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On the histological anatomy of *Marimermis maritima* Rubzov & Platonova, 1974 (Nematoda: Enoplia: Marimermithida), parasite of a sea urchin

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Summary - *Marimermis maritima* Rubzov & Platonova, 1974 was found for the first time since its original description. A female over 8 cm long, parasitizing the body cavity of *Strongylocentrotus polyacanthus* (Echinodermata: Echinoidea) was collected in the upper sublittoral zone of Ushishir Island (Kuril Islands, north-eastern Pacific). The specimen resembles free-living nematodes in having well developed cephalic and cervical setae. Contrary to its first diagnosis *M. maritima* is provided with a normal alimentary tract, including muscular pharynx, polycytous intestine, rectum and anus. The female genital tract is paired, outstretched and contains numerous small oocytes. In the region of the vagina the body cavity is filled with a fibrous matrix and different cells including myocytes. Specialized vulvar muscles are absent. An emended diagnosis of Marimermithida and list of genera are provided. Because of the anterior sensilla pattern (6+10), anterior position of the pharyngeal gland openings, triradial internal lumen of the cardia, this taxon should be referred to Enoplia.

Résumé - ***Anatomie de* Marimermis maritima *Rubzov & Platonova, 1974 (Nematoda: Enoplia: Marimermithida), parasite d'un oursin*** - *Marimermis maritima* Rubzov & Platonova, 1974 a été trouvé pour la première fois depuis sa description originale. Une femelle de plus de 8 cm de longueur, parasitant la cavité générale de *Strongylocentrotus polyacanthus* (Echinodermata : Echinoidea), a été collectée dans la zone sublitorale supérieure de l'île Ushishir (Iles Kouriles, nord-est du Pacifique). Le spécimen ressemble à un nématode libre, ayant des soies céphaliques et cervicales bien développées. Contrairement à la diagnose originale, *M. maritima* possède un canal alimentaire normal, comprenant pharynx musculariséé, intestin pluricellulaire, rectum et anus. Le système génital femelle est pair, replié, avec de nombreux petits oocytes. Dans la région vaginale, la cavité est remplie d'une gangue fibreuse et de différentes cellules, y compris des cellules musculaires. Il n'y a pas de muscles vulvaires spécialisés. Une diagnose amendée des Marimermithida et un liste des genres sont données. En raison de l'arrangement des sensilles antérieures (6+10), de la position antérieure des ouvertures des débouchés des glandes pharyngiennes, de la lumière triradiée du cardia, le taxon étudié se rapporterait aux Enoplia.

Key-words: anatomy, *Marimermis,* Marimermithida, Marimermithidae, nematodes, sea-urchins, taxonomy.

Marimermithid nematodes are known as rare parasites of marine invertebrates. These nematodes were first described by Rubzov and Platonova (1974) from starfishes and sediment samples taken in the Kuril Islands and Kergelen Island waters. The authors established the taxa *Marimermis* and *Trophomera* as well as the family Marimermithidae Rubzov & Platonova, 1974 housing both genera. For the marimermithids, Rubzov and Platonova (1974) postulated larval parasitism in the body cavity of echinoderms and subsequent free living (evidently without feeding) and reproducing adult stages in bottom sediments. In the anatomy of marimermithids they also indicated some similarities to true Mermithida, larval parasites of aquatic and terrestrial invertebrates, mostly insects. Later, several other genera were described and included in Marimermithidae by Rubzov (1977, 1985*a*, *b*), and Tchesunov and Spiridonov (1985). But the species of the first genus, *Marimermis* Rubzov & Platonova, 1974, have long remained known only from type specimens. Here a new finding of *Marimermis maritima* Rubzov & Platonova, 1974 is reported together with new observations on its anatomy and some considerations on the taxonomy.

Methods

The living nematode was collected at Kuril Islands in north-eastern Pacific, more precisely at Ushishir Island, at a depth of 20 m, on July 1988, where it was extracted from the body cavity of a sea urchin (*Strongylocentrotus polyacanthus;* Echinodermata: Echinoidea: Regularia), and fixed with 4% formaldehyde in sea water.

