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Do 'Eyeless' Shrimp See the Light of Glowing Deep-Sea Vents?

by

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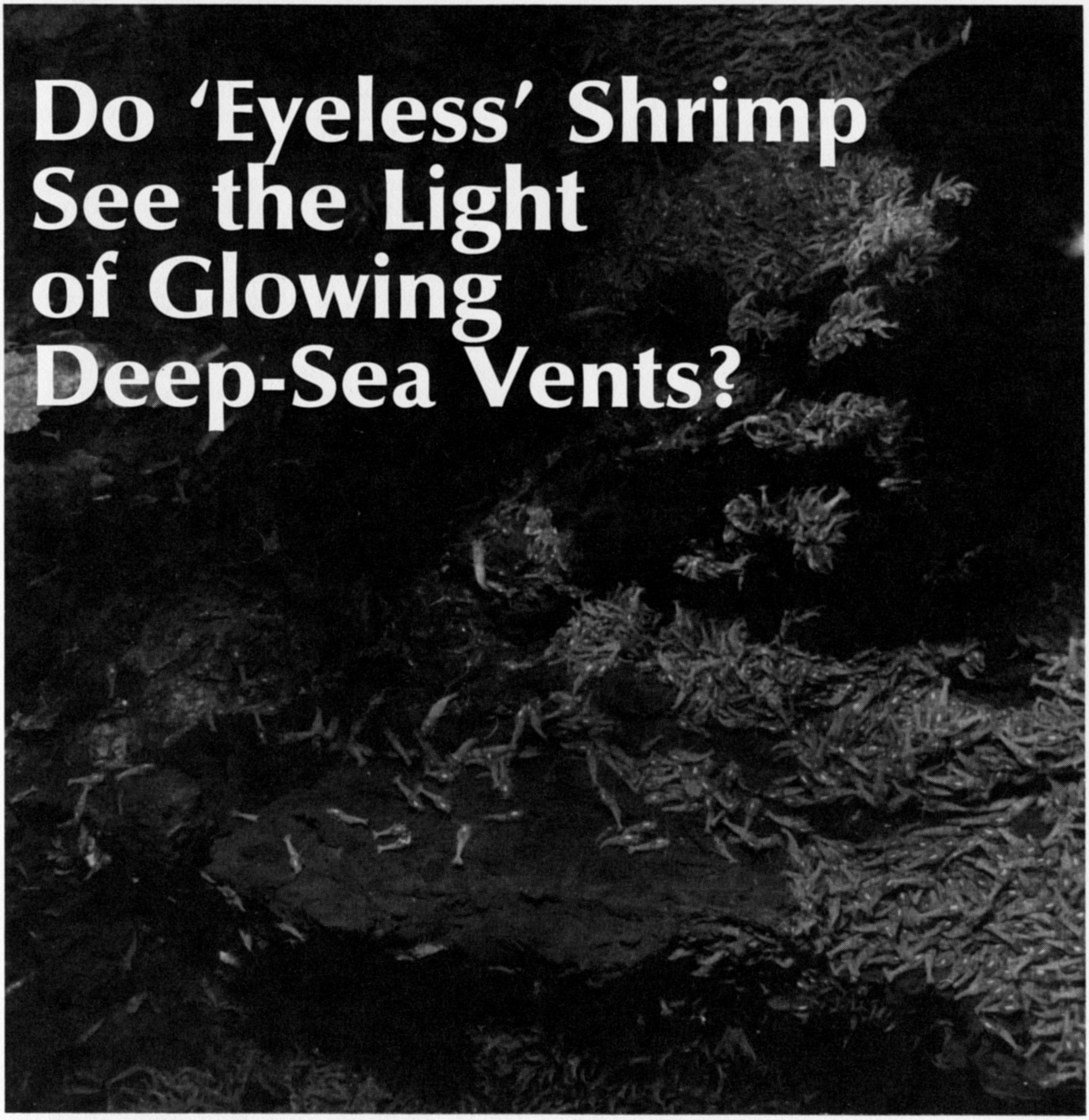

