

Draconematidae (Nematoda) from cold-water corals in the Porcupine Seabight: The genus *Tenuidraconema* Decraemer, 1989

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Abstract

A new species of *Tenuidraconema* Decraemer, 1989 is described from a cold-water coral degradation zone in the Porcupine Seabight (NE Atlantic). *Tenuidraconema microsperma* sp. n. is distinguished from all other species of *Tenuidraconema* by the combination of 10 CAT located posterior to the amphidial fovea, SIAT alternately long and short, male amphidial fovea composed of an inner and an outer loop, with ventral arm of inner loop as long as high, external labial sensilla papilliform, compact, jagged sperm cells with large, refractive inclusions, the shape of the gubernaculum and the number of tail rings. Additional descriptive data are provided for *T. koreense* Rho & Kim, 2004, from specimens found in the Porcupine Seabight. Additionally, the fourth-stage juvenile is described for the first time, the species diagnosis is emended, and the biogeography in the North Atlantic is discussed. The diagnosis of *Tenuidraconema* is emended, and a dichotomic identification key to the five included species is provided.

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Keywords: Marine nematodes; Taxonomy; *Tenuidraconema*; Porcupine Seabight; Cold-water corals

Introduction

The present paper is part of an extensive study dealing with the nematofauna associated with a cold-water coral degradation zone in the Porcupine Seabight (continental slope, northeast Atlantic Ocean). This is an area where the living cold-water coral framework is being gradually degraded due to a constant bioerosion process, resulting in the presence of dead fragments of the framework-building coral, *Lophelia pertusa* (Linnaeus, 1758), and of skeletons of the glass sponge *Aphrocallistes bocagei*

Schultze, 1886, clogged together with sediment. Compared to the associated sediment, the coral fragments themselves are characterised by higher abundances of typically epifaunal nematode taxa, such as Epsilonematidae and Draconematidae. Several genera and species belonging to these two closely related families show significant microhabitat preferences for dead *Lophelia* fragments (Raes and Vanreusel 2006; Raes et al. 2008). This is explained by the feeding behaviour and particular way of locomotion of these animals: they move forward over a certain surface like inchworms, alternately attaching and releasing the anterior and posterior ends of the body (Stauffer 1924; Lorenzen 1973). Draconematidae use both cephalic adhesion tubes (CAT) and posterior adhesion tubes (PAT) for attachment.

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Only few Draconematidae have been described from the deep sea. Kito (1983) described two species of *Cephalochaetosoma* Kito, 1983 from a depth of 5549–5551 m in the western North Pacific. For one of these species, Decraemer et al. (1997) have erected the genus *Bathychaetosoma* Decraemer, Gourbault & Backeljau, 1997. In his doctoral dissertation, Bussau (1993) proposed the genus *Eudraconema* from the East Pacific (depth: 4100–4200 m). It has since been encountered in the Central Pacific (depth: 4990 m) by Decraemer and Gourbault (1997). These authors also described a species of *Dinetia* Decraemer & Gourbault, 1997 from the East Pacific Rise (depth: 2600 m), and a new subspecies of *Cephalochaetosoma pacificum* Kito, 1983 from the West Pacific deep sea (1707 m).

Several new species of Epsilonematidae have already been described from the coral degradation zone in the Porcupine Seabight (Raes et al. 2003, 2006). In the present paper, a new species of *Tenuidraconema* Decraemer, 1989 is described and additional information is provided for *T. koreense* Rho & Kim, 2004. The latter species was originally described from the east coast of South Korea, where it was found at depths of 150–250 m (Rho and Kim 2004). Although a large number of individuals was examined, only few measurements from one male and one female were given in the original description. More information on intraspecific variation and more detailed observations on the different morphological features are added here. Moreover, information on juvenile stages is provided for the first time. An identification key for the species in *Tenuidraconema* is also given.

Material and methods

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

Rather than all material examined, only the best-preserved specimens were stored in such museum collections; these specimens are listed under “Voucher material” for the respective species.

For further information on material and methods, see Raes et al. (2009) elsewhere in this ODE issue.

Additional abbreviations used

LdCAT	length of laterodorsal cephalic adhesion tube
LvATa	length of anteriormost lateroventral posterior adhesion tube
LvATp	length of posteriormost lateroventral posterior adhesion tube

MdCATa	length of anteriormost mediodorsal cephalic adhesion tube
MdCATp	length of posteriormost mediodorsal cephalic adhesion tube
SICATa	length of anteriormost sublateral cephalic adhesion tube
SICATp	length of posteriormost sublateral cephalic adhesion tube

Taxonomic section

Family Draconematidae Filipjev, 1918

Subfamily Draconematinae Filipjev, 1918

Genus *Tenuidraconema* Decraemer, 1989

Type species. *Tenuidraconema fiersi* Decraemer, 1989.

Valid species included. *Tenuidraconema fiersi*; *T. koreense* Rho & Kim, 2004; *T. microsperma* sp. n.; *T. philippinense* Rho & Kim, 2005; *T. tongaense* Rho, Min & Kim, 2007.

Diagnosis. See the corresponding discussion section below.

Tenuidraconema microsperma sp. n.

(Figs. 1–4, 5B)

Etymology. The specific epithet is derived from the Greek adjective mikros, meaning ‘small’, and the Greek noun sperma, meaning ‘sperm’: the combined word reflects the observation that this species has small sperm cells. The epithet is to be treated as a noun phrase in apposition for the purposes of nomenclature.

Voucher material. Holotype male on slide UGMD 104129 (UGent): Porcupine Seabight, Belgica mound province, 51°24'48.2"N 11°45'55.4"W, 17/06/2000, depth 1005 m.

Paratypes (collecting data as for holotype): Allotype female on slide UGMD 104133 (UGent); three males on slides UGMD 104133 (one specimen; UGent), RIT 739 (one specimen; KBIN), 2008.583 (one specimen; NHM); two females on slides UGMD 104029 (one specimen; UGent), RIT 737 (one specimen; KBIN); two fourth-stage juveniles on slides UGMD 104131 (one specimen; UGent), RIT 738 (one specimen; KBIN).

Habitat. At the type locality, the species was found in 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). Specimens were collected from dead coral fragments and dead sponge skeletons (*Aphrocallistes bocagei* Schultze). At other localities, the species also occurred in sediment underlying the sediment-clogged coral framework.

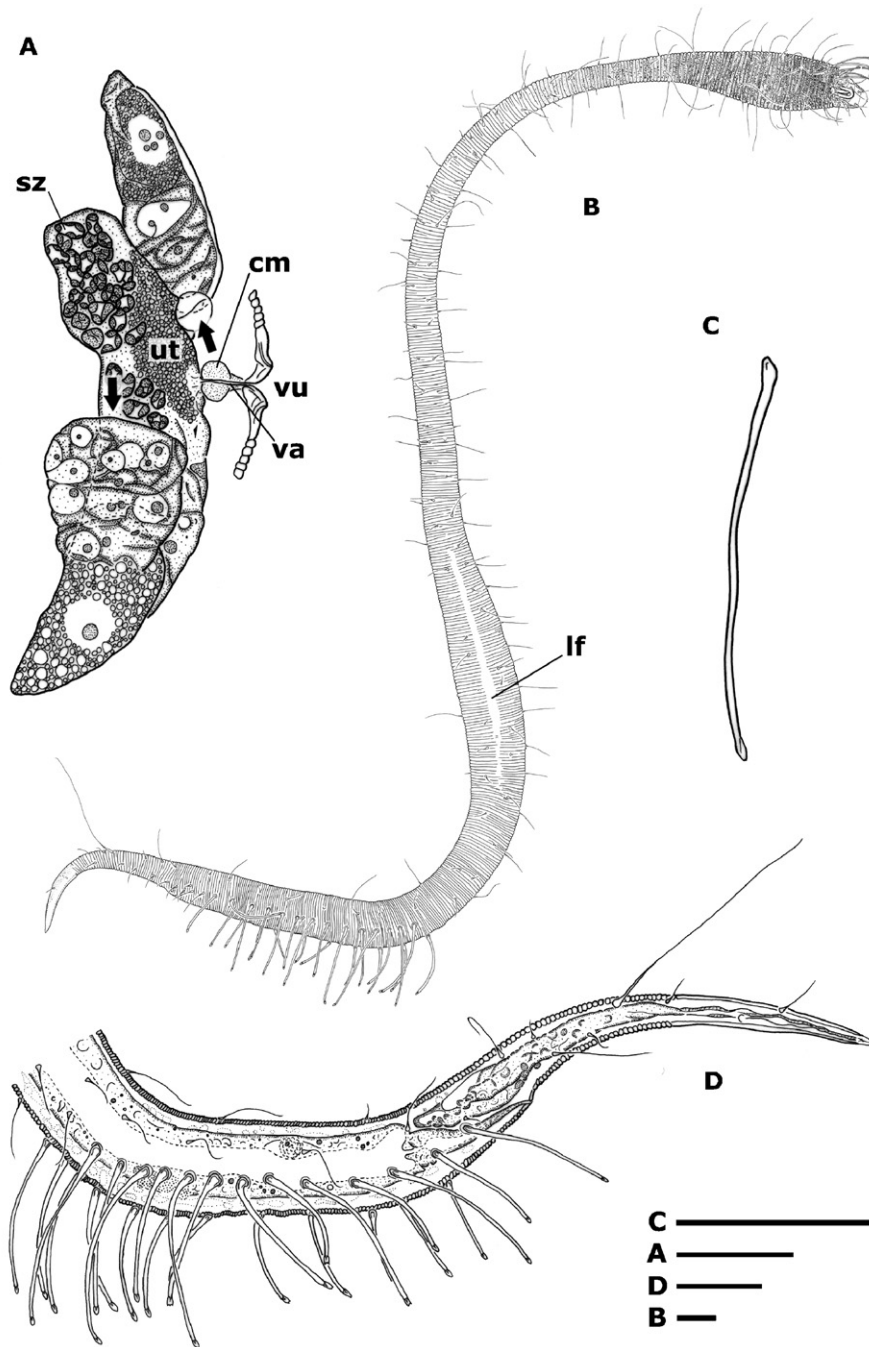


Fig. 1. *Tenuidraconema microsperma* sp. n. (A) Paratype female, reproductive system; arrows indicate distal tips of ovaria. (B) Holotype male, external habitus. (C) Holotype male, SIAT. (D) Paratype female, posterior body region and tail. cm = contractor muscle, lf = lateral field, sz = spermatozoon, ut = uterus, va = vagina, vu = vulva. Scale bars = 20 μ m.

Relative abundance. At the type locality, *T. microsperma* constituted 0.53% of the total nematode community.

Morphological measurements. See Table 1.

