

Light Production by the Arm Tips of the Deep-Sea Cephalopod *Vampyroteuthis infernalis*

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Abstract. The archaic, deep-sea cephalopod *Vampyroteuthis infernalis* occurs in dark, oxygen-poor waters below 600 m off Monterey Bay, California. Living specimens, collected gently with a remotely operated vehicle (ROV) and quickly transported to a laboratory ashore, have revealed two hitherto undescribed means of bioluminescent expression for the species. In the first, light is produced by a new type of organ located at the tips of all eight arms. In the second, a viscous fluid containing microscopic luminous particles is released from the arm tips to form a glowing cloud around the animal. Both modes of light production are apparently linked to anti-predation strategies. Use of the tip-lights is readily elicited by contact stimuli, while fluid expulsion has a much higher triggering threshold. Coelenterazine and luciferase are the chemical precursors of light production. This paper presents observations on the structure and operation of the arm-tip light organs, the character of the luminous cloud, and how the light they produce is incorporated into behavioral patterns.

Introduction

Vampyroteuthis infernalis Chun, 1903 (Fig. 1) is the lone occupant of the cephalopod order Vampyromorpha. Its unique morphological characteristics, combining features of both the octopodiformes and decapodiformes, suggest that it represents an evolutionary position intermediate between the two groups (Young, 1977; Healy, 1989); and it may be a relic from an ancestral cephalopod line (Pickford, 1946). This phylogenetic issue has not yet been clearly resolved,

which only adds to the enigmatic status of the species (Young *et al.*, 1998). *Vampyroteuthis* inhabits temperate and tropical waters of the Pacific, Atlantic, and Indian Oceans, typically between 600 and 1200 m. At these depths, sunlight is dim or absent altogether, oxygen content is low, and temperatures range from about 2° to 6°C (Pickford, 1946). In waters over the Monterey Submarine Canyon, we have found *Vampyroteuthis* throughout the year at depths between 600 and 900 m and at oxygen concentrations centered around 0.4 ml/l.

When observed in its natural habitat, *Vampyroteuthis* has the appearance of a robust and substantial animal, but this impression is somewhat misleading. Manipulation *in situ* and in the laboratory reveals that its body is very soft, with watery tissues and little dense musculature. It has a very low metabolic rate and lives at extremely low oxygen concentrations, yet it is capable of relatively high swimming speeds, relying on its fins rather than jet propulsion (Hunt, 1996; Seibel *et al.*, 1997, 1998, 1999).

Vampyroteuthis has been reported to feed upon copepods, prawns, and cnidarians (Young, 1977; Nixon, 1987), but dietary evidence is very scarce. In the laboratory, members of this species will take euphausiids and pieces of fish when the food is placed in contact with the oral surface of the arms, although this is hardly natural feeding. In turn, *Vampyroteuthis* beaks have been reported from the stomachs of large, deep-diving fishes, pinnipeds, and whales, and from benthopelagic fishes (*e.g.*, Percy and Ambler, 1974; Antonelis *et al.*, 1987; Fiscus *et al.*, 1989; Clarke *et al.*, 1996; Clarke and Young, 1998; Drazen *et al.*, 2001). All but the whales are visually cued predators with large eyes that function effectively in dim, monochromatic light.

Cephalopods, particularly deep-water squids, employ a diverse suite of light-producing organs that can occur on the mantle, fins, arms, tentacles, head, eyes, viscera, or else-

Received 10 February 2003; accepted 15 July 2003.

