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A new cyst nematode, Heterodera tropica sp. n. (Tylenchida: Heteroderidae) parasitising the breadnut tree, Brosimum alicastrum from a tropical forest in Veracruz State, Mexico

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Summary. A new species of cyst nematode of the genus *Heterodera* belonging to the *Humuli* group is described from rhizosphere soil and roots of the breadnut tree, *Brosimum alicastrum* (family Moraceae) in a tropical forest in La Mancha of Veracruz State, Mexico. The breadnut cyst nematode, *Heterodera tropica* sp. n. is characterised by small ambifenestral cysts without bullae and a weak underbridge. Second-stage juveniles have well-developed stylet 20-24 μm long, conical tail, 32-56 μm long with hyaline region, 17-28 μm. Phylogenetic relationships of *H. tropica* sp. n. with other species of the *Humuli* group were reconstructed using the D2-D3 expansion segments of 28S rRNA, ITS rRNA and *COI* gene sequences. The new species is morphologically and molecularly similar to the fig cyst nematode, *H. fici* and these two cyst nematodes are shown to be sister species in phylogenetic trees reconstructed using the ITS rRNA and *COI* gene sequences. With the description of the breadnut cyst nematode, together with *H. humuli* and *H. fici,* the number of species of *Humuli* group reported in North America increased to three.

Keywords: 28S rRNA gene, *COI* gene, *Humuli* group, new species, phylogeny, Veracruz State.

Presently, four valid species of the genus *Heterodera* Schmidt, 1871: *H. carotae* Jones, 1950, *H. cyperi* Golden, Rau & Cobb, 1962, *H. humuli* Filipjev, 1934 and *H. schachtii* A. Schmidt, 1871, and several unidentified species of cyst-forming nematodes of this genus have been reported in Mexico (Escobar-Avila *et al.,* 2018; Subbotin *et al.,* 2021). In 2023-2025, during nematological surveys in different Mexico states, a few cysts of the genus *Heterodera* were collected from rhizosphere soil and roots of the breadnut tree, *Brosimum alicastrum* Sw. (family Moraceae) in the jungle area near the Ecological Station La Mancha, Ecology Institute of Jalapa, Veracruz State. After morphological, morphometric and molecular studies, these cysts were identified as belonging to a new species of the *Humuli* group of the genus *Heterodera*. Morphological description and molecular characterisation of the new species, *Heterodera tropica* sp. n. is provided in this study.

MATERIALS AND METHODS

Nematode samples. Soil and root samples were collected from the breadnut tree, *B. alicastrum* in a tropical forest near the Ecological Station La Mancha, Ecology Institute of Jalapa, Veracruz State, Mexico. Second-stage juveniles (J2) and cysts were extracted by using the centrifugal-flotation method (Jenkins,

1964) and sieving technique (Ayoub, 1977). Cysts and J2 specimens were hand-picked under a stereomicroscope and used for morphological study or transferred to 70% ethanol for molecular study.

Morphological study. Second-stage juveniles were killed by heating in a drop of water at 50°C and fixed in Golden solution (Hooper, 1970). They were transferred to 20 ml vials and stored at room temperature for 10 days. The nematodes were then processed to dehydrated glycerin using a modification of the Seinhorst (1959) method and mounted on slides for light microscopy (LM) and scanning electron microscopy (SEM) as described by Cid Del Prado Vera and Subbotin (2012). Vulval cone sections were mounted in glycerin-gelatine. Measurements and drawings of cysts and J2 were made using a drawing tube and photographs were taken with a digital camera mounted on an American Optical compound microscope (AO, USA).

DNA extraction, PCR and sequencing of nematode samples. DNA was extracted from several J2 individuals using a standard protocol with proteinase K. PCR and sequencing were performed as described by Subbotin *et al.* (2021). Several primer sets were used: Het-coxiF (5' - TAG TTG ATC GTA ATT TTA ATG G - 3') and Het-coxiR (5' - CCT AAA ACA TAA TGA AAA TGW GC - 3') primers for amplification of the partial *COI* gene;TW81 (5' - GTT TCC GTA GGT GAA CCT GC - 3') and AB28 (5' - ATA TGC TTA AGT TCA GCG GGT - 3') primers for amplification of the ITS1-5.8S-ITS2 rRNA gene and D2A (5' - ACA AGT ACC GTG AGG GAA AGT TG-3') and D3B (5' - TCG GAA GGA ACC AGC TAC TA - 3') primers for amplification of the D2-D3 expansion segments of 28S rRNA gene (Subbotin *et al.,* 2021, 2022). The sequencing was performed by Azenta (California, USA). New nematode sequences were submitted to GenBank under accession numbers: PV962729 (D2D3 of 28S rRNA gene), PV962730 (ITS rRNA gene), PV962830 (*COI* gene) and indicated in phylogenetic trees.

Phylogenetic analysis of nematode samples. New sequences were aligned with corresponding published D2-D3 of 28S rRNA, ITS rRNA and *COI* gene sequences (Subbotin *et al*., 2001, 2022; Fanelli *et al*., 2019; Jiang *et al.,* 2021; Sakata & Kushida, 2024; Yang *et al.,* 2024; Ni *et al.,* 2025) using ClustalX 1.83 (Chenna *et al.,* 2003) with default parameters. Alignments were analysed with Bayesian inference (BI) using MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003). BI analysis for each gene was initiated with a random starting tree and was run with four chains for 1.0×10^6 generations. Posterior probabilities (PP) are given on appropriate clades. Sequence analysis of alignments was performed with PAUP 4b10 (Swofford, 2003). Pairwise divergences between taxa were computed as absolute distance values and as percentage mean distance values based on whole alignment, with adjustment for missing data.

