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Research Article

Occurrence and Identification of Mermithid Nematode Parasites Associated with Grasshoppers (Orthoptera: Acrididae) in Mongolian Rangelands

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ABSTRACT

Grasshoppers are important herbivorous insects in Mongolian grasslands and may serve as hosts for parasitic nematodes, including members of the family Mermithidae. This study investigated nematode parasitism in the light-winged grasshopper (*Calliptamus abbreviatus* Ikonnikov, 1913) and Barabens' grasshopper (*Angaracris barabensis* Pallas, 1773) and characterized the associated nematodes using molecular analysis. A total of 1,012 grasshopper specimens were collected, comprising 503 *C. abbreviatus* and 509 *A. barabensis*. Of 200 individuals of each species examined by dissection, six individuals of each species were infected with nematodes, corresponding to a prevalence of 3% in both hosts. Molecular identification was performed by PCR amplification and sequencing of the ribosomal DNA region, yielding an approximately 950-bp fragment. BLAST analysis of the 919-bp sequences showed a 99.3% nucleotide identity with *Mermis nigrescens* (KF886020). The sequences obtained from Mongolian specimens were deposited in the DDBJ database under accession numbers OM293674 and OM293675. These findings provide molecular evidence for the occurrence of *M. nigrescens* in Mongolia and document its parasitism in *C. abbreviatus* and *A. barabensis*. The results expand the known host associations and geographical distribution of *M. nigrescens* and provide baseline information for further studies on mermithid–grasshopper interactions and their potential significance in the natural regulation of grasshopper populations.

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Introduction

Animal husbandry is the primary engine of Mongolia's society and economy, making pasture management a critical issue. However, the country's pastureland resources are severely degrading due to extensive destruction by harmful organisms and environmental shifts (Khan et al., 2024). This degradation is driven by global warming, desertification, pasture desiccation, the loss of traditional seasonal migration and rotation practices, rapidly increasing livestock numbers, and biological factors such as grasshopper outbreaks. Consequently, over 70% of Mongolia's pastures have deteriorated in both plant cover and botanical composition due to overgrazing, high livestock density

and grasshopper distribution.

Harmful insects and rodents, particularly grasshoppers and voles, reduce pasture yields by 10% to 40%. As major biological stressors in livestock pastures, grasshopper outbreaks directly threaten winter forage availability and animal food security. In the grasslands of Mongolia's forest-steppe region, which host 53 botanical families and 69 distinct plant species, grasshoppers selectively forage on 9 species of 7 genera, significantly degrading rangeland resources (Batnaran, 2022).

Parasites that infest grasshoppers and other orthopteran insects include grasshopper nematodes such as *Agamermis decaudata*, *Amphimermis bonaerensis*, *A. dichroplusi*, *A. ronderosi*, *Hexamermis cochlearius*, *H. ovistriata*, Longimermis acridophila, and *Mermis nigrescens*; nematomorph hairworms such as *Paragordius varius* and *Spinochordodes tellinii*; red mites; tachinid flies (Tachinidae); and sarcophagid flies (Sarcophagidae) such as *Blaesoxipha caridei* and *B. angustifrons* (Batnaran, 2015; Rusconia et al., 2017; Salas-Araiza et al., 2025; Singh et al., 2025). Nematodes belonging to the genus *Mermis* are widely distributed across North America, Europe, and Asia, but are rarely reported from Africa. These nematodes are well adapted to moist environments and parasitize grasshoppers during their larval stages. During the third or fourth larval stage, they emerge from the host insect, complete their development, and lay eggs on plant surfaces. Herbivorous insects, particularly grasshoppers, become infected by ingesting the eggs while feeding. Upon emergence from the host, the nematodes remain in the larval stage and complete their development in the soil, a process that ultimately results in host mortality (Capinera, 2011). Studies conducted in Australia indicate that two species of the genus *Mermis* (*M. quirindiensis* and *M. athysanota*) play a significant role in regulating grasshopper populations in regions with high precipitation. In contrast, these parasites are rarely observed in the arid western regions of the continent (Batnaran, 2008).

