Brief Notes

Derivatives of Cilia in the Distal Sense Cells of the Retina of *Pecten**.

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The scallop, *Pecten*, a bivalved mollusk, has approximately 100 brilliantly colored blue-green eyes a millimeter or so in diameter located along the free margins of the mantle. Each eye contains a double retina which is separated from the lens by a thin connective tissue septum. Just beneath the septum lies the distal retina with its two cell types: the distal sense cell (Dakin's (1910) terminology), which is associated with the distal ramus of the optic nerve, and the external interstitial supporting cell. The proximal retina (which will be described in a subsequent communication) is just beneath the distal retina, and it contains rod cells associated with the proximal ramus of the optic nerve and internal interstitial supporting cells. This note describes observations concerning the fine structure of appendages on the specially differentiated septal border of the distal sense cells.

Methods

Eyes of freshly dredged *Pecten irradians* were excised and fixed for 60 minutes at 4°C. in an aqueous solution: 4 per cent OsO_4, 2 per cent $K_2Cr_2O_7$, 0.2 per cent KOH, and 0.810 M sucrose. The eyes were dehydrated in ethyl alcohol and embedded in a 4:1 mixture of butyl and methyl methacrylate, sectioned with a Porter-Blum microtome, and examined with a Philips EM-100A electron microscope.

OBSERVATIONS

Along the septal border of each distal sense cell are a small number of oval structures a micron or so in diameter. Fig. 1 is an electron micrograph depicting one such structure. It is composed of alternate lightly and densely stained bands which are arranged concentrically and show gradations in spacing.

These bands originate in the basal bodies of cilia, as can be seen in favorably oriented sections (such as Fig. 2). Rows of both basal bodies and ciliary stalks are seen on the bottom half of Fig. 2 and on the left side of Fig. 1. That these structures are ciliary basal bodies and stalks is illustrated by Fig. 3, which is an electron micrograph of one such stalk in transverse section showing nine dense loci, some of which appear to be double, arranged around the circumference. This corresponds closely to the structure of cilia in animals from diverse phyla which have been examined by Fawcett and Porter (1954) and others. In Fig. 2 ciliary stalks in longitudinal section (indicated by lines parallel to the stalks) are seen to be continuous with the bands. The entire concentrically banded structure, connected as it is to the cell by ciliary stalks, should be considered an appendage to the cell.

In Fig. 4, which shows an appendage at higher magnification, the dark bands are seen to consist of parallel linear limits, which are interpreted as membranes, and a contained space of about 25 mμ. In this micrograph the dense bands are repeated roughly every 70 mμ.

In many micrographs of sections taken in different planes, the concentric banding has been a constant feature, and for this reason it is assumed that the distal sense cell appendages are spherical. However, their three-dimensional morphology is not yet completely understood and will be taken up later in a fuller treatment of the structure of the eye of *Pecten*.

DISCUSSION

To Hesse belongs the credit for recognizing the nature of the specially differentiated septal border of the distal sense cell. In his first study of the *Pecten* eye (1900), he was undecided as to whether the distal sense cells were ciliated epithelium, but in a later account (Hesse, 1908) he regarded the septal edge as the part of the cell specialized for photoreception ("*Stiftchensaum*"). Küpfer (1916) thought these structural elements of the septal border were neurofibrils continuous with the distal ramus of the optic nerve, while Dakin first thought of them as "cilia-like processes" (Dakin, 1910), then changed his mind and agreed with Küpfer (Dakin, 1928). Roche (1925), using Bielshowsky's silver impregnation method, was also in agreement with Küpfer.

As a result of the finding that the distal sense

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cell appendages are derived from cilia, just as are the vertebrate rod outer segments (De Robertis, 1956; Porter, 1957), it is tempting to assume that they, too, are photoreceptors. In spite of the fact that the vertebrates and mollusks are widely separated phyla, light microscope investigations by Hesse (1908) tend to support this homologization. He found that the sense cells in the retina of the gastropod mollusk, *Limax maximus*, have appendages similar to those of *Pecten's* distal sense cell, which are also derived from cilia. Since *Limax* has a single-layered retina with only one type of sense cell, this evidence tends to lend credence to the idea that the distal sense cell appendages are indeed photoreceptor structures.

The physiology of the eye of *Pecten* has been investigated by Hartline (1938), who showed (1) that the axons from the proximal retina discharge impulses during steady illumination of the eye, but (2) that the axons from the distal retina discharge impulses only in response to a decrease in illumination of the eye. Hartline discussed the possibility, in view of the latter finding, that the distal sense cell may be an "off receptor." Recent investigations by Ratliff and Mueller (1957) show that an "off response" may be generated by interaction among receptors that usually respond as "on elements." On this basis one might postulate that the distal sense cell is actually excited during illumination, but is inhibited by the activity of the proximal retina, and that the distal sense cell's activity appears as an after-discharge when the inhibition is released on reduction of the illumination. At present, details of the relationship between the proximal and distal retinas are unknown, and there is no direct evidence to support this speculation. Be that as it may, the finding that, like the vertebrate rod outer segments, the distal sense cell appendages are derived from cilia does suggest they are photoreceptors. Proof of this will have to await the exact localization of the photochemical pigments, as has already been accomplished in the case of the vertebrate rod outer segment and the arthropod rhabdom (Wald and Hubbard, 1957).

