

Postembryonic Morphology in Epsilonematidae, with a Discussion on the Variability of Caudal Gland Outlets

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Abstract: A new species of *Akanthepsilonema* and the first-stage juvenile of *Glochinema trispinatum* are described. Furthermore, additional morphological information is provided for *Trieptilonema tripapillata*. Animals originate from a cold-water coral degradation zone in the Porcupine Seabight area (North-East Atlantic Ocean). *Akanthepsilonema sinicornibus* sp. n. differs from *A. helleouetae* in number of body annules, sexual dimorphism in amphid size, absence of copulatory thorns in males, absence of large spines and horns, shape of the copulatory apparatus, and position of ambulatory setae relative to vulva in females. The genus diagnosis for *Akanthepsilonema* is adjusted to incorporate the new species. *Akanthepsilonema* mainly differs from every other genus in the family by the combination of six rows of ambulatory setae situated around the vulva in females and eight subcephalic setae not displaced toward the anterior part of the head capsule. Small differences between the Papua New Guinea and the Porcupine Seabight populations of *T. tripapillata* indicate minimal intraspecific variability. Second-stage juveniles from Papua New Guinea have two rows of three ambulatory setae, whereas Porcupine Seabight specimens have two rows of four ambulatory setae. First- and fourth-stage juveniles of *T. tripapillata* are described for the first time. Literature data and personal observations showed that the molting of first-stage juveniles into second-stage juveniles and of third-stage juveniles into fourth-stage juveniles involves a decrease in the number of body rings, resulting in a loss of flexibility which is possibly compensated for by the development (I-II) or the doubling of the number of rows (III-IV) of ambulatory setae. This decrease is also linked with the formation of the head capsule and the smooth tail tip, although intergeneric variability is evident. The molting of second-stage juveniles into third-stage juveniles and of fourth-stage juveniles into adults is also subject to intergeneric variability. The variability in the number and orientation of caudal gland outlets among different nematode taxa is discussed. The presence of separate outlets for the caudal glands seems to be widespread within the family Epsilonematidae and has also been observed in various other, unrelated taxa of free-living aquatic nematodes, although their arrangement in Epsilonematidae is opposite. This aberrant arrangement is probably related to the aberrant locomotory pattern in this family.

Key words: *Akanthepsilonema sinicornibus*, caudal glands, cold-water corals, epsilonematids, *Glochinema trispinatum*, ontogeny, Porcupine Seabight, taxonomy, *Trieptilonema tripapillata*.

The family Epsilonematidae Steiner, 1927 is composed of three subfamilies: Epsilonematinae Steiner, 1927; Glochinematinae Lorenzen, 1974; and the monospecific Keratonematinae Gourbault and Decraemer, 1986. Epsilonematid nematodes are frequently found among the supralittoral or intertidal interstitial marine fauna, and recently several species were found in the deep sea (Neira et al., 2001; Gad, 2002; Raes et al., 2003; Gad, 2004). Samples originating from a cold-water coral degradation zone in the Porcupine Seabight yielded a rich nematode community, including several new species for this family (Raes et al.,

2003). Coral fragments, such as those of the framework-building cold-water coral *Lophelia pertusa* (Linnaeus, 1758), can be regarded as ideal substrates for epifaunal nematodes such as Epsilonematidae. Nematodes belonging to this family are characterized by an ε-shaped body and the presence of ambulatory setae on the ventral side of their posterior body region. These structures are used in their looper-caterpillarlike locomotion (Stauffer, 1924; Lorenzen, 1973a).

A new species of *Akanthepsilonema* Gourbault and Decraemer, 1991, with aberrant features for the genus, will be described here. Additional information is given for *Trieptilonema tripapillata* Decraemer, 1982, a species originally described from an intertidal lagoon in Papua New Guinea based on only one male, one female, one second-stage juvenile, and one third-stage juvenile. Clearly, there was a need for additional information to incorporate intraspecific variability. Strikingly, this species was found to be very abundant in the sampled cold-water coral degradation zone. The complete juvenile series is illustrated in this paper. *Glochinema trispinatum* Raes, Vanreusel and Decraemer, 2003, was originally described from the Porcupine Seabight area. New material from this area yielded a first-stage juvenile. Because the present study produced a lot of new information on juvenile stages within the Epsilonematidae, the ontogenetic morphology of this family will be discussed. The redescription of *T. tripapillata*, a species with pronounced caudal papillae bearing the separate outlets of the caudal glands, resulted in an extensive review of the number and orientation of caudal gland outlets in nematodes.

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MATERIAL AND METHODS

The epsilonematids studied in this paper originated from three NIOZ (Netherlands Institute for Sea Research) box corers (32-cm-diam.) that were collected with the RV Belgica during the June 2000 and May 2001 sampling campaigns. These box cores were taken on the top and slope of a seabed mound situated in the Belgica mound province of the Porcupine Seabight (Box IV 2000 [depth: 1,005 m]: 51°24'48.2" N, 11°45'55.4" W; Box V 2000 [depth: 1,000 m]: 51°24'49.4" N, 11°45'55.9" W; Box IV 2001 [depth: 972 m]: 51°25'7.7" N, 11°46'9.3" W). The Porcupine Seabight is a large embayment of the European continental slope, located in the North-East Atlantic Ocean, southwest of Ireland (Fig. 1). The Belgica mound province is one of the three seamount provinces in this area, characterized by the presence of 21 large, outcropping, and conical mounds, aligned on four along-slope-trending ridges (Van Rooij et al., 2003). These mounds are known to be associated with cold-water coral banks, mainly constructed by the framework builder *Lophelia pertusa* (L.) and associated fauna such as the glass sponge *Aphrocallystes bocagei* Schultze, 1886. The samples used in the present study originated from a cold-water coral reef degradation zone, covered with sediment-clogged dead coral framework (Freiwald et al., 2002) and skeletons of *Aphrocallystes bocagei*. Only a very small amount of living coral was present. After removal of these large biogenic substrates, three sediment cores (surface area 10 cm²) were collected from

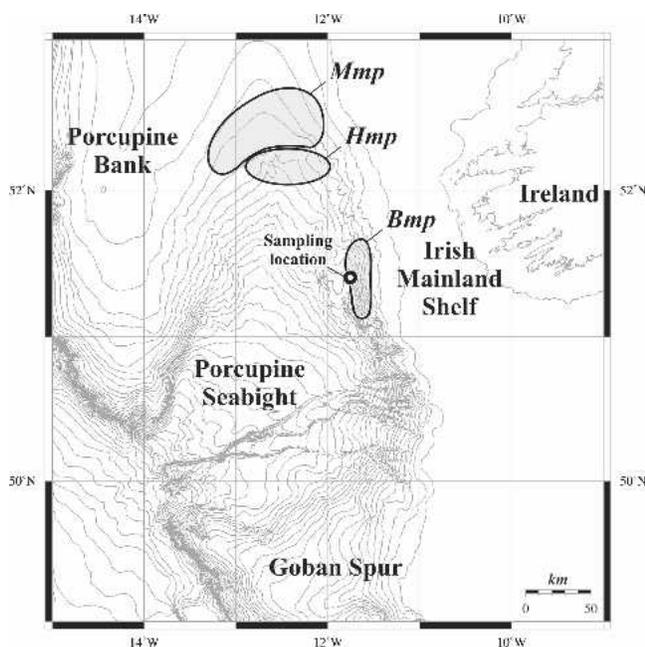


FIG. 1. Map of the Porcupine Seabight area (after Van Rooij et al., 2003). The sampling location is indicated. A detailed overview of the Belgica mound province with an indication of the exact box core locations is given in Raes and Vanreusel (2005, Fig. 1). *Mmp* = Magellan mound province; *Hmp* = Hovland mound province; *Bmp* = Belgica mound province.

each box core. The sediment was poorly sorted, containing small coral and sponge fragments as well as some small mollusc shells and echinoid radiolas. All material was fixed with 4% neutralized formalin.

Each *Lophelia* and *Aphrocallystes* fragment was rinsed thoroughly over a 1-mm and a 32- μ m sieve to separate macrofauna and meiofauna. Meiofauna was extracted from the underlying or remaining sediment by density gradient centrifugation, using Ludox (a colloidal silica polymer; specific gravity 1.18) as a flotation medium (Heip et al., 1985; Vincx, 1996). Some of the material was stained with Rose Bengal. Nematodes were picked out individually and subsequently mounted onto slides for detailed morphological observation with a Leica DMLB light microscope, using the formalin-ethanol-glycerol technique described by Seinhorst (1959) and Vincx (1996). A Leitz Dialux 20 microscope, Sanyo CCD video camera, and Quantimet 500 software were used to perform measurements. Scanning electron micrographs were taken from the formalin-fixed specimens. After ultrasonic treatment (to remove detritus attached to the body), the specimens were transferred to OsO₄, dehydrated, subjected to critical-point drying, and coated with gold particles.

Type material is deposited in the collections of Ghent University, Museum voor Dierkunde (UGent), the Koninklijk Belgisch Instituut voor Natuurwetenschappen in Brussels (KBIN), and the Natural History Museum in London (NHM).

ABBREVIATIONS USED

L: total body length.

N: number of cuticular rings, smooth tail tip included (remark: all annules counted dorsally).

dcs: distance from the anterior edge of the head capsule to the insertion point of the cephalic setae.

hdw: maximal width of the head capsule.

hdl: length of the head capsule.

bda: body diameter at the level of the amphids.

amphw: amphidial width.

amph%: $(\text{Amphw} / \text{Hdw}) \times 100$.

ph: pharyngeal length, measured from the anterior end of the head capsule up to the posterior border of the pharyngeal bulb, lips (when protruding) and cardia not included.

lvAsl: length of the anteriormost lateroventral ambulatory seta.

osvAsl: length of the anteriormost ambulatory seta in the outer subventral rows.

isvAsl: length of the anteriormost ambulatory seta in the inner subventral rows.

asup: length of the anteriormost modified somatic or supporting seta.

psup: length of the posteriormost modified somatic or supporting seta.

tail: tail length.

tmr: length of the smooth tail tip.

mbd ph: body diameter at level of the pharyngeal bulb.

mbd: maximal diameter of the posterior body region.

(mbd): minimal body diameter.

mbd/(mbd): proportion of the minimal body diameter to the maximal body diameter.

abd: anal body diameter.

spic: length of the spicule, measured along the arc.

gub: length of the gubernaculum.

V%: position of the vulva, expressed as a percentage of L, measured from the anterior end.

a: de Man a-ratio, i.e., L/mbd.

b: de Man b-ratio, i.e., L/ph.

c: de Man c-ratio, i.e., L/tail.

DESCRIPTIONS

Familia Epsilonematidae Steiner, 1927

Subfamilia Epsilonematinae Steiner, 1927

Genus *Akanthepsilonema* Gourbault and Decraemer, 1991

Akanthepsilonema sinecornibus sp. n. (Figs. 2-4)

Type specimens. Holotype male on slide RI 682 (KBIN). Paratype males on slides UGMD 104095 (UGent), RI 681, RI 677 (KBIN) and stored as 2005.2684 (NHM). Additional male: 2005.2657 (NHM). Allotype female on slide RI 681 (KBIN). Paratype females on slides UGMD 104093 (UGent), RI 681, RI 678 (KBIN) and stored as 2005.2675 (NHM). Paratype third-stage juveniles on slides UGMD 104094 (UGent) and RI 678 (KBIN). Paratype fourth-stage juveniles on slides UGMD 104092 (UGent), RI 676 (KBIN) and stored as 2005.2666 (NHM).

Type locality. Porcupine Seabight, Belgica mound province. Coordinates: 51°24'49.4" N, 11°45'55.9" W (material collected on 6/17/2000; depth: 1,000 m).

