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Bioluminescence in Pelagic Octopods[1]

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ABSTRACT: A peculiar circumoral organ in a pelagic bolitaenid octopus luminesced brilliantly when treated with H_2O_2. This is the first confirmed luminescent organ in an octopus. Similar organs are found only in females of *Eledonella pygmaea*, *Japetella diaphana* (sensu lato) approaching sexual maturity. The luminescent organs may function to attract mates.

A NUMBER OF REPORTS have suggested that bioluminescence occurs in octopods, but none of them have been substantiated. Chun (1910) suggested that modified suckers in the blind, bathypelagic octopod, *Cirrothauma murrayi*, were photogenic but when Aldred, Nixon, and Young (1978) re-examined this species they discounted Chun's hypothesis. Harvey (1952) considered that scattered early observations on bioluminescence in octopods resulted from infection by luminous bacteria. More recently Taki's report (1964) of luminescence in the neritic octopus *Callistoctopus arakawai* does not eliminate the possibility that the light resulted from reflection of low ambient light by iridophores. Herring (1977) suggested that the "luminescence" observations of Akimushkin (1965) on the epipelagic octopus *Tremoctopus lucifer* also resulted from reflection rather than emission of light. Young et al. (1979) detected a luminescent compound in the digestive glands of two species of midwater octopods belonging to the family Bolitaenidae. However, they did not eliminate the possibility that the compound was a nonfunctional derivative of the diet. We report on a photogenic organ and on observations of its light-producing capability, in midwater octopods also belonging to the family Bolitaenidae.

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MATERIALS AND METHODS

The octopus observed to luminesce was captured from the R/V *Thomas Washington* in an open midwater trawl (RMT–8; Clarke 1969) that fished obliquely between the surface and 2000 m at lat. 30°52.2′ N and long. 157°50.6′ W in August 1978. The animal was fixed in 10 percent formalin and later preserved in 50 percent isopropyl alcohol. A piece of photogenic organ was subsequently embedded in Epon 812, sectioned with a glass knife, and stained with Richardson's stain. Specimens of *Eledonella pygmaea* sectioned were prepared in a similar manner. Tissues from the region where the luminescent organ is found were embedded from 2 males and 3 females of this species. An additional 9 specimens of *E. pygmaea* (20–45 mm Mantle Length) from Hawaiian waters were examined under the dissecting microscope. A further 15 specimens of *Japetella diaphana* (35 mm ML to about 80 mm ML) from Hawaiian waters were examined under the dissecting microscope as were 2 specimens of *J. heathi* from waters off the coasts of Oregon (> 70 mm ML, damaged) and California (70 mm ML).

RESULTS

Observations on Bioluminescence

The specimen stimulated to luminesce was badly damaged during capture (Figure 1*A*). Nevertheless the animal could be identified to the family Bolitaenidae on the basis of its hemispherical eyes, uniserial arrangement of suckers, and ctenoglossan radula. Judging from its size (roughly estimated to be about

