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*(TRIDACNA MAXIMA)*

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INTRODUCTION

The giant clam *Tridacna maxima* Röding, 1798, has been observed to retract within its shell when an object passes even some distance above the exposed mantle lobes (Stasek, 1965). The shadow cast by the object need not fall upon the mollusk for retraction to occur. The nature and location of the receptors involved in this undoubtedly visual response have been hitherto debatable because the only structures that can be said to be eye-like in appearance are the numerous "hyaline organs," which lie in the superficial tissues of the upwardly directed mantle lobes. However, the hyaline organs have been thought not to function as eyes because nervous connections have never been demonstrated (Yonge, 1936). Nevertheless, the behavior of *Tridacna* suggested that structures capable of perceiving moving objects must be present and led me to renewed investigations of the hyaline organs as the most likely sites of photoreception. I began with an attempt to ascertain histologically whether or not they were innervated. This paper records my findings in this regard and also describes a sensory structure found in association with the hyaline organ, but which has not been previously reported in the Tridacnidae.

## MATERIALS AND METHODS

Hyaline organs were obtained from living specimens of *Tridacna maxima* taken from coral reefs at Eniwetok Atoll, Marshall Islands, and at Fanning Island, Line Islands, Central Pacific Ocean. Baker's formaldehyde-calcium and Bouin's fluid were used to fix the tissues. About 50 specimens were serially sectioned at 12 micra and stained either with hematoxylin-eosin, Masson's trichrome, Bodian's Protargol, or by the periodic-acid Schiff-reaction (PAS) methods. The most revealing techniques proved to be those employing hematoxylin-eosin and Masson's trichrome stains. Even with some experimentation Bodian's Protargol, a nerve stain, was unsuccessful in indicating nervous tissue in *Tridacna*. Similarly, control sections of the eyes of the pectinid *Hinnites* were unsuccessfully stained with Protargol. Regardless of technique, nervous tissue was only lightly stained, but with few exceptions, nerves could be clearly traced. All sectioning and staining was done in the Department of Zoology, University of California, Berkeley, by Mr. Richard Nishioka and Mrs. Diane Dunlop.

