



Research article

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Are juveniles of the enigmatic deep-sea nematode *Rhaptothyreus* (Rhaptothyreida: Rhaptothyreidae) parasitic?

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Abstract. *Rhaptothyreus* is arguably the most enigmatic nematode taxon due to a combination of unusual morphological features (e.g., large feather-like amphids, vestigial mouth, trophosome, single spicule), unclear phylogenetic relationships (possible affinities with the Enoplida, Mermithida and Benthimermithida) and a distribution restricted to the deep sea. Here I provide the first record of the genus in the Western Pacific Ocean and describe new morphological features of a moulting juvenile. This specimen is characterised by features that differ markedly from those of the adults, the most prominent being the absence of cephalic sensillae and amphids and the presence of a stylet-like structure in the buccal cavity. Similar contrasts in morphology are found between adults and juveniles of the order Benthimermithida, which is characterised by free-living adults and parasitic juveniles. Other morphological (large body size, presence of trophosome) and distributional characteristics (predominantly deep-sea distribution, juveniles rare / absent in sediments) are also common to both groups. Published records show that *Rhaptothyreus* is commonly found in oligotrophic environments (e.g., abyssal plain) where organisms bearing symbiotic bacteria are not typically found, which makes the presence of endosymbiotic bacteria inside the trophosome unlikely. These observations are consistent with the existence of a parasitic juvenile life stage in *Rhaptothyreus*.

Keywords. Benthimermithida, continental slope, ontogeny, *Rhaptothyreus typicus*, New Zealand

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Introduction

The deep-sea nematode *Rhaptothyreus typicus* Hope & Murphy, 1969 is characterised by several unusual morphological features, including a vestigial mouth and pharynx, presence of a trophosome, large feather-like amphids and a single spicule. The phylogenetic relationships of this enigmatic taxon remain unclear, but affinities with the Enoplida (Hope & Murphy 1969; Miljutin 2014b), Mermithida (Hope 1977; Petter 1980) and Marimermithidae or Benthimermithidae (Inglis 1983) have been suggested. In the original description of the species, Hope & Murphy (1969: 72) state that "... the possibility of a change in the structure of the amphid during development, suggest that younger juveniles may possess certain morphological features that would provide a clue to the phylogenetic relationships of this species." All specimens that have been collected since, however, are either specimens with a heavily cuticularized spicule (usually referred to as males) or late-stage moulting juveniles with a lightly cuticularized spicule

(but otherwise similar to the males); no females have yet been observed. It has also been suggested that males may in fact be juveniles due to the lack of well-defined testes in specimens with a strongly cuticularized spicule (Miljutin *et al.* 2006).

The absence of a mouth and alimentary canal indicates that *Rhaptothyreus* does not feed, and the trophosome is thought to serve either as a food reserve or as an organ housing endosymbiotic bacteria (Miljutin *et al.* 2006). A detailed morphological study using transmission and scanning electron microscopy did not unequivocally demonstrate the presence of bacteria in the trophosome of *Rhaptothyreus typicus* (Miljutin *et al.* 2006). The absence of bacterial symbionts would suggest that the trophosome acts as a food reserve for the non-feeding adults, as in the mouthless adults of the order Benthimermithida (Miljutin 2014a). Juveniles of benthimermithid nematodes parasitize a range of invertebrate hosts and emerge as free-living adults in the sediments. *Rhaptothyreus* may have a similar life cycle, but no parasitic juveniles have yet been found, perhaps due to pronounced morphological divergence (as was suggested to explain the apparent absence of females; Hope & Murphy 1969).

Rhaptothyreus is exclusively found in the deep sea and is widely distributed on the continental slope and abyssal plain of the North and South Atlantic Oceans, as well as in the Eastern Pacific Ocean on the continental margin of South America (see summary by Miljutin *et al.* 2006). Here the first record of the genus in the Western Pacific Ocean is provided, and new evidence for a parasitic life cycle similar to that found in benthimermithids is presented based on morphological differences between male and juvenile specimens.

Material and methods

Samples were obtained from New Zealand's southern Hikurangi margin, Southwest Pacific. They were collected during National Institute of Water and Atmospheric Research (NIWA) cruise TAN1004 (1046 m water depth) on 15 April 2010 using an Ocean Instruments MC-800A multicorer (MUC; core internal diameter = 9.5 cm). The top five centimetres of sediment were fixed in 10% formalin and stained with Rose Bengal. The sample was rinsed on a 1 mm sieve to remove large particles and on a 45 µm sieve to retain nematodes. Nematodes were extracted from the remaining sediments by Ludox flotation and transferred to pure glycerol (Sommerfield & Warwick 1996). Observations were made from glycerol mounts using differential interference contrast microscopy and drawings were made with the aid of a camera lucida. Specimens for scanning electron microscopy (SEM) were transferred to a 2% glutaraldehyde solution with sodium cacodylate buffer overnight and then transferred to a 4% osmium tetroxide solution for 2 hours. Specimens were gradually transferred to pure ethanol using a graded ethanol series, critical point dried, and mounted onto stubs before coating with gold using a sputter coater. Observations were made using a Hitachi TM3000 tabletop SEM at high vacuum mode.