Swarms of shrimp cover the surface of a black smoker chimney in a Mid-Atlantic Ridge hydrothermal vent field. (Photo courtesy of the author)

by Cindy Lee Van Dover

My visitors quickly focus on the heart of the matter. "But do they turn pink when they're cooked?" I'm asked, as I try to describe the gray shrimp living at hot springs deep in the Atlantic Ocean. It is a reasonable enough question, since the shrimp crowd around plumes of black, 350-degree-Celsius water pouring out of sulfide chimneys on the seafloor. The shrimp are protected from the cauldron, though, by seawater drawn up beside the rising plume. Further, the heat escaping from the earth's interior is quickly absorbed by the surrounding seawater. Within a few centimeters above the chimney orifice, the temperature of the plume is a comfortable 20 degrees, and within a meter it is an icy 2 degrees. Still, wouldn't the occasional shrimp find itself caught up in water hot enough to turn it instantly to deep-sea bouillabaise?

It was a geologist, Peter A. Rona with the National Oceanic and Atmospheric Administration laboratory in Miami, who first discovered hot springs in the Atlantic in 1985 (Location 2, map, p. 44), and collected shrimp for biologists to examine. Using a dredge to sample the

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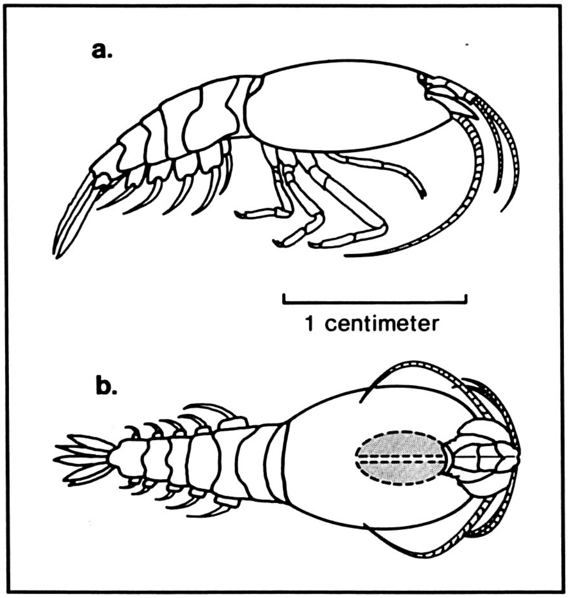

Figure 1. (a) Side, and (b) dorsal views of Rimicaris exoculata. *Shaded area indicates the location of the unique "eyes," visible as bright spots in the photo on page 47.*

seafloor from a surface ship, Rona picked up hundreds of shrimp and pieces of black sulfide chimneys. Most of the shrimp (Figure 1) quickly found their way to the Smithsonian Institution in Washington, D.C., where Austin B. Williams, one of the world's experts on animals such as shrimp, lobsters, and crabs—collectively known as decapod crustaceans—studied them. Williams and Rona published descriptions of two new species of shrimp, assigning them the names *Rimicaris exoculata* and *Rimicaris chacei*. The generic designation, *Rimicaris*, is from the Latin *rima*, meaning rift or fissure, and refers to the Mid-Atlantic Rift; and *caris* means shrimp. The specific name *exoculata* refers to the fact that this species is deprived of any vestige of the usual shrimp eyestalk or cornea; *chacei* is named in honor of Fenner A. Chace, a renowned taxonomist of decapod crustaceans. Both species are members of same taxonomic family as the shrimp that are known from Pacific hydrothermal vents.

