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Diversity of plant-parasitic nematodes associated with chickpea (*Cicer arietinum* L.) in the main growing areas of Ethiopia

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Summary – Chickpea is one of the most important legume crops in Ethiopia; however, its production is far below the mean international chickpea production due to biotic and abiotic stressors. Plant-parasitic nematode infestation is extensive in chickpea-growing areas worldwide. The distribution and population density of plant-parasitic nematodes in chickpea were determined during the September-December 2021 growing season. Ten plant-parasitic nematode taxa were identified from 27 localities across ten districts in the main chickpea-growing areas in Ethiopia. *Pratylenchus* had the highest prominence values, followed by *Rotylenchulus* and *Meloidogyne* spp. *Helicotylenchus*, *Hoplolaimus*, *Scutellonema* and *Quinisulcius* were more prevalent than *Criconemoides* and *Ditylenchus*. Sequences of different molecular markers, including D2-D3 of 28S rDNA, ITS of rDNA, and *COI* and Nad5 of mtDNA, revealed the presence of *Meloidogyne javanica*, *Rotylenchulus parvus*, *Scutellonema clathricaudatum* and *Helicotylenchus caudatus*. *Helicotylenchus caudatus* and *R. parvus* are the first reports from Ethiopia and chickpea, while *S. clathricaudatum* is the first report for chickpea. This study provides essential baseline information of nematode pest occurrence on chickpea in Ethiopia. This information will raise awareness among growers, agricultural officers, and extension advisors, enabling them to develop effective nematode management strategies for the chickpea production system in Ethiopia.

Keywords – 28S rDNA, *COI*, frequency of occurrence, ITS rDNA, molecular data, morphology, Nad5, prominence value.

Chickpea (*Cicer arietinum* L.) is a significant legume crop, with Ethiopia being the first and fifth largest producer in Africa and worldwide, respectively (Fikre *et al*., 2014; FAOSTAT, 2021). The crop is nutritionally rich and pivotal in ensuring global food security as it is cultivated in tropical, subtropical, and temperate regions (Singh *et al*., 2008; FAOSTAT, 2021). Chickpea is extensively grown in various parts of Ethiopia and is cultivated by smallholder farmers, either as a sole crop or in double cropping systems, utilising residual moisture on vertisols (Fikre *et al*., 2020). During the main cropping season of 2019-2020, pulses occupied 12.16% of Ethiopia's total grain crop area, of which 1.63% (*ca* 208 838 ha) was allo-

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cated to chickpea cultivation (Central Statistical Auhtority (CSA), 2019-2020).

In the sub-Saharan African region (SSA), plant-parasitic nematode problems, their economic significance and overall management have been overshadowed by other pests and pathogens (Coyne *et al*., 2018), particularly in Ethiopia (Abebe *et al*., 2015). However, economically important nematode species have caused yield losses ranging from 7% to 50% in sub-Saharan African countries (Talwana *et al*., 2015), with challenges stemming from farmers' lack of awareness of nematode issues and limited nematode surveys (De Waele & Elsen, 2007). Plant-parasitic nematodes are also well recognised as major constraints to legume production (Sikora *et al*., 2018) but have received limited attention concerning chickpea cultivation in Ethiopia (Sharma & McDonald, 1990; Sharma *et al*., 1992). Studies have associated various nematode species with the crop, including root-knot nematodes (*Meloidogyne* spp.), root-lesion nematodes (*Pratylenchus* spp.), cyst nematodes (*Heterodera* spp.), reniform nematodes (*Rotylenchulus* spp.), stunt and spiral nematodes, ring and pin nematodes and stem nematodes (Castillo *et al*., 2008; Sikora *et al*., 2018; Zwart *et al*., 2019). These nematodes contribute to yield losses of 14.6% globally in chickpeas (Sharma & McDonald, 1990).

Despite Ethiopia's prominence as a primary chickpea producer in Africa (Shiferaw *et al*., 2007; Bekele *et al*., 2019), the diversity and prevalence of nematodes affecting chickpea have not been assessed and remain largely unexplored. Only *Pratylenchus delattrei* Luc, 1958 and *Quinisulcius capitatus* (Allen, 1955) Siddiqi, 1971 have been characterised from chickpea in Ethiopia (Kefelegn *et al*., 2023). In this context, a comprehensive survey of nematodes was conducted in the primary cultivation areas of Ethiopia, with the following key objectives: *i*) to identify the diversity and density of plant-parasitic nematode genera associated with chickpea in Ethiopia's main cropping areas; and *ii*) to characterise some important plant-parasitic nematode species using both morphological and molecular tools. Our study has contributed to a better understanding of the nematode diversity of Ethiopia and, most importantly, identified nematode species that could potentially harm chickpea production.

Materials and methods

Field survey sampling

Nematode surveys were conducted in chickpea fields during the main growing season (September-December) in 2021, mainly from 27 localities of the nine districts (Minjar, Adea, Liben (Chekolla), Sodo, South Sodo, Abeshege, Sebeta Hawas, Lemen Zuria and Mesekan) where chickpea is most grown (Fig. 1). Within each of the selected districts/localities, 8-26 fields were randomly sampled, and from each field a bulk soil and root sample was taken (every soil sample corresponds with a root sample). This comprehensive effort resulted in a total sampling of approximately 304 fields. More specifically, 15-20 cm deep soil cores from the chickpea rhizosphere were collected by traversing the field in a zig-zag pattern, using a 3 cm diam. metal tube after removing the top 1-2 cm of dry soil. These soil cores were mixed to form a 500 g composite soil sample. Simultaneously, chickpea roots were sampled from ten randomly chosen plants in each field. For each sampling location the geographical coordinates and altitude were recorded (Fig. 1). The soil and root samples were put into a clean and labelled polythene bag, sealed and transported to Jimma University's Plant Disease Diagnostics Laboratory (PPDL) using insulated containers and stored at 4°C until extraction and further processing to maintain and prevent any changes to nematode populations (Barker *et al*., 1969).

Sample processing

Soil and root samples were processed separately. Chickpea roots were carefully washed free of adhering soil and chopped into 2 cm pieces and sub-samples of 10 g roots were used for nematode extraction. Soil samples were thoroughly mixed and homogenised, and an aliquot of 100 ml was used for nematode extraction. Nematodes were extracted using the modified Baermann tray method over a period of 48 h for soil and 6 days for root samples (Hooper *et al*., 2005). The nematodes were collected on a 38 μm sieve, rinsed into 70 ml plastic cups and stored at 4°C until counting. The suspension volume was reduced to 10 ml and densities were determined from 1 ml aliquots using a compound microscope (40×). Nematode densities in soil and roots were calculated and expressed per 100 ml soil or 10 g root, respectively.