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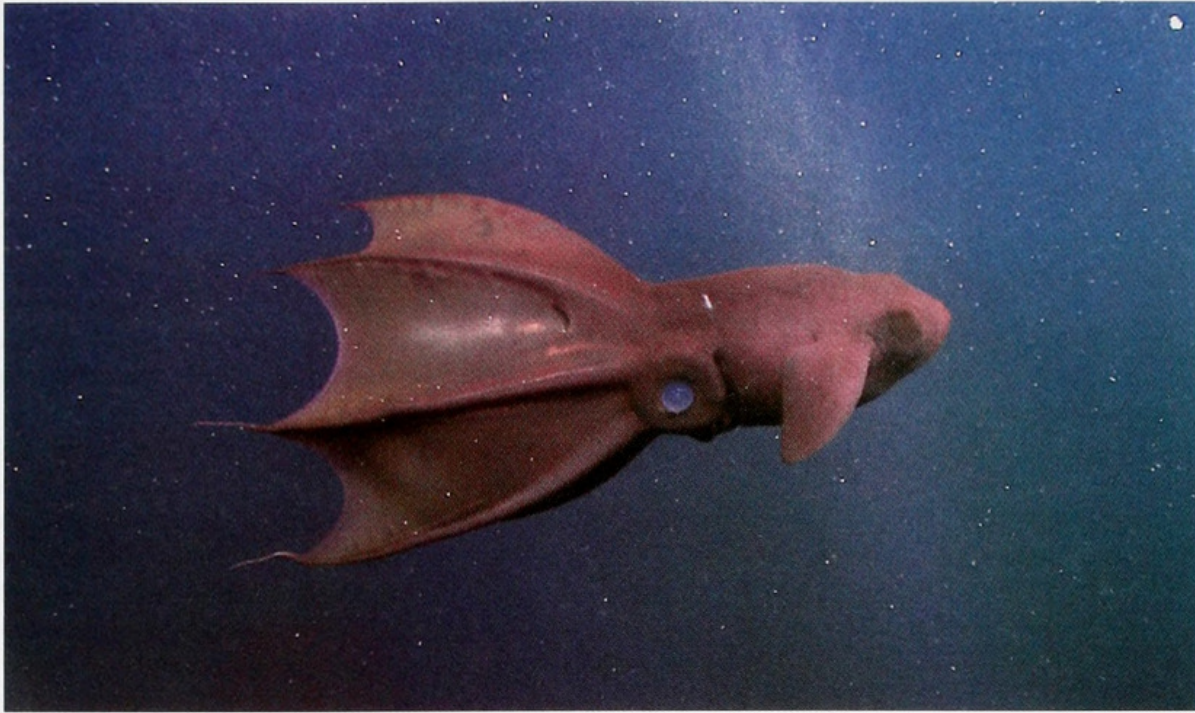


Figure 1. *Vampyroteuthis infernalis*, frame grab from high-definition video footage shot at a depth of 717 m in Monterey Bay, California. Mantle length = 10.2 cm. The fin-base photophore is located behind the dark patch of skin, posterior to (to the right of) the fin. The composite organ is the small, elongate white patch dorsal to and on a line just behind the eye. Minute epidermal organs are scattered over the surface of the mantle and the arms, but not on the web. The new arm-tip light organs described here are located on the oral surface of the filamentous portion of each arm, beyond the margin of the web.

where, depending on the species (Herring, 1977). The light they produce is used for attracting prey, deterring predators, and presumably for intraspecific communication. Luminous secretions are found in a number of deep-living invertebrates but are rare among cephalopods and fishes (Herring, 1977, 1988).

Three types of light-emitting organs have been described in *Vampyroteuthis infernalis*: large, paired, complex photophores at the bases of the fins; small, simple, epidermal organs scattered over the surface of the animal; and composite organs—two clusters of small, pale nodules located dorsally on a line just behind the eyes (Pickford, 1949). Light production has been observed only from the fin-base photophores; emission spectra of these organs were measured at 460 nm by Herring (1983) and 461–466 nm by Widder *et al.* (1983). Herring *et al.* (1994) examined all three organ types and, based on detailed histological evidence, concluded that the composite organs are probably extraocular photoreceptors, while the epidermal organs are most likely light producers. They also found that the reflective surfaces in the light organs were collagen instead of the iridosomal platelets found in other modern cephalopods. To date, no one has observed light from the epidermal organs, nor has there been any behavioral evidence of light sensitivity by the composite organs. We have discovered two new forms of bioluminescent expression in *Vampyroteuthis*:

light produced by organs at the tips of all eight arms, and luminous fluid released by the arm tips.

