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Research article

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Two new genera and five new species of Selachinematidae (Nematoda, Chromadorida) from the continental slope of New Zealand

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Abstract. Two new genera and five new species of Selachinematidae are described from the New Zealand upper continental slope (350-1240 m depth). Synonchiella rotundicauda sp. nov. is characterised by cephalic setae 0.25 cbd long, mandibles each with two pairs of hooks and two wing-like projections laterally, eight cup-shaped pre-cloacal supplements and short rounded tail. *Pseudocheironchus* gen. nov. is similar to *Cheironchus*, but differs from the latter in having a cuticle without lateral differentiation, cephalic setae only slightly longer than the outer labial sensillae, and a posterior buccal cavity with three equal mandibles. Pseudocheironchus ingluviosus gen. et sp. nov. is characterised by mandibles with eight blunt teeth, multispiral amphideal fovea with five turns, and a short rounded tail. Males of this new species with 17-19 cup-shaped pre-cloacal supplements. Males of the genus Cobbionema are described for the first time; C. trigamma sp. nov. is characterised by four long cephalic setae and six smaller outer labial setae in one circle, six rhabdions surrounding the anterior buccal cavity, each with two pairs of pointed projections at their posterior extremities, posterior buccal cavity widening posteriorly, with three pairs of rhabdions fused posteriorly and widening anteriorly, males with two testes pointing anteriorly and with reflexed posterior testis, and no pre-cloacal supplements. Gammanema agglutinans sp. nov. is characterised by a short, stout body often covered in adhering mucus and detritus, cuticle with minute spines, leaf-shaped somatic setae with ducts, sexual dimorphism in the shape of the amphideal fovea (loop-shaped in males and spiral in females), posterior buccal cavity with three pairs of broad, column-shaped rhabdions fused anteriorly, intestine cells with orange-brown granules, and small tubular pre-cloacal supplements. Bendiella gen. nov. is most similar to Halichoanolaimus, but differs from the latter, and all other genera of the family Selachinematidae, in having a cuticle with lateral differentiation consisting of longitudinal rows of larger dots, and from all other genera of the Choniolaiminae in lacking pre-cloacal supplements. Bendiella thalassa gen. et sp. nov. is characterised by amphideal fovea with 5.25 turns, anterior buccal cavity with twelve rhabdions, each with a pair of pointed projections at posterior extremity, posterior buccal cavity with three Y-shaped pairs of slender rhabdions fused from two thirds of distance from anterior ends, and conico-cylindrical tail.

Key words. Selachinematinae, Choniolaiminae, marine predatory nematodes, bathyal, Southwest Pacific.

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Introduction

The family Selachinematidae Cobb, 1915 is a group of predatory nematodes widespread in the world's oceans (e.g., Jensen 1987; Pereira *et al.* 2009). The taxonomy of the group was revised in detail by Gerlach (1964). A key to the genus *Synonchiella* Cobb, 1933 was provided by Fadeeva (1988), and, more recently, Tchesunov & Okhlopkov (2006) reviewed and described some selachinematid specimens from the Northeast Atlantic and provided an emended diagnosis for the genus *Cheironchus* Cobb, 1917. Selachinematids are most often reported from relatively coarse sediments in shallow water environments (e.g., Warwick 1971; Okhlopkov 2002; Tchesunov & Okhlopkov 2006). They also occur in deep-sea habitats, with eight species belonging to three genera recorded from water depths >400 m worldwide (Miljutin *et al.* 2010).

Only two species of Selachinematidae are presently known from the New Zealand Exclusive Economic Zone, *viz.*, *Halichoanolaimus ovalis* Ditlevsen, 1921 and *H. robustus* (Bastian, 1865) (Leduc & Gwyther 2008). Here, two new genera and five new species of Selachinematidae are described from the continental slope of New Zealand (350-1240 m depth).

Material and Methods

Sediment samples were obtained from the Chatham Rise and Challenger Plateau, two major bathymetric features of the continental slope of New Zealand. Details of the study region and sampling sites are given in Leduc *et al.* (2012a, 2012b). Briefly, samples were collected along a transect at 178°30′ E across the Chatham Rise (nine sites, 350-3100 m depth) in austral spring (September-October) 2001 during National Institute of Water and Atmospheric Research (NIWA) cruise TAN0116. Twenty-three additional sites between 240 and 1300 m depths on the Chatham Rise and Challenger Plateau were sampled in austral autumn-early winter (March-April and May-June) 2007 (NIWA cruises TAN0705 and TAN0707, respectively). Additional samples were obtained in February 2011 (NIWA cruise TAN1103) from a site near the middle of Chatham Rise crest at 350 m depth, and in November 2011 (NIWA cruise TAN1116) from a site on the northern flank of Chatham Rise at 470 m depth.

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 1 mm sieve to remove large particles and on a 45 μ m 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. All measurements are in μ m, and all curved structures are measured along the arc. Type specimens are held in the NIWA Invertebrate Collection (NIC), Wellington. Abbreviations in the text are as follows:

a = body length/maximum body diameter

abd = anal body diameter

b = body length/pharynx length c = body length/tail length cbd = corresponding body diameter

L = body length

n = number of specimens

%V = vulva distance from anterior end of body \times 100/total body length

Results

Class Chromadorea Inglis, 1983 Subclass Chromadoria Pearse, 1942 Order Chromadorida Chitwood, 1933 Suborder Chromadorina Filipjev, 1929 Superfamily Chromadoroidea Filipjev, 1917 Family Selachinematidae Cobb, 1915

Diagnosis

(Modified from Decraemer & Smol 2006.) Body usually stout. Cuticle punctated with or without lateral differentiation. Head sensillae may be jointed. Amphideal fovea usually multispiral, rarely loop-shaped. Buccal cavity spacious, divided into two compartments, either reinforced by cuticularised rhabdions in both portions (Choniolaiminae), or with posterior rhabdions modified into protrusible mandibles (Selachinematinae). Pharynx with or without posterior bulb, anterior bulb sometimes present (*Cheironchus* and *Pseudocheironchus* gen. nov.). Males usually with two outstretched testes, either on same or different sides of the intestine; pre-cloacal supplements usually present, usually cup-shaped, sometimes setose, papilliform, rarely tubular. Female didelphic-amphidelphic with reflexed ovaries.

Remarks

The holophyly of the family Selachinematidae is based on the holapomorphy of a spacious buccal cavity without teeth or, if teeth are present, they are not homologous with teeth found in other Chromadorida (Lorenzen 1981). The family placement of *Richtersia* Steiner, 1916 and *Desmotersia* Neira & Decraemer, 2009 remains uncertain and these genera are considered by some as intermediate between the Selachinematidae and Desmodoroidea (e.g., Pastor de Ward & Lo Russo 2007; Neira & Decraemer 2009). The genus *Dignathonema* Filipjev, 1918 was synonymised with *Cheironchus* Cobb, 1917 by Filipjev (1926). *Trogolaimus* Cobb, 1920 was classified in the subfamily Selachinematinae by Gerlach (1964), but, as Tchesunov & Okhlopkov (2006) noted, this genus should be assigned to the Choniolaiminae based on the structure of the buccal cavity. The latter authors considered *Trogolaimus* to be a synonym of *Gammanema* Cobb, 1920. *Nunema* Cobb, 1933 and *Pteronium* Cobb, 1933 were considered doubtful by Hope & Murphy (1972).

Subfamily Selachinematinae Cobb, 1915

Diagnosis

Anterior portion of buccal cavity reduced, posterior portion with three denticulate mandibles (modified rhabdions); dorsal mandible may be reduced.

Valid genera

Cheironchus Cobb, 1917 Demonema Cobb, 1894 Kosswigonema Gerlach, 1964 Synonchiella Cobb, 1933 Synonchium Cobb, 1920

Genus Synonchiella Cobb, 1933

Type species

Synonchiella truncata Cobb, 1933

Diagnosis

Cuticle without lateral differentiation. Outer labial setae and cephalic setae usually in one circle. Buccal cavity with three equal mandibles made of two branches fused posteriorly; the two branches completely fused in some species (e.g., *S. rotundicauda* sp. nov.). Pharynx without posterior or anterior bulb. Cupshaped pre-cloacal supplements present.

Remarks

Synonchiella denticulata Cobb, 1933, *S. ferox* Cobb, 1933 and *S. siphonolaimoides* (Allgén, 1940) were considered doubtful by Gerlach (1964) due to incomplete descriptions. The latter author also transferred *S. annulata* Gerlach, 1952 and *S. orcina* Gerlach, 1952 to the genus *Latronema*.

Valid species

- S. dilarae Fadeeva, 1988
- S. edax Aissa & Vitiello, 1970
- S. forceps (Gerlach, 1957)
- S. hopperi Ott, 1972
- S. japonica Fadeeva, 1988
- S. lutosa Gagarin & Klerman, 2007
- S. major Murphy, 1965
- S. micramphis (Schuurmans-Stekhoven, 1950)
- S. microspiculoides (Schuurmans-Stekhoven, 1946)
- S. minor Murphy, 1965
- S. minuta Vitiello, 1970
- S. riemanni Warwick, 1970
- S. roscoffiensis De Coninck, 1965
- S. siphonolaimoides (Allgén, 1940)
- S. spiculora Murphy, 1962
- S. truncata Cobb, 1933

Synonchiella rotundicauda sp. nov.