Swarms at hot vents

The Pacific shrimp live inconspicuously as ordinary scavengers among groups of other animals at deep, warm (2- to 20-degree-Celsius) water springs. But the Atlantic branch of the family is far and away the more remarkable in terms of its ecology. For one thing, *Rimicaris exoculata* has been found only on active, high-temperature sulfide chimneys; investigations of chimneys venting "cooler" (200-degree) water have yet to show any presence of *R. exoculata*. In this environment they encounter extreme water temperature gradients—only a few millimeters may separate 350-degree water from 2-degree water. Spectacular crowds of these shrimp, with as many as 1,500 individuals per square meter, have been observed completely obscuring the surface beneath them. And they don't just sit quietly, but constantly move about in such a way as to prompt John M. Edmond, a geochemist at the Massachusetts Institute of Technology who has visited the Atlantic hot springs in *DSV Alvin*, to describe them as "disgustingly like swarming maggots on a hunk of rotten meat." While I might have opted for a more engaging analogy—say, "bees dancing on a hive"—Edmond's imagery does justice to the sight.

Another extraordinary feature of the Atlantic shrimp is that they dominate the fauna at Atlantic hot springs. This contrasts sharply with springs of the eastern Pacific, where lush, exotic communities of tubeworms and bivalves crowd around cracks in the seafloor through which warm water issues (article, pp. 41–46). It is the tubeworms and bivalves that have become famous for their symbiotic associations with sulfur-oxidizing bacteria, housed within special tissues, and producing most, if not all, of the animals' nutrition. The Atlantic shrimp, however, do not host symbiotic bacteria. Instead, the shrimp appear to gather their food by mining the sulfide surface of the black smoker chimneys on which they live. The tips of the legs of these shrimp have strong, file-like spines that may be used for rasping. Their first pair of legs, located very near the mouth, have scoop-shaped claws that look well-designed for picking up small bits of loosened sulfide; a brush-like appendage then sweeps the sulfides out of the scoop and into the mouth (Figures 2 and 3).

On post-mortem examinations of collected specimens, I found every stomach packed solidly full of sulfide minerals. Of course, there isn't much nutrition to be gained from the sulfide minerals themselves. But we think that associated with the sulfides are tremendous numbers of free-living bacteria. Like the symbiotic bacteria of the eastern Pacific, these bacteria would have to grow by using the chemical energy in reduced sulfur compounds (plentiful in the hot vent water) to convert carbon dioxide and water into bacterial tissue, in much the same way as green plants use the energy of sunlight to convert carbon dioxide and water into plant tissue. Bacteria-laden sulfide minerals are ingested by the shrimp, the bacteria are digested, and the undigested minerals are eliminated. This mode of feeding would account for the determined way the shrimp seem to attack the sulfide chimneys, as if desperate to glean yet more bacteria from an otherwise unpalatable substrate.

Palatability raises another issue: are the shrimp good to eat? The opportunity to address this question arose during the visit of a very distinguished and discriminating colleague from the University of Newcastle, Great Britain, J. R. Cann. In the true spirit of scientific experimentation, we gathered around the laboratory Bunsen burner one afternoon, took one of the shrimp from the freezer, and boiled it. It did not turn an appetizing pink. If anything, it turned a still more unappealing shade of gray. As we might have expected, given the sulfide environment of the shrimp, the flesh tasted of rotten egg, and if that were not enough, the texture of the beast was as I imagine a rubber band might be. Perhaps it was overcooked. We concluded from our experiment that there will be no market for these shrimp among the gourmandizing public.

To see, or not to see?

In studying photographs and videotapes of the shrimp to learn about their behavior, I could not help but notice a bright reflective spot on the dorsal surface, or back, of the shrimp. Knowing that sooner or later someone would ask me about those spots, I carefully looked at some preserved specimens and discovered that the spots correspond to the paired lobes of a very large and unusual organ just beneath the thin, transparent carapace. Each lobe was connected to the brain of the shrimp by a large nerve cord. Despite the absence of lenses or another image-forming device, I guessed that the lobes corresponded to eyes of a sort never encountered before. My guess was hardly proof, as my colleagues were quick to point out, so I set out to find what was needed to prove that they were indeed some sort of weird eye in this otherwise eyeless shrimp.