Materials and Methods

In situ behavioral observations and quantitative video surveys of meso- and bathypelagic cephalopods have been a component of MBARI's midwater research program since 1991 (Hunt, 1996). The program is based on the use of remotely operated vehicles, or ROVs. Over a 10-year time span we have carefully observed 57 individuals of *Vampyroteuthis in situ* and have collected 18 to establish in laboratory aquaria. Specimens in this study included adult males and females with mantle lengths ranging from 7.9 to 12.1 cm. All were gently collected with the ROV *Ventana* (Robison, 1993) at a time-series station 1600 m deep over the axis of the Monterey Submarine Canyon. Field observations and collections occurred under full illumination from the ROV's four 500-W, broad-spectrum lights. Once the ROV was recovered, the animals were placed in darkened containers and were quickly transferred to our laboratory ashore. In the shoreside facility they were maintained in the dark, at 4° to 6° C, in circular, 260-l kreisel tanks (Hamner, 1990) for as long as 2 months.

Most of the specimens appeared to be temporarily blinded by the vehicle's lights during capture. After several hours in the dark, they responded to point sources of white

light by moving away, and by contracting the iris-like sphincter muscle (Pickford, 1949) that surrounds the front of the eye. Laboratory observations were made both under red light and in the dark, often with an image intensifier classified as Gen II+ according to the U.S. Army Night Vision Laboratory's criteria. Light production was recorded with a variety of low-light video cameras.

For chemical assays of arm-tip light organs, we removed the distal portions of arms from several specimens and used them either fresh or after they had been frozen in liquid nitrogen. Light output from each assay listed below was measured with a Hamamatsu HC-124 photomultiplier tube, in a custom-built integrating sphere, for at least 20 s.

Coelenterazine assay: To test for the presence of coelenterazine, we homogenized individual arm tips in 500 μ l of methanol (approximately 10:1 by volume). One milliliter of purified *Oplophorus* luciferase in a solution of 20 mM Tris and 100 mM NaCl was injected into 200 μ l of the sample solution. Mantle tissue with epidermal light organs and web tissue (which lacks the epidermal light organs) were also assayed for the presence of this luciferin.

Luciferase assay: Sample arm tips to be tested for luciferase activity were extracted in an aqueous solution of 100 mM Tris pH 8.1 and 50 mM EDTA. Calcium chloride addition caused no light output, indicating that a calcium-activated photoprotein was not involved. The test solution was added to 20 μ l of coelenterazine in 0.5 μ g/ μ l MeOH, and the light production was measured. For negative controls, tissue from the web was homogenized, and the extracts were added to methanol.

Bacterial luciferase assay: Assays for luminous bacteria

in the arm-tip light organs, the ejecta from the organs, and the surrounding water followed the reduced flavin assay described in Hastings *et al.* (1978), with the flavin reduced by bubbling with H₂ gas in the presence of platinized carbon. Cultured *Vibrio harveyi* were used as positive controls for this assay. We also tested for the presence of luminous bacteria in samples of arm-tip exudate that were streaked on seawater agar plates kept at 4°C for 2 weeks.

Fluorescence microscopy: Autofluorescence images of arm-tip light organs and ejecta were obtained with a Zeiss Axioplan microscope using 10 $\times$ and 40 $\times$ Neofluar objectives, under DAPI illumination.

Electron microscopy: Material was fixed in 2% glutaraldehyde with 0.1 M cacodylate buffer. Samples were post-fixed using osmium tetroxide and embedded in Epon. Thick (1–2 μ m) sections through the light-producing region of the arm tip were stained with toluidine blue. Thin sections from the same region were stained with uranyl acetate and lead citrate.

Results

In the laboratory we observed that the tips of all eight arms often glowed when an animal was handled (Fig. 2). The bright blue lights usually appeared as a tight chain of 4 to 6 small discs, tapering in size distally along the oral surface of each arm tip. Occasionally there was a different pattern, in which the light appeared as two parallel lines separated by a dark gap. With a mild contact stimulus, the arms and web flared outward, with the arm tips glowing. With stronger prodding, the arms were curled, writhing up



Figure 2. Frame grab from a low-light video recording, showing the glowing arm tips of *Vampyroteuthis infernalis*. The animal is oriented such that its head and beak are directed toward the camera, with the arms and web beginning to flare outward.

