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Zoomorphology

Ultrastructure of transrectal coelomoducts in the sea cucumber *Parastichopus californicus* (Echinodermata, Holothuroida)

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Summary. The perivisceral coelom of the sea cucumber *Parastichopus californicus* is connected to the lumen of the hindgut by as many as 200 short transrectal ducts. Each duct is lined by a pseudostratified epithelium composed of: (i) monociliated, tonofilament-containing cells, (ii) myoepithelial cells, (iii) bundles of neurites, and (iv) granule-containing cells. In most places the lumen of each duct is lined by the monociliated, tonofilament-containing cells. The myoepithelial cells are predominantly basal in position and circular in orientation, but some border the lumen and parallel the long axis of the duct. The epithelium of a duct consists of the same types of cells as occur in the peritoneum covering the rectum and differs markedly from the nonciliated, cuticularized epithelium that lines the lumen of the rectum. Based on ultrastructural characteristics, the transrectal ducts represent evaginations of the peritoneum overlying the rectum and are thus "coelomoducts" *sensu* Goodrich. The possibility is discussed that perivisceral coelomoducts of holothuroids function in regulating coelomic volumes.

A. Introduction

The perivisceral coelom of most echinoderms is believed to be isolated from the external environment. Crinoids and a few species of sea cucumbers have, however, short ducts connecting the perivisceral coelom to the outside of the body (Hyman 1955; Anderson 1966). Among holothuroids, an open perivisceral coelom has been considered a unique feature of certain apodan species that have unusual burrowing or brooding habits. These apodans include *Synaptula hydriformis* (Lesueur, 1824) [=*Synapta vivipara* (Oersted, 1851)], *Labidoplax buski* (McIntosh, 1866), and *Leptosynapta clarki* Heding, 1928 (Clark 1898; Becher 1912; Anderson 1966). The coelomic ducts are thought to enable intracoelomic fertilization (Clark 1898; Everingham 1961; Estabrooks 1984), the birth of embryos brooded in the coelom (Anderson 1966; Vaney 1925), or the venting of coelomic fluid to reduce body size during escape responses (Anderson 1966). Similar ducts connecting the perivisceral coelom with the posterior end of the rectum were described for the burrowing molpadonian holothuroid *Caudina chilensis* (J. Müller, 1850) (Kawamoto 1927), but Kitao (1935) subsequently proposed that the ducts of this species represent transient breaks that arise from overly strong contractions of body wall muscles. Recently, transrectal coelomic ducts have been found in two epibenthic, nonbrooding holothuroids: the aspidochirote *Parastichopus californicus* (Stimpson, 1857) and the dendrochirote *Cucumaria miniata* (Brandt, 1835) (Shinn 1985). The discovery of coelomic ducts in widely divergent orders suggests that the ducts may occur routinely in holothuroids and have more general functions than previously hypothesized.

In this paper, we provide the first ultrastructural description of the perivisceral coelomoducts of a sea cucumber, *P. californicus*, and compare the morphology of these ducts with the structure of other tissues located in the rectal wall. Functions of the transrectal ducts of *P. californicus* and other holothuroids are discussed with respect to their possible involvement in regulation of fluid volume in the perivisceral coelom.

B. Materials and methods

Adult *P. californicus* (20–30 cm long) were collected by divers from Shady Cove, San Juan Island, Washington, USA (48°33′ N, 123°00′ W; 2–10 m depth). Juveniles (3–4 cm long) were obtained from sea water aquaria at the Friday Harbor Laboratories. These specimens had apparently settled in the aquaria as larvae. Measurements were made on specimens that had been anesthetized in a 1:1 solution of 7.5% $MgCl_2$: sea water. Except where specified otherwise, the results are based on adult animals.

The posterior part of the body (2–3 cm of adults; 1 cm of juveniles) was removed using a razor blade, sliced open longitudinally to expose the rectal lumen, and then flooded with fixative (*see below*). Fixative was subsequently squirted with a Pasteur pipette into the coelomic space between the rectum and body wall.

For plastic sections, tissues were fixed for 1–2 h in one of the following solutions: (1) 2.5% glutaraldehyde in filtered sea water, (2) 2% glutaraldehyde in a ruthenium red/sodium cacodylate solution (Cavey and Cloney 1972), or (3) 3% glutaraldehyde in phosphate buffer (McLean 1984). After the tissues had hardened (15–60 min), they were cut into smaller pieces and transferred to fresh fixative for one

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additional hour. The pieces were decalcified for 6 days in 6% EDTA (ethylenediaminetetraacetic acid) adjusted to pH 7.4, refixed for 1 h, and then postfixed in 2% bicarbonate-buffered OsO_4 for 1 h (Stricker and Cloney 1981). Tissues fixed in sea water-glutaraldehyde were dehydrated in ethanol, transferred through three changes of propylene oxide, and then embedded in "Medcast" resin (Pelco, Inc.). Other tissues were dehydrated in isopropyl alcohol and embedded in a 1:1 mixture of LX-112 resin and Araldite (Ladd Research Industries, Inc.). Specimens were examined with a JEOL JEM-100S transmission electron microscope.

For scanning electron microscopy, specimens were fixed for 2 h in 2% OsO_4 in filtered sea water. The tissues were subsequently dehydrated in acetone, critical-point dried using CO_2, coated with gold-palladium, and examined with a JEOL JSM-35 scanning electron microscope.

C. Results

1. Morphology of the rectum

The digestive tract of *P. californicus* terminates posteriorly in a tubular rectum (="cloaca"). The rectum receives the intestine on its ventral side and extends anteriorly as the common trunk for a pair of branched respiratory trees (Fig. 1). The posterior end of the intestine bears a sphincter that can isolate the intestinal lumen from the rectal lumen. A ring-shaped fold of the posterior body wall guards the anal opening (Figs. 1, 2). The fold contains a separate anal coelom around which are arranged the anal sphincter muscles (Figs. 1, 2, 14). The rectum is surrounded by the perivisceral coelom and is connected to the body wall by numerous tissue strands that contain the radially arranged rectal suspensor muscles.

