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Ultrastructure of the Head of *Okranema eileenae* Greenslade and Nicholas, 1991 (Thoracostomopsidae: Nematoda)

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Abstract: *Okranema eileenae* is a marine nematode from Australian sandy beaches. The structure of its cephalic region is described by light, scanning, and transmission electron microscopy. Three large lips, separated by three deep clefts and surmounted by flexible liplets, surround the mouth. Transverse and longitudinal sections of the head have been used to investigate the ultrastructure of the lips, buccal cavity, mandibles, and cephalic sensilla. The pharyngeal muscles are attached to the external head cuticle over a broad band, forming the cephalic capsule, which terminates in the three connected cuticular cephalic arches—one in each lip. Three mandibles form the central core of each lip, cuticular structures from which two small teeth—denticles and one large central tooth, the onchium—project into the buccal cavity. The onchia are anterior extensions of the pharynx that contain the ducts of pharyngeal glands that discharge into the buccal cavity. Epidermal tissue extends anteriorly as far as the cephalic arch. Cephalic structures, apart from sensory setae, are formed from an expanded cephalic cuticle.

The inner labial, outer labial, and cephalic setae each contain two dendritic processes. Aspects of amphidial structure are described for the first time in Thoracostomopsidae. The external apertures are illustrated by scanning electron microscopy and the internal structure in sections by transmission electron microscopy. Two bundles of about 100 dendritic processes are enclosed by the amphidial sheath cell, as well as a group of four other dendritic processes. Two amphidial duct cells are present on each side of the head, but without containing dendritic processes. However, the ultrastructural description of the amphids is incomplete.

Key words: amphid, head, lip region, marine, morphology, nematode, Thoracostomopsidae, scanning electron microscopy, transmission electron microscopy, ultrastructure.

The Enoplolaiminae, to which *Okranema eileenae* Greenslade and Nicholas, 1991 belongs, are common predatory nematodes on some sandy beaches in Australia (Greenslade and Nicholas, 1991; Nicholas and Hodda, 1999). They possess a spacious buccal cavity partially enclosed by three large lips and bearing prominent teeth. Inglis (1964) described the structure of the head of Enoplida, and in particular detail that of the Enoplidae, from light microscopy. The Enoplolaiminae were included within the Enoplidae by Inglis, but this subfamily has subsequently been placed in the Thoracostomopsidae by Lorenzen (1981).

As described by Inglis, the enoplolaimid head comprises a cephalic capsule in which the external cuticle is differentiated from the rest of the body cuticle. The pharyngeal musculature attaches to the external body wall over a broad band at the posterior edge of the cephalic capsule (Inglis uses ''oesophagus'' for what is more correctly termed the pharynx). The anterior limit of this band is marked by a thickening of the cuticle, termed the cephalic ring by Inglis, although the structure forms three connected arches rather than a ring and is so described in this paper. Each arch reaches its apex at the center of a lip and dips down to join the adjacent arches just below the deepest extremity of the clefts separating the lips. Anterior to the cephalic arch, the cephalic region forms three deeply incised lips surmounted by cuticular liplets. Inglis distinguishes a buccal cavity anterior to the cephalic ring (arch) from an onchial cavity enclosed by pharyngeal musculature. In this paper the term ''buccal cavity'' is used for both parts of the expanded anterior end of the alimentary canal with a triangular cross section. Posterior to the buccal cavity, the alimentary canal becomes narrower with a triradiate cross section. In describing the ultrastructure of the cuticle, the terminology of Bird and Bird (1991) is used.

Within the tissues of each lip lies a mandibular plate of complex shape from which, at its anterior extremity, two denticles protrude into the buccal cavity. Farther posterior in the buccal cavity, where it is backed by pharyngeal muscle, three more teeth protrude into the buccal cavity. The correct name for these teeth is questionable. The term onchium—plural onchia—is used here following Inglis (1964) and Lorenzen (1981), although Bird and Bird (1991) prefer odontium. Inglis (1964) distinguishes between a mandibular plate, backed by buccal tissue, and an onchial plate, backed by pharyngeal musculature. However, both are parts of a single cuticular plate operated as a single grasping structure by the anterior two tiers of pharyngeal muscles.

The head of *Rhabdodemania minima* (Rhabdodemaniidae) has been described from light and transmission electron microscopy (TEM) by Hope (1988). The relationships of the family Rhabdodemaniidae within the Enoplida are controversial (Lorenzen, 1981), but the cephalic region of *Rhabdodemania* shows interesting similarities and differences from *Okranema* at the ultrastructural level. *Rhabdodemania minima* has a deep tripartite buccal cavity bearing onchia and odontia but lacks the deeply incised lips and mandibular plates found in *Okranema*.

The external openings of the amphids, situated post labially in Adenophorea, are generally clearly visible at high magnification by light microscopy (LM) and are important taxonomically. Their structure has been reviewed by Lorenzen (1981). The amphids have not pre-

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viously been described in Thoracostomopsidae, and their presence has been overlooked in almost all taxonomic descriptions of this family, although Warwick (1977) figures the external amphidial aperture in *Epacanthion mawsoni*. In the present work, the external appearance of the amphid aperture is described from scanning electron microscopy (SEM), and many observations on the internal structure of the amphids have been made by TEM. However, a complete description of their internal structure has not been achieved.

Descriptive terminology applied to the amphids in this paper follows that of Bird and Bird (1991) and Coomans and De Grisse (1981), although the differences between their structure in *Okranema* from that in other previously described nematodes makes it difficult to apply the terminology appropriately.

Material and Methods

Specimens of *Okranema eileenae* were collected from between the tide marks at Dolphin Beach, south of Moruya Heads in New South Wales, on the southeast coast of Australia. They were extracted from the sand by sedimentation and sieving in sea water and individually picked up and identified under the microscope prior to fixation.

Several specimens were fixed with 5% formalin in sea water for LM. These were subsequently washed in distilled water and transferred to 5% aqueous glycerol, which was allowed to evaporate at 40°C in an oven. They were then transferred to anhydrous glycerol and mounted on slides for microscopy.

The fixative used for specimens for TEM was comprised of 2.5% glutaraldehyde, 3.7% formalin, 0.1 M sodium cacodylate, 2 mM $MgCl_2$, 5 nM EGTA, and 0.14 M sucrose. For SEM, several males were post-fixed in 1% OsO_4 in the same buffer solution, minus the glutaraldehyde and formalin, for 30 minutes, washed in the solution without osmium, and then freeze-dried. They were mounted on metal stubs and coated with gold/palladium before examination by SEM. For TEM, several males, preserved in the above fixative, were washed in the same buffer solution, without fixatives. The specimens were cut in half and the head end was progressively dehydrated in graded ethanol solutions. From ethanol they were transferred in stages through 100% ethanol to propylene oxide and finally to Spurr epoxy resin (Spurr, 1969) in capsules. After hardening the resin, sections were cut with a diamond knife, transferred to slot grids on formvar film, and stained with uranyl acetate and Reynolds lead citrate (Reynolds, 1963) before TEM examination. Two males were sectioned transversely and two longitudinally.