Figs 1-3, Table 1

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Diagnosis

Synonchiella rotundicauda sp. nov. is characterised by cephalic setae 0.25 cbd long, mandibles each with two pairs of hooks and two wing-like projections laterally, multispiral amphideal fovea with 3.5 turns, eight cup-shaped pre-cloacal supplements, and short tail (2.2. abd) with rounded extremity.

Etymology

The species name is derived from the Latin *rotundus* (= round, circular) and *cauda* (= tail), referring to the unusual rounded shape of the tail.

Material examined

Holotype

NEW ZEALAND: &, NIWA 88354, 17 Apr. 2007, NIWA cruise TAN0705, station 172, eastern Chatham Rise crest, 43.5162° S, 178.6167° W, 422 m, fine sand (53.5%), silt/clay (23.5%), very fine sand (18.9%).

Paratype

NEW ZEALAND: 1 \, NIWA 88355, 15 Nov. 2011, NIWA cruise TAN1116, station 107, northern flank of Chatham Rise, 42.8625° S, 177.9253° E, 467 m.

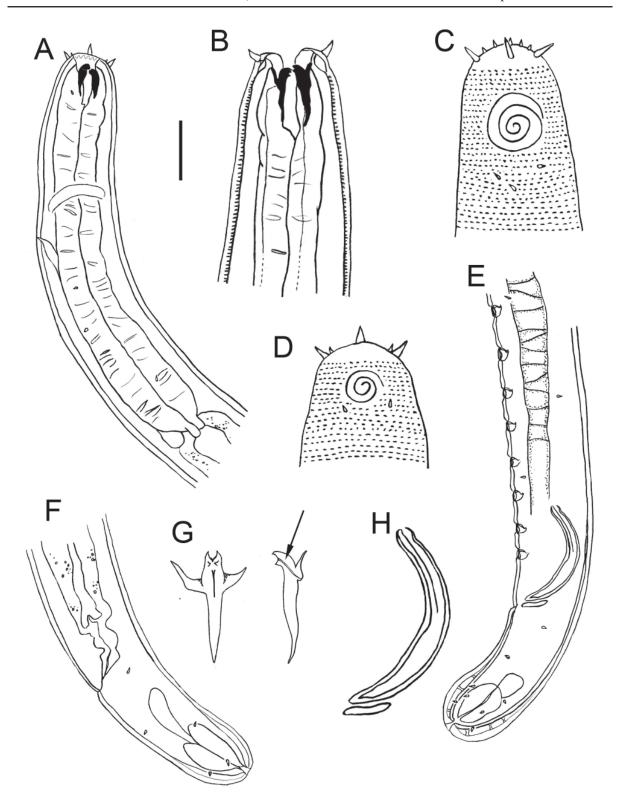


Fig. 1. *Synonchiella rotundicauda* sp. nov. **A.** Anterior body region of female. **B.** Male head. **C.** Surface view of male head. **D.** Surface view of female head. **E.** Male posterior body region. **F.** Female posterior body region. **G.** Mandibles, en face (left) and lateral (right) views. **H.** Spicule and gubernaculum. Arrow shows position of duct connecting anterior end of marginal tube and buccal cavity. Scale bar: A, E-F = $25 \mu m$; B-D = $15 \mu m$; G = $8 \mu m$; H = $13 \mu m$.

Description

Male

Body cylindrical, tapering slightly towards anterior extremity. Cuticle $\sim 2.0~\mu m$ thick throughout body, thicker in tail region, 4 μm , with transverse rows of punctations, without lateral differentiation. Somatic setae short and sparse, in four sublateral rows. Head blunt, rounded, not set off. Six conical inner labial papillae, $\sim 1.5~\mu m$ long; six longer outer labial setae, 4 μm long, and four cephalic setae, $\sim 1~\mu m$ long, situated close to or slightly anteriorly to outer labial setae (Fig. 1C). Amphideal fovea cuticularised, multispiral, 3.5 turns. Anterior portion of buccal cavity short and narrow, with inconspicuous rhabdions at anterior extremity. Posterior buccal cavity with three equal mandibles, 15 μm long, with one mandible situated dorsally and two sub-ventrally; each mandible with two pairs of hooks at anterior extremity and two larger wing-like projections emerging laterally and pointing anteriorly; mandible also with small duct apparently connecting anterior extremity of marginal tubes and opening into buccal cavity near anterior end of mandible (Fig. 1G). Posterior buccal cavity surrounded by slightly swollen pharyngeal

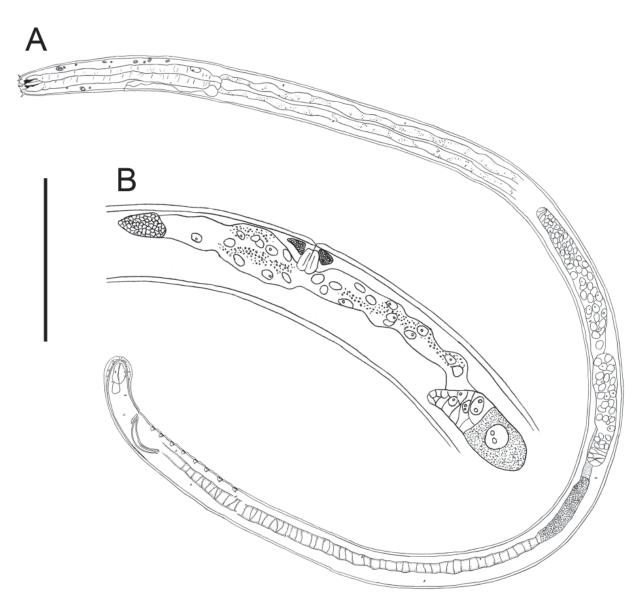


Fig. 2. Synonchiella rotundicauda sp. nov. **A**. Entire male. **B**. Female reproductive system. Scale bar: $A = 150 \ \mu m$; $B = 75 \ \mu m$.

tissue, pharynx widening posteriorly, not forming true bulb. Several light refractive, golden-brown corpuscules present in pharyngeal region (also present in tail; Fig. 3A, B). Nerve ring at 45% of pharynx length from anterior end. Secretory-excretory (S-E) system present, cellular body of ventral gland small, situated immediatly posterior to pharynx, pore situated ~ 0.5 cbd posterior to nerve ring.

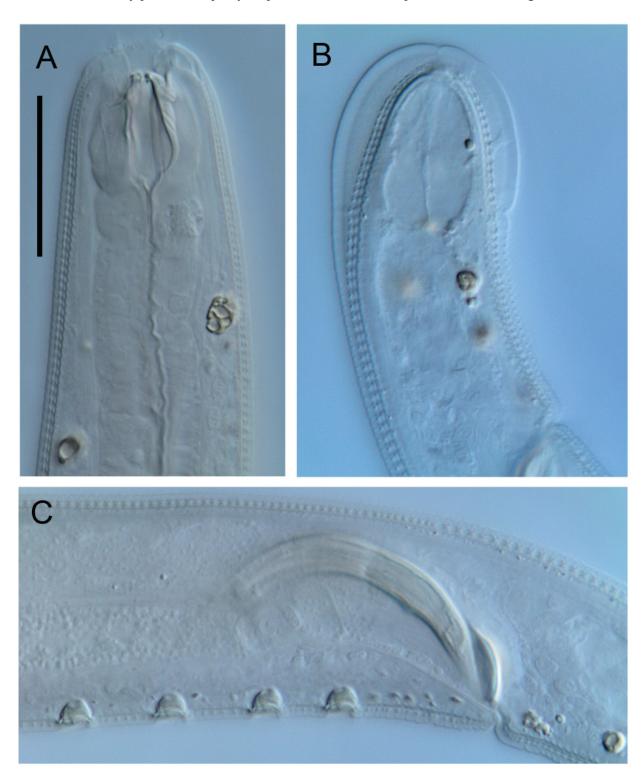


Fig. 3. *Synonchiella rotundicauda* sp. nov. Light micrographs. **A.** Anterior body region of male showing buccal cavity. **B.** Tail of male. **C.** Spicular apparatus. Scale bar = $25 \mu m$.

maximum body diameter; abd = anal body diameter; b = body length/pharynx length; c = body length/tail length; cbd = corresponding body **Table 1.** Morphometrics (μm) of *Synonchiella rotundicauda* sp. nov. and *Pseudocheironchus ingluviosus* gen. et sp. nov. — a = body length/ diameter; L = body length; n = number of specimens; V = vulva distance from anterior end of body; <math>%V = V/total body length.

