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Research article

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New nematode species and genera (Nematoda: Chromadorea) from cold seeps on Hikurangi Margin, New Zealand

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Abstract. Relatively little is known about the taxonomy and ecology of deep-sea nematode species inhabiting cold seep habitats. The available data show that cold seep nematode communities are typically characterized by low diversity and are often dominated by a single species, although no nematode taxon appears to have a strong association with methane seepage. In July 2019, a research voyage to New Zealand’s Hikurangi Margin provided an opportunity to characterize the nematode species communities of New Zealand cold seeps, which had not been investigated until now. Here, six new species and two new nematode genera of the class Chromadorea are described from macrofauna cores obtained at three seep sites (Mungaroa, Glendhu, and Uruti South) on Hikurangi Margin from 1227 to 2077 m depth. The species described here represent a wide range of feeding groups, ranging from deposit feeders (*Linhomoeus pycnocricus* sp. nov., *Deraionema barbatum* gen. et sp. nov.) to microvores (*Aulostomonema abyssum* gen. et sp. nov., *Aegialoalaimus magnus* sp. nov.) and epigrowth feeders (*Desmodora parapilosa* sp. nov.). The diet of *Siphonolaimus curtisensillus* sp. nov., which is characterized by an unusual stylet-like feeding apparatus, remains to be determined, however the presence of several different feeding modes in the species described here indicates that a range of food sources are exploited by macrofaunal nematodes at the study sites. *Desmodora*, *Linhomoeus*, and *Aegialoalaimus* have been reported from cold seep habitats previously, however no records of *Siphonolaimus* from cold seeps could be found in the literature. *Aulostomonema* gen. nov. does not appear to have a close association with seeps, whilst *Deraionema* gen. nov. appears to be restricted to the centre of the seep sites where methane seepage is likely strongest. Ongoing work on the ecology and distribution of nematode communities at the Hikurangi Margin seep sites will help determine spatial patterns in abundance and species distributions in more detail, including the identification of any species/taxa with affinities with methane seepage.

Keywords. Xyalidae, Linhomoeidae, Aegialoalaimidae, Desmodoridae, macrofauna.

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Introduction

Cold seeps are areas of where methane-rich fluids emerge from the seafloor, leading to the establishment of specialized biological communities that rely on chemosynthesis for their nutrition (Paull *et al.* 1984,

Table 1. Details of cold seep sites and sampling stations (NIWA voyage TAN1904). Only stations from which nematode specimens are described in the present study are included.

Seep site	Station	Distance from centre of seep site (m)	Depth (m)	Lat (S)	Long (E)
Mungaroa	15	386	2070	41.9354	175.3076
Mungaroa	18	17	2075	41.9376	175.3112
Mungaroa	19	0	2075	41.9378	175.3112
Mungaroa	21	149	2077	41.9382	175.3128
Mungaroa	23	479	2019	41.9403	175.3157
Glendhu	40	11	1993	41.7695	176.0882
Uruti South	61	105	1227	41.4251	176.3510
Uruti South	62	116	1226	41.4250	176.3510
Uruti South	64	275	1245	41.4279	176.3485
Uruti South	66	101	1230	41.4266	176.3497
Uruti South	68	0	1237	41.4260	176.3506
Uruti South	70	82	1235	41.4253	176.3509

1985). Assemblages that rely directly or indirectly on this chemosynthesis are known as methane or cold seep communities. To date, most of the research on cold seep communities has focused on bacteria as well as macro- and megafaunal taxa (Levin 2005; Cordes *et al.* 2009). Relatively little is known about nematodes, a taxon particularly abundant in meiofaunal samples but which is also common in macrofaunal samples (Vanreusel *et al.* 2010a). Nematodes are usually the most abundant metazoan taxon in the benthos and are common in all deep-sea sediment habitats, including cold seeps (Vanreusel *et al.* 2010b). In their review, Vanreusel *et al.* (2010a) found that nematodes are sometimes substantially more abundant in cold seep sediments than at nearby background sites. Nematode communities at cold seeps are typically characterized by low diversity and are often dominated by a single species. There does not appear to be any strong association with any particular nematode taxon and cold seeps, with high variability in community structure among seeps (Vanreusel *et al.* 2010a). Investigations conducted since the review by Vanreusel *et al.* (2010a) largely confirm these observations (e.g., Hauquier *et al.* 2011; Pape *et al.* 2011; Portnova *et al.* 2011; Guilini *et al.* 2012).

Rosli *et al.* (2016) provided the first data on the abundance of deep-sea cold seep meiofauna in the New Zealand region. They found that seep meiofauna abundance at Opouawe bank (at ca 1000 m water depth) on Hikurangi Margin was similar to that of meiofauna from slope and seamount habitats at similar depths, and lower than meiofauna from canyon habitats. Meiofaunal community structure was shown to differ between seep and all other deep-sea habitats, mainly due to a greater abundance of nauplii and amphipods in the seep samples relative to slope, canyon and seamount samples. No data were obtained, however, on species or genus nematode communities at the seep sites (Rosli *et al.* 2016, 2018).

In July 2019, a research voyage to New Zealand’s Hikurangi Margin took place as part of the research programme “Gas Hydrates: Economic Opportunities and Environmental Implications” (HYDEE). The goal of this voyage was to obtain biological and biogeochemical data to investigate the potential impact of changes in seafloor methane flux on marine ecosystems. This voyage provided an opportunity to characterize the nematode species communities of New Zealand cold seeps, which until now have not been investigated, and to study deeper (> 1200 m) seep locations unimpacted by anthropogenic disturbance. Nematodes were obtained from both meiofauna (29 mm diameter, 45 µm mesh size) and macrofauna cores

(95 mm diameter, 300 µm mesh size). Here, six new species and two new nematode genera of the class Chromadorea are described from macrofauna cores obtained at three seep sites on Hikurangi Margin.

Material and methods

Samples were obtained from the southern end of the Hikurangi subduction margin, off the east coast of New Zealand's North Island, in a region where the Pacific Plate subducts obliquely beneath the Australian Plate. Three cold seep sites were targeted during National Institute of Water and Atmospheric Research (NIWA) voyage TAN1904 (July 2019): Mungaroa and Glendhu at ca 2000 m depth, and Uruti South at ca 1250 m depth. Each site was approximately 1 km in diameter, at the centre of which was an active cold seep of approximately 200–300 m in diameter as determined by the extent of the seafloor backscatter signal for the carbonate rock that forms at the main seepage location. At each site, a video-guided multicorer was deployed at 9–10 locations along a transect spanning the outer periphery of the site, the edge of the seep, and the centre of the seep (Table 1). The Ocean Instruments MC-800A multicorer was equipped with cores of 9.5 cm internal diameter. The top 5 cm of sediment was fixed in 10% formalin and stained with Rose Bengal. Samples were rinsed on a 300 µm sieve to retain macro-infauna, and nematodes were handpicked under a stereo microscope and transferred to pure glycerol (Somerfield & Warwick 1996).

Species descriptions were made from glycerol mounts using differential interference contrast microscopy and drawings were made with the aid of a camera lucida. Measurements were obtained using an Olympus BX53 compound microscope with cellSens Standard software for digital image analysis. All measurements are in µm (unless stated otherwise), and all curved structures are measured along the arc. The terminology used for describing the arrangement of morphological features such as setae follows Coomans (1979), terminology of stoma structures follows Decraemer *et al.* (2014). Type specimens are held in the NIWA Invertebrate Collection (Wellington).

List of abbreviations

- a = body length/maximum body diameter
- b = body length/pharynx length
- c = body length/tail length
- c' = tail length/anal or cloacal body diameter
- cbd = corresponding body diameter
- L = total body length
- n = number of specimens
- V = vulva distance from anterior end of body
- %V = $V/\text{total body length} \times 100$

Results

Phylum Nematoda Cobb, 1932
 Class Chromadorea Inglis, 1932
 Order Monhysterida Filipjev, 1929
 Superfamily Siphonolaimoidea Filipjev, 1918

Family **Siphonolaimidae** Filipjev, 1918

Diagnosis (from Fonseca & Bezerra 2014)

Body generally long and slender. Rounded anterior and posterior ends. Cuticle striated. Anterior sensilla variable: 6 + 6 + 4 in the Siphonolaiminae and 0 + 6 + 4 or 0 + 0 + 4 in the Astomonematinae. Amphids

circular. One or two gonads may be present. Gubernaculum apophysis oriented dorsocaudally. Tail shortened by histolysis.

Subfamily **Siphonolaiminae** Filipjev, 1918

Diagnosis (from Fonseca & Bezerra 2014)

Six + four cephalic setae situated at more or less same level. Outer labial setae always shorter than cephalic setae. Amphids circular. Buccal cavity may contain axial cuticularized spear-like structure (siphon). Pharynx narrow anteriorly and widening posteriorly. One anterior outstretched gonad.

Genus ***Siphonolaimus*** de Man, 1893

Anthraconema zur Strassen, 1904: 302.

Chromagaster Cobb, 1894: 419.

Type species

Siphonolaimus niger de Man, 1893.

Diagnosis (from Zograf *et al.* 2015)

Cuticle striated. Buccal cavity containing an axial cuticularized spear-like structure (siphon). Six outer labial setae and four cephalic setae situated more or less at same level, the six always shorter than the four. Amphids circular. One anterior outstretched ovary. Single anterior testis. Gonad located to the left of intestine.

Remarks

A key to males of all 21 valid species of *Siphonolaimus* was provided by Zograf *et al.* (2015).

***Siphonolaimus curtisensillus* sp. nov.**

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Figs 1–3, Table 2

Diagnosis

Siphonolaimus curtisensillus sp. nov. is characterized by body length 3.5–5.3 mm, papillose outer labial sensilla, short cephalic setae (3 µm or 0.21–0.27 cbd), 2–3 µm long subcephalic setae, amphids 36–41% cbd wide, arcuate spicules 1.2–1.7 cloacal body diameters long, gubernaculum with sharply bent crurae and dorsocaudal apophyses, at least 30 inconspicuous precloacal supplements, vulva located at 68–76% of body length from anterior extremity, uterus wall slightly cuticularized opposite vulva, and tail conical and gradually tapering.

Differential diagnosis

The new species is most similar to *S. banyulensis* Boucher, 1971 (known only from males), *S. mejillinus* Pastor de Ward, 1989 and *S. japonicus* Zograf, Trebukhova & Pavlyuk, 2015 in having papillose outer labial sensilla as well as short (< 0.3 cbd) cephalic setae. *Siphonolaimus curtisensillus* sp. nov. can be differentiated from *S. banyulensis* by the shorter body length (in males: 3.5–5.3 vs 7.8–8.3 mm in *S. banyulensis*), shorter spicules (1.2–1.7 vs 3.0–3.7 cloacal diameters in *S. banyulensis*), and longer tail (in males: 2.8–4.0 vs 1.5–1.8 cloacal body diameters in *S. banyulensis*), from *S. mejillinus* by the shorter body length (3.5–5.3 vs 7.0–8.3 mm in *S. mejillinus*), larger amphids (36–41 vs 18–19% cbd in *S. mejillinus*), and tail shape (elongated conical vs short and rounded in *S. mejillinus*) and from

S. japonicus by the higher a ratio ($a = 63\text{--}76$ vs $32\text{--}55$ in *S. japonicus*), longer siphon ($44\text{--}64$ vs $32\text{--}41$ μm in *S. japonicus*), longer tail ($c' = 2.8\text{--}5.6$ vs $2.0\text{--}2.3$ in *S. japonicus*) and number of precloacal supplements (at least 30 vs 15 in *S. japonicus*).

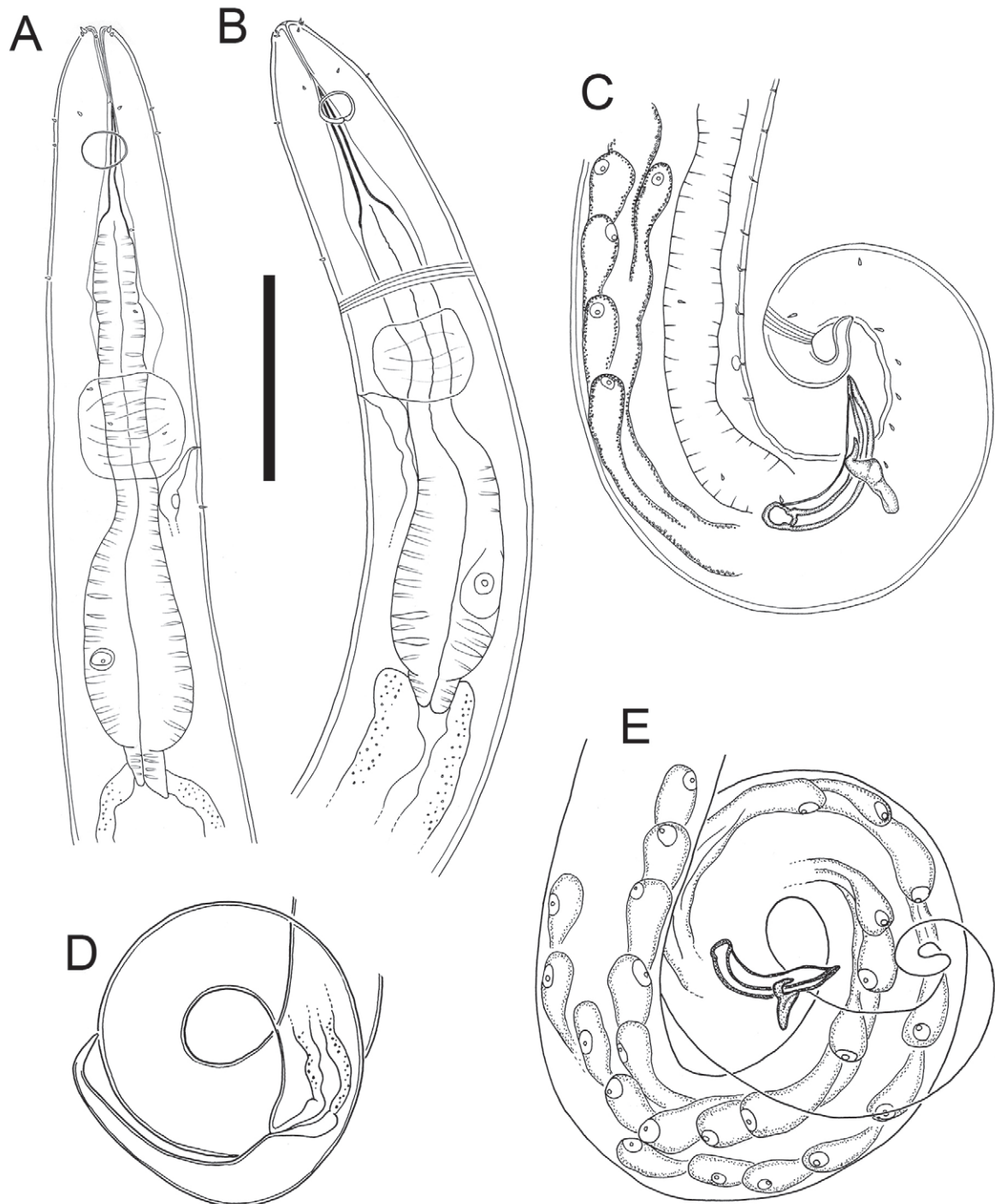


Fig. 1. *Siphonolaimus curtisensillus* sp. nov. **A, C.** Holotype (NIWA154903). **B, D,** Paratype (NIWA 154904). **E.** Paratype (NIWA154905). **A.** Male anterior body region. **B.** Female anterior body region. **C.** Male posterior body region. **D.** Female posterior body region. **E.** Male posterior body region. Scale bar: A–B = 75 μm ; C = 70 μm ; D = 85 μm ; E = 125 μm .

Etymology

The species name is derived from the Latin ‘*curtus*’ meaning ‘short’ and diminutive of Latin ‘*sensus*’ meaning ‘perceive’, ‘feel’, and refers to the short cephalic sensilla characteristic of the species.

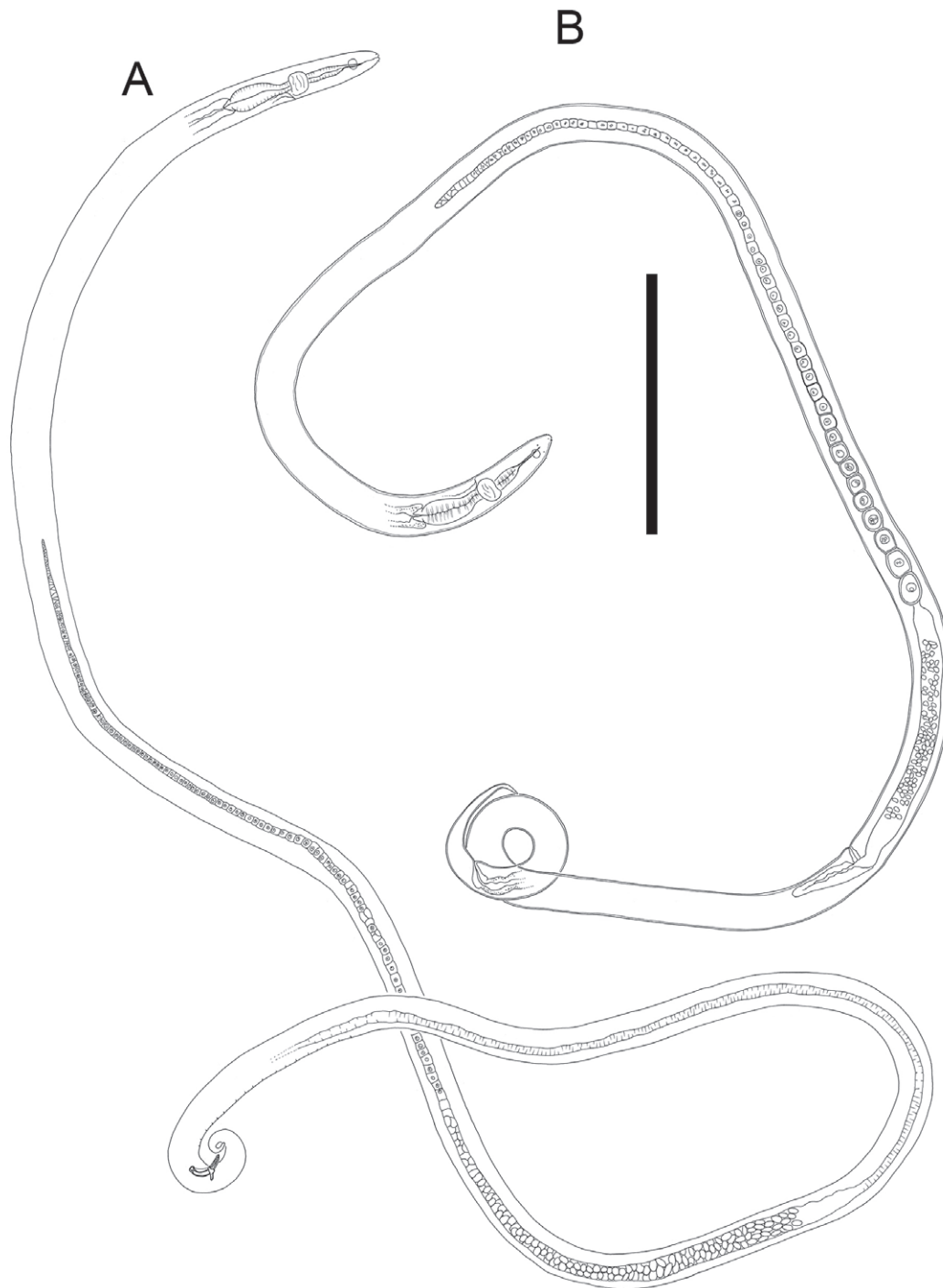


Fig. 2. *Siphonolaimus curtisensillus* sp. nov. **A.** Entire male, holotype (NIWA154903). **B.** Entire female, paratype (NIWA154904). Scale bar = 400 μ m.