Given the limited information available on insect-parasitizing nematodes and hairworms in Mongolia, particularly their diversity, host associations, distribution, and potential role in regulating grasshopper populations, systematic investigations are needed to address this knowledge gap. Therefore, the present study was undertaken to investigate the occurrence and diversity of parasitic nematodes associated with grasshoppers in Mongolian rangelands and to characterize their host–parasite associations. The study specifically aimed to (i) identify the nematode parasites associated with grasshopper species, (ii) determine their prevalence and distribution among grasshopper hosts and sampling locations, and (iii) assess their potential significance as naturally occurring biological control agents for the sustainable management of grasshopper populations in Mongolia. The findings are expected to provide baseline information on autochthonous entomopathogenic nematodes and contribute to the development of environmentally sustainable approaches for protecting Mongolia's vulnerable pasture ecosystems.

Materials and Methods

Grasshoppers and nematodes

A field study to determine the species composition and distribution of grasshoppers in the central region of Mongolia was conducted during 2016–2017 at Zaisan Tolgoi (49°08′02.4″ N, 104°49′30.1″ E), located 7 km east west of the center of Baruunburen soum, Selenge Province, on the right bank of the Burgaltai River, at an elevation of 892 m above sea level. The study area lies within the mountain steppe zone of the middle mountainous region of the Selenge–Orkhon river basin, which forms part of the Khangai–Khentii mountain system (Figure 1).

Adult specimens of the light-winged grasshopper, *Calliptamus abbreviatus* Ikonnikov, 1913, and Barabens' grasshopper, *Angaracris barabensis* Pallas, 1773, were collected from Baruunburen soum, Selenge Province, northern Mongolia, using a standard sweep net. Grasshopper specimens were collected from natural and pasture habitats and transferred to the laboratory in ventilated containers for further examination. Species identification was performed based on external morphological characteristics using the identification keys of GJa and Mistshenko (1951).

A total of 400 adult grasshopper specimens were examined for nematode infection. Individual grasshoppers were dissected under a stereomicroscope, and their internal organs and body cavity were carefully examined for the presence of nematodes. Recovered nematodes were removed using sterile fine-tipped forceps and rinsed thoroughly with sterile distilled water to remove adhering host tissues and debris. The nematodes were subsequently preserved in 70% ethanol and stored until morphological and molecular analyses were performed (Figure 2). Representative specimens were used for DNA extraction and molecular identification.

