




Research article

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Three new nematode species (Chromadorida: Selachinematidae) from the continental slope of New Zealand

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Abstract. Three new species of selachinematid nematodes, *Choanolaimus serieporus* sp. nov., *C. sparsiporus* sp. nov. and *Gammanema lunatum* sp. nov., are described from the continental slope of New Zealand. We also provide partial ribosomal DNA SSU and LSU D2–D3 sequences for *Gammanema lunatum* sp. nov. and another selachinematid species, *Halichoanolaimus funestus* Leduc, 2020. Until now, the genus *Choanolaimus* de Man, 1880 comprised a single species restricted to coastal dunes, beaches and estuarine environments of the North Sea, Northeast Atlantic and Northeast Pacific. To our knowledge, the present study provides the first record of the genus from the southern hemisphere and from the deep-sea environment (>250 m depth). The two new species of *Choanolaimus* are characterised by two longitudinal dorsosublateral rows of pore complexes, which differ in arrangement between species thus providing a taxonomically informative character. The presence of pore complexes in *Choanolaimus* is consistent with previous findings, which show that within the Selachinematidae Cobb, 1915, pore complexes are only found in genera with a blind intestine. The two species of *Gammanema* Cobb, 1920 known so far from New Zealand share characters not found in any other species of the genus, i.e., loop-shaped amphids in males and the presence of cuticle spines, which indicates that these two species may have evolved from a common ancestor. The SSU and LSU D2–D3 consensus trees are largely congruent. Our molecular phylogenetic analyses confirm previous results, which support the monophyly of the family Selachinematidae but not of the subfamilies Selachinematinae and Choniolaiminae, with some genera placed in different clades despite sharing strong morphological similarities. We have found no support for the monophyly of the genus *Halichoanolaimus* de Man, 1886, which forms a well-supported clade with the genera *Bendiella* Leduc, 2013, *Cobbionema* Filipjev, 1922 and *Demonema* Cobb, 1894.

Keywords. Blind intestine, pore complexes, Bounty Trough, Papanui Canyon, Otago fan complex, 18S rDNA, 28S rDNA.

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Introduction

The Selachinematidae Cobb, 1915 is a globally distributed family of predatory nematodes that occurs in both shallow water (Warwick 1971; Okhlopkov 2002; Tchesunov & Okhlopkov 2006) and deep-sea environments (Miljutin *et al.* 2010). The family is currently divided into two subfamilies, the Selachinematinae Cobb, 1915 and Choniolaiminae Schuurmans-Stekhoven & Adam, 1931, based on the buccal cavity armature (Tchesunov 2014); however, the monophyly of these two subfamilies is not supported by molecular phylogenetic analyses (Leduc & Zhao 2016; Ahmed *et al.* 2020). Within the Choniolaiminae, the genus *Choanolaimus* de Man, 1880 comprises only one species, *C. psammophilus* de Man, 1880, which occurs in coastal dunes, beaches and estuarine environments. The genus *Gammanema* Cobb, 1920 is more common and speciose, with 14 valid species in coastal and deep-water environments (Tchesunov *et al.* 2020). Fourteen selachinematid species have so far been recorded from the New Zealand region, including one species of *Gammanema* (Leduc 2013, 2020). The genus *Choanolaimus* has not yet been found in the region.

The Bounty Trough is a mid-Cretaceous feature located off the east coast of New Zealand's South Island bounded on the north by the Chatham Rise and on the south by the Campbell Plateau (Fig. 1). The system is fed by sediment from the eastern South Island shelf, through the Otago Fan complex via the 800-km-long Bounty Channel to the distal Bounty Fan at the mouth of the Bounty Trough (Carter & Carter 1987). A voyage to the Bounty Trough was undertaken in early 2024 as part of a partnership between the Nippon Foundation-Nekton Ocean Census programme, the National Institute of Water and Atmospheric Research (NIWA) and Museum of New Zealand Te Papa Tongarewa (Mills *et al.* 2024). The goal of this voyage was to accelerate the discovery of species from the New Zealand region by visiting the Bounty Trough area, which was very under-sampled based on records from the New Zealand scientific collections and databases. Here, we describe three new species of selachinematid nematodes, *Choanolaimus serieporus* sp. nov., *C. sparsiporus* sp. nov. and *Gammanema lunatum* sp. nov., from samples obtained during the Bounty Trough voyage and at other New Zealand continental margin sites. We provide ribosomal DNA SSU and LSU D2–D3 sequences for *Gammanema lunatum* sp. nov. and another selachinematid species, *Halichoanolaimus funestus* Leduc, 2020, and present the result of molecular phylogenetic analyses for the family.

Material and methods

Sampling and morphological analyses

The RV *Tangaroa* voyage TAN2402 to the Bounty Trough was undertaken in February 2024. Sites were sampled in the Otago Fan complex, the main Bounty Channel and adjacent slope, and the Bounty Fan (Fig. 1). Additional specimens from the same region (RV *Tangaroa* voyage TAN1902) and from Challenger Plateau located off the west coast of New Zealand's North Island (RV *Tangaroa* voyage TAN0707) were also used for the present study (Table 1).

Sediment samples were collected using a Van Veen grab (0.2 m² surface area) and an Ocean Instruments MC-800A multicorer (core internal diameter = 9.5 cm). Each meiofauna sample consisted of one subcore of internal diameter 29 mm taken to a depth of 5 cm. Samples for morphological analyses were sliced into 0–1 and 1–5 cm sediment depth layers, fixed in 10% formalin and stained with Rose Bengal. Samples for molecular sequencing were taken immediately adjacent to the samples for morphological analyses and were treated in the same way but were preserved in 99% ethanol instead of formalin. Samples were subsequently rinsed on a 32 µm sieve to retain nematodes. Nematodes were extracted from the remaining sediments by Ludox flotation, with samples for morphological analyses transferred to pure glycerol (Somerfield & Warwick 1996), and samples for molecular analyses kept in 99% ethanol.

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 taken 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) and terminology of cuticular pore-like structures follows Leduc & Zhao (2018). Because females of *Choanolaimus* have a blind intestine and lack the anus, the tail length has been measured beginning from the posterior extremity of the intestine. Type specimens are held in the NIWA Invertebrate Collection (Wellington).

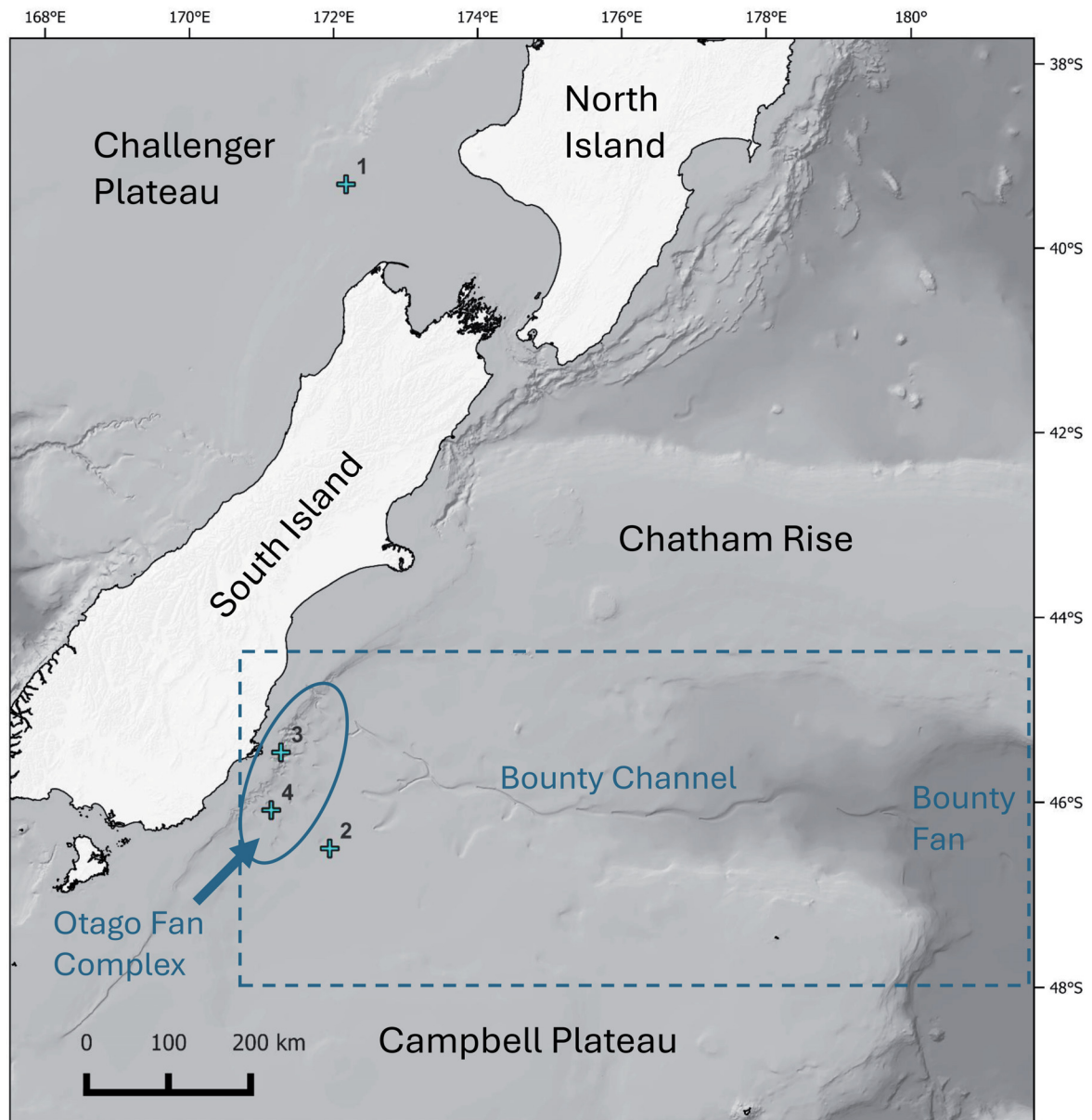


Fig. 1. The New Zealand region with the Bounty Trough area targeted during RV *Tangaroa* voyage TAN2402 (dotted line; comprising the Otago Fan complex, Bounty Channel and Bounty Fan), other bathymetric features and study sites (numbered crosses). See Table 1 for details of the study sites.