Other localities. Porcupine Seabight, Belgica mound province. Coordinates: 51°24'48.2" N, 11°45'55.4" W

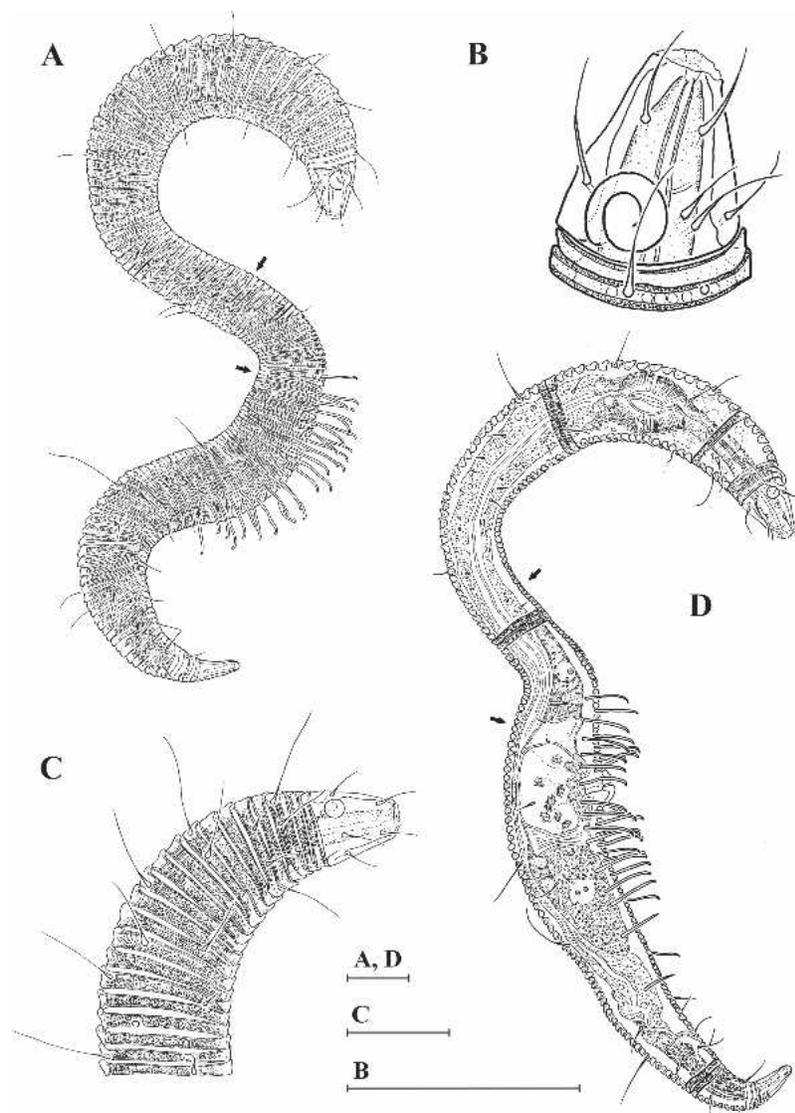


FIG. 2. *Akanthepsilonema sinecornibus* sp. n. A) Holotype ♂, habitus. B) Additional ♂, head capsule (lateral view). C) Paratype ♀, pharyngeal region (lateral view). D) Paratype ♀, habitus. Arrows indicate inversion of annular orientation. Scale bars: 20 μm.

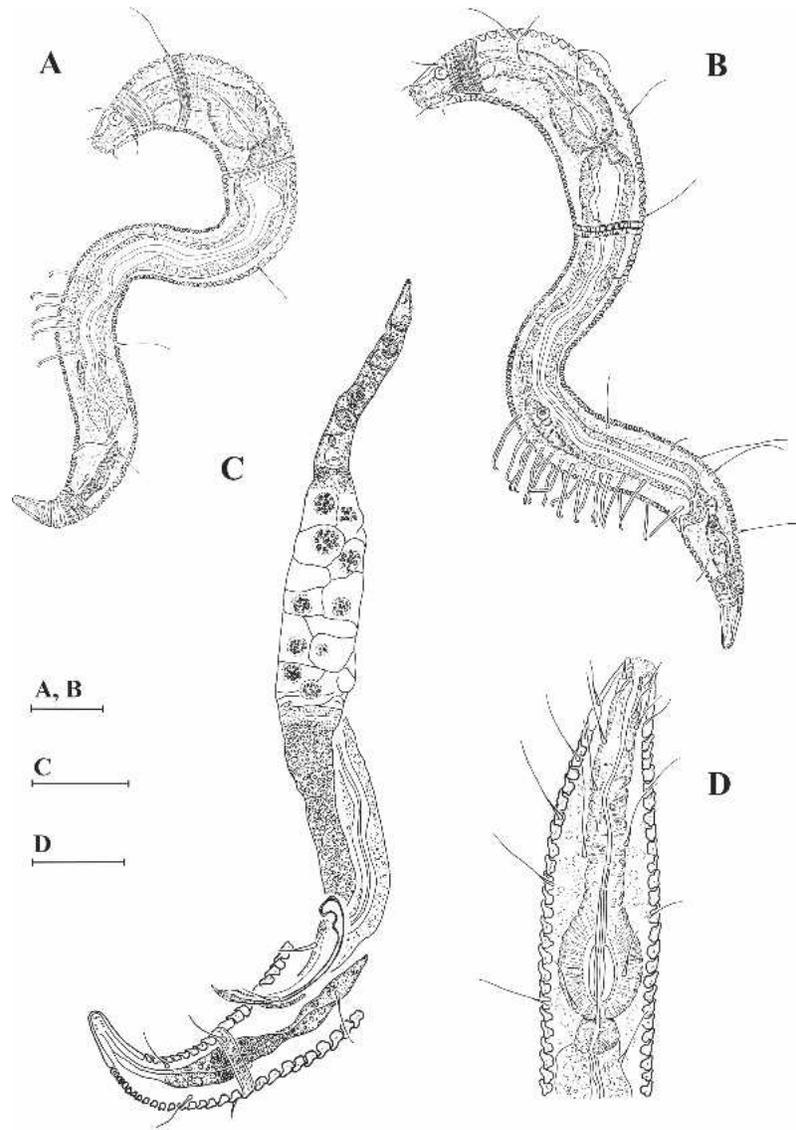


FIG. 3. *Akanthepsilonema sinicornibus* sp. n. A) Third-stage juvenile, habitus. B) Fourth-stage juvenile, habitus. C) Paratype ♂, testis. D) Paratype ♂, pharyngeal region (lateral view). Scale bars: 20 μ m.

(material collected on 6/17/2000; depth: 1,005 m); 51°25'7.7" N, 11°46'9.3" W (material collected on 5/07/2001; depth: 972 m).

Date of collection. 17 June 2000 and 7 May 2001.

Type habitat. A cold-water coral degradation zone on the flank and near the top of a seabed mound. Associated with sediment-clogged framework of the cold-water coral *Lophelia pertusa* (Linnaeus, 1758). It was found on dead coral fragments and within the underlying sediment.

Relative abundance. This species comprises 0.46% of the total nematode community at the type locality.

Etymology. The species name means "without horns," as opposed to the key diagnostic feature formerly delimiting the genus, the presence of large mediadorsal horns just anterior to the ventral curvature. From the Latin preposition *sine* (without) and the ablative plural of the Latin noun *cornu*, *cornus* (horn).

Measurements. Table 1.

Males

Body typically ϵ -shaped, rather small and noticeably slender with only slight enlargements at level of pharynx and ambulatory setae. Region between anterior-most dorsal curvature and ventral curvature strikingly long and slender (Figs. 2A,4A). Body cuticle with 145 to 163 body annules (155 in holotype). Annules broadest at level of pharynx and cloaca and finest at level of ambulatory setae. Annules only minimally overlapping. Anterior-most annules with anteriorly directed margin. Ventrally, inversion of orientation between annules 56 and 67 (predominantly between annule 59 and 60; between 60 and 61 in holotype). Dorsally, inversion between annules 69 and 79 (predominantly between annule 77 and 78, as in holotype). Annules in pharyngeal region with irregular, sometimes mosaic-like pattern of

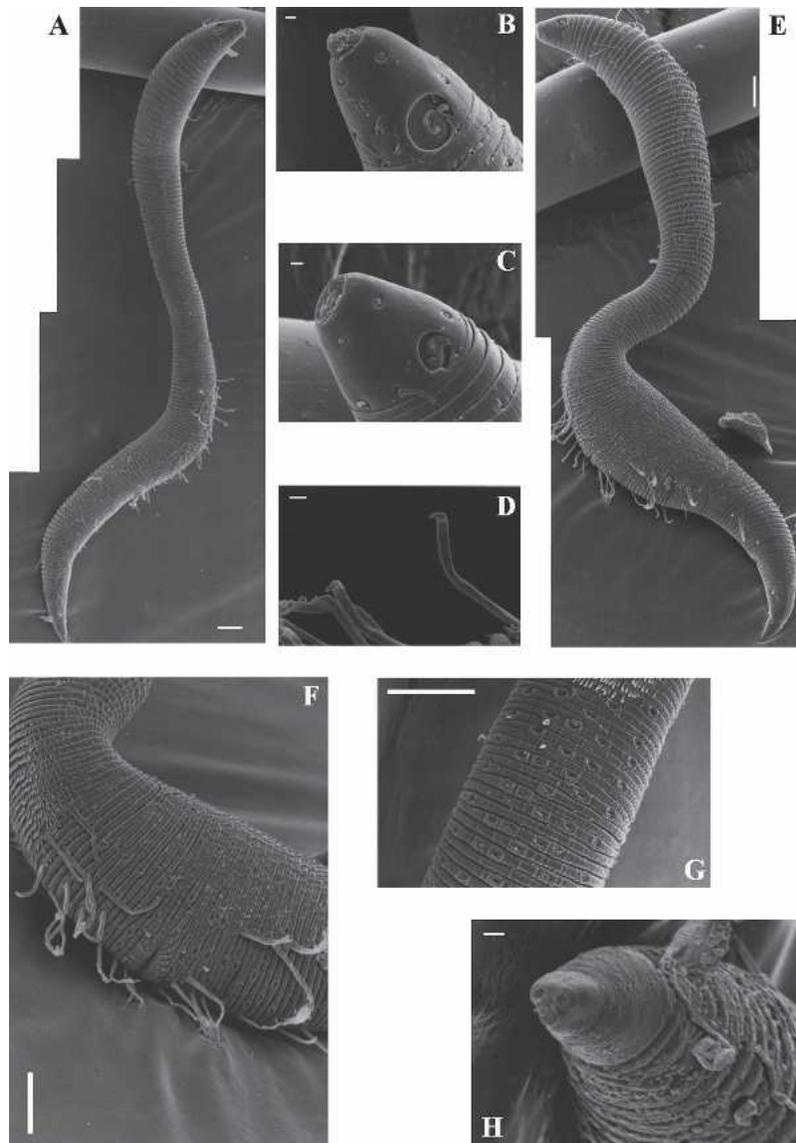


FIG. 4. *Akanthepsilonema sinicornibus* sp. n. A) ♂, habitus. B) ♂, head capsule (lateral view). C) ♀, head capsule (lateral view). D) ♀, ambulatory setae. E) ♀, habitus. F) ♀, vulva and ambulatory setae (lateral-ventral view). G) ♂, insertion sites of ambulatory setae (ventral view). H) ♂, tail tip with outlets of caudal glands. Scale bars: 10 μ m in A, E, F, and G; 1 μ m in B, C, D, and H.

heterogeneous vacuoles of various sizes (Fig. 2A). Annules in slender region posterior to pharynx with cuticular ornamentation comparable to that of pharyngeal region. Both regions dorsally with strongly built, longitudinal ridges delimiting more regularly shaped vacuoles. Annules at level of ambulatory setae ornamented with one transverse row of small vacuoles. Annules in posterior body region and anteriormost tail annules either with one row of irregular vacuoles or with mosaic of smaller heterogeneous vacuoles. More posteriorly on tail, vacuoles progressively smaller and one to six annules immediately anterior to tail tip completely smooth or only with indistinct vacuoles. Ventral field of hair-like spines present anterior to ambulatory setae (Fig. 2A). Short spines present dorsally in region of ambulatory setae.

Somatic setae in pharyngeal region and region ante-

rior to ambulatory setae arranged in 10 longitudinal rows: one mediadorsal row, two subdorsal rows, two laterodorsal rows, two lateroventral rows, two subventral rows, and one medioventral row. Mediodorsal, subdorsal, and laterodorsal setae especially long. Somatic setae at level of ambulatory setae arranged in five longitudinal rows: one mediadorsal row and two subdorsal rows with long setae and two mediolateral rows with short setae. In this region, no somatic setae on ventral side of body. Ambulatory setae strongly built and slightly s-shaped, all with curved tip (see female in Fig. 4D) and arranged in six longitudinal rows: outer rows with eight to 15 lateroventral setae, intermediate rows with 12 to 18 subventral setae, and inner rows with six to 12 almost medioventral setae (Figs. 2A,4G). Ambulatory setae in lateroventral row straighter than other ambulatory setae. Lateroventral row almost immedi-

TABLE 1. Measurements of specimens of *Akantheptionema sinecornibus* sp. n. (ranges and means). All absolute values are in μm . The number of specimens that was measured, when different from the total number of specimens, is indicated between brackets in superscript.