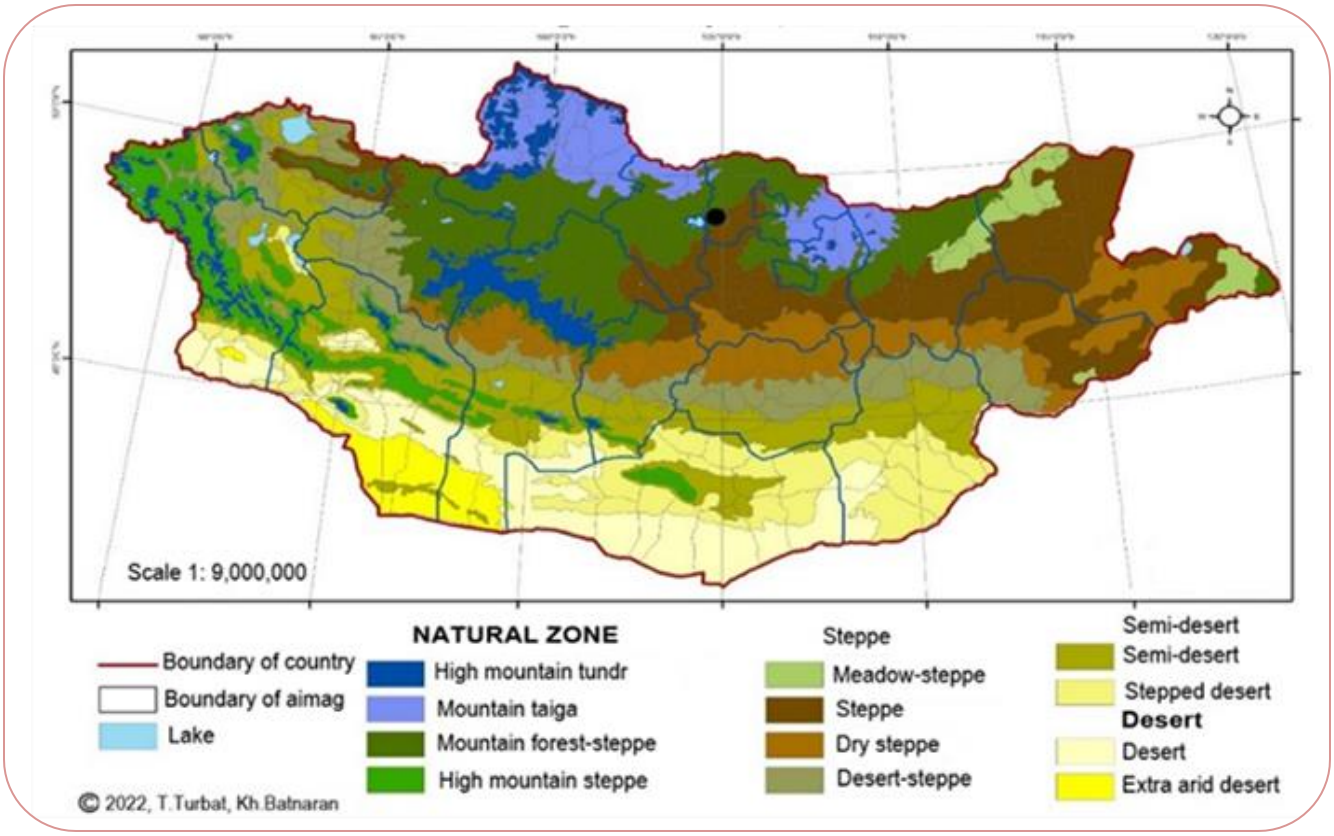

Figure 1. Geographic location of the grasshopper collection site in Mongolia.

Figure 2. Nematode detection process.

Extraction of nematode DNA and polymerase chain reaction

Total genomic DNA was extracted from individual nematode specimens using the NucleoSpin® DNA Insect Mini Kit (Macherey-Nagel, PA, USA), following the manufacturer's instructions. Briefly, nematode specimens were transferred to sterile microcentrifuge tubes, excess ethanol was removed, and the specimens were processed using the lysis, binding, washing, and elution steps recommended by the manufacturer. The extracted DNA

was eluted in the recommended elution buffer and stored at −30°C until further analysis.

The internal transcribed spacer (ITS) region of the ribosomal DNA was amplified by polymerase chain reaction (PCR) using the universal nematode primers ITS1 (5′-ACCTACCGATTGGAGATTCGATGA-3′) and ITS4 (5′-ACCGCTAGAACAACAATAGCAGTT-3′). PCR amplification was carried out in a final reaction volume of 50 µL containing 1 µg of template DNA, 100 pmol of each primer, 1× PCR buffer, 5 mM $MgCl_2$, 1 mM dNTPs, 1 U RNase inhibitor, and 5 U DreamTaq DNA polymerase (Thermo Fisher Scientific, USA). Appropriate negative controls were included to monitor potential contamination.

PCR amplification was performed in a thermal cycler under the following conditions: initial denaturation at 94°C for 5 min; 35 cycles of denaturation at 94°C for 30 sec, primer annealing at 56°C for 30 sec, and extension at 72°C for 1 min; followed by a final extension at 72°C for 5 min. The amplified products were separated by electrophoresis on 1.5% agarose gels and visualized under UV illumination after staining with ethidium bromide. PCR products showing bands of the expected size were purified and subjected to nucleotide sequencing.

DNA sequencing and molecular identification

The PCR-amplified products were subjected to nucleotide sequencing using the ABI PRISM™ Dye Primer Cycle Sequencing Ready Reaction Kit (PerkinElmer, USA) according to the manufacturer's protocol. Sequencing reactions were analyzed using an ABI 377A automated DNA sequences. The resulting chromatograms were examined manually, and low-quality regions and ambiguous nucleotide positions were removed. The sequences were assembled and edited using GENETYX version 6.1 software (Genetyx Corporation, Tokyo, Japan).

The resulting ribosomal DNA sequences were compared with homologous sequences available in the National Center for Biotechnology Information (NCBI) GenBank database using the Basic Local Alignment Search Tool (BLAST) to determine their closest taxonomic matches (Benson et al., 2002). Putative species identification was based on sequence similarity together with the morphological characteristics of the recovered nematodes. The obtained sequences were identified as corresponding to *Mermis nigrescens*.

