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Draconematidae (Nematoda) from cold-water corals in the Porcupine Seabight: The genus *Cygnonema* Allen & Noffsinger, 1978

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Abstract

Two new and closely related species of the genus *Cygnonema* Allen & Noffsinger, 1978 are described from a cold-water coral degradation zone in the Porcupine Seabight (NE Atlantic). Both species differ from *C. steineri* Allen & Noffsinger, 1978 by more pronounced pharyngeal and posterior swellings, a smaller body, a shorter pharynx in relation to body length, a higher number of CAT, and by the absence of a dorsal tooth. *Cygnonema verum* sp. n. differs from *C. belgicae* sp. n. by its greater body length, the relatively larger head capsule, a higher number of CAT, a more anteriorly positioned anteriormost laterodorsal CAT, a higher number of PAT, by the external labial sensilla being setiform, a higher number of subcephalic setae, and by a more anterior position of the amphidial fovea on the head capsule. Males of *C. verum* sp. n. are easily recognised by the presence of two large subventral, precloacal corniform setae. They also differ from males of *C. belgicae* sp. n. in the smaller amount of cytoplasm in the sperm cells, a knob-like capitulum, and a relatively shorter tail tip. The diagnosis of *Cygnonema* is emended, a dichotomic identification key to the three species is provided, and their biogeography is discussed.

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

Introduction

The genus *Cygnonema* Allen & Noffsinger, 1978 was originally described by Allen and Noffsinger (1978) from McMurdo Sound, Antarctica, where the type species, *C. steineri* Allen & Noffsinger, 1978, was collected at a depth of 457 m. Within the family Draconematidae, it is the genus with the most slender body shape. It can be distinguished by characteristic, non-modified cephalic adhesion tubes (i.e. with tube base enlarged), extending up to a length of more than two times the diameter of the head capsule along the cervical region (Decraemer et al. 1997).

This 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, north-east Atlantic Ocean). Compared to the associated sediment, the coral fragments themselves are characterised by higher abundances of Epsilonematidae

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and Draconematidae (Raes and Vanreusel 2006), which is mainly attributed to these animals' particular way of locomotion and capacity for attachment (Stauffer 1924; Lorenzen 1973). Draconematidae use both Cephalic Adhesion Tubes (CAT) and Posterior Adhesion Tubes (PAT) for attachment to the coral surface. Several new species of Epsilonematidae have already been described from the same location (Raes et al. 2003, 2006). In the present paper, two new and closely related species of *Cygnonema* are described, a dichotomic identification key to the three species in the genus is provided, and their biogeography is discussed.

Material and methods

All specimens were collected from dead coral fragments of *Lophelia pertusa* (Linnaeus, 1758) and, to a lesser extent, *Madrepora oculata* Linnaeus, 1758, from skeletons of *Aphrocallistes bocagei* Schultze, 1886, and from the sediment directly beneath these large biogenic substrates. Material was collected with a NIOZ box corer (diam. 32 cm) during the June 2000 and May 2001 sampling campaigns of the RV Belgica. Box cores were taken on the top and slope of one seabed mound situated in the Belgica mound province of the Porcupine Seabight: Box IV 2000 (51°24′48.2″N 11°45′55.4″W; depth 1005 m), Box V 2000 (51°24′49.4″N 11°45′55.9″W; depth 1000 m), Box IV 2001 (51°25′7.7″N 11°46′9.3″W; depth 972 m). The Porcupine Seabight is a large embayment of the European continental slope, located in the North-East Atlantic, southwest of Ireland. Living cold-water coral framework (mainly *Lophelia pertusa*) and associated fauna is present on the mounds in the Belgica mound province. Our samples were taken in the sediment-clogged cold-water coral framework facies (Freiwald et al. 2002) and contained mainly dead material. After removal of the large biogenic substrata, three sediment cores (surface area: 10 cm^2) were pushed into the sediment of each box core. The sediment consisted of fine to medium sand but was poorly sorted, containing small coral and sponge fragments as well as some mollusc-shell fragments and echinoid spines. All material was fixed with a 4% neutralised formalin solution.

Each coral and sponge fragment was rinsed thoroughly over a 1 mm and a 32 µm sieve to separate macrofauna and meiofauna. Meiofauna was extracted from the underlying or remaining sediment by density gradient centrifugation, using Ludox HS-40 (a colloidal silica polymer; specific gravity 1.18) as a flotation medium (Heip et al. 1985; Vincx 1996). Material was stained with Rose Bengal. Nematodes were individually picked out from the meiofauna and subsequently mounted onto slides using the formalin–ethanol–glycerol technique described by Seinhorst (1959) and Vincx (1996). Detailed morphological observation was carried out with a Leica DMLB light microscope. A Leitz Dialux 20 microscope, Sanyo CCD video camera, and the Quantimet 500 software were utilised for measurements. Scanning electron micrographs were taken from the glycerol-fixed specimens. After ultrasonic treatment (to remove detritus attached to the body), the specimens were transferred to OsO_4, dehydrated, subjected to critical-point drying, and coated with gold particles.

Juvenile stages were distinguished based on the size of the genital primordium, the number and arrangement of cephalic and posterior adhesion tubes, and the number of subcephalic setae.

Type material 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). Non-type specimens are denoted as 'additional' material throughout the text.

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.

Abbreviations used

a	de Man a-ratio, i.e. L/mbd
abd	body diameter at level of anal or cloacal opening
Amphl	length of amphidial fovea
Amphw	width of amphidial fovea
Amph%	(Amphw/Hdw) × 100
b	de Man b-ratio, i.e. L/ph
Bda	body width at level of amphidial fovea (in first-stage juveniles only)
c	de Man c-ratio, i.e. L/tail
CAT	cephalic adhesion tube
Corn-set	length of precloacal corniform setae
gub	length of gubernaculum
Hdl	length of head capsule
Hdw	maximal width of head capsule
L	total body length
LdCATa	length of anteriormost laterodorsal cephalic adhesion tube
LdCATp	length of posteriormost laterodorsal cephalic adhesion tube
mbd	maximal diameter of posterior body region
(mbd)	minimal body diameter
mbd/(mbd)	ratio of maximal diameter of posterior body region to minimal body diameter
mbd ph	body diameter at level of pharyngeal bulb

MdCAT	length of mediodorsal cephalic adhesion tube
MvATa	length of anteriormost medioventral posterior adhesion tube
MvATp	length of posteriormost medioventral posterior adhesion tube
PAT	posterior adhesion tube
ph	pharyngeal length, measured from anterior end of head capsule to posterior border of pharyngeal bulb, lips (when protruding) and cardia not included
SdCATa	length of anteriormost subdorsal cephalic adhesion tube
SdCATp	length of posteriormost subdorsal cephalic adhesion tube
SlATa	length of anteriormost sublateral posterior adhesion tube
SlATp	length of posteriormost sublateral posterior adhesion tube
spic	length of spicule, measured along arc
SvATa	length of anteriormost subventral posterior adhesion tube
SvATp	length of posteriormost subventral posterior adhesion tube
tail	length of tail
tmr	length of tail tip
V%	position of vulva, expressed as percentage of L, measured from anterior end

Taxonomic section

Family Draconematidae Filipjev, 1918
Subfamily Prochaetosomatinae Allen & Noffsinger, 1978

Genus *Cygnonema* Allen & Noffsinger, 1978

Type species. *Cygnonema steineri* Allen & Noffsinger, 1978.

Valid species included. *Cygnonema belgicae* sp. n., *C. steineri* Allen & Noffsinger, *C. verum* sp. n.

Emended diagnosis

Prochaetosomatinae. Length 1.0–3.1 mm. Body slender, S-shaped, slightly enlarged at level of genital system, and either with conspicuous enlargement at level of pharynx or only slightly swollen at base of pharynx. Annules smooth or with inconspicuous subcuticular granulation. CAT with enlarged base and with fine or slightly swollen tip. Number of CAT variable between 10 and 16. All CAT posterior to head capsule, extending posterior to head capsule for up to more than two head capsule diameters, and arranged in four longitudinal rows: two subdorsal and two sublateral. Two sublateral and two subventral rows of PAT with bell-shaped tip. Tail tip with 2–6 setae. Rostrum bullet-shaped, either smooth or with faint markings. Subcephalic setae present, variable in number (between 2 and 18). Amphidial fovea located centrally on head capsule or near posterior border of head capsule. Male amphidial fovea loop-shaped with longer dorsal arm. Shape of amphidial fovea sexually dimorphic in some species: female fovea may be inconspicuous and tubular. Buccal cavity weakly developed, either without teeth or with conspicuous dorsal tooth. Pharynx long and cylindrical, with well-developed, oval or elongated terminal bulb and with slight anterior swellings. Terminal bulb without thickened lumen wall. Cloacal/anal flap may be present. Female with either four setiform or twelve short, truncated, tube-like paravulval setae. Male with or without two large subventral corniform setae.

Cygnonema verum sp. n.

(Figs. 1–3)

Etymology. The specific epithet is the neuter form of the Latin adjective verus, meaning 'real', 'true'. Compared to *Cygnonema steineri*, the new species, with its posteriorly more enlarged body and its broader pharyngeal region, shows more obvious resemblance to a floating swan (*Cygnonema* means 'swan nematode').

Voucher material. Holotype male on slide UGMD 104128 (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 104125 (UGent); three males on slides UGMD 104129 (one specimen; UGent), RIT 736 (one specimen; KBIN), 2008.558 (one specimen; NHM); two second-stage juveniles on slide UGMD 104128 (two specimens; UGent); four third-stage juveniles on slides UGMD 104126 (one specimen; UGent), UGMD 104133 (one specimen; UGent), RIT 735 (one specimen; KBIN), 2008.549 (one specimen; NHM); two fourth-stage juveniles on slides UGMD 104130 (one specimen; UGent), RIT 735 (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, 1758). Specimens were collected from dead coral fragments.

Relative abundance. At the type locality, *C. verum* constituted 0.26% of the total nematode community.

Morphological measurements. See Table 1.

Male

Body S-shaped, enlarged at level of pharynx and along reproductive system in posterior body half (Fig. 1A). Head capsule and anterior part of pharyngeal

Table 1. Morphological measurements in *Cygnonema verum* sp. n.

