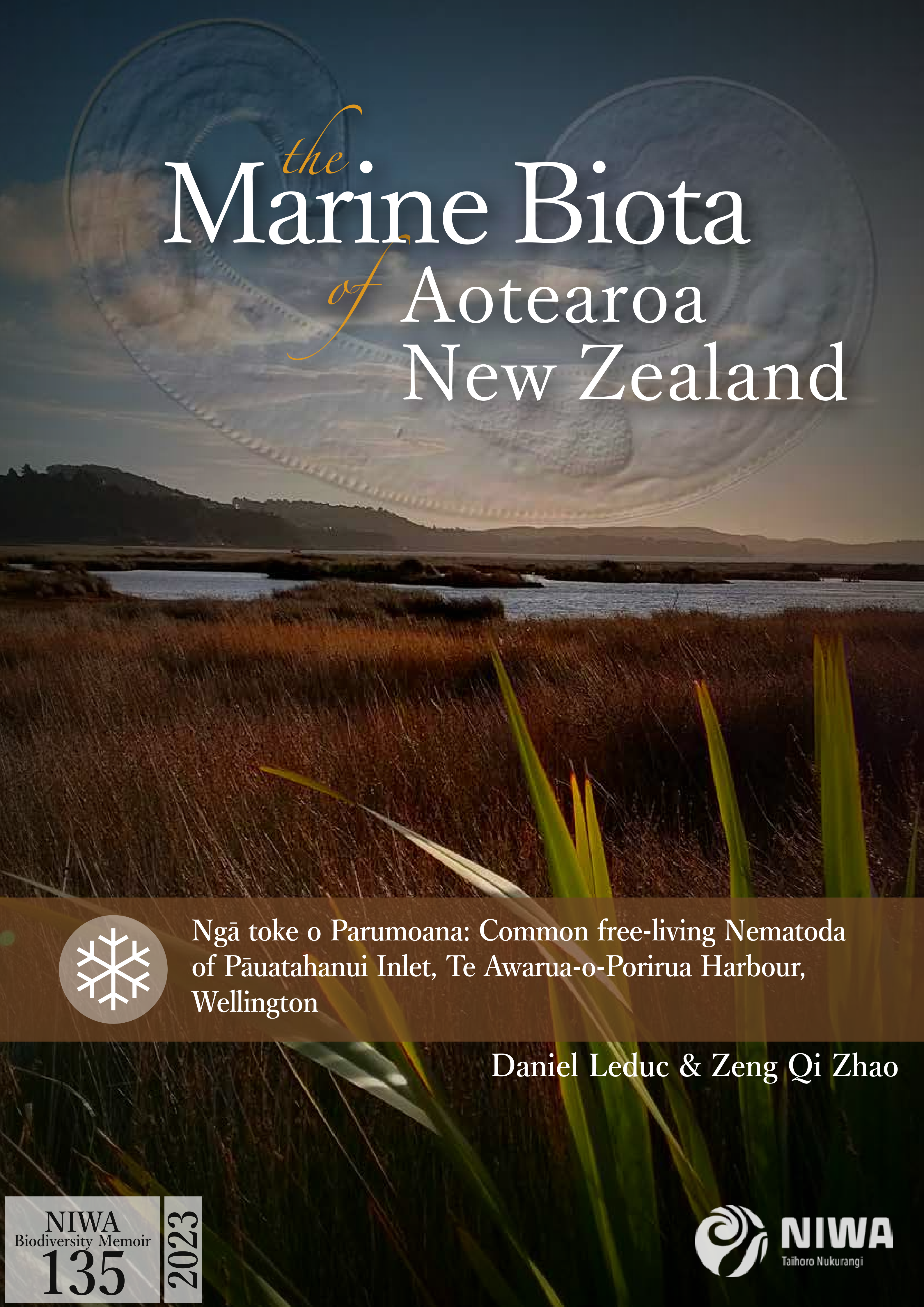

# the Marine Biota of Aotearoa New Zealand

## Ngā toke o Parumoana: Common free-living Nematoda of Pāuatahanui Inlet, Te Awarua-o-Porirua Harbour, Wellington

Daniel Leduc & Zeng Qi Zhao

NIWA Biodiversity Memoir 135
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Taihoro Nukurangi

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Cover image
Pāuatahanui Inlet, a drowned river valley and one of two arms of Te Awarua-o-Porirua Harbour, Wellington, New Zealand; upper impression, light micrograph of free-living, female nematode, *Microlaimus* sp. (Microlaimida Leduc, Verdon & Zhao, 2018), from Figure 4C.

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# PREFACE

# Ngā toke o Parumoana: Common free-living Nematoda of Pāuatahanui Inlet, Te Awarua-o-Porirua Harbour, Wellington

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## Abstract

The phylum Nematoda Cobb, 1932, also known as roundworms, is the most abundant metazoan taxon in aquatic sediments worldwide, as well as one of the most diverse. Despite their ubiquitous distribution, our knowledge of nematode taxonomy and diversity in Aotearoa New Zealand, and in particular, free-living species in marine sediments, remains very limited. The nematode fauna of New Zealand's marine environments, ranging from the most accessible beaches to abyssal plains, remains poorly known, with the total biodiversity of the free-living marine nematode fauna in the New Zealand Exclusive Economic Zone estimated at several thousand species. Prior to this work, the total number of free-living marine nematode species known from the New Zealand region was 190 species.

Unlike previous recent NIWA Biodiversity Memoirs which focus on a particular taxon group rather than a specific region, this work focuses on the nematode fauna of Pāuatahanui Inlet, a drowned river valley and one of two arms of Te Awarua-o-Porirua Harbour in the Wellington region. The main reason for this regional approach is that the New Zealand marine nematode fauna remains largely uninvestigated, and very few specimen collections are available. The most efficient way to increase our knowledge of free-living marine nematode taxonomy in New Zealand is therefore to begin describing the fauna from an easily accessible environment. Pāuatahanui Inlet was chosen because, while it has high ecological and cultural significance, it is also subject to anthropogenic impacts associated with changes in surrounding land use and pollution. A better knowledge of the nematode fauna will thus bring a more complete understanding of the ecological value of this ecosystem and should facilitate ecological monitoring in the future.

A total of 55 nematodes species belonging to two classes, eight orders, 19 families and 41 genera were found. Thirty-nine of the most common species are described here, 26 of which are new to science, four of which are new records for New Zealand, and seven of which [*Bathylaimus* cf. *australis* Cobb, 1894; *Tripyloides* cf. *marinus* (Bütschli, 1874) de Man, 1886; *Chromadora* cf. *nudicapitata* Bastian, 1865; *Chromadorina germanica* (Bütschli, 1874) Wieser, 1954; *Cobbia trefusiaeformis* de Man, 1907; *Terschellingia* cf. *longicaudata* de Man, 1907; *Litoditis* cf. *marina* (Bastian, 1865) Sudhaus, 2011] are cosmopolitan species or species complexes. Together, these species are to be called 'Ngā toke o Parumoana': 'ngā toke' referring to the worms, and 'parumoana' referring to the tidal areas of Te Awarua-o-Porirua which consist of two elements, i.e., the brown mud flats (paru) and the sea (moana).

In addition to line drawings and light micrographs, scanning electron micrographs and molecular sequences are provided for 12 and 28 of the species described here, respectively. Eight seemingly cosmopolitan species, some of which are likely to be cryptic species complexes, were found to occur in the inlet, but the identity of the Pāuatahanui Inlet populations could not be confirmed due to a lack of published molecular sequence data. It is highly likely that additional nematode species not listed here will be found in the inlet as sampling continues in the future. Currently, free-living nematodes are estimated to represent about 40% of the total infaunal diversity in Pāuatahanui Inlet.

## Non-technical summary

Roundworms, or nematodes, are the most numerous and diverse animals living on and in the seabed and are widely distributed in shallow and deep marine environments across the globe. Despite their widespread distribution, our knowledge of nematode taxonomy and diversity in Aotearoa New Zealand remains very limited. The nematode fauna of New Zealand's marine environments, ranging from the most accessible beaches to abyssal plains, remains poorly known, with the total biodiversity of the free-living marine nematode fauna in the New Zealand Exclusive Economic Zone estimated at several thousand species. Prior to this work, the total number of free-living (non-parasitic) marine nematode species known from the New Zealand region was 190 species.

Unlike previous recent NIWA Biodiversity Memoirs which focus on a particular group of organisms rather than a specific region, this work focuses on the nematode fauna of Pāuatahanui Inlet, a drowned river valley and one of two arms of Te Awarua-o-Porirua Harbour in the Wellington region. The main reason for this approach is that the New Zealand marine nematode fauna remains largely uninvestigated, and very few specimen collections are available. The most efficient approach to increase our knowledge of marine nematode taxonomy in New Zealand is therefore to begin describing the fauna from an easily accessible environment. Pāuatahanui Inlet was chosen because, while it has high ecological and cultural significance, it is also subject to anthropogenic impacts associated with changes in land use and pollution. A better knowledge of the nematode fauna will thus bring a more complete understanding of the ecological value of this ecosystem and should facilitate ecological monitoring in the future.

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In addition to line drawings and light micrographs, scanning electron micrographs and molecular sequences are provided for 12 and 28 of the species described here, respectively. The identity of eight species resembling species with apparently worldwide distributions could not be confirmed due to the lack of published molecular sequence data. It is highly likely that additional nematode species not listed here will be found in the inlet as sampling continues in the future. Currently, nematodes are estimated to represent about 40% of the total diversity of animals living in Pāuatahanui Inlet sediments.

## Keywords

Nematodes, Enoplea, Enoplida, Chromadorea, Araeolaimida, Chromadorida, Desmodorida, Microlaimida, Monhysterida, Plectida, Rhabditida, taxonomy, new species, New Zealand, Wellington, Porirua, intertidal, scanning electron microscopy, D2–D3 region of large subunit 28S ribosomal DNA gene, small subunit 18S ribosomal DNA gene, mitochondrial cytochrome oxidase c subunit 1 (COI) gene

## Introduction

The phylum Nematoda Cobb, 1932 comprises mostly small, unsegmented worms that live interstitially in aquatic sediments and soils, or as parasites of plants and animals. Nematodes belong to a wider clade, the informally named Ecdysozoa (moulting animals), proposed by Aguinaldo *et al.* (1997), on the basis of molecular analyses. This group includes other phyla such as tardigrades, kinorhynchs, and arthropods (Giribet & Edgecombe 2017). Nematodes are one of the most successful groups of animals, as demonstrated by their ability to adapt to a wide variety of environmental conditions. In the marine environment, nematodes thrive in habitats ranging from the deepest trenches to wave-exposed beaches, and parasitise a wide range of invertebrate, fish, and mammal hosts. Free-living nematodes typically reach densities of several hundred thousand to millions of individuals per square meter of seabed, making them by far the most common and abundant metazoans in marine sediments (Heip *et al.* 1985). They are also highly diverse, with a handful of sediment typically containing anywhere from about 10 to 100 species, depending on the environment (Boucher & Lambshead 1995; Leduc *et al.* 2010). On Chatham Rise, a submarine ridge east of New Zealand's South Island, 247 morphospecies were identified from a single site at 1240 m water depth (Leduc *et al.* 2010). Globally, approximately 5000–6750 free-living marine nematode species have been described to date, which is thought to represent about 10–15% of the true total global diversity (Appeltans *et al.* 2012; Hodda 2022; Nemys eds. (2022); N. Smol pers. com.). Many parts of the oceans have not been investigated, particularly the deep sea, where only about 700 nematode species have been described so far, even though this environment is known to have very high nematode species richness (Boucher & Lambshead 1995; Miljutin *et al.* 2010; Zeppilli *et al.* 2018).

Work on the taxonomy of free-living nematodes in the New Zealand region began with the descriptions of Ditlevsen (1921, 1930) and Allgén (1927a, 1932, 1950), based on material from the coast of the Campbell and Auckland Islands and also a few locations on Stewart Island, Three Kings Islands, and North Island. A few more species were later described by Wieser (1956b), based on material obtained during the *Galathea* expeditions (1950–1952), and Sudhaus (1974) and Sudhaus & Nimrich (1989), who focused on rhabditid nematodes in the upper intertidal zone. Together, these authors described a total of 112 valid species of free-living marine nematodes from the region by the end of the 20th century (Leduc & Gwyther 2008). Between 2000 and end of 2020, 93 additional species were recorded or described from deep-sea and coastal environments of New Zealand (Leduc & Presswell in press), and the first New Zealand type specimen collection of free-living marine nematodes was established within the NIWA Invertebrate Collection (NIC) in Wellington. It has been estimated that anywhere between 1250 to 5000 species occur in the New Zealand region, which at the current rate of description would take one to three centuries to describe (Leduc & Presswell in press). Unlike in places such as Europe and parts of North America, where free-living marine nematodes have been relatively well studied, new species continue to be encountered from samples wherever they are obtained in the New Zealand Exclusive Economic Zone, including accessible environments such as urban beaches and estuaries.

Beside the newly established collection of nematode type specimens at NIC, there are very few free-living marine nematode specimens held in natural history collections in museums and research or academic institutions across the country. Because of their small size (ca. 1 mm in length), nematodes are not routinely collected as part of oceanographic sampling expeditions. Unfortunately, samples inspected under a microscope, such as sediment core samples obtained for analyses of infauna, are usually sieved over a mesh of 300 µm to 1 mm, resulting in the loss of most nematode specimens. Any nematodes present may not be noticed due their size and simple morphology (the Greek *nematos*, after all, means thread), or when noticed they may be arbitrarily excluded or ignored as they are perceived as being difficult to identify, or if counted they are often later discarded. Although the isolation and preparation of nematode specimens for observation does require the use of a relatively fine mesh (20–63 µm), a stereomicroscope, and some agility when preparing slides, this is largely counterbalanced by the ease with which numerous and diverse nematode specimens can be collected in small samples from just about any aquatic environment except the water column.

The current, most widely used classification of the phylum Nematoda was proposed by De Ley & Blaxter (2002, 2004) based on molecular phylogenetic analyses of SSU rDNA sequences, as well as morphological, ontogenetic, and biological characters. However, recent molecular phylogenetic investigations suggest that updates to this higher level classification are required, including: (1) moving the Benthimermithidae Petter, 1980 (previously classified within their own separate order) to the order Plectida Gadea, 1973 (Leduc &

Zhao 2019a), (2) moving the Rhaptothyreidae Hope & Murphy, 1969 (previously classified within their own separate order) to the order Enoplida Filipjev, 1929 (Leduc *et al.* 2018a), and (3) moving the Microlaimoidea Micoletzky, 1922 (previously classified within the Desmodorida De Coninck, 1965) to their own separate order Microlaimida Leduc, Verdon & Zhao, 2018 (Leduc *et al.* 2018b; Leduc *et al.* 2019). The latter change is only moderately well supported by the available molecular evidence, but better reflects the lack of any morphological synapomorphy between the Microlaimoidea and the taxa classified within the Desmodorida. In the classification of De Ley & Blaxter (2002, 2004), nematodes are divided into two classes, the Enoplea Inglis, 1983 and Chromadorea Inglis, 1983. Within the class Enoplea, most of the free-living marine nematode taxa belong to order Enoplida, although a few are also found within the closely related (but largely terrestrial or freshwater) Triplonchida Cobb, 1920. Within the class Chromadorea, free-living marine species are found in seven orders: the Chromadorida Chitwood, 1933, Desmodorida, Araeolaimida De Coninck & Schuurmans Stekhoven, 1933, Monhysterida Filipjev, 1929, Plectida, Rhabditida Chitwood, 1933, and the newly erected Microlaimida. The present work includes representatives of all these orders except the Triplonchida.

Unlike previous recent NIWA Biodiversity Memoirs which focus on a particular taxon, this work focuses on a geographical location (Pāuatahanui Inlet). The primary reasons for this regional approach are twofold: (1) building a nematode collection from scratch was required, as extensive collections of nematode specimens were not previously available; and (2) the nematode fauna of the New Zealand region is very poorly known. Therefore, the most efficient approach to increase our knowledge of free-living marine nematode taxonomy in this part of the world was to begin describing the fauna from an easily accessible environment. This approach also has the advantage of providing a comprehensive overview of the fauna that characterises a particular type of ecosystem. A total of 55 nematodes species belonging to two classes, eight orders, 19 families and 41 genera were found in the inlet as part of this work. Thirty-nine of these species are described here, 26 of which are new to science and four are new records for New Zealand. Together, these species are to be called 'Ngā toke o Parumoana': 'ngā toke' referring to the worms, and 'parumoana' referring to the tidal areas of Te Awarua-o-Porirua which consist of two elements, i.e., the brown mud flats (paru), and the sea (moana). Scanning electron micrographs and molecular sequences were obtained for 12 and 28 of the species described here, respectively. The species not described here are species that were less common or rare, and which could not be described due to insufficient material. It is virtually certain that more species are present in Pāuatahanui Inlet; however, the fauna described here represents the most common species likely to be encountered.

## Biology of nematodes

Although the earliest nematode fossils date back to the early Devonian (395 mya), the phylum is considered to be older and to have originated in the Precambrian (Poinar 2011). One result of the potentially earlier origins of this group might be that the genetic and genomic variance is high even among closely related nematode taxa (Sommer & Streit 2011). Nematodes exhibit gonochoristic, hermaphroditic, and parthenogenetic modes of reproduction, although most free-living marine species follow a gonochoristic mode of reproduction with equal numbers of males and females (although in some species, males can be relatively rare) (Schierenberg & Sommer 2014). Females of free-living marine species typically lay their eggs directly in the sediment, although some species are known to carry their eggs using specialised structures (Verschelde & Vincx 1995), and others are ovoviviparous (Fu *et al.* 2017). Nematodes have four juvenile stages separated by moulting events, with each juvenile stage closely resembling the adults apart from an underdeveloped reproductive system. Marine nematodes typically have rapid generation times lasting days to weeks (Moens & Vincx 1998), although longer generation times are likely to occur in cold, low-productivity environments such as the deep sea (e.g., Tietjen & Lee 1972).

Nematodes can feed on a variety of food sources. Although the diet of a particular species can vary depending on available food sources (Moens *et al.* 2004), buccal morphology can provide a broad indication of nematode feeding modes. Wieser (1953a) devised a feeding type classification for free-living aquatic nematodes based on buccal morphology. The first group comprised nematodes without buccal armature (i.e., lacking teeth or mandibles), which he split into group 1A with a small buccal cavity (selective deposit feeders or bacterial feeders) and 1B with a large buccal cavity (non-selective deposit feeders or detritus feeders). The second group comprised nematodes with a buccal armature, which he divided into group 2A with relatively small buccal cavities and teeth (epistrate or microalgal feeders) and group 2B with larger buccal cavities usually with larger teeth or mandibles (predators and omnivores). This scheme is still widely used in the literature for investigating ecological patterns, although some authors have suggested various modifications (e.g., Jensen 1987; Moens & Vincx 1997). Research has shown that marine nematodes can be both highly selective, even targeting particular strains of bacteria over others (Derycke *et al.* 2016), and flexible with potential food sources ranging from dissolved organic matter to other nematodes (Chia & Warwick 1969; Moens & Vinx 1997). Because of their high abundance in marine sediments and high turnover rates, nematodes play an important role in benthic food webs both as consumers and as prey for other organisms, including commercially important fish species (see reviews by Heip *et al.* 1985; Gee 1989; Coull 1990; Schratzberger & Ingels 2018).

Because nematodes have very limited locomotion or swimming ability and lack a pelagic larval stage, they have long been assumed to have low dispersal capability. However, nematodes can passively disperse via water currents, rafting, zoochory (including bird feet and turtle carapaces) and via human-mediated vectors such as on ship hulls and in the ballast tanks of ships (Chan *et al.* 2016; Ptatscheck & Transpurger 2020). Nevertheless, whilst gene flow can be substantial at scales < 50 km, it is generally restricted at larger spatial scales (100s km) (Derycke *et al.* 2013). Molecular evidence to date suggests the presence of cryptic nematode species complexes (genetically distinct but morphologically identical species) some of which are widespread while others may be geographically restricted (Bhadury *et al.* 2008; Bik *et al.* 2010; Derycke *et al.* 2010). In New Zealand, for example, the identity of *Litoditis mediterranea* (Sudhaus, 1974) Sudhaus, 2011 specimens from Otago Harbour was confirmed through crossbreeding experiments with cultures from Europe, where the species was originally described (Leduc & Gwyther 2008). These results demonstrate that some nematode species do have a cosmopolitan distribution, which in the case of *L. mediterranea*, an opportunistic species associated with drift macroalgae, may have been facilitated by natural or anthropogenic vectors. Other species, on the other hand, may appear similar to species recorded from overseas but in fact be quite distinct. For example, specimens very similar to the so-called cosmopolitan species *Spirinia parasitifera* (Bastian, 1865) Gerlach, 1963 were found in Pāuatahanui Inlet, but comparison of SSU rDNA sequences revealed the New Zealand population to be a distinct species, *Spirinia antipodea* Leduc, 2018 (Leduc & Zhao 2018). It is therefore important, whenever possible, to include molecular sequence data in nematode species descriptions in order to obtain a more accurate picture of their diversity and allow comparisons with morphologically similar populations from other localities. In the present study, we were able to obtain molecular sequences for 28 species; to our knowledge, this is the first time that a taxonomic monograph on free-living marine nematodes includes molecular data.

## Study location

Te Awarua-o-Porirua Harbour, commonly known as Porirua Harbour, is an inlet surrounded by the city of Porirua on the west coast of the lower North Island, in the Wellington region (Fig. 1, 2). With the exception of Wellington Harbour, Porirua Harbour is the largest estuary system in the Wellington region. The entrance of the harbour is about 150 m wide at its narrowest point and opens opposite Mana Island. The inlet comprises two arms, the Onepoto arm (2.4 $km^2$) to the south and the Pāuatahanui Inlet arm (4.7 $km^2$) to the northeast. Both arms are shallow drowned river valleys composed of sandflats, with about 37% of Pāuatahanui Inlet being exposed at low tide (Stevens & Robertson 2014). Most of this exposed habitat consists of unvegetated, firm, muddy sands. The deepest part of Pāuatahanui inlet, at about 8–10 m below chart datum, is located in the narrow channel at the inlet's entrance, but most of the inlet is less than 2 m deep (Gibb & Cox 2009). Despite the lack of large river flows into the harbour, the largest streams in the Porirua Harbour catchment (Porirua, Pāuatahanui, and Horokiri streams) enter at the heads of each arm of the harbour, defining it as an estuary: it has free tidal exchange with the open ocean, and significant dilution by freshwater inputs does occur (Dalrymple *et al.* 1992). Residence time in Pāuatahanui Inlet is approximately three days (Healy 1980). This relatively rapid exchange of water is mainly driven by the semidiurnal tides.

Porirua Harbour has been described as potentially the most completely hard-edged estuary in New Zealand, i.e., the most completely surrounded by road, rail, and walkway or cycleway embankments (Blaschke *et al.* 2010), which has implications for pollution from vehicle emissions and road wash, wave refraction, estuarine erosion and loss of the absorptive capacity of the Harbour edges from storm surges, direct coastal habitat loss, and loss of potential habitat for estuarine species retreating from rising sea levels. The Porirua

Harbour catchment is composed mostly of exotic grassland (46%), exotic forest (14%) and urban area (14%) (Blaschke *et al.* 2010). Following heavy rain, streams within the catchment often contain elevated levels of faecal contamination from agriculture, septic tanks, and urban stormwater, as well as nutrient concentrations sufficiently elevated to result in growth of nuisance algae (Blaschke *et al.* 2010). Contaminants such as zinc and other metals, DDT, and polycyclic aromatic hydrocarbons have been recorded in streams of the Porirua harbour catchment, sometimes exceeding ANZECC threshold values (Cameron 2001; Milne & Watts 2008). Analyses of bioavailable metals in harbour sediment indicate that most metal concentrations are below ANZECC guideline levels (Milne *et al.* 2004; Stephenson & Mills 2006); however, zinc and lead concentrations sometimes exceed guideline concentrations (Williamson *et al.* 2004). Potentially toxic organic compounds, such as tributyltin and DDT have been found in the sediments in Pāuatahanui Inlet at levels which may have affected benthic communities (Milne *et al.* 2004; Williamson *et al.* 2004; Sorensen & Milne 2009).

Increased sedimentation is considered to be the most pervasive contaminant affecting estuaries and sheltered coastal embayments in New Zealand, and Pāuatahanui Inlet is no exception (Thrush *et al.* 2004; Matheson & Schwarz 2007). High sedimentation rates are probably responsible for the disappearance of seagrass from the inner parts of the inlet (Matheson & Schwarz 2007; Zabarte-Maeztu *et al.* 2020), and probably influence invertebrate and fish populations. Swales *et al.* (2005) estimated the present average sediment accumulation rates in Pāuatahanui Inlet at 4.6 mm $yr^{-1}$, well above the pre-colonisation rates of ~1 mm $yr^{-1}$. If current sedimentation rates remain unchanged, sediments will infill the inlet and turn it into saline swamp by 2180 (± 25 years) (Gibbs & Cox 2009).

Like other estuaries, Porirua Harbour is an important centre of diversity for shore and wading birds, fish, invertebrates, macroalgae, and flowering plants such as seagrass. However, because it is one of the largest estuaries in the Wellington region, the biodiversity value of Porirua Harbour is considerably elevated. Pāuatahanui Inlet is classified by the Department of Conservation (DOC) as a site of national significance under its Sites of Special Wildlife Interest (SSWI) criteria and was listed as a site of national significance for indigenous vegetation (saltmarsh and seagrass) and significant habitats for indigenous fauna in the Regional Policy Statement (WRC 1995). The inlet was also classified in the Wellington Regional Coastal Plan as an Area of Significant Conservation Value based on the natural, conservation, geological, and scientific values (GRWC 2000). The 50-hectare Pāuatahanui Wildlife Management Reserve, owned by DOC and Forest and Bird, lies at the head of the inlet. Mana Bank, which is located on the western side of Pāuatahanui Inlet, was identified as a key aquatic habitat of high ecological value during the environmental impact assessment of Porirua roading options (WRC 1989a). The sediment on Mana Bank consists of open rippled uncompacted sand, which is not found on a similar scale anywhere else in the harbour. The high abundance of harpacticoid copepods has been shown to support a wide range of fish species including flounder, kahawai, spotted dogfish, and sole (Jones & Hadfield 1985). The area was also identified as an important habitat for the paddle crab, as the soft sands provide shelter during the moulting season (WRC 1989b). Seagrass beds, which cover an area of about 37 hectares in the outer part of Pāuatahanui Inlet (Stevens & Robertson 2014), also provide important habitat for both invertebrates and juvenile fish (e.g., Bell & Hicks 1991).

Numerous studies exist on the benthic fauna of Pāuatahanui Inlet. Coull & Wells (1981) published the first ecological study of meiofauna in New Zealand, comparing densities of major meiofaunal taxa such as nematodes, harpacticoid copepods, and kinorhynchs from Waiwhetu Stream, Hutt River estuary, and Pāuatahanui Inlet. Harpacticoid copepods were the topic of several subsequent studies in the inlet, including investigations of their diversity, community structure, distribution, movement, and predation (Hicks 1985, 1988, 1989, 1992; Bell & Hicks 1991; Iwasaki 1993). The macrofauna of Porirua Harbour has been extensively studied, including relatively recent systematic surveys in both arms (Stephenson & Mills 2006; Milne 2008). In their review of the available information on the benthic communities in Porirua Harbour, Blaschke *et al.* (2010) concluded that polychaete worms dominated macrofaunal communities numerically (> 50%), followed by bivalve molluscs, crustaceans, and gastropod molluscs. Stevens & Robertson (2008) described the macrofaunal communities in the harbour as 'unbalanced', as they are dominated by species tolerant of moderate sedimentation and enrichment. However, because of its size and moderately healthy status (Coull & Wells 1981; Stevens & Robertson 2008), the Porirua Harbour is likely to be the most significant area for estuarine invertebrates in the Wellington region. Indeed, eight invertebrate species (a polychaete,

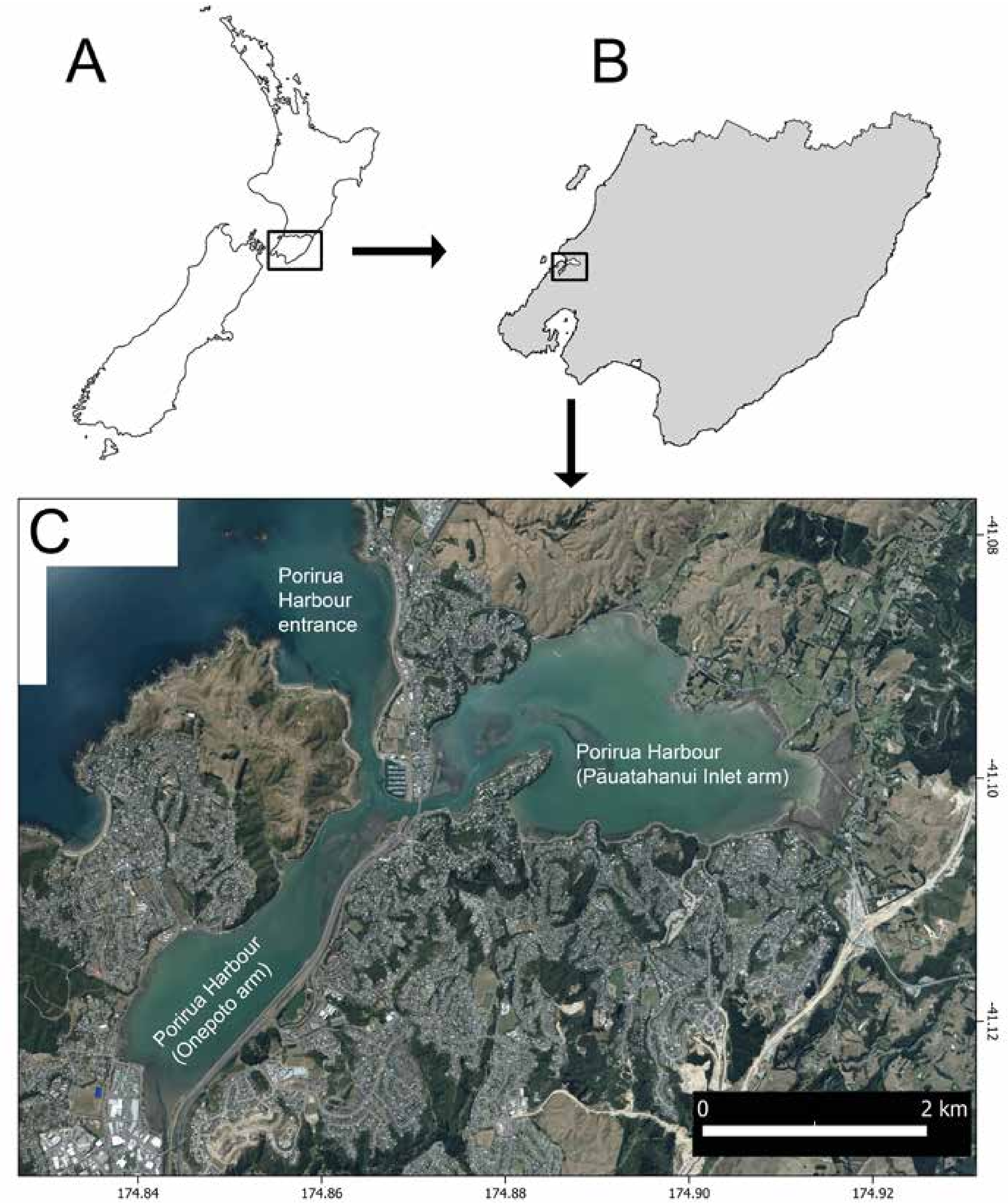


**Figure 1.** Study location: **A.** Map of New Zealand with inset of Wellington region in the lower North Island; **B.** Location of Porirua Harbour within the Wellington region; **C.** Aerial view of Porirua Harbour, which is composed of the Onepoto and Pāuatahanui Inlet arms. Aerial map obtained from LINZ (*Sourced from the LINZ Data Service (https://data.linz.govt.nz/layer/105727-wellington-03m-rural-aerial-photos-2021/) and licensed by Greater Wellington Regional Council for re-use under the Creative Commons Attribution 4.0 International licence*).

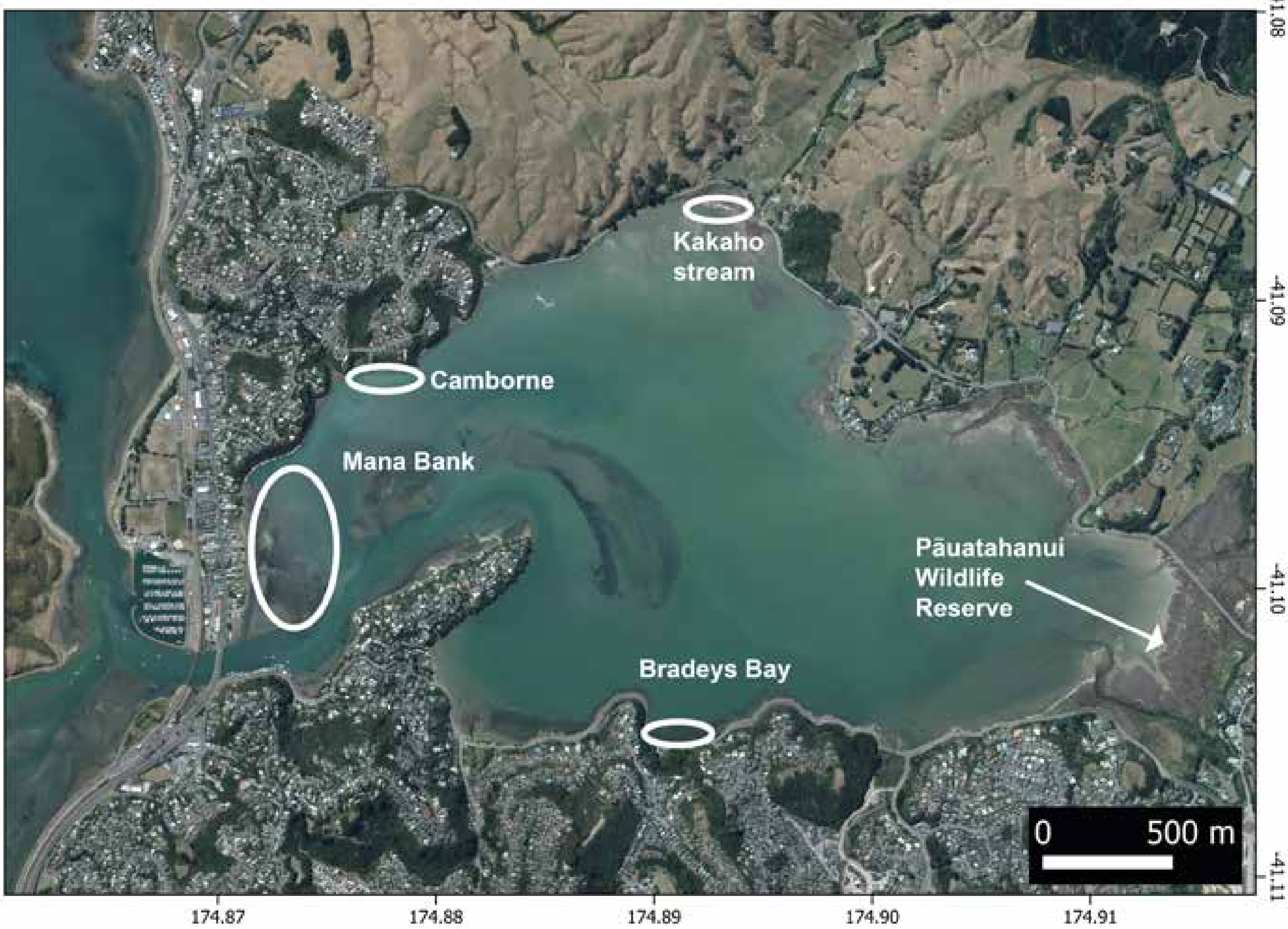


**Figure 2.** Aerial view of Pāuatahanui Inlet showing the location of sampling sites. Aerial map obtained from LINZ (Sourced from the LINZ Data Service (https://data.linz.govt.nz/layer/105727-wellington-03m-rural-aerial-photos-2021/) and licensed by Greater Wellington Regional Council for re-use under the Creative Commons Attribution 4.0 International licence).

a snail, and six copepod species) were first described and identified from Porirua Harbour (Ponder 1972; Kudenov & Read 1977; Wells *et al*. 1982).

Te Awarua-o-Porirua is integral to the identity of Ngāti Toa. The harbour has played a fundamental role over the generations in sustaining their physical and cultural needs. According to iwi tradition, Awarua-o-Porirua was valued because it was the richest harbour for kaimoana and other resources south of Kawhia, which is north of Taranaki on the West Coast of the North Island. Shellfish such as pipi, pūpū (winkle or cat's eye), paua, mussels and oysters, kina (sea urchin), and a range of fish sustained the people of Ngāti Toa. Because of the life-sustaining abundance and variety provided by Te Awarua-o-Porirua and its tributaries, as well as the surrounding coast and ocean, a large number of Ngāti Toa settlements were located in and around the harbour. Until the 1930s and 1940s, the people of Ngāti Toa were still substantially dependent on the marine resources taken from the area. Over time, however, the lands, harbours, and waterways of Te Awarua-o-Porirua have been adversely impacted by settlement and urban development, and the area is no longer a rich source of kaimoana.

Recently, the ecological significance of Pāuatahanui Inlet has been increasingly recognised by the local community. In 1991, a local community group founded the Guardians of Pāuatahanui Inlet (GOPI). GOPI and community volunteers have carried out ten triennial surveys of cockles (*Austrovenus stutchburyi* (Wood, 1828) in Pāuatahanui Inlet since 1992, making it the longest-running citizens' science project in New Zealand. The surveys show that the cockle population is in an improving state, although concerns about health risks remain, given the ability of filter-feeding shellfish to accumulate heavy metals and other contaminants. In 2014, in response to the National Policy Statement for Freshwater Management, the Te Awarua-o-Porirua Whaitua committee, comprising Ngāti Toa, community members, local and regional council officers, and elected officials, was established. The committee was tasked with recommending ways to improve the management of land and water within Te Awarua-o-Porirua catchment to achieve an improvement in water quality and ecology. The Ngāti Toa Statement (https://www.gw.govt.nz/assets/Whaitua/ngatitoataopwhaituastatement.pdf) and the Te Awarua-o-Porirua Whaitua Implementation Programme (WIP) (https://www.gw.govt.nz/assets/Whaitua/Porirua-WIP-web.pdf) containing these recommendations were finalised in April 2019.

## Methods and materials

**Sampling and specimen preparation.** Sediment samples (~0–5 cm sediment depth) were obtained by scooping approximately the top 5 cm of sediment by hand in the intertidal zone of Pāuatahanui Inlet, during periods of low tide, in July 2016, September 2018, January 2018, February 2019, October 2019, December 2019, and July 2020. Several locations were sampled, including Mana Bank, the intertidal zone bordering the Camborne Walkway, Bradeys Bay, and the upper intertidal zone near the Kakaho Stream (Fig. 2). Several areas in the uppermost parts of the inlet near the Pauatahanui Wildlife Reserve and Horokiri Stream were also sampled on multiple occasions between 2016 and 2020, but these samples yielded very few nematode specimens and as a result no species were described from the upper part of the inlet. Sediment samples were refrigerated overnight, and live nematodes were extracted the following day by repeated manual elutriation followed by decantation onto a 45 μm mesh and sorted into morphospecies under a dissecting microscope (Heip *et al.* 1985). Whenever possible, live adult specimens were obtained for molecular sequencing (see below); each specimen was mounted in a drop of seawater on a temporary slide to confirm its identity, and images of key morphological features were taken to provide image vouchers. The remaining specimens were fixed in 5% buffered formalin for morphological analyses. Formalin-fixed specimens for light microscopy were transferred to glycerol and mounted onto permanent slides as per the method of Somerfield & Warwick (1996). All measurements are in μm (unless stated otherwise), and all curved structures are measured along the arc.

Specimens for scanning electron microscopy (SEM) were transferred to a 2% glutaraldehyde solution with sodium cacodylate buffer for two days and transferred to a 4% osmium tetroxide solution overnight. Specimens were then gradually transferred to pure ethanol using a graded ethanol series, critical point dried, and mounted onto stubs before coating with gold & palladium using a sputter coater. Observations were made using a Hitachi TM3000 tabletop SEM in high-vacuum mode.

**Description format.** Each new species description is provided with the following sections: **Description**, **Species diagnosis** and **Differential diagnosis**. The **Description** section is structured into a description of male morphology based on observations of both holotype and any paratype(s), followed by a description of female morphology (if available). To avoid duplication, the description text contains little if any of the measurement data presented in the table of morphological measurements of the corresponding species. The species description is followed by a **Species diagnosis** section summarising the key morphological features of the species, including relevant morphological measurements from the corresponding table. The purpose of this section is to list and describe the main traits needed for identification. The **Differential diagnosis** section provides a detailed comparison of morphological features between the new species and other similar species within the same genus. The purpose of this section is to explain why a new species was erected and to help differentiate it from similar species. Morphological features which are considered useful in differentiating between similar species must be either: absent in one species and present in the other, be different in shape/structure, or have a non-overlapping range of dimensions. In a small number of cases, features which have slight overlap in dimensions are also listed, but only when they may aid identification and when other, obvious morphological differences are also present. In some cases, a **Remarks** section is also included, in which information is provided about the significance of unusual morphological features, behaviour, or general ecology.

For known species or species that are similar to existing species ('cf.'), a **Diagnosis** section is provided outlining the main morphological features, followed by a **Remarks** section outlining the relationship between the Pāuatahanui Inlet specimens and specimens previously described in the literature.

**Nematode identification and morphology.** The Plymouth monographs on British free-living marine nematodes, published by Platt & Warwick (1983, 1988) and Warwick *et al.* (1998), include illustrated keys to worldwide genera which are widely used for genus identification. However, the identification keys are now somewhat out of date, due to changes in the classification of various taxa and the description of new genera. A volume of the *Handbook of Zoology* was published in 2014 which provides a comprehensive and updated overview of the taxonomy of almost every nematode order (Schmidt-Rhaesa 2014) and is a useful resource for checking genus identifications. Species identification requires an examination of the primary literature, much of which can now be accessed through the online Nemys database by registered users (https://nemys.ugent.be). This resource, created by researchers at Ghent University in Belgium, also provides species lists and interactive identification keys for some taxa.

The most common method for the observation and identification of nematodes is light microscopy (LM). Formalin-fixed specimens are typically transferred to glycerol, which over time, renders the animal more transparent and facilitates observations of both the external and internal features. For most nematodes, observations with a compound microscope equipped with differential interference contrast (DIC) at 1000× magnification, is needed to provide a sufficiently detailed picture of features such as the buccal cavity and distribution of body hairs (setae) and enable identification (Fig. 3). Although this level of magnification is generally sufficient to capture all of the morphological features required for species identification and descriptions, in some cases SEM observations can reveal details which are either difficult or impossible to observe using LM alone, thus providing additional morphological data. Morphological observations are most clearly summarised and illustrated using drawings, which can capture both the internal and external morphology. Illustrations typically show a lateral view of the animal, mainly because the bodies of fixed nematodes tend to be curved along the dorso-ventral plane, resulting in the animal lying on its side. A lateral view allows sensory and copulatory structures to be shown clearly; however, ventral and dorsal views can also help to illustrate the structure and arrangement of morphological features. Light micrographs are often used in species descriptions, but their usefulness may be limited by their typically shallow focal plane, which can only capture a limited range of structures in one image. Scanning electron micrographs are sometimes included in species descriptions, but their use in the literature is limited due to the time-consuming nature of specimen preparation methods. This is, however, the best method for observing the finer details of external structures in nematodes.

Nematodes are characterised by a relatively simple body plan consisting of a tube (a one-way alimentary tract) within a tube (the body wall). When using a stereomicroscope at low (100× or less) magnification, there may appear to be little if any difference between one nematode specimen and the next. However, observation of appropriately fixed specimens using a compound microscope at high (100–1000×) magnification will reveal a multitude of morphological characters that can be used to differentiate between taxa. Although most nematodes are characterised by an unsegmented, thread-like body shape with a more-or-less rounded anterior extremity and a tapering posterior extremity, variation in body shape does occur among taxa (Fig. 4). For example, some taxa within the Desmoscolecida Filipjev, 1929 are characterised by a short, stout body shape as well as the presence of cuticle spines or body rings giving a "furry" or segmented appearance. Others, such as microlaimids, have bodies that are both short and relatively thin, making them easy to miss when sorting through samples. Some desmodorid taxa have very characteristic S-shaped bodies with a swollen mid-body region, while other taxa have extremely slender and thin bodies, which in the case of stilbonematine nematodes can be covered in a layer of tiny bacteria. The anterior (cephalic) body region is often rounded, but in some cases can be truncated, swollen, or tapering. Tail shape is also variable, ranging from rounded to conical, conicocylindrical, or filiform, with a posterior extremity which may be tapering or club-shaped (clavate).

After body shape, the next most obvious trait that can be observed is the body cuticle, which covers the entire surface of the nematode. The cuticle varies in thickness and is made up of several layers, i.e., the epicuticle (outer surface), the cortical zone, the median zone, and the basal zone. The surface of the cuticle can be smooth (as in most taxa within the order Enoplida), striated (i.e., with shallow transverse grooves, as in many taxa within the order Monhysterida), annulated (i.e., with deep transverse grooves, as in some taxa within the order Desmodorida) or punctated (i.e., with numerous small 'dots', as found in the order Chromadorida and family Comesomatidae Filipjev, 1918). When observed using LM, cuticle punctations are seen as numerous 'dots' which can vary in size, and which may be irregularly arranged or in transverse or longitudinal rows (Fig. 5). These 'dots' are in fact columnar structures in the median cuticle layer not usually visible on the outer surface of the animal, as shown by SEM. Cuticle punctations can be homogeneous, i.e., of similar size and distribution laterally and/or longitudinally, or heterogeneous, i.e., with differences in punctation size and spacing laterally and/or longitudinally. The cuticle often bears somatic setae which can be arranged in four, six, or eight longitudinal rows, and which may or may not be connected to epidermal glands. In some taxa, such as the family Cyatholaimidae Filipjev, 1918, structures such as pore complexes and lateral pore-like structures are also present (see *Paracanthonchus wellsi* **sp. nov.** and Fig. 6).

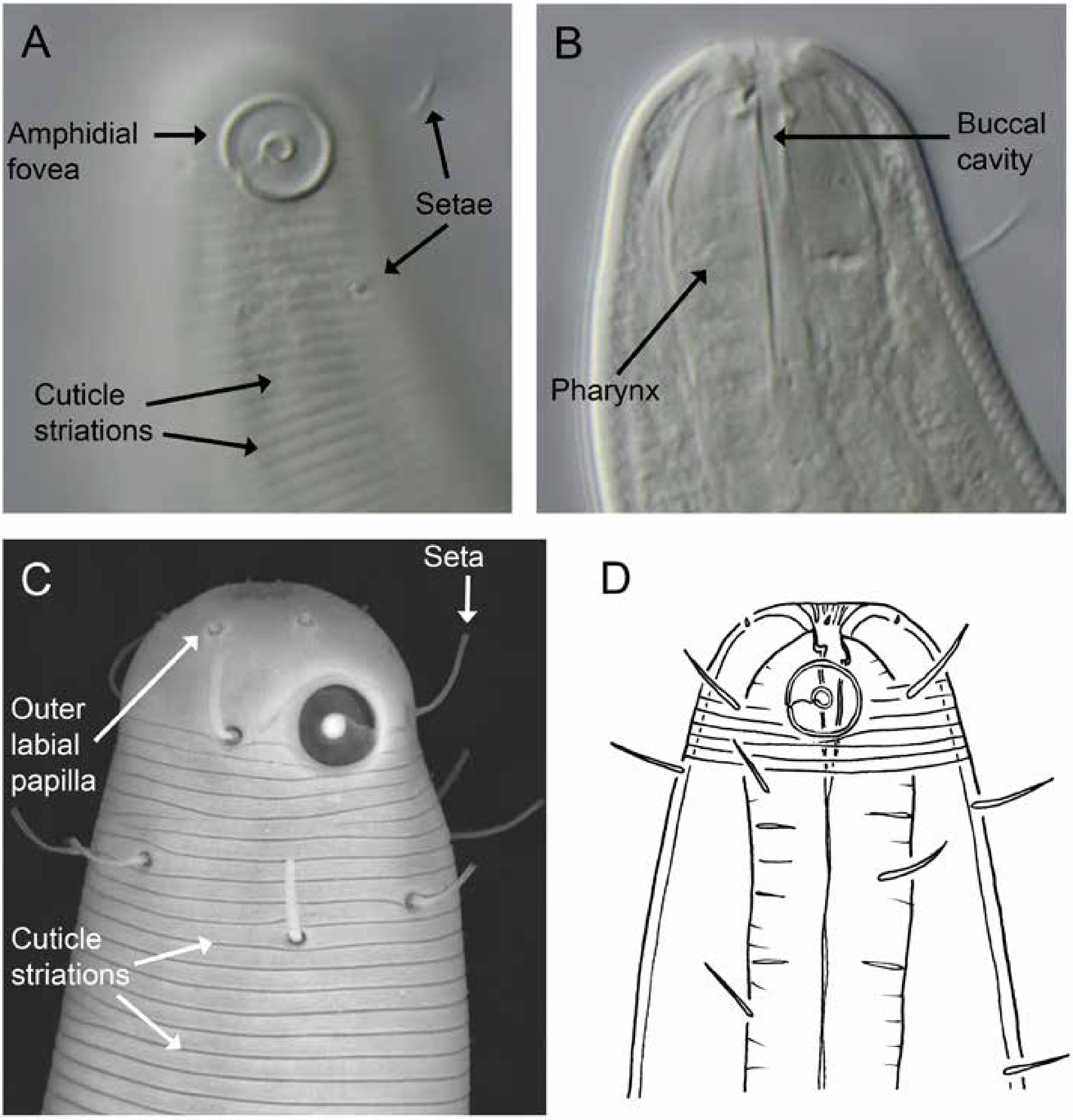


**Figure 3.** Methods for the observations and illustration of nematode morphology, exemplified by the cephalic region of *Spirinia antipodea* Leduc & Zhao, 2019: **A.** Light micrograph taken at 1000 × magnification using differential interference contrast, showing surface view of cuticle, amphidial fovea and setae; **B.** Light micrograph showing optical cross-section of buccal cavity and anterior pharyngeal region; **C.** Scanning electron micrograph showing detailed surface ornamentation and the position of the minute outer labial papillae and cuticle striation pattern; **D.** Drawing illustrating both external and internal morphology.

The nematode body plan is built around two axes of symmetry; whilst the pharynx (anterior portion of alimentary tract), buccal cavity, and lip region follow a triradial symmetry composed of one dorsal sector and two ventrosublateral sectors, all other structures (including the cephalic region and body wall) follow a bilateral symmetry. Describing the position of various morphological features on the nematode body requires different terminologies depending on whether they are distributed along bilaterally or triradially symmetrical axes. This is particularly important for the anterior body region, where most of the sensory structures are located and where the lip region (triradial symmetry) and cephalic region (bilateral symmetry) meet (Fig. 7).

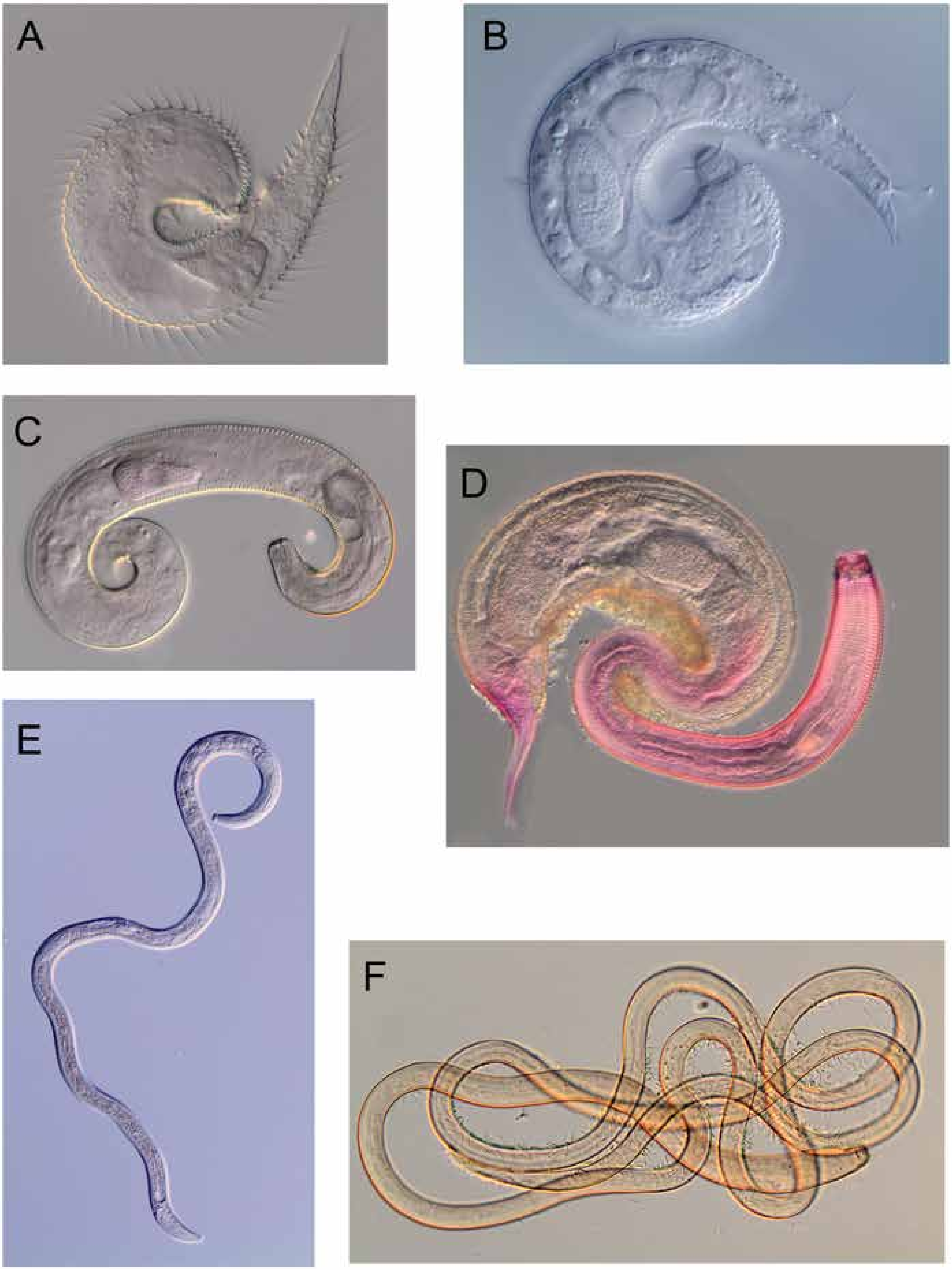


**Figure 4.** Free-living marine nematode body shapes, ranging from stout to slender: **A.** Male *Greeffiella* sp. (Desmoscolecida); **B.** Female *Hapalomus* sp. (Desmoscolecida); **C.** Female *Microlaimus* sp. (Microlaimida); **D.** Female *Desmodorella* sp. (Desmodorida); **E.** Female *Sabatieria* sp. (Araeolaimida); **F.** Juvenile *Eubostrichus* sp. (Desmodorida).

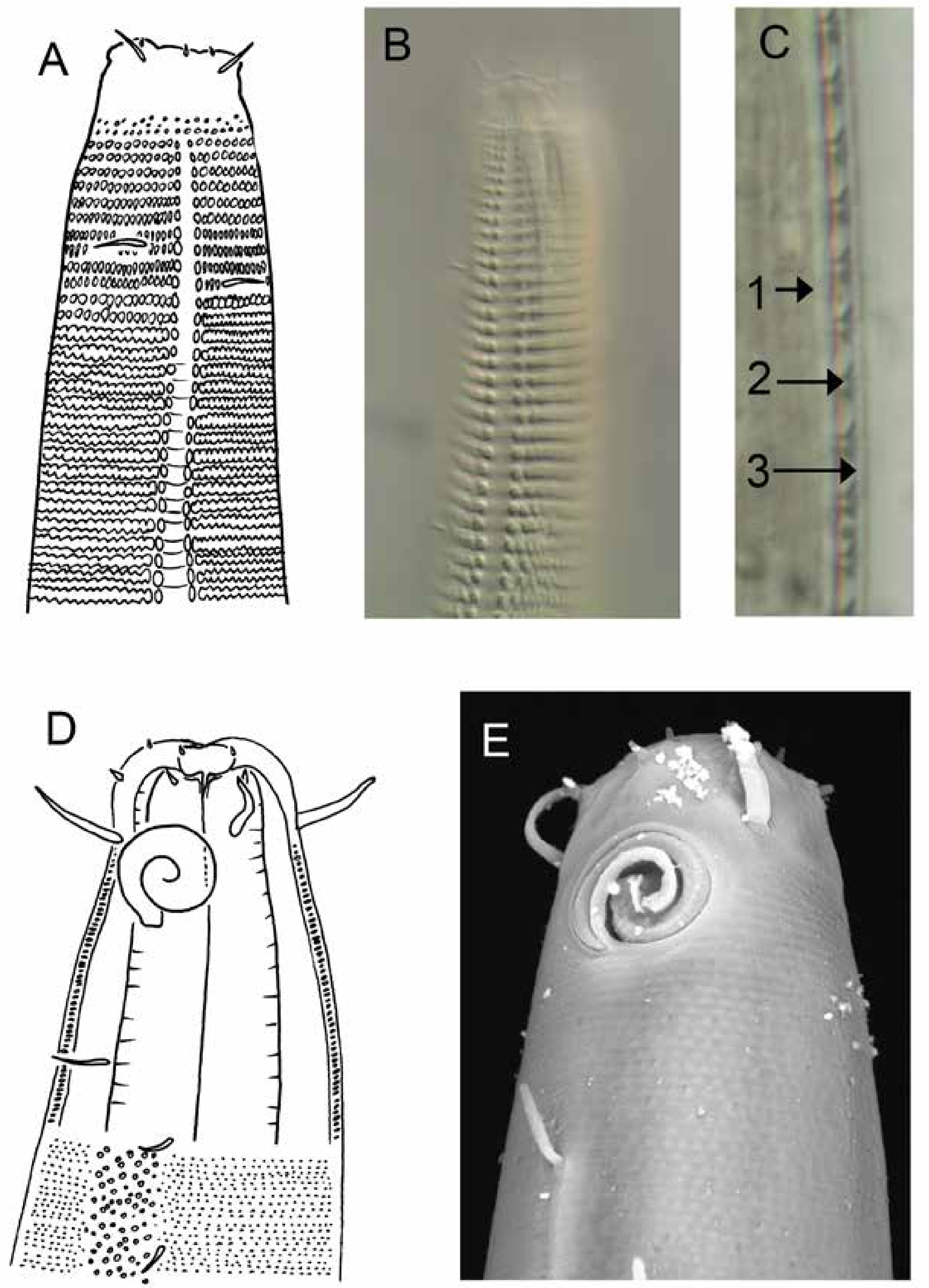


**Figure 5.** Cuticle punctations in marine nematodes, exemplified by *Ptycholaimellus spiculuncus* **sp. nov.** (A–C) and *Sabatieria* cf. *granifer* (D–E): **A.** Drawing of lateral view of cephalic region showing two longitudinal rows of enlarged cuticle punctations with transverse rows of smaller, distinct to partially fused punctations; **B.** Light micrograph showing the same features as in A; **C.** Light micrograph showing a transverse optical section of cuticle, mid-body region, with the basal (1), median (2) and cortical zones (3) of the cuticle; **D.** Cephalic region showing lateral differentiation of irregularly-arranged large punctations flanked by transverse rows of small punctations; **E.** Scanning electron micrograph showing presence of very fine striations on cuticle surface, as well as transverse rows of minute bumps, created by the presence of underlying column structures in the median cuticle zone, giving the appearance of punctations under light microscopy.

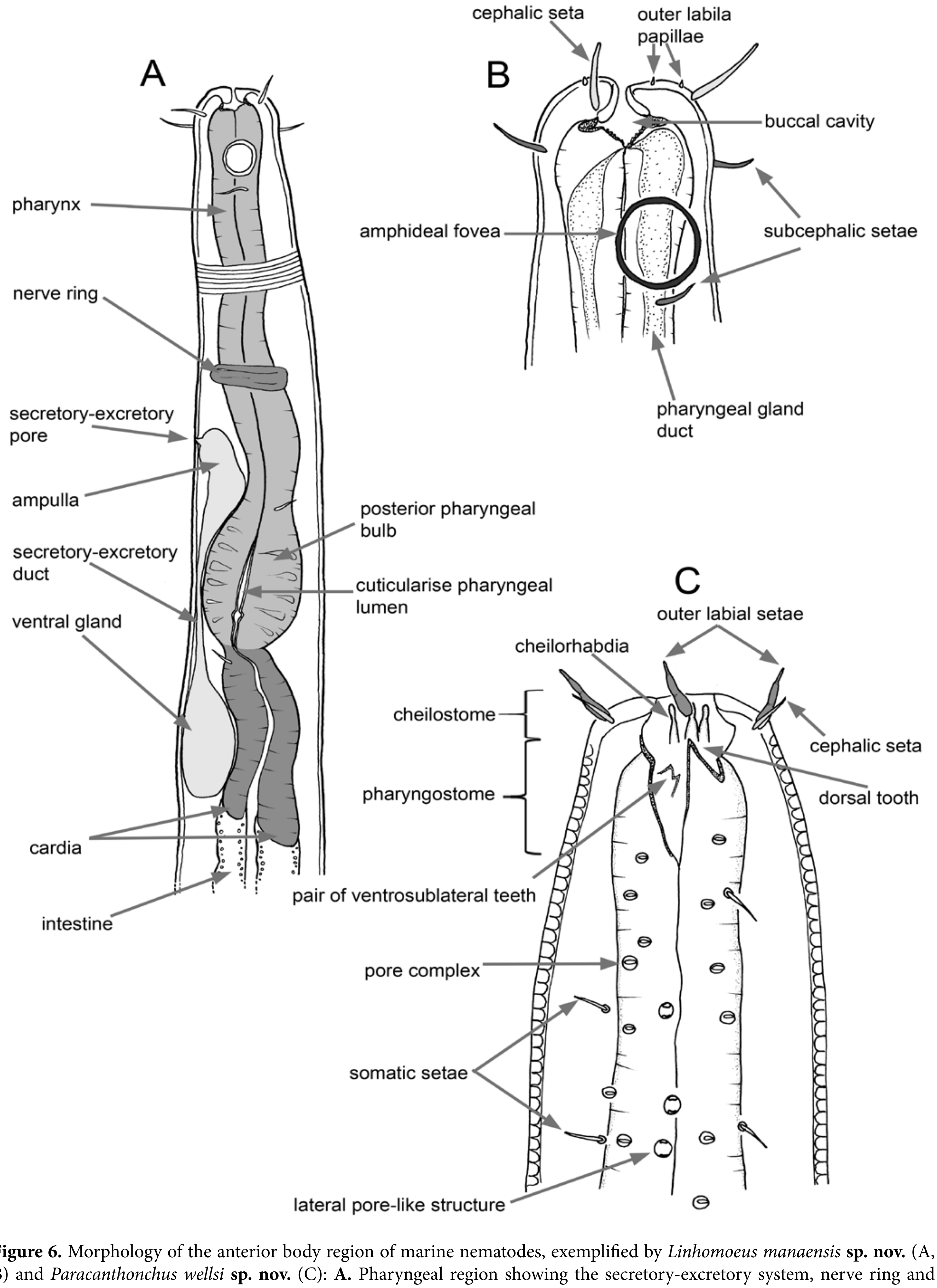


**Figure 6.** Morphology of the anterior body region of marine nematodes, exemplified by *Linhomoeus manaensis* **sp. nov.** (A, B) and *Paracanthonchus wellsi* **sp. nov.** (C): **A.** Pharyngeal region showing the secretory-excretory system, nerve ring and pharynx; **B.** Cephalic region showing details of cephalic sensilla (six outer labial papilla in a circle anterior to four much longer cephalic setae), subcephalic setae, amphid (circular), and buccal cavity with minute teeth-like projections; **C.** Cephalic region with six outer labial setae at same level as four shorter cephalic setae, buccal cavity with large dorsal tooth and pair of ventro-sublateral teeth, and cuticle with pore complexes, lateral pore-like structures and somatic setae.

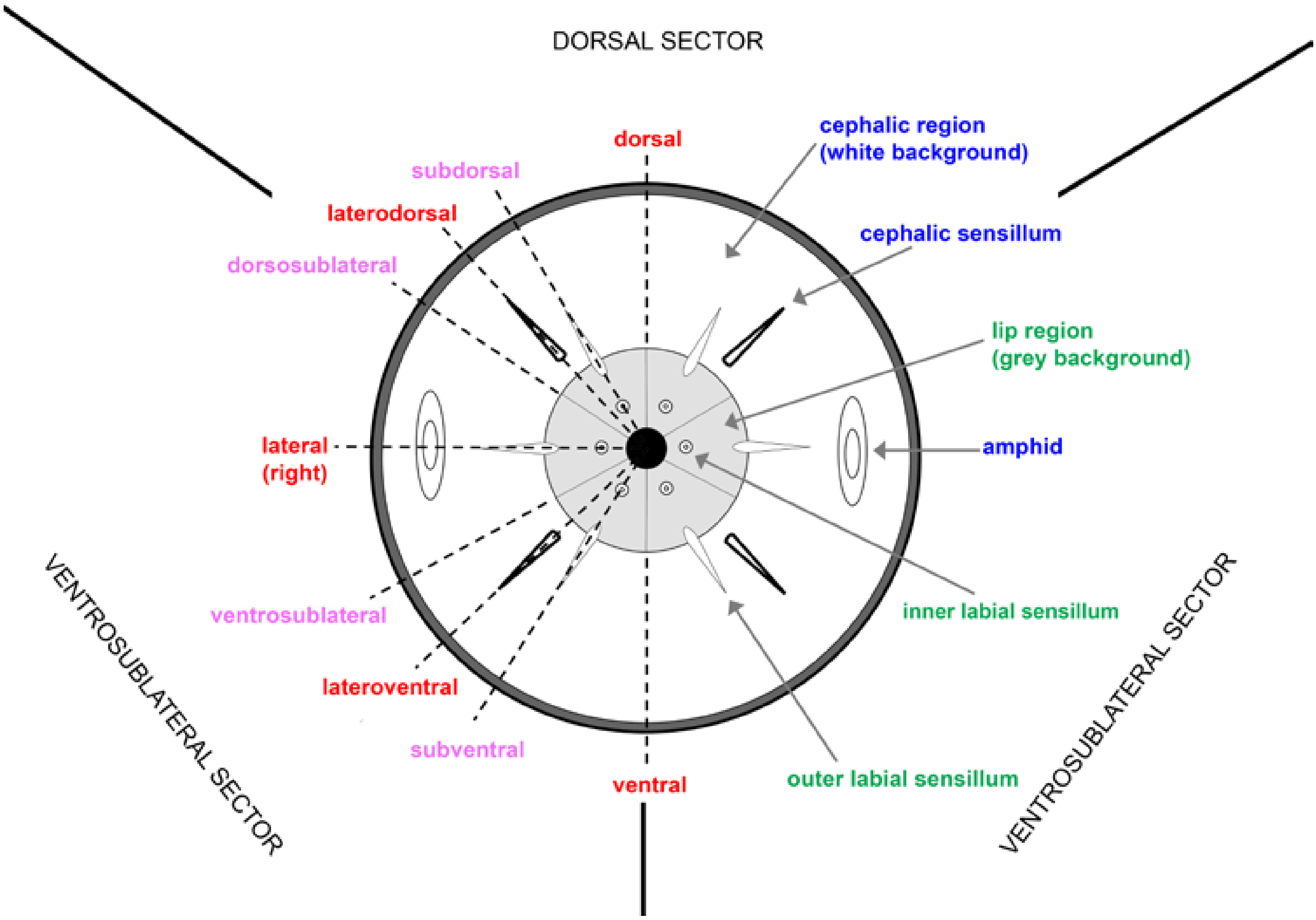


**Figure 7.** Schematic *en face* view of nematode anterior body extremity, with details of terminology used to describe the position of cephalic structures arranged along bilaterally (i.e., cephalic sensilla and amphids on cephalic region, white background) and triradially symmetrical axes (i.e., inner and outer labial sensilla on lip region, grey background). The terminology used for describing the position of cephalic structures is shown with bilateral terminology in red font and triradial terminology in magenta font. Morphological structures and body regions are labelled with bilaterally arranged/divided structures/body regions in blue font and triradially arranged/divided structures/body regions shown in green font.

The lip region typically bears a circle of six inner labial sensilla (two located subdorsally, two laterally, and two subventrally) and a circle of six outer labial sensilla in the same arrangement but slightly posterior to the inner labial sensilla. The cephalic region (immediately posterior to the lip region) bears a circle of four cephalic sensilla (two located lateroventrally and two laterodorsally) posterior to the outer labial sensilla. The inner labial, outer labial, and cephalic sensilla can either be papilliform (< 2 **µm** in length) or setiform (> 2 **µm**). In some taxa the outer labial sensilla are located at the same level as the cephalic sensilla, resulting in a 6 + 10 arrangement instead of the typical 6 + 6 + 4 arrangement of anterior sensilla. In some cases, additional setae are also present at the same level as the cephalic sensilla or between the circles of cephalic sensilla and outer labial sensilla (e.g., in *Theristus vivax* **sp. nov.**). These additional setae can be located adjacent to the outer labial sensilla or the cephalic sensilla, or somewhere between them (e.g., in *Theristus vivax* **sp. nov.**). Within the family Linhomoeidae the number of additional setae can sometimes vary within species (e.g., in *Linhomoeus manaensis* **sp. nov.**). For more details on symmetry in nematodes and the terminology of the body regions, see De Coninck (1965) and Coomans (1979).

The main sensory organs of nematodes are the amphids, which are thought to be involved in chemoreception. Each of the two amphids is normally located laterally posterior to the lip region (Fig. 6). Amphids consist of the amphidial fovea, an internal pocket or cavity connected to the exterior via the amphidial aperture. In enoplids, the amphidial fovea is often pocket-shaped with a narrow slit-like aperture. In most of the order Monhysterida and Microlaimida, both the amphidial fovea and aperture are circular and usually similar in size, although in some cases the amphidial aperture can be smaller than the amphidial fovea resulting in the appearance of a ring when their outlines are superimposed. In other taxa, the amphidial fovea can be uni- or multispiral (e.g., order Desmodorida, family Comesomatidae), loop-shaped (e.g., Axonolaimidae De Coninck & Schuurmans Stekhoven, 1933), or a narrow slit (e.g., family Chromadoridae Filipjev, 1917). It is not uncommon for some degree of dimorphism to be present, with amphids often larger in males than females, or of a different shape.

The digestive system consists of the mouth opening, buccal cavity, pharynx, intestine, and rectum. The mouth opening is normally located apically on the lip region, and can be circular or triangular, reflecting the triradial symmetry which characterises this region. The mouth (or buccal) cavity is divided into two main portions, the cheilostome and the pharyngostome (Fig. 6). The cheilostome is the anteriormost portion of the buccal cavity; it is not surrounded by pharyngeal tissue and is sometimes characterised by the presence of internal folds called cheilorhabdia (e.g., order Desmodorida, Chromadorida, and Microlaimida). The pharyngostome is located immediately posterior to the cheilostome and is surrounded by pharyngeal tissue. The pharyngostome sometimes contains teeth, usually located dorsally and ventrosublaterally, various arrangements of denticles (small teeth), or can be without teeth or denticles. Teeth can be used to pierce microalgal cells or scrape organic material from the surface of sediment grains (e.g., family Chromadoridae), or to feed on nematode and other prey (e.g., some taxa within the order Enoplida). The pharynx is a muscular and glandular organ with a triradial lumen separating the dorsal and ventrosublateral sectors. The posterior part of each sector contains a gland which opens into the pharyngeal lumen or buccal cavity (pharyngostome), although these can often be difficult to observe. The pharynx is sometimes characterised by the presence of anterior, median, and/or posterior swellings (bulbs). The pharynx is separated from the intestine by the cardia, a muscular one-way valve which delivers food to the intestine. Cardia can be very short or elongated as in *Linhomoeus manaensis* **sp. nov.** (Fig. 6). The intestine occupies the length of the animal between the cardia and the rectum, and often contains partially digested items such as microalgal cells, amorphous detritus, or nematode prey. The rectum is connected to the intestine by a valve surrounded by a sphincter muscle. The rectum lumen is lined with cuticle continuous with the body cuticle.

The secretory-excretory system in most marine nematodes consists of a ventral gland (sometimes called renette cell or secretory-excretory gland) which is typically located ventrally near the anterior part of the intestine or in the pharyngeal region (Fig. 6). The gland is connected via a duct to a ventral secretory-excretory pore typically located further anteriorly in the pharyngeal or cephalic region. In some taxa, additional glands are present adjacent to the ventral gland. Three caudal glands are typically found in the tail region, and these open to the exterior at the tail tip through a spinneret (Fig. 8). Two smaller additional glands may also be present (Adam & Tyler 1980). In some cases, the caudal glands are located anterior to the cloaca or anus (e.g., in *Viscosia dossena* **sp. nov.**).

The female reproductive system consists of one (monodelphic) or two genital branches (didelphic), each consisting of an ovary, oviduct, and uterus, and connected to a single vagina opening by a mid-ventral vulva (Fig. 8). The ovaries may be reflexed (bent) or outstretched. In some taxa a spermatheca may be associated with each genital branch. The male reproductive system comprises either one (monorchic) or two testes (diorchic) that open into a common gonoduct (vas deferens) (Fig. 8). Like the ovaries, testes can either be reflexed or outstretched. Sperm dimorphism is sometimes observed in species with two testes. The vas deferens joins the rectum and opens into the cloaca. The copulatory apparatus typically consists of two cuticularised spicules and the associated gubernaculum (Fig. 8). The spicules are protracted during copulation, during which they keep the vulva open allowing sperm to flow into the female. Spicules are typically symmetrical and can be differentiated into a head (capitulum) offset from a narrower shaft tapering into a fine distal end. Structures such as ventral vela (singular velum; thin cuticularised flanges) or lamella (internal cuticularised ridge) may be present. The gubernaculum may be simple or complex and may comprise the corpus (main part), cuneus (central projections between the spicules), crurae (lateral guiding pieces), and apophyses (prominent structures). In the region surrounding the cloacal opening and in the caudal area, accessory genital structures such as precloacal supplements, spines, papillae, or bursa may be present. Variation in the morphology of the copulatory apparatus and associated genital structures

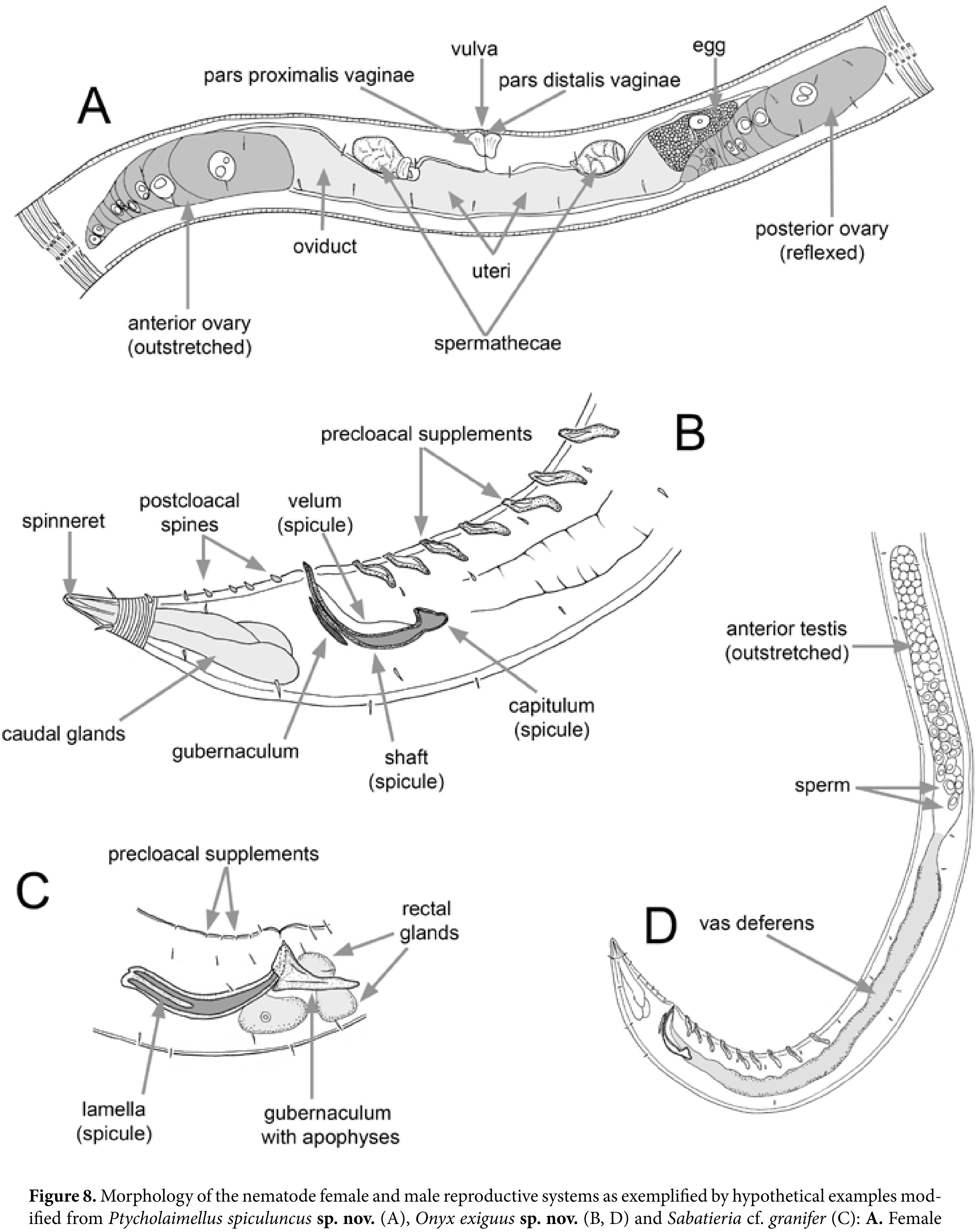


**Figure 8.** Morphology of the nematode female and male reproductive systems as exemplified by hypothetical examples modified from *Ptycholaimellus spiculuncus* **sp. nov.** (A), *Onyx exiguus* **sp. nov.** (B, D) and *Sabatieria* cf. *granifer* (C): **A.** Female reproductive system with two opposed ovaries (amphidelphic); **B.** Male posterior body region and copulatory apparatus (spicules, gubernaculum and precloacal supplements); **C.** Male copulatory apparatus; **D.** Male posterior body region showing single anterior outstretched testis (monorchic) and copulatory apparatus.

is often used for differentiating among closely related nematode species.

**Registration of type and general material.** Most primary and secondary type materials are accessioned within the NIWA Invertebrate Collection (NIC) at the National Institute of Water & Atmospheric Research (NIWA) at Greta Point, Wellington (prefix NIWA—). A number of paratype specimens were lodged in the National Nematode Collection of New Zealand (NNCNZ), now part of the New Zealand Arthropod Collection (NZAC) held by Manaaki Whenua – Landcare Research in Auckland (prefix NNCNZ—).

**ZooBank registration.** This published work and the nomenclatural acts that it contains (i.e., creation of new species) have been registered in ZooBank (http://www.zoobank.org/), the official registry of Zoological Nomenclature. The ZooBank Life Science Identifier for this publication is urn:lsid:zoobank.org:pub:58AA50AE-8BCC-489B-92A8-42FD45BDE187. New scientific names and other comments are registered in ZooBank, and the registration details are included as part of the descriptions under the subheading 'ZooBank registration'.

**DNA extraction, PCR, and sequencing.** A single specimen of each species freshly extracted from the sediments was 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). COI primers were forward primer LCO1490, 5'-GGTCAACAAATCATAAAGATATTGG-3', and reverse primer HCO2198, 5'-TAAACTTCAGGGTGACCAAAAAATCA-3' (Folmer *et al.* 1994). For SSU, LSU and COI, the 20 µl PCR contained 10 µl Go Tag® Green Master Mix (Promega Corporation, Madison, WI, USA), 1 µl (5 µM) each of forward and reverse primers, and 2 µl of DNA template. 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 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 4.8 (Gene Codes Corp.).

**Sequence alignment and phylogenetic inference.** The ribosomal DNA SSU and LSU D2–D3 sequences as well as COI sequence were deposited in GenBank. The accession numbers are provided in the species descriptions, along with comparison with any publicly available sequences for Pāuatahanui Inlet species that are morphologically similar to known species from outside New Zealand.

A phylogenetic analysis was conducted using all of the Pāuatahanui Inlet SSU sequences, except for the *Paracanthonchus wellsi* **sp. nov.** and *Steineria preclara* **sp. nov.** sequences, which were too short to be included (< 550 bp). Sixty-two GenBank sequences (> 850 bp) belonging to the same species, genus, or family as the Pāuatahanui Inlet sequences were included in the analysis for comparison and to provide context. DNA sequences were aligned by MUSCLE alignment algorithm (Edgar 2004a, b) with default parameters. ModelTest 3.04 (Posada & Crandall 1998) in conjunction with PAUP*4.0b10 (Swofford 2002) and jModeTest 2.1.7 software (Darriba *et al.* 2012; Guindon & Gascuel 2003) were used to select the best fit model of DNA evolution with the Akaike Information Criterion (AIC). A Bayesian tree was obtained with MrBayes 3.2.6 (Ronquist & Huelsenbeck 2003) in Geneious 10.1.6 (http://www.geneious.com, Kearse *et al.* 2012). Four MCMC chains were run for 1,100,000 generations under the best-fit model (GTR + I + G). 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, burnin of 110,000 generations and thinning interval of 200. The perimeter files from multiple runs were inspected for chain convergence with Trace in Geneious 10.1.6 (http://www.geneious.com, Kearse *et al.* 2012) and trees were edited in FigTree v1.4.3. 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 10.1.3 with default settings and 1000 bootstrap replicates (Guindon & Gascuel 2003).

The SSU and COI sequences of *Terschellingia* cf. *longicaudata* de Man, 1907 were compared with those of taxa within the same family for which sequences were available in GenBank. To help visual interpretation of the tree, SSU sequences which were identical and both from the same study and location were not included in the analyses. The final SSU dataset included 26 *T. longicaudata* sequences, 7 other *Terschellingia* de Man, 1888 sequences, and 11 sequences from other closely related genera. The phylogenetic trees were built using the same method as described above.

## Terminology

Morphological terminology for nematodes follows Decraemer *et al.* (2014). See Belogurov & Belogurova (1989) for detailed discussion of the specialised morphological features of oncholaimids, Hope & Aryuthaka (2009) for a discussion on the morphology of rectal and ejaculatory glands, Lorenzen (1981, 1994) for a description of dereids, Leduc & Verschelde (2013) for discussion on cephalic region and amphidial fovea and aperture terminology, and Leduc & Zhao (2018) for a discussion of pore complexes and lateral pore-like structures in cyatholaimids.

**additional setae** – setae located at level of posterior-most circle of cephalic sensilla or slightly anterior to it, and which may be located in various positions immediately adjacent to, or between, the cephalic and outer labial sensilla; most commonly encountered in Xyalidae and Linhomoeidae

**alae** – longitudinal thickening of the cuticle forming wing-like expansions

**amphid** – paired lateral sense organs thought to be involved in chemoreception which generally open posterior to the lip region

**amphidial aperture** – opening of the amphidial fovea

**amphidial fovea** – invagination of the cuticle forming a pocket connected to the nervous system via the amphidial duct and to the exterior through the amphidial aperture

**amphidelphic** – female reproductive system with two opposed ovaries

**ampulla** – a membranous sac or vesicle, sometimes present as part of secretory-excretory system in proximity to pore

**annulation** – deep transverse striae which occur at regular intervals in the cuticle

**antidromous** – changing direction, e.g., antidromously reflexed ovary

**arcade tissue** – a mass of cells surrounding the buccal cavity

**bursal alae** – alae surrounding the cloacal opening

**capitulum** – the enlarged, cephalated proximal portion of the spicule

**cardia** – a muscular structure at the base of the pharynx opening into the intestine

**caudal glands** – usually three unicellular cells in or near the tail, discharging into a common ampulla at the spinneret

**cephalic capsule** – non-annulated, well set off cephalic region with an extra thick (inner) layer of the cuticle

**cervical setae** – setae located in the anterior pharyngeal region (well posterior to amphids) which can be differentiated from the somatic setae located further posteriorly due to their length or appearance or arrangement

**cheilorhabdia** – internal folds or rugae near anterior extremity of the buccal cavity (cheilostome), normally twelve in number; most commonly found in Desmodorida, Microlaimida, and Chromadorida

**cheilostome** – the anterior region of the buccal cavity located within lip region, delimited anteriorly by the mouth opening and posteriorly by the pharyngostome

**chords** – four longitudinal lines of hypodermal thickening lying on the inner side of the hypodermis and variously termed the dorsal, lateral, and ventral chords. The chords contain the nuclei of the hypodermis

**clavate** – swollen or club-shaped

**cloaca** – in the male a common chamber lined with cuticle which receives the products of the intestinal and reproductive tracts and empties to the exterior via the cloacal opening

**copulatory apparatus** – the sex organs of the male employed in the act of copulation, normally spicules, gubernaculum, and any supplements

**corpus** – main part of gubernaculum

**crura** – lateral guiding piece of the gubernaculum

**cryptocircular** - an amphidial fovea with similar outline as a cryptospiral amphidial fovea but without a central spot

**cryptospiral** – term used to describe an amphidial fovea with an outline that is comma-shaped or an interrupted circle (i.e., start- and end-points of the circle do not meet), and with a central spot

**cuneus** – central projection of gubernaculum between the two spicules

**cuticle** – semi-permeable exoskeleton composed of a complex extracellular matrix, which may be relatively thin or thick and multilayered; the cuticle covers the entire surface of the animal and invaginates at openings and lines the buccal cavity, rectum, and cloaca in males, the vulva in females, the secretory-excretory duct and some sensory organs

**demanian system** – a more or less complex seminal receptacle found in females of most oncholaimid genera; sperm are kept alive by secretions from the osmium, which consists of modified intestinal epithelium connected to the demanian system

**deirid** – sense organ taking the form of papillae or short setae located at same level as, or slightly posterior to, nerve ring, located laterally, or slightly dislaced dorsally; exclusive to Enoplida

**didelphic** – female reproductive system with two ovaries

**diorchic** – male reproductive system with two testes

**ejaculatory glands** – series of glands located on both left and right-hand sides of intestine, each with a long duct extending posteriorly and which may open into the vas deferens or cloaca; commonly found in Monhysterida and Araeolaimida

**endocupola** – dome-shaped structure formed by the splitting of the inner and outer cuticle layers in cephalic region of oncholaimids

**gubernaculum** – in male nematodes a grooved cuticularised structure, sometimes paired, which guides the spicules

**gubernacular apophyses** – prominent cuticularised structures on the gubernaculum, generally directed dorsally, dorsocaudally, or caudally

**gymnostome** – anterior portion of pharyngostome or posterior buccal cavity surrounded by arcade tissue

**labial sensilla** – sensilla located on the lips

**lamella** – inner longitudinal cuticularised partition of the spicule

**lateral alae** – lateral or sublateral extensions of the cuticle which extend along the body

**lateral pore-like structure** – circular or elliptical cuticularised opening on the cuticle supported by a modified (or possibly fused) punctuation at each of the anterior and posterior extremities, and with central, non-cuticularised dome; underlying gland cells absent; found in some Chromadorida

**metaneme** – filamentous organs, thought to act as stretch receptors, located in or near lateral chords of enoplid nematodes, with a central scapulus and anterior and posterior filaments

**monodelphic** – female reproductive system with one ovary

**monorchic** – male reproductive system with one testis

**nerve ring** – prominent part of the nervous system surrounding the pharynx

**odontium** – a labial tooth (teeth) situated on the pharyngeal wall but formed in the pharynx and oriented forward

**opisthodelphic** – female reproductive system with single ovary posterior to the vulva

**orthometaneme** – metanemes running parallel to the longitudinal axis of the body

**papilla** – cephalic or body sensilla less than 2 μm in length, usually conical or hemispherical

**pars distalis vaginae** – the distal part of the vagina with cuticular lining continuous with that of the exterior of the body

**pars proximalis vaginae** – the proximal section of the vaginal canal with hyaline walls

**pharyngostome** – posterior region of the buccal cavity, consisting of specialised anterior part of the pharynx, itself divided into the gymnostome (anterior portion not surrounded by pharyngeal tissue) and stegostome (posterior portion surrounded by pharyngeal tissue)

**pharyngeal sleeve** – thin layer of pharyngeal tissue surrounding stegostome (posterior buccal cavity)

**phasmid** – the lateral caudal papillae connected with the lateral precaudal glands; paired postanal lateral chemoreceptor sensory organs

**pore complex** – cuticularised ring in middle cuticle layer with slit-like transverse pore; underlying gland cells present, often difficult to distinguish; found in some Chromadorida

**prodelphic** – female reproductive system with a single ovary anterior to the vulva

**pseudocoel** – fluid-filled body cavity between the body wall and intestine lacking an epithelial lining

**pseudocoelomocytes** – cells lying in the pseudocoelom

**punctated** – term used to describe cuticle with numerous small 'dots', which may be arranged irregularly or in transverse or longitudinal rows; the appearance of dots stems from the presence of column- or rod-like structures separating the basal and cortical layers of the cuticle

**radial tube** – longitudinal tube formed by the cuticular lining of the pharyngeal lumen

**rectal glands** –unicellular glands, often three or six in number, which produce refractive granules and connected to the anterior part of the rectum

**setae** – cephalic or body sensilla 2 µm or more in length

**spicules** – male intromittent organs functioning during copulation for the transfer of sperm, often paired; each an elongate cuticularised piece, extrusible through the cloacal opening

**stomatoidal ring** – zone of contact between the endocupola and wall of buccal cavity in oncholaimids

**striations** – transverse grooves or shallow depressions which occur at regular intervals in the cuticle

**subcephalic setae** – setae located between cephalic sensilla and near posterior edge of amphids

**secretory-excretory system** – specialised excretory structure which in most aquatic nematodes generally consists of an excretory gland cell, also known as ventral gland or renette cell, located in the pseudocoelom and connected to a canal opening midventrally through a pore in the pharyngeal body region

**spermatheca** – the enlarged portion of the female reproductive system which functions as a reservoir in receiving and holding sperm

**spine** – a stout, pointed process of the cuticle

**spinneret** – outlet of the caudal glands

**stegostome** – posterior portion of pharyngostome, or posterior buccal cavity

**supplements** – in males, ventromedian organs of contact reception, secretion, and attachment, located anteriorly or posteriorly to the cloaca, derived of cuticle, and functioning during copulation

**unispiral** – term used to describe an amphidial fovea with a circular outline and a central spot

**vas deferens** – a slender muscular tube extending from the ejaculatory duct to the testis

**velum** – a delicate cuticular membrane on the inner side of the spicule

**ventral gland** – the secretory-excretory gland, also known as renette cell, connected through a duct to the secretory-excretory pore located midventrally

## Abbreviations

| | |
|---|---|
| **abd** | Anal body diameter |
| **ANZECC** | Australian and New Zealand Environment and Conservation Council |
| **a** | Body length/maximum body width |
| **b** | Body length/pharynx length |
| **bp** | Base pairs |
| **c** | Body length/tail length |
| **c’** | Tail length/anal or cloacal body diameter |
| **cbd** | Corresponding body diameter |
| **COI** | Mitochondrial protein-coding gene, cytochrome c oxidase subunit I |
| **DDT** | Dichlorodiphenyltrichloroethane |
| **DNA** | Deoxyribonucleic acid |
| **DOC** | Department of Conservation |
| **D2–D3 of LSU rDNA** | D2–D3 region of large subunit 28S ribosomal DNA gene |
| **GOPI** | Guardians of Pāuatahanui Inlet |
| **GRWC** | Greater Wellington Regional Council |
| **L** | Length |
| **n** | Number of specimens |
| **NNCNZ** | National nematode collection of New Zealand |
| **NIWA** | National Institute of Water and Atmospheric Research, Wellington, New Zealand |
| **NZAC** | New Zealand arthropod collection |
| **PCC** | Porirua City Council |
| **PCR** | Polymerase chain reaction |
| **PHT** | Porirua Harbour and Catchment Community Trust |
| **rDNA** | ribosomal DNA |
| **SSU** | Small subunit 18S |
| **SSWI** | Sites of Special Wildlife Interest |
| **USDA** | United States Department of Agriculture |
| **V** | Vulva distance from anterior body extremity |
| **%V** | Vulva distance from anterior end of body × 100/total body length |
| **WIP** | Whaitua Implementation Programme |
| **WRC** | Wellington Regional Council |

## Acknowledgments

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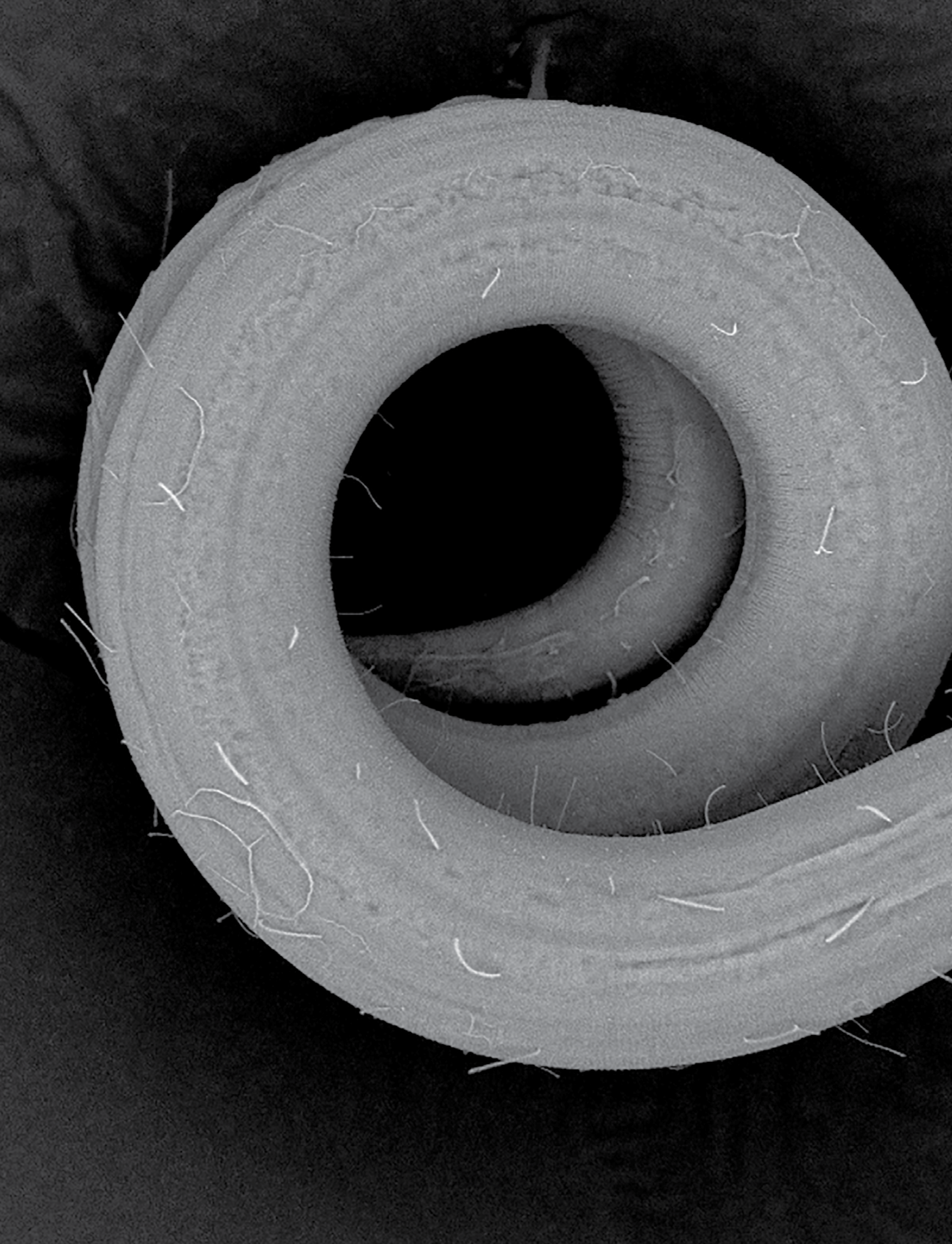


Scanning electron micrograph of free-living nematode, *Steineria preclara* Leduc & Zhao, 2023 (Enoplea Inglis, 1983, Monhysterida Filipjev, 1929, Xyalidae Chitwood, 1951)

# TAXONOMY & SYSTEMATICS

## Checklist of nematode species from Pāuatahanui Inlet, Te Awarua-o-Porirua Harbour, Wellington, Aotearoa New Zealand

The classification of De Ley & Blaxter (2002, 2004) was used; however, we followed Leduc *et al.* (2018b) in treating the Microlaimida as a separate order instead of a superfamily within the order Desmodorida.

Phylum NEMATODA Cobb, 1932
Class ENOPLEA Inglis, 1983
  Order ENOPLIDA Filipjev, 1929
    Family ANOPLOSTOMATIDAE Gerlach & Riemann, 1974
      Genus ***Anoplostoma*** Bütschli, 1874
        *Anoplostoma amphicystum* **sp. nov.**
    Family ENCHELIDIIDAE Filipjev, 1918
      Genus ***Ledovitia*** Filipjev, 1927
        *Ledovitia gutturosa* **sp. nov.**
    Family ONCHOLAIMIDAE Filipjev, 1916
      Genus ***Viscosia*** de Man, 1890
        *Viscosia dossena* **sp. nov.**
    Family OXYSTOMINIDAE Chitwood, 1935
      Genus ***Litinium*** Cobb, 1920
        *Litinium ankistronidum* **sp. nov.**
    Family THORACOSTOMOPSIDAE Filipjev, 1927
      Genus ***Oxyonchus*** Filipjev, 1927
        *Oxyonchus* sp. 1 (NIWA 154881, short body & cephalic setae, Mana Bank, Leduc & Zhao)
    Family TRIPYLOIDIDAE Filipjev, 1918
      Genus ***Bathylaimus*** Cobb, 1894
        *Bathylaimus* cf. *australis* Cobb, 1894
      Genus ***Tripyloides*** de Man, 1886
        *Tripyloides* cf. *marinus* (Bütschli, 1874) de Man, 1886

Class CHROMADOREA Inglis, 1983
  Order ARAEOLAIMIDA De Coninck & Schuurmans Stekhoven
    Family AXONOLAIMIDAE Filipjev, 1918
      Genus ***Axonolaimus*** de Man, 1889
        *Axonolaimus glandifer* **sp. nov.**
      Genus ***Odontophora*** Bütschli, 1874
        *Odontophora atrox* Leduc & Zhao, 2016
    Family COMESOMATIDAE Filipjev, 1918
      Genus ***Sabatieria*** Rouville, 1903
        *Sabatieria* cf. *granifer* Wieser, 1954
        *Sabatieria paramacramphis* **sp. nov.**
  Order CHROMADORIDA Chitwood, 1933
    Family CHROMADORIDAE Filipjev, 1917
    Subfamily CHROMADORINAE Filipjev, 1917
      Genus ***Chromadora*** Bastian, 1865
        *Chromadora* cf. *nudicapitata* Bastian, 1865
      Genus ***Chromadorina*** Filipjev, 1918
        *Chromadorina germanica* (Bütschli, 1874) Wieser, 1954
    Subfamily HYPODONTOLAIMINAE de Coninck, 1965
      Genus ***Chromadorita*** Filipjev, 1922
        *Chromadorita spinicauda* **sp. nov.**
      Genus ***Ptycholaimellus*** Cobb, 1920
        *Ptycholaimellus spiculuncus* **sp. nov.**
    Family CYATHOLAIMIDAE Filipjev, 1918
    Subfamily CYATHOLAIMINAE Filipjev, 1918
      Genus ***Paracanthonchus*** Micoletzky, 1924
        *Paracanthonchus wellsi* **sp. nov.**

Order DESMODORIDA De Coninck, 1965
Family DESMODORIDAE Filipjev, 1922
Subfamily DESMODORINAE Filipjev, 1922
Genus ***Pseudochromadora*** Daday, 1899
*Pseudochromadora plurichela* **sp. nov.**
Subfamily SPIRINIINAE Chitwood, 1936
Genus ***Chromaspirina*** Filipjev, 1918
*Chromaspirina stilbonematinops* **sp. nov.**
Genus ***Onyx*** Cobb, 1891
*Onyx exiguus* **sp. nov.**
Genus ***Spirinia*** Gerlach, 1963
*Spirinia antipodea* Leduc, 2018
Order MICROLAIMIDA Leduc, Verdon & Zhao, 2018
Family MICROLAIMIDAE Micoletzky, 1922
Genus ***Microlaimus*** de Man, 1880
*Microlaimus korari* Leduc, 2016
Order MONHYSTERIDA Filipjev, 1929
Family LINHOMOEIDAE Filipjev, 1922
Genus ***Eleutherolaimus*** Filipjev, 1922
*Eleutherolaimus paraschneideri* **sp. nov.**
Genus ***Linhomoeus*** Bastian, 1865
*Linhomoeus manaensis* **sp. nov.**
Genus ***Metalinhomoeus*** de Man, 1907
*Metalinhomoeus bifidosetus* **sp. nov.**
*Metalinhomoeus trinimirmecius* **sp. nov.**
Genus ***Terschellingia*** de Man, 1888
*Terschellingia* cf. *longicaudata* de Man, 1907
Family SPHAEROLAIMIDAE Filipjev, 1918
Genus ***Metasphaerolaimus*** Gourbault & Boucher, 1981
*Metasphaerolaimus* sp. 1 (NIWA 154880, dorsocaudal apophyses & conicocylindrical tail, Mana Bank, Leduc & Zhao)
Family XYALIDAE Chitwood, 1951
Genus ***Cobbia*** de Man, 1907
*Cobbia trefusiaeformis* de Man, 1907
Genus ***Daptonema*** Cobb, 1920
*Daptonema falcatispiculum* **sp. nov.**
*Daptonema carnulentum* **sp. nov.**
Genus ***Omicronema*** Cobb, 1920
*Omicronema nicholasi* **sp. nov.**
Genus ***Paramonohystera*** Steiner, 1916
*Paramonohystera leptamphida* **sp. nov.**
Genus ***Promonhystera*** Wieser, 1956a
*Promonhystera crinita* **sp. nov.**
Genus ***Steineria*** Micoletzky 1922
*Steineria preclara* **sp. nov.**
Genus ***Theristus*** Bastian, 1865
*Theristus arcuatospiculus* **sp. nov.**
*Theristus levicapitulus* **sp. nov.**
*Theristus vivax* **sp. nov.**
Order PLECTIDA Gadea, 1973
Family CAMACOLAIMIDAE Micoletzky, 1924
Genus ***Deontolaimus*** de Man, 1880
*Deontolaimus poriruaensis* **sp. nov.**
Order RHABDITIDA Chitwood, 1933
Family PELODERIDAE Andrássy, 1976
Genus ***Litoditis*** Sudhaus, 2011
*Litoditis* cf. *marina* (Bastian, 1865) Sudhaus, 2011

## Molecular taxonomy

Near complete or partial SSU rDNA sequences were obtained for 28 species (one specimen per species) representing 27 genera belonging to 12 families, seven orders and two classes. Near complete or partial D2–D3 of LSU rDNA sequences were obtained for a subset of 21 of these 28 species. A single mitochondrial cytochrome oxidase c subunit 1 (COI) sequence was obtained for *Terschellingia* cf. *longicaudata*. A SSU rDNA phylogenetic tree was built using all of the Pāuatahanui inlet sequences (Fig. 9), except for the *Paracanthonchus wellsi* **sp. nov.** and *Steineria preclara* **sp. nov.** sequences which were too short (< 550 bp) resulting in anomalous placement in the tree. Sequences from Genbank representing the same species, genera, or families as the Pāuatahanui Inlet sequences were included in the phylogenetic tree for comparison and to provide broader context.

The classes Chromadorea and Enoplea were recovered as well-supported monophyletic groups (100% posterior probability and 92% bootstrap support). The Enoplea was represented by a single order, the Enoplida, which in turn comprised three families and four genera, all of which were recovered as well-supported monophyletic clades (100% posterior probability and 99–100% bootstrap support). Within the Chromadorea, some of the orders were recovered as monophyletic (i.e., Microlaimida, Desmodorida, Chromadorida, and Rhabditida) while others were not (Monhysterida and Araeolaimida), which is similar to previous SSU phylogenies (Holterman *et al.* 2006; Meldal *et al.* 2007; Leduc et al. 2018b). It is not yet clear how best to resolve the disagreement between the current classification scheme based on a combination of both morphological and SSU phylogenetic methods and the results of increasingly detailed and comprehensive SSU phylogenies that include a growing number of marine taxa, but approaches such as mitogenomics and phylogenomics may help provide some solutions in the future (Smythe *et al.* 2019; Kern *et al.* 2020).

Overall, the Pāuatahanui Inlet sequences were placed as expected in the SSU tree, at least genera/species for which sequences of sufficient length were available in Genbank. The only exception to this was *Ptycholaimellus spiculuncus* **sp. nov.** which, although correctly placed within the Chromadoridae, was not placed close to the only other *Ptycholaimellus* Cobb, 1920 sequence available (FJO40472). However, it is relatively common to find that marine nematode genera do not form monophyletic clades in SSU phylogenies (e.g., Armenteros *et al.* 2014a; Leduc & Zhao 2018). Wherever possible, the SSU sequences of Pāuatahanui Inlet specimens that are morphologically similar to known species were compared to available sequences in the individual species descriptions below. Note that most of these comparisons were severely limited by the lack of available sequences. More detailed phylogenetic comparisons, however, were conducted for *Terschellingia* cf. *longicaudata* because several SSU sequences were available.

## Systematics

Phylum **Nematoda** Cobb, 1932
Class **Enoplea** Inglis, 1983
Order **Enoplida** Filipjev, 1929

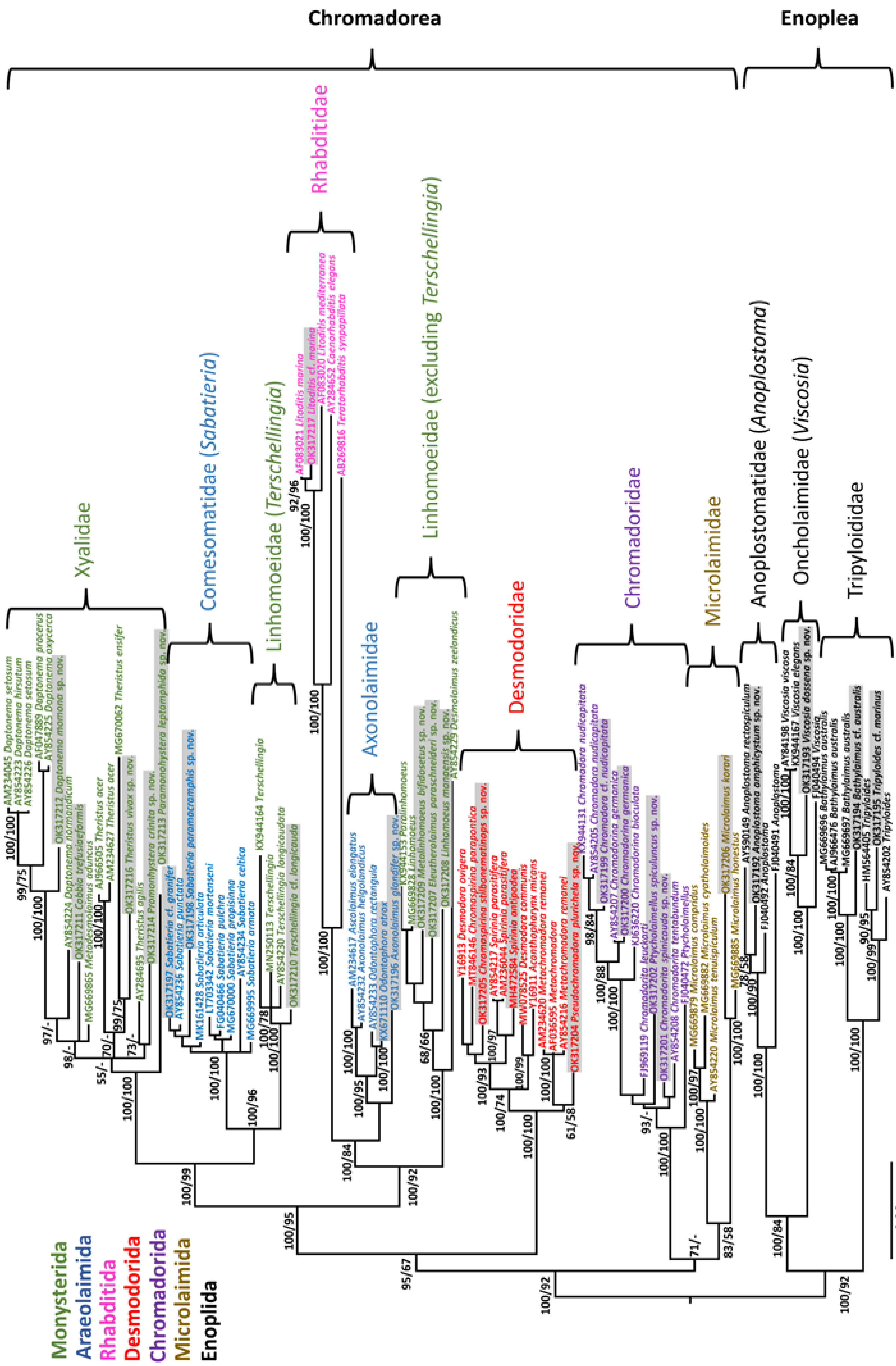
Family **Anoplostomatidae** Gerlach & Riemann, 1974
Subfamily **Anoplostomatinae** Gerlach & Riemann, 1974

Anoplostomatinae Gerlach & Riemann, 1974: 554.

