

# Two New Species of Free-living Marine Nematodes (Nematoda: Axonolaimidae and Tripyloididae) from the Coast of Antarctica

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Two new species of free-living marine nematodes, *Odontophora odontophoroides* sp. nov. and *Parabathylaimus jare* sp. nov., are described from the coastal sand of Langhovde, Lützow-Holm Bay, Dronning Maud Land, Antarctica. *Odontophora odontophoroides* sp. nov. is the only species in *Odontophora* Bütschli, 1874 that has bicuspidate odontia. *Odontophora odontophoroides* sp. nov. is similar to species in *Odontophoroides* Boucher and Helléouët, 1977 and *Synodontium* Cobb, 1920 in having bicuspidate odontia, but differs in having a didelphic reproductive system in females. *Parabathylaimus jare* sp. nov. differs from congeners in the unjointed inner labial and cephalic sensilla, the outer labial sensilla three-jointed in males and two-jointed in females, the position of the amphids, the shorter spicules, and the conical tail without long subterminal setae. Modified generic diagnoses and keys to species are included for *Odontophora* and *Parabathylaimus* De Coninck and Schuurmans Stekhoven, 1933. A new combination, *Parabathylaimus arthropappus* (Wieser and Hopper, 1967) comb. nov., is established.

**Key Words:** Araeolaimida, Enoplida, littoral, meiobenthos, meiofauna, JARE 56.

## Introduction

There have been a number of taxonomic and ecological works on the free-living marine nematode fauna of Antarctic and Subantarctic regions (Ingels et al. 2014). The first taxonomic result for Antarctic Continent was provided by Cobb (1914), who described 25 new species from Adelie Land. Up to the present time, more than 160 species have been described from Antarctic Continent including several deep-sea sites (Cobb 1930; Steiner 1931a, b; Allgén 1946, 1959, 1960; Mawson 1956, 1958; Inglis 1958; Lorenzen 1973, 1986; Hope 1974; Decraemer 1976, 1991; Allen and Noffsinger 1978; Timm 1978a, b; Platt 1983; Blome and Schrage 1985; Decraemer and Noffsinger 1992; Blome and Riemann 1999; Vermeeren et al. 2004; Fonseca et al. 2006; Leduc 2014, 2016; Shimada et al. 2017, 2019). Steiner (1931a, b) established 125 species and eight subspecies of Epsilonematidae based on Antarctic and Subantarctic specimens, but Lorenzen (1973) synonymized them to only three valid species.

During the 56th Japanese Antarctic Research Expedition (JARE 56), a faunal survey of the littoral meiobenthos around Syowa Station, a Japanese research station, revealed

two undescribed species of free-living marine nematodes belonging to Axonolaimidae and Tripyloididae. This is the third nematode publication arising from the National Institute of Polar Research (NIPR) workshop on marine invertebrates collected during JARE operations, following Shimada et al. (2017, 2019).

## Materials and Methods

Specimens were collected by ACS on 31 January 2015 from the coast of Langhovde (69°14'24.3"S, 39°42'55.8"E), about 20 km south of Syowa Station, Lützow-Holm Bay, Dronning Maud Land, Antarctica. Intertidal and upper subtidal sandy sediments were sampled with a shovel and washed in fresh water; the supernatant was then filtered through 32 µm mesh, and the extract was fixed in 10% formalin. In the laboratory, nematodes were sorted under a stereomicroscope, transferred into 10% glycerin in 30% ethanol, placed in a thermostatic chamber at 40°C for 72 hours, and mounted individually in anhydrous glycerin on glass slides supported by a paraffin wax ring (Hooper 1986a) and sealed with Canada balsam for differential interfer-

ence contrast microscope (Olympus BX51) observation. For scanning electron microscope (SEM; Hitachi S-3000N) observation, nematodes were dried in a critical-point dryer and sputter-coated with gold (Au) to 200 Å thickness. Light microscopic photographs were taken with a digital camera (ASONE PCM500) and edited with GIMP ver. 2.10 (<https://www.gimp.org/>). Measurements and drawings were made from digital images by using Inkscape ver. 1.0 (<https://inkscape.org/>). All specimens examined were deposited in the Invertebrate Collection of Hokkaido University Museum (ICHUM), Sapporo, Japan.

De Man's ratios (cf. Hooper 1986b) were: a, ratio of body length to maximum body diameter; b, ratio of body length to pharyngeal length; c, ratio of body length to tail length; c', ratio of tail length to cloacal/anal body diameter; and V, position of vulva from anterior body end, expressed as percentage of body length.

## Results

Order **Araeolaimida** De Coninck and Schuurmans Stekhoven, 1933  
 Family **Axonolaimidae** Filipjev, 1918  
 Genus **Odontophora** Bütschli, 1874

**Type species.** *Odontophora marina* Bütschli, 1874

**Diagnosis modified from Leduc and Zhao (2016).** Cuticle smooth or striated; inner labial sensilla indistinct; six papilliform outer labial sensilla and four setiform cephalic sensilla in separate circles; buccal cavity funnel-shaped or conical with well-developed cuticular wall; six well-developed odontia present in cheilostoma; amphids loop-shaped with longitudinally elongate (inverted U-shaped) or circular (O-shaped) aperture; long subterminal setae on tail present or absent; spicules shorter than 2.0 cloacal body diameters; gubernacula usually with dorso-caudal apophysis, without anterior branch sometimes mistakenly called "telamon" (cf. Tchesunov 2014; Shimada et al. 2019); precloacal pore and supplements present or absent; male diorchic; female didelphic, ovaries outstretched.

**Remarks.** Leduc and Zhao (2016) listed 33 valid species and eight *species inquirendae* in *Odontophora*, providing a taxonomic key to all valid species. We add four valid species: *O. sinapophysis* Pinto and Neres, 2020, which was described after the work by Leduc and Zhao (2016); *O. hawksbiensis* Turpeenniemi, Nasira, and Maqbool, 2001, and *O. serrata* Hourston and Warwick, 2010, which were overlooked by Leduc and Zhao (2016); and *O. polaris* (Cobb, 1914), which De Coninck and Schuurmans Stekhoven (1933) regarded as a *species inquirenda*. Leduc and Zhao (2016) followed De Coninck and Schuurmans Stekhoven (1933), probably because of the incomplete original description by Cobb (1914) based only on an immature specimen, although Cobb (1930) and Timm (1978b) later provided descriptions of both sexes. In addition, we consider *O. longicaudata* Schuurmans Stekhoven and De Coninck, 1933 to be a *species inquirenda*, because this species was established

based only on a juvenile. Thus, the genus *Odontophora* now contains the following 36 valid species (Cobb 1914; Turpeenniemi et al. 2001; Hourston and Warwick 2010; Leduc and Zhao 2016; Pinto and Neres 2020).

- O. angustilaima* (Filipjev, 1918) Allgén, 1929  
 = *Conolaimus angustilaimus* Filipjev, 1918  
 non *O. angustilaimus* sensu Schuurmans Stekhoven (1950)
- O. armata* (Ditlevsen, 1918) Allgén, 1929  
 = *Trigonolaimus armatus* Ditlevsen, 1918  
 = *Conolaimus armatus* (Ditlevsen, 1918) Allgén, 1930  
 = *Trigonolaimus intermedius* Allgén, 1929  
 = *Conolaimus intermedius* (Allgén, 1929) Allgén, 1934  
 = *O. intermedius* (Allgén, 1929) Allgén, 1930  
 = *Trigonolaimus minor* Ditlevsen, 1918  
 = *O. minor* (Allgén, 1929) Allgén, 1930  
 non *O. armata* sensu De Coninck and Schuurmans Stekhoven (1933)  
 non *O. armata* sensu Schuurmans Stekhoven (1935) (in part)
- O. articulata* Keppner, 1988
- O. atrox* Leduc and Zhao, 2016
- O. bermudensis* Jensen and Gerlach, 1976
- O. brevispicula* Keppner, 1988
- O. carrolli* Keppner, 1988
- O. deconincki* Galtsova, 1976  
 = *O. armata* sensu De Coninck and Schuurmans Stekhoven (1933)  
 = *O. armata* sensu Schuurmans Stekhoven (1935) (in part)
- O. exharena* Warwick and Platt, 1973
- O. falcifera* Ott, 1972
- O. fatisca* Vitiello, 1971
- O. furcata* Wieser, 1956
- O. hawksbiensis* Turpeenniemi, Nasira, and Maqbool, 2001
- O. lituifera* Wieser, 1959
- O. longisetosa* (Allgén, 1928) Allgén, 1929  
 = *Conolaimus longisetosus* Allgén, 1928  
 non *Conolaimus longisetosus* sensu Schuurmans Stekhoven (1931)
- O. mercurialis* Wieser, 1959
- O. mucronata* Wieser, 1959
- O. octoseta* Boucher and Helléouët, 1977
- O. ornata* Lorenzen, 1971
- O. paravilloti* Blome, 1982
- O. peritricha* Wieser, 1956
- O. phalarata* Lorenzen, 1971
- O. polaris* (Cobb, 1914) De Coninck and Schuurmans Stekhoven, 1933  
 = *Axonolaimus polaris* Cobb, 1914
- O. polynesiae* Boucher, 1973
- O. rectangula* Lorenzen, 1971
- O. regalia* Nichols and Musselman, 1979
- O. serrata* Hourston and Warwick, 2010
- O. setosa* (Allgén, 1929) Allgén, 1929  
 = *Trigonolaimus setosus* Allgén, 1929

