Digestive System of *Trichodorus porosus*[1]

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Abstract: The onchiostyle of *Trichodorus porosus* has an anterior outer portion, a fine inner spear and a posterior onchiostyle extension. The extension has a ventral lumen and is fused to the pharynx wall. The inner spear enters the dorsal wall of the outer onchiostyle posterior to the guide ring and extends anteriorly inside the anterior portion of the onchiostyle. Muscle cells are absent in the basal position of the esophagus. The glandular portion of the basal part of the esophagus consists mainly of endoplasmic reticulum lined with ribosomes. A sinus empties into the lumen through the dorsal esophageal gland orifice. The configuration of the intesinal lumen is highly variable. The rectum is attached to the dorsal and ventral walls of the body cavity by striated rectal muscle cells. *Key Words: Trichodorus porosus,* Digestive system, Ultrastructure, Rough endoplasmic reticulum, Onchiostyle, Esophagus, Intestine.

In 1935, Cobb (4) called the protrusible feeding apparatus of *Trichodorus obtusus* Cobb a long, slender and flexible cutting or pricking organ. Thorne (9) described it as a fused spear without basal bulbs. Allen (1) described several other features of the digestive system of the genus *Trichodorus*. A histological study of *T. elegans* Allen indicated the onchiostyle was a type of dorsally located tooth and that the lumen was ventral to the spear, emptying into the pharynx at the guide ring. The esophagus was described as dorylaimoid, with a slender anterior portion expanding into a pyriform or elongate basal bulb containing five esophageal gland nuclei.

Chen *et al.* (3) reported the spear of *T. christiei* to consist of two main structures. Raski *et al.* (8) concluded that the spear of *T. allius* Jensen had a tooth-like anterior odontostyle and a posterior odontostyle extension, and observed a sinus-like branching structure associated with the lumen in the glandular portion of the esophagus. In 1968, Hirumi *et al.* (5) described two parts in the feeding apparatus of *T. christiei,* an outer spear and a fine inner spear with the anterior part of the outer spear containing the inner spear and the posterior portion of the outer spear or onchiostyle extension fused to the dorsal wall of the pharynx. The inner spear passed through a dorsal opening in the middle of the outer spear. Pharyngeal muscles were shown attached to the surface of the onchiostyle extension. Hirumi and Hung (6) saw that the intestine of *T. christiei* had both a microvillous and a granular region. Bird (2) reported the posterior part of *T. porosus* had dorsolateral actin and myosin muscle cell filaments extending from the hypodermis to the intestine, dividing the dorsal body cavity into three sectors.

The object of the present investigation was to study the morphology and ultrastructure of the digestive system of *T. porosus* and compare it with the partial descriptions of the digestive systems of *T. allius* and *T. christiei.*

Materials and Methods

Heat-relaxed *T. porosus* females were fixed 1.5 hr at room temperature in a mixture of 3% glutaraldehyde and 3% acrolein in 0.1 M sodium cacodylate-buffer solution; post-fixed in 1% osmium tetroxide in a dilute salt solution for 1 hr; given three 15-min washes of dilute salt solution, and dehydrated in a graded ethanol series with a final dehydration in propylene oxide. They were embedded for sectioning by placement in a 1:1 mixture of propylene oxide-resin (1:1 mixture of Araldite 6005 and dodecanyl succinic anhy-

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dride) for 12 hr at 35 C and then in 100% resin at 35 C for 8 hr. Solutions were changed by allowing the nematodes to settle to the bottom of containers and decanting the supernatant liquid. Embedding was carried out under a dissecting microscope. The final embedding medium of 98% resin and 2% DMP-30 was first cured at room temperature for 12 hr, then 8 hr at 35 C, 16 hr at 45 C, and finally 24 hr at 60 C.