	Holotype male	Males (n = 14)	Allotype female	Females (n = 15)
L	435	335–500 (430)	435	345–475 (405) ⁽¹⁴⁾
N	155	145–163 (154)	155	151–163 (155)
hdw	16	14–16 (15.0)	14.5	14–16 (14.9) ⁽¹⁴⁾
hdl	16	13.5–16.5 (14.9) ⁽¹³⁾	13.5	12.5–16 (14.4) ⁽¹⁰⁾
amphw	6.5	6–8 (6.7) ⁽¹³⁾	4	4–5 (4.6) ⁽¹³⁾
amph%	40.5	37.5–53.5 (44.7) ⁽¹³⁾	28	28–35 (30.7) ⁽¹³⁾
ph	77	66.5–83 (75.2)	79	69–86.5 (76.6) ⁽¹³⁾
IvAsI	16	13–19.5 (16.9) ⁽¹³⁾	15.5	13.5–19 (16.2) ⁽¹²⁾
osvAsI	12.5	11.5–16 (13.7) ⁽¹²⁾	10	11.5–16 (13.8) ⁽¹⁴⁾
isvAsI	12	13–16 (14.0) ⁽¹¹⁾		11–16 (14.0) ⁽¹²⁾
psup	11	7.5–13 (10.8) ⁽¹¹⁾	11	11.5–15.5 (13.0)
tail	48.5	40–55.5 (48.6) ⁽¹³⁾	39.5	39–50.5 (45.2) ⁽¹³⁾
tmr	14.5	12.5–16.5 (14.7) ⁽¹³⁾		10.5–16 (13.5)
mbd ph	26.5	25–27.5 (26.4)	26.5	25.5–28.5 (27.1)
mbd	26.5	23–28 (26.4)	36	26.5–38.5 (33.4)
(mbd)	19.5	17–19.5 (18.6)	20	18–20.5 (19.4)
mbd/(mbd)	1.3	1.3–1.5 (1.4)	1.8	1.4–1.9 (1.7)
abd	19.5	19–21 (19.6)	17	16–19 (17.4) ⁽¹⁴⁾
spic	39.5	37–44.5 (41.1) ⁽¹³⁾		
gub	10	6–9.5 (8.1) ⁽¹²⁾		
V%			285.5	61.5–69 (64.1) ⁽¹⁴⁾
a	16.4	13.6–18.3 (16.3)	12.1	10.2–13.8 (12.0) ⁽¹⁴⁾
b	5.6	5.0–6.5 (5.7)	5.5	4.4–5.9 (5.3) ⁽¹⁴⁾
c	8.9	7.1–9.7 (8.9) ⁽¹³⁾	11.0	7.8–10.0 (8.8) ⁽¹³⁾
		Juvenile stage III (n = 3)		Juvenile stage IV (n = 7)
L		225–275 (255)		270–345 (305)
N		166–185 (178)		162–171 (166)
hdw		11–12 (11.4)		12–13.5 (13.0)
hdl		10.5–12.5 (11.3) ⁽²⁾		11–13.5 (12.0)
amphw		3–4 (3.6)		3.5–4.5 (4.1)
amph%		29.5–32.5 (31.2)		26.5–35.5 (31.3)
ph		52–59 (56.1)		60.5–69.5 (65.1)
IvAsI				
osvAsI				16.5–18.5 (17.4) ⁽⁵⁾
isvAsI		15.5–16 (15.7)		13.5–16.5 (15.1) ⁽⁵⁾
psup		13–15.5 (14.3)		13–15.5 (14.4) ⁽⁶⁾
tail		35–37 (36.1)		37.5–45.5 (41.8)
tmr		9.5–13 (11.0)		11.5–13 (12.6) ⁽⁶⁾
mbd ph		20.5–23.5 (21.9)		24.5–27.5 (25.8)
mbd		14–18 (16.4)		19–26 (21.9)
(mbd)		14–17.5 (15.3)		16.5–20.5 (18.4)
mbd/(mbd)		1.0–1.2 (1.1)		1.1–1.3 (1.2)
abd		13–16 (14.7)		16.5–19.5 (18.1)
spic				
gub				
V%				
a		15.1–16.0 (15.6)		13.4–14.8 (13.9)
b		4.3–4.6 (4.5)		4.2–5.7 (4.7)
c		6.4–7.6 (7.0)		6.2–8.2 (7.3)

ately followed by four to five lateroventral short, slender, straight, slightly modified, somatic setae with straight, pointed tip. Slightly modified somatic setae gradually decreasing in length and width toward posterior end and eventually becoming indistinguishable from normal, subventral-lateroventral somatic setae on tail.

Head capsule a smooth truncated cone (Figs. 2B,4B), often with lip region partially protruding. Head capsule

with four cephalic setae and eight subcephalic setae, the latter all located at level of amphids. On each side of head capsule subcephalic setae arranged as follows: one subdorsal seta immediately anterior to amphid, one ventrosublateral seta at same level as subdorsal one, one lateroventral seta immediately posterior to sublateral seta, and one subventral seta variable in position, i.e., at level of subdorsal and sublateral seta (as in holotype) (Fig. 2B), at level of lateroventral seta, or in

between sublateral and lateroventral seta. Amphids situated near base of head capsule and clearly shifted dorsally. Amphidial fovea large (40.5% of corresponding head width in holotype), ventrally wound spiral usually consisting of 1.6 coils (1.8 coils in Fig. 2B). Buccal cavity very narrow. Two minute teeth (one dorsal, one ventral) present or absent where buccal cavity grades into pharyngeal lumen (Fig. 2B). Pharynx short, extending into well-developed, oval, muscular terminal bulb. Pharyngeal lumen wall strongly cuticularized, especially in posterior part of bulb where lumen wall is differentiated into well-developed cuticular valves (Fig. 3D). Cardia short and triangular. Intestine granular, with thick conspicuous brush border.

Male reproductive system (Fig. 3C) with single anterior, outstretched testis extending far into region between anteriormost dorsal curvature and ventral curvature. Testis positioned ventrally around intestine, sometimes shifted somewhat to left or right side. Narrow anterior germinal and growth zones followed by wider vesicula seminalis consisting of large, opaque sperm cells, each with clear, round nucleus containing radiate pattern of small nucleoli. Spicules slender and strongly curved, with hook-shaped capitulum. Calomus thin, with small bulge at base of capitulum, where velum originates. Gubernaculum thin, slightly bent, adjacent to spicules except for proximal end. Copulatory thorns absent.

Tail short and conical, with 16 to 20 complete annules, including smooth tail tip (18 in holotype). Anterior end of conical tail tip dorsally with one to five incomplete annules (three in holotype). Anteriormost tail annule split ventrally around cloaca. Tail with subdorsal and subventral-lateroventral somatic setae. Three caudal glands extending anteriorly beyond cloaca (Fig. 3C), up to two-thirds of spicule length. Each of these glands ending in a separate pore (Fig. 4H).

Females

Females similar to males in size and shape, although posterior body enlargement more pronounced (Figs. 2D,4E). Cuticle composed of 151 to 163 annules (155 in allotype female), comparable to males. Inversion of orientation between annules 57 and 68 (between 60 and 61 in allotype female) ventrally and between annules 68 and 82 (between 80 and 81 in allotype female) dorsally. Cuticular ornamentation similar to that of males (Figs. 2C,4F).

Position of rows of somatic setae in females identical to that of males, except for absence of medioventral row in pharyngeal region and presence of an additional medioventral seta immediately anterior to anus. Ambulatory setae similar to those of males, arranged in six to seven longitudinal rows. Outer, lateroventral rows with 14 to 20 setae: five to eight setae situated anterior to vulva, eight to 11 setae posterior to vulva, and in some

cases one seta at level of vulva. Intermediate, subventral rows with 11 to 18 setae, of which five to eight are situated anterior to vulva, five to 10 posterior to vulva, and one seta present or absent at level of vulva. Inner subventral rows with seven to 10 setae: one to five setae anterior to vulva and four to seven setae posterior to it. Ambulatory setae in lateroventral rows longer, straighter, and more robust than those in subventral rows. As many as two medioventral setae may be present between both inner subventral rows. In total, 27 to 38 setae situated anterior to vulva and 42 to 49 setae posterior to it. Number of ambulatory setae anterior to vulva always less than posterior to it. Each lateroventral row of ambulatory setae followed by two or three modified somatic setae considered supporting setae because they are longer (11–15.5 μm in females vs. 7.5–13 μm in males) and much more strongly built than in males. Each supporting seta similar to ambulatory setae in length and girth, but differing from them by being straight and usually lacking a curved tip, except for anteriormost supporting seta with minute, sometimes slightly curved, set-off tip. From anterior to posterior there is a gradual morphological transformation from ambulatory setae via supporting setae to normal somatic setae, expressed by changes in length, girth, and structure of distal tip (Fig. 2D).

Sexual dimorphism evident from position of subcephalic setae and size and shape of amphids. Eight subcephalic setae: on each side one subdorsal seta, one lateroventral seta, and one subventral seta immediately anterior to amphid and one laterodorsal seta immediately posterior to it (Fig. 2C). As a result, females with only six subcephalic setae at level of amphids. Amphids situated near base of head capsule and shifted dorsally. Amphids spiral, ventrally wound with 1.6 coils, but, unlike males, circular in outline and much smaller (28% of corresponding head width in allotype female) (Fig. 4C).

Female reproductive system didelphic and amphidelphic, with antidromously reflexed ovaries, situated ventrally from intestine. Anterior ovary reflexed toward left side, and posterior ovary reflexed toward right side. Vagina bipartite, with *pars distalis* shorter than, or as long as, *pars proximalis*. Uterus often filled with sperm cells (no. 10–24), recognizable by highly refractile nuclear material. Vulva surrounded externally by numerous radial cuticular ridges, ornamented with small tubercles (Fig. 4F). No somatic setae around vulva.

Tail with 16 to 19 complete annules, including smooth tail tip (18 in allotype female). Conical tail tip with one to five incomplete annules on dorsal side (three in allotype female). As in males, anteriormost tail annule split around anus and separate outlets for each caudal gland.

Juveniles

First- and second-stage juveniles

Not found.

Third-stage juveniles

Three juvenile males. Body comparable to male adults in shape (Fig. 3A) but smaller and with more constant body diameter. Cuticle with 166 to 185 narrow annules, which is more than in adults. Annules in pharyngeal region with one row of more or less irregular vacuoles occupying entire width of each annule. Annules in slender region posterior to pharynx with one row of tiny vacuoles. Annules smooth at level of ambulatory setae and in posterior body region. Anteriormost tail annules with one row of tiny vacuoles. Vacuoles larger and more irregular more posteriorly on tail.

Except for region of ambulatory and supporting setae, somatic setae arranged in five longitudinal rows: one mediodorsal row, two laterodorsal rows, and two lateroventral rows. No lateroventral somatic setae in region of ambulatory and supporting setae. Two subventral rows with 10 to 11 slender, slightly s-shaped ambulatory setae with curved tip. Two posteriormost ambulatory setae on each side slightly broader and situated slightly more dorsally than other ambulatory setae, but distinguishable from supporting setae by presence of curved tip. One strongly developed, straight, dorsosublateral supporting seta with straight tip, situated just anterior to cloaca.

Five subcephalic setae, all situated near posterior edge of head capsule: one mediodorsal seta and on each side of head one laterodorsal and one lateroventral seta. Relative width of amphids comparable to that of females (29.5–32.5% of corresponding head width). Amphids with 1.6 coils.

Tail with 24 to 28 complete annules, including smooth tail tip, with one or two incomplete annules on dorsal side. As in adults, anteriormost tail annule split around anus.

Fourth-stage juveniles

Four juvenile males and three juvenile females, all comparable to male adults in body shape, but smaller (Fig. 3B). Number of annules (162–171) comparable to that of third-stage juveniles. Cuticular ornamentation in pharyngeal region as described in males. Annules in slender region posterior to pharynx ornamented with single row of vacuoles. Annules smooth at level of ambulatory setae. Annules in posterior body region and anteriormost tail annules with single row of rectangular vacuoles. The vacuoles become more irregular in shape more posteriorly on the tail.

Somatic setae in pharyngeal region and at level of anteriormost dorsal curvature arranged in five longitudinal rows as in third-stage juveniles. Somatic setae in region of ambulatory setae and in caudal region arranged as follows: one row of mediodorsal setae, two dorsosublateral rows, and two lateroventral rows. Five longitudinal rows of ambulatory setae: two outer subventral rows with eight to 11 s-shaped setae with curved

tip, two inner subventral rows of five to eight thinner and shorter s-shaped setae with curved tip, and two medioventral setae at level of first two supporting setae, comparable in shape with inner subventral setae. Each outer subventral row of ambulatory setae followed by three more heavily built supporting setae with straight tip. Anteriormost supporting seta close to posteriormost ambulatory seta but distinguishable from ambulatory setae by its more robust appearance and absence of a distinctly curved tip.

Six to seven subcephalic setae: on each side, one subventral and one lateroventral seta always present. Juvenile males with two subdorsal setae; juvenile females with one mediodorsal seta and two laterodorsal setae posterior to amphid. Relative width of amphids comparable to that in adult females (26.5–35.5% of corresponding head width). Amphids spiral, consisting of 1.6 coils.