The abbreviations used to label the photomicrographs are listed in Table 1.

Table 1. List of abbreviations used in the figures.

AA - amphid aperture
AD - amphidial duct
AG - amphidial gland
BL - base of inner labial seta
BM - body wall longitudinal muscles
CA - cephalic arch
CC - cephalic capsule
CL - cortical layer of cuticle
CR - cortical ribs
CS - cephalic seta
CV - cephalic ventricle
DN - denticle
DP - dendritic processes
ED - epidermis
GD - duct of amphidial gland
HD - hemidesmosomes
ICL - inner cortical layer
IL - inner labial seta
LL - liplet
ML - median layer of cuticle
MN - mandible
MV - multivillous body of amphid
MT - metaneme
OCL - outer cortical layer
OL - outer labial seta
ON - onchium
PB - basal laminar of pharynx
PC - pharyngeal cuticle
PG - duct of pharyngeal gland
PL - pharyngeal lumen
PM - pharyngeal muscle
SR4 - group of four amphid dendritic processes
SRB - sheath receptor bundle

Results

An external view of the head capsule by SEM (Fig. 1A) shows the smooth outer surface of the dorsal lip, demarcated from the annulated body cuticle by a circumferential groove. Four of the six outer labial setae (near the base of the cephalic capsule) and four of the inner labial setae (at the top of the lips) are evident. Only one of the four cephalic setae is clearly separable from the outer labial setae. A liplet arises from the top of each lip. In Figure 1B the mouth is wide open and the interior of the buccal cavity is visible by SEM. The three lips—one dorsal and two ventrolateral—separated by deep clefts, are evident. Viewed from within the mouth, two pointed denticles protrude into the buccal cavity from one lip, just below one of the liplets. An onchium protruding into the buccal cavity is visible at the center of this lip. Figure 1C, which looks deeper into the buccal cavity, shows the transition from the capacious triangular buccal cavity from the triradiate pharynx. Figure 1D shows the anterior body by LM.

Several specimens were examined by SEM, but the measurements given below are taken from one of the two male specimens shown in Figure 1 that happened to be favorably situated on the supporting stub, except for measurements of the labial setae, which were measured under LM (Fig. 1D). The cephalic capsule is 39

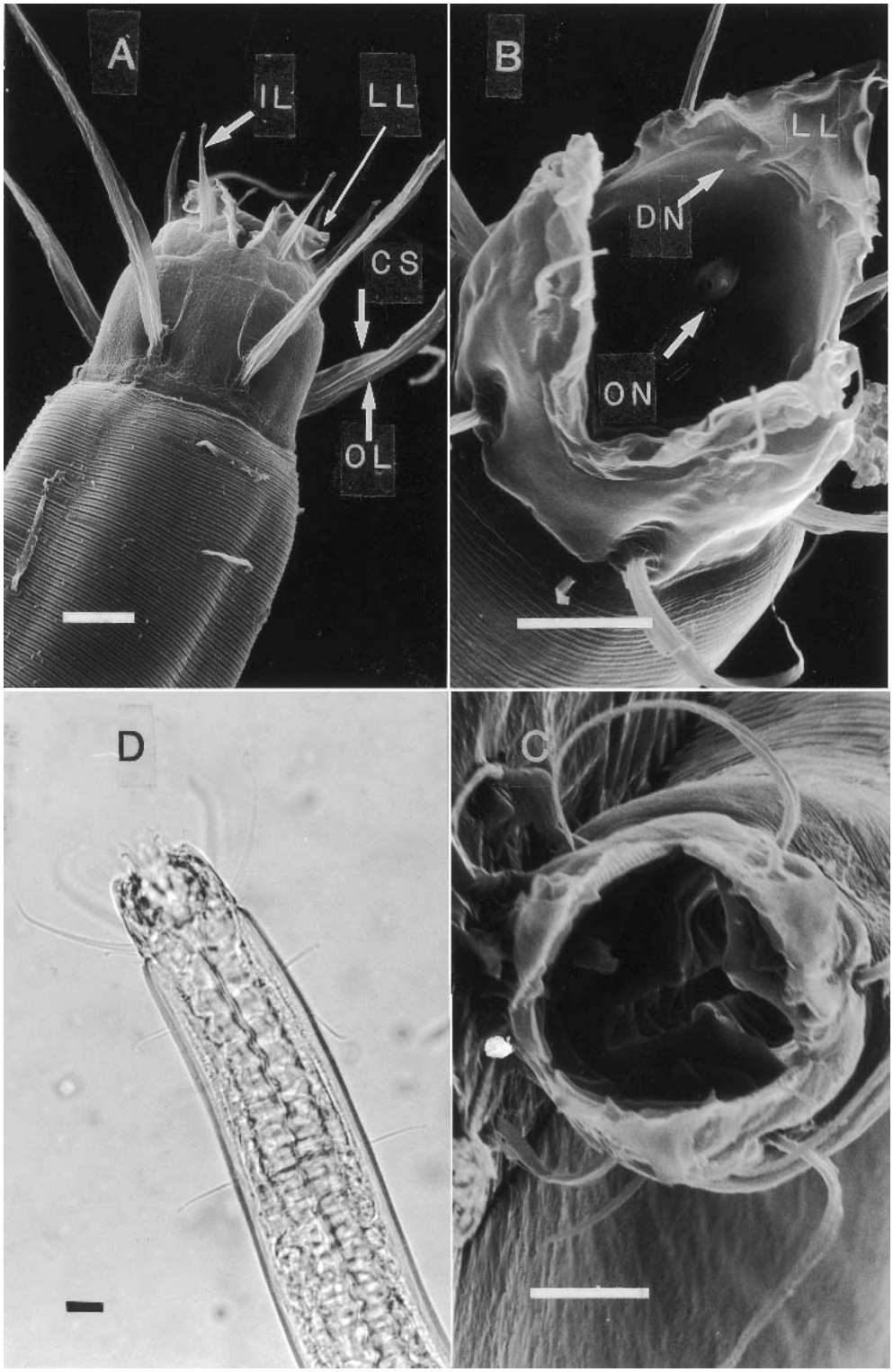

FIG. 1. The head and anterior body of *Okranema eileenae* by SEM and LM. A) The head from a dorsal perspective. B) The interior of one lip showing two denticles and one of the onchia viewed through the open mouth. C) The full depth of the buccal cavity and entrance to the pharynx viewed through the open mouth. D) The anterior of the body by LM. (Scale bar = 10 μm)

μm high and 31 μm wide. Annulations immediately posterior to the groove are about 0.9 μm wide but increase to a little over 1 μm farther posteriorly. Six outer labial setae (34 μm long) and four cephalic setae (23 μm long) are inserted anterior to this groove. Four cephalic setae are inserted adjacent and posterior to four of the outer labial setae and adhere to these setae. Six inner labial setae (16 μm long) are inserted at the front of the head at the base of six flexible liplets. The liplets are 9 μm high and appear to have flexible borders supported

by an internal rod. The buccal cavity is wide and about 30 μm deep. The margins of the three lips are deeply incised to 60% of the lip height. Within the tissues of each lip a rod forms a mandible with an onchium (tooth) at its base. Two denticles project into the buccal cavity from the anterior extremity of the mandible. The sharp tips of the denticles are 7.8 μm apart. The tip of the onchium is about 22 μm from the top of the lips and just anterior to the limit of the cleft between the lips.