The proof required turned out to be the unequivocal demonstration of the presence of a light-sensitive visual pigment. There are two straightforward ways of doing this: one relies on immunological techniques, which identify molecules on the basis of structure; and the other is a biochemical assay, which identifies molecules on the basis of function. Ete Z. Szuts, a sensory physiologist at the Marine Biological Laboratory in Woods Hole, was willing to perform the biochemical assay. Together we dissected the organs from frozen shrimp under the surreal conditions of a red-lit laboratory. Then Szuts purified the membranous material that should contain the visual pigment, and

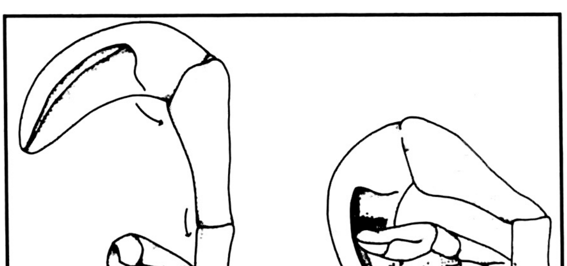

Figure 2. The first pair of legs, or chelae, of the shrimp are scoop-shaped. Sulfide particles with encrusting bacteria are scraped from the chimney surface, and shoveled into the shrimp's mouth using them.

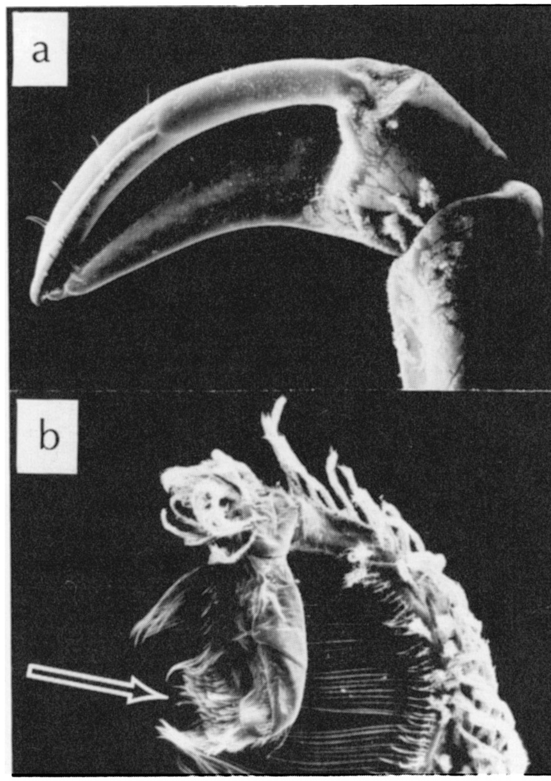

Figure 3. (a) Scanning electron micrograph of claw of first leg. (b) Arrow points to brush that sweeps sulfide particles into shrimp's mouth. Arrow also indicates scale, length = 1 millimeter.

extracted whatever pigment there was in the membranes with a mild detergent. We used a spectrophotometer to measure the amount of light at different wavelengths absorbed by this extracted material, first in the dark and then after bleaching the extract with a light. The two measurements are necessary since visual pigments are light-sensitive, and have characteristic absorption spectra under these different light conditions.

It is an elegant procedure, producing satisfyingly concrete evidence when it works, as it did for us. In the extracted material, there was a substance that absorbed maximally in the long wavelength, blue-green part of the spectrum; on bleaching, the product absorbed maximally at shorter wavelengths. The shape of the absorption spectra of the shrimp pigment closely match those of rhodopsin, the visual pigment found in eyes of both vertebrates and invertebrates.

Building on this evidence, we turned to Steven C. Chamberlin of the Institute for Sensory Research at Syracuse University, New York, for a morphological description of this novel organ. His work, involving the laborious preparation and sectioning of material for microscopy, identified the photoreceptor, or light-sensitive, cells. These cells are grouped into six-cell clusters, with 1,300 to 1,500 clusters per lobe. Each cell has a cylindrical region filled with rhabdomeral membranes, the membranes containing the visual pigment. A thin stalk leads down from the rhabdomeral region to the cell nucleus, beyond which is the junction with a nerve cell.