Species	Synonchiella	Synonchiella rotundicauda sp. nov.	Pseudochei	Pseudocheironchus ingluviosus gen. et sp. nov.	s gen. et sp. nov.
	Male Holotype	Female Paratype	Males Holotype	les Paratype	Female Paratypes
٢	ı			_	,
	1411	1172	1034	992	940, 1209
l ल	43	32	25	25	25, 27
Р	~	7	12	6	9, 12
၁	23	20	24	22	21, 26
Body diameter at level of cephalic setae	16	18	20	18	18, 21
Body diameter at level of amphids	26	30	23	24	25, 29
Length of cephalic setae	4	4-5	2	2	2, 3
Amphid height	14	7	6	12	7
Amphid width	14	10	17	16	10
Amphid width/cbd (%)	54	33	74	29	40
Amphid from anterior end	12	11	4	9	2, 5
Length of mandibles	15	14	18-20	19-21	22, 24
Nerve ring from anterior end	79	54	49	54	53, 54
Nerve ring cbd	33	36	39	35	38, 42
Exeretory pore from anterior end	86	75	84	94	•
Pharynx length	180	163	88	105	99, 104
Pharynx diameter at base	24	24	25	24	29, 31
Pharynx cbd at base	36	38	40	37	39, 41
Max. body diam.	33	37	41	39	38, 44
Spicule length	51	1	51	48	1
Gubernaculum length	11	ı	11	6	
Anal body diam.	28	27	30	31	27, 32
Tail length	61	09	43	46	44, 46
Tail length/abd	2.2	2.2	1.4	1.5	1.4, 1.6
Λ	•	573	•		438, 555
$\Lambda\%$	1	49	ı	1	46, 47
Vulval body diameter		37		1	38, 43

Reproductive system diorchic with outsretched testes. Both anterior and posterior testes on right of intestine. Oval-shaped, nucleated sperm cells, $\sim 6 \times 7~\mu m$. Spicules paired, strongly curved, 1.8 abd long, widest in middle portion and tapering distally; thin cuticular projection extending from proximal end over almost half of spicule length. Gubernaculum small, plate-like, without lateral pieces, parallel to distal end of spicules. Mid-ventral row of eight cup-shaped pre-cloacal supplements, $\sim 4~\mu m$ wide and 4 μm deep, situated 6-8 μm apart; distance between supplements increasing slightly anteriorly. Pre-cloacal supplements thickly cuticularised with nerve entering anterior side of cup. No pre-or post-cloacal setae or papillae observed. Tail short, with rounded posterior extremity, posterior half with few short setae and ducts, some of which are not connected to setae; terminal setae not observed. Three caudal glands and small spinneret present.

Female

Similar to males, but with smaller amphideal fovea, 2.5 turns. Reproductive system with posterior ovary reflexed, on right of intestine; anterior ovary poorly developed (Fig. 2B). Vulva located at mid-body. Vaginal glands present, *pars proximalis vaginae* surrounded by constrictor muscle.

Remarks

In contrast to *Synonchiella rotundicauda* sp. nov., all other *Synonchiella* species are characterised by relatively long, conico-cylindrical tails with a thin cylindrical portion. *S. minor* is characterised by a relatively short conical tail (2.9 abd), but can be distinguished from *S. rotundicauda* sp. nov. in having smaller amphid with 1.75 turns (*vs.* 2.5 turns in *S. rotundicauda* sp. nov.), longer spicules (200 *vs.* 51 µm), and more pre-cloacal supplements (42-46 *vs.* 8).

Genus *Pseudocheironchus* gen. nov. urn:lsid:zoobank.org:act:D308E75C-FF14-44AB-9DA3-E2297C691AF6

Type species

Pseudocheironchus ingluviosus gen. et sp. nov.

Diagnosis

Cuticle without lateral differentiation or only weak lateral differentiation. Outer labial sensillae and cephalic setae in one circle; cephalic setae slightly longer than outer labial sensillae. Anterior portion of buccal cavity reduced, with six thin, slightly cuticularised rhabdions; posterior buccal cavity with three equal mandibles. Pharynx short, with well-developed anterior and posterior bulbs. Male with cupshaped pre-cloacal supplements. Tail short.

Etymology

This generic name refers to the close similarity between the new genus and *Cheironchus*. The two genera share a feature not found in any other genus of the Selachinematidae, *viz.*, a pharynx with conspicuous anterior and posterior bulbs.

Remarks

Pseudocheironchus gen. nov. is similar to Cheironchus in having a pharynx with well-developed anterior and posterior bulbs and cup-shaped pre-cloacal supplements. Pseudocheironchus gen. nov. differs from the latter in having a cuticle without or only weak lateral differentiation (vs. lateral differentiation of larger, irregularly spaced punctations in Cheironchus), cephalic setae only slightly longer than the outer labial sensillae (vs. cephalic setae much longer than outer labia sensillae), and a posterior buccal cavity with three equal mandibles (vs. dorsal mandible reduced). Pseudocheironchus gen. nov. is also similar

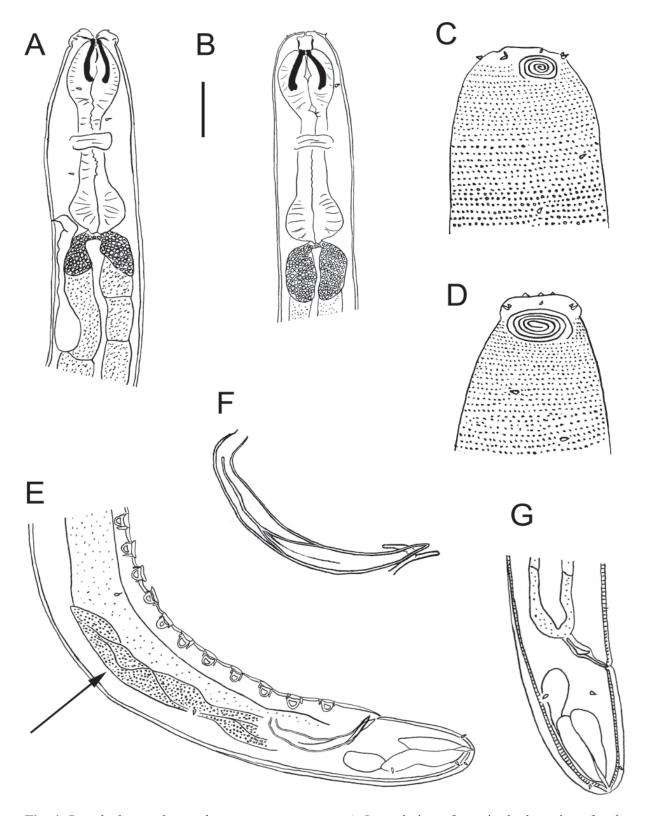


Fig. 4. *Pseudocheironchus ingluviosus* gen. et sp. nov. **A.** Lateral view of anterior body region of male. **B.** Sublateral view of anterior body region of female. **C.** Surface view of female head. **D.** Surface view of male head. **E.** Male posterior body region. **F.** Spicule and gubernaculum. **G.** Female posterior body region. Arrow shows location of ejaculatory glands. Scale bar: A-B = 25 μm; C-D = 15 μm; E, G = 62 μm; $F = 10 \mu m$.

to *Synonchiella* in having three equal mandibles in the posterior buccal cavity, but differs from the latter in having a pharynx with anterior and posterior bulbs (*vs.* no pharyngeal bulb in *Synonchiella*).

Pseudocheironchus ingluviosus gen. et sp. nov.

Figs 4-7, Table 1

urn:lsid:zoobank.org:act:258E6E4A-6142-4A49-88B9-9A6E9B765309

Diagnosis

Pseudocheironchus ingluviosus gen. et sp. nov. is characterised by mandibles, each with two pairs of four blunt hooks, mandibles joined by a membrane with slender cuticularised ridges at their junction, multispiral amphideal fovea with 5.0 turns, short conical tail with rounded end, and males with spicules 1.5-1.7 abd long and 17-19 cup-shaped pre-cloacal supplements.

Etymology

The species name comes from the Latin *ingluviosus* (= voracious, gluttonous), and refers to the well-developed feeding apparatus of the species.

Material examined

Holotype

NEW ZEALAND: *3*, NIWA 88356, 5 Apr. 2007, NIWA cruise TAN0705, station 38, western Chatham Rise crest, 43.8266° S, 176.7043° E, 478 m, medium sand (45.3%), fine sand (43.9%).

Paratypes

NEW ZEALAND: 1 \circlearrowleft , NIWA 88357, 20 Feb. 2011, NIWA cruise TAN1103, station 69, central Chatham Rise, 43.331° S, 178.288° E, 350 m, sediment depth 1-5 cm, mean grain size 55-59 μ m, 55-57% sand, particle sorting (geometric) 4.1-4.3. 1 \circlearrowleft , 1 \circlearrowleft , NIWA 88358, 5 Oct. 2001, NIWA cruise TAN0116, station U2582, Chatham Rise crest, 43.4333° S, 178.5000° E, 350 m, silt/clay (37.5%), fine sand (23.4%), medium sand (21.4%).

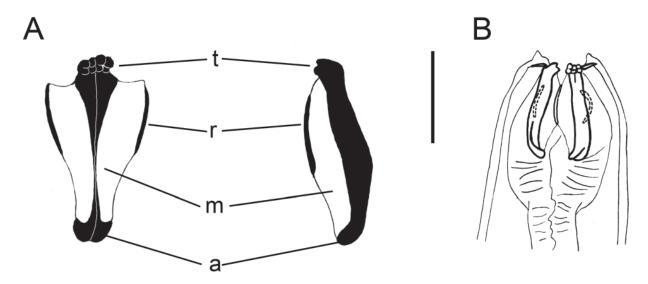


Fig. 5. *Pseudocheironchus ingluviosus* gen. et sp. nov. **A.** En face and side views (left and right, respectively) of mandibles. **B.** Sub-lateral view of female head showing position of mandibles and cuticularised ridges. a = mandible axis; m = membrane; r = cuticularised ridge; t = teeth. Scale bar: $A = 10 \mu \text{m}$; $B = 20 \mu \text{m}$.

