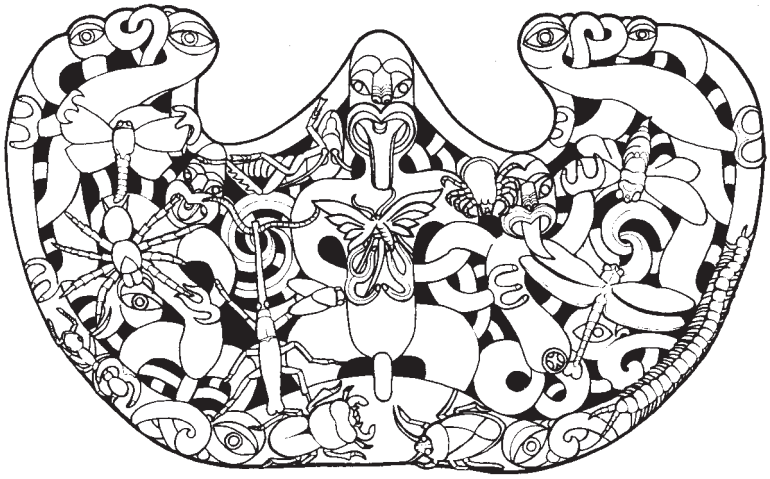

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Root-Knot Nematodes (*Meloidogyne* spp.) (Nematoda: Rhabditida, Meloidogynidae)

by

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POPULAR SUMMARY

Phylum **Nematoda**

Class **Chromadorea**

Order **Rhabditida**

Superfamily **Tylenchoidea**

Family **Meloidogynidae**

Root-knot nematodes (RKNs) (*Meloidogyne* Goeldi, 1887) are plant endoparasites that induce galls on roots and cause severe economic damage to a wide range of plants worldwide. They were first recorded from New Zealand in 1908. However, they are a difficult group taxonomically and the identification and distribution of RKN in New Zealand is not well documented. Correct identification of RKN to species level is an important component of crop and pasture management, especially for developing resistant varieties and effective crop rotations. It is also important for international trade and biosecurity. Descriptions of locally derived specimens are given of the seven RKN species with pest status in New Zealand, and their phylogenetic relationships are presented. The damage caused and possible means of control are discussed, and areas for future investigation are presented.

Ko ngā nematode pona-pakiaka (ngā RKN) (*Meloidogyne* Goeldi, 1887) ko ngā pirinoa rāroto ā-tipu ka āki i ngā puku ki ngā pakiaka, ā, ka pūtakea mai te tūkino ā-ōhanga tino kino ki ngā tipu maha puta noa i te ao. I tuhia tuatahitia ēnei i Aotearoa i te tau 1908. Heoi anō, he uaua te rōpū nei i te taha o te pūnaha whakarōpū, ā, kāore i te pai te tuhi i te tautuhinga me te horahanga o te RKN i Aotearoa. Ko te tautuhi tika i te RKN ki te taumata ā-momo ko tētahi wāhanga tino hira o te whakahaere huanga, whakahaere pātiki karaehe hoki, inā koa mō te whakawhanake momo ārai, me ngā hurihanga huanga whaihua. He mea hira anō hoki mō te tauhoko tāwāhi me te haumaru koiora. Ka tukuna he whakaahuaranga mō ngā tauira i takea mai ā-takiwā o ngā momo RKN e whitu he tūnga kīrehe ō rātou i Aotearoa, ā, ka whakaatuhia hoki ngā hononga o ngā kāwai whakaheke. Ka kōrerohia te tūkino ka pūtakea mai me ngā tikanga ka tāmihia pea ērā, ā, ka whakaatuhia ngā wāhanga hei whakatewhatewha ā muri ake nei.

CONTRIBUTORS

Contributor **Zeng-Qi Zhao** was born in Shanxi Province in the north of China. He gained a Bachelor of Agricultural Science degree from Shanxi Agricultural University, P.R. China in 1985. After graduation, he was employed at Shanxi Agricultural University for 14 years (1985–1999) in teaching, research and administration. He was promoted as Department Head at the Department of Agronomy in 1996. After arriving in Australia in 1999, he worked and studied in the School of Agriculture, Food and Wine, University of Adelaide for 7 years. His Ph.D. project focussed on the taxonomy, biology, ecology and pathogenicity of above-ground nematodes in pine plantations in Australia. Since joining Manaaki Whenua - Landcare Research in 2007, Zeng-Qi has concentrated his research efforts on free living nematodes, including the family Tripylidae, but retains a broad interest in Nematoda, particularly plant-parasitic nematodes. As a Nematologist, he has also been contracted by MPI since he started his work with Manaaki Whenua. Zengqi is the author of over 70 scientific papers and a book on marine nematodes of New Zealand.

Kaikōhai **Zeng-Qi Zhao** i whānau mai i te Porowini o Shanxi i te raki o Haina. I whiwhi ia i te Tohu Paetahi Pūtaiao Ahuwhenua mai i te Whare Wānanga Ahuwhenua o Shanxi, Haina i te tau 1985. Whai muri i tana tohu, i mahi ia i te Whare Wānanga Ahuwhenua o Shanxi mō ngā tau 14 (1985–1999) i roto i te whakaako, te rangahau me te whakahaere. I whakatairangahia ia hei Kaiwhakahaere Tari i te Tari Ahuwhenua i te tau 1996. I te taenga mai ki Ahitereiria i te tau 1999, i mahi me te ako ia i te Kura Ahuwhenua, Ngā Kai me te Wāina, Te Whare Wānanga o Adelaide mō ngā tau e 7. Ko tana kaupapa Ph.D. i aro ki te whakarōpūtanga, te koiora, te mātai pūnaha rauropi me te kaikiri o ngā nematode ki runga ake i te whenua i ngā ngahere paina i Ahitereiria. Mai i te whakaurunga ki Manaaki Whenua - Landcare Research i te tau 2007, kua arotahi a Zeng-Qi ki ngā nematode whai oranga, tae atu ki te whānau Tripylidae, engari kei te whānui tonu tana aro ki te Nematoda, inā koa ngā nematode whakararu tipu. Hei Kaimātai Nematode, kua kirimana hoki ia e te MPI mai i tana tīmatanga mahi ki Manaaki Whenua. Ko Zeng-Qi te kaituhi o ngā pepa pūtaiao nui atu i te 70 me tētahi pukapuka mō ngā nematode moana o Aotearoa.

Contributor **Kerrie Davies** was brought up on a mixed farm on the Liverpool Plains of NSW, Australia. She spent her undergraduate days at the University of New England, Armidale, NSW (B.Sc. Hons, 1968). At the Waite Agricultural Research Institute, she studied locust physiology for her Ph.D. (The University of Adelaide, 1972). After its completion, Kerrie became a post-doctoral fellow (1972–74) with Dr John Fisher working on cereal cyst nematodes. Later, with John she examined the physiology of moulting in *Aphelenchus avenae*. After John's retirement, Kerrie was lecturer in Nematology (1993–99), teaching undergraduates and supervising post-graduate students. She also taught short courses on "Nematodes in Cropping Systems—Identification and Techniques" with Dr. Mike Hodda (CSIRO Ecosystem Sciences). Kerrie supervised projects on *Pratylenchus*, *Anguina*, nematodes as biocontrol agents of pest snails and millipedes, induced resistance to *Heterodera* in white clover, *Heterorhabditis,* brassicas as green manures, and aphelenchid nematodes associated with pine trees. Since 2000, she has been a Visiting Research Fellow at the University of Adelaide. Her research interests include the gall-former *Fergusobia* and nematodes of fig sycones. She has ca 100 scientific publications, including 15 in collaboration with Zeng-Qi Zhao.

I whakatipuria te kaituhi a **Kerrie Davies** i tētahi pāmu whakauruuru o ngā Paparua o Liverpool o NSW, Ahitereiria. I ngā rā o te tohu paetahi i ako ia i te University of New England, Armidale, NSW (B.Sc. Hons, 1968). I te Waite Agricultural Research Institute, i ako ia i te koiora o te locust mō tana Tohu Kairangi (The University of Adelaide, 1972). Ina oti ana te tohu, ka tū a Kerrie hei hoa-rangahau whai muri i te tohu kairangi (1972–74) ki te taha o Tākuta John Fisher e whai ana i te kaupapa o ngā cereal cyst nematodes. I muri ake, i mātai rāua ko John i ngā āhuatanga o te koiora o te whakamāunu i a *Aphelenchus avenae*. I muri i te whakatānga o John, ka tū a Kerrie hei pūkenga i te Mātai Nematology (1993–99), e whakaako ana i ngā tauira tohu paetahi, e whakahaere tikanga ana i ngā tauira tohu paerua hoki. I whakaako hoki ia i ngā akoranga poto mō "Ngā Nematode i ngā Pūnaha Ahuwhenua—Te Tautuhi me ngā Tikanga" tahi ki a Tākuta Mike Hodda (CSIRO Ecosystem Sciences). I whakahaere tikanga a Kerrie i ngā kaupapa mō ngā nematode *Pratylenchus, Anguina* hoki hei taputapu tāmi ā-koiora i ngā hātaretare, i ngā millipede hoki, mō te ātete i ākina ki te *Heterodera* i te korowa mā, mō

Heterorhabditis, mō ngā tipu brassica hei whakahaumako ā-tipu, mō ngā aphelenchid nematodes e whirinaki ana ki ngā rākau paina hoki. Mai i te tau 2000, kua noho ia hei Hoa Rangahau Manuhiri i te University of Adelaide. I roto i ōna aronga rangahau ko te kaihanga-puku *Fergusobia* me ngā nematode o ngā sycone kei ngā piki. Ko tōna 100 ngā putanga pūtaiao i whakaputaina e ia, i roto nei ko te 15 he mahinga ngātahitanga nā rāua ko Zeng-Qi Zhao.

Contributor **Chris Mercer** gained a Bachelor of Agricultural Science degree from Massey University, Palmerston North, in 1971 and was then employed as a technician/senior technician with the Insect Control and Organic Chemistry Group of the Ministry of Agriculture at Ruakura from 1973–1979. He then studied at the University of Auckland from 1979–1981 gaining an M.Sc. in Insect Pathology. He trained in Nematology with the potato cyst nematode group of DSIR at the Mt. Albert Research Centre. In 1982, Chris was appointed as a scientist to DSIR in Palmerston North to research the nematode pathogens attacking white clover. His principal work was the identification of resistance to the clover cyst and clover root-knot nematodes in clovers. A single locus conferring complete resistance to the clover root-knot nematode was found in Kenya white clover. Chris tested resistant material in field trials and incorporated it into seed lines for further evaluation in the AgResearch Grasslands breeding programmes. Chris retired in December 2012 and is leading a native bush restoration project.

I riro i te kaituhi a **Chris Mercer** te Tohu Paetahi Pūtaiao Ahuwhenua mai i Te Kunenga ki Pūrehuroa, i Te Papaioea, i te tau 1971, ā, kātahi ka mahi ia hei pūkenga/pūkenga matua ki te Rōpū Whakahaere Pepeke me te Matū Pūtaiao o te Manatū Ahuwhenua i Ruakura mai i te tau 1973 ki te 1979. I muri mai ka ako ia i Waipapa Taumata Rau mai i te tau 1979 ki te 1981, ā, i whakawhiwhia ia ki te Tohu Paerua Pūtaiao mō te Mātai Mate Pepeke. I whakangungua ia i te Mātai Nematology ki te rōpū potato cyst nematode o DSIR i te Mt. Albert Research Centre. I te tau 1982, i whakatūria a Chris hei kaipūtaiao ki a DSIR i Te Papaioea ki te rangahau i ngā tukumate nematode e patu ana i te korowa mā. Ko tana mahi matua ko te tautuhi i te ātete ki te clover cyst, ki ngā clover root-knot nematodes hoki i ngā korowa. I kitea tētahi pūtau kotahi e tuku ana i te ātete katoa ki te nematode puku-pakiaka o te korowa i te korowa mā o Kenya. I whakamātau a Chris i ngā matū ātete i ngā whakamātau ā-whīra, ā, i whakaurua ki ngā kāwai kākano hei arotake atu anō i ngā hōtaka whakatupu o AgResearch Grasslands. I whakatā a Chris i te Hakihea 2012, ā, kei te ārahi ia i tētahi kaupapa whakaora ngahere māori.

Contributor **Farhat Shah** completed his undergraduate studies (B. Sc. Hons) and his M.Sc. in Plant Pathology at the Agriculture University, Peshawar, Pakistan. From 1989 to 1994, he conducted research in the Department of Agriculture, for the Government of KPK Pakistan, including work on seed potato production. He graduated from Lincoln University, Canterbury, New Zealand, with a Ph.D. in Plant Pathology in 1999 and since then has conducted research as a member of Crop and Food Research in Lincoln in New Zealand. He has engaged in the diagnosis and management of soil-borne pathogens including plant-parasitic nematodes; studied yield gaps of potatoes due to biotic and abiotic constraints; studied the biology of nematodes in potatoes and other crops; screened potato and forage brassica cultivars for resistance and tolerance against plant-parasitic nematodes; and performed diagnostics of soil-borne pathogenic fungi and plant-parasitic nematodes. Farhat has also carried out extension activities, presenting his work to farmers and others at field days and to scientists at workshops and international conferences. He has more than 20 peer-reviewed scientific publications.

I whakaoti te kautuhi a **Farhat Shah** i ana akoranga tohu paetahi (B. Sc. Hons) me tana M.Sc. i te Mate Tipu i te Agriculture University, Peshawar, Pakitāne. Mai i te tau 1989 ki te tau 1994, i mahi ia i ngā rangahau i te Tari Ahuwhenua, mō te Kāwanatanga o KPK Pakitāne, tae atu ki te mahi mō te whakaputa tinaku rīwai. I puta ia i Te Whare Wānaka o Aoraki, i Waitaha, i Aotearoa, ki te Tohu Kairangi i te Mātai Mate Tipu i te tau 1999, ā, mai i taua wā kua mahi ia i ngā rangahau hei mema o Crop and Food Research, i Lincoln, i Aotearoa. I whai wāhi ia ki te tautohu, ki te whakahaere hoki i ngā tukumate o te oneone tae atu ki ngā nematode pirinoa ā-tipu; i rangahau ia i ngā āputa o ngā hua rīwai nā ngā here koiora, nā ngā here koiora kore hoki; i rangahau ia i te koiora o ngā nematode i roto i ngā rīwai, i ētahi atu huanga hoki; i āta whakarōpū ia i ngā momo rīwai, i ngā momo brassica hei kai mā ngā kararehe hoki, mō te ātete, mō te parenga hoki ki ngā nematode pirinoa ā-tipu; ā, i mahi ia i ngā tautuhinga o ngā hekaheka tukumate o te oneone me ngā nematode pirinoa ā-tipu. Kua kawea hoki e Farhat ngā mahi toronga, e whakaatu ana i tana mahi ki ngā kaipāmumā i ngā rā whīra, ā, ki ngā kaipūtaiao i ngā awheawhe me ngā hui ā-ao anō hoki. Neke atu i te 20 āna putanga pūtaiao i arotake ā-hoapātia.

Contributor Lee Aalders was born in Southland, New Zealand. She gained a Master of Science degree from the University of Otago in 1999 and has worked as a Research Technician and a Research Associate for AgResearch Ltd at the Ruakura campus in Hamilton since then. During that time, her research has involved plant-parasitic

nematodes in agriculture, nematodes as biosecurity risks in the Better Border Biosecurity programme, and free-living nematodes as indicators of environmental change. She is the author of 25 scientific papers.

I whānau mai te kaituhi a **Lee Aalders** ki Murihiku, i Aotearoa. I whakawhiwhia ia ki tana Tohu Paerua Pūtaiao mai i Ōtākou Whakaihu Waka i te tau 1999, ā, kua mahi ia hei Pūkenga Rangahau, hei Hoa Rangahau hoki mō AgResearch Ltd i te wāhi o Ruakura i Kirikiriroa mai i taua wā. I roto i tērā wā, i whai wāhi ki tana rangahau ko ngā nematode pirinoa ā-tipu i roto i te ahuwhenua, ko ngā nematode hei tūraru haumaru koiora i te hōtaka Better Border Biosecurity, ko ngā nematode ora-wātea hei tohu o te huringa taiao. Ko ia te kaituhi o ngā pepa pūtaiao e 25.

Contributor Nigel Bell obtained his Bachelor of Science, Master of Science (Entomology); and Ph. D. (Nematology) from the University of Massey. He is now a team leader at AgResearch Ltd; working on plant invertebrate interactions and soil biology. Nigel's work is focused on nematodes and microbes in agricultural systems. He and his team conduct research on many aspects of nematode biology and ecology from population to community level, including using nematodes as bioindicators, control of plant feeding nematodes and preventing entry of unwanted nematodes into New Zealand. He is author of about 80 scientific publications.

I whakawhiwhia te kaituhi a **Nigel Bell** ki tana Tohu Paetahi Pūtaiao, ki tana Tohu Paerua Pūtaiao (Mātai Pepeke), ki tana Tohu Kairangi (Mātai Nematology) hoki mai i Te Kunenga ki Pūrehuroa. I tēnei wā he kaiārahi rōpū ia i AgResearch Ltd; ā, e mahi ana ia e pā ana ki ngā pāhekoheko a ngā tuaiwi-kore ā-tipu, ki te koiora ā-oneone hoki. E aro ana tā Nigel mahi ki ngā nematode me ngā moroiti i roto i ngā pūnaha ahuwhenua. Kei te mahi rangahau rātou ko tōna rōpū e pā ana ki ngā āhuatanga maha o te koiora me te mātai hauropi o te nematode mai i te taumata o te taupori ki te taumata o te hapori, tae atu ki te whakamahi i ngā nematode hei tohu koiora, ki te whakahaere i ngā nematode kai tipu, ki te ārai i te urunga mai o ngā nematode kāore e hiahiatia ana ki Aotearoa anō hoki. Ko ia te kaituhi o ngā pepa pūtaiao tata ki te 80.

ABSTRACT

Root-knot nematodes (RKNs) (*Meloidogyne* Goeldi, 1887) are plant endoparasites that induce galls on roots and cause severe economic damage to a wide range of plants worldwide. They were first recorded from New Zealand by Kirk in 1908. However, they are a difficult group taxonomically and the identification and distribution of RKN in New Zealand is not well documented. Correct identification of RKN to species level is an important component of crop and pasture management, especially for developing resistant varieties and effective crop rotations. It is also important for international trade and biosecurity.

The present study was conducted with the objective of identifying the RKN species in New Zealand, summarising the work done, and indicating the areas where future research is needed. Nematodes were isolated from cultivated fields, pastures and orchards. Seven RKN species were characterised using both morphological and molecular approaches. PCR-based molecular analyses confirmed the presence in New Zealand of some highly polyphagous apomictic RKN species. Analyses using sequences of SSU, ITS and LSU allowed consistent discrimination between *Meloidogyne fallax*, *M. hapla*, *M. minor*, *M. naasi*, and *M. trifoliophila*, and also distinguished them from *M. incognita*, *M. javanica*, and *M. hapla*. In contrast, they did not separate *M. incognita*, *M. javanica*, and *M. hapla*, respectively. A properly designed survey, using additional sequences in a molecular study, is now needed to clarify whether other RKN species are present in New Zealand, possibly on indigenous plant species. This study also confirmed that *M. hapla* infects kiwifruit in New Zealand.

Keywords: D2-D3 region of large subunit (LSU) 28S rDNA gene, molecular phylogeny, *Meloidogyne* spp., morphology, nematode identification, perineal patterns, plant-parasitic nematodes, potatoes, root-knot nematodes, PCR, internal transcribed spacer (ITS) region of rDNA, isozyme patterns, kiwifruit, white clover, tomatoes, small subunit (SSU) 18S rDNA gene.

http://www.zoobank.org/urn:lsid:zoobank.org:pub:C81DBEF8-A42F-43D7-BD51-99121EB4561A

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CHECKLIST OF TAXA

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INTRODUCTION

Root-knot nematodes (*Meloidogyne* Goeldi, 1887) (RKN) are plant endoparasites that induce galls on roots and can cause severe economic damage to a wide range of plants worldwide. There are at least 100 nominal species of RKN (Hunt & Handoo 2009, James *et al*. 2019). Economically, they are the most important group of plant-parasitic nematodes (Jones *et al.* 2013). They are polyphagous, significantly damage most important food crops, and have a world-wide distribution. The four most common and damaging species are *M. arenaria* (Neal 1889) Chitwood, 1949, *M. hapla* Chitwood, 1949 (Moens *et al*. 2009), *M. incognita* (Kofoid & White, 1919) Chitwood, 1949, and *M. javanica* (Treub, 1885) Chitwood, 1949. These four species all have very wide host ranges. However, most species of RKN, usually more recently described, are not serious pests and have narrower host ranges and local distribution. Species identification of RKNs is very challenging because specific techniques are required for morphological studies, *i.e*., specialist training is needed, and they tend to have high levels of intraspecific variability both in morphology and in genetics (e.g., Hartman & Sasser 1985, Hunt & Handoo 2009). Molecular (sequencing), biochemical (esterase tests), and biological (differential host tests) techniques are therefore needed in addition to morphological studies.

Above-ground symptoms of RKN attack in the field are usually non-specific, resembling nutrient deficiencies including yellowing, stunting, easy wilting and reduced growth. Below-ground, RKNs induce specific galls on roots, which may vary in form according to RKN species, the type of host plant and its susceptibility, and the numbers of nematodes attacking the plant. In tuber-forming plants like potatoes, brown spots and rotting of tubers may occur, and small galls may develop on the surface of the tuber causing cosmetic damage. Roots of plants like carrots and parsnips may be deformed. Heavily galled roots are unable to efficiently absorb water and nutrients, leading to poor growth and decreased yield and reduced persistence. Root-knot nematodes, like other plant-parasitic nematodes, damage host roots as they feed and/or move within them, causing loss of root exudates into the soil. These may attract other pathogenic organisms such as root-rotting fungi. Thus, RKNs are not only primary pathogens but also cause disease complex within the soil around host roots.

The life cycle of RKNs (Fig. 1) is complex (e.g., Jones & Payne 1978; Barker *et al.* 1985; Moens *et al.* 2009; Chitwood & Perry 2009). They are endo-sedentary parasitic nematodes. As plant parasites of the Superfamily Tylenchoidea, they have a modified stoma or mouth which carries a stylet—a hollow, needle-like structure made of cuticle. The first moult occurs within the egg, and the nematode hatches as the J2, which is the infective stage. The J2 migrates through the soil towards the growing tip of a suitable root, attracted by plant root exudates and CO_2 gradients. This stage has a much-enlarged subventral oesophageal gland, which produces and secretes proteins and peptides called effectors (Vieira & Gleason 2019), molecules that target host pathways to facilitate parasitism. The infective juvenile uses thrusts of its stylet, together with enzymes secreted from the subventral gland, to soften the cell walls and allow penetration of the root. It then migrates (intercellularly, thus avoiding much of the host's immune receptors) through the cortex to a suitable spot near the vascular cylinder, where it becomes immobile. There, the juvenile uses its stylet to penetrate the walls of five to seven cells near its head and begins to feed on the plant cell cytoplasm. As part of this procedure, it injects further secretions into the cells, which interact with the host plant's molecular pathways and induce specialised feeding structures which become giant cells. The affected cells undergo repeated cycles of mitosis without cell division, *i.e.,* they become multinucleate. The nuclei enlarge and the cytoplasm appears granular. The cells hypertrophy, and the surrounding parenchyma cells divide repeatedly, and eventually form the galls diagnostic of RKNs. The giant cells act as a nutrient sink and as transfer cells and are metabolically very active. They probably transfer solutes to the feeding tubes secreted by the nematode and attached to its stylet. The nematode then moults a further three times. In many species of RKN, males are rare or absent, and in some are induced by exposure to extreme environmental conditions such as heat greater than 35ºC. Males are vermiform and motile, and do not feed. Females remain sedentary and develop into the pear-shape typical of RKN. Where present, males are attracted to females via pheromones, and mating and insemination occur. Eggs are laid into a gelatinous matrix produced by glands near the female's anus. The matrix apparently contains antibiotics to prevent bacteria from attacking the eggs and it also protects them from desiccation. Twenty to thirty per cent of these eggs will hatch within a month but the others are in some sort of dormancy or diapause, which allows some eggs to be carried over from season to season. In general, hatching of RKN eggs is dependent only on suitable temperature and moisture conditions, with no stimulus from host plants being required. In some cases, root diffusates and generation number within a season can influence the hatching

response (Curtis *et al*. 2009). Some species of *Meloidogyne*, e.g., *M. naasi* (Antoniou & Evans 1987) require a period of cold to induce hatching.

Some *Meloidogyne* spp. have become important, economically significant agricultural pests, and enormous research efforts have been and are continuing to be made to understand how they interact with host plants (Rutter *et al*. 2022). This work has been aided by the recent technological advancements in molecular studies (Rehman *et al.* 2016; Vieira & Gleason 2019). For example, mass spectrometry has been used to identify 486 proteins secreted by second stage juveniles of *M. incognita*, most from the subventral oesophageal gland (Bellafiore *et al.* 2008). These function in protein synthesis and secretion, modification of plant cell walls, cell cycle modulation, protection from host cell defences and giant cell formation – all important for plant parasitism by the nematode. The full genomes of *M. incognita* (Abad *et al.* 2008), *M. hapla* (Opperman *et al*. 2008), *M. arenaria* (Sato *et al.* 2018) and *M. enterolobii* (Koutsovoulos *et al*. 2020) and some other species of RKN are now known, aiding in the identification of putative effectors. The genomes of all RKNs examined have a set of genes encoding plant cell wall-degrading enzymes, apparently linked to their plant-parasitic lifestyle, and not found in other animals (Danchin *et al.* 2009).

Root-knot nematodes have a wide variety of reproductive strategies, ranging from amphimixis to obligatory mitotic parthenogenesis (Chitwood & Perry 2009). There are no sex chromosomes (Triantaphyllou 1973). Sex ratios vary, with males being rare in some species and produced in others via sex-reversal under environmental stress (these have two not one gonad). The form of parthenogenesis also varies, being mitotic in *M. incognita, M. arenaria,* and *M. javanica*. However, *M. hapla* is a facultative parthenogen; its form of reproduction depends on the race. Meiotic parthenogenesis occurs in *M. naasi, M. fallax,* and *M. trifoliophila.* There is no pairing of homologous chromosomes in mitotic parthenogenesis, and no sexual meiotic recombination occurs in *M. incognita* (Castagnone-Sereno 2006). *Meloidogyne incognita, M. arenaria,* and *M. javanica* are all polyploid, and they have highly divergent genomes that have probably resulted from different hybridizations. This structure is associated with different gene expression patterns, which may favour their polyphagous habits. Castagnone-Sereno *et al*. (2019) have suggested that variations in the number of gene copies are involved in adaptive processes of the nematode. This could explain the development of host races in mitotic species of RKN (Eisenback & Triantaphyllou 1991). Evolution of races can be used to differentiate some species (Hartmann & Sasser 1985).

Temperate RKN species such as *M. chitwoodi*, *M. fallax* and *M. hapla* are diploid and may reproduce sexually or parthenogenetically, whereas the tropical species such as *M. arenaria, M. javanica* and *M. incognita* are mitotically apomictic (Castagnone-Sereno 2006). The nature of reproduction in the tropical apomicts leads to reticulate evolution (Hugall *et al.* 1999), which occurs when a lineage arises from partial merging of two ancestor lineages. The reticulate pattern, seen in phylogenetic trees derived from DNA sequences of apomictic organisms, results from how such species evolve via processes including symbiosis, lateral gene transfer and interspecific hybridization (Gontier 2015; Lunt 2008). Over time, large differences in allelic sequences in one species may arise from accumulation of mutations. This makes analyses of the genomes of apomictic species like *M. javanica* and *M. incognita* more complicated than for sexually reproducing forms.

Correct identification of RKN species is important for crop and pasture management, particularly for the development of host plant resistance and crop rotation as a strategy for reduction in nematode populations (Hunt & Handoo 2009) and for trade. Traditional identification of RKNs based upon morphology requires considerable expertise, and inexperience can easily lead to incorrect diagnoses. While examination of perineal patterns (Fig. 2) and biochemical markers have been important for identification of RKNs, molecular techniques are increasingly used for species differentiation and diagnostics (Blok & Powers 2009). Ribosomal DNA regions and the cytochrome oxidase (COII) - 16S rRNA gene region of mtDNA have been utilised to examine the phylogenetic relationships of RKNs (Hugall *et al.* 1997). McClure (2012) used sequence and phylogenetic analyses of 18S rRNA, D2-D3 of 28S rRNA, internal transcribed spacer-rRNA and mitochondrial DNA gene sequences to identify RKN species from golf courses in the United States of America. PCR diagnostic assays based on ribosomal sequence information or sequence characterised amplified regions (SCAR) have been used for rapid and sensitive species diagnosis (e.g., Tigano *et al.* 2010; Wishart *et al.* 2002; Zijlstra 2000). Adam *et al*. (2007) assembled a collection of these molecular marker assays into a diagnostic key for distinguishing a range of RKN. While molecular techniques are now the preferred methods for distinguishing RKN species, challenges to their application for fully identifying all RKNs remain, due to inter- and intra-specific sequence variation (e.g., Blok & Powers 2009; Hunt & Handoo 2009).

Meloidogyne nematodes were first recorded from New Zealand by Kirk (1908). Since then, they have been reported to infect a wide range of host plants in New Zealand (Dale 1972). However, the identification and distribution of RKNs in New Zealand have been less studied (Hodda & Nobbs 2008) than in many countries. To date, various named RKN species (*M. ardenensis, M. arenaria, M. fallax, M. hapla, M. incognita, M. javanica, M. minor, M. naasi, M. trifoliophila*), along with a number of undefined RKN isolates have been reported from New Zealand (Anon. 1967 in Dale 1972; Clark 1963; Knight *et al.* 1997a; New Zealand Ministry of Agriculture and Forestry 2001; Marshall *et al.* 2001; Mercer *et al*. 2007; Zhao *et al*., 2017; Bell personal communication, 2020). *Meloidogyne ardenensis* has been collected and reported from New Zealand on four occasions, all from *Prunus* spp. (Dale 1972). All these identifications were based on morphology alone. While *Prunus*, as a woody dicotyledonous plant, is a suitable host for this species (Thomas & Brown 1981), it is difficult to separate *M. ardenensis* from *M. incognita* on morphological grounds (Santos 1967) and the actual identity of the nematodes from *Prunus* cannot be confirmed in the absence of molecular tests. It is not considered to be an economic threat (Thomas & Brown 1981). In addition, there are no specimens of putative *M. ardenensis* collected in New Zealand available for study. Thus, *M. ardenensis* is not included in this work. *Meloidogyne arenaria* has a world-wide distribution and was apparently collected in New Zealand from *Ficus elastica* by an unknown person in 1967 (Dale 1972). Dale (1972) also reported it as a new record for New Zealand, collected from elm (*Ulmus* sp.). Sequences of *M. arenaria* used in molecular studies of New Zealand materials were supplied by Zijlstra (1997) and were not from indigenous specimens. The 2006 list of regulated pests for importation of nursery stock (New Zealand Standard 155.02.06) includes *M. arenaria, i.e*., it is not recognised in New Zealand. Many reports of *Meloidogyne* from New Zealand have been of *M. hapla* from a broad range of hosts including pasture species but these were often mis-identified and were actually *M. trifoliophila* (Watson & Mercer 2000). Recently, *M. fallax* has been reported infecting fodder beet and white clovers and is threatening the pasture industry in New Zealand (Rohan *et al.* 2016). Both *M. fallax* and *M. hapla* infest kiwifruit (*Actinidia deliciosa*), an important crop in New Zealand (Knight *et al.* 1997a; Farhat Shah personal communication 2020). Because the species *M. fallax, M. hapla, M. incognita, M. javanica, M. minor, M. naasi,* and *M. trifoliophila* have been widely collected and characterised in New Zealand, they are included here.

The pest status of any given nematode species can be estimated from its population density and frequency of association with particular host plants, its unique symptoms (where they occur), and the degree of increased productivity following use of nematicide or soil pasteurisation (Mercer 1994). The major economic plants affected by RKN in New Zealand are, in terms of export value, white clover and kiwifruit; and for domestic value, potatoes and tomatoes (Mercer 1994). In New Zealand pastures, white clover roots are attacked by several nematodes, mainly clover root-knot nematodes (*Meloidogyne* spp.), clover cyst nematode (*Heterodera trifolii*) and root lesion nematodes (*Pratylenchus* spp.). These attacks reduce plant vigour, increase the rate of stolon death, and compromise vegetative persistence (Watson & Mercer 2000). Prior to 1994, many reports of *M. hapla* were from clover species (*Trifolium* spp.), but the RKN commonly infecting clovers has since been recognised as *M. trifoliophila*, the most widespread RKN species in New Zealand pastures (Bernard & Eisenback 1997; Watson & Mercer 2000; Mercer *et al.* 2008). In vegetables, *M. fallax* is increasingly common in New Zealand potato crops, particularly in the North Island (Shah *et al.* 2010). *Meloidogyne naasi* has been reported from several grasses and some cereal crops in New Zealand (Grbavac *et al.* 1978; Sheridan & Grbavac 1979), and *M. minor* was recognised as a recent incursion in turf grasses (Zhao *et al*. 2017).

Grazing of sheep (for meat and wool) and cattle (for meat and dairy products) is vital to the New Zealand economy and relies on pastures in which white clover (*Trifolium repens*) is the main forage legume, grown in combination with perennial ryegrass (*Lolium perenne*) (Ford *et al*. 2015). White clover is important also for nitrogen fixation, estimated to have an annual value in NZ $1.49 billion, with herbage production value $1.33 billion, an enhanced value of $22 million, honey production value $30 million, and seed production $30 million (ceresfarm.co.nz/clover.htm#Top, accessed 28 November 2023; https://www.ceresfarm.co.nz). White clover fixes approximately 1.57 million tonnes of nitrogen annually, contributing approximately $1.49 billion to the New Zealand economy (Caradus *et al*. 1996). The annual financial contribution of white clover through fixed nitrogen, forage yield, seed production and honey production is estimated as $3.095 billion (Caradus *et al.* 1996). Dairy exports make up about 30% of New Zealand's annual agricultural exports (Ford *et al.* 2015), with a value of *ca* NZ $20 billion in 2020 (NZ Dept. of Statistics). It is difficult to distinguish the value of the damage respective

invertebrate pests are causing to pastures, as they often co-exist in the field. Thus, RKN often occurs with more damaging pests such as weevils, scarab grass grubs, and porina moth, and with other nematodes (particularly *Heterodera* and *Pratylenchus*). The nematode most commonly found in pastures is *Pratylenchus*, occurring in about 90% of all pasture soil samples in New Zealand (Yeates 1981; Knight 2001; McNeil *et al.* 2015). In general, in the North Island, populations of *Heterodera* peak in the spring and autumn, while those of RKN are highest in summer and early autumn (Ferguson *et al.* 2018).

Yeates (1977) concluded that RKNs were primary pathogens significantly affecting clover growth and nitrogen fixation. Field trials in which nematicides were used to control nematodes (including RKN) resulted in an increase of 40% in clover production, a lift of 57% in N fixation, and improved ability of white clover to recover from drought (Watson *et al*. 1985; 1993). More recent work on trials with soil pasteurization (Wakelin *et al.* 2016) has estimated the cost of root disease (which includes unquantified levels of RKN) in white clover. They found an increase of 12–64 % (ave. 28.5%) in white clover production after pasteurization; and estimated that root diseases cost (NZ) \$750 ha^{-1}year in Southland; \$715 ha^{-1}year in Canterbury, and \$1506 ha^{-1}year in Waikato (important dairy regions of New Zealand). More recently, Ferguson *et al*. (2018) estimated that pasture nematodes cost dairy farmers up to NZ \$274 million p.a. and sheep and beef farmers NZ \$326 million p.a.

Kiwifruit is also economically important for New Zealand. Exports of the fruit were valued at about NZ \$3 billion in 2021 (Overseas Trade Statistics 2021; N.Z. Department of Statistics). Putative *M. hapla* is commonly isolated from kiwifruit vines (Watson *et al*. 1992; Knight 1997a), but apparently causes little reduction in yield (Sale 1985). Potatoes are particularly important in New Zealand in crop rotations with pastures (export value NZ \$105,838 million p.a. and total value NZ \$1,160 million p.a. in 2020 (Annual Report of Potatoes New Zealand Inc.)), and while *Globodera* spp. is the major nematode problem for this plant (Marshall 1993), *M. naasi* causes both cosmetic and manufacturing problems. New Zealand uses more land for growing potatoes than for any other crop, with over 10,000 hectares grown each year, and the industry is expanding.

Tomatoes are the major vegetable grown for domestic consumption in New Zealand, with an estimated value of NZ \$60 million in 1992 (NZ Vegetable and Potato Growers Federation), but most are grown hydroponically. Several species of RKN are well known to reduce yield of tomatoes grown in soil, but losses in New Zealand have not been measured (Nigel Bell and Farhat Shah, personal communication, 2022).

From the above summary, it is evident that RKNs are a significant problem for New Zealand agricultural production. As a first step to future identification and surveys of the RKNs in New Zealand, we here characterise (morphologically and with molecular markers including ITS sequences) various isolates of New Zealand RKNs. These New Zealand studies are by no means complete and have often been carried out on an *ad hoc* basis. We present them here as much to indicate what is not known of this group in New Zealand as to show what is. We consider the current understanding of the distribution and hosts of these nematodes, both for New Zealand and the world, and comment on possible management regimes and future research. Our aim has been to indicate the research needed to establish just what species of RKN are present in New Zealand; for development of a more rational basis for plant breeding programmes for resistance and tolerance to RKN; and to support crop rotation recommendations and other suggestions for management of these pest nematodes.

Abbreviations

BT—bootstrap; D2–D3—sequences of the expansion segments of the 28S ribosomal RNA domain 2 and 3; EPPO—The European and Mediterranean Plant Protection Organization; ITS — sequences for internal transcribed spacer-rRNA; J2—second stage juvenile nematode, but also the name for a particular esterase phenotype; LM—light microscope; LSU—sequences for large subunit ribosomal RNA; MAF—Ministry of Agriculture and Forestry; NNCNZ—National Nematode Collection New Zealand; NCBI—National Center for Biotechnology Information. PP—posterior probability; RKN—root-knot nematode; SSU sequences for small subunit ribosomal RNA.

The following two letter geographical codes (Crosby *et al.* 1998) refer to specific regions of New Zealand, from where the collections listed in this publication were made: AK—Auckland; BP—Bay of Plenty; CL—Coromandel; CO—Central Otago; DN—Dunedin; GB—Gisborne; HB—Hawkes Bay; MC — Mid Canterbury; NC—North Canterbury; ND—Northland; NN—Nelson; RI—Rangitikei; SC—South Canterbury; SL—Southland; TK—Taranaki; WA—Wairarapa; WD— Westland; WI—Wanganui; WO—Waikato.

MATERIALS AND METHODS

Cultures

Cultures of various *Meloidogyne* species were initiated from egg masses hand-picked from roots (see Table 1 for details of collection sites and host plants). *Meloidogyne fallax, M. hapla, M. incognita*, and *M. javanica* were maintained in pots with tomato (*Solanum lycopersicum* Mill. Cv. Rutgers), and *M. trifoliophila* was maintained in pots on white clover (*Trifolium repens* L. Cv. Grasslands Sustain), grown in a glasshouse with range 15–25ºC.

Table 1. *Meloidogyne* species collected in New Zealand; with host plant, site collection, voucher number and GenBank accession number.

Species	Host plant	Site of collection	Voucher No.	GenBankAcc.#		
				SSU	ITS	LSU
fallax	Fodder beet (*Beta vulgaris*)	Taupo	NNCNZ 4000–4019	PP789162	KP825333	PP792552
hapla	Kiwifruit (*Actinidia chinensis*)	Te Puke	NNCNZ 4029–4039 MPI nematode collection slide nos 1032, 1057, 1064. 1109	PP789163	JX465582	PP792553
incognita	Tamarillo (*Solanum betaceum*)	Keri Keri	NNCNZ 4040–4053	PP789164	JX465583	PP792554
javanica	Courgette (*Cucurbita pepo*)	Keri Keri	NNCNZ 4054–4064 MPI nematode collection slide nos 1265, 2265	PP789165	JX465564	PP792555
minor	Perennial ryegrass (*Lolium perenne*)	Hagley Oval, Christchurch	NNCNZ 3210–3237	KX671111	KX671108	KX671113
naasi	Perennial ryegrass (*Lolium perenne*)		NNCNZ 4065–4076 MPI nematode collection slide no. 3310	PP789166	PP784305	PP792556
trifoliophila	White clover (Cv. Sustain) (*Trifolium repens*)	Fitzherbert West, Palmerston North	NNCNZ 4077–4097	PP789167	JX465593	PP792557

Extraction

Nematodes were extracted from root and soil samples using a modification of the Whitehead & Hemming (1965) tray method (Bell & Watson 2001). Root knots (galls) and egg masses were collected from the root samples, and mature females were dissected from the galls. Adult males and second stage juveniles that emerged from the root mass were collected from the fluid in the base of the trays.

Morphological examination

For morphological examination, some nematodes were heat-killed and mounted in water on glass slides (Davies & Giblin-Davis 2004) as temporary specimens. Others were heat-killed, fixed in 3% formalin and transferred to glycerol for mounting on slides as 'permanent' specimens (Davies & Giblin-Davis 2004). A total of seven species, involving 15 populations, comprising more than 283 nematodes, including 78 females, 76 males, 129 juveniles, mounted on slides from the NNCNZ and the Nematology Collection of MPI, New Zealand, were studied and examined using interference contrast microscopy (Nikon, Eclipse 90*i*). Measurement of specimens both in water and in glycerol were made using a NIS-Elements Basic Research microscope (Nikon, Version 2.32). Maximum body diameter was measured at mid-body length for males and second stage juveniles, respectively. Body length was measured along the mid-line. De Man's ratios were determined. Micrographs (digital images) were made using a camera attached to the microscope (Nikon Camera Head DS-Fi1) (Zhao *et al.* 2015). Where RKN species were cultured, eggs could be collected and measured, but this was not possible for some field collections.

Molecular methods

1. For species identification

A single second stage juvenile, a male, and a mature female were each used separately for DNA extraction for all RKN species identification. A modification of the method of Zheng *et al*. (2002) was followed for DNA extraction. A single nematode was transferred into a 200 µl PCR tube, with 20 µl of nematode lysis buffer (125 mM KCI, 25 mM Tris-CI pH 8.3, 3.75 mM $MgCI_2$, 2.5 mM DTT, 1.125% Tween 20) and 2 µl of proteinase K (600 µg/ml). The tube was incubated at 65 ºC for 60 min, followed by 95 ºC for 10 min. Total genomic DNA was extracted using worm lysis buffer containing proteinase K (Williams *et al*. 1992).

The following primers were used for polymerase chain reaction (PCR): for rDNA small subunit (SSU)–first SSU 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 2646R, 5'-GCTACCTTGTTACGACTTTT-3' (Holterman *et al*. 2006); for rDNA D2-D3 expansion segments of the large subunit (LSU), the forward primer D2A, 5'-ACAAGTACCGTGAGGGAAAGT-3' and the reverse primer D3B, 5'-TGCGAAGGAACCAGCTACTA-3' (Nunn 1992); for ITS 1 and 2, the forward primers ITS5, 5'-GGAAGTAAAAGTCGTAACAAGG-3' (Howlett *et al*. 1992) and the reverse primer ITS26, 5'- GCGGATCCATATGCTTAAGTTCAGCGGGT-3' (AB28, Howlett *et al*. 1992); for mtDNA cytochrome c oxidase II (COII), the forward primer C2F3, 5'-GGTCAATGTTCAGAAATTTGTGG-3' and reverse primer 1108, 5'-TACCTTTGACCAATCACGCT-3' (Powers & Harris 1993) were used.

The 20 µl PCR reactions contained 10 µl 2x Go Taq®Green master Mix (Promega Corporation, Madison, WI, USA), 1 µl (5µM) each forward and reverse primer and 2 µl of DNA template. The thermal cycling programme was as follows: denaturation at 95 ºC for 3 min, flowed by 40 cycles of denaturation at 95 ºC for 30 sec, annealing at 55 ºC for 30 sec and extension at 72 ºC for 45 sec. A final extension was at 72 ºC for 7 min. The amplicons were electrophoresed on 1.2% agarose (in 1x TAE) gel stained with SYBR® Safe and visualised using a Gel Doc Software system (BioRad, Hercules, CA, USA).

Successfully amplified products were sequenced bi-directionally using the amplification primers by EcoGene® (Auckland, New Zealand). The DNA sequences obtained were edited against the GenBank database (Altschul *et al.* 1990). The sequences were deposited in GenBank with the accession numbers listed in Table 1.

Published sequences of *Meloidogyne* species for SSU (35), ITS (61) and D2-D3 (53) from GenBank were included in the phylogenetic analysis (because Cox II sequences were only obtained from *M. minor*, no phylogenetic study is made here using those sequences). Nematode species and GenBank accession numbers are listed for each taxon in the phylogenetic trees (Figs 3–5). Sequences generated in the work reported here are in bold. DNA sequences were aligned in ClustalX2 (Larkin *et al.* 2007) using default parameter values. ModelTest 3.04 (Posada & Crandall1998) and PAUP*4.0b10 (Swofford 2002) were used to select the best fitting model using the Akaike Information Criteria (AIC). A Bayesian phylogenetic tree was constructed using MrBayes 3.1.2 (Ronquist & Huesenback 2003) with four MCMC chains run for $1x10^6$ generations. The best fitting model for SSU was GTR + I + G; for D2-D3 GTR + G; and for ITS it was GTR + G. Prior distributions were as follows: ratepr = variable, revmatpr = dirichlet (1,2,1,1,2,1), shapepr = exponential (5), brlenspr = unconstrained: exponential (10). We started analysis from a random topology and used a temperature of 0.2, a burnin of 10% and a thinning interval of 1,000. Multiple runs were performed to ensure convergence. We also performed a maximum parsimony analysis in PAUP*4.0b10 (Swofford 2002) with bootstrapping. For the bootstrapping we used 100 replicates with 100 random addition replicates from stepwise addition trees and TBR branch swapping. The trees were rooted using *Meloidogyne marylandi*, which is sufficiently divergent from the species considered here to function as an outgroup.

2. For sampling of pastures for RKN

Between 2010 and 2017 an *ad hoc* survey was conducted to examine changes in the distributions of RKN species. While this was not comprehensive, it was what could be achieved with the staff and funding available. Root-knot nematodes were isolated from pasture soil extractions from various locations around New Zealand. Individual J2s were initially identified based on their tail morphology and identification was then confirmed using molecular methods.

For DNA identification of *Meloidogyne* species from this survey, individual J2s were placed on a concave slide with UltraPure™ DNase/RNase-Free Distilled Water (Thermofisher Scientific) and then transferred to another concave slide containing prepGEM™ buffer. The nematode was ruptured with a sterile blade then transferred, using a glass micropipette, to a sterile tube containing 20 µl of prepGEM™ buffer.

DNA was extracted from each specimen using the prepGEM™ tissue kit (ZyGEM Corporation Ltd, New Zealand) according to manufacturer's instructions. The ribosomal internal transcribed spacer (ITS) was amplified using the primers ITS5 (White *et al.* 1990) and ITS26 (AB28, Howlett *et al.* 1992). DNA was amplified in 25µl reactions comprising of 2 µl of template DNA, using 1x buffer (Hi-Fi Buffer, Bioline), 1mM dNTPs, 0.4µM of each primer, 0.2 mg/ml BSA and 1 unit of *Taq* polymerase (Velocity *Taq*, Bioline). Thermo-cycling included an initial denaturing at 98ºC for 2 min, then for 40 cycles, 98ºC for 30 sec, 55ºC 30 sec, 72ºC for 45 sec, with a final extension step of 72ºC for 5 min. The product was purified using the Gene JET PCR purification kit (Thermofisher Scientific). Where there was a sequence heterogeniety (*i.e*., the presence of two overlapping peaks of identical size in the electropherograms), the purified products were cloned in the pCR4-TOPO vector (Invitrogen), prior to DNA sequencing of individual clones. The fragments were sequenced by Massey Genome Service (Massey University, New Zealand) and cleaned using Geneious™ 8.1.5 (http://www.geneious.com, Kearse *et al*. 2012). The sequences were compared to nematode sequences listed on the BLAST (Basic Local Alignment Search Tool) website (http://blast.ncbi.nlm.nih.gov/).

Gel electrophoresis for esterase and malate dehydrogenase isozymes

Isozyme phenotypes were determined for mature females of isolates of *M. hapla, M. javanica, M. incognita* and *M. trifoliophila* from cultures on tomato or white clover (Mercer *et al.* 1997). A minimum of eight females for each species, together with their associated egg masses, were macerated individually in 0.1 M phosphate extraction buffer (pH 7.4) with 20% sucrose, 2% Triton X-100, and 0.1% bromophenol blue. Electrophoretic separation of esterase and malate dehydrogenase isozymes was made with an automated Phastsystem (Pharmacia, Uppsala, Sweden). Esterase and malate dehydrogenase isozymes were detected by staining for enzymatic activity according to the protocols of Esbenshade & Triantaphyllou (1985, 1990).

Mapping of nematode distributions

The two letter geographical codes of Crosby *et al.* (1998), which refer to specific regions, were used to define collection areas in New Zealand. Distribution maps were produced using ESRI. ArcGIS Pro. Version 3.0.3. Nov. 30, 2022. URL: https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview.

Sites from which the individual RKN species were collected were taken from Bell *et al*. (2006), from unpublished morphological lists put together by K. Knight and/or D. Sturhan, and from molecular identifications made by Lee Aalders and Farhat Shah.

MOLECULAR PHYLOGENETIC RELATIONSHIPS

Sequences for partial SSU, ITS and D2-D3 were amplified from the following specimens collected in New Zealand: a female, male and juvenile of *M. fallax. M. hapla, M. incognita, M. javanica, M. minor, M. naasi,* and *M. trifoliophila,* respectively. The sequences of female, male and juvenile were identical, and these were deposited in GenBank with the accession numbers (Table 1). All the obtained sequences aligned with the GenBank sequences for the corresponding species of *Meloidogyne.* The phylogenetic trees inferred from these analyses are shown in Figs 3–5. Molecular phylogeny of near full length SSU, the ITS region and D2-D3 expansion segments of LSU indicate that the specimens collected in New Zealand are phylogenetically close to the corresponding species of RKN. All three trees, derived from SSU, ITS and D2-D3 sequences, grouped the New Zealand isolates of *Meloidogyne* spp. together with the corresponding isolates of species from other countries.