The specimen was later dissected. The cephalic end was rinsed in distilled water, transferred to anhydrous

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glycerin by slow evaporation, and mounted in apical and lateral position in glycerin slides. Other selected body portions were washed in distilled water and postfixed with 1% osmium tetroxide for several days in a refrigerator. Postfixed portions were progressively transferred through a graded ethanol series to acetone and embedded into Epon resin. After the resin hardened at 60°C for 48 h, transversal sections of 2 μm thickness were cut with glass knives. The sections were stained with methylene blue and azur II during 3-4 min at 60°, then rinsed with basic fuchsin for a few minutes at room temperature.

Marimermis maritima Rubzov & Platonova, 1974

(Figs 1-4)

Mensurations

L = 81.5 mm; a = 131; b = 92; c = 325; V = 60.6. Body diameters, at the level of cephalic setae = 66 μm, of nerve ring = 240 μm, of cardia = 320 μm, at mitbody = 620 μm, at anus = 360 μm.

Description

Body long, cylindrical, thread-like, whitish, barely transparent. Thick smooth cuticle without visible lateral differentiation. Scarce and short somatic setae distributed along the entire body. Cephalic end in the shape of a rounded truncate cone. Body cuticle thinning anteriorly 10 μm (amphid level) to 4 μm apically. Mouth opening small, triangular. Three minute blunt inconspicuous projections or odontia present interradially. Six small inner labial papillae in oval depressions present around the mouth. Outer circle of ten thin setae 22-23 μm long (six outer labial setae a little longer than the four cephalic setae). Further posteriorly, somatic setae dispersed in lateromedian quadrants; these setae anteriorly nearly equal to outer labial setae. Amphid a minute pore behind the lateral outer labial seta, pore (amphidial aperture) followed by a small subcuticular sack (amphidial fovea), then by an amphidial nerve. Body wall consisting of cuti-

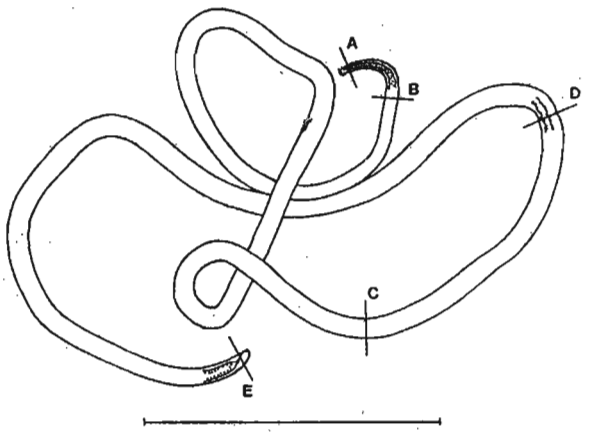

Fig. 1. Marimermis maritima, *female, total view. (Cross-lines marked with letters indicate sites of the sections represented on Fig. 3; scale bar = 1 μm).*