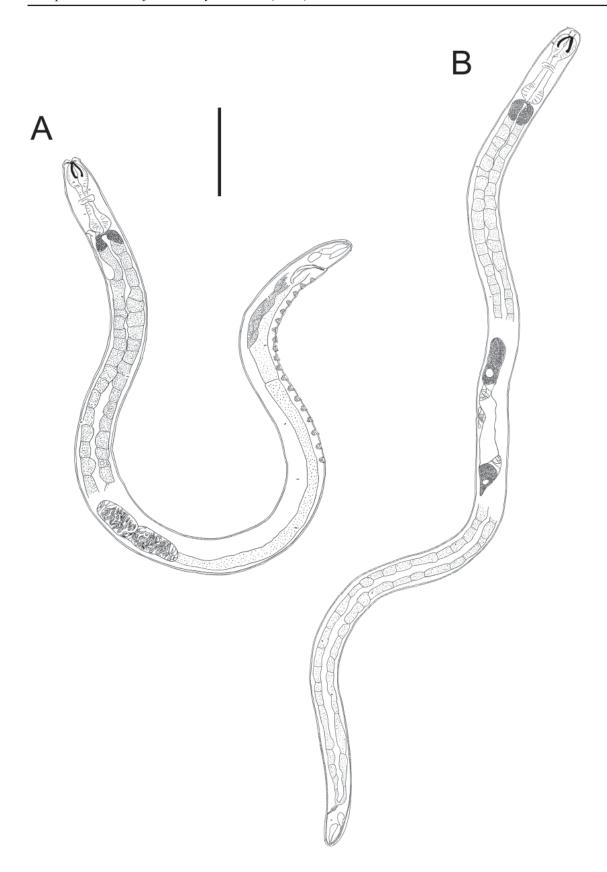


Fig. 6. *Pseudocheironchus ingluviosus* gen. et sp. nov. **A**. Entire male. **B**. Entire female. Scale bar = $100 \, \mu m$.

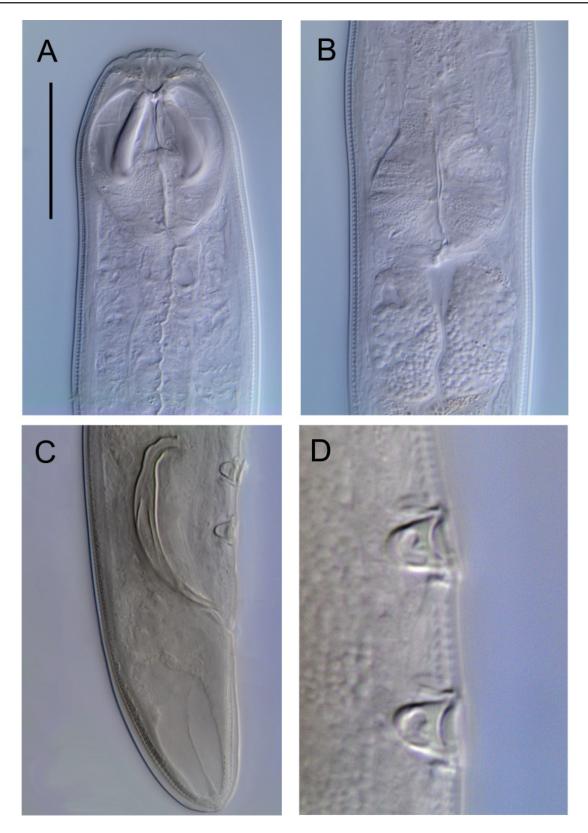


Fig. 7. Pseudocheironchus ingluviosus gen. et sp. nov. Light micrographs. **A.** Female head region showing buccal cavity and mandibles. **B.** Female posterior pharyngeal bulb and anterior portion of intestine. **C.** Male posterior body region showing right spicule and cup-shaped supplements. **D.** Detail of pre-cloacal supplements. Scale bar: $A-C = 30 \mu m$; $D = 10 \mu m$.

Description

Males

Body cylindrical, tapering slightly towards both extremities. Cuticle 1.5-1.8 µm thick throughout body, thicker in tail region, 3-4 µm, with transverse rows of punctations, without lateral differentiation or differentiation consisting of slightly larger punctations. Somatic setae short and sparse, in four sublateral rows. Head slightly set off by constriction at level of amphid. Six conical inner labial papillae; six small outer labial setae and four slightly longer cephalic setae (~ 0.1 cbd) situated in one circle. Amphideal fovea situated near anterior extremity, multispiral with 5.0 turns and transversely oval outline. Anterior portion of buccal cavity short, with six pairs of thin, cuticularised rhabdions fused proximally, ~ 6 μm long. Posterior buccal cavity with three equal mandibles, 18-21 μm long, with one mandible situated dorsally and two sub-ventrally. Each mandible consists of a heavily cuticularised axis with a longitudinal groove (Fig. 5A); axis is thinnest in middle portion and widens towards the posterior and anterior extremities; anterior portion consists of two sets of four blunt hooks; posterior extremity of axis rounded. Two thin membranes extend laterally from the entire length of each mandible (often difficult to observe); a thin, slightly bent, cuticularised ridge is found at the junction of the membranes, one situated ventrally and two sub-dorsally (Fig. 5A, B). Pharynx short, with conspicuous oval-shaped anterior bulb surrounding posterior portion of buccal cavity, 23 µm wide, 29 µm long, and rounded posterior bulb, 25 μm wide. Nerve ring at middle of pharynx. Secretory-excretory (S-E) system present, cellular body of ventral gland situated ~ 1.5 cbd posterior to pharynx, pore situated near posterior extremity of posterior pharyngeal bulb. Intestine cells with numerous round inclusions, most dense in cells immediately posterior to pharynx (Fig. 4A).

Reproductive system diorchic with short, $\sim 50~\mu m$ long, outstretched testes. Anterior testis on left of intestine, posterior testis on right of intestine. Small, nucleated sperm cells, oval or elongated with pointed ends, $\sim 6 \times 2~\mu m$. Spicules paired, curved, 1.5-1.7 abd long, widest in middle portion and tapering distally. Gubernaculum small, slightly bent, median part (cuneus) with hook-shaped projection pointing dorsally (Fig. 4F). Three, perhaps four pairs of ejaculatory glands situated anterior to spicules (Fig. 4E). Mid-ventral row of 17-19 cup-shaped pre-cloacal supplements, $\sim 5~\mu m$ wide and 5 μm deep, situated 5-8 μm apart. Pre-cloacal supplements thickly cuticularised, with nerve entering anterior side of cup. No pre-cloacal seta observed. Post-cloacal setae/papillae not observed. Tail short, conical, with rounded posterior extremity and three small terminal setae. Three caudal glands and small spinneret present.

Females

Similar to males, but with smaller amphideal fovea with circular outline. Reproductive system didelphic-amphidelphic with reflexed ovaries. Anterior ovary on left of intestine, posterior ovary on right of intestine. Vulva located slightly pre-median. Vaginal glands present, *pars proximalis vaginae* surrounded by constrictor muscle.

Subfamily Choniolaiminae Schuurmans-Stekhoven & Adam, 1931

Diagnosis

Buccal cavity with broad, cup-shaped anterior portion and relatively narrow posterior portion, both reinforced by radially arranged, cuticularised rhabdions. Mandibles absent.

Valid genera

Choniolaimus Ditlevsen, 1921 Choanolaimus De Man, 1880 Cobbionema Filipjev, 1922 Gammanema Cobb, 1920 Halichoanolaimus De Man, 1886 Latronema Wieser, 1954

Genus Cobbionema Filipjev, 1922

Type species

Cobbionema acrocerca Filipjev, 1922

Diagnosis

Four cephalic setae conspicuously longer than the outer labial sensillae, buccal cavity surrounded by anterior pharyngeal bulb. Male with two testes pointing anteriorly and reflexed posterior testis. Short conico-cylindrical tail.

Remarks

Cobbionema cylindrilaimoides (Schuurmans-Stekhoven, 1950) was synonymised with *C. acrocerca* by Gerlach (1964) in his review of the Selachinematidae. Species descriptions were until now all based on female specimens only.

Valid species

C. acrocerca Filipjev, 1922 C. capense Furstenberg & Vincx, 1987

Cobbionema trigamma sp. nov.

Figs. 8-10, Table 2

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Diagnosis

Cobbionema trigamma sp. nov. is characterised by four long cephalic setae and six smaller outer labial setae in one circle, amphideal fovea with 4.25 turns, six rhabdions surrounding anterior buccal cavity, each with two pairs of pointed projections at their posterior extremities, posterior buccal cavity widening posteriorly and with three pairs of rhabdions fused posteriorly and widening anteriorly, males with two testes pointing anteriorly and with reflexed posterior testis, spicules 2.5 abd long, and no pre-cloacal supplements.

Etymology

The species name is derived from the Greek letter γ (gamma), and refers to the presence of three pairs of rhabdions fused posteriorly (*i.e.*, gamma-shaped) in the posterior buccal cavity.

Material examined

Holotype

NEW ZEALAND: *3*, NIWA 88359, 6 Apr. 2007, NIWA cruise TAN0705, station 45, southern flank of Chatham Rise, 44.4864° S, 177.1407° E, 1238 m, silt/clay (93.9%).

