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# Taxonomy, morphology and ultrastructure of the free–living marine nematode *Pselionema simplex* De Coninck, 1942 (Chromadoria: Ceramonematidae)

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**Summary.** The free-living marine nematode *Pselionema simplex* De Coninck, 1942 (Ceramonematidae) is redescribed together with an examination of some ultastructural details. The species is recorded in the White Sea for the first time. The body cuticle consists of broad rigid annules connected with thinner flexible interconnections. The annules are ultrastructurally simple and formed with a thick electron-lucent layer with thin electron-dense coverings on the external and internal sides. Interconnections are multilayered. The annule electron-lucent material corresponds to the exocuticle, and interconnections - to the endocuticle. The cuticle of the cephalic end is very slightly modified. The pharynx consists of the procorpus, elongated narrowed isthmus and posterior widening. Radial myofilaments are revealed in the procorpus and isthmus only, whereas the posterior widening is built with pharyngeal gland cell bodies. The midgut is composed of four epithelial cells as viewed in transversal sections. The recto-intestinal valve cells possess rather long microvilli directed into the rectal lumen; a cuticular covering is not present.

**Key words:** *Pselionema simplex*, Ceramonematidae, redescription, ultrastructure, cuticle, pharynx, cephalic end, rectum.

The family Ceramonematidae contains nematodes with a very thick cuticle divided into broad rigid annules connected by thin flexible membranes, hence, ceramonematid nematodes appear to be encased in armour. This cuticular annulation is further complicated by the presence of longitudinal ridges, thin plates (zygapophyses) overlapping the neighbouring rings and different width of the rings. Cuticular organization visible in light microscopy was summarized by Haspeslagh (1973, 1979) and ultrastructural examinations of ceramonematids bv Nicholas & Stewart (1990), Stewart & Nicholas (1992, 1994) and Fürstenberg & Vincx (1993).

The present study includes a redescription of *Pselionema simplex* from the White Sea together with observations on its ultrastructure.

## MATERIAL AND METHODS

Nematodes were sampled by SCUBA-diving in the White Sea near the Biological Station of Moscow State University (Kanadalaksha Bay, Karela Shore, Kassian Island, sublittoral bottom depression of 20 m depth, silt, 4 August 1987).

Extraction of nematodes was done bv a decanting and sieving methods. For light microscopy several living specimens were picked up with a fine needle, fixed in 4% formalin in sea water, washed in distilled water, and transferred to anhydrous glycerol by slow evaporation. The specimens were mounted in glycerol and examined in permanent glycerol slides.

For transmission electron microscopy, specimens were fixed at room temperature in 2.5% glutaraldehyde in cacodylate buffer (pH=7.4), containing 13.1% sucrose during 2 hr. After washing with the same buffer they were postfixed in 2% osmium tetroxide for a night in a refrigerator. Postfixed specimens were progressively transferred through graded an ethanol series to acetone and embedded into Epon resin. After hardening, the resin at 60° C for 48 hours, ultrathin

sections were cut with glass knives, stained with aqueous uranyl acetate and Reynolds lead citrate on formvar coated grids. Ultrathin sections were viewed with a Jeol JEM-100B at 80 kV.

## RESULTS

### Light microscopy redescription (Fig. 1)

**Males** (n=3): L = 520-660 μm, a = 35.8-38.8, b = 4.5-4.7, c = 6.3-6.6. Body diameter at the level of cephalic setae = 7-8.5 μm, nerve ring = 15.5-18.5 μm, cardia = 15.5-18 μm, midbody = 13.5-17 μm, anus = 13.5-15.5 μm.

**Females** (n=2): L = 566-580 μm, a = 31.3, b = 4.2, c = 6.5-7.1. Body diameter at the level of cephalic setae = 7 μm, nerve ring = 17 μm, cardia = 18 μm, midbody = 18.5 μm, anus = 12 μm.

Body rather cylindrical in males, with maximal diameter situated anteriorly whereas the body is slightly fusiform in females. Body cuticle composed of broad and thick annules. Cephalic capsule situated anteriorly, and a terminal cone posteriorly; none having annulation or plates. The total number of annules between the cephalic end and terminal cone is 91-99 in males and 76 in a female. The annules are distributed along the male body as follows: oesophageal region - 17-19 annules, intestinal region - 55-64, tail region - 15-19. In the female body the annules are distributed as 17, 46, 13 in these regions.

Cephalic capsule bullet-shaped; cuticle thin at the apex, but thickens gradually posterior to the base where cuticle thickness is equal to that of further (postcephalic) annules. Cephalic capsule is 18-20.5 μm long in males exceeding the basal diameter in 1.35-1.4 times. In females the same measurements are respectively 21-22 μm and 1.5-1.6.

Postcephalic annules in optical section are thickly dense and lens-like; they are joined with intermediate membranes of thin, flexible cuticle. Vacuolization not present. Annules are unequal in width: they increase gradually from the first postcephalic annule to annule numbers 32 to 36 in males, or number 31 in female, just posteriorly to the cardia and measure between 3.5 μm and 8.5 μm (males) or 5.5 μm and 10 μm (females) in width. Smaller annules follow the wide annules at 31/36 where posteriorly they again increase gradually to the widest anal annule. Males have tail annules dorsally broader then ventrally. The tail annules decrease in width gradually to the terminal cone. Zygapophyses are weak and sinusoid. Eight longitudinal ridges (two sublateral and two submedian pairs) extend from the posterior margin of the cephalic capsule along the body to the tail cone. The ridges are formed by thin cuticular vanes on each annule. The vanes appear slightly S-shaped with the anterior tips bent dorsally and posterior ventrally at the left side, and *vice versa* at the right side, overlapping with the anterior and posterior vanes.

Mouth opening small. Four thin cephalic setae, 3.5-7 μm long in males, and 5-6 μm long in females. Somatic setae not observed further posterior to anal region. Amphid loopshaped, bent ventrally, situated on the posterior half of the cephalic capsule. Dorsal and ventral branches of the amphid are almost equal. In males the amphids are 7.5-9.5 μm long, and 4-4.5 μm wide (33-37% of corresponding body diameter). The same measurements of female are respectively 7 μm, 4.5 μm, and 33%.

Stoma is not differentiated. Oesophagus consists of three compartments: 1. anterior procorpus, slightly narrowing posteriorly and thin with distinct radial muscular striation, 2. intermediate narrowed isthmus without a discernible radial striation, 3. basal pear-shaped swelling without a radial striation. Cardia compact, embedded in the intestinal tissue. Rectum very long (38 μm in a male, 29 μm in a female) and proximally widened.

Nerve ring at the anterior isthmus. Renette cell behind the cardia, ventrally to the intestine. Cell neck of the renette extends anteriorly terminating with an ampulla and excretory pore between the nerve ring and cardia. The excretory pore in a male is situated on the 13th postcephalic annule (84 μm behind the cephalic end) and in female on 13th annule, too (115 μm behind the cephalic end).

Ovaries paired, antidromous. One of the females with a vulva between the 37th and 38th postcephalic annules, the other one - between the 38th and 39th annules. The largest and most developed oocyte in the ovary displaces a small spermatheca containing small round-shaped spermatozoans as well as a germinal zone to the vulva, or even further.