Cooled resin blocks were trimmed, oriented, and ultrathin (silver-gold) transverse and longitudinal sections of *T. porosus* were cut on a Porter-Blum MT-2 ultra-microtome with a diamond knife. Two ribbons of ten serial sections each were placed on separate coated grids. The sections were stained 15 min in a saturated uranyl acetate and 3 min in lead citrate. Sections were observed and electron micrographs taken on a Zeiss 9A electron microscope.

RESULTS AND DISCUSSION

ONCHIOSTYLE: The protrusible feeding apparatus of *T. porosus* is composed of an anterior outer onchiostyle and an inner spear similar to that of *T. christiei* (5), and a posterior onchiostyle extension like that described for *T. allius* (8). The inner spear enters the dorsal wall of the outer onchiostyle posterior to the guide ring and extends anteriad to at least 4 μ from the anterior end. In transverse section the anterior part of the inner spear appears as a small electron-dense dot. The posterior onchiostyle extension is fused to the pharynx wall and has a ventral lumen which is triangular when expanded. The lumen walls are fused to the onchiostyle extension and appear to be of similar composition (Fig. 1). The dorsal and lateral walls of the base of the onchiostyle extension are attached to the myofibrils of the muscle cells (Fig. 1, 2). The posterior half of the onchiostyle extension has numerous transverse striations (Fig. 2).

In general, the observations of the onchiostyle of *T. porosus* were consistent with those illustrated in the electron micrographs of *T. christiei* (5) and *T. allius* (8). The inner spear of *T. porosus* extended further forward than that reported for *T. christiei* (5), appearing in transverse sections of the anterior portion of the onchiostyle as a fine electron-dense dot. A similar electron-dense structure is present in the micrographs of the anterior regions of the onchiostyles of both *T. christiei* (5) and *T. allius* (8).

The author considers the stomatal armature of *T. porosus* an onchiostyle, because it is formed *in situ* in first-stage juveniles, molted stylets have not been observed in cast cuticles, and new stylets have not been observed developing in the esophagus. Observations of *T. christiei* (7) have indicated that no portion of the stylet is shed during molting.

ESOPHAGUS. The slender anterior portion of the esophagus (Fig. 2) is attached to the base of the onchiostyle extension and the lumen of these organs is continuous and of similar composition. This indicates that when the onchiostyle is protruded from the nematode body, the anterior portion of the esophagus must move in an anteriad direction. This is possible since this part of the esophagus of *T. porosus* is usually compressed or S-shaped when the onchiostyle is retracted. The slender anterior part of the esophagus is surrounded by the nerve ring through its entire length when the onchiostyle is retracted (Fig. 2, 3).

The enlarged basal portion of the dorylaimoid esophagus is composed of a triradiate lumen and dorsal and sub-ventral glandular regions (Figs. 3, 4, 5). No musculature is present in this region. Three areas of cytoplasm containing nuclei and mitochondria are adjacent to each ray of the esophagus lumen and the glandular regions are between these. A lateral esophagus nucleus was ob-

served with marginal clumps of chromatin (Fig. 4).

The glandular regions of the basal part of the esophagus are composed of numerous mitochondria, a few Golgi bodies, and large areas of endoplasmic reticulum lined with ribosomes (Fig. 6, 7). The presence of large areas of rough endoplasmic reticulum supports the theory that this is an area of high metabolic activity, possibly involved in synthesis of digestive substances.

The dorsal esophageal gland of *T. porosus* has a sinus in the anterior portion of the basal part of the esophagus (Fig. 3), similar to that described for *T. allius* (8). In longitudinal section the sinus is fan-shaped, with its base next to the esophageal lumen and the other surfaces adjacent to the rough endoplasmic reticulum (Fig. 3). A transverse section through the center of the sinus showed the dorsal esophageal gland orifice of the sinus opening into the lumen (Fig. 4). The sinus is probably a structure for the accumulation of digestive substances prior to their secretion into the esophageal lumen.