Paratypes

NEW ZEALAND: 1 \circlearrowleft , NIWA 88360, 8 Oct. 2001, TAN0116, station U2593A, southern flank of Chatham Rise, 44.3333° S, 178.5000° E, 1200 m, silt/clay (63.8%), fine sand (16.0%), very fine sand (13.6%). 1 \circlearrowleft , NIWA 88361, 26 Apr. 2007, NIWA cruise TAN0705, station 271, northern flank of Chatham Rise, 42.6216° S, 175.9262° E, 1210 m, fine sand (60.3%), medium sand (29.3%).

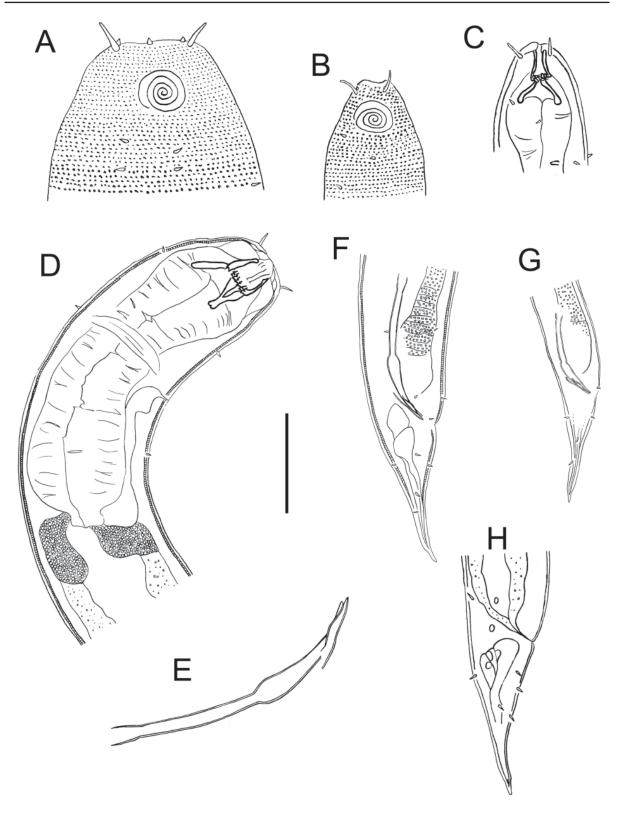


Fig. 8. *Cobbionema trigamma* sp. nov. **A.** Surface view of holotype head. **B.** Surface view of paratype male head. **C.** Buccal cavity of paratype male. **D.** Holotype anterior body region. **E.** Spicule and gubernaculum of holotype. **F.** Holotype posterior body region. **G.** Paratype male posterior body region. **H.** Female posterior body region. Scale bar: $A-C = 30 \mu m$; $D = 80 \mu m$; $E = 36 \mu m$; $E = 70 \mu m$; $E = 40 \mu m$.

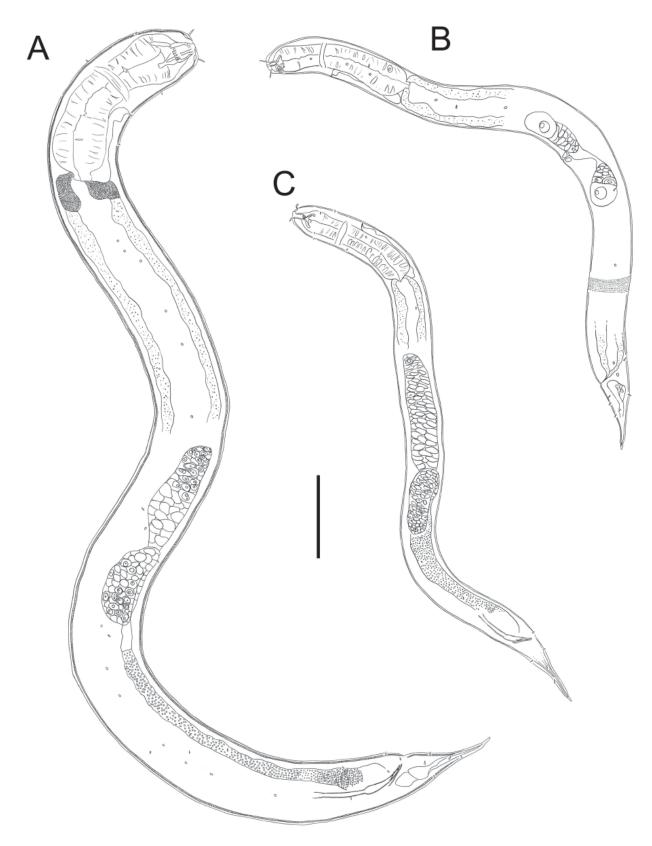


Fig. 9. Cobbionema trigamma sp. nov. A. Entire holotype. B. Entire female. C. Entire male paratype. Scale bar = $100 \ \mu m$.

Description

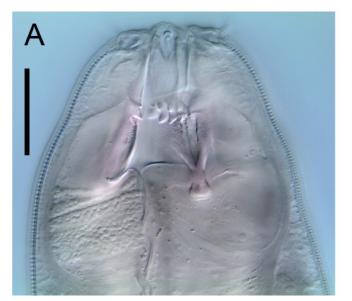
Males

Body cylindrical, tapering slightly towards both extremities. Cuticle 1.5-3.0 μm thick, thickest in tail region, with transverse rows of punctations, without lateral differentiation except in mid-body region, where punctations are irregularly spaced and further apart; lateral rows of oval-shaped cuticle pores, 1.5-2 × 2-3 µm, beginning from halfway down pharynx to anterior portion of tail (Fig. 10B). Somatic setae short and sparse, irregularly distributed. Head blunt, not set off, with six lips surrounding mouth opening. Inner labial papillae minute; six small outer labial setae situated slightly anterior to four conspicuously longer cephalic setae, 0.3-0.5 cbd. Amphideal fovea multispiral with 4.25 turns, with circular outline. Buccal cavity voluminous, divided into anterior and posterior portion. Anterior portion of buccal cavity cylindrical, with six cuticularised rhabdions, each with two pairs of large, pointed projections at posterior extremity (Fig. 10A). Posterior buccal cavity cone-shaped, widest at posterior extremity, with three pairs of rhabdions fused posteriorly and gradually widening anteriorly (Fig. 10A). Pharynx with conspicuous anterior bulb surrounding posterior portion of buccal cavity and part of anterior buccal cavity; pharynx widens posteriorly but not forming true posterior bulb. Nerve ring at 45% of pharynx length from anterior. Secretory-excretory (S-E) system present, cellular body of ventral gland situated immediately posterior to pharynx, pore situated 0.1-0.5 cbd posterior to nerve ring. Intestine cells with numerous round inclusions, most dense in cells immediately posterior to pharynx (Fig. 8D).

Reproductive system with two testes pointing anteriorly, with outstretched anterior testis and reflected posterior testis. Anterior testis on left of intestine, posterior testis on right of intestine. Large globular sperm cells, $6\text{-}9\times10\text{-}13~\mu m$. Spicules paired, 2.5 abd long, curved, swollen at proximal end and at \sim 55% of spicule length from proximal portion, then tapering distally. Gubernaculum bent, with lateral pieces (crurae) flanking distal ends of spicules. Pre-cloacal supplements absent; one small pre-cloacal seta. Tail conico-cylindrical with short, sparse setae and pointed extremity. Three caudal glands and spinneret present.

Female

Similar to male. Reproductive system didelphic-amphidelphic with reflected ovaries. Anterior ovary on left of intestine, posterior ovary on right of intestine. Vulva located at $\sim 40\%$ of body length from anterior



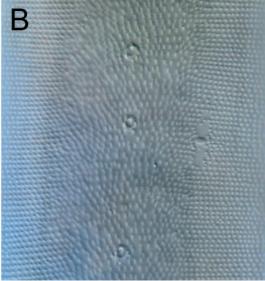


Fig. 10. Cobbionema trigamma sp. nov. Light micrographs. A. Buccal cavity of holotype. B. Cuticle of holotype, showing cuticle pores. Scale bar: $A = 25 \mu m$; $B = 12 \mu m$.

extremity. *Pars proximalis vaginae* surrounded by constrictor muscle, vaginal glands not observed. Anus not observed.

Remarks

Cobbionema trigamma sp. nov. is similar to C. acrocerca but differs from the latter in having a posterior buccal cavity with three pairs of rhabdions fused posteriorly and widening anteriorly, whereas C. acrocerca possesses a posterior buccal cavity with three irregularly-spaced rhabdions narrowing posteriorly and bearing hooks at their anterior extremities. C. trigamma sp. nov. differs from C. capense in the absence of denticles in the buccal cavity, and in the number (24 in C.trigamma sp. nov. vs. 7 in C. capense) and orientation of pointed projections (all pointing posteriorly vs. some pointing anteriorly in C. capense; pointed projections referred to as "teeth" in Furstenberg & Heyns 1987).

There was a substantial (> 2-fold) difference in size between the holotype and the paratype male. The two males also differed in the size of the amphid (0.28 vs. 0.52 cbd) and tail length (2.2. vs. 2.8 abd), but were identical in the size and arrangement of head sensillae, buccal cavity structure, and copulatory apparatus.

The buccal cavity of *Cobbionema trigamma* sp. nov. closely resembles that of *Halichoanolaimus*. *H. robustus* (Bastian, 1865), *H. consimilis* Allgén, 1933, *H. quattuordecimpapillatus* Chitwood, 1951 and *H. dolichurus* Ssaweljev, 1912, for example, all have an anterior buccal cavity surrounded by rhabdions with pointed projections or hooks (the latter often in pairs) and a posterior buccal cavity surrounded by three pairs of rhabdions fused posteriorly (see figs 6-9 in Gerlach 1964).