Table 1. Details of sampling sites. See Fig. 1 for the map of the study area.

| Site | Voyage_station | Location | Gear | Date | Depth, m | Latitude S | Longitude E |
|------|----------------|---------------------------------------|------------|--------------|----------|------------|-------------|
| 1 | TAN0707_134 | Challenger Plateau | Multicorer | 7 Jun. 2007 | 266 | 39.6450 | 172.1533 |
| 2 | TAN1902_130 | Slope | Multicorer | 14 Mar. 2019 | 1338 | 46.9320 | 171.7847 |
| 3 | TAN2402_2 | Papanui Canyon (Otago Fan complex) | Grab | 9 Feb. 2024 | 680 | 45.8668 | 171.0415 |
| 4 | TAN2402_34 | Slope (Otago Fan complex) | Multicorer | 13 Feb. 2024 | 992 | 46.4971 | 170.8644 |

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 = $V/\text{total body length} \times 100$

DNA extraction, PCR and sequencing

Male specimens of *Gammanema lunatum* sp. nov. and *Halichoanolaimus funestus* Leduc, 2020 were picked out of the ethanol preserved sample (TAN2402, stn 2) and were placed on a temporary slide to confirm their identity. Morphological vouchers of *H. funestus* were also obtained from the corresponding formalin-fixed sample and transferred onto slides (see above; NIWA 181635). Specimens for sequencing were transferred to lysis buffer and kept frozen at -80°C prior to molecular analyses. DNA was extracted by the method of Zheng *et al.* (2002) with minor modifications. The DNA extract was transferred into a new tube and stored at -20°C until used as PCR template. The sequenced specimens were destroyed during DNA extraction and, as a result, were not registered in NIC. Primers for LSU amplification were forward primer D2A (5'-ACAAGTACCGTGAGGGAAAGT 3') and reverse primer D3B (5' TGCGAAGGAACCAGCTACTA-3') (Nunn 1992). Primers for the rDNA small subunit (SSU) were the first fragment forward primer 1096F, 5'-GGTAATTCTGGAGCTAATAC-3' and reverse primer 1912R, 5'-TTTACGGTCAGAACTAGGG-3', and the second fragment forward primer 1813F, 5'-CTGCGTGAGAGGTGAAAT-3' and reverse primer 2646R, 5'-GCTACCTTGTTACGACTTTT-3', respectively (Holterman *et al.* 2006). For SSU and LSU, the 20 µl PCR contained 10 µl Go Tag® Green Master Mix (Promega Corporation, Madison, WI, USA), 1 µl each of forward and reverse primers (5 µM), 2 µl of DNA template and 6 µl of distilled water. The thermal cycling program was as follows: denaturation at 95°C for 3 min, followed by 35 cycles of denaturation at 94°C for 15 s, annealing at 53°C for 30 s, and extension at 72°C for 45 s. A final extension was performed at 72°C for 7 min. The amplicons were electrophoresed on 1% TAE-agarose gel stained with SYBR® Safe, observed under UV illumination using the Gel-Doc system (BioRad, Hercules, CA, USA), and images processed using the Quantity One 1-D analysis software (BioRad). The PCR products were diluted with distilled water 3–5 times and sequenced bi-directionally using the amplification primers by EcoGene (Auckland, New Zealand). Sequences were obtained with a 3130xl Genetic Analyzer (Applied Biosystems, USA) and assembled and edited with Sequencher ver. 4.8 (Gene Codes Corp.).

Sequence alignment and phylogenetic inference

The ribosomal DNA SSU and LSU D2–D3 sequences were deposited in GenBank (accession nos PQ286529, PQ286530 and PQ301196, PQ301197). Phylogenetic analyses were conducted using available Selachinematidae sequences. DNA sequences were aligned by MUSCLE alignment algorithm (Edgar 2004a, 2004b) with default parameters. ModelTest ver. 3.04 (Posada & Crandall 1998) in conjunction with PAUP* ver. 4.0b10 (Swofford 2002) and jModelTest ver. 2.1.10 software (Guindon & Gascuel 2003; Darriba *et al.* 2012) were used to select the best fit model of DNA evolution with the Akaike Information Criterion (AIC). A Bayesian tree was obtained with MrBayes ver. 3.2.6 (Huelsenbeck & Ronquist 2001) in Geneious ver. 10.2.6 (<https://www.geneious.com>, Kearse *et al.* 2012). Four MCMC chains were run for 1 000 000 generations under the best-fit model (GTR + I + G) for both SSU and LSU D2–D3. Prior distributions were as follows: revmatpr = dirichlet (1,2,1,1,2,1), shapepr = exponential (5), brlenspr = unconstrained: exponential (10). Analysis was started from a random topology and with temperature of 0.2, burning of 100 000 generations and thinning interval of 200. The perimeter files from multiple runs were 24 inspected for chain convergence with Trace in Geneious ver. 10.2.6 and trees were edited in FigTree ver. 1.4.3. The results of the phylogenetic analysis described above were tested using maximum likelihood analysis as an alternative tree-building method. These analyses were conducted in Geneious ver. 10.2.6 with default settings and 1000 bootstrap replicates (Guindon & Gascuel 2003).

Results

Taxonomy

Class Chromadorea Inglis, 1932
Order Chromadorida Chitwood, 1933
Family Selachinematidae Cobb, 1915
Subfamily Choniolaiminae Schuurmans-Stekhoven & Adam, 1931

Genus *Choanolaimus* de Man, 1880

Type species

Choanolaimus psammophilus de Man, 1880 (= *Halichoanolaimus obtusicaudatus* Schulz, 1934).

Diagnosis (emended from Tchesunov 2014)

All the anterior sensilla are papilliform. Cuticle is laterally differentiated with larger, more widely separated punctations. Spiral amphidial fovea with two or more turns. Rhabdions of the anterior cup-shaped buccal chamber posteriorly bicuspid. Pharynx cylindrical or with weak posterior bulb. Intestine blind; anus absent. Precloacal supplements are papilla pierced by fine pores. Tail very short, rounded conical or semicircular.

Remarks

The type species of the genus occurs in dunes (“about roots of beach spermatophytes”; de Man 1880: 50) and estuarine environments (Riemann 1966). *Halichoanolaimus obtusicaudatus* Schulz, 1934 was synonymised with *Choanolaimus psammophilus* by Gerlach (1964). The diagnosis is emended to reflect the blind intestine and the absence of the anus in representatives of this genus.

Choanolaimus serieporus sp. nov.
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Figs 2–4; Tables 2–3

Diagnosis

Body length 1321–1688 µm, cephalic region with slight constriction at level of amphids, amphidial fovea large, 0.51–0.56 cbd wide and with 4–5 turns, short pharynx with posterior bulb, each side of body

with two to three groups of 8–11 dorsosublateral pore complexes arranged in longitudinal rows and located between pharyngeal and tail regions, spicule length 1.2–1.6 body diameters at level of cloacal opening, gubernaculum 36 μm long, three or four precloacal supplements, tail short and rounded, 0.7 body diameters long at level of cloacal opening in males.

Differential diagnosis

The new species is most readily distinguished from *Choanolaimus psammophilus* by the large amphidial fovea 0.51–0.56 cbd wide with 4–5 turns (vs amphidial fovea ≤ 0.3 cbd wide with 2–2¼ turns in *C. psammophilus*), arrangement of pore complexes (dorsosublateral vs dorso- and ventrosublateral in *C. psammophilus*), shape of the inner labial sensilla (papilliform vs ‘flap-like’ or on swollen lobes in *C. psammophilus*), short 125–155 μm long pharynx with posterior bulb (vs pharynx > 200 μm long without posterior bulb in *C. psammophilus*), longer spicules (1.1–1.6 vs ≤ 1.0 body diameters at cloacal opening in *C. psammophilus*) and fewer precloacal supplements (3–4 vs 6–7 in *C. psammophilus*).

Choanolaimus serieporus sp. nov. can be distinguished from *C. sparsiporus* sp. nov. by the slightly longer body (1321–1682 vs 1272 μm in *C. sparsiporus*), lower a ratio (17–18 vs 24 in *C. sparsiporus*), higher b and c ratios (11 and 32–38 vs 8 and 27, respectively, in *C. sparsiporus*), arrangement of pore complexes (groups of 8–11 pore complexes vs sparsely distributed in *C. sparsiporus*), and number of precloacal supplements (3–4 vs 2 in *C. sparsiporus*).

Etymology

The species name is derived from the Latin ‘series’ (= ‘row, succession’) and ‘porus’ (= ‘hole’) and refers to the arrangement of the pore complexes in rows in this species.

Type material examined

Holotype

NEW ZEALAND • ♂; Otago Fan complex, Papanui Canyon; 45.8668° S, 171.0415° E; 680 m water depth; 9 Feb. 2024; sandy mud sediments; voyage TAN2402, stn 2; NIWA 181629.

Paratypes

NEW ZEALAND • 1 ♂; Otago Fan complex, continental slope; 46.9320° S, 171.7847° E; 1338 m water depth; 14 Mar. 2019; voyage TAN1902, stn 130; NIWA 181630 • 1 ♀; Challenger Plateau, continental slope; 30.6450° S, 172.1533° E; 266 m water depth; 7 Jun. 2007; voyage TAN0707, stn 134; NIWA 181631.

Type habitat and locality

Continental slope, New Zealand.

