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Brachiopod Tentacles: Ultrastructure and Functional Significance of the Connective Tissue and Myoepithelial Cells in *Terebratalia*

Christopher G. Reed* and Richard A. Cloney

Department of Zoology, University of Washington, Seattle, Washington, U.S.A.

Summary. The fine structure of the tentacles of the articulate brachiopod *Terebratalia transversa* has been studied by light and electron microscopy. The epidermis consists of a simple epithelium that is ciliated in frontal and paired latero-frontal or latero-abfrontal longitudinal tracts. Bundles of unsheathed nerve fibers extend longitudinally between the bases of the frontal epidermal cells and appear to end on the connective tissue cylinder; no myoneural junctions were found. The acellular connective tissue cylinder in each tentacle is composed of orthogonal arrays of collagen fibrils embedded in an amorphous matrix. Baffles of parallel crimped collagen fibrils traverse the connective tissue cylinder in regions where it buckles during flexion of the tentacle.

The tentacular peritoneum consists of four cell types: 1) common peritoneal cells that line the lateral walls of the coelomic canal, 2) striated and 3) smooth myoepithelial cells that extend along the frontal and abfrontal sides of the coelomic canal, and 4) squamous smooth myoepithelial cells that comprise the tentacular blood channel.

Experimental manipulations of a tentacle indicate that its movements are effected by the interaction of the tentacular contractile apparatus and the resilience of the supportive connective tissue cylinder. The frontal contractile bundle is composed of a central group of striated fibers and two lateral groups of smooth fibers which function to flex the tentacle and to hold it down, respectively. The small abfrontal group of smooth myoepithelial cells effects the re-extension of the tentacle, in conjunction with the passive resiliency of the connective tissue cylinder and the concomitant relaxation of the frontal contractile bundle.

Key words: Brachiopod tentacles – Connective tissue – Myoepithelial cells – Ultrastructure.

Send offprint requests to: Christopher G. Reed, Department of Zoology, NJ-15, University of Washington, Seattle, Washington 98195, U.S.A.

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Introduction

The general histology of brachiopod tentacles has been reviewed by Helmcke (1937), Hyman (1959), Beauchamp (1960), and Williams and Rowell (1965). Each tentacle consists of three tubular layers of tissue: 1) an outer layer of epidermis that is ciliated in certain tracts, 2) an intermediate layer of connective tissue, and 3) an inner peritoneal layer that lines a central coelomic canal. Nerves extend the length of each tentacle immediately beneath the frontal epidermis in inarticulate brachiopods (Blochmann, 1892, 1900), or within the connective tissue beneath the epidermis in articulate brachiopods (Bemmelen, 1883). The connective tissue has a supportive role (Chuang, 1956) and has often been described as cartilaginous or cartilagelike (Hancock, 1859; Hyman, 1959; Rudwick, 1970; McCammon and Reynolds, 1976; Storch and Welsch, 1976), but its mechanical and chemical properties have not been properly investigated.

A blood channel that is closed at its distal end extends the length of each tentacular coelomic canal adherent to the frontal peritoneum (Beauchamp, 1960; Williams and Rowell, 1965). It is considered to be contractile although rhythmic contractions have not yet been demonstrated (Beauchamp, 1960). Atkins (1959a) described fine "muscle fibers" in the walls of the tentacular blood channels of *Macandrevia;* Storch and Welsch (1976) subsequently demonstrated by electron microscopy that the tentacular blood channels in *Lingula* are composed of peritoneal cells that contain myofilaments.

Several investigators have claimed that the contractile apparatus in brachiopod tentacles consists of bundles of muscle fibers that extend longitudinally beneath the peritoneum on opposite sides of the coelomic canals (Huxley, 1854; Hancock, 1859; Hyman, 1959; Reynolds and McCammon, 1977). It has also been reported that the tentacular peritoneum itself is partly composed of longitudinal "muscle fibers" (Helmcke, 1937; Chuang, 1956; Beauchamp, 1960; Williams and Rowell, 1965) and recently Storch and Welsch (1976) have described peritoneal myoepithelial cells in the tentacles of *Lingula.*

The contractile tissue has been described as smooth in some genera and striated in others. On the basis of the movements of the tentacles of the articulate brachiopods *Pumilus antiquatus* and *Platidia davidsoni,* Atkins (1958) suggested that the contractile apparatus may be composed of both smooth and striated "muscle fibers". She attributed the coiling of the tentacles to the striated "muscle" and suggested that the ability of the tentacles to remain coiled for long periods indicated the presence of smooth "muscle fibers". Atkins (1959b) also implied a composite organization for the contractile apparatus in the tentacles of *Terebratalia transversa* when she noted that "certain of the (muscle) fibers are striated".

Some of the inconsistencies and hypotheses in the literature can be resolved or tested by ultrastructural studies. Storch and Welsch (1976) have examined the ultrastructure of the lophophore of an inarticulate brachiopod (*Lingula unguis*). In this study the fine structure of the tentacles of an articulate brachiopod (*Terebratalia transversa*) is described for the first time. The diversity of myoepithelial cell types in the tentacular peritoneum is discussed in conjunction with the skeletal role of the tentacular connective tissue, and a model is proposed to explain the movements of brachiopod tentacles.

Materials and Methods

Specimens

Subtidal specimens of *Terebratalia transversa* Sowerby (1846) with smooth shells were dredged at two different locations in San Juan Channel in the San Juan archipelago, Washington, during the winters of 1973–74 and 1975–76. Intertidal specimens with ribbed shells were also collected on San Juan Island in the fall of 1975. All observations in this paper were made on the subtidal brachiopods unless otherwise indicated.

Preparation of Specimens for Microscopy

Tentacles from the lateral arms and the median coils of fully developed lophophores were excised and fixed immediately at room temperature in 2.5% glutaraldehyde and 0.14M NaCl buffered at pH 7.4 in 0.2M Millonig's phosphate buffer. The final osmolality was about 960 milliosmoles. After two hours in the primary fixative the tentacles were rinsed briefly and postfixed in 2% osmium tetroxide buffered at pH 7.4 in 1.25% sodium bicarbonate for one hour at room temperature (Wood and Luft, 1965).

Some tentacles were relaxed in chloral hydrate and fixed in another fixative that improved the preservation of the sarcoplasmic reticulum (Cavey and Cloney, 1972). After relaxation the tentacles were transferred to a solution of 2% glutaraldehyde and 0.27M sucrose containing 0.05% unpurified ruthenium red buffered at pH 7.4 in 0.2M cacodylate buffer. The final osmolality was about 900 milliosmoles. After 4 h of fixation at room temperature the tentacles were rinsed briefly and postfixed in 2% osmium tetroxide buffered at pH 7.4 in 1.25% sodium bicarbonate for 2 h in an ice bath. After post fixation the tentacles were rinsed in distilled water for 30 s to remove the excess fixative. They were then dehydrated in ethanol, transferred through three changes of propylene oxide, and infiltrated and embedded in Epon according to the method of Luft (1961).

One micron sections for light microscopy were cut with glass knives on a Sorvall Porter-Blum MT-1 ultramicrotome and stained with an alkaline solution of methylene blue and azure II (Richardson et al., 1960). Photomicrographs were made with Kodak Panatomic X film or Kodak High Contrast Copy film. Thin sections about 60 nm thick for electron microscopy were cut with a diamond knife on a Sorvall Porter-Blum MT2-B ultramicrotome and mounted on copper grids. Thin sections were stained with saturated aqueous uranyl acetate and lead citrate (Reynolds, 1963). Electron micrographs were made with a Philips EM-300 electron microscope.

Measurements on the dimensions of the myoepithelial cells were obtained by relaxing the lophophore with chloral hydrate and allowing it to decompose for 2 days. After the tentacular epidermis had sloughed off, the connective tissue cylinders were cut off and examined with a Zeiss Standard Universal microscope equipped with polarizing optics.

Paraffin sections of lophophores that were fixed in Bouin's fluid were stained with toluidine blue to determine if the connective tissue was metachromatic.

Results

General Description of the Lophophore

The lophophore of *Terebratalia transversa* Sowerby consists of a pair of lateral arms and a median coil fringed along their margins by two rows of staggered tentacles. A flap of tissue called the brachial fold runs mesad to the lophophoral fringe bearing the tentacles, delimiting a heavily ciliated brachial groove that carries food to the mouth (Fig. 1). Orton (1914) designated the side of the tentacles facing the brachial groove "frontal" and the opposite side "abfrontal". The tentacles that form the row closest to the brachial groove have paired latero-abfrontal epidermal ridges while each tentacle of the outer row has a grooved frontal surface and paired latero-frontal epidermal ridges (Fig. 2, 3). Each tentacle contains a central

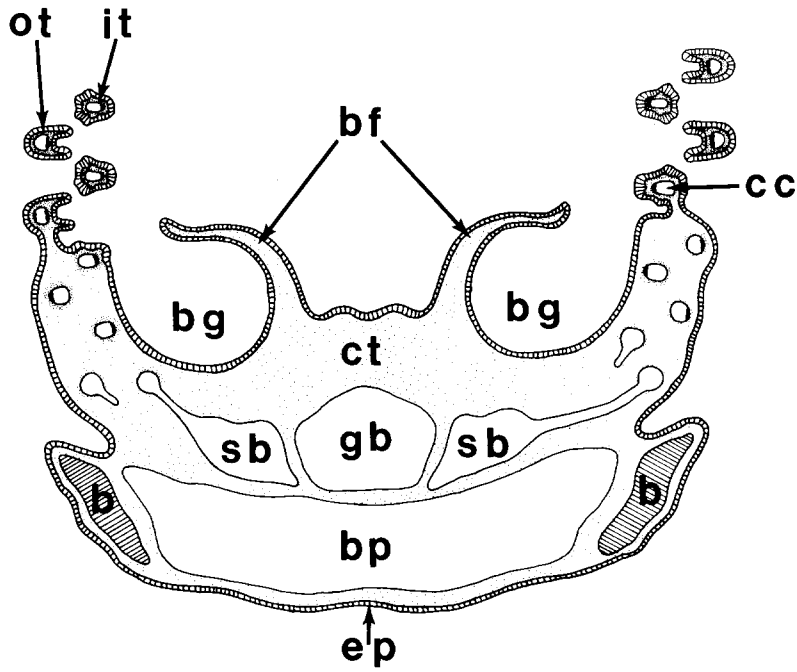

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Fig. 1. Schematic diagram of a slightly oblique section of one of the lateral arms of a lophophore, showing the organization of the coelomic canal systems and the arrangement of the two types of tentacles as they arise from the margin of the lophophore. The peritoneum that lines the coelomic canals is not shown. The dense connective tissue of the lophophore (stippled area) extends into the tentacles as stiff collagenous tubes. The greater brachial canal occupies a central position along the main axis of the lateral arm. The smaller brachial canal system courses below the lophophoral margin and gives rise to coelomic extensions into the tentacles. A large metacoelic brachial pouch extends into each lateral arm in close proximity to the calcareous brachidium. The brachial fold runs along the lophophoral fringe, forming the brachial groove at the base of the tentacles

