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Research article

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New and known *Halichoanolaimus* de Man, 1886 species (Nematoda: Selachinematidae) from New Zealand's continental margin

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Abstract. The Selachinematidae is a globally distributed family of predatory nematodes found from shallow waters to the abyssal plain. Here, three new species of *Halichoanolaimus* de Man, 1886 (*H. ossilagulus* sp. nov., *H. funestus* sp. nov. and *H. pumilus* sp. nov.) and one known species (*H. ovalis* Ditlevsen, 1921) are described from the New Zealand continental margin, thus bringing the total number of selachinematid species recorded from the New Zealand region to 14 and the total number of species of *Halichoanolaimus* to 26. The range of *H. ovalis* is extended from the Southern Ocean to the Southwest Pacific Ocean (latitude 42° S to 53° S); the depth range of this species, which was originally described from the littoral zone, is also extended to 1061 m depth. Dorsosublateral rows of pore complexes and pseudocoelomocytes, features that have either rarely or not been recorded previously in the genus, were observed in all four species described here. The taxonomic significance of these features remains to be ascertained for the family and will require observations of other species of *Halichoanolaimus* and selachinematid genera. Pseudocoelomocytes and pore complexes may have an excretory function, thus aiding to process the waste products of digestion in selachinematid taxa with a blind intestine.

Keywords. Blind intestine, pseudocoelomocytes, pore complexes, continental slope, Kaikōura Canyon.

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Introduction

The Selachinematidae Cobb, 1915 is a globally distributed family of predatory nematodes most commonly reported from shallow water environments (Warwick 1971; Okhlopkov 2002; Tchesunov & Okhlopkov 2006), but occurring as deep as the abyssal plain (Miljutin *et al.* 2010). The family is characterized by a large buccal cavity with cuticularized rhabdions and/or mandibles, and is currently divided into two subfamilies, the Selachinematinae and Choniolaiminae Schuurmans-Stekhoven & Adam, 1931 based on buccal cavity armature (Tchesunov 2014). The monophyly of these two subfamilies, however, is not supported by molecular phylogenetic analyses (Leduc & Zhao 2016). The predatory feeding habits of selachinematids has been repeatedly confirmed by observations of nematode prey remnants in the intestine of several species (e.g., Allgén 1933; Okhlopkov 2003). Some selachinematid genera,

i.e., *Halichoanolaimus* de Man, 1886, *Cobbionema* Filipjev, 1922 and *Bendiella* Leduc, 2013 are characterized by a blind intestine, an unusual feature among free-living nematodes.

In the New Zealand Exclusive Economic Zone, three selachinematid species have been reported from coastal waters (Leduc & Gwyther 2008; Leduc & Zhao 2015) and a further eight species have been described from the shelf and continental slope down to a depth of 1240 m (Leduc 2013; Leduc & Zhao 2016). *Halichoanolaimus* is the most common and diverse genus of the Selachinematidae, with 23 valid species described to date (Zograf *et al.* 2015; Leduc & Zhao 2016), three of which have been recorded from the New Zealand region. Here, I describe three new species from continental slope and submarine canyon habitats of New Zealand and provide a new deep-sea record for *Halichoanolaimus ovalis* Ditlevsen, 1921, which was originally described from the littoral zone of New Zealand's subantarctic islands.

Material & Methods

Samples were obtained from three of New Zealand's major bathymetric features: Kaikōura Canyon, Chatham Rise and Challenger Plateau. Kaikōura Canyon lies to the east of the South Island (~42°S) and has been described as one of the most productive deep-sea benthic habitats known (De Leo *et al.* 2010). Chatham Rise is a submarine ridge that extends eastwards from the South Island of New Zealand, over water depths ranging from ca 250 to 3000 m. The rise lies beneath the Subtropical Front (STF), a region associated with heightened primary productivity (Bradford-Grieve *et al.* 1997; Murphy *et al.* 2001). Challenger Plateau encompasses water depths ranging from ca 400 to 3000 m in an area of generally low biological productivity to the northwest of the South Island (Murphy *et al.* 2001). Several sites (405–1420 m water depth) were sampled along the Kaikōura Canyon axis in May 2010 during National Institute of Water and Atmospheric Research (NIWA) cruise TAN1006. Samples were collected across a similar water depth range on Chatham Rise and Challenger Plateau in 2007 during NIWA cruise TAN0705 (March–April) and TAN0707 (May–June), respectively.

Sediment samples were collected using an Ocean Instruments MC-800A multicorer (core internal diameter = 9.5 cm). Each sample consisted of one subcore of internal diameter 26 mm taken to a depth of 5 cm. Samples were fixed in 10% formalin and stained with Rose Bengal. Samples were subsequently rinsed on a 45 µm sieve to retain nematodes. Nematodes were extracted from the remaining sediments by Ludox flotation 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), the terminology of stoma structures follows Decraemer *et al.* (2014) and the terminology of cuticular pore-like structures follows Leduc & Zhao (2018). The ratio 'F' expressing the length of the cylindrical portion of the tail as a percentage of total tail length was calculated following Zograf *et al.* (2015). Because females of *Halichoanolaimus* have a blind intestine and lack an anus, tail length was measured beginning from the posterior extremity of the intestine. Type specimens are held in the NIWA Invertebrate Collection (Wellington), and the National Nematode Collection of New Zealand (Auckland).

List of abbreviations

- a = body length/maximum body diameter
- b = body length/pharynx length
- c = body length/tail length
- c' = tail length/body width at level of cloacal opening or anus

cbd	=	corresponding body diameter
F	=	length of cylindrical portion of tail as % of total tail length
L	=	total body length;
n	=	number of specimens
V	=	vulva distance from anterior end of body
%V	=	V/total body length × 100

Results

Phylum Nematoda Cobb, 1932
 Class Chromadorea Inglis, 1983
 Subclass Chromadoria Adamson, 1987
 Order Chromadorida Chitwood, 1933
 Family Selachinematidae Cobb, 1915
 Subfamily Choniolaiminae Schuurmans Stekhoven & Adam, 1931

Genus *Halichoanolaimus* de Man, 1886

Smalsundia Allgén, 1929: 454.

Type species

Halichoanolaimus robustus (Bastian, 1865) de Man, 1886.

Diagnosis (modified from Tchesunov 2014)

Cuticle with lateral differentiation in the form of larger and more widely spaced punctations. All anterior sensilla usually papilliform. Cuticularized rhabdions of anterior buccal cavity (gymnostome) with pointed teeth (denticles) at posterior extremity; posterior portion of buccal cavity (stegostome) surrounded by three Y-shaped pairs of cuticularized rhabdions. Pharynx without anterior or posterior bulb. Intestine of adult stages blind. Precloacal supplements usually papilliform or setiform. Tail with cylindrical proximal portion and often elongated cylindrical distal portion.

Remarks

A key to males of all 22 valid species of *Halichoanolaimus* was provided by Zograf *et al.* (2015). An additional species was subsequently described by Leduc & Zhao (2016).

Halichoanolaimus ovalis Ditlevsen, 1921

Table 1, Figs 1–3

Material examined

NEW ZEALAND • 2 ♂♂, 1 ♀; Kaikōura Canyon, 42.5082° S, 173.6325° E; water depth 1061 m; voyage TAN1006 station 7, site K4; 3 May 2010; NIWA 139245.

Type locality

North Arm of Carnley Harbour, Auckland Islands.

Description

Males

BODY. Cylindrical, tapering slightly towards anterior extremity. Cuticle with transverse rows of punctations; lateral differentiation consisting of larger, more widely spaced punctations. Two dorsosublateral rows of

Table 1. Morphometrics (μm) of three new and one known species of *Halichoanolaimus* de Man, 1886 from New Zealand’s continental margin. Abbreviations = a, body length/maximum body diameter; b, body length/pharynx length; c, body length/tail length; c’, tail length/body diameter at level of cloacal opening or anus; cbd, corresponding body diameter; F, length of cylindrical portion of tail as % of total tail length; L, total body length; V, vulva distance from anterior end of body; %V, V/total body length \times 100. *Because females lack an anus, tail length in females was measured from posterior edge of blind intestine, and the commonly used morphometric “anal body diameter” was measured at posterior edge of the blind intestine.

Species	<i>Halichoanolaimus ovalis</i> Ditlevsen, 1921			<i>Halichoanolaimus ossilagulus</i> sp. nov.			<i>Halichoanolaimus funestus</i> sp. nov.			<i>Halichoanolaimus pumilus</i> sp. nov.	
	Males	Female		Males	Females		Males	Females		Male	Female
Specimen	M1	M2	F1	Holotype M1	Paratype M2	Paratype F1	Paratype F2	Holotype M1	Paratype F1	Paratype F2	Holotype
L	1461	1453	1356	1068	966	1192	1267	2709	3006	2786	756
a	22	22	24	22	17	18	17	23	20	20	15
b	7	7	5	7	6	7	8	7	9	9	7
c*	8	9	7	11	9	13	9	8	10	9	6
c’*	4.1	3.7	5.0	2.9	3.0	2.4	3.2	6.3	5.7	5.1	4.7
Head diam. at ceph. setae	29	29	30	20	23	24	23	40	46	44	20
Length of outer labial sensilla	2	2	2	1–2	1–2	1–2	1–2	3–4	4	3	3–4
Length of cephalic sensilla	2	2	2	1–2	1–2	1–2	1–2	3–4	4	3	3–4
Amphid height	12	12	12	8	8	8	9	15	12	13	10
Amphid width	15	16	16	12	11	11	11	17	17	17	15
Amphid width/cbd (%)	38	38	40	43	37	33	33	29	27	30	58
Amphid from anterior end	15	15	16	6	7	8	11	26	24	23	8
Nerve ring from anterior end	103	87	114	83	89	99	92	156	145	154	65
Nerve ring cbd	54	61	50	44	51	54	56	94	117	113	40
Excretory pore from anterior end	117	105	147	95	96	111	101	212	183	184	84
Pharynx length	211	209	256	150	151	162	160	377	348	317	115
Pharyngeal diam. at base	43	46	38	33	39	42	56	81	90	93	30
Pharynx cbd	61	64	53	47	53	56	64	110	125	121	42
Max. body diam.	65	66	56	48	58	68	75	120	148	141	49
Spicule length	68	73	–	56	59	–	–	97	–	–	49
Gubernacular apophyses length	37	43	–	26	24	–	–	47	–	–	24
Cloacal/anal body diam.*	45	46	40	33	36	38	46	54	55	62	29
Tail length*	183	170	200	95	109	91	147	341	311	317	136
F	68	65	66	54	57	48	72	77	80	77	61
V	–	–	639	–	–	625	574	–	1341	1288	–
%V	–	–	47	–	–	52	45	–	45	46	–
Vulval body diam.	–	–	56	–	–	68	75	–	130	137	–