	Male holotype	Male paratypes ($n = 3$)	Female allotype	Juvenile stage II ($n = 2$)	Juvenile stage III ($n = 5$)	Juvenile stage IV ($n = 2$)
L	1625	1325–1525 (1440)	1415	450–480 (465)	580–770 (660)	1085–1125 (1105)
Hdw	20.5	19–20.5 (19.9)	21	12–13 (12.7)	15–16.5 (15.8)	17.5–20 (18.7)
Hdl	27	20.5–24.5 (22.6)	22	12–15 (13.4)	15.5–18.5 (16.9)	17.5–18.5 (17.9)
Amphw	5	5–6 (5.5)	5	3–3.5 (3.4)	3.5–4 (3.8)	3.5
Amphl	8.5	7–7.5 (7.5)	6.5	6–6.5 (6.3)	6–7.5 (6.7)	6
Amph%	23.3	26.5–29.1 (27.4)	22.7	26.5–27.5 (27.0)	21.7–24.9 (23.7)	17.2–19.8 (18.5)
ph	160.5	126–148.5 (137.5)	137.5	84.5–96.5 (90.5)	95–123.5 (105.6)	111 (1)
MdCAT				19.5–20.5 (20.0)	19–25.5 (22.4)	
SdCATa	25.5	25–26.5 (25.9)	27			25.5–26 (25.6)
SdCATp	43.5	33.5–39 (37.0)	35.5			30–31.5 (30.9)
LdCAT					24.5–25.5 (24.9)	27–28 (27.4)
SlCATa	31	25.5–29.5 (27.1)	28			
SlCATp	36.5	32.5–35 (33.6)	39.5			
SlATa	56.5	54–56.5 (55.0)	52.5	32.5–35 (34.0)	34.5–41.5 (39.1)	40–42.5 (41.1)
SlATp	35.5	33.5–36.5 (35.4)	38.5	24–25.5 (24.8)	22.5–26 (24.1)	26.5–29 (27.8)
SvATa	39	35.5–39 (36.9)	38.5			
SvATp	19.5	19.5–22 (20.9)	23.5			
MvATa						30–33 (31.5)
MvATp						17–19.5 (18.1)
Corn–set	10	10–12.5 (10.7)				
tail	165	121–148.5 (138.9)	123	56–60.5 (58.2)	95.5–75 (69.8)	86–91 (88,3)
tmr	37.5	36–36.5 (36.2)	43.5	24.5	29.5–34 (31.5)	35–38 (36.3)
mbd ph	49	42–46.5 (43.8)	41	26.5–29.5 (27.9)	32–37 (34.3)	35.5–46.5 (41.1)
mbd	65	35.5–64.5 (50.9)	61	20.5–21 (20.9)	25.5–33.5 (29.1)	36–40.5 (38.5)
(mbd)	16.5	15.5–19 (17.7)	16	15	15–16.5 (15.7)	15–17.5 (16.3)
mbd/(mbd)	3.9	2.3–3.5 (2.8)	3.8	1.4	1.7–2.0 (1.9)	2.3–2.5 (2.4)
abd	29.5	27–31 (29.4)	17	13.5–15 (14.3)	15–16.5 (15.9)	18–31 (24.4)
spic	85	79.5–85 (82.9)				
gub	24.5	20.5–25 (23.0)				
V%			60.2			
a	25.1	23.7–37.1 (29.6)	23.2	21.9–22.6 (22.2)	21.1–24.9 (22.7)	26.7–31.1 (28.9)
b	10.1	10.3–10.6 (10.5)	10.3	4.7–5.7 (5.2)	6.1–6.3 (6.2)	10.2 (1)
c	9.9	9.9–10.9 (10.4)	11.5	7.9–8.1 (8.0)	8.6–10.2 (9.4)	12.4–12.7 (12.5)

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.

region conspicuously narrow. Body width gradually increasing along pharynx until reaching maximal pharyngeal width immediately anterior to pharyngeal bulb (Fig. 2B). Width minimal immediately anterior to intestine. More posteriorly, body very slender but gradually increasing in width until maximal width at level of vesicula seminalis. Posteriorly to vesicula seminalis, body width constant, then decreasing between corniform setae and tail. Tail conico-cylindrical. Swollen pharyngeal region 11.9–12.5% of total body length. Body with fine transverse striation, hereafter specified as 'annulation'. Broadest annules immediately posterior to head capsule, finest annules at level of testis. All annules smooth. Posterior body region often littered with fine detritus.

CAT (14–16) arranged in four longitudinal rows: two laterodorsal rows consisting of two tubes, and two subdorsal rows of 5–6 tubes (Fig. 2B). CAT slender but strongly built, with enlarged base, gradually decreasing in width up to the slightly swollen, fusiform tip. Anteriormost tubes in all four rows on annules 4–6. Posteriormost tubes in laterodorsal rows on annules 9–11, and in subdorsal rows on annules 23–32. Robust PAT with swollen base and well-developed bell-shaped tip, arranged in two rows of 9–12 SlAT and two subventral rows converging towards posterior, together consisting of 24–28 SvAT. Total number of PAT 48–51. Width of anteriormost SlAT 1.8–2.7 μm at 10 μm from base of tube. PAT gradually decreasing in length towards posterior. Glands associated with PAT situated either on right or on left side of vas deferens. Each gland with duct connecting it to PAT. Anteriormost PAT situated at 73.6–78.5% of body length. Region with PAT taking up 7.9–8.6% of total body length.

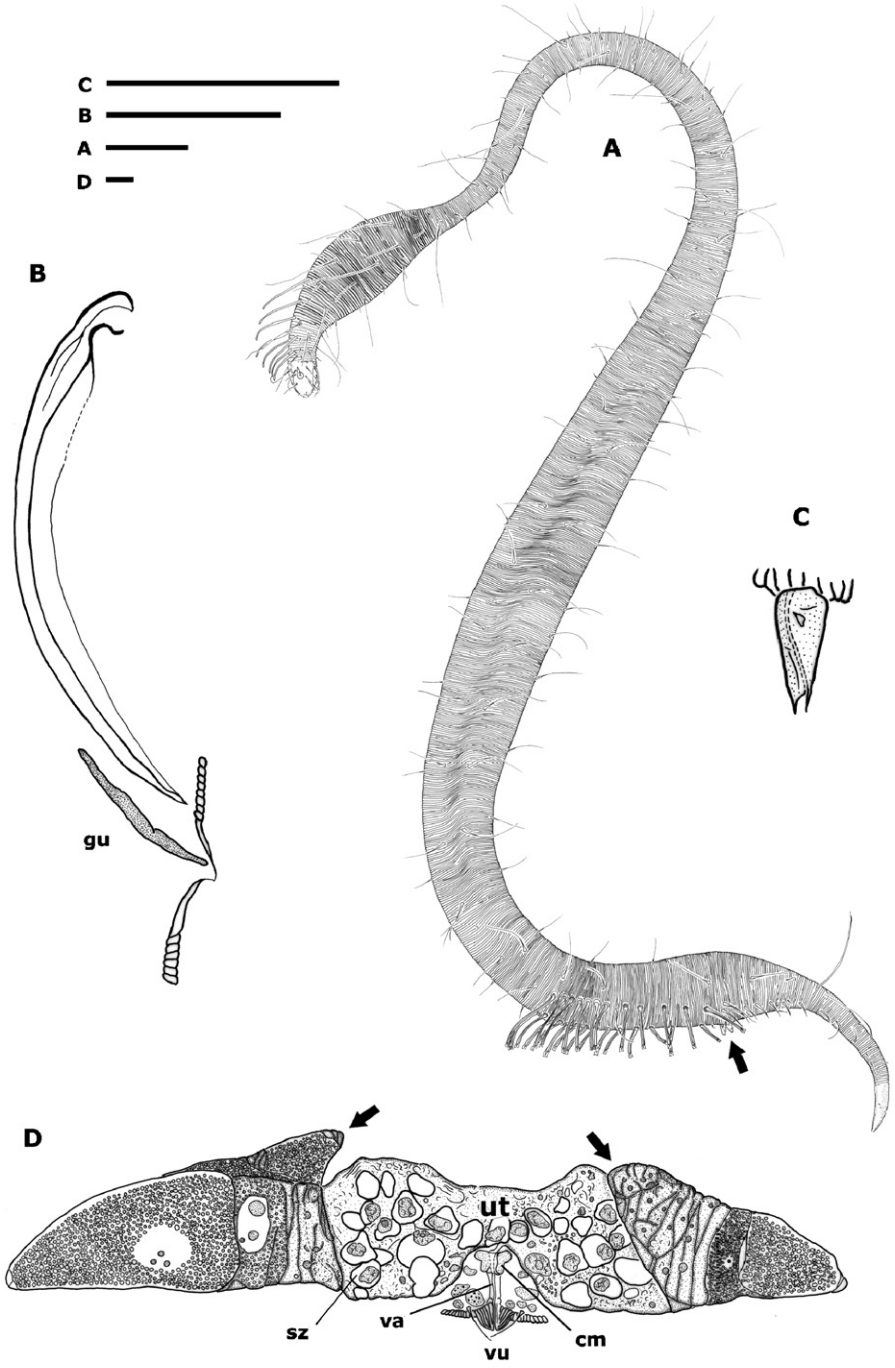

Fig. 1. *Cygnonema verum* sp. n. (A) Holotype male, external habitus; arrow indicates position of corniform setae. (B) Paratype male, spicule and gubernaculum. (C) Paratype male, corniform seta. (D) Allotype female, reproductive system; arrows indicate distal tips of ovaria. cm = contractor muscle, gu = gubernaculum, sz = spermatozoon, ut = uterus, va = vagina, vu = vulva. Scale bars = 20 μm.

Somatic setae in pharyngeal region arranged in 12 rows: one mediodorsal row of short setae, two subdorsal and two laterodorsal rows of long setae, two mediolateral rows of short setae, two lateroventral and two subventral rows of long setae, and one medioventral row of short setae (Fig. 2B). Some pores may be present between laterodorsal and mediolateral rows. Body between pharyngeal region and region of PAT with one mediodorsal row, two laterodorsal rows, two lateroventral rows and one medioventral row of long somatic setae. Lateroventral setae alternately long and short. In region of PAT somatic setae arranged in one mediodorsal row, two sublateral rows in dorsal sector, and two sublateral rows in line with SlAT. At level of