- = *Conolaimus setosus* (Allgén, 1929) Allgén, 1930  
 = *Axonolaimus elegans* Schulz, 1932  
 = *Conolaimus longisetosus* sensu Schuurmans Stekhoven (1931)  
*O. setosoides* Timm, 1952  
*O. sinapophysis* Pinto and Neres, 2020  
*O. spiculodentata* Pastor de Ward, 1984  
*O. tenuicaudata* Allgén, 1935  
*O. urothrix* Gerlach, 1957  
*O. variabilis* Wieser and Hopper, 1967  
*O. villoti* Luc and De Coninck, 1959  
*O. wieseri* Luc and De Coninck, 1959

species inquirendae

- O. angustilaimoides* Chitwood, 1951  
*O. axonolaimoides* Timm, 1952  
*O. insulana* Belogurov, 1978  
*O. longicaudata* Schuurmans Stekhoven and De Coninck, 1933  
*O. marina* Bütschli, 1874  
 = *Conolaimus marinus* (Bütschli, 1874) Allgén, 1930  
*O. parangustilaima* Wieser, 1956  
 = *O. angustilaimus* sensu Schuurmans Stekhoven (1950)  
*O. parasetosa* (Allgén, 1929) Allgén, 1929  
 = *Trigonolaimus parasetosus* Allgén, 1929  
 = *Conolaimus parasetosus* (Allgén, 1929) Allgén, 1930  
*O. paratenuicaudata* Allgén, 1942

***Odontophora odontophoroides*** Shimada, sp. nov.  
 (Figs 1–3)

Axonolaimidae gen. sp. in Shimada et al. (2017): table 1.

**Material examined.** *Holotype.* Male (ICHUM 5373), formalin fixed, whole mount in glycerin, upper subtidal sandy sediment, Langhovde (69°14'24.3"S, 39°42'55.8"E), Lützow-Holm Bay, Dronning Maud Land, Antarctica. *Paratypes.* Five males (ICHUM 5484–5488) and five females (ICHUM 5374, 5489–5492), formalin fixed, whole mount in glycerin, same collection data as for holotype. *Other material.* One male, formalin fixed, dissected for observation from ventral side. Two males and one female, Au-coated for SEM, same collection data as for holotype.

**Etymology.** The specific name *odontophoroides* is a noun in apposition (in the nominative case), referring to the bicuspidate odontia similar to those in the genus *Odontophoroides* Boucher and Helléouët, 1977.

**Diagnosis.** Six bicuspidate odontia; amphids with longitudinally elongate aperture at level of pharyngostoma; cephalic sensilla shorter than cephalic body diameter; no subcephalic sensilla; conical tail with slightly expanded tip, without long subterminal setae; arcuate spicules with capitulum at proximal end and two spine-like structures at distal end; gubernacula with dorso-caudal apophysis; precloacal pore and supplements present.

**Measurements.** See Table 1.

**Description of males.** Body (Fig. 1A) cylindrical, gradu-

ally tapering toward both ends. Cuticle colorless, 3–6 µm thick, with very fine, indistinct transverse striations. Somatic sensilla absent except in cervical, cloacal, and caudal regions. Head (Figs 1B, C, 2A–C) truncate at anterior end. Six lips low, inconspicuous under light microscope. Inner labial sensilla not observed. Six papilliform outer labial sensilla, located at anterior body end. Four setiform cephalic sensilla, 0.5–0.7 cephalic diameters long, located 0.4–0.6 cephalic diameters from anterior body end. Subcephalic sensilla absent. Amphids (Figs 1C, 2B, D) loop-shaped with longitudinally elongate aperture, dorsal and ventral branches equal in length, 1.0–1.2 cephalic diameters long, 0.25–0.35 cephalic diameters wide (length/width=3.0–4.3), located at level of pharyngostoma, beginning just posterior to cephalic sensilla and ending at level of posterior end of buccal cavity. Buccal cavity (Figs 1C, 2A) funnel-shaped or conical, with well-developed cuticular walls, 1.4–1.7 cephalic diameters long, divided into two sections: cheilostoma 5–7 µm long, movable by linkage with lips, equipped with six bicuspidate odontia (5–6 µm long, 4–5 µm wide) (Figs 1C, 2B, C) similar in shape to odontia in *Odontophoroides*; pharyngostoma immovable, 19–23 µm or 1.1–1.4 cephalic diameters long, at most 7–10 µm or 0.2–0.4 cephalic diameters wide. Other solid structures in buccal cavity, e.g., “accessory buccal structures” reported in *O. atrox* by Leduc and Zhao (2016), absent. Pharynx (Fig. 1B, C) surrounding posterior 20–40% of buccal cavity, nearly cylindrical, slightly enlarged at posterior end but not forming distinct bulb. Nerve ring located at 60–70% of pharyngeal length. Secretory-excretory system well developed; pore 1.4–2.1 buccal cavity lengths from anterior body end; renette cell 1.3–1.5 pharyngeal lengths from anterior end, 0.4–0.6 corresponding body diameters wide, accompanied by two smaller ventrolateral cells. Cervical sensilla setiform, shorter than cephalic sensilla, 0.4–0.6 cephalic diameters long, arranged in four longitudinal rows, dense in anterior half of cervical region and sparser posteriorly, anteriormost setae located at level of amphids. Cardia short, surrounded by intestine. Tail (Fig. 1D) conical, slightly expanded at tip, 3.3–4.3 cloacal body diameters long, with three terminal setae (4–9 µm long). Long subterminal setae absent. Rows of ventrolateral setae (5–12 µm long) and sparser dorsolateral setae (4–7 µm long) present on each side in cloacal and caudal regions. Number and position of setae differ among specimens. Three caudal glands located postcloacally. Spinneret present. Spicules (Figs 1D–G, 2E) paired, belonging to arcuate type in Leduc and Zhao’s (2016) classification, as long as 1.1–1.4 cloacal body diameters or 0.3–0.4 tail lengths, with capitulum at proximal end and two spine-like structures at distal end. Gubernacula (Figs 1D–G, 2F, G) also paired, as long as 0.4–0.6 cloacal body diameters or 0.3–0.4 spicule lengths, located between spicules, with twisted dorso-caudal apophysis. Precloacal pore (Figs 1D, E, 2H) present with gland cell 8–14 µm anterior to cloaca. Precloacal supplements (Figs 1D, E, 2I) papilliform, 16–23 in number, each with gland cell; anteriormost supplement 377–492 µm or 6.2–8.8 cloacal body diameters from cloaca. Reproductive system (Figs 1A, 2J, K) diorchic with opposed, outstretched testes: anterior testis beginning at 18–27%