Chamberlain's morphological evidence suggests that the unusual organs of *Rimicaris* are modified compound eyes, specialized for high sensitivity by:

- Extreme proliferation of rhabdomeral membranes, and high concentrations of visual pigment.
- Absence of lenses or other image-forming devices, thereby minimizing the potential for absorbance of photons by non-photoreceptive tissues.
- Presence of reflective properties that might allow reflected light a chance to be absorbed by the photoreceptors.

A full-sized "Dudley Unit" (plywood mannequin of Dudley Foster) standing in front of a sulfide chimney, in 2,500 meters of water at the Juan de Fuca Ridge. Mannequin was used to show the scale of the chimney, and to test the CCD camera. (Photo by Milton Smith, University of Washington)

As these lines of research progress, and as we become more confident that we are indeed dealing with a visual organ, the issue turns to what the shrimp may be looking at. Without lenses, they cannot be seeing an image. Instead, we guess that the shrimp are detecting gradients of light. Based on the structure of the organ, we hypothesize that it is particularly well-adapted for detecting low levels of light. What sources of light are there in the deep sea? These shrimp live 3,600 meters below the surface of the sea, far beyond the reach of sunlight; it is a pitch-black environment, seemingly darker than one can even imagine. From *Alvin*, the only light to be glimpsed at that depth is the occasional, eerily blue-green flash from a bioluminescent organism. Normal shrimp eyes can detect this type of light; but why should the vent shrimp have evolved such an unusual eye if this was all it was looking at? We began to wonder about other sources of light that might be peculiar to the extreme hydrothermal vent environment.

Glowing hydrothermal vents

The dominant physical features of the Mid-Atlantic Ridge vents are the sulfide chimneys on which *Rimicaris* lives. Could there be light, detectable by the shrimp, associated with the springs of 350-degree-Celsius water? The advantages to the shrimp of such a situation are clear; the light could serve as a beacon to draw them to areas where they can feed, and such a light could also serve as a warning signal to deter them from too close an encounter with water hot enough to cook them instantly.

We know that hot things glow with thermal radiation, a phenomenon known as "black body" radiation. Are black smokers hot enough to be emitting light visible to the shrimp? Rough calculations, based on estimates of the threshold light intensity necessary for vision, the emission spectrum of a black body radiator, and the absorption spectrum of the visual pigment of the shrimp, indicate that the shrimp may indeed be able to see such a glow, even though it might be too dim for a human eye to detect.

Testing this hypothesis means returning to Mid-Atlantic Ridge vents with *Alvin,* carefully measuring light levels and wavelengths at the chimneys, studying the shrimp's behavior in response to experimental light stimuli, and shipboard physiological experimentation. The earliest we could hope to visit the Mid-Atlantic Ridge is next summer; after that, *Alvin* heads into the Pacific for an extended period, leaving studies in the Atlantic on hold indefinitely.

Logic led us to believe that our hypothetical light at Mid-Atlantic Ridge vents could be a universal phenomenon at similar high-temperature vents elsewhere in the deep sea. Thus, while we could not immediately find out what light *Rimicaris* may be detecting, we could ask a simpler question: What are the ambient light conditions at other black smoker chimneys?

The opportunity to begin answering this question came unexpectedly and quickly. John R. Delaney, a professor of Geology at the University of Washington, invited me to participate as the biologist on a cruise to hydrothermal vent sites on the Endeavour segment of the Juan de Fuca Ridge, 180 miles off the coast of Vancouver, Canada (Figure 4). I learned that he was to use an electronic charge-coupled device (CCD) camera to create a digital mosaic of seafloor images in the vicinity of these vents. At about the same time, I was reminded by Alan D. Chave, a scientist at AT&T Bell Laboratories, in Murray Hill, New Jersey, that such a camera ought to be sensitive enough to detect the levels of light I expected the shrimp to be seeing. Conventional photographic emulsions would have to have an ASA rating on the order of 50,000 to 100,000 to detect the same level of light. CCD cameras are