The rectum serves principally as a muscular pump for moving sea water into the respiratory trees, although it also functions in defecation. In life, the lumen of the rectum is usually filled with sea water. The thickness of the rectal wall varies continuously during the rhythmic expansions and contractions of respiration; it is typically 200–300 μm thick.

2. Histology of rectal wall

The rectal wall consists of an adluminal epithelium (Figs. 3–5), a thick connective tissue layer (Figs. 3, 6, 7), and an overlying peritoneum (Figs. 7–10).

The adluminal epithelium is a single layer of pleomorphic cells underlain by a contorted basal lamina (Figs. 3–5). The cells have broad, interconnecting apical expansions and relatively narrow perikarya sunken, in groups, into the subjacent connective tissue layer. The apical plasmalemma of the cells is elaborated into a reticulum of microlamellae which support a thin cuticle. The latter dis-

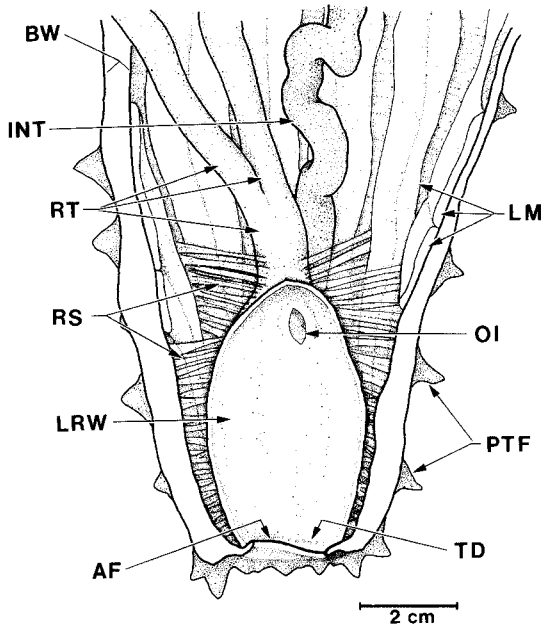

Fig. 1. Diagram of posterior end of *Parastichopus californicus* that has been dissected by a longitudinal incision through the dorsal body wall. The rectum has been opened to reveal the luminal surface of the rectal wall. For clarity the lateral pockets of the respiratory trees are not shown

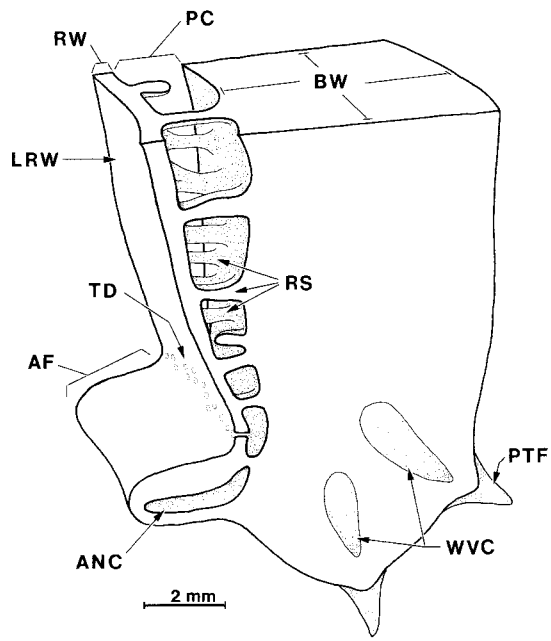

Fig. 2. Diagram of piece of tissue from posterior end of *Parastichopus californicus*. Note the transrectal ducts located just internal to the anal fold

Fig. 3. Transmission electron micrograph (*TEM*) of transverse section through rectal wall showing adluminal epithelium and subepithelial connective tissue. *Arrowheads* indicate the convoluted basal lamina of the epithelium. The cuticle was not preserved

Fig. 4. Apex of adluminal epithelium of rectum (*TEM*). *Arrowheads* indicate the cuticle that overlies the non-ciliated epithelium

Fig. 5. Oblique section through apex of adluminal epithelium revealing that the apical microlamellae are interconnected (*TEM*)

Fig. 6. Transverse section through rectum showing a bundle of muscle fibers, neurites, and processes of granule-containing cells which traverse the connective tissue layer (*TEM*)