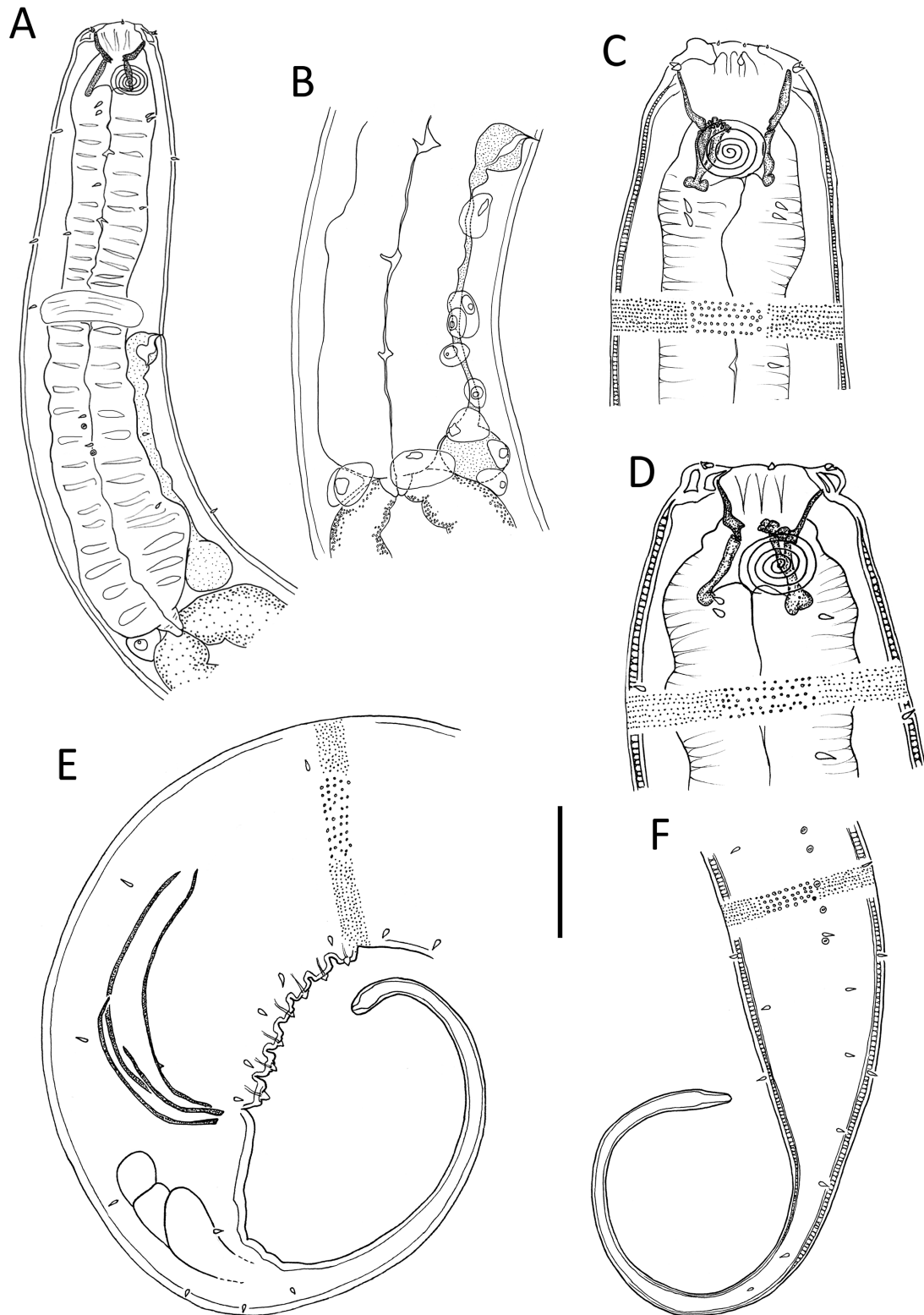


Fig. 1. *Halichoanolaimus ovalis* Ditlevsen, 1921 **A.** Male anterior body region. **B.** Posterior male pharyngeal region and anterior intestinal region showing location of pseudocoelomocytes. **C.** Female cephalic region. **D.** Male cephalic region. **E.** Male posterior body region. **F.** Female posterior body region. Scale bar: A = 50 μ m; B = 37 μ m; C, E = 27 μ m; D = 25 μ m; F = 35 μ m.

pore complexes extending from posterior to nerve ring to cloacal region, each pore complex ca 1.5 μm in diameter, becoming more closely spaced posteriorly. Up to two or three ventrosublateral pore complexes also present in pharyngeal region or slightly posterior to pharynx. Eight longitudinal rows of short, sparse somatic setae, 2–3 μm long. Cephalic region slightly rounded, with slight indentation immediately posterior to cephalic setae. Lip region not conspicuously differentiated, bearing six inner labial papillae. Six short

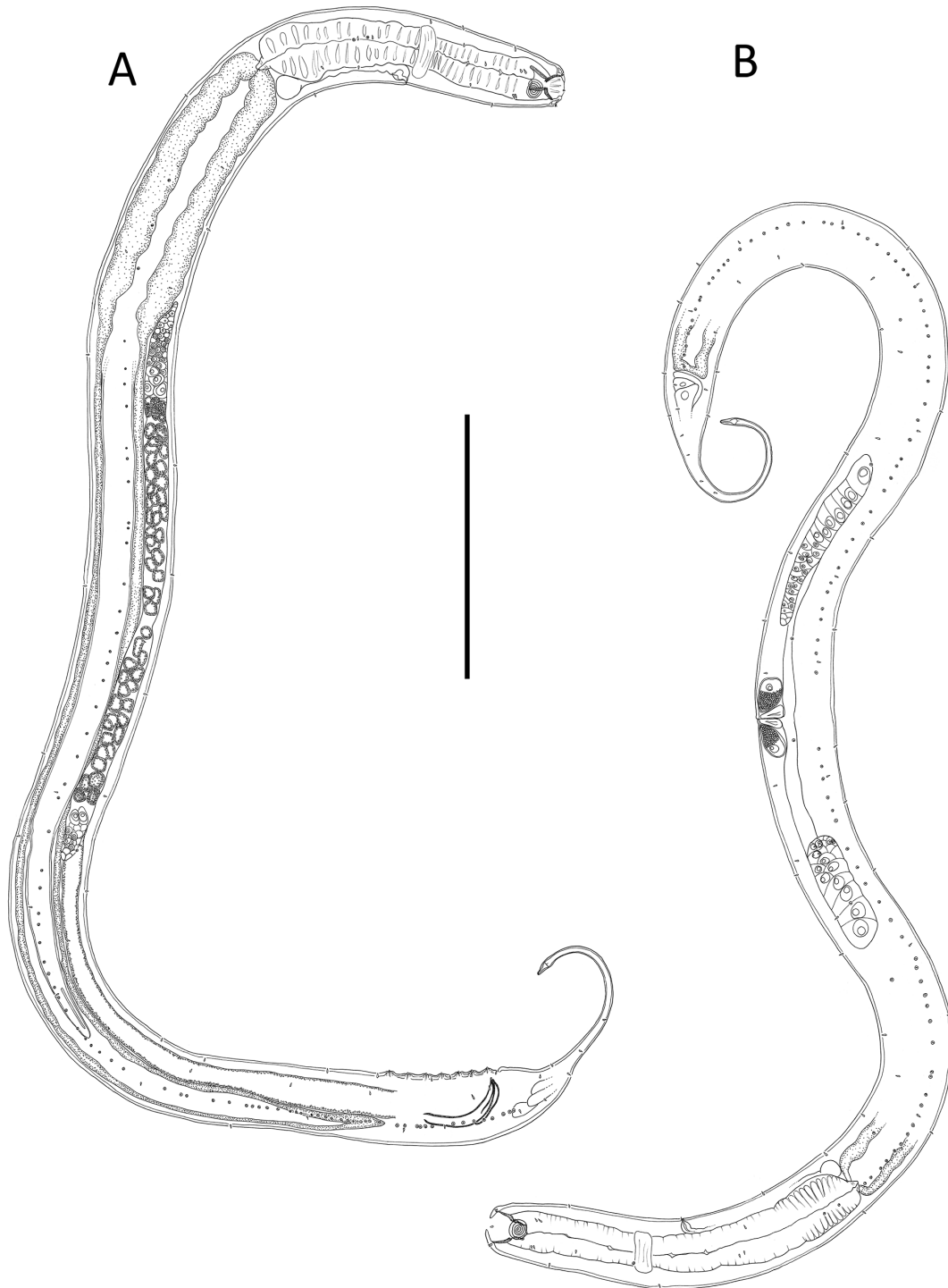


Fig. 2. *Halichoanolaimus ovalis* Ditlevsen, 1921 A. Entire ♂. B. Entire ♀. Scale bar: 200 μm .

outer labial papillae, 2 μm long, located at base of labial region and at same level as four cephalic papillae of same length. Amphideal fovea multispiral with 5.0 to 5.25 turns, situated ~ 0.4 cbd from anterior end. Buccal cavity (pharyngostome) large, 25–30 μm deep, divided into anterior (gymnostome) and posterior