**Diagnosis.** Three lips, each with short inner and outer labial sensilla. Buccal cavity spacious, cylindrical, toothless, and surrounded by pharyngeal tissue only in the posterior section. Pharynx musculature not inserting at base of cephalic capsule. Amphids with small aperture and relatively large fovea, similar in both sexes and always situated behind the cephalic capsule. Only dorsolateral loxometanemes present, predominantly of type I, some of type II and all with caudal filament. Three pharyngeal glands open directly posterior to the buccal cavity. Outline of pharynx smooth. Of the secretory-excretory system, only the pore was observed. Males diorchic, the posterior testis proceeds forward slightly and is then reflexed. Female reproductive system didelphic-amphidelphic with antidromously reflexed ovaries. Gonads positioned to the left of the intestine. Three caudal glands penetrate the pre-caudal region (after Smol *et al.* 2014).

**Type genus.** *Anoplostoma* Bütschli, 1874

**Figure 9** (*opposite*)**.** 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. Posterior probabilities (left) and bootstrap values (right) greater than or equal to 50% are given on appropriate clades; for clarity, values are not shown for all clades. Orders are denoted by different colours as shown on legend on upper left-hand corner. New sequences are shown on grey background. Scale stands for substitutions per site. Hyphen (-) indicates less than 50% bootstrap support.



Chromadorea
Enoplea
Xyalidae
Comesomatidae (Sabatieria)
Linhomoeidae (Terschellingia)
Rhabditidae
Axonolaimidae
Linhomoeidae (excluding Terschellingia)
Desmodoridae
Chromadoridae
Microlaimidae
Anoplostomatidae (Anoplostoma)
Oncholaimidae (Viscosia)
Tripyloididae
Monysterida
Araeolaimida
Rhabditida
Desmodorida
Chromadorida
Microlaimida
Enoplida
0.06

## Genus *Anoplostoma* Bütschli, 1874

*Anoplostoma* Bütschli, 1874: 36–38, figs 20, 21.

**Diagnosis.** Body tapering towards both extremities. Cuticle smooth. Triangular mouth opening surrounded by six inner labial papillae. Circle of six outer labial setae situated only slightly anterior to circle of four slightly shorter cephalic setae. Amphids pocket-shaped, located posterior to buccal cavity, equal in males and females; amphidial aperture small, ovoid, or circular. Buccal cavity voluminous and toothless, formed by parallel cuticularised walls not surrounded by pharyngeal musculature. Pharynx muscular. Outlets of pharyngeal glands just posterior to the buccal cavity. Secretory-excretory pore known only from few species, situated well behind buccal cavity. Male reproductive system with two testes; female reproductive system with two antidromously reflexed ovaries. Male with paired bursal alae supported by sublateral spines and possibly smaller papillae. Tail conicocylindrical (modified from Tchesunov & Nguyen Vu Thanh 2010).

**Remarks.** *Anoplostoma* is the only genus of the subfamily. It was revised by Wieser (1953b), Chitwood (1960), and most recently by Tchesunov & Nguyen Vu Thanh (2010), who provided a key to the fourteen valid species. The latter authors state that the posterior testis in *Anoplostoma* is reflexed; however, both testes are clearly outstretched in *Anoplostoma amphicystum* **sp. nov.** Additional *Anoplostoma* species have been described more recently by Gagarin (2015), Nguyen Vu Thanh & Gagarin (2015), and Li & Guo (2016).

**Type species.** *Anoplostoma viviparum* (Bastian, 1865) Bütschli, 1874

### *Anoplostoma amphicystum* sp. nov.

Figs 10–12; Table 1

**Material examined. Holotype** NIWA 139299, NIWA Stn Z18746, 41.098° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 28 Jul 2016, fine sand, male. **Paratypes** NIWA 139300, two females, same data as for holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet Wellington region, lower North Island, New Zealand.

**Description. Males.** Body relatively stout, tapering towards both extremities, particularly anterior extremity. Cuticle smooth; cervical and somatic setae absent. Cephalic region narrow, not set off by constriction. Six internal labial papillae on labial region; circle of six outer labial setae, 1.1–1.3 cbd long, situated at level of buccal cavity and slightly anterior to four slightly shorter cephalic setae. Amphidial fovea cup-shaped, situated 2.1–2.3 cbd posterior to buccal cavity; amphidial aperture circular or oval, small, 2 µm wide. Buccal cavity with conical cheilostome and cuticularised cheilirhabdions; three cuticularised structures (called 'muniments' by Belogurov & Alekseev (1977) in their description of *A. cuticularia* Belogurov & Alekseev, 1977) at level of anterior third of gymonostome inserted in the inner layer of the endocupola. Gymnostome cylindrical, without teeth, with heavily cuticularised walls, 11 µm deep and 3–4 µm wide. Pharynx muscular, cylindrical, widening slightly towards posterior extremity; ducts of pharyngeal glands opening at base of buccal cavity. Nerve ring located posteriorly to middle of pharynx. Secretory-excretory system not observed. Cardia medium-sized, surrounded by intestinal tissue. Male reproductive system with two opposed and outstretched testes located to the left of intestine. Spicules 2.4 cloacal body diameters long, slender, slightly curved and tapering distally, with central lamella two-thirds along proximal two-thirds. Gubernaculum narrow, almost straight, with small, curved apophyses. Bursal alae indistinct; paired lateroventral spine-like setae, 5 µm long, located ca. one cloacal body diameter posterior to cloaca. Three precloacal caudal glands present (exact location not clear). Tail long, conicocylindrical, with slightly swollen tip bearing two or possibly three short, ca. 2 µm long, setae.

**Females.** Similar to males but tail without short terminal setae; precloacal caudal glands located to the left of intestine, approximately halfway between anus and posterior extremity of posterior ovary. Female reproductive system with two opposed and reflexed ovaries both located to the left of intestine. Eggs, 63–69 × 23–28 µm. Each genital branch with proximal sphincter and large, bladder-like spermatheca, 23–25 × 15–16 µm; sperm not observed in spermatheca. Three pairs of vaginal glands located posteriorly and anteriorly to vulva. Vulva located slightly anterior to mid-body.

**Etymology.** The species name is derived from the Greek *amphis* (= double, on both sides), and *kystis* (= bladder, sac) and refers to the female reproductive system with two bladder-like spermathecae.

**Species diagnosis.** *Anoplostoma amphicystum* **sp. nov.** is characterised by relatively stout body (a = 32–33), outer labial setae 1.1–1.3 cbd long, amphidial fovea situated 2.1–2.3 cbd posterior to buccal cavity, tail 6.6–8.4 cloacal or anal body diameters long, with two or three short terminal setae in males, three precloacal caudal glands, male reproductive system with two

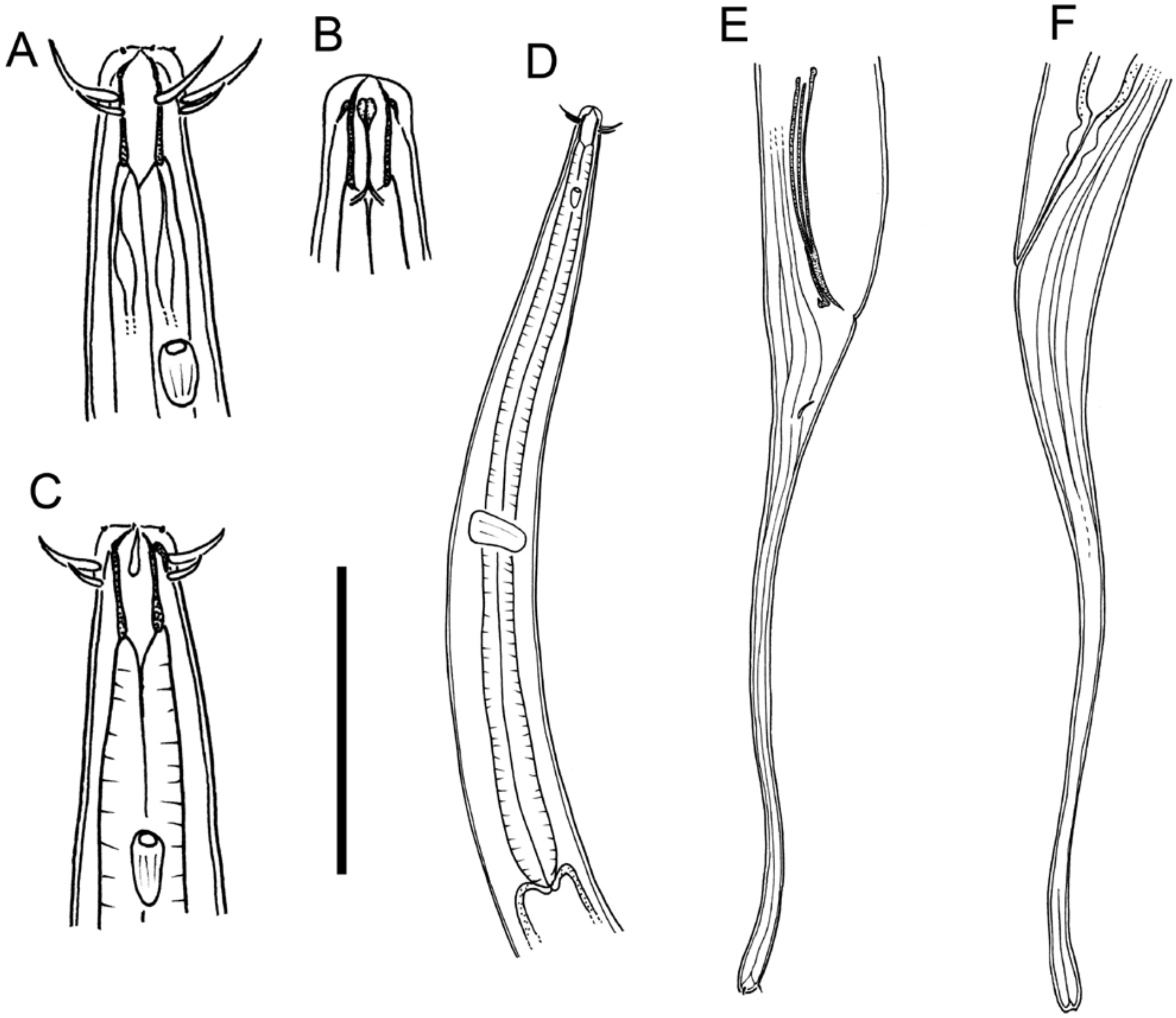



**Figure 10.** *Anoplostoma ampicystum* **sp. nov.**: **A.** Anterior body region of female paratype NIWA 139300; **B.** Female paratype cephalic region NIWA 139300; **C.** Male holotype anterior body region (NIWA 139299); **D.** Female paratype pharyngeal body region NIWA 139300; **E.** Male holotype posterior body region NIWA 139299; **F.** Female paratype posterior body region NIWA 139300. Scale bar: A, B, C = 30 µm; D = 48 µm; E, F = 75 µm.

outstretched testes, slender spicules 2.4 cloacal body diameters long and with central lamella, gubernaculum with small, curved apophyses, indistinct bursal alae, and female reproductive system with large bladder-like spermatheca, three pairs of vaginal glands and vulva slightly anterior to mid-body.

**Differential diagnosis.** *Anoplostoma amphicystum* **sp. nov.** is similar to *A. heterurum* (Cobb, 1914) Kreis, 1934 (Virginia, USA; freshwater), *A. hirtum* Gerlach, 1956 (South Atlantic), *A. subulatum* Gerlach, 1957 (South Atlantic), *A. sunderbanae* Timm, 1967 (Bay of Bengal), and *A. viviparum* (Bastian, 1865) Bütschli, 1874 (North Atlantic) in the length of the tail expressed as ratio c′ and oviparous reproduction (except for *A. viviparum*, which is viviparous). The new species can be differentiated from *A. heterurum* by the ratio of a (32–33 *versus* 35 in *A. heterurum*), ratio of c (8–9 *versus* 11), length of outer labial setae (1.1–1.3 *versus* 1.0 cbd), and presence of short gubernacular apophyses (*versus* no gubernacular apophyses); from *A. hirtum* by the ratio of a (32–33 *versus* 46–47), length of outer labial setae (1.1–1.3 *versus* 2.1 cbd), length of spicules (56 *versus* 65–67 µm), and number of lateroventral setae in cloacal region (one pair *versus* three pairs); from *A. subulatum* by the ratio of a (32–33 *versus* 42), length of outer labial setae (1.1–1.3 *versus* 0.75), and length of spicules (56 *versus* 86–101 µm); and from *A. viviparum* by the shorter body length (<1400 *versus* 1600–2100 µm), length of outer labial setae (1.1–1.3 *versus* 0.8–1.0), and the reproductive strategy (viviparous in *A. viviparum*). The new species is also similar to *A. tumidum* Li & Guo, 2016 but differs from the latter in having a shorter body (1274–1364 *versus* 1503–1739 µm), somewhat shorter tail (c′ = 6.6–8.4 *versus* 8.3–10.4), spicule shape

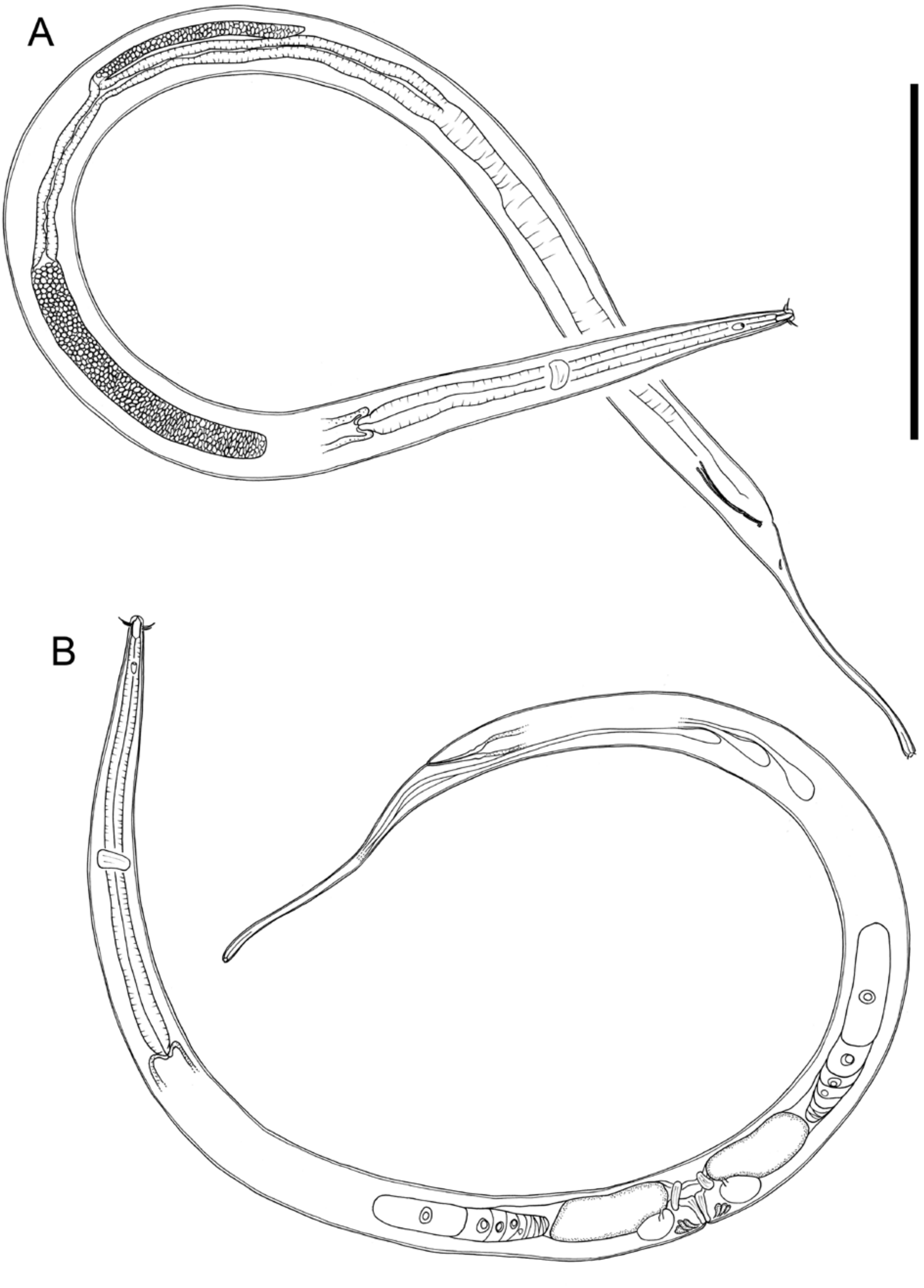



**Figure 11.** *Anoplostoma amphicystum* **sp. nov.**: **A.** Entire male holotype NIWA 139299; **B.** Entire female paratype NIWA 139300. Scale bar = 200 µm.

**Figure 12.** *Anoplostoma amphicystum* **sp. nov.** light micrograph: Vulva and proximal portion of genital branches with spermathecae, female paratype NIWA 139300. Scale bar = 10 μm.

**Table 1.** Morphometrics (μm) of *Anoplostoma amphicystum* **sp. nov.,** given as individual values, or a range of values from several specimens.

| Parameter | Male Holotype | Females Paratypes |
|---|---|---|
| Number of specimens | 1 | 2 |
| L | 1274 | 1328, 1364 |
| a | 33 | 32, 33 |
| b | 5 | 5, 6 |
| c | 8 | 8, 9 |
| c' | 6.6 | 7.3, 8.4 |
| Body diameter at cephalic setae | 8 | 7, 8 |
| Body diameter at amphids | 14 | 12, 13 |
| Length of outer labial setae | 9 | 9–10 |
| Length of cephalic setae | 5 | 4–5 |
| Amphid height | 1 | 2 |
| Amphid width | 2 | 2 |
| Amphid width/cbd (%) | 14 | 14, 15 |
| Amphid from anterior end | 29 | 27, 30 |
| Nerve ring from anterior end | 136 | 136, 139 |
| Nerve ring cbd | 29 | 27, 28 |
| Pharynx length | 242 | 238, 254 |
| Pharyngeal diameter at base | 16 | 15, 17 |
| Pharynx cbd at base | 36 | 34, 37 |
| Maximum body diameter | 39 | 41 |
| Spicule length | 56 | – |
| Gubernacular apophysis length | 16 | – |
| Cloacal/anal body diameter | 23 | 20, 21 |
| Tail length | 153 | 153, 168 |
| V | – | 622, 659 |
| %V | – | 47, 48 |
| Vulval body diameter | – | 38, 41 |

(spicule not swollen distally *versus* swollen distally), and presence of bladder-like spermathecae. In addition to the morphological differences outlined above, *A. amphicystum* **sp. nov.** differs from most species of the genus in the presence of spermatheca, although they have been noted in *A. exceptum* Schulz, 1935 and *A. viviparum* by Rachor (1969).

**Sequence data.** Partial SSU rDNA sequence (752 bp; Genbank OK317192).

**ZooBank registration.** *Anoplostoma amphicystum* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:F150D110-4BAA-48CE-815C-3EB11928E339.

## Family **Enchelidiidae** Filipjev, 1918

Enchelidiidae Filipjev, 1918: 144–109, fig. 28, table 4, 5.

**Diagnosis.** Buccal cavity with three unequal teeth, of which the dominant can be extended at least in some genera. Right ventrosublateral tooth usually larger than the left ventrosublateral. Sexual dimorphisms in the shape of the buccal cavity and pharynx in the organs concerned are reduced in males of some genera. Amphidial opening in part non-spiral and in part dorsally spiral. Outline of pharynx crenate. Females didelphic-amphidelphic. Demanian system always absent. Males with or without precloacal supplements (modified from Smol *et al.* (2014)).

**Type genus.** *Enchelidium* Ehrenberg, 1836

## Genus *Ledovitia* Filipjev, 1927

*Ledovitia* Filipjev, 1927: 180, pl. 2 fig. 62c, d; pl. 6 fig. 62a, b.

**Diagnosis.** Buccal cavity divided into two or three parts by several rows of denticles: three teeth, right ventrosublateral largest and acute. Pharynx without posterior bulb. Males with well-developed precloacal supplements, cup-shaped and cuticularised, with or without winged bases. Gubernaculum with or without apophyes. Caudal glands present (modified from Smol *et al.* (2014)).

**Remarks.** The genus was revised by Wieser (1953b) and Belogurov *et al.* (1983). Hong & Lee (2014) provided a key to the eight valid species of the genus known before the present study.

**Type species.** *Ledovitia hirsuta* Filipjev, 1927

### *Ledovitia gutturosa* sp. nov. Figs 13–14; Table 2

**Material examined. Holotype** NIWA 154866, NIWA Stn Z18746, 41.102° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 9 Dec 2019, fine sand, male. **Paratypes** NIWA 154867, two males and three females, same data as for holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Males.** Body cylindrical, tapering strongly towards anterior extremity but only slightly towards posterior extremity. Cuticle smooth. Fine, long cervical setae present, arranged irregularly, not in circles; cuticularised ring and short duct present at base of each cervical seta. Somatic setae absent. Cephalic region demarcated by slight constriction at level of buccal cavity. Lips short, thin, each bearing a single internal labial papilla at base. Six outer labial setae and four cephalic setae similar in length and in single circle, always shorter than cervical setae. Amphidial fovea loop-shaped, bent ventrally, outline not cuticularised; amphidial aperture kidney-shaped; amphidial aperture narrow, located at top of amphidial fovea loop. Buccal cavity with heavily cuticularised walls, not surrounded by pharyngeal tissue, 10 µm deep and up to 5–6 µm wide, divided into three compartments by two transverse rings of small denticles. Right ventrosublateral tooth acute and conspicuously larger than left ventrosublateral and dorsal teeth; the latter sometimes difficult to discern depending on specimen orientation. Pharynx muscular, cylindrical; anterior-most portion with conspicuously widened and cuticularised lumen to about half of distance between anterior extremity and nerve ring. Nerve ring located slightly less than halfway down length of pharynx. Secretory-excretory system not observed. Cardia medium-sized, surrounded by intestinal tissue. Reproductive system with two opposed and outstretched testes both located to the right of intestine. Sperm cells globular, 12–14 × 10–11 µm. Spicules arcuate, strongly cuticularised, with central cuticularised lamella extending from the outer to the inner spicule wall and weakly defined capitulum. Gubernaculum with bent apophyses and lateral crurae consisting of tapering projections parallel to the spicules. Two large, strongly cuticularised precloacal supplements present, each consisting of a central cup-shaped portion flanked by two wing-shaped structures each 5–10 µm long; posterior-most supplement located 109–135 µm from cloaca, anterior-most supplement located 79–93 µm from posterior-most supplement. Pair of precloacal setae present ventrally. Three precloacal caudal glands present, of varying position relative to intestine, with single opening terminally. Tail conicocylindrical, with slightly swollen distal portion, with two rows of subventral setae and six subterminal setae 6–8 µm long.

**Females.** Similar to males but with longer body, slightly higher c ratio, smaller amphids, longer tail, wider cephalic region, and tail with fewer setae. Reproductive system with two opposed and reflexed ovaries both located to the right of intestine, sphincter muscle sometimes visible at base of each genital branch. Vagina short, vaginal glands apparently absent. Eggs, 111–203 × 43–66 µm. Vulva located at or near mid-body.

**Etymology.** The species name is derived from the Latin *gutturosus* (= with enlarged throat) and refers to the structure of the anterior half of the pharynx with wide, distinctly cuticularised lumen.

**Species diagnosis.** *Ledovitia gutturosa* **sp. nov.** is characterised by outer labial and cephalic setae of similar length, cervical setae 9–16 µm long, loop-shaped amphidial fovea and kidney-shaped amphidial aperture, buccal cavity separated into three portions by two transverse bands of small denticles, pharyngeal lumen conspicuously widened and cuticularised anteriorly and caudal glands located well anterior to cloaca; male with strongly cuticularised arcuate spicules 52–76 µm long, gubernacular apophyses 10–14 µm long, two strongly cuticularised precloacal supplements with central cup-shaped portion flanked by two wing-shaped structures, pair of precloacal setae, and conicocylindrical tail with six subterminal setae.

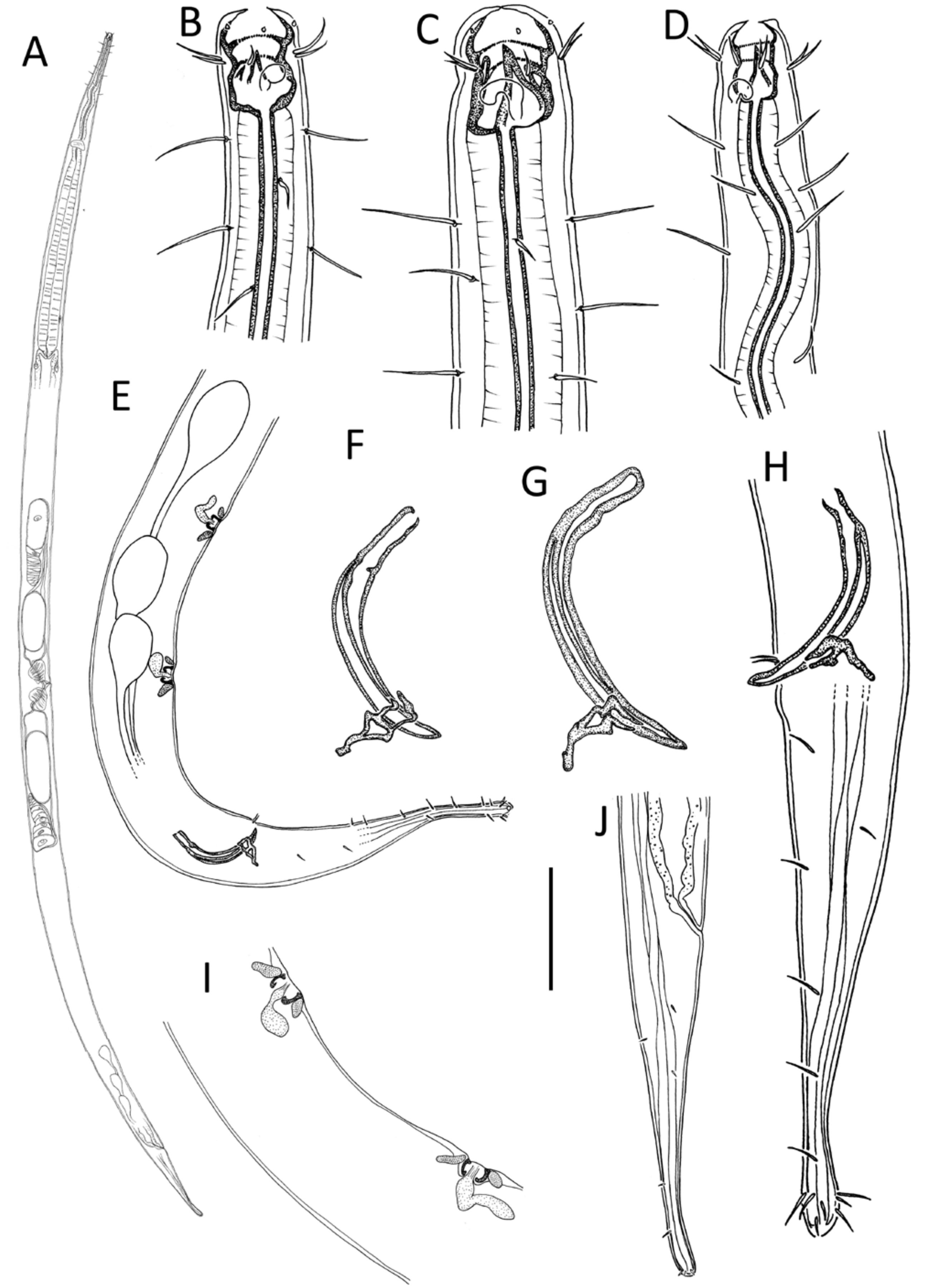



**Figure 13.** *Ledovitia gutturosa* **sp. nov**.: **A.** Entire female paratype NIWA 154867; **B–C.** Female paratype cephalic region NIWA 154867; **D.** Male holotype cephalic region NIWA 154866; **E.** Male holotype posterior body region NIWA 154866; **F.** Spicular apparatus, male holotype NIWA 154866; **G.** Spicular apparatus, male paratype NIWA 154867; **H.** Male paratype posterior body region NIWA 154867; **I.** Precloacal supplements, male holotype NIWA 154867; **J.** Female paratype posterior body region NIWA 154867. Scale bar: A = 350 µm; B = 20 µm; C = 18 µm; D = 15 µm; E = 65 µm; F, G = 25 µm; H = 28 µm; I = 38 µm; J = 75 µm.

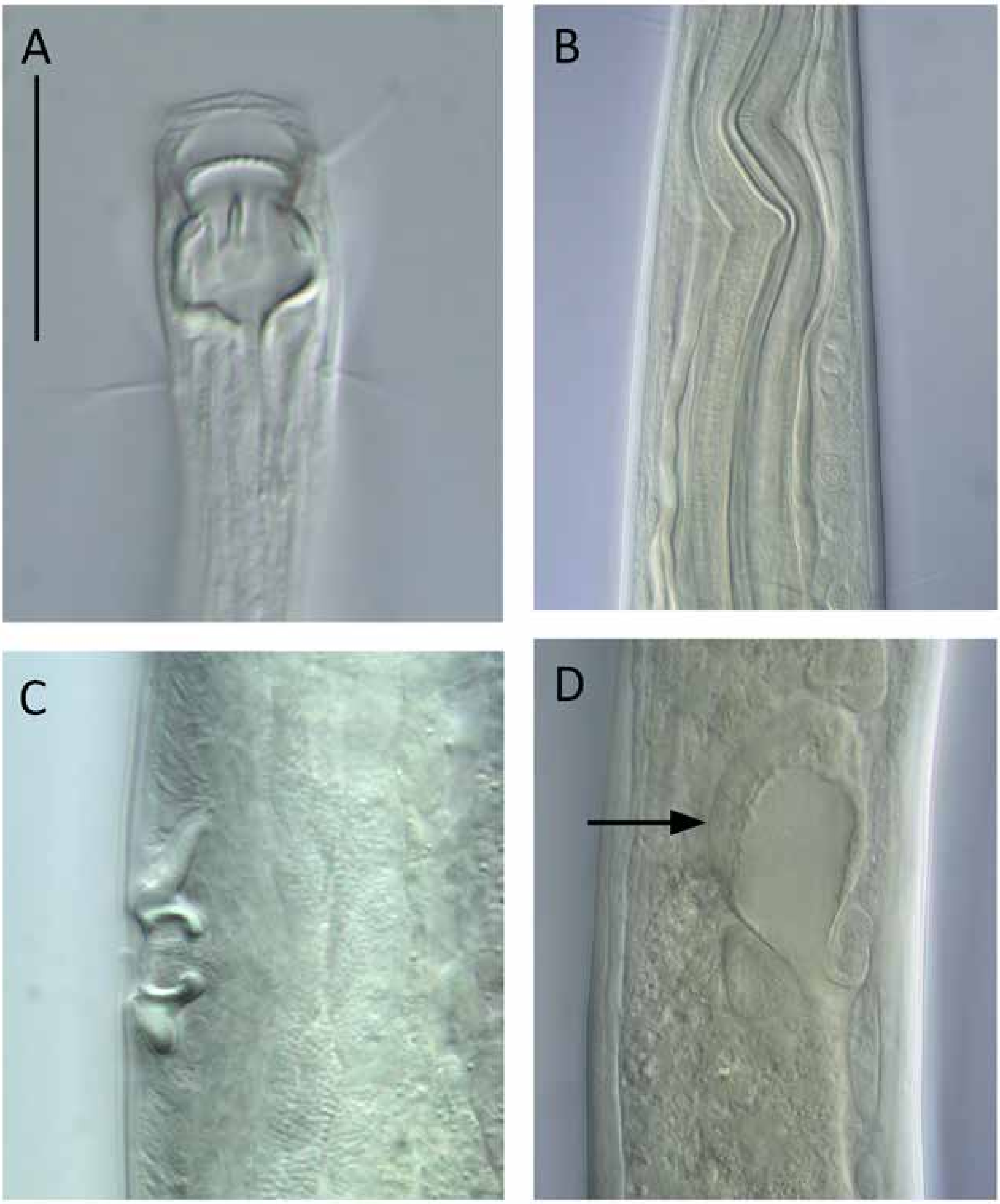



**Figure 14.** *Ledovitia gutturosa* **sp. nov.**, light micrographs: **A.** Female paratype cephalic region showing buccal cavity NIWA 154867; **B.** Anterior portion of pharynx showing expanded and cuticularised pharyngeal lumen, female paratype NIWA 154867; **C.** Precloacal supplement, male holotype NIWA 154866; **D.** Caudal gland and duct below, male holotype NIWA 154867. Arrow shows position of caudal gland. Scale bar: A = 20 µm; B = 50 µm; C = 130 µm; D = 40 µm.

**Differential diagnosis.** *Ledovitia gutturosa* **sp. nov.** is most similar to *L. pharetrata* Wieser, 1953b (Chilean coast) in body length, ratios of a, b, c and c', roughly equal outer labial and cephalic setae, structure of the spicular apparatus, presence of two precloacal setae, presence of caudal setae, and tail length. The new species, however, is clearly distinct from *L. pharetrata* in the position of the caudal glands, which are located posterior to the cloaca in *L. pharetrata* but well anterior to the cloaca in *L. gutturosa* **sp. nov.** Wieser's (1953b) observations on the position of the caudal glands in *L. pharetrata* are considered credible as he described other closely related species of the same family with caudal glands located well anterior to the cloaca. *Ledovitia gutturosa* **sp. nov.** is also characterised by vulva located slightly more posteriorly (%V = 49–54 *versus* 41–48 in *L. pharetrata*), shorter spicules (52–76 *versus* ca. 100 µm in *L. pharetrata* as measured along the arc), and shorter cervical setae (9–16 *versus* 18 µm in *L. pharetrata*). The new species is also similar to *L. brevis* Hong & Lee, 2014 (Korean coast) in having roughly equal outer labial and cephalic setae, two pre-cloacal setae, and caudal setae in males. The new species differs from *L. brevis* in having higher c ratios (13–17 *versus* 11 in *L. brevis*), longer spicules (52–76 *versus* 39–41 µm in *L. brevis*), and longer gubernacular apophyses (10–14 *versus* 4 in *L. brevis*). The structure of the spicules also differs between the two species: a central lamella is present in the spicules of *L. gutturosa* **sp. nov.** but not in *L. brevis*, and the gubernaculum in *L. gutturosa* **sp. nov.** has a more complex structure than in *L. brevis*. Finally, we note that the thickly cuticularised pharyngeal lumen observed in *L. gutturosa* **sp. nov.** does not appear to have been observed in other species of the genus. It is possible, however, that this feature is present in other species but was not included in the descriptions.

**ZooBank registration.** *Ledovitia gutturosa* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:DD0FE8DD-52E4-4B25-BCAC-48E6A1049F88.

**Table 2.** Morphometrics (µm) of *Ledovitia gutturosa* **sp. nov.**, given as individual values, or a range of values from several specimens.

| Parameter | Males | | Females |
|---|---|---|---|
| | Holotype | Paratypes | Paratypes |
| Number of specimens | 1 | 2 | 3 |
| L | 1762 | 1846, 1868 | 2486–3344 |
| a | 45 | 32, 35 | 36–37 |
| b | 4 | 4 | 4 |
| c | 15 | 13, 14 | 16–17 |
| c' | 3.8 | 2.6, 4.2 | 4.4–5.1 |
| Body diameter at cephalic setae | 9 | 9, 10 | 14–17 |
| Body diameter at amphids | 10 | 10, 12 | 14–18 |
| Length of outer labial setae | 8–9 | 9–10 | 6–9 |
| Length of cephalic setae | 8–9 | 8–10 | 8–10 |
| Length of cervical setae | 9–13 | 9–16 | 10–15 |
| Amphidial fovea height | 7 | 6, 7 | 4–7 |
| Amphidial fovea width | 5 | 5, 6 | 4–7 |
| Amphid width/cbd (%) | 50 | 50 | 29–39 |
| Amphid from anterior end | 7 | 6, 7 | 6–10 |
| Nerve ring from anterior end | 167 | 192, 241 | 215–318 |
| Nerve ring cbd | 34 | 26, 38 | 40–57 |
| Pharynx length | 408 | 453, 495 | 574–868 |
| Pharyngeal diameter at base | 18 | 21, 27 | 35–58 |
| Pharynx cbd at base | 37 | 44, 49 | 56–80 |
| Maximum body diameter | 39 | 53, 57 | 67–91 |
| Spicule length | 52 | 55, 76 | – |
| Gubernacular apophysis length | 10 | 11, 14 | – |
| Cloacal/anal body diameter | 31 | 32, 35 | 31–48 |
| Tail length | 118 | 134, 144 | 146–213 |
| V | – | – | 1236–1805 |
| %V | – | – | 49–54 |
| Vulval body diameter | – | – | 66–89 |

## Family **Oncholaimidae** Filipjev, 1916
## Subfamily **Oncholaimellinae** De Coninck, 1965

Oncholaimellinae De Coninck, 1965: 660, fig. 470.

**Diagnosis** Cuticle smooth. Buccal cavity free; right ventrosublateral tooth always larger than other teeth, if the other teeth occur at all. Females didelphic-amphidelphic, rarely monodelphic-prodelphic. Demanian system absent or present and, if present, simple. Bursa present or absent (after Smol *et al.* (2014)).

**Type genus.** *Oncholaimellus* de Man, 1890

## Genus ***Viscosia*** de Man, 1890

*Viscosia* de Man, 1890: 184, pl. 5, fig. 9.
*Meroviscosia* Kreis, 1932: 52.
*Mononcholaimus* Kreis, 1924: 13–15, fig. 8.

**Diagnosis** Buccal cavity large, right ventrosublateral tooth usually largest. Females didelphic-amphidelphic with reflexed ovaries. Spicules short. Gubernaculum absent. Demanian system present and simple, consisting of prolongation of the ovary at the reflexed point that connects it with intestine through the osmosium (after Smol *et al.* (2014)).

**Remarks.** *Viscosia* is a diverse genus containing 87 valid species (Smol *et al.* 2014). It occurs in marine, brackish, and freshwater sediments. The most recent species descriptions were provided by Gagarin (2020a) and Nguyen Vu Thanh & Gagarin (2013).

**Type species.** *Viscosia viscosa* (Bastian, 1865) de Man, 1890

***Viscosia dossena* sp. nov.** Figs 15–18; Table 3

**Material examined. Holotype** NIWA 139267, NIWA Stn Z18745, 41.093° S, 174.876° E, Pāuatahanui Inlet near Camborne Walkway, upper intertidal, 28 Jul 2016, gravelly sand, male. **Paratypes** NIWA 139268, two male and four females, same data as holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Males.** Body relatively stout, tapering slightly towards both extremities. Cuticle smooth, often with adhering diatoms of various sizes. Somatic setae 3–4 µm long, sparse, present only in anterior-most portion of pharyngeal region. Cephalic region demarcated by slight constriction and basal groove. Six lips present, each bearing a single internal labial papilla. Six outer labial setae and four slightly longer cephalic setae in single circle. Amphidial fovea cup-shaped, slightly posterior to circle of outer labial and cephalic setae; amphidial aperture narrow, up to 2 µm wide, located at level of basal groove. Buccal cavity heavily cuticularised, 31–35 µm deep and 14–15 µm wide. Left ventrosublateral and dorsal teeth single-tipped and similar in size, smaller than right ventrosublateral tooth; all three teeth hollow and with subterminal ducts connected to pharyngeal glands. Cuticularised wall of buccal cavity connected anteriorly to cuticle by cuticularised endocupola with simple stomatoidal ring. Pharynx muscular, cylindrical, widening slightly towards posterior extremity. Nerve ring located approximately halfway down length of pharynx. Secretory-excretory system present; excretory pore located slightly posterior to nerve ring. Long duct with well-defined and relatively thick walls extends from excretory pore down to at least middle of body on right side of pharynx and intestine, becoming indistinct posteriorly. Ventral gland not observed. Cardia medium-sized, surrounded by intestinal tissue. Reproductive system with two opposed and outstretched testes located to the right of intestine. Spicules short, straight, slightly swollen proximally and tapering distally. Gubernaculum absent. Two subventral transverse row of short setae surrounding anterior half of cloaca; first anterior-most row with six setae, second row with five slightly smaller setae. One pair of stout subventral papillae also present immediately anterior to cloaca, and one pair of short setae immediately posterior to cloaca. Three precloacal caudal glands present, of varying position relative to intestine, with single opening terminally. Tail conical, with slightly swollen distal portion, with several short setae mainly located subventrally

**Females.** Similar to males but with slightly smaller amphids, several anal glands, and tail without setae. Reproductive system with two opposed and reflexed ovaries both located to the right of intestine. Eggs, 63–65 × 84–94 µm. Demanian system typical of the genus, consisting of a pocket off each ovary at point of flexure; distally, each pocket is surrounded by sphincter muscle and connected to several small glands, and joins to intestine through osmosium. Vulva located at mid-body.

**Etymology.** The species name is derived from the Latin *dossenus* (= jester) and refers to the appearance of the lips resembling a jester hat, and the unusual appearance of this species resulting from adhering diatoms on the cuticle.

**Species diagnosis.** *Viscosia dossena* **sp. nov.** is characterised by relatively stout body (a = 21–26), outer labial setae 2–3 µm long and cephalic setae 4–6 µm long, amphidial fovea 31–35% cbd wide in males and 19–30% cbd in females, secretory-excretory system characterised by long duct with conspicuously thickened walls extending to at least mid-body on right side of digestive system and apparently without ventral gland, males with two transverse subventral rows of setae surrounding anterior half of cloaca, and with one pair of subventral papillae immediately anterior to cloaca and one pair of short setae immediately posterior to cloaca, pockets of demanian system each with several small glands and sphincter muscle distally, all three caudal glands located anterior to cloaca/anus, and short conical tail.

**Differential diagnosis.** *Viscosia dossena* **sp. nov.** can be differentiated from all other species of the genus by the structure of the secretory-excretory system, which is characterised by the apparent lack of ventral gland, and a long duct with thickened and well-defined walls extending to at least half of body length on the right side of the body. When present, the secretory-excretory system in other species of the genus is always characterised by a more-or-less defined ventral gland usually located slightly posterior to pharynx (and always in anterior half of body), and the walls of the duct connecting the ventral gland to the excretory pore are never conspicuously thickened. The new species also differs from most other species of the genus by its stout body shape (a = 21–26). Other species of the genus with a ratio of a lower than 30 are: *V. brachylaimoides* Chitwood, 1937 (North Atlantic; a = 21–57), *V. crassa* Kreis, 1934 (Malay Archipelago; a = 20–21), *V. franzii* Boucher, 1977 (North Sea; a = 27–64), *V. floridana* Keppner, 1987 (North Atlantic; a = 25–28), *V. papillatula* Lorenzen, 1981 (North Atlantic; a = 22–35), *V. rectangula* Wieser, 1953b (Chilean coast; a = 22–28),

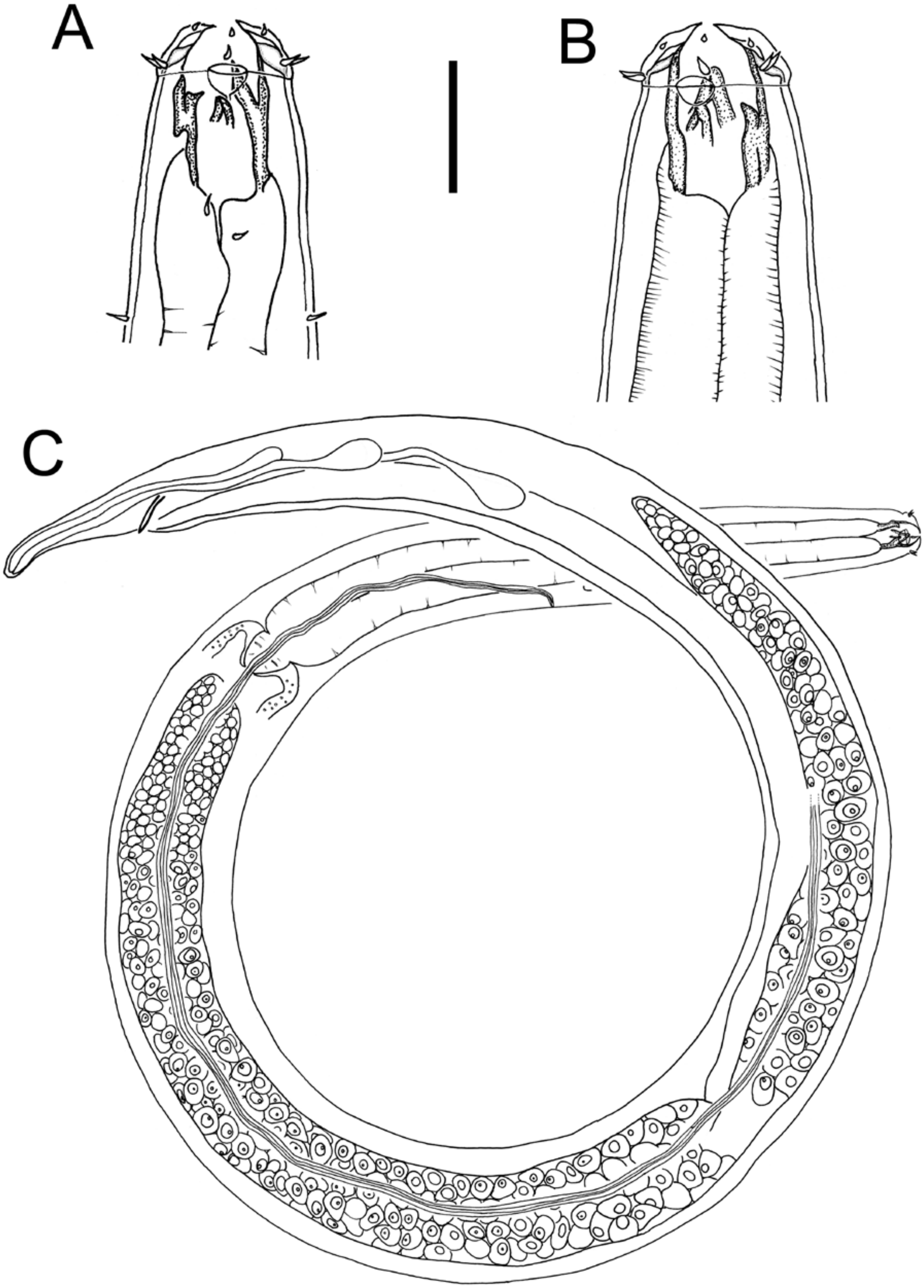



**Figure 15.** *Viscosia dossena* **sp. nov.**: **A.** Male holotype cephalic region NIWA 139267; **B.** Female paratype cephalic region NIWA 139268; **C.** Entire male paratype NIWA 139268. Scale bar: A, B = 25 μm; C = 85 μm.

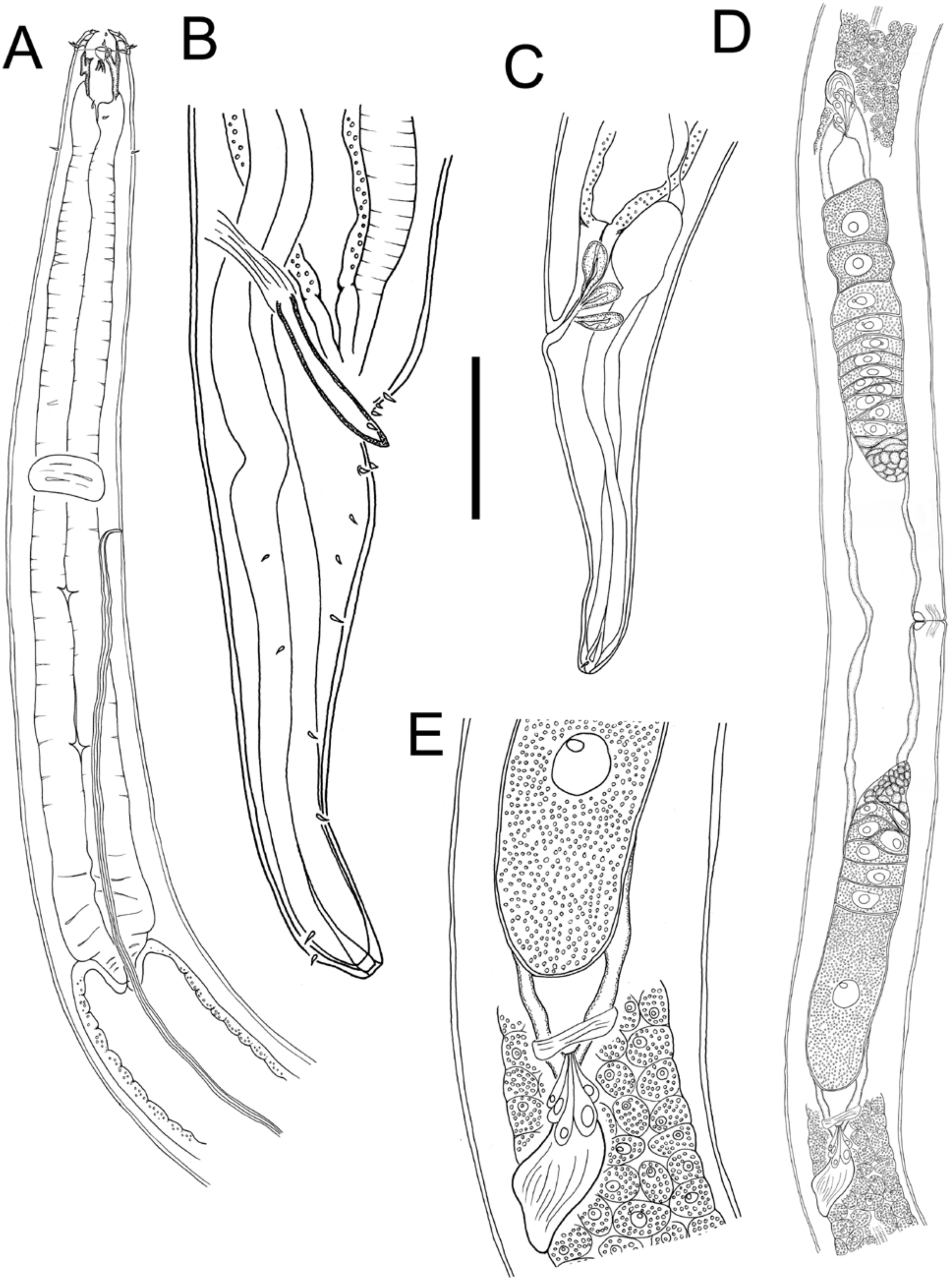



**Figure 16.** *Viscosia dossena* **sp. nov.**: **A.** Male holotype anterior body region NIWA 139267; **B.** Male paratype posterior body region NIWA 139268; **C.** Female paratype posterior body region NIWA 139268; **D.** Female paratype reproductive system NIWA 139268; **E.** Detail of demanian system, female paratype NIWA 139268. Scale bar: A = 75 µm; B = 30 µm; C, E = 50 µm; D = 115 µm.

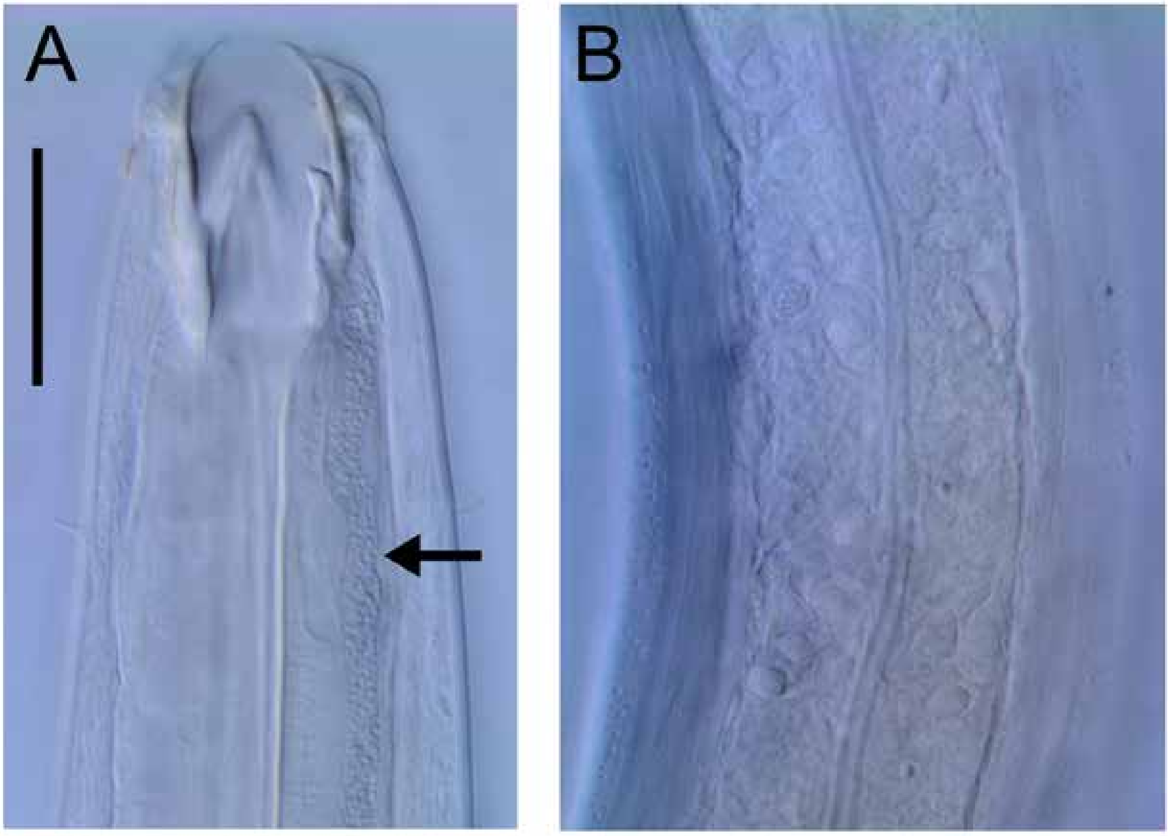



**Figure 17.** *Viscosia dossena* **sp. nov.**, light micrographs: **A.** Lateral view of male paratype cephalic region NIWA 139268; **B.** Lateral view of male paratype mid-body region showing lateral chord and duct of secretory-excretory system NIWA 139268. Arrow shows location of dorsal pharyngeal gland duct. Scale bar = 25 µm.

and *V. wieseri* Mawson, 1958 (Southern Ocean; a = 29–46). Note that although *V. brachylaimoides* and *V. franzii* are both currently classified within the genus *Viscosia*, they are both characterised by a buccal cavity with a large left ventrosublateral tooth instead of large right ventrosublateral tooth, indicating that these species do not belong to *Viscosia*. Because of this conflicting trait, and the lack of information on the structure of the female reproductive system for these two species, we consider both to be *incertae sedis* for the time being. *Viscosia dossena* **sp. nov.** differs from *V. crassa* and *V. papillatula* by the position of the vulva (52–53% from anterior in *V. dossena* **sp. nov.** *versus* 58–59% and 67 % in *V. crassa* and *V. papillatula*, respectively), and length of the cephalic setae (4–6 µm in *V. dossena* **sp. nov.** *versus* $\leq$2 µm in *V. crassa* and *V. papillatula*), from *V. floridana* by the length of outer labial sensilla (setose in *V. dossena* **sp. nov.** *versus* papillose in *V. floridana*), from *V. rectangula* by the shape of the tail (clavate tip in *V. dossena* **sp. nov.** *versus* tapering in *V. rectangula*) and depth of buccal cavity (31–35 µm deep in *V. dossena* **sp. nov.** *versus* 60 µm deep in *V. rectangula*), and from *V. wieseri* by the shape of the tail (conical in *V. dossena* **sp. nov.** *versus* conicocylindrical in *V. wieseri*).

**Remarks.** The only other record of an oncholaimid nematode with pennate diatom ectocommensals was provided for *Oncholaimus vulgaris* Bastian, 1865 by Bastian (1865). Records of diatoms on the cuticle were also provided for *Spirinia parasitifera* (Bastian, 1865) by Bastian (1865), *Desmodora pontica* Filipjev, 1922 and *Metachromadora onyxoides* Chitwood, 1936 by Tietjen (1971), and *Croconema ovigerum* (Ott, 1976) by Ott *et al.* (1991) (order Desmodorida). It is unclear whether the diatoms are used as a food source by *Viscosia dossena* **sp. nov.** Observations of gut contents revealed the presence of amorphous green material, presumably of algal origin, but no diatom frustules were seen. Oncholaimids are generally regarded as facultative predators that may feed on other nematodes, protozoans, animal carcasses, or detritus (Moens & Vincx 1997; Moens *et al.* 2005; Leduc 2009).

The structure of the secretory-excretory system in *Viscosia dossena* **sp. nov**. is unusual and as far as we are aware it has not been described previously for any other nematode species. It is unclear what the function of a duct extending at least halfway down the body length (always on right side of intestine) may be. Secretory-excretory gland(s) are presumably present, but they

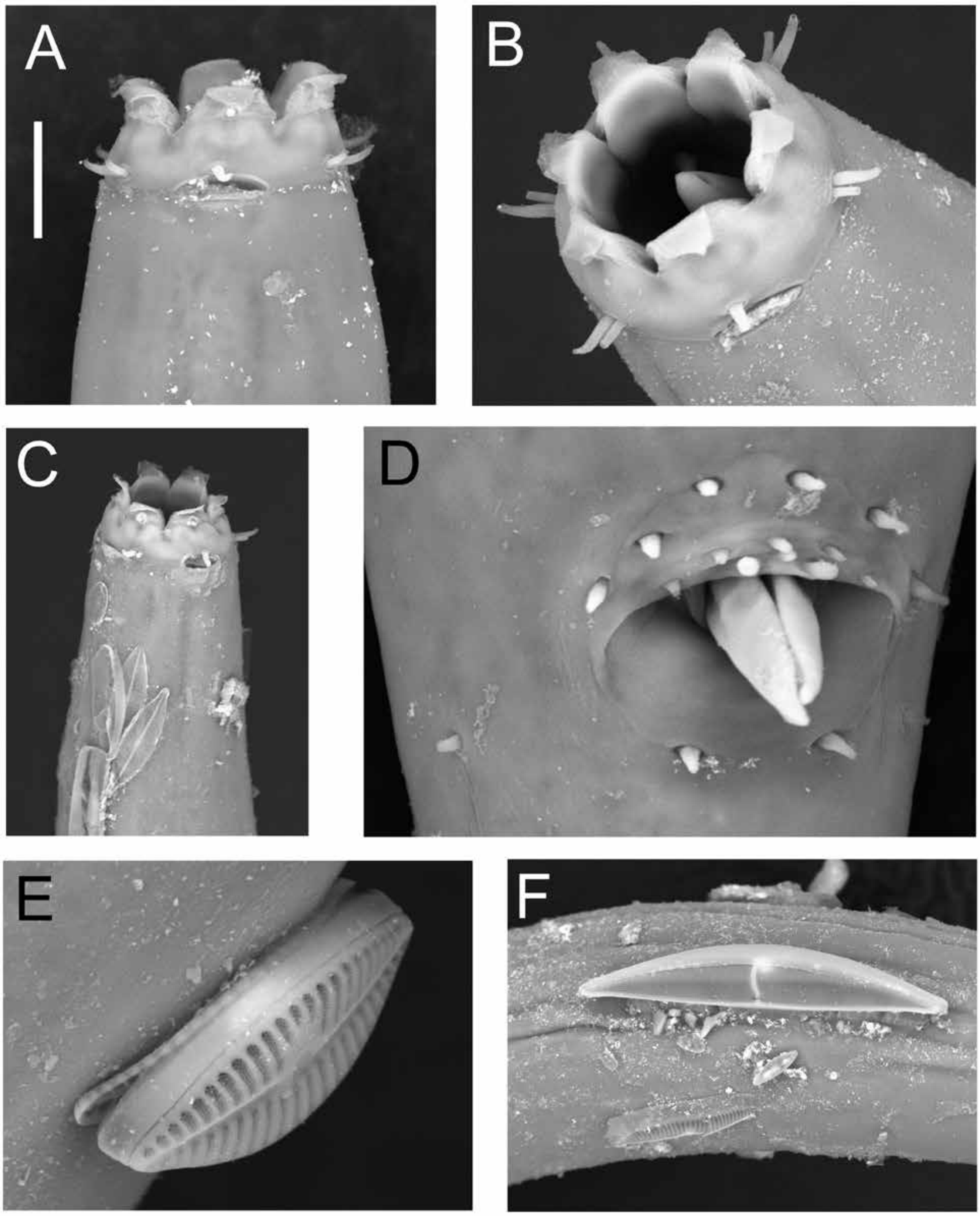



**Figure 18.** *Viscosia dossena* **sp. nov.**, scanning electron micrographs: **A.** Lateral view of male cephalic region; **B.** Subterminal view of male cephalic region, showing mouth opening and tip of right ventrosublateral tooth; **C.** Anterior body region of male, showing remnants of adhering diatoms; **D.** Ventral view of cloaca showing protruding spicules and arrangement of pre- and postcloacal sensilla; **E–F.** Diatoms adhering to the cuticle of main body region. Scale bar: A = 10 µm; B = 8 µm; C = 18 µm; D, E = 5 µm; F = 22 µm.

could not be detected despite careful observations.

**Sequence data.** Partial SSU rDNA (1571 bp; Genbank OK317193) and D2–D3 of LSU rDNA (706 bp; Genbank OK317218).

**ZooBank registration.** *Viscosia dossena* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:9A68BD1A-189E-48AE-9C17-E56D0E94F8F1.

**Table 3.** Morphometrics (µm) of *Viscosia dossena* **sp. nov.**, given as individual values, or a range of values from several specimens.

| Parameter | Males | | Females |
|---|---|---|---|
| | Holotype | Paratypes | Paratypes |
| Number of specimens | 1 | 2 | 3 |
| L | 1759 | 2038, 2048 | 2106–2249 |
| a | 23 | 24, 25 | 21–26 |
| b | 6 | 5, 6 | 5 |
| c | 19 | 19, 20 | 20–22 |
| c' | 3.0 | 3.0 | 3.0–3.2 |
| Body diameter at cephalic setae | 25 | 25, 27 | 28–30 |
| Body diameter at amphids | 26 | 26, 27 | 30–32 |
| Length of outer labial setae | 3 | 3 | 2–3 |
| Length of cephalic setae | 5–6 | 4–6 | 4–6 |
| Amphid height | 6 | 6, 7 | 5–6 |
| Amphid width | 8 | 9 | 6–9 |
| Amphid width/cbd (%) | 31 | 33, 35 | 19–30 |
| Amphid from anterior end | 7 | 7, 9 | 8–10 |
| Nerve ring from anterior end | 192 | 206, 213 | 210–217 |
| Nerve ring cbd | 54 | 63, 71 | 62–69 |
| Excretory pore from anterior end | 230 | 251, 255 | 248–260 |
| Pharynx length | 282 | 420, 432 | 453–474 |
| Pharyngeal diameter at base | 46 | 47, 50 | 53–56 |
| Pharynx cbd at base | 65 | 47, 50 | 74–82 |
| Maximum body diameter | 75 | 82, 85 | 83–105 |
| Spicule length | 27 | 32, 33 | – |
| Cloacal/anal body diameter | 30 | 33, 35 | 32–35 |
| Tail length | 91 | 100, 106 | 101–108 |
| V | – | – | 1090–1189 |
| %V | – | – | 52–53 |
| Vulval body diameter | – | – | 83–99 |

## Family **Oxystominidae** Chitwood, 1935
## Subfamily **Oxystomininae** Chitwood, 1935

Oxystomininae Chitwood, 1935: 53.

**Diagnosis** Only dorsolateral orthometanemes. Ventral gland present and confined within the pharyngeal region. Females monodelphic-opisthodelphic. Caudal glands extend into the precaudal region (from Smol *et al.* (2014)).

**Type genus.** *Oxystomina* Filipjev, 1921

## Genus ***Litinium*** Cobb, 1920

*Litinium* Cobb, 1920: 234, fig. 8.

**Diagnosis.** Circles of six inner and six outer labial setae situated close together on the anterior end, subapically, with a circle of four cephalic setae posterior to the circles of inner and outer labial setae. Amphidial fovea situated between the circles of the outer labial and cephalic setae. Amphidial fovea varies in shape between species and may differ in males and females of the same species: may be ovoid with an anterior round aperture, horseshoe-like or crescent contoured or more complex. An only posterior antidromously reflexed ovary present; vulva shifted anteriorly. Tail never clavate, more-or-less short, cylindrical or occasionally conical, with rounded tip; terminal caudal capsule absent or weakly developed (after Tchesunov *et al.* (2014c)).

**Remarks.** *Litinium* was most recently revised by Tchesunov *et al.* (2014c). Two additional species were subsequently described by Yu & Xu (2018) and Martelli *et al.* (2017). The latter authors list 17 valid species in the genus but did not include the species described by Yu & Xu (2018). Another *Litinium* species was recently described from the Kermadec Trench by Leduc & Zhao (2021).

**Type species.** *Litinium aequale* Cobb, 1920

### ***Litinium ankistronidum*** **sp. nov.**

Figs 19–20; Table 4

**Material examined. Holotype** NIWA 154870, NIWA Stn Z19170, 41.102° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 27 Jul 2020, fine sand, male. **Paratypes** NIWA 154871, three females, same data as for holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Males.** Body long, tapering slightly towards anterior extremity. Cuticle smooth, without ornamentation, 1.25–1.5 µm thick throughout entire body. Somatic setae absent, except on tail of some specimens. Cephalic region demarcated by very slight constriction at level of amphidial fovea. Setose internal and outer labial sensilla in separate circles close to each other and four slightly longer cephalic setae, 0.6–0.7 cbd long, situated far posteriorly ca. 1.4–1.6 body diameters at level of amphids from posterior edge of amphids. Amphidial fovea located immediately posterior to outer labial setae, ovoid, with lightly cuticularised outline; amphidial aperture circular, ca. 2.5 µm in diameter, located in upper half of amphidial fovea. Buccal cavity narrow, cylindrical, not cuticularised and without armature. Pharynx muscular, cylindrical, surrounding

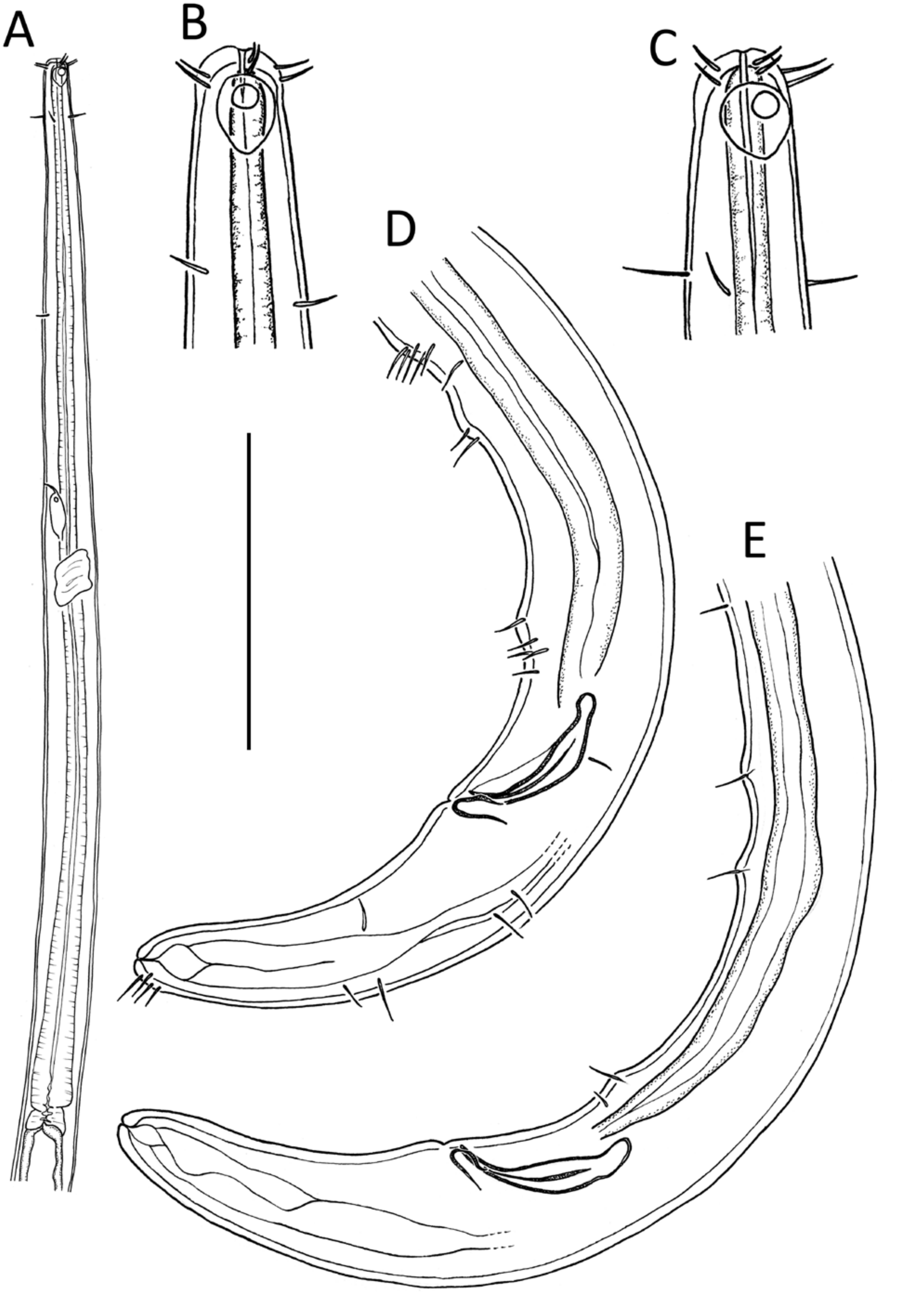



**Figure 19.** *Litinium ankistronidum* **sp. nov.**, holotype male NIWA 154870: **A.** Pharyngeal region, male paratype NIWA 154871; **B.** Cephalic region, male paratype NIWA 154871; **C.** Cephalic region, male holotype NIWA 154870; **D.** Posterior body region, male holotype NIWA 154870; **E.** Posterior body region, male paratype NIWA 154871. Scale bar: A = 100 µm; B, C = 25 µm; D, E = 38 µm.

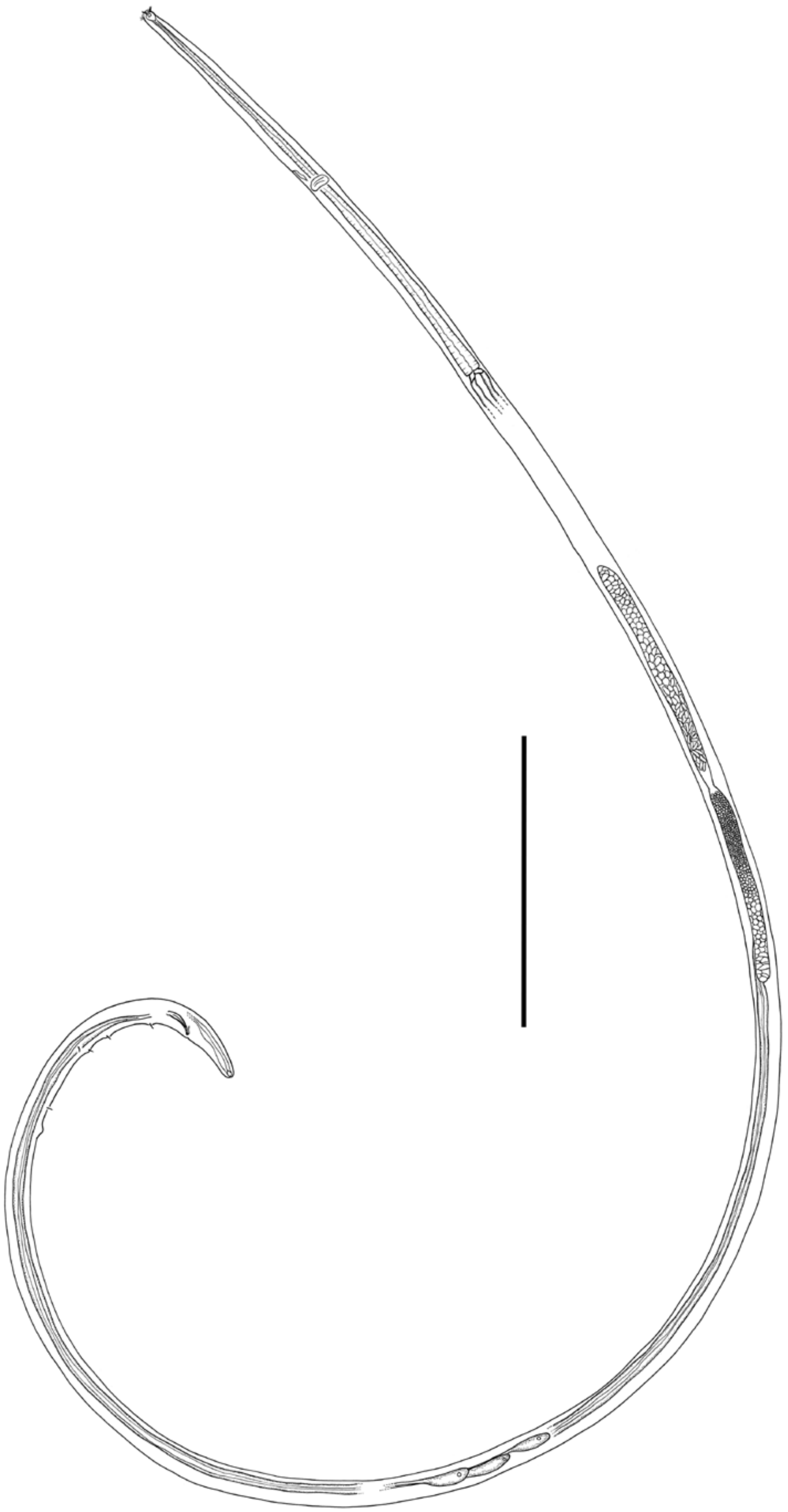


**Figure 20.** *Litinium ankistronidum* **sp. nov.**, entire male paratype NIWA 154871. Scale bar = 200 µm.

posterior portion of buccal cavity, widening gradually towards posterior extremity but not forming true bulb. Nerve ring located approximately halfway down length of pharynx or slightly anterior to halfway. Secretory-excretory system present; excretory pore and ampulla located slightly anterior to nerve ring; ventral gland not observed. Cardia well-developed, not surrounded by intestinal tissue. Reproductive system with two opposed and outstretched testes; anterior testis located to the right of intestine, posterior testis located to the right or left of intestine. Mature sperm in anterior testis elongated, 8–14 × 2–4 µm; mature sperm in posterior testis smaller, globular, 1.4 × 1.5–1.6 µm. Spicules short, 1.3 cloacal body diameters long, slightly arcuate, with lamella extending ca. three-quarters of spicule length from distal end; pointed distal end and rounded capitulum. Gubernaculum consisting of two detached u-shaped lateral pieces (crurae), median portion of gubernaculum (corpus and cuneus) not visible. Three or four precloacal supplements consisting of cuticular swellings each with an internal duct; the first two posterior-most supplements located 26–32 µm apart, third supplement located 12–17 µm further anteriorly, and when present, fourth supplement located 65 µm from third supplement. Single or multiple setae, 3–4 µm long, associated with each precloacal supplement. Three precloacal caudal glands present, about halfway between cloaca and posterior edge of posterior testis, of varying position relative to intestine, with single opening at tail tip. Tail conical, gradually tapering and with rounded tip; setae sometimes present subdorsally and sublaterally, 3–4 µm long.

**Table 4.** Morphometrics (µm) of *Litinium ankistronidum* **sp. nov.**, given as individual values, or a range of values from several specimens.

| Parameter | Male Holotype | Females Paratypes |
|---|---|---|
| Number of specimens | 1 | 3 |
| L | 2022 | 1895–2030 |
| a | 106 | 100–103 |
| b | 6 | 6 |
| c | 46 | 39–43 |
| c' | 2.4 | 2.4–2.7 |
| Body diameter at cephalic setae | 6 | 6–9 |
| Body diameter at amphids | 7 | 7–8 |
| Length of outer + inner labial setae | 3–3 | 3–4 |
| Length of cephalic setae | 4–4 | 4–5 |
| Amphid height | 6 | 6–7 |
| Amphid width | 5 | 5 |
| Amphid width/cbd (%) | 71 | 63–71 |
| Amphid from anterior end | 2 | 2–3 |
| Nerve ring from anterior end | 150 | 151–163 |
| Nerve ring cbd | 18 | 17–18 |
| Excretory pore from anterior end | 126 | 124–136 |
| Pharynx length | 347 | 329–353 |
| Pharyngeal diameter at base | 11 | 12–13 |
| Pharynx cbd at base | 17 | 18–19 |
| Maximum body diameter | 19 | 19–20 |
| Spicule length | 24 | 23–24 |
| Gubernaculum length | 8 | 6–7 |
| Cloacal/anal body diameter | 18 | 18–19 |
| Tail length | 44 | 43–52 |

**Etymology.** The species name is derived from the Greek *ankistron* (= fishhook), and *eidos* (= form, figure, likeness) and refers to the shape of the curved body.

**Species diagnosis.** *Litinium ankistronidum* **sp. nov.** is characterised by body length 1895–2030 µm, inner and outer labial setae 3–4 µm long, cephalic setae 4–5 µm long situated far posteriorly (1.4–1.6 body diameters at level of amphids from posterior edge of amphids), ovoid amphidial fovea and circular amphidial aperture, walls of buccal cavity not cuticularised, spicules 1.3 cloacal body diameters long, gubernaculum consisting of two detached u-shaped lateral pieces, 3–4 precloacal supplements, and gradually tapering conical tail 2.4–2.7 cloacal body diameters long.

**Differential diagnosis.** The new species is most similar to *L. profundorum* Tchesunov, Thanh & Tu, 2014 (South Atlantic) in amphid shape, the length of anterior sensilla, spicule length and presence of precloacal supplements bearing a single seta each. *Litinium ankistronidum* **sp. nov.** differs from the latter in body length (1895–2030 *versus* 1196 µm in *L. profundorum*), ratio of a (100–106 *versus* 52 in *L. profundorum*), cephalic setae position well posterior to amphids *versus* immediately posterior to amphids in *L. profundorum*), number of precloacal supplements (3–4 *versus* 2 in *L. profundorum*), and longer tail (c′ = 2.4–2.7 *versus* 1.2 in *L. profundorum*).

**ZooBank registration.** *Litinium ankistronidum* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:8E4F2CBB-6BAC-4D4F-B5E8-7D8676FF57E8.

## Family **Thoracostomopsidae** Filipjev, 1927
## Subfamily **Enoplolaiminae** De Coninck, 1965

Enoplolaiminae De Coninck, 1965: 656, fig. 464.

**Diagnosis.** Three high lips. Buccal cavity always with three mandibles and three teeth. One mandible and one tooth together form a unit which can be moved back and forth by specialised pharyngeal muscles, whereby the frontal section of the unit is moved in line with the body axis. A pharyngeal gland opens through each tooth. All three teeth have the same length, or the dorsal tooth is distinctly smaller than the two ventrosublateral teeth; the two ventrosublateral teeth are always equal in length (from Smol *et al.* (2014)).

**Type genus.** *Enoplolaimus* de Man, 1893

### Genus ***Oxyonchus*** Filipjev, 1927

*Oxyonchus* Filipjev, 1927: 144.

**Diagnosis.** Cuticle smooth or striated. Lips high or low. Cephalic organ present or absent. Cephalic capsule well developed, broad, with well-developed fenestrae and incisions; posteriorly can be divided into six lobes or undulate. Anterior edge of cephalic capsule strengthened with mandibular ring of cuticle associated with mandibles. Mandibles well-developed, arc-shaped, rods connected by broad transverse bar with claws, denticles can be present on inner surface of mandibular plate. Teeth (onchia) unequal; two large ventrosublateral teeth that extend to anterior end of mandibles. Dorsal tooth small. Spicules short (1–3 cloacal body diameters). Pre-cloacal supplement present or absent. Gubernaculum with or without apophyses (from Fadeeva *et al.* (2012)).

**Remarks.** A tabular key to the 17 valid species of the genus is provided by Fadeeva *et al.* (2012).

**Type species.** *Oxyonchus hamatus* (Steiner, 1916) Filipjev, 1927

### ***Oxyonchus* sp. 1** (NIWA 154881, short body & cephalic setae, Mana Bank, Leduc & Zhao) **sp. indet.**

Figs 21–23; Table 5

**Material examined.** NIWA 154881, NIWA Stn Z19168, 41.098° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 22 Feb 2019, fine sand, male.

**Description. Male.** Body cylindrical, tapering slightly towards anterior extremity. Cuticle smooth. Sparsely distributed somatic setae present in anterior half of pharyngeal region, 6–8 µm long. Orthometanemes present in lateral fields from posterior to cephalic region to slightly anterior to cloacal region, each consisting of a cuticularised frontal filament gradually narrowing anteriorly, ca. 150 µm long, and scapulus 8 µm long and 5 µm wide; caudal filaments not observed. Mouth opening surrounded by one dorsal and two ventrosublateral lips separated by deep clefts, each bearing a very thin lip lobe at apex bearing two relatively stout labial setae. Outer labial setae in same circle as cephalic setae, the former slightly longer (0.4 cbd) than the latter (0.3 cbd). Cervical setae present laterally and sublaterally near base of cephalic capsule, in groups of three or single, 8–13 µm long. Cephalic organ, amphidial fovea, and amphidial aperture not observed. Cephalic capsule well-developed, 38 µm high and 40 µm wide at base, with deep incisions, strengthened by thin cuticularised band surrounding its base; double arcs of cuticularisation also present along anterior edge of cephalic capsule, joined to cuticularisation at base. Each mandibular plate bearing at least 12–15 denticles on inner surface; two large, triangular ventrosublateral onchia 13 µm long, and short dorsal onchium, barely larger than surrounding denticles. Pharynx muscular, cylindrical with wavy appearance and widening gradually posteriorly; anterior-most portion swollen, connecting with inner surface of cephalic capsule and surrounding mandibular plates. Nerve ring located relatively far anteriorly, less than one-third of pharynx length from anterior. Secretory-excretory system not observed. Cardia medium-sized, surrounded by intestinal tissue. Green algal material observed in anterior portion of intestinal lumen. Reproductive system with two opposed and outstretched testes both located to the left of intestine. Sperm cells small, globular, 3–4 × 5–7 µm. Spicules equal, arcuate, 2.0 cloacal body diameters long, with relatively broad velum and weakly defined capitulum. Gubernaculum with strongly cuticularised, straight apophyses and lateral crurae consisting of thin, curved, and distally pointed projections. Tubular precloacal supplements present, strongly cuticularised, 18 µm long, located 2.7 cloacal body diameters anterior to cloaca. Tail conicocylindrical, with clavate tip and sparsely distributed subdorsal and subventral setae; no terminal setae. Three caudal glands present, apparently extending into precloacal region.

**Species diagnosis.** *Oxyonchus* sp. 1 **sp. indet.** is characterised by body length 2733 µm, orthometanemes present in lateral fields, outer labial setae in same circle as cephalic setae, cervical setae present laterally and sublaterally near base of cephalic capsule, 8–13 µm long, mandibular plate bearing at least 12–15 denticles, two large ventrosublateral onchia and short dorsal onchium, nerve ring located less than one-third of pharynx length from anterior, spicules two cloacal body diameters long, gubernaculum with apophyses and lateral crurae, tubular precloacal supplements 18 µm long located 2.7 cloacal body diameters anterior to cloaca.

**Differential diagnosis.** The Pāuatahanui Inlet specimen resembles *O. orientalis* Fadeeva, Mordukhovich & Zograf, 2012 (Sea of Japan), and *O. nicholasi* Faddeva, Mordukhovich & Zograf, 2012

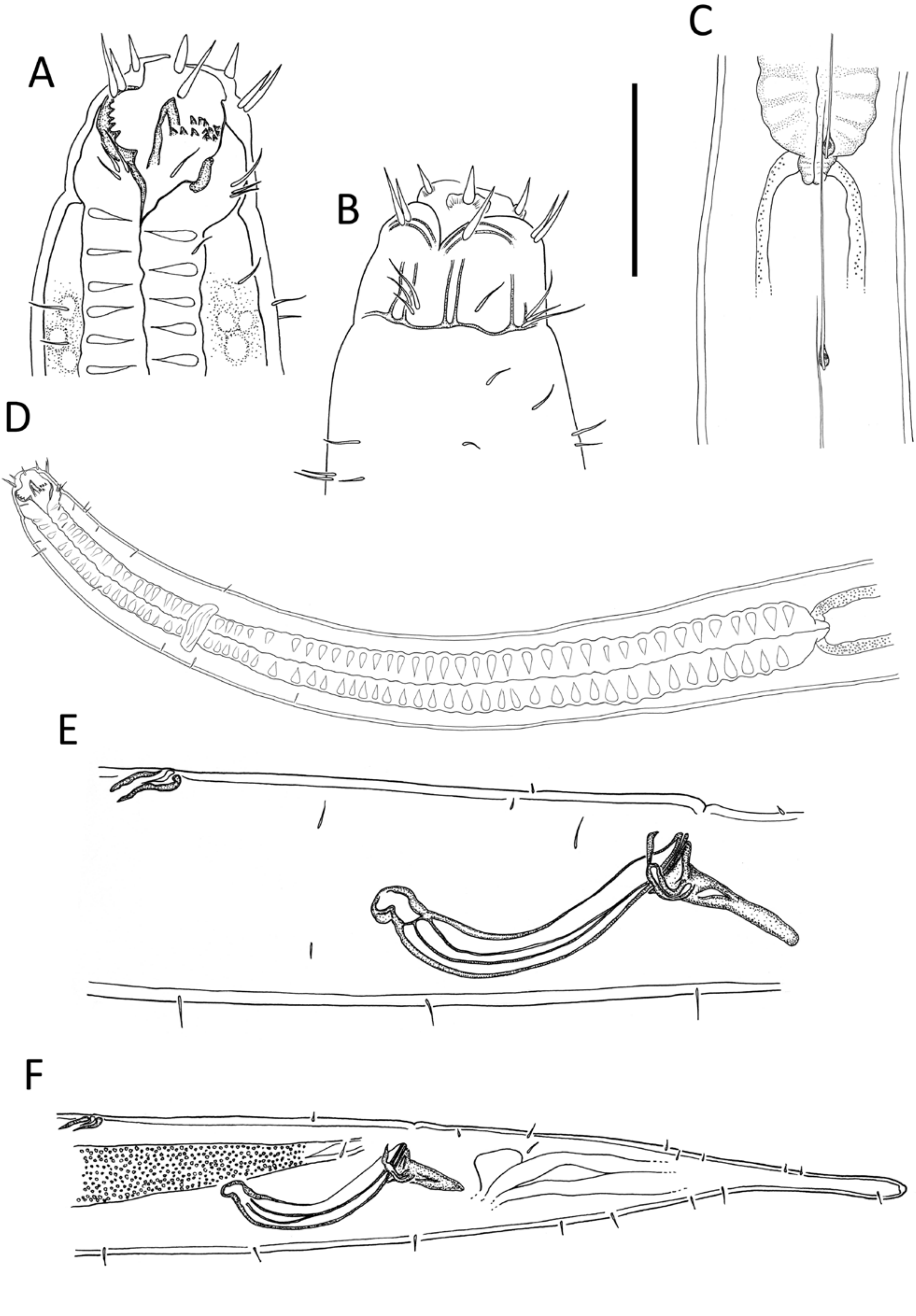



**Figure 21.** *Oxyonchus* sp. 1 (NIWA 154881, short body & cephalic setae, Mana Bank, Leduc & Zhao) **sp. indet.**, male: **A–B.** Cephalic region; **C.** Posterior pharyngeal region, showing lateral orthometanemes; **D.** Pharyngeal region; **E.** Spicular apparatus; **F.** Posterior body region. Scale bar: A, B = 40 μm; C = 100 μm; D = 160 μm; E = 60 μm; F = 95 μm.

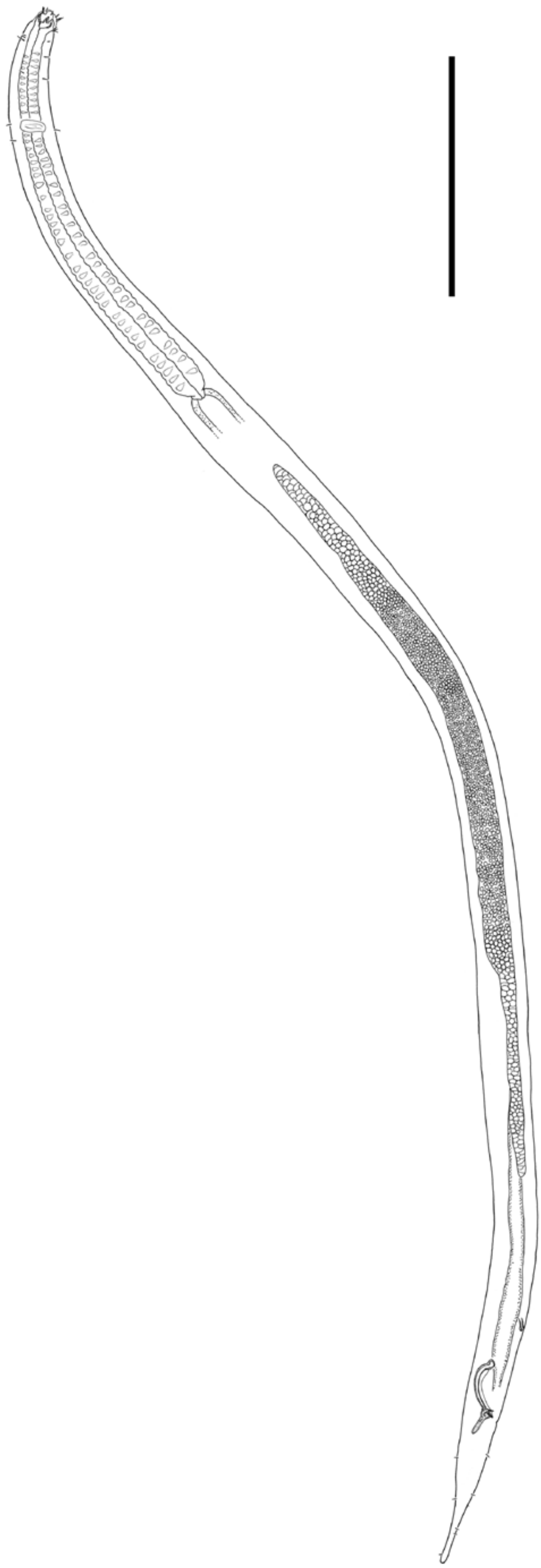


**Figure 22.** *Oxyonchus* sp. 1 (NIWA 154881, short body & cephalic setae, Mana Bank, Leduc & Zhao) **sp. indet.**, entire male. Scale bar = 400 µm.

**Figure 23.** *Oxyonchus* sp. 1 (NIWA 154881, short body & cephalic setae, Mana Bank, Leduc & Zhao) **sp. indet.**, light micrograph of junction of pharynx and intestine showing green algal material in intestine lumen. Scale bar = 10 µm.

(Sea of Okchotsk) in having mandibles with denticles, cephalic setae less than 1 cbd long, arcuate spicules, gubernaculum with apophyses, presence of precloacal supplement, and tail less than 5 cloacal body diameters long. The Pāuatahanui Inlet specimen differs from both species in having shorter body length (2733 *versus* 3045–4155 µm in *O. orientalis* and *O. nicholasi*), shorter cephalic setae (0.3 *versus* 0.5–0.8 cbd in *O. orientalis* and *O. nicholasi*), and longer cephalic capsule (38 *versus* 23–27 µm in *O. orientalis* and *O. nicholasi*). The Pāuatahanui Inlet specimen also resembles *O. acantholaimus* (Ssaweljev, 1912) Filipjev, 1927 in having short (< 0.5 cbd) cephalic setae and mandibles with denticles but differs from the latter in body length (2733 *versus* 4600 µm in males of *O. acantholaimus*), cephalic capsule length (38 *versus* 45–50 µm in *O. acantholaimus*), presence of setae on tail (*versus* absent in *O. acantholaimus*), and tail length (4.1 *versus* 5.9

**Table 5.** Morphometrics (µm) of *Oxyonchus* sp. 1 (NIWA 154881, short body & cephalic setae, Mana Bank, Leduc & Zhao) **sp. indet.**

| Parameter | Male |
|---|---|
| Number of specimens | 1 |
| L | 2733 |
| a | 28 |
| b | 4 |
| c | 11 |
| c' | 4.1 |
| Body diameter at cephalic setae | 32 |
| Length of inner labial setae | 8–10 |
| Length of outer labial setae | 14 |
| Length of cephalic setae | 9, 10 |
| Body diameter at base of cephalic capsule | 40 |
| Cephalic capsule height | 38 |
| Stoma depth | 37 |
| Nerve ring from anterior end | 189 |
| Nerve ring cbd | 68 |
| Pharynx length | 677 |
| Pharyngeal diameter at base | 58 |
| Pharynx cbd at base | 95 |
| Maximum body diameter | 99 |
| Spicule length | 116 |
| Gubernacular apophysis length | 33 |
| Cloacal body diameter | 59 |
| Cloaca to supplement | 158 |
| Tail length | 244 |

cloacal body diameters in *O. acantholaimus*) (no information is available on the structure of the spicular apparatus in *O. acantholaimus*). While a number of body measurements have non-overlapping ranges compared to other species of the genus, it is possible that the discovery of more specimens will decrease or eliminate these gaps; we have refrained from erecting a new species for the Pāuatahanui Inlet specimen accordingly.

## Family **Tripyloididae** Filipjev, 1918

Tripyloididae Filipjev, 1918: 128, fig. 35, table 6.

**Diagnosis.** Metanemes, when present, almost exclusively ventrolateral loxometanemes of type II, whereas dorsolateral loxometanemes occur only rarely or are absent altogether. Two circles of anterior sensilla: first circle with six inner labial sensilla often setiform; second circle of six outer labial + four cephalic setae, which may be jointed. Buccal cavity consists of one or three or four portions that lie one behind the other; tooth-like projections are common, of which the dorsal tooth can be dominant (after Smol *et al.* (2014)).

**Type genus.** *Tripyloides* de Man, 1886

## Genus ***Bathylaimus*** Cobb, 1894

*Bathylaimus* Cobb, 1894: 409, fig. 9.
*Cothonolaimus* Ditlevsen, 1919: 168, pl. 4, fig. 2, 4, 8. pl. 6, fig. 6.
*Parabathylaimus* De Coninck & Schuurmans Stekhoven, 1933: 120.
*Bathylaimoides* Allgén, 1947: 22, fig. 16.

**Diagnosis.** Lips deeply incised. Buccal cavity large and deep, consisting of two parts, with teeth or cuticular projections in posterior part. Males with large gubernaculum (after Smol *et al.* (2014)).

**Remarks.** *Bathylaimus* comprises 31 valid species. This genus occurs mainly in marine environment and also in brackish waters (Smol *et al.* 2014).

**Type species.** *Bathylaimus australis* Cobb, 1894

### ***Bathylaimus* cf. *australis* Cobb, 1894**

Figs 24–27; Table 6

*Bathylaimus assimilis* de Man, 1922: 119–120, fig 2.
*Bathylaimus ponticus* Filipjev, 1922: 107–108, fig 6.

**Material examined.** NIWA 139261, NIWA Stn Z18745, 41.093° S, 174.876° E, Pāuatahanui Inlet near Camborne Walkway, upper intertidal, 28 Jul 2016, gravelly sand, three males and three females.

**Type & locality.** Holotype, Port Jackson, New South Wales, Australia, 1891. Type specimens could not be located in USDA Nematode Collection (Dr Zafar Handoo, curator, pers. com.)

**Distribution.** Cosmopolitan, including records from the coast of New Zealand, Australia, eastern United States of America, Brazil, Red Sea, Mediterranean Sea, North Sea, and Black Sea (Gerlach & Riemann 1973/1974, Leduc & Gwyther 2008).

**Diagnosis.** The *Bathylaimus* cf. *australis* specimens from Pāuatahanui Inlet are characterised by body cylindrical, colourless, tapering slightly towards both extremities, 2093–2364 µm long. Cuticle smooth. Eight rows of sparse somatic setae in pharyngeal region, 4–6 µm long; few sparse, shorter somatic setae present on rest of body. Cephalic region demarcated by very slight constriction at level of buccal cavity. Three deeply incised lips, each bearing two internal labial setae, 4 µm long. Six triple-jointed outer labial setae and four markedly shorter cephalic setae in single circle. Amphidial fovea circular or cryptocircular, 0.8 cbd from anterior extremity; smaller circular amphidial aperture, 3–4 µm diameter. Buccal cavity large, with cuticularised walls; anterior portion of buccal cavity 29–34 µm deep, 11–16 µm wide, posterior buccal cavity smaller, 16–18 µm

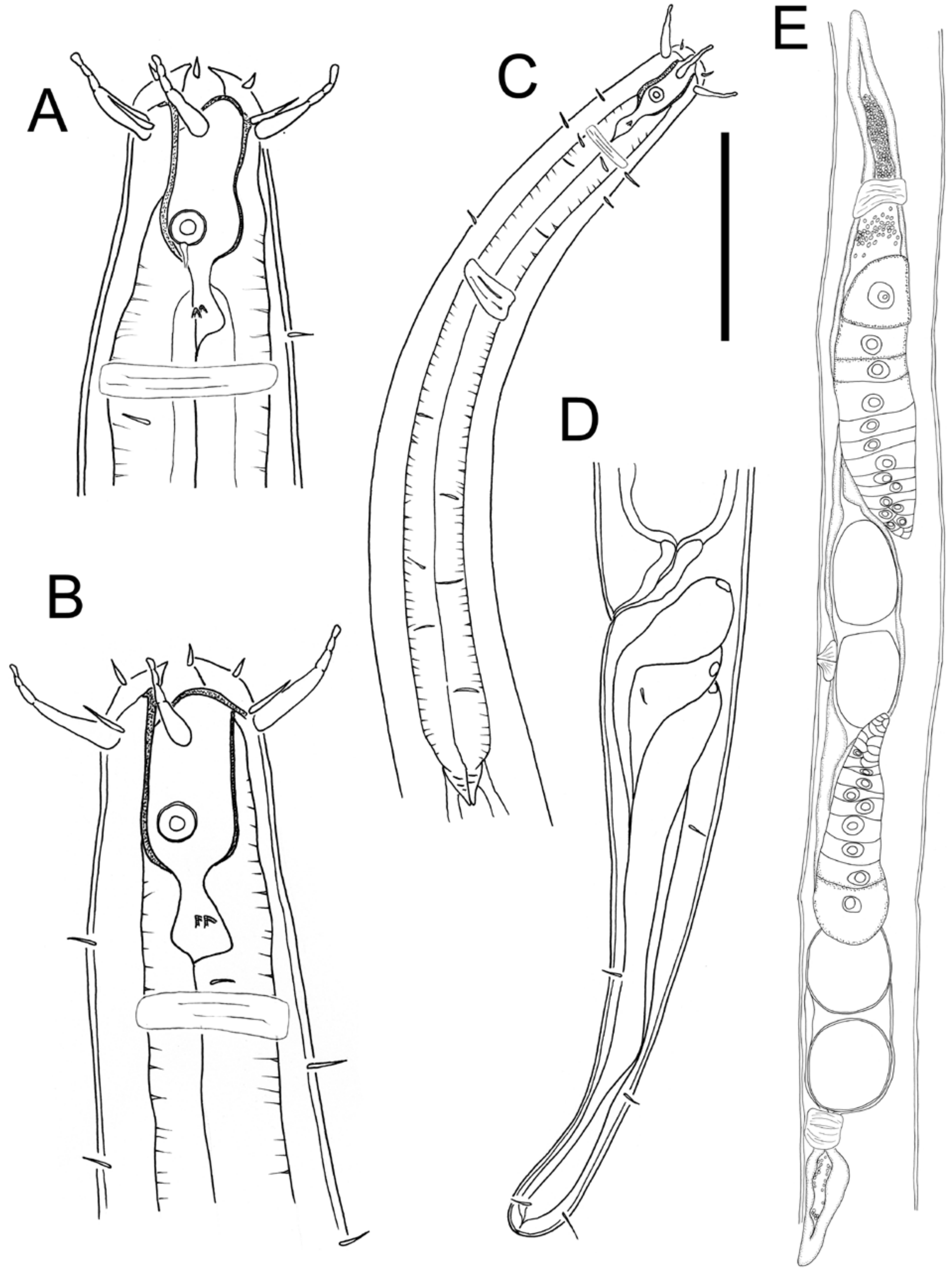



**Figure 24.** *Bathylaimus* cf. *australis* Cobb, 1894, NIWA 139261: **A.** Male cephalic region showing nerve ring-like structure; **B.** Female cephalic region showing nerve ring-like structure; **C.** Male anterior body region; **D.** Female posterior body region; **E.** Female reproductive system. Scale bar: A, B = 40 μm; C = 105 μm; D = 55 μm; E = 135 μm.

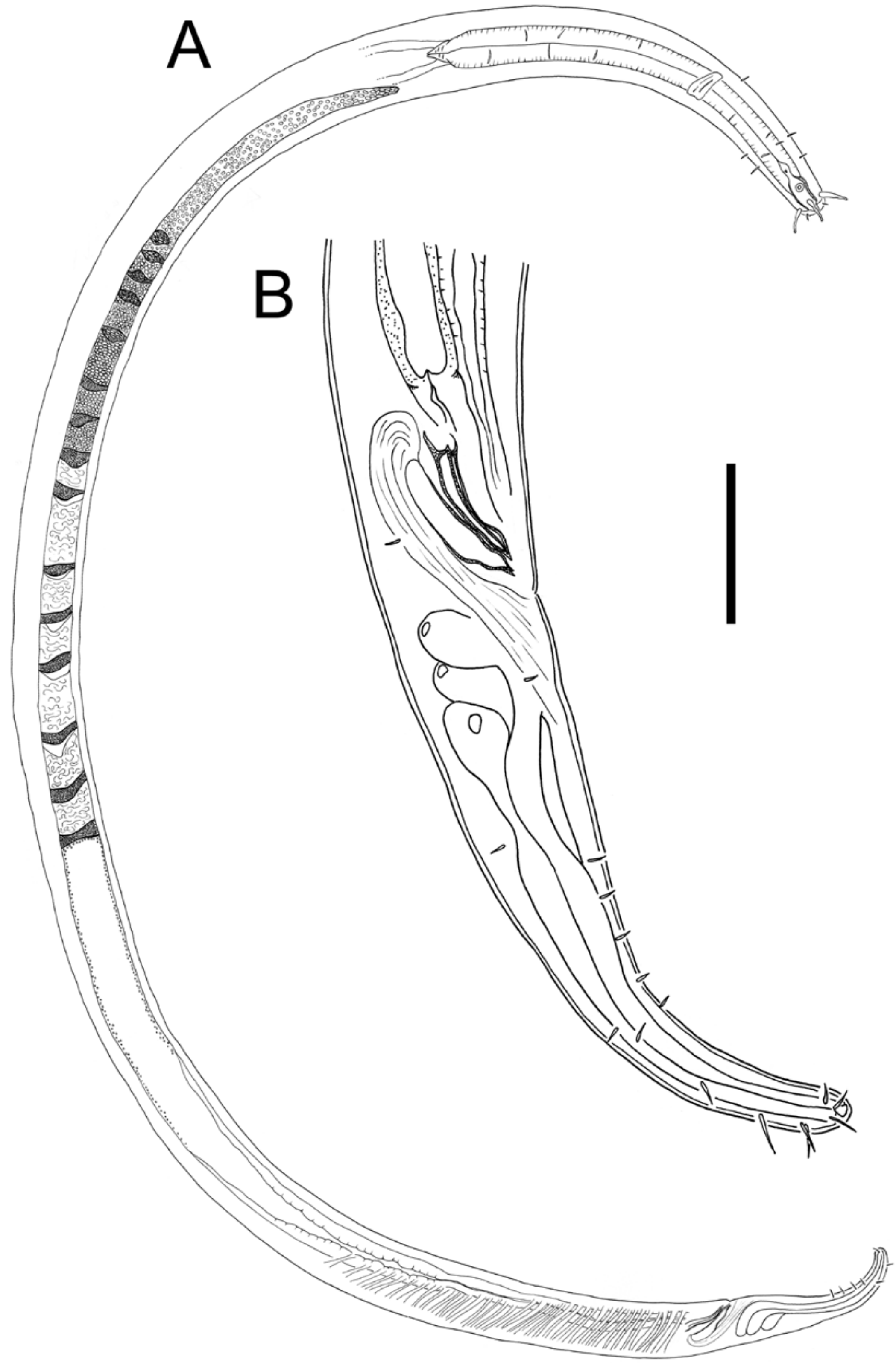



**Figure 25.** *Bathylaimus* cf. *australis* Cobb, 1894, NIWA 139261: **A.** Entire male; **B.** Male posterior body region. Scale bar: A = 150 µm; B = 40 µm.

deep, 8–11 µm wide, with pair of ventrosublateral teeth. Ducts of pharyngeal glands connected to base of posterior portion of buccal cavity. Pharynx muscular, cylindrical, widening slightly towards posterior extremity. Nerve ring located approximately 40% down length of pharynx from anterior. Additional nerve ring-like structure visible slightly posterior to the buccal cavity in all specimens. Secretory-excretory system

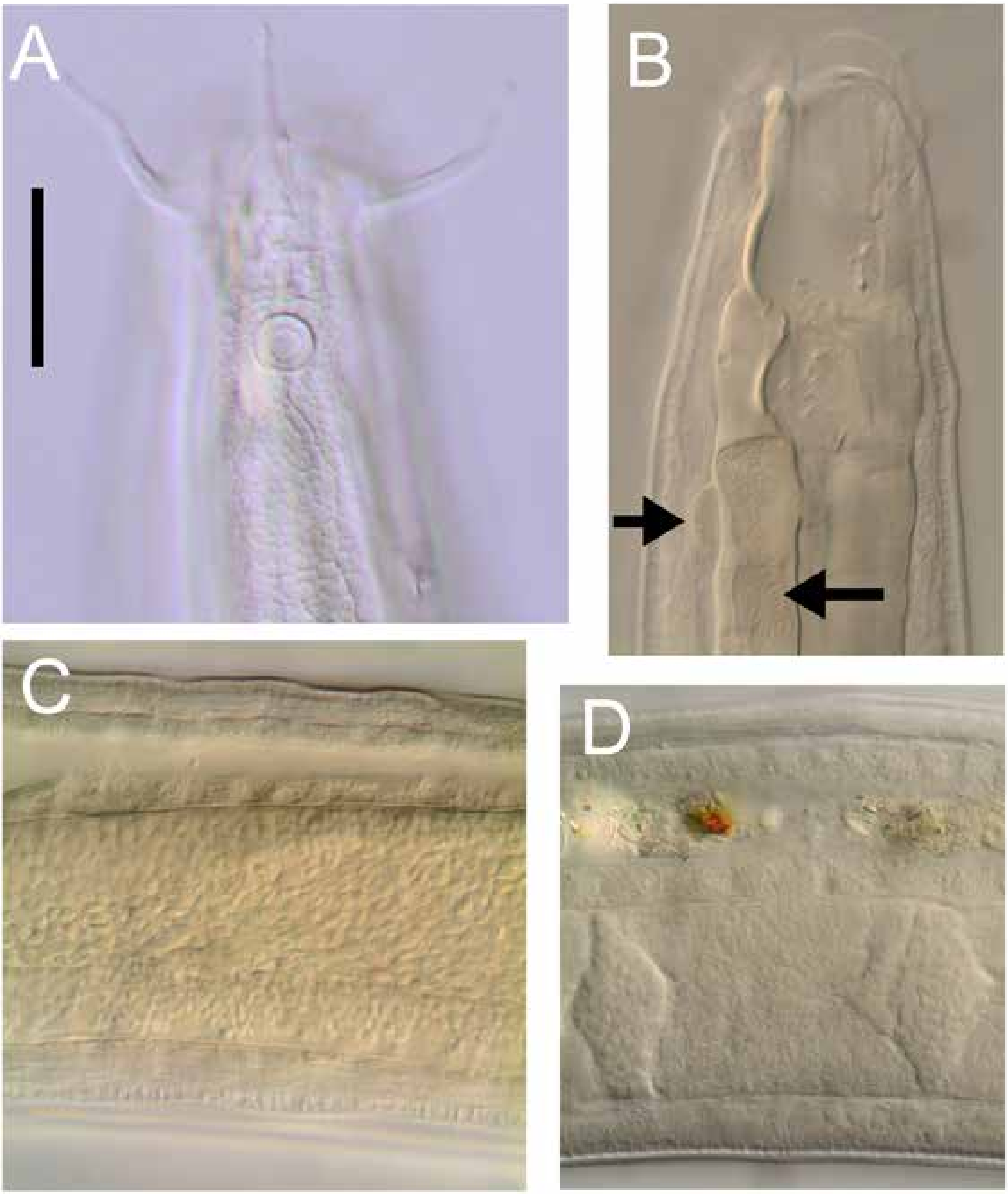



**Figure 26.** *Bathylaimus* cf. *australis* Cobb, 1894, NIWA 139261, light micrographs: **A.** Lateral view of male cephalic region; **B.** Optical cross-section of female cephalic region, showing buccal cavity; **C.** Anterior portion of vas deferens showing mature sperm cells; **D.** Middle portion of testis showing banding pattern, intestine also visible above testis. In B), top arrow shows position of anterior nerve ring-like structure and bottom arrow shows position of duct of pharyngeal gland. Scale bar: A = 20 µm; B = 22 µm; C, D = 24 µm.

not observed. Cardia medium-sized, surrounded by intestinal tissue. Male reproductive system with single outstretched testis located ventrally relative to intestine, with characteristic banding pattern created by clusters of tightly-packed sperm. Spicules short, slightly bent and swollen proximally. Gubernaculum relatively large, paired, each half with a pair of ventrolaterally directed teeth, connected proximally to large muscle. Precloacal supplements not observed. Tail conicocylindrical, with several short setae mainly located subventrally, and longer setae near tail tip, 610 µm long. Three caudal glands present. Females similar to males but with slightly wider body, and tail slightly swollen distally with fewer setae. Reproductive system with two opposed and reflexed ovaries of variable position relative to intestine, on opposite sides, or same side. Eggs, 54–55 × 63–68 µm. Spermathecae present, consisting of a pocket off each ovary at point of flexure; each spermatheca is surrounded by sphincter muscle proximally. Vulva located slightly anterior to mid-body.

