Journal of Helminthology

www.cambridge.org/jhl

A new species of the genus *Hexamermis* Steiner, 1924 (Nematoda: Mermithidae) from northern Iran: a nematode with an unusual uterine morphology

N. Vazifeh[1], G. Niknam[1], N.B. Camino[2] and F. Abootalebi[1]

[1]Department of Plant Protection, Faculty of Agriculture, University of Tabriz, Tabriz, Iran and [2]Investigador CIC Centro de Estudios Parasitológicos y de Vectores, CEPAVE, Facultad de Ciencias Naturales y Museo, UNLP, Argentine

Research Paper

Cite this article: Vazifeh N, Niknam G, Camino NB and Abootalebi F (2024). A new species of the genus *Hexamermis* Steiner, 1924 (Nematoda: Mermithidae) from northern Iran: a nematode with an unusual uterine morphology. *Journal of Helminthology*, **98**, e29, 1–8
https://doi.org/10.1017/S0022149X24000063.

Received: 20 November 2023
Revised: 05 January 2024
Accepted: 14 January 2024

Keywords:
D2-D3 28S-rRNA; description; morphometry; taxonomy; Zirab

Corresponding author:
G. Niknam;
Email: g_niknam@tabrizu.ac.ir

Abstract

Hexamermis zirabi sp. n., recovered from a natural habitat of Mazandaran province, north of Iran, is described based on morphological and molecular data. The new species is characterized by its six cephalic papillae; cuticle with distinct cross fibers; conoid or sharply tapered head; mouth terminal; six hypodermal cords; J-shaped vagina oriented to the anterior end of body; uterus with Z-organs or sclerotized bodies; tail similar in both sexes and bluntly rounded; spicules paired, separate, slightly curved, shorter than body width at cloaca, with rounded tip; and male genital papillae arranged in five rows. In addition to the morphological study, molecular phylogenetic analyses using a partial large subunit (28S D2-D3) were also performed, and the new species formed a highly supported (1.00% Bayesian posterior probability (BPP)) clade with *Hexamermis popilliae*.

Introduction

Mermithid nematodes are obligate invertebrate parasites dating back to the Early Cretaceous. Their fossil records are exceedingly sparse, especially before the Cenozoic era. Thus, little is known about their early host associations (Luo *et al*. 2023). The family Mermithidae Braun, 1883, comprises a group of parasitic nematodes with developmental hosts in the Arthropoda and Mollusca (Poinar 1983). Their hosts include species of at least 15 different orders of insects (Nickle 1972).

Integrated pest management approaches aim to avoid causing harm to beneficial organisms in agroecosystems; among them, mermithids can be considered very useful candidates because their potential as entomoparasites has already been realized and documented.

Hexamermis Steiner 1924 has been widely used in studies where agricultural pests are infested by entomopathogenic nematodes (Achinelly & Camino 2008). The genus is classified under Mermithidae and characterized by a morphological pattern very similar to what is observed in *Agamermis* (Cobb *et al.* 1923), with a very significant difference of presence (*vs* absence) of tail tip appendage that is always preserved after final molt (Hernández-Crespo & Santiago-Álvarez 1997). *Hexamermis* species are generally characterized by their six cephalic papillae; cuticle with distinct cross fibers; mouth central and terminal; small amphids; six hypodermal cords; J, V, or rarely a modified S-shaped vagina; and paired and separate spicules (Poinar & Linares 1985).

Until now, only one species of *Hexamermis*, namely *Hexamermis albicans* (Siebold 1848) Steiner 1923, has been reported from Iran (Nikdel *et al.* 2011). A new population of this genus was recovered during a recent nematological survey conducted to explore mermithid diversity in the soils of Mazandaran province, north of Iran. The study of the population confirmed that it belongs to an unknown species, whose characterization is the aim of the present contribution.

Material and methods

Sampling, morphological, and morphometric study

Soil samples were collected from the rhizosphere of *Diospyros lotus* from a natural habitat in Mazandaran province, northern Iran. The modified Brown and Boag (1988) method was used to extract the nematodes. The extracted nematodes were killed and processed to dehydrated glycerin, according to De Grisse (1969), and permanent slides were prepared. Nematodes were measured using an Olympus BX41 light microscope with differential interference contrast optics and a drawing tube. Microphotographs were taken using the same microscope equipped with a DP50 digital camera. Raw photographs were edited using Adobe Photoshop CS. Line drawings were done based on the digital images using CorelDRAW software, v12.