Tail with 17 to 25 complete annules, including smooth tail tip. Tail tip with one to seven incomplete annules on dorsal side. As in adults, anteriormost tail annule split around anus.

Diagnosis

Akanthepsilonema sinicornibus sp. n. is characterized by 145 to 163 annules in males and 151 to 163 annules in females. Large spines or horns absent. Most ambulatory setae situated posterior to vulva. Amphids in females clearly smaller than in males. Spicules 37 to 44.5 µm in length, with hook-shaped capitulum. Copulatory thorns absent.

Differential diagnosis

Akanthepsilonema sinicornibus sp. n. resembles *A. helleouetae* Gourbault and Decraemer, 1991, the only other species within this genus, in the following features: (i) the elongation of the anterior body region, (ii) a maximum-to-minimum body diameter ratio lower than two, (iii) the cuticular ornamentation, (iv) the presence of eight subcephalic setae on the head capsule, (v) the presence of six rows of ambulatory setae in adults, and (vi) supporting setae differentiated only in females and juveniles.

It differs from this species in the following features: (i) a higher number of annules, (ii) the total absence of large spines or horns, (iii) amphids wider in males than in females, (iv) shorter spicules with a hook-shaped capitulum in males, (v) absence of copulatory thorns in males, and (vi) most ambulatory setae situated posterior to the vulva in females.

Relationships with other genera

The genus *Akanthepsilonema* Gourbault and Decraemer, 1991, was originally established to accommodate *A. helleouetae*, an epsilonematid with conspicuous copulatory thorns, fine ventral and dorsal spines, and large

dorsal horns. These features made *Akantheptionema* one of the easiest recognizable genera in the family.

However, the genus also differs from every other genus in the family by the combination of six rows of ambulatory setae situated around the vulva and eight subcephalic setae not displaced toward the anterior part of the head capsule. Given these features, the new species *A. sinicornibus* sp. n. clearly belongs to this genus. Moreover, Gad (2002) argued that cuticular protrusions such as spines or dorsal horns can evolve in response to similar environmental conditions, and similarities between species with such structures may therefore be interpreted as the result of convergent evolution. Therefore, the presence of such structures is of low diagnostic value and cannot be used to separate genera.

Except for the presence or absence of copulatory thorns, large spines, and horns, there is one other important diagnostic character that separates both species; in *A. helleouetae*, most ambulatory setae are situated anterior to the vulva, whereas in *A. sinicornibus* sp. n. most ambulatory setae are situated posterior to the vulva. The arrangement of ambulatory setae in relation to the vulva was considered a character suitable for discriminating between genera by Gourbault and Decraemer (1996), with only the genus *Archeptionema* Steiner, 1931, having more ambulatory setae posterior to the vulva. In contrast to *A. sinicornibus* sp. n., however, all ambulatory setae in *Archeptionema* are situated at the level of the vulva or posterior to it and are arranged in only four rows (Steiner, 1931). Because the position of the ambulatory setae in relation to the vulva is a character that does not apply to males and juveniles, this character alone should not be used to erect a new genus. Therefore, *A. sinicornibus* is put in the genus *Akantheptionema*.

Within the subfamily Epsilonematinae Steiner, 1927, the only genera with ambulatory setae arranged in six longitudinal rows are *Akantheptionema*, *Bathyptionema* Steiner, 1931, *Leptptionema* Clasing, 1983, *Polkeptionema* Verschelde and Vincx, 1992, and *Pterneptionema* Verschelde and Vincx, 1992. Among these genera only *Akantheptionema*, *Bathyptionema*, and *Leptptionema* possess eight subcephalic setae. However, we do not consider it advisable to draw any conclusions about relationships between genera within the family until molecular phylogenetic data are available to assess both the phylogenetic significance and the diagnostic value of morphological characters.

Emended genus diagnosis

Akantheptionema Gourbault and Decraemer, 1991. Epsilonematidae. This genus is characterized by the combination of an elongated anterior body region, a maximum-to-minimum body diameter ratio of less than two, six rows of ambulatory setae situated around the vulva, supporting setae only differentiated in females

and juveniles, and eight subcephalic setae not displaced toward the anterior part of the head capsule. Copulatory thorns, large spines, and horns are present or absent. The majority of the ambulatory setae are situated either anterior or posterior to the vulva.

Type species: *Akantheptionema helleouetae* Gourbault and Decraemer, 1991.

Other species: *Akantheptionema sinicornibus* sp. n.

Remark on juvenile stage III as described for A. helleouetae Gourbault and Decraemer, 1991

A detailed analysis of the arrangement of ambulatory setae in the juvenile stages of *A. sinicornibus* sp. n., *Bathyptionema*, and *Leptptionema* showed that: (i) in all second-stage juveniles of these genera, the ambulatory setae are arranged in two rows of three to eight setae; (ii) in all third-stage juveniles of these genera, the ambulatory setae are arranged in two rows of eight to 15 setae; (iii) in all fourth-stage juveniles of these genera, the ambulatory setae are arranged in four to five rows with four to 11 setae in the internal rows and seven to 16 setae in the external rows.

The third-stage juvenile of *A. helleouetae* has four rows of ambulatory setae: the internal rows with four setae and the external rows with nine setae (Gourbault and Decraemer, 1991). This agrees with the abovementioned arrangement for a fourth-stage juvenile and not with that of a third-stage juvenile. Therefore, we conclude that the third-stage juvenile of *A. helleouetae* as described by Gourbault and Decraemer (1991) is actually a fourth-stage juvenile.

Familia Epsilonematidae Steiner, 1927

Subfamilia Epsilonematinae Steiner, 1927

Genus *Triptionema* Decraemer, 1982

Triptionema tripapillata Decraemer, 1982 (Figs. 5–6)

Type specimens. Holotype male on slide RIT 27, paratype female and juvenile III on slide RIT 28, and paratype juvenile II on slide RIT 29 (KBIN).

Additional specimens.

Additional males on slides UGMD 104092, UGMD 104096, and UGMD 104098 (UGent), RI 683 and RI 679 (KBIN), stored as 2005.2696, 2005.2706, 2005.2708–2005.2712 (NHM).

Additional females on slides UGMD 104096 and UGMD 104098 (UGent), RI 683 and RI 679 (KBIN), stored as 2005.2705, 2005.2707 (NHM).

Additional first-stage juveniles on slides UGMD 104096, UGMD 104097 (UGent), RI 676 and RI 678 (KBIN), stored as 2005.2694 (NHM).

Additional second-stage juveniles on slides UGMD 104096 (UGent), RI 677 (KBIN), stored as 2005.2662 and 2005.2693 (NHM).

Additional third-stage juveniles on slides UGMD 104098 (UGent), RI 679 (KBIN), stored as 2005.2703 (NHM).

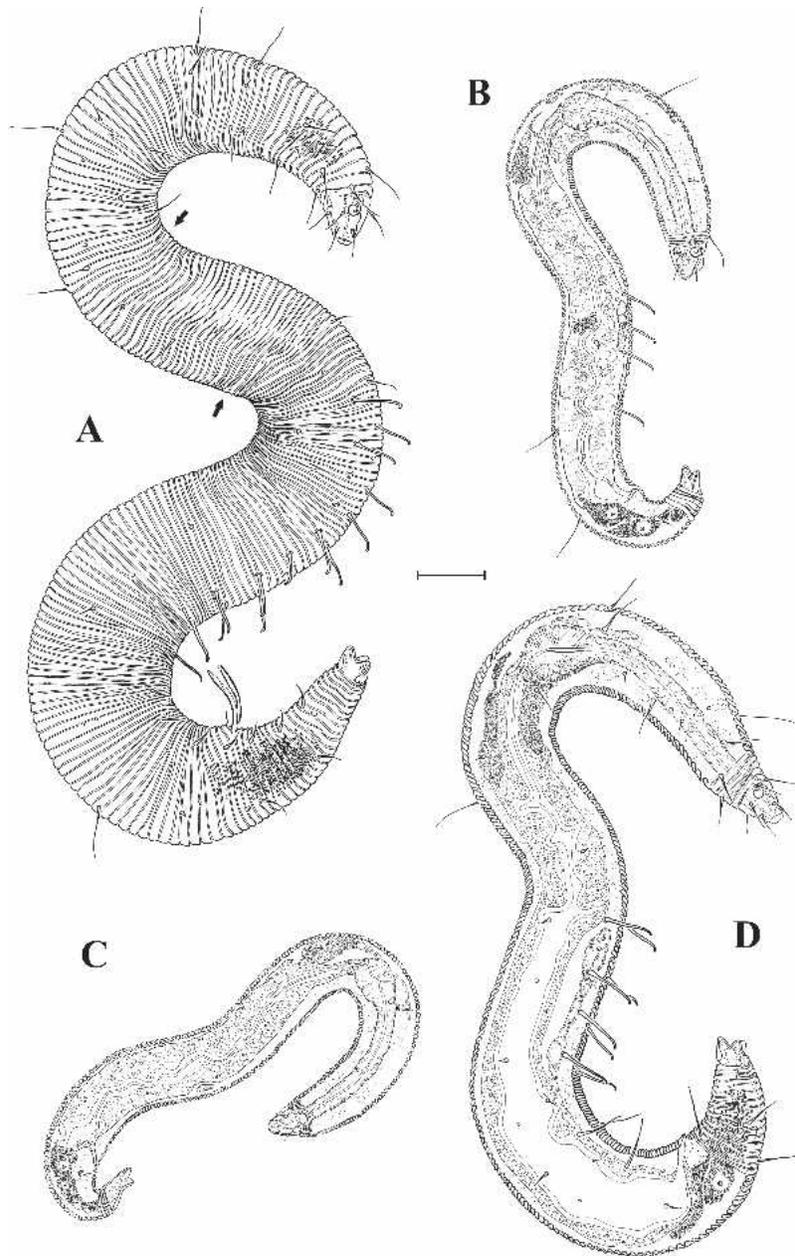


FIG. 5. *Triepsilonema tripapillata* Decraemer, 1982 (Porcupine Seabight specimens). A) ♂, habitus. B) Second-stage juvenile, habitus. C) First-stage juvenile, habitus. D) Fourth-stage juvenile, habitus. Arrows indicate inversion of annular orientation. Scale bar: 20 µm.

Additional fourth-stage juveniles on slides UGMD 104096 and UGMD 104098 (UGent), RI 683 and RI 679 (KBIN), stored as 2005.2690, 2005.2695, 2005.2704 (NHM).

Type locality. Laing Island, Hansa Bay, Madang Province, Papua New Guinea.

New locality. Porcupine Seabight, Belgica mound province. Coordinates: 51°24'48.2" N, 11°45'55.4" W (material collected on 6/17/2000; depth: 1,005 m); 51°24'49.4" N, 11°45'55.9" W (material collected on 6/17/2000; depth: 1,000 m); 51°25'7.7" N, 11°46'9.3" W (material collected on 5/7/2001; depth: 972 m). It has also been recorded from 51°24'47.5" N, 11°45'55.7" W (material collected on 5/25/2003; depth: 994 m).

Date of collection. Type material: 5 May 1977. Porcupine Seabight material: 17 June 2000 and 7 May 2001.

Type habitat. Between the marine alga *Halimeda*. Samples originated from a lagoon.

New habitat. A cold-water coral degradation zone on the flank and near the top of a seabed mound. Associated with sediment-clogged framework of the cold-water coral *Lophelia pertusa* (Linnaeus, 1758). It was found on dead coral fragments, on dead sponge skeletons (*Aphrocallistes bocagei* Schultze, 1886), and within the underlying sediment.

Relative abundance at new locality. This species comprises 2.0% of the total nematode community in the Porcupine Seabight samples.

Measurements. Table 2.