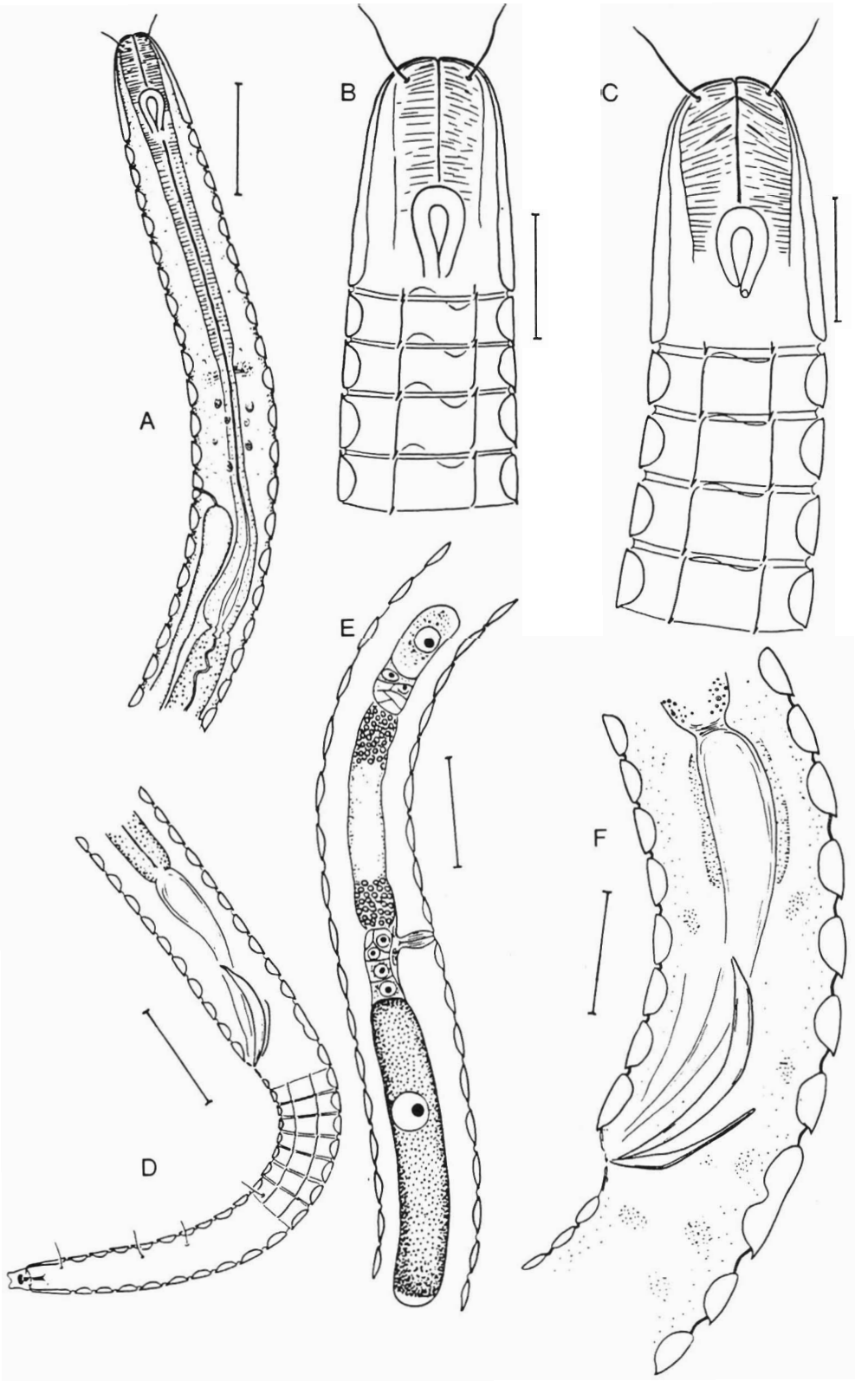


**Fig. 1.** *Pselionema simplex* (light microscopy drawings). A: Anterior body; B: Cephalic end of male; C: Cephalic end of female; D: Posterior body of male; E: Female gonad; F: Hindgut and copulatory apparatus of male. Scale bars: A, D, E - 20 μm, B, C, F - 10 μm