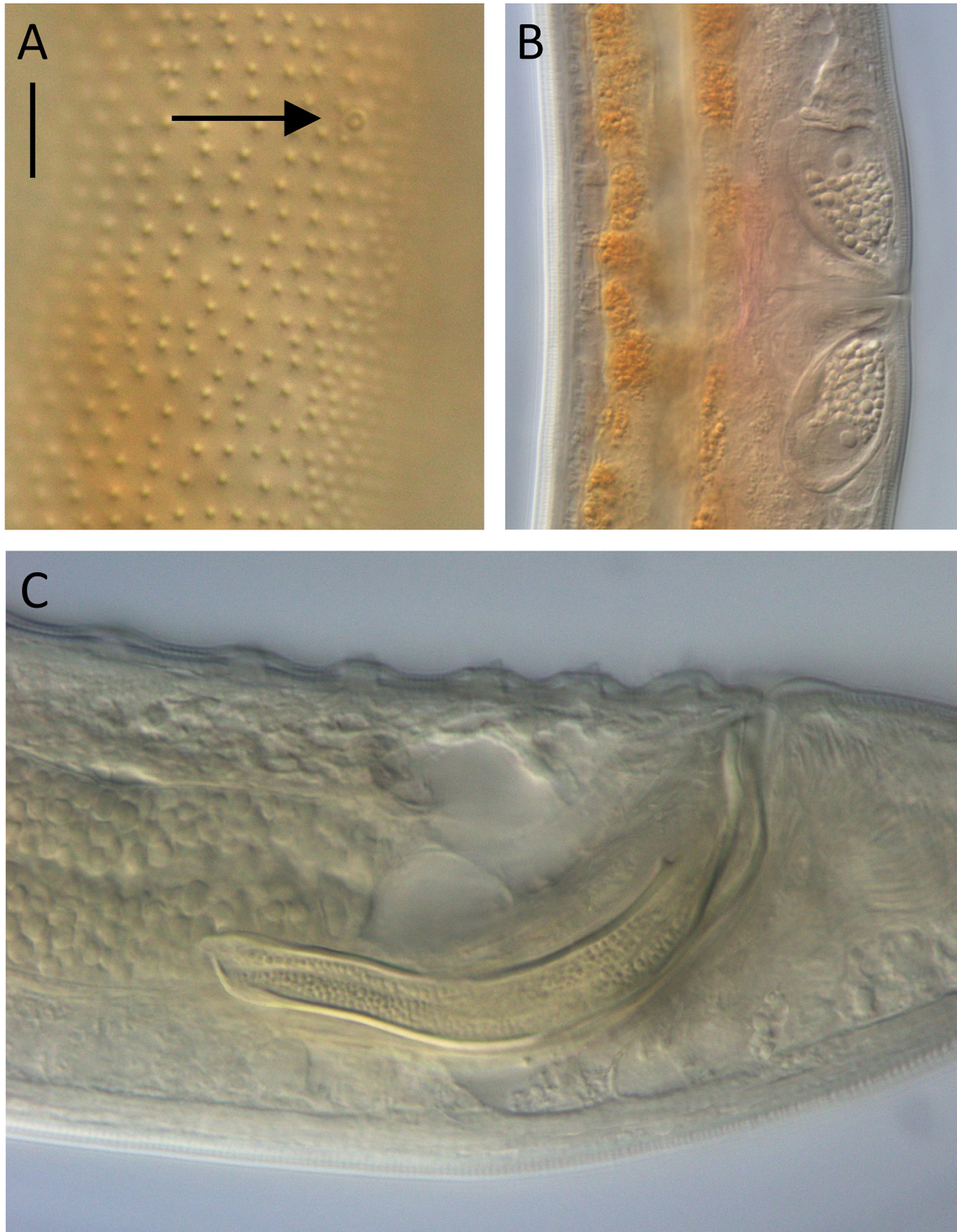


Fig. 3. *Halichoanolaimus ovalis* Ditlevsen, 1921. Light micrographs. **A.** Female cuticle showing lateral differentiation and pore complexes (arrow). **B.** Vulva, showing vaginal glands. **C.** Copulatory apparatus. Scale bar: A, C = 5 μm ; B = 15 μm .

portions (stegostome). Anterior portion of buccal cavity cup-shaped, with three sets of six cuticularized rhabdions, 12–14 μm long, terminating in three sets of at least six pairs (one anterior and one posterior) of denticles; posterior portion of buccal cavity narrower, cylindrical, surrounded by three Y-shaped pairs of cuticularized rhabdions with swollen bases, 15–17 μm long. Pharynx cylindrical, muscular, without anterior or posterior bulb. Nerve ring at ca 45–50% of pharynx length from anterior. Secretory-excretory system present; renette cell up to 18 μm wide and 18 μm long, situated at level of cardia. Several nucleated pseudocoelomocytes also present around base of pharynx and either side of secretory-excretory duct; ampulla slightly smaller than renette cell, pore situated posterior to nerve ring. Cardia small, surrounded by intestine; posterior extremity of intestine blind.

REPRODUCTIVE SYSTEM. Diorchic with outstretched testes. Anterior testis to the right or ventrally to intestine, posterior testis to the left side of intestine. Sperm cells globular, 8–12 \times 15–17 μm . Spicules paired, curved, tapering distally, length 1.5–1.6 body diameters at level of cloacal opening; minute ventral denticle present at one third of spicule length from distal tip, interior of spicules granular in appearance. Gubernaculum consisting of two detached lateral pieces (crurae) tapering distally, median portion of gubernaculum (corpus and cuneus) not visible. Seven precloacal supplements present, consisting of conical papillae set on cylindrical cuticular elevations each with internal duct, supplements located 10–14 μm from each other. Tail conicocylindrical with cylindrical portion ca two thirds of total tail length; a few short and sparse somatic setae present subventrally and subdorsally. Three caudal glands located posterior to spicules, spinneret present.

Females

Similar to males but with slightly longer tail. Reproductive system didelphic-amphidelphic, with reflexed ovaries. Anterior ovary to the left of intestine and posterior ovary to the right of intestine. Vulva situated at mid-body. Mature eggs not observed. Proximal portion of vagina surrounded by constrictor muscle, two large and conspicuous vaginal glands with coarsely granulated cytoplasm and large nucleus present. Intestine blind, no rectum or anus.

Remarks

Halichoanolaimus ovalis was originally described by Ditlevsen (1921) based on two females from the Auckland Islands, and males were later described from the littoral zone of Campbell Island by Allgén (1927) (both Auckland and Campbell islands are located in the Southern Ocean directly south of New Zealand's South Island). The female specimen from Kaikōura Canyon broadly resembles the original description of Ditlevsen (1921), although the Kaikōura Canyon female is shorter (body length 1.4 vs 1.8 mm in *H. ovalis*) and has a higher ratio of 'a' (24 vs 18). Ditlevsen (1921) states that the amphideal fovea of *H. ovalis* females has six turns; however, his figure shows only five turns, which is consistent with the Kaikōura Canyon specimen. The present description is also consistent with the observation of conspicuous vaginal glands with coarsely granulated cytoplasm by Ditlevsen (1921). The two male specimens from Kaikōura Canyon agree well with the description of Allgén (1927) in general body dimensions, although like the Auckland Islands specimens, the Campbell Island specimens are somewhat stouter as indicated by a lower value of 'a' (17) relative to the Kaikōura Canyon specimens (22). In addition, Allgén counted only four amphideal fovea turns in his male specimens compared to five in the Kaikōura Canyon specimens. However, the structure of the copulatory apparatus, as well as the shape and number of precloacal supplements, are the same.

The intestine of one of the male *H. ovalis* specimens contained the anterior half of a nematode prey which was identified as belonging to *Halalaimus* de Man, 1888 based on the structure of the cuticle, amphideal fovea and buccal cavity. The intestine of the other *H. ovalis* male (from the same sample) contained the posterior half of a nematode, possibly also belonging to the genus *Halalaimus*.

Halichoanolaimus ossilagulus sp. nov.

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Table 1, Figs 4–6

Diagnosis

Halichoanolaimus ossilagulus sp. nov. is characterized by a body length of 966–1267 μm , amphideal fovea with 4.5 turns in both males and females, rhabdions of anterior portion of buccal cavity ending in three sets of 10 pairs of denticles with single raised denticle in centre of each set, pharyngeal lumen conspicuously cuticularized, single pseudocoelomocyte associated with SE system and located dorsally opposite renette cell, spicule length 1.6–1.7 body diameters at level of cloacal opening, gubernaculum 24–26 μm long, two or three precloacal supplements and tail 2.4–3.2 cbd long with cylindrical portion comprising about half (or three quarters in one female) of total tail length.

Differential diagnosis

The new species is most similar to *H. consimilis* Allg en, 1933 in general body dimensions and number of amphideal fovea turns, but differs from the latter in having shorter spicules (56–59 vs 72 μm in *H. consimilis*), fewer precloacal supplements (2–3 vs 4 supplements), and shorter tail (males: 2.9–3.2 vs 3.7 cbd in *H. consimilis*; females: 2.4–3.2 vs 5.2 cbd in *H. consimilis*) (note that the tail dimensions for *H. consimilis* were derived from Allg en’s drawings using the blind end of the intestine as starting point for the tail region in females). In addition to the morphological differences noted above, the arrangement of the precloacal supplements differs between the two species: in *H. consimilis* the four precloacal supplements are equidistant, whereas in *H. ossilagulus* sp. nov. the distance between the second and third (when present) anterior-most supplements is much greater than the distance between the two posterior-most supplements.

Etymology

The species name is derived from the Latin *ossilago* ('bony hardness') and *gula* ('gullet', 'throat') and refers to the cuticularized pharyngeal lumen of this species.

Material examined**Holotype**

NEW ZEALAND • 1 ♂; Southern flank of Chatham Rise, 1241 m water depth (44.4853° S, 177.1410° E, voyage TAN0705, station 45), sandy mud (83% silt/clay, 17% sand); NIWA 139246.

Paratypes

NEW ZEALAND • 1 ♂, 2 ♀♀; same location as for holotype; 6 April 2007; NIWA 139247.

Type habitat and locality

Southern flank of Chatham Rise, 1241 m water depth (44.4853° S, 177.1410° E, voyage TAN0705, station 45), sandy mud (83% silt/clay, 17% sand).

