

## *Thalassomermis megamphis* n. gen., n. sp. (Mermithidae: Nemata) from the Bathyal South Atlantic Ocean

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**Abstract:** *Thalassomermis megamphis* n. gen., n. sp. (Mermithidae: Nemata) was extracted from sediment collected off the coast of Brazil at a depth of approximately 1,000 m. Although the food of this new nematode is unknown, the reduction of the stoma and esophagus and presence of a trophosome indicate that it is parasitic in its juvenile stages. *Thalassomermis megamphis* n. gen., n. sp. is assigned to Mermithidae because of its similarity to that family in the appearance of the cephalic sensory receptors, the long and tubular vagina, and copulatory muscles of the male extending posteriorly throughout most of the length of the tail. *Thalassomermis megamphis* n. gen., n. sp. differs from all other members of Mermithidae by the large, lenticular, intracuticular amphidial fovea with coiled, emergent terminal filaments as well as the small amphidial aperture situated over the center of the fovea.

**Key words:** Abyssal, Benthimermithidae, deep-sea, Foraminifera, marine nematode, Mermithidae, parasite, Rhaptothyreidae, *Thalassomermis megamphis* n. gen., n. sp., taxonomy.

Several species of nematodes recently found in the marine environment superficially resemble one another in having at least some degree of specialized reduction of the digestive system. In most cases this specialization includes transformation of the mid-gut to a trophosome or trophosome-like structure. The first such nematode to be described was *Rhaptothyreus typicus* Hope & Murphy, 1969, in which the mouth is absent, the esophagus is reduced, and the region of the mid-gut is occupied by a loose assemblage of cells, between which are bacterium-like endosymbionts (Hope and Murphy, 1969; Riemann, 1993). It is likely that these nematodes, for which only males are known, are free-living.

Search for females of *Rhaptothyreus* led to the discovery of more than 100 female and three male nematodes, all with a vestigial stoma and esophagus, and a trophosome instead of a gut. Although several new genera and species of nematodes were represented,

none were closely related to *Rhaptothyreus*. Juveniles, the youngest of which were armed with a stylet but otherwise resembled the free-living adults, parasitized ostracods of the genus *Zabythocypris* Maddocks, 1969 (Hope, 1977). These and related species were subsequently described by Petter (1980, 1981a, 1981b, 1982a, 1982b, 1983a, 1983b, 1987) and Tchesunov (1988a, 1988b) and assigned to the genus *Benthimermis* Petter, 1980 (Benthimermithidae). Other genera added to the family include *Abos* Rubzov, 1980 and *Adenodelphis* Petter, 1983. Nematodes, polychaetes, amphipods, isopods, cumaceans, and tanaids have been added to the list of known hosts of juvenile Benthimermithidae (Petter, 1980, 1983b; Petter and Gourbault, 1985; Tchesunov, 1995).

Mermithoidea, which includes Mermithidae and Tetradonematidae, are usually parasites of freshwater or terrestrial invertebrates and are not generally known to have representatives in the marine environment. However, *Echinomermella grayi* (Gemmill, 1901) Chitwood, 1933, which was originally collected from the body cavity of a sea urchin (*Echinus esculentus* Linnaeus, 1758) by Gemmill (1901), was assigned to Mermithidae by Chitwood (1933) because it has "... some similarities to the Mermithidae, namely, the character of the esophagus and the cuticle." Chitwood's (1933) assignment of this species to Mermithidae was provisional because, as he noted, a stylet had not

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been observed and the gut was not degenerate as in the Mermithidae. *Echinomermella matsi* Jones & Hagen, 1987 also parasitize sea urchins and was assigned to Mermithoidea, but is unique in that it is parasitic in the adult stage, not in the juvenile stages, and is ovoviviparous (Jones and Hagen, 1987). In this respect this species is more similar to *Heleidomermis magnapapula* Poinar & Mullens, 1987 (Mermithoidea: Mermithidae) and members of Tetradonematidae (Mermithoidea). The most recent report of a marine mermithid is *Nematimermis enoplivora* Tchesunov & Spiridonov, 1993 (Tetradonematidae), a parasite in the pseudocoelom of two marine *Enoplus* spp. (Tchesunov and Spiridonov, 1993).

Rubzov and Platonova (1974) also proposed the family Marimermithidae, which now includes *Marimermis* Rubzov & Platonova, 1974; *Ananus* Rubzov, 1977; *Australonema* Tchesunov & Spiridonov, 1993; and *Thalassonema* Ward, 1933 (Tchesunov, 1995). Whereas the known hosts of the marimermithid parasitic juveniles are echinoderms and polychaetes, the adults are free-living in sediments, where they apparently exist on nutrient reserves acquired in their juvenile stages. The stoma and esophagus of these nematodes are not degenerate, nor is the gut transformed into a trophosome.

From sediment samples taken off the coast of Brazil, we found another new genus and new species in which the digestive system is reduced and a trophosome instead of a normal gut is present. On the basis of these and other characters, it is assigned to the family Mermithidae and becomes the first well-documented example of a marine representative of that family.

#### MATERIALS AND METHODS

One male and one female were fixed in 10% formalin in sea water, processed into glycerol by the evaporation method, and mounted in anhydrous glycerol. Observations, camera lucida drawings, and photomicrographs were made with a Zeiss Photomicroscope II equipped with interference contrast optics.

#### SYSTEMATICS

##### *Thalassomermis* n. gen.

Body cylindrical. Cuticle thick with fine surface circumferential striations. Sixteen pore-like cephalic sensilla situated in single circle of six groups; two in each of two lateral, and three in each of four submedian groups. Amphidial fovea circular and large, but perimeter barely distinguishable. Aperture of amphidial canal near center of fovea with emergent terminal filaments coiled around perimeter of fovea.

Rudiment of oral aperture situated terminally. Vestigial esophagus slender, extending posteriorly from vestige of stoma through nerve ring to level of trophosome with sinuous lumen. Stichocytes not apparent. Vestigial esophagus without direct connection to trophosome. Trophosome cylindrical, filled with vacuoles and without internal lumen. Rectum and anus absent.

Males diorchic; gonads opposed and outstretched. Spiculum single, short, and dagger-like with retractor and protractor muscles attached to capitulum. Gubernaculum absent. Well-developed copulatory musculature present throughout length of tail as well as anterior to cloaca. Pre- and post-cloacal subventral supplements present on right and left sides of body. Tail bluntly rounded, and caudal glands absent. Female reproductive system amphidelphic and outstretched; vagina relatively long; eggs small and spherical.

*Type species: Thalassomermis megamphis* n. gen., n. sp.

*Thalassomermis megamphis* n. gen., n. sp.