Molecular identification of plant material. The plant host was identified using the ITS rRNA gene sequences. DNA from roots was extracted using QIAgen DNeasy Plant Mini Kit (Qiagen, USA). PCR was performed with Premix Ex Taq (Takara Bio Inc., Japan). The ITS5 (5' - GGA AGT AAA AGT CGT AAC AAG G - 3') and 26S-25R (5' - TAT GCT TAA AYT CAG CGG GT - 3') (Liston *et al.,* 1996) primers were used for amplification of the ITS1-5.8S-ITS2 rRNA gene. The new plant ITS rRNA gene sequence was compared with those deposited in the GenBank using Blastn (https://www.ncbi.nlm.nih.gov/ genbank/). New plant ITS rRNA gene sequence was submitted to GenBank under accession number: PV959259.

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RESULTS

Heterodera tropica sp. n. (Figs 1-4)

Measurements: see Tables 1 and 2.

Cyst. Body basically lemon-shaped, light brown colour, with a short neck that is straight or curved 41.2±9.0 (20-58) µm long, without a subcrystalline layer. Vulval cone distinct, with zig-zag ridges surrounding the fenestra. Ambifenestrate with symmetrical semifenestra, bullae absent, underbridge weak.

Second stage juveniles. Body vermiform, lip region slightly set off, with three to four annuli. Stylet well-developed, basal knobs rounded, directed slightly anteriorly. Median bulb ovoid. Pharyngeal lobe 122-156 µm long, overlapping intestine dorsally. Excretory pore at level of the first third of the pharyngeal lobe. Cuticle with conspicuous annulation. Lateral field with four incisures, areolated in the external bands and a few areolation in the internal band in the middle region. Genital primordium posterior to the mid-body, 10-17 µm long by 6-7 µm wide. Anus distinct. Tail conical with terminus almost acute. Phasmids 5.0-12 (7.8) µm posterior to anus. Hyaline part about 50% of tail length.

White female: not found.

Male: not found.

Eggs (n=37): Shells hyaline, without surface markings. Length (L) = 89.6±2.8 (82-95) µm; width (W) = 39.8±1.6 (37-43) µm; L/W = 2.3±0.1 (2.1-2.5).

Etymology. The specific epithet is derived from the tropical locality from which the species is described.

Type host and locality. The breadnut cyst nematode, *H. tropica* sp. n. was collected from roots of the breadnut, *Brosimum alicastrum* Sw. (family Moraceae) in a tropical forest in La Mancha, Actopan County, Veracruz State, Mexico (N 19°35'.820; W 96°22'.550), 2 m above sea level.

