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Ultrastructure of the Feeding Apparatus of *Rhabdodemania minima* Chitwood, 1936 (Enoplida: Rhabdodemaniidae)

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Abstract: The feeding apparatus of the marine nematode *Rhabdodemania minima* Chitwood, 1936 has been examined with light and transmission electron microscopy. The buccal capsule consists of a posterior region with smooth walls bearing three sets of three minute denticles at its posterior end and three large onchia in its mid region; a middle region with grooved walls; and an anterior region with costae and six odontia. The anterior and middle portions of the buccal capsule are enveloped by the cephalic cuticle, whereas the posterior region, which is set off from the middle region by a buccal seam, is partially enveloped by the anterior end of the esophagus. Two subventral esophageal glands open into the lumen of the esophagus. Secretions of each of three paraesophageal glands are conveyed through a duct in each of the three corresponding corners of the buccal wall to an opening between labia. A pair of wing-like thickenings, termed pterons, embraces the duct of each paraesophageal gland in the posterior and middle regions of the buccal capsule. A model of how the buccal capsule operates is proposed and tested. Morphological and functional aspects of the buccal apparatus and cephalic cuticle are compared with those of other taxa of the Enoplida, and their phylogenetic implications are discussed.

Key words: buccal capsule, cephalic cuticle, comparative morphology, esophagus, feeding apparatus, functional morphology, gland, marine nematode, morphology, *Rhabdodemania minima,* ultrastructure.

The genus *Rhabdodemania* Baylis and Daubney, 1926, the only valid genus in the family Rhabdodemaniidae, presently includes 26 nominal species. Members of the genus are readily identified by a unique combination of characters among which are the following: a relatively large, goblet-shaped buccal capsule that with light microscopy appears to be divided by at least one transverse buccal seam (two or more by some interpretations); three or rarely two teeth (onchia) in the posterior region of the buccal capsule; and, in the anterior region, a pair of odontia at each corner of the buccal capsule, as well as obliquely oriented striations on each of the three anterior walls. The term "odontium" is used here in reference to teeth in the anterior region of the buccal capsule. The term is used as a matter of convenience and does not necessarily imply homology.

Difficulties in interpreting these structures from whole mounts have prevented the recognition of possible homologies with comparable structures in other taxa. This has contributed to the problems of understanding the evolutionary relationships of *Rhabdodemania.* As a result, Rhabdodemaniidae has been allied with Leptosomatidae (5,10,27,28), Enoplidae (7,12, 15,22,31), Oncholaimidae (8,29), and Enchelidiidae (15). Enoplidae, as it is used in this case, precedes the revision of Lorenzen (19) and, therefore, includes Enoplinae and Enoplolaiminae. Of these proposed relationships, that between Rhabdodemaniidae and Enoplidae has been most frequently favored, and it has been supported by the assumption that the odontia of members of Rhabdodemaniidae are homologous with the jaws of members of Enoplidae (15,23,31).

This is in disagreement with Lorenzen (19), however, whose phylogenetic analyses concerning *Rhabdodemania* were largely based on structures other than those con-

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cerned with the head and buccal capsule. He removed Rhabdodemaniidae from Enoplina to the only other suborder of Enoplida, Tripyloidina, thus refuting the possibility of a close phylogenetic relationship between Rhabdodemaniidae on the one hand and Enoplidae and Enoplolaiminae on the other. Furthermore, he identified morphological similarities between members of Rhabdodemaniidae and members of Pandolaimidae (Tripyloidina) and suggested that a close phylogenetic relationship may exist between these two families.

Inglis (17) subsequently removed Rhabdodemaniidae from Tripyloidina and assigned it to a new suborder, Leptosomatina, along with Leptosomatidae, Oxystominidae, and Pandolaimidae. Although this action implies that the taxa assigned to Leptosomatina share one or more derived characters, none were identified.

In connection with a taxonomic study of the genus *Rhabdodemania*, a study, using light and transmission electron microscopy, of the head and feeding apparatus of *R. minima* was undertaken to provide morphological data that may clarify the evolutionary relationships of the genus, especially among members of Enoplina and Tripyloidina. Also, it was anticipated that this investigation would provide information concerning how the buccal capsule functions in the process of feeding.

Although there are no other ultrastructural studies of enoplids with which to compare the results of this investigation, it is possible to compare the results on a limited basis with previous studies in which only light microscopy was employed (14,15, 23,31). It is anticipated that this study will provide a basis for comparison in future ultrastructural investigations on enoplids.

MATERIALS AND METHODS

Specimens of *R. minima* used in this investigation include material previously collected, fixed, and embedded by Rieger and Ruppert (26) during an investigation on the mass embedding of meiofauna, as well as new material collected and processed specifically for this investigation. In both cases, specimens were obtained in November from muddy sand collected from the White Oak River at Swansboro, North Carolina, near its confluence with the Atlantic Ocean. Specimens were extracted from sediment in laboratories at the Institute of Marine Sciences, University of North Carolina, Morehead City, North Carolina.

Specimens for light microscopy were fixed in 4% formalin in sea water for 48 hours and processed into anhydrous glycerine for preparation of permanent, glycerine whole mounts. The slide numbers of these specimens are USNM catalog numbers 77053–77067.

Specimens for transmission electron microscopy were fixed for 3 hours at 4 C in 3.5% glutaraldehyde in 0.1 M Sorensen's Phosphate Buffer and 10% sucrose. They were postfixed for 1.5 hours at 4 C with 1% osmium tetroxide in 0.1 M phosphate buffer, dehydrated in ethanol, and embedded in Epon-Araldite. Sections (70–80 nm) were stained by the method of S. C. Chang (pers. comm.) with aqueous uranyl acetate at 56 C for 10 minutes and lead citrate at room temperature for 5 minutes. Sections were examined with a Zeiss EM9S-2 transmission electron microscope.

Light microscopic observations of whole specimens that had been fixed with the protractor muscles fully contracted were needed to test the model proposed in this study to explain how the buccal apparatus functions. Because the only available specimens of this species were those in which these muscles were relaxed or only partially contracted, it was necessary to make supplementary observations of the buccal capsule in specimens of another species in which the protractor muscles were fully contracted. The specimen used for this purpose are of an undescribed species of *Rhabdodemania* collected by A. C. Tarjan from east of Sea Horse Key and northwest of North Key, Florida. These specimens, two of which appear in Figures 10B, C, have buccal capsules that are essentially identical to those of *R. minima*. They are

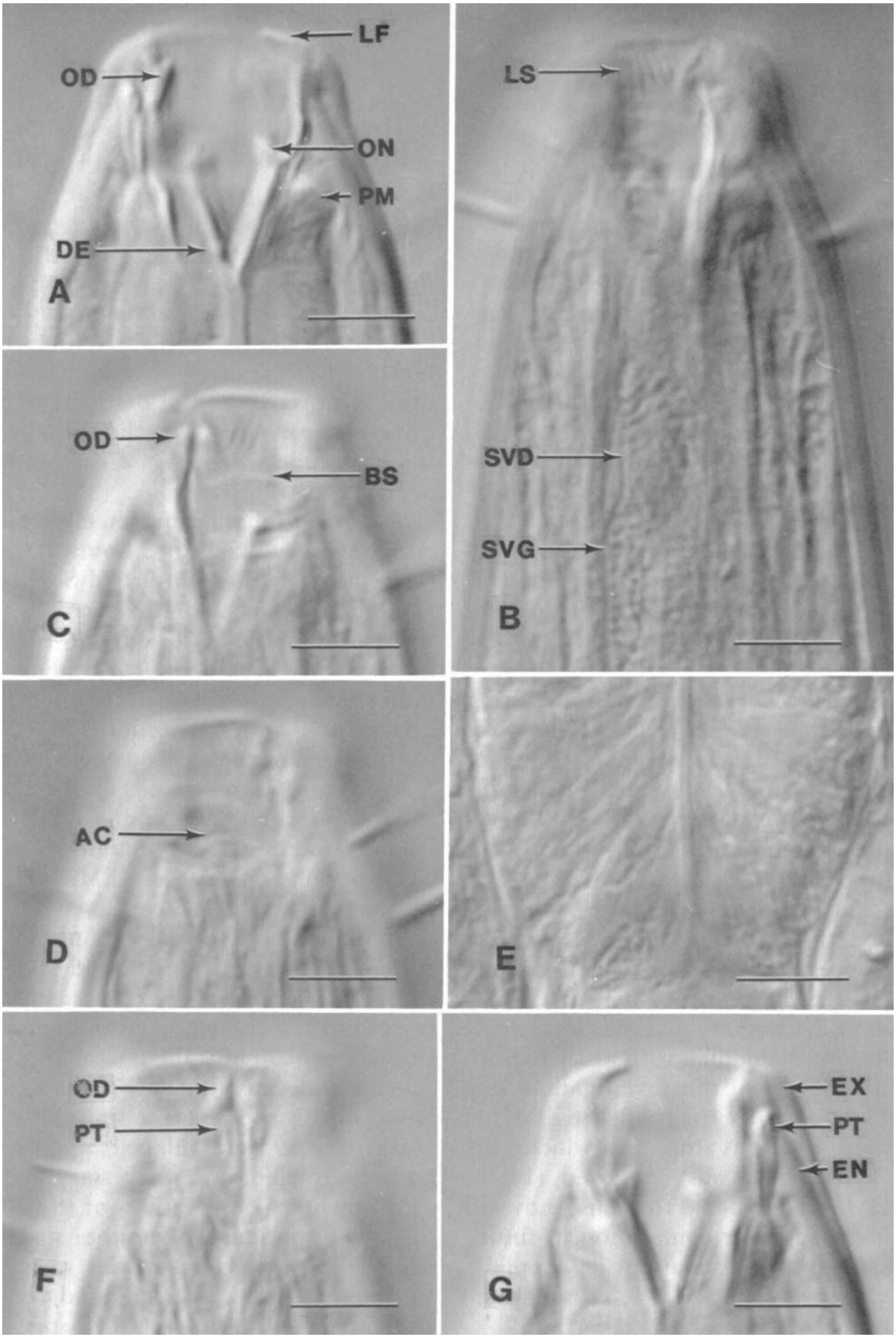

FIG. 1. *Rhabdodemania minima.* Photomicrographs of optical longitudinal sections. Bar = 5 μm. A–D, F, G) Buccal capsule with protractor muscles relaxed. E) Posterior end of esophagus with protractor muscles relaxed.