The consensus trees inferred from SSU, ITS and D2-D3 (Figs 3–5) are all similar in that they suggest that the New Zealand isolates of *Meloidogyne* fall within two clades with five sub-clades. The SSU analysis (Fig. 3) suggested a cluster of *M. minor*, *M. fallax* and *M. chitwoodi*, but with poor (62% posterior probability and less than 50% bootstrap) support. This group was sister to a clade of *M. naasi* and *M. trifoliophila,* which has 100% PP and

100% BT support. Sequences from *M. incognita, M. javanica*, and *M. arenaria* were in one large clade (100% PP and 93% BT support overall) but lacked support for groupings of individual species within it. Finally, there is a strongly supported (100% PP and 100% BT) clade of sequences from *M. hapla*, which is sister to all the other clades in the analysis. The arrangement of clades in the ITS analysis (Fig. 4) was similar to that for D2-D3 (Fig. 5). *M. fallax* clustered with *M. chitwoodi* in a clade with 100% PP and 100% BT support for ITS, and with 100% PP and 100% BT support for D2-D3, respectively, which was sister to a clade comprising sequences from *M. minor* (again with 88% PP and 69% BT support for ITS, and with 97% PP and 66% BT support for D2-D3, respectively). In turn, this combined group was sister to a clade comprising sequences from *M. naasi* and *M. trifoliophila* with 100% PP and 98% BT support for ITS, respectively, and with 100% PP and 96% BT support for D2-D3, respectively. These three sub-clades were then sister to a cluster of two sub-clades; one comprising sequences of *M. javanica*, *M. incognita* and *M. arenaria*, and the other with sequences of *M. hapla* (Figs. 3 and 4). In turn, these were sister to a well-supported clade of *M. enterolobii* (sequences only available for ITS), and a poorly supported grouping of *M. incognita* and *M. hapla*, and a well-supported group of sequences from *M. hapla*. These analyses suggest considerable variability in the sequences of these isolates.

In summary, analyses using sequences of SSU, ITS and LSU allowed consistent discrimination between *Meloidogyne fallax*, *M. hapla, M. minor, M. naasi*, and *M. trifoliophila*, and also distinguished them from *M. incognita, M. javanica, and M. hapla*. In contrast, the sequencing of the three ribosomal genes reported here was unable to discriminate between *M. javanica*, *M. incognita* and *M. arenaria*, or between *M. hapla* and *M. incognita*. This lack of discrimination is similar to the findings of Blok *et al.* (1997) and others.

The work described here was not intended to be a detailed molecular phylogenetic study of RKN, and hence only one recent study from the literature is included in this discussion. The most comprehensive phylogeny of RKN yet published is probably that of Alvarez-Ortega, Brito & Subbotin (2019), who used sequences of five genes (18S, D2-D3, ITS, mitochondrial cytochrome oxidase subunit 1, and the cytochrome oxidase subunit II-16S rRNA intergeneric fragment) from 56 valid species of *Meloidogyne* to infer their tree. The species they used represent more than half the known RKN species. They inferred 11 distinct clades, but 75% of the species were in seven clades within a *Meloidogyne* super-clade. Of these, their Clade I corresponds to the *M. javanica/incognita/ arenaria* clade observed in the analyses reported here; Clade II includes *M. hapla*; and Clade III has two groupings: one including *M. trifoliophila/naasi* and the other *M. fallax/minor*. The clades/groupings inferred in our work agree with those found by Alvarez-Ortega *et al*. (2019) for the corresponding nematode species. Thus, the *Meloidogyne* species known from New Zealand fall into three of the eleven clades proposed by Alvarez-Ortega *et al*. (2019) (Clades I, II and III). Biologically, most of the species falling within Clade I are polyphagous, polyploid mitotic parthenogens, and make up what is known as the 'tropical RKN complex'; Clade II includes species attacking monocotyledons and dicotyledons, having differing modes of reproduction; and Clade III has species which are all meiotic parthenogens, and parasitize both monocots and dicots. Species falling into the remaining eight clades of RKNs apparently have narrower host ranges and do not have world-wide distributions. At present, no species of RKN from New Zealand is known to belong to these clades.

This study, sampling pastures for RKN, has confirmed the presence of several temperate and tropical parthenogenetic RKN species in agricultural areas of New Zealand. Some of these species appear to have variable genetic sequences. When aligned, ITS PCR fragments cloned and sequenced from single specimens of putative *M. incognita*, *M. javanica* and *M. hapla* from agricultural areas of New Zealand (Farhat Shah, personal communication, December 2020) were highly variable, with 99 variable positions in 8 clones from *M. incognita*, 89 variable positions in 8 clones from *M. incognita*, and 100 variable positions in 10 clones from *M. hapla*. Hugall *et al*. (1999) demonstrated that sequence variation in *M. arenaria*, *M. javanica* and *M. incognita* ranged up to 18% with 26 different sequences out of 31 clones. The ribosomal sequences from the New Zealand isolates of *M. javanica* and *M. incognita* had bi-partite phylogenetic clustering similar to that reported by Hugall *et al*. (1999) (Farhat Shah, personal communication, December 2020), with one group of sequences having little variation and a second with much greater divergence. This pattern of ITS variation could result from hybridisation between RKN species (Hugall *et al.* 1999; Lunt 2008).

Preliminary attempts to conduct isozyme tests for New Zealand species of RKN were made using standard methodologies (Bell, personal communication 2023). Unfortunately, these efforts yielded inconclusive results.

They are, however, mentioned below in the Remarks on individual species. It is recommended that any future work on identification of New Zealand RKN should include these tests.

SYSTEMATICS

Inter- and intraspecific variability has long made identification of root-knot nematodes a 'tricky procedure' (e.g., Rammah & Hirschmann 1990; Kaur & Attri 2013). While the development of isozyme (enzymes that differ in amino acid sequence but catalyze the same chemical reaction) and molecular methodologies has allowed greater precision in diagnosis than is possible using morphology alone, even these have encountered problems with variability (e.g., Blok *et al.* 1997; Blok & Powers 2009). Nuclear genome sequencing has shown that *M. incognita, M. arenaria* and *M. javanica* have divergent copies of many loci (Hugall *et al*. 1999; Lunt 2008; Szitenberg *et al*. 2017). Hybridization and genome multiplications during the evolution of these species has meant that species identifications and phylogenetic analyses relying on nuclear gene sequences are difficult. Morphological characters commonly used for identification have included use of the perineal pattern (striations in the cuticle around the terminal end of the globose female, forming characteristic but variable patterns like a finger-print) and positions of the excretory pore and phasmids in mature females; length of the stylet and tail, and position of the phasmids in males; and stylet length and tail length and form in second stage juveniles (e.g., Hunt & Handoo 2009; Subbotin, Palomares-Rius & Castillo 2021). Given the variability, considerable experience and expertise is needed for reliable identifications based on morphology alone, and a suite of characters must be used, and identifications should be confirmed with molecular techniques.

In this section, we present morphological and morphometric data on seven RKN isolated from New Zealand. *Meloidogyne incognita, M. javanica,* and *M. hapla* are economic pests of the potato, pasture and horticulture industries. *Meloidogyne fallax* is widespread on potatoes, as is *M. trifoliophila* on white clover. *Meloidogyne naasi* has been isolated from both North and South Islands of New Zealand, has potential to be a serious pest of pastures, crops and potatoes, and is therefore included here. *Meloidogyne minor* is a recent incursion, and while not widespread at present, it could become a pest of turf grasses and potatoes.

Species descriptions

Descriptions are presented in alphabetical order. All measurements are based on specimens isolated from cultures by Lee Aalders and/or from infested plants by Zengqi Zhao, fixed and mounted on slides kept in the NNCNZ. Additional material, stored on slides in the MAF collection, is detailed here but most was not specifically examined for this work.

Meloidogyne fallax Karrsen, 1996

English common name: False Columbia root-knot nematode
EPPO Code: MELGFA
Figs 6–11.

Measurements: See Table 2.

Morphology

Females: Body annulated, 398–758 µm long, 223–464 µm wide, pearly white, globular to pear shaped, no posterior protuberance, a distinct neck region (124–295 µm long) usually projecting vertically from the body axis but occasionally at an angle of up to 90º to one side. Head region not clearly off-set from body, marked with one or two annules. Head cap distinct but variable in shape; labial disc slightly elevated. Cephalic framework weakly sclerotized; vestibule extension distinct. Stylet 13–15 µm long, cone dorsally curved and shaft cylindrical; knobs large, off-set, rounded to transversely ovoid, slightly sloping posteriorly from the shaft. Excretory pore located about two stylet lengths behind the anterior end of the nematode. One or two small vesicles present along the lumen lining. Pharyngeal glands variable in size and shape. Lateral fields indistinct when viewed with LM. Perineal pattern (Fig. 8) round to ovoid in shape. Dorsal arch ranging from low to moderately high, occasionally angular in form, with coarse striae. Tail terminus indistinct, without punctations. Phasmids too small for clear

observation. Vulva a transverse slit. Perivulval area without striae. Ventral pattern region oval to angular in shape; striae moderately coarse.

Table 2. Morphometrics of adult and second stage juveniles (J2) of *Meloidogyne fallax* isolated from New Zealand. Measurements are in µm and in the form: mean ± SD (range).

Character	Female	Male	J2
n	11	15	21
L	556±112 (398–758)	1190±143 (1047–1432)	343±7.2 (328–352)
a	1.7±0.2 (1.2–2.0)	38.6±4.1 (33.3–44.8)	27.0±1.5 (24.6–29.2)
b		14.7±1.5(11.7–16.6)	6.3±0.3 (5.7–6.9)
c	-	160.1±37.3 (130.4–203.7)	8.2±0.4 (7.5–8.9)
c’	-	-	4.4±0.4 (4.0–5.2)
T	-	61.0±7.0 (52.8–69.7)	
Greatest body diam.	327.4±79.9 (222.8–463.8)	31.2±4.0 (26.9–36.4)	12.7±0.6 (12.1–13.5)
Body diam. at stylet knobs	-	16.2±0.6 (15.2–16.9)	8.7±0.3 (8.3–9.4)
Body diam. at excretory pore	-	22.4±1.1 (20.9–24.4)	11.5±0.3 (11.0–12.0)
Body diam. at anus	-	12.1±1.3 (9.6–13.8)	9.2±0.9 (8.8–10.3)
Head region height	-	3.7±0.3 (3.2–4.3)	1.8±0.3 (1.4–2.3)
Head region diam.	-	9.8±0.5 (8.7–10.7)	4.9±0.6 (4.0–5.7)
Neck length	175.9±44.0 (123.8–259.5)	-	-
Neck diam.	76.7±18.3 (51.8–110.9)	-	-
Stylet	14.0±0.6 (13.1–14.6)	17.9±0.7 (16.7–18.7)	10.0±0.6 (9.0–10.8)
Stylet cone	-	9.6±0.5 (9.1–10.2)	-
Stylet knob height	1.8±0.2 (1.5–2.0)	2.0±0.2 (1.8–2.4)	0.9±0.2 (0.7–1.3)
Stylet knob width	3.9±0.3 (3.4–4.2)	3.9±0.3 (3.3–4.2)	1.7±0.2 (1.4–1.9)
DGO	4.2±0.3 (3.9–4.8)	4.0±0.5 (3.3–4.7)	4.2±0.3 (3.7–4.4)
Ant. end to metacorpus	-	80.3±5.8 (72.3–94.0)	54.8±2.5 (50.0–62.0)
Metacorpus length	37.6±4.7 (31.9–44.3)	18.5±1.9 (14.8–20.6)	12.4±0.9 (10.5–13.2)
Metacorpus diam.	32.1±2.8 (29.8–37.4)	8.8±2.3 (8.6–11.5)	7.1±0.4 (6.4–7.2)
Metacorpus valve length	13.2±0.7 (12.6–13.9)	6.2±0.9 (5.0–7.1)	3.8±0.3 (3.3–4.5)
Metacorpus valve width	9.2±0.7 (8.3–10.3)	3.8±0.4 (3.4–4.6)	2.7±0.2 (2.4–2.9)
Ant. end to end of gland lobe	-	227.0.9±42.6 (177.1–290.7)	-
Excretory pore-ant. end	29.6±5.1 (23.4–34.7)	128.2±9.7 (114.1–143.3)	68.3±2.6 (62.0–71.0)
Tail length	-	7.7±1.2 (6.0–9.2)	42.1±2.6 (38.2–46.4)
Hyaline tail terminus	-	-	13.5±1.5 (11.2–16.5)
Phasmids from anus	-	10.8±0.4 (10.5–11.3)	-
Spicule	-	28.3±1.4 (26.5–30.9)	-
Gubernaculum	-	7.6±1.2 (5.9–9.1)	-
Testis	-	746.0±74.9 (645.2–860.3)	-
Vulva slit length	21.24±3.7 (18.5–26.5)	-	-
Vulva-anus	12.6±1.7 (10.0–13.9)	-	-
Body length/neck length	3.1±0.4 (2.8–3.7)	-	-
Stylet knob width/height	2.2±0.4 (1.8–2.8)	1.9±0.2 (1.6–2.3)	1.9±0.2 (1.7–2.2)
Metacorpus length/width	1.1±0.1 (1.1–1.3)	-	1.8±0.2 (1.5–1.9)
(Excretory pore/L) x 100	-	10.8±1.2 (9.1–12.3)	19.8±0.9 (17.6–20.8)

Females of *M. fallax* are found associated with distinctive galls (Fig. 11). Unlike those induced by other species of RKN, galls induced by *M. fallax* are smaller, globular, and strung out along host roots.

Males: Body vermiform, 1047–1432 µm long, slightly tapering anteriorly, bluntly rounded posteriorly. Cuticle with distinct annules. Lateral field with four incisures; not aereolated. Head slightly off-set, with a single post-labial annule (or head region) usually partly or fully subdivided by a transverse incisure. Labial disc rounded, not elevated. Cephalic framework moderately sclerotized, vestibule extension distinct. Stylet 17–19 µm long, cone straight; shaft cylindrical; knobs large, bifid, rounded, off-set from the shaft. Pharynx with slender procorpus, metacorpus oval shaped with pronounced valve. Ventrally overlapping pharyngeal gland lobe variable in length. Hemizonid 2–3 µm in length, two to four annules anterior to excretory pore. Testis usually long, monorchic, with reflexed or outstretched germinal zone. Tail short (6–9 µm) and twisted. Spicules 26–31 µm long, slender, cephalated, slightly curved ventrally; gubernaculum crescent shaped. Phasmids located anterior to cloaca.

Second-stage Juveniles: Body 328–352 µm long, vermiform, tapering at both ends but posteriorly more than anteriorly. Body annules fine but distinct. Lateral field with four incisures, not areolated. Head region truncate, slightly off-set from body. Head cap not raised, narrower than head region. Cephalic framework weakly sclerotized, vestibule extension distinct. Stylet slender and moderately long (9.0–10.8 µm), cone straight; shaft cylindrical; knobs small, rounded and off-set from the shaft. Pharynx with faintly outlined procorpus and oval shaped meta-corpus with distinct valve. Oesophageal gland lobe variable in length, overlapping intestine ventrally. Hemizonid distinct, at level of excretory pore, which opens behind level of metacorpus. Moderately sized tail (38–46 µm long), gradually tapering to hyaline tail terminus (11–16.5 µm long), with inflated proctodeum. Phasmids not observed. A rounded hypodermis marks the anterior position of the hyaline tail terminus; tail terminus ending in a broadly rounded tip. Terminus usually marked by faint irregular cuticular constrictions.

Eggs: not measured.

Differential diagnosis. The New Zealand isolate of *Meloidogyne fallax* is characterised by having females with a dorsally curved stylet, excretory pore opening between the knobs and metacorpus, and an ovoid perineal pattern with a moderately high dorsal arch and coarse striae. Males have a labial disc with raised lateral edges. J2s have the hemizonid at the same level as the excretory pore, and a short tail with a broadly rounded tip. The New Zealand isolate is morphologically closest to the original description of *M. fallax* (Karssen 1996), and mature females fully fit the original description. However, the New Zealand males differ in having stylets with bifid knobs (as opposed to undivided round knobs). The second stage juveniles are smaller (328–352 *vs* 381–435 µm in length), but size of J2s is so variable that it is not a good character for differentiation of most species of *Meloidogyne* (Rammah & Hirschmann 1990; Kaur & Attri 2013). Galls are typically small and globular, and strung out along roots.

The New Zealand isolate of *M. fallax* is morphologically separated from the other known New Zealand isolates of RKN by the position of the excretory pore in mature females (opening at approximately half the distance between the anterior end and the metacorpus in *M. fallax*, *vs* close to the stylet knobs in *M. incognita, M. minor* and *M. naasi*; at the level of the anterior metacorpus in *M. javanica*; and at about 75% of the distance from anterior end to the metacorpus in *M. hapla* and *M. trifoliophila*). It is further separated from *M. incognita* in having a shorter stylet (13–15 *vs* 16–17.5 µm long). The perineal pattern of *M. fallax* is circular to ovoid, with coarse striae and a high dorsal arch; and lacking the 'wings' and punctations of *M. hapla* and the distinct lateral fields present in *M. javanica*. Males of the New Zealand isolate of *M. fallax* have an arcuate spicule and gubernaculum unlike those of *M. javanica*, which are strongly curved, and have a shorter tail (6–9 *vs* 14–17 µm long). The phasmids on the tail of *M. fallax* male are closer to the anus than in *M. incognita* (10.5–11 *vs* 12–17 µm distant). Body length of the second stage juveniles separates the New Zealand isolate of *M. fallax* from those of *M. incognita, M. javanica, M. naasi,* and *M. trifoliophila* (respectively, 328–352 *vs* 358–412, 354–426, 370–390, and 397–467µm long). They tend to have a short tail with a broadly rounded tip (length 38–46 µm *vs* 43–59 µm in *M. hapla*; 46–61 µm in *M. javanica*; 53–63 µm in *M. minor*; 51–78 µm in *M. naasi*; and 62–77.5 µm in *M. trifoliophila*). The length of the hyaline section of the tail is shorter in *M. fallax* than in *M. naasi* and *M. trifoliophila* (11–16.5 *vs* 20–27 and 17–26 µm long). They lack the digitate tail tip of second stage juveniles of *M. trifoliophila.* Morphologically, it cannot be distinguished from *M. chitwoodi* but sequencing of the ITS region and COI confirms that they are different species (Handoo *et al*. 2004; Janssen *et al*. 2016).

Material examined. Non-type specimens. Eleven females (slide nos NNCNZ 4000–4007), 15 males (slide nos NNCNZ 4008–4011) and 21 juveniles (slide nos NNCNZ 4012–4019) deposited at the National Nematode Collection, New Zealand.

Other material. The MAF collection contains five slides with specimens.

Distribution (Map 1). Based on material examined: New Zealand: **North Island:** AgResearch Campus, Hamilton, WO. **South Island:** Lincoln, Canterbury, MC.

Based on collections: Widely distributed throughout New Zealand, in both the North and South Islands, and the Chatham Islands. North Island: AK, WO, BP, TO, GB, TK, RI, HB, WI, WA, WN. South Island: NN, MC, SC, DN, CO, SO and CH.

For world distributions see Table 3.

Habitat and hosts. Based on material examined: New Zealand: potato (*Solanum tuberosa*) tubers, tomato (*Solanum lycopersicum*).

Based on literature: New Zealand: *Lepinella* spp. (cotula), *Beta vulgaris* (fodder beet), *Solanum physalifolium* (hairy nightshade), *Solanum tuberosa* (potato tubers), *Solanum lycopersicum* (tomato plants), *Trifolium repens* (white clover). For international hosts see Table 3.

Remarks. *Meloidogyne fallax* is identified by the short, broadly rounded tail terminus of J2s, and by inducing relatively small, globular galls strung out along roots (Hunt & Handoo 2009). On potatoes, tubers have raised, blister-like swellings on tuber surfaces. The J2 also has the hemizonid at the level of the excretory pore. The mature female has a curved stylet and an oval shaped perineal pattern with coarse striae and a high dorsal arch.

Meloidogyne fallax was first recorded in New Zealand in 1998 from potato tubers, and infected cotula roots from lawn-bowling greens (Marshall *et al*. 2001; Rohan *et al*., 2015). It has recently been positively identified from kiwifruit (Farhat Shah, personal communication, September 2022). While uncommon in potato crops, occasional outbreaks do occur, as in Southland in 1998 (Marshall *et al*., 2001). In the Canterbury district, it was once confined to wetter areas only (Nigel Bell, personal communication, September 2022). However, with the introduction of irrigation, *i.e*., a change in land-use, it is now found throughout the district. Although only recognised in New Zealand since 1998 (Marshall *et al.* 2001), it is now known from both the North and the South Islands (Ferguson *et al.* 2018).

DNA sequencing of J2s from galls on beet tubers (Shah *et al*. 2010) confirmed morphological observations that they were *M. fallax*. Morphological, sequencing and inoculation tests confirmed that white clover can support development of *M. fallax* (Rohan *et al.* 2016). Both morphological observations and ITS sequences (99.8 % match with *M. fallax* NCBI Genbank accession from the Netherlands (AY281853)) confirmed that J2s arising from single egg masses on white clover were *M. fallax* (Shah *et al*. 2010). The phylogenetic analyses from this study (Figs 3–5) show *M. fallax* is grouped in a clade with *M. chitwoodi* and *M. minor*.

Meloidogyne fallax reproduces by facultative meiotic parthenogenesis (Karrsen 1996). It is regarded as cool climate RKN but has been found widely within both the North and South Island of New Zealand from both cropping and pasture fields (Marshall *et al*. 2001; Shah *et al.* 2010) and the incidence in fields appears to be increasing (Shah *et al*. 2010). *Meloidogyne fallax* is known to develop on a wide range of monocotyledonous and dicotyledonous plants (see Table 3). It was recorded in Australia, on potato, in 2001 (Nobbs *et al*. 2001).

Growers and farmers in New Zealand try to avoid including two or more host plants in a rotation to minimise the risk of building up damaging populations of pests. An earlier assessment (Bell *et al*. 2006) of rotations for management of root-knot nematode populations in pasture (considered to be *M. trifoliophila* and/or *M. hapla* in that assessment) suggested that inclusion of successive crops of turnips (*Brassica rapa* var *rapa*), Italian ryegrass and turnips before re-establishing pasture would be successful. Whether this would still be the case with *M. fallax* is unclear as the host suitability of turnips to this nematode appears to be unknown. Common weeds such as nightshade can be hosts for *M. fallax* (Shah *et al.* 2010). Maize (*Zea mays*) is a poor host for *M. fallax* (Davis & Venette 2004), so could be useful for pasture rotation to manage the nematode. Crop rotation of potato and pasture is common in New Zealand (Cheah *et al.* 2008), partly for management of populations of the potato cyst nematodes *Globodera pallida* and *G. rostochiensis* (Marshall 1993). *Meloidogyne fallax* populations can increase in both potatoes and white clover and ryegrass in pasture, are becoming more prevalent (Shah *et al.* 2010), and may come to restrict yields of both potatoes and pasture crops. It is not clear how much damage *Globodera* and RKN respectively do to potatoes, but both will contribute to disease complexes by weakening the host plants and

promoting entry to roots of soil pathogens like *Verticillium* and *Fusarium*. *Meloidogyne fallax* hatches well in water and does not require hatch stimulation from root diffusate (Wesemael *et al*. 2006).

Table 3. Species, world distribution and hosts of seven species of *Meloidogyne* (while every effort has been made to find records of these nematodes, some will have been missed and not listed here).

Species	Distribution	Hosts	References
M. fallax	Australia, Belgium, Bulgaria, Chile, France, Germany, The Netherlands, New Zealand, Norway, South Africa, Sweden, Switzerland, UK, USA, South Africa	*Beta vulgaris, Cynara cardunculus* var. *scolymus, Daucus carota, Fragaria* × *ananassa, Hemerocallis* sp., *Lactuca sativa, Lamprocapnos spectabilis, Medicago sativa, Oenothera erythrosepala*, *Phacelia tanacetifolia*, *Scorzonera hispanica*, *Solanum americanum, Solanum lycopersicum, Solanum physalifolium, Solanum tuberosum, Zea mays*	CABI 2013; Daher *et al.* 1996; EPPO 2003, 2021; Fourie *et al.* 2001; Hay & Pethybridge 2005; Karssen 1996; Marshall *et al.* 2001; Nambiar *et al.* 2008; Nischwitz *et al.* 2013; Nobbs *et al.* 2001; Rohan *et al.* 2016 Schmitz *et al.* 1998; Shah *et al.* 2010; Topalović *et al.* 2017; van der Sommen *et al.* 2005; Waeyenberge & Moens 2001; Wesemael *et al.* 2011
M. hapla	Algeria, Argentina, Armenia, Australia, Belarus, Belgium, Brazil, Bulgaria, Canada, Chile, China, Colombia, Costa Rica, Côte d'Ivoire, Czechia, Ecuador, Egypt, Estonia, Ethiopia, Yugoslavia, Finland, France, Germany, Greece, Guatemala, Hungary, India, Indonesia, Iran, Israel, Italy, Japan, Kazakhstan, Kenya, Kyrgyzstan, Latvia, Libya, Lithuania, Malawi, Malaysia, Mexico, Moldova, Mongolia, Morocco, The Netherlands, New Zealand, Nigeria, Norfolk Island, North Macedonia, Norway, Pakistan, Panama, Papua, New Guinea, Paraguay, Peru, Philippines, Poland, Portugal, Romania, Russia, Serbia and Montenegro, Slovakia, Slovenia, South Africa, South Korea, Spain, Sri Lanka, Sweden, Switzerland, Tajikistan, Tanzania, Thailand, the Mediterranean Basin, Turkey, Turkmenistan, Uganda, Ukraine, Russia, UK, USA, Uruguay, Uzbekistan, Venezuela, Zimbabwe	Over 550 plant host species including**:** *Actinidia chinensis, Actinidia deliciosa, Ageratina adenophora, Ageratina trapezoideum, Allium cepa, Apios americana, Arachis hypogaea, Beta vulgaris, Brassica napus* var. *napus, Brassica oleracea* var. *capitata, Cajanus cajan, Camellia sinensis, Capsicum annuum, Chenopodium album, Chenopodium quinoa, Tanacetum cinerariifolium, Cichorium intybus, Codonopsis pilosula, Coffea arabica, Convolvulus arvensis, Daucus carota, Daucus carota* subsp. *sativus, Dianthus caryophyllus, Dioscorea polystachya, Eustoma grandiflorum, Ficus carica, Fragaria* × *ananassa, Glycine max, Gypsophila paniculata, Lactuca sativa, Limonium sinuatum, Linum usitatissimum, Medicago sativa, Mentha* sp., *Nicotiana tabacum, Olea europaea* subsp. *europaea, Paeonia lactiflora, Paulownia tomentosa, Raphanus raphanistrum, Rosa pendulina, Sinapis alba, Solanum americanum, Solanum lycopersicum, Solanum muricatum, Solanum tuberosum, Tanacetum cinerariifolium, Trifolium ambiguum*, *T. argutum*, *T. arvense, T. dubium*, *T. glomeratum*, *T. hybridum*, *T. medium*, *T. micranthum*, *T. nigrescens*, *T. occidentale*, *T. pratense*, *T. repens*, *T. semipilosum*, *T. striatum*, *T. subterraneum*, *Vitis vinifera*	Abrantes *et al.* 2008; Akyazİ *et al.* 2012, 2017; Ambrogioni 1969; Arutyunov 1992; Berbec 1972; Berge *et al.* 1972; Bridge 1988; Brinkman 1975; Chaves & Torres 1993; Chitwood 1949; Choi 1981; Colbran 1958; Coolen & Hendrickx 1972; Dabaj & Jenser 1987; Dale 1973; Dong *et al.* 2015; Efremenko & Klimakova 1972; Erenfelde 1984; Gladkaya 1983; Goyal *et al.* 1976; Grujicic & Paunovic 1971; Gugino *et al.* 2006; Gul & Saeed 1990; Handoo 2005; Hernandez *et al.* 2004; Hu *et al.* 1997; Jepson, 1987; Johnson *et al.* 1996; LaMondia 2002; Li *et al.* 2020; Lordello & Monteiro 1974; Maafi & Mahdavian 1997; Martin 1961; Mennan *et al.* 2006; Mercer & Miller 1997; Meressa *et al.*, 2014; Minz 1956; Mitsui *et al.* 1976; Muhammad 1992; Nyoike *et al.* 2012; Pérez & Lewis 2004; Pethybridge *et al.* 2008; Philippi *et al.* 1996; Pinochet *et al.* 1989; Pokharel & Kruchina 1991; Potter *et al.* 1972; Pyrowolakis 1975; Ratanaprapa & Chunram 1988; Robertson *et al.* 2006; Romascu *et al.* 1974; Ruelo 1981; Saka 1990; Santos *et al.* 1987; Seebens *et al.* 2017; Širca *et al.* 2003; Skwiercz *et al.* 2019; Stoeen 1974; Stoyanov 1980; Sturhan 1976; Tiilikkala 1991; Triantaphyllou 1966; Tzortzakakis *et al.* 2019; Vallotton 1981; Van Der Linde 1956; Vargas & Pajuelo 1973; Villain *et al.* 2013; Vovlas *et al.* 2010; Wheeler *et al.* 2000; Whitehead 1969; Zouhar *et al.* 2003
M. incognita	Afghanistan, Albania, Algeria, Angola, American Samoa, Antigua and Barbuda,	Over 700 species and varieties including *Abelmoschus esculentus, Abelmoschus manihot*, *Abutilon theophrasti, Acacia confusa, Achillea millefolium, Achyranthes*	Abrantes *et al.*, 2008; Adesiyan & Odihirin 1978; Affokpon *et al.*, 2011; Ahmed 1975; Ali & Sharma 2003; Alvarez Argudin 1970; Anwar *et al.*

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Species	Distribution	Hosts	References
M. incognita	Armenia, Argentina, Australia, Azerbaijan, Bangladesh, Barbados, Belarus, Belize, Belgium, Bermuda, Benin, Bolivia, Bosnia and Herzegovina, Botswana, Brazil, Brunei, Burkina Faso, Bulgaria, Cabo Verde, Cameroon, Canada, Central African Republic, Chile, Colombia, Congo, Costa Rica, Cuba, China, Côte d'Ivoire, Cyprus, Czechia, Belarus, Dominica, Dominican Republic, Ecuador, Egypt, El Salvador, Eritrea, Estonia, Ethiopia, Federal Republic of Yugoslavia, Fiji, France, French Guiana, Gambia, Georgia, Germany, Ghana, Greece, Guadeloupe, Guatemala, Guinea, Guyana, Haiti, Honduras, Hungary, Iceland, India, Indonesia, Iran, Iraq, Israel, Italy, Jamaica, Japan, Jordan, Kazakhstan, Kenya, Kiribati; Kyrgyzstan, Latvia, Lebanon, Liberia, Libya, Lithuania, Macedonia, Madagascar, Malaysia, Malawi, Mali, Malta, Martinique, Mauritania, Mauritius, Mexico, Moldova, Moldavia, Mongolia, Montserrat, Montenegro, Morocco, Mozambique, Myanmar, Niger, Netherlands, New Caledonia, New Zealand, Nicaragua, Nigeria, Niue, Nepal, Norfolk Island, North Macedonia, Oman, Papua, New Guinea, Pakistan, Panama, Philippines, Paraguay, Peru, Poland, Portugal, Puerto Rico, Réunion, Romania, Russia, Saint Lucia, Saint Vincent and the Grenadines, Saudi Arabia, Senegal, Serbia, Serbia and Montenegro, Seychelles, Sierra Leone,	*aspera, Actinidia deliciosa, Ageratum conyzoides, Albizia lebbeck, Alcea rosea, Allium cepa, Allium fistulosum, Aloe vera, Amaranthus blitoides, Amaranthus blitum, Amaranthus deflexus, Amaranthus graecizans, Amaranthus hybridus, Amaranthus retroflexus, Amaranthus spinosus, Amaranthus viridis, Ampelamus laevis, Anacardium occidentale, Ananas comosus, Anchusa azurea, Anethum graveolens, Apium graveolens, Arabidopsis thaliana, Araujia sericifera, Areca catechu, Asparagus officinalis, Basella alba, Bassia scoparia, Bertholletia excelsa, Beta vulgaris, Bidens pilosa, Borreria hispida, Brassica oleracea, Brassica rapa, Brachiaria reptans, Bryophyllum fedtschenkoi, Calendula officinalis, Canavalia ensiformis, Canna indica, Cannabis sativa, Capsicum annuum, Capsicum chinense, Cardiospermum halicacabum, Carica papaya, Celosia argentea, Chenopodium album, Chenopodium murale, Cicer arietinum, Citrullus lanatus, Cleome viscosa, Clitoria ternatea, Cnidoscolus urens* var. *stimulosus, Cocos nucifera, Coffea arabica, Coffea canephora, Colocasia esculenta, Commelina benghalensis, Convolvulus arvensis, Cordia myxa, Cordyline fruticosa, Coriandrum sativum, Cucumis anguria, Cucumis melo, Cucumis sativus, Cucurbita argyrosperma, Cucurbita maxima, Cucurbita moschata, Cucurbita pepo, Cullen corylifolium, Curcuma alismatifolia, Curcuma longa, Cynodon dactylon, Cyperus esculentus, Cyperus haspan, Cyperus rotundus, Dahlia coccinea, Datura metel, Datura stramonium, Daucus carota, Dichondra repens, Digitaria horizontalis, Digitaria insularis, Digitaria sanguinalis, Dioscorea alata, Dioscorea batatas, Dioscorea cayennensis, Dioscorea esculenta, Dioscorea cayennensis* subsp. *rotundata, Duranta erecta, Echinochloa crus-galli, Eleusine indica, Emilia sonchifolia, Eragrostis ciliaris, Eryngium foetidum, Euphorbia heterophylla, Euphorbia hirta, Euphorbia prostrata, Euphorbia tirucalli, Ficus benjamina, Ficus carica, Ficus elastica, Ficus religiosa, Galinsoga parviflora, Gerbera jamesonii, Glycine max, Gomphrena globosa, Gossypium hirsutum, Helianthus annuus, Hevea brasiliensis, Hibiscus cannabinus, Hibiscus rosa-sinensis, Hibiscus syriacus, Hibiscus trionum, Ipomoea batatas, Ipomoea nil, Ipomoea purpurea, Ipomoea triloba, Jacquemontia pentanthos, Jasminum multiflorum, Jasminum sambac, Juglans regia, Lactuca sativa, Lactuca serriola, Lagenaria siceraria, Lantana camara, Launaea intybacea, Lavandula angustifolia, Lens culinaris, Leonotis nepetifolia, Leucas aspera, Lotus corniculatus, Luffa acutan-*	2009; Anwar & McKenry 2010; Araki & Nakasono 1987; Artyunov 1985; AVA 2001; Aydınlı 2018; Bačić *et al.* 2016; Bahmani *et al.* 2013; Bala 1984; Batyr & Kozhokaru 1985; Bhardwaj & Högger 1984; Bhat & Kaul 1994; Bora 1970; Bridge 1978, 1988; Bridge *et al.* 1991; Brooks 2002; Cabrera *et al.* 2013; Campbell & Griffin 1975; Castillo *et al.* 2008; Castillo & Jiménez-Díaz 2003; Chaudhary *et al.* 2013; Chen *et al.* 1991; Chunram 1972; Colombo *et al.* 2008; Crill *et al.* 1973; Cuadra *et al.* 1988; Curi & Silveira 1978; da Ponte 1968; da Ponte *et al.* 1977; Daramola *et al.* 2013; de Cara *et al.* 2011; d'Errico *et al.* 2014; de Moura *et al.* 2010; Doucet & Pinochet 1992; Dzhuraeva 1976; Echeverrigaray *et al.* 2010; Eissa & Hyder 1981; Eloh *et al.* 2020; El-Sherbiny 2011; Fortuner 1981; Freire 1976; Freire & Ferraz 1977; Freire & Ponte 1976; Fukudome 1978; Galbieri *et al.* 2020; Gautier 1975; Gharabadiyan *et al.* 2012; Gill & Firoza 2014; Gladkaya 1981; Goes *et al.* 1982; Goodey *et al.* 1965; Grujicic 1974; Gushchin & Efremenko 1975; Guzman-Plazola *et al.* 2006; Hall *et al.* 2017; Hashim 1979; Hunt 1977; Huu Tien Nguyen *et al.* 2019; Ibrahim & Handoo 2016; Ibrahim *et al.* 1972; Ibrahim *et al.* 2010; Jamily *et al.* 2018; Johnson & Potter 1980; Johnson *et al.* 1996; Kaur *et al.* 2007; Kalvelage & Brose 1990; Kanyagia 1979; Karshe 1993; Katcho 1972; Kaur *et al.* 2007; Karuri *et al.* 2017; Kaur & Attri 2013; Keetch & Buckley 1984; Kepenekci & Dura 2017; Kermarrec 1974; Khan & Dabaj 1980; Khan *et al.* 2007, 2017; Khanzada *et al.* 2007; Kozhokaru 1972; Krnjaic 1977; Kruger *et al.* 2007; Kwerepe & Labuschagne 2004; Kyrou 1976; Lamberti *et al.* 1987, 1988; Li et al. 1992; Lima *et al.* 2005; 2013; Liu 1977; Lopes & Lordello 1980; López 1985; Lordello & Lordello 1972; Lordello & Marini 1974; Lordello *et al.* 1986; Luc *et al.* 1964; Mallikarjuna *et al.* 2010; Mar'enko 1989; Martin & Armstrong 1975; Mathur & Khera 1991; Mathur *et al.* 1970; Mavlyanov 1972; Mercer & Miller 1997; Mishra 1991; Moens 1985; Moye *et al.* 2018; Murga-Gutierrez *et al.* 2012; Nasira *et al.* 2011; Oever & Mangane 1992; Onkendi *et al.* 2014; Orton Williams 1973; Pajovic *et al.* 2007; Pallum 1972; Phan *et al.* 2018; Philis 1983; Pinochet 1977; Pogosyan & Karapetyan 1976; Poornima *et al.* 2017; Powell 1974; Price 1994; Quénéhervé *et al.* 2011; Qureshi *et al.* 1984; Radoi *et al.* 2019; Ramyabharathi *et al.* 2014;

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Species	Distribution	Hosts	References
M. incognita	Singapore, Slovakia, Slovenia, Somalia, South Africa, South Korea, Samoa, Solomon Islands, Spain, Sri Lanka, Sudan, Siberia, Suriname, Switzerland, Syria, Tajikistan, Tanzania, Thailand, Tonga, Trinidad and Tobago, Turkey, Turkmenistan, Tuvalu, Togo, Tunisia, Turkey, UK, Uganda, Ukraine, Uruguay, USA, Uzbekistan, Vanuatu, Venezuela, Vietnam, Yemen, Zambia, Zimbabwe	*gula, Luffa cylindrica, Malachra alceifolia, Malpighia emarginata, Malpighia glabra, Malva neglecta, Malva pusilla, Mangifera indica, Manihot esculenta, Medicago sativa, Melilotus indicus, Mentha × piperita, Mentha spicata, Mesembryanthemum cordifolium, Miconia cinnamomifolia, Momordica charantia, Morinda citrifolia, Morus alba, Morus nigra, Murraya paniculata, Musa acuminata, Musa × paradisiaca, Nicotiana tabacum, Ocimum basilicum, Ocimum americanum, Oenanthe javanica, Olea europaea, Ophiopogon japonicus, Oryza sativa, Parthenium hysterophorus, Passiflora edulis, Paulownia elongata, Petroselinum crispum, Phaseolus vulgaris, Phoenix dactylifera, Phyla nodiflora, Phytolacca americana, Piper methysticum, Piper nigrum, Pisum sativum, Pithecellobium dulce, Pittosporum tobira, Plantago lanceolata, Polianthes tuberosa, Polygonum aviculare, Polygonum lanceolatum, Persicaria maculosa, Polygonum posumbu, Pongamia pinnata, Portulaca oleracea, Portulaca quadrifida, Prosopis juliflora, Prunus domestica, Prunus persica, Prunus salicina, Psidium guajava, Psophocarpus tetragonolobus, Ptychosperma elegans, Punica granatum, Radermachera sinica, Raphanus raphanistrum* subsp. *sativus, Rhaponticum repens, Ricinus communis, Rollinia mucosa, Rosmarinus officinalis, Rumex acetosa, Rumex dentatus, Saccharum officinarum, Salvia miltiorrhiza, Samanea saman, Sansevieria trifasciata, Schinus terebinthifolius, Sesamum indicum, Setaria viridis, Sida acuta, Sida rhombifolia, Sinapis alba, Solanum americanum, Solanum dulcamara, Solanum lycopersicum, Solanum lycopersicum* var. *cerasiforme, Solanum melongena, Solanum nigrum, Solanum sisymbriifolium, Solanum tuberosum, Spinacia oleracea, Tabebuia serratifolia, Tagetes erecta, Tephrosia vogelii*, *Trachyspermum ammi*, *Trifolium ambiguum*, *T. argutum*, *T. arvense*, *T. dubium*, *T. glomeratum*, *T. hybridum*, *T. medium*, *T. micranthum*, *T. nigrescens*, *T. occidentale*, *T. pratense*, *T. repens*, *T. semipilosum*, *T. striatum*, *T. subterraneum*, *Triticum aestivum, Veitchia merrillii, Vernonia cinerea, Vigna angularis, Vigna mungo, Vigna radiata, Vigna unguiculata, Viola pilosa, Vitex agnus-castus, Vitex trifolia, Vitis vinifera, Washingtonia robusta, Zea mays, Zingiber officinale*	Rasina 1970; Rathour *et al.* 2006; Raveendran & Nadakal 1975; Reddy 1977; Rich *et al.* 2008; Roman & Grullon 1975; Romascu *et al.* 1974; Ruanpanun & Khun-in 2015; Rudzyavichene *et al.* 1975; Saad & Tanveer 1972; Sahu *et al.* 2011; Saigusa & Matsumoto 1961; Salam 1991; Santos 1983; Sarawak 1975; Shiabova 1977; Scotto La Massese 1961; Shahid *et al.* 2007; Sharma & McDonald 1990; Shen *et al.* 1990; Shepherd & Barker 1990; Sikora *et al*. 1988; Singh *et al.* 2010, 2012; Širca *et al.* 2003; Sivapalan 1978; Song *et al.* 2019; Sosa Moss 1985; Stirling 1976; Stoyanov 1980; Tariq *et al.* 2007; Tarjan 1953; Taylor 1975; Taylor *et al.* 1982; Tesařová *et al.* 2003; Timchenko 1981; Timm 1965; Tiwari & Dave 1985; Touré *et al.* 2019; Treskova & Sadykhov 1982; Tsai *et al.* 2020; Tzortzakakis *et al.* 2016; Vargas & Pajuelo 1973; Velastegui & Fiallos 1987; Villain *et al.* 2013; Vovlas *et al.* 2004; Vyas *et al.* 2008; Walker *et al.* 1974; Waller & Bridge 1978; Walters & Barker 1994; Wang & Hughes 1976; Wesemael *et al.* 2011; Williams-Woodward & Davis 2001; Wu & Xue 1986; Yamada & Takakura 1975; Yang *et al.* 1991; Ye *et al.* 2015; Zarina & Shahina 2010; Zarina & Shaheen 2014; Zeng *et al.* 2014; Zhang *et al.* 1998; Zhao *et al.* 2017
M. javanica	Africa, Algeria, Angola, Argentina, Armenia, Australia, Bangladesh, Bolivia, Bosnia and Herzegovina, Botswana, Brazil, Bulgaria, Burundi, Brazil, Brunei, Ceylon, China, Chile,	Over 770 host species or varieties including *Abelmoschus esculentus,Actinidia deliciosa*, *Agathosma betulina, Ageratum conyzoides, Albizia saman, Allium cepa, Anagallis arvensis, Ananas comosus, Antirrhinum majus, Apios americana, Apium graveolens, Arachis hypogaea, Arachis pintoi, Arctium lappa, Artemisia absinthium, Basella alba,*	Abivardi & Sharafeh 1973; Adesiyan & Odihirin 1978; Agudelo *et al.* 2006; Ahmed 1975; Ali *et al.* 2014, 2019; Ali & Sharma 2003; de Araújo *et al.* 2012; de Araújo Filho *et al.* 2012; Archidona-Yuste *et al*. 2020; Artyunov 1985; Awol Seid *et al.* 2019; Batyr & Kozhokaru 1985; Behdani *et al.* 2017; Bala 1984;

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Species	Distribution	Hosts	References
M. javanica	Colombia, Comoros, Congos, Cook Islands, Costa Rica, Côte d'Ivoire, Cyprus, Cuba, Ecuador, Egypt, El Salvador, Eritrea, Ethiopia, Federal Republic of Yugoslavia, Fiji, France, Gabon, Gambia, Germany, Ghana, Greece, Guadeloupe, Honduras, Guatemala, Hungary, Iceland, India, Iran, Iraq, Israel, Italy, Jamaica, Japan, Jordan, Kenya, Kazakhstan, Kiribati, Lebanon, Liberia, Libya, Madagascar, Malawi, Martinique, Malta, Mauritania, Mauritius, Malaysia, Mexico, Moldavia, Moldova, Morocco, Montenegro, Mozambique, Myanmar, Nepal, Nicaragua, Nigeria, Niue, North Macedonia, Oman, Papua New Guinea, Pakistan, Panama, Paraguay, Peru, Philippines, Poland, Portugal, Puerto Rico, Réunion, Russia, Rwanda, Samoa, Saudi Arabia, Senegal, Serbia and Montenegro, Singapore, Solomon Islands, Sri Lanka, South Africa, Sudan, Suriname, South America, South Korea, Spain, Syria, Tanzania, Tajikistan, Thailand, Tonga, Trinidad and Tobago, Tunisia, Turkey, Turkmenistan, Uganda, UK, Ukraine, USA, Uruguay, Uzbekistan, Venezuela, Vietnam, Yemen, Zambia, Zimbabwe	*Bauhinia purpurea, Berberis vulgaris, Borago officinalis, Calendula officinalis, Callistemon viminalis, Camellia sinensis, Canna indica, Cannabis sativa, Capsicum annuum, Carica papaya, Carissa macrocarpa, Castanea dentata, Catharanthus roseus, Chamaerops humilis, Chenopodium album, Chrysanthemum morifolium, Cicer arietinum, Citrullus lanatus, Clitoria ternatea, Coleus forskohlii, Convolvulus arvensis, Corchorus olitorius, Cordyline fruticosa, Cucumis melo, Cucumis sativus, Cucurbita pepo, Cullen corylifolium, Curcuma longa, Daucus carota, Dioscorea polystachya, Duranta erecta, Ecclinusa ramiflora, Echinochloa crus-galli, Erigeron bonariensis, Euphorbia prostrata, Euphorbia tirucalli, Eustoma grandiflorum, Exacum affine, Fragaria × ananassa, Gochnatia polymorpha, Gomphrena globosa, Gossypium hirsutum, Graptophyllum pictum, Helianthus tuberosus, Heliconia rostrata, Hibiscus tilliaceus, Holmskioldia sanguinea, Humulus lupulus, Hyeronima alchorneoides, Ipomoea batatas, Jasminum multiflorum, Jasminum sambac, Manihot esculenta, Melaleuca alternifolia, Melia azedarach, Melissa officinalis, Miconia cinnamomifolia, Morinda citrifolia, Musa × paradisiaca, Nicotiana plumbaginifolia, Nicotiana tabacum, Olea europaea, Oryza sativa, Oxalis corniculata, Parthenium hysterophorus, Passiflora edulis, Paulownia elongata, Paulownia fortunei, Phaseolus vulgaris, Phoenix canariensis, Phoenix dactylifera, Piper nigrum, Pisum sativum, Pittosporum tobira, Plukenetia volubilis, Portulaca oleracea, Prunus domestica, Prunus persica, Prunus salicina, Psidium guajava, Punica granatum, Ricinus communis, Rosmarinus officinalis, Rubia tinctorum, Ruta graveolens, Sabal palmetto, Saccharum officinarum, Salvia officinalis, Sesamum indicum, Sesbania cannabina, Sesbania sesban, Sinningia speciosa, Solanum americanum, Solanum lycopersicum, Solanum melongena, Solanum tuberosum, Tectona grandis, Tephrosia vogelii, Terminalia catappa, Trichosanthes dioica, Trifolium ambiguum, T. argutum, T. arvense, T. dubium, T. glomeratum, T. hybridum, T. medium, T. micranthum, T. nigrescens, T. occidentale, T. pratense, T. repens, T. semipilosum, T. striatum, T. subterraneum, Vigna unguiculata, Vitis vinifera, Zantedeschia aethiopica, Zea mays, Zingiber officinale, Zinnia elegans, Ziziphus spina-christi*	Bellé *et al.* 2019; Bhardwaj & Högger 1984; Bhatti & Musarrat 2008; Bridge 1988; Brito *et al.* 2018; Carneiro *et al.* 2003; Cho *et al.* 1987; Costilla *et al.* 1976; Dabaj & Jenser 1987; Dzhuraeva 1976; de Araújo *et al.* 2012; Deimi & Mitkowski 2010; Desaeger & Rao 2000; Doucet & Pinochet 1992; Eissa 1982; Egunjobi 1985; El-Sherbiny 2011; EPPO 2021; Fortuner 1981; Fukudome 1978; Galbieri *et al.* 2020; Gu *et al.* 2021; Gul & Saeed 1987; Gushchin & Efremenko 1975; Hajihassani *et al.* 2019; Ibrahim *et al.* 2010; Ibrahim & Handoo 2016; Ito *et al.* 2015; Janati *et al.* 2018; Jiskani *et al.* 2009; Kanjanasoon 1964; Kaur *et al.* 2007; Kamran *et al.* 2010; Kanyagia 1979; Keetch & Buckley 1984; Khair 1986; Khan *et al.* 2005, 2007; Khanzada & Khan 2008; Klein *et al.* 2012; Kolombia *et al.* 2017; Kondratenko 1985; Kondratenko & Metlitskii 1989; Lamberti *et al.* 1986; Lamberti *et al.* 1987; Lima *et al.* 2005, 2013; Liu 1977; Loubser 1988; Ma *et al.* 2007; Machado *et al.* 2013; Machado *et al.* 2014; Madamba 1981; Malan *et al.* 2004; Mani *et al.* 2005; Mar'enko 1989; Martin & Armstrong 1975; Medina *et al.* 2017; Mercer & Miller 1997; Meza *et al.* 2016; Moosavi 2015; Mukhopadhyay & Roy 2006; Narayanaswamy & Setty 1979; Nascimento *et al.* 2020; Oka 2012; Orton Williams 1972; Onkendi *et al.* 2014; Pajovic *et al*. 2007; Perera *et al.* 2005; Perera *et al.* 2008; Phong *et al.*2020; Philis 1983; Pinochet 1977; Pyrowolakis 1975; Qaiser *et al.* 2009; Sasser & Carter 1985; Saad & Tanveer 1972; Salam 1991; Santos *et al.* 1987; Sahu *et al.* 2011; Shagalina & Shagalin 1987; Shahid *et al.* 2007; Sharma 1980; Silva *et al.* 2014; Singh & Gupta 2011; Sivapalan 1978; Sosa Moss 1985; Song *et al.* 2017; Spatafora *et al.* 2004; Srivastava *et al.* 2012; Stephan 1978, 1980; Tarjan 1953; Tariq *et al.* 2007; Tariq-Khan *et al.* 2020; Taylor *et al.* 1982; Tzortzakakis 2009; Tzortzakakis *et al.* 2016; van den Oever & Mangane 1992; Vovlas *et al.* 2015; Walker *et al.* 2002; Waller & Bridge 1978; Waldmann1971; Wang *et al.* 2014; Wesemael *et al.* 2011; Wu *et al.* 2011; Yang et al. 1991; Yasir *et al.* 2018; Zarina & Shahina 2010; Muhammad *et al.* 2012; Quénéhervé *et al.* 2011; Zeng *et al.* 2018; Zhao *et al.* 2017; Zia *et al.* 2014
M. minor	The Netherlands, Belgium, Ireland, Portugal, Chile, USA, UK, Ireland,	*Agrostis stolonifera, Anagallis arvensis, Avena sativa, Daucus carota, Festuca* sp., *Hordeum vulgare, Lactuca sativa, Lolium multiflorum, Lolium perenne, Medicago*	EPPO 2021; Karssen *et al.* 2004; McClure *et al.* 2012; Viaene *et al.* 2007; Wesemael *et al.* 2011, 2014; Zhao *et al.* 2017

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Species	Distribution	Hosts	References
M. minor	New Zealand	*lupulina*, *Medicago sativa, Phacelia tanacetifolia, Phleum pratense, Poa* sp., *Solanum lycopersicum, Solanum tuberosum, Tagetes erecta, Trifolium pratense, Trifolium repens, Trifolium* sp., *Triticum aestivum, Vicia sativa, Zea mays*	
M. naasi	Argentina, Belgium, Canada, Chile, Czech Republc, France, former Yugoslavia, former Soviet Union, Germany, Hungary, India, Iran, Ireland, Italy, Mozambique, Poland, Thailand, New Zealand, The Netherlands, Portugal, Serbia, UK, USA	*Agrostis idahoensis*, *Agrostis stolonifera*, *Allium cepa, Avena sativa, Beta vulgaris*, *Cestrum aurantiacum, Coronilla scorpioides*, *Dactylis glomerata, Digitaria sanguinalis*, *Festuca arundinacea, Festuca pratensis, Glycine max*, *Gossypium hirsutum, Hordeum vulgare*, *Lolium* × *hybridum, Lolium multiflorum*, *Lolium perenne, Medicago polymorpha*, *Medicago sativa*, *Melilotus sulcatus, Manihot esculenta, Phragmites australis, Phaseolus vulgaris*, *Pisum sativum*, *Plantago lanceolata*, *Poa annua*, *Poa nemoralis*, *Poa pratensis, Poa trivialis*, *Secale cereal, Solanum peruvianum, Sorghum bicolor, Stellaria media*, *Triticum aestivum, Triticum durum, Trifolium alexandrinum*, *Trifolium hybridum*, *Vicia villosa*	Ayton & Dickerson 1969; Amin & Budal 1994; Bélair *et al.* 2006; Caubel *et al.* 1972; Coyne *et al.* 2006; Dos Santos *et al.* 2020; Echevarría & Chaves 1998; Franklin 1965; Golden & Taylor 1967; Gooris 1968; Hallmann *et al.* 2007; Jensen *et al.* 1968; Karssen 2002; Kilpatrick *et al.* 1976; Kornobis 2001; Lewis & Webley 1996; McClure *et al.* 2012; Michell *et al.* 1973; Radewald *et al.* 1970; Sheridan & Grbavac 1979; Sikora *et al.* 1972; Simard *et al.* 2008; Suresh *et al.* 2017; Taylor *et al.* 1971; Vandenbossche *et al.* 2011; Yeates 2010; Zhao *et al.* 2017
M. trifoliophila	Australia, New Zealand, USA	*Arachis hypogaea*, *Kummerowia stipulacea, Melilotus albus*, *Phaseolus vulgaris, Pisum sativum*, *Trifolium ambiguum*, *T. argutum*, *T. arvense*, *T. dubium*, *T. glomeratum*, *T. hybridum*, *T.medium*, *T. micranthum*, *T. nigrescens*, *T. occidentale*, *T. pratense*, *T. repens*, *T. semipilosum*, *T. subterraneum*, *Vicia faba*, *Vicia sativa*	Bernard & Eisenback 1997; Bernard & Jennings 1997; Mercer *et al.* 1997; Mercer & Miller 1997; Zahid *et al.* 2000

Meloidogyne fallax has an isozyme pattern with a unique malate dehydrogenase (N1b) and no major esterase band EST (Karrsen 1996; Hunt & Handoo 2009). In our test gels, one band was observed on the tomato (Beet) host and two bands on white clover for esterase, while for malate dehydrogenase, one band was observed on tomato (Beet) host and two bands on white clover.