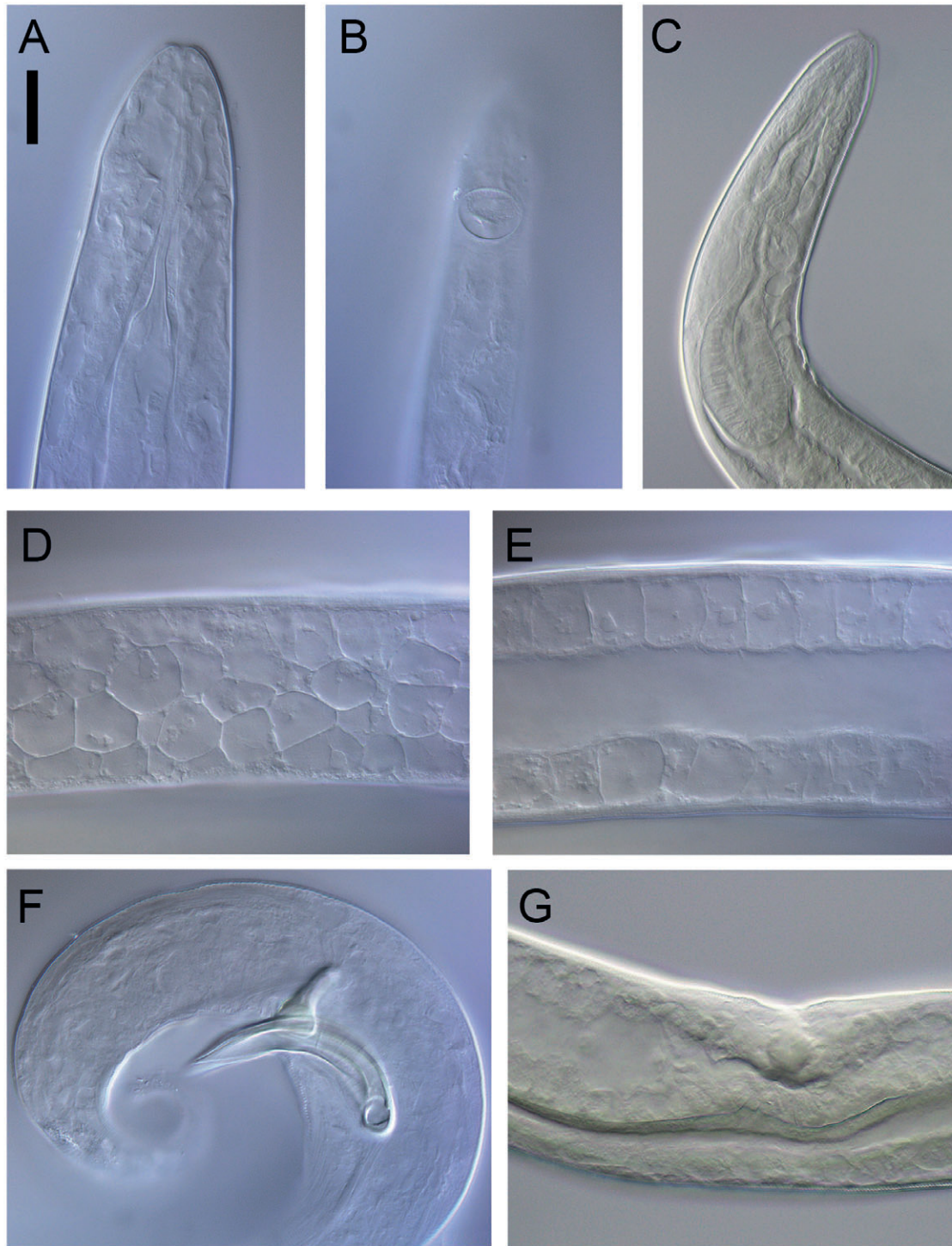


Fig. 3. *Siphonolaimus curtisensillus* sp. nov. Light micrographs. **A–B, F.** Holotype (NIWA154903). **C.** Paratype (NIWA154905). **D–E, G.** Paratype (NIWA154904). **A.** Male cephalic region showing pharynx and stylet. **B.** Male cephalic region showing amphid. **C.** Female anterior body region. **D–E.** Male intestine. **F.** Copulatory apparatus. **G.** Vulva and proximal portion of female genital branch. Scale bar: A–B = 20 μ m; C–F = 10 μ m; G = 15 μ m.

Table 2. Morphometrics (μm) of *Siphonolaimus curtisensillus* sp. nov. Abbreviations: a = body length/maximum body diameter; b = body length/pharynx length; c = body length/tail length; c' = tail length/anal or cloacal body diameter; cbd = corresponding body diameter; L = total body length; V = vulva distance from anterior end of body; %V = $V/\text{total body length} \times 100$.

	Males			Females			
	Holotype	Paratypes		Paratypes			
Specimen	M1	M2	M3	F1	F2	F3	F4
L	5302	4792	3507	3965	4617	4663	4165
a	76	70	65	63	68	68	66
b	25	25	20	22	25	26	23
c	29	29	25	20	29	21	20
c'	4.0	2.8	3.5	4.7	4.4	5.5	5.6
Body diam. at cephalic setae	14	11	13	15	12	11	12
Body diam. at amphids	43	45	44	43	46	45	41
Length of cephalic sensilla	3	3	3	3	3	3	3
Amphideal fovea height	15	16	15	14	15	15	14
Amphideal fovea width	18	17	16	16	18	16	17
Amphideal fovea width/cbd (%)	42	38	36	37	39	36	41
Amphideal fovea from anterior end	34	37	30	37	41	35	33
Nerve ring from anterior end	134	125	102	115	114	113	111
Nerve ring cbd	56	54	51	53	56	60	55
Excretory pore from anterior	155	149	128	140	144	142	142
Pharynx length	208	195	172	180	185	181	183
Pharyngeal bulb diam.	41	43	39	41	46	47	44
Pharynx cbd at base	61	61	59	63	67	71	64
Max. body diam.	70	68	54	63	68	69	63
Spicule length	75	70	68				
Gubernacular apophyses length	15	14	13				
Cloacal/anal body diam.	46	60	41	43	37	40	37
Tail length	186	168	142	200	161	219	208
V	–	–	–	2695	3500	3537	3082
%V	–	–	–	68	76	76	74
Vulval body diam.	–	–	–	62	57	64	51

Material examined

Holotype

NEW ZEALAND • ♂; Hikurangi Margin, Mungaroa cold seep site; 41.9382° S, 175.3128° E; 2076 m water depth; collected on 7 Jul. 2019; sandy mud (96% silt/clay, mean particle size 20 μm), voyage TAN1904, station 21; NIWA 154903.

Paratypes

NEW ZEALAND • 1 ♂, 2 ♀♀; same collection data as for holotype; NIWA154904 • 1 ♂, 2 ♀♀; Hikurangi Margin, Mungaroa cold seep site; 41.9378° S, 175.3112° E; 2075 m water depth; collected on

7 Jul. 2019; sandy mud (97% silt/clay, mean particle size 15 μm), voyage TAN1904, station 18; NIWA 154905.

Type habitat and locality

New Zealand continental slope, Hikurangi Margin, Mungaroa cold seep.

Description

Male

Body colourless, long, cylindrical, tapering slightly towards both extremities. Cuticle with fine transverse striations without lateral differentiation. A few sparse, short somatic setae, ca 2 μm long, present in pharyngeal and posterior body regions. Cephalic region slightly rounded, no lip region visible. Inner labial papillae not observed; six short outer labial papillae, 1.5–2.0 μm long, at about same level as four slightly longer cephalic setae, 3 μm long (0.21–0.27 cbd). Ring of eight short subcephalic setae, 2–3 μm long, slightly anterior to amphid, and two subcephalic setae located ventrally and dorsally at level of amphid. Amphideal fovea circular with slightly cuticularized outline, situated 0.7–0.8 cbd from anterior end. Buccal cavity with spear-like siphon, 44–64 μm long or 26–33% of pharynx length. Pharynx cylindrical, muscular, with elongated posterior bulb; pharyngeal lumen not cuticularised. Nerve ring at 60–65% of pharynx length from anterior. Secretory-excretory system present; pore located at or immediately posterior to level of nerve ring, ampulla small, renette cell not observed. Cardia small, 11–13 μm long, partially surrounded by intestine. Intestine wall consists of numerous clear cells each with nucleus.

Reproductive system monorchic with single anterior outstretched testis. Position of testis relative to intestine could not be determined. Sperm cells globular, 15–19 \times 14–16 μm . Spicules paired, curved, tapering distally, 1.2–1.7 cloacal body diameters long. Gubernaculum with sharply bent lateral pieces (crurae) and almost straight dorso-caudal apophyses. Two rows of 10–13 ejaculatory glands located on either side of vas deferens. At least 30 inconspicuous papillose precloacal supplements present, located 18–22 μm apart. Tail conical, gradually tapering distally, 2.8–4.5 cloacal body diameters long; a few short and sparse somatic setae present subventrally and subdorsally. Caudal glands and spinneret not observed.

Females

Similar to males, but with slightly longer tail, 4.4–5.6 anal body diameters long. Reproductive system monodelphic with single anterior ovary located to the left of intestine; mature eggs ca 135 \times 42 μm . Spermatheca present posterior to vulva. Vulva situated slightly posterior to two thirds of body length from anterior extremity. Proximal portion of vagina surrounded by constrictor muscle, vaginal glands not observed. Proximal portion of uterus opposite vulva slightly cuticularized over ca two corresponding body diameters.

Family **Linhomoeidae** Filipjev, 1922

Diagnosis (from Fonseca & Bezerra 2014)

Cuticle often striated and seldom smooth. Inner labial sensilla as papilla or not visible. Amphids circular in most cases; seldom curved into a round bow-like shape. Inner side of labial region often formed by an annular, soft skinned pad that narrows the buccal aperture. Cardia noticeably lengthened. Two outstretched gonads facing opposite directions, seldom single gonad. Anterior gonad to the left or right of intestine, and posterior gonad to opposite side.

Remarks

The Linhomoeidae comprises three subfamilies: the Linhomoeinae Filipjev, 1922, Desmolaiminae Schneider, 1926 and Eletherolaiminae Filipjev, 1922. These subfamilies are differentiated mainly based on the arrangement of cephalic sensilla and structure of the buccal cavity.

Subfamily **Linhomoeinae** Filipjev, 1922

Diagnosis (modified from Fonseca & Bezerra 2014)

Anterior sensilla in two circles (6 + 10) with or without additional setae. Amphids with circular or oval outline, usually cuticularized. Buccal cavity shallow, cup-shaped, seldom cylindrical, more or less cuticularized. Pharynx widening posteriorly, sometimes forming a distinct bulb. Tail conical or conicocylindrical.

Genus **Linhomoeus** Bastian, 1865

Paralinhomoeus De Man, 1907: 240.

Eulinhomoeus De Man, 1907: 239.

Type species

Linhomoeus elongatus Bastian, 1865.

Diagnosis (modified from Fonseca & Bezerra 2014)

Cuticle finely striated. Six inner labial papillae; six outer labial setae and four cephalic setae in one circle with the cephalic setae longer than the outer labial setae; additional setae may be present. Amphids circular, cryptospiral or cryptocircular. Buccal cavity cup-shaped, more or less cuticularized, sometimes with teeth or plates, and sometimes divided by a cuticular ring. Pharynx posteriorly enlarged, without forming a distinct bulb. Cardia usually conspicuous and elongated. Two outstretched ovaries. Gubernaculum with dorsal apophyses. Tail conical or conicocylindrical.

Remarks

Linhomoeus was synonymised with *Paralihomoeus* De Man, 1907 by Fonseca & Bezerra (2014) because no clear diagnoses could be provided to distinguish these genera. According to the latter authors, a total of 59 species now belong to *Linhomoeus*.

***Linhomoeus pycnocricus* sp. nov.**

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Figs 4–6, Table 3

Diagnosis

Linhomoeus pycnocricus sp. nov. is characterized by body length 3.8–5.6 mm, ratio of a = 40–50, 6 + 16 arrangement of cephalic sensilla with six outer labial setae 5–6 µm or 17–25% cbd long, four slightly shorter cephalic setae 3–4 µm or 10–16% cbd long, and six additional setae similar in length to outer labial setae; eight subcephalic setae present, 4–6 µm long; strongly cuticularized amphidial fovea 35–40% cbd wide; buccal cavity cup-shaped with strongly cuticularized base and walls; secretory-excretory pore located at level of nerve ring or immediately posterior or anterior; spicules 0.9–1.1 cloacal body diameters long, gubernaculum with straight dorsocaudal apophyses, 25–27 papilliform preloacal supplements present; conicocylindrical tail, 5.5–9.8 cloacal/anal body diameters long.

Differential diagnosis

The new species is most similar to *L. anteporus* (Vitiello, 1969) Fonseca & Bezerra, 2014, *L. bocki* (Schuurmans Stekhoven, 1946) Fonseca & Bezerra, 2014, *L. brevisetosus* Schuurmans Stekhoven, 1946, *L. caxinus* (Vitiello, 1969) Fonseca & Bezerra, 2014, *L. conicaudatus* (Allg en, 1930) Fonseca & Bezerra, 2014, *L. deconincki* (Groza-Rojancovski, 1972) Fonseca & Bezerra, 2014, *L. ordinarius* (Wieser, 1956) Fonseca & Bezerra, 2014, and *L. undulatus* Wieser, 1959, 2014, and in having relatively short cephalic setae and outer labial setae (< 40% cbd).

Linhomoeus pycnocricus sp. nov. differs from *L. anteporus* in longer body length (3.8–5.6 vs 1.7–1.9 mm in *L. anteporus*), higher ratio of a (40–50 vs 37–40 in *L. anteporus*) and b (16–17 vs 8 in *L. anteporus*), position of secretory-excretory pore (at or slightly anterior or posterior to nerve ring vs well anterior to nerve ring in *L. anteporus*), longer spicules (70–81 vs 33 µm) and shorter cephalic and outer labial setae (10–25 vs 35 µm in *L. anteporus*), from *L. bocki* in lower ratio of a (40–50 vs 75–88 in *L. bocki*), position of secretory-excretory pore (at or slightly anterior or posterior to nerve ring vs halfway between nerve ring and anterior body extremity in *L. bocki*), and presence of preloacal papillae and caudal setae (vs absent in *L. bocki*), from *L. brevisetosus* in shorter body length (3.8–5.6 vs 8.6 mm in *L. brevisetosus*), lower ratio of a (40–50 vs 119), b (16–17 vs 25 in *L. brevisetosus*), and c (8–11 vs 18 in *L. brevisetosus*), and in tail shape having (elongated conicocylindrical vs short and conical in *L. brevisetosus*), from *L. caxinus* in longer body length (3.8–5.6 vs 1.5–2.1 mm in *L. caxinus*), lower ratio of a (40–50 vs 58–73 in *L. caxinus*), shorter cephalic and outer labial setae (10–25 vs 36–40% cbd in *L. caxinus*) and longer spicules (70–81 vs 16–20 µm in *L. caxinus*), from *L. conicaudatus* in lower ratio of a (40–50 vs 60–61 in *L. conicaudatus*), shorter cephalic and outer labial setae (10–25 vs 30% cbd in *L. conicaudatus*) and tail shape (elongated conicocylindrical vs short and conical), from *L. deconincki* in the lower ratio of a (40–50 vs 64–82 in *L. deconincki*), position of vulva (49–55 vs 44% of body length from anterior in *L. deconincki*), number of preloacal supplements (25–27 vs 10 in *L. deconincki*) and larger amphid (35–42 vs 28% cbd in *L. deconincki*), from *L. ordinarius* in the lower ratio of a (40–50 vs 90–95 in *L. ordinarius*) and b (16–17 vs 13–14 in *L. ordinarius*), slightly shorter cephalic and outer labial setae (10–25 vs 27–30% cbd in *L. ordinarius*), larger amphids (35–42 vs 30–33% cbd in *L. ordinarius*), and buccal cavity armature (strongly cuticularized vs not cuticularized in *L. ordinarius*), and from *L. undulatus* in longer body longer length (3.8–5.6 vs 2.3 mm in *L. undulatus*), tail shape (conicocylindrical without subventral papillae vs conical with seven pairs of subventral papillae in *L. undulatus*), and larger amphid (35–42 vs 25% cbd in *L. undulatus*).

Etymology

The species name is derived from the Greek ‘*pycnos*’ (= dense, thick) and ‘*krikos*’ (= ring), and refers to the thickly cuticularized amphideal fovea of the species.

Material examined

Holotype

NEW ZEALAND • ♂; Hikurangi Margin, Uruti South cold seep site; 41.4251° S, 176.3510° E; 1227 m water depth; collected on 13 Jul. 2019; sandy mud (96% silt/clay, mean particle size 17 µm), voyage TAN1904, station 61; NIWA 154906.

