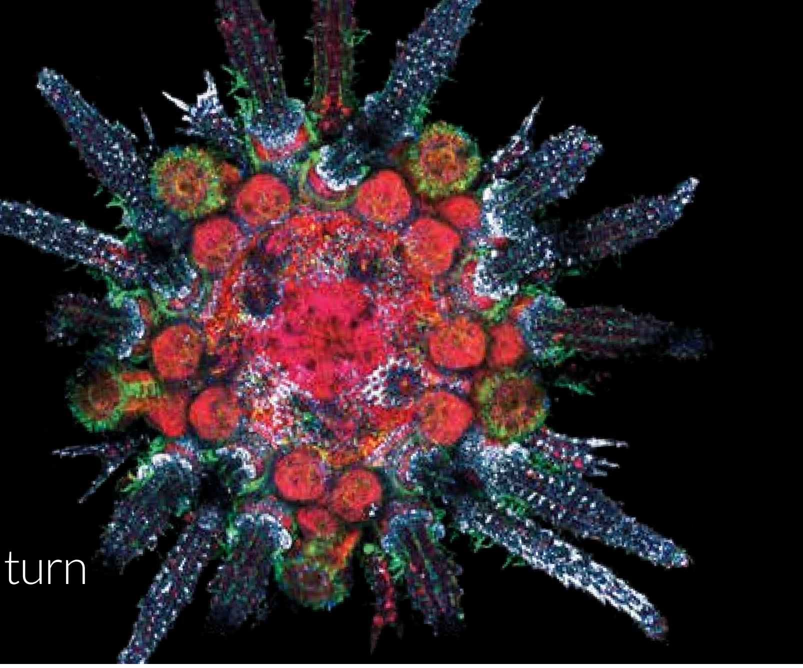
FEATURE

Strange VISIONS

The study of animal sight takes a turn toward the bizarre

By Susan Milius



A lab image of a juvenile purple sea urchin (*Strongylocentrotus purpuratus*) — without obvious eyes — shows an abundance of light-detecting proteins, such as c-opsins (red).

It sounds like a riddling trick: How can an animal with no eyes still see? But it's a serious scientific question — the trickiest kind of riddle.

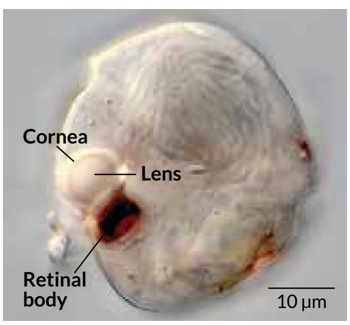
Sea urchins don't have anything that people recognize as an eye, says Sönke Johnsen of Duke University. Urchin bodies are mobile pincushions in purples and pinks to browns and blacks, bristling with a mix of spiky spines and soft, stretchy tube feet.

Yet at times urchins act as if they "see" large-enough somethings in their world, even if the how and what of their visual systems have been hard to pin down. "Maddening," Johnsen says. "They almost always have what looks like purposeful behavior, but you can't quite put your finger on it because there's something so alien about them."

Thus 21st century science has come to take seriously the idea that an urchin doesn't have an eye, but *is* an eye. Earth may be home to creatures whose whole bodies serve as big eyeballs crawling on a thousand tiny, soft feet.

This crawling-eyeball hypothesis illustrates a surge of interest in exotic vision. For decades, a few vertebrates (including humans, goldfish and cats) plus fewer insects (mostly honeybees) dominated vision research. No more. "We're not just focusing on eyes that look like our eyes," Johnsen says.

More recent investigations explore eyeballs in creatures too small to have brains to use them, skin with a light-sense of its own, vision in scallops and octopuses and in butterflies that, via the twists of evolution, developed eyes on their heads as well as light sensors on their rumps. Looking into such a wide array of strange eyes or almost-eyes reveals how evolution has solved the basic problem of extracting information from light in an extraordinary variety of ways.



What looks a bit like a vertebrate eye, with cornea, lens and light-catching retinal body, evolved in a tiny single-cell warnowiid (*Proterythropsis* shown).

"What it means to be an eye is so much broader than we originally thought," Johnsen says. In all this diversity, who's to say an urchin can't be its own spiny eyeball? The idea has been challenging to test, with brainstorms bumping against frustrations. Years of research delved into parts of the idea, and then a burst of discovery about genes for opsins, the main light-catching molecules in animal vision, changed the rules. Through it all, urchins continue to be maddening wonders.