All measurements are in µm, and all curved structures are measured along the arc. Type specimens are held in the NIWA Invertebrate Collection (NIC), Wellington, New Zealand. Abbreviations in the text are as follows:

- a = body length / maximum body diameter
- abd = anal body diameter
- c = body length / tail length
- cbd = corresponding body diameter

Miljutin *et al.* (2006) questioned whether specimens with a well-developed spicule are indeed male, as they do not possess obvious testes. For the purpose of this study, specimens with a heavily cuticularized spicule are referred to as males; all other specimens are referred to as juveniles.

Results

Order Rhaphothyreida Tchesunov, 1995
 Family Rhaphothyreidae Hope & Murphy, 1969
Rhaphothyreus Hope & Murphy, 1969

Rhaphothyreus typicus Hope & Murphy, 1969
 Figs 1-4, Table 1

Material examined

NEW ZEALAND: 3 ♂♂ (NIWA 88370; two specimens processed for SEM after observations under light microscopy), 15 Apr. 2007, NIWA cruise TAN1004, st. 4, southern Hikurangi margin, 175.6642° E, 41.6837° S, open slope habitat, 1046 m, mean particle size (geometric) 12 µm, silt / clay content 94.7%, CaCO₃ content 2.1%, organic carbon content 1.0%. One juvenile (processed for SEM after observations under light microscopy), same data as ♂♂.

Description

Male

Body cylindrical, tapering slightly towards anterior and posterior ends. Cuticle with light striations 1–2 µm apart, confined to innermost cuticle layer (Fig. 2B), but also visible on SEM micrographs (Fig. 4A, D), 2.0–2.5 µm thick in mid-body, thickening gradually towards head and tail regions (up to 5 µm thick) due to expansion of median layer (Fig. 1A). Eight longitudinal rows of short somatic setae, ~1 µm long, beginning from anterior edge or mid-level of amphid and extending ~2 cbd posterior to nerve ring; each seta in small pit; anteriormost setae with conspicuous ducts; rest of body devoid of somatic setae (confirmed using SEM). Chords consisting of two longitudinal rows of cells, often poorly defined, with clear round inclusions (Figs 1E, 2C). Longitudinal muscle fibres 2–5 µm thick, beginning at level of amphids and most conspicuous in anterior body region. Metanemes not observed.

Remnant of oral aperture pore-like or not discernible. Six inner and six outer labial papillae in pairs and in one circle (presence of paired inner and outer labial papillae difficult to observe with light microscopy), ~1 µm long and 5–7 µm from anterior end, each pair of setae in small pit with conspicuous duct; second circle of four submedian papilliform sensillae of similar length and structure to setae of first circle, 12–14 µm from anterior end. Amphid large, oblong, ~1.3 cbd in height and 0.5–0.6 cbd wide, with strongly cuticularized outline (Fig. 2A). Amphideal fovea covered by a thin layer of cuticle with central longitudinal rib tapering anteriorly; thin layer of cuticle with transverse rows of minute perforations. Amphideal canal strongly cuticularized, splitting into two ducts directly underneath amphideal fovea (Fig. 2A). No clear buccal cavity present; pharynx with indistinct contours, remnant of pharyngeal lumen sometimes visible as continuous, longitudinal slit extending from oral region to slightly posterior to nerve ring. Nerve ring conspicuous. Secretory-excretory system not observed.

Trophosome present, tapering anteriorly, beginning 169–183 µm from anterior end, filled with numerous small, rod-shaped structures, 0.7–1.4 × 1.2–2.3 µm. No cellular structure discernible in anterior portion of trophosome; one specimen with clear globular inclusions, possibly remnant of cell nuclei. Four or five longitudinal rows of nucleated, oval-shaped turgescient cells, 7–17 × 17–25 µm, situated dorsally and subdorsally and extending from anterior end of trophosome to slightly anterior to spicules (Figs 1E, 2B). At ~90% of body length from anterior, trophosome appearance changes abruptly to rows of large, strongly stained, nucleated cells with minute round inclusions, ~1 µm in diameter (Fig. 3B). Cells decrease in size slightly posteriorly and form a short duct (possibly vas deferens) anterior to spicule.