INTESTINE: The intestine wall of *T. porosus* is a single layer 0.2 to 0.6 μ thick. No cell boundaries, microvillous layer, or granular regions were observed; however, only posterior areas of the intestine were studied. Therefore, at least portions of the intestine of *T. porosus* differ from that described by Hirumi and Hung (6) for *T. christiei*. The configuration of the lumen of the intestine is highly variable in transverse section, being lobed with numerous small invaginations (Fig. 8).

In transverse section the anterior portion of the lumen of the rectum is oval. The rectal wall is 0.2 to 0.6 μ thick, with an outer layer having a composition resembling the intestine wall, and an inner cuticular layer. The cuticular portion is composed of an electron-dense layer lining the lumen and an outer granular layer (Fig. 9, 10, 11).

The lateral surfaces of the rectum of *T. porosus* are attached to two ventral rectal muscles (Fig. 10). The sub-dorsal surfaces of the rectum are attached to two dorsal muscles extending from the sub-dorsal walls of the rectum to just inside the sub-dorsal walls of the body cavity, dividing the body cavity into three sectors (Fig. 9). The rectal muscles are striated, exhibiting both actin and myosin filaments.

In transverse section the posterior portion of the rectum is crescent-shaped (Fig. 12). The cuticular portion of the rectal wall is enlarged, having a thickness of 0.3 to 1.2 μ. The subterminal caudal pores appear as spheres (Fig. 12). The crescent-shaped lumen of the anus is completely and solely surrounded by a thick layer of cuticle (Fig. 13).

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FIG. 1. Transverse section of onchiostyle extension (St E). Lumen (Lu), filamentous portion of protractor muscles (Fl), muscle attachment (At) to extension, nucleus (N). × 21,600.

FIG. 2. Longitudinal section of onchiostyle extension (St E) and slender anterior part of esophagus (E). Filamentous portion of protractor muscle cells (Fl), esophagus lumen (Lu), nuclei (N), mitochondria (M), dorsal nerve (DN), sub-ventral nerve (SN), nerve ring (NR). × 12,600.

FIG. 3. Longitudinal section of esophagus. Lumen (Lu), sinus (Si), slender anterior bulb (AB), enlarged posterior bulb (PB), esophagus wall (EW), dorsal nerve (DN). × 14,400.

FIG. 4. Transverse section of basal portion of esophagus. Endoplasmic reticulum (ER), cytoplasm devoid of ER (Fl_1, Fl_2, Fl_3) adjacent to lumen (Lu) ray, sinus (Si), esophagus lumen (Lu), Dorsal esophageal gland orifice (Dego), lateral muscle nucleus (N) with marginal clumps of chromatin. × 15,000.

FIG. 5. Transverse section of basal portion of esophagus. Esophagus lumen (Lu), esophagus wall (EW), cytoplasm devoid of endoplasmic reticulum (Fl), cuticle (Cu), somatic musculature (SM), endoplasmic reticulum (ER). × 7,203.

FIG. 6. Sagittal section of basal glandular portion of esophagus between two lumen rays. Mitochondria (M), esophageal walls (EW), endoplasmic reticulum (ER), Golgi body (G). × 17,798.

FIG. 7. Transverse section of dorsal esophageal gland. Rough endoplasmic reticulum (ER) with ribosomes. × 55,064.

FIG. 8. Transverse section of intestine. Somatic musculature (SM), cuticle (Cu), intestine lumen (Lu). × 5,340.

FIG. 9. Transverse section of rectum. Cuticle (Cu), somatic muscle cell (SM) with nucleus (MN), rectum lumen (Lu), filamentous portions of dorsal rectal muscle cells (RM). × 6,257.

FIG. 10. Transverse section of rectum. Rectal lumen (Lu), rectal wall (RW), dorsal rectal muscle (DRM), filamentous portion of ventral rectal muscle (VRM), terminus of somatic muscle cell (SM), and cuticle (Cu). × 8,899.

FIG. 11. Transverse section of rectum. Rectal lumen (Lu), rectal wall (RW). × 28,366.