*Male holotype:* L = 3.19 mm; a = 36.7; b = 5.3; c = 22.6. Body cylindrical, shorter, and thinner than female (Fig. 1A). Head region slightly conical with rounded oral surface (Fig. 2A); tail slightly conical with taper mostly on dorsal side and terminus rounded; caudal glands and aperture absent; tail length 1.9 cloacal body diameters (Fig. 4). Body diameter at level of cephalic sensilla 27  $\mu$ m; at amphidial pore 46  $\mu$ m; at

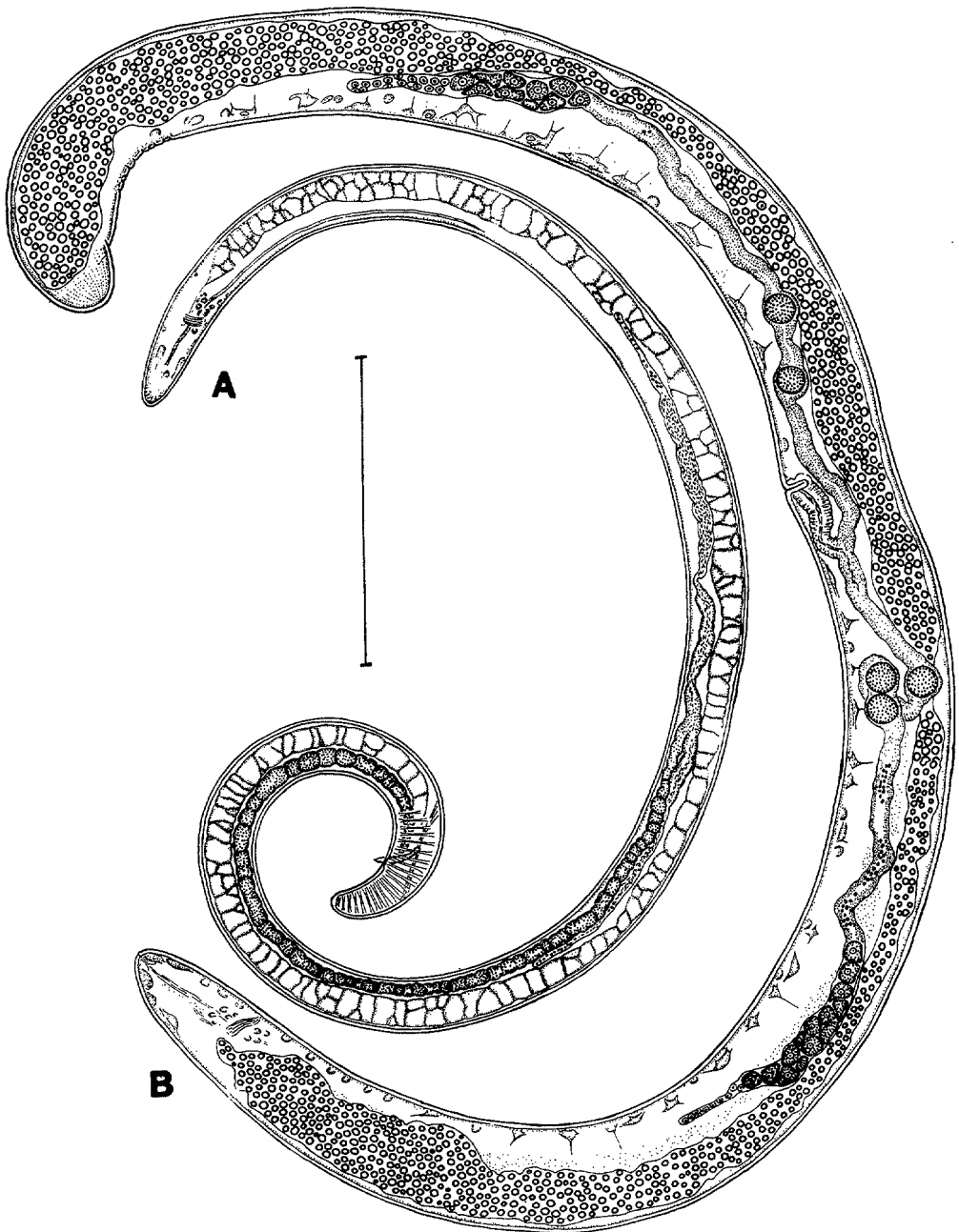


FIG. 1. *Thalassomermis megamphis* n. gen., n. sp. A) Male holotype. B) Female allotype. Scale = 500  $\mu$ m.

nerve ring 75  $\mu$ m; at midbody 87  $\mu$ m; at cloaca 71  $\mu$ m.

Cuticle thick; four layers apparent with light microscopic observations (Fig. 5A). External surface of cuticle with fine circumferential striations and with at least two layers of oblique, crossing, intracuticular fibers

(Fig. 5C). Anterior termination of somatic muscle on cephalic rim (slight internal ridge-like thickening of cuticle situated at beginning of cephalic taper) 48  $\mu$ m from anterior surface of head (Figs. 3A,5A). Thickness of cuticle anterior and posterior to ridge 4 and 3  $\mu$ m, respectively at mid-

