Unique Envelope of a Jellyfish Ovum: The Armed Egg

Abstract. *The eggs of* Bougainvillia multitentaculata *are spawned with an envelope consisting of a single layer of cnidocytes. The cnidocytes are surficial on eggs, cleavage stages, and young blastulae. During gastrulation, the cnidocytes are gradually incorporated into the ectoderm and become an integral part of the planula.*

Most eggs are enveloped by coats which vary in origin, strength, and morphological complexity. Eggs of hydromedusae usually appear naked; at best, a thin jelly layer surrounds them. The eggs of the anthomedusa *Bougainvillia multitentaculata*, however, have a layer of maternal cnidocytes (Figs. 1 and 3). Eggs of a large number of medusae found in the waters of the Pacific off the shores of Washington were examined subsequently, and no other was found to carry cnidocytes. A survey of the literature failed to disclose a report of similar findings.

Free-swimming medusae of *B. multitentaculata* were collected in May and June off the floats at the Friday Harbor Laboratories, University of Washington. The medusae spawn twice daily; in the evening and in the morning. The eggs were observed by phase-contrast microscopy. The entire egg is surrounded by a continuous single layer of cnidocytes (Figs. 1 and 3). These appear to be in close contact with the egg surface and are embedded in a barely detectable jelly layer 30 to 50 μ thick. The density of cnidocytes seems to be uniform over the entire egg surface, approximately 18 per 100 μ^2. When the seawater is acidified with acetic acid, the nematocysts are discharged and their filament is extruded (Fig. 2). During activation a large number of the cnidocytes separate from the ovum; if the eggs are then agitated, the cnidocytes fall off and the eggs become naked. The fertilizing and supernumerary spermatozoa in the eggs' environment and the fertilization reaction fail to trigger the nematocysts. A variety of agents, such as ethylenediaminetetraacetate, glutathione, and electric stimulation, also failed to initiate this reaction.

The eggs of *B. multitentaculata* remain covered with cnidocytes during cleavage. They demonstrate a "heart-shaped" or unilateral cleavage (*1*) typical for eggs of cnideria. During initial phases of cytokinesis, cnidocytes follow the infolding cell membrane, but no cnidocytes were detected at the depth of the furrow; after completion of cleavage, cnidocytes were seen only on the external cell surfaces. In young blastulae, the location of cnidocytes remains surficial (Fig. 4), and they separate cleanly from the blastulae after the nematocysts have been triggered. The layer of cnidocytes does not interfere with flagellar development and activity. In late blastulae and gastrulae, the cnidocytes seem to become more firmly associated with the embryo and become positioned between the dividing ectodermal cells, which are now much smaller in size. In planulae, the cnidocytes no longer protrude from the ectoderm (Fig. 5). Sections prepared from planulae fixed in glutaraldehyde and osmium and embedded in epoxy (Fig. 6) disclose that the cnidocytes have been incorporated histologically

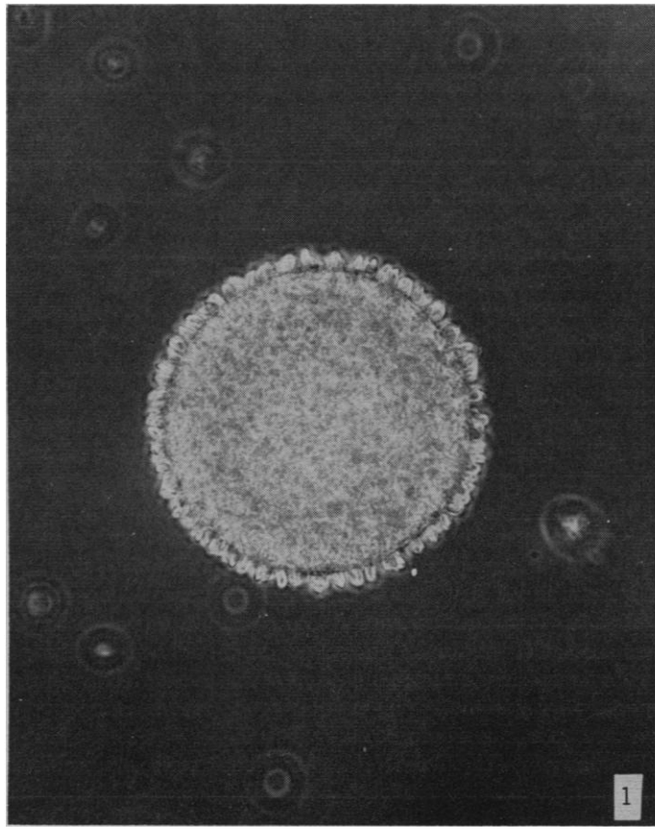


Fig. 1. *Bougainvillia multitentaculata* egg with an envelope of cnidocytes (× 270).