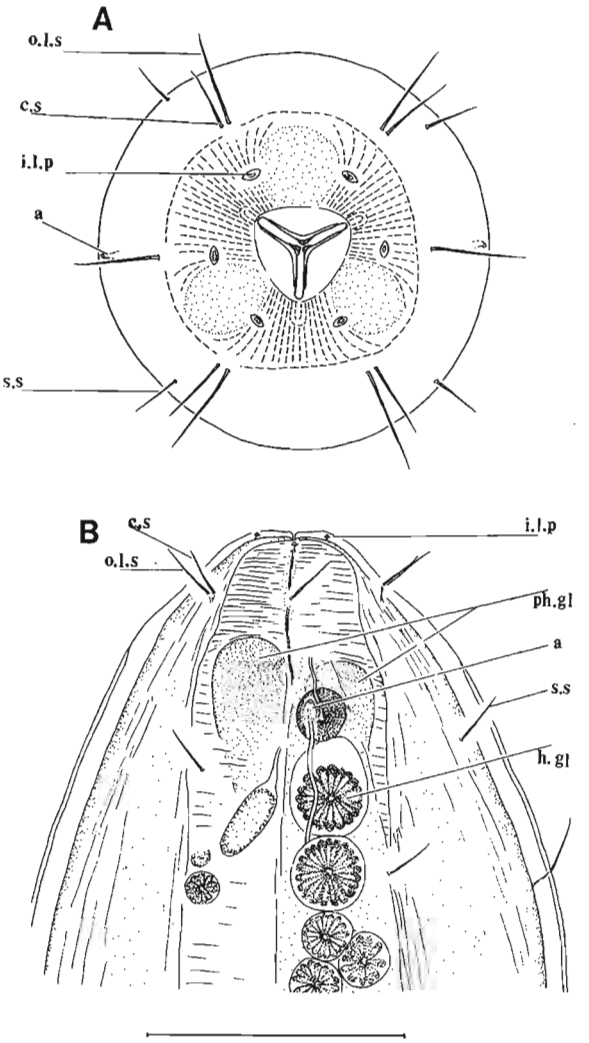

Fig. 2. Marimermis maritima, *female. A: Cephalic end, apical view; B: Cephalic end, lateral view (Scale bar = 100 μm). Abbreviations: a = amphid; c = cardia; c.s = cephalic setae; cu.m = circumuterial musculature; h.gl. = hypodermal glands; i = intestine; ic.ma = intercellular matrix; i.l.p = inner labial papilla; l.ch = lateral hypodermal chord; m = myocyte; md.ch = middorsal hypodermal chord; mv.ch = midventral hypodermal chord; o = oocyte; o.l.s = outer labial setae; ov.e = ovarial epithelium; ph = pharynx; ph.gl. = pharyngeal glands; r = rectum; r.p = rectal projections; sc = satellite cells; s.s = somatic setae; subd.ch = subdorsal hypodermal chord; subv.ch = subventral hypodermal chord; u = uterus; v = vulva; v.m = vaginal musculature.*