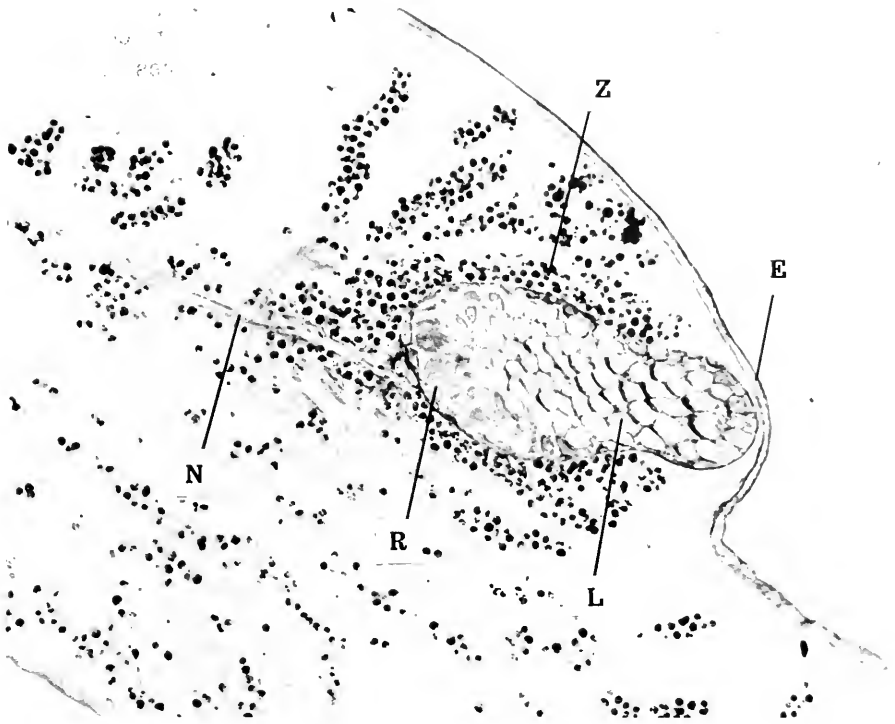
## OBSERVATIONS

The hyaline organs are variable in form and in histological appearance, but each is essentially a rounded body, usually elliptical, with a protuberance on the side nearest the surface of the mantle (figs. 1 and 3). This protuberance, transparent in life, is composed of an irregularly arranged mass of large spheroidal cells, each with a peripheral nucleus (fig. 1, L). The cytoplasm of these cells appears granular after staining, and is often polarized as a result of slow penetration of the fixing agent. Staining with hematoxylin and eosin gives these cells a reddish hue. An irregular layer of cells staining light violet with hematoxylin and eosin forms the curved proximal wall of the organ (figs. 1 and 3, R). Cell membranes are not always clearly discernible in this layer, and tangential or oblique sections give the impression that there is more than one layer of this kind of cell. In several tangential sections, and in especially propitious sections made through the middle of the organ, the proximal ends of these cells could be seen to give rise to fibers (fig. 4, F) that extend along the periphery of the

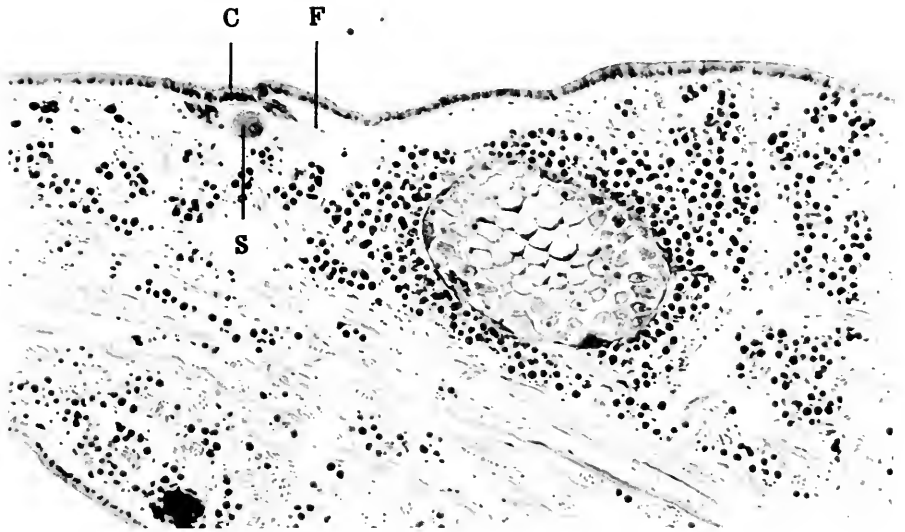
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Figure 1. Near mid-section of a hyaline organ showing the retina (R), multicellular lens (L), optic nerve (N), overlying epithelium (E), and zooxanthellae (Z) lying in what is presumed to be a circum-optic hemocoelic space. Lateral is to the lower right. Overall length of the organ is about 0.3 mm. PAS stain.

Figure 2. Section of a hyaline organ showing the associated ciliary sense organ (C), fibers (F) emerging from nerve cell bodies, and the large cell (S) nested among the nerve cell bodies. Lateral is to the left. Hematoxylin-eosin stain.



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organ to emerge, usually eccentrically and either separately or as small bundles, from near the proximal end of the organ. These fibers or bundles join to form a small nerve that passes off into the mantle tissues (fig. 1, N). In a few instances that I attributed to difficulties in staining nervous tissue, fibers emerging from the hyaline organ could not be detected, although the usual small nerve lay in adjacent tissues.

Surrounding the whole of the hyaline organ is a light scattering of minute, very dense bodies that I have tentatively identified as pigment granules. These granules, best seen in tangential sections, only rarely seem to be intracellular, in which instances they appear to be situated in the tips of processes emerging from stellate cells. The entire hyaline organ lies in a space, probably hemocoelic, that is packed with zooxanthellae (fig. 1, Z). Concentrations of these plant cells are also found elsewhere in the mantle tissues, and, where the spaces are fairly large, the long axes of the concentrations are oriented more or less perpendicular to the upper mantle surfaces (fig. 1). In many sections, the spaces accommodating the zooxanthellae extend to the epithelium, which is occasionally ruptured, whether naturally or as an artifact, I cannot say.