List of abbreviations for Figures 1–10: AC—Arch of exocuticle; **AE**—Anterior edge of endocuticle; **AR**—Anterior region of buccal capsule; **BG**—Groove in buccal wall; **BR**—Ridge in buccal wall; **BS**—Buccal seam; **BV**—Base of "V" formed by buccal ridges; **CO**—Costa; **DE**—Denticles; **EF**—Endocephalic fibers; **EN**—Endocuticle; **EP**—Epicuticle; **EX**—Exocuticle; **FZ**—Fibrous zone; **HD**—Hypodermis; **L**—Lumen of permanently mounted in anhydrous glycerine on microscope slides bearing USNM catalog numbers 77068–77096.

The range and, in parentheses, the mean and one standard deviation are given for all morphometric data.

RESULTS

Light microscopy

The esophagus is cylindrical, although slightly wider posteriorly. Its muscle fibers are radial, except in the region where the esophagus overlaps the buccal capsule (Fig. 1A) and at the posterior end of the esophagus (Fig. 1E), where the fibers are oblique to the longitudinal axis of the esophagus. At the anterior end of the esophagus the fibers extend posteriorly and mesad from their origin to their insertion on the cuticular lining of the lumen of the esophagus. At the posterior end the fibers extend anteriorly and mesad from their origin to their insertion on the cuticular lining. The subventral esophageal glands open into the lumen of the esophagus at ca. 1.6 head diameters from the anterior terminus of the head. No gland comparable to the subventral glands was detected in the dorsal sector.

The goblet-shaped buccal capsule tapers mostly posteriorly and slightly anteriorly where the labial flaps arch over and partially close the oral aperture (Fig. 1A). Approximately the posterior one-third of the buccal capsule is enveloped by the anterior muscles of the esophagus. In this region the dorsal and each subventral wall of the buccal capsule, all of which are heavily cuticularized, bear an onchium that projects into the lumen of the buccal capsule (Fig. 1A). There appear to be three minute, tooth-like projections (denticles) situated near the posterior end of the buccal capsule, one dorsal and one on each subventral wall (Fig. 1A). The transition between the cuticle of the buccal capsule and that lining the lumen of the esophagus is typically without demarcation.

The buccal cavity is divided transversely by a buccal seam situated slightly anterior to the esophageal tissue (Fig. 1C). Anterior to this buccal seam, oblique longitudinal striations occur on the dorsal and each subventral wall of the buccal capsule. Striae in each half of each wall are angled slightly toward the striae in the other half of the same wall (Fig. 1B, C). Thus, the striae converge toward the median longitudinal plane of each buccal wall.

An odontium is situated on each side of each inside corner of the buccal capsule slightly posterior to the labial flaps and in the general region of the longitudinal striations (Fig. 1A, C, F). A pair of wing-like structures (pterons) occur in the somatic cuticle at each outside corner of the buccal capsule, slightly posterior to the level of the odontia (Fig. 1F, G). That portion of the buccal capsule that extends anteriorly beyond the esophagus is enveloped by the cephalic cuticle (Fig. 1A, G), which consists of two visible layers, an endocuticle and an exocuticle (Fig. 1G).

Ultrastructure

Anterior esophagus and paraesophageal glands: The cuticular lining of the triradiate lumen of the esophagus is homogeneous and slightly thicker along the proximal third of each ray (Fig. 3A). Six radial muscle fibers appear in each transverse section of the esophagus, with two fibers in each of the three sectors. Each muscle fiber is one sarcomere in length, and each has its origin on the basal lamina of the esophagus and its insertion on the thickened, cuticular wall of a corresponding ray of the lumen. The distal portion of each ray is

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buccal capsule; **LF**—Labial flap; **LS**—Longitudinal buccal striae; **MC**—Marginal cell; **MR**—Middle region of buccal capsule; **MV**—Microvilli; **OD**—Odontium; **ON**—Onchium; **PD**—Duct of paraesophageal gland; **PG**—Paraesophageal gland; **PL**—Plasmalemma of paraesophageal gland; **PM**—Protractor muscle; **PR**—Posterior region of buccal capsule; **PT**—Pteron of paraesophageal gland duct; **SDG**—Subdorsal esophageal gland; **SVD**—Subventral esophageal gland duct; **SVG**—Subventral esophageal gland; **ZA**—Zonula adherens.

enveloped by marginal cells (Fig. 3A, B), whose filaments extend from the end of the ray to the external surface of the esophagus.

An esophageal gland extends anteriorly through the center of each subventral sector of the esophagus. Each gland opens into the lumen of the esophagus by way of a prominent cuticularized duct 17.6–21.9 (18.2 ± 1.4) μm from the anterior surface of the head (Figs. 2, 3A). The secretions of the glands, in at least one phase of their existence, are spheres 478–611 (559 ± 58) nm d with an electron-dense cortex and a fibrous interior (Fig. 3D). In the center of the dorsal sector, a gland comparable to the gland in each subventral sector was not observed. If such a gland is present, its opening into the lumen of the esophagus is posterior to the region sectioned in this investigation. Two subdorsal glands, one on the dorsal side of each subdorsal ray, taper anteriorly and end near the posterior end of the buccal capsule. The products of these glands are fine granular substances in membrane-bound spheres (Fig. 3A, B). An opening for these glands was not observed.

There is only one muscle fiber in each sector of the esophagus where the latter overlaps the posterior end of the buccal capsule. For the purposes of this investigation, the posterior limit of the buccal capsule is arbitrarily designated as the level of the posterior margin of the insertion of the anterior esophageal muscle cells. Each of these three muscle fibers, and to a lesser extent the next muscle fibers posterior to each, are obliquely oriented with their contractile filaments extending radially and anteriorly from the point of origin to the point of insertion (Figs. 2, 3C, 4A, B). The angle from the median longitudinal axis of the head to the filaments of the anterior fibers is 40–52 (44 ± 4) degrees. A zonula adherens occurs at the juncture between the anterior muscle fiber and the adjacent hypodermis (Fig. 2).

Three glands lie in the body cavity adjacent to the basal lamina of the esophagus, one paralleling each ray of the esophageal lumen (Figs. 3C, E–H, 4A). The distance to which these glands extend posteriorly is unknown. Anteriorly at about the level of the denticles in the posterior end of the buccal capsule, infoldings of the apical plasmalemma of each gland cell occur around a duct with a lightly stained wall (Fig. 3E–H). Farther anterior, where the esophagus overlaps the buccal capsule, each duct emerges from its respective gland cell, passes mesad between the lobes of esophageal muscle (Figs. 4A, 9), and continues anteriorly where its wall merges with the cuticle at a corner of the posterior buccal capsule (Figs. 4B, 9). Thus, products of the paraesophageal gland cells are conveyed through tubular channels in the cuticular wall of the posterior region of the buccal capsule.

Cephalic cuticle and hypodermis: The cephalic cuticle is the external cuticle that covers the head region. In the general area of the buccal capsule, the cephalic cuticle is comprised of three layers, which are identified by the terminology of Maggenti (20). A fourth layer, the mesocuticle, which is present in the cuticle covering the remainder of the body, is absent.

The most external layer is the epicuticle. This layer extends from the external surface of the head (Fig. 2) across the labial flaps and into the buccal cavity. It becomes the mesal layer of the cuticular buccal wall.

The next layer, the exocuticle, is composed of a fine-grained, homogeneous matrix in which are embedded fine fibers and possibly granules (Figs. 2, 5B, 6A, 7A, 9). The exocuticle is also the principal component of the labial flaps (Fig. 2). At the level of the posterior end of the buccal capsule, the exocuticle is 124–338 (238 ± 67) nm thick. It gradually becomes wider toward the anterior region of the buccal cavity, where it attains a maximum width of 1,651–2,534 (2,174 ± 282) nm. The exocuticle and underlying hypodermis, at 5.1–7.9 (6.9 ± 0.6) nm from the anterior end of the head, project posteriorly between the tissue of the esophagus and the cuticular lining of the buccal capsule (Fig. 2). This posterior extension of exocuticle

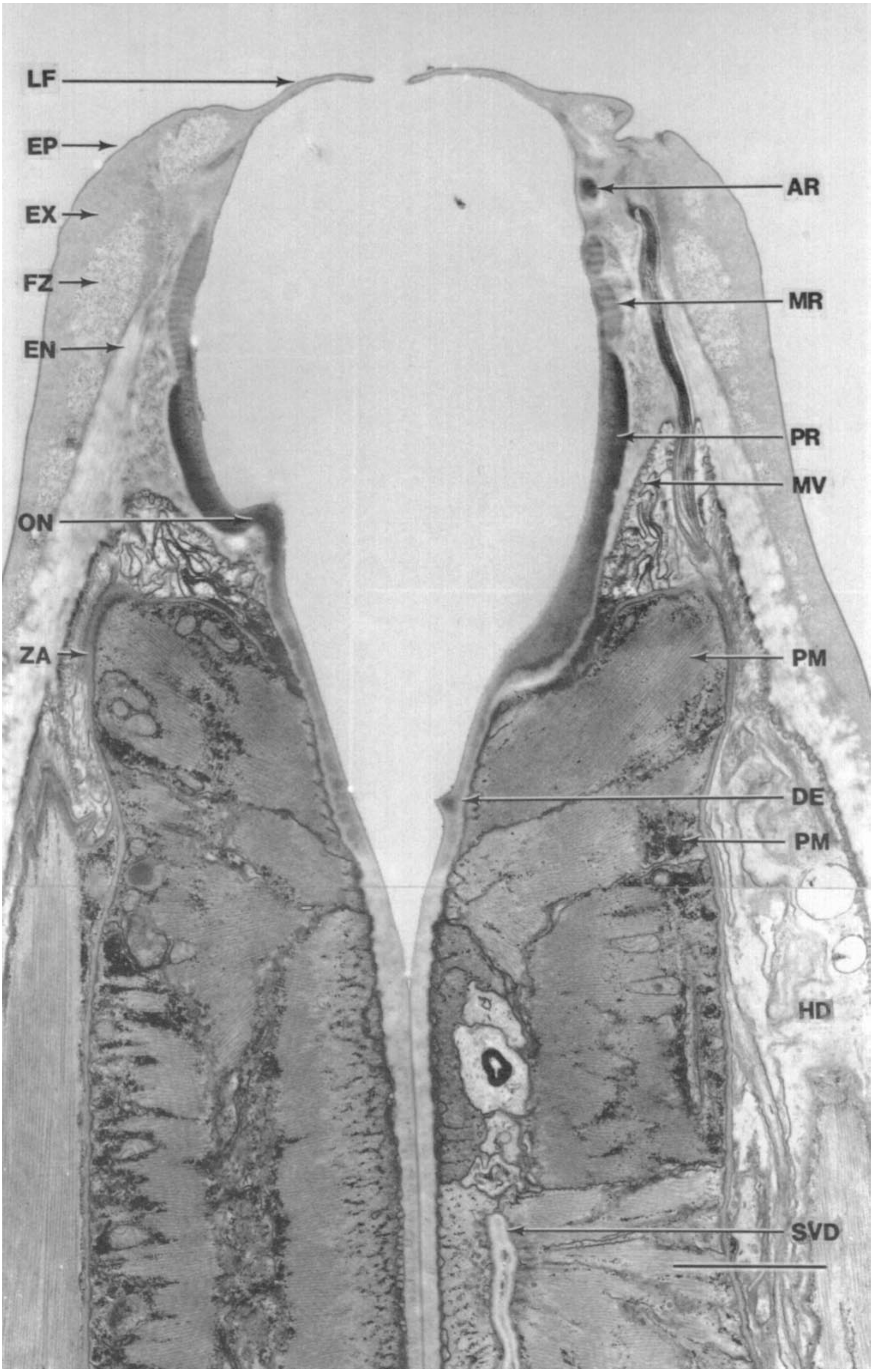

FIG. 2. *Rhabdodemania minima.* Transmission electron micrograph of a longitudinal section through base of dorsal onchium and right subventral esophageal gland duct. Bar = 2.5 μm. Refer to Figure 1 for abbreviations.