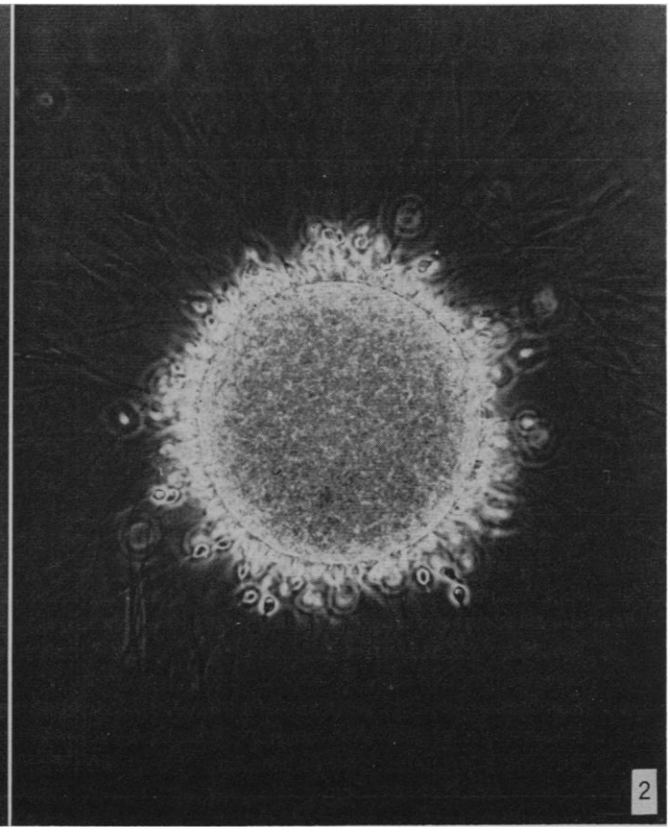
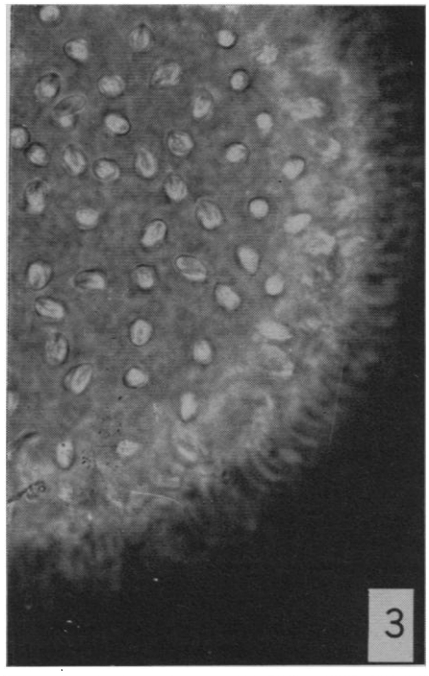
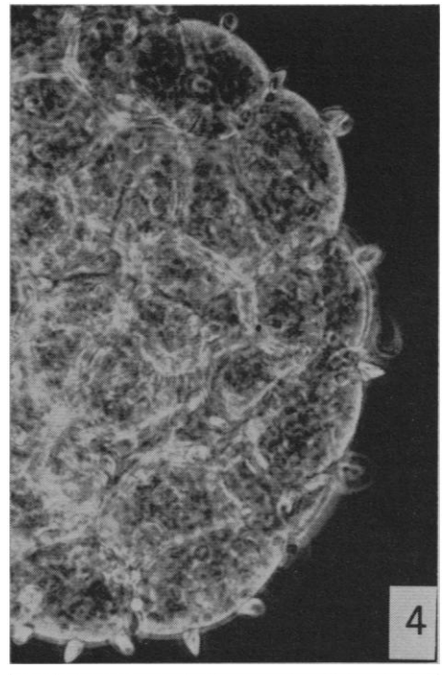


Fig. 2. Discharged nematocysts (× 270).

into the ectodermal layer. The ovoid cnidocytes are nested between slender, very tall, columnar cells abutting the thin mesoglea. A cnidocil projects from the free surface of the cnidocytes. When the nematocysts are triggered artificially only a few cnidocytes separate from the planula, demonstrating further their more intimate association with their neighboring cells.

