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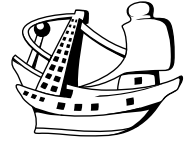
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Two new species of *Trophomera* Rubtzov & Platonova, 1974 (Nematoda: Plectida: Benthimermithidae) from the Clarion-Clipperton Fracture Zone, North Pacific

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Abstract: Two new species of the genus *Trophomera* Rubtzov & Platonova, 1974 (Nematoda: Plectida: Benthimermithidae) from the deep-sea bottom of the Clarion-Clipperton Fracture Zone, North Pacific are described. *Trophomera mangani* sp. nov. differs from its congeners in terms of its large body size, preamphidial cervical lateral alae extending the whole distance from the cephalic apex to amphid, a cone-shaped tail with a terminal spine, and reproductive system with two testes arranged consecutively in tandem and connected by a joint spermaduct. *Trophomera fodinae* sp. nov. can be distinguished from its congeners by its setiform cephalic sensilla, a pharynx that connects with the anterior end of the trophosome, a rounded tail with a terminal spine possessing additional cuticular layers and granular inclusions, the presence of an anus and a rectum, the anterior position of the vulva, and its short reproductive system with two telogonic reflected ovaries. Dichotomous keys to male and female of *Trophomera* are provided.

Résumé : Deux nouvelles espèces de *Trophomera* Rubtzov & Platonova, 1974 (Nematoda : Plectida : Benthimermithidae) de la zone de fracture de Clarion-Clipperton, Pacifique nord. Deux nouvelles espèces du genre *Trophomera* Rubtzov & Platonova, 1974 (Nematoda : Plectida : Benthimermithidae) des fonds marins de la zone de fracture de Clarion-Clipperton dans le nord Pacifique sont décrites. *Trophomera mangani* sp. nov. diffère de ses congénères par sa large taille, ses ailes latérales cervicales préamphidiales s'étendant sur toute la distance de l'apex céphalique à l'amphide, une queue en forme de cône avec une épine terminale et un système reproducteur avec deux testicules disposés consécutivement en tandem et reliés par un spermaduct. *Trophomera fodinae* sp. nov. se distingue de ses congénères par sa sensille céphalique sétiforme, un pharynx qui se connecte à l'extrémité antérieure du trophosome, une queue arrondie avec une épine terminale possédant des couches cuticulaires supplémentaires et des inclusions granulaires, la présence d'un anus et d'un rectum, la position antérieure de la vulve et son système reproducteur court avec deux ovaires télégoniques réfléchis. Les clés dichotomiques mâles et femelles sont fournies.

Keywords: Marine nematodes • Deep sea • CCFZ • Taxonomy • *Trophomera mangani* sp. nov. • *Trophomera fodinae* sp. nov.

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Introduction

The genus *Trophomera* Rubtzov & Platonova, 1974 (= *Abos* Rubtzov, 1980 = *Benthimermis* Petter, 1980) belongs to the family Benthimermithidae Petter, 1980 together with two monospecific genera, namely *Adenodelphis* Petter, 1983 and *Bathynema* Miljutin & Miljutina, 2009. Formerly, Benthimermithidae was the only family of the order Benthimermithida Tchesunov, 1995; however, molecular phylogenetic analyses have shown that Benthimermithidae is a member of Plectida Gadea, 1973 (Holovachov et al., 2013; Leduc & Zhao, 2018). In the juvenile stage, benthimermithid nematodes are parasites of various deep-sea invertebrates; in the adult stage, they are free-living (Miljutin, 2014). Although *Trophomera* contains 40 nominal species, only three species, viz. *T. australis* (Petter, 1983), *T. petterae* (Miljutin, 2004), and *T. granovitchi* Tchesunov & Rozenberg, 2011, have been described based on both sexes and most species were established based on single specimens (Rubtzov & Platonova, 1974; Petter, 1980, 1981a & b, 1982a & b, 1983 & 1987; Rubtzov, 1980; Chesunov, 1988a & b; Bussau, 1993; Miljutin & Tchesunov, 2001; Miljutin, 2004, 2006 & 2011; Miljutin & Miljutina, 2009; Tchesunov & Rozenberg, 2011; Holovachov et al., 2013). Of these species, *T. abyssalis* (Bussau, 1993) and *T. regalis* (Bussau, 1993) were established in the doctoral thesis of Bussau (1993) (cf. Tchesunov, 2017); nevertheless, Holovachov (2020) indicated that they are valid under the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999).

In the present study, two new species of *Trophomera*, collected from the Deep Ocean Resources Development Co., Ltd. (DORD)-licensed area in the Clarion-Clipperton Fracture Zone (CCFZ), are described. Details of the DORD surveys and previous studies on free-living nematodes from the CCFZ including five *Trophomera* species (Miljutin & Miljutina, 2009) were previously described by Shimada et al. (2020).

Materials and Methods

Deep-sea sediments containing free-living marine nematodes were collected from a DORD licensed area of the CCFZ using spade corers onboard the research vessels *Hakurei-maru No. 2* (Japan Oil, Gas and Metals National Corporation) in 2011 and *Ka'imikai-O-Kanaloa* (University of Hawai'i Marine Center) in 2016. The methods used for extraction,

fixation, preparation, differential interference contrast microscopy, photography measurement, and illustration were those described by Shimada et al. (2020). Specimens were deposited in the National Museum of Nature and Science (NMST), Tsukuba, Japan. The terminology used follows that of Miljutin (2014).

Descriptions

Family Benthimermithidae Petter, 1980

Genus *Trophomera* Rubtzov & Platonova, 1974

Trophomera mangani Shimada, sp. nov.