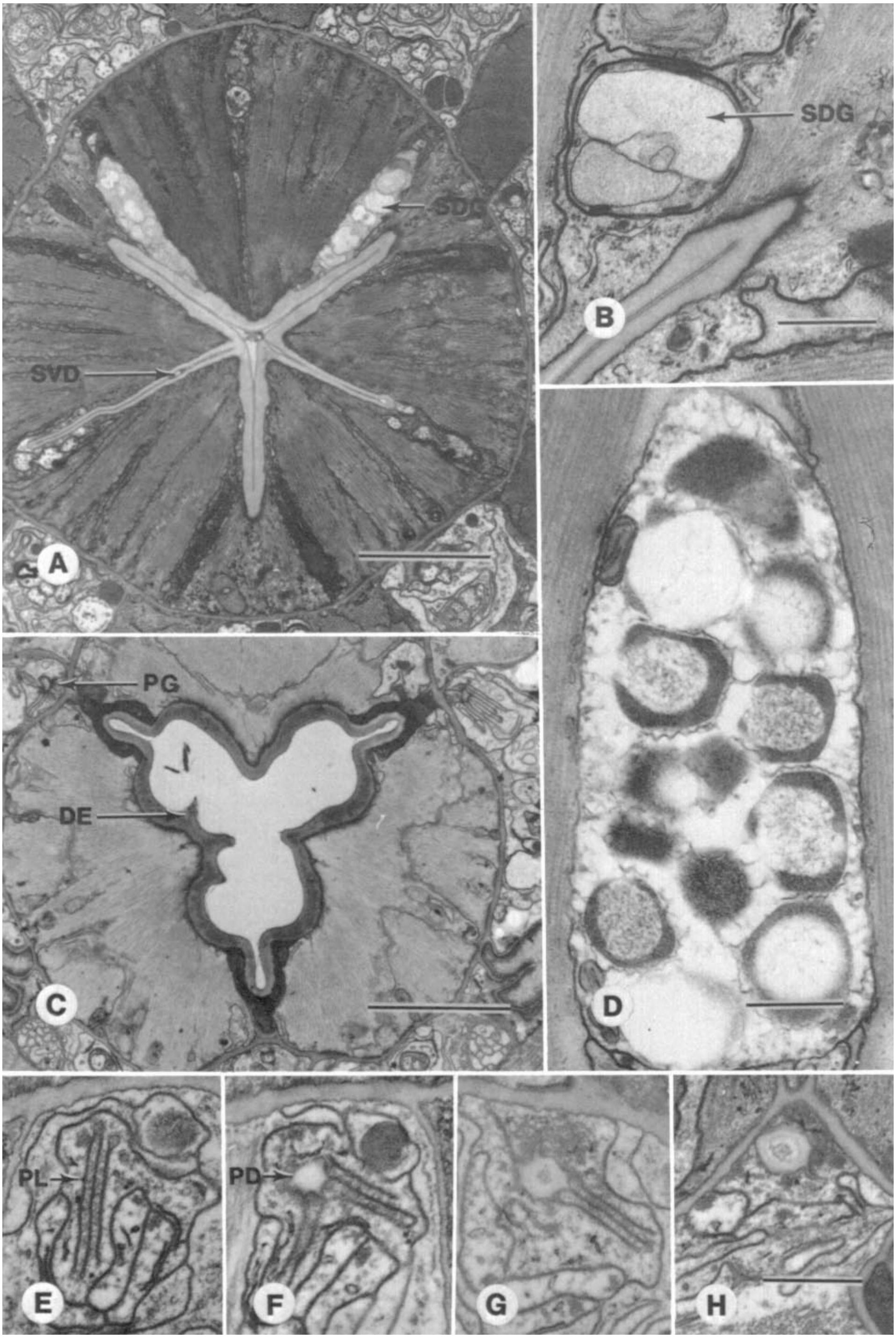

FIG. 3. *Rhabdodemania minima.* Transmission electron micrographs of transverse sections. Except for D, dorsal at top. A) Esophagus at level of subventral esophageal gland ducts. Bar = 2.5 μm. B) Dorsal ray of esophagus and subdorsal esophageal gland near anterior end. Bar = 0.5 μm. C) Posterior end of buccal capsule at level of denticles. Only one set of three denticles is in the plane of section. Bar = 2.5 μm. D) Subventral esophageal gland near its anterior end. Bar = 0.5 μm. E–H) Paraesophageal gland in series of posterior to anterior sections through infoldings of plasmalemma and cuticularized duct. Bar = 0.5 μm. Refer to Figure 1 for abbreviations.

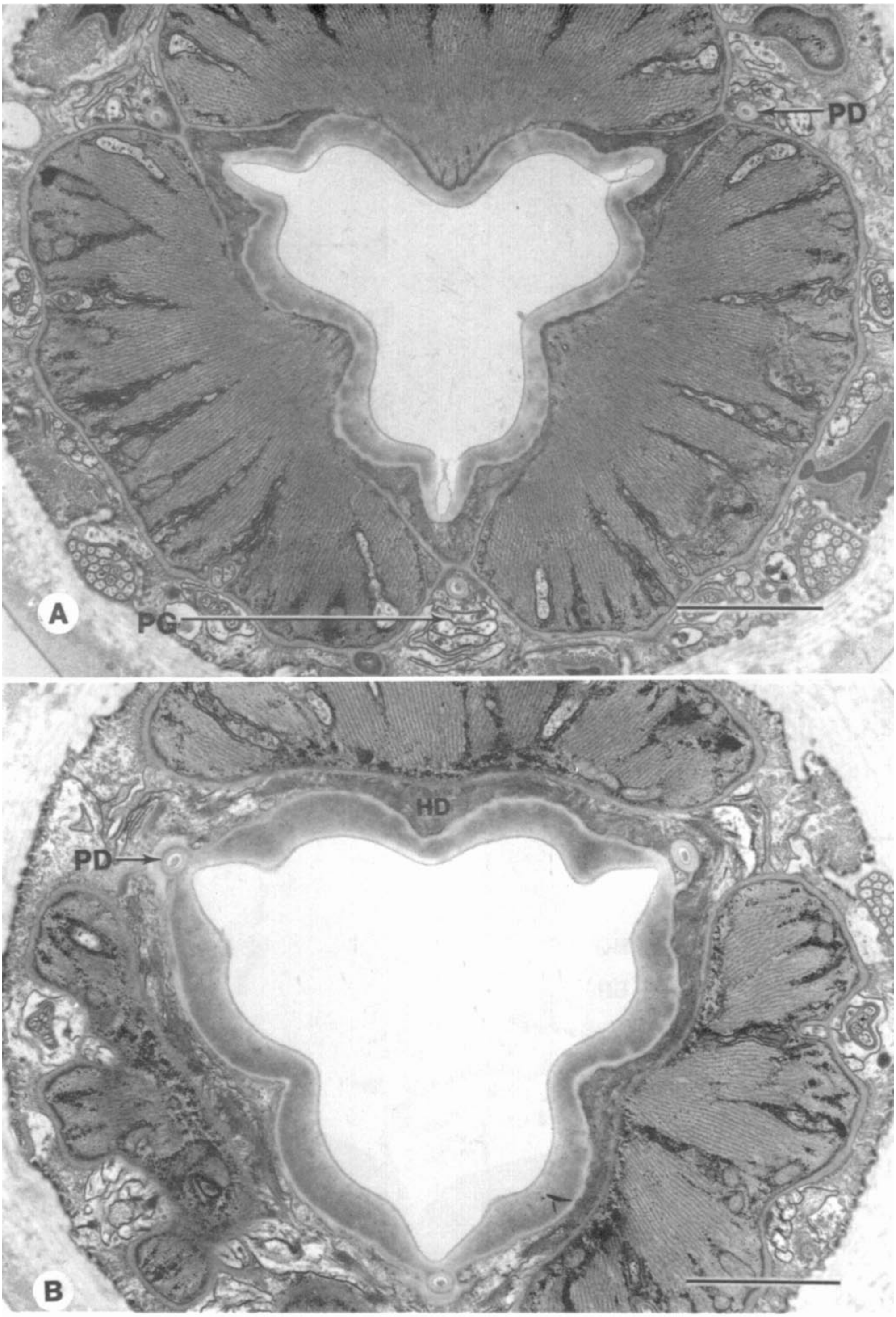

FIG. 4. *Rhabdodemania minima.* Transmission electron micrographs of transverse sections. Dorsal is at top. A) Posterior region of buccal capsule at a level near mid region of anterior protractor muscles. Bar = 2.0 μm. B) Posterior region of buccal capsule at a level near anterior end of anterior protractor muscles. Bar = 2.0 μm. Refer to Figure 1 for abbreviations.