Overlying the hyaline organ at the surface of the mantle is either an intact layer of cuboidal (sometimes squamous) epithelium with basal nuclei (fig. 1, E) or a thin covering composed of basement membrane and connective tissue, the epithelium having been torn or worn away (fig. 3, B). In either instance the upper mantle surface over the hyaline organ bulges upwardly and laterally (fig. 1), or else the organs are situated on papillae and thus raised above the general mantle surface.

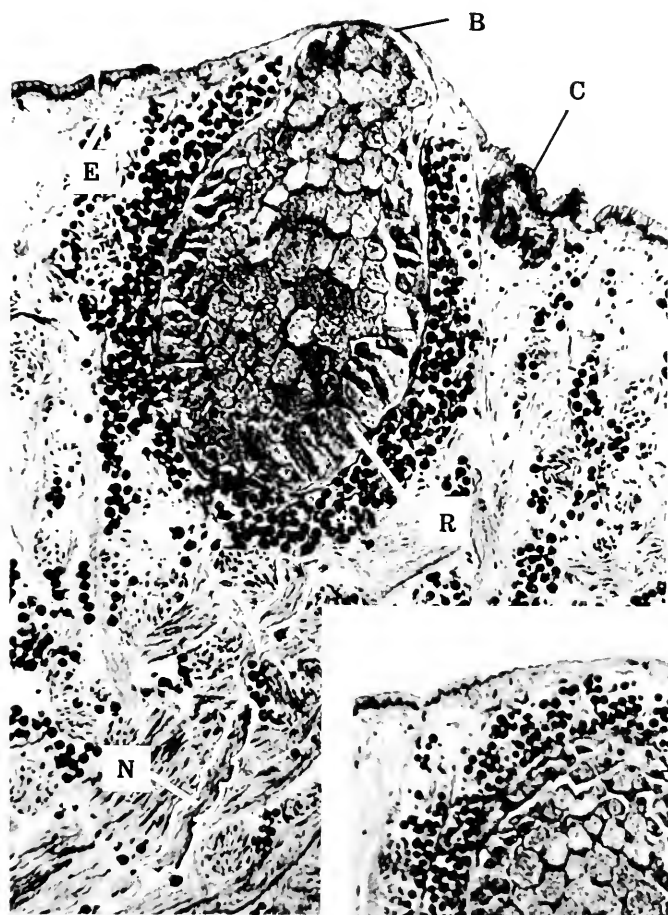
Joining the nerve that emerges from the hyaline organ is an additional bundle of fibers having as its source a slightly thickened patch of epithelium lying near, and lateral to the protuberance of the hyaline organ (figs. 2 and 3, C). The appearance of this patch of cells is highly variable. The cells are sometimes cuboidal, sometimes columnar. Sometimes the patch is flattened or its center is only slightly rounded above the general surface of the mantle. Occasionally the patch lies in a pit. In many sections the cells of this patch bear cilia (fig. 2). Where cilia are not in evidence, their absence is probably an artifact of fixation. Below this modified epithelial region is a group of darkly staining cell bodies, each tapering to a long proxi-

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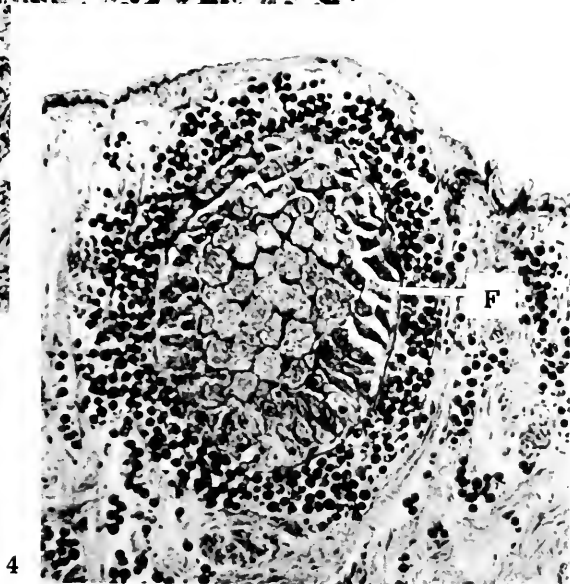
Figure 3. Near mid-section of a hyaline organ and its associated sense organ (C), showing the basement membrane/connective tissue covering of the lens (B), epithelium with basal nuclei (E), retina (R), and elements of the common nerve (N), which have been outlined in ink. Overall length of the organ is about 0.4 mm. Mason's trichrome stain.