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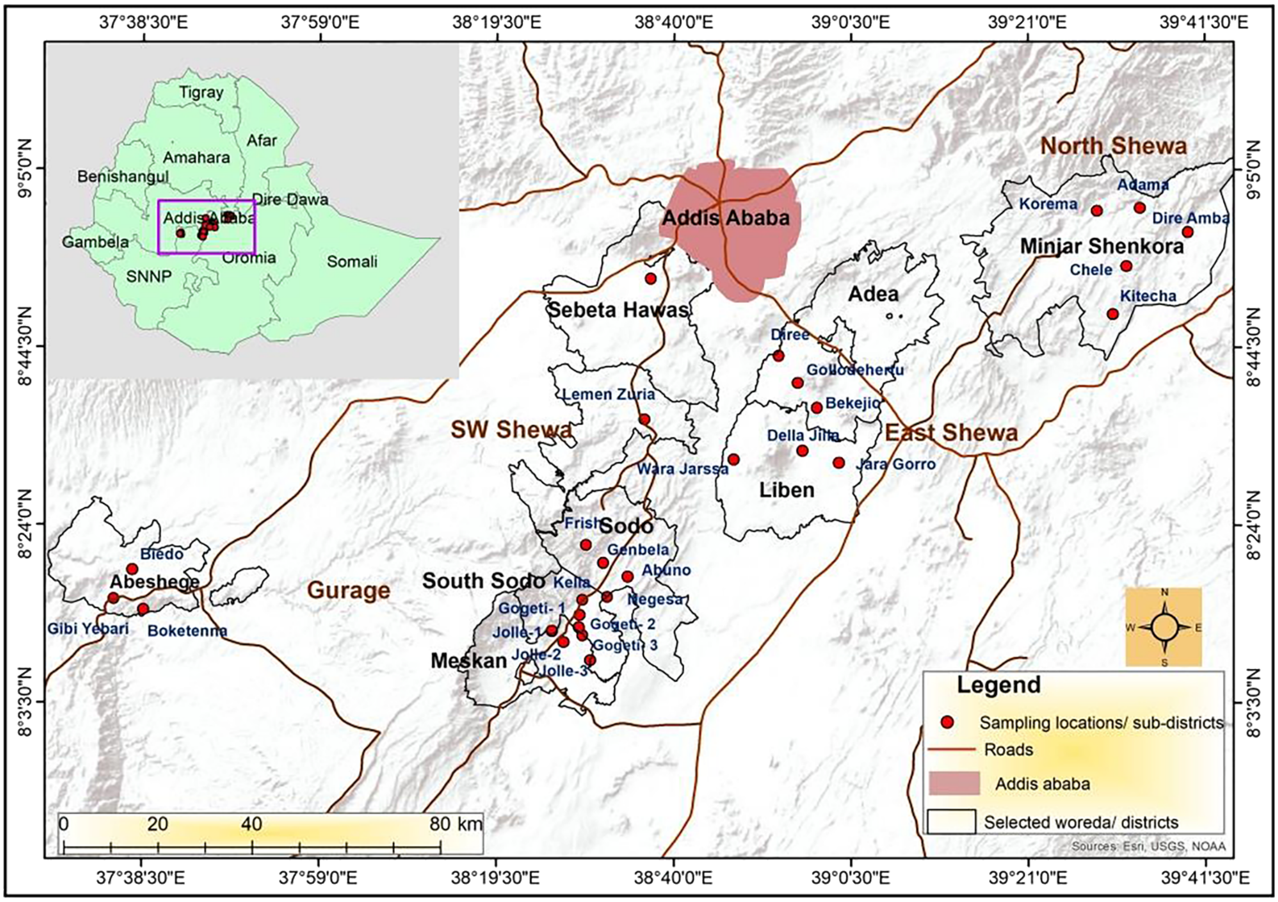

Fig. 1. A map showing sampling localities (red circles) where nematode survey samples were obtained from chickpea fields during the main growing season (September-December, 2021).

Data analysis

Data analyses were done using scripts written in RStudio 2022.12.0+353 and run in R version 4.2.1. The nematode population densities, the frequency of occurrence and the prominence values of each nematode genus per districts were estimated separately for the soil and root samples. The mean numbers of nematodes were presented graphically to reveal the distribution pattern, while details of the frequency of occurrence and prominence values along with population densities are presented in tables. The frequency of occurrence (FO%) of each genus was calculated using the formula: FO = (number of fields where a genus detected/total number of fields sampled) × 100, and prominence value (PV) of each genus was calculated using the formula: $PV = (\text{population density} \times \sqrt{\text{Frequency of occurrence}})/10$ (De Waele & Jordaan, 1988).

Morphological analysis

Morphological and morphometric data were recorded from both live and fixed nematodes using temporary and permanent slides as described in Singh *et al*. (2019). To link molecular data with morphological vouchers of individual nematodes, live nematodes were heat-relaxed by quickly passing them over a flame, and examined, photographed and measured using an Olympus BX51 DIC Microscope (Olympus Optical) equipped with an HD Ultra camera. Each specimen was subsequently recovered from a temporary slide for genomic DNA extraction. For permanent slides, nematode suspensions were concentrated in a drop of water in an embryo glass dish, with a few drops of fixative (4% formalin and 1% glycerol (in water). Nematodes were immediately heated in a microwave (700 W) for approximately 4 s and left at room temperature for 1 h and at 4°C for 24 h. This was followed

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by gradual transfer to anhydrous glycerin, which was then mounted on glass slides, as described by Seinhorst (1959).

MOLECULAR ANALYSIS

Nematode morphological vouchers were prepared prior to DNA extraction. These vouchers were made with light microscopy of individual nematodes on a temporary slide. Then, each nematode was individually removed from the temporary slide and cut into 2-3 pieces, and the pieces were transferred to a PCR tube containing 20 μl of worm lysis buffer (50 mM KCl, 10 mM Tris (pH 8.3), 2.5 mM $MgCl_2$, 0.45% NP 40 (Tergitol, Sigma) and 0.45% Tween-20). The genomic DNA of *Meloidogyne* spp. was thus extracted from six second-stage juveniles obtained from the chickpea roots. The PCR tubes were then frozen at −20°C for 10 min followed by addition of 1 μl of proteinase K (1.2 mg ml^{-1}), incubation at 65°C (1 h) and 95°C (10 min), and finally centrifugation of the mixture at 14 000 *g* for 1 min (Singh *et al*., 2019).