Description**Males**

BODY. Cylindrical, tapering slightly towards both extremities. Cuticle with transverse rows of punctations; lateral differentiation consisting of larger, more widely spaced punctations. Two dorsosublateral rows of pore complexes extending from posterior end of pharynx to cloacal region, more or less equally distributed along each row; each pore complex ca 1.5 μm in diameter. Somatic setae short, 1–2 μm long, sparse, irregularly arranged along body. Cephalic region slightly rounded, lip region raised and offset. Six inner labial papillae; six short outer labial papillae, 1–2 μm long, at same level as four cephalic

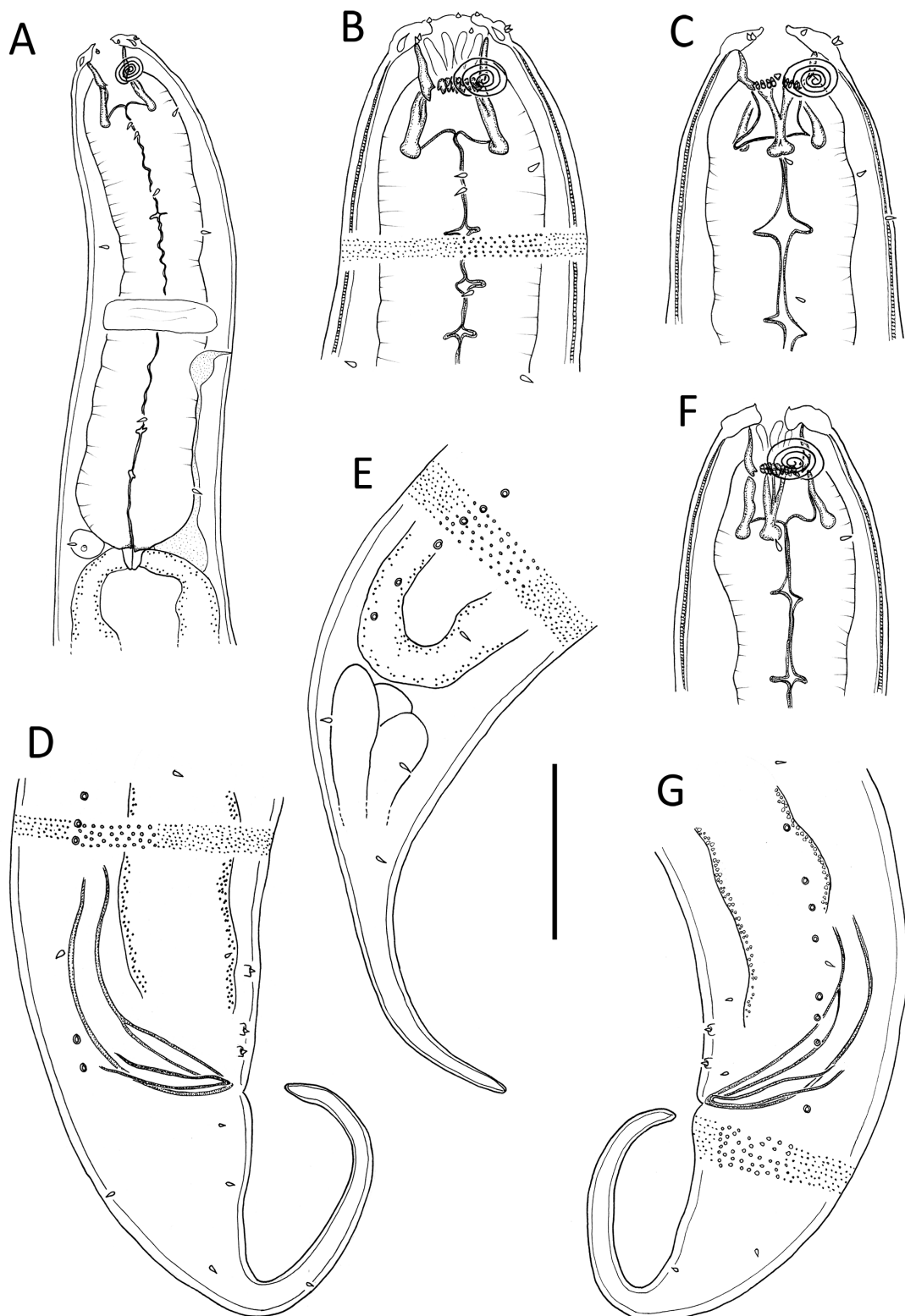


Fig. 4. *Halichoanolaimus ossilagulus* sp. nov. A. Holotype ♂ (NIWA 139246), anterior body region. B. Paratype ♀ (NIWA 139247), cephalic region. C. Paratype ♂ (NIWA 139247), cephalic region. D. Paratype ♂, posterior body region. E. Paratype ♀, posterior body region. F. Holotype ♂, cephalic region. G. Holotype ♂, posterior body region. Scale bar: A = 50 µm; B–C, E–F = 35 µm; D = 30 µm; G = 32 µm.

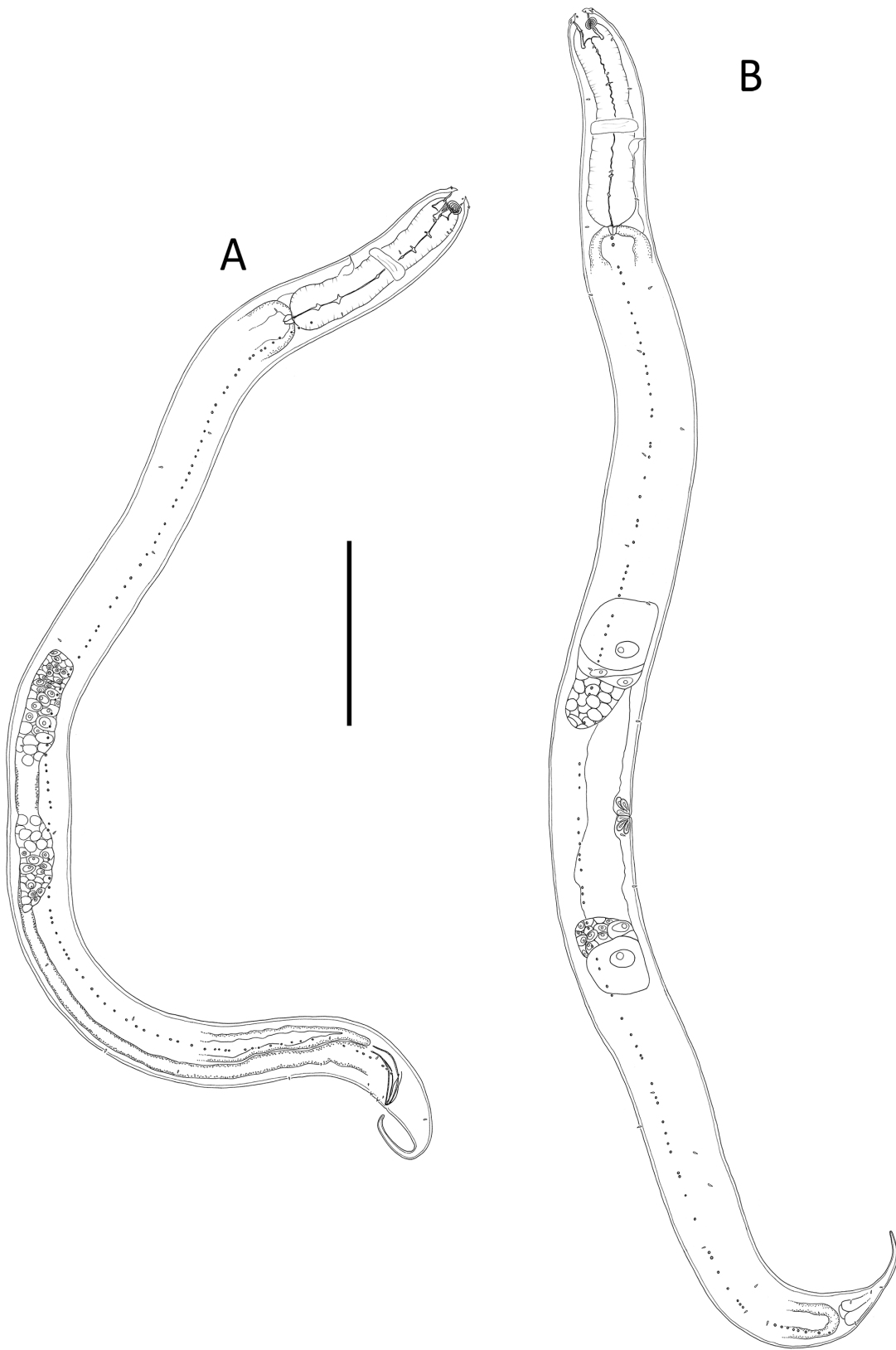


Fig. 5. *Halichoanolaimus ossilagulus* sp. nov. **A.** Entire holotype ♂ (NIWA 139246). **B.** Entire paratype ♀ (NIWA 139247). Scale bar = 150 μ m.

papillae of same length. Amphideal fovea multispiral with 4.5 turns, situated <0.3 cbd from anterior end. Buccal cavity (pharyngostome) large, ca $20\ \mu\text{m}$ deep, divided into anterior (gymnostome) and posterior portions (stegostome). Anterior portion of buccal cavity cup-shaped, with three sets of three cuticularized rhabdions, $8\text{--}10\ \mu\text{m}$ long, terminating in three sets of 10 pairs of teeth (denticles), with raised central denticle located in middle of each set; posterior portion of buccal cavity narrower, cylindrical, surrounded by three Y-shaped pairs of cuticularized rhabdions with swollen bases, $13\ \mu\text{m}$ long. Pharynx

