Australasian Plant Pathology (2026) 55:20
https://doi.org/10.1007/s13313-026-01108-y

ORIGINAL RESEARCH ARTICLE

Two unknown species of Mermithidae (Nematoda) parasitising fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in Australia

Daniel C. Huston[1] · **Cüneyt Caglar**[1] · **Sarah Bonney**[2] · **Samantha J. Bond**[2] · **Wathsala Ratnayake**[2] · **Brian Thistleton**[2] · **Frezzel Praise J. Tadle**[3] · **Siva Subramaniam**[3] · **Mike Hodda**[1]

Received: 29 April 2025 / Accepted: 14 October 2025

Abstract

Fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae) is an invasive and important pest of multiple crops including grains and vegetables. The moth was first detected in Australia in 2020 and has since established populations across the north of the continent with further spread expected. Surveys for parasites and pathogens impacting Australian fall armyworm populations were undertaken between 2020 and 2025. Here, we report on two distinct genetic lineages of parasitic nematode of the family Mermithidae collected from *S. frugiperda* caterpillars during this period. Because the specimens available were post-parasitic juveniles, they could not be reliably identified morphologically beyond the family level. Phylogenetic analyses using two ribosomal (18S, 28S) and one mitochondrial (COI) gene demonstrated the presence of two distinct species-level lineages (one in Queensland and one in the Northern Territory) but they did not resolve the taxonomic position of either. Thus, neither lineage can be reliably assigned to any known genus and are therefore given informal placeholder assignments: Mermithidae sp. FA-QLD and Mermithidae sp. FA-NT. Mermithid nematodes likely represent an important component of natural population regulation for fall armyworm and join a growing list of organisms which have been found parasitising this moth in Australia.

Keywords Mermithida · Parasite · Parasitoid · Biocontrol · Natural enemy · Management

Introduction

The fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) is a seriously damaging pest of grains and other crops such as vegetables, cotton and sugarcane (Montezano et al. 2018). The moth is native to the Americas but since 2016 has spread to over 80 countries, primarily in Africa, Asia and Oceania (Maino et al. 2021; Nguyen et al. 2021; Piggott et al. 2021; Qi et al. 2021; Rane et al. 2023; FAO 2025). Fall armyworm was first detected in Australia in 2020, initially in the Torres Strait and Far North Queensland, and has subsequently spread west to the Northern Territory and Western Australia, and south through Queensland to New South Wales, Victoria and Tasmania (Piggott et al. 2021; Qi et al. 2021; Rane et al. 2023). Fall armyworm has established populations across northern Australia and some more southernly locations and, as eradication is not considered feasible, further spread throughout the continent appears inevitable (Qi et al. 2021). This species thus represents a serious threat to multiple Australian agricultural industries and requires management.

Control of fall armyworm relies primarily on synthetic insecticides and genetically modified crops containing toxins derived from the soil bacterium *Bacillus thuringiensis* (Montezano et al. 2018). However, various populations of fall armyworm exhibit resistance to insecticides and *B.*

✉ Daniel C. Huston
Daniel.Huston@csiro.au

[1] Australian National Insect Collection, National Research Collections Australia, CSIRO, PO Box 1700, Canberra, ACT 2601, Australia

[2] Department of Agriculture and Fisheries, Northern Territory Government, Plant Health Laboratories, Berrimah Farm Science Precinct. GPO, Box 3000, Darwin, NT 0801, Australia

[3] Department of Agriculture and Fisheries (QDAF), Queensland, Brisbane, Australia

thuringiensis toxins (Togola et al. 2018; Sisay et al. 2019) and such resistance has already been detected in Australian fall armyworm (Bird et al. 2022; Tay et al. 2022). Because of the negative impacts of pesticides on environmental health and an increasingly restrictive regulatory landscape, there is a critical need for the development of new and integrative management strategies for pests such as fall armyworm. Parasitic organisms as biocontrol agents are likely to represent an important component of such future strategies.

Numerous parasites and pathogens have been reported from fall armyworm in its native range in the Americas, including viruses, fungi, wasps, flies and nematodes (e.g., Ashley 1979; Ashley et al. 1982; Hamm et al. 1986; Molina-Ochoa et al. 2003). Escape from the Americas has not, however, resulted in fall armyworm escaping parasites and disease. Viruses, fungi, wasps, flies and nematodes have already been reported parasitising fall armyworm across its invasive range (Sisay et al. 2019; Firake and Behere 2020; Koffi et al. 2020; Sun et al. 2020; Otim et al. 2021; Fagan-Jeffries et al. 2024). In Australia, the entomopathogenic fungi *Metarhizium rileyi* has been observed parasitising fall armyworm in the field (AusVeg 2020). Twelve species of parasitoid wasps have also been formally reported from fall armyworm in Australia, five of which were considered new to science (Fagan-Jeffries et al. 2024). Furthermore, Fagan-Jeffries et al. (2024) noted that several parasitoid flies had been collected, although they have not yet been further reported on. Additional parasites and pathogens of fall armyworm in Australia also await reporting.