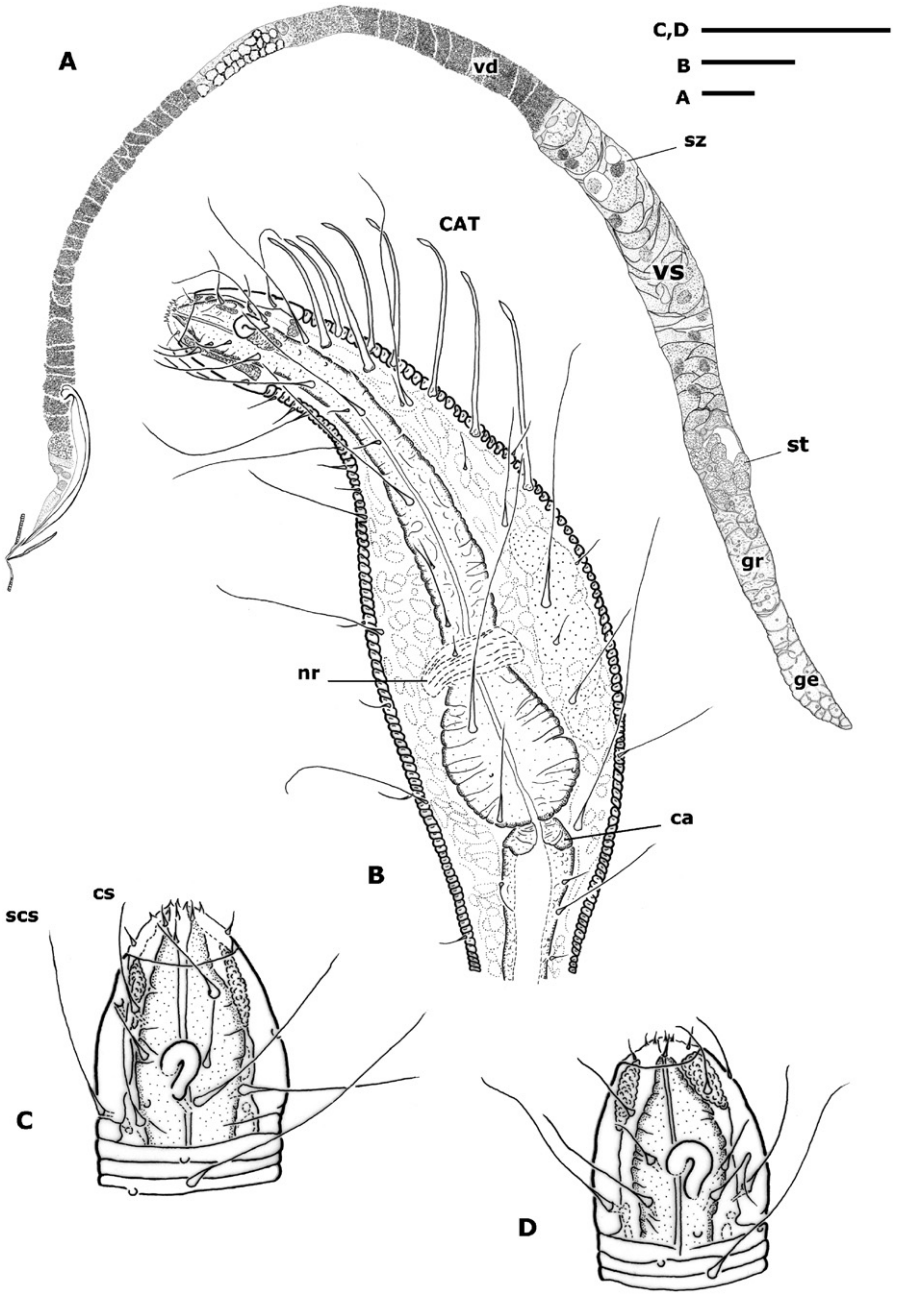

Fig. 2. *Cygnonema verum* sp. n. (A) Paratype male, reproductive system. (B) Holotype male, head capsule and pharynx. (C) Allotype female, head capsule. (D) Paratype male, head capsule. ca = cardia, CAT = cephalic adhesion tube, cs = cephalic seta, ge = germinal zone, gr = growth zone, nr = nerve ring, scs = subcephalic seta, st = spermatid, sz = spermatozoon, vd = vas deferens, vs = vesicula seminalis. Scale bars = 20 μm.

corniform setae one or two sublateral setae and one subventral seta on each side. Two or four subventral setae between this subventral seta and cloacal opening on each side. On each side, one subventral seta at level of cloacal opening. One small lateroventral seta may be present anterior to cloacal opening on each side. Tail with four or six subventral setae, two very long subdorsal setae (broken off in holotype; 57 and 66.5 μm in paratype male), and several tiny subdorsal setae on each side. Tail tip on each side with one lateroventral and one tiny subdorsal seta.

Head capsule smooth, bullet-shaped; labial region protruded (Fig. 2D). Head capsule length 16.1–16.9% of pharynx length; head capsule width 42.1–47.0% of pharynx width. Labial region with numerous small rod-like protrusions. Six small setiform external labial sensilla, four cephalic setae, and 15–18 subcephalic setae. Subcephalic setae on each side located subdorsally,

subventrally and at both sides of amphidial fovea. Additional setae may occur scattered on head capsule. Amphidial fovea question mark-shaped, with longer dorsal arm, located centrally on head capsule. Length of amphidial fovea 30.9–34.6% of head capsule length. Buccal cavity tiny, elongated. Teeth absent. Anterior part of head capsule with gold-coloured granules. Anterior part of pharynx long and cylindrical; pharynx with well-developed terminal bulb and slight swellings at level of head capsule and immediately anterior to terminal bulb. Large nerve ring (Fig. 2B, nr) between both posteriormost swellings. Terminal bulb without thickened lumen wall. Cardia (Fig. 2B, ca) short. Intestine granular, with inconspicuous or thin brush border. Cloacal flap present (Fig. 1B).

Male reproductive system located ventrally to intestine, monorchic (single testis), with outstretched testis extending far anteriorly (i.e. tip of testis located at 40.7–45.2% of total body length) (Fig. 2A). Germinal zone (Fig. 2A, ge) granular, with developing spermatogonia. Growth zone (Fig. 2A, gr) with several compact, fully grown spermatids (Fig. 2A, st) with irregular border, 10 μm in diameter on average, without perceptible nucleus. Vesicula seminalis (Fig. 2A, vs) elongated, with large (19 μm on average), irregular spermatozoa (Fig. 2A, sz). Each spermatozoon with marginal cytoplasm, well-developed halo and granular nucleus. Vas deferens (Fig. 2A, vd) slender and granular. Spicule length 5.5–6% of total body length. Spicules large, slender and curved (Figs. 1B, 2A). Capitulum set off, knob-like. Velum conspicuous, starting at base of capitulum. Gubernaculum (Fig. 1B, gu) parallel to spicules. Two large subventral corniform setae with open tip and internal duct, located immediately behind posteriormost SvAT (Fig. 1A, C).

Tail conico-cylindrical, with 66–81 complete annules (81 in holotype), including tail tip. Tail tip 22.7–29.9% of tail length, dorsally with numerous tiny vacuoles, sometimes with one incomplete annule dorsally (e.g. in holotype) or two incomplete annules ventrally. Caudal glands extending up to halfway spicule length.

Female

Habitus similar to male, but body clearly more enlarged at level of female reproductive system. Swollen pharyngeal region 14.6% of total body length. Annulation as in male.

CAT morphology as in male; CAT arranged in two laterodorsal rows consisting of two tubes and two subdorsal rows of five tubes. Anteriormost LdCAT on annules 4 and 5, posteriormost LdCAT on annules 7 and 10. Anteriormost SdCAT on annule 4, posteriormost SdCAT on annule 23. PAT morphology as in male; PAT arranged in two rows of 11–12 SlAT and two subventral rows converging towards posterior, together consisting of 25 SvAT. Total number of PAT 48. Width of anteriormost SlAT 1.9 μm at 10 μm from base of tube. PAT gradually decreasing in length towards posterior.

Somatic setae in pharyngeal region, region anterior to PAT and region of PAT arranged as in male, except for presence of subventral setae instead of medioventral setae around vulva. Between posteriormost SvAT and anal opening one medioventral seta, two latero-ventral-subventral setae, two sublateral setae in dorsal sector, and one subdorsal seta on each side. Tail with two short subdorsal setae, two very long subdorsal setae (51 and 63 μm in allotype female), and two short subventral setae on each side. Tail tip on each side with one lateroventral and one tiny subdorsal seta.

Shape of head capsule as in male (Fig. 2C). Labial region protruded. Head capsule length 16.1% of pharynx length; head capsule width 50.7% of pharynx width. Four cephalic setae (Fig. 2C, cs) and 18 subcephalic setae (Fig. 2C, scs), arranged as in male. No sexual dimorphism in shape or location of amphidial fovea (Fig. 2C). Length of amphidial fovea 29.8% of head capsule length. Digestive system as in male. Anal flap present.

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. 1D). Anterior ovary reflexed along right side, posterior ovary reflexed along left side. Uterus (Fig. 1D, ut) with numerous sperm cells (Fig. 1D, sz) with condensed nucleus. Vulva (Fig. 1D, vu) bulged out. Vagina (Fig. 1D, va) bipartite, proximal part surrounded by contractor muscles (Fig. 1D, cm). Four paravulval setae.

Tail conico-cylindrical, with 54 complete annules, including tail tip. Tail tip 35.2% of tail length, dorsally with numerous tiny vacuoles. No incomplete annules.

Juveniles

First-stage juvenile. Not found.

Second-stage juvenile (Fig. 3A). Posterior body region not enlarged; slight pharyngeal swelling. Body finely annulated. All annules smooth, as in adults.

One slender, mediodorsal CAT with enlarged base and slightly swollen tip, located on annules 5–8. PAT slender, strongly cuticularised, with enlarged base and bell-shaped tip, arranged in two sublateral longitudinal rows, each consisting of two tubes. Width of anteriormost SlAT 1.8–1.9 μm at 10 μm from 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, all with long setae. Between pharyngeal region and region of PAT two laterodorsal rows and two lateroventral rows of relatively long setae. In region of PAT, relatively long somatic setae in two sublateral rows in dorsal sector.

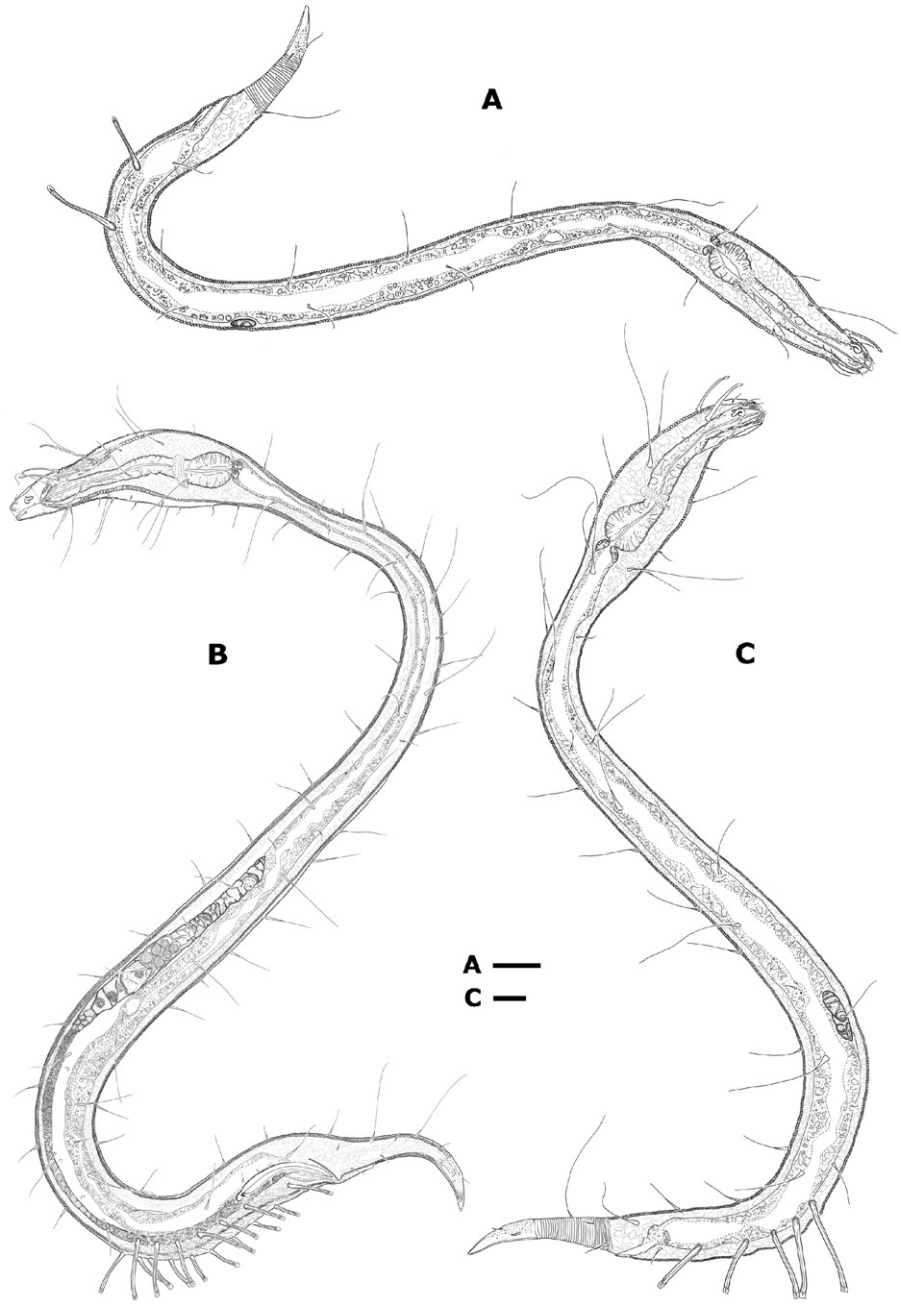

Fig. 3. *Cygnonema verum* sp. n., juvenile habitus. (A) Paratype, second stage. (B) Paratype, fourth stage. (C) Paratype, third stage. Scale bars = 20 μm.