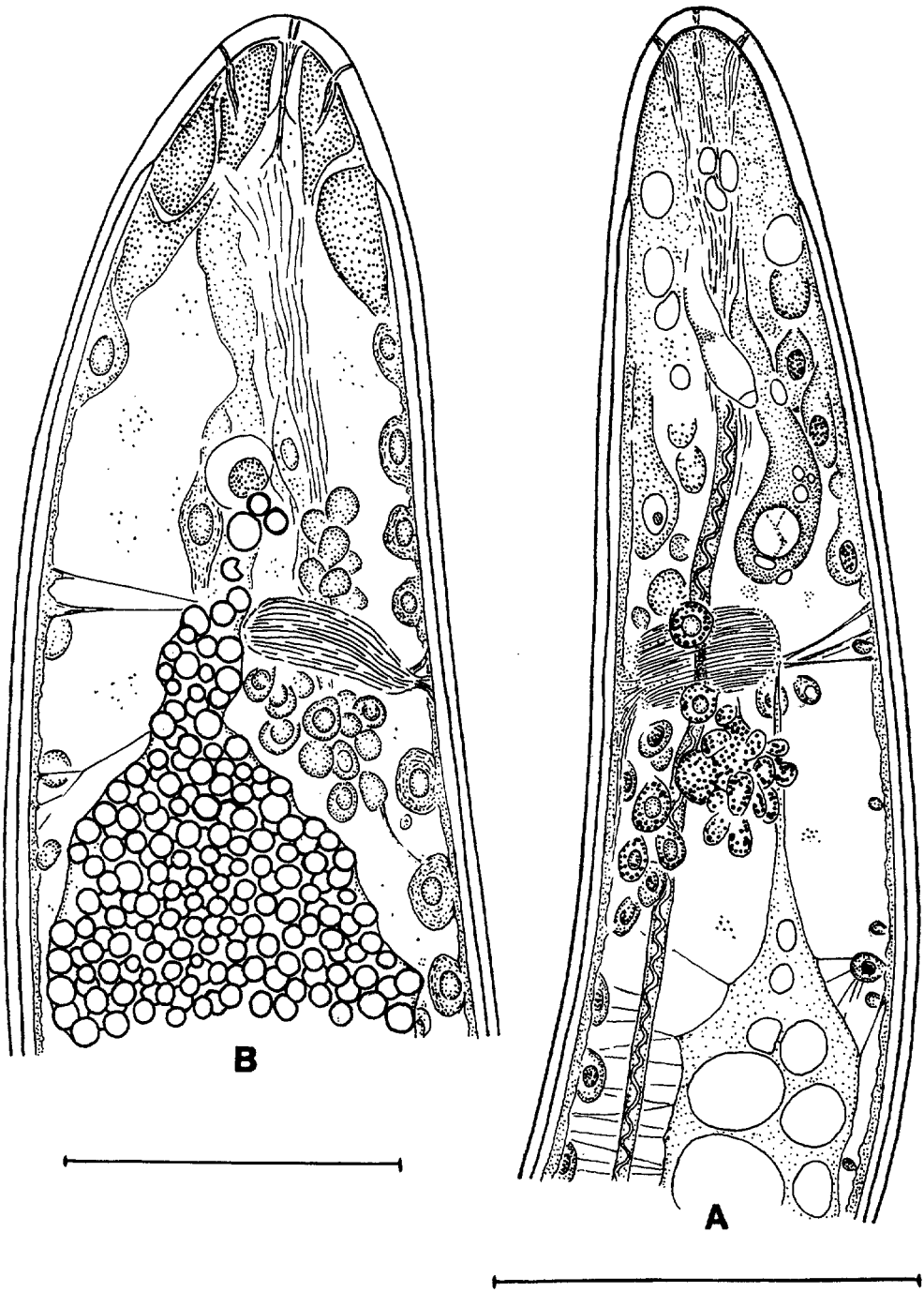


FIG. 2. *Thalassomermis megamphis* n. gen., n. sp. Optical sections of head and neck regions. A) Male holotype. B) Female allotype. Scales = 100  $\mu\text{m}$ .

body 2.5–3.5  $\mu\text{m}$ ; at mid-tail 8.5  $\mu\text{m}$ . Number of longitudinal hypodermal chords not determined. Lateral longitudinal chords 2.0–3.0  $\mu\text{m}$  wide posterior to amphid, 5.0  $\mu\text{m}$  at anterior end of trophosome, 6.5  $\mu\text{m}$  at

mid-body, and 7.5  $\mu\text{m}$  at level of cloacal vent.

Head with single circle of six cephalic sensory receptors, each surrounded by small, oval area of smooth cuticle (Figs. 3,6A);

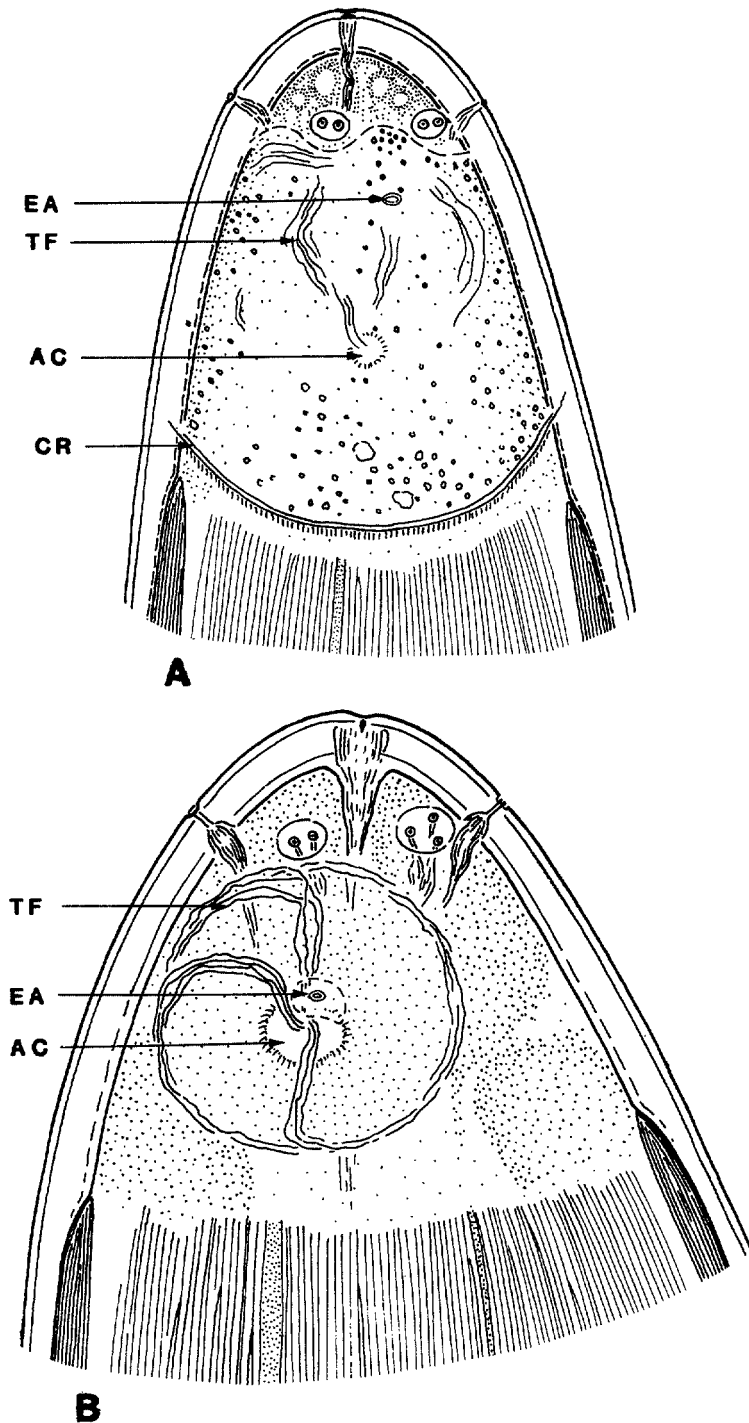


FIG. 3. *Thalassomermis megamphis* n. gen., n. sp. Optical sections of head regions. A) Male holotype. B) Female allotype. Scale = 50  $\mu$ m. AC = aperture of amphidial canal; CR = cephalic rim; EA = external aperture of amphidial fovea; TF = terminal filaments.

each lateral cephalic sensory receptor with two sensilla; number of sensilla in submedian receptors unknown. Amphidial fovea

intracuticular, lenticular, 46  $\mu$ m in diameter (1 corresponding body diameter); anterior rim scarcely visible, situated 13  $\mu$ m from oral