over the head to the apex of the mantle, exposing the suckers and cirri and placing the glowing arm tips in a cluster at the top. When an animal rolled the arms and mantle back down to their normal position, it frequently tucked the arm tips within the web, where they were shielded from view. This behavior, which was observed both in the field and in the laboratory, is similar to a nonluminous pattern seen in octopuses attacked by moray eels (Hanlon and Messenger, 1996). The eight arm-tip light organs of *Vampyroteuthis* always glowed and dimmed simultaneously. They flashed 1 to 3 times per second, or glowed steadily, but rarely for longer than one minute. The pulsing could include complete extinction of the light, or just dimming, before returning to the previous level of intensity. There is a dark, densely pigmented layer of skin on the aboral surface and on the sides of each arm tip, but the oral surface is generally unpigmented.

The structure of the oral surface of the arm tips continues the basic pattern found along the entire length of the arm—a series of central plates alternating with paired lateral plates (Fig. 3). In the proximal and medial portions of the arm, the lateral plates support cirri, while the central plates are the bases for suckers (Pickford, 1949, plate VI, fig. 20). Plates, cirri, and suckers get smaller toward the distal end; near the tip, the plates bear mere rudiments. Proximally, the plates are pale and opaque, but as they approach the distal tip they become translucent. Within this window at the tip of the arm are subdermal clusters of particles that impart an iridescent green and yellow sheen to the plates. When the arm is viewed from the side, the central plates appear bulbous and extend outward beyond the lateral plates (Pickford, 1949, plate VI, fig. 19). Light expressed from the central plates alone may be the source of the pattern that appears as a chain of discs, while light coming from just the lateral plates would show as parallel lines. The light-producing area of the arm tip can be occluded by the edges of the dark skin along both sides, which close together along the midline of the oral surface. This means of controlling light output is similar to that described for the arm-tip photophores of *Taningia danae* by Herring *et al.* (1992).

Given a strong contact stimulus to the arms or body, the arm tips exuded a viscous fluid containing small glowing particles. As the arms swept up over the head and mantle, the particles dispersed, enveloping the animal in a luminous cloud (Fig. 4). To all observers, the light from the cloud was much dimmer than that of the fin lights and arm tips, but we were unable to measure its intensity. The number of particles released varied from a few dozen to several hundred, usually related to the strength of the stimulus. Cloud luminescence persisted for 2 to 3 min, and individual particles glowed for as long as 9 min (Hunt, 1996). Once the particles had gone dark, stirring the water did not re-initiate luminescence. After several such displays, production of the luminous fluid ceased, and while the arm tips could still be



Figure 3. Arm tip of a living specimen of *Vampyroteuthis infernalis*, showing the distal light-producing region, and patches of small, green particles in the lateral plates that are associated with the luminous ejecta. cp = central plate; lp = lateral plate; scale bar = 1 mm; the arrows point to patches of iridescent particles that are not present after an extensive luminous cloud has been created.

stimulated to glow, the dense clusters of particles in the arm tips were gone. The fluid matrix that bears the luminous particles is viscous and somewhat sticky. Arm tips that brushed across the inner surface of a kreisel during a bioluminescent display usually left behind a lingering streak of light. The release of luminous particles often preceded an escape response by the animal.

The chemical assays provided clear evidence of the presence of coelenterazine (luciferin) and luciferase in the arm-tip light organs of *Vampyroteuthis* (Fig. 5), which indicates that these compounds are the basis for light production. No calcium-activated photoprotein activity was detected in any assay. Small amounts of coelenterazine were found in the mantle epidermal tissue. These results support the conclusion by Herring *et al.* (1994) that the epidermal organs produce light. Assays for luciferin and luciferase in the web tissue were negative. The assay for bacterial luciferase in

