

Ultrastructure of anterior and mid-regions of infective juveniles of *Steinernema feltiae* ⁽¹⁾

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Summary – The anterior region of infective third stage juveniles of *Steinernema feltiae* consists of an elongated buccal cavity supported by an invaginated body cuticle and regions of the buccal cuticle. The buccal cavity in the mid-region is slightly collapsed but enlarged posteriad. The buccal cavity can be divided into seven regions with region 1 corresponding to the cheilostom lined by the body cuticle, region 2 surrounded by arcade cells, and regions 3-7 lined by cuticle and surrounded by muscle cells designated M1-M5. The corpus of the esophagus consists of a central triradiate lumen supported by myofilaments of marginal and radial cells. The dorsal gland orifice is located at the base of the buccal cavity whereas the outlets of the subventral glands are slightly anterior to the nerve ring. Cuticular duct and supporting cells of the secretory-excretory gland in the vicinity of the nerve ring extend posteriad to occupy a major part of the body cavity near the esophago-intestinal valve and anterior region of the intestine. Within the basal bulb of the esophagus, the lumen expands to form a pump cavity enclosed by a dentate-corrugated cuticle supported by myofilaments of marginal and radial cells. Bacteria located between the esophago-intestinal valve and the ventricular region of the intestine are surrounded by microvilli.

Résumé – *Ultrastructure des régions antérieure et moyenne des juvéniles infestants de Steinernema feltiae* – La région antérieure des juvéniles infestants de troisième stade de *Steinernema feltiae* consiste en une cavité buccale allongée soutenue par une invagination de la cuticule du corps et par certaines zones de la cuticule buccale. La cavité buccale est rétrécie dans sa partie moyenne et élargie postérieurement. La cavité buccale peut être divisée en sept régions, la région 1 correspondant au cheilostome bordé par la cuticule du corps, la région 2 étant bordée par les cellules en arcade, les régions 3 à 7 bordées par la cuticule et entourées par les cellules musculaires désignées comme M1 à M5. Le corpus œsophagien consiste en une lumière triradiée soutenue par les myofibrilles des cellules marginales et radiales. L'orifice de la glande dorsale est situé à la base de la cavité buccale tandis que ceux des glandes subventrales sont légèrement antérieurs à l'anneau nerveux. Le conduit cuticularisé et les cellules de soutien de la glande sécrétrice/excrétrice située à proximité de l'anneau nerveux s'étendent postérieurement et occupent la majeure partie de la cavité du corps au niveau de la valve œsophago-intestinale et de la région antérieure de l'intestin. Au centre du bulbe basal de l'œsophage, la lumière s'élargit pour former la cavité de la « pompe », entourée par une cuticule rugueuse et denticulée soutenue par les cellules marginales et radiales. Les bactéries localisées entre la valve œsophago-intestinale et la région ventriculaire de l'intestin sont entourées de microvillosités.

Key-words : Electron microscopy, insect parasite, *Steinernema feltiae*, Nematoda.

Bacterial species, such as *Xenorhabdus bovienii* contained in the vesicles of *Steinernema feltiae* (Filipjev, 1934) (= *S. bibionis* Bovien, 1937), are released in the insect body cavity where they multiply and kill the host insect within 48 h (Poinar, 1993; Wouts, 1984). With the current trends to reduce the use of chemical pesticides, there is an active interest in utilizing steinernematid and heterorhabditid species as biological control agents of soil inhabiting insects in pest management systems (Poinar, 1979; Gaugler & Kaya, 1990). Interest in the ultrastructure of *Steinernema* was focused on the intestinal vesicle, which is a modified portion of the steinernematid intestine. Large populations of symbiotic bacteria (*Xenorhabdus* spp.) are usually present within

these vesicles which show considerable variation in morphology among different steinernematids (Bird & Akhurst, 1983; Bird & Bird, 1991).

Our electron microscope observations of the buccal cavity, esophagus, and intestine of *S. feltiae* provide additional data for comparing entomopathogenic nematodes and related nematodes (Poinar, 1993; Van de Velde *et al.*, 1994). These ultrastructural studies may provide an insight on the functional anatomy of steinernematid nematodes and their effectiveness as biological control agents of insect pests. (Dutky, 1959; Gaugler, 1987; Ghally 1987; Gaugler & Kaya, 1990; Kondo & Ishibashi, 1990; Nickle & Cantelo, 1991).

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Materials and methods

Infective third stage juveniles (J3) of *Steinernema feltiae* from an alginate gel pad provided by Biosys, Inc. were released in water. The infective juveniles were then concentrated and suspended in water, mixed with warm liquified 2% agar, and poured into small grooves cut in agar-filled Petri dishes. A sample of infective juveniles was injected into the body cavity of the greater wax moth, *Galleria mellonella*. After 4 h, juveniles were dissected from the insect and processed in the manner used for the non-injected J3 infective juveniles. The solidified agar containing the nematodes was diced into 2-3 mm blocks that were transferred to glass vials containing buffered 3% glutaraldehyde for chemical fixation (1.5 h) of the juveniles. This was followed by washing in six changes of buffer over a period of 1 h, postfixation in 2% osmium tetroxide for 2 h, dehydration in an acetone series (Endo & Wergin, 1973; Wergin & Endo, 1976) and infiltration with a low viscosity embedding medium (Spurr, 1969). Silver-gray sections of selected nematodes were cut with a diamond knife and mounted on uncoated 75 × 300 mesh copper grids. The sections were stained with uranyl acetate (10 min) and lead citrate (5 min) and viewed with a Philips 400T electron microscope operated at 60 kV with a 30 μm objective aperture.

Results

BUCCAL CAVITY

The cheilostom of the buccal cavity of 3rd stage juveniles of *Steinernema feltiae* is lined by the body cuticle that extends posteriad and widens to form a triradiate cavity before attaching to the cuticular terminus of the esophagus and forming the buccal ring (Fig. 2). In using the terminology proposed by Van de Velde *et al.* (1994), the cheilostom of the buccal cavity is region 1 (Fig. 2). Correspondingly, the cuticle lining region 2 of the buccal cavity is surrounded by arcade cells of hypodermal origin. The anterior-most muscle cells of the esophagus surround regions 3-7 of the cuticle-lined buccal cavity. The cuticle lining regions 2-3 of the buccal cavity forms a modified cylindroid, but the cavity is diminished in regions 3-4 and moderately expanded in region 5. The buccal regions 3-7 show dense myofilaments within radial cells M1-M5 inserted on the cuticle surface (Fig. 2). In region 7 and posteriad from the closure of the central lumen of the esophagus, the lumen extends laterally into the triradiate arms of the cuticle lined lumen to form radial tubuli (Figs 2, 3B).

CORPUS

The corpus region comprising the procorpus and metacarpus of the esophagus is muscular and has hemidesmosome contacts along the periphery of the cuticle from which myofilaments extend to the basal lamina of the esophagus (Figs 1, 5). The dorsal gland extension

traverses the full length of the esophagus and terminates as a cuticular port that occurs adjacent to M5 and region 7 of the stoma (Figs 2, 3C). The triradiate arms of the cuticularized lumen of the corpus broaden terminally and have paired internal cuticular ridges that, when in contact, delimit the radial tubuli along the length of the procorpus (Figs 3B, 5). The cuticle forming the radial tubuli has an alternating pattern of electron density (Figs 2, 3B).

ISTHMUS AND BULBUS REGIONS

The contents of the subventral glands have access to the esophageal lumen via openings that are part of a short cuticular duct that terminates as a valve in the anterior terminus of a subventral gland extension (Fig. 6). The valve, shown in longitudinal section, occurs just anterior to the isthmus and nerve ring (Fig. 1B). Similarly, a subventral valve in transverse section is surrounded by nerve ring components (Fig. 6B). The diameter of the esophagus in the region of the nerve ring is about 1/6 the width of the nematode body. The triradiate termini of the cuticularized lumen are narrow and pointed and lack the rounded tubular shape observed in the procorpus (Fig. 8). The isthmus of the esophagus is surrounded by neurons of the nerve ring (Fig. 6) and by components of the secretory-excretory cell (Figs 1B, 8). Bilateral branches of the secretory-excretory cell extend posteriad and adjacent to the base of the esophagus and the intestinal epithelium (Fig. 13C). The terminal cuticular secretory-excretory duct is prominent from the secretory-excretory pore to the vicinity of the secretory-excretory gland cell and adjacent secretory-excretory canals (Figs 1, 8 inset, 12). Non-cuticular ducts occur in the secretory-excretory canals that are located adjacent to the esophago-intestinal valve and the anterior region of the intestine. The secretory-excretory canals lie in lateral grooves formed by the bi-layered dorso-ventral oriented intestinal epithelium (Fig. 16).

The dorsal or subventral glands in the basal bulb of the esophagus were not clearly defined. However, the presence of cells with Golgi apparatus, secretory granules and dense ribosome populations signified the presence of glandular tissue (Figs 9, 10). The pump within the basal bulb of an infective juvenile is characterized by a pump chamber with a lumen extending from the central esophagus to the esophago-intestinal valve (Figs 1B, 9, 10, 11). Longitudinal sections through the valve reveal that the highly convoluted, regularly shaped cuticular wall of the pump chamber is bounded externally by myofilaments of radial and marginal cells (Fig. 10). Muscle elements are attached to the basal lamina of the esophagus by hemidesmosomes. In addition to the lateral orientation of muscle filaments extending from the cuticular surface of the pump, moderate to strong posteriad oriented myofilaments are attached to the posteriad basal lamina of the esophagus (Figs 9, 11).