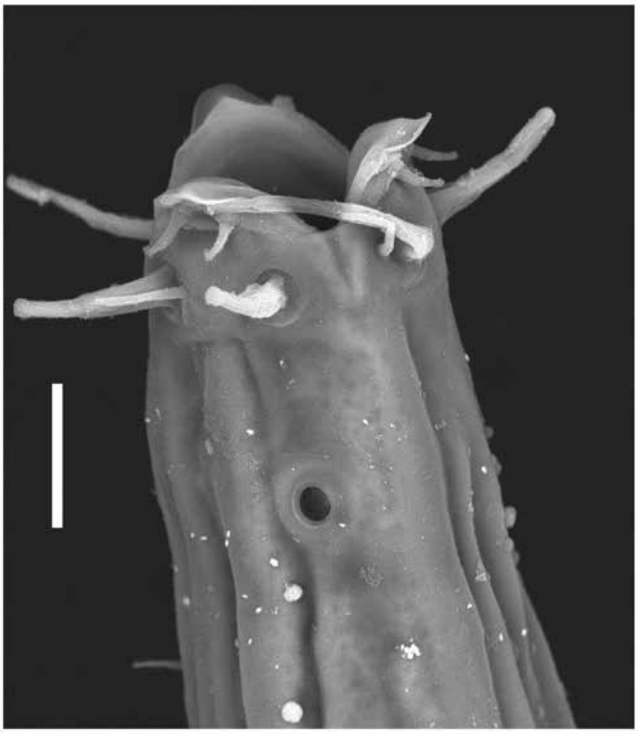


**Figure 27.** *Bathylaimus* cf. *australis* Cobb, 1894 scanning electron micrograph of female cephalic region. Scale bar = 10 µm.

**Remarks.** The Pāuatahanui Inlet specimens agree well with the original description of the species by Cobb (1894). However, the secretory-excretory system, which was noted in the original description, was not observed here. Our observations show that the amphids in *Bathylaimus australis* are best described as circular or cryptocircular, and not spiral or unispiral as per the descriptions of Cobb (1894) and of De Coninck & Schuurmans Stekhoven (1933). The appearance of a spiral arises from the superimposition of the outlines of the amphidial aperture and amphidial fovea, the latter being characterised by a greater diameter than the former.

Two morphological features were noted in the Pāuatahanui Inlet specimens which had not been observed in previous descriptions of the species. A nerve ring-like structure was noted in all specimens observed, surrounding the pharynx slightly posterior to the buccal cavity. Two nerve rings have been observed in several *Longidorus* and *Paralongidorus* species by Goodey & Hooper (1963) but have not been observed in the Enoplida. Although the dorsal sector of the nerve ring-like structure in *Bathylaimus australis* specimens was always readily observable, it is easily overlooked, which may explain why it has not been noted in earlier descriptions of the species. Spermathecae were also observed for the first time for this species; these structures were relatively difficult to see in some of the female specimens, which may be why they have not been noticed previously.

**Table 6.** Morphometrics (µm) of *Bathylaimus* cf. *australis* Cobb, 1894, given as a range of values from several specimens.

| Parameter | Males | Females |
|---|---|---|
| Number of specimens | 3 | 3 |
| L | 2093–2353 | 2169–2364 |
| a | 34–38 | 28–33 |
| b | 6 | 6 |
| c | 14–15 | 13–15 |
| c' | 3.7–4.2 | 4.0–4.7 |
| Body diameter at cephalic setae | 25–27 | 26–28 |
| Body diameter at amphids | 28–31 | 31–32 |
| Length of outer labial setae | 20–25 | 21–24 |
| Length of cephalic setae | 8 | 6–8 |
| Amphid height | 6–7 | 6 |
| Amphid width | 6–7 | 6 |
| Amphid width/cbd (%) | 21–23 | 19 |
| Amphid from anterior end | 21–26 | 22–27 |
| Nerve ring from anterior end | 140–155 | 146–156 |
| Nerve ring cbd | 45–49 | 52–58 |
| Pharynx length | 370–386 | 393–404 |
| Pharyngeal diameter at base | 31–34 | 34–37 |
| Pharynx cbd at base | 63–68 | 69–75 |
| Maximum body diameter | 61–62 | 72–81 |
| Spicule length | 40–46 | – |
| Gubernaculum length | 34–47 | – |
| Cloacal/anal body diameter | 38–41 | 35–41 |
| Tail length | 142–165 | 163–164 |
| V | – | 1019–1114 |
| %V | – | 47–48 |
| Vulval body diameter | – | 74–81 |

**Sequence data.** Partial SSU rDNA (1578 bp; Genbank OK317194) and D2–D3 of LSU rDNA (777 bp; Genbank OK317219). The Pāuatahanui Inlet SSU sequence differs from other available *Bathylaimus australis* sequences (AJ966476, MG669696, MG669697) by 4–5%, which would suggest that the Pāuatahanui Inlet specimens belong to a separate species. The Genbank sequences were obtained from specimens from the coast of the Netherlands, however, and no sequences are available from the type locality in Australia (Port Jackson). Ascertaining the identity of the Pāuatahanui Inlet specimens will require molecular data from the type locality; however, given the divergence between the New Zealand and European sequences, *B. australis* is likely to comprise several cryptic species.

## Genus *Tripyloides* de Man, 1886

*Nannonchus* Cobb, 1913: 442.

**Diagnosis.** Lips low and only lightly incised. Anterior sensilla in two circles: six inner labial papillae or short setae, six long and mostly jointed outer labial setae and four shorter cephalic setae (not jointed). Amphidial fovea cryptospiral. Buccal cavity consisting of several parts with teeth or cuticular projections. Males sometimes with circular musculature surrounding the spicular apparatus (from Smol *et al.* (2014)).

**Remarks.** The genus was revised by Wieser (1956a) and Tchesunov *et al.* (2010). Fu *et al.* (2018) provided a key to species of the genus. Wieser (1956a, p.35) noted that "the status of the species of this genus has to be revised completely" and Tchesunov (2010) later commented on how observations of some key features which have been used to differentiate between *Tripyloides* species, such as buccal cavity and amphid structure, depends largely on the state of preservation of the specimens as well as the angle of observation. The genus has yet to be comprehensively revised, and it is likely that the taxonomic status of several *Tripyloides* species will need to change in the future.

The type species of the genus, as designated by de Man in Stiles & Hassall (1905), *T. vulgaris* de Man, 1886, was synonimised with *T. marinus* by De Coninck & Schuurmans Stekhoven (1933). According to the International Code of Zoological Nomenclature, the latter authors could have fixed as type species, the species that would, in their judgment, best serve stability and universality, either the nominal species previously cited as type species, or the taxonomic species actually involved in the misidentification. They did not, however, fix the type species. We propose that the type species of the genus *Tripyloides* be now fixed (under Article 70.3 of the Code) as *T. marinus* (Bütschli, 1874) de Man, 1886, misidentified as *Tripyloides vulgaris* de Man, 1886 in the original designation by de Man in Stiles & Hassall (1905, p.146).

**Type species.** *Tripyloides marinus* (Bütschli, 1874) de Man, 1886

### *Tripyloides* cf. *marinus* (Bütschli, 1874) de Man, 1886

Figs 28–30; Table 7

*Tripyla marina* Bütschli, 1874: 33–34; figs 12a–c.
*Tripyloides demani* Filipjev, 1918: 181–183; fig. 35.
*Tripyloides issatschenkovi* Paramonov, 1929: 93–94; fig. 14.
*Tripyloides vulgaris* de Man, 1886: 61–66; figs 1–11.

**Material examined.** NIWA 154863, NIWA Stn Z19169, 41.102° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 9 Dec 2019, fine sand, four males and two females.

**Type & locality.** Bay of Kiel, Baltic Sea, Germany, beach sand, 1874. de Man's type collection is located in the Naturalis Invertebrate Collection, Naturalis, Leiden, the Netherlands, but registration details of the holotype were not confirmed prior to publication.

**Distribution.** Cosmopolitan, including records from the Baltic Sea, Barents Sea, North Sea, Mediterranean Sea, Black Sea, Caspian Sea, Red Sea, North Atlantic (Nova Scotia), and South Pacific (Chile) (Gerlach & Riemann 1973/1974; Tchesunov 1981a).

**Diagnosis.** *Tripyloides* cf. *marinus* from Pāuatahanui Inlet are characterised by a cylindrical, colourless body that tapers slightly towards both extremities, 857–1301 µm long. Cuticle smooth. Eight longitudinal rows of short somatic setae in pharyngeal region, 2–3 µm long, sparse on rest of body except in precloacal region where two rows of 3–4 subventral setae are present, and caudal region where several subventral, sublateral and subdorsal setae are present. Cephalic region demarcated by very slight constriction at level of buccal cavity. Three lips present, not deeply incised, each bearing two small internal labial papillae; six double-jointed outer labial setae with truncate tips and four shorter, unjointed cephalic setae in single circle. Amphidial fovea cryptocircular, 0.8–1.0 cbd from anterior extremity, lightly cuticularised; smaller circular amphidial aperture, 2–3 µm diameter, not cuticularised. Buccal cavity medium-sized, 16–17 µm deep and up to 5–6 µm wide, with cuticularised walls, and divided into three compartments, although depending on state of preservation four compartments can sometimes be distinguished; single dorsal cuticularised tooth present at base of buccal cavity. Buccal cavity compartments delimited by pointed projections of buccal cavity wall forming incomplete rings around buccal cavity and sometimes resembling a tooth; each compartment becoming narrower posteriorly. Pharynx muscular, cylindrical, widening slightly towards posterior extremity; ducts of pharyngeal glands not observed. Nerve ring located around middle of pharynx. Secretory-excretory system not observed. Cardia medium-sized, completely or partially surrounded by intestinal tissue. Male reproductive system with single outstretched testis located ventrally relative to intestine. Sperm cells elongated, with long, thin central nucleus. Spicules short, slightly bent with central lamella and weak capitulum. Gubernaculum relatively large,

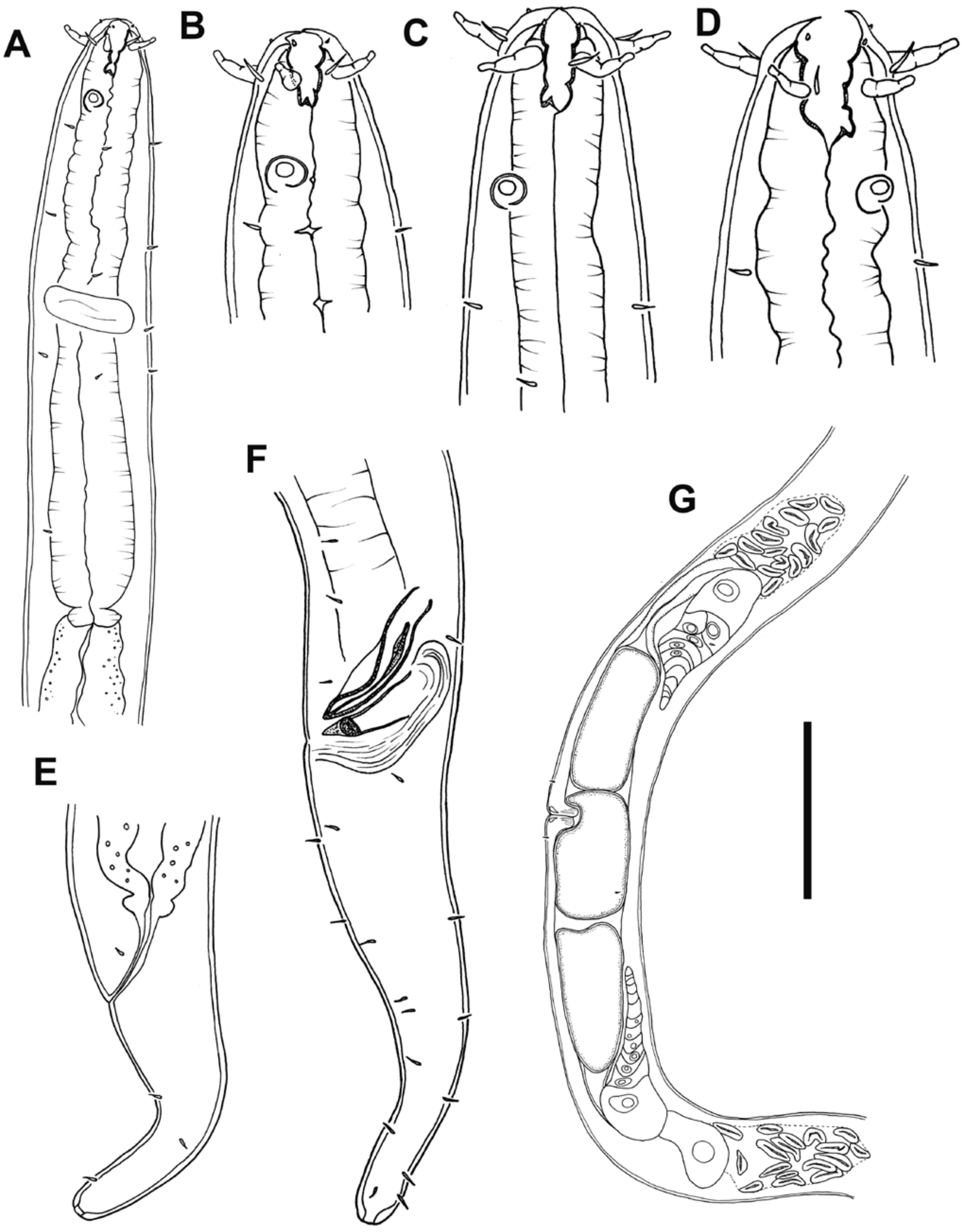



**Figure 28.** *Tripyloides* cf. *marinus* (Bütschli, 1874) de Man, 1886, NIWA 154863: **A.** Male anterior body region; **B–C.** Male cephalic region; **D.** Female cephalic region; **E.** Female posterior body region; **F.** Male posterior body region; **G.** Female reproductive system. Scale bar: A = 50 µm; B–F = 30 µm; G = 80 µm.

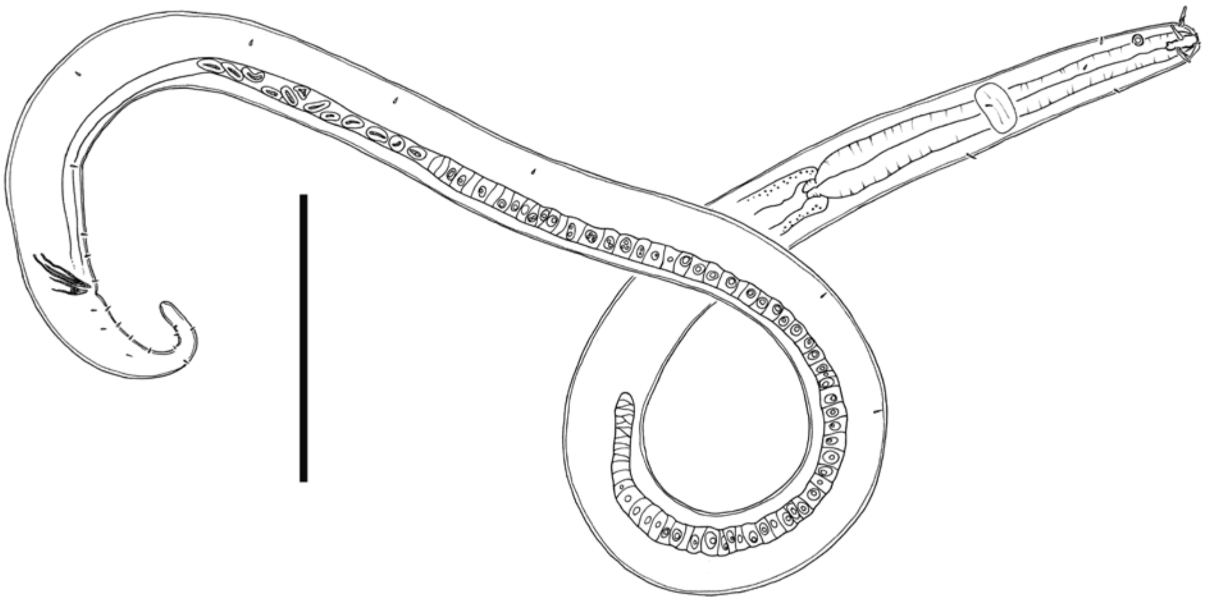


**Figure 29.** *Tripyloides* cf. *marinus* (Bütschli, 1874) de Man, 1886, NIWA 154863, entire male. Scale bar = 150 µm.

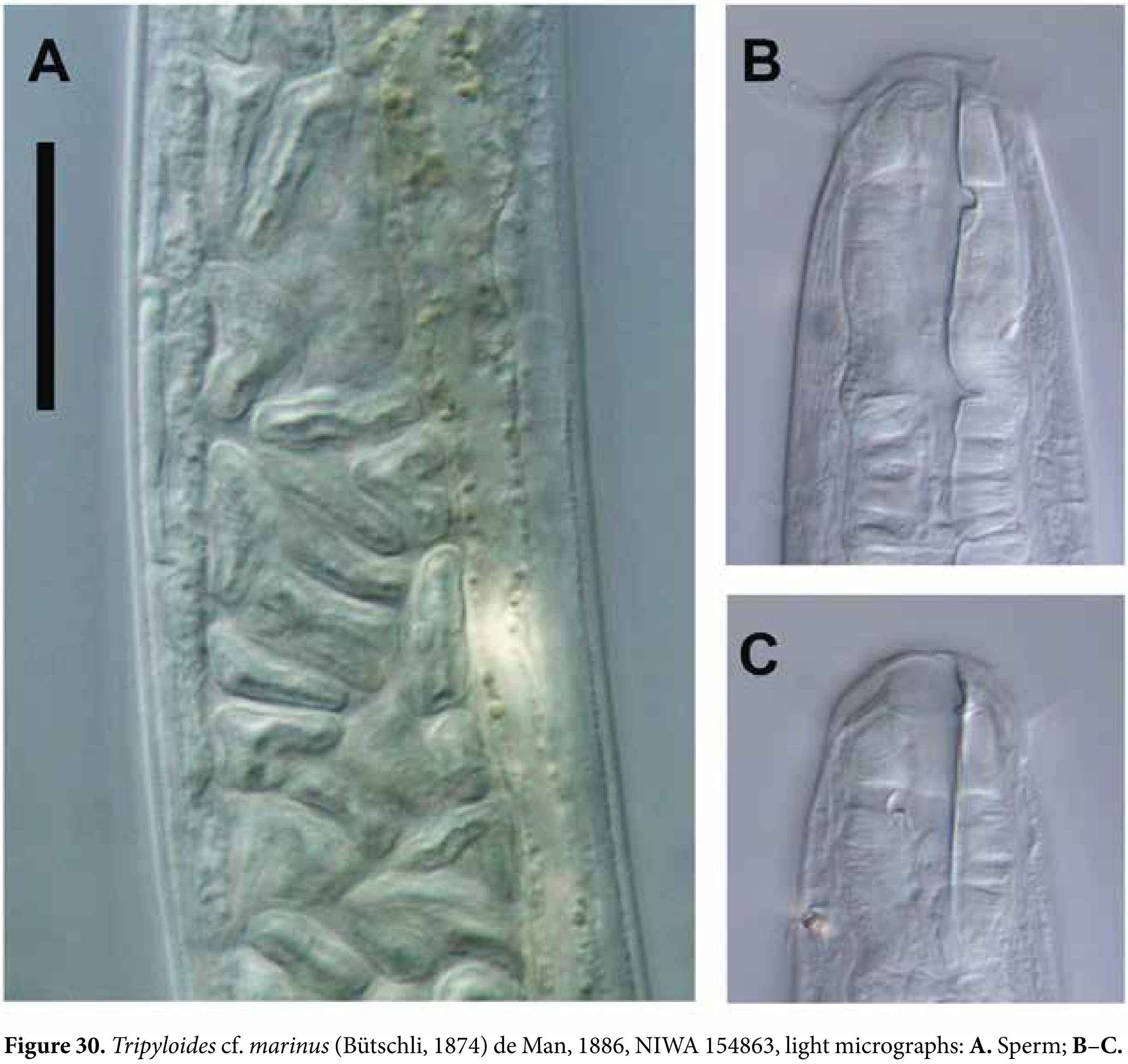



**Figure 30.** *Tripyloides* cf. *marinus* (Bütschli, 1874) de Man, 1886, NIWA 154863, light micrographs: **A.** Sperm; **B–C.** Optical cross-section of female cephalic region, showing buccal cavity and lips. Scale bar: A = 20 µm; B, C = 25 µm.

**Table 7.** Morphometrics (μm) of *Tripyloides* cf. *marinus* (Bütschli, 1874) de Man, 1886, given as a range of values from several specimens.

| Parameter | Males | Females |
|---|---|---|
| Number of specimens | 4 | 4 |
| L | 857–1301 | 937–1020 |
| a | 24–33 | 23–28 |
| b | 6–7 | 5–7 |
| c | 10–14 | 12–17 |
| c' | 2.5–3.5 | 2.5–3.3 |
| Body diameter at cephalic setae | 16–19 | 18–19 |
| Body diameter at amphids | 25–28 | 26–27 |
| Length of outer labial setae | 8–10 | 8–10 |
| Length of cephalic setae | 5–6 | 4–6 |
| Amphid height | 5–7 | 5–6 |
| Amphid width | 5–6 | 5 |
| Amphid width/cbd (%) | 18–24 | 19 |
| Amphid from anterior end | 20–27 | 23–25 |
| Nerve ring from anterior end | 63–114 | 74–96 |
| Nerve ring cbd | 31–35 | 34 |
| Pharynx length | 125–212 | 151–176 |
| Pharyngeal diameter at base | 22–24 | 22–24 |
| Pharynx cbd at base | 32–39 | 35–36 |
| Maximum body diameter | 35–42 | 34–47 |
| Spicule length | 24–32 | – |
| Gubernacular apophysis length | 20–21 | – |
| Cloacal/anal body diameter | 25–33 | 22–26 |
| Tail length | 83–104 | 54–86 |
| V | – | 485–594 |
| %V | – | 52–56 |
| Vulval body diameter | – | 34–47 |

paired, lightly cuticularised along most of its length, pointed distally and with strongly cuticularised lateral projections near distal tip, connected proximally to large muscle attached ventrally to body wall. Precloacal supplements not observed. Tail conicocylindrical, with short cylindrical distal portion. Caudal glands not observed, spinneret present. Female reproductive system with two opposed and reflexed ovaries situated ventrally relative to intestine. Eggs, 28–35 × 61–73 μm. Spermathecae present, consisting of a pocket off each ovary at point of flexure, each with numerous sperm cells; wall of spermatheca and structure of connection to ovary difficult to distinguish. Vulva located slightly posterior to mid-body.

**Remarks.** The Pāuatahanui Inlet specimens agree well with the original description of the species by Bütschli (1874) and falls within the range of morphometric parameters recorded for this species by various authors as reported in the review by Tchesunov *et al.* (2010). Riemann (1966) recognized two forms of the species, one stout and one elongated, which differed in body dimensions, tail shape, and the structure of borders delimiting the buccal cavity compartments, but which both had four-chambered buccal cavities. Lorenzen (1969) also distinguished between stout and elongated forms of *T. marinus*, which differed in body dimensions but showed different numbers of buccal cavity compartments (three in the stout form and four in the elongated form). Tchesunov *et al.* (2010) hypothesized that these two forms may are in fact different species, with the stout form corresponding to *T. marinus* and the elongated form corresponding to *T. gracilis* (Ditlevsen, 1919) Filipjev, 1927. The Pāuatahanui Inlet specimens appear most similar to the stout form of Riemann (1966) and Lorenzen (1969) in general body dimensions and tail shape but comparing buccal cavity structure is not straight-forward due to the variation we observed among the Pāuatahanui Inlet specimens, as well as inconsistencies between the descriptions of Riemann (1966) and Lorenzen (1969).

Early decriptions of *Tripyloides* species did not differentiate between amphidial fovea and amphidial apertures, which is the likely reason behind the diversity of amphid shapes described for *T. marinus*, including spiral, unispiral, cryptospiral and cryptocircular (De Coninck & Schuurmans Stekhoven 1933, Riemann 1966, Lorenzen, 1969). In the Pāuatahanui Inlet specimens, the amphidial fovea is always cryptocircular and the amphidial aperture is always circular.

Spermathecae were observed for the first time for this species; these structures were relatively difficult to observe, and their presence was first detected by the presence of dense aggregations of sperm cells. These structures, which are similar to the spermathecae also observed in *Bathylaimus australis* for the first time here, are likely to have been overlooked in previous desriptions of *T. marinus* and perhaps other *Tripyloides* species.

**Sequence data.** Partial SSU rDNA (798 bp; Genbank OK317195) and D2–D3 of LSU rDNA (728 bp; Genbank OK317220).

## Class **Chromadorea** Inglis, 1983
## Order **Araeolaimida** De Coninck & Schuurmans Stekhoven, 1933
## Family **Axonolaimidae** Filipjev, 1918

Axonolaimidae Filipjev, 1918: 317.

**Diagnosis.** Cuticle finely striated or smooth. Anterior end with four cephalic setae. Four subcephalic setae posterior to the amphids. Amphids loop-shaped, longitudinally elongated, placed at the base of the stoma. Buccal cavity conical without odontia. Ovaries outstretched. Testis outstretched. Spicules arcuate. Apophyses oriented caudally. Several postcloacal setae in the ventral side (from Fonseca & Bezerra (2014b)).

**Type genus.** *Cylindrolaimus* de Man, 1880

## Genus ***Axonolaimus*** de Man, 1889

*Axonolaimus* de Man, 1889: 3, fig. 70, 71.

**Diagnosis.** Cuticle finely striated or smooth. Anterior end with four cephalic setae. Cervical setae (often called 'subcephalic setae') present posterior to the amphids. Amphids loop-shaped, longitudinally elongated or with rounded outline, at level of buccal cavity. Buccal cavity funnel-shaped, without odontia. Females with two opposed, outstretched ovaries; males with one outstretched testis, sometimes two testes present. Spicules arcuate. Apophyses oriented dorso-caudally. Small tubular or pit-like recloacal supplements sometimes present. Male tail with subventral rows of setae (from Fonseca & Bezerra (2014b)).

**Type species.** *Axonolaimus spinosus* (Bütschli, 1874) de Man, 1889

### ***Axonolaimus glandifer*** **sp. nov.**

Figs 31–33; Table 8

**Material examined. Holotype** NIWA 139284, NIWA Stn Z19166, 41.102° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, mid-intertidal, 31 Jan 2018, fine sand, male. **Paratypes** NIWA 139285, four males and two females, same data as for holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Males.** Body colourless, cylindrical, tapering slightly towards both extremities. Cuticle smooth. Two laterodorsal and two lateroventral rows of somatic setae present along entire body length, 3–8 µm long. Lateral chords with numerous small vacuoles, mostly visible posterior to pharynx and in tail region. Blunt, slightly rounded cephalic region, slightly narrower than rest of body; lips short. Inner and outer labial sensilla not observed; four cephalic setae, 0.6–0.8 cbd long. Two pairs of lateroventral and two pairs of laterodorsal cervical setae, 6–8 µm long, situated slightly posterior to amphids. Amphidial fovea loop-shaped, situated slightly posterior to cephalic setae, about as long as buccal cavity is deep or slightly shorter; outline elongated, with parallel dorsal and ventral branches, lightly cuticularised. Buccal cavity funnel-shaped, with cuticularised walls, 20–22 µm deep, up to 6 µm wide, without odontia. Pharynx muscular, anterior portion surrounding posterior of buccal cavity, widening slightly posteriorly. Anterior portion of pharyngeal gland ducts visible, beginning at about one fifth of pharynx length from anterior. Nerve ring located at about two-thirds of pharynx length from anterior. Secretory-excretory gland, 32–50 × 15–24 µm, located up to 40 µm posterior to pharynx; secretory-excretory pore situated far anteriorly at level of anterior edge of amphids. Cardia short, surrounded by intestinal tissue. Reproductive system with two opposed outstretched testes, anterior testis to the right of intestine, posterior testis to the left of intestine; sperm cells globular, 9–11 × 7–8 µm. Spicules short, arcuate, strongly cuticularised, with straight capitulum. Gubernaculum with strongly cuticularised dorsocaudal apophyses, without crurae. Between 54 and 74 small, equidistant, tubular precloacal supplements present, sometimes indistinct; each supplement connected to a conspicuous gland. Tail conicocylindrical, with two dense rows of subventral setae and sparse subdorsal setae. Three caudal glands present.

**Females.** Similar to males but with 8–12 cervical setae, slightly smaller amphidial fovea, and tail with fewer setae. Reproductive system with two opposed, outstretched ovaries; anterior ovary to the right of intestine, posterior ovaryto the left of intestine. Eggs, 64–72 × 31–34 µm. Spermatheca not obseved. Vulva located near mid-body. Three pairs of vaginal glands present.

**Etymology.** The species name is derived from the Latin *glandis* (= acorn) and *fero* (= carry, bear), and refers to the presence of conspicuous glands associated with the precloacal supplements.

**Species diagnosis.** *Axonolaimus glandifer* **sp. nov.** is characterised by body length 1440–1690 µm in males and 1660–1790 µm in females; cephalic setae 0.6–0.8 cbd long; eight cervical setae in males (8–12 in females); amphidial fovea with elongated outline,

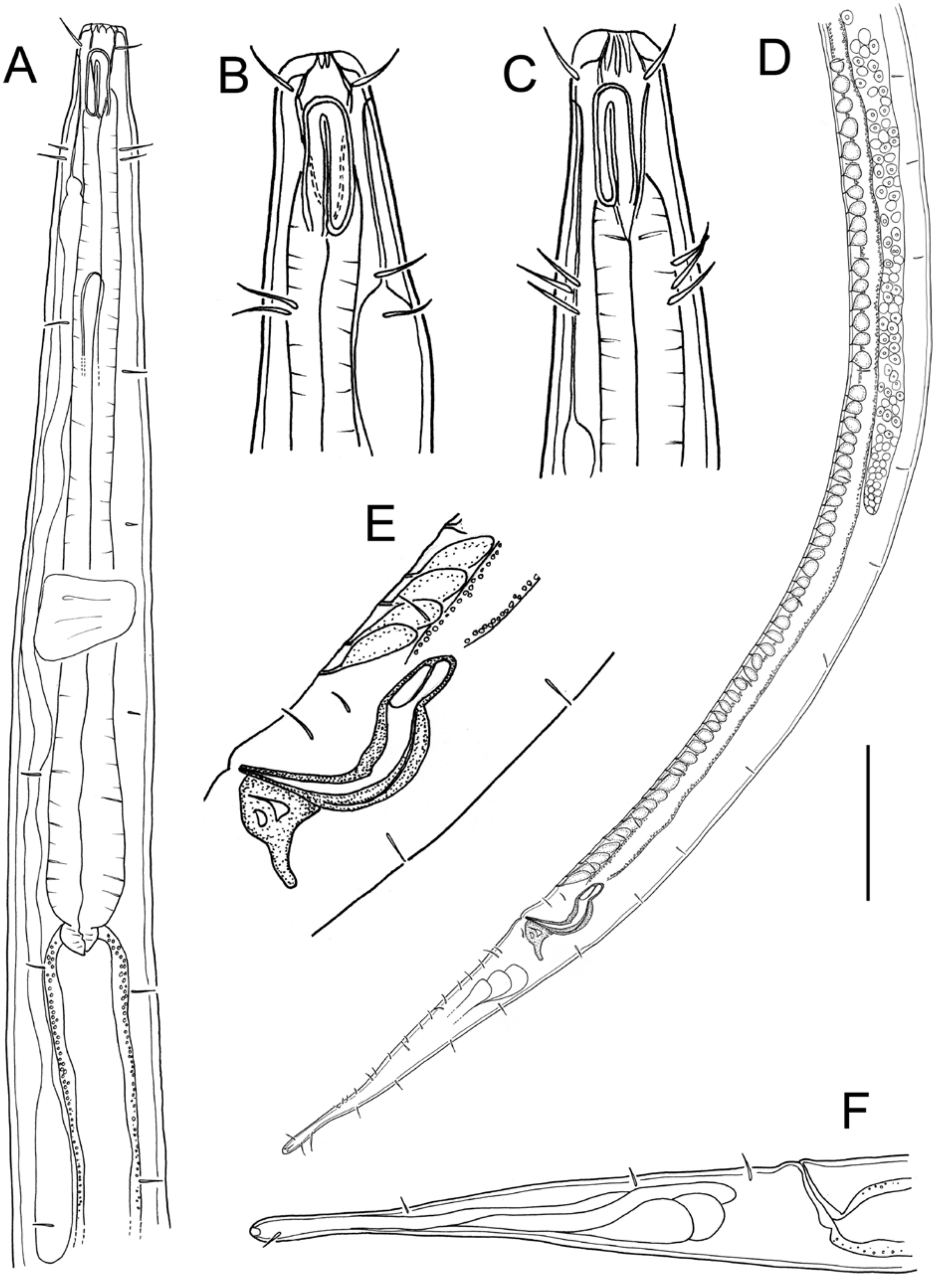



**Figure 31.** *Axonolaimus glandifer* **sp. nov.**: **A.** Anterior body region of male holotype NIWA 139284; **B.** Male paratype cephalic region NIWA 139285; **C.** Female paratype cephalic region NIWA 139285; **D.** Male holotype posterior body region NIWA 139284; **E.** Copulatory apparatus, male holotype NIWA 139284; **F.** Female paratype posterior body region NIWA 139285. Scale bar: A = 38 µm; B, C = 20 µm; D = 90 µm; E = 30 µm; F = 50 µm.

approximately as long as buccal cavity is deep or slightly shorter, and with parallel dorsal and ventral branches; secretory-excretory pore located far anteriorly at level of anterior edge of amphids; males with short, arcuate, strongly cuticularised spicules, gubernaculum with dorsocaudal apohyses, and 54–74 tubular precloacal supplements each connected to a conspicuous gland; conicocylindrical tail with dense subventral rows of setae in males.

**Differential diagnosis.** The new species is similar to *Axonolaimus arcuatus* Schuurmans Stekhoven, 1950 (Mediterranean Sea), *A. paraponticus* Hopper, 1963 (Gulf of Mexico), and *A. spinosus* (North Atlantic) in the shape and size of the amphids but can be differentiated from the latter by the position of the secretory-excretory pore at level of anterior edge of amphids (*versus* at level of mid amphid or further posteriorly in the other species). *Axonolaimus glandifer* **sp. nov.** differs from all species of the genus by the presence of a large number (> 50) of equidistant, tubular precloacal supplements associated with conspicuous glands. When present, the number of precloacal supplements in other species of the genus never exceeds 30, and associated glands are not usually conspicuous (e.g., *A. helgolandicus* Lorenzen, 1971, *A. deconincki* Vincx & Furstenberg, 1989, *A. orcombensis* Warwick, 1970, *A. hexapilus* Wieser & Hopper, 1967).

**Sequence data.** Partial SSU rDNA (1555 bp; Genbank OK317196) and D2–D3 of LSU rDNA (712 bp; Genbank OK317221).

**ZooBank registration.** *Axonolaimus glandifer* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:4617AF28-E626-4471-9C33-225CC30046E9.

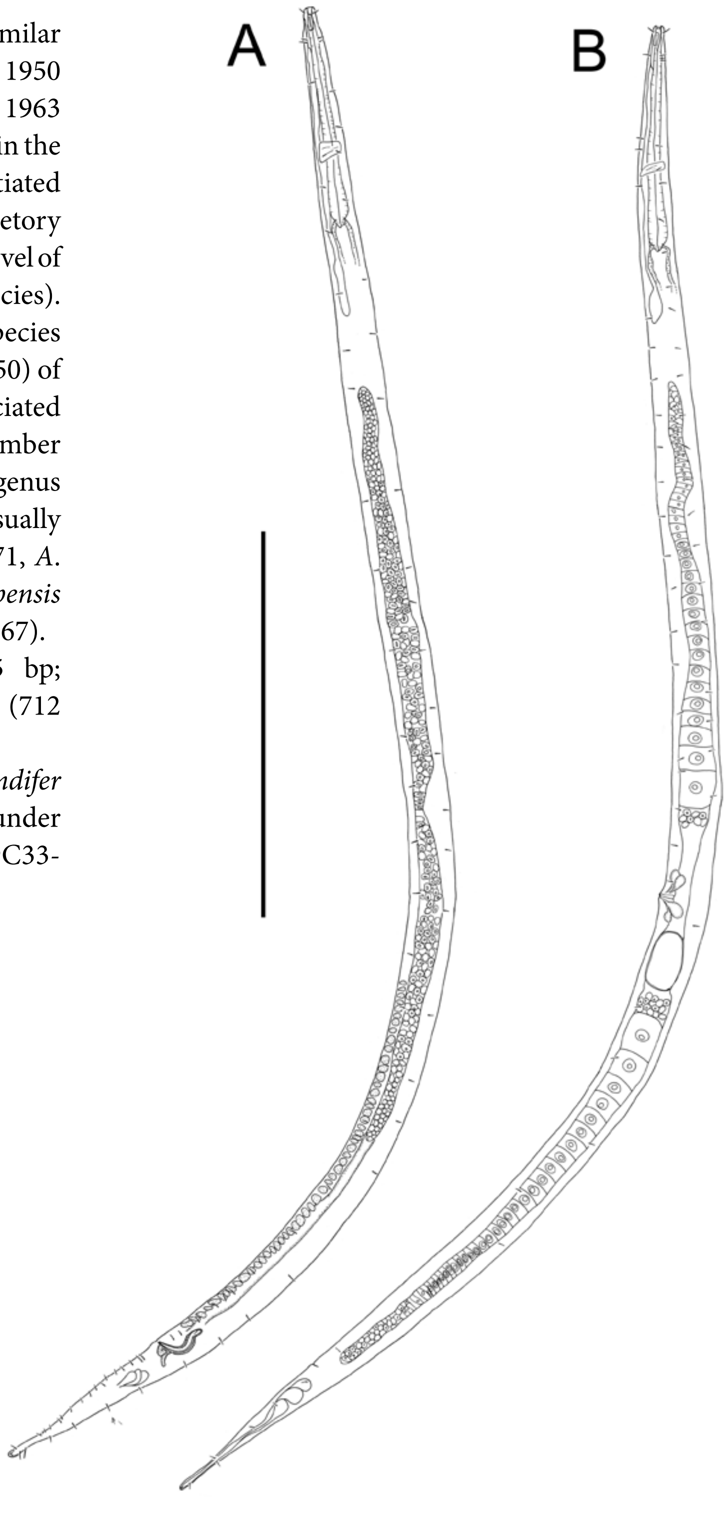



**Figure 32.** *Axonolaimus glandifer* **sp. nov.**: **A.** Entire male holotype NIWA 139284; **B.** Entire female paratype NIWA 139285. Scale bar = 400 µm.

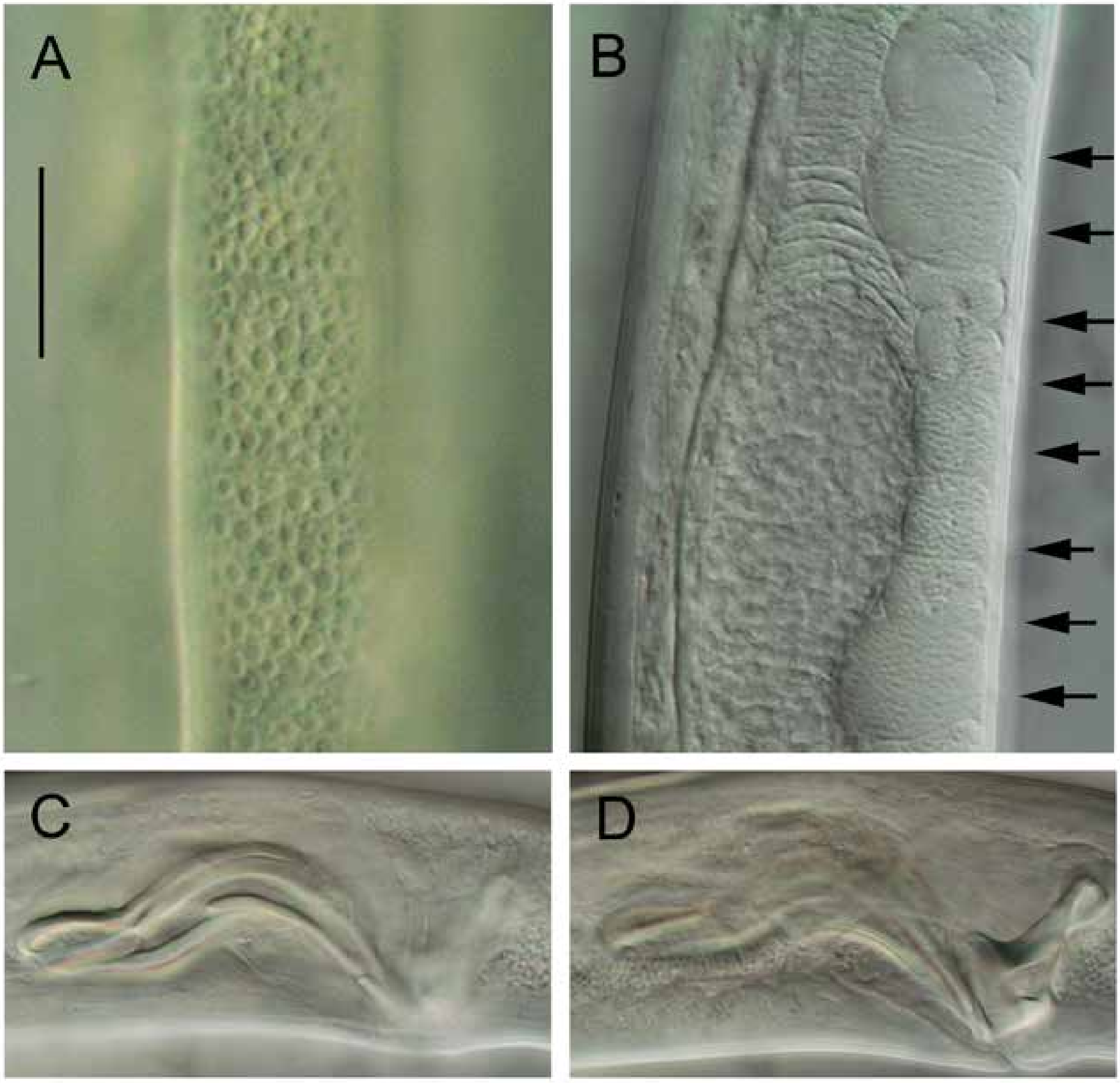



**Figure 33.** *Axonolaimus glandifer* **sp. nov.**, light micrographs: **A.** Lateral chord of female paratype NIWA 139285; **B.** Male holotype precloacal region, showing intestine (left), vas deferens (middle), and glands (right) associated with the precloacal supplements (shown by arrows) NIWA 139284; **C.** Spicule, male holotype NIWA 139284; **D.** Gubernaculum, male holotype NIWA 139284. Scale bar: A = 10 µm; B = 20 µm; C, D = 24 µm.

## Genus ***Odontophora*** Bütschli, 1874

*Odontophora* Bütschli, 1874: 49, fig. 13, table 3.
*Conolaimus* Filipjev, 1918: 323–324, fig. 72, table 10..
*Trigonolaimus* Ditlevsen, 1919: 177–180, plate 8, figs 1, 4, 5, 6, 7, 9, plate 9, figs 4, 5.

**Diagnosis.** Tapering anterior end with rounded cephalic region. Cuticle smooth or finely striated. Cephalic setae long; four to twelve cervical setae (often called 'subcephalic setae') present. Amphidial fovea loop-shaped, longitudinally elongated or with almost circular outline. Buccal cavity deep and funnel-shaped, with six odontia in anterior portion. One or two circles of cuticularised accessory buccal structures often present, alternating with odontia and often oval- or kidney-shaped or denticulated. Pharynx gradually widening posteriorly or with weak posterior bulb. Females with two oustretched ovaries and males with two opposed testes. Spicules arcuate, bent, or L-shaped; gubernacular apophyses present. Pore-like or tubular precloacal supplements present or absent. Tail usually conical, less commonly conicocylindrical (after Leduc & Zhao (2016)).

**Remarks.** The genus was recently revised by Leduc & Zhao (2016), who also provided an identification key for all 34 valid species. Another *Odontophora* species was later described by Pinto & Neres (2020).

**Type species.** *Odontophora marina* Bütschli, 1874

**Table 8.** Morphometrics (μm) of *Axonolaimus glandifer* **sp. nov.**, given as individual values, or a range of values from several specimens.

| Parameter | Males | | Females |
|---|---|---|---|
| | Holotype | Paratypes | Paratypes |
| Number of specimens | 1 | 4 | 3 |
| L | 1677 | 1435–1693 | 1656, 1785 |
| a | 35 | 33–39 | 32 |
| b | 8 | 8–9 | 8 |
| c | 9 | 8–9 | 9, 10 |
| c' | 5.0 | 4.9–5.4 | 5.1, 5.7 |
| Body diameter at cephalic setae | 12 | 12–13 | 12 |
| Body diameter at amphids | 14 | 14–15 | 14, 15 |
| Length of cervical setae | 6–8 | 6–8 | 7–8 |
| Length of cephalic setae | 7–8 | 8–9 | 7–8 |
| Amphid height | 16 | 17–18 | 15, 16 |
| Amphid width | 6 | 6 | 5 |
| Amphid width/cbd (%) | 43 | 40–43 | 33, 36 |
| Amphid from anterior end | 7 | 4–6 | 6 |
| Nerve ring from anterior end | 137 | 110–122 | 130, 144 |
| Nerve ring cbd | 34 | 29–32 | 31, 39 |
| Excretory pore from anterior end | 5 | 6–7 | 7, 8 |
| Pharynx length | 214 | 186–213 | 211, 229 |
| Pharyngeal diameter at base | 19 | 19–21 | 21 |
| Pharynx cbd at base | 36 | 34–37 | 36 |
| Maximum body diameter | 48 | 41–49 | 51, 56 |
| Spicule length | 57 | 53–61 | – |
| Gubernacular apophysis length | 16 | 18–22 | – |
| Cloacal/anal body diameter | 38 | 35–37 | 33, 34 |
| Tail length | 191 | 181–193 | 174, 189 |
| V | – | – | 843, 932 |
| %V | – | – | 51, 56 |
| Vulval body diameter | – | – | 51, 56 |

### ***Odontophora atrox*** **Leduc & Zhao, 2016**

Figs 34, 35

*Odontophora atrox* Leduc & Zhao, 2016: 1125, figs 3–6, table 1.

**Type & locality. Holotype** NIWA 99787, NIWA Stn Z19172, 41.304° S, 174.806° E, Greta Point, Wellington, lower intertidal, 2 Mar 2016, coarse sand and gravel. **Paratypes** NIWA 99788, NNCNZ 3240-2, same data as for holotype.

**Additional material examined.** NIWA 139275, NIWA Stn Z18745, 41.093° S, 174.876° E, Pāuatahanui Inlet near Camborne Walkway, upper intertidal, 28 July 2016, gravelly sand, one male and one female.

**Distribution.** Wellington Harbour and Pāuatahanui Inlet Wellington region, lower North Island, New Zealand.

**Diagnosis.** *Odontophora atrox* is characterised by body length 2055–2490 μm, cephalic setae 1.1–1.5 cbd long, twelve cervical setae, eight of which are slightly shorter and four of which are markedly shorter than the cephalic setae, excretory pore located slightly posterior to the amphids, and nerve ring located at two-thirds to three quarters of pharynx length from anterior; males are characterised by weakly arcuate spicules and tapering gubernacular apophyses, 9–10 small tubular precloacal supplements, cloaca flanked by two sets of heavily cuticularised and evertible spines, and two elongated laterodorsal setae near tail tip, 33–43 μm long.

**Sequence data.** Partial SSU rDNA (1596 bp; Genbank KX671110) and D2–D3 of LSU rDNA (704 bp; Genbank KX671112).

## Family **Comesomatidae** Filipjev, 1918
## Subfamily **Sabatieriinae** Filipjev, 1918

Subfamily Comesomatinae Filipjev, 1918: 239.

**Diagnosis.** Anterior sensilla in three separate crowns, second and third crowns very close together. Buccal cavity rather weakly cuticularised; anterior portion globular to cup-shaped, sometimes very small; posterior portion never strongly cuticularised and never cylindrical or conical, but always a narrow, collapsed tube. Spicules bent, usually enlarged proximally. Apophyses usually directed dorsocaudally and paired; if directed dorsally, apophysis is single, small, and rudimentary (after Fonseca & Bezerra (2014b)).

**Type genus.** *Sabatieria* Rouville, 1903

### Genus ***Sabatieria*** Rouville, 1903

*Sabatieria* Rouville, 1903: 1529.
*Parasabatieria* de Man, 1907: 237.

**Diagnosis.** Cuticle sometimes striated, more commonly with transverse rows of punctations, lateral differentiation as larger regular or irregular punctuation may occur. Anterior sensilla arranged in three circles. Cephalic setae longer than the outer labial setae. Anterior portion of buccal cavity globular to cup-shaped, posterior portion narrow and tubular, weakly cuticularised; sometimes with small projections of the wall at the border between the two portions. Male excretory system with two additional uninucleate subventral gland cells far behind the cardia. Spicules usually enlarged proxi-

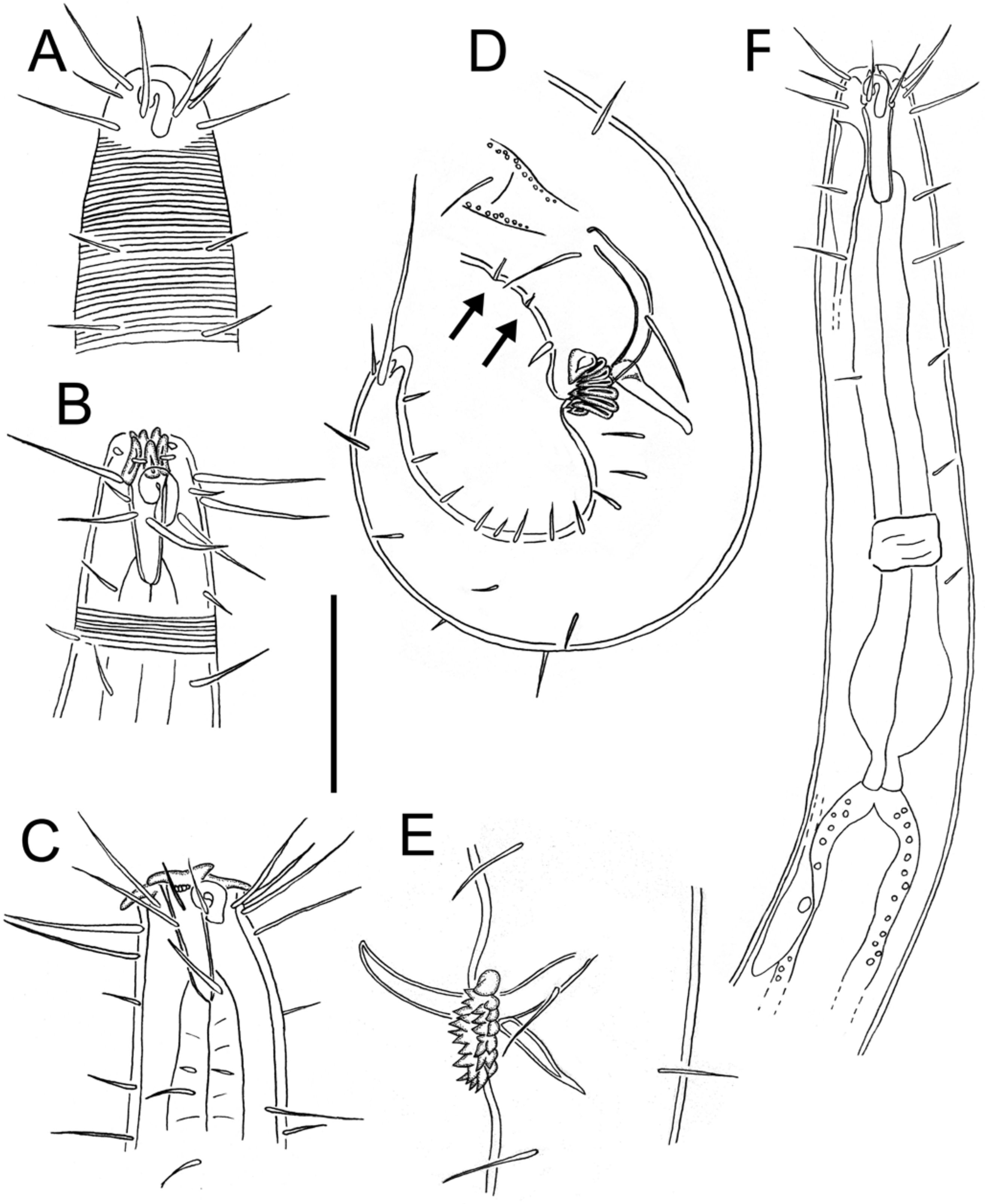



**Figure 34.** *Odontophora atrox* Leduc & Zhao, 2016, males: **A.** Lateral surface view of cephalic region; **B–C.** Lateral view of cephalic region; **D.** Posterior body region with inverted cloacal spines; **E.** Copulatory apparatus showing everted precloacal spines; **F.** Anterior body region. Scale bar: A–D = 30 µm; E = 26 µm; F = 40 µm. Modified from Leduc & Zhao (2016) with permission from E.J. Brill/ Dr W. Backhuys, Leiden publishers.

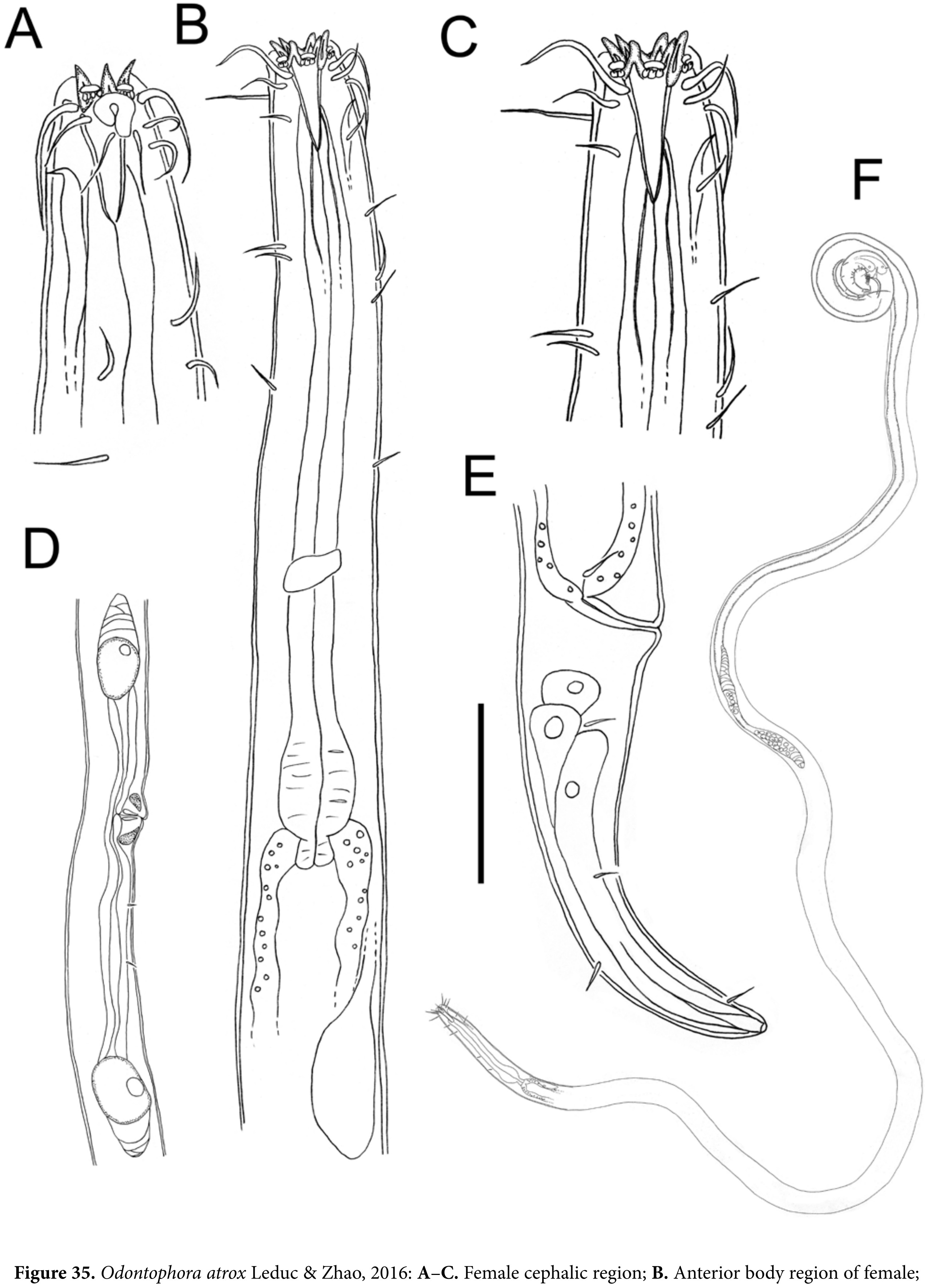



**Figure 35.** *Odontophora atrox* Leduc & Zhao, 2016: **A–C.** Female cephalic region; **B.** Anterior body region of female; **D.** Female reproductive system; **E.** Female posterior body region; **F.** Entire male. Scale bar: A, C, E = 30 µm; B = 40 µm; D = 90 µm; F = 220 µm. Modified from Leduc & Zhao (2016) with permission from E.J. Brill/ Dr W. Backhuys, Leiden publishers.

mally, apophyses usually directed dorsocaudally or caudally (from Fonseca & Bezerra (2014b)).

**Remarks.** Seventy-six valid *Sabatieria* species have been described to date (Platt 1985; Fonseca & Bezerra 2014b; Botelho *et al.* 2014; Rosli *et al.* 2014; Leduc 2017; Guo *et al.* 2018; Fu *et al.* 2019; Yang *et al.* 2019; Zhai *et al.* 2020). Because of the large number of species in the genus, Platt (1985) suggested splitting the genus into the following five species groups to facilitate species identification based on morphological differences:

*Praedatrix* species group (49 species): Most species with lateral cuticle differentiation of larger, more widely spaced punctations and amphids with three turns, but two or four turns may also occur. Spicules without central lamella distinct from the internal projection from proximal end. Simple tubular or pore-like supplements and straight gubernacular apophyses. This large group is relatively loosely defined, and unlike the other groups it is not characterised by any autapomorphic features.

*Armata* species group (6 species): Similar to *Praedatrix* group except for the elongated cephalic setae (>1.7 cbd) and usually slender bodies (a >65 except in *S. migrans* Jensen & Gerlach, 1977). Amphids usually with three turns but four turns may also occur. Simple tubular supplements.

*Pulchra* species group (10 species): Pairs of short and relatively stout cervical setae present. Amphids with three to four turns. Five to nine conspicuous precloacal supplements. Gubernaculum characterised by median piece (cuneus) with a well-developed caudally directed bar extending from its proximal end.

*Celtica* species group (5 species): Amphids with three turns. Body relatively large and stout. Curved gubernacular apophyses and conspicuous precloacal supplements.

*Ornata* species group (6 species): Amphids usually with three turns. Similar to *Celtica* group except for the presence of a posterior group of more closely situated precloacal supplements.

**Type species.** *Sabatieria cettensis* Rouville, 1903

### *Sabatieria* cf. *granifer* Wieser, 1954

Figs 36–39; Table 9

*Sabatieria granifer* Wieser, 1954: 130, fig. 169.

**Type & locality.** Golfo de Ancud, Chile, 41.917° S, 72.966° W. Types presumed lost; curators at Lund University in Sweden where parasitic nematodes collected during same Chile expedition are stored do not know where free-living nematode types might be located.

**Additional material examined.** NIWA 139276, NIWA Stn Z18745, 41.093° S, 174.877 ° E, Pāuatahanui Inlet near Camborne Walkway, upper intertidal, 28 Jul 2016, gravelly sand, six males and four females.

**Distribution.** Golfo de Ancud (Chile) and Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Diagnosis.** *Sabatieria* cf. *granifer* specimens from Pāuatahanui Inlet are characterised by colourless body, 2280–2820 μm long. Cuticle with lateral differentiation of larger, irregularly spaced punctations; eight longitudinal rows of somatic setae, most dense in pharyngeal region. Six inner labial papillae and six outer labial papillae in separate circles; cephalic setae 6–10 μm (0.33–0.56 cbd) long, located posterior to outer labial papillae at level with anterior edge of amphids. Amphidial fovea with 2.25 turns, 0.50–0.58 cbd wide in males and 0.40–0.50 cbd wide in females. Cuticularised cup-shaped buccal cavity with minute pointed projections at base. Secretory-excretory system present with excretory pore slightly posterior to nerve ring and ventral gland immediately posterior to pharynx. Pharynx muscular, cylindrical, widening posteriorly but not forming true bulb; pharyngeal gland ducts clearly visible. Males with spicules 92–105 μm long (1.6–2.1 cloacal body diameters), 35–43 μm long dorsocaudal gubernacular apophyses with wide base, tapering distally and surrounding spicules distally. Rectal glands present. At least 14 indistinct tubular supplements present. Conicocylindrical tail 3.9–4.5 cloacal body diameters long with three terminal setae. Three caudal glands and spinneret present. Vulva at 44–45% of body length from anterior; vaginal glands present. Female tail 4.9–5.4 anal body diameters long with sparse setae.

**Remarks.** The Pāuatahanui Inlet specimens are morphologically very close to *Sabatieria granifer* in most respects, except for the following minor differences: slightly smaller amphids (in males: 10–11 *versus* 12 μm and 0.50–0.58 *versus* 0.66 cbd; in females: 8–9 *versus* 11 μm and 0.40–0.50 *versus* 0.50 cbd), longer spicules (1.6–2.1 *versus* 1.5 cloacal body diameters), and shorter gubernacular apophyses (35–43 *versus* 54 μm). It is possible that the two geographically disparate populations in fact represent different species, but unfortunately no molecular sequence is available from the Chile population to test this hypothesis.

**Sequence data.** Partial SSU rDNA (1519 bp; Genbank OK317197) and D2–D3 of LSU rDNA (733 bp; Genbank OK317222).

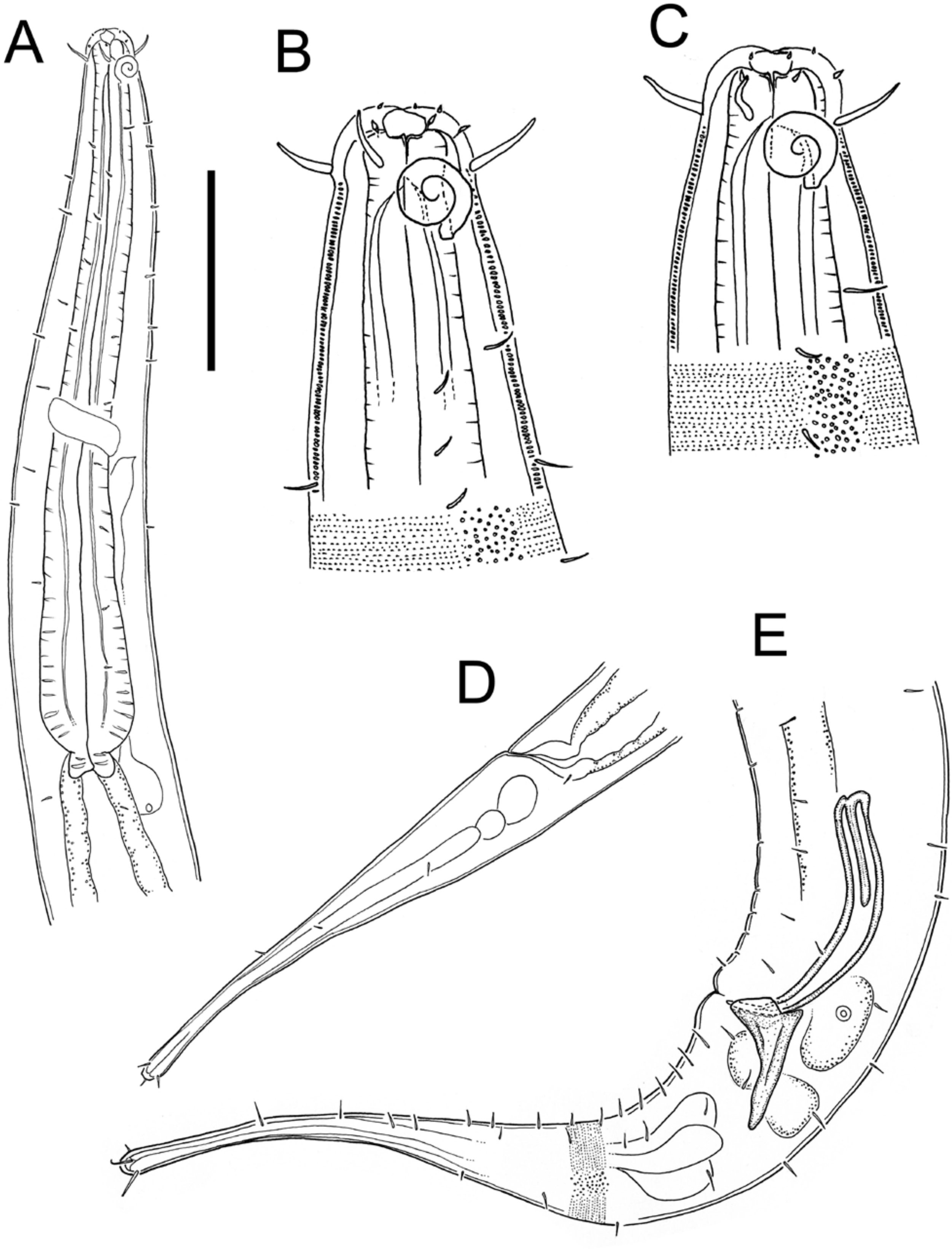



**Figure 36.** *Sabatieria* cf. *granifer* Wieser, 1954, NIWA 139276: **A.** Male anterior body region; **B.** Male cephalic region; **C.** Female cephalic region; **D.** Female posterior body region; **E.** Male posterior body region. Scale bar: A = 75 µm; B, C = 26 µm; D = 100 µm; E = 65 µm.

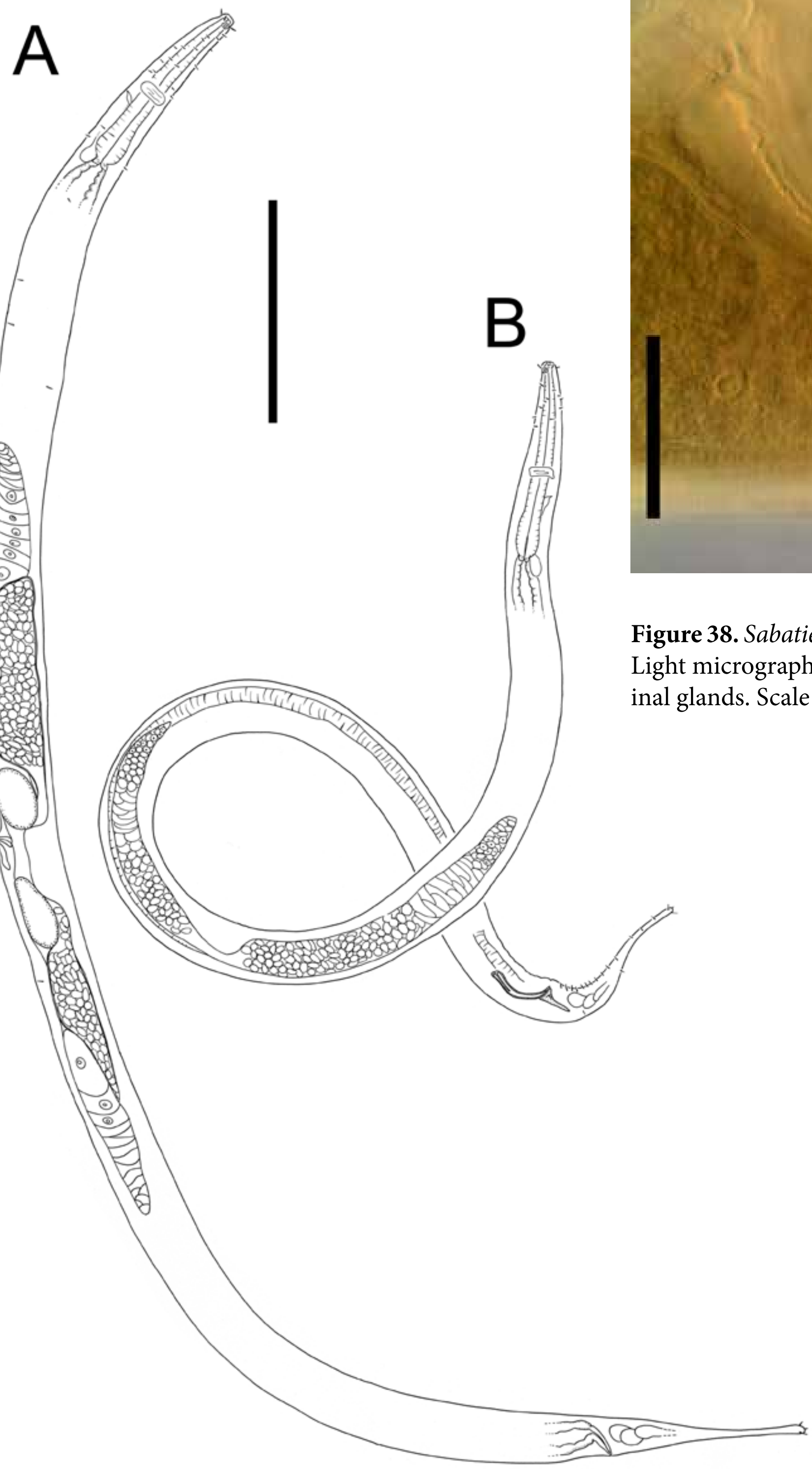



**Figure 37.** *Sabatieria* cf. *granifer* Wieser, 1954, NIWA 139276: **A.** Entire female; **B.** Entire male. Scale bar = 250 µm.

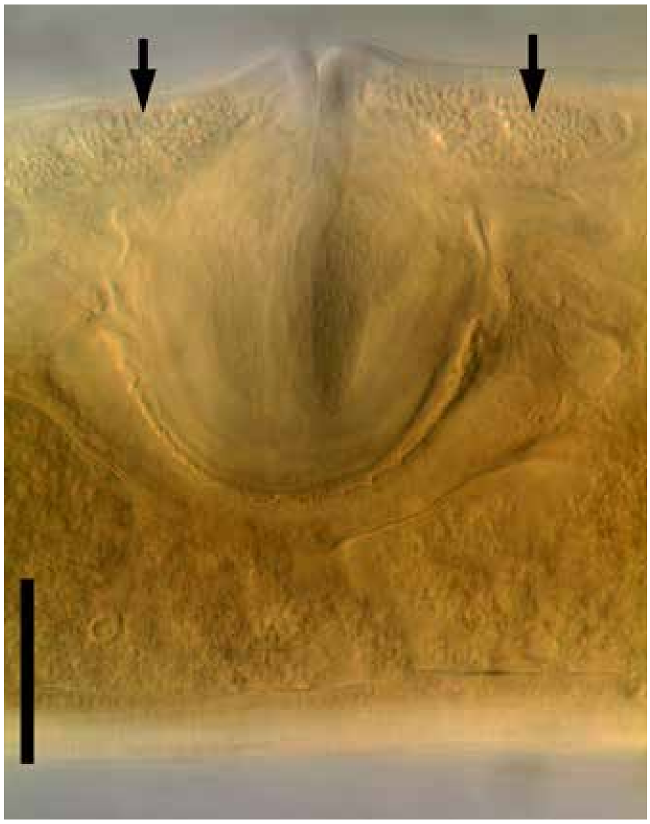


**Figure 38.** *Sabatieria* cf. *granifer* Wieser, 1954, NIWA 139276: Light micrograph of vagina, arrows showing location of vaginal glands. Scale bar = 20 µm.

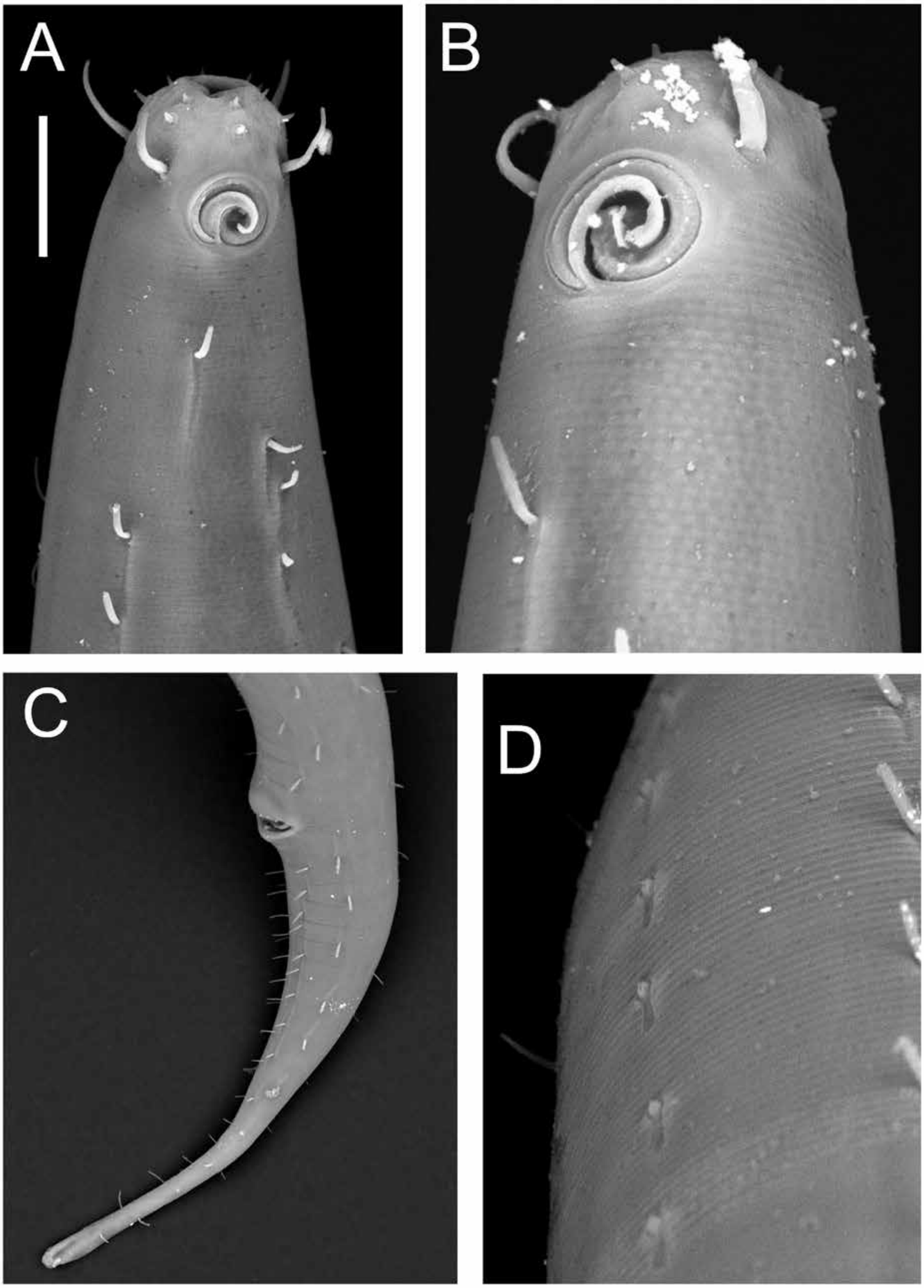



**Figure 39.** *Sabatieria* cf. *granifer* Wieser, 1954 Scanning electron micrographs: **A.** Female anterior body region; **B.** Male cephalic region; **C.** Male posterior body region; **D.** Surface view of precloacal supplements. Scale bar: A = 10 µm; B = 5 µm; C = 35 µm; D = 7 µm.

**Table 9.** Morphometrics (µm) of *Sabatieria* cf. *granifer* Wieser, 1954, given as a range of values from several specimens.

| Parameter | Males | Females |
|---|---|---|
| Number of specimens | 4 | 3 |
| L | 2283–2826 | 2496–2593 |
| a | 33–37 | 31–38 |
| b | 9–11 | 10 |
| c | 10–11 | 10–11 |
| c' | 3.9–4.5 | 4.9–5.4 |
| Body diameter at cephalic setae | 17–18 | 18 |
| Body diameter at amphids | 18–20 | 18–20 |
| Length of cephalic setae | 7–10 | 6–10 |
| Amphid height | 8–11 | 10 |
| Amphid width | 10–11 | 8–9 |
| Amphid width/cbd (%) | 50–58 | 40–50 |
| Amphid from anterior end | 6–7 | 6–9 |
| Nerve ring from anterior end | 123–141 | 135–140 |
| Nerve ring cbd | 43–51 | 43–49 |
| Excretory pore from anterior end | 150–175 | 158–162 |
| Pharynx length | 237–257 | 248–265 |
| Pharyngeal diameter at base | 31–38 | 33–36 |
| Pharynx cbd at base | 49–59 | 54–59 |
| Maximum body diameter | 61–77 | 69–82 |
| Spicule length | 92–105 | – |
| Gubernacular apophysis length | 35–43 | – |
| Cloacal/anal body diameter | 50–58 | 44–50 |
| Tail length | 220–263 | 233–252 |
| V | – | 1115–1138 |
| %V | – | 44–45 |
| Vulval body diameter | – | 69–82 |

## *Sabatieria paramacramphis* sp. nov.

Figs 40, 41; Table 10

**Material examined. Holotype** NIWA 139286, NIWA Stn Z18746, 41.098° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 28 Jul 2016, fine sand, male. **Paratype** NIWA 139287, one female, same data as for holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Male.** Body colourless, cylindrical, tapering slightly towards both extremities. Cuticle punctated, with lateral differentiation of slightly larger punctations. Sparsely distributed somatic setae present along entire body length, 4–7 µm long. Blunt, slightly rounded cephalic region, set off from rest of body by slight constriction at level of amphids. Six small inner labial papillae present on lip region; six outer labial papillae in a separate circle and four cephalic setae situated further posteriorly, 1.1 cbd long. Amphidial fovea large, spiral, situated immediately posterior to cephalic setae, with slightly less than 2.5 turns. Buccal cavity medium-sized, cup-shaped, with small cuticularised teeth. Pharynx muscular, not surrounding buccal cavity, widening posteriorly but not forming true bulb. Anterior portion of pharyngeal gland ducts visible, connecting with pharyngeal lumen at level of amphids. Nerve ring located near half of pharynx length. Secretory-excretory gland located immediately posterior to pharynx; secretory-excretory pore situated ca. 1.0 cbd posterior to nerve ring, with two small, nucleated accessory glands. Cardia short, surrounded by intestinal tissue. Reproductive system with two opposed outstretched testes; both testes to the right of intestine, sperm cells globular, nucleated, 3–6 × 7–11 µm. Spicules paired, equal, arcuate, 1.4 cloacal body diameters long, with short central cuticularised projection (lamella) in proximal portion, tapering distally. Gubernaculum with bent apophyses and small crurae. Ejaculatory glands present but outline indistinct; rectal glands not observed. Precloacal seta not observed. Twelve tubular precloacal supplements present; five posterior-most supplements conspicuously closer to each other than anterior supplements. Tail conicocylindrical, with sparse subventral setae and sparse subdorsal setae; three terminal setae, 5–6 µm long. Three caudal glands present.

**Female.** Similar to males but with longer body length, higher ratio of b and c, slightly shorter cephalic setae 0.9 cbd long, smaller amphidial fovea 0.6 cbd wide, and tail with fewer setae. Reproductive system with two opposed, outstretched ovaries; anterior ovary to the left of intestine, posterior ovary to the right of intestine. Eggs, 91 × 33–34 µm. Small spermatheca present, pocket-shaped, one in each genital branch. Vulva located near mid-body; vaginal glands not observed.

**Etymology.** The species name alludes to the similarity between the new species and *Sabatieria macramphis* Lorenzen, 1971, which like the new species is characterised by large amphids.

**Species diagnosis.** *Sabatieria paramacramphis* **sp. nov.** is characterised by relatively slender body (a = 59–62); body length 1990 µm in male and 2460 µm in female; cephalic setae 0.9–1.1 cbd long; cuticle with lateral differentiation of slightly larger punctations; male with large amphids (0.8 cbd wide) with ca. 2.5 turns, female with smaller amphid (0.6 cbd wide) with ca. 2.5 turns; buccal cavity with small cuticularised

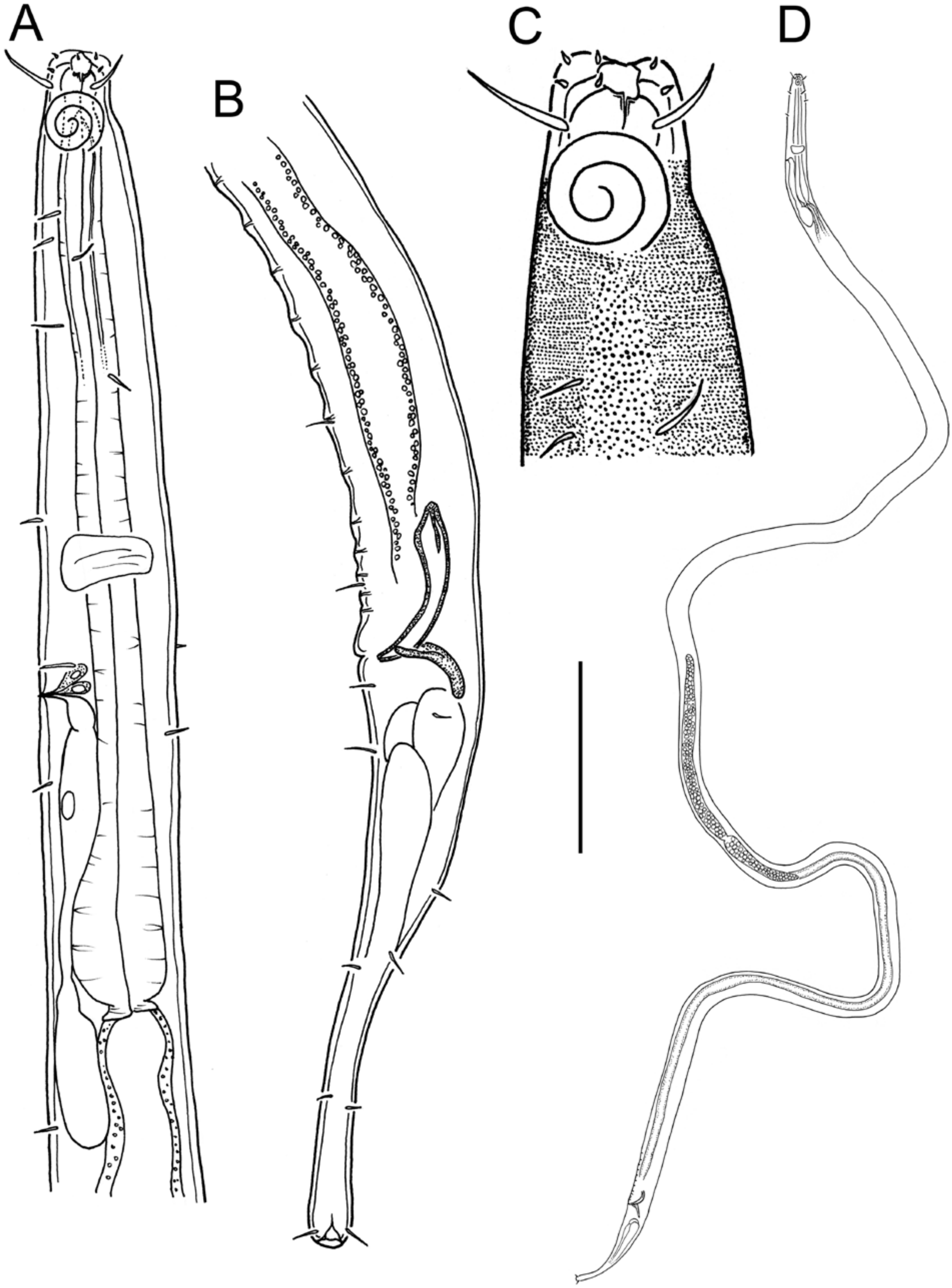



**Figure 40.** *Sabatieria paramacramphis* **sp. nov.**: **A.** Anterior body region, male holotype NIWA 139286; **B.** Posterior body region, male holotype NIWA 139286; **C.** Cephalic region, male holotype NIWA 139286; **D.** Entire male paratype NIWA 139287. Scale bar: A = 40 μm; B = 42 μm; C = 20 μm; D = 275 μm.

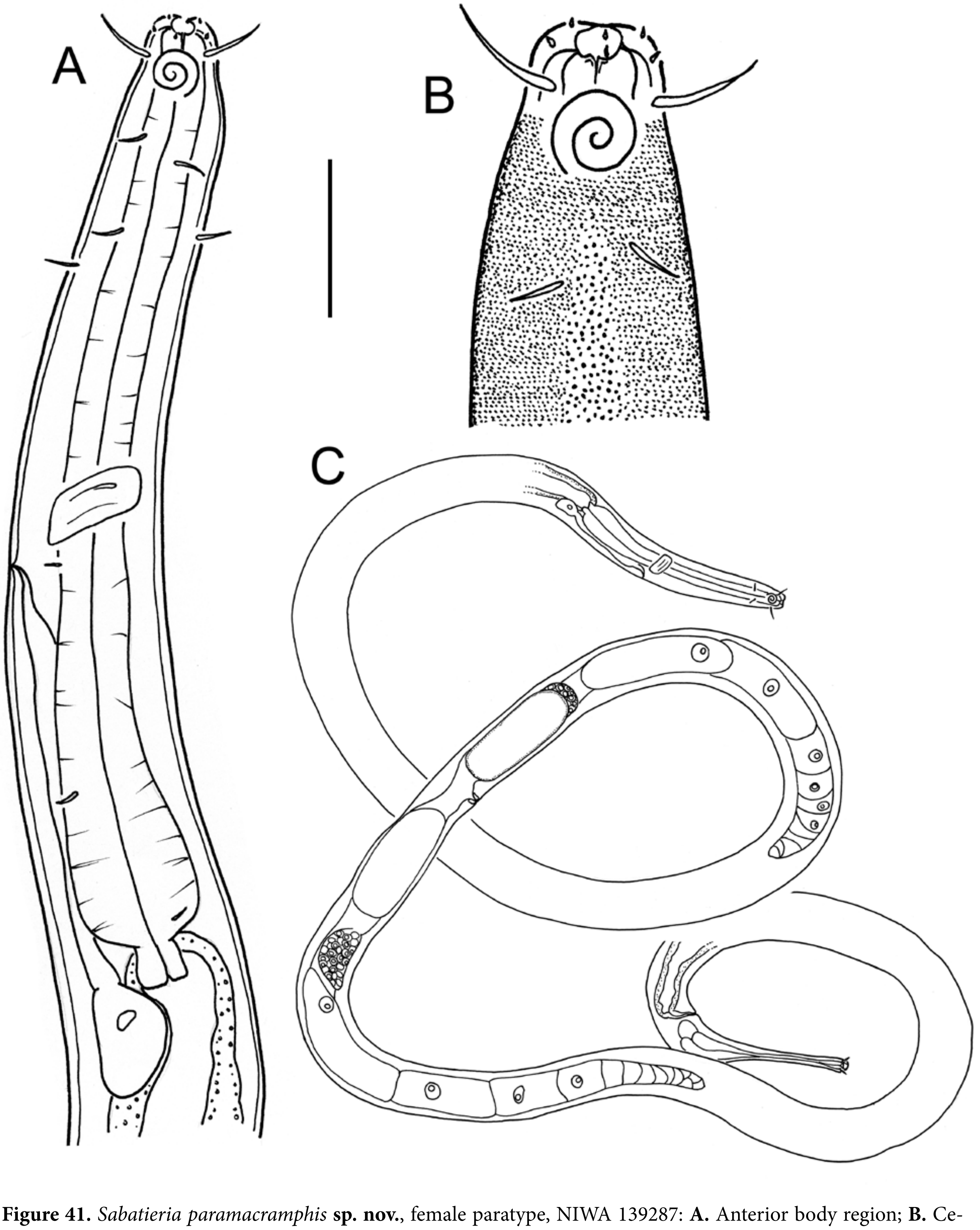



**Figure 41.** *Sabatieria paramacramphis* **sp. nov.**, female paratype, NIWA 139287: **A.** Anterior body region; **B.** Cephalic region; **C.** Entire female. Scale bar: A = 25 µm; B = 13 µm; C = 114 µm.

teeth; secretory-excretory system with pore slightly posterior to nerve ring; male with spicules 1.4 cloacal body diameters long, curved gubernacular apophyses, and twelve tubular precloacal supplements with five posterior-most supplements closer together than anterior supplements; conicocylindrical tail 4.2–4.6 cloacal/anal body diameters long.

**Differential diagnosis.** The new species belongs to the *ornata* species group of Platt (1985) due to the presence of a bent gubernaculum and of a posterior group of more closely situated precloacal supplements. *Sabatieria paramacramphis* **sp. nov.** most closely resembles *S. macramphis* (North Atlantic), *S. longisetosa* (Kreis, 1929) Wieser, 1954 (North Atlantic), and *S. strigosa* Lorenzen, 1971 (North Atlantic) in the relatively large amphid and long cephalic setae. *Sabatieria paramacramphis* **sp. nov.** can be differentiated from *S. longisetosa* by the longer body (1990–2460 µm *versus* 1300–1600 µm in *S. longisetosa*), greater ratio of a (59–62 *versus* 42–46 in *S. longisetosa*), presence of somatic setae in pharyngeal region (*versus* absent in *S. longisetosa*) and cuticularised buccal cavity with teeth (*versus* not cuticularised and without teeth in *S. longisetosa*). *Sabatieria paramacramphis* **sp. nov.** can be differentiated from *S. macramphis* by the shorter cephalic setae (11–14 µm and 0.9–1.1 cbd *versus* 18–20 µm and 1.4–1.7 cbd in *S. macramphis*) and structure of the spicules (40 µm long, bent, with short lamella, and without distal hook versus 27–31 µm long, almost straight, without lamella and with distal hook in *S. macramphis*). *Sabatieria paramacramphis* **sp. nov.** differs from *S. strigosa* in the greater ratio of c (15–20 *versus* 13–14 in *S. strigosa*), shorter cephalic setae (11–14 µm *versus* 17–23 µm in *S. strigosa*) and longer spicules (40 µm *versus* 28–31 µm in *S. strigosa*).

**Table 10.** Morphometrics (µm) of *Sabatieria paramacramphis* **sp. nov.**, given as individual values.

| Parameter | Male Holotype | Female Paratype |
|---|---|---|
| Number of specimens | 1 | 1 |
| L | 1994 | 2458 |
| a | 62 | 59 |
| b | 10 | 16 |
| c | 15 | 20 |
| c' | 4.5 | 4.2 |
| Body diameter at cephalic setae | 13 | 12 |
| Body diameter at amphids | 15 | 13 |
| Length of cephalic setae | 14 | 11 |
| Amphid height | 12 | 7 |
| Amphid width | 12 | 8 |
| Amphid width/cbd (%) | 80 | 62 |
| Amphid from anterior end | 8 | 6 |
| Nerve ring from anterior end | 104 | 85 |
| Nerve ring cbd | 28 | 26 |
| Excretory pore from anterior end | 135 | 107 |
| Pharynx length | 193 | 157 |
| Pharyngeal diameter at base | 20 | 20 |
| Pharynx cbd at base | 29 | 31 |
| Maximum body diameter | 32 | 42 |
| Spicule length | 40 | – |
| Gubernacular apophysis length | 15 | – |
| Cloacal/anal body diameter | 29 | 30 |
| Tail length | 131 | 125 |
| V | – | 1271 |
| %V | – | 52 |
| Vulval body diameter | – | 36 |

**Sequence data.** Partial SSU rDNA (1262 bp; Genbank OK317198) and D2–D3 of LSU rDNA (777 bp; Genbank OK317223).

**ZooBank registration.** *Sabatieria paramacramphis* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:6090ABD7-F88E-4A01-B616-EF39F371A00D.

## Order **Chromadorida** Chitwood
## Family **Chromadoridae** Filipjev, 1917
## Subfamily **Chromadorinae** Filipjev, 1917

Chromadorinae Filipjev, 1917: 24.

**Diagnosis.** Cuticle homo- or heterogeneous, usually without or with slight lateral differentiation made by larger dots. Outer labial papilliform sensilla and four cephalic setae in two separate circles. Amphidial fovea transverse slit-like, difficult to observe under light microscopy. Buccal cavity armed with three nearly equal solid teeth. Pharyngeal tissue not enlarged around the buccal cavity. Simple and distinctly defined posterior pharyngeal bulb. Precloacal cup-shaped supplementary organs usually present (after Tchesunov (2014a)).

**Type genus.** *Chromadora* Bastian, 1865

## Genus ***Chromadora*** Bastian, 1865

*Chromadora* Bastian, 1865: 167, plate 13, figs 230–248.

**Diagnosis.** Homogeneous punctated body cuticle pattern along the body, with lateral differentiation of larger punctations. Transverse slit-like amphidial fovea. Pharyngostome with three solid teeth, the dorsal tooth larger than the ventrosublateral teeth. Ocelli may be present. Males usually with cup-shaped precloacal supplements (from Tchesunov (2014a)).

**Type species.** *Chromadora nudicapitata* Bastian, 1865

### ***Chromadora* cf. *nudicapitata* Bastian, 1865**

Figs 42, 43; Table 11

*Chromadora chlorophthalma* de Man, 1876: 114–115.
*Chromadora flamionensis* Daday, 1901: 453–453.
*Prochromadora longitubus* Wieser, 1951: 470–472, fig. 12.
*Chromadora micropapillata* Schuurmans Stekhoven, 1942: 170–172.
*Chromadora micropapillata* subsp. *crucifera* Wieser, 1954: 97, fig. 149.
*Chromadora natans* Bastian, 1865: 168–169, plate 13, figs 236–238.
*Chromadora quadrilinea* Filipjev, 1918: 181, fig. 51, table 8.
*Chromadora quadrilineoides* Chitwood, 1951: 634.
*Chromadora quarnerensis* Daday, 1901: 454–456.
*Chromadora siciliana* Wieser, 1954: 203–205, fig. 20.
*Chromadorella trilinea* Paramonov, 1927: 49.

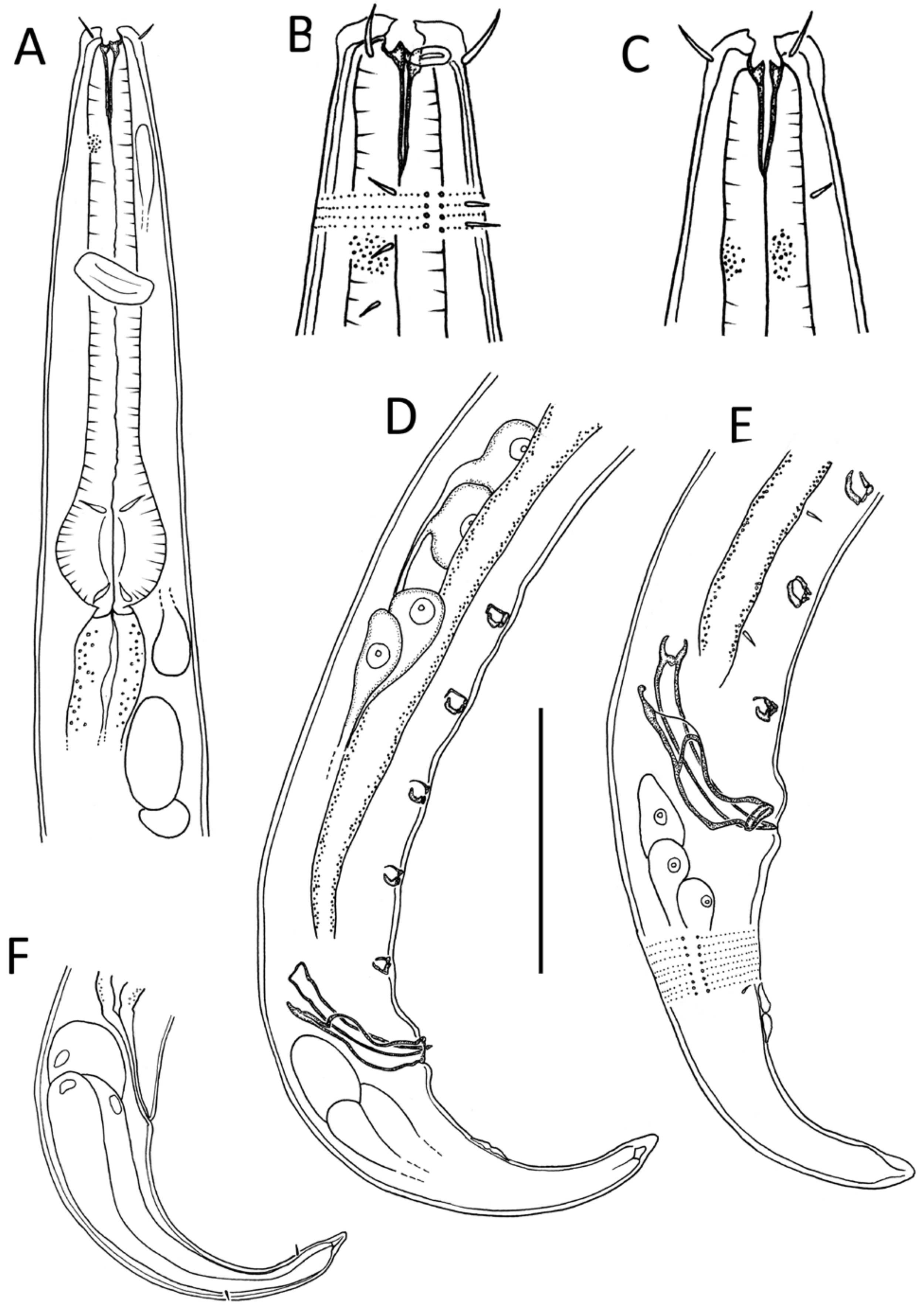



**Figure 42.** *Chromadora* cf. *nudicapitata* Bastian, 1865 NIWA 154872: **A.** Male anterior body region; **B.** Male cephalic region; **C.** Female cephalic region; **D–E.** Male posterior body region; **F.** Female posterior body region. Scale bar: A, D = 50 μm; B, C = 22 μm; E = 40 μm; F = 60 μm.

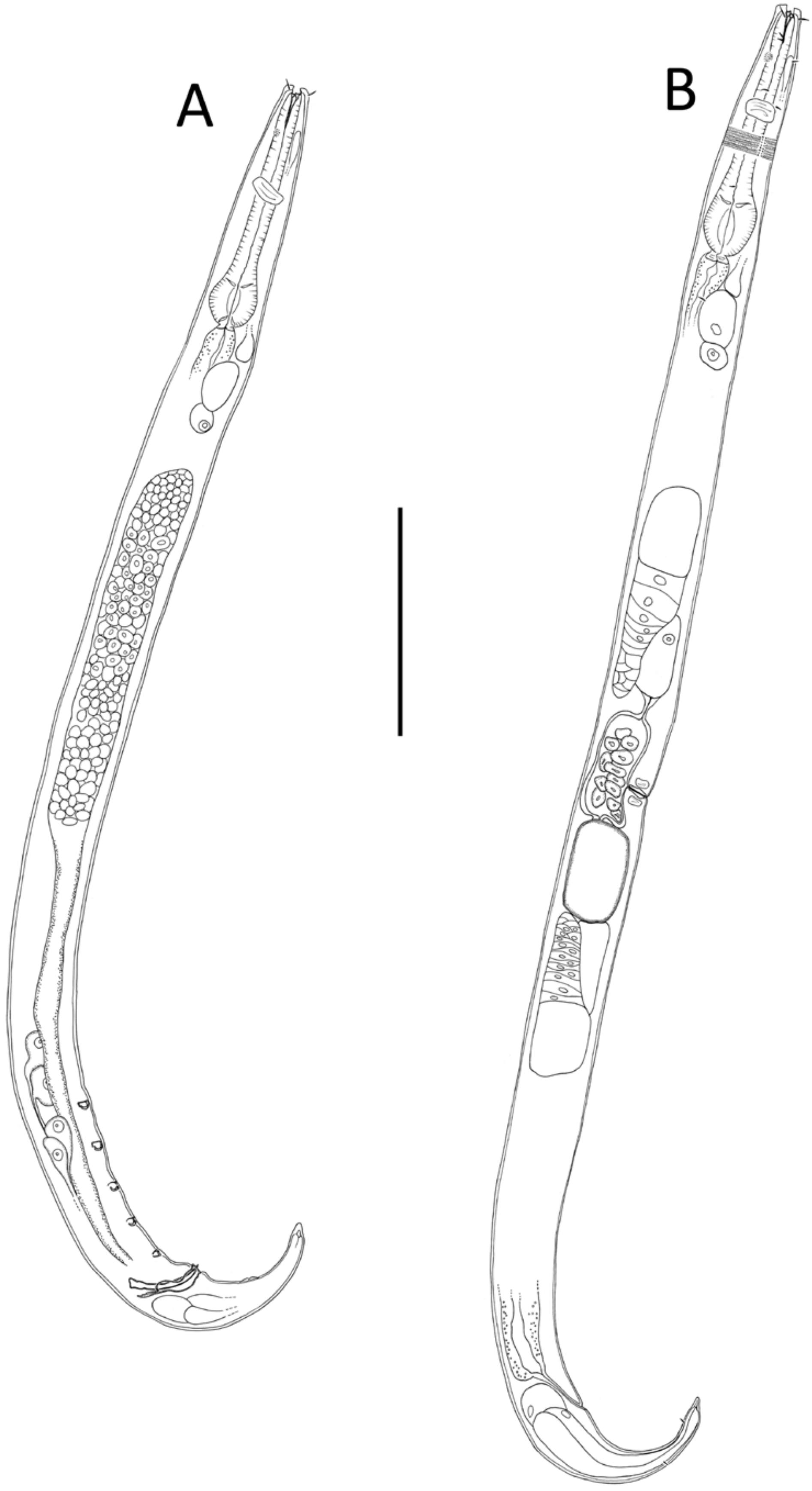



**Figure 43.** *Chromadora* cf. *nudicapitata* Bastian, 1865, NIWA 154872: **A.** Entire male; **B.** Entire female. Scale bar = 100 µm.

**Type & locality.** English Channel, North Sea. Bastian's types are presumably located at The Natural History Museum, London, but registration details of the holotype were not confirmed prior to publication.

**Additional material examined.** NIWA 154872, NIWA Stn Z19170, 41.098° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 27 Jul 2020, fine sand, seven males and six females.

**Distribution.** Cosmopolitan, including the North Sea, Mediterranean Sea, Red Sea, Black Sea, Eastern Pacific, Sea of Japan, North and South Atlantic, Australia and New Zealand (Campbell Island, South Island and Pāuatahanui Inlet).