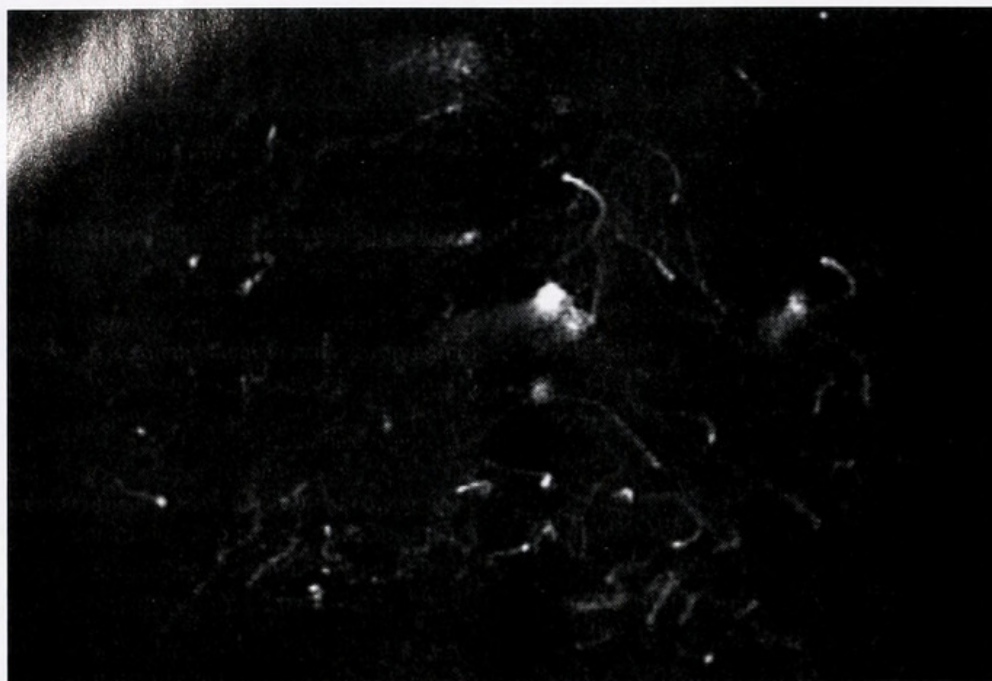


Figure 4. Frame grab from a low-light video recording showing the release of glowing particles from the arm tips of *Vampyroteuthis infernalis*. The head of the specimen is directed toward the camera. Particles in the cloud are swirled by movements of the arms and web, and by water jetting through the siphon. "Tails" on the glowing particles are caused by electronic lag in the camera's image intensifier.

the tip lights was negative, as were the culturing efforts to demonstrate the presence of luminous bacteria in the arm tips and their exudate.

Microscopic examination of the iridescent clusters in the arm tips of animals that had not yet secreted luminous material revealed extensive patches of rounded yellow particles that glowed blue-green under fluorescent illumination (Fig. 6). No pores that might release the fluid were evident on the arm tips, although the rudimentary suckers are likely sites. The particles matched, in size and configuration, particles culled from the arm-tip exudate and from the water in which a luminous cloud had been produced. Sections of the arm tips showed a low-density central core with prominent nuclei on the oral side and sparse muscle tissue on the aboral. We saw no evidence of an iridosomal reflective layer nor of layered collagen fibers like those found by Herring *et al.* (1994) in the fin-base photophores.

A comparison of our specimens with others collected by trawling in Monterey Bay and elsewhere in the North Pacific revealed that, in almost every case, the arm-tip light organs had broken off the trawl-caught specimens. This observation is similar to that made on *Octopoteuthis* (Herring *et al.*, 1992) and may explain why the arm-tip light organs of *Vampyroteuthis* were not discovered until we could collect the animals in perfect condition. On two of our ROV-caught specimens, we found a short, apparently regenerated arm, each with what appeared to be a small light source at its tip.

Over a gradient of stimuli, the fin lights were the most readily illuminated, and although this pair always worked

together, they could operate independently of the other two light sources. Light emission from the fin lights was regulated by chromatophores and by iris-like skin closures similar to those that shield the eyes. The arm-tip lights seldom glowed without the fin lights also being on, and all 10 could pulse in concert. The luminous ejecta was never observed without the tip lights glowing as well.