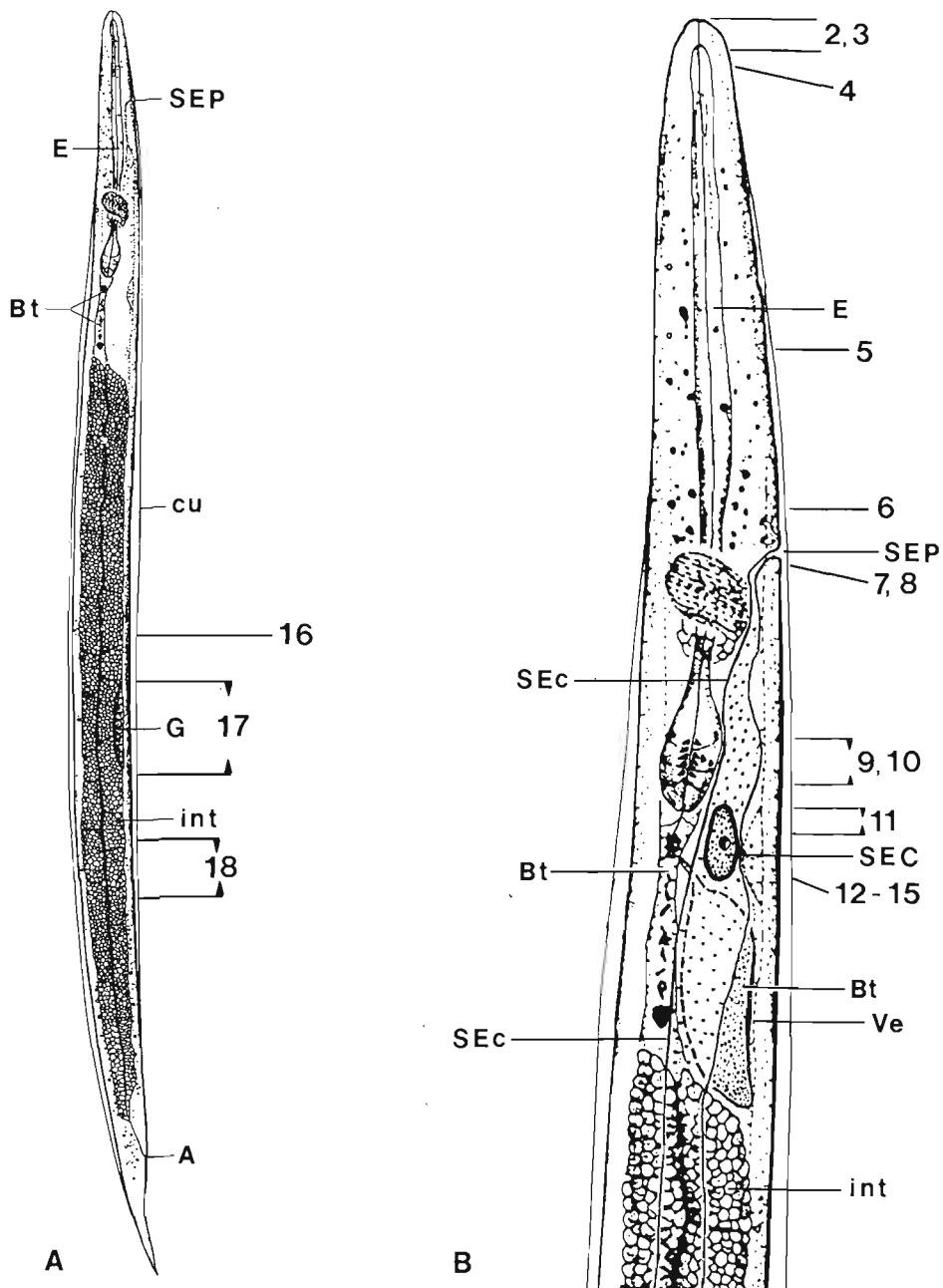


Fig. 1. Diagrams to compare infective third stage juveniles (J3) of *Neoplectana carpocapsae* with *Steinernema feltiae*. Numbers correspond to micrographs in text. **A:** Diagram of *Neoplectana carpocapsae* (genus synonymized as *Steinernema*) shows location of symbiotic bacteria, *Xenorhabdus nematophilus* (Bt) in ventricular region of intestine. (E: esophagus; SEP: secretory-excretory pore; cu: ensheathing second-stage cuticle; G: gonad primordium; int: intestine; A: anus). **B.** Modified and enlarged diagram of Figure 1A representing *S. feltiae* and showing locations of secretory-excretory pore (SEP), cell (SEC) and canals (SEc) in relation to bacterial vesicle (Ve). (bt: bacteria; E: esophagus; int: intestine).

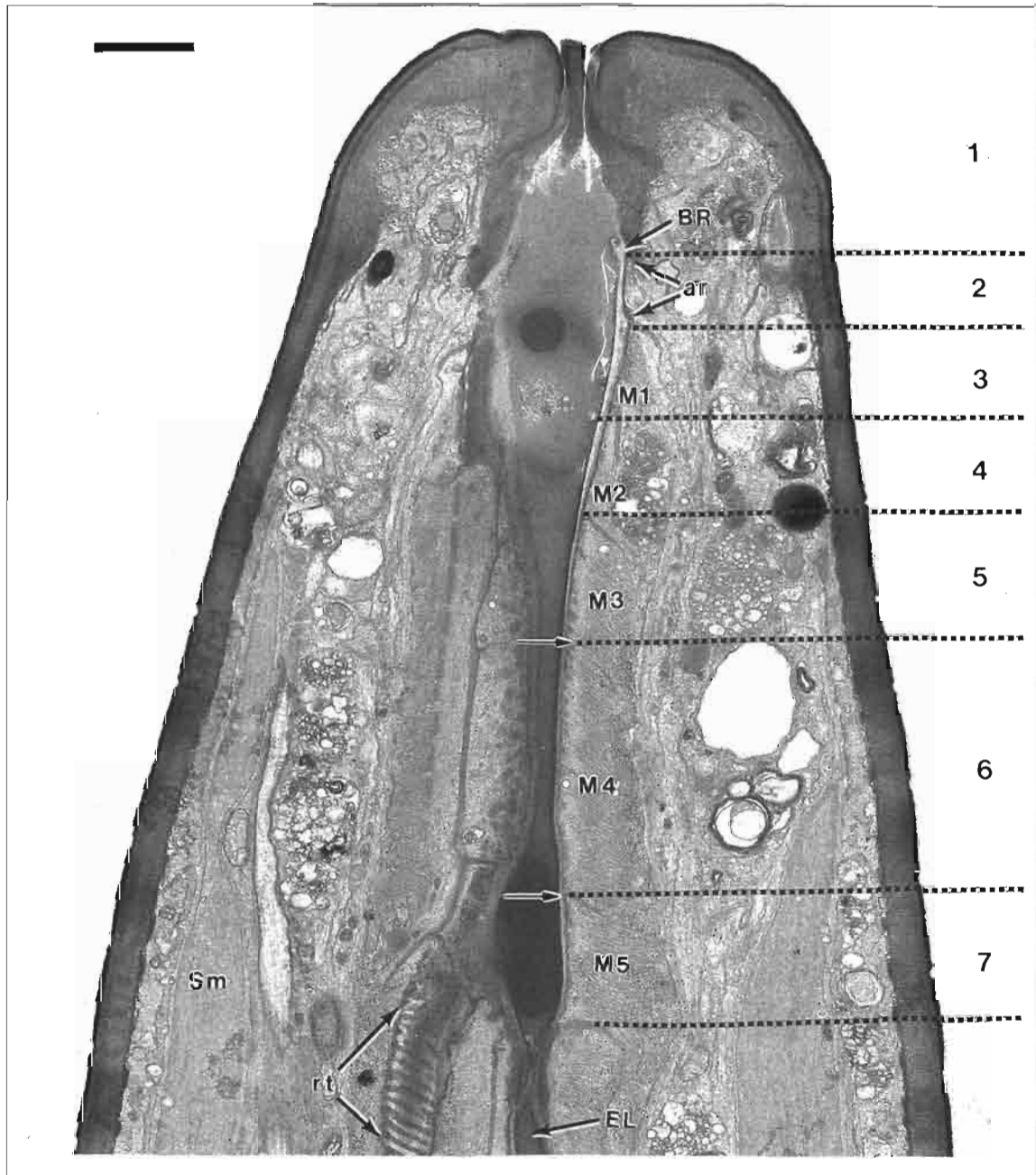


Fig. 2. Longitudinal section of buccal cavity region of third stage juvenile (J3) of *Steinernema feltiae*. Buccal cavity divided into seven regions with region 1 corresponding to the cheilostom lined by the body cuticle, regions 2-7 lined by the esophageal cuticle. Region 2 surrounded by arcade cells (ar), and regions 3-7 surrounded by muscle cells designated M1-M5. Boundary between body cuticle and esophageal cuticle forms a buccal ring (BR). Duct of dorsal esophageal gland valve illustrated as (Dd) in Fig. 3C is located near buccal region 7 and muscle cell M5. (EL : esophageal lumen; M1 : muscle inserted on buccal region 3; M2 : muscle inserted on buccal region 4; Sm : somatic muscle; rt : radial tubulus; arrows indicate cell boundaries of radial cell muscle inserted on buccal cuticle. Bar = 1.0 μ m).