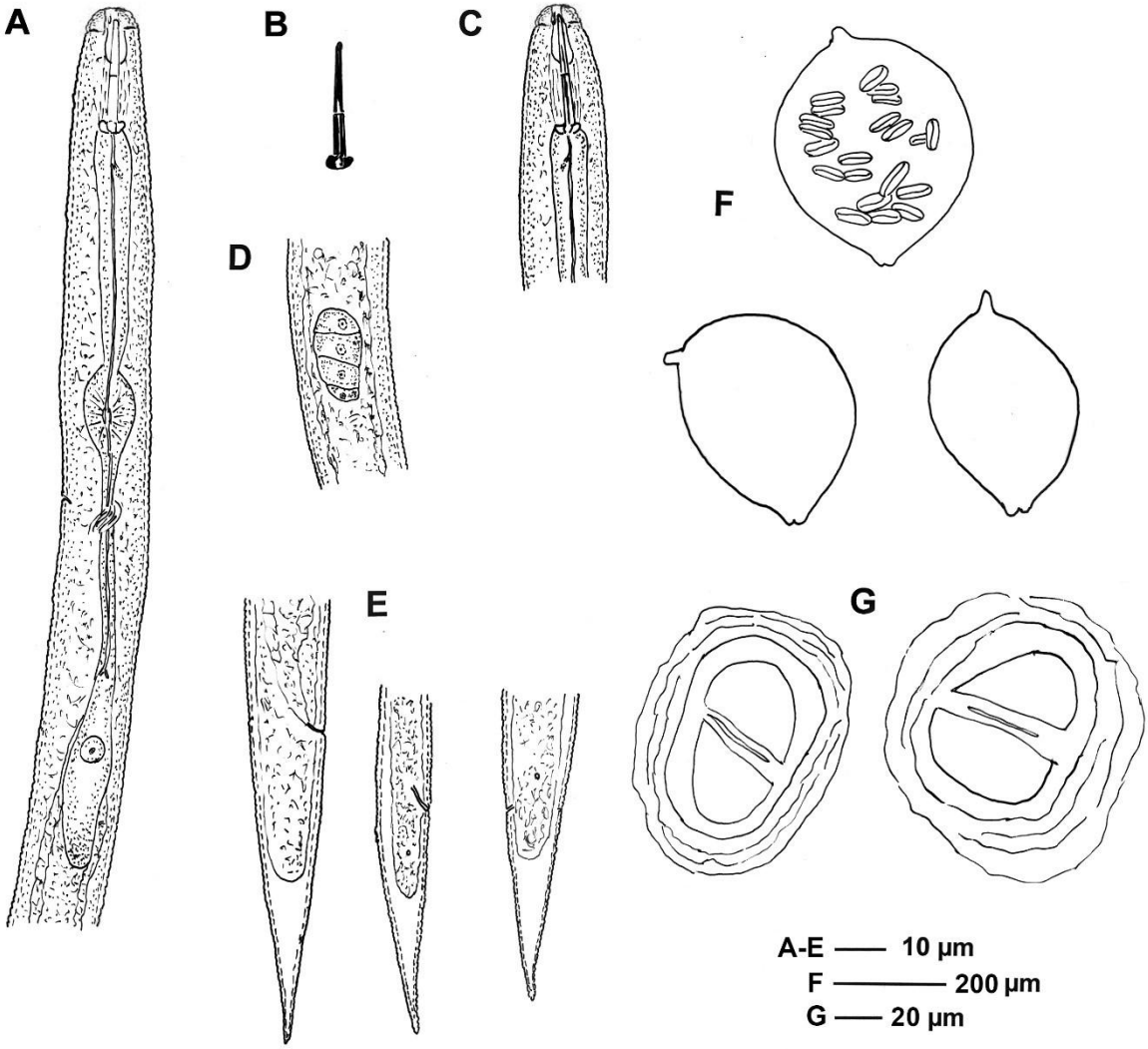

Fig. 1. *Heterodera tropica* sp. n. A-E: Second stage juvenile. A: Anterior region; B: Stylet; C: Lip region; D. Genital primordium; E: Tails; F: Cysts; G: Ambifenestrate vulval plates.

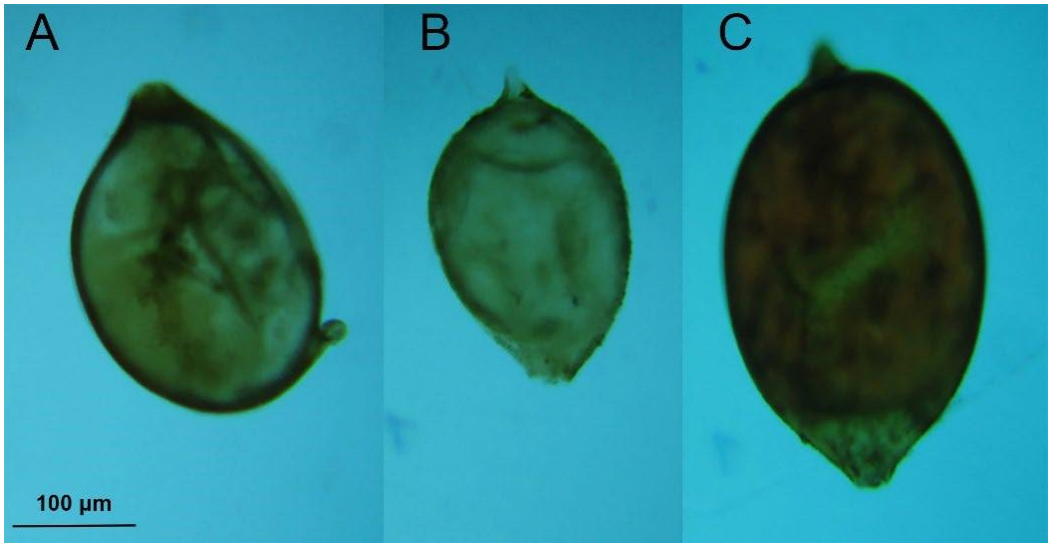

Fig. 2. *Heterodera tropica* sp. n. Light microscope photographs. A-C: Cyst shape.