On one occasion, male and female specimens were collected on the same day and were then placed in separate kreisels less than a meter apart, in the darkened laboratory ashore. When the female was disturbed and began to flash her arm-tip lights, the undisturbed male quickly and vigorously responded with tip-light flashes. This reaction was repeated twice (Hunt, 1996). We saw no evidence of differential light production by females and males. In the Cranchiidae and Lycoteuthidae, arm-tip photophores develop as secondary sexual characters (Herring *et al.*, 1992). We detected no sexual dimorphism in the light organs of *Vampyroteuthis*. Luminous suckers on the deep-sea octopus *Stauroteuthis syrtensis* may be used for intraspecific communication (Johnsen *et al.*, 1999a, b), but the structure of the light organs in this species is not at all like the arm-tip lights of *Vampyroteuthis*. Although animals in kreisels reacted to point sources of artificial light by shading their eyes with their arms and web, or by moving away from the light, the response of *Vampyroteuthis* to artificial light never included luminescence.

Supplemental images (*in situ* video, laboratory low-light video, digital stills, and electron micrographs) are available online at <http://www.mbari.org/midwater/vamp>.

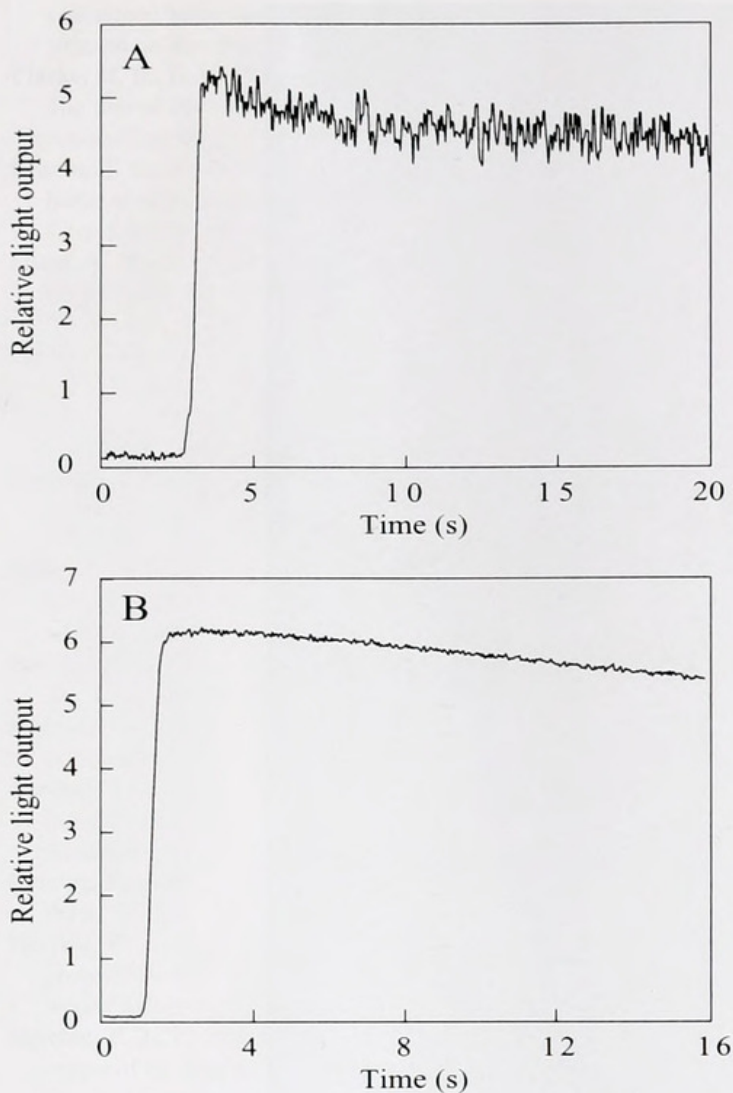


Figure 5. Luciferin and luciferase assays for arm-tip light organs of *Vampyroteuthis infernalis*. (A) Light produced by methanolic extracts upon the addition of *Oplophorus* luciferase indicates the presence of the luciferin coelenterazine. (B) Addition of coelenterazine to aqueous extracts shows high luciferase activity. Negative controls for both assays (omitted here for clarity) did not deviate measurably from the pre-injection baseline. The higher noise associated with the coelenterazine assay is due to the higher gain setting required to detect the presence of that molecule.