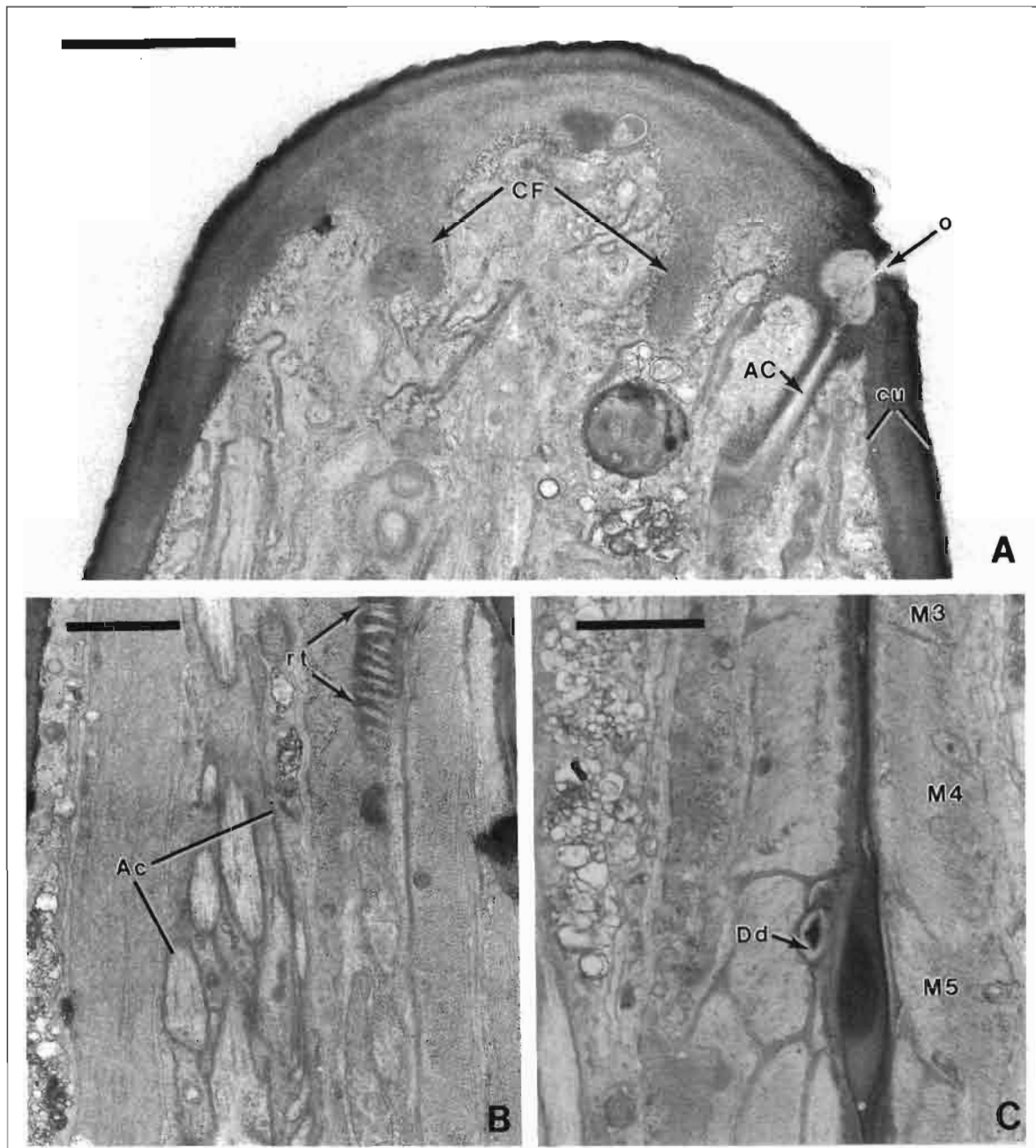


Fig. 3. Submedian, longitudinal sections of anterior region of *Steinernema feltiae* J3. *A*: Anterior terminal shows orifice (*o*) of amphidial gland extension. (*AC*: amphidial canal; *CF*: cephalic framework; *cu*: cuticle); *B*: Basal region of amphidial gland cilia (*Ac*). (*rt*: radial tubulus); *C*: Sections through *M3*, *M4*, and *M5* muscles inserted on cuticle of posteriad region of buccal cavity. (Portion of dorsal gland duct (*Dd*) lies adjacent to a muscle cell (*M5*)). Bars = 1.0 μm .

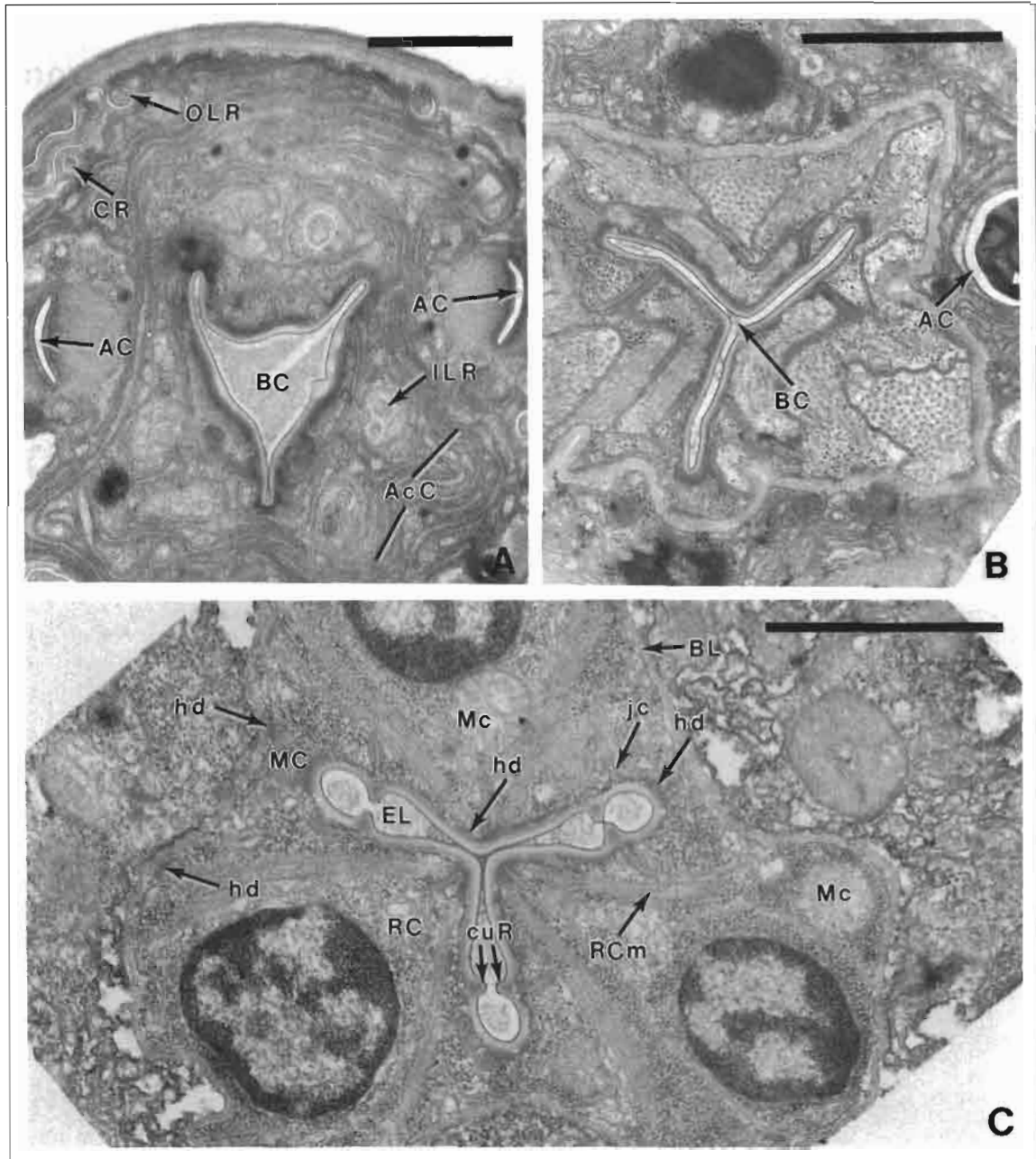


Fig. 4. Transverse sections through buccal cavity and esophagus of *Steinernema feltiae* ♂. *A*: Anterior region of triradiate buccal cavity (BC) shows stoma in open position and supported by thin layer of cuticle. (ACC: accessory cilia; AC: amphidial canal; CR: cephalic receptor; ILR, inner labial receptor; OLR, outer labial receptor); *B*: Posterior region of buccal cavity (BC) shows cavity in a closed position. (AC: amphidial canal); *C*: Section shows club-shaped arms of triradiate esophageal lumen. Radial (RC) and marginal (MC) muscles cell attached to esophageal lumen cuticle (EL) and basal lamina (BL) of esophagus by hemidesmosomes (hd). Cuticular ridges (cuR) extend into lumen of esophagus opposite junctional complexes (jc) between marginal and radial cells in anterior region of esophagus. (Mc: mitochondria; RCm: radial muscle cell. Bars = 1.0 μm).



Fig. 5. Longitudinal section through mid-region of esophagus corpus of *Steinernema feltiae* J3. Central part of esophageal lumen shows evenly spaced hemidesmosomes (hd) on cuticle surface and their association with radial muscle cell (RC). Irregular cuticular branches (Icu) of irradiate lumen caused by slight folding of esophagus during fixation procedures. (Sm : somatic muscle. Bar = 1.0 μ m).