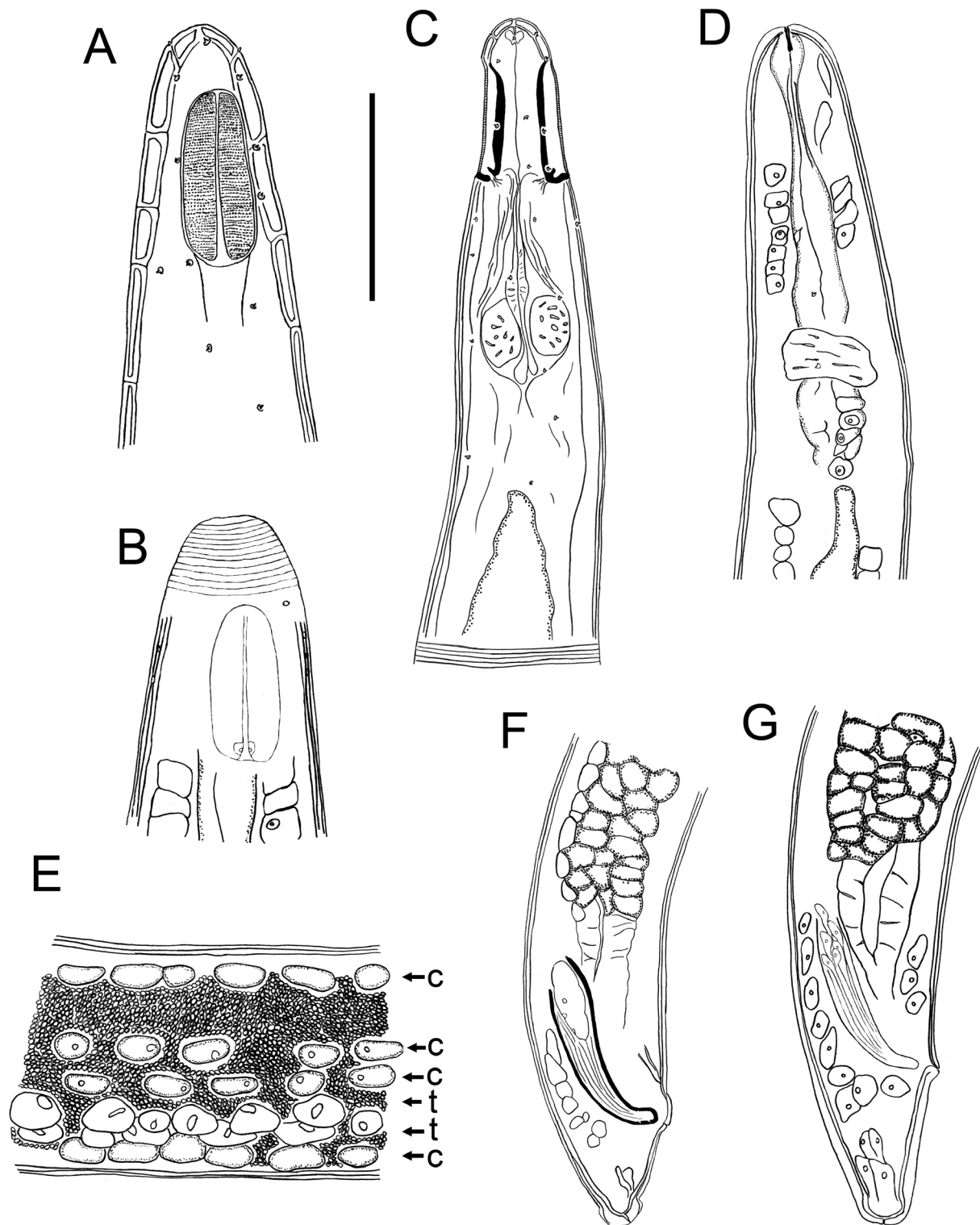


Fig. 1. *Rhaptothyreus typicus* Hope & Murphy, 1969. Line drawings. **A.** Lateral view of male head. **B.** Lateral view of moulting juvenile head, with details of surface striations on outer cuticle and outline of amphid under moulting cuticle. **C.** Anterior body region of male. **D.** Anterior body region of juvenile. **E.** Lateral view of male mid-body region. **F.** Posterior body region of male. **G.** Posterior body region of juvenile. Arrows show the position of the chord (c) and turgescens cells (t). Scale bar: A–B = 50 μ m, C–D = 75 μ m, E = 60 μ m, F–G = 70 μ m.