Paratypes

NEW ZEALAND – Uruti South cold seep site • 1 ♂; 41.4250° S, 176.3510° E; 1226 m depth, collected on 13 Jul. 2019; voyage TAN1904, station 62; NIWA154908 • 1 ♀; 41.4279° S, 176.3485° E; 1245 m depth, collected on 14 Jul. 2019; sandy mud (97% silt/clay, mean grain size 14.2 µm), voyage TAN1904, station 64; NIWA154910 • 3 ♂♂; 41.4266° S, 176.3497° E; 1230 m depth, collected on 14 Jul. 2019;

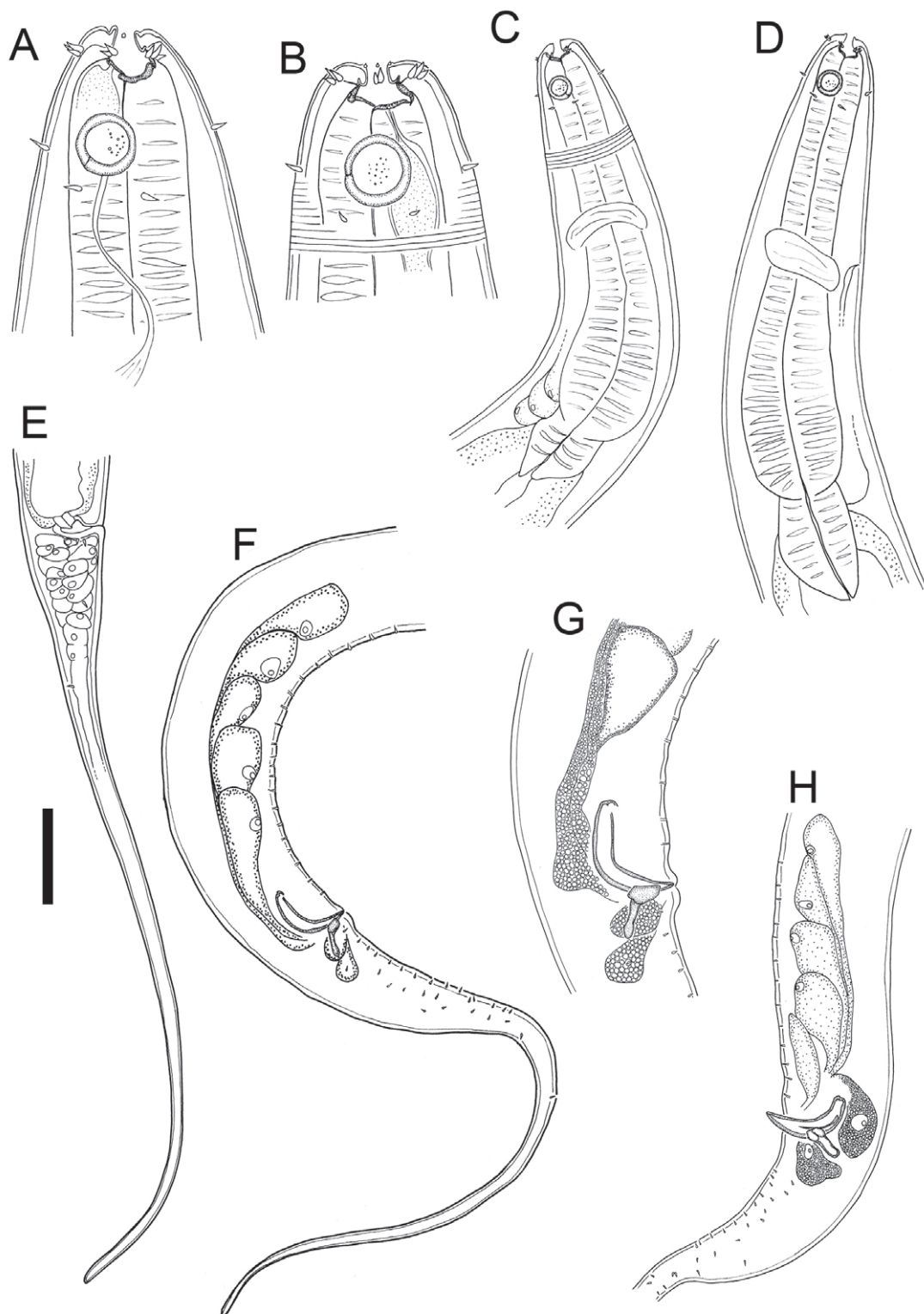


Fig. 4. *Linhomoeus pycnocricus* sp. nov. **A, D.** Paratype (NIWA154910). **B, F–G.** Paratype (NIWA154907). **C, H.** Paratype (NIWA154908). **E.** Paratype (NIWA154909). **A.** Female cephalic region. **B.** Male cephalic region. **C.** Male anterior body region. **D.** Female anterior body region. **E.** Female posterior body region. **F.** Male posterior body region. **G.** Copulatory apparatus. **H.** Copulatory apparatus and ejaculatory glands. Scale bar: A–B = 25 μ m; C–D = 75 μ m; E = 85 μ m; F = 80 μ m; G = 50 μ m; H = 70 μ m.

sandy mud (97% silt/clay, mean grain size 19 μm); voyage TAN1904, station 66; NIWA154907 • 2 ♀♀; 41.4260° S, 176.3506° E; 1237 m depth, collected on 14 Jul. 2019; sandy mud (94% silt/clay, mean grain size 18 μm); voyage TAN1904, station 68; NIWA154909.

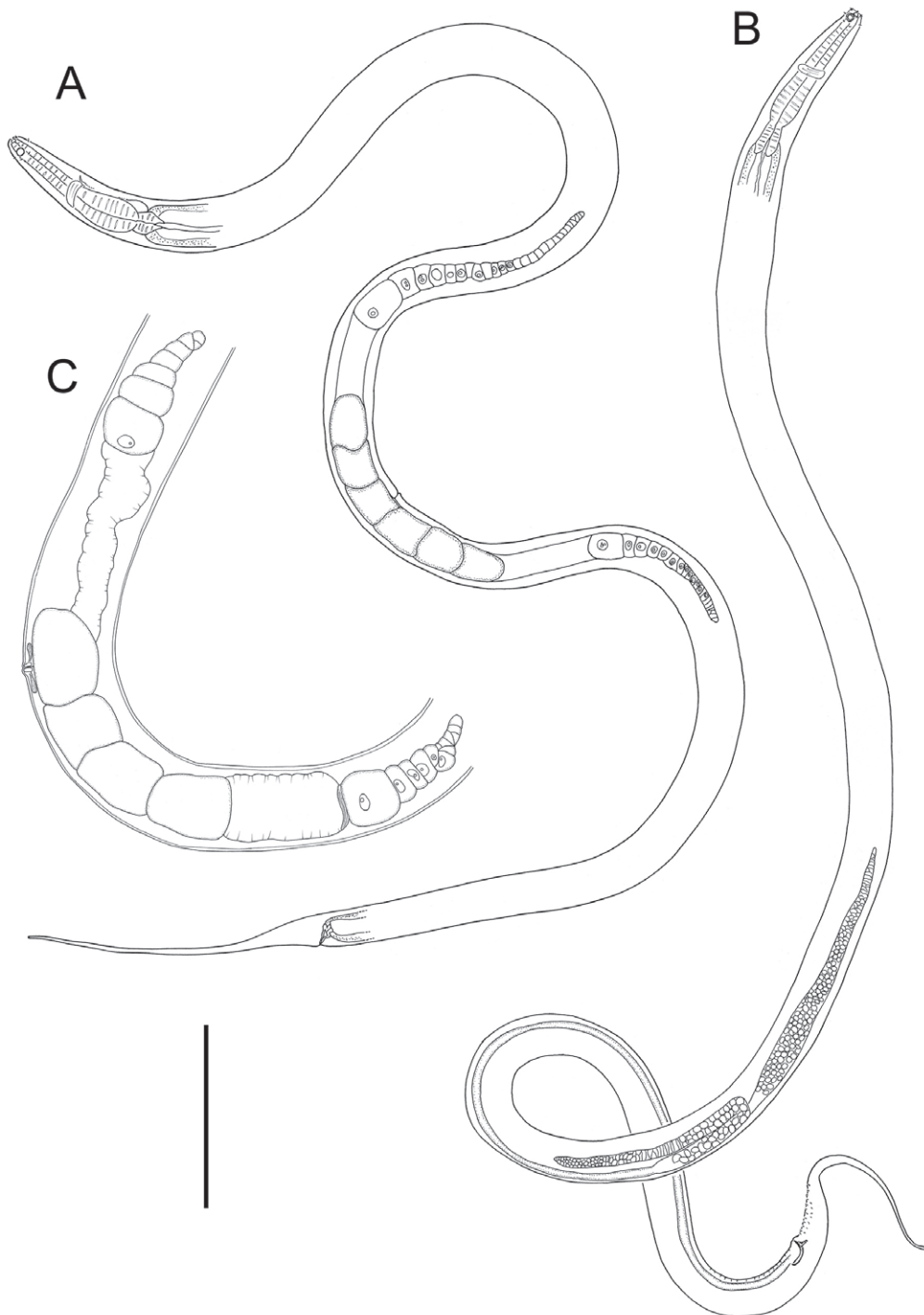


Fig. 5. *Linhomoeus pycnocricus* sp. nov. **A.** Entire female, paratype (NIWA154909). **B.** Entire male, paratype (NIWA154907). **C.** Female reproductive system, paratype (NIWA154910). Scale bar: A–B = 500 μm ; C = 275 μm .

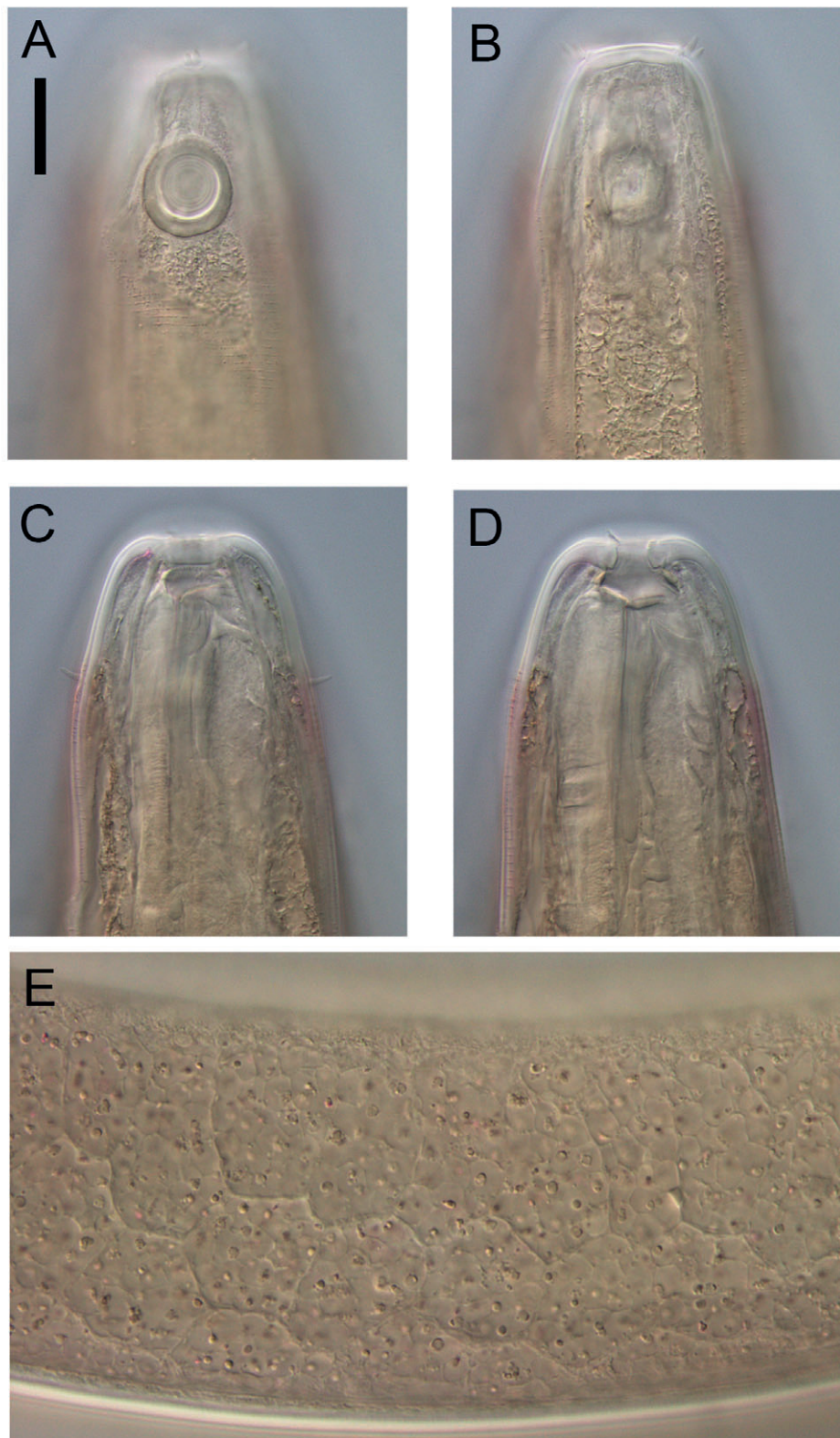


Fig. 6. *Linhomoeus pycnocricus* sp. nov. Light micrographs of male, paratype (NIWA154907). **A.** Cephalic region showing amphid. **B.** Cephalic region showing cephalic sensilla. **C.** Cephalic region showing subcephalic sensilla. **D.** Cephalic region showing buccal cavity and pharynx. **E.** Intestine. Scale bar: A–D = 20 μ m; E = 15 μ m.

Table 3. Morphometrics (μm) of *Linhomoemus pycnocricus* sp. nov. Abbreviations: a = body length/maximum body diameter; b = body length/pharynx length; c = body length/tail length; c' = tail length/anal or cloacal body diameter; cbd = corresponding body diameter; L = total body length; V = vulva distance from anterior end of body; %V = $V/\text{total body length} \times 100$.

	Males					Females		
	Holotype	Paratypes				Paratypes		
Specimen	M1	M2	M3	M4	M5	F1	F2	F3
L	3800	5662	4979	4984	5112	5520	5593	5460
a	46	48	44	45	43	41	40	50
b	16	17	17	16	16	16	17	17
c	10	9	9	10	11	8	10	9
c'	6.3	8.0	7.0	6.2	5.5	9.8	7.8	9.4
Body diam. at cephalic setae	29	24	26	27	30	26	26	24
Body diam. at amphids	38	48	43	50	51	52	50	47
Length of cephalic sensilla	3–4	3–4	3	3–4	3	3	4	3
Amphideal fovea height	17	19	18	21	19	18	18	19
Amphideal fovea width	16	19	17	19	18	19	18	18
Amphideal fovea width/cbd (%)	42	40	40	38	35	37	36	38
Amphideal fovea from anterior end	13	14	16	19	21	20	16	17
Nerve ring from anterior end	113	135	129	161	138	152	150	151
Nerve ring cbd	64	86	85	95	85	98	98	87
Excretory pore from anterior	123	123	139	–	148	148	–	160
Pharynx length	242	339	293	304	320	348	332	326
Pharyngeal diam. at base	55	70	74	78	80	92	86	72
Pharynx cbd at base	74	102	108	111	112	125	122	104
Max. body diam.	82	118	114	111	119	134	140	110
Spicule length	70	81	78	77	77	–	–	–
Gubernacular apophyses length	27	25	15	18	18	–	–	–
Cloacal/anal body diam.	62	77	76	77	83	72	73	67
Tail length	392	613	530	477	456	706	571	632
V	–	–	–	–	–	2720	3051	2707
%V	–	–	–	–	–	49	55	50
Vulval body diam.	–	–	–	–	–	154	138	110

Type habitat and locality

New Zealand continental slope, Hikurangi Margin, Uruti South cold seep.

Description

Male

Body mostly colourless except for slight brown colouration in pharyngeal region and presence of brown granules in intestine wall, cylindrical, tapering slightly towards both extremities. Cuticle finely striated, no lateral differentiation. Somatic setae apparently absent. Blunt to rounded cephalic region, not set-off from rest of body. Narrow mouth opening surrounded by bulge of inner portion of lip region. Six minute inner labial papillae surrounding mouth opening. Six outer labial setae, 5–6 μm or 17–25% cbd long, situated

at same level as four slightly shorter cephalic setae; 3–4 µm or 10–16% cbd. Six additional setae present at same level as cephalic and outer labial setae in most specimens; additional setae similar in length to outer labial setae or slightly shorter, situated laterally, lateroventrally and laterodorsally, resulting in a 6 + 16 arrangement of cephalic sensilla. Eight subcephalic setae present, 4–6 µm long; two subdorsal and two subventral setae situated at level of amphid, and two sublateral setae located slightly posterior to each amphid. Amphidial fovea circular; outline strongly cuticularized, usually with pitted appearance in centre, surrounded by cuticle striations, ca 0.3–0.4 cbd from anterior extremity. Buccal cavity cup-shaped, 10–15 µm deep, up to 15 µm wide, with strongly cuticularized base and walls; teeth-like projections not observed. Ducts of pharyngeal glands visible, emptying at base of buccal cavity. Pharynx muscular, anterior portion surrounding base of buccal cavity, not swollen; posterior portion of pharynx slightly swollen but not forming a true bulb. Nerve ring located near middle of pharynx or slightly anteriorly or posteriorly. Secretory-excretory system present, small ventral gland situated at level of cardia; excretory pore located at level of nerve ring or immediately posterior or anterior to it. Cardia well-developed, 43–93 µm long.

Reproductive system with two opposed testes; outstretched anterior testis, posterior testis may be outstretched or reflexed. Anterior and posterior located either both to the right or both to the left of intestine. Sperm cells globular, 17–20 × 18–23 µm. Spicules short, arcuate, 0.9–1.1 cloacal body diameters long, strongly cuticularized, tapering distally. Gubernaculum with straight dorsocaudal apophyses. Twenty-five to twenty-seven papilliform preloacal supplements, beginning 15–30 µm anterior to cloaca and 9–28 µm apart. Tail conicocylindrical, with short subventral setae on anterior conical portion; terminal setae not observed. Caudal glands not well defined.

Female

Similar to males but with fewer caudal setae. Reproductive system with two opposed outstretched ovaries both located to the left of intestine. Spermatheca not observed. Vulva located near mid-body. Vaginal glands present. Pars proximalis vaginae surrounded by constrictor muscle.

Genus *Aulostomonema* gen. nov.

urn:lsid:zoobank.org:act:E4C34AE7-53F3-4B0A-9C5F-6BF6A7668A8E

Type species

Aulostomonema abyssum gen. et sp. nov.

Diagnosis

Cuticle finely striated. Six outer labial setae and four cephalic setae of similar length and located in one circle; additional setae and subcephalic setae absent. Amphids circular. Mouth opening narrow, followed by elongated constriction of the anteriormost portion of the pharyngostome separating the lip region from the cuticularized, cylindrical buccal cavity. Pharynx not surrounding buccal cavity anteriorly; posterior bulb present. Cardia well developed. Male reproductive system with single anterior outstretched testis. Gubernaculum with dorsal apophyses. Tail conical.