PCR amplification of the D2-D3 expansion segment of the 28S rDNA of rDNA was performed using the primer pairs D2A (5′-ACA AGT ACC GTG AGG GAA AGT TG-3′) and D3B (5′-TCC TCG GAA GGA ACC AGC TAC TA-3′), and the partial ITS region of rDNA was amplified using the primers Vrain2F (5′-CTT TGT ACA CAC CGC CCG TCG CT-3′) and Vrain2R (5′-TTT CAC TCG CCG TTA CTA AGG GAA TC-3′) (Vrain *et al*., 1992; Subbotin *et al*., 2007). The primer pair JB3 (5′-TTT TTT GGG CAT CCT GAG GTT TAT-3′) and JB4.5 (5′-TAA AGA AAG AAC ATA ATG AAA ATG-3′) were used to amplify the *COI* region of mtDNA (Derycke *et al*., 2010) following the thermal profile as described by Singh *et al*. (2019). The mitochondrial NADH dehydrogenase subunit 5 gene fragment (Nad5) was using primer pair NAD5F2 (5′-TAT TTT TTG TTT GAG ATA TAT TAG-3′) and NAD5R1 (5′-CGT GAA TCT TGA TTT TCC ATT TTT-3′) (Janssen *et al*., 2016).

All the PCR products were stained using GelRed (Biotium) and visualised in a 1% agarose gel under UV light illumination. The successful PCR products were finally cleaned using alkaline phosphatase (1 U ml^{-1}) and exonuclease I (20 U ml^{-1}) and sequenced from two directions at the Macrogen sequencing facility service (https://dna.macrogen.com, Europe). Contigs were made from the newly produced forward and reverse sequences using Geneious Prime 2022. 1 (https://www.geneious.com) and deposited in GenBank. Sequences of the Nad5 gene of *Meloidogyne* spp. were aligned with 79 *Meloidogyne* from reference Nad5 sequences for species identification (Janssen *et al*., 2016).

PHYLOGENETIC ANALYSES

The obtained sequences were analysed along with other relevant sequences available in GenBank. All analyses were done within Geneious Prime 2022.1. Multiple alignments of the different DNA sequences were made using MUSCLE with the default parameters, and the poorly aligned ends were manually trimmed. Bayesian phylogenetic analysis was carried out using the GTR + I + G model for both genes, analyses were run under 1×10^6 generations (two independent runs with four chains) and Markov chains were sampled every 100 generations and 20% of the converged runs were regarded as ‘burnin’ (Huelsenbeck & Ronquist, 2001).

Results

DIVERSITY OF PLANT-PARASITIC NEMATODES IN CHICKPEA FIELDS

From the 27 localities across in the nine districts, ten different genera of plant-parasitic nematode were identified from soil and root samples: *Pratylenchus*, *Meloidogyne*, *Rotylenchulus*, *Quinisulcius*, *Scutellonema*, *Helicotylenchus*, *Hoplolaimus*, *Criconemoides*, *Ditylenchus* and *Heterodera* (Tables 1, 2). Only *Pratylenchus* and *Meloidogyne* were recovered from the roots (Table 2). Pooled soil and root data for each sample in each district showed variation in the diversity and mean number of nematodes among the districts (Figs 2, 3). Site-level details are presented in the supplementary information (Suppl. Tables S1, S2). The genus *Pratylenchus* had the highest population density, prominence and frequency of occurrence followed by *Rotylenchulus* and *Meloidogyne* (Table 1). The PVs for *Pratylenchus* ranged from 32 (Sebeta) to 170 (Minjar), and this genus was present in up to 100% of the fields (Table 1). *Rotylenchulus* individuals were present in up to 100% of the fields with PVs ranging from 3 (Abeshege) to 235 (Mesekan) (Table 1). *Meloidogyne* was the third most important genus presented in the fields up to 100% with PVs ranging from 3 (Chekolla) to 62 (Minjar) districts. In all the sampled districts, six or more nematode genera were identified, except Lemmen Zuria where only three genera (*Ditylenchus*, *Meloidogyn*e and *Pratylenchus*) were recorded (Fig. 2). The highest population density of *Pratylenchus* (170 individuals

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Table 1. Population densities (PD), frequencies of occurrence (FO) and prominence values (PV) at genus level per districts recovered from 100 ml of soil from 27 localities across nine districts.

Nematode genus	Sampling districts														
	Minjar			Adea			Chekolla			Lemen Zuria			Sebeta		
	PD	FO (%)	PV	PD	FO (%)	PV	PD	FO (%)	PV	PD	FO (%)	PV	PD	FO (%)	PV
Criconemoides	6	53	4	1	13	–	3	8	1	–	–	–	–	–	–
Ditylenchus	2	13	1	1	21	1	1	4	–	1	11	–	2	11	1
Helicotylenchus	–	–	–	–	–	–	2	17	1	–	–	–	1	11	–
Heterodera	–	–	–	–	–	–	–	–	–	–	–	–	6	44	4
Hoplolaimus	20	58	15	7	8	2	6	13	2	–	–	–	–	–	–
Meloidogyne	63	98	62	8	42	5	4	42	3	49	100	49	17	67	14
Pratylenchus	170	100	170	18	58	14	23	50	16	58	100	58	34	89	32
Rotylenchulus	94	100	94	20	67	16	9	54	7	–	–	–	13	67	11
Scutellonema	12	53	9	12	29	7	8	29	4	–	–	–	3	33	2
Quinisulcius	2	5	–	5	17	2	1	4	–	–	–	–	5	22	2

Nematode genus	Sampling districts											
	Sodo			South Sodo			Abeshegie			Mesekan		
	PD	FO (%)	PV	PD	FO (%)	PV	PD	FO (%)	PV	PD	FO (%)	PV
Criconemoides	1	13	–	1	8	–	–	–	–	2	17	1
Ditylenchus	6	30	3	1	6	–	3	8	1	1	2	–
Helicotylenchus	20	72	17	58	53	42	7	31	4	6	31	3
Heterodera	–	–	–	–	–	–	–	–	–	–	–	–
Hoplolaimus	4	13	–	1	15	–	2	21	1	–	–	–
Meloidogyne	34	68	28	14	63	11	20	53	15	46	74	40
Pratylenchus	85	96	83	53	85	49	88	79	78	155	98	153
Rotylenchulus	27	50	19	115	87	107	7	23	3	237	98	235
Scutellonema	4	38	2	20	75	17	49	67	40	6	55	4
Quinisulcius	2	6	–	3	19	1	–	–	–	115	81	104