The structure of the head, as seen by LM at x 1,000, is shown in Figure 2. Within the tissues surrounding the buccal cavity are supporting skeletal elements whose structure can be understood only from sections observed by TEM, which also reveals sensory neurons associated with the labial setae and the amphids.

Figure 3A is a transverse section through the three lips, which, at mid-capsule level, are well separated with thin cuticle and apparently flexible margins. At the center of two of the lips lies an electron-dense central mandibular plate. On each side of the plate is a set of up to 23 supporting cuticular ribs in transverse section. In one lip, cut slightly anterior to the other two, a pair of smaller skeletal elements supplement the diminished mandible. External to the mandible, several cuticular skeletal structures are evident in each lip. The cortical cuticle layer on the outer surface of the lip is electron-dense but much thinner on the inner surface and at the flexible margins. The electron-lucent bulk of the lip appears to be an extension of the cuticle median layer. In two lips a discrete body of amorphous tissue lies within this space—the cephalic ventricle, better seen in longitudinal section (Fig. 5A). Two groups of dendritic processes (terminal elements of sensory neurons) flank the mandibular plate.

Figure 3B is a transverse section through the base of one of the inner labial setae. An inner labial seta in transverse section is shown in Figure 6B. The external cortical layer of the cuticle encloses a diffuse median layer at the base of the labial seta. The basal layer closely surrounds two eccentrically placed sensory dendritic processes. In Figure 3C the solid base of one of the denticles, two of which project into the buccal cavity from each of the three mandibles, is present in trans-

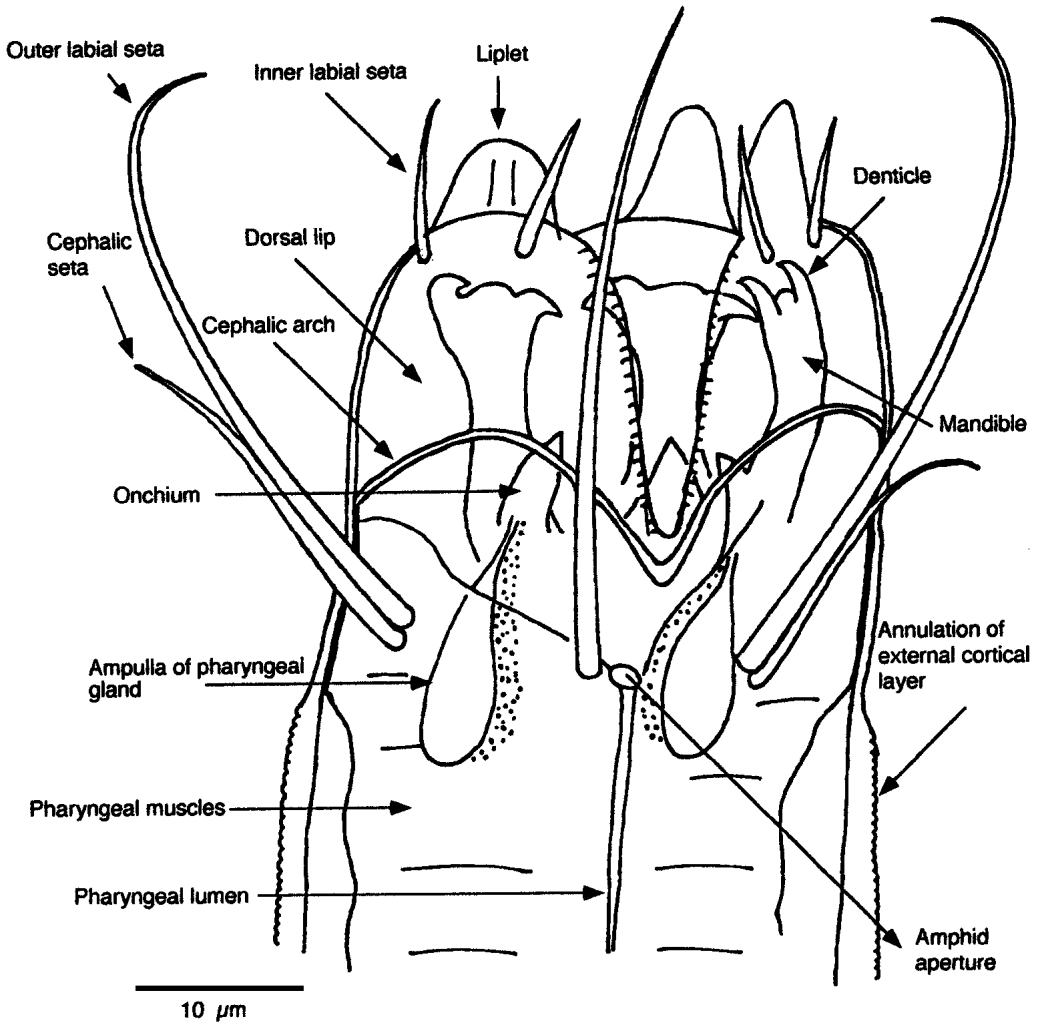

FIG. 2. The structure of the head of *Okranema eileenae* as seen by LM. (Scale bar = 10 μm)