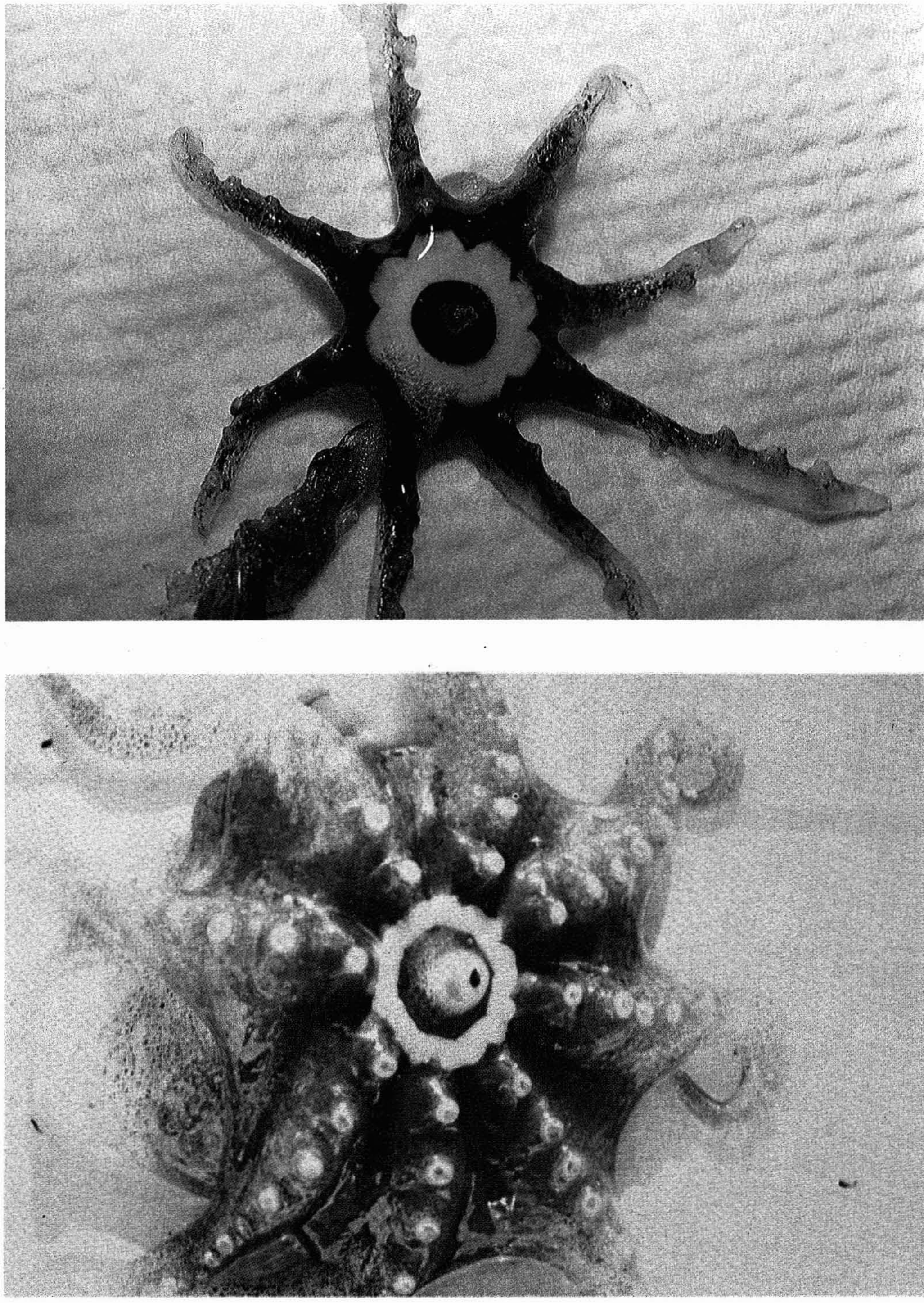

FIGURE 1*A*. Oral surface of the buccal crown of the luminescent octopus, possibly *Eledonella pygmaea*, prior to fixation. The yellow structure is the bioluminescent circumoral organ. Bubbles at one edge of the organ resulted from the H_2O_2 treatment. *B*. Oral surface of the buccal crown of the Oregon specimen of *Japetella*. Note that the shape of the yellow circumoral organ differs slightly from that in Figure 1*A*. Photograph provided by W. Pearcy, Oregon State University.