Members of the nematode family Mermithidae have been reported parasitising fall armyworm outside of its native range, including in Africa (Ahissou et al. 2021), India (Firake and Behere 2020) and China (Sun et al. 2020). The life cycles of mermithids comprise both free-living and parasitic stages (Petersen 1985; Kaiser 1991). In terrestrial species, adults dwell in the soil where they mate, and females produce eggs. Depending on species, females may either release eggs into the soil or migrate to the surface and lay eggs on vegetation (e.g., Kaburaki and Imamura 1932; Christie 1936; Baker 1983). In the former life-cycle strategy infective juveniles hatch from the eggs, search for and infect, suitable hosts. In the latter strategy, the host becomes infected by consuming the eggs. Developmental time for the parasitic juveniles varies between species, ranging from one to 12 weeks (Hagmeier 1912; Cobb 1926; Christie 1936, 1937; Poinar and Gyrisco 1962; Cuthbert 1968). After completing development, the post-parasitic juvenile ruptures a hole in the host cuticle through mechanical pressure; this process almost always kills the host (Petersen 1985). After emergence, post-parasitic juveniles migrate into the soil, where they moult and mature into adults. The broad host specificity of many mermithid species (Nickle 1972; Petersen 1985; Kaiser 1991) has clearly facilitated parasitism of fall armyworm across its invasive range. Here, we report on the first collections of mermithid nematodes from Australian fall armyworm populations.

Methods

Fall armyworm caterpillars were collected between 2020 and 2025 from crops (e.g., sweet corn, sorghum, capsicum) and weeds in commercial operations and experimental field plots in the tropical north of Australia: Queensland (Bowen and Burdekin regions) and the Northern Territory (Darwin and Katherine regions). Collections occurred primarily during the wet season (November-April). Caterpillars were collected alive and transported to the laboratory where they were maintained in individual containers at 25–28 °C and 60–80% relative humidity until they matured to adult moths or parasites were detected. Density of fall armyworm was not estimated in the field so no data on infection prevalence is available. Emerged nematodes (Fig. 1) were preserved in 80–100% ethanol. Nematodes were preliminarily identified as post-parasitic stages of nematodes in the family Mermithidae based on general morphological characteristics of the family: highly elongate and slender macroscopic body with excessive coiling and a piercing stylet in the stoma (Nickle 1972). Because post-parasitic juvenile mermithids have few taxonomic characters and cannot usually be identified to species (Nickle 1972; Kaiser 1991), no further morphological studies were undertaken.

Genomic DNA was extracted from specimens using DNeasy Blood and Tissue kits (Qiagen®) following the manufacturer's instructions. Three molecular markers were targeted: the mitochondrial cytochrome c oxidase I (COI) gene region, the small subunit ribosomal RNA (18S rRNA), and the large subunit ribosomal RNA (28S rRNA). These markers were chosen as they are the most commonly employed barcodes for the identification of nematodes. The COI region was amplified using the forward primer JB3 (5′-TTT TTT GGG CAT CCT GAG GTT TAT-3′) (Bowles et al. 1992) and reverse JB5 (5′-AGC ACC TAA ACT TAA AAC ATA ATG AAA ATG-3′) (Derycke et al. 2005). The 18S region was amplified in two fragments, with the first fragment using the forward primer G18S4 (5′-GCT TGT CTC AAA GAT TAA GCC-3′) (Blaxter et al. 1998) and reverse R18Ty11 (5′-GGT CCA AGA ATT TCA CCT CTC-3′) (Chizhov et al. 2006) and the second fragment using the forward primer F18Ty12 (5′-CAG CCG CGG TAA TTC CAG C-3′) (Chizhov et al. 2006) and reverse R18Ty12 (5′-CGG TGT GTA CAA AGG GCA GG-3′) (Chizhov et al. 2006). The 28S region was amplified using the forward primer D2A (5′-ACA AGT ACC GTG AGG GAA AGT TG-3′) and

Fig. 1 Mermithid nematodes (Mermithidae sp. FA-NT) emerging from a fall armyworm (*Spodoptera frugiperda*) caterpillar. Specimens collected near Darwin, Northern Territory, Australia. Photograph credit: Wathsala Ratnayake, NT DITT. Scale bar = 1 mm

reverse primer D2B (5′-TCG GAA GGA ACC AGC TAC TA′) (Nunn 1992). PCR and clean-up followed Huston et al. (2023) and was the same for all three gene regions. PCR products were sent to the Biomolecular Resource Facility, Australian National University, Canberra, for Sanger sequencing and sequenced using the amplification primers. Resultant reads were assembled and edited using Geneious Prime® v2025.0.3 (Biomatters).