**Diagnosis.** *Chromadora nudicapitata* specimens from Pāuatahanui Inlet are characterised by body length 604–720 µm. Homogeneous cuticle with transverse rows of punctations with lateral differentiation consisting of two longitudinal sublateral rows of larger punctations. Cephalic setae 5–6 µm (0.4–0.5 cbd) long, cervical setae 3–5 µm long. Ocelli present and located 18–25 µm from anterior extremity. Unispiral or slit-like amphids 4 µm wide. Buccal cavity with solid dorsal tooth slightly larger than the two solid ventrosublateral teeth. Pharynx with conspicuous rounded posterior bulb. Secretory-excretory system with ventral gland immediately posterior to pharynx, two nucleated accessory glands situated immediately posterior to ventral gland, and ampulla at level of ocelli (pore not observed). Males with spicules 35–37 µm long (1.3–1.6 cloacal body diameters), gubernaculum 28–31 µm long with minute denticles distally, five cup-shaped precloacal supplements located 17–20 µm from each other, and one pair of ejaculatory glands located on left and right side of vas deferens (four glands in total). Precloacal seta absent, but midventral patch of thickened cuticle with thin central duct 24–28 µm posterior to cloacal opening. Single anterior testis to the right or ventrally located relative to intestine. Conical tail 2.5–2.8 cloacal body diameters long. Female reproductive system with anterior ovary to the right of intestine and posterior ovary to the left of intestine, vulva at 47–50% of body length from anterior and tail 3.3–4.3 abd long.

**Remarks.** The Pāuatahanui Inlet specimens are morphologically similar to the specimens originally described for *Chromadora nudicapitata* from the type locality (North Sea) by Bastian (1865) and Platt & Warwick (1988), but have shorter body length (604–720 *versus* 770–1000 µm in the North Sea specimens), higher c ratio (8–10 *versus* 7 in the specimens described by Bastian (1865)), shorter spicules (24–28 *versus* 29–30 µm in the North Sea specimens), and shorter tail (2.5–2.8 *versus* 3.1–5.5 cloacal/anal body diameters in the specimens described by Platt & Warwick (1988).

**Table 11.** Morphometrics (µm) of *Chromadora* cf. *nudicapitata* Bastian, 1865, given as a range of values from several specimens.

| Parameter | Males | Females |
|---|---|---|
| Number of specimens | 4 | 4 |
| L | 604–675 | 669–752 |
| a | 19–21 | 19–20 |
| b | 6 | 6–7 |
| c | 9–10 | 8–9 |
| c' | 2.5–2.8 | 3.1–4.3 |
| Body diameter at cephalic setae | 11–12 | 11–12 |
| Body diameter at amphids | 11–12 | 12 |
| Length of cephalic setae | 5–6 | 5–6 |
| Amphid height | 2–3 | 2–3 |
| Amphid width | 4 | 4 |
| Amphid width/cbd (%) | 33–36 | 33 |
| Amphid from anterior end | 2–5 | 4–5 |
| Nerve ring from anterior end | 59–65 | 59–63 |
| Nerve ring cbd | 24–26 | 22–28 |
| Pharynx length | 101–111 | 100–120 |
| Pharyngeal bulb diameter | 21 | 21–25 |
| Pharynx bulb cbd | 26–28 | 26–32 |
| Maximum body diameter | 30–33 | 35–39 |
| Spicule length | 35–37 | – |
| Gubernaculum length | 28–31 | – |
| Cloacal/anal body diameter | 23–26 | 20–28 |
| Tail length | 63–72 | 77–89 |
| V | – | 315–365 |
| %V | – | 47–50 |
| Vulval body diameter | – | 34–39 |

**Sequence data.** Partial SSU rDNA (801 bp; Genbank OK317199) and D2–D3 of LSU rDNA (744 bp; Genbank OK317224). The Pāuatahanui Inlet SSU sequence was identical to the *Chromadora nudicapitata* sequence from the United Kingdom (Southampton; AY854205) over their region of overlap (477 bp). There was no overlap between the Pāuatahanui Inlet sequence and the only other available *Chromadora nudicapitata* sequence (Portugal; KX944131), which could therefore not be compared.

## Genus ***Chromadorina*** Filipjev, 1918

*Chromadorina* Filipjev, 1918: 162–163, fig. 44, table 7.

**Diagnosis.** Homogeneous cuticle with transverse rows of punctations but without obvious lateral differentiation. Amphidial fovea transverse slit-like (when visible). Pharyngostoma with three nearly equal solid teeth. Ocelli may be present. Cup-shaped precloacal supplements present (from Tchesunov (2014a)).

**Type species.** *Chromadorina obtusa* Filipjev, 1918

## *Chromadorina germanica* (Bütschli, 1874) Wieser, 1954

Figs 44, 45; Table 12

*Chromadora germanica* Bütschli, 1874: 48, fig. 25a, b, table 6.
*Prochromadorella germanica* De Coninck & Schuurmans Stekhoven, 1933: 73, figs 49–51.
*Heterochromadora germanica* Wieser, 1951: 466, fig. 10 a–d.
*Chromadora droebachiensis* Allgén, 1931: 244, fig. 10a–b.
*Chromadora minor* Cobb, 1894: 394, fig. 6.

**Type & locality.** Kiel Harbour, Baltic Sea, 54.366° N, 10.173° E. Types presumed lost.

**Additional material examined.** NIWA 139294, NIWA Stn Z18747, 41.106° S, 174.891° E, Bradeys Bay, Pāuatahanui Inlet, upper intertidal, 25 Sep 2018, partly anoxic gravelly sand, four males and three females.

**Distribution.** Cosmopolitan, including the Baltic Sea, North Sea, Mediterranean Sea, the east and west coasts of North America, Bay of Bengal, Australia, and New Zealand (Pāuatahanui Inlet Wellington region, lower North Island, New Zealand.).

**Diagnosis.** The *Chromadorina germanica* specimens from Pāuatahanui Inlet are characterised by body length 711–926 µm, homogeneous cuticle with transverse rows of punctations without lateral differentiation, cephalic setae 4–6 µm (0.31–0.50 cbd) long, 6–8 sublateral cervical setae mostly arranged in pairs and 1.5 cbd from anterior extremity, ocelli usually present and located 20–22 µm from anterior extremity (at same level as cervical setae), slit-like amphids 4–5 µm wide, buccal cavity with three more-or-less equal solid teeth (one dorsal and two ventrosublateral), pharynx with conspicuous rounded posterior bulb, secretory-excretory system with elongated ventral gland, a smaller accessory gland situated immediately posterior to ventral gland, and excretory pore at level of amphids. Males with spicules 26–31 µm (1.0–1.2 cloacal body diameters), gubernaculum 15–19 µm long, 17–19 precloacal supplements, a single precloacal seta, and conical tail 3.3–4.1 cloacal body diameters long. Female reproductive system with two opposed and reflexed ovaries.Vulva at 47–49% of body length from anterior and tail 5.2–5.8 abd long.

**Remarks.** The Pāuatahanui Inlet specimens are morphologically indistinguishable from the Baltic Sea specimens originally described for *Chromadorina germanica* by Bütschli (1874), and subsequent descriptions by Cobb (1894) based on Australian specimens, Wieser (1954) based on Chilean specimens, and Platt & Warwick (1988) based on North Sea specimens.

**Sequence data.** Partial SSU rDNA (1532 bp; Genbank OK317200) and D2–D3 of LSU rDNA (787 bp; Genbank OK317225). The Pāuatahanui Inlet SSU sequence differed from the *Chromadorina germanica* sequence from the United Kingdom (Southampton) by 0.16% (2 in 1270 bp). It is not clear whether this degree of divergence is sufficient to consider the Pāuatahanui Inlet specimens as a separate species. For example, some cryptic and co-generic species have identical SSU sequences (Tchesunov *et al.* 2015; Kanzaki *et al.* 2016), while other co-generic species differ by 1–2% (Tchesunov *et al.* 2015; Tandingan De Ley *et al.* 2007). Given the strong morphological similarities and paucity of molecular data, the Pāuatahanui Inlet specimens are considered to represent a population of *Chromadorina germanica* for the time being.

## Subfamily **Hypodontolaiminae** de Coninck, 1965

Hypodontolaiminae de Coninck, 1965: 636, fig. 440.

**Diagnosis.** Cuticle punctated heterogeneously or rarely homogeneously, with or without lateral differentiation. Six outer labial papillae and four cephalic setae in two separate circles. Amphidial fovea distinct or obscure, transversely flattened or oval; generally located between the four cephalic setae. Stoma funnel-shaped, armed with hollow teeth; the large dorsal tooth may be opposed by smaller ventrosublateral teeth, denticles may be present; anterior part of pharynx often with prominent dorsal muscular swelling. Males with cup-like precloacal supplements, rarely absent (after Tchesunov (2014a)).

**Type genus.** *Hypodontolaimus* de Man, 1886

### Genus *Chromadorita* Filipjev, 1922

*Chromadorita* Filipjev, 1922: 138–139.
*Allgeniella* Strand, 1934: 271.

**Diagnosis.** Cuticle ornamentation homogeneous, rarely with slightly more pronounced punctations laterally. Hollow teeth, mostly one dorsal and one or two ventrosublateral, rarely one indistinct dorsal tooth only; sometimes tiny denticles may be present. Pharynx may be swollen anteriorly in various degrees, posterior bulb single. Precloacal supplements present or absent (after Tchesunov (2014a)).

**Remarks.** Platt & Warwick (1988) noted that *Chromadorita* and the closely related genus *Innocuonema* Inglis, 1969 are very similar and that they will therefore both require revision. Baldrighi *et al.* (2018) provided a key to species of the genus.

**Type species.** *Chromadorita demaniana* Filipjev, 1922

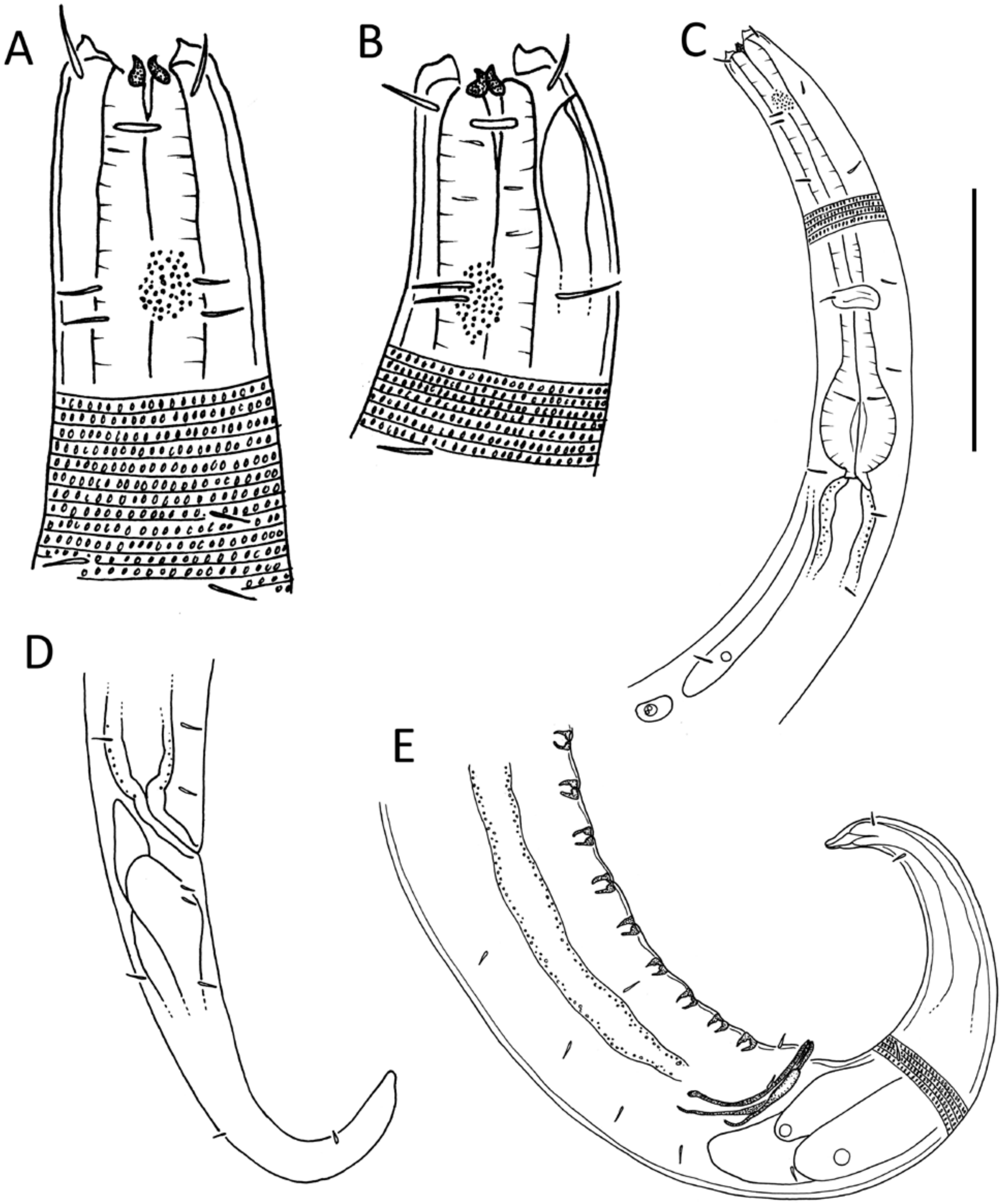



**Figure 44.** *Chromadorina germanica* (Bütschli, 1874) Wieser, 1954 NIWA 139294: **A.** Male cephalic region; **B.** Female cephalic region; **C.** Male anterior body region; **D.** Female posterior body region; **E.** Male posterior body region. Scale bar: A, B = 20 µm; C = 75 µm; D = 60 µm; E = 50 µm.

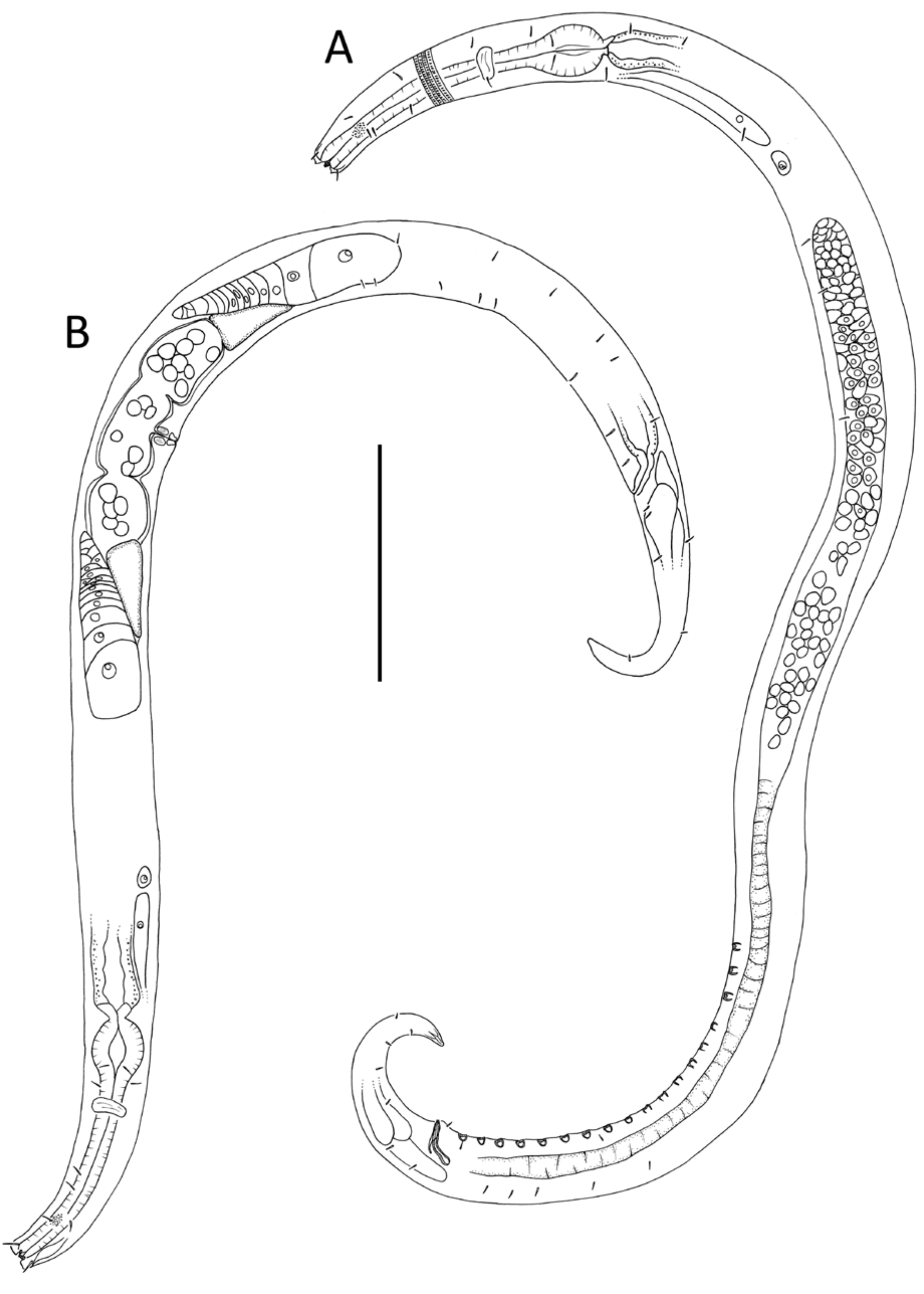



**Figure 45.** *Chromadorina germanica* (Bütschli, 1874) Wieser, 1954, NIWA 139294: **A.** Entire male; **B.** Entire female. Scale bar = 100 µm.

**Table 12.** Morphometrics (μm) of *Chromadorina germanica* (Bütschli, 1874) Wieser, 1954, given as a range of values from several specimens.

| Parameter | Males | Females |
|---|---|---|
| Number of specimens | 4 | 3 |
| L | 711–926 | 748–814 |
| a | 22–27 | 21–25 |
| b | 6–8 | 7 |
| c | 7–10 | 6–7 |
| c' | 3.3–4.1 | 5.2–5.8 |
| Body diameter at cephalic setae | 12–13 | 13–14 |
| Body diameter at amphids | 14 | 14 |
| Length of cephalic setae | 5–6 | 4–6 |
| Amphid height | 1–2 | 1–2 |
| Amphid width | 4 | 4–5 |
| Amphid width/cbd (%) | 29–36 | 36 |
| Amphid from anterior end | 4–7 | 4–5 |
| Nerve ring from anterior end | 66–81 | 62–74 |
| Nerve ring cbd | 24–27 | 25–26 |
| Pharynx length | 112–134 | 109–124 |
| Pharyngeal bulb diameter | 20–22 | 22 |
| Pharynx bulb cbd | 25–29 | 27–29 |
| Maximum body diameter | 26–42 | 32–36 |
| Spicule length | 26–31 | – |
| Gubernacular apophysis length | 17–19 | – |
| Cloacal/anal body diameter | 23–28 | 21–22 |
| Tail length | 90–96 | 109–127 |
| V | – | 359–386 |
| %V | – | 47–49 |
| Vulval body diameter | – | 32–35 |

## *Chromadorita spinicauda* sp. nov.

Figs 46–48; Table 13

**Material examined. Holotype** NIWA 139280, NIWA Stn Z18746, 41.098° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 28 Jul 2016, fine sand, male. **Paratypes** NIWA 139281, three males and two females, same data as for holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Males.** Body stout, cylindrical, colourless, tapering slightly towards anterior extremity. Cuticle annulations interspersed with transverse rows of punctations without lateral differentiation and homogeneous throughout body. Two longitudinal lateral rows of 14–15 oval cuticle pores distributed more-or-less evenly along entire length of body. Eight rows of short, 6–7 μm long somatic setae present. Blunt, slightly rounded cephalic region; lips short. Inner labial and outer labial sensilla not observed; four cephalic setae, ca. 0.31–0.38 cbd long, at level of amphids. Amphidial fovea narrow oval to slit-shaped, not surrounded by cuticle annulations, less than 0.5 cbd from anterior extremity. Cheilostome with twelve cheilorhabdia. Buccal cavity medium-sized, with large heavily cuticularised dorsal tooth with weakly cuticularised, outer raised portion protruding from pharyngeal tissue (giving buccal cavity appearance of can opener), two smaller ventrosublateral teeth present. Ducts of pharyngeal glands not observed. Pharynx muscular, with anterior portion conspicuously swollen dorsally; lumen not cuticularised. Round to oval-shaped posterior pharyngeal bulb present. Nerve ring located slightly posterior to middle of pharynx. Secretory-excretory system consisting of four glands, 12–13 × 21 μm, situated laterally, dorsally, and ventrally immediately posterior to pharynx and surrounding intestine; excretory pore located immediately anterior to cephalic setae. Cardia short, not surrounded by intestinal tissue. Reproductive system with single outstretched testis located ventrally relative to intestine; sperm cells globular or spherical, 4 × 4–6 μm. Spicules 1.7–1.8 cloacal body diameters long, arcuate, with central lamella along entire length. Short gubernaculum not surrounding spicules distally, with curved dorsocaudal apophyses. Precloacal supplements not observed. Tail conical, with sparse subventral and subdorsal setae; two subventral rows of 6–7 stout spines beginning from middle of tail length. Three caudal glands and spinneret present.

**Females.** Similar to males. Reproductive system with two opposed and reflexed ovaries; anterior ovary to the right of intestine, posterior ovary to the left of intestine. Mature eggs not observed. One spermathecum present in proximal portion of each genital branch; spermatheca rounded with thin walls and full of sperm. Vulva located near mid-body. Pars proximalis vaginae surrounded by constrictor muscle; two vaginal glands present.

**Etymology.** The species name is derived from the Latin term *spina* (= thorn) and *cauda* (= tail) and refers to the presence of subventral spines on the tail of male specimens.

**Species diagnosis.** *Chromadorita spinicauda* **sp. nov.** is characterised by body length 580–600 μm in males and 590–620 μm in females, annulated cuticle with interspersed transverse rows of punctations without lateral differentation and homogeneous throughout body, two longitudinal lateral rows of cuticle pores and eight longitudinal rows of short somatic setae, buccal cavity with large cuticularised dorsal tooth with

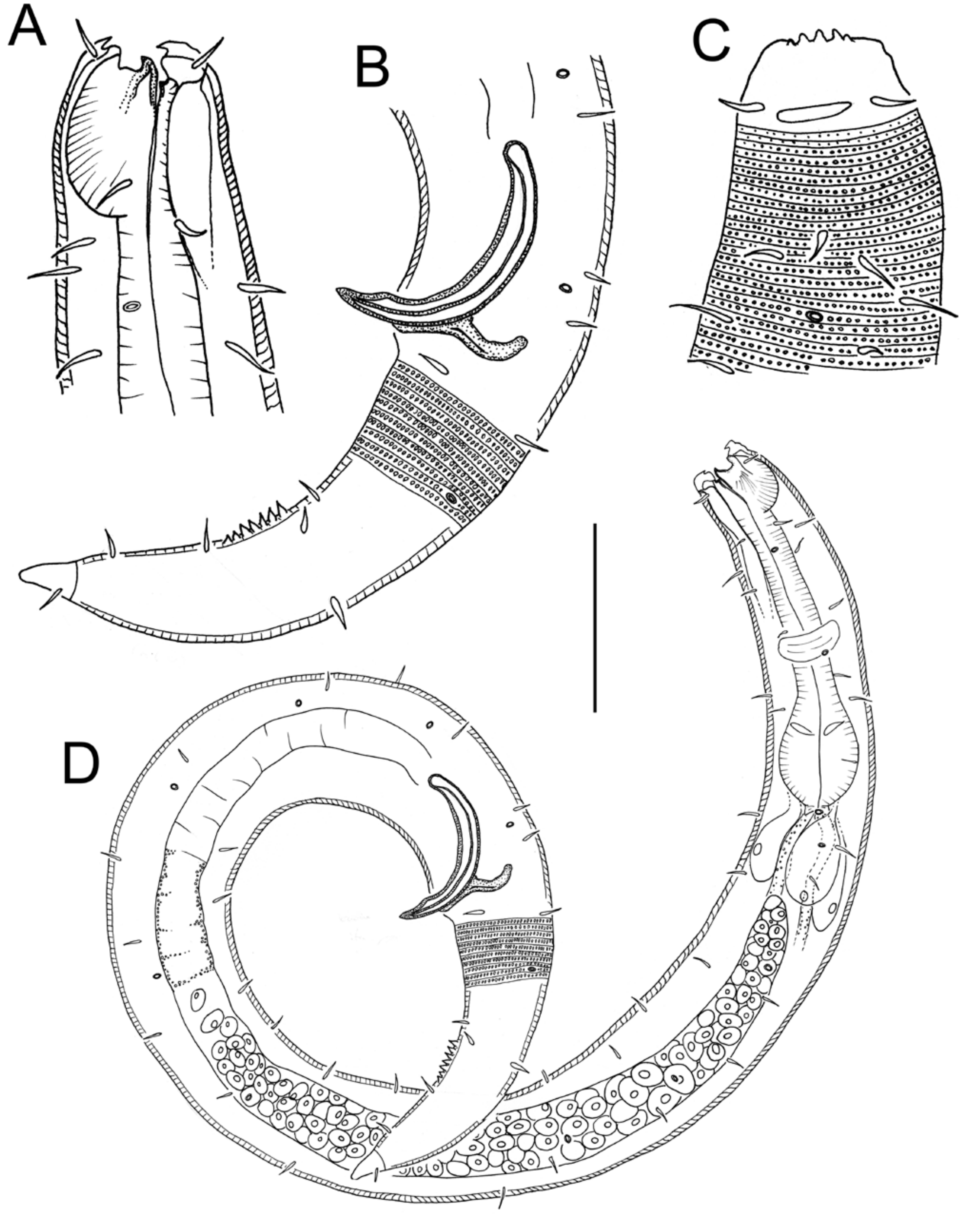



**Figure 46.** *Chromadorita spinicauda* **sp. nov.**: **A.** Cephalic region, male paratype NIWA 139281; **B.** Posterior body region, male holotype NIWA 139280; **C.** Surface view of cephalic region, male paratype NIWA 139281; **D.** Entire male holotype NIWA 139280. Scale bar: A, C = 20 µm; B = 30 µm; D = 50 µm.

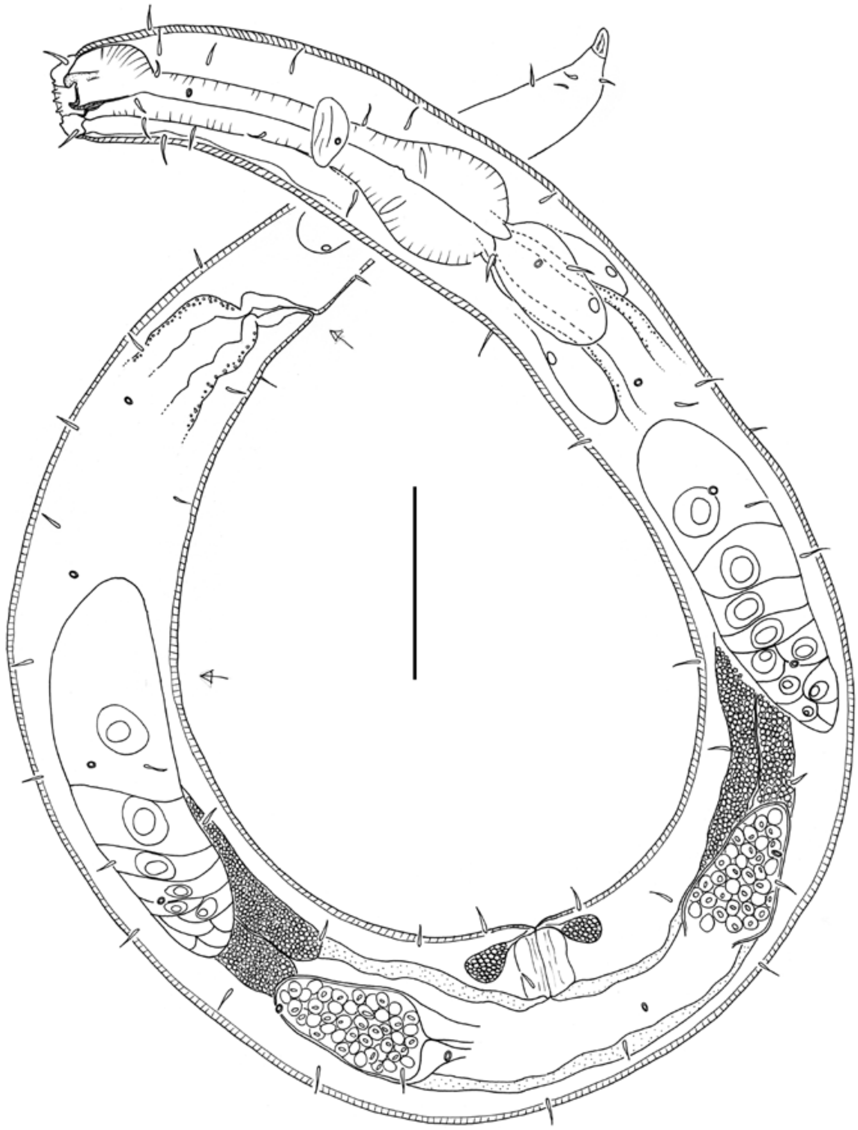


**Figure 47.** *Chromadorita spinicauda* **sp. nov.**, entire female paratype, NIWA 139281. Scale bar = 40 µm.

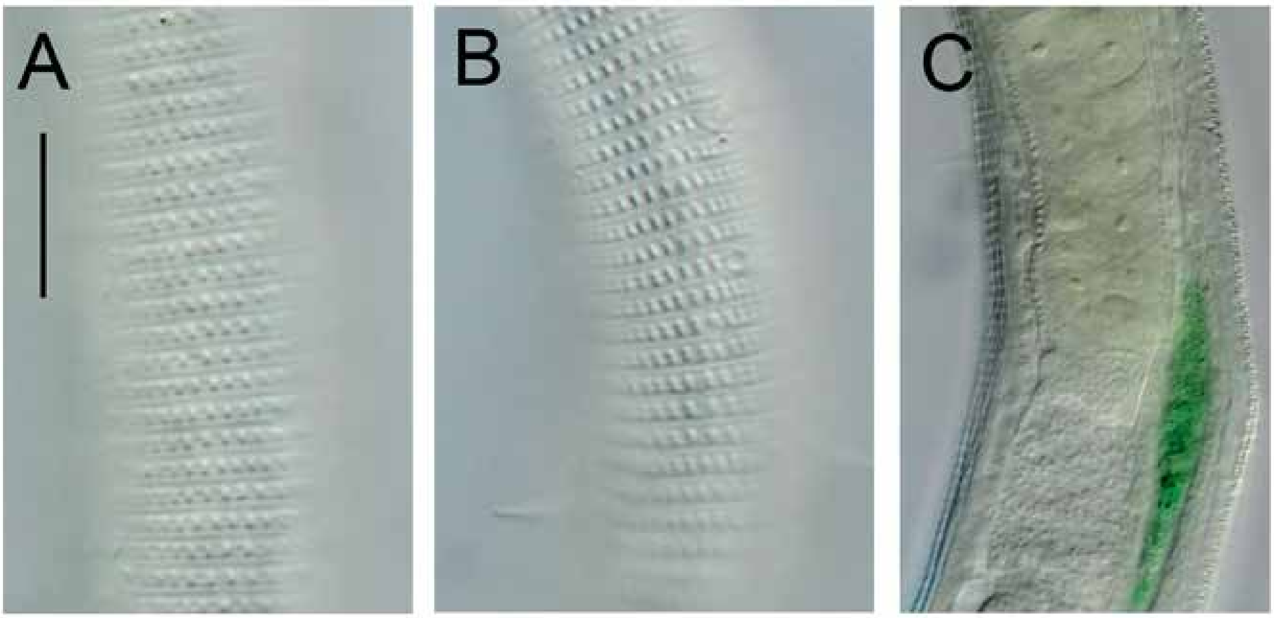



**Figure 48.** *Chromadorita spinicauda* **sp. nov.** NIWA 139281, light micrographs: **A.** Cuticle punctations, male paratype mid-body region; **B.** Cuticle punctations, male paratype cloacal body region; **C.** Posterior end of testis and intestine with pigmented contents, female paratype. Scale bar: A, B = 10 µm; C = 17 µm.

**Table 13.** Morphometrics (µm) of *Chromadorita spinicauda* **sp. nov.**, given as individual values, or a range of values from several specimens.

| Parameter | Males | | Females |
|---|---|---|---|
| | Holotype | Paratypes | Paratypes |
| Number of specimens | 1 | 3 | 2 |
| L | 583 | 581–598 | 591, 621 |
| a | 17 | 19–21 | 17, 18 |
| b | 6 | 6–7 | 6, 7 |
| c | 7 | 6 | 7, 8 |
| c' | 3.0 | 3.0–3.5 | 3.3, 3.6 |
| Body diameter at cephalic setae | 16 | 13–16 | 15, 17 |
| Body diameter at amphids | 18 | 15–17 | 18, 19 |
| Length of cephalic setae | 5 | 5 | 5–6 |
| Amphid height | 3 | 2 | 2 |
| Amphid width | 10 | 9 | 9, 10 |
| Amphid width/cbd (%) | 56 | 53–60 | 47, 56 |
| Amphid from anterior end | 6 | 2–4 | 4, 5 |
| Nerve ring from anterior end | 50 | 42–50 | 52 |
| Nerve ring cbd | 27 | 27–28 | 30 |
| Excretory pore from anterior end | 4 | 3–5 | 4 |
| Pharynx length | 93 | 84–94 | 87, 92 |
| Pharyngeal bulb diameter | 21 | 20–23 | 22, 25 |
| Pharyngeal bulb cbd | 29 | 28–29 | 29, 33 |
| Maximum body diameter | 34 | 29–31 | 33, 37 |
| Spicule length | 51 | 49–51 | – |
| Gubernacular apophysis length | 13 | 10–13 | – |
| Cloacal/anal body diameter | 30 | 28 | 23, 24 |
| Tail length | 89 | 94–105 | 75, 87 |
| V | – | – | 281, 308 |
| %V | – | – | 48, 50 |
| Vulval body diameter | – | – | 33, 37 |

outer raised portion and two ventrosublateral teeth, secretory-excretory system with four glands and pore immediately anterior to cephalic setae, males with arcuate spicules 1.7–1.8 cloacal body diameters long, curved gubernacular apophyses and tail with two subventral rows of 6–7 stout spines, and females with spermatheca and vulva situated at mid-body.

**Differential diagnosis.** The new species most closely resembles *C. brevisetosa* Gerlach, 1953 (Mediterranean Sea), *C. nephramphida* Blome 1985 (Galápagos Islands), *C. abyssalis* Bussau, 1993 (East Pacific), *C. mucrocaudata* Boucher, 1976 (North Atlantic), *C. nana* Lorenzen, 1973 (North Atlantic), *C. minima* (Kreis, 1929) Wieser, 1954 (North Atlantic), *C. obliqua* (Gerlach, 1953) Wieser, 1954 (Mediterranean Sea), *C. minor* (Allgén, 1927b) Wieser, 1954 (Southwest Pacific), *C. pharetra* Ott, 1972 (North Atlantic) as well as *Innocuonema tentabunda* (de Man, 1890) Inglis, 1969 (North Atlantic), which are all characterised by short body length (<1500 µm) and lack of precloacal supplements. The new species differs from all of these species in the presence of postcloacal spines. In addition, the new species differs from *C. brevisetosa* in stouter body shape (a = 17–21 *versus* 22–33 in *C. brevisetosa*), from *C. nephramphida* in the shape of the amphid (oval to slit-like versus kidney-shaped in *C. nephramphida*), from *C. abyssalis* in the absence of lateral differentiation in the cuticle (present in *C. abyssalis*), from *C. mucrocaudata* in the length of somatic setae (<0.5 cbd versus 1.0 cbd in *C. mucrocaudata*) and presence of gubernacular apophyses (gubernacular apophyses absent in *C. mucrocaudata*), from *C. nana* in the shape of the gubernacular apophyses (narrow and curved *versus* wide and short in *C. nana*) and spicule length (49–51 versus 22–23 µm in *C. nana*), from *C. pharetra* in the absence of ventromedial papillae (present in *C. pharetra*), and from *Innocuonema tentabunda* in spicule length (49–51 versus 35 µm in *I. tentabunda*).

**Sequence data.** Partial SSU rDNA (1533 bp; Genbank OK317201) and D2–D3 of LSU rDNA (721 bp; Genbank OK317226).

**ZooBank registration.** *Chromadorita spinicauda* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:C18ABC37-BF7F-433D-A423-888241CC86C4.

## Genus *Ptycholaimellus* Cobb, 1920

*Ptycholaimellus* Cobb, 1920: 337–338.

**Diagnosis** Cuticle with punctated ornamentation of two longitudinal rows of larger punctations. Labial region usually offset and narrower than the rest of cephalic region. Dorsal tooth in the buccal cavity large, hollow, with a dorsal apophysis. Peribuccal pharyngeal tissue swollen dorsally to accommodate the dorsal tooth. A pair of small globular cuticular bodies may be present on the outside of the peribuccal swelling. Posterior pharyngeal bulb double. Precloacal supplements usually absent (after Tchesunov (2014a)).

**Remarks.** The genus was last revised by Jensen & Nehring (1992) and a key to species was provided by Chunming *et al.* (2015). The genus currently comprises 22 valid species (Huang & Gao 2016).

**Type species.** *Ptycholaimellus carinatus* Cobb, 1920

***Ptycholaimellus spiculuncus* sp. nov.**

Figs 49–51; Table 14

**Material examined. Holotype** NIWA139292, NIWA Stn Z18746, 41.098° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 28 Jul 2016, fine sand, male. **Paratypes** NIWA 139293, three males and five females, same data as for holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Males.** Body cylindrical, colourless, tapering slightly towards anterior extremity. Cuticle annulated, ten annulations per 17–20 µm, with transverse rows of punctations most conspicuous near anterior body extremity and near cloacal region. Two longitudinal lateral rows of larger punctations, 3–4 µm apart, extending from 6–8 µm posterior to anterior body extremity to near tail tip; cuticle above two lateral rows of punctations raised and forming lateral alae. Two lateroventral and two laterodorsal rows of 4–6 µm long somatic setae extending from anterior pharyngeal region to near tail tip, located adjacent to longitudinal rows of larger punctations; anterior-most somatic setae sometimes in pairs. Cephalic region blunt, somewhat rounded and slightly narrower than rest of body; lips sometimes extended. Inner labial sensilla not observed; inner labial papillae located slightly anterior to four cephalic setae, ca. 0.24–0.32 cbd long, situated at base of labial region. Amphidial fovea not observed. Cheilostome with twelve cheilorhabdia, not cuticularised. Buccal cavity medium-sized, with cuticularised walls and large heavily cuticularised dorsal tooth; ventrosublateral teeth not observed. Duct of dorsal pharyngeal glands empties through narrow duct at base of dorsal tooth. Pharynx muscular, with anterior portion swollen dorsally. Well-developed posterior pharyngeal bulb, 43–45 µm long (27–30% of pharynx length) split into two roughly equal portions by discontinuity in pharyngeal tissue; lumen of posterior pharyngeal bulb heavily cuticularised. Nerve ring located slightly anterior to posterior pharyngeal bulb. Secretory-excretory system with pore situated slightly posterior to cephalic setae and medium-sized ventral gland situated slightly posterior to pharyngeal bulb. Cardia short, surrounded by intestinal tissue. Reproductive system with single outstretched testis located to the right of intestine; sperm cells globular or spherical, 3–4 × 5–7 µm. Spicules 1.3–1.4 cloacal body diameters long, L-shaped, with two small hook-shaped structure at distal tip and small pointed projection near distal tip. Short, curved gubernaculum pointed proximally, with pointed, curved crurae, no dorsocaudal apophyses. Precloacal supplements not observed. Tail conical; three caudal glands and spinneret present.

**Females.** Similar to males, but with slightly longer tail. Reproductive system with two opposed and reflexed ovaries; anterior ovary to the right of intestine, posterior ovary to the left of intestine. One small spermathecum present in proximal portion of each genital branch; spermatheca rounded with thin walls and sphincter muscle at base. Vulva located near mid-body. Pars proximalis vaginae surrounded by constrictor muscle; no vaginal glands observed.

**Etymology.** The species name is derived from the Latin *uncus* (= hook, barb) and refers to the presence of small hooks at the distal tip of the spicules.

**Species diagnosis.** *Ptycholaimellus spiculuncus* **sp. nov.** is characterised by body length 985–1136 µm in males and 1013–1247 µm in females, maximum body diameter 38–50 µm, four sublateral rows of short somatic setae along entire length of body, relatively short cephalic setae 0.3–0.4 cbd long, posterior pharyngeal bulb 43–45 µm long in males (27–30% of pharynx length) and 36–58 µm in females (25–34% of pharynx length), L-shaped spicules with small distal hooks and small pointed projection near distal tip, gubernaculum with pointed proximal end and without dorsocaudal apophyses, and precloacal supplements absent.

**Differential diagnosis.** The new species is most similar to *P. macrodentatus* (Timm, 1961) Wieser & Hopper, 1967 (Bay of Bengal) and *P. vincxae* Jensen & Nehring, 1992 (North Atlantic) in having a relatively slender body (maximum body diameter ≤ 0 µm), short cephalic setae (< 1 cbd), short posterior bulb (< 35% of total pharynx length), ventral gland shorter than pharyngeal length, and lack of precloacal supplements. *Ptycholaimellus spiculuncus* **sp. nov.** can be differentiated from *P. macrodentatus* mainly by the structure of the spicules (bent at about middle of spicule length and with small distal hooks and projection *versus* bent at one-third of spicule length from proximal length and without hooks or projection in *P. macrodentatus*), the markedly smaller ventral gland, and presence of spermatheca (versus absent in *P. macrodentatus*). *Ptycholaimellus spiculuncus* **sp. nov.** can be most easily differentiated from *P. vincxae* by the structure of the

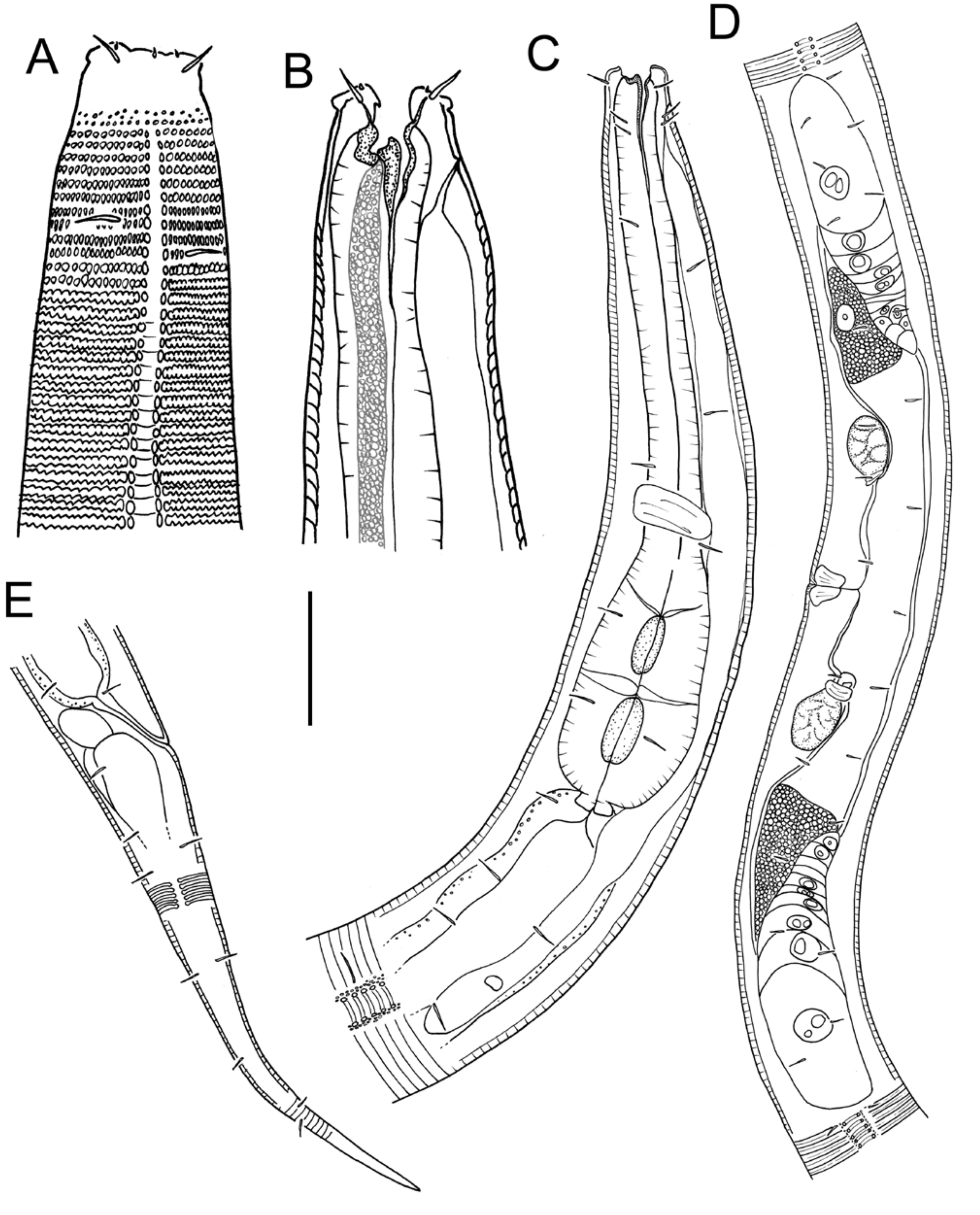



**Figure 49.** *Ptycholaimellus spiculuncus* **sp. nov.**: **A.** Surface view of male holotype cephalic region NIWA 139292; **B.** Cross-section view of holotype male cephalic region NIWA 139292; **C.** Female paratype anterior body region NIWA 139293; **D.** Female paratype reproductive system NIWA139293; **E.** Female paratype posterior body region NIWA 139293. Scale bar: A, B = 20 µm; C = 32 µm; D = 47 µm; E = 40 µm.

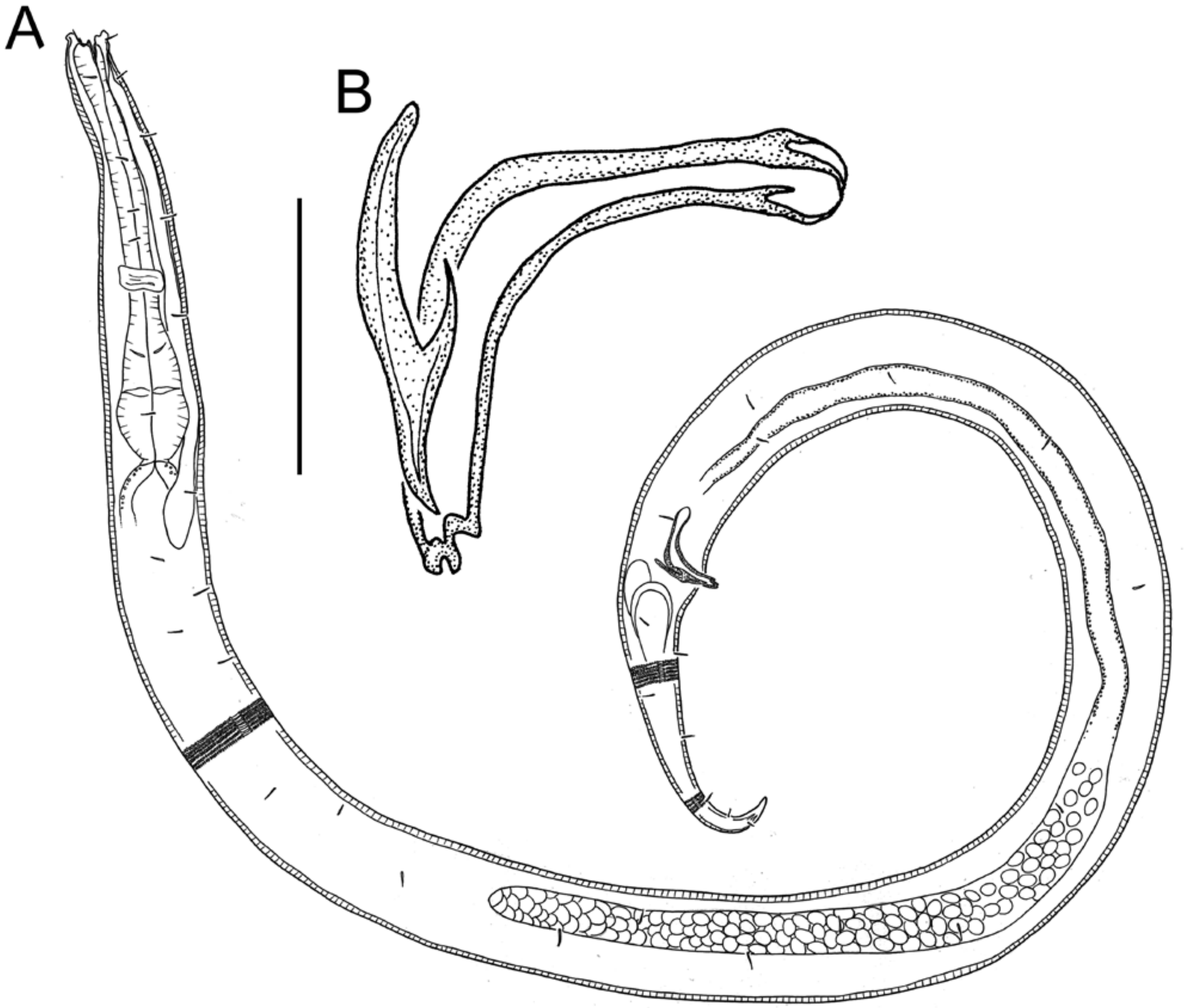



**Figure 50.** *Ptycholaimellus spiculuncus* **sp. nov.**, male paratype NIWA139293: **A.** Entire male; **B.** Copulatory apparatus. Scale bar: A = 100 µm; B = 16 µm.

spicules (with small distal hooks and projection *versus* without hooks or projection in *P. vincxae*), structure of the gubernaculum (without dorsocaudal apophyses *versus* dorsocaudal apophyses present in *P. vincxae*), and shorter cephalic setae (2–5 versus 15–17 µm long in P. *vincxae*).

**Sequence data.** Partial SSU rDNA (1631 bp; Genbank OK317202) and D2–D3 of LSU rDNA (823 bp; Genbank OK317227).

**ZooBank registration.** *Ptycholaimellus spiculuncus* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:8C590298-D5F7-49AF-8567-C40D7D3898F9.

## Family **Cyatholaimidae** Filipjev, 1918
## Subfamily **Cyatholaiminae** Filipjev, 1918

Cyatholaiminae Filipjev, 1918: 134–135.

**Diagnosis.** Body cuticle with homogeneous punctation, usually without lateral differentiation. Precloacal supplements usually absent; gubernaculum usually unpaired proximally (after Tchesunov (2014a)).

**Type genus.** *Cyatholaimus* Bastian, 1865

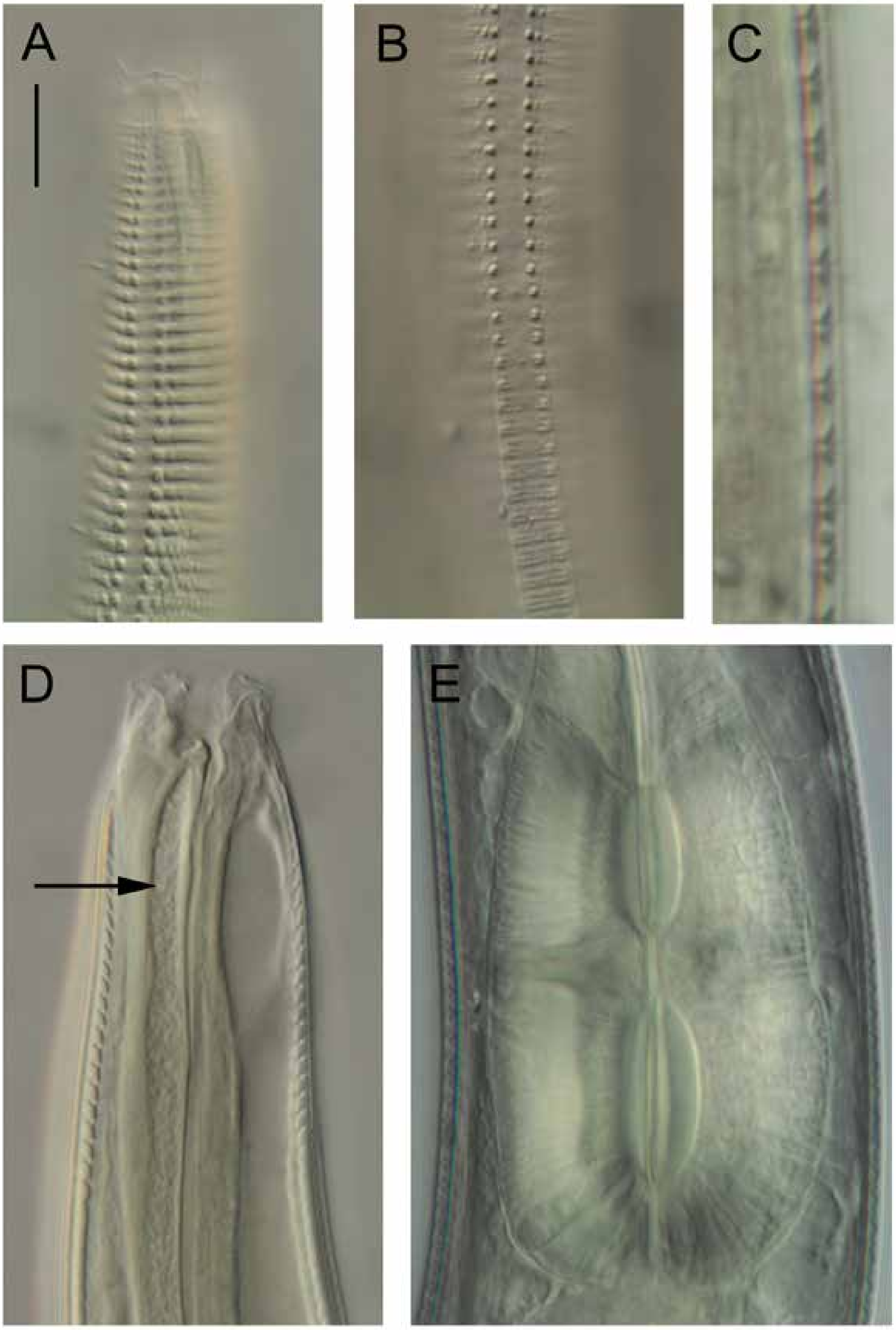



**Figure 51.** *Ptycholaimellus spiculuncus* **sp. nov.**, light micrographs: **A.** Cuticle ornamentation, anterior body region of female paratype NIWA 139293; **B.** Cuticle ornamentation, cloacal body region of female paratype NIWA 139293 (focus shifts from cuticle surface at bottom of image to below cuticle surface in middle and top of image); **C.** Transverse optical section of female paratype cuticle, mid-body region NIWA 139293; **D.** Anterior body region of holotype male, showing buccal cavity, pharynx, and ampulla NIWA 139292; **E.** posterior pharyngeal bulb of female paratype (NIWA 139293). Arrow shows position of pharyngeal tube. Scale bar: A–B, D–E = 10 µm; C = 7 µm.

**Table 14.** Morphometrics (μm) of *Ptycholaimellus sipunculus* **sp. nov.**, given as individual values, or a range of values from several specimens.

| Parameter | | | |
|---|---|---|---|
| Males | | Females | |
| | Holotype | Paratypes | Paratypes |
| Number of specimens | 1 | 3 | 5 |
| L | 1136 | 985–1116 | 1013–1247 |
| a | 26 | 23–27 | 22–28 |
| b | 7 | 7 | 6–8 |
| c | 9 | 8–10 | 7–9 |
| c' | 4.1 | 3.5–4.1 | 5.1–6.3 |
| Body diameter at cephalic setae | 13 | 13–17 | 13–14 |
| Length of cephalic setae | 4 | 3–4 | 2–5 |
| Nerve ring from anterior end | 89 | 72–92 | 75–88 |
| Nerve ring cbd | 33 | 30–32 | 26–33 |
| Excretory pore from anterior end | 9 | 11 | 6–9 |
| Pharynx length | 154 | 142–166 | 144–174 |
| Pharyngeal bulb maximum width | 31 | 29 | 25–33 |
| Pharyngeal bulb cbd | 41 | 37–39 | 33–41 |
| Maximum body diameter | 43 | 42–44 | 42–50 |
| Spicule length | 41 | 38–41 | – |
| Gubernacular apophysis length | 22 | 22–25 | – |
| Cloacal/anal body diameter | 31 | 29–32 | 24–29 |
| Tail length | 127 | 112–118 | 128–169 |
| V | – | – | 463–623 |
| %V | – | – | 46–51 |
| Vulval body diameter | – | – | 38–48 |

## Genus *Paracanthonchus* Micoletzky, 1924

*Paracanthonchus* Micoletzky, 1924: 138–140.
*Harveyjohnstonia* Mawson, 1953: 39-40, figs 12–14.
*Paraseuratiella* Schuurmans Stekhoven, 1950: 100–101, fig. 55a–c.

**Diagnosis.** Body cuticle with transverse rows of fine punctations, which laterally may be slightly larger or irregularly arranged. Buccal cavity with larger pointed dorsal tooth and smaller ventrosublateral teeth. Gubernaculum proximally paired, distally expanded, and dentate. Tubular precloacal supplements (after Tchesunov (2014a)).

**Remarks.** The genus was revised by Miljutina & Miljutin (2015), who provided a tabular key to the 63 species considered valid at the time. Two additional species were subsequently described by Tchesunov (2015) and Leduc & Zhao (2018).

**Type species.** *Paracanthonchus caecus* (Bastian, 1865) Micoletzky, 1924

### ***Paracanthonchus wellsi* sp. nov.**

Figs 52–55; Table 15

**Material examined. Holotype** NIWA 139264, NIWA Stn Z18747, 41.106° S, 174.891° E, Bradeys Bay in Pāuatahanui Inlet, upper intertidal, 25 Sep 2018, partly anoxic gravelly sand, male. **Paratypes** NIWA 139265, one male and two females, same data as for holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Males.** Body cylindrical, tapering slightly towards both extremities. Cuticle with transverse rows of punctations; lateral differentiation consisting of slightly larger punctations visible from level of cloaca to near tail tip. Four longitudinal rows of somatic setae, 4–7 μm long, located laterodorsally and lateroventrally from posterior to amphids to near tail tip. Longitudinal row of lateral pore like structures present along each mediolateral line from posterior to amphids to two-thirds of pharynx length from anterior; lateral pore-like structures difficult to distinguish in some specimens. Eight longitudinal rows of pore complexes situated subventrally (2 rows), subdorsally (2 rows), and sublaterally (4 rows), extending from posterior to amphids to near tail tip. Blunt cephalic region not offset from rest of body; lip region short. Anterior sensilla arranged in two crowns: first crown consisting of six short inner labial setae, 2 μm long, second crown consisting of six double-jointed outer labial setae and four slightly shorter and unjointed cephalic setae. Multispiral amphidial fovea with 5 turns and circular outline, situated slightly posterior to second crown of anterior sensilla. Buccal cavity consisting of wide, cup-shaped cheilostome with twelve cheilorhabdia and narrow funnel-shaped pharyngostoma with large cuticularised dorsal tooth and two pairs of smaller ventrosublateral teeth. Cylindrical, muscular pharynx narrowest in middle portion and widening slightly towards anterior and posterior extremities. Ocelli not observed (in either live or formalin-fixed specimens). Nerve ring located near mid-pharynx. Secretory-excretory system present, excretory pore located about 0.5–1.0 cbd anterior to nerve ring; ventral gland not observed. Cardia small, not surrounded by intestinal tissue. Reproductive system with anterior outstretched testis lying to the right of intestine. Sperm cells small, globular, 5 × 3 μm. Spicules paired, equal, lightly

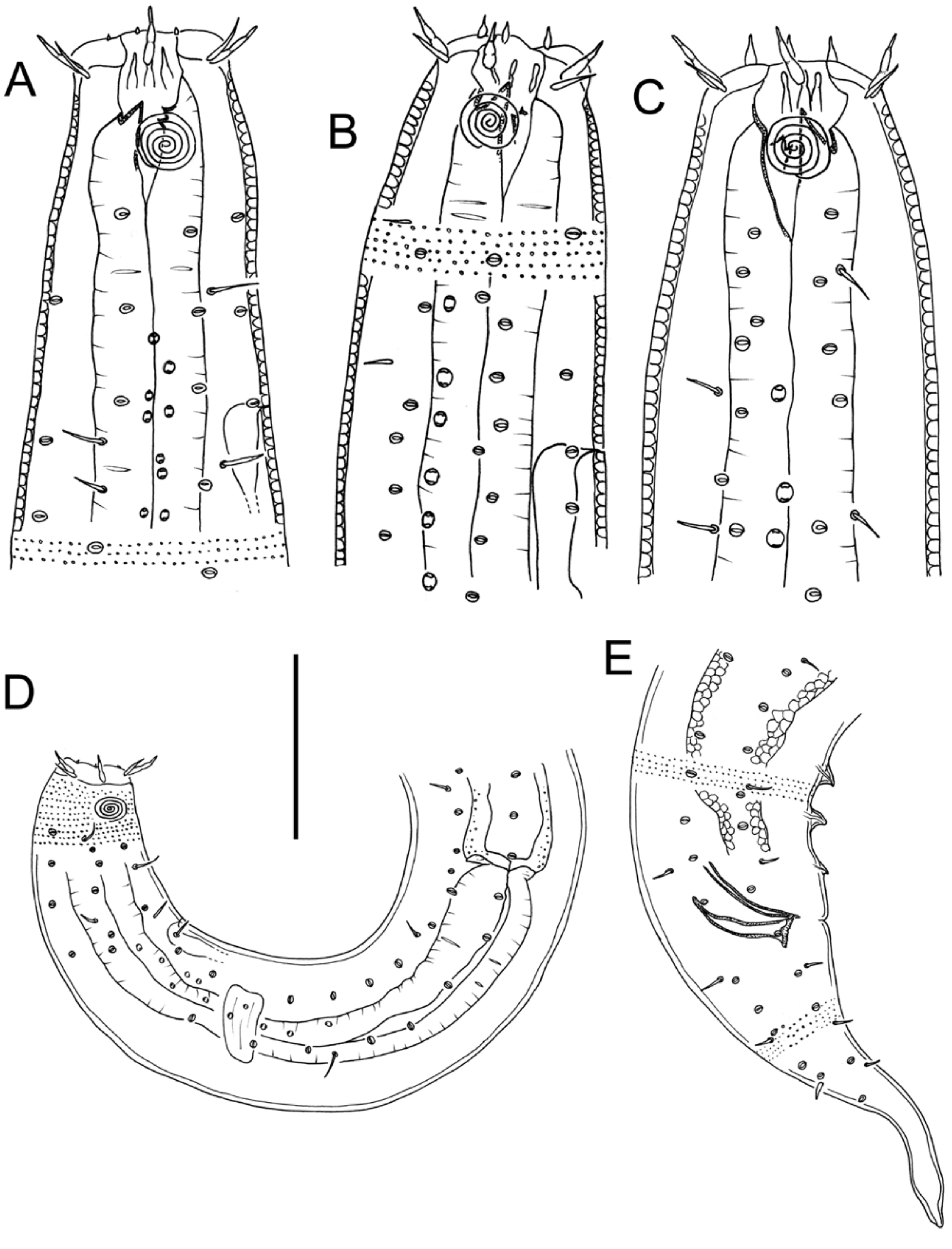



**Figure 52.** *Paracanthonchus wellsi* **sp. nov.**: **A.** Anterior body region of male paratype NIWA 139265; **B–C.** Anterior body region of female paratype NIWA 139265; **D.** Pharyngeal body region of male holotype NIWA 139264; **E.** Posterior body region of male holotype NIWA 139264. Scale bar: A, B, C = 30 µm; D = 55 µm; E = 45 µm.

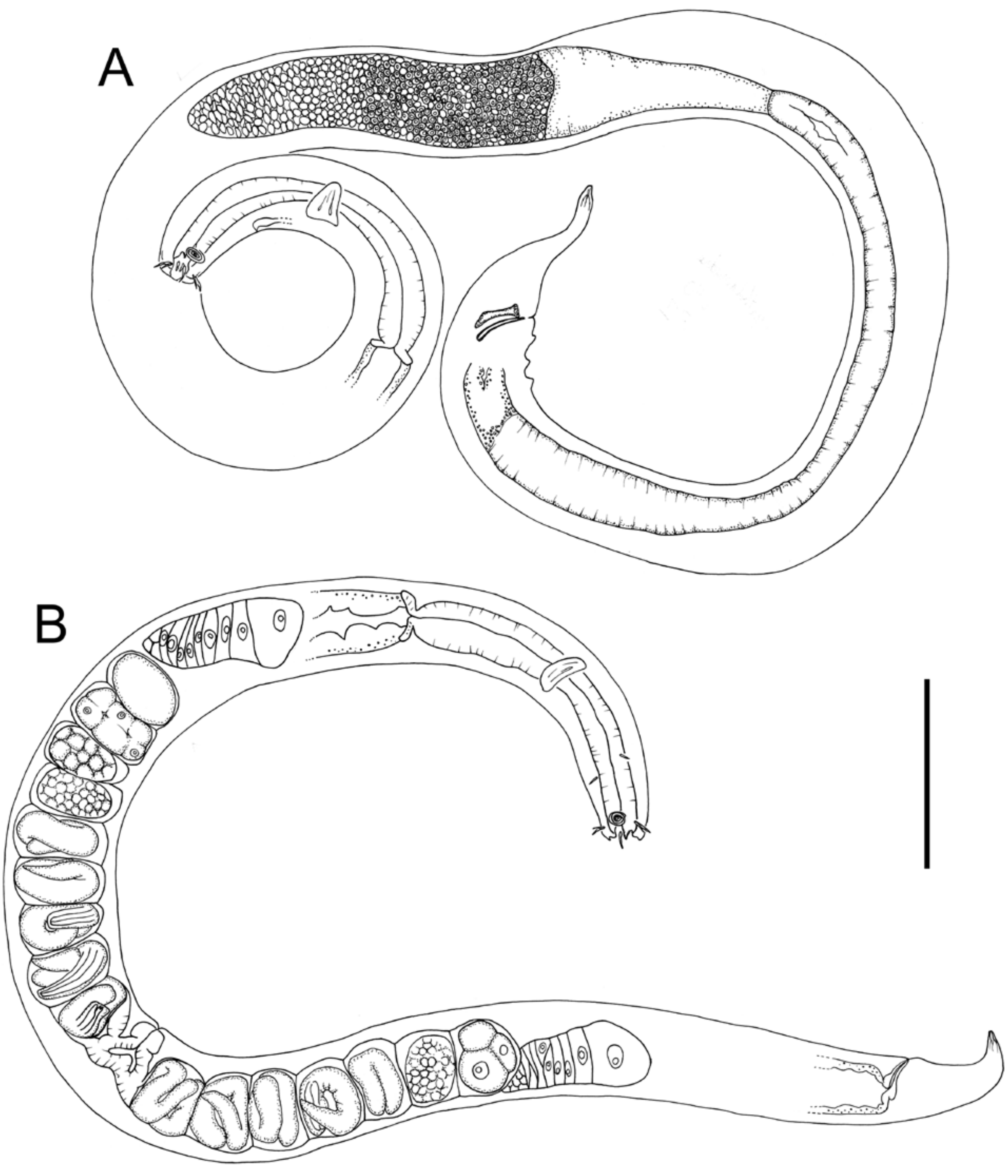



**Figure 53.** *Paracanthonchus wellsi* **sp. nov.**: **A.** Entire male holotype NIWA 139264; **B.** Entire female paratype NIWA 139265. Scale bar: A = 100 µm; B = 130 µm.

cuticularised, slightly bent and gradually narrowing distally. Gubernaculum proximally and distally paired (not fused), shorter than spicules, heavily cuticularised; distal end with numerous small pointed projections. Three precloacal supplements consisting of tubes within conical papilloid projections, either equidistant or gradually further apart from posterior-most to anterior-most supplement; posterior-most supplement 10–12 µm from cloaca. Short conicocylindrical tail with slightly swollen tip; three caudal glands and spinneret present.

**Females.** Similar to males but with lower ratio of a, inner labial papilla 3–4 µm long, amphids with 4.5–5.0 turns, more numerous pore complexes, larger, more

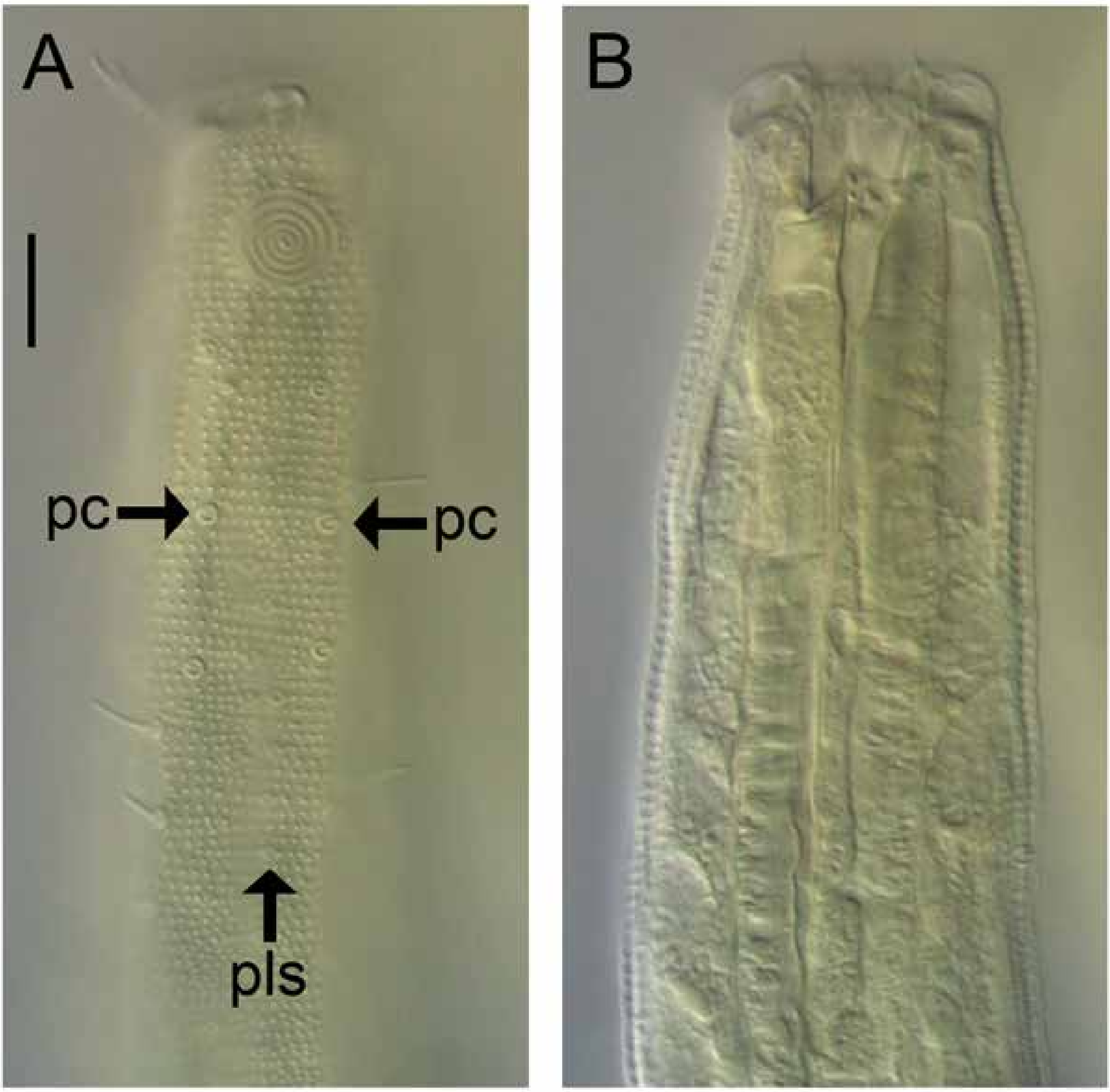



**Figure 54.** *Paracanthonchus wellsi* **sp. nov.**, light micrographs of male paratype, NIWA 139265: **A.** Surface view of anterior body region, showing row of lateral pore-like structures (pls) and two rows of sublateral pore complexes (pc), indicated by arrows; **B.** Optical cross-section of anterior body region. Scale bar = 10 µm.

conspicuous lateral pore-like structures present in pharyngeal, main body and caudal regions, and conical tail. Ovoviviparous with two opposed and reflexed ovaries; anterior ovary to the right of intestine, posterior ovary to the left of intestine. Thick vaginal and uterine walls; vulva near mid-body.

**Etymology.** The species is named after John Berkeley James Wells, an international authority on the biology and taxonomy of harpacticoid copepods (Huys 2021). He pioneered meiofaunal research in New Zealand, including research on the Pāuatahanui Inlet fauna and was a trustee of the Pāuatahanui Inlet Community Trust and chairperson of the Guardians of Pāuatahanui Inlet.

**Species diagnosis.** *Paracanthonchus wellsi* **sp. nov.** is characterised by body length ca. 1470–1600 µm, presence of lateral pore-like structure in males (pharyngeal region only) and females (entire body), presence of eight longitudinal rows of pore complexes in both sexes but more numerous in females, two laterodorsal and two lateroventral rows of somatic setae, amphid with 5.0 turns in males and 4.5–5.0 turns

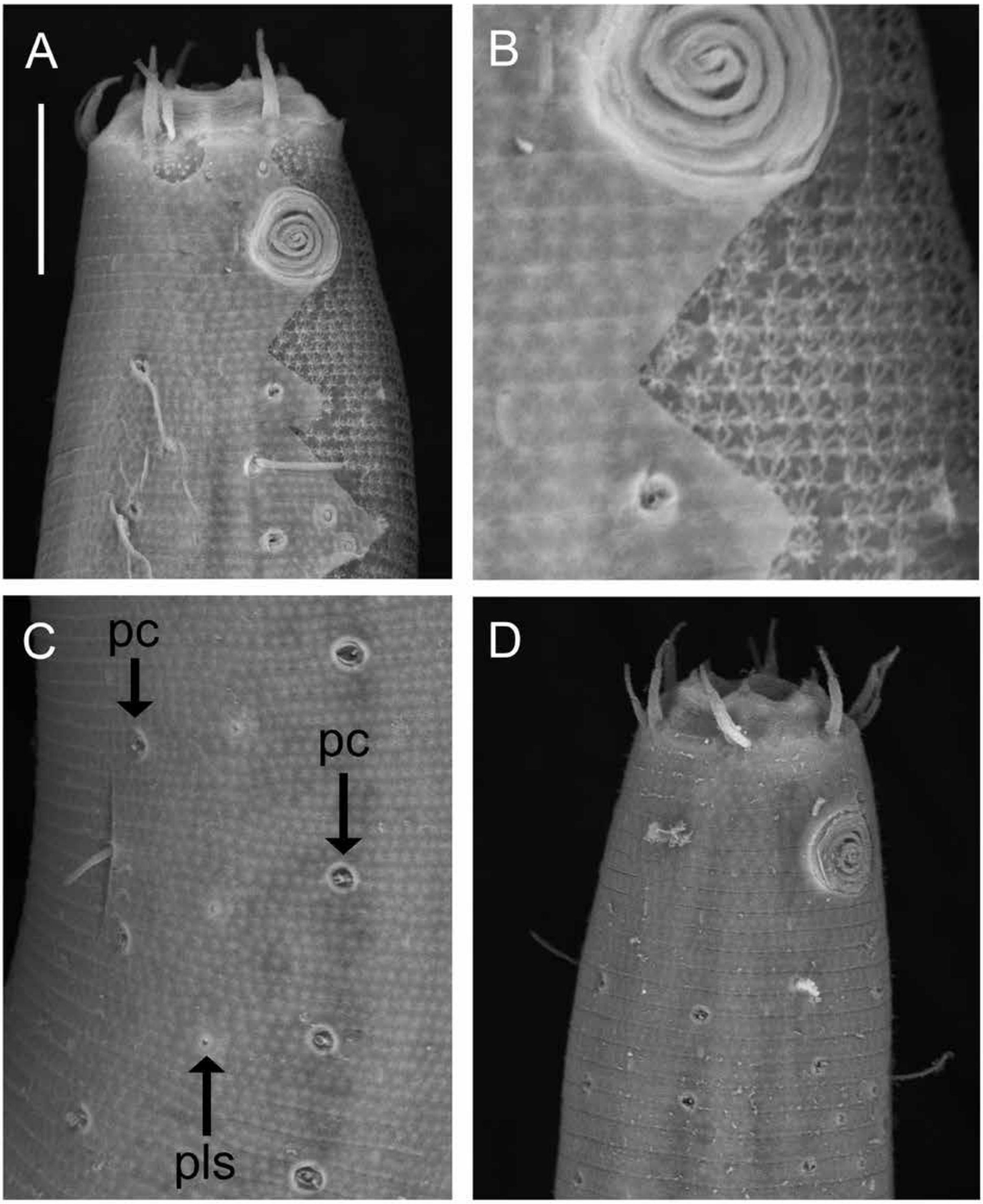



**Figure 55.** *Paracanthonchus wellsi* **sp. nov.**, scanning electron micrographs of male: **A.** Anterior body region, with epicuticle partially removed; **B.** Detail of cuticle, showing details of median layer of cuticle revealed by removal of epicuticle; **C.** Cuticle in mid-body region, showing row of lateral pore-like structures (pls) and two rows of sub-lateral pore complexes (pc), indicated by arrows; **D.** Anterior body region. Scale bar: A, D = 25 μm; B = 4 μm; C = 8 μm.

in female, buccal cavity with large dorsal tooth and two pairs of smaller ventrosublateral teeth, excretory pore 0.5–1.0 cbd anterior to nerve ring, ocelli absent, male with slightly bent spicules, gubernaculum with numerous small pointed projections distally, three precloacal supplements consisting of tubes within conical papilloid projections and short conicocylindrical tail, and ovoviviparous female with short conical tail.

**Differential diagnosis.** *Paracanthonchus wellsi* **sp. nov.** resembles *P. latens* Gourbault, 1980 (South Atlantic), *P. mamubiae* Miljutina & Miljutin, 2015 (Northwest Pacific), *P. nannodontus* (Shulz, 1932) Wieser, 1954 (North Atlantic), *P. tumepapillatus* Timm, 1957 (Caribbean Sea) and *P. olgae* Tchesunov,

**Table 15.** Morphometrics (μm) of *Paracanthonchus wellsi* **sp. nov.**, given as individual values, or a range of values from several specimens.

| Parameter | Males | | Females |
|---|---|---|---|
| | Holotype | Paratype | Paratypes |
| Number of specimens | 1 | 1 | 3 |
| L | 1485 | 1512 | 1465–1595 |
| a | 25 | 28 | 18–20 |
| b | 7 | 7 | 6 |
| c | 16 | 14 | 11–16 |
| c' | 2.3 | 2.7 | 2.1–3.0 |
| Body diameter at cephalic setae | 22 | 25 | 23–30 |
| Body diameter at amphids | 31 | 37 | 32–34 |
| Length of outer labial setae | 10 | 8 | 10–11 |
| Length of cephalic setae | 8–9 | 7–8 | 8 |
| Amphid height | 7 | 9 | 9–10 |
| Amphid width | 10 | 10 | 10 |
| Amphid width/cbd (%) | 32 | 37 | 29–31 |
| Amphid from anterior end | 11 | 11 | 8–13 |
| Nerve ring from anterior end | 104 | 111 | 121–128 |
| Nerve ring cbd | 46 | 40 | 47–54 |
| Excretory pore from anterior end | 52 | 55 | 64–65 |
| Pharynx length | 208 | 219 | 250–279 |
| Pharyngeal diameter at base | 25 | 24 | 29–37 |
| Pharynx cbd at base | 50 | 45 | 53–61 |
| Maximum body diameter | 60 | 54 | 78–83 |
| Spicule length | 36 | 37 | – |
| Gubernacular apophysis length | 28 | 31 | – |
| Cloacal/anal body diameter | 40 | 41 | 44–46 |
| Tail length | 92 | 109 | 94–140 |
| V | – | – | 772–851 |
| %V | – | – | 52–53 |
| Vulval body diameter | – | – | 75–79 |
| Laterodorsal pore complexes (pharynx) | 14 | 14 | 37–41 |
| Laterodorsal pore complexes (central body) | 94 | 82 | 156–158 |
| Laterodorsal pore complexes (tail) | 7 | 6 | 9–12 |
| Lateroventral pore complexes (pharynx) | 11 | 14 | 34 |
| Lateroventral pore complexes (central body) | 82 | 69 | 122–151 |
| Lateroventral pore complexes (tail) | 4 | 5 | 10–13 |
| Lateral pore-like structures (pharynx) | 14 | 16 | 11–14 |
| Lateral pore-like structures (central body) | – | – | 38–50 |
| Lateral pore-like structures (tail) | – | – | 4–5 |

2015 (North Atlantic) in having a small number of precloacal supplements (<5) and a gubernaculum with numerous pointed projections distally. The new species can be differentiated from *P. latens* by the smaller body size (1465–1595 *versus* 1733–2458 μm in *P. latens*), smaller amphid relative to corresponding body diameter (29–37 *versus* 40% in *P. latens*), fewer amphid turns (4.5–5 *versus* 6.5 turns in *P. latens*), shorter spicules (36 *versus* 84–87 μm in *P. latens*, and shorter gubernaculum (28 *versus* 43–50 μm in *P. latens*), from *P. mamubiae* by the shape and length of the tail (conical and 92–140 μm long *versus* conicocylindrical and 152–352 μm long in *P. mamubiae*), position of the amphids (8–13 μm *versus* 3–7 um from anterior extremity in *P. mamubiae*), and length of the cephalic setae (7–9 *versus* 2–4 μm in *P. mamubiae*), from *P. nannodontus* by the number of amphid turns (4.5–5.0 *versus* 3.5 turns in *P. nannodontus*), length of inner labial sensilla (setose and 2–4 μm long *versus* papillose in *P. nannodontus*), and length of cephalic setae (7–9 *versus* 5–6 μm in *P. nannodontus*), from *P. tumepapillatus* by the number of subventral teeth (four *versus* two subventral teeth in *P. tumepapillatus*), and *P. olgae* by the ratio of a (19–28 *versus* 25–43 in *P. olgae*), length of the spicules (36 *versus* 45–64 μm in *P. olgae*), length of the gubernaculum (28 *versus* 42–69 μm in *P. olgae*), and presence of lateral pore-like structures (absent in *P. olgae*).

**Remarks**. Ovoviviparity has been noted in two other *Paracanthonchus* species to dates: *P. stateni* Allgén, 1930 (Tierra del Fuego) and *P. heterodontus* (Schulz, 1932) Vincx *et al.* (1982) (Baltic Sea).

**Sequence data.** Partial SSU rDNA (542 bp; Genbank OK317203).

**ZooBank registration.** *Paracanthonchus wellsi* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:D41E799D-6CBB-4927-9BC3-37B7E397FFE9.

## Order **Desmodorida** De Coninck, 1965

## Family **Desmodoridae** Filipjev, 1922

## Subfamily **Desmodorinae** Filipjev, 1922

Desmodorinae Filipjev, 1922: 117.

**Diagnosis.** Cuticle annulated except in cephalic region. Cephalic region with thickened cuticle except in lip region and set off as conspicuous cephalic capsule. Amphidial fovea generally not surrounded by annulation of body cuticle; may be located on a cuticularised plate. Buccal cavity mostly with distinct teeth. Pharyngeal bulb round to elongated (modified from Tchesunov (2014b)).

**Type genus.** *Desmodora* de Man, 1889

### Genus *Pseudochromadora* Daday, 1899

*Pseudochromadora* Daday, 1899: 562–563.
*Micromicron* Cobb, 1920: 324–325.
*Bradylaimoides* Timm, 1961: 63.

**Diagnosis.** Short cylindrical body with short cephalic capsule and short conical tail. Lateral alae usually extending from posterior to the pharynx (except in *P. plurichela* **sp. nov.** where it extends from about mid-pharynx) to the tail region. Short somatic setae arranged in six or eight longitudinal rows. Cephalic capsule usually consisting of slender labial portion followed by main part of cephalic capsule characterised by thickened cuticle; a sutura sometimes present between the two portions. Four cephalic setae located on labial portion of cephalic capsule on anterior rim of the main portion. Unispiral amphidial fovea located on main portion of cephalic capsule. Short cylindrical pharynx with conspicuous posterior bulb. Male of most species with copulatory and postcloacal thorns, arched spicules, and gubernaculum with capitulum (modified from Mordukhovich *et al.* (2015)).

**Remarks.** The genus currently comprises 13 valid species, with recent species description by Mordukhovich *et al.* (2015), Datta *et al.* (2018a) and Zograf *et al.* (2021).

**Type species.** *Pseudochromadora quadripapillata* Daday, 1899

### *Pseudochromadora plurichela* sp. nov.

Figs 56, 57; Table 16

**Material examined. Holotype** NIWA 139282, NIWA Z18746, 41.098° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 28 Jul 2016, fine sand, male. **Paratypes** NIWA 139283, one male and three females, same data as holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Males.** Body short, stout, cylindrical, with slight golden brown colouration, widest in precloacal region, tapering slightly towards anterior extremity. Cuticle annulated, no lateral differentiation; lateral alae extending from near mid-pharynx to slightly posterior to cloaca, cuticle annulations sometimes interdigitate at level of lateral alae. Body covered in layer of fine debris and mucous; presence of minute, filiform spines likely but cannot be confirmed without scanning electron microscopy. Eight longitudinal rows of somatic setae present, 8–15 µm long, associated hypodermal glands or glandular sensory organs not observed. Blunt, slightly rounded cephalic region, slightly offset from rest of body. Cephalic capsule with main portion surrounded by thickened cuticle and lip region usually folded inwards; no sutura separating main and lip regions. Circle of six small inner labial papillae followed by circle of six slightly larger outer labial papillae. Four cephalic setae, ca. 0.25–0.30 cbd long, at level of anterior edge of amphids. Amphidial fovea large, unispiral, located on main portion of cephalic capsule. Buccal cavity medium-sized, with large, conspicuous, cuticularised dorsal tooth and two smaller ventrosublateral teeth. Ducts of pharyngeal glands not observed. Pharynx muscular, lumen not cuticularised; anterior portion surrounding buccal cavity, slightly swollen. Well-developed posterior pharyngeal bulb present, 35–40 µm long, without conspicuous partitions. Nerve ring located slightly posterior to middle of pharynx. Secretory-excretory system not observed. Cardia short, not surrounded by intestinal tissue. Reproductive system with single outstretched testis located to the left of intestine; sperm cells globular or spherical, 8–10 × 10–11 µm. Spicules short, 1.5–1.6 cloacal body diameters long, arcuate, with swollen proximal portion (capitulum); velum not observed. Small, curved gubernaculum not surrounding spicules distally. Ventral row of ten precloacal supplements consisting of claw-like cuticularised projections, more-or-less equidistant and separated by folds of cuticle. Copulatory and postcloacal thorns absent. Tail conical, with short subventral and subdorsal setae. Three caudal glands and spinneret present.

**Females.** Similar to males but with markedly smaller, cryptospiral amphidial fovea and unispiral amphidial aperture, lower values of a, and slightly longer tail. Reproductive system with two opposed and reflexed ovaries; anterior ovary to the left or right of intestine, posterior ovary to the opposite side of intestine. Mature eggs and spermatheca not observed. Vulva located at about two-thirds of body length from anterior. Pars proximalis vaginae surrounded by constrictor muscle.

**Etymology.** The species name is derived from the Latin *pluris* (= more) and *chela* (= claw) and refers to the presence of multiple claw-like precloacal supplements in males.

**Species diagnosis.** *Pseudochromadora plurichela* **sp. nov.** is characterised by body length ca. 800–900 µm, lateral alae extending from mid-pharynx to beyond cloaca/anus and with interdigitation of cuticle annulations, eight longitudinal rows of somatic setae,

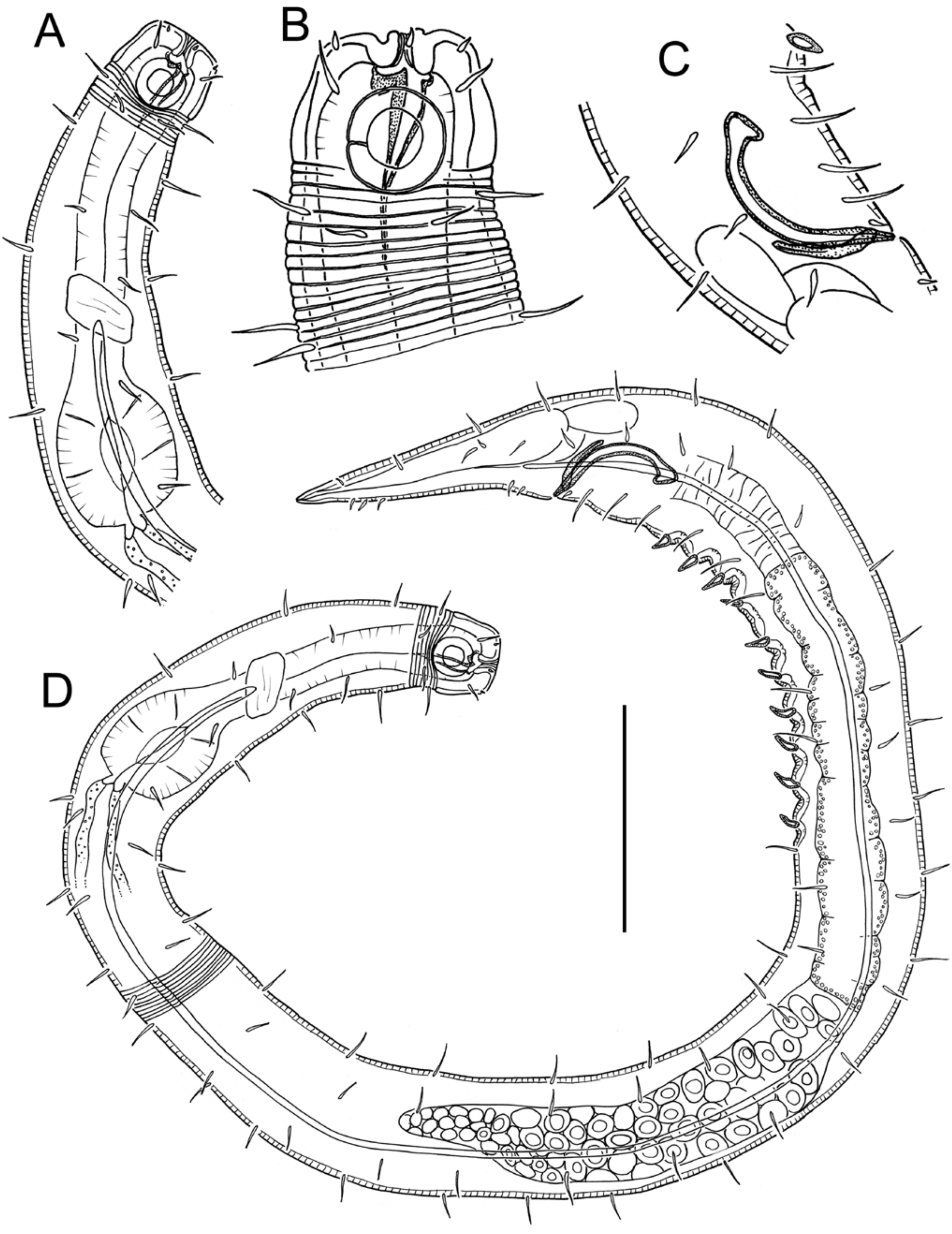



**Figure 56.** *Pseudochromadora plurichela* **sp. nov.**, male holotype NIWA 139282: **A.** Anterior body region; **B.** Cephalic region; **C.** Copulatory apparatus; **D.** Entire male. Scale bar: A = 65 µm; B = 30 µm; C = 45 µm; D = 80 µm.

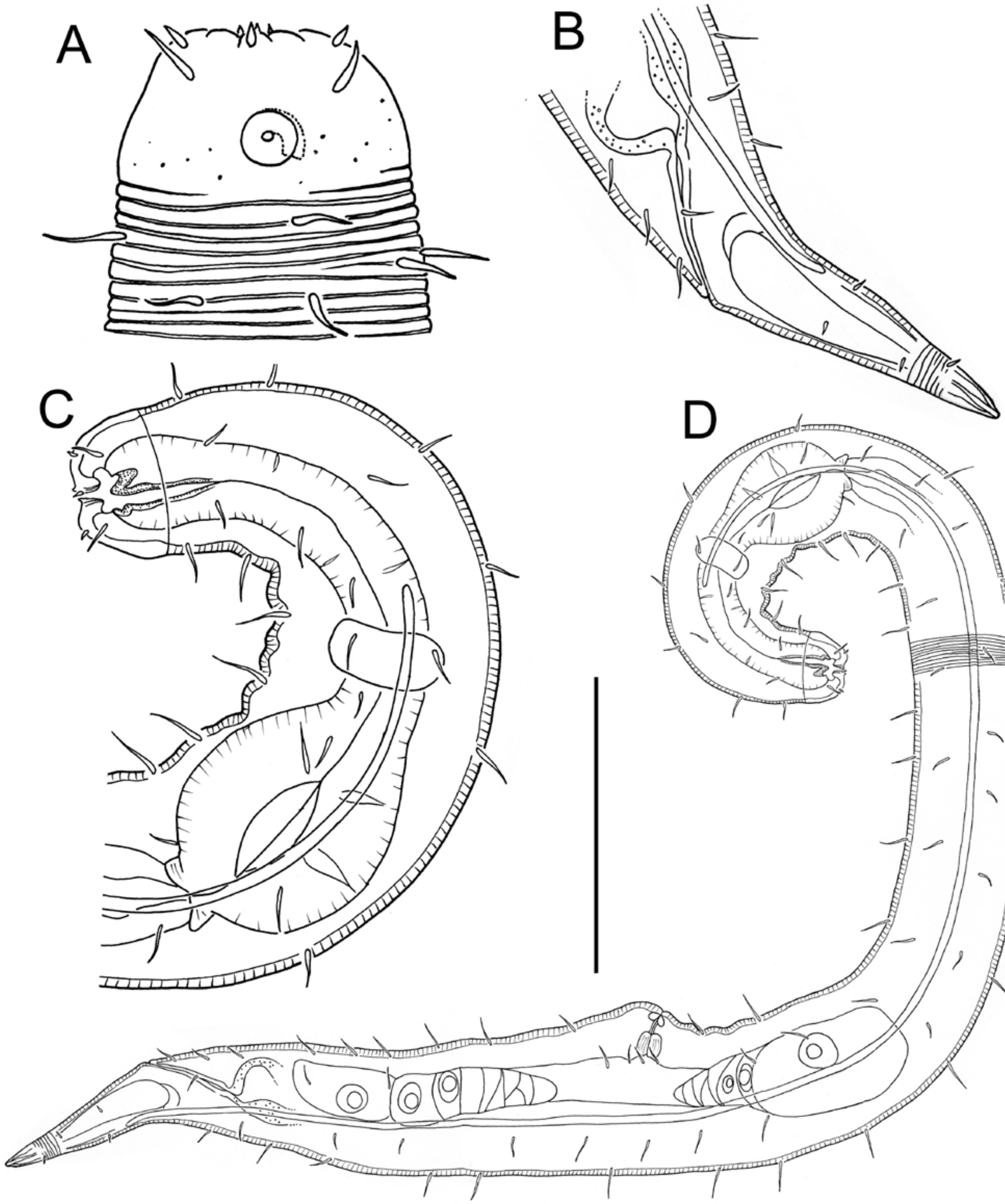



**Figure 57.** *Pseudochromadora plurichela* **sp. nov.**, female paratype NIWA 139283: **A.** Surface view of cephalic region; **B.** Posterior body region; **C.** Anterior body region; **D.** Entire female. Scale bar: A = 30 µm; B = 66 µm; C = 60 µm; D = 125 µm.

cephalic capsule with lip region not set off from main region, sexual dimorphism in the size and shape of the amphidial fovea (large unispiral in males, small cyptospiral in females), pharyngeal bulb without conspicuous partitions, female without thorns, male with ten claw-like precloacal supplements but without copulatory or postcloacal thorns.

**Differential diagnosis.** *Pseudochromadora plurichela* **sp. nov.** can be differentiated from all other *Pseudochromadora* species by the lateral alae extending from near mid-pharynx level instead of from posterior to the pharynx. The new species resembles *P. reathae* Leduc & Wharton, 2010 (New Zealand coast) in the presence of several conspicuous cuticularised

**Table 16.** Morphometrics (µm) of *Pseudochromadora plurichela* **sp. nov.**, given as individual values, or a range of values from several specimens.

| Parameter | Males | | Females |
|---|---|---|---|
| | Holotype | Paratype | Paratypes |
| n | 1 | 1 | 3 |
| L | 830 | 802 | 789–895 |
| a | 18 | 18 | 11–15 |
| b | 6 | 6 | 6–7 |
| c | 10 | 10 | 11–12 |
| c' | 2.4 | 2.2 | 2.8–3.2 |
| Body diameter at cephalic setae | 24 | 22 | 25–29 |
| Body diameter at amphids | 27 | 26 | 26–29 |
| Length of outer labial setae | 2–3 | 2–3 | 2–3 |
| Length of cephalic setae | 6–7 | 6–7 | 6–7 |
| Amphid height | 14 | 14 | 5–6 |
| Amphid width | 13 | 13 | 6–7 |
| Amphid width/cbd (%) | 48 | 50 | 21–24 |
| Amphid from anterior end | 7 | 5 | 7–9 |
| Nerve ring from anterior end | 74 | 75 | 68–79 |
| Nerve ring cbd | 37 | 35 | 37–46 |
| Pharynx length | 140 | 129 | 134–142 |
| Pharyngeal bulb diameter | 34 | 34 | 38–42 |
| Pharyngeal bulb cbd | 43 | 44 | 49–52 |
| Maximum body diameter | 45 | 45 | 59–74 |
| Spicule length | 55 | 53 | – |
| Gubernaculum length | 21 | 20 | – |
| Cloacal/anal body diameter | 35 | 36 | 22–27 |
| Tail length | 85 | 80 | 71–78 |
| V | – | – | 526–594 |
| %V | – | – | 65–67 |
| Vulval body diameter | – | – | 59–74 |

precloacal supplements but differs from the latter in the shape of the amphidial fovea in males (loop-shaped in *P. reathae*, unispiral in *P. plurichela* **sp. nov.**). The new species also ressembles *Pseudochromadora incubans* Gourbault & Vincx, 1990 (Caribbean Sea), *P. buccobulbosa* Verschelde & Vincx, 1995 (Indian Ocean), *P. commansi* Verschelde & Vincx, 1995 (Indian Ocean), *P. rossica* Mordukhovich, Fadeeva, Semenchenko & Zograf, 2015 (Sea of Japan), *P. cazca* (Gerlach, 1956) Gerlach, 1963 (South Atlantic), and *P. interdigitatum* Muthumbi, Verschelde & Vincx, 1995 (Indian Ocean) in having a rounded cephalic capsule with a lip region not set off from the main part of the cephalic capsule, but differs from the latter by the absence of thorns in both males and females.

*Pseudochromadora plurichela* **sp. nov.** is similar to the monospecific genus *Psammonema* due to the anterior portion of the lateral alae overlapping with the pharynx. The new species, however, differs from *Psammonema* Verschelde & Vincx, 1995 in the position of the amphids (middle of main region of cephalic capsule *versus* anterior of main region of cephalic capsule in *Psammonema*), absence of denticles in buccal cavity (*versus* denticles present in *Psammonema*), shape of pharyngeal bulb (rounded and without partitions *versus* elongated and tripartite in *Psammonema*), and absence of differentiation of somatic setae in females (*versus* presence of different types of somatic setae in *Psammonema*).

**Sequence data.** Partial SSU rDNA (1530 bp; Genbank OK317204).

**ZooBank registration.** *Pseudochromadora plurichela* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:289656D1-0E06-4185-89BA-38B70A2E6B3F.

## Subfamily **Spiriniinae** Chitwood, 1936

Spiriniinae Chitwood, 1936: 1.
Metchromadorinae Chitwood, 1936: 1.

**Diagnosis.** Body cuticle finely striated. Head cuticle not thickened, not modified, and not demarcated as a cephalic capsule. Amphidial fovea a simple spiral, usually located close to the apex and surrounded with cuticular striation. Buccal cavity rather tight, typically with a distinct or minute dorsal tooth; two smaller ventrosublateral teeth may be present or absent. Posterior pharyngeal bulb usually present, either round or oval (modified from Tchesunov (2014b)).

**Type genus.** *Spirinia* Gerlach, 1963

### Genus ***Chromaspirina*** Filipjev, 1918

*Chromaspirina* Filipjev, 1918: 229, fig. 45, table 7.
*Bolbolaimus* Cobb, 1920: 319–321.
*Mesodorus* Cobb, 1920: 325–326.

**Diagnosis.** Body robust, rarely slender, with rounded or rectangular cephalic region and short conical tail; fine body annulations. Annulated or non-annulated cephalic region; body annulations envelop the amphidial fovea partly, entirely, or only begin at posterior edge of amphids. Amphidial fovea uni-, crypto- or multispiral, or loop-shaped. Cephalic setae at anterior edge or further posteriorly alongside amphids. Distinct buccal cavity, conspicuously cuticularised; large dorsal tooth and smaller subventral teeth; ventral field of denticles may be present. Pharynx with round or oval posterior bulb, sometimes weakly developed, and without cuticularised lumen. Precloacal supplements may be present (modified from Leduc & Verschelde (2015)).

**Remarks.** The genus, which currently comprises 17 valid species, was revised by Leduc & Verschelde (2015). A new species was recently described by Revkova & Revkov (2022).

**Type species.** *Chromaspirina pontica* Filipjev, 1918

### *Chromaspirina stilbonematinops* sp. nov.

Figs 58–61; Table 17

**Material examined. Holotype** NIWA 139262, NIWA Stn Z18746, 41.098° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 28 Jul 2016, fine sand, male. **Paratypes** NIWA 139263, five males and two females, same data as for holotype.

**Additional material** Portobello Marine Laboratory reference collection slides 0058 0008, 0059 0008 & 0060 0008, 45.85° S, 170.68° E, Papanui Inlet, January 2006, *Zostera* sediments, one male and two females.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, and Papanui Inlet, Otago Peninsula, New Zealand.

**Description. Males.** Body cylindrical, slender, with slightly pink colouration, tapering slightly towards anterior extremity. Cuticle annulated, no lateral differentiation. Some specimens partially covered with by single layer of densely-packed rod-shaped bacteria, 0.9–1.1 × 1.2–1.4 µm. Eight rows of short somatic setae present, initially of similar length to cephalic setae, gradually decreasing in length towards posterior end of pharynx; no hypodermal glands or glandular sensory organs observed. Blunt, slightly rounded cephalic region; circle of six minute inner labial papillae followed by circle of six slightly larger outer labial papillae. Four cephalic setae, ca. 0.28–0.34 cbd long, at level of anterior edge of amphids. Amphidial fovea unispiral, or multispiral with 1.25 turns, partially surrounded by cuticle annulations, less than 0.5 cbd from anterior extremity. Cheilostome with twelve cheilorhabdia. Buccal cavity medium-sized, with conspicuous cuticularised dorsal tooth and two smaller ventrosublateral teeth. Ducts of pharyngeal glands not observed. Pharynx muscular, lumen not cuticularised; anterior portion surrounding buccal cavity, sometimes slightly swollen, posterior pharyngeal bulb oval-shaped. Nerve ring located slightly posterior to middle of pharynx. Secretory-excretory system not observed. Cardia ca. 10 µm long, not surrounded by intestinal tissue. Reproductive system with single outstretched testis located to the left or right of intestine; sperm cells globular or spherical, 4–6 × 6–8 µm. Spicules short, 1.2–1.6 cloacal body diameters long, arcuate, with swollen proximal portion (capitulum), and velum. Curved gubernaculum not surrounding spicules distally. Precloacal supplements present, consisting of 3–4 shallow, cup-shaped supplements beginning 20–30 µm anteriorly from cloaca and 8–10 µm apart, followed by 15–21 large, heavily cuticularised tubular supplements, 8 µm long, 6–8 µm apart. Tail conical, with sparse subventral and subdorsal setae. Three caudal glands and spinneret present.

**Females.** Similar to males but with slightly smaller amphids. Reproductive system with two opposed and reflexed ovaries; anterior ovary to the left of intestine, posterior ovary to the right of intestine. Mature eggs and spermatheca not observed. Vulva located slightly posterior to mid-body. Pars proximalis vaginae surrounded by constrictor muscle.

**Etymology.** The species name refers to the closely related stilbonematine nematodes (family Desmodoridae), which resemble the new species in their slender body shape and cuticular cover of ectosymbiotic bacteria.

**Species diagnosis.** *Chromaspirina stilbonematinops* **sp. nov.** is characterised by body with pink colouration, body length 1150–1630 µm, a slender body shape (a = 58–82, maximum body diameter 18–23 µm), some specimens partially covered by layer of densely packed rod-shaped bacteria, amphidial fovea unispiral or multispiral with 1.25 turns and partially surrounded by cuticle annulations, oval pharyngeal bulb, spicules 1.2–1.6 cloacal body diameters long, curved gubernaculum without apophyses, and 3–4 cup-shaped and 15–21 heavily cuticularised tubular precloacal supplements.

**Differential diagnosis.** *Chromaspirina stilbonematinops* **sp. nov.** is most similar to *C. chabaudi* Boucher, 1975 (North Atlantic), *C. multipapillata* Jayasree & Warwick, 1970 (North Atlantic) and *C. vanreuselae* Verschelde & Vincx, 1996 (Indian Ocean) in having a slender body (a > 50) and precloacal supplements. The new species can be differentiated from these species by the narrower body (maximum body diameter of 18–23 µm in *C. stilbonematinops* **sp. nov.** *versus* 24–56 µm in the other species), the

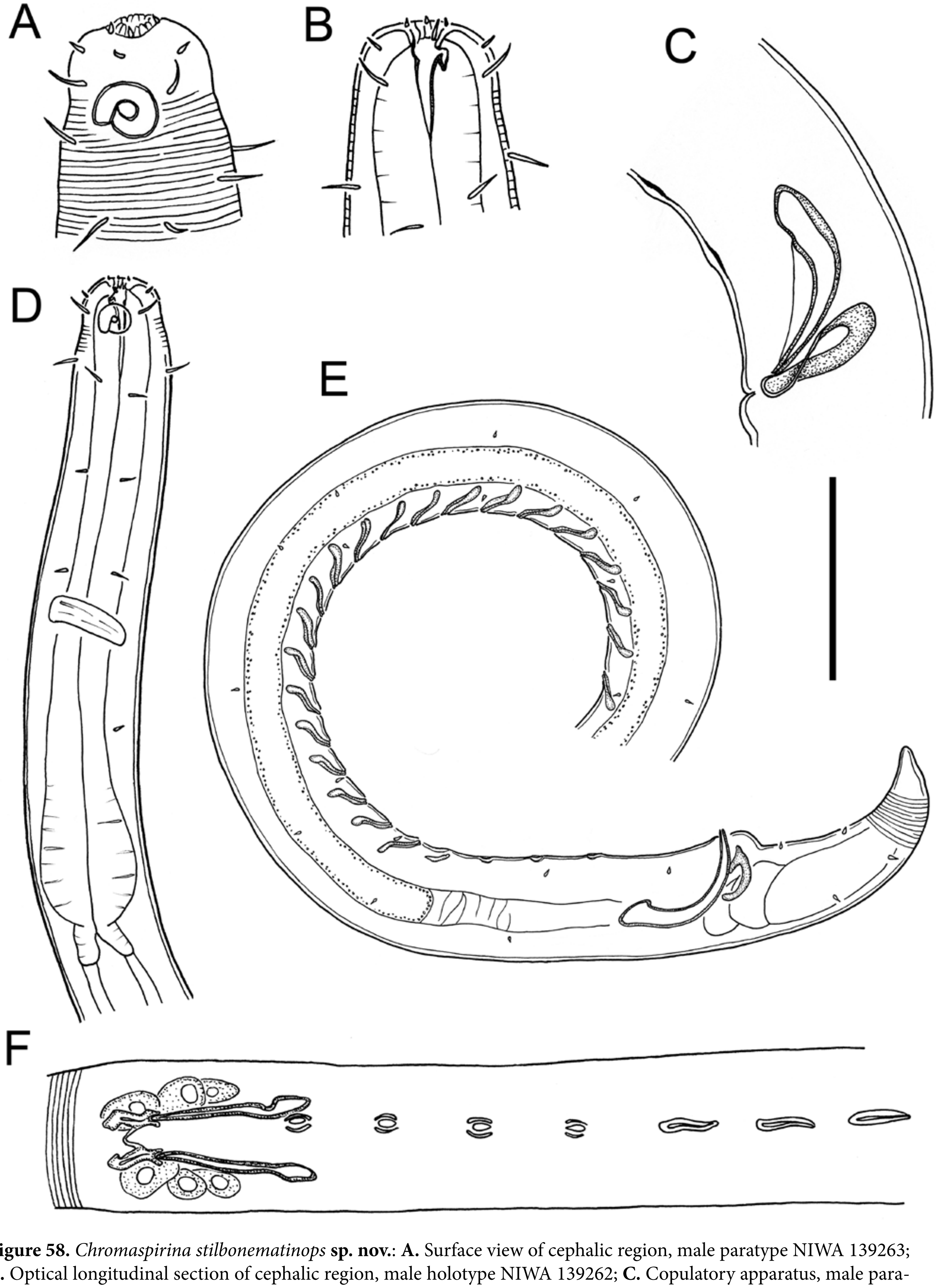



**Figure 58.** *Chromaspirina stilbonematinops* **sp. nov.**: **A.** Surface view of cephalic region, male paratype NIWA 139263; **B.** Optical longitudinal section of cephalic region, male holotype NIWA 139262; **C.** Copulatory apparatus, male paratype NIWA 139263; **D.** Anterior body region, male holotype NIWA 139262; **E.** Lateral view of posterior body region, male paratype NIWA 139263; **F.** Ventral view of copulatory apparatus, male paratype NIWA 139263. Scale bar: A, B, C = 20 μm; D, E = 35 μm; F = 35 μm.