The ribosomal RNA gene sequences of *M. nigrescens* isolated from grasshoppers in Mongolia were deposited in the DNA Data Bank of Japan (DDBJ) under accession numbers OM293674 and OM293675.

Results

As a result of the field survey, a total of 1.012 grasshopper specimens (Orthoptera: *Acrididae*) were collected, including the light-winged grasshopper (*Calliptamus abbreviatus* Ikonnikov, 1913) and Barabens' grasshopper (*Angaracris barabensis* Pallas, 1773). Of the 503 specimens of *C. abbreviatus* (198 males and 305 females; 49.7% of the total), 200 individuals meeting the study criteria were dissected, revealing nematode parasitism in six females (3%). Similarly, of the 509 specimens of *A. barabensis* (211 males and 298 females; 50.3% of the total), 200 individuals were dissected, among which six grasshoppers (four males and two females; 3%) were infected with nematodes.

In addition to morphological identification, molecular sequence data were utilized to compare the nematode sequences with those available in the GenBank database. Genomic DNA was extracted from the nematodes using the NucleoSpin® DNA Insect Mini Kit, followed by PCR amplification. Analysis of the PCR products revealed successful amplification of the expected ~950 bp fragment (Figure 3).

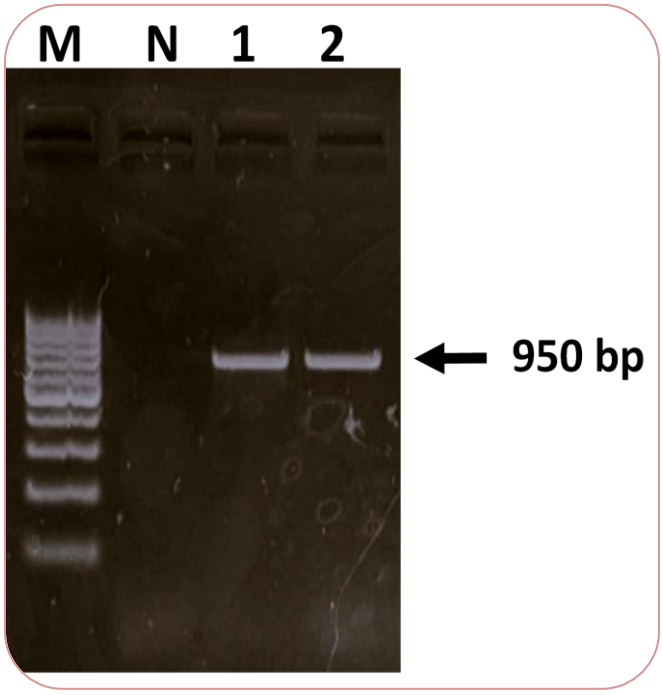

Figure 3. Agarose gel electrophoresis of PCR-amplified DNA (~950 bp) from nematode samples, showing distinct bands indicative of successful amplification.