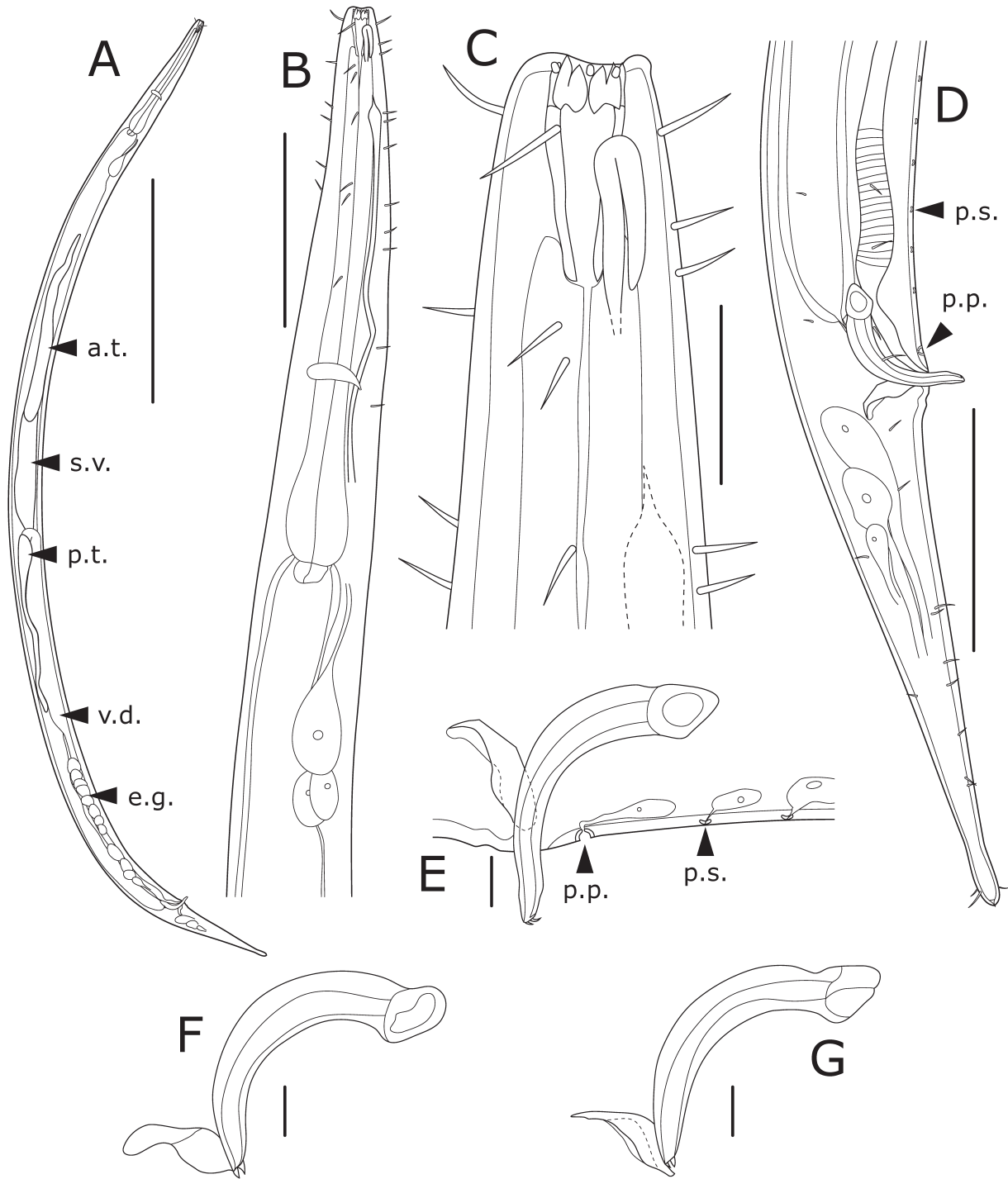


Fig. 1. *Odontophora odontophoroides* sp. nov. A, male body (holotype); B, male anterior region (holotype); C, male head with closed mouth (holotype); D, male posterior region (holotype); E, male genital apparatus (holotype); F, G, spicule and gubernaculum (ICHUM 5486 and 5488, respectively). Abbreviations: a.t., anterior testis; e.g., ejaculatory glands; p.p., precloacal pore; p.s., precloacal supplement; p.t., posterior testis; s.v., seminal vesicle; v.d., vas deferens. Scale bars: A, 500  $\mu$ m; B, D, 100  $\mu$ m; C, 20  $\mu$ m; E–G, 10  $\mu$ m.

of body length from anterior body end, as long as 11–20% of body length, located on right side of intestine in four specimens including holotype but on left side in two other specimens (ICHUM 5486 and 5488); posterior testis ending 63–75% of body length from anterior body end, as long as 16–20% of body length, located on left side of intestine in three specimens including holotype but on right side in three other specimens (two testes located on opposite sides

of intestine in five specimens including holotype, but both on right side in ICHUM 5487). In total length, reproductive system (from anterior end of anterior testis to posterior end of posterior testis) 44–55% of body length. Seminal vesicle well developed, located between two testes, beginning at 34–43% of body length and ending at 47–58%, filled with globular sperm (10–20  $\mu$ m in diameter). Vas deferens (Fig. 1A, D) distinct, strongly muscular in posterior part, with 10



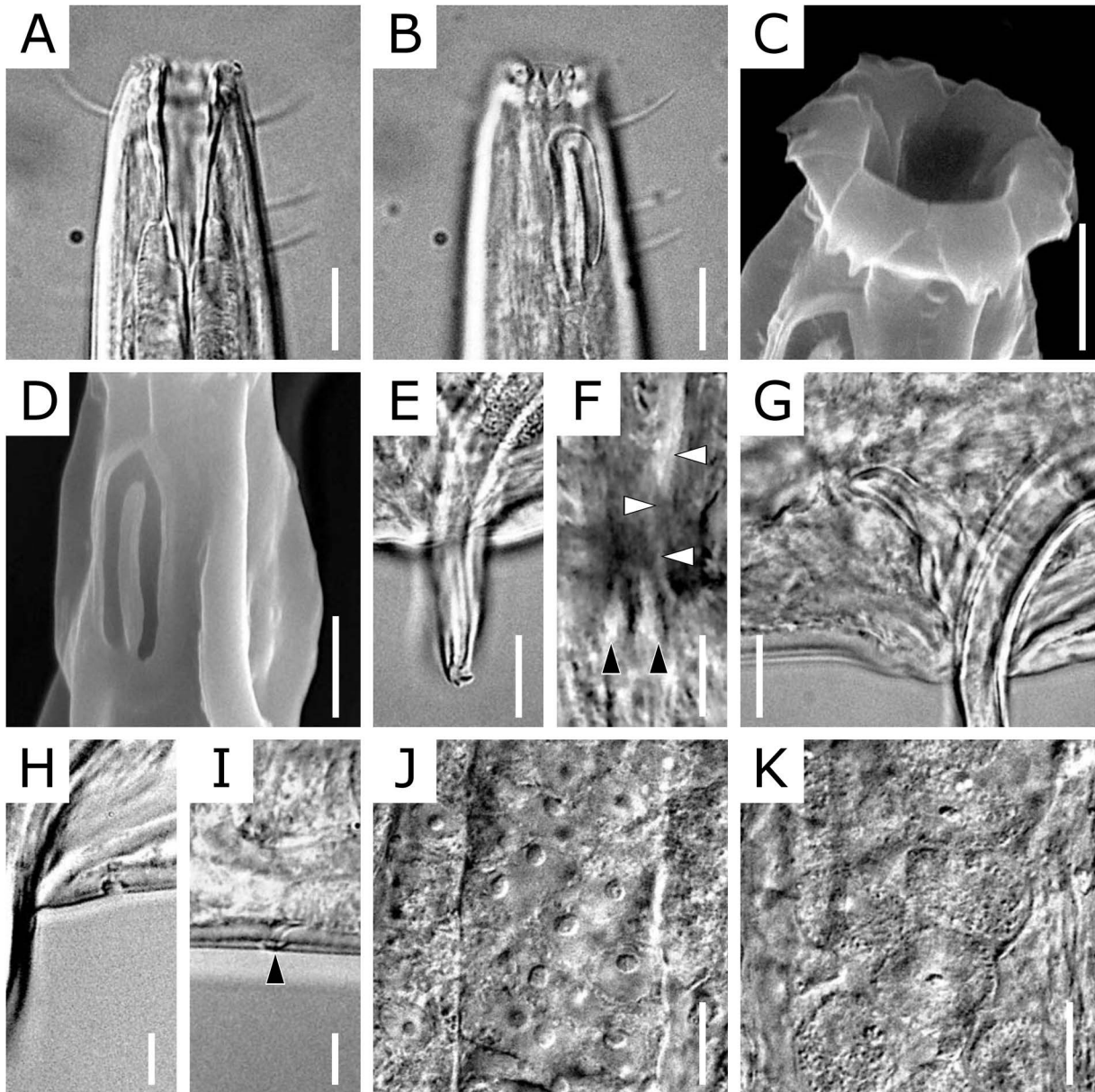


Fig. 2. *Odontophora odontophoroides* sp. nov. A, B, E–J, differential interference contrast photomicrographs; C, D, SEM images. A, inner view of head (holotype); B, amphid and odontia (holotype); C, mouth opening with odontia (non-type male); D, amphidial aperture (non-type male); E, distal end of spicule with spine-like structures (holotype); F, ventral view of left spicule (white arrowheads) and gubernacula (black arrowheads) (dissected non-type); G, gubernaculum (holotype); H, preloacal pore (holotype); I, preloacal supplement (black arrowhead) (holotype); J, contents of testis (holotype); K, sperms in seminal vesicle (holotype). Scale bars: A–G, J, K, 10  $\mu$ m; H, I, 5  $\mu$ m.

or more large (20–40  $\mu$ m in diameter) ejaculatory gland cells on both sides.