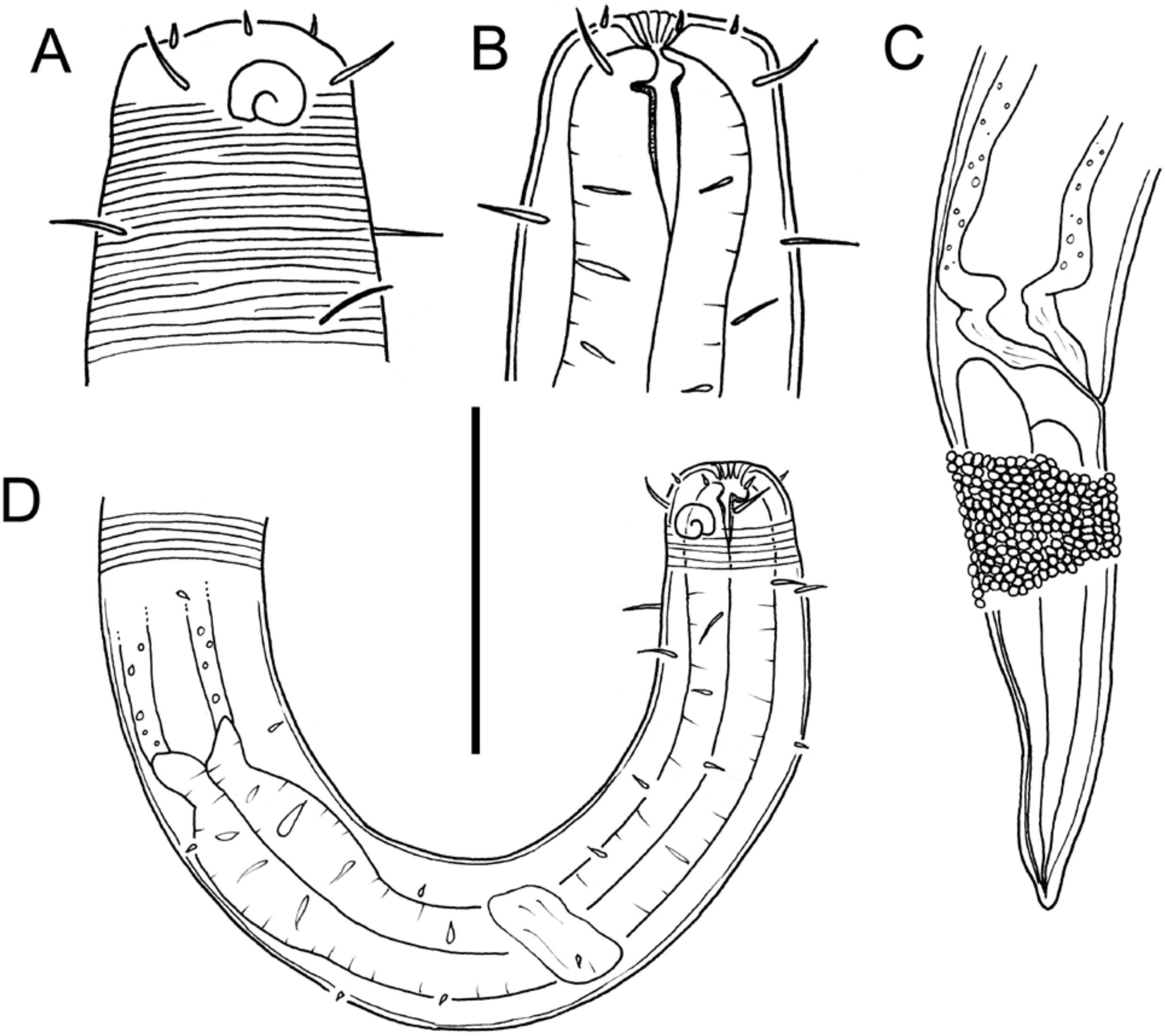


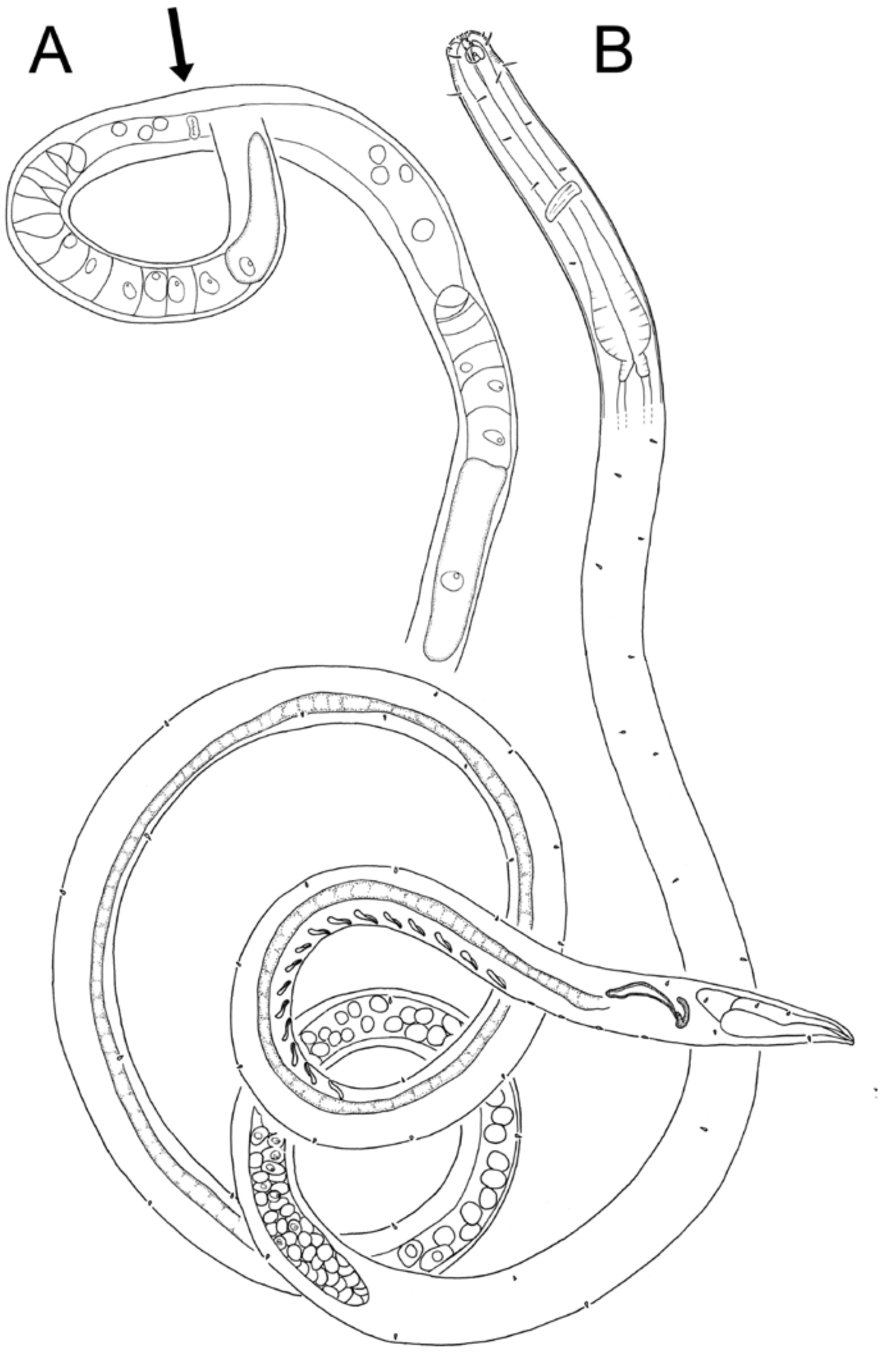

**Figure 59.** *Chromaspirina stilbonematinops* **sp. nov.**, female paratype NIWA 139263: **A.** Surface view of cephalic region; **B.** Optical longitudinal section of cephalic region; **C.** Posterior body region; **D.** Anterior body region. Scale bar: A, B = 20 µm; C = 35 µm; D = 45 µm.

shape of precloacal supplements (cup-shaped and heavily cuticularised tubular supplements in *C. stilbonematinops* **sp. nov.** *versus* fine tubular or thorn-like supplements in the other species), and presence of dense bacteria layer on the cuticle (*versus* bacteria absent in the other species).

The resemblance between the new species and the closely related Stilbonematinae Chitwood, 1936 lies mainly in the presence of a dense layer of bacteria on the cuticle and a relatively long and thin body. The new species, like other species of the genus *Chromaspirina*, differs from the Stilbonematinae in having a buccal cavity with teeth (*versus* teeth absent in Stilbonematinae) and a relatively long pharynx not differentiated into three regions (*versus* a short pharynx divided into three regions in the Stilbonematinae).

**Remarks.** To our knowledge, this is the first record of a dense rod-shaped bacteria cover on the cuticle of a marine nematode species outside of the Stilbonematinae (family Desmodoridae). The nature of the relationship between *C. stilbonematinops* **sp. nov.** hosts and bacteria remains unclear, but may be similar to the symbiosis involving stilbonematine nematodes and their ectosymbiotic sulphur-reducing bacteria; the former migrate through the sediment to provide their bacterial ectosymbionts with both reduced sulphur compounds and oxygen, and the bacteria are in turn ingested by their nematode host (Ott *et al.* 1991). The new species appears to lack specialised sensory glandular organs, which in the Stilbonematinae are involved in sustaining the bacterial association through the secretion of a mucus envelope (Bulgheresi *et al.* 2006). Such

**Figure 60.** *Chromaspirina stilbonematinops* **sp. nov.**: **A.** Female paratype reproductive system NIWA 139263; **B.** Entire male holotype NIWA 139262. Arrow shows position of vulva. Scale bar = 50 µm.




organs, however, are not present in all stilbonematine species (e.g., *Eubostrichus hortulanus* Leduc, 2013) and may not be strictly necessary for maintaining the symbiotic relationship. It is also interesting to note that *C. stilbonematinops* **sp. nov.** is characterised by a body diameter smaller than any of the other species of the genus, a feature resulting in a higher surface to volume ratio that maximises the attachment surface for bacteria. It is likely that all *C. stilbonematinops* **sp. nov.** have a more extensive bacterial cover than observed in the examined specimens, and that the majority of the bacteria were lost during specimen extraction, a phenomenon also known occur in some stilbonematines (Ott *et al.* 1995, 2014).

*Chromaspirina stilbonematinops* **sp. nov.** was among the most common species recorded in an ecological study of the fauna of Papanui Inlet, Otago Peninsula ("*Chromaspirina* sp.1" in Leduc & Probert 2011).

**Sequence data.** Partial SSU rDNA (1538 bp; Genbank OK317205).

**ZooBank registration.** *Chromaspirina stilbonematinops* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:362EFF71-6162-4140-9782-1C975A493B7B.

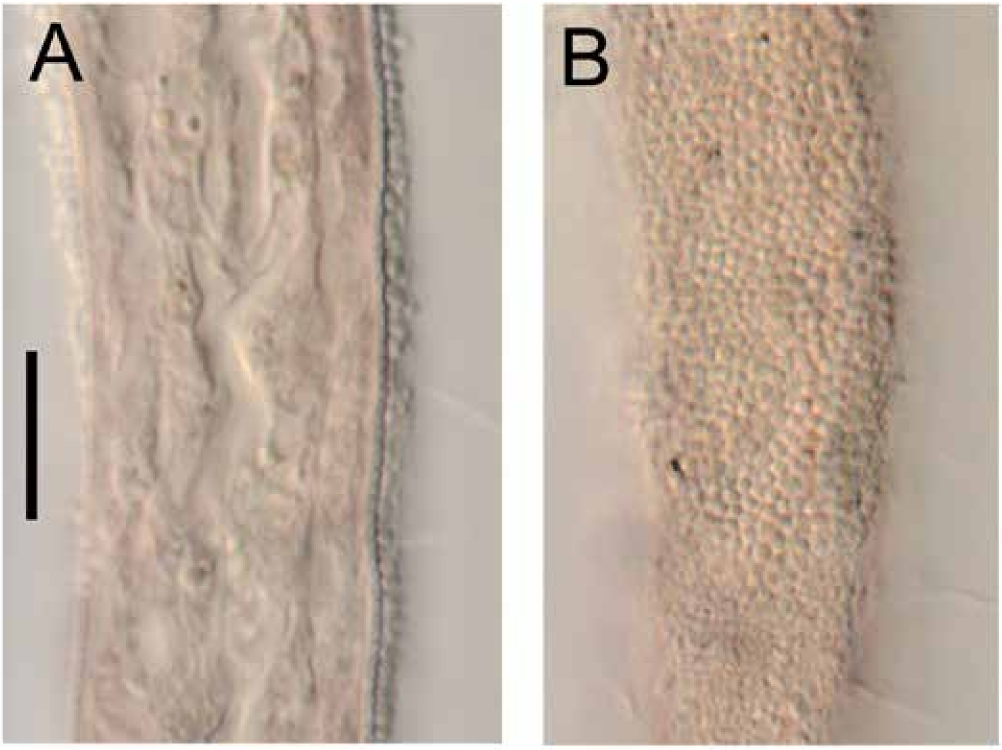



**Figure 61.** *Chromaspirina stilbonematinops* **sp. nov.**, light micrographs of male paratype NIWA 139263: **A.** Optical transverse section of middle body region showing single layer of bacteria; **B.** Surface view of middle body region. Scale bar = 10 µm.

## Genus ***Onyx*** Cobb, 1891

*Onyx* Cobb, 1891: 146–155.
*Oistolaimus* Ditlevsen, 1921: 4–6, plate 1, figs 2, 10, 11.

**Diagnosis.** Body usually slender, sometimes stout, with rounded cephalic region and conical tail; fine body striations sometimes envelop the amphidial fovea partly, entirely, or only begin at posterior edge of amphids. Amphidial fovea uni-, crypto- or multispiral, loop-shaped, or circular, located near anterior body extremity. Outer labial sensilla usually setose, either in same circle as or very close to cephalic setae. Buccal cavity with a long spear-like dorsal tooth and sometimes with numerous small denticles. Pharynx with single or double posterior bulb, usually without cuticularised lumen. Strongly cuticularised, tubular precloacal supplements, often S-shaped (modified from Blome & Riemann (1994) and Platt & Warwick (1988)).

**Remarks.** The genus was revised by Blome & Riemann (1994), who also provided a key to species. The key was later updated by Huang & Wang (2015), who omitted three species which had previously been transferred from the genus *Sigmophoranema* Hope & Murphy, 1972 to *Onyx* by Armenteros *et al.* (2014b): *Onyx brevispiculatus* (Inglis, 1963) Armenteros, Ruiz-Abierno & Decraemer, 2014, *Onyx litorale* (Schulz, 1939) Armenteros, Ruiz-Abierno & Decraemer, 2014 and *O. monstrosum* (Gerlach, 1956), Armenteros, Ruiz-Abierno & Decraemer, 2014. The genus was most recently revised by Tchesunov *et al.* (2022), who provided a key to valid species. *Onyx* now comprises 24 valid species, including the new species described herein.

**Type species.** *Onyx perfectus* Cobb, 1891

### ***Onyx exiguus*** **sp. nov.**

Figs 62, 63; Table 18

**Material examined. Holotype** NIWA 154861, NIWA Stn Z19169, 41.102° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 9 Dec 2019, fine sand, male. **Paratypes** NIWA 154862, two males and three females, same data as for holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Males.** Body short, cylindrical, with slight golden-brown colouration, tapering slightly towards anterior extremity, often with several protists attached to pharyngeal, mid-body and/or tail region(s).

**Table 17.** Morphometrics (μm) of *Chromaspirinia stilbonematinops* **sp. nov.**, given as individual values, or a range of values from several specimens.

| Parameter | Males | | Females |
|---|---|---|---|
| | Holotype | Paratypes | Paratypes |
| Number of specimens | 1 | 5 | 2 |
| L | 1406 | 1150–1632 | 1413, 1418 |
| a | 70 | 58–82 | 62, 72 |
| b | 13 | 11–14 | 13, 15 |
| c | 30 | 23–32 | 28 |
| c' | 2.5 | 2.4–3.2 | 3.1 |
| Body diameter at cephalic setae | 14 | 12–14 | 13 |
| Body diameter at amphids | 14 | 13–15 | 14 |
| Length of outer labial papillae | 1–2 | 1–2 | 1–2 |
| Length of cephalic setae | 4 | 4–5 | 4–5 |
| Amphid height | 5 | 4–5 | 4 |
| Amphid width | 6 | 5–6 | 5 |
| Amphid width/cbd (%) | 43 | 38–40 | 36 |
| Amphid from anterior end | 4 | 3–6 | 3–5 |
| Nerve ring from anterior end | 57 | 56–63 | 58 |
| Nerve ring cbd | 20 | 19–20 | 19 |
| Excretory pore from anterior end | – | – | – |
| Pharynx length | 108 | 106–120 | 95, 112 |
| Pharyngeal diameter at base | 17 | 15–16 | 16 |
| Pharynx cbd at base | 20 | 18–20 | 20 |
| Maximum body diameter | 20 | 18–20 | 20, 23 |
| Spicule length | 26 | 24–29 | – |
| Gubernacular apophysis length | 9 | 9–11 | – |
| Cloacal/anal body diameter | 19 | 18–20 | 17 |
| Tail length | 47 | 45–64 | 52 |
| V | – | – | 803, 851 |
| %V | – | – | 56, 60 |
| Vulval body diameter | – | – | 19, 21 |

Cuticle with fine striations beginning from level of cephalic setae, without lateral differentiation. Eight longitudinal rows of short, 3–4 μm long, sparsely distributed somatic setae. Rounded cephalic region not set-off from rest of body. Lip region folded inwards; inner labial sensilla not observed. Six outer labial setae, 0.4–0.5 cbd long, located in same circle as the four markedly longer cephalic setae 0.8–1.5 cbd long; the two lateral outer labial sensilla displaced dorsally by anterior edge of amphid. Ring of subcephalic setae, 8–10 μm long, located sublaterally, subventrally and subdorsally at level of posterior edge of amphids; 8–12 subcephalic setae located further posteriorly also in subventral, subventral, and subdorsal positions. Amphidial fovea unispiral, with circular, slightly cuticularised outline, located near anterior body extremity, surrounded by cuticle annulations. Cheilostome with twelve cheilorhabdia. Buccal cavity cup-shaped, with cuticularised walls and strongly cuticularised, spear-like dorsal tooth, 21–28 μm long; two smaller ventrosublateral teeth also present. Pharynx muscular, lumen not cuticularised; anterior portion surrounding buccal cavity, sometimes slightly swollen anteriorly; posterior pharyngeal bulb elongated or oval-shaped. Dorsal pharyngeal gland and duct sometimes visible. Nerve ring located slightly posterior to middle of pharynx. Secretory-excretory system not observed. Cardia small. Reproductive system with single outstretched testis located to the left of intestine; sperm cells oval-shaped to globular, 5–7 × 8–12 μm. Spicules short, 1.3–1.4 cloacal body diameters long, arcuate, with swollen proximal portion (capitulum), thin and tapering distal portion, and velum. Slightly curved gubernaculum not surrounding or flanking spicules distally. Precloacal supplements present, consisting of 8–9 S-shaped, strongly cuticularised tubes beginning 10–11 μm anterior from cloaca, more-or-less equidistant from each other (7–11 μm apart) except for two anterior-most supplements which are further apart (10–15 μm). Tail conical, with two subventral rows of 5–6 short, 2 μm long, stout spines and sparse sublateral and subdorsal setae, 3–4 μm long. Three caudal glands and spinneret present.

**Females.** Similar to males but with slightly higher c′ ratio and without subventral spines on tail. Reproductive system with two opposed and reflexed ovaries; both ovaries located ventrally or anterior ovary to the left of intestine and posterior ovary to the right of intestine. Mature eggs, 28 × 59–64 μm. Vulva located slightly posterior to mid-body. Vagina straight; pars proximalis vaginae surrounded by constrictor muscle.

**Etymology.** The species name is derived from the Latin *exiguus* (= little, short, meagre) and refers to the small size of this species.

**Species diagnosis.** *Onyx exiguus* **sp. nov.** is characterised by short body (525–762 μm), lateral outer labial setae displaced dorsally, cephalic setae 12–16 μm long, unispiral amphidial fovea, ring of eight subbcephalic setae, 8–10 μm long, at level of posterior edge of amphids and ring of additional subcephalic setae further posteriorly, buccal cavity without denticles, pharynx with simple pharyngeal bulb with uncuticularised lumen, males with 8–9 S-shaped and strongly cuticularised supplements more-or-less equidistant except for anterior-most two supplements which are slightly further apart, and two subventral rows of stout spines on tail.

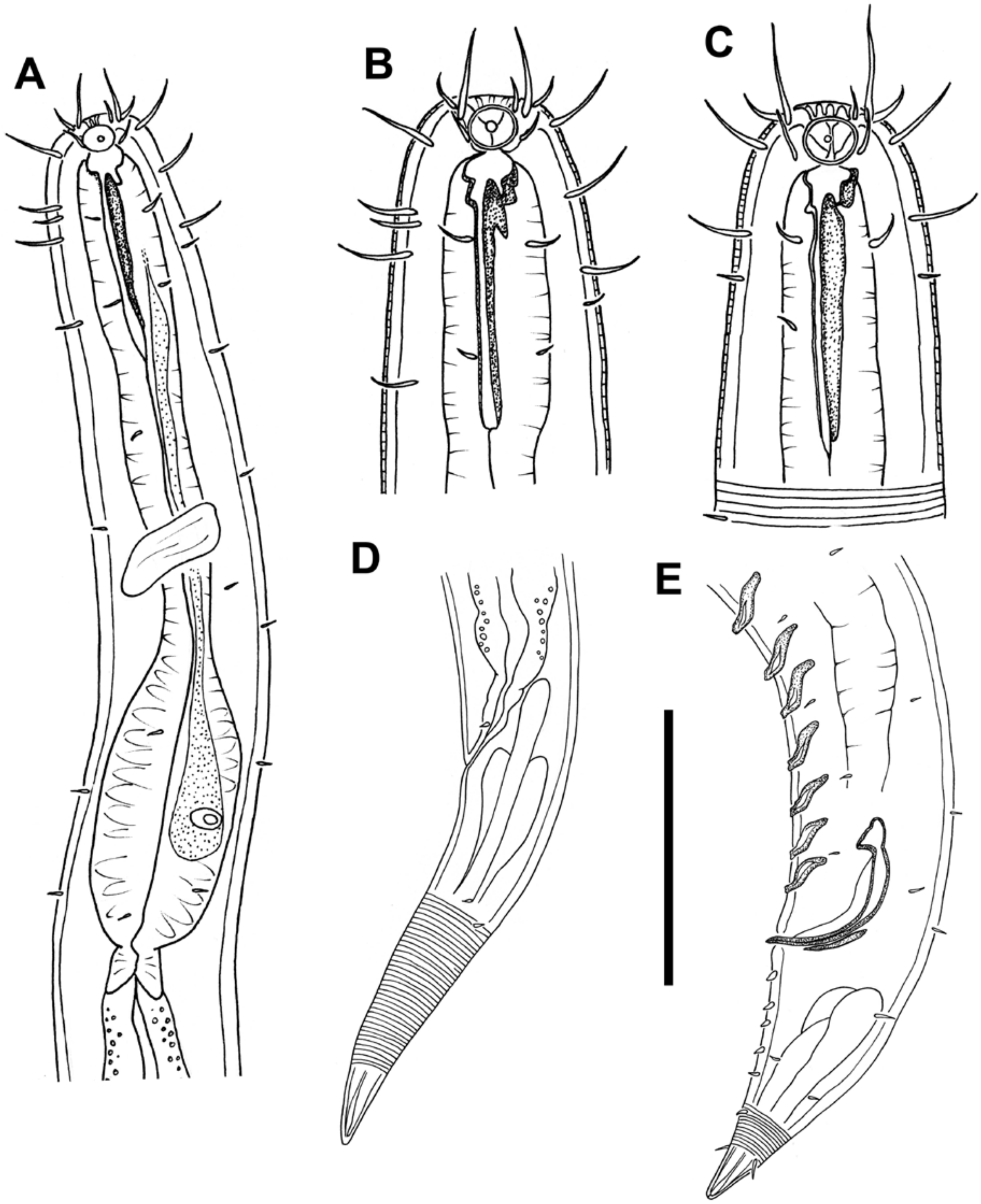



**Figure 62.** *Onyx exiguus* **sp. nov.**: **A.** Female paratype anterior body region NIWA 154862; **B.** Female paratype cephalic region NIWA 154862; **C.** Male holotype cephalic region NIWA 154861; **D.** Female paratype posterior body region NIWA 154862; **E.** Male holotype posterior body region NIWA 154861. Scale bar: A = 50 µm; B, C = 30 µm; D = 60 µm; E = 54 µm.

**Species diagnosis.** The new species is similar to *O. cangionensis* Tu, Smol, Vanreusel, & Thanh, 2011 (coastal Vietnam), *O. blomei* Nguyen Dinh Tu, Smol, Vanreusel, & Thanh, 2011 (coastal Vietnam), *O. mangrovi* Tu, Smol, Vanreusel, & Thanh, 2011 (coastal Vietnam), and *O. macramphis* Blome & Riemann, 1994 (coastal Australia) in the short (< 900 µm) body length. The new species can be differentiated from *O. cangionensis* by the shape of the amphidial fovea (unispiral *versus* loop-shaped in *O. cangionensis*), number of precloacal supplements (8–9 *versus* 14 in *O. cangionensis*) and presence of subcephalic setae (absent in *O. cangionensis*), from *O. blomei* by the shape of the amphidial fovea (unispiral *versus* multispiral in

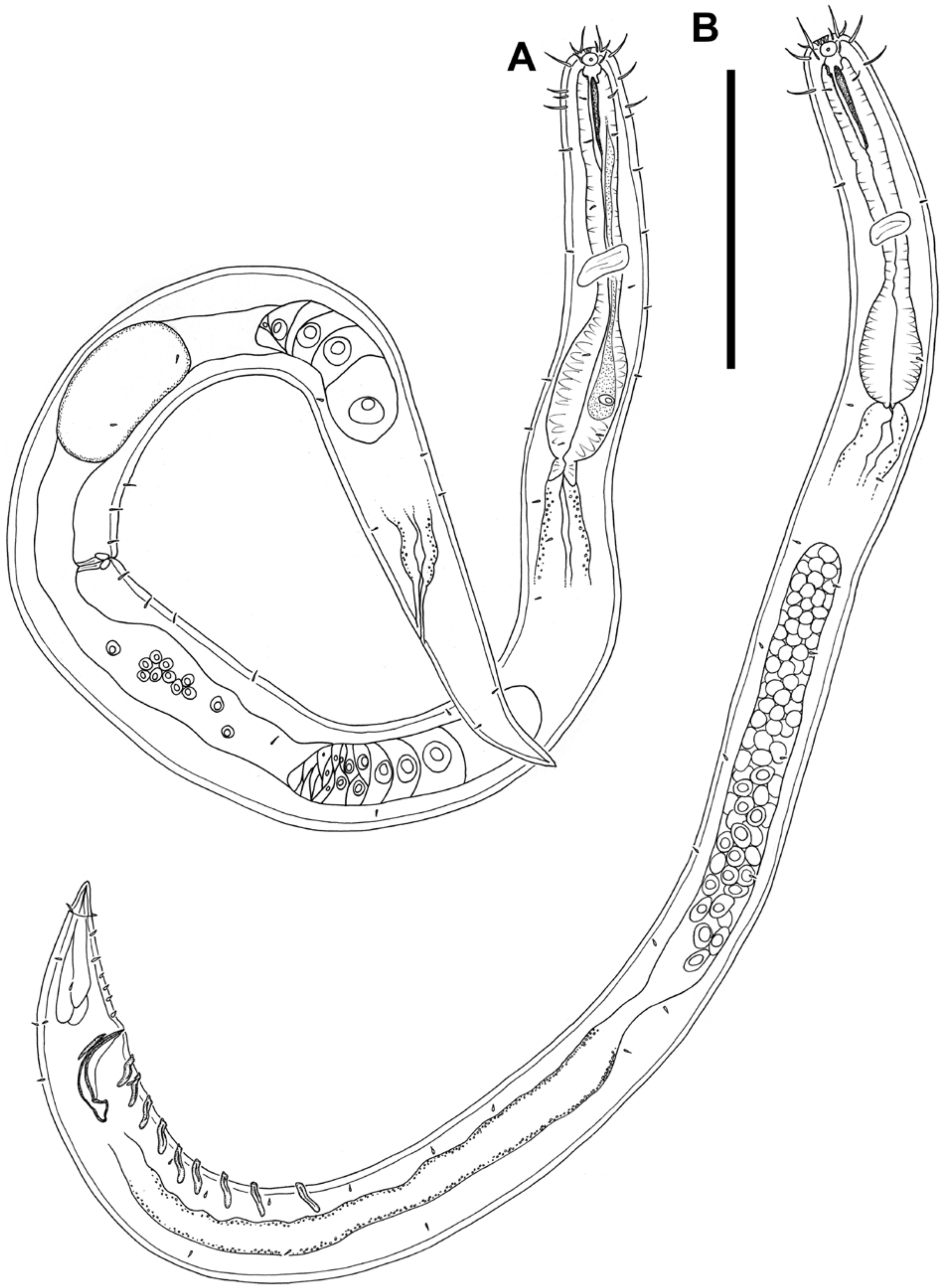



**Figure 63.** *Onyx exiguus* **sp. nov.**: **A.** Entire female paratype NIWA 154862; **B.** Entire male holotype NIWA 154861. Scale bar = 100 µm.

**Table 18.** Morphometrics (μm) of *Onyx exiguus* **sp. nov.**, given as individual values, or a range of values from several specimens.

| Parameter | Males | | Females |
|---|---|---|---|
| | Holotype | Paratypes | Paratypes |
| Number of specimens | 1 | 2 | 3 |
| L | 636 | 602, 607 | 525–762 |
| a | 20 | 20, 23 | 13–20 |
| b | 5 | 7 | 5–6 |
| c | 12 | 9, 10 | 10–12 |
| c' | 1.8 | 2.3, 2.4 | 1.9–2.7 |
| Body diameter at cephalic setae | 10 | 15, 18 | 11–15 |
| Body diameter at amphids | 17 | 19, 20 | 16–21 |
| Length of outer labial setae | 5–6 | 6 | 5–6 |
| Length of cephalic setae | 15–16 | 15–16 | 12–15 |
| Amphid height | 6 | 6, 7 | 6 |
| Amphid width | 6 | 6, 7 | 6 |
| Amphid width/cbd (%) | 35 | 32, 35 | 29–38 |
| Amphid from anterior end | 2 | 4, 5 | 1–2 |
| Nerve ring from anterior end | 76 | 46, 50 | 72–84 |
| Nerve ring cbd | 30 | 30, 31 | 29–31 |
| Pharynx length | 117 | 81, 91 | 110–139 |
| Pharyngeal bulb diameter | 20 | 19, 23 | 24–25 |
| Pharyngeal bulb length | 36 | 30, 32 | 40–50 |
| Pharynx cbd at base | 31 | 25, 29 | 32–33 |
| Maximum body diameter | 32 | 26, 30 | 38–43 |
| Spicule length | 39 | 37, 40 | – |
| Gubernacular apophysis length | 13 | 11, 12 | – |
| Cloacal/anal body diameter | 29 | 26, 28 | 23–27 |
| Tail length | 52 | 60, 66 | 51–66 |
| V | – | – | 279–439 |
| %V | – | – | 53–58 |
| Vulval body diameter | – | – | 36–41 |

*O. blomei*) and number of subcephalic setae (8 + 8–12 *versus* 4 in *O. blomei*), from *O. mangrovi* by the shape of the outer labial sensilla (setose *versus* indistinct *in O. mangrovi*), tail length (1.8–2.7 *versus* 1.0–1.3 cloacal/anal body diameters in *O. mangrovi*), and number of precloacal supplements (8–9 *versus* 17–23 in *O. mangrovi*), and from *O. macramphis* by the shape of the amphidial fovea (unispiral *versus* multispiral in *O. macramphis*), length of cephalic setae (12–16 *versus* 8 μm in *O. macramnphis*), and number of precloacal supplements (8–9 *versus* 14 in *O. macramphis*).

**ZooBank registration.** *Onyx exiguus* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:64FF7527-6B33-4A64-BA3A-CC7A5DFA598A.

## Genus *Spirinia* Gerlach, 1963

*Spirinia* Gerlach, 1963: 67.

**Diagnosis.** Body with fine body annulations and rounded or conical cephalic region. Annulated cephalic region; body annulations normally completely surround the amphidial fovea, with few exceptions. Spiral amphidial fovea. Bucca cavity narrow, lightly cuticularised; no or small/inconspicuous dorsal tooth, no or minute ventrosublateral teeth. Pharynx with small pyriform, oval, or rounded posterior bulb without cuticularised lumen. Precloacal supplements usually absent. Short conical tail (from Leduc & Verschelde (2015)).

**Remarks.** The genus, which currently comprises 14 valid species, was revised by Leduc & Verschelde (2015).

**Type species.** *Spirinia parasitifera* (Bastian, 1865)

### *Spirinia antipodea* Leduc, 2019

Figs 64–67

*Spirinia antipodea* Leduc, 2019: 93–102, figs 1–3, table 1.

**Type & locality. Holotype** NIWA 115466, NIWA Stn Z18745, 41.093° S, 174.876° E, Pāuatahanui Inlet near Camborne Walkway, upper intertidal, 28 Jul 2016, gravelly sand. **Paratypes** NIWA 115467, NNCNZ 3315–3317, same data as holotype, five males and three females.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Species diagnosis.** *Spirinia antipodea* is characterised by relatively slender body (a = 44–59), body length = 2180–2350 μm in males (mean = 2270 μm) and 2210–2560 μm in females (mean = 2363 μm), eight longitudinal rows of somatic setae associated with hypodermal glands in pharyngeal region replaced by pores without visible glands in rest of body, cephalic setae 0.25–0.35 cbd long, unispiral amphidial fovea partially surrounded by cuticle annulations and less than 0.5 cbd from anterior extremity, arcuate spicules 52–59 μm long (mean = 57 μm), gubernaculum with short tapering apophyses, vulva located at mid-body, and tail length 3.7–4.7 cloacal/anal body diameter long.

**Remarks.** *Spirinia antipodea* closely resembles *Spirinia parasitifera* (Bastian, 1865) Gerlach, 1963 due to similarities in the length and arrangement of cephalic sensilla, structure of the buccal cavity, size and shape of the amphids, and structure of the pharynx and

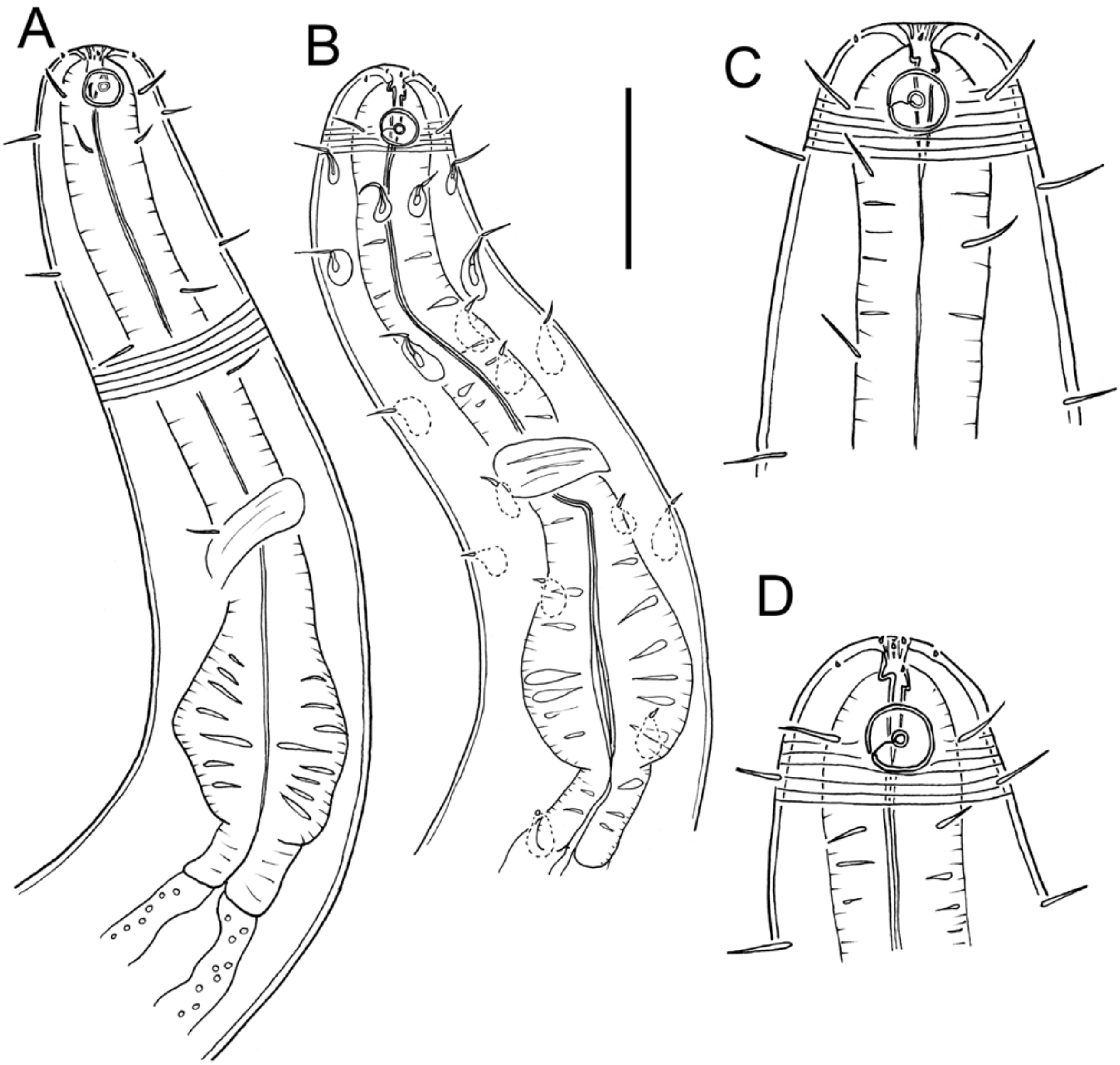


**Figure 64.** *Spirinia antipodea* Leduc, 2019: **A.** Male anterior body region; **B.** Female anterior body region; **C.** Male cephalic region; **D**. Female cephalic region. Scale bar: A, B = 30 µm; C, D = 20 µm. Modified from Leduc & Zhao (2019b) with permission from E.J. Brill/ Dr W. Backhuys, Leiden publishers.

male copulatory apparatus. *Spirinia parasitifera* has been recorded from multiple localities across the globe (although no records exist from New Zealand waters) and exhibits a relatively high degree of variability in some key body dimensions; it is therefore likely to constitute a species complex (Armenteros *et al*. 2014b; Leduc & Zhao 2019b). *Spirinia antipodea* is best differentiated from *S. parasitifera* based on SSU sequences rather than D2–D3 of LSU sequences or morphological characters, at least until more information is available on morphological and molecular variability within the *S. parasitifera* species complex.

**Sequence data.** Partial SSU rDNA (1521 bp; Genbank MH472584) and D2–D3 of LSU rDNA (388 bp; Genbank MH472585).

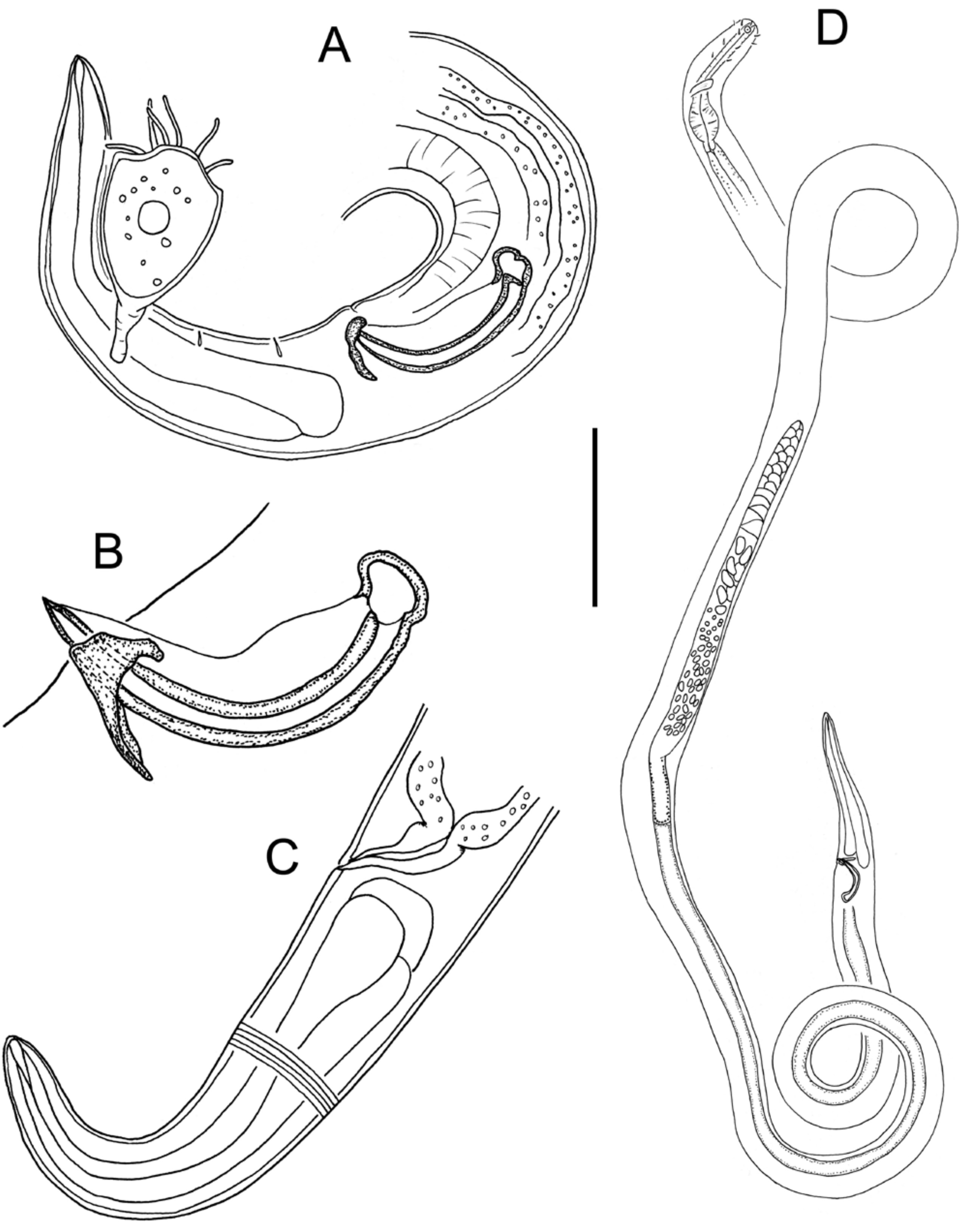



**Figure 65.** *Spirinia antipodea* Leduc, 2019: **A.** Male posterior body region; **B.** Spicule and gubernaculum; **C.** Female posterior body region; **D.** Entire male. Scale bar: A = 40 µm; B = 17 µm; C = 35 µm; D = 150 µm. Modified from Leduc & Zhao (2019b) with permission from E.J. Brill/ Dr W. Backhuys, Leiden publishers.

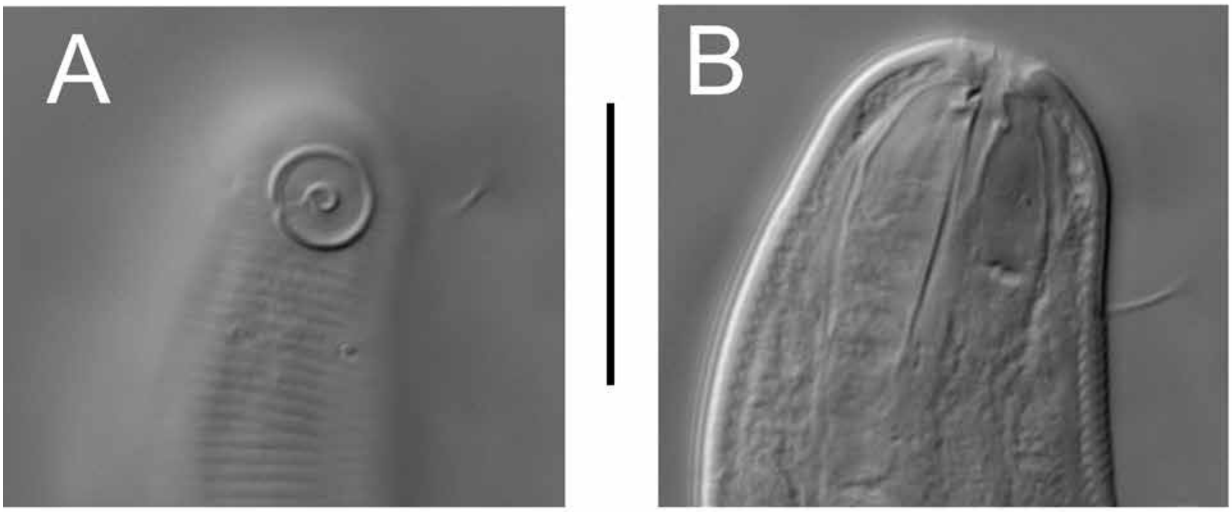



**Figure 66.** *Spirinia antipodea* Leduc, 2019 light micrographs: **A.** Surface view of female cephalic region; **B.** Optical section of female cephalic region. Scale bar = 20 µm. Modified from Leduc & Zhao (2019b) with permission from E.J. Brill/ Dr W. Backhuys, Leiden publishers.

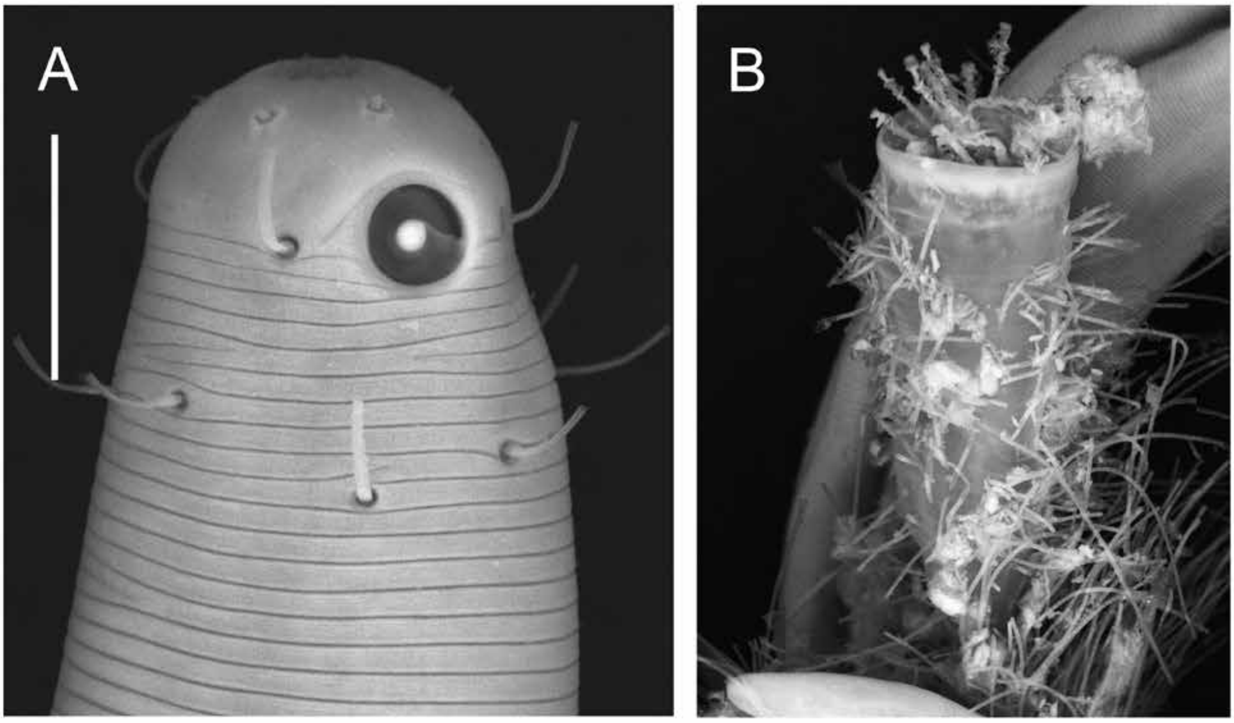



**Figure 67.** *Spirinia antipodea* Leduc, 2019, scanning electron micrographs of male: **A.** Anterior body region; **B.** Protist and bacteria attached to tail. Scale bar: A = 10 µm; B = 20 µm.

## Order **Microlaimida** Leduc, Verdon & Zhao, 2018

## Family **Microlaimidae** Micoletzky, 1922

Microlaimidae Micoletzky, 1922: 370–373.

**Diagnosis.** Body often brownish yellow. Cuticle usually distinctly annulated, without lateral differentiation; finely punctated or spiny in some species. Head cuticle smooth but not thickened or modified in a cephalic capsule; head usually slightly set off the body. Anterior sensilla six + six + four, inner labial sensilla as minute papillae, outer labial sensilla as papillae or short setae, cephalic sensilla as usually longer setae. Amphidial fovea circular with postero-dorsal interruption, more seldom uni- or even multispiral. Cheilostome with twelve weak longitudinal folds. Pharyngostome with cuticularised walls; small dorsal tooth and two opposite, even lesser, teeth usually present, or unarmed. Pharynx with posterior rounded muscular bulb. Ventral pore usually posterior to nerve ring. Two opposed outstretched ovaries. Two opposed testes or only anterior testis. Tail conical (modified from Tchesunov (2014b)).

**Type genus.** *Microlaimus* de Man, 1880

## Genus ***Microlaimus*** de Man, 1880

*Microlaimus* de Man, 1880: 15–16.
*Microlaimoides* Hoeppli, 1926: 241–242.
*Paracothonolaimus* Schulz, 1932: 366–368, fig. 18.

**Diagnosis.** Cuticle annulated, in some species also showing punctations or longitudinal bars. Cephalic region slightly set off. Spicules usually short and arcuate, seldom long and slender; gubernaculum present, often bent distally but without dorso-caudal apophyses. Papilloid precloacal supplements may be present (modified from Tchesunov (2014b)).

**Remarks.** Kovalyev & Tchesunov (2005) provided a list of 70 valid *Microlaimus* species. An updated list comprising 83 valid species was provided by Leduc (2016). Since then, two *Microlaimus* species were described by Revkova (2017, 2020a) and Gagarin (2020b). Shi & Xu (2017) transferred two *Microlaimus* species to the genus *Molgolaimus* Ditlevsen, 1921 based on the structure of the female reproductive system.

**Type species.** *Microlaimus globiceps* de Man, 1880

### ***Microlaimus korari*** **Leduc, 2016**

Figs 68–70; Table 19

*Microlaimus korari* Leduc, 2016: 259–264, figs 1–2, table 1.

**Material examined.** NIWA 139295, NIWA Stn Z19168, 41.102° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, mid-intertidal, 22 Feb 2019, fine sand, three males and two females.

**Type & locality. Holotype** NIWA 99774, NIWA Stn TAN0707/23, 38.620° S, 168.945° E, Challenger Plateau (west of New Zealand), 482 m, 28 May 2007, male. **Paratypes** NIWA 99775, same data as for holotype, female; NIWA 99776, NIWA Stn TAN0802/233, 67.620° S, 178.829° W, abyssal plain near Scott Seamount, Ross Sea, Antarctica, 3543 m, 6 Mar 2008, female.

**Distribution.** Challenger Plateau, Ross Sea abyssal plain, and Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand

**Diagnosis.** Pāuatahanui Inlet specimens characterised by a colourless or somewhat yellowish body, and are cylindrical, tapering towards anterior body extremity. Cuticle annulated from immediately posterior to cephalic setae to near tail tip; very faint longitudinal bars visible at level of pharyngeal bulb and posteriorly. Two subventral rows of short, stout somatic setae observed in pre-cloacal region, one subdorsal pair also present at level of spicules; somatic setae apparently absent elsewhere. Cuticle pores and epidermal glands not observed. Head rounded, slightly set off by constriction immediately posterior to cephalic setae. Six inner labial papillae and six outer labial papillae in two separate circles; four short cephalic setae situated further posteriorly, 0.13–0.19 corresponding body diameter (cbd) long. Circular or cryptocircular amphidial fovea with cuticularised outline, situated about 0.75 cbd from anterior extremity. Buccal cavity large, funnel-shaped, heavily cuticularised, with large dorsal tooth and two smaller subventral teeth; right subventral tooth situated approximately 4 µm anteriorly relative to left subventral tooth. Cheilostome with twelve cheilorhabdia. Pharynx surrounding buccal cavity slightly swollen and forming a small bulb; large, muscular posterior pharyngeal bulb present, oval-shaped. Secretory-excretory system present; ventral gland situated slightly posterior to cardia and excretory pore situated slightly anterior to nerve ring. Nerve ring situated at almost two-thirds of pharynx length from anterior. Cardia 7 µm long, not surrounded by intestinal tissue. Reproductive system diorchic, testes opposed and outstretched both to the right of intestine. Sperm cells globular, 6–8 × 7–9 µm. Two equal spicules, very long (2.6–3.8 cloacal body diameters) and slender, with swollen proximal end and pointed distal end. Gubernaculum 0.8–1.1 cloacal body diameters long, with distal end curving laterally and swollen proximal end, situated dorsally relative to spicules and without crurae. Precloacal supplements not observed. Tail conical, with five pairs of short and stout subventral setae and three pairs of subdorsal setae. Three caudal glands and spinneret present. Females similar to males in most respects, but with lower values of a, slightly smaller amphids, and without caudal setae. Reproductive system didelphic, with opposed and outstretched genital branches both situated ventrally relative to intestine. Vulva situated slightly posterior to mid-body. Proximal portion of vagina surrounded by constrictor muscle.

**Remarks.** The Pāuatahanui Inlet specimens agree well with the original description of *M. korari* based on continental slope and abyssal specimens, particularly in the shape and structure of the cephalic region, heavily cuticularised buccal cavity, cuticle ornamentation with longitudinal bars, and structure of the copulatory apparatus including long spicules and gubernaculum with curved proximal end. A few inconsistencies were

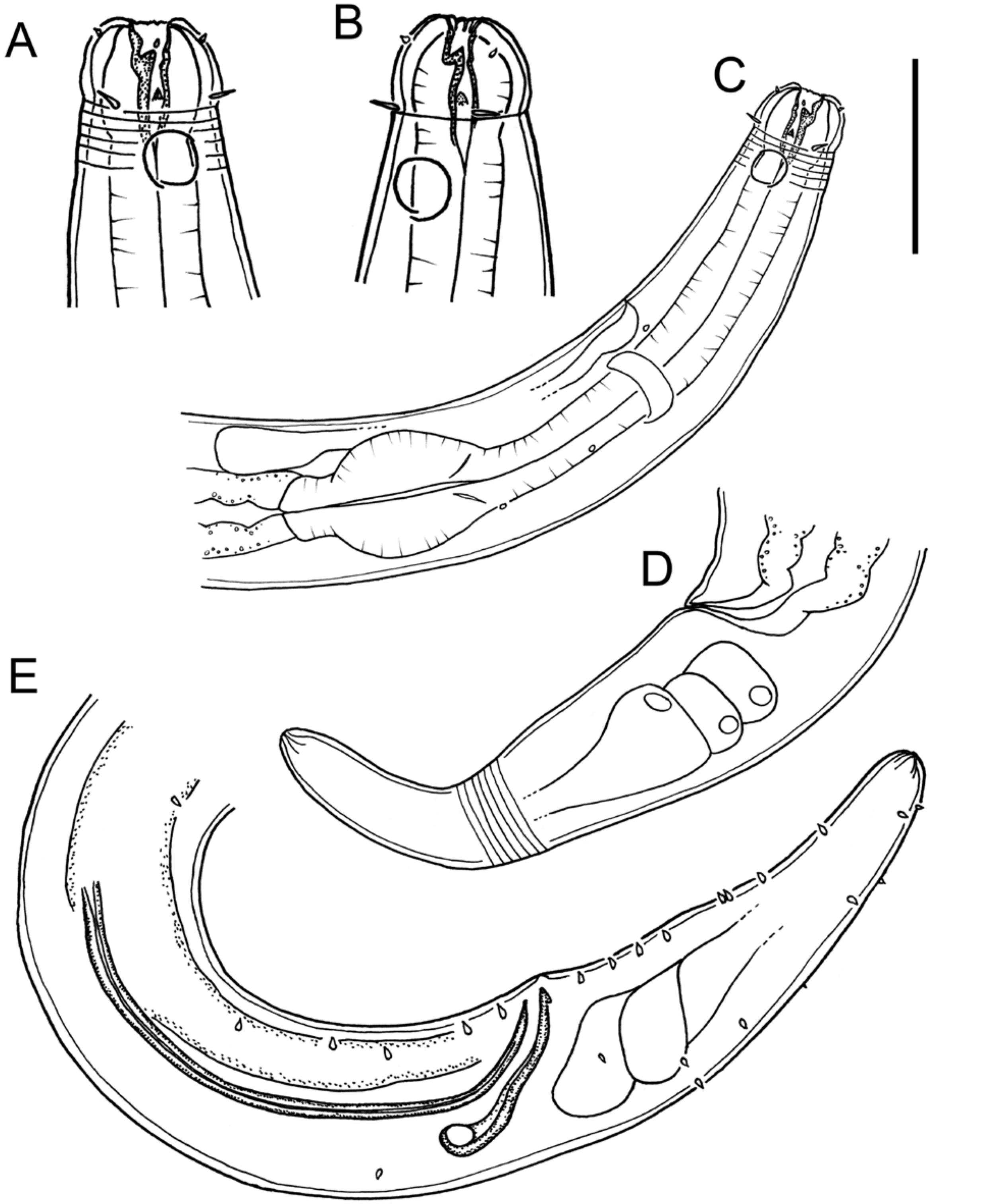



**Figure 68.** *Microlaimus korari* Leduc, 2016 NIWA 139295: **A.** Cephalic region of male; **B.** Cephalic region of female; **C.** Anterior body region of male; **D.** Posterior body region of female; **E.** Posterior body region of male. Scale bar: A, B = 20 µm; C = 30 µm; D, E = 25 µm.

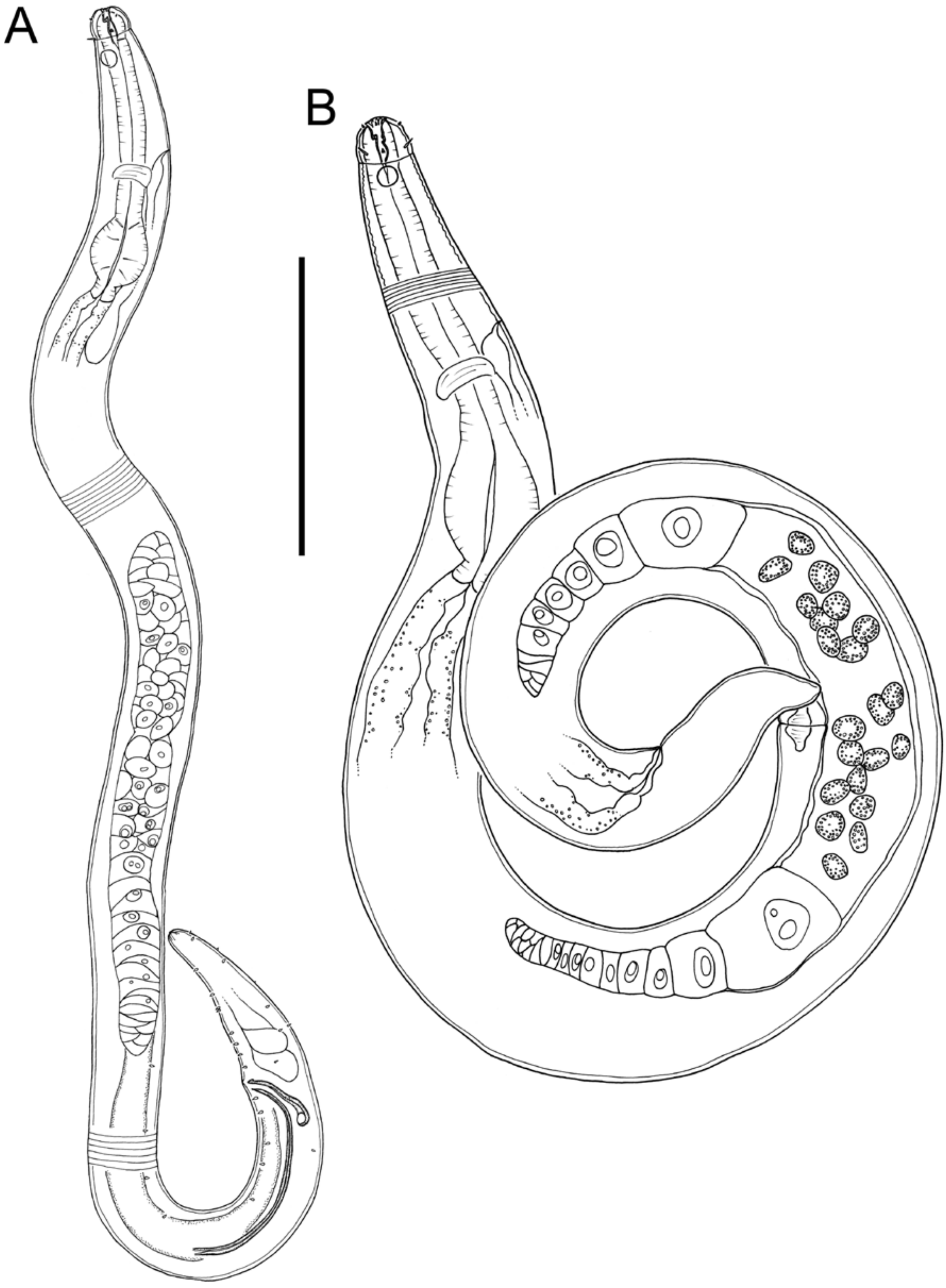



**Figure 69.** *Microlaimus korari* Leduc, 2016 NIWA 139295: **A.** Entire male; **B.** Entire female. Scale bar: A = 100 µm; B = 72 µm.

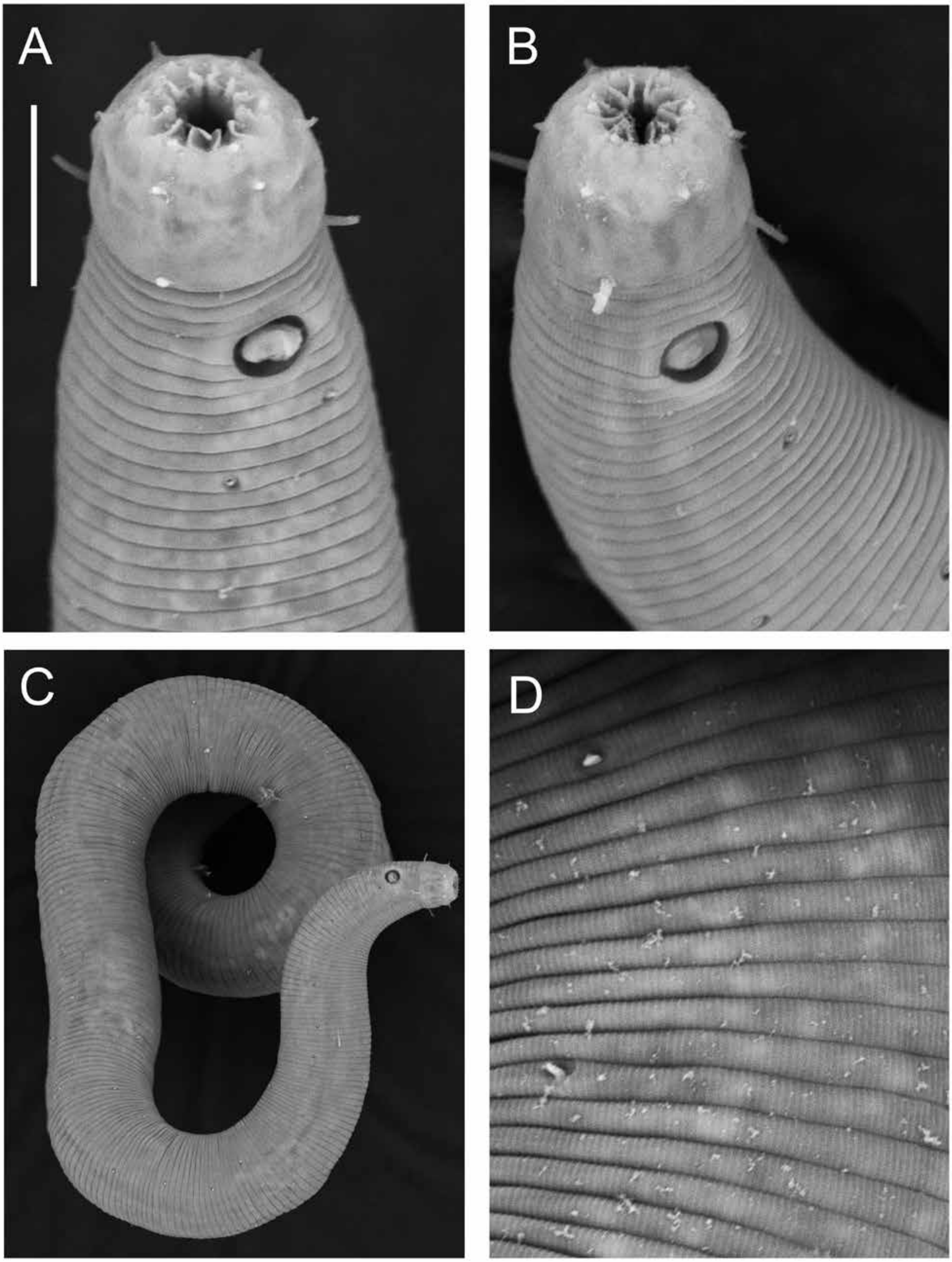


**Figure 70.** *Microlaimus korari* Leduc, 2016, scanning electron micrographs: **A–B.** Cephalic region of male; **C.** Entire juvenile; **D.** Detail of cuticle in lateral, mid-body region of female. Scale bar: A, B = 8 µm; C = 37 µm; D = 7 µm.

**Table 19.** Morphometrics (µm) of *Microlaimus korari* Leduc, 2016, given as a range of values from several specimens.

| Parameter | Males | Females |
|---|---|---|
| Number of specimens | 3 | 2 |
| L | 575–664 | 602, 642 |
| a | 20–24 | 15 |
| b | 5–7 | 5, 6 |
| c | 10–12 | 9, 13 |
| c' | 2.0–2.5 | 2.1, 3.0 |
| Body diameter at cephalic setae | 13–15 | 14, 15 |
| Body diameter at amphids | 15–16 | 16, 17 |
| Length of cephalic setae | 2–3 | 2 |
| Amphid height | 6 | 5 |
| Amphid width | 6 | 5 |
| Amphid width/cbd (%) | 38 | 29–31 |
| Amphid from anterior end | 12 | 12, 13 |
| Nerve ring from anterior end | 42–61 | 65 |
| Nerve ring cbd | 24–25 | 28 |
| Excretory pore from anterior end | 47–55 | 62 |
| Pharynx length | 83–115 | 113, 114 |
| Pharyngeal bulb diameter | 21–23 | 24, 25 |
| Pharynx cbd at base | 26–27 | 31 |
| Maximum body diameter | 28–30 | 40, 43 |
| Spicule length | 64–90 | – |
| Gubernaculum length | 21–27 | – |
| Cloacal/anal body diameter | 24–25 | 22, 24 |
| Tail length | 51–60 | 47, 71 |
| V | – | 357, 371 |
| %V | – | 58, 59 |
| Vulval body diameter | – | 40, 43 |

noted in the Pāuatahanui Inlet specimens however, namely slightly longer body length (505–537 *versus* 575–664 µm in the Pāuatahanui Inlet specimens), higher c ratio (8 *versus* 9–13), shorter tail (3.5–3.9 *versus* 2.0–3.0 cloacal/anal body diameters), slightly larger amphids in males (6 *versus* 5 µm diameter), shorter spicules (4.4 versus 2.6–3.8 cloacal body diameters), and slightly shorter gubernaculum (1.2 versus 0.8–1.1 cloacal body diameters). Given these morphological inconsistencies, and the difference in habitat between the populations (deep-sea *versus* intertidal), it is possible that the Pāuatahanui Inlet represent a different species. No molecular data, however, are available for the type population to test this hypothesis.

**Sequence data.** Partial SSU rDNA (1489 bp; Genbank OK317206) and D2–D3 of LSU rDNA (685 bp; Genbank OK317228).

## Order **Monhysterida Filipjev**
## Family **Linhomoeidae** Filipjev, 1922

Linhomoeidae Filipjev, 1922: 171–173.

**Diagnosis.** Cuticle often striated and seldom smooth. Inner labial sensilla as papilla or not recognizable at all. Amphids circular in most cases; or curved into a round, bow-like shape in some genera. Inner side of the labial region formed by an annular, soft-skinned pad that narrows the buccal aperture. Cardia noticeably lengthened. Two outstretched gonads facing opposite directions, seldom single gonad present. Anterior gonad to the left or right of intestine, and the posterior gonad to the opposite side (from Fonseca & Bezerra (2014a)).

**Type genus.** *Linhomoeus* Bastian, 1865

## Genus ***Eleutherolaimus*** Filipjev, 1922

*Eleutherolaimus* Filipjev, 1922: 173–175, fig. 34, table 4.

**Diagnosis.** Body slender. Anterior sensilla arranged in three circles; six inner labial papilla and two successive circles of four setae located lateroventrally and laterodorsally. The pattern may be supplemented with two mediolateral setae in pre- or postamphidial positions as well as one medioventral seta and one mediodorsal seta, resulting in 4 + 2 + 4, 4 + 6, or 6 + 4. Amphidial fovea circular, usually interrupted posteriorly. Buccal cavity cylindrical, short, with parallel cuticularised walls. Pharynx slender, without a distinct posterior bulb. Cardia elongate. Ventral pore in vicinity of nerve ring. Ovaries paired. Spicules curved. Gubernacular apophyses dorsocaudally oriented. Tail conical with rounded tip, conicocylindrical or cylindrical (modified from Fonseca & Bezerra (2014a)).

**Remarks.** A tabular and pictorial key to all 14 valid species of the genus was provided by Tchesunov & Miljutin (2006).

**Type species.** *Eleutherolaimus longus* Filipjev, 1922

### ***Eleutherolaimus paraschneideri*** **sp. nov.**

Figs 71, 72; Table 20

**Material examined. Holotype** NIWA 139290, NIWA Stn Z18746, 41.093° S, 174.876° E, Pāuatahanui Inlet near Camborne Walkway, upper intertidal, 28 Jul 2016, gravelly sand, male. **Paratype** NIWA 139291, one female, same data as for holotype.

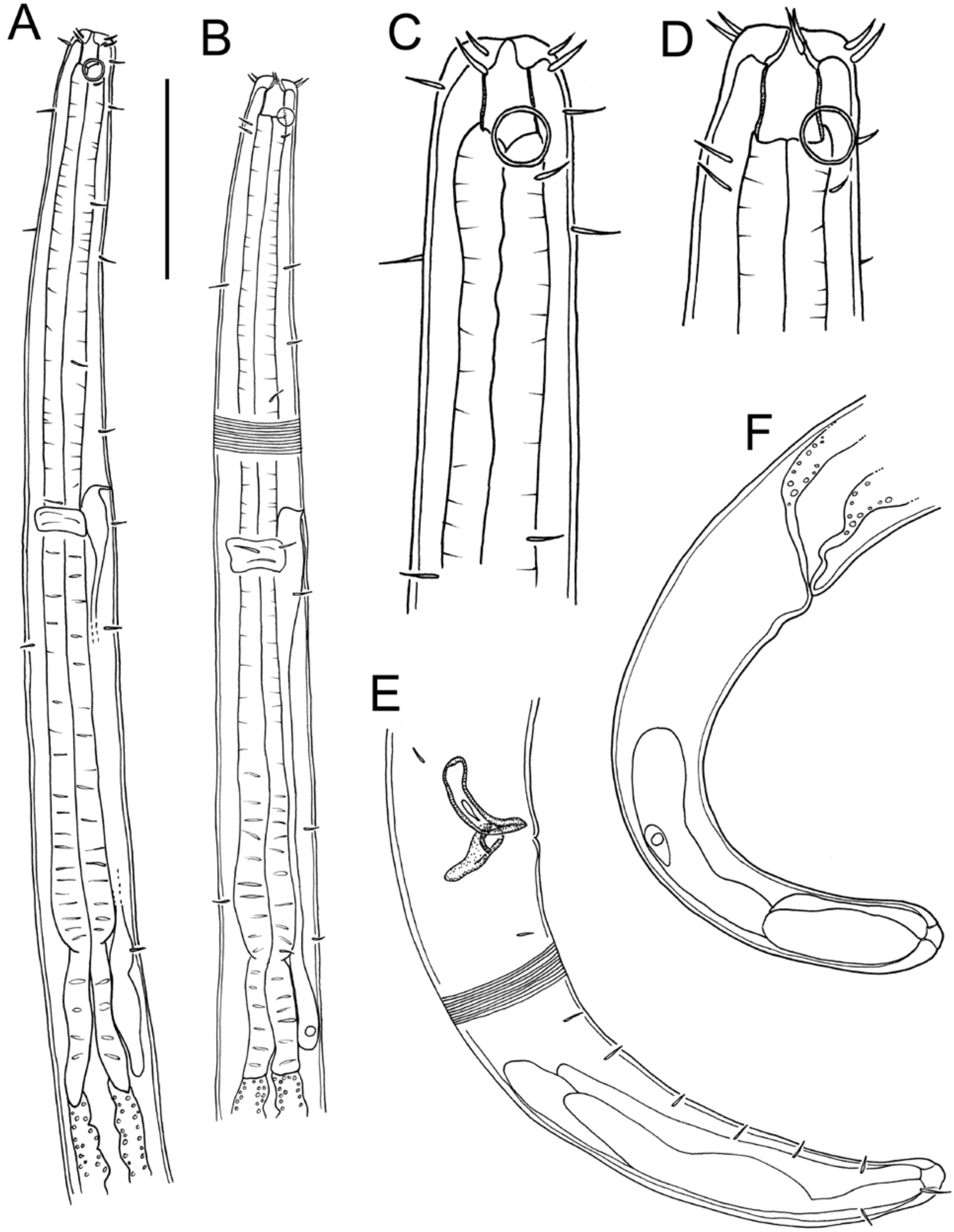



**Figure 71.** *Eleutherolaimus paraschneideri* **sp. nov.**: **A.** Male holotype anterior body region NIWA 139290; **B.** Female paratype anterior body region NIWA 139291; **C.** Male holotype cephalic region NIWA 139290; **D.** Female paratype cephalic region NIWA 139291; **E.** Male holotype posterior body region NIWA 139290; **F.** Female paratype posterior body region NIWA 139291. Scale bar: A, B = 50 µm; C, D = 17 µm; E, F = 35 µm.

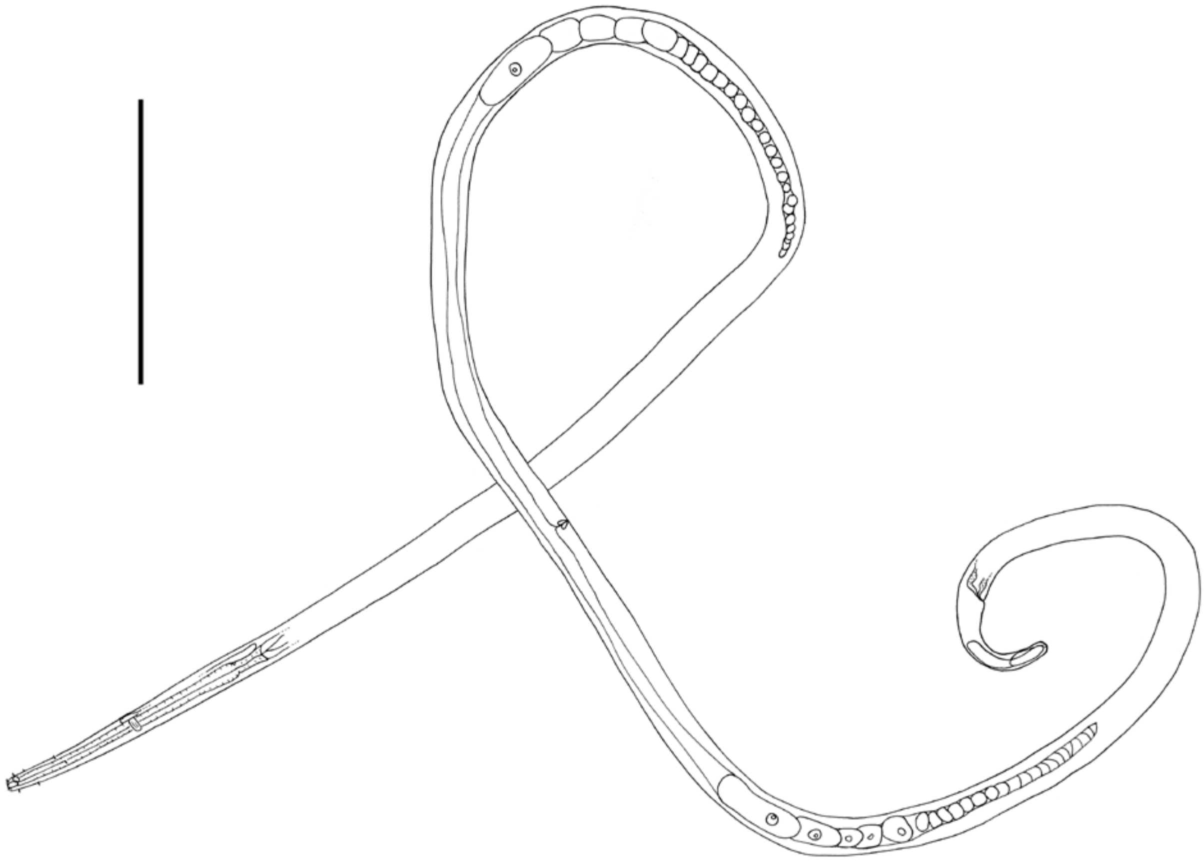


**Figure 72.** *Eleutherolaimus paraschneideri* **sp. nov.** Entire female paratype NIWA 139291. Scale bar = 250 µm.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Male.** Body colourless, slender, cylindrical, tapering slightly towards both extremities. Cuticle finely striated, no lateral differentiation. Short somatic setae largely absent except in pharyngeal and cloacal regions, sparsely distributed, 4 µm long. Slightly rounded cephalic region, not set-off. Narrow mouth opening surrounded by bulge of inner portion of lip region. Inner labial papillae not observed. Two separate circles of four cephalic setae located lateroventrally and laterodorsally on lip region; setae of posterior circle 0.3–0.4 cbd long, slightly longer than setae in anterior circle. One medioventral seta and one mediodorsal seta situated between amphid and posterior circle of cephalic setae, 4 µm long; one mediolateral seta situated immediately posterior to each amphid, 4 µm long. Amphidial fovea circular, outline slightly cuticularised, not broken, at level of junction of buccal cavity and pharynx. Buccal cavity cylindrical, 4 µm wide, 9 µm deep, with cuticularised walls, without cuticularised ring, not surrounded by pharyngeal tissue. Ducts of pharyngeal glands not observed. Pharynx muscular, widening slightly posteriorly but not forming true bulb; lumen not cuticularised. Nerve ring located slightly posterior to middle of pharynx. Secretory-excretory system with small ventral gland situated immediately posterior to pharyngeal bulb; excretory pore slightly anterior to nerve ring. Cardia long, conspicuous, ca. 35 µm long. Reproductive system with two opposed testes; position of testes relative to intestine unclear. Spicules short, 0.8 cloacal body diameters long, cuticularised, arcuate; slightly swollen proximal portion and short lamella present. Gubernaculum with strongly cuticularised dorsocaudal apophyses, slightly bent. Precloacal supplements not observed. Tail conical with rounded tip; two rows of subventral setae, 3–4 µm long, and two pairs of subdorsal setae near tail tip. Three caudal glands located mostly in posterior half of tail; spinneret present.

**Female.** Similar to males but with medioventral and mediodorsal seta located further posteriorly at level of amphids and tail almost cylindrical with slightly swollen tip and without setae. Reproductive system with two opposed outstretched ovaries; anterior ovary to the left of intestine, posterior ovary to the right of intestine.

**Table 20.** Morphometrics (µm) of *Eleutherolaimus paraschneideri* **sp. nov.**, given as individual values.

| Parameter | Male Holotype | Female Paratype |
|---|---|---|
| Number of specimens | 1 | 1 |
| L | 2620 | 2816 |
| a | 90 | 85 |
| b | 12 | 13 |
| c | 22 | 24 |
| c' | 4.6 | 4.9 |
| Body diameter at cephalic setae | 10 | 11 |
| Body diameter at amphids | 12 | 13 |
| Length of cephalic setae | 3–4 | 3–5 |
| Amphid height | 5 | 5 |
| Amphid width | 5 | 5 |
| Amphid width/cbd (%) | 42 | 38 |
| Amphid from anterior end | 6 | 7 |
| Nerve ring from anterior end | 118 | 120 |
| Nerve ring cbd | 23 | 23 |
| Excretory pore from anterior end | 112 | 111 |
| Pharynx length | 215 | 217 |
| Pharyngeal diameter at base | 15 | 15 |
| Pharynx cbd at base | 25 | 25 |
| Maximum body diameter | 29 | 33 |
| Spicule length | 21 | – |
| Gubernacular apophysis length | 13 | – |
| Cloacal/anal body diameter | 26 | 24 |
| Tail length | 119 | 118 |
| V | – | 1720 |
| %V | – | 61 |
| Vulval body diameter | – | 30 |

Spermatheca not observed. Vulva slightly posterior to mid-body. Vaginal gland not observed. Pars proximalis vaginae surrounded by constrictor muscle.

**Etymology.** The species name refers to the similarity between the new species and *Eleutherolaimus schneideri* Turpeenniemi, 1997.

**Species diagnosis.** *Eleutherolaimus paraschneideri* **sp. nov.** is characterised by body length 2620 µm in male and 2816 µm in female, length of cephalic setae in posterior circle 3–5 µm (0.3–0.4 cbd), medioventral and mediodorsal setae situated between amphid and posterior circle of cephalic setae in male and at level of amphids in female, one mediolateral seta situated immediately posterior to each amphid, amphid situated at level of junction of buccal cavity and pharynx, 0.38–0.42 cbd wide, secretory-excretory pore situated slightly anterior to nerve ring, spicules 21 µm long (0.8 cbd), tail conical, 4.6 cloacal body diameters with subventral and subdorsal setae 4 µm long in male, and tail almost cylindrical, 4.9 anal body diameters long and without setae in females.

**Differential diagnosis.** The new species is most similar to *Eleutherolaimus schneideri* (Baltic Sea) in the length, number and arrangement of the two circles of cephalic setae and additional medioventral, mediodorsal, and postamphidial setae, the size of the buccal cavity, size and placement of amphids, structure of the copulatory apparatus, and shape of the tail. *Eleutherolaimus paraschneideri* **sp. nov.** differs from *E. schneideri* in the position of the secretory-excretory pore relative to the nerve ring (anterior to nerve ring *versus* posterior to nerve ring in *E. schneideri*), distribution and length of somatic setae (4 µm long and mostly present in pharyngeal and cloacal regions *versus* 2–13 µm long and present throughout body in *E. schneideri*), absence of cuticularised ring in buccal cavity (*versus* cuticularised ring present in *E. schneideri*), and higher values of b (12–13 versus 9–10 in *E. schneideri*) and c (22–24 versus 13–22 in *E. schneideri*).

**Sequence data.** Partial SSU rDNA (1589 bp; Genbank OK317207) and D2–D3 of LSU rDNA (731 bp; Genbank OK317229).

**ZooBank registration.** *Eleutherolaimus paraschneideri* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:56DF0481-9AAD-41C9-AA58-91D9DE80A5D0.

## Genus ***Linhomoeus*** Bastian, 1865

*Linhomoeus* Bastian, 1865: 94.
*Paralinhomoeus* de Man, 1907: 74–81, plate 4, fig. 15.
*Eulinhomoeus* de Man, 1907: 74.

**Diagnosis.** Cuticle finely striated. Six inner labial papillae; six outer labial setae and four cephalic setae in one circle with the cephalic setae longer than the outer labial setae; sometimes additional setae are present. Amphids circular, cryptospiral or cryptocircular. Buccal cavity cup-shaped, more-or-less cuticularised, sometimes with teeth or plates, and sometimes divided by a cuticular ring. Pharynx posteriorly enlarged, without forming a distinct bulb. Cardia usually conspicuous and elongated. Two outstretched ovaries. Gubernaculum with dorsal apophyses. Tail conical or conicocylindrical (modified from Fonseca & Bezerra (2014a)).

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

**Type species.** *Linhomoeus elongatus* Bastian, 1865

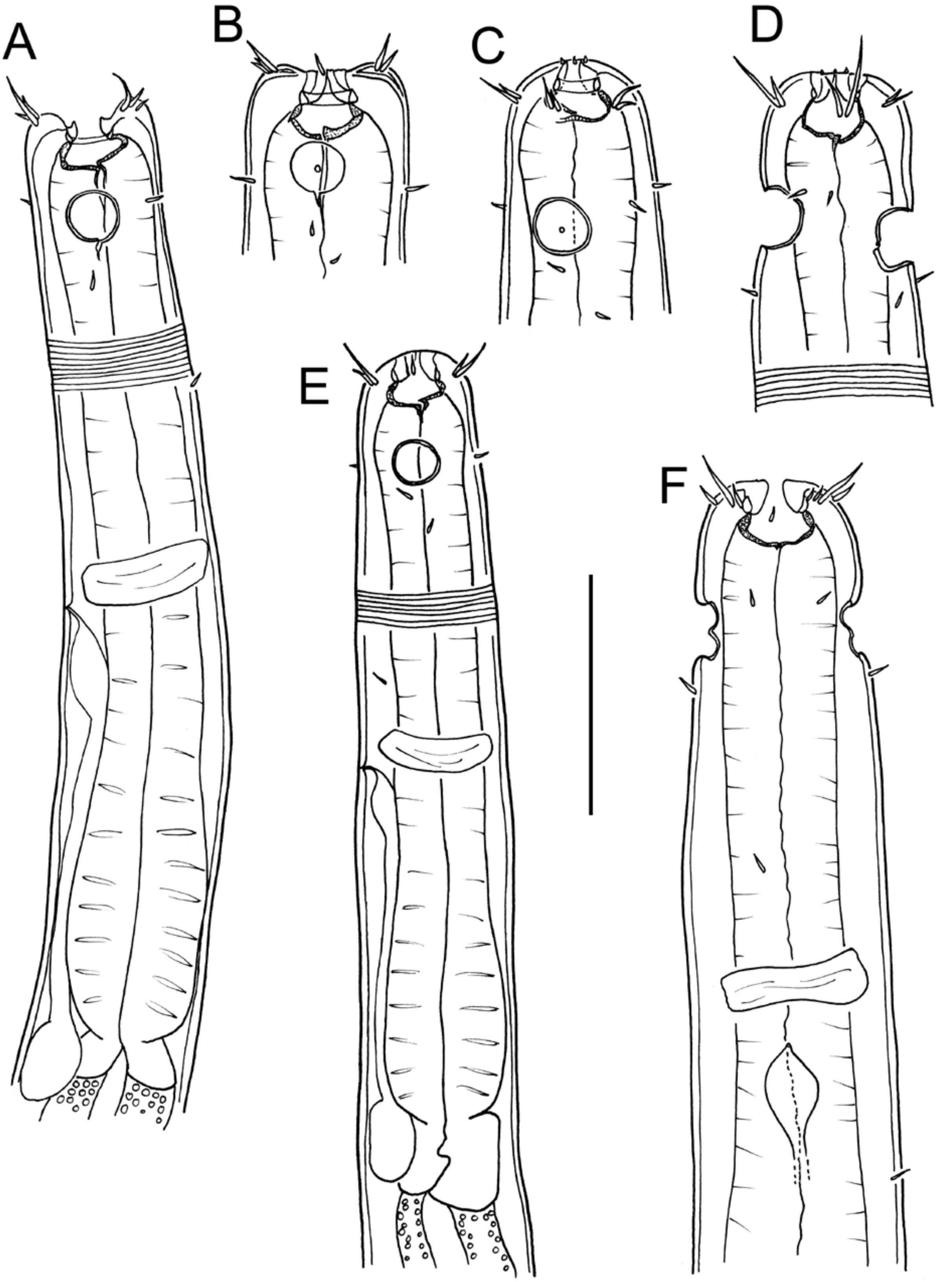



**Figure 73.** *Linhomoeus manaensis* **sp. nov.**: **A.** Female paratype anterior body region NIWA 139289; **B.** Male holotype cephalic region NIWA 139288; **C.** Male paratype cephalic region NIWA 139289; **D.** Male paratype cephalic region NIWA 139289; **E.** Male paratype anterior body region NIWA 139289; **F.** Ventral view of male paratype anterior body region NIWA 139289. Scale bar: A = 40 µm; B, C, D = 36 µm; E = 42 µm; F = 33 µm.

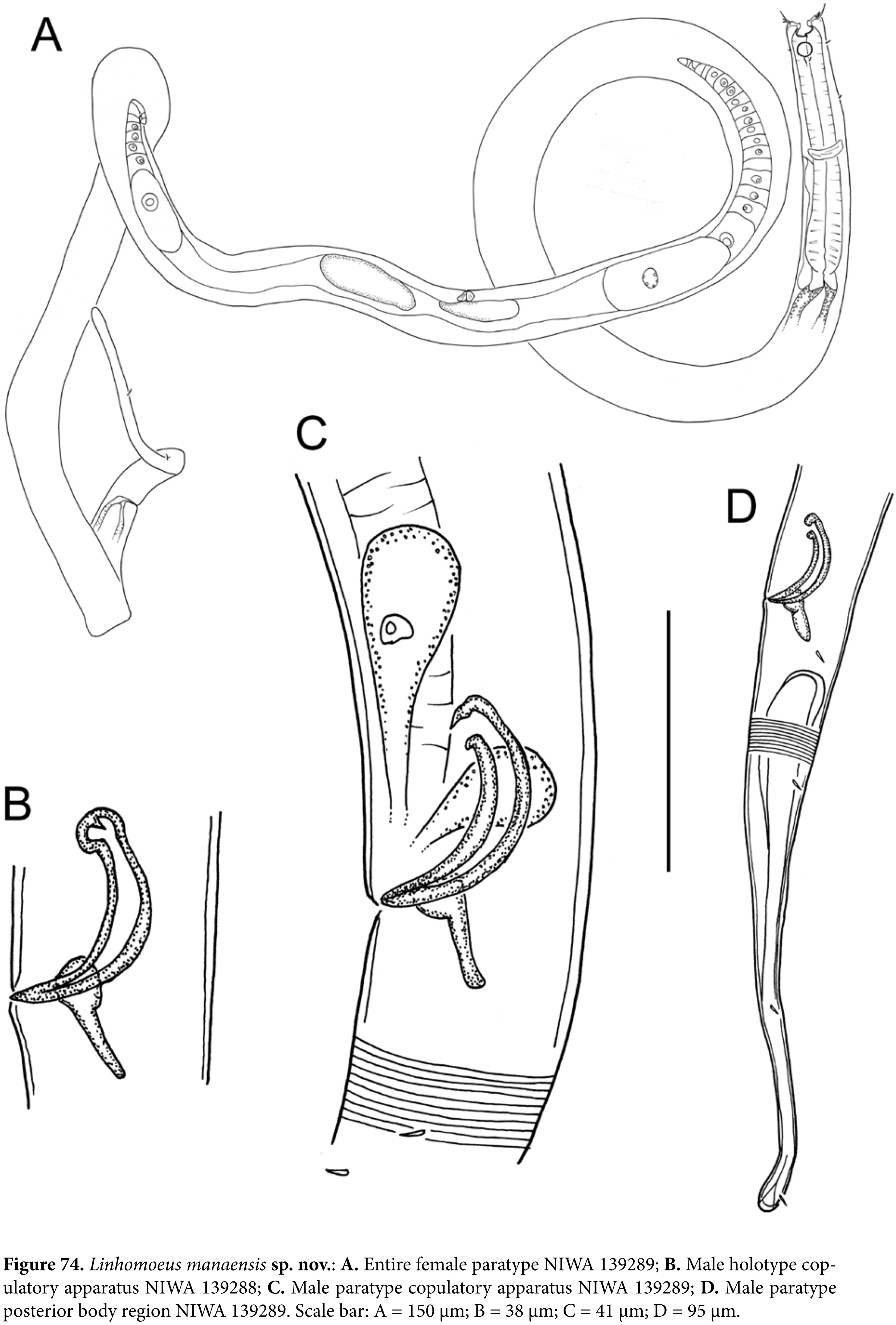



**Figure 74.** *Linhomoeus manaensis* **sp. nov.**: **A.** Entire female paratype NIWA 139289; **B.** Male holotype copulatory apparatus NIWA 139288; **C.** Male paratype copulatory apparatus NIWA 139289; **D.** Male paratype posterior body region NIWA 139289. Scale bar: A = 150 µm; B = 38 µm; C = 41 µm; D = 95 µm.

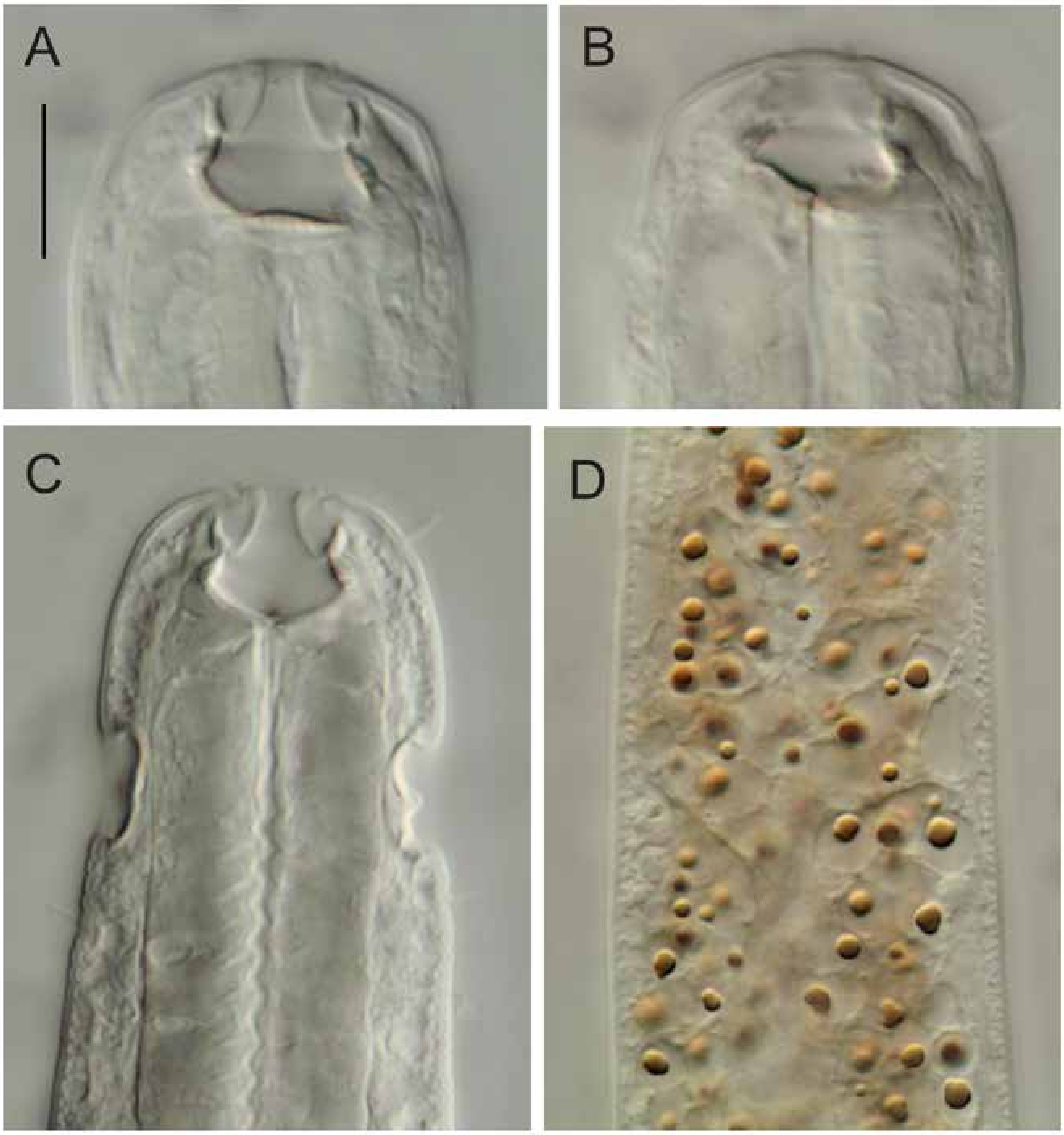



**Figure 75.** *Linhomoeus manaensis* **sp. nov.**, light micrographs: **A.** Lateral view of holotype male cephalic region showing buccal cavity and mouth opening NIWA 139288; **B.** Lateral view of male holotype cephalic region showing buccal cavity with tooth-like projection NIWA 139288; **C.** Ventral view of male paratype cephalic region NIWA 139289; **D.** Intestine with brown globules, female paratype NIWA 139289. Scale bar: A, B = 10 µm; C = 12 µm; D = 14 µm.

## *Linhomoeus manaensis* sp. nov.

Figs 73–76; Table 21

**Material examined. Holotype** NIWA 139288, Z19166, 41.102° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, mid-intertidal, 31 Jan 2018, fine sand, male. **Paratypes** NIWA 139289, three males and one female, same data as for holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Males.** Body colourless except for presence of brown granules in intestine wall, cylindrical, tapering slightly towards both extremities. Cuticle finely striated, no lateral differentiation. Somatic setae

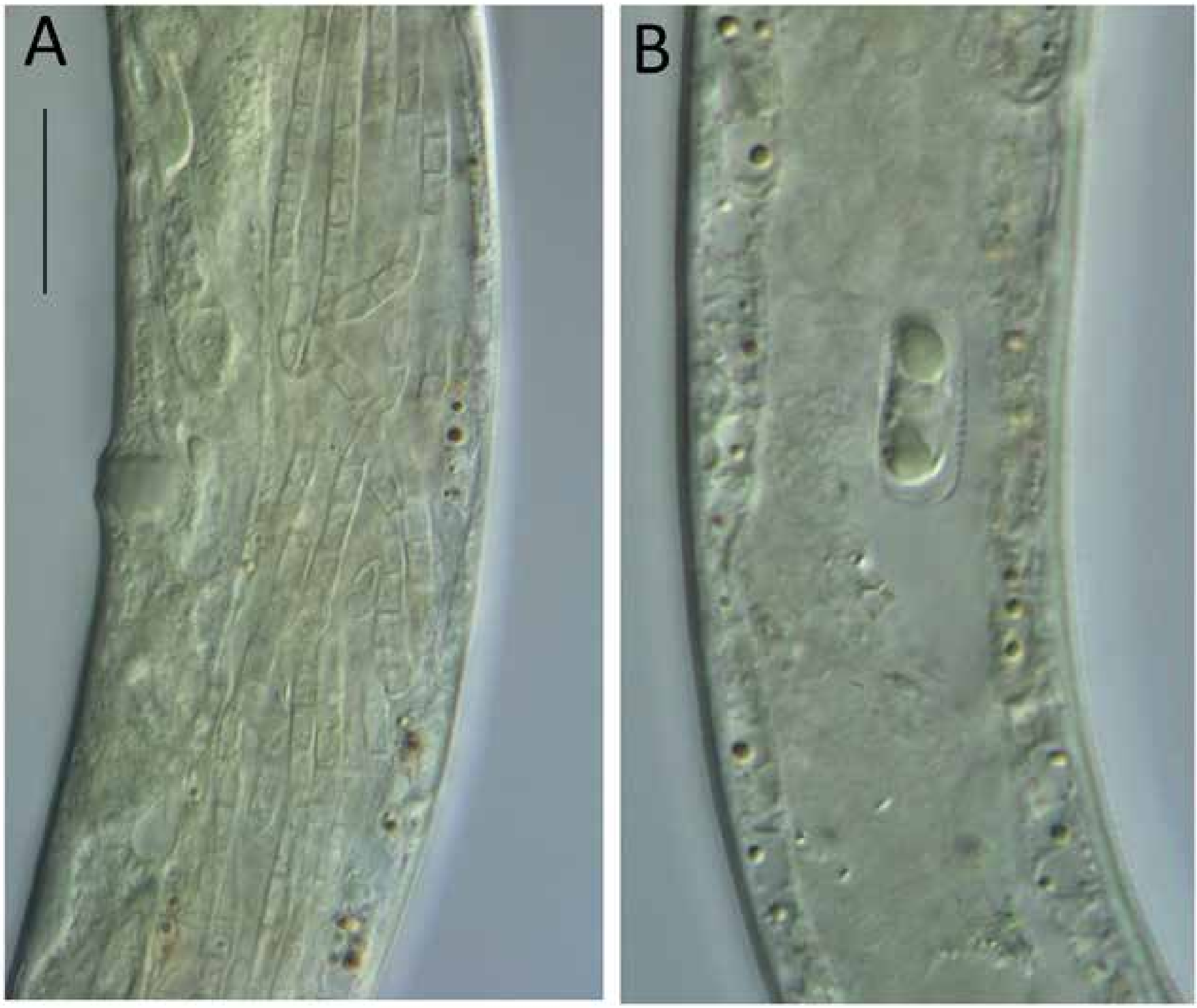



**Figure 76.** *Linhomoeus manaensis* **sp. nov.**, light micrographs of female paratype NIWA 139289: **A.** Lateral view of vagina and intestine containing cyanobacteria filaments; **B.** Diatom in intestine of same specimen. Scale bar: A = 20 µm; B = 12 µm.

largely absent except in pharyngeal and cloacal regions, sparsely distributed. Blunt to rounded cephalic region, not set-off from rest of body. Narrow mouth opening surrounded by bulge of inner portion of lip region. Six minute inner labial papillae surrounding mouth opening. Six outer labial setae situated at same level as four longer cephalic setae, ca. 0.4–0.5 cbd long. Two or four additional setae present at same level as cephalic and outer labial setae in most specimens; additional setae similar in length to outer labial setae or slightly shorter, situated either laterally or lateroventrally and laterodorsally, resulting in either a 6 + 10 (no additional setae), 6 + 12 (two lateral additional setae), or 6 + 14 (two laterodorsal and two lateroventral additional setae) overall arrangement of cephalic sensilla. Eight subcephalic setae present, 3 µm long; a circle of two subdorsal and two subventral setae situated at level of amphid, and two sublateral setae located slightly posterior to each amphid. Amphidial fovea circular; outline slightly cuticularised, sometime broken, often with central fleck, surrounded by cuticle striations, ca. 0.5–0.7 cbd from anterior extremity. Buccal cavity cup-shaped, 7–9 µm deep, up to 9 µm wide, with slightly cuticularised ring and heavily cuticularised walls and base; depending on angle of observation, teeth-like projections and toothed ('rasping') ridges can be seen. Ducts of pharyngeal glands not visible. Pharynx muscular, anterior portion slightly swollen and surrounding base of buccal cavity; posterior portion of pharynx slightly swollen but not forming a true bulb. Nerve ring located near middle of pharynx. Secretory-excretory system with small ventral gland situated immediately posterior to pharyngeal bulb; excretory pore located immediately posterior to nerve ring. Cardia relatively short, 12–20 µm long. Reproductive system with two opposed, outstretched testes; anterior

**Table 21.** Morphometrics (μm) of *Linhomoeus manaensis* **sp. nov.**, given as individual values, or a range of values from several specimens.

| Parameter | Males | | Female |
|---|---|---|---|
| | Holotype | Paratypes | Paratype |
| Number of specimens | 1 | 3 | 1 |
| L | 1719 | 1432–1478 | 1815 |
| a | 54 | 45–47 | 52 |
| b | 11 | 11 | 12 |
| c | 10 | 8–9 | 11 |
| c' | 6.9 | 6.7–7.0 | 7.5 |
| Body diameter at cephalic setae | 20 | 17–18 | 18 |
| Body diameter at amphids | 25 | 22–24 | 22 |
| Length of outer labial setae | 3 | 2–3 | 3 |
| Length of cephalic setae | 7 | 7–9 | 8 |
| Amphid height | 8 | 8–9 | 8 |
| Amphid width | 8 | 8 | 8 |
| Amphid width/cbd (%) | 32 | 35–36 | 36 |
| Amphid from anterior end | 13 | 15–20 | 14 |
| Nerve ring from anterior end | 74 | 68–71 | 77 |
| Nerve ring cbd | 31 | 26–28 | 27 |
| Excretory pore from anterior end | 93 | 75–82 | 82 |
| Pharynx length | 154 | 135–137 | 146 |
| Pharyngeal bulb diameter | 24 | 22–23 | 23 |
| Pharynx bulb cbd | 31 | 29–30 | 28 |
| Maximum body diameter | 32 | 31–33 | 35 |
| Spicule length | 32 | 29–35 | – |
| Gubernacular apophysis length | 10 | 10–11 | – |
| Cloacal/anal body diameter | 25 | 23–25 | 21 |
| Tail length | 173 | 156–176 | 158 |
| V | – | – | 921 |
| %V | – | – | 51 |
| Vulval body diameter | – | – | 33 |

testis located to the left of intestine, posterior testis to the right of intestine. Sperm cells globular, 5–9 × 7–10 μm. Spicules short, arcuate, 1.3 cloacal body diameters long, strongly cuticularised, with slightly swollen proximal portion. Gubernaculum with straight, strongly cuticularised dorsocaudal apophyses. Precloacal supplements not observed. Tail conicocylindrical, with short, sparse setae; one subterminal seta sometimes present. Three caudal glands present.

**Female.** Similar to males but with slightly higher value of c and c′, additional setae absent, and only one subcephalic seta posterior to each amphid. Reproductive system with two opposed outstretched ovaries; anterior ovary to the left of intestine, posterior ovary to the right of intestine. Spermatheca not observed. Vulva located near mid-body. Vaginal gland not observed. Pars proximalis vaginae surrounded by constrictor muscle.