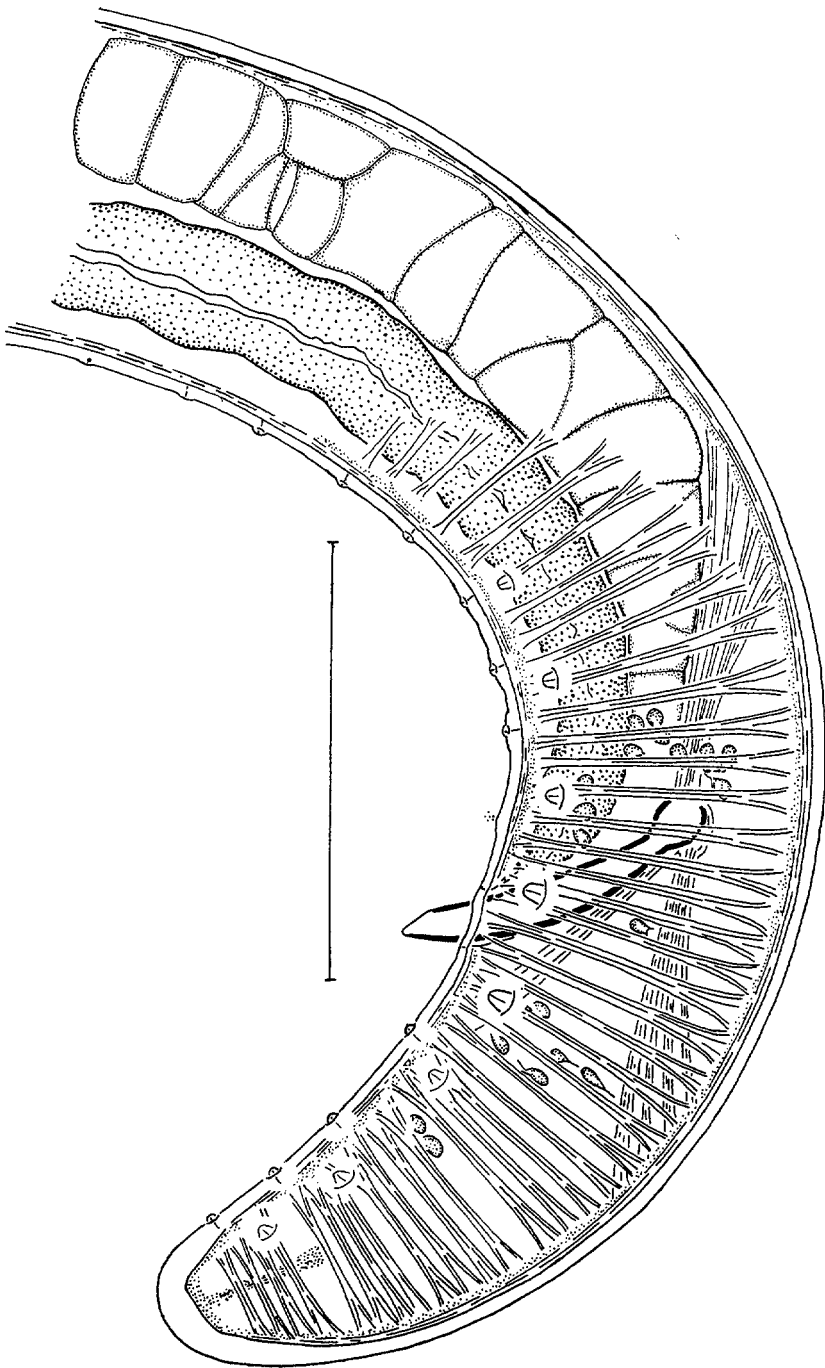


FIG. 4. *Thalassomermis megamphis* n. gen., n. sp. Tail region of male holotype. Scale = 100  $\mu$ m.

surface; posterior rim more distinct, arched, 58  $\mu$ m from oral surface. External aperture of amphidial fovea 2  $\mu$ m in diameter and situated 25  $\mu$ m from oral surface (Figs. 3A,5C). Aperture of amphidial canal 45  $\mu$ m

from oral surface (Figs. 3A,6A) and 5  $\mu$ m in diameter. Emergent terminal filaments (sensory cilia?) elongate, coiled around perimeter of fovea and presumably enveloped by *corpus gelatum* (Fig. 3A). Cervical and so-