cle, hypodermis, and layer of longitudinal muscles (Fig. 3 A-C, E, F). Body cuticle smooth, 7.5-12 μm thick. No metanemes observed. Hypodermis composed of eight longitudinal chords separated by thin subcuticular layer. Subcuticle several times thinner than the cuticle. Lateral chords very broad, often more or less lobate, deeply protruding into the pseudocoelom (especially close to the anterior and posterior body ends). Clear cell borders present in the lateral chords. Cell bodies forming the lateral chords possibly differing to one another in content (strongly vacuolated or reticulate). Hypodermal nuclei concentrated in the lateral chords. Median and submedian chords very close to one another and much thinner than the lateral chords. Nerves could not be observed with certainty on cross-sections in the ventral and dorsal chords. Middorsal and midventral chords possibly containing nuclei in the pharyngeal portion of the body; subdorsal and subventral chords devoid of nuclei. Peculiar glandular structures present in the lateral chords, as spherical radially-structured bodies in large transparent vacuoles, looking like rosettes on cross-sections (Figs. 2 B; 3 A, B). Small rounded cavity with distinct wall present in the center of the rosette. A thin cuticularized canal running from the central cavity outwards to and through the body cuticle and obviously terminating in an external pore. Rosettes very numerous from the anterior part to the nerve ring region; less numerous posteriorly but occurring along the entire body down to the tail. In the pharyngeal and anterior intestinal regions, body musculature coelomyarian supplied with voluminous hyaline processes containing nuclei. In the anterior body region (from nerve ring to anterior part of intestine), presence of eight to ten myocytes between lateral and submedian hypodermal chords, three to seven myocytes between submedian and median chords on cross-sections (Fig. 3 A, B). In the middle of the body, myocytes less numerous: six to eigth between lateral and submedian chords, two to four between submedian and median chords. In that area, the myocytes are flattened against the body wall by internal organs; hyaline processes extremely scarce in the mid-body. Apparently, myocytes situated at mid-body much longer than those in the anterior and posterior regions. Number of myocytes per circumference on cross-section increasing again towards the posterior end. Just anteriorly to the rectum, presence of eight to twelve myocytes between the lateral and submedian chords and three to five myocytes between submedian and median chords. In sections of the hindbody region, the cell bodies of the myocytes again more numerous and projecting freely into the pseudocoelom (Fig. 3 F). Alimentary tract: buccal cavity not developed. Pharynx muscular, nearly cylindrical, gradually widening posteriad. Terminal ampullae of pharyngeal glands visible in the anterior inflated region of the pharynx; outlets of the glands located in the same region, at about the same level (Fig. 2 B). Pharynx with distinct cuticular internal lining throughout its entire length. In the posterior pharyngeal region, pharyngeal glands enlarged at the detriment of muscles. Cardia (pharyngo-intestinal valve) small, sunk into the intestine and with triradial internal lumen (Fig. 4 A). Midgut with a distinct internal lumen along its entire length, and consisting of numerous mononuclear cells. Anteriorly, intestine rather slender and, on cross-sections, with about 30 cells with distinct intercellular borders (Fig. 3 B). In gonadal region, intestine broadening; intestine and genital tract occupying almost the entire internal space of the body (Fig. 3 C). Epithelial intestinal cells in this region high columnar and about twice as numerous as in the anterior region. Intercellular borders hardly visible, perhaps because of dense granularity, big inclusions and vacuoles. In the uterus region, intestine thinner, the cells less in number and more flattened, especially ventrally (Fig. 3 E). Posteriorly, intestinal cells lower, and their number reduced to 20-30 on cross-section. Hindgut or rectum slightly dorso-ventrally flattened and with thick internal cuticular lining. Dorsally, three lobes or projections of epithelial tissue (rectal projections) adjoining the proximal rectum (Fig. 3 F). Female genital system amphidelphic, outstretched. Both branches very long: the anterior branch extending nearly to the cardia, the posterior one nearly to the anus. Gonads surrounded by a thin cellular epithelial layer (Figs. 3 C-E; 4 B, C). Germinal zone terminal. Gonads densely filled with oocytes gradually increasing in size towards the vagina. Distal oocytes rather small, with nuclei and nucleoles, and coarse granularity (vitelline droplets?). Genital branches becoming larger towards the vagina. Large proximal oocytes densely granulated by differently stained, coarse glo-bules with nuclei not so visible. Very dense intercellular matrix in distal regions of the gonad. In the same sites presence of groups of small oval cells (satellite cells) in narrow interstices between masses of intercellular substance and oocytes (Figs 3 D; 4 C). Satellite cells with transparent cytoplasm with vesicules and relatively big nuclei with nucleoli. The most proximal region of the genital branch (uterus) formed of cubic epithelium with distinct basal lamina and low cells with polarized cytoplasm and oval nuclei with nucleoli (Fig. 3 E). Uterus surrounded with non-cellular fibrosity; longitudinal circomyarian myocytes without visible cytoplasmic processes over the uterus inside and above the fibrosity. On cross-sections, vagina in form of a simple invagination of the body wall involving also the muscle layer (Fig. 3 E). No specialized dilatator muscles detected in the vulva region, but small short myocytes