Between posteriormost PAT and anus on each side one sublateral seta in dorsal sector and one lateroventral seta. Tail with one very long subdorsal seta on each side and one short, truncated lateroventral seta immediately anterior to tail tip. Tail tip with one short mediodorsal seta.

Shape of head capsule and shape of amphidial fovea as in adults. Head capsule length 12.5–17.5% of pharynx length; head capsule width 41.5–50.1% of pharynx width. Six setiform labial sensilla, four cephalic setae and two subcephalic setae: on each side of head capsule one seta situated dorsally to posterior end of amphidial fovea. Amphidial fovea located centrally on head capsule or slightly shifted to anterior. Length of amphidial fovea 41.8–53.7% of head capsule length.

Tail with 36–37 complete annules, including tail tip. Tail tip 40.7–43.6% of tail length, ornamented with numerous tiny vacuoles, and with 1–2 incomplete annules dorsally.

Third-stage juvenile (Fig. 3C). Pharyngeal and posterior body region more swollen than in second-stage juveniles; pharyngeal swelling and subsequent thin

region conspicuous. Body finely annulated. All annules smooth, as in adults.

Three slender CAT, broader at base and with slightly swollen tip: one mediodorsal tube and two laterodorsal tubes, all located on annules 6–10. PAT slender, strongly cuticularised, with enlarged base and bell-shaped tip, arranged in two sublateral longitudinal rows, each consisting of five tubes. Width of anteriormost SlAT 1.7–2.1 μm at 10 μm from base of tube.

Somatic setae in pharyngeal region arranged in eight rows: one mediodorsal row, two laterodorsal rows and two lateroventral rows with both long and short setae, two subventral rows with long setae, and one medioventral row with short setae. Body between pharyngeal region and region of PAT with one mediodorsal row, two laterodorsal rows and two lateroventral rows of relatively long setae. In region of PAT somatic setae in one mediodorsal row of relatively long setae and two sublateral rows of short setae in dorsal sector. Between posteriormost PAT and anus one mediodorsal seta and on each side one laterodorsal seta and one short sublateral seta in ventral sector, in line with PAT. One short lateroventral seta at level of anus. Tail with one short and one very long subdorsal seta on each side. Tail tip on each side with one short subdorsal seta and one lateroventral truncated seta or pore.

Shape of head capsule and shape of amphidial fovea as in adults. Head capsule length 13.6–18.2% of pharynx length; head capsule width 42.6–50% of pharynx width. Six setiform labial sensilla, four cephalic setae and two subcephalic setae, arranged as in second-stage juveniles. Amphidial fovea located centrally on head capsule or slightly shifted to posterior. Length of amphidial fovea 36.7–44.5% of head capsule length.

Tail with 34–43 complete annules, including tail tip. Tail tip 42.3–50.1% of tail length, ornamented with numerous tiny vacuoles and either without incomplete annules, with 1–3 incomplete annules dorsally or with one incomplete annule ventrally.

Fourth-stage juvenile. (Fig. 3B). Posterior enlargement less pronounced than in adults. All annules smooth, as in adults.

Six fine CAT with swollen base and slightly enlarged tip: four subdorsal tubes arranged in two longitudinal rows and two laterodorsal tubes at level of anteriormost subdorsal CAT. Anteriormost laterodorsal CAT on annule 8, anteriormost subdorsal CAT on annule 9, posteriormost subdorsal CAT on annules 18–22. PAT robust, with slightly enlarged base and well-developed bell-shaped tip, arranged in three rows: two sublateral rows of 6–7 tubes and one medioventral row of nine tubes. Total number of PAT 22–23. Width of anteriormost SlAT 2.3 μm at 10 μm from base of tube.

Somatic setae in pharyngeal region arranged in 10 rows: one mediodorsal row of short setae, two subdorsal and two laterodorsal rows of long setae, two lateroventral and two subventral rows of long setae, and one medioventral row of short setae. Body between pharyngeal region and region of PAT with one mediodorsal row, two laterodorsal rows, two lateroventral rows and one medioventral row of long somatic setae, as in adults. In region of PAT, somatic setae also arranged as in male. Between posteriormost PAT and anus, mediodorsal, laterodorsal, sublateral, and lateroventral setae may be present, as well as one lateroventral seta immediately anterior to anus. Tail with two subventral setae, two very long subdorsal setae and several tiny subdorsal setae on each side. Tail tip on each side with one lateroventral and one subdorsal pore.

Shape of head capsule and shape of amphidial fovea as in adults. Head capsule length 16.5% of pharynx length; head capsule width 42.6–49.2% of pharyngeal width. Six setiform labial sensilla, four cephalic setae and four subcephalic setae: on each side of head capsule one seta situated dorsally and one seta situated ventrally to amphidial fovea. Amphidial fovea located centrally on head capsule or slightly shifted to posterior. Length of amphidial fovea 32.4–34.7% of head capsule length. Digestive system as in adults. Male reproductive system already well-developed, especially in moulting specimen. Several spermatids and spermatozoa already present in this specimen.

Tail with 42–46 complete annules, including tail tip. Tail tip 38.3–44.2% of tail length, ornamented with numerous tiny vacuoles, and with either two incomplete annules dorsally or two incomplete annules ventrally. Caudal glands may be unclear, extending in front of anus.

Diagnosis

Cygnonema verum sp. n. is characterised by (1) general body shape (slender with pronounced enlargements at level of pharynx), (2) body size (1325–1625 μm in male, 1415 μm in female), (3) length of head capsule relative to length of pharynx (16.1–16.9% in male, 16.1% in female), (4) width of head capsule relative to width of pharynx (42.1–47.0% in male, 50.7% in female), (5) 14–16 CAT, (6) anteriormost CAT located on annules 4–6, (7) 48–51 PAT, (8) setiform external labial sensilla, (9) 15–18 subcephalic setae, (10) amphidial fovea located centrally on head capsule, (11) spermatozoa with well-developed halo and only small amount of cytoplasm, (12) capitula of spicules knob-like, (13) two large subventral corniform setae in males, and (14) male tail tip 22.7–29.9% of tail length.

For differential diagnosis, see the corresponding text section after the description of the following species.

Cygnonema belgicae sp. n.

(Figs. 4–9)

Etymology. The species is named in honour of the crew of the R.V. Belgica, in appreciation of their ready

help on several sampling campaigns. The specific epithet is to be treated as a noun in the genitive case for the purposes of nomenclature.

Voucher material. Holotype male on slide RI 677 (KBIN): Porcupine Seabight, Belgica mound province, 51°24′49.4″N 11°45′55.9″W, 17/06/2000, depth 1000 m.

Paratypes (collecting data as for holotype): Allotype female on slide RIT 742 (KBIN); one male on slide RI 677 (KBIN); two females on slides UGMD 104093 (one specimen; UGent), 2008.610 (one specimen; NHM); two second-stage juveniles on slides UGMD 104093 (one specimen; UGent), RIT 743 (one specimen; KBIN); two third-stage juveniles on slides UGMD 104093 (one specimen; UGent), RI 677 (one specimen; KBIN).

Additional specimens. Porcupine Seabight, Belgica mound province, 51°24′48.2″N 11°45′55.4″W, 17/06/2000, depth 1005 m: Two males on slides UGMD 104129 (one specimen; UGent), 2008.567 (one specimen; NHM); one first-stage juvenile on slide UGMD 104135 (UGent); two second-stage juveniles on slides UGMD 104130 (one specimen; UGent), UGMD 104134 (one specimen; UGent); one third-stage juvenile on slide UGMD 104029 (UGent); three fourth-stage juveniles on slides UGMD 104127 (two specimens; UGent), UGMD 104128 (one specimen; UGent). Specimens from Porcupine Seabight, Belgica mound province, 51°25′7.7″N 11°46′9.3″W, 07/05/2001, depth 972 m: One male on slide UGMD 104136 (UGent); one fourth-stage juvenile on slide RIT 740 (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. At other localities the species also occurred on dead sponge skeletons (*Aphrocallistes bocagei* Schultze) and within the underlying sediment.

Relative abundance. At the type locality, *C. belgicae* constituted 0.71% of the total nematode community.

Morphological measurements. See Table 2.

Male

Slender S-shaped body, enlarged at level of pharynx and along reproductive system (Figs. 4A, 8A). Head capsule and anterior part of pharyngeal region strikingly narrow. Body width gradually increasing along pharynx, reaching maximal pharyngeal width immediately anterior to nerve ring. Posterior to this point, body width gradually decreasing again; body width minimal immediately anterior to intestine. More posteriorly, body very narrow, slightly increasing in width until reaching maximal width at level of vesicula seminalis. Posterior to vesicula seminalis, body remaining wide, decreasing again behind posteriormost SvAT. Tail slender, conico-cylindrical. Swollen pharyngeal region 13.0–15.1% of total body length. Body finely annulated. Broadest annules in pharyngeal region, finest annules at level of testis. All annules smooth. Posterior body region often littered with fine detritus (Fig. 8C).

CAT (12) arranged in four longitudinal rows: two laterodorsal rows consisting of two tubes and two subdorsal rows of four tubes (Figs. 5D, 8E, 9A). CAT slender, with enlarged base, gradually decreasing in width towards distal end, except for slightly swollen tip. Anteriormost tubes in laterodorsal rows on annules 7–10, posteriormost tubes in laterodorsal rows on annules 13–16. Anteriormost tubes in subdorsal rows on annules 11–14, posteriormost tubes in subdorsal rows on annules 26–32. Robust PAT with swollen base and well-developed bell-shaped tip, arranged in two rows of 8–11 SlAT and two subventral rows converging towards posterior, together consisting of 17–20 SvAT (Figs. 4A, 8C, 9E). Total number of PAT 34–41. Width of anteriormost SlAT 2.0–2.3 μm at 10 μm from base of tube. PAT gradually decreasing in length towards posterior. Glands associated with PAT, situated either on right or on left side of vas deferens. Anteriormost PAT situated at 71.9–76.9% of body length. Region with PAT taking up 7.8–11.8% of total body length.