FIG. 12. Transverse section of posterior part of rectum. Rectal muscles (RM), rectal wall (RW), lumen (Lu), subterminal caudal pores. × 5,340.

FIG. 13. Transverse section of posterior end of *T. porosus*. Terminus of body cavity (T), anal lumen (Lu), thickened cuticle (Cu). × 5,340.

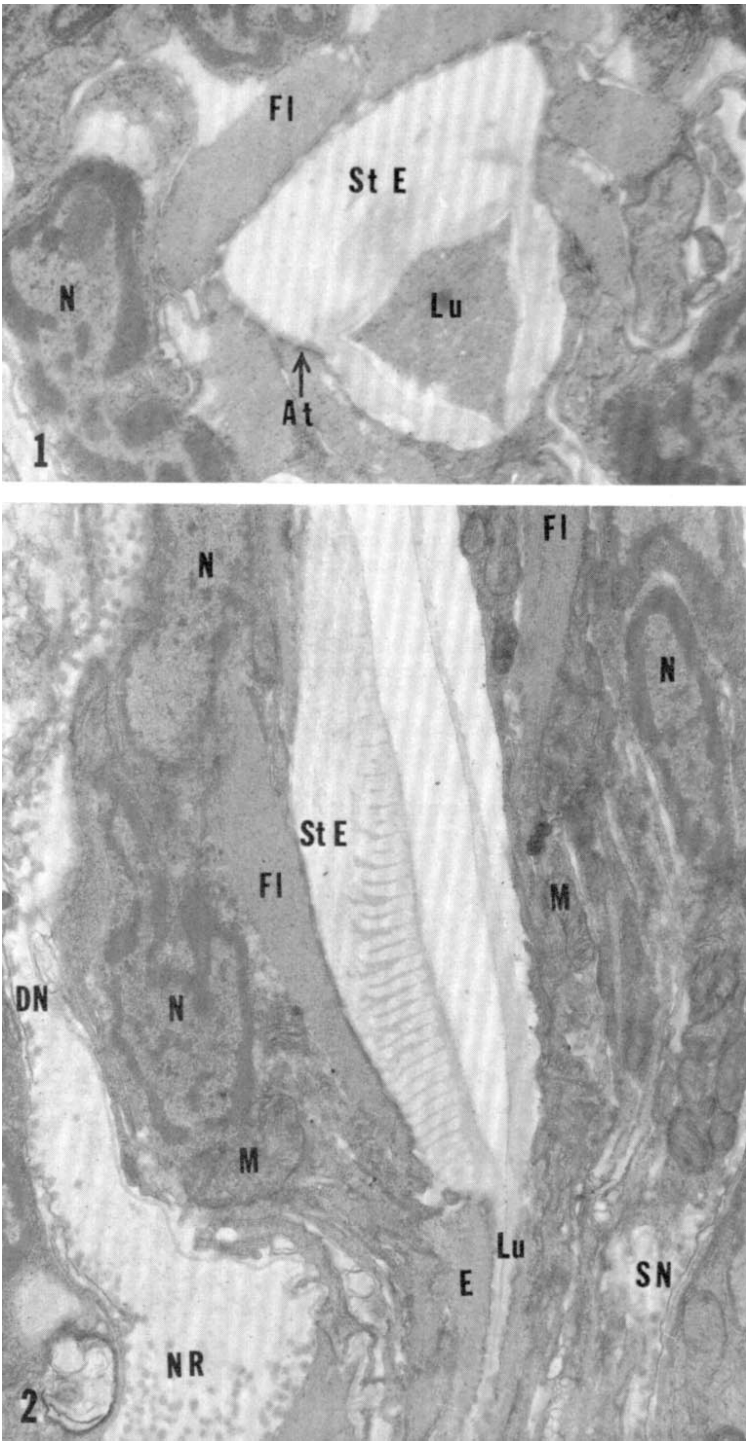
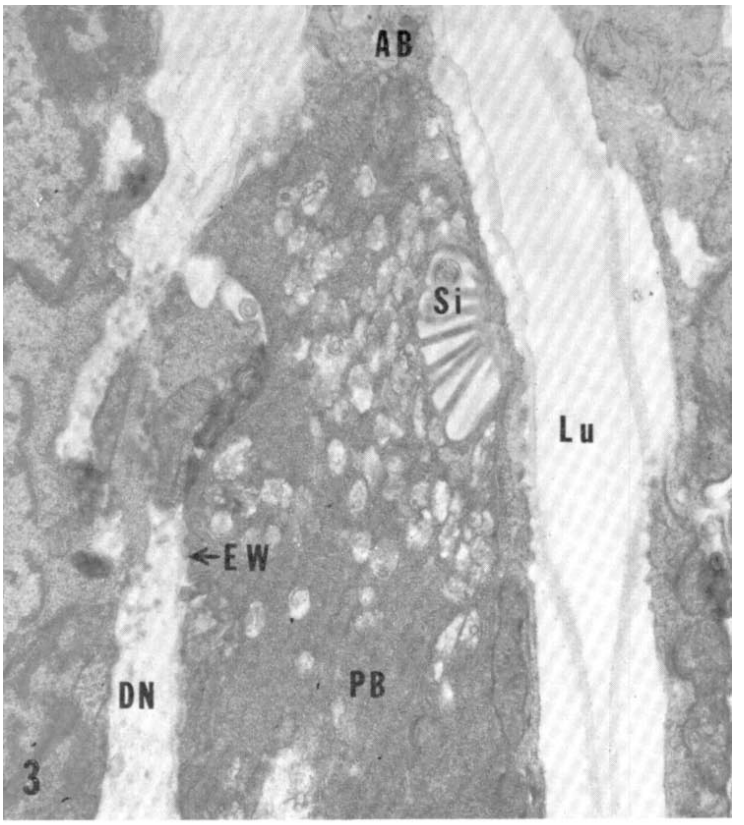