Phylogenetic trees including SSU, ITS and D2-D3 of LSU rDNA sequences of the New Zealand *M. fallax* populations showed that they clustered with other *M. fallax* populations in one clade (Figs 3–5).

Meloidogyne hapla **Chitwood, 1949**

English common name: Northern root-knot nematode

EPPO Code: MELGHA

Figs 12–17.

Measurements. Table 4.

Morphology. Females: Body annulated, 467–767 µm long, 300–512 µm wide, pearly white, almost globular to pear shaped; no posterior protuberance; a distinct neck region (48–166 µm long) projecting laterally from the body axis. Cuticle thicker in posterior half of body. Head region off-set from body, may be marked with two annules. Head cap distinct but variable in shape; labial disc slightly elevated. Cephalic framework weakly sclerotized; vestibule extension distinct. Stylet 12–14 µm long, moderately slender, cone dorsally curved and shaft cylindrical; knobs large, off-set, rounded to transversely ovoid, slightly sloping posteriorly from the shaft. Excretory pore located between anterior head end and level of metacorpus, opening at anterior end of latter. No vesicles located along the lumen lining. Pharyngeal glands variable in size and shape. Perineal pattern rounded (Fig. 14). Dorsal arch low, may be extended into lateral wings on one or both sides, with fine striae. Lateral field with clear separation of dorsal and ventral striae but no distinct lines. Tail terminus indistinct, punctations present

between anus and terminus. Phasmids small and difficult to observe. Vulva a transverse slit. Perivulval area devoid of striae. Ventral pattern region usually oval, may be angular in shape; striae fine.

Table 4. Morphometrics of adult and second stage juveniles (J2) of *Meloidogyne hapla* isolated from New Zealand. Measurements are in µm and in the form: mean ± SD (range).

Character	Female	Male	J2
n	14	15	11
L	613±97 (467–767)	1133±155 (819–1368)	357±30.9 (310–386)
a	1.5±0.2 (1.3–1.9)	34.3±5.1 (26.0–47.5)	25.3±3.5 (18.8–28.4)
b		16.9±2.2 (12.8–21.0)	7.1±0.5 (6.6–7.7)
c	-	181.9±58.0 (131.7–327.7)	7.4±0.4 (6.9–8.2)
c’	-	0.4±0.1 (0.2–0.6)	4.8±0.4 (4.3–5.3)
T	-	58.3±8.4 (37.4–70.0)	
Greatest body diam.	411.9±69.1 (299.6–512.1)	33.4±4.7 (25.7–40.8)	14.4±2.6 (12.3–20.6)
Body diam. at stylet knobs	-	17.0±1.5 (15.5–20.1)	8.6±0.6 (8.0–8.6)
Body diam. at excretory pore	-	22.9±2.8 (19.5–27.7)	11.5±0.3 (11.3–11.9)
Body diam. at anus	-	15.7±1.4 (14.7–18.5)	10.0±0.5 (9.2–11.0)
Head region height	-	5.0±0.4 (4.4–5.9)	1.8±0.1 (1.6–2.0)
Head region diam.	-	9.4±0.8 (7.9–10.7)	4.8±0.3 (4.3–5.2)
Neck length	88.3±31.3 (48.4–165.8)	-	-
Neck diam.	62.9±14.2 (45.3–84.7)	-	-
Stylet	13.1±0.7 (12.5–14.1)	19.6±1.2 (17.8–21.2)	10.6±1.1 (9.0–11.7)
Stylet cone	6.1±0.7 (5.5–7.2)	10.8±0.9 (9.4–12.7)	-
Stylet knob height	1.8±0.4 (1.3–2.7)	1.9±0.3 (1.6–2.3)	1.0±0.2 (0.9–1.3)
Stylet knob width	3.3±0.6 (2.5–4.2)	3.3±0.3 (3.0–3.8)	1.6±0.1 (1.5–1.7)
DGO	4.0±0.2 (3.8–4.3)	4.1±0.6 (3.6–4.8)	4.7±0.5 (4.3–5.2)
Ant. end to metacorpus	81.6±6.7 (70.3–89.1)	67.1±8.5 (53.7–76.2)	51.2±5.6 (41.5–58.6)
Metacorpus length	37.7±4.4 (30.1–44.7)	16.9±2.9 (13.1–22.4)	13.4±2.5 (11.3–18.0)
Metacorpus diam.	32.1±4.8 (22.6–36.7)	10.1±1.7 (7.8–13.1)	8.1±1.4 (6.6–10.7)
Metacorpus valve length	13.9±0.8 (12.6–14.6)	5.4±0.3 (5.0–5.7)	3.8±0.1 (3.7–4.0)
Metacorpus valve width	9.9±1.2 (8.1–11.0)	4.0±0.6 (3.7–4.7)	2.9±0.1 (2.8–2.9)
Ant. end to end of gland lobe	-	118.9±16.1 (96.8–131.5)	-
Excretory pore-ant. end	33.8±4.0 (28.8–38.5)	118.9±16.1 (96.8–142.2)	70.5±10.9 (53.3–85.8)
Tail length	-	6.6±1.5 (3.5–8.9)	48.0±5.0 (42.4–58.7)
Hyaline tail terminus	-	-	13.8±2.9 (9.3–18.3)
Phasmids from anus	-	6.3±2.5 (3.0–8.9)	20.4±1.2 (17.2–25.6)
Spicule	-	27.7±2.4 (25.2–32.0)	-
Gubernaculum	-	7.7±1.1 (6.2–8.9)	-
Testis	-	658.1±121.5 (468.5–806.1)	-
Vulva slit length	20.2±1.1 (18.4–21.7)	-	-
Vulva-anus	15.6±1.7 (12.4–17.8)	-	-
Body length/neck length	7.9±2.5 (4.0–13.8)	-	-
Stylet knob width/height	2.0±0.6 (1.4–2.7)	1.8±0.3 (1.3–2.4)	1.6±0.3 (1.2–1.8)
Metacorpus length/width	1.2±0.1 (1.0–1.3)	1.7±0.3 (1.2–2.1)	1.7±0.2 (1.4–1.9)
(Excretory pore/L) x 100	-	16.0±2.8 (11.9–17.8)	19.0±1.7 (15.9–21.0)

Males: Body vermiform, 819–1368 µm long, slightly tapering anteriorly, bluntly rounded posteriorly. Cuticle with distinct annules. Lateral field with four incisures. Head slightly or not off-set, with a single post-labial annule. Labial disc rounded, not elevated. Cephalic framework moderately sclerotized, vestibule extension distinct. Stylet 18–21 µm long, cone straight; shaft cylindrical; knobs large and rounded, barely off-set from the shaft. Pharynx with slender procorpus, metacorpus oval shaped with pronounced valve. Ventrally overlapping pharyngeal gland lobe variable in length. Hemizonid, 2–3 µm in length, two to four annules anterior to excretory pore, which opens about two bulb lengths posterior to the metacorpus. Testis usually long, monorchic, with reflexed or outstretched germinal zone. Tail short and twisted. Spicules slender, 25–32 µm long, weakly cephalated, slightly ventrally curved; small gubernaculum also arcuate. Phasmids located level with or slightly anterior to cloaca.

Second-stage juveniles: Body 310–386 µm long, vermiform, tapering at both ends but posteriorly more than anteriorly. Body annules small but distinct. Lateral field with four incisures, not areolated. Head region truncate, slightly off-set from body. Head cap low and narrower than head region. Cephalic framework weakly sclerotized, vestibule extension distinct. Stylet slender and moderately long (9–12 µm), cone straight; shaft cylindrical; knobs distinct, rounded and off-set from the shaft. Pharynx with faintly outlined procorpus and oval shaped meta-corpus with distinct valve. Oesophageal gland lobe variable in length, overlapping intestine ventrally. Hemizonid distinct at level of or anterior to excretory pore, just posterior to nerve ring. Moderately sized tail (43–59 µm), gradually tapering to hyaline tail terminus (9–18 µm), proctodeum not inflated. Phasmids difficult to observe, small, slightly posterior to anus. A rounded hypodermis marks the anterior position of the smooth hyaline tail terminus; tail tip variable in shape, from narrowly rounded to bifurcate.

Eggs (n = 38)**:** Length 73–100 (83.6 ± 6.1) µm; width 35–47 (40.1 ± 3.2) µm.

Differential diagnosis. The New Zealand isolate of *Meloidogyne hapla* is characterised by having mature females with a distinctive rounded perineal pattern with a low dorsal arch and clear lateral fields separating dorsal and ventral striae, and punctuations near the anus. Juveniles have a finely rounded tail tip. Morphologically, the isolate is closest to the description of *M. hapla* (Hunt & Handoo 2009). However, it varies from the original description in having J2s that are generally smaller than those described by Hunt & Handoo (2009) (310–386 *vs* 360–500 µm long). Galls have lateral roots growing from them (Fig. 17).

The New Zealand isolate of *M. hapla* is morphologically separated from the other known New Zealand isolates of RKN by the form of the perineal pattern of mature females. It has a low dorsal arch which may be extended into lateral wings on one or both sides, with fine striae—not seen in the other known species of RKN in New Zealand. The tail has punctations between the anus and terminus, again not present in other New Zealand species of RKN. The position of the excretory pore in mature females (opening at approximately 75% of the distance between the anterior end and the metacorpus in *M. hapla vs* close to the stylet knobs in *M. incognita, M. minor* and *M. naasi*; and at the level of the anterior metacorpus in *M. javanica)* is also useful for morphological separation. It is further separated from *M. incognita* and *M. javanica* in having a shorter style (respectively, 12.5–14 *vs* 16–17.5 and 14–18 µm long). Males of the New Zealand isolate of *M. hapla* have phasmids which are closer to the anus than in other known New Zealand RKN (3–9 µm vs 10.5–11 in *M. fallax*; 12–17 µm in *M. incognita*; 8–19 µm in *M. javanica*, 10.5–11 in *M. minor*; 10.5–112 in *M. naasi*; and 8.5–16 in *M. trifoliophila*). They also have four *vs* the six or seven lateral lines of *M. trifoliophila*. The second stage juvenile of *M. hapla* from New Zealand is difficult to separate from those of other New Zealand species of RKN. It has been measured at 310–386 µm in length; smaller than those of *M. naasi* (397–467 µm long). The tail is just longer (43–59 µm) than in *M. fallax* (38–46 µm), and the hyaline area (9–18 µm long) is shorter than in *M. naasi* (20–27 µm long. Second stage juveniles lack the inflated proctodeum of *M. javanica*, *M. minor* and *M. incognita.* Juveniles of *M. hapla* lack the digitate tail tip present *M. trifoliophila* and tend to be smaller (body length mean 357, range 310–386 µm *vs* mean 412, range 378–461 µm) and to have tails with a shorter hyaline section [13.8 (41–59 µm) *vs* 20.1 (17–26 µm) long].

Material examined. Non-type specimens. Fourteen females (slide nos NNCNZ 4020–4028), 15 males (MPI nematode collection slide nos 1032, 1057, 1064, 1109) and 11 juveniles (slide nos NNCNZ 4029–4039) deposited at the National Nematode Collection, New Zealand.

Other material. The MAF collection contains 132 slides with specimens.

Distribution (Map 2). Based on material examined: New Zealand: **North Island:** AgResearch Campus, Hamilton, WO; Te Puke, BP.

Based on collections: Found throughout New Zealand, particularly the North Island. North Island: ND, AK, WO, BP, TO, GB, HB, TK, WI, WA, WN. South Island: NN, MB, NC, MC, SC, DN, CO.

For world distributions see Table 3.

Habitat and hosts. Based on material examined: New Zealand: kiwifruit (*Actinidia deliciosa)*, potato (*Solanum tuberosa*) tubers, tomato roots (*Solanum lycopersicum*), white clover (*Trifolium repens*).

Based on literature: New Zealand: *Actinidia deliciosa* (kiwifruit), *Allium cepa* (onion), *Apium graveolens* (celery), *Aster* sp. (aster), *Begonia andifolia, Beta vulgaris* (mangold/ silverbeet/beetroot), *Boronia heterophylla* (boronia), *Boronia megastigma* (scented boronia), *Brassica rapa* (turnip), *Capsicum ammum* (ornamental pepper), *Chenopodium album* (fat hen), *Cirsium arvense* (perennial thistle), *Cirsium vulgare* (spear thistle), *Convolvulus aroensis* (field bindweed), *Cyphomandra betacea* (tamarillo), *Daucus carota* (carrot), *Deutzia* x hydrida (deutzia), *Gerbera jamesonii* (African daisy), *Helichrysum bracteatum* (straw flower), *Hypericum* sp. (St. John's wort), *Ipomoea batatas* (kumara), *Lactuca sativa* (lettuce), *Leptinella* spp. (cotula), *Lotus pendunculalus* (lotus major), *Lupinus* sp., *Medicago saliva* (lucerne), *Paeonia* sp. (peony rose), *Pastinaca sativa* (parsnip), *Pelargonium inodorum* (kopata), *Phebalium squameum (=P. billatdien)*, *Phlox* sp., *Pisum sativum* (pea), *Prunella vulgaris* (self heal), *Ranunculus repens* (creeping buttercup), *Ribes sylvestre* (red currant), *Rosa* sp. (rose), *Rumex obtusifolius* (broad-leaved dock), *Rumex* sp. (dock), *Scabiosa* sp., *Scorzonera hispanica* (black salsify), *Senecio jacobaea* (ragwort), *Solanum ayiculare* (poroporo), *Solanum lycopersicum* (tomato), *Solanum nigrum* (black nightshade), *Solanum tuberosum* (potato), *Trifolium ambiguum*, *T. argutum*, *T. arvense*, *T. dubium*, *T. glomeratum*, *T. hybridum*, *T. medium*, *T. micranthum*, *T. nigrescens*, *T. occidentale*, *T. pratense*, *T. repens* (white clover), *T. semipilosum*, *T. striatum*, *T. subterraneum* (subterranean clover), *Viburnum japonicum, Vitis vinifera* (grape). For international hosts see Table 3.

Remarks. *Meloidogyne hapla* is identified by the cuticular markings in the perineal area of the mature female. Typically, it has a low upper arch and the area is often extended into lateral wings on one or both sides. It is also characterised by having punctations in the tail region. It is one of the four most common species of *Meloidogyne* worldwide (Hunt & Handoo 2009), with a very wide host range. As such, there are no quarantine implications for New Zealand for this nematode.

This RKN was first recorded from New Zealand in 1963 (Clark 1963), from potato, parsnip, *Chenopodium, Circium*, *Cyphomandra* and *Phebalium*. It is known to be tolerant of cold conditions (Hunt & Handoo 2009) and is often described as a cool climate RKN. It is the dominant RKN in areas with lighter, volcanic ash soils (Watson & Mercer 2000). There are no quarantine implications for this species. While it is known that *M. hapla* is a facultative parthenogen, its mode of reproduction in New Zealand is unknown. However, both males and females are commonly found in the field, *i.e*., parthenogenesis is unlikely in New Zealand (Farhat Shah, personal communication, September 2022).

Meloidogyne hapla has a very wide host range (more than 550 host species have been recognised), including both cultivated and perennial broad-leaved plants, including potato, and clovers in pastures. However, it does not develop on grasses. Given that other RKN species within pastures do multiply on graminaceous plants and that potatoes are often used as an inter-rotation crop, it is difficult to design rotations for control of the nematodes on potatoes in New Zealand. Galls induced by this RKN on white clover are small, rounded, inconspicuous, and often have lateral roots growing from them (Hunt & Handoo 2009).

A question of special interest with respect to New Zealand RKNs is the identity of nematodes infecting kiwifruit crops. The kiwifruit industry is the biggest sector in New Zealand's horticultural industry, and in 2019/20 gross sales were worth NZ $2.96 billion with export of about 150 million trays of fruit. Records of RKN infestations of kiwifruit form about 30% of all RKN reports from New Zealand, always listed as *M. hapla*, but without molecular confirmation. Sequences from nematodes from the *M. hapla* Te Puke sem G culture, collected from kiwifruit (Figs 3–5) confirmed this isolate as *M. hapla*. The damage done to productivity of kiwifruit by *M. hapla* has not been quantified. However, in damaging the roots of the vines RKN will make kiwifruit more susceptible to other soil-borne pathogens, e.g., *Fusarium*. Grandison (1983) found the possible use of nematicides to improve yield of kiwifruit impractical, given that RKN were recorded on roots in soil at depths of more than a metre (Farhat Shah, personal communication, September 2022). In the field, it is not practical to introduce nematicides to soil at that depth, meaning chemical control is not feasible for RKN in kiwifruit.

Most but not all populations of *M. hapla* have the H1 phenotype of malate dehydrogenase (Esbenshade & Triantaphyllou 1985 a,b), which is unique to the species. In our preliminary gels, two bands were seen for malate dehydrogenase, and one for the esterase (Lee Aalders, personal communication, December 2023).

Meloidogyne hapla is phylogenetically distinct from other RKNs, forming monospecific clades in both our SSU and D2-D3 of LSU rDNA sequences analyses (Figs 3 & 5).

***Meloidogyne incognita* (Kofoid & White, 1919) Chitwood, 1949**

English common name: Southern root-knot or cotton root-knot nematode

Figs 18–22.

Measurements. Table 5.

Morphology. Females: Body annulated, 501–912 µm long, 216–646 µm wide, pearly white, globular to pear shaped, no posterior protuberance, a distinct neck region projecting from the body axis at an angle of up to 90º to one side. Cuticle thickens at level of retracted stylet knobs. Head region off-set from body, marked with two annules. Head cap distinct but variable in shape; labial disc slightly elevated. Cephalic framework weakly sclerotized; vestibule extension distinct. Stylet 16–17.5 µm long, robust, cone straight and shaft cylindrical; knobs large, off-set, rounded, slightly sloping posteriorly from the shaft. Excretory pore located just posterior to level of stylet knobs, at level of opening of dorsal gland. One or two large vesicles and several smaller ones located along the lumen lining. Pharyngeal glands variable in size and shape. Perineal pattern variable, rounded to oval shaped; dorsal arch low, rounded, with long, smooth to wavy striae (Fig. 19). Tail terminus indistinct without punctations. Phasmids small and difficult to observe. Perivulval area devoid of striae. Lateral fields present, clearly dividing dorsal and ventral striae, but no lateral lines. Ventral pattern region oval to angular shaped; striae moderately coarse.

Males: Body vermiform, 851–1620 µm long, slightly tapering anteriorly, bluntly rounded posteriorly. Cuticle with distinct annules. Lateral field with four incisures; outer bands irregularly areolated. Head slightly off-set, with two post-labial annules. Labial disc rounded, elevated. Cephalic framework moderately sclerotized, vestibule extension distinct. Stylet 18–23 µm long, cone straight; shaft cylindrical; knobs large and rounded, off-set from the shaft. Pharynx with slender procorpus, metacorpus oval shaped with pronounced valve. Ventrally overlapping pharyngeal gland lobe variable in length. Hemizonid two to five annules anterior to excretory pore which opens about two bulb lengths behind the metacorpus. Testis usually long, monorchic, with reflexed or outstretched germinal zone. Tail short (7.5–16 µm long), twisted. Spicules 28–32 µm long, slender, barely cephalated, slightly ventrally arcuate; gubernaculum also arcuate. Phasmids located level with or slightly anterior to cloaca.

Second-stage Juveniles: Body 358–412 µm long, vermiform, tapering at both ends but posteriorly more than anteriorly. Body annules small but distinct. Lateral field with four incisures, not areolated. Head region truncate, slightly off-set from body. Head cap low and narrower than head region. Cephalic framework weakly sclerotized, vestibule extension distinct. Stylet slender and moderately long (10.5–12 µm), cone straight; shaft cylindrical; small knobs, rounded and off-set from the shaft. Pharynx with faintly outlined procorpus and oval shaped metacorpus with distinct valve. Oesophageal gland lobe variable in length, overlapping intestine ventrally. Hemizonid distinct at level of or immediately anterior to excretory pore which opens slightly less than one bulb length behind the metacorpus. Proctodeum inflated. Moderately sized tail (45–56 µm long), gradually tapering to relatively short hyaline narrow tail terminus (11–15 µm long). Phasmids not observed. A rounded hypodermis marks the anterior position of the hyaline tail terminus; tail terminus ending in a narrowly rounded tip. Terminus smooth, may have cuticular constrictions.

Eggs (n = 6)**:** Length 67–91 µm (81.2 ± 10.3); width 41–52 µm (44.8 ± 3.8).

Differential diagnosis. The New Zealand isolate of *Meloidogyne incognita* is morphologically closest to the descriptions of the species given by Jepson (1987) and Hunt & Handoo (2009). However, none of the nematodes examined here had the high square dorsal arch said to be typical of the *M. incognita* perineal pattern. Jepson (1987) suggested that the *M. incognita* perineal pattern is probably the most variable of all *Meloidogyne* spp., the dorsal arches are typically high and squared, and that the lateral fields are indistinct. The specimens studied here were different in these two aspects of perineal form, with low arches and clear differentiation of dorsal and ventral striae. Galls are typically large and irregular (Fig. 22).

The mature female of the New Zealand isolate of *M. incognita* can be separated from those of *M. fallax, M. hapla, M. javanica*, *M. minor*, *M. naasi*, and *M. trifoliophila* in having the excretory pore opening close to but posterior to the stylet knobs, a clear distinction. It also has a longer stylet (16–17.5 µm in length) than that of *M. fallax, M. hapla, M. minor, M. naasi*, and *M. trifoliophila* (respectively, 13–15, 12.5–14, 13–14, 13–14, and 11–13 µm in length). It differs from *M. javanica* in the form of the perineal pattern; while the ventral and dorsal striae are clearly differentiated in both, *M. incognita* lacks the clear lateral field with parallel sides that is present in *M. javanica*. Morphometrics of the male of the New Zealand isolate of *M. incognita* overlapped with most of those of the other RKN species recognised. However, the phasmids were further from the anus (a distance of 12–17 µm)

than in *M. fallax, M. hapla, M. minor,* and *M. naasi* (respectively, 10.5–11, 3–9, 10.5–11, 10.5–11 µm). In addition, the stylet was longer than in males of *M. naasi* (18–23 *vs* 15–17 µm long), and the spicule and gubernaculum were less curved than in *M. javanica* (arcuate *vs* ventrally curved). It is separated from *M. trifoliophila* by the number of lateral lines (4 *vs* more than 6). The second stage juveniles of the New Zealand isolate of *M. incognita* were also morphologically variable, making it difficult to separate them from other RKN species of the same stage. However, in body length (358–412 µm) they are larger than *M. fallax* (328–352 µm long); they have a shorter tail than in *M. trifoliophila* (45–58 *vs* 62–77.5 µm long) and lack its digitate tip; and the hyaline portion of the tail is shorter than in *M. naasi* (11–15 *vs* 20–27 µm long). They have an inflated proctodeum, absent in juveniles of *M. hapla.*

Material examined. Non-type specimens. Thirteen females (slide nos NNCNZ 4040–4042 containing nine specimens; four of the 13 females examined were temporary specimens), eight males (slide nos NNCNZ 4043–4045) and 22 juveniles (slide nos NNCNZ 4046–4053) deposited at the National Nematode Collection, New Zealand.

Other material. MAF collection contains 67 slides with specimens.

Distribution (Map 3). Based on material examined: New Zealand: **North Island:** Auckland, AK; AgResearch Campus, Hamilton, WO. **South Island:** Lincoln, Canterbury, MC.

Based on collections: More widespread on North Island than South Island. **North Island:** AK; BP; GB; HB; ND; WO; WN. **South Island:** MC.

For world distributions see Table 3.

Habitat and hosts. Based on material examined: New Zealand: potato (*Solanum tuberosum*) tubers, tomato (*Solanum lycopersicum).*

Based on literature: New Zealand: *Allium cepa* (onion), *Beta vulgaris* (beetroot), *Carica papaya* (pawpaw), *Carica pubescens* (mountain pawpaw), *Cucunis sativus* (cucumber), *Cyclamen* sp. (cyclamen), *Cyphomandra betacea* (tamarillo), *Daucus carota* (carrot), *Delphinium cultorum* (delphinium), *Fragaria* sp. (strawberry), *Gerbera jamesonii* (African daisy), *Ipomoea batatas* (kumara), *Leptinella dioica* (dioica), *Leptinella* spp. (cotula), *Nicotiana tabacum* (tobacco), *Nothofagus truncato* (hard beech), *Pastinaca sativa* (parsnip), *Phaseolus angularis* (adzuki bean), *Phaseolus coccineus* (multiflora bean/scarlet runner), *Phytolacca octandra* (pokeweed), *Saintpaulia* sp. (African violet), *Solanum aviculare* (poroporo), *Solanum lycopersicum* (tomato), *Solanum melongena* (egg plant), *Solanum nuricatum* (pepino), *Solanum physalifolium* (hairy nightshade), *Solanum tuberosum* (potato), *Trifolium ambiguum*, *T. argutum*, *T. arvense*, *T. dubium*, *T. glomeratum*, *T. hybridum*, *T. medium*, *T. micranthum*, *T. nigrescens*, *T. occidentale*, *T. pratense*, *T. repens* (white clover), *T. semipilosum*, *T. striatum*, *T. subterraneum* (subterranean clover). For international hosts see Table 3.

Remarks. In an attempt to determine how much intraspecific morphological and morphometrical variation occurred in *M. incognita*, specimens from four districts of Punjab, India and five different host plants were examined and measured (Kaur & Attri 2013). It was concluded that, in mature females, body length and width, neck length, ratio 'a', distance from anus to tail terminus, interphasmid distance, and perineal patterns could all be used reliably for identification. In the Indian study, no characters from J2 nematodes were sufficiently stable for use in ID. Thus, future morphological identifications of *M. incognita* in New Zealand could possibly be made using the mature female only.

Meloidogyne incognita is one of four species of the genus with a world-wide, largely tropical and temperate distribution (Hunt & Handoo 2009), *i.e*., there are no quarantine implications for it. It is a mitotic parthenogen. It is generally regarded as a temperate climate RKN (Hunt & Handoo 2009), reflected in its NZ distribution with most records from the North Island and none from the cool south of the South Island. De Guiron (1979) noted that 10–20% (up to 80%) of living undifferentiated eggs of *M. incognita* were in diapause, which explains the persistence of the nematode in the soil in the absence of host plants and following periods of climatic stress (e.g., drought, cold).

The first New Zealand record of *M. incognita* was from potato and it was subsequently recorded from onion, pawpaw, gerberas, and tomatoes (Clark 1963). It has a broad host range, including white clover (Mercer & Miller 1997) and many weeds, but does not multiply on graminaceous plants. The galls it induces are large and irregular in shape.

Table 5. Morphometrics of adult and second stage juveniles (J2) of *Meloidogyne incognita* isolated from New Zealand. Measurements are in µm and in the form: mean ± SD (range).

Character	Female	Male	J2
n	13	8	22
L	681±125 (501–912)	1299±439 (851–1620)	396±14.6 (358–412)
a	1.7±0.6 (1.3–3.6)	38.1±7.2 (26.8–48.6)	28.2±1.9 (24.2–31.2)
b		13.5±2.0 (10.1–16.5)	6.5±0.4 (5.9–7.6)
c	-	111.6±36.2 (79.1–183.3)	7.7±0.5 (7.0–9.0)
c’	-	0.7±0.1 (0.5–0.9)	5.5±0.5 (4.7–6.4)
T	-	53.9±3.8 (49.0–58.0)	-
Greatest body diam.	430.4±110.5 (216–646)	34.4±5.2 (29.2–40.9)	14.0±0.9 (12.8–16.7)
Body diam. at stylet knobs	-	18.0±2.7 (12.3–20.4)	9.4±0.5 (8.7–9.9)
Body diam. at excretory pore	-	25.6±3.3 (19.8–29.6)	12.3±0.4 (12.0–12.9)
Body diam. at anus	-	18.6±3.6 (13.5–23.1)	9.6±0.7 (8.7–10.8)
Head region height	-	4.0±0.7 (3.2–5.1)	1.6±0.4 (1.0–2.0)
Head region diam.	-	12.0±2.3 (10.2–12.1)	5.3±0.6 (4.2–6.1)
Neck length	190.7±77.8 (50.2–307.9)	-	-
Neck diam.	91.3±42.1 (39.9–160.8)	-	-
Stylet	17.0±0.4 (16.3–17.5)	21.1±1.7 (17.8–23.1)	11.1±0.4 (10.5–11.7)
Stylet cone	9.2±0.4 (8.7–9.6)	11.3±1.0 (9.1–12.3)	6.3±0.6 (4.9–6.8)
Stylet knob height	2.0±0.4 (1.7–2.4)	2.0±0.4 (1.5–2.5)	1.1±0.1 (0.8–1.2)
Stylet knob width	3.5±0.7 (3.0–4.0)	4.9±0.5 (4.0–5.4)	2.1±0.2 (1.8–2.4)
DGO	4.9±0.6 (4.1–5.3)	3.2±0.6 (2.5–4.0)	3.6±0.6 (2.9–4.2)
Ant. end to metacorpus	123.5±11.4 (109.5–137.3)	95.8±9.8 (84.3–112.0)	60.8±3.2 (53.4–66.3)
Metacorpus length	43.9±6.2 (36.2–54.5)	26.2±3.7 (20.3–31.8)	12.6±1.4 (9.8–14.7)
Metacorpus diam.	35.1±6.8 (28.3–50.0)	12.6±1.4 (10.8–14.1)	7.4±0.6 (6.7–8.6)
Metacorpus valve length	16.2±2.4 (12.5–18.8)	10.1±0.9 (8.8–11.5)	4.8±0.3 (4.1–5.2)
Metacorpus valve width	11.9±1.4 (9.0–13.5)	6.7±0.8 (5.9–7.5)	3.5±0.3 (2.9–4.2)
Ant. end to end of gland lobe	-	220.6±8.0 (211.4–226.2)	-
Excretory pore-ant. end	31.4±4.6 (25.9–40.0)	154.8±14.7 (148.1–171.7)	78.2±3.1 (76.4–81.6)
Tail length	-	12.3±3.7 (7.5–15.8)	51.8±2.8 (45.1–55.7)
Hyaline tail terminus	-	-	12.9±1.2 (10.9–14.6)
Phasmids from anus	-	14.0±2.0 (12.2–16.8)	27.4±1.3 (25.7–28.1)
Spicule	-	29.5±2.0 (27.8–31.9)	-
Gubernaculum	-	7.3±0.7 (6.2–8.0)	-
Testis	-	674.4±157.3 (493.3–675.4)	-
Vulva slit length	24.8±3.0 (20.3–28.5)	-	-
Vulva-anus	16.1±2.5 (13.1–18.5)	-	-
Body length/neck length	4.4±2.4 (2.1–9.9)	-	-
Stylet knob width/height	1.7±0.1 (1.6–1.7)	2.5±0.5 (2.0–2.5)	2.0±0.5 (1.4–3.1)
Metacorpus length/width	1.3±0.1 (1.1–1.5)	2.1±0.3 (1.5–2.3)	1.7±0.1 (1.5–1.9)
(Excretory pore/L) x 100	-	11.0±0.6 (10.6–11.7)	19.6±0.4 (19.3–20.1)

Given that *M. incognita* could potentially co-exist in pastures with *M. trifoliophila* and *M. hapla*, and other pest nematodes such as *Heterodera trifolii* and *Pratylenchus* spp., it will be difficult to design rotations for control with plants that are not hosts for one or other pest species. In addition, many weeds act as reservoirs for future infestations. As the nematodes feed on host plant roots, they leave them open to attack by soil pathogens, *i.e*., they form part of a disease complex, and as such it is difficult to determine which nematode pathogen is causing the greatest reduction in yield.

Esbenshade & Triantaphyllou (1985 a,b) described a unique esterase for *M. incognita*, together with a malate dehydrogenase of the N1 type. In our initial gel electrophoresis, it was not possible to separate gel patterns from *M. javanica* and *M. incognita*. One band was observed for malate dehydrogenase, while three bands were detected for esterase, also observed in *M. javanica*. Here, as in other phylogenetic analyses of RKN, sequences from *M. incognita* (Figs 3–5) were in a large clade with *M. javanica* and *M. arenaria*, without clear groups of the respective species.

***Meloidogyne javanica* (Treub, 1885) Chitwood, 1949**

English common name: Javanese root-knot nematode

EPPO Code: MELGJA

Figs 23–28.

Measurements. Table 6.

Morphology. Females: Body annulated, 588–1194 µm long, 274–784 µm wide, pearly white, usually pear shaped, no posterior protuberance, a distinct neck region (192–330 µm long) projecting from the body axis at an angle of up to 90 ° to one side. Head region barely off-set from body, marked with one or two annules. Head cap distinct but variable in shape; labial disc slightly elevated. Cephalic framework weakly sclerotized; vestibule extension distinct. Stylet 14–18 µm long, robust, cone dorsally curved and shaft cylindrical; knobs large, off-set, rounded to transversely ovoid, slightly sloping posteriorly from the shaft. Excretory pore located at 70% of distance between stylet knobs and anterior end of metacorpus, or 2.5 stylet lengths posterior to head end. Pharyngeal glands variable in size and shape. Perineal pattern dorso-ventrally ovoid to oval shaped; with deep lateral incisures (lateral fields), which are not crossed by striae (Fig. 25). Dorsal arch ranging from low to moderately high; with fine, wavy, mostly continuous striae. Lateral lines distinct, more or less parallel to each other. Tail whorl usually present; terminus indistinct without punctations. Phasmids small and difficult to observe, posterior to anus. Vulva a straight or arcuate slit. Perivulval area devoid of or with faint broken striae. Ventral pattern region round to oval in shape; striae fine.

Males: Body vermiform, 1030–1448 µm long, slightly tapering anteriorly, bluntly rounded posteriorly. Cuticle with distinct transverse striae. Lateral field with four incisures. Head off-set, with a single post-labial annule. Labial disc rounded, not elevated. Cephalic framework strongly sclerotized, vestibule extension distinct. Stylet 21–22 µm long; cone straight; shaft cylindrical; knobs rounded, off-set, sloping posteriorly from the shaft. Pharynx with slender procorpus, metacorpus oval shaped with pronounced valve. Ventrally overlapping pharyngeal gland lobe variable in length. Hemizonid 2–3 µm in length, two to four annules anterior to excretory pore, which opens posterior to metacorpus. Testis usually long, monorchic, with reflexed or outstretched germinal zone. Tail short (14–17 µm long) and twisted. Spicules slender, 29–37 µm long, not cephalated, curved ventrally; gubernaculum more curved than spicule. Prominent phasmids located level with or slightly posterior to cloaca.

Second-stage Juveniles: Body 354–426 µm long, vermiform, tapering at both ends but posteriorly more than anteriorly. Body annules small but distinct. Lateral field with four incisures. Head region truncate, slightly off-set from body. Head cap low and narrower than head region. Cephalic framework weakly sclerotized, vestibule extension distinct. Stylet slender (8–12 µm long), cone straight; shaft cylindrical; knobs distinct, rounded and set-off from the shaft. Pharynx with faintly outlined procorpus and oval shaped meta-corpus with distinct valve. Oesophageal gland lobe variable in length, overlapping intestine ventrally. Hemizonid immediately anterior to level of excretory pore, which opens posterior to metacorpus. Moderately sized tail (46–61 µm long), gradually tapering to hyaline tail terminus (12–17 µm long), with inflated proctodeum. Phasmids not observed. A rounded hypodermis marks anterior position of the hyaline tail terminus; tail terminus ending in a finely to broadly rounded tip. Terminus often has faint cuticular constrictions.

Eggs: (n=5); Length 75–95 µm (84.4 ± 7.9); width 36–44 µm (40.1 ± 3.2).

Table 6. Morphometrics of adult and second stage juveniles (J2) of *Meloidogyne javanica* isolated from New Zealand. Measurements are in µm and in the form: mean ± SD (range).

Character	Female	Male	J2
n	12	4	23
L	788±175 (588–1194)	1204±197 (1030–1448)	402±20.9 (354–426)
a	1.8±0.4 (1.4–2.5)	29.7±4.5 (25.0–35.7)	29.1±1.9 (24.7–31.8)
b		11.7±1.6 (10.7–14.0)	6.7±0.4 (5.8–7.3)
c	-	79.9±18.3 (61.3–103.9)	7.9±0.6 (6.3–8.4)
c’	-	-	5.9±0.6 (4.7–6.9)
T	-	39.6–39.9	-
Greatest body diam.	462.5±143.4 (273.7–784.3)	40.8±6.2 (35.8–49.4)	13.9±1.0 (11.1–16.2)
Body diam. at stylet knobs	-	22.6±3.3 (19.9–27.3)	10.6±1.7 (8.8–13.2)
Body diam. at excretory pore	-	33.0.0±4.0 (29.5–37.4)	12.4±0.5 (11.8–13.2)
Body diam. at anus	-	21.2±7.0 (16.2–29.1)	8.9±0.8 (7.8–10.8)
Head region height	-	5.0±0.9 (3.8–6.0)	1.9±0.3 (1.5–2.3)
Head region diam.	-	12.7±0.3 (12.4–13.1)	5.1±0.4 (4.7–5.7)
Neck length	253.0±86.2 (192.2–330.5)	-	-
Neck diam.	108.3±26.2 (70.0–162.8)	-	-
Stylet	15.6±1.4 (14.0–17.6)	21.8±0.4 (21.1–22.1)	11.0±0.5 (8.2–11.6)
Stylet cone	-	11.9±0.5 (11.2–12.3)	5.8±0.6 (8.2–11.6)
Stylet knob height	2.0±0.4 (1.7–2.4)	2.1±0.2 (1.8–2.3)	1.1±0.1 (1.0–1.2)
Stylet knob width	4.6±0.3 (4.4–4.9)	4.6±0.3 (4.2–4.9)	2.0±0.2 (1.9–2.2)
DGO	3.7±0.3 (3.4–3.9)	3.0±0.3 (2.7–3.2)	2.9±0.4 (2.4–3.1)
Ant. end to metacorpus	-	103.1±11.7 (90.7–118.6)	60.0±4.7 (51.0–65.3)
Metacorpus length	41.0±10.1 (29.3–47.4)	21.0±3.8 (17.3–24.9)	13.9±1.1 (11.8–15.1)
Metacorpus diam.	28.4±2.8 (26.6–31.6)	15.6±1.5 (14.5–17.3)	8.0±0.9 (6.9–9.6)
Metacorpus valve length	15.9±1.7 (14.7–17.1)	10.0±0.4 (9.5–10.4)	4.6±0.5 (3.9–5.1)
Metacorpus valve width	10.4±0.7 (9.9–10.9)	6.9±0.8 (6.0–7.9)	3.3±0.3 (2.9–3.7)
Ant. end to end of gland lobe	-	240.7 (233.4, 247.0)	-
Excretory pore-ant. end	41.9±7.9 (34.8–53.1)	155.7±28.7 (133.0–187.9)	78.1±5.3 (73.6–88.3)
Tail length	-	15.3±1.5 (13.9–17.3)	51.7±4.4 (45.9–61.3)
Hyaline tail terminus	-	-	14.7±1.7 (12.1–17.1)
Phasmids from anus	-	13.1±5.5 (8.7–19.3)	-
Spicule	-	31.4±4.0 (28.6–37.2)	-
Gubernaculum	-	8.5±1.7 (7.0–10.9)	-
Testis	-	492.4±114.6 (411.4–573.4)	-
Vulva slit length	24.5±3.3 (16.8–28.5)	-	-
Vulva-anus	16.8±2.5 (13.3–20.8)	-	-
Body length/neck length	3.3±0.8 (1.9–4.4)	-	-
Stylet knob width/height	2.3±0.6 (1.8–2.9)	2.2±0.2 (2.1–2.2)	1.9±0.2 (1.7–2.3)
Metacorpus length/width	1.4±0.3 (1.1–1.8)	1.5±0.2 (1.3–1.7)	1.7±0.3 (1.4–2.1)
(Excretory pore/L) x 100	-	12.9±4.6 (10.1–18.2)	19.1±1.4 (18.1–21.8)

Differential diagnosis. The New Zealand isolate of *Meloidogyne javanica* is characterised by having mature females with perineal patterns with distinct lateral fields and lines. It is morphologically closest to the description of *M. javanica* given by Hunt & Handoo (2009). However, males differ from the description given by Hunt & Handoo (2009) in having an off-set *vs* not off-set labial region. On most hosts, gall form is large and irregular.

The mature female of the New Zealand isolate of *M. javanica* is separated from all other RKN species isolated there by having perineal patterns which are dorso-ventrally ovoid to oval shaped; and have deep lateral incisures (lateral fields), which are not crossed by striae and have almost parallel walls. Such lateral fields have only been seen in *M. javanica*. In body shape, it differs from those of *M. hapla*, *M. minor* and *M. naasi* in having a long neck (respectively, 192–330 µm *vs* 48–166, 80–139 and 75–143 µm long); but the ratio of body length:neck length is highly variable and overlaps with that of the other species. The opening of the excretory pore, at about the level of the anterior end and the metacorpus, is more posterior than in *M. incognita, M. minor* and *M. naasi*, in which it opens close to the stylet knobs; and in *M. fallax, M. hapla* and *M. trifoliophila* it is more anterior. *Meloidogyne javanica* has a longer stylet than the female of *M. trifoliophila* (14–18 vs 11–13 µm in length), but it is similar in length to that of other species examined from New Zealand. The adult male of *M. javanica* in New Zealand has a spicule and gubernaculum that are more curved than in other RKN males isolated there. At 14–17 µm, the tail of these isolates of male *M. javanica* is longer than in *M. fallax, M. hapla, M. minor, M. naasi* and *M. trifoliophila* (respectively, 6–9, 3.5–9, 7.5–11, 3–11, and 7–12 µm long). The males of New Zealand isolates of *M. javanica* also have a longer stylet than those of *M. fallax, M. hapla, M. minor, M. naasi*, and *M. trifoliophila* (respectively, 21–22 vs 17–19, 18–21, 16–19, 15–17, and 16–19 µm long). Most of the morphometrics of the second stage juveniles of the New Zealand isolate of *M. javanica* overlap those of the other species of RKN isolated. However, it can be separated from *M. fallax* in having a longer tail (46–61 µm *vs* 38–46 µm) and from *M. trifoliophila* in having a shorter one (46–61 µm vs 62–77.5 µm long) without a digitate tip; and having a shorter length of the hyaline part of the tail separates it from *M. naasi* and *M. trifoliophila* (respectively, 12–17 *vs* 20–27 and 17–26 µm in length). It has an inflated proctodeum; not present in juveniles of *M. hapla*.

Material examined. Non-type specimens. Twelve females (slide nos NNCNZ 4054–4059), four males (slide nos NNCNZ 4060; MPI nematode collection slide nos 1265, 2265) and 23 juveniles (slide nos NNCNZ 4061–4064) deposited at the National Nematode Collection, New Zealand.

Other material. MAF collection contains 20 slides with specimens.

Distribution (Map 4). Based on material examined: New Zealand: **North Island:** AgResearch Campus, Hamilton, WO. **South Island:** Lincoln, Canterbury, MC.

Based on collections: Widespread on North Island; limited distribution on South Island. **North Island:** AK; BP; ND; CL; GB; WO. **South Island:** MC.

For world distributions see Table 3.

Habitat and hosts. *Meloidogyne javanica* has more than 770 recorded host species (Subbotin *et al*. 2021). Based on material examined: New Zealand: potato (*Solanum tuberosa*) tubers, tomato (*Solanum lycopersicum*).

Based on literature: New Zealand: *Cucunis sativus* (cucumber), *Cucurbita pepo* (marrow/courgette), *Dianthus caryophyllus* (carnation), *Gerbera jamesonii* (African daisy), *Pastinaca sativa* (parsnip), *Saintpaulia* sp. (African violet), *Solanum nigrum* (black nightshade), *Trifolium ambiguum*, *T. argutum*, *T. arvense*, *T. dubium*, *T. glomeratum*, *T. hybridum*, *T. medium*, *T. micranthum*, *T. nigrescens*, *T. occidentale*, *T. pratense*, *T. repens* (white clover), *T. semipilosum*, *T. striatum*, *T. subterraneum* (subterranean clover). For international hosts see Table 3.

Remarks. In an attempt to determine how much intraspecific morphological and morphometrical variation occurred in *M. javanica*, specimens from six populations and three host races were examined and measured (Rammah & Hirschmann 1990). From that study, it was concluded that, in mature females of *M. javanica*, stylet morphology and perineal patterns could be used reliably for identification. Head and stylet morphology of males was also useful. Other characters were too variable to be used. There was no morphological basis for differentiation of host races of *M. javanica*. This suggests that future morphological identifications of *M. javanica* could be made on the basis of perineal patterns and stylet morphology in adults.

Meloidogyne javanica is one of four species of the genus with a world-wide distribution (Hunt & Handoo 2009), *i.e*., there are no quarantine implications for it. It is generally regarded as a warm climate RKN (Subbotin *et al.* 2021), reflected in its NZ distribution with most records from the North Island and few from the cooler South Island.

The first formal New Zealand record of *M. javanica* was by Dale (1972), from cucumber. However, he also reported an unpublished record of it on *Gerbera*, from the Entomology Department, which was undated, so it was

presumably recognised earlier. It has a broad host range but does not multiply on graminaceous plants. Zhao (personal communication, September 2022) commented that it is frequently collected from tomatoes grown in the field.

While there have been no pot trials with nematicides to test how much *M. javanica* reduces yield of host plants in New Zealand, fumigation is practised in areas with high nematode pressure, e.g., where tomatoes are grown in the field and in apple nurseries (Farhat Shah, personal communication, September 2022). Rotations are most commonly used to keep populations low. Given that *M. javanica* co-exists in pastures with *M. incognita*, *M. trifoliophila* and *M. fallax*, and other pest nematodes such as clover cyst nematode and *Pratylenchus* spp., it is difficult to design rotations with plants that are not hosts for one or other pest species.

Galls of *M. javanica* are similar to those of *M. incognita*, being large and irregular in form (Fig. 28). Like *incognita*, it is a mitotic parthenogen.

Meloidogyne javanica has an esterase phenotype of the J3, J2 or J2a form (Esbenshade & Triantaphyllou 1985 a,b; Tomaszewski *et al.* 1994; Castro *et al.* 2003). Its malate dehydrogenase is of the N1 type (Esbenshade & Triantaphyllou 1885 a,b). In our preliminary gels for *M. javanica* one band was observed for malate dehydrogenase, while three bands were detected for esterase, also observed in gels for *M. incognita*. It was not possible to separate gel patterns from *M. javanica* and *M. incognita*. Here, as in other phylogenetic analyses of RKN, sequences from *M. javanica* were in a large clade with *M. incognita* and *M. arenaria*, without clear groups of the respective species.