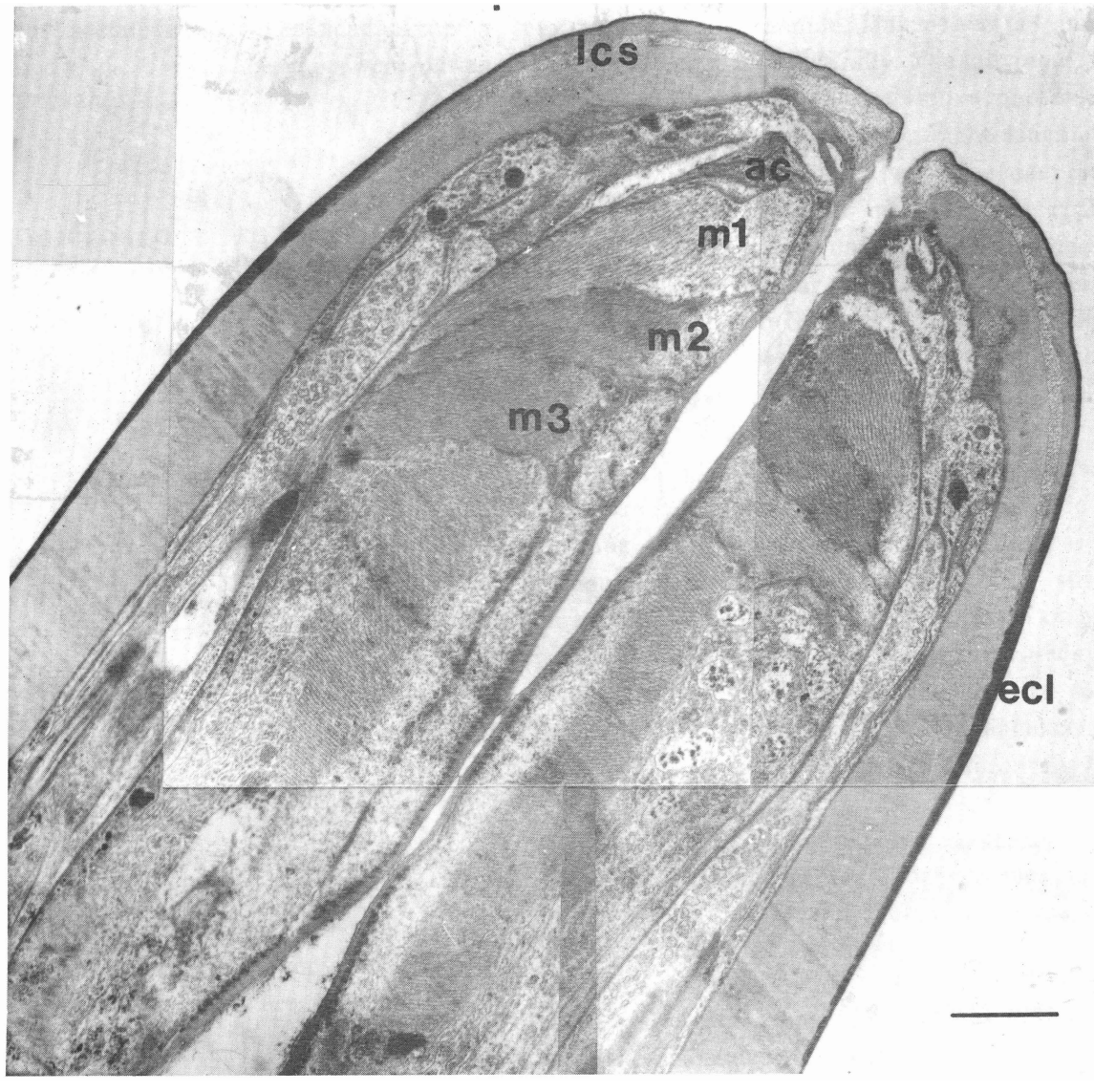


**Fig. 2.** Longitudinal section through the cephalic end and buccal cavity of *Pselionema simplex*. Magnification: x 6 000. Scale bar: 1 $\mu$m. Abbreviations to the figures: **ac** - arcade cells; **af** - amphidial fovea; **am** - adradial muscle; **bc** - buccal cavity; **c** - body cuticle; **ecl** - external cuticular layer; **en** - endocuticle; **ex** - exocuticle; **hd** - hemidesmosome; **ic** - interconnection between body cuticle annules; **icl** - internal layer of cuticle annules; **il** - intestinal lumen; **ld** - labial dendrite; **lcs** - loose cuticular sublayer; **ls** - labial sheath cell; **m1, m2, m3** - first, second, and third tiers of buccal muscle cells; **mc** - marginal cell; **mf** - myofilaments of the pharyngeal muscle cells; **mvi** - microvilli of the intestine; **mvr** - microvilli of the rectointestinal valve cells; **np** - neuropile of the nerve ring; **pg** - pharyngeal gland; **pl** - pharyngeal lumen; **pm** - paramarginal process; **pn** - pharyngeal nerve; **rl** - rectal lumen; **rvc** - rectointestinal valve cells; **sm** - somatic muscle cell; **tf** - tonofilaments of pharyngeal marginal cells; **z** - zygapophysis (overlapping projection of cuticle annule).

Testes paired. Spicules short (20-22 $\mu$m along the chord), arched, acuted at both tips. Gubernaculum a thin parallel plate 13.5 $\mu$m long. Cloaca region shaped by two annules fused dorsally.

Tail cylindro-conical, 6.6-6.8 anal diameters long in males, 7.8-8.1 in females. Tail annule gradually decreasing in width posteriorly. Terminal cone in a male is 11 $\mu$m long, in a female 13 $\mu$m long. Four pairs of lateroventral setae 6-7 $\mu$m long present on the male tail. A single setae on the female tail, absent in some specimens.

## Transmission electron microscopy

**Somatic cuticle.** The body cuticle consists of thick, dense annules with flexible interconnections between them. In longitudinal sections the annules are lens-shaped with external flat and internal convex surfaces (Figs. 6C & 7A). In the annules the external surface cuticular layer is very electron-dense, about 170-250 nm thick; it forms the overlapping projections or zygapophyses (Figs. 2, 3, 4 & 5D). Thickness of the

external layer is irregular being maximal at the zygapophysis's base. A trilaminar construction is not revealed in the external layer, as in *Metadasynemoides cristatus* (Nicholas & Stewart, 1990) but unlike the cuticle of *Ceramonema carinatum* (Stewart & Nicholas, 1992). Therefore, it is not evident whether the external layer corresponds to epicuticle in the general pattern of nematode cuticle (Maggenti, 1979; Bird & Bird, 1991). The bulk of the annule is an amorphous electron-lucent material about 1.05-1.47 $\mu$m thick in different places. This layer contains scarced vague radial veins. The veins are more distinct in the middle region of the electron-lucent bulk; they appear as canals with a thingranular content (Figs. 4C & 5D). The internal surface cuticular basal layer of the annule is homogeneous, thinner and less electron-dense than external one (38-60 nm, Fig. 4B, C). The interconnections between annules are bent inside the body and are 3-4 times thinner (0.6-0.7 $\mu$m) than the latter ones (Figs. 3C,D & 6C). The external surface layer of the interconnections is electron-dense and osmiophilic as a continuation of the external layer of the annule. The interconnection is sharply separated from the annule and shows a flaky laminar construction where six - seven parallel electron-lucent and electron-dense laminas alternate. The laminas are not very distinct and may become indistinct towards the internal surface.

**Cephalic end.** The cuticle of the cephalic capsule is only weakly modified or almost identical to that of the body annules (Fig. 2). The cuticle narrows gradually from the cephalic base to the mouth opening and is not accompanied by a perioral enlargement. A thin sublayer of friable granular material is present adjacent to the mouth opening in the electron-lucent median layer (Fig. 2). This sublayer also resembles a friable undifferentiated mesocuticle present in some monhysterid nematodes with normal generalized cuticle (Tchesunov, 1990b). The median elecron-lucent homogen layer is cleaved by the sublayer into two strata differing in some details: the internal stratum retains the original ultrastructure and the thinner external stratum is finely granulated with a densed subsurface zone.

**Pharynx.** The buccal capsule is not differentiated (Fig. 2). The walls of the cheilostoma are formed by somatic cuticle. A thin surface layer of the internal pharyngeal lumen wall appears slightly dense. The cuticle of the anterior division of the oesophastoma (buccal compartment) is thin (about 95 nm), more dense than cuticle of the cheilostoma and not separated by a seam from the latter. This cuticle continues posteriorly in the pharynx and appears only slightly modified. The anteriormost buccal compartment is surrounded by an arcade tissue (Fig. 2). There are three tiers of the oesophageal muscles separated by cell membranes in the oesophastoma region. The muscles appear almost wedge-shaped with narrow ends turned to the basal lamina and wider ones to the cuticular lining of the pharynx. Myofilaments of the muscles are directed obliquely to the longitudinal body axis (Fig. 2). There are no cross cell membranes further posterior along the anterior muscular pharynx.

At the level of cephalic setae the pharynx is three-lobed in cross section (Fig. 8A). There are two muscles in each interradius: the anteriormost muscle occupies a periferal position whereas the second muscle is displaced by a cuticular lining. At this point each muscle contains a single interradial fan of the myofilaments. Marginal cells join to the cuticular radii. The marginal cells contain tonofilaments connecting the inner cuticular lining with the basal lamina. Each marginal cell is surrounded by two cell processes of unknown origin, here named paramarginal cells; these processes do not have any specific cytostructures (Figs. 4A & 8A, B). They probably refer to the anteriormost pharyngeal cells. There are six nerve chords, each of them situated between paramarginal process and the cuticle (Fig. 8A). The nerve chords consist of three or four fibers.