(Figs 1-2 & Table 1)

Type material

Holotype. Adult male, formalin fixed, whole mount in glycerin (NSMT-As 4626), collected by Yoshiro Sekido, Habato Furuta, & Tomoko Tsuboi (Marine Biological Research Institute of Japan Co., Ltd.: MBRIJ) on 9 October 2016.

Type locality and habitat

Seafloor sediment from the CCFZ (10°30.1495'N-148°59.5538'W), water depth: 5331 m, sediment depth: 2-3 cm.

Etymology

The specific name *mangani* is the genitive case of a Latin noun *manganum* (manganese). It refers to the type locality, which is known as a deep-sea mining area for manganese nodules.

Measurements

See table 1.

Description

Male. Body (Fig 1A) cylindrical, gradually tapering toward both ends, strongly tapering in cephalic and caudal regions. Cuticle colorless, 5-10 µm thick, with fine (0.8-1.2 µm wide) transverse striations (Fig. 2A). Somatic sensilla (Figs 1B-D & 2A) papilliform or short (1-2 µm) setiform, each connecting to a gland cell (40-60 µm in long diameter but smaller in cervical and caudal regions) (Figs 1B & 2B), arranged in eight longitudinal rows throughout body length except in caudal region, two rows in each dorsal and ventral field and in both lateral fields. Head (Fig. 1B-C) rounded at anterior end. Lips and inner labial sensilla not observed. Six outer labial sensilla subcuticular. Four

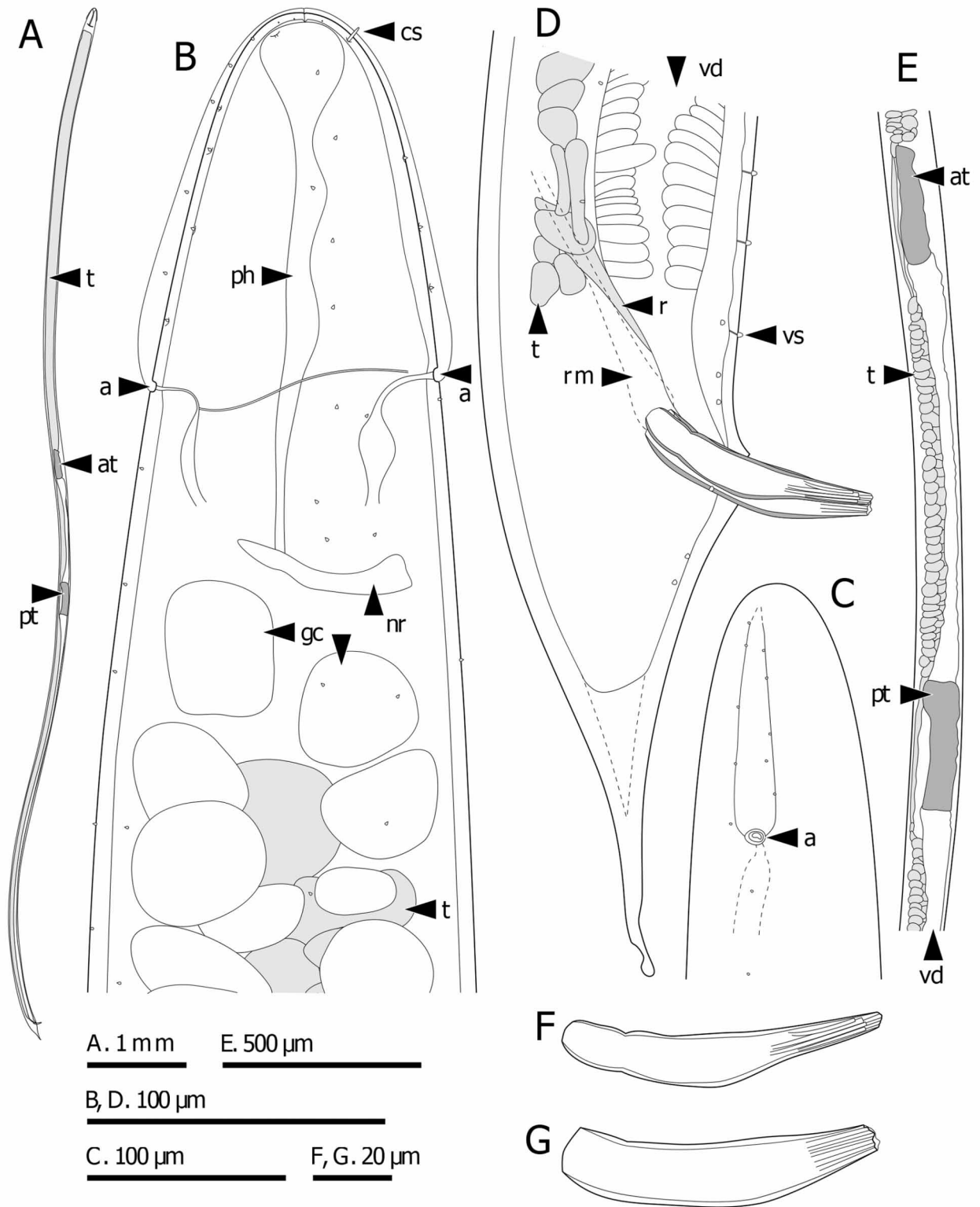


Figure 1. *Trophomera mangani* sp. nov. **A.** Body with trophosome and reproductive system. **B.** Anterior region, ventral view. **C.** Head with amphid and cervical lateral ala, lateral view. **D.** Posterior region, lateral view. **E.** Reproductive system. **F.** Right spicule. **G.** Left spicule. Abbreviations: a, amphid; at, anterior testis; cs, cephalic sensillum; gc, gland cell of somatic sensillum; nr, nerve ring; ph, pharynx; pt, posterior testis; r, rectum; rm, retractor muscle of spicule; t, trophosome; vd, vas deferens; vs, ventromedian supplement.