**Description of females.** Body (Fig. 3A) similar to males, with following differences. Cephalic and cervical sensilla (Fig. 3B) slightly shorter than in males: cephalic sensilla 0.3–0.6 cephalic diameters long; cervical sensilla 0.25–0.5 cephalic diameters long. Buccal cavity slightly larger than in males, 1.5–1.8 cephalic diameters long and 0.4–0.5 cephalic diameters wide. Somatic sensilla absent in preanal region. Tail (Fig. 3C) not sexually dimorphic. Arrangement of caudal sensilla as in males, but ventrolateral sensilla as short as dorsolateral setae (4–7  $\mu$ m long) and sparser, often not observed in anterior half of tail. Reproductive system (Fig. 3A, D) didelphic, with opposed, outstretched ovaries: anterior

ovary beginning at 20–26% of body length from anterior body end and ending at 43–48%, as long as 20–25% of body length, located on right side of intestine in four specimens but on left side in another specimen (ICHUM 5489); posterior ovary beginning at 60–66% of body length and ending at 83–86%; as long as 17–25% of body length, located on opposite side of intestine from anterior ovary. In total length, reproductive system 60–65% of body length. Mature eggs 75–95  $\mu$ m long, 50–60  $\mu$ m wide. One egg present in each uterus in two specimens (ICHUM 5489 and 5490); one egg present only in anterior uterus in ICHUM 5374; and no egg present in two specimens. Vulva slit-like, located at 54–55% of body length. Vagina sclerotized, 30–37  $\mu$ m long, with well-developed vaginal glands. Sperm not observed in ovi-

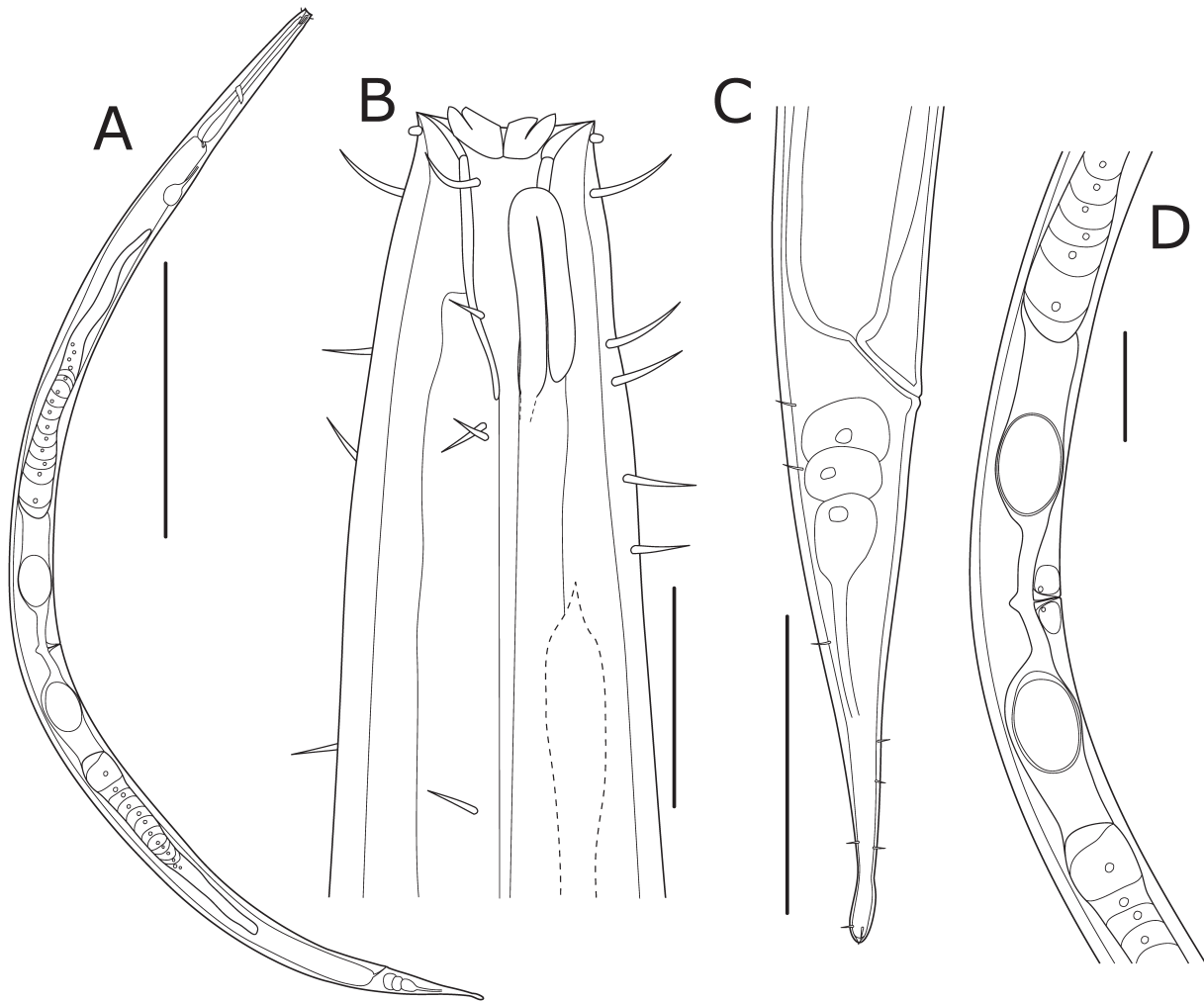


Fig. 3. *Odontophora odontophoroides* sp. nov. A, female body (ICHUM 5490); B, female head with open mouth (ICHUM 5490); C, female posterior region (ICHUM 5490); D, vaginal region (ICHUM 5490). Scale bars: A, 500 µm; B, 20 µm; C, D, 100 µm.

ducts or uteri.

**Remarks.** *Odontophora odontophoroides* sp. nov. differs from congeners in having anteriorly bicuspidate odontia. Most species in *Odontophora* have a single anterior cusp on each odontium, but nine species have odontia with three or more cusps: *O. brevispicula*, *O. fatisca*, *O. furcata*, *O. paravilloti*, and *O. villoti* have three cusps (Luc and De Coninck 1959; Gerlach 1962; Vitiello 1971; Blome 1982; Keppner 1988); *O. articulata*, *O. bermudensis*, and *O. carrolli*, five cusps (Jensen and Gerlach 1976; Keppner 1988); and *O. serrata*, seven cusps (Hourston and Warwick 2010). Species in *Odontophoroides* and *Synodontium* Cobb, 1920, also have bicuspidate odontia, but differ from *O. odontophoroides* sp. nov. in having only a posterior ovary, rather than two ovaries (cf. Bütschli 1874; Cobb 1920; Wieser 1956; Boucher and Helléouët 1977; Tarjan and Nguyen 1988; Fonseca and Bezerra 2014).

Following is a taxonomic key to males of *Odontophora* species, modified from Leduc and Zhao (2016). Although Leduc and Zhao (2016) used presence or absence of the subcephalic sensilla located just posterior to the cephalic sensilla (group C) as a diagnostic character, we did not use this character, as presence/absence was difficult to distinguish in

several species (cf. Cobb 1914; Ditlevsen 1918; Filipjev 1918; Allgén 1928, 1929, 1935; De Coninck and Schuurmans Stekhoven 1933; Timm 1952; Wieser 1956, 1959; Gerlach 1957; Luc and De Coninck 1959; Wieser and Hopper 1967; Lorenzen 1971; Vitiello 1971; Ott 1972; Boucher 1973; Warwick and Platt 1973; Galtsova 1976; Jensen and Gerlach 1976; Boucher and Helléouët 1977; Nichols and Musselman 1979; Blome 1982; Pastor de Ward 1984; Keppner 1988; Turpeenniemi et al. 2001; Hourston and Warwick 2010; Leduc and Zhao 2016; Pinto and Neres 2020):

1. Single lateral subcephalic sensillum present just posterior to each amphid..... 2
- Lateral subcephalic sensillum absent just posterior to each amphid..... 5
2. Pair of long subterminal setae present on tail.....  
.....*O. wieseri*
- Long subterminal setae absent..... 3
3. Tail conico-cylindrical..... *O. tenuicaudata*
- Tail conical..... 4
4. Gubernaculum with dorso-caudal apophysis.....  
.....*O. octoseta*
- Gubernaculum without dorso-caudal apophysis.....  
.....*O. sinapophysis*

Table 1. Morphometrics of *Odontophora odontophoroides* sp. nov. Measurements are in micrometers, with the mean value followed by the range in parentheses. \*Distance from anterior body end; n, sample size; a to V, de Man's ratios.