The pharynx becomes round in cross section at the level of the anterior amphids (Figs. 4 & 8B). There are two muscles in each oesophageal sector; each muscle contains two bundles of myofilaments and many tiny vesicles, but mitochondria are not visible. Marginal cells develop lobes surrounding the cuticular radii. Each marginal cell has two paramarginal processes laterally (perhaps these are posterior continuations of the anterior paramarginal processes). There are three nerve strings composed of four fibers situated between the muscles of each pairs, close to the basal lamina.

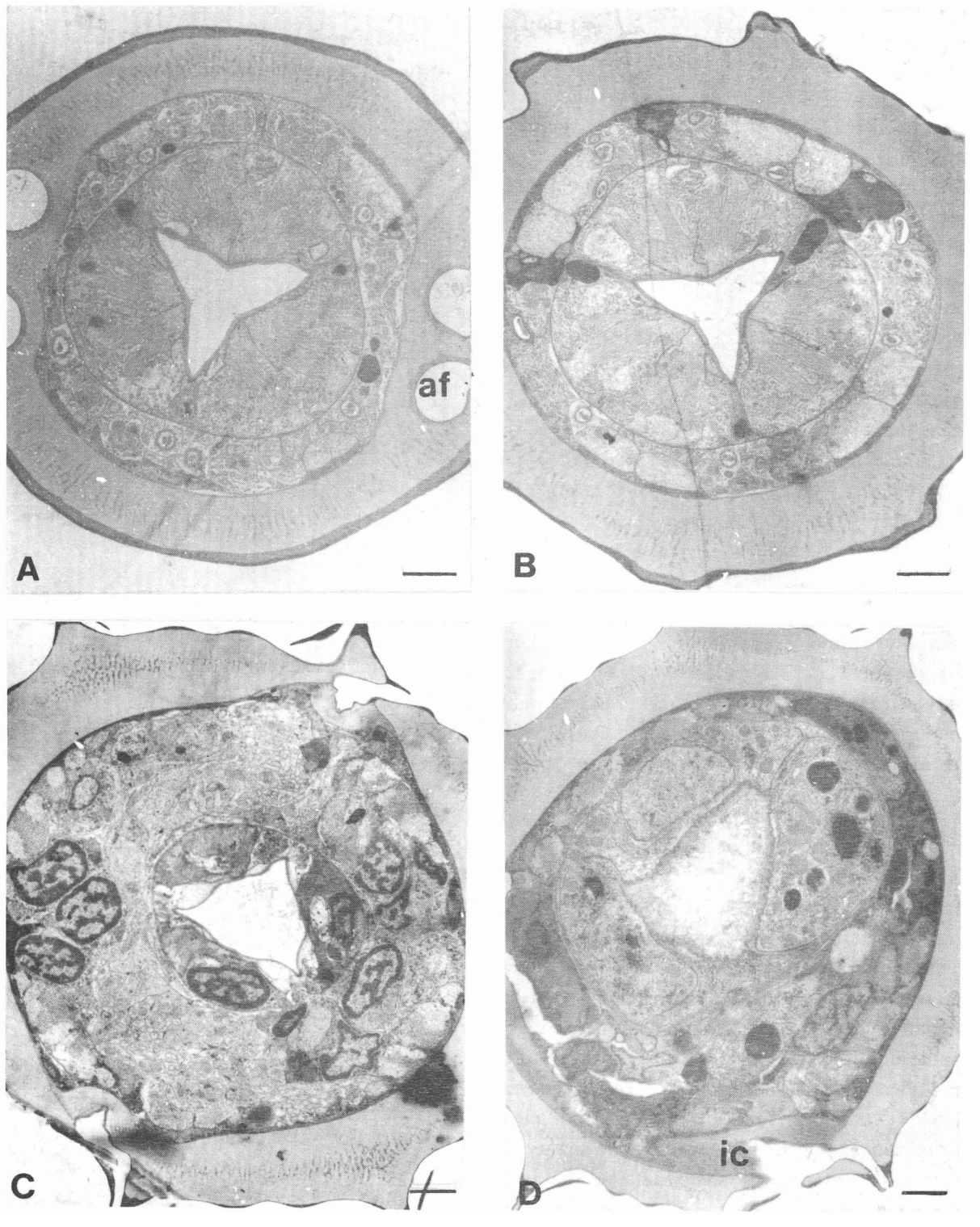


**Fig. 3.** Transversal sections of *Pselionema simplex*. A: At the level of amphids; B: Cephalic capsule posterior to amphids; C: At level of the median narrowed pharynx and the nerve ring; D: Anterior intestine. Magnifications: A, B - x 6 000; C, D - x 5 000. Scale bars: 1 μm.