Differential diagnosis

The new genus is tentatively placed within the Linhomoeidae, as it matches almost all aspects of the diagnosis of the family, including the arrangement of the cephalic sensilla, amphid shape, elongated cardia, and copulatory apparatus. However, *Aulostomonema* gen. nov. is characterized by a unique feature not found in other genera of the family, i.e., a constriction in the anteriormost portion of the buccal region (pharyngostome) separating the cylindrical buccal cavity from the lip region. This feature should not be confused with the inner soft skinned pad of the lip region (cheilostome) narrowing the buccal aperture of many Linhomoeidae. The constriction in the anteriormost portion of the buccal region

of *Aulostomonema* is similar to the constriction found in the Siphonolaiminae (family Siphonolaimidae), anteriorly to the spear-like siphon. The new genus, however, lacks the siphon which characterizes the Siphonolaiminae and possesses six outer labial setae and four cephalic setae in one circle instead of two separate circles as in the Siphonolaiminae.

The new genus is tentatively placed within the Linhomoeinae due to the arrangement of the cephalic sensilla (i.e., six outer labial setae and four cephalic setae in one circle) and the cuticularised buccal cavity. *Aulostomonema* gen. nov. differs from all genera within the Linhomoeinae in having an elongated cylindrical buccal cavity, compared to a cup-shaped buccal cavity in all other genera within the Linhomoeinae.

Aulostomonema gen. nov. differs from the genera in the subfamily Desmolaiminae which are characterized by a minute or conical buccal cavity, and which never have setiform outer labial sensilla and cephalic setae in a single circle. Within the Desmolaiminae, *Aulostomonema* gen. nov. is most similar to the genus *Terschellingoides* Timm, 1967 (subfamily Desmolaiminae) in having an elongated cylindrical buccal cavity and a single anterior outstretched testis, but differs from the latter in the arrangement of the cephalic sensilla, i.e., a single circle of six outer labial setae and four cephalic setae vs four cephalic setae only in *Terschellingoides*.

The new genus has some affinities with the closely-related Eleutherolaiminae Filipjev, 1922 due to the cylindrical buccal cavity. However, *Aulostomonema* gen. nov. differs from all genera in this subfamily in having an elongated buccal cavity (vs short buccal cavity in the other genera) and in the arrangement of the cephalic sensilla, which in Eleutherolaiminae consists of a 4 + 2 + 4, 4 + 6 or 6 + 4 arrangement.

Etymology

The genus name is derived from the Greek ‘*aulos*’ meaning ‘flute’, ‘pipe’, ‘tube’, ‘*stoma*’ for ‘mouth’ and ‘*nema*’ for ‘thread’ and refers to the shape of the buccal cavity in this genus of nematode.

Aulostomonema abyssum gen. et sp. nov.

urn:lsid:zoobank.org:act:105F5B86-DC27-4689-8279-10549DAC2C21

Figs 7–9, Table 4

Diagnosis

Aulostomonema abyssum gen. et sp. nov. is characterized by body length 7.1–8.8 mm; short, 3 µm long outer labial setae and cephalic setae in single circle; amphids ca 0.5 cbd from anterior extremity; narrow mouth opening followed by constriction expanding posteriorly into cuticularized, cylindrical buccal cavity 19–23 µm long and 3 µm in diameter; excretory pore located at level of nerve ring or slightly posterior; spicules 1.5 cloacal body diameters long, gubernaculum with dorsocaudal apophyses, at least 10–13 papilliform precloacal supplements present; short conical tail with rounded posterior extremity.

Etymology

The species name is derived from the Latin ‘*abyssus*’ meaning ‘a deep pit, the deep sea’, ‘hell’ and refers to the deep type locality.

Material examined

Holotype

NEW ZEALAND • ♂; Hikurangi Margin, Mungaroa cold seep site; 41.9382° S, 175.3128° E; 2077 m water depth; collected on 7 Jul. 2019; sandy mud (96% silt/clay, mean particle size 20 µm), voyage TAN1904, station 21; NIWA154911.

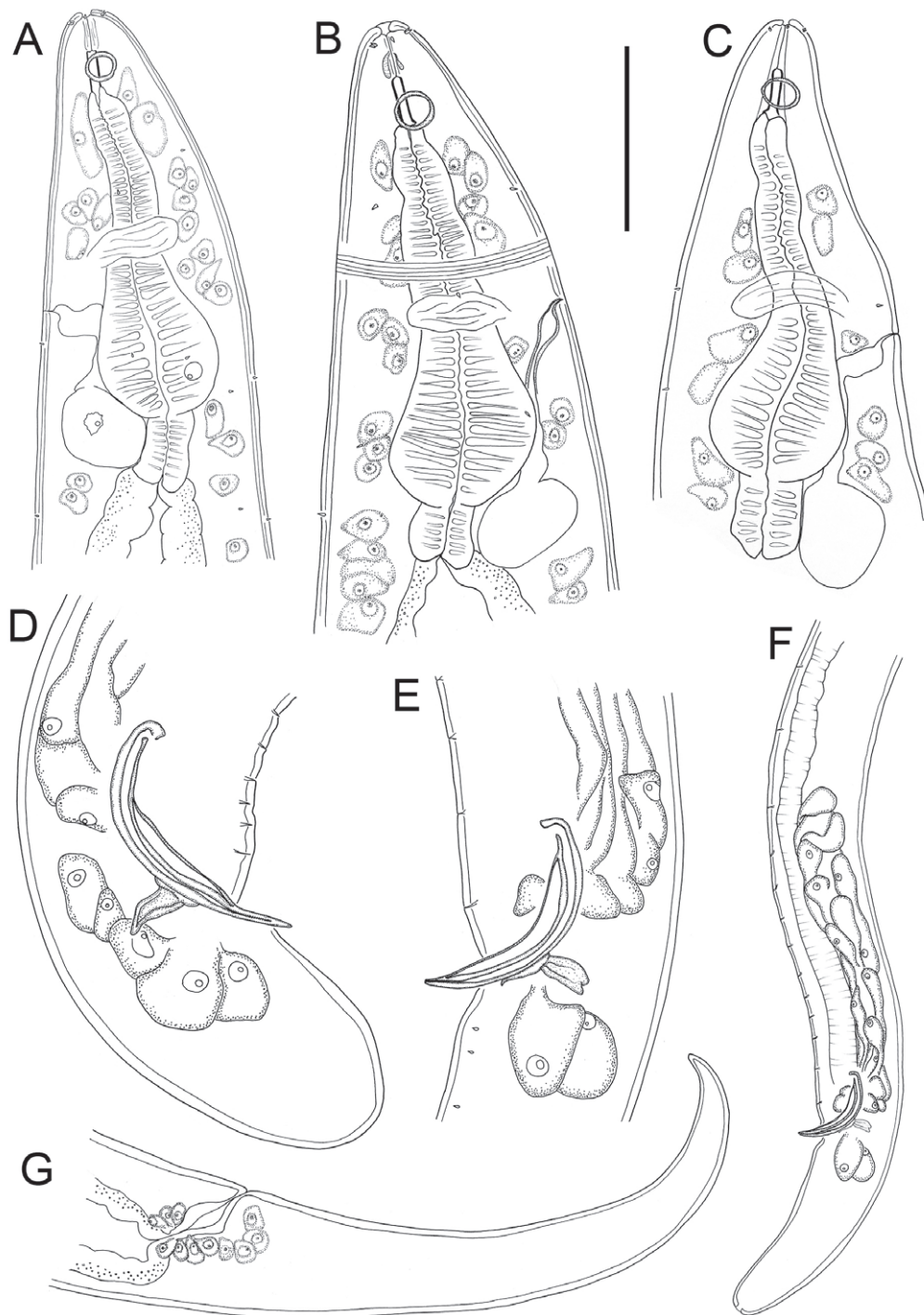


Fig. 7. *Aulostomonema abyssum* gen. et sp. nov. **A, E–F.** Holotype (NIWA154911). **B, D.** Paratype (NIWA154912). **C, G.** Paratype (NIWA154913). **A–B.** Anterior body portion of male. **C.** Anterior body region of juvenile. **D.** Posterior body region of male. **E.** Copulatory apparatus. **F.** Posterior body region of male. **G.** Posterior body region of juvenile. Scale bar: A = 100 μ m; B, D, G = 75 μ m; C = 70 μ m; E = 80 μ m; F = 200 μ m.

Paratypes

NEW ZEALAND – **Hikurangi Margin, Mungaroa cold seep site** • 1 ♂; 41.9403° S, 175.3157° E; 2091 m water depth; collected on 7 Jul. 2019; sandy mud (98% silt/clay, mean particle size 16 µm), voyage TAN1904, station 23; NIWA154912 • 2 juveniles; 41.9354° S, 175.3076° E; 2070 m water

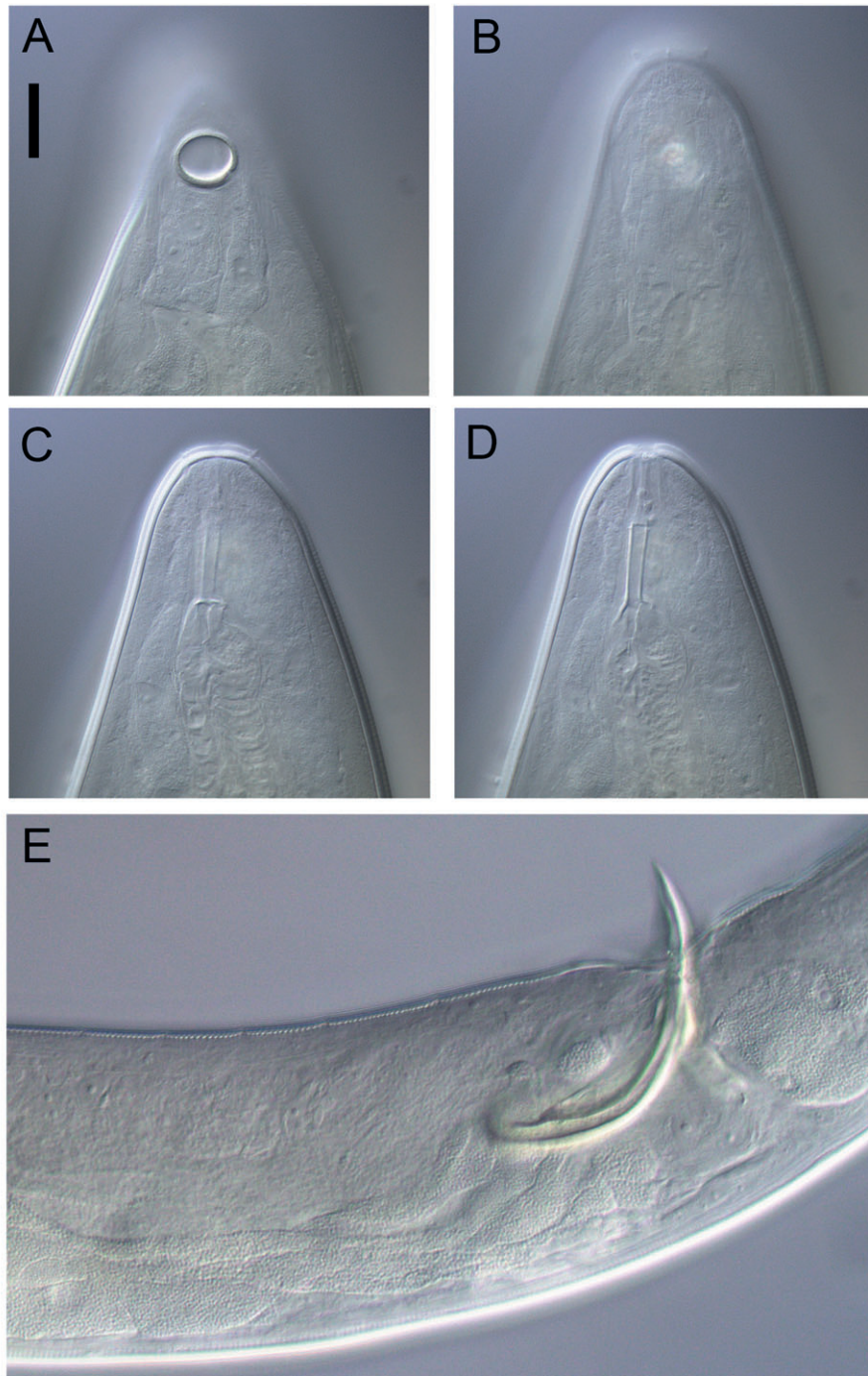


Fig. 8. *Aulostomonema abyssum* gen. et sp. nov. Light micrographs of male, holotype (NIWA154911). **A.** Cephalic region showing amphid. **B.** Cephalic region showing anterior sensilla. **C.** Cephalic region showing pharynx. **D.** Cephalic region showing buccal cavity. **E.** Copulatory apparatus and precloacal supplements. Scale bar: A–D = 20 µm; E = 18 µm.

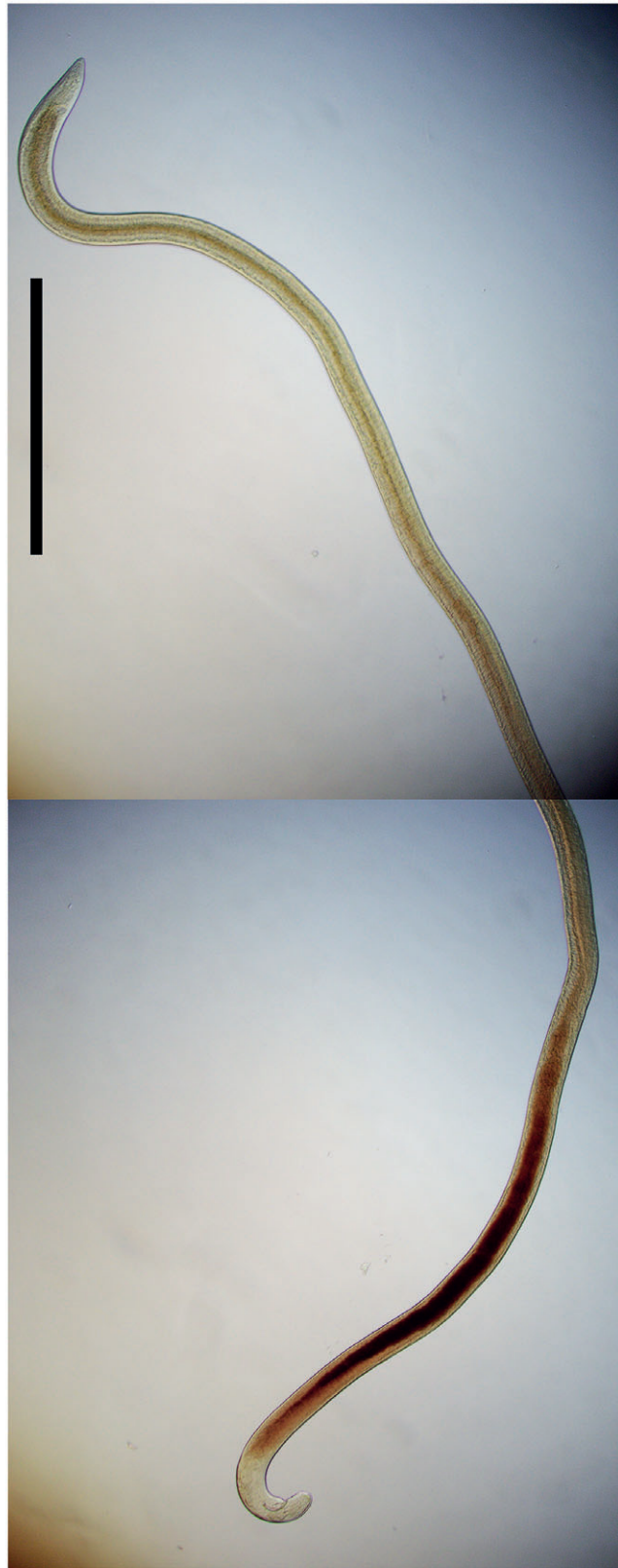


Fig. 9. *Aulostomonema abyssum* gen. et sp. nov. Composite light micrograph image of entire male, paratype (NIWA154912). Scale bar = 1000 μ m.

Table 4. Morphometrics (μm) of *Aulostomonema abyssum* gen. et sp. nov. Abbreviations: a = body length/maximum body diameter; b = body length/pharynx length; c = body length/tail length; c' = tail length/anal or cloacal body diameter; cbd = corresponding body diameter; L = total body length; V = vulva distance from anterior end of body; %V = V/total body length \times 100.

	Males		Juveniles	
	Holotype	Paratype	Paratypes	
Specimen	M1	M2	J1	J2
L	8790	7146	5506	3770
a	65	52	47	42
b	49	46	37	26
c	39	68	22	17
c'	2.7	1.3	4.5	4.8
Body diam. at cephalic setae	23	21	16	13
Body diam. at amphids	51	47	40	31
Length of cephalic sensilla	3	3	3	2
Amphideal fovea height	15	14	12	13
Amphideal fovea width	18	16	15	14
Amphideal fovea width/cbd (%)	35	34	38	45
Amphideal fovea from anterior end	24	26	23	22
Nerve ring from anterior end	125	107	101	95
Nerve ring cbd	102	92	84	59
Excretory pore from anterior	159	109	123	122
Pharynx length	181	156	150	143
Pharyngeal bulb diam.	65	60	52	41
Pharynx cbd at base	117	109	99	70
Max. body diam.	135	138	117	89
Spicule length	124	123	–	–
Gubernacular apophyses length	21	20	–	–
Cloacal/anal body diam.	84	83	57	47
Tail length	227	105	256	224

depth; collected on 7 Jul. 2019; sandy mud (98% silt/clay, mean particle size 16 μm), voyage TAN1904, station 15; NIWA154913.

Type habitat and locality

New Zealand continental slope, Hikurangi Margin, Mungaroa cold seep.

Description

Male

Body cylindrical, colourless, tapering slightly towards both extremities. Cuticle finely striated, no lateral differentiation. Somatic setae short and sparse. Rounded cephalic region, not set-off from rest of body. Lip region poorly developed; inner labial papillae not observed. Six short outer labial setae, 3 μm or 13–14% cbd long, situated at same level as four cephalic setae of same length. Additional and subcephalic setae absent. Amphidial fovea circular; outline cuticularized, surrounded by cuticle striations, ca 0.5

cbd from anterior extremity. Narrow mouth opening followed by constriction 20–22 μm in length, apparently surrounded by several small glands, expanding posteriorly into cuticularized, cylindrical buccal cavity, 19–23 μm long and 3 μm in diameter. Pharynx muscular, not surrounding cylindrical buccal cavity; posterior portion of pharynx swollen into pharyngeal bulb; ducts of pharyngeal glands not observed. Nerve ring located slightly posterior to middle of pharynx. Secretory-excretory system with large ventral gland situated at level of cardia; excretory pore located at level of nerve ring or slightly posterior. Cardia not surrounded by intestine, well-developed, 43–93 μm long. Multiple pseudocoelomocytes present in pharyngeal region. Intestine with amorphous brown content.