The female of *Cobbionema trigamma* sp. nov. appears to lack an anus, a feature that has also been observed in several *Halichoanolaimus* species (Gourbault & Vincx 1985). The absence of an anus was also noted by Schuurmans-Stekhoven (1950) in *C. cylindrolaimoides* ("the anal cleft could not be located"). The latter author cast doubt on the observations of Filipjev (1922), who drew the anus of *C. acrocerca* very far posteriorly near the cylindrical portion of the tail, which could suggest that the anus is in fact absent in *C. acrocerca* as well.

Cobbionema trigamma sp. nov. is unusual among the Selachinematidae in the structure of the testes (two testes anteriorly with posterior testis reflexed), and Choniolaiminae in lacking pre-cloacal supplements. Because this is the first time that male *Cobbionema* specimens are described, it remains unclear whether these are characteristic of other species of the genus.

Genus Gammanema Cobb, 1920

Type species

Gammanema ferox Cobb, 1920 (junior synonym of Gammanema rapax (Ssaweljev, 1912)).

Diagnosis

Cuticle without lateral differentiation, four slender cephalic setae; outer labia either papillose or setose. Amphideal fovea usually spiral, rarely loop-shaped. Anterior buccal cavity large, cup-shaped, surrounded by rhabdions with pointed projections at their posterior ends; posterior buccal cavity smaller, often with broad column-shaped rhabdions. Pharynx without anterior or posterior bulb. Pre-cloacal supplements present, usually cup-shaped, rarely setose or tubular. Short conical tail.

Remarks

Gammanema paramenzeli (Allgén, 1935) was considered doubtful by Gerlach (1964), *Trogolaimus uniformis* Cobb, 1920 was transferred to *Gammanema* by Tchesunov & Okhlopkov (2006) and *G. fennicum* Gerlach, 1953 was re-established as a valid species by Okhlopkov (2002).

a = body length/maximum body diameter; abd = anal body diameter; b = body length/pharynx length; c = body length/tail length; cbd = corresponding Table 2. Morphometrics (μm) of Cobbionema trigamma sp. nov., Gammanema agglutinans sp. nov., and Bendiella thalassa gen. et sp. nov. body diameter; L = body length; n = number of specimens; V = vulva distance from anterior end of body; %V = V/total body length.

Male Holotype	s Paratype 11 600 55 9 9 9 25 5-6	Female Paratype 1 566	Males	000				E1
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n anterior end 88 79 from anterior end 120 200	2	6	9	6	12, 13	12	16	15
from anterior end 120 200	54	53	09	54	91, 93	62	75	67-84
from anterior end 120 200	34	36	59	47	57, 69	34	30	29-31
200	99	89	ı	1	1	84	105	96-28
	124	127	154	136	213, 220	153	171	165-172
	28	32	41	31	47, 51	25	21	20-23
	37	38	56	43	60, 65	35	31	30-35
	36	41	64	52	60, 72	35	30	30-35
	57		36	34	1	39	38	1
	17	1	19	19	1	20	20	ı
	23	27*	45	35	30, 39	27	26	23-27*
	55	29*	58	42	46, 58	201	140	124-138*
Tail length/abd 2.2 2.8	2.8	1.1*	1.3	1.2	1.5	7.0	5.4	4.6-6.0*
		294	ı	ı	493, 578	ı	1	472-486
Λ0%		52	1	1	63, 65	1	1	47-50
Vulval body diam.		41	1	1	60, 72	1	1	30-35

*approximate values only since no anus was observed in female specimens

Valid species

- G. anthostoma Okhlopkov, 2002
- G. cancellatum Gerlach, 1955
- G. curvata Gagarin & Klerman, 2007
- G. conicauda Gerlach, 1953
- G. fennicum Gerlach, 1953
- G. kosswigi Gerlach, 1964
- G. mediterraneum Vitiello, 1970
- G. polydonta Murphy, 1965
- G. rapax (Ssaweljev, 1912)
- G. smithi Murphy, 1964
- G. tchesunovi Gagarin & Klerman, 2007
- G. uniformis (Cobb, 1920)

Gammanema agglutinans sp. nov.

Figs 11-13, Table 2

urn:lsid:zoobank.org:act:3AEBAD01-7722-489F-B9FF-818C5B1B8617

Diagnosis

Gammanema agglutinans sp. nov. is characterised by short, stout body (a = 10-15), cuticle with minute spines, leaf-shaped somatic setae with ducts, sexual dimorphism in the shape of the amphideal fovea (loop-shaped in males and spiral in females), posterior buccal cavity with three pairs of broad, column-shaped rhabdions fused anteriorly, intestine cells conspicuous with orange-brown granules, slightly curved spicules, 0.8-1.0 abd long, and small tubular pre-cloacal supplements.

Etymology

The species name is derived from the Latin word *glutino* (= glue, paste together) and refers to the mucus and debris adhering to cuticle of this species.

Material examined

Holotype

NEW ZEALAND: \circlearrowleft , NIWA 88362, 20 Feb. 2011, NIWA cruise TAN1103, station 69, central Chatham Rise, 43.331° S, 178.288° E, 350 m, sediment depth 1-5 cm, mean grain size 55-59 μ m, 55-57% sand, particle sorting (geometric) 4.1-4.3.

Paratypes

Description

Males

Body short, stout, cylindrical, tapering slightly towards anterior extremity, covered with thin layer of adhering mucus and small detrital particles. Cuticle ~ 1.0 -1.5 µm thick, with transverse rows of punctations, without lateral differentiation, each punctation terminating into a minute spine (spines often difficult to observe due to presence of adhering particles). Four sub-lateral rows of leaf-shaped somatic setae (*i.e.*, with narrow base, wide middle portion, and tapering distal end), each with a central duct,

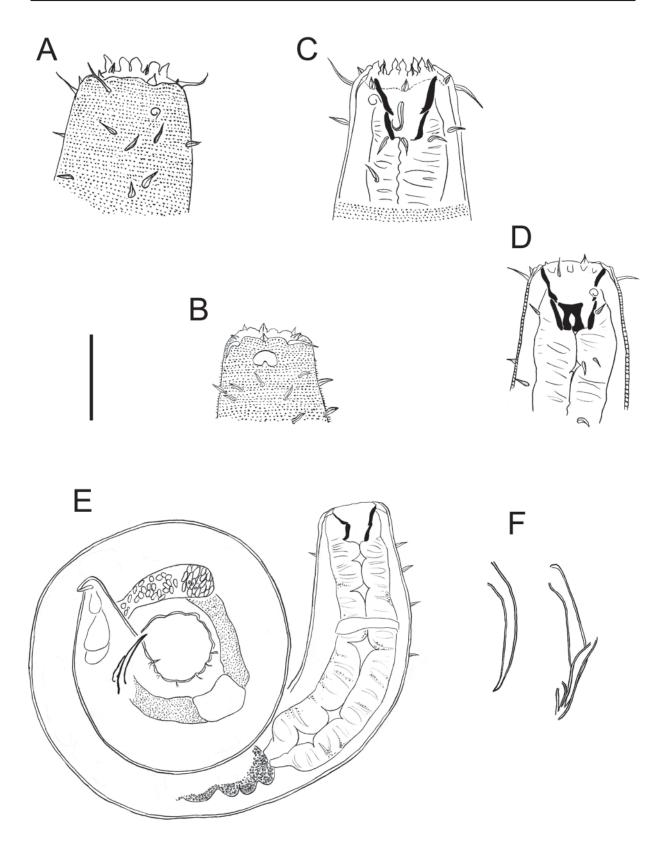


Fig. 11. *Gammanema agglutinans* sp. nov. **A.** Surface view of female head. **B.** Surface view of male head. **C.** Female head, showing buccal cavity. **D.** Female head, showing buccal cavity. **E.** Entire male. **F.** Spicule and gubernaculum. Scale bar: $A-D=30~\mu m$; $E=40~\mu m$; $F=18~\mu m$.