DNA extraction, PCR, and sequencing

Following morphological confirmation, one fresh specimen of *Hexamermis zirabi* sp. n., was selected for DNA extraction. DNA was extracted using a method from Archidona-Yuste *et al.* (2016). The DNA sample was stored at –20°C until used as a polymerase chain reaction (PCR) template. The D2-D3 expansion segments of 28S rRNA were amplified using forward D2A (5′-ACAAGTACCGT GAGGGAAAGTTG-3′) and reverse D3B (5′-TCGGAAGGAAC CAGCTACTA-3′) primers (Nunn 1992). A 25 µL PCR reaction mixture was composed of 10 µL ddH_2O, 12.5 µL PCR master mix (Ampliqon), 0.75 µL of each forward and reverse primers, and 1 µL of DNA template. The PCR cycle conditions were as follows: one denaturation cycle of 94°C for 15 min, followed by 35 cycles of 94° C for 45s; an annealing cycle of 55°C for 45s; an extension cycle of 72° C for 45s, and finally, one extension cycle of 72°C for 5 min. The PCR products were purified and sequenced directly for both strands using the same primers with Applied Biosystems 3730/3730xl DNA Analyzer in South Korea. The newly generated sequence of the 28S region was submitted to the GenBank database under accession number OR614376.

Phylogenetic analyses

The recently obtained sequence was aligned with 21 other D2-D3 expansion segments of 28S rRNA gene sequences available in GenBank, using Muscle software implemented in MEGA6 (Tamura *et al.* 2013). *Mononchus truncates* Bastian, 1865 (AY593064) was chosen as an outgroup taxon. The sequence dataset was analyzed with the Bayesian inference method using MrBayes 3.1.2 (Ronquist & Hulesenbeck 2003). The best-fit model of nucleotide substitution used for the phylogenetic analysis was statistically selected using MrModel test 2.3 (Nylander 2004) with an Akaike-supported model accompanied by PAUP* version 4.0b10 (Swofford 2003). After discarding burn-in samples and evaluating convergence, the remaining samples were retained for further analysis. The tree was visualized and saved with FigTree v1.4.3.

Results

Hexamermis zirabi sp. n.

Material examined

Six females and one male from one location were well preserved.

Description

These were small-sized mermithids. The body was mostly straight to J-shaped upon fixation, cylindrical, visibly narrowing toward the anterior end and less toward the posterior end since the caudal region is rounded. The color of the trophosome was yellow. Cuticle possessing distinct cross fibers, 4.5 – 6 µm thick in the anterior region, 6 – 9 µm at mid-body, and 8 – 11 µm in the tail region. The stoma was small and thin. The mouth opening was central and terminal. The head was conoid or sharply tapered, with a cephalic cap surrounding the mouth opening. Six cephalic (head) papillae were at the same plane, but there were no lip papillae. Amphids were oval-shaped and small, with an opening behind the lateral head papillae. Their aperture was circular, 5.5 – 7 µm wide, and occupying 19 – 21% lip region diameter. Six hypodermal chords were located at mid-body. Trophosome begins after the nerve ring, narrows at the anterior part, and is extended to near the end of the body in the female, but in the male, continues far beyond the head of the spicules and does not reach the level of the cloaca. The nerve ring encircled the pharynx's anterior part and was at 2.5 – 2.8% of the body length. Vulva, a longitudinal slit, was located post-equatorially. Vulval lips were lacking or greatly reduced, and the cuticular cone was well developed (sclerotized), 30 – 32 µm long. The vagina was J-shaped, muscular, oriented to the anterior end of body and curved at the distal portion where it meets the branches of the uteri, extending inward 73 – 75% of the body diameter in lateral view. The uterus had Z-organs or sclerotized bodies. The tail was similar in both sexes and was bluntly rounded. Spicules were paired, separate, slightly curved, equal, 11.7 times as long as wide, and shorter than the body width at the cloaca, with rounded tips. The male genital papillae were arranged in five rows: the lateral with 4 papillae as the outer row and 11 papillae in the middle or lateroventral one; the ventral row starts from near the head of the spicules and continues up to tail end, with seven pre-anal papillae: two simples and five triplets; six post-anal: four triplets, one double and one simple, with four genital papillae surrounding cloaca: Post-parasitic juveniles not found (Figs. 1 and 2).

Measurements

Female (n = 6): body length 5.85 – 9.68 (7.54) mm, width of the head at the level of cephalic papillae 29 – 38 (32) µm, body diameter at the level of nerve ring 87 – 106 (98) µm, body diameter at vulval region 140 – 175 (165) µm, distance from head to the nerve ring 169 – 250 (225) µm, body diameter at posterior end of the trophosome 112 – 138 (128) µm, length of vagina 161 – 212 (188) µm, width of vagina 62 – 83 (75) µm, V% = 57 – 60 (59), distance from end of trophosme to tail tip 60 – 80 (74) µm (Table 1).

Male (n = 1): body length 10.20 mm, width of the head at the level of cephalic papillae 43.7 µm, body diameter at the level of nerve ring 125 µm, greatest diameter of the body 158 µm, body diameter at cloaca 142 µm, distance from the head to the nerve ring 260 µm, length of spicules 117 µm, width of spicules 10 µm.

Molecular characterization

A 28S rRNA sequence of *Hexamermis zirabi* sp. n., was obtained, having 762 bp (OR614376).