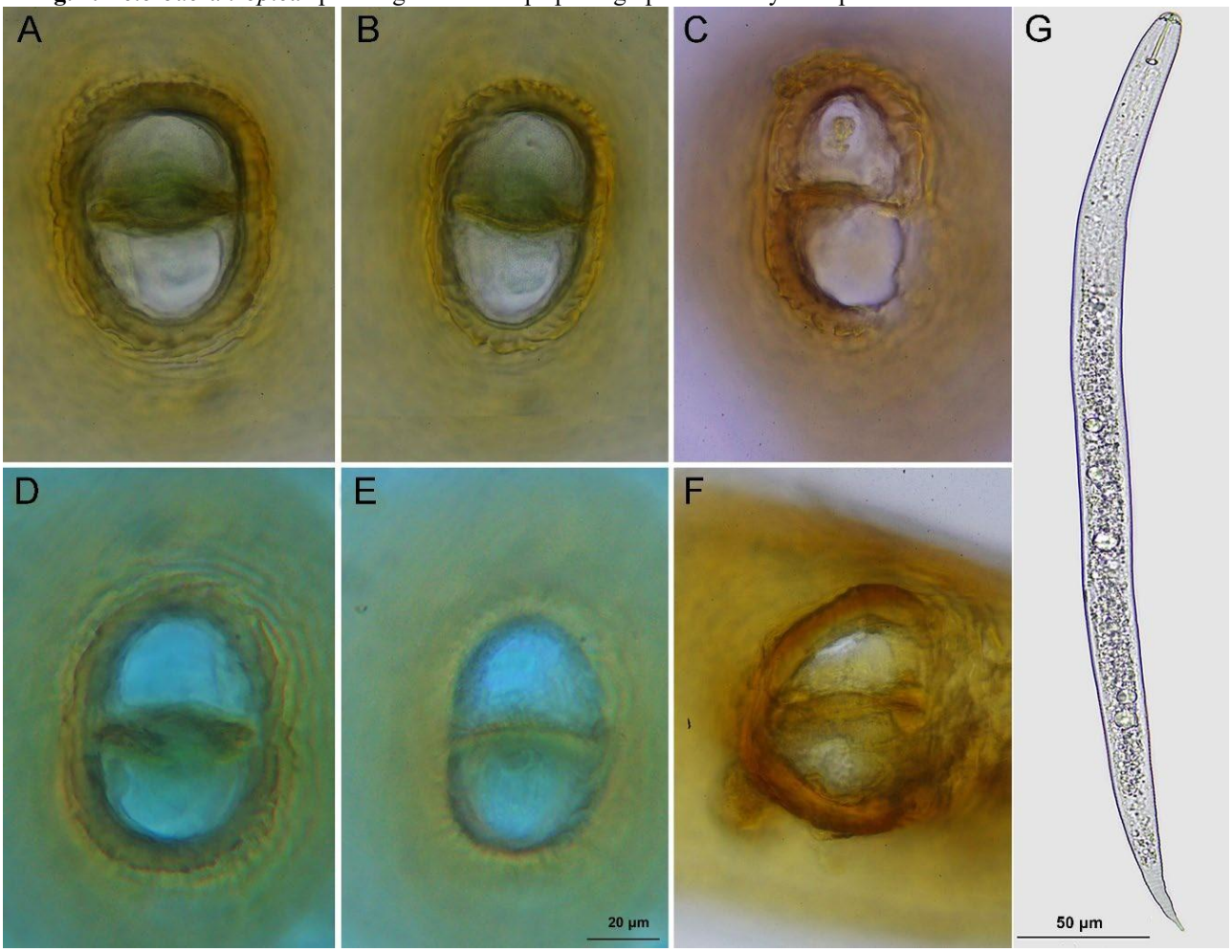

Fig. 3. *Heterodera tropica* sp. n. Light microscope photographs. A-F: Ambifenestrate vulval plate; G: Entire body of second stage juvenile.

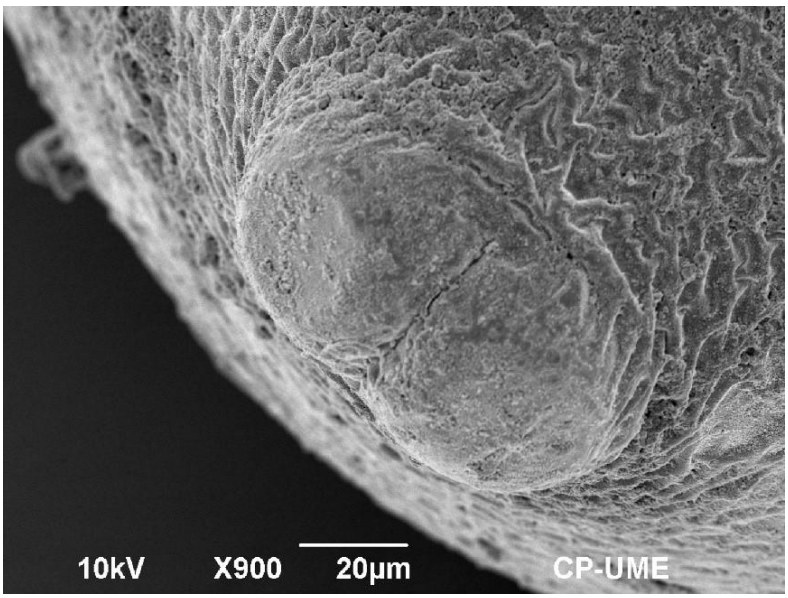

Fig. 4. *Heterodera tropica* sp. n. Scanning electron microscope photograph. Vulval region of cyst.

Table 1. Measurements of cysts of *Heterodera tropica* sp. n.
All measurements are in µm and in the form: mean ± s.d. (range).

Samples / Character	Holotype	Paratypes
n	1	15
Body length (L) without neck	334	432 ± 58.9 (246-536)
L with neck	374	446 ±6 4 (294-540)
Body width (W)	230	326 ± 48.4 (196- 574)
L/W (without neck)	1.45	1.29 ± 0.24 (0.78-1.82)
L/W (with neck)	1.63	1.39 ± 0.24 (0.89-1.76)
n	-	8
Fenestra length	-	46.8 ± 7.9 (32-55)
Fenestra width	-	34 ± 6.2 (25-41)
Vulva slit	-	34.5 ± 6.5 (26-40)

Table 2. Morphometrics of second-stage juveniles of *Heterodera tropica* sp. n.
All measurements are in µm and in the form: mean ± s.d. (range).

Samples / Character	Paratypes Fixed	Immobilised by heating
n	5	11
L	380 ± 1.0 (370-400)	410 ± 3.0 (350-460)
a	22.7 ± 0.7 (21.9-23.6)	21.6 ± 2.3 (16-24)
b	4.4 ± 0.3(4.0-4.9)	3.9 ± 0.4 (3.3-4.5)
b'	2.6 ± 0.3 (2.3-3.0)	3.0 ± 0.1 (2.5-3.3)
c	9.7 ± 1.8 (7.9-11.7)	8.2 ± 0.5 (7.6-9.3)
c'	3.4 ± 0.7 (2.5-4.3)	3.9 ± 0.6 (3.0-4.8)
Stylet length	21.8 ± 0.5 (21.0-22.0)	22.3 ± 1.0 (20-24)
Stylet knob width	4.3 ± 0.5 (4.0-5.0)	4.0
Lip region width	8.0	8.3 ± 0.5 (8.0-9.0)
Lip region height	4.0	4.0
DGO	4.3 ± 0.96 (3.0-5.0)	5.6 ± 0.8 (4.0-7.0)
Median bulb valve to anterior end distance	65.0 ± 7.4 (53-72)	67.9 ± 5.3 (56-73)
Body width (maximum)	16.8 ± 0.5 (16-17)	19.1 ± 2.2 (16-24)
Excretory pore to anterior end distance	140.8 ± 16.4 (122-156)	104.5 ± 7.8 (94-119)
Tail length	40.4 ± 8.6 (32-51)	49.7 ± 4.1 (43-56)
Hyaline part of tail length	22.2 ± 3.4 (17-26)	25.3 ± 1.9 (22-28)