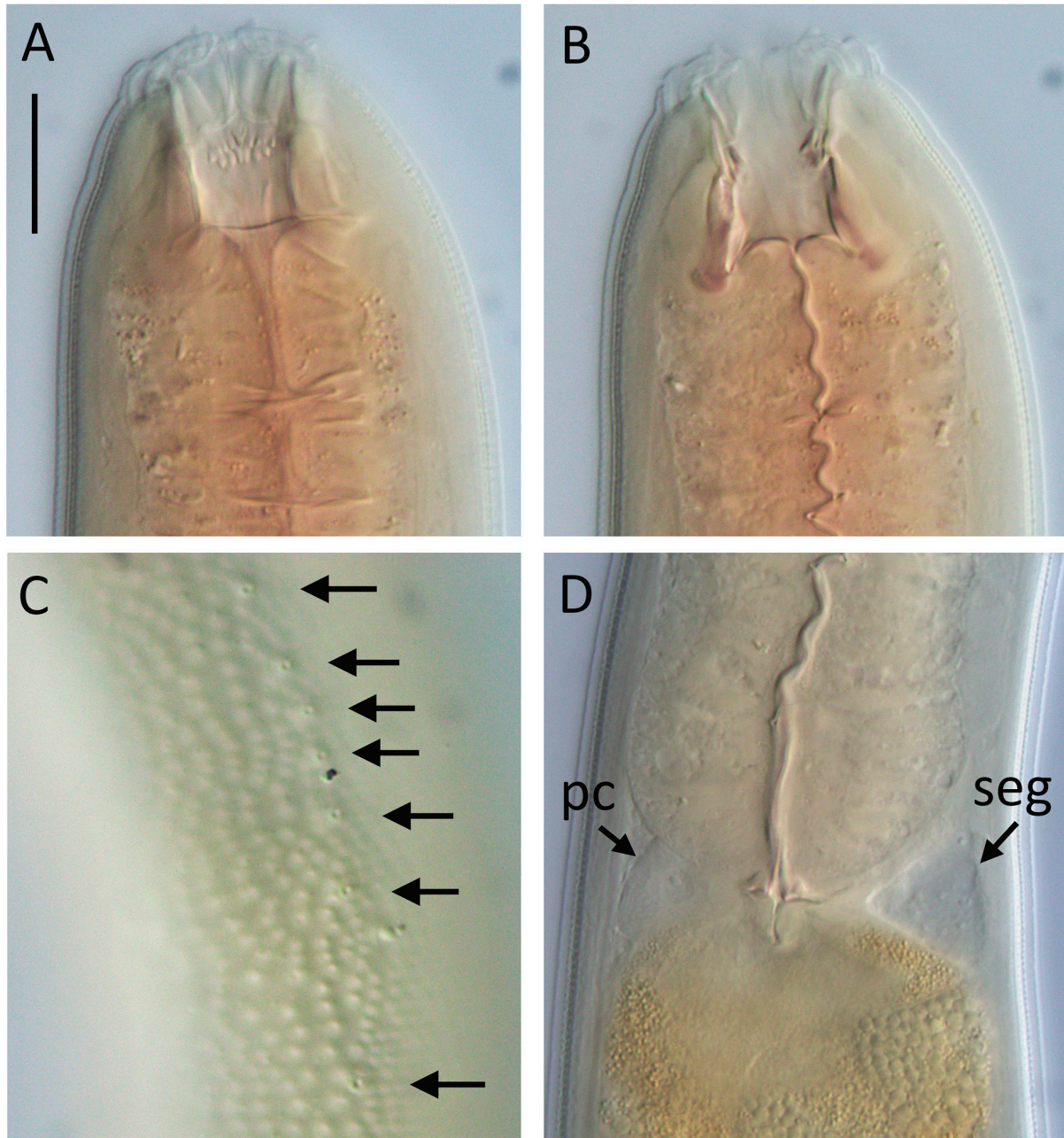


Fig. 6. *Halichoanolaimus ossilagulus* sp. nov. Light micrographs. **A, B.** Cephalic region of paratype ♀ (NIWA 139247), showing structure of buccal cavity. **C.** Cloacal region of holotype ♂ (NIWA 139246), showing cuticle ornamentation and pore complexes (arrows). **D.** Junction of pharynx and intestine of paratype ♀ showing position of secretory-excretory gland (seg) and pseudoceolomocyte (pc). Scale bar: A–B = $15\ \mu\text{m}$; C = $11\ \mu\text{m}$; D = $17\ \mu\text{m}$.

cylindrical, muscular, without anterior or posterior bulb; pharyngeal lumen conspicuously cuticularized. Nerve ring at 55–60% of pharynx length from anterior. Secretory-excretory system present. Renette cell 13–15 µm long, 7–14 µm wide, situated at level of cardia; single nucleated pseudocoelomocyte present dorsally and opposite renette cell, ampulla small, pore situated slightly posterior to nerve ring. Cardia small, surrounded by intestine. Posterior extremity of intestine blind, rectum absent.

REPRODUCTIVE SYSTEM. Diorchic with short outstretched testes. Anterior testis to the left of intestine, posterior testis to the right of intestine. Sperm cells globular, 7–8 × 8–10 µm. Spicules paired, curved, tapering distally, length 1.6–1.7 body diameters at level of cloacal opening; gubernaculum consisting of two detached lateral pieces (crurae) tapering distally, median portion of gubernaculum (corpus and cuneus) not visible. Two or three precloacal supplements present, consisting of conical papillae set on cylindrical cuticular elevations. When present, third anterior-most supplement conspicuously further away from other two supplements (12 µm) than two posterior-most supplements are from each other (4–6 µm). Tail conicocylindrical, cylindrical portion ca half of total tail length; a few short and sparse somatic setae present. Caudal glands not observed.

Females

Similar to males; one female with cylindrical portion of tail comprising ca three quarters of total tail length. Reproductive system didelphic-amphidelphic, with reflexed ovaries. Anterior ovary to the left of intestine and posterior ovary to the right of intestine. Vulva situated near mid-body. Proximal portion of vagina surrounded by constrictor muscle, two pairs of vaginal glands present. Intestine blind, anus not observed.

Halichoanolaimus funestus sp. nov.

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Table 1, Figs 7–9

Diagnosis

Halichoanolaimus funestus sp. nov. is characterized by relatively large body, 2.7–3.0 mm long, amphideal fovea spiral with 4.5–5.0 turns, rhabdions of anterior portion of buccal cavity ending in three sets of 10 pairs of denticles with single raised denticle in centre of each set, several pseudocoelomocytes associated with SE system surrounding base of pharynx, spicule length 1.8 body diameters at level of cloacal opening with ventral protrusion near distal tip, gubernaculum 47 µm long, seven inconspicuous papillose precloacal supplements and tail 5.1–6.3 cbd long with cylindrical portion comprising slightly more than three quarters of total tail length.

Differential diagnosis

The new species is most similar to *H. dolichurus* Ssaweljev, 1912 in body length, shape of the copulatory apparatus, number of precloacal supplements and tail length, but can be differentiated from the latter by the lower ‘a’ ratio (20–23 vs 30–40 in *H. dolichurus*) and number of amphideal fovea turns (4.5–5.0 vs 3.75–4.0 turns in *H. dolichurus*). The new species is also similar to *H. ovalis* in the number of amphideal fovea turns, structure of the spicular apparatus and number of precloacal supplements, but can be differentiated from the latter by the longer body (2.7–3.0 vs 1.3–1.8 mm in *H. ovalis*), higher ‘a’ ratio (20–23 vs 17–18 in *H. ovalis*), longer tail (in males, 5.7–6.3 vs 3.6 cbd in *H. ovalis*) and longer spicules (97 vs 60 µm in *H. ovalis*).

Etymology

The species name is derived from the Latin *funestus* ('causing death', 'calamity, deadly') and refers to the ability of this species to feed on relatively large nematodes owing to its voluminous armed buccal cavity and large body size.

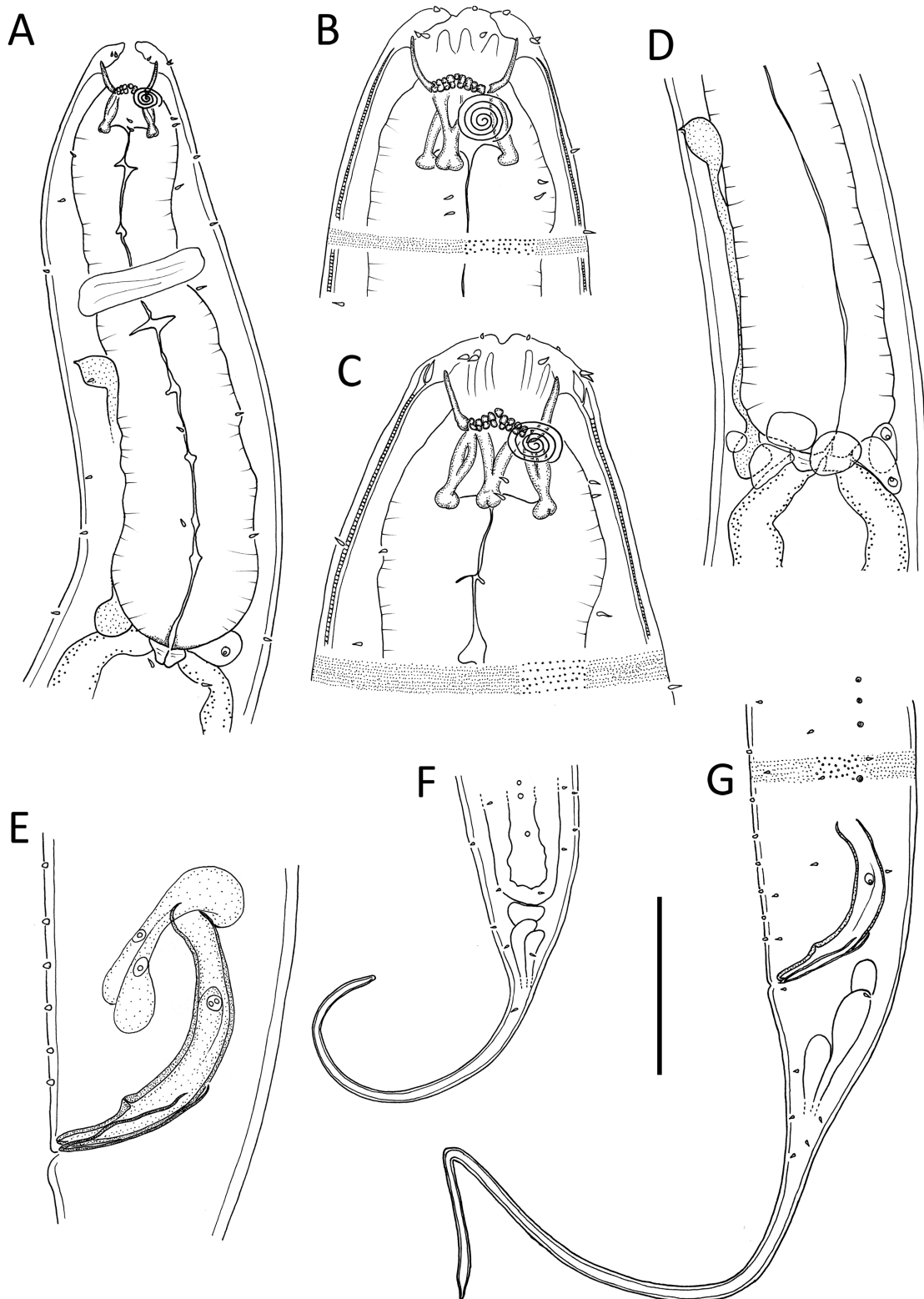


Fig. 7. *Halichoanolaimus funestus* sp. nov. **A.** Anterior body region of paratype ♀ (NIWA 139249). **B.** Holotype ♂ (NIWA 139248), cephalic region. **C.** Paratype ♀, cephalic region. **D.** Holotype ♂, posterior pharyngeal region and anterior intestinal region showing location of pseudocoelomocytes. **E.** Holotype ♂, spicular apparatus. **F.** Paratype ♀, posterior body region. **G.** Holotype ♂, posterior body region. Scale bar: A = 112 µm; B–C, E = 50 µm; D = 105 µm; F = 115 µm; G = 75 µm.