Description

Males

Body cylindrical, tapering slightly towards both extremities, mostly colourless except for light brown intestine wall. Cuticle 3–4 μm thick, with faint annulations ca 2.0–2.5 μm apart; transverse rows of cuticle punctations with lateral differentiation consisting of larger, more widely spaced punctations beginning from about middle of pharynx length to proximal portion of tail. On each side of body, two to three groups of 8–11 dorsosublateral pore complexes arranged in longitudinal rows and located between pharyngeal and tail regions; each pore complex ca 1.5–2.5 μm in diameter. Somatic setae short, ca 2 μm long, sparse, irregularly arranged along body. Cephalic region slightly rounded, with slight constriction at level of amphids. Lip region short, slightly raised. Six inner labial papillae; six short outer labial

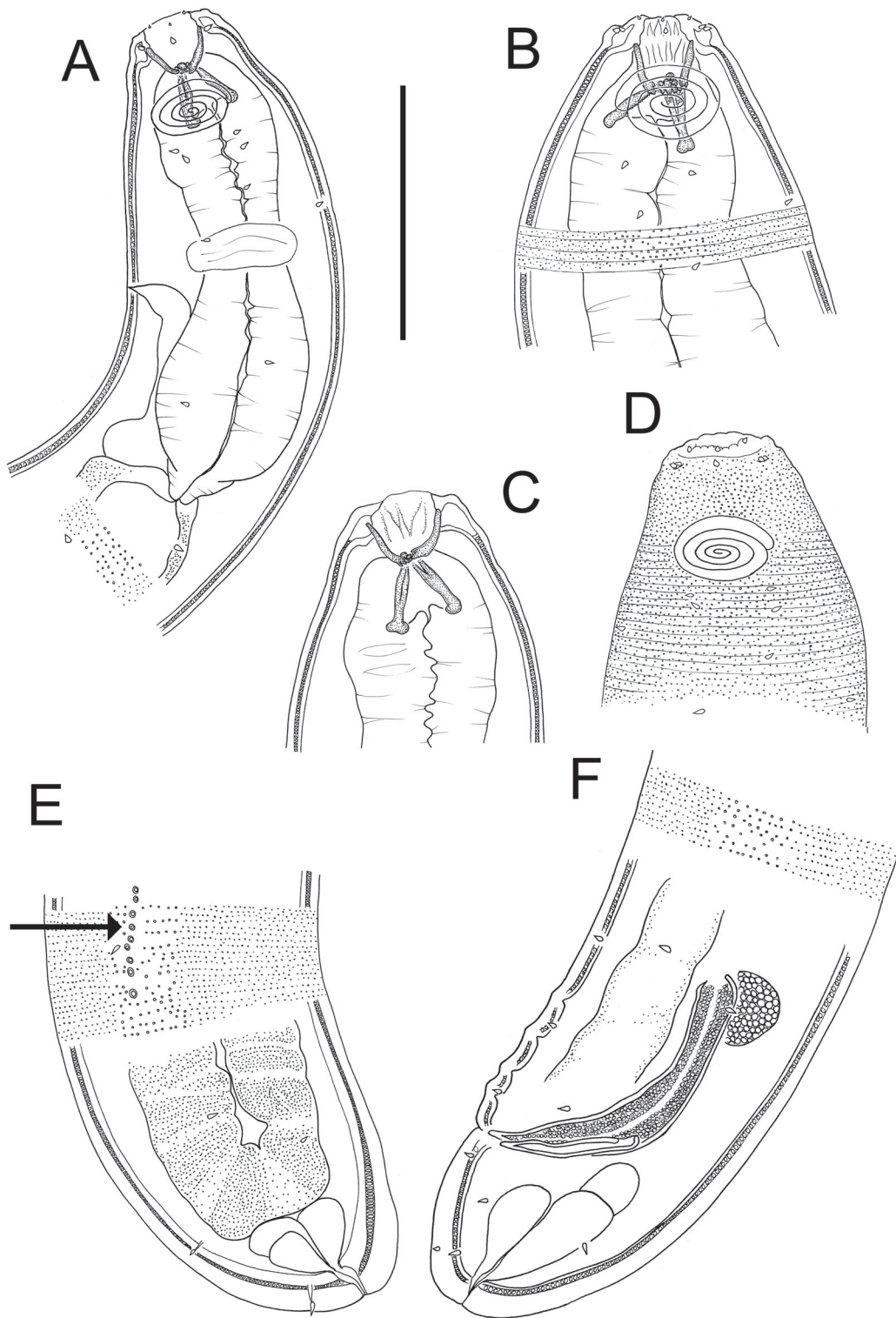


Fig. 2. *Choanolaimus serieporus* sp. nov. **A.** Anterior body region of holotype, ♂ (NIWA 181629). **B.** Cephalic region of paratype, ♀ (NIWA 181631). **C–D.** Cephalic region of paratype, ♂ (NIWA 181630). **C.** Optical cross-section. **D.** Surface view. **E.** Posterior body region of paratype, ♀ (NIWA 181631). **F.** Posterior body region of holotype, ♂ (NIWA 181629). Arrow shows group of dorsosublateral pore complexes. Scale bar: A = 75 µm; B–F = 60 µm.

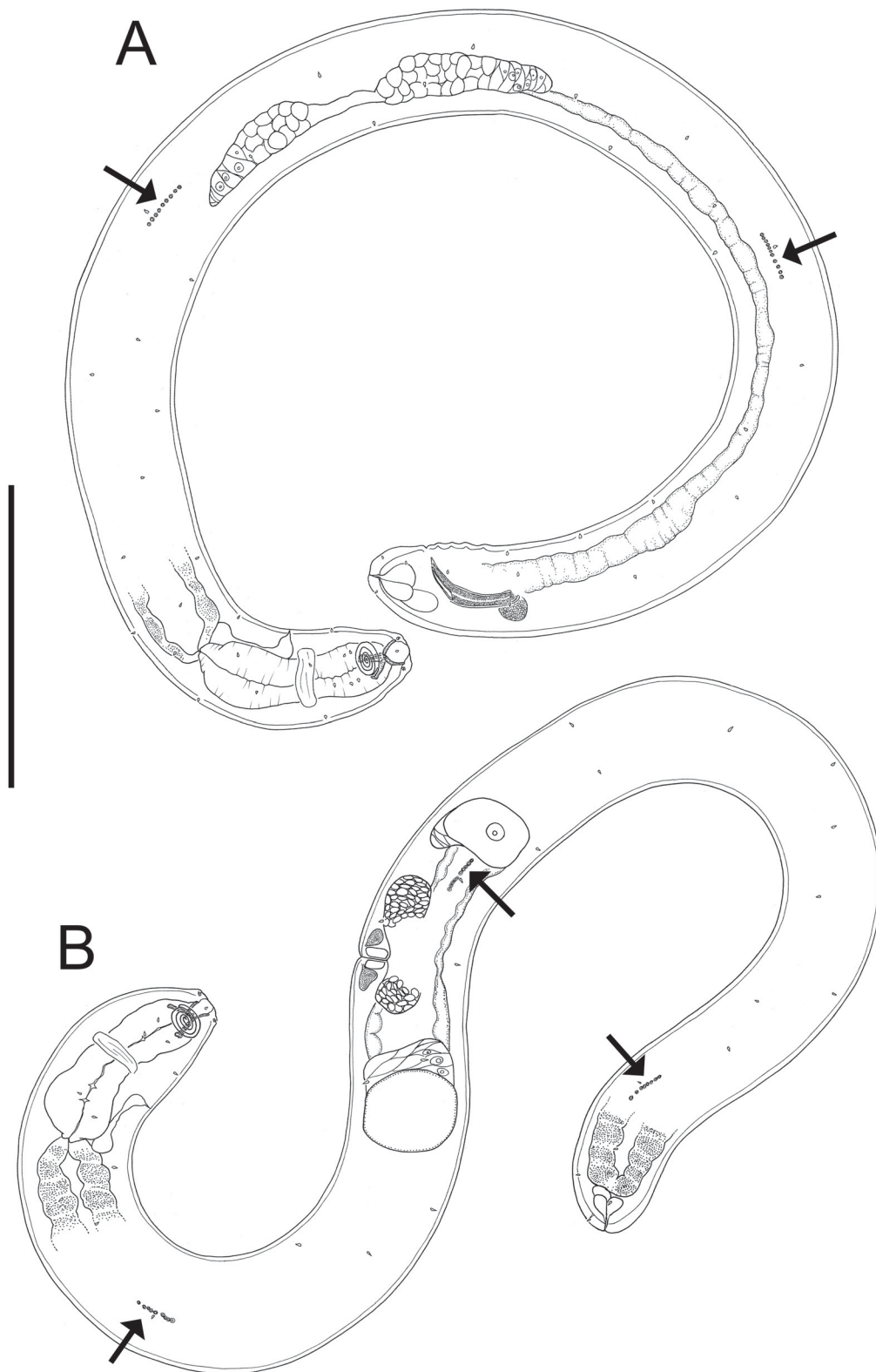


Fig. 3. *Choanolaimus serieporus* sp. nov. **A.** Entire holotype, ♂ (NIWA 181629). **B.** Entire paratype, ♀ (NIWA 181631). Arrows show groups of dorsosublateral pore complexes. Scale bar = 200 µm.