Somatic setae in pharyngeal region arranged in 12 rows: one mediodorsal row of short setae, two subdorsal rows (only one seta on each side) and two laterodorsal rows of long setae, two mediolateral rows of short setae, two lateroventral and two subventral rows of long setae, and one medioventral row of short setae (Fig. 5D). Mediolateral setae not always in one row. Body between pharyngeal region and region of PAT with one mediodorsal row, two laterodorsal rows, two lateroventral rows and one medioventral row of long somatic setae. In region of PAT, somatic setae arranged in one mediodorsal row and two sublateral rows in dorsal sector. Between posteriormost SlAT and cloacal opening three lateroventral-subventral somatic setae on each side. Tail with two or three subventral setae, two very long subdorsal setae (46.5 and 59 μm in holotype) and several tiny subdorsal setae on each side. Tail tip on each side with two lateroventral setae and one tiny subdorsal seta (Fig. 9F).

Head capsule smooth, bullet-shaped; labial region protruded (Figs. 5A, 9C). Head capsule length 12.2–14.8% of pharynx length; head capsule width 36.7–41.7% of pharynx width. Labial sensilla short, inconspicuous. Four cephalic setae and 4–6 subcephalic setae: on each side one laterodorsal and one lateroventral seta; additional setae may be present. Amphidial fovea loop- or question mark-shaped (question mark-shaped in holotype) with longer dorsal arm, located at or near posterior border of head capsule. Length of amphidial fovea 32.2–40.4% of head capsule length. Buccal cavity tiny and elongated. Teeth absent. Anterior

Table 2. Morphological measurements in *Cygnonema belgicae* sp. n.

	Male holotype	Other males ($n = 8$)	Female allotype	Other females ($n = 7$)	Juvenile stage I ($n = 1$)	Juvenile stage II ($n = 10$)	Juvenile stage III ($n = 8$)	Juvenile stage IV ($n = 7$)
L	1095	980–1195 (1100)	1275	1055–1305 (1215)	350	260–460 (385)	475–760 (590)	745–980 (840)
Hdw	12.5	12.5–13.5 (13.2)	13	13–13.5 (13.4)	7.5	10–11.5 (10.5)	10.5–12.5 (11.4)	11.5–13.5 (12.4)
Hdl	17.5	15–17 (15.8)	17	15–16.5 (15.6)	3.5	12–14 (13.3) [9]	12.5–15 (14.0)	13.5–17 (15.2)
Bda					9.5			
Amphw	4.5	3–4.5 (3.9)	3.5	3.5–4 (3.6)	3	3–4 (3.4) [9]	3–4 (3.5)	3.5–4 (3.7)
Amphl	6	5–6.5 (5.5)	5	4.5–5.5 (5.0)	4	4.5–6 (5.1)	4.5–5 (4.9)	4.5–5 (4.8)
Amph%	34.9	24.4–34.7 (29.7)	27.6	26.3–27.7 (27.2)	29.5	28.7–38.4 (32.3) [9]	26.9–35.1 (30.7)	26.9–34.2 (29.7)
ph	121	107–127 (119.3)	134.5	116–133.5 (126.1)	77	62.5–84 (76.7)	73.5–101 (91.0)	103–126.5 (111.4)
MdCAT						17.5–21 (18.5) [9]	13.5–20 (18.0) [7]	
SdCATa	16	16–19.5 (18.0)	15.5	17–19 (17.9) [6]				20–22 (21.0) [6]
SdCATp	28	25–29.5 (27.4)	28	25.5–28.5 (27.5)				
LdCAT							13.5–19.5 (17.3)	16.5–23 (20.2) [6]
SlCATa	17	17–20.5 (18.5)	17	15.5–20 (18.2) [5]				
SlCATp	23	20–23 (21.5)	21	18–23.5 (21.3) [6]				
SlATa	49	44.5–50 (47.6)	50.5	47–54 (51.7)		34–38.5 (36.5) [9]	30–40.5 (36.6)	41–44 (42.8)
SlATp	27	27.5–32 (29.1)	26.5	23–30 (26.2)		25–29.5 (27.5) [9]	20–24.5 (22.2)	22.5–25.5 (23.7)
SvATa	38.5	33.5–39 (36.4)	39.5	35–40 (37.7)				
SvATp	19	15–20 (17.8)	17	14–19 (17.6) [6]				
MvATa								28.5–35 (33.3)
MvATp								14.5–18.5 (16.6)
tail	122	120–136.5 (128.0)	122.5	111–154 (136.4)	49	44.5–62.5 (53.9) [8]	57–77 (69.8)	79.5–117.5 (94.1)
tmr	42.5	40.5–47 (42.8)	44	43–50.5 (46.1)	6.5	22–25.5 (23.5) [9]	27–32.5 (31.1)	33.5–38.5 (36.9)
mbd ph	33.5	32–35 (33.7)	33.5	31.5–39 (33.6)	21	18–25 (21.2)	22.5–29.5 (26.3)	27.5–33.5 (30.1)
mbd	31.5	31.5–40.5 (36.4)	49.5	40–57.5 (48.0)	15	12.5–21 (16.8)	18.5–26.5 (22.2)	22–33.5 (28.7)
(mbd)	13	12.5–14 (13.2)	13.5	13–14 (13.3)	11.5	10–13.5 (11.9)	12–14.5 (12.8)	12–14.5 (13.2)
mbd/(mbd)	2.4	2.4–3.0 (2.8)	3.7	3.0–4.4 (3.6)	1.3	1.2–1.6 (1.4)	1.5–2.0 (1.7)	1.8–2.5 (2.2)
abd	18.5	18–20.5 (19.3)	16	14–17 (15.5)	13.5	9.5–14 (12.1) [8]	9.5–15 (12.9)	12–21.5 (15.4)
spic	57.5	54–64 (58.8)						
gub	17.5	15.5–19 (17.3)						
V%			63.2	57.5–61.9 (59.7)				
a	35.1	28.4–31.8 (30.2)	25.7	22.5–28.0 (25.5)	23.4	20.6–26.9 (23.1)	24.7–30.2 (26.6)	25.0–34.0 (29.5)
b	9.1	8.5–9.9 (9.2)	9.5	8.6–10.3 (9.7)	4.5	4.1–5.8 (5.0)	5.6–8.3 (6.5)	6.5–9.3 (7.5)
c	9	7.6–9.3 (8.6)	10.4	8.4–10.6 (9.0)	7.1	5.8–8.3 (7.2) [8]	6.9–9.9 (8.5)	8.3–9.7 (8.9)

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.

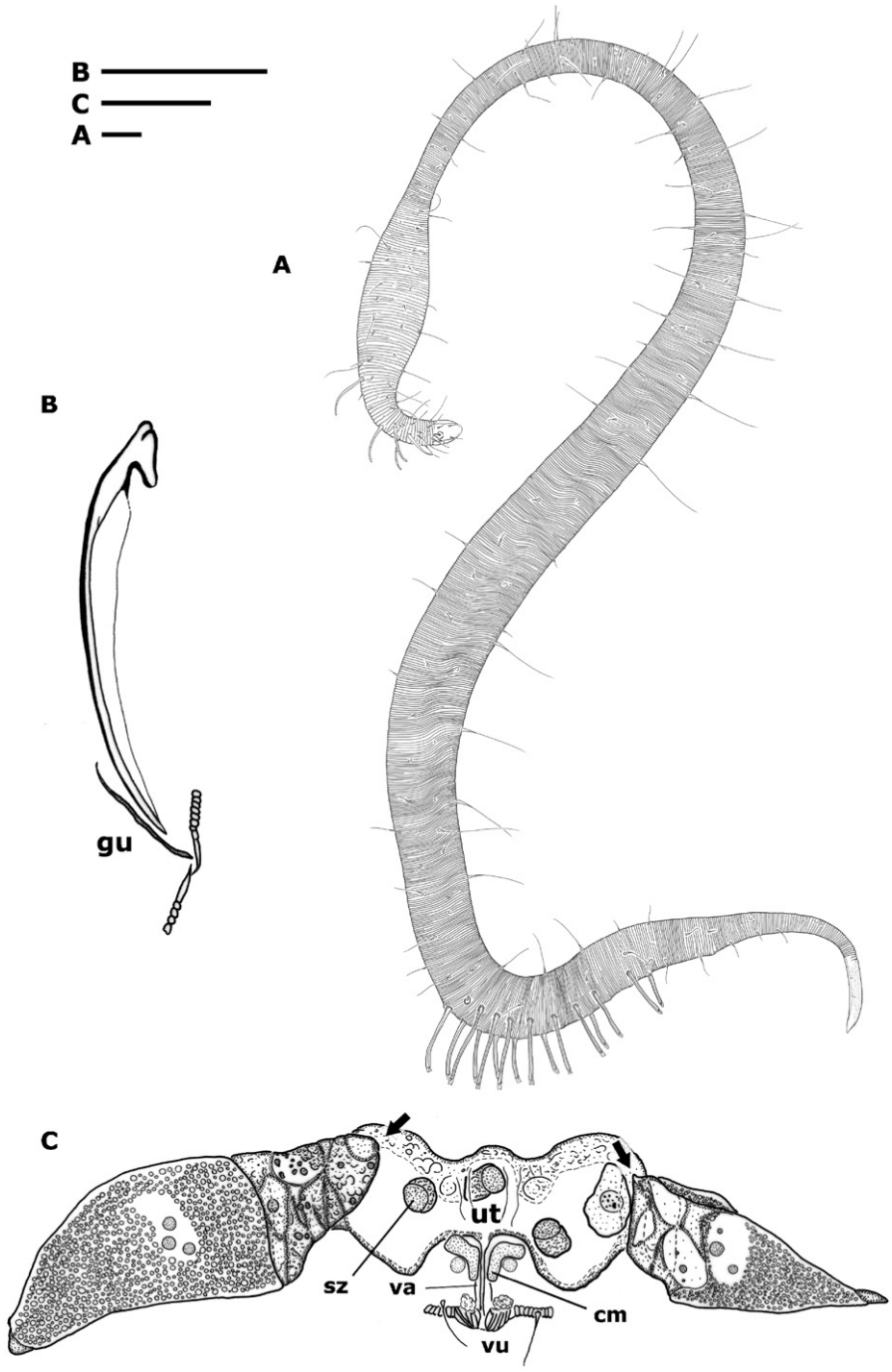

Fig. 4. *Cygnonema belgicae* sp. n. (A) Holotype male, external habitus. (B) Additional male, spicule and gubernaculum. (C) Additional female, reproductive system; arrows indicate distal tips of ovaria. cm = contractor muscle, gu = gubernaculum, sz = spermatozoon, ut = uterus, va = vagina, vu = vulva. Scale bars = 20 μm.

part of head capsule with gold-coloured granules. Anterior part of pharynx long and cylindrical; pharynx with well-developed terminal bulb (Fig. 5D). Large nerve ring (Fig. 5D, nr) immediately anterior to pharyngeal bulb. Terminal bulb without thickened lumen wall. Cardia (Fig. 5D, ca) short. Intestine granular, with inconspicuous or thin brush border. Cloacal flap present or absent (absent in holotype).