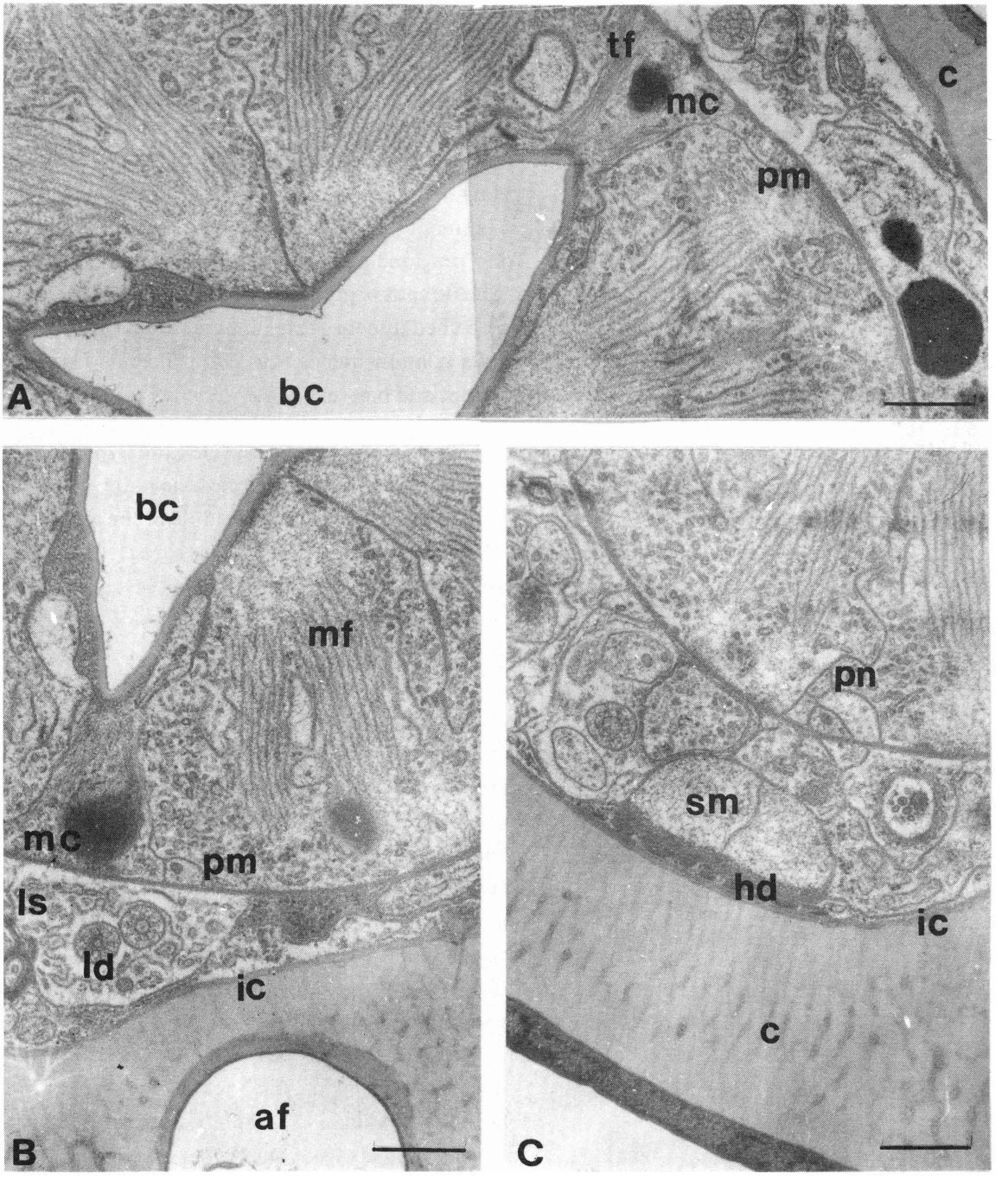


**Fig. 4.** Transversal sections of *Pselionema simplex* at the level of amphids (enlargement of parts of Figure 3A). A: Dorsal part of the pharynx; B: Dorsolateral part of the section showing marginal cell and cephalic sensilla dendrites; C: Ventrolateral part of section showing anterior ends of myocytes. Magnifications: x 20 000, Scale bars: 0.5 μm.

At the level of the posterior amphids, and posterior to the buccal capsule, the pharynx remains strongly muscular. The pattern of muscles is the same as described previously (Figs. 3A, B & 8C). In this section the muscles possess two bundles of myofilaments in oblique angle one to another, and mitochondria are present. The cytoplasm in the central region close to the cuticle is electron-lucent. The marginal cells contain nuclei surrounding the cuticular radii with their lobes. Paramarginal processes are not present. There are pharyngeal glands situated beween the muscles of each pair of sector. Outlets of the

pharyngeal gland cells were not detected, but it is probably that they are situated in the anterior pharynx. Nerve cell bodies containing nuclei are situated between the muscles at perifery of each sector pair in the pharyngeal glands. These nerve cells are identified by having numerous tiny vesicles in their cytoplasm.

The pharynx narrows to the isthmus region just anteriorly to the nerve ring (Figs. 3C & 8D). The cuticle of the radii at this position is electron-lucent, slightly inflated in places where they are surrounded by the lobes of the marginal cells. The cell pattern in the isthmus is simple. Each pharyngeal sector possesses only one muscle cell with two bundles of myofilaments. Each bundle contains 7 to 11 myofilaments. The myofilament bundle number is twice reduced and the isthmus region is less muscular than the anterior procorpus. There is a pharyngeal gland cell within each sector muscle. The marginal cells contain tonofilaments.

The pharynx forms a pear-shaped thickening at the posterior end. The cuticle is strongly inflated and at this location is electron-lucent interradially. The general cell pattern is identical to that in the isthmus, however, the interradial cells do not contain myofilaments (Fig. 8E). The bulk volume of the interradial cell is occupied by the pharyngeal cell body. The cytoplasm of the gland cell contains rough endoplasmatic reticulum and secretory globules. The latters are different in the dorsal and the fine granulated subventral glands: subventral globules appear more condensed. Both the interradial and gland cell bodies contain nuclei. The marginal cells are voluminous, lobate, with nuclei and electron-lucent cytoplasm, but without tonofilaments.

**Midgut.** In cross-section the intestine consists four cells (Figs. 3D & 8F). The internal surface cell membrane forms short, almost conical microvilli (120 - 150 nm long) with apical osmiophilic dense tips. The microvilli are submerged in a glycocalyx layer comparable in its density to that of a peritrophic membrane. The intestinal cells have amorphous osmiophilic inclusions in vacuoles, mitochondria and well developed endoplasmatic reticulum. The cells possess lobate projections underlying the adjacent cells basally (Figs. 5C, D & 6A).

**Hindgut.** The rectum is elongated and expanded anteriorly to the recto-intestinal valve (Fig. 6A, C). The rectal cuticle is thin (60-70 nm), structurally simple, amorphous and gradually narrowing from the anus to the valve. There are rounded cells with long microvilli (1.3-2 $\mu$m long, 0.06-0.07 $\mu$m wide) protruding into of the proximal expanded lumen of the rectum. These cells are not covered with a cuticle but are provided only with a plasmalemma. Long entangled threads of glycocalyx attached to the microvilli are stretched into the rectal lumen. The microvilli-bearing cells contain nuclei; the cytoplasm is elecrontransparent and has very few organelles (Fig. 6B).

**Body wall: somatic muscles and hypodermis.** The front ends of the anteriormost somatic myocytes are situated at the level of the middle of the amphid (Figs. 3A & 4C). The myocytes are disposed in two subdorsal and two subventral pairs. At this level the myocytes occupy totally 22% of the body wall circumference (Fig. 3B).

At the level of the middle procorpus the myocytes are arranged in pairs but are broader here and occupy in total 40% of the body wall circumference. There are additional longitudinal myocytes at this level which adjoin to the pharyngeal basal lamina and not to the subcuticular hypodermis. These are a total of six circumpharyngeal myocytes: two lateral, two subdorsal and two subventral. The subdorsal and subventral circumpharyngeal muscles are displaced respectively dorsally and ventrally from lateromedian pairs of the parietal myocytes.

At the level of posterior procorpus the muscle bands consist of four myocytes. The muscles occupy here 47% of the body wall circumference. There are no circumpharyngeal muscles at this level.

At the level of the nerve ring (anterior isthmus) each muscle band is composed of three myocytes, and the muscle layer covers 42% of the body wall circumference (Fig. 3C).

In the region of the anterior midgut the lateral hypodermal chords are very wide and displace the muscle bands medially. Each muscle band consists of three myocytes. The layer of longitudinal muscles occupies in sum 40% of the body wall circumference (Fig. 3D).