Male

Body very slender, sigmoid, enlarged in pharyngeal region and at level of testis and vesicula seminalis

(Figs. 1B, 3A). Swollen pharyngeal region 12.3–16.2% of total body length. Region between pharyngeal bulb and anterior tip of testis conspicuously long and slender: body width decreasing behind pharynx, reaching minimal width immediately posterior to pharyngeal bulb, slightly broadening again until reaching maximal width at level of vesicula seminalis. More posteriorly, width

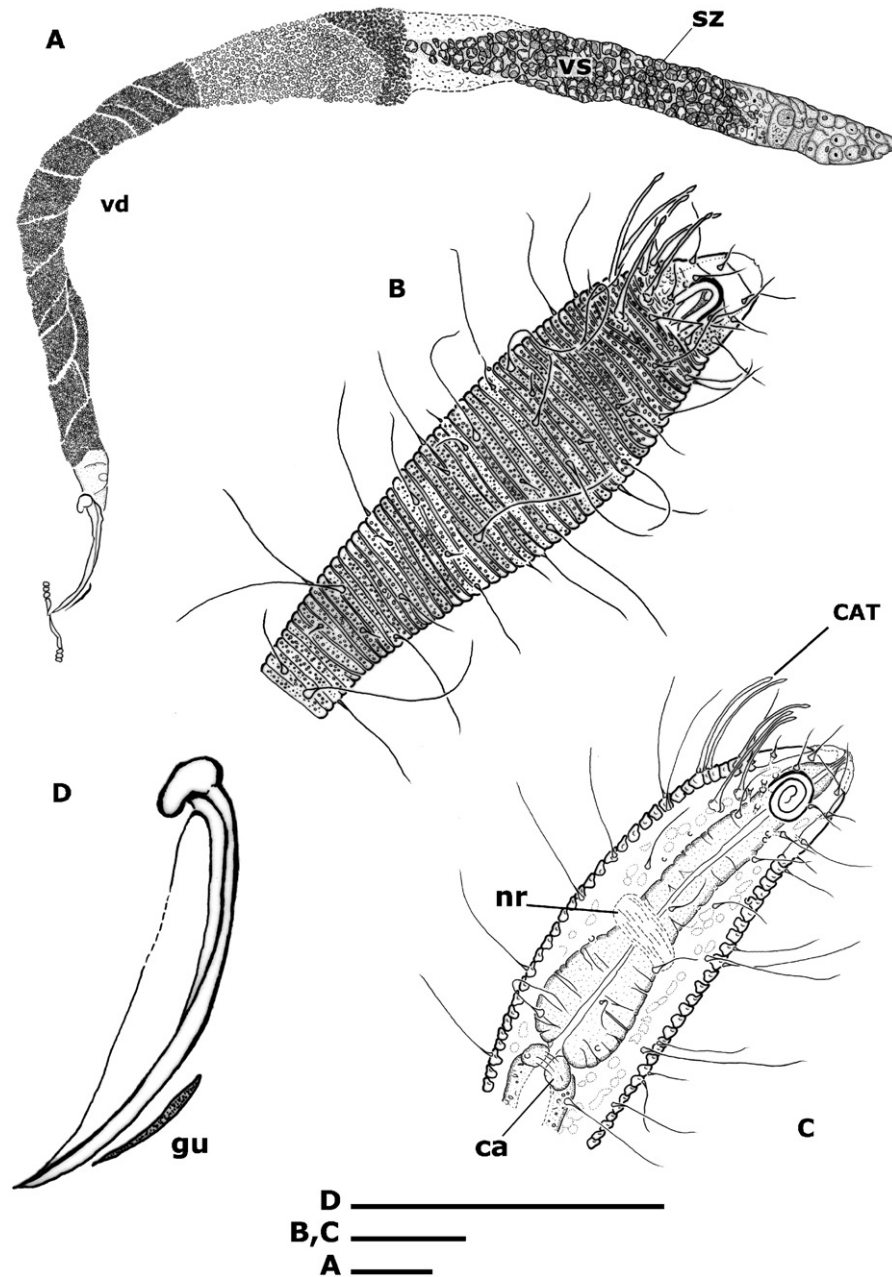


Fig. 2. *Tenuidraconema microsperma* sp. n. (A) Paratype male, reproductive system. (B) Holotype male, head capsule and pharyngeal region, external view. (C) Additional female, head capsule and pharyngeal region internal view. (D) Paratype male, spicule and gubernaculum. ca = cardia, CAT = cephalic adhesion tube, gu = gubernaculum, nr = nerve ring, sz = spermatozoon, vd = vas deferens, vs = vesicula seminalis. Scale bars = 20 μ m.

slightly decreasing, then constant up to cloacal opening. At level of cloacal opening, body width decreases abruptly. Tail conico-cylindrical. Slender body region posterior to pharynx without attached ciliates.

Body completely annulated. Annules not overlapping, broadest in pharyngeal region and narrow region posterior to pharynx. Annules gradually decreasing in width along testis, finest immediately anterior to PAT

and at level of PAT, and gradually increasing posterior to PAT. Annule width constant on tail. Beginning at level of anterior tip of testis, annules laterally interrupted by narrow lateral field extending up to level of vesicula seminalis (Fig. 1B, 1f). Lateral field 67–154 μ m in length, 2.3–3.0 μ m in width. Occasionally, lateral field present as local constriction of annules instead of actual interruption (Fig. 4C). One or two

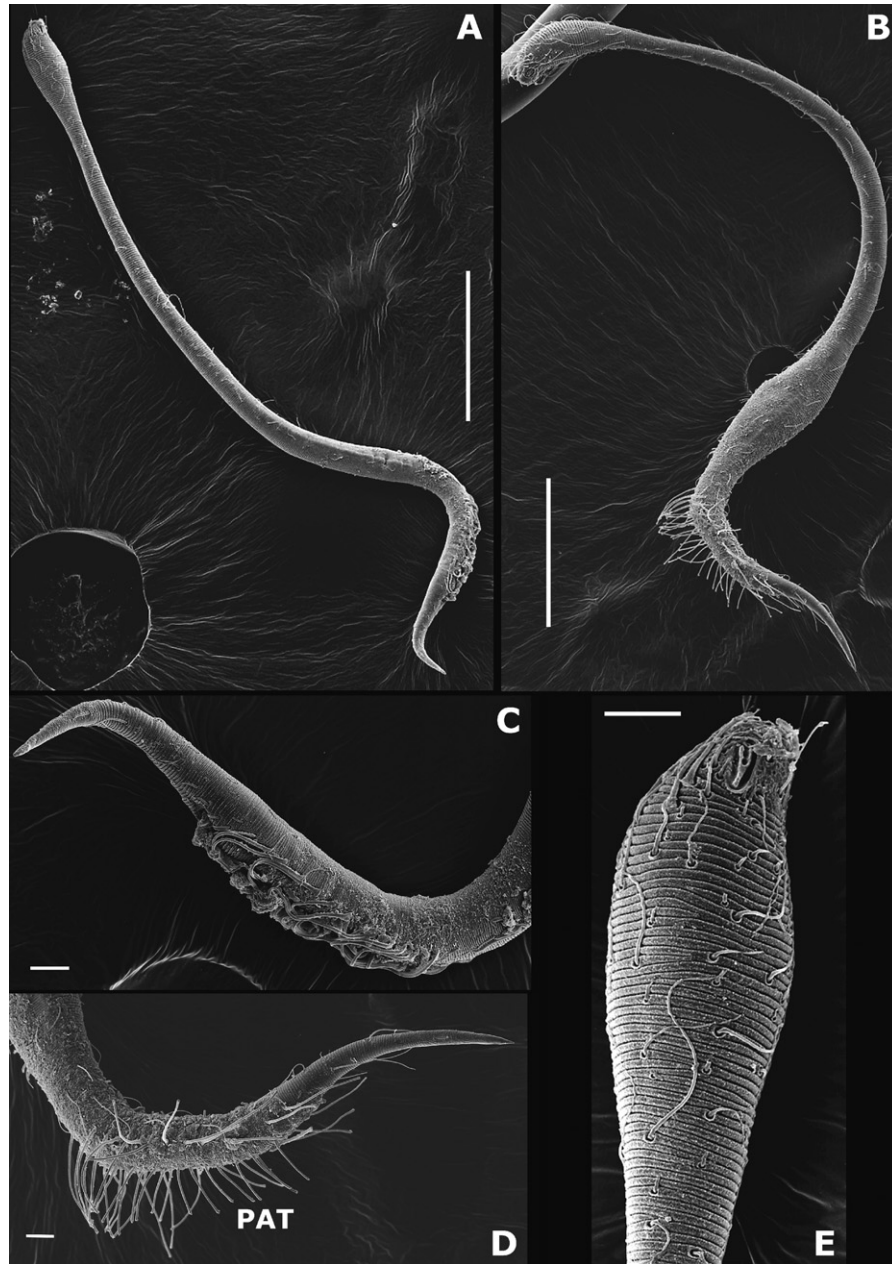


Fig. 3. *Tenuidraconema microsperma* sp. n. (A) Additional male, external habitus. (B) Paratype female, external habitus. (C) Additional male, posterior body region and tail. (D) Paratype female, posterior body region and tail; PAT = posterior adhesion tubes. (E) Additional male, head capsule and pharyngeal region. Scale bars A, B = 100 μ m, C–E = 10 μ m.

rows of numerous small and irregular vacuoles present on annules in pharyngeal region and slender anterior body region (Fig. 2B), one row at level of testis and around cloacal opening. Except for pharyngeal region, vacuoles may be faint or even indistinguishable. Annules in posterior body region with rough, somewhat granular edges and littered with detritus.

Ten CAT, arranged in five longitudinal rows, each row consisting of two very slender tubes with swollen insertion base and slightly swollen tip (Fig. 2B).

Antermost CAT in each row located on posterior border of head capsule or on first annule, i.e. at posterior border of amphidial fovea. Second CAT in each row located either on head capsule or on annules 1–4. PAT very slender, bent backwards, with swollen base and bell-shaped tip (Fig. 1C). Width of anteriormost SIAT 0.8–1.0 μ m at 10 μ m from base. PAT arranged in four rows: two rows of 12–14 SIAT and two rows of 7–10 SvAT (Fig. 3C). First SIAT 38.5–53.5 μ m in length, second SIAT either comparable

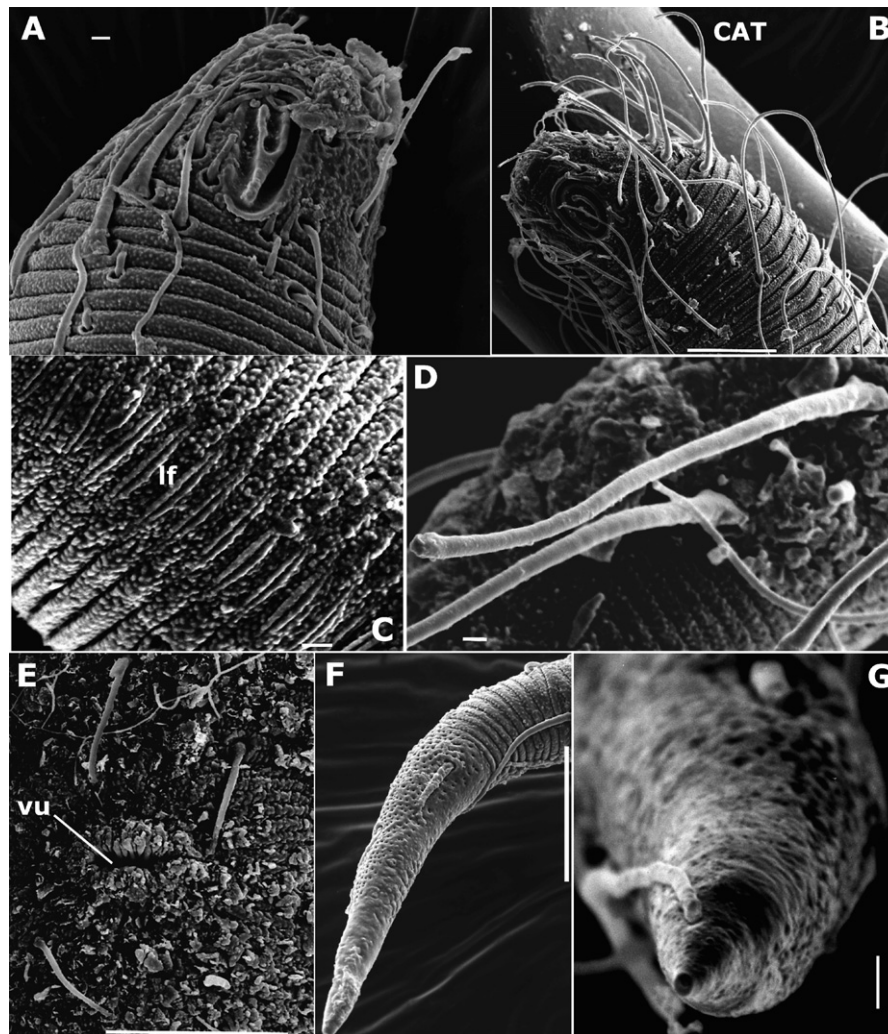


Fig. 4. *Tenuidraconema microsperma* sp. n. (A) Additional male, head capsule and CAT, lateral view. (B) Paratype female, head capsule and CAT, lateral view. (C) Additional male, lateral field. (D) Paratype female, PAT. (E) Paratype female, vulva. (F) Additional male, tail tip. (G) Paratype female, tail tip. CAT = cephalic adhesion tube, lf = lateral field, vu = vulva. Scale bars B, E, F = 10 μ m, A, C, D, G = 1 μ m.

in length or clearly shorter. Third SIAT always clearly shorter than first SIAT. Posterior to third SIAT, SIAT alternately long and short. SvAT gradually decreasing towards posterior. PAT clearly associated with glands, which appear as two longitudinal rows of several separate compartments located near insertion sites of PAT. First PAT located at 69.0–78.8% of body length. Distance between first and last PAT 10.9–15.4% of total body length.