**Etymology.** The species name is derived from the type locality (Mana Bank) in Pāuatahanui Inlet.

**Species diagnosis.** *Linhomoeus manaensis* **sp. nov.** is characterised by a relatively short body length (males 1432–1719 μm and female 1815 μm) and low values of a (45–54) and b (11–12), cephalic setae 0.4–0.5 cbd long, presence of either 4, 2 or no additional setae in males, eight subcephalic setae slightly posterior to, and at level of, amphids, amphids 0.32–0.36 cbd wide, relatively large and heavily cuticularised buccal cavity with cuticularised ring and tooth-like projection and/or ridge, secretory-excretory pore situated immediately posterior to nerve ring, spicules 1.3 cloacal body diameters long, gubernacular apophyses 10–11 μm long, and conicocylindrical tail with rounded tip, 6.7–7.5 cloacal/anal body diameters long.

**Differential diagnosis.** The new species shares a number of traits including length and arrangement of cephalic sensilla, size and structure of the buccal cavity, amphid size and position, structure of the copulatory apparatus, and/or length and shape of the tail with a number of other *Linhomoeus* species. However, it can be differentiated from all other species of the genus by the number, size, and arrangement of the subcephalic setae.

*Linhomoeus manaensis* **sp. nov.** resembles *Linhomoeus macramphis* Schuurmans Stekhoven, 1942 (Mediterranean Sea) in body length, body dimensions, and general structure and size of the buccal cavity, amphids, copulatory apparatus, and tail. The latter species, however, is characterised by the presence of only four long subcephalic setae (*versus* six or eight relatively short subcephalic setae in *L. manaensis* **sp. nov.**) located mid-way between the cephalic setae and anterior edge of the amphids (*versus* at level of, and immediately posterior to, amphids in *L. manaensis* **sp. nov.**) and posterior pharynx lumen with teeth-like cuticularised projection (*versus* no cuticularisation of lumen in *L. manaensis* **sp. nov.**).

*Linhomoeus manaensis* **sp. nov.** resembles *L. filiformis* (Filipjev, 1918) Fonseca & Bezerra (2014a) (Black Sea) in general body dimensions and most features of the cephalic region, but differs from the latter in having shorter cephalic setae (5–9 μm *versus* 11 μm in *L. filiformis*) and subcephalic setae slightly posterior to amphids (*versus* absent in *L. filiformis*), smaller amphids (8 μm wide and 0.3–0.4 cbd *versus* 10 μm wide and 0.5 cbd) in *L. filiformis*, and markedly shorter gubernacular apophyses (11 *versus* 25 μm in *L. filiformis*).

The new species is similar to *L. bocki* (Schuurmans Stekhoven, 1946) Fonseca & Bezerra (2014a) (North

Atlantic) in the structure of the buccal cavity, size and position of the amphids, pharynx and cardia dimensions, and structure of the copulatory apparatus, but differs from the latter in having subcephalic setae (*versus* no subcephalic setae in *L. bocki*) and in the position of the secretory-excretory pore (immediately posterior to nerve ring *versus* well anterior to nerve ring in *L. bocki*).

*Linhomoeus manaensis* **sp. nov.** resembles *L. caxinus* Vitiello, 1969 (Mediterranean Sea), but differs from the latter in the arrangement of subcephalic setae (four subcephalic setae, two of which are situated anterior to the amphids *versus* six or eight subcephalic setae located at level of, or posterior to, amphids), and size and shape of the tail (conicocylindrical with clavate tip and 6.7–7.5 cloacal/anal body diameters long *versus* filiform with pointed tip and 9.2–11.3 cloacal/anal body diameters long).

*Linhomoeus manaensis* **sp. nov.** is similar to *L. flevensis* Bouwman, 1981 and *L. fuscacephalus* (Cobb, 1920) Gerlach, 1963 (both North Atlantic) in the structure of the buccal cavity and amphids. The new species differs from *L. flevensis* in body size (1432–1815 *versus* 2600–4100 µm), lower values of a (45–54 *versus* 62–78), b (11–12 *versus* 15–20) and c (8–11 *versus* 11–22), and absence of lateral subcephalic setae anterior to amphids (*versus* present in *L. flevensis*), and from *L. fuscacephalus* in body size (1432–1815 versus 4900 µm), larger amphids (0.3–0.4 *versus* 0.2 cbd), and position of subcephalic setae (at level of, and posterior to, amphids *versus* anterior to amphids in *L. fuscacephalus*).

**Sequence data.** Partial SSU rDNA (1605 bp; Genbank OK317208) and D2–D3 of LSU rDNA (693 bp; Genbank OK317230).

**ZooBank registration.** *Linhomoeus manaensis* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:541BD507-A5C3-45DA-AC19-372DB8797D96.

## Genus ***Metalinhomoeus*** de Man, 1907

*Metalinhomoeus* de Man, 1907: 81–84, plate 3, fig. 16 e, g, i, plate 4, fig. 16 a–d, f, h.
*Monhystriella* Kreis, 1929: 67–68, fig. 28 a–c, table 5.

**Diagnosis.** Cuticle finely striated. Only the four cephalic setae normally recognisable under light microscopy. Four additional subcephalic setae present. Amphids circular, sometimes with broken outline. Buccal cavity cup-shaped, cuticularised, rarely armed with denticles, without cuticularised ring. Pharyngeal bulb well-developed. Cardia elongated. Ventral gland opening between bulb and nerve ring. Tail conical or conicocylindrical with the cylindrical portion of variable length (modified from Fonseca & Bezerra (2014a)).

**Type species.** *Metalinhomoeus typicus* de Man, 1907

### ***Metalinhomoeus bifidosetus*** **sp. nov.**

Figs 77–80; Table 22

**Material examined. Holotype** NIWA 139273, NIWA Stn Z18745, 41.093° S, 174.876° E, Pāuatahanui Inlet near Camborne Walkway, upper intertidal, 28 Jul 2016, gravelly sand, male. **Paratypes** NIWA 139274, one male and four females, same data as for holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Males.** Body colourless, cylindrical, tapering slightly towards both extremities. Cuticle striated, no lateral differentiation. Somatic setae largely absent except in pharyngeal and cloacal regions, sparsely distributed. Blunt to rounded cephalic region, set-off by slight constriction at level of amphids. Narrow mouth opening surrounded by bulge of inner portion of lip region. Six minute inner labial papillae surrounding mouth opening, only visible using scanning electron microscopy. Six outer labial papillae, situated anteriorly to four cephalic setae, ca. 0.6 cbd long. Four subcephalic setae present, 4–6 µm long; two subcephalic setae (one ventral and one dorsal) situated slightly posterior to buccal cavity; one subcephalic seta situated immediately posterior to each amphid. Amphidial fovea circular; outline cuticularised, sometime broken, surrounded by cuticle striations, ca. 0.7 cbd from anterior extremity. Buccal cavity funnel-shaped, 5–6 µm deep, with cuticularised walls; cuticularised base with numerous minute denticles. Ducts of pharyngeal glands sometimes visible, emptying at base of buccal cavity. Pharynx muscular, anterior portion slightly swollen and surrounding buccal cavity; posterior bulb well-developed, oval shaped, with slightly cuticularised lumen. Nerve ring located slightly posterior to middle of pharynx. Secretory-excretory system with large ventral gland situated immediately posterior to pharyngeal bulb; excretory pore between nerve ring and pharyngeal bulb. Cardia long, conspicuous, 35–50 µm long. Reproductive system with two opposed, outstretched testes both located to the left of intestine; sperm cells globular, 10 × 12–13 µm. Spicules short, 1.3 cloacal body diameters long, strongly cuticularised, arcuate; slightly swollen proximal portion. Gubernaculum with strongly cuticularised dorsocaudal apophyses.

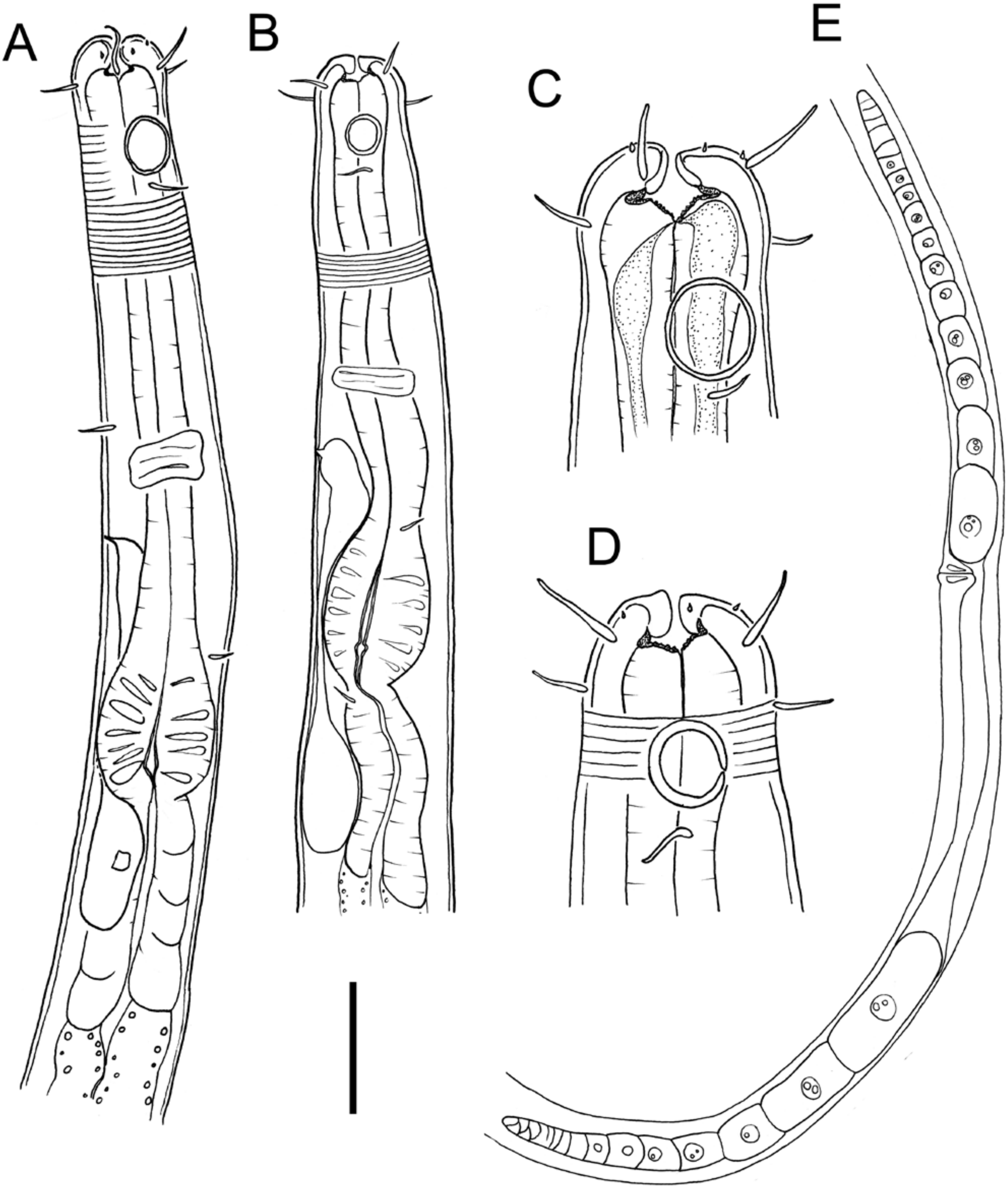



**Figure 77.** *Metalinhomoeus bifidosetus* **sp. nov.**: **A.** Male holotype anterior body region NIWA 139273; **B.** Female paratype anterior body region NIWA 139274; **C.** Male paratype cephalic region NIWA 139274; **D.** Female paratype cephalic region NIWA 139274; **E.** Female paratype reproductive system NIWA 139274. Scale bar: A, B = 25 µm; C, D = 12 µm; E = 65 µm.

One tubular precloacal supplement present, situated ca. 1.0 cbd from cloaca. Tail conical, with pair of stout subventral spines, 4 µm long, ca. one-third of tail length from cloaca; 12–13 subventral pairs of stout bifid (claw-like) spines in posterior half of tail. Sparse subdorsal and subventral caudal setae present, 4–7 µm long. Three caudal glands present.

**Females.** Similar to males but with slightly lower values of a, b, and c, smaller amphids, and longer conicocylindrical tail without setae or spines. Reproductive system with two opposed outstretched ovaries; anterior ovary to the left of intestine, posterior ovary to the right of intestine. Spermatheca absent. Egg, ca. 70 × 20–25 µm. Vulva located near mid-body.

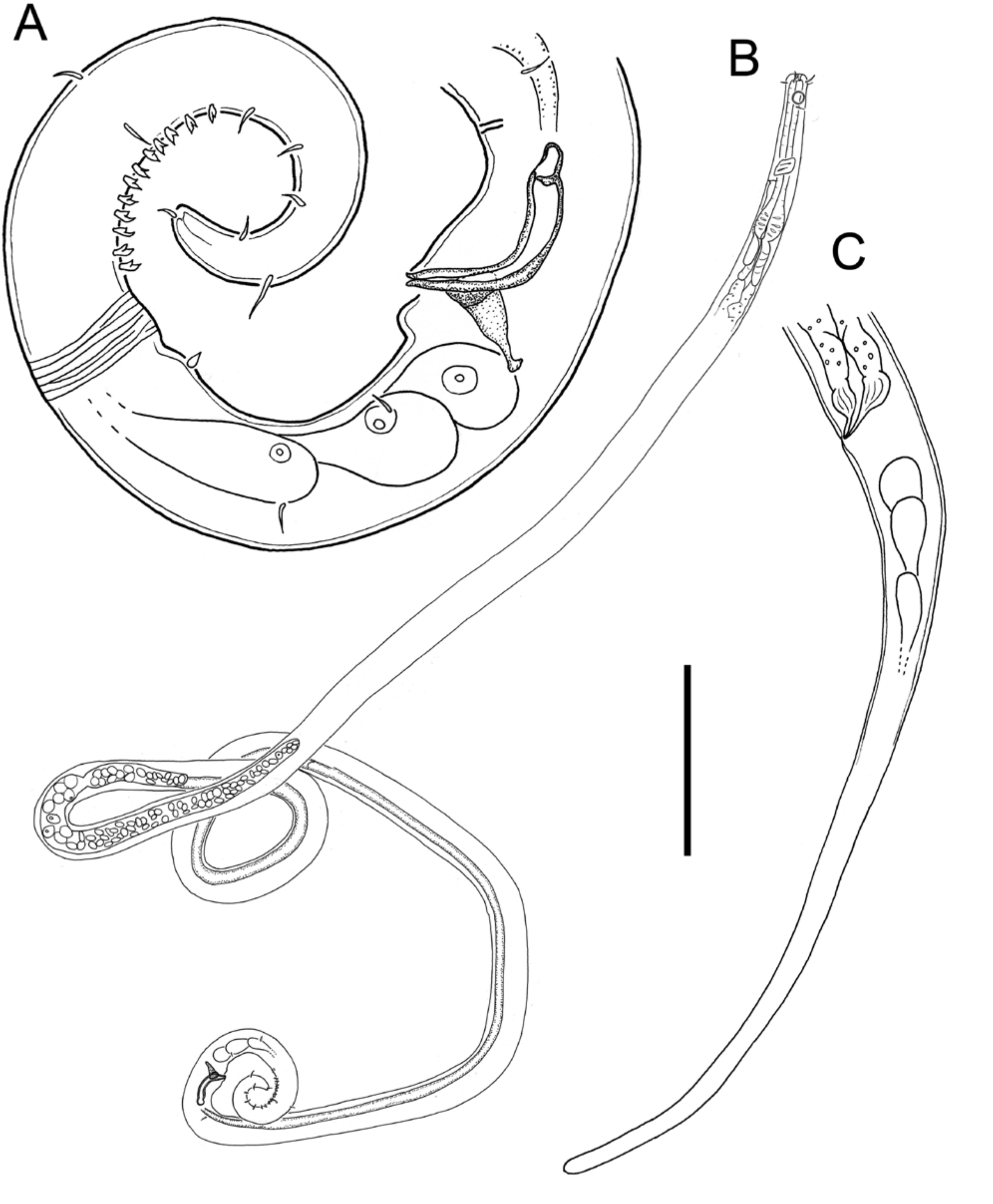



**Figure 78.** *Metalinhomoeus bifidosetus* **sp. nov.**: **A.** Male holotype posterior body region NIWA 139273; **B.** Entire male holotype NIWA 139273; **C.** Female paratype posterior body region NIWA 139274. Scale bar: A = 25 µm; B = 140 µm; C = 45 µm.

Vaginal gland not observed. Pars proximalis vaginae surrounded by constrictor muscle.

**Etymology.** The species name is derived from the Latin *bifidus* (= two-cleft, forked), and *seta* (= bristle) and refers to the bifid spines on the tail of the males.

**Species diagnosis.** *Metalinhomoeus bifidosetus* **sp. nov.** is characterised by body length 1990–2345 µm, cephalic setae 8–11 µm (ca. 0.6 cbd) long, four subcephalic setae, 4–6 µm long; amphids 0.5 cbd wide in males, 0.3–0.4 cbd wide in females, 0.7 cbd from

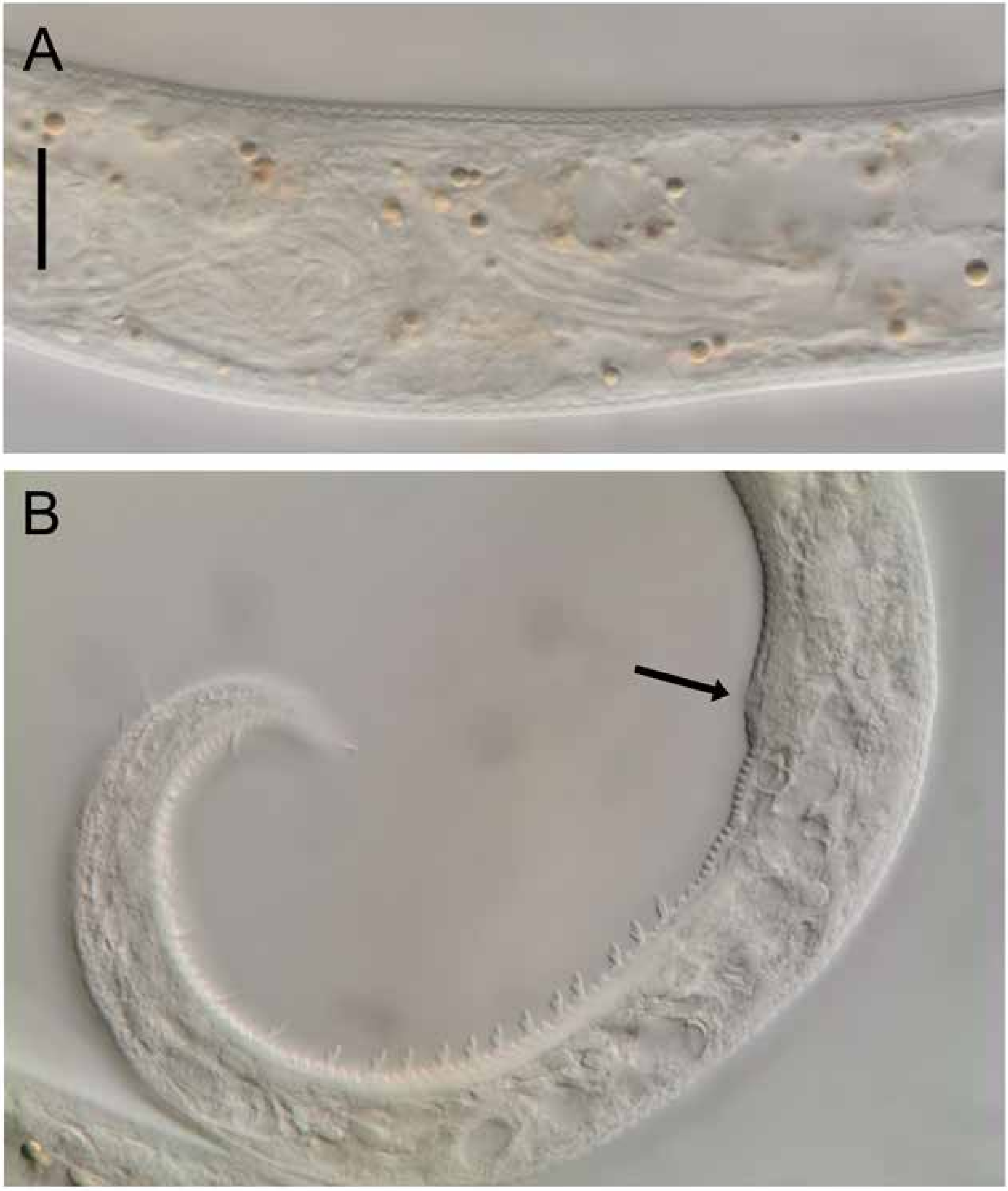



**Figure 79.** *Metalinhomoeus bifidosetus* **sp. nov.** Light micrographs: **A.** Intestine of paratype male with bacteria NIWA 139274; **B.** Male holotype tail, showing stout and bifid subventral spines NIWA 139273. Arrow shows position of stout spine. Scale bar: A = 10 µm: B = 13 µm.

anterior extremity; buccal cavity with cuticularised walls and base and with numerous minute denticles; one tubular precloacal supplement present, spicules1.3 cloacal body diameters long, gubernaculum with dorso-caudal apophyses; tail of male conical, 7.2–9.1 cloacal body diameters long, with pair of stout subventral spines at one-third of tail length from cloaca, posterior half of tail with 12–13 subventral pairs of bifid spines; female with conicocylindrical tail, 11.4–14.9 anal body diameters long, without spines or setae.

**Differential diagnosis.** The new species differ from all other species of the genus by the buccal cavity with numerous minute denticles and presence of subventral pairs of bifid spines on the tail of males. *Metalinhomoeus bifidosetus* **sp. nov.** is most similar to *M. insularis* Timm, 1967 (Arabian Sea) and *M. filiformis* (de Man, 1907)

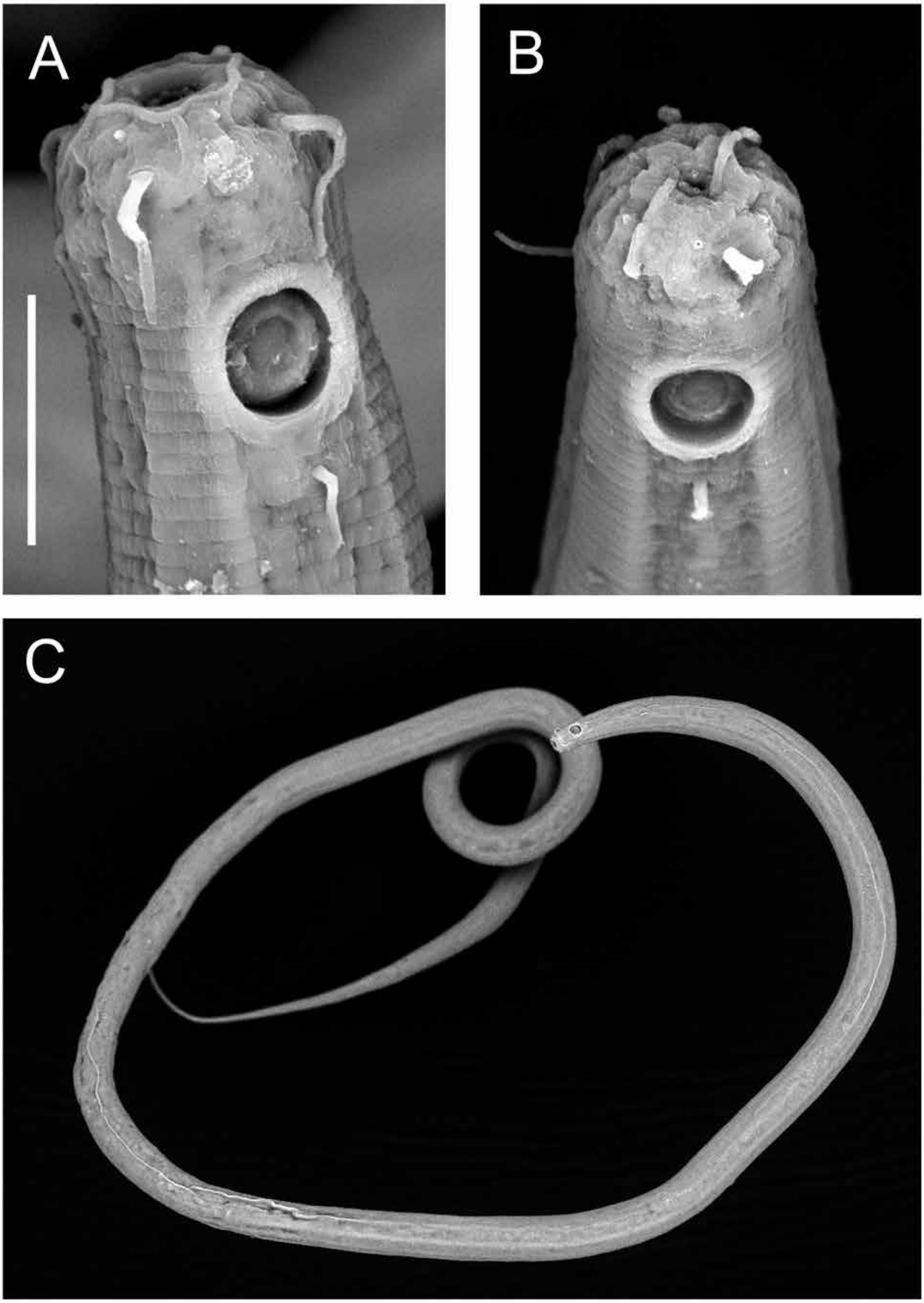



**Figure 80.** *Metalinhomoeus bifidosetus* **sp. nov.** scanning electron micrographs: **A.** Cephalic region of male; **B.** Cephalic region of female; **C**. Entire female. Scale bar: A = 10 µm; B = 11 µm; C = 115 µm.

**Table 22.** Morphometrics (µm) of *Metalinhomoeus bifidosetus* **sp. nov.**, given as individual values, or a range of values from several specimens.

| Parameter | Males | | Females |
|---|---|---|---|
| | Holotype | Paratypes | Paratypes |
| n | 1 | 1 | 4 |
| L | 2133 | 2337 | 1993–2345 |
| a | 82 | 75 | 66–72 |
| b | 17 | 18 | 15–19 |
| c | 12 | 11 | 8–9 |
| c' | 7.2 | 9.1 | 11.4–14.9 |
| Head diameter at cephalic setae | 15 | 15 | 14–16 |
| Head diameter at amphids | 16 | 17 | 17–18 |
| Length of sub-cephalic setae | 5–6 | 5–6 | 4–6 |
| Length of cephalic setae | 8–9 | 9 | 8–11 |
| Amphid height | 10 | 10 | 7–8 |
| Amphid width | 8 | 8 | 6–7 |
| Amphid width/cbd (%) | 50 | 47 | 33–41 |
| Amphid from anterior end | 12 | 12 | 11–13 |
| Nerve ring from anterior end | 71 | 72 | 59–69 |
| Nerve ring cbd | 21 | 22 | 22–24 |
| Pharynx length | 125 | 128 | 116–132 |
| Pharyngeal bulb diameter | 22 | 24 | 22–23 |
| Pharynx cbd at base | 24 | 26 | 26 |
| Maximum body diameter | 26 | 31 | 30–34 |
| Spicule length | 33 | 31 | – |
| Gubernaculum length | 10 | 10 | – |
| Cloacal/anal body diameter | 25 | 23 | 18–22 |
| Tail length | 179 | 209 | 249–297 |
| V | – | – | 929–1120 |
| %V | – | – | 47–52 |
| Vulval body diameter | – | – | 29–30 |

(North Atlantic) in the size and position of the cephalic sensilla and amphids but differs from the former by the shorter tail in females (11.4–14.9 abd long in *M. bifidosetus* **sp. nov.** *versus* 17.3–21.0 abd in *M. insularis*) and longer cardia (35–50 µm long in *M. bifidosetus* **sp. nov.** *versus* 20 µm in *M. insularis*), and from the latter by the shorter body length (< 2.4 mm in *M. bifidosetus* **sp. nov.** *versus* 2.9–3.3 mm in *M. filiformis*), lower values of a (66–82 in *M. bifidosetus* **sp. nov.** *versus* 130–150 in *M. filiformis*) and tail shape in females (conicocylindrical in *M. bifidosetus* **sp. nov.** *versus* conical in *M. filiformis*).

**Sequence data.** Partial SSU rDNA (1563 bp; Genbank OK317209) and D2–D3 of LSU rDNA (683 bp; Genbank OK317231).

**ZooBank registration.** *Metalinhomoeus bifidosetus* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:61A23D1B-C578-4315-8A5F-AC6F4B414AC5.

## *Metalinhomoeus trinimirmecius* sp. nov.

Figs 81, 82; Table 23

**Material examined. Holotype** NIWA 154868, NIWA Stn Z19167, 41.102° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 25 Sep 2018, fine sand, male. **Paratype** NIWA 154869, one female, same data as for holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Male.** Body colourless except for brownish granules inside intestine wall, cylindrical, tapering slightly towards anterior extremities. Cuticle striated, no lateral differentiation. Somatic setae absent. Blunt to slightly rounded cephalic region, not set-off from rest of body. Narrow mouth opening surrounded by bulge of inner portion of lip region. Six minute inner labial papillae surrounding mouth opening; six outer labial papillae, situated anteriorly to four cephalic setae, 0.4 cbd long. Two subventral and two subdorsal subcephalic setae present, 1 µm long, situated at level of amphids or slightly posterior. Amphidial fovea circular; outline cuticularised, surrounded by cuticle striations, ca. 0.7 cbd from anterior extremity. Buccal cavity small, funnel-shaped, shallow, 3 µm deep, with cuticularised wall. Pharynx muscular, anterior portion partially surrounding buccal cavity; posterior bulb oval shaped, lumen not cuticularised. Nerve ring located slightly posterior to middle of pharynx. Secretory-excretory system with excretory pore between nerve ring and pharyngeal bulb; ventral gland not observed. Cardia ca. 15 µm long, not surrounded by intestine. Reproductive system with two opposed, outstretched testes; anterior testis to the left of intestine, posterior testis to the right of intestine. Sperm cells small, globular, 1 × 1–2 µm. Spicules short, 0.9 cloacal body diameters long, arcuate; slightly swollen proximal portion and tapering distal portion. Gubernaculum with lightly cuticularised dorsocaudal apophyses. Short precloacal seta present, 1 µm long. One tubular precloacal supplement present, situated ca. 0.5 cbd from cloaca. Tail conicocylindrical, with three wart-like postcloacal supplements each bearing a minute papilla, beginning 26 µm posterior to cloaca. Three caudal glands and spinneret present.

**Female.** Similar to males but with smaller amphids, longer cardia 31 µm long, and longer tail without supplements. Reproductive system with two opposed outstretched ovaries; anterior ovary to the right of intestine, posterior ovary located ventrally.

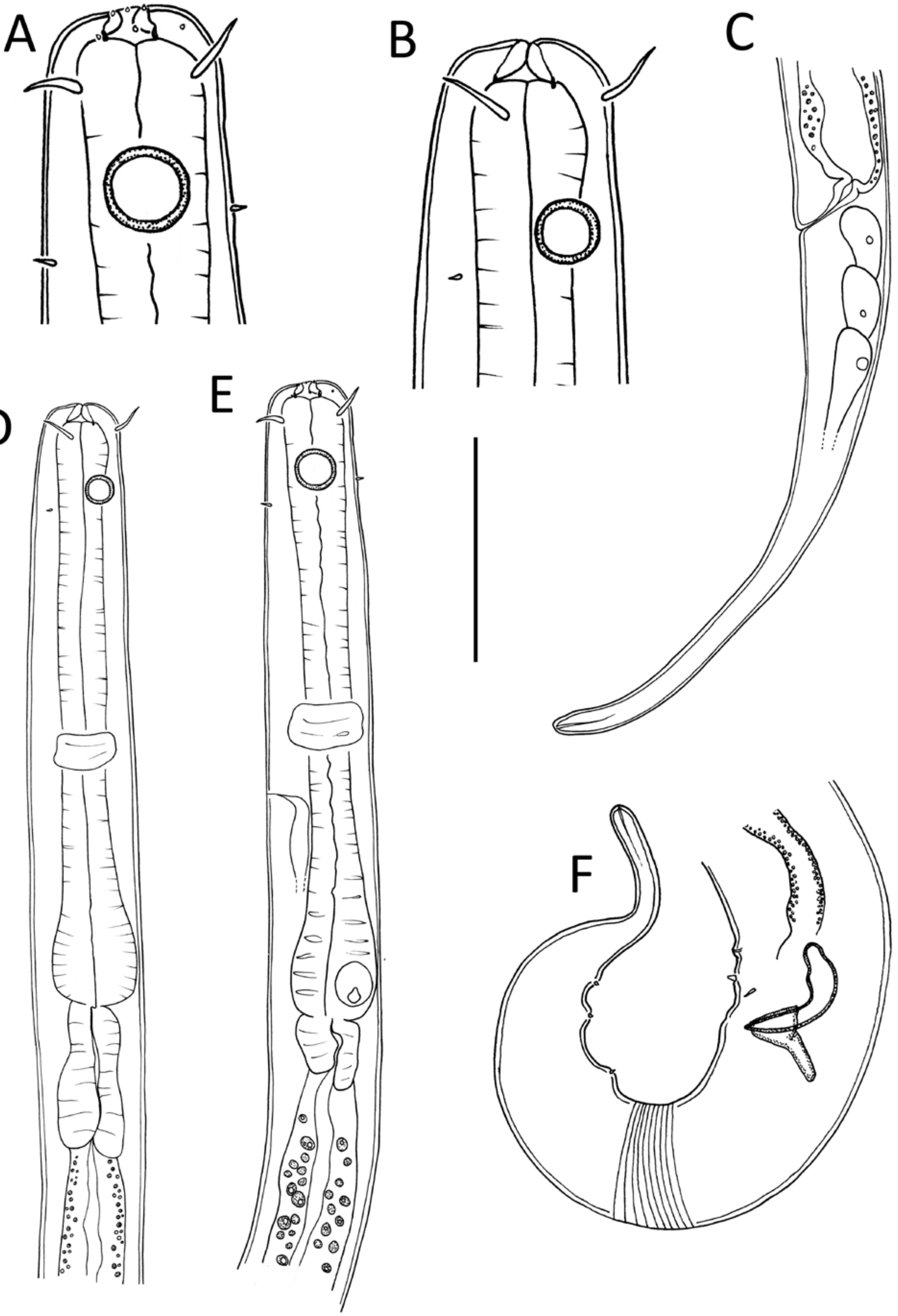



**Figure 81.** ***Metalinhomoeus trinimirmecius*** **sp. nov.**: **A.** Male holotype cephalic region NIWA 154868; **B.** Female paratype cephalic region NIWA 154869; **C.** Female paratype posterior body region NIWA 154869; **D.** Female paratype anterior body region NIWA 154869; **E.** Male holotype anterior body region NIWA 154868; **F.** Male holotype posterior body region NIWA 154868. Scale bar: A, B = 20 µm; C = 50 µm; D, E = 45 µm; F = 33 µm.

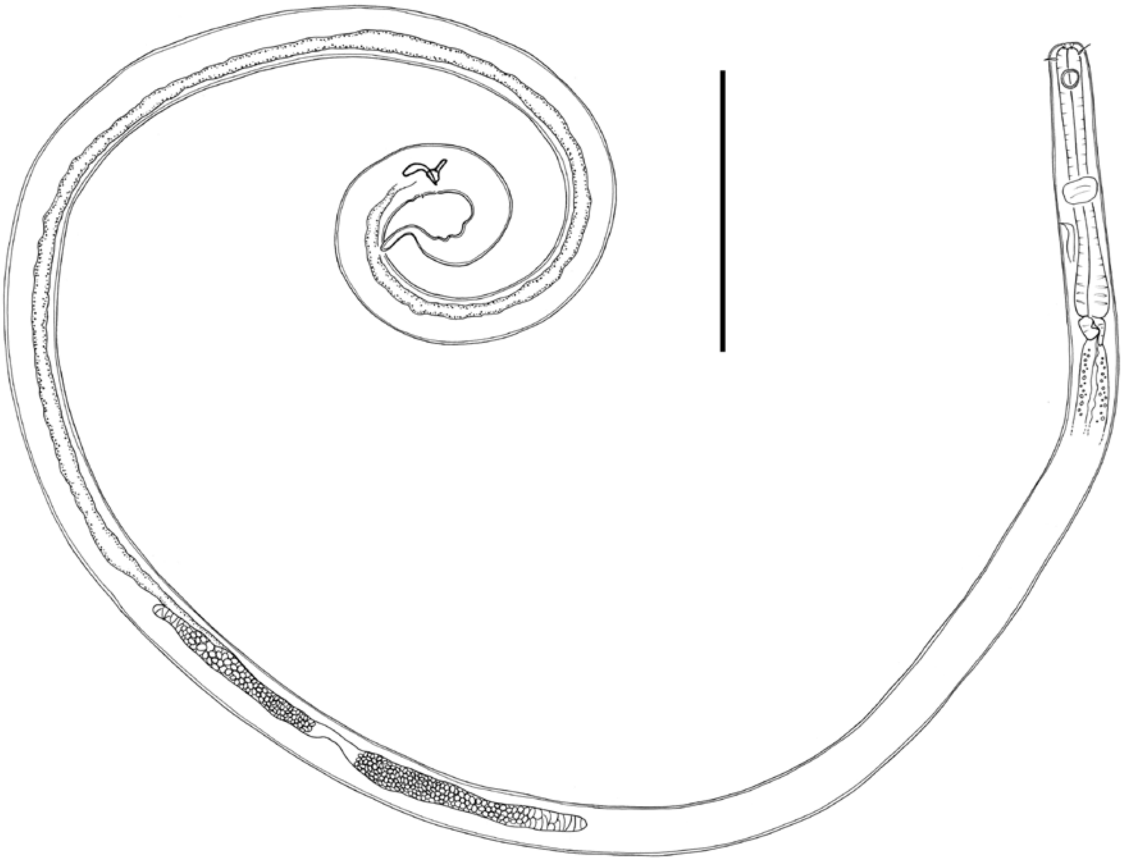


**Figure 82.** *Metalinhomoeus trinimirmecius* **sp. nov.** Entire holotype male NIWA 154868. Scale bar = 120 µm.

Spermatheca not observed. Vulva located far anteriorly at ca. one-third of body length from anterior extremity. Vaginal glands not observed. Pars proximalis vaginae surrounded by constrictor muscle.

**Etymology.** The species name is derived from the Greek *trinus* (= three) and *myrmekia* (= anthill, wart), and refers to the presence of three ventral postcloacal supplements on the tail of the male.

**Species diagnosis.** *Metalinhomoeus trinimirmecius* **sp. nov.** is characterised by body length 1438–1794 µm, cephalic setae 6 µm (0.4 cbd) long, two subventral and two subdorsal subcephalic setae, 1 µm long; amphids ca. 0.5 cbd wide in males, 0.3 cbd wide in females, located 0.7 cbd from anterior extremity; buccal cavity shallow with cuticularised walls; male with precloacal seta and one tubular precloacal supplement present, spicules 0.9 cloacal body diameters long, gubernaculum with dorso-caudal apophyses, ventral row of three wart-like postcloacal supplements each bearing a minute papilla; conicocylindrical tail 4.5 cloacal body diameters long in the male and 7.1 anal body diameters long in the female.

**Differential diagnosis.** The new species differs from most other species of the genus, except *M. biratus* Vitiello, 1969 (Mediterranean Sea), *M. numidicus* Aissa & Vitiello, 1977 (Mediterranean Sea), *M. musaecauda* Lorenzen, 1966 (North Atlantic), *M. torosus* Jensen & Gerlach, 1976 (Western Atlantic), and *M. variabilis* Murphy, 1965 (Chilean coast), by the presence of pre- and/or postcloacal supplements in males. *Metalinhomoeus trinimirmecius* **sp. nov.** differs from *M. biratus* by the presence of postcloacal supplements (*versus* absent in *M. biratus*), shape of the precloacal supplements (tubular *versus* slight swellings in *M. biratus*), absence of subcephalic setae posterior to amphids (*versus* single subcephalic setae posterior to each amphid in *M. biratus*), and shorter tail (4.5 cloacal body diameters *versus* 6.2–13.0 cloacal body dimaters in males of *M. biratus*); from *M. numidicus* by the shorter body length (1438–1794 *versus* 2494–3440 µm in *M. numidicus*), ratio of a (65–75 *versus* 83–113), number of postcloacal supplements (three *versus* 5–9 in *M. numidicus*), and presence of precloacal seta and tubular supplement (*versus* absent in *M. numidicus*); from *M. musaecauda* by the higher ratio of a (65–75 *versus* 47–63 in *M. musaecauda*), number and shape of precloacal supplements (one tubular supplement versus four cuticular thickenings in *M. musaecauda*)

**Table 23.** Morphometrics (μm) of *Metalinhomoeus trinimirmecius* **sp. nov.**, given as individual values.

| Parameter | Male Holotype | Female Paratype |
|---|---|---|
| Number of specimens | 1 | 1 |
| L | 1438 | 1794 |
| a | 65 | 75 |
| b | 12 | 15 |
| c | 15 | 13 |
| c' | 4.5 | 7.1 |
| Body diameter at cephalic setae | 15 | 15 |
| Body diameter at amphids | 17 | 19 |
| Length of sub-cephalic sensilla | 1 | 1 |
| Length of cephalic setae | 6 | 6 |
| Amphid height | 8 | 7 |
| Amphid width | 8 | 6 |
| Amphid width/cbd (%) | 47 | 32 |
| Amphid from anterior end | 12 | 14 |
| Nerve ring from anterior end | 62 | 59 |
| Nerve ring cbd | 21 | 21 |
| Excretory pore from anterior end | 78 | 80 |
| Pharynx length | 116 | 117 |
| Pharyngeal diameter at base | 16 | 17 |
| Pharynx cbd at base | 22 | 21 |
| Maximum body diameter | 22 | 24 |
| Spicule length | 20 | – |
| Gubernacular apophysis length | 8 | – |
| Cloacal/anal body diameter | 22 | 20 |
| Tail length | 98 | 141 |
| V | – | 571 |
| %V | – | 32 |
| Vulval body diameter | – | 22 |

and presence of postcloacal supplements (versus absent in *M. musaecauda*); from *M. torosus* by the shape of the outer labial sensilla (papillose *versus* setose in *M. torosus*) and the much shorter subcephalic setae (1 *versus* 9–12 μm in *M. torosus*); and from *M. variabilis* by the much shorter body length (1438–1794 *versus* 5000–8680 μm in *M. variabilis*), longer cephalic setae (6 *versus* 2.5 μm in *M. variabilis*) and shorter spicules (20 *versus* 73 μm in *M. variabilis*). The new species also differs from all other species of the genus in having a vulva located far anteriorly at about one-third of body length from anterior. In all other species of the genus for which data is available, the vulva is located at least 40% of body length from anterior body extremity. The only other exception is *M. torosus*, which has a vulva located at 35% of body length from anterior. However, the latter species should probably be moved to the genus *Linhomoeus* on account of the setose outer labial sensilla located close to the cephalic setae (Fonseca & Bezerra 2014a).

**ZooBank registration.** *Metalinhomoeus trinimirmecius* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:43578AC3-A62C-4AAF-BB0C-BDC51D4D7B6F.

## Genus *Terschellingia* de Man, 1888

*Terschellingia* de Man, 1888: 11–12, plate 1, fig. 7.

**Diagnosis.** Cuticle finely striated, may appear smooth under light microscope. Amphids circular, usually located far anteriorly in the cephalic region. Inner labial sensilla minute, often not visible; outer labial sensilla papilliform, located anteriorly to, or in same circle as, the four cephalic setae. Buccal cavity absent or minute, cuticularised structure rarely present. Pharynx with posterior bulb. Cardia well-developed. Secretory-excretory pore located posterior to nerve ring. Female didelphic-amphidelphic (rarely monodelphic-prodelphic), ovaries outstretched, vulva at about mid-body. Male monorchic or diorchic, posterior testis sometimes reflexed; spicules curved, gubernaculum usually with apophyses. Tail conicocylindrical; tail tip rounded, without terminal setae (modified from Armenteros *et al.* (2009)).

**Remarks.** The genus was most recently revised by Armenteros *et al.* (2009), and a key to the 24 valid species of the genus was provided by Wang *et al.* (2017). The diagnosis provided by Armenteros *et al.* (2009) states that males are diorchic; however, *Terschellingia brevicauda* Ott, 1972 possesses only one testis. The number and structure of the testes remains unknown for several species of the genus including *T. gourbaultae* Austen, 1989 and *T. capitata* Vitiello, 1969.

**Type species.** *Terschellingia communis* de Man, 1888

### *Terschellingia* cf. *longicaudata* de Man, 1907

Figs 83–88; Table 24

*Terschellingia longicaudata* de Man, 1907: 39–41, plate 1, fig. 4.
*Terschellingia antonovi* Filipjev, 1922: 204–205.
*Terschellingia baltica* Schulz, 1932: 409–410, fig. 43 a–c.
*Terschellingia heterospiculum* Allgén, 1933: 102–103, fig. 65.
*Terschellingia heteroseta* Schuurmans Stekhoven, 1950: 190–191, fig. 123 a, b.

**Additional material examined.** NIWA 139279, NIWA Stn Z18745, 41.093° S, 174.876° E, Pāuatahanui Inlet near Camborne Walkway, upper intertidal, 28 Jul 2016, gravelly sand, two males and three females.

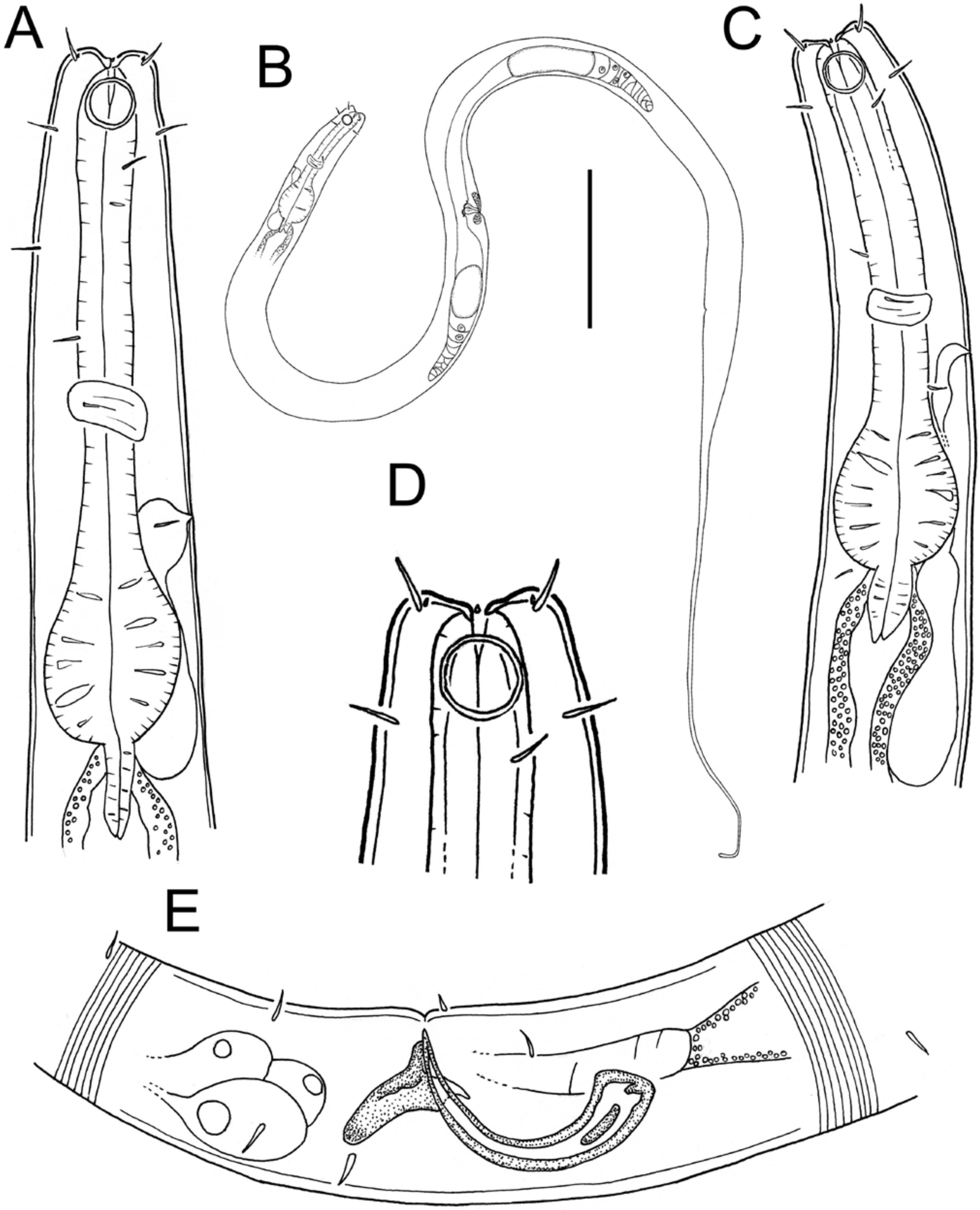



**Figure 83.** *Terschellingia* cf. *longicaudata* de Man, 1907 NIWA 139279: **A.** Male anterior body region; **B.** Entire female; **C.** Female anterior body region; **D.** Female cephalic region; **E.** Male copulatory apparatus. Scale bar: A = 30 µm; B = 145 µm; C = 40 µm; D = 20 µm; E = 23 µm.

**Type and locality.** Coast of Eastern Scheldt, the Netherlands. De Man's type collection is located in the Naturalis Invertebrate Collection, Naturalis, Leiden, the Netherlands, but registration details of the holotype were not confirmed prior to publication.

**Distribution.** Cosmopolitan.

**Diagnosis.** *Terschellingia longicaudata* specimens from Pāuatahanui Inlet are characterised by body length 1511–1727 µm, light brown colouration throughout body except for colourless cylindrical portion of tail, and most conspicuous in vicinity of cephalic and cloacal regions. Somatic setae largely absent except in pharyngeal and cloacal regions, sparsely distributed, six minute inner labial papillae surrounding mouth opening, only visible using scanning electron microscopy. Six outer labial papillae, situated at same level as four cephalic setae, ca. 0.3 cbd long. Six subcephalic setae present, 5–7 µm long; two subdorsal and two subventral subcephalic setae at level of posterior edge of amphids, two lateroventral subcephalic setae posterior to the amphids. Amphidial fovea circular, ca. 0.3 cbd from anterior extremity. Buccal cavity narrow, tubular, 5–9 µm deep, not cuticularised. Secretory-excretory system with large ventral gland situated immediately posterior to pharyngeal bulb; well-developed ampulla; excretory pore between nerve ring and pharyngeal bulb. Male reproductive system with two opposed, outstretched testes both located either ventrally or to the right of intestine; spicules arcuate, 1.7–1.8 cloacal body diameters long. Gubernaculum with strongly cuticularised dorsocaudal apophyses and pointed central piece (cuneus). Precloacal supplements not observed. Tail conicocylindrical, with very long conical distal portion. Female reproductive system with two opposed outstretched ovaries either both to the right or left of intestine.

**Remarks.** The Pāuatahanui Inlet specimens are very similar to the original description of *T. longicaudata* by de Man 1907 based on specimens collected in the North Sea. The only differences are the slightly wider amphids in the Pāuatahanui Inlet specimens (0.4 *versus* 0.3 cbd) and the number and arrangement of subcephalic setae. In the Pāuatahanui Inlet specimens, six subcephalic setae are present (two subdorsal and two subventral setae at level of posterior edge of amphids, and two lateroventral setae posterior to the amphids), whereas in *T. longicaudata* type specimens eight subcephalic setae are present (two subdorsal and two subventral setae at level of amphids and two pairs of sublateral setae posterior to the amphids). Although

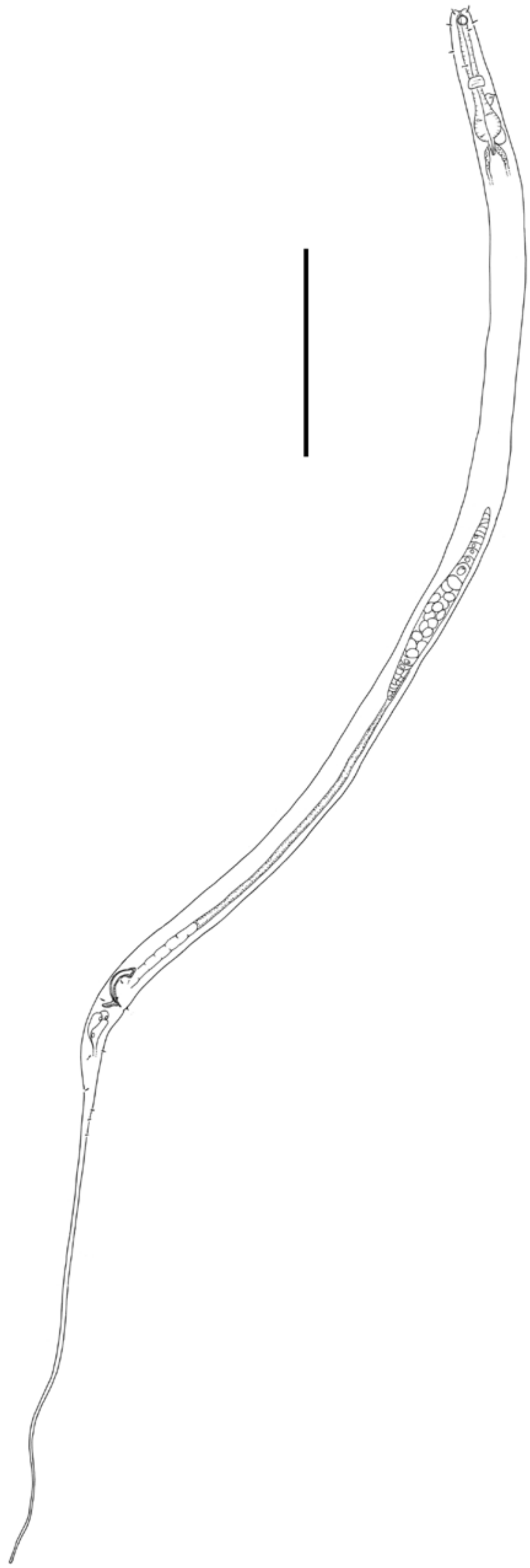


**Figure 84.** *Terschellingia* cf. *longicaudata* de Man, 1907, Entire male, NIWA 139279. Scale bar = 200 µm.

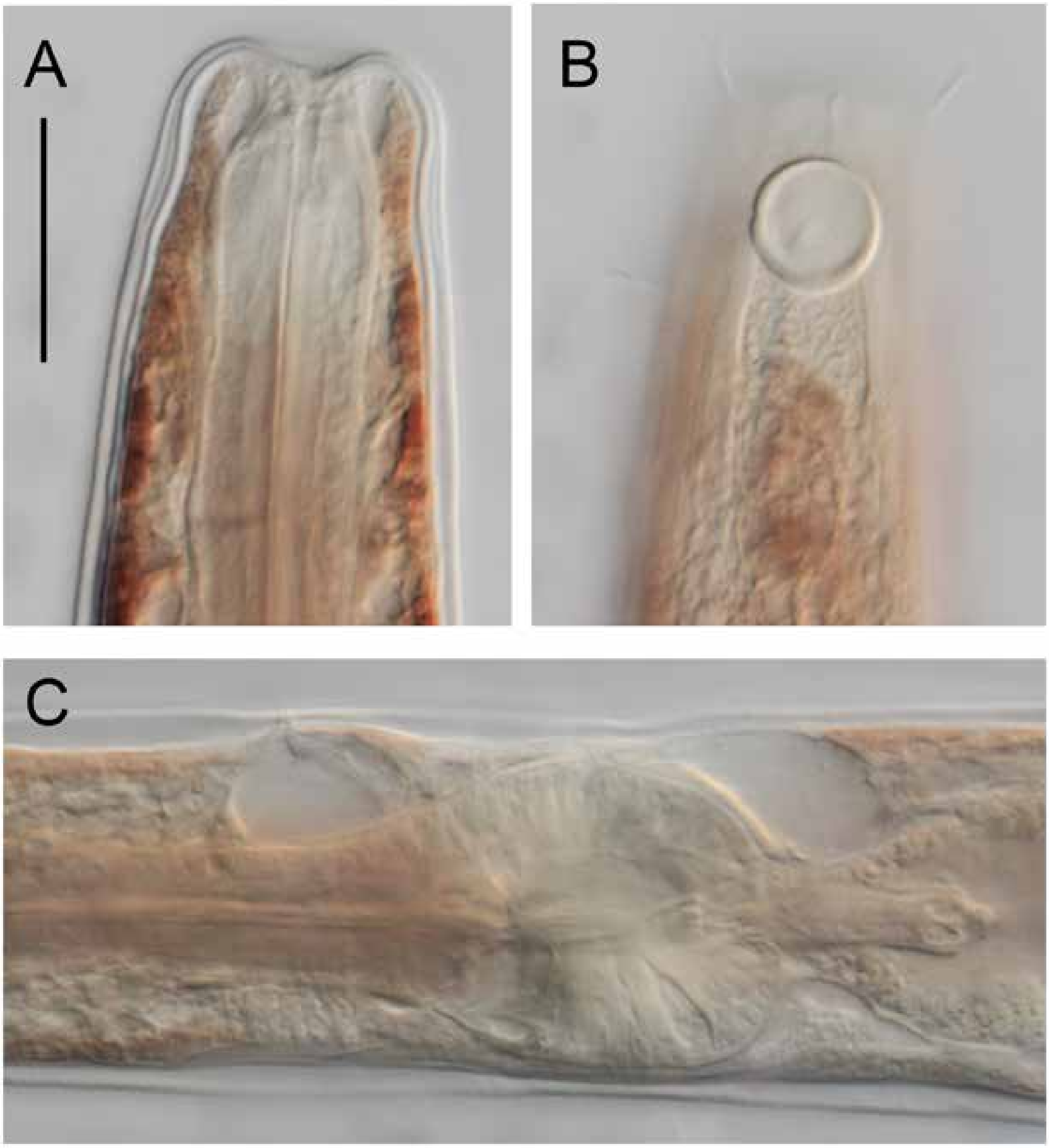



**Figure 85.** *Terschellingia* cf. *longicaudata* de Man, 1907, NIWA 139279, light micrographs: **A.** Optical cross-section of male anterior body region showing buccal cavity, pharynx, and brown pigmentation; **B.** Surface view of male anterior body region showing cephalic sensilla and amphid; **C.** Optical cross-section of male showing posterior portion of pharynx, cardia, and secretory-excretory system. Scale bar: A, B = 17 µm; C = 20 µm.

variability in several morphological characters of *T. longicaudata* has been noted previously (e.g., body dimensions, amphid size, spicule length), variability in the number and arrangement of subcephalic setae is yet to be assessed. For example, whilst *T. longicaudata* specimens described from the Arabian Sea by Timm (1962) and from the British Isles by Warwick *et al.* (1998) are characterised by the same number and arrangement of subcephalic setae as in the original description of the species, specimens described from the Caribbean Sea have only four subcephalic setae (Armenteros *et al.* 2009) and specimens from the Hakon Mosby mud volcano (NE Atlantic, 1250 m depth) lack subcephalic setae altogether (Portnova 2009). In their description of *T. longicauda* based on specimens from the Florida coast, Wieser & Hopper (1967) describe two morphotypes: one from Biscayne Bay with subcephalic setae arranged as in the original description of *T. longicaudata* by de Man (1907), and another from Vero Beach with subcephalic setae arranged as in the Pāuatahanui Inlet specimens. *Terschellingia gerlachi*, which was described from New Caledonia and was

**Figure 86.** *Terschellingia* cf. *longicaudata* de Man, 1907, scanning electron micrograph of cephalic region of juvenile, showing cuticle striations, position of cephalic sensilla, and amphid. Scale bar = 5 µm.

synonymised with *T. longicaudata* by Armenteros *et al.* (2009), lacks postamphidial subcephalic setae, whilst *T. longispiculata* from the Florida coast is characterised by the same number and arrangement of subcephalic setae as in the original description of *T. longicaudata* (Wieser & Hopper 1967). Further work is needed to assess whether subcephalic setae can be used to differentiate among *Terschellingia* species.

*Terschellingia longicaudata* is the most common and widely distributed species of the genus. A study by Bhadury *et al.* (2008) based on 18S rRNA analyses showed that morphologically defined *T. longicaudata* sharing identical sequences are distributed from the British Isles to Malaysia. On the other hand, other morphologically defined *T. longicaudata* specimens possessed highly divergent sequences, which led the authors to conclude that: (1) *T. longicaudata* in fact constitutes a species complex; and (2) morphological characters may not allow one to discriminate among species of this species complex. Armenteros *et al.* (2009) observed considerable variability in some of the morphological characters of *T. longicaudata*, including body size, tail length, and presence/absence of precloacal supplements. This variability is also demonstrated by the high number of *Terschellingia* species that have been synonymised with *T. longicaudata*. Morphological characters are clearly not informative enough for differentiating among species of the *T. longicaudata* species complex, and a combination of morphological information and molecular sequences is needed for accurate identification (Bhadury *et al.* 2008; Sahrean *et al.* 2017). It is not yet clear, however, how to differentiate between the different *T. longicaudata* lineages identified in 18S rRNA phylogenies based on morphology (Sahrean *et al.* 2017).

**Sequence data.** Partial SSU rDNA (1563 bp; Genbank OK317210) and COI sequence (604 bp; Genbank OK314957).

**Table 24.** Morphometrics (μm) of *Terschellingia* cf. *longicaudata* de Man, 1907, given as a range of values from several specimens.

| Parameter | Males | Females |
|---|---|---|
| Number of specimens | 2 | 3 |
| L | 1511, 1640 | 1568–1727 |
| a | 43, 47 | 35–48 |
| b | 12, 13 | 12–14 |
| c | 3 | 3–4 |
| c' | 15.8, 19.9 | 16.1–17.7 |
| Body diameter at cephalic setae | 17, 18 | 17–19 |
| Body diameter at amphids | 21 | 22–25 |
| Length of cephalic setae | 5–6 | 5–6 |
| Length of subcephalic setae | 5–7 | 5–8 |
| Amphid height | 9 | 9–10 |
| Amphid width | 9 | 9–10 |
| Amphid width/cbd (%) | 43 | 40–43 |
| Amphid from anterior end | 4, 6 | 5–9 |
| Nerve ring from anterior end | 52 | 57–65 |
| Nerve ring cbd | 31 | 32–34 |
| Excretory pore from anterior end | 77, 90 | 79–89 |
| Pharynx length | 122, 126 | 124–132 |
| Pharyngeal bulb diameter | 24, 26 | 30–31 |
| Pharynx bulb cbd | 32 | 35–37 |
| Maximum body diameter | 35 | 36–45 |
| Spicule length | 49, 50 | – |
| Gubernacular apophysis length | 11, 15 | – |
| Cloacal/anal body diameter | 28, 29 | 38–34 |
| Tail length | 457, 558 | 574–663 |
| V | – | 574–663 |
| %V | – | 33–40 |
| Vulval body diameter | – | 36–43 |

**Phylogenetic analyses.** *Terschellingia* sequences formed a well-supported (100% posterior probability and bootstrap support) monophyletic clade in the SSU consensus tree (Fig. 87). *Terschellingia lissa* and *T. obesa* sequences were nested within the clade comprising all *Terschellingia longicaudata* sequences; therefore, the *T. longicaudata* species complex is not monophyletic. The tree recovered the six *T. longicaudata* SSU clades identified by Sahraean *et al.* (2017). Clade 1 was moderately to well supported (100% posterior probability and 76% bootstrap support) and comprised sequences from Portugal, the Mediterranean, Iran, the United Kingdom, Mexico, and the Netherlands; clade 2 comprised identical sequences from the United Kingdom; clade 3 was well supported (100% posterior probability and 94% bootstrap support) and comprised sequences from the United Kingdom and Mexico; clade 4 was well supported (100% posterior probability and 97% bootstrap support) and comprised sequences from Taiwan; clade 5 was well supported (100% posterior probability and bootstrap support) and comprised sequences from Iran, and clade 6 comprised identical sequences from Iran. The *Terschellingia lissa* sequence was most similar to a *Terschellingia longicaudata* sequence from the Netherlands (LT795765; clade 1 in Sahraean *et al.* (2017)) but differed from the latter by 9.1%, whereas *T. obesa* was most similar to a *Terschellingia longicaudata* sequence from Taiwan (GU937776; clade 4 in Sahraean *et al.* (2017)) but differed from the latter by 15.6%. The SSU sequence from the Pāuatahanui Inlet specimen was placed within a well-supported clade (100% posterior probability and 97% bootstrap support) composed of sequences identified as *T. longicaudata* or *Terschellingia* including the Sahraean *et al.* clades 1, 2, 3, and 4; however, it was not placed within any of the *T. longicaudata* SSU clades identified by the latter authors. The Pāuatahanui Inlet sequence was most similar to a *T. longicaudata* sequence (AY854230) from the United Kingdom belonging to clade 1 and differed from the latter by 1.7%.

*Terschellingia* sequences formed a moderately supported (73% posterior probability and 74% bootstrap support) monophyletic clade in the COI consensus tree (Fig. 88). The *T. longicaudata* sequence from Pāuatahanui Inlet was included in a well-supported clade (100% posterior probability and bootstrap support) comprising two identical *T. longicaudata* sequences (one from the Netherlands and one from Iran; haplotype 1 in Sahraean *et al.* (2017)) and another *T. longicaudata* sequence from Iran (haplotype 2 in Sahraean *et al.* (2017)). Within this clade, the New Zealand *T. longicaudata* was grouped with the Sahraean *et al.* haplotype 1 with moderate support (89% posterior probability and 88% bootstrap support). The Pāuatahanui Inlet sequence differed from the Sahraean *et al.* haplotype 1 by 1.5% and from haplotype 2 by 4.3%.

Overall, we observed relatively limited genetic divergence between the Pāuatahanui Inlet specimen and *T. longicaudata* populations from other localities. Studies of marine free-living nematodes have shown that intra-specific COI divergence does not exceed 4%, whereas inter-specific divergence exceeds 5% (Derycke *et al.* 2005; Fonseca *et al.* 2008; Derycke *et al.* 2010; de Oliveira *et al.* 2012; Armenteros *et al.* 2014a). The low dissimilarity (1.5%) between the New Zealand COI sequence and the Sahraean *et al.* haplotype 1 from

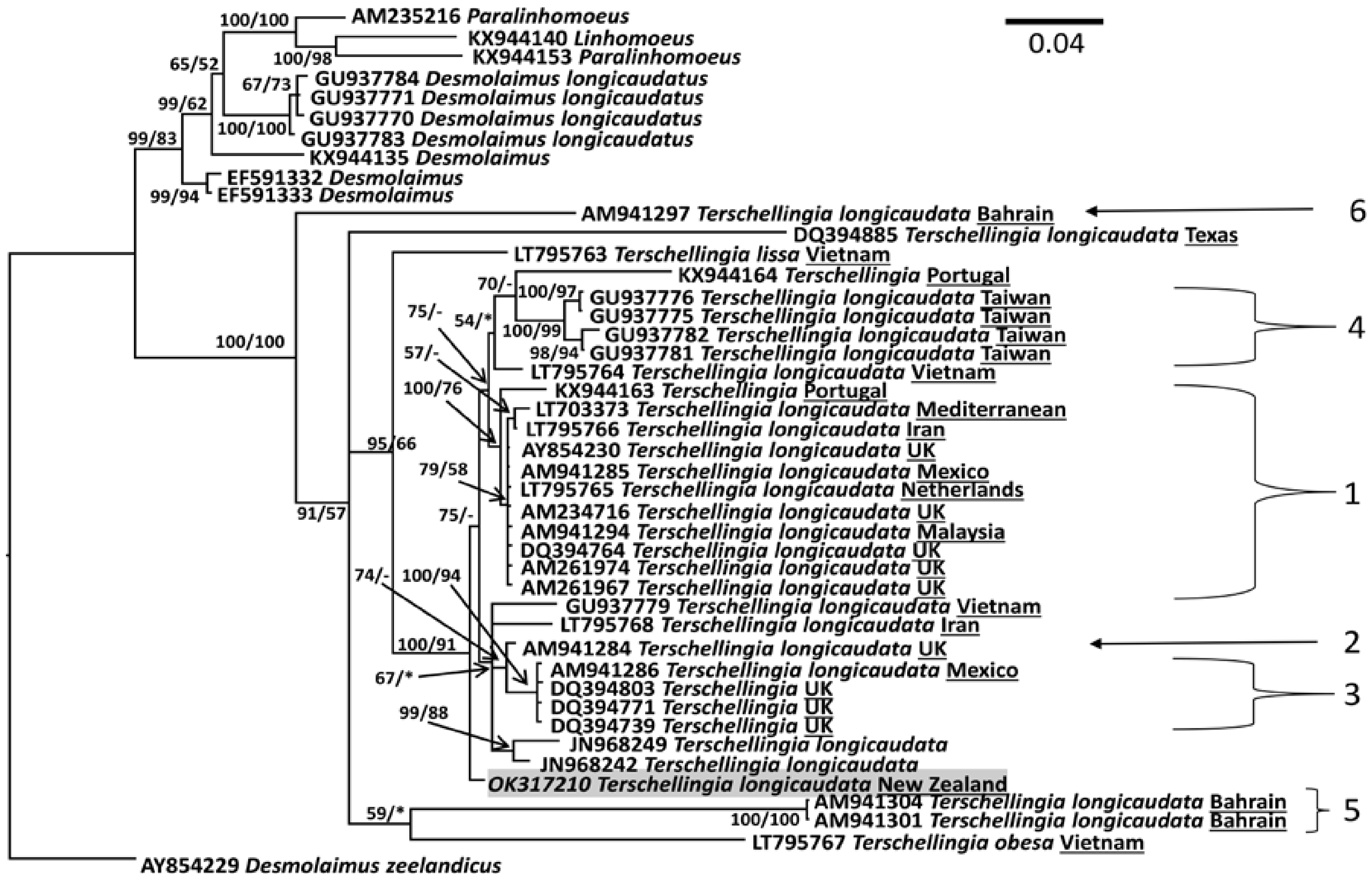



**Figure 87.** Bayesian tree inferred from SSU sequences, aligned using the MUSCLE alignment under the general time-reversible (GTR) + gamma distribution (G) model. Posterior probabilities (left) and bootstrap values (right) from the ML analyses greater than or equal to 50% are given on appropriate clades. Dashes (-) indicate low (<50%) bootstrap support and asterisks (*) indicate no bootstrap support. When known, sampling location is given for *Terschellingia* species (underlined). The sequence generated in the present study is indicated by grey background. The six *Terschellingia longicaudata* clades identified by Sahraean *et al.* (2017) are identified by numbers on the right of the tree. The scale stands for substitutions per site.

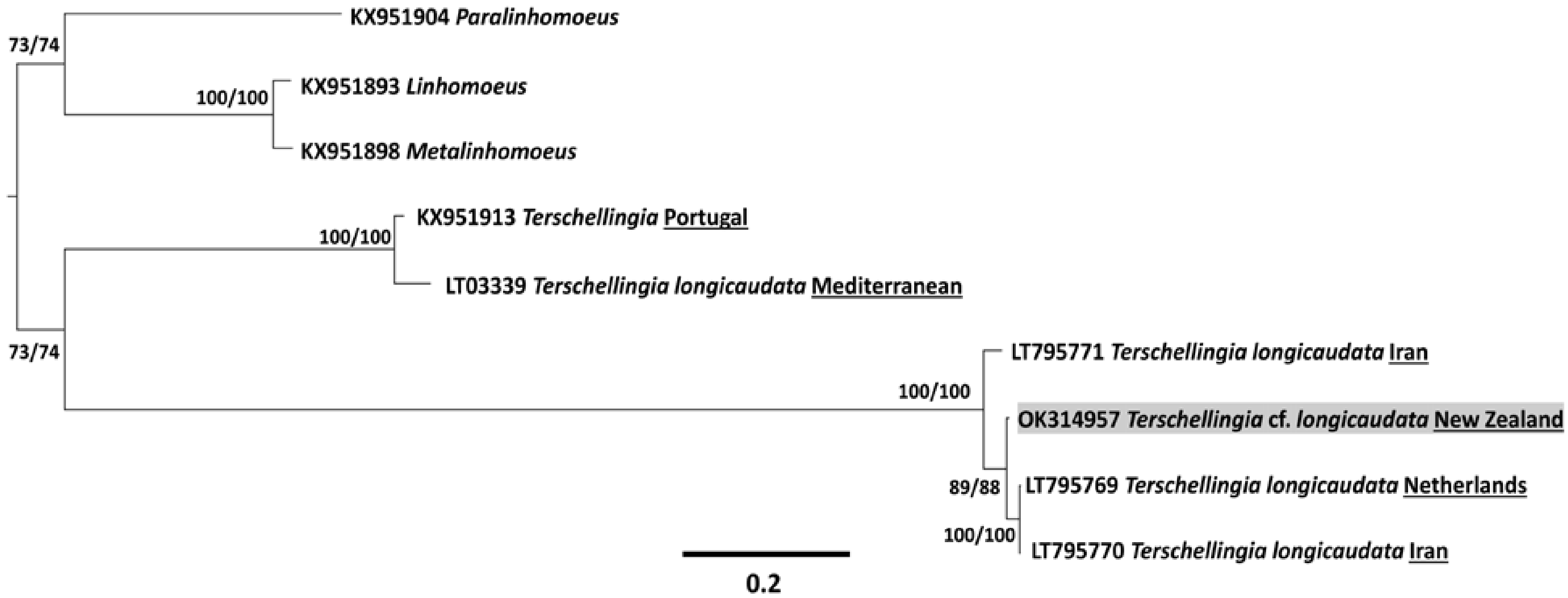



**Figure 88.** Bayesian tree inferred from COI sequences, aligned using the MUSCLE alignment under the general time-reversible (GTR) + gamma distribution (G) model. Posterior probabilities (left) and bootstrap values (right) from the ML analyses are given on the appropriate clades. The sequence generated in the present study is indicated by grey background. Sampling location is given for *Terschellingia* species (underlined). The scale stands for substitutions per site.

Iran and the Netherlands therefore suggests that they belong to the same species. The SSU phylogenetic analyses, however, were not entirely consistent with the COI results. Sahraean *et al.* (2017) found that *T. longicaudata* specimens belonging to haplotype 1 all belonged to the globally distributed, SSU-defined clade 1, which has been recorded from the United Kingdom, the Netherlands, Mediterranean Sea, Iran, Mexico and Malaysia. In contrast, the New Zealand specimen was placed outside clade 1 in our SSU phylogenetic analysis. Nevertheless, the Pāuatahanui Inlet SSU sequence showed strongest similarity to sequences from clade 1, differing by as little as 1.7%.

The inconsistency between the SSU and COI phylogenetic analyses could indicate that the Pāuatahanui Inlet population in fact represents a clade distinct from those identified by previous authors, but verifying this hypothesis will require more extensive sampling of *T. longicaudata* from Pāuatahanui Inlet and other New Zealand coastal locations, and, ideally, coastal habitats from across the wider Southwestern Pacific region. Since previous studies have shown that more than one *T. longicaudata* lineage can be present in a given region (Bhadury *et al.* 2008; Sahrean *et al.* 2017), it seems likely that further sampling in the New Zealand region will also reveal the presence of additional *T. longicaudata* clades distinct from the Pāuatahanui Inlet population.

## Family **Sphaerolaimidae** Filipjev, 1918
## Subfamily **Sphaerolaiminae** Filipjev, 1918

Sphaerolaiminae Filipjev, 1918: 223.

**Diagnosis.** Body slender. Cuticle finely striated. Anterior sensilla arranged in three crowns six + six + eight; with the third crown having four adjacent subcephalic setae (each seta of the third crown is isolated). Scattered cervical setae. Amphids circular. Buccal cavity barrel-shaped, with the anterior portion having longitudinal ribs and the posterior with strongly cuticularised walls. Pharynx culindrical with cuticularised lumen. Vulva posterior to the midbody region. Tail conical with scattered somatic setae (after Fonseca & Bezerra (2014a)).

## Genus ***Metasphaerolaimus*** Gourbault & Boucher, 1981

*Metasphaerolaimus* Gourbault & Boucher, 1981: 1045–1051, figs 5–7.
*Ceratosphaerolaimus* Fadeeva, 1983: 1329–1332, fig. 5.

**Diagnosis.** Cuticle finely striated. Six inner labial papillae; six outer labial setae at same level as four longer cephalic setae; eight groups of sub-cephalic setae. Amphidial fovea circular, situated posteriorly to buccal cavity. Buccal cavity strongly cuticularised with six H- or X-shaped cuticularised structures lining the inner buccal cavity wall, hooked anteriorly and articuLating on cuticularised rim posteriorly. Pharynx cylindrical with strongly cuticularised lumen (after Leduc (2015a)).

**Remarks.** A tabular key to the ten valid species of the genus is provided by Leduc (2015a).

**Type species.** *Metasphaerolaimus cancellatus* Gourbault & Boucher, 1981

### ***Metasphaerolaimus* sp. 1** (NIWA 154880, dorsocaudal apophyses & conicocylindrical tail, Mana Bank, Leduc & Zhao) **sp. indet.**

Figs 89–91; Table 25

**Material examined.** NIWA 154880, NIWA Stn Z19168, 41.098° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 22 Feb 2019, fine sand, male.

**Description. Male.** Body golden-brown, cylindrical. Cuticle striated, no lateral differentiation. Eight rows of somatic setae present throughout body, 12–26 μm long, most dense in pharyngeal region. Lips high, bearing six minute inner labial papillae. Six outer labial setae, 0.2 cbd long, in same circle as four slightly shorter cephalic setae. Additional setae not observed. Eight groups of 4–5 sub-cephalic setae, 8–27 μm long, at level of buccal cavity. Amphidial fovea circular, with cuticularised outline and entirely surrounded by cuticle striations, situated immediately posterior to buccal cavity ca. 1.0 cbd from anterior extremity. Buccal cavity large, 25 μm deep and 20 μm wide; six X-shaped cuticularised structures lining the inner buccal cavity wall (sometimes called mandibles) hooked anteriorly and with wide base articulating onto cuticularised rim posteriorly. Posterior portion of buccal cavity surrounded by pharyngeal tissue. Pharynx muscular, cylindrical, with strongly cuticularised lumen. Cardia surrounded by intestine. Nerve ring situated slightly anterior to middle of pharynx length. Secretory-excretory system present; ampulla and pore situated slightly posterior to nerve ring; ventral gland not observed. Structure of the genital branch could not be observed. Spicules equal, broadly arcuate, 2.3 cloacal body diameters long, strongly cuticularised proximally;

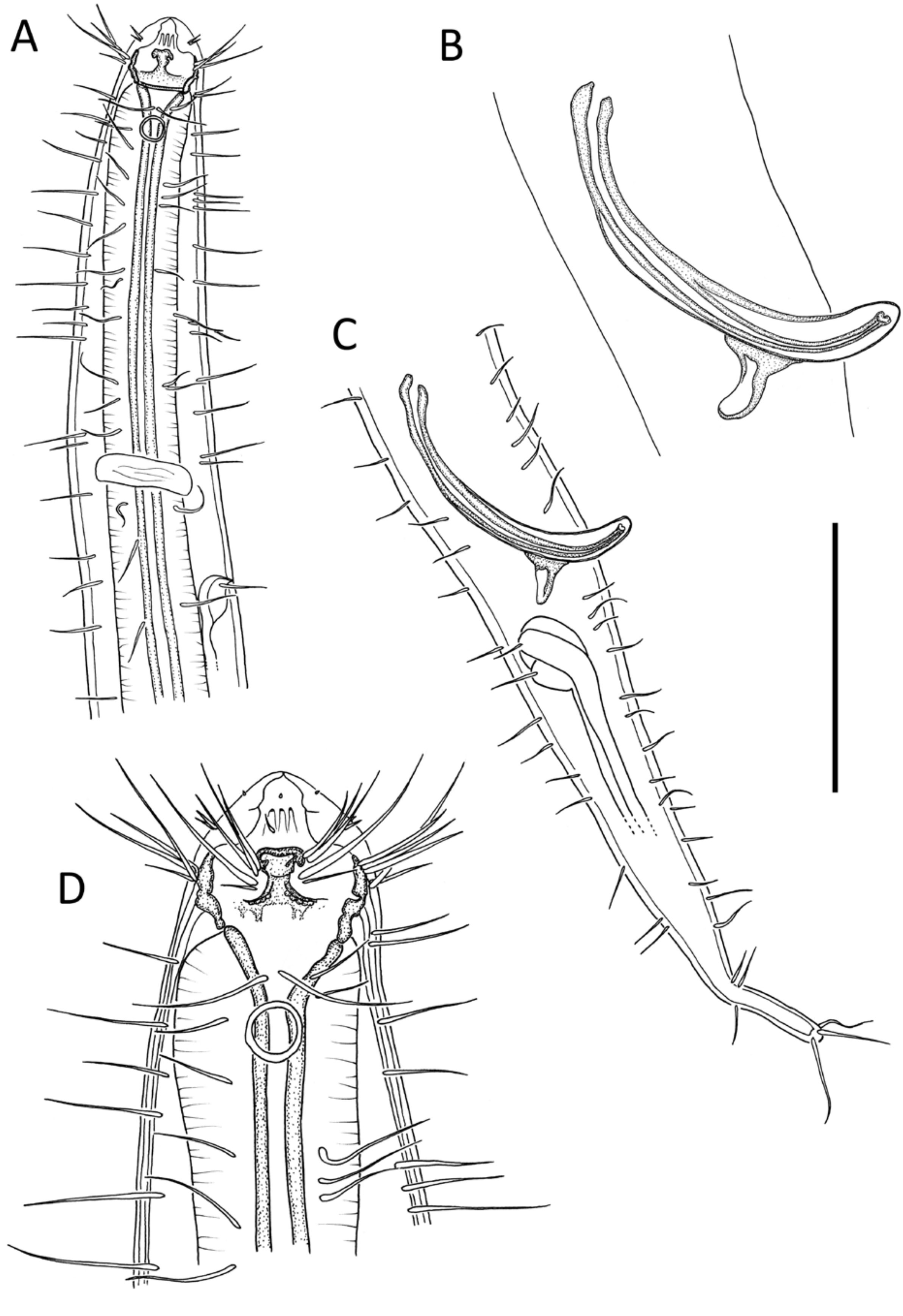



**Figure 89.** *Metasphaerolaimus* sp. 1 (NIWA 154880, dorsocaudal apophyses & conicocylindrical tail, Mana Bank, Leduc & Zhao) **sp. indet.**, male: **A.** Anterior body region; **B.** Copulatory apparatus; **C.** Posterior body region; **D.** Cephalic region. Scale bar: A = 100 μm; B = 55 μm; C = 90 μm; D = 40 μm.

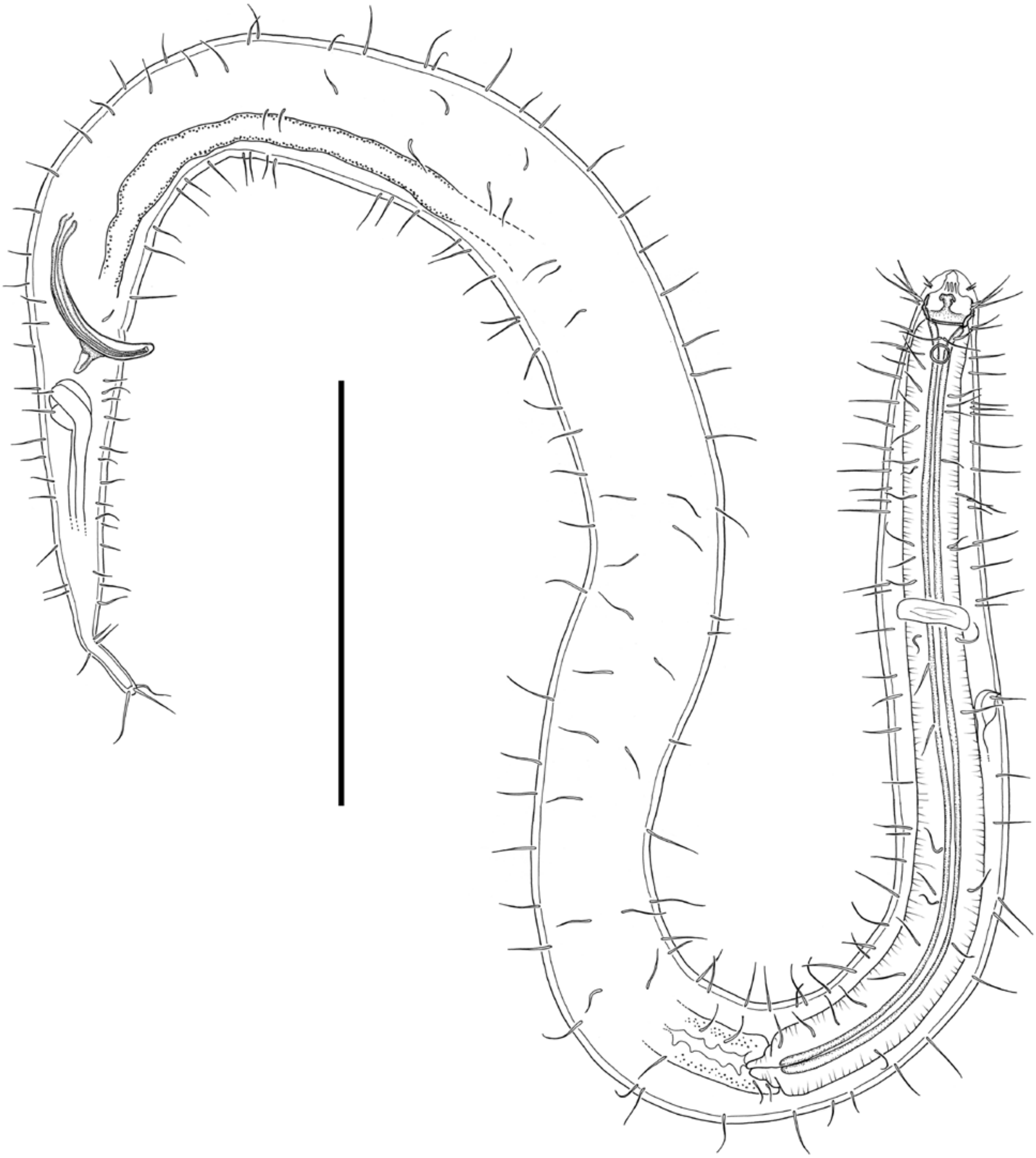


**Figure 90.** *Metasphaerolaimus* sp. 1 (NIWA 154880, dorsocaudal apophyses & conicocylindrical tail, Mana Bank, Leduc & Zhao) **sp. indet.**, entire male. Scale bar = 200 µm.

distal portion with thinly cuticularised margins and narrow central thick cuticularisation bending laterally at tip. Gubernaculum not surrounding spicules, with slightly curved dorsocaudal apophyses. Precloacal seta, supplements and ejaculatory glands not observed. Tail conicocylindrical with subventral and subdorsal rows of setae and three 24–22 µm long terminal setae. Three small caudal glands present.

**Species diagnosis.** *Metasphaerolaimus* sp. 1 **sp. indet.** is characterised by body length 1418 µm, eight rows of 12–26 µm long somatic setae, eight groups of 4–5, 8–27 µm long sub-cephalic setae, amphidial

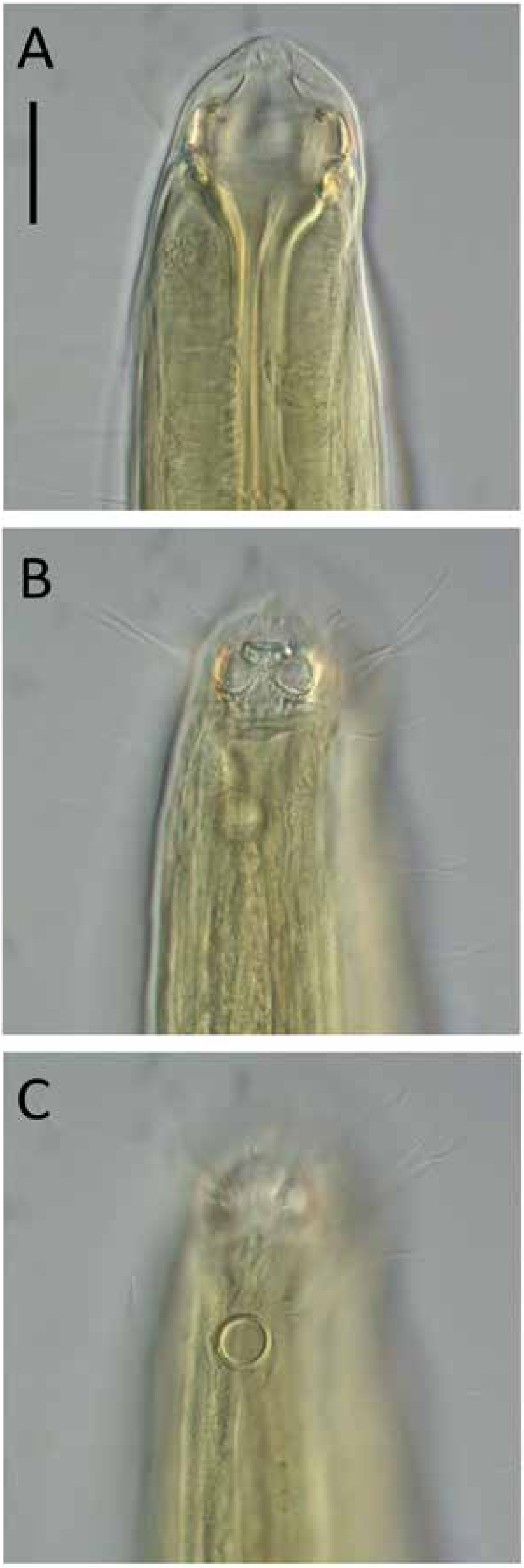



**Figure 91.** *Metasphaerolaimus* sp. 1 (NIWA 154880, dorsocaudal apophyses & conicocylindrical tail, Mana Bank, Leduc & Zhao) **sp. indet.**, light micrographs of male anterior body region showing: **A.** Buccal cavity, pharynx, and lips; **B.** Anterior sensilla; **C.** Amphidial fovea. Scale bar = 20 µm.

**Table 25.** Morphometrics (µm) of *Metasphaerolaimus* sp. 1 (NIWA 154880, dorsocaudal apophyses & conicocylindrical tail, Mana Bank, Leduc & Zhao) **sp. indet.**, given as individual values.

| Parameter | Male |
|---|---|
| Number of specimens | 1 |
| L | 1418 |
| a | 20 |
| b | 3 |
| c | 8 |
| c’ | 4.0 |
| Body diameter at cephalic setae | 22 |
| Body diameter at amphids | 37 |
| Length of outer labial setae | 4 |
| Length of cephalic setae | 2–3 |
| Amphid height | 10 |
| Amphid width | 9 |
| Amphid width/cbd (%) | 24 |
| Amphid from anterior end | 36 |
| Nerve ring from anterior end | 158 |
| Nerve ring cbd | 55 |
| Excretory pore from anterior end | 213 |
| Pharynx length | 416 |
| Pharyngeal diameter at base | 36 |
| Pharynx cbd at base | 57 |
| Maximum body diameter | 71 |
| Spicule length | 103 |
| Gubernacular apophysis length | 14 |
| Cloacal body diameter | 45 |
| Tail length | 180 |

fovea immediately posterior to buccal cavity, spicules 2.3 cloacal body diameters long, gubernaculum with slightly curved dorsocaudal apophyses.

**Differential diagnosis.** Only three species of the genus *Metasphaerolaimus* have a gubernaculum with dorsocaudal apophyses: *M. campbelli* (Allgén, 1927b) Gourbault & Boucher, 1981 (Campbell Island), *M. horrendus* (Sergeeva, 1981) Gourbault & Boucher, 1981 (Black Sea), and *M. japonicus* (Fadeeva, 1983) Gourbault & Boucher, 1981 (Sea of Japan) (see Leduc 2015a). The Pāuatahanui Inlet specimens differ from *M. horrendus* in having a conicocylindrical tail (versus conical in *M. horrendus*). *Metapshaerolaimus campbelli* and *M. japonicus* differ from *Metasphaerolaimus* sp. 1 in having larger amphidial fovea (35–37 *versus* 24% of cbd in *Metasphaerolaimus* sp. 1) and shorter spicules (41 and 63–78 µm, respectively, *versus* 103 µm in *Metasphaerolaimus* sp. 1). These differences, however, are relatively minor (especially between *Metasphaerolaimus* sp. 1 and *M. japonicus*, which have relatively long spicules), and so we refrain from erecting a new species for the Pāuatahanui Inlet specimens until more specimens are found.

## Family **Xyalidae** Chitwood, 1951

Xyalidae Chitwood, 1951: 655.

**Diagnosis.** Cuticle striated. Six outer labial setae and four cephalic setae in one circlet, with cephalic setae shorter than or at most equal to labial ones. Often additional cephalic setae and occasionally eight groups of sub-cephalic setae are present. Stoma usually funnel-shaped, completely, or only at the base surrounded by pharyngeal tissue. Ventral gland mostly absent (or invisible under light microscopy). Females with one (anterior) ovary to the left side of intestine. Males usually with two testes, the anterior one to the left side of intestine, the posterior one (may be absent) to the right side (from Fonseca & Bezerra (2014a)).

**Type genus.** *Xyala* Cobb, 1920

## Genus ***Cobbia*** de Man, 1907

*Cobbia* de Man, 1907: 232–233.

**Diagnosis.** Cuticle finely striated or annulated. Anterior sensilla arranged in two circles of six + ten, inner labial sensilla setiform, outer labial setae at same level as, and longer than the cephalic setae. Short additional setae may be present at level of outer labial setae and cephalic setae. Buccal cavity conical, partially surrounded by pharyngeal musculature and equipped with one or three teeth (one dorsal, two subventral). Amphids circular. Male reproductive system with two testes; anterior to the left of intestine, posterior to the right. Opening of the caudal glands probably separated. Tail conical or conical cylindrical without terminal setae (modified from Fonseca & Bezerra (2014a)).

**Remarks.** Keys to valid *Cobbia* species were provided by Datta *et al.* (2018b) and Wang *et al.* (2018). There are currently ten valid species in the genus.

**Type species.** *Cobbia trefusiaeformis* de Man, 1907

### ***Cobbia trefusiaeformis* de Man, 1907**

Figs 92–94; Table 26

*Cobbia trefusiaeformis* de Man, 1907: 233.

**Material examined.** NIWA 139298, NIWA Stn Z19168, 41.098º S, 174.872º E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 22 Feb 2019, fine sand, two males, and one female.

**Type & locality.** Coast of Eastern Scheldt, the Netherlands. De Man's type collection is located at the Naturalis Invertebrate Collection, Naturalis, Leiden, the Netherlands, but registration details of the holotype were not confirmed prior to publication.

**Distribution.** Cosmopolitan, including records from southern Japan, the Red Sea, the Mediterranean, the Baltic Sea, the White Sea, and the North Sea (Gerlach & Riemann 1973/1974; Lorenzen 1977; Aryuthaka 1989; Tchesunov *et al.* 2008; Semprucci 2013).

**Diagnosis.** *Cobbia trefusiaeformis* specimens from Pāuatahanui Inlet are characterised by colourless, cylindrical body. Cuticle striated, no lateral differentiation. Six rows of somatic setae present in pharyngeal region, 5–12 µm long, sparse elsewhere. Cephalic region not set-off; thin lips bearing six 3–4 µm long inner labial setae. Six outer labial setae, 1.1–1.4 cbd long, in same circle as four shorter cephalic setae, 0.9–1.1 cbd long. Two additional setae, 4 µm long, located slightly ventrally to each lateral outer labial seta; additional setae at same level or slightly anterior to the circle of outer labial setae and cephalic setae. Amphidial fovea medium-sized, circular, with lightly cuticularised outline and entirely surrounded by cuticle striations, ca. 1.25–1.5 cbd from anterior extremity. Buccal cavity with lightly cuticularised, barrel-shaped cheilostome; pharyngostome funnel-shaped with three weakly cuticularised teeth, dorsal tooth slightly larger than the two ventrosublateral teeth. Pharyngeal glands open at tip of each tooth. Pharynx muscular, cylindrical, without posterior bulb. Nerve ring located at ca. 40% of pharynx length from anterior. Secretory-excretory system not observed. Cardia ca. 8 µm long, surrounded by intestinal tissue. Male reproductive system with two outstretched testes; anterior testis to the left of intestine, posterior testis to the right of intestine. Sperm cells globular, nucleated, 9 × 9 µm. Spicules equal, strongly bent (L-shaped), 1.3–1.4 cloacal body diameters long, strongly cuticularised, with swollen proximal ends and distal end with two small, pointed projections. Lightly cuticularised gubernaculum surrounding distal end of spicules, without apophyses. Precloacal seta, supplements and ejaculatory glands not observed. Tail conicocylindrical with elongated filiform portion; subventral and subdorsal setae present in cloacal region and conical portion of tail, 3–9 µm long, no terminal setae. Three small caudal glands present. Female similar to males but with only one additional seta between lateral outer labial setae and lateral inner labial setae and slightly ventrosublaterally, and longer tail with sparser setae. Reproductive system with single

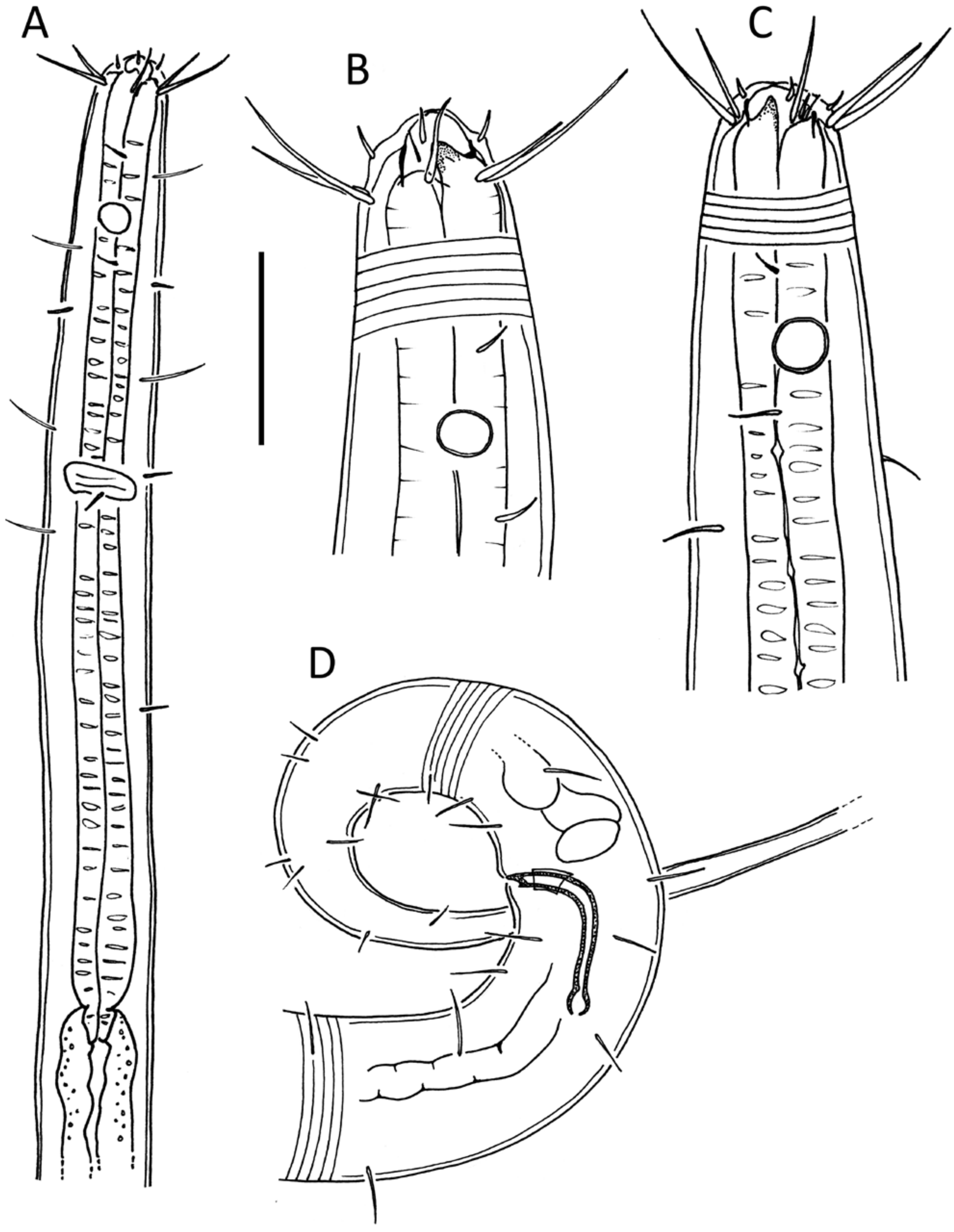



**Figure 92.** *Cobbia trefusiaeformis* de Man, 1907 NIWA 139298: **A.** Anterior body region of male; **B.** Cephalic region of female; **C.** Cephalic region of male; **D.** Posterior body region of male. Scale bar: A = 40 μm; B = 19 μm; C = 22 μm; D = 32 μm.

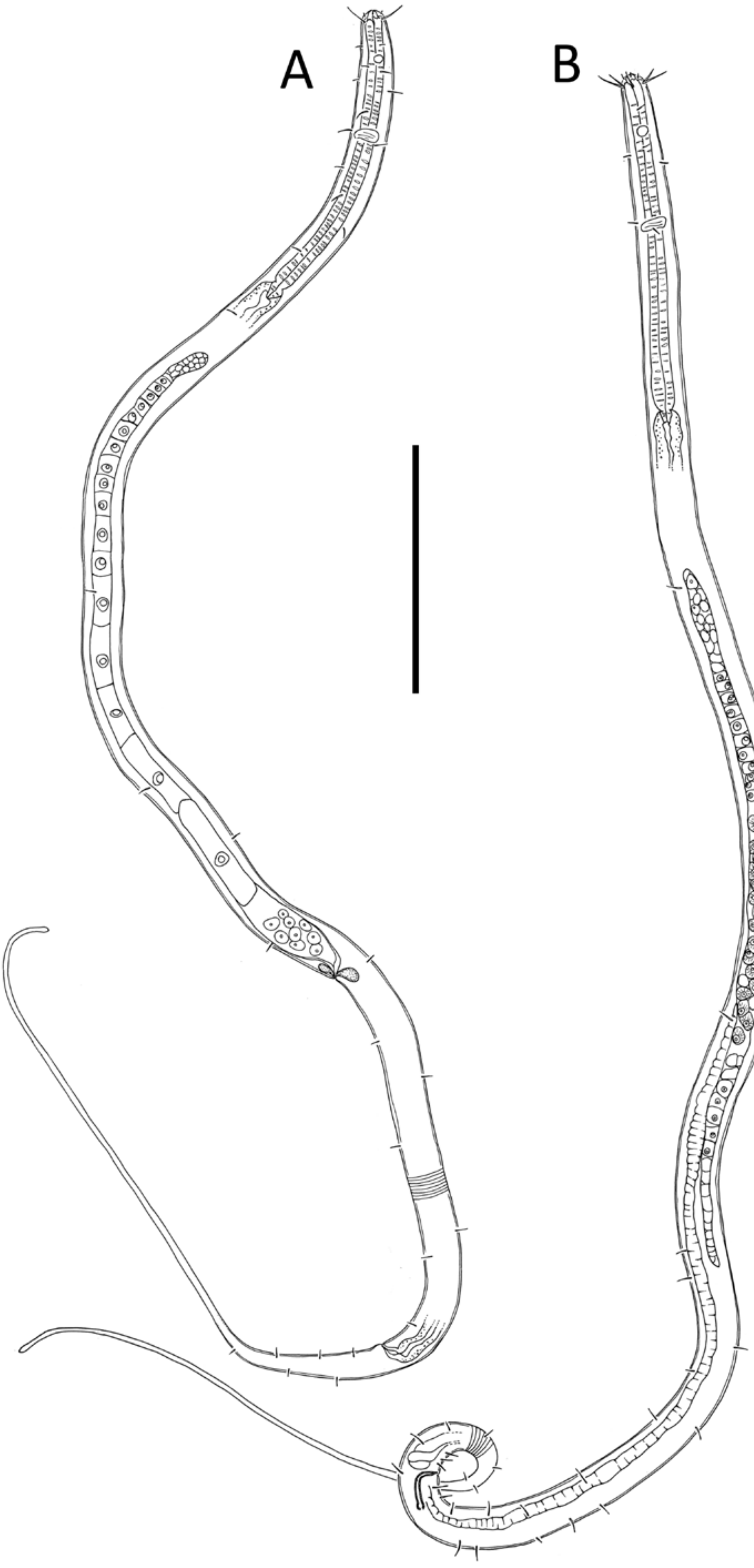



**Figure 93.** *Cobbia trefusiaeformis* de Man, 1907 NIWA 139298: **A.** Entire male; **B.** Entire female. Scale bar = 150 µm.

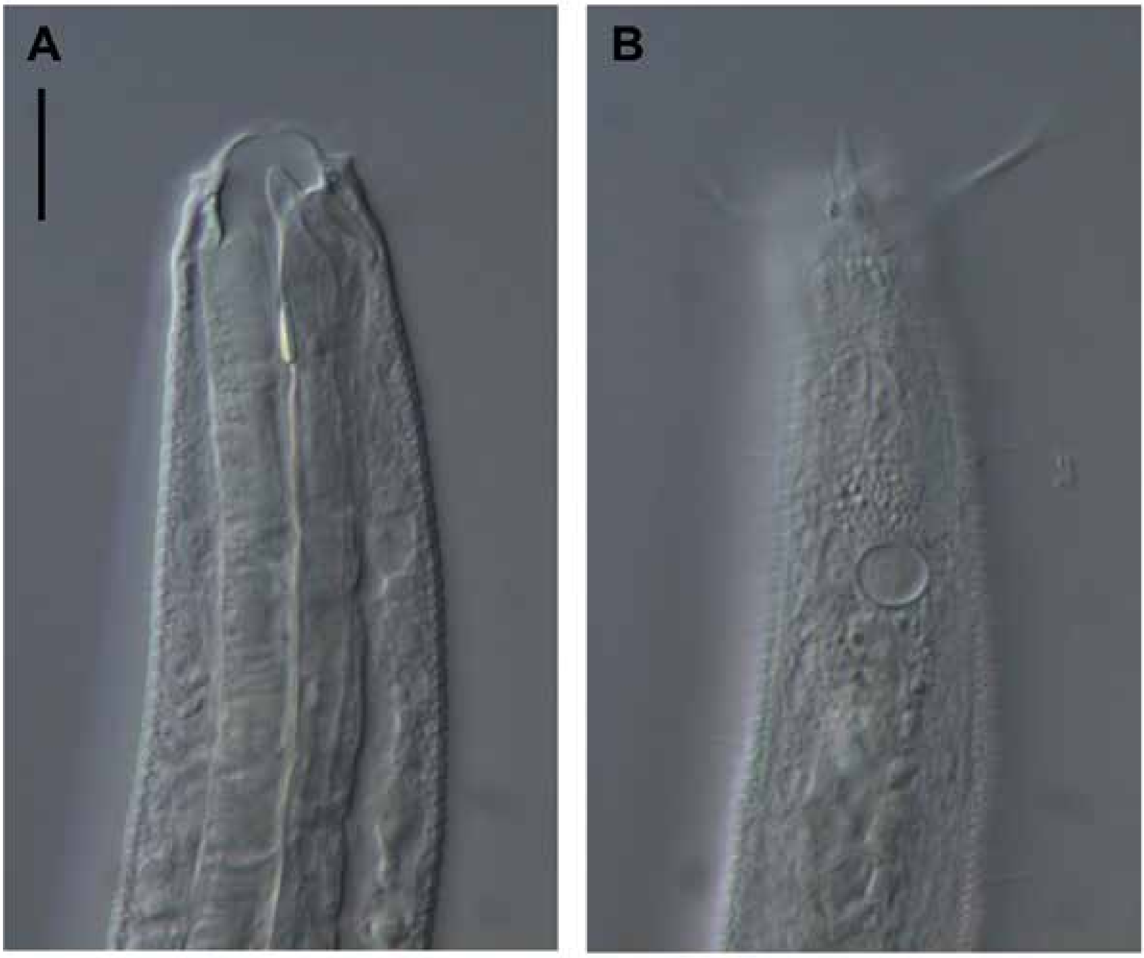



**Figure 94.** *Cobbia trefusiaeformis* de Man, 1907 NIWA 139298, light micrographs of female: **A.** Optical cross-section of cephalic region showing lips, buccal cavity, and pharynx; **B.** Surface view of cephalic region showing anterior sensilla, cuticle ornamentation, and amphid. Scale bar = 10 µm.

outstretched ovary to the left of intestine. Spermatheca and post- and prevulval sac not observed; vulval glands present. Vulva located near mid-body. No constrictor muscle observed surrounding pars proximalis vaginae.