	Male		Female
	Holotype	Paratypes	Paratypes
n	—	5	5
Body length	2396	2378 (2114–2749)	2514 (2161–2975)
a	31.9	28.8 (22.5–38.2)	28.5 (26.4–30.4)
b	8.2	8.0 (7.0–8.7)	8.4 (7.8–9.4)
c	10.9	10.8 (9.0–12.0)	12.3 (11.9–12.6)
c'	3.9	3.8 (3.3–4.3)	3.9 (3.5–4.2)
V	—	—	54.4 (54.0–54.7)
Cephalic diameter	18	17 (16–18)	16 (15–17)
Maximum body diameter	75	84 (72–94)	89 (71–105)
Vulval body diameter	—	—	83 (63–99)
Cloacal/anal body diameter	56	59 (52–66)	54 (49–61)
Cephalic sensilla length	9.3–12.9	9.7 (7.9–12.1)	8.0 (6.0–9.8)
Cervical sensilla length	6.9–7.2	7.9 (6.9–9.6)	6.2 (4.6–7.8)
Amphid*	9.6	8.4 (5.7–9.5)	8.1 (7.7–9.0)
Amphid length	19	19 (18–21)	18 (17–20)
Amphid width	4.8	5.3 (4.8–6.0)	4.9 (4.3–5.4)
Buccal cavity length	27	26 (24–29)	27 (24–29)
Pore of secretory-excretory system*	48	48 (36–57)	47 (39–59)
Nerve ring*	181	194 (176–218)	174 (159–199)
Pharyngeal length	293	299 (282–315)	297 (277–317)
End of renette cell*	400	421 (401–462)	430 (382–483)
Tail length on arc	220	220 (207–234)	212 (190–251)
Spicule length on arc	73, 75	73 (70–79)	—
Gubernaculum length on arc	27, 27	28 (24–29)	—
Precloacal pore from cloaca	8.5	11.4 (7.7–13.8)	—
Number of precloacal supplements	23	19 (16–21)	—
Anterior end of anterior gonad*	557	495 (412–743)	556 (446–644)
Posterior end of posterior gonad*	1623	1697 (1397–2072)	2128 (1857–2460)
Vulva*	—	—	1367 (1181–1607)

- |   |  |
|---|--|
| 5. Pair of sublateral subcephalic sensilla at mid-level of each amphid . . . . . 6        | 15. Spicules without capitulum . . . . . <i>O. paravilloti</i>                           |
| — Pair of sublateral subcephalic sensilla absent . . . . . 10                             | — Spicules with capitulum . . . . . <i>O. furcata</i>                                    |
| 6. Pair of long subterminal setae on tail . . . . . 7                                     | 16. Each odontium with seven cusps . . . . . <i>O. serrata</i>                           |
| — Long subterminal setae absent . . . . . 9   | — Each odontium with five cusps . . . . . 17   |
| 7. Cuticularized lateral spines in cloacal region . . . . . <i>O. atrox</i>               | 17. Precloacal supplements large, with cuticular elevations . . . . . <i>O. carrolli</i> |
| — Cuticularized lateral spines absent . . . . . 8   | — Precloacal supplements minute . . . . . <i>O. bermudensis</i>                          |
| 8. Each odontium with three cusps . . . . . <i>O. villoti</i>                             | 18. Pair of long subterminal setae on tail . . . . . 19                                  |
| — Each odontium with single cusp . . . . . <i>O. variabilis</i>                           | — Long subterminal setae absent . . . . . 29   |
| 9. Precloacal supplements large, with cuticular elevations . . . . . <i>O. articulata</i> | 19. Distal end of spicules hook-shaped . . . . . <i>O. mercurialis</i>                   |
| — Precloacal supplements minute . . . . . <i>O. setosa</i>                                | — Distal end of spicules not hook-shaped . . . . . 20                                    |
| 10. Each odontium with two or more cusps . . . . . 11                                     | 20. Spicules without capitulum . . . . . 21  |
| — Each odontium with single cusp . . . . . 18   | — Spicules with capitulum . . . . . 22   |
| 11. Each odontium with two cusps . . . . . <i>O. odontophoroides</i> sp. nov.             | 21. Amphidial aperture longitudinally elongate . . . . . <i>O. ornata</i>                |
| — Each odontium with three or more cusps . . . . . 12                                     | — Amphidial aperture circular . . . . . <i>O. mucronata</i>                              |
| 12. Each odontium with three cusps . . . . . 13   | 22. Capitulum of spicules pointed dorsally . . . . . <i>O. peritricha</i>                |
| — Each odontium with five or more cusps . . . . . 16                                      | — Capitulum of spicules not pointed dorsally . . . . . 23                                |
| 13. Pair of long subterminal setae on tail . . . . . 14                                   | 23. Spicules L-shaped (sharply bent in middle) . . . . . <i>O. rectangula</i>            |
| — Long subterminal setae absent . . . . . <i>O. fatisca</i>                               | — Spicules gradually bent . . . . . 24   |
| 14. Distal end of spicule unequally bicuspid . . . . . <i>O. brevispicula</i>             | 24. Amphidial aperture longitudinally elongate . . . . . <i>O. exharena</i>              |
| — Distal end of spicule not bicuspid . . . . . 15   | — Amphidial aperture circular . . . . . 25   |
|   | 25. Precloacal supplements present . . . . . 26  |



- Precloacal supplements absent ..... 27
- 26. Subterminal setae on tail much longer than cloacal body diameter ..... *O. phalarata*
- Subterminal setae on tail shorter than cloacal body diameter ..... *O. longisetosa*
- 27. Cephalic sensilla shorter than cephalic body diameter ..... *O. angustilaima*
- Cephalic sensilla much longer than cephalic body diameter ..... 28
- 28. Longest cervical sensilla as long as cephalic sensilla ... *O. falcifera*
- Longest cervical sensilla much shorter than cephalic sensilla ..... *O. urothrix*
- 29. Spicules with capitulum ..... 30
- Spicules without capitulum ..... 33
- 30. Amphids at level of pharyngostoma .... *O. deconincki*
- Amphids at level of cheilostoma ..... 31
- 31. Cephalic sensilla longer than 1.5 cephalic body diameters. .... *O. polynesiae*
- Cephalic sensilla shorter than cephalic body diameter ..... 32
- 32. Spicules as long as cloacal body diameter ... *O. armata*
- Spicules longer than 1.5 cloacal body diameters. .... *O. setosoides*
- 33. Spicules L-shaped ..... *O. polaris*
- Spicules gradually bent ..... 34
- 34. Amphidial aperture longitudinally elongate ..... *O. hawksbiensis*
- Amphidial aperture circular ..... 35
- 35. Cervical sensilla equal to or longer than cephalic body diameter ..... *O. regalia*
- Cervical sensilla much shorter than cephalic body diameter ..... 36
- 36. Cephalic sensilla as long as cephalic body diameter. ... *O. spiculodentata*
- Cephalic sensilla twice as long as cephalic body diameter ..... *O. lituifera*

Order **Enoplida** Filipjev, 1929  
 Family **Tripyloidea** Filipjev, 1928  
 Genus ***Parabathylaimus*** De Coninck and  
 Schuurmans Stekhoven, 1933

**Type species.** *Bathylaimus ponticus* Filipjev, 1922

**Diagnosis modified from De Coninck and Schuurmans Stekhoven (1933).** Cuticle smooth or striated; three lips high, deeply incised; anterior sensilla all setiform; inner labial and cephalic sensilla jointed or not; outer labial sensilla jointed; buccal cavity not divided; teeth absent; amphids unispiral; long subterminal setae on tail present or absent; spicules shorter than 2.0 cloacal body diameters; gubernaculum with projection(s) at distal end; male monorchic; female didelphic.