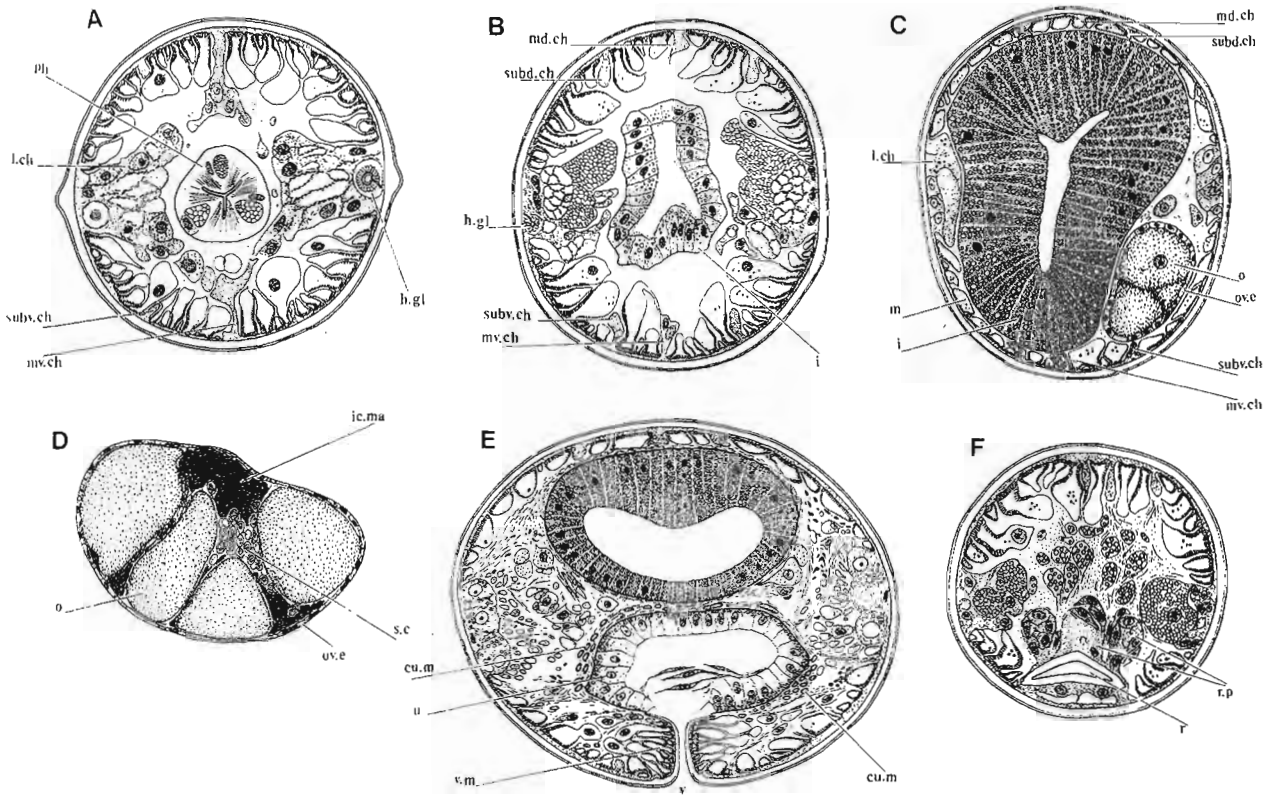

Fig. 3. Marimermis maritima, *female: A: Cross-section at the level of the pharynx just behind the nerve ring (level "A" on the Fig. 1); B: Cross-section at the level of anterior intestine between cardia and tip of the anterior gonad (level "B" on the Fig. 1); C: Cross-section at the level of the anterior female genital branch with oocytes within (level "C" on Fig. 1); D: Cross-section of the anterior female genital branch (between the levels of "C" and "D" on Fig. 1); E: Cross-section at the level of vulva (level "D" on Fig. 1); F: Cross-section at the level of rectum (level "E" on Fig. 1). (For abbreviations, see Fig. 2).*

with cytoplasmic bodies present, overlying one another along the walls of the vagina, and so possibly forming a contractile ring around the vagina. In the anterior part of the body, from the nerve ring to the anterior intestine, body cavity voluminous and filled with a liquid (pseudocoelom) (Fig. 3 A, B). Intercellular aggregates of a granular substance and separate cells present in the pseudocoelom. In the mid-body region, voluminous intestine and genital tract occupying nearly all of the internal space, reducing the body cavity to interstices between the internal organs and the body wall (Fig. 3 C). In this region, pseudocoelom filled here and there with undefinite scattered or concentrated fibres with sparse cells having big granular inclusions. At the level of uteri and vagina, internal space occupied with rather dense heterogenous granular-fibrous material with drops of an amorphous substance (Fig. 3 E). Fibres (scattered or concentrated) forming a layer of parallel fibres around the intestine and the uteri. Uteri surrounded with irregular groups of longitudinal myocytes. Apart from that, presence of rather big cells (some of them having coarse granular cytoplasm) with processes inserted into the intercellular material. Other longitudinal cell processes also numerous in the intercellular material near the lateral chords. Close to the rectum, internal space extending and containing granular-fibrous material with vesicular bodies, cells with processes and vacuolated cells inserted (Fig. 3 F).