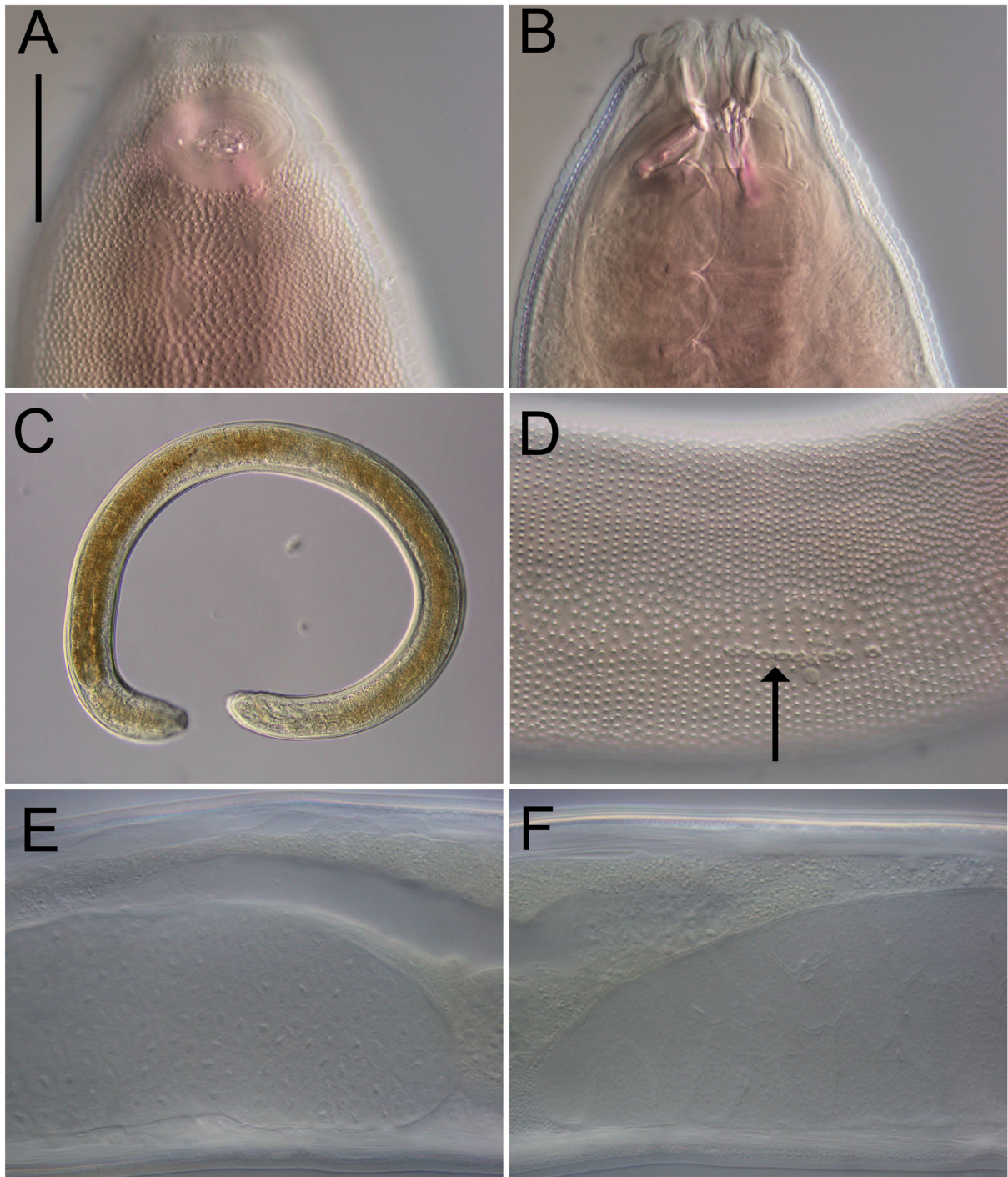


Fig. 4. *Choanolaimus serieporus* sp. nov., light micrographs. **A–B.** Cephalic region of paratype, ♀ (NIWA 181631). **A.** Surface view. **B.** Cross-section view. **C.** Entire paratype, ♂ (NIWA 181630). **D.** Lateral view of mid-body cuticle of paratype, ♀ (NIWA 181631). **E.** Proximal portion of posterior testis of paratype, ♂ (NIWA 181630). **F.** Proximal portion of anterior testis of paratype, ♂ (NIWA 181630). Arrow shows group of dorsosublateral pore complexes. Scale bar: A, B, D = 25 µm; C = 125 µm; E–F = 40 µm.

Table 2. Measurements (μm) and ratios in three new species of Selachinematidae Cobb, 1915 from New Zealand’s continental slope. 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; n = number of specimens; V = vulva distance from anterior end of body; %V = V/total body length \times 100; * = measurements of anal body diameter and tail length based on location of distal end of blind intestine.

| Species | <i>Choanolaimus serieporus</i> sp. nov. | | | | <i>Choanolaimus sparsiporus</i> sp. nov. | | | | <i>Gammanema lunatum</i> sp. nov. | | | |
|---------------------------------|---|----------|----------|----------|--|----------|----------|----------|-----------------------------------|----------|----------|----------|
| | Males | | Female | | Male | | Female | | Males | | Female | |
| | Holotype | Paratype | Paratype | Paratype | Holotype | Holotype | Paratype | Paratype | Holotype | Paratype | Paratype | Paratype |
| L | 1339 | 1688 | 1321 | | 1272 | 1196 | 754 | | 1196 | 754 | 1817 | |
| a | 18 | 17 | 17 | | 24 | 15 | 13 | | 15 | 13 | 16 | |
| b | 11 | 11 | 11 | | 8 | 5 | 6 | | 5 | 6 | 5 | |
| c | 35 | 32 | 38* | | 27 | 13 | 20 | | 13 | 20 | 19 | |
| c’ | 0.7 | 0.7 | 0.6* | | 1.1 | 1.6 | 1.3 | | 1.6 | 1.3 | 1.6 | |
| Head diam. at cephalic setae | 30 | 37 | 26 | | 26 | 55 | 34 | | 55 | 34 | 74 | |
| Head diam. at amphids | 47 | 56 | 45 | | 41 | 62 | 37 | | 62 | 37 | 77 | |
| Length of inner labial sensilla | 1–2 | 1–2 | 1–2 | | 1–2 | 4 | 2 | | 4 | 2 | 4–5 | |
| Length of outer labial sensilla | 1.5–2.0 | 2–3 | 1.5–2.0 | | 1.5–2.0 | 4 | 2 | | 4 | 2 | 4–5 | |
| Length of cephalic setae | 1.5–2.0 | 2–3 | 1.5–2.0 | | 1.5–2.0 | 20 | 8–9 | | 20 | 8–9 | 19 | |
| Amphid height | 15 | 20 | 18 | | 17 | 13 | 14 | | 13 | 14 | 6 | |
| Amphid width | 24 | 29 | 25 | | 23 | 17 | 17 | | 17 | 17 | 8 | |
| Amphid width/cbd (%) | 51 | 52 | 56 | | 56 | 27 | 46 | | 27 | 46 | 30 | |
| Amphid from anterior end | 19 | 13 | 12 | | 14 | 21 | 16 | | 21 | 16 | 22 | |
| Nerve ring from anterior end | 68 | 89 | 60 | | 76 | 96 | 60 | | 96 | 60 | 144 | |
| Nerve ring cbd | 63 | 82 | 75 | | 51 | 77 | 49 | | 77 | 49 | 94 | |
| Pharynx length | 125 | 155 | 125 | | 158 | 240 | 137 | | 240 | 137 | 376 | |
| Pharyngeal diam. at base | – | – | – | | – | 50 | 37 | | 50 | 37 | 69 | |
| Pharyngeal bulb diam. | 39 | 57 | 52 | | 36 | – | – | | – | – | – | |
| Pharynx cbd at base | 67 | 86 | 75 | | 51 | 70 | 51 | | 70 | 51 | 97 | |
| Max. body diam. | 73 | 102 | 77 | | 52 | 78 | 56 | | 78 | 56 | 113 | |
| Spicule length | 83 | 87 | – | | 65 | 46 | 35 | | 46 | 35 | – | |
| Gubernaculum length | 36 | 36 | – | | 24 | 29 | 24 | | 29 | 24 | – | |
| Cloacal/anal body diam. | 53 | 71 | 57* | | 42 | 57 | 38 | | 57 | 38 | 61 | |
| Tail length | 38 | 52 | 35* | | 47 | 94 | 49 | | 94 | 49 | 96 | |
| V | – | – | 624 | | – | – | – | | – | – | 1120 | |
| %V | – | – | 47 | | – | – | – | | – | – | 62 | |
| Vulval body diam. | – | – | 77 | | – | – | – | | – | – | 113 | |

papillae, ca 1.5–3.0 μm long, at same level as four cephalic papillae of same length. Amphidial fovea large, multispiral with $4\frac{3}{4}$ –5 turns, situated ca 0.4 cbd from anterior end. Buccal cavity (pharyngostome) large, divided into anterior (gymnostome) and posterior portions (stegostome). Anterior portion of buccal cavity cup-shaped, 16–26 μm deep, with three sets of three cuticularised rhabdions, 14–21 μm long, terminating in three sets of small bifid 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 cuticularised rhabdions with swollen bases, of similar length to anterior rhabdions. Pharynx short, muscular, slightly swollen anteriorly and with posterior bulb; pharyngeal lumen not conspicuously cuticularised. Nerve ring near middle of pharynx length. Secretory-excretory system present; renette cell situated at level of cardia, ampulla small, pore situated immediately posterior to nerve ring. Cardia small, ca 6 μm long, partially surrounded by intestine. Posterior extremity of intestine blind, rectum absent.

Reproductive system diorchic with opposed, outstretched testes. Anterior testis to the right of intestine, posterior testis to the left or ventrally relative to intestine. Sperm cells globular; in holotype, sperm cells of similar dimensions in both anterior and posterior testes ($10\text{--}11 \times 13\text{--}15 \mu\text{m}$). In paratype, sperm cells markedly larger in anterior testis ($14\text{--}16 \times 17\text{--}24 \mu\text{m}$) relative to posterior testis ($6 \times 10 \mu\text{m}$). Spicules paired, curved, tapering distally, length 1.2–1.6 body diameters at level of cloacal opening; gubernaculum consisting of two detached lateral pieces (crurae) tapering distally, ca 0.4 spicule length, median portion of gubernaculum (corpus and cuneus) apparently absent. Three or four precloacal supplements present, consisting of raised areas of cuticle; posteriormost supplement 11–12 μm from cloaca, remaining supplements 8–13 μm apart. Tail short, rounded, cuticle gradually doubling in thickness posteriorly, reaching 7 μm thick distally; a few short and sparse somatic setae present. Three caudal glands located posterior to cloacal opening, spinneret present.