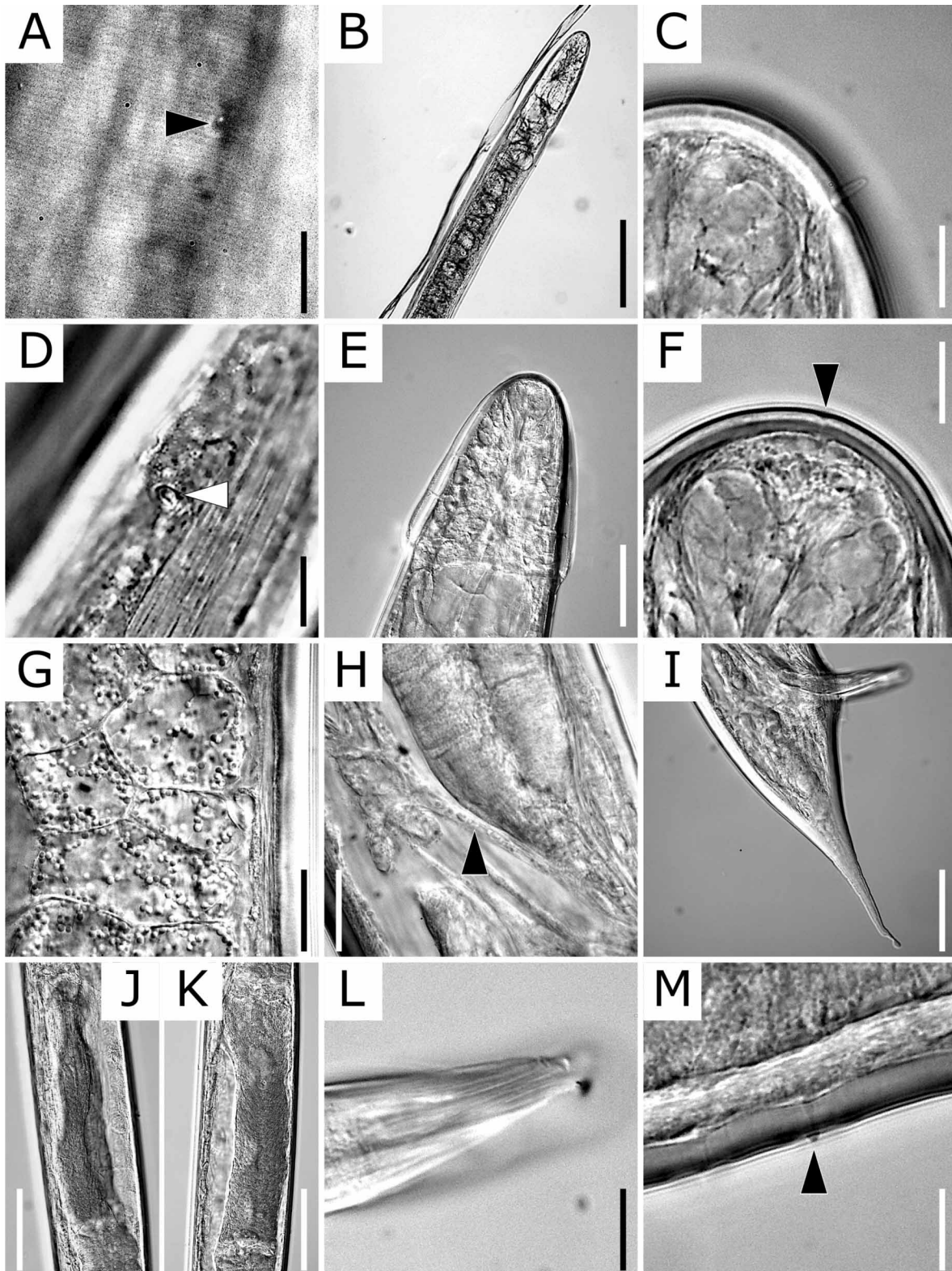


Figure 2. *Trophomera mangani* sp. nov. Differential interference contrast micrographs. **A.** Cuticular striations with somatic sensillum (arrowhead). **B.** Anterior region with dark-colored trophosome and colorless gland cells. **C.** Cephalic sensillum. **D.** Amphidial aperture (arrowhead). **E.** Cervical lateral alae. **F.** Anterior apex with mouth opening (arrowhead). **G.** Trophosome. **H.** Rectum (arrowhead) and vas deferens. **I.** Tail. **J.** Anterior testis. **K.** Posterior testis. **L.** Distal end of spicule with striations. **M.** Precloacal supplement (arrowhead). Scale bars: A, C, F, L & M, 10 μ m; B, 200 μ m; D, G & H, 20 μ m; E & I, 50 μ m; J & K, 100 μ m.

Table 1. Morphometrics of *Trophomera mangani* sp. nov. and *T. fodinae* sp. nov. Measurements are in micrometers. *Distance from anterior body end.