Figure 4. Section of the organ shown in figure 3, indicating fibers (F) emerging from the retinal cells.

mal fiber, as suggested in figure 2, F. These fibers pass inwardly and eventually coalesce to form the nerve bundle mentioned above. The distal ends of the cell bodies are also tapered and lie in close approximation to the thickened epithelium, which they appear to penetrate either partially as dark



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rods (fig. 2) or entirely as extremely thin fibrils that emerge from cone-shaped pores in the epithelium. Because of the limitations of microscopic resolution the actual details of these relationships remain obscure. An isolated cell, spherical and relatively large, is often found in close proximity to the cell bodies described above (fig. 2, S).

Rarely, as was true for the hyaline organ shown in figure 1, as associated ciliary organ is lacking. Conversely, ciliated patches with their underlying cell bodies may sometimes be found unassociated with a hyaline organ. In all such instances that I have observed, these isolated ciliated patches were situated near the very edge of the mantle.

#### CONCLUSIONS AND DISCUSSION

While visual function of any eye is probably best evidenced by electrophysiological means whereby, at the time of illumination, an action potential is directly recorded from the regions presumed to be the retina or the optic nerve, relatively few invertebrate "eyes" have been so tested. In the absence of physiological proof of photoreception, structures have been termed "eyes" if they superficially appeared to be such, if there were behavioral responses seeming to be elicited by visual stimuli, and if there was innervation of the structures. In *Tridacna* the latter two criteria have been unfulfilled until recently when I observed that *Tridacna maxima* reacts to moving objects (Stasek, 1965) and, in the present paper, that there are nerves passing from the hyaline organs. Therefore, by the same criteria used to support a similar contention for the "eyes" of most invertebrates, there is reason to believe that the hyaline organs function in photoreception. The proximal layer of cells is thus interpretable as a retina. The fibers from the ends of these cells are therefore held to carry visual information to an optic nerve formed by the fibers as they come together outside the body of the eye. The cells filling the interior of the eye are interpretable as comprising a multicellular lens. Electron microscopical studies, such as those summarized by Eakin (1965), would be a reasonable next-step in the investigation of these eyes. Most importantly, studies of the ultrastructure would indicate which, if any, elements of the presumed and rather disorderly retina are anatomically comparable to cells known to be light sensitive in other organisms.

The function of the ciliated accessory organ, underlaid by what are interpreted to be bipolar nerve cell bodies, is unknown but may be either a tactile or a chemosensory one. In view of the relatively complex behavioral responses to local mechanical irritation, as reported previously (Stasek, 1965), my present opinion is that the accessory organs are mechanoreceptors. No function can be offered for the spherical cell nested within the group of nerve cell bodies of the accessory organ. A diagrammatic reconstruction of the eye and its accessory organ appears in figure 5.