350-degree-Celsius water, glowing eerily as it rises from a vent in the Endeavour Ridge hydrothermal vent field. The glow, predicted by the author, is yet to be fully explained. (Photo by Milton Smith, University of Washington)

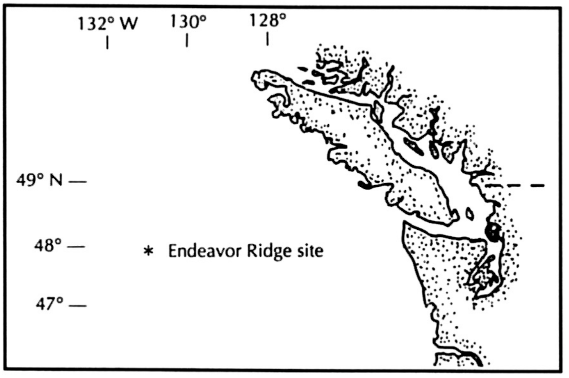

Figure 4. Location of the Endeavour Ridge segment of the Juan de Fuca Ridge, where the glow of hydrothermal vents was first discovered.

used extensively in astronomy to capture light from distant galaxies; there is a satisfying, if somewhat pre-Copernican, symmetry in turning to the same technology in oceanography to capture light emissions fueled by the core of our own planet.

On reaching *R/V Atlantis II* and meeting Delaney, I suggested aiming the CCD camera at a black smoker orifice, while all of *Alvin*'s outside lights were extinguished, and letting it record what was there. John enthusiastically agreed to try this simple experiment. Dudley B. Foster, *Alvin*'s chief pilot and expedition leader (article, pp. 17–21), agreed to work the submersible for brief periods of time without external lights.

What initially sounded like a simple experiment in fact required a great deal of effort and many unsung heroes, not the least of whom were the *Alvin* pilots and technicians. Together with Milton Smith, an expert in remote sensing at the University of Washington, the *Alvin* crew worked into overtime to configure the camera so that it could collect the required information. This group usually remains nameless; but this efficient, wonderfully competent team makes *Alvin* and *Alvin*-dependent research so successful. In addition to Foster, they are pilots Gary Rajcula, Pat Hickey, and Tom Tengdin; pilots-in-training Steve Etchemendy and Tim Connors; and technician Soc Carello.

The author displays a specimen of Rimicaris exoculata *that escaped the gastronomic experiment. (Photo by Rob Brown, WHOI)*

Finally, on the last dive of a 19-dive series, *Alvin* was lifted off the deck, carrying the CCD camera mounted on the front basket. Inside the pressure hull were Foster, Delaney, and Smith. That day I haunted the lab where surface communication with the submersible takes place every half hour. In response to brief surface queries about their status, only a "busy" signal was returned in Morse code. At the end of the dive, as the submersible began its hour-long ascent, I gave up on learning anything about the success of the experiment, and left the room. On returning, I was handed a note by Hickey, the dive's surface controller. It was a message relayed up from the submersible, a message with only two words: VENTS GLOW.

With *Alvin* on deck, scientists and pilots gathered around the computer work station as Smith was recalling images of the glow. I expected to see some ambiguous hint of a fuzz which, if one was willing to stretch the imagination, might be called a glow; I doubt that I was alone in that expectation. Instead, what came up on the screen was a dramatic, unequivocal glow with a sharply-defined edge at the interface between the sulfide chimney and the vent water. Just a centimeter or two above this interface, the glow became very diffuse, disappearing altogether within 5 centimeters. The same phenomenon was documented at two different 350-degree chimneys within the same vent field.

The discovery of this glow at high-temperature vents opens up a new area of research. At the moment, the glow is an intriguing and aesthetically-pleasing phenomenon; its importance will be judged by what we will learn in the future about the mechanisms of its production and its biological consequences.