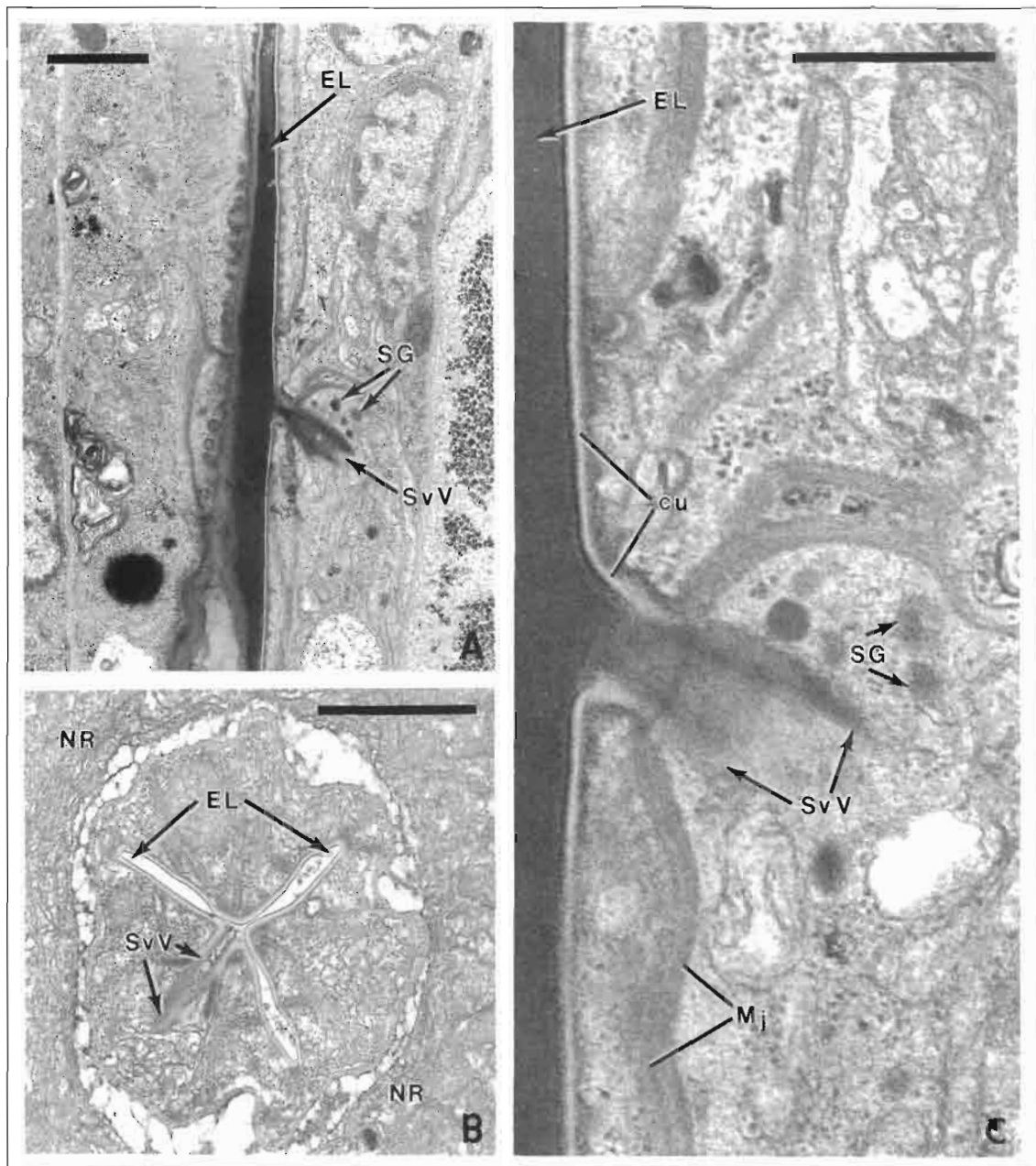


Fig. 6. Longitudinal and transverse sections through subventral gland valve of *Steinernema feltiae* ♂3. *A*: Section through elongated subventral gland valve (SvV) projecting into ampulla of gland extension. (EL: esophageal lumen; SG: secretory granules); *B*: Transverse section through posterior region of esophagus showing portion of subventral gland valve (SvV) with entry point into esophageal lumen (EL) of the esophagus. (Bars 1.0 μm); *C*: Different level of sectioning from Figure 5A, shows well defined cuticle (cu) boundaries of esophageal lumen (EL) and base of subventral gland valve (SvV). (Mj: membrane junction; SG: secretory granules. Bar = 0.5 μm).



Fig. 7. Longitudinal section of postcorpus region of *Steinernema feltiae* J3 shows isthmus of esophagus (E) surrounded by axons and/or dendrites which constitute the nerve ring (NR). (EL : esophageal lumen. Bar = 1.0 μ m).

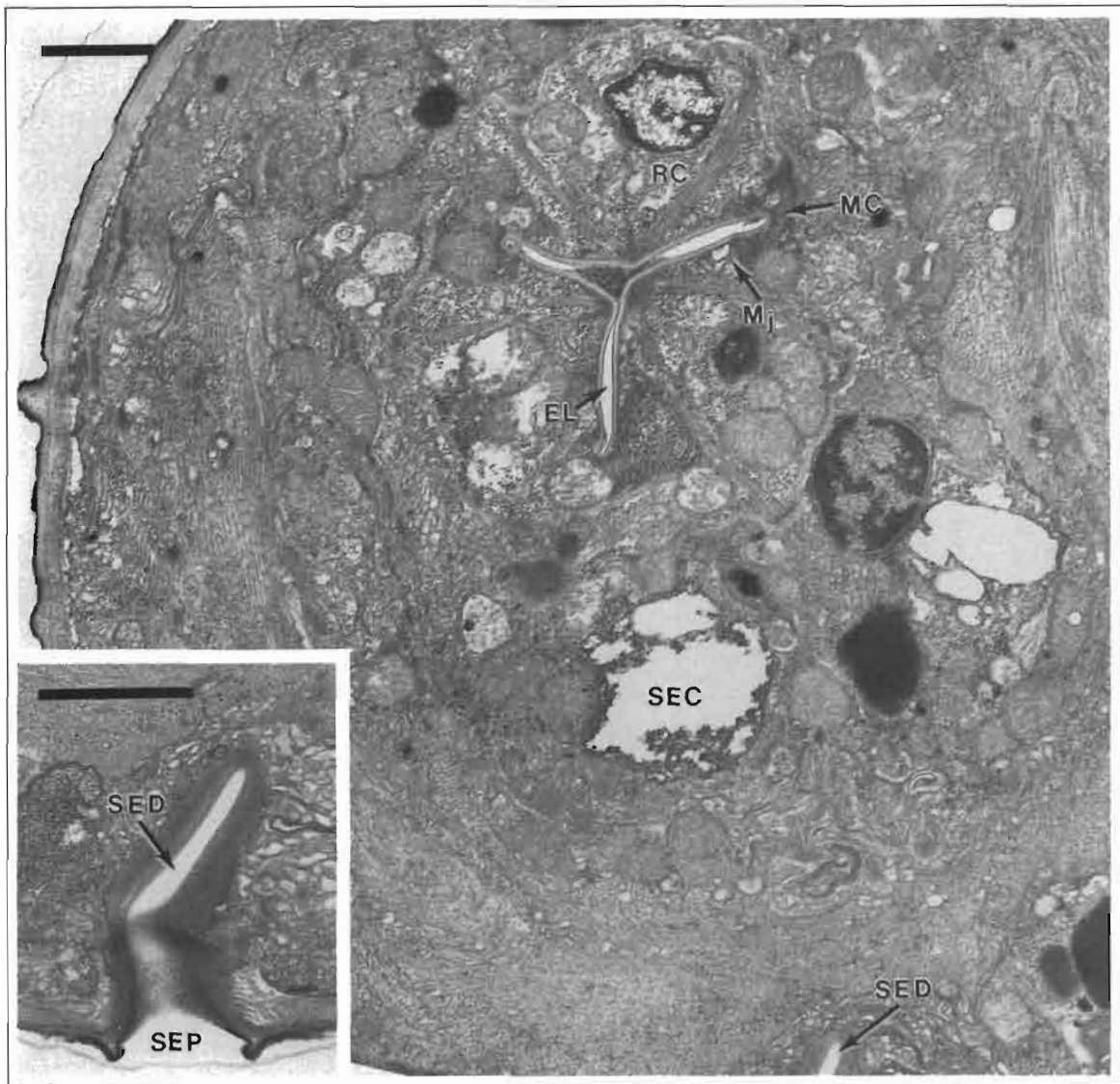


Fig. 8. Transverse section through the esophagus of *Steinernema feltiae* J3, slightly posterior to the nerve ring. Triradiate esophageal lumen lacks radial tubuli as described in Figure 3C. Arms of esophageal cuticle are flattened and supported by marginal cell (MC) terminally. Larger radial cells (RC) form lateral membrane junctions (Mj) with the marginal cells. (SEC : secretory excretory cell). Inset shows secretory-excretory duct (SED) joining invaginated body cuticle to form secretory-excretory pore (SEP). (Bar = 1.0 μ m).

ESOPHAGO-INTESTINAL VALVE AND BACTERIA-LADEN VESICLE

Three tiers of nonmuscular cells apparently control the aperture of the esophago-intestinal valve. The base of the third tier of cells merges with the microvilli-lined ventricular region of the intestine (Figs 1B, 12, 13 A-B, 14). A mid-longitudinal section through a bacteria-laden vesicle shows that this vesicle lies at the base of the esophago-intestinal valve. The bacteria in the vesicle has continuity with bacteria located within or at the junction

of the esophago-intestinal valve and intestinal lumen (Figs 1, 14, 15). Other specimens have bacteria-filled vesicles that extend posteriad and ventrally along the base of the intestine. In transverse sections, some bacteria-laden vesicles have narrow anteriad extensions that are flanked dorso-laterally by secretory-excretory canals and intestinal epithelia (Fig. 15 & inset).