**Remarks**. The Pāuatahanui Inlet specimens are largely consistent with the description of *C. trefusiaeformis* by de Man (1907) based on specimens from the Netherlands. However, the following discrepancies were observed between specimens from Pāuatahanui Inlet and the Netherlands: shorter body length (1.3–1.6 *versus* 2.0 mm in the type specimens), lower ratio of a (46–52 *versus* 55–60), shorter outer labial setae (16–20 *versus* 25 µm), and slightly smaller amphids (6–7 *versus* 8 µm). Key morphological traits defining the species, namely the presence of additional setae in the cephalic region, number and arrangement of teeth in the buccal cavity, position of the amphids, structure of the male and female reproductive systems, structure of the male copulatory apparatus, and tail shape are all consistent between the Pāuatahanui and Netherlands specimens. The species has been recorded in locations across the globe, with descriptions of specimens provided from the Baltic Sea (Lorenzen 1977), Ireland and Scotland (Warwick *et al.* 1998), and southern Japan (Aryuthaka 1989). *Cobbia trefusiaeformis* therefore appears to be cosmopolitan, but this hypothesis will need to be tested using molecular data, which are not currently available from *C. trefusiaeformis* populations outside New Zealand.

**Sequence data.** Partial SSU rDNA (1244 bp; Genbank OK317211) and D2–D3 of LSU rDNA (677 bp; Genbank OK317232).

## Genus ***Daptonema*** Cobb, 1920

*Daptonema* Cobb, 1920: 281–282.

**Diagnosis.** Cuticle striated or annulated. Somatic setae usually present, generally shorter than 1.5 times the corresponding body diameter. Inner labial sensilla papilliform; outer labial and cephalic setae in single circle. Additional setae sometimes present at level of cephalic and outer labial setae. Amphids circular and of varying

**Table 26.** Morphometrics (µm) of *Cobbia trefusiaeformis* de Man, 1907, given as individual values.

| Parameter | Males | Female |
|---|---|---|
| Number of specimens | 2 | 1 |
| L | 1331, 1475 | 1555 |
| a | 46, 51 | 52 |
| b | 7 | 8 |
| c | 4 | 3 |
| c' | 13.0, 16.2 | 23.6 |
| Body diameter at cephalic setae | 14 | 14 |
| Body diameter at amphids | 20, 21 | 22 |
| Length of outer labial setae | 16–19 | 16–20 |
| Length of cephalic setae | 12–15 | 12–16 |
| Amphid height | 6 | 6 |
| Amphid width | 6, 7 | 6 |
| Amphid width/cbd (%) | 30, 33 | 27 |
| Amphid from anterior end | 25, 31 | 31 |
| Nerve ring from anterior end | 76, 89 | 78 |
| Nerve ring cbd | 24 | 24 |
| Pharynx length | 194, 207 | 202 |
| Pharyngeal diameter at base | 14, 15 | 13 |
| Pharynx cbd at base | 25 | 26 |
| Maximum body diameter | 29 | 30 |
| Spicule length | 33, 34 | – |
| Cloacal/anal body diameter | 25 | 20 |
| Tail length | 324, 405 | 471 |
| V | – | 786 |
| %V | – | 51 |
| Vulval body diameter | – | 26 |

size and position from the anterior end. Buccal cavity conical, weakly cuticularised. Cardia small, surrounded by intestine. Ventral gland absent. Post- and prevulval sac may be present. Spicules usually short (1.5–2.0 times the anal body diameter) and strongly curved or L-shaped. Gubernaculum usually present, sometimes with lateral guiding pieces and/or dorso-caudal apophyses. Tail conicocylindrical with 2–4 terminal setae (from Fonseca & Bezerra (2014a)).

**Remarks.** A list of 116 valid *Daptonema* species was provided by Venekey *et al.* (2014). Additional *Daptonema* species were later described by Nguyen Din Tu *et al.* (2014), Leduc (2015b), Sun & Huang (2017), Wang *et al.* (2018), Aryuthaka & Kito (2018), Huang *et al.* (2019), Sun *et al.* (2019), Qiao & Huang (2020), Long *et al.* (2020) and Gagarin (2021).

**Type species.** *Daptonema fissidens* Cobb, 1920

### *Daptonema falcatispiculum* sp. nov.

Figs 95, 96; Table 27

**Material examined. Holotype** NIWA 154878, NIWA Stn Z18747, 41.106° S, 174.891° E, Bradeys Bay in Pāuatahanui Inlet, upper intertidal, 25 Sep 2018, partly anoxic gravelly sand, male. **Paratypes** NIWA 154879, one male and one female, same data as for holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Males.** Body relatively stout, colourless, cylindrical, tapering slightly towards both extremities. Cuticle with transverse annulations, no lateral differentiation. Eight rows of short somatic setae present mainly in pharyngeal region, sparse elsewhere, ca. 2 µm long. Epidermal cells in anterior half of pharyngeal region large, with well-defined boundaries and highly transparent. Truncated cephalic region with slightly set-off lip region; each of the six lips bearing a minute inner labial papilla. Six unjointed outer labial setae, 0.36–0.38 cbd long, in same circle as four unjointed, shorter cephalic setae, 0.23–0.27 cbd long. No additional setae present. Amphidial fovea relatively small, circular, with lightly cuticularised outline, surrounded by cuticle annulations, ca. 0.6–0.7 cbd from anterior extremity. Buccal cavity funnel-shaped, not cuticularised, 9–10 µm deep, 5 µm wide, without teeth. Ducts of pharyngeal glands not observed. Pharynx muscular, anterior portion surrounding funnel-shaped portion of buccal cavity, widening slightly posteriorly. Nerve ring located slightly anterior to middle of pharynx. Secretory-excretory system not observed. Cardia, ca. 12 µm long, partially surrounded by intestinal tissue. Reproductive system with two outstretched testes; anterior testis to the left of intestine and posterior testis to the right of intestine. Sperm cells globular, 6–9 × 9–12 µm. Spicules equal, arcuate, strongly cuticularised, 2.0–2.1 cloacal body diameters long, slightly swollen proximally, with lateral hook near distal tip. Gubernaculum slightly longer than half of spicule length, without apophyses, surrounding distal end of spicules; precloacal supplements not observed. Ejaculatory glands not observed. Tail conicocylindrical with rows of subventral and subdorsal setae, 3–6 µm long; three terminal setae, 6 µm long. Three caudal glands present.

**Female.** Similar to males but tail without subventral or subdorsal setae. Reproductive system with single

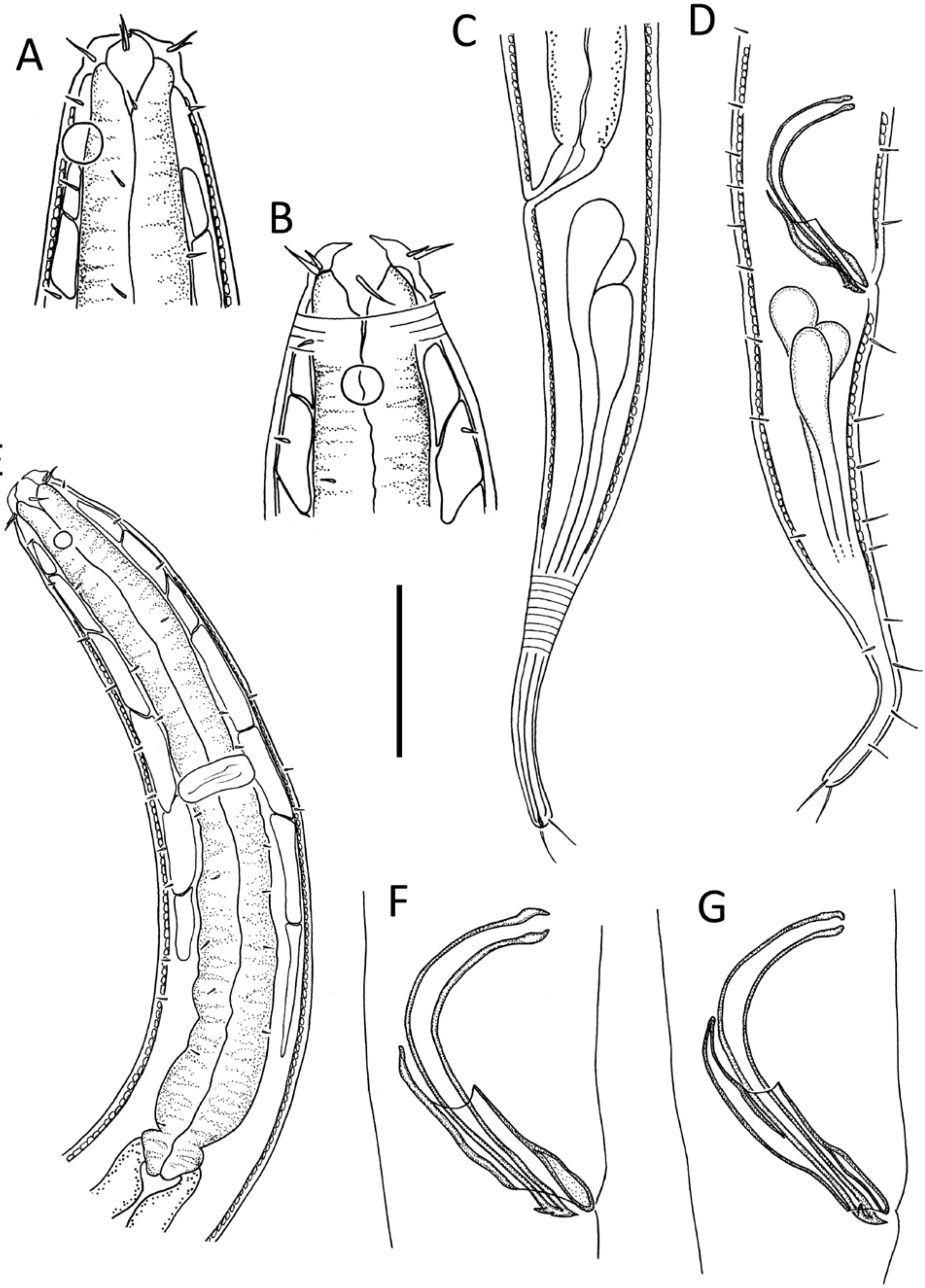



**Figure 95.** *Daptonema falcatispiculum* **sp. nov.**: **A.** Cephalic region of female paratype NIWA 154879; **B.** Cephalic region of male holotype NIWA 154878; **C.** Female paratype posterior body region NIWA 154879; **D.** Male paratype posterior body region NIWA 154879; **E.** Female paratype pharyngeal region NIWA 154879; **F.** Copulatory apparatus, paratype male NIWA 154879 **G.** Copulatory apparatus, holotype male NIWA 154878. Scale bar: A, B = 20 µm; C, D = 40 µm; E = 23 µm; F, G = 26 µm.

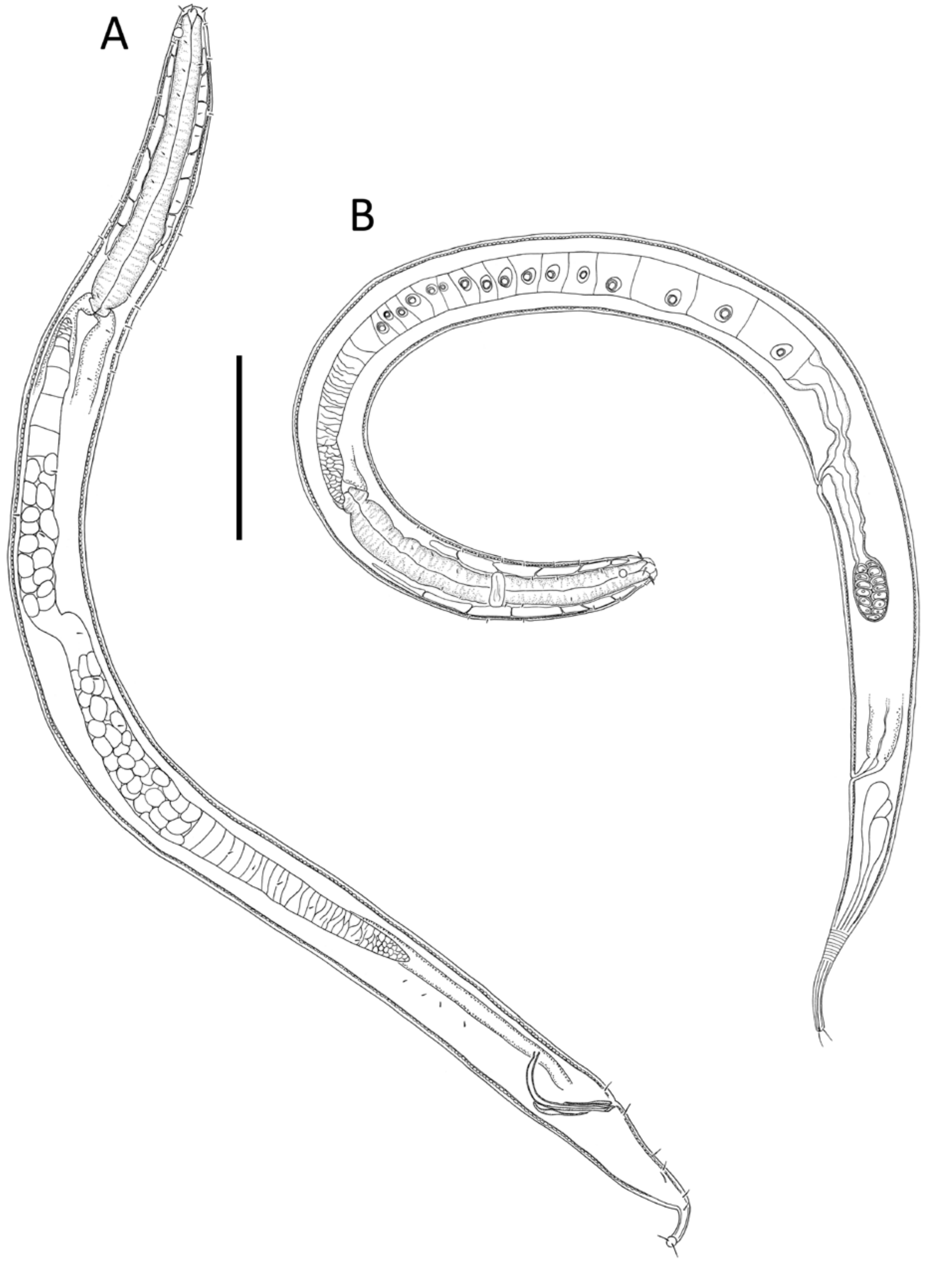



**Figure 96.** *Daptonema falcatispiculum* **sp. nov.**: **A.** Entire holotype male NIWA 154878; **B.** Entire paratype female NIWA 154879. Scale bar = 100 µm.

**Table 27.** Morphometrics (μm) of *Daptonema falcatispiculum* **sp. nov.**, given as individual values.

| Parameter | Males | | Female |
|---|---|---|---|
| | Holotype | Paratype | Paratype |
| Number of specimens | 1 | 1 | 1 |
| L | 776 | 741 | 933 |
| a | 19 | 17 | 20 |
| b | 5 | 6 | 5 |
| c | 10 | 6 | 6 |
| c' | 2.6 | 3.9 | 4.8 |
| Body diameter at cephalic setae | 11 | 12 | 13 |
| Body diameter at amphids | 17 | 19 | 21 |
| Length of outer labial setae | 4 | 5 | 5 |
| Length of cephalic setae | 3 | 3 | 3 |
| Amphid height | 5 | 5 | 5 |
| Amphid width | 5 | 5 | 5 |
| Amphid width/cbd (%) | 29 | 26 | 24 |
| Amphid from anterior end | 10 | 13 | 15 |
| Nerve ring from anterior end | 71 | 63 | 77 |
| Nerve ring cbd | 32 | 32 | 34 |
| Pharynx length | 153 | 134 | 180 |
| Pharyngeal diameter at base | 19 | 16 | 22 |
| Pharynx cbd at base | 38 | 38 | 40 |
| Maximum body diameter | 40 | 43 | 46 |
| Spicule length | 62 | 66 | – |
| Gubernaculum length | 39 | 35 | – |
| Cloacal/anal body diameter | 31 | 32 | 31 |
| Tail length | 80 | 125 | 149 |
| V | – | – | 616 |
| %V | – | – | 66 |
| Vulval body diameter | – | – | 45 |

outstretched ovary to the left of intestine; anterior extremity of ovary overlaps with cardia. Mature eggs not observed. Postvulval sac present, oval-shaped, not cuticularised, 38 × 20 μm, connected to vagina by 45 μm long duct. Vulva located at two-thirds of body length from anterior. Vaginal glands not observed

**Etymology.** The species name is derived from the Latin *falcatus* (= sickle-shaped, curved), and refers to the arcuate shape of the spicules.

**Species diagnosis.** *Daptonema falcatispiculum* **sp. nov.** is characterised by body length 741–933 μm, moderately stout body shape (a = 17–20), truncated cephalic region with slightly set-off lip region, short (0.2–0.4 cbd long) unjointed outer labial setae and cephalic setae, no additional setae, conspicuous epidermal cells in anterior half of pharyngeal region, male with two testes, long (2.0 cloacal body diameters) arcuate spicules with lateral hooks and 35–39 μm long gubernaculum without apophyses, females with vulva at two-thirds of body length from anterior and postvulval sac.

**Differential diagnosis.** *Daptonema falcatispiculum* **sp. nov.** differs from most other species of the genus in having relatively long arcuate spicules. A similar spicular apparatus is found only in *D. curvispicula* Tchesunov & Miljutin, 2006 (Arctic Ocean) and *D. curvispiculum* (Gerlach, 1951) Wieser, 1959 (Mediterranean Sea). The new species differs from *D. curvispicula* by the smaller amphids (5 *versus* 17–18 μm diameter in *D. curvispicula*) and the presence of lateral hooks near the tip of the spicules (*versus* no distal hooks in *D. curvispicula*), and from *D. curvispiculum* by the shorter body length (741–933 *versus* 1127–1200 μm), lower values of a (17–20 versus 27–38), and absence of gubernacular apophyses (*versus* present in *D. curvispiculum*).

**ZooBank registration.** *Daptonema falcatispiculum* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:76BF549D-80A2-4F38-ADA6-559A0B398E3D.

## *Daptonema carnulentum* sp. nov.

Figs 97–99; Table 28

**Material examined. Holotype** NIWA 139269, NIWA Stn Z18745, 41.093° S, 174.876° E, Pāuatahanui Inlet near Camborne Walkway, upper intertidal, 28 Jul 2016, gravelly sand, male. **Paratypes** NIWA 139270, two males and three females, same data as for holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Males.** Body stout, colourless, cylindrical, tapering slightly towards both extremities. Cuticle with transverse annulations, no lateral differentiation. Eight rows of somatic setae present mainly in pharyngeal region, sparse elsewhere, 2–3 μm long. Epidermal cells in anterior half of pharyngeal region large, with well-defined boundaries and highly transparent. Truncated cephalic region with conspicuously set-off lip region extending up to 10 μm anteriorly; each of the six lips bearing a minute inner labial papilla. Six triple-jointed outer labial setae, 0.45–0.58 cbd long, in same circle as four triple-jointed, shorter cephalic setae, 0.28–0.47 cbd long. One additional seta, ca. 5 μm long, apparently jointed, situated immediately next to each of the lateral outer labial setae. Amphidial fovea oval to almost circular, medium-sized, with lightly cuticularised outline, surrounded by cuticle annulations, ca. 0.5 cbd from

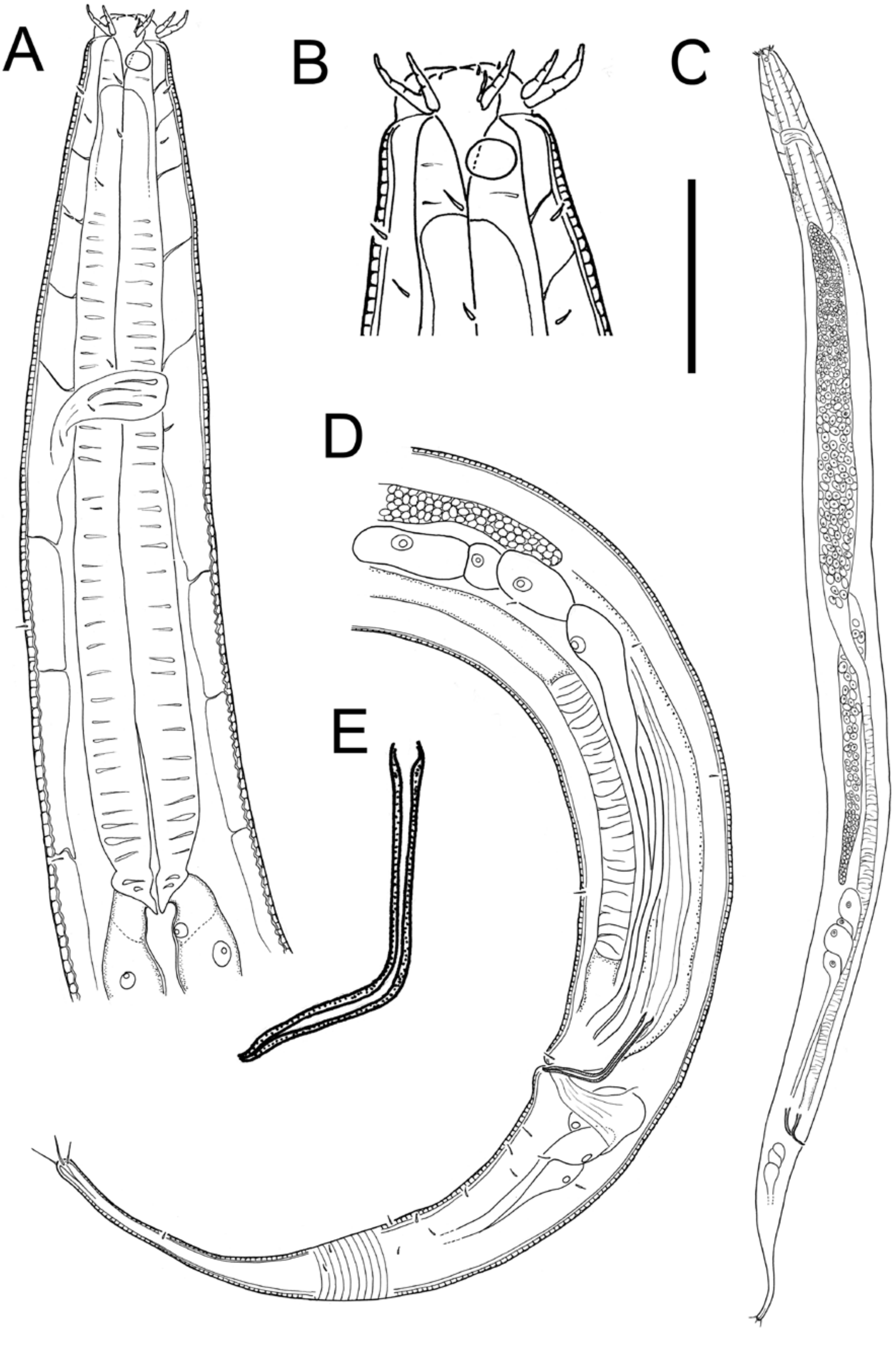



**Figure 97.** *Daptonema carnulentum* **sp. nov.** Male: **A.** Anterior body region, holotype NIWA 139269; **B.** Cephalic region, holotype NIWA 139269; **C.** Entire holotype male NIWA 139269; **D.** Posterior body region, paratype NIWA 139270; **E.** Spicule, paratype NIWA 139270. Scale bar: A = 60 µm; B = 30 µm; C = 275 µm; D = 80 µm; E = 25 µm.

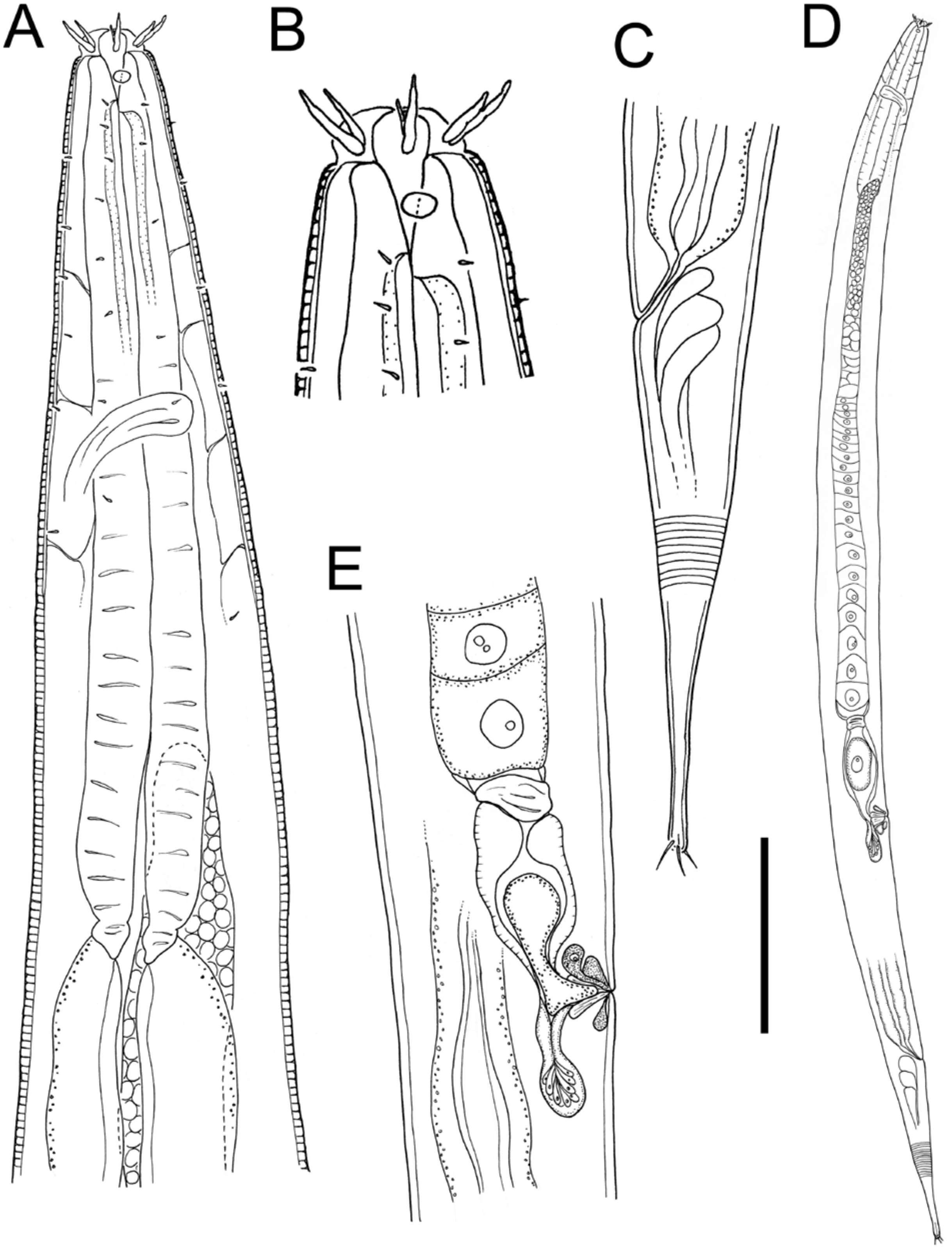



**Figure 98.** *Daptonema carnulentum* **sp. nov.**, paratype female NIWA 139270: **A.** Anterior body region; **B.** Cephalic region; **C.** Posterior body region; **D.** Entire female; **E.** Vulva and posterior portion of reproductive system. Scale bar: A = 60 μm; B = 32 μm; C = 95 μm; D = 315 μm; E = 80 μm.

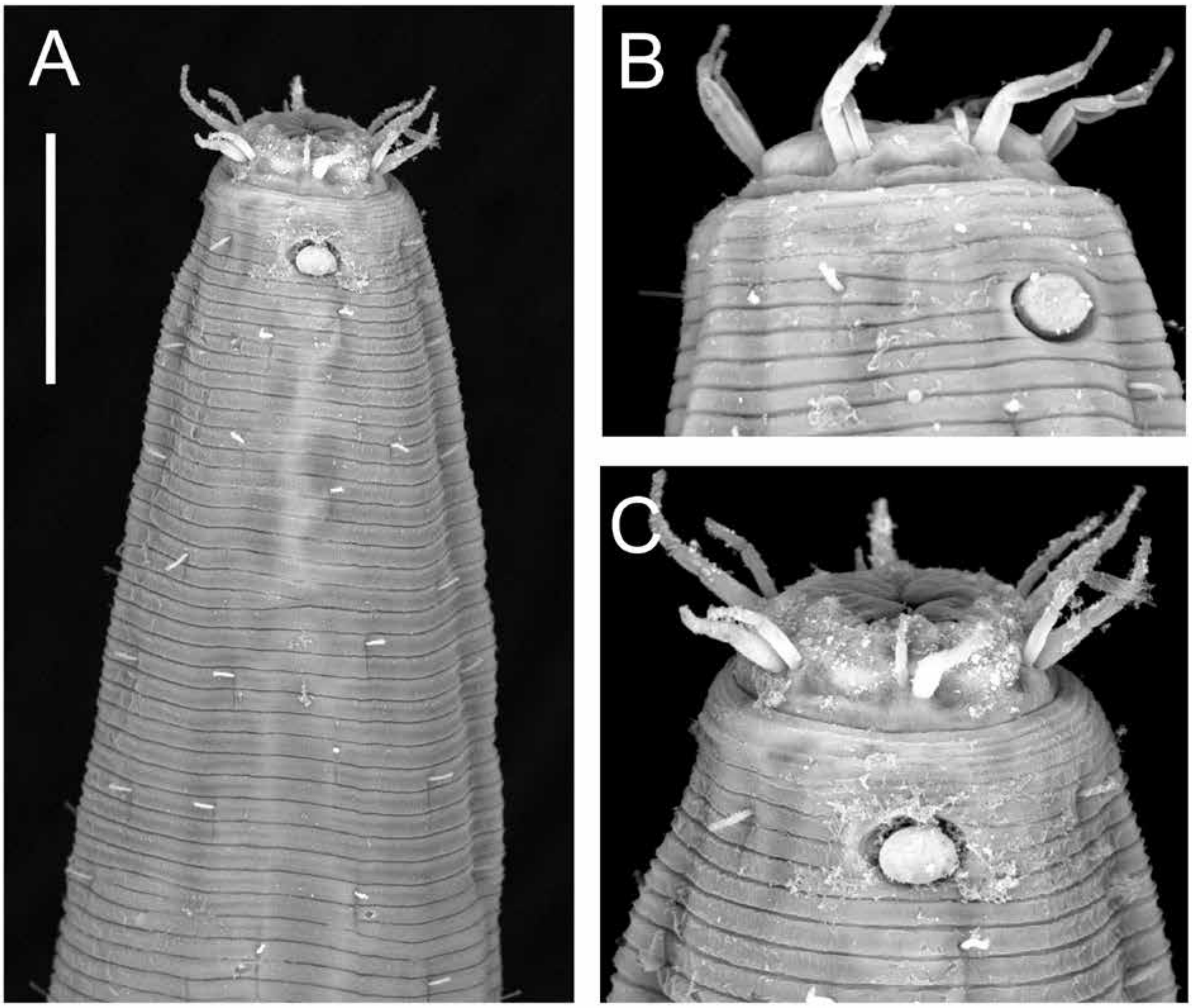



**Figure 99.** *Daptonema carnulentum* **sp. nov.**, scanning electron micrographs: **A.** Anterior body region of female; **B–C.** Female cephalic region. Scale bar: A = 25 µm, B = 11 µm, C = 13 µm.

anterior extremity. Buccal cavity funnel-shaped, not cuticularised, 11–15 µm deep, 8–10 µm wide, without teeth. Ducts of pharyngeal glands sometimes visible in anterior portion of pharynx. Pharynx muscular, anterior portion surrounding funnel-shaped portion of buccal cavity, widening slightly posteriorly. Nerve ring located slightly anterior to middle of pharynx. Secretory-excretory system not observed. Cardia ca. 12 µm long, surrounded by intestinal tissue. Reproductive system with two outstretched testes; anterior testis to the left of intestine and posterior testis to the right of intestine. Anterior extremity of anterior testis overlaps with posterior portion of pharynx. Sperm cells globular, 8–9 × 11–12 µm. Spicules short, thin L-shaped, strongly cuticularised. Gubernaculum and precloacal supplements not observed. One row of four ejaculatory glands present either side of vas deferens. Tail conicocylindrical with rows of subventral setae and sparse subdorsal setae; three terminal setae present, 9–12 µm long. Three caudal glands and spinneret present.

**Females.** Similar to males but with generally lower values of a, wider body diameter in cephalic region, slightly smaller amphidial fovea, tail without subventral or subdorsal setae, and longer terminal setae 9–20 µm. Reproductive system with single outstretched ovary to the left of intestine. Anterior extremity of ovary overlaps with posterior portion of pharynx; base of ovary surrounded by sphincter muscle. Mature eggs ca. 45 × 75 µm. Spermatheca and prevulval sac not observed; post-vulval sac present. Vulva located near two-thirds of body length from anterior. Pars proximalis vaginae surrounded by constrictor muscle; at least three small vaginal glands present.

**Etymology.** The species name is derived from the Latin term *carnuentus* (= fleshy, corpulent, fat), and refers to both the stout body shape of this species as well as large size of the gonads in males and females.

**Table 28.** Morphometrics (µm) of *Daptonema carnulentum* **sp. nov.**, given as individual values, or a range of values from several specimens.

| Parameter | Males | | Females |
|---|---|---|---|
| | Holotype | Paratypes | Paratypes |
| Number of specimens | 1 | 2 | 3 |
| L | 1726 | 1535, 1723 | 1198–1819 |
| a | 18 | 16, 17 | 13–18 |
| b | 7 | 6 | 6–7 |
| c | 7 | 6, 7 | 6–7 |
| c' | 5.0 | 4.2, 4.8 | 3.6–4.7 |
| Body diameter at cephalic setae | 19 | 18 | 20–24 |
| Body diameter at amphids | 27 | 26 | 28–32 |
| Length of outer labial setae | 11 | 8–10 | 12–14 |
| Length of cephalic setae | 7–9 | 5–6 | 7–10 |
| Amphid height | 5 | 5 | 5 |
| Amphid width | 6 | 5, 6 | 5–6 |
| Amphid width/cbd (%) | 22 | 19, 23 | 18–19 |
| Amphid from anterior end | 11 | 12, 13 | 12–16 |
| Nerve ring from anterior end | 112 | 109, 110 | 68–121 |
| Nerve ring cbd | 57 | 52, 59 | 57–58 |
| Pharynx length | 253 | 250, 271 | 203–279 |
| Pharyngeal diameter at base | 34 | 32, 40 | 38–49 |
| Pharynx cbd at base | 65 | 63, 77 | 71–84 |
| Maximum body diameter | 96 | 93, 106 | 91–122 |
| Spicule length | 53 | 48, 55 | – |
| Cloacal/anal body diameter | 51 | 53, 61 | 54–61 |
| Tail length | 255 | 257, 258 | 208–280 |
| V | – | – | 772–1188 |
| %V | – | – | 64–65 |
| Vulval body diameter | – | – | 79–105 |

**Species diagnosis.** *Daptonema carnulentum* **sp. nov.** is characterised by body length 1200–1820 µm, stout body shape (a = 13–18), truncated cephalic region with conspicuously set-off lip region, triple-jointed outer labial and cephalic setae, two additional setae situated laterally at level of outer labial setae, conspicuous epidermal cells in anterior half of pharyngeal region, male and female gonads overlapping with posterior portion of pharynx, male with two testes, short L-shaped spicules and no gubernaculum, females with vulva at two-thirds of body length from anterior, post-vulval multicellular gland, and pre- and post-vulval sacs absent.

**Differential diagnosis**. *Daptonema carnulentum* **sp. nov.** resembles *D. oxycerca* (de Man, 1888) (North Atlantic) and *D. williamsi* Vincx & Coomans, 1983 (Solomon Islands) most in body size and shape, length and arrangement of cephalic sensilla, size and shape of the amphids and spicules, and tail length. The new species differ from the latter two species mainly by the absence of gubernaculum and presence of a large multicellular postvulval gland. The new species also differs from *D. oxycerca* in having a vulva located further anteriorly (64–65% *versus* 74–75% of body length from anterior), and from *D. williamsi* by the smaller number of ejaculatory glands (3–4 *versus* 5).

**Sequence data.** Partial SSU rDNA (1566 bp; Genbank OK317212) and D2–D3 of LSU rDNA (742 bp; Genbank OK317233).

**ZooBank registration.** *Daptonema carnulentum* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:4AC898B2-5ED1-4FBA-9114-E1AC6368E700.

## Genus *Omicronema* Cobb, 1920

*Omicronema* Cobb, 1920: 265.

**Diagnosis.** Cuticle coarsely annulated with longitudinal bars and without projections or crests. Somatic setae present along the body. Six thin hyaline lips. Anterior sensilla in two circles; inner labial sensilla setiform; second circle with additional setae at lateral fields. Amphid circular, relatively large, without sharply defined rims, and cryptospiral. Buccal cavity deep with strongly cuticularise walls. Tail conical or conicocylindrical, with or without terminal setae (modified from Fonseca & Bezerra (2014a)).

**Remarks.** Six valid *Omicronema* species are listed by Venekey *et al.* (2014); no other species have been described since.

**Type species.** *Omicronema litorium* Cobb, 1920

### *Omicronema nicholasi* sp. nov.

Figs 100, 101; Table 29

**Material examined. Holotype** NIWA 154873, NIWA Stn Z19169, 41.102° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 9 Dec 2019, fine sand, male.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Males.** Body colourless, cylindrical, tapering slightly towards both extremities. Cuticle annulated, each annulation ca. 2 µm apart, with numerous longitudinal bars ca 0.6 µm apart; no lateral differentiation. Sparse somatic setae present posterior to amphid, throughout pharyngeal region, and cloacal/caudal regions, 4 µm long. Thin, 5 µm high lips bearing 4 µm long inner labial setae; six outer labial setae 0.9–1.1

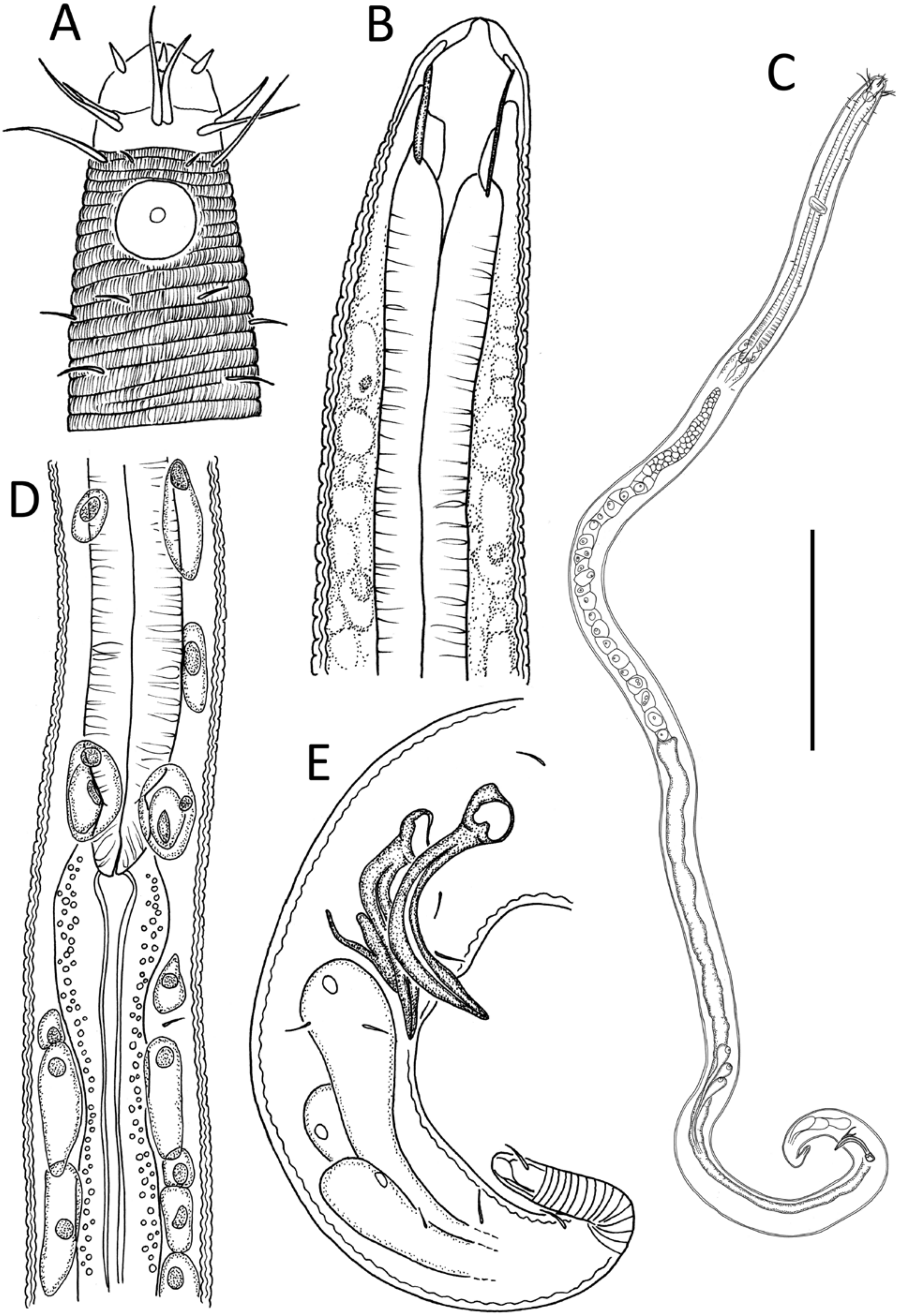



**Figure 100.** *Omicronema nicholasi* **sp. nov.**, male holotype NIWA 154873: **A–B.** Cephalic region; **C.** Entire male; **D.** Junction of pharynx and intestine; **E.** Posterior body region. Scale bar: A, B = 25 μm; C = 170 μm; D = 35 μm; E = 30 μm.

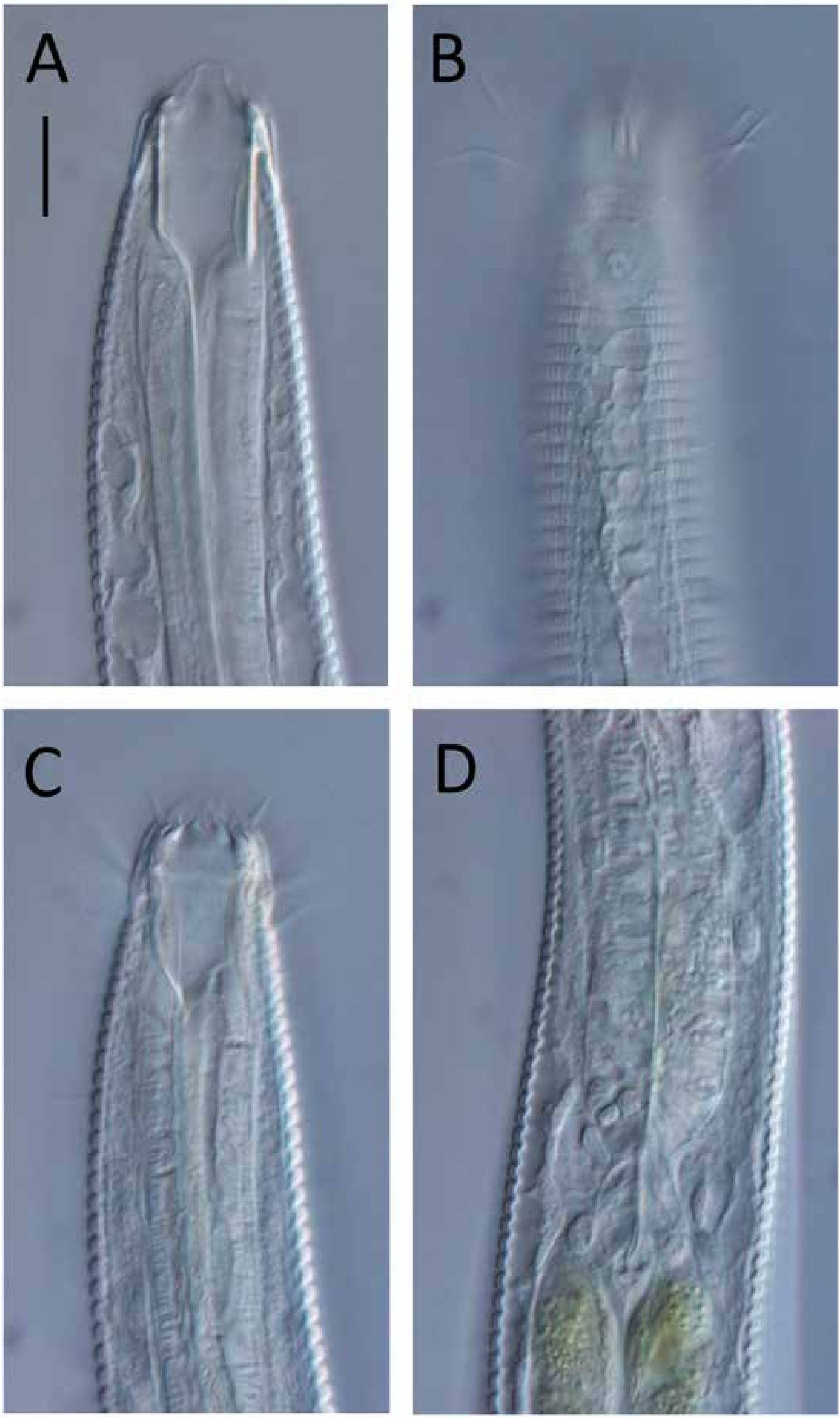



**Figure 101.** *Omicronema nicholasi* **sp. nov.**, light micrographs of male holotype NIWA 154873: **A.** Optical cross-section of cephalic region showing buccal cavity and lips; **B.** Optical cross-section of cephalic region showing inner labial sensilla; **C.** Surface view of cephalic region showing cuticle ornamentation, amphidial fovea, and outer labial and cephalic setae; **D.** Optical cross-section of junction of pharynx and intestine. Scale bar = 10 µm.

**Table 29.** Morphometrics (µm) of *Omicronema nicholasi* **sp. nov.**, given as individual values.

| Parameter | Male Holotype |
|---|---|
| Number of specimens | 1 |
| L | 1283 |
| a | 41 |
| b | 5 |
| c | 13 |
| c' | 3.7 |
| Body diameter at cephalic setae | 15 |
| Body diameter at amphids | 18 |
| Length of outer labial setae | 13–16 |
| Length of cephalic setae | 12–15 |
| Amphid height | 9 |
| Amphid width | 9 |
| Amphid width/cbd (%) | 50 |
| Amphid from anterior end | 16 |
| Nerve ring from anterior end | 116 |
| Nerve ring cbd | 26 |
| Pharynx length | 237 |
| Pharyngeal diameter at base | 15 |
| Pharynx cbd at base | 26 |
| Maximum body diameter | 31 |
| Spicule length | 44 |
| Gubernacular apophysis length | 11 |
| Cloacal body diameter | 26 |
| Tail length | 96 |

cbd long, in same circle as four slightly shorter cephalic setae, 0.8–01.0 cbd long. One additional seta adjacent to each lateral outer labial seta, of similar length to cephalic setae. Two pairs of short (3 µm long) sublateral subcephalic setae; two subdorsal and two subventral subcephalic setae, 7–13 µm long. Amphidial fovea large, circular, with central weakly defined outline, surrounded by cuticle annulations, ca. 1.0 cbd from anterior extremity. Buccal cavity large, 21 µm deep, 8 µm wide, cylindrical, with strongly cuticularised walls and at least four (possibly six) thin longitudinal folds in posterior portion. Ducts of pharyngeal glands not observed. Pharynx muscular, cylindrical, only partly surrounding posterior portion of buccal cavity, widening slightly posteriorly but not forming a posterior bulb. Nerve ring located at approximately middle of pharynx. Secretory-excretory system not observed. Cardia 15 µm long, partly surrounded by intestinal tissue. Numerous pseudocoelomocytes present in pharyngeal region and throughout body (except tail region), each with well-defined, circular, dense nucleus. Reproductive system with single outstretched testis located to the left of intestine; sperm cells globular, 9–12 × 9–12 µm. Spicules short, 1.7 cloacal body diameters long, arcuate, strongly cuticularised; swollen proximal portion (capitulum) and pointed distal ends. Gubernaculum not surrounding spicules distally, with curved dorsal apophyses. Precloacal supplements and seta not observed. Tail conical; three caudal glands and spinneret present. No terminal setae.

**Etymology.** The species is posthumously named after nematologist Warwick. L. Nicholas (Australian National University, Canberra) who, amongst many other achievements, contributed to the taxonomy of free-living marine nematodes in Austalia and beyond.

**Diagnosis**. *Omicronema nicholasi* **sp. nov.** is characterised by body length 1283 µm, ratio of a 41, ratio of c′ 3.7, outer labial setae 13–16 µm (0.9–1.1 cbd), cephalic setae 12–15 µm (0.8–1.0 cbd), two additional lateral setae of similar length to cephalic setae, eight subcephalic setae located slightly posterior to the cephalic setae and anterior to the amphids (four short sublateral, two long subdorsal, and two long subventral), sparse somatic setae 4 µm long, amphidial fovea 9 µm in diameter (0.5 cbd), buccal cavity 21 µm deep, 8 µm wide and with thin longitudinal folds, numerous pseudocoelomocytes throughout most of body, arcuate spicules 1.7 cloacal body diameters long, gubernaulum with curved dorsal apophyses.

**Differential diagnosis.** The new species can be differentiated from all other *Omicronema* species by the presence of subcephalic setae (subcephalic setae are absent in all other species). *Omicronema nicholasi* **sp. nov.** is most similar to *O. australis* Stewart & Nicholas, 1994 (coastal Australia) but can be differentiated from the latter based on shorter body length (1283 *versus* 1850–2898 µm in *O. australis*), shorter outer labial setae (13–16 *versus* 28 µm in *O. australis*), and larger amphidial fovea (0.5 *versus* 0.3 cbd in *O. australis*).

**ZooBank registration.** *Omicronema nicholasi* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:CF1E88ED-D2E5-4BC8-99D3-F643E8BDB017.

## Genus *Paramonohystera* Steiner, 1916

*Paramonohystera* Steiner, 1916: 639–641, fig.39 a–c, table 33.

**Diagnosis.** Conspicuous lip region bearing six inner labial papillae. Six outer labial setae and four cephalic setae situated in single circle at base of lip region; two additional lateral setae sometimes present. Medium to large buccal cavity funnel-shaped. Amphids circular or elliptical. Spicules elongate (≥ 2 cloacal body diameter long), gubernaculum usually tubular and without apophyses (modified from Yu & Xu (2015) and Fonseca & Bezerra (2014a)).

**Remarks.** Gerlach & Riemann (1973) noted that *Paramonhystera* as used by Filipjev (1918; p.279) and several subsequent workers is an invalid emendation. The genus was most recently revised by Yu & Xu (2015), who also provided a key to 14 valid species. This review, however, omitted the species *Paramonohystera brevicaudata* Gagarin & Nguyen ThiThu, 2008. An additional species was later described by Huang & Sun (2019).

**Type species.** *Paramonohystera megacephala* (Steiner, 1916) Wieser, 1956a

### *Paramonohystera leptamphida* sp. nov.

Figs 102–104; Table 30

**Material examined. Holotype** NIWA 139277, NIWA Stn Z18745, 41.093° S, 174.876° E, Pāuatahanui Inlet near Camborne Walkway, upper intertidal, 28 Jul 2016, gravelly sand, male. **Paratypes** NIWA 139278, one male and four females, same data as holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Males.** Body colourless, cylindrical, tapering slightly towards both extremities. Cuticle striated, no lateral differentiation. Eight rows of somatic setae present in pharyngeal region, with anterior-most somatic setae often arranged in pairs or triplets, sparse elsewhere, 8–14 µm long. Cephalic region set-off by slight constriction at level of amphids; well-developed lip region extending bearing six 2 µm long inner labial papillae. Six outer labial setae, 0.60–0.70 cbd long, in same circle as four slightly shorter cephalic setae, 0.45–0.55 cbd long. Eight short, 2–3 µm long sucephalic setae present: two sublateral pairs immediately posterior to the outer labial setae, and one subdorsal and one subventral pair of subcephalic setae at level of amphids. Amphidial fovea large, elliptical or kidney-shaped, with weak outline and almost entirely surrounded by cuticle striations, ca. 0.35–0.55 cbd from anterior extremity. Buccal cavity large, funnel-shaped, with lightly cuticularised walls, 15–25 µm deep, 13–17 µm wide, without teeth. Pharynx muscular, anterior portion surrounding buccal cavity, widening slightly posteriorly. Nerve ring located slightly anterior to middle of pharynx. Secretory-excretory system not observed. Cardia ca. 9 µm long, surrounded by intestinal tissue. Reproductive system with two outstretched testes; anterior testis to the left of intestine and extending almost to level of pharynx, posterior testis to the right of intestine. Sperm cells globular, nucleated, 5–7 × 7–8 µm. Spicules thin, elongated, 5.0–5.3 cloacal body diameters long, with thick but lightly cuticularised walls and slightly swollen proximal ends. Gubernaculum surrounding distal end of spicules and with dorscaudal apophyses tapering distally. A single short precloacal seta present; precloacal supplements and ejaculatory glands not observed. Tail conicocylindrical with rows of subventral setae and sparse sublateral and subdorsal setae; three terminal setae present, 15–17 µm long. Three caudal glands and spinneret present.

**Females.** Similar to males but with generally wider cephalic and body diameter, somatic setae occurring singly and not in pairs or triplets, and tail with sparse subventral setae. Reproductive system with single outstretched ovary to the left of intestine. Anterior extremity of ovary overlaps with posterior portion of pharynx. Spermatheca and post- and prevulval sac not observed; post-vulval gland present. Vulva located at almost two-thirds of body length from anterior. Pars proximalis vaginae surrounded by constrictor muscle.

**Etymology.** The species name *leptamphida* is derived from the Greek term *leptos* (= thin, fine, subtle, delicate), and refers to the weak outline of the amphids in this species.

**Species diagnosis.** *Paramonohystera leptamphida* **sp. nov.** is characterised by body length 1320–1690 µm in males and 1650–1860 µm in females, six inner labial papillae 2 µm long, six outer labial setae slightly longer than the four cephalic setae, eight short subcephalic setae at level of, and anterior to, amphids, eight longitudinal rows of 8–14 µm long somatic setae in pharyngeal region, with somatic setae often arranged in pairs or triplets in males and singly in females, and large (ca. 0.65–0.75 cbd) elliptical or kidney-shaped amphids with weak outline. Males with spicules 5.0–5.3 cloacal body diameters long and gubernaculum with distally tapering dorsocaudal apophyses.

**Differential diagnosis.** The new species can be differentiated from all other species of the genus by the presence of gubernacular apophyses, which are absent in all other species. *Paramonohystera leptamphida* **sp. nov.** resembles *P. geraerti* Chen & Vincx, 2000 (coastal Chile), *P. megacephala* (Arctic Ocean), and *P. sinica* Xu & Wu, 2015 (East China Sea) in having very long (≥ 4.0 cloacal body diameters) spicules but can be differentiated from them by the shape of the amphid (elliptical or kidney shaped in *P. leptamphida* **sp. nov.** versus circular in the other species), and the

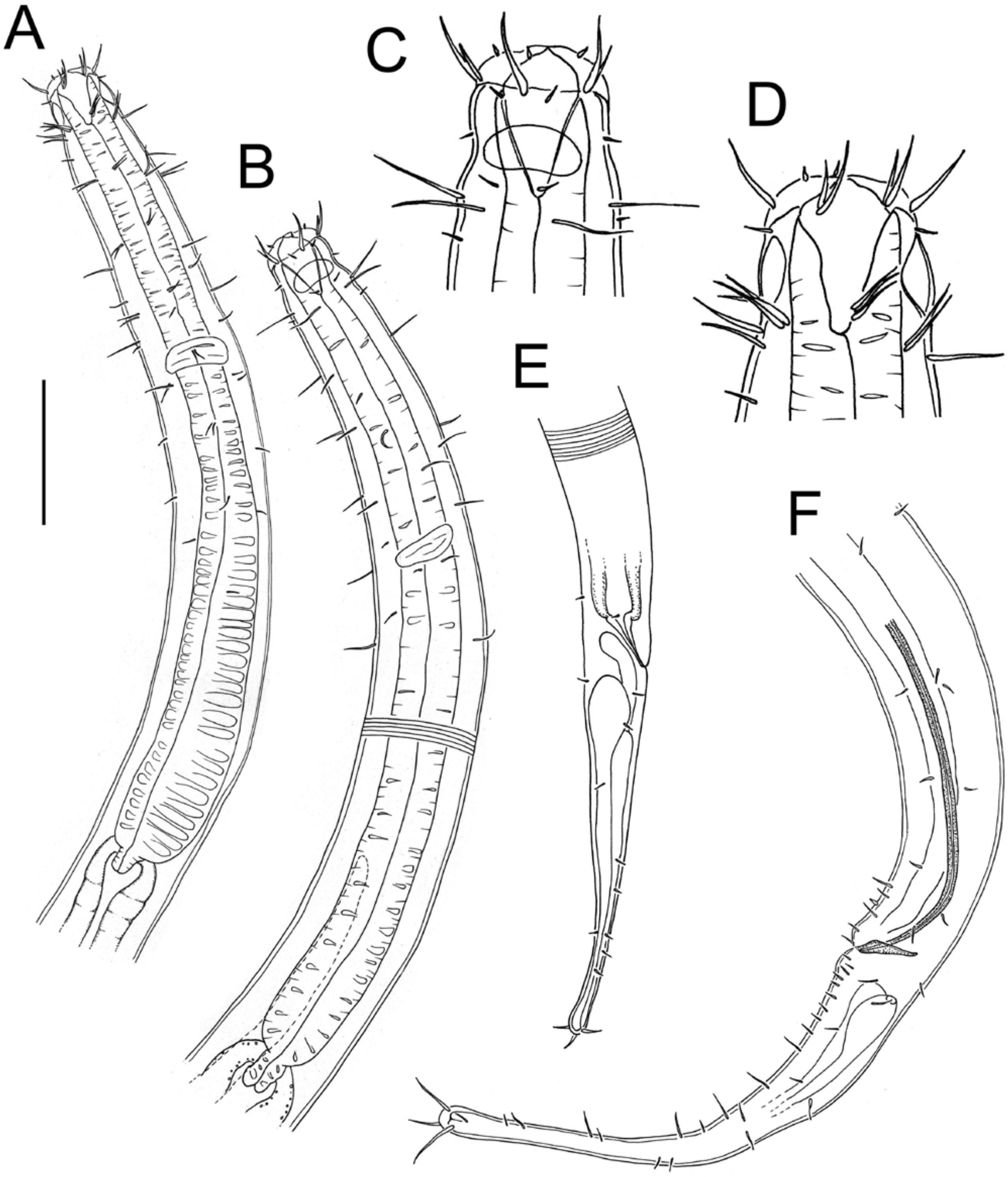



**Figure 102.** *Paramonohystera leptamphida* **sp. nov.**: **A.** Holotype male anterior body region NIWA 139277; **B.** Female paratype anterior body region NIWA 139278; **C.** Female paratype cephalic region NIWA 139278; **D.** Male holotype cephalic region NIWA 139277; **E.** Female paratype posterior body region NIWA 139278; **F.** Male paratype posterior body region NIWA 139277. Scale bar: A = 42 µm; B = 35 µm; C = 28 µm; D = 22 µm; E = 82 µm; F = 40 µm.

arrangement of somatic setae in pairs and triplets in the males (versus somatic setae occurring singly in the other species).

**Sequence data.** Partial SSU rDNA (1543 bp; Genbank OK317213) and D2–D3 of LSU rDNA (708 bp; Genbank OK317234).

**ZooBank registration.** *Paramonohystera leptamphida* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:542D223A-CD35-4F30-8337-4939DD08532C.

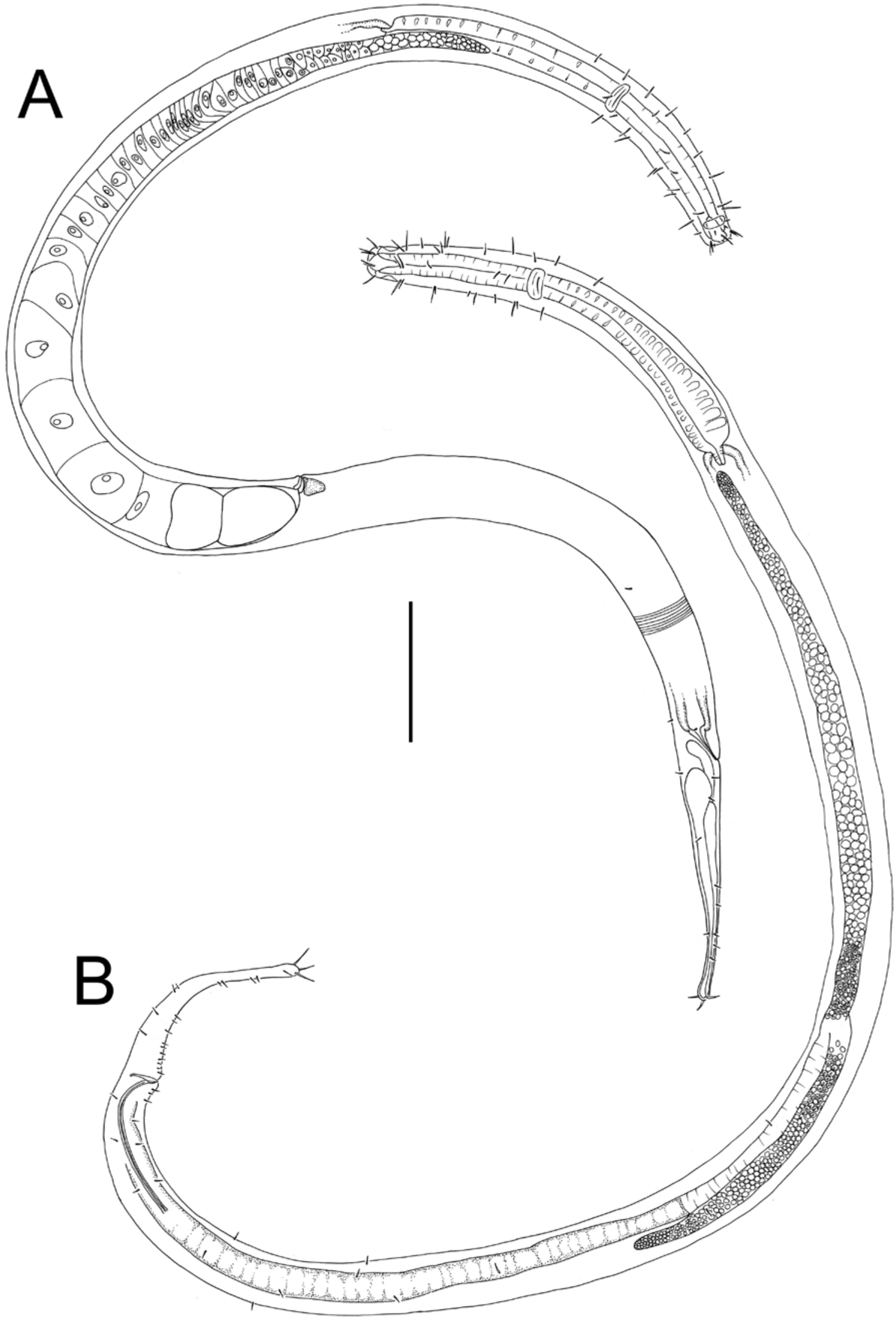



**Figure 103.** *Paramonohystera leptamphida* **sp. nov.**: **A.** Entire female paratype NIWA 139278; **B.** Entire male paratype NIWA 139278. Scale bar: A =125 µm; B = 82 µm.

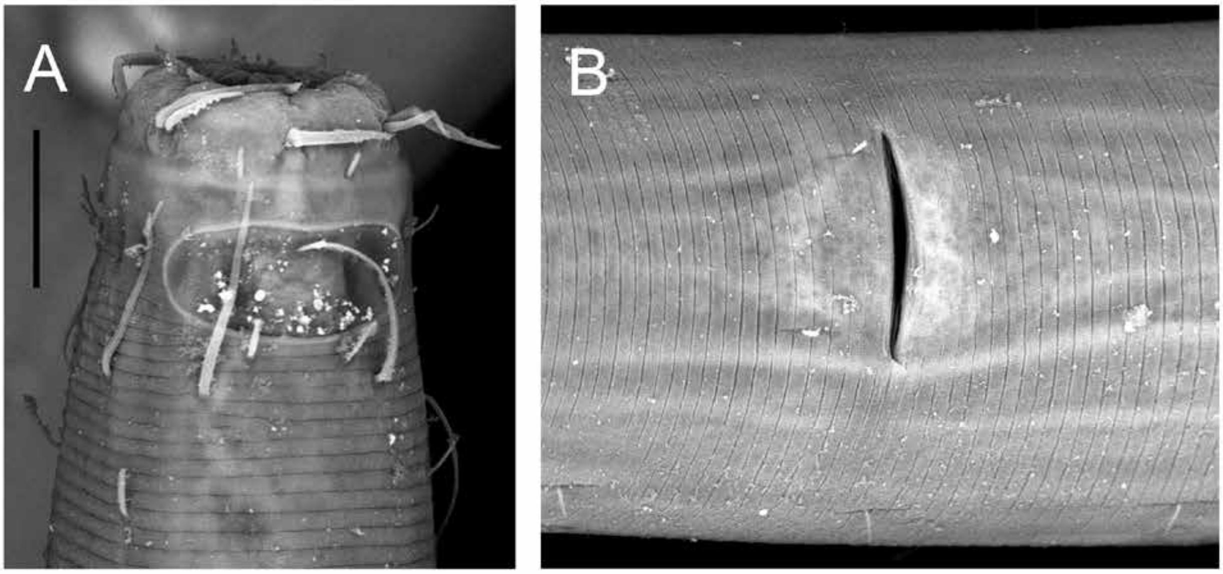



**Figure 104.** *Paramonohystera leptamphida* **sp. nov.**, scanning electron micrographs: **A.** Cephalic region of juvenile; **B.** Vulva. Scale bar: A = 10 µm; B = 12 µm.

**Table 30.** Morphometrics (µm) of *Paramonohystera leptamphida* **sp. nov.**, given as individual values, or a range of values from several specimens.

| Parameter | Males | | Females |
|---|---|---|---|
| | Holotype | Paratype | Paratypes |
| Number of specimens | 1 | 1 | 4 |
| L | 1685 | 1322 | 1653–1864 |
| a | 37 | 31 | 27–35 |
| b | 5 | 6 | 8 |
| c | 11 | 9 | 8–11 |
| c' | 5.9 | 6.3 | 4.7–5.9 |
| Body diameter at cephalic setae | 21 | 20 | 24–26 |
| Body diameter at amphids | 26 | 23 | 26–27 |
| Length of outer labial setae | 12–14 | 13–14 | 13–16 |
| Length of cephalic setae | 9–10 | 11 | 7–10 |
| Amphid height | 11 | 11 | 9–10 |
| Amphid width | 19 | 19 | 18–19 |
| Amphid width/cbd (%) | 73 | 73 | 67–73 |
| Amphid from anterior end | 9 | 13 | 13–16 |
| Nerve ring from anterior end | 118 | 92 | 136–141 |
| Nerve ring cbd | 40 | 40 | 43–47 |
| Pharynx length | 330 | 224 | 336–368 |
| Pharyngeal diameter at base | 34 | 31 | 29–35 |
| Pharynx cbd at base | 44 | 41 | 48–55 |
| Maximum body diameter | 46 | 42 | 50–70 |
| Spicule length | 131 | 123 | – |
| Gubernacular apophysis length | 10 | 8 | – |
| Cloacal/anal body diameter | 26 | 23 | 34–36 |
| Tail length | 154 | 145 | 169–213 |
| V | – | – | 1016–1161 |
| %V | – | – | 61–63 |
| Vulval body diameter | – | – | 50–59 |

## Genus ***Promonhystera*** Wieser, 1956a

*Promonhystera* Wieser, 1956a: 72–74, fig. 229 a–d, fig. 230 a–f.

**Diagnosis.** Cuticle striated. Anterior sensilla in two circles; first circle comprising setiform inner labial sensilla, second circle comprising outer labial setae and cephalic setae, additional lateral setae may be present. Amphids circular. Buccal cavity conical. Spicules short or elongated; gubernaculum without apophyses. Tail conical or conicocylindrical with terminal setae (modified from Fonseca & Bezerra (2014a)).

**Remarks.** *Promonhystera albigensis* Riemann, 1966 was transferred to *Daptonema* by Hopper (1968) but was subsequently returned to *Promonhystera* by Yu & Xu (2015) because of the presence of setose inner labial sensilla. The diagnosis of *Promonhystera* given by Fonseca & Bezerra (2014a) states that the amphid in *Promonhystera* is vesicular; however, the descriptions of all three valid species of the genus by Wieser (1956a) and Riemann (1966) show small to medium-sized amphids with well-defined outline. Additional lateral setae are not included in the diagnosis of Fonseca & Bezerra (2014a), but the illustrations of *P. albigensis* Riemann, 1966 clearly show the presence of additional lateral setae, a feature also found in *P. crinita* **sp. nov.** The genus diagnosis was further modified to accommodate the presence of relatively short spicules in *P. crinita* **sp. nov.**

**Type species.** *Promonhystera faber* Wieser, 1956a

***Promonhystera crinita* sp. nov.**

Figs 105–107; Table 31

**Material examined. Holotype** NIWA 154864, NIWA Stn Z19169, 41.102° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 9 Dec 2019, fine sand, male. **Paratypes** NIWA 154865, two males and four females, same data as for holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Males.** Body cylindrical. Cuticle colourless, striated, without lateral differentiation. Longitudinal rows of somatic setae present; eight rows (two subdorsal, two subventral and four sublateral) in pharyngeal region, and four sublateral rows in middle body region. Somatic setae very long; length of longest somatic seta 3.3–4.0 cbd (76–88 μm), long somatic setae sometimes paired with shorter seta less than 1.0 cbd long. Cephalic region not set-off; lip region bearing six 4–5 μm long inner labial setae. Six outer labial setae, ca. 0.8 cbd long, in same circle as four shorter cephalic setae, 0.4–0.7 cbd long; one or two lateral setae present next to each lateral outer labial seta, 0.4–0.7 cbd long. Sixteen subcephalic setae present: two short subdorsal and two short subventral setae at level of amphids, and a ring of setae slightly posterior to amphids consisting of two long subdorsal and two long subventral setae, and four sublateral pairs of setae, each pair consisting one long seta and one short seta. Amphidial fovea medium-sized, circular, with slightly cuticularised outline and entirely surrounded by cuticle striations, ca. 0.6 cbd from anterior extremity. Buccal cavity relatively spacious, funnel-shaped, with lightly cuticularised walls, 13–17 μm deep, 11 μm wide at widest point, without teeth. Pharynx muscular, anterior portion surrounding buccal cavity, not widening posteriorly. Nerve ring located slightly anterior to middle of pharynx. Secretory-excretory system not observed. Cardia ca. 9–10 μm long. Reproductive system with single outstretched anterior testis to the left of intestine. Sperm cells globular, nucleated, 4–6 × 4–5 μm. Spicules thin, 1.4–1.6 cloacal body diameters long, slightly curved, with slightly swollen proximal ends; velum absent. Gubernaculum short, weakly cuticularised, surrounding distal end of spicules, without apophyses. Precloacal supplements and ejaculatory glands not observed. Tail conicocylindrical with subventral rows of mostly short subventral setae 3–9 μm long and some long setae 20–46 μm long; sparse sublateral and subdorsal setae also present in posterior half of tail. Two long terminal setae 33–47 μm long. Caudal glands not observed.

**Females.** Similar to males but with generally wider body diameter, higher a ratio, lower c ratio, somatic setae occurring singly and not in pairs, longest somatic seta 2.5–2.8 cbd (68–75 μm) long, only one additional seta present next to each lateral outer labial seta, and longer tail. Reproductive system with single outstretched ovary to the left of intestine. Spermatheca present; post- and prevulval sac not observed. Vulva located at almost two-thirds of body length from anterior; pre- and post-vulval glands present. Pars proximalis vaginae surrounded by constrictor muscle.

**Etymology.** The species name is derived from the Latin term *crinitus* (= hairy, long-haired), and refers to the long somatic setae found in this species.

**Species diagnosis.** *Promonhystera crinita* **sp. nov.** is characterised by longest somatic seta 2.5–4.0 cbd (68–88 μm) long, inner labial setae 4–5 μm long, presence of one or two additional lateral setae next to each outer labial seta, sixteen subcephalic setae at same level as, and slightly posterior to, amphids, amphid ca. 0.3 cbd wide, and conicocylindrical tail with two terminal setae; male with single anterior outstretched testis, spicules 1.4–1.6 cloacal body diameters long, simple gubernaculum without distal pointed projections, and female with vulva at 64–70% of body length from anterior, spermatheca present, and pre- and post-vulvar glands present.

**Differential diagnosis.** The new species ressembles the other three known species of the genus in the arrangement and length of the inner labial setae, outer labial setae, and cephalic setae, as well as size and shape of the buccal cavity and amphids, but differs from all other species in having relatively short spicules (26–27 μm or 1.4–1.6 cloacal body diameters *versus* 58–85 μm or 2.0–2.7 cloacal body diameters). *Promonhystera crinita* **sp. nov.** is most similar to *P. albigensis* (North Atlantic) in the presence of additional lateral setae, long somatic setae, and conicocylindrical tail, but differs from the latter in shorter body length (880–1062 *versus* 1480–1620 μm in *P. albigensis*), lower a ratios in males (38–44 *versus* 53 in *P. albigensis*) and females (28–32 *versus* 39–40 in *P. albigensis*), shorter spicules (26–27 μm or 1.4–1.6 cloacal body diameters versus 71 μm or 2.7 cloacal body diameters in *P. albigensis*) and gubernaculum without pointed projections (*versus* distal pointed projections present in *P. albigensis*).

*Promonhystera* is similar to the closely-related genus *Metadesmolaimus* Schuurmans Stekhoven, 1935 in having setose inner labial sensilla. Up to now, the two genera differed by spicule length (elongated or short in

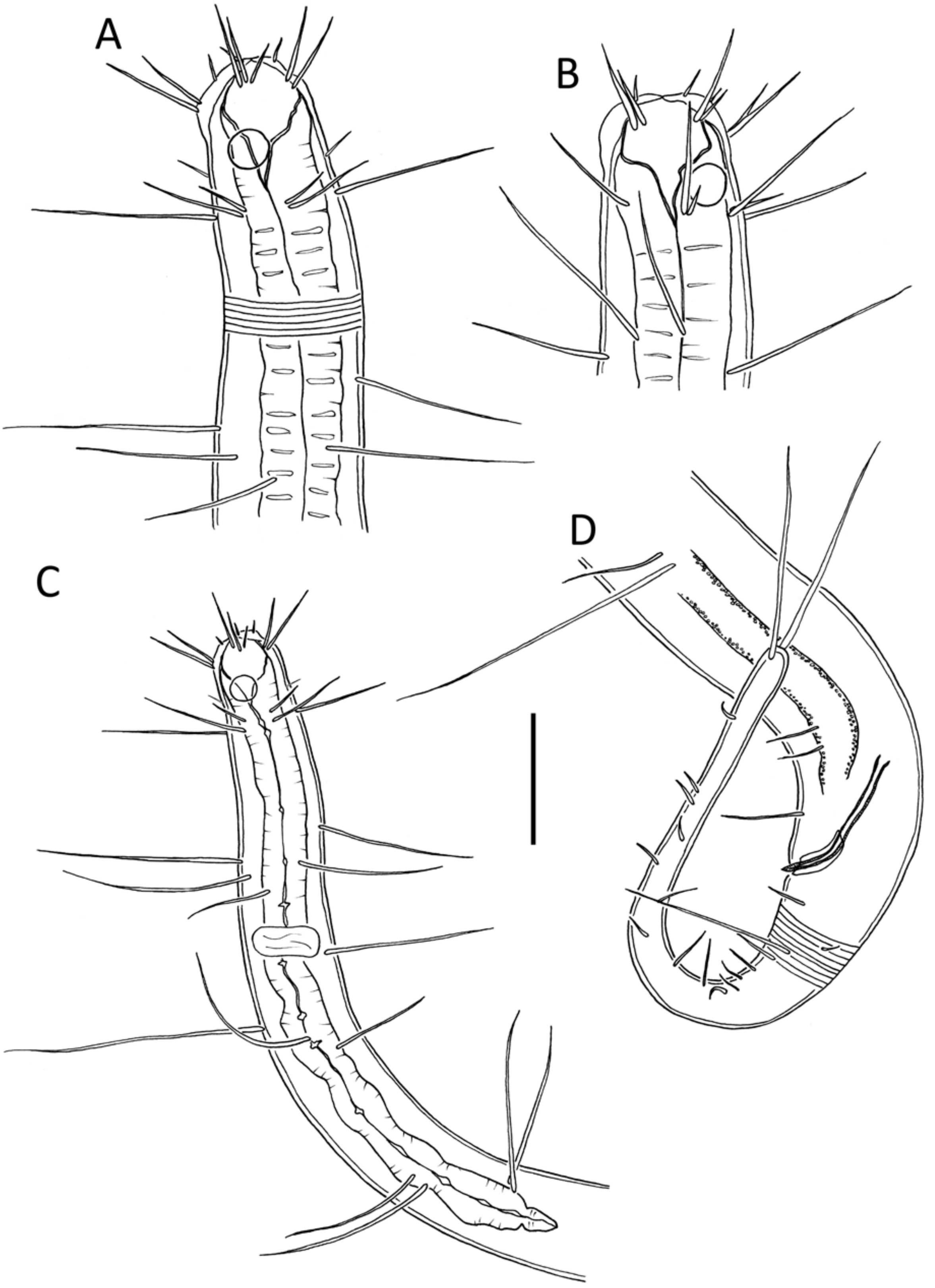



**Figure 105.** *Promonhystera crinita* **sp. nov.**: **A.** Male holotype cephalic region NIWA 154864; **B.** Female paratype cephalic region NIWA 154865; **C.** Male holotype anterior body region NIWA 154864; **D.** Male holotype posterior body region NIWA 154864. Scale bar: A, D = 20 μm; B = 33 μm; C = 22 μm.

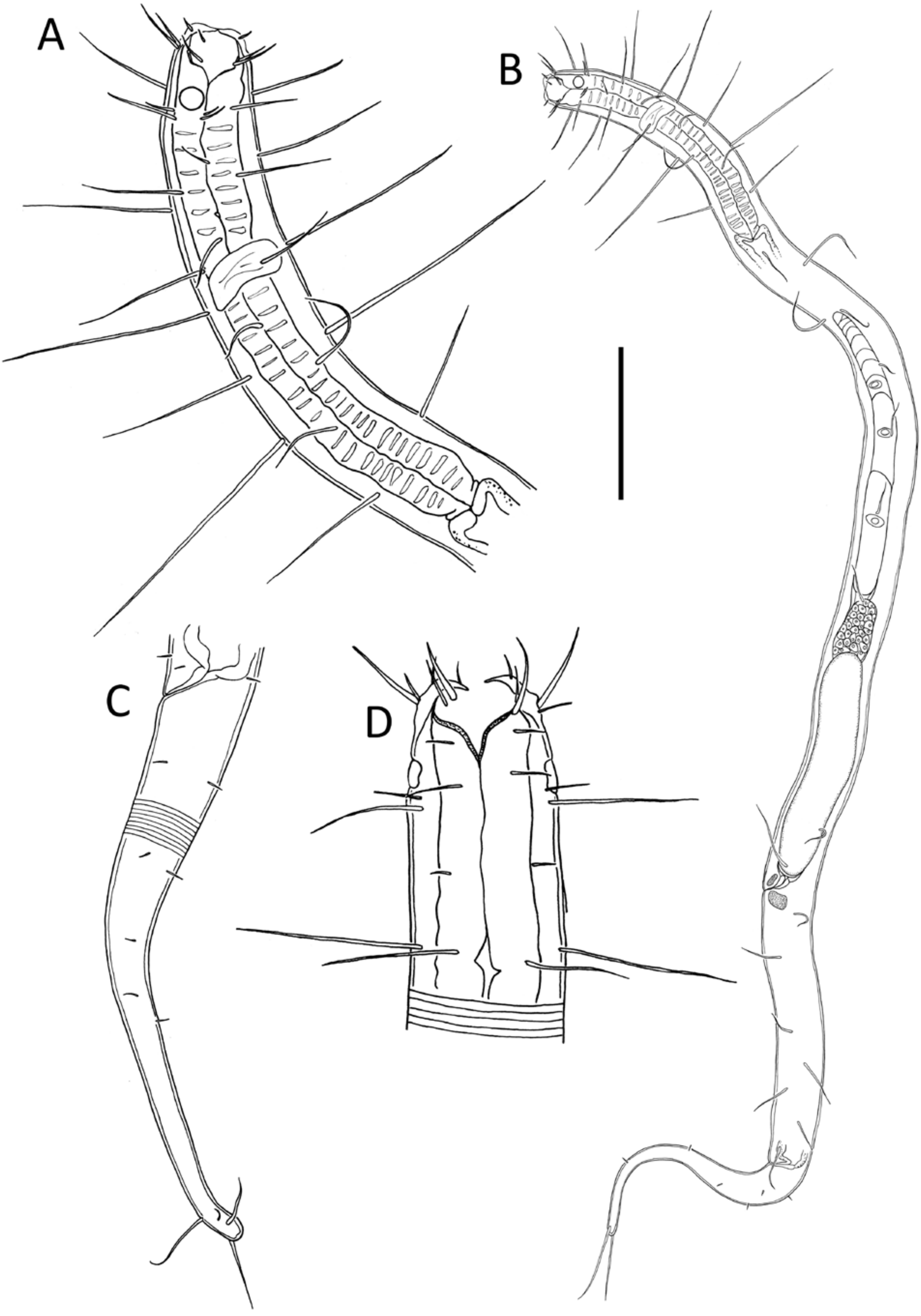



**Figure 106.** *Promonhystera crinita* **sp. nov.**, female paratype NIWA 154865: **A.** Anterior body region; **B.** Entire female; **C.** Posterior body region; **D.** Ventral view of cephalic region. Scale bar: A = 40 μm; B = 85 μm; C = 42 μm; D = 26 μm.

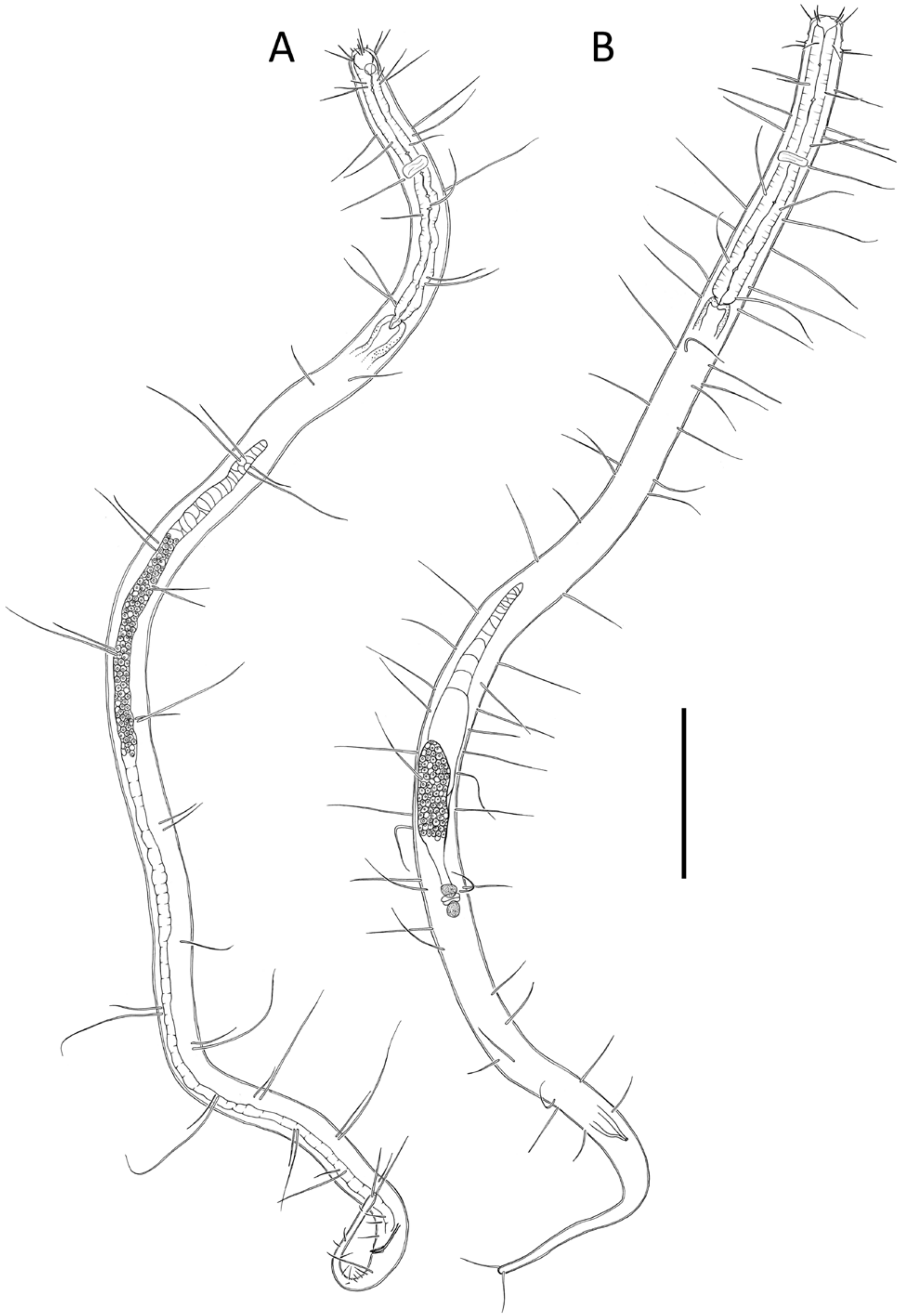



**Figure 107.** *Promonhystera crinita* **sp. nov.**: **A.** Entire male holotype NIWA 154864; **B.** Entire female paratype NIWA 154865. Scale bar = 100 µm.

**Table 31.** Morphometrics (µm) of *Promonhystera crinita* **sp. nov.**, given as individual values, or a range of values from several specimens.

| Parameter | Males | | Females |
|---|---|---|---|
| | Holotype | Paratypes | Paratypes |
| Number of specimens | 1 | 2 | 4 |
| L | 949 | 993, 1062 | 880–1010 |
| a | 38 | 41, 44 | 28–32 |
| b | 6 | 6 | 5–6 |
| c | 10 | 11, 14 | 6–7 |
| c' | 5.8 | 3.9, 5.9 | 6.0–6.5 |
| Body diameter at cephalic setae | 17 | 17, 18 | 18–20 |
| Body diameter at amphids | 18 | 18 | 22–25 |
| Length of outer labial setae | 14 | 15–16 | 14–16 |
| Length of cephalic setae | 7 | 10–12 | 9–13 |
| Amphid height | 6 | 6 | 6 |
| Amphid width | 6 | 6 | 6 |
| Amphid width/cbd (%) | 33 | 33, 35 | 24–27 |
| Amphid from anterior end | 10 | 9, 13 | 13–18 |
| Nerve ring from anterior end | 89 | 78, 80 | 86–92 |
| Nerve ring cbd | 22 | 22, 23 | 27 |
| Pharynx length | 166 | 154, 177 | 145–198 |
| Pharyngeal diameter at base | 12 | 14 | 17–18 |
| Pharynx cbd at base | 23 | 23, 24 | 26–28 |
| Maximum body diameter | 25 | 24 | 30–32 |
| Spicule length | 27 | 26 | – |
| Gubernaculum length | 8 | 9 | – |
| Cloacal/anal body diameter | 17 | 16, 18 | 22–27 |
| Tail length | 98 | 71, 94 | 143–151 |
| V | – | – | 584–694 |
| %V | – | – | 64–70 |
| Vulval body diameter | – | – | 29–31 |

*Metadesmolaimus*, always elongated in *Promonhystera*), but this distinction no longer exists following the inclusion of *P. crinita* within *Promonhystera*. We also note that the diagnosis of *Metadesmolaimus* given by Fonseca & Bezerra (2014a) states that terminal setae are absent in *Metadesmolaimus*; however, several species such as *M. gelana* Warwick & Platt, 1973, *M. psammophilus* Tchesunov, 1990 and *M. zhangi* Guo, Chen & Liu, 2016 have terminal setae. Nevertheless, the two genera still differ in some key morphological traits, i.e., cuticle colouration (brownish in *Metadesmolaimus*, colourless in *Promonhystera*), structure of the outer labial setae (jointed in *Metadesmolaimus*, simple in *Promonhystera*), and structure of the buccal cavity (extended, divided into two parts by a cuticularised ring in *Metadesmolaimus*, simple and without a ring in *Promonhystera*).

*Promonhystera* is also very similar to *Daptonema*, with *P. crinita* **sp. nov.** showing particularly strong resemblance to *Daptonema* species with long (> 2 cbd) somatic setae, i.e., *D. floridanum* (Wieser & Hopper, 1967) Aryuthaka & Kito, 2018, *D. galeatum* (Wieser & Hopper, 1967) Aryuthaka & Kito, 2018, *D. invagiferoum* (Platt, 1973) Lorenzen, 1977, *D. mirabilis* (Schuurmans Stekhoven & De Coninck, 1933) Tchesunov, 1990, *D. stylosum* (Lorenzen, 1973) Lorenzen, 1977 and *D. voskresenkii* Tchesunov, 1990 (see Table 4 in Aryuthaka & Kito 2018). *Promonhystera*, however, differs from *Daptonema* in having setose inner labial sensilla (papillose in *Daptonema*).

**Sequence data.** Partial SSU rDNA (862 bp; Genbank OK317214) and D2–D3 of LSU rDNA (755 bp; Genbank OK317235).

**ZooBank registration.** *Promonhystera crinita* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:50466A6D-7248-4D8C-BD12-2AD25D5468DD.

## Genus *Steineria* Micoletzky 1922

*Steineria* Micoletzky 1922: 168.

**Diagnosis.** Cuticle usually striated, rarely punctated. Anterior sensilla in two circles as seen with light microscopy; anterior circle papilliform, posterior setiform comprising outer labial setae, cephalic setae, additional setae (may be obscured or absent) and subcephalic setae. Subcephaic setae at same level or immediately posterior and adjacent to cephalic and outer labial setae and arranged in eight-radiate symmetry; number and length variable. Groups of long cervical setae also present anteriorly to, at same level as, or slightly posterior to, the amphids. Amphids circular with lightly cuticularised outline. Buccal cavity conical, cuticular ring sometimes present in anterior portion. Somatic setae present or absent, may be long or short. Spicules simple, short, either slightly bent, arcuate, or L-shaped; gubernacular apophyses present or absent. Tail conic-cylindrical with two or three terminal setae (modified from Fonseca & Bezerra (2014a)).

**Remarks.** Our SEM observations show that pairs of additional setae are present at the same level as the outer labial and cephalic setae in *Steineria preclara* **sp. nov.** These additional setae, which are located subdorsally and subventrally, are differentiated from the outer labial and cephalic setae by their relatively short length. In addition, our SEM observations show that the subcephalic setae are located slightly posterior to the circle of outer labial and cephalic setae in *Steineria preclara* **sp. nov.** This is also clearly the case in other species, such as *S. sinica* Huang & Wu, 2011. In addition, several species, i.e., *S. punctata* Gerlach, 1955, *S. aquatica* Alekseev & Belogurov, 1973 and *S. marsiana* Alekseev & Belogurov, 1973, have a punctated cuticle. The diagnosis of the genus, which previously did not include the presence of additional setae, the slight posterior position of the subcephalic setae (in some species), and the punctated cuticle (in some species), is therefore amended here.

A key to the species of *Steineria* was provided by Wieser (1956a). Gerlach & Riemann (1973/1974) later provided a list of 21 valid *Steineria* species. An additional six species were later described by Alekseev & Belogurov (1973), Ott (1977), Fadeeva (1991), Huang & Wu (2011), and Gagarin (2013). Two species, *S. pavo* Gerlach, 1957 and *S. pulchra* Mawson, 1957, were transferred to the genus *Peudosteineria* Wieser, 1956a by Fadeeva (1986). We also recommend moving *Steineria marcorum* Gerlach, 1956 to *Pseudosteineria* because of the position of the subcephalic setae at same level as the amphids. The genus *Steineria* currently comprises 24 valid species.

**Type species.** *Steineria polychaeta* (Steiner, 1915) Micoletzky, 1922

### *Steineria preclara* sp. nov.

Figs 108–111; Table 32

**Material examined. Holotype** NIWA 139296, NIWA Stn Z19168, 41.098° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 22 Feb 2019, fine sand, male. **Paratypes** NIWA 139297, four males and three females, same data as holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Males.** Body colourless, cylindrical, tapering slightly towards both extremities. Cuticle striated, no lateral differentiation. Eight rows of somatic setae present from posterior to amphids to tail region, consisting of short (3–10 μm) and long (14–26 μm) setae. Cephalic region slightly rounded, with slight constriction between amphids and cephalic sensilla; six short and thin lips. Six inner labial papillae, slightly posterior to lips. Six outer labial setae, 11–14 μm long, in same circle as four slightly shorter cephalic setae, 9–13 μm long; four pairs of additional setae located sublaterally and at same level as outer labial and cephalic setae, 7–9 μm long. Eight groups of subcephalic setae located in single circle immediately posterior to circle of outer labial, cephalic and additional setae; each group consists of three setae with longest setae 46–56 μm long, shortest setae 18–37 μm long and one seta of intermediate length. Two sublateral pairs of cervical setae located slightly anterior to each amphid and posterior to subcephalic setae, each pair consisting of one long seta 42–47 μm long and one shorter seta 21–26 μm long. Amphidial fovea circular, with slightly cuticlarised outline, located 0.8–0.9 cbd from anterior extremity. Buccal cavity narrow, funnel-shaped, with cuticularised ring anteriorly, without teeth. Pharynx muscular, cylindrical, without posterior bulb. Nerve ring located 34–44% of pharynx length from anterior. Pore of secretory-excretory system located at about middle of pharynx; ventral gland located slightly posterior to pharynx, sometimes indistinct. Cardia 10–12 μm long, surrounded by intestinal tissue. Reproductive system with two opposed and reflexed testes; anterior testis to the right of intestine, posterior testis to the left of intestine. Sperm cells globular, ca. 9 × 8 μm. Spicules strongly cuticularised, slightly bent, with weak capitulum, 0.9–1.1 cloacal body diameters long. Gubernaculum surrounding distal end of spicules and with bent dorsocaudal apophyses. Cloaca flanked by two rows of 10–11 subventral setae, 7–21 μm long. Precloacal seta and supplements not observed; 5–6 pairs of ejaculatory glands present. Tail conicocylindrical with rows of subventral setae and sparse subdorsal setae; two terminal setae present, 38–53 μm long. Three caudal glands present.

**Females.** Similar to males except ventral gland located at level of pharynx at least in one specimen (indistinct in other specimens). Reproductive system with single reflexed ovary to the right of intestine. Spermatheca present, without sperm in the sepcimens observed; post- and prevulval sacs not observed. Vulva located at almost two-thirds of body length from anterior; two large vulval glands present. Pars proximalis vaginae surrounded by constrictor muscle.

**Etymology.** The species name *preclara* is derived from the Latin term *preclarus* (= very beautiful, splendid), and refers to the long cephalic, subcephalic and cervical setae that characterise this species.

**Species diagnosis.** *Steineria preclara* **sp. nov.** is characterised by presence of four sublateral pairs of short additional setae at level of outer labial and cephalic setae, eight groups of subcephalic setae immediately posterior to circle of outer labial, cephalic and additional setae, with each group consisting of one long, one short, and one intermediate length seta, two sublateral pairs of cervical setae anterior to each amphid, eight longitudinal rows of long and short somatic setae, buccal cavity with cutilarised ring anteriorly, amphid

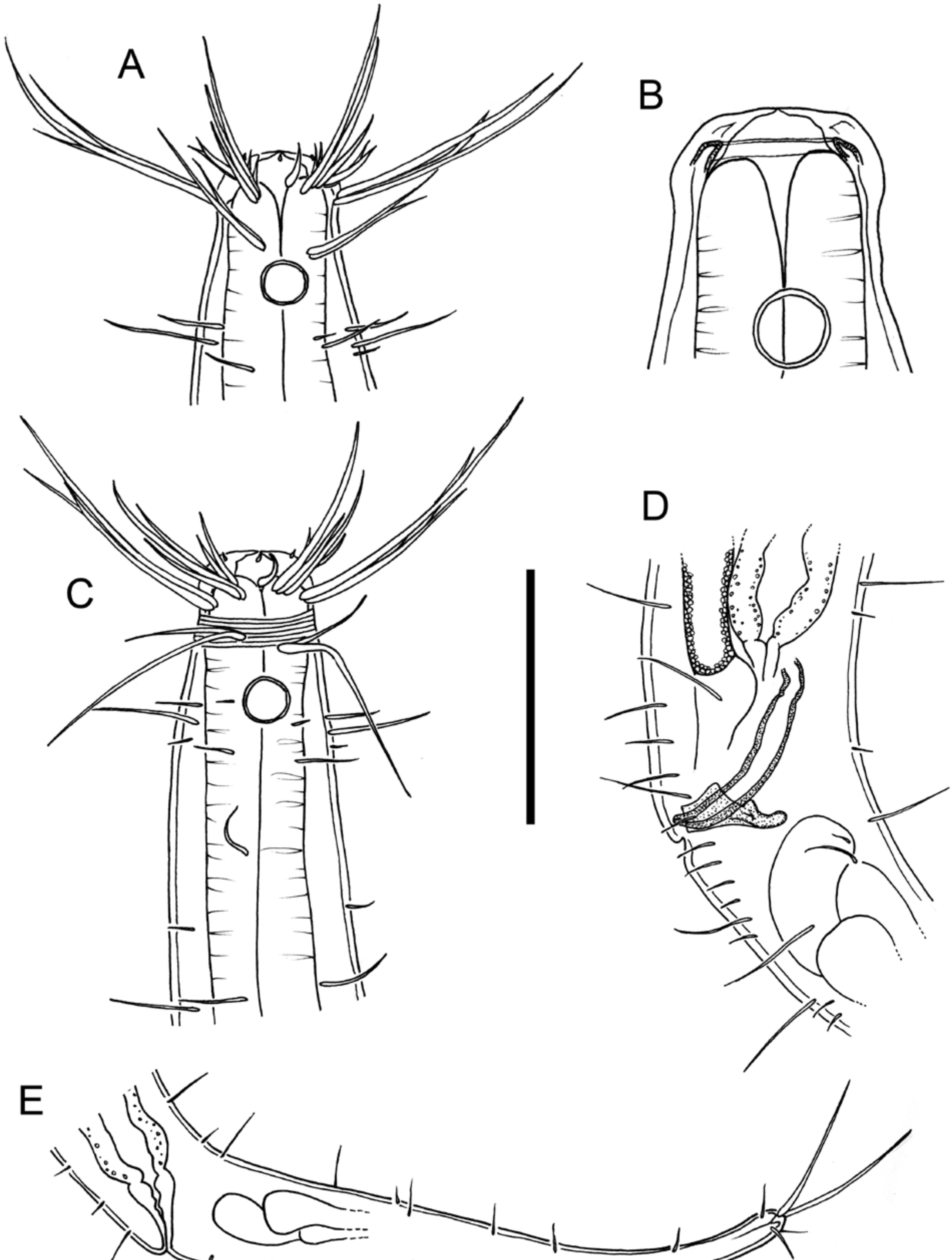



**Figure 108.** *Steineria preclara* **sp. nov.**: **A.** Cephalic region of female paratype showing arrangement of anterior sensilla NIWA 139297; **B.** Cephalic region of female paratype showing buccal cavity NIWA 139297; **C.** Anterior body region of male holotype NIWA 139296; **D.** Male holotype copulatory apparatus NIWA 139296; **E.** Female paratype posterior body region NIWA 139297. Scale bar: A, C = 50 µm; B = 28 µm; D = 48 µm; E = 70 µm.

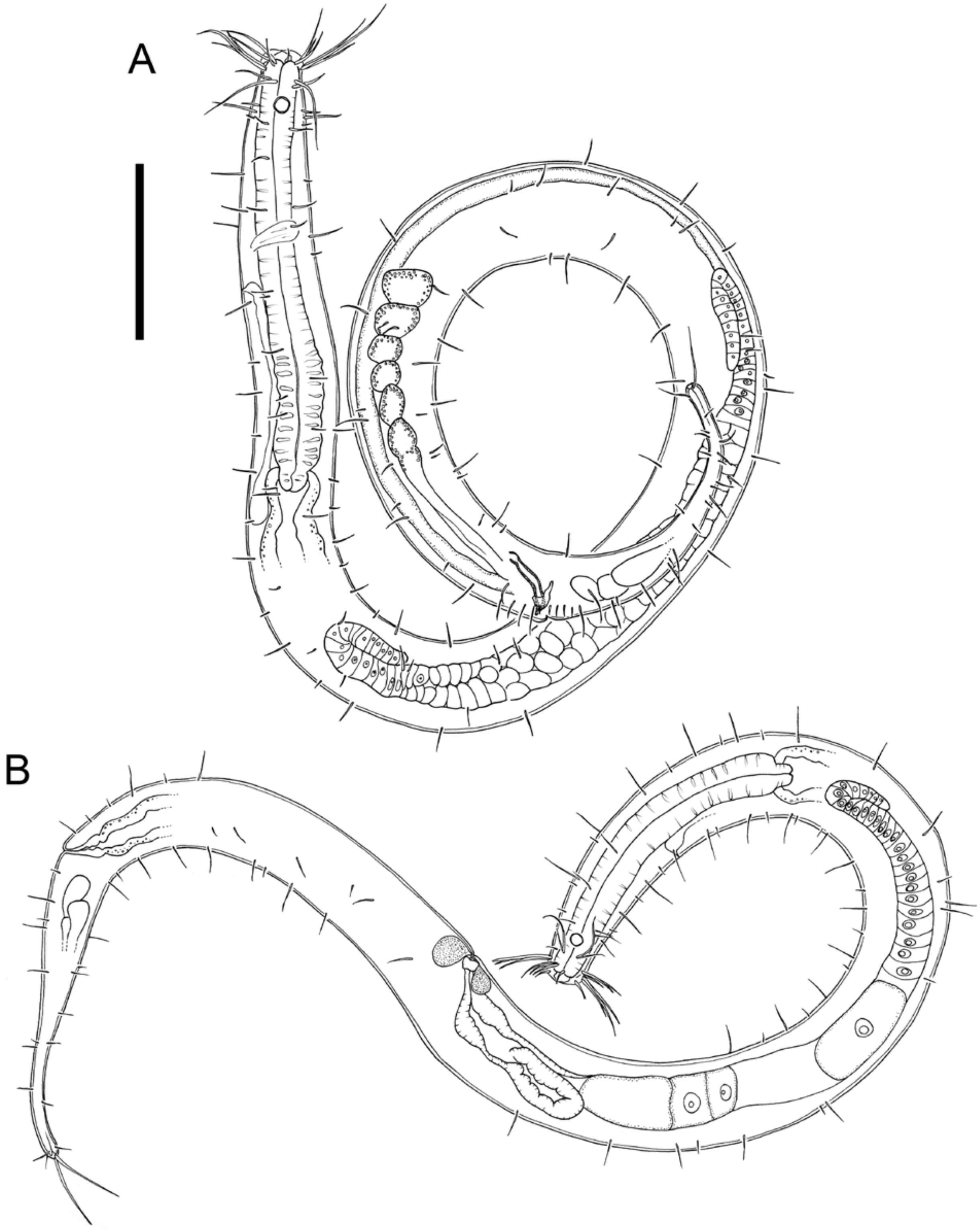



**Figure 109.** *Steineria preclara* **sp. nov.**: **A.** Entire male holotype NIWA 139296; **B.** Entire female paratype NIWA 139297. Scale bar = 100 µm.

located 0.8–0.9 cbd from anterior extremity, male and female reproductive systems with reflexed genital branches, males with slightly bent spicules 0.9–1.1 cloacal body diameters long and bent dorso-caudal apophyses, and females with vulva at almost two-thirds of body length from anterior.

**Differential diagnosis.** The new species is most similar to *S. chiliensis* Murphy, 1966 (coastal Chile),

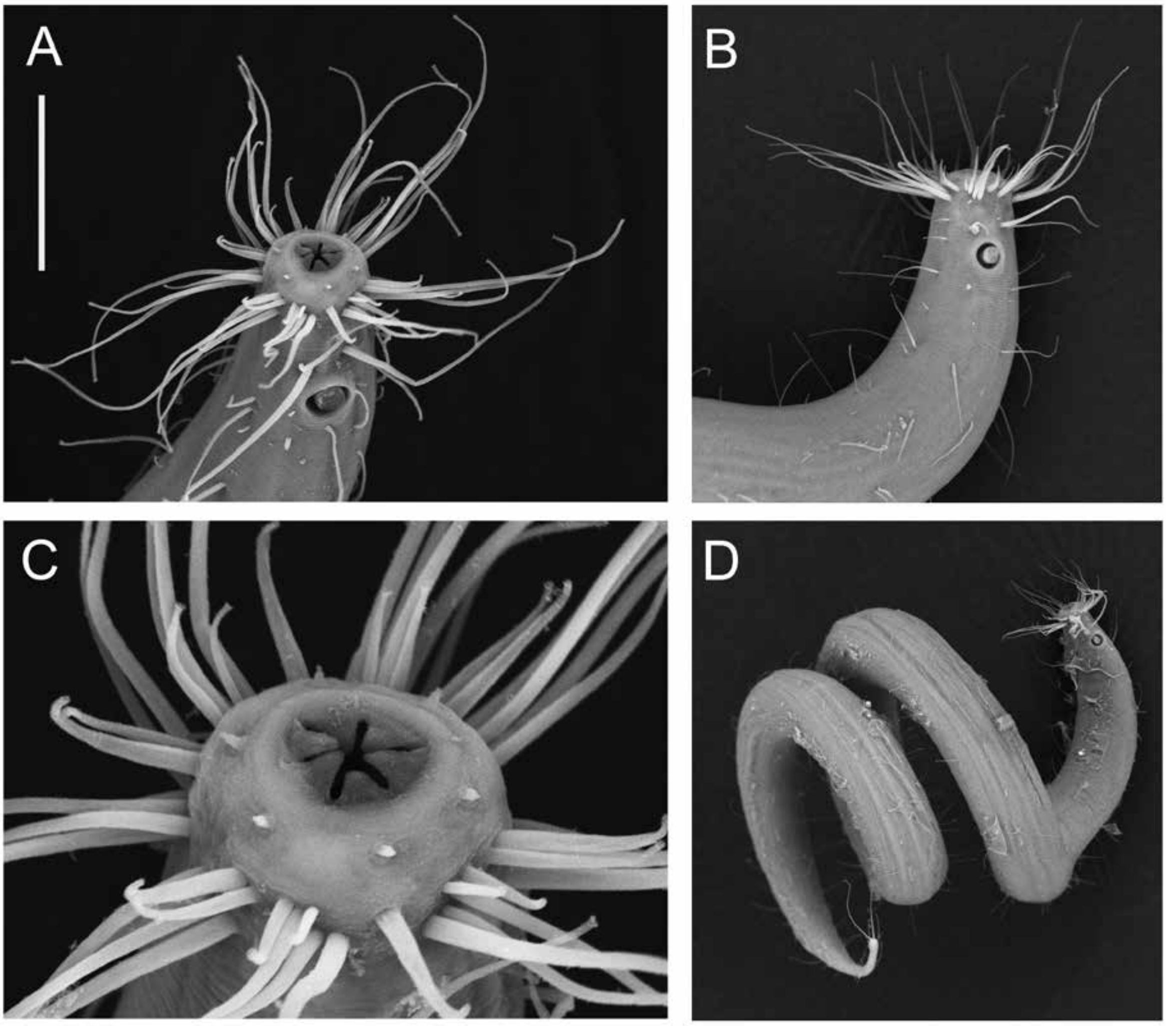



**Figure 110.** *Steineria preclara* **sp. nov.** Scanning electron micrographs: **A–B.** Anterior body region of female; **C.** Cephalic region of female; **D**. Entire juvenile. Scale bar: A = 25 µm; B = 38 µm; C = 8 µm; D = 80 µm.