Reproductive system with one anterior outstretched testis located to the left of intestine. Sperm cells globular 12–17 \times 18–22 μm . Spicules short, arcuate, with velum, 1.5 cloacal body diameters long, strongly cuticularized, tapering distally. Gubernaculum with dorsocaudal apophyses tapering distally or with bifid tip. At least 10–13 papilliform precloacal supplements present, difficult to observe, beginning ca 30 μm anterior to cloaca and 30–80 μm apart. Several large rectal glands present; multiple ejaculatory glands present on either side of vas deferens extending 5–6 cloacal body diameters anterior to cloaca. Tail short, conical with rounded posterior extremity. Caudal glands not observed.

Juvenile

Similar to males but with shorter body length, lower ratios of a, b and c, slightly smaller amphids, and longer conical tail with pointed posterior extremity.

Superfamily Sphaerolaimidae Filipjev, 1918

Family Xyalidae Chitwood, 1951

Diagnosis (from Fonseca & Bezerra 2014)

Cuticle striated. Six outer labial setae and four cephalic setae in one circle, with cephalic setae shorter than or at most equal to outer labial setae. Often additional setae and occasionally eight groups of subcephalic setae present. Buccal cavity usually funnel-shaped, completely or only at the base surrounded by pharyngeal tissue. Ventral gland mostly absent. Females with one anterior ovary to the left of intestine. Males usually with two testes, the anterior one to the left of intestine, the posterior one to the right of intestine (or absent).

Remarks

A list of valid genera and species of the family Xyalidae was provided by Venekey *et al.* (2014). The Xyalidae is a large and diverse family of nematodes currently comprising 50 valid genera (Venekey *et al.* 2014; Jiang & Huang 2015; Leduc 2015; Yu & Xu 2015; Gagarin 2020).

Genus *Deraionema* gen. nov.

urn:lsid:zoobank.org:act:BF025843-A358-490E-8C22-0CA5B967BF79

Type species

Deraionema barbatum gen. et sp. nov.

Diagnosis

Cuticle finely striated; sixteen longitudinal rows of subcephalic setae posterior to amphids; sexual dimorphism in amphid shape: in males, amphideal fovea and aperture form a single, narrow band (or ‘collar’) around the entire circumference of the cephalic region, presumably resulting from the fusion of the left and right amphids, in females, amphids are transversely oval with faint outline; large conical

buccal cavity; male reproductive system with two opposed testes; spicules slender and elongated; gubernaculum without apophyses; conicocylindrical tail with terminal setae.

Differential diagnosis

The new genus differs from all other genera within the Xyalidae, and indeed all genera within the entire phylum Nematoda, in having males with a single annular amphideal fovea and aperture surrounding the entire circumference of the cephalic region. Within the Xyalidae, amphids are most commonly rounded or oval-shaped, or can be spindle-shaped (*Xenolaimus* Cobb, 1920) or indistinct (e.g., *Gnomoxyala* Lorenzen, 1977). In some genera such as *Pseudoechinotheristus* Blome, 2002, the oval amphids are transversely elongated and may occupy close to 100% of the corresponding body diameter, but the two amphids always remain distinct. In *Deraionema* gen. nov., it appears that the two amphids have become so wide as to become fused, thus forming a single structure. In some specimens, it is possible to discern the amphideal nerve extending posteriorly from the amphid, which allows to determine the position of the lateral sectors.

Deraionema gen. nov. is most similar to *Paramonohystera* Steiner, 1916 in the conical buccal cavity, structure of the copulatory apparatus (i.e., elongated, slender spicules and gubernaculum without apophyses) and conicocylindrical tail with terminal setae. In addition to differences in male amphid shape, the two genera can be differentiated by the presence of 16 longitudinal rows of subcephalic setae in *Deraionema* gen. nov. (vs absent in *Paramonohystera*).

Etymology

The species name is derived from the Greek ‘*deraion*’ meaning ‘necklace’, ‘collar’ and ‘*nema*’ meaning ‘thread’, and refers to the shape of the amphids in males.

Deraionema barbatum gen. et sp. nov.

urn:lsid:zoobank.org:act:2ACBF50F-E281-48D6-9866-D7ED15F5D3BD

Figs 10–12, Table 5

Diagnosis

Deraionema barbatum gen. et sp. nov. is characterized by body length 2.1–3.2 mm; outer labial setae 6–8 µm long and cephalic setae 4–5 µm long; short and sparse subcephalic setae present anterior to amphids; sixteen longitudinal rows of subcephalic setae present posterior to amphids, increasing in length posteriorly; pronounced sexual dimorphism in amphid shape: in males, amphideal fovea and aperture form a single, narrow band around the entire circumference of the cephalic region, presumably resulting from the fusion of the left and right amphids, in females, amphids are transversely oval with faint outline; large conical buccal cavity with cuticularized ring (cheilostome) and three transverse cuticularized pieces (pharyngostome); slender, elongated spicules 2.4–3.9 cloacal body diameters long with lateral extensions distally bearing minute spines; gubernaculum long and thin, without apophyses or crurae; conicocylindrical tail 3.3–4.8 cloacal/anal body diameters long.

Etymology

The species name is derived from the Latin ‘*barbatus*’ meaning ‘bearded’ and refers to the longitudinal rows of subcephalic setae.

Material examined

Holotype

NEW ZEALAND • ♂; Hikurangi Margin, Uruti South cold seep site; 41.4251° S, 176.3510° E; 1227 m water depth; collected on 13 Jul. 2019; voyage TAN1904, station 61; NIWA154914.

Paratypes

NEW ZEALAND • 2 ♂♂; same collection data as for holotype; NIWA 154915 • 1 ♂, 1 ♀; Hikurangi Margin, Uruti South cold seep site; 41.4250° S, 176.3510° E; 1226 m water depth; collected on 13 Jul.

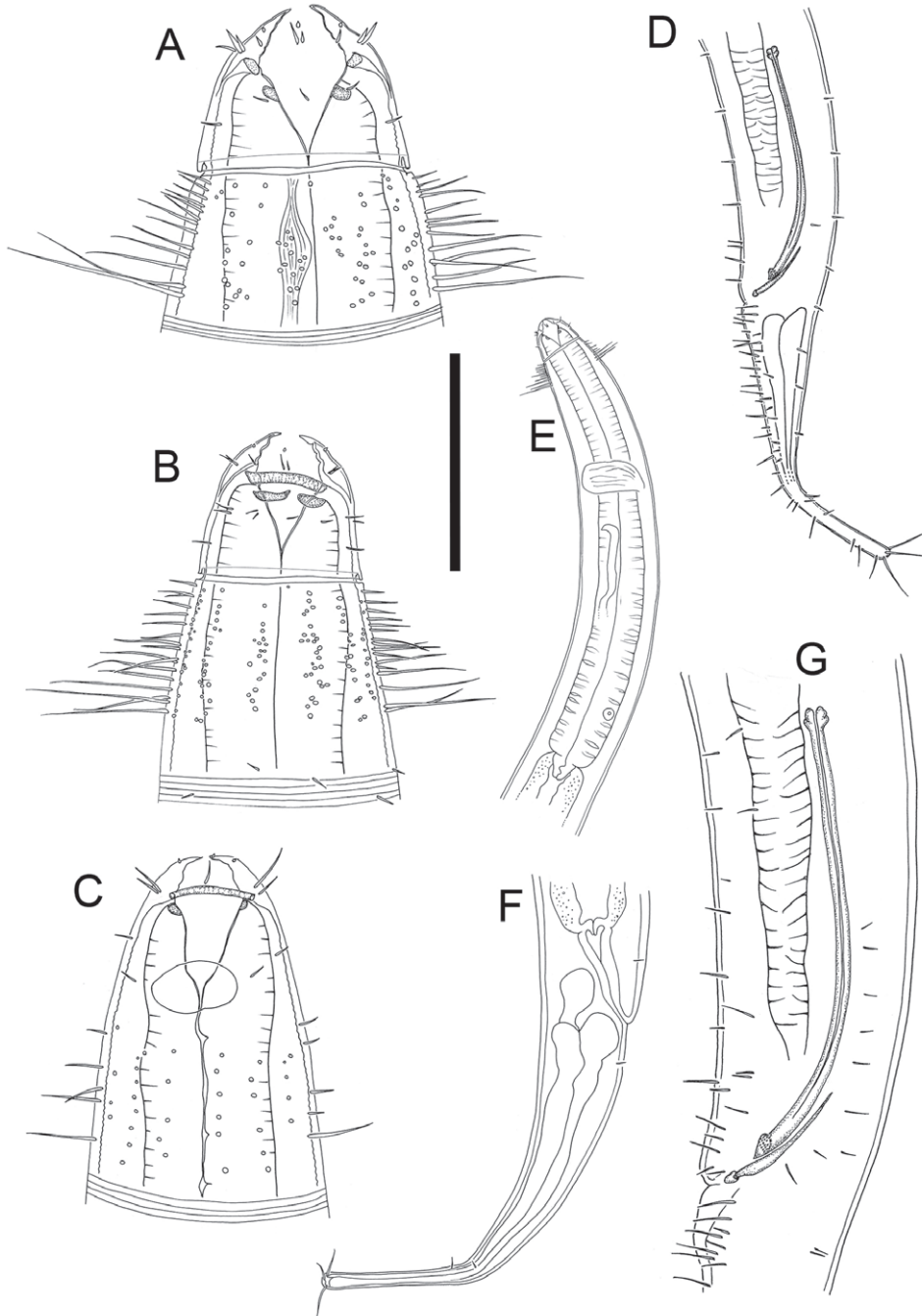


Fig. 10. *Deraionema barbatum* gen. et sp. nov. **A, D, G.** Paratype (NIWA154915). **B, E.** Holotype (NIWA 154914). **C, F.** Paratype (NIWA154917). **A–B.** Lateral view of male cephalic region. **C.** Female cephalic region. **D.** Male posterior body region. **E.** Male anterior body region. **F.** Female posterior body region. **G.** Copulatory apparatus. Scale bar: A = 50 μ m; B = 65 μ m; C = 55 μ m; D = 140 μ m; E = 240 μ m; F = 120 μ m; G = 70 μ m.

2019; sandy mud (91% silt/clay, mean particle size 24 μm); voyage TAN1904, station 61; NIWA 154916
 • 3 ♂♂; Mungaroo cold seep site; 41.9378° S, 175.3112° E; 2075 m water depth; collected on 7 Jul.
 2019; sandy mud (96% silt/clay, mean grain size 17 μm); voyage TAN1904, station 19; NIWA 154917.

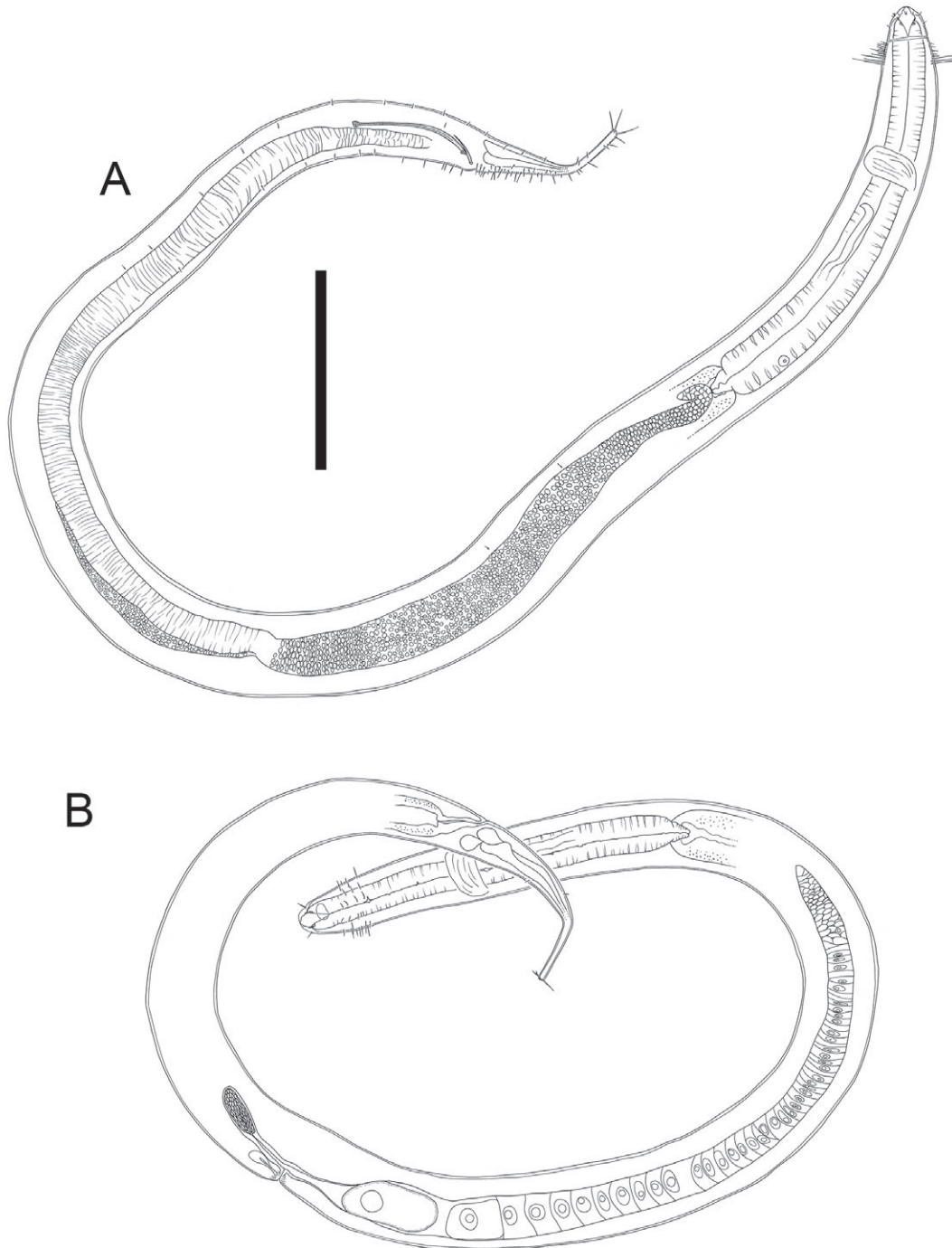


Fig. 11. *Deraionema barbatum* gen. et sp. nov. **A.** Entire male, holotype (NIWA154914). **B.** Entire female, paratype (NIWA154917). Scale bar = 250 μm .

Type habitat and locality

New Zealand continental slope, Hikurangi Margin, Uruti South and Mungaroa cold seeps.

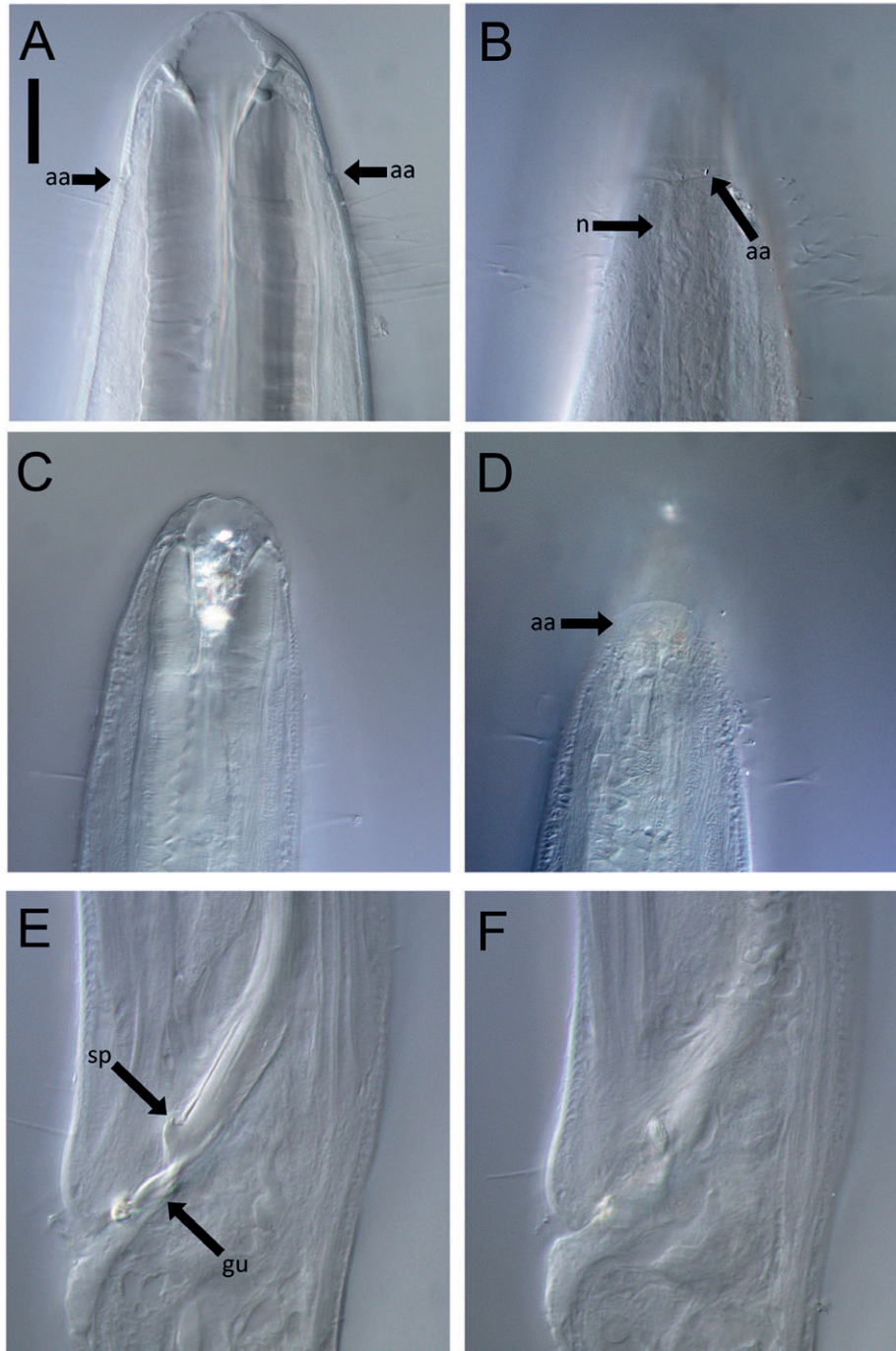


Fig. 12. *Deraionema barbatum* gen. et sp. nov. Light micrographs. **A–B, E–F.** Paratype (NIWA154915). **C–D.** Holotype (NIWA154917). **A.** Male cephalic region showing lips, buccal cavity, pharynx and subcephalic setae. **B.** Male cephalic region showing amphideal aperture. **C.** Female cephalic region showing lips, buccal cavity and pharynx. **D.** Female cephalic region showing amphideal aperture and subcephalic setae. **E–F.** Copulatory apparatus. Abbreviations: aa = amphideal aperture; gu = gubernaculum; n = amphideal nerve; sp = spicule. Scale bar = 20 μ m.