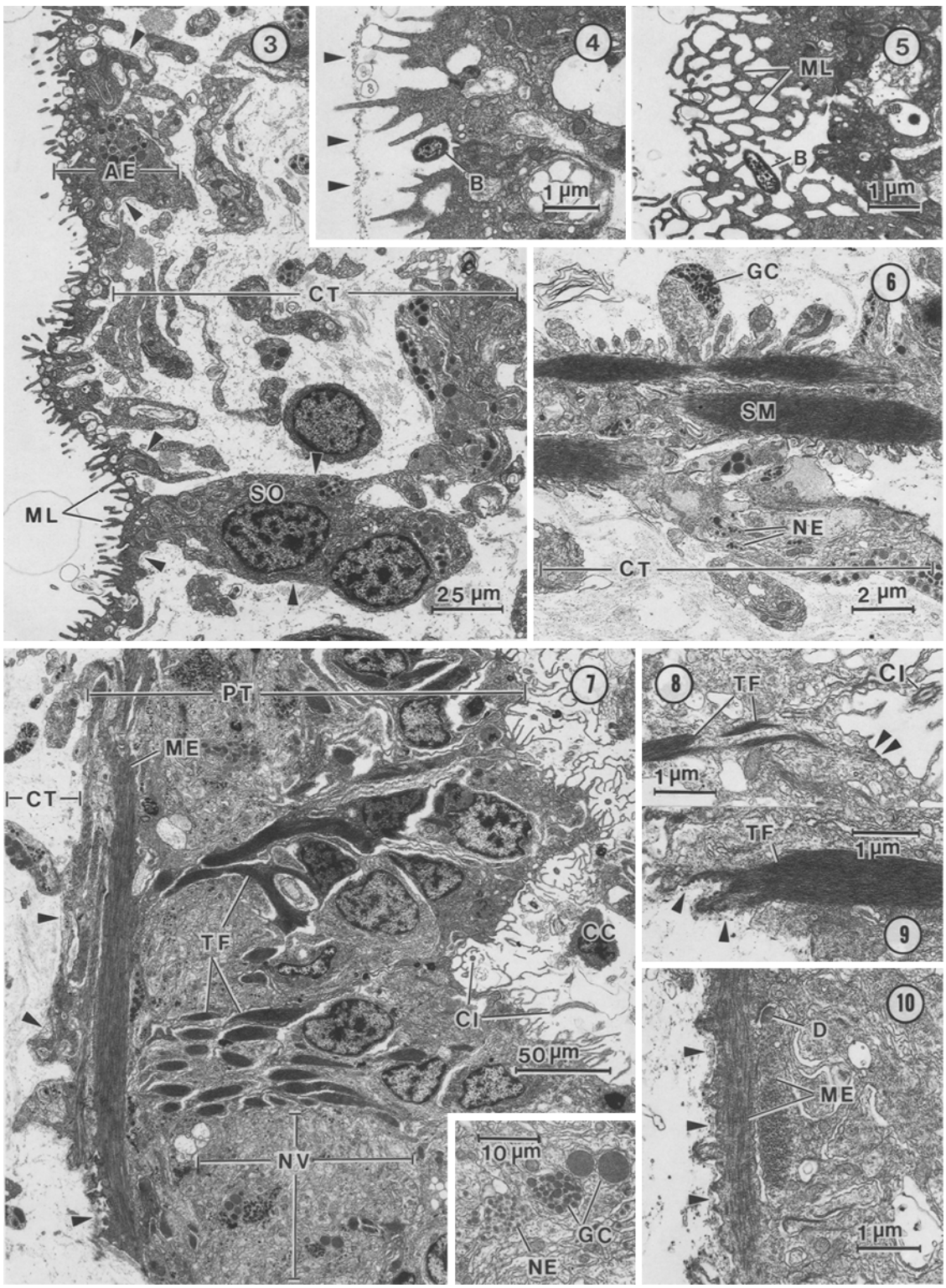

Fig. 7. Slightly oblique transverse section through peritoneum overlying the rectum (*TEM*). *Arrowheads* indicate the basal lamina of the peritoneum. *Inset* shows cross-section through part of a nerve

Fig. 8. Apical part of ciliated, tonofilament-containing peritoneal cells (*TEM*). *Arrowheads* indicate densities of the apical plasmalemma at which tonofilaments may terminate

Fig. 9. Basal part of ciliated, tonofilament-containing peritoneal cell (*TEM*). *Arrowheads* indicate the basal lamina

Fig. 10. Basal processes of myoepithelial peritoneal cells (*TEM*). *Arrowheads* indicate the basal lamina

solves during some fixation procedures for electron microscopy (e.g. Fig. 3). Zonular intermediate and septate junctions connect the apical expansions of adjacent cells. All adluminal epithelial cells appear to be secretory in young animals, but only some of these cells exhibit secretory activity in older animals. The adluminal epithelium is neither muscularized nor underlain by subepithelial muscles, and its cells lack cilia.

The connective tissue of the rectal wall consists of moderately densely packed collagen fibrils and isolated fibroblasts in an abundant ground substance (Figs. 3, 6, 30). Bundles of cell processes, which include unstriated muscle fibers, neurites, and granule-containing cells, cross the connective tissue layer (Fig. 6). The neurites contain small (80–130 nm in diameter), dense-cored vesicles. Granule-containing cells have larger inclusions (250–650 nm in maximal dimension) of more variable shape (spherical-to-cylindrical) and electron density than inclusions in the neurites. Axon-like processes of the granule-containing cells extend among and parallel the neurites. The nuclei of muscle and nerve cells were not seen within the connective tissue layer of the rectal wall. An external lamina ensheaths and separates each bundle of cell processes from the surrounding collagen fibrils of the connective tissue.

The peritoneum consists of monociliated cells containing bundles of 12 nm tonofilaments (Figs. 7–9), basally located unstriated myoepithelial cells (Figs. 7, 10), nerves, and granule-containing cells (Fig. 7). The muscle fibers are predominantly circular in orientation, but some are longitudinal (Figs. 7, 10). Most of the nerves lie immediately apical to the muscle fibers. Occasional large nerves protrude towards the connective tissue of the rectum but remain above the basal lamina that delimits the peritoneum. The nerves contain neurites and processes of granule-containing cells similar in appearance to those in the connective tissue layer. Individual neurites extend among or subjacent to the muscle cells.

3. General morphology of the transrectal coelomic ducts

The coelomic ducts of *P. californicus* traverse the wall of the posterior end of the rectum, just internal to the anal sphincter (Figs. 1, 2, 11–17). They are visible by light microscopy in live specimens but are more evident in tissues that have been made opaque by fixation (Shinn 1985). Adult specimens contain 50–200 ducts spaced 100–700 μm apart in pinned-out preparations. The ducts occupy a continuous, narrow band within which they are arranged irregularly or in short diagonal rows of 3–5 ducts.

The luminal ends of the ducts open flush with the apical surface of the rectal epithelium or upon papillae (Figs. 11, 13–15). The coelomic ends of the ducts open into shallow, densely ciliated depressions in the rectal wall (Figs. 12, 17). The ducts, usually simple, straight tubes, measure about 200 μm long and 50 μm in outside diameter. Occasional pairs of ducts join and hence share a common opening into the rectal lumen. The triradiate lumina of the ducts appear to be closed (Fig. 16). Whether or not the ducts are usually closed in life has not been established.

The pseudostratified epithelium of a transrectal duct has the following cellular components: monociliated, tonofilament-containing cells, unstriated myoepithelial cells, granule-containing cells, and tracts of neurites. The monociliated, tonofilament-containing cells occupy most of the apical volume of the epithelium (Fig. 18), whereas myoepithelial cells occupy most of the basal volume (Figs. 18, 25). The somata of the granule-containing cells and the tracts of neurites typically have an intermediate position (see below).