In pharyngeal region, somatic setae arranged in 10 longitudinal rows: one mediodorsal row, two subdorsal rows, two laterodorsal rows, two lateroventral rows, two subventral rows, and one medioventral row (Figs. 2B, 3E). Mediolateral setae sometimes present. Slender region posterior to pharyngeal bulb and region anterior to PAT with one mediodorsal row, two

laterodorsal rows, two lateroventral rows, and one medioventral row of somatic setae. Region of PAT with one mediodorsal row and two sublateral rows of somatic setae in dorsal sector. In some cases, one subventral seta present in front of or behind posteriormost SIAT. Additionally, two lateroventral setae usually present behind posteriormost SIAT. These lateroventral setae usually followed by 4–5 subventral, pericloacal ('anal') setae: two precloacal, two postcloacal setae, and sometimes one seta at level of cloacal opening. Anteriormost pericloacal seta slightly longer than other pericloacal setae. Tail on each side with several subventral setae and subdorsal setae, including longest somatic setae on entire body (62.5 μ m in holotype). Tail tip with one short lateroventral and one short subdorsal seta on each side.

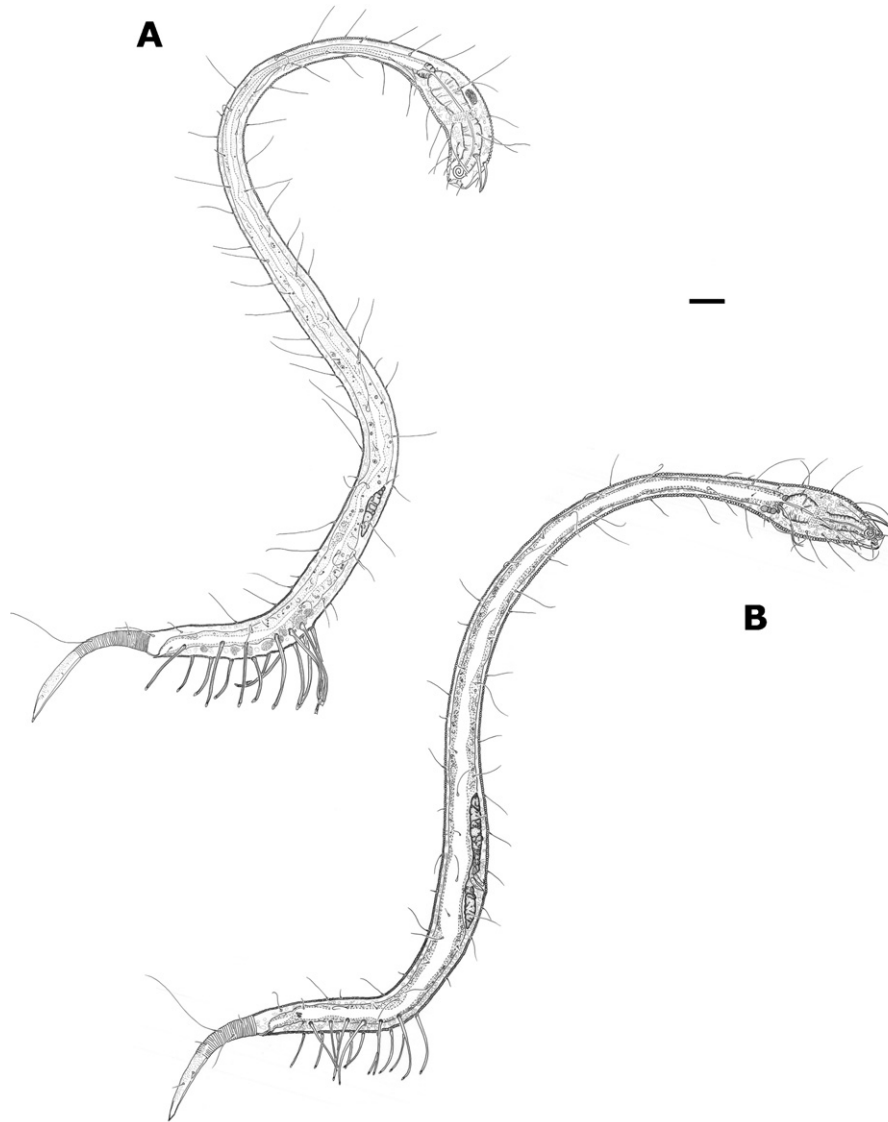


Fig. 5. (A) *Tenuidraconema koreense* Rho & Kim, 2004 additional fourth-stage juvenile. (B) *T. microsperma* sp. n., additional fourth-stage juvenile. Scale bar = 20 μ m.

Head capsule a broad, truncated cone, either smooth or ornamented with small vacuoles, which may be faint (Figs. 2B, 4A). Labial sensilla papilliform. Four cephalic and 20–28 subcephalic setae, arranged in eight rows: generally two subdorsal rows of three setae, two laterodorsal rows of four setae, two lateroventral rows of two setae and two subventral rows of two setae. Next to this, scattered pores may be present near posterior border of head capsule. Amphidial fovea long, between 52.4% and 76.0% of length of head capsule, located near posterior border of head capsule. Amphidial fovea composed of conspicuous outer loop and vague inner loop. Ventral arm in outer loop longer than dorsal arm; ventral arm in inner loop only a short bulge. Long arms of both loops joining at posterior

border of head capsule. Buccal cavity narrow and unarmed, surrounded by gold-coloured granules. Anterior part of pharynx cylindrical, with oval, muscular terminal bulb without thickened lumen wall. Large nerve ring (Fig. 2C, nr) immediately in front of terminal bulb. Cardia (Fig. 2C, ca) flattened antero-posteriorly. Intestine granular, with slightly thickened brush border. Cloacal flap absent; cloacal opening sometimes ending on bulge.

Male reproductive system monorchic (single testis), with outstretched testis extending far anteriorly (testis tip located at 48.8–58.7% of total body length in holotype) (Fig. 2A). Germinal and growth zones finely granular, usually slender, situated ventrally to intestine: either medioventrally or shifted to the

Table 1. Morphological measurements in *Tenuidraconema microsperma* sp. n.

	Male holotype	Male paratypes (n = 10)	Female allotype	Other female paratypes (n = 6)	Juvenile stage IV (n = 9)
L	930	750–1060 (905)	895	810–965 (925)	445–735 (640)
Hdw	18.5	18.5–21 (19.8)	20.5	19.5–21 (20.6)	17.5–18.5 (18.0) ⁽⁸⁾
Hdl	17.5	15–19 (16.7)	17	16.5–20 (18)	13–15.5 (14.3) ⁽⁸⁾
Amphw	5.5	4.5–6 (5.5)	6.5	6–7.5 (7) (5)	5–6.5 (5.8) ⁽⁸⁾
Amphl	10.5	9.5–11.5 (10.3)	9	8.5–9.5 (8.7)	5.5–7 (6.1) ⁽⁸⁾
Amph%	29	24.4–30.1 (27.8)	31.2	29.6–38.3 (34.5) ⁽⁵⁾	29.0–36.7 (32.1) ⁽⁸⁾
ph	76	67.5–80.5 (74.8)	77	71.5–80.5 (74.8)	50–65 (61.0) ⁽⁶⁾
MdCATa	16.5	15–19.5 (17.1) ⁽⁹⁾	16.5	17–19.5 (18.1)	
MdCATp	24	20–25 (22.2) ⁽⁹⁾	26.5	21–25 (22.9)	
SdCATa	17.5	17–21 (18.8) ⁽⁹⁾	17.5	16.5–20 (18.5)	17–20.5 (18.1) ⁽⁸⁾
SdCATp	22.5	21.5–26 (23.2) ⁽⁹⁾	25.5	21.5–29 (24.2)	
LdCAT					18.5–24.5 (21.2) ⁽⁷⁾
SICATa	20.5	17–23.5 (21.1)	20	20.5–22 (21.2)	
SICATp	21	23–29 (25.3)	22.5	24.5–27.5 (25.9)	
SIATa	46	38.5–53.5 (46.2)	54	41–49 (44.7)	
SIATp	27.5	25–46.5 (34.4)	39	28.5–41 (35.6)	
LvATa					29–47 (38.1)
LvATp					24–36 (31.2)
SvATa	40.5	36–43.5 (39.4)	37	30.5–42 (38.3)	
SvATp	19	17–24 (21.4)	19	16.5–22.5 (19.6)	
MvATa					24–37 (32.5)
MvATp					12.5–22.5 (18.8) ⁽⁸⁾
tail	102.5	87.5–129.5 (111.1)	105	94.5–122.5 (107.7)	68–87 (79.5)
tmr	39	36–43 (41.3) ⁽⁹⁾	53.5	49.5–53.5 (51.2)	40–49.5 (44.4)
mbd ph	30.5	21.5–31.5 (29.2)	31.5	29.5–33 (31.1)	25.5–36 (29.8)
mbd	32.5	25.5–37 (29.6)	51.5	38.5–52 (48.8)	19.5–38.5 (27.7)
(mbd)	12	11.5–13 (12.3)	12	12–13.5 (12.9)	10–15 (12.9)
mbd/(mbd)	2.7	1.9–3.0 (2.4)	4.3	2.9–4.4 (3.8)	1.5–2.7 (2.2)
abd	18	17.5–20 (18.8)	16.5	15–18 (15.7)	12.5–18.5 (14.8)
spic	38	31–39.5 (36.6)			
gub	12	8–12.5 (10.4)			
V%			64.7	63.3–64.6 (64.0)	
a	28.4	28.0–36.3 (30.8)	17.4	18.1–20.9 (19.1)	17.0–29.6 (24.0)
b	12.2	10.4–13.2 (12.1)	11.6	11.4–13.5 (12.4)	8.9–11.0 (10.3) ⁽⁶⁾
c	9.1	7.6–10.2 (8.2)	8.5	7.8–9.1 (8.6)	6.4–9.3 (8.1)

All absolute values in μm . Ranges followed by average values between brackets. Number of specimens measured between brackets in superscript where different from number of available specimens.

left or right. Vesicula seminalis (Fig. 2A, vs) only slightly wider than vas deferens (Fig. 2A, vd), variable in length and located ventrally to and usually on left side of intestine. Sperm cells (Fig. 2A, sz) compact, jagged and opaque, with several large, refractive, spherical or rounded inclusions. Diameter of sperm cells $3.5\mu\text{m}$ on average. Vas deferens granular, usually wide and located ventrally to and usually on right side of intestine. Spicule length 3.5–4.9% of total body length. Spicules arcuate, with set off, ventrally oriented, usually beak-like capitulum (Fig. 2D). Velum well-developed, connected to base of capitulum. Gubernaculum (Fig. 2A, gu) narrow, slightly curved and parallel to spicules.