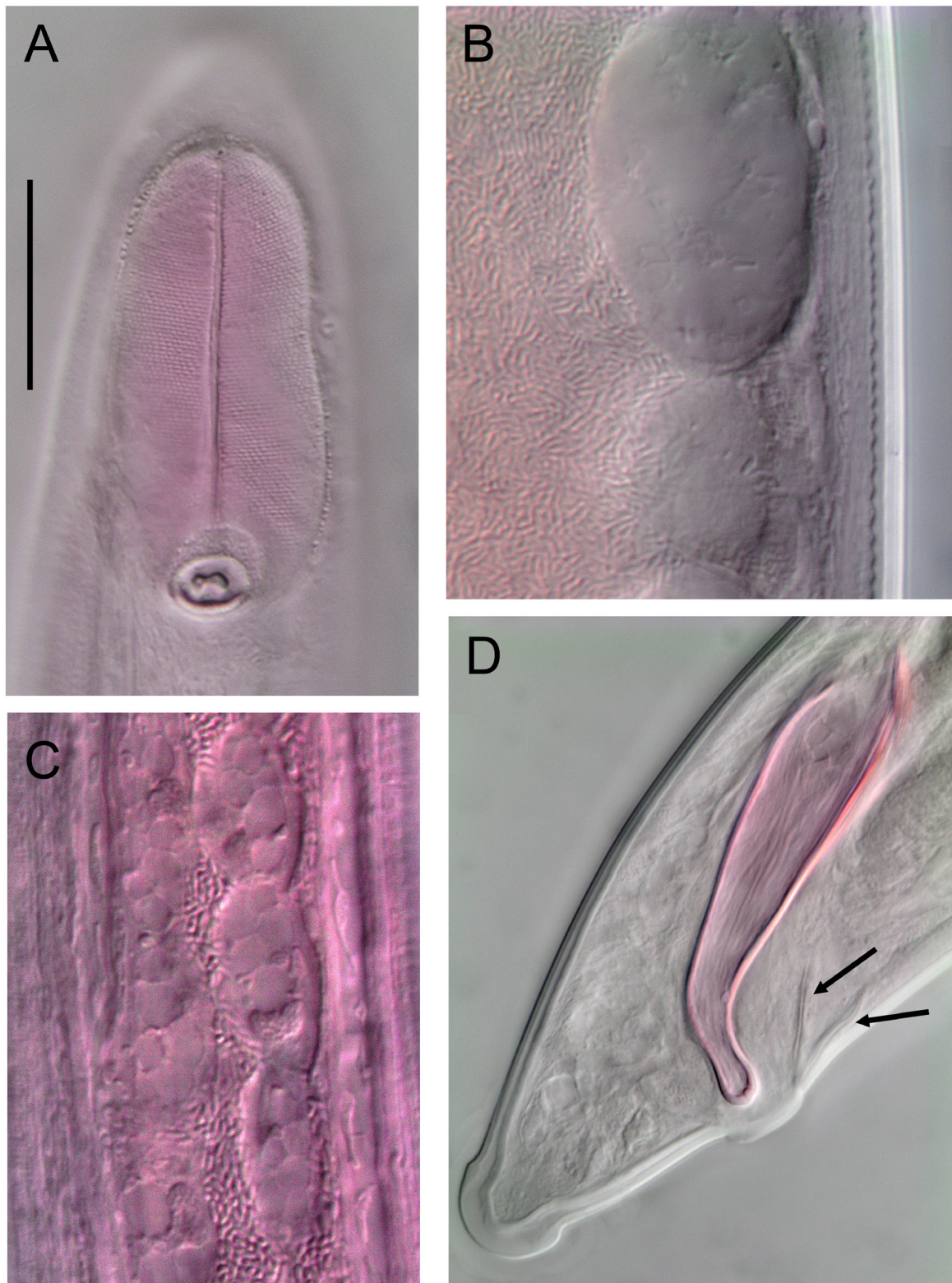


Fig. 2. *Rhaphtothyreus typicus* Hope & Murphy, 1969. Light micrographs (♂). **A.** Lateral view of head showing amphid. **B.** Mid-body region showing cuticle, turgescence and portion of anterior trophosome with rod-shaped structures. **C.** Cells of lateral chord with clear, round inclusions. **D.** Posterior body region. Arrows show the position of the two small ducts apparently joining just prior to the cloacal opening. Scale bar: A, C = 20 μ m, B = 18 μ m, C = 30 μ m.