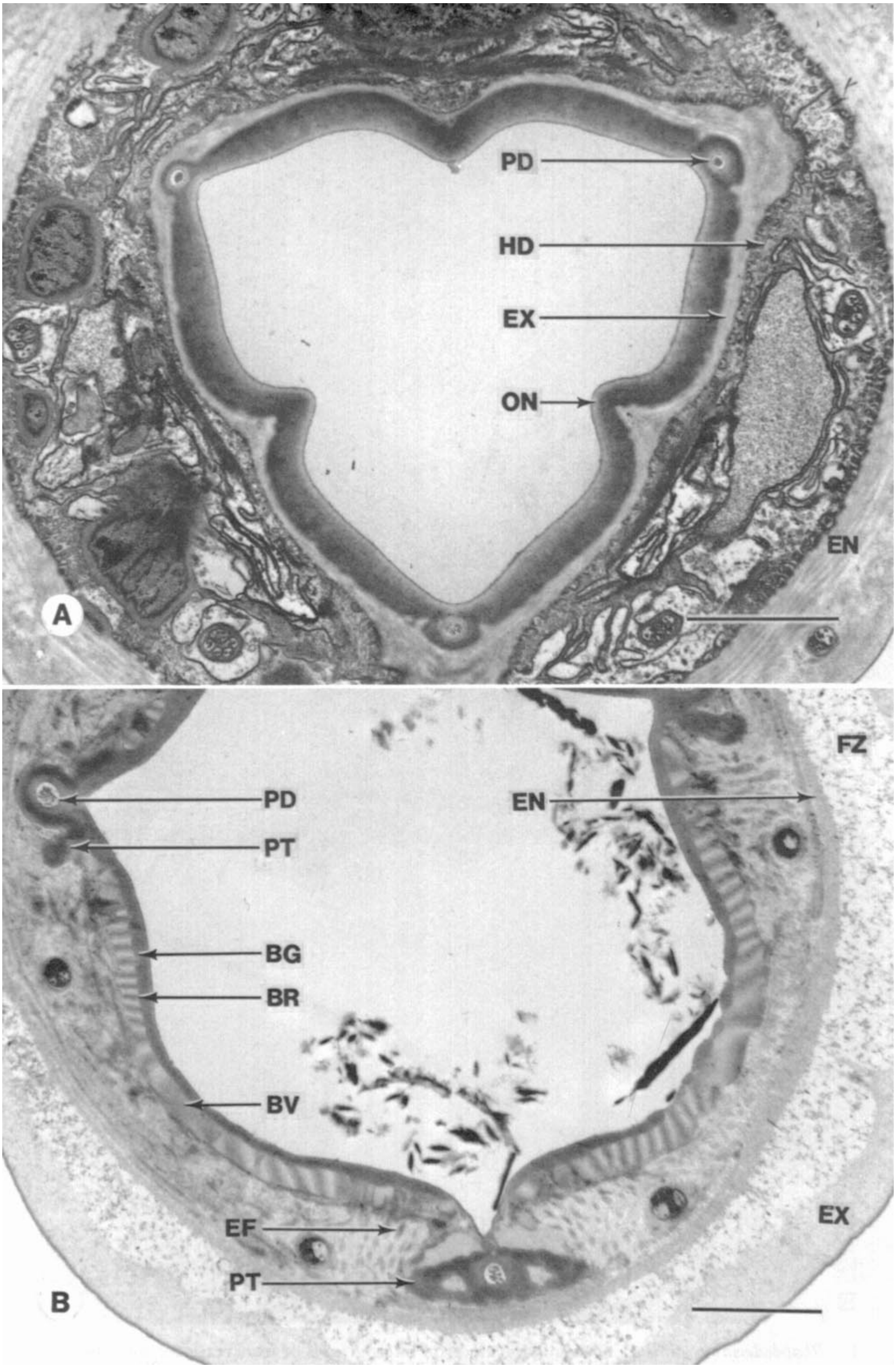

FIG. 5. *Rhabdodemania minima.* Transmission electron micrographs of transverse sections. Dorsal is at top. A) Posterior region of buccal capsule at level of hypodermal collar and posterior ends of onchia. Bar = 2.0 μm. B) Middle region of buccal capsule. Section is inclined, so dorsal side of section is more posterior than ventral side. Bar = 2.0 μm. Refer to Figure 1 for abbreviations.

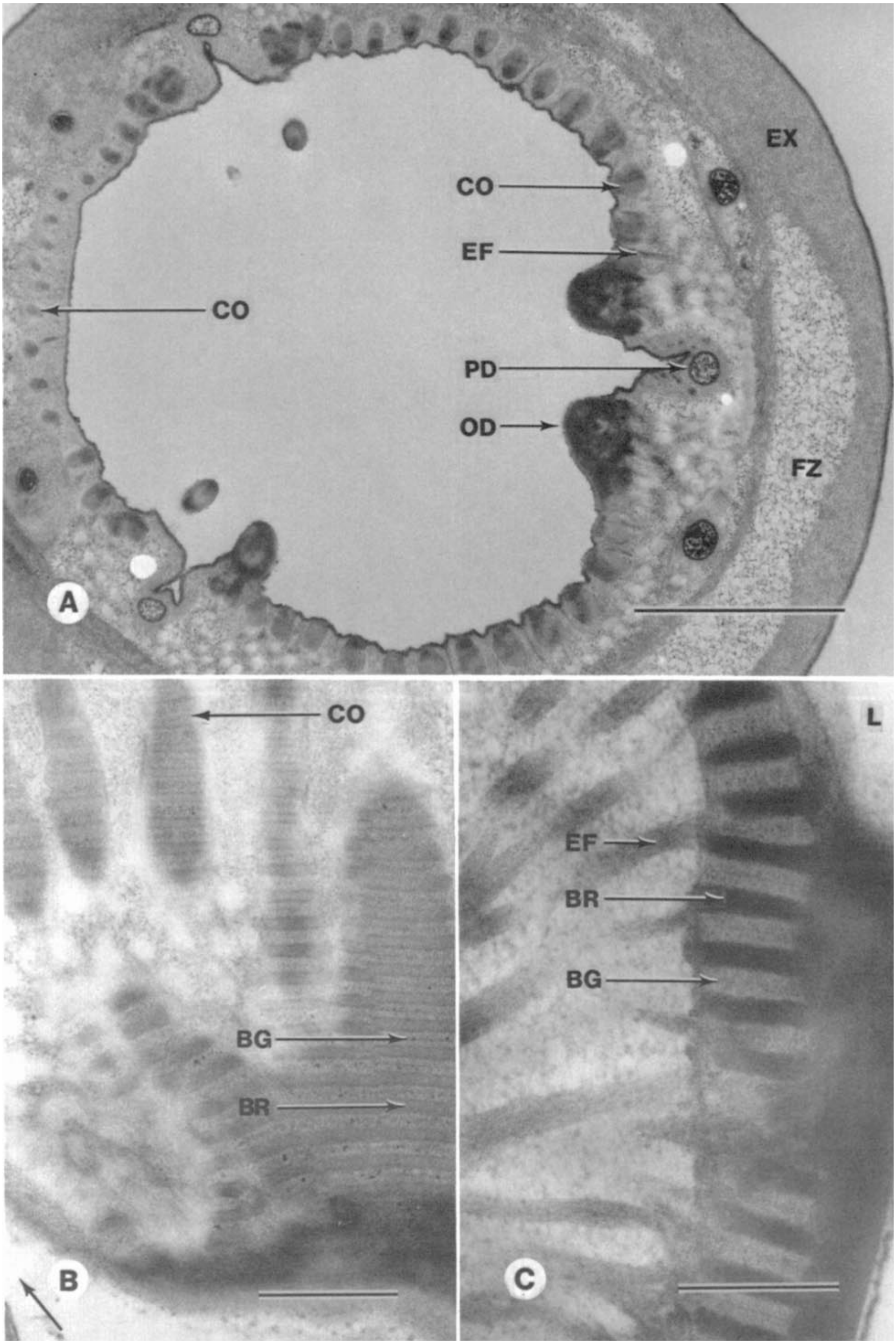

FIG. 6. *Rhabdodemania minima*. Transmission electron micrographs of transverse (A) and longitudinal (B, C) sections. A) Anterior region of buccal capsule at level of the odontia. Section is inclined, so left is more anterior and through tips of odontia, whereas right is more posterior and through bases of odontia. Bar = 2.0 μm. B) Tangential section of buccal walls of middle (lower) and anterior (upper) regions of buccal capsule. Anterior is up. Arrow in corner of buccal capsule indicates direction of longitudinal axis of buccal capsule. Bar = 500 nm. C) Buccal wall of middle region of buccal capsule. Anterior is up. Bar = 250 nm. Refer to Figure 1 for abbreviations.