FIG. 1–2



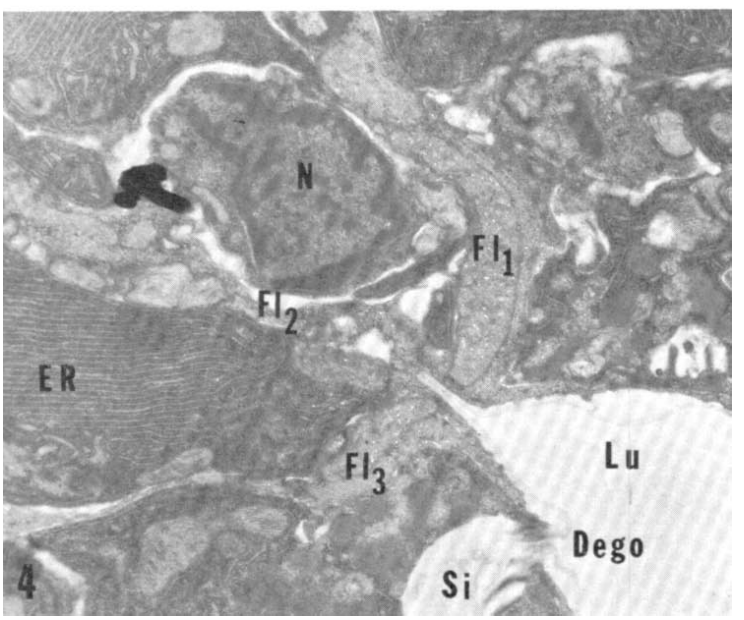


FIG. 3–4

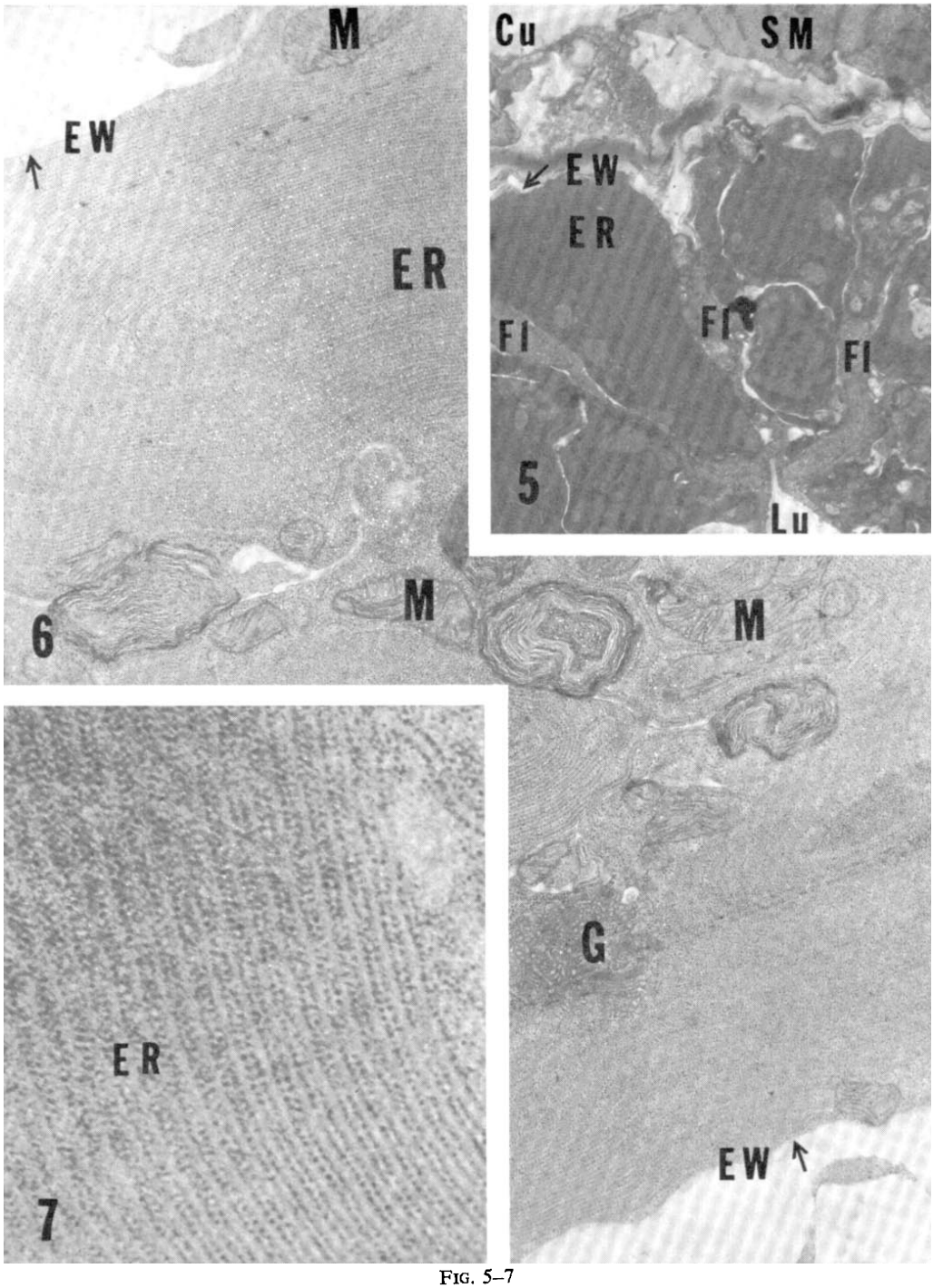
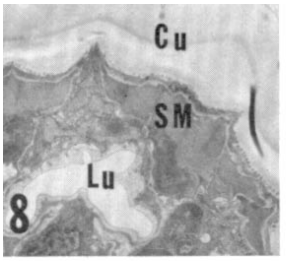
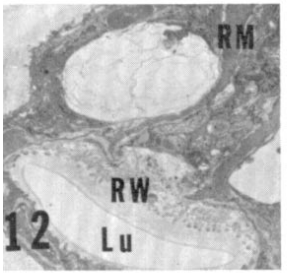
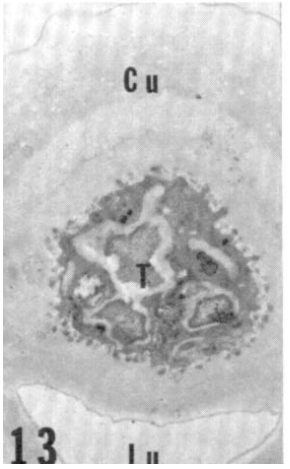