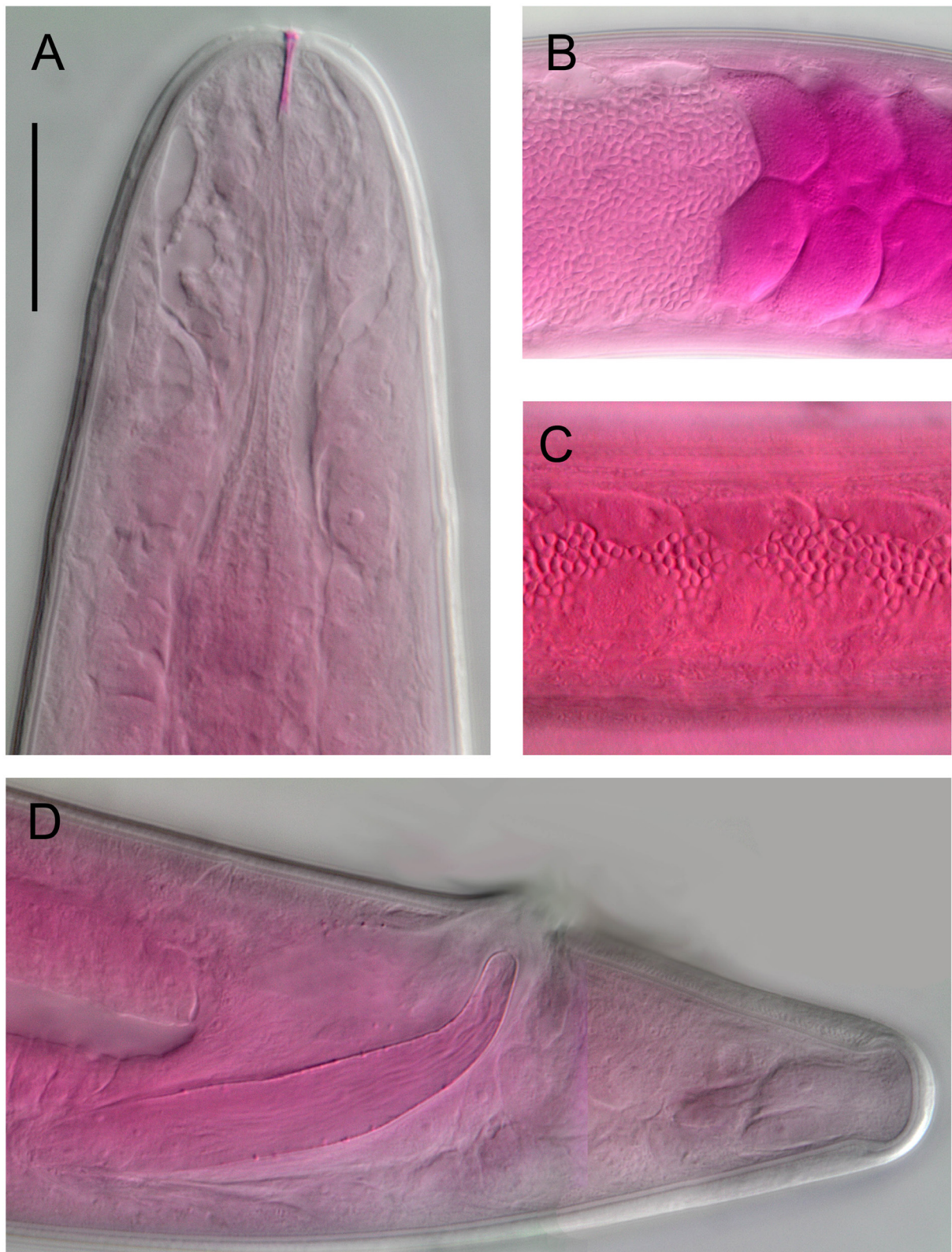


Fig. 3. *Rhaptothyreus typicus* Hope & Murphy, 1969. Light micrographs (moulting juvenile). **A.** Lateral view of head, showing stylet-like structure. **B.** Sharp transition between anterior (left) and posterior trophosome (right). **C.** Lateral chord, mid-body region. **D.** Posterior body region. Scale bar: A = 20 μm , B = 40 μm , C = 28 μm , D = 25 μm .

Table 1. Morphometrics (μm) of specimens of *Rhaphtothyreus typicus* from New Zealand's southern Hikurangi margin. a = body length/maximum body diameter; abd = anal body diameter; c = body length / tail length; cbd = corresponding body diameter; L = body length.