*S. polychaeta* (Steiner, 1915 Micoletzky, 1922 (coastal Indonesia), *S. sinica* Huang & Wu, 2011 (Yellow Sea) and *S. sterreri* Ott, 1977 (West Atlantic) in body dimensions and arrangement of anterior sensilla. *Steineria preclara* **sp. nov.** can be distinguished from *S. chiliensis* by the position of the cervical setae (anterior to amphids in *S. preclara* **sp. nov.** *versus* slightly posterior to amphids in *S. chiliensis*) and shape of the gubernacular apophyses (long and curved *versus* short and straight in *S. chiliensis*); from *S. polychaeta* by the shape of the copulatory apparatus (slightly bent spicules and well-cuticularised gubernacular apohyses *versus* L-shaped spicules and thin gubernacular apphyses in *S. polychaeta*), longer body (males: 1080–1260 *versus* 742 µm in *S. polychaeta*), and number of additional setae (eight versus four in *S. polychaeta*); from *S. sinica* by the number of cervical setae (four groups of two cervical setae *versus* eight groups of two cervical setae in *S. sinica*), presence of additional setae (absent in *S. sinica*) and number of terminal setae (two *versus* three in *S. sinica*); from *S. sterreri* by the length of the cervical setae (up to 47 µm versus 20 µm or less in *S. sterreri*), length of longest subcephalic setae (46–6 *versus* 85–95 µm in *S. sterreri*), and smaller amphid diameter (8–9 *versus* 12 µm diameter).

**Remarks.** Additional setae have been observed in a number of Xyalidae species, but they have not been mentioned in previous descriptions of *Steineria* species. Some illustrations show the presence of distinctively shorter "subcephalic setae" located sublaterally which we interpret as additional setae similar to the ones observed in *S. preclara* **sp. nov.** Based on drawings, additional setae appear to be present in a number of *Steineria* species, namely *S. gerlachi* Wieser, 1959, *S. chiliensis*, *S. ericia* Gerlach, 1956, *S. polychaetoides* Gerlach, 1951, *S. sterreri*, and *S. polychaeta*. Because there are numerous setae in the cephalic region of *Steineria*, the presence of additional setae is best ascertained using either SEM (*S. preclara* **sp. nov.**, present description) or en face light microscopy observations (*S. chiliensis*, Murphy 1966).

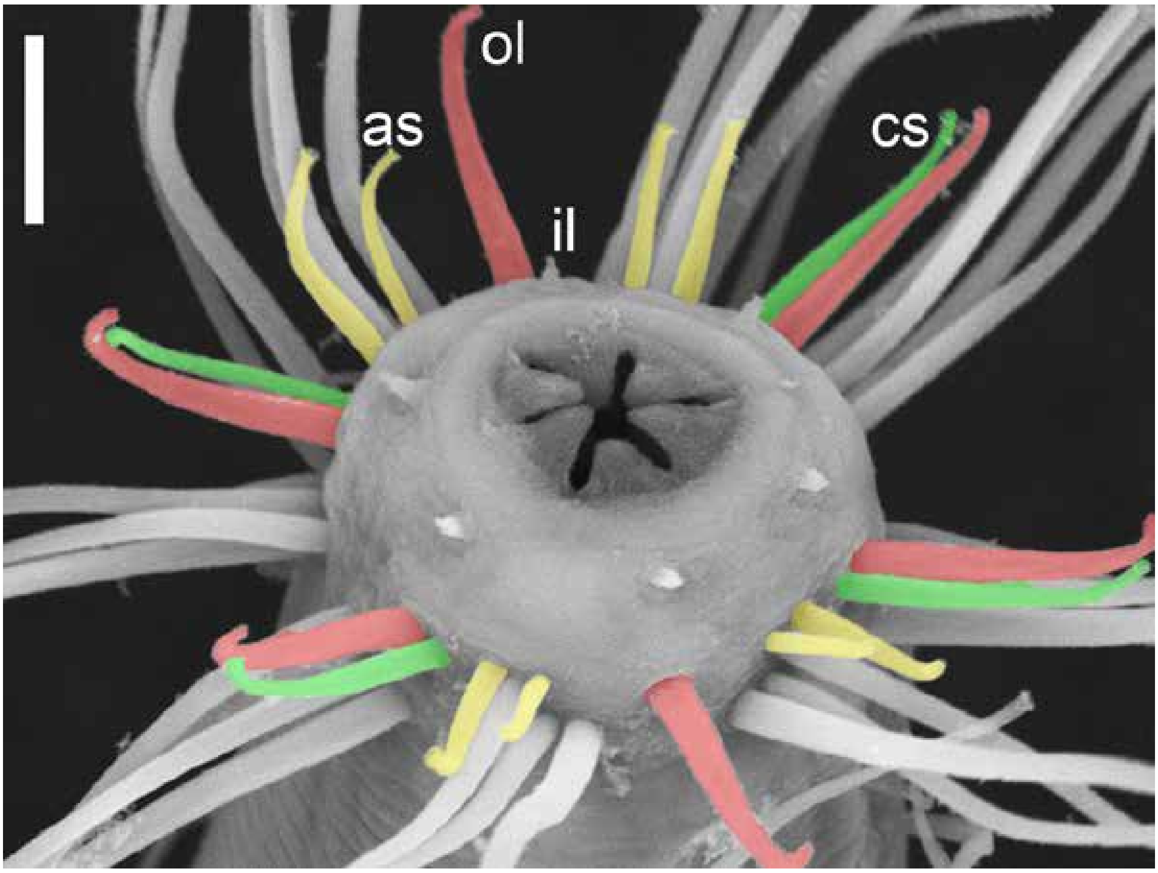



**Figure 111.** *Steineria preclara* **sp. nov.**, scanning electron micrograph of female cephalic region, showing arrangement of cephalic sensilla. as = additional setae (yellow); cs = cephalic setae (green); il = inner labial papillae; ol = outer labial setae (red). Scale bar = 5 µm.

The presence of reflexed genital branches in both males and females of *S. preclara* **sp. nov.** is unusual for the genus and indeed the order Monhysterida. Drawings of *Steineria pontica* Groza-Rojancovski, 1972, however, show a reflexed anterior ovary in this species, but it is not clear if the posterior ovary is also reflexed. We were not able to find any evidence of reflexed testes in other species of the genus, although many species descriptions do not give information on the structure of the male genital branches.

**Sequence data.** Partial SSU rDNA (519 bp; Genbank OK317215).

**ZooBank registration.** *Steineria preclara* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:B30E5271-CD82-4FAC-A56D-1616CC3E8CFB.

## Genus ***Theristus*** Bastian, 1865

*Theristus* Bastian, 1865: 156–157, plate 13, figs 187–191.
*Penzancia* de Man, 1889: 7–8.
*Theristus* (*Penzancia*) de Man, 1889: 7–8.

**Diagnosis.** Cuticle striated. Somatic setae usually present. Anterior sensilla in two circles; inner labial papilliform or setiform and outer labial and cephalic setae setiform. Additional setae sometime present in lateral fields at level of outer labial setae. Ocelli occasionally present. Buccal cavity funnel-shaped. One or two testes. Spicules usually curved, sometimes very long but primarily as long as the cloacal body diameter. Gubernaculum with or without dorsal apophyses. Tail conical, without terminal setae (after Fonseca & Bezerra (2014a)).

**Remarks.** A list of 92 valid *Theristus* species was provided by Venekey *et al.* (2014). Additional *Theristus* species were later described by Nguyen Dinh Tu & Gagarin (2017) and Revkova (2020b).

**Type species.** *Theristus acer* Bastian, 1865

### ***Theristus arcuatospiculus*** **sp. nov.**

Figs 112, 113; Table 33

**Material examined. Holotype** NIWA 154877, NIWA Stn Z19170, 41.102° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 27 Jul 2020, fine sand, male.

**Table 32.** Morphometrics (μm) of *Steineria preclara* **sp. nov.**, given as individual values, or a range of values from several specimens.

| Parameter | Males | | Females |
|---|---|---|---|
| | Holotype | Paratypes | Paratypes |
| Number of specimens | 1 | 4 | 3 |
| L | 1260 | 1084–1210 | 1155–1294 |
| a | 26 | 22–24 | 21–23 |
| b | 6 | 5–6 | 6 |
| c | 7 | 7 | 6–7 |
| c' | 4.5 | 4.3–4.4 | 4.5–5.5 |
| Body diameter at cephalic setae | 20 | 20–21 | 20–22 |
| Body diameter at amphids | 29 | 25–28 | 27–31 |
| Length of outer labial setae | 13 | 11–14 | 13–14 |
| Length of cephalic setae | 10–11 | 9–13 | 9–12 |
| Length of additional setae | 8 | 7–9 | 9 |
| Length of longest subcephalic setae | 48–57 | 46–57 | 51–60 |
| Length of shortest subcephalic setae | 18–37 | 20–35 | 32–35 |
| Length of longest cervical setae | 45–47 | 40–46 | 45–47 |
| Length of shortest cervical setae | 21–22 | 21–26 | 19–25 |
| Amphid height | 9 | 8–9 | 8 |
| Amphid width | 8 | 8 | 8 |
| Amphid width/cbd (%) | 28 | 29–32 | 26–30 |
| Amphid from anterior end | 25 | 17–24 | 19–27 |
| Nerve ring from anterior end | 98 | 67–87 | 69–91 |
| Nerve ring cbd | 40 | 37–40 | 39–44 |
| Excretory pore from anterior end | 126 | 107–124 | 108–126 |
| Pharynx length | 224 | 198–214 | 183–224 |
| Pharyngeal diameter at base | 28 | 24–27 | 29–31 |
| Pharynx cbd at base | 48 | 42–47 | 49–54 |
| Maximum body diameter | 49 | 46–52 | 53–59 |
| Spicule length | 40 | 36–42 | – |
| Gubernacular apophysis length | 8 | 9–11 | – |
| Cloacal/anal body diameter | 38 | 35–39 | 33–37 |
| Tail length | 172 | 164–169 | 167–184 |
| V | – | – | 697–815 |
| %V | – | – | 60–63 |
| Vulval body diameter | – | – | 53–59 |

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Male.** Body colourless, cylindrical, tapering slightly towards both extremities. Cuticle striated, no lateral differentiation. Four sublateral longitudinal rows of somatic setae present in pharyngeal region and slightly posterior to pharyngeal region, 3–4 μm long, not visible in middle body region. Cephalic region rounded, with swollen and well-developed lips bearing six inner labial papillae. Six outer labial setae 0.6 cbd long, in same circle as four slightly shorter cephalic setae, 0.4 cbd long. No additional setae present. Amphidial fovea large, circular, with lightly cuticularised outline, surrounded by cuticle striations, ca. 1.0 cbd from anterior extremity. Buccal cavity 7 μm wide, 4 μm deep, funnel-shaped, with lightly cuticularised walls, without teeth. Ducts of pharyngeal glands not observed. Pharynx muscular, anterior portion slightly surrounding base of buccal cavity, not widening posteriorly and without posterior bulb. Nerve ring located near middle of pharynx. Secretory-excretory system not observed. Cardia 5 μm long, partially surrounded by intestinal tissue. Reproductive system with two outstretched testes; anterior testis located to the left of intestine; posterior testis located to the right of intestine. Sperm cells globular, ca. 5 × 6 μm. Spicules paired, symmetrical, arcuate, 2.4 cloacal body diameters long, gradually tapering distally and terminating into slight hook, strongly cuticularised. Gubernaculum surrounding spicules distally and with large, thickly cuticularised dorso-caudal apophyses ca. one-third of spicule length. Ejacualatory glands and precloacal supplements not observed. Tail conical, with sparse, short setae; caudal glands not observed.

**Etymology.** The species name is derived from the Latin *arcuatus* (= bent like a bow) and refers to the shape of the spicules.

**Species diagnosis.** *Theristus arcuatospiculus* **sp. nov.** is characterised by swollen and well-developed lip region, 3–4 μm long somatic setae arranged in four sublateral rows, papillose inner labial sensilla, outer labial setae 6 μm long, cephalic setae 4 μm long, large amphidial fovea 0.8 cbd wide, male reproductive system with two testes, long arcuate spicules 2.4 cloacal body diameters long, gubernaculum with conspicuous dorso-caudal apophyses ca. one-third of spicule length, and conical tail 6.5 cloacal body diameters long.

**Differential diagnosis.** The new species belongs to the '*Theristus acer-pertenuis*' group of species characterised by symmetrical spicules and conspicuous dorsocaudal gubernacular apophyses (Jensen 1986). This group comprises the following species: *T. acer* Bastian, 1865, *T. copulatus* Jensen, 1986, *T. gracilis* (de Man, 1876) Filipjev, 1918, *T. longisetosus* Schuurmans Stekhoven & De Coninck, 1933, *T. manicatus* Wieser, 1956a, *T. modicus* Wieser, 1956a, *T. pertenuis* Schuurmans Stekhoven, 1935, *T. pictus* Gerlach, 1951, *T. subacer* Pavlijuk, 1984, and *T. subcurvatus* Lorenzen, 1977. *Theristus arcuatospiculus* **sp. nov.** differs from most of these species except *T. manicatus* (coastal Chile) and *T. subcurvatus* (North Atlantic) in having markedly larger amphidial fovea (0.8 cbd *versus* ≤ 0.6 cbd). The

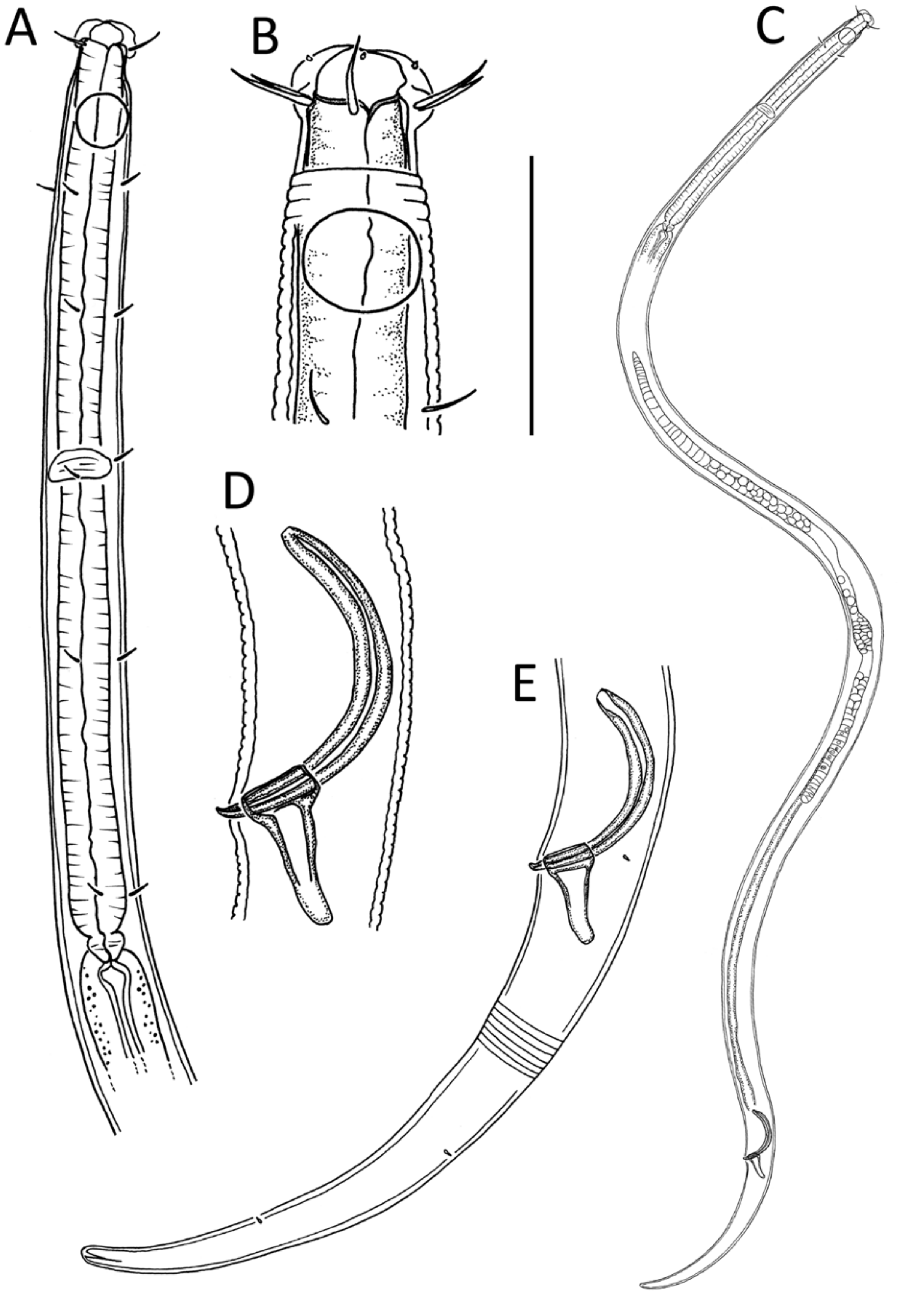



**Figure 112.** *Theristus arcuatospiculus* **sp. nov.**, male holotype NIWA 154877: **A.** Pharyngeal region; **B.** Cephalic region; **C.** Entire male; **D.** Copulatory apparatus; E. Posterior body region. Scale bar: A = 50 µm; B = 20 µm; C = 150 µm; D = 25 µm; E = 40 µm.

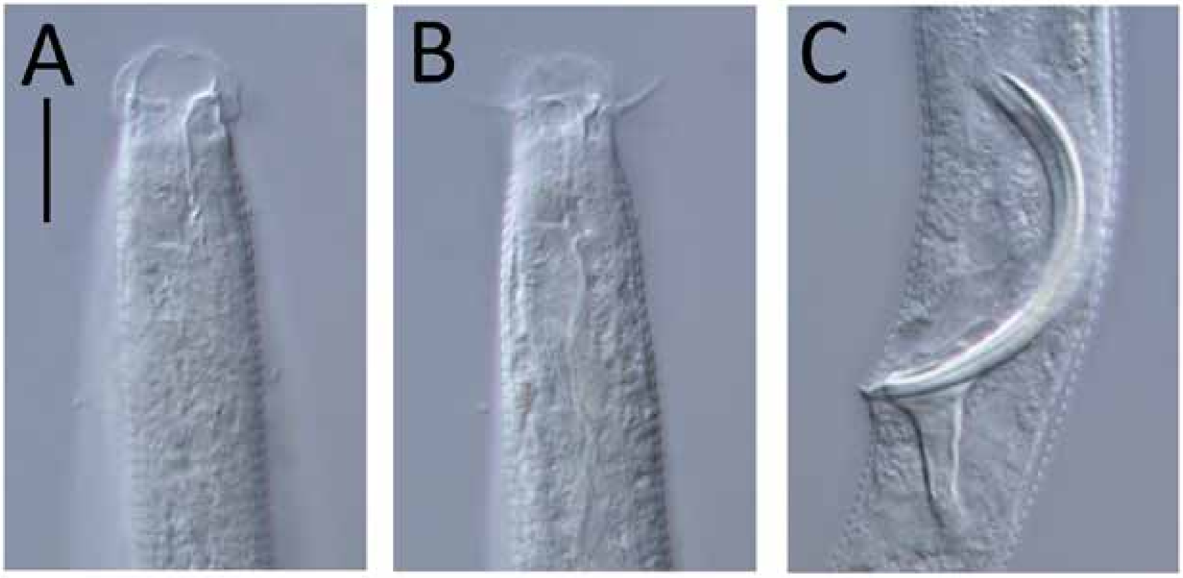



**Figure 113.** *Theristus arcuatospiculus* **sp. nov.**, light micrographs of male holotype NIWA 154877: **A–B.** Optical cross-section of cephalic region showing lips, buccal cavity and anterior sensilla; **C.** Copulatory apparatus. Scale bar = 10 µm.

**Table 33.** Morphometrics (µm) of *Theristus arcuatospiculus* **sp. nov.**, given as individual values.

| Parameter | Male Holotype |
|---|---|
| Number of specimens | 1 |
| L | 836 |
| a | 44 |
| b | 5 |
| c | 8 |
| c' | 6.5 |
| Body diameter at cephalic setae | 10 |
| Body diameter at amphids | 11 |
| Length of outer labial setae | 6 |
| Length of cephalic setae | 4 |
| Amphid height | 8 |
| Amphid width | 9 |
| Amphid width/cbd (%) | 82 |
| Amphid from anterior end | 12 |
| Nerve ring from anterior end | 72 |
| Nerve ring cbd | 15 |
| Pharynx length | 155 |
| Pharyngeal diameter at base | 9 |
| Pharynx cbd at base | 15 |
| Maximum body diameter | 19 |
| Spicule length | 39 |
| Gubernacular apophysis length | 12 |
| Cloacal/anal body diameter | 16 |
| Tail length | 104 |

new species can be distinguished from *T. manicatus* by the length and shape of the spicules (arcuate and 2.4 cloacal body diameters long *versus* S-shaped and 1.0 cloacal body diameters long in *T. manicatus*) and length and shape of the gubernacular apophyses (rounded distally and one-third of spicule length *versus* pointed distally and half of spicule length in *T. manicatus*). *Theristus arcuatospiculus* **sp. nov.** can be differentiated from *T. subcurvatus* by the spicule cuticularisation and length (thickly cuticularised and 2.4 cloacal body diameters long *versus* lightly cuticularised and <1.5 cloacal body diameters long in *T. subcurvatus*) and the length of the gubernacular apophyses (12 *versus* 4 µm in *T. subcurvatus*).

**ZooBank registration.** *Theristus arcuatospiculus* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:937836FD-961D-4A12-AF56-D3858639FBAE.

## *Theristus levicapitulus* sp. nov.

Figs 114, 115; Table 34

**Material examined. Holotype** NIWA 154876, NIWA Stn Z18747, 41.106° S, 174.891° E, Bradeys Bay in Pāuatahanui Inlet, upper intertidal, 25 Sep 2018, partly anoxic gravelly sand, male.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Male.** Body colourless, cylindrical, tapering slightly towards both extremities. Cuticle striated, no lateral differentiation. Eight rows of somatic setae present in pharyngeal region and immediately anterior to cloacal region, 4–10 µm long, sometimes in pairs, absent in middle body region. Cephalic region rounded, smooth, set-off from body by constriction slightly anterior to amphids; lips bearing six inner labial setae 3 µm long. Six outer labial setae 0.6–0.8 cbd long, in same circle as four cephalic setae, 0.6 cbd long. Two lateral and two subdorsal additional setae present at same level as outer labial setae and cephalic setae, 0.6 cbd long. Amphidial fovea medium-sized, circular, with lightly cuticularised outline, surrounded by cuticle striations, ca. 1.0 cbd from anterior extremity. Buccal cavity broad, 14 µm wide, 10 µm deep, funnel-shaped, with cuticularised walls, without teeth. Ducts of pharyngeal glands not observed. Pharynx muscular, anterior portion slightly swollen and surrounding buccal cavity, not widening posteriorly and without posterior bulb. Nerve ring located slightly posterior to middle of pharynx. Secretory-excretory system not observed. Cardia 10 µm long, partially surrounded by intestinal tissue. Reproductive system with two outstretched testes both located to the left of intestine; sperm cells globular, ca. 10 × 15 µm. Spicules paired, symmetrical, slightly arcuate, 1.9 cloacal body diameters long, strongly cuticularised and with central lamella one-third of spicule length from distal tip; slightly rounded and set off proximal portion. Gubernaculum with relatively large distal triangular plates on either side of spicules; ventral and dorsal pairs of thin, curved extensions proximally, no apophyses. Precloacal supplements not observed. Two pairs of ejaculatory glands ca. four cloacal body diameters anterior to cloacal opening. Tail conical, with rows of subventral and subdorsal setae, 3–5 µm long Three caudal glands present.

**Etymology.** The species name is derived from the Latin *levis* (= smooth, bald) and *capitulum* (= head) and refers to the characteristic unstriated cephalic region of this species.

**Species diagnosis.** *Theristus levicapitulus* **sp. nov.** is characterised by smooth cephalic region set-off from rest of body by constriction slightly anterior to amphids, inner labial setae 3 µm long, outer labial setae 14–17 µm long, cephalic setae 13 µm long, amphidial fovea 8 µm in diameter, buccal cavity with cuticularised walls, male reproductive system with two testes, spicules 1.9 cloacal body diameters long, gubernaculum 34 µm long without apophyses but with distal triangular plates flanking the spicules, and conical tail 6.1 cloacal body diameters long.

**Differential diagnosis.** The new species belongs to the '*Theristus flevensis*' species group of Wieser & Hopper (1967) and Tchesunov (1981b) characterised by a gubernaculum with distal hooks or triangular plates. This group includes the following thirteen species: *T. borosi* Andrássy, 1958, *T. bipunctatus* (Schneider, 1906) Filipjev, 1929, *T. calx* Wieser & Hopper, 1967, *T. flevensis* Schuurmans Stekhoven, 1935, *T. longisetifer* Kito & Aryuthaka, 1998, *T. macroflevensis* Gerlach, 1954, *T. marinae* Tchesunov, 1981b, *T. metaflevensis* Gerlach, 1955, *T. minimus* Gagarin & Nguyen Vu Thanh, 2011, *T. polychaetophilus* Hopper, 1966, *T. pratti* Murphy & Canaris, 1964, *T. scanicus* Allgén, 1949 and *T. siwaschensis* Revkova, 2020. *Theristus ambronensis* Schulz, 1937 was also previously included in this species group but was recently synonymised with *T. flevensis* by Revkova (2020)). Morphological variation within this group is relatively limited, but *T. levicapitulus* **sp. nov.** differs from all other species of the group by the unstriated, set-off cephalic region. The description of *T. ambronensis* by Schulz (1937) (North Sea) does not clearly show the extent of cuticle striation and shows a cephalic region narrower than the rest of the body; however, the new species can be differentiated from *T. ambronensis* by the markedly longer spicules (61 *versus* 30–31 µm in *T. ambronensis*), higher ratio of a (45 *versus* 25–26 in males of *T. ambronensis*) and b (8 *versus* 5 in males of *T. ambronensis*), and presence of eight rows of somatic setae in pharyngeal region (*versus* sparsely distributed somatic setae in *T. ambronensis*).

**ZooBank registration.** *Theristus levicapitulus* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:92D59D44-1755-489A-8110-B2FC9EF85C30.

### ***Theristus vivax*** **sp. nov.**

Figs 116–118; Table 35

**Material examined. Holotype** NIWA 139271, NIWA Stn Z18745, 41.093° S, 174.876° E, Pāuatahanui Inlet near Camborne Walkway, upper intertidal, 28 Jul 2016, gravelly sand, male. **Paratypes** NIWA 139272, four males and three females, same data as holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Males.** Body colourless, cylindrical, tapering slightly towards both extremities. Cuticle striated, no lateral differentiation. Eight rows of

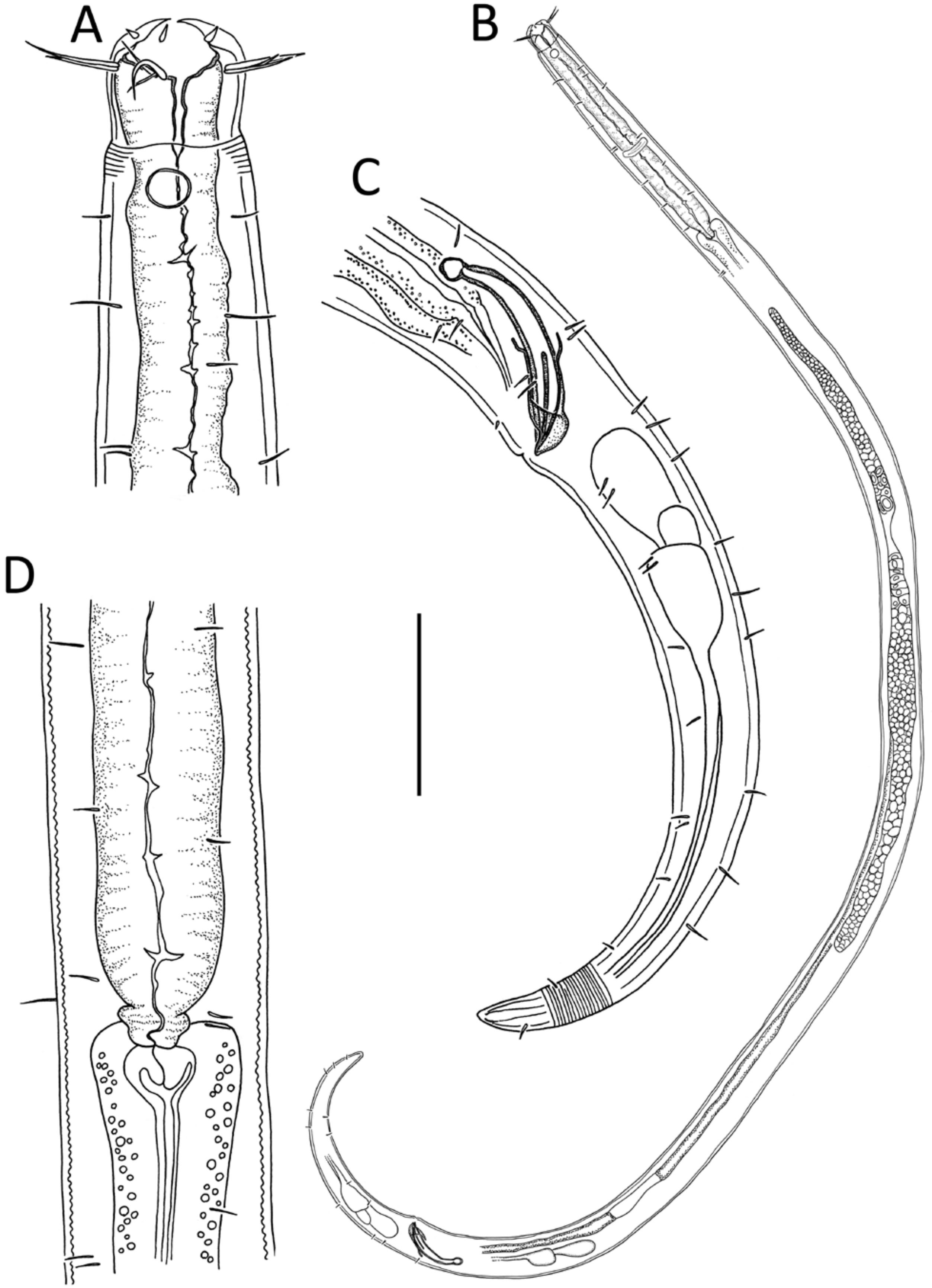



**Figure 114.** *Theristus levicapitulus* **sp. nov.**, male holotype NIWA 154876: **A.** Cephalic region; **B.** Entire male; **C.** Junction of pharynx and intestine; **D.** Posterior body region. Scale bar: A, D = 30 µm; B = 145 µm; C = 45 µm.

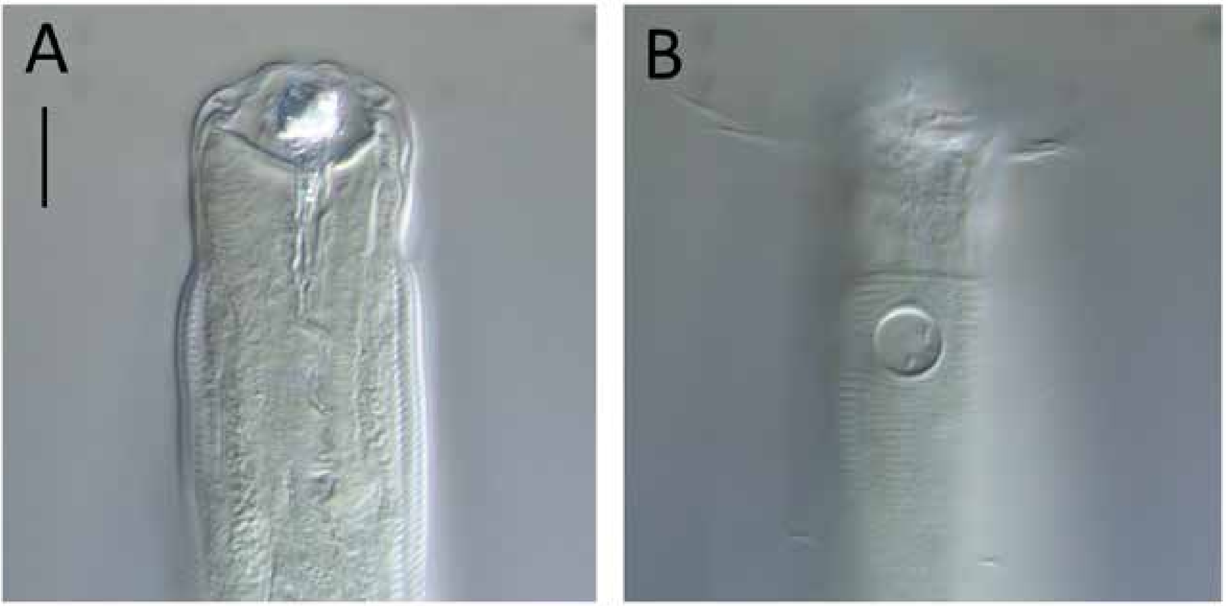



**Figure 115.** *Theristus levicapitulus* **sp. nov.**, light micrographs of male holotype NIWA 154876: **A.** Optical cross-section of cephalic region showing buccal cavity and lips; **B.** Surface view of cephalic region showing cuticle ornamentation, amphidial fovea, and anterior sensilla. Scale bar = 10 µm.

**Table 34.** Morphometrics (µm) of *Theristus levicapitulus* **sp. nov.**, given as individual values.

| Parameter | Male Holotype |
|---|---|
| Number of specimens | 1 |
| L | 1523 |
| a | 45 |
| b | 7 |
| c | 8 |
| c' | 6.1 |
| Body diameter at cephalic setae | 22 |
| Body diameter at amphids | 25 |
| Length of outer labial setae | 14–17 |
| Length of cephalic setae | 13 |
| Amphid height | 8 |
| Amphid width | 8 |
| Amphid width/cbd (%) | 32 |
| Amphid from anterior end | 24 |
| Nerve ring from anterior end | 135 |
| Nerve ring cbd | 34 |
| Pharynx length | 210 |
| Pharyngeal diameter at base | 22 |
| Pharynx cbd at base | 35 |
| Maximum body diameter | 35 |
| Spicule length | 61 |
| Gubernacular apophysis length | – |
| Cloacal/anal body diameter | 32 |
| Tail length | 194 |

somatic setae present along entire body length, 12–16 µm long. Slightly rounded cephalic region, not set-off from body; lips bearing six inner labial setae 2 µm long. Six outer labial setae 0.8–0.9 cbd long, in same circle as four slightly shorter cephalic setae, 0.5–0.6 cbd long. Two pairs of additional setae, 2–3 µm long, situated subventrally between level of inner labial setae and cephalic setae. Amphidial fovea circular, with lightly cuticularised outline, surrounded by cuticle striations, ca. 1.0 cbd from anterior extremity. Buccal cavity funnel-shaped, with lightly cuticularised walls, 10–13 µm deep, 10 µm wide, without teeth. Ducts of pharyngeal glands not observed. Pharynx muscular, anterior portion surrounding buccal cavity, widening slightly posteriorly. Nerve ring located slightly anterior to middle of pharynx. Secretory-excretory system not observed. Cardia 10 µm long, surrounded by intestinal tissue. Reproductive system with single outstretched testis located to the left of intestine; sperm cells globular, 7–8 × 10–11 µm. Spicules short, L-shaped, strongly cuticularised; slightly swollen proximal portion, sometimes with small gland visible. Gubernaculum with strongly cuticularised dorsocaudal apophyses; relatively well-developed crurae flanking the spicules distally, sometimes directed laterally and less visible. Precloacal supplements not observed. Tail conical, with rows of subventral and subdorsal setae. Three caudal glands present.

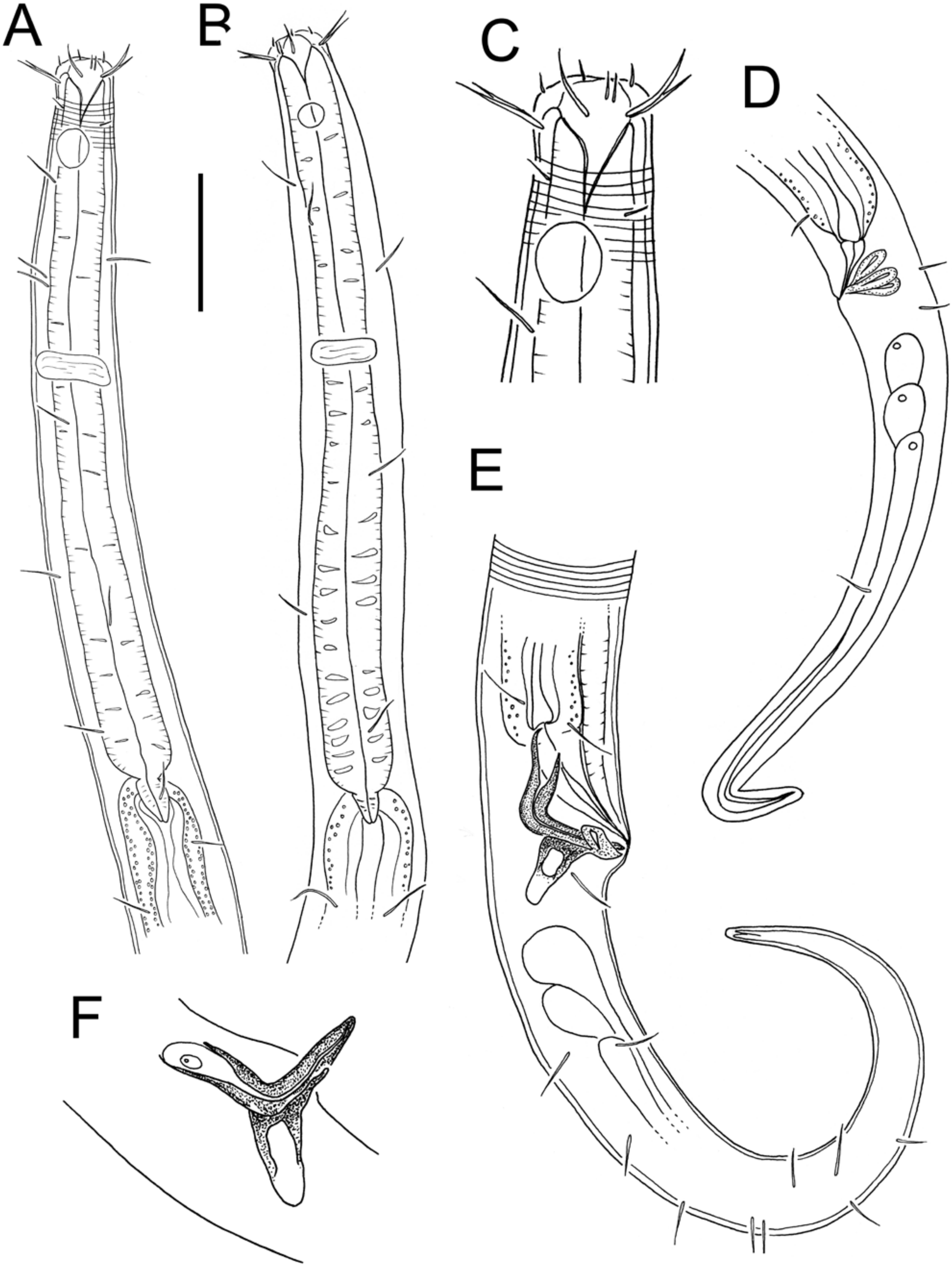



**Figure 116.** *Theristus vivax* **sp. nov.**: **A.** Anterior body region of male holotype NIWA 139271; **B.** Anterior body region of female paratype NIWA 139272; **C.** Cephalic region of male holotype NIWA 139271; **D.** Posterior body region of female paratype NIWA 139272; **E.** Posterior body region of male holotype NIWA 139271; **F.** Male paratype copulatory apparatus NIWA 139272. Scale bar: A, B = 40 µm; C = 20 µm; D = 35 µm; E = 27 µm; F = 22 µm.

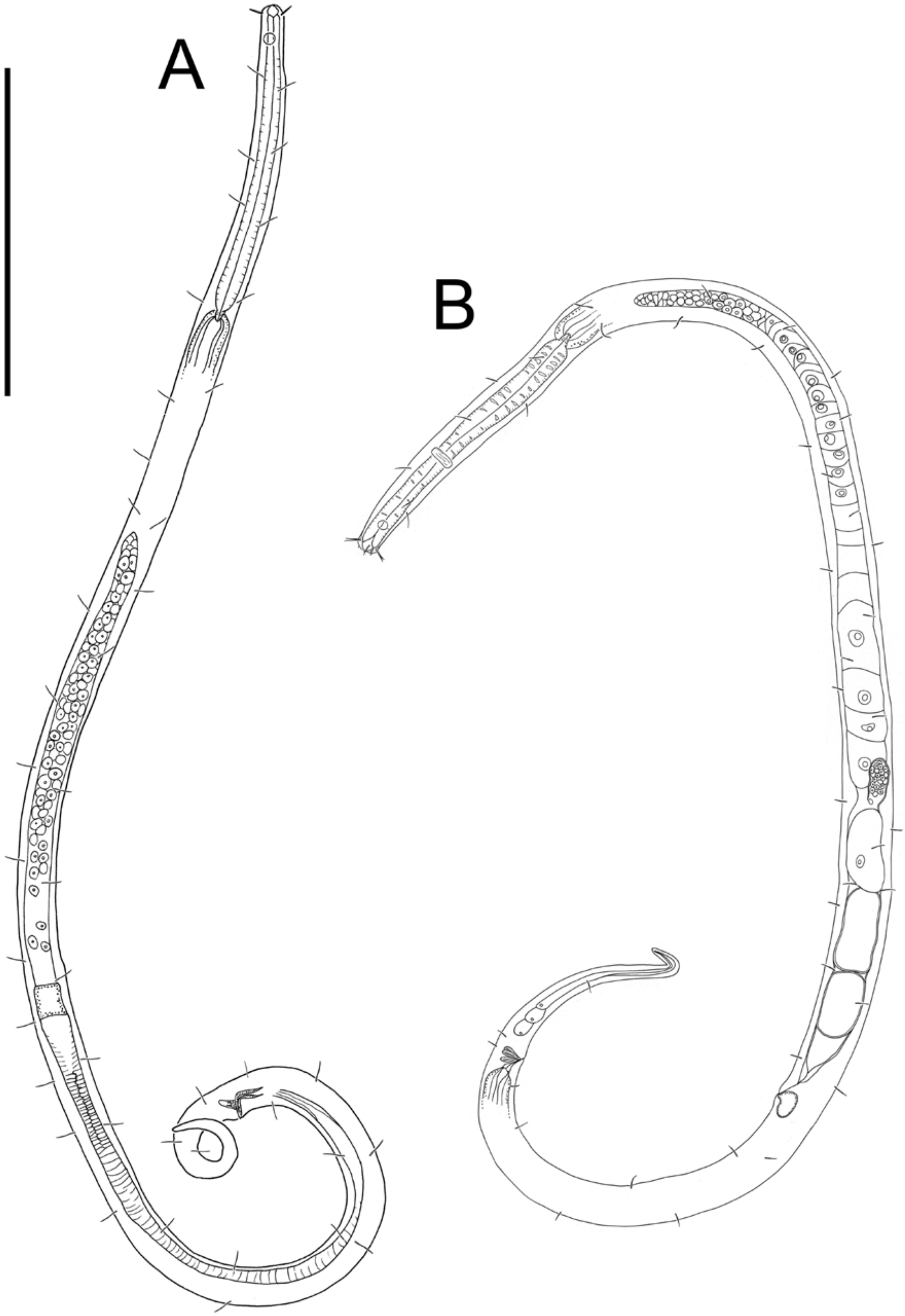



**Figure 117.** *Theristus vivax* **sp. nov.**: **A.** Entire male paratype NIWA 139272; **B.** Entire female paratype NIWA 139272. Scale bar = 250 µm.

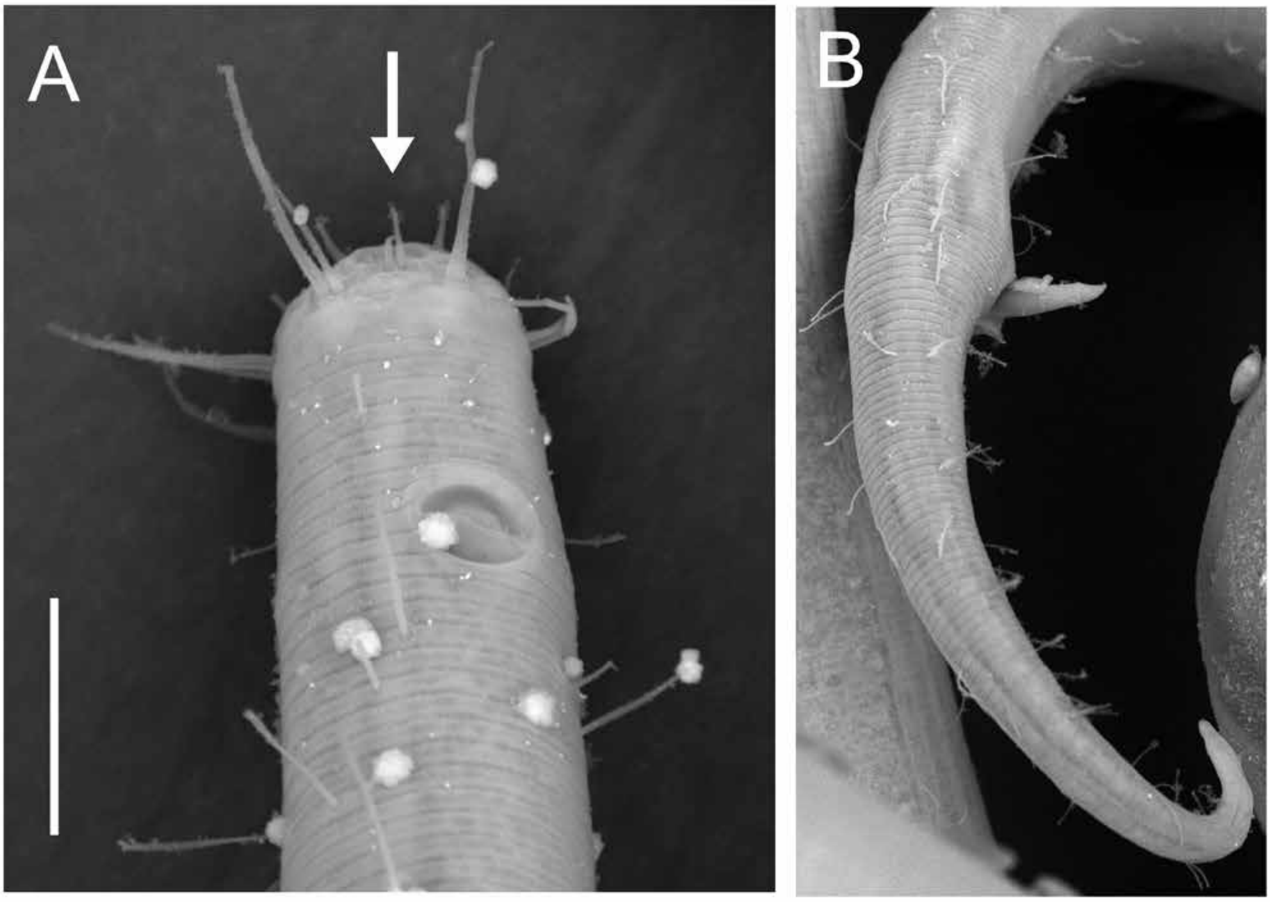



**Figure 118.** *Theristus vivax* **sp. nov.**, scanning electron micrographs: **A.** Cephalic region of male; **B.** Posterior body region of male. Arrow shows position of additional setae. Scale bar: A = 20 µm; B = 33 µm.

**Females.** Similar to males but with lower values of a, smaller amphidial fovea, and longer tail with fewer setae. Reproductive system with single outstretched ovary to the left of intestine. Eggs 25–28 × 50–60 µm. Single spermatheca present. Vulva located near two-thirds of body length from anterior. Large vaginal gland present.

**Etymology.** The species name is derived from the Latin *vivacis* (= vigorous, lively), and refers to the particularly vigorous swimming of freshly caught specimens.

**Species diagnosis.** *Theristus vivax* sp. nov. is characterised by body length 1440–1600 µm, ratio of a 36–56, six outer labial setae (0.8–0.9 cbd) in same circle as four slightly shorter cephalic setae (0.5–0.6 cbd), two pairs of short additional setae, situated subventrally between level of inner labial setae and cephalic/outer labial setae, somatic setae 12–16 µm; amphid 0.40–0.50 cbd wide in males and ca. 0.35 cbd wide in females, located 1.0 cbd from anterior extremity; short L-shaped spicules, gubernaculum with strongly cuticularised dorsocaudal apophyses and well-developed crurae flanking the spicules distally, absence of precloacal supplements; vulva at 65–67% of body length from anterior extremity; tail 5.9–8.6 cloacal/anal body diameters long.

**Differential diagnosis.** The new species can be differentiated from all other *Theristus* species by the presence of two additional setae situated subventrally between level of inner labial setae and cephalic/outer labial setae. *Theristus vivax* sp. nov. is similar to *T. acer* Bastian, 1865 (North Atlantic) in the ratio of a, structure of the male copulatory apparatus, size and position of amphids, and position of vulva, but can be differentiated from the latter in the somewhat shorter body length ($\leq$ 1600 µm in *T. vivax* sp. nov. *versus* $\geq$ 1600 µm in *T. acer*), setose inner labial sensilla (*versus* papillose in *T. acer*), and position of the additional setae (slightly anterior to cephalic setae in *T. vivax* **sp. nov.** *versus* same level as cephalic setae in *T. acer*). The new species is also similar to *T. interstitialis* Warwick, 1970 (North Atlantic) in body length, ratio of a, papillose inner labial sensilla, size and position of amphids, and copulatory apparatus, but can be differentiated from the latter by the position and length of the additional setae (two pairs of short additional setae situated subventrally in *T. vivax* **sp. nov.** *versus* two long and two short additional setae flanking the lateral outer labial

**Table 35.** Morphometrics (µm) of *Theristus vivax* **sp. nov.**, given as individual values, or a range of values from several specimens.

| Parameter | Males | | Females |
|---|---|---|---|
| | Holotype | Paratypes | Paratypes |
| Number of specimens | 1 | 4 | 3 |
| L | 1470 | 1445–1564 | 1457–1602 |
| a | 47 | 51–56 | 36–39 |
| b | 7 | 6–7 | 6–7 |
| c | 8 | 9–10 | 8 |
| c' | 6.4 | 5.9–6.2 | 7.4–8.6 |
| Body diameter at cephalic setae | 17 | 17–19 | 16–17 |
| Body diameter at amphids | 19 | 19–21 | 19–20 |
| Length of outer labial setae | 15 | 13–16 | 13 |
| Length of cephalic setae | 11 | 8–10 | 7–9 |
| Amphid height | 11 | 9–10 | 6–8 |
| Amphid width | 9 | 9–10 | 7 |
| Amphid width/cbd (%) | 47 | 40–50 | 35–37 |
| Amphid from anterior end | 22 | 21–25 | 20–21 |
| Nerve ring from anterior end | 84 | 95–105 | 95–111 |
| Nerve ring cbd | 25 | 24–25 | 25–28 |
| Pharynx length | 199 | 202–245 | 215–260 |
| Pharyngeal diameter at base | 19 | 16–18 | 18–20 |
| Pharynx cbd at base | 29 | 26–27 | 28–29 |
| Maximum body diameter | 31 | 40–42 | 40–42 |
| Spicule length | 35 | 38–40 | – |
| Gubernacular apophysis length | 14 | 13–15 | – |
| Cloacal/anal body diameter | 28 | 25–30 | 23–25 |
| Tail length | 179 | 147–177 | 173–206 |
| V | – | – | 967–1037 |
| %V | – | – | 65–67 |
| Vulval body diameter | – | – | 36–38 |

setae in *T. interstitialis*) and gubernaculum without teeth distally (*versus* gubernaculum with two pairs of teeth distally in *T. interstitialis*). *Theristus vivax* **sp. nov.** also shows similarities with *T. pertenuis* Bresslau & Schuurmans Stekhoven in Schuurmans Stekhoven, 1935 (North Atlantic, also Mediterranean and Red Sea) in ratio of a, number and length of cephalic sensilla, and structure of copulatory apparatus, but differs from the latter in the longer body length (1440–1600 µm in *T. vivax* **sp. nov.** *versus* 1000–1100 µm in *T. pertenuis*) presence of additional setae (*versus* absent in *T. pertenuis*), longer somatic setae (12–16 µm in *T. vivax* **sp. nov.** *versus* 3–4 µm in *T. pertenuis*), larger amphids (6–11 µm diameter in *T. vivax* **sp. nov.** *versus* 6 µm diameter in *T. pertenuis*), and longer spicules (35–40 µm in *T. vivax* **sp. nov.** versus 23 µm in *T. pertenuis*).

**Remarks**. *Theristus vivax* **sp. nov.** was by far the most abundant species in the sample collected from near the Camborne Walkway in July 2016, and common in most samples obtained from the inlet. Live specimens are particularly vigorous swimmers.

**Sequence data.** Partial SSU rDNA (1567 bp; Genbank OK317216) and D2–D3 of LSU rDNA (690 bp; Genbank OK317236).

**ZooBank registration.** *Theristus vivax* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:870789B2-10ED-4DCB-B4D4-C0CBA30E86FB.

## Order **Plectida** Gadea, 1973
## Family **Camacolaimidae** Micoletzky, 1924

Camacolaimidae Micoletzky, 1924: 227

**Diagnosis.** Cuticle annulated, annules smooth or with fine longitudinal striation. Lateral alae usually present, single band of smooth cuticle. Epidermal glands and body pores sometimes present. Somatic sensilla present, not connected to epidermal glands. Labial region rounded, continuous with body contour, lips fused basally or completely, forming small cephalic capsule. First annulus is located posterior to amphids and cephalic setae bases. Inner labial sensilla indistinct. Outer labial sensilla usually papilliform, located on outer surface of lips. Cephalic sensilla setiform or papilliform; their bases often located posterior to amphids. Subcephalic sensilla not usually present; cervical sensilla and deirid absent. Amphidial aperture ventrally-unispiral, in some species with distinct central elevation, or transversely oval; amphidial fovea usually located at level of, or slightly anterior to, cephalic setae. Secretory-excretory system usually present; renette cell located opposite to ventral side of intestine. Excretory ampulla present, located at level of the mid-pharynx. Cuticularised excretory duct very short, opens outside at about the level of the midpharynx or on the ventral side of the labial region. Oral opening triangular or rounded. Buccal cavity often with complicated armament. Cheilostome is always undifferentiated. Gymnostom with either three radial or two subventral odontia pointing forward, single dorsal odontium pointing forward, or undifferentiated; stegostom morphology variable. Pharyngeal tubes absent. Dorsal gland orifice penetrates pharyngeal lumen at stoma base; subventral gland orifices not seen. Pharynx cylindrical anteriorly, gradually widening posteriorly; uniformly muscular all the way through or only in anterior part; in the latter case, the dorsal and often subventral glandular sectors of the pharynx are enlarged; pharyngeal lumen uniformly thickened; valv-ular apparatus absent. Cardia surrounded by intestinal tissue. Female reproductive system didelphic-amphidelphic or monodelphic-opisthodelphic; ovary branches reflexed antidromously. Spermatheca present, axial; located between oviduct and uterus. Vulva equatorial, transverse. Vagina straight; pars proximalis vaginae encircled by a single sphincter muscle; pars refringens vaginae and epiptygmatha absent. Male reproductive system diorchic; testes directed forward (outstretched) or opposed, with posterior testis reflexed. Spicules symmetrical, arcuate; often with ventrally inclined capitulum; gubernaculum present. Copulatory apparatus composed of midventral row of supplements, precloacal papilliform sensillum that is located somewhat anterior to cloaca, and a pair of postcloacal papilliform sensilla. Either alveolar or tubular, or both types of supplements are present; in the latter case, alveolar supplements are located more anteriorly than the tubular.

The genus *Deontolaimus* de Man, 1880 has alveolar supplements that are located only along the pharyngeal region of the body, and postcloacal sensilla on the tail; no tubular supplement and no precloacal sensilla. Some have no supplements at all, no precloacal sensilla and only have post-cloacal sensilla. Tail conoid. Three caudal glands present, their nuclei are incaudal. Spinneret functional, weakly or strongly cuticularised, often long conoid or arcuate toward dorsal body side (modified from Holovachov (2014)).

## Genus *Deontolaimus* de Man, 1880

*Deontolaimus* de Man, 1880: 3–4.
*Camacolaimus* de Man, 1889: 8.
*Camacolaimoides* De Coninck & Schuurmans Stekhoven, 1933: 113.
*Acontiolaimus* Filipjev, 1918: 187–188, fig. 36, table 6.
*Digitonchus* Cobb, 1920: 314.
*Ypsilon* Cobb, 1920: 314.

**Diagnosis.** Cuticle annulated, annules smooth, without ornamentation. Lateral alae absent or present, single band of smooth cuticle. Epidermal glands absent. Somatic setae present, not connected to epidermal glands. Labial region rounded or truncated, continuous with body contour, lips basally fused. First annulus posterior to amphids and cephalic setae bases. Inner labial sensilla papilliform, located on anterior surface of lips. Outer labial sensilla papilliform, located on outer surface of lips. Cephalic sensilla setiform; their bases usually located at level with, or posterior to, amphids (anterior to amphids in one species). Subcephalic and cervical sensilla, deirid and ocelli absent. Amphidial fovea ventrally-unispiral or ventrally-multispiral. Secretory-excretory system: ventral gland located opposite to left-hand side of intestine; excretory canal short, extending from pore along ventral region of pharynx towards excretory ampulla. Excretory pore located at level with nerve ring or along anterior-most part of the pharynx (close to anterior body end). Oral opening elongate-ovoid in sagittal plane. Buccal cavity narrow, with dorsal armament: cheilostome undifferentiated; gymnostome with a single dorsal odontium pointing forward; stegostome funnel-shaped, with dorsal onchiostyle; odontium and odontostyle joined together. Radial tubes absent. Dorsal gland orifice penetrates pharyngeal lumen at stoma base. Subventral gland orifices not seen. Pharynx weakly muscularised and cylindrical anteriorly, more glandular and gradually widening posteriorly; with uniformly thickened lumen throughout, lacking valves and bulbs. Cardia embedded in intestine. Female reproductive system didelphic, amphidelphic or monodelphic, opisthodelphic; ovary branches reflexed antidromously; spermatheca axial; vulva equatorial; vagina straight; pars proximalis vaginae encircled by a single sphincter muscle; pars refringens vaginae absent. Male reproductive system diorchic; testes directed forward (outstretched); spicules arcuate, with ovoid ventrally inclined capitulum, narrowing shaft and thin velum; gubernaculum plate-like. Copulatory apparatus: up to 250 or more alveolar supplements along the midventral body line, one or two postcloacal sensilla. Tail elongate-conoid. Three caudal glands present, their nuclei are incaudal. Spinneret functional, weakly cuticularised (after Holovachov & Boström (2015)).

**Remarks.** Holovachov & Boström (2015) reviewed the genus *Deontolaimus* and provided a key to all 17 valid species of the genus. Two new species have since been described by Nguyen Dinh Tu *et al.* (2016).

**Type species.** *Deontolaimus papillatus* de Man, 1880

### *Deontolaimus poriruaensis* sp. nov.

Figs 119, 120; Table 36

**Material examined. Holotype** NIWA 154874, NIWA Stn Z19170, 41.102° S, 174.872° E, Mana Bank, Pāuatahanui Inlet, upper intertidal, 27 Jul 2020, fine sand, male. **Paratypes** NIWA 154875, two males and one female, same data as holotype.

**Type locality.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Distribution.** Pāuatahanui Inlet, Wellington region, lower North Island, New Zealand.

**Description. Males.** Body colourless, cylindrical, tapering slightly towards both extremities. Cuticle annulated; annules without ornamentation, located 1.5–1.7 μm apart in pharyngeal region and 1.0 μm

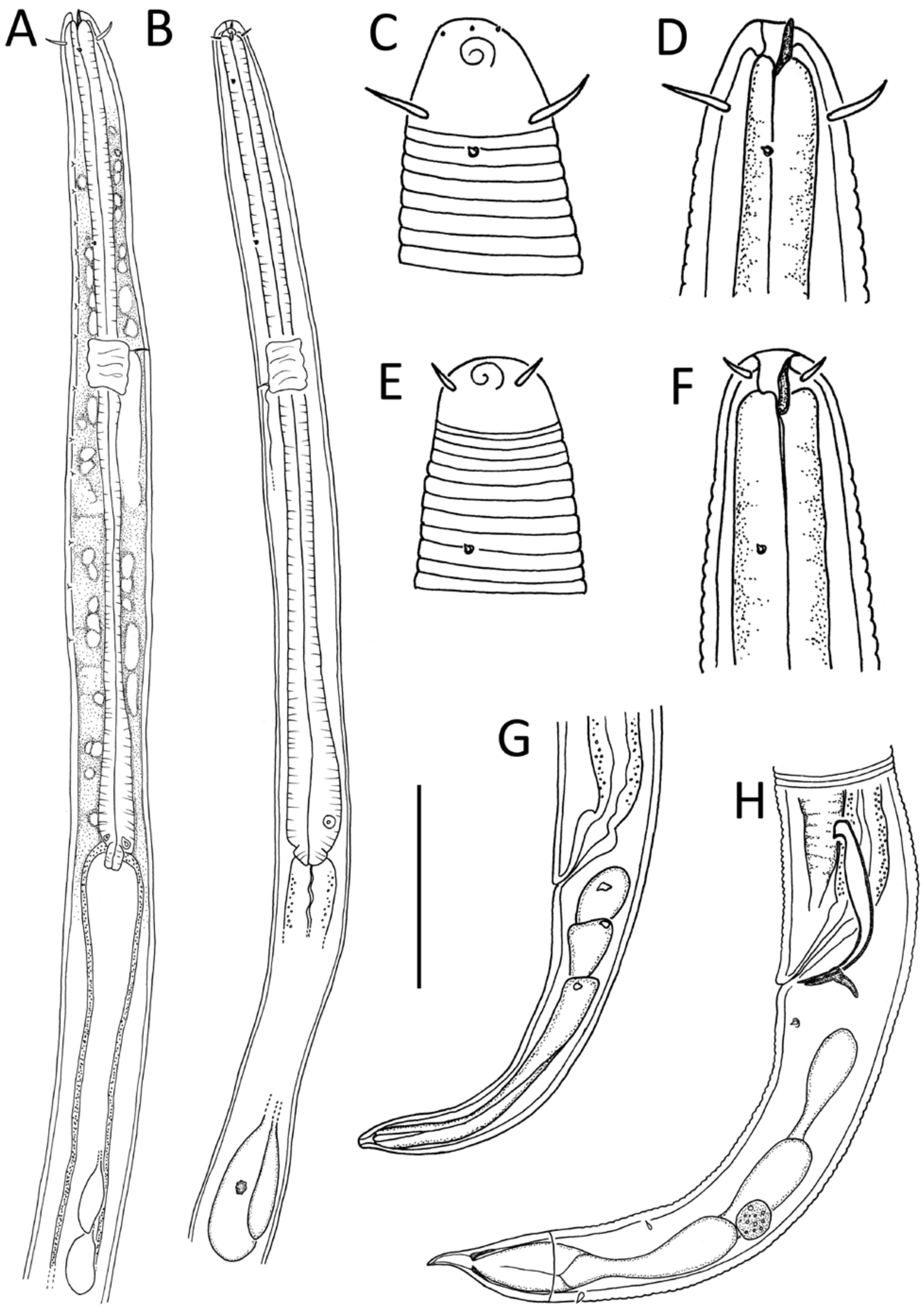



**Figure 119.** *Deontolaimus poriruaensis* **sp. nov.**: **A.** Pharyngeal region of male holotype NIWA 154874; **B.** Pharyngeal region of female paratype NIWA 154875; **C–D.** Male holotype cephalic region NIWA 154874; **E–F.** Female paratype cephalic region NIWA 154875; **G.** Female paratype posterior body region NIWA 154875; **H.** Male holotype posterior body region NIWA 154874. Scale bar: A, B = 50 µm; C, D, E, F = 17 µm; G = 40 µm; H = 30 µm.

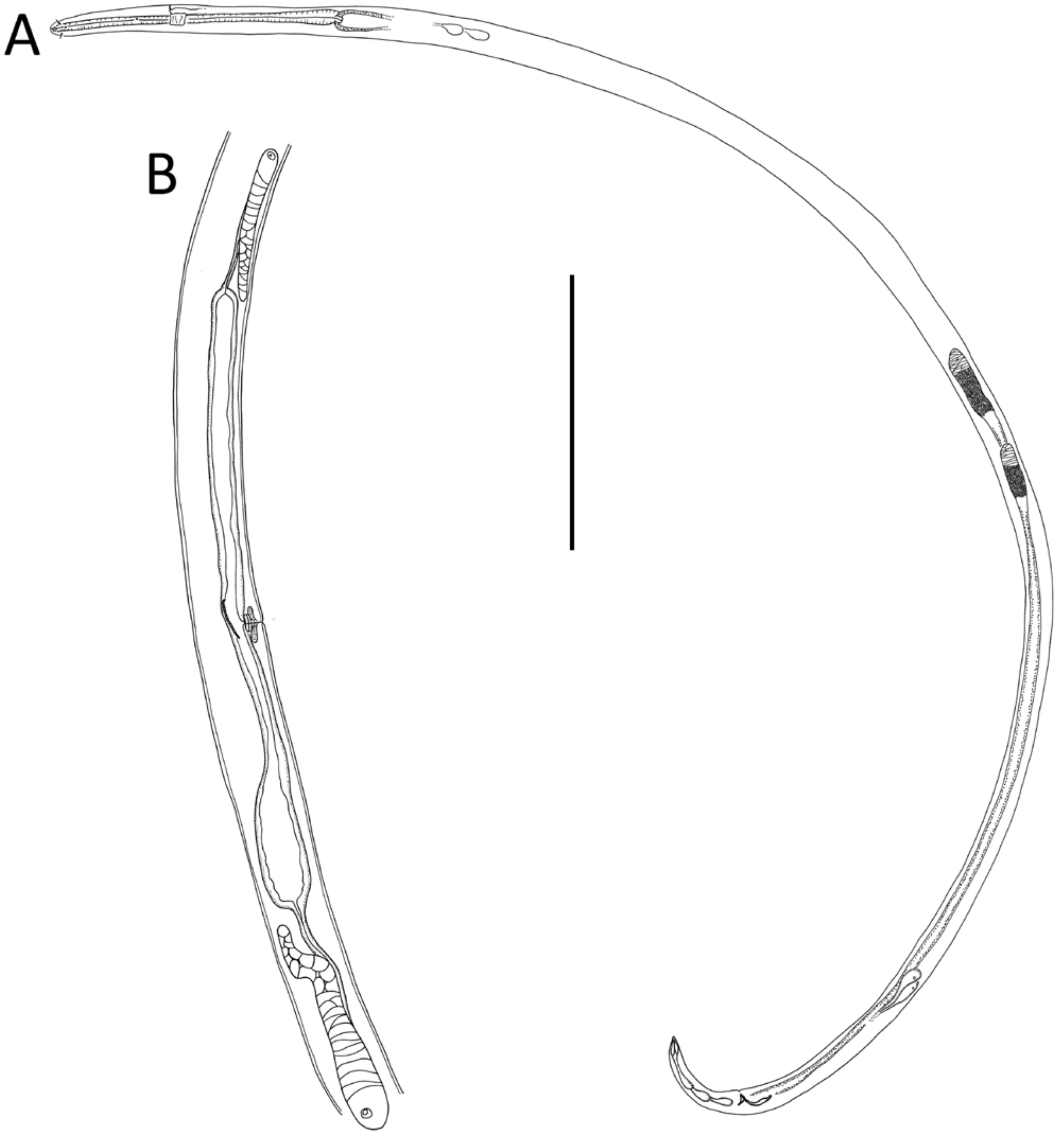



**Figure 120.** *Deontolaimus poriruaensis* **sp. nov.**: **A.** Entire male holotype NIWA 154874; **B.** Female paratype reproductive system NIWA 154875. Scale bar: A = 200 µm; B = 110 µm.

apart in posterior body region. Cuticle without lateral differentiation. Two pairs of lateral body pores in anterior half of pharyngeal region, each with short protruding papilla; anterior-most body pores ca. 1.0 cbd from anterior extremity. Other somatic sensilla not observed except for two pairs of subventral papillae and one pair of subdorsal papillae on tail. Labial region rounded, continuous with body contour; lips fused. Anterior-most annule appearing posterior to amphid and cephalic sensilla bases. One circle of minute papilliform anterior sensilla visible on the anterior surface of labial region. Cephalic sensilla setiform, 0.6–0.7 cbd long, their bases located 6–8 µm from the anterior body extremity and posterior to amphid. Amphidial fovea ventrally spiral with 1.5 turns, located anterior to cephalic sensilla bases. Oral opening terminal. Buccal cavity tubular, with dorsal onchiostyle. Onchiostyle with blunt tip and subcylindrical body.

**Table 36.** Morphometrics (µm) of *Deontolaimus poriruaensis* **sp. nov.**, given as individual values, or a range of values from several specimens.

| Parameter | Males | | Female |
|---|---|---|---|
| | Holotype | Paratypes | Paratype |
| Number of specimens | 1 | 2 | 1 |
| L | 1489 | 1417, 1607 | 1906 |
| a | 62 | 70, 71 | 64 |
| b | 7 | 7, 8 | 7 |
| c | 18 | 18, 20 | 22 |
| c' | 4.3 | 3.8, 4.4 | 4.6 |
| Body diameter at cephalic setae | 10 | 10, 11 | 10 |
| Body diameter at amphids | 8 | 7,8 | 10 |
| Length of cephalic setae | 6 | 7, 8 | 4 |
| Amphid height | 2 | 3 | 3 |
| Amphid width | 3 | 3 | 3 |
| Amphid width/cbd (%) | 38 | 38, 43 | 30 |
| Amphid from anterior end | 1.5 | 1.8, 1.8 | 0.8 |
| Onchiostyle length | 4.5 | 3.6, 3.8 | 5.3 |
| Anterior-most body pore | 9 | 9 | 17 |
| Nerve ring from anterior end | 92 | 87 | 90 |
| Nerve ring cbd | 21 | 20 | 21 |
| Pharynx length | 209 | 202, 204 | 268 |
| Pharyngeal diameter at base | 10 | 10, 13 | 18 |
| Pharynx cbd at base | 20 | 20, 21 | 24 |
| Maximum body diameter | 24 | 20, 23 | 30 |
| Spicule length | 31 | 31, 33 | – |
| Gurbenacular apophyses length | 4 | 4, 6 | – |
| Cloacal/anal body diameter | 19 | 18, 21 | 19 |
| Tail length | 81 | 79, 80 | 87 |
| V | – | – | 910 |
| %V | – | – | 48 |
| Vulval body diameter | – | – | 29 |

Pharynx muscular throughout entire length, widening posteriorly, not subdivided into sections, without bulbs or valvular apparatus. Dorsal pharyngeal gland usually visible, opening indistinct; subventral pharyngeal glands indistinct. Nerve ring located slightly anterior to middle of pharynx length. Secretory-excretory system present; pore located at level of nerve ring; two glands located 46–84 µm posterior to pharynx, to the left of intestine. Cardia 5–8 µm long, embedded in intestine. Reproductive system diorchic, both testes outstretched and directed anteriorly; anterior testis to the right of intestine, posterior testis to the left of intestine. Sperm cells small, globular, 1.2–1.3 × 1.2–1.3 µm. Two pairs of ejaculatory glands located either side of vas deferens, ca. 65–140 µm from cloacal opening. Spicules paired, symmetrical, 1.6–1.7 cloacal body diameters long, with arcuate subcylindrical shaft and capitulum. Gubernaculum with paired dorsocaudal apophyses. Ventral row of ca. 13 small alveolar supplements present in pharyngeal region, not observed elsewhere. Tubular supplements not present. Tail conical with three caudal glands opening through cuticularised, pointed terminal spinneret.

**Females.** Similar to males but with anterior-most body pore located further posteriorly; cephalic setae located further anteriorly and closer to amphid than in males likely due to retraction of lip region. Reproductive system with two opposed, reflexed ovaries; anterior ovary to the right of intestine, posterior ovary located ventrally relative to intestine. Spermathecae not observed. Vagina straight, ca. 0.3 times vulval body diameter. Vulva located near mid-body. Two vaginal glands and sphincter muscle present; uterus with thin cuticularised plate at level of vagina.

**Etymology.** The species name is derived from Porirua, the city in which Pāuatahanui Inlet is located.

**Species diagnosis.** *Deontolaimus poriruaensis* **sp. nov.** is characterised by body length 1417–1906 µm; annulated cuticle without lateral differentiation; anterior-most body pore 0.9–1.2 cbd from anterior extremity; cephalic setae bases posterior to amphid and 0.6–0.7 cbd long; amphidial fovea ventrally spiral with 1.5 turns, onchiostyle short (ca. 4–5 µm long), with blunt tip; male with ventral row of small alveolar supplements in pharyngeal region, tubular supplements absent, spicules 31–33 µm long; and didelphic female reproductive system.

**Differential diagnosis.** The new species is most similar to *D uniformis* (Cobb, 1920) Holovachov & Boström, 2015 (North Atlantic) in having cuticle without lateral fields/alae, cephalic setae located posterior to amphids, excretory pore near level of nerve ring, multispiral amphids, and female reproductive system with both ovaries equally developed. *Deontolaimus poriruaensis* **sp. nov.** differs from *D. uniformis* in the location of the anterior-most body pore (9–17 *versus* 41–42 µm from anterior extremity in *D. uniformis*), slightly fewer amphidial fovea turns (1.5 *versus* 2 turns in *D. uniformis*), shorter onchiostyle (4–5 *versus* 12–13 µm in *D. uniformis*), shorter spicules (31–33 versus 43–46 µm in *D. uniformis*), and distribution of alveolar supplements (pharyngeal region only *versus* almost entire body length in *D. uniformis*).

**ZooBank registration.** *Deontolaimus poriruaensis* Leduc & Zhao, 2023 is registered in ZooBank under urn:lsid:zoobank.org:act:BBD06547-E184-4276-A6BA-F3C189C9955D.

Order **Rhabditida** Chitwood, 1933
Family **Peloderidae** Andrássy, 1976

Peloderidae Andrássy, 1976: 150.

**Diagnosis.** Lips hardly separate, papillae very small. Stoma well developed. Cheilostome not cuticularised; gymnostome and promesostegostome with parallel walls; metastegostome with glottoid apparatus and either with small warts or with bristle-like denticles. Pharyngeal corpus swollen, bulb-like. Female genital organ paired, amphidelphic; vulva at or near mid-body region. Tail of female conoid- to cupola-like. Spicules fused distally. Bursa well developed, with mid-bursa phasmid position (after Abolafia (2006)).

Genus ***Litoditis*** Sudhaus, 2011

*Litoditis* Sudhaus, 2011: 133–134.
*Phasmarhabditis* Andrássy, 1976: 151
*Rhabditis* (*Pellioditis*) Dougherty, 1953: 71
*Pellioditis* (Dougherty, 1953) Timm, 1960: 150
*Rhabditis* Dujardin, 1845: 239-244.

**Diagnosis.** Lateral field of cuticle with three to seven ridges. Glottoid apparatus and pharyngeal sleeve present. Pharynx with distinct median bulb as wide as, or wider than, the posterior pharyngeal bulb. Intestine with constriction posteriorly forming a pre-rectum. Female with two opposed and reflexed genital branches, male with single anterior reflexed testis. Nine pairs of subventral genital papillae, three of which are precloacal; phasmid opening ventrally at base of seventh genital papilla. Gubernaculum forked. Female tail conical; juveniles always with rounded tail tip (after Sudhaus (2011)).

**Remarks.** Sudhaus (2011) lists four valid species within the genus.

**Type species.** *Litoditis marina* (Bastian, 1865) Sudhaus, 2011

### *Litoditis* cf. *marina* (Bastian, 1865) Sudhaus, 2011

Figs 121–123; Table 37

*Rhabditis marina* Bastian, 1865: 129–130, plate 10, figs 60–62.
*Rhabditis* (*Caenorhabditis*) *marina* (Bastian, 1865) Osche, 1952: 265.
*Rhabditis* (*Choriorhabditis*) *marina marina* (Bastian, 1865) Osche, 1954: 247, fig. 1 a–f.
*Rhabditis* (*Pellioditis*) *marina* (Bastian, 1865) Dougherty, 1953: 71.
*Rhabditis marina marina* Steiner, 1921: 9, fig. 1, table 1.
*Pellioditis marina* (Bastian, 1865) Andrássy, 1983: 102.

**Material examined.** NIWA 139266, NIWA Stn Z18748, 41.087° S, 174.892° E, upper Pāuatahanui Inlet in sand covered by stranded *Ulva* near Kakaho Stream, upper intertidal, 14 Oct 2019, four males and three females; Portobello Marine Laboratory collection slides 0001–0005, 45.846° S, 170.703° E, live *Zostera* blades, Papanui Inlet, January 2006, three females and two males.

**Type & locality.** Falmouth, England, sand from tide-pools, 1965. Bastian's type is presumably located at The Natural History Museum, London, but registration details of the holotype were not confirmed prior to publication.

**Distribution.** Cosmopolitan, including records from the coast of New Zealand (South Island and Campbell Island), Japan, Mediterranean Sea, and the North Atlantic (Sudhaus 1974, Kito 1981, Leduc & Gwyther 2008).

**Diagnosis.** *Litoditis* cf. *marina* specimens from Pāuatahanui Inlet are characterised by body cylindrical, colourless, tapering slightly towards anterior extremity. Cuticle with fine transverse striations; lateral field of cuticle with four to six ridges from posterior region of pharynx to caudal region. Somatic setae not observed. Cephalic region not set-off from rest of body. Inner labial sensilla not observed. Six outer labial papillae, one on each lip; four cephalic papillae present slightly posteriorly. Amphidial fovea minute, sometimes indistinct, oval-shaped, located at same level or slighlty posterior to cephalic papillae. Buccal cavity cylindrical, toothless, with cuticularised walls; cylindrical portion 12–15 µm deep and 3–5 µm wide, almost entirely surrounded by pharyngeal tissue ("sleeve"). Glottoid apparatus consisting of short, cylindrical cavity with cuticularised wall slightly narrower than main buccal cavity and set-off from the latter by a constriction. Ducts of pharyngeal glands empty immediately posterior to glottoid apparatus. Pharynx slightly swollen immediately posterior to buccal cavity, with well-developed median bulb slightly wider than the posteror pharyngeal bulb; the latter with cuticularised valvular appartus. Nerve ring located immediately posterior to median bulb. Secretory-excretory system not observed. Lateral deirids present slightly posterior to level of nerve ring. Cardia medium-sized, surrounded by thin intestine tissue. Pre-rectum not observed. Male reproductive system with single reflexed testis bent ventrally and located to the right of intestine. Sperm cells spherical or globular, 4 × 4–5 µm, nucleated. Spicules equal, short,

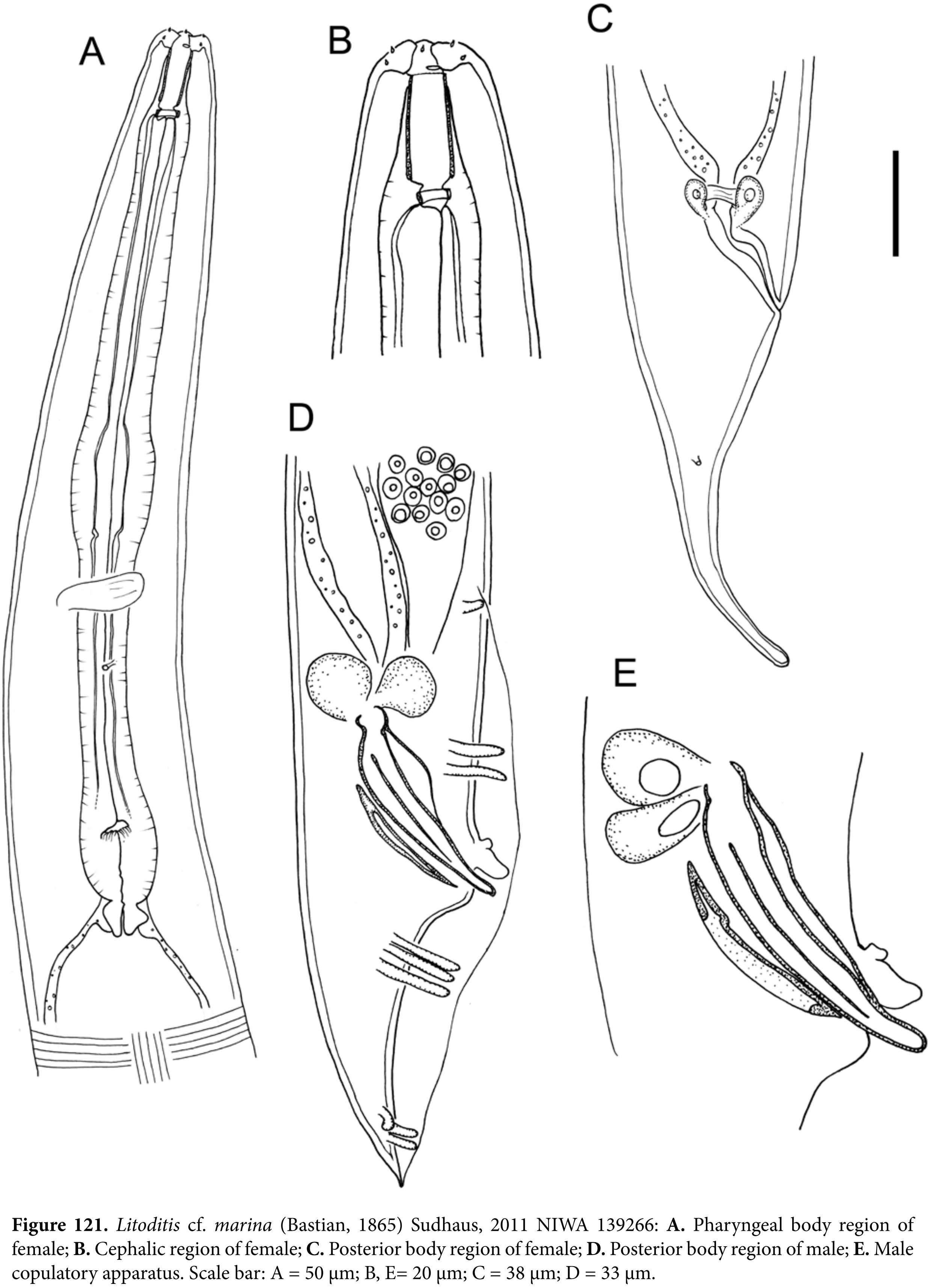



**Figure 121.** *Litoditis* cf. *marina* (Bastian, 1865) Sudhaus, 2011 NIWA 139266: **A.** Pharyngeal body region of female; **B.** Cephalic region of female; **C.** Posterior body region of female; **D.** Posterior body region of male; **E.** Male copulatory apparatus. Scale bar: A = 50 µm; B, E= 20 µm; C = 38 µm; D = 33 µm.

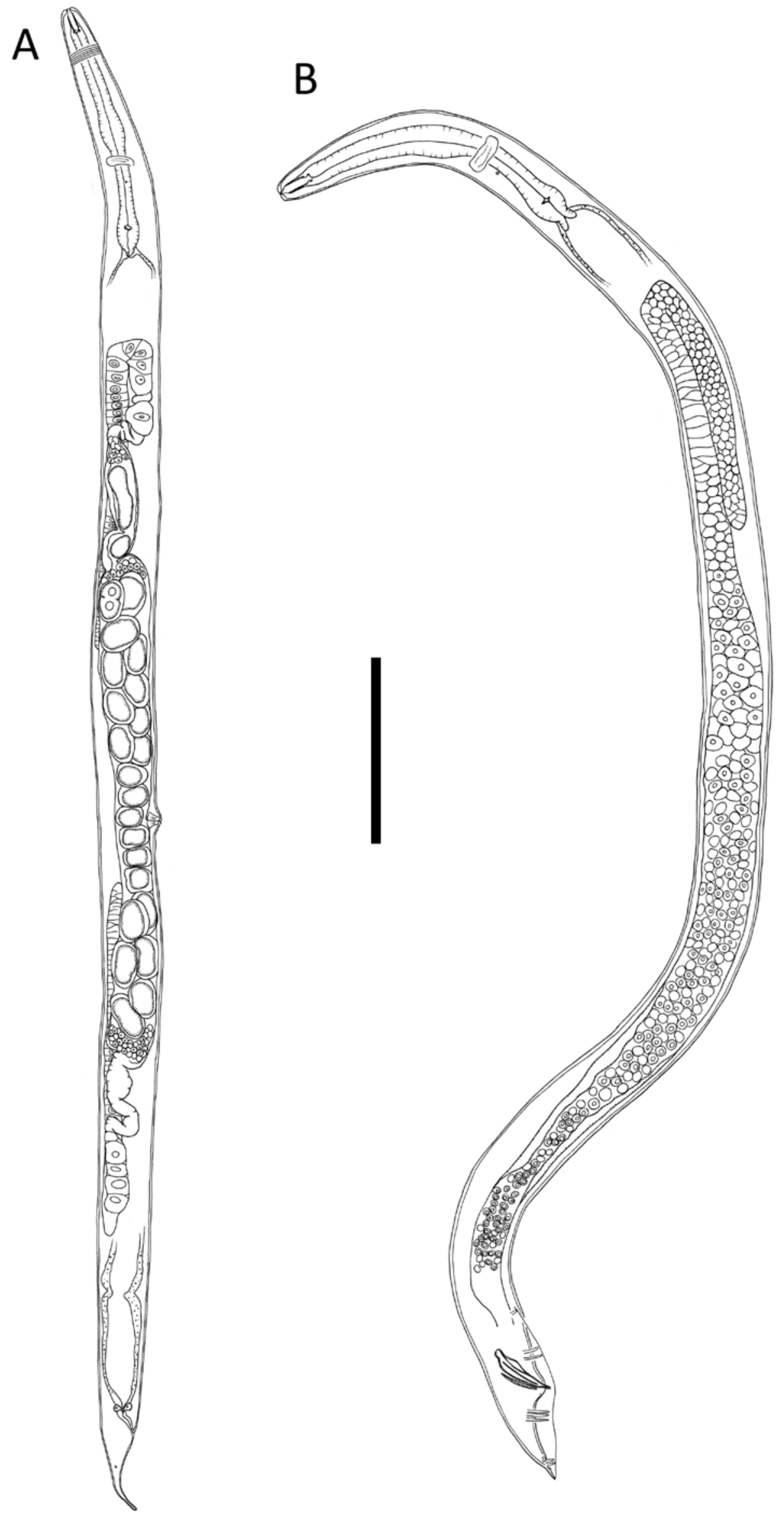



**Figure 122.** *Litoditis* cf. *marina* (Bastian, 1865) Sudhaus, 2011 NIWA 139266: **A.** Entire female; **B.** Entire male. Scale bar: A = 200 µm; B = 125 µm.

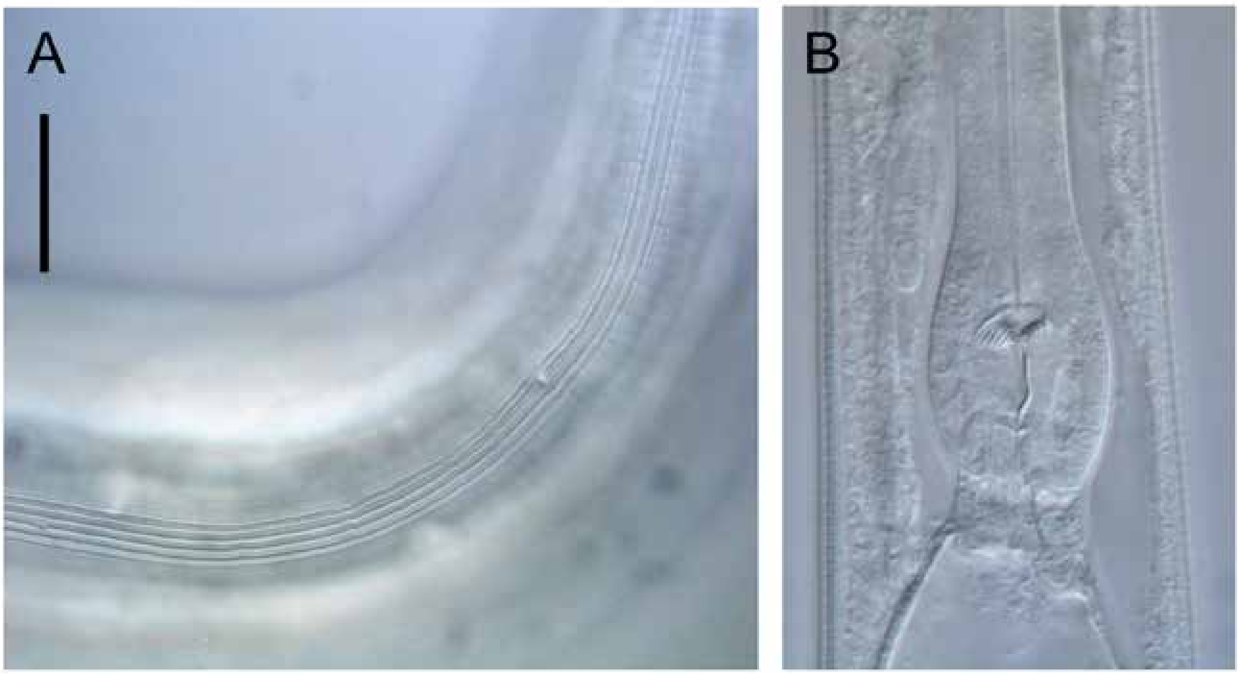



**Figure 123.** *Litoditis* cf. *marina* (Bastian, 1865) Sudhaus, 2011 NIWA 139266: **A.** Lateral surface view of female cuticle at level of posterior end of pharynx (top right-hand side) and anterior end of intestine (bottom left-hand side) showing lateral cuticular ridges and striations; **B.** Posterior bulb of male with cuticularised valvular apparatus. Scale bar: A = 25 µm; B = 15 µm.

slightly bent, with velum and median cuticularised strip, distal end blunt and proximal end with slight capitulum; two, possibly three glands emptying into proximal portion of each spicule. Gubernaculum parallel to spicules, slightly bent, pointed distally and proximally, about half of spicule length. Precloacal supplements and setae not observed. Leaf-shaped flap of cuticle present immediately anterior to cloaca. Bursa present, 95–127 µm long, smooth, supported on both sides by nine long and narrow genital papillae arranged in groups of 1, 2, 3 and 3. Seventh genital papilla from anterior usually bent laterally. Tail short, conical, with pointed tip; caudal glands and spinneret indistinct. Females similar to males but with longer body, lower ratio of a, and longer conical tail with rounded tip and phasmids 35–38 µm posterior to anus. Intestine with constriction posteriorly forming a pre-rectum; rectum ca. 30 µm long (slightly less than anal diameter) with at least two rectal glands at its junction with the intestine. Reproductive system with two opposed and reflexed ovaries; anterior ovary to the right of intestine and posterior ovary to the left of intestine. Eggs 23–30 × 31–40 µm. Spermathecae not observed. Vulva a transverse slit located slightly posterior to mid-body.

**Table 37.** Morphometrics (µm) of *Litoditis* cf. *marina* (Bastian, 1865) Sudhaus, 2011, given as a range of values from several specimens.

| Parameter | Males | Females |
|---|---|---|
| Number of specimens | 4 | 3 |
| L | 973–1154 | 1174–1646 |
| a | 24–27 | 20–24 |
| b | 5–6 | 5–6 |
| c | 16–19 | 13–17 |
| c' | 1.7–2.2 | 2.6–2.8 |
| Lips height | 3–4 | 4–5 |
| Body diameter at cephalic papillae | 12–13 | 14–15 |
| Stoma depth | 12–15 | 13–16 |
| Stoma width | 3–5 | 5–6 |
| Nerve ring from anterior end | 126–140 | 143–170 |
| Nerve ring cbd | 35–38 | 45–54 |
| Deirid from anterior end | 156–165 | 170–200 |
| Pharynx length | 195–216 | 228–265 |
| Median bulb width | 21–23 | 24–28 |
| Isthmus width | 12–14 | 15–16 |
| Posterior bulb width | 21–22 | 24–27 |
| Posterior bulb cbd | 39–40 | 48–61 |
| Maximum body diameter | 41–44 | 53–69 |
| Spicule length | 44–46 | – |
| Gubernacular apophysis length | 26–29 | – |
| Bursa length | 95–127 | – |
| Cloacal/anal body diameter | 32–35 | 30–37 |
| Tail length | 61–73 | 85–96 |
| V | – | 614–886 |
| %V | – | 52–54 |
| Vulval body diameter | – | 53–68 |

**Remarks.** According to Sudhaus (1974), the only morphological differences between *Litoditis mediterranea* and the closely-related *Litoditis marina* are the appearance of the bursa (smooth in *L. mediterranea versus* scaly in *L. marina*) and the shape of the tail (pointed in females of *L. mediterranea versus* rounded in females of *L. marina*). The Pāuatahanui Inlet specimens are intermediate due to the presence of a smooth bursa (consistent with *L. mediterranea*) and a tail with rounded tip (consistent with *L. marina*). The Pāuatahanui Inlet specimens agree well in most respects with the five specimens (three females and two males) from Papanui Inlet (in New Zealand's South Island) that we were able to examine, the only discrepancy being that the tail of one Papanui female specimen has a pointed end instead of a rounded end. The Papanui Inlet population was identified as belonging to *Litoditis mediterranea* based on a cross-breeding experiment with cultures from Europe conducted by Walter Sudhaus (Leduc & Gwyther 2008). The SSU molecular data from the Pāuatahanui Inlet specimen, however, suggests a closer affinity with *L. marina* (see below).

**Sequence data.** Partial SSU rDNA (1334 bp; Genbank OK317217). The Pāuatahanui SSU sequence differed from a *Litoditis mediterranea* sequence by 4% (AF083020) and from a *Litoditis marina* sequence by 0.5% (AF083021). A study has shown that dissimilarities between SSU rDNA sequences of different *Caenorhabditis* species (family Rhabditidae) range from about 0.8 to 1.8% (Fitch *et al.* 1995). This range is higher than the 0.5% dissimilarity observed between the Pāuatahanui Inlet sequence and *L. marina*, suggesting that the latter may belong to the same species. *Litoditis marina,* however, has been shown to be a species complex, based on mitochondrial COI, nuclear ITS and D2D3 regions (Derycke *et al.* 2005, 2008).

## Discussion

Coull & Wells (1981) published the first ecological study of meiofauna in New Zealand, which included data on the distribution of meiofaunal taxa (nematodes, copepods, kinorhynchs and oligochaetes) in Pāuatahanui Inlet; subsequent studies were published on the ecology and taxonomy of the harpacticoid copepod fauna for the same area. The present study is the first investigation of nematode species diversity in Pāuatahanui Inlet. Sufficient material (usually at least one male and one female in good condition) was obtained to allow identification or description of 39 of the most common species from the inlet, 26 of which (67%) are new to science. Specimens belonging to an additional 16 species were also collected but they did not provide sufficient material for description or species identification (Table 38). These 16 species belong to a total of 12 genera, 12 families, and seven orders. The total number of nematode species found in the inlet is thus 55. However, because sampling did not extend to the subtidal parts of the inlet, and because most nematode species within a given environment are usually rare, it is expected that more species will be found in Pāuatahanui Inlet.

There have been only two studies of nematode species communities in New Zealand coastal environments to date. Warwick *et al.* (1997) investigated nematode communities in shallow subtidal sediments of Mahurangi Harbour (muddy sediments) and Martins Bay (sandy sediments), northeast of Auckland. They found a total of 74 morphospecies at their Mahurangi Harbour site and 104 morphospecies at their Martins Bay site. The study did not provide data on the identity of the species (which were identified to genus and labelled sp. A, B, etc.) except for records of the cosmopolitan species complex *Terschellingia longicaudata* at both locations. The second study of New Zealand coastal nematode species communities was conducted in the intertidal zone of Papanui Inlet in the Otago region (Leduc & Probert 2011) and uncovered a total of 84 nematode morphospecies. As in the Warwick *et al.* (1997) study, limited data on species identity were provided, with only eight named species identified. The available data suggests at least some overlap in species composition between Papanui and Pāuatahanui inlets. *Chromaspirina stilbonematinops* **sp. nov.** was noted by the lead author in samples from Papanui Inlet (Leduc & Probert 2011; referred to as "*Chromaspirina* sp. 1" therein). *Chromadora* cf. *nudicapitata*, *Bathylaimus* cf. *australis,* and *Litoditis* cf. *marina* also occur in both Papanui and Pāuatahanui

**Table 38.** List of the 16 species collected from Pāuatahanui Inlet for which insufficient material was available to allow species description or full identification.

| Order | Family | Genus | NIWA # | Specimens |
|---|---|---|---|---|
| Enoplida Filipjev, 1929 | Oncholaimidae Filipjev, 1916 | *Oncholaimus* Dujardin, 1845 | NIWA 154888 | One male |
| | Oxystominidae Chitwood, 1935 | *Oxystomina* Filipjev, 1921 | NIWA 154883 | One male |
| | Thoracostomopsidae Filipjev, 1927 | *Mesacanthion* Filipjev, 1927 | NIWA 154886 | Ten females |
| | Trefusiidae Gerlach, 1966 | *Rhabdocoma* Cobb, 1920 | NIWA 154890 | One male, one female |
| Araeolaimida De Coninck & Schuurmans Stekhoven, 1933 | Axonolaimidae Filipjev, 1918 | *Odontophora* Bütschli, 1874 | NIWA 154893 | Two males, one juvenile |
| Chromadorida Chitwood, 1933 | Chromadoridae Filipjev, 1917 | *Prochromadorella* Micoletzky, 1924 | NIWA 154894 | One male |
| | Cyatholaimidae Filipjev, 1918 | *Paracanthonchus* Micoletzky, 1924 | NIWA 154889 | One male |
| Desmoscolecida Filipjev, 1929 | Cyartonematidae Tchesunov, 1989 | *Cyartonema* Cobb, 1920 | NIWA 154891 | One male |
| Desmodorida De Coninck, 1965 | Desmodoridae Filipjev, 1922 | *Eubostrichus* Certes, 1899 | NIWA 154884 | One male, two females |
| Microlaimida Leduc, Verdon & Zhao, 2018 | Microlaimidae Micoletzky, 1922 | *Microlaimus* de Man, 1880 | NIWA 154882 | Two males, one female, one juvenile |
| | | | NIWA 154892 | One male |
| Monhysterida Filipjev, 1929 | Linhomoeidae Filipjev, 1922 | *Metalinhomoeus* de Man, 1907 | NIWA 154887 | One male, two females |
| | | | NIWA 154896 | One juvenile |
| | | | NIWA 154897 | One female |
| | | | NIWA 154898 | One female |
| | Xyalidae Chitwood, 1951 | *Daptonema* Cobb, 1920 | NIWA 154895 | One female |

inlets (Leduc & Gwyther 2008), which is perhaps not surprising given their seemingly cosmopolitan distributions. On the other hand, some common species described or recorded from Papanui Inlet, i.e., *Microlaimus falciferus* Leduc & Wharton 2008, *Aponema subtile* Leduc & Wharton 2008, *Desmolaimus courti* Leduc & Gwyther, 2008, *Sabatieria mortenseni* (Ditlevsen, 1921) Filipjev, 1922, *Oncholaimus moanae* Leduc, 2009 and *Pseudochromadora reathae* Leduc & Wharton, 2010 were not encountered in Pāuatahanui Inlet, and vice versa for the common Pāuatahani Inlet species *Spirinia antipodea*.

Despite our incomplete knowledge, it is clear that nematodes represent a significant proportion of the infaunal diversity in Pāuatahanui Inlet, representing about 40% of the total known infaunal diversity. Read (1984) listed 22 species of polychaetes in the inlet, although this is likely an underestimate as samples were restricted to the intertidal zone and the eastern end of the inlet. Arthropods, molluscs, and other macrofauna are represented by about 40 morphospecies in total (Milne *et al.* 2009), and harpacticoid copepods, which have been relatively well-studied, comprise 29 species (Iwasaki 1993). It is likely that nematodes represent a similarly high percentage of infaunal species diversity in other sheltered soft sediment environments around New Zealand.

The present work focused on the taxonomy of nematodes, and consequently no attempt was made to quantify and compare nematode species communities and richness in different parts of the inlet. However, the fact that most (57%) of the species were described from Mana Bank samples suggest that this area is particularly biodiverse (Table 39). Eleven species (30%) were described from the Camborne walkway area, four from Bradeys Bay (11%), and one from the vicinity of Kakaho stream (3%; Fig. 124). Whilst not quantitative, these numbers suggest the existence of a strong declining gradient in nematode species diversity from the lower parts of the inlet in the west to the upper parts of the inlet towards Pāuatahanui Wildlife Reserve in the east, where insufficient specimens could be obtained for species descriptions. Mana Bank was identified as a key habitat of high ecological value due to the high variety of crustacean species, high abundance of juvenile fish such as flounders, and use of this habitat by paddle crabs (WRC 1989a, b). Our observations seem to provide support for the ecological importance of Mana Bank as benthic habitat, although a quantitative ecological survey will be required to


**Figure 124.** Total number of named species described from the Pāuatahanui Inlet sampling locations.

obtain a reliable picture of nematode diversity patterns within the inlet. High sedimentation rates as well as the high concentrations of pollutants may be partly responsible for the seemingly low nematode densities in the upper portion of the inlet (Williamson *et al.* 2004; Swales *et al.* 2005). Surveys of macrofauna in the inlet appear to show lower species richness and abundance in the uppar parts of the inlet (Milne & Sorensen 2009). Macrofaunal community structure in Pāuatahanui Inlet has been linked to concentrations of metal contaminant, although contaminats tend to co-vary with other variables including sediment grain size and organic matter content (Milne & Sorensen 2009).

The availability of molecular data remains limited for most marine nematode species, but it is hoped that the molecular data obtained in the present work will be useful for future comparisons as molecular data become increasingly common. Determining the identity of some species remains problematic, even for species such *as Terschellingia longicaudata* for which a relatively large number of sequences have been obtained. This problem will persist until molecular data are accompanied by morphological descriptions and until populations from type localities of commonly encountered and seemingly widely distributed species or species complexes are sequenced. The provision of sequence data should also facilitate the application of molecular approaches such as environmental DNA for the study of ecological patterns in Pāuatahanui Inlet and other similar habitats across New Zealand.

The present study brings the total number of free-living marine nematode species known from the New Zealand region to 245 at the time of publication. It is estimated that in the order of 1000–5000 additional free-living species are yet to be recorded and described from the region (Leduc & Preswell submitted). Of the 39 species described here, seven [*Bathylaimus* cf. *australis* Cobb, 1894; *Tripyloides* cf. *marinus* (Bütschli, 1874) de Man, 1886; *Chromadora* cf. *nudicapitata* Bastian, 1865; *Chromadorina germanica* (Bütschli, 1874) Wieser, 1954; *Cobbia trefusiaeformis* de Man, 1907; *Terschellingia* cf. *longicaudata* de Man, 1907; *Litoditis* cf. *marina* (Bastian, 1865) Sudhaus, 2011] are cosmopolitan species or species complexes, and an additional two species have been recorded outside New Zealand (Table 39). However, given the state of our knowledge on the taxonomy and distribution of nematode species in New Zealand and elsewhere, it is not possible to speculate about biogeographical patterns or degree of endemicity.

**Table 39.** List of named Pāuatahanui Inlet species with details of their distribution in the inlet and of any other New Zealand or overseas records.

| Site | Species | Other NZ records? | World distribution |
|---|---|---|---|
| Kakaho | *Litoditis* cf. *marina* | Yes | Cosmopolitan |
| Bradeys Bay | *Paracanthonchus wellsi* **sp. nov.** | - | - |
| | *Daptonema falcatispiculum* **sp. nov.** | - | - |
| | *Theristus levicapitulus* **sp. nov.** | - | - |
| | *Chromadorina germanica* | - | Cosmopolitan |
| Camborne | *Viscosia dossena* **sp. nov.** | - | - |
| | *Spirinia antipodea* | - | - |
| | *Eleutherolaimus paraschneideri* **sp. nov.** | - | - |
| | *Metalinhomoeus bifidosetus* **sp. nov.** | - | - |
| | *Daptonema carnulentum* **sp. nov.** | - | - |
| | *Paramonhystera leptamphida* **sp. nov.** | - | - |
| | *Theristus vivax* **sp. nov.** | - | - |
| | *Odontophora atrox* | Yes | - |
| | *Sabatieria* cf. *granifer* | - | Chile |
| | *Bathylaimus* cf. *australis* | Yes | Cosmopolitan |
| | *Terschellingia* cf. *longicaudata* | Yes | Cosmopolitan |
| Mana | *Anoplostoma amphicystum* **sp. nov.** | - | - |
| | *Ledovitia gutturosa* **sp. nov.** | - | - |
| | *Litinium ankistrodinum* **sp. nov.** | - | - |
| | *Axonolaimus glandifer* **sp. nov.** | - | - |
| | *Sabatieria paramacramphis* **sp. nov.** | - | - |
| | *Chromadorita spinicauda* **sp. nov.** | - | - |
| | *Ptycholaimellus spiculuncus* **sp. nov.** | - | - |
| | *Pseudochromadora plurichela* **sp. nov.** | - | - |
| | *Chromaspirinia stilbonematinops* **sp. nov.** | - | - |
| | *Onyx exiguus* **sp. nov.** | - | - |
| | *Linhomoeus manaensis* **sp. nov.** | - | - |
| | *Metalinhomoeus trinimirmecius* **sp. nov.** | - | - |
| | *Omicronema nicholasi* **sp. nov.** | - | - |
| | *Promonhystera crinita* **sp. nov.** | - | - |
| | *Steineria preclara* **sp. nov.** | - | - |
| | *Theristus arcuatospiculus* **sp. nov.** | - | - |
| | *Deontolaimus poriruaensis* **sp. nov.** | - | - |
| | *Cobbia trefusiaeformis* | - | Cosmopolitan |
| | *Tripyloides* cf. *marinus* | - | Cosmopolitan |
| | *Chromadora* cf. *nudicapitata* | Yes | Cosmopolitan |
| | *Microlaimus korari* | Yes | Ross Sea |

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## Taxonomic index

Principal taxonomic account is in bold font; species illustrations are in bold italic.

A checklist of nematode species from Pāuatahanui Inlet, Te Awarua-o-Porirua Harbour, Wellington, Aotearoa New Zealand is given on pages 30–31. Bayesian trees inferred from SSU sequences are given on pages 33 and 141.

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