Table 5. Morphometrics (μm) of *Deraionema barbatum* gen. et sp. nov. Abbreviations: a = body length/maximum body diameter; b = body length/pharynx length; c = body length/tail length; c' = tail length/anal or cloacal body diameter; cbd = corresponding body diameter; L = total body length; V = vulva distance from anterior end of body; %V = $V/\text{total body length} \times 100$.

	Males				Females			
	Holotype	Paratypes			Paratypes			
Specimen	M1	M2	M3	M4	F1	F2	F3	F4
L	2619	2577	2420	2388	2279	2085	2336	3217
a	20	23	21	23	28	21	21	25
b	15	5	5	4	6	5	6	5
c	14	13	13	12	11	10	12	13
c'	4.0	4.4	3.3	3.6	4.8	4.6	3.6	3.8
Body diam. at cephalic setae	30	32	29	33	28	29	30	37
Body diam. at amphids	49	51	53	49	46	44	43	60
Length of cephalic sensilla	4	4	5	3–4	6	5	5	5
Amphideal fovea height	5	5	5	4	12	13	14	7
Amphideal aperture height	2	1	1	1	12	13	14	7
Amphideal fovea width	49	51	53	49	18	20	16	22
Amphideal fovea width/cbd (%)	100	100	100	100	39	45	37	37
Amphideal fovea from anterior end	37	42	46	39	32	29	29	39
Nerve ring from anterior end	174	177	180	178	166	146	167	205
Nerve ring cbd	83	88	84	81	65	63	68	100
Excretory pore from anterior	255	254	266	ND	240	164	ND	297
Pharynx length	537	513	532	548	398	385	380	628
Pharyngeal diam. at base	61	59	69	53	39	46	50	63
Pharynx cbd at base	99	97	102	86	72	79	87	114
Max. body diam.	128	113	117	106	81	99	113	127
Spicule length	158	178	168	147	–	–	–	–
Gubernacular apophyses length	45	47	48	54	–	–	–	–
Cloacal/anal body diam.	49	46	56	58	45	46	55	63
Tail length	194	201	183	206	216	213	196	241
V	–	–	–	–	1403	1278	1425	2184
%V	–	–	–	–	62	61	61	68
Vulval body diam.	–	–	–	–	78	95	103	112

Description

Male

Body cylindrical, colourless, tapering slightly towards both extremities. Cuticle finely striated, no lateral differentiation. Eight longitudinal rows of short and sparse somatic setae short and sparse. Rounded cephalic region, not set-off from rest of body. Lip region well developed with six inner labial papillae. Six outer labial setae, 20–22% cbd long, situated at same level as four slightly shorter cephalic setae, 13–17% cbd. Up to six additional setae present at same level as outer labial and cephalic setae, either

adjacent to outer labial and cephalic setae or halfway between outer labial setae, 4 μm long. Variable number of subcephalic setae (up to 20) present at level of buccal cavity and anterior to amphids, 4–5 μm long. Sixteen longitudinal rows of 12–20 subcephalic setae present beginning immediately posterior to amphids, increasing in length posteriorly, 4–47 μm long. Amphidial fovea a single, continuous narrow band around entire circumference of cephalic region, 5 μm in height, located 0.8–0.9 cbd from anterior body extremity; amphideal aperture narrower than amphideal fovea, 2 μm in height, consisting of a single narrow opening surrounding entire circumference of cephalic region. Buccal cavity large, 26–38 μm deep and up to 19 μm wide, conical; cuticularized ring present at base of cheilostome; wall of pharyngostome lightly cuticularized and with three transverse cuticularized pieces arranged in a broken ring, one in each of the dorsal and ventrosublateral sectors. Pharynx muscular, surrounding most of buccal cavity, without posterior bulb; ducts of pharyngeal glands not observed. Nerve ring located at one third of pharynx length from anterior. Secretory-excretory system usually indistinct; pore located posterior to nerve ring near middle of pharynx, ventral gland not observed. Cardia surrounded by intestine, 18–30 μm long.

Reproductive system diorchic with two opposed and outstretched testes; anterior testis located to the left of intestine and posterior testis to the right of intestine. Sperm cells globular, small, 4–5 \times 5–7 μm . Spicules slender, 2.5–3.9 cloacal body diameters long, strongly cuticularised, with rounded lateral extensions distally bearing numerous minute spines. Gubernaculum elongated, thin proximally, without dorsocaudal apophyses or crurae. Precloacal supplements absent. Rectal glands and ejaculatory glands not observed. Tail conicocylindrical, with numerous subventral setae and sparse subdorsal setae, 6–14 μm long, three terminal setae 26–33 μm long. Three caudal glands present.

Female

Similar to males but additional setae absent, rows of subcephalic setae posterior to amphids with fewer (5–8) setae, oval amphids with faint contours, and tail with sparsely distributed setae. Reproductive system with single anterior outstretched ovary located to the left of intestine, mature egg 49 \times 101 μm ; spermatheca present posterior to vulva. Vulva located at two thirds of body length from anterior body extremity; single vaginal gland present.

Family incertae sedis **Aegialoalaimidae** Lorenzen, 1981

Diagnosis (emended from Holovachov 2015)

Cuticle smooth or finely annulated. Lateral alae absent. Epidermal glands absent. Somatic sensilla present. Labial region rounded, continuous with body contour. Inner labial sensilla indistinct. Outer labial sensilla pore-like or papilliform, located on outer surface of lips. Cephalic sensilla papilliform or setiform, located at base of labial region, anterior to amphid. Amphidial aperture circular. Subcephalic and cervical sensilla, deirid and ocelli absent. Secretory-excretory system present; renette cell located opposite to ventral side of pharynx, cardia or anterior part of intestine. Excretory ampulla present. Excretory duct very short, usually opens near level of nerve ring in males and further anteriorly in females. Stoma small, undifferentiated. Pharynx divided into anterior long tubular section with strongly cuticularised lumen and weakly developed tissue, and strongly muscularized oval basal bulb. Cardia cylindrical or conoid, partly enveloped by intestinal tissue in its posterior part. Female reproductive system didelphic, amphidelphic, ovary branches reflexed antidromously. Spermatheca present, axial. Vulva equatorial, transverse. Vagina thick; pars refringens vaginae absent. Male reproductive system diorchic, both testes outstretched. Spicules symmetrical, straight or arcuate; gubernaculum present or absent. Copulatory apparatus composed of a row of midventral precloacal sensilla (absent in some species). Postcloacal sensilla absent. Tail similar between sexes, conoid or subcylindrical with rounded terminus. Three caudal glands present, with common or multiple openings.

Remarks

This family was placed within the order Plectida by De Ley & Blaxter (2004) but was later considered incertae sedis by Holovachov (2014) due to lack of molecular data and unclear phylogenetic affinities. The placement of this family remains uncertain despite recent molecular analyses (Leduc & Zhao 2021).

Genus *Aegialoalaimus* de Man, 1907

Tubuligula Boucher & Helléuët, 1977: 29 op. Jensen, 1978: 229–230

Type species

Aegialoalaimus elegans de Man, 1907.

Diagnosis (from Holovachov 2015)

See family diagnosis.

Remarks

The genus currently comprises five valid species (Leduc & Zhao 2021) and was revised by Holovachov (2015).

Aegialoalaimus magnus sp. nov.

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Figs 13–15, Table 6

Diagnosis

Aegialoalaimus magnus sp. nov. is characterized by body length 2.8–3.3 mm, papilliform cephalic sensilla, amphids with strongly cuticularized outline and central region with pitted appearance, radiating, cuticularized processes surrounding junction of pharyngostome and cheilostome, secretory-excretory pore located at or near level of nerve ring and ventral gland well posterior to cardia, spicules 1.4–1.6 cloacal body diameters long, well-developed gubernacular apophyses, 11–12 inconspicuous preloacal supplements, and conical tail 2.8–3.5 cloacal or anal body diameters long.

Differential diagnosis

The new species differs from all other species of the genus in the longer body (2.8–3.3 vs < 2.0 mm in all other species), gubernaculum with conspicuous apophyses (vs apophyses absent in all other species) and greater number of preloacal supplements (11–12 vs 0–8 in all other species).

Etymology

The species name is derived from the Latin ‘*magnus*’ meaning ‘large’, ‘great’ and refers to the relatively large size of the species.

Material examined**Holotype**

NEW ZEALAND • ♂; Hikurangi Margin, Mungaroa cold seep site; 41.9376° S, 175.3110° E; 2075 m water depth; collected on 7 Jul. 2019; sandy mud sediment (97% silt/clay, mean particle size 19 µm), voyage TAN1904, station 18; NIWA154918.

Paratypes

NEW ZEALAND • 2 ♀♀; same collection data as for holotype; NIWA154920 • 1 ♂; Glendhu cold seep site; 41.7695° S, 176.0882° E; 1993 m depth; collected 10 Jul. 2019; sandy mud sediment (88% silt/clay, mean particle size 27 µm), voyage TAN1904, station 40; NIWA 154919.

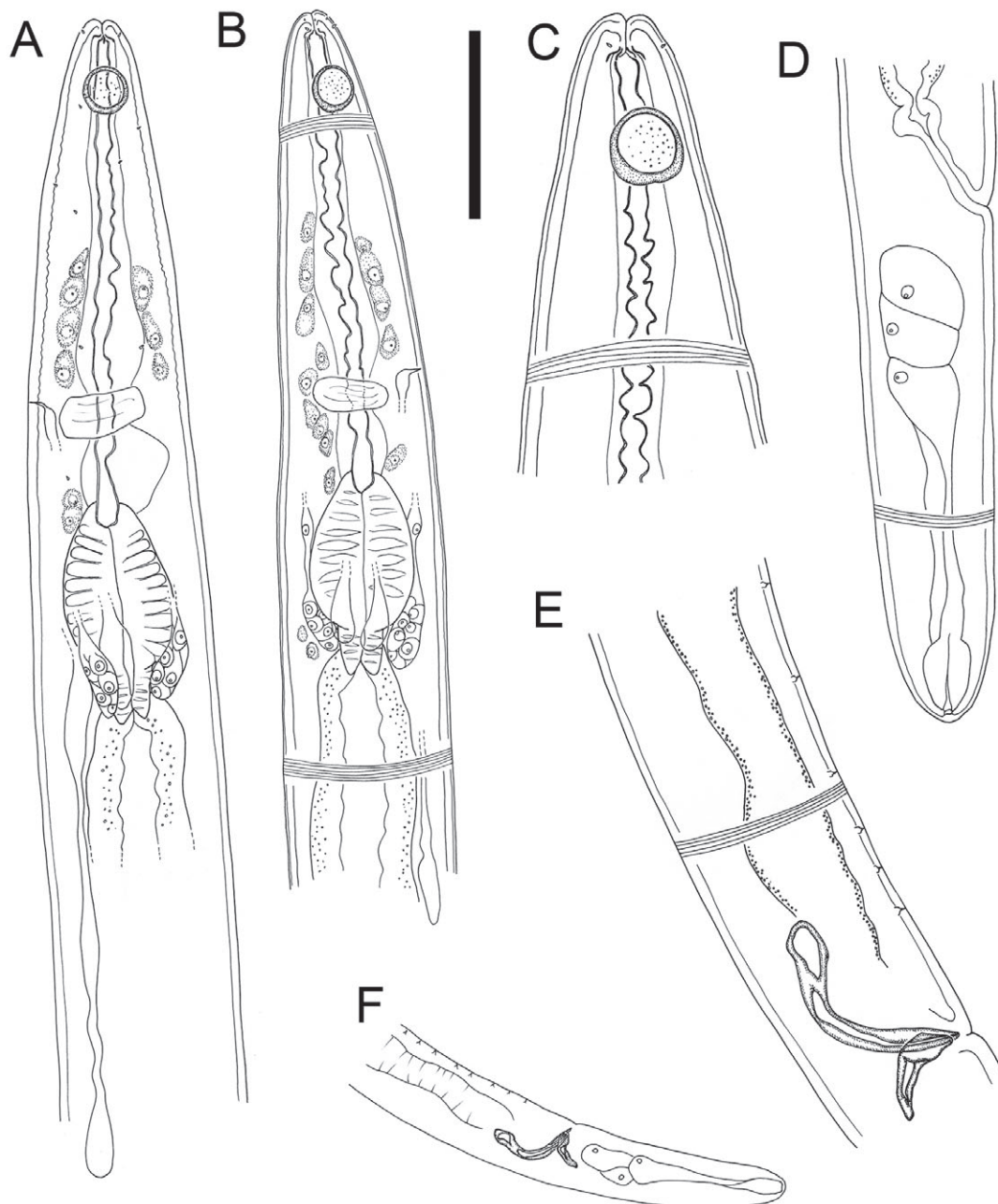


Fig. 13. *Aegialoalaimus magnus* sp. nov. **A–B, D.** Paratype (NIWA154920). **C, E–F.** Holotype (NIWA 154918). **A–B.** Female anterior body region. **C.** Male cephalic region. **D.** Female posterior body region. **E.** Male copulatory apparatus. **F.** Male posterior body region. Scale bar: A–B = 100 µm; C = 60 µm; D–E = 50 µm; F = 125 µm.

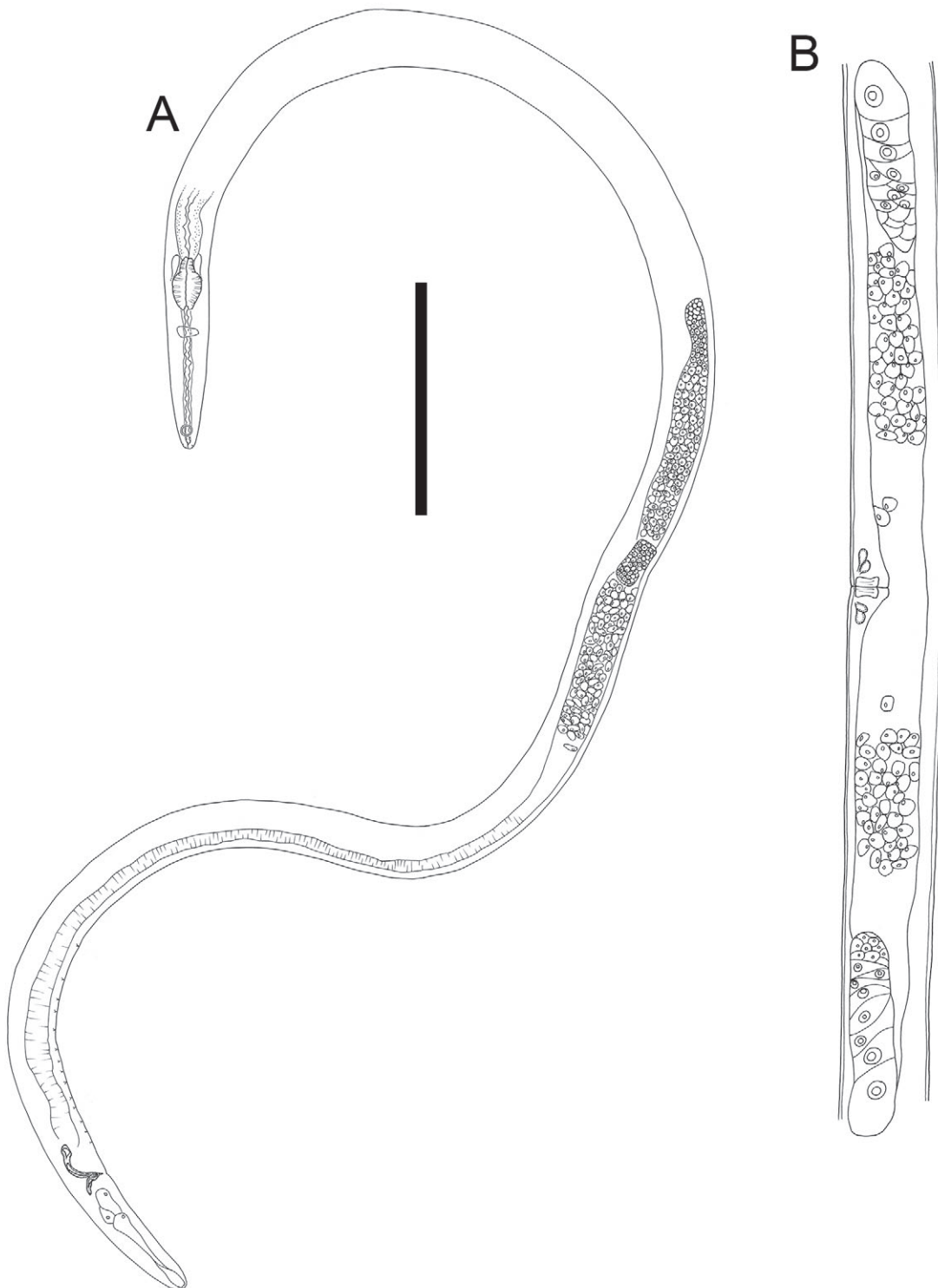


Fig. 14. *Aegialoalaimus magnus* sp. nov. **A.** Entire male, holotype (NIWA154918). **B.** Female reproductive system, paratype (NIWA154920). Scale bar: A = 300 μ m; B = 175 μ m.

Type habitat and locality

New Zealand continental slope, Hikurangi Margin, Mungaroa and Glendhu cold seeps.