***Meloidogyne minor* Karrsen, Bolk, van Aelst, van den Beld, Kox, Korthals, Molendijk, Zijlstra, van Hoof & Cook, 2004**

English common name: None

EPPO Code: MELGMI

Figs 29–33.

Measurements. Table 7.

Morphology. Females: Body relatively small, 332–534 µm long, 199–363 µm wide, weakly annulated, pearly white, usually globose, sometimes elongated; neck region distinct, often bent; young females with but mature females lacking a slight posterior protuberance. Head region off-set from the body. Labial cap distinct and highly variable in shape, labial disk elevated, lateral lips prominent; cephalic framework weakly sclerotized. Stylet 13–14 µm long, conus slightly curved dorsally, shaft cylindrical, knobs transversely ovoid and slightly sloping backwards from shaft. Excretory pore located at level of stylet knobs. Pharyngeal glands variable in size and shape. Perineal pattern small, rounded, with fine striae, dorsal arch low with coarse striae (Fig. 30). Tail remnant area distinct, without punctuations; in some weak lateral lines present; phasmids large, visible, located anterior to covered anus. Egg mass five to six times larger than female body size.

Males: Body vermiform, slightly tapering anteriorly, 818–1689 µm long and 25–52 µm in diameter, bluntly rounded posteriorly and annulated, usually not twisted, tail region arcuate. Four incisures present in raised lateral field, one or two incomplete central incisures near mid-body in some specimens; outer bands irregularly areolated. Head not off-set from body, one post-labial annule present often with one or two incomplete transverse incisures. Labial disc rounded. Cephalic framework strongly sclerotized; vestibule extension distinct. Stylet with straight conus and cylindrical shaft; 16–19 µm long, large transversely ovoid knobs, sloping slightly backwards from the shaft. Dorsal gland orifice close to stylet knobs. Pharynx with slender procorpus and oval-shaped metacorpus. Pharyngeal gland lobe ventrally overlapping intestine, two subventral gland nuclei present. Hemizonid not seen; excretory pore opens posterior to the nerve ring. Testis long, single, with outstretched germinal zone. Tail usually curved ventrally, short, 7–11 µm long, conical with bluntly rounded tip. Spicule and gubernaculum slender, arcuate. Phasmids large and located level with or slightly anterior to cloaca.

Second-stage Juveniles: Body vermiform, 370–390 µm long, 13–22 µm in diameter, annulated; anterior part tapering behind stylet-knob level, posterior part slightly ventrally curved when heat relaxed. Lateral field with four incisures, areolation not seen. Head region rounded, not off-set from body. Head cap narrower than head region. Cephalic framework weakly sclerotized, vestibule extension distinct. Stylet small, conus straight, shaft cylindrical; knobs transversely ovoid and slightly sloping backwards. Metacorpus relatively large, ovoid, triradiate lumen with clear sclerotized lining. Pharyngeal gland lobe relatively long, ventral overlap of intestine clearly visible, three gland nuclei present. Hemizonid width of one annule in length, at posterior end of excretory pore and adjacent to it;

Table 7. Morphometrics of adult and second stage juveniles (J2) of *Meloidogyne minor* isolated from New Zealand. Measurements are in µm and in the form: mean ± SD (range).

Character	Female	Male	J2
n	11	11	13
L	413±70 (332–534)	1219±271 (818–1689)	377±8.0 (370–390)
a	1.6±0.2 (1.4–1.9)	29.8±6.7 (19.2–37.7)	22.8±3.4 (17.7–28.7)
b		18.1±4.0 (14.0–22.0)	6.5±0.2 (6.1–6.8)
c	-	136.5±11.7 (121.1–146.3)	6.9±0.4 (6.1–7.8)
c’	-	-	4.8±5.5 (3.7–5.4)
T	-	58–60	-
Greatest body diam.	258±47 (199–363)	42±11 (25–52)	17±3 (13–22)
Body diam. at stylet knobs	-	17.3±3.1 (15.3–20.8)	-
Body diam. at excretory pore	-	42.0±38 (37.6–44.9)	-
Body diam. at anus	-	22.4±2.7 (22.5–26.4)	11.3±1.5 (9.3–13.5)
Head region height	-	4.3±1.0 (3.4–6.1)	2.6±0.4 (2.0–3.2)
Head region diam.	-	10.7±1.2 (9.1–12.3)	5.8±0.4 (5.2–6.1)
Neck length	104.9±23.5 (80.5–138.8)	-	-
Neck diam.	62.9±8.7 (51.3–63.9)	-	-
Stylet	13.3±0.4 (12.8–13.8)	17.9±0.8 (16.3–18.8)	11.3±1.2 (9.7–12.8)
Stylet cone	-	11.2±0.4 (10.4–11.6)	-
Stylet knob height	1.4±0.3 (1.1–1.7)	2.0±0.3 (1.6–2.6)	1.1±0.2 (1–1.5)
Stylet knob width	2.5±0.3 (2.1–2.8)	3.9±0.3 (3.3–4.3)	2.0±0.3 (1.5–2.5)
DGO	4.6±0.5 (4.2–5.5)	4.4±0.4 (3.7–4.8)	3.4±0.5 (2.7–4.2)
Ant. end to metacorpus	-	73.2±3.0 (70.7–76.58)	58.2±2.4 (54.9–63.7)
Metacorpus length	30.2±6.7 (22.7–41.0)	23.6±4.3 (20.6–26.6)	14.6±1.0 (13.5–17.1)
Metacorpus diam.	24.9±4.4 (20.2–31.8)	10.9±1.4 (9.3–12.0)	8.9±0.1 (8.9–9.3)
Metacorpus valve length	10.3±1.5 (7.8–12.3)	6.3±0.6 (5.5–6.9)	3.9±0.4 (3.6–4.5)
Metacorpus valve width	7.6±0.9 (6.0–8.5)	4.0±0.3 (3.5–4.3)	2.8±0.2 (2.7–3.1)
Excretory pore-ant. end	13.1±1.4 (11.6–14.4)	115.7±31.5 (77.9–160.3)	72.3±6.2 (64.9–77.9)
Tail length	-	9.2±1.6 (7.4–11.2)	54.8±4.3 (52.9–62.6)
Hyaline tail terminus	-	-	15.9±1.1 (14.0–18.0)
Phasmids from anus	-	10.8±0.4 (10.5–11.3)	11.7±1.3 (10.8–12.6)
Spicule	-	26.4±2.0 (23.1–28.7)	-
Gubernaculum	-	7.6±0.7 (7.1–8.3)	-
Testis	-	602.1±36.4 (576.4–627.8)	-
Vulva slit length	23.8±4.8 (17.0–29.4)	-	-
Vulva-anus	14.1±2.2 (11.5–15.9)	-	-
Body length/neck length	4.0±0.6 (3.3–5.4)	-	-
Stylet knob width/height	1.8±0.5 (1.2–2.4)	2.0±0.3 (1.3–2.5)	-
Metacorpus length/width	1.2±0.1 (1.1–1.4)	-	-
(Excretory pore/L) x 100	-	10.2±2.0 (8.1–12.1)	19.1±1.8 (17.3–23.6)

pore opens behind the level of the nerve ring. Tail straight, 53–63 µm in length, slender, sometimes slightly curved ventrally, gradually tapering until finely pointed tail tip; rectum usually weakly inflated. Hyaline tail terminus distinct, 14–18 µm in length, relatively long and narrow, often one or two cuticular constrictions present on tail terminus. Phasmids posterior to anus, at about 26% (21–32%) of tail length, small, difficult to see.

Eggs: (n=12); Length 73–98 µm (82.0 ± 7.6); width 36–43 µm (40.1 ± 2.6).

Differential diagnosis: The New Zealand isolate of *Meloidogyne minor* is morphologically closest to the original description of *M. minor* (Karrsen *et al*., 2004). However, it varies from the original description in having phasmid positions that are sexually dimorphic. In the original description, the male phasmids were posterior to the anus, but in the New Zealand specimens of *M. minor*, they are slightly anterior to or at the same level as the anus (Fig. 31). Karrsen *et al.* (2004) stated that in the female the phasmids are small and usually not visible, but in the New Zealand specimens they are large and clearly visible (Fig. 32).

The New Zealand isolate of *M. minor* is morphologically separated from the other known New Zealand isolates of RKN by a relatively small, circular perineal pattern in mature females, lacking the 'wings' and punctations of *M. hapla* and the distinct lateral fields present in *M. javanica*. It is further separated from other species of RKN from New Zealand by having large, prominent phasmids. The position of the excretory pore in mature females (opening close to the stylet knobs) separates it from *M. fallax* (opening at approximately half the distance between the anterior end and the metacorpus), from *M. javanica* (opening at the level of the anterior metacorpus), and from *M. hapla* and *M. trifoliophila* (opening at about 75% of the distance from anterior end to the metacorpus). Males of the New Zealand isolate of *M. minor* have a curved rather than the twisted tail seen in the other species of RKN isolated in New Zealand. They also have an arcuate spicule and gubernaculum unlike those of *M. javanica* which are strongly curved and have a shorter tail (7.5–11 *vs* 14–17 µm long). The phasmids on the tail of male *M. minor* are further from the anus than in *M. hapla* (10.5–11 *vs* 3–9 µm distant), but closer than in *M. incognita* (12–17 µm distant). Body length of the second stage juveniles separates the New Zealand isolate of *M. minor* from those of *M. incognita, M. javanica and M. naasi* (respectively, 370–390 *vs* 358–412, 354–426, and 397–467µm long). Their tail is longer than that of *M. fallax* (53–63 *vs* 38–46 µm long), and the length of the hyaline section of the tail is shorter than in *M. naasi* and *M. trifoliophila* (14–18 *vs* 20–27 and 17–26 µm long). They lack the digitate tail tip of second stage juveniles of *M. trifoliophila.* Juveniles have an inflated proctodeum, not present in *M. hapla*.

Material examined. Non-type specimens. Three females (slide nos NNCNZ 3210–3214), 12 males (slide nos NNCNZ 3215–3225) and 12 juveniles (slide nos NNCNZ 3226–3237) deposited at the National Nematode Collection, New Zealand.

Distribution (Map 5). Based on material examined: New Zealand: **North Island:** Not recorded. **South Island:** MC.

Based on collections: **North Island:** Not recorded. **South Island:** a sports ground in Christchurch, MC.

For world distributions see Table 3.

Habitat and hosts. Based on material examined: New Zealand: perennial ryegrass (*Lolium perenne*).

Based on literature: New Zealand: *Lolium perenne* (perennial ryegrass). For international hosts see Table 3.

Remarks. The key diagnostic features of *M. minor* are the small rounded perineal pattern of the mature female, the presence of lateral fields in some specimens, and large phasmids. Females are usually globular but may be elongated. Males usually have a curved, but not twisted, tail. The hemizonid is at the level of the excretory pore in second stage juveniles. It is a facultative meiotic parthenogen.

Meloidogyne minor was first recorded in New Zealand, from turf, by Zhao *et al*. (2017). It is regarded as an emerging pest species in Europe (Moens *et al.* 2009). It has not been recorded from Australia.

In the UK and the USA, mixed populations of *M. minor* and *M. naasi* have been found on golf courses (Karrsen *et al*. 2004; McLure *et al.* 2012). On Washington golf courses, there was about one *M. minor* for every four *M. naasi* (McLure *et al.* 2012). Extraordinarily high numbers of juvenile *M. minor* were found in the New Zealand sample—with more than 7800 juveniles in an 80 g soil sample (Zhao *et al.* 2017); much greater than any damage threshold. However, it was only detected at the one site in Christchurch, suggesting a recent incursion.

In New Zealand, *M. minor* caused yellow patch disease on ryegrass turf within 18 months of the laying of the turf (Zhao *et al.* 2017). It has potential to spread and become a significant pest, as eradication (using methyl bromide, problematic in itself) is unlikely and would be very expensive. Ongoing efforts will be required to prevent

spread, e.g., on sand attached to boots. On potatoes, *M. minor* has galls similar to those induced by *M. fallax*—appearing as small, pimple-like raised blisters.

Meloidogyne minor has a N1a malate dehydrogenase (Mdh) pattern with two additional weaker bands after prolonged staining of electrophoretic gels, and one very weak VS1 esterase band (Karrsen *et al*. 2004). No gels are available for New Zealand isolates of *M. minor*. In our analyses, molecular sequencing grouped the New Zealand isolate of *M. minor* with isolates of the nematode from other countries (Figs 3–5), and phylogenetic analyses grouped it with *M. fallax* and *M. chitwoodi*. This supports the inferences of Alvarez-Ortega *et al.* (2019).

***Meloidogyne naasi* Franklin, 1965**

English common name: Barley root-knot nematode

EPPO Code: MELGNA

Figs 34–38.

Measurements. Table 8.

Morphology. Females: Body annulated, relatively broad and short for the genus, 332–534 µm long, 199–363 µm wide, pearly white, globular to pear shaped, with slight posterior protuberance bearing vulva, and a distinct neck region (80–139 µm long) projecting from the body axis at an angle of up to 90º to one side. Head region off-set from body, marked with one or two annules. Head cap distinct but variable in shape; labial disc slightly elevated. Cephalic framework weakly sclerotized; vestibule extension distinct. Stylet 13–14 µm long, cone slender, dorsally curved and shaft cylindrical; knobs large, rounded to transversely ovoid, slightly sloping posteriorly from the shaft. Excretory pore opening at level of the stylet knobs. One or two large vesicles and several smaller ones located along the lumen lining of metacorpus. Pharyngeal glands variable in size and shape. Perineal pattern dorsoventrally oval; dorsal arch ranging from low to moderately high, with coarse striae (Fig. 36). Tail terminus indistinct, without punctations. Anus covered by cuticular fold. Phasmids relatively large, anterior to anus. Broken cuticular lines around and between phasmids. Perivulval area with a few faint striae. Lateral field marked by interrupted striae. Ventral pattern region oval to angular in shape; striae moderately coarse.

Males: Body vermiform, 796–1215 µm long, slightly tapering anteriorly, bluntly rounded posteriorly. Cuticle with distinct transverse striae. Lateral field with four incisures. Head slightly off-set, with a single post-labial annule usually partly subdivided by a transverse incisure. Labial disc rounded, elevated. Cephalic framework moderately sclerotized, vestibule extension distinct. Stylet 15–17 µm long, cone straight; shaft cylindrical; knobs large and rounded, off-set from the shaft. Pharynx with slender procorpus, metacorpus ovoid to elongate oval shape with pronounced valve. Ventrally overlapping pharyngeal gland lobe variable in length. Hemizonid 2–3 µm in length, two to four annules anterior to excretory pore, which opens 2–3 bulb lengths behind the metacorpus. Testis usually long, monorchic, with reflexed or outstretched germinal zone. Tail short and twisted. Spicules slender, 25–31 µm long, slightly ventrally arcuate; gubernaculum a little more curved. Phasmids located level with or slightly anterior to cloaca.

Second-stage Juveniles: Body 397–467 µm long, vermiform, tapering at both ends but posteriorly more than anteriorly. Body annules small but distinct. Lateral field with four incisures, not areolated. Head region truncate, slightly off-set from body. Head cap low and narrower than head region. Cephalic framework weakly sclerotized, vestibule extension distinct. Stylet slender and moderately long (11–12 µm), cone straight; shaft cylindrical; knobs distinct, rounded and off-set from the shaft. Pharynx with faintly outlined procorpus and oval or sub-ovoid shaped metacorpus with distinct valve. Oesophageal gland lobe variable in length, overlapping intestine ventrally. Hemizonid distinct, 2–3 um long, at level of excretory pore which opens at level of nerve ring; inflated proctodeum. Moderately sized slender tail (51–78 µm long), gradually tapering to hyaline tail terminus (20–27 µm long). Phasmids not observed. A rounded hypodermis marks the anterior position of the smooth narrow hyaline tail terminus; tail terminus ending in a narrowly rounded tip. Terminus generally marked by faint cuticular constrictions.

Eggs: not measured (not collected from field).

Differential diagnosis. The New Zealand isolate of *Meloidogyne naasi* is characterised by its perineal pattern, with a moderately high dorsal arch, covered anus, and prominent phasmids in females. It is morphologically closest to the original description of *M. naasi* (Franklin, 1965). However, it varies from the original description in having a ventral perineal pattern which may be angular. Galls on barley are terminal,

cylindrical, club-shaped, hook-shaped or spiral, but more or less globular on lateral roots of sugar beet (Franklin 1965; dos Santos *et al.* 2020).

Table 8. Morphometrics of adult and second stage juveniles (J2) of *Meloidogyne naasi* isolated from New Zealand. Measurements are in µm and in the form: mean ± SD (range).

Character	Female	Male	J2
n	4	12	17
L	413±70 (332–534)	1008±113 (796–1215)	429±15.7 (397–467)
a	1.6±0.2 (1.4–1.9)	34.3±6.0 (21.8–44.3)	27.0±1.9 (24.2–30.7)
b		16.9±3.4 (12.1–20.5)	7.1±0.5 (6.6–8.0)
c	-	187.3±76.0 (85.6–240.7)	6.5±0.9 (5.6–8.3)
c’	-	-	6.5±0.6 (5.3–7.8)
T	-	66.1±8.9 (54.5–76.5)	-
Greatest body diam.	258±47 (199–363)	30.2±6.7 (21.8–44.93)	15.9±0.7 (14.4–17.3)
Body diam. at stylet knobs	-	15.5±3.2 (12.6–22.4)	9.8±0.2 (9.5–10.0)
Body diam. at excretory pore	-	22.1±3.6 (19.3–22.3)	13.6±0.4 (12.8–14.0)
Body diam. at anus	-	10.8±3.1 (7.0–16.8)	10.4±1.4 (9.5–12.5)
Head region height	-	2.9±0.8 (2.2–4.0)	1.6±0.3 (1.3–2.2)
Head region diam.	-	7.1±1.8 (6.1–9.7)	5.0±0.6 (4.6–5.6)
Neck length	104.9±23.5 (80.5–138.8)	-	-
Neck diam.	62.9±8.7 (51.3–63.9)	-	-
Stylet	13.3±0.4 (12.8–13.8)	15.8±0.7 (15.0–16.7)	11.7±0.6 (10.8–12.2)
Stylet cone	-	8.1±0.6 (7.5–8.9)	-
Stylet knob height	1.4±0.3 (1.1–1.7)	1.7±0.3 (1.3–2.1)	1.3±0.2 (1.2–1.5)
Stylet knob width	2.5±0.3 (2.1–2.8)	3.4±0.5 (2.6–4.1)	2.0±0.2 (1.7–2.2)
DGO	4.6±0.5 (4.2–5.5)	3.1±0.5 (2.2–3.7)	2.6±0.2 (2.3–2.7)
Ant. end to metacorpus	-	61.7±8.7 (55.2–80.94)	60.4±3.9 (55.8–66.8)
Metacorpus length	30.2±6.7 (22.7–41.0)	16.4±2.2 (14.1–19.7)	11.7±1.0 (10.2–13.0)
Metacorpus diam.	24.9±4.4 (20.2–31.8)	10.6±0.5 (9.8–11.0)	7.7±0.2 (7.3–7.9)
Metacorpus valve length	10.3±1.5 (7.8–12.3)	6.0±1.3 (4.1–7.7)	4.0±0.2 (3.9–4.4)
Metacorpus valve width	7.6±0.9 (6.0–8.5)	4.1±0.9 (3.2–5.5)	3.0±0.3 (2.4–3.3)
Ant. end to end of gland lobe	-	207.1±26.3 (174.9–235.7)	-
Excretory pore-ant. end	13.1±1.4 (11.6–14.4)	112.5±16.4 (99.6–140.7)	70.0±2.3 (67.4–72.6)
Tail length	-	6.2±2.4 (3.0–11.5)	67.2±8.8 (51.0–78.0)
Hyaline tail terminus	-	-	24.7±2.5 (19.6–27.4)
Phasmids from anus	-	5.9±0.6 (5.1–6.5)	-
Spicule	-	28.1±1.6 (25.5–30.7)	-
Gubernaculum	-	6.1±0.9 (5.1–7.1)	-
Testis	-	696±116 (546–819)	-
Vulva slit length	23.8±4.8 (17.0–29.4)	-	-
Vulva-anus	14.1±2.2 (11.5–15.9)	-	-
Body length/neck length	4.0±0.6 (3.3–5.4)	-	-
Stylet knob width/height	1.8±0.5 (1.2–2.4)	2.0±0.1 (1.8–2.1)	1.5±0.2 (1.3–1.8)
Metacorpus length/width	1.2±0.1 (1.1–1.4)	1.6±0.2 (1.3–1.9)	1.5±0.1 (1.4–1.7)
(Excretory pore/L) x 100	-	10.7±0.8 (10.0–11.6)	15.4±17.2 (16.4–0.6)

The New Zealand isolate of *M. naasi* is morphologically separated from the other known New Zealand isolates of RKN by having a perineal pattern that is dorsoventrally ovoid with a low to moderately high dorsal arch, a covered anus, and relatively large phasmids, anterior to the anus. The pattern lacks the 'wings' and punctations of *M. hapla* and the distinct lateral fields present in *M. javanica*. It is further separated from other species of RKN from New Zealand by the position of the excretory pore in mature females (opening close to the stylet knobs), separating it from *M. fallax* (opening at approximately half the distance between the anterior end and the metacorpus), from *M. javanica* (opening at the level of the anterior metacorpus), and from *M. hapla* and *M. trifoliophila* (opening at about 75% of the distance from anterior end to the metacorpus). Males of the New Zealand isolate of *M. naasi* have a twisted rather than the curved tail seen in the *M. minor* isolated in New Zealand. They also have an arcuate spicule and gubernaculum unlike those of *M. javanica* which are more strongly curved and have a shorter tail (3–11 *vs* 14–17 µm long). The phasmids on the tail of male *M. naasi* are closer to the anus than in *M. incognita* and *M. trifoliophila* (respectively, 5–6.5 *vs* 12–17 and 8.4–16 µm distant). The stylets of males of *M. naasi* are smaller than those of *M. hapla* (15–17 *vs* 18–21 µm long). Body length of the second stage juveniles separates the New Zealand isolate of *M. naasi* from those of *M. incognita, M. javanica* and *M. minor* (respectively, 397–467 *vs* 358–412, 354–426, and 370–390 µm long). Their tail is longer than that of *M. fallax* (51–78 *vs* 38–46 µm long), and the length of the hyaline section of the tail is longer than in *M. fallax, M. hapla, M. incognita, M. javanica*, and *M. minor* (20–27 *vs* 11–16.5, 9–18, 11–15, 12–17, and 14–18 µm long). They lack the digitate tail tip of second stage juveniles of *M. trifoliophila.*

Material examined. Non-type specimens. Four females (slide nos NNCNZ 4065, 4066), 12 males (MPI nematode collection slide no 3310) and 17 juveniles (slide nos NNCNZ 4067–4076) deposited at the National Nematode Collection, New Zealand.

Other material. MAF collection contains 8 slides with specimens.

Distribution (Map 6). Based on material examined: New Zealand: **North Island:** WN; AK. **South Island:** MC.

For world distributions see Table 3.

Habitat and hosts. Based on material examined: New Zealand: Wheat (*Triticum aestivum*), perennial ryegrass (*Lolium perenne*).

Based on literature: New Zealand: *Agrostis tenuis* (brown top), *Avena sativa* (oat), *Daucus carota* (carrot), *Glyceria fluitans* (floating sweet grass), *Hordeum vulgare* (barley), *Lolium perenne* (perennial ryegrass), *Lolium* sp., *Poa annua* (poa), *Polygonum persicaria* (willow weed), *Secale cereale* (rye/ryecorn), *Triticum aestivum* (wheat). For international hosts see Table 3.

Remarks. *Meloidogyne naasi* is characterised by having a perineal pattern that can be described as a 'monkey face', with the phasmids the eyes, the anus the nose and the vulva a wide mouth.

This RKN was first reported from New Zealand by Grbavac *et al.* (1978). *Meloidogyne naasi* is regarded as a cool climate RKN but is found widely on both the North Island and the cooler South Island of New Zealand. Its eggs require a period of chilling for hatching to occur *i.e*., have a temperature dormancy (Antoniou & Evans 1987). Thus, *M. naasi* has one generation per year. It is a meiotic parthenogen.

Meloidogyne naasi has been found in both pastures and from perennial ryegrass samples taken from golf-courses (Zhao *et al*. 2017). It has a wide host range (more than 60 recorded host species), developing on both graminaceous crops such as oats and barley and ryegrass and on broad leaf plants like carrot (Grbavac *et al*. 1978; Sheridan & Grbavac 1979).

Meloidogyne naasi has not been recorded from Australia. While it needs cold to induce hatch of eggs (Antoniou & Evans 1987); such temperatures do occur in cereal growing and/or dairying areas in southern New South Wales and Victoria, and the South-East of South Australia, *i.e.,* it could possibly develop there. Thus, there are quarantine implications for this nematode.

In Europe and America, *M. naasi* has been found on golf courses together with *M. minor* (Zhao *et al*. 2017). In New Zealand, it was not found in turf with *M. minor* (Zhao *et al*. 2017) but has been collected from perennial ryegrass in pastures (Knight *et al.* 1997). Galls induced by this nematode on barley are cylindrical, terminal, club-shaped, hook-shaped or spiral (Franklin 1965). On the lateral roots of sugar-beet they are more or less globular. Egg masses are retained within the roots.

Isozyme patterns as reported by Esbenshade & Triantaphyllou (1990) show that the esterase from *M. naasi* is VF1, which is shared with that of *M. exigua*. However, the pattern for N1a malate dehydrogenase (Mdh) is unique in *M. naasi*. Thus two enzyme patterns are necessary to distinguish these two species. No electrophoretic gels are available for New Zealand isolates of *M. naasi*. Phylogenetic analyses of sequences obtained here (Figs 3–5) placed *M. naasi* in a clade with *M. trifoliophila*, similar to the results obtained by Alvarez-Ortega *et al.* (2019) in their large study.

***Meloidogyne trifoliophila* Bernard & Eisenback, 1997**

English common name: Clover root-knot nematode

EPPO Code: MELGTR

Figs 39–45.

Measurements. Table 9.

Morphology. Females: Body 425–607 µm long, 308–550 µm wide, pearly white, globular to pear shaped, with a slight posterior protuberance which carries the vulva, and a distinct neck region projecting from the body axis, usually at an angle of up to 90º to the ventral side. Head region barely off-set from body, marked with one or two annules. Lip region distinct but variable in shape; labial disc not elevated. Cephalic framework weakly sclerotized; vestibule extension distinct. Stylet 11–13 µm long, cone straight or dorsally curved and shaft cylindrical; knobs large, may be bifid, off-set, rounded to transversely ovoid. Excretory pore about two stylet lengths posterior to head end, slightly anterior to metacorpus. Pharyngeal glands variable in size and shape. Perineal pattern rounded to ovoid, dorsal arch rounded, striae weak, long, smooth (Fig. 41). Tail terminus indistinct without punctations. Phasmids small and difficult to observe; posterior to anus. Perivulval area devoid of striae. Vulval slit often arcuate. Lateral lines not present. Ventral pattern region rounded; striae smooth or wavy, short or long.

Males: Body vermiform, 840–1376 µm long, slightly tapering anteriorly, bluntly rounded posteriorly. Cuticle with distinct transverse striae. Lateral field prominent, with more than four incisures; most (7) at anterior end, decreasing to six in posterior region. Head slightly off-set, with a single post-labial annule usually partly subdivided by a transverse incisure. Labial disc rounded, barely elevated. Cephalic framework moderately sclerotized, vestibule extension distinct. Stylet sturdy, 16–19 µm long, cone straight; shaft cylindrical; knobs large and rounded, off-set from the shaft and slightly sloping backwards from it. Pharynx with slender procorpus, metacorpus oval shaped with pronounced valve. Ventrally overlapping pharyngeal gland lobe variable in length. Hemizonid 2–3 µm in length, at level of or one or two annules posterior to excretory pore, which opens about one bulb length posterior to the metacorpus. Testis usually long, monorchic, with reflexed or outstretched germinal zone. Tail short (7–12 µm long) and twisted. Spicules slender, 27–31 µm in length, slightly ventrally arcuate, barely cephalated; gubernaculum slender, weakly sclerotised, barely arcuate. Phasmids located level with or slightly anterior to cloaca.

Second-stage Juveniles: Body 378–461 µm long, vermiform, tapering at both ends but posteriorly more than anteriorly. Body annules small but distinct. Lateral field with four incisures, not areolated. Head region truncate, slightly off-set from body. Head cap low and narrower than head region. Cephalic framework weakly sclerotized, vestibule extension distinct. Stylet slender and moderately long (9–13 µm), cone straight; shaft cylindrical; knobs distinct, rounded and off-set from the shaft. Pharynx with faintly outlined procorpus and oval shaped metacorpus with distinct valve. Oesophageal gland lobe variable in length, overlapping intestine ventrally. Hemizonid distinct, at level of excretory pore, which opens through it. Inflated proctodeum. Moderate to long tail (51–79 µm long), gradually tapering to hyaline tail terminus (17–26 µm long) from which level it narrows rapidly on ventral side. Phasmids not observed. A rounded hypodermis marks the anterior position of the hyaline tail terminus; tail terminus digitate, ending in a narrowly rounded tip.

Eggs: n=5; Length 73–100 µm (89.6 ± 11.0); width 36–44 µm (40.3 ± 2.0).

Differential diagnosis. The New Zealand isolate of *Meloidogyne trifoliophila* is characterised by the form of the perineal pattern in mature females, being rounded with weak smooth striae, and by having males with more than four lateral lines. It is morphologically closest to the original description of *M. trifoliophila* (Bernard and Eisenback 1997). However, it varies from the original description in having mature females with a slight posterior protuberance which carries the vulva, and which tend to have a smaller stylet (11–13 µm long; females of other RKN species from New Zealand have stylets longer than 13 µm). Galls are large and elongate (Fig. 45).

Table 9. Morphometrics of adult and second stage juveniles (J2) of *Meloidogyne trifoliophila* isolated from New Zealand. Measurements are in µm and in the form: mean ± SD (range).

Character	Female	Male	J2
n	14	12	24
L	488±49 (425–607)	1116±157 (840–1376)	412±19.3 (378–461)
a	1.3±0.2 (1.0–1.7)	36.1±9.9 (18.2–46.9)	28.0±3.2 (23.2–33.6)
b		14.9±3.1 (12.8–22.7)	7.1±0.5 (6.1–8.2)
c	-	125.8±25.6 (96.3–172.2)	6.8±0.6 (6.2–8.5)
c’	-	-	6.1±0.1 (4.0–8.5)
T	-	58.9±9.4 (51.3–73.3)	-
Greatest body diam.	374±62 (308–550)	32.9±9.2 (21.8–46.1)	14.8±1.4 (12.6–16.5)
Body diam. at stylet knobs	-	16.1±2.7 (13.7–21.8)	9.4±0.6 (8.6–10.7)
Body diam. at excretory pore	-	20.5±1.0 (19.1–22.3)	12.9±1.3 (11.9–13.0)
Body diam. at anus	-	17.6±2.4 (12.6–19.6)	10.1±1.7 (8.0–12.6)
Head region height	2.3±0.6 (1.7–3.0)	3.2±0.4 (2.7–3.8)	1.7±0.3 (1.2–2.0)
Head region diam.	6.4±0.5 (5.7–7.2)	9.0±0.7 (8.4–10.2)	5.1±0.4 (4.4–5.6)
Neck length	105.4±43.5 (32.7–215.4)	-	-
Neck diam.	55.1±19.9 (30.8–100.3)	-	-
Stylet	12.1±0.7 (11.2–12.7)	17.3±0.9 (15.7–18.8)	11.1±0.8 (9.1–12.7)
Stylet cone	5.8±0.9 (4.6–6.7)	8.5±0.5 (7.7–9.2)	-
Stylet knob height	1.7±0.2 (1.3–1.9)	2.1±0.3 (1.7–2.7)	1.2±0.1 (1–1.4)
Stylet knob width	3.5±0.3 (3.2–3.9)	3.6±0.2 (3.4–3.9)	1.8±0.2 (1.5–2.0)
DGO	4.3±0.6 (3.4–5.0)	4.8±0.7 (3.6–5.8)	4.3±0.5 (3.8–4.9)
Ant. end to metacorpus	73.8±7.7 (65.0–87.0)	77.6±7.1 (60.1–84.7)	58.4±5.6 (50.1–67.1)
Metacorpus length	30.7±6.0 (23.9–43.2)	17.9±2.7 (14.9–22.6)	11.6±1.1 (10.2–13.3)
Metacorpus diam.	27.5±2.7 (23.9–32.1)	11.7±2.3 (9.3–15.9)	7.7±0.7 (6.7–8.7)
Metacorpus valve length	10.8±1.7 (8.9–13.4)	5.9±0.6 (4.8–6.5)	4.3±0.2 (3.9–4.5)
Metacorpus valve width	8.2±1.3 (5.6–9.5)	4.5±0.5 (3.7–5.3)	3.4±0.2 (3.2–3.7)
Ant. end to end of gland lobe	-	192.3±21.9 (174.0–222.3)	-
Excretory pore-ant. end	26.7±5.2 (20.4–32.9)	110.0±7.0 (97.6–117.0)	71.1±4.8 (61.9–77.5)
Tail length	-	9.1±1.7 (7.1–11.7)	60.9±5.5 (50.9–78.6)
Hyaline tail terminus	-	-	20.1±1.9 (16.8–26.2)
Phasmids from anus	-	11.8±3.9 (8.4–16.0)	-
Spicule	-	29.6±1.5 (27.4–30.7)	-
Gubernaculum	-	7.6±1.2 (5.9–8.8)	-
Testis	-	687.1±194.8 (490.2–1008.3)	-
Vulva slit length	13.4±0.9 (11.5–14.3)	-	-
Vulva-anus	11.0±1.0 (9.9–12.9)	-	-
Body length/neck length	5.5±2.9 (2.6–14.3)	-	-
Stylet knob width/height	2.1±0.3 (1.9–2.6)	1.8±0.3 (1.6–2.4)	1.5±0.2 (1.1–1.9)
Metacorpus length/width	1.1±0.2 (0.9–1.3)	-	-
(Excretory pore/L) x 100	-	10.3±1.6 (8.5–13.9)	17.5±0.6 (16.4–18.3)

The New Zealand isolate of *M. trifoliophila* is morphologically separated from the other known New Zealand isolates of RKN by having a perineal pattern that is rounded or oval, with long, weak smooth striae. The pattern lacks the 'wings' and punctations of *M. hapla* and the distinct lateral fields present in *M. javanica*. The small phasmids are posterior to the anus, separating *M. trifoliophila* from *M. naasi,* in which they are anterior. It is further separated from other species of RKN from New Zealand by the position of the excretory pore in mature females (opening close to the stylet knobs), separating it from *M. fallax* (opening at approximately half the distance between the anterior end and the metacorpus), from *M. javanica* (opening at the level of the anterior metacorpus), and from *M. hapla* and *M. trifoliophila* (opening at about 75% of the distance from anterior end to the metacorpus). Males of the New Zealand isolate of *M. trifoliophila* have a twisted rather than the curved tail seen in the *M. minor* isolated in New Zealand. They also have an arcuate spicule and gubernaculum unlike those of *M. javanica,* which are more curved, and have a shorter tail (7–12 *vs* 14–17 µm long). The distance to the anus of the phasmids on the tail of male *M. trifoliophila* is variable (8.5–16 µm distant), overlapping that of other species of New Zealand RKN. There are more than six lateral lines, compared to four in other species of RKN from New Zealand. Body length of the second stage juveniles separates the New Zealand isolate of *M. trifoliophila* from those of *M. fallax* (respectively, 378–461 *vs* 328–352 µm long). Their tail is longer than that of *M. fallax, M. incognita* and *M. javanica* (62–77.5 *vs* 38–46 45–56 and 46–61 µm long), and the length of the hyaline section of the tail is longer than in *M. fallax, M. incognita* and *M. minor* (17–26 *vs* 11–16.5, 11–15 and 14–18 µm long). The digitate tail tip is not present in any of the other New Zealand species of RKN. With the exception of this last character, it is not possible to clearly separate second stage juveniles of *M. trifoliophila* from those of *M. hapla*. They tend to be longer (body length mean 412 µm, range 378–461 µm *vs* mean 357 µm, range 310–386 µm), and to have tails with a longer hyaline section (mean length 20.1 µm, range 17–26 µm *vs* mean 13.8 µm, range 41–59 µm).

Material examined. Non-type specimens. Fourteen females (slide nos NNCNZ 4077–4089), 12 males (slide nos NNCNZ 4090, 4091) and 24 juveniles (slide nos NNCNZ 4092–4097) deposited at the National Nematode Collection, New Zealand.

Distribution (Map 7). Based on material examined: New Zealand: North Island: AgResearch Campus, Hamilton, WO.

Based on collections: Widespread through the North Island but has a limited distribution in the South Island.

North Island: ND, AK, WO, BP, GB, HB, TK, WI, WA, WN. **South Island:** WD.

For world distributions see Table 3.

Habitat and host. Based on material examined: New Zealand: white clover (*Trifolium repens*).

Based on literature: New Zealand: *Trifolium ambiguum*, *T. argutum*, *T. arvense*, *T. dubium*, *T. glomeratum*, T. *hybridum*, *T. medium*, *T. micranthum*, *T. nigrescens*, *T. occidentale*, *T. pratense*, *T. repens*, *T. semipilosum*, *T. subterraneum*. For international hosts see Table 3.

Remarks. The New Zealand isolate of *Meloidogyne trifoliophila* is characterised by a combination of characters: having females with a round perineal pattern with long, smooth striae, no distinct lateral field, and a slightly protuberant vulva; males with up to 8 lateral lines which may be forked or broken; and second stage juveniles with a short slender stylet and tail with a digitate tip.

Meloidogyne trifoliophila is known to significantly impact the productivity of white clover (Ferguson *et al.* 2018; Zahid *et al*. 2001). It is mostly recorded from the North Island and is more widespread and abundant than *M. hapla* (Mercer *et al*. 1997). It has been found only on the northern and western parts of the South Island (Mercer *et al.* 1997; Ferguson *et al.* 2018). This suggests that it is a temperate climate RKN. Galls induced by this RKN on white clover are large, elongate and smooth in form, and lack lateral roots. Egg masses are retained within the gall.

Grasses are rarely hosts of *M. trifoliophila* (Bernard & Eisenback 1997; Mercer *et al*. 1997). In New Zealand, this RKN has been isolated from cultivated white clover. Mercer (1990) found that, in sterilised soil in a glasshouse, 460 *M. trifoliophila* eggs per 100g of soil (incorrectly identified as *M. hapla*, Mercer *et al.* 1997) reduced white clover growth by 20%. An initial population of 50 juveniles per 100 g of soil caused severe damage to potato tubers in a pot test (Wesemael *et al.* 2014). Given that *M. trifoliophila* does not develop on grasses, it may be possible in some areas to rotate white clover/rye grass swards with grasses alone. However, control of broad-leaved weeds in such pastures would be critical. It should be noted that white clover partially resistant to *M. trifoliophila* was susceptible to *M. hapla* (Mercer *et al*. 1997), complicating attempts to control RKN in mixed pastures. In addition, success of such a rotation assumes that egg hatch is induced by moisture alone, *i.e*., that there

are no hatching factors associated with host roots, and that there is no carry-over of viable eggs from season to season as with potato and cereal cyst nematodes.

Meloidogyne trifoliophila has been recorded from Australia (Zahid *et al*. 2000).

Mercer *et al*. (1997) compared isozyme phenotypes of various isolates of *M. trifoliophila* with those of other RKN species. For *M. trifoliophila*, they observed a single esterase isozyme with an electrophoretic mobility of 0.32, which differentiated the species from *M. hapla, M. javanica, M. arenaria* and *M. incognita*. They found two bands of malate dehydrogenase activity in extracts of *M. trifoliophila*, with respective activities of 0.45 and 0.53. No consistent variation with malate dehydrogenase was seen among the isolates of *M. trifoliophila* and *M. hapla*. In test gels for *M. trifoliophila*, one band was observed for malate dehydrogenase, and two bands were observed for esterase isozyme, respectively. These distinct patterns effectively differentiate *M. trifoliophila* from all the other New Zealand RKN species tested. Phylogenetic analyses (Figs 3–5) of sequences obtained here placed *M. trifoliophila* in a clade with *M. naasi*, similar to the results inferred by Alvarez-Ortega *et al.* (2019) in their study of 56 species of RKN.

DISCUSSION

Most of the *Meloidogyne* species collected and identified from New Zealand are representatives of species with world-wide distributions on cultivated plants. A comprehensive survey of New Zealand RKNs is needed, with examination of their molecular biology and information on their morphology, morphometrics, host range, and distribution, because: a) eight of the proposed eleven clades (Alvarez-Ortega *et al*. 2019) of the genus have not been recognised in New Zealand, b) it is a relatively isolated area of the world with many unique plant species on which species of RKN may have evolved, and c) considerable variation has been observed in sequences of several RKNs from New Zealand. It should be noted, however, that most of the pest species discussed here are known to have world-wide distributions, *i.e*., are unlikely to have originated in indigenous New Zealand vegetation. Only *M. fallax* is thought to have possibly originated in New Zealand (Rohan *et al*. 2016). While land was cleared for most New Zealand pastures about a century ago, other local pest species of RKN have not emerged on pastures, suggesting that any indigenous forms found will not have a broad host range.

In 1965, Harry Wallace published a blue-print for research on the cereal cyst nematode *Heterodera avenae,* then a serious problem on cereal crops in southern Australia. He outlined ten key research areas, as applicable to RKN now as to cereal cyst nematode then. These were: (i) the distribution of the nematode, especially in areas outside regions where it was recognised as a pest; (ii) estimation of yield losses; (iii) interactions between the nematode's physiology and the environment; (iv) understanding how different soil types affected distribution and abundance; (v) the taxonomic status of local populations and possible existence of different races; (vi) host preferences of different populations and races; (vii) changes in population density with season, soil type and crop locality; (viii) the relationship between crop damage and nematode population density under different environmental conditions; (ix) the testing of host plant varieties for resistance to the nematode; and (x) the use of nematicides in badly-infested areas. The one management research area not listed by Wallace was that of biocontrol. These recommendations are still generally accepted (Starr *et al.* 2002; Hunt & Handoo 2009). In the 1970s, 80s and 90s, these recommendations were acted upon in Australia, and cereal cyst nematode is now managed world-wide through a combination of resistant and tolerant varieties and crop rotation. However, where *Heterodera* was the only cyst-forming species in high densities on lighter soils in cereal-growing areas of Australia, and developed only on grasses, in New Zealand several species of RKN and other plant-parasitic nematodes may co-exist in any one situation and most have very wide host-ranges. This means that, while rotations have been used world-wide, for many years (e.g., Allen *et al.* 1988; Zahid *et al.* 2002), designing effective rotations for RKN is difficult. Management for broad-acre cropping currently relies on the use of both host plant rotations and growing resistant and tolerant cultivars. Use of nematicides is too costly for broad-acre use, and too dangerous both for user and the environment (Zahid *et al.* 2002). In New Zealand, intensive horticultural industries do use fumigation methods for controlling disease in their soils but rotations and soil amendments remain the major practice (Nigel Bell, personal communication, September 2022). For example, carrot seedlings may be treated prophylactically with pesticides at the time of planting (Nigel Bell, personal communication, September 2022).

A brief discussion of the methods for and possible future of control of RKN in New Zealand's most economically important agricultural exports follows. Breeding programmes for improvement of white clover in New Zealand began in about 1930, when clovers were selected for improved productivity and persistence under grazing (Brock *et al*. 1989). In the 1980's–1990's, there were active research programmes seeking resistance and tolerance of root-knot and cyst nematodes. Mercer (1994) stated that to increase white clover productivity there should be i) breeding programmes to improve resistance and tolerance of white clover to nematodes, ii) introduction of pasture management systems to reduce the damage done by nematodes, and iii) improving the biological control of the nematodes. Early results seeking resistance to RKN in *T. repens* were not encouraging (Kouame *et al.* 1998; van den Bosch & Mercer 1996). Quesenberry *et al*. (1986) suggested that resistance to RKN in clovers was quantitative, *i.e*., that recurrent selection using large populations would be needed to develop resistance. No resistance was found in a screening of 134 lines of subterranean clover (Kouame *et al.* 1989). Caradus *et al.* (1996a) wrote that, along with various agronomic characters, breeding should include incorporation of resistance to nematodes attacking roots (and other invertebrate pests).

In New Zealand, two long-term concurrent breeding programmes were established, involving recurrent crossing and selection; one for resistance under known nematode pressure (at Grasslands Research Centre, Palmerston North) and the other for tolerance to high nematode loadings in the field (Ruakura Research Centre, Hamilton) (Watson & Mercer 2000). Screening for resistance was carried out in pots in a glasshouse (Mercer 1994). Individual plants on which fewest nematodes reproduced were selected, and crossed, over generations. No immunity to *M. trifoliophila* was found in white clover, but there was evidence of partial resistance, and wide differences in susceptibility (van den Bosch & Mercer 1996b). By the third generation of crosses, there were significant differences in the numbers of *M. trifoliophila* on susceptible and resistant plants, with resistant selections having only 43% of the number of galls per gram of root of the susceptible plants (van den Bosch & Mercer 1996a). By the sixth generation, this resistance had not significantly increased (45%) (Mercer *et al.* 2000). The resistance reaction was recognised as a form of hypersensitivity (Mercer *et al*. 2004), involving several genes. There was a tendency for cultivars of *T. repens* to be resistant to clover cyst nematode but susceptible to *M. trifoliophila* (Mercer 1994), which made breeding for resistance to both clover cyst nematode and RKN more difficult. The most resistant plants came from lines with larger leaves, and the most susceptible were from smaller leaved lines (van den Bosch & Mercer 1996b). For research purposes, the most resistant lines were crossed with commercial seed lines (Mercer *et al.* 1999; Mercer *et al.* 2008).

When these white clovers were tested in grazed field trails, alongside lines selected for tolerance, lines selected for resistance were more productive than those selected for susceptibility. However, cross-resistance to clover cyst nematode and *M. trifoliophila* was not expressed. Tolerant lines did not carry fewer nematodes, and it was concluded that their tolerance was related to other factors, e.g., an ability to cope better with nematode-induced stress (Watson & Mercer 2000). Complete resistance to RKN was found in 10–20% of seedlings of *Trifolium semipilosum* cv. Safari (native to northern Africa and the Arabian Peninsula) (Barrett *et al*., 2005; Mercer & Barrett 2006), and the locus conferring this was identified and markers for it were developed. Unfortunately, the resistance to *M. trifoliophila* in *T. repens* and *T. semipilosum* was temperature sensitive (Mercer 2005), *i.e*., it broke down in hot dry summers. While clover cyst nematode populations were suppressed by the perennial Caucasian clover (*T. ambiguum)* over a period of 6 years, RKN populations increased more in such soils than in those with white clover (Watson *et al*. 2000) *i.e*., the long-term usefulness of Caucasian clover is doubtful.

The incursion of the destructive clover root weevil *Sitona lepidus* in 1996 (Gerard *et al.* 2013) changed management priorities. However, when the weevil was present, a nematode-tolerant line was the only white clover in the top ten of 62 white and red clover lines or cultivars evaluated (2002–2005) under both dairy and sheep/beef grazing in the North Island (Crush *et al.* 2005).

In the last 25 years, breeding programmes in New Zealand have concentrated on selecting white clover cultivars with adaptations for wet hill country or for dairy farming (Widdup *et al.* 2015). Farmers still have no white clover cultivar with resistance to both cyst and root-knot nematodes that could be used in managing the pests, *i.e*., white clover yields remain well below their potential. Over time, distribution and numbers of *M. hapla* in pastures have increased significantly (Farhat Shah, personal communication, September 2022), which will make future breeding programmes more difficult.

In New Zealand, *Globodera* nematodes are more important for potato production than RKN, given their significance for export of rural products (https://www.mpi.govt.nz/export/food/fruit-and-vegetables/steps-to-exporting-fresh-vegetables/potatoes-extra-requirements). Of the species of *Meloidogyne* that attack potatoes in New Zealand, *M. fallax* is the most damaging. There is no commercial potato cultivar available with resistance to *Meloidogyne* spp. Resistance to *M. fallax, M. incognita*, *M. javanica* and *M. hapla* has been reported in wild potato species (Brown *et al*. 1991, 1995; Janssen *et al.* 1996) and attempts have been made to introgress these into breeding lines to develop resistant potato cultivars. There have also been efforts to produce transgenic cultivars with resistance. For example, Dinh *et al*. (2015) generated transgenic potato lines with an RNA interference transgene that silenced a *Meloidogyne* effector gene. These lines had significant resistance to all the *Meloidogyne* species tested. More recently, the bacterium *Bacillus subtilis* was engineered to secrete a plant-defence elicitor peptide, and potato roots were pre-treated with suspensions of it (Zhang & Gleason 2020). Such roots were significantly protected against galling. Thus, genetic engineering may lead to cultivars resistant to RKN, but the public would then have to be convinced that it was safe to consume such potatoes. For now, the only management tool available to farmers is the use of rotations, with solanaceous crops grown one year in four. Unfortunately, given the very wide host range of *M. fallax* and recent reports of its ability to infect fodder beet and white clover (Rohan *et al.* 2016), such rotations will not be suitable for control of this species of RKN.

Knight *et al*. (1997) listed tomatoes as a host plant for *M. arenaria, M. hapla, M. incognita,* and *M. javanica* in New Zealand, but because most are grown hydroponically in glasshouses there has been no attempt to assess losses caused by these nematodes in the field. Tomatoes can be protected against RKN attack by growth of cultivars incorporating the Mi gene for resistance (Roberts & Thomason, 1996; Kaloshian *et al.* 1998). However, this resistance can be broken by high temperatures (e.g., Dropkin 1969; Veremis & Roberts 1996) and in Europe continuous cultivation of tomatoes led to the breaking of resistance within a few generations (Gowen & Tzortzakakis 1996). Screening of five common tomato cultivars at Lincoln University has identified one with complete resistance to RKN (Tran 2020). This may be a new source of resistance and should be further investigated. New Zealand farmers growing tomatoes in the field use fumigation and rotations with, e.g., brassicas, to control populations of RKN.

On the basis of morphological studies, *M. hapla* was reported from kiwifruit by various researchers (Dale 1971a; Knight *et al*. 1997). This identification was confirmed by Mercer, Shah and Bulman (Farhat Shah, pers. com., December 2020) using molecular sequencing, and again here. However, the pathogenicity of this nematode to the vine is unknown, and there is no known source of resistance or tolerance. Recently, *M. fallax* has been recorded as developing on kiwifruit. Since the incursion of kiwifruit vine canker (*Pseudomonas syringae actinidiae*; also known as Psa) in 2010 (Vanneste *et al*. 2014), which has a high impact on vine productivity, it may be that problems with RKN have become insignificant for this industry. However, Shah (personal communication, September 2022) pointed out that not only does root damage caused by the nematodes allow entry to the vines by soil born fungal pathogens such as *Fusarium*, it may also promote invasion by Psa. In March 2021, various organisms were listed for risk to kiwifruit, and RKN was not included (https://kvh.org.nz/biosecurity/kiwifruits-most-unwanted). *Meloidogyne arenaria* has been recorded from kiwifruit in Turkey (Akyazi *et al.* 2012), so could possibly attack the vine in New Zealand. While border controls appear to have prevented incursion of *M. arenaria* into New Zealand for now, vigilance must be maintained.