Female

Similar to males but amphids with 4 turns. Reproductive system didelphic-amphidelphic, with reflexed ovaries; anterior ovary to the right of intestine, posterior ovary to the left of intestine. Vulva situated near mid-body. Proximal portion of vagina surrounded by constrictor muscle, vaginal glands present. Intestine blind, anus absent.

Choanolaimus sparsiporus sp. nov.

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Fig. 5; Tables 2–3

Diagnosis

Body length 1272 μm , large amphidial fovea, 0.56 cbd wide and with $5\frac{1}{4}$ turns, pharynx with posterior bulb, two dorsosublateral rows of small pore complexes sparsely distributed between pharyngeal and tail regions, spicule length ca 1.5 body diameters at level of cloacal opening, gubernaculum 24 μm long, two papilliform precloacal supplements, tail short, conical, 1.1 body diameters long at level of cloacal opening.

Differential diagnosis

The new species is most readily distinguished from *Choanolaimus psammophilus* by the large amphidial fovea 0.56 cbd wide with $5\frac{1}{4}$ turns (vs amphidial fovea ≤ 0.3 cbd wide with $2\text{--}2\frac{1}{4}$ turns in *C. psammophilus*), arrangement of pore complexes (dorsosublateral vs dorso- and ventrosublateral in *C. psammophilus*), shape of the inner labial sensilla (papilliform vs ‘flap-like’ or on swollen lobes in *C. psammophilus*), pharynx with posterior bulb (vs pharynx without posterior bulb in *C. psammophilus*), longer spicules (1.5 vs ≤ 1.0 body diameters at cloacal opening in *C. psammophilus*) and fewer precloacal supplements (2 vs 6–7 in *C. psammophilus*).

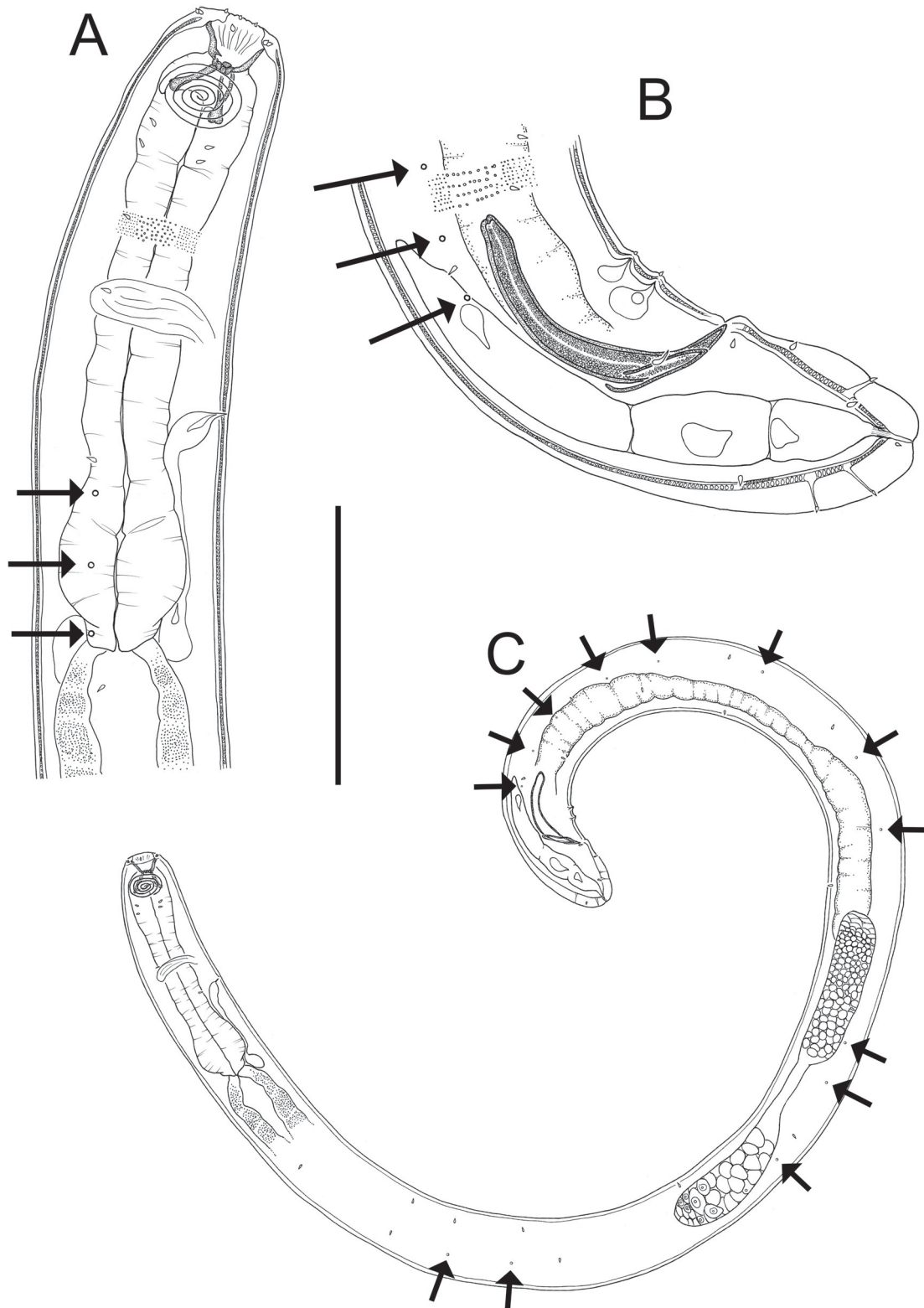


Fig. 5. *Choanolaimus sparsiporus* sp. nov., holotype, ♂ (NIWA 181632) **A.** Anterior body region. **B.** Posterior body region. **C.** Entire specimen. Arrows show position of dorsosublateral pore complexes. Scale bar: A = 75 μ m; B = 60 μ m; C = 200 μ m.

Choanolaimus sparsiporus sp. nov. can be distinguished from *C. serieporus* sp. nov. by the slightly shorter body (1272 vs 1321–1682 μm in *C. serieporus*), higher a ratio (24 vs 17–18 in *C. serieporus*), lower b and c ratios (8 and 27 vs 11 and 32–38, respectively, in *C. serieporus*), arrangement of pore complexes (sparsely distributed vs groups of 8–11 pore complexes in *C. serieporus*), and number of precloacal supplements (two vs 3–4 in *C. serieporus*).

Etymology

The species name is derived from the Latin ‘*sparsus*’ (= ‘few, rare, scattered’) and ‘*porus*’ (= ‘hole’) and refers to the scattered arrangement of the pore complexes in this species.

Type material examined

Holotype

NEW ZEALAND • ♂; Otago Fan complex, continental slope; 46.4971° S, 170.8644° E; 992 m water depth; 13 Feb. 2024; voyage TAN2402, stn 34; NIWA 181632.

Type habitat and locality

Continental slope, New Zealand.

Description

Male

Body cylindrical, tapering slightly towards both extremities, mostly colourless except for light brown intestine wall. Cuticle 3.0–3.5 μm thick, without annulations; transverse rows of cuticle punctations with lateral differentiation consisting of larger, more widely spaced punctations beginning from posterior to amphids to tail region. Two dorsosublateral rows of small pore complexes sparsely distributed between pharyngeal and tail regions; each pore complex ca 1.5 μm in diameter. Somatic setae short, 2.0–2.5 μm long, sparse, located dorsosublaterally and ventrosilaterally. Cephalic region somewhat rounded; lip region short, bearing six inner labial papillae. Six short outer labial papillae located slightly further posteriorly, ca 1.5–2.0 μm long, at same level as four cephalic papillae of same length. Amphidial fovea large, multispiral with $5\frac{1}{4}$ turns, situated ca 0.3 cbd from anterior end. Buccal cavity (pharyngostome) large, divided into anterior (gymnostome) and posterior portions (stegostome). Anterior portion of buccal cavity cup-shaped, 13 μm deep, with three sets of three cuticularised rhabdions, 11 μm long, terminating in three sets of small bifid 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 cuticularised rhabdions with swollen bases, 14 μm long. Pharynx muscular, slightly swollen anteriorly and with posterior bulb; pharyngeal lumen not conspicuously cuticularised. Nerve ring near middle of pharynx length. Secretory-excretory system present; renette cell situated at level of cardia, pore situated slightly posterior to nerve ring. Cardia small, partially surrounded by intestine. Posterior extremity of intestine blind, rectum absent.

Reproductive system diorchic with opposed, outstretched testes. Anterior testis to the right of intestine, posterior testis to the left of intestine. Sperm cells spherical to globular, larger in anterior testis (11×11 – $14 \mu\text{m}$) relative to posterior testis ($6 \times 6 \mu\text{m}$). Spicules paired, curved, tapering distally, length 1.5 body diameters at level of cloacal opening; gubernaculum consisting of two detached lateral pieces (crurae) tapering distally, ca 0.4 spicule length, median portion of gubernaculum (corpus and cuneus) apparently absent. Two precloacal supplements present, consisting of small papillae on swollen portion of cuticle and connected to a hypodermal gland; posteriormost supplement 17 μm from cloaca, supplements 7 μm apart. Tail short, conical, rounded distally, cuticle gradually doubling in thickness posteriorly, reaching 10 μm thick distally; a few short and sparse somatic setae present. Three caudal glands, one of which extends well anterior to cloacal opening; spinneret present.