Diagnosis

Six cephalic papillae; cuticle with distinct cross fibers; head conoid or sharply tapered; mouth central and terminal; amphids small and oval shaped; six hypodermal cords; vulva a longitudinal slit and located post-equatorially; vulval cuticular cone well developed (sclerotized); vagina J-shaped and oriented to the anterior end of body; uterus with Z-organs or sclerotized bodies; tail similar in both sexes, bluntly rounded; spicules paired, separate, slightly curved, shorter than body width at cloaca, with rounded tip; male genital papillae arranged in five rows: the lateral with 4 papillae as the outer row and 11 papillae in the middle or lateroventral

https://doi.org/10.1017/S0022149X24000063 Published online by Cambridge University Press

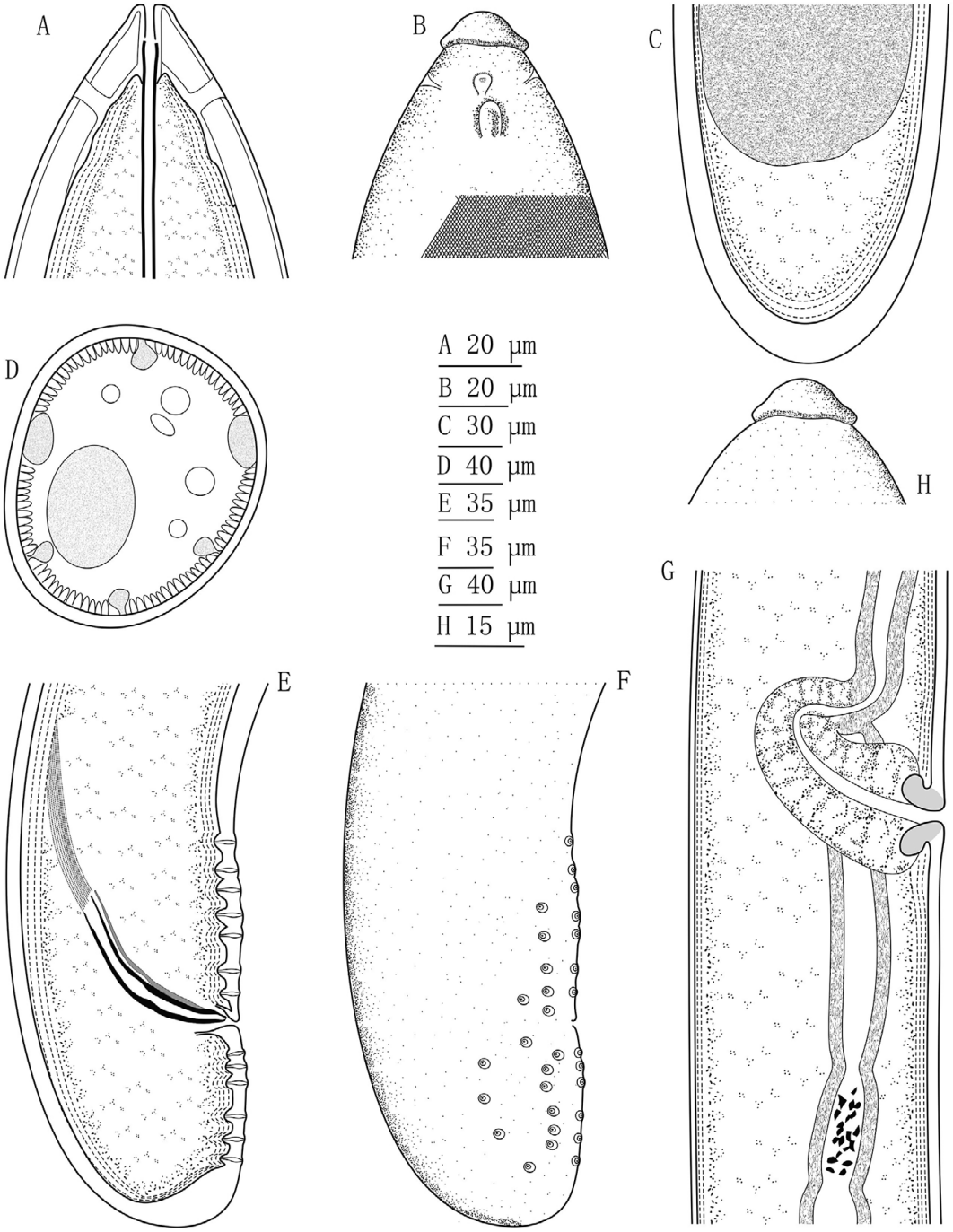

Figure 1. *Hexamermis zirabi* sp. n. (A) Anterior region in lateral median view; (B and H) Anterior region in lateral surface view; (C) Female caudal region; (D) Cross-section, mid-body; (E) Male caudal region in lateral median view; (F) Male caudal region in lateral surface view; (G) Vulval region and vagina.

one; the ventral row starts from near the head of the spicules and continues up to the tail end, with seven pre-anal papillae: two simples and five triplets; and six post-anal: four triplets, one double and one simple, with four genital papillae surrounding cloaca, separate the new species from previously described members of *Hexamermis*.