SUMMARY

Located along the septal border of the distal sense cell are a small number of appendages approximately a micron in diameter. In electron micrographs these appendages are seen to consist of lightly and densely stained bands which are arranged concentrically. These bands are continuous with the stalks of cilia which originate in basal bodies. Evidence for the concept that these distal sense cell appendages are photoreceptor structures is discussed.

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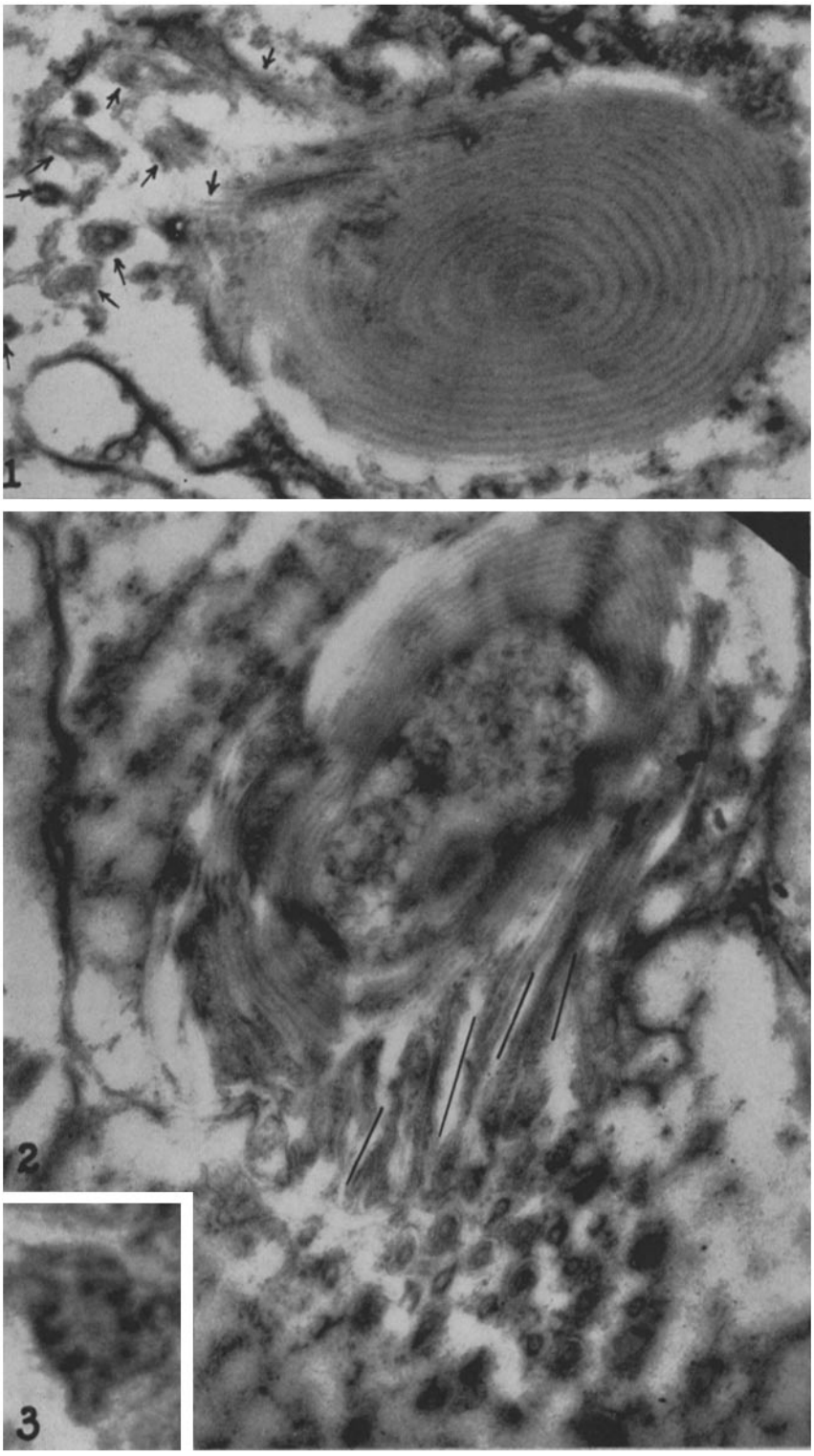
EXPLANATION OF PLATES

PLATE 120

FIG. 1. Electron micrograph of an appendage on the septal border of a distal sense cell. The structure is composed of alternate lightly and densely stained bands arranged concentrically. The basal bodies and stalks of cilia from which this appendage is derived are seen on the left side of the micrograph (arrows). × 20,000.