4-8 μ m long and 2 μ m wide (Fig. 13E). Head blunt, only slightly rounded, not set off. Mouth opening surrounded by six pairs of thin, leaf-shaped cuticle extensions, 3-4 μ m long (Fig. 11A, B). Labial sensillae in three separate circles; inner and outer labial setae conical, $\sim 2 \mu$ m long, each with central duct; four cephalic setae, each with central duct, <0.3 cbd. Loop-shaped amphideal fovea, situated <0.2 cbd from anterior extremity. Buccal cavity divided into anterior and posterior portions; anterior portion of buccal cavity large, funnel-shaped, with twelve cuticularised rhabdions, each with one pair of pointed

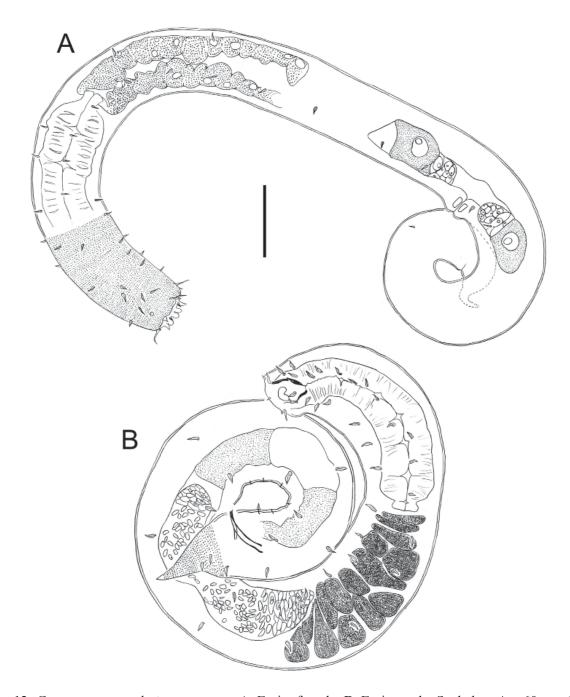


Fig. 12. *Gammanema agglutinans* sp. nov. **A**. Entire female. **B**. Entire male. Scale bar: $A = 60 \mu m$; $B = 50 \mu m$.

projections at posterior extremity (Fig. 13D). Posterior buccal cavity narrow, cylindrical, surrounded by three pairs of broad, column-shaped rhabdions fused in anterior half (Fig. 13B). Pharynx without anterior bulb; pharynx widens posteriorly but not forming true posterior bulb. Nerve ring at $\sim 40\%$ of

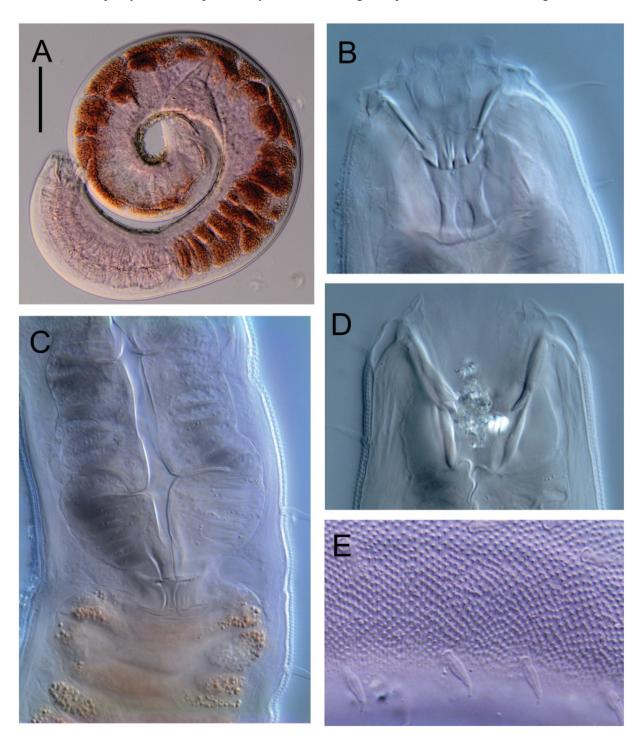


Fig. 13. Gammanema agglutinans sp. nov. Light micrographs. **A.** Entire male. **B.** Buccal cavity of female, showing paired rhabdions in posterior buccal cavity. **C.** Posterior region of pharynx, cardia, and anterior region of intestine of female. **D.** Buccal cavity of female, showing pointed projections at posterior extremity of rhabdions in anterior buccal cavity. **E.** Cuticle of male, showing punctations, spines, and somatic setae. Scale bar $A = 30 \mu m$; $B, D = 15 \mu m$; $C = 12 \mu m$; $E = 7 \mu m$.

pharynx length from anterior. Secretory-excretory (S-E) system not observed. Intestine cells large, well-defined, with numerous round, orange-brown inclusions (Fig. 13A).

Reproductive system diorchic with short, outsretched testes. Testes situated either both ventrally or with anterior testis on left of intestine and posterior testis on right of intestine; small, globular to oval-shaped sperm cells, $2\text{-}4\times5~\mu m$. Spicules paired, 0.8-1.0 abd long, slightly curved, with slight constriction near proximal extremity and tapering distally. Gubernaculum small, slightly bent at proximal end, with lateral pieces (crurae) flanking the distal end of the spicules and a small cuneus with two small, drop-shaped projections anteriorly (not visible in paratype male). At least six small tubular pre-cloacal supplements, difficult to observe due to adhering particles; pre-cloacal seta present. Tail short, conical, with few sparse sub-dorsal setae. Three caudal glands and spinneret present.

Females

Similar to male, but with conspicuously smaller spiral amphideal fovea, 1.5 turns. Reproductive system didelphic-amphidelphic, with reflected ovaries. Anterior ovary on left of intestine, posterior ovary on right of intestine. Vulva located at two thirds of body length from anterior extremity. *Pars proximalis vaginae* surrounded by constrictor muscle, vaginal glands not observed.

Remarks

G. agglutinans sp. nov. differs from all other species in the genus in having a cuticle with spines (vs. spines absent in all other species), males with loop-shaped amphids (vs. multispiral amphids) and leaf-shaped somatic setae with ducts (vs. slender setae without ducts). In addition, species of the genus are characterised by either cup-shaped or setose pre-cloacal supplements, whereas G. agglutinans sp. nov. is characterised by tubular supplements.

Genus *Bendiella* gen. nov. urn:lsid:zoobank.org:act:8E1879A0-8BBA-4564-AAC8-E6BF123EDF0E

Type species

Bendiella thalassa gen. et sp. nov.

Diagnosis

Cuticle with lateral differentiation in the form of longitudinal rows of larger punctations. Outer labial sensillae and cephalic setae in one circle; cephalic setae slightly longer than outer labial sensillae. Buccal cavity large; anterior portion of buccal cavity cylindrical to funnel-shaped, with twelve cuticularised rhabdions, each with pointed projections at posterior extremity. Posterior buccal cavity narrower, cylindrical, surrounded by three Y-shaped pairs of slender rhabdions. Pre-cloacal supplements absent. Tail long.

Etymology

The genus is named after Bendis, the Thracian goddess of the hunt.

Remarks

Bendiella gen. nov. is most similar to Halichoanolaimus in the shape and arrangement of the head sensillae, structure of the buccal cavity, and in having a relatively long tail. Bendiella gen. nov. differs from the latter, and from all other genera of the family Selachinematidae, in having a cuticle with lateral differentiation consisting of longitudinal rows of larger dots, and from all other genera of the Choniolaiminae (except the species Gammanema anthostoma Okhlopkov, 2002) in lacking pre-cloacal supplements.

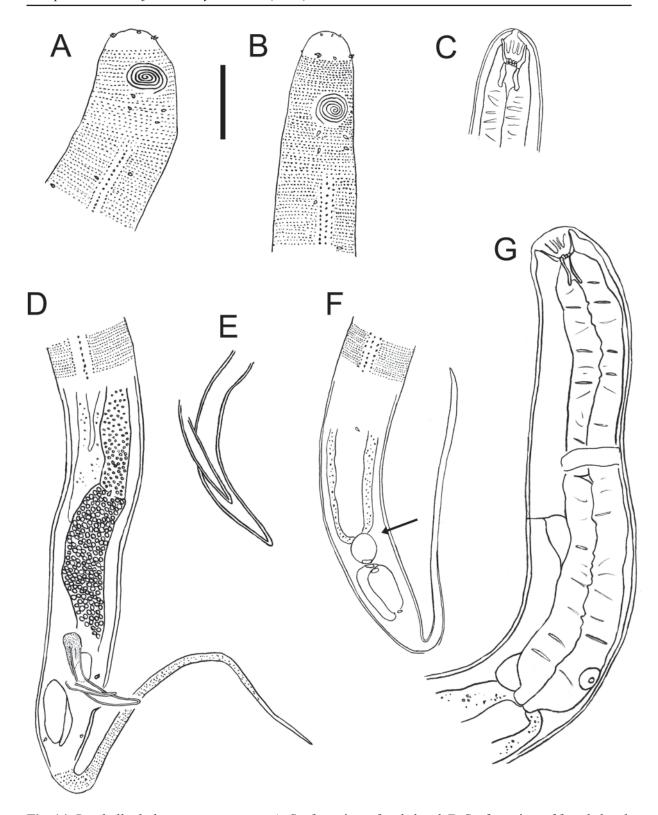


Fig. 14. *Bendiella thalassa* gen. et sp. nov. **A**. Surface view of male head. **B**. Surface view of female head. **C**. Female head, showing buccal cavity. **D**. Posterior body region of male. **E**. Spicule and gubernaculum. **F**. Posterior body region of female. **G**. Anterior body region of male. Arrow shows position of lateral hypodermal gland near posterior end of intestine. Scale bar: A-C, $G = 25 \mu m$; D, $F = 32 \mu m$; $E = 13 \mu m$.