Abbreviations for Figures. A sarcomeric A-band; *ab* abfrontal side of tentacle; *b* brachidium; *ba* baffles; *bb* basal body; *bc* blood channel; *bf* brachial fold; *bg* brachial groove; *bl* basal lamina; *bp* brachial pouch; *c* cilium; *cc* tentacular coelomic canal; *cct* circumferential layer of connective tissue; *cp* common peritoneal cell; *cr* ciliary rootlet; *cs* ciliary stump; *ct* connective tissue; *ep* epidermis; *f* frontal side of tentacle; *gb* greater brachial canal; *gc* glycocalyx; *gl* glycogen particles/rosettes; *go* Golgi complex; *H* sarcomeric H-band; *hd* hemidesmosome; *I* sarcomeric I-band; *it* inner tentacle; *l* lateral side of tentacle; *lct* longitudinal layer of connective tissue; *lu* lumen of blood channel; *ly* putative secondary lysosome; *mc* mucous cell; *md* mucous droplet; *mf* myofilament field; *mt* mitochondrion; *mv* microvilli; *n* nerves; *nf* nerve fibers; *nu* nucleus; *nt* putative nerve terminal; *ot* outer tentacle; *p* peritoneum; *pc* peripheral coupling; *rr* rough endoplasmic reticulum; *sb* smaller brachial canal; *sc* subsarcolemmal cisterna; *sd* septate desmosome; *sm* smooth myoepithelial cell; *sq* squamous myoepithelial cell of the blood channel; *sr* sarcoplasmic reticulum; *st* striated myoepithelial cell; *Z* sarcomeric Z-line; *za* zonula adhaerens

Abbreviations for Captions. Ch chloral hydrate; *Gc* cacodylate-buffered glutaraldehyde; *Gp* phosphate-buffered glutaraldehyde; *Os* bicarbonate-buffered osmium tetroxide

cylindrical extension of the mesocoel. The dense acellular connective tissue in each tentacle forms a stiff cylinder that is covered externally by the epidermis and internally by the peritoneum. A frontal involution of the peritoneum in each tentacle forms a blood channel that extends the length of the tentacular coelomic canal (Fig. 2).

Movements of the Tentacles

The tentacles are extended during feeding but they curl up toward the brachial groove when disturbed. After several moments the tentacles slowly uncurl, but they can remain curled for longer periods if the source of irritation persists. If the tips of the tentacles are cut off to expose the coelomic canals to the external medium, the tentacles curl and uncurl like intact tentacles, indifferent to any loss of coelomic pressure. A similar experiment was conducted by Chuang (1956) on the inarticulate brachiopod *Lingula unguis* with identical results.

If the tentacular peritoneum is disrupted by crushing the tentacles with forceps, the connective tissue cylinders regain their original shape and the tentacles remain extended. When intact tentacles are relaxed with chloral hydrate they also uncurl; the extended tentacles can be bent in any direction and they will immediately straighten out again. Manipulations of the connective tissue cylinders of partially decomposed tentacles give the same results, demonstrating that the resiliency of the tentacles resides in their connective tissue cylinders.

Ultrastructure of the Tentacles

Epidermis. Each outer tentacle is covered by a simple epithelium that consists of columnar cells on the frontal side and cuboidal cells on the abfrontal side of the tentacle; the inner tentacles are completely covered by a single layer of columnar epidermal cells. The ciliated epidermal cells in both types of tentacles are primarily restricted to longitudinal tracts on the epidermal ridges, but a weaker frontal ciliary tract is present and the remaining surface of the tentacle is sparsely ciliated.

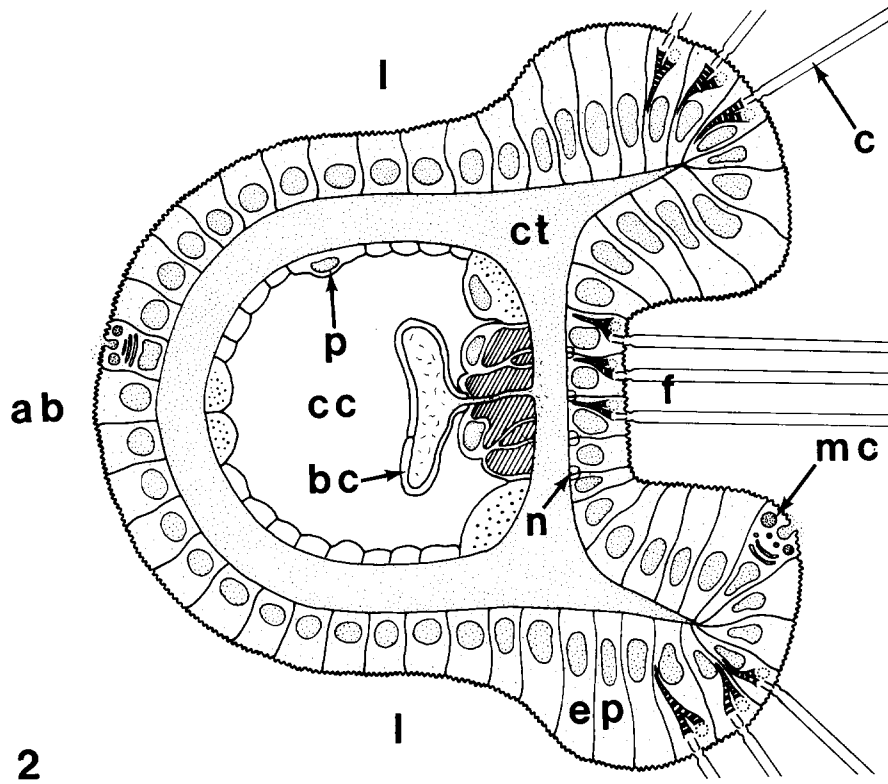
The free surface of each epidermal cell has a microvillous border about 0.7 μ thick that is coated with a glycocalyx of low electron density. Putative secondary lysosomes are common in the apical cytoplasm, and dark secretory granules often occur in various stages of condensation near Golgi cisternae and vesicles (Fig. 5). An ovoid nucleus is located in the middle of each cell and oblong mitochondria are abundant in the juxtanuclear cytoplasm. Glycogen rosettes up to 140 mμ in diameter are dispersed throughout the cytoplasm.

Each cell in a ciliary tract gives rise to a single cilium. Two centrioles are oriented at right angles to each other in the apical cytoplasm at the base of each cilium. A ciliary rootlet with a periodicity of 70 nm arises from the two centrioles and extends basally past the nucleus. Another short ciliary rootlet may extend laterally from the basal body, parallel to the apical plasmalemma.

Mucous cells are scattered throughout the epidermis and increase in number near the bases of the tentacles. Each mucous cell contains prominent supranuclear Golgi complexes and mucous droplets up to 1.0 μ in diameter that accumulate in the apical cytoplasm, excluding other inclusions and organelles.

The apices of all the epidermal cells are joined by zonulae adhaerentes, and tonofilaments converge on their basal plasmalemmata to form hemidesmosomes. Septate desmosomes join the cells at the level of their nuclei. A basal lamina about 47 nm thick underlies the epidermis, separating it from the connective tissue cylinder.

A proliferation of round cells occurs in the frontal epidermis at the base of each tentacle (Fig. 4).



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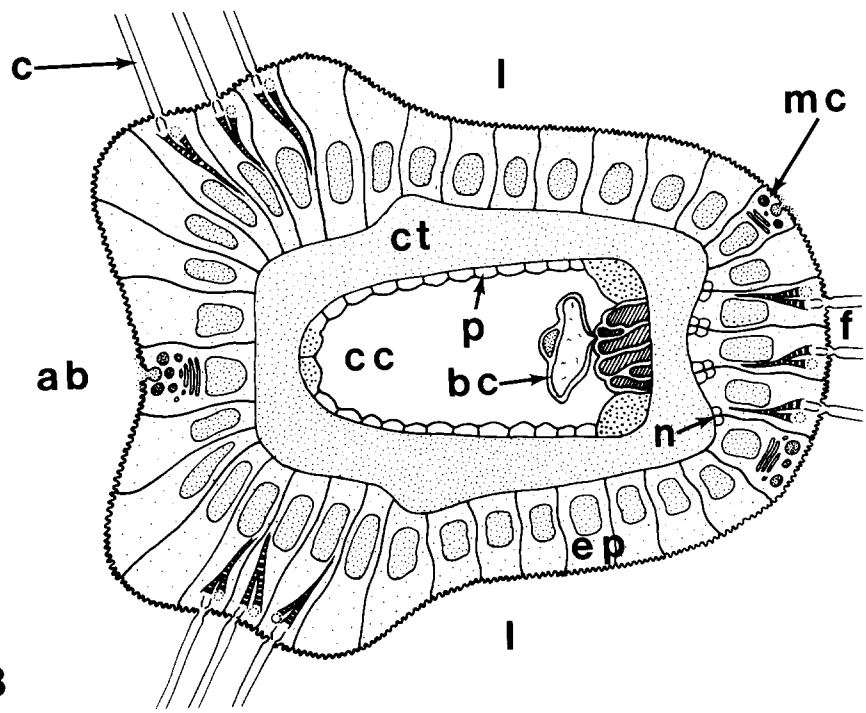

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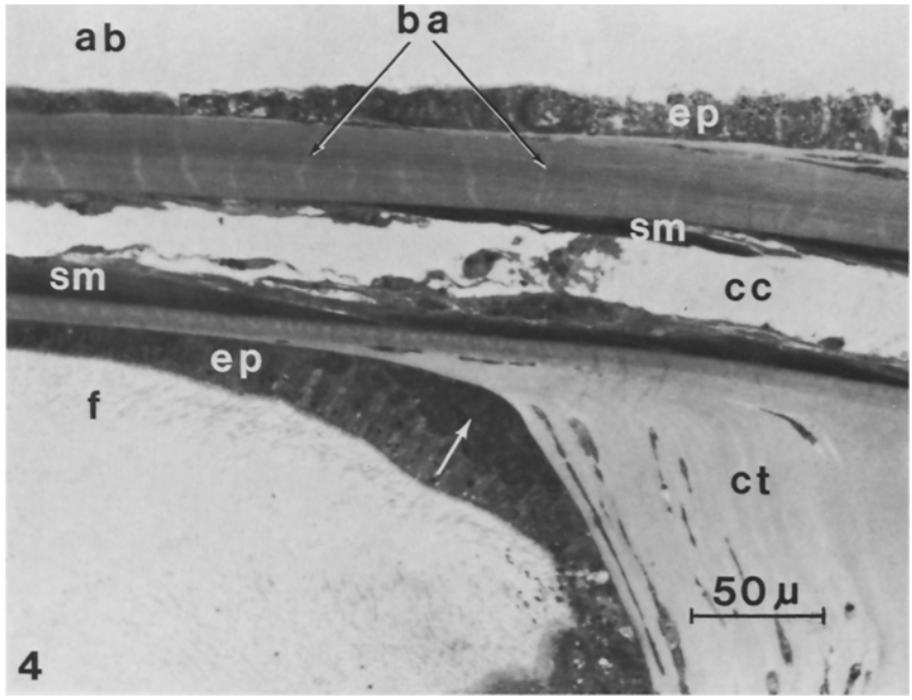