Sex	<i>T. mangani</i>	<i>T. fodinae</i>
	sp. nov.	sp. nov.
	Male	Female
Body length	10600	7275
a (body length/maximum body diameter)	81.5	63.3
b (body length/pharyngeal length)	41.6	48.2
c (body length/tail length)	64.2	58.7
V (vulval position/body length, in %)	-	47.1
Body diameter at cephalic sensilla	36	26
Body diameter at amphid	94	66
Body diameter at anterior end of trophosome	125	91
Maximum body diameter	130	115
Body diameter at vulva	-	115
Body diameter at cloaca/anus	85	62
Cephalic sensilla*	9.3	8.6
Cephalic sensilla length	3.6	4.5-4.7
Amphid*	122	70
Nerve ring*	183	114
Trophosome* (= pharyngeal length)	255	151
Tail length on arc	165	124
Spicule length on arc (right/left)	80/80	-
Anterior gonad*	4525	3020
Anterior gonad length	305	222
Posterior gonad*	5880	3713
Posterior gonad length	325	209
Vulva*	-	3430

cephalic sensilla (Figs 1B & 2C) setiform, 0.1 cephalic diameters long, at 0.25 cephalic body diameters from anterior end: only left lateroventral sensilla exist and other three sensilla lost (pores and nerves present) in holotype. Subcephalic sensilla absent. Amphids (Figs 1B-C & 2D) at 3.4 cephalic diameters, 1.3 corresponding body diameters, or 1/89 of body length from anterior body end: aperture transversely elliptical, surrounded by double contour cuticular wall; fovea narrow and tube-like, not sclerotized. Transverse cord-like structure (Fig. 1B) present at level of amphids. Cervical lateral alae (Figs 1B-C & 2E) belonging to type A from classification of Miljutin & Miljutina (2009), preamphidial, extending the whole distance from the cephalic apex to amphid, 2 μ m high at anterior body end, 10 μ m high at posterior end. Several somatic sensilla present on cervical lateral alae. Mouth opening (Fig. 2F) present but vestigial, minute pore at cephalic apex. Buccal cavity reduced to thin channel between mouth opening and pharynx, 4.5 μ m long. Pharynx

(Fig. 1B) nonmuscular, without lumen, not observed posteriorly. Nerve ring (Fig. 1B) at 72% of distance from anterior body end to midgut. Midgut modified to oligocellular trophosome (Figs 1A-B, 1D-E, 2B & 2G) with numerous black or brown granules and without lumen, filling area of body between pharyngeal and caudal regions, ending anterior to cloaca. Rectum (Figs 1D & 2H) thin, as long as cloacal body diameter, including trophosome granules. Tail (Figs 1D & 2I) cone-shaped (gradually tapering) with terminal spine, 1.9 cloacal body diameters long including terminal spine, belonging to type 2d from classification of Miljutin & Miljutina (2009): terminal spine completely cuticular with inner axis of another cuticular layer in proximal half, not possessing cytoplasmic inclusion, as long as 40% of entire tail length, strongly constricted at distal end. Caudal glands and spinneret absent. Caudal sensilla (Fig. 1D) papilliform, arranged in two subventral rows as continuation of somatic sensilla. Reproductive system (Figs 1A & 1E) diorchic, belonging to type C from classification of Petter (1982b) and Miljutin (2004). Two testes (Figs 1E & 2J-K) possessing homogeneous dark brownish content, much darker than trophosome under light microscope, arranged consecutively in tandem, connected by joint spermaduct: anterior testis located at 43-46% of body length; posterior testis located at 55-59% of body length. Total length of reproductive system equal to 16% of body length. Vas deferens (Figs 1D-E & 2H) muscular, expanded just anterior to cloaca. Spermaduct and vas deferens situated at left side of trophosome. Mature sperms not observed. Spicules (Figs 1D, 1F-G & 2L) paired, slightly bent, longitudinally striated distally and jagged at distal end, both equal to 0.95 cloacal body diameters or 0.5 tail lengths, showing slight deference in shape: right spicule (Fig. 1F) with capitulum, tapering toward both ends, maximal 0.18 cloacal body diameters wide; left spicule (Fig. 1G) without capitulum, thicker than right spicule at both ends, maximal 0.21 cloacal body diameters wide. Spicule retractor muscles (Fig. 1D) well-developed. Gubernaculum absent. Thirty-four precloacal ventromedian supplements (Figs 1D & 2M) papilliform. Anterior-most supplement at 11.4 cloacal body diameters from cloaca.

Female. Not found.

Diagnosis and discussion

Trophomera mangani sp. nov. is characterized by its large body size (ca. 10 mm long), preamphidial

cervical lateral alae extending the entire distance from the cephalic apex to amphid (type A), long (1.9 cloacal body diameters) cone-shaped tail with terminal spine (type 2d), and reproductive system with two testes arranged consecutively in tandem and connected by a joint spermaduct (type C).

Of 17 known *Trophomera* species described based on male specimens, *T. mangani* sp. nov. is most similar to the *T. acuticauda* (Petter, 1981b) in having the type A cervical lateral alae, type C male reproductive system, and a tail with a terminal spine. However, *T. mangani* sp. nov. can be distinguished from *T. acuticauda* by the type 2d cone-shaped tail (vs. the type 1b rounded tail with a terminal spine in *T. acuticauda*) (cf. Petter, 1981b). Although Miljutin & Miljutina (2009) classified *T. acuticauda* with a type 2c tail, we suggest that its tail classification should be type 1b based on the figures in the original description by Petter (1981b).

Although *Trophomera* contains 40 nominal species, 37 of them were described from only males (14 species) or females (23 species). Only three species, *T. australis*, *T. petterae*, and *T. granovitchi*, have been described based on both sexes. The males and females collected from the same sediment samples were considered as in the same species, but they are not completely similar in morphological characteristics. Male of *T. australis* differs from female in having type 1a tail (vs. type 2d in female) and male of *T. petterae* can be distinguished from female in having type 2b or 2c tail (vs. type 2d in female) (Petter, 1983; Miljutin, 2004; Miljutin & Miljutina, 2009). In *T. granovitchi*, tail shape of male is unknown due to injury of the only specimen (Tchesunov & Rozenberg, 2011). Therefore, it is suggested that there is a sexual dimorphism in *Trophomera* species and that males and females of the same species are regarded as different species.