(100 ml soil)$^{-1}$) was recorded in Minjar district (Table 1), while the highest population densities of *Meloidogyne* (63 juveniles, males and females (100 ml soil)$^{-1}$) and *Rotylenchulus* (237 individuals (100 ml soil)$^{-1}$) were observed in Minjar and Meskean districts, respectively (Table 1). In addition to the three most important genera, namely, *Pratylenchus*, *Rotylenchulus* and *Meloidogyne*, other genera such as *Helicotylenchus*, *Hoplolaimus*, *Scutellonema* and *Quinisulcius* were also commonly detected, each with population densities ranging from 1 to 58, 1 to 20, 1 to 49 and 1 to 115, respectively (Table 1). From the roots, the PVs of *Meloidogyne* spp. ranged from 2 (South Sodo and Mesekan) to 97 (Minjar), with densities of 3-107 juveniles, males and females (10 g roots)$^{-1}$ (Fig. 3) and presented in fields in up to 83% of the samples (Table 2). For *Pratylenchus*, PVs ranged from 1 (Chekolla) to 46 (Minjar), with densities of 2-49 individuals (10 g roots)$^{-1}$ (Fig. 3) and presented in fields in up to 88% of the root samples (Table 2). Roots infected with *Meloidogyne* exhibited visible galling damage (Fig. 4), while no obvious damage was associated with *Pratylenchus* species.

Characterisation of the most predominant nematode species

Root-knot nematodes

Meloidogyne javanica from chickpea roots was identified based on its identity with Nad5 *Meloidogyne* reference sequences (Janssen *et al*., 2016). *Meloidogyne* populations from 22 sequences corresponding with eight samples were 100% identical to *M. javanica*. However, *Meloidogyne* populations from seven sequences corresponding to two samples could not be unequivocally linked to a reference sequence.

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Table 2. Population densities (PD), frequencies of occurrence (FO) and prominence values (PV) at genus level per districts recovered from 10 g roots from 27 localities across eight districts.

Nematode genus	Sampling districts																							
	Minjar			Adea			Chekolla			Lemen Zuria			Sodo			S/Sodo			Abeshegie			Meskan		
	PD	FO (%)	PV	PD	FO (%)	PV	PD	FO (%)	PV	PD	FO (%)	PV	PD	FO (%)	PV	PD	FO (%)	PV	PD	FO (%)	PV	PD	FO (%)	PV
Meloidogyne	107	83	97	15	33	9	7	25	3	19	50	13	4	33	3	4	14	2	7	33	4	3	36	2
Pratylenchus	49	88	46	5	46	4	2	13	1	33	75	28	23	59	18	10	41	6	39	63	31	22	58	17

Helicotylenchus caudatus Sultan, 1985
(Fig. 5; Table 3)

Female

Body spiral-shaped after heat-killing. Lip region not set off, hemispherical to flattened, with 3-4 annuli (Fig. 5). Stylet well developed with rounded knobs. Excretory pore located at the level of the pharyngo-intestine junction. Ventrally overlapping pharyngeal glands. Tail conical, distinctly annulated, curved dorsally, ending in finger-like or ventral projections, terminally rounded tip variable in length and terminally rounded.

Molecular characterisation

Four identical D2-D3 of 28S rDNA sequences (OP647413-OP647416; 445 bp) and one ITS rDNA sequence (OP650246; 887 bp) were generated for *H. caudatus* in this study (Figs 6, 7). The D2-D3 sequences formed a maximally supported clade with seven *H. caudatus* sequences (MN764331-MN764337) and one unidentified *Helicotylenchus* sp. (KM506847) from South Korea, which are 96-97% similar. The first ITS sequence of *H. caudatus* formed a weakly supported sister relation with *H. dihystera*, *H. paxilli*, *H. pseudorobustus*, *H. digonicus*, *H. scoticus*, *H. broadbalkiensis*, *H. crenacauda*, *H.* sp. and *H. microlobus* (Fig. 7).

Male

Not found.

Remarks

Helicotylenchus caudatus was reported for the first time in Ethiopia from the rhizosphere of chickpea, marking the first documented association of *H. caudatus* with chickpea (Table 1). This species has also been reported in other countries, including India (potato) and Korea (grass) (Sultan, 1985; Mwamula *et al.*, 2020). The morphology and morphometric characteristics of the studied females align with the original description (Sultan, 1985) and subsequent descriptions by Mwamula *et al.* (2020), except a longer body length (704-719 *vs* 520-610 μm) and higher b indices (5.9-6.6 *vs* 4.5-5.2). Additionally, the tail length is slightly shorter in comparison to Korean populations (16.3-19.8 *vs* 17.1-22.1 μm) (Table 4). Hence, despite the sister position with the other *H. caudatus* sequences (also not from type material) and the molecular differences, this

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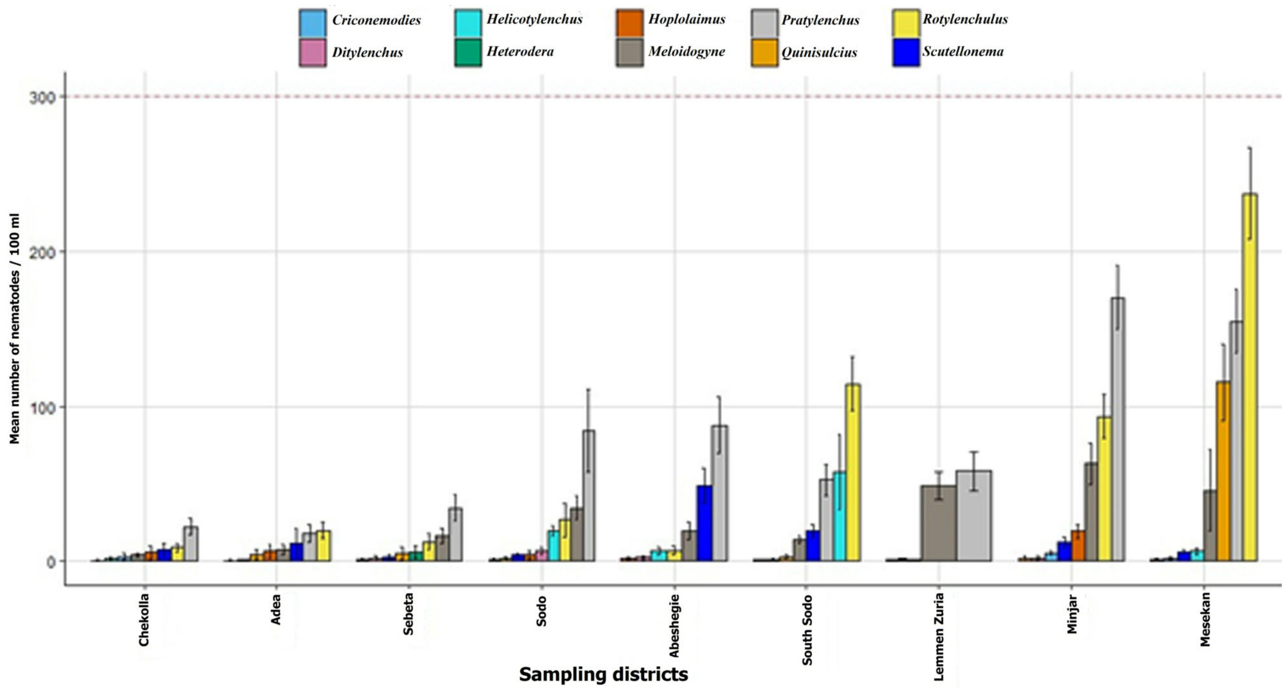

Fig. 2. Mean number of nematodes recovered from 100 ml of soil.