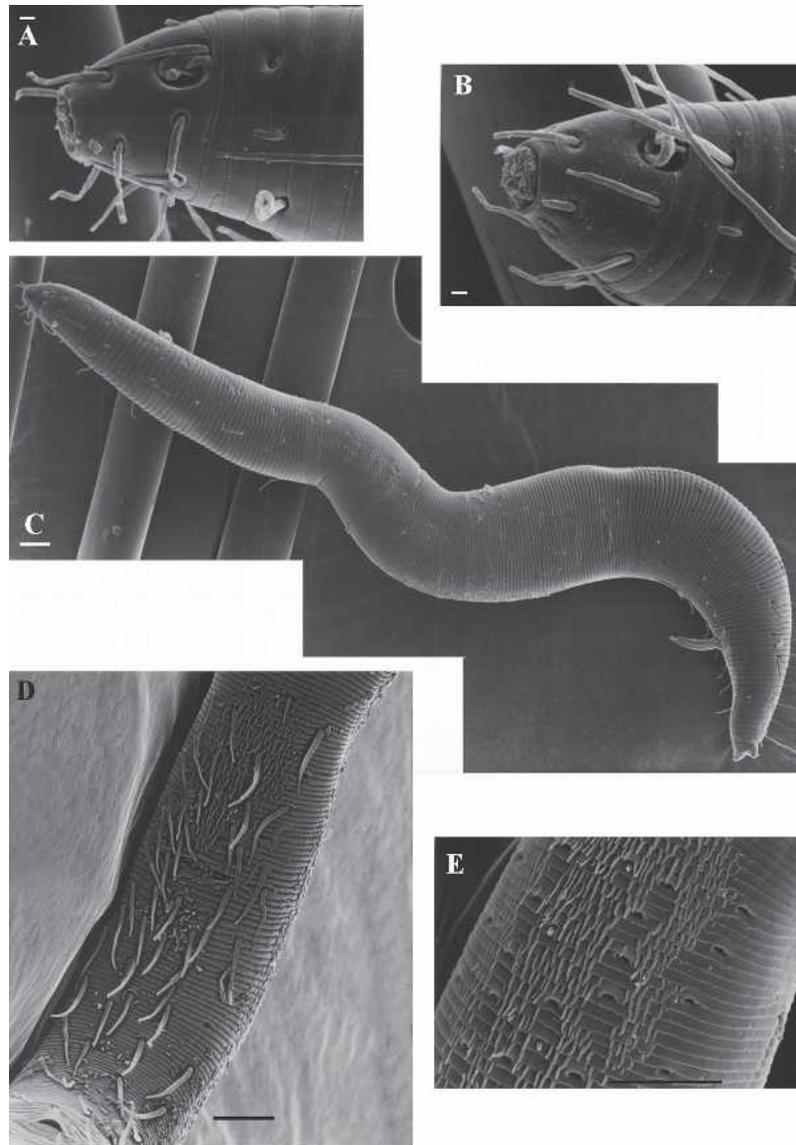


FIG. 6. *Triepsilonema tripapillata* Decraemer, 1982 (Porcupine Seabight specimens). A) ♂, head capsule (lateral view). B) ♀, head capsule (lateral view). C) ♂, habitus. D) ♀, vulva and ambulatory setae (ventral view). E) ♂, insertion sites of ambulatory setae (ventral view). Scale bars: 1 μm in A and B; 10 μm in C, D, and E.

Redescription and additional information

Males

Body slender, almost cylindrical, and ϵ -shaped (Figs. 5A,6C). No marked enlargements but widest at level of testis: body width gradually increasing from anterior end up to cloacal region and gradually decreasing again along tail. Posterior body region laterally often with large refractile bodies. Cuticle with 198 annules in holotype and 206 to 227 annules in Porcupine Seabight specimens. Annules fine, broadest at level of pharynx and on tail, finest at mid-body. Annules overlapping, with hyaline outer layer. Anteriormost annules with anteriorly directed margin. Ventrally, inversion of orientation on annule 42 in holotype and between annules 52 and 62 in Porcupine Seabight specimens (i.e., at level of anteriormost dorsal curvature), dorsally on annule 77 in holotype, and between 79 and 90 in Porcu-

pine Seabight specimens (i.e., at level of ventral curvature). Body rings in holotype male without ornamentation, except for a few tail annules with small, transversally elongated vacuoles. Porcupine Seabight specimens with scattered cuticular ornamentation. Anteriormost annules generally without ornamentation, although several small vacuoles may occur. Annules in pharyngeal region either smooth or ornamented with numerous tiny vacuoles, often gradually increasing in size until becoming transversally elongated and then gradually decreasing in size again. Annules at level of pharyngeal bulb either smooth or ornamented with tiny vacuoles. Annules between pharyngeal bulb and posterior body region always smooth. Annules anterior to cloaca with numerous tiny vacuoles, often gradually increasing in size until forming a network of transversally elongated vacuoles at level of cloaca and then gradually decreasing in size toward posterior end of

TABLE 2. Measurements of type specimens from Papua New Guinea (first four columns) and Porcupine Seabight specimens of *Trieptisolenema tripapillata* Decraemer, 1982 (ranges and means). All absolute values are in μm . The number of specimens that was measured, when different from the total number of specimens, is indicated between brackets in superscript.

	Holotype male	Paratype female	Paratype juvenile stage II	Paratype juvenile stage III	
L	400	370	190	295	
N	198	195	164	201	
hdw	12.5	12.5	12	12	
hdl	12	11	10	8	
bda					
amphw	3.5	3.5	3.5	2.5	
amph%	29	28.5	29	21.5	
ph	88	93		82.5	
osvAsI	17	14.5	10	11.5	
isvAsI	13.5	13			
asup	9.5				
tail	58.5	46	26	35.5	
tmr	7	6	5.5	7	
mbd ph	25.5	36.5	25	30.5	
mbd	38.5	48.5	25	38.5	
(mbd)	29	38.5	23.5	33.5	
mbd/(mbd)	1.3	1.3	1.1	1.1	
abd	26.5	30.5	22	25.5	
spic	42.5				
gub	11.5				
V%		58.5			
a	10.4	7.6	7.7	7.67	
b	4.5	4.0		3.58	
c	6.8	8.0	7.4	8.36	

	Males (n = 10)	Females (n = 10)	Juvenile stage I (n = 10)	Juvenile stage II (n = 10)	Juvenile stage III (n = 10)	Juvenile stage IV (n = 10)
L	385–575 (495)	480–580 (540)	185–280 (225)	210–340 (280)	270–395 (335)	365–505 (435)
N	206–227 (217)	209–231 (218)	179–200 (191)	163–193 (182)	227–242 (232)	215–239 (225)
hdw	13–14.5 (14.0)	13.5–15 (14.2)	8.5–9.5 (9.2)	10.5–12 (11.1)	11–13 (12.1)	12.5–13.5 (12.9)
hdl	10–13 (11.5)	10.5–15 (12.5)	5.5–8 (6.8) ⁽⁹⁾	8.5–10 (9.4)	8.5–11.5 (9.9)	9.5–11.5 (10.9)
bda			11–12.5 (11.7)			
amphw	3–4 (3.8)	3.5–4 (3.8)	3.5–4.5 (4.0)	3.5–4 (3.8)	3.5–4.5 ((3.9)	3.5–4 (3.8)
amph%	28–43 (33.4)	24.5–36 (30.8)	29.5–38 (34.1)	28.5–36.5 (34.0)	29–34.5 (32.4)	24.5–32.5 (29.6)
ph	106.5–120 (112.7)	104.5–122 (113.2)	69–78 (73.2)	67.5–87 (78.8)	76–98 (88.7)	92–108.5 (98.9)
osvAsI	16.5–19.5 (18.0) ⁽⁹⁾	15.5–21 (17.4) ⁽⁹⁾		10–15 (12.8)	12.5–16.5 (14.9)	15.5–18.5 (16.9)
isvAsI	13–15 (13.9) ⁽⁸⁾	10.5–15 (12.7) ⁽⁹⁾				11.5–14.5 (13.1)
asup	7.5–11 (9.6)					
tail	49.5–61.5 (55.8)	45.5–58.5 (50.5)	32.5–37.5 (35.2)	20.5–41 (33.1)	34.5–45 (38.9)	39.5–49 (44.9)
tmr	8.5–10 (9.3)	7.5–10.5 (9.6)	10.5–12.5 (11.6)	6.5–9 (7.7)	7.5–9 (7.9)	7.5–9.5 (8.5) ⁽⁹⁾
mbd ph	29–34 (31.7)	30–38 (33.6)	18–24 (20.1)	19.5–29.5 (23.1)	23–31 (26.1)	25.5–35 (30.2)
mbd	37.5–47.5 (41.9)	42.5–57 (49.0)	19–25 (21.0)	19–34 (25.4)	25–37.5 (30.1)	29.5–52.5 (37.6)
(mbd)	30–35.5 (32.0)	30.5–39.5 (34.3)	18–23.5 (19.9)	18.5–30 (23.2)	22.5–30.5 (26.4)	25–39.5 (31.2)
mbd/(mbd)	1.2–1.4 (1.3)	1.3–1.6 (1.4)	1.0–1.1 (1.1)	1.0–1.2 (1.1)	1.1–1.3 (1.1)	1.1–1.3 (1.2)
abd	29–34.5 (31.2)	27–32 (30.3)	17.5–21 (19.2)	17.5–30 (21.5)	22–29.5 (25.1)	25–33.5 (28.6)
spic	42.5–49.5 (46.5)					
gub	12–15.5 (13.4)					
V%		50.5–60 (55.4)				
a	10.1–14.0 (11.8)	9.4–13.9 (11.6)	8.5–12.1 (10.7)	9.0–13.0 (11.0)	9.9–12.9 (11.2)	9.7–13.6 (11.7)
b	3.5–5.3 (4.4)	4.3–5.3 (4.8)	2.6–3.6 (3.1)	2.7–4.1 (3.5)	3.0–4.1 (3.8)	3.9–5.1 (4.4)
c	6.9–10.1 (8.8)	9.3–11.9 (10.7)	5.4–7.5 (6.3)	6.8–13.7 (8.6)	7.6–10.4 (8.6)	8.7–11.1 (9.7)

tail. Posteriormost annules without ornamentation. Ventral field of hair-like spines present at level of ambulatory setae (Fig. 6E).

Somatic setae flattened. Somatic setae in pharyngeal region and region anterior to ambulatory setae arranged in eight longitudinal rows: two subdorsal rows, two laterodorsal rows, two lateroventral rows, and two subventral rows. At level of ambulatory setae, somatic setae arranged in two dorsosublateral rows. Somatic setae at level of “fine” (i.e., slightly modified somatic)

setae situated in subdorsal, laterodorsal, dorsosublateral, lateroventral, subventral, and medioventral position. Two fine somatic setae present immediately anterior to cloaca. Somatic setae on tail arranged in two subdorsal rows, two laterodorsal rows, two ventrosublateral-lateroventral rows, and two subventral rows. Ambulatory setae slender, slightly s-shaped, with curved tip, arranged in four longitudinal rows with some scattered setae in between (Fig. 6E): two outer subventral rows with six to nine setae, two inner subventral rows with

eight to 13 setae, and two to six setae scattered in between those two latter rows. Inner subventral rows converging toward cloaca. In holotype, outer subventral rows of ambulatory setae immediately followed by six (right side) and seven (left side) subventral, short, fine setae with straight and fine tip: three and four setae, respectively, anterior to cloaca, one seta at level of cloaca on right side and two and three setae, respectively, posterior to it, the latter gradually becoming shorter and finer. Porcupine Seabight specimens with nine to 14 subventral fine setae: five to 10 setae anterior to cloaca, often one seta at level of cloaca and another three to four posterior to it, gradually becoming shorter and finer. Posteriormost subventral fine seta situated immediately anterior to smooth tail tip.

Head capsule a smooth, rounded, truncated cone, slightly lopsided with longer dorsal side (Fig. 6A). Labial region with two crowns of six labial papillae, often partially protruding and then partly surrounded by a small rim of the head capsule. Four cephalic and eight subcephalic setae. Subcephalic setae arranged on each side as follows: one subdorsal seta, one laterodorsal seta, one lateroventral seta, and one subventral seta. All subcephalic setae located at anterior border of amphids except for laterodorsal setae, which are situated posterior to amphids at posterior edge of head capsule. Amphids situated near base of head capsule, slightly shifted dorsally (laterodorsal position). Amphidial fovea a small (29% of the corresponding head width in holotype), ventrally wound open spiral with 1.25 turns. Buccal cavity narrow and cylindrical. Two subventral tooth-like projections in lumen may be present, opposite with corresponding indentation of dorsal lumen wall, where buccal cavity grades into pharyngeal lumen. Pharynx long (88 μm in holotype male and 106.5–120 μm in Porcupine Seabight specimens) and slender, gradually widening into an oval, partly glandular terminal bulb. Terminal bulb ventrally, laterally, and dorsally surrounded by glandular mass. Pharyngeal lumen wall slightly cuticularized. Cardia inconspicuous. Intestine often granular, although internal structure highly variable. Intestinal brush border conspicuous.

Male reproductive system with a single wide, anteriorly outstretched testis situated ventrally to intestine and extending beyond ventral curvature. Vesicula seminalis with several large, opaque sperm cells. Each sperm cell with a large round or slightly jagged nucleus containing numerous small nucleoli. Spicules often protruding (Fig. 5A), curved, and rather robust, with triangular or beak-like capitulum and well-developed velum. Narrow, slightly s-shaped gubernaculum with clear triangular cuneus, adjacent to spicules, except for proximal part, which curves away from spicules. Copulatory thorns absent.

Tail short and conical, completely annulated, with 17 to 20 annules ventrally and 18 to 22 annules dorsally, including smooth tail tip. Smooth tail tip usually without incomplete annules. Three caudal glands extend-

ing anteriorly beyond cloaca. Caudal glands ending posteriorly in one medioventral and two laterodorsal, smooth papillae, 4 to 5 μm in length. Each papilla with terminal spinneret, forming a separate outlet for one of the three caudal glands (Fig. 8A).