Male reproductive system located ventrally to intestine, monorchic (single testis), with outstretched testis extending far anteriorly (i.e. tip of testis located at 41.5–50.9% of total body length) (Fig. 5C). Germinal zone (Fig. 5C, ge) granular, with developing spermatogonia. Growth zone (Fig. 5C, gr) with several compact, fully grown spermatids (Fig. 5C, st) with irregular border, 10.5 μm in diameter on average, without

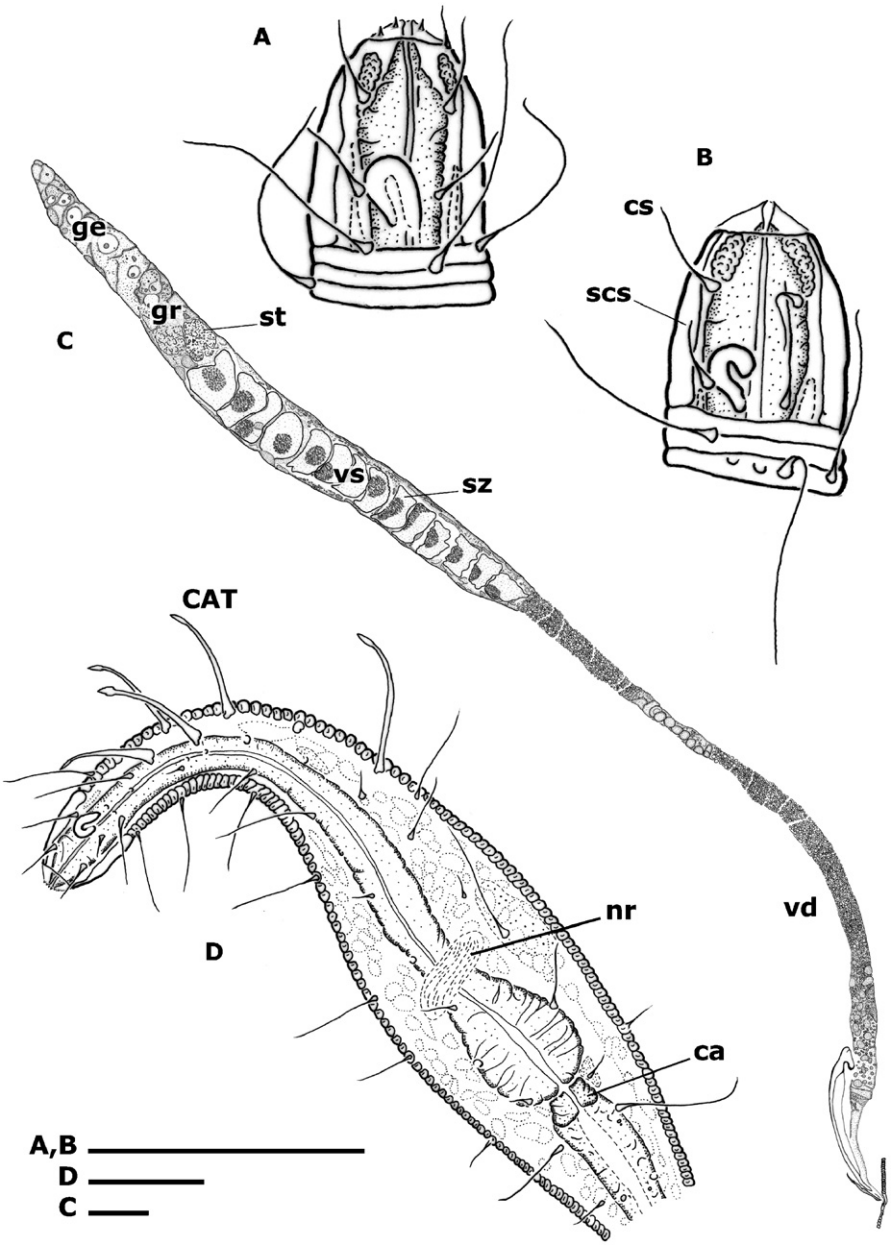

Fig. 5. *Cygnonema belgicae* sp. n. (A) Additional male, head capsule. (B) Additional female, head capsule. (C) Additional male, reproductive system. (D) Holotype male, head capsule and pharynx. ca = cardia, CAT = cephalic adhesion tube, cs = cephalic seta, ge = germinal zone, gr = growth zone, nr = nerve ring, scs = subcephalic seta, st = spermatid, sz = spermatozoon, vd = vas deferens, vs = vesicula seminalis. Scale bars = 20 µm.

perceptible nucleus. Vesicula seminalis (Fig. 5C, vs) elongated, with large (15.5 µm on average) spermatozoa (Fig. 5C, sz), each with large amount of cytoplasm and granular nucleus. Vas deferens (Fig. 5C, vd) slender, granular. Percentage of spicule length to total body length 4.6–5.8%. Spicules large, slender, gently curved (Fig. 4B). Capitulum set off, beak-shaped. Velum conspicuous, starting at base of capitulum. Gubernaculum (Fig. 4B, gu) parallel to spicules. No corniform seta.

Tail conico-cylindrical, with 75–81 complete annules (78 in holotype), including tail tip. Tail tip 31.0–36.6% of tail length, dorsally with numerous tiny vacuoles, sometimes with 1–2 incomplete annules dorsally (two in holotype) or two incomplete annules ventrally. Caudal glands extending up to halfway spicule length, ending in a single, common outlet (Fig. 9F).

Female

Habitus as in male, but slightly more enlarged at level of reproductive system (Fig. 8B). Swollen pharyngeal region 12.3–17.3% of total body length. Body finely annulated. Annulation as in male.

Arrangement and structure of CAT as in male (Fig. 9B). Anteriormost tubes in laterodorsal rows on annules 8–13, posteriormost tubes in laterodorsal rows on annules 13–18. Anteriormost tubes in subdorsal rows on annules 9–15, posteriormost tubes in subdorsal rows on annules 28–33. PAT structured as in male, arranged in two rows of 8–13 SlAT and two subventral rows converging towards posterior, together consisting of 18–22 SvAT (Fig. 8D). Total number of PAT 37–45. Width of anteriormost SlAT 1.8–2.2 μm at 10 μm from base of tube. PAT gradually decreasing in length towards posterior.

Somatic setae in pharyngeal region, region anterior to PAT and region of PAT arranged as in male, except for presence of subventral setae instead of medioventral setae around vulva (Figs. 4C, 9H, vu). Between posteriormost SvAT and anal opening one medioventral seta, 2–3 lateroventral-subventral setae, one sublateral seta in dorsal sector, one subdorsal seta, and one mediodorsal seta on each side. Tail with several short subdorsal setae, two long subdorsal setae (broken off in allotype female; 37 and 51.5 μm in one paratype female), and one short subventral seta on each side. Tail tip on each side with one lateroventral and one subdorsal seta.

Shape of head capsule similar to that in male (Figs. 5B, 9D). Head capsule length 11.6–13.0% of pharynx length; head capsule width 34.9–42.1% of pharynx width. Four cephalic setae (Fig. 5B, cs) and 2–4 subcephalic setae (Fig. 5B, scs), arranged as in male. Shape and location of amphidial fovea as in male. Length of amphidial fovea 29–35% of head capsule length. Digestive system as in male. 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. 4C). Anterior ovary reflexed along right side, posterior ovary reflexed along left side. Uterus (Fig. 4C, ut) often with numerous sperm cells (Fig. 4C, sz), each with large amount of cytoplasm and condensed nucleus. Vagina (Fig. 4C, va) bipartite: proximal and distal part equally long; proximal part surrounded by contractor muscle (Fig. 4C, cm). Four paravulval setae.

Tail conico-cylindrical, with 65–74 complete annules (65 in allotype), including tail tip. Tail tip 31.8–38.7% of tail length, ornamented with numerous tiny vacuoles, sometimes with 1–3 incomplete annules ventrally (none in allotype). Caudal glands ending in a common outlet (Fig. 9G).

Juveniles

First-stage juvenile (Fig. 6A). Body width almost uniform, with only slight pharyngeal swelling. Body finely annulated, with smooth annules, as in adults.

Adhesion tubes absent. Only four somatic setae: on each side one mediolateral seta in pharyngeal region and one subdorsal seta at level of anus. Subdorsal setae broken off, only insertion sites visible. Head capsule short. Six labial sensilla: two dorsalmost sensilla large (3.8 μm in length) and hook-shaped; remaining sensilla shorter, triangular. Amphidial fovea small, circular in outline, located posterior to head capsule.

Tail with 61 complete annules, including tail tip. Tail tip short (12.8% of tail length), smooth, conical, with well-developed spinneret.

Second-stage juvenile (Fig. 6B). Body width almost uniform; only slight pharyngeal swelling. Body finely annulated, with smooth annules, as in adults.

One slender, mediodorsal CAT with enlarged base and barely swollen tip, located on annules 9–13. PAT slender, strongly cuticularised, with slightly enlarged base and bell-shaped tip, arranged in two sublateral longitudinal rows, each consisting of two tubes. Width of anteriormost SlAT 1.6–1.9 μm at 10 μm from base of tube.

Somatic setae in pharyngeal region arranged in six rows: one mediodorsal row with relatively long setae, two laterodorsal rows with long setae, two lateroventral rows with short and long setae, and one medioventral row with relatively long setae. Between pharyngeal region and region of PAT two laterodorsal rows and two lateroventral rows of relatively long setae. In region of PAT somatic setae in two sublateral rows of relatively long setae in dorsal sector. Between posteriormost PAT and anus on each side one sublateral seta in dorsal sector and one lateroventral seta. Tail with one very long subdorsal seta on each side and one short, truncated lateroventral seta immediately anterior to tail tip. This seta sometimes absent or located on tail tip. Tail tip also with one short mediodorsal seta.

Shape of head capsule and shape of amphidial fovea as in adults. Head capsule length 15.1–19.8% of pharynx length; head capsule width 43.9–58.0% of pharynx width. Two subcephalic setae: on each side of head capsule one seta situated dorsally to posterior end of amphidial fovea. Amphidial fovea located posteriorly on head capsule, sometimes near its posterior border. Length of amphidial fovea 33.2–43.0% of head capsule length.

Tail with 36–42 complete annules, including tail tip. Tail tip 35.1–52.5% of tail length, ornamented with numerous tiny vacuoles, either without incomplete annules, with two incomplete annules dorsally or with 1–2 incomplete annules ventrally.

Third-stage juvenile (Fig. 6C). Body shape comparable to adults, but with less pronounced posterior enlargement. Body finely annulated, with smooth annules, as in adults.