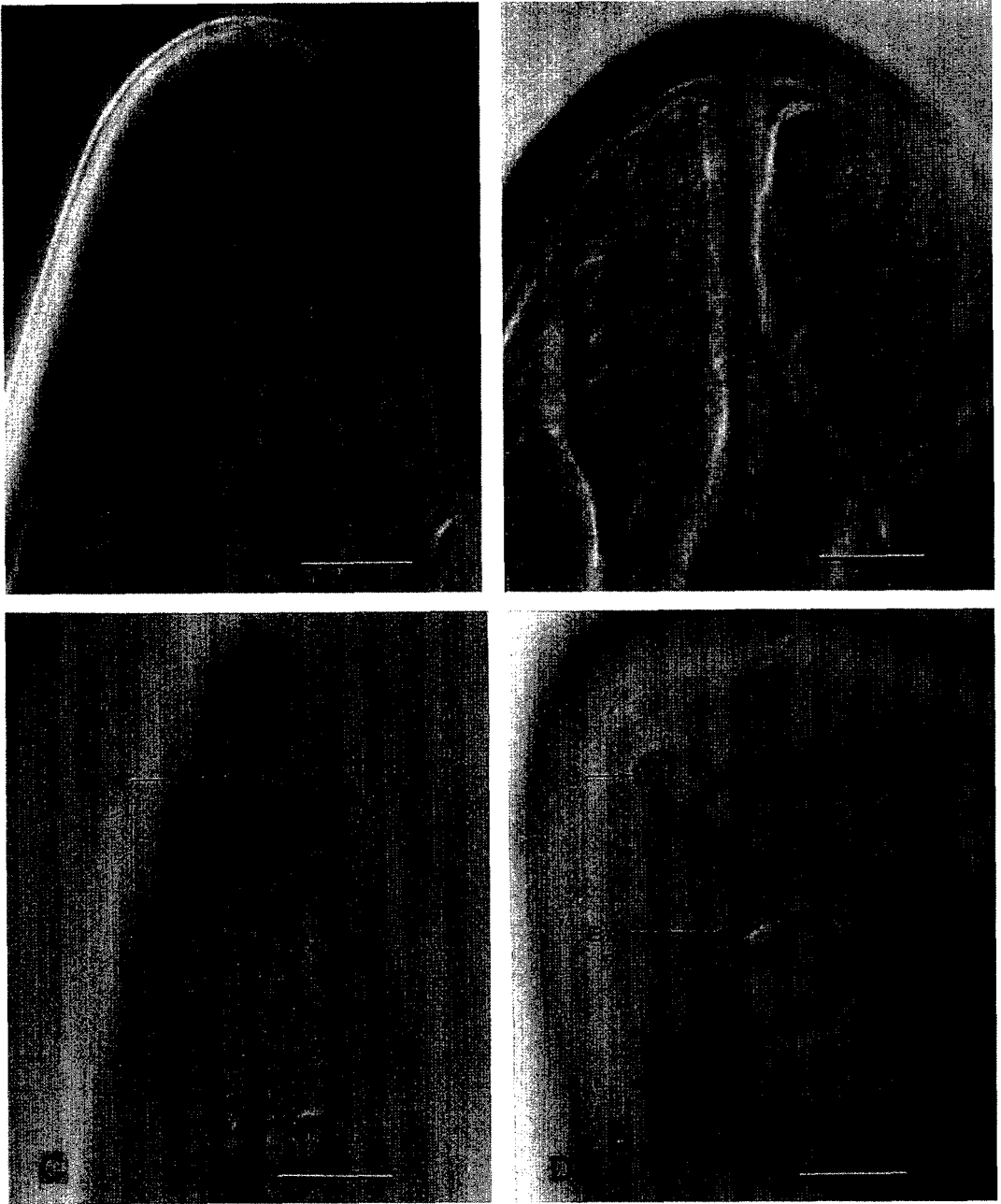


FIG. 5. *Thalassomermis megamphis* n. gen., n. sp. A) Optical section of head of male holotype. B) Optical section of head of female allotype. C) Lateral surface of head of male holotype. D) Lateral surface of head of female allotype. Scales = 10  $\mu$ m. CR = cephalic rim; CS = cephalic sensory receptor; EA = external aperture of amphidial fovea.

matic sensory sensilla, except ventromedian and subventral supplements, absent.

Stomatal vestige narrow and apparently without external aperture (Figs. 3A,5A). Esophagus slender, extending posteriorly

from stomatal vestige through nerve ring (Fig. 2A) and continuing ventral to trophosome for about one-sixth of body length. Lumen of esophagus slightly cuticularized and sinusoidal anterior and posterior to nerve

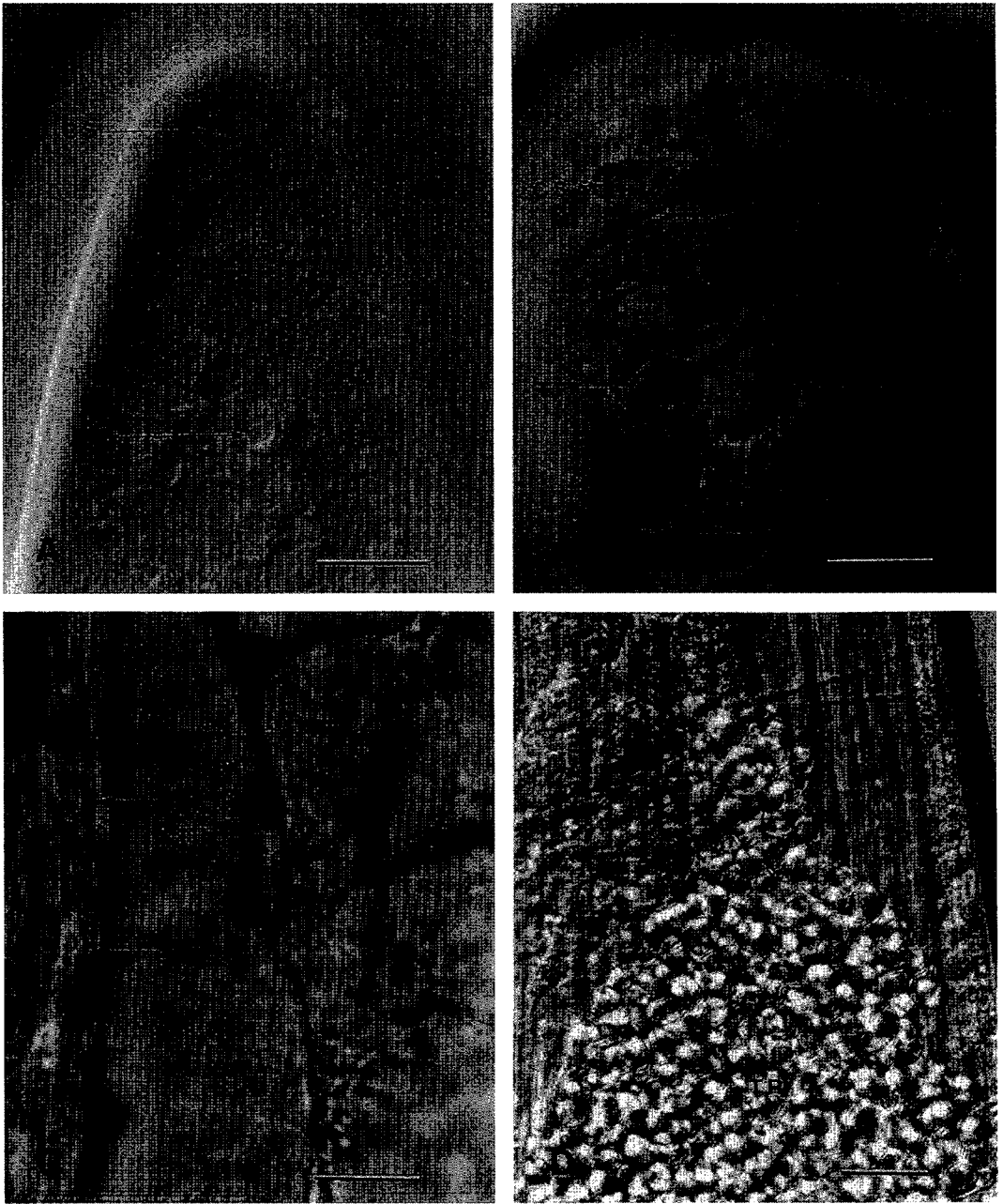


FIG. 6. *Thalassomermis megamphis* n. gen., n. sp. A) Optical section of head of male holotype showing cephalic sensilla and aperture of amphidial canal; scale = 10  $\mu$ m. B) Optical section of lateral surface of head of female allotype showing cephalic sensilla, amphidial fovea, aperture of amphidial canal, and terminal filaments; scale = 10  $\mu$ m. C) Optical section of esophagus and trophosome of male holotype; scale = 10  $\mu$ m. D) Optical section of trophosome of female allotype; scale = 5  $\mu$ m. AC = aperture of amphidial canal; CS = cephalic sensory receptor; LE = lumen of esophagus; PE = post-neural esophagus; TF = terminal filaments; TR = trophosome.