The revised taxonomic key for male *Trophomera* species, modified from the table key of Miljutin & Miljutina (2009), is as follows:

1. Reproductive system monorchic
.....*T. improvisa* (Miljutin, 2004)
Reproductive system diorchic 2
2. Two testes directed anteriorly 3
Two testes tandem 5
3. Lateral cervical alae absent
.. *T. granovitchi* (Tchesunov & Rozenberg, 2011)
Lateral cervical alae present 4
4. Amphids at ca. 3.0 corresponding body diameters
from anterior body end *T. breviptera* (Petter,
1982b)
Amphids at ca. 1.0 corresponding body diameter
from anterior body end *T. crozetensis* (Petter,
1983)
5. Lateral cervical alae reaching anterior body end 6
Lateral cervical alae not reaching anterior body
end 11
6. Tail with terminal spine 7
Tail without terminal spine 8
7. Tail rounded *T. acuticauda* (Petter, 1981b)
Tail cone-shaped ***T. mangani* sp. nov.**
8. Tail rounded 9
Tail cone-shaped 10
9. Tail as long as 0.8 cloacal body diameters
..... *T. platyptera* (Miljutin, 2004)
Tail very short, cloaca just anterior to body end ..
..... *T. rotundicauda* (Petter, 1981b)
10. Tail with a small mucron
..... *T. australis* (Petter, 1983)
Tail without mucron .. *T. leptosoma* (Petter, 1981b)
11. Lateral cervical alae preamphidial 12
Lateral cervical alae preamphidial and
postamphidial 15
12. Lateral cervical alae shorter than amphidial body
diameter *T. aptera* (Petter, 1982b)
Lateral cervical alae longer than amphidial body
diameter 13
13. Posterior testis with anterior cecum
..... *T. petterae* (Miljutin, 2004)
Posterior testis without anterior cecum 14
14. Distal end of spicules jagged
..... *T. abyssalis* (Bussau, 1993)
Distal end of spicules not jagged
..... *T. rosaliae* (Chesunov, 1988b)
15. Tail rounded *T. gracilis* (Petter, 1982a)
Tail cone-shaped 16
16. Preamphidial branch of alae as long as
postamphidial branch *T. litoralis* Miljutin, 2006
Preamphidial branch of alae much shorter than
postamphidial branch 17
17. Posterior end of alae bifurcated
..... *T. diploptera* (Petter, 1981a)
Posterior end of alae not bifurcated
..... *T. regalis* (Bussau, 1993)

***Trophomera fodinae* Shimada, sp. nov.**
(Figs 3-4 & Table 1)

Type material

Holotype. Adult female, formalin fixed, whole mount in glycerin (NSMT-As 4613), collected by Yoshiro Sekido and Yasushi Miyazaki (MBRIJ) on 10 November 2011.

Type locality and habitat

Seafloor sediment from the CCFZ (9°14.9090'N-146°15.6008'W); water depth: 5369 m, sediment depth: 1-2 cm.

Etymology

The specific name *fodinae* is the genitive case of a Latin noun *fodina* (mine, quarry). It refers to the type locality, which is known as a deep-sea mining area for manganese nodules.

Measurements

See table 1.

Description

Female. Body (Fig. 3A) almost cylindrical, gradually tapering toward both ends. Cuticle colorless, 2-5 μm thick, with fine (0.8-1.2 μm wide) transverse striations (Fig. 4A). Somatic sensilla papilliform, arranged in four longitudinal rows along four epidermal chords: ventral and dorsal rows present only in cervical region; right and left lateral rows present throughout body length except caudal region. Gland cells of somatic sensilla (Figs 3B & 4B) much smaller (10-20 μm in long diameter) than those of *T. mangani* sp. nov. Large nucleus in each epidermal cell (Fig. 4B). Somatic muscles under epidermis (Figs 3B & 3C) conspicuous. Head (Figs 3B & 4C) truncate at anterior end. Lips and inner labial sensilla not observed. Six outer labial sensilla subcuticular. Four cephalic sensilla (Figs 3B & 4C) setiform, 0.15-0.20 cephalic diameters long, at 0.33 cephalic body diameters from anterior end. Subcephalic sensilla absent. Amphids (Figs 3B & 4D) pore-like, at 2.7 cephalic diameters, 0.9 corresponding body diameters, or 1/104 of body length from anterior body end. Amphidial fovea strongly sclerotized. Transverse cord-like structure absent. Mouth opening (Fig. 4C) vestigial, small pore at anterior body end, more obvious than that of *T. mangani* sp. nov. Buccal cavity reduced to thin channel, 3.5 μm long. Pharynx (Figs 3B & 4E) nonmuscular and without lumen, but conspicuous and connecting with midgut. Nerve ring (Fig. 3B) at 75% of pharyngeal length from anterior body end. Midgut modified to oligocellular trophosome (Figs 3A-D & 4F-G) with numerous black or brown granules and without lumen. Rectum (Figs 3C & 4H) present, 0.7 anal body diameters long, connecting posterior end of trophosome and anal opening. Tail (Figs 3C & 4I-J) rounded with terminal spine possessing additional cuticular layers and granular inclusions, belonging to

type 1c from classification of Miljutin & Miljutina (2009), 2.0 cloacal body diameters long: terminal spine as long as 70% of entire tail length; additional cuticular layers forming longitudinally striated axis; granular inclusions present only at middle of spine. Cuticular ring (Figs 3C & 4K) present at base of terminal spine, possible artificial characteristic from injury during collection or fixation. Caudal glands and spinneret absent. Reproductive system (Fig. 3A & 3D) didelphic-amphidelphic, belonging to type A from classification of Miljutin (2004). Two ovaries (Figs 3D & 4L-M) telogonic, reflected, brownish-yellow in color but paler than trophosome under light microscope, both situated at right side of trophosome: anterior ovary located at 42-45% of body length; posterior ovary located at 51-54% of body length. Oviducts conspicuous, situated at left side of ovaries. Uteri not developed, without mature egg. Total length of reproductive system equivalent to 12% of body length. Vulva (Figs 3A, 3D & 4N) at 47% of body length. Vagina (Fig. 4N-O) sclerotized and strongly muscular, 35 μm or 0.3 vaginal body diameters long, with ca. 10 well-developed vaginal glands at both lateral sides.