**Remarks.** *Parabathylaimus* was established by De Coninck and Schuurmans Stekhoven (1933) based on three known species transferred from *Bathylaimus* Cobb, 1894: *P. denticaudatus* (Allgén, 1930), *P. ponticus* (Filipjev, 1922), and *P. profundis* (Filipjev, 1927). *Parabathylaimus* differs

from *Bathylaimus* in having the single buccal cavity, without teeth, whereas the buccal cavity in *Bathylaimus* is divided into two parts, with several teeth in the posterior part (De Coninck and Schuurmans Stekhoven 1933). Allgén (1947) transferred *Bathylaimus brachylaimus* Allgén, 1935 to *Parabathylaimus*, but this species has teeth, and Wieser (1956) considered it to be a synonym of *B. zostericola* (Allgén, 1933). Gerlach (1951) subsequently treated *Parabathylaimus* as a junior synonym of *Bathylaimus*, because the presence or absence of the posterior part of the buccal cavity and teeth is sometimes difficult to discern. However, we consider *Parabathylaimus* to be distinct from *Bathylaimus*, because all of our specimens obviously lack the posterior part of the buccal cavity and teeth. In a literature survey of the 34 valid species in *Bathylaimus* (Gerlach and Riemann 1974; Keppner 1988; Huang and Zhang 2009; Gagarin and Nguyen 2011; Smirnova and Fadeeva 2011; Chen and Guo 2014), except for the three *Parabathylaimus* species previously mentioned, we found that only *B. arthropappus* Wieser and Hopper, 1967 lacks the posterior part of buccal cavity and teeth (Wieser and Hopper 1967). *Bathylaimus austrogeorgiae* Allgén, 1959 and *B. jacobseni* Allgén, 1954 possibly belong in *Parabathylaimus*, but the original descriptions and figures by Allgén (1954, 1959) are too simple for a conclusion to be reached.

De Coninck and Schuurmans Stekhoven (1933) considered *P. denticaudatus* to be a junior synonym of *P. ponticus*, but we consider them to be distinct species, based on the length of the spicules (ca. 2.0 cloacal body diameters in *P. ponticus*; 1.0 cloacal body diameters in *P. denticaudatus*) (Filipjev 1922; Luc and De Coninck 1959). On the basis of having shorter spicules, *P. ponticus* sensu Schuurmans Stekhoven (1935) is actually *P. denticaudatus* (cf. Schuurmans Stekhoven 1935). *Parabathylaimus* includes the following four valid species.

*P. arthropappus* (Wieser and Hopper, 1967) Shimada, comb. nov.

= *Bathylaimus arthropappus* Wieser and Hopper, 1967

*P. denticaudatus* (Allgén, 1930) De Coninck and Schuurmans Stekhoven, 1933

= *Bathylaimus denticaudatus* Allgén, 1930

= *P. ponticus* sensu Schuurmans Stekhoven (1935)

*P. ponticus* (Filipjev, 1922) De Coninck and Schuurmans Stekhoven, 1933

= *Bathylaimus ponticus* Filipjev, 1922

non *P. ponticus* sensu Schuurmans Stekhoven (1935)

*P. profundis* (Filipjev, 1927) De Coninck and Schuurmans Stekhoven, 1933

= *Bathylaimus profundis* Filipjev, 1927

***Parabathylaimus jare*** Shimada, sp. nov.

(Figs 4–6)

*Tripyloidea* gen. sp. in Shimada et al. (2017): table 1.

**Material examined.** *Holotype*. Male (ICHUM 5375), formalin fixed, whole mount in glycerin, upper subtidal sandy



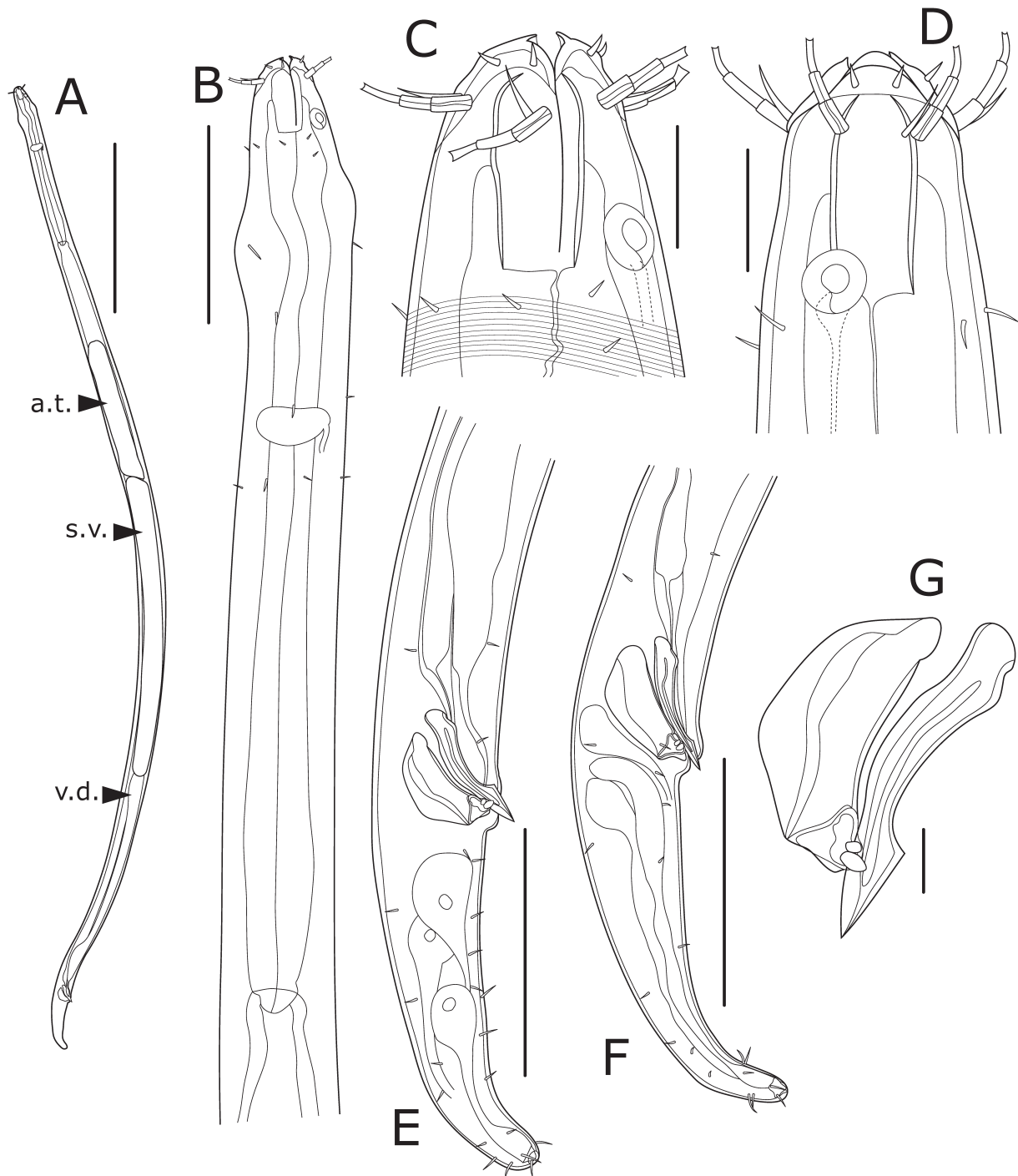


Fig. 4. *Parabathylaimus jare* sp. nov. A, male body (holotype); B, male anterior region (holotype); C, male head, dorso-lateral view (holotype); D, male head, lateral view (ICHUM 5377); E, male posterior region (holotype); F, male posterior region (ICHUM 5377); G, spicule and gubernaculum (holotype). Abbreviations: a.t., anterior testis; s.v., seminal vesicle; v.d., vas deferens. Scale bars: A, 500  $\mu$ m; B, E, F, 100  $\mu$ m; C, D, 20  $\mu$ m; G, 10  $\mu$ m.

sediment, Langhovde (69°14'24.3"S, 39°42'55.8"E), Lützow-Holm Bay, Dronning Maud Land, Antarctica. *Paratypes*. Three males (ICHUM 5376–5378) and one female (ICHUM 5493), formalin fixed, whole mount in glycerin, same collection data as for holotype. *Other material*. One male, Au-coated for SEM, same collection data as for holotype.

**Etymology.** The specific name *jare* is derived from the expedition name JARE 56, and thus treated as indeclinable.

**Diagnosis.** Six inner labial and four cephalic sensilla not

jointed; six outer labial sensilla three-jointed in males and two-jointed in females; amphids at level of posterior end of buccal cavity; spicules short (as long as cloacal body diameter); conical tail without long subterminal setae.