INTESTINE

The restricted lumen of the intestine is surrounded by membranous boundaries of paired layers of epithelial



Fig. 9. Longitudinal, submedian section through the cuticularized pump in basal bulb of *Steinernema feltiae* ♂3. Myofilaments (*my*) in tangential view are related to muscle elements inserted on the surface of corrugated cuticle of basal bulb pump as also shown in Figure 10. (*bl*: basal lamina of esophagus; *bm*: basal membrane. Bar = 1.0 μm).

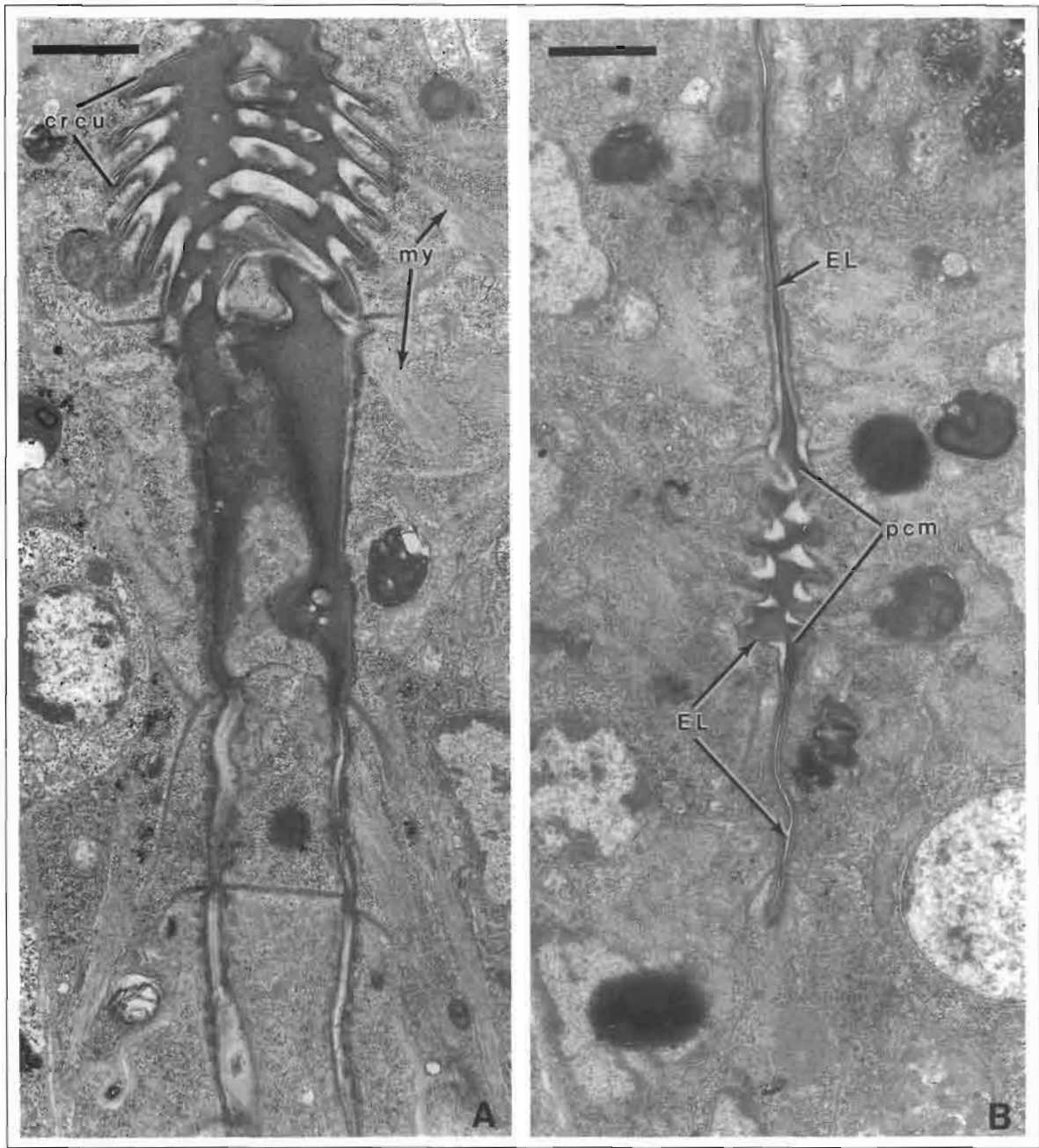


Fig. 10. Longitudinal, median sections through pump chamber of *Steinernema feltiae* J3. *A*: Slightly expanded lumen of pump chamber supported by corrugated cuticle (*cru*) with inserted muscle elements in lateral-posteriad orientation. (*my*: myofilaments); *B*: Submedian section through pump chamber (*pcm*) shows merging of cuticular walls of esophageal lumen (*EL*). (Bars = 1.0 μm).



Fig. 11. Longitudinal section of esophago-intestinal junction of *Steinernema feltiae* ♀3. Cuticle-lined lumen extends from pump chamber and basal lamina (bl) into 2 tiers of cells of esophago-intestinal junction and into a 3rd tier which constitutes the anterior-most region of the intestinal epithelium. (E: esophagus; EL: esophageal lumen; my: myofilaments; N: nucleus of esophago-intestinal junction. Bar = 1.0 μm).

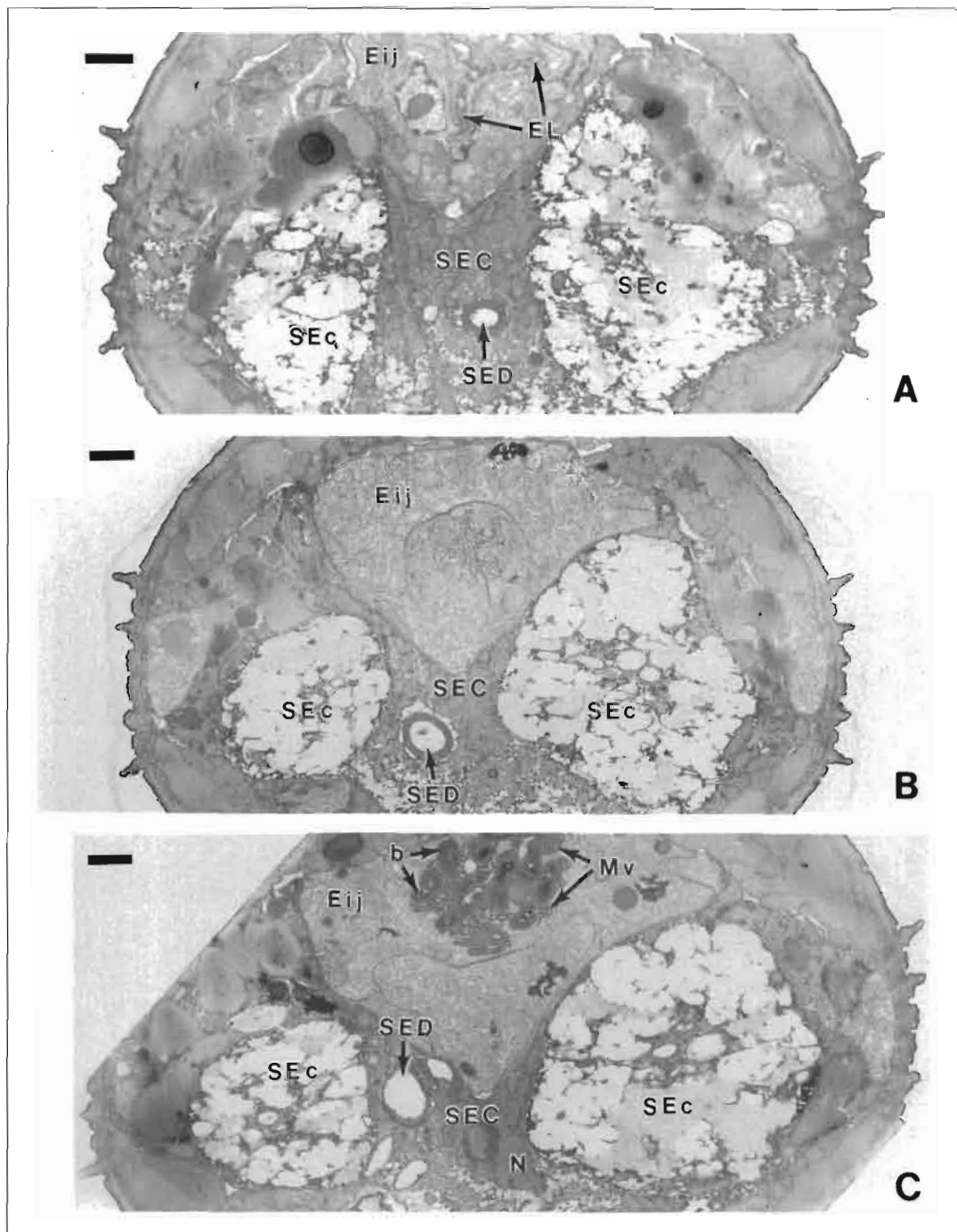


Fig. 12. Transverse sections through regions of esophago-intestinal junction of *Steinernema feltiae* ♂3. **A**: Anteriad section through esophago-intestinal junction (*Eij*) shows triradiate, convoluted, thinly cuticularized lumen (*EL*). Secretary-excretory canals (*SEc*) and part of central secretory cell (*SEC*) occupy a large cross sectional area of body cavity; **B**: Section at terminus of esophago-intestinal junction (*Eij*) shows irregular pattern of lumen wall within 3rd tier cell. (*SEc*: secretary-excretory canal; *SED*: secretary-excretory duct); **C**: Section through anteriad region of intestine shows bacteria (*b*) extending from bacteria-filled vesicle. Microvilli (*Mv*) surround perimeter of bacteria (*b*) accumulated at terminus of the esophago-intestinal valve and entrance to intestine. (*SEC*: secretary-excretory cell; *SEc*: secretary-excretory canal; *N*: nucleus of secretary-excretory cell; *SED*: secretary-excretory duct. Bars = 1.0 μ m).