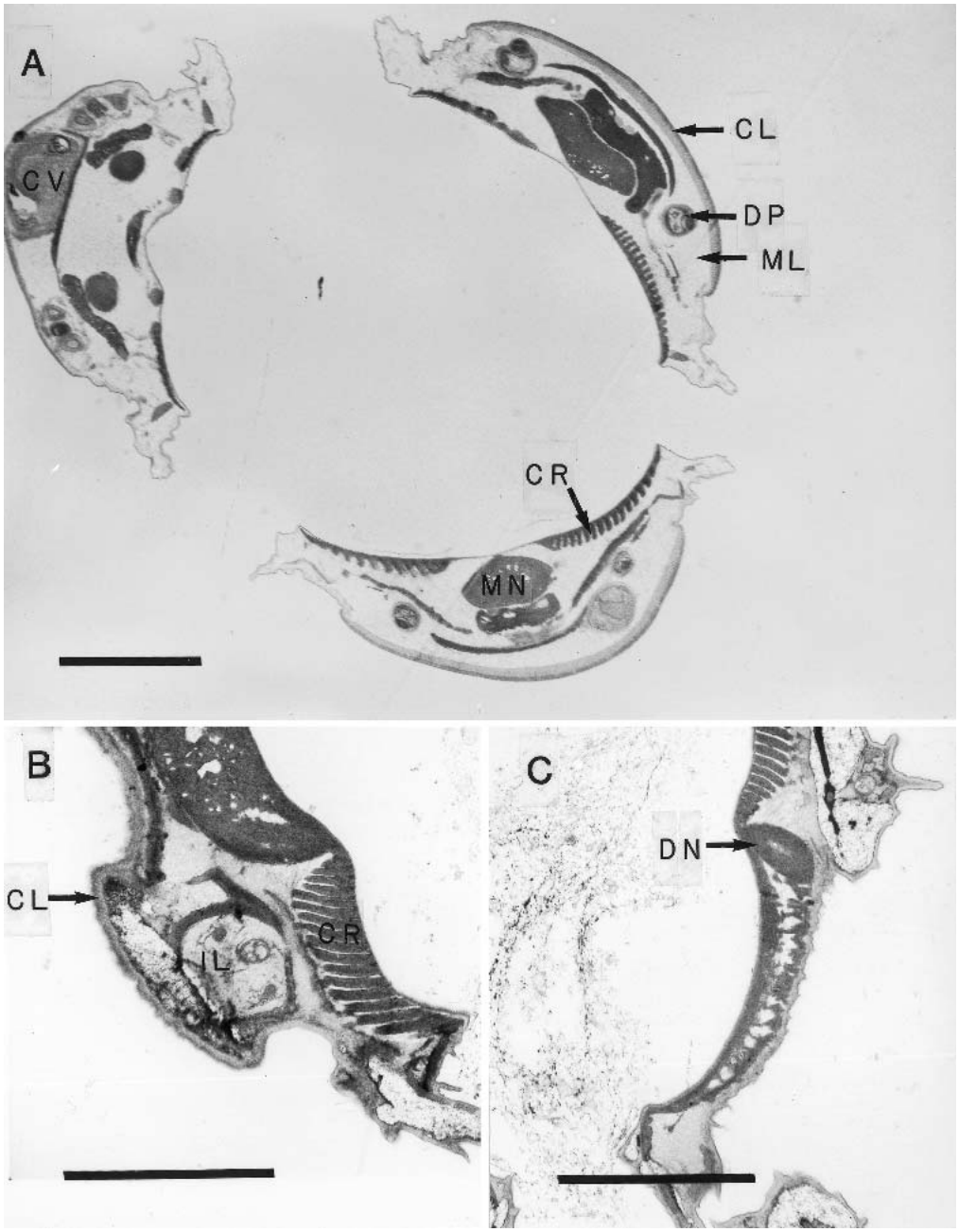

FIG. 3. Transverse sections through the anterior of the lips by TEM. A) Section through all three lips. B) Section through the base of one of the inner labial setae. C) Section through one of the denticles. (Scale bar = 5 μm)

verse section as well as at the base of an inner labial seta.

In Figure 4, the transverse section cuts the cephalic capsule at the base of the cleft between two of the lips. The tip of one of the three onchia is visible. The section is not quite transverse. One lip, not joined to the other two, shows cuticular ribs on either side of the electron-dense mandible plate. Ribs are present only near the borders of the other two lips. Behind the mandibular plate in one lip lies part of the electron-dense cuticular arch and tissue supporting one of the inner labial setae. In the other two lips, one sarcomere of the first tier of pharyngeal radial muscle cells fills almost all the space between the mandible and the electron-dense cuticle lining the buccal cavity. The pharyngeal muscle cells abut the cortical layer of the external cuticle, separated by only a very narrow epidermal layer, forming the cephalic capsule. Hemidesmosomes, not visible at this magnification, bind the muscle to the epidermis and the epidermis to the basal layer of the cuticle.

A longitudinal section (Fig. 5A) through the buccal cavity cuts through two of the onchia. The section does not cut through the lip at its apex. The core of the onchia holds the duct of a pharyngeal gland and cytoplasmic tissue. The duct and cytoplasmic tissue, containing endoplasmic reticulum, are more clearly evi-

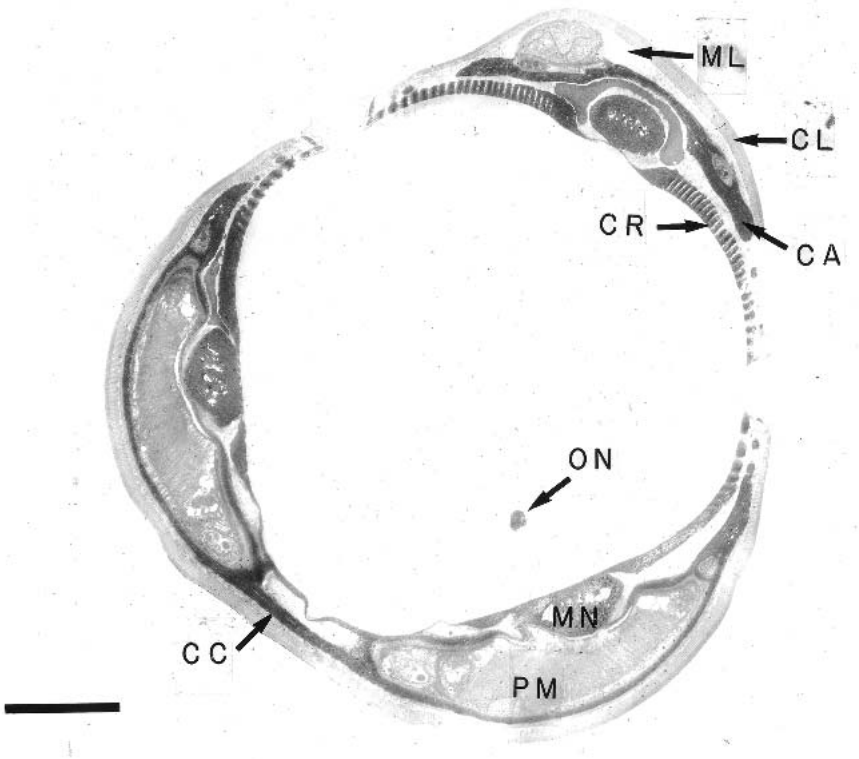

FIG. 4. Transverse section at the base of the lips. One lip sectioned anterior to the junction with the other two lips; the other two sectioned just posterior to their junction. (Scale bar = 5 μm)

dent in the right-hand onchium and in two transverse sections (Figure 5B,C). Light microscopy shows the duct arises from the ampulla of a pharyngeal gland (Fig. 2). The left-hand side of the section shows much more of the capsule than the right. The lower parts of the onchia lie within the first and second tier of pharyngeal muscle cells, and their electron-dense cuticle is continuous with the less-dense buccal cuticle. The upper parts of the onchia extend well beyond the pharyngeal muscles protruding into the buccal cavity.