Tail very slender and conico-cylindrical, with 38–53 complete annules (49 in holotype), including long (32.8–45.4% of tail length) and pointed tail tip (Fig. 4F). Tail tip with tiny vacuoles on dorsal side, sometimes with one or two incomplete annules ventrally (one in holotype). Caudal glands inconspicuous, but ending in a common terminal outlet.

Female

Similar to male in size and shape, but mid-body enlargement (at level of vulva) much more pronounced (Fig. 3B). Swollen pharyngeal region 12.8–16.3% of total body length. Annules broadest in pharyngeal region and in narrow region posterior to pharynx,

gradually decreasing in width along anterior ovary. Annules finest at level of anterior PAT, gradually increasing along tail. In most cases, lateral field absent or inconspicuous. When present, lateral field (Fig. 4C, lf) either as lateral interruption or lateral constriction of annules and extending from 9.6 μm in front of anterior ovary up to level of anterior ovary (width 3.0 μm , length 51 μm). Cuticular ornamentation similar to male.

Shape of CAT and PAT as in male (Fig. 4D). CAT arranged in five longitudinal rows on dorsal side, each consisting of two tubes. Anteriormost CAT in each row at posterior border of head capsule or on first annule, i.e. either well posterior to amphidial fovea or at level of posterior border of amphidial fovea. Second CAT in each row situated on annules 1–4. Width of anteriormost SIAT 0.9–1.2 μm at 10 μm from base of tube. PAT arranged in four rows: two of 12–17 SIAT and two of 8–13 SvAT (Figs. 1D, 3D). SIAT alternately long and short.

In pharyngeal region, somatic setae arranged in 12 or 14 longitudinal rows. Twelve rows arranged as follows: one mediodorsal row, two subdorsal rows, two laterodorsal rows, two mediolateral rows, two lateroventral rows, two subventral rows, and one medioventral row. If somatic setae arranged in 14 rows, each mediolateral row replaced by two sublateral rows of setae: one in dorsal and one in ventral sector. In slender region posterior to pharyngeal bulb, region anterior to PAT and region of PAT somatic setae arranged as in male, though with two subventral setae on each side at level of vulva (Figs. 1A, 4E, vu) and without medioventral setae in this region. Each side with one short seta behind posteriormost PAT. No anal setae. Tail on each side with three subventral setae and five subdorsal setae, including longest somatic setae on entire body (47.0 μm in allotype) (Fig. 1D). Tail tip on each side with one short lateroventral and one short subdorsal seta.

Head capsule a broad, truncated cone as in male, either smooth or ornamented with small vacuoles (Figs. 2C, 4B). Labial sensilla papilliform. Four cephalic setae and 23–28 subcephalic setae, arranged in eight rows: generally two subdorsal rows of three setae, two laterodorsal rows of five setae (not entirely in one row but closely together), two lateroventral rows of three setae and two subventral rows of two setae. Additional pores may be present near posterior border of head capsule. Sexual dimorphism obvious from shape of amphidial fovea: female fovea a large, longitudinally elongated, ventrally wound spiral consisting of 2.5–2.7 coils, situated centrally on or at posterior border of head capsule. Length of amphidial fovea 41.7–52.9% of head capsule length. Buccal cavity narrow and unarmed, surrounded by gold-coloured granules. Digestive system as in male. Anal flap absent; anus sometimes ending on bulge.

Female reproductive system situated ventrally to intestine, slightly shifted to right side, didelphic and

amphidelphic (two ovaria: one directed anteriorly, the other posteriorly), with antidromously reflexed ovaries (area of germinal and growth zones folded entirely over alongside oviduct) (Fig. 1A). Anterior ovary reflexed to posterior usually along left side, posterior ovary reflexed to anterior usually along right side. Uterus (Fig. 1A, ut) often with numerous small, jagged sperm cells with refractive rim (Fig. 1A, sz). Vagina bipartite: proximal and distal part equal in length (Fig. 1A, va). Proximal part thin-walled but surrounded by strongly refractive contractor muscle (Fig. 1A, cm). No paravulval setae.

Tail with 34–45 complete annules (42 in allotype), including long (40.5–52.4% of tail length) and pointed tail tip. Tail tip either without incomplete annules (condition in allotype), with 1–2 incomplete annules dorsally or with one incomplete annule ventrally. Caudal glands ending in a common outlet (Fig. 4G).

Juveniles

First-, second- and third-stage juveniles could not be distinguished from the corresponding stages of *T. koreense* Rho & Kim. For description of these stages, see the separate text section below.

Fourth-stage juvenile (Fig. 5B). Very slender body, enlarged at level of pharynx; posterior body region only slightly swollen. Posterior swelling best developed in juvenile females. Annules in pharyngeal region ornamented with one row of irregular vacuoles. Slender region posterior to pharynx either smooth or with one row of faint vacuoles. Remainder of annules smooth. Lateral field absent, inconspicuous or present as lateral interruption of annules, located in front of genital primordium, or at level of germinal and growth zones in male.

Four slender CAT (two subdorsal and two laterodorsal), with swollen base and slightly swollen tip, located on posterior border of head capsule or on annules 1–3, i.e. always clearly posterior to amphidial fovea. One medioventral row of nine PAT and two lateroventral rows of 6–7 PAT. PAT long, very slender, with swollen base and fine, bell-shaped tip. MvAT gradually decreasing in width towards posterior. Long and short LvAT, not alternating. Width of anteriormost LvAT 0.8–1.1 μm at 10 μm of base of tube.

Somatic setae in pharyngeal region arranged in eight rows: two subdorsal, two laterodorsal, two lateroventral, and two subventral rows. Region between pharynx and PAT with one mediodorsal row, two laterodorsal rows, two lateroventral rows, and one medioventral row of somatic setae. At level of PAT somatic setae in one mediodorsal and two sublateral rows in dorsal sector. On each side, one short subventral seta sometimes present immediately in front of anus. Tail with one subventral and three subdorsal somatic setae on each side, including very long subdorsal setae. Tail tip with one short lateroventral and one short subdorsal seta on each side.

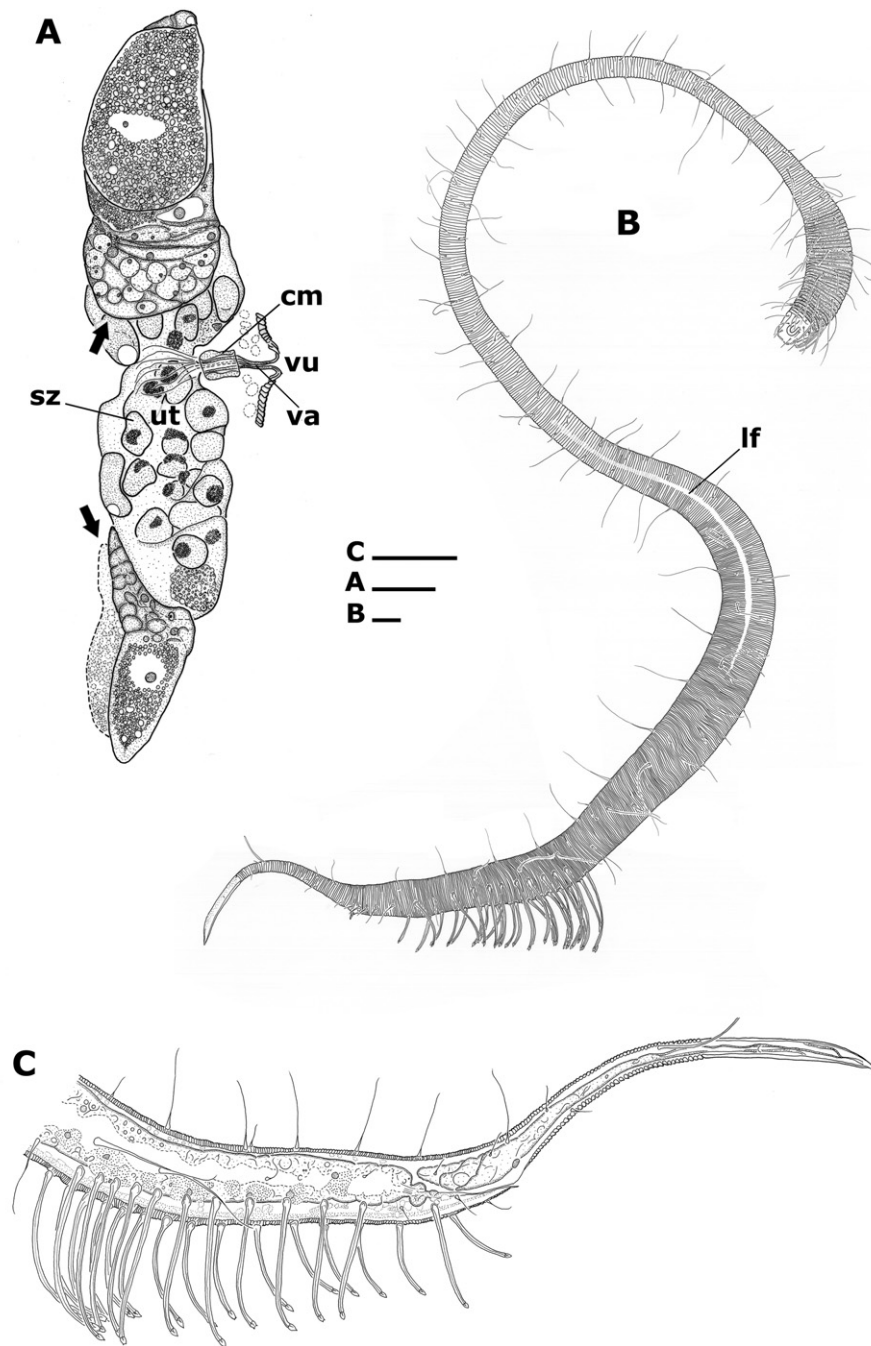


Fig. 6. *Tenuidraconema koreense* Rho & Kim, 2004 (A) Additional female, reproductive system; arrows indicate distal tips of ovaria. (B) Additional male, external habitus. (C) Additional female, posterior body region and tail. cm = contractor muscle, lf = lateral field, sz = spermatheca, ut = uterus, va = vagina, vu = vulva. Scale bars = 20 μ m.

Head capsule a truncated cone, ornamented with small vacuoles. Four cephalic and 12–17 subcephalic setae, arranged in two subdorsal rows, two laterodorsal rows, two lateroventral rows, and two subventral rows. Amphidial fovea spiral, ventrally wound, consisting of 2.1–2.6 loops, usually antero-posteriorly elongated. Amphidial fovea located centrally on head capsule.

Length of amphidial fovea 34.8–49.8% of length of head capsule. Digestive system as in adults. One moulting individual with fully developed spicules and spermatozoa as in adult male.