Eye icon

The eye has held a special place in biology since Victorian eyeballs caught sight of, and possibly squinted skeptically at, Chapter VI in *On the Origin of Species*. Under "Difficulties of the Theory," Charles Darwin chose the eyeball as an example of "organs of extreme perfection and complications." To imagine that such a marvel arose by mere evolutionary happenstance, he wrote, "seems, I freely confess, absurd in the highest degree."

Of course he doesn't really allow this alleged absurdity to ding his lifework's theory. He immediately proposes a way for extreme perfection to start simple: The building blocks of a fancy eye, he points out, could themselves in their simple form "be useful to any animal under changing conditions of life." Minimal light-sensitive cells might not manage even the blurriest image, but could sense big changes such as day turning to night.

Darwin's absurd eyeball was presumably a camera-style belonging to a vertebrate. (Light enters through a cornea and lens, which focus it on the "film," the swath of light-sensitive photoreceptor cells at the back.) Current research excursions far beyond vertebrate eyeballs are taking the ideas in Chapter VI to new places.

A paper published last year in *Nature*

traced the origin of the simpler parts of a camera-style structure, the parts that Darwin thought must have been useful in themselves. The structure, however, was not in a human or even an animal but in single-celled marine plankton.

A microscopic lens-and-film structure, an ocelloid as it's called, peers out cyclopslike from one side of certain predatory warnowiids. Flicking a little flagellum tail sends a warnowiid corkscrewing through the ocean, the ocelloid scanning as the cell turns.

The diameter of the film in the plankton's microcamera is tiny even compared with the wavelengths of light it receives, says study coauthor Gregory Gavelis of the University of British Columbia in Vancouver. The view through such an "eye," if "you were to project it on a screen, would probably look like one pixel," he says.

Simpler sensitive spots let other microbes swim toward, or flee, light according to their needs. So Gavelis wonders if warnowiids do something more complex with their ocelloid. That single pixel could be useful, he speculates, if it detected some quirk of light, maybe polarization, reflecting off prey.

Even at this scale, Darwin was correct about eye components evolving from simpler structures that had their own uses. The main clear bulge that serves as lens and cornea in warnowiids evolved from what were once mitochondria, vital power stations in the cell. And the swath of photoreceptors that act as film in the camera came from a stolen chloroplast, a nugget that had transformed sunlight into carbohydrates to feed some ancient red alga.

Scaling up to actual animals finds new and odd examples of eye parts useful in their simplified form, even in animals that also have complex image-forming eyes.

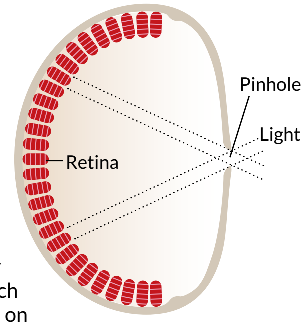
Octopuses stare out of camera-style eyes that are remarkably like vertebrates'. But octopus skin also has photoreceptors that detect light and then cue color changes, Todd Oakley and Desmond Ramirez of the University of California, Santa Barbara reported in 2015 in the *Journal of Experimental Biology*. Shifting color can communicate or camouflage. Exposure to light can trigger waves of yellow and brown even in bits of skin completely detached from the octopus — no connection to a brain needed (*SN: 6/27/15, p. 10*).

Backup sensors for awkward body parts might explain eyespots in Asian swallowtail butterflies (*Papilio xuthus*). They flap pale, stained-glass wings, and their insect-style, compound eyes can outdo human vision to detect ultraviolet or polarized light. Despite these capable eyes, both males and females of the species have eyespots, the most basic of light-sensing organs — just a cluster of photoreceptors — on their genitals.

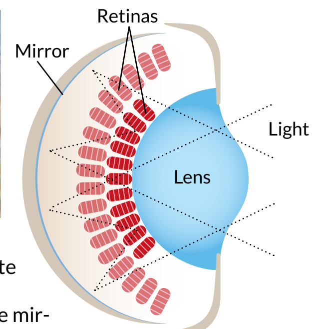
The genital eyespots may help with basic butterfly positioning, suggests Kentaro Arikawa of the Graduate University for Advanced Studies in Hayama, Japan. In his tests, males that had their eyespots removed fumbled during mating as if having trouble orienting themselves. Spotless females had a different problem. They mated and found leaves on which to lay their eggs, as they normally do. But without feedback from eyespots,

Oddball eyes

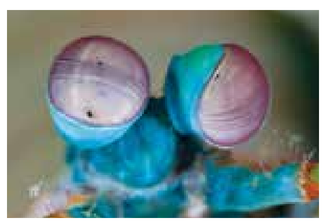
The familiar vertebrate eyeball with a lens focusing light on a retina is just one of 10 basic kinds of visual organs that have evolved in animals. Here are four underwater standouts.