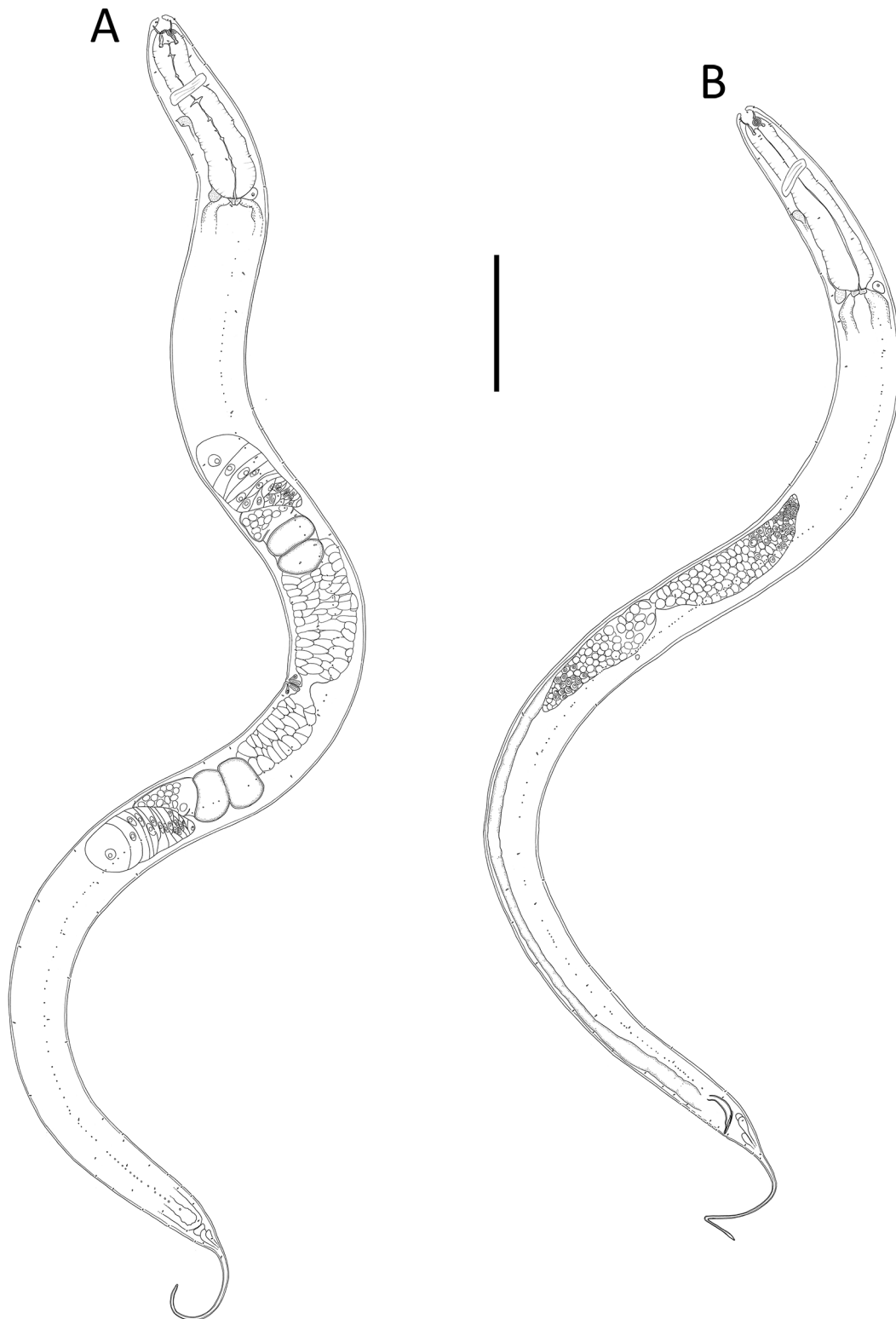


Fig. 8. *Halichoanolaimus funestus* sp. nov. **A.** Entire paratype ♀ (NIWA 139249). **B.** Entire holotype ♂ (NIWA 139248). Scale bar = 250 µm.

Material examined

Holotype

NEW ZEALAND • 1 ♂; Main axis of Kaikōura Canyon, 1061 m water depth (42.5082° S, 173. 6325° E, voyage TAN1006, station 7, site K4); NIWA 139248.

Paratypes

NEW ZEALAND • 2 ♀♀; same location as for holotype; 3 May 2010; NIWA 139249.

Type habitat and locality

Main axis of Kaikōura Canyon, 1061 m water depth (42.5082° S, 173. 6325° E, voyage TAN1006, station 7, site K4).

Description

Male

BODY. Cylindrical, tapering slightly towards both extremities. Cuticle with transverse rows of punctations; lateral differentiation consisting of larger, more widely spaced punctations. Two dorsosublateral rows of pore complexes extending from posterior end of pharynx to cloacal region, becoming more closely spaced posteriorly; each pore complex ca 2 µm in diameter in middle body region and ca 3 µm in diameter near cloacal region. Somatic setae 2–5 µm long, sparse, arranged in eight longitudinal rows along body. Cephalic region slightly rounded, lip region slightly offset. Six inner labial papillae; six short outer labial setae, 3–4 µm long, at same level as four cephalic papillae of same length. Amphideal fovea multispiral with 5.0 turns, situated 0.4–0.5 cbd from anterior end. Buccal cavity (pharyngostome) large, ca 45–50 µm deep, divided into anterior (gymnostome) and posterior portions (stegostome). Anterior portion of buccal cavity cup-shaped, with three sets of three cuticularized rhabdions, 17–25 µm long, terminating in three sets of 10 pairs of teeth (denticles), with raised central denticle located in middle of each set; posterior portion of buccal cavity narrower, cylindrical, surrounded by three Y-shaped pairs

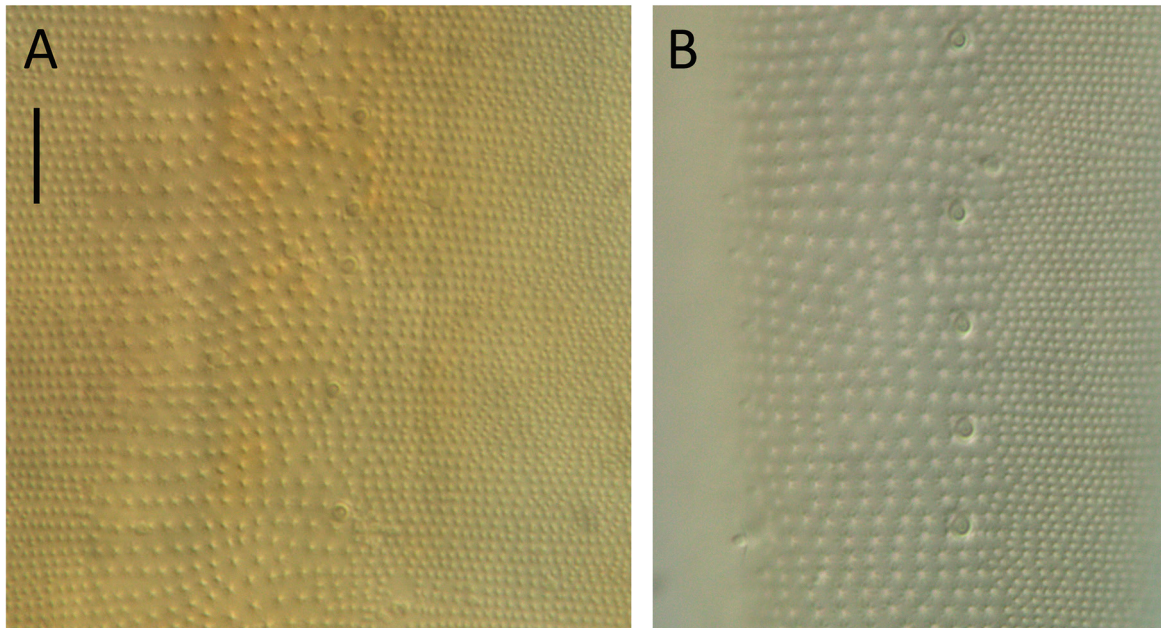


Fig. 9. *Halichoanolaimus funestus* sp. nov. Light micrographs of paratype ♀ (NIWA 139249). **A.** Cuticle in mid-body region showing arrangement of pore complexes. **B.** Cuticle near tail region showing arrangement of pore complexes. Scale bar = 10 µm.

of cuticularized rhabdions with swollen bases, 24–27 µm long. Pharynx cylindrical, muscular, without anterior or posterior bulb; pharyngeal lumen not cuticularized. Nerve ring at 40–50% of pharynx length from anterior. Secretory-excretory system present. Renette cell 24–32 µm long, 21–33 µm wide, situated at level of cardia; several nucleated pseudocoelomocytes surrounding base of pharynx, ampulla small, pore situated slightly posterior to nerve ring. Cardia small, surrounded by intestine. Posterior extremity of intestine blind, rectum absent.