A thin, dense continuation of the onchial cuticle lines the anterior parts of the buccal cuticle. Behind this cuticle, anterior to the left-hand onchium, lie eight cuticular ribs in longitudinal section. Anterior to the onchium and enclosing the ribs is a circumscribed area of amorphous material of moderate electron density, corresponding to the cephalic ventricle described by LM. A column of cytoplasmic tissue forms the base of an inner labial seta. Exterior to the ventricle, the median layer of the body cuticle—of low electron-density granular material—expands to form the profile of the lip. An electron-lucid external cuticle layer and thin epicuticle—the latter invisible at this magnification—form the outer surface of the head.

The anterior pharyngeal muscle sarcomeres are closely applied to the external body cuticle, separated by a thin sheet of epidermis, forming the cephalic capsule. Hemidesmosomes bind the muscle cells to the epidermis and the epidermis to the basal layer (Fig. 6E). In this region the outer cortical, medial, and basal layers of the cuticle are of similar thickness. At this magnification the epicuticle cannot be resolved. Level with the mid-point of the onchia, the epidermis and cuticle basal layer thicken to form a section of the cephalic arch. A dense cuticular bar joins the cephalic arch to the onchium, forming the anterior border of the pharyngeal muscles.

The principal external aperture of the amphid is shown by SEM in Figure 6A. It lies close to the posterior edge of the cephalic capsule and between the insertion of an outer labial seta and a short additional seta. Its circumferentially elongated slit, 1.7 μm long, lies on an elliptical bump, 3 μm wide by 2 μm long, surrounded by a groove. Two small apertures beside the main aperture are present. A longitudinal section (Fig. 6C) passes through an amphidial aperture—probably one of the smaller additional apertures. The internal structure of the amphids is partially described by TEM in Figure 6C and Figures 7–9. In Figure 6C, the amphidial sheath cell extends anteriorly to the aperture, enclosing a bundle of numerous sheath receptors (dendritic processes) and a microvillous body. The electron-dense basal layer of the cuticle—the cephalic capsule—extends posteriorly as far as the anterior edge of the outer labial seta and the amphid cell, but loses its density thereafter.

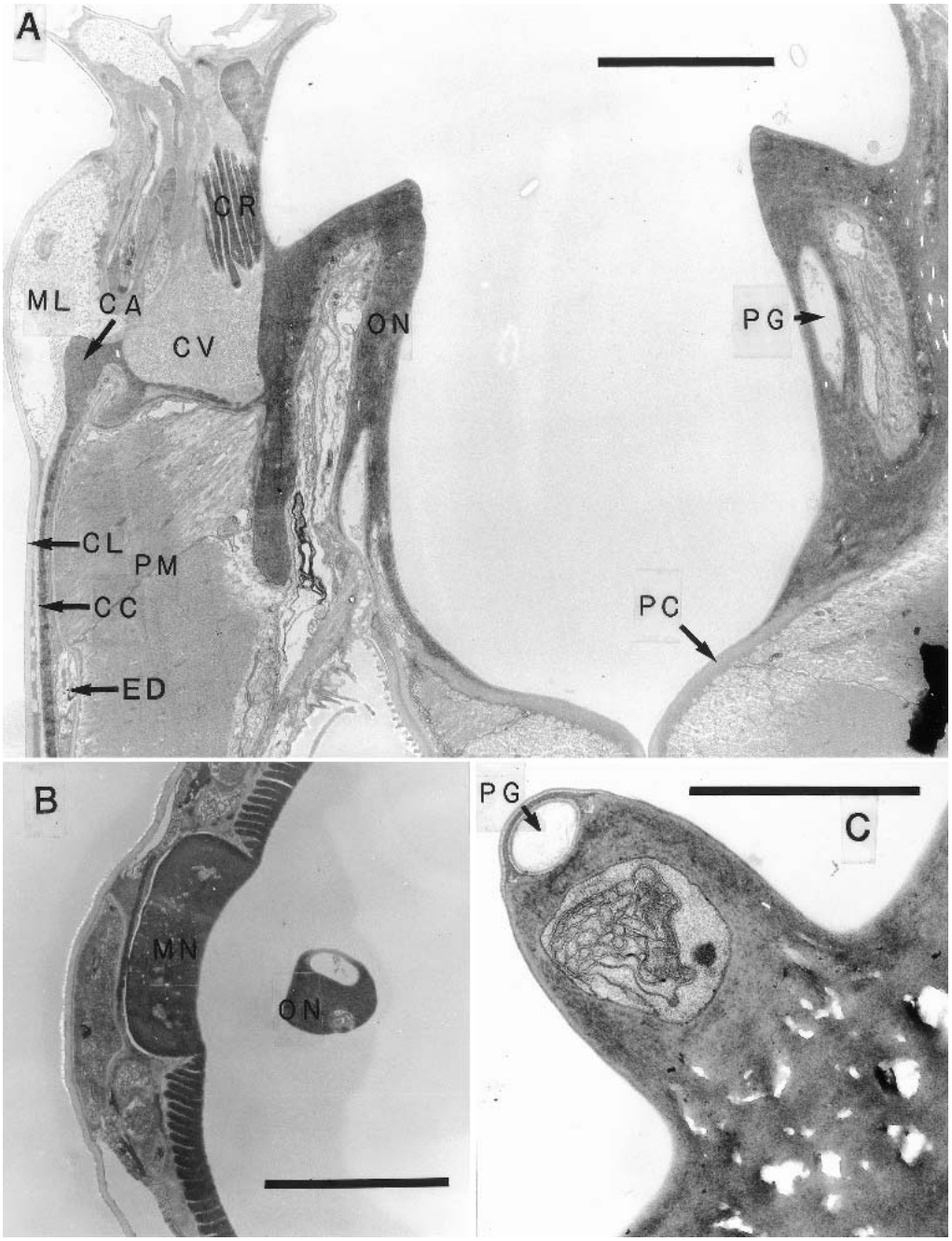

FIG. 5. Sections through the onchia. A) Longitudinal section passing through two of the three onchia. B) Transverse section near tip of onchium. C) Transverse section through base of onchium. (Scale bar = 5 μm)

The outer labial seta and the cephalic seta (Fig. 6C, D) each contain two dendritic processes. Other details are not clearly resolved in either of the sections, but there appear to be some muscle filaments and a denser supporting material. The inner labial setae also contain two dendritic processes Fig. 6B. In the pharyngeal region (Fig. 6E) the dendritic processes of the two inner labial setae from each lip run together in a single cytoplasmic extension. Each has a ring of nine microtubules, with each tubule connected by a bar to nine peripheral microtubules.

A slightly oblique transverse section through the base of the buccal cavity (Fig. 7A) passes through, on one side of the head, the insertion of a lateral outer labial seta and the posterior part of the cephalic capsule. On the other side it cuts through the head just posterior to the insertion of the opposite outer labial seta and the cephalic capsule. At this level it cuts through the amphidial sheath cell on this side of the head but misses the sheath cell on the other side. The sheath cell encloses two bundles of sheath receptors.