	Males			Juvenile
L	5578	6010	4484	4931
a	77	80	58	69
c	119	140	118	90
Head diameter at level of mid-amphid	34	35	35	41
Amphid height	44	45	46	39
Amphid width	21	19	–	18
Amphid width / cbd (%)	62	54	–	44
Amphid from anterior end	14	18	17	22
Nerve ring from anterior end	111	112	101	111
Nerve ring cbd	52	52	51	53
Maximum body diameter	72	75	77	71
Spicule length	70	71	78	70
Anal body diameter	42	42	44	46
Tail length	47	43	38	55
Tail length / abd	1.1	1.0	0.9	1.2

Single unpaired spicule, 1.5–1.8 abd long, strongly cuticularized, tapering distally and with sharp bend at $\sim 1/5$ of spicule length from distal tip; distal tip slightly swollen (Fig. 2D). Proximal part of spicule contains several small glandular cells; longitudinal structures along spicule length may be ducts connecting glands and small pores (discontinuities in cuticle) near distal tip of spicule (Fig. 1F). Spicule almost completely surrounded by muscular tissue (sheath); at least three pairs of muscles attached to dorsal and ventral body wall. Two small ducts, apparently joining before cloacal opening, visible in two specimens (Fig. 2D). Tail short, conical, with conspicuous terminal cap (Figs 2D, 4D). Terminal or subterminal pore present; caudal glands not observed.

Moulting juvenile

Similar to males in general appearance. Striations of innermost cuticle layer not discernible except in posterior body region; surface of cuticle with fine striations. Small granules separating outer and inner layers of head cuticle (Fig. 3A). A few sparse somatic setae present in pharyngeal region, each with a small pit, not in obvious rows. Chords consist of two rows of well defined oval-shaped, nucleated cells without inclusions (Fig. 3C).

Cephalic sensillae not observed. No amphideal aperture visible on moulting cuticle (Fig. 4C); amphid of similar size and shape as male amphid, located underneath moulting cuticle, barely visible, not cuticularized (Fig. 1B). Oral aperture minute. Small, cuticularized, stylet-like structure, 10 μm long, narrowest in middle region, situated directly underneath oral aperture; may be remnants of narrow, cuticularized buccal cavity (Fig. 3A). Outline of vestigial pharynx with anterior portion of lightly cuticularized pharyngeal tubes visible, with small anterior bulb surrounding stylet-like structure and with posterior bulb immediately posterior to a conspicuous nerve ring.