Type material. Slides with holotype cyst (CNHE 12357) and paratypes cysts and second-stage juveniles (CNHE 12358) were deposited in the Laboratorio de Helmintología del Instituto de Biología, UNAM, Mexico and the Colegio de Postgraduados Nematode Collection (CPNC)

(A128). LSIDurn:lsid:zoobank.org:act:5B35CE37-DC71-47DC-A0B4-BE5FAD9632F9

Differential diagnosis and relationships. By morphological and molecular characteristics, *Heterodera tropica* sp. n. belongs to the *Humuli* group of *Heterodera* spp. It is characterised by ambifenestrate cyst, absence of bullae and weak underbridge.

Heterodera tropica sp. n. is similar to *H. fici* Kirjanova, 1954, measurements of cysts and J2 of these species overlap. Both species have an ambifenestrate vulval cone. *Heterodera tropica* sp. n. differs from *H. fici* by the somewhat shorter length of cysts: 246-536 µm *vs* 432-688 µm, 400-640 µm (Golden *et al.,* 1988) and 420-680 µm (Fanelli *et al.,* 2019) and shorter fenestral length: 32-55 µm *vs* 5864 µm, 48-62 µm (Golden *et al.,* 1988) and 46-72 µm (Fanelli *et al.,* 2019).

Heterodera tropica sp. n. and *H. fici* differ from all other species of the *Humuli* group by having ambifenestrate cysts.

Molecular characterisation of *H. tropica* sp. n.

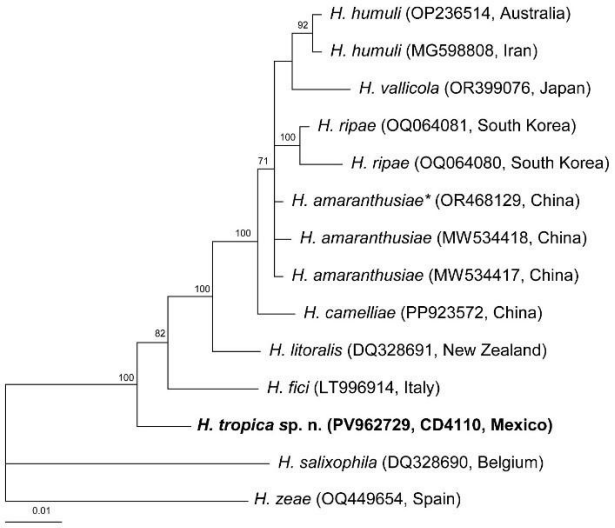

Fig. 5. Phylogenetic relationships of *Heterodera tropica* sp. n. from Mexico with other representatives of the *Humuli* group of the genus *Heterodera*: Bayesian 50% majority rule consensus tree from two runs as inferred from analysis of the D2-D3 of 28S rRNA gene sequence alignment under the GTR + I + G model. Posterior probabilities equal to, or more than, 70% are given for appropriate clades. The new sequence is indicated in bold. * - identified as *H. ripae* by Yang *et al.* (2024).

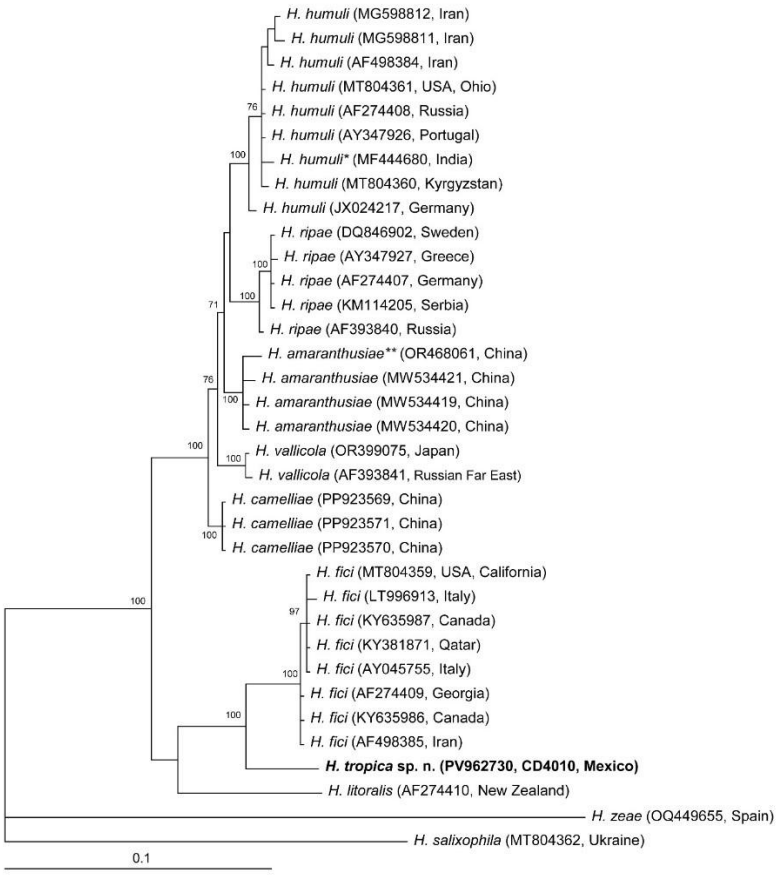

Fig. 6. Phylogenetic relationships of *Heterodera tropica* sp. n. from Mexico with other representatives of the *Humuli* group of the genus *Heterodera*: Bayesian 50% majority rule consensus tree from two runs as inferred from analysis of the ITS rRNA gene sequence alignment under the GTR + I + G model. Posterior probabilities equal to, or more than, 70% are given for appropriate clades. The new sequence is indicated in bold. * - identified as *H. skohensis* in the GenBank, ** - identified as *H. ripae* by Yang *et al.* (2024).