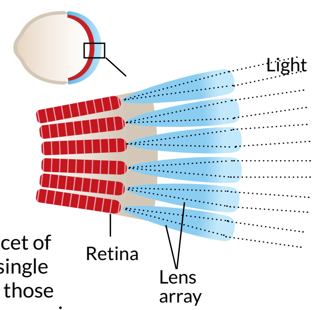


Nautilus This invertebrate relative of squids doesn't use a lens. The tiny eye opening restricts light entry much as a pinhole allows an image to form on film inside the simplest cameras.

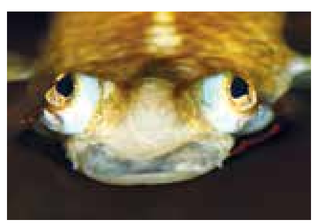


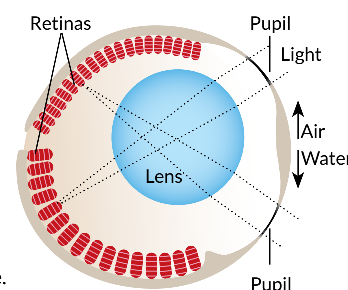
Scallop The tiny eyes rimming the body of a scallop look like vertebrate eyes, but in the 1960s, researchers showed that it's not the lens but the mirror at the rear that's focusing the light.





Mantis shrimp Each clear outer facet of this compound eye sends light to a single photosensitive structure. A zone of those structures (band across middle of the eye in image) holds the color-detecting sensors.





Four-eyed fish These are vertebrate eyes with special features handy for swimming at the surface. Light from the airy world enters through a different opening and registers on a separate retina than light from water below.

SOURCES: NAUTILUS AND FISH: T.W. CRONIN *ET AL*/*VISUAL ECOLOGY* PRINCETON UNIV. PRESS, 2014; D.I. SPEISER, E.R. LOEW, AND S. JOHNSEN/*J. EXPT. BIOL.* 2011; T.W. CRONIN

PHOTOS FROM TOP: ATESE/ISTOCKPHOTO; S. JOHNSEN/DUKE UNIV.; © SCUBAZOO/ALAMY STOCK PHOTO; H. ZELL/WIKIMEDIA COMMONS (CC BY-SA 3.0); DRAWINGS: E. OTWELL the females failed to actually lay any eggs, Arikawa reported in 2001.

Simple parts can be reworked in different combinations for lots of eye diversity. Giant clams, sometimes larger than a soup tureen, watch for danger with many tiny pinhole cameras punctuating the lips of their mantle. So-called four-eyed fish double each of their two eyes, one half better tuned to seeing above water and the other better for below the surface.

Scallops at first glance look as if they have vertebrate eyes, a rim of dozens of mini-marble eyeballs, some sky-blue with a dark spot of pupil. Scallops and people have eyed each other for millennia, but not until the 1960s did Michael Land of the University of Sussex in England demonstrate that the mirrored surface at the back of the mollusk's eyeball does most of the image focusing, as does the lens in a vertebrate eye.

Scallop eyes have a "squishy" lens that makes only minor adjustments as light streams in and hits the eyeball's inner mirror, says Daniel Speiser of the University of South Carolina in Columbia. As the light bounces forward again, the mirror's curve focuses it mainly on one of two retinas stacked well within the eyeball. After more than a decade of puzzling over what a second retina might do in scallop eyes, Speiser says "they remain confounding." But their focusing mirror beat Newton's reflecting telescope by millennia.

Inscrutable urchins

Where urchins fit in this parade of animal vision remains to be seen.

To be a crawling eyeball in the best sense of the term means detecting not just light but also where it comes from. "If you just have a ball, the ball can't really see," Johnsen says. Its own bulk might shade light on one side from reaching the other, but that's not much use for pinpointing light direction. To detect objects or form images, an eye needs more detailed information about where light is and isn't. Some structure has to restrict the incoming light for the photoreceptors. Putting together multiple bits of visual information is what yields an image.