REPRODUCTIVE SYSTEM. Dioecious with outstretched testes. Anterior testis to the left of intestine, posterior testis to the right of intestine. Sperm cells globular, 21–22 × 22–25 µm. Spicules paired, curved, tapering distally, length 1.8 body diameters at level of cloacal opening, with ventral protrusion near distal tip. Gubernaculum consisting of two detached lateral pieces (crurae) tapering distally, median portion of gubernaculum (corpus and cuneus) not visible. Seven inconspicuous papillose precloacal supplements present; posteriormost four supplements 10–13 µm apart, anteriormost three supplements 16–21 µm apart. Tail long, conicocylindrical, cylindrical portion slightly more than three quarters of total tail length; a few short and sparse somatic setae present. Three caudal glands present.

Females

Similar to males, but with slightly lower 'a' ratio and slightly fewer (4.5–4.75) amphideal fovea turns. Reproductive system didelphic-amphidelphic, with reflexed ovaries. Anterior ovary to the left of intestine and posterior ovary to the right of intestine. Mature eggs 95–99 × 48–53 µm. Vulva situated slightly pre-median. Proximal portion of vagina surrounded by constrictor muscle, two small vaginal glands present. Intestine blind, anus not observed.

Remarks

A nematode belonging to the genus *Parodontophora* Timm, 1963 was observed in the intestine of the holotype, and a nematode of the genus *Sabatieria* Rouville, 1903 was observed in the intestine of one of the female paratypes.

Halichoanolaimus pumilus sp. nov.

[urn:lsid:zoobank.org:act:027D24CF-2A62-472D-B6D9-F7E3EBB12487](https://doi.org/10.21203/rs.3.rs-1234567/v1)

Table 1, Figs 10–11

Diagnosis

Halichoanolaimus pumilus sp. nov. is characterized by short body length, 756 µm long, two dorsosublateral rows of pore complexes with five pore complexes in anterior part of intestine and 10 pore complexes anterior to cloacal region, amphideal fovea with 6.5 turns, pharyngeal lumen distinctly cuticularized, spicule length 1.8 body diameters at level of cloacal opening, gubernaculum 24 µm long and tail 4.7 cbd long with cylindrical portion comprising ca 60% of total tail length.

Differential diagnosis

The new species is most similar to *H. brandtae* Zograf, Trebukhova & Pavlyuk, 2015 in tail shape (cylindrical portion < 75% of total tail length) and high number of amphideal fovea turns (6.5). The new species differs from the latter by the markedly shorter body length (756 vs 1600–1700 µm in *H. brandtae*), larger amphideal fovea (58 vs <40% cbd in *H. brandtae*), shorter spicules (49 vs 82 µm in *H. brandtae*), shape and number of precloacal supplements (three supplements in shape of cylindrical cuticularized structures vs five papillose precloacal supplements in *H. brandtae*), and number and arrangement of cuticular pore structures (row of five dorsosublateral pore complexes in anterior part of intestine and 10 pore complexes anterior to cloacal opening vs row of 13–15 lateral 'cuticular pores' in posterior part of intestine in *H. brandtae*). *Halichoanolaimus pumilus* sp. nov. is also similar to *H. minutissimus* Timm, 1961 in the short body length (< 800 µm) but can easily be distinguished from

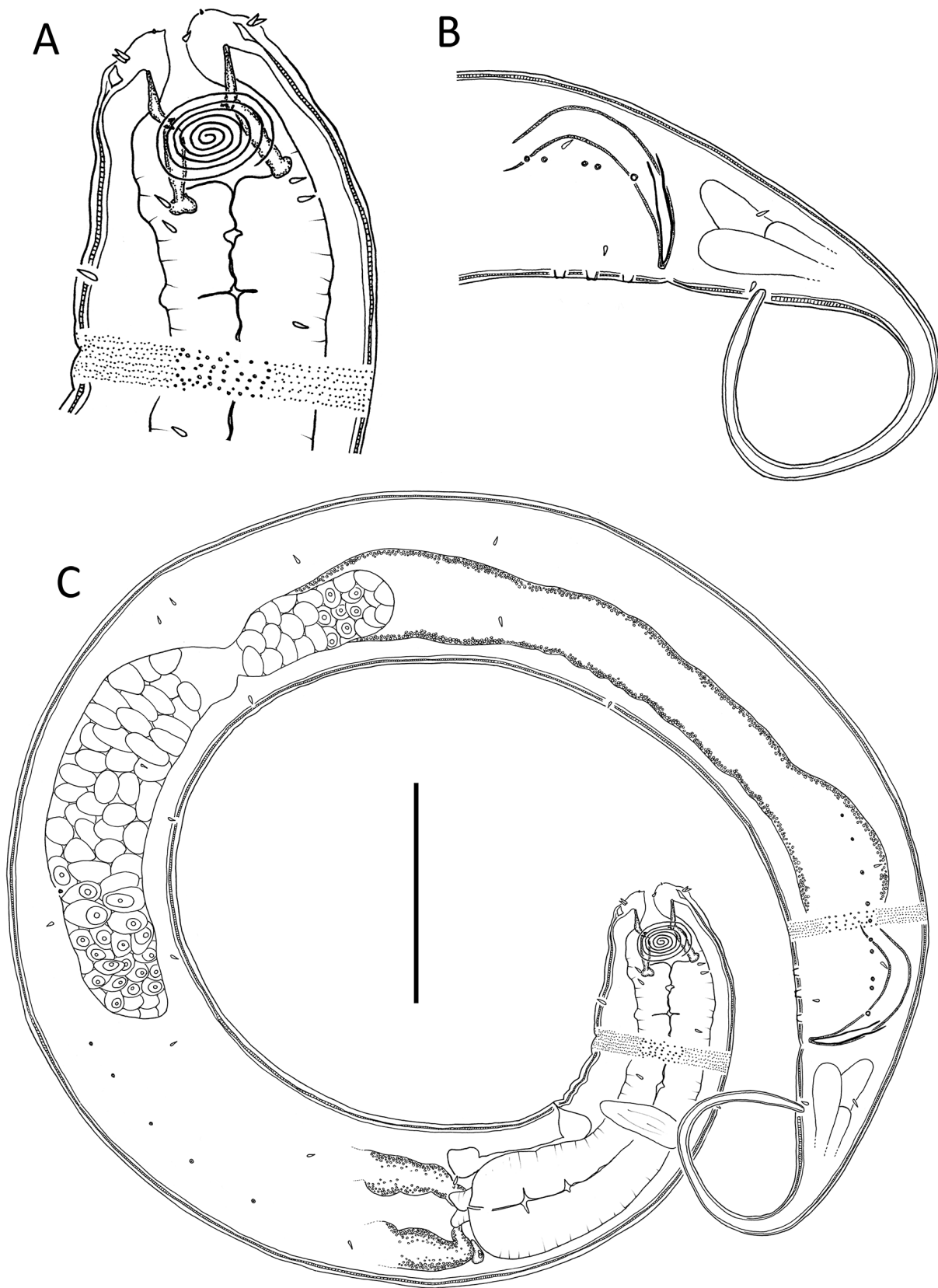


Fig. 10. *Halichoanolaimus pumilus* sp. nov. Holotype ♂, NIWA 139250. A. Anterior body region. B. Posterior body region. C. Entire ♂. Scale bar: A = 25 μ m; B = 42 μ m; C = 60 μ m.

the latter by the much shorter tail (4.7 vs 11.0 cbd in *H. minutissimus*) and number of amphideal fovea turns (6.5 vs 3.5 in *H. minutissimus*).

Etymology

The species name is derived from the Latin *pumilus* ('dwarfish', 'little') and refers to the small size of this species relative to most other species of *Halichoanolaimus*.