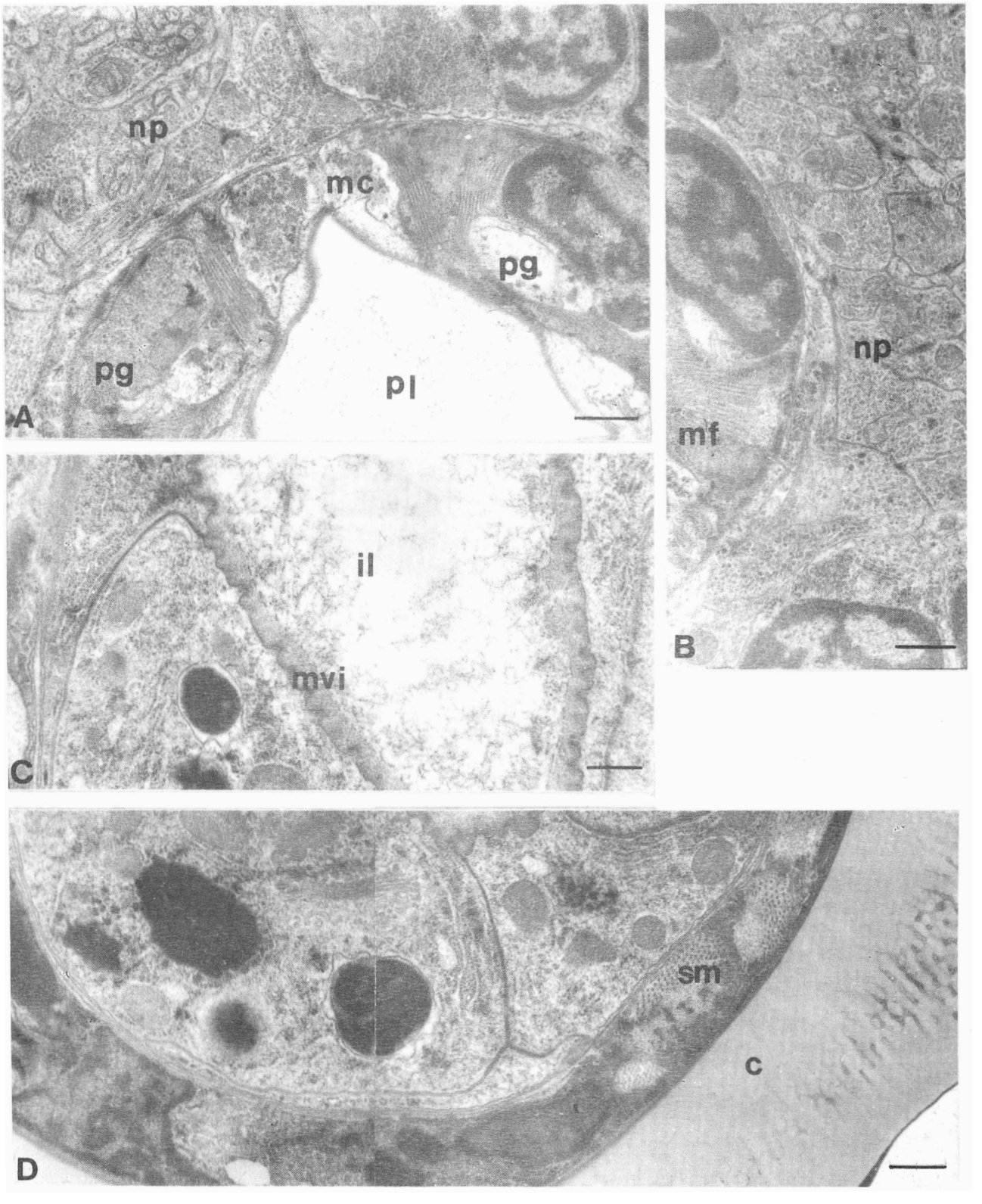


Fig. 5. Transversal sections of *Pselionema simplex*. A & B: At the level of median narrowed amphid and the nerve ring (enlargement of parts of Figure 3C); C & D: Anterior intestine (enlargements of parts of Figure 3D). Magnifications: x 15 000. Scale bars: 0.5 μm.

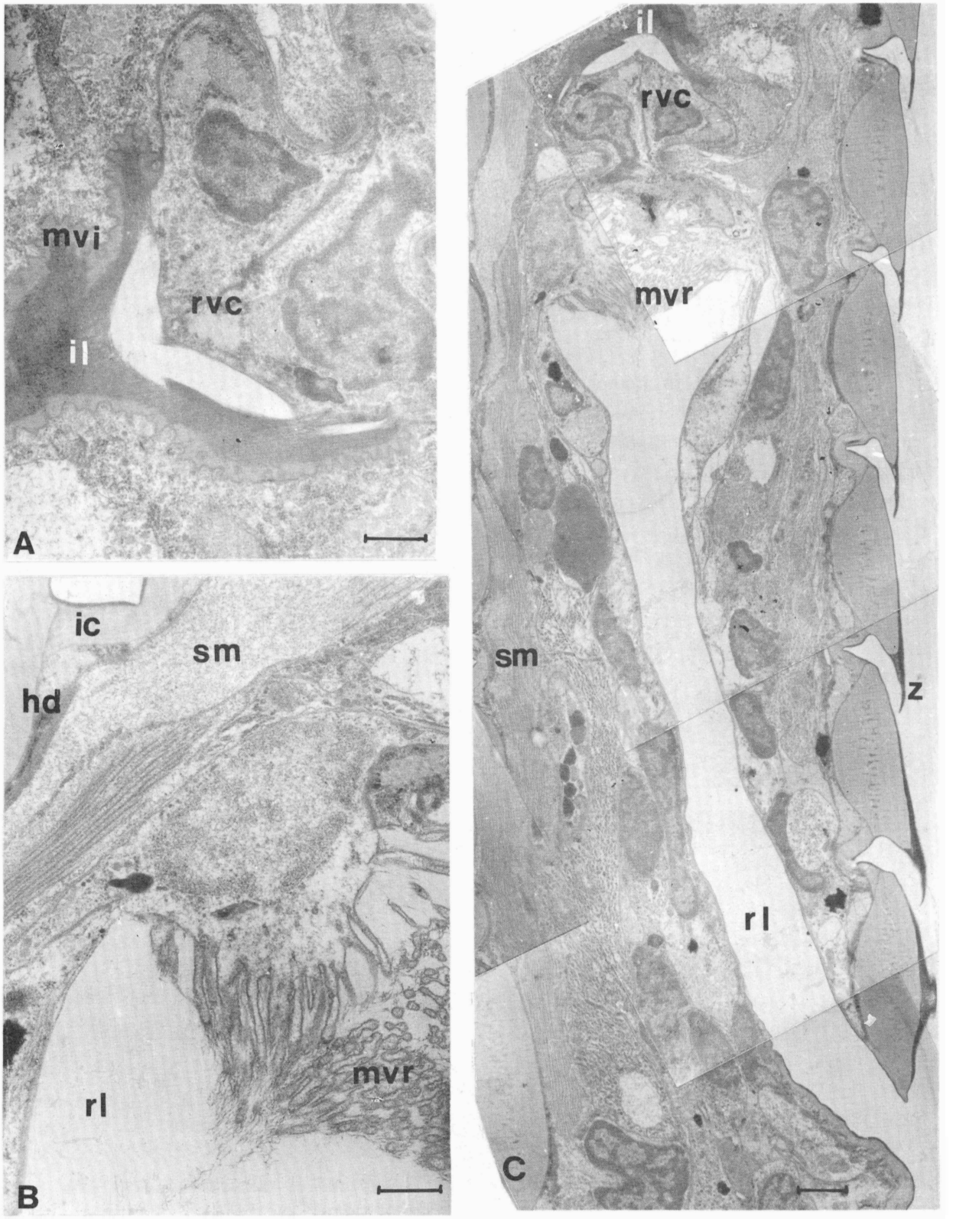


Fig. 6. Longitudinal (sagittal) section of *Pselionema simplex* through the rectum region. A: Rectum and rectointestinal valve; B: Valve cells (enlargement of part of Figure 6A); C: Microvillar cells (enlargement of part of Figure 6A). Magnifications: A, B - x 15 000, C - x 6 000. Scale bars: A, B - 0.5 μm, C - 1 μm.