Tail with 35–39 complete annules, including long (51.1–58.4% of tail length) and pointed tail tip ornamented with tiny vacuoles. Tail tip either without

incomplete annules, with 1–7 incomplete annules dorsally or with 3–6 incomplete annules ventrally.

Diagnosis

Tenuidraconema microsperma sp. n. is characterised by the following combination of character states: (1) 10 CAT, arranged in five longitudinal rows; (2) all CAT

located posterior to amphidial fovea; (3) length of anteriormost SIAT 38.5–53.5 μm in male, 41–49 μm in female; (4) length of anteriormost SvAT 36–43.5 μm in male, 30.5–42 μm in female; (5) width of anteriormost SIAT 0.8–1.0 μm in male, 0.9–1.2 μm in female; (6) distance between first and last PAT 10.9–15.4% of total length in male; (7) SIAT alternately long and short;

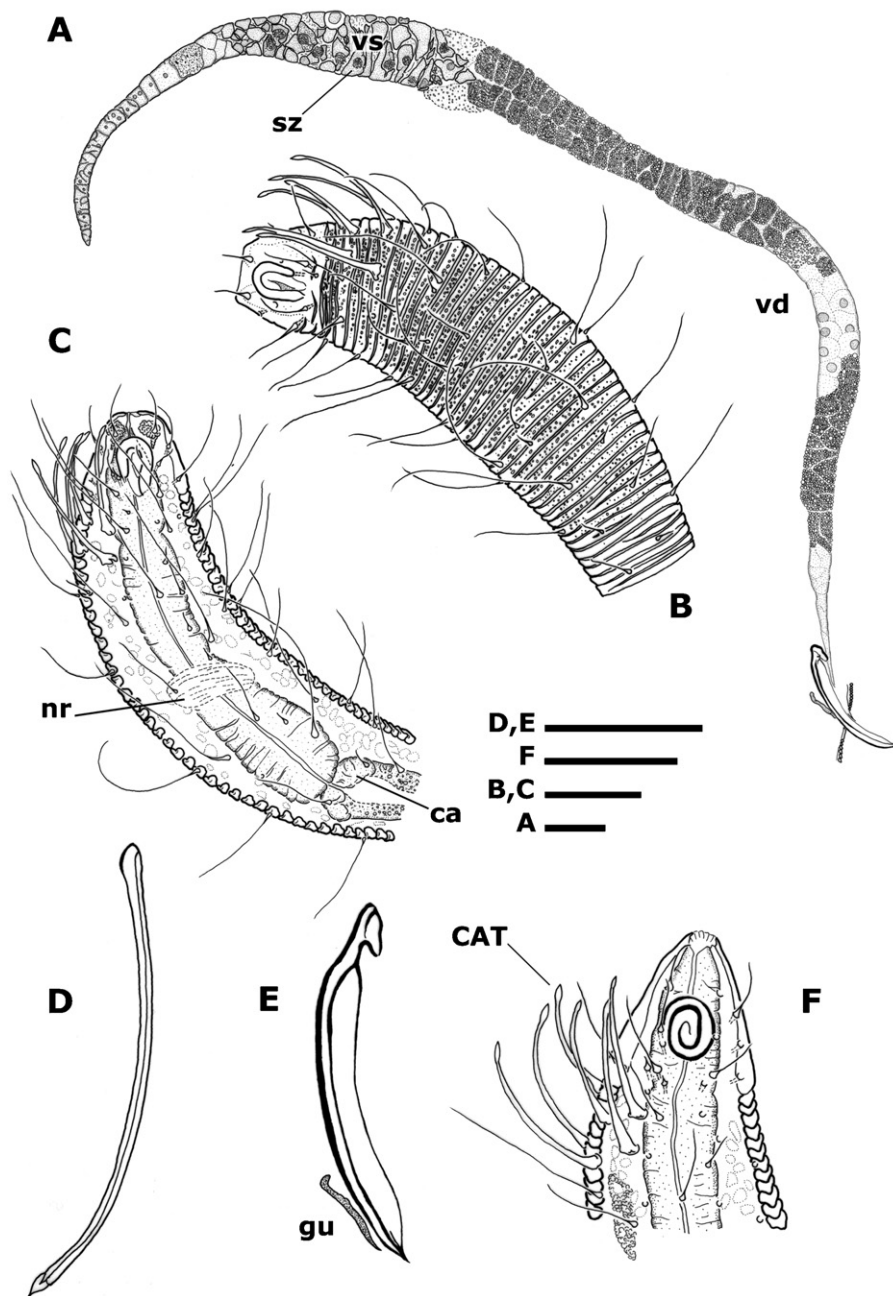


Fig. 7. *Tenuidraconema koreense* Rho & Kim, 2004 (A) Additional male, reproductive system. (B) Additional male, head capsule and pharyngeal region, external view. (C) Additional male, head capsule and pharyngeal region internal view. (D) Additional male, SIAT. (E) Additional male, spicule and gubernaculum. (F) Additional female, head capsule and CAT. ca = cardia, CAT = cephalic adhesion tube, gu = gubernaculum, nr = nerve ring, sz = spermatozoon, vd = vas deferens, vs = vesicula seminalis. Scale bars = 20 μm .

(8) labial sensilla papilliform; (9) male amphidial fovea composed of an inner and an outer loop, with ventral arm of inner loop as long as high; (10) sperm cells compact, jagged, with several large, refractive, spherical inclusions, diameter 3.5 µm on average; (11) proximal part of gubernaculum parallel to spicules; (12) 38–53 tail rings in male, 34–45 in female.

See also the key to the species of *Tenuidraconema* in the discussion section below.

***Tenuidraconema koreense* Rho & Kim, 2004**

(Figs. 5A, 6, 7)

Together with *T. microsperma* sp. n., a North-Atlantic population of *T. koreense* was encountered. The Porcupine

Seabight specimens agree well with the original description (from the Pacific Ocean), but also provide more information on intraspecific variability of certain features. For example, the original description contains morphometric data for only one male and one female, information on the morphology of the male reproductive system is limited to the spicules and the gubernaculum, and sperm-cell structure is not mentioned at all. The text below contains morphological observations of the Porcupine Seabight specimens concerning features not mentioned in the original description of the Pacific population, notes differences between the two populations, and describes the fourth-stage juvenile for the first time.

Type locality. South Korea, Namae, 37°57'07"N 128°46'41"E, 21/04/2000, 150–250 m.

Table 2. Morphological measurements of Porcupine Seabight specimens of *Tenuidraconema koreense* Rho & Kim, 2004.

Character	Male (n = 11)	Female (n = 10)	Juvenile stage IV (n = 9)
L	845–1405 (1190)	715–1485 (1075)	610–1030 (795)
Hdw	21.5–27 (23.2)	19.5–25 (23.1)	16.5–24.5 (21.1)
Hdl	15–20.5 (17.6)	12.5–20 (16.7) ⁽⁹⁾	14–20 (15.9) ⁽⁸⁾
Amphw	5.5–8 (6.9)	7–8 (7.5)	5–7.5 (6.5) ⁽⁸⁾
Amphl	10–12.5 (11.3)	7.5–10.5 (8.9)	6–9 (7.3) ⁽⁸⁾
Amph%	25.7–34.5 (29.9)	29.2–34.7 (32.3)	23.9–36.3 (31.4) ⁽⁸⁾
ph	70–99.5 (88.8)	64.5–103 (83.7)	61–83.5 (75.6) ⁽⁶⁾
MdCATa	17–22.5 (19.7)	15.5–21 (18.7) ⁽⁸⁾	
MdCATp	22–30 (27.3)	20.5–29 (25.8) ⁽⁸⁾	
SdCATa	18–22.5 (21.4)	17–24 (20.6) ⁽⁹⁾	14–22 (18.7) ⁽⁷⁾
SdCATp	23–31 (27.8)	22–29.5 (25.4) ⁽⁹⁾	
LdCAT			17.5–25 (21.4) ⁽⁷⁾
SlCATa	22–25.5 (23.8)	19–26.5 (22.8)	
SlCATp	25–30.5 (27.8)	22–31 (26.7)	
SlATa	46–66 (57.2)	39–66 (55.3)	
SlATp	30–44.5 (35.7)	31–46 (38.1)	
LvATa			33–53.5 (44.1)
LvATp			22–39.5 (34.1)
SvATa	41–62.5 (56.5)	33.5–62 (50.3) ⁽⁹⁾	
SvATp	21.5–27.5 (24.4)	19.5–28 (24.6)	
MvATa			32–56 (43.4)
MvATp			14.5–27.5 (22.6)
tail	85–151 (128.9) ⁽¹⁰⁾	106–161 (131.3)	82.5–116.5 (97.9)
tmr	40–58 (52.2) ⁽¹⁰⁾	43.5–66.5 (55.2)	30–55.5 (44.1)
mbd ph	30–41 (34.2)	32.5–37 (34.3)	26–39 (33.5)
mbd	30–47 (38.6)	40–57.5 (47.4)	24.5–43.5 (32.3)
(mbd)	11.5–14 (13.4)	11.5–16 (13.6)	12–17 (14.3)
mbd/(mbd)	2.5–3.5 (2.9)	3.0–4.1 (3.5)	2.0–2.7 (2.3)
abd	16–22.5 (19.2)	14.5–18.5 (16.0)	14–18.5 (15.7)
spic	34–53 (47.6)		
gub	11–16 (14.1) ⁽⁹⁾		
V%		54.0–67.7 (62.2)	
a	23.5–34.1 (30.8)	16.1–27.6 (22.4)	14.0–29.7 (25.2)
b	12.0–14.2 (13.3)	9.0–15.1 (12.7)	8.8–13.0 (10.8) ⁽⁶⁾
c	8.3–12.3 (9.3)	6.0–9.8 (8.1)	6.4–10.6 (8.1)

All absolute values in µm. Ranges followed by average values between brackets. Number of specimens measured between brackets in superscript where different from number of available specimens.

Voucher material. Additional specimens from Porcupine Seabight, Belgica mound province, 51°24'48.2"N 11°45'55.4"W, 17/06/2000, depth 1005 m: Four males on slides UGMD 104124 (one specimen; UGent), UGMD 104133 (one specimen; UGent), RIT 739 (one specimen; KBIN), 2008.566 (one specimen; NHM); three females on slides UGMD 104132 (one specimen; UGent), UGMD 104133 (one specimen; UGent), 2008.582 (one specimen; NHM); one fourth-stage juvenile on slide 2008.565 (NHM). Additional specimen from Porcupine Seabight, Belgica mound province, 51°25'7.7"N 11°46'9.3"W, 07/05/2001, depth 972 m: One fourth-stage juvenile on slide RIT 741 (KBIN). Additional specimens from Porcupine Seabight, Belgica mound province, 51°24'49.4"N 11°45'55.9"W, 17/06/2000, depth 1000 m: Four males on slides UGMD 104093 (one specimen; UGent), RIT 744 (two specimens; KBIN), 2008.602 (one specimen; NHM); two females on slides RIT 744 (one specimen; KBIN), 2008.587 (one specimen; NHM); one fourth-stage juvenile on slide UGMD 104137 (UGent).

Other localities. (1) Porcupine Seabight, Belgica mound province. Coordinates: 51°24'48.2"N 11°45'55.4"W (17/06/2000; depth 1005 m), 51°24'49.4"N 11°45'55.9"W (17/06/2000; depth 1000 m), 51°25'7.7"N 11°46'9.3"W (07/05/2001; depth 972 m), and 51°24'49"N 11°45'56.3"W (25/05/2003; depth 1004 m). (2) Plateau of the Great Meteor Seamount. Coordinates: 30°02'00"N 28°32'00"W (Station 518; 14/09/1998; depth 293 m), 30°06'00"N 28°24'18"W (Station 520; 14/09/1998; depth 422 m), 29°53'54"N 28°22'00"W (Station 552; 18/09/1998; depth 332 m).