Discussion

Comparison with the original description

The only previous record of *M. maritima* is from the coast of Simushir Island (Kuril Islands, North-Eastern Pacific), at 10 m depth, on a stony bottom; six female specimens were found free (Rubzov & Platonova, 1974). All measurements of the newly described specimen correspond well to those of the type females (L = 54 - 99 mm; a = 106 - 136; b = 68 -

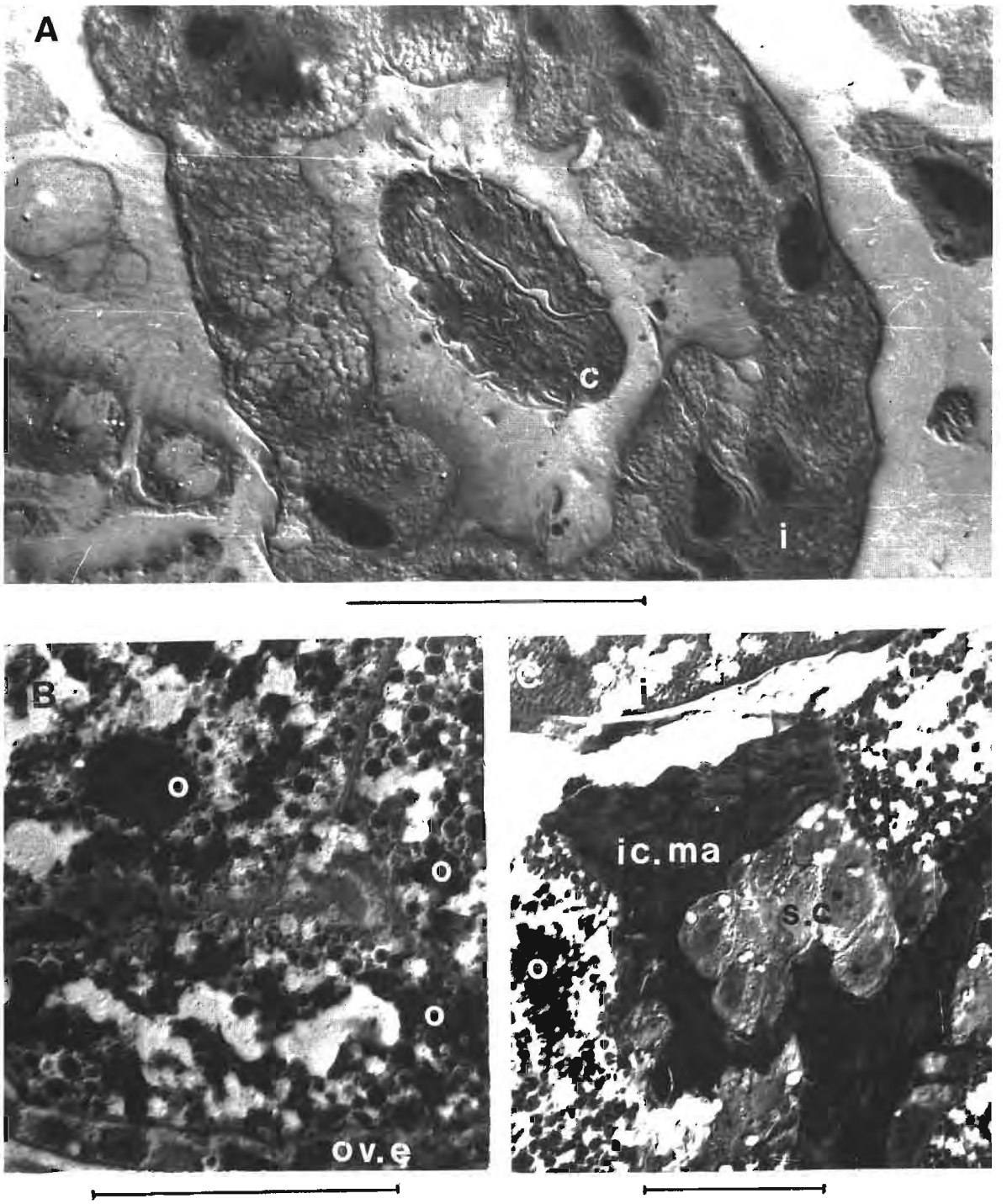

Fig. 4. Marimermis maritima, *female. A: Cross-section at the level of cardia; B-C: Cross-section of the ovary. (Scale bars = 100 μm; for abbreviations see Fig. 2).*