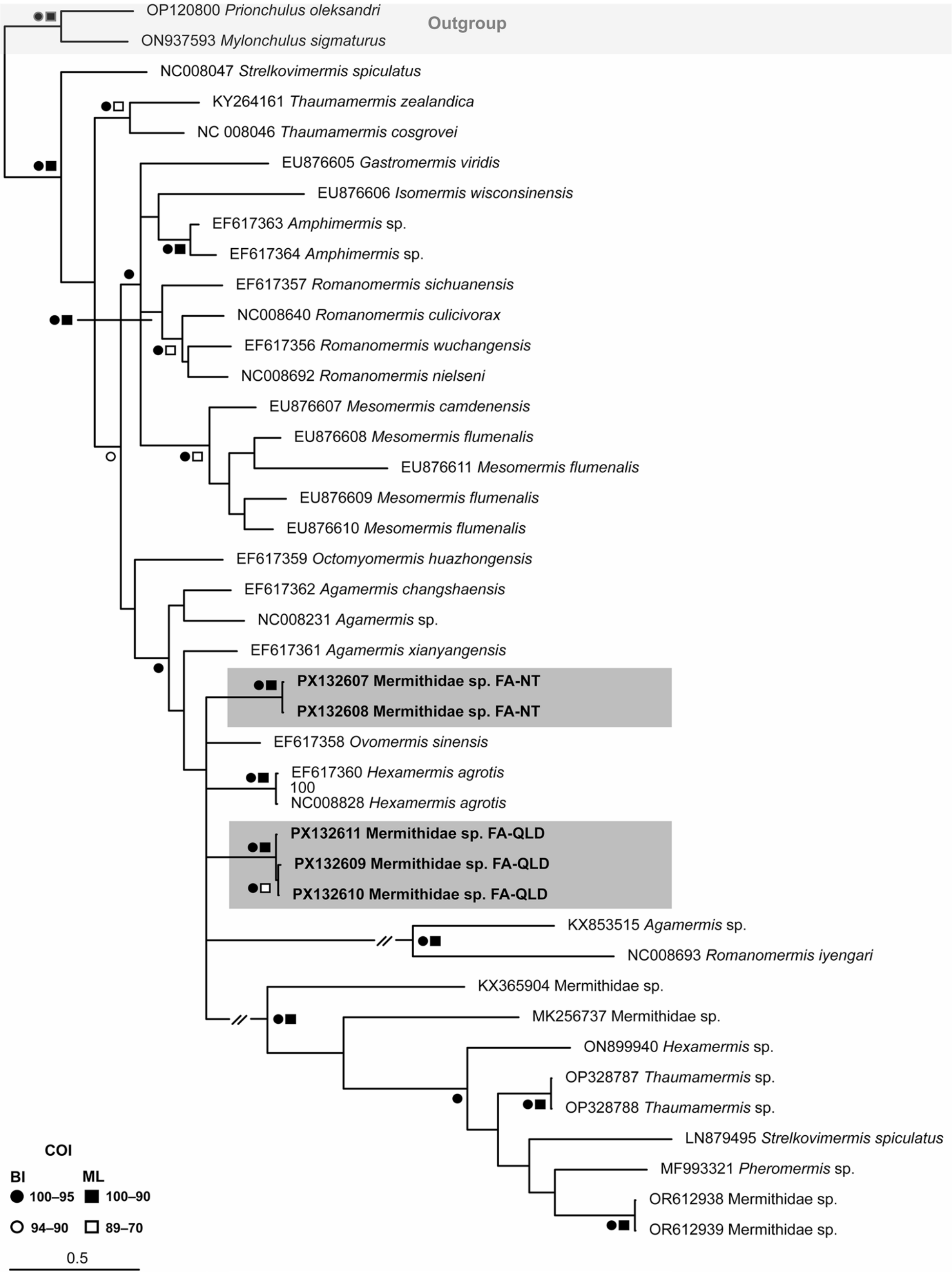
Newly generated sequences were first confirmed as representing species of the Mermithidae through comparison against the NCBI GenBank database via BLAST (Altschul et al. 1990). Intraspecific variation among newly generated sequences was evaluated through alignment using MUSCLE (Edgar 2004) as implemented in MEGA11 (Tamura et al. 2021). Newly generated sequences representing all unique variants detected for each gene region were aligned with those of other members of the Mermithidae using MUSCLE and MEGA11 as above. Best-fit nucleotide substitution models for phylogenetic analyses were evaluated for the COI, 18S and 28S datasets using MEGA11 and the GTR + G substitution model was selected for all three. Phylogenetic analyses were performed on XSEDE (Towns et al. 2014) accessed through the CIPRES portal (Miller et al. 2010), using sequences of two species of the Mononchida as outgroup taxa. Majority-rule consensus trees were constructed using Bayesian inference (BI) and maximum likelihood (ML) analyses. Bayesian inference was performed using MrBayes v3.2.6 (Ronquist et al. 2012) with default priors and four chains sampled every 1,000 of 10,000,000 generations; the first 2,500 samples were discarded as burn-in. Maximum likelihood analyses were performed using RAxML (Stamatakis 2014) with 1,000 bootstrap pseudoreplicates. Combined BI/ML trees were edited and annotated in Adobe Illustrator CS6.

Results

Small numbers of mermithid nematodes were collected from fall armyworm in each year between 2020 and 2025. We generated molecular sequence data for each of the three targeted gene regions for three individual mermithids from Queensland and four individual mermithids from the Northern Territory. Comparison of sequences from Queensland and the Northern Territory indicated the presence of two distinct mermithid species-level lineages, one present at each locality. These species are hereafter referred to as Mermithidae sp. FA-QLD and Mermithidae sp. FA-NT. No intraspecific variation was detected in the 18S and 28S sequence data for either species. COI sequences of Mermithidae sp. FA-QLD differed from one another by 2–4 bp (< 1%); those of Mermithidae sp. FA-NT differed from one another by 0–1 bp (< 1%). Mermithidae sp. FA-QLD differed from Mermithidae sp. FA-NT by 84–89 bp (22–23%), 26–27 bp (2%), and 90–91 bp (12–13%) in the COI, 18S and 28S gene regions, respectively. Representative sequences are deposited on GenBank under the accession numbers PX132607-PX132611 (COI); PX132969, PX132970 (18S); PX132971, PX132972 (28S).

Most nodes were poorly resolved across all phylogenetic analyses, with abundant polytomies and repeated instances of non-monophyly for multiple genera. Overall, analyses did not permit placement of either Mermithidae sp. FA-QLD or Mermithidae sp. FA-NT into a named genus. Tree topologies derived from BI and ML analyses of the COI dataset (Fig. 2) were largely congruent. Sequences of Mermithidae sp. FA-QLD and Mermithidae sp. FA-NT resolved in a large clade comprised of species of *Agamermis*, *Hexamermis*, *Ovomermis sinensis*, *Thaumamermis* sp., *Pheromermis* sp., *Romanomermis iyengari*, *Strelkovimermis spiculatus* and several unidentified mermithids with strong support in BI.