4. Tonofilament-containing cells

Tonofilament-containing cells span the entire thickness of the ductal epithelium (Fig. 18). They possess distinctive 12 nm filaments grouped into bundles up to 1 μm in diameter (Figs. 18–21). The attenuated basal part of each cell appears to have a single bundle of filaments which attaches to the plasmalemma (Figs. 20, 21). The bundles commonly branch just below the nucleus so that two or more bundles of filaments are typically evident at or above the level of the nucleus (Fig. 19). The bundles taper apically. We could not discern attachment of the filaments to the apical plasmalemma (but see Fig. 8 for apical attachments of tonofilament bundles in rectal peritoneal cells). The filament bundles of some cells show transverse bands with a periodicity of about 350 nm (Figs. 18, 20). Other bundles of tonofilaments are unbanded (Figs. 21, 25). The latter have the same electron density as the darker parts of banded bundles.

Tonofilament-containing cells have Golgi bodies, numerous small, electron-lucent vacuoles, mitochondria, and rough endoplasmic reticulum (RER) (Fig. 18). Apical specializations of the tonofilament-containing cells include zonular intermediate and septate junctions, microvilli, microlamellar folds, and cilia (Figs. 18, 22). The single cilium of each cell emerges from an apical invagination. The short, banded rootlet extending from the ciliary basal body has a periodicity of about 65 nm (Fig. 22). Band periodicity distinguishes the ciliary rootlets from banded bundles of tonofilaments. The ciliary axonemes display the $9\times2+2$ arrangement of microtubules typical of kinocilia (Fig. 22, inset).

5. Myoepithelial cells

Myoepithelial cells are interspersed with the tonofilament-containing cells throughout the epithelium of each duct (Figs. 18, 25). The unstriated muscle fibers are predominantly basal in position and circular in orientation (Figs. 18, 25, 26). In some myoepithelial cells, however, the contractile processes border the ductal lumen and parallel the long axis of the duct (Figs. 27, 28). The ducts evidently lack dilator muscles.

Myoepithelial cells attach to adjacent myoepithelial cells by scattered desmosomes, although the junctions were often disrupted in our material. The apical, longitudinally oriented muscle fibers connect to adjacent cells, usually tonofilament-containing cells, by zonular intermediate and septate junctions (Fig. 27). The myoepithelial cells adhere by basal hemidesmosomes to the same basal lamina that underlies the tonofilament-containing cells (Figs. 25, 26).

6. Granule-containing cells

Cell bodies with membrane-bounded granules are situated well above the basal lamina of the ductal epithelium, scattered among the tonofilament-containing cells and myoepithelial cells (Fig. 23). Granule-containing perikarya usually lie adjacent to a nerve (see below) and send their axon-

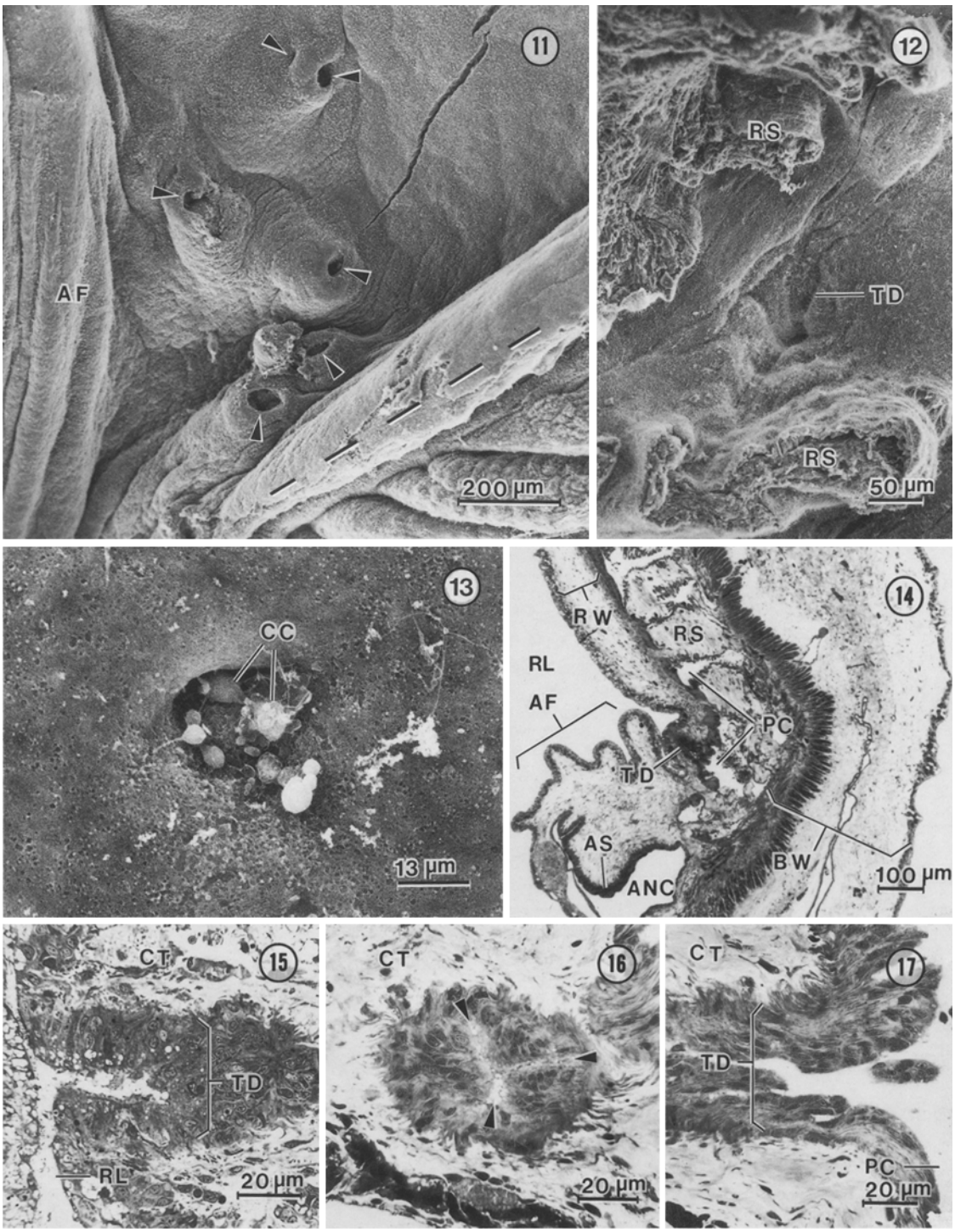

Fig. 11. Scanning electron micrograph (*SEM*) of luminal surface of rectal wall showing openings of transrectal ducts (*arrowheads*) into the posterior end of rectum. *Dashed line* indicates cut edge of rectal wall