Discussion

The effect of arm-tip luminescent displays on the dark-adapted human eye is striking; coupled with the bright blue light emitted by the two fin-base photophores, these displays produce a complex and dynamic visual field. The fundamental question they raise is, how does *Vampyroteuthis* use the light? Because these responses can be elicited by mechanical stimuli, we assume that production of light from the arm-tip organs and the cloud of luminous particles are elements of an anti-predation strategy based on startling or distracting a potential predator, thus allowing for escape (Young, 1983). The visual predators that we know about are all better swimmers than *Vampyroteuthis*, so its escape strategy must rely on more than speed. Deceptive, deimatic

behavior, such as chromatophore displays and unpredictable protean behavior, is often coupled with locomotion in cephalopod escape strategies (Hanlon and Messenger, 1996). In the darkness of its habitat, *Vampyroteuthis* may substitute luminescence for chromatophore displays in an otherwise familiar cephalopod behavior pattern of deception, diversion, and flight.

Arm-tip light organs, which can be bitten or broken off and then regenerated, may serve as sacrificial diversions for predators (Herring, 1977). Tip lights are found in several deep-living squids such as *Chiroteuthis* and *Octopoteuthis*, where they may also serve as lures for prey, thus functioning like the escae of anglerfish and the barbels of stomiid fishes (Herring, 1977; Young, 1983). Our observations of apparently regenerated light organs at the ends of shortened arms in *Vampyroteuthis* may be evidence of their potential as sacrificial structures. The characteristics of the arm-tip displays indicate that there is direct neural control of their luminescence.

The production of luminous clouds is common among other deep-living pelagic invertebrates but rare in cephalopods. Anecdotal evidence for the production of luminous clouds by squids was summarized by Young *et al.* (1979), who suggested that renal fluid might be the luminous substrate. The only well-documented case is the sepiolid *Heteroteuthis*, which ejects a cloud of luminous particles when it is disturbed, presumably as a distraction to predators (Herring, 1977). The ejecta is produced by glands within the mantle that contain dense populations of light-producing bacteria, which are combined with ink and mucus during release through the siphon (Herring, 1988, 2002). The glands themselves emit light and have complex internal reflectors, which suggests that they have multiple uses (Herring, 1988). Structurally and operationally, the release of luminous fluids appears to be a completely different process in *Vampyroteuthis* than it is in *Heteroteuthis*.

Visual trickery is common within the depth range and light regime that *Vampyroteuthis* occupies (Robison, 1995, 1999; Herring, 2002), and our observations suggest some additional ways that its luminescence may be employed. Because the luminous fluid released by *Vampyroteuthis* is sticky, it would adhere to a potential predator and might initiate a "burglar alarm" consequence by painting it with bioluminescence that cannot be turned off or readily removed, thus making the attacker vulnerable to secondary predators. A similar behavior has been described for the bathypelagic holothurian *Eynpniasites eximia* (Robison, 1992). Glowing particles in the ejecta might be used to attract smaller prey such as copepods, which would then become trapped by the viscous matrix. This function has been proposed for the twinkling bioluminescent suckers and mucous glands of the cirrate octopus *Stauroteuthis syrtensis* (Johnsen *et al.*, 1999b). It is tempting to correlate the size and abundance of light sources in the cloud with the epi-