Fig. 4. Photomicrograph of a median sagittal section through the base of an outer tentacle. The frontal epidermis contains a cluster of round cells (white arrow). The acellular cylinder of connective tissue that immediately surrounds the tentacular coelomic canal is denser than the connective tissue in the rest of the lophophore and is traversed by numerous baffles. The section passes through smooth myoepithelial cells on the frontal and abfrontal sides of the coelomic canal. (Gp-Os fixation.) × 1060

Nerves. Bundles of naked neuronal processes extend along the frontal side of each tentacle between the bases of the epidermal cells (Fig. 5). These basiepithelial nerve fibers are on the epidermal side of the basal lamina and have never been observed crossing the connective tissue cylinder to form myoneural junctions. Instead, neuronal processes filled with both dense and clear vesicles that range in diameter from 100 to 140 nm appear to end on the connective tissue cylinder (Fig. 10). The

Fig. 2. Schematic diagram of a transverse section of an outer tentacle. The epidermis is ciliated in longitudinal tracts on the frontal surface and on the latero-frontal epidermal ridges. Nerves extend longitudinally between the bases of the frontal epidermal cells. A thick layer of acellular connective tissue separates the epidermis from the peritoneum. The peritoneum consists of myoepithelial cells on the frontal and the abfrontal sides of the tentacular coelomic canal. The frontal contractile bundle has both smooth (stippled) and striated (slashed) fibers, but the small abfrontal contractile bundle has only smooth fibers. A blood channel is formed by an involution of the frontal peritoneum

Fig. 3. Schematic diagram of a transverse section of an inner tentacle. The ciliary tracts arise from the frontal epidermis and the paired latero-abfrontal epidermal ridges. The rest of the histological organization is similar to that of the outer tentacle in Figure 2

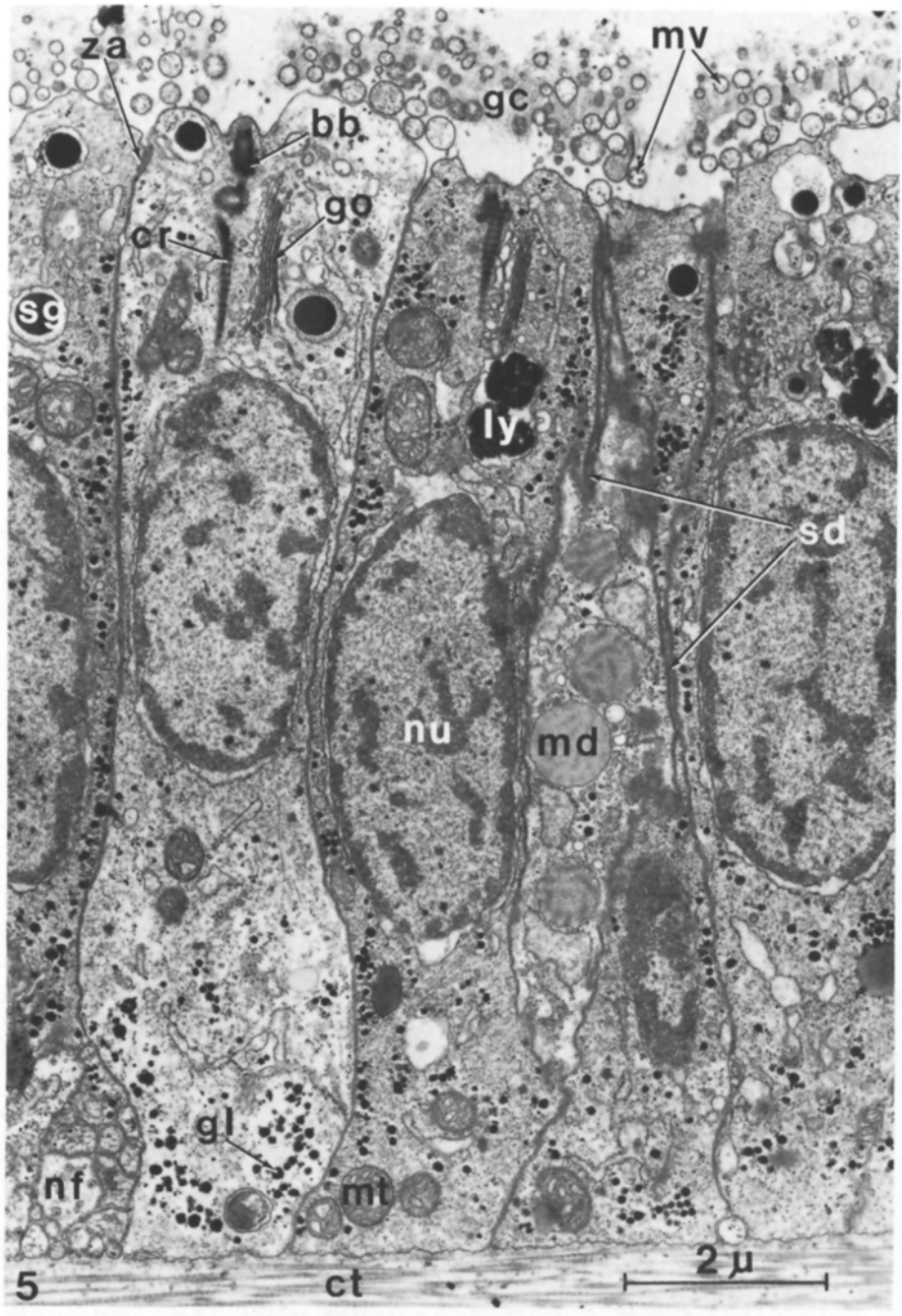
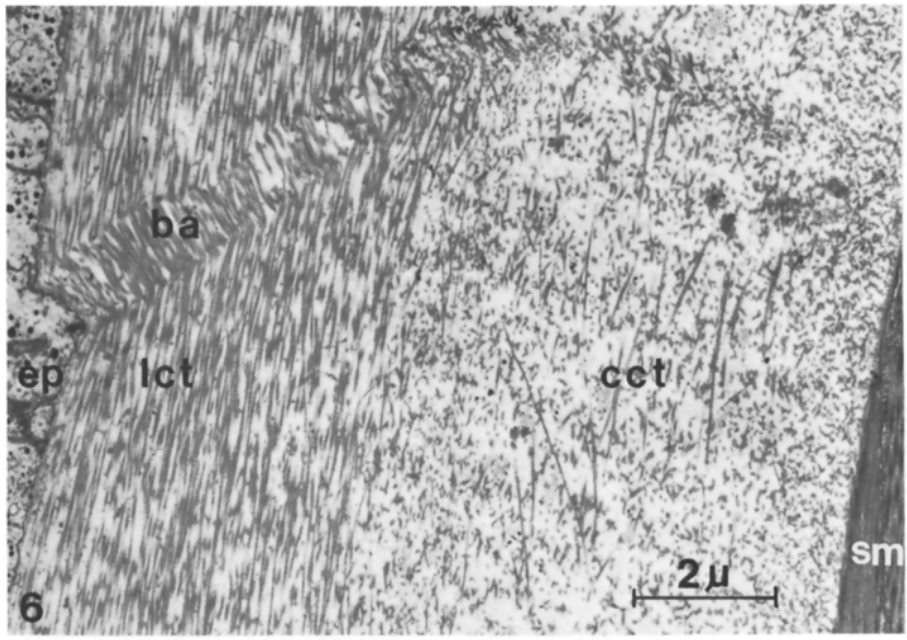


Fig. 5. Electron micrograph of a transverse thin section of the frontal epidermis near the base of an outer tentacle. The columnar epidermal cells are joined apically by zonulae adhaerentes and at the level of their nuclei by septate desmosomes. Surface modifications of the apical plasmalemma in each cell consist of a single cilium surrounded by sinuous microvilli that perforate a faint glycocalyx. The apical cytoplasm in each cell is characterized by secretory granules, putative secondary lysosomes, and a supranuclear Golgi complex next to the basal body and the ciliary rootlet of the cilium. Glycogen rosettes and occasional lipid droplets are also found dispersed throughout the cytoplasm. The section passes through part of a mucous cell containing large mucous droplets. A bundle of unsheathed nerve fibers is positioned between the bases of two epidermal cells in the lower left corner. (Gp-Os fixation.) ×13,740



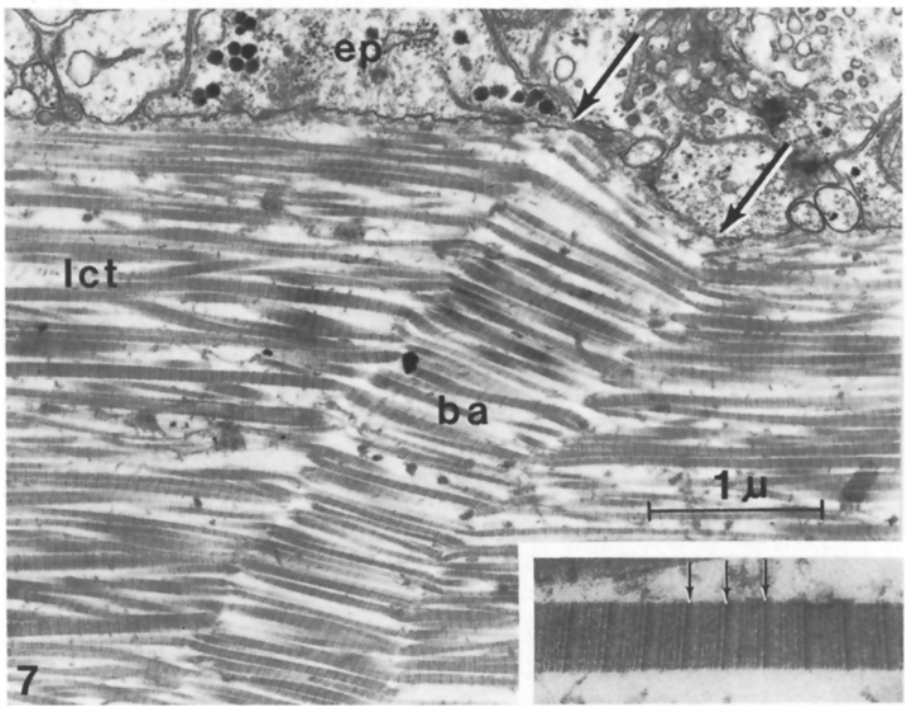
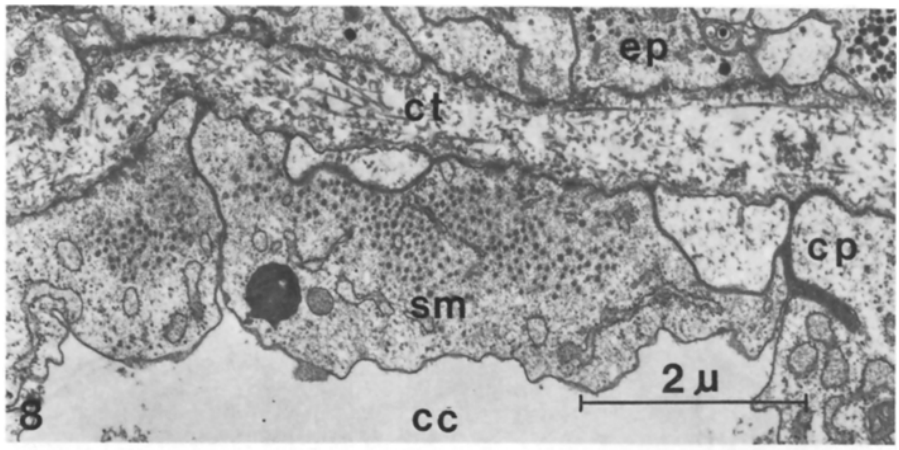