Male. Not found.

Diagnosis and discussion

Trophomera fodinae sp. nov. is characterized by its setiform cephalic sensilla, a pharynx that connects with the anterior end of the trophosome, a rounded tail with a terminal spine possessing additional cuticular layers and granular inclusions (type 1c), the presence of an anus and a rectum, the anterior position (47% of body length) of its vulva, and its short reproductive system (12% of body length) with two telogonic reflected ovaries (type A).

Of the 26 known *Trophomera* species described based on female specimens, *T. fodinae* sp. nov. most closely resembles *T. filiformis* (Petter, 1987) and *T. marionensis* (Petter, 1983) in having the type 1c tail and the type A reproductive system. However, *T. fodinae* sp. nov. can be distinguished from *T. filiformis* by the complete pharynx that connects with the trophosome, setiform cephalic sensilla (vs. papilliform in *T. filiformis*), and shorter reproductive system (12% of body length in *T. fodinae* sp. nov. vs. ca. 35% in *T. filiformis*) (cf. Petter, 1987). *Trophomera fodinae* sp. nov. also differs from the type series of *T. filiformis* collected from the Norwegian Sea by the position of its amphids (at 5.0 cephalic diameters or ca. 1/100 of the body length from the anterior end in *T. fodinae* sp. nov. vs. at 2-3 cephalic diameters or ca. 1/50-1/30 of

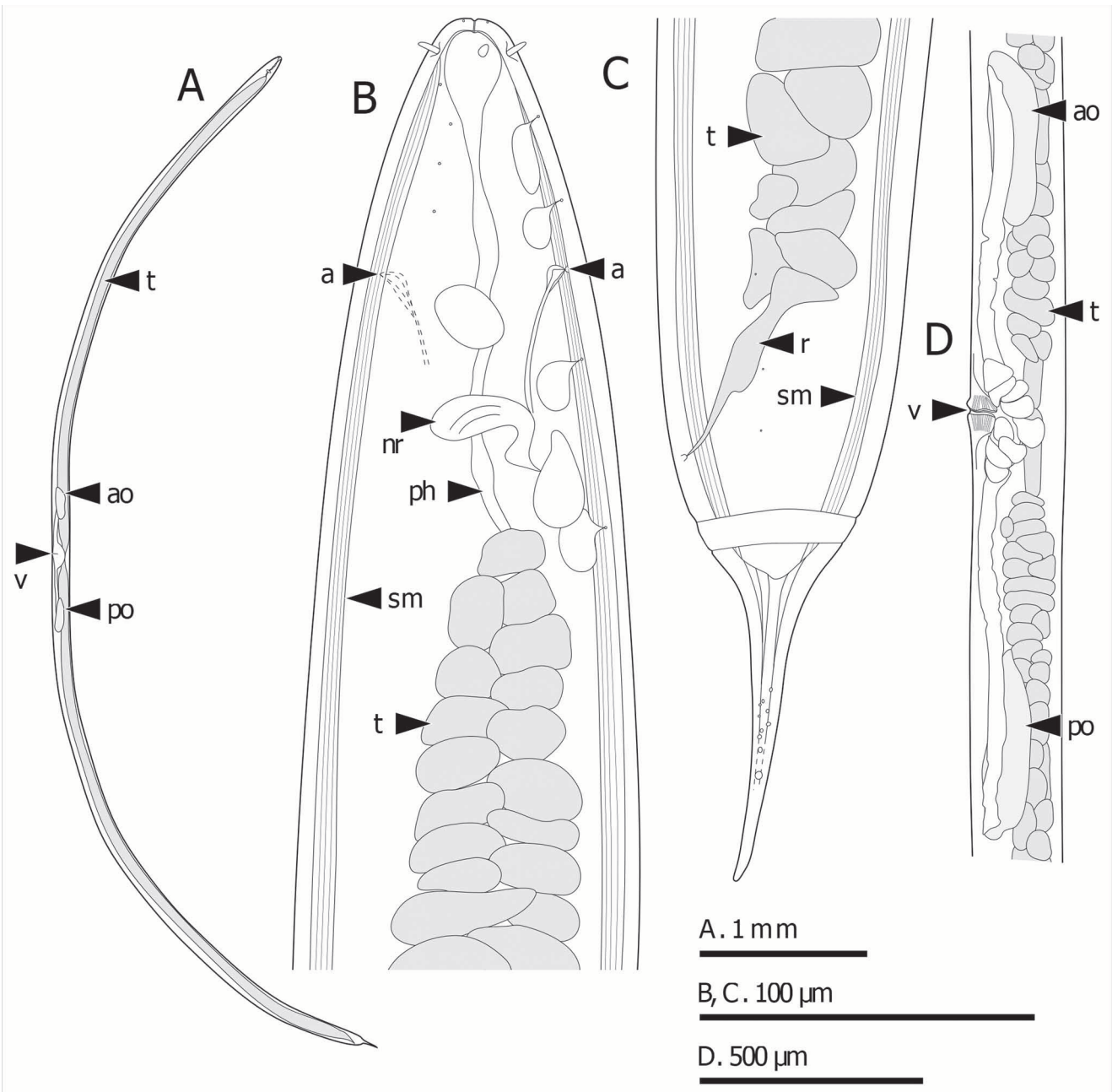


Figure 3. *Trophomera fodinae* sp. nov. **A.** Body with trophosome and reproductive system. **B.** Anterior region, ventral view. **C.** Posterior region, lateral view. **D.** Reproductive system. Abbreviations: a, amphid; ao, anterior ovary; nr, nerve ring; ph, pharynx; po, posterior ovary; r, rectum; sm, somatic muscle; t, trophosome; v, vulva.