Females

Females similar to males in most respects. Body cuticle with 195 annules in Papua New Guinea specimen and 209 to 231 annules in Porcupine Seabight specimens, which is comparable to males. Inversion of orientation between annules 55 and 65 ventrally (i.e., at level of anteriormost dorsal curvature) and between annules 77 and 87 dorsally (i.e., at level of ventral curvature). Annules often smooth, sometimes ornamented with transversally elongated vacuoles in pharyngeal region and on tail. Ventral field of hair-like spines present in region of ambulatory setae (Fig. 6D).

Somatic setae flattened as in males. Number and position of longitudinal rows of somatic setae in females similar to that in males. Ambulatory setae slender, slightly s-shaped, with curved tip and arranged in four longitudinal rows with some scattered setae in between, as in males. No clear separation between ambulatory and fine (somatic) setae, but a gradual transition from the one type into the other, i.e., becoming finer, straighter and with a straighter distal tip (Fig. 6D). Somatic setae on tail posteriorly also becoming shorter. Two outer subventral rows with 14 to 18 setae, gradually changing from ambulatory setae anteriorly to somatic setae posteriorly: four to six setae anterior to vulva, sometimes one seta at level of vulva, seven to nine setae between vulva and anus, sometimes one seta at level of anus and two to three setae on tail. Posteriormost setae in outer subventral rows situated immediately anterior to smooth tail tip. Two inner subventral rows with 11 to 17 setae: three to six setae anterior to vulva, sometimes one seta at level of vulva and seven to 10 setae between vulva and anus. Posteriormost setae in inner subventral rows clearly finer than setae situated more anteriorly. Four to seven ambulatory setae scattered between inner subventral rows: one to five anterior to vulva and one to five posterior to it.

Shape of head capsule, number and position of subcephalic setae, shape and size of amphids, buccal cavity and pharynx as in males (Fig. 6B).

Female reproductive system didelphic and amphidelphic with outstretched ovaries, situated ventrally to intestine. Anterior ovary shifted slightly to right side, posterior ovary to left side. In mature females, anterior ovary extending up to anteriormost dorsal curvature (close to pharyngeal bulb) and posterior ovary up to anus. Vagina bipartite, with cuticularized *pars distalis* shorter and narrower than *pars proximalis*, connected to anterior region of uterus. Uterus with or without large sperm cells, each with distinct nucleus. Spermathecae absent. Vulva situated at 50.5% to 60% of total body

length from anterior, surrounded by several radial cuticular folds. Paravulval setae absent.

Tail with 15 annules ventrally and 16 annules dorsally in Papua New Guinea specimen and 17 to 19 annules ventrally and 18 to 22 annules dorsally in Porcupine Seabight specimens, always including smooth tail tip. Smooth tail tip without incomplete annules. Caudal glands ending separately in three smooth papillae as in males (Fig. 8B).

Juveniles

First-stage juveniles

Twenty-one specimens, only from Porcupine Seabight area. Habitus as in adults, although smaller (Fig. 5C). Number of annules 179 to 200, which is slightly less than in adults. Annules thin, non-overlapping, and largely without ornamentation, except for some slightly broader annules on tail, ornamented with single row of small vacuoles.

Only four rather short and flattened somatic setae present along body: on each side one seta at level of pharyngeal bulb and one at level of anus. Each seta with distinct circular insertion site. Ambulatory setae absent.

Head capsule a short truncated cone, with four long (5.9 μm on average) cephalic setae. Subcephalic setae absent. Amphids positioned mediolaterally between annules one and five posterior to head capsule. Amphidial fovea small (average width: 4.0 μm ; average length: 2.0 μm), antero-posteriorly flattened, oval, and unispiral, dorsally wound with posterior aperture. Pharynx long and slender, partly glandular, with well-developed endbulb. Clear glandular structures laterally at level of pharyngeal bulb and dorsally posterior to pharyngeal bulb. Intestine granular. Genital primordium minute.

Tail with 16 to 18 annules ventrally and 19 to 24 annules dorsally, including smooth tail tip. Tail tip triangular, relatively longer than in adults due to an extended basis and without incomplete annules. Tail with three distinct caudal glands extending anterior to anus. Only two terminal papillae: ventral one (average length: 3.4 μm) longer than dorsal one (average length: 2.7 μm).

Second-stage juveniles

One specimen originating from Papua New Guinea and 22 specimens from Porcupine Seabight area. General body shape as in adults (Fig. 5B). Body about equally wide, tapered toward both ends, 190 to 340 μm in length. Number of annules 163 to 193, which is slightly less than in first-stage juveniles. Annules fine, non-overlapping, and mostly smooth except for some tail annules ornamented with one or two rows of small, oval vacuoles. Ventral field of small hair-like spines present anterior to ambulatory setae.

Somatic setae in pharyngeal region and region anterior to ambulatory setae arranged in five longitudinal

rows: one mediodorsal row, two laterodorsal rows, and two lateroventral rows. Antermost mediodorsal seta situated on second or third annule posterior to head capsule. Posterior body region with long mediodorsal setae and shorter laterodorsal setae. Tail with one lateroventral seta on each side. Somatic setae flattened, except mediodorsal ones. Two lateroventral rows of three (Papua New Guinea specimen) or four (Porcupine Seabight specimens) slender, slightly bent ambulatory setae with curved tip. Posteriormost ambulatory seta in Porcupine Seabight specimens slightly separated from other three setae.

Head capsule conical and truncated as in adults, with four cephalic setae and two long, laterodorsal subcephalic setae at base of head capsule, situated posterior to amphid and immediately anterior to first complete body ring. Labial sensilla apparently situated on two rows. Amphids similar to those of adults. Pharynx long and slender, partly glandular, with well-developed endbulb. Endbulb surrounded by glandular material. Intestine granular. Genital primordium small.

Tail with 12 annules ventrally and 19 annules dorsally in Papua New Guinea specimen, 14 to 17 annules ventrally and 19 to 25 annules dorsally in Porcupine Seabight specimens, including smooth tail tip. Smooth tail tip without incomplete annules. Tail tip as in adults, ending on two small laterodorsal papillae and one longer medioventral papilla, each with the outlet of a caudal gland.

Third-stage juveniles

One specimen originating from Papua New Guinea and 17 specimens from Porcupine Seabight area (sexes not evident). Habitus as in adults. Cuticle with 201 annules in Papua New Guinea specimen and 227 to 242 annules in Porcupine Seabight specimens. Annules fine, non-overlapping, and mostly smooth, except for annules on tail, ornamented with numerous small, irregular (mostly elongated) vacuoles. Vacuoles inconspicuous (but present) in third-stage juvenile from Papua New Guinea (RIT 28). Annules finest at mid-body, widest in pharyngeal region and tail region.

Somatic setae in pharyngeal region arranged in five longitudinal rows: one mediodorsal row, two laterodorsal rows, and two lateroventral rows. Somatic setae in region between anteriormost dorsal curvature and ambulatory setae located in one mediodorsal and two laterodorsal rows. One short lateroventral seta on each side, immediately anterior to ambulatory setae. Several short dorsosublateral setae as well as some long mediodorsal setae present at level of ambulatory setae. One laterodorsal seta present on each side immediately anterior to anus. Tail on each side with one lateroventral seta and one mediodorsal seta immediately anterior to tail tip. Somatic setae flattened, except mediodorsal ones. Two lateroventral rows of seven almost straight ambulatory setae with curved tip. Posteriormost ambu-

latory seta situated anterior to anus, slightly finer than other ambulatory setae and with almost straight distal tip.

Head capsule a truncated cone, shorter in Papua New Guinea specimen (8 μm) than in Porcupine Seabight specimens (on average: 9.9 μm). Head with four cephalic and five subcephalic setae: one medio-dorsal seta, two laterodorsal setae, one lateroventral seta, and one medioventral seta. Lateroventral seta positioned on right side in Papua New Guinea specimen and predominantly on left side in Porcupine Seabight specimens. All subcephalic setae situated at base of head. Amphids as in adults. Pharynx long, slender, partly glandular and with well-developed endbulb. Endbulb surrounded by glandular material. Intestine granular. Genital primordium variable in size.

Tail with 15 annules ventrally and 16 annules dorsally in Papua New Guinea specimen, 18 to 22 annules ventrally, and 19 to 24 annules dorsally in Porcupine Seabight specimens, including smooth tail tip. Tail tip without incomplete annules, ending on one medioventral and two laterodorsal papillae, all of equal size.

Fourth-stage juveniles

Twelve juvenile male and nine juvenile female specimens, all from Porcupine Seabight area (Fig. 5D). Habitus as in adults. Cuticle with 215 to 239 annules, which is comparable to adults. Annules smooth, except for annules on tail ornamented with numerous elongated, irregular vacuoles. Annules finest at mid-body, widest in pharyngeal region and tail region.

Somatic setae in pharyngeal region and region between anteriormost dorsal curvature and ambulatory setae arranged in five longitudinal rows: one mediodorsal row, two laterodorsal rows, and two lateroventral rows. Several short dorsosublateral and lateroventral setae, as well as some long mediodorsal setae present at level of ambulatory and modified somatic setae. One medioventral, straight somatic seta usually present between posteriormost inner subventral ambulatory seta and anus. One laterodorsal seta on each side, immediately anterior to anus. Tail with one laterodorsal and one lateroventral somatic seta on each side and one mediodorsal seta.

Ambulatory setae arranged in two inner and two outer subventral rows. Each outer subventral row with four to seven s-shaped ambulatory setae with curved tip, positioned closely together posterior to ventral curvature. More posteriorly, ambulatory setae followed by two setae gradually becoming more somatic, i.e., finer, straighter, and with straighter distal tip. At level of anus, a subventral slightly modified somatic seta constitutes the endpoint of this progressive series. Inner subventral rows with three to five ambulatory setae, slightly shorter and finer than those of outer subventral rows.

Head capsule conical and truncated as in adults. Four cephalic and eight subcephalic setae, arranged as

in adults. Amphids as in adults. Long, slender, partly glandular pharynx with well-developed endbulb. Endbulb surrounded by glandular material. Genital primordium in juvenile females variable in size: 41.5 to 57.5 μm .

Tail with 19 to 22 annules ventrally and 19 to 23 annules dorsally, including smooth tail tip. Tail tip without incomplete annules, ending on one medioventral and two laterodorsal papillae, all of equal size.

One aberrant specimen with vacuoles on head and pharyngeal region, similar to those on tail, and four papillae on smooth tail tip with small tubercle in between.

Emended diagnosis

Triepsilonema tripapillata Decraemer, 1982, is characterized by the three large caudal papillae, by the cuticular body rings, either lacking ornamentation or ornamented with transversally elongated vacuoles, and by the shape of the copulatory apparatus.

Emended genus diagnosis

Triepsilonema Decraemer, 1982. Epsilonematidae. Body almost cylindrical and slightly epsilon-shaped, with 200 to 230 body annules in adults. Ambulatory setae slender, slightly s-shaped, with bent tip, arranged in four longitudinal rows with some scattered setae in between. In males, ambulatory setae in outer subventral rows followed by short, fine setae. In females, outer subventral rows exhibiting a gradual transition from ambulatory setae to somatic setae toward the tail. Amphids rather small spiral structures with 1.25 turns; no sexual dimorphism. Head capsule with four cephalic and eight subcephalic setae in adults. Two crowns of labial sensilla. Pharynx long and slender, gradually widening into an oval, partly glandular terminal bulb. Ovaries outstretched. Three caudal glands extending anteriorly beyond cloaca, each with a separate outlet. Smooth tail tip very short, with one medioventral and two subdorsal, smooth papillae, each with the outlet of one of the caudal glands. First-stage juveniles without ambulatory setae and with only two smooth papillae on tail tip. Second-stage juveniles with two rows of three or four ambulatory setae and two subcephalic setae. Third-stage juveniles with two rows of seven ambulatory setae and five subcephalic setae. Fourth stage juveniles with four rows of ambulatory setae and eight subcephalic setae.

Type species: *Triepsilonema tripapillata* Decraemer, 1982.

Variability of features

Detailed observations on the type material from Papua New Guinea and the new material from the Porcupine Seabight showed that, although both populations are geographically and bathymetrically well isolated, they are morphologically remarkably similar.

Whether this reflects either active gene flow or the conservation of character states is not clear, but the former seems unlikely. Nevertheless, a recent discovery of *T. tripapillata* on coral rubble from the Kenyan coast (Kurwitu) suggests that this species could be cosmopolitan (M. Raes, pers. obs.). The differences between both populations, although limited, might point to the presence of two cryptic species. This might well be the case, although in the absence of molecular (sequence) data for both populations it is inadvisable to discuss this matter here. Moreover, one should focus on the astonishing morphological similarity between these two populations that live so distantly from each other, rather than on the differences.