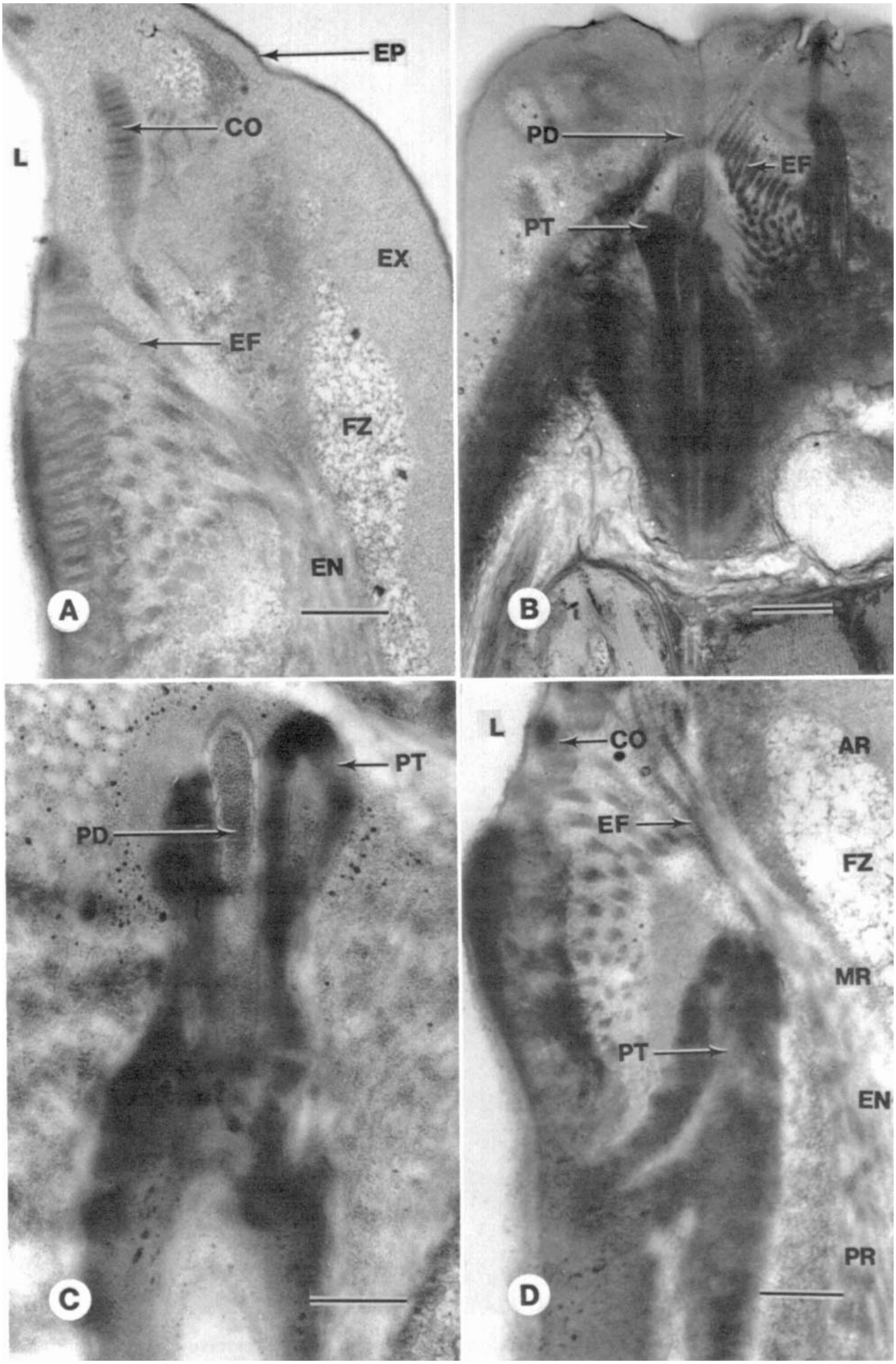

FIG. 7. *Rhabdodemania minima.* Transmission electron micrographs of longitudinal sections. Anterior at top. A) Buccal wall and cephalic cuticle at middle and anterior regions of buccal capsule. Bar = 0.5 μm. B) Paraesophageal gland duct through posterior, middle, and anterior regions of buccal capsule. Bar = 0.5 μm. C) Paraesophageal gland duct and duct pterons. Bar = 0.5 μm. D) Wall of posterior, middle, and anterior regions of buccal capsule with pteron of paraesophageal gland duct. Bar = 1.0 μm. Refer to Figure 1 for abbreviations.

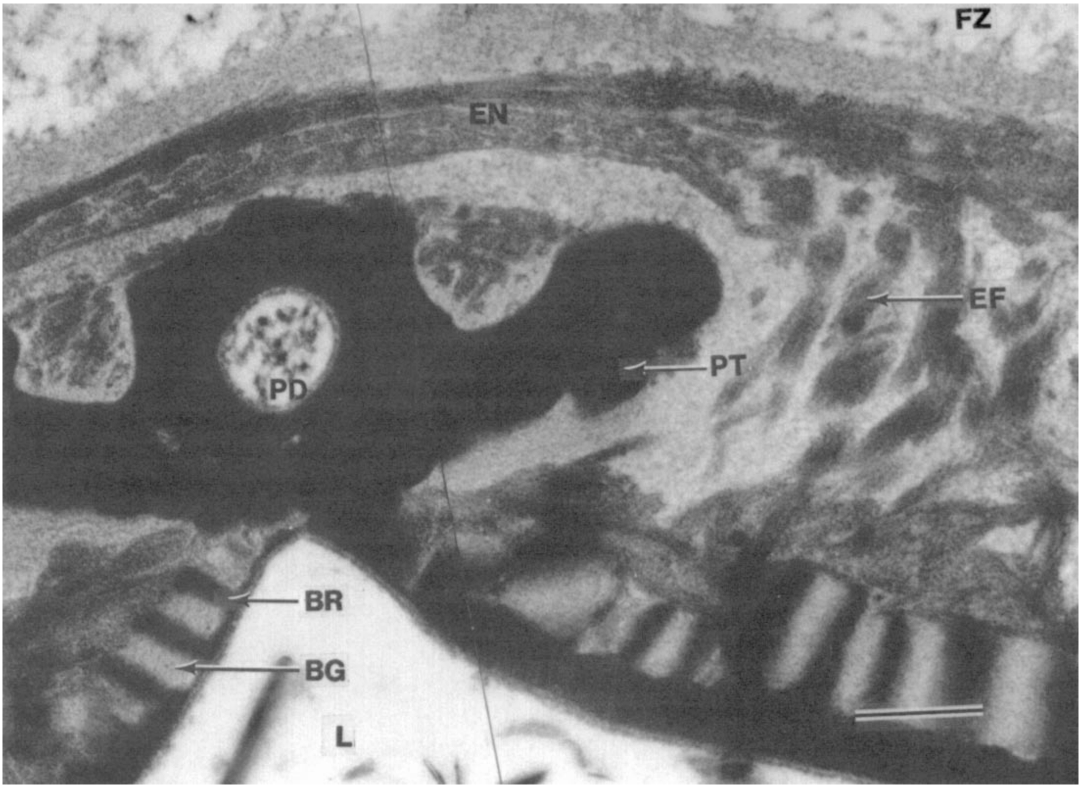

FIG. 8. *Rhabdodemania minima*. Transmission electron micrographs of a transverse section through wall of middle region of buccal capsule and paraesophageal gland duct with pterons. Bar = 250 nm. Refer to Figure 1 for abbreviations.

gradually becomes thinner and ends near the middle region of the anterior esophageal muscle cells at a distance of 7–10 (9 ± 1) μm from the anterior end of the head. The endocuticle is not involved in this posterior extension of the cephalic cuticle.

Within the exocuticle there is an irregular zone of loosely packed fibers that passes around the head (Figs. 2, 5B, 6A, 7A, 8, 9). This zone of fibers extends anteriorly from a level near the posterior end of the buccal capsule, increases to a maximum width of 554–1,259 (880 ± 259) nm and tapers to an end anterior to the buccal seam. It occurs as a smaller zone at the base of the lips, and it may occur elsewhere within the cephalic exocuticle as small, isolated pockets (Figs. 2, 7A). As far as is known, these zones of fibers occur only in the head.

The endocuticle, innermost layer of the cephalic cuticle, is 542–1,025 (820 ± 137) nm thick at the level of the posterior end of the buccal capsule. It is comprised alternately of electron-dense and relatively translucent layers (Figs. 2, 5A, B, 7A, D, 8, 9). The endocuticle extends anteriorly to near the junction of the middle and anterior regions of the buccal capsule, where, with a reduction in the number of layers, it tapers to an end.

A cephalic capsule, which is a typical component of the endocuticle in many of the taxa in Enoplida, is absent. This is in agreement with light microscopic observations for all species of *Rhabdodemania*.

The hypodermis at the level of the posterior end of the buccal capsule is 1.03–1.98 (1.49 ± 0.29) μm thick. Between the protractor muscles and cuticle, at the level of the zonula adherens, the hypodermis is 0.17–0.42 (0.29 ± 0.09) μm thick. Cytoplasmic filaments associated with the zonula adherens span the width of the hypodermis and attach to its external surface and the cuticle (Fig. 2). Each of the anterior muscle fibers of the esophagus (protractor

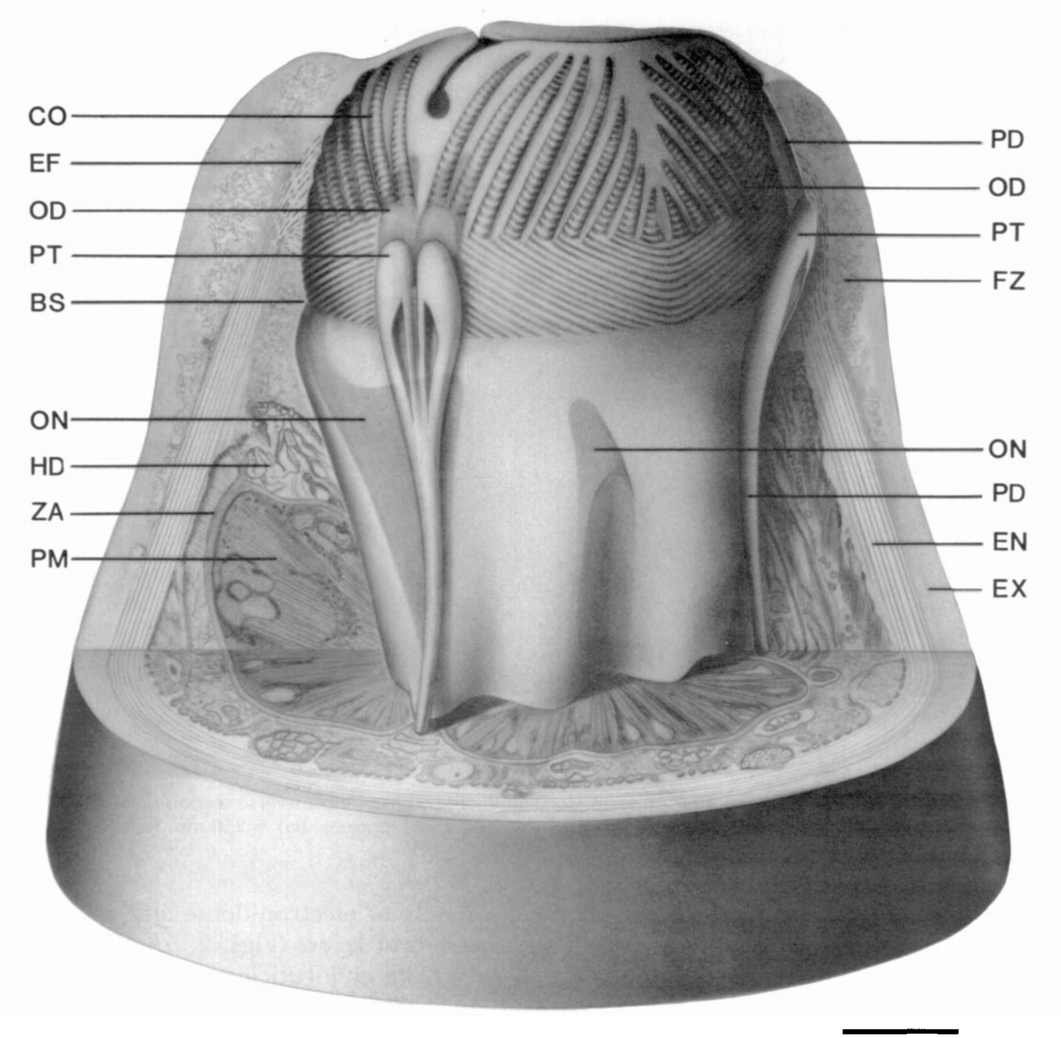

FIG. 9. *Rhabdodemania minima.* Illustrated cutaway view of buccal capsule. Layers of cephalic cuticle have been removed leaving only buccal wall, including costae and pterons. Odontia and onchia are visible through buccal wall. Frontal plane of cut passes through paraesophageal gland duct anterior to pteron on ventral (right) side of head. Bar = 2.0 μm. Refer to Figure 1 for abbreviations.

muscles of the buccal capsule), therefore, is attached to the external cuticle.