Habitat. At the type locality, the species was found in subtidal coarse sediment and on various invertebrates (hermit crabs, sponges, and bryozoans). Other habitats consisted of (1) a cold-water coral degradation zone on the flank and near the top of a seabed mound, where specimens were associated with sediment-clogged framework of the cold-water coral *Lophelia pertusa* (Linnaeus) and were found on dead coral fragments, on dead sponge skeletons (*Aphrocallistes bocagei* Schultze) or within the underlying sediment; (2) biogenic coarse sand composed of coral fragments and mollusc shells.

Morphological measurements. See Tables 2 and 3.

Additional information and variability of features

Male

Swollen pharyngeal region 8% (type specimens) or 11.3–13.2% (Porcupine Seabight specimens) of total body length. Body thinnest immediately behind pharynx (Fig. 6B). Region between pharyngeal bulb and anterior tip of testis conspicuously long and slim. In some cases, sessile ciliates attached to this region. Body widest at level of vesicula seminalis. More posteriorly, width

Table 3. Morphological measurements of Great Meteor Seamount specimens of *Tenuidraconema koreense* Rho & Kim, 2004.

Character	Male	Female
L	1105	935
Hdw	22.5	22
Hdl	15	14.5
Amphw	6.5	8.5
Amphl	10.5	8
Amph%	28	38.4
ph	75.5	77.5
MdCATa	15	15
MdCATp	23.5	22
SdCATa	17	17
SdCATp	21.5	22.5
SICATa	21.5	19
SICATp	26.5	22.5
SIATa	51	46.5
SIATp	30	28
SvATa	42	34.5
SvATp	19	18
tail	111.5	108
tmr	43	49
mbd ph	31.5	32.5
mbd	32	45
(mbd)	13.5	13
mbd/(mbd)	2.4	3.4
abd	18.5	14.5
spic	51.5	
gub	11	
V%		66.2
a	34.8	20.8
b	14.6	12.1
c	9.9	8.7

All absolute values in μm .

slightly decreasing, then constant up to cloacal opening. Body abruptly narrowing posterior to cloacal opening. Beginning 30–94 μm in front of anterior tip of testis, annules laterally interrupted by narrow lateral field, extending up to level of vesicula seminalis (Fig. 6B, lf). Lateral interruption 166–250 μm in length and 2.2–3.0 μm in width, sometimes faint or absent. Annules in posterior body region with rough, somewhat granular edges and littered with detritus.

One Porcupine Seabight specimen exceptionally with two rows of CAT carrying three tubes instead of two. Anteriormost CAT in each row at posterior border of head capsule (type and some Porcupine Seabight specimens) or on annules 1–3 (some Porcupine Seabight specimens): generally well posterior to amphidial fovea, sometimes at level of posterior border of amphidial fovea. Second CAT in each row located on annules 3–6. Width of anteriormost SIAT 1.3–2.0 μm at 10 μm from base. PAT (Fig. 7D) arranged in four rows: two rows of

8–12 SIAT (12 in type specimens) and two rows of 7–15 SvAT (15 in type specimens). SIAT slightly and gradually decreasing in length towards posterior. SvAT more strongly decreasing in length towards posterior. PAT clearly associated with glands, appearing as two longitudinal rows of several separate compartments at base of PAT. First PAT located at 56.5–81.5% of body length. Distance between first and last PAT 8.5–15.8% of total body length.

Somatic setae in pharyngeal region arranged in eight (two subdorsal rows, four sublateral rows, two subventral rows: type specimens), 12 or 14 (one mediodorsal row, two subdorsal rows, two laterodorsal rows, two mediolateral or four sublateral rows, two lateroventral rows, two subventral rows, and one medioventral row: Porcupine Seabight specimens) longitudinal rows. Slender region behind pharyngeal bulb and region anterior to PAT with one mediodorsal row, two laterodorsal rows, two lateroventral rows, and one medioventral row of somatic setae. Posterior to each posteriormost SIAT one lateroventral seta usually present. This seta usually followed by four (type specimens) or five (Porcupine Seabight specimens), subventral, pericloacal ('anal') setae: two (type specimens) or three (Porcupine Seabight specimens) precloacal and two postcloacal. Anteriormost pericloacal seta longest. Some smaller Porcupine Seabight individuals with only three pericloacal setae on each side: two precloacal and one postcloacal. Annulated tail on each side with two subventral setae and several subdorsal setae. Longest somatic setae on entire body located subdorsally, either in pharyngeal region (type specimens: 65 µm) or on tail (Porcupine Seabight specimens: 51.3 µm on average; sometimes truncated and then on average 25.1 µm in length). Tail tip with three (type specimens: one sublateral and two mediolateral setae) or two (Porcupine Seabight specimens: one short lateroventral and one short subdorsal seta) somatic setae on each side.

Head capsule a broad, truncated cone, either smooth or ornamented with small vacuoles (Fig. 7B). Six small and setiform external labial sensilla, sometimes visible when labial region protruded (which is rarely the case). Head capsule with 21–24 subcephalic setae, arranged in eight rows: generally two subdorsal rows of three setae, two laterodorsal rows of five setae, two lateroventral rows of two setae and two subventral rows of two setae. Occasionally, additional scattered pores present near posterior border of head capsule. Amphidial fovea 51.8–78.4% of length of head capsule, located centrally on head capsule or near posterior border of head capsule; sometimes surrounded by first annule (Fig. 7B, C). Amphidial fovea composed of conspicuous outer loop and vague inner loop. Dorsal arm in outer loop shorter than ventral arm; dorsal arm in inner loop longer than ventral arm. Long arms of both loops joining at

posterior border of head capsule, sometimes penetrating into first annules. Ventral arm of inner loop longer than high. Buccal cavity surrounded by four cephalic glands with gold-coloured granules. Pharynx with elongated, muscular terminal bulb and two less pronounced anterior swellings divided by an indentation at level of posterior border of head capsule. Large nerve ring (Fig. 7C, nr) situated immediately in front of terminal bulb. Cardia (Fig. 7C, ca) triangular or antero-posteriorly flattened. Intestine granular, with slightly thickened brush border. Cloacal flap present or absent.

Testis extending far anteriorly (tip located at 47.9–57.4% of total body length). Germinal and growth zones finely granular, usually slender, forming broad band curved ventrally around intestine, slightly shifted to the left. Vesicula seminalis (Fig. 7A, vs) usually wider than former zones, located ventrally to and partially on left side of intestine. Seminal vesicle containing several large, irregularly shaped, elongated, opaque sperm cells (Fig. 7A, sz), each with large amount of cytoplasm, narrow halo and one round or slightly jagged nucleus filled with numerous tiny nucleoli. Length of sperm cells 12 µm on average. Vas deferens (Fig. 7A, vd) granular, usually wide, located ventrally to and in most cases on right side of intestine. Spicule length 3.7–4.3% of total body length. Spicules with set off, ventrally oriented, triangular or beak-like capitulum and usually with ventral apophysis at base of manubrium, connected to velum (Fig. 7E). Gubernaculum (Fig. 7E, gu) narrow; distal part parallel to lamina, proximal part bent away from spicules, sometimes hook-shaped.

Tail with 54–78 complete annules, including long (34% of tail length in type specimens, 36.2–43.1% in Porcupine Seabight specimens) and pointed tail tip. Tail tip sometimes (not in holotype) with one incomplete annule dorsally or 1–5 incomplete annules ventrally.

Female

Swollen pharyngeal region 9.9–16.4% of total body length. In most cases, lateral field absent or inconspicuous. When present, lateral field usually narrower than in male (width 1.5–2.8 µm) and extending from slightly anterior of genital system up to level of uterus (length 65–158 µm). One Porcupine Seabight specimen exceptionally with decoration of fine vacuoles in slender region behind pharyngeal bulb.

Anteriormost CAT in each row at posterior border of head capsule (type and some Porcupine Seabight specimens) or on annules 1–3 (some Porcupine Seabight specimens); generally well posterior to amphidial fovea, sometimes at level of posterior border of amphidial fovea (Fig. 7F). Second CAT in each row situated on annules 1–6. Width of anteriormost SIAT 1.2–1.8 µm at 10 µm from base of tube. PAT arranged in two rows of 11–13 SIAT (13 in type specimens) and two rows

of 7–19 SvAT (19 in type specimens, 7–16 in Porcupine Seabight specimens) (Fig. 6C). PAT gradually decreasing in length towards posterior.

In pharyngeal region, somatic setae arranged in 12 or 16 longitudinal rows: one mediodorsal row, two subdorsal rows, two or four laterodorsal rows, two mediolateral rows, two or four lateroventral rows, two subventral rows, and one medioventral row. In slender region behind pharyngeal bulb, in region anterior to PAT and in region of PAT somatic setae arranged as in male, although with two subventral setae on each side at level of vulva and without medioventral setae in this region. Each side with or without one short seta between two posteriormost SIAT. Posterior to last SIAT, one or two short sublateral setae usually present on each side. One subventral anal seta on each side at level of anus or one medioventral seta anterior to anus. Tail on each side with one subventral seta, 3–4 laterodorsal setae and one very long subdorsal seta (37.5 μm in female from Porcupine Seabight). Tail tip on each side with one short lateroventral and 1–2 short subdorsal setae.

Six labial sensilla, four cephalic setae and 21–29 subcephalic setae, arranged in eight rows: maximally two subdorsal rows of three setae, two laterodorsal rows of six setae (not entirely in one row but closely together), two lateroventral rows of three setae and two subventral rows of three setae. Amphidial fovea consisting of 2.5–2.7 coils, situated centrally on head capsule. Length of amphidial fovea 49.1–67.5% of head capsule length. Buccal cavity surrounded by gold-coloured granules. Anal flap present or absent.

Female reproductive system situated ventrally to intestine, didelphic and amphidelphic (two ovaria: one directed anteriorly, the other posteriorly), with antidromously reflexed ovaries (area of germinal and growth zones folded entirely over alongside oviduct) (Fig. 6A). Anterior ovary reflexed along right side, posterior ovary reflexed along left side. Uterus (Fig. 6A, ut) often with numerous opaque sperm cells (Fig. 6A, sz), each with considerable amount of cytoplasm and more condensed nucleus than in male. Vagina (Fig. 6A, va) bipartite, proximal and distal part equal in length; proximal part surrounded by strongly refractive contractor muscle (Fig. 6A, cm). Four paravulval setae around vulva (Fig. 6A, vu) in type specimens, no paravulval setae in Porcupine Seabight specimens.

Tail with 50–76 complete annules, including long (39.2–46.7% of tail length) and pointed tail tip. Tail tip either without incomplete annules, with 1–3 incomplete annules dorsally (three in allotype) or with one incomplete annule ventrally.

Juveniles

First-, second- and third-stage juveniles could not be distinguished from the corresponding stages of

T. microsperma sp. n. For description of these stages, see the separate text section below.

Fourth-stage juvenile (Fig. 5A). Slender body, obviously enlarged at level of pharynx. Posterior swelling less pronounced, especially in juvenile males. Annules in pharyngeal region ornamented with one or two rows of irregular vacuoles. Slender region posterior to pharynx sometimes with one row of vacuoles. Remainder of annules smooth. Lateral field absent or present as lateral interruption of annules, anterior to genital system or at level of germinal and growth zones in some juvenile males.