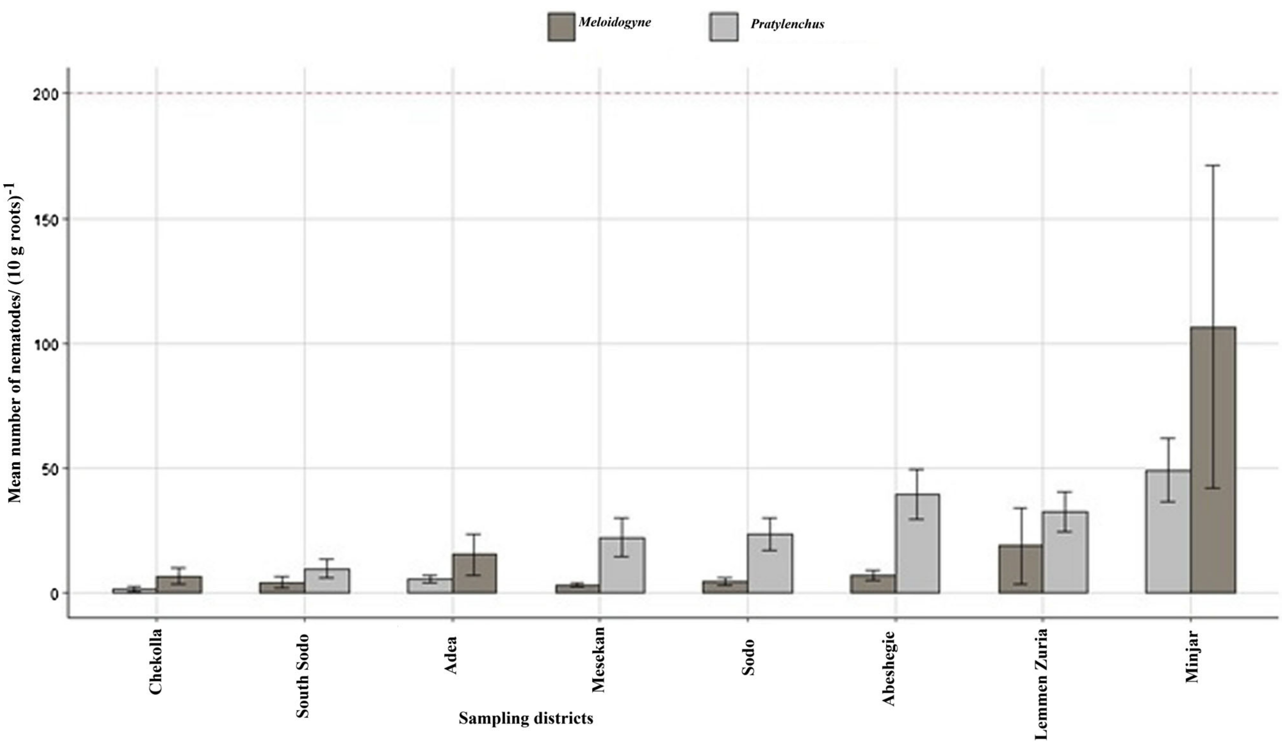

Fig. 3. Mean number of nematodes recovered from 10 g of chickpea roots.

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Fig. 4. Chickpea root samples showing heavy galling caused by *Meloidogyne* spp.

species is identified as *H. caudatus*. This study links for the first time an ITS sequence to *H. caudatus*.

Scutellonema clathricaudatum Whitehead, 1959
(Fig. 8; Table 4)

Female

Body C-shaped when heat-killed. Hemispherical to conical and slightly flattened lip region with 6-8 lip annuli. Well-developed stylet with rounded to oval-shaped basal knob. Excretory pore located at the level of anterior end of pharyngeal gland lobe. Indistinct genital tract with poorly developed spermatheca. Ventrally actuated conoid and rounded to squarish tail with variable terminus shapes.

Male

Not found.

Molecular characterisation

Three identical sequences each of D2-D3 of 28S of rDNA (OP644684-OP644686; 487 bp), ITS rDNA (OP650243-OP650245; 456 bp) as well as *COI* mtDNA (OP645381-OP645383; 408 bp), were generated (Figs 9-11). The D2-D3 sequences of the Ethiopian *S. clathricaudatum* sequences were 99% similar to *S. clathricaudatum* type D (KY639314 and KY639315; 4 bp differences) and in a well-supported sister position with these *S. clathricaudatum* type D sequences. The obtained sequences form a well-supported clade (0.88 PP) with *S. clathricaudatum* types B, C and D, and *Scutellonema* sp. D (Fig. 9). Our ITS rDNA sequences formed a maximally supported clade (1.00 PP) with *Scutellonema* sp. D (Fig. 10). The three identical *COI* sequences were in a well-supported clade (0.94 PP) with *S. clathricaudatum* types B, C and D (Fig. 11).

Remarks

This species is reported for the first time from the rhizosphere of chickpea (Table 1). It has also been reported from Ethiopia (*Acacia* sp. and maize), Niger (pigeon pea), Tanzania (cotton), South Africa (sugarcane) and West Africa (yam, peanut, millet, groundnut, sorghum and cowpea) (Whitehead, 1959; Sharma *et al*., 1993; Baujard & Martiny, 1995; Nene *et al*., 1996; Van Den Berg & Mekete, 2010; Van den Berg *et al*., 2013, 2017; Kolombia *et al*., 2017). The studied females are morphologically and morphometrically similar to the original description (Whitehead, 1959), and subsequent descriptions (Kolombia *et al*., 2017), except a slightly longer stylet in our specimens compared to the original descriptions (28.1-29.7 *vs* 21-25 μm). Based on the D2-D3 sequences, the Ethiopian *S. clathricaudatum* is very similar to the *S. clathricaudatum* type D associated with yam (Kolombia *et al*., 2017).