Biological control of plant-parasitic nematodes via antagonistic micro-organisms has been investigated now for decades but remains a largely elusive goal in practice (Stirling 2019; Hallman *et al*. 2009; Benedetti *et al*. 2021). However, it is known that increasing the organic content of soils improves its biodiversity and promotes biocontrol. Organisms which have been investigated as biocontrol agents of RKN species include the bacterium *Pasteuria* (with host specificity making it potentially very attractive as a biocontrol agent) (Bishop *et al.* 2007), but it is difficult to mass produce, e.g., Hallmann *et al.* (2009). *Trichoderma*, mycorrhizal and endophytic fungi are used against nematodes as resistance inducers. They reduce the damage caused by plant-parasitic nematodes directly by parasitism, antibiosis, paralysis and by the production of lytic enzymes. They also minimize harm by competing with nematodes for space and resources and provide higher nutrient and water uptake to the plant. They may modify root morphology and/or rhizosphere interactions in ways promoting plant-growth. In addition, filamentous fungi can induce plant resistance against nematodes by activating hormone-mediated (salicylic and jasmonic acid, strigolactones among others) plant-defence mechanisms (Hallmann *et al*. 2009).

There is increasing awareness that soil ecosystems have been disrupted and modified by agricultural practices (Stirling 2019), and recognition that some soils can act as suppressors of cyst and root-knot nematodes (Kerry & Crump 1980; Adam *et al.* 2014). Recent molecular techniques allow study of such soils. For example, tomatoes grown in three unpasteurised arable soils were infested by lower populations of *M. hapla* than those grown in pasteurised soils (Adam *et al*. 2014), and a diverse microflora was found to specifically adhere to J2s in the former soil. Presumably, this microflora affected female fecundity, reducing numbers of eggs by up to 93% in the unpasteurised soil. In New Zealand, Bell *et al*. (2016) examined ten local soils and found two with suppressive activity against *M. hapla*. Use of next generation sequencing identified the presence of nematode-trapping fungi (Orbiliomycetes) in these soils. These fungi include the genera *Arthrobotrys, Drechslerella* and *Dactylellina,* all recognised nematode trapping fungi. It may be possible to use Orbiliomycetes as bioindicators of suppressive soils (Bell *et al*. 2016), and such knowledge could then be used to inform farmers making decisions on, e.g., soil cultivation which is known to disrupt biocontrol mechanisms. Future work could look at ways to promote soil biodiversity and suppressiveness, e.g., by incorporation of organic material into soils.

Extensive work is now going into the diversity and functional analysis of effector proteins secreted by plant-parasitic nematodes, including RKNs (Rehman *et al.* 2016; Vieira & Gleason 2019). Most of those identified in RKNs since 2016 (summarized in Vieira & Gleason 2016) have been effectors suppressing the host immune response, but one interferes with metabolic and signalling pathways. These new methodologies also allow examination of plant responses to nematode attack, e.g., the work of Islam *et al.* (2015) on white clover in New Zealand. These workers compared the expression of various genes in white clover following infection with *H. trifolii* and *M. trifoliophila* and found large differences with time from infection and between the two nematode species. Second stage juveniles of plant-parasitic nematodes can be treated with double stranded (ds) RNA to temporarily silence endogenous target genes coding for effectors (RNAi), preventing subsequent parasitism (Rehman *et al.* 2016). However, as Vieira & Gleason (2019) point out, at present genetic transformation is not practical for plant-parasitic nematodes, and until such technologies become available it will not be possible to use RNAi for control of nematodes in the field.

Finally, a phylogenetic analysis of 87 sequences of 18S rRNA from various *Meloidogyne* species having sequences in common with *M. javanica*, *M. incognita* and *M. arenaria* revealed greatest similarity with *M. enterolobii* and five strains *of M. incognita* and *M. javanica* (Islam *et al*. 2020). It is likely that, as a part of the evolutionary process, some of these strains will adapt (possibly hybridize) to produce new, more virulent forms (Islam *et al*. 2020). In their unpublished analyses of the sequences of various isolates of *M. hapla*, *M. javanica* and *M. incognita* from New Zealand, Mercer, Shah and Bulman (Farhat Shah, personal communication, 2020) found considerable variability within these pest species. While host test ranges have not been carried out, this variability increases the chances of the emergence of new strains. Thus, ongoing vigilance will be necessary to protect New Zealand agriculture from emerging virulent strains of RKNs, both from within the country and as incursions. In addition, there is a continuing risk of incursions of existing pest species, e.g., *M. enterolobii*, recently recorded from Australia (https://www.appsnetorg/nematodes/pdf/PSN 040 Meloidogyne enterolobii.pdf) (accessed November 2023).

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Addendum. Since this manuscript was originally drafted, *M. hispanica* Hirschman 1986 has been identified in New Zealand (Zhao, personal communication, December 2023). This new record further stresses the importance of vigilance against possible incursions, and the need for a comprehensive, co-ordinated survey and identification of *Meloidogyne* in New Zealand.

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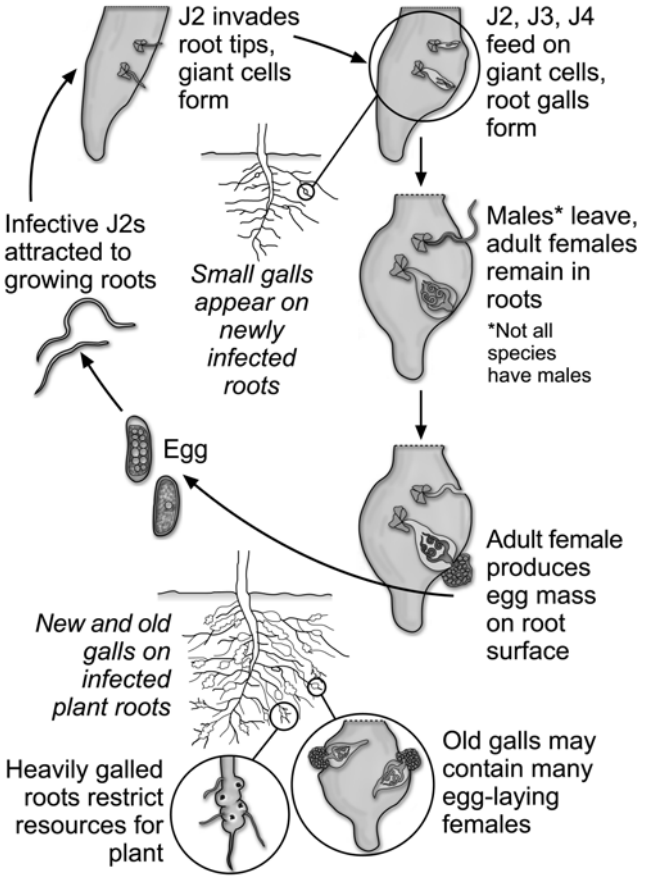


Fig. 1. Schematic life cycle of *Meloidogyne* nematodes. Drawn by Pauline Hunt, AgResearch; reproduced with permission from New Zealand Journal of Agricultural Research.

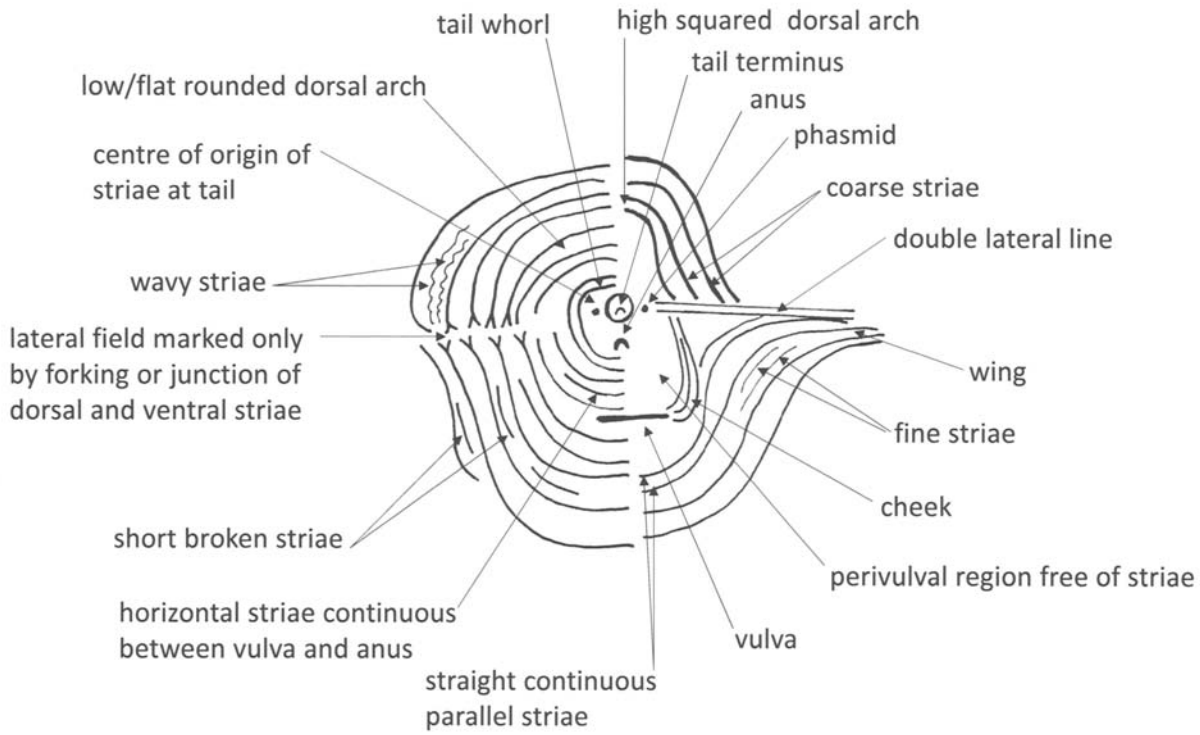


Fig. 2. General morphology of perineal patterns of *Meloidogyne* females. Re-drawn from Jepson (1987).

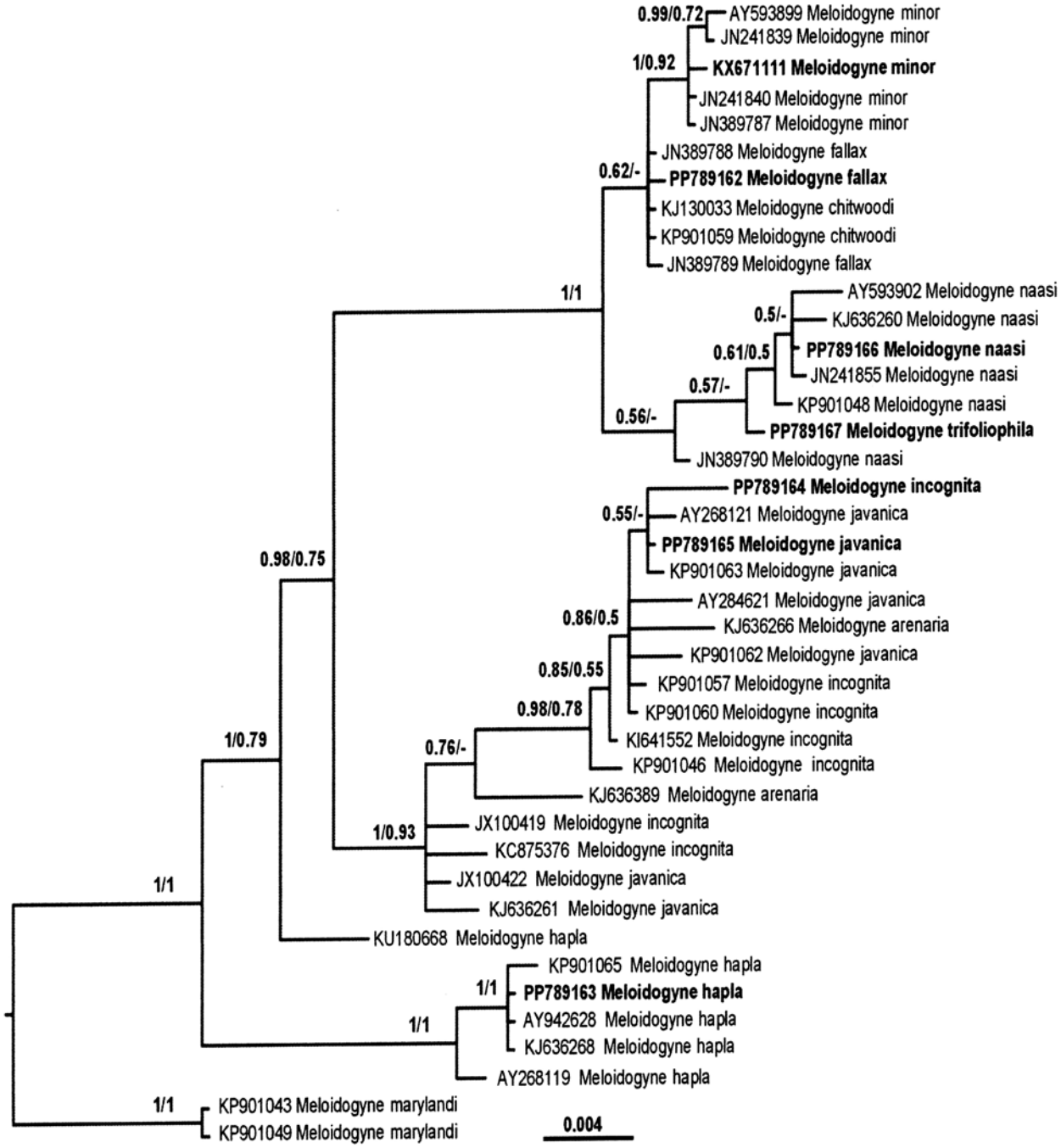


Fig. 3. Bayesian consensus tree of species of *Meloidogyne* isolated from New Zealand; inferred from SSU sequences under GTR+I+G model. Posterior probability values exceeding 50% are given on appropriate clades. Newly obtained sequences in this study are in bold. The scale stands for substitutions per site. - : less than 50% bootstrap support.

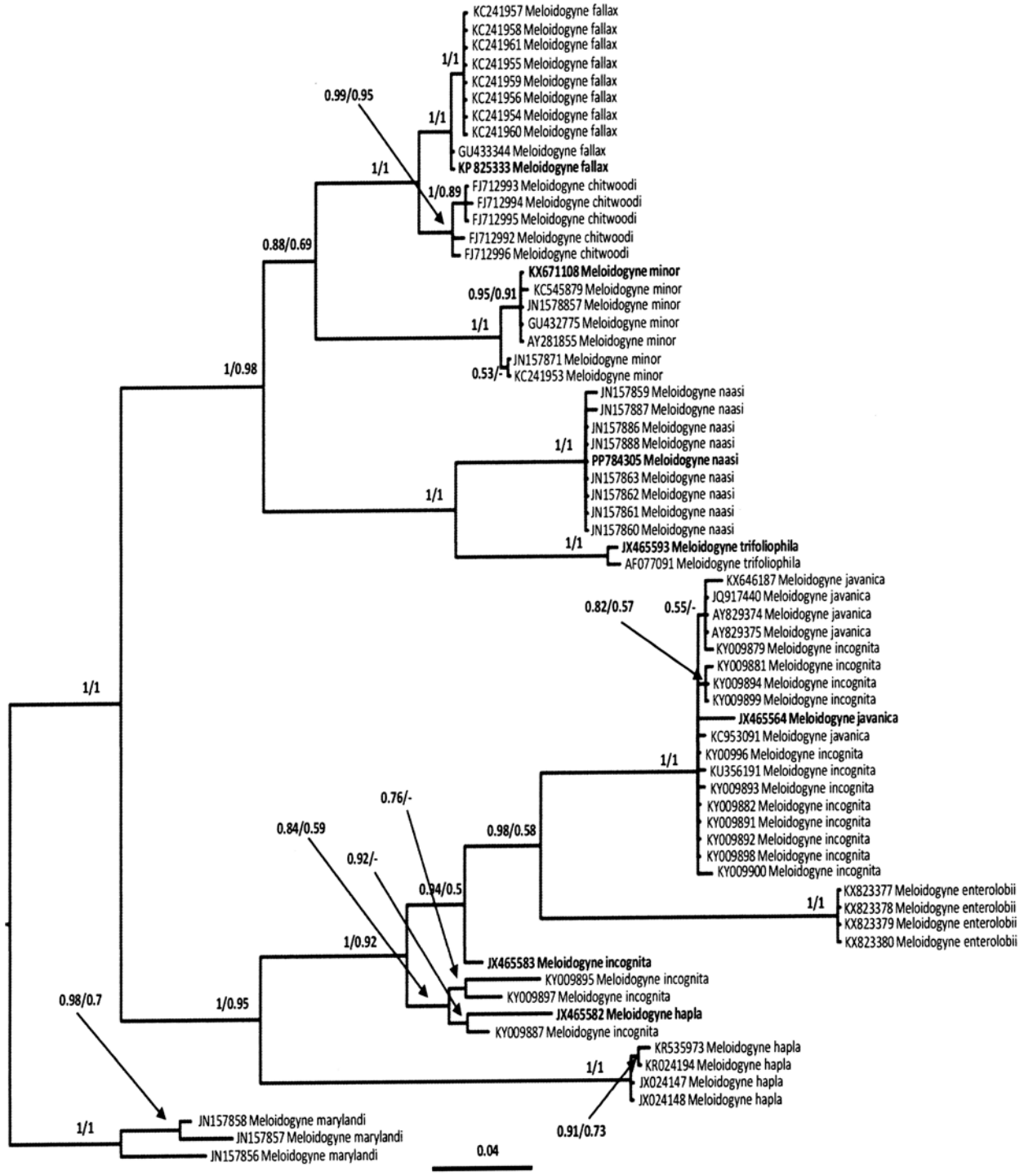


Fig. 4. Bayesian consensus tree of species of *Meloidogyne* isolated from New Zealand; inferred from ITS sequences under GTR+G model. Posterior probability values exceeding 50% are given on appropriate clades. Newly obtained sequences in this study are in bold. The scale stands for substitutions per site. * : no bootstrap support; - : less than 50% bootstrap support.

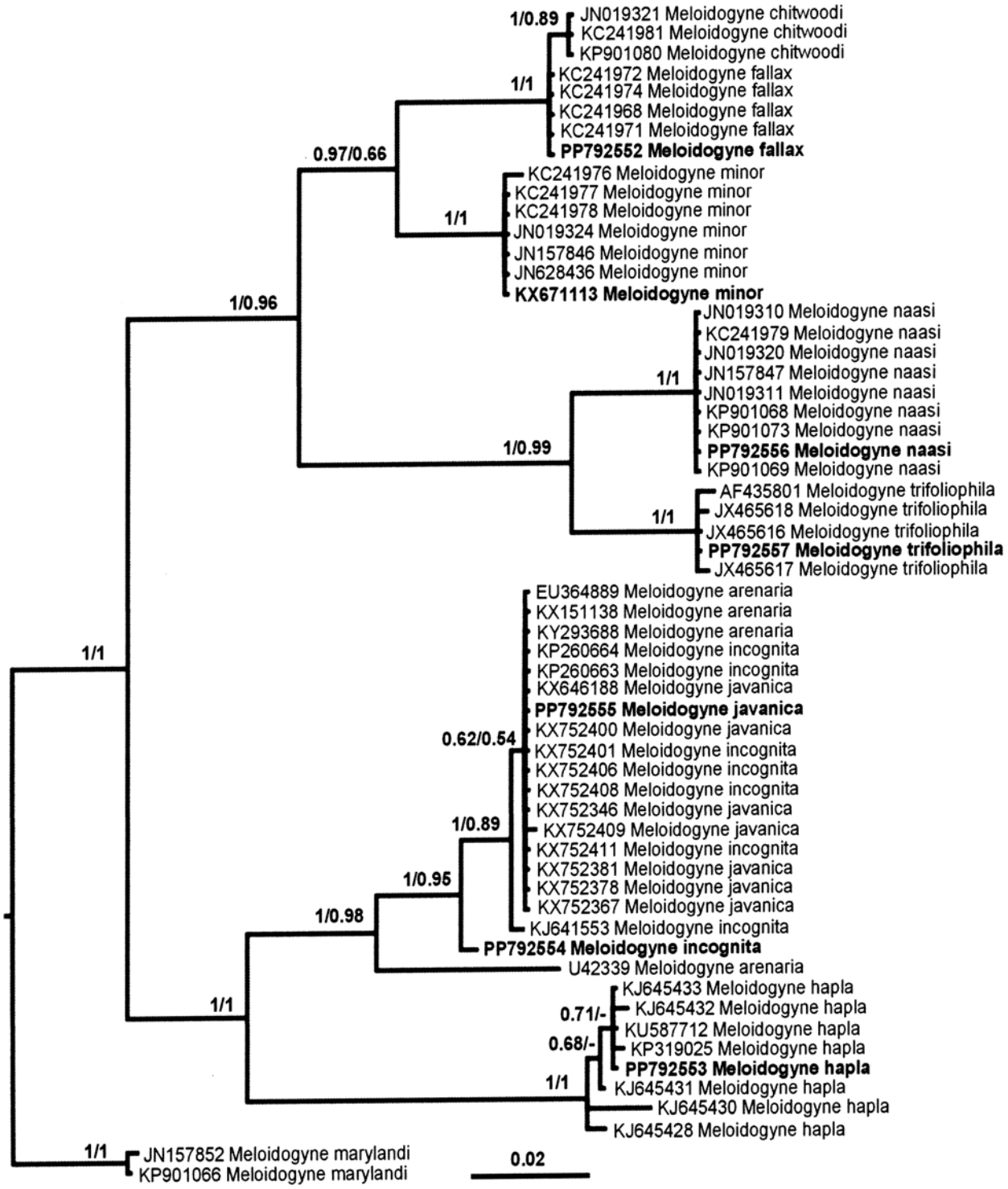


Fig. 5. Bayesian consensus tree of species of *Meloidogyne* isolated from New Zealand; inferred from LSU D2/D3 sequences under GTR+G model. Posterior probability values exceeding 50% are given on appropriate clades. Newly obtained sequences in this study are in bold. The scale stands for substitutions per site. - : less than 50% bootstrap support.

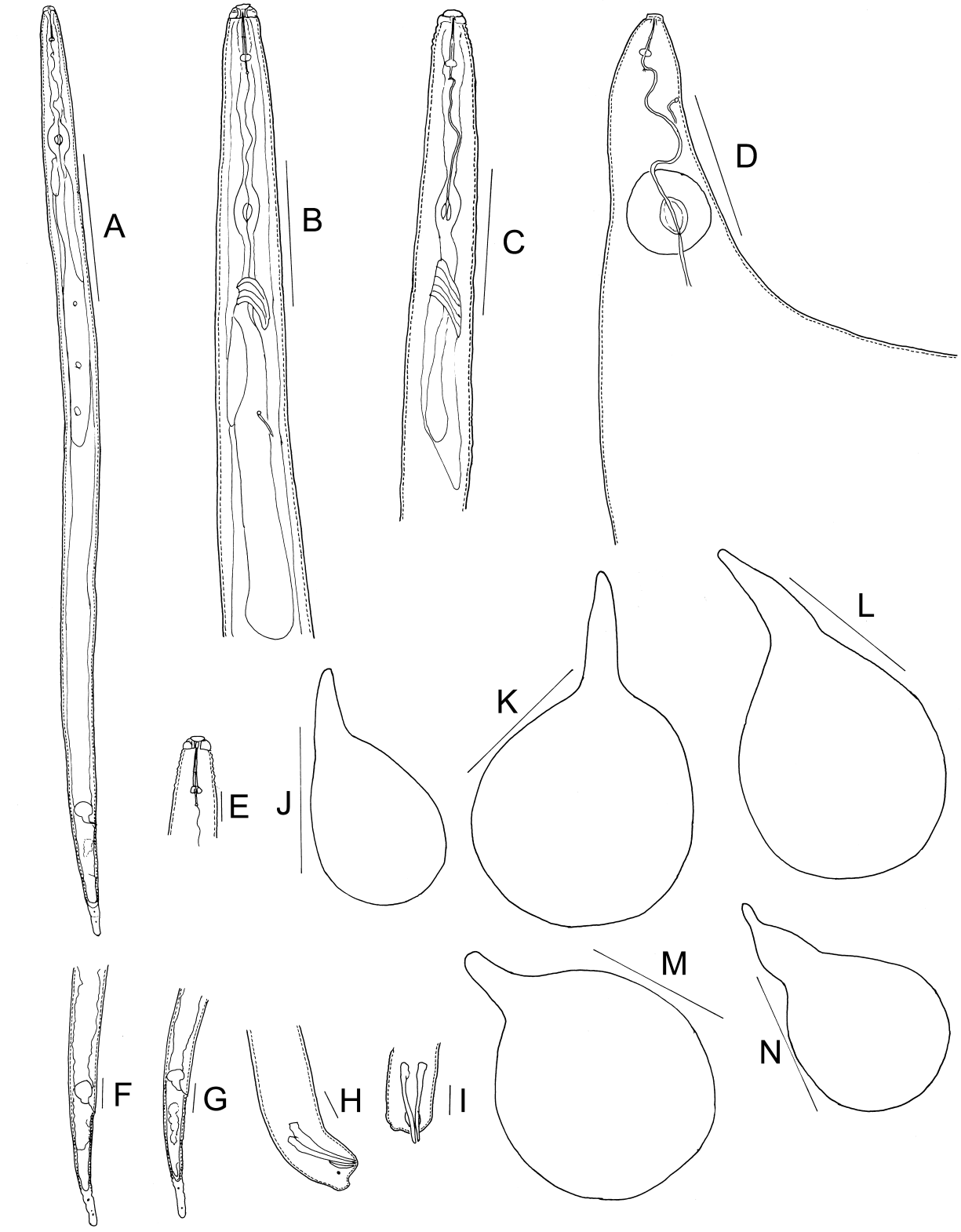


Fig. 6. Line drawings of *Meloidogyne fallax* mature females, males and second stage juveniles isolated from New Zealand. A: Second stage juvenile; B, C: Anterior ends of males; D: Anterior end of mature female; E: Stylet and lip region of second stage juvenile; F, G: Tails of second stage juvenile; H: Lateral view of male tail; I: Ventral view of male tail; J, K, L, M, N: Outlines of body shapes of mature females. Scale bars: A, B, C 50 µm; D 100 µm; E, F, G, H, I 10 µm; J, K, L, M, N: 250 µm.

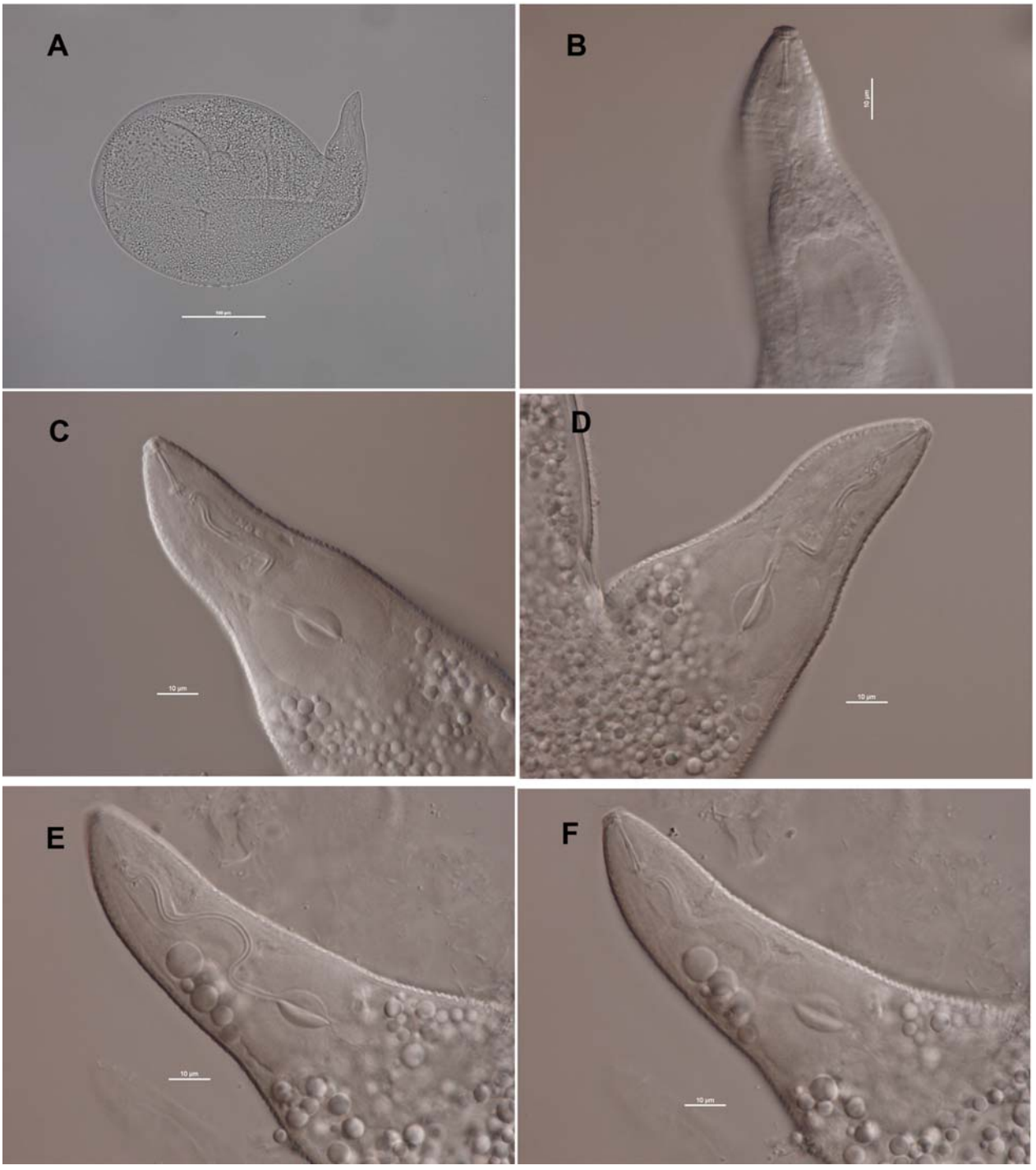


Fig. 7. Micrographs of mature female of *Meloidogyne fallax* isolated from New Zealand. A: Whole body; B: Anterior end; C: Showing lip region and stylet; D: Anterior end showing metacorpus; E: Anterior end; F: Anterior end showing stylet and excretory tract.

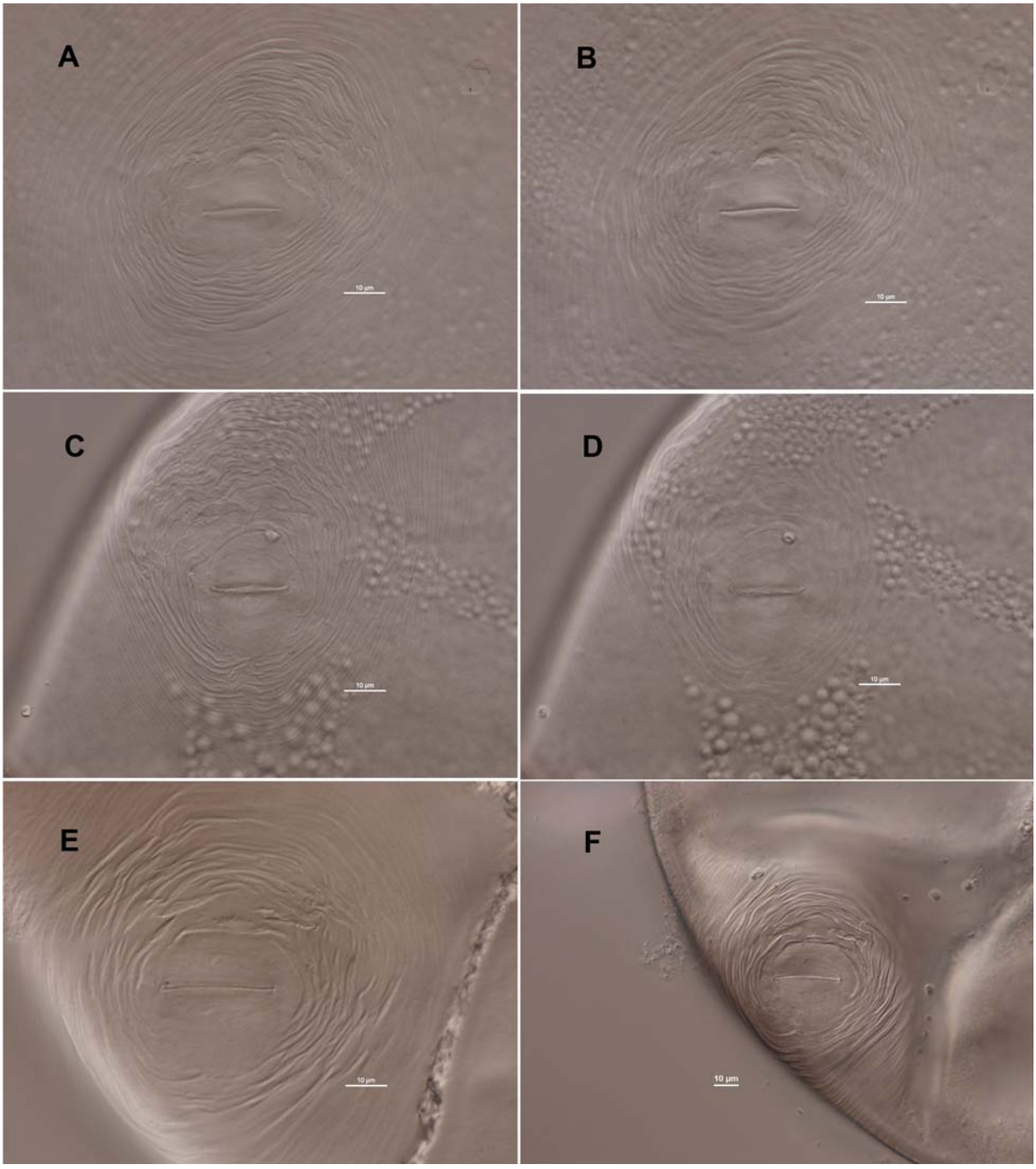


Fig. 8. Micrographs of perineal patterns from mature females of *Meloidogyne fallax*.

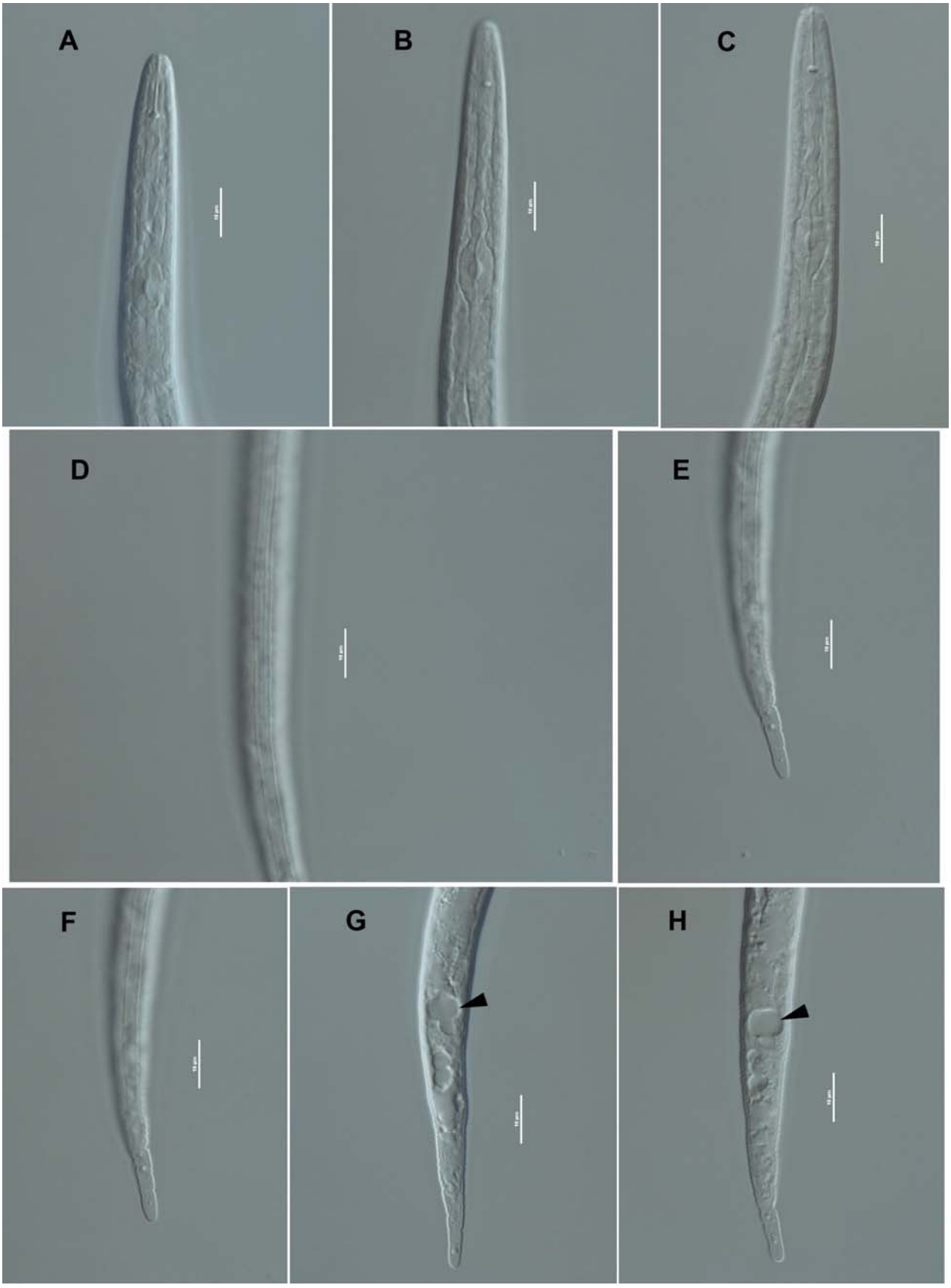


Fig. 9. Micrographs of second stage juveniles of *Meloidogyne fallax*. A: Anterior end, showing head region and stylet; B: Anterior end, showing metacorpus; C: Anterior end showing stylet and metacorpus; D: Lateral field and lines; E, F, G, H: Tails, showing inflated proctodeum (arrowed), hyaline region and phasmids.

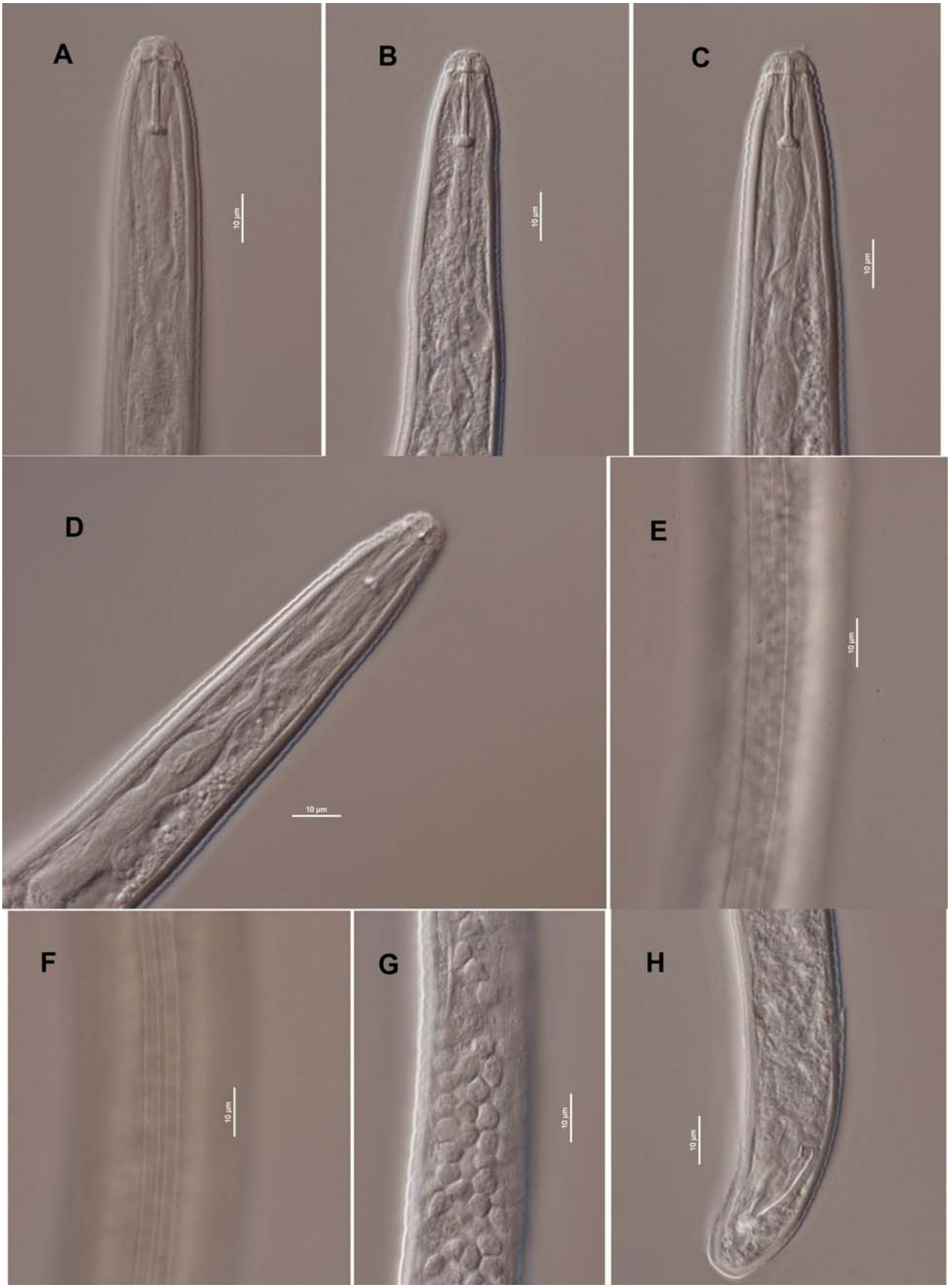


Fig 10. Micrographs of males of *Meloidogyne fallax*. A, B, C, D: Anterior end, showing stylet, lip region, excretory pore and metacorpus; E, F: Lateral field; G: Spermatozoa; H: Ventral view of tail tip with spicules.

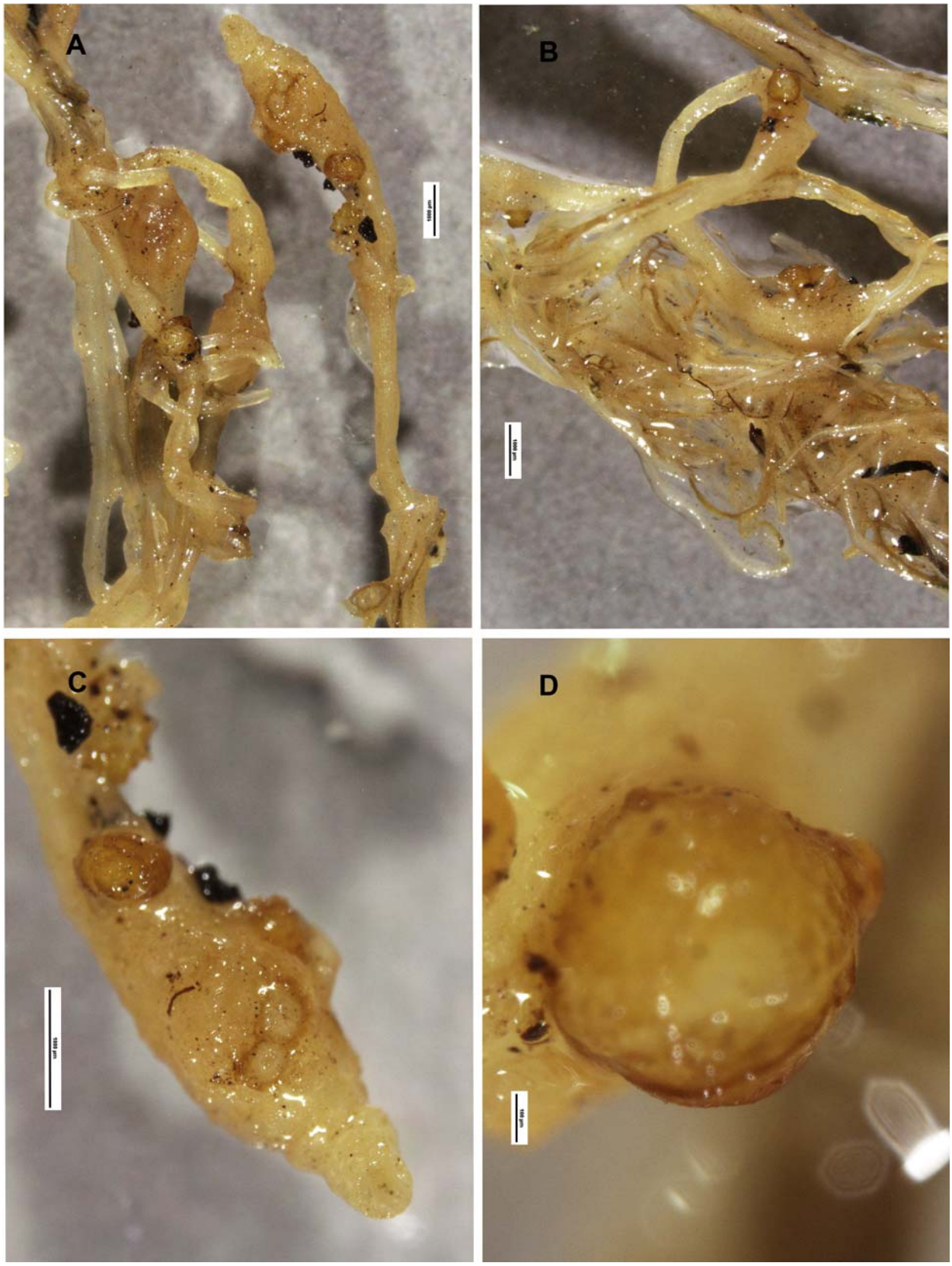


Fig. 11. Micrographs of galling induced by *Meloidogyne fallax* on tomato roots (*Solanum lycopersicum* L.). A, B, C: Roots with galls; D: Close-up of mature female protruding from plant root.

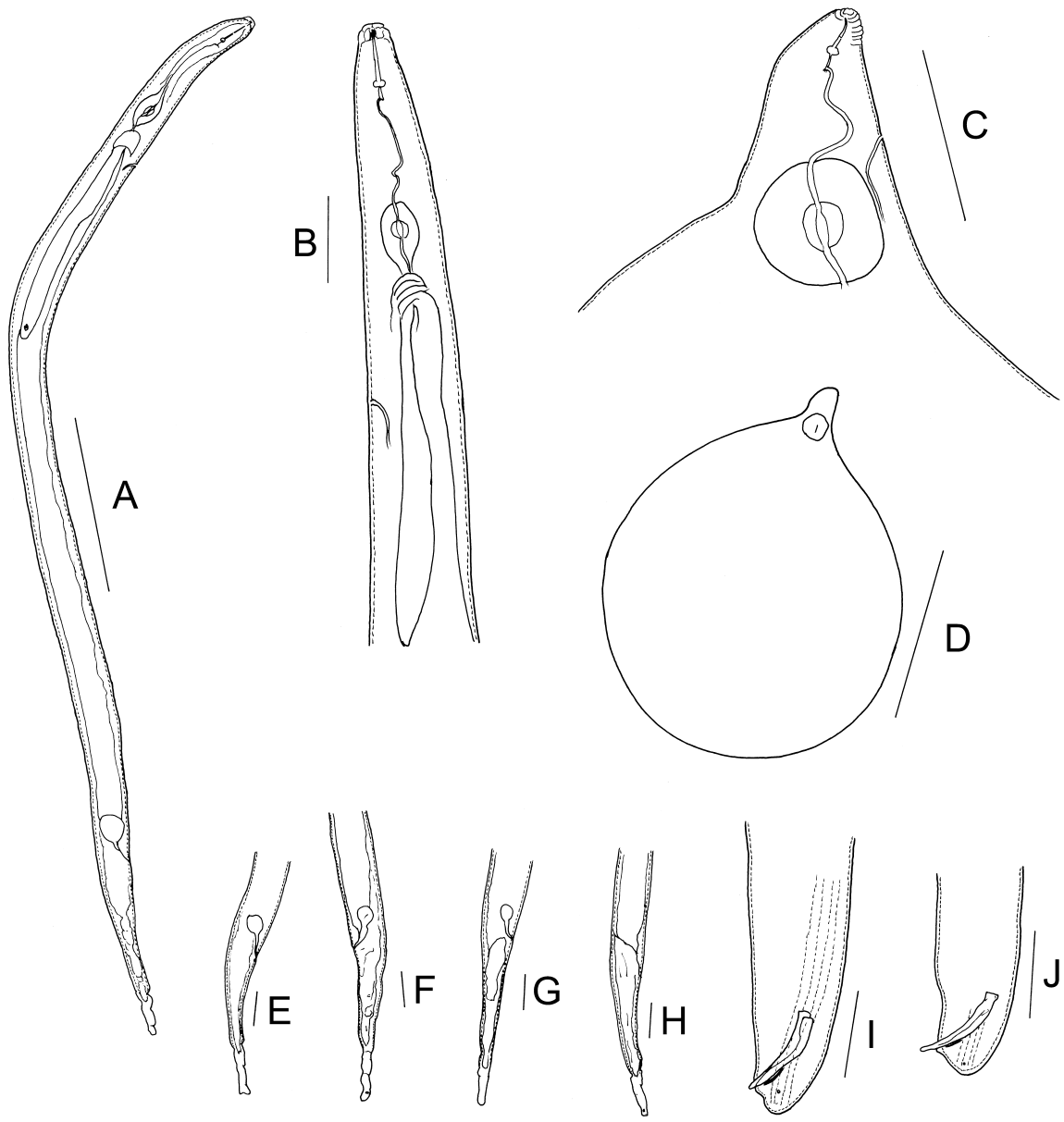


Fig. 12. Line drawings of *Meloidogyne hapla* mature females, males and second stage juveniles. A: Second stage juvenile; B: Anterior end of male; C: Anterior end of female; D: Outline of body shape of mature female; E, F, G, H: Tails of second stage juveniles; I, J: Lateral view of male tails. Scale bars: A: 50 µm; B: 25 µm; C: 50 µm; D: 250 µm; E–J: 10 µm.