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MNG_OM293674   1:CTACCGATTGGAGATTCGATGAGAACTTTGGACTGGGCGTGAAGTGGCCTAAAAACC
MNG_OM293675   1:CTACCGATTGGAGATTCGATGAGAACTTTGGACTGGGCGTGAAGTGGCCTAAAAACC
NZ_KF886020    1:CTACCGATTGGAGATTCGATGAGAACTTTGGACTGGGCGTGAAGTGGCCTAAAAACC
MNG_OM293674  58:GCTACACTGCCTGGAAAGATGTTCAAATCGTATCTTCTAGAGGAAGTAAAAGTCGTA
MNG_OM293675  58:GCTACACTGCCTGGAAAGATGTTCAAATCGTATCTTCTAGAGGAAGTAAAAGTCGTA
NZ_KF886020   58:GCTACACTGCCTGGAAAGATGTTCAAATCGTATCTTCTAGAGGAAGTAAAAGTCGTA
MNG_OM293674 115:ACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTAGCGAGTGCTCGAAAGAGTG
MNG_OM293675 115:ACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTAGCGAGTGCTCGAAAGAGTG
NZ_KF886020  115:ACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTAGCGAGTGCTCGAAAGAGTG
MNG_OM293674 172:TATCGTTATGGGCGTTGAGCGCGAATATGCGGTGGGCGCTAGTCGCTAATCCGTCGC
MNG_OM293675 172:TATCGTTATGGGCGTTGAGCGCGAATATGCGGTGGGCGCTAGTCGCTAATCCGTCGC
NZ_KF886020  172:TATCGTTATGGGCGTTGAGCGCGAATATGCGGTGGGCGCTAGTCGCTAATCCGTCGC
MNG_OM293674 229:CTCTATCGTCAACAGTCGGCTGGGAGTATGCTCGTTCTGTGTAGAGTGCTAGTCGCT
MNG_OM293675 229:CTCTATCGTCAACAGTCGGCTGGGAGTATGCTCGTTCTGTGTAGAGTGCTAGTCGCT
NZ_KF886020  229:CTCTATCGTCAACAGTCGGCTGGGAGTATGCTCGTTCTGTGTAGAGTGCTAGTCGCT
MNG_OM293674 286:CTTGTCTGCAGGGGCTGCTCCATACAGTTTGACTTTTTATCTTAACAGACGTTTTAC
MNG_OM293675 286:CTTGTCTGCAGGGGCTGCTCCATACAGTTTGACTTTTTATCTTAACAGACGTTTTAC
NZ_KF886020  286:CTTGTCTGCAGGGGCTGCTCCATACAGTTTGACTTTTAATCTTAACAGACGTTTTAC
MNG_OM293674 342:CGGGGGTATTTATTCCGACGTTGGGTAGTTGTCTGGCTACGCGTTTGCACGTCGGGG
MNG_OM293675 342:CGGGGGTATTTATTCCGACGTTGGGTAGTTGTCTGGCTACGCGTTTGCACGTCGGGG
NZ_KF886020  342:CGGGGGTATTTATTCCGACGTTGGGTAGTTGTCTGGCTACGCGTTTGCACGTCGGGG
MNG_OM293674 400:TAACTGGACGCCTTTTTTGTCCAGCTGAAATTCAATGAGTAGCGCCTGGCGTTACCG
MNG_OM293675 400:TAACTGGACGCCTTTTTTGTCCAGCTGAAATTCAATGAGTAGCGCCTGGCGTTACCG
NZ_KF886020  400:TAACTGGACGCCTTTTTTGTCCAGCTGAAATTCAATGAGTAGCGCCTGGCGTTACCG
MNG_OM293674 457:CCCCCGAATGGAATTGACGGATGTATTTTGTGGGGTATCTGTGGAGCGGAAGCGCCA
MNG_OM293675 457:CCCCCGAATGGAATTGACGGATGTATTTTGTGGGGTATCTGTGGAGCGGAAGCGCCA
NZ_KF886020  457:CCCCCGAATGGAATTGACGGATGTATTTTGTCGGGTATCTGTGGAGCGGAAGCGCCA
MNG_OM293674 514:GCACCCCATACGACCTGATTAAAGGATGGGGAAGATACAATGAAGAGATAGAGTATT
MNG_OM293675 514:GCACCCCATACGACCTGATTAAAGGATGGGGAAGATACAATGAAGAGATAGAGTATT
NZ_KF886020  514:GCACCCCATACGACCTGATTAAAGGATGGGGAAGATACAATGAAGAGATGGAGTATT
MNG_OM293674 571:GCGGCACACGCGCGCCGATTCCTGAAGGTCAGGGGAATCGATGCGAGATTGGTCGAA
MNG_OM293675 571:GCGGCACACGCGCGCCGATTCCTGAAGGTCAGGGGAATCGATGCGAGATTGGTCGAA
NZ_KF886020  571:GCGGCACACGCGCGCCGATTCCTGAAGGTCAGGGGAATCGATGCGAGATTGGTCGAA
MNG_OM293674 628:GTGCTCATTAAGGTCTCTCGCCCGCAAAATACTAATGGCGTTTGTTGGTCTCTAGGG
MNG_OM293675 628:GTGCTCATTAAGGTCTCTCGCCCGCAAAATACTAATGGCGTTTGTTGGTCTCTAGGG
NZ_KF886020  628:GTGCTCATTAAGGTCTCTCGCCCGCAAAATACTAATGGCGTTTGTTGGTCTCTAGGG
MNG_OM293674 685:CTGGAGATGCGTGCGCATACTGACGGCCGAAACCTCATACGGTCTGATCGAATGTGT
MNG_OM293675 685:CTGGAGATGCGTGCGCATACTGACGGCCGAAACCTCATACGGTCTGATCGAATGTGT
NZ_KF886020  685:CTGGAGATGCGTGCGCATACTTACGGCCGAAACCTCATACGGTCTGATCGAATGTGT
MNG_OM293674 742:ATGGGGAAGAGACAGAGAAAATGGGCAGTGCAGGGCGAGTTATGGACCAAGGACTCG
MNG_OM293675 742:ATGGGGAAGAGACAGAGAAAATGGGCAGTGCAGGGCGAGTTATGGACCAAGGACTCG
NZ_KF886020  742:ATGGGGAAGAGACAGAGAAAATGGGCAGTGCAGCGCGAGTTATGGACCAAGGACTCG
MNG_OM293674 799:CCGGGCTGTTTTGTCGAAAGCACTCTGCTTCGCCCATTTTCCGCCAGCAAATGCAAC
MNG_OM293675 799:CCGGGCTGTTTTGTCGAAAGCACTCTGCTTCGCCCATTTTCCGCCAGCAAATGCAAC
NZ_KF886020  799:CCGGGCTGTTTTGTCGAAAGCACTCTGCTTCGCCCATTTTCCGCCAGCAAATGCAAC
MNG_OM293674 856:CTAACTTATCGGACTGAATCGTTTTAGCTCAGTGATGGGCGAAAGTGCTATTGTTGT
MNG_OM293675 856:CTAACTTATCGGACTGAATCGTTTTAGCTCAGTGATGGGCGAAAGTGCTATTGTTGT
NZ_KF886020  856:CTAACTTATCGGACTGAATCGTTTTAGCTCAGTGATGGGCGAAAGTGGTATTGTTGT
MNG_OM293674 913:TCTAGCG
MNG_OM293675 913:TCTAGCG
NZ_KF886020  913:TCTAGCG
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Figure 4. Nucleotide sequence alignment of *M. nigrescens* isolates from Mongolia (MNG; GenBank accession numbers OM293674 and OM293675) and New Zealand (NZ; GenBank accession number KF886020), representing members of the family Mermithidae.