the body length in *T. filiformis*) and the presence of the granular inclusions of the terminal spine (cf. Petter, 1987); however, it falls in the range of intraspecific variation based on redescribed specimens from the Atlantic and Indian Ocean (position of amphids at 2-8 cephalic diameters or ca. 1/100-1/30 of the body length, and a specimen with granular inclusions) (cf. Miljutin, 2004). *Trophomera fodinae* sp. nov. differs

from *T. marionensis* by the connecting type of pharynx and trophosome (junction located at the anterior end of the trophosome in *T. fodinae* sp. nov. vs. junction located more posteriorly and the trophosome forming an anterior cecum in *T. marionensis*) and the anterior position of the vulva (at 47% of the body length in *T. fodinae* sp. nov. vs. 50-58% of the body length in *T. marionensis*) (cf. Petter, 1983; Bussau, 1993; Miljutin,

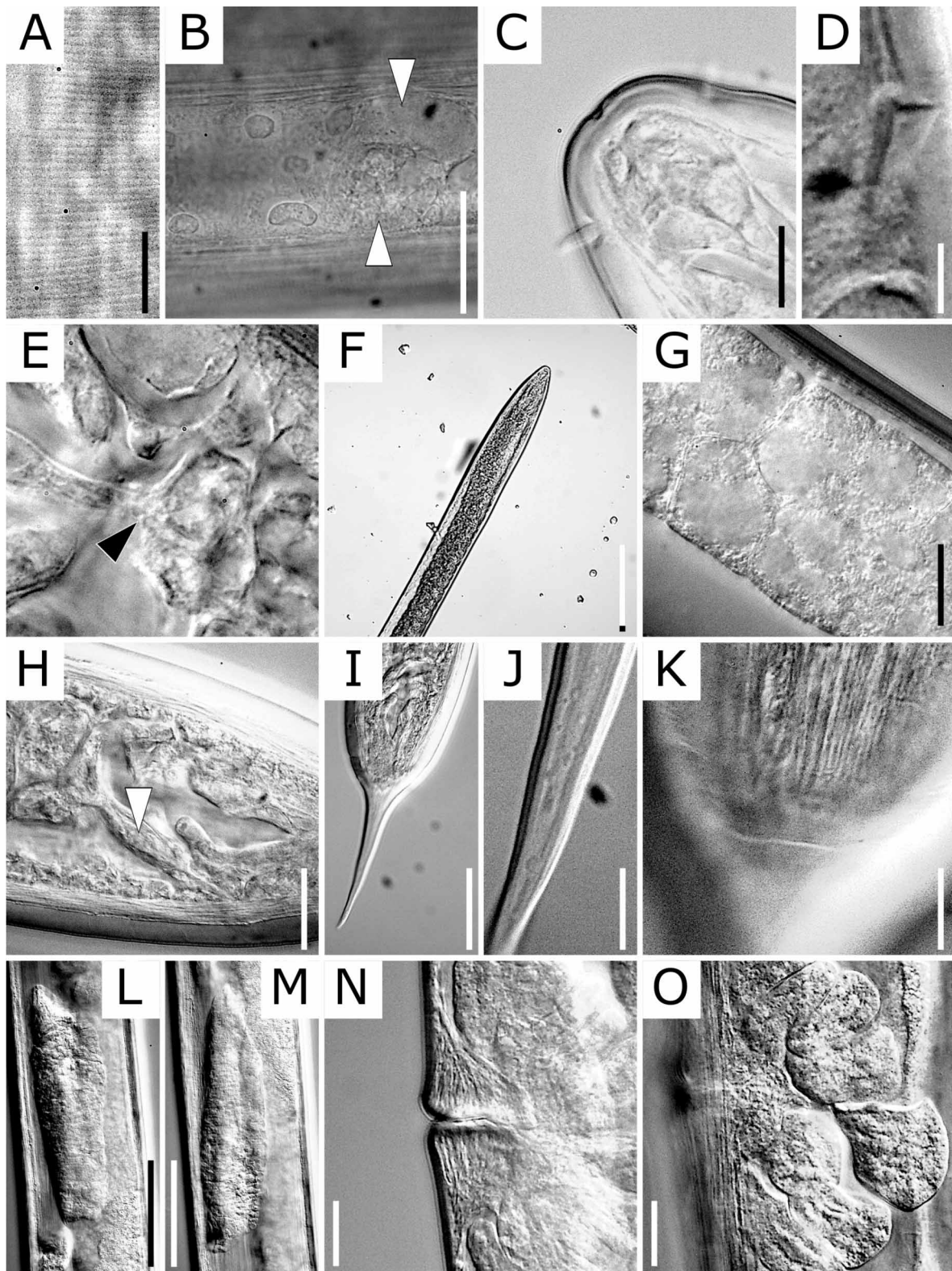


Figure 4. *Trophomera fodinae* sp. nov. Differential interference contrast micrographs. **A.** Cuticular striations. **B.** Epidermal chord with gland cells (arrowheads). **C.** Head with cephalic sensilla and mouth opening. **D.** Amphidial fovea. **E.** Junction of pharynx and trophosome (arrowhead). **F.** Anterior region with dark-colored trophosome. **G.** Trophosome. **H.** Rectum (arrowhead). **I.** Tail. **J.** Granular inclusions in terminal spine. **K.** Cuticular ring on tail. **L.** Anterior ovary. **M.** Posterior ovary. **N.** vaginal region. **O.** vaginal glands. Scale bars: A-C, E, J & K, 10 μ m; D, 5 μ m; F, 200 μ m; G, H, N & O, 20 μ m; I, 50 μ m; L & M, 100 μ m.