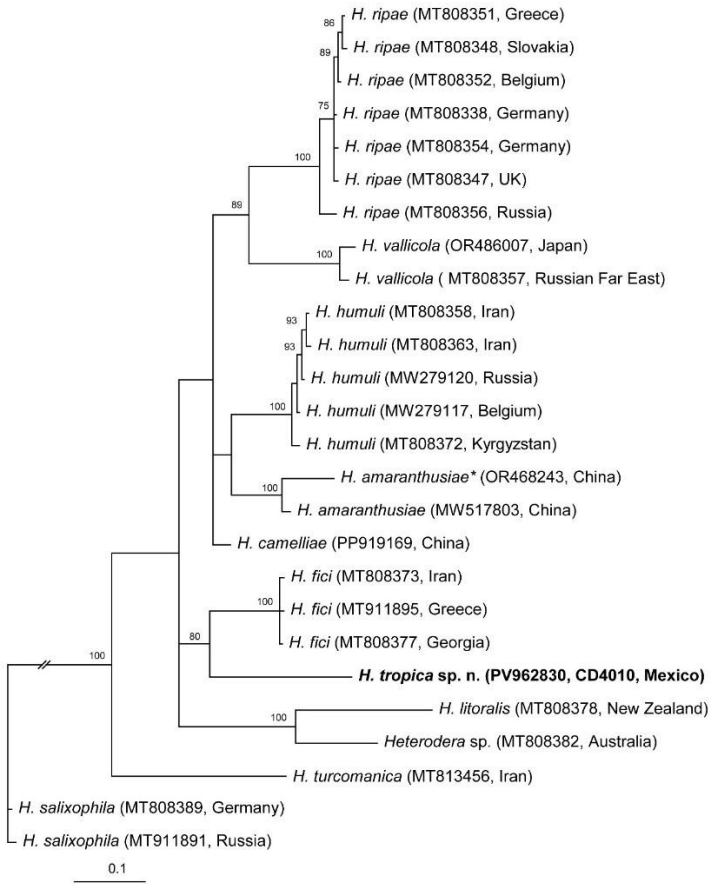

Fig. 7. Phylogenetic relationships of *Heterodera tropica* sp. n. from Mexico with other representatives of the *Humuli* group of the genus *Heterodera*: Bayesian 50% majority rule consensus tree from two runs as inferred from analysis of the *COI* gene sequence alignment under the GTR + I + G model. Posterior probabilities equal to, or more than, 70% are given for appropriate clades. The new sequence is indicated in bold. * - identified as *H. ripae* by Yang *et al.* (2024).

The D2-D3 of 28S rRNA gene. The alignment included 12 sequences of 8 species from the *Humuli* group and two sequences of outgroup taxa and was 718 bp in length. One sequence of *Heterodera tropica* sp. n. was obtained in this study. Phylogenetic relationships of *H. tropica* sp. n. with other representatives of the *Humuli* group, as inferred from analysis of the D2-D3 of 28S rRNA gene sequence alignment, are given in Figure 5. The sequence of *H. tropica* sp. n. differed from that of *H. fici* by 2.3% (16 bp). The sequence (OR468129) identified as *H. ripae* Subbotin, Sturhan, Rumpenhorst & Moens, 2003 by Yang *et al.* (2024) did not form a clade with sequences of this species and it is considered here to be a representative of *H. amaranthusiae* Jiang *et al.,* 2021.

The ITS rRNA gene. The alignment included 33 sequences of eight species from the *Humuli* group and two sequences of an outgroup taxa was 986 bp in length. One sequence of *H. tropica* sp. n. was obtained in this study. Phylogenetic relationships of *H. tropica* sp. n. with other representatives of the *Humuli* group as inferred from analysis of the ITS rRNA gene sequence alignment are given in Figure 6. The sequence of *H. tropica* sp. n. differed from those of *H. fici* by 3.7-4.0% (33-36 bp). Maximal intraspecific sequence variations were 0.3% for *H. fici,* 0.4% for *H. ripae* and *H. humuli*. The sequence (OR468061) identified as *H. ripae* by Yang *et al.* (2024), formed a clade with sequences of *H. amaranthusiae* and it is considered here as a representative of *H. amaranthusiae.* Intraspecific sequence variation for *H. amaranthusiae* was 0.6%.

The *COI* gene. The alignment included 24 sequences of 10 species from the *Humuli* group and two sequences of outgroup taxa and was 424 bp in length. One sequence of *H. tropica* sp. n. was obtained in this study. Phylogenetic relationships of *H. tropica* sp. n. with other representatives of the *Humuli* group as inferred from analysis of the *COI* gene sequence alignment are given in Figure 7. The sequence of *H. tropica* sp. n. differed from those of

H. fici by 11.8-12.1% (49-50 bp). Maximal intraspecific sequence variations were 0.9% for *H. ripae*, 0.5% for *H. fici* and 1.4% for *H. humuli*. The sequence (OR468243), identified as *H. ripae* by Yang *et al.* (2024), formed a clade with sequences of *H. amaranthusiae* and it is considered here as a representative of *H. amaranthusiae*. Intraspecific sequence variation for *H. amaranthusiae* was 4.1%.