Fig. 12. Ciliated coelomic end of transrectal duct (*SEM*)

Fig. 13. Luminal opening of transrectal duct (*SEM*). Note the cuticle covering the adluminal epithelium of the rectum

Fig. 14. Light micrograph (*LM*) of longitudinal section through the posterior end of *Parastichopus californicus*. 1 µm Epon section

Fig. 15. Longitudinal section through luminal end of transrectal duct (*LM*). 1 µm Epon section

Fig. 16. Transverse section through transrectal duct (*LM*). *Arrowheads* indicate the three radii of the lumen. 1 µm Epon section

Fig. 17. Longitudinal section through coelomic end of transrectal duct (*LM*). 1 µm Epon section

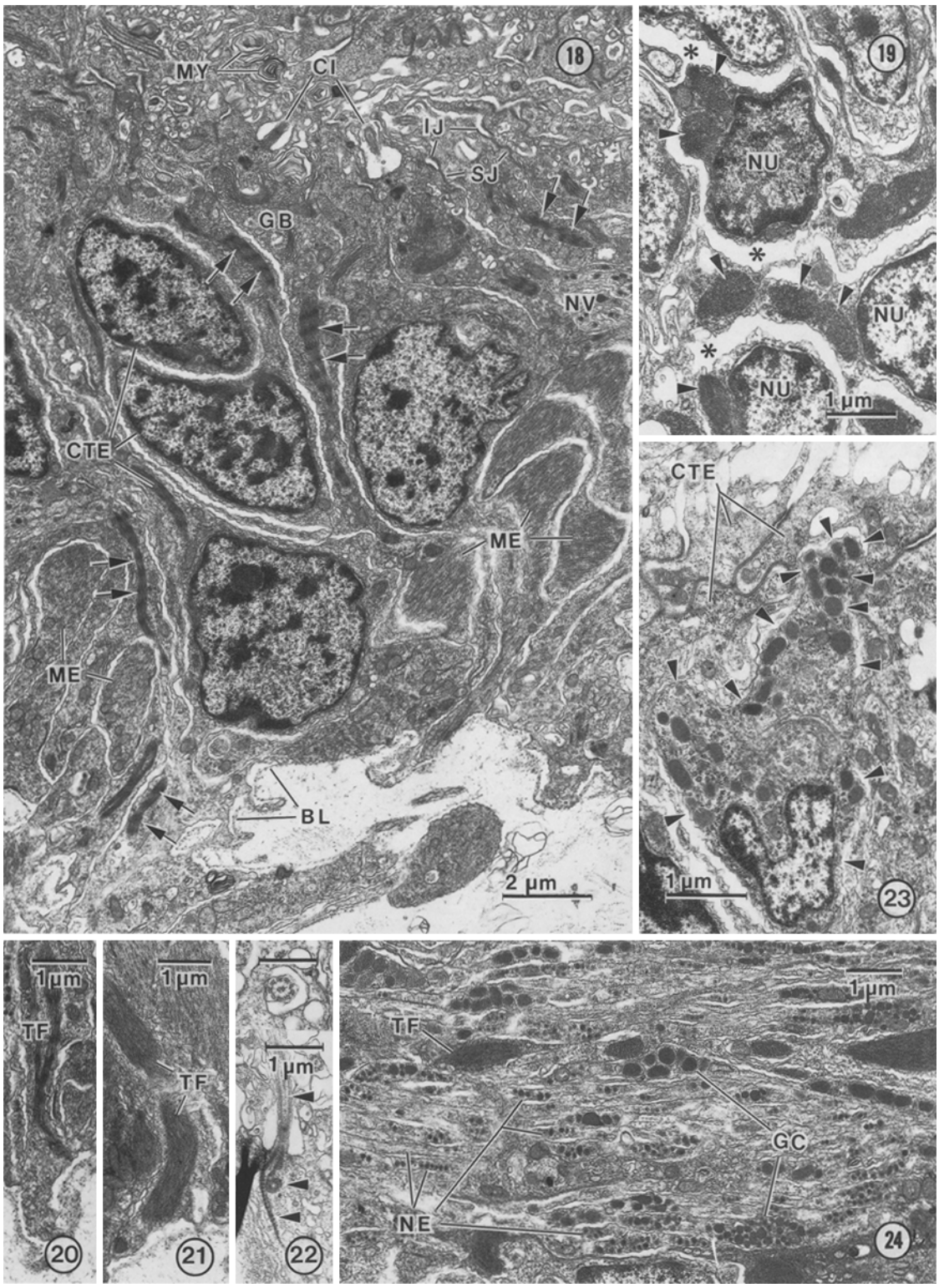

Fig. 18. Slightly oblique, longitudinal section through the epithelium of a transrectal duct (*TEM*). *Paired arrows* indicate bundles of tonofilaments in ciliated, tonofilament-containing cells. The lumen of the duct (at top) is nearly collapsed

Fig. 19. Tangential section through the epithelium of a transrectal duct showing cross-sections of bundles of tonofilaments (*arrowheads*) (*TEM*). Intercellular spaces (*asterisks*) were probably exaggerated by fixation

Fig. 20. Basal end of banded bundle of tonofilaments (*TEM*)

Fig. 21. Non-banded bundle of tonofilaments (*TEM*)

Fig. 22. Apical end of cilated, tonofilament-containing cell (*TEM*). *Arrowheads* indicate, from top to bottom, the base of a cilium, the accessory centriole and the ciliary rootlet. *Inset*: transverse section through cilium of tonofilament-containing cell