Anteriorly, the hypodermis arches mesad between the anterior end of the esophagus and the cephalic cuticle, forming a collar around the posterior region of the buccal capsule. This hypodermal collar (cephalic ventricle) is 1.44–4.24 (2.25 ± 0.80) μm in its anterior to posterior dimension. It appears to be penetrated by nerve endings and bears numerous microvilli at its interface with the cephalic cuticle (Fig. 2).

Buccal capsule: Three major regions of the buccal capsule are identifiable from longitudinal sections: 1) a posterior region 10.3–15.3 (14.1 ± 1.6) μm long with solid, electron-dense walls; 2) a middle region 1.3–1.9 (1.6 ± 0.2) μm long with transversely striated walls; and 3) an anterior region, 2.6–3.6 (3.2 ± 0.4) μm long, in which the walls are divided into longitudinal costae (Figs. 2, 9). At least the anterior and middle regions of the buccal capsule are lined with epicuticle.

The posterior end of the buccal capsule in transverse section is basically triradiate, but the lumen is more spacious than that of the esophagus. The cuticle of the posterior region of the buccal capsule is 403–620 (494 ± 64) nm at its thickest. Posteriorly, the cuticle decreases in thickness to 200–454 (350 ± 79) nm and gradually becomes less electron dense until slightly posterior to the denticles where the electron density abruptly diminishes (Fig. 2; compare A and C of Fig. 3). The denticles, which appear in light microscopy as a single, mesad projection from each wall of the buccal capsule, are revealed in electron microscopy to be three sets of three solid denticles. There is one set at each angle where the adjacent rays of the buccal capsule wall merge (Fig. 3C).

More anteriorly, the posterior region of the buccal capsule becomes more voluminous and in cross section changes in shape from triradiate to triangular (Fig. 4B). An onchium is situated on each buccal wall near the level of the hypodermal collar. Each onchium is a mesad fold of the buccal wall into which projects endocuticle and, sometimes, hypodermis from that which envelops the posterior buccal capsule (Figs. 2, 5A).

The structure of the buccal walls, exclusive of the epicuticle, abruptly changes at the junction of the posterior and middle regions of the buccal capsule. This junction is the buccal seam visible in light microscopic observations. The electron-dense layer of the posterior buccal wall continues anteriorly, but from the buccal seam forward it is incised on its external surface by a series of transverse, parallel grooves. These grooves are 38–64 (52 ± 7) nm wide, 171–226 (193 ± 21) nm deep, and separated from one another by a wall of electron-dense cuticle 37–51 (44 ± 4) nm wide (Figs. 2, 5B, 6B, C, 7A, 8, 9). The cuticle within the grooves is not an intrusion of the exocuticle, but, rather, is occupied by a substance, possibly a mat-like condensation of endocephalic fibers that is intermediate in electron density between that of the ridges and exocuticle. A band of minute, electron-dense granules occurs in the center of each groove (Fig. 6B, C).

The parallel grooves extend from corner to corner across the dorsal and subventral buccal walls, slanting posteriorly from the corners of the buccal capsule at an angle of 115–130 (120 ± 7; n = 4) degrees (Figs. 6B, 9). Grooves reaching the median longitudinal plane of each buccal wall are continuous with grooves from the other half of the wall and appear as stacked "V"s (Fig. 9). Cross sections at this level of the head reveal the broader, tangential sections through the base of the Vs midway between buccal corners (Fig. 5B).

Slightly posterior to the buccal seam, a pair of wing-like processes, each process here termed a pteron, projects into the cephalic cuticle from each outside corner of the buccal capsule (Figs. 5B, 7B, C, 8, 9). Each pteron becomes wider as it proceeds anteriorly, then folds back toward, and fuses with, the external surface of the wall of the paraesophageal gland duct (Figs. 5B, 9). As each pteron folds back upon itself, it encloses a pocket of cephalic cuticle at each side of the gland duct (Figs. 5B, 7C). Anteriorly, the pterons become solid as the cuticular pockets within them end blindly (Fig. 7C). Slightly anterior to the buccal seam, the paraesophageal gland ducts, with pterons, separate from the corner of the buccal capsule and project anteriorly into the exocuticle (Figs. 5B, 7D, 9). The gland duct wall, apparently an extension of the buccal wall, ends at about the midlength of the middle region of the buccal capsule. Each pteron, however, continues anteriorly for a short distance as a rounded lobe (Figs. 7B, C, 9). From where the gland duct wall ends, conveyance of the glandular products continues anteriorly through a tubular duct in the exocuticle (Figs. 6A, 7B, 9). Each tubular duct is lined by a thin electron-dense layer that may be an inward extension of epicuticle. Each duct closely parallels a corner of the buccal cavity and opens to the exterior in the base of the notch between labia.

The middle region of the buccal capsule extends anteriorly from the buccal seam for a distance of 730–2,100 (1,506 ± 403) nm, where the anterior region of the buccal capsule begins with the division of the buccal wall into anteriorly directed and tapered costae (Figs. 6B, 9). The costae, which extend to the base of the labial flaps, are inclined obliquely toward the median longitudinal plane of the corresponding head sector at an angle similar to that of the parallel grooves (Figs. 6B, 9). Because the costae are an extension of the middle region of the buccal capsule, their composition is similar to it; namely, each costa appears to have a mesal electron-dense layer and parallel grooves (Figs. 6A, B, 9). Consequently, each costa is distinct from the surrounding exocuticle by its banding and greater overall electron density.

The posterior portion of each costa contacts the epicuticle that lines the lumen of the buccal capsule and here, between each costa, there is a shallow longitudinal groove in the mesal surface of the buccal wall (Fig. 6A). Anteriorly, each costa separates from the epicuticle and the longitudinal grooves disappear.

The middle region of the buccal capsule is subtriangular in cross section, and the wall between each pair of corners is arched outward (Fig. 5B). Toward the anterior end of the buccal capsule, the shape gradually becomes circular in cross section with a shallow notch at the anterior extensions of the buccal corners. On each side of each notch in the anterior region, there is a solid odontium that projects into the lumen of the buccal capsule (Figs. 6A, 9). The core of each odontium is continuous with, and composed of, the mesal, electron-dense layer of the buccal wall.

Numerous, densely packed bundles of electron-dense fibers, here termed endocephalic fibers, emerge from the external surface of the middle and anterior regions of the buccal capsule and posteriorly merge with the electron dense concentric layers of the endocuticle (Figs. 5B, 6A, C, 7A, B, D, 8, 9). Fibers emerging from the middle region tend to be concentrated near the corners of the buccal capsule, where they pass to the outside of the endocephalic pterons and then posteriorly into the endocuticle (Figs. 5B, 7D). In the anterior region, endocephalic fibers emerge from the external surface of each costa and from the epicuticle between costae and pass directly posterior into the endocuticle (Fig. 6A). Many bundles of fibers also emerge from the external surface of the electron-dense core of each odontium, passing posteriorly and externally to the pterons into the electron-dense layers of the endocuticle (Fig. 6A).

The buccal capsule is partially closed anteriorly by three labial flaps, one extending mesad from each of the dorsal and subventral labial surfaces of the head (Fig. 2). Adjacent flaps may slightly overlap each other at their bases, but even when the stoma is at rest they leave a small, central, triangular oral opening.

DISCUSSION

Functional morphology

For the genus *Rhabdodemania*, there has not been a published description, based upon actual observations, of the manner in which the buccal capsule functions during food ingestion. Wieser (30), in his classification of feeding types among marine nematodes, placed the genus *Rhabdodemania* in category 2–B, which includes mostly predators with "big and powerful armature" and whose prey is swallowed whole or pierced by means of spears or teeth. In his description of *R. illgi*, Wieser (31) considered the "cuticular projections" (onchia) described for members of *Rhabdodemania* as being homologous with the teeth of "other enoplid genera," and the three pairs of longer onchia (odontia) as being homologous with the mandibles. The concept that members of *Rhabdodemania* possess mandibles or jaws, as was proposed by Wieser, has been supported by other researchers (3,15,18,23–25). It is at least implicit in these assessments that members of *Rhabdodemania* have "jaws," that pairs of odontia are homologous with the paired, pointed tips of each jaw occurring among members of Enoplinae and Enoplolaiminae, and that there are similarities in the way by which the mouth parts operate during feeding.

On the basis of the ultrastructural observations in this study, it is possible to postulate more precisely how the buccal capsule functions during feeding. For this analysis it is assumed that the more electron-dense cuticle of the buccal walls is relatively hard and inflexible. By contrast, the less electron-dense exocuticle occurring in the head region (especially in the fibrous zones of the exocuticle) and the cuticle of intermediate electron density situated in the grooves in the wall of the middle and anterior regions of the buccal capsule are relatively more elastic.

The dynamics of the model are based upon the oblique arrangement of the most anterior muscle cells of the esophagus. When contracted, these muscles may not only dilate the posterior triradiate region of the buccal capsule, but also pull the dense cuticle of the posterior buccal capsule in an anterior direction. It is evident that the anterior muscle fiber in each sector of the esophagus is a protractor muscle because of its point of insertion on the posterior buccal wall, its oblique orientation, and its attachment by way of a zonula adherens to the external body wall. Undoubtedly, the latter provides a secure anchor from which the buccal capsule may be pulled.

The protractor muscles are one sarcomere in length. Therefore, it is theoretically possible to subtract the length of the A band from the total length of the sarcomere to obtain the maximum distance by which each muscle shortens, assuming that shearing of the myofilaments does not occur. In this study, however, this was not possible because, in the available material, the A bands of the protractor muscles were not sufficiently distinct to measure.

The contraction of the protractor muscles and forward movement of the posterior region of the buccal capsule also exert a forward force on the walls of the middle and anterior regions. However, walls of the middle and anterior regions cannot move forward, at least not by an appreciable amount, because they are attached to the anterior rim of the endocuticle by endocephalic fibers. Consequently, the buccal walls bend at the buccal seam and the walls of the middle and anterior region expand outward over the anterior rim of the endocuticle. Thus, the walls of the middle and anterior regions become obliquely radial to the median, longitudinal axis of the buccal cavity; the anterior region of the buccal capsule and oral aperture dilate; and the odontia are moved to the rim of the oral aperture. The labial flaps remain folded into the buccal cavity. The length of each flap, from its base to its rim, is insufficient to reach and overlap the odontia. Also, it is possible that, as the oral aperture is dilated, the labial flaps are stretched between corners of the buccal capsule, which may further reduce their length. As a result, the tips of the odontia are fully exposed in this position.