Relationships

Morphologically, *Hexamermis zirabi* sp. n. is readily recognized and distinguished from its congeners by the peculiar morphology of its uterus, which has Z-organs or sclerotized bodies *vs* the absence of such structures in the uterus. Additionally, leaving aside *H. cavicola* (Welch 1963), an Australian species, the new species can be separated from other *Hexamermis* members by its conoid or sharply tapered head region. It differs from *H. cavicola* by the body length (5.85 – 10 *vs* 60 – 160 mm), presence of seven pre- and six post-anal *vs* eight pre- and ten post-anal genital papillae, spicules length (117 *vs* 470 – 550 µm), vulva location (57 – 60% *vs* 53 – 56%) and other characters (for more comparison, see Welch, 1963). The new species is also comparable to *H. albicans*, Costa Rican population, which is distinguished by

https://doi.org/10.1017/S0022149X24000063 Published online by Cambridge University Press

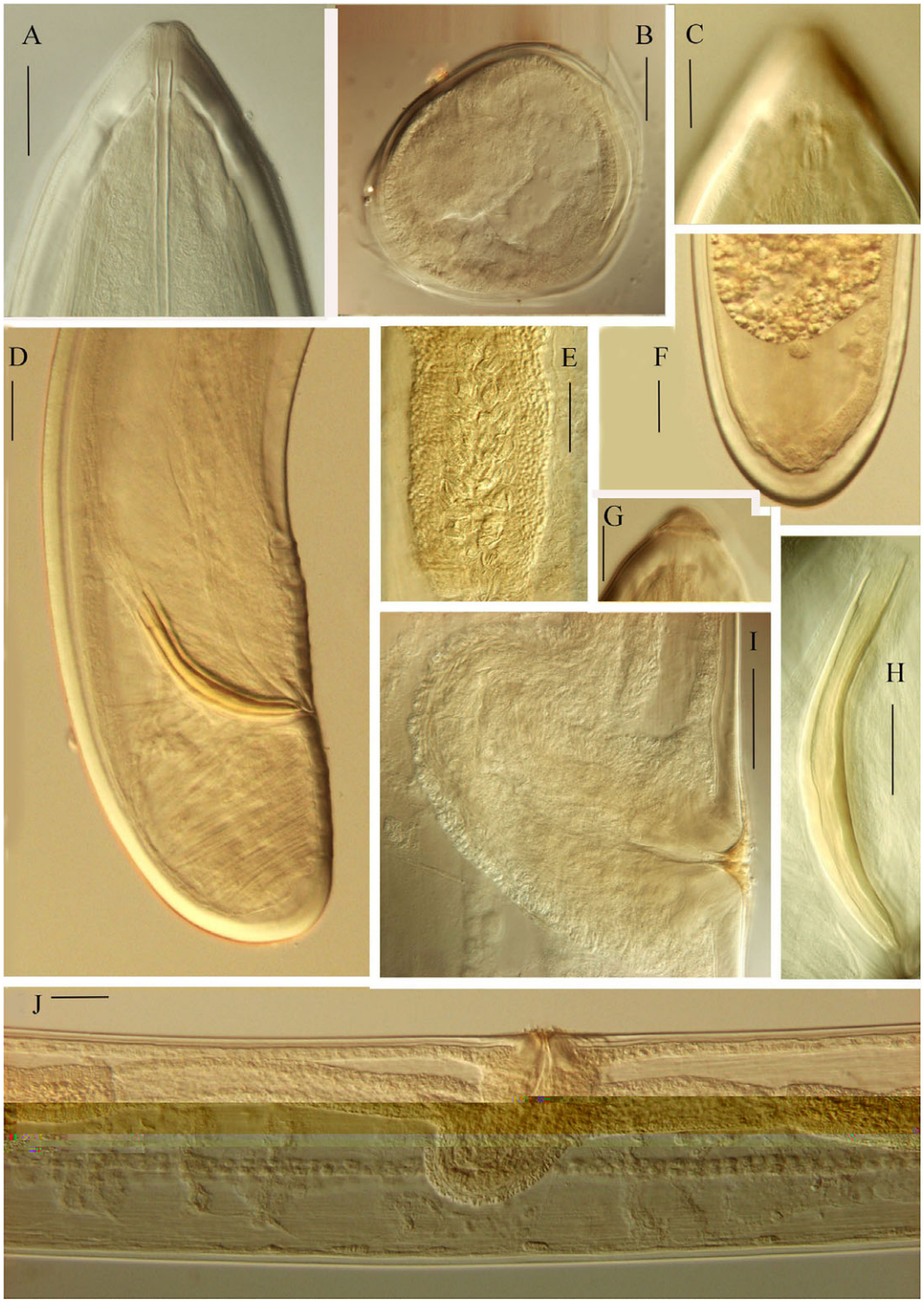

Figure 2. *Hexamermis zirabi* sp. n. (A) Anterior region in lateral median view; (B) Cross-section, mid-body; (C and G) Anterior region in lateral surface view; (D) Male caudal region in lateral median view; (E) Z-organs; F: Female caudal region; (G) Cross fibers; (H) Spicules; (I and J) Vulval region and vagina. Scale bars: (A, C, E) (H) 20 μm; (B) (J) 40 μm; (D) 35 μm; (F) (I) 40 μm; (G) 15 μm.