85; V = about 52; body diameters: at the level of cephalic seta = 76 - 80 μm, of nerve ring = 270 - 290 μm, at midbody = 500 - 650 μm, at posterior end of the intestine = 400 - 460 μm).

However, some anatomical differences in the specimen described here are more significant than described earlier and contradict sharply both specific and generic original diagnoses: *i*) the pharynx is of a generalized nematode type, muscular, cylindrical, without stichocytes; *ii*) midgut does not present a trophosome but rather a normal intestine with distinct internal lumen; *iii*) the intestine is connected with a normal rectum without any indication of reduction. Therefore the alimentary tract is not strongly modified but, rather, resembles that of the majority of other nematodes. The original description did not mention the rosette-like bodies which are glandular structures with an internal central reservoir inside. The differences between the original and present descriptions are supposed to be due to difference in methods, as Rubzov and Platonova (1974) inspected non-stained cross-sections hand-made in glycerin-gelatin with a razor; such sections are too thick to allow an accurate observation of the anatomical details.

Peculiar features in the morphology of *Marimermis maritima*

M. maritima, as well as its congeners, differs sharply from typical parasitic nematodes in having long and numerous cephalic and somatic setae as well as amphids in a lateral position behind the labial region. In these respects, they resemble free-living nematodes. From what can be seen into cross-sections the alimentary tract serves for normal feeding, *i.e.,* it does not resemble that of true mermithids. On the other hand, *M. maritima* exhibits some noticeable features discussed below.

Similar prominent and deeply protruding lateral chords were shown by Timm (1953) for the large marine free-living nematode *Leptosomatum acephalatum* (Enoplida: Leptosomatidae). *M. maritima* generally resembles leptosomatids in cephalic structures and overall habitus. The majority of adult *Marimermis* specimens were found by Rubzov and Platonova (1974) free in sediments. Hence, it is supposed that adult specimens abandon their hosts for reproduction outside in environment. Can they also feed there as free-living nematodes? However, unlike free-living nematodes, the adult females of *M. maritima* lack caudal glands and are provided with female gonads producing a large number of comparatively small eggs.

Internal space constitutes a true pseudocoelom in the anterior body, while the pseudocoelom is reduced to narrow spaces between the body wall and internal organs in the midbody. In the vaginal region, this internal space is filled with a granular substance which surrounds numerous cells. Such condition is unusual for nematodes (cf. Chitwood & Chitwood, 1950; Bird & Bird, 1991).

The last structure to be emphasized is the vagina. Unlike the majority of nematodes in which a system of specialized muscles opens the vagina, that of *M. maritima* seems to possess a vagina formed by a simple invagination of the body wall including the longitudinal muscles.

Systematic position of *Marimermis*

Rubzov and Platonova (1974) erected the new family Marimermithidae including *Marimermis* together with two other genera, *Trophomera* Rubzov & Platonova, 1974 and *Thalassonema* Ward, 1933, which were the only genera known at the time. Later, the genera *Ananus* Rubzov, 1977, *Acronema* Rubzov, 1978 and *Australonema* Tchesunov & Spiridonov, 1985 were described and included in Marimermithidae (Rubzov, 1977, 1978, 1985*a*,*b*; Tchesunov & Spiridonov, 1985). Rubzov (1980, 1985*b*) also proposed a new order, Marimermithida Rubzov, 1980, including the genera *Benthimermis* Petter, 1980, *Abos* Rubzov, 1980, and *Adenodelphis* Petter, 1983.