FIG. 2. Micrograph of an appendage illustrating origin of the concentric bands. Rows containing basal bodies and ciliary stalks are seen on the bottom half of this figure. Ciliary stalks sectioned longitudinally which are seen to be continuous with the bands of the appendage are indicated by lines between and parallel with the stalks. The closed outlines in the center of the appendage are similar to those found in the crown cell, a ciliary derivative described by Bargmann and Knopp (1955), and by Porter (1957). × 17,000.

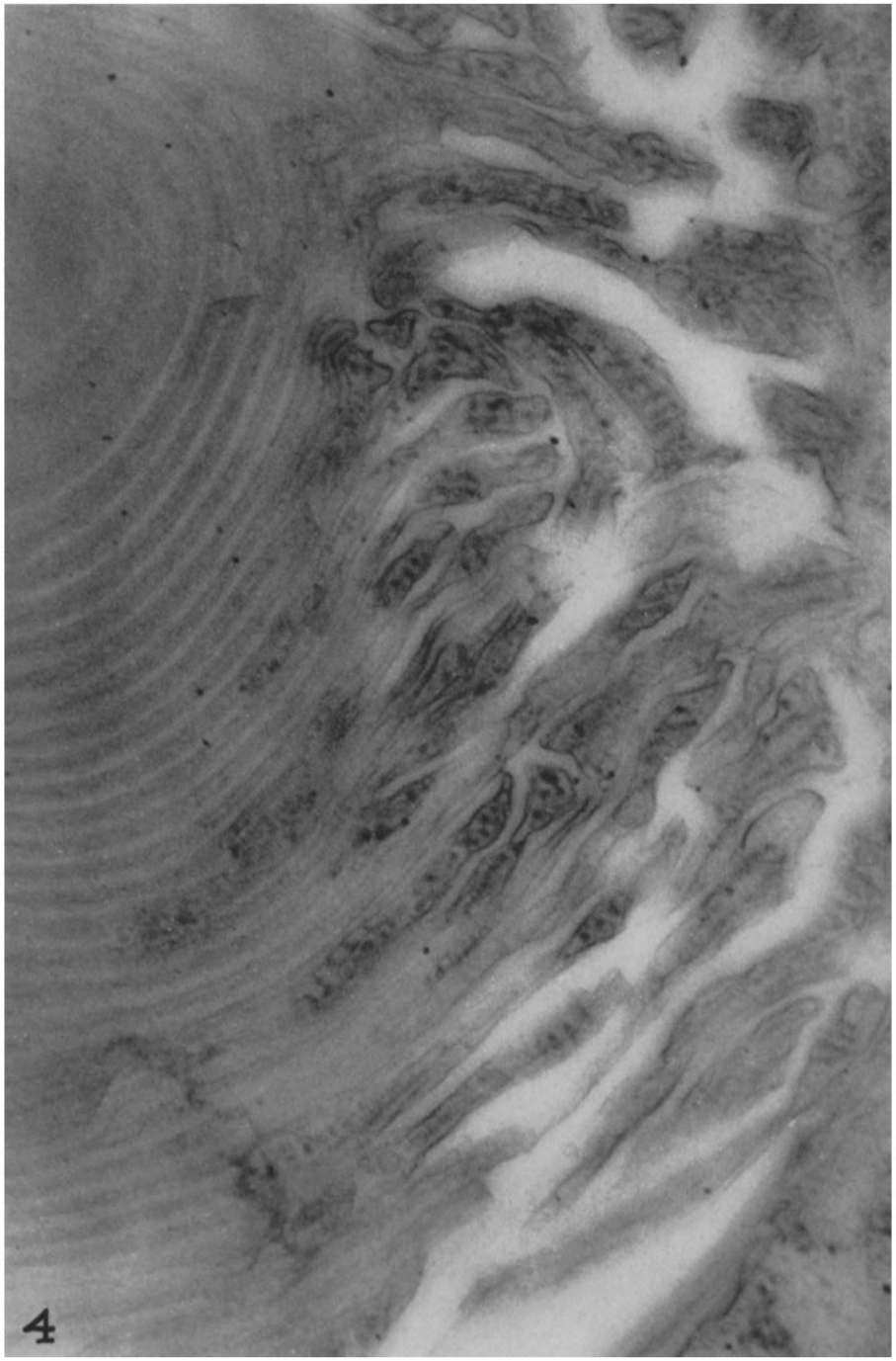
FIG. 3. Ciliary stalk in transverse section. Nine dense loci, some of which appear to be double, are arranged around the circumference. (No definite densely stained material is seen in the center.) × 100,000.



(Miller: Ciliary derivatives in *Pecten*'s retina)

PLATE 121

FIG. 4. Micrograph of distal sense cell appendage. The densely stained bands are composed of parallel linear limits which are interpreted as membranes. Ciliary stalks within which are many dense markings are seen on the right-hand side of this figure. × 44,000.



(Miller: Ciliary derivatives in *Pecten*'s retina)