Fig. 2 Bayesian majority-rule consensus tree of the COI dataset. Bayesian inference (BI) posterior probabilities (pp) for nodes represented by circles, maximum likelihood (ML) bootstrap support (bs) represented by squares. Support values less than 0.90 (pp) and 70 (bs) not shown. The scale-bar indicates the expected number of substitutions per site. GenBank accession number presented before taxa name. Taxa sequenced in the present study are presented in bold and highlighted



However, this clade formed an eight-way polytomy and the relationships between Mermithidae sp. FA-QLD, Mermithidae sp. FA-NT and other mermithids in the group were unclear. BI and ML analyses of the 18S dataset (Fig. 3) also produced generally congruent topologies, but the positions of Mermithidae sp. FA-QLD and Mermithidae sp. FA-NT were not resolved. These two species once again clustered with species of *Agamermis* and *Hexamermis*, but with no support. Notably, the sequences of the QLD and NT species were not resolved in the supported clade which included sequences of *Ovomermis sinensis*, a known mermithid parasite of fall armyworm (Sun et al. 2020). Results of BI and ML analyses of the 28S dataset were generally similar to analyses of the COI and 18S datasets; the QLD and NT species resolved in a clade comprised largely of species of *Agamermis* and *Hexamermis*, but with no clear relationship with any of these taxa (Fig. 4).

Discussion

Because postparasitic larvae of mermithiids have very few morphological characters useful for identification (Nickle 1972; Kaiser 1991) and our phylogenetic analyses provide

Fig. 3 Bayesian majority-rule consensus tree of the 18S dataset. Bayesian inference (BI) posterior probabilities (pp) for nodes represented by circles, maximum likelihood (ML) bootstrap support (bs) represented by squares. Support values less than 0.90 (pp) and 70 (bs) not shown. The scale-bar indicates the expected number of substitutions per site. GenBank accession number presented before taxa name. Taxa sequenced in the present study are presented in bold and highlighted

no further taxonomic resolution, we cannot presently assign Mermithidae sp. FA-QLD and Mermithidae sp. FA-NT to any known genus. At the very least, our analyses do provide some evidence of which groups these two species are not likely to belong to such as *Romanomermis* and *Mesomermis*. Species of these genera are primarily aquatic and parasites of mosquitos (Galloway and Brust 1979) and black flies (St-Onge et al. 2008), respectively. It also seems relatively clear that these two species do not represent *Hexamermis sinensis* (syn. *Ovomermis sinensis*) a species which has been reported to parasitise fall armyworm in China (Sun et al. 2020). Mermithidae sp. FA-QLD and Mermithidae sp. FA-NT cluster with species of *Agamermis* and *Hexamermis* consistently across our analyses (although without any support) and species of both of these genera have been reported to parasitise larval lepidoptera (Nickle 1972; Petersen 1985; Kaiser 1991). It is probable that Mermithidae sp. FA-QLD and Mermithidae sp. FA-NT will fall into one of these genera, but this cannot be confirmed until adults of both species are found, or future revisionary taxonomic and phylogenetic work provide a better picture of the mermithid phylogeny.

Mermithid nematodes are important regulators of insects and other arthropods in aquatic and terrestrial ecosystems (Nickle 1981; Petersen 1985; Baker 1986; Baker and Capinera 1997). At the end of the parasitic phase of their life cycle, mermithids almost always kill their hosts and can thus be useful biocontrol agents (Nickle 1981; Petersen 1985; Kaiser 1991). Mermithids are especially promising for integrated pest management in agricultural systems because some species are tolerant of a variety of pesticides and other agricultural chemicals (Petersen 1985; Kaya 1994). Several species have been investigated intensively for biocontrol, primarily those which parasitise mosquitos (e.g., Nickle 1979; Achinelly and Micieli 2011; Alavo et al. 2015). The mermithid *Romanomermis culicivorax* was available commercially in North America for the control of mosquitos in the mid-to-late 1970s under the trade name 'Skeeter Doom' (Nickle 1979). The first company marketing *R. culicivorax* during this period found that while production was economical, shipping and handling were not (Cupello et al. 1982; Petersen 1985). The second company to enter the market invested significant resources into improving shipping and handling (Cupello et al. 1982), but subsequently shifted away from biocontrol research and thus never actually marketed *R. culicivorax* (Petersen 1985). Improvements in materials technologies since the 1980s and the speed and efficiency of