Fig. 23. Soma of granule-containing cell (*TEM*). *Arrowheads* indicate limits of the cell

Fig. 24. Longitudinal section through epithelium of a transrectal duct, showing bundle of axons (*TEM*). The latter are of several types that differ in the size, shape, and electron density of their vesicles

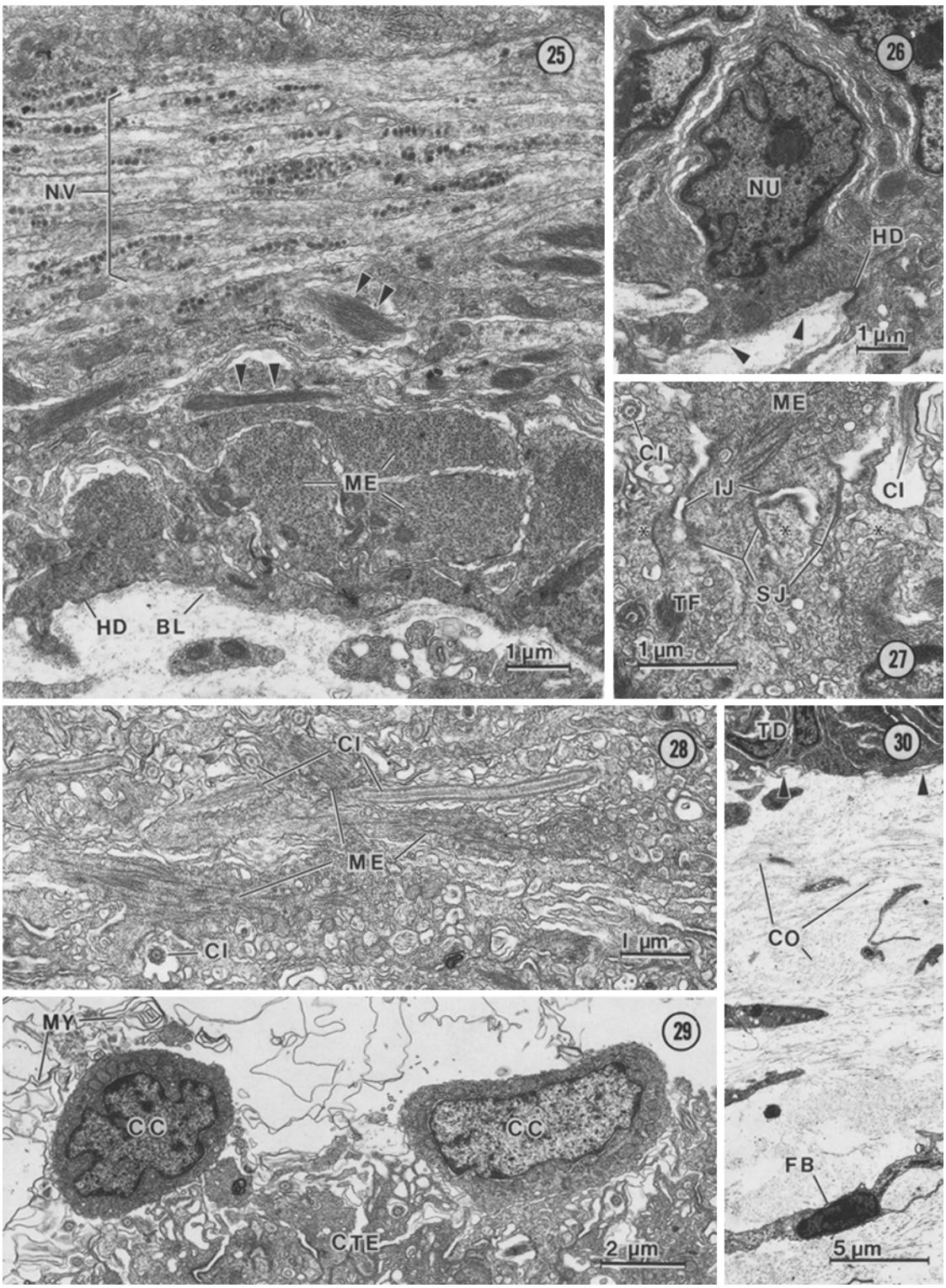

Fig. 25. Longitudinal section of transrectal duct, showing profiles of basally located, circular, myoepithelial cells and a nerve whose constituent axons contain small, dense-cored vesicles (*TEM*). *Double arrows* indicate bundle of tonofilaments in a ciliated tonofilament containing cell

Fig. 26. Soma of myoepithelial cell (*TEM*). *Arrowheads* indicate basal lamina

Fig. 27. Apex of transrectal duct showing intercellular junctions between a myoepithelial cell and ciliated, tonofilament-containing cells (*TEM*)

Fig. 28. Tangential section through apex of a transrectal duct (*TEM*). Filaments in the apices of myoepithelial cells parallel the long axis of the duct

Fig. 29. Longitudinal section through a transrectal duct, showing the apices of ciliated, tonofilament-containing cells and coelomocytes in the ductal lumen (*TEM*)

Fig. 30. Connective tissue surrounding a transrectal duct. *Arrowheads* indicate the basal lamina (*TEM*)

like processes into the nerve. The granules, spherical to cylindrical in shape (maximal dimensions: 350 nm in diameter, 650 nm × 350 nm, respectively), vary in electron density. These cells lack histological specializations typical of epithelial cells. For example, the cells do not extend directly to the basal lamina. Where cell processes that contain similar appearing granules approach the basal lamina, no hemidesmosomes or other specialized attachments are evident. Granule-containing cells were never found to border the ductal lumen, and no junctional complexes have been observed between granule-containing cells and other epithelial cells.