having small body size (5.85 – 9.68 *vs* 42 – 83.8 mm), narrower lip region (29 – 43.7 *vs* 51.7 – 53.5 μm), the more posterior position of the vulva (57 – 60% *vs* 40 – 54%) and the presence of seven pre- and six post-anal *vs* three pre- and six post-anal genital papillae (Table 1).

Phylogenetically, *Hexamermis zirabi* sp. n. is related to *H. popillae* (Mazza *et al.* 2017), an Italian species, but can be differentiated by the conoid or sharply tapered *vs* obtuse head region, amphidial openings small *vs* large, female body length (5.85 – 9.68 *vs* 18 – 50 mm), size of the vagina (62 – 83 × 161 –

https://doi.org/10.1017/S0022149X24000063 Published online by Cambridge University Press

212 *vs* 154 – 176 × 224 – 384 µm) and male genital papillae arrangement in a row (*vs* clustered).

Type locality and habitat

Zirab County, Mazandaran province, north of Iran (GPS coordinates: 36°10′68″ N 052°57′86″E, altitude 500 m a.s.l.), in the rhizosphere of *Diospyros lotus.*

Type material

Holotype female, five paratype females and males were deposited at the Nematode Collection of the Department of Plant Protection, Faculty of Agriculture, University of Tabriz, Tabriz, Iran.

Etymology

The name of the species refers to the location of the new species, Zirab County, Mazandaran province, north of Iran.

On the phylogeny

The evolutionary relationships of *Hexamermis zirabi* sp. n., as derived from molecular analysis along with other mermithids, are presented in Figure 3. The average nucleotide composition is as follows: 22.37% A, 21.86% C, 29.97% G, and 25.81% T. The new species forms a highly supported (1.00% Bayesian posterior probability (BPP)) clade with *Hexamermis popilliae.* The new 28S sequence in the pairwise comparison with *Hexamermis popilliae* (MF040825) presents 81.89% identity (28 bp differences: insertions,