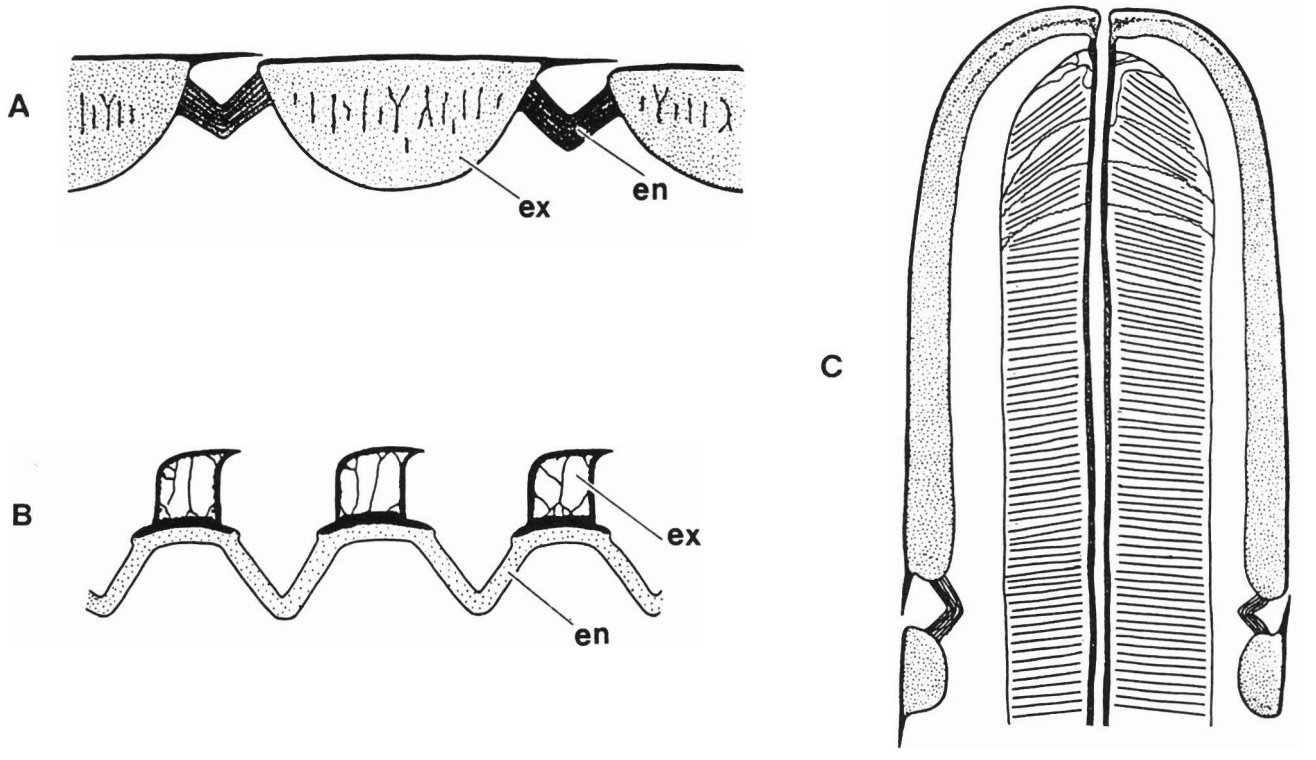


Fig. 7. Comparative schematic representation of the cuticle of (A) *Pselionema simplex* and (B) *Metadasynemoides cristatus* (cf. Nicholas & Stewart, 1990). C: Schematic drawing of cephalic end of *Pselionema simplex*.

In all body regions examined the pharynx and intestine are flattened tightly to the muscles and hypodermis of the body wall, i. e. there are almost no interspaces. Therefore, there is almost no true body cavity in the pharyngeal and anterior intestinal regions.

## DISCUSSION

**Taxonomy.** *Pselionema simplex* was described by De Coninck (1942) based on males from the Mediterranean Sea and has not been redescribed. The White Sea specimens described here differ slightly from the original diagnosis in several measurements and ratios such as body length (520-660 $\mu$m *vs* 425-546 $\mu$m), spicule length (20-22 $\mu$m *vs* 16-19 $\mu$m), «b» (4.5-4.7 *vs* 3.1-3.3), «c» (6.3-6.6 *vs* 4.35-4.6) and number of cuticle annules (91-99 *vs* 70-76). These differences are regarded as intraspecific variations.

*Pselionema simplex* is the first ceramonematid nematode species reported from the White Sea.

**Cuticle.** The cuticle of *Pselionema simplex* differs from that of general nematode pattern which is comprised of the following layers: epicuticle, cortical zone, median zone and basal zone (Bird & Bird, 1991) or epicuticle, exocuticle, mesocuticle, and endocuticle (Maggenti, 1979). The cuticle of *P. simplex* (Fig. 7A) is composed of solid rings (like sclerites) alternating with flexible interconnections (like articulate membranes) possibly comparable superficially with cuticles of other segmented animals such as arthropods and especially kinorhynchs (Adrianov et al., 1990) than with generalized nematode cuticles.

It is has not been determined which zones, if any, in the cuticle of *Pselionema simplex* correspond to the layers defined by Maggenti and Bird & Bird. To resolve the problem the highly specialized cuticle of *P. simplex* can be compared with that of *Metadasynemoides cristatus* investigated by Nicholas & Stewart (1990). The cuticle of *M. cristatus* appears more generalized or plesiomorph as it consists of many (600-800)