Figure 7B,C includes photomicrographs of opposite sides of the same section through the pharyngeal region posterior to the buccal cavity where the pharynx

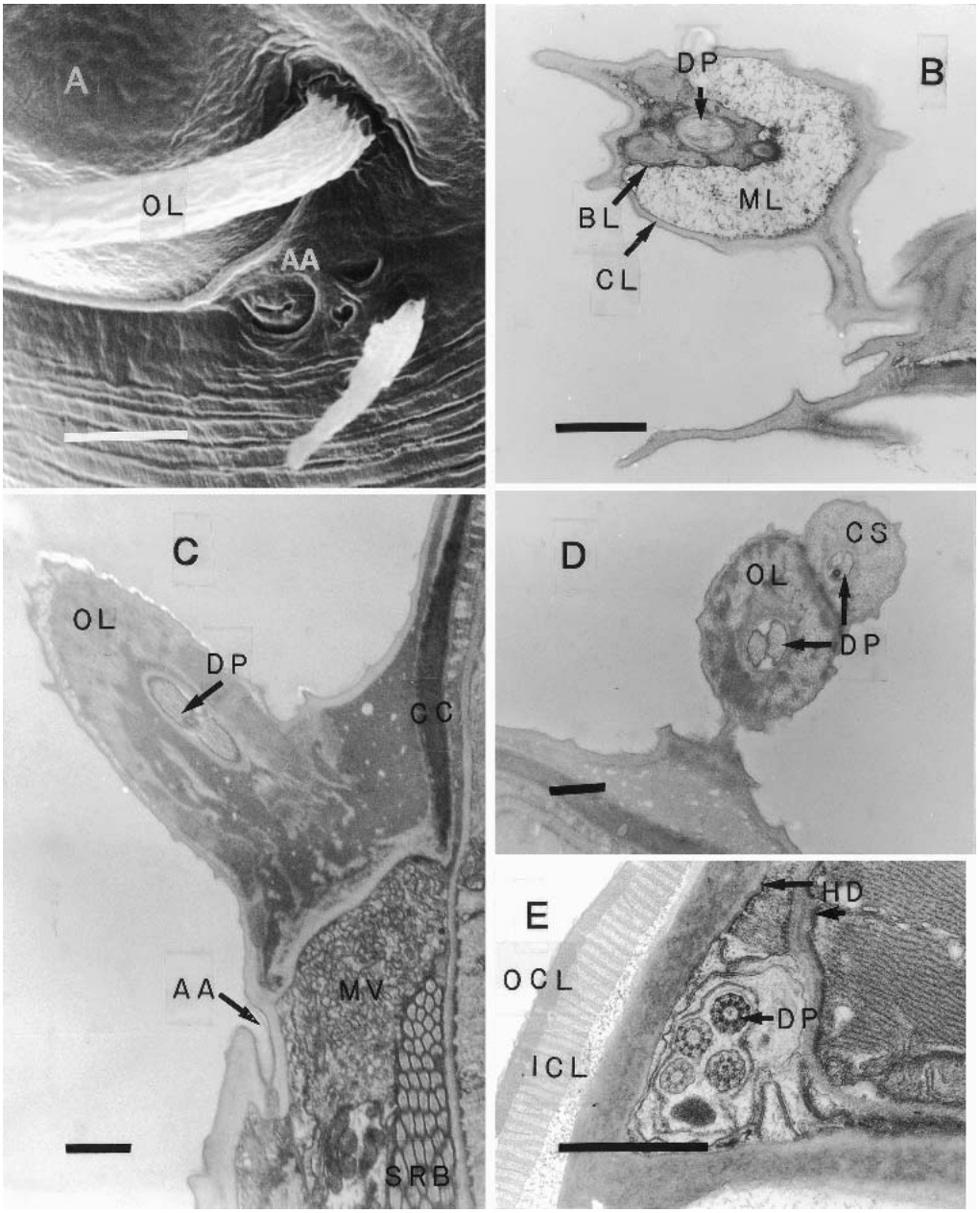

FIG. 6. A) External amphidial apertures (SEM). B) Transverse section through inner labial seta. C) Longitudinal section through outer labial seta and anterior extent of amphid. D) Transverse section through juxtaposed outer labial and cephalic setae. E) Transverse section through dendritic processes of two inner labial setae just anterior to cephalic arch. (Scale bars: *A* = 5 μm; B-E = 1 μm)

has a triradiate lumen. The photomicrographs show the amphidial sheath cells on opposite sides of the body. At this level, only a single bundle of sheath receptors is enclosed by the sheath cell. Other sections, at a more anterior level, show two adjacent bundles of sheath receptors (Fig. 7A). The sheath cells contain numerous mitochondria (Fig. 7C) and microvillous bodies (Figs. 6C, 9). A large gland cell is separated from the sheath cell by a bulge in the pharynx (Fig. 7B,C).

At higher magnification (Fig. 8A) the sheath cell contains a compact group of four dendritic processes in addition to the sheath receptor bundle of dendritic processes. Figure 8B,C shows, respectively, the bundle and the group of four dendritic processes at still higher magnification. The bundle has up to at least 87 dendritic processes, each containing between five and nine microtubules. The disposition of microtubules in the group of four differs. Two contain nine microtubule doublets a third 20 doublets in an outer ring, and 17 inside the ring; and in the fourth, the two rings of microtubule doublets are less regularly arranged.

Associated with the sheath cell in the pharyngeal region are three amphidial gland cells. Figure 9 shows two cells containing a cuticle-lined duct into which empty vesicles discharge. The third cell contains empty vesicles and numerous mitochondria. The three cells