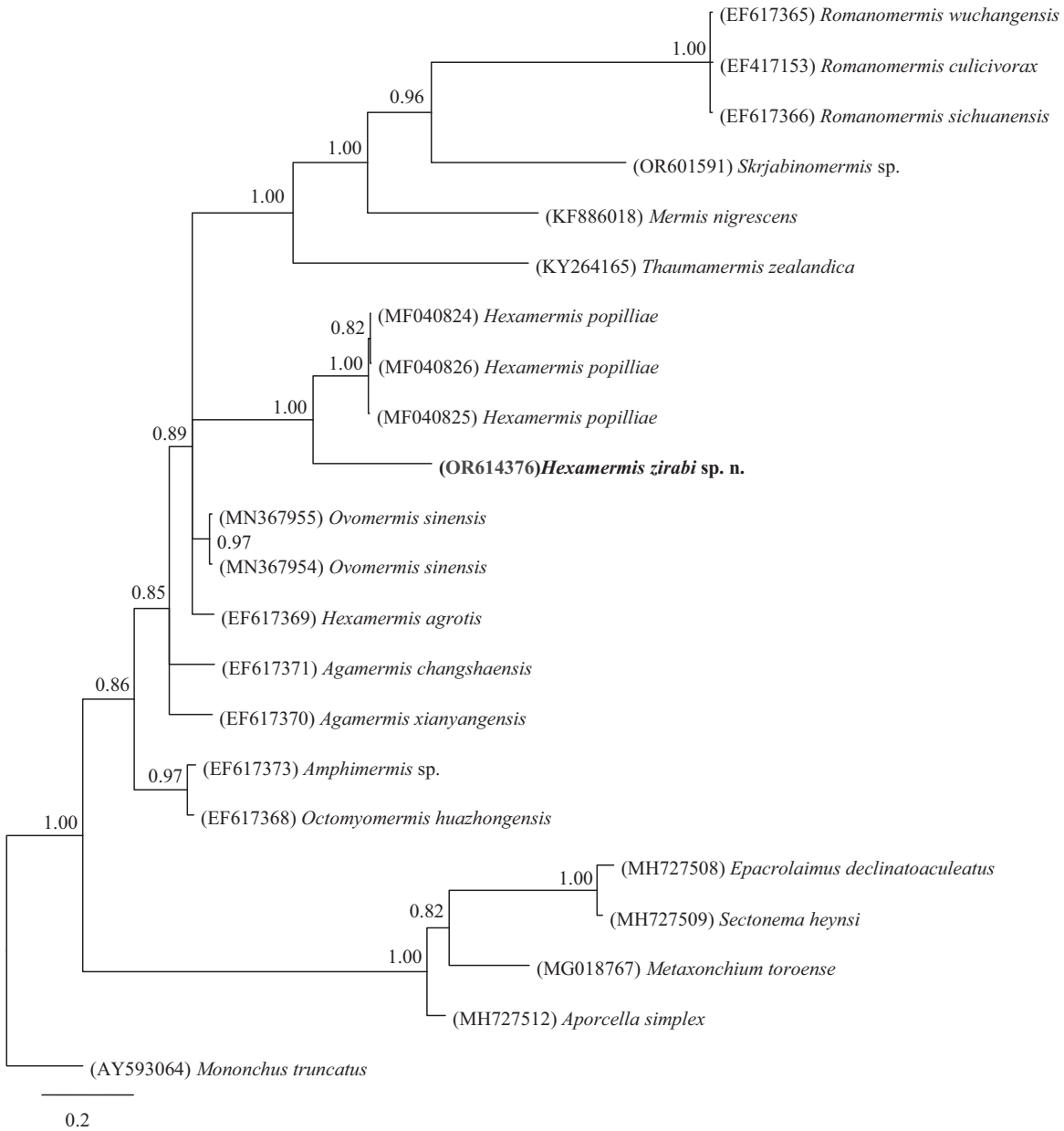

Figure 3. Consensus 50% majority rule Bayesian phylogenetic tree of *Hexamermis zirabi* sp. n. based on 28S rRNA D2-D3 sequences under the GTR+I+G model. Posterior probabilities >50% are given for appropriate clades. The newly obtained sequence is in bold.

https://doi.org/10.1017/S0022149X24000063 Published online by Cambridge University Press

Table 1. Main morphometrics of *Hexamermis zirabi* sp. n. and its three close species of the genus *Hexamermis.* All measurements in μm (except body length in mm)

Characters	*H. zirabi* sp. n.		*H. cavicola* (Welch 1963)		*H. popilliae* (Mazza *et al.* 2017)		*H. albicans* (Nickle & Grijpma 1974)	
	Female	Male	Female	Male	Female	Male	Female	Male
n	6	1	4	6	6	6	4	5
Body length	5.85 – 9.68	10.20	123 – 160	60 – 90	18 – 50	10 – 13	42 – 83.8	11 – 33.2
Width of the head at the level of cephalic papillae	29 – 38	43.7	74 – 90	58 – 84	–	–	51.7[a]	53.5[a]
Body diameter at the level of nerve ring	87 – 106	125	240 – 270	160 – 230	153 – 172	–	–	–
Greatest diameter of the body	140 – 175	158	580 – 650	300 – 460	256 – 320	190 – 240	157 – 220	114 – 136.8
Distance from head to the nerve ring	169 – 250	260	400 – 510	350 – 530	–	120-132	–	–
Body diameter at posterior end of the trophosome/at cloaca	112 – 138	142	–	260 – 300	–	112 – 128	138[a]	–
Length of vagina	160 – 212	–	–	–	224 – 384	–	170[a]	–
Width of vagina	62 – 83	–	–	–	154 – 176	–	116[a]	–
V%	57 – 60	–	53 – 56	–	–	–	40 – 54	–
Length of spicules	–	117	–	470 – 550	–	108 – 120	–	92.6 – 130

[a]Calculated from Nickle and Grijpma (1974) illustration.

Table 2. Insects reported from Zirab County, Mazandaran province, north of Iran

Superfamily	Family	Genus	species
Papilionoidea Latreille, 1802	Papilionoidae Latreille, 1802	*Iphichlides* Hubner, 1819	*Iphichlides podalirius* Linnaeus, 1758
	Pieridae, Duponchel, 1835	*Pieris* Schrank, 1801	*Pieris brassicae* Linnaeus, 1758
			Pieris rapae Linnaeus, 1758
		Pontia Fabricius, 1807	*Pontia (Daplidice) edusa* Fabricius, 1777
		Anthocharis Boisduval, Rambur, Dumenil, & Graslin, 1833	*Anthocharis cardamines* Linnaeus, 1758
		Colias Fabricius, 1807	*Colias (Eriocolias) crocea* Fourcroy, 1758
		Gonepteryx Leach, 1815	*Gonepteryx rhamni* Linnaeus, 1758
	Lycaenidae Leach, 1815	*Lycaena* Fabricius, 1807	*Lycaena tityrus* Poda, 1761
			Lycaena phlaeas Linnaeus, 1761
		Polyommatus Latreille, 1804	*Polyommatus (Polyommatus) icarus* Rottemburg, 1775
	Nymphalidae Swainson, 1827	*Limenitis* Fabricius, 1807	*Limenitis reducta* Staudinger, 1901
		Vanessa Fabricius, 1807	*Vanessa (Cynthia) atalanta* Linnaeus, 1758
			Vanessa (Cynthia) cardui Linnaeus, 1758
		Agiais Dalman, 1816	*Aglais urticae turcicae* Staudinger, 1861
			Aglais io Linnaeus, 1758
		Argynnis Fabricius, 1807	*Argynnis (Argynnis) paphia masandaranensis* Gross & Ebert, 1975
			Argynnis (Pandoriana) pandora Denis & Schiffermuller, 1775
		Issoria Hubner, 1819	*Issoria lathonia* Linnaeus, 1758
		Lasiommata Westwood, 1841	*Lasiommata megera transcaspica* Staudinger, 1901
			Lasiommata adrastoides Bienert, 1869
		Maniola Schrank, 1801	*Maniola jurtina phorima* Fruhstorfer, 1909
		Chazara Moore, 1893	*Chazara briseis meridionalis* Staudinger, 1886
	Libytheidae Boisduval, 1833	*Libythea* Fabricius, 1807	*Libythea celtis* Laicharting, 1782