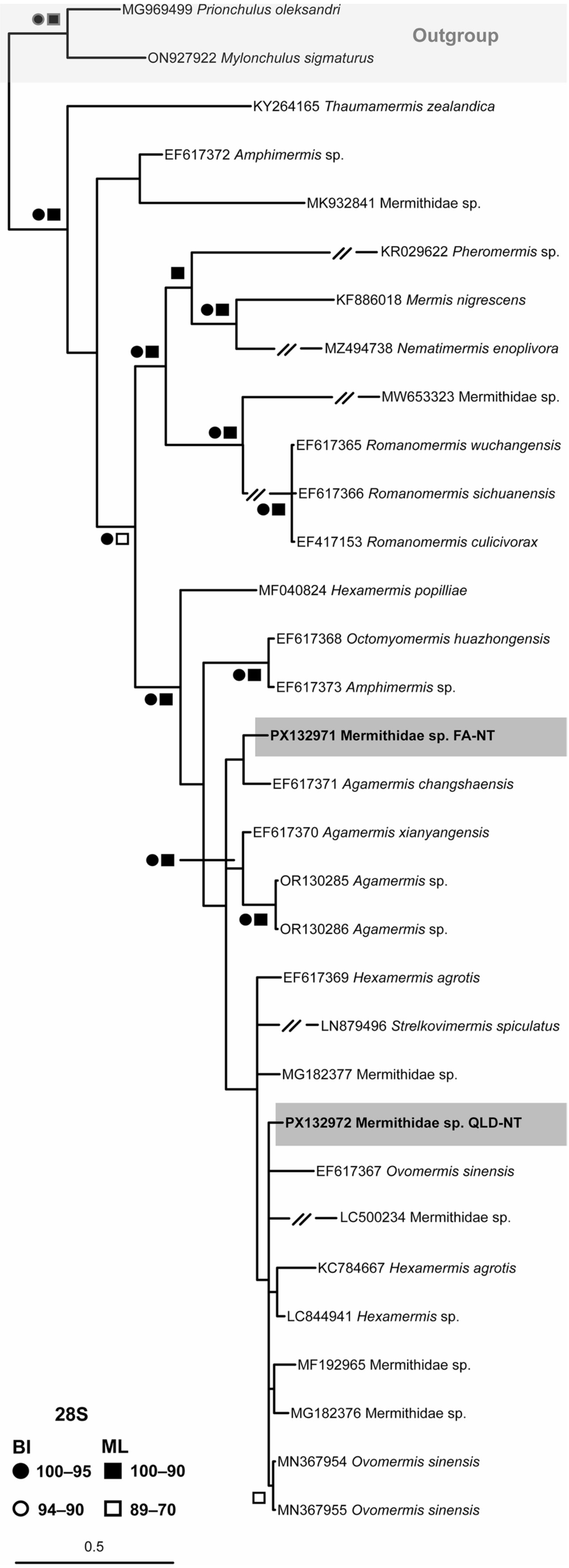


Fig. 4 Bayesian majority-rule consensus tree of the 28S dataset. Bayesian inference (BI) posterior probabilities (pp) for nodes represented by circles, maximum likelihood (ML) bootstrap support (bs) represented by squares. Support values less than 0.90 (pp) and 70 (bs) not shown. The scale-bar indicates the expected number of substitutions per site. GenBank accession number presented before taxa name. Taxa sequenced in the present study are presented in bold and highlighted

modern shipping along with a critical need for less reliance on chemical control of pests suggests new investigations into mermithids as biocontrol agents are warranted.

The exact timing of infection and length of development in Mermithidae sp. FA-QLD and Mermithidae sp. FA-NT is presently unknown. Anecdotal evidence from rearing field collected fall armyworm caterpillars suggests the developmental time for these nematodes is probably between four and ten weeks, like those of other known terrestrial mermithids (Hagmeier 1912; Cobb 1926; Christie 1936; Baker 1983). Thus, infected caterpillars still have the opportunity to cause significant crop damage before being killed by these parasites. Biological control using these nematodes would thus focus more on suppressing population densities of fall armyworm across years and seasons, rather than complete elimination at a specific time point.

These two nematode species are already present in some Australian cropping areas affected by fall armyworm and have been found parasitising caterpillars across four years. Thus, fall armyworm is essentially already undergoing biological control by mermithid parasites at the population level in at least some areas of Australia's tropical north. However, it is still likely that growers can take specific actions to further promote parasitism of fall armyworm by these nematodes. The life cycles of Mermithidae sp. FA-QLD and Mermithidae sp. FA-NT are yet to be elucidated, but rainfall is the major factor influencing movement of infective juveniles as well as female emergence and egg laying, and higher levels of rainfall stimulate a higher proportion of the mermithid population to emerge (Baker 1983; Kaiser 1991). Irrigation could potentially be used to induce parasitism at desired time points during a growing season. To promote higher rates of parasitism, strong knowledge of the life history of these mermithids is needed.

Another potential option is translocation of mermithid species. Mermithidae sp. FA-QLD was found only in Queensland and Mermithidae sp. FA-NT was found only in the Northern Territory. Assuming that these species are truly geographically isolated from one another, translocating these mermithids could place additional pressure on fall armyworm populations. Mermithids have been successfully introduced outside their native range to control mosquitos in some experiments. The native range of *Romanomermis culicivorax* is the southern United States, but this species was successfully introduced into the northern state of Maryland, where a self-sustaining population was established despite subzero winter temperatures (Nickle 1979). Other experiments have introduced *Romanomermis culivivorax* to countries beyond North America, including Taiwan (Mitchell et al. 1974; Chen 1976), Thailand (Chapman et al. 1972), and El Salvador (Petersen 1978; Willis et al. 1980). However, elucidating the natural history of Mermithidae sp. FA-QLD and Mermithidae sp. FA-NT would be a critical step before such translocation activities could be recommended to ensure for suitable environmental factors and to avoid potential impact on non-target species.