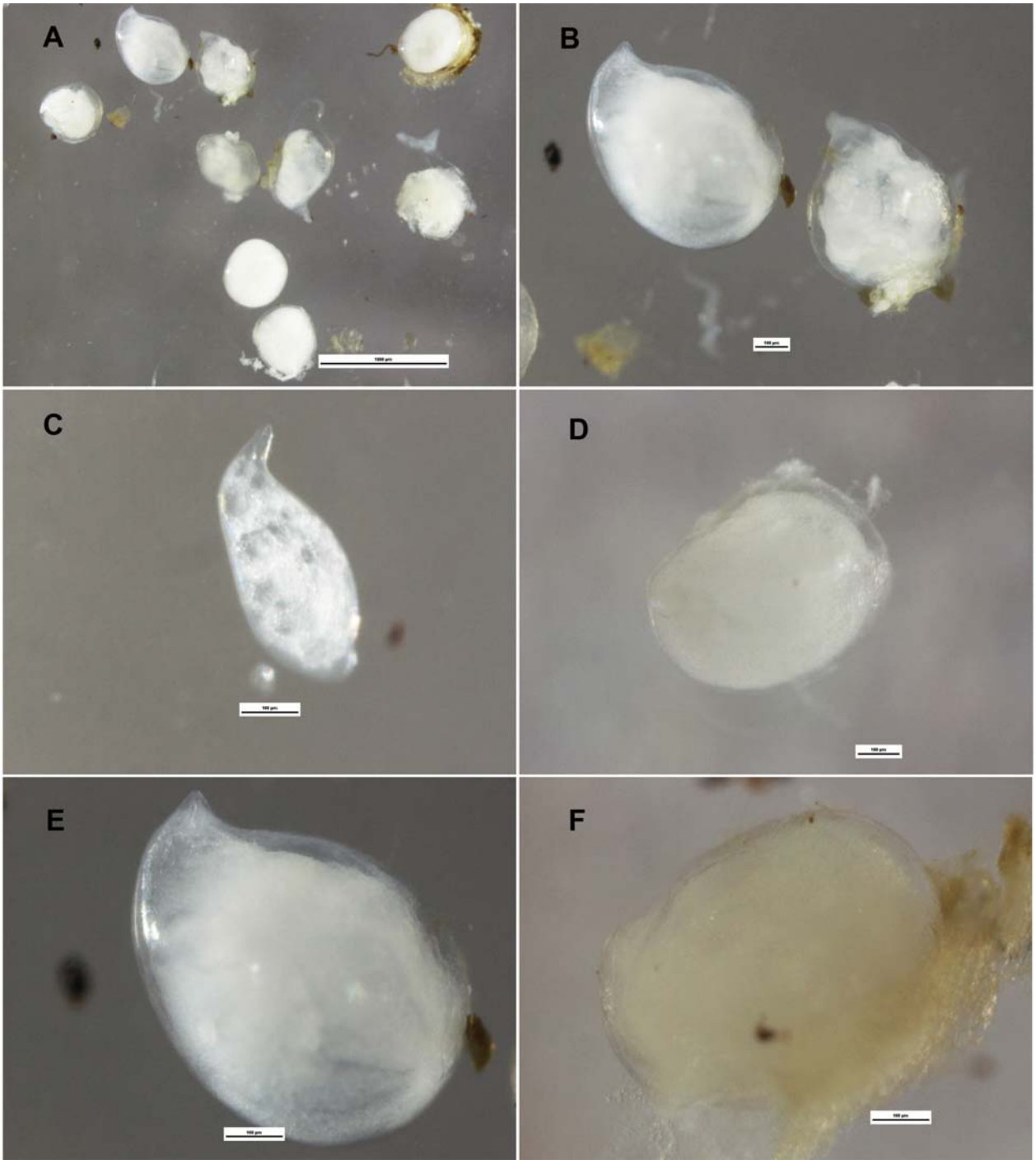


Fig. 13. Micrographs of mature females of *Meloidogyne hapla*. A–E: Whole body of mature (white) females; F: Mature female on a piece of root.

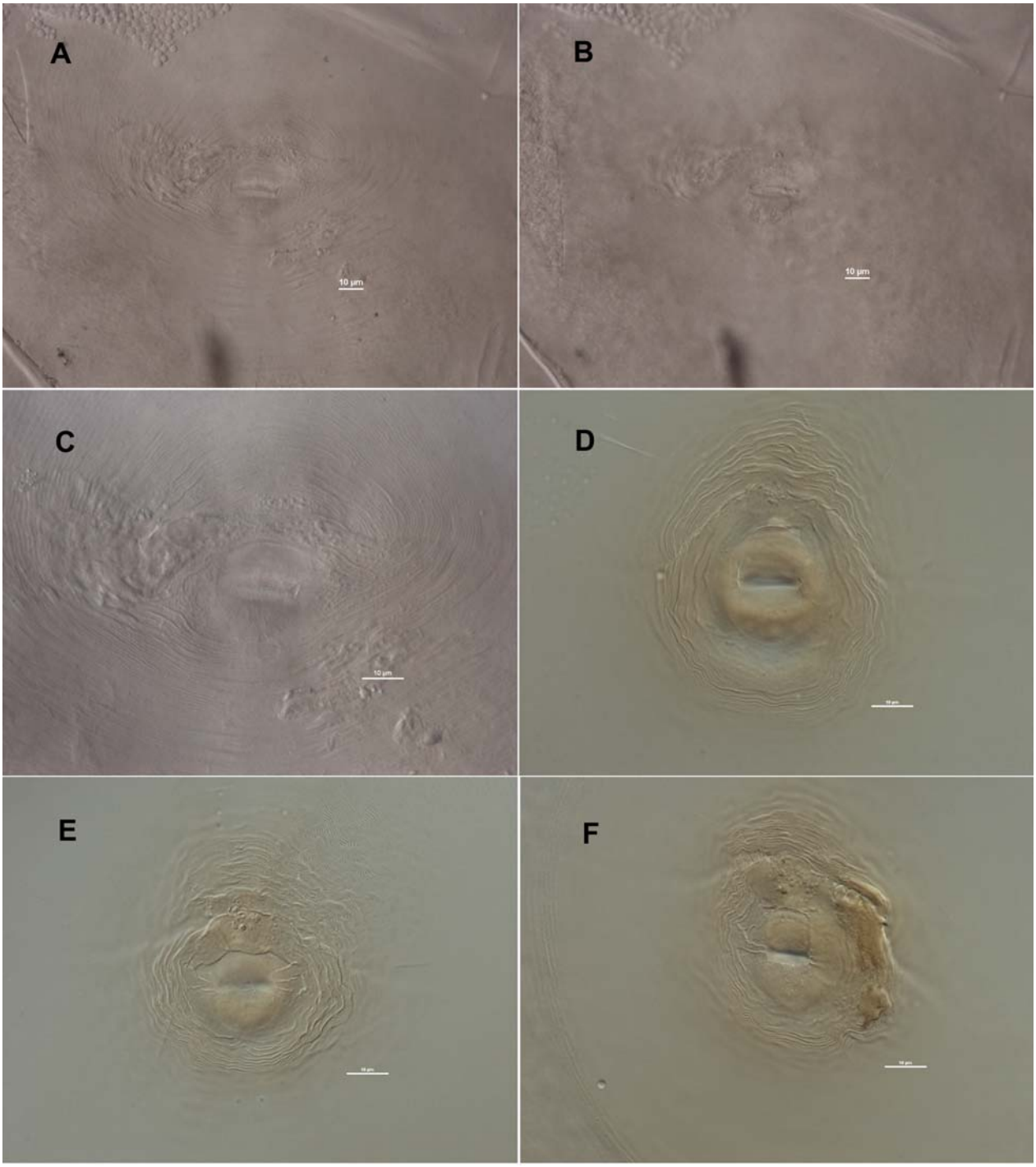


Fig. 14. Micrographs of perineal patterns from mature females of *Meloidogyne hapla*.

Fig. 15. Micrographs of males of *Meloidogyne hapla*. A, B: Anterior end, showing stylet; C: Lateral lines; D, E, F: Lateral view of tail with spicules.

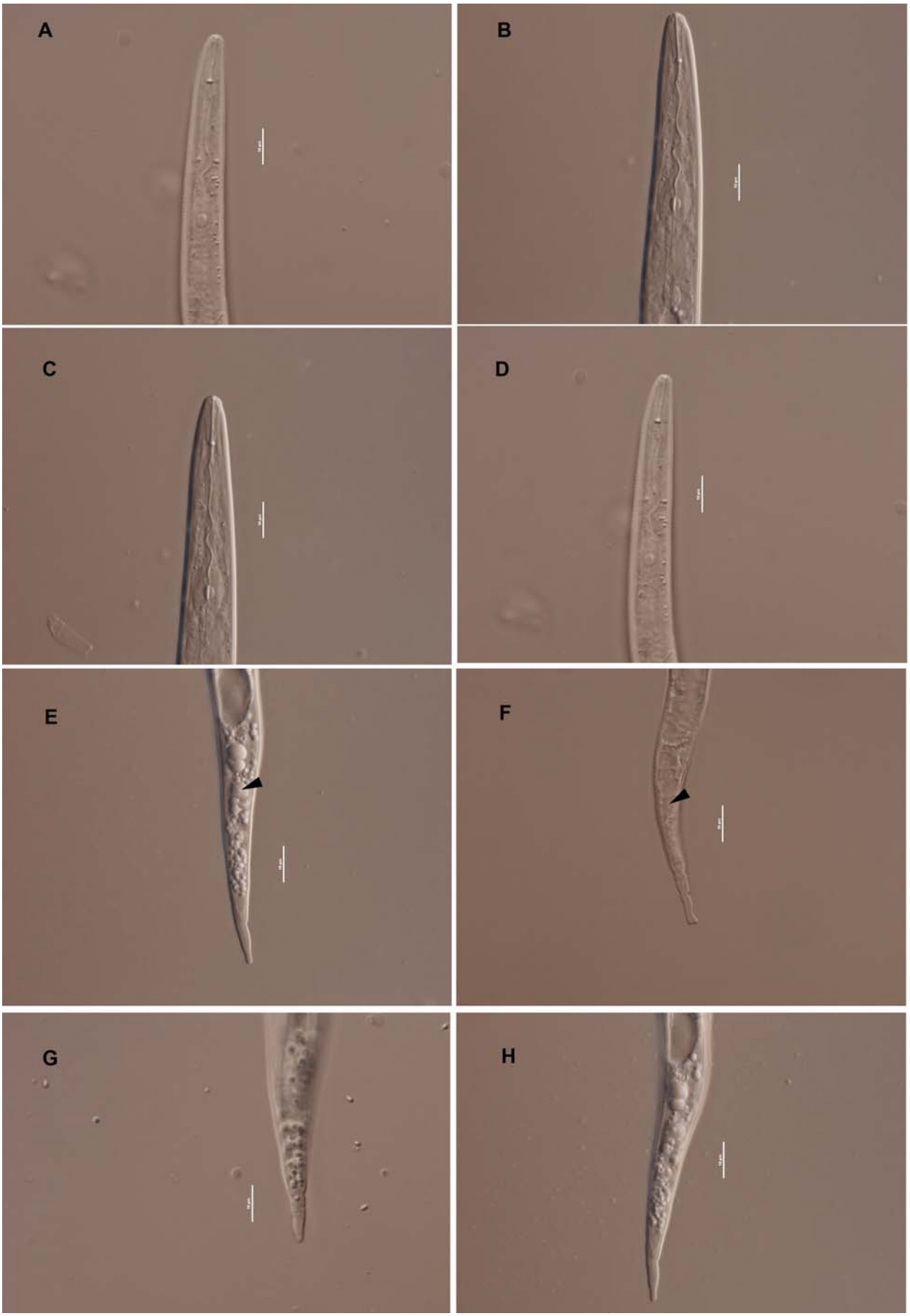


Fig 16. Micrographs of second stage juvenile of *Meloidogyne hapla* isolated from New Zealand. A–D: Anterior end, showing head region and stylet, metacorpus; E, F: Tails, showing phasmids (arrowed); G–H: Tails, showing hyaline region.

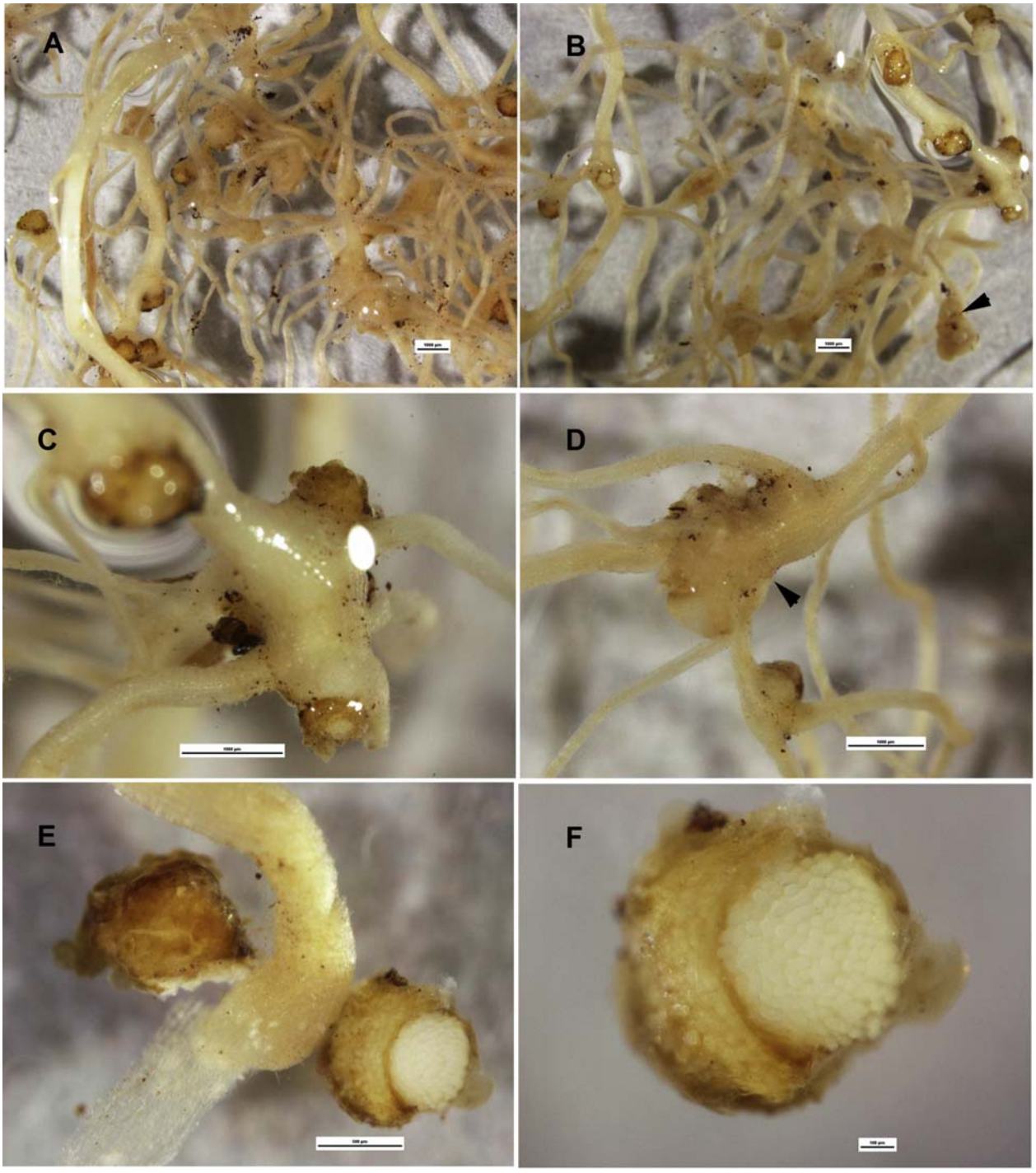


Fig. 17. Micrographs of galling induced by *Meloidogyne hapla* on tomato roots (*Solanum lycopersicum* L.). A, B, C, D: Roots with galls (arrowed); E, F: Close-up of egg mass from plant root.

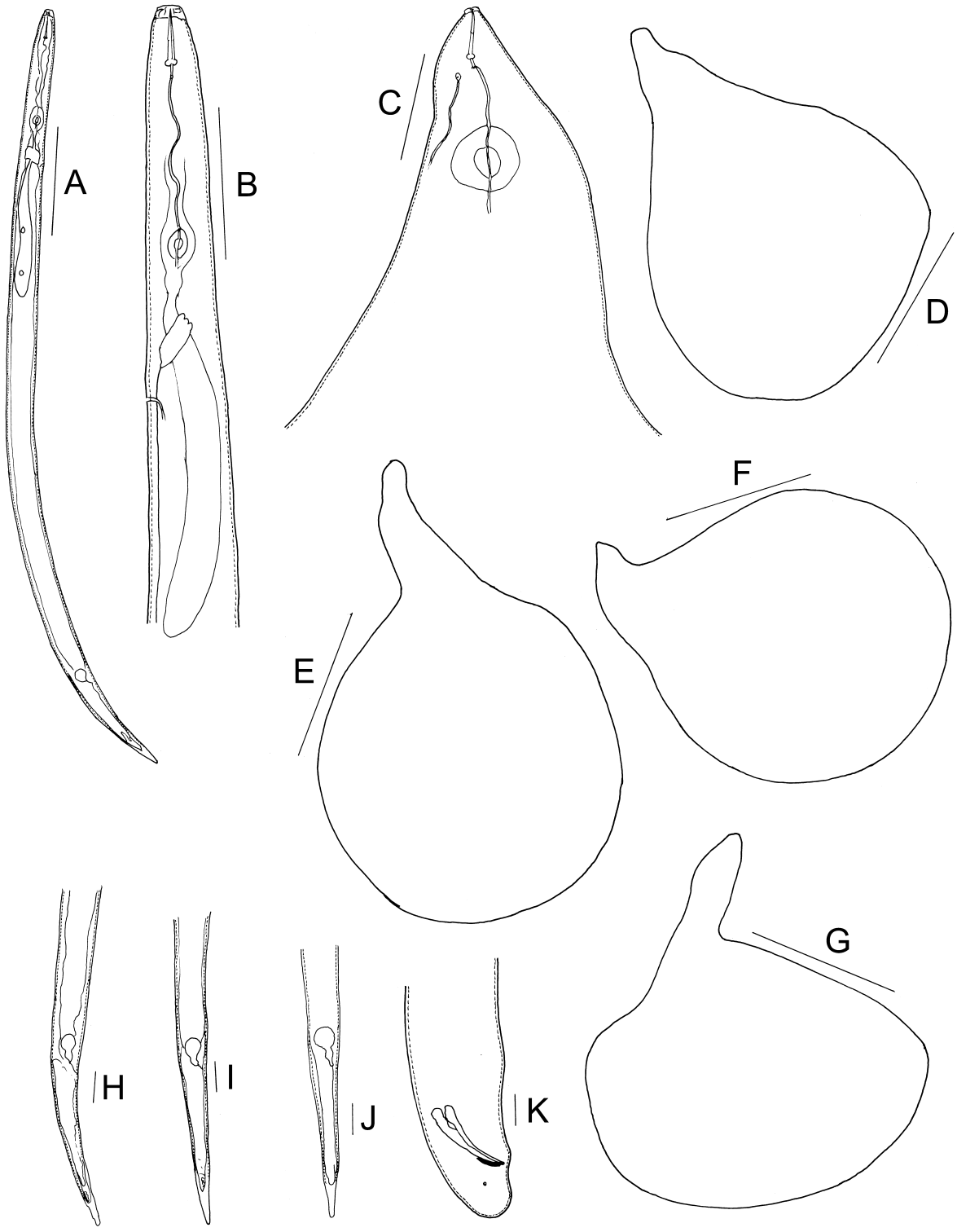


Fig. 18. Line drawings of *Meloidogyne incognita* mature females, males and second stage juveniles. A: Second stage juvenile; B: Anterior end of male; C: Anterior end of female; D, E, F, G: Outlines of body shapes of mature females; H, I, J: Tails of second stage juveniles; K: Lateral view of male tail. Scale bars: A–C: 50 µm; D–G: 250 µm; H–K: 10 µm.

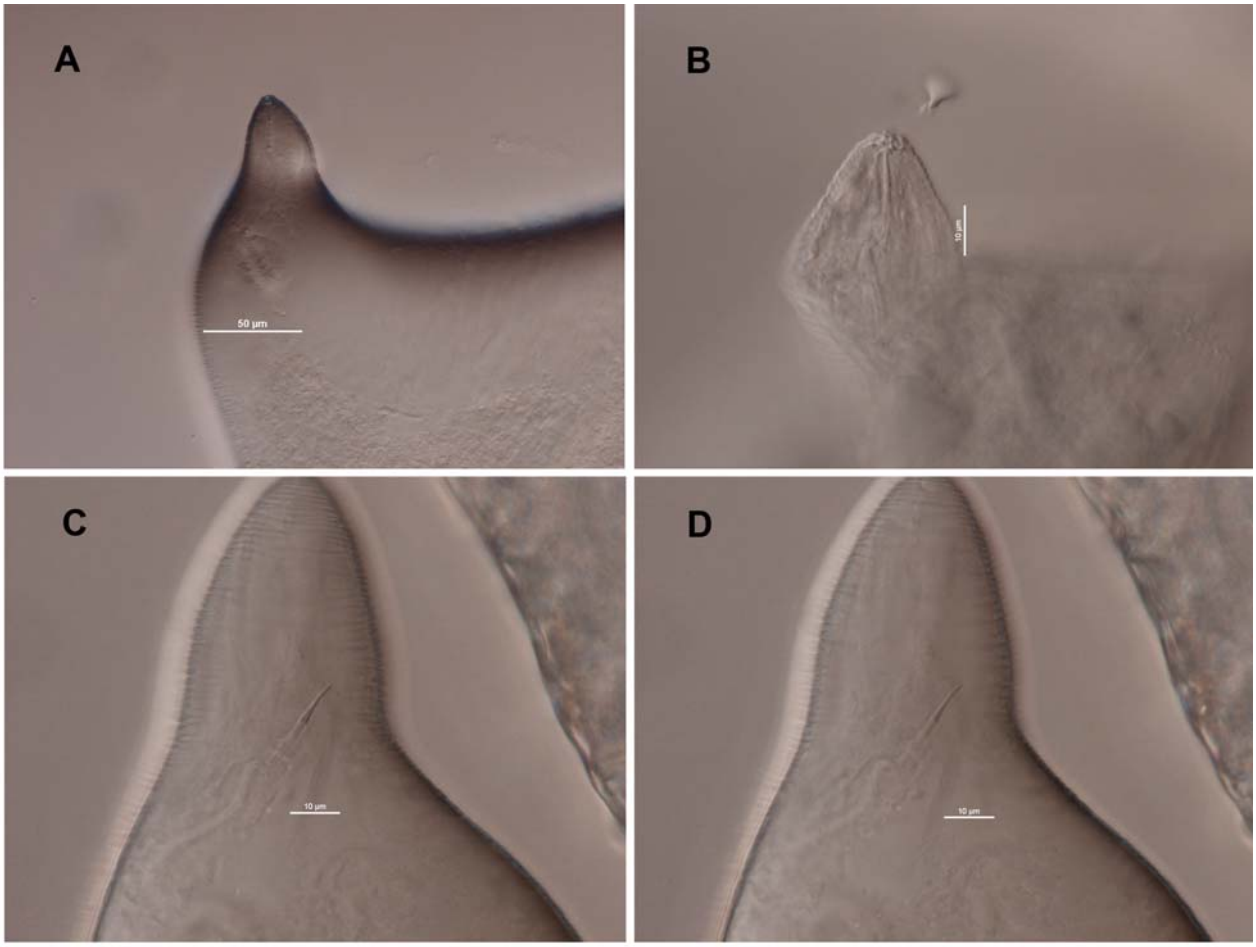


Fig. 19. Micrographs of mature female of *Meloidogyne incognita*. A: Anterior end; B: Showing lip region and stylet; C, D: Stylet at different focal levels.

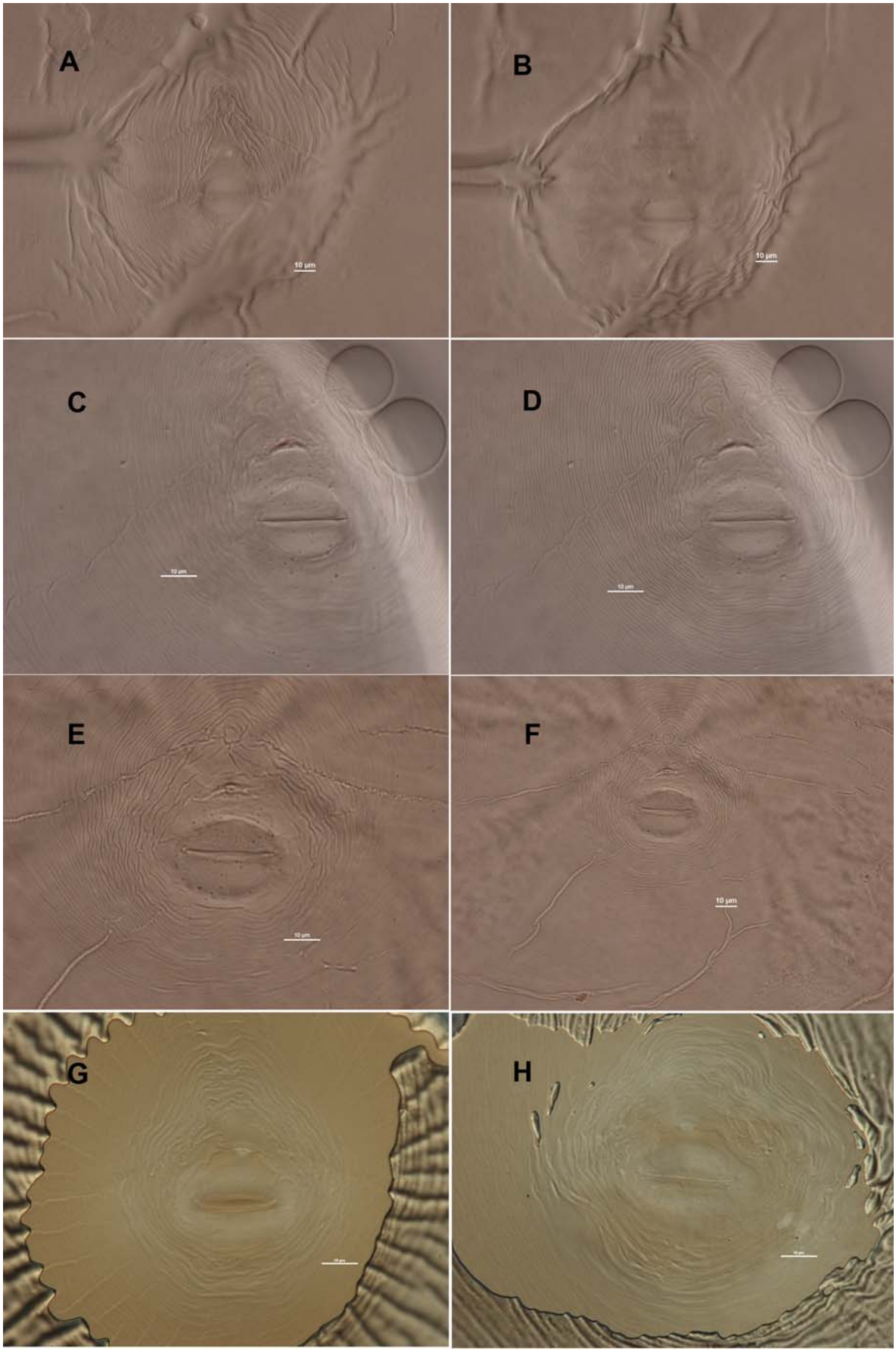


Fig. 20. Micrographs of perineal patterns from mature females of *Meloidogyne incognita*.

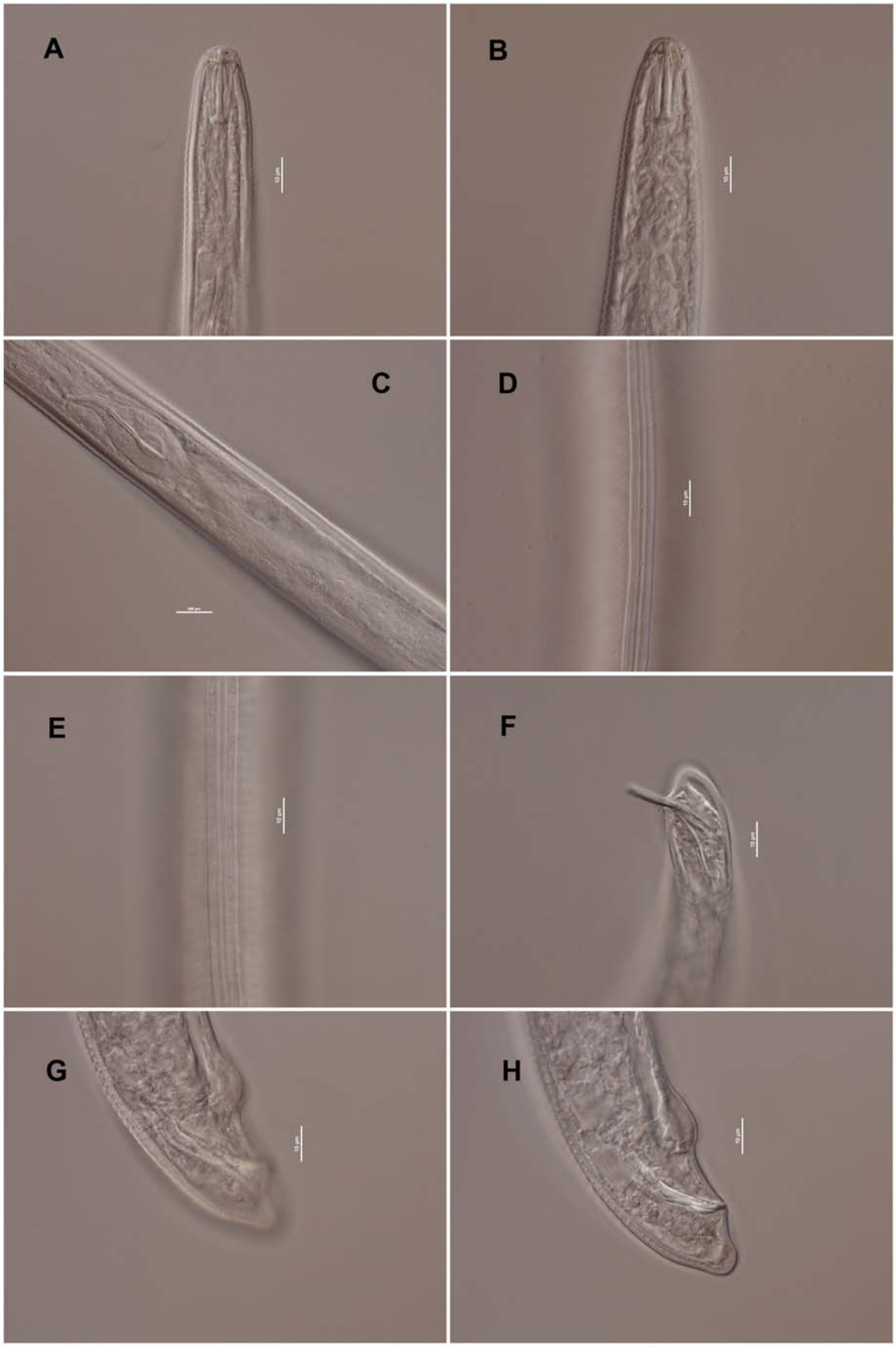


Fig. 21. Micrographs of males of *Meloidogyne incognita*. A, B: Anterior end, showing stylet, lip region, excretory pore; C: Metacorpus; D, E: Lateral field; F, G, H: Tail tip with spicules, phasmids.

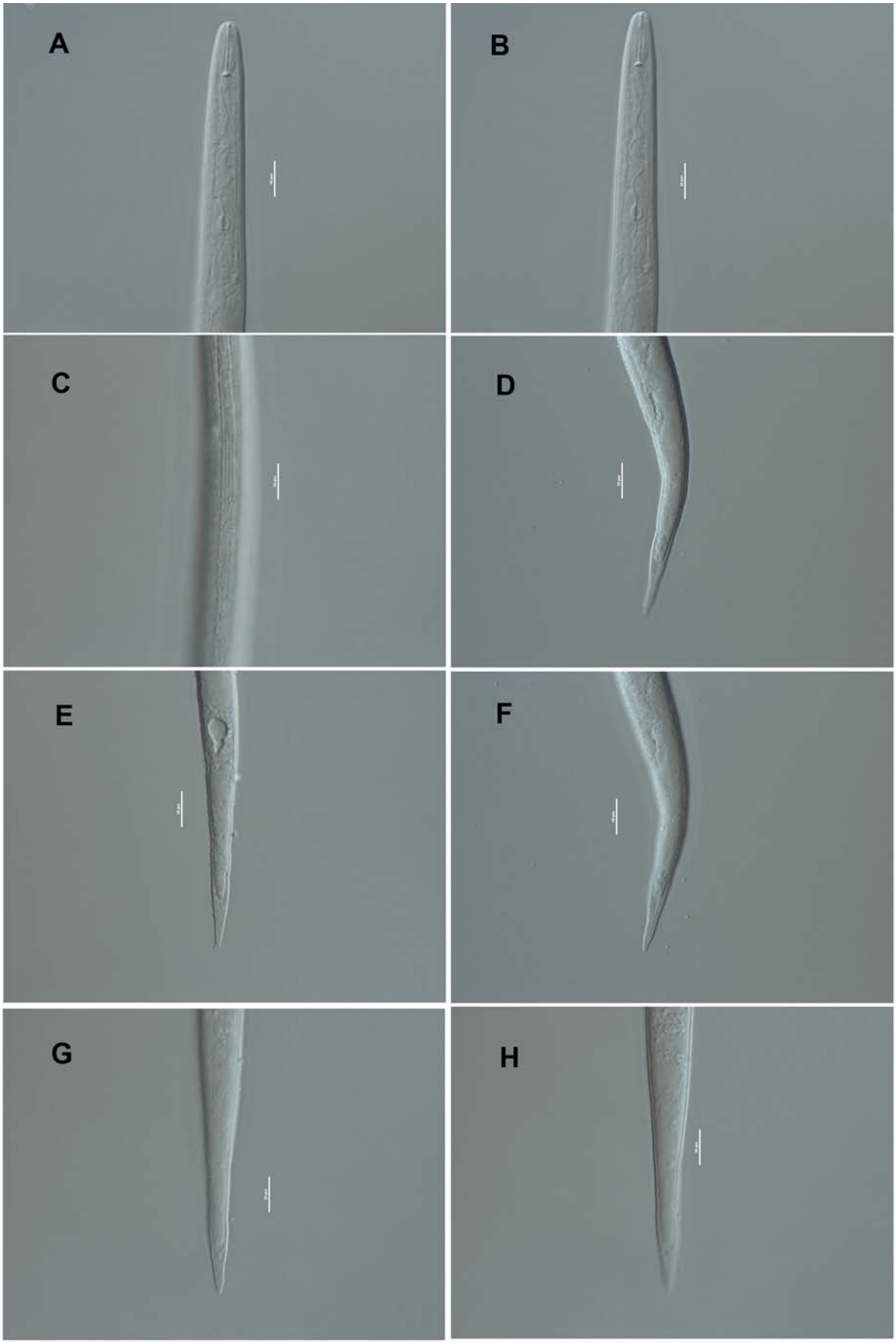


Fig. 22. Micrographs of second stage juvenile of *Meloidogyne incognita* from New Zealand. A, B: Anterior end, showing head region and stylet; C: Lateral field and lines; D, E, F, G, H: Tails, showing inflated proctodeum and hyaline region.

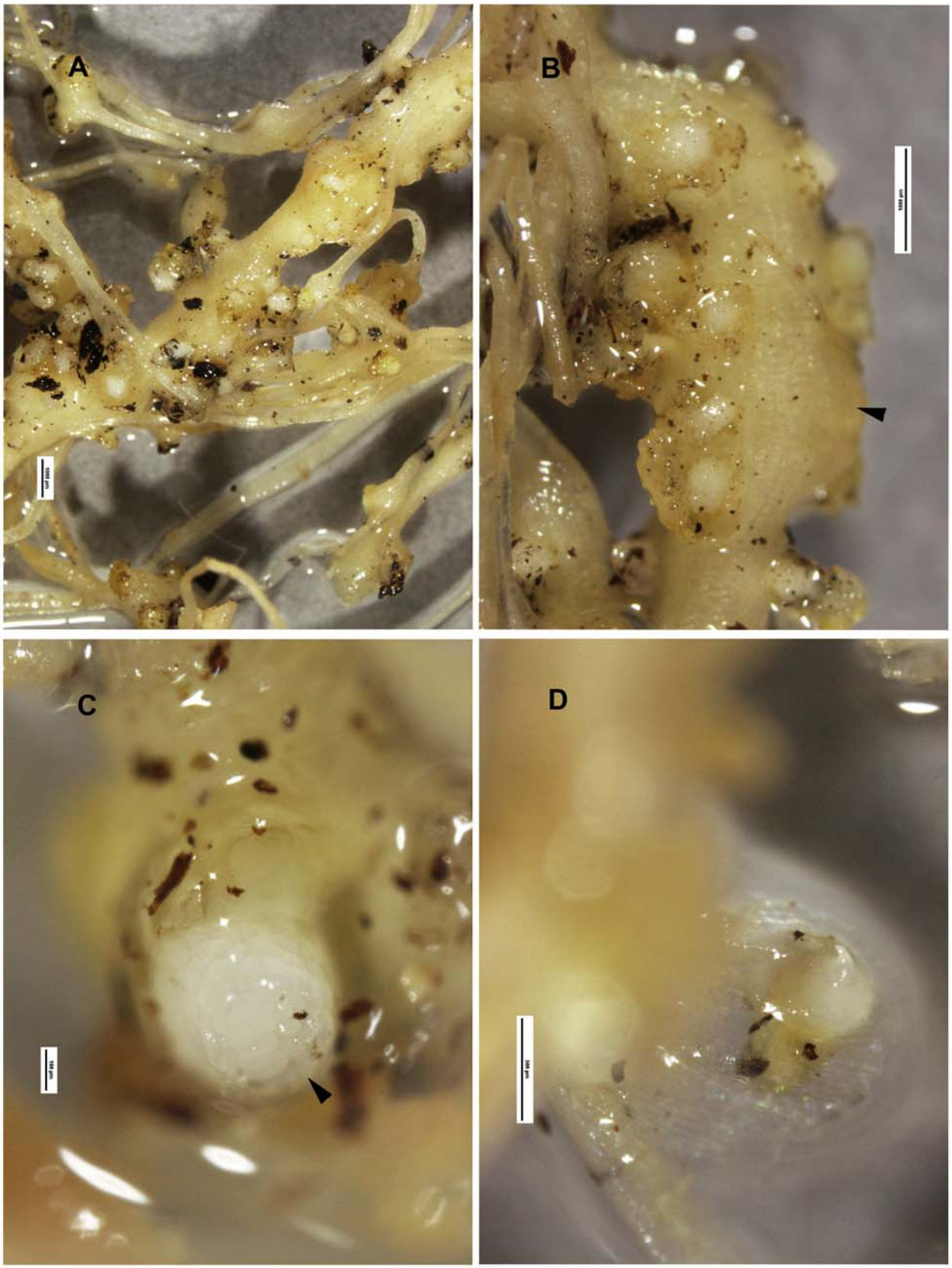


Fig. 23. Micrographs of galling induced by *Meloidogyne incognita* on tomato roots (*Solanum lycopersicum* L.). A, B: Roots with galls (arrowed); C: Close-up of egg mass from plant root (arrowed); D: female protruding from root.

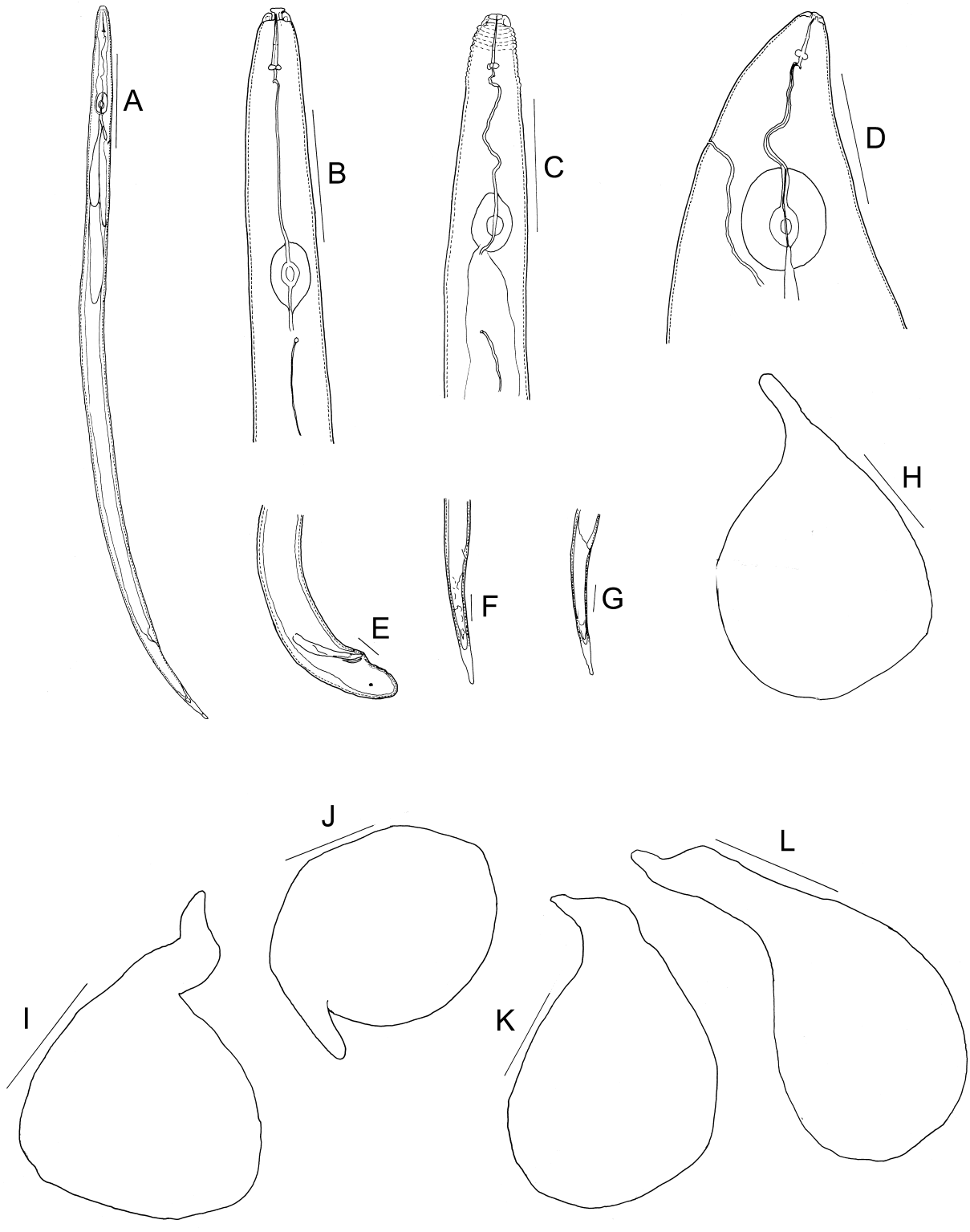


Fig. 24. Line drawings of *Meloidogyne javanica* mature females, males and second stage juveniles isolated from New Zealand. A: Second stage juvenile; B, C: Anterior ends of males; D: Anterior end of mature female; E: Male tail; F, G: Tails of second stage juveniles; H, I, J, K, L: Outlines of bodies of mature females. Scale bars: A–D: 50 µm; E–G: 10 µm; H–L: 250 µm.

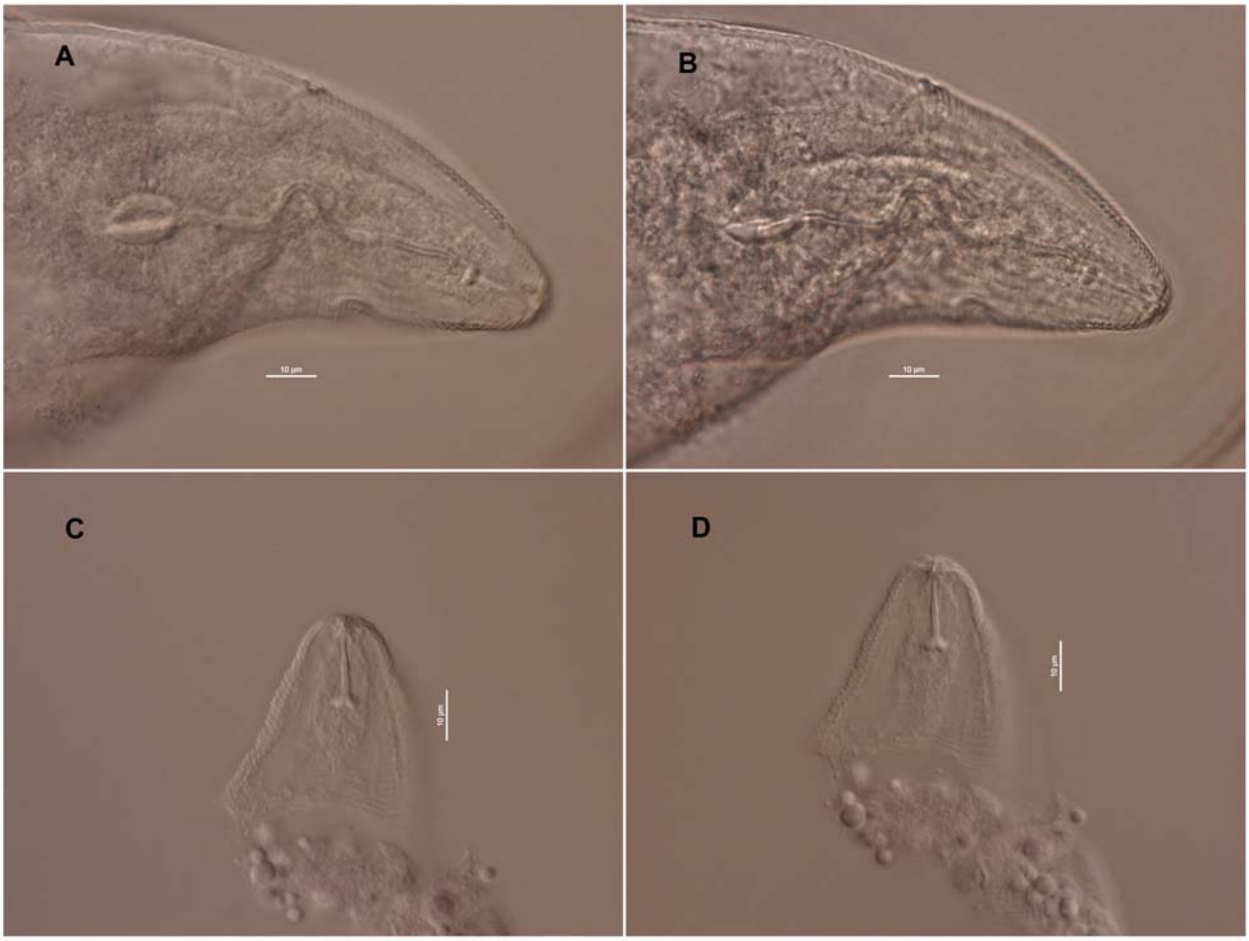


Fig. 25. Micrographs of mature female of *Meloidogyne javanica* isolated from New Zealand. A, B: Anterior end, at different focal levels, showing excretory pore and duct, metacorpus, stylet and annulations, C, D: Labial region at different focal levels, showing stylet, lip region.

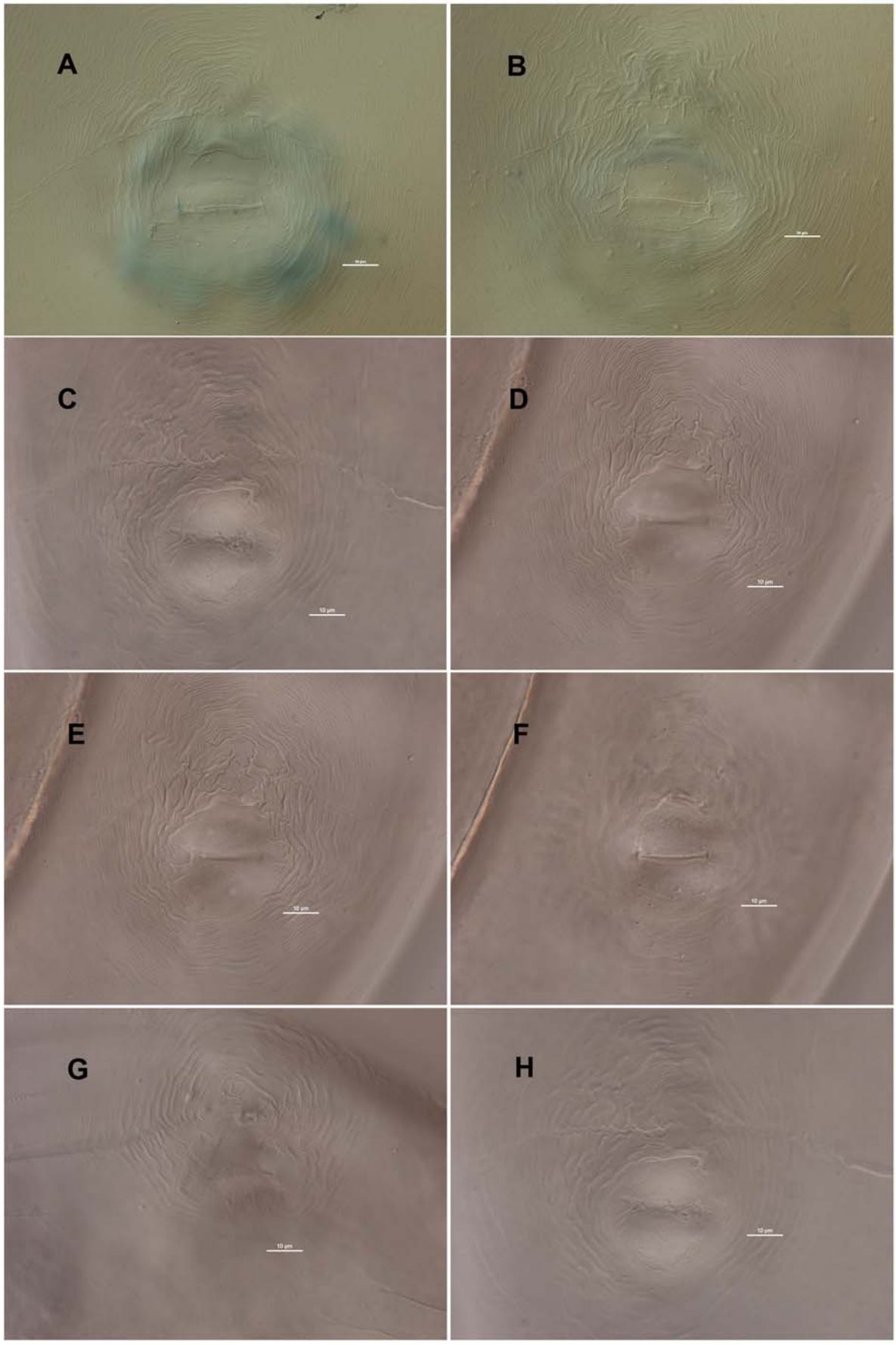


Fig. 26. Micrographs of perineal patterns from mature females of *Meloidogyne javanica*.