The cephalic cuticle also plays an important role in the function of the buccal capsule. For example, the endocuticle, which has a laminated substructure and, presumably, is more resistant to deformation than the exocuticle, gradually tapers to an end at the level of the middle region of the buccal capsule. Therefore, it is excluded from that region of the cephalic cuticle most likely to be distorted by protraction of the buccal capsule and dilation of the oral aperture. Conversely, the greatest portion of the cephalic cuticle is comprised of exocuticle, which has no obvious infrastructure. There are no striations on the surface, organized layers of fibers, or other inclusions that might serve to strengthen this cuticle or reduce its flexibility. In fact, the loosely packed fibers, amorphic composition, and, especially, the circumoral zones or pockets of loosely packed fibers probably accommodate distortion (compression and stretching) of the cephalic cuticle when the anterior buccal capsule is dilated.

The function of the paraesophageal glands remains uncertain, but their ontogenetic origin and, most likely, their function differ from that of the subventral esophageal glands that open on the lip re-

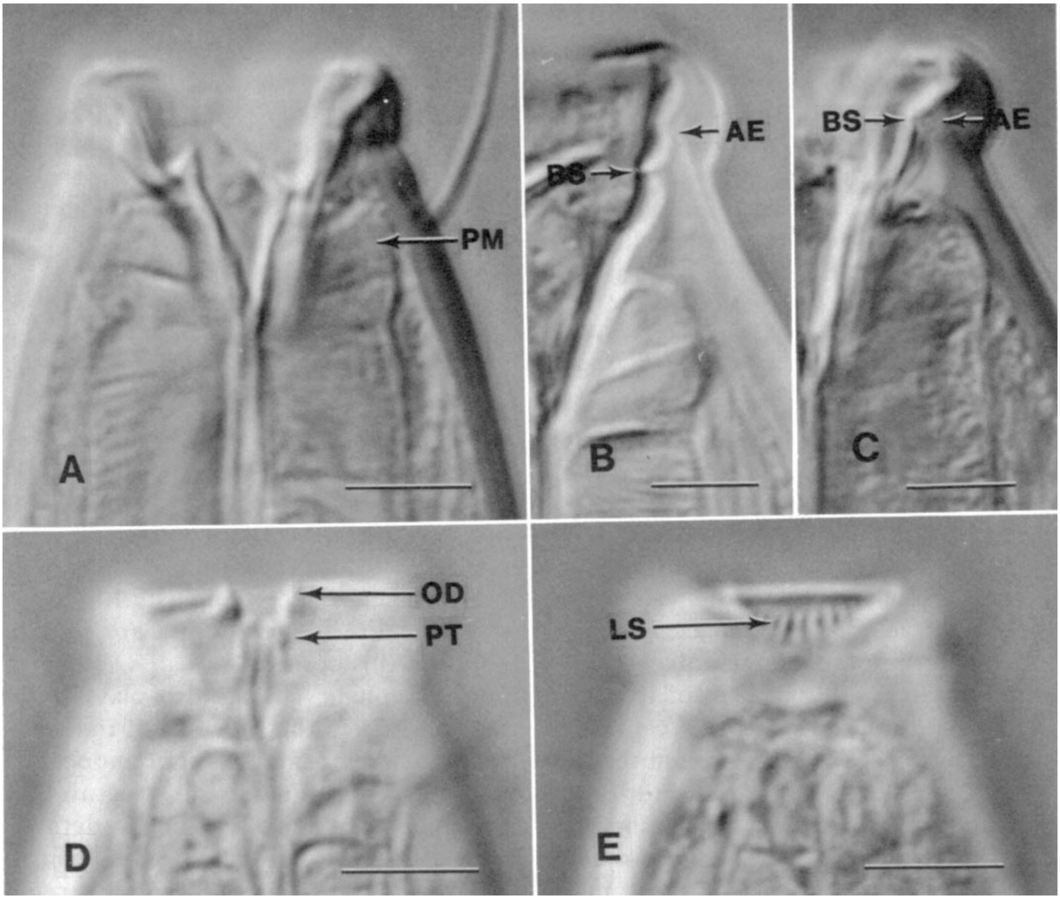

FIG. 10. *Rhabdodemania minima* (A, D, E) and specimens of an undescribed species of *Rhabdodemania* (B, C). Photomicrographs of optical longitudinal sections. Bar = 5 µm. A, C–E) Buccal capsule with protractor muscles contracted. B) Buccal capsule with protractor muscles relaxed. Refer to Figure 1 for abbreviations.

gion of at least some members of the suborder Enoplina (14). The pterons of each paraesophageal gland duct may give support to the ducts of the paraesophageal glands, preventing them from being pinched shut when the anterior and middle regions of the buccal capsule are dilated.

Some of the assumptions and conclusions made for this model have been tested by examination of whole-mount specimens to see if there is a correlation between contraction of the protractor muscles and dilation of the buccal capsule, at least as far as may be determined with the light microscope. Unfortunately, in the material at hand, there is only one specimen of *R. minima* in which the protractor muscle is contracted, and it appears to be only partially contracted (Fig. 10A D, E). Therefore, additional observations were made on specimens of an undescribed species of *Rhabdodemania* in which the protractor muscles in some specimens are fully relaxed (Fig. 10B) and in others fully contracted (Fig. 10C). In the latter specimens, the angle of the protractor muscle to the median axis of the nematode was increased as a result of forward movement of the buccal capsule (Fig. 10A), the buccal seam had been moved to the level of the anterior rim of the endocuticle (compare B and C of Fig. 10), the walls of the middle region of the buccal capsule in optical longitudinal section became obliquely radial to the longitudinal axis of the buccal capsule (Fig. 10A, C), and the odontia were moved to the anterior rim of the buccal aperture (Fig. 10D). By comparing specimens of *R. minima* of similar size, it was determined that the inside diameter of the buccal capsule is ca. 7 μm when the protractor muscles are relaxed and 10 μm when they are partially contracted.

It also appeared from comparative light microscopic observations that the wall of the middle region is compressed when the buccal capsule is dilated. If this is true, it may be that compression is accommodated by the transverse grooves in its walls, and the angle of the grooves may in some way be functionally significant. It is also possible that the grooves and ridges provide an increased surface area for the attachment of the endocephalic fibers.

The costae also become thicker and the distance between them increases slightly when the buccal cavity is dilated (compare Figs. 1B and 10E), probably due to compression. Whereas the costae may be important in giving mechanical support to the anterior region of the buccal walls, the longitudinal separations between them are equally important in allowing the elastic exocuticle in which they are embedded to stretch radially. This would accommodate an increase in the circumference of the buccal capsule as it is dilated and could account for the increased distance between costae (Fig. 10E).

There are no retractor muscles in the head region that return the buccal capsule to its resting mode. Retraction may, in part, be accomplished by the resiliency of the cephalic cuticle and buccal wall. However, it is possible that retraction is accomplished by the obliquely oriented dilator muscles of the posterior region of the esophagus, the contractile filaments of which have their mesal insertion anterior to the distal origin (Fig. 1E). When the dilator muscles of the posterior end of the esophagus contract, perhaps in the process of swallowing, they may pull the cuticular lining of the esophagus and buccal capsule in a posterior direction, thus returning the buccal capsule to a resting position.

While it is possible that individuals of the genus *Rhabdodemania* are epistrate feeders and feed by dilating the buccal capsule and scraping material from a substrate with the odontia, they could also be predators that suck protozoans or minute metazoans into the buccal capsule, where the prey's body wall is pierced by the anteriorly directed odontia and onchia and possibly lacerated by the posterior denticles. In either case, the manner of feeding is different from the way in which members of the Enoplidae are believed to grasp and (or) crush prey with their opposable mandibles.

Comparative morphology and phylogenetic considerations

Cephalic cuticle: An important aspect of the structure and function of the feeding apparatus of many enoplids is related to the increased thickness of the cephalic cuticle overlying the anterior end of the esophagus. This is a means by which the buccal capsule has been increased in depth and structural complexity. Several theories have been proposed to explain how the thickening has been achieved. Filipjev (11) proposed that it resulted from the cuticle of the head region being folded inward upon itself at the stoma doubling its thickness. This interpretation has been accepted by others (4,6,7,13). More recent studies attribute the increased depth of the cephalic cuticle to splitting of the cuticle into additional layers (2) or to thickening of the cephalic cuticle (14,22,24). Inglis (15) attributed the increased distance between the oral aperture and the anterior end of the esophagus in Enoplida to the presence of a fluid-filled cavity, the cephalic ventricle.

The present study provides additional evidence that a thickening of the head cuticle results from an expansion of a layer of cuticle, which in this case is the exocuticle. This is different from observations in which the mesocuticle (21) and "X" layer (14) are thickened. It is consistent, however, with the conclusion (24) that the layer involved in the thickening is not the same in all taxa. If additional transmission electron microscopy confirms that this is true, it will be necessary to conclude that the thickened cuticle over the anterior region of the head is not homologous among all taxa of Enoplina, and this may not be used as a synapomorphic character by which monophyly is determined for this suborder.

This study also confirms the observations of Inglis (15) that, among members of *Rhabdodemania,* a cavity (cephalic ventricle) exists between the anterior end of the esophagus and the cephalic cuticle, but, rather than being fluid filled, it is occupied by hypodermal tissue and, probably, nerve cell processes.

Another result of the cuticle of the head region being thickened is a decrease in the effectiveness with which the normally radial, anterior esophageal muscles dilate or otherwise manipulate the oral aperture and anterior portion of the buccal capsule. This problem has been overcome by different specializations. In leptosomatids, it is the dilator muscles attached to apodemes that together effect the retraction of the lip region from around the oral aperture to expose the odontia and dilate the lumen of the stoma (14). It has been overcome in *Rhabdodemania* by a complex mechanism involving the protractor muscles of the buccal capsule, modifications of the anterior region of the buccal walls, and endocephalic fibers. Analysis of such mechanisms may provide further clues to evolutionary relationships among members of Enoplina.