Mermithids are generally thought to be good biocontrol candidates because their host-specificity protects non-target organisms. Mermithids fall along a spectrum of host-specificity, with some species being capable of infecting only a single host species, others infecting multiple species within a genus or family, and others which may parasitise hosts across multiple orders (Petersen 1985; Kaiser 1991). Because fall armyworm has only recently arrived in Australia on the wing (Qi et al. 2021; Rane et al. 2023), and Mermithidae sp. FA-QLD and Mermithidae sp. FA-NT parasitise caterpillars, these nematodes are most likely Australian natives with at least generic-level host specificity. There are several other species of exotic *Spodoptera* established in Australia along with a number of native species (Nielsen et al. 1996; Braby 2000). For example, *Spodoptera litura* is native to South-East Asia and Oceania and is a minor pest of cotton in Northern Australia (Farrow and McDonald 1987; Wilson et al. 2013). It is likely that the normal hosts of Mermithidae sp. FA-QLD and Mermithidae sp. FA-NT include native species of *Spodoptera*. Follow-up work exploring the host breadth for these two mermithiids is needed.

Mermithid nematodes can now be added to the growing list of native and naturalised organisms which have been found parasitising fall armyworm in Australia. The broad range of *Spodoptera frugiperda* establishment across Australia also suggests that additional mermithid nematodes parasitising this moth are likely to be found. Mermithid nematodes may prove useful for managing populations of *S. frugiperda*, along with other biocontrol agents such as fungi (AusVeg 2020) and parasitoid wasps (Fagan-Jeffries et al. 2024). There is thus a critical need for a thorough investigation into the natural history of the two mermithid nematodes reported on here to determine how they may best be included into fall armyworm management strategies. Culture methods should also be explored as this may lead to efficient methods of high-density deployment.

Funding Open access funding provided by CSIRO Library Services. This project received no specific funding.

Data availability Data are available from the corresponding author upon reasonable request.

Declarations

Ethical approval Not applicable.

Competing interests The authors declare no competing interests.

References

Achinelly FM, Micieli VM (2011) Optimizing laboratory production of *Strelkovimermis spiculatus* (Nematoda: Mermithidae) with a discussion of potential release strategies for mosquito biological control. Biol Control 57(1):31–36

Ahissou BR, Sawadogo WM, Bonzi S, Baimey H, Somda I, Bokonon-Ganta A, Verheggen F (2021) Natural enemies of the fall armyworm *Spodoptera Frugiperda* (Smith) (Lepidoptera: Noctuidae) in Burkina Faso. Tropicultura 39(3):1–21

Alavo TBC, Abagli AZ, Pérez-Pacheco R, Platzer EG (2015) Large-scale production of the malaria vector biocontrol agent *Romanomermis iyengari* (Nematoda: Mermithidae) in Benin, West Africa. MalariaWorld Journal 6:1–5. https://doi.org/10.5281/zenodo.10869973

Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ (1990) Basic local alignment search tool. J Mol Biol 215(3):403–410. https://doi.org/10.1016/S0022-2836(05)80360-2

Ashley TR (1979) Classification and distribution of fall armyworm parasites. Fla Entomol 62:114–123

Ashley TR, Waddill VH, Mitchell ER, Rye J (1982) Impact of native parasites on the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), in South Florida and release of the exotic parasite, *Eiphosoma vitticole* (Hymenoptera: Ichnuemonidae). Environ Entomol 11(4):833–837

AusVeg (2020) Management of fall armyworm in vegetable crops in Australia

Baker GL (1983) Parasites of locusts and grasshoppers. Agfacts, New South Wales Department of Agriculture, Sydney

Baker GL (1986) The ecology of mermithid nematode parasites of grasshoppers and locusts in south-east Australia. In: Samson RA, Vlak JM, Peters D (eds) Fundamental and Applied Aspects of Invertebrate Pathology. Foundation of the Fourth International Colloquium of Invertebrate Pathology, Wageningen, Netherlands, pp 277–280

Baker GL, Capinera JL (1997) Nematodes and nematomorphs as control agents of grasshoppers and locusts. Mem Entomol Soc Can 129:157–211

Bird L, Miles M, Quade A, Spafford H (2022) Insecticide resistance in Australian *Spodoptera frugiperda* (JE Smith) and development of testing procedures for resistance surveillance. PLoS One 17(2):e0263677. https://doi.org/10.1371/journal.pone.0263677

Blaxter ML, De Ley P, Garey JR, Liu LX, Scheldeman P, Vierstraete A, Vanfleteren JR, Mackey LY, Dorris M, Frisse LM (1998) A molecular evolutionary framework for the phylum Nematoda. Nature 392(6671):71–75. https://doi.org/10.1038/32160

Bowles J, Blair D, McManus DP (1992) Genetic variants within the genus *Echinococcus* identified by mitochondrial DNA sequencing. Mol Biochem Parasitol 54(2):165–173

Braby MF (2000) Butterflies of australia: their identification, biology and distribution. CSIRO, Collingwood, Australia

Chapman HC, Pant CP, Mathis HL, Nelsen MJ, Phantomachinda B (1972) Field release of the nematode <Emphasis Type="Italic">Reesimermis nielseni</Emphasis> for the control of <Emphasis Type="Italic">Culex p</Emphasis>. <Emphasis Type="Italic">fatigans</Emphasis> in Bangkok, Thailand. WHO/BC 412:1–7

Chen P-S (1976) A study on *Reesimermis nielseni* for control of *Culex pipiens fatigans* in Taiwan. Bull Inst Zool Acad Sin 15:21–28

Chizhov VN, Chumakova OA, Subbotin SA, Baldwin JG (2006) Morphological and molecular characterization of foliar nematodes of the genus *Aphelenchoides*: *A. fragariae* and *A. ritzemabosi* (Nematoda: Aphelenchoididae) from the main botanical garden of the Russian academy of sciences. Russ J Nematol 14(2):179–184