Adapted from Khayrandish *et al.* 2011

https://doi.org/10.1017/S0022149X24000063 Published online by Cambridge University Press

deletions, or substitutions/no gaps). GenBank database is very poor in large subunit sequences deposited from Mermithidae, and more sequences of the species belonging to the family are required to enable a detailed discussion on the molecular phylogeny of the group.

Discussion

There has been little study about the mermithids fauna in Iran. The only available taxonomic document is a paper published by Nikdel *et al.* (2011) in which they described *Hexamermis albicans* parasitizing the abdominal cavity of larvae of two lepidopterans, *Euproctis chrysorrhoea* and *Lymantria dispar* (Lymantriidae) during a survey conducted to study mermithids in Arasbaran area, northwest of Iran. Although the study on mermithids is still in its early stages in Iran, our recent sampling showed that the group is species-rich in the understudied regions. So, as a part of the survey results, an unknown species of the genus *Hexamermis* was collected, described, and illustrated in this contribution. *Hexamermis zirabi* sp. n. was recovered from rhizospheric soil samples of *Diospyros lotus* from the north of Iran.

The presence of sclerotized bodies in the uterus of the new species and a sharply narrower head region differentiated the species from all the previously described species of the genus. Regarding the function of uterine differentiation, there is no report on the structures in the mermitid's uterus. Still, several possible functions have been proposed for uterine differentiation in *Xiphinema* (Cobb 1913), which may also be the case in mermithids. Kruger (1988) pointed out (p. 250) that 'These vary from slowing the passage of eggs through the uterus during shell formation, the prevention of sperm reflux from the spermatheca during egg movement, and the secretion of certain substances from the globular structures for eggshell formation'. Z-organs in the understudy population of the new species are triangular to rhomboid and 6.5 – 9 µm long and are seen as a complex structure inside the uterus. Additional histochemical and physiological investigations may elucidate uterine differentiation's actual function(s) in the future.

Morphological differences of *Hexamermis zirabi* sp. n. compared with the closely related species were discussed in the earlier parts of the text. We tried several times to find this species' associated or potential hosts, but unfortunately, it was not possible. According to the insect fauna reported from this area (Table 2), its possible host(s) may be a member of the order Lepidoptera. As mentioned above, *Hexamermis albicans* was previously isolated and reported from two species of this order in Arasbaran forests of Iran.

The present study's phylogenic analysis was based on one LSU D2-D3 marker. However, the monophyly of the genus was not confirmed, and further sequences of other representatives of the genus are needed to assess their monophyly. In our tree, *Hexamermis agrotis* with accession number EF617369 was placed in a branch far from the *Hexamermis* spp. Morphological data of the abovementioned species was not available and its identity may need further confirmation.

As we claimed above, regarding the richness of species of mermithids in Iran, we have identified two new genera and several new species belonging to the different genera of mermithids whose descriptions are in preparation.

Financial support. This research received no specific grant from any funding agency, commercial or not-for-profit sectors.

Competing interest. The authors have no competing interests.

References

Achinelly MF and Camino NB (2008) *Hexamermis paranaense* new species (Nematoda, Mermithidae): a parasite of *Diloboderus abderus* (Coleoptera, Scarabaeidae) in Argentina. *Iheringia Serie Zoologia* **98**, 460–463.

Archidona-Yuste A, Navas-Cortés JA, Cantalapiedra-Navarrete C, Palomares-Rius JE and Castillo P (2016) Cryptic diversity and species delimitation in the *Xiphinema americanum*-group complex (Nematoda: Longidoridae) as inferred from morphometric and molecular markers. *Zoological Journal of the Linnean Society* **176**(**2**), 231–265.

Bastian HC (1865) II. Monograph of the Anguillulidae, or free nematoids, marine, land, and freshwater, with descriptions of 100 new species. *Transactions of the Linnean Society of London* **25**, 73–184.