Fig. 6. Longitudinal section of the frontal side of the connective tissue cylinder in an inner tentacle. The cylinder consists of a subepidermal longitudinal layer and a subperitoneal circumferential layer of fibrils embedded in an amorphous matrix. A zone of crimped and displaced fibrils corresponds to one of the bands, or baffles, observed by light microscopy. (Gp-Os fixation.) ×9520

Fig. 7. Longitudinal section of the subepidermal connective tissue on the frontal side of the cylinder. The region between the arrows corresponds to part of one of the baffles observed by light microscopy. It consists of a zone where the parallel fibrils are crimped and oriented at a different angle than they are in the rest of the cylinder. The fibrils have a major axial periodicity of 63 nm (inset: distance between arrows) that is diagnostic of native vertebrate collagen fibrils. (Gp-Os fixation.) ×23,200. *Inset:* ×83,860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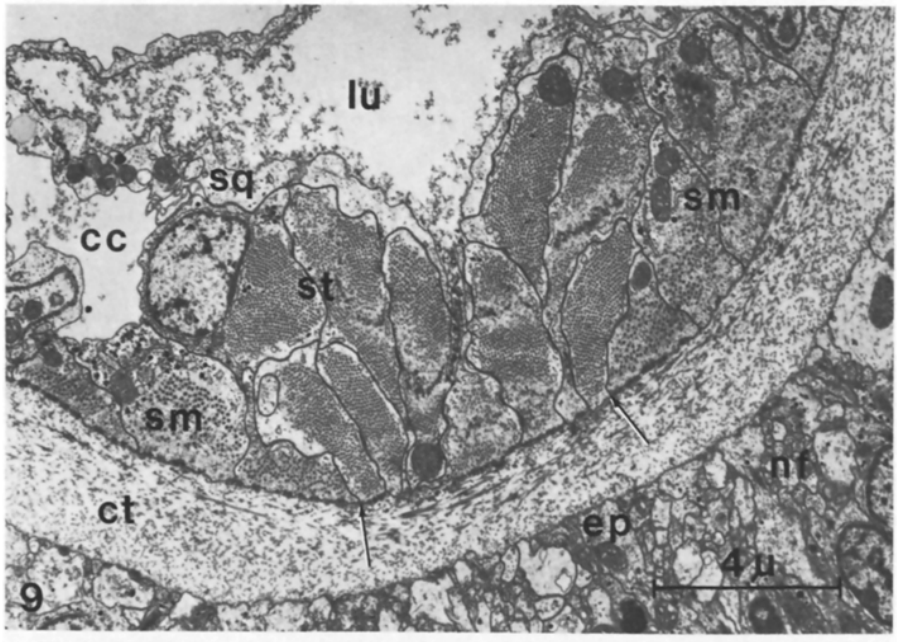
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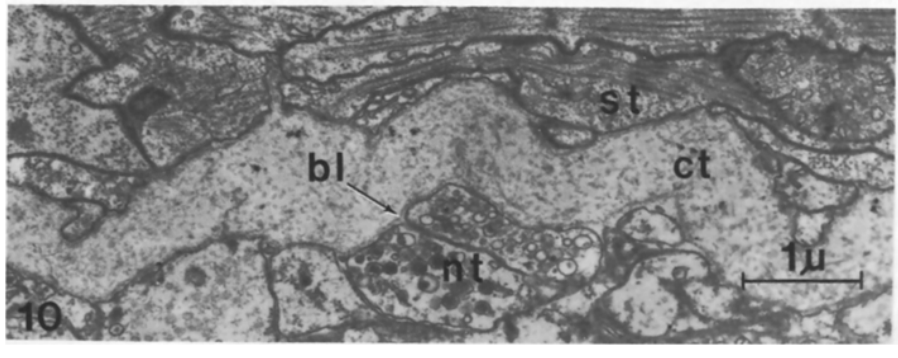
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contractile apparatus of the tentacle remains separated from these apparent nerve terminals by a layer of connective tissue about 1.0 μ thick. No intraperitoneal nerve fibers were found.

Connective Tissue. The connective-tissue cylinder in each tentacle is bounded by a basal lamina beneath the epidermis and by another one beneath the peritoneum. This tube diminishes in thickness distally and varies in shape in the two types of tentacles. It is an ovoid cylinder in the inner tentacles, but in the outer tentacles the cylinder extends into the latero-frontal epidermal ridges, forming a pair of connective tissue ridges that run the length of each tentacle (Fig. 2).

The tentacular connective tissue is distinguished from the connective tissue in the rest of the lophophore by an absence of cells and a lack of metachromasia when stained with toluidine blue. The dense acellular connective tissue of the tentacles consists of a fibrous component embedded in a matrix of amorphous ground substance. The fibrils range in diameter from 15 nm to 100 nm and have a mean axial periodicity of 63 nm (Fig. 7). They are primarily arranged in two layers within each cylinder: a thick outer longitudinal subepidermal layer and an inner circumferential layer subjacent to the peritoneum (Fig. 6). This organization loses its integrity near the tip of the tentacle. Small bundles of thin (20 nm in diameter) electron dense filaments with fuzzy boundaries are infrequently found in the cylinder. Flocculent material from the blood channel is also found dispersed in the homogeneous matrix in regions where the lumen of the blood channel communicates with the connective tissue.

By light microscopy numerous bands, or baffles, are visible traversing the connective tissue cylinder at irregular intervals (Fig. 4). When viewed with a polarizing microscope it is clear that the fibrous components of the baffles are oriented in a different axis than the fibrils in the rest of the cylinder. Examination with the electron microscope reveals that these baffles are actually zonulae of parallel crimped collagen fibrils in regions where the cylinder buckles during flexion (Fig. 6, 7).

Fig. 8. Transverse section of the abfrontal contractile bundle near the distal end of an inner tentacle (refer to Figure 2). The smooth myoepithelial cells are exposed apically to the tentacular coelomic canal (bottom) and are bordered laterally by the common peritoneal cells and basally by the connective tissue cylinder. (Gp-Os fixation.) ×15,480

Fig. 9. Transverse section of the frontal contractile bundle near the distal end of an inner tentacle. Approximately 10 striated myoepithelial cells occupy the central part of the contractile bundle (between the arrows) and are bordered on either side by a group of 3 smooth myoepithelial cells (outside the arrows). The striated fibers adjoin the squamous peritoneal cells that comprise the tentacular blood channel. The acellular connective tissue cylinder separates the myoepithelial cells from the epidermis and the neuronal processes at the bottom of the picture. (Gp-Os fixation.) ×6190

Fig. 10. Longitudinal section of two putative nerve terminals near the distal end of an inner tentacle. The neuronal processes are filled with dense and clear vesicles but remain separated from the frontal myoepithelial cells by the acellular connective tissue cylinder. Some of the vesicles appear to contact the neurolemma facing the basal lamina. (Gc-Os fixation.) ×16,100