Rotylenchulus parvus (Williams, 1960a, b) Sher, 1961
(Fig. 12; Table 5)

The morphology and morphometrics of females (n = 10) and males (n = 4) from our specimen agree with the original description of *R. parvus* (= *Helicotylenchus parvus*) by Williams (1960a) and subsequent descriptions by Van Den Berg *et al*. (2016) and Singh *et al*. (2020). Nine D2-D3 of 28S rDNA (OP734810-OP734818; 603-

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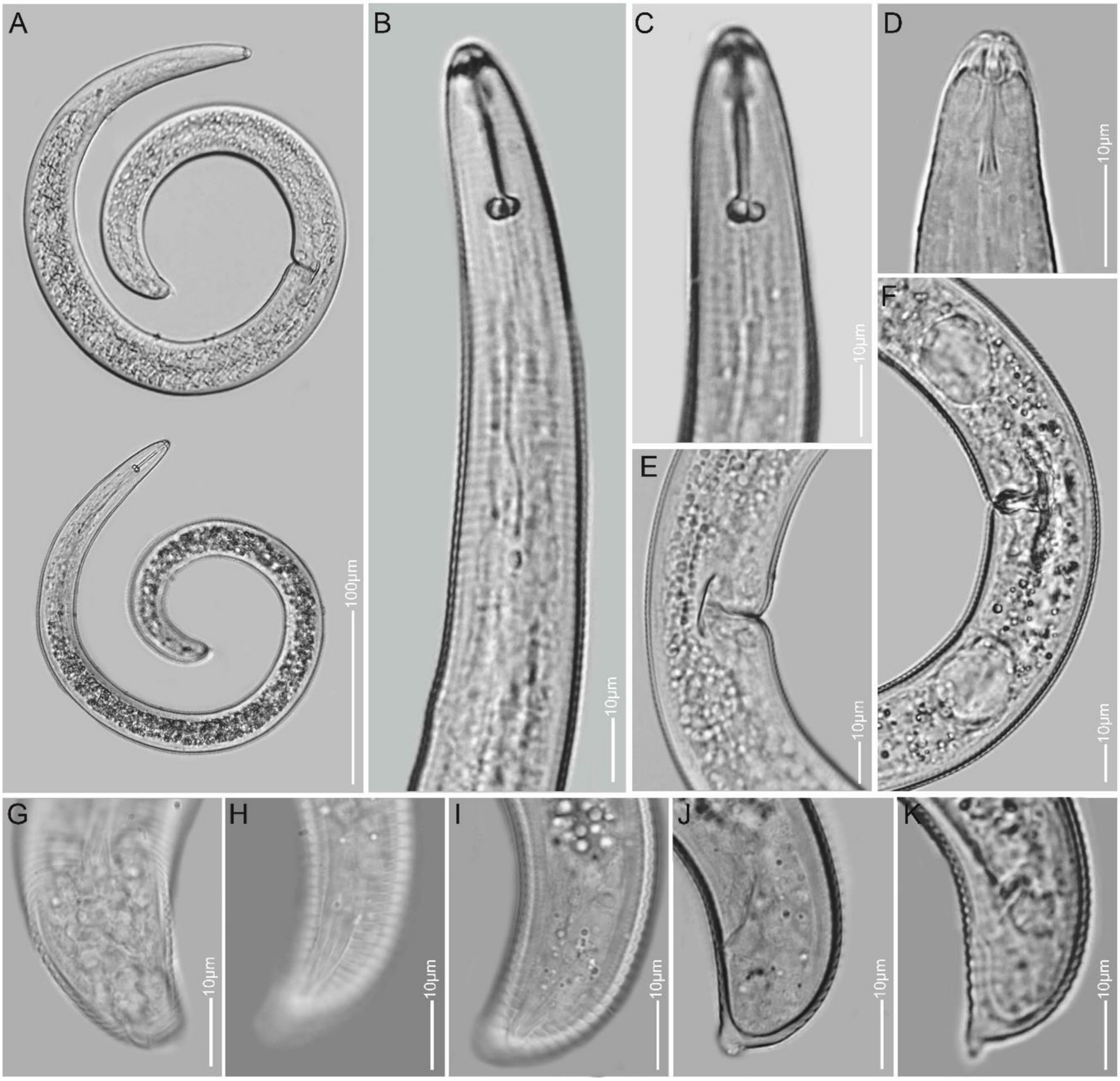

Fig. 5. Light microscopy images of *Helicotylenchus caudatus*. A: Total bodies; B: Anterior region up to the median bulb; C: Lip region, stylet and dorsal gland orifice; D: Lip region and conus; E, F: Mid-body regions showing vulva; G-K: Posterior regions showing tails, anus, tail mucron and tail annuli.

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Table 3. Comparison of morphometrical data of *Helicotylenchus caudatus* found in chickpea in Ethiopia with other populations from India (Sultan, 1985) and Korea (Mwamula *et al*., 2020). All measurements are in μm and in the form: mean ± s.d. (range).