Three slender CAT, broader at base, gradually decreasing in width up to slightly swollen distal tip:

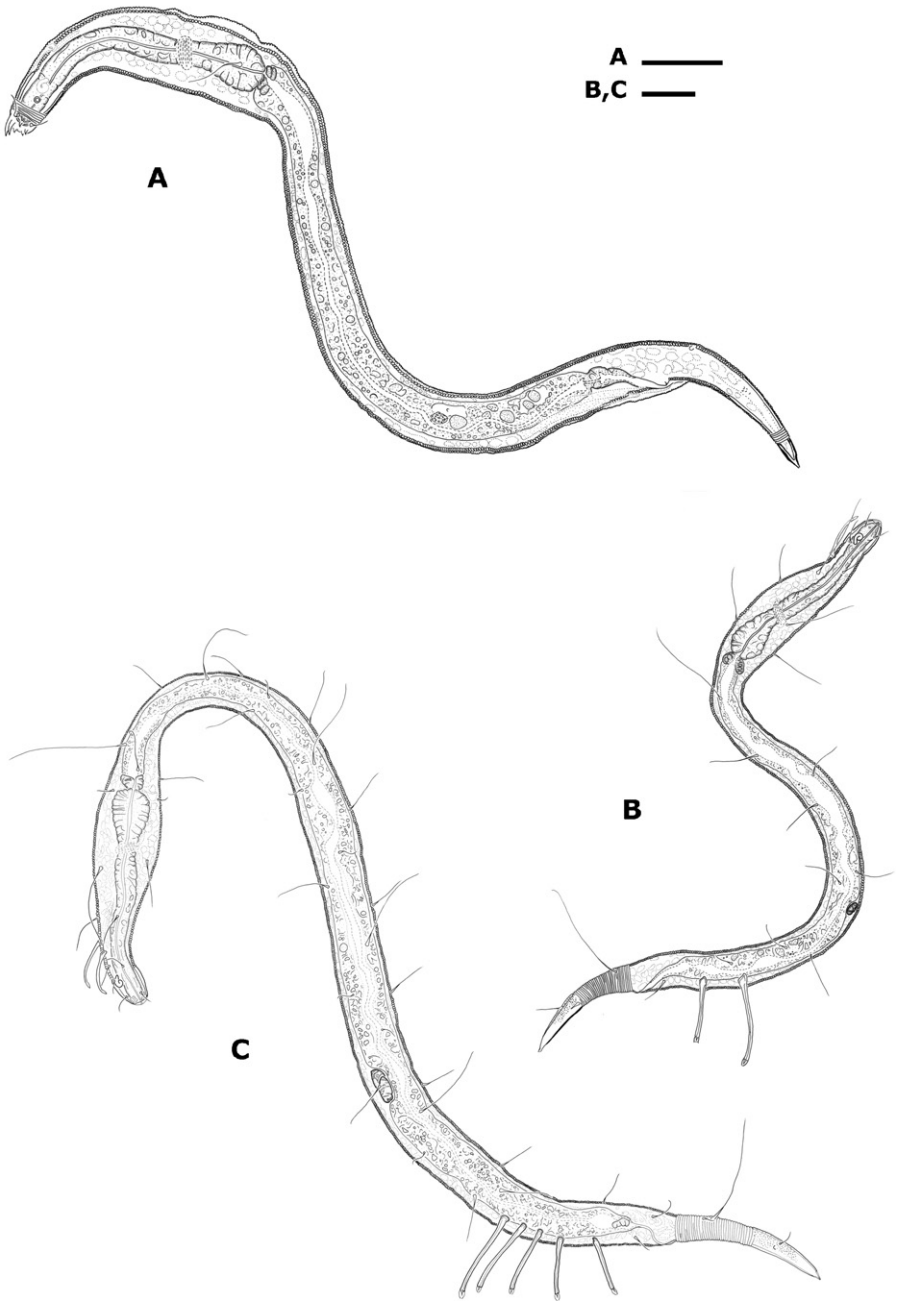

Fig. 6. *Cygnonema belgicae* sp. n., juvenile habitus. (A) Additional specimen, first stage. (B) Additional specimen, second stage. (C) Additional specimen, third stage. Scale bars = 20 μm.

one mediodorsal tube located on annules 14–16, two laterodorsal tubes located more anteriorly, on annules 11–12. PAT slender, strongly cuticularised, with enlarged base and bell-shaped tip, arranged in two sublateral longitudinal rows, each consisting of five tubes. Width of anteriormost SlAT 1.7–2.0 μm at 10 μm from base of tube.

Somatic setae in pharyngeal region arranged in eight rows: one mediodorsal row, two laterodorsal rows and two lateroventral rows with both long and short setae, two subventral rows with long setae, and one medioventral row with short setae. Body between pharyngeal region and region of PAT with one mediodorsal row, two laterodorsal rows and two lateroventral rows of relatively long setae. In region of PAT somatic setae in one mediodorsal row; two sublateral rows of short setae in dorsal sector may be present, but usually are inconspicuous or absent. One mediodorsal seta present between posteriormost PAT and anus. At level of anus, one laterodorsal and one lateroventral seta present on each side. Tail with one short and one very long subdorsal seta on each side.

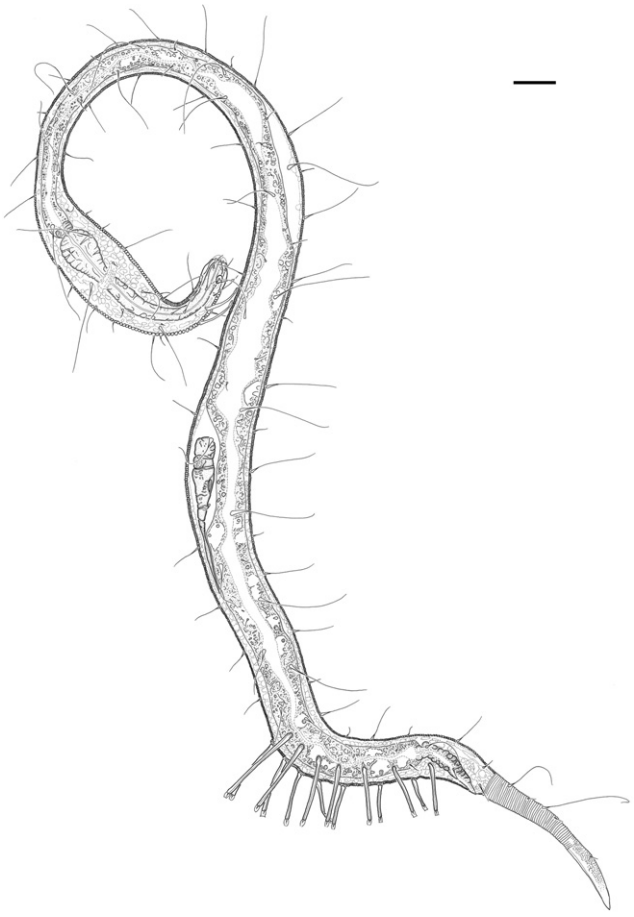

Fig. 7. *Cygnonema belgicae* sp. n., additional fourth-stage juvenile, habitus. Scale bar = 20 μm.

Tail tip on each side with one short subdorsal seta and one lateroventral pore.

Shape of head capsule and shape of amphidial fovea as in adults. Head capsule length 12.3–19.9% of pharynx length; head capsule width 38.3–48.0% of pharynx width. Two subcephalic setae: on each side of head capsule one seta situated dorsally to posterior end of amphidial fovea. Amphidial fovea located posteriorly on head capsule, near posterior border. Length of amphidial fovea 31.6–40.4% of head capsule length.

Tail with 39–47 complete annules, including tail tip. Tail tip 41.6–54.6% of tail length, ornamented with numerous tiny vacuoles, either without incomplete annules, with one incomplete annule dorsally or with 1–3 incomplete annules ventrally.

Fourth-stage juvenile (Fig. 7). Body slender as in adults, although slightly less enlarged posteriorly. All annules smooth, as in adults.

Four slender CAT, gradually decreasing in width towards slightly swollen tip: two subdorsal and two laterodorsal tubes. Laterodorsal tubes located on annules 10–13; subdorsal tubes always located more posteriorly, on annules 14–17. PAT slender but strongly cuticularised, with enlarged base and well-developed bell-shaped tip, arranged in two sublateral rows and one medioventral row; each row with seven tubes. Total number of PAT 21. Width of anteriormost SlAT 1.8–2.0 μm at 10 μm from base of tube.

Somatic setae in pharyngeal region arranged in 10 rows: one mediodorsal row of short setae, two subdorsal rows and two laterodorsal rows of long setae, two lateroventral and two subventral rows of long setae, and one medioventral row of short setae. Somatic setae between pharyngeal region and posteriormost PAT arranged as in adults. Between posteriormost SlAT and anus one mediodorsal seta and on each side one subdorsal seta and two lateroventral setae; subdorsal seta and posteriormost lateroventral seta situated immediately anterior to anus or at level of anus. Tail usually with one subventral seta, two very long subdorsal setae and several tiny subdorsal setae on each side. Tail tip on each side with one subdorsal seta and one lateroventral pore.

Shape of head capsule, shape and location of amphidial fovea as in adults. Head capsule length 10.7–15.4% of pharynx length; head capsule width 38.4–44.4% of pharynx width. Four subcephalic setae: on each side of head capsule one seta situated laterodorsally at level of amphidial fovea and one seta lateroventrally at posterior border of head capsule. Length of amphidial fovea 29.3–34.6% of head capsule length. Digestive system as in adults. Genital system in males long and slender; genital system in females small, although uterus and two ovaria already recognisable.

Tail with 52–60 complete annules, including tail tip. Tail tip 32.8–46.1% of tail length, ornamented with numerous tiny vacuoles, either with 1–3 incomplete annules dorsally or with 1–3 incomplete annules ventrally.

Diagnosis

Cygnonema belgicae sp. n. is characterised by (1) general body shape (slender with pronounced enlargements at level of pharynx), (2) body size (980–1195 μm in male, 1055–1305 μm in female, (3) length of head capsule relative to length of pharynx (12.2–14.8% in male, 11.6–13.0% in female), (4) width of head capsule relative to width of pharynx (36.7–41.7% in male, 34.9–42.1% in female), (5) 12 CAT, (6) anteriormost laterodorsal CAT located on annules 7–10 in male, on annules 8–13 in female, (7) 34–45 PAT, (8) 4–6 subcephalic setae in male, 2–4 subcephalic setae in female, (9) amphidial fovea located at or near posterior border of head capsule, (10) spermatozoa with large amount of cytoplasm, (11) capitulum beak-shaped, and (12) male tail tip 31.0–36.6% of tail length.