Johnsen credits J.D. Woodley, then at the University of the West Indies in Jamaica, as an early source of the idea that urchins are roving eyeballs with an outer surface that is generally sensitive to light. What made an urchin's bun-shaped body able to locate where light comes from, he proposed, was shading from its many spines. In 1982, during a talk at the International Echinoderm Conference in Tampa, Fla., Woodley suggested that for any patch of urchin body, the forest of spines would allow only restricted shafts of light to penetrate. "It's like being down a well," Johnsen says. "You can only look up."

Experimenting with urchins and their echinoderm relatives is notoriously difficult. "You can have this whole group of animals that will do something that makes a lot of sense. But then you test them a few days later, or test a different batch, and you get a totally different answer," he says.

Nevertheless, Johnsen and his students built "a glorified wading pool" with a glass bottom raised enough for a person to slide underneath and look up at urchins moving on the bottom. "Like watching paint dry," he says. "They're painfully slow."

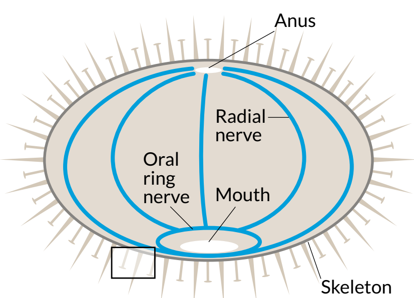
To give urchins a read-the-letters eye test, student Erin Blevins fastened various circles of black plastic one at a time to the pool's wall and released an urchin in the center. Two species of burrow-dwelling *Echinometra* urchins didn't seem to notice spots covering a small part, only 16 or 26 degrees, of the 360-degree view. But a larger, 33-degree spot drew urchins toward it, possibly by mimicking the dark entrance to a burrow, she and Johnsen reported in 2004. These urchins may not be great at resolving details, but they do more than just tell day from night.

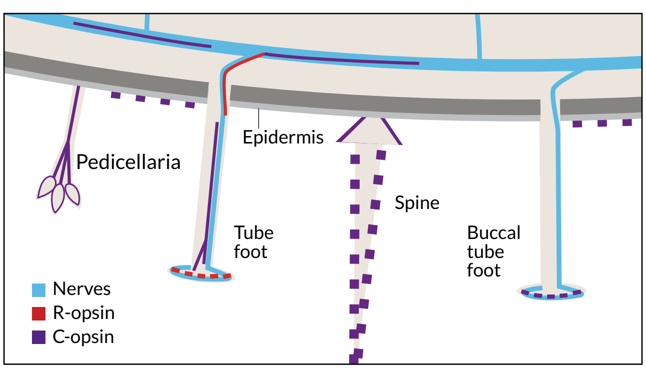
Testing another piece of Woodley's idea about spines, a later student, Divya Yerramilli, and Johnsen considered spine density. They hypothesized that urchins with dense spines might resolve details better than those with sparser coverings. The more tightly packed spines, in theory, would divide the light-sensitive urchin surface into a greater number of little areas with narrow views, a bit like more pixels reducing blur on a computer screen.

The two reported just that in 2010. Densely spined purple urchins (*Strongylocentrotus purpuratus*) detected a smaller spot than the more loosely spined species in earlier experiments. In the pool, the urchins detected a 10-degree black spot and tended to creep toward it or away. (The mix of retreat and advance may mean the spot was scary ... or inviting, hard to tell with alien minds.)

These results fit with the notion of spines shading the urchin surface, but they didn't prove that's what makes the vision work. "Figuring it out from there gets a little tougher,"

The details A sea urchin (schematic, right) has no centralized brain, just large nerves (blue) that connect to a ring around its mouth. However, its outer surface (below), with defensive spines, tube feet and pedicellariae grippers, has two kinds of light-detecting opsin proteins.

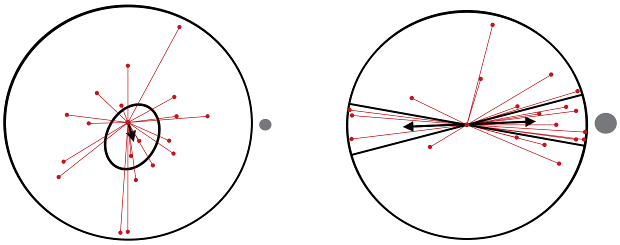




SOURCE: E.M. ULLRICH-LÜTER *ET AL/INTEGR. COMP. BIOL.* 2013

E. OTWELL

Seeing spots In a lab test for vision, purple urchins crawled from the center of a pool in random directions (left) as if they didn't see the small spot on the outer wall. With a larger spot, most urchins noticed, either approaching it or fleeing (right).