Table 3. Key morphological trait comparison among all valid species of the genus *Choanolaimus* de Man, 1880. *Abbreviations:* cbd = corresponding body diameter; ND = no data; PC = pore complex.

| Reference | <i>C. psammophilus</i> de Man, 1880 | | | | | <i>C. serieporus</i> sp. nov. | <i>C. sparsiporus</i> sp. nov. |
|---|-------------------------------------|------------------------|--|--|---|--|--|
| Habitat & location | de Man 1880 | Loof 1961** | Chitwood 1960 | Riemann 1966 | Platt & Warwick 1988 | Bussau 1990 | Present study |
| | Sand dunes; Holland | Sand dunes; Holland | Beach spermatophytes; California | Coastal (high water line); Germany | Coastal subsoil; New Hebrides | Dunes; Germany and Denmark coast | Continental slope; New Zealand |
| Body length (µm) | 1700-2000 | 1270-1360 | 1600 | 1600-2120 | 1300-2400 | 1260-1310 | 1321-1688 |
| a | 25 | 20-22 | 29 | 22 | 16-19 | 15 | 17-18 |
| b | 7 | 6-7 | 7 | 7 | ND | 6-7 | 11 |
| c | 35-50 | 33-38 | 39 | 43 | ND | 27-28 | 32-38 |
| Inner labial sensilla | Papilliform? | Papilliform | Papilliform on lobes | Papilliform on lobes | Flap-like | Papilliform on lobes* | Papilliform |
| Amphideal fovea width (% cbd) | ND | 27* | 27* | 23 | 30 | 23* | 56 |
| Amphideal fovea t urns | ND | 2¼ | 2* | 2¼ | 2¼ | 2½* | 5¼ |
| Pharynx length | ND | ND | ND | 245 | ND | ND | 158 |
| Posterior pharynx | ND | Swollen posteriorly | Cylindrical | Slightly swollen posteriorly | Cylindrical | ND | Bulb present |
| PC arrangement*** | ND | ND | ND | Dorsosublateral and ventrosublateral; regularly-spaced* | Dorsosublateral and ventrosublateral; regularly-spaced* | Dorsosublateral and ventrosublateral; regularly-spaced* | Dorsosublateral; two or three groups of 8-11 PC sparsely distributed |
| Ratio of spicule length to body diameter at level of cloacal opening | ND | 0.9* | 0.7* | 0.7 | 1.0 | 0.8* | 1.2-1.6 |
| Number of precloacal supplements | ND | 7 | 7 | 6 | 6-7 | ND | 2 |

* From figure
** Redescription based on de Man's (1880) type specimens
*** It is unclear whether the structures observed by Riemann (1966), Platt & Warwick (1988) and Bussau (1990) are pore complexes or pores associated with somatic setae.

Genus *Gammanema* Cobb, 1920

= *Trogolaimus* Cobb, 1920

Type species

Gammanema ferox Cobb, 1920.

Diagnosis (from Tchesunov *et al.* 2020)

Cuticle with homogenous annulations, without longitudinal ridges or lateral differentiation. Six inner and six outer labial sensilla, either setose or papillose; four cephalic setae, often slender and longer; outer labial and cephalic sensilla often combined in common circle of 10, with dorso- and ventrosublateral sensilla arranged in four pairs with cephalic sensilla. Amphidial fovea spiral or loop-shaped, usually noticeably larger in males than in females. Somatic setae in irregular longitudinal rows; anterior cervical setae may be as long as cephalic setae. Mouth opening surrounded by partly fused lips shaping a circumoral membrane with fine longitudinal striation. Twelve projections, from small and inconspicuous to prominent and elaborate, at rim of mouth opening. Buccal cavity (pharyngostome) with two chambers, anterior cup-shaped and posterior cylindrical; walls of each chamber strengthened with three cuticularized rhabdions; rhabdions of anterior chamber terminate posteriorly in minute denticles. Pharynx cylindroids, evenly muscular and devoid of terminal bulb. Alimentary tract terminates by rectum and anus. Precloacal midventral supplementary organs sucker-like, cup-shaped, tubular, or absent. Tail short, conical, cuticle of its terminal cone levigated or smooth.

Remarks

The genus was revised by Tchesunov *et al.* (2020), who also provided a pictorial key to valid species. Prior to this study, 14 species were considered valid, while three (*G. ferox* Cobb, 1920, *G. menzelii* (Ditlevsen, 1918) Gerlach, 1964 and *G. rapax* (Ssaweljev, 1912) Gerlach 1964) are considered species inquirendae (Tchesunov *et al.* 2020). *Gammanema rapax* was considered as dubious by Murphy (1965) because the original description lacks illustrations and type specimens are evidently lacking. This decision was ignored or overlooked in some subsequent taxonomic publications (e.g., Platt & Warwick 1988; Okhlopkov 2002; Ahmed *et al.* 2020) but was accepted in the recent review of Tchesunov *et al.* (2020).

Gammanema lunatum sp. nov.

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Figs 6–8; Table 2

Diagnosis

Gammanema lunatum sp. nov. is characterised by body length 754–1817 µm, cuticle with minute spines mostly visible in tail region, amphideal fovea large and loop-shaped in males and small and unispiral in females, inner and outer labial setae of similar length (2–4 µm), conical and on broad cuticle bases, cephalic setae 0.25–0.35 cbd long, spicules relatively short (length = 0.8–0.9 body diameter at level of cloacal opening), gubernaculum ca 2/3 of spicule length, six to ten sup-shaped precloacal supplements, vulva at almost 2/3 of body length from anterior extremity, tail length 1.3–1.6 cloacal/anal body diameters.

Differential diagnosis

The new species differs from most other species of the genus, except *Gammanema agglutinans* Leduc, 2013, in males having loop-shaped amphidial fovea instead of unispiral (*G. conicauda* Gerlach, 1953) or multispiral amphidial fovea (all other species of *Gammanema*). The new species also differs in the shape of the amphidial fovea in females, which is multispiral in all other species of the genus for which

observations are available, except *G. conicauda* which is characterised by the unispiral amphidial fovea. In addition, the new species differs from most congeners, except *G. agglutinans*, in having minute cuticular spines.

Gammanema lunatum sp. nov. differs from *G. agglutinans* in the shape of the amphidial fovea in males ($\frac{3}{4}$ vs $\frac{1}{2}$ turn in *G. agglutinans*) and females (1.0 vs 1.5 turns in *G. agglutinans*), larger amphidial fovea size in males (17 vs 10 μm wide in *G. agglutinans*) and females (8 vs 5 μm in *G. agglutinans*), and the shape of precloacal supplements (cup-shaped vs tubular in *G. agglutinans*). *Gammanema lunatum* differs from *G. conicauda* in the shorter body (754–1817 vs 1985–3724 μm in *G. conicauda*), markedly lower a ratio (13–16 vs 30–43 in *G. conicauda*), shorter outer labial setae (2–4 vs 16 μm in *G. conicauda*), shorter cephalic setae (8–20 vs 30–33 μm in *G. conicauda*), and fewer precloacal supplements (6–10 cup-shaped supplements vs 22 papilliform precloacal supplement in *G. conicauda*).

Etymology

The species name is derived from the Latin ‘*lunatus*’ (= ‘shaped like a crescent moon’) and refers to characteristic shape of the amphids in males.

Type material examined

Holotype

NEW ZEALAND • ♂; Otago Fan complex, Papanui Canyon; 45.8668° S, 171.0415° E; 680 m water depth; 9 Feb. 2024; sandy mud sediments; voyage TAN2402, stn 2; NIWA 181633.

Paratypes

NEW ZEALAND • 1 ♂, 1 ♀; same data as for holotype; NIWA 181634.

Type habitat and locality

Upper continental slope, New Zealand.

Description

Males

Body cylindrical, relatively stout, tapering slightly towards both extremities; no colouration except for light to dark brown intestine wall. Cuticle ca 2–3 μm thick, with faint transverse annulations ca 1 μm apart and transverse rows of punctations without lateral differentiation; minute spines visible mainly in tail region, may be present in mid-body region and apparently absent in pharyngeal region. Eight longitudinal rows of somatic setae, 4–7 μm long in pharyngeal and tail regions, 2–4 μm long in mid-body region; pore complexes not observed. Cephalic region blunt, slightly rounded. Mouth opening surrounded by 12 membranous projections of varying shape located in internal circle surrounded by the lips. Partly fused lips each bearing a conical inner labial seta, 2–4 μm long, on a broad cuticle base. Six outer labial setae of same size and shape located further posteriorly at base of lip region; four longer (ca 0.25–0.35 cbd long) and thinner cephalic setae located immediately posterior to outer labial setae, without broad base. Amphideal fovea relatively large, loop-shaped, situated slightly posterior to cephalic setae; amphidial aperture slightly shorter than amphidial fovea. Buccal cavity (pharyngostome) divided into anterior (gymnostome) and posterior portions (stegostome). Anterior portion of buccal cavity cup-shaped, ca 14–23 μm deep, with three sets of cuticularised rhabdions, 18–20 μm long, terminating posteriorly in pairs of small teeth or denticles; posterior portion of buccal cavity narrower, cylindrical, surrounded by three Y-shaped pairs of cuticularised rhabdions with swollen bases, of similar length to anterior rhabdions. Pharynx cylindrical, muscular, without anterior or posterior bulb; pharyngeal lumen not conspicuously cuticularized or partitioned. Nerve ring at ca 40% of pharynx length from