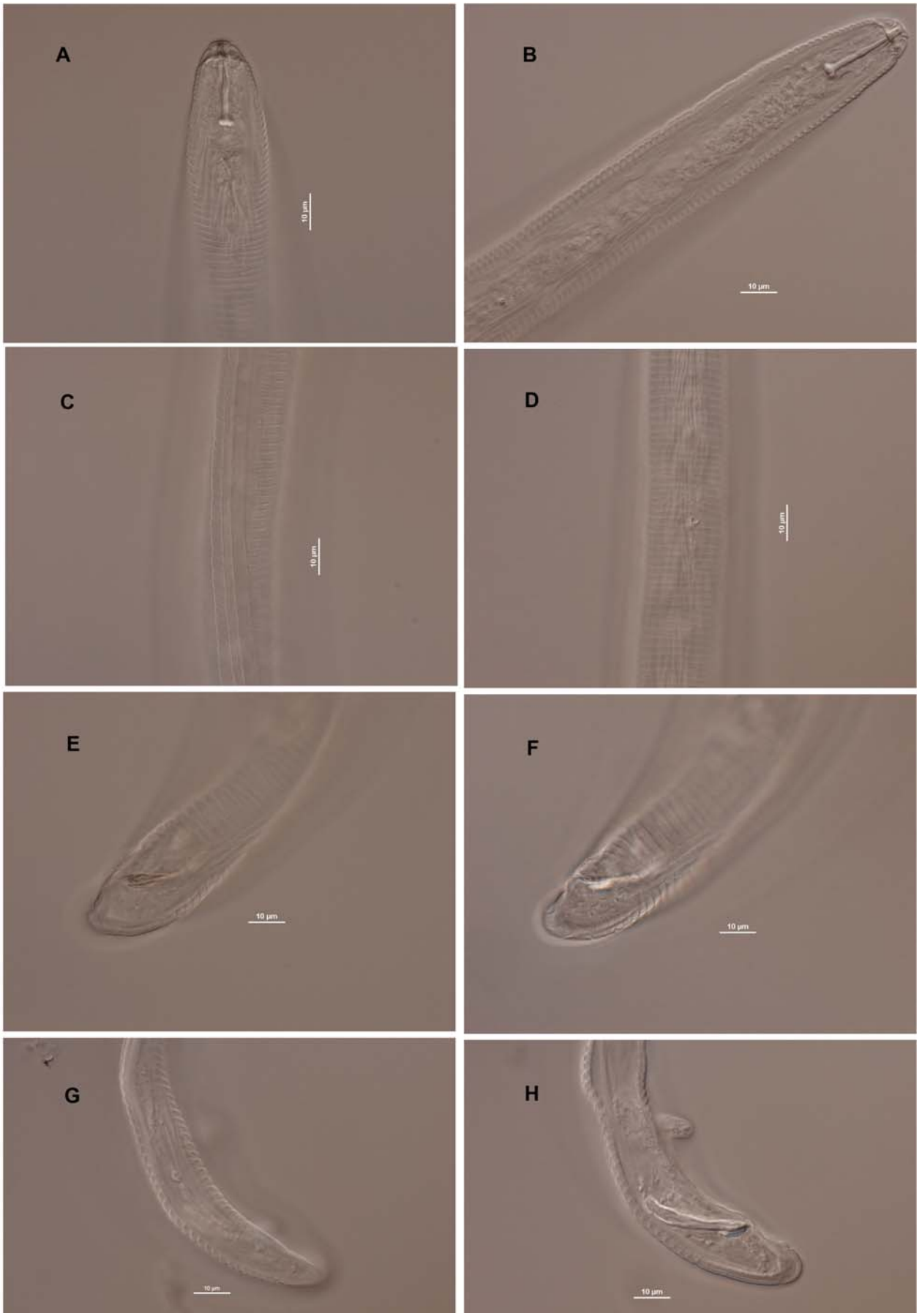


Fig. 27. Micrographs of males of *Meloidogyne javanica.* A, B: Anterior ends showing stylets; C: Lateral lines; D: Opening of excretory pore; E, F: Sub-ventral views of tail; G: Lateral view of tail showing phasmid; H: Lateral view of tail with spicules and gubernaculum.

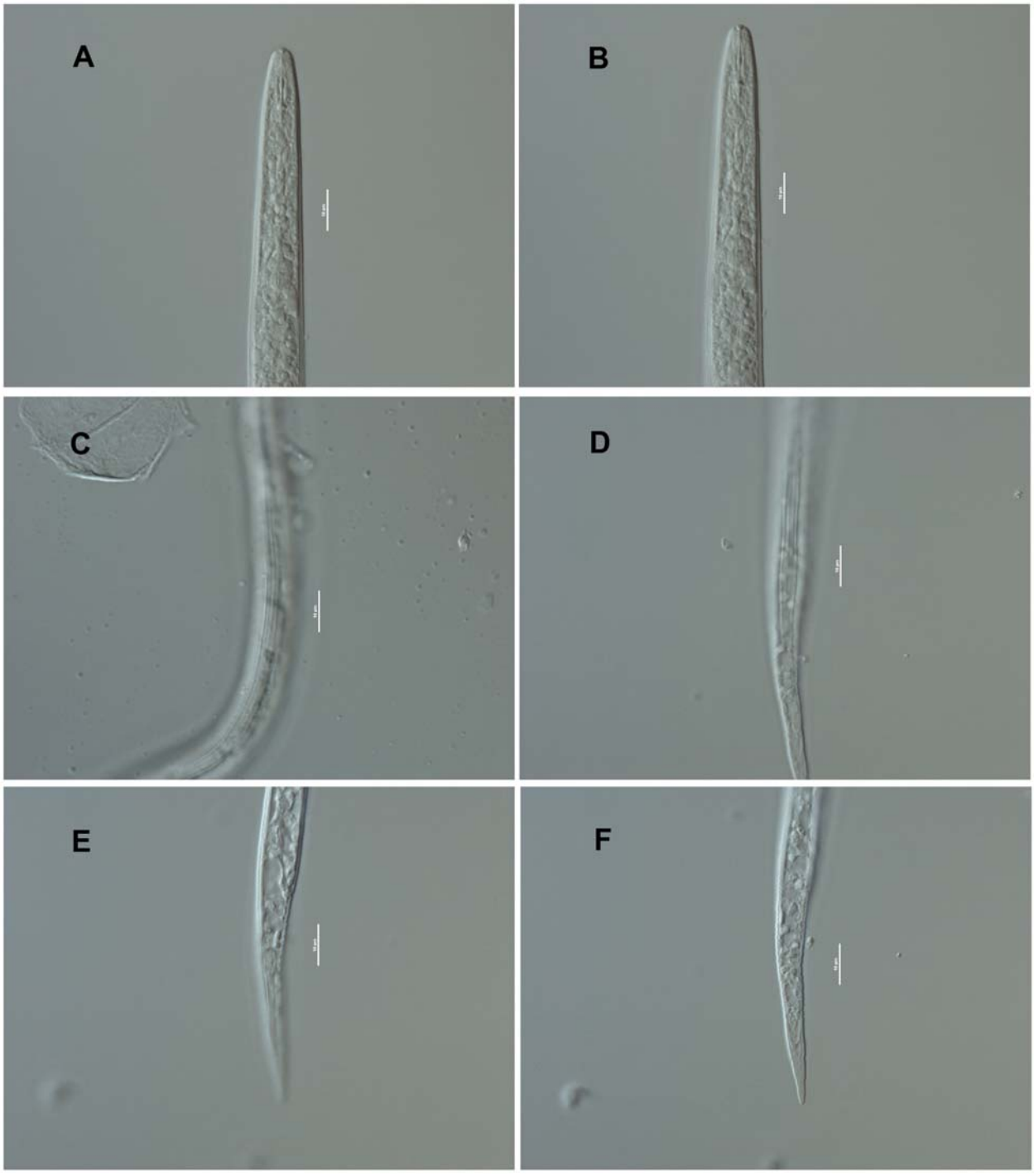


Fig. 28. Micrographs of second stage juvenile of *Meloidogyne javanica* isolated from New Zealand. A, B: Anterior ends, showing stylet and metacorpus; C, D: Lateral lines at different levels of body; E, F: Tail region, showing anus, hyaline region and tip.

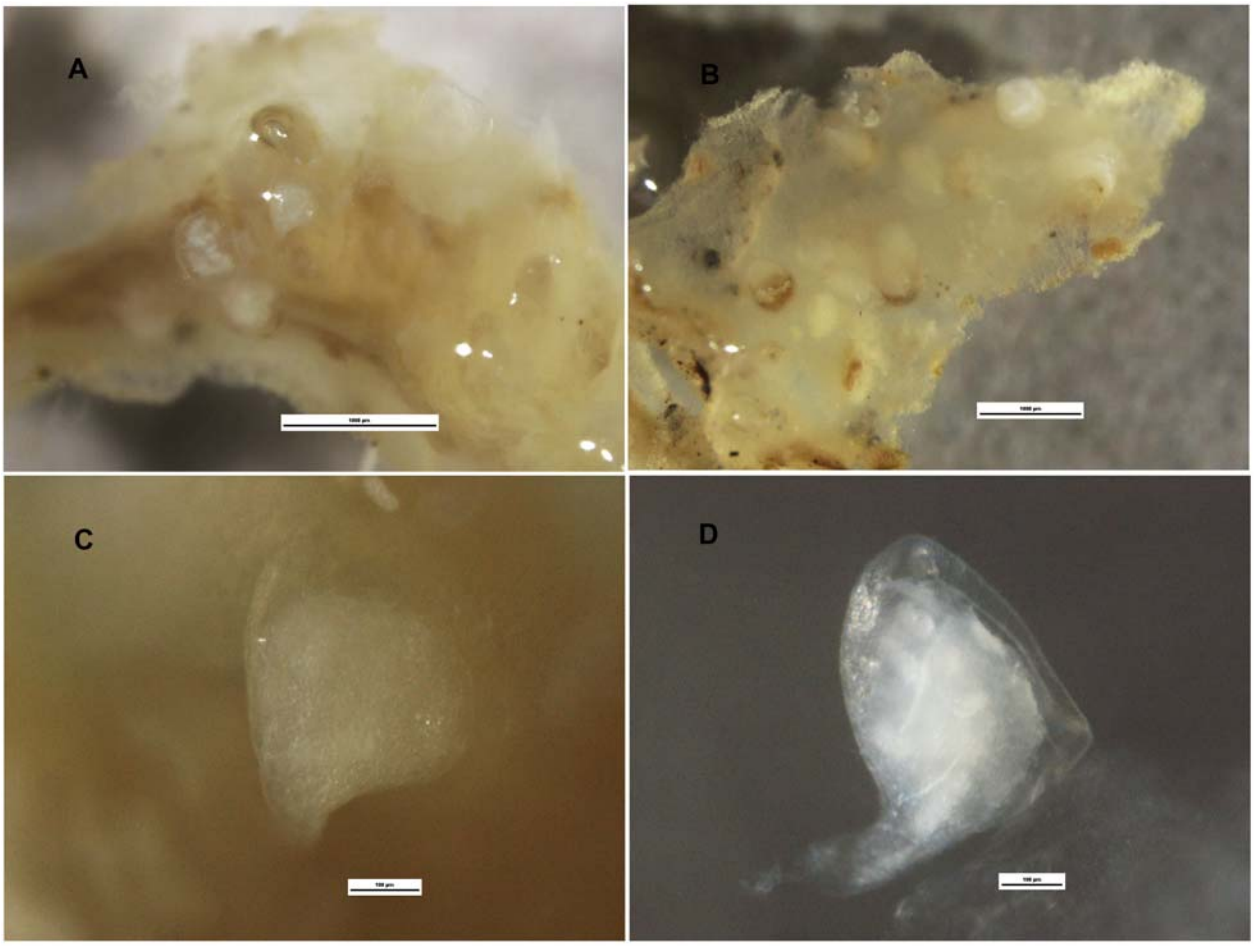


Fig. 29. Micrographs of galling induced by *Meloidogyne javanica* on tomato roots (*Solanum lycopersicum* L.). A, B, C: Roots with galls; D: Close-up of mature female protruding from plant root.

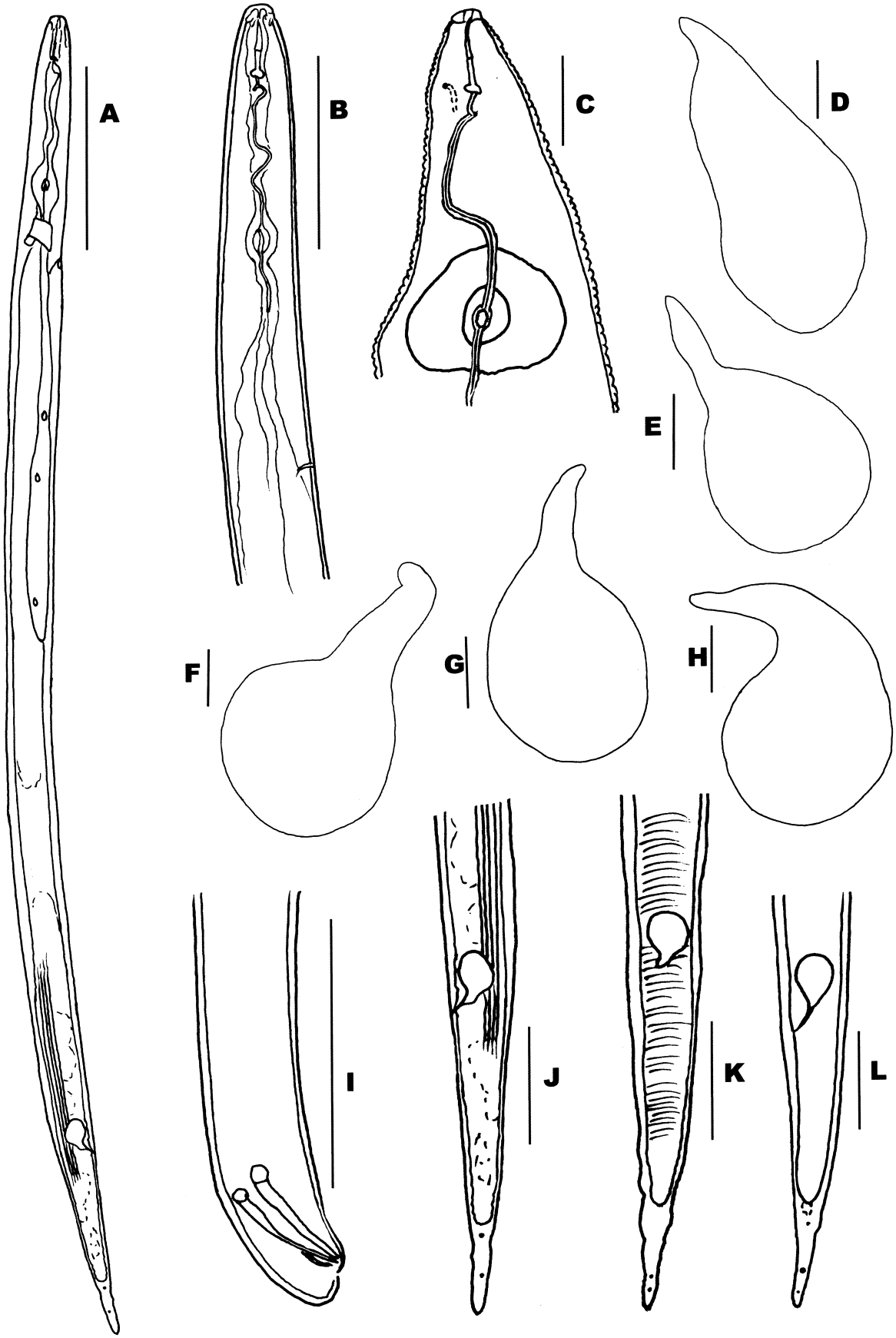


Fig. 30. Line drawings of *Meloidogyne minor* mature females, males and second stage juveniles isolated from New Zealand. A: Second stage juvenile; B: Anterior end of male; C: Anterior end of female, showing stylet and excretory pore; D, E, F, G, H: Outlines of bodies of mature females; I, Male tail; J, K, L: Tails of infective juveniles. J: Lateral lines; K, L: Form of hyaline areas. Scale bars: A–I: 50 µm; J–L: 10 µm.

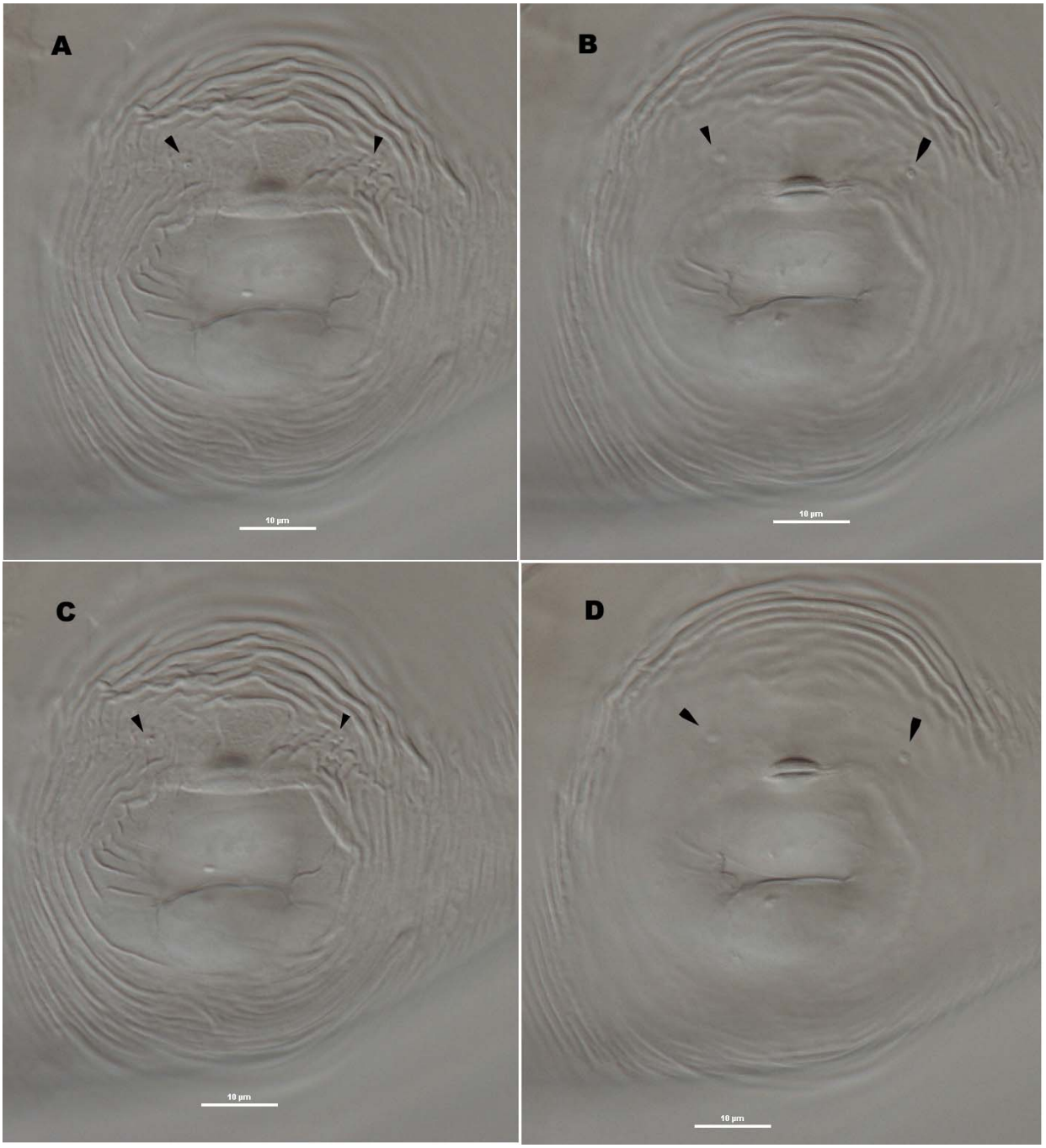


Fig. 31. Micrographs of perineal patterns from mature females of *Meloidogyne minor*. Phasmids arrowed.

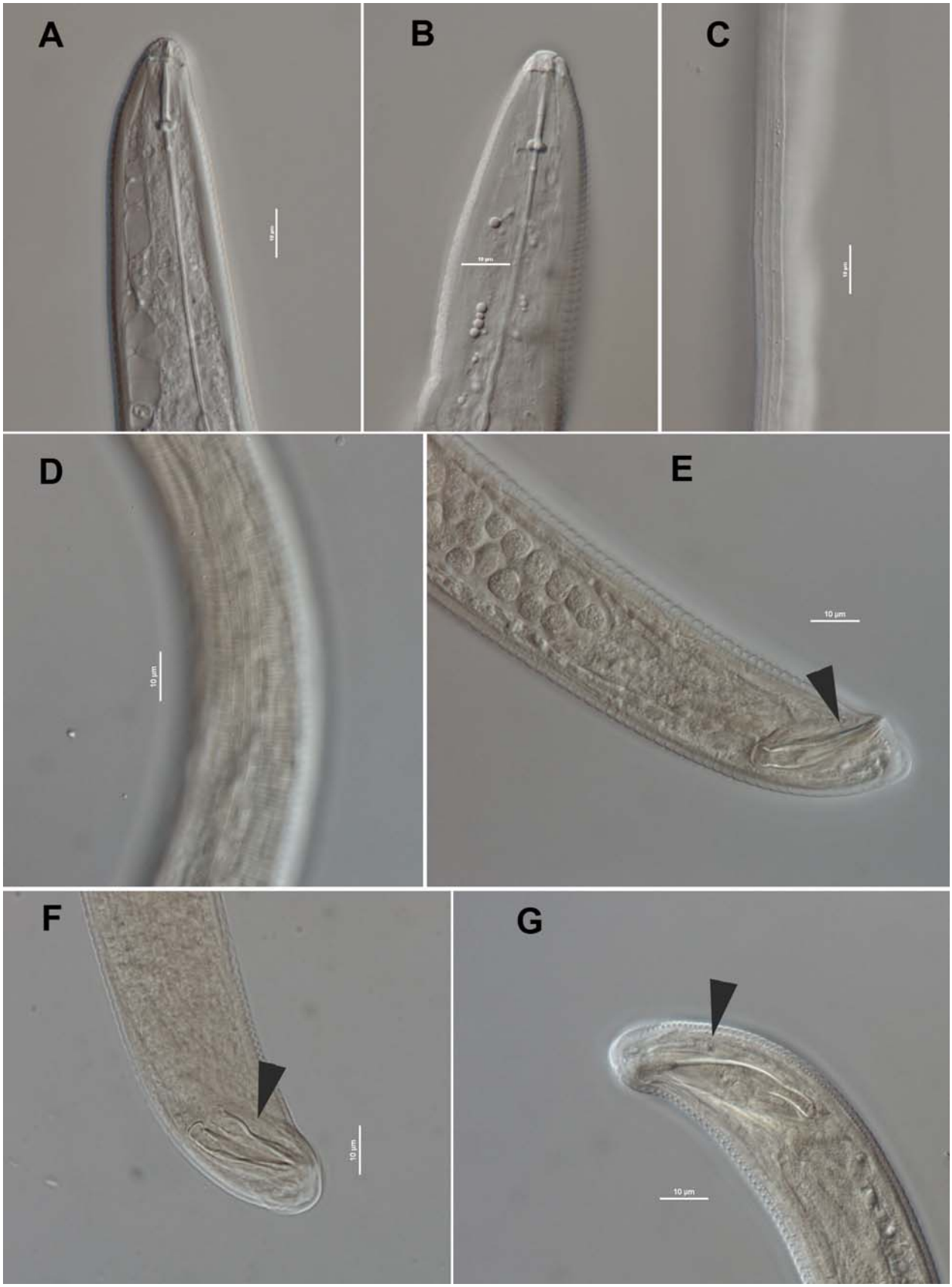


Fig. 32. Micrographs of males of *Meloidogyne minor*. A, B: Anterior ends, showing labial lips and stylets; C, D: Lateral lines; E: Lateral view of tail showing spicules (arrowed); F, G: Lateral views of tail showing phasmids (arrowed).

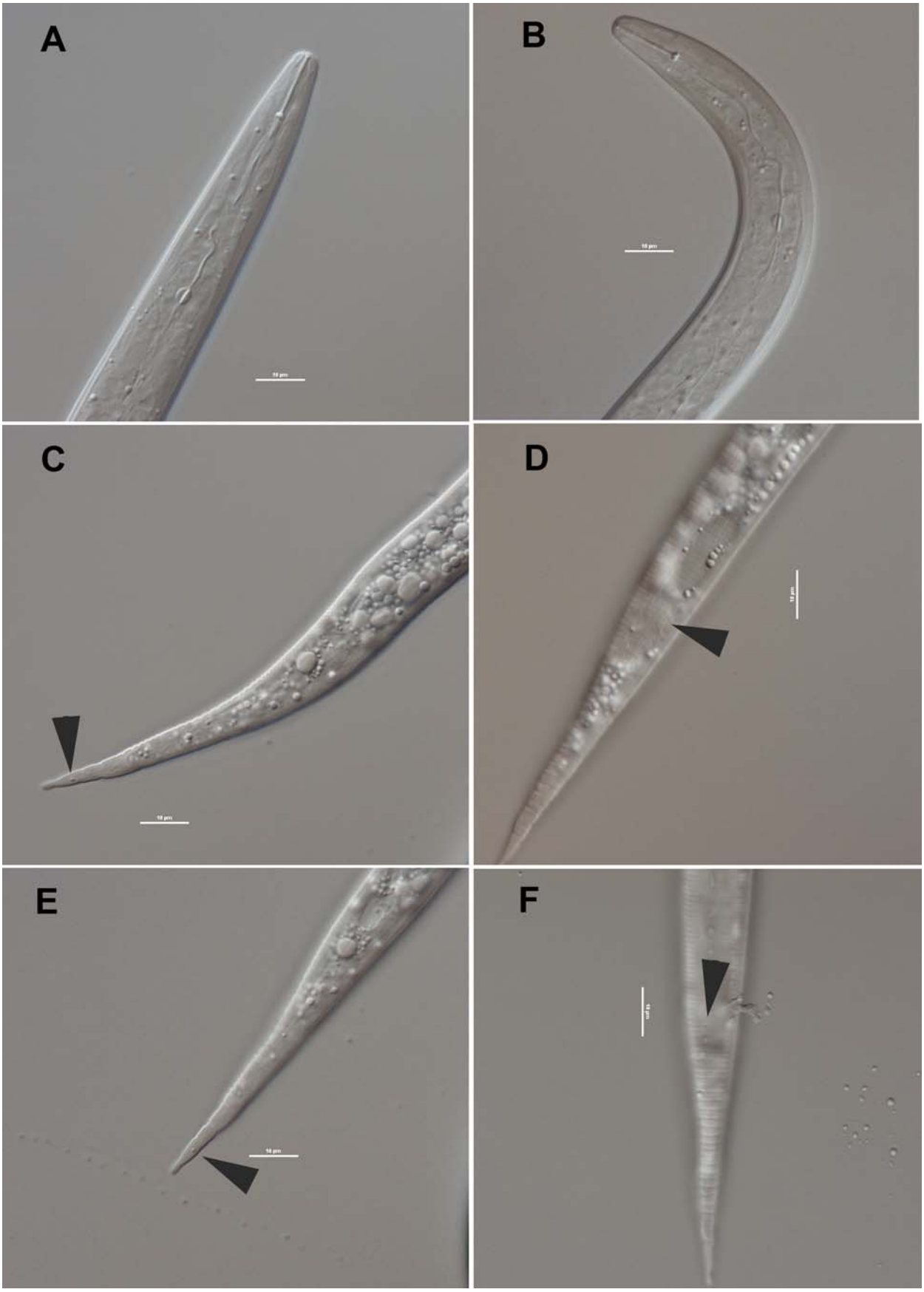


Fig. 33. Micrographs of second stage juveniles of *Meloidogyne minor*. A, B: Anterior end showing stylet and metacorpus; C: Tails of second stage juveniles showing position of fat droplets (arrowed); D: Lateral lines (arrowed); E: Position of fat droplets on tail (arrowed); F: Lateral view of tail showing phasmids (arrowed).

Fig. 34. A. Micrographs of galling induced by *Meloidogyne minor.* A: galls (arrowed) on perennial ryegrass (*Lolium perenne* L.). B: mature white female (arrowed).

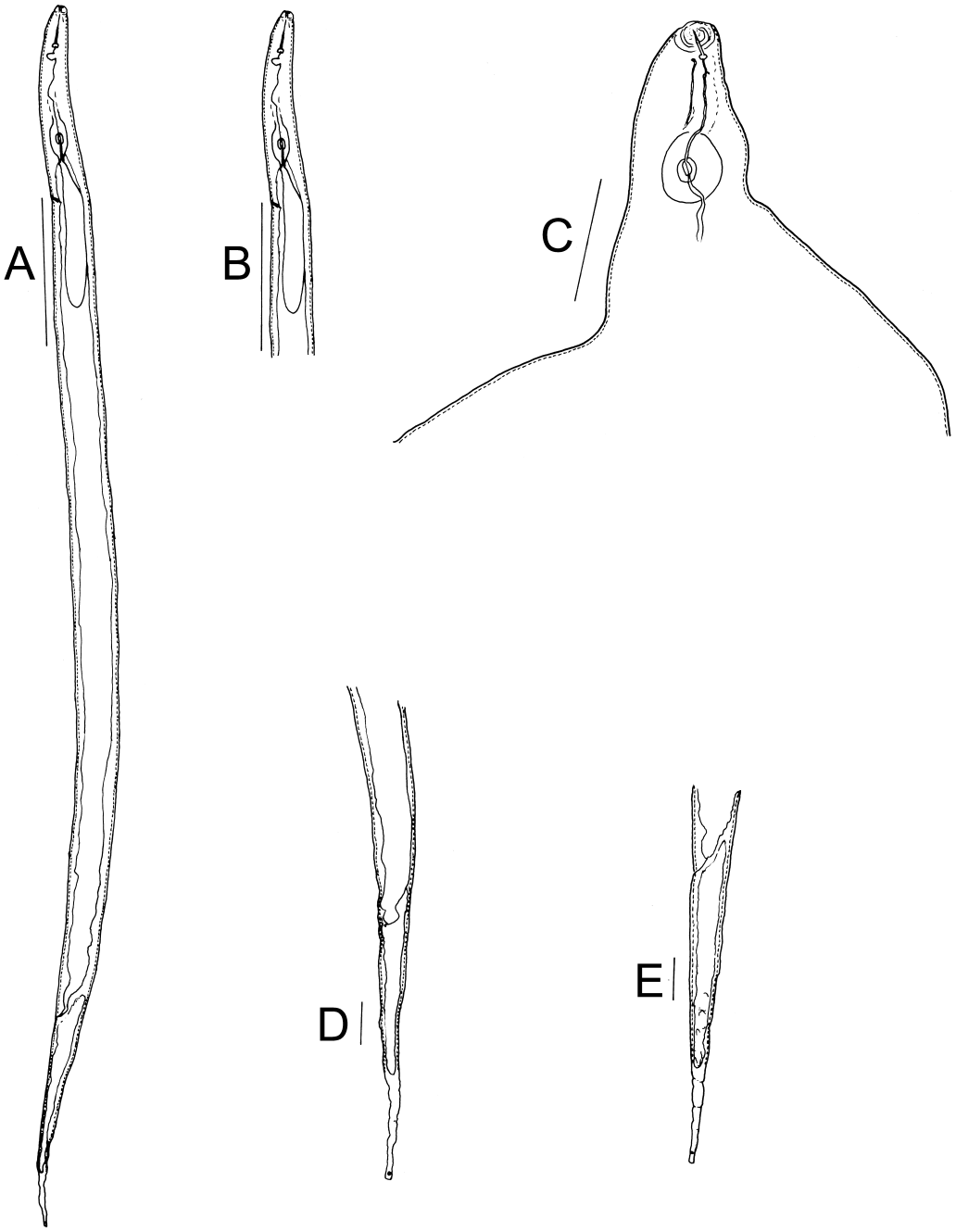


Fig. 35. Line drawings of *Meloidogyne naasi* mature female, male and second stage juveniles isolated from New Zealand. A: Second stage juvenile; B: Anterior end of male: C: Anterior end of female; D, E: Tails of second stage juveniles. Scale bars: A–C: 50 µm; D, E: 10 µm.

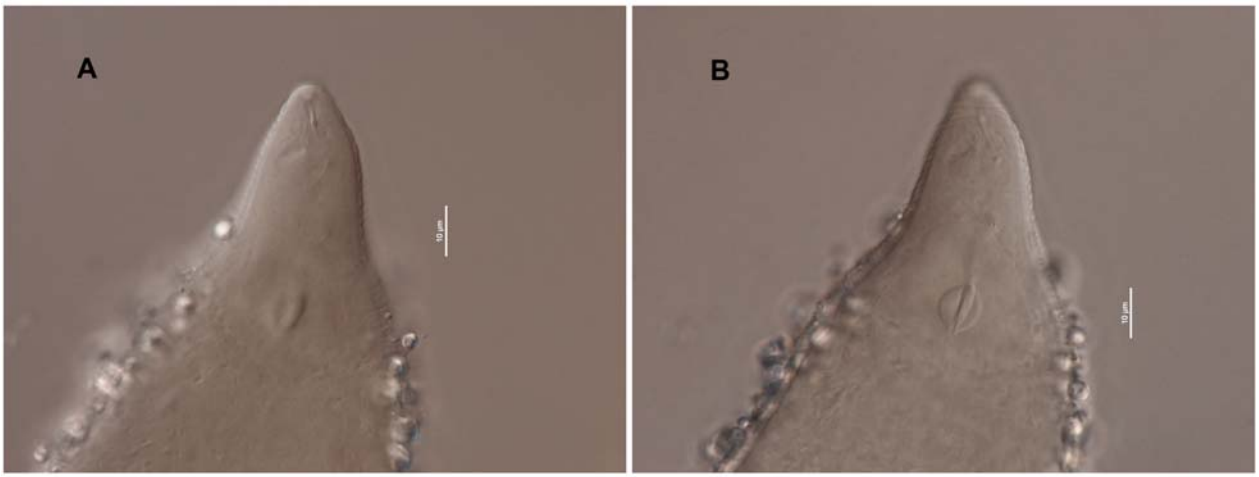


Fig. 36. Micrographs of mature female of *Meloidogyne naasi* isolated from New Zealand. A, B: Anterior end at different focal planes, showing stylet and metacorpus.

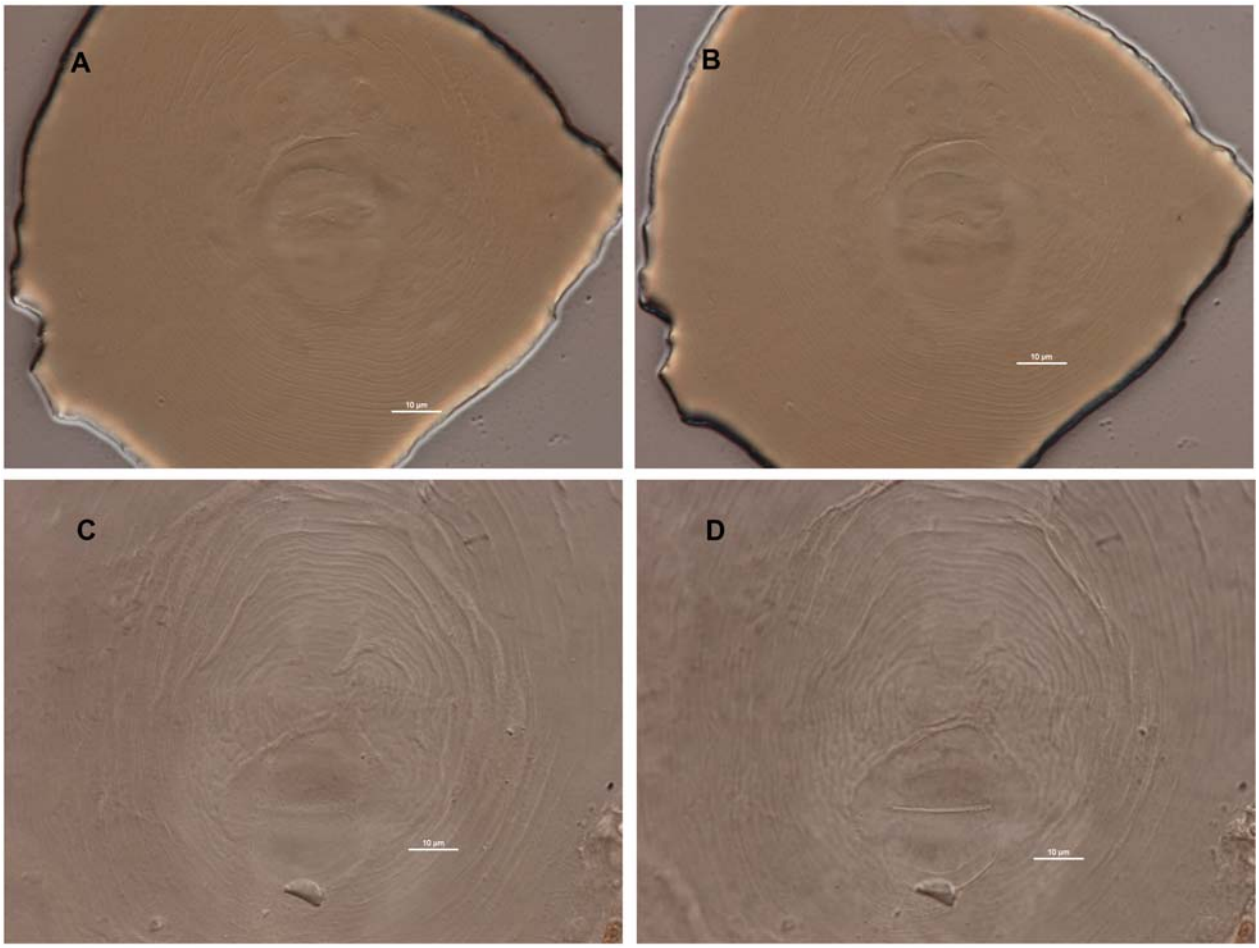


Fig. 37. Micrographs of perineal patterns from mature females of *Meloidogyne naasi.*

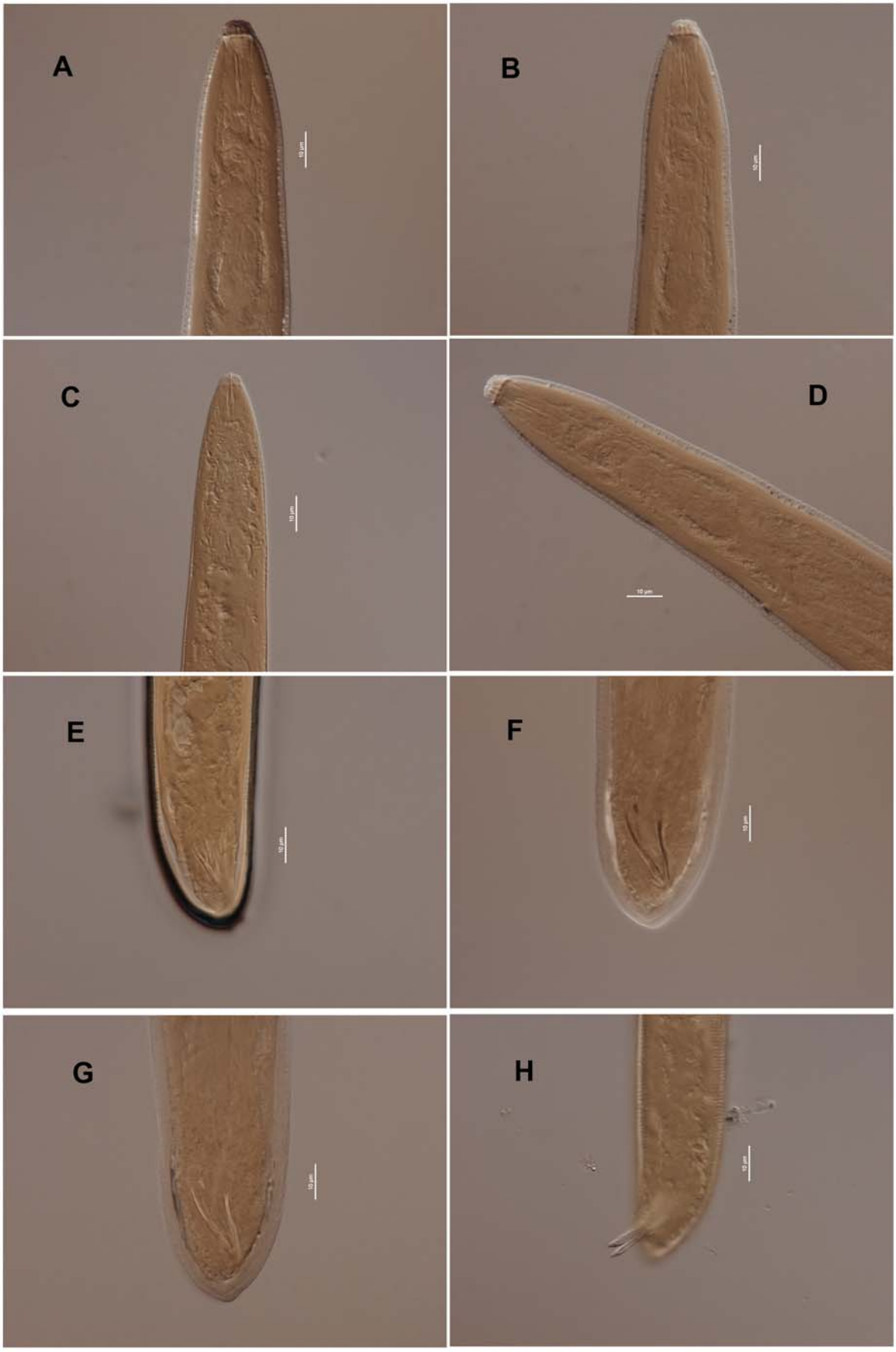


Fig. 38. Micrographs of males of *Meloidogyne naasi*. A, B, C, D: Anterior ends, showing stylets and metacorpus; E, F, G, H: Tails at different focal points, showing spicules.

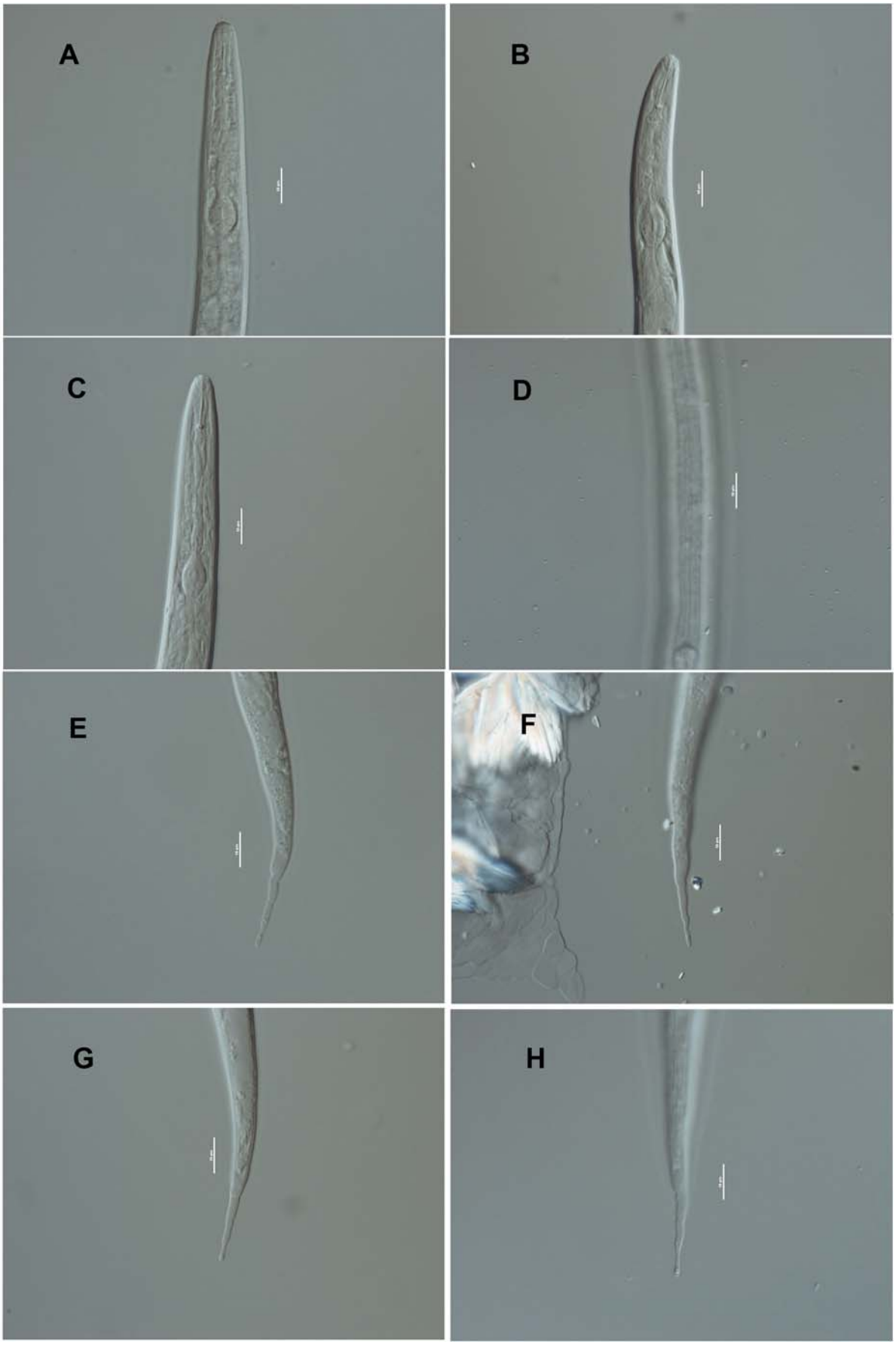


Fig. 39. Micrographs of second stage juveniles of *Meloidogyne naasi*. A, B, C: Anterior ends, showing stylet and metacorpus; D: Lateral lines; E, F, G, H: Tails, showing hyaline regions.

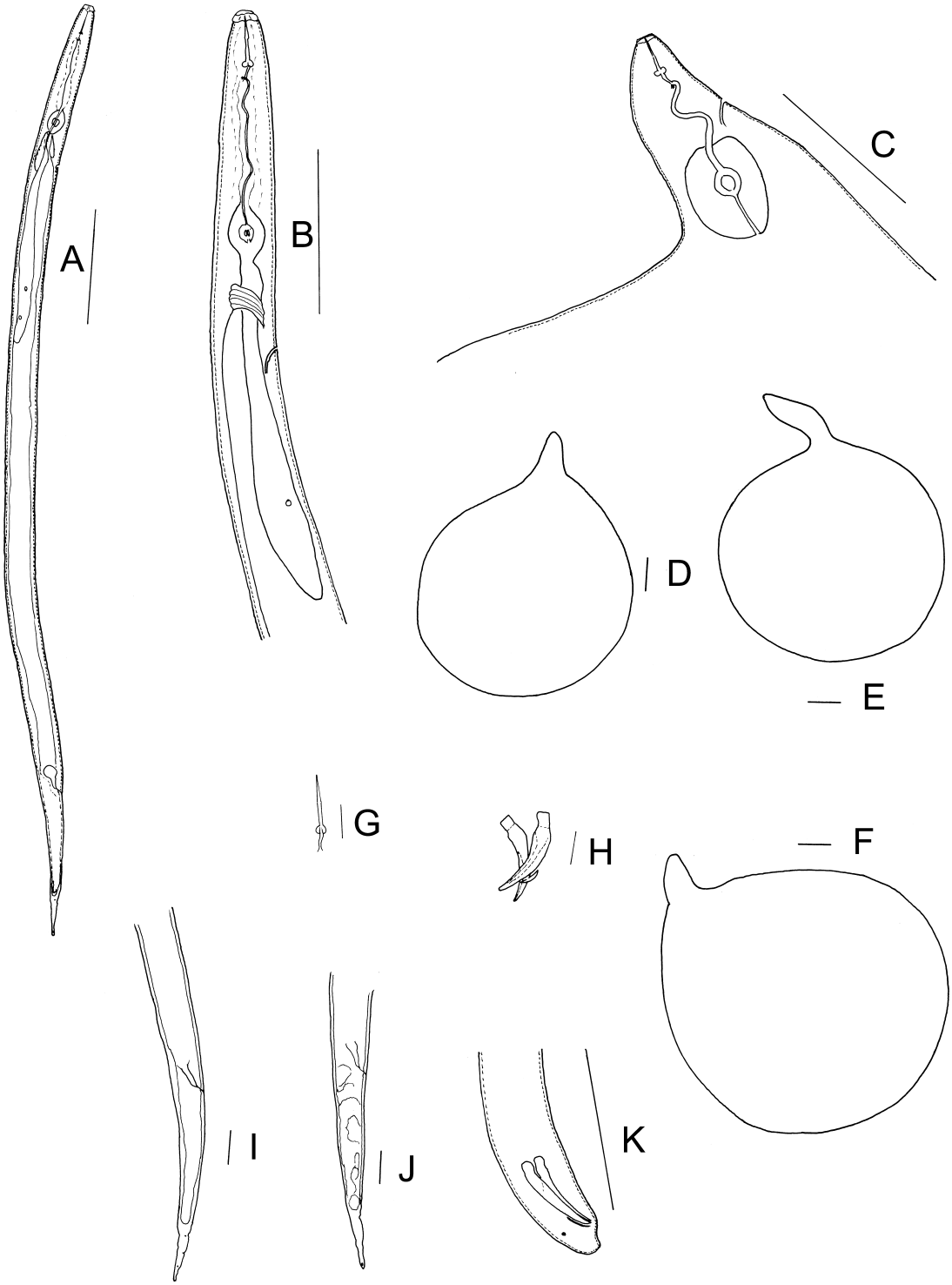


Fig. 40. Line drawings of *Meloidogyne trifoliophila* mature females, males and second stage juveniles isolated from New Zealand. A: Second stage juvenile; B: Anterior end of male; C: Anterior end of mature female; D, E, F: Outline of bodies of mature females; G: Stylet of male; H: Spicules and gubernaculum; I, J: Tails of second stage juveniles; K: Lateral view of male tail showing spicules, gubernaculum and phasmid. Scale bars: A–C: 50 µm; D–F: 25 µm; G–J: 10 µm; K: 50 µm.