ring (Figs. 2A,6C). Nerve ring 130  $\mu$ m from oral surface. Posterior end of esophagus without connection to trophosome. Trophosome (Figs. 1A,2A,4,6C) apparently cellular

and filled with large, translucent vacuoles with thin cytoplasmic interlayers, but nuclei not seen; internal lumen absent (Figs. 1A,2A,4,6D). Anteriorly trophosome at-



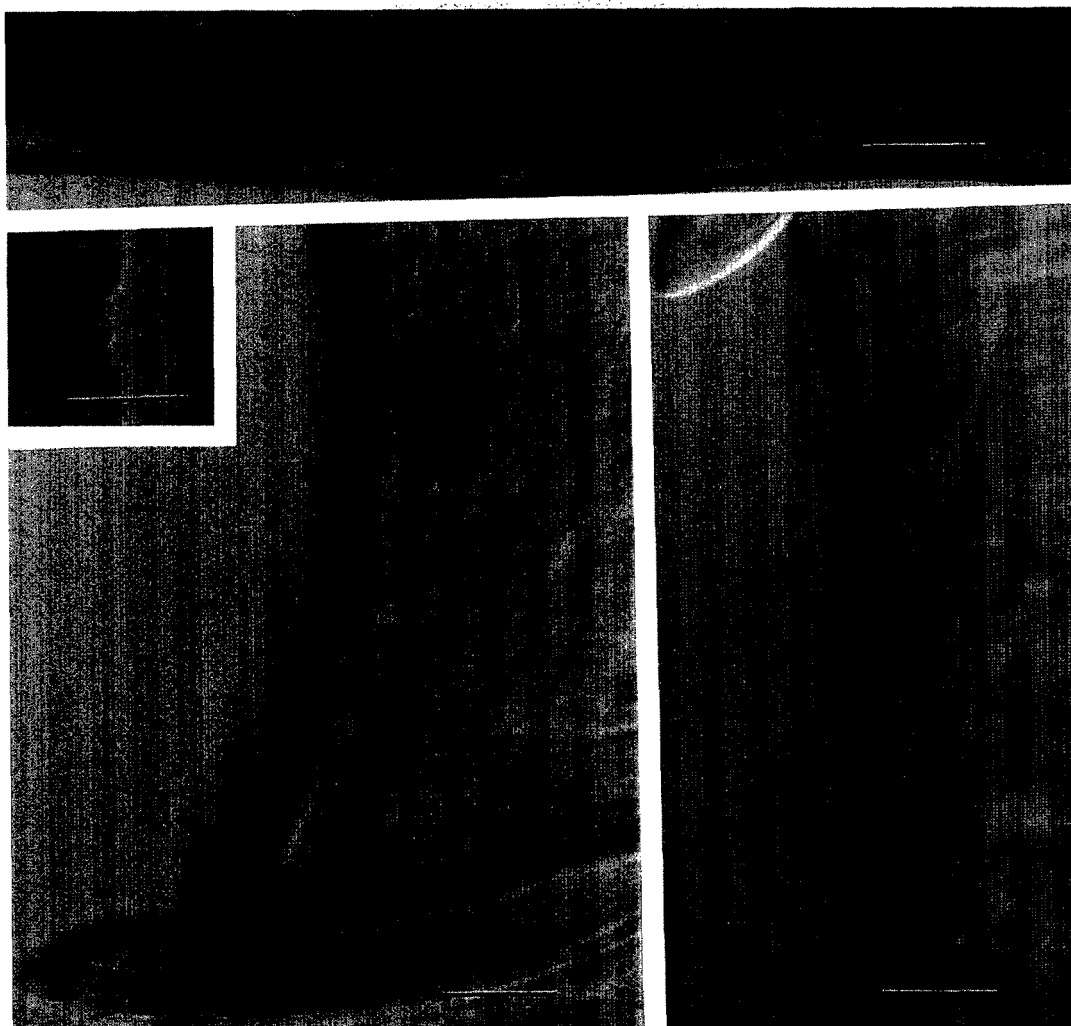


FIG. 7. *Thalassomermis megamphis* n. gen., n. sp. A) Vagina of the allotype. B) Spiculum and precloacal, ventromedian supplements of holotype. Inset: Precloacal, subventral supplements on right side of holotype. C) Postcloacal, ventromedian supplements on left side of holotype. Scale A = 50  $\mu$ m; scales B-C = 10  $\mu$ m.

tached to nerve ring area by thin cytoplasmic process.

Reproductive system diorchic, opposed, testes outstretched (Fig. 1A). Anterior and posterior testes similar in structure and size (Fig. 1A). Distal portion of testes occupied by small, oval primary spermatocytes; nuclei of spermatocytes 4.0  $\mu$ m in diameter and granular. Testis enlarged proximally and densely filled with cylindrical, vermiculate spermatozoans (spermatids?). Anterior and posterior testes joined to common, thick-walled, convoluted duct extending to cloaca (Fig. 1A); common duct without apparent

specialized regions of seminal vesicle and ejaculatory duct. Ejaculatory glands absent.

Spiculum single, siculiform, 73  $\mu$ m long, 10  $\mu$ m wide (Figs. 4,7B). Protractor and retractor muscles inserted on distinct capitulum. Gubernaculum absent. Copulatory musculature composed of approximately 20 pre- and 20 postcloacal, dorsoventrally oriented fibers (Fig. 4). Nine papilloid ventromedian supplements anterior to cloaca, and four ventromedian supplements posterior to cloaca (Figs. 4,7B,C). Two pre- and four postcloacal subventral supplements on right side; two precloacal supplements on right

juxtaposed (Fig. 7B; inset). Four pre- and four postcloacal, papilloid subventral supplements on left side of body (Fig. 4). Each supplement in ventromedian and subventral series comprised of hemispherical protuberance and central duct with sensillum; two farthest anterior ventromedian supplements with duct through cuticle, but without hemispherical protuberance. Tail bluntly rounded (Fig. 4).

*Female allotype*: L = 3.83 mm; a = 22.3; b = 24.3; c = 71.3; V = 52.1%.

Body cylindrical and greater in length and diameter than male (Fig. 1B). Body diameter at level of cephalic sensilla 37  $\mu$ m; at amphidial pore 66  $\mu$ m; at nerve ring 131  $\mu$ m; at midbody 172  $\mu$ m; at posterior end of trophosome 123  $\mu$ m. Cuticle with four layers apparent with light microscope (Fig. 5B); oblique, crisscross, intracuticular fibers present. Cephalic rim with anterior termination of somatic muscles 66  $\mu$ m from oral surface (Fig. 3B). Thickness of cuticle between cephalic sensilla and vestige of stoma 5.0  $\mu$ m; posterior to cephalic sensilla 3.5  $\mu$ m; at midbody 3.5  $\mu$ m; on tail 10  $\mu$ m. Hypodermis evidently with eight longitudinal chords; lateral longitudinal chords 6.5  $\mu$ m wide posterior to amphid, 5.0  $\mu$ m at level of nerve ring, 8.5  $\mu$ m at mid-body, and 15  $\mu$ m at posterior end of trophosome. Head region with large, granular hypodermal cells and nerve cell processes.