Character	*H. caudatus* from chickpea in Ethiopia (this study)	*H. caudatus* from potato in India (Sultan, 1985)	*H. caudatus* from grass in Korea (Mwamula *et al*., 2020)	
			Korea (YS4)	Korea (KP-2)
n	10	9	15	6
L	711 ± 5.7 (704-719)	580 (520-610)	755 ± 63.1 (650-852)	707 ± 65.2 (634-793)
a	24.9 ± 1.8 (23.0-28.1)	24 (23-25)	25.5 ± 1.4 (22.4-27.7)	24.8 ± 1.6 (22.9-27.0)
b	6.1 ± 0.2 (5.9-6.6)	4.9 (4.5-5.2)	6.4 ± 0.7 (5.4-8.0)	6.2 ± 0.6 (5.5-7.0)
b′	5.0 ± 0.1 (4.9-5.2)	4.2 (3.8-4.5)	5.2 ± 0.5 (4.2-5.9)	4.8 ± 0.5 (4.1-5.4)
c	40.3 ± 2.4 (36.3-43.2)	34 (32-36)	39.2 ± 5.2 (33.2-49.1)	37.2 ± 3.5 (34.8-44.1)
c′	1.0 ± 0.1 (1.0-1.2)	1.2 (0.8-1.5)	1.1 ± 0.1 (0.9-1.3)	1.0 ± 0.0 (1.0-1.1)
V	62.8 ± 0.6 (62.2-63.9)	65 (63-66)	62.8 ± 2.3 (58.4-65.8)	64.1 ± 1.4 (62.3-65.2)
Vulva position	447 ± 7.0 (441-460)	–	–	–
m	–	52 (52-53)	43.7 ± 2.4 (40.2-47.3)	43.5 ± 1.8 (41.1-46.0)
O	–	31 (29-37)	44.0 ± 2.8 (38.9-48.2)	44.2 ± 3.3 (39.1-48.8)
Stylet length	25.3 ± 0.6 (24.3-26.0)	25-28	25.2 ± 0.7 (24.1-26.5)	25.1 ± 0.4 (24.7-25.8)
Lip height	4.1 ± 0.2 (3.7-4.5)	–	4.0 ± 0.3 (3.6-4.4)	3.8 ± 0.2 (3.4-4.1)
Lip width	7.2 ± 0.5 (6.7-8.1)	–	6.7 ± 0.3 (6.3-7.6)	6.9 ± 0.3 (6.5-7.3)
DGO	10.0 ± 0.3 (9.5-10.5)		11.1 ± 0.6 (10.3-12.1)	11.0 ± 1.0 (9.3-12.1)
Pharyngeal length	117 ± 3.5 (110-120)	–	118 ± 7.7 (104-128)	115 ± 2.8 (111-120)
Pharyngeal overlap	141 ± 2.1 (139-145)	–	147 ± 8.1 (124-159)	149 ± 2.5 (147-153)
SE pore from anterior end	110 ± 2.1 (110-113)	–	115 ± 7.3 (106-125)	120 ± 5.0 (113-128)
Mid-body diam.	28.7 ± 2.1 (25.6-30.9)	21-27	29.6 ± 2.1 (23.5-32.3)	28.5 ± 1.5 (26.3-30.5)
Tail length	17.7 ± 1.2 (16.3-19.8)	–	19.4 ± 1.6 (17.1-22.1)	19.0 ± 1.1 (18.0-20.9)
Anal body diam.	17.2 ± 1.0 (15.6-18.5)	–	17.0 ± 0.9 (15.5-18.5)	18.4 ± 0.9 (17.2-19.5)

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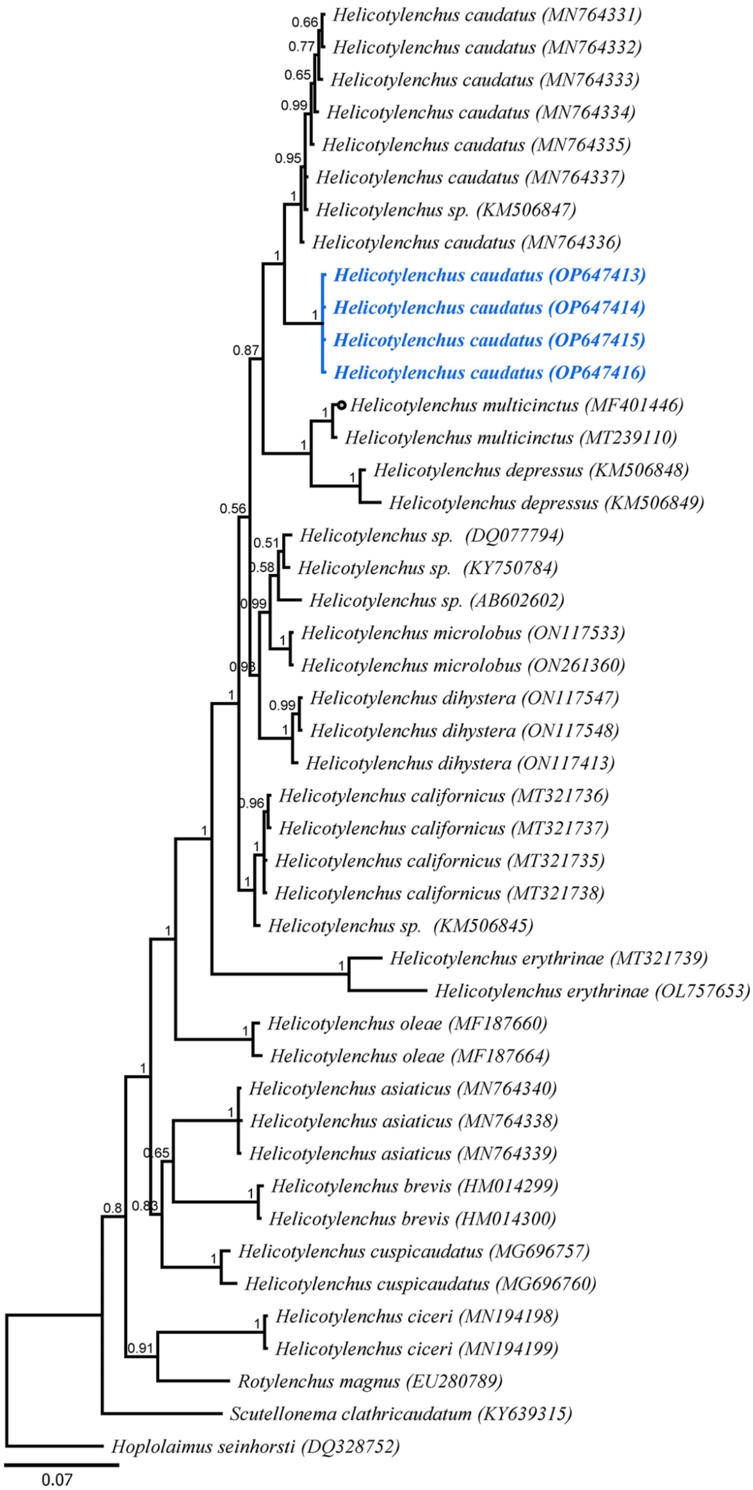

Fig. 6. Bayesian 50% majority rule consensus phylogeny of *Helicotylenchus caudatus* from Ethiopia and related species based on D2-D3 of 28S rDNA sequences using a GTR model. Branch support is indicated with PP. The sequences from this study are shown in blue.