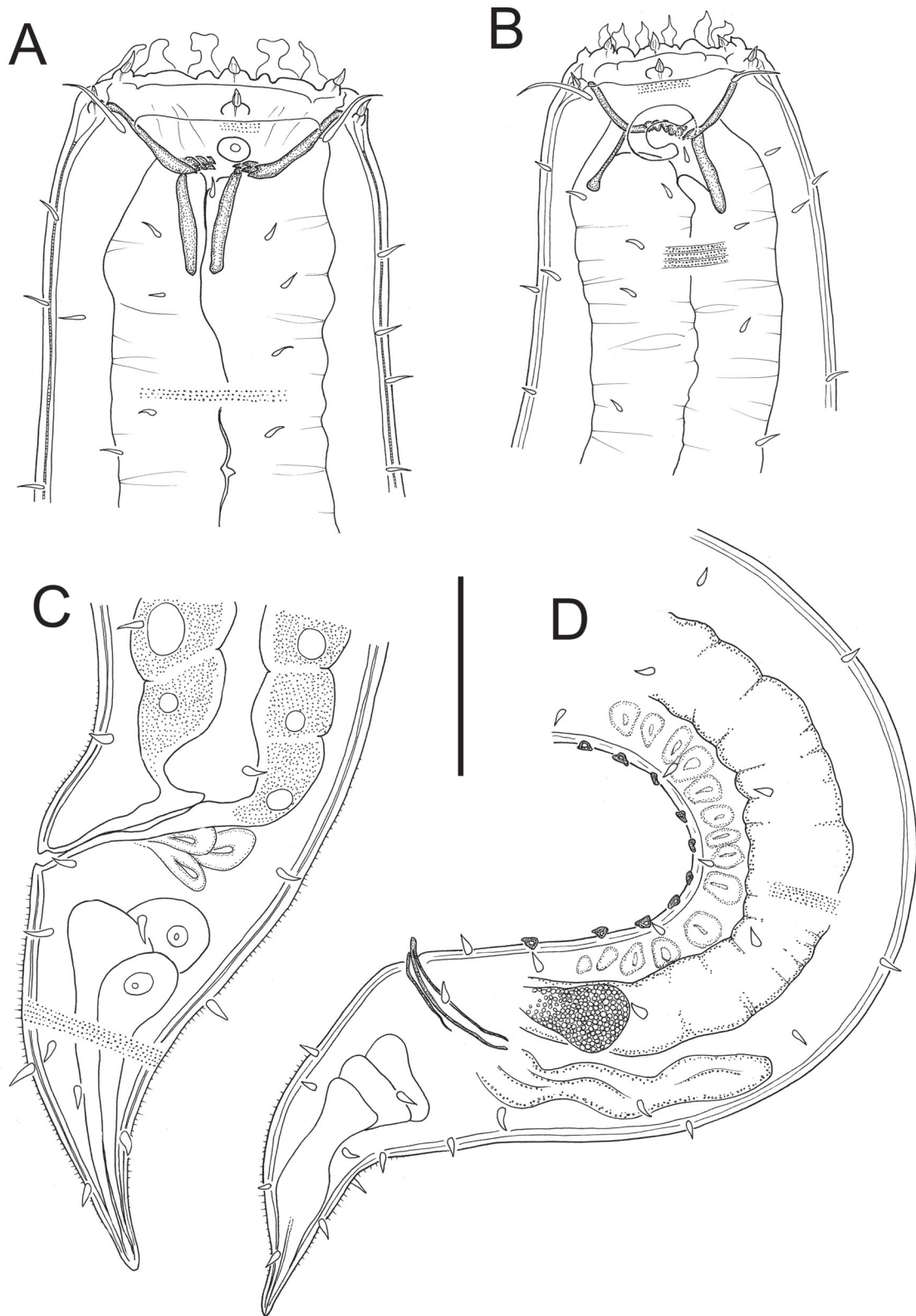


Fig. 6. *Gammanema lunatum* sp. nov. **A.** Cephalic region of paratype, ♀ (NIWA 181634). **B.** Cephalic region of holotype, ♂ (NIWA 181633). **C.** Posterior body region of paratype, ♀ (NIWA 181634). **D.** Posterior body region of holotype, ♂ (NIWA 181633). Scale bar: A–C = 50 µm; D = 58 µm.

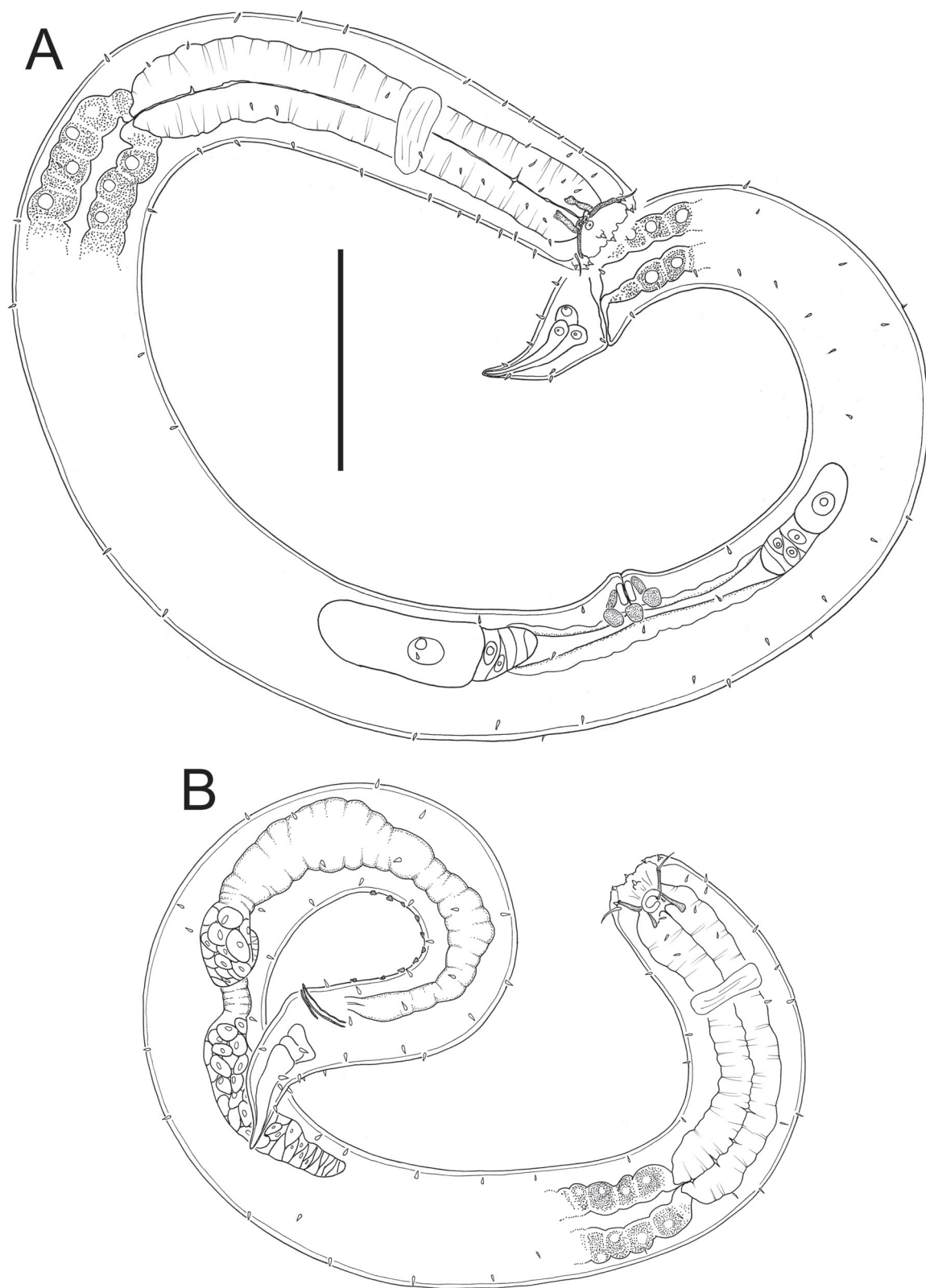


Fig. 7. *Gammanema lunatum* sp. nov. **A.** Entire paratype, ♂ (NIWA 181634). **B.** Entire holotype, ♂ (NIWA 181633). Scale bar = 150 µm.