**Measurements.** See Table 2.

**Description of males.** Body (Fig. 4A) cylindrical, gradually tapering toward both ends. Cuticle colorless, 2–4  $\mu$ m thick, with fine transverse striations. Somatic sensilla sparse except in cervical, cloacal, and caudal regions. Head (Figs

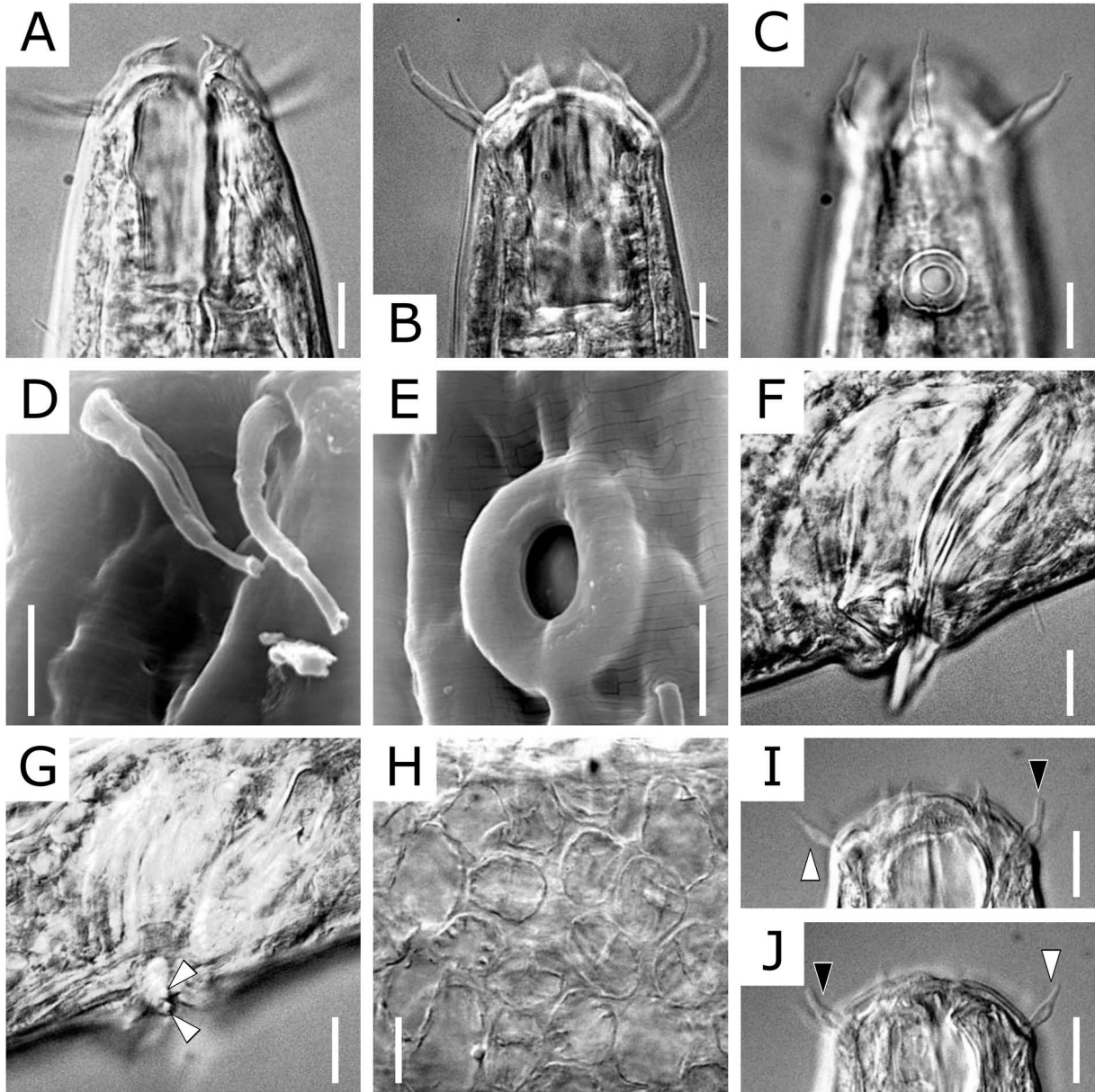


Fig. 5. *Parabathylaimus jare* sp. nov. A–C, F–J, differential interference contrast photomicrographs; D, E, SEM images. A, inner view of head (holotype); B, inner view of head with male anterior sensilla (ICHUM 5377); C, male anterior sensilla and amphid (ICHUM 5376); D, outer labial and cephalic sensilla (non-type male); E, amphidial aperture and cuticular ring (non-type male); F, spicule and gubernaculum (holotype); G, distal tooth-like structures of gubernaculum (white arrowheads) (holotype); H, sperms in seminal vesicle (holotype); I, J, female outer labial sensilla (black arrowheads) and cephalic sensilla (white arrowheads) (ICHUM 5493). Scale bars: A–D, F–J, 10  $\mu$ m; E, 5  $\mu$ m.

4B–D, 5A–C) rounded at anterior end. Three lips high, deeply incised. Six setiform inner labial sensilla unjointed, acute at distal end, 0.10–0.15 cephalic diameters long, 0.10–0.25 cephalic diameters from anterior body end. Six setiform outer labial sensilla (Figs 4C, D, 5B–D) three-jointed, flared at distal end, 0.5–0.7 cephalic diameters long, located 0.4–0.6 cephalic diameters from anterior end. Four setiform cephalic sensilla (Figs 4C, D, 5B–D) unjointed, acute at distal end, 0.3–0.4 cephalic diameters long, arranged in single circle together with outer labial sensilla. Subcephalic sensilla absent. Amphids (Figs 4C, D, 5C, E) unispiral with circular or oval aperture and thick cuticular ring, 0.3–0.4 cephalic diameters wide, 1.0–1.1 cephalic diameters or 0.7–0.8 buccal cavity lengths from anterior end (posterior end of amphids

at level of posterior end of buccal cavity). Amphidial ducts conspicuous. Buccal cavity (Figs 4C, D, 5A, B) single, nearly cylindrical in shape, 1.3–1.5 cephalic diameters long and ca. 0.5 cephalic diameters wide (length/width=2.7–2.9). Teeth absent. Pharynx (Fig. 4B–D) surrounding posterior 35–45% of buccal cavity, nearly cylindrical, not expanded at posterior end. Holotype crushed flat in anterior part of pharynx during fixation. Nerve ring located at 35–40% of pharyngeal length. Secretory-excretory system not observed. Cervical sensilla setiform, slightly longer than inner labial sensilla, arranged in eight longitudinal rows, beginning just posterior to buccal cavity, sparser in posterior half of cervical region. Cardia short, surrounded by intestine. Tail (Fig. 4E, F) nearly conical in shape, rounded at posterior end, 3.2–3.5 clo-