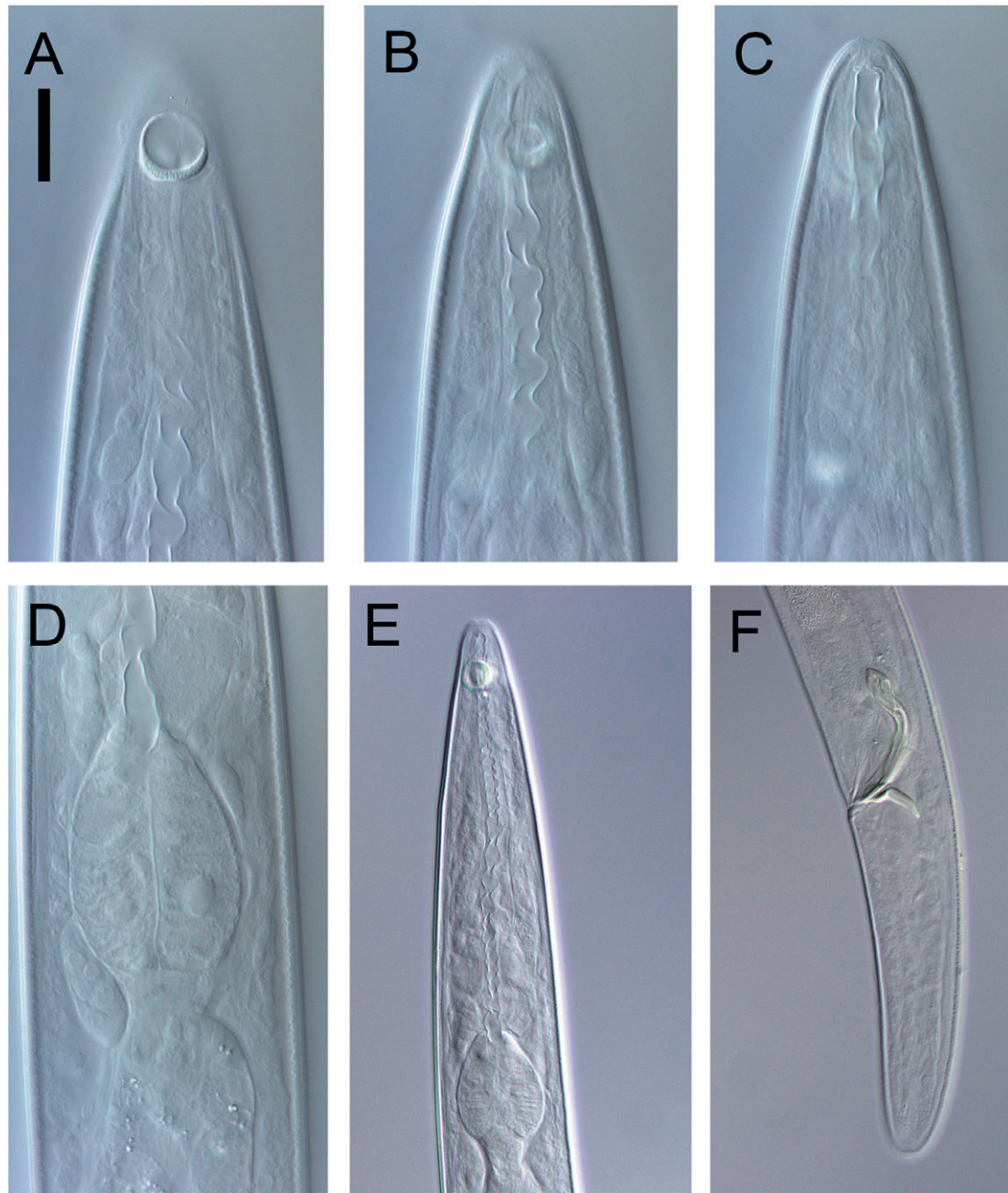


Fig. 15. *Aegialoalaimus magnus* sp. nov. Light micrographs. **A–D.** Paratype (NIWA154920). **E–F.** Holotype (NIWA154918). **A.** Anterior portion of female showing amphid. **B.** Anterior portion of female showing cephalic sensilla and buccal cavity. **C.** Anterior portion of female showing buccal cavity. **D.** Junction of pharynx and intestine. **E.** Anterior body portion of male. **F.** Posterior body portion of male. Scale bar: A–D = 20 μ m; E = 44 μ m; F = 50 μ m.

Table 6. Morphometrics (μm) of *Aegialoaliamus magnus* sp. nov. Abbreviations: a = body length/maximum body diameter; b = body length/pharynx length; c = body length/tail length; c' = tail length/anal or cloacal body diameter; cbd = corresponding body diameter; L = total body length; V = vulva distance from anterior end of body; %V = $V/\text{total body length} \times 100$.

	Males		Females	
	Holotype	Paratype	Paratypes	
Specimen	M1	M2	F1	F2
L	3261	2925	3068	2846
a	43	42	39	42
b	14	14	14	13
c	16	17	18	16
c'	3.3	2.8	3.1	3.5
Body diam. at cephalic setae	16	19	16	15
Body diam. at amphids	27	26	29	26
Length of cephalic sensilla	1	1	1	1
Amphideal fovea height	16	15	16	15
Amphideal fovea width	14	16	14	15
Amphideal fovea width/cbd (%)	52	62	48	58
Amphideal fovea from anterior end	19	17	17	17
Nerve ring from anterior end	160	124	127	126
Nerve ring cbd	59	61	56	55
Pharynx length	238	211	214	214
Pharyngeal bulb diam.	43	41	42	37
Pharyngeal bulb length	53	55	53	55
Pharynx cbd at base	65	66	63	62
Max. body diam.	76	70	78	67
Spicule length	93	86	–	–
Gubernacular apophyses length	25	26	–	–
Cloacal/anal body diam.	60	60	56	51
Tail length	199	169	172	178
V	–	–	1531	1428
%V	–	–	50	50
Vulval body diam.	–	–	78	67

Description

Male

Body colourless, cylindrical along most of its length, tapering slightly towards both extremities. Cuticle with fine transverse striations without lateral differentiation. Body pores and epidermal glands absent. A few sparse, short somatic papillae, 1 μm long, present in anterior pharyngeal region. Cephalic region slightly rounded; lip region poorly developed, continuous with body contour, lips fused. Inner labial papillae not observed; six short outer labial papillae, < 1 μm long, located slightly anterior to four slightly longer cephalic papillae, 1–1.5 μm long. Subcephalic setae absent. Amphideal fovea circular with strongly cuticularized outline and central region with pitted appearance, situated well posterior to cephalic sensilla, 0.6–0.7 cbd from anterior end. Ocelli

absent. Oral opening termina. Cheilostome is a narrow tube 7–8 μm long; pharyngostome 4–6 μm wide, indistinguishable from the cuticularised lumen of the pharynx. Six short and cuticularized radiating processes surrounding junction of pharyngostome and cheilostome, S-shaped. Pharynx divided into two sections: anterior tubular part and posterior (basal) bulb. Tubular part of the pharynx is 163–196 μm long, 4–8 μm wide, with irregular contour, surrounded by thin sheath of non-muscular tissue. Posterior bulb muscular, oval-shaped, surrounded by six elongated glands with ducts extending anteriorly, each comprised of multiple nucleated cells. Pharyngeal glands sometimes visible. Nerve ring located at 59–67% of pharynx length from anterior. Secretory-excretory system present; pore located at or immediately posterior to level of nerve ring, ampulla small, renette cell located 1.5–2.5 cbd posterior to pharyngeal bulb. Cardia ca 15–18 μm long, partially surrounded by intestine.

Reproductive system diorchic with with two anteriorly-directed testes both located ventrally or to the left of intestine; anterior testis outstretched, posterior testis reflexed. Sperm cells globular, 13–17 \times 9–13 μm , of similar shape and dimensions in both testes. Spicules paired, equal, strongly cuticularized, arcuate and 1.4–1.6 cloacal body diameters long; tapered distal end swollen proximal end (capitulum). Gubernaculum dorso-caudal apophyses slightly bent distally. Ejaculatory and rectal glands not observed. Eleven to twelve inconspicuous tubular precloacal supplements located 15–48 μm apart. Tail conical, with rounded tip, 2.8–3.3 cloacal body diameters long, without somatic setae. Three caudal glands and spinneret present.

Female

Similar to males, but with excretory pore located at or slightly anterior to level of nerve ring. Reproductive system didelphic with two opposed and reflexed ovaries both located ventrally or to the left of intestine; spermatheca absent. Vulva situated at mid-body. Proximal portion of vagina surrounded by constrictor muscle, small vaginal glands present. Uterus wall not cuticularized.

Order Desmodorida De Coninck, 1965

Family **Desmodoridae** Filipjev, 1922

Diagnosis (from Tchesunov 2014)

Cuticle annulated, without dots, but spines, fringes or longitudinal ornamentation may be present. No specialised ambulatory setae at anterior and posterior body ends.

Subfamily **Desmodorinae** Filipjev, 1922

Diagnosis (from Tchesunov 2014)

Cuticle annulated except in cephalic region. Cephalic region with thickened cuticle except in lip region and set off as a conspicuous cephalic capsule. Amphideal fovea generally not surrounded by cuticle annulations; may be located on a cuticularized plate. Buccal cavity mostly with distinct teeth. Pharyngeal bulb round or elongated.

Genus **Desmodora** de Man, 1889

Type species

Desmodora communis (Bütschli, 1874).

Diagnosis (modified from Verschelde *et al.* 1998)

Cuticle without ridges or spines. Cephalic capsule either smooth or partly to entirely ornamented with structures resembling pores or small vacuoles, which have been shown by scanning electron microscopy to not be visible on the cuticle surface (e.g., Fadeeva *et al.* 2016); cephalic setae located either in the lip region or on main part of head capsule. Subcephalic setae sometimes present, when present few in number and mainly located posteriorly to amphideal fovea. Amphideal fovea cryptospiral or multispiral, seldom loop-shaped. Buccal cavity with large dorsal tooth and smaller subventral teeth. Pharynx with oval or circular posterior bulb. Spicules short, arcuate, with capitulum and velum. Precloacal supplements sometimes present, usually pore-like, seldom consisting of cuticular swellings or flaps. Tail usually conical, seldom conico-cylindrical.

***Desmodora parapilosa* sp. nov.**

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Figs 16–18, Tables 7–8

Diagnosis

Desmodora parapilosa sp. nov. is characterized by body length 2.3–3.2 mm, jointed inner labial setae, outer labial setae and cephalic setae, main portion of cephalic capsule with numerous, irregularly distributed pores (or vacuoles), large amphideal fovea with 2.25 turns in males (smaller in females with 1.75–2.0 turns), buccal cavity with large cuticularised dorsal tooth, two smaller ventrosublateral teeth and two lateral, transverse rows of small denticles, arcuate spicules 1.3–1.5 cloacal body diameters long, short, plate-like gubernaculum, vulva at almost two thirds of body length from anterior and conical tail 2.6–3.5 cloacal or anal body diameters long.

Differential diagnosis

The new species is most similar to *Desmodora pilosa* Ditlevsen, 1926 in the shape of the amphids (spiral), presence of pores/vacuoles in the cephalic capsule, buccal cavity armature with rows of denticles and structure of the copulatory apparatus. *Desmodora parapilosa* sp. nov. can be differentiated from the latter by the jointed anterior sensilla (vs not jointed in *D. pilosa*), larger amphids (in males: 51–63 vs 37 % cbd in *D. pilosa*), number of amphid turns (2.25 in males and 1.75–2.0 in females vs 1.25 turns in males and females of *D. pilosa*), and shorter spicules (61–66 vs 72–96 µm in *D. pilosa*).

Etymology

The species name refers to the morphologically similar species *Desmodora pilosa* Ditlevsen, 1926.

Material examined**Holotype**

NEW ZEALAND • ♂; Hikurangi Margin, Uruti South cold seep site; 41.4251° S, 176.3510° E; 1226 m water depth; collected on 13 Jul. 2019; sandy mud sediment (91% silt/clay, mean particle size 23 µm), voyage TAN1904, station 62; NIWA154921.

Paratypes

NEW ZEALAND – Uruti South cold seep site • 3 ♂♂; same collection data as for holotype; NIWA 154922 • 1 ♀; 41.4260° S, 176.3506° E; 1237 m water depth; collected on 14 Jul. 2019; sandy mud sediment (94% silt/clay, mean particle size 18 µm); voyage TAN1904, station 68; NIWA154923 • 1 ♀; Uruti South cold seep site; 41.4253° S, 176.3509° E; 1235 m water depth; collected on 14 Jul. 2019; voyage TAN1904, station 70; NIWA154924.

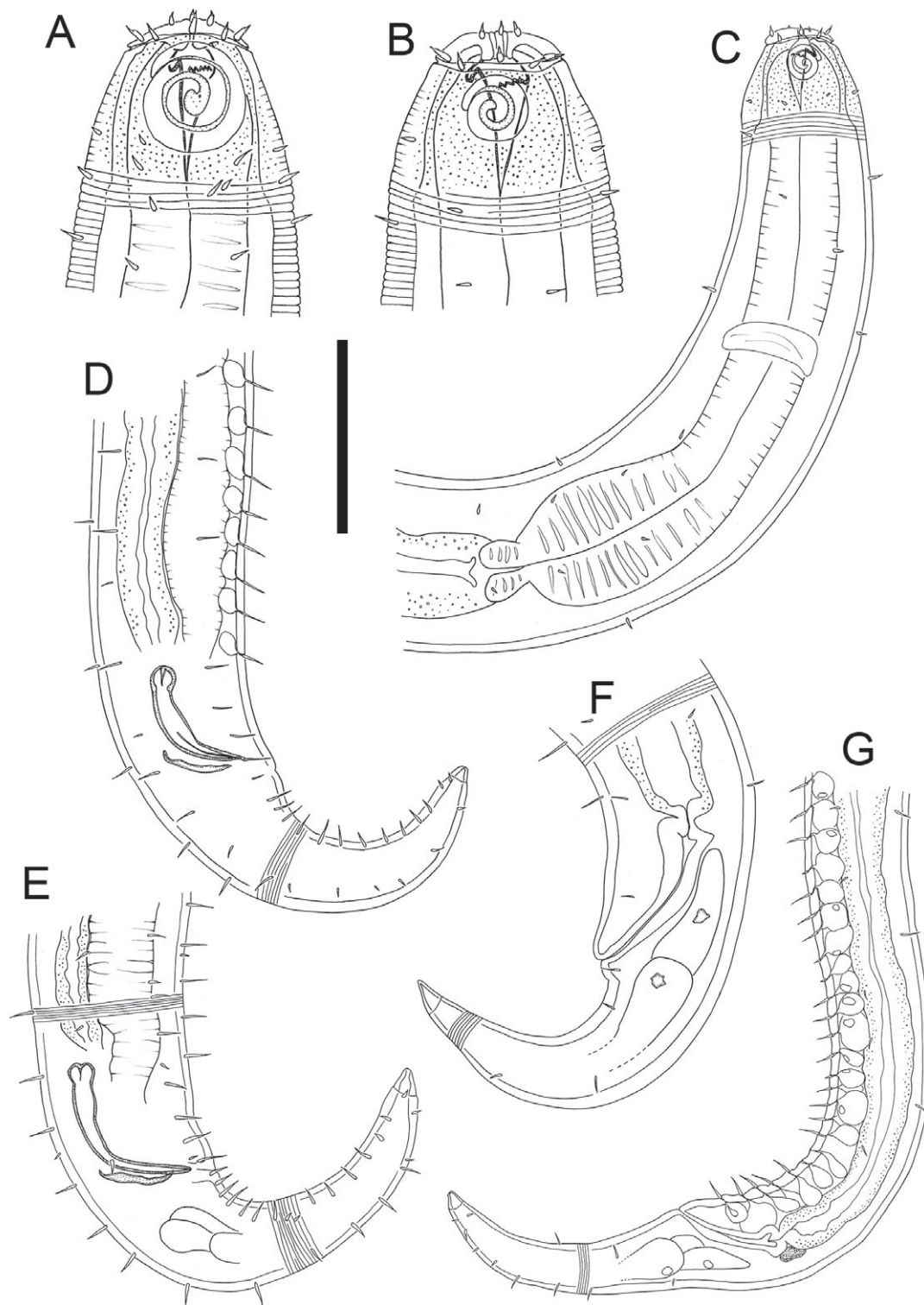


Fig. 16. *Desmodora parapilosa* sp. nov. **A, E.** Holotype (NIWA154921). **B–C, F–G.** Paratype (NIWA 154923). **D.** Paratype (NIWA154922). **A.** Male cephalic region. **B.** Female cephalic region. **C.** Female anterior body region. **D–E.** Male posterior body region. **F–G.** Female posterior body region. Scale bar: A = 50 μ m; B = 40 μ m; C = 75 μ m; D–E = 70 μ m; F = 60 μ m; G = 100 μ m.

Type habitat and locality

New Zealand continental slope, Hikurangi Margin, Uruti South cold seep.