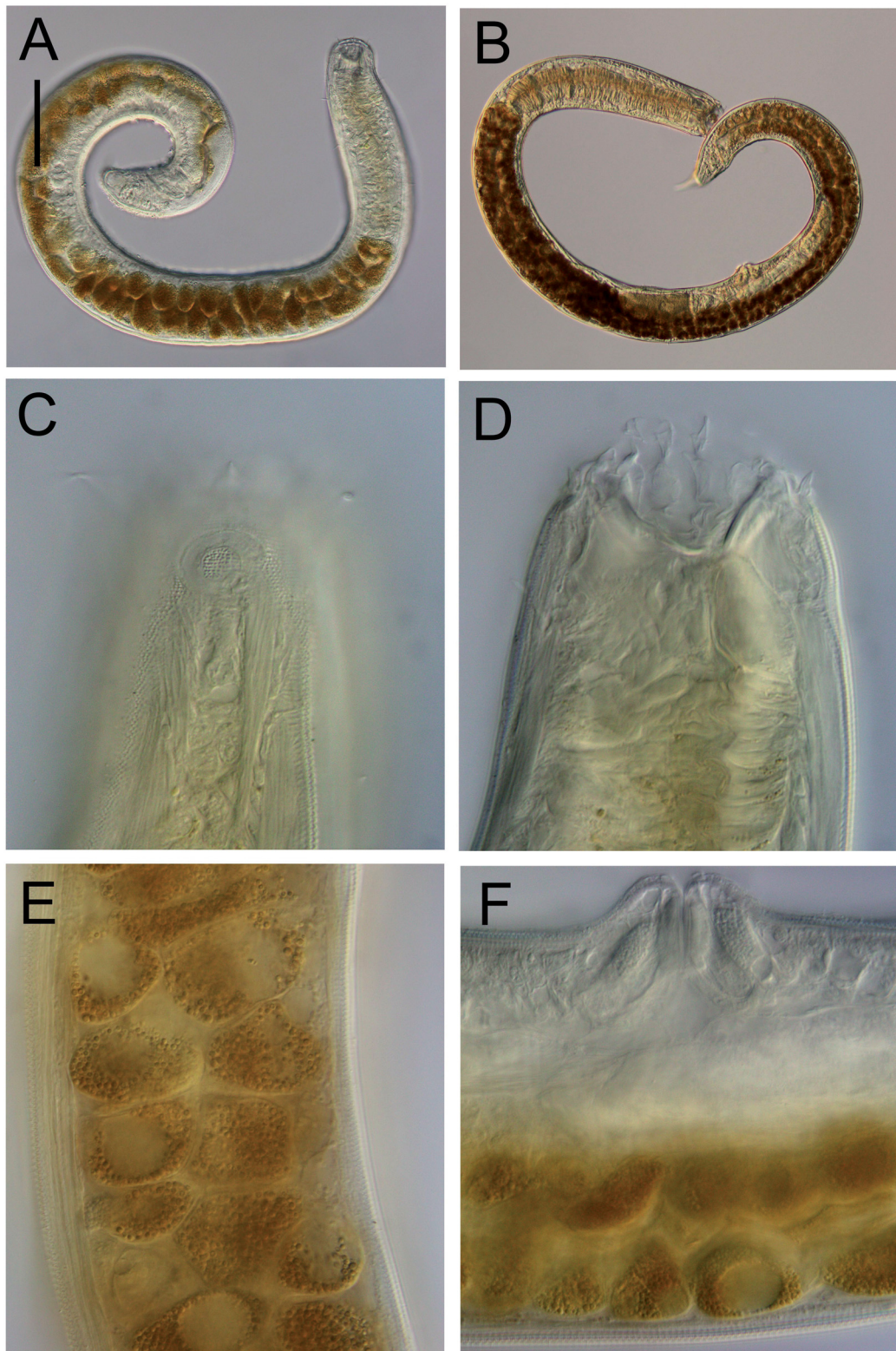


Fig. 8. *Gammanema lunatum* sp. nov. **A.** Entire paratype, ♂ (NIWA 181634). **B.** Entire paratype, ♀ (NIWA 181634). **C–D.** Cephalic region of holotype, ♂ (NIWA 181633). **C.** Surface view. **D.** Cross-section view. **E.** Intestine of paratype, ♀ (NIWA 181634). **F.** Vulva of paratype, ♀ (NIWA 181634). Scale bar: A = 125 µm; B = 165 µm; C–D = 16 µm; E–F = 20 µm.

anterior. Secretory-excretory system not observed. Cardia small, surrounded by intestine. Intestine and vas deferens join posteriorly into cloaca, opening to the exterior via cloacal opening.

Reproductive system diorchic with two short and opposed testes located ventrally relative to intestine; anterior testis outstretched, posterior testis reflexed. Sperm cells globular, longest diameter up to 23 μm , ca 1.5–2.0 greater than shortest diameter. Spicules paired, slightly curved, tapering distally, length 0.8–0.9 body diameters at level of cloacal opening; gubernaculum consisting of two flat detached lateral pieces (crurae), ca $\frac{2}{3}$ of spicule length; median portion of gubernaculum (corpus and cuneus) apparently absent. Six to ten cup-shaped precloacal supplements; posteriormost supplement 18–32 μm anterior to cloacal opening, supplements located 5–17 μm apart. Tail short, conical; three caudal glands and spinneret present.

Female

Similar to males, except for conspicuously smaller, unispiral amphidial fovea and aperture. Reproductive system didelphic-amphidelphic, with reflexed ovaries located ventrally relative to intestine. Vulval opening on conspicuously swollen body region, situated almost two thirds of body length from anterior extremity. Proximal portion of vagina surrounded by constrictor muscle; several vaginal glands present surrounding vulval region. Rectum and anus present.

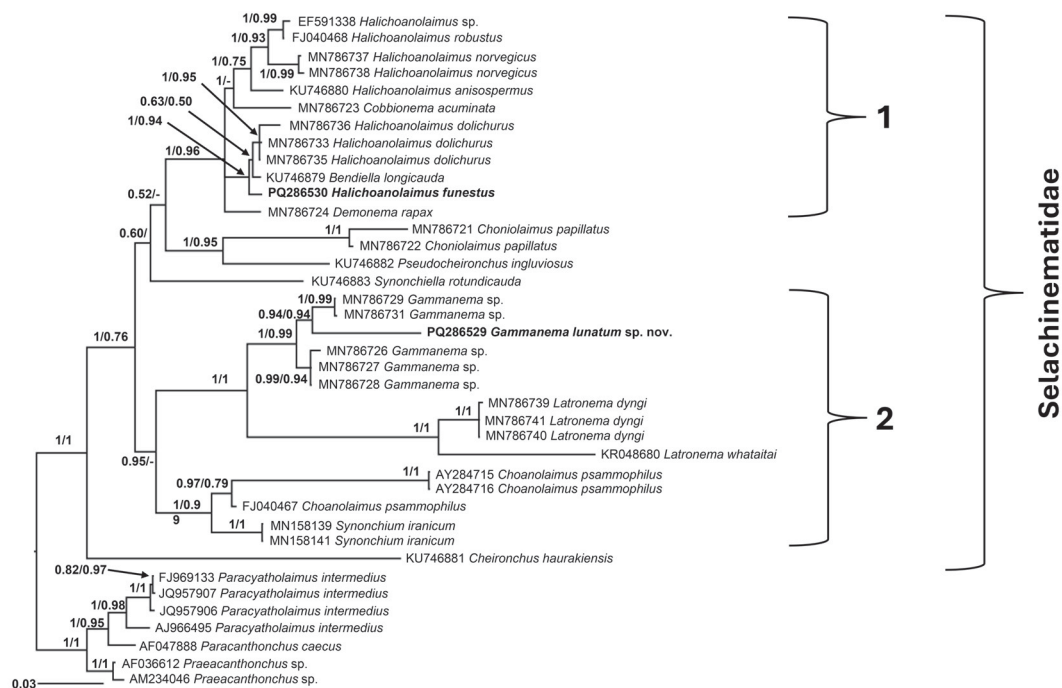


Fig. 9. Bayesian tree inferred from SSU sequences, aligned using the MUSCLE alignment algorithm under the general time-reversible (GTR) + I (proportion of invariable sites) + gamma distribution (G) model. The new sequences are shown in bold font. Posterior probabilities (left) and bootstrap values (right) greater than or equal to 50% are given on appropriate clades. Sequence FJ040468 is labelled *Synonchiella* sp. in Genbank but is changed here to *Halichoanolaimus robustus* (Bastian, 1865) de Man 1886, based on a reinvestigation of the images of the voucher specimen used for sequencing by Ahmed *et al.* (2020). Note that sequences MN786729 & MN786731 and MN786726–8 published by Ahmed *et al.* (2020) were labelled *Gammanema rapax* sensu Platt & Warick (1988) and *Gammanema rapax*, respectively; however, given the uncertain status of this species (Tchesunov *et al.* 2020), the sequences are instead labelled “*Gammanema* sp.”. The scale stands for substitutions per site. - = less than 50% bootstrap support.

Discussion

The present study brings total number of selachinematid species recorded from the New Zealand region to 17 (Leduc 2020). Until now, the genus *Choanolaimus* comprised a single species restricted to coastal dunes, beaches and estuarine environments of the North Sea, Northeast Atlantic and Northeast Pacific (de Man 1880; Chitwood 1960; Riemann 1966; Platt & Warwick 1988). To our knowledge, this is the first time that *Choanolaimus* is recorded from the Southern Hemisphere and from deep-sea environments (266–1338 m depth). Although the two new species described here correspond well to the genus diagnosis in terms of the structure of the anterior sensilla (all papilliform), cuticle ornamentation (with lateral differentiation) and tail shape (short and conical/rounded), they both differ from the type species in having a posterior pharyngeal bulb. By itself, however, this difference does not justify the erection of a new genus to accommodate the New Zealand species. The two new species are both characterised by two longitudinal dorsosublateral rows of pore complexes (defined by Leduc & Zhao (2018) as circular structures with slit-like pore and ring-like development of dense material in the middle cuticle layer) in both males and females. The arrangement of these pore complexes differs between *C. serieporus* sp. nov. and *C. sparsiporus* sp. nov., thus providing a taxonomically informative character for recognition of the species. Pore complexes may also be present in *C. psammophilus*; the descriptions of Gerlach (1952) and Riemann (1966) show the presence of ventro- and dorsosublateral pore-like structures in the anterior and posterior body regions of this species; however, the observations of Platt & Warwick (1988) suggest that they may be associated with somatic setae. Pore complexes have so far only been found in selachinematid genera with a blind intestine (i.e., *Halichoanolaimus*, *Bendiella*, *Cobbionema* and *Choanolaimus*), and not in genera with an intestine connecting to a cloaca/rectum (*Synonchiella*, *Cheironchus*, *Pseudocheironchus*, *Latronema*) (Leduc 2020).

Gammanema lunatum sp. nov. is the second species of the genus recorded from the New Zealand region. It is morphologically similar to *G. agglutinans*, which was described from Chatham Rise, a topographic feature adjoining the Bounty Trough to the north (see Fig. 1; Leduc 2013). The two New Zealand species share characters not found in any other species of *Gammanema*, i.e., loop-shaped amphids in males and the presence of cuticle spines. These similarities indicate that these two species may have evolved from a common ancestor.

Our phylogenetic analyses confirm previous published results which supported the monophyly of the family Selachinematidae but not of the subfamilies Selachinematinae and Choniolaiminae (Leduc & Zhao 2016; Ahmed *et al.* 2020). Similar to Ahmed *et al.* (2020), we have found strong support for a clade comprising *Halichoanolaimus*, *Bendiella*, *Cobbionema* and *Demonema* (clade 1 in Figs 9–10). While the first three genera have very similar buccal morphology (anterior and posterior portions of buccal cavity reinforced by radially arranged cuticularized rhabdions, with anterior rhabdions terminating in denticles), *Demonema* is much more similar to *Cheironchus* (anterior portion of buccal cavity reduced, and rhabdions of posterior portion modified into denticulate mandibles), which is placed outside of clade 1. Other genera sharing strong morphological similarities have also been placed in different clades, including *Gammanema* and *Choniolaimus*, which differ only in the presence or absence of a posterior pharyngeal bulb, and *Synonchiella* and *Synonchium*, which share similar buccal cavity morphology. The limited sequence data available suggest that *Gammanema* and *Latronema* are monophyletic; however, we found no support for the monophyly of *Halichoanolaimus*, for which more data are available.

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