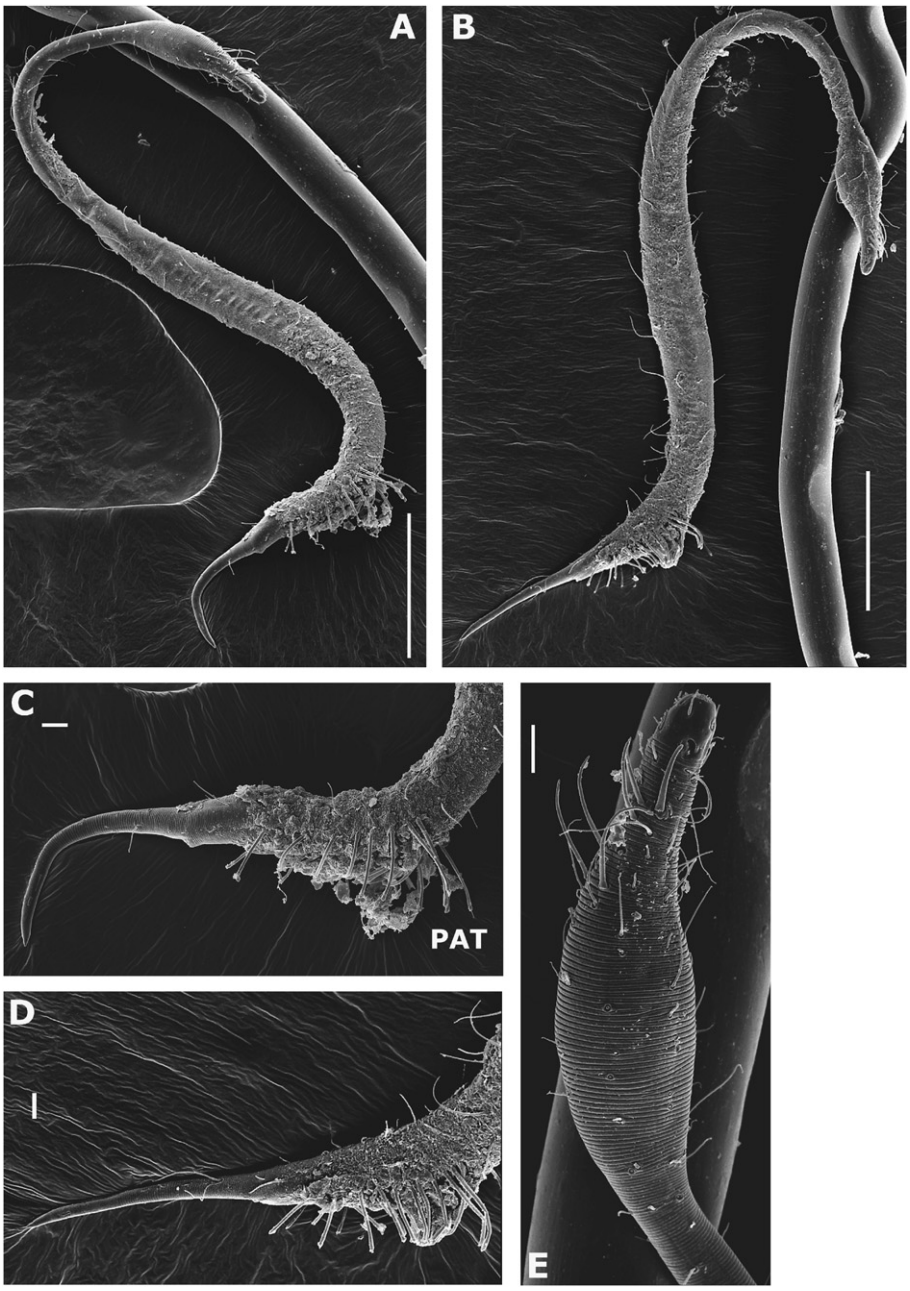

Fig. 8. *Cygnonema belgicae* sp. n. (A) Additional male, habitus. (B) Additional female, habitus. (C) Additional male, posterior body region. (D) Additional female, posterior body region. (E) Additional male, head capsule and pharyngeal region. PAT = posterior adhesion tubes. Scale bars A, B = 100 µm, C–E = 10 µm.

Differential diagnosis

Adults of *C. verum* sp. n. and *C. belgicae* sp. n. differ from the type species, *C. steineri*, in (1) general body shape (*C. steineri* is much more slender), (2) size (*C. steineri* is larger: 1700–3100 µm vs. 1325–1625 µm in *C. verum* sp. n. and 980–1305 µm in *C. belgicae* sp. n.), (3) length of pharynx in relation to body length (much longer in *C. steineri*: de Man b-ratio 3.9–6.3 vs. 10.1–10.6 in *C. verum* sp. n. and 8.5–10.3 in *C. belgicae* sp. n.), (4) number of CAT (10 in *C. steineri* vs. 14–16 in *C. verum* sp. n. and 12 in *C. belgicae* sp. n.), and (5) absence of a dorsal tooth. Adults of *C. verum* sp. n. differ from those of *C. belgicae* sp. n. in (1) size (*C. verum* sp. n. is longer), (2) larger head capsule (head capsule length relative to pharynx length, and head capsule width relative to pharynx width higher in *C. verum* sp. n.), (3) higher number of CAT, (4) position

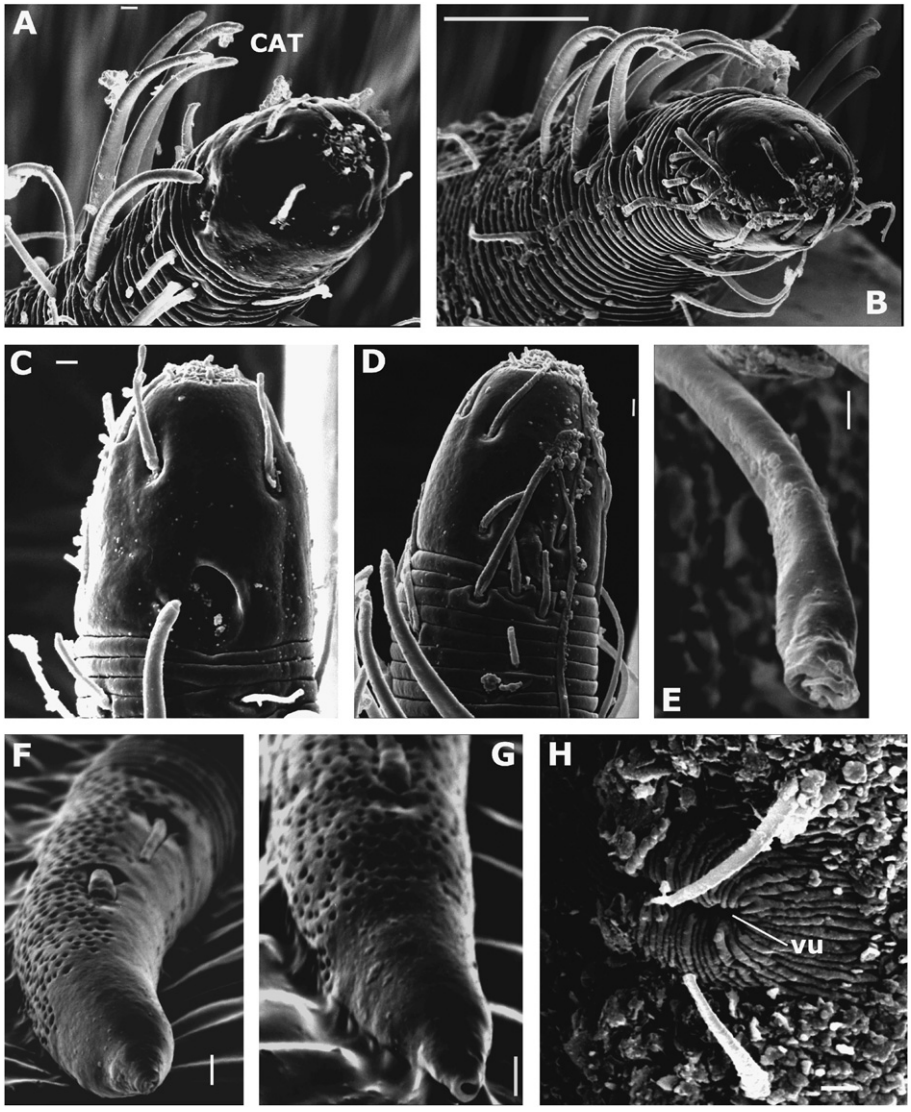

Fig. 9. *Cygnonema belgicae* sp. n. (A) Additional male, anterior region, subfrontal view. (B) Additional female, anterior region, subfrontal view. (C) Additional male, head capsule, lateral view. (D) Additional female, head capsule, lateral view. (E) Additional male, PAT tip. (F) Additional male, smooth tail tip. (G) Additional female, smooth tail tip. (H) Additional female, vulva. CAT = cephalic adhesion tube, vu = vulva. Scale bars A, C–H = 1 μm, B = 10 μm.

of anteriormost laterodorsal CAT (more anteriorly in *C. verum* sp. n.), (5) higher number of PAT, (6) the setiform external labial sensilla, (7) higher number of subcephalic setae, and (8) location of amphidial fovea (centrally on head capsule instead of near posterior border as in *C. belgicae* sp. n.). Moreover, males of *C. verum* sp. n. can easily be distinguished from those of the other species in the genus by the presence of two large subventral corniform setae immediately behind posteriormost SvAT. They differ from males of *C. belgicae* sp. n. in (1) the small amount of cytoplasm, (2) a knob-like instead of beak-shaped capitulum, and (3) a relatively shorter tail tip.

Fourth-stage juveniles of *C. verum* sp. n. differ from those of *C. belgicae* sp. n. in (1) size (cf. adults), (2) width of head capsule (cf. adults), (3) location of amphidial fovea (cf. adults), (4) number of CAT (six in *C. verum* sp. n. vs. four in *C. belgicae* sp. n.), and (5) 9 MvAT vs. 7 in *C. belgicae* sp. n.

Earlier juvenile stages of *C. verum* sp. n. can be distinguished from those of *C. belgicae* sp. n. by (1) width of head capsule, (2) location of amphidial fovea, and (3) location of MdCAT (at level of LdCAT in *C. verum* sp. n. vs. posterior to LdCAT in *C. belgicae* sp. n.).

The three species of *Cygnonema* can easily be identified as follows.

Key to the species of *Cygnonema*

1. Very slender body, only slightly swollen at base of pharynx; length at least 1700 μm; de Man b lower than 7; 10 CAT; dorsal tooth evident..... *C. steineri* Allen & Noffsinger, 1978
– Slender body with conspicuous enlargement at level of pharynx; length less than 1700 μm; de Man b higher than 7; 12–16 CAT; teeth absent..... 2
2. 14–16 CAT; 48–51 PAT; setiform external labial sensilla; 15–18 subcephalic setae; amphidial fovea located centrally on head capsule; male with two large subventral corniform setae; spermatozoa with small amount of cytoplasm; capitulum knob-like..... *C. verum* sp. n.
– 12 CAT; 34–45 PAT; external labial sensilla inconspicuous; 2–6 subcephalic setae; amphidial fovea located near posterior border of head capsule; male without corniform setae; spermatozoa with large amount of cytoplasm; capitulum beak-shaped..... *C. belgicae* sp. n.

Biogeography

Cygnonema verum sp. n. and *C. belgicae* sp. n. are two new species in a previously monospecific genus. The type species, *C. steineri*, was described from a site at 457 m depth opposite Hut Point, McMurdo Sound, Antarctica (77°51′S, 166°38′E). It was also found at Duke Ernst Bay (77°40′S, 35°30′W), Gauβ station (66°03′S, 89°38′E) and Scott Base (77°51′S, 166°45′E), all in the Antarctic. Our new finding is the first outside of the Antarctic zoogeographical region. It is known that although the Antarctic Convergence isolates the Antarctic pelagic species, this surface ocean feature is no barrier for the benthos (Clarke 2003). As a result, abyssal Antarctic faunas have a strong link to other oceans, particularly the Atlantic (Brandt et al. 2007). A molecular genetic study on three species of benthic Foraminifera suggested even substantial levels of gene flow from Antarctic to Arctic populations, but very low levels in the opposite direction (Pawlowski et al. 2007). Although the *Cygnonema* species from the Porcupine Seabight are clearly morphologically different from their Antarctic congener, the occurrence of representatives of this genus in both areas might also indicate a faunal connection between them. The genus might have its origin in the Antarctic, from where it could have spread through the Atlantic Ocean, at least up to the Porcupine Seabight area. However, this idea is still highly hypothetical and can only be confirmed by molecular genetic studies and the discovery of more *Cygnonema* specimens in other parts of the Atlantic Ocean.

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