Description

Male

Long cylindrical body, widest at level of pharynx, with slight golden-brown colouration throughout except for main portion of cephalic capsule and intestine wall which which may be strongly stained

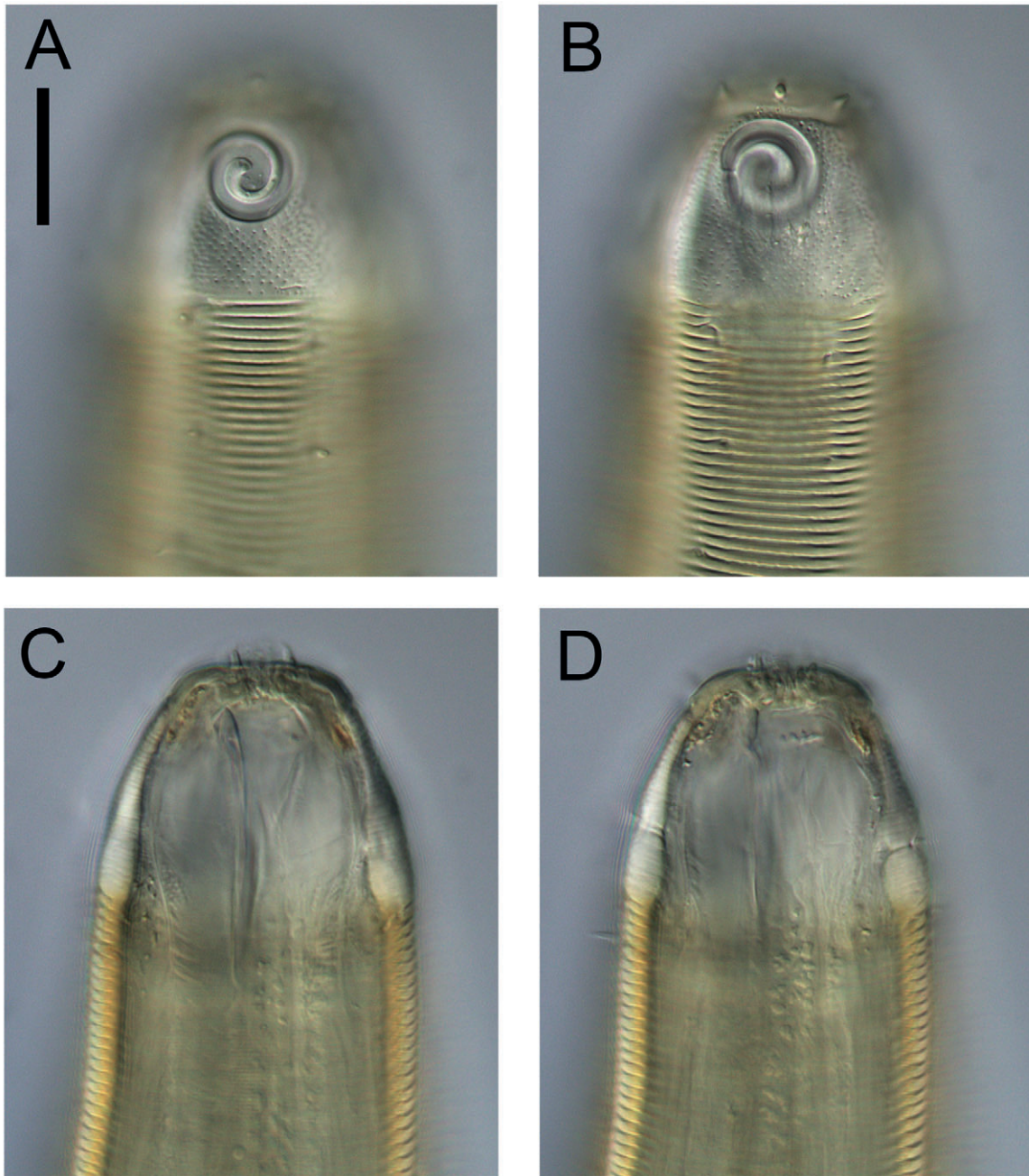


Fig. 17. *Desmodora parapilosa* sp. nov. Light micrographs, paratype (NIWA154923). **A–B.** Female cephalic region showing cuticle, amphid, and cephalic sensilla. **C–D.** Female cephalic region showing buccal cavity. Scale bar = 20 μ m.

by Rose bengal; rounded anterior end and conical tail. Cuticle coarsely annulated with annulations ca 1.2 μm apart; minute cuticle spines present on surface of cuticle, difficult to observe using light microscopy. Several protists often attached throughout body length and some specimens with patches of dense rod-shaped bacteria on outer cuticle, 4–8 μm long. Eight longitudinal rows of somatic setae along entire body length, 4–6 μm long in pharyngeal and mid-body regions, and up to 10 μm long in precloacal region; subventral row of precloacal somatic setae associated with conspicuous epidermal glands. Well-developed cephalic capsule, 40–46 μm wide and 40–46 μm high, consisting of two parts separated by a sutura: a lip portion with relatively thin cuticle and extendable anterior portion and a main region with

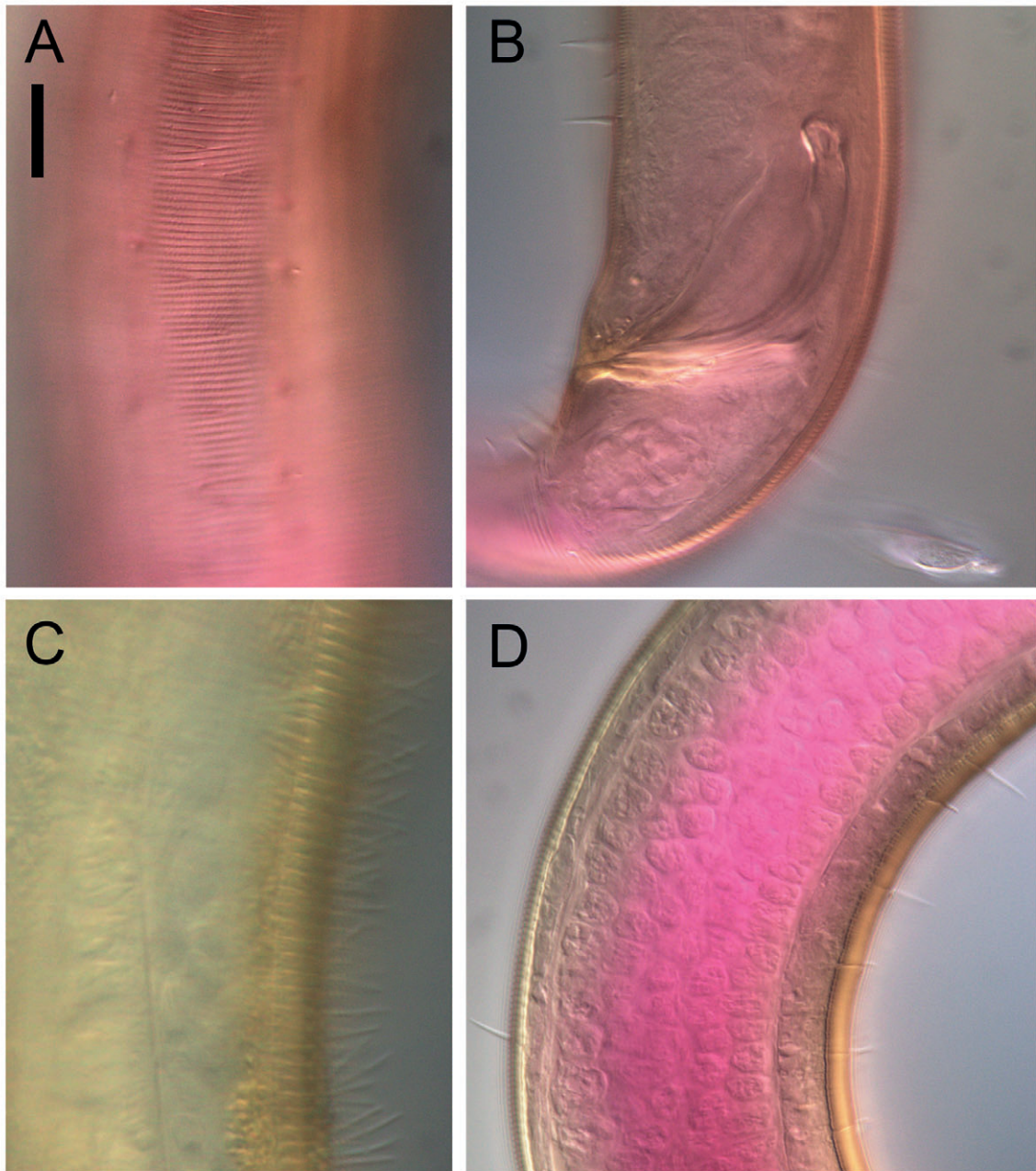


Fig. 18. *Desmodora parapilosa* sp. nov. Light micrographs of male, paratype (NIWA154922). **A.** Cuticle, mid-body region. **B.** Copulatory apparatus. **C.** Cuticle with attached bacteria. **D.** Sperm. Scale bar: A = 20 μm ; B, D = 17 μm ; C = 13 μm .

Table 7. Morphometrics (μm) of *Desmodora parapilosa* sp. nov. Abbreviations: a = body length/maximum body diameter; b = body length/pharynx length; c = body length/tail length; c' = tail length/anal or cloacal body diameter; cbd = corresponding body diameter; L = total body length; V = vulva distance from anterior end of body; %V = V/total body length \times 100.

	Males				Females	
	Holotype	Paratypes			Paratypes	
Specimen	M1	M2	M3	M4	F1	F2
L	2503	2265	2492	2641	2649	3252
a	37	35	39	38	34	37
b	12	12	11	12	10	13
c	20	20	19	19	19	23
c'	2.6	2.7	3.0	3.1	3.3	3.5
Body diam. at cephalic setae	27	26	25	22	22	22
Body diam. at amphids	43	43	39	43	39	38
Length of cephalic sensilla	3–4	3–4	5	4–5	4	4
Amphideal fovea height	29	27	28	30	16	15
Amphideal fovea width	27	22	24	23	14	14
Amphideal fovea width/cbd (%)	63	51	62	53	36	37
Amphideal fovea from anterior end	10	12	4	10	8	11
Nerve ring from anterior end	112	101	118	129	146	133
Nerve ring cbd	61	62	60	65	67	64
Pharynx length	215	196	234	227	254	258
Pharyngeal bulb diam.	44	44	45	46	49	48
Pharynx cbd at base	64	64	64	69	68	69
Max. body diam.	68	64	64	69	78	89
Spicule length	63	66	63	61	–	–
Gubernacular apophyses length	32	36	34	33	–	–
Cloacal/anal body diam.	48	43	45	46	42	40
Tail length	127	114	133	142	138	141
V	–	–	–	–	–	–
%V	–	–	–	–	–	–
Vulval body diam.	–	–	–	–	–	–

thickened cuticle (up to 7 μm thick) and comprising at least three quarters of cephalic capsule. Main portion of cephalic capsule with numerous, dense pores (or vacuoles) irregularly distributed except near base where pores may be arranged in transverse rows; sparse subcephalic setae present at base of cephalic capsule, 2–6 μm long. Six inner and six outer labial setae present on lip region; inner labial setae 2–4 μm long, outer labial setae 4–6 μm long. Four cephalic setae present at level of sutura, 3–5 μm long. Inner labial setae, outer labial setae and cephalic setae all with a single joint near tip where sensilla becomes markedly narrower. Amphideal fovea and aperture large, spiral with 2.25 turns and cuticularized outline, located on main portion of cephalic capsule; amphideal fovea slightly wider than amphideal aperture. Buccal cavity with large cuticularised dorsal tooth and two smaller ventrosublateral teeth; two lateral, transverse rows of small denticles also present. Cylindrical pharynx slightly swollen anteriorly and

Table 8. Comparison of morphometric data of *Desmodora parapilosa* sp. nov. and *Desmodora pilosa* Ditlevsen, 1926 from the literature (modified from Leduc 2021). Abbreviations: ND = no data; * = estimated from figure; ** = morphometric data of females not provided; *** = *Desmodora gorbunovi* Filipjev, 1946 and *D. gorbunovi perforata* Filipjev, 1946 were synonymised with *D. pilosa* by Gerlach (1963); # = Pores present in *D. gorbunovi perforata* but absent in *D. gorbunovi*.

	<i>Desmodora parapilosa</i> sp. nov.		<i>Desmodora aff. pilosa</i>		<i>Desmodora pilosa</i>		<i>Desmodora gorbunovi</i> and <i>D. gorbunovi perforata</i> ***	
Reference	Present study		Leduc (2021)		Ditlevsen (1926)	Jensen (1991)**	Filipjev (1946)	
Location	SW Pacific		SW Pacific		NW Atlantic	Norwegian Sea	Arctic Ocean	
Water depth (m)	1226–1237		6080		1048–1096	970–3062	410–510	
Sex	Males	Females	Male	Female	Female	Females	Males	Females
L	2265–2641	2649–3252	2562	2776	3000	2820, 3180	2950–3600	3300–3400
a	35–39	34–37	43	49	30	30, 34	45–50	35–40
b	11–12	10–13	9	11	13	8, 10	10–11	10–13
c	19–20	19–23	22	21	18	16, 19	18–22	19–21
c'	2.6–3.1	3.3–3.5	2.3	3.2	3.5*	2.5, 2.7*	3.0*	3.2*
Length of inner labial setae	2–4	3	4	4–5	ND	6	5*	ND
Length of outer labial setae	4–6	4–5	3	3	ND	9	6*	ND
Length of cephalic setae	3–5	4	5	4	ND	9	5*	ND
Cephalic sensilla jointed?	Y	Y	N	N	N	N	N	N
Amphid height	27–30	15–16	24	16	ND	21	17*	ND
Amphid width	22–27	14	19	13	ND	20	17*	ND
Amphid width/cbd (%)	51–63	36–37	49	31	37*	23	37*	ND
Amphid turns	2.25	1.75–2.0	1.5	1.25	1.25	1.25	1.25	1.25
Buccal cavity armature	Dorsal + smaller ventrosublateral teeth and two lateral transverse rows of denticles		Dorsal + smaller ventrosublateral teeth and two lateral transverse rows of denticles		ND	Dorsal + smaller ventrosublateral teeth and band of denticles along ventral sector	Small dorsal tooth (ventrosublateral teeth may be present)	
Spicule length	61–66	–	75	–	ND	85, 96	72–80	–
Gubernaculum length	32–36	–	30	–	ND	36, 45	40	–
%V	–	63–64	–	54	56	ND	–	62–65
Cephalic capsule with vacuoles?	Yes	Yes	Yes	Yes	No	Yes	Variable#	Variable#

with oval posterior pharyngeal bulb. Secretory-excretory system not observed. Cardia 12–19 µm long, partially surrounded by intestine.

Reproductive system monorchic with outstretched testis located to the right or left of intestine. Mature sperm cells globular or spherical, 8 × 8–10 µm. Short, arcuate spicules with well-developed capitulum, tapering shaft and distal end, 1.3–1.5 cloacal body diameters long; short, plate-like gubernaculum.

Precloacal supplements and seta not observed. Conical tail with subventral and subdorsal rows of setae. Non-annulated tail tip without perforations. Caudal glands and spinneret present.

Female

Similar to males, but with smaller amphideal fovea with 1.75–2.0 turns and slightly longer tail. Reproductive system didelphic, amphidelphic with reflexed ovaries; position of ovaries relative to intestine not clear in one specimen, in other specimen, anterior ovary located to the left of intestine and posterior ovary to the right. Spermatheca not observed. Vulva located at almost two thirds of body length from anterior. Proximal portion of vagina cuticularised; proximal portion of vagina surrounded by constrictor muscle. Vaginal glands present.

Remarks

The original description of *D. pilosa* by Ditlevsen (1926) based on Northwest Atlantic specimens did not include observations of male specimens or of buccal cavity armature. Ditlevsen (1926) did not describe pores in the cephalic capsule. *Desmodora gorbunovi* Filipjev, 1946 and *Desmodora gorbunovi perforata* Filipjev, 1946 were described based on Arctic Ocean specimens and later synonymized with *D. pilosa* by Gerlach (1963). The former lacks pores in the cephalic capsule whereas the latter is characterized by numerous pores in the cephalic capsule. Both of these are described by Filipjev (1946) as having a buccal cavity with a small dorsal tooth (although small ventrosublateral teeth may be present based on the drawings) without denticles. In his redescription of *D. pilosa* based on specimens from the Norwegian Sea, Jensen (1991) noted strong similarities between his specimens and *Desmodora gorbunovi* including the cephalic capsule with numerous pores, size and arrangement of anterior sensilla and somatic setae, structure of the amphideal fovea, and tail shape. Jensen's specimens, however, have a buccal cavity with a band of numerous denticles, whereas Filipjev's specimens do not have denticles. The descriptions of Filipjev (1946) and Jensen (1991) also show some inconsistencies in body dimensions and size of anterior sensilla and amphideal fovea (Table 8).

Leduc (2021) recently described abyssal nematode specimens from the Southwest Pacific showing similarities to *D. pilosa* although inconsistencies in body size, dimensions, amphid size and cuticle ornamentation were noted. Despite the morphological differences between the Southwest Pacific specimens and the specimens described by Ditlevsen (1926), Filipjev (1946) and Jensen (1991), Leduc (2021) did not erect a new species because further data are required from the type locality of *D. pilosa* (upper continental slope of NW Atlantic) to determine the structure of the buccal cavity armature, presence or absence of pores in the cephalic capsule and male morphology of this species.

A new species, *Desmodora parapilosa* sp. nov., is erected here because the Hikurangi margin specimens can be differentiated from the specimens described by Ditlevsen (1926), Filipjev (1946), Jensen (1991) and Leduc (2021) based on several key characters, i.e., the jointed anterior sensilla, larger amphids with greater number of turns, and shorter spicules. The new species also differs from the Southwest Pacific abyssal specimens in having a lower ratio of a, longer tail, longer gubernaculum, and smaller sperm ($8 \times 8\text{--}10 \mu\text{m}$ vs $10\text{--}11 \times 16\text{--}19 \mu\text{m}$) (Table 8).

Discussion

The core samples used in this study were relatively large (ca 70 cm²) and were processed using a coarse mesh (300 μm), unlike most studies of nematodes and other meiofauna which are typically based on relatively small core samples (< 10 cm²) and processed using a finer (20–63 μm) mesh (Leduc *et al.* 2010). The methodology used in the present study allows to focus on macrofaunal nematode species which are larger and often less abundant than nematode species from meiobenthic samples, and which are therefore often overlooked. Despite their relatively low abundance, these larger species make a

disproportionate contribution to total nematode biomass and are therefore likely to play an important role in benthic food webs (Sharma *et al.* 2022).

The species describe here represent a wide range of feeding groups, ranging from deposit feeders (*Linhomoeus pycnocricus* sp. nov., *Deraionema barbatum* gen. et sp. nov.) to microvores (*Aulostomonema abyssum* gen. et sp. nov., *Aegialoalaimus magnus* sp. nov.) and epigrowth feeders (*Desmodora parapilosa* sp. nov.) (Moens & Vincx 1997). The stylet-like feeding apparatus found in the genus *Siphonolaimus* is unique among marine nematodes and is similar to the feeding apparatus of the parasitic Tylenchida Thorne, 1949 which mostly attack plant roots but also other parts of plants as well as fungi and terrestrial arthropods (Subbotin 2014). There have been no observations of feeding behaviour of *Siphonolaimus* to date and their diet remains to be determined. *Siphonolaimus* belongs to the same subfamily as *Astomonema* Ott, Rieger, Rieger & Enderes, 1982 and *Parastomonema* Kito, 1989, two genera characterized by lack of buccal cavity and which host endosymbiotic bacteria. There are however no signs of endosymbiosis in *Siphonolaimus*. Further analyses will be required to determine the distribution of different feeding types across seep and background locations, but the presence of several different feeding modes in the species described here indicates that a range of food sources are exploited by macrofaunal nematodes at the Hikurangi Margin seep sites.

The present study is the first to provide data on cold seep nematode species in the New Zealand region. *Desmodora*, *Linhomoeus*, and *Aegialoalaimus* have been reported from cold seep habitats previously (Vanreusel *et al.* 2010b; Pape *et al.* 2011), however no records of *Siphonolaimus* from cold seeps could be found in the literature. This genus has been recorded at a number of deep-sea sites from shelf depths to 4220 m, including canyon or channel habitats (Miljutin *et al.* 2010). The newly described genus *Aulostomonema* gen. nov. does not appear to have a close association with seeps, as the type specimens were obtained from the seep edge and outer periphery of the Mungaroa seep site. The specimens of *Deraionema* gen. nov. described here, however, come from the seep centres of the Uruti South and Mungaroa seep sites, indicating a potential close association for this genus with methane seepage. Ongoing work on the taxonomy, ecology and distribution of nematode communities at the Hikurangi Margin seep sites will help determine spatial patterns in abundance and species distributions in more detail, including the identification of species/taxa with affinities with methane seepage.

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