These genera, however, differ from one another in significant morphological features. *Benthimermis* contrary to *Marimermis* and allies has an abnormal alimentary tract, namely a trophosome built of big cells retaining only a thin capillary lumen, scarcely connected within the reduced pharynx and rectum. The other features of *Benthimermis,* cephalic sensilla pattern (six more or less reduced papilla + four short setae), rows of tiny lateral setae along the body, reflexed ovaries, also place it apart from Marimermithidae. Petter (1980) erected the new family Benthimermithidae for *Benthimermis* and subsequently placed *Abos* and *Adenodelphis* in this family. The genus *Trophomera* is very similar to these three genera in being provided with cephalic sensilla and alimentary tract; therefore, it is suggested to include it in Benthimermithidae as well. Like true marimermithids, the larval stages of benthimermithids are parasites in body cavities and other internal organs of deep-sea bottom-dwelling invertebrates, while free adults inhabit sediments where they obviously spend their trophosome food stock and reproduce. The family Benthimermithidae is provided with such peculiar characters that it can not be included in one of the existing nematode orders; therefore it was proposed to rise this taxon up to order level (Tchesunov, 1995).

The species *Acronema antarcticum* Rubzov, 1978 does not fit in either Marimermithidae or Benthimermithidae. The original description is based on a single juvenile specimen found near the Antarctic Continent in bottom sediment at the depth 230-

250 m (Rubzov, 1978). It probably belongs to one of the secernentean parasitic groups.

The order Marimermithida diagnosed below should be classified in Enoplia owing to the following features: optically smooth cuticle, uncoiled amphid in lateral position, six + ten pattern of cephalic sensilla, anterior position of dorsal and subventral pharyngeal gland openings, cylindrical pharynx without a terminal bulb, cardia with triangular internal lumen (the characters of higher subdivisions of Nematoda are summarized from Maggenti, 1963; Andrássy, 1976; Lorenzen, 1981; Adamson, 1987). Among other enoplian orders, the Marimermithida is close to the most generalized Enoplida. However, the order Marimermithida differs from Enoplida not only by its parasitic habits, but also by outstretched (*vs* anti-dromously reflexed) female genital tract, absence of caudal glands in adults, and probably by absence of metanemes. Overall resemblance to Mermithida as emphasized by Rubzov and Platonova (1974) consists in larval parasitism in invertebrates and subsequent free-living of adults. The marimermithids share almost no specific features with true mermithids, which are larval parasites of mainly fresh-water and terrestrial invertebrates.

Order Marimermithida Rubzov, 1980

Enoplia. Large nematodes up to 15 cm long. Cuticle thick and optically smooth. Cephalic sensilla: six papilla + ten setae. Uncoiled pore-like amphids. Cervical or somatic setae possibly present. Mouth opening triangular. Stoma not differentiated. Pharynx muscular, cylindrical, with triradial cuticularized internal lining of the lumen. Outlets of dorsal and two subventral pharyngeal glands at the same level in the anterior pharynx. Cardia with triangular lumen. Midgut polycytous, with true internal lumen. Rectum and anus generally present. Excretory system obscure; in genera *Ananus,* and *Australonema,* two parallel canals possibly observed in pseudocoelom, ventrally to the pharynx and the anterior midgut. Eight hypodermal chords; lateral chords wide, lobate, polycytous; median and submedian chords very thin. Female reproductive system amphidelphic with outstretched ovaries producing numerous small eggs. No caudal glands.

SINGLE FAMILY

Marimermithidae Rubzov & Platonova, 1974

TYPE GENUS

Marimermis Rubzov & Platonova, 1974

OTHER GENERA

Thalassonema Ward, 1933

Ananus Rubzov, 1977

Australonema Tchesunov & Spiridonov, 1985

Marimermis is well defined by long cephalic and somatic setae and rosette-like hypodermal glands. The other genera have much shorter cephalic setae and absence of visible somatic sensilla and rosette-like glands, which clearly differentiates them from *Marimermis*. On the contrary, *Ananus, Australonema* and *Thalassonema* differ from one another in obscured and, poorly studied characters such as presence/absence of anus or excretory canals. The subsequent synonymization of these three taxa is possible.

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