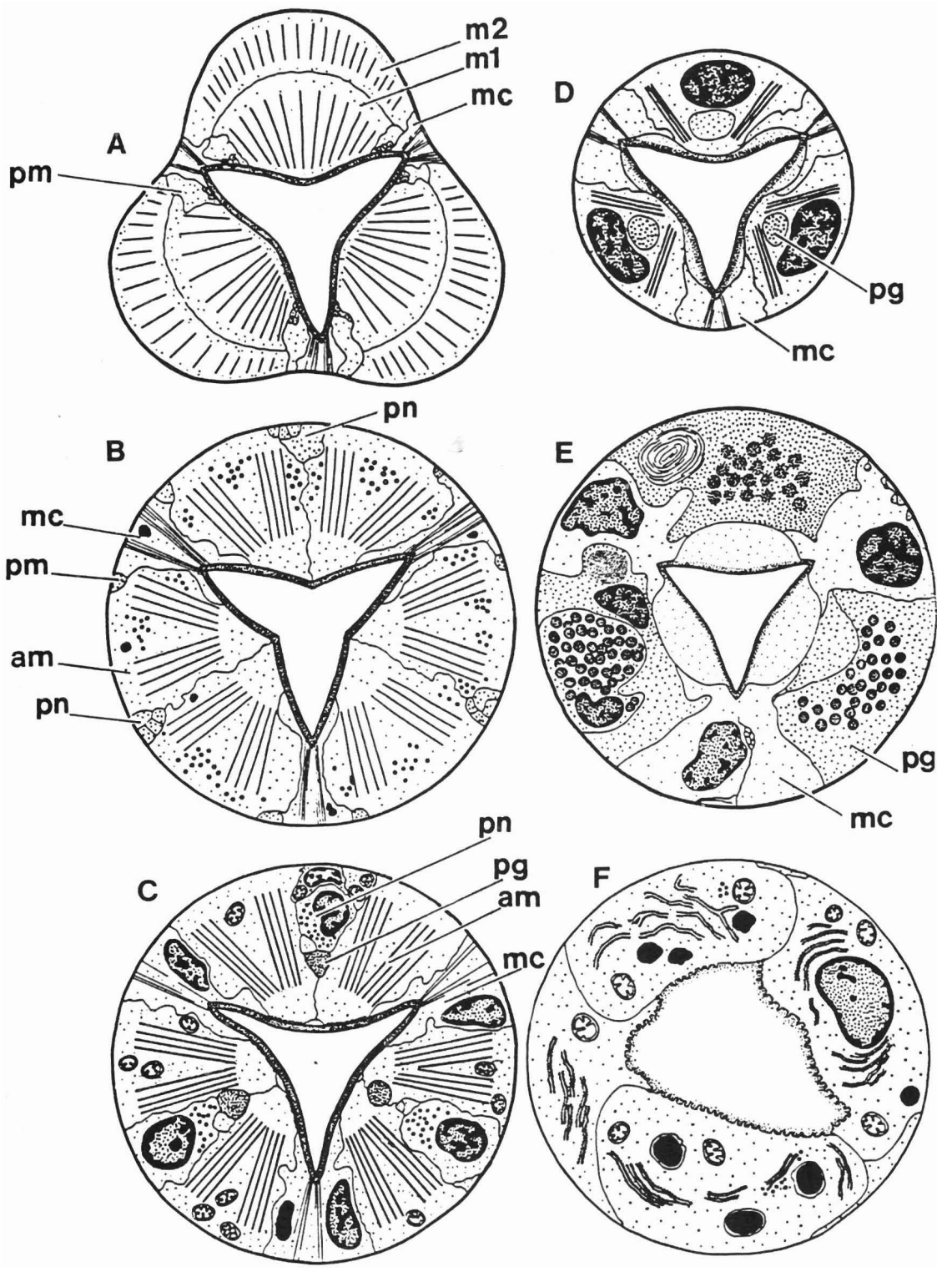


Fig. 8. Diagrammatic illustration of transversal sections of the alimentary tract of *Pselionema simplex* at the level of (A) cephalic setae, (B) amphids, (C) just posterior to the cephalic capsule, (D) median narrowed part of the pharynx (isthmus), (E) posterior widening of the pharynx, (F) anterior part of the midgut.

narrow annules without any noticeable zygapophyses. The flexible interconnections extend to the annules to underlye them as a basal layer (Fig. 7B). Therefore, this continuous basal layer may be designated as endocuticle (Maggenti, 1979) or basal zone (Bird & Bird, 1991). In *P. simplex* the striated flexible interconnections consequently represent also an endocuticle, but it is absent (evidently reduced) in the annules. The endocuticular flexible interconnections of the cuticle of *P. simplex* discontinuously alternate with that of the exocuticular annules in a manner similar to that of *Ceramonema carinatum* (Stewart & Nicholas, 1992).

**Pharynx.** The buccal cavity does not differ from the subsequent internal pharyngeal lumen neither in shape nor in cuticular lining. Therefore, this stoma type may be considered as being primitive for nematodes. It is possible however to identify the same three tiers of buccal muscle cells indicated in *Ceramonema carinatum* by Stewart & Nicholas (1994) and also in the monhysterid nematodes *Geomonhystera disjuncta* and *Diplolaimella dievengatensis* by Van de Velde & Coomans (1991). According to the latter authors the muscle cell tiers correspond to divisions of the buccal cavity into consecutive regions.

The pharynx (or oesophagus) consists of three distinct regions: anterior muscular procorpus, middle narrowed isthmus, posterior glandular pear-like widening. Lorenzen (1981) observed with the aid of optical microscopy a similar pharynx type in two ceramonematid nematodes, *Dasynemella sexalineata* and *Pselionema dissimile*. The pharynx of other ceramonematids is not or poorly described, apparently because usually it is almost indistinct when viewed through the dense cuticle.

Such a tripartite pharynx type is broadly distributed among marine nematode families which are not closely related, especially in smaller representatives: Diplopeltoididae s. str., Cyartonematidae, Camacolaimidae, Tarvaiidae, and also in certain genera of Leptolaimidae, Xyalidae (*Ammotheristus*), Tubolaimoididae (*Chitwoodia*), Desmodoridae (*Robbea*) (Tchesunov, 1990a). This phenomenon was considered a common trend in the evolution of marine nematodes and not evidence of phylogenetical relationships (Tchesunov, 1990a).

**Rectum.** The presence of the surface membrane microvilli in ectodermal cells not covered with a cuticle is a very rare character within Nematoda. Normally the cuticle lines the whole nematode body including all openings and invaginations such as buccal cavity, pharynx lumen, and cardia, vulva and vagina, openings of sensilles, distal portion of excretory canal (Bird & Bird, 1991). The body surface microvilli, as processes of hypodermal cytoplasm with absence of cuticle, are known in some entomophagous tylenchids absorbing nutrients from the haemocoel of host insects (Riding, 1970; Subbotin et al., 1993).

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**Чесунов А. В.** Таксономия, морфология и ультраструктура свободноживущей морской нематоды *Pselionema simplex* De Coninck, 1942 (Chromadoria: Ceramonematidae).

**Резюме.** Описание морфологии и деталей ультраструктуры *Pselionema simplex* (Ceramonematidae), вида впервые обнаруженного в Белом море. Туловищная кутикула очень своеобразна: панцырная, плотная, состоит из широких и толстых ригидных колец, соединенных гибкими сочленовными мембранами. Кольца ультраструктурно просты и образованы гомогенным электронно-светлым материалом, покрытым с наружной и внутренней сторон тонким электронно-плотным слоем. Сочленовные мебраны с параллельной поверхности тела слоистостью. Показано, что светлый основной слой колец соответствует экзокутикуле, а сочленовная мембрана - эндокутикуле в генерализованной схеме расположения слоев кутикулы нематод. Соматическая кутикула головного конца очень слабо модифицирована. Фаринкс состоит из прокорпуса, суженного удлиненного истмуса и прекардиального расширения. Радиальные миофибриллы имеются только в прокорпусе и истмусе; прекардиальное расширение образовано телами фарингеальных желез. Кишка на поперечном срезе состоит из четырех клеток. В клетках ректоинтестинального клапана имеются длинные микровилли, обращенные в просвет задней кишки; кутикулярного покрытия здесь нет.