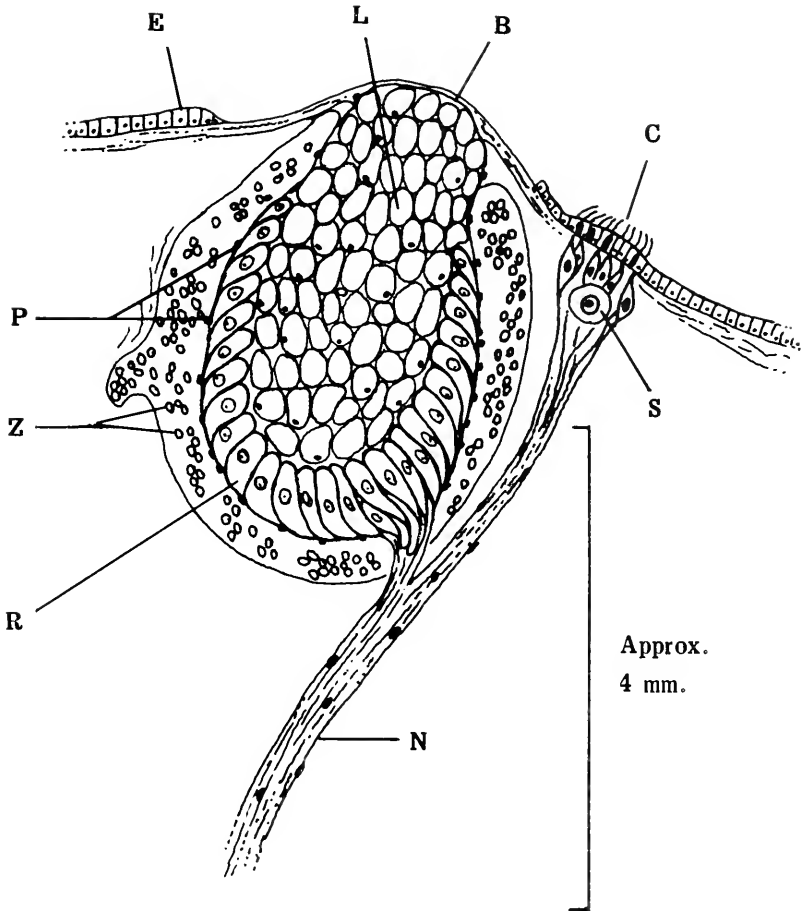


Figure 5. Diagrammatic reconstruction of the eye of *Tridacna maxima*, showing overlying membrane (B), ciliary sense organ (C), epithelium (E), multicellular lens (L), common nerve (N) and its bifurcation, pigment granules (P), retina (R), spherical cell (S) associated with the nerve cell bodies of the accessory organ, and circum-optic space filled with zooxanthellae (Z).

The Tridacnidae are usually ranked with the Cardiidae in the superfamily Cardiaceae. The existence of siphonal eyes in members of the Cardiidae has been known for many years. Roche (1925) reviewed much of the earlier literature and briefly described the eye and associated ciliated sense organ in *Cardium edule*. Unlike the eye of *Tridacna*, that of *Cardium* is of the inverse type; that is, the retinal nerve fibers pass between the retina and the lens before joining to form the optic nerve. In both species the eyes are rather simple. Pelseneer (1911, pl. 20) figured sections of the more com-

plex eye of *Cardium australe*, and while he did not fully describe it in his text (p. 56), he did note the existence of an inverted retina and of a ciliated accessory organ in that species. The lenses of these eyes, as well as that of *Pecten* (in Carthy, 1958, p. 9), are multicellular. It may be noted here that the accessory organs of *Tridacna crocea* were apparently mistaken to be incipient hyaline organs by Yonge (1936, p. 303).

Placed with *Tridacna* in the Tridacnidae is the monotypic genus *Hippopus*, which has been reported to lack hyaline organs. If *Hippopus* is, in fact, blind, comparative studies should reveal behavioral differences. Rosewater (1965) observed that *Hippopus* reacts to shadows, but response to shadows is not to be regarded as equivalent to the "sight" reaction of *Tridacna*. It may be that eyes do exist in *Hippopus*, but lie more deeply embedded in the mantle tissues.

Neither Yonge (1936) nor Brock, whose investigations Yonge reviewed, were able to demonstrate innervation of the hyaline organs. Yonge, therefore, believed the hyaline organs to function not as lenses associated with perception, but as windows that concentrate sunlight and distribute it deep into the tissues of the mantle. There, growth of zooxanthellae, known to live symbiotically within the mantle lobes, would be facilitated. Yonge thought that this relationship comprised a built-in food source for the clam. In a later paper, Yonge (1953, p. 468) recognized that there were features shared by the hyaline organs of *Tridacna* and the siphonal eyes of *Cardium*, although he held that the former had lost both retina and nerves. As reviewed by Wenrich (1916, p. 312), Patten in 1886, regarded the visual structures of *Pecten* and *Arca* not as eyes but as organs for the direct absorption of energy from the sun, terming them "heliophags." The hyaline organs of *Tridacna*, until now thought to serve indirectly in the conversion of the sun's energy to the benefit of the mollusk, are the last molluscan eyes to be relegated to the same fictitious status as the heliophags of other sighted bivalves.

#### ACKNOWLEDGMENTS

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