Molecular plant host identification. The plant ITS rRNA gene sequence (PV959259) was 99.85% identical (96% coverage) and 99.42% identical (100% coverage) to the sequences of *Brosimum alicastrum* (OR606404 and MT726054) deposited by Vianna-Filho *et al.* (unpublished) and Bogun *et al.* (2024), respectively.

DISCUSSION

The *Humuli* group of *Heterodera* contains species that parasitise dicotyledonous plants and are characterised by a lemon-shaped cyst having a bifenestrate cone (except for *H. fici* and *H. tropica* sp. n. which both have an ambifenestrate vulval cone), long vulval slit, weak underbridge and absence of bullae. With the description of *H. tropica* sp. n., the total number of species from the *Humuli* group becomes nine (Subbotin *et al.,* 2022; Ni *et al.,* 2025). Until now, only two species from the *Humuli* group, the hop cyst nematode, *H. humuli* parasitising roots of hop plants and the fig cyst nematode, *H. fici* parasitising roots of various species of *Ficus* trees, have been reported in North America; they are considered to be agricultural pests. By the description of the breadnut cyst nematode, the number of species of *Humuli* group increases to three, and two of them are parasitic on woody plants. *Heterodera tropica* sp. n. has been found in only one location in Mexico, but the host plant is widely distributed along the west coast of central Mexico and in southern Mexico (Yucatán, Campeche), Guatemala, El Salvador, the Caribbean, and the Amazon basin. Breadnut leaves are commonly used as forage for livestock during the dry season in Central America. The fruits and seeds are also used to feed many kinds of domestic animals (Fairchild, 1945; Gardner, *et al.,* 2021).

Heterodera tropica sp. n. and *H. fici* are morphologically and morphometrically very similar, they also share related plant hosts belonging to the family Moraceae. In phylogenetic trees reconstructed using the ITS rRNA and *COI* gene sequences, these nematodes are considered sister species. Reliable differentiation and identification of these species can be done using rRNA and *COI* gene sequences only. Testing to determine any overlap of host ranges of the two species is necessary for determining their agricultural importance and for determining the degree of resolution needed for management decisions.

Yang *et al.* (2024) recently reported *H. ripae* from the rhizosphere soil of *Fagopyrum esculentum* (Polygonaceae) in Liupanshui, Guizhou Province, China, representing the first finding of *H. ripae* from plants other than *Urtica* spp. However, the present phylogenetic and sequence analysis revealed that the published sequences of this nematode do not belong to *H. ripae* but rather to *H. amaranthusiae*, the species previously known parasitising only *Amaranthus retroflexus* (Amaranthaceae) in Yunnan Province, China. We believe, based on our finding, the report by Yang *et al.* (2024) should be considered as the first record of *H. amaranthusiae* on *F. esculentum.*

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REFERENCES

AYOUB, S.M. 1977. *Plant Nematology: An Agricultural Training Aid*, State of California. 157 pp.

BOGUN, A.C., PAREDES-VILLANUEVA, K., MASCARELLO, M. & MAGEL, E.A. 2024. Development of a DNA macroarray for the molecular biological identification of trade-relevant tropical CITES timber species and their look-alikes. *Holzforschung* 78: 471-486. DOI: 10.1515/hf-2023-0114

CHENNA, R., SUGAWARA, H., KOIKE, T., LOPEZ, R., GIBSON, T.J., HIGGINS, D.G. & THOMPSON, J.D. 2003. Multiple sequence alignment with the Clustal series of programs. *Nucleic Acids Research* 31: 3497-3500. DOI: 10.1093/nar/gkg500

CID DEL PRADO VERA, I. & SUBBOTIN, S.A. 2012. *Belonolaimus maluceroi* sp. n. (Tylenchida: Belonolaimidae) from a tropical forest in Mexico and key to the species of *Belonolaimus*. *Nematropica* 42: 201-210.

ESCOBAR-AVILA, I.M., LOPEZ-VILLEGAS, E.O., SUBBOTIN, S.A. & TOVAR-SOTO, A. 2018. First report of carrot cyst nematode *Heterodera carotae* in Mexico: morphological, molecular characterization, and host range study. *Journal of Nematology* 50: 229-242.

FAIRCHILD, D. 1945. The ramon tree of Yucatan (*Brosimum alicastrum*). *Florida State Horticultural Society Proceedings* 58: 198-200.

FANELLI, E., VOVLAS, A., SANTORO, S., TROCCOLI, A., LUCARELLI, G., TRISCIUZZI, N. & DE LUCA, F. 2019. Integrative diagnosis, biological observations, and histopathology of the fig cyst nematode *Heterodera fici*

Kirjanova (1954) associated with *Ficus carica* L. in southern Italy. *ZooKeys* 824: 1-19. DOI: 10.3897/zookeys.824.26820

GARDNER, E.M., AUDI, L., ZHANG, Q., SAUQUET, H., MONRO, A.K. & ZEREGA, N.J.C. 2021. Phylogenomics of *Brosimum* (Moraceae) and allied genera, including a revised subgeneric system. *Taxon* 70: 778-792. DOI: 10.1002/tax.12503

GOLDEN, A.M., MAQBOOL, M.A. & SHAHINA, F. 1988. Redescription of *Heterodera fici* (Nematoda: Heteroderidae) with SEM observations. *Journal of Nematology* 20: 381-391.

HOOPER, D.J. 1970. Handling, fixing, staining and mounting nematodes. In: *Laboratory Methods for Work with Plant and Soil Nematodes.* (J.F. Southey Ed.) Technical Bulletin, Ministry of Agriculture, Fisheries and Food, (5th edition). London, H.M.S.O.