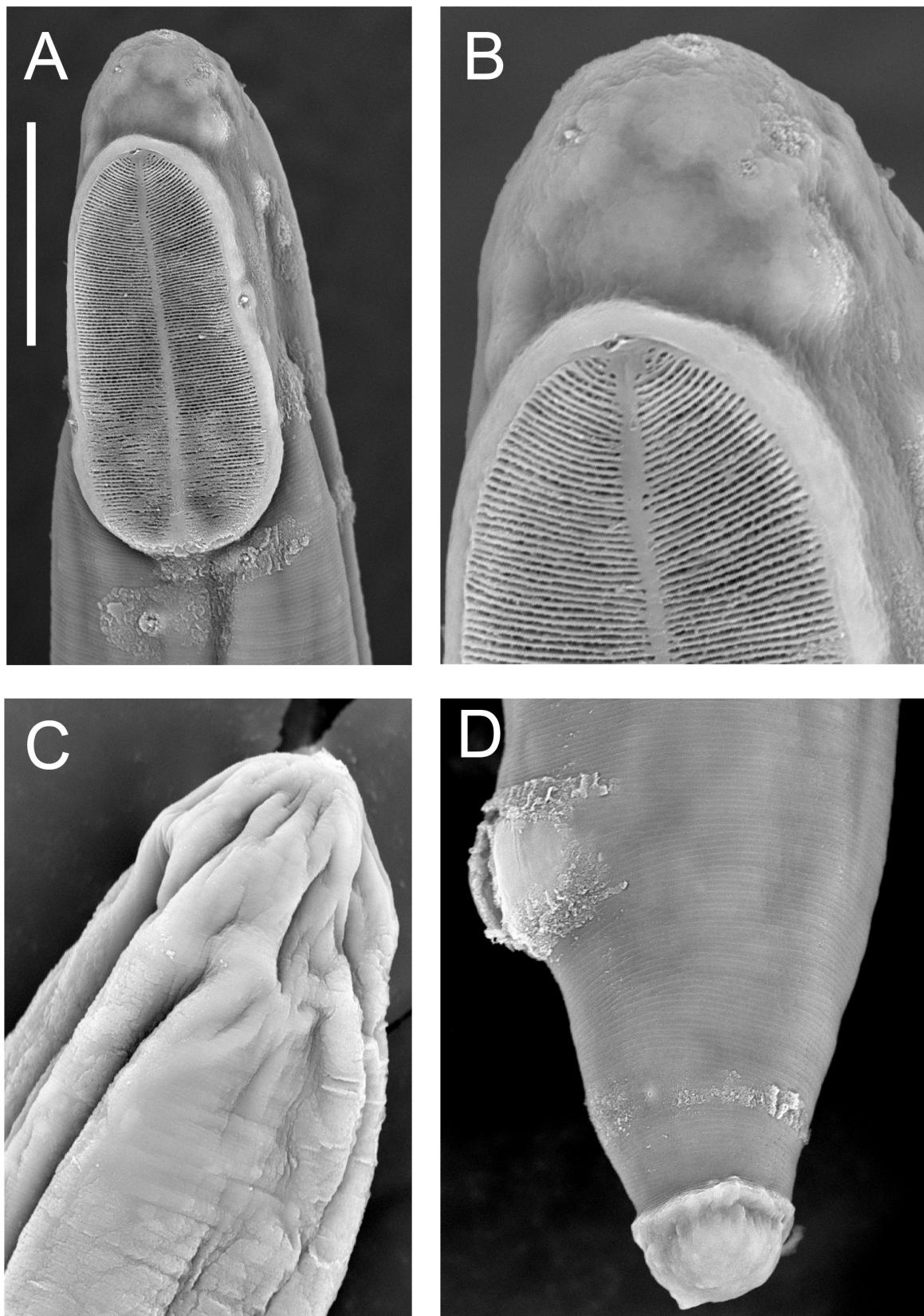


Fig. 4. *Rhaptothyreus typicus* Hope & Murphy, 1969. Scanning electron micrographs. **A–B.** Male head. **C.** Juvenile head. **D.** Male posterior body region. Scale bar: A = 20 μm , B = 8 μm , C = 12 μm , D = 16 μm .

Intestine modified into trophosome; anterior and posterior parts of trophosome similar in structure to that of males, but with globular, not rod-shaped, structures (Fig. 3B). Four rows of turgescient cells present dorsally and subdorsally. Spicule similar in shape to that of male specimens, but lightly cuticularized (Fig. 3D). Tail short, conical, without terminal cap. Terminal pore present.

Remarks

The Hikurangi margin male specimens agree well with the description of *R. typicus* by Hope & Murphy (1969), although a few inconsistencies were noted. The Hikurangi margin specimens are characterised by short body length relative to the type specimens (4,484–6,010 vs. 6,990–12,800 μm), but within the range reported by Miljutin *et al.* (2006) for the same species. The longitudinal rows of turgescient cells observed in the Hikurangi specimens were not observed in the original description of the species by Hope & Murphy (1969) or the description by Miljutin *et al.* (2006); Riemann (1993), however, described the presence of longitudinal rows of turgescient cells in the dorsal region of the type specimens of *R. typicus*. In addition, the ventral transverse ridge observed on the ventral side of the tail of the type specimens by Hope & Murphy (1969) and mentioned in the description of Miljutin *et al.* (2006) was not present in the specimens observed in the present study; furthermore, this feature was not noted in Riemann's (1993) description.

Discussion

Some conspicuous differences in morphology were observed between the males and the juvenile specimen. Most notably, the amphideal aperture, cephalic sensillae and tail terminal cap found in the males were not observed in the juvenile, whereas a stylet-like structure and relatively well defined (but vestigial) pharynx were observed in the juvenile specimen but not the males. These and other morphological differences are consistent with the description of a juvenile by Hope & Murphy (1969), who noted that the stoma was more evident in juveniles than in males, while the terminal cap on the tail was absent and the amphids and spicule less strongly cuticularized. It appears that the Hikurangi margin specimen represents an earlier stage juvenile, as it has retained more juvenile features than those observed by Hope & Murphy (1969). The latter specimens were referred to as fourth-stage juveniles, but they may be better described as recently moulted males; the sexual maturity of so-called males (i.e., specimens with a heavily cuticularized spicule) is yet to be confirmed, however, and it is unclear what stage the juvenile specimen described here may be. The pronounced morphological differentiation between male and juvenile *Rhaphothyreus* is unusual among nematodes (particularly free-living taxa; De Coninck 1965) and could help explain why juvenile stages have not yet been found.