PCR products were purified from agarose gels using GENECLEAN kit II (MP Biomedicals, Solon, OH) and were sent to Macrogen, Korea (https://dna.macrogen.com) for sequencing. Nucleotide sequence of Mermithidae sp. ITS1 rRNA gene (n = 2) fragments produced significant alignments with *M. nigrescens* nematode. The nucleotide sequences of the ribosomal RNA gene of *M. nigrescens* isolated from Mongolia were submitted to the DDBJ database under accession no. OM293674 and OM293675. A Basic Local Alignment Search Tool (BLAST) through GenBank noted the small subunit ribosomal RNA gene and internal transcribed spacer 1 (ITS1) sequence of *M. nigrescens* (919 bp; OM293674 and OM293675) had the closest match to *M. nigrescens* ITS1 gene (KF886020; 99.3% identity) (Figure 4, Table 1).

Table 1. Partial Gene Sequence Comparison for ITS1of the Mermis nigrescens

GenBank accession numbers	OM293674	OM293675	KF886020.1	KF886021.1
OM293674		100.0%	99.3%	99.3%
OM293675	100.0%		99.3%	99.3%
KF886020.1*	99.3%	99.3%		100.0%
KF886021.1*	99.3%	99.3%	100.0%	

Discussion

According to the research results carried out in Mongolia before 1990, researchers have discovered several parasites in Orthoptera insects, especially grasshoppers, and noted their distribution. Grasshoppers in Mongolia were frequently infested with red mites (*Eutrombidium* sp.) and tachinid flies (*Tachina magna*) (Batnaran, 2015). However, detailed studies have not been conducted on the biology, parasite–host interactions, microhabitat associations for free-living adult and juvenile stages, and ecology of these parasites that are infested on grasshoppers, as well as their potential use in plant protection.