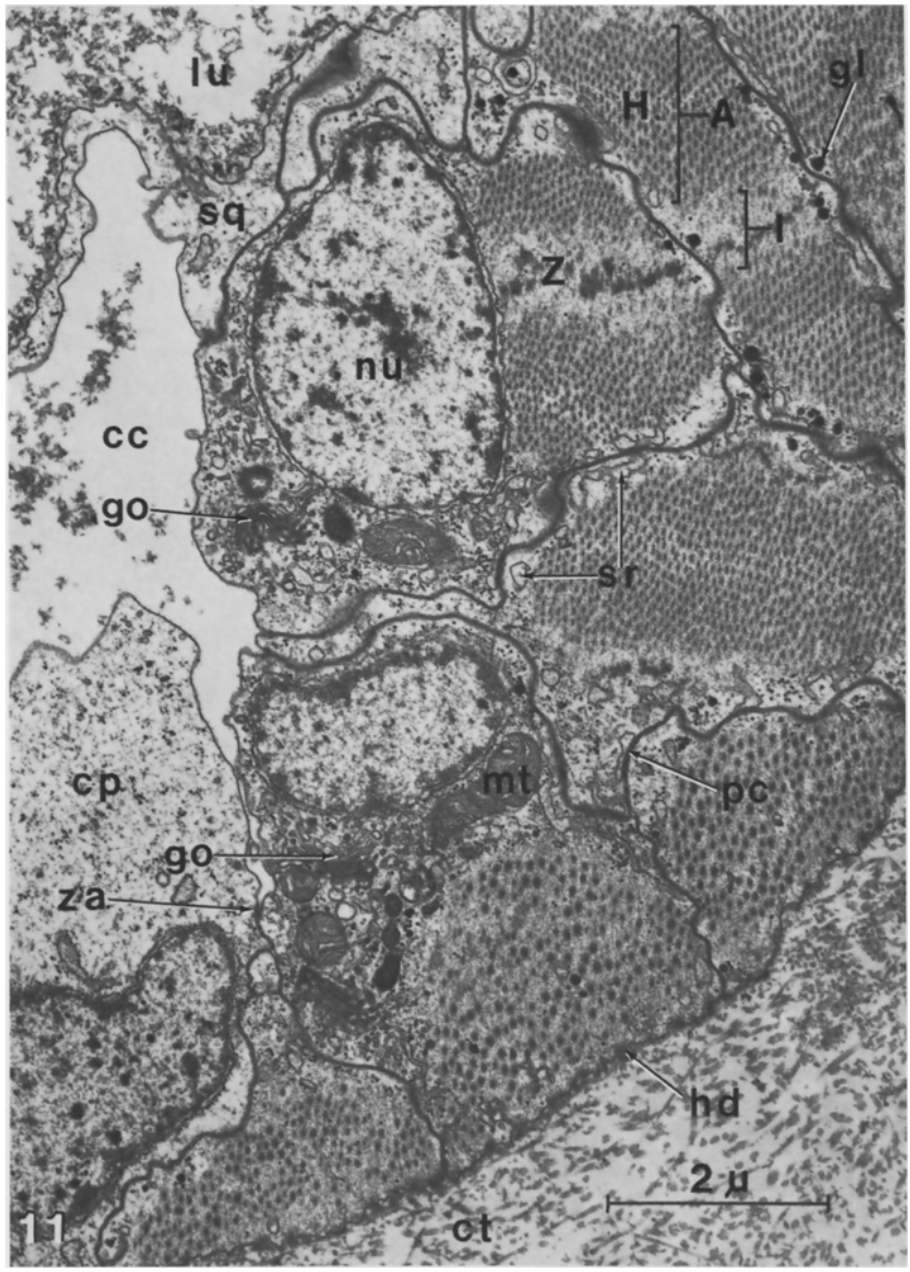


Fig. 11. Slightly oblique section of the smooth (bottom) and the striated (top) myoepithelial cells of the frontal contractile bundle. The apices of the myoepithelial cells are exposed to the tentacular coelomic canal on the left and adjoin to each other and to adjacent peritoneal cells by zonulae adhaerentes. A single nucleus is located in the centro-apical cytoplasm of each cell and Golgi complexes and mitochondria are present in the juxtanuclear cytoplasm. The obliquity of the plane of section allows visualization of the sarcomeric regions in the striated myofilament fields. The myofilament field in each smooth fiber consists of much thicker filaments surrounded by many thin filaments. The sarcoplasmic reticulum (SR) is more abundant and the peripheral couplings are more frequent in the striated fibers. Hemidesmosomes attach the myoepithelial cells firmly to the connective tissue cylinder (lower right). (Gp-Os fixation.) $\times 14{,}750$

Peritoneum. The simple epithelium lining each tentacular coelomic canal consists of four cell types found in specific regions within the tentacle: 1) common peritoneal cells, 2) striated myoepithelial cells, 3) smooth myoepithelial cells, and 4) squamous smooth myoepithelial cells that form the tentacular blood channel.

Common Peritoneal Cells

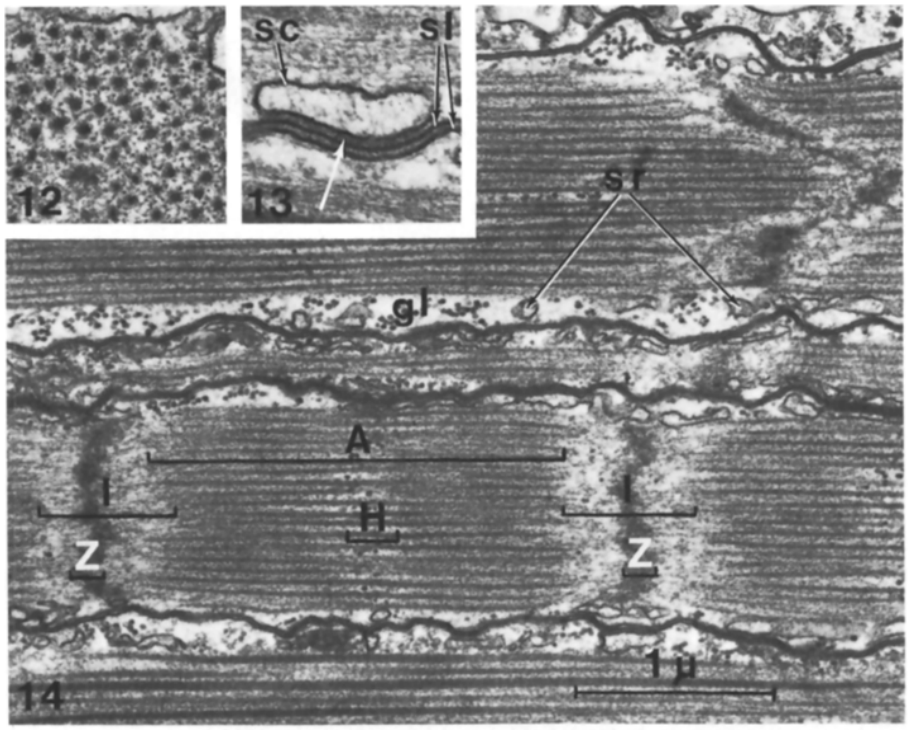
The lateral walls of each tentacular coelomic canal are lined by elongate peritoneal cells that are joined by juxtaluminal zonulae adhaerentes. Rough endoplasmic reticulum is abundant in the cytoplasm of each cell, and the outer membrane of the nuclear envelope is studded with ribosomes. The cells are underlain by a basal lamina 30 nm thick.

Striated and Smooth Myoepithelial Cells

Organization within the Tentacle. Longitudinal rows of fusiform myoepithelial cells extend the length of each tentacle on opposite sides of the coelomic canal. A bundle of myofilaments is confined to the basal cytoplasm in each of the cells. The frontal myoepithelial cells consist of a central group of striated fibers and two lateral groups of smooth fibers (Fig. 9, 11). The striated myoepithelial cells are oriented parallel to the longitudinal axis of the tentacle and are contiguous with the squamous myoepithelial cells that comprise the blood channel. The smooth myoepithelial cells are oriented at an angle of about 12.5° from the longitudinal axis of the tentacle. These fibers and the small group of abfrontal smooth myoepithelial cells (Fig. 8) are contiguous with the common peritoneal cells. The mean length and mean width, at the center, of both types of myoepithelial cells was determined to be 106 μ and 3.0 μ, respectively. The cells have an approximate overlap of 80 %, so that the central perinuclear region of each cell is juxtaposed to the tapering basal processes of adjacent myoepithelial cells.

The above observations hold for all the subtidal smooth shelled specimens examined. In the six intertidal specimens sampled, however, no striated myoepithelial cells were found in the tentacles. The contractile apparatus in each tentacle consisted entirely of smooth fibers (Fig. 17).

Common Characteristics of the Striated and Smooth Myoepithelial Cells. The apical parts of the striated and the smooth myoepithelial cells have a similar composition of organelles. Tubular mitochondria with lamellar cristae accompany the nucleus in the centroapical cytoplasm and occur above the bundle of myofilaments along the length of both types of myoepithelial cells. The juxtanuclear cytoplasm is further distinguished by Golgi complexes and sparse profiles of rough endoplasmic reticulum. Glycogen is abundant throughout the cells, both in the form of scattered beta particles (approximately 30 nm in diameter) and in rosettes up to 125 mμ in diameter arranged in clusters. Cilia are sometimes found in the tentacular coelomic canal, and in one instance a basal body was observed in a smooth myoepithelial cell, but microvilli are lacking. The apices of the myoepithelial cells are joined together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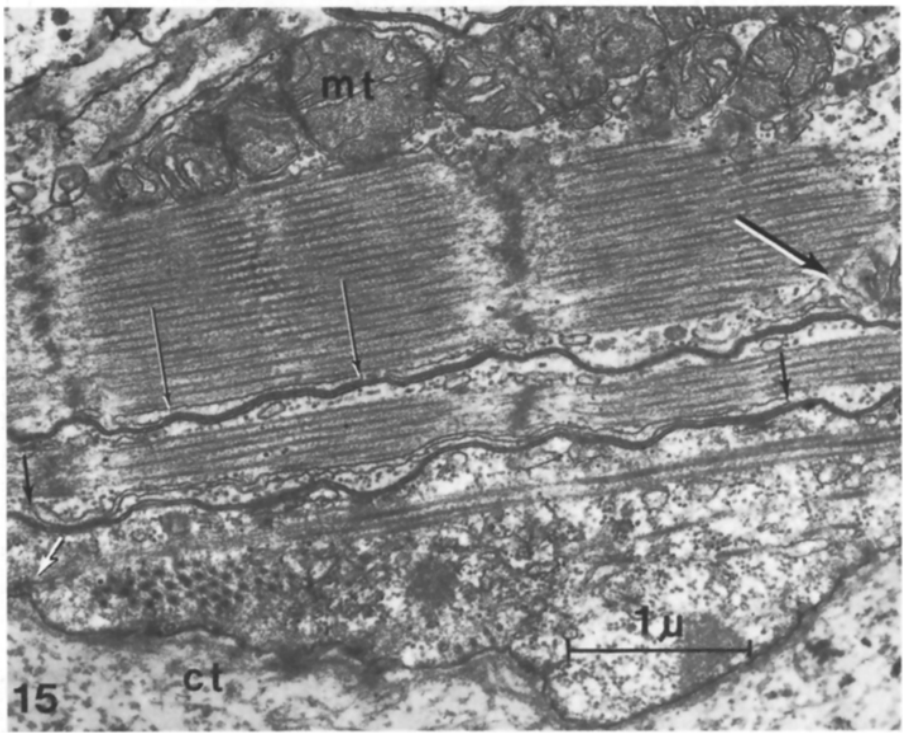
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and to the apices of the common peritoneal cells and to the squamous myoepithelial cells of the blood channel by zonulae adhaerentes. The flattened basal surfaces of both types of myoepithelial cells have numerous hemidesmosomes and adjoin a basal lamina 66 nm thick (Fig. 9, 11). Schematic models of the striated and the smooth myoepithelial cells are presented in Figures 20, and 21.

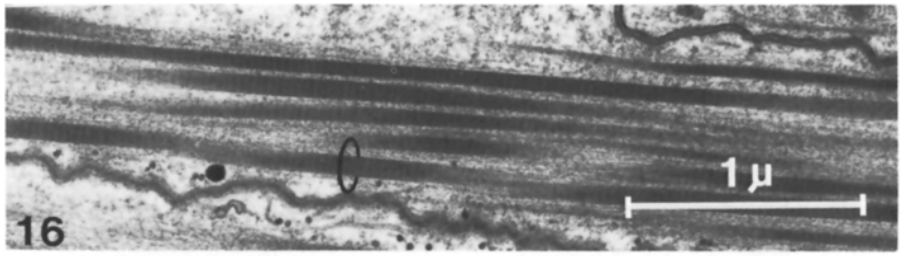
Myofilament Field and Sarcoplasmic Reticulum of the Striated Myoepithelial Cells. The myofilament field is composed of interdigitating thick and thin myofilaments that produce the cross-striations visible by light microscopy. Each sarcomere averages 2.5 μ long in tentacles relaxed with chloral hydrate (Fig. 14, 15). A mean A-band width of 2.0 μ corresponds to the length of the thick myofilaments. The widths of the I-band and the H-band average 0.5 μ and 0.18 μ respectively. There is no visible M-line. The thin myofilaments are about 1.0 μ long and insert into an indistinct, wavy Z-line 0.1 μ wide. Rarely a myoepithelial cell contains unusually long myofilaments, with correspondingly longer sarcomeres (Fig. 14). Each thick (22 nm in diameter) myofilament is surrounded by 12 thin (7 nm in diameter) myofilaments, producing a thin: thick myofilament ratio of 6:1 (Fig. 12). The thin myofilaments appear to insert into hemidesmosomes on the basal sarcolemma. The sarcomeres of adjacent myoepithelial cells are usually aligned (Fig. 15). Beta glycogen particles are generally excluded from the interfilamentous sarcoplasm, except in the H-band where they occupy the regions between the thick myofilaments where thin myofilaments are absent.