Head conically rounded (Figs. 1B,3B), tail bluntly rounded (Fig. 1B). Head with single circle of six cephalic sensory receptors, each surrounded by small, oval area of smooth cuticle (Figs. 3B,6B); each lateral receptor with two sensilla and each submedian receptor apparently with three sensilla. Amphidial fovea intracuticular, lenticular, and with indistinct peripheral margin evident only by presence of coiled terminal filaments (Figs. 3B,6B); fovea 36  $\mu$ m in diameter situated 20  $\mu$ m from oral surface. External aperture of amphidial fovea 2.0  $\mu$ m in diameter, situated 38  $\mu$ m posteriorly from oral surface (Figs. 3B,5D). Aperture of amphidial canal 40  $\mu$ m from oral surface (Figs. 3B,6B), transversely oval, 7 by 10  $\mu$ m in diameter; canal aperture with three emergent bundles of

filaments (sensory sensilla), two directed anteriorly and one posteriorly, all coiled counter-clockwise in amphidial fovea, and presumably enveloped by *corpus gelatum* (Figs. 3B,6B). Additional somatic sensory sensilla absent.

Buccal aperture closed, evident only as slight depression on oral surface. Vestigial stoma fibrous, cylindrical, and without external aperture (Figs. 3B,5B); intra-pseudo-coelomic extension of stoma cord-like, fibrous, and gradually tapered. Esophagus slender, cylindrical, and with slightly cuticularized lumen; esophagus not observed posterior to nerve ring (Fig. 2B). Connection between esophagus and trophosome apparently absent. Trophosome variable in thickness and densely filled with spherical vacuoles of homogeneous substance (Fig. 2B); intercellular borders and lumen not apparent. Rectum and anus absent. Body cavity spacious. Cells with distinct cytoplasmic processes, probably neurons, distributed ventrally along most of body length (Fig. 1B).

Female reproductive system amphidelphic, each gonoduct outstretched (Fig. 1B). Distal end of ovary filled with minute oögonia without evidence of nuclei; farther proximally in gonoduct, oocytes with granular cytoplasm and distinct nuclei. Ova *in utero* about 40  $\mu$ m in diameter, but without evidence of nuclei (Figs. 1B,7A). Vulva transverse; vagina long, slightly curved and directed anteriorly along ventral body wall (Figs. 1B,7A). Sperm present in both branches of uterus (Fig. 1B). Tail rounded; caudal glands and spinneret absent.

#### *Type locality*

One male and one female collected from sieved sediment samples obtained during cruise 167 of the Woods Hole Oceanographic Institute's research vessel Atlantis II. The sediment was collected off the coast of Brazil on 20 February 1967 by an epibenthic sled at a depth of 943-1,007 m, at 07° 58.0' to 07° 50.0' S latitude and 34° 17.0' W longitude.

#### *Type specimens*

Male holotype on slide bearing USNM number 175426, and female allotype on slide bearing USNM number 175427.

### Diagnosis

*Thalassomermis megamphis* n. gen., n. sp. differs from all other members of Mermithidae by the large, lenticular, intracuticular, amphidial fovea; location of the aperture of the amphidial canal near the center of the fovea; and the emergent terminal amphidial filaments coiled around the perimeter of the fovea. The absence of stichocytes may be another difference between *T. megamphis* n. gen., n. sp. and adult members of Mermithidae. However, stichocytes are present in juveniles and absent in adult mermithids (G. O. Poinar, Jr., pers. comm.).

### DISCUSSION

#### Biology

The presence of a trophosome indicates that feeding in *T. megamphis* n. gen., n. sp. is unlike that of the majority of other marine nematodes. Two possibilities are suggested: i) Nutritional requirements may be derived through a symbiotic relationship with an internal procaryotic organism, such as is known for *Astomonema* and relatives (Ott et al., 1982) and suspected for members of Rhaptothyreidae (Hope and Murphy, 1969; Riemann, 1993). In such cases it is assumed that the nematodes dwell in the sediment throughout their lives, and their endosymbionts play some obligate role in metabolizing nutrients absorbed from the external environment through the nematode's body wall. ii) Juveniles, as endoparasites of other invertebrates, may acquire and store food reserves in what will later become the trophosome. Food reserves in the trophosome are later utilized by the free-living, sediment-dwelling adults.

Whereas both those nematodes with endosymbionts and those with parasitic life styles possess a more-or-less reduced or transformed alimentary tract, making normal food uptake improbable, we believe that the second alternative is more likely for *T. megamphis* n. gen., n. sp. This is based on lack of evidence for bacteria-like symbionts within the trophosome, and overall morphological similarity between *T. megamphis* n.

gen., n. sp. and benthimermithid and mermithid nematodes, for which parasitism is firmly established. Thus, we consider individuals of this new species to be free-living during at least part of their adult life, and parasites of an unknown host during the juvenile stages.

Judging from a comparison of the trophosome of the male and female of *T. megamphis* n. gen., n. sp., we assume the male specimen was older than the female. The trophosome of the female is densely filled with spherical, homogeneous inclusions (food reserves), whereas such inclusions apparently have been depleted from the trophosome of the male.

#### Relationships

*Thalassomermis megamphis* n. gen., n. sp. is not closely related to either Rhaptothyreidae or Marimermithidae. Members of *Rhaptothyreus* have large and structurally unique amphids and harbor bacterial endosymbionts (Hope and Murphy, 1969; Riemann, 1993). Members of Marimermithidae have setiform cephalic and cervical sensilla and a muscular esophagus with a triradiate lumen. Marimermithids more closely resemble free-living marine nematodes of the order Enoplida than they do any of the other taxa of nematodes parasitizing marine invertebrates (Tchesunov, 1995).