SAKATA, I. & KUSHIDA, A. 2024. First report of *Heterodera vallicola*, a Japanese elm parasitic cyst nematode species, in Japan. *Nematological Research* 54: 29-32.

JENKINS, W.R. 1964. A rapid centrifugal flotation technique for separating nematodes from soil. *Plant Disease Reporter* 48: 692.

JIANG, R., HU, X., LI, Y., BIAN, Y., HUANG, L., GU, J., LIU, P., HUANG, W., KONG, L., LIU, S., PENG, H. & PENG, D. 2021. *Heterodera amaranthusiae* n. sp. (Nematoda: Heteroderidae), a new cyst nematode parasitising *Amaranthus retroflexus* L. in China. *Nematology* 24: 289-305. DOI: 10.1163/15685411-bja10131

LISTON, A., ROBINSON, W.A., OLIPHANT, J.M. & ALVAREZ-BUYILLA, E. 1996. Length variation in the nuclear ribosomal DNA internal transcribed spacer region of non-flowering seed plants. *Systematic Botany* 21: 109-120. DOI: 10.2307/2419742

NI, C.H., LI, Q.Y., YANG, Z.F., XU, C.L. & XIE, H. 2025. Morphology and molecular analysis of *Heterodera camelliae* n. sp. (Nematoda: Heteroderinae), a new species of cyst-forming nematode parasitizing tea plants in China. *European Journal of Plant Pathology* 171: 407-420. DOI: 10.1007/s10658-024-02956-4

RONQUIST, F. & HUELSENBECK, J.P. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572-1574. DOI: 10.1093/bioinformatics/btg180

SEINHORST, J. 1959. A rapid method for the transfer of nematodes from fixative to anhydrous glycerine. *Nematologica* 4: 67-69. DOI: 10.1163/187529259X00381

SUBBOTIN, S.A. 2021. Molecular identification of nematodes using polymerase chain reaction (PCR). In: *Techniques for Work with Plant and Soil Nematodes* (R.N. Perry, D.J. Hunt & S.A. Subbotin. Eds). pp. 218239. Wallingford, UK, CAB International. DOI: 10.1079/9781786391759.0012

SUBBOTIN, S.A., VIERSTRAETE, A., DE LEY, P., ROWE, J., WAEYENBERGE, L., MOENS, M. & VANFLETEREN, J.R. 2001. Phylogenetic relationships within the cystforming nematodes (Nematoda, Heteroderidae) based on analysis of sequences from the ITS regions of ribosomal DNA. *Molecular Phylogenetics and Evolution* 21: 1-16. DOI: 10.1006/mpev.2001.0998

SUBBOTIN, S.A., SWART, A., CID DEL PRADO VERA, I., TANHA MAAFI, Z. & CHIZHOV, V.N. 2021. DNA barcoding and phylogeny of some cyst nematode species from the genus *Heterodera* (Tylenchida: Heteroderidae) parasitising monocots. *Russian Journal of Nematology* 29: 93-100. DOI: 10.24412/0869-6918-2021-2-93-99

SUBBOTIN, S.A., ROUBTSOVA, T.V., BOSTOCK, R.M., TANHA MAAFI, Z. & CHIZHOV, V.N. 2022. DNA barcoding, phylogeny and phylogeography of the cyst nematode species of the *Humuli* group from the genus *Heterodera* (Tylenchida: Heteroderidae). *Nematology* 24: 873-886. DOI: 10.1163/15685411-bja10292

SWOFFORD, D.L. 2003. *PAUP*: Phylogenetic Analysis Using Parsimony and Other Methods.* Version 4.0b10. Sunderland, MA, USA, Sinauer Associates

YANG, Z., ZHANG, H., JIANG, Z., WU, Y. & LIU, M. 2024. Morphological and molecular characterization of *Heterodera ripae,* a new record cyst nematode in the rhizosphere soil of *Fagopyrum esculentum*. *Scientific Reports* 14: 9958. DOI: 10.1038/s41598-024-60826-9

I. Cid del Prado Vera, E.S. Perez, H. Ferris and S.A. Subbotin. Новая цистообразующая нематода *Heterodera tropica* sp. n. (Tylenchida: Heteroderidae), паразитирующая на хлебном дереве *Brosimum alicastrum* в тропическом лесу штата Веракрус, Мексика.

Резюме. Новый вид цистообразующей нематоды рода *Heterodera*, относящийся к группе *Humuli*, описан из ризосферной почвы и корней хлебного дерева *Brosimum alicastrum* (семейство Moraceae) в тропическом лесу в Ла-Манче штата Веракрус, Мексика. Хлебная цистообразующая нематода *Heterodera tropica* sp. n. характеризуется небольшими амбифенестральными цистами без булле и тонким задним мостом. Личинка второй стадии имеет хорошо развитый стилет длиной 20-24 мкм, конический хвост длиной 32-56 мкм с гиалиновой областью длиной 17-28 мкм. Филогенетические связи *H. tropica* sp. n. с другими видами группы *Humuli* были реконструированы с использованием

последовательностей генов D2-D3 28S рРНК, ITS рРНК и COI. Новый вид морфологически и генетически близок к фиговой цистообразующей нематоде *H. fici*, и эти две цистообразующие нематоды, как показано на филограммах, реконструированных с использованием последовательностей рРНК ITS и гена COI, являются сестринскими видами. С описанием цистообразующей нематоды, число видов группы *Humuli*, зарегистрированных в Северной Америке, наряду с *H. humuli* и *H. fici,* увеличилось до трёх.