Bendiella thalassa gen. et sp. nov. Figs. 14-16, Table 2 urn:lsid:zoobank.org:act:31AB5540-964C-41F2-B592-F329369969DC

Diagnosis

Bendiella thalassa gen. et sp. nov. is characterised by amphideal fovea with 5.25 turns, anterior buccal cavity with twelve rhabdions, each with a pair of pointed projections at posterior extremity, posterior buccal cavity with three Y-shaped pairs of slender rhabdions fused from two thirds of distance from

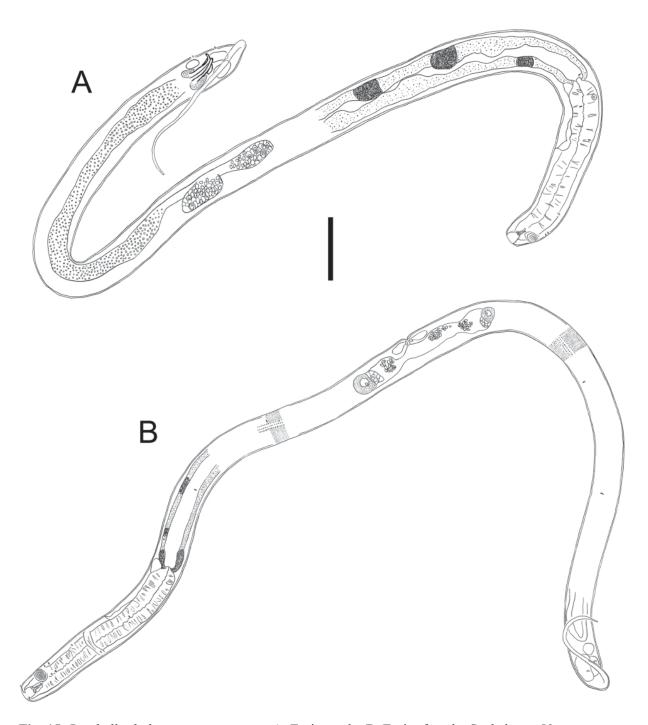


Fig. 15. Bendiella thalassa gen. et sp. nov. A. Entire male. B. Entire female. Scale bar = $50 \mu m$.

anterior ends, spicules 1.4 abd, gubernaculum consisting of two detached lateral pieces (crurae) without median portion (corpus or cuneus), and conico-cylindrical tail, 7.0 abd long.

Etymology

The species name is derived from the Greek word *thalassa* (= sea).

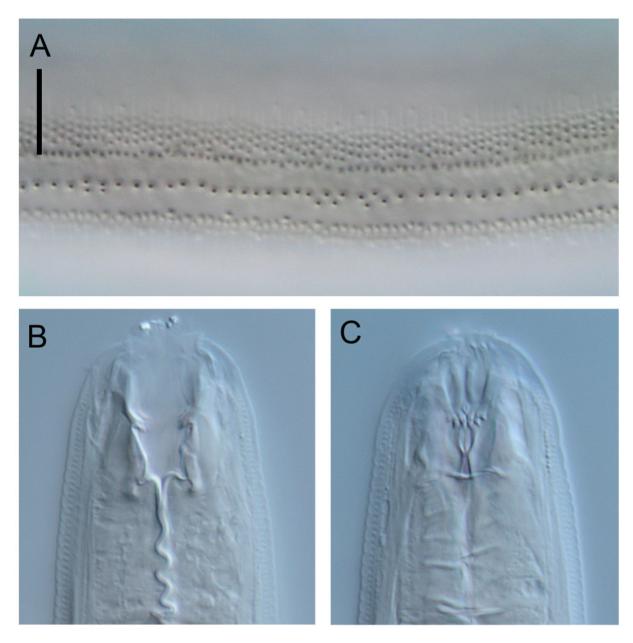


Fig. 16. Bendiella thalassa gen. et sp. nov. Light micrographs. **A.** Lateral view of male cuticle. **B.** Female head, showing shape of buccal cavity. **C.** Female head, showing details of rhabdions in anterior and posterior buccal cavity. Scale bar = $10 \mu m$.

Material examined

Holotype

NEW ZEALAND: *3*, NIWA 88365, 6 Apr. 2007, NIWA cruise TAN0705, station 45, southern flank of Chatham Rise, 44.4864° S, 177.1407° E, 1238 m, silt/clay (93.9%).

Paratypes

NEW ZEALAND: 1 \circlearrowleft , 3 \circlearrowleft \circlearrowleft , NIWA 88366, 4 Jun. 2007, NIWA cruise TAN0707, station 98, eastern Challenger Plateau, 40.1264° S, 170.2217° E, 804 m, silt/clay (83.3%), very fine sand (6.6%).

Description

Males

Body cylindrical, tapering slightly towards anterior extremity. Cuticle $\sim 1.5~\mu m$ thick, with transverse rows of punctations, lateral differentiation beginning $\sim 1.0~c$ bd posterior to amphid and ending at level of cloaca, consisting of three longitudinal rows of slightly larger dots (Fig. 16A). Somatic setae short and sparse, irregularly spaced. Head blunt, rounded, not set off. Inner labial papillae minute; six small outer labial setae situated in same circle as four slightly longer cephalic setae, <0.1 cbd. Amphideal fovea multispiral with 5.25 turns, situated $\sim 0.5~c$ bd from anterior extremity. Buccal cavity large, divided into anterior and posterior portions. Anterior portion of buccal cavity cylindrical to funnel-shaped, with twelve cuticularised rhabdions, each with one pair of pointed projections at posterior extremity (Fig. 16B, C). Posterior buccal cavity narrower, cylindrical, surrounded by three Y-shaped pairs of slender rhabdions fused from two thirds of distance from anterior ends (Fig. 16C). Pharynx without anterior bulb; pharynx widens posteriorly but not forming true posterior bulb. Nerve ring at $\sim 40\%$ of pharynx length from anterior. Secretory-excretory (S-E) system present, cellular body of ventral gland small, situated at posterior end of pharynx, pore situated $\sim 0.6~c$ bd posterior to nerve ring. Intestine cells with numerous round inclusions, some cells differentiated by presence of more numerous and closely packed inclusions (Fig. 15).

Reproductive system diorchic with short, $\sim 40\text{-}45~\mu m$ long, outsretched testes. Anterior testis on right of intestine, posterior testis on left of intestine; small, round sperm cells, 2 μm in diameter. Spicules paired, 1.4 abd long, curved, tapering distally. Gubernaculum consisting of two detached lateral pieces (crurae) tapering distally; median portion of gubernaculum (corpus and cuneus) apparently absent. Precloacal supplements and seta absent. Two round hypodermal glands situated laterally at level of cloaca, each connected to short seta. Tail 7.0 abd long, conico-cylindrical, with short, sparse setae and pointed extremity. Three caudal glands and spinneret present.

Females

Similar to male, but with slightly smaller amphid situated 1.0 cbd from anterior extremity. Reproductive system didelphic-amphidelphic, with reflected ovaries. Anterior ovary on left of intestine, posterior ovary on right of intestine. Vulva located slightly pre-median. *Pars proximalis vaginae* surrounded by constrictor muscle, vaginal glands not observed. Anus not observed.

Discussion

The present study brings the total number of deep-sea selachinematid species to thirteen (Miljutin *et al.* 2010). Of the species described in the present study, *Gammanema agglutinans* sp. nov. was by far the most common, with records from fourteen sites on Chatham Rise and Challenger Plateau (Fig. 17). *Bendiella thalassa* gen. et sp. nov. was also recorded from Chatham Rise and Challenger Plateau (three sites), whereas *Cobbionema trigamma* sp. nov., *Pseudocheironchus ingluviosus* sp. nov., and *Synonchiella rotundicauda* sp. nov. were only recorded at Chatham Rise sites.

Acknowledgements

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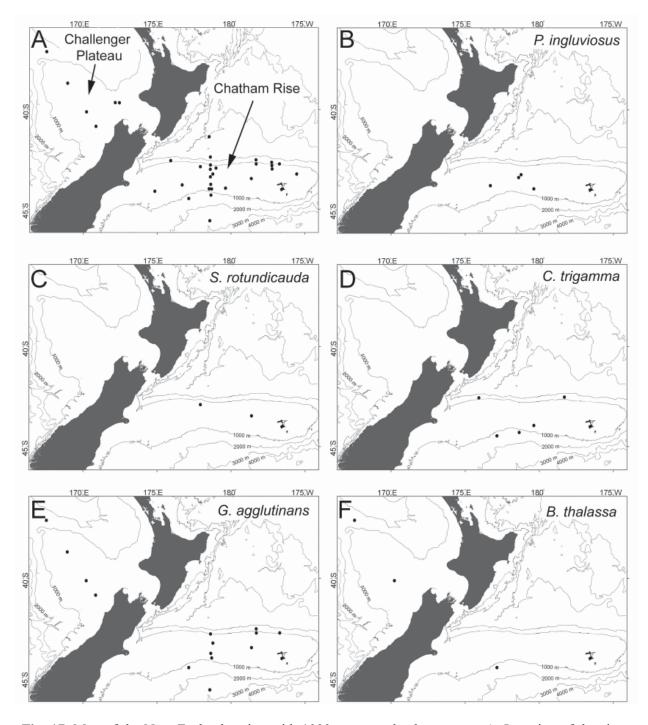


Fig. 17. Map of the New Zealand region with 1000 m water depth contours. **A.** Location of the sites sampled on Chatham Rise and Challenger Plateau. – **B-F.** Distributions of individual species. – **B.** *Pseudocheironchus ingluviosus* gen. et sp. nov. **C.** *Synonchiella rotundicauda* sp. nov. **D.** *Cobbionema trigamma* sp. nov. **E.** *Gammanema agglutinans* sp. nov. **F.** *Bendiella thalassa* gen. et sp. nov.

Conservation and NIWA, for permission to use the data and samples. I also acknowledge the other participants of voyages TAN0116, TAN0705, TAN0707, TAN1103, and TAN1116, and the officers and crew of the RV *Tangaroa*. I am grateful to Natalia Fadeeva and an anonymous reviewer for providing constructive criticisms on an early draft of the manuscript.

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