Christie JR (1936) Life history of *Agamermis decaudata*, a nematode parasite of grasshoppers and other insects. J Agric Res 52:161–178

Christie JR (1937) *Mermis subnigrescens*, a nematode parasite of grasshoppers. J Agric Res 55:353–364

Cobb NA (1926) The species of *Mermis*: a group of very remarkable nemas infesting insects. J Parasitol 13(1):66–72

Cupello JM, Petersen JJ, Chauthani AR (1982) An improved method for long-distance shipping the mosquito parasite *Romanomermis culicivorax*. J Nematol 14(1):121–125

Cuthbert FP (1968) Bionomics of a mermithid (nematode) parasite of soil-inhabiting larvae of certain chrysomelids (coleoptera). J Invertebr Pathol 12(3):283–287

Derycke S, Remerie T, Vierstraete A, Backeljau T, Vanfleteren J, Vincx M, Moens T (2005) Mitochondrial DNA variation and cryptic speciation within the free-living marine nematode *Pellioditis marina*. Mar Ecol Prog Ser 300:91–103

Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res 32(5):1792–1797. https://doi.org/10.1093/nar/gkh340

Fagan-Jeffries EP, Miles MM, Atkin-Zaldivar TCC, Howe AG, Subramaniam S, Chambers DM, Tadle FPJ, Adnan SM, Sivasubramaniam V, Woodward A (2024) Hymenopteran parasitoids of fall armyworm (*Spodoptera Frugiperda* (JE Smith)(Lepidoptera: Noctuidae)) in Australia, with the description of five new species in the families Braconidae and eulophidae. Austral Entomol 63(2):136–174. https://doi.org/10.1111/aen.12682

FAO (Food and Agricultural Organization of the United Nations) (2025) Global Action for Fall Armyworm Control. Monitoring, Fall Armyworm Map. https://www.fao.org/fall-armyworm/monitoring-tools/faw-map/en. Accessed 30 April 2025

Farrow RA, McDonald G (1987) Migration strategies and outbreaks of noctuid pests in Australia. Int J Trop Insect Sci 8:531–542

Firake DM, Behere GT (2020) Natural mortality of invasive fall armyworm, *Spodoptera frugiperda* (JE Smith) (Lepidoptera: Noctuidae) in maize agroecosystems of northeast India. Biol Control 148:104303. https://doi.org/10.1016/j.biocontrol.2020.104303

Galloway TD, Brust RA (1979) Review of the genus *Romanomermis* (Nematoda: Mermithidae) with a description of *R. communensis* sp. n. from Canada. Can J Zool 57(2):281–289

Hagmeier A (1912) Beiträge Zur Kenntnis der Mermithiden. I. Biologische notizen und systematische beschreibung Einiger alter und Neuer Arten. Zool Jahrb Abt Syst Geogr Biol Tiere 49:521–612

Hamm JJ, Pair SD, Marti Jr OG (1986) Incidence and host range of a new ascovirus isolated from fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Fla Entomol 69:524–531

Huston DC, Khudhir M, Hodda M (2023) Phylogenetic position of *Ptychaphelenchus eucalypticola* Hodda, 2009 within the Aphelenchoidoidea Skarbilovich, 1947 (Siddiqi, 1980) inferred from partial 18S and 28S rDNA gene sequences. Nematology 25:59–76. https://doi.org/10.1163/15685411-bja10206

Kaburaki T, Imamura S (1932) A new mermithid-worm parasitic in the rice borer, with notes on its life history and habits. Proc Imp Acad Japan 8(3):109–112

Kaiser H (1991) Terrestrial and semiterrestrial Mermithidae. In: Nickle WR (ed) Manual of Agricultural Nematology. Marcel Dekker, New York, New York, pp 899–966

Kaya HK (1994) Biological control of the brown planthopper by a mermithid nematode. Korean J Appl Entomol 33(4):207–215

Koffi D, Kyerematen R, Eziah VY, Agboka K, Adom M, Goergen G, Meagher RL (2020) Natural enemies of the fall armyworm, *Spodoptera frugiperda* (JE Smith)(Lepidoptera: Noctuidae) in Ghana. Fla Entomol 103(1):85–90. https://doi.org/10.1653/024.103.0414

Maino JL, Schouten R, Overton K, Day R, Ekesi S, Bett B, Barton M, Gregg PC, Umina PA, Reynolds OL (2021) Regional and seasonal activity predictions for fall armyworm in Australia. Curr Res Insect Sci 1:100010. https://doi.org/10.1016/j.cris.2021.100010

Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE)., New Orleans, LA. pp 1–8. https://doi.org/10.1109/GCE.2010.5676129

Mitchell CJ, Chen PS, Chapman HC (1974) Exploratory trials utilizing a mermithid nematode as a control agent for *Culex* mosquitos in Taiwan. J Formos Med Assoc 73:241–254

Molina-Ochoa J, Lezama-Gutierrez R, Gonzalez-Ramirez M, Lopez-Edwards M, Rodriguez-Vega MA, Arceo-Palacios F (2003) Pathogens and parasitic nematodes associated with populations of fall armyworm (Lepidoptera: Noctuidae) larvae in Mexico. Fla Entomol 86(3):244–253

Montezano DG, Sosa-Gómez DR, Specht A, Roque-Specht VF, Sousa-Silva JC, Paula-Moraes SVd, Peterson JA, Hunt TE (2018) Host plants of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in the Americas. Afr Entomol 26(2):286–300