In contrast to eggs and cleavage stages in planulae, cnidocytes become differentially distributed. The narrower pole which will form the oral portion after settling down shows a higher density than any other segment.





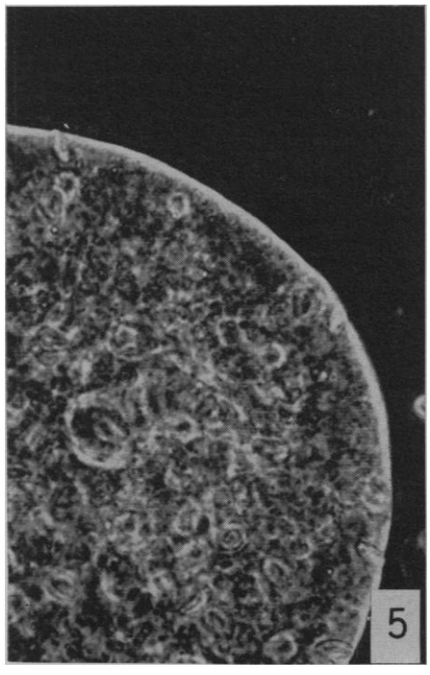


Fig. 3. Surface view of an egg with unreacted nematocysts (× 650). Fig. 4. Surficial cnidocytes in young blastulae (× 430). Fig. 5. The rounded wider pole of a *B. multitentaculata* planula is smooth. Cnidocytes have been incorporated into the larval ectoderm (× 650). Fig. 6. A sagittal section of a planula fixed in 4 percent glutaraldehyde, postosmicated, and embedded in Epon. The section was stained with Richardson's alkaline methylene blue-Azure II stain. The cnidocytes have been incorporated among the slender columnar epithelial cells of the ectoderm (× 2050).

The behavior of cnidocytes during embryonic development of *B. multitentaculata* is of great interest because the association between germ cells and highly specialized maternal somatic cells appears to be permanent. The superficially located cnidocytes become fully integrated into the embryonal ectoderm and seem to be compatible with it. The cnidocytes are, thus, not merely passively carried along as protective "equipment." In a few experiments we attempted to ascertain whether the maternal cnidocytes are obligatory components of normal development. It has been reported that trypsin treatment triggered nematocysts in sea anemone (*2*). When eggs, cleavage stages, and young blastulae of *B. multitentaculata* were treated with trypsin, a large number but not all nematocysts were discharged. After being returned to seawater, the further development of such embryos was apparently unaffected. From the experiments thus far, it is not known whether the demonstrable cnidocytes at this time are all of maternal origin or whether some might be newly differentiated as described during normal development of a number of coelenterates (*3*). The development of *B. multitentaculata* is apparently not affected when the number of cnidocytes is reduced or, possibly, even if they were eliminated altogether.

No information could be found about the ecology of *Bougainvillia multitentaculata*. It is not known which animals prey on its eggs and larvae in the plankton. The presence of armor, that is, nematocysts, would undoubtedly give them an improved chance for escaping predators and constitute a very advantageous adaptive mechanism.

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References and Notes

1. K. Dan and J. C. Dan, *Biol. Bull.* **93**, 163 (1947).
2. L. E. R. Picken and R. J. Skaer, in *The Cnidaria and Their Evolution*, W. J. Rees, Ed. (Academic Press, New York, 1966), pp. 19–50; T. M. Yanagita, *Jap. J. Zool.* **12**, 361 (1959).
3. F. Bodo and J. Bouillon, *Cah. Biol. Mar.* **9**, 69 (1968); L. H. Hyman, in *The Invertebrates*, vol. 1, *Protozoa Through Ctenophora* (McGraw-Hill, New York, 1940), p. 433.
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