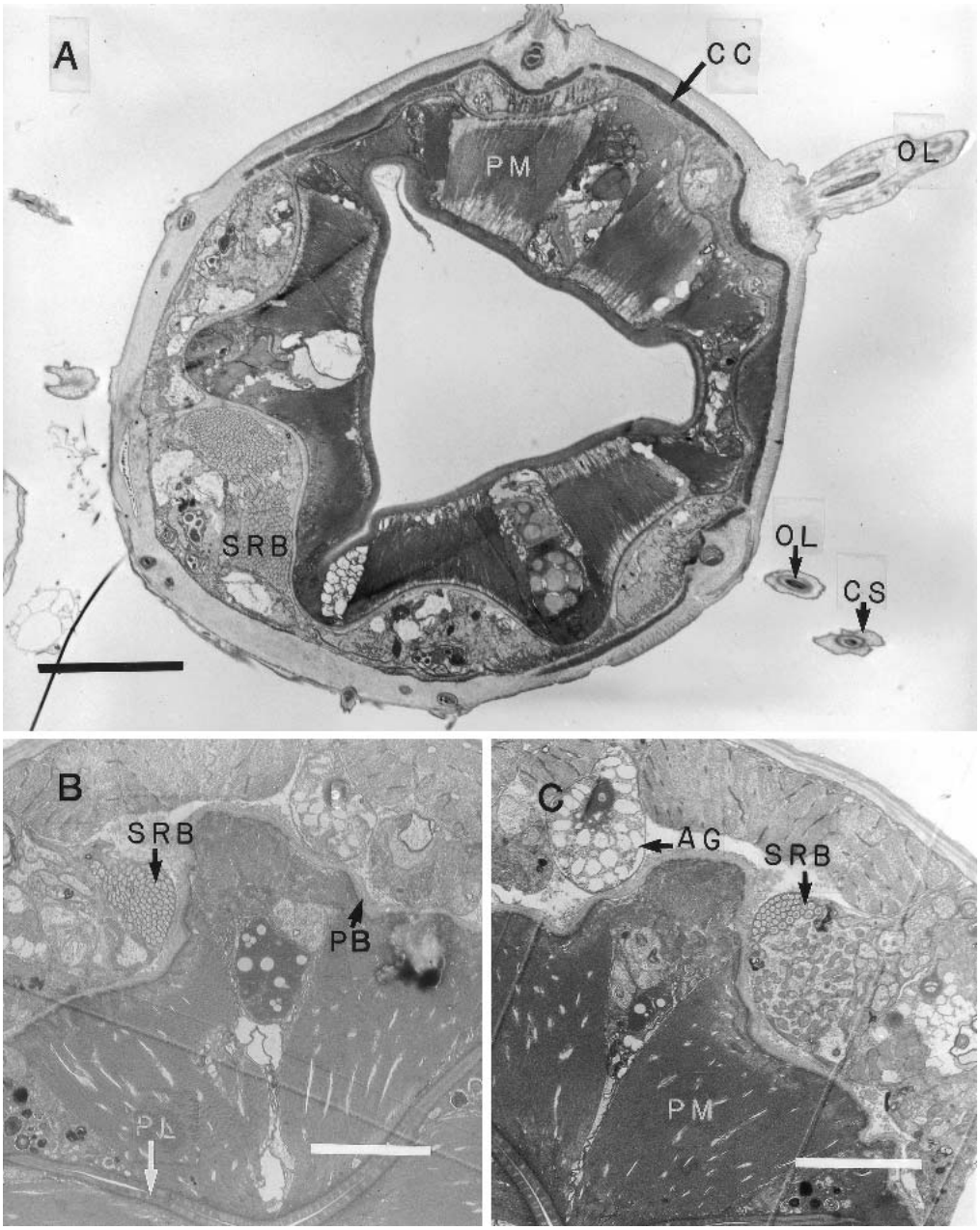

FIG. 7. Transverse sections through the amphids at the base of the buccal cavity. A) Slightly oblique transverse section through amphid receptor bundles on one side of head, posterior to cephalic capsule, and the base of cephalic capsule on the other side, anterior to the receptor bundles. B, C) Two parts of a single transverse section through the anterior pharyngeal region comparing the structure of the amphids on the two sides of the body. (Scale bar = 5 μm)

abut the sheath cell, which has a bundle of sheath receptors. The three gland cells, only two of which possess ducts, can be traced forward in a series of sections as far as the amphidial aperture, but any opening to the aperture, if indeed it occurs, has not been observed—nor have the posterior origins of the gland cells been observed.

DISCUSSION

Characteristic of the Enoplolaiminae is an inflated cephalic region (Inglis, 1964). An expansion and splitting of the cephalic cuticle contributes to this inflation. In *O. eileenae,* the typical nematode four-layered body cuticle (Bird and Bird, 1991) splits at the level of the cephalic arch. The epicuticle and cortical layer form the surface contour of the head and are reflected at the mouth opening to form the inner lining of the buccal cavity as far as the cephalic arch, which separates the anterior buccal cavity from that part enclosed by pharyngeal musculature. The median layer, of low electron density, thickens to fill most of the volume of the anterior cephalic region including the liplets. The inner cortical layer, according to this interpretation, forms

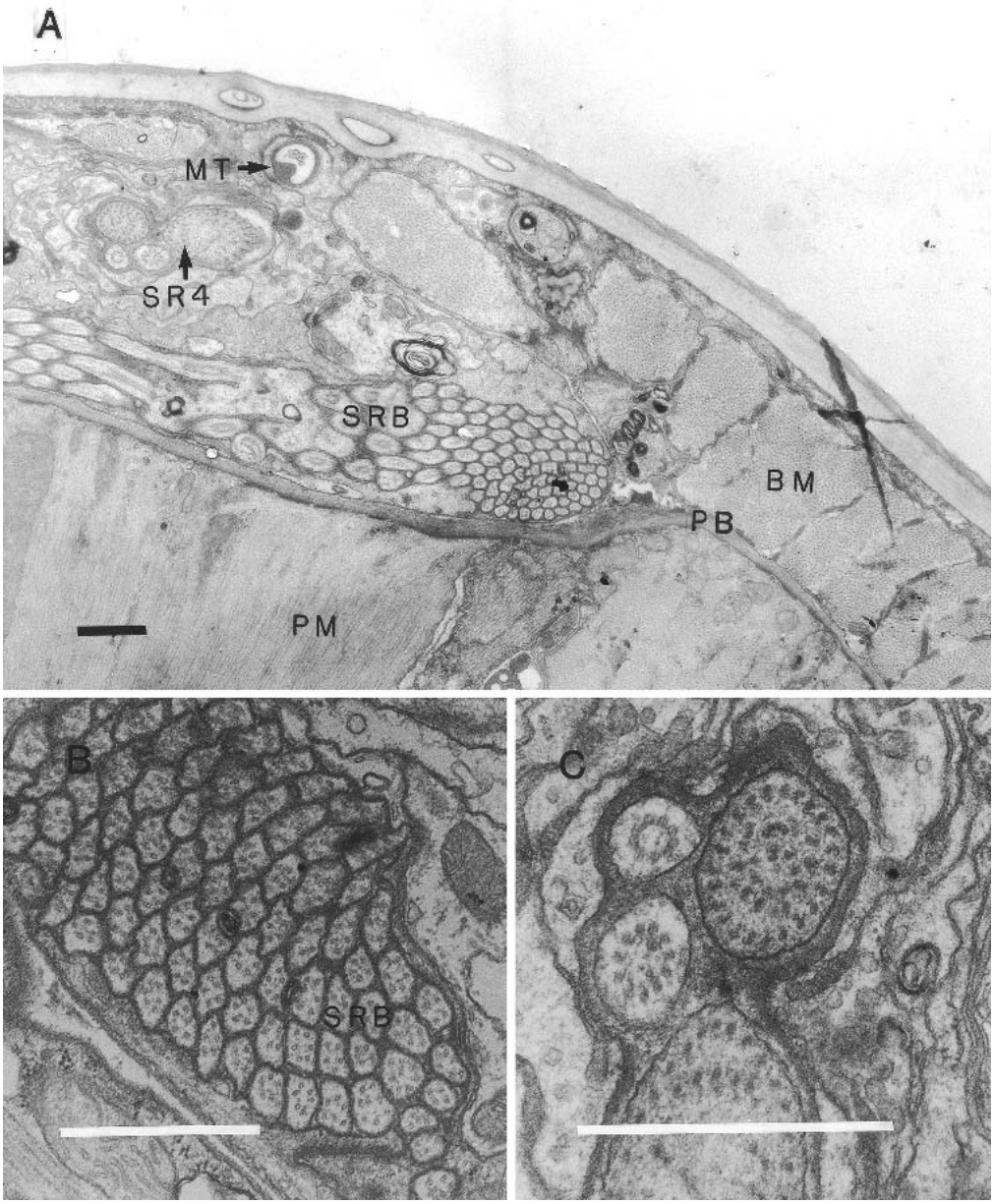

FIG. 8. Transverse sections through anterior pharyngeal region showing amphidial structure. A) Amphid receptor bundle and group of four dendritic processes. B) Amphid receptor bundle at higher magnification. C) Group of four amphid dendritic processes at higher magnification. (Scale bar = 1 μm)