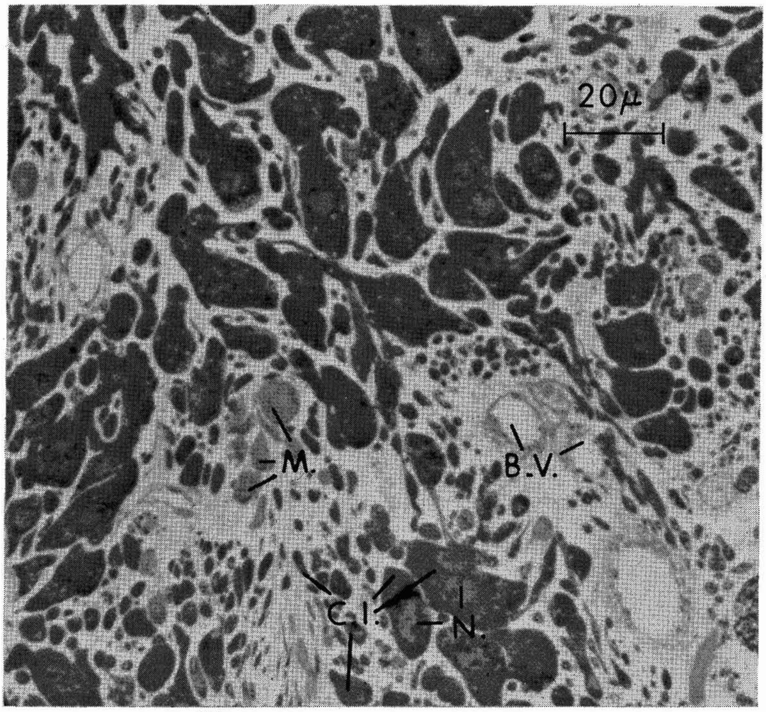

FIGURE 2. Midportion of a cross section through the circumoral organ. *B.V.*, blood vessel; *C.I.*, cytoplasmic inclusion; *M*, muscle; *N*, nucleus.

30–35 mm ML) and heavy pigmentation, it could be a mature individual of the common species *Eledonella pygmaea*.

The octopus had a bright yellow organ (we designate this the circumoral organ) surrounding the mouth (Figure 1). Because of this unusual pigmentation, the freshly captured specimen was taken into a darkroom and H_2O_2 (U.S.P. 3%, 5 ml) was poured over the oral surface. This action caused the ring to produce a very bright luminescence which, to the eye, seemed to be definitely in the green range. The light diminished after a few minutes but was twice regenerated with additional applications of H_2O_2. Light production was restricted to the circumoral organ while the surrounding tissues remained dark. The distinctive shape of the brilliant organ was clear at a distance of 3 m.

Description of the Organ

The large circumoral organ lies beneath transparent integument on the oral surface of the buccal region and forms a thick (1.5 mm deep by 3 mm wide) ring around the mouth. The brilliant yellow color found throughout the organ changed in preservation to a pale orange. The aboral surface of the organ is covered by the dense pigmentation of the buccal region. No iridophores are present. Short lobes of the circumoral organ extend slightly onto the bases of the arms and give it a flower-like appearance.

In spite of the poor fixation, the general organization of the organ could be determined. Numerous blood vessels and muscles pass through the organ, which otherwise contains predominantly a single cell type (Figure 2). The dominant cell possesses a large nucleus surrounded by a dark-staining material with well-defined margins lying within the cytoplasm. Poorly staining vesicles and/or tubes lie within this deeply staining cytoplasmic inclusion. Commonly, slender extensions of the cells that also contained extensions of the dark-staining inclusions were observed. Near the distal edge of the organ, these extensions were less common and the tissue was dominated by broad cytoplasmic inclusions. In the proximal portions of the organ, nuclei were rarely seen, and the tissue seems to consist of an interwoven mass of cell extensions containing slender, dark cytoplasmic inclusions. The source of the yellow pigment could not be found.

This structural pattern neither confirms nor denies the photogenic nature of the organ. The presence of extensive cytoplasmic inclusions, however, is also found in the photocytes of the dorsal mantle photophore of the squid *Ommastrephes pteropus* (Girsch, Herring, and McCapra 1976).

In bolitaenid octopods without a circumoral organ, a narrow unpigmented oral muscular ring occupies approximately the same position as the circumoral organ. The fibers of the ring connect alternate arms. No such muscular ring could be found beneath the circumoral organ of the present specimen, although muscle fibers pass through the organ and along its aboral surface.

Comparison with Other Bolitaenid Octopods

At least two species of bolitaenid octopods were examined for the presence of a circumoral organ: *Eledonella pygmaea* and *Japetella diaphana*. The name *Japetella heathi* applied to specimens from waters off Oregon and California may be a junior synonym of *J. diaphana* (Thore 1949, Young 1972). *E. pygmaea* was examined in greatest detail. No trace of a circumoral organ could be found in any of the males of this species. While no males carrying spermatophores were examined, one nearly mature specimen was sectioned that had a well developed hectocotylus, greatly enlarged suckers, and a large penis. The smallest immature female sectioned (22 mm ML) had small ova (0.14 × 0.12 mm). The only trace found of a circumoral organ consisted of scattered large cells interspersed among the muscle cells of the oral muscular ring. A larger female (37 mm ML), with larger and more elongate ova (0.5 × 0.17), had numerous large cells among the muscle cells but these lacked the characteristic cytoplasmic inclusions. In dissection, this specimen's oral muscular ring appeared slightly swollen. This octopus showed no evidence of the dark pigmentation characteristic of the mature animal. The third female (47 mm ML) had spawned and was apparently brooding its young when captured (see Young 1978). The oral muscular ring was slightly enlarged but rather flat and flaccid. Sections revealed large regions of loose connective tissue and occasional muscle strands but no clear remnant of the circumoral organ. One pigmented female specimen (45 mm ML) that was not sectioned possessed an orange circumoral organ with a shape very similar to that described, although the organ was considerably less swollen. While the ovary of this specimen was packed with eggs (1 mm in length), the ovary was small and the eggs appeared to be in a state of deterioration. This octopus may be a spent female whose circumoral organ is in the initial stages of resorption. In the remaining specimens examined, the morphological trends seen were the same as those exhibited by the specimens sectioned.