Four slender CAT with swollen base and slightly swollen tip, located on posterior border of head capsule or on annules 1–5, always clearly posterior to amphidial fovea: two subdorsal and two laterodorsal tubes. One medioventral row of 7–9 PAT and two lateroventral rows of 6–7 PAT. PAT long, robust, with swollen base and well-developed bell-shaped tip, gradually decreasing in length towards posterior. Width of anteriormost LvAT 1.2–1.8 μm at 10 μm of base of tube.

Somatic setae in pharyngeal region arranged in eight rows: two subdorsal rows, two laterodorsal rows, two lateroventral rows, and two subventral rows. Region between pharynx and PAT with one mediodorsal row, two laterodorsal rows, two lateroventral rows, and one medioventral row of somatic setae. At level of PAT somatic setae in one mediodorsal and two sublateral rows in dorsal sector. On each side, one short subventral seta anterior to anus. Tail with one subventral and three subdorsal somatic setae on each side, including very long subdorsal setae. Tail tip with one short lateroventral and one short subdorsal seta on each side.

Head capsule a short, truncated cone, ornamented with small vacuoles. Four cephalic and 11–17 subcephalic setae, arranged in two subdorsal rows, two laterodorsal rows, two lateroventral rows, and two subventral rows. Amphidial fovea spiral, ventrally wound, consisting of 2–2.6 loops, usually longer than wide. Amphidial fovea located either centrally on head capsule or slightly shifted to anterior. Length of amphidial fovea 32.6–51.7% of length of head capsule. Digestive system as in adults. Genital system well-developed in moulting individuals: juvenile females with reflexed ovaries.

Tail with 44–64 complete annules, including long (36.5–49.1% of tail length) and pointed tail tip ornamented with tiny vacuoles. Tail tip either without incomplete annules, with two incomplete annules dorsally or with one incomplete annule ventrally.

Emended species diagnosis

The species is characterised by the following combination of character states: (1) 12 CAT, arranged in six longitudinal rows; (2) all CAT located posterior to amphidial fovea; (3) length of anteriormost SIAT 46–66 μm in male, 39–66 μm in female; (4) length of

Table 4. Morphological measurements of juveniles of *Tenuidraconema* species.

Character	Stage III (<i>n</i> = 10)	Stage II (<i>n</i> = 10)	Stage I (<i>n</i> = 5)
L	380–685 (555)	315–490 (380)	240–295 (260)
Hdw	15.5–19 (17.1) ⁽⁹⁾	12.5–16 (14.3)	
Hdl	12.5–15 (13.7) ⁽⁹⁾	7–13 (10.9) ⁽⁹⁾	
Bda			10.5–13 (11.7) ⁽⁴⁾
Amphw	4.5–7 (5.8) ⁽⁹⁾	4–6 (4.8) ⁽⁹⁾	1.4–1.6 (1.5) ⁽³⁾
Amphl	5.5–8 (6.3) ⁽⁹⁾	4–5.5 (4.6) ⁽⁸⁾	1.4–1.9 (1.5) ⁽⁴⁾
Amph%	29.4–38.9 (34.0) ⁽⁹⁾	30.4–38.3 (33.6) ⁽⁹⁾	13.1–13.4 (13.3) ⁽³⁾
ph	56.5–69.5 (62.1) ⁽⁹⁾	43.5–63 (53.6)	40.5–56 (48.8)
MdCAT	15–21.5 (18.5) ⁽⁸⁾	13.5–19 (16.4) ⁽⁹⁾	
LdCAT	16–23.5 (21.1) ⁽⁹⁾		
LvATa	33–50 (42.7)	32–49 (40.9)	
LvATp	21–38.5 (30.2)	28.5–49 (39.1)	
tail	66.5–86 (77.3)	52.5–73 (60.5)	50.5–60 (54.9) ⁽⁴⁾
tmr	32.5–45 (39.8)	24.5–35 (29.8)	3.5–6.5 (5.5)
mbd ph	20.5–29.5 (25.6)	18–26 (21.6)	16.5–23 (19.4)
mbd	14–23 (18.4)	12.5–19.5 (14.9)	12–14 (12.7)
(mbd)	8.5–13 (10.9)	9–12 (10.4)	9–14.5 (11.0)
mbd/(mbd)	1.6–1.9 (1.7)	1.3–1.6 (1.4)	1.2–1.4 (1.3)
abd	9.5–15 (12.4)	8.5–13.5 (11.1)	10–13 (10.9) ⁽⁴⁾
a	16.4–37.4 (30.7)	16.2–35.4 (26.5)	17.7–22.5 (19.9)
b	6.5–10.1 (8.9)	5.9–7.8 (7.1)	4.9–6.2 (5.4)
c	5.7–8.3 (7.2)	5.6–7.9 (6.3)	4.5–5.0 (4.8) ⁽⁴⁾

All absolute values in μm . Ranges followed by average values between brackets. Number of specimens measured between brackets in superscript where different from number of available specimens.

anteriormost SvAT 41–62.5 μm in male, 33.5–62 μm in female; (5) width of anteriormost SIAT 1.3–2.0 μm in male, 1.2–1.8 μm in female; (6) distance between first and last PAT 8.5–15.8% of total length in male; (7) external labial sensilla setiform; (8) male amphidial fovea composed of an inner and an outer loop, with ventral arm of inner loop longer than high; (9) sperm cells elongated, irregularly shaped, with large amount of cytoplasm, narrow halo and one nucleus, 12 μm in length on average; (10) proximal part of gubernaculum often hook-shaped, bent away from spicules; (11) velum well-developed and cuticularised; (12) 54–78 tail rings in male, 50–76 in female.

See also the key to the species of *Tenuidraconema* in the discussion section below.

Early-stage juveniles in *Tenuidraconema*

The respective first-, second- and third-stage juveniles of *T. koreense* and *T. microsperma* sp. n. could not be distinguished from each other, thus are described below (for morphological measurements, see Table 4).

First-stage juvenile

(Fig. 8A)

Slender body, slightly S-shaped and only slightly enlarged at level of pharynx. Body finely annulated.

No adhesion tubes. On each side one mediolateral somatic seta at level of pharynx and one shorter mediolateral seta on tail. Head capsule short, anteriorly with six hook-shaped labial sensilla. Four cephalic setae; no subcephalic setae. Amphidial fovea a tiny circle (diameter 1.4–1.9 μm), situated posterior to head capsule.

Tail with 56–64 complete annules, including pointed tail tip. Tail tip smooth, with conspicuous spinneret, taking up only 6.3–12.5% of tail length. Tail tip either with four incomplete annules dorsally or with five incomplete annules ventrally.

Second-stage juvenile

(Fig. 8B)

Very slender body, enlarged at level of pharynx. Entire body finely annulated; no cuticular ornamentation. Lateral field absent, or present either as local differentiation of cuticle or as lateral interruption of annules, between first dorsal curvature and ventral curvature.

One robust, mediodorsal CAT, broadest at its base and gradually decreasing in width, with barely swollen tip, located on posterior border of head capsule or on annules 1–3, i.e. always well posterior to amphidial fovea. Two lateroventral rows of two PAT. PAT long and slender, with slightly swollen base and fine,

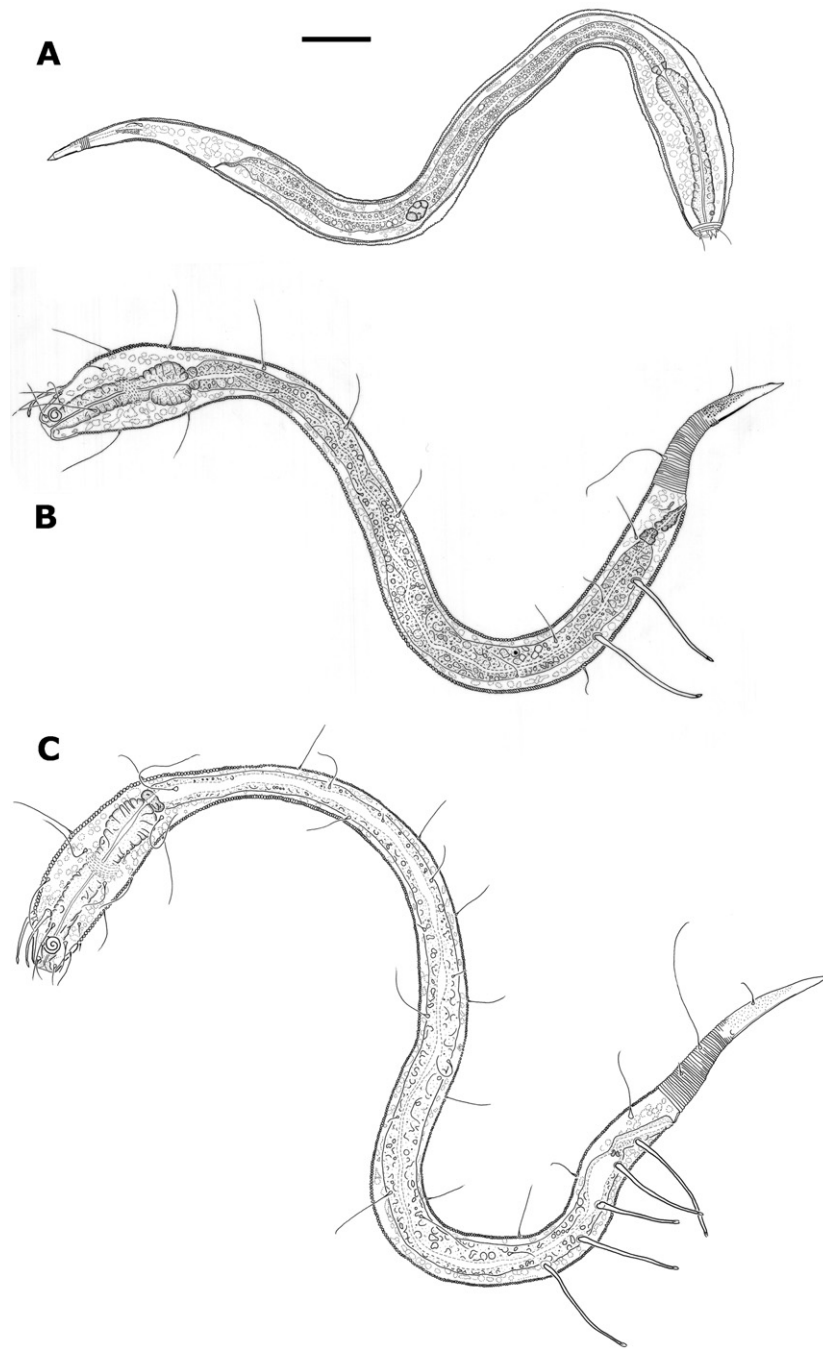


Fig. 8. *Tenuidraconema* sp., juvenile habitus. (A) First stage. (B) Second stage. (C) Third stage. Scale bar = 20 μ m.

bell-shaped tip. Width of anteriormost LvAT 1.0–1.8 μ m at 10 μ m of base of tube.

Somatic setae in pharyngeal region arranged in six rows: one mediodorsal row, two laterodorsal rows, two lateroventral rows, and one medioventral row. Region between pharynx and PAT with two laterodorsal rows and two lateroventral rows of somatic setae. At level of PAT somatic setae on two sublateral rows in dorsal sector. Immediately in front of anus, one lateroventral

seta present on both sides. Tail with one very long subdorsal somatic seta on each side. Tail tip with one mediodorsal seta.