The populations differ in: (i) size of females (clearly smaller in Papua New Guinea), (ii) length of the pharynx (clearly shorter in Papua New Guinea specimens), (iii) number of annules (slightly lower in Papua New Guinea specimens), (iv) inversion of annule orientation in males (more anterior in Papua New Guinea specimens), (v) ornamentation of annules (almost completely smooth in Papua New Guinea specimens), (vi) number of fine setae following outer subventral rows of ambulatory setae in males (clearly fewer in Papua New Guinea specimens), and (vii) number of ambulatory setae in second-stage juveniles.

Relationships with other genera

Decraemer (1982) considered *Triepsilonema* close to *Bathypsilonema* mainly because both possess six rows of ambulatory setae. However, thorough observation of the new material and a subsequent re-examination of the type material revealed that the ventralmost ambulatory setae are not really arranged in two rows, but rather are scattered between the inner subventral rows (Fig. 6E). There are no obvious features linking *Triepsilonema* with any other epsilonematid, although its body shape may suggest some relation with *Archepsilonema*, a genus however characterized by only four rows of ambulatory setae. Nevertheless, the presence of three conical caudal papillae and outstretched ovaries in combination with an almost cylindrical body shape makes this genus unique within the family.

Familia Epsilonematidae Steiner, 1927

Subfamilia Glochinematinae Lorenzen, 1974

Genus *Glochinema* Lorenzen, 1974

Glochinema trispinatum Raes, Vanreusel and Decraemer, 2003 (Fig. 7)

Specimen juvenile stage I. Slide RI680 (KBIN).

Locality. Porcupine Seabight, Belgica mound province. Coordinates: 51°25'7.7" N, 11°46'9.3" W (material collected on 5/07/2001; depth: 972 m).

Date of collection. 7 May 2001.

Habitat. A cold-water coral degradation zone on the flank and near the top of a seabed mound. Associated with sediment-clogged framework of the cold-water

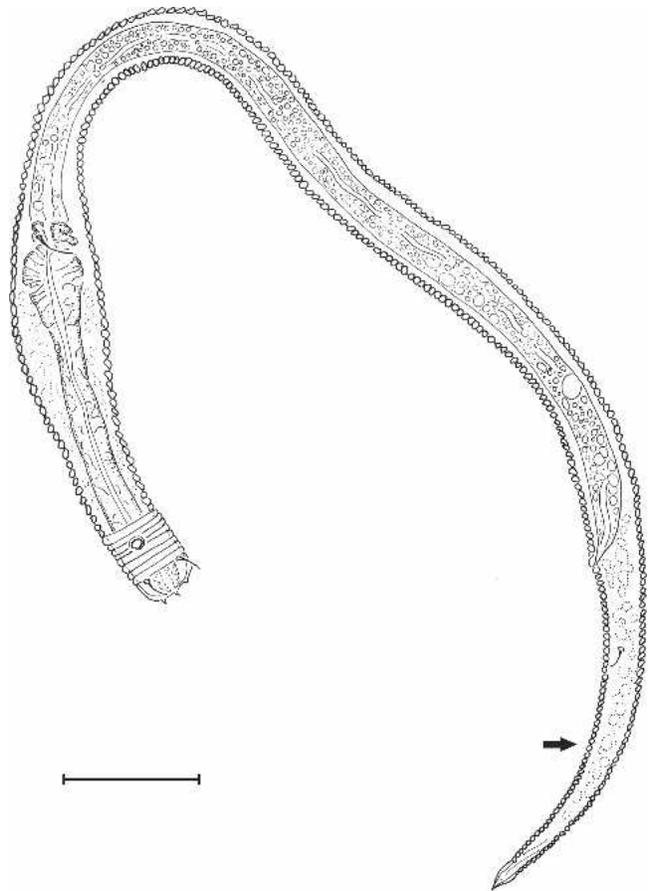


FIG. 7. *Glochinema trispinatum* Raes, Vanreusel and Decraemer, 2003. Habitus of first-stage juvenile. The arrow indicates the position of the caudal somatic seta on the right side. Scale bar: 20 μ m.

coral *Lophelia pertusa* (Linnaeus, 1758). It was found on dead coral fragments.

Measurements. Table 3.

First-stage juvenile

One specimen. Small, with almost constant body diameter, except for enlarged pharyngeal region and more slender tail (Fig. 7). Pharynx remarkably long compared to adults. Cuticle with 227 fine annules, uniform in shape, non-overlapping, and without ornamentation.

Only four somatic setae, all situated mediolaterally: on each side one seta at level of pharyngeal bulb and one seta on tail. Seta on left side of tail positioned more anteriorly than seta on right side. Head capsule short, with six labial sensilla at anterior end, of which four most dorsal sensilla hook-shaped and two most ventral sensilla only short, blunt protrusions. Four cephalic setae, situated at posterior edge of head capsule. Head capsule together with first eight body annules assumed to be positionally homologous with head capsule in second-stage juveniles. Amphids small, oval, unispiral, situated at level of annules four to six. Pharynx slender with well-developed endbulb. Tail with 57 annules, including short smooth tail tip with long spinneret.

siderable degree of overlap. The observed overlap during the later molting stages is explained by the fact that there are simply more data available. Variability is high in *Polkepsilonema* and *Glochinema*.

Lorenzen (1973a) suggested that the pattern of change in the number of annules during ontogeny could be genus specific; he observed that the first two juvenile stages in *Epsilonema* and *Perepsilonema* have fewer and the last two stages more annules than the adults, whereas the opposite is true for *Bathyepsilonema*. For *Epsilonema* and *Bathyepsilonema*, these observations are confirmed by other literature data on the changes during molting from second-stage juveniles into third-stage and from fourth-stage juveniles into adults (Table 4). The examples below also confirm intergeneric variability.

A general decrease in the number of body rings, e.g., as observed in the I-II and III-IV transitions, could be related to the creation of: (i) broader annules, (ii) the head capsule, or (iii) the tail tip. Indeed, annules in first-stage juveniles are clearly narrower than in second-stage juveniles. Moreover, there seems to be a positional homology of certain annules from first-stage juveniles with parts of the annules, head capsule, or tail tip in second-stage juveniles. This can be clearly observed in molting first-stage juveniles. As the cuticle is presumably completely resynthesized during molting, there will probably be no straightforward fusion of the annules of first-stage juveniles into the annules of second-stage juveniles during the process; either (i) a lower number of (broader) annules is newly formed, or (ii) the same number of annules is formed and these annules fuse in a later stage of the molting process. In the latter case, the observed body length increase during transitions between juvenile stages can be explained only by an additional broadening of body rings after or simultaneously with this annular fusion.

It is not entirely clear why these changes occur, although it is obvious that a higher number of annules in first-stage juveniles (compared to second-stage juveniles) allows for higher mobility, important in freeing itself from the egg and moving forward without the help of ambulatory setae, which are absent in first-stage juveniles. Something similar could be true for the III-IV transition in *Akantheepsilonema*, *Epsilonema*, *Leptepsilonema*, *Metepsilonema*, and *Triepsilonema*, where the number of rows of ambulatory setae doubles from two to four (or five as in *Akantheepsilonema sinicornibus* sp. n.), resulting in increased stability and mobility, which might compensate for the loss in flexibility. In contrast, this decrease in the number of annules was also observed in *Perepsilonema* (absence of ambulatory setae) and *Polkepsilonema* (both third- and fourth-stage juveniles with four rows of ambulatory setae). Moreover, a similar decrease was not observed in representatives of the genus *Bathyepsilonema*, despite doubling in the number of rows of ambulatory setae.

Head capsule and position of the amphids: Judging by the position of the amphids, the cephalic setae, and the

cervical constriction, it was postulated that the head capsule and the eight anteriormost annules in the first-stage juvenile of *Glochinema trispinatum* (Fig. 7) are positionally homologous with the head capsule in second-stage juveniles. Indeed, the head capsule in the first-stage juvenile of *G. trispinatum* is very short, the cephalic setae are at the base of this short head capsule, and the amphids are positioned posterior to it; this is no longer the case in second-stage juveniles. The same was observed in *Epsilonema byssicola* Lorenzen, 1973, and *Triepsilonema tripapillata*. In contrast, the amphids in first-stage juveniles of *Metepsilonema* and *Bathyepsilonema* are already situated on the head capsule, the head capsule is already well-developed, and the cephalic setae are already situated anteriorly on the head capsule. Intergeneric variability is evident.

By way of comparison, intrageneric variability in the position of amphids and cephalic setae in first-stage juveniles has been observed within *Desmodora*, a representative of the closely related family Desmodoridae. In first-stage juveniles of *Desmodora minuta* Wieser, 1954 (Clasing, 1980), the cephalic setae are situated at the base of the head capsule and the amphids are situated in the annulated region posterior to the head capsule; in first-stage juveniles of *D. schultzi* Gerlach, 1950, cephalic setae and amphids are already situated anteriorly on the head capsule. In second-stage juveniles of both species, amphids are located on the head capsule and cephalic setae are shifted to the anterior.

In first-stage juveniles belonging to the closely related family Draconematidae, cephalic setae are always at the posterior border of the head capsule and amphids are always surrounded by the anterior annules, posterior to the head capsule. Evidence for this has been found in *Dracograllus chiloensis* Clasing, 1980, *Draconema antarcticum* Allen and Noffsinger, 1978, *Cygnonema* sp. (a new species from the Porcupine Seabight), and *Tenuidraconema* sp. (a new species from the Porcupine Seabight). All these species are characterized by a well-developed head capsule in adults.

Tail tip: It is clear from Figure 7 that the smooth tail tip in the first-stage juvenile of *G. trispinatum* is very short compared to the tail tip in the second-stage juvenile (Fig. 2A in Raes et al., 2003). Again, there seems to be a positional homology of the tail tip together with several tail annules in first-stage juveniles with the tail tip of second-stage juveniles. In *Metepsilonema*, the tail tip is also slightly shorter in first-stage juveniles compared to second-stage juveniles. In contrast, the smooth tail tip in first-stage juveniles of *T. tripapillata* is longer than in second-stage juveniles. In *Epsilonema*, the tail tip in first-stage juveniles is also longer than in second-stage juveniles. Again, intergeneric variability is present.

THE TAXONOMIC AND PHYLOGENETIC IMPORTANCE OF CAUDAL GLANDS

Within the family Epsilonematidae, the introduction of the new genus *Triepsilonema* by Decraemer (1982)

was, apart from its habitus and the structure of its female reproductive system, mainly based upon the presence of separate outlets for the three caudal glands, with each outlet located at the end of a pronounced papilla (Fig. 8A,B). So far, caudal glands have been considered to be of great taxonomic importance at high taxonomic level (e.g., to distinguish between Adenophorea and Secernentea) as well as at low taxonomic level (e.g., to distinguish certain genera such as *Ixonema* Lorenzen, 1971). Emphasis was placed mainly on the (i) presence or absence of caudal glands, (ii) number of gland cells, and (iii) presence of either a common outlet or separate outlets for the caudal glands.

Within the family Epsilonematidae (order Desmo-

dorida), the presence of separate outlets for the three caudal glands seems relatively widespread. It has been observed in representatives of seven genera (*Akanthepsilonema*, *Bathyepsilonema*, *Epsilonema*, *Perepsilonema*, *Polkepsilonema*, *Pternepsilonema*, and *Triepsilonema*). However, current information is based on few specimens per taxon and data on possible intrageneric variability, intraspecific variability, or the presence of sexual dimorphism are rare.