Little work has been done to document the incidence of mermithid infections in insect populations. Prevalence of mermithid infection was reported 0 to 4.12% in Hawaiian kipuka spiders (Vandergast and Roderick, 2003), 0.2% in bumble bees in USA (Tripodi and Strange, 2018), 3.2% in stink bugs *Megacopta cribraria* in USA (Stubbins et al., 2016) and 9.6% in European earwigs in New Zealand (Presswell et al., 2015). The nematodes were identified as belonging to the species *M. nigrescens*, according to the presence of the main diagnostic features (Kaya and Stock, 1997; Presswell et al., 2015). The nematodes were uniformly white-colored, rounded at the anterior surrounded by slight swelling and slightly flattened ventrally at the posterior end. Each parasite was coiled several times within the host's abdominal cavity. The average length of the nematodes was 132.4 ± 34 mm. Although there is not enough data to identify the mermithids found in the Orthoptera by genus or species, our reported parasites were similar to European earwigs inhabiting mermithids from New Zealand. Moreover, as a known grasshopper's nemathode, *M. nigrescens*, categorized in the entomopathogenic nematodes (EPNs) used for biological control, alongside families such as Steinernematidae and Heterorhabditidae. These EPNs are noted for their symbiotic relationship with entomopathogenic bacteria (*Xenorhabdus nematophila* strain BA2 and *Photorhabdus luminescens* strain EGAP3), which they release into the host haemocoel to induce lethal septicemia (Muhammad et al., 2025; Singh et al., 2025). Some Ascaridids, including mermithids use grasshoppers as intermediate hosts to infect vertebrates like birds or mammals (Baker and Capinera, 1997).

Over 14 sampling dates, 1,012 specimens of light-winged grasshopper (*C. abbreviatus* Ikonnikov, 1913) and Baraben's grasshopper (*A. barabensis* Pallas, 1773) male and females belonging to the Orthoptera family were collected, of which 400 were dissected (40%), with 12 were parasitized by *M. nigrescens* nematodes (3%). This study represents the first attempt to quantify the prevalence of mermithid infection in grasshoppers in Mongolia. In this study, we confirmed *M. nigrescens* Dujardin, 1842 by morphology identification and sequence analysis. Blast search analysis of our sequences showed 99.3% identity with *M. nigrescens* nematode from New Zealand. Mermithids can be effective tools for host population densities and have often been targeted as biocontrol organisms for harmful insects of plants (Welch, 1965; Mongkolkiti and Hosford Jr, 1971). It will be important to investigate the host range of these mermithids among orthopteran species.

This study is the first documentation of grasshopper mermithids in Mongolia. Results suggest that the prevalence of parasitism in grasshopper specimens. Further work remains, including completing a definitive morphological species identification, determining free-living adult and juvenile stages of nematodes, and identifying possible other Orthoptera hosts and intermediate hosts. Mermithid infestations of grasshoppers could be considered as bioregulator agents against these and other insect pests in agricultural areas of Mongolia.

Conclusion

In this study, *Mermis nigrescens* Dujardin, 1842 was detected and confirmed based on both morphological and molecular sequence analyses from grasshopper species *Calliptamus abbreviatus* (Ikonnikov, 1913) and *Angaracris barabensis* (Pallas, 1773). Comparative sequence alignment revealed that the ITS1 rRNA gene of the Mongolian specimens exhibited 99.3% identity to *M. nigrescens* from New Zealand, confirming the species identification.

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Author Contributions

KB and GT conceptualized and designed the experiment. GG and RG conducted the field investigations and experimental work. KB supervised the study and ensured methodological and analytical consistency. DB performed the molecular analyses. DI prepared the initial manuscript draft. All authors critically reviewed and refined the manuscript, verified the data and analyses, and approved the final version for submission.

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Conflict of Interest

The authors declare no conflict of interest.

Sustainable Development Goals Targeted

SDG 2: Zero Hunger
SDG 12: Responsible Consumption and Production
SDG 15: Life on Land

Policy Addressed

Naturally occurring mermithid nematodes should be conserved and further investigated as potential components of integrated grasshopper management. Further studies on their prevalence, host specificity, pathogenicity, environmental requirements, and population-level effects are needed before practical application.

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