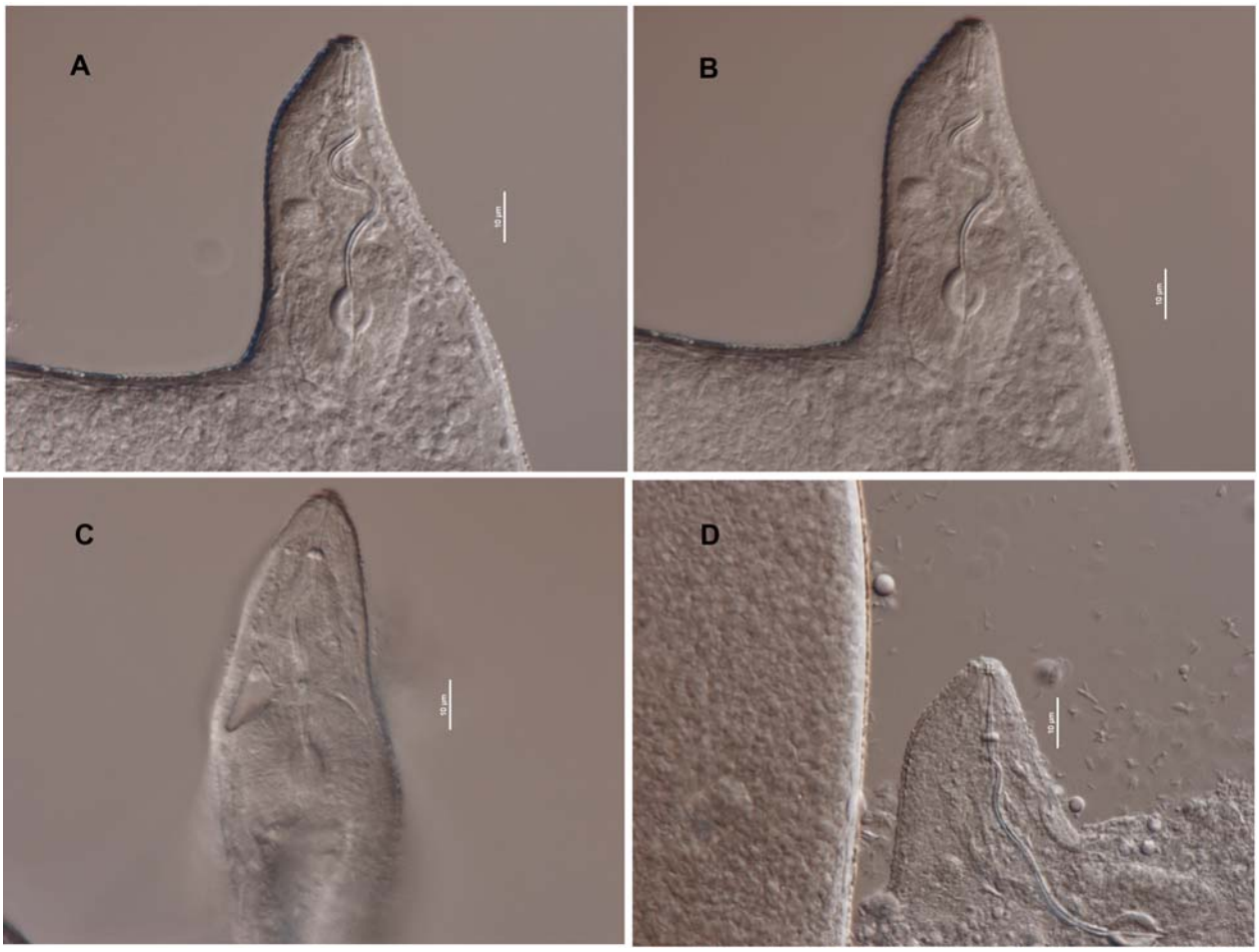


Fig. 41. Micrographs of mature females of *Meloidogyne trifoliophila* isolated from New Zealand. A, B: Anterior end at different focal planes, showing stylet and metacorpus; C: Stylet; D: Lateral lips and stylet. Scale bars: A–D: 10 µm.

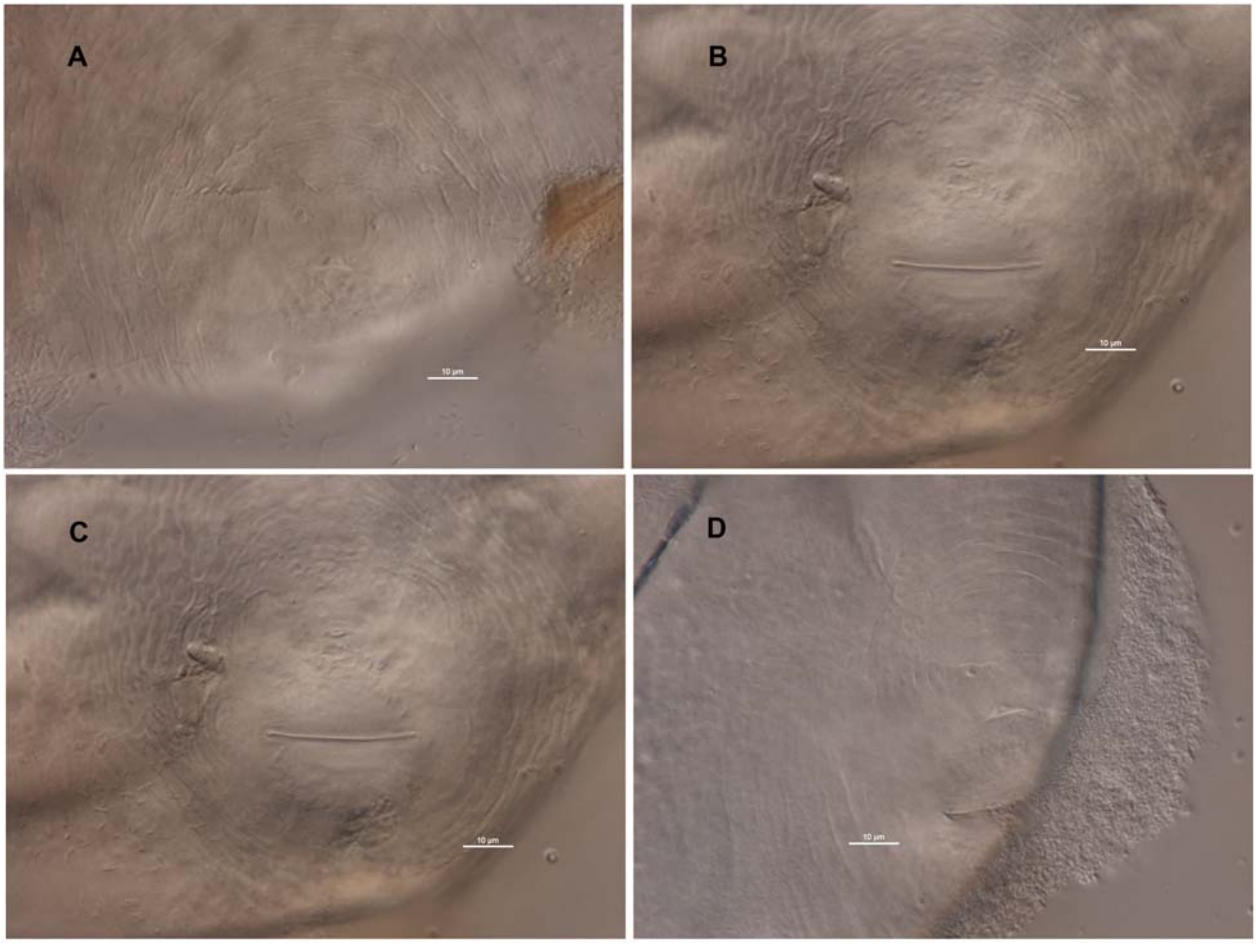


Fig. 42. Micrographs of perineal patterns from mature females of *Meloidogyne trifoliophila*.

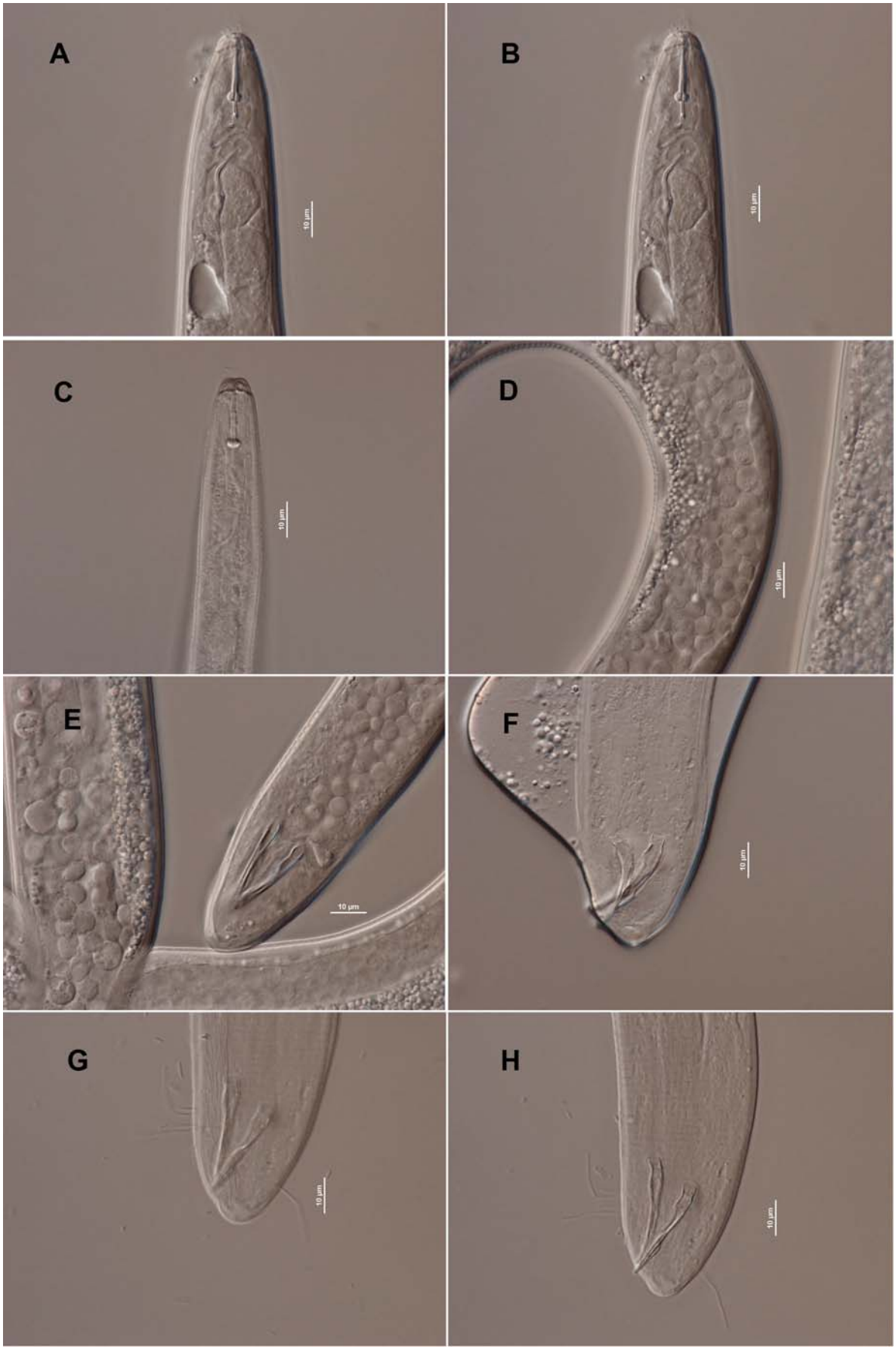


Fig. 43. Micrographs of males of *Meloidogyne trifoliophila.* A, B, C: Anterior ends showing stylet, metacorpus and head capsule; D: Spermatozoa; E, F, G, H: Lateral views of tails, showing spicules and gubernaculum.

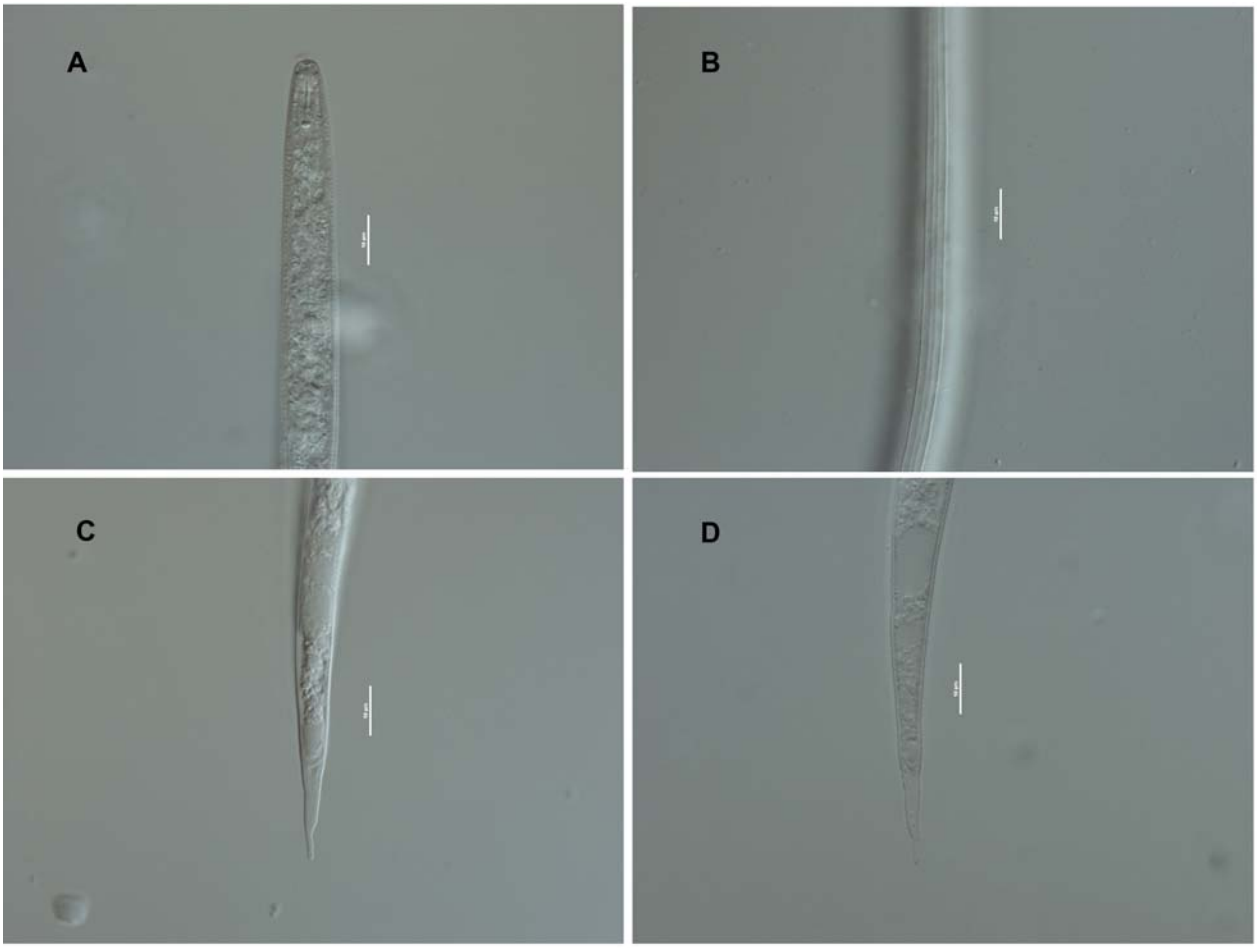


Fig. 44. Micrographs of second stage juveniles of *Meloidogyne trifoliophila.* A: Anterior end showing head cap and stylet; B: Lateral lines; C, D: Tail, showing hyaline region and digitate tip.

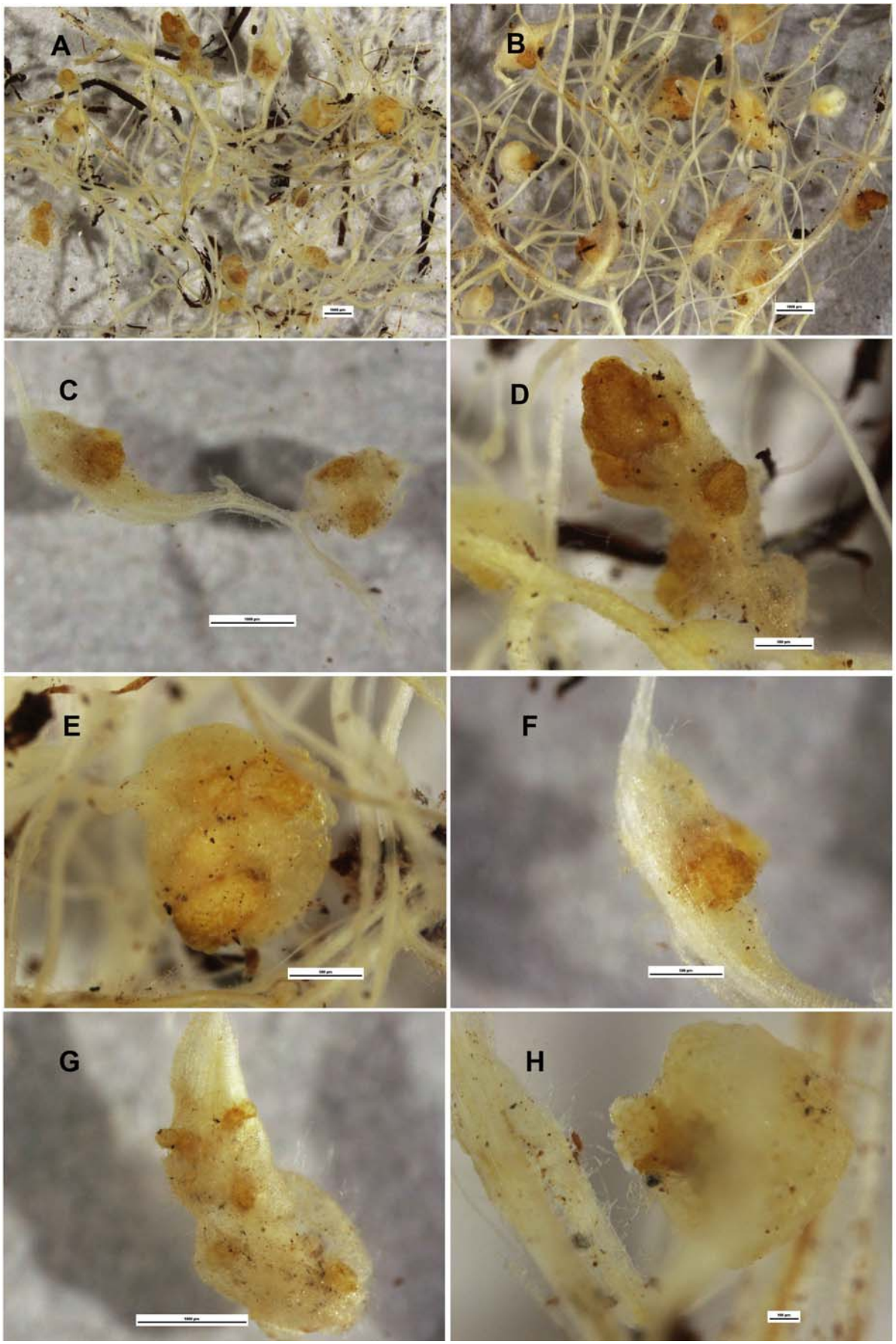
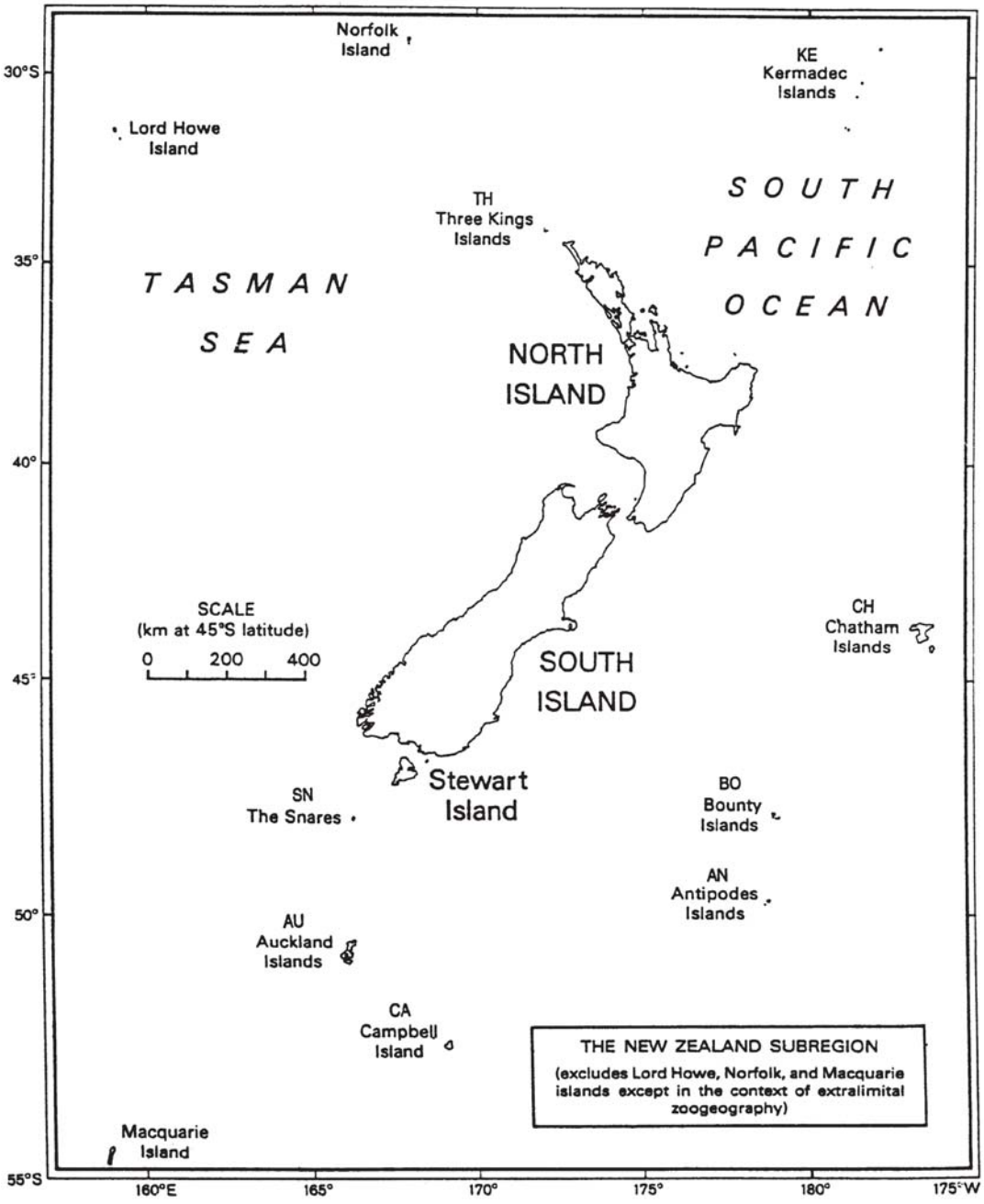
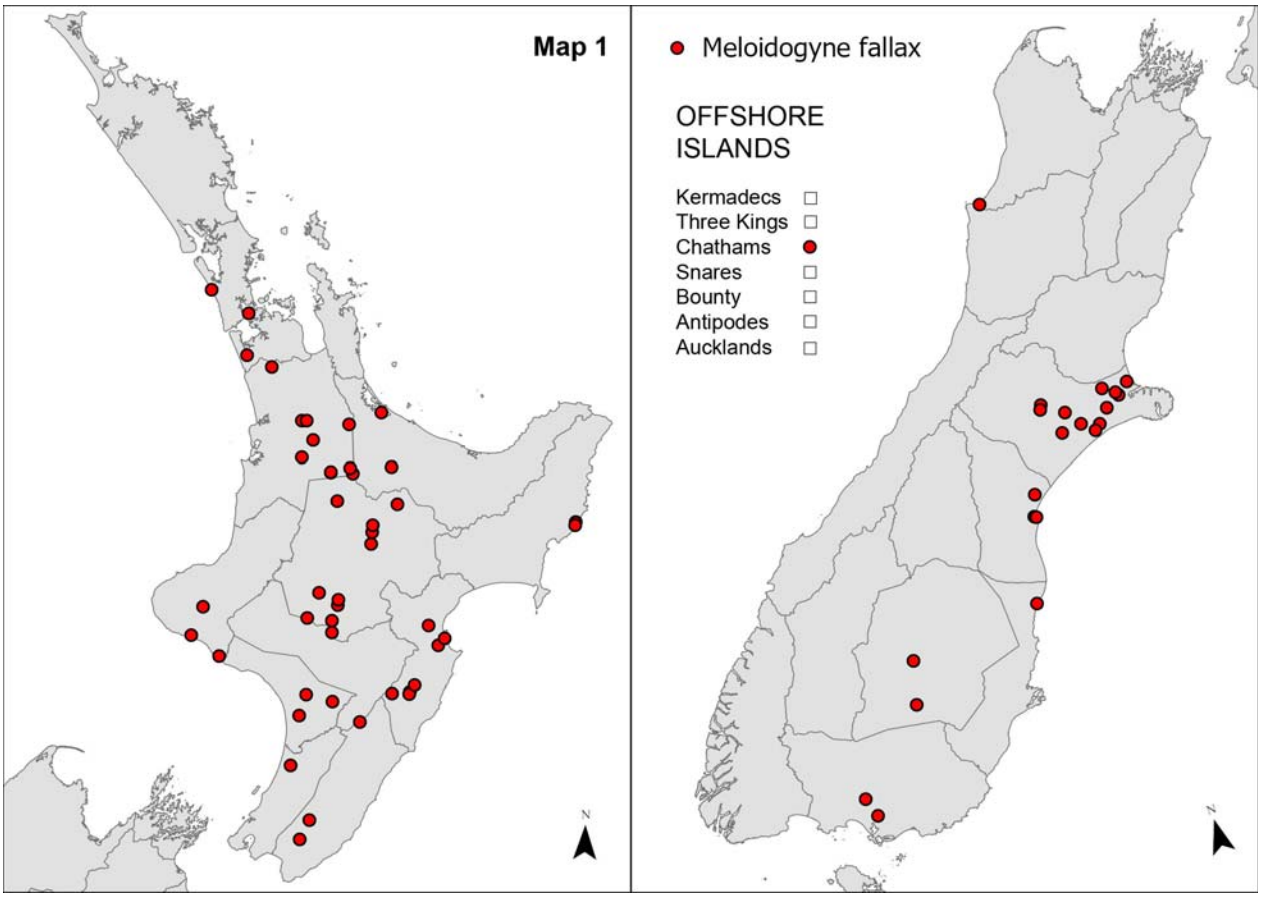
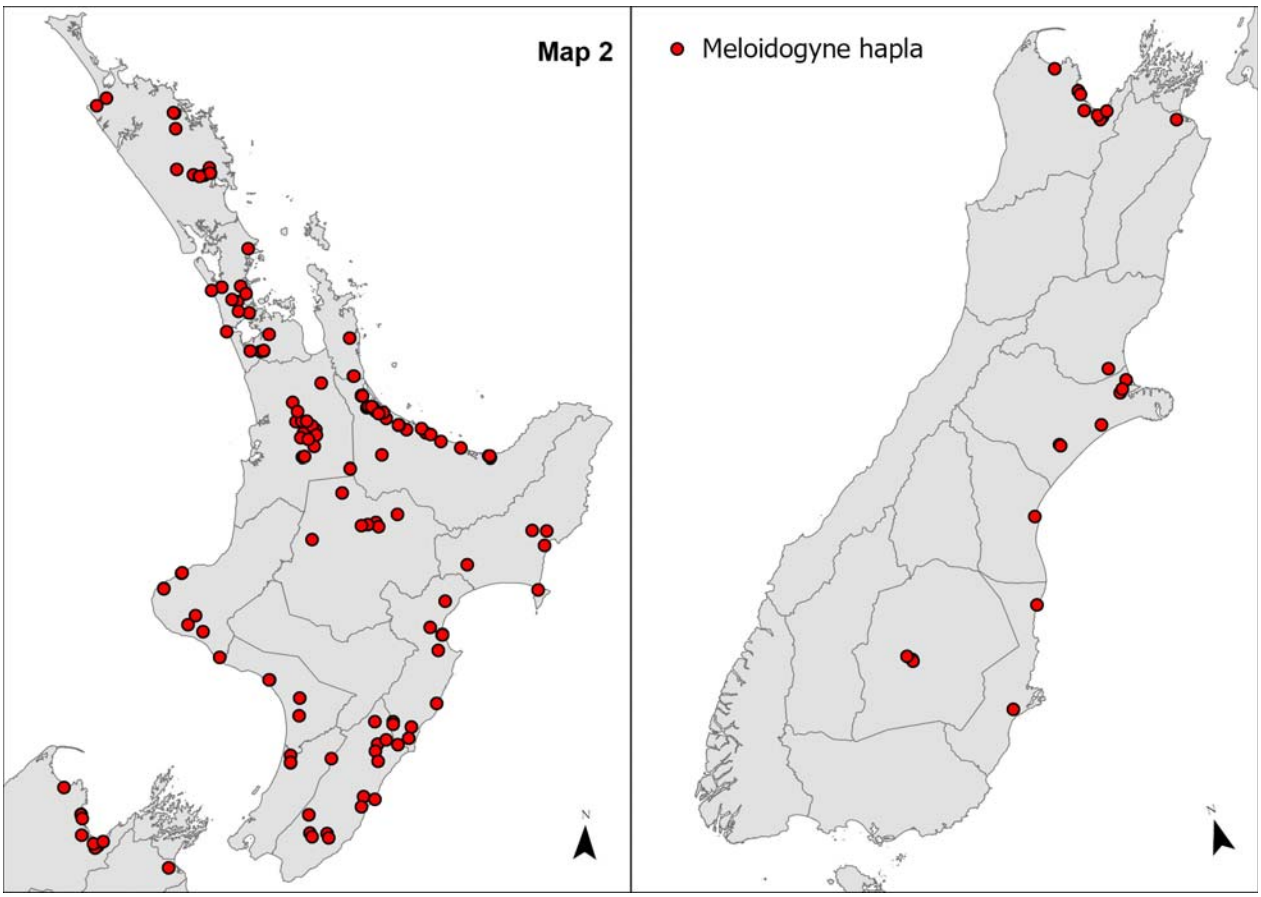
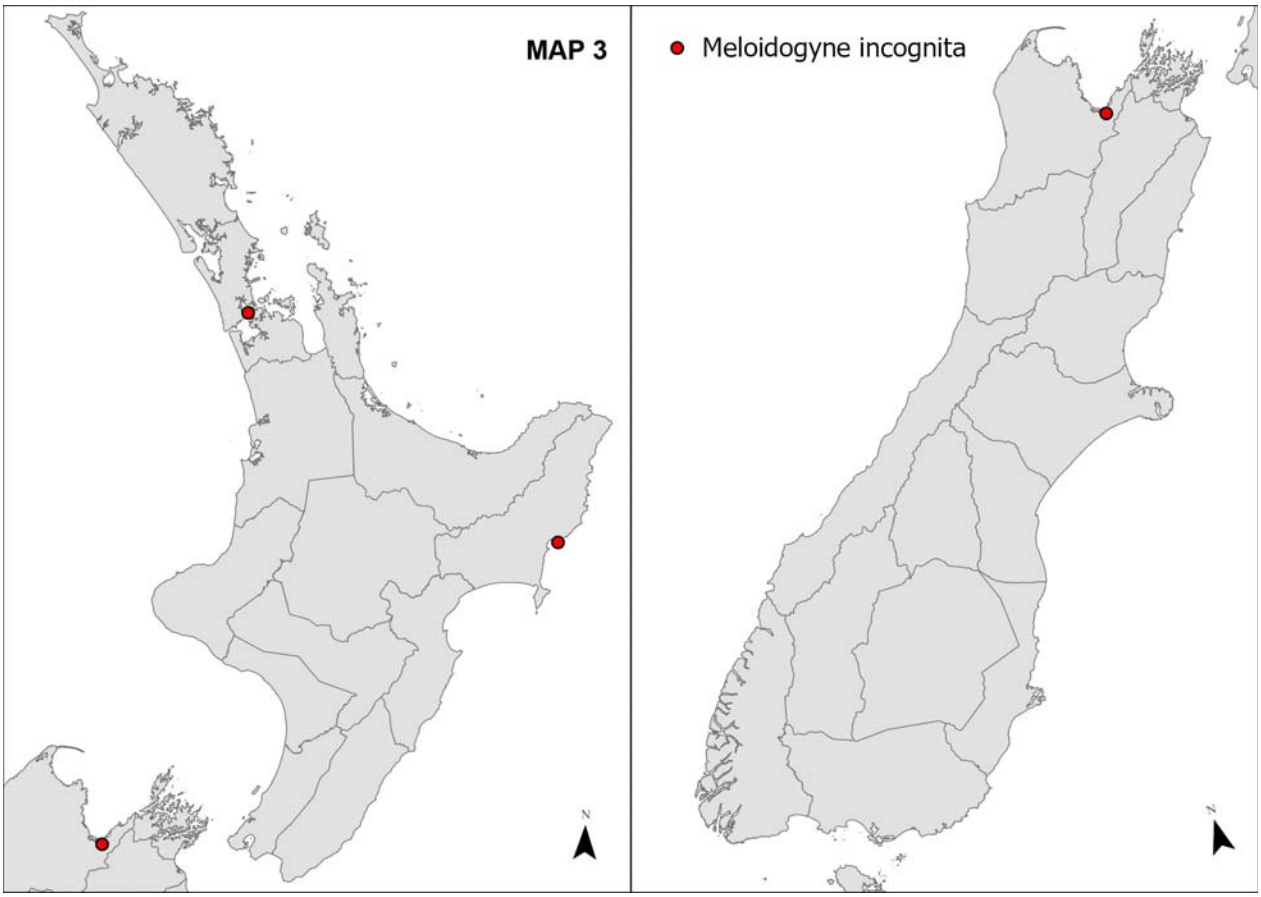


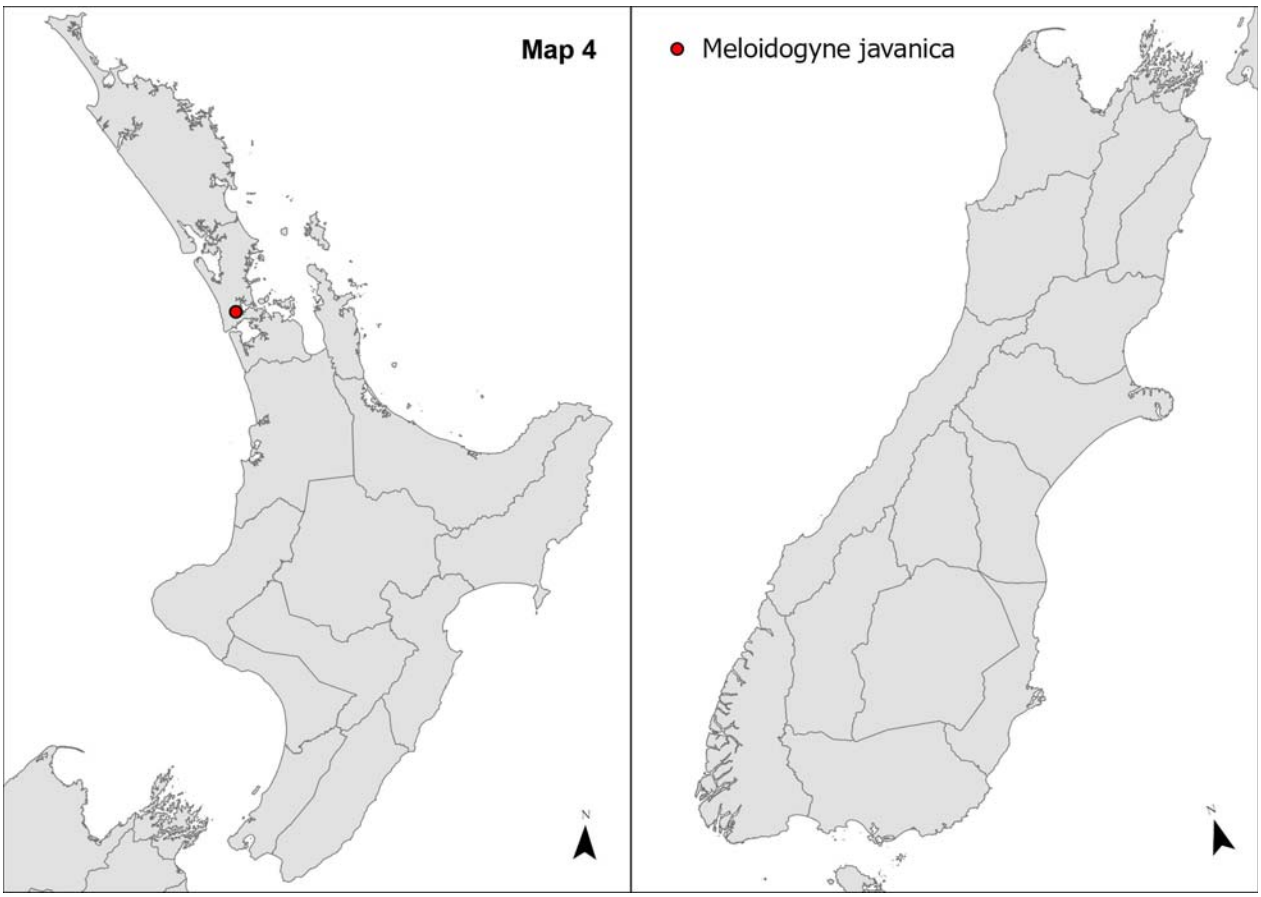
Fig. 45. Micrographs of galling induced by *Meloidogyne trifoliophila* on white clover roots (*Trifolium repens*). A, B: Roots with galls; C–G: Close-ups of galls and protruding females; H: close-up of egg mass from plant root.

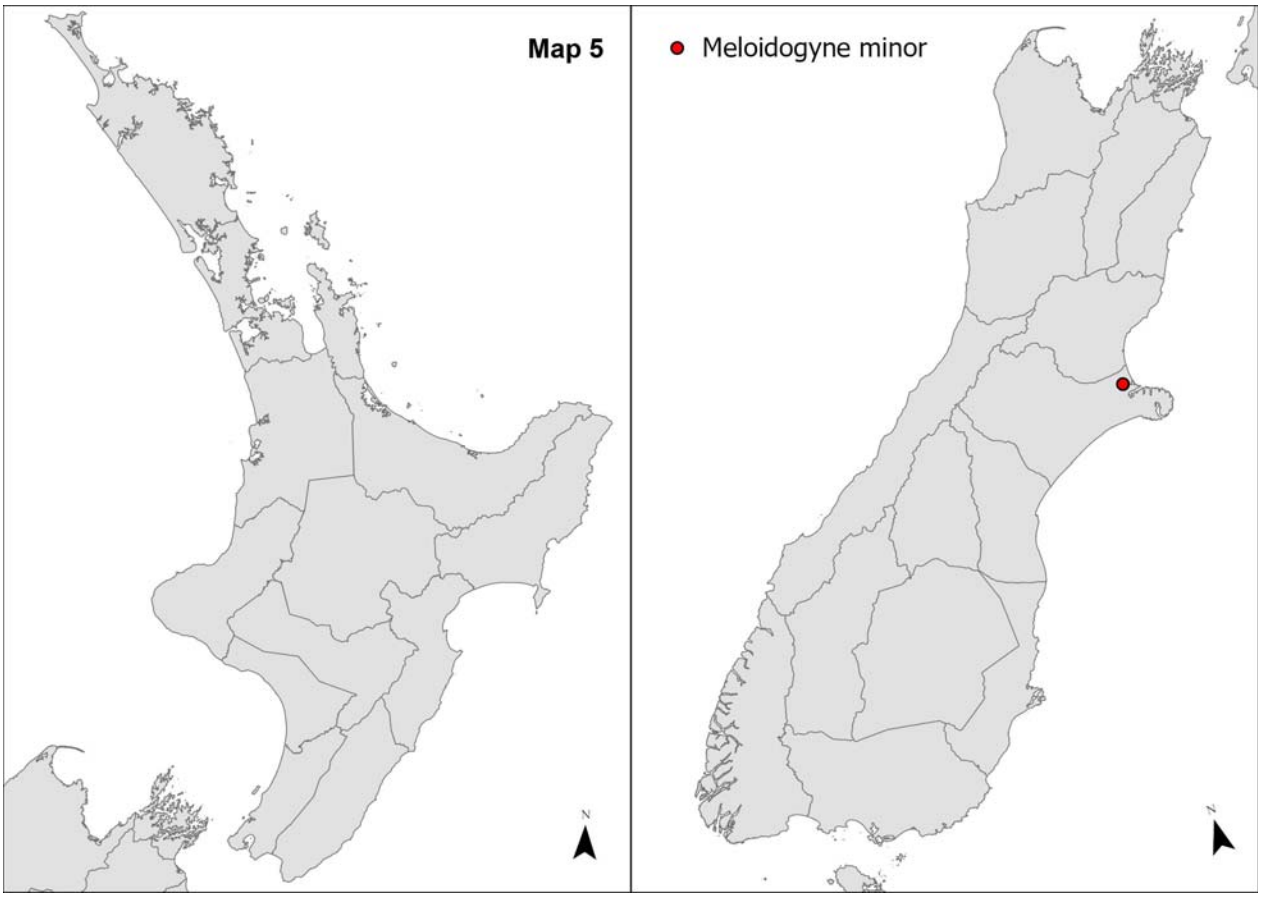

Norfolk Island
KE Kermadec Islands
Lord Howe Island
TH Three Kings Islands
SOUTH PACIFIC OCEAN
TASMAN SEA
NORTH ISLAND
SOUTH ISLAND
Stewart Island
SCALE (km at 45°S latitude)
0 200 400
CH Chatham Islands
SN The Snares
BO Bounty Islands
AN Antipodes Islands
AU Auckland Islands
CA Campbell Island
Macquarie Island
THE NEW ZEALAND SUBREGION
(excludes Lord Howe, Norfolk, and Macquarie islands except in the context of extralimital zoogeography)
30°S
35°
40°
45°
50°
55°S
160°E
165°
170°
175°
180°
175°W

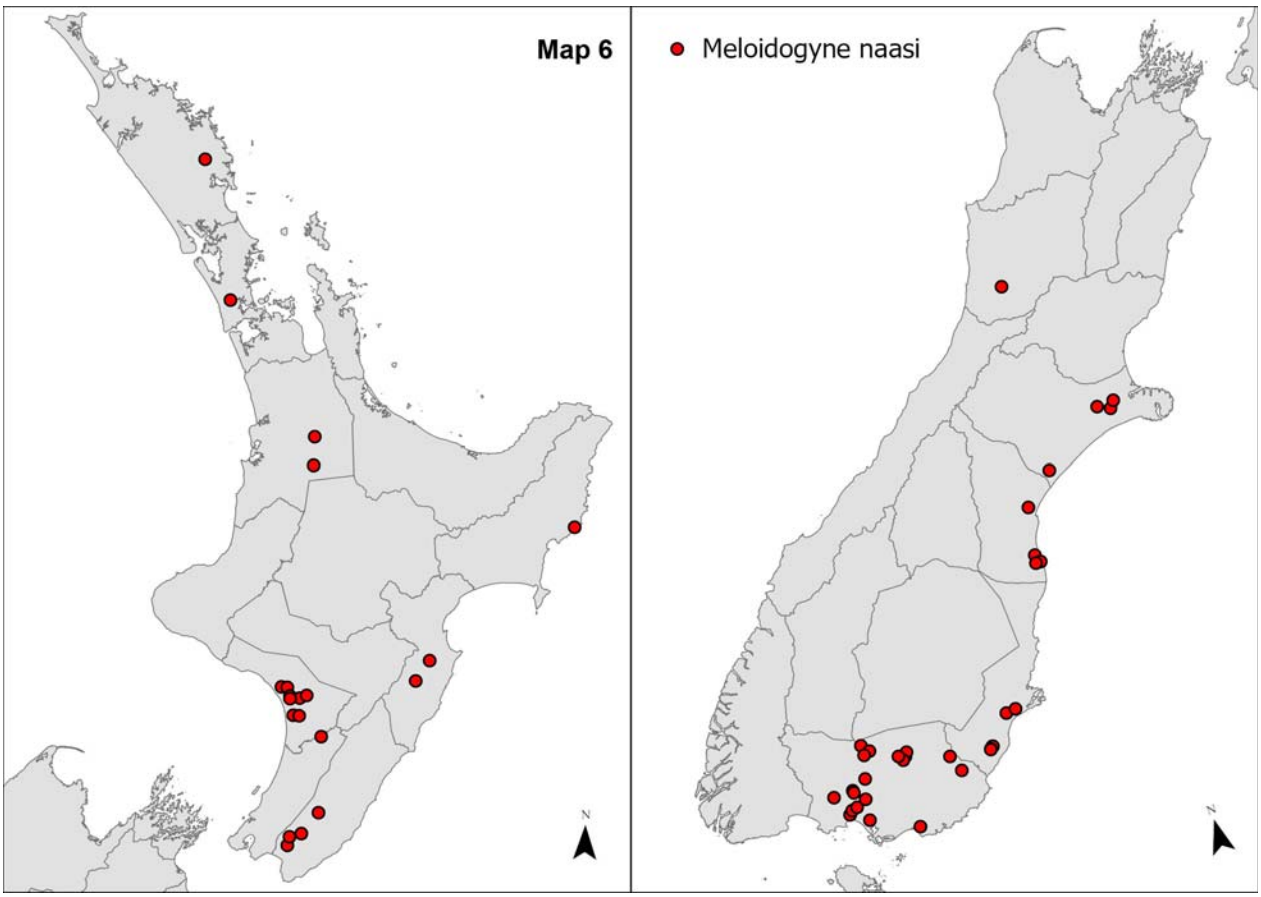

Map 1
Meloidogyne fallax
OFFSHORE ISLANDS
Kermadecs
Three Kings
Chathams
Snares
Bounty
Antipodes
Aucklands

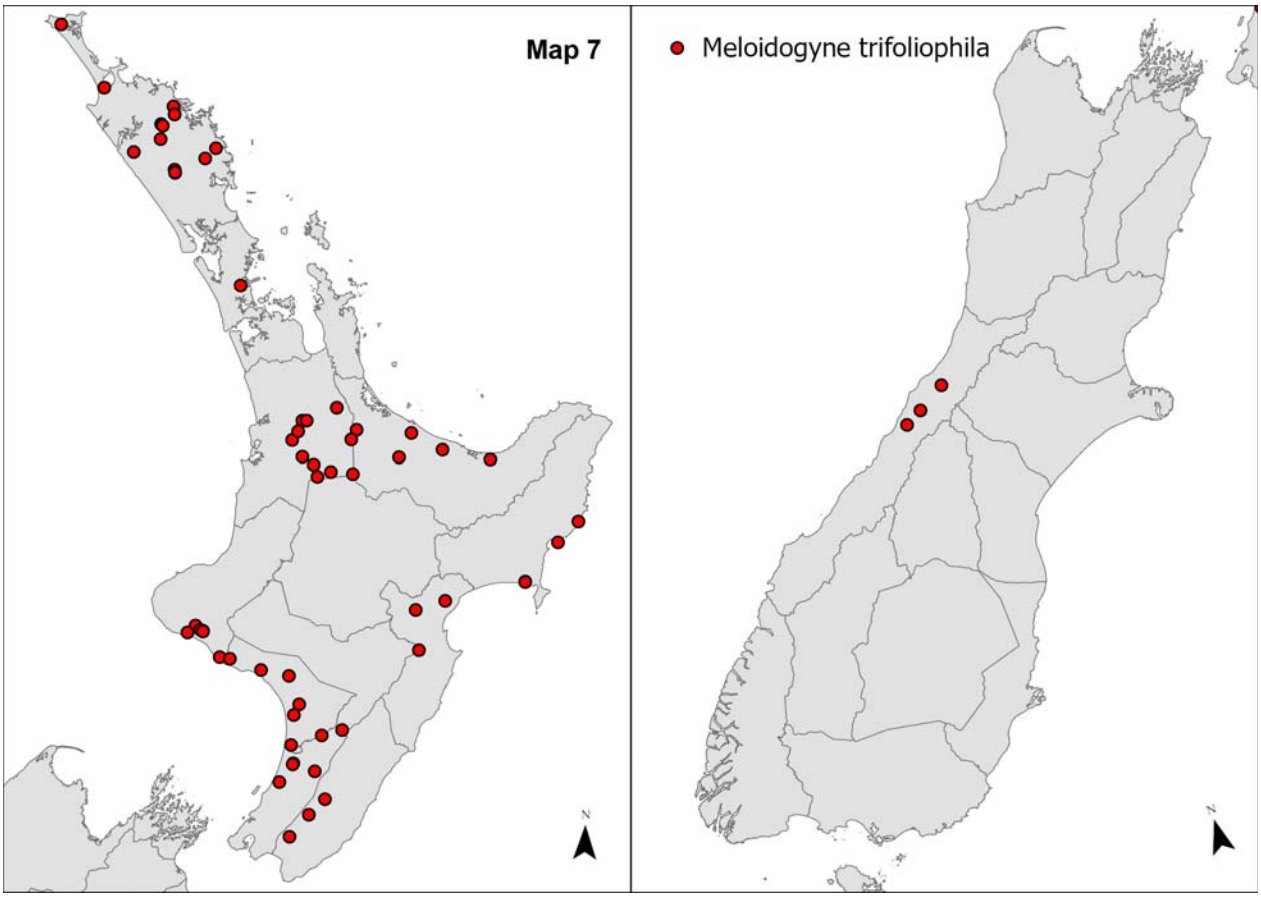

Map 2
Meloidogyne hapla


MAP 3
Meloidogyne incognita
N
N


Map 4
Meloidogyne javanica
N
N


Map 5
Meloidogyne minor
N
N


Map 6
Meloidogyne naasi
N
N


Map 7
Meloidogyne trifoliophila
N
N

TAXONOMIC INDEX

This index covers the nominal taxa mentioned in the text, regardless of their current status in taxonomy. Taxa in **bold** type are those included in the checklist. Page number in **bold** type denotes the start of a description, and in **italic** type a figure.

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He titiro whāiti tā tēnei pukapuka ki ngā mea noho whenua, kāore he tuarā; i pēnei ai i te mea kei te mōhio whānuitia ngā mea whai tuarā, ā, ko ngā mea noho moana, koirā te tino kaupapa o te huinga pukapuka *NIWA Biodiversity Memoirs.*

Ka āhei te tangata ki te **whakauru tuhituhinga** mehemea kei a ia ngā tohungatanga me ngā rauemi e tutuki pai ai tana mahi. Heoi anō, e wātea ana te Kohinga Angawaho o Aotearoa hei āta tirotiro mā te tangata mehemea he āwhina kei reira.

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