The separate outlets of the three caudal glands in epsilonematids, when present, are arranged as follows: one medioventral outlet and two laterodorsal ones, as can be seen in Figure 8C of a male of *Epsilonema multispiralum* Raes, Vanreusel and Decraemer, 2003, and Figure 4H of a male of *Akanthepsilonema sinicornibus*

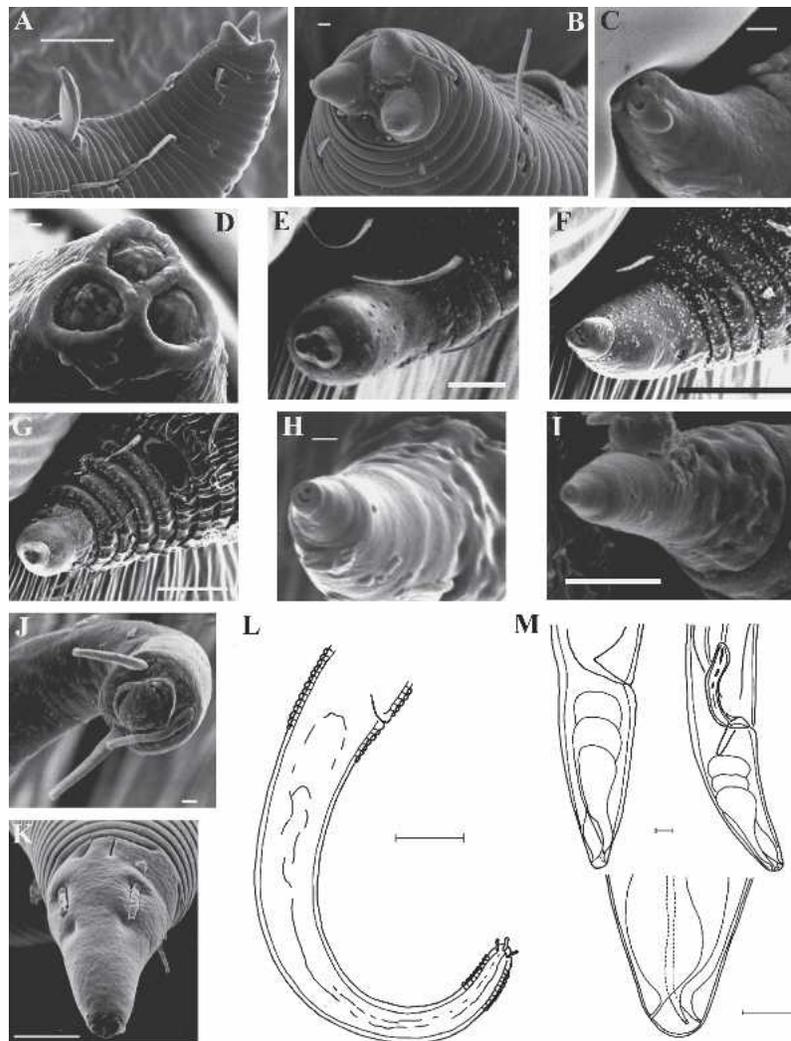


FIG. 8. Caudal gland outlets. A) *Triepsilonema tripapillata* Decraemer, 1982 (male). B) *Triepsilonema tripapillata* Decraemer, 1982 (female). C) *Epsilonema multispiralum* Raes, Vanreusel and Decraemer, 2003 (male) (after Raes et al., 2003). D) *Epsilonema pustulatum* Lorenzen, 1973 (male) (after Karssen et al., 2000). E) *Pternepsilonema servaesae* Verschelde and Vincx, 1993 (female) (after Verschelde and Vincx, 1993). F) *Polkepsilonema mombasae* Verschelde and Vincx, 1993 (male) (after Verschelde and Vincx, 1993). G) *Polkepsilonema mombasae* Verschelde and Vincx, 1993 (female) (after Verschelde and Vincx, 1993). H) *Bathyepsilonema lopheliae* Raes, Vanreusel and Decraemer, 2003 (male) (after Raes et al., 2003). I) *Bathyepsilonema lopheliae* Raes, Vanreusel and Decraemer, 2003 (female) (after Raes et al., 2003). J) *Dorylaimopsis variabilis* Muthumbi, Soetaert and Vincx, 1997 (male) (after Muthumbi et al., 1997). K) *Leptonemella vestari* Hoschitz, Buchholz and Ott, 1999 (female) (after Hoschitz et al., 1999). L) *Deontolaimus papillatus* De Man, 1880 (female) (modified from Meyl, 1954). M) *Diplopeltula incisa* (Southern, 1914) (one female and two males) (modified from Gerlach, 1950). Scale bars: 100 nm in D; 1 μ m in B, C, H, and J; 5 μ m in E, I, and K; 10 μ m in A, F, G, L, and M.

sp. n. An SEM illustration by Karssen et al. (2000) shows three well developed caudal gland papillae in a male of *Epsilonema pustulatum* Lorenzen, 1973, which have a similar position as the caudal gland outlets in the species mentioned above (Fig. 8D). Males and females of *Pterepsilonema servaesae* Verschelde and Vincx, 1993, have been described with a spinneret bearing three separate pore-like outlets. Scanning electron microscope (SEM) micrographs of a female specimen, however, show these outlets as short protruding tubes: a medioventral one and two laterodorsal ones (Fig. 8E).

The caudal gland outlets may show inter- and intraspecific differences in shape and number, e.g., in *Polkepsilonema mombasae* Verschelde and Vincx, 1993, males have been described with three times three pores, although it is clear from Figure 8F that there are only three pores, filled with secretion particles. In contrast to males, females have seven, possibly eight, or nine pores. The SEM micrograph (Fig. 8G) shows a more-or-less triangular tail tip with the outlets arranged in three groups: a medioventral group with two pores and two laterodorsal groups with three pores each. In *Bathyepsilonema lopheliae* Raes, Vanreusel and Decraemer, 2003, sexual dimorphism in the nature of caudal gland outlets is also clear from SEM micrographs (Figs. 8H,I); the male shows a medioventral pore opposite a curved slit-like opening, which could be the result of fusion of the laterodorsal pores; the female, on the other hand, has only a single terminal pore. A single outlet has also been observed in a female of *Glochinema trispinatum* Raes, Vanreusel and Decraemer, 2003 (Fig. 4B in Raes et al., 2003). In *Perepsilonema ritae* Verschelde and Vincx, 1994, males possess a spinneret provided with one medioventral and two laterodorsal groups of two pores each.

Within a species, the nature of caudal gland outlets also may differ between stages of development; the first-stage juvenile of *Triepsilonema tripapillata* Decraemer, 1982, described in the current paper possesses only two caudal papillae (a medioventral and a mediodorsal one), whereas all later stages possess three caudal papillae.

Scanning electron microscope (SEM) observations of two species belonging to the closely related family Dracoenematidae Filipjev, 1918, *i.c.* *Dracognomus simplex* (Gerlach, 1954) Allen and Noffsinger, 1978 (Karssen and Van Aelst, 2002), and a new, undescribed *Cygnonema* species (M. Raes, pers. obs.), show a single common outlet for the three caudal glands.

In spite of the taxonomic importance of caudal glands, little is known about their ultrastructure and physiology. For a long time, caudal glands have been considered to be of one type with a single secretory function, *i.e.*, involved in the attachment of the nematode to the substrate. Later, a second function was attributed to caudal glands, the secretion of a sticky mucus that serves as a trap for food particles (Riemann and

Schrage, 1978). Ultrastructural studies undertaken to better understand the locomotion of certain nematodes revealed the presence of two sets of caudal glands in several taxa, such as *Perepsilonema* (Adams and Tyler, 1980; Turpeenniemi and Hyvärinen, 1996). Both sets play a role in locomotion; one set of three viscid gland cells is responsible for attaching the nematode to the substrate, and another set of smaller cells is responsible for releasing it from the substrate again. The ducts of both types of gland cells may have a common pore at the tail tip either with a spinneret apparatus (*Perepsilonema conifer* Lorenzen, 1973, Epsilonematidae) or without such an apparatus (*Theristus caudasaliens* Adams and Tyler, 1980, Xyalidae). In contrast, the ducts of the different gland cell types may open through different pores (*Sphaerolaimus gracilis* de Man, 1876, Sphaerolaimidae) (Turpeenniemi and Hyvärinen, 1996). Thus, the number and type of caudal gland outlets does not necessarily indicate the presence of one or two sets of caudal glands.

Caudal glands are present in the majority of aquatic nematodes belonging to the Enoplea and the non-rhabditidan (= non-secernentean) taxa of the class Chromadorea. In terrestrial forms, there is a tendency toward reduction or absence of these structures.

According to Lorenzen (1978), caudal glands rarely open through separate ducts or pores except in the families Xyalidae (e.g., in *Echinotheristus cimbricus* Von Thun and Riemann, 1967, and *E. teutonicus* Von Thun and Riemann, 1967) and Sphaerolaimidae (Monhysteroidea), where separate outlets are more common. A single common duct and opening in the other family of the superfamily Monhysteroidea, the Monhysteridae, is regarded as a synapomorphy for this family.

Currently, separate outlets for the three caudal glands have been observed in various unrelated taxa of free-living aquatic nematodes. Within the order Araeolaimida, several taxa belonging to the superfamily Axonolaimoidea, e.g., *Diplopeltula incisa* (Southern, 1914) Gerlach, 1962, *D. breviceps* Gerlach, 1950, and *Pararaeolaimus nudus* (Gerlach, 1951) Timm, 1961, have separate caudal gland outlets. These data were gathered either by light microscopic observations (Diplopeltidae) or by SEM observations, e.g., of a male of *Dorylaimopsis variabilis* Muthumbi, Soetaert and Vincx (1997) (Comesomatidae) (Fig. 8J).

Within the order Desmodorida, separate outlets for the three caudal glands have been observed in representatives of the families Epsilonematidae (Desmodoroidea, see above), Desmodoridae (Desmodoroidea), and Microlaimidae (Microlaimoidea). Hoschitz et al. (1999) described three small, separate, pore-like outlets in *Leptonemella vestari* and illustrated this with an SEM micrograph of the tail tip (Fig. 8K). The orientation of the outlets was not described and could not be deduced from the illustration. A representative of the Micro-

laimidae, *Ixonema*, also possesses separate outlets, with each outlet located on a papilla (M. Raes, pers. obs.).

Within the order Plectida sensu De Ley and Blaxter (2002), separate outlets were also observed. The caudal gland outlets in *Deontolaimus papillatus* de Man, 1880 (Camacolaiminae, Leptolaimidae), described by Meyl (1954) as one tube-like outlet next to two short papillae, were later reinterpreted as three separate caudal gland outlets by Lorenzen (1973b) (Fig. 8L).

In contrast to the situation in the family Epsilonematidae, there are always one mediodorsal and two lateroventral outlets in former examples, as illustrated in Figure 8J of *Dorylaimopsis variabilis* (Muthumbi et al., 1997).

Lorenzen (1978) regarded the presence of three separate outlets for the caudal glands as a plesiomorphic character in nematodes, based upon the observations and hypotheses of Ossche (1955, 1958) and on outgroup comparison, e.g., with the Gastrotricha. Ossche (1955, 1958) observed that in several secernentean species without caudal glands, the tail tip showed three protuberances, of which one was always mediodorsal in position and the remaining two always lateroventral. He interpreted these protuberances (currently termed mucrones or mucros) as rudiments of caudal gland openings because this arrangement appeared constant and was similar to that of the three separate caudal gland openings in most free-living aquatic nematodes (e.g., *Diplopeltula incisa* (Southern, 1914) Gerlach, 1962 [Fig. 8M]). So, according to Ossche, the absence of caudal glands within the Secernentea is at a secondary rather than at a primary level.

Discussion: Although Ossche (1955, 1958) showed that tail tips with three protuberances are present in several secernentean taxa, these protuberances may be quite variable in number, position, and shape and may be accompanied by additional structures such as spines. The presence of protuberances may well be a useful diagnostic character at species level (e.g., within the genus *Chronogaster* in Chronogasteridae, Plectoidea), although the homology of mucrones with caudal gland outlets, as hypothesized by Ossche (1955), is questionable. The orientation of the three tail protuberances could be related to body symmetry and locomotion. The majority of nematodes have a slender, cylindrical body and usually crawl or swim with undulatory movements in a dorso-ventral plane (Stauffer, 1924; Decraemer and Hunt, 2005). Aberrant body shapes may be related to an aberrant locomotory pattern as in Epsilonematidae and Draconematidae, which move like inchworms on their ventral side. The aberrant (i.e., opposite) arrangement of the separate outlets of the three caudal glands in Epsilonematidae taxa compared with other nematodes could be related to their aberrant mode of locomotion and is considered an apomorphy for this family of nematodes. It has already been mentioned above that Draconematidae have only a single

outlet, which indicates that caudal glands might not play an important role in locomotion here because locomotion in Draconematidae relies mainly on the presence of large locomotory adhesion tubes.

Within the family Epsilonematidae, the genus *Triepsilonema* differs from most other genera because of its more-or-less cylindrical body, comparable to most taxa within the Desmodorida. This character could be interpreted as primitive based upon outgroup comparison. If we accept Lorenzen's hypothesis that the presence of separate outlets for the caudal glands is a primitive character, this would provide an additional argument for the hypothesis that the genus *Triepsilonema* is a primitive genus within the family Epsilonematidae. On the other hand, *Triepsilonema* possesses the aberrant arrangement of caudal gland outlets typical for Epsilonematidae, which is a derived character. Next to that, *Triepsilonema* females differ from the other Epsilonematidae taxa by the possession of outstretched ovaries, a character considered as derived (Lorenzen, 1981, 1994). Based on the last two features, it seems that the more cylindrical body shape in *Triepsilonema* is at a secondary (loss of aberrant body shape typical to all other Epsilonematidae) rather than primary (preservation of cylindrical body) level.

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