Fig. 12. Transverse section of the myofilament field of a striated myoepithelial cell. An orbital of 12 thin filaments surrounds each thick filament, producing a thin:thick myofilament ratio of 6:1. The thick filaments are 22 nm in diameter and the thin filaments are 7 nm in diameter. (Ch relaxation; Gc-Os fixation.) × 56,640

Fig. 13. Longitudinal section of a peripheral coupling in a striated myoepithelial cell. The outer membrane of the subsarcolemmal cisterna closely parallels the sarcolemma, and a thin line of electron dense material can be distinguished within the 15 nm intermembrane gap (white arrow). The lumen of the subsarcolemmal cisterna is electron lucent. (Gp-Os fixation.) × 63,000

Fig. 14. Longitudinal section of the myofilament fields of several striated myoepithelial cells. The sarcomeres are usually about 2.5 μ long, but infrequently longer sarcomeres may be encountered (top). Glycogen granules are generally restricted to the cell periphery along with the SR, but they are found in the myofilament field in the H-band regions where the thin filaments are absent. No M-line is visible. Part of the myofilament field of an adjacent smooth myoepithelial cell is visible at the bottom of the picture. (Ch relaxation; Gc-Os fixation.) × 27,130

Fig. 15. Longitudinal grazing section of a striated myofilament field. Oblique tubules of SR arise from meandering longitudinal tubules in the peripheral sarcoplasm (large arrow). Occasionally the SR component of a peripheral coupling consists of a long tubule rather than a saccule (small long arrows). The section also passes through a longitudinal tubule of SR approximately 4 μ long (between short black arrows). The sarcomeres are aligned in adjacent fibers. A smooth myoepithelial cell (bottom) contains a small bundle of myofilaments perpendicular to the main myofilament field. The thin filaments in the smooth fiber appear to insert on the basal sarcolemma in densities that resemble hemidesmosomes (white arrow). (Ch relaxation; Gc-Os fixation.) × 24,150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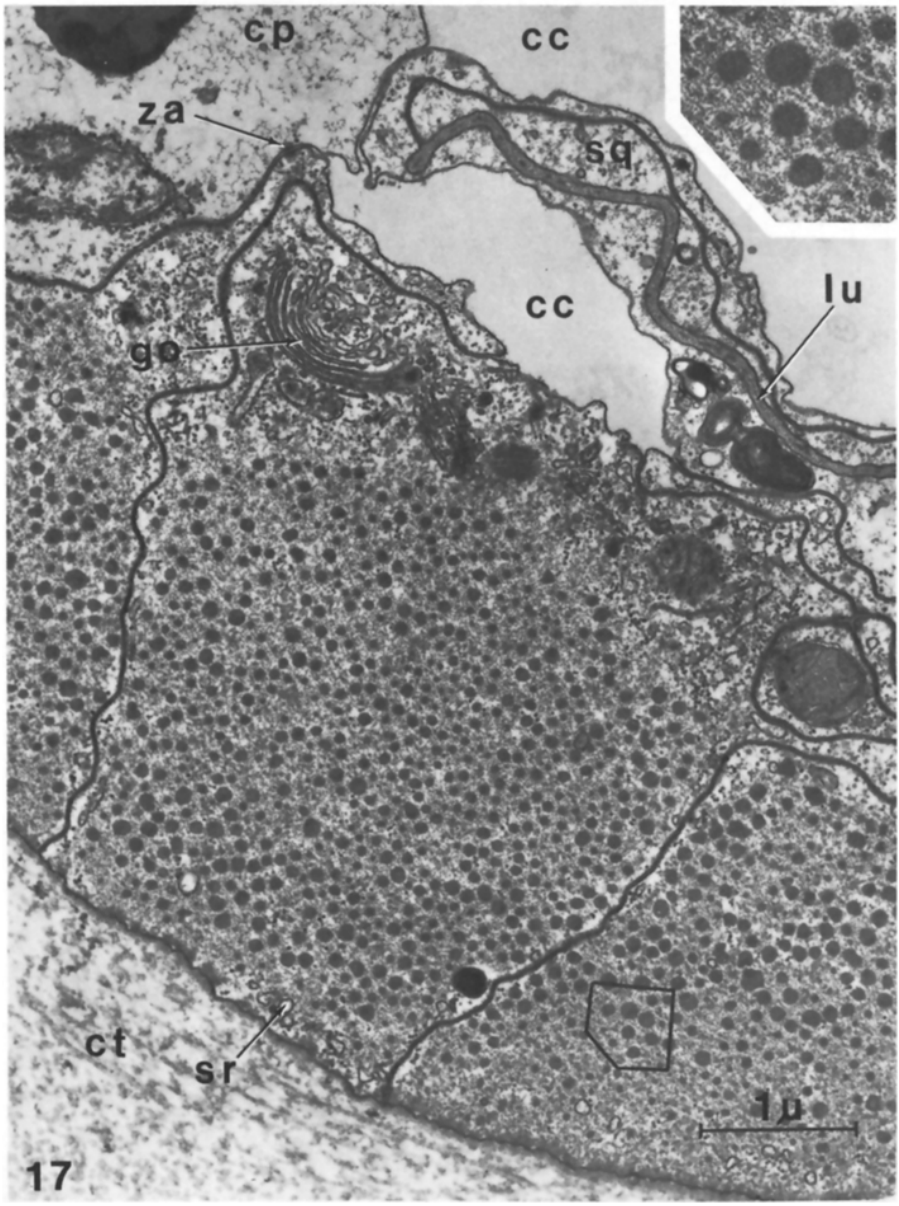
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A smooth membranous system of tubules, the sarcoplasmic reticulum (SR), is arranged peripheral to the myofilament field. It consists of meandering longitudinal tubules ranging from 80 to 110 mμ in diameter that are connected by short transverse or oblique tubules (Fig. 15). The SR is not well developed and does not show regional amplification along the length of a sarcomere. No evidence of a T-system was found. Instead, the tubular SR frequently forms subsarcolemmal cisternae that are closely applied to the lateral sarcolemma, forming *peripheral couplings* (after the terminology of Johnson and Sommer, 1967; Fig. 11). The outer membrane of the saccule of SR and the corresponding region of sarcolemma are parallel and separated by a 15 nm gap containing an electron dense plaque equidistant between the two apposed membranes (Fig. 13). Each coupled cisterna of SR is further characterized by a lumen of low electron density. The peripheral couplings are often found directly opposite one another in adjacent myoepithelial cells, but their location in specific sarcomeric regions is irregular.

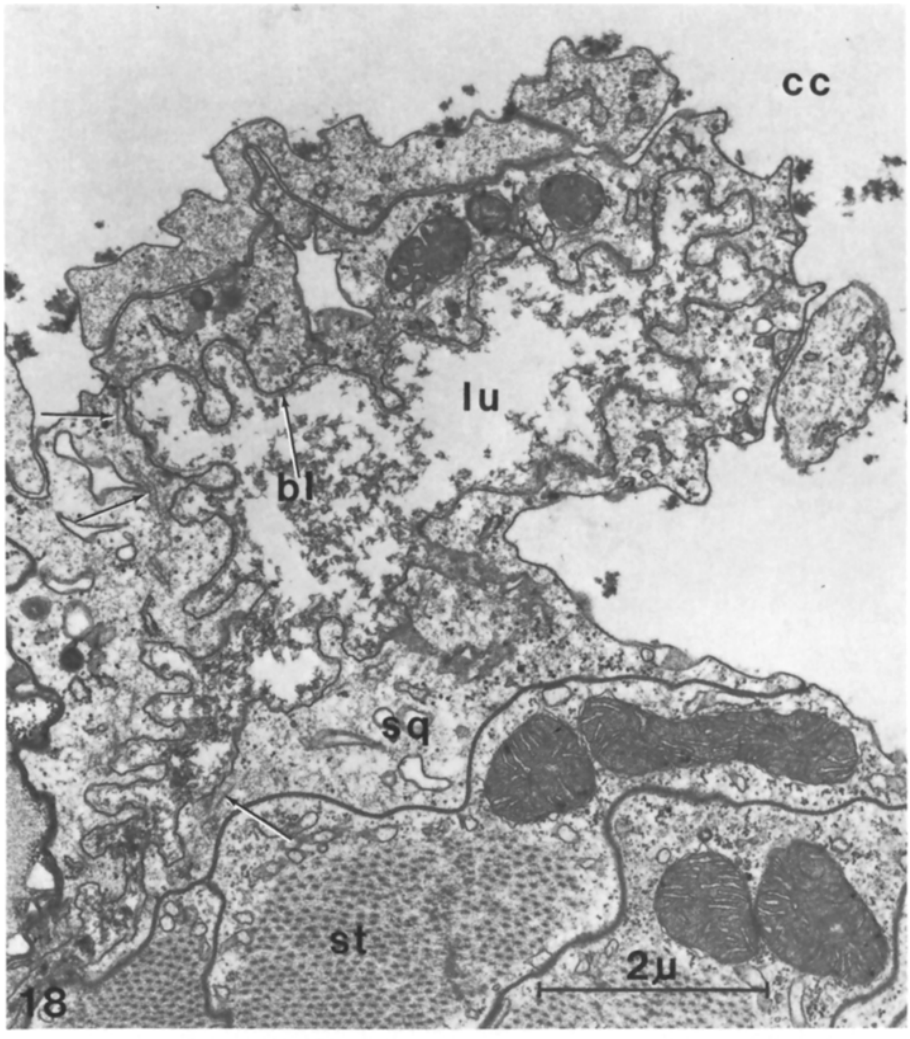
Sometimes the area of close apposition of the sarcolemma with the SR is not limited to a cisterna but involves a considerable length of a longitudinal tubule of SR (Fig. 15). Except for their size, these subsarcolemmal tubules have the same micromorphology as the subsarcolemmal cisternae described above, and they are considered to be functionally equivalent.

Myofilament Field and Sarcoplasmic Reticulum of the Smooth Myoepithelial Cells. Thick and thin myofilaments of indefinite length are staggered throughout the myofilament field. The thick myofilaments are fusiform and resemble the paramyosin myofilaments of bivalve tonic adductor muscles in their dimensions. They average 110 nm in diameter at their thickest point and taper at about 30 nm in diameter near their tips. They also have a major axial periodicity of 32 nm (Fig. 16), equivalent to one of the several periodicities characteristic of paramyosin myofilaments (Heyer and Kater, 1973). A profusion of thin myofilaments 7 nm in diameter surrounds each thick myofilament (Fig. 17). A thin: thick myofilament ratio could not be established owing to the staggered arrangement of the thick myofilaments and the abundance and disorder of the thin myofilaments.