The new observations on the juvenile described herein may provide some clues as to the life cycle of *Rhaphothyreus*. There are similarities between the Hikurangi margin juvenile and juveniles of benthimermithid nematodes (Hope 1977; Tchesunov & Rozenberg 2011). Species of this family parasitize a variety of marine invertebrate hosts as juveniles and emerge as non-feeding adults surviving in the sediments on stored food reserves in the trophosome. Although very little is known about the biology of juveniles, available morphological data provide a basis for comparisons. For example, juveniles of *Trophomera granovitchi* Tchesunov & Rozenberg, 2011 are characterised by the absence of cephalic sensillae and amphideal aperture, presence of a stylet-like structure in the buccal cavity region, vestigial pharynx and midgut with internal lumen, whereas adult specimens have well-developed cephalic sensillae and amphids, while lacking a stylet-like structure, pharynx and intestine. Similar differences were observed between the *R. typicus* juvenile and adults, although no intestine was observed in the juvenile. These contrasts observed between males and juveniles of both species may suggest that *R. typicus* juveniles are parasitic, i.e., they are equipped with a feeding apparatus but mostly lacking sense organs, as they are not necessary inside the host. Adults, on the other hand, are free-living in the sediments and are presumed to be reproductive; a feeding apparatus is no longer required as they survive

on energy reserves, but sense organs such as cephalic sensillae and amphids are required for finding a mate. Another morphological similarity between *Rhaptothyreus* and benthimermithid adults is their large body length (~4–12 mm) relative to most free-living, deep-sea nematode species (which rarely exceed 3 mm; D. Leduc personal observations).

A life cycle similar to that of benthimermithids would imply that the rod-shaped structures in the anterior trophosome of male *Rhaptothyreus* are not bacteria. Although the size and shape of these structures is consistent with bacteria, detailed observations with transmission electron microscopy could not confirm the presence of bacteria in the trophosome of *R. typicus* (Miljutin *et al.* 2006). Moreover, the only deep-sea nematode with bacterial symbionts known to date, *Astomonema southwardorum* Austen *et al.*, 2013, is characterised by bacteria of a different shape (spherical to ovoid *vs.* rod-shaped in *R. typicus*) and size ($7\text{--}10 \times 3\text{--}5 \mu\text{m}$ *vs.* $\sim 1 \times 2 \mu\text{m}$ in *R. typicus*) (Tchesunov *et al.* 2012). Nematodes bearing internal symbionts are normally found in reducing environments associated with high organic matter input (Ott *et al.* 1982) or methane seepage (Austen *et al.* 1993); they are therefore rare in the deep sea and have so far only been found in highly productive canyon habitats (Tchesunov *et al.* 2012; Ingels *et al.* 2011). *Rhaptothyreus*, however, has been found at low productivity abyssal sites (see summary in Miljutin *et al.* 2006). The distribution of *Rhaptothyreus* is similar to that of benthimermithids, i.e., they are rare and found mostly (or exclusively in the case of *Rhaptothyreus*) in the deep sea. *Rhaptothyreus* juveniles are rarely encountered and juvenile specimens collected to date are all near maturity and/or presumably undergoing their final moult, which is consistent with a life cycle where only adults are free-living (as in benthimermithids). Finally, the nematode community at the southern Hikurangi margin sampling site was dominated by *Mudwigglus* Leduc, 2013, *Paramonohystera* Steiner, 1916 and *Aegialoalaimus* de Man, 1907, genera that are widespread in the open slope habitats of New Zealand and without particular affinity for chemosynthetic or highly productive environments (D. Leduc unpublished data; Leduc *et al.* 2012).

It is possible that the trophosome of *R. typicus* is, in fact, a testis. This structure, in some of the specimens from New Zealand, is characterised by a hollow, vas deferens-like posterior portion which appears to be connected to the cloacal opening (although this could not be confirmed with certainty). If this were the case, however, it is unclear where food reserves would be stored.

Rhaptothyreus shows some similarities with mermithid nematodes, which are usually parasites of freshwater or terrestrial invertebrates, but are also found in the deep sea (Tchesunov & Hope 1997). The amphideal fovea in adults of the marine mermithid *Thalassomermis megamphis* Tchesunov & Hope, 1977 is large, whereas the amphideal aperture is minute, as in *Rhaptothyreus*. In addition, juvenile mermithids have a protrusible stylet that is absent in adults. Finally, several mermithid genera have only one spicule (e.g., *Thalassomermis* Tchesunov & Hope, 1977 and *Limnomermis* Daday, 1911), a feature that they share with *Rhaptothyreus* but otherwise is rare in nematodes.

In conclusion, new morphological observations of a juvenile *R. typicus*, as well as the distributional pattern of the genus, suggest that *Rhaptothyreus* has a life cycle similar to that of benthimermithids. Further tests of this hypothesis will require either determining the identity of the rod-shaped structures inside the trophosome (i.e., are they bacteria or not?), or, more significantly, finding juvenile *Rhaptothyreus* specimens inside a host (if they are indeed parasitic). Comparisons with adult specimens may be difficult due to the different morphologies of adults and juveniles, and molecular tools will be required to confirm the identity of juvenile specimens.

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