Johnsen says. "You have to do something gruesome like take the little spines off and the urchins sort of like — die."

Opsins everywhere

Then advances in automated genetic analysis led to a rush of discoveries of opsin molecules that told a twistier urchin story.

Opsins are the proteins that make animal eyes possible. People also have other light-sensing molecules, such as the cryptochromes that surge and fade to keep the body's day-night rhythms. But opsins are the celebrity molecules that let photoreceptors in the retinas of humans and other animals see.

A sea urchin close-up shows surface spines as well as darker, stretching tube feet possibly involved in vision.

The various opsins lie embedded in cell membranes and share the basic structure of a cluster of seven dangling curlicues. A naked opsin isn't of much use for vision, but its superpower is the ability to maintain a connection with a catcher's mitt of a molecule called a chromophore. The mitt absorbs a photon of light and unkinks itself into a longer, straighter form. That shape change triggers the attached opsin to change shape too, which sets off the biochemical cascade that ends up with a brain seeing, say, a carrot in all its orangeness. In humans and most other animals, chromophores are forms of retinal, derived from vitamin A, abundant in those showy carrots.

Thanks to DNA studies, the growth in sheer numbers of opsin forms being discovered is "explosive," says Thomas Cronin of the University of Maryland, Baltimore County. In 2012, Cronin's then-student Megan Porter and their colleagues published a family tree of the proteins' evolutionary relationships, created by using 889 opsins. "Probably the number of opsins that have been sequenced since then is 50 percent to 100 percent higher," Cronin says.

"We're at this point where we have all this information about the opsins that exist," says Porter, now at the University of Hawaii at Manoa. "But for a lot of these, we don't know what they're doing."

Some might not have anything to do with light at all. Opsins appear in sperm of mice and men, Michael Eisenbach of the Weizmann Institute of Science in Rehovot, Israel, and colleagues wrote last year in *Scientific Reports*. The opsins are sensitive to heat and may help sperm navigate their way by temperature, the researchers propose. If so, sperm opsins do it splendidly. A single sperm reacts to a difference of less than 0.0006 degrees Celsius across its body length. Rather than crawling eyeballs, sperm might just be swimming thermometers.

Urchins 2.0

Esther Ullrich-Lüter's opsin search was all about sea urchins when she worked in Maria Ina Arnone's lab at the Anton Dohrn Zoological Station in Naples, Italy. A big international collaboration had unveiled the majority of genes for the purple sea urchin in 2006, confirming that the animal without obvious eyes had genes for light-catching opsins. In fact, urchins have genes for at least eight different opsins.

With the genes' sequences in hand, Ullrich-Lüter could do molecular studies to locate them in the urchin body. This project started looking for particular opsin forms in urchin larvae (which are easy to get). After a year of slow progress, the researchers added adults as test subjects. In a what-if whim born of frustration, Ullrich-Lüter tested the adult tube feet. Bingo.

The soft extendible foot projections rise among the spines over the whole body of the urchin. At the tips of the feet and in a cavity at the base of each foot were concentrations of rhabdomeric opsins, which are vital to invertebrate vision, Ullrich-Lüter and the Arnone team reported in 2011. But these r-opsins were not scattered across the urchin surface, which would have supported the spine-shading idea. Ullrich-Lüter instead proposed that opsins in the little cavities at the bases of the tube feet would be shaded enough to detect light direction.

Plowing forward, the researchers uncovered a whole second visual system in the urchin, based on a different set of opsins. Ciliary opsins, or c-opsins, were scattered all over the urchin surface, Ullrich-Lüter and colleagues reported in 2013. "We thought, oh my god, this could be the reason for this long-proposed dermal light sense," she says. But it wasn't that simple.

The same study found c-opsins on the spines and tube feet too. If the spines themselves perceive light, she asks, how could they offer shading? Ullrich-Lüter and collaborators at Lund University in Sweden continue to study the puzzling animals. Her best bet is that the cavities around the feet are the key to urchin vision. Johnsen's current opinion: "Tough to say."

There may indeed be eyes in the maddening urchins. But it's going to take more science to see them. ■

Explore more

- Thomas W. Cronin *et al.* *Visual Ecology*. Princeton University Press, 2014.