Bioluminescent and Red-Fluorescent Lures in a Deep-Sea Siphonophore

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Examples of bioluminescent lures in the sea are quite rare, posited only for a few fish and cephalopods (*1*). In many marine organisms, including siphonophores, luminescence is thought to serve defensive purposes. Siphonophores are colonial hydrozoans (phylum Cnidaria) that are dominant predators in the ocean, some reaching tens of meters in length. Nearly all members of this group are luminous (*2*), but because of their fragility, they are rarely observed alive.

Using a submersible at depths between 1600 m and 2300 m (*3*), we collected three specimens of an undescribed species in the genus *Erenna* (Fig. 1A and movie S1). Unlike most siphonophores, *Erenna* do not feed on crustaceans but prey instead upon fish (*4*), remnants of which were found inside two of our specimens. At great depths where chance encounters with vertebrates are rare, it is unclear how they obtain prey. Here we show that the nonvisual *Erenna* sp. we captured possesses red-emitting bioluminescent appendages that may act as lures for fish prey.

Erenna tentacles have numerous side branches (tentilla), each consisting of a large cnidoband (an array of ~3000 stinging cells) attached to a central stalk (Fig. 1, B and C). The transparent stalk terminates in a bulb containing white spots, historically called "ocelli" (*4*). We found that, when ruptured in $CaCl_2$, these spots produced luminescence, indicating that they are in fact photophores filled with Ca^{2+}-regulated photoproteins. Unlike typical cnidarian photocytes, these terminal photophores did not readily flash upon direct stimulation.

Photophores of young tentilla (Fig. 1B) contained only bioluminescent tissue, but when mature, they were surrounded by red fluorescent material (Fig. 1C). This substance produced a multimodal fluorescence emission, spanning yellow to red (583, 620, and 680 nm) (Fig. 1, D and E). These mature tentilla also displayed a unique rhythmic flicking behavior (movie S1).

We observed blue-green (immature) and orange-red (mature) in vivo emission by eye, but we were unable to record bioluminescence emission spectra because of the scarcity of specimens and the small size of the photophores. We expect bioluminescence spectra to be similar to fluorescence emissions, as is the case in other cnidarians (*2*).

Among all marine organisms, only the rare scaleless dragonfishes (Stomiidae) have been known to produce red luminescence (*1*), but red fluorescent substances have been noted in several marine phyla (*5*–*7*). The fluorescent material of *Erenna* does not appear to belong to the green fluorescent protein family (*5*), nor does it resemble the biliproteins of the siphonophore *Physalia* (*6*). On the basis of emission and absorption spectra, with a Soret band at 406 nm and secondary Q bands at 570 and 583 nm (Fig. 1, F and G), the main constituents are most similar to porphyrins found in medusae and fish (*7*).

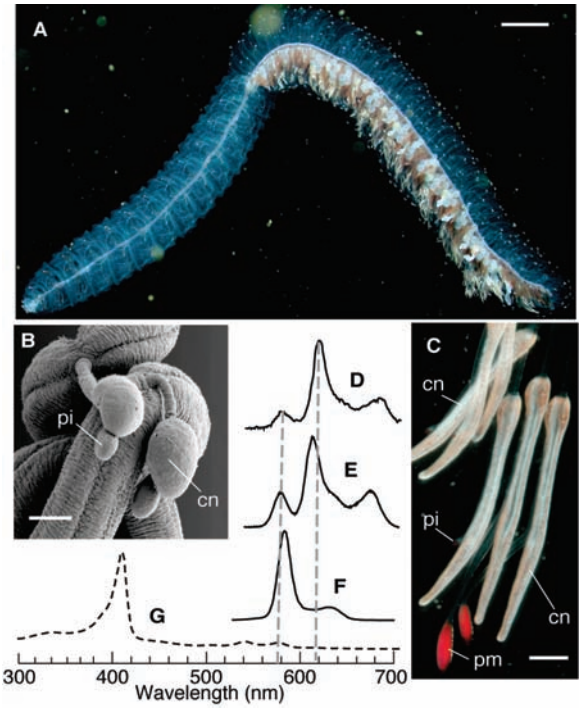

Fig. 1. (**A**) *Erenna* sp. at 1662 m. Scale bar, 2 cm. (**B**) Scanning electron micrograph of immature photophore (pi) and cnidoband (cn). Scale bar, 200 μm. (**C**) Live tentilla with mature photophores (pm). Scale bar, 1 mm. (**D** to **F**) Fluorescence emission spectra of (D) a live mature photophore (excitation wavelength λ_{ex} = 410 nm), (E) unpurified extract (λ_{ex} = 473 nm), and (F) purified extract (λ_{ex} = 410 nm). Dashed vertical lines show primary conserved emission peaks. (**G**) The absorbance spectrum of purified photophore extract.

Given the characteristic flicking of the bioluminescent and fluorescent filaments, we concluded that the siphonophore *Erenna* uses them as lures to attract fish. Fluorescent structures may serve as lures in a diverse assemblage of nonluminous taxa, from cnidarians to crustaceans, and we have found examples of putative lures in several other siphonophores and medusae. In shallow waters, fluorescence could be excited by ambient blue light rather than by bioluminescence as in deep-dwelling *Erenna*.

The assertion that red light acts as an attractant is at odds with the prevailing view that deep-living creatures cannot detect long wavelengths; however, our knowledge of deep-sea visual abilities is limited. For example, the eyes of *Cyclothone*, an abundant deep-sea fish, have not yet been studied, and evidence for red sensitivity in a deep myctophid fish has been presented only recently (*8*). Our findings suggest that the role of long-wavelength light in marine visual ecology merits a closer look.

References and Notes

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Supporting Online Material
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Materials and Methods
Movie S1

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