The SR is considerably reduced and consists of a few longitudinal or oblique tubules that run peripheral to the myofilament field. Peripheral couplings are rare but are identical to those found in the striated myoepithelial cells.

Fig. 16. Longitudinal section through part of the myofilament field of a smooth myoepithelial cell. The thick filaments have an axial periodicity of 32 nm and are extremely long, passing in and out of the plane of section. They are staggered throughout the myofilament field and are accompanied by numerous thin filaments 7 nm in diameter. The circled thick filament is 88 nm in diameter. (Gp-Os fixation.) × 32,000

Fig. 17. Transverse section of the frontal contractile bundle in an inner tentacle of one of the intertidal brachiopods examined. The contractile bundle consists entirely of smooth myoepithelial cells with staggered thick paramyosinoid filaments surrounded by numerous thin filaments. (Ch relaxation; Gc-Os fixation.) × 21,130. *Inset:* Higher magnification of the area of the myofilament field within the box in Figure 17. The thick filaments vary in diameter depending on the level they are sectioned at, and are surrounded by a profusion of thin filaments. × 53,690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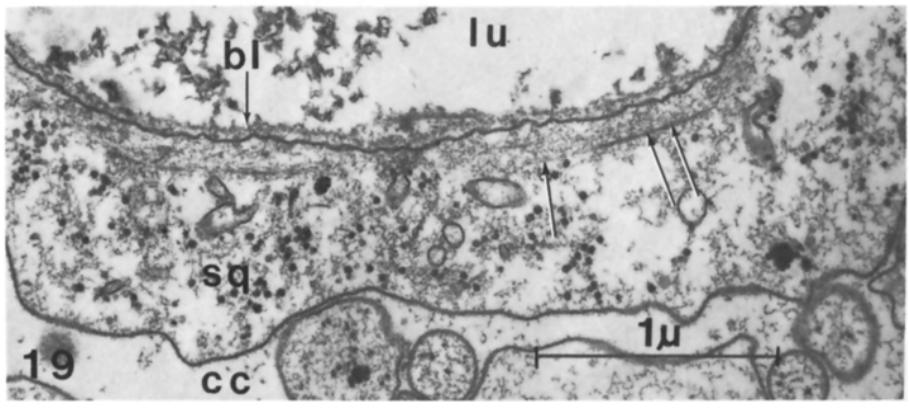
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Cells of the Blood Channel

The blood channel is composed of a single layer of squamous myoepithelial cells with a basal lamina 44 nm thick on their luminal, or basal, surfaces (Fig. 18). The apical surfaces of the cells are exposed to the tentacular coelomic canal. Each cell contains inconspicuous thick (22 nm in diameter) and thin (70 nm in diameter) myofilaments oriented parallel to each other in the juxtaluminal cytoplasm circumferential to the lumen of the blood channel. After routine fixation the basal plasmalemmata of these cells are often thrown into numerous folds. In the dilated region of the blood channel, however, the folds are absent and the myofilaments are parallel to the basal plasmalemmata (Fig. 19).

Discussion

*Epidermis.*The frontal epidermis of the tentacles of *Laqueus californicus* has been described as a stratified columnar epithelium by Reynolds and McCammon (1977), but in *Terebratalia transversa* it consists of a simple columnar epithelium. Stratified epithelia are rare in the invertebrates, and the tentacles of *Laqueus* should be re-examined by electron microscopy to verify their observation.

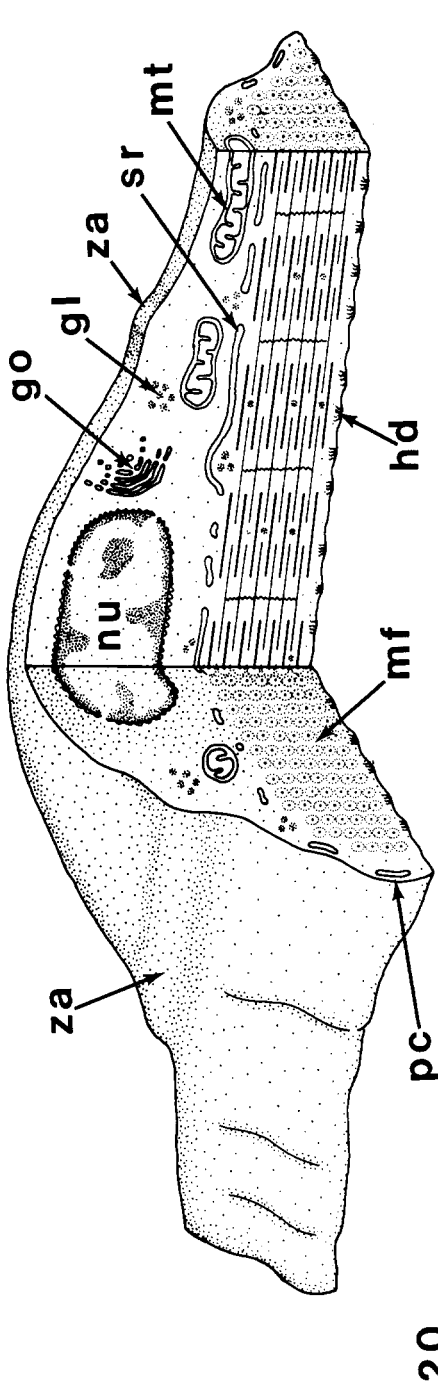
McCammon and Reynolds (1976) used autoradiography to demonstrate the absorption of organic nutrients by the tentacles and brachial groove of *Terebratalia transversa*. They postulated that the nutrients are initially bound by mucins on the surface of the epidermal cells, which may correspond to the glycocalyx described in this paper. The lophophore, in addition to collecting and transporting food particles to the mouth, is considered to be a primary site for gaseous exchange in brachiopods (Hyman, 1959). The presence of microvilli on the tentacular epidermal cells is consistent with both the absorption of nutrients and external respiration.

The presence of putative secondary lysosomes suggests that the epidermal cells are also involved in heterophagy, but it will be necessary to demonstrate the uptake of mass tracers by these cells and the presence of lysosomal enzymes to test this hypothesis. Another possibility is that the structures which appear to be residual bodies are products of autophagy.

The intraepidermal clusters of round cells at the base of each tentacle may correspond to the "amoebocytes" described by Chuang (1956) or the "coelomocytes" described by Storch and Welsch (1976) in the tentacular epidermis of *Lingula unguis*.

Fig. 18. Transverse section of a tentacular blood channel. Squamous cells with myofilaments in their juxtaluminal cytoplasm (arrows) comprise the walls of the blood channel. Their basal (luminal) plasmalemmata are thrown into folds, indicating that the cells have been fixed in the contracted state. The blood channel is laterally contiguous with the striated myoepithelial cells of the frontal contractile bundle. (Gp-Os fixation.) ×15,370

Fig. 19. Transverse section of the wall of a dilated part of the blood channel. The lumen of the blood channel is at the top. Both thick (double arrows) and thin (single arrow) myofilaments are circumferentially arranged in the juxtaluminal cytoplasm parallel to the relatively straight basal plasmalemma. (Gp-Os fixation.) ×32,800



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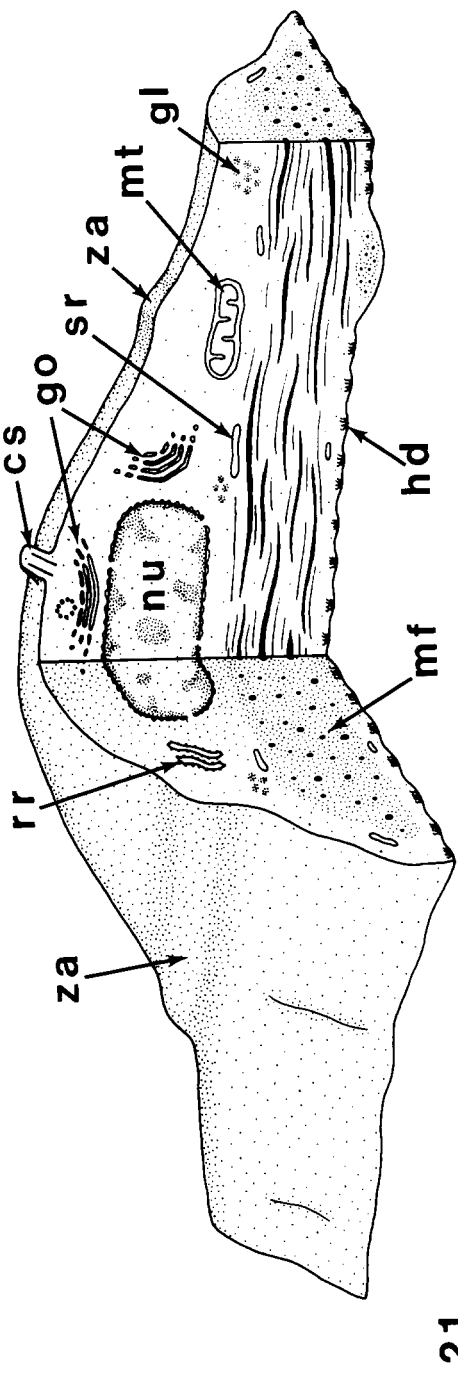

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Nerves. The position of the tentacular nerves above the epidermal basal lamina in *Terebratalia transversa* is consistent with Blochmann's interpretation of the nervous system in inarticulate brachiopods (Blochmann, 1892; 1900). Such intraepithelial nerves are considered to be characteristic of rather primitive nervous systems (Bullock and Horridge, 1965, pp. 50). The basiepithelial bundles of unsheathed nerve fibers in the tentacles of *Terebratalia* resemble the tentacular nerves of phoronids (Silén, 1954), bryozoans (Lutaud, 1973), pterobranchs (Dilly, 1972), and pogonophores (Gupta and Little, 1969) in their intraepidermal position and their simple histological organization.

A more extensive search for myoneural junctions must be conducted. The only apparent nerve endings observed in this study were separated from the myoepithelial cells by a thick layer of connective tissue. Myoneural synapses may simply be out of the plane of section, or there may be a diffusion of transmitter across the connective tissue cylinder to initiate contraction of the myoepithelial cells, as postulated by Florey and Cahill (1977) for the tube feet of echinoids. On the other hand, the putative nerve terminals may actually be innervating the ciliated epidermal cells.

Connective Tissue. The connective tissue in the tentacles of *Terebratalia transversa* is similar in its ultrastructure and mechanical properties to fibrous cartilage, but it lacks cells and does not have metachromatic staining properties. It is more appropriately designated as dense fibrous connective tissue until the chemical composition of the matrix is known in greater detail. The connective tissue in the rest of the lophophore has a metachromatic matrix and qualifies as cartilage according to the criteria of Person and Philpott (1969).