Braun M (1883) *Die thierisher Parasiten des Menchen nebst einer Anleitung zur praktischen Beschaeftigung mit der Helminthologie fuer Stadierende und Aertze*. Anon, Wurzburg. 233 pp.

Brown DJF and Boag B (1988) An examination of methods used to extract virus-vector nematodes (Nematoda: Longidoridae and Trichodoridae) from soil samples. *Nematologia Mediterranea* **16**, 93–99.

Cobb NA (1913). New nematode genera found inhabiting fresh water and non-brackish soils. *Journal of the Washington Academy of Sciences* **3**, 432–444.

Cobb NA, Steiner G and Christie LR (1923) *Agamermis decaudata*: a nema parasite of grasshoppers and other insects. *Journal of Agricultural Research* **11**, 921–926.

De Grisse AT (1969) Redescription ou modification de quelques techniques utilisées dans l´étude des nematodes phytoparasitaires. *Mededelingen Rijksfaculteit Landbouwwetenschappen Gent* **34**, 351–69.

Hernández-Crespo P and Santiago-Álvarez C (1997) Description of *Hexamermis serenensis* sp. n. (Nematoda: Mermithidae) a parasite of *Dociostaurus macroccanus* (Thunberg) (Orthoptera: Acrididae) in Spain. *Fundamental and applied Nematology* **20**, 37–42.

Khayrandish A, Ahmadzade F and Naderi A (2011) Investigation of Rhopalocera butterflies from Zirab Savad-kooh. *Iranian Journal of Biology* **23**(**5**), 752–760.

Kruger JC de W (1988) The uterine differentiation in *Xiphinema*. *Phytophylactica* **20**, 233–251.

Luo C, Poinar GOJr, Xu C, Zhuo D, Jarzembowski EA, and Wang B (2023). Widespread mermithid nematode parasitism of Cretaceous insects. *eLife*, **12**, e86283.

Mazza G, Paoli F, Strangi A, Torrini G, Marianelli L, Peverieri GS, Binazzi F, Bosio G, Sacchi S, Benvenuti C, Venanzio D, Giacometto E, Roversi PF and Poinar GO Jr (2017) *Hexamermis popilliae* n. sp. (Nematoda: Mermithidae) parasitizing the Japanese beetle *Popillia japonica* Newman (Coleoptera: Scarabaeidae) in Italy. *Systematic Parasitology* **94**(**8**), 915–926.

Nikdel M, Kaiser H and Niknam G (2011) First record of *Hexamermis* cf. *albicans* (Siebold, 1848) (Nematoda: Mermithidae) infecting lepidopteran larvae from Iran. *Nematologia Mediterranea* **39**(**1**), 81–83.

Nickle WR (1972) A contribution to our knowledge of the Mermithidae (Nematoda). *Journal of Nematology* **4**, 113–146.

Nickle WR and Grijpma P (1974) *Hexamermis albicans* (Siebold) (Nematoda: Mermithidae) a parasite of the larva. *Turrialba* **24**, 70–74.

Nunn GB (1992) *Nematode Molecular Evolution. An Investigation of Evolutionary Patterns among Nematodes based on DNA Sequences*. Nottingham, UK, University of Nottingham.

Nylander JAA (2004) *MrModeltest v2. Program distributed by the author*. Sweden, Uppsala University, Evolutionary Biology Centre.

Ronquist F and Huelsenbeck JP (2003) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* **19**, 1572–1574.

Poinar GO Jr and Linares B (1985) *Hexamermis dactylocercus* sp. n. (Mermithidae: Nematoda), a parasite of *Aeneolamia varia* (Cercopidae: Homoptera) in Venezuela. *Revue de Nématologie* **8**(**2**), 109–111.

https://doi.org/10.1017/S0022149X24000063 Published online by Cambridge University Press

Poinar GO Jr (1983) *The Natural History of Nematodes*. Prentice Hall, Englewood Cliffs, New Jersey. 323 pp.

Siebold ThVon (1848) Ueber die Fadenwiirmer der Insecten. *Stettiner Entomologische Zeitung* **9**, 290–300.

Steiner G (1923) Limicole Mermithiden aus dem Sarekgebirge und der Torne Lappmark. (Beitrag von Dr I. G. de Man.) *Naturw Untersuch Sarekgeb* **4**(**8**), 805–828.

Steiner G (1924) Mermithids parasitic in the tea bug (*Helopeltis antoniisign*). *Mededell. Proefst. Thee* **44**, 10–16.

Swofford DL (2003) *PAUP*: phylogenetic analysis using parsimony (*and other methods), version 4.0b 10*. Sunderland, MA, Sinauer Associates.

Tamura K, **Stecher G**, **Peterson D**, **Filipski A and Kumar S** (2013) MEGA6: molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution* **30**, 2725–2729.

Welch HE (1963) *Amphimermis bogongae* sp. nov. and *Hexamermis cavicola* sp. nov. from the Australian bogong moth. *Parasitology* **53**, 55–62.

https://doi.org/10.1017/S0022149X24000063 Published online by Cambridge University Press