2004 & 2011; Miljutin & Miljutina, 2009). *Trophomera marionensis* sensu Chesunov (1988b) is suggested to be an undescribed species because of disagreements with the original description as well as other redescriptions related to the strongly constricted cephalic region and the much more anterior position of the vulva (37% of body length). As *T. marionensis* is a cosmopolitan species collected from the Pacific (including the CCFZ), Atlantic, and Indian Oceans (Petter, 1983; Bussau, 1993; Miljutin, 2004 & 2011; Miljutin & Miljutina, 2009), Miljutin (2011) suggested that the identity of *T. marionensis* from the different localities should be tested using molecular methods.

The revised taxonomic key for female *Trophomera* species modified from the table key of Miljutin & Miljutina (2009), is as follows:

- | | | | |
|---|----------------------------------|---|--|
| 1. Tail rounded without terminal spine | 2 | 15. Reproductive system as long as 0.5 body lengths | <i>T. americana</i> Miljutin, 2011 |
| Other type tail | 8 | Reproductive system as long as 0.15-0.25 body lengths | 16 |
| 2. Tail with terminal knob | 3 | 16. Tail rounded cone-shaped | <i>T. elegantis</i> Miljutin & Miljutina, 2009 |
| Tail without terminal knob | 4 | Tail cone-shaped | <i>T. hureaui</i> (Petter, 1983) |
| 3. Ovaries not reflected <i>T. bathycola</i> (Rubtzov, 1980) | | 17. Tail with abnormal terminal spine | |
| Ovaries reflected | <i>T. arnaudi</i> (Petter, 1983) | <i>T. turpicauda</i> (Miljutin, 2004) | |
| 4. Ovaries not reflected | | Tail with normal terminal spine | 18 |
| <i>T. pseudominuta</i> (Miljutin, 2004) | | 18. Terminal spine with additional cuticular layers and granular inclusions | 19 |
| Ovaries reflected | 5 | Terminal spine without additional cuticular layers and granular inclusions | 23 |
| 5. Amphids at 1/50 of body length | 6 | 19. Tail cone-shaped | |
| Amphids at 1/160-1/90 of body length | 7 | <i>T. pacifica</i> Miljutin & Miljutina, 2009 | |
| 6. Body shorter than 1 mm | | Tail rounded | 20 |
| <i>T. minutissima</i> Miljutin & Miljutina, 2009 | | 20. Body longer than 50 mm | |
| Body longer than 2 mm <i>T. minuta</i> (Petter, 1987) | | <i>T. megala</i> (Petter, 1987) | |
| 7. Body length/tail length = 70 | | Body shorter than 20 mm | 21 |
| <i>T. ifremeri</i> (Miljutin, 2004) | | 21. Pharynx not connected with trophosome | |
| Body length/tail length > 100 | | <i>T. filiformis</i> (Petter, 1987) | |
| <i>T. edouardensis</i> (Petter, 1983) | | Pharynx connected with trophosome | 22 |
| 8. Tail without terminal spine | 9 | 22. Anterior end of trophosome forming cecum | |
| Tail with terminal spine | 17 | <i>T. marionensis</i> (Petter, 1983) | |
| 9. Cephalic sensilla as long as 30 μ m | | Anterior end of trophosome not forming cecum .. | |
| <i>T. iturupiensis</i> Rubtzov & Platonova, 1974 | | <i>T. fodinae</i> sp. nov. | |
| Cephalic sensilla shorter than 10 μ m | 10 | 23. Body longer than 20 mm | |
| 10. Tail with attenuatous tip .. <i>T. hopei</i> (Petter, 1980) | | <i>T. conchicola</i> Holovachov et al., 2013 | |
| Tail without attenuatous tip | 11 | Body shorter than 10 mm | 24 |
| 11. Ovaries not reflected | 12 | 24. Rectum and anus absent | |
| Ovaries reflected | 13 | <i>T. petterae</i> (Miljutin, 2004) | |
| 12. Cephalic sensilla papilliform | | Rectum and anus present | 25 |
| <i>T. senckenbergi</i> Miljutin & Miljutina, 2009 | | 25. Ovaries not reflected <i>T. laubieri</i> (Petter, 1987) | |
| Cephalic sensilla setiform | | Ovaries reflected | 26 |
| <i>T. longiovaris</i> Miljutin, 2011 | | 26. Tail rounded | |
| 13. Cephalic sensilla papilliform | 14 | <i>T. granovitchi</i> Tchesunov & Rozenberg, 2011 | |
| Cephalic sensilla setiform | 15 | Tail cone-shaped | <i>T. australis</i> (Petter, 1983) |
| 14. Tail as long as anal body diameter | | | |
| <i>T. tchesunovi</i> (Miljutin, 2004) | | | |
| Tail twice as long as anal body diameter | | | |
| <i>T. conicauda</i> (Petter, 1987) | | | |

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