The absence of cells in the tentacular connective tissue cylinders described in this paper contradicts the findings of McCammon and Reynolds (1976), who postulated that connective tissue cells have a role in the transport of nutrients from the epidermal cells to the tentacular coelomic canals in *Terebratalia*. Another hypothesis is needed to explain their results.

Fig. 20. Schematic model of a striated myoepithelial cell. The cell is fusiform and normally is extremely elongated basally along the axis of the myofilament field, but the contractile process is truncated at either end of the perikaryon in the diagram. The apical cytoplasm contains a single ovoid nucleus accompanied by tubular mitochondria, clusters of glycogen rosettes, and a Golgi complex. The basal part of the cell is occupied by an extensive striated myofilament field embraced peripherally by meandering tubules of SR. The tubular SR forms peripheral couplings with the lateral sarcolemma. A juxtaluminal zonula adhaerens forms a band around the apex of the cell. Hemidesmosomes attach the cell basally and transmit the force of contraction to the connective tissue cylinder

Fig. 21. Schematic model of a smooth myoepithelial cell. The cell is shaped like a striated myoepithelial cell, and the elongated basal contractile process has also been truncated at either end of the perikaryon. Juxtanuclear Golgi complexes are more common and may be found in close association with the basal body of a ciliary stump that arises from the apical surface. The apical cytoplasm is further distinguished by occasional profiles of rough endoplasmic reticulum, mitochondria, and glycogen rosettes. A sparse tubular SR courses over the periphery of the myofilament field, which contains very thick fusiform filaments surrounded by many thin filaments. Occasionally a small bundle of filaments is oriented perpendicular to the filaments of the main myofilament field. A zonula adhaerens rims the apex of the cell and numerous hemidesmosomes attach the cell basally to the connective tissue cylinder

The source of the connective tissue in the tentacles is problematic. It may be secreted by epithelial cells or by fibroblasts that leave the connective tissue cylinders after they are formed. Tentacular peritoneal cells are purported to secrete the connective tissue cylinders in the polypide primordia of bryozoans (Gordon, 1974), but studies of the postlarval development of the lophophore or the regeneration of tentacles will be necessary to demonstrate the origin of the connective tissue in brachiopod tentacles.

The significance of the connective tissue cylinders in the support and the movements of brachiopod tentacles was demonstrated by Chuang (1956). The fibrils in the tentacular connective tissue of *Terebratalia* have a periodicity characteristic of native vertebrate collagen fibrils, and we assume that the mechanical properties are similar. We envision that the fibrils impart a stiffness to the connective tissue that is enhanced by their orientation within each cylinder. The longitudinal layer of collagen fibrils would resist elongation of the cylinder and the circumferential layer of fibrils would resist changes in the diameter of the cylinder, resulting in a stiff, inextensible tube.

Orthogonal arrays of fibrils are also found in the connective tissue cylinders of echinoid tube feet (Florey and Cahill, 1977), but unlike the connective tissue cylinders of brachiopod tentacles, these are capable of great extension and compression. These properties may be a consequence of different degrees of interfibrillar cross-linking and/or intrinsic differences in the mechanical properties of the matrices of the two systems.

The natural movements of brachiopod tentacles and the experimental manipulations of the connective tissue cylinders described in this paper demonstrate that the cylinders are endowed with some elasticity. Since it is our interpretation that the collagen component confers tensile strength to the cylinders, the elastic property of the connective tissue cylinders may reside in the matrix. Elastic properties have been demonstrated for the matrices of other invertebrate connective tissues (Gosline, 1971).

The mechanical significance of the baffles is still in question. During flexion of a tentacle the frontal side of the connective tissue cylinder is compressed and the abfrontal side is stretched, deforming the cylinder at the baffles. The baffles may therefore be sites of strain in the cylinder that store the potential energy that serves to re-extend the tentacle when the myoepithelial cells relax. A more extensive study is needed to elucidate the combination of factors that are responsible for the mechanical properties of the connective tissue cylinders in brachiopod tentacles.

Peritoneum. It is clear that the contractile cells in the tentacles of the articulate brachiopod *Terebratalia transversa* are myoepithelial cells, not subperitoneal muscle fibers as described by Reynolds and McCammon (1977). Myoepithelial cells have also been demonstrated by electron microscopy in the tentacles of the inarticulate brachiopod *Lingula unguis* (Storch and Welsch, 1976), and it seems likely that they are characteristic of the phylum. The peritoneum also forms a myoepithelium in the tentacles of bryozoans (Gordon, 1974; Cloney, unpublished observations), pterobranchs (Dilly, 1972), and pogonophores (Gupta and Little, 1969). In the tentacles of entoprocts, however, there is no peritoneum and the contractile apparatus consists of true muscle fibers and epidermal myoepithelial cells (Nielsen, 1976).

The peritoneum in the tentacles of brachiopods has a greater diversity of cell types than the tentacular peritonea of the other coelomate phyla mentioned. The composite organization of the tentacular contractile apparatus that was anticipated by Atkins is confirmed by our study. In the subtidal *Terebratalia* examined, the frontal contractile bundle is composed of both smooth and striated myoepithelial cells, and squamous smooth myoepithelial cells form the blood channels. Several types of fibers are common in skeletal muscles, but such heterogeneity has not been previously demonstrated in a continuous myoepithelium.

Figures 20 and 21 compare the structure of the striated and the smooth myoepithelial cells described in this paper. The thick myofilaments in the smooth myoepithelial cells have the dimensions of filaments known to have a high paramyosin content (Levine et al., 1976), and paramyosin has been isolated from other brachiopod muscles (Winkelman, 1976). Myofilaments with high paramyosin: myosin ratios are usually found in tonic muscles capable of a prolonged maintenance of tension without an excessive expenditure of energy (Prosser, 1967). Other structural features of the smooth fibers that correlate with a tonic capacity are the irregular organization of the myofilament field, the high thin: thick myofilament ratio, and the paucity of SR and peripheral couplings.

The SR is more extensive in the striated myoepithelial cells, but they do not have the elaborate tubular system characteristic of larger phasic muscle fibers. The striated myofilament field apparently is small enough that a sparse SR is sufficient to effectuate calcium ion diffusion. We suggest that the peripheral junctions of the SR with the sarcolemma are functionally equivalent to peripheral couplings, but physiological studies are needed to confirm their suspected role in excitation-contraction coupling. The absence of intracisternal and intratubular densities within the coupled subsarcolemmal cisternae and tubules distinguishes the peripheral couplings in the myoepithelial cells of brachiopod tentacles from the peripheral couplings in ascidian muscle (Cavey and Cloney, 1972) and myocardium (Oliphant and Cloney, 1972) and in vertebrate skeletal (Schiaffino and Margreth, 1969) and cardiac (Fawcett and McNutt, 1969) muscle.

The higher organization of the myofilament field, the lower thin:thick myofilament ratio, the larger volume of SR, and the greater frequency of peripheral couplings suggest a phasic competence for the striated myoepithelial cells.

Myofilaments have now been demonstrated in the peritoneal cells that comprise the tentacular blood channels in both inarticulate (Storch and Welsch, 1976) and articulate brachiopods (this paper). The blood channels in the tentacles of phoronids (Zimmer, personal communication) and pogonophores (Gupta and Little, 1969) are also formed by involutions of a contractile peritoneum. In the case of brachiopods and phoronids, the contractile blood channels in the tentacles have closed distal ends (Beauchamp, 1960; Williams and Rowell, 1965; Dawydoff and Grassé, 1959), suggesting structural and functional homologies of possible phyletic significance.

The role of the blood vascular system in the physiology of brachiopods is uncertain. The coelomic fluid functions both in the circulation of the respiratory pigment and in the conveyance of nutrients and metabolic wastes (Hyman, 1959). The coagulum within the tentacular blood channel suggests that it also contains metabolites. Periodic contractions of the tentacular blood channels would force

blood plasma into the tissue spaces and into the lophophore, facilitating internal transport.

A model for the movements of the tentacles of subtidal *Terebratalia transversa* can now be formulated that takes into account the skeletal role of the tentacular connective tissue cylinders and the physiological implications of the observed morphologies of the different myoepithelial cells.

We suggest that three sets of myoepithelial cells have the following functions in the movements of each tentacle. 1) The striated myoepithelial cells of the frontal contractile bundle (the flexor set) are responsible for flicking motions and for the initial flexion of the tentacle, as anticipated by Atkins (1958). 2) The smooth myoepithelial cells of the frontal contractile bundle (the tonic set) hold the tentacle down for long periods against the resiliency of the connective tissue cylinder. 3) The abfrontal contractile bundle (the extensor set) initiates the return of the tentacle to the extended position, along with the concomitant relaxation of the frontal contractile bundle and the resiliency of the connective tissue cylinder.

The morphology of the myoepithelial cells correlates well with their presumed functions in the movements of the tentacles, but physiological confirmation is lacking. The postulated roles of the smooth and striated fibers can be tested by making observations on their responses to neurotransmitters and on their respective speeds and durations of contraction and relaxation. Information should also be gathered on the intrinsic properties of the different myoepithelial cells (myosin ATPase activities; Ca^{++} binding abilities of their respective SR systems) that may ultimately govern their respective functions.

Variations of the model proposed above are to be expected in brachiopod tentacles that have different degrees of mobility. The tentacles of *Crania anomala* extend between the valves during feeding and must withdraw quickly when the valves snap shut (Atkins and Rudwick, 1962); the striated fibers in these tentacles should be well developed. On the other hand, in tentacles with limited mobility and/or in which the speed of retraction is not critical, smooth fibers may predominate and serve also as the flexor set (i.e., *Lingula*; Chuang, 1956; Storch and Welsch, 1976). Both smooth and striated "muscle fibers" have been described in the tentacles of *Pumilus antiquatus* and *Platidia davidsoni,* which probably have a mobility comparable to that described for the tentacles of the subtidal *Terebratalia* examined in this study.

We suggest two hypotheses to explain the absence of striated myoepithelial cells in the tentacles of the intertidal *Terebratalia transversa* sampled: 1) It represents an adaptation within the species to environmental conditions that accompany an intertidal existence, or 2) The specimens examined represent two different taxa of brachiopods with different histological characteristics. The second hypothesis appears credible because *Terebratalia transversa* was formerly divided into two species based primarily on shell morphology. *Terebratalia transversa* Sowerby (1846) originally encompassed only those specimens with smooth shells, while Gould (1850) applied the name *Terebratalia caurina* to those specimens with ribbed shells. *T. caurina* was regarded as a subspecies of *T. transversa* by Dall (1921), but Thomson (1927) considered them separate species and described different depth ranges for them. Mattox (1955) subsequently decided that their differences did not warrant their distinction as separate taxa and placed them together as *Terebratalia*

transversa. This decision should be reconsidered now that there is evidence that the two morphs may also have histological differences. These hypotheses can be tested by sampling specimens with ribbed or smooth shells from various intertidal and subtidal localities; these studies are now in progress.

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