Although *Thalassomermis megamphis* n. gen., n. sp. has several characters in common with members of Benthimermithidae, we are of the opinion that *Thalassomermis* n. gen. does not have a close phylogenetic affinity with that family, even though there are several shared similarities. The reasons are as follows: i) *Thalassomermis* n. gen. has oblique fibers in the cuticle, whereas they appear to be absent among members of Benthimermithidae (W. D. Hope, unpubl.); however, such fibers are illustrated in the original description of *Benthimermis megala* Petter, 1987 (Petter, 1987; Fig. 1G). ii) *Thalassomermis* n. gen. has six short papilliform or pore-like cephalic sensory receptors in a single circle. Each submedian receptor is provided with three sensilla, at least in the female, and each lateral receptor is pro-

vided with two sensilla. In Benthimermithidae there may be one or two circles of receptors (6 + 4). If there is only one circle, it is the anterior that is absent. The receptors of the anterior circle, when present, are always papilliform, whereas those of the posterior circle are setiform. iii) The amphidial fovea is large and intracuticular, whereas in Benthimermithidae the amphid is small, tubular, or rounded, and pore-like. iv) *Thalassomermis* n. gen. lacks somatic sensilla, whereas there are lateral rows of minute somatic setae in Benthimermithidae. v) The esophagus in the male is a thin chord with a thin, cuticular, sinuous lumen, extending from the vestigial mouth through the nerve ring and then farther posteriorly for a distance equal to one-sixth of the body length. In females the cuticular lumen is not discernible in the preneuronal remnant of the esophagus, and there is no evidence of an esophagus posterior to the nerve ring. In adult benthimermithids the esophagus is more obvious and with a greater diameter, but cellular detail and a cuticularly lined lumen are absent. vi) The female reproductive system is outstretched vs. a reflexed system in Benthimermithidae, except in the case of *Benthimermis laubieri* Petter, 1987, in which the female gonoducts are also outstretched. vii) The vagina is elongated and curved vs. a very short straight vagina among benthimermithids. viii) There is a single spiculum in *Thalassomermis megamphis* n. gen., n. sp., and it is also single in *Agamomeris* Stiles, 1903, *Eumermis* Daday, 1911, *Gastromermis* Micoletzky, 1923, *Limnomermis* Daday, 1911, and *Paramermis* Linstow, 1898, all of which are genera of Mermithidae (Rubzov, 1977). Conversely, spicula are paired in benthimermithids. ix) Testes are opposed in *Thalassomermis megamphis* n. gen., n. sp., whereas they are tandemly oriented among members of Benthimermithidae.

Features possessed by *Thalassomermis megamphis* n. gen., n. sp., but absent in Benthimermithidae, do occur among some terrestrial and fresh-water members of Mermithoidea, i.e. Mermithidae and Tetradonematidae. The most important feature, which we consider to be diagnostic for

Mermithoidea, is the post-cloacal distribution of copulatory muscles. According to our observations (unpubl.), this character is present in most species of Mermithidae and appears to occur in the tetradonematid genera *Corethrellonema* Nickle, 1969 and *Mermithonema* Goodey, 1941.

*Thalassomermis megamphis* n. gen., n. sp. resembles members of Mermithoidea in having either very short papilliform or pore-like cephalic sensory sensilla and an esophagus reduced to a narrow cord of tissue with a thin, cuticularized lumen. The mermithoid esophagus extends posteriorly for 15% to nearly 100% of the body length and consists of a distinct cuticular tube ensheathed, at least in juveniles, by well-defined stichocytes (Kaiser, 1991). The apparent absence of stichocytes in the adults of *Thalassomermis megamphis* n. gen., n. sp. may not be significant because in mermithids these cells degenerate after sexual maturity is reached. Another similarity is in the female gonoducts, which are outstretched in *Thalassomermis* n. gen. and Tetradonematidae (Ferris and Ferris, 1966), and may be straight or reflexed in Mermithidae (Rubzov, 1977). The vagina among members of *Thalassomermis* n. gen. is elongate and tubular, as is often the case among members of Mermithidae (Rubzov, 1977; Kaiser, 1991).

Between the two families of Mermithoidea, we are of the opinion that *Thalassomermis* n. gen. has its closest phylogenetic affinity with Mermithidae and is here assigned to that family. This conclusion is based on similarities in the structure of the cephalic sensilla, and the long and tubular vagina. *Thalassomermis* n. gen. differs from Tetradonematidae in the absence of the three to eight large cells (originally designated tetrads (Cobb, 1919); possibly modified stichocytes) associated with the esophagus behind the nerve ring of most tetradonematids, and the elongated vagina, which is always short among Tetradonematidae.

A review of life cycles provides further evidence that *Thalassomermis megamphis* n. gen., n. sp. is more closely related to members of Mermithidae than to Tetradonematidae. In the case of tetradonematids, sexual maturation

tion and copulation occur within the host, after which the females usually escape to the external environment for egg deposition, as in *Corethrellonema grandispiculosum* Nickle, 1969 and *Tetradonema plicans* Cobb, 1919 (Cobb, 1919; Nickle, 1969). The same trend occurs in the females of *Heterogonema ovomaculis* Van Waerebeke & Remillet, 1973, where the females migrate from the body cavity to the lumen of the gut of their insect host. There the female bursts, presumably because of osmotic pressure, with the liberation of her ova (Van Waerebeke and Remillet, 1973). In another species, *Aproctonema chapmani* Keilin, 1917, details of the life cycle are unknown, although Keilin (1917) assumed that mature females also escape from the host to deposit their eggs. However, in all of the foregoing cases, it seems unlikely that tetradonematid males ever leave the host.

Most members of Mermithidae have a different life cycle in which juveniles of both sexes leave the host and reach sexual maturity in the external environment. One exception is *Heleidomermis magnapapula* Poinar & Mullens, 1987, in which sexual maturation is reached within the insect host (Poinar and Mullens, 1987). Nonetheless, the free-living, sediment-dwelling male of *Thalassomermis megamphs* n. gen., n. sp. indicates this species has a life cycle similar to most members of Mermithidae.

The relationships of *Thalassomermis* n. gen. with Mermithidae and Tetradonematidae may be more complex than the above discussion implies. Kaiser (1983) suggested that neoteny appears to be a general evolutionary trend in mermithids, and that the Tetradonematidae may be a miscellaneous assemblage of independently evolved, neotenic mermithids. Consequently, the Tetradonematidae may be polyphyletic (Kaiser, 1983).

As previously mentioned, other species believed to be mermithids parasitizing marine invertebrates are *Echinomermella grayi*, *E. matsi*, and *Nematimermis enoplivora*. Not enough is known about *E. grayi* to place it with certainty in the Mermithoidea, but *N. enoplivora*, for which females and juveniles

are known, is undoubtedly a mermithoid properly referred to Tetradonematidae because it reaches sexual maturity within its host. The known hosts of *N. enoplivora* are either of two species of the marine nematodes, *Enoplus communis* Bastian, 1865 and *E. brevis* Bastian, 1865. *Nematimermis enoplivora* also resembles Tetradonematidae in that juveniles have in tandem four large and two smaller stichocytes, which probably are homologous with the tetrads characteristic of Tetradonematidae (Tchesunov and Spiridonov, 1993). Adult females of *N. enoplivora* differ from *T. megamphs* n. gen., n. sp. by apparent absence of the cephalic sensilla and amphids; ventrad shift of the vestigial stoma; an obscure vulva, which, along with the absence of males implies parthenogenetic reproduction; and embryonation of ova within the female.

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