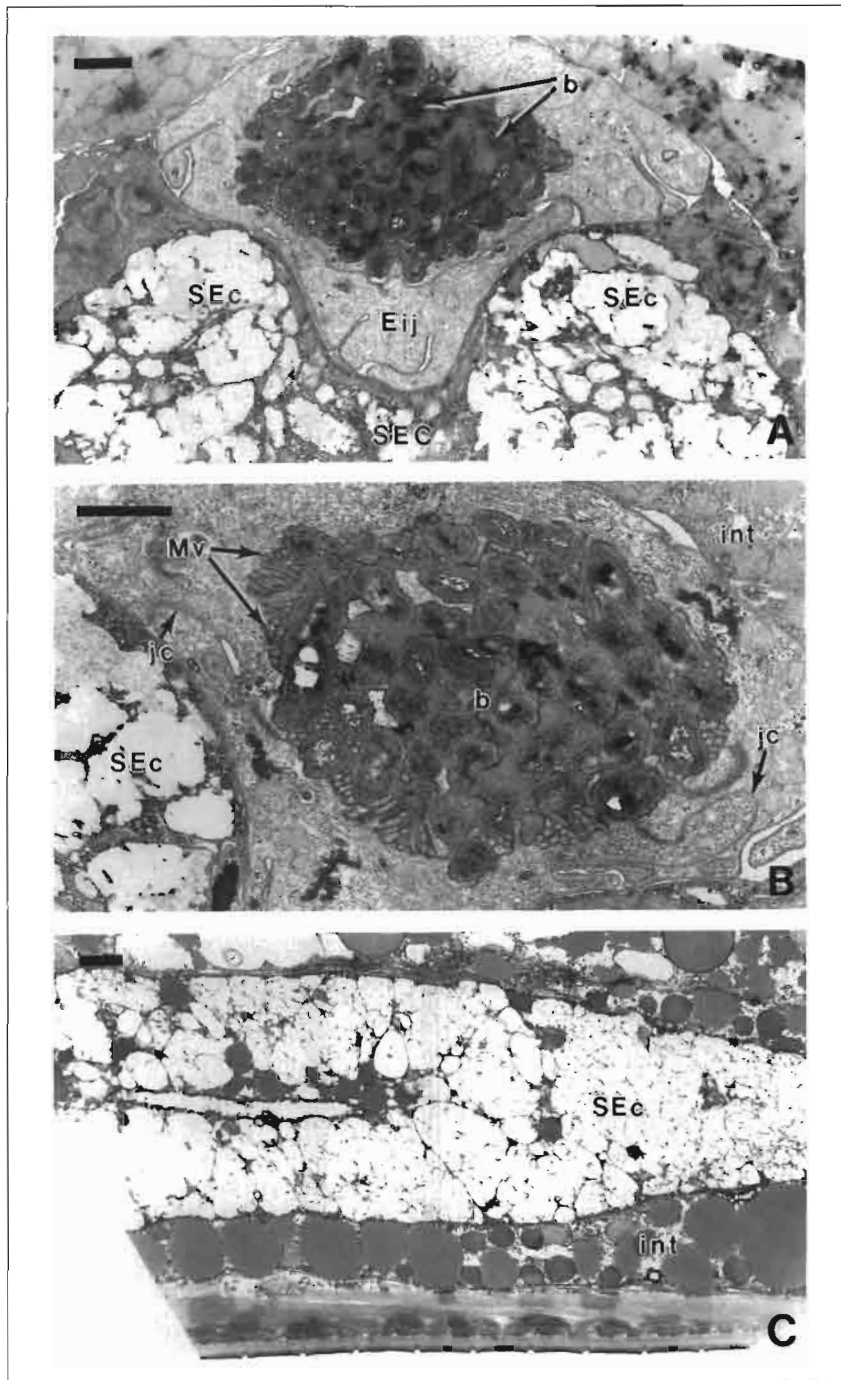


Fig. 13. Sequence of transverse sections and longitudinal section of esophago-intestinal junction and intestine of *Steinernema feltiae* J3. *A* : Esophago-intestinal junction cell with concentrations of bacteria (*b*) in esophageal lumen leading into intestine. Note secretory granules within secretory-excretory canals (*SEc*) and part of secretory-excretory cell (*SEC*); *B* : Section posteriad from Figure 13*A* shows bacteria (*b*) in lumen of intestinal (*int*) epithelium lined with microvilli (*Mv*). Two-celled cross sectional view of intestine defined by junctional complexes (*jc*) between adjacent cells; *C* : Longitudinal view of secretory-excretory canal (*SEc*) bordered by intestinal (*int*) epithelium filled with electron dense lipid granules. (Bars = 1.0 μm).



Fig. 14. Longitudinal section through cells (C1, C2, C3) of esophago-intestinal junction (Eij) of *Steinernema feltiae* J3 surrounded posteriad and ventrally by bacteria (b) filled vesicle. Intestinal lumen (L) located near dorsal region of nematode. (E : esophagus. Bar = 1.0 μ m).

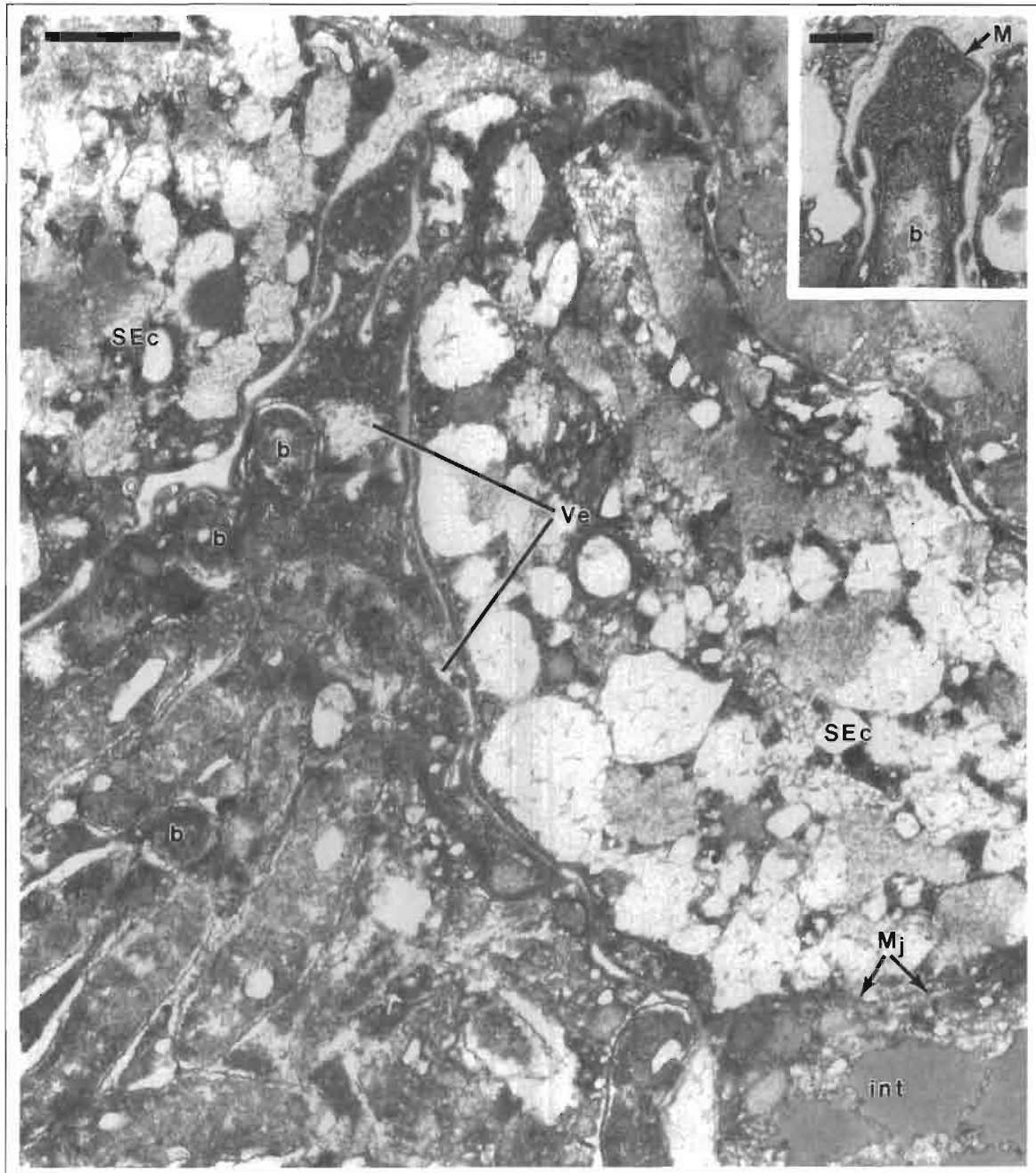


Fig. 15. Section near apex of bacteria filled vesicle (Ve) in *Steinernema feltiae* ♂3. Thin vesicle wall shows invaginations of membrane surfaces around main body regions and some evaginations containing bacteria (b) near entrance into intestinal lumen (int). (Bar = 1.0 μ m). Inset shows terminal region of vesicle with enclosed bacterium (b). (M : membrane of vesicle; Mj : membrane junction. Bar = 0.5 μ m).