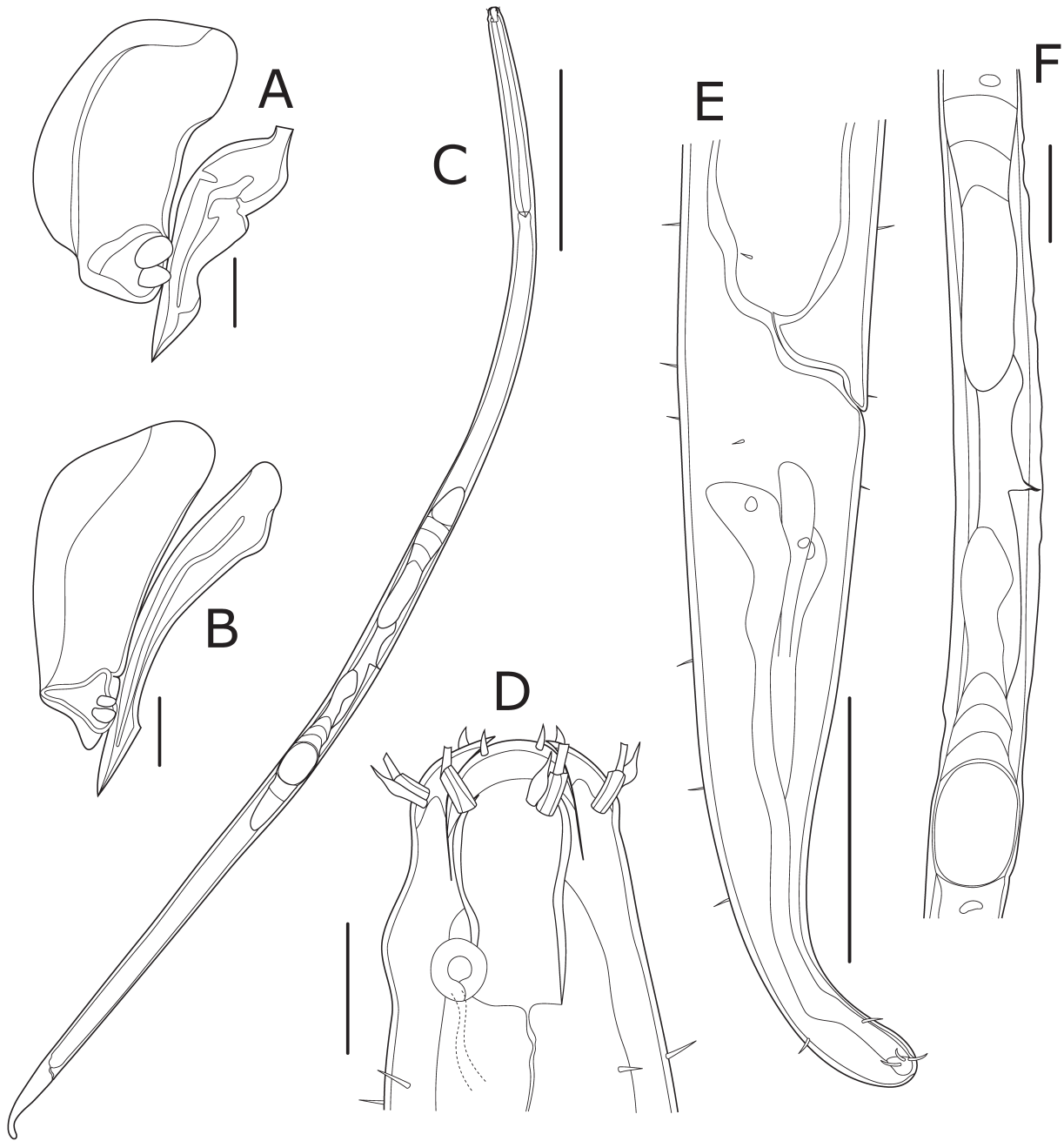


Fig. 6. *Parabathylaimus jare* sp. nov. A, malformed spicule and gubernaculum (ICHUM 5376); B, spicule and gubernaculum (ICHUM 5377); C, female body (ICHUM 5493); D, female head (ICHUM 5493); E, female posterior region (ICHUM 5493); F, vaginal region (ICHUM 5493). Scale bars: A, B, 10  $\mu$ m; C, 500  $\mu$ m; D, 20  $\mu$ m; E, F, 100  $\mu$ m.

cal body diameters long, with three terminal setae (8–9  $\mu$ m long). Long subterminal setae absent. Rows of ventrolateral and dorsolateral setae (5–8  $\mu$ m long) on each side in cloacal and caudal regions. Number and position of setae differ among specimens. Three caudal glands located postcloacally. Spinneret distinct. Spicules (Figs 4G, 5F, 6A, B) paired, as long as 1.0–1.2 cloacal body diameters or 0.3–0.4 tail lengths, slightly arcuate, constricted proximally but not forming distinct capitulum, acute at distal end, with median lamella and heel-shaped ventral projection. Left spicule in ICHUM 5376 (Fig. 6A) malformed; right spicule similar to those in other males. Gubernaculum (Figs 4G, 5F, G, 6A, B) single plate-like, as long as 0.9–1.2 cloacal body diameters or 0.8–1.1

spicule lengths, located between spicules, with distal swelling having two tooth-like projections on each side. Preclonal supplement absent. Reproductive system (Fig. 4A) monorchic with outstretched anterior testis, not well developed in ICHUM 5377 or 5378. Testis located on left side of intestine, beginning at 27% of body length from anterior body end, as long as 15% of body length in holotype. Seminal vesicle well developed in holotype but not observed in other specimens, as long as 30% of body length, filled with globular sperm (5–10  $\mu$ m in diameter) (Fig. 5H). Vas deferens observed in all specimens, not strongly muscular.

**Description of female.** Body (Fig. 6C) similar to males, with following differences. Outer labial sensilla (Figs 5I, J,

Table 2. Morphometrics of *Parabathylaimus jare* sp. nov. Measurements are in micrometers, with the mean value followed by the range in parentheses. \*Distance from anterior body end; n, sample size; a to V, de Man's ratios.

	Male		Female
	Holotype	Paratypes	Paratype
n	—	3	1
Body length	2968	3177 (2982–3492)	3590
a	34.5	41.9 (38.0–45.6)	37.8
b	6.3	6.3 (6.1–6.7)	6.4
c	18.3	18.7 (18.0–19.7)	17.3
c'	3.2	3.4 (3.3–3.5)	3.8
V	—	—	55.0
Cephalic diameter	28	29 (28–29)	32
Maximum body diameter	86	77 (67–92)	95
Vulval body diameter	—	—	91
Cloacal/anal body diameter	51	49 (48–50)	54
Inner labial sensilla length	3.3–3.8	3.9 (3.3–4.6)	3.6–4.3
Outer labial sensilla length	16–18	18 (16–19)	9–11
Cephalic sensilla length	9–10	11 (8–12)	7–9
Cervical sensilla length	4.3–4.4	5.1 (4.0–6.4)	4.4–5.9
Amphid*	27	31 (30–32)	30
Amphid diameter	11	10 (10–11)	9
Buccal cavity length	38	41 (40–43)	41
Buccal cavity width	13	15 (14–15)	14
Nerve ring*	178	191 (177–202)	—
Pharyngeal length	472	501 (490–522)	565
Tail length on arc	162	170 (166–177)	207
Spicule length on arc	56, 56	54 (49–59)	—
Gubernaculum length on arc	46	54 (49–58)	—
Anterior end of anterior gonad*	791	789 (700–868)	1361
Posterior end of posterior gonad*	—	—	2375
Vulva*	—	—	1973

6D) two-jointed, much shorter than in males, 0.3–0.4 cephalic diameters long, 0.3 cephalic diameters from anterior end. Cephalic sensilla (Figs 5I, J, 6D) unjointed, expanded in middle, 0.2–0.3 cephalic diameters long. Nerve ring indistinct. Tail (Fig. 6E) similar to males in shape but slightly longer, 3.8 anal body diameters long. Ventrolateral and dorsolateral setae also present, but ventrolateral setae sparser than in males. Reproductive system (Fig. 6C, F) didelphic, with opposed, reflexed ovaries: anterior ovary on right side of intestine, beginning at 51% of body length and ending at 38%, as long as 13% of body length; posterior ovary also on right side of intestine, beginning at 58% of body length and ending at 66%, as long as 8% of body length. Total length of reproductive system 28% of body length. No egg present in uteri. Vulva slit-like, located at 55% of body length. Vagina weakly sclerotized, 15 µm long. Sperm not observed in oviduct or uteri.

**Remarks.** *Parabathylaimus jare* sp. nov. differs from *P. arthropappus* in having much shorter outer labial sensilla (shorter than cephalic diameter in *P. jare* sp. nov.; ca. 1.5 cephalic diameters long in *P. arthropappus*), in having the amphids positioned more anteriorly (at the level of the buccal cavity in *P. jare* sp. nov.; posterior to the buccal cavity in *P. arthropappus*), and in lacking subterminal setae as long as the cloacal body diameter at the tail tip (present in *P. arthropappus*) (cf. Wieser and Hopper 1967); from *P. ponticus* in

the shorter spicules (as long as the cloacal body diameter in *P. jare* sp. nov.; twice as long as the cloacal body diameter in *P. ponticus*) (cf. Filipjev 1922); from *P. profundis* in the shape of tail (conical, 3.2–3.8 cloacal/anal body diameters long in *P. jare* sp. nov.; conico-cylindrical, ca. 7.5 anal body diameters long in *P. profundis*) (cf. Filipjev 1927); and from *P. denticaudatus* in having unjointed inner labial and cephalic sensilla (jointed in *P. denticaudatus*), and having the outer labial sensilla three-jointed in males and two-jointed in females (four-jointed in both sexes in *P. denticaudatus*) (cf. Schuurmans Stekhoven 1935; Luc and De Coninck 1959).

Following is a taxonomic key to *Parabathylaimus* species (cf. Filipjev 1922, 1927; Allgén 1930; De Coninck and Schuurmans Stekhoven 1933; Wieser and Hopper 1967):

1. Tail conico-cylindrical, with filiform posterior portion.  
..... *P. profundis*
- Tail conical or clavate ..... 2
2. Spicules twice as long as cloacal body diameter .....  
..... *P. ponticus*
- Spicules as long as or shorter than cloacal body diameter ..... 3
3. Amphids located posterior to buccal cavity. ....  
..... *P. arthropappus*
- Amphids located at level of buccal cavity. .... 4
4. Inner labial and cephalic sensilla two-jointed, outer labial sensilla four-jointed in both sexes .....



- ..... *P. denticaudatus*  
 — Inner labial and cephalic sensilla unjointed, outer labial sensilla three-jointed in males and two-jointed in females ..... *P. jare* sp. nov.

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