Nguyen DT, Chen Y, Herron GA (2021) Preliminary characterisation of known pesticide resistance alleles in *Spodoptera Frugiperda* (Lepidoptera: Noctuidae) in its invasive Australian range. Austral Entomol 60(4):782–790. https://doi.org/10.1111/aen.12570

Nickle WR (1972) A contribution to our knowledge of the Mermithidae (Nematoda). J Nematol 4(2):113–146

Nickle WR (1979) Probable establishment and overwintering of a mermithid nematode parasite of mosquitoes in Maryland. Proc Helminthol Soc Wash 46:21–27

Nickle WR (1981) Mermithid parasites of agricultural pest insects. J Nematol 13(3):262–266

Nielsen ES, Edwards ED, Rangsi TV (1996) Checklist of the lepidoptera of Australia. CSIRO, Melbourne, Australia

Nunn GB (1992) Nematode molecular evolution: an investigation of evolutionary patterns among nematodes based upon DNA sequences. Ph. D. Thesis, University of Nottingham, Nottingham, UK

Otim MH, Adumo Aropet S, Opio M, Kanyesigye D, Nakelet Opolot H, Tek Tay W (2021) Parasitoid distribution and parasitism of the fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in different maize producing regions of Uganda. Insects 12(2):121. https://doi.org/10.3390/insects12020121

Petersen JJ (1978) Observations on the mass production of *Romanomermis culicivorax*, a nematode parasite of mosquitoes. Mosquito News 38:83–86

Petersen JJ (1985) Nematodes as biological control agents: part I. Mermithidae. Adv Parasitol 24:307–344

Piggott MP, Tadle FPJ, Patel S, Cardenas Gomez K, Thistleton B (2021) Corn-strain or rice-strain? Detection of fall armyworm, <Emphasis Type="Italic">Spodoptera frugiperda</Emphasis> (JE Smith)(Lepidoptera: Noctuidae), in northern Australia. Int J Trop Insect Sci 41(4):2607–2615. https://doi.org/10.1007/s42690-021-00441-7

Poinar GO, Gyrisco GG (1962) Studies on the bionomics of *Hexamermis arvalis* poinar and Gyrisco, a Mermithid parasite of the alfalfa weevil, *Hypera postica* (Gyllenhal). J Insect Pathol 4:469–483

Qi G-J, Ma J, Wan J, Ren Y-L, McKirdy S, Hu G, Zhang Z-F (2021) Source regions of the first immigration of fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae) invading Australia. Insects 12(12):1104

Rane R, Walsh TK, Lenancker P, Gock A, Dao TH, Nguyen VL, Khin TN, Amalin D, Chittarath K, Faheem M (2023) Complex multiple introductions drive fall armyworm invasions into Asia and Australia. Sci Rep 13(1):660. https://doi.org/10.1038/s41598-023-27501-x

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst Biol 61(3):539–542. https://doi.org/10.1093/sysbio/sys029

Sisay B, Simiyu J, Mendesil E, Likhayo P, Ayalew G, Mohamed S, Subramanian S, Tefera T (2019) Fall armyworm, *Spodoptera frugiperda* infestations in East Africa: assessment of damage and parasitism. Insects 10(7):195. https://doi.org/10.3390/insects10070195

St-Onge M, LaRue B, Charpentier G (2008) A molecular revision of the taxonomic status of mermithid parasites of black flies from Quebec (Canada). J Invertebr Pathol 98(3):299–306. https://doi.org/10.1016/j.jip.2008.04.001

Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinform 30(9):1312–1313

Sun B, Li F, He X, Cao F, Bandason E, Shapiro-Ilan D, Ruan W, Wu S (2020) First report of *Ovomermis sinensis* (Nematoda: Mermithidae) parasitizing fall armyworm *Spodoptera frugiperda* (Lepidoptera: Noctuidae) in China. J Nematol 52:1–7. https://doi.org/10.21307/jofnem-2020-050

Tamura K, Stecher G, Kumar S (2021) MEGA11: molecular evolutionary genetics analysis version 11. Mol Biol Evol 38(7):3022–3027. https://doi.org/10.1093/molbev/msab120

Tay WT, Rane RV, James W, Gordon KHJ, Downes S, Kim J, Kuniata L, Walsh TK (2022) Resistance bioassays and allele characterization inform analysis of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) introduction pathways in Asia and Australia. J Econ Entomol 115(6):1790–1805. https://doi.org/10.1093/jee/toac151

Togola A, Meseka S, Menkir A, Badu-Apraku B, Boukar O, Tamò M, Djouaka R (2018) Measurement of pesticide residues from chemical control of the invasive *Spodoptera Frugiperda* (Lepidoptera: Noctuidae) in a maize experimental field in Mokwa, Nigeria. Int J Environ Res Public Health 15(5):849. https://doi.org/10.3390/ijerph15050849

Towns J, Cockerill T, Dahan M, Foster I, Gaither K, Grimshaw A, Hazlewood V, Lathrop S, Lifka D, Peterson GD (2014) XSEDE: accelerating scientific discovery. Comput Sci Eng 16(5):62–74. https://doi.org/10.1109/MCSE.2014.80

Willis OR, Chapman HC, Petersen JJ (1980) Additional field testing of the mermithidparasite Romanomermis culicivorax against Anopheles albimanus in El Salvador. MosquitoNews 40:71–73

Wilson L, Downes S, Khan M, Whitehouse M, Baker G, Grundy P, Maas S (2013) Ipm inthe transgenic era: a review of the challenges from emerging pests in Australian cottonsystems. Crop Pasture Sci 64(8):737–749. https://doi.org/10.1071/CP13070