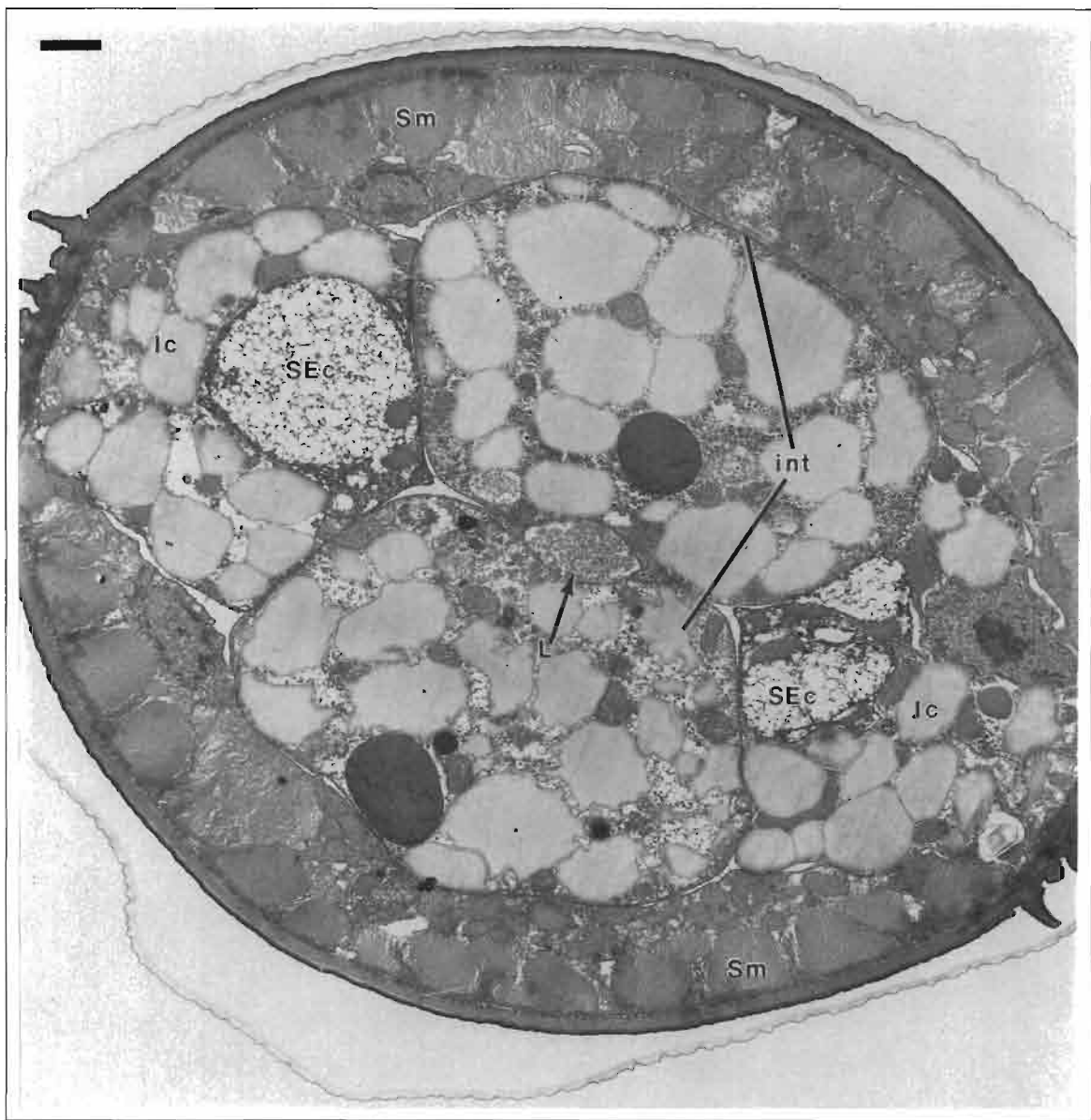


Fig. 16. Transverse section through mid-region of *Steinernema feltiae* ♂3 showing paired cell epithelium enclosing lumen (L) of intestine (int). Intestine flanked by extensions of secretory-excretory canals (SEc) and lateral cord (lc) of hypodermis. (SM : somatic muscle. Bar = 1.0 μ m).

cells that extend through most of the length of the nematode (Fig. 16). Transverse and longitudinal sections through the intestinal region show the relative space occupied by narrowing branches of the secretory-excretory cell and the developing tissues of the gonad (Figs 1, 17). The parallel arrays of cells comprising the intestinal epithelium are nucleated and joined longitudinally end-to-end and dorso-ventrally by membrane junctions (Fig. 18). Membrane junctions at common boundaries

of the pair of cells surround the intestinal lumen (Fig. 16). The restricted opening within the lumen shows a wide contrast to that of a related genus *Heterorhabditis* in which bacteria are distributed throughout the intestinal lumen of infective juveniles (Fig. 19).

DISCUSSION

The buccal cavity of *Steinernema feltiae* differs ultrastructurally from the related entomopathogenic nema-

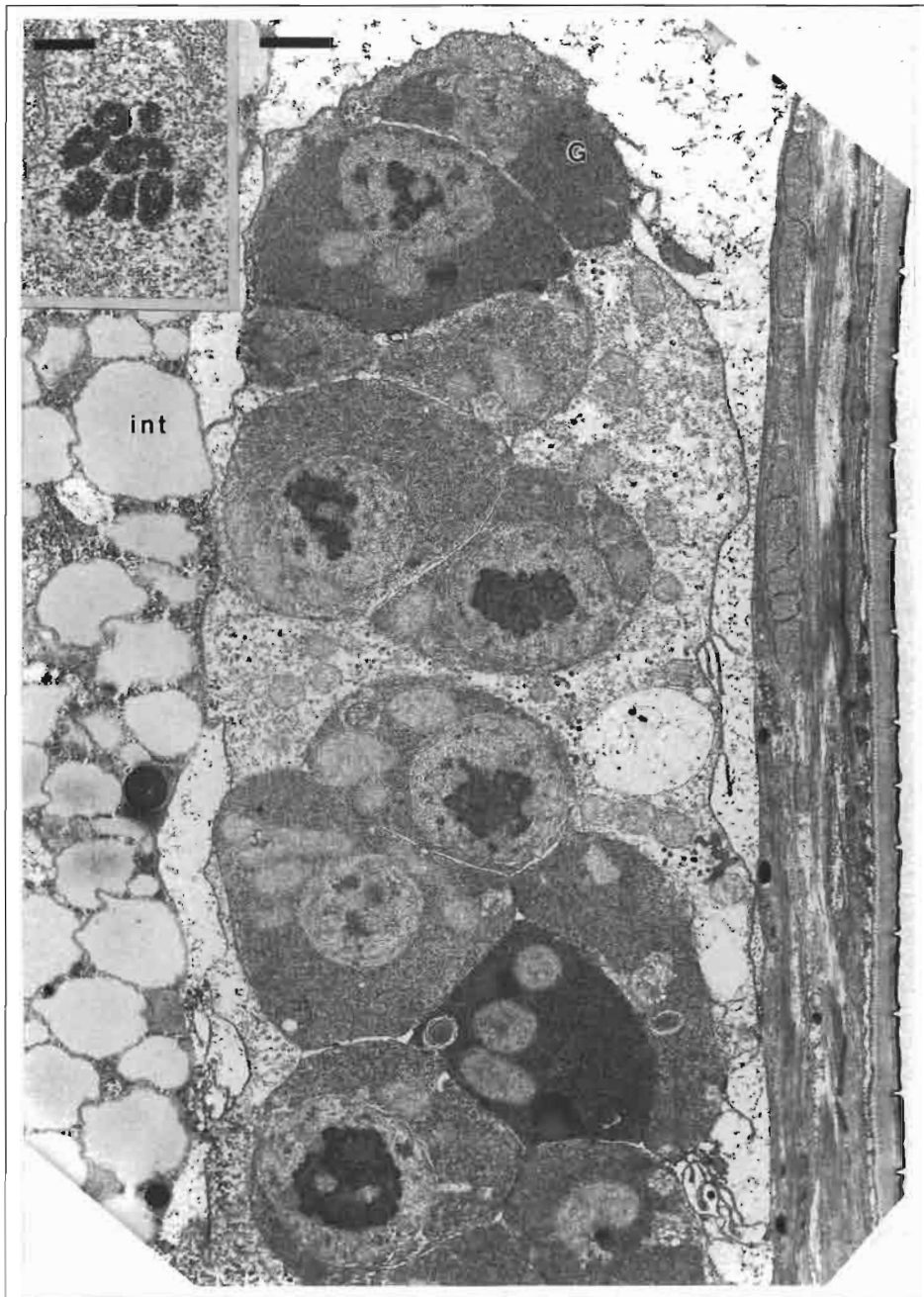


Fig. 17. Longitudinal section through gonad of *Steinernema feltiae* ♂3. Gonad (G) bordered dorsally by intestine (int). (Bar = 1.0 μm). Inset shows cell near gonad terminus with several metaphase chromosomes. (Bar = 0.5 μm).