7. Nerves

Nerves containing up to 50 or more neurites form a conspicuous part of the ductal epithelium (Figs. 18, 24, 25). The nerves typically parallel the long axis of the duct. One or more layers of myoepithelial cell processes usually separate the nerves from the basal lamina; tonofilament-containing cells or myoepithelial cells invariably overlie the nerves and isolate them from the ductal lumen. The nerves may be composed exclusively of neurites containing small (80–130 nm diameter), dense-cored vesicles (Fig. 25) or, as in the peritoneum overlying the rectum, the constituent neurites may intermix with processes of granule-containing cells (*see above*; Fig. 24). Individual neurites containing small, dense-cored vesicles are also woven among myoepithelial cells and the bases of tonofilament-containing cells.

In addition to the numerous membrane-bounded vesicles, neurites contain abundant microtubules and mitochondria. No specialized junctions have been observed between adjacent neurites in a bundle or between neurites and neighboring epithelial cells. We have been able to locate only one soma containing small dense-cored vesicles. Its position and morphology were similar to those of the granule-containing cells described above. Most somata of nerve cells that contain small, dense-cored vesicles presumably lie outside the ductal epithelium.

8. Contents of ductal lumen

The ductal lumen contains scattered coelomocytes (Fig. 29) and whorled and irregularly folded sheets of myelin-like material (Figs. 18, 29). Myelin-like material also occurs above the peritoneal cells of the perivisceral coelom and in scattered pockets within the connective tissue compartment of the rectal wall. These whorls could represent coagulates of coelomic or interstitial fluids, or they could arise as artifacts of fixation.

9. Connective tissue surrounding the ductal epithelium

A moderately dense collagenous connective tissue underlies the ductal epithelium (Fig. 30). An irregular meshwork of unbanded fibrils occurs immediately subjacent to the basal lamina of the epithelium. This subepithelial meshwork is surrounded by banded fibrils (70 nm periodicity) arranged either circumferentially or parallel to the long axis of the duct. There are no subepithelial muscles or hemal vessels specifically associated with the perivisceral coelomic ducts. No special association was evident between the ductal epithelium and those bundles of muscle and neuronal processes that traverse the connective tissue of the rectal wall in the vicinity of the ducts.

D. Discussion

1. Histology and occurrence of coelomic ducts in holothuroids

This study reveals that the transrectal ducts of *P. californicus* are real organs that have specific morphological attributes. The ducts are not merely breaks in the rectal wall as suggested by Kitao (1935) for similarly located openings in *Caudina chilensis*. Both Kawamoto (1927) and Kitao (1935) present photomicrographs of transrectal ducts (= "coelo-anal pores") of *C. chilensis* that were lined by an epithelium. This suggests to us that the ducts of that species are also real and distinct from various transient breaks that may form in the rectal wall (Kitao 1935). The transrectal ducts are evidently absent from juveniles (< 3 cm long, Kitao 1933), and ducts in the process of formation are common in large specimens (Kitao 1935). Thus, the ducts may appear only late in the ontogeny of *C. chilensis*.

The epithelium of the transrectal ducts of *P. californicus* is composed of the same cell types as the peritoneum covering the rectal wall and various other organs in *P. californicus* and holothuroids in general (Cameron and Fankboner 1984; Doyle 1967; Herreid et al. 1976, 1977; Jensen 1975; Kawaguti 1964; Bouland et al. 1982). In contrast, the types of cells composing the transrectal ductal epithelium differ markedly from those found in the epithelium that lines the rectum of *P. californicus*. The holothuroid rectum arises from a proctodeal invagination (Feral and Massin 1982) and its lining epithelium is histologically similar to the epidermis (Cameron and Fankboner 1984; Bouland et al. 1982; Holland and Nealson 1978; Menton and Eisen 1970; Smith 1983). Morphological characteristics of fully formed ducts lead us to conclude that the transrectal ducts of *P. californicus* represent evaginations of the perivisceral peritoneum rather than invaginations of the rectal mucosa. Stages in the formation of transrectal ducts remain to be elucidated, however.

Although lacking detail, previous descriptions of the histology of perivisceral coelomic ducts of holothuroids are generally consistent with our observations of the ducts of *P. californicus*. In *C. chilensis* and *Leptosynapta clarki* the ducts are reportedly lined by a simple epithelium (Kawamoto 1927; Anderson 1966, respectively). The transrectal ducts of *C. chilensis* are not cuticularized but Kawamoto (1927) reported no muscles. The epithelium of the circumanal ducts of *L. clarki* is squamous, similar to that lining the coelom, and surrounded by circular muscles (Anderson 1966). Whether the muscles are subepidermal or intraepidermal in that species remains to be determined by transmission electron microscopy.

2. Comparative cytology of the transrectal ducts

The ciliated, tonofilament-containing cells of the transrectal duct of *P. californicus* are equivalent to the "adluminal cells" of Wood and Cavey (1981), the "flagellated epithelial cells" of Jensen (1975) and the "coelomic epithelial cells" and "peritoneal cells" of several authors (Doyle 1967; Herried et al. 1976; Kawaguti 1964; Bouland et al. 1982). Although ciliated cells are common components of echinoderm peritonea (Rieger and Lombardi 1987), bundles of tonofilaments are not unique to peritoneal cells. Long bundles of tonofilaments are present in epidermal cells of the tentacles and tube feet of various holothuroids (Bouland et al. 1982; Menton and Eisen 1970; Smith 1983). We be-

lieve the banded and unbanded bundles of tonofilaments in the transrectal ducts of *P. californicus* to be different forms of the same organelle. Crossbanding of tonofilament bundles of echinoderms has been reported by Bouland et al. (1982) who supposed the bundles to be contractile. At present, there is no evidence to support that supposition. If the bundles are contractile, however, the tonofilament-containing cells, being radially disposed, could function in dilating the transrectal ducts. Alternatively, the tonofilaments may be tension-bearing structures that passively slide past one another in response to changes in the height of the epithelium caused by contractions of surrounding myoepithelial cells. A similar passive mechanism is envisioned for changes in the length of collagen fibers in the catch ligaments of echinoid spines (Smith et al. 1981).

In the transrectal ducts of *P. californicus*, the basally located myofibrils encircle the ducts and form sphincters by which the ducts can be closed. The apically situated myofilament bundles that parallel the long axis of the duct probably help accommodate changes in the lengths of ducts as the rectum dilates and contracts during respiration.