the cuticular arch and the lining of the anterior buccal cavity. It forms the electron-dense skeletal elements such as the mandibular arms, denticles, and supporting ribs. This is consistent with Inglis's (1964) interpretation that the mesocuticle—using Maggenti's (1979) terminology—forms much of the volume of the cephalic region and the liplets, but Inglis did not believe that the endocuticle contributed to this region. He considered the cuticular reinforced lining of the anterior buccal cavity to be a thicker extension of the pharyngeal cuticle. In *Rhabdodemania minima,* Hope (1988) described the endocuticle of the outer cephalic cuticle to turn in at the mouth to intrude beneath the buccal cuticle. Hope believed that the fluid-filled ventricle described by Inglis is a mistaken interpretation of hypodermal (= epidermal) tissue anterior to the cephalic ring. In *Okranema* there is no epiderminal tissue anterior to the cephalic arch. The non-cytoplasmic material in the position of the cephalic ventricle may be fluid or a low-density gel prior to fixation. A thin sheet of epidermal tissue lies between the pharyngeal muscles and the body cuticle posterior to the cephalic arch.

The onchia are extensions of the pharyngeal cuticle and contain the ducts of pharyngeal glands. The pharyngeal muscle cells are, in fact, myoepithelial cells that secrete the buccal cuticle (Bird and Bird, 1991). An

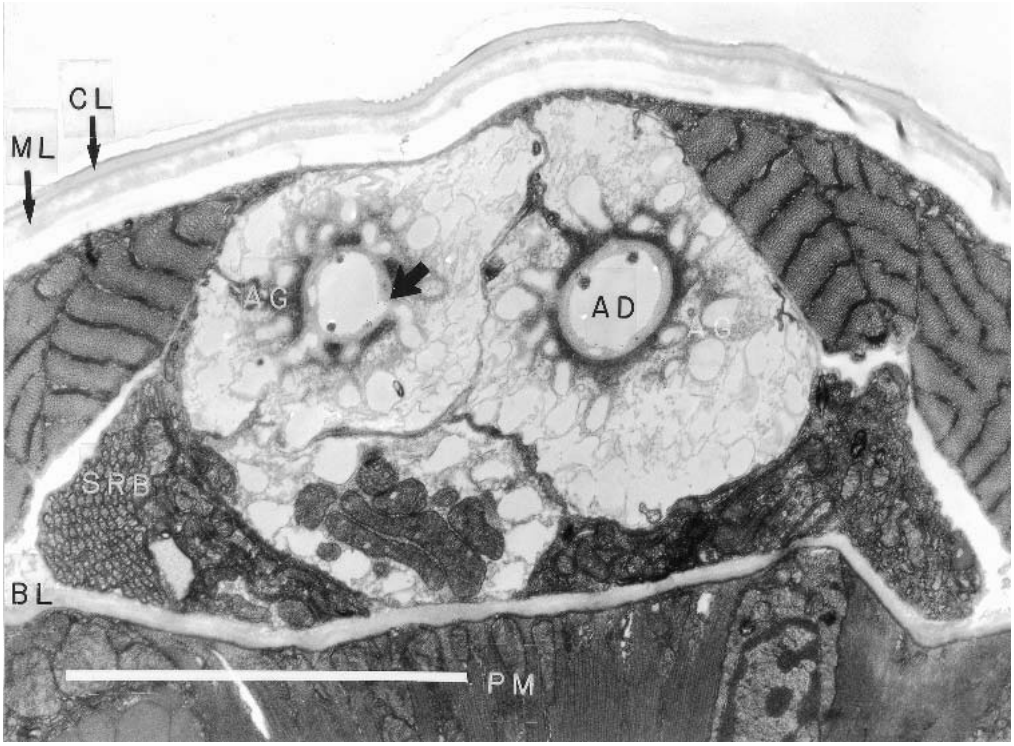

FIG. 9. Transverse section through amphidial gland cells and ducts at level of anterior end of pharynx. Arrow head marks point where vesicle opens into duct. (Scale bar = 5 μm)

alternative interpretation of the cuticular skeleton anterior to the onchia and cephalic arch is that the whole mandibular plate is a product of pharyngeal cells, while the inflated cephalic capsule, with an expanded low-density median layer, is a product of epidermal cells posterior to the cephalic arch. The cuticular arch would be the inner cortical layer of the cuticle. Following this interpretation the whole mandible, the onchia, and the supporting ribs may be the product of pharyngeal cells. In nematodes the external body cuticle and the pharyngeal cuticle are shed at each moult. The odontostyle in Dorylaimida (Enoplea) is developed prior to moulting within pharyngeal tissue and subsequently moved forward to lie in the buccal cavity (Grootaert and Coomans, 1980). Only a study of the moulting process can reveal which tissues secrete the cuticular skeleton of the head. *Okranema* in the process of moulting has not been found in collections made at all times of the year over 2 years (Nicholas and Hodda, 1999).

The external aperture of the amphids has been described for the first time in any species of Thoracostomopsidae. The ultrastructure of the amphids in many nematodes—the majority described belonging to the Secernentea—has been reviewed by Coomans and De Grisse (1981) and Bird and Bird (1991). The basic structure can be viewed as variations of that described in *C. elegans* (Ward et al., 1975). The structure of the amphids in the marine nematode *Ceramonema carinatum* (Chromadoria) was also interpreted by Stewart and Nicholas (1994) as a variation of that of *C. elegans*. Their ultrastructure in *Okranema* is not so easily interpreted as a variation of that form. Sheath receptors enclosed by the amphidial sheath cell may be equivalent to the sheath receptors in *C. elegans* but much more numerous. Numbers of sheath receptors vary considerably among different nematodes, and in some species may ramify and subdivide, as in *C. elegans*. Three gland cells are associated with the amphid sheath cell—two with cuticular ducts—but no duct receptors have been observed. The relationships between the ducts and the external amphid apertures, and with the sheath cell, are unknown. Clearly, much more work must be done before there is a satisfactory description of the amphids in Enoplia.

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