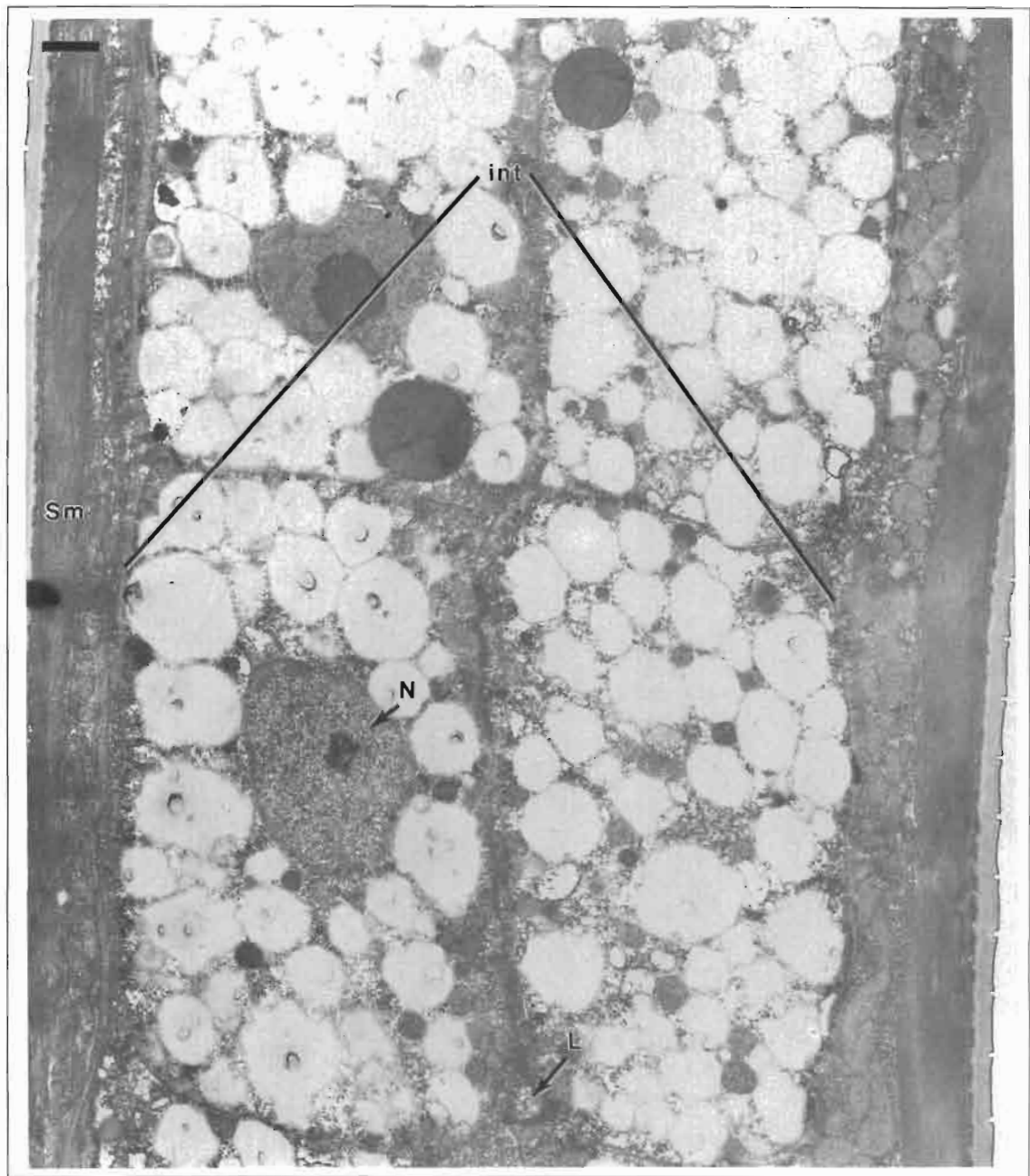


Fig. 18. Longitudinal section through intestine of *Steinernema feltiae* J3 shows parallel arrays of intestinal cells filled with lipid granules. (*int* : intestine; *L* : lumen of intestine; *N* : nucleus; *Sm* : somatic musculature. Bar = 1.0 μm).



Fig. 19. Longitudinal section through intestinal lumen of infective third stage juvenile of *Heterorhabditis bacteriophora*. Large population of bacteria within intestine in *H. bacteriophora* contrasts with the nonfunctional nature of the midgut region of *S. feltiae* shown in Figure 18. (Bar = 1.0 μm).

tode, *Heterorhabditis bacteriophora* (Poinar, 1975; Endo & Nickle, 1991). The cuticle of the cheilostom of *S. feltiae* joins the cuticle of the expanded anterior-most region of the buccal cavity to form the buccal ring. The thin cuticle that forms the buccal cavity of *S. feltiae* differs from the relatively thick cuticle that supports the triangular cylindroid buccal capsule in *Caenorhabditis elegans* (Wright & Thomson, 1981) and *H. bacteriophora* (Endo & Nickle, 1994). However, *S. feltiae* and *H. bacteriophora* are similar in that the muscle-supported cuticles forming the buccal cavities are more extensive than in *C. elegans*. The relatively thin wall of the buccal capsule of *S. feltiae* and the wide bands of muscle filaments inserted on the buccal wall cuticle, designated as regions 6 and 7, may relate to the feeding behavior of the species. The genera *Heterorhabditis* and *Steinernema* have related ancestral forms of stomatal structures that show their adaptability to feed in a semi-liquid habitat as found in an insect cadaver (Poinar, 1993). Each species represents two well recognized nematode families with capabilities of harboring symbiotic bacteria and invading insect hosts. The bacteria released from the nematode multiply rapidly in the insect to cause septicemia that results in the destruction of the host insect (Wouts, 1984; Gaugler, 1987).

In transverse section, the triradiate cuticular lining of the procorpus lumen of *S. feltiae* has radial tubuli as observed in *C. elegans* (Albertson & Thomson, 1976) and *S. carpocapsae* (Poinar & Leutenegger, 1968). This is in contrast to the pointed cuticular arms in the procorpus of *H. bacteriophora* (Endo & Nickle, 1994). The marginal arms of the procorpus of *Rhabditis* were described as having "tubes" and those of the metacarpus having smaller "tubes" when observed by light microscopy (Chitwood & Chitwood, 1950). Regardless of the shape of the arms of the triaradiate lumen, myofilaments and corresponding hemidesmosomes of marginal and radial muscles cells apparently support and expand the esophageal lumen during food uptake in a manner described for other species that have muscular esophagi (Chitwood & Chitwood, 1950; Mapes, 1965). The dentate cuticular wall of the bulbar valve or pump present in longitudinal sections of *S. feltiae* appears similar to the cuticular folds of *C. elegans* observed in transverse sections (Albertson & Thomson, 1976). Vertical and oblique orientations of the muscle elements of *S. feltiae* are readily discernable and similar to that described for the bulbar valve of rhabditids (Chitwood & Chitwood, 1950). The posteriad direction of the dentate projections of the bulbar valve relates to the bands of longitudinally oriented muscles that extend posteriad and attach to the basal lamina at the base of the esophagus. The esophago-intestinal valve of *S. feltiae* appears to have a three-tier configuration between the basal lamina of the esophagus and the anterior-most region of the microvilli lined intestine, as in *H. bacteriophora* (Endo & Nickle, 1991). Symbiotic bacteria, *Xenorhabdus luminescens*

(Poinar *et al.*, 1977; Thomas & Poinar, 1979), reclassified as *Photorhabdus luminescens* (Boemare *et al.*, 1993) are distributed throughout the length of the intestinal lumen of *H. bacteriophora*; whereas in infective juveniles of steinernematids, bacteria are retained within vesicles (Bird & Alkhurst, 1983). In infective juveniles of *S. feltiae*, bacteria can occur in an enlarged vesicle with its terminal portion extended towards the lumen of the ventricular region of the intestine. Thus, the bacteria from the vesicle would have ready access to the main channel of the intestine where they can multiply and be discharged into an insect host. The differences in electron density of bacteria among the specimens of *S. feltiae* may be due to variations in fixation or resin infiltration. However, their presence within a vesicle and their apparent entry point into the anterior-most region of the intestinal lumen is consistent. Studies are needed to determine the precise time required for the release of the symbiotic bacteria into the host insect and their subsequent multiplication and release in the hemocoel.

Physiological and light microscopic studies of the secretory-excretory system of juvenile stages of *C. elegans* showed that excretory cell, duct cell and pore cell functions are essential for normal survival. When either of these cells were ablated with a laser microbeam, the juveniles were filled with fluid within 12-24 h and died within a few days. Observations of pulsations of the excretory duct of dauer juveniles under differing levels of osmolarity led to the conclusion that one of the functions of the excretory system is osmoregulation (Nelson & Riddle, 1984). Our ultrastructural observations of the related rhabditid species show a very extensive secretory-excretory (SE) system in which the SE canal occupy a large volume of the body cavity along-side the intestine. The lateral bodies within the hypodermal cords reported in juveniles of *S. carpocapsae* (Poinar & Leutenegger, 1968) should be interpreted as transverse sections through canals of the secretory-excretory system as shown in *S. feltiae*. In a review of other secernentean nematodes, it was reported that the function of the SE system is quite variable and that in addition to osmoregulation, this system secretes enzymes or glycoproteins of a protective or lubricating nature (Bird & Bird, 1991).

The anterior sensilla of *S. feltiae* are similar to those described for *H. bacteriophora* and other secernentean nematodes (Baldwin & Hirschmann, 1973; Ward *et al.*, 1975; De Grisse, 1977; Coomans, 1979; Wright, 1980); they have twelve labial sensilla, four cephalic sensilla, and two amphids. Each of the inner labial sensilla consists of two receptors, whereas the outer labial sensilla have single receptors. The cephalic sensilla each possess one receptor. The lamellae-like structures in the head region of *S. feltiae* are similar to nerve structures in *Heterodera glycines* (Endo, 1980), *Meloidogyne incognita* (Endo & Wergin, 1977), and *Heterorhabditis bacteriophora* (Endo & Nickle, 1994). The direct relationship between these nerve structures to lateral accessory sensilla

was demonstrated in the citrus nematode, *Tylenchulus semipenetrans* (Natasasmita, 1979).

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