Japetella diaphana (including *J. heathi*) is a much larger species but is simlar to *Eledonella pygmaea* in its heavy pigmentation and lack of silvery tissues in mature specimens. The circumoral organ of *Japetella* is similar to that described above but differs somewhat in shape (Figure 1*B*). In the four specimens examined that possessed the organ, it appeared as a thick (5 mm wide in the largest specimen) lobular ring lacking extensions onto the arms. The firm, fully formed organ may be somewhat flat but curled over the oral surface of the oral muscular ring, or it may be formed nearly into a cord (i.e., a disc in cross-section). In a fresh specimen the organ was yellow but in preservation it was orange to pale orange.

No trace of a circumoral organ was found in males. None of the males examined had spermatophores; however, one large male (60 mm ML) with a large penis and enlarged suckers was nearly mature. Of the four specimens that had circumoral organs, all were large females. Three were well pigmented, and iridophores had been lost in two of these. The lightly pigmented Hawaiian specimen (about 70 mm ML) had eggs of 0.9 × 0.2 mm and a slender circumoral organ (2 mm thick). The Oregon specimen had lost most of the ovary during capture. The largest of the remaining eggs measured about 3 × 1 mm. The smaller California specimen had ova measuring 2 × 0.6 mm. The larger Hawaiian specimen (about 80 mm ML) had completely lost the ovary during capture. The circumoral organ of this specimen was not firm and appeared to be in an early stage of resorption. Immature females up to about 50 mm ML showed no trace of the organ. Two spent (presumably brooding) females exhibited a flaccid oral muscular ring and lacked a circumoral organ.

In spite of limited material available, the pattern of development of the circumoral organ is clear and identical in both genera. The organ is absent in males. In females, only the slightest trace of the presumptive organ is present in young specimens. The organ is fully formed only in large octopods near maturity that have either undergone or are in the process of undergoing pigmentary changes associated with sexual maturity. In brooding females the organ has been resorbed.

DISCUSSION

The bright luminescence repeatedly produced by treating the circumoral organ with H_2O_2 leaves little doubt that this peculiar organ is bioluminescent. Two features of the organ, its color and its location, are unusual. The dense yellow pigmentation could alter the color of blue-green light typically produced by luminous tissue (Young 1981), which may contribute to the green color of the observed luminescence.

The location of photogenic tissue surrounding the mouth is unique among cephalopods (personal observation, see Herring 1977). Indeed, except for photophores at the tips of the arms or embedded in the tentacles, orally directed photophores are not found on the oral surfaces of the arms, web, or buccal membrane in other cephalopods.

In an octopus a luminous lure surrounding the mouth and ringed by eight outstretched arms would seem to be a nearly ideal trap. Such a trap, however, would lack a trigger. With arms spread, the eyes would lose sight of an approaching prey, and lacking any counterpart of a lateral line system (Wells 1978), the prey could well bite the light organ before being detected. The color of the organ also suggests that it is not intended to be detected by a large audience, most of whom have eyes attuned to the blue region of the spectrum (e.g., Fernandez 1978, Muntz and Johnson 1978).

Since the organ is found only in females approaching sexual maturity, we suggest that it acts to attract a mate. Both *Japetella diaphana* and *Eledonella pygmaea* apparently mate at the lower end of their vertical range (Young 1978). At these great depths (i.e., around 1000 m and 1400 m respectively) reduced predation pressure may make sexual signaling less risky. Attracting a mate with a signal whose color is poorly visible to hungry onlookers but brilliant to an appropriately adapted mate may reduce the risk even further. In addition, the attracting signal would be distinct against background bioluminescent "noise" in both its color and its unusual shape.

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