Buccal capsule: The taxonomic position of Rhabdodemaniidae within the order Enoplida remains uncertain. There is no evidence that the suborder Tripyloidina, to which it is now assigned, is monophyletic; that is, members of this suborder are not known to share one or more synapomorphic characters. By contrast, the suborder Enoplina is allegedly monophyletic, because most of its members share the synapomorphic condition of having the caudal glands extend into the precaudal cavity of the body (19). Because members of Rhabdodemaniidae have caudal glands that are confined to the tail region, this family is excluded from Enoplina and, by default, assigned to Tripyloidina. As noted by Lorenzen (19), however, the caudal glands in members of *Enoplus* (Enoplidae), Anticomidae, Halalaiminae (Oxystominidae), and some members of Ironidae are confined to the caudal region. Yet they are indisputably members of Enoplina, because they share synapomorphic characters with other subtaxa of the suborder. To this list of exceptions I add the genus *Pseudocella* (Leptosomatidae), in which the caudal glands are confined to the tail, but which, for many other reasons, appears to be closely related to *Thoracostoma.* Considering the foregoing exceptions, it is possible that Rhabdodemaniidae is a representative of Enoplina, even though the caudal glands of its members are confined to the caudal region. Therefore, it is appropriate to include taxa from Tripyloidina and Enoplina in a discussion of the possible phylogenetic affinities of Rhabdodemaniidae.

Enoplidae, as noted, has been the family most frequently compared with Rhabdodemaniidae (3,15,16,18,23–25,31). Although the subfamily Enoplolaiminae has not specifically been mentioned in these studies, it is most likely that members of this subfamily were being compared with *Rhabdodemania* because they, unlike members of Enoplinae, possess three onchia in addition to the paired, conical tips of each mandible that may have been derived from odontia. Because there is no ultrastructural information on the onchia of enoplolaimids, it is not possible to make additional conclusions in this study concerning their homology with the onchia of *Rhabdodemania.*

Indeed, the mandibles of members of Enoplidae may in part be derived from the fusion of odontia. However, if that component of the enoplid jaw is homologous with the odontia of *Rhabdodemania,* it does not necessarily follow that the odontia in members of *Rhabdodemania* are components of mandibles. Data from this investigation suggest that there is less similarity between the mandibles of enoplid genera and the structure of the anterior region of the buccal capsule among members of

Rhabdodemania than is implied or assumed from previous investigations. For example, as noted, Wieser (31) concluded that the three pairs of longer onchia (odontia) in *Rhabdodemania* are homologous with the mandibles of enoplid genera. Platonova (23) and Platonova and Gal'tsova (25) agreed with Wieser and gave more detailed analyses of the armature of the anterior region of the buccal capsule. In these analyses, three seams or sutures circumscribing the walls of the anterior region are illustrated and described, the most anterior of which is an arc at the posterior end of the longitudinal striae (costae of this study). Platonova (23) interpreted the region between the most anterior and middle seams as a mandible and the odontia as the tips of the mandibles and concluded that they are homologous with the mandibles of enoplids. She designated the region between the middle and posterior seams as the mandibular ring and the processes extending from the external surface of each mandibular ring into the cuticle of the head region as mandibular processes. A function was not suggested for either the mandibular ring or mandibular process.

Observations in the present study do not support the existence of an anterior seam. It is assumed that the appearance of such a seam in light microscopy is attributable to the uniform alignment of the posterior ends of the costae and (or) the intercostal separations. The second seam is the buccal seam of this study. The region between the posterior ends of the costae and buccal seam, as demonstrated in ultrastructural observations of *R. minima*, is not a mandible but the walls of the striated, and presumably compressible, middle region of the buccal capsule. It is structurally unlike the solid, and presumably inflexible, jaws of the members of the Enoplidae, and it likely does not function in the same way. The third seam described by Platonova, the most posterior of the three, is interpreted here to be the bend at which the exocuticle extends posteriorly and envelops the posterior region of the buccal capsule (Fig. 1D). Because the "mandibular ring" is delimited anteriorly by a structure of the buccal wall (buccal seam) and delimited posteriorly by a feature of the cephalic cuticle, it is not a structural or functional entity. Finally, the mandibular processes are the pterons in this study, which also are not involved with mandibles.

Given that the middle and anterior regions of the buccal capsule have no apparent structural or functional similarity to the mandibles of enoplids, the terms mandible, mandibular ring and mandibular process, especially when making comparisons to the mandibles of enoplids, are inappropriate and should not be applied to members of *Rhabdodemania*. Other dissimilarities between the enoplids and *Rhabdodemania* include the modification of the anterior muscles of the esophagus for abducting and adducting the jaws in members of Enoplinae (15), whereas in the latter taxon they dilate and slightly protrude the anterior region of the buccal capsule. Although the esophageal glands of enoplids and *Rhabdodemania* open into the lumen of the esophagus, it is not known if paraesophageal glands occur in enoplids.

Concerning the family Leptosomatidae, it is apparent that the feeding apparatus and head structure among most of its members demonstrate little similarity to those of *Rhabdodemania*. In contrast to *Rhabdodemania*, all leptosomatids have a cephalic capsule; the esophageal glands open on the lip region; paraesophageal glands are absent; the buccal capsule, at least among members of *Deontostoma* and presumably among most other leptosomatid genera, when at rest is closed from its pseudokampters (false corners) to its eukampters (true corners) and when dilated is opened fully to its eukampters; the buccal capsule is dilated by labial retractor muscles; and longitudinal striations in the buccal capsule and labial flaps are absent.

The odontia in members of Deontostomatinae and Synonchinae, at least superficially resemble those of *Rhabdodemania* in number, position and form (19), thus raising the question of homology concerning the odontia of members of Leptosomatidae and Rhabdodemaniidae. However, histological sections have revealed that each odontium in members of *Deontostoma californicum* Steiner and Albin, 1933, and, presumably, in other members of Leptosomatidae as well, is a conical fold of the layer of cuticle that lines the buccal cavity with a core of exocuticle that projects into each odontium from its base (14). This is in contrast to the odontium of members of *Rhabdodemania,* which lacks a distinct core and may be derived from a costa or an amalgamation of costae. It is concluded, therefore, that the similarity between odontia of members of *Rhabdodemania* on the one hand and Deontostomatinae and, presumably, Synonchinae on the other is the result of convergence.

Among members of the subfamilies Barbonematinae, Platycominae, and Leptosomatinae, there is even less similarity to the buccal capsule of *Rhabdodemania,* where odontia are absent, and when at rest the buccal capsule appears to be completely closed (pseudokampters absent).

Within Leptosomatidae, the buccal capsule with greatest apparent similarity to that among members of Rhabdodemaniidae is found in members of *Cylicolaimus* (Cylicolaiminae), as has been observed by Filipjev (9). The buccal capsule in members of *Cylicolaimus* is goblet shaped and spacious when at rest, and the posterior end of the buccal capsule is enveloped by the muscles of the anterior end of the esophagus. As reported previously (14), however, each subventral esophageal gland duct of *Cylicolaimus* extends anteriorly through the wall of the buccal capsule and opens on the lip region midway, in an en face view, between the ventral corner and a subdorsal corner of the buccal capsule; and the oral aperture is surrounded by three microlabia. These morphological features clearly demonstrate close phylogenetic affinity between Cylicolaiminae and other members of the Leptosomatidae, but not with Rhabdodemaniidae.

This study of the head and buccal capsule provides no evidence that Rhabdodemaniidae shares one or more synapomorphic characters with either Enoplidae or Leptosomatidae, and it supports the conclusions of Lorenzen (19) that the family Rhabdodemaniidae is not closely related to members of the family "Enoplidae" or Enoplolaiminae.

The buccal capsule among members of other families of Enoplina—namely, Ironidae, Oxystominidae, Anticomidae, and Phanodermatidae—do not have apparent similarities to that among members of *Rhabdodemania,* and further consideration of these families is without justification.

The possibility of a monophyletic relationship between *Rhabdodemania* and *Pandolaimus latilaimus* (Allgén, 1929) Stekhoven, 1935, the only nominal species of the genus and family Pandolaimidae, is much more plausible. Lorenzen (19) has already identified derived characters shared only by these two taxa, none of which are concerned with the structure of the head or buccal capsule. Specifically, representatives of both genera have wide lateral hypodermal chords (a character unique within Enoplida), a single anterior testis, and two caudal glands confined to the tail. Although Lorenzen did not include the structure of the amphid as a shared character, the amphidial aperture in members of both genera is not readily visible with the light microscope, a condition that may have resulted from homology.

Personal observations of specimens of *P. latilaimus* not only confirmed the observations of Lorenzen (19), but revealed some additional similarities in the structure of the buccal capsule. The buccal wall bears three equally spaced, longitudinal furrows that may correspond to the corners of the buccal capsule of *Rhabdodemania;* the esophageal glands open into the lumen of the esophagus; and the posterior end of the buccal capsule is enveloped by the anterior end of the esophagus. What appears to be the anterior muscle in each sector of the esophagus is even closer to a longitudinal orientation than in specimens of *Rhabdodemania,* and the origins of these muscles appears to be on the mesal surface of the cephalic cuticle, as it is in *Rhabdo-*

demania. These observations corroborate the conclusions of Lorenzen (19) concerning the possibility of a phylogenetic relationship between species of *Rhabdodemania* and *Pandolaimus*. However, more conclusive evidence for homologous structures of the head and buccal capsule will require comparable ultrastructural observations of *P. latilaimus*.

Before Lorenzen's (19) revision, the genus *Pandolaimus*, along with *Anoplostoma*, had been assigned to the family Anoplostomatidae by Jensen (18). In addition to *Pandolaimus* and *Anoplostoma* having a buccal capsule of similar shape and size, these two genera were assigned to the same family because in both taxa the esophageal glands open into the esophagus, rather than into the buccal capsule, and the buccal capsule was believed to be constructed of three plates with furrows at their joints.

Although there is also a similarity between *Anoplostoma* and *Rhabdodemania* in the general shape and size of the buccal capsule, there has been no further evidence that the buccal capsules are homologous, nor are these two genera known to share synapomorphic characters concerned with any other region of the body. A possible exception, not previously reported, however, is suggested by the similarity between the pterons of *Rhabdodemania* and the muniments of *Anoplostoma*, the latter described by Belogurov and Alekseev (1) for *Anoplostoma cuticularia* Belogurov and Alekseev, 1977. The pterons and muniments are similar to each other, at least with the light microscope, in general shape, size, number, and position. This raises the possibility that the buccal capsule of *Anoplostoma* is homologous with that of *Rhabdodemania* and *Pandolaimus*, and by this apparently unique, character complex, these genera may be recognized as part of a monophyletic group. However, in the absence of any conclusive evidence of homology between the buccal capsule of *Anoplostoma* on the one hand and *Rhabdodemania* and *Pandolaimus* on the other, no conclusion may be drawn without further ultrastructural investigations.

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