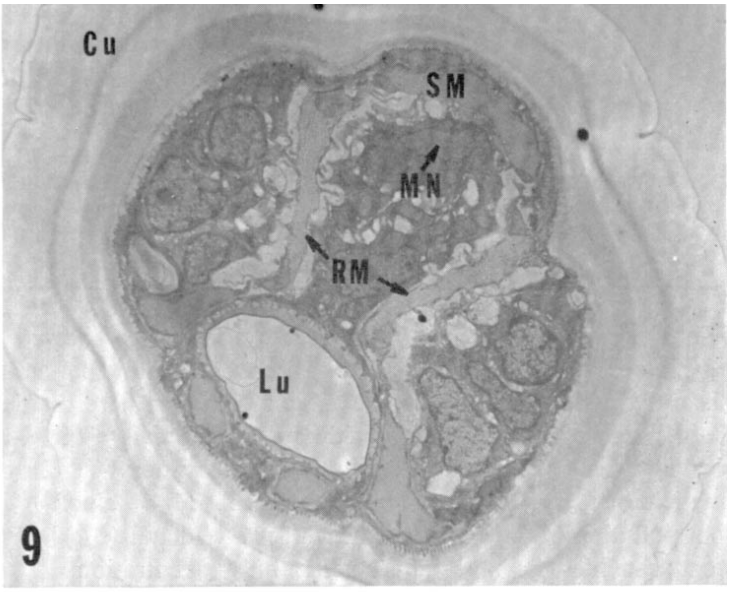
FIG. 5–7


Cu
SM
Lu
8


Lu
RW
11


RM
RW
12
Lu


Cu
T
13
Lu


Cu
SM
MN
RM
Lu
9

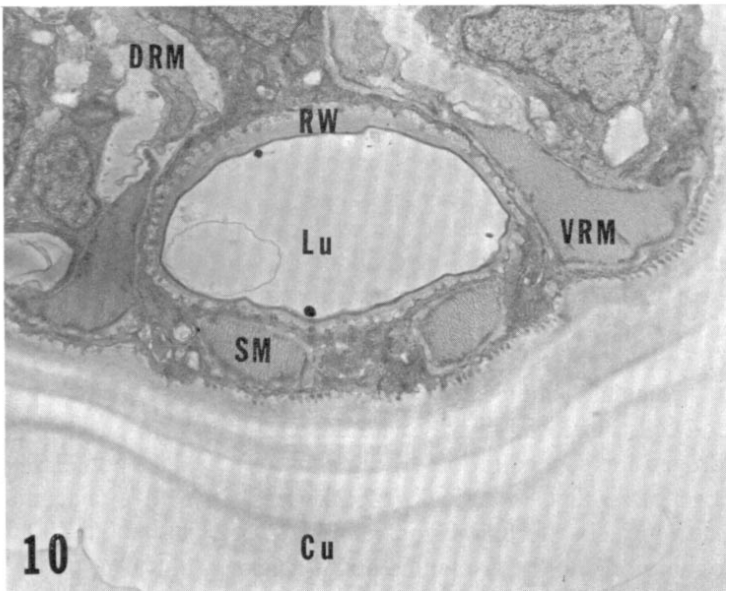

DRM
RW
Lu
VRM
SM
10
Cu

FIG. 8–13