Head capsule dome-shaped, sometimes ornamented with small vacuoles. Labial region usually clearly set off immediately anterior to amphidial fovea. Four cephalic and four subcephalic setae: on each side one laterodorsal subcephalic seta immediately posterior to amphidial fovea and one subdorsal subcephalic

seta at posterior border of head capsule. Amphidial fovea ventrally wound into spiral consisting of 1.4–1.9 coils, located anteriorly on head capsule. Length of amphidial fovea 35.2–54.8% of length of head capsule.

Tail with 30–52 complete annules, including long (42.6–54.8% of tail length) and pointed tail tip. Tail tip ornamented with vacuoles. Tail tip either without incomplete annules, with 1–11 incomplete annules dorsally or with three incomplete annules ventrally.

Third-stage juvenile

(Fig. 8C)

Slender body, enlarged in pharyngeal region. Annules in pharyngeal region sometimes with one row of tiny, irregular vacuoles. All other annules completely smooth. Lateral field absent, or present either as lateral interruption or as local differentiation of cuticle, extending up to anterior part of genital primordium.

Three slender CAT with swollen base and slightly swollen tip: one mediodorsal tube and two laterodorsal tubes. All CAT located on posterior border of head capsule or on annules 1–7, i.e. always posterior to amphidial fovea. Two lateroventral rows of 5 PAT. PAT long, relatively slender, with slightly swollen base and fine, bell-shaped tip. Width of anteriormost LvAT 0.9–1.6 μm at 10 μm of base of tube.

Somatic setae in pharyngeal region arranged in eight rows: two subdorsal rows, two laterodorsal rows, two lateroventral rows, and two subventral rows. Region between pharynx and PAT with one mediodorsal row, two laterodorsal rows and two lateroventral rows of somatic setae. At level of PAT somatic setae on one mediodorsal and two sublateral rows in dorsal sector. Immediately in front of anus one short subventral seta sometimes present on each side. Tail with two subdorsal setae on each side, including very long subdorsal seta. Tail tip with few short subdorsal and subventral setae.

Head capsule a truncated cone, ornamented with small vacuoles. Four cephalic and 7–10 subcephalic setae, arranged in two subdorsal rows, two laterodorsal rows, two lateroventral rows, and two subventral rows. Amphidial fovea a ventrally wound spiral consisting of 2.1–2.2 coils. Amphidial fovea located centrally or anteriorly on head capsule. Length of amphidial fovea 36.1–57.8% of length of head capsule. Digestive system as in adults.

Tail with 39–57 complete annules, including long (47.0–58.7% of tail length) and pointed tail tip ornamented with vacuoles. Tail tip either without incomplete annules, with 2–4 incomplete annules dorsally or with 1–2 incomplete annules ventrally.

Discussion

According to Decraemer (1989), the genus *Tenuidraconema* is, among other character states, characterised by the presence of a lateral field. This feature should be utilised with caution, however, as the lateral field may be inconspicuous or absent even in adults of both *T. koreense* and *T. microsperma* sp. n. Moreover, it may be present as either a lateral interruption of the annules or as a lateral differentiation of the cuticle. The location of CAT relative to the head capsule is variable within the genus, too, which is an important observation given the diagnostic importance Decraemer et al. (1997) have ascribed to this feature for the distinction between genera in the family Draconematidae. The same is, however, also the case in the genus *Dracognomus* Allen & Noffsinger, 1978.

Light-microscopic morphology of sperm cells is not commonly used as a diagnostic feature in nematode taxonomy. Moreover, only few studies have attempted to construct a classification based on nematode sperm types (for an overview, see Justine 2002), and most phylogenetic studies based on nematode sperm deal with ultrastructural aspects and spermatogenesis (Yushin and Malakhov 2004). However, sperm morphology can be used as a diagnostic feature here to distinguish between *T. koreense* and *T. microsperma*: the sperm cells of these two species are strikingly different from each other, and each type consequently occurs in individuals with either 10 or 12 CAT. The same is true for sperm cells found in the uterus of females of both species.

Identification and variability of features

Prior to the present study, four species of *Tenuidraconema* have been described: *T. fiersi*, *T. koreense*, *T. philippinense*, and *T. tongaense*. Rho and Kim (2005) and Rho et al. (2007) compared the features they believed to be of diagnostic value for these species. However, the results presented here show that some of those features are variable within a species. For example, the position of the anteriormost CAT may be either on the head capsule or posterior to it in both *T. koreense* and *T. microsperma*. Besides, in the Porcupine Seabight specimens of *T. koreense* the amphidial fovea may or may not reach the first body annules. Furthermore, the presence and position of somatic setae intermingled between the SIAT is variable among males of *T. koreense* from the Porcupine Seabight. The number of SIAT and SvAT is also variable and overlaps between species. Nevertheless, the different species can still be distinguished easily:

Tenuidraconema tongaense is clearly very close to *T. fiersi*, as both show a similar, slender body. In addition, both species clearly differ from all others by

the position of the CAT, i.e. all on the head capsule in *T. fiersi* and *T. tongaense* versus at least some located on the anteriormost annules in the other species. The two species share with *T. philippinense* the shape of the male amphidial fovea, which consists of a single loop instead of an inner and an outer loop as in *T. koreense* and *T. microsperma*. Moreover, *T. fiersi* and *T. microsperma* have papilliform external labial sensilla, whereas in the other species these sensilla are setiform.

Tenuidraconema philippinense and *T. microsperma* are clearly closely related, judging from the overall body shape and especially the shape, width and organisation of the SIAT, i.e. the fact that they are fine and alternately long and short. Nevertheless, *T. microsperma* differs from *T. philippinense* in (1) the shape of the male amphidial fovea, which consists of a double loop and (2) the tail shape (more slender in *T. philippinense*). It also differs from all other species in the number of CAT (10 instead of 12). Furthermore, it can be clearly distinguished from *T. koreense* in (1) the size and shape of the sperm cells (larger and with more cytoplasm in *T. koreense*), (2) the shape of the ventral arm of the inner loop in the male amphidial fovea (longer in *T. koreense*), (3) the location of the proximal part of the gubernaculum relative to the spicules (bent away from the spicules in *T. koreense*), and (4) the number of tail rings (generally more in *T. koreense*). It must be added here that the number of tail rings cannot be used as a diagnostic feature for Great Meteor Seamount specimens of *T. koreense*. Fourth-stage juveniles of *T. koreense* and *T. microsperma* from the Porcupine Seabight area can be distinguished by (1) the width of the anteriormost SIAT and (2) the number of tail rings. *Tenuidraconema koreense* and *T. philippinense* differ from each other in the shape of the male amphidial fovea and in the shape, width, and arrangement of the SIATs.

Emended diagnosis of *Tenuidraconema*

Draconematinae. Body slender, sigmoid; swollen pharyngeal region 8–16.4% of total body length. Body cuticle with vacuolar ornamentation at level of pharynx, on slender body region posterior to pharynx, at level of testis, and around cloacal opening. Cuticle at mid-body interrupted by a more or less conspicuous lateral field. Ten or twelve CAT with widened base and slightly enlarged tip, located either on head capsule or posterior to amphidial fovea within a distance of one head capsule width. Amphidial fovea loop-shaped or consisting of an inner and an outer loop in males, spiral in females and juveniles. Anterior part of pharynx cylindrical, with elongated, muscular terminal bulb and with or without less pronounced anterior swellings, the latter around mid-corpus and/or at level of head capsule. Terminal bulb without thickened lumen wall. Buccal cavity short and narrow, without teeth. Tail with numerous annules.

Biogeography and dispersal of *T. koreense*

The species was originally described from Namae, South Korea, where it was collected at a depth of 150–250 m (Rho and Kim 2004). It is remarkable that the same species, with only limited morphological differences, is now found in the North Atlantic at a depth of 1000 m. Judging from the geographical and bathymetrical differences, as well as the assumed complexity of dispersion routes that could link both populations, it is possible that these populations are genetically isolated from each other and may represent different cryptic species (Raes et al. 2008).

One male and one female specimen belonging to this species have been found on the plateau of the Great Meteor Seamount (measurements in Table 3). These individuals are morphologically and morphometrically

Key to the species of *Tenuidraconema*

The five species of *Tenuidraconema* can be identified as follows:

1. CAT located at level of amphidial fovea, i.e. on head capsule.....2
- CAT located posterior to amphidial fovea, i.e. on posterior border of head capsule or posterior to head capsule.....3
2. External labial sensilla papilliform; spicule length up to 30 µm.....*T. fiersi* Decraemer, 1989
- External labial sensilla setiform; spicule length exceeds 40 µm.....*T. tongaense* Rho, Min & Kim, 2007
3. Ten CAT, arranged in five longitudinal rows; external labial sensilla papilliform.....*T. microsperma* sp. n.
- Twelve CAT, arranged in six longitudinal rows; external labial sensilla setiform.....4
4. Male amphidial fovea consisting of an inner and an outer loop; SIAT slender but robust, gradually decreasing in length towards posterior.....*T. koreense* Rho & Kim, 2004
- Male amphidial fovea consisting of a single loop; SIAT slender, alternating long and short.....*T. philippinense* Rho & Kim, 2005

almost identical to those from the type locality and Porcupine Seabight, although the number of tail annules is slightly lower: 49 in the male and 43 in the female. Moreover, another new species of *Tenuidraconema* has been found on this seamount (G. Gad, pers. comm.). These observations agree well with the hypothesis of Gad (2004) that cold-water coral reefs could be regarded as a source for the colonisation of the Great Meteor Seamount by Epsilonematidae and Draconematidae, and for genetic exchange. It is, however, still unclear how this takes place. According to Gad (2004) and Gad and Schminke (2004), the colonisation of the Great Meteor Seamount by meiofauna could occur through continuous transport by the outflow of Mediterranean water and between the Great Meteor Seamount and the north-western coast of Africa. According to these authors, this trans-oceanic colonisation is not the result of a single long-distance dispersive action but a gradual process using seamounts, the Canary Islands and the Island of Madeira as 'stepping stones', i.e. intermediate stations where a new population can be established, which can then serve as a source for further colonisation. If this is the case, then the presence and distribution of *Lophelia pertusa* might be an essential aspect in this hypothesis. The plateau of the Great Meteor Seamount is known to be covered by biogenic coarse sand, which is partially composed of coral fragments. Subfossil remains of the cold-water coral *Lophelia pertusa* have been found on this seamount, and this coral species has also been recorded on the nearby Atlantis Seamount, near Madeira, near the Canary Islands and near the Azores (Rogers 1999). The possibility that Mediterranean Outflow Water (MOW) may play a role in the distribution of *L. pertusa* and the dispersal of its larvae, both northward along the north-western European continental margin (up to the Norwegian Sea and also reaching the Porcupine Seabight at a depth of 800–1000 m) and westward across the Atlantic, has already been put forward by De Mol et al. (2002). According to Le Goff-Vitry et al. (2004), it could be the Shelf Edge Current (SEC), a surface current which follows the northward branch of the MOW and reaches the Porcupine Seabight at a depth of 100–200 m, that transports the larvae of *L. pertusa* along the continental margin from the Iberian margin up to the Norwegian Sea. However, only the MOW is able to reach both the Porcupine Seabight and the Great Meteor Seamount. We hypothesise here that at least part of the nematofauna associated with *L. pertusa* fragments follows the same trajectory as the larvae of this coral species, resulting in a co-occurrence of the coral and these nematodes. Following this hypothesis, the source for colonisation would be somewhere in the Mediterranean Sea or near the MOW outflow point in the North Atlantic. Moreover, this should ensure continuing long-distance genetic exchange,

whether via stepping stones or not. It is, however, also possible that nematodes such as *T. koreense* are more widely distributed in the region but able to establish a population only in the presence of *L. pertusa* fragments or other biogenic substrata.

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