Details of the innervation of the transrectal ducts are, as yet, unresolved. Given the abundance of nervous tissue in the ductal epithelium, it seems probable that both myoepithelial cells and tonofilament-containing cells are innervated. This suggestion is not easily reconciled with most previous studies of echinoderm neurons, however. While there is limited evidence that some neurons with small, dense-cored granules, such as predominate in the transrectal ducts of *P. californicus*, may be motor neurons (Bachmann and Goldschmid 1978; Cobb and Raymond 1979), neurons of this appearance are generally believed to be interneurons (Pentreath and Cobb 1972). Echinoderm muscles are typically innervated by axons containing electron-lucent secretory vesicles (reviewed by Pentreath and Cobb 1972; Cobb and Raymond 1979), whereas neurites of this type are conspicuously absent from the transrectal ducts of *P. californicus*. Cells resembling the granule-containing cells in the transrectal ducts occur in many echinoderms and are variously hypothesized to be neurosecretory (Doyle 1967; Holland 1970; Motokawa 1982; Smiley and Cloney 1985; Wilkie 1979) or to contain neuromuscular transmitters (Pentreath and Cobb 1972). Byrne (1984) and Wilkie (1984) have cautioned that echinoderms may contain several classes of these cells. Thus, the functions of these cells in the transrectal ducts remain enigmatic.

3. Functions of perivisceral coelomic ducts of holothuroids

Functions of the transrectal coelomoducts of *P. californicus* and other holothuroids have scarcely been studied. In *P. californicus*, the ducts provide a pathway by which masses of coelomocytes enclosing foreign bodies exit the perivisceral coelom (Shinn 1985; Dybas and Fankboner 1986). Many of the coelomocytes composing the masses are believed to contain metabolic wastes (Jangoux 1982). Thus the transrectal ducts may be involved in both excretion and cellular defense mechanisms. A more basic function of the ducts may be the regulation of fluid volume within the perivisceral coelom. The holothuroids *L. clarki*, *C. chilensis*, and *C. miniata* rapidly reduce their size by expelling coelomic fluid through their perivisceral coelomic ducts (Anderson 1966; Kawamoto 1927; Shinn unpublished observations, respectively). Rapid reductions in body size are reported for *P. californicus* and several additional species of holothuroids, but the mechanism for this has not been established (Clark 1898; Costello 1946; Glynn 1965; Margolin 1976; Pantin and Sawaya 1953). Transrectal ducts, such as described in the present paper, may constitute a routine part of holothuroid anatomy providing a morphological mechanism for altering body size.

Transport of materials through transrectal ducts could be accomplished by several mechanisms. An increase in coelomic pressure caused by contraction of the body wall muscles and simultaneous relaxation of the circular myoepithelial cells of the transrectal ducts could force either coelomic fluid or masses of coelomocytes out of the coelom. In species that have the ducts internal to the anal sphincter, an increase in rectal pressure caused by simultaneous contraction of the rectal wall and anal sphincter could force materials into the coelom. Transport either into or out of the coelom could be caused by peristaltic contractions of the circular myoepithelial cells of the ductal epithelium or by beating of cilia of the ductal tonofilament-containing cells.

4. A "primitive" coelomoduct

The present study reveals that the transrectal coelomoducts of *P. californicus* are simple evaginations of myoepithelial peritoneum. We suggest that the transrectal ducts function most basically as components of the hydrostatic skeleton. These points relate directly to two significant, recent advances in our understanding of coeloms. First, Clark (1964, 1979) convincingly argued that the primitive function of the coelom was as a hydrostatic skeleton. Second, coelomic linings typically include myoepithelial cells and may have consisted primitively of a simple monociliated myoepithelium (Gardiner and Rieger 1980; Rieger 1986; Rieger and Lombardi 1987; Turbeville and Ruppert 1985; Welsch and Storch 1982). Application of these principles to the widely accepted concept of coelomoducts as elaborations of the peritoneum yields the following postulates which parallel our observations and inferences: (i) coelomoducts are primitively a component of the hydrostatic skeleton and functioned in exchanging the fluid in or regulating the volume of the coelom, and (ii) the coelomoducts of primitive coelomates were lined by a simple monociliated myoepithelium (i.e., an epithelium resembling the peritoneum). The first postulate is compatible with the well-established fact that coelomoducts, like coeloms, commonly have multiple functions, e.g., as gonoducts or nephridial ducts (Goodrich 1946), although it argues against the hypothesis elaborated by Goodrich (1946) that coelomoducts of coelomate animals are most basically gonoducts and evolved from the gonoducts of acoelomate or pseudocoelomate phyla. The second postulate elaborates on Goodrich's morphological concept of the primitive coelomoduct as a simple ciliated tubule. In conclusion, we believe that the transrectal perivisceral coelomoducts of *P. californicus* represent a relatively unmodified form of coelomoduct.

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Abbreviations

AE	adluminal epithelium
AF	anal fold
ANC	anal coelom
AS	anal sphincter muscle
B	bacterium
BL	basal lamina
BW	body wall
CC	coelomocyte
CI	cilium
CO	collagen fibers
CT	connective tissue
CTE	ciliated, tonofilament-containing epithelial cell
D	desmosome-like junction
FB	fibroblast
GB	Golgi bodies
GC	axon-like process of granule-containing cell
HD	hemidesmosome
IJ	intermediate junction
INT	intestine
LM	longitudinal muscles of body wall
LRW	luminal surface of rectal wall
ME	myoepithelial cell
ML	microlamellae
MY	myelin-like material
NE	neurite
NV	nerve
NU	nucleus
OI	opening of intestine into rectum
PC	perivisceral coelom
PT	peritoneum
PTF	papilliform tube feet
RW	rectal wall
RL	rectal lumen
RS	rectal suspensor
RT	respiratory trees
SJ	septate junction
SO	soma of adluminal epithelial cell
SM	subepidermal muscle
TD	transrectal duct
TF	tonofilaments
WVC	lateral water vascular canals

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