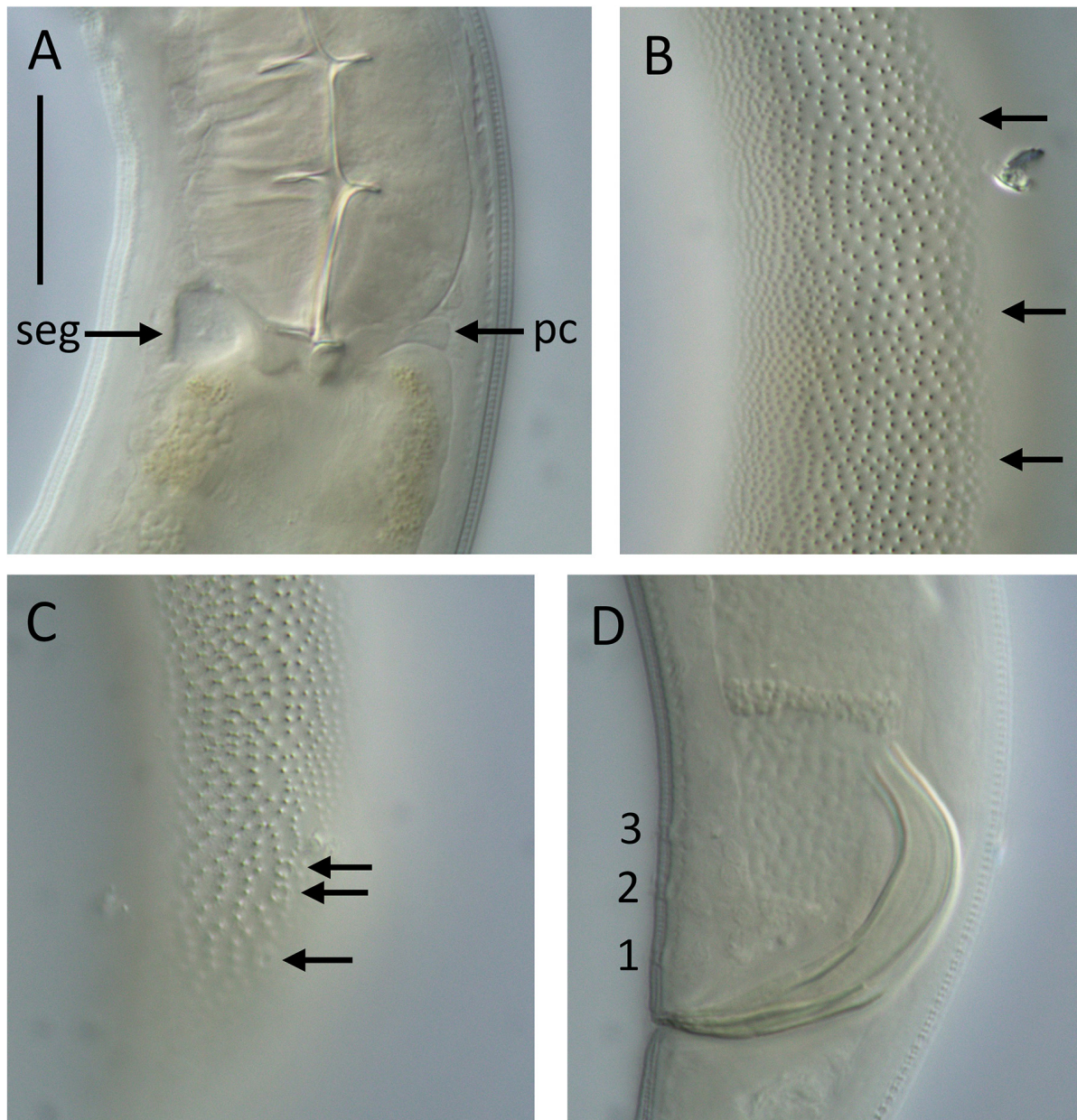


Fig. 11. *Halichoanolaimus pumilus* sp. nov. Light micrographs of holotype ♂ (NIWA 139250). **A.** Junction of pharynx and intestine, showing position of secretory-excretory gland (seg) and pseudocoelomocyte (pc). **B.** Mid-body cuticle, showing position of pore complexes (arrows). **C.** Cuticle near tail region, showing position of pore complexes (arrows). **D.** Spicular apparatus and preloacal supplements (numbered 1 to 3). Scale bar = 20 μ m.

Material examined

Holotype

NEW ZEALAND • ♂; Challenger Plateau, 803 m water depth (40.1313° S, 170.2132° E, voyage TAN0707, station 98), sandy mud (82% silt/clay, 18% sand); 6 Apr. 2007; NIWA 139250.

Type habitat and locality

Challenger Plateau, 803 m water depth (40.1313° S, 170.2132° E, voyage TAN0707, station 98), sandy mud (82% silt/clay, 18% sand).

Description

Male

BODY. Cylindrical, tapering slightly towards both extremities. Cuticle with transverse rows of punctations; lateral differentiation consisting of larger, more widely spaced punctations. Two dorsosublateral rows of pore complexes with five pore complexes in anterior part of intestine and 10 pore complexes anterior to cloacal region; each pore complex ca 2 µm in diameter. Somatic setae short, 3 µm long, sparsely distributed. Cephalic region slightly rounded, lip region slightly offset. Six inner labial papillae; six short outer labial setae, 3–4 µm long, at same level as four cephalic papillae of same length. Amphideal fovea relatively large, multispiral with 6.5 turns, situated ca 0.5 cbd from anterior end. Buccal cavity (pharyngostome) large, ca 20 µm deep, divided into anterior (gymnostome) and posterior portions (stegostome). Anterior portion of buccal cavity cup-shaped, with three sets of three cuticularized rhabdions, 8 µm long, terminating in three sets of paired teeth (denticles; exact number could not be determined); posterior portion of buccal cavity narrower, cylindrical, surrounded by three Y-shaped pairs of cuticularized rhabdions with swollen bases, 10 µm long. Pharynx cylindrical, muscular, without anterior or posterior bulb; pharyngeal lumen cuticularized. Nerve ring at ca 55% of pharynx length from anterior. Secretory-excretory system present. Renette cell small, 9 µm long, 7 µm wide, situated at level of cardia; single nucleated pseudocoelomocyte situated dorsally and opposite renette cell, pore situated slightly posterior to nerve ring. Cardia small, partially surrounded by intestine. Posterior extremity of intestine blind, rectum absent.

REPRODUCTIVE SYSTEM. Dioecious with outstretched testes. Anterior testis to the left of intestine, posterior testis to the right of intestine. Sperm cells globular, 6–10 × 8–14 µm. Spicules paired, curved, tapering distally, length 1.7 body diameters at level of cloacal opening. Gubernaculum consisting of two detached lateral pieces (crurae) tapering distally, median portion of gubernaculum (corpus and cuneus) not visible. Three precloacal supplements in shape of cylindrical cuticularized structures located 8–9 µm apart. Tail conicocylindrical, cylindrical portion ca 60% of total tail length; a few short and sparse somatic setae present. Three caudal glands and spinneret present.

Discussion

The present study brings the total number of valid species of *Halichoanolaimus* from 23 to 26, and the total number of selachinematid species recorded from the New Zealand region from 11 to 14. I also provide a new record for *H. ovalis* and extend its known range from about 53° S in the Southern Ocean to 42° S in the Southwest Pacific Ocean. The water depth range of this species, which was originally described from the littoral zone, is also extended to include the deep sea (1061 m depth). The nematode communities of Kaikōura Canyon (where *H. ovalis* was recorded) are characterized by high abundance, low diversity as well as the presence of taxa such as *Sabatieria pulchra* (Schneider, 1906) which are most commonly found in eutrophic environments and not in deep-sea habitats (Leduc *et al.* 2014). It is possible that high food availability and abundant nematode populations in the canyon provide a suitable environment for predatory nematodes such as *Halichoanolaimus*, perhaps facilitating colonisation of a deep-sea environment by shallow water species.

Examination of the four species described here has revealed the presence of morphological features which have either rarely or not yet been recorded in *Halichoanolaimus*. In all four species, longitudinal dorsosublateral rows of pore complexes were seen to extend from posterior to the pharyngeal region to the posterior portion of the intestine of both males and females, and tended to be slightly larger and/or more conspicuously cuticularized near the posterior end of the intestine, as well as more closely spaced, and least visible in the middle body region. The term “pore complex” was used to describe the cuticular pore structures seen in the four species of *Halichoanolaimus*, following the terminology provided by Leduc & Zhao (2018) for the Cyatholaimidae. In the latter study, pore complexes were defined as “circular structures arranged in sublateral, subventral and subdorsal longitudinal rows, with slit-like pore and ring-like development of dense material in the middle cuticle layer”. Overall, the position and structure of the cuticle pores observed in the four species of *Halichoanolaimus* fit the definition given by Leduc & Zhao (2018). These authors used the term “lateral pore-like structures” for cuticle pores distributed mediolaterally and with unmodified or modified/fused punctations supporting the cuticular opening at the anterior and posterior ends. This type of structure was not observed in any of the species of *Halichoanolaimus* described here.

Across the genus *Halichoanolaimus*, cuticle pores have so far only been observed in *H. brandtae* and *H. bispirae* Daschenko & Belogurov, 1991. In *H. brandtae*, lateral rows of cuticle pores located in the posterior part of the intestine are described based on SEM observations (Zograf *et al.* 2015); these structures were not seen in specimens observed with light microscopy due to their small size. In *H. bispirae*, lateral rows of cuticular pore structures were described just posterior to the nerve ring and in the posterior portion of the intestine (Daschenko & Belogurov 1991). The drawings of Daschenko & Belogurov (1991), however, show that these structures are in fact located dorsosublaterally (at least in the posterior body region), not laterally. I hypothesize that the cuticular structures described by Zograf *et al.* (2015) in *H. brandtae* are in fact also located dorsosublaterally, but this cannot be ascertained as the body symmetry is difficult to determine from the SEM micrographs.

Because it can be difficult to observe pore complexes using light microscopy, particularly in the middle body region where pore complexes tend to be smaller and less well defined, it is possible that they have been overlooked in other species of *Halichoanolaimus*. For example, my observations of type specimens of *H. anisospermus* Leduc & Zhao, 2016 show that dorsosublateral rows of pore complexes are present in both males and females of this species even though these structures were not noted in the original description. Dorsosublateral pore complexes have also been observed in the closely related selachinematid *Bendiella longicauda* Leduc & Zhao, 2016, but they are apparently not present in *B. thalassa* Leduc, 2013 (D. Leduc, pers. obs.). Rows of mediolateral pores similar to the lateral pore-like structures described by Leduc & Zhao (2018) are present in several *Cobbionema* species (Leduc 2013; Ahmed *et al.* 2020). In *Gammanema agglutinans* Leduc, 2013, no pore complexes can be observed, although the somatic setae, which are arranged in four longitudinal sublateral rows, each have a cuticularized ring at their base which show similarities to pore complexes (D. Leduc, pers. obs.). Further observations by the author show that cuticle pores are absent in *Synonchiella rotundicauda* Leduc, 2013, *Pseudocheironchus ingluviosus* Leduc, 2013, *Cheironchus haurakiensis* Leduc & Zhao, 2016 and *Latronema whataitai* Leduc & Zhao, 2015. More detailed investigation of cuticle pores in selachinematids is required in order to evaluate their potential taxonomic significance. The function of these cuticular pores remains unclear; however, the fact that they are often most dense and slightly larger near the posterior extremity of the blind intestine may imply some kind of excretory function. Pore complexes and lateral pore-like structures appear to be found only in genera with a blind intestine (*Halichoanolaimus*, *Bendiella* and *Cobbionema*), while being absent in genera with an intestine connecting to a cloaca/rectum (*Synonchiella* Cobb, 1933, *Cheironchus* Cobb, 1917, *Pseudocheironchus* Leduc, 2013, *Latronema* Wieser, 1954), which may also indicate an excretory function.

All of the four species of *Halichoanolaimus* described here were found to possess pseudocoelomocytes apparently associated with the secretory-excretory system. In two of the species only one pseudocoelomocyte was observed; in the other two species several were seen surrounding the base of the pharynx and in *H. ovalis* they were also present along the duct linking the renette cell and ampulla. The function of pseudocoelomocytes in nematodes is not entirely clear, although an excretory function is possible in species where pseudocoelomocytes are associated with the SE system, as in *Hemiplectus muscorum* Zell, 1991 (Holovachov *et al.* 2009; Decraemer *et al.* 2014). Given the blind intestine of *Halichoanolaimus*, pseudocoelomocytes may help process the waste products of digestion.

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