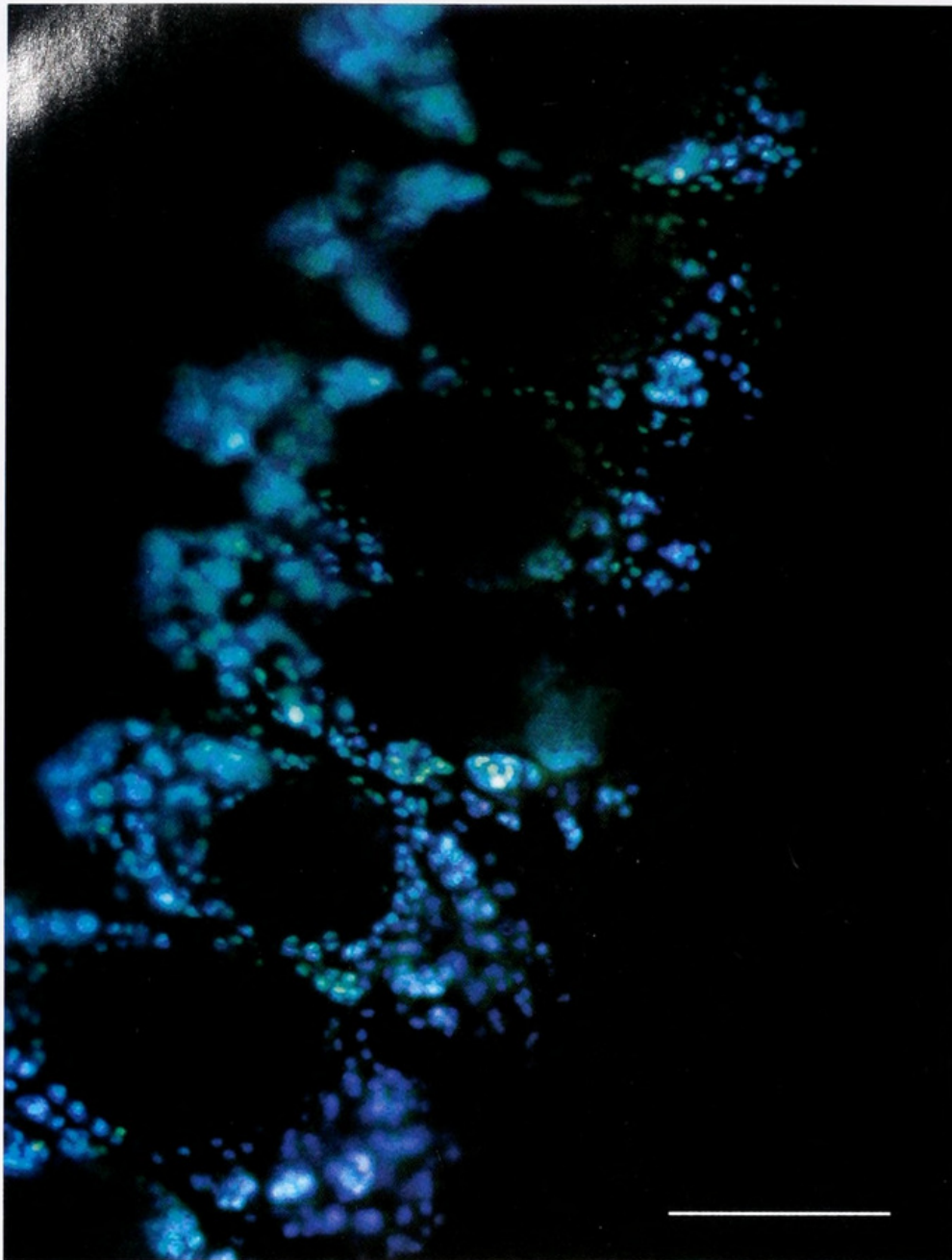


Figure 6. Epifluorescence micrograph of the oral surface of an arm tip of *Vampyroteuthis infernalis*, showing patches of clustered particles. The dark areas along the midline are in the central plates, which bear suckers or their rudiments. Scale bar = 1 mm. Individual particles ranged from 10 to 15 μm in greatest dimension.

dermal organs of *Vampyroteuthis*, but we have never seen the latter luminesce.

The luminous secretion from the arm tips of *Vampyroteuthis* is unique among the known cephalopod bioluminescent systems. Likewise, the arm-tip light organs are structurally distinct from all others. Predator avoidance seems the most likely function of the luminous behavior we have seen, but clearly, much is yet to be learned from observing these animals in their natural habitat.

Acknowledgments

R. E. Sherlock provided invaluable support both at sea and ashore. We gratefully acknowledge the skills and ded-

ication of the ROV *Ventana*'s pilots and the crew of the R/V *Point Lobos*. Coelenterazine, synthesized by S. Inoue, and *Oplophorus* luciferase, purified by Y. Haneda, were kindly provided by O. Shimomura. M. Haygood and J. W. Hastings gave us advice on the bacterial luciferase assays. We thank J. F. Case for a helpful review of the paper. Supported by the David and Lucile Packard Foundation.

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Robison, Bruce H et al. 2003. "Light Production by the Arm Tips of the Deep-Sea Cephalopod *Vampyroteuthis infernalis*." *The Biological bulletin* 205, 102–109. <https://doi.org/10.2307/1543231>.

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