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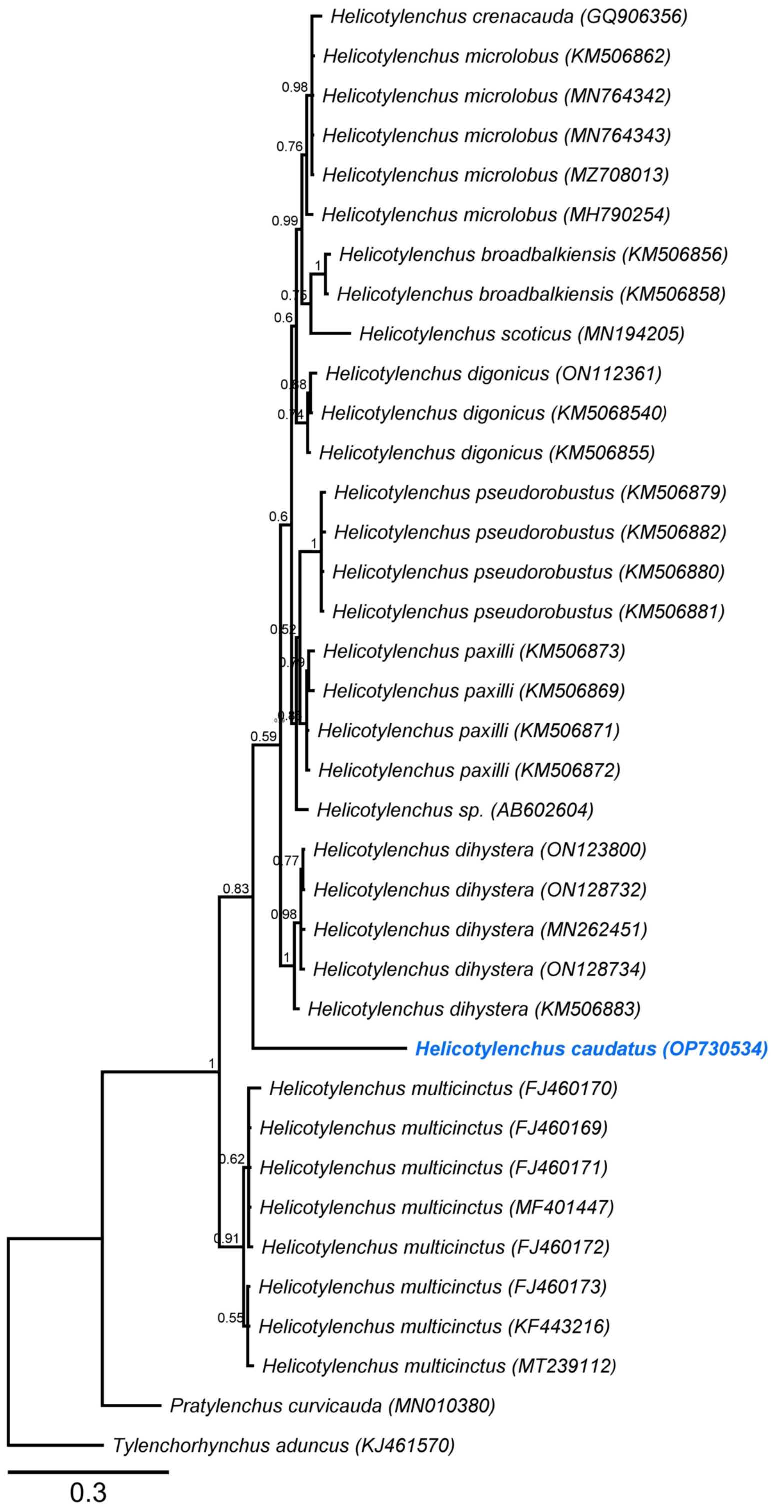

Fig. 7. Bayesian 50% majority rule consensus phylogeny of *Helicotylenchus caudatus* from Ethiopia and related species based on ITS rDNA sequences using a GTR model. Branch support is indicated with PP. The sequences from this study are shown in blue.

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Table 4. Comparison of morphometrics of the Ethiopian *Scutellonema clathricaudatum* from chickpea with the original description from Tanzania (Whitehead, 1959a), and other *S. clathricaudatum* populations from yam fields in Ghana and Nigeria. All measurements are in μm and in the form: mean ± s.d. (range).

Character	*S. clathricaudatum* from chickpea in Ethiopia (this study)	*S. clathricaudatum* from cotton in Tanzania (Whitehead, 1959)	*S. clathricaudatum* from yam in Ghana and Nigeria (Kolombia *et al*., 2017)		
			Type A		Type D
			2NS35-9	L17	L28
n	10	15	5	4	3
L	683 ± 15.6 (659-701)	596-747	826 ± 40 (784-888)	648 ± 91 (512-710)	822 ± 112 (699-919)
a	25.0 ± 0.7 (24.0-26.3)	19.1-25.4	24.6 ± 3.6 (18.8-28.2)	20.4 ± 3.3 (16.5-24.5)	20.5 ± 1.2 (19.3-21.6)
b	5.6 ± 0.2 (5.4-5.9)	4.7-6.9	7.8 ± 1.4 (6.8-9.8)	7.4 ± 1.4 (5.7-8.9)	8.8 ± 1.1 (7.6-9.7)
b′	5.1 ± 0.2 (4.8-5.3)	–	6.7 ± 1.5 (5.3-8.8)	5.6 ± 0.95 (4.7-6.6)	6.9 ± 1.5 (5.9-8.0)
c	42.1 ± 1.1 (40.6-44.3)	27.0-47.5	45.3 ± 5.3 (37.8-50.9)	39 ± 7.0 (30.1-44.7)	26.2 ± 3.9 (23.7-30.6)
c′	0.8 ± 0.0 (0.8-0.9)	–	0.77 ± 0.12 (0.7-0.98)	0.71 ± 0.04 (0.67-0.76)	1.2 ± 0.11 (1.1-1.3)
V	56.6 ± 1.6 (53.8– 58.6)	51.2-60.3	57.1 ± 1.5 (54.8-58.8)	54.2 ± 2.7 (52.2-57.3)	54.7 ± 1.3 (53.4-56.1)
Stylet length	28.9 ± 0.6 (28.1-29.7)	21-25	26.7 ± 1.3 (25.5-28.5)	25.9 ± 1.4 (24.5-27.5)	27.7 ± 1.3 (26.5-29.0)
Conus	–	–	11.2 ± 1.3 (10.0-13.0)	11.3 ± 1.0 (10.0-12.5)	12.7 ± 1.3 (11.5-14.0)
Shaft and knobs	–	–	15.5 ± 0.71 (14.5-16.5)	14.6 ± 0.75 (13.5-15.0)	15 ± 2.2 (12.5-16.5)
Stylet width	–	–	2.4 ± 0.19 (2.3-2.7)	2.0 ± 0.28 (1.6-2.3)	2.4 ± 0.45 (2.1-2.7)
m	–	–	41.9 ± 3.3 (37.7-45.6)	43.4 ± 2.5 (40.0-45.5)	45.9 ± 6.0 (41.8-52.8)
Stylet knob height	3.6 ± 0.3 (3.1-3.9)	–	3.2 ± 0.64 (2.7-3.9)	3.3 ± 0.43 (2.9-3.7)	3.1 ± 0.52 (2.7-3.5)
Stylet knob width	4.5 ± 0.7 (3.4-5.3)	–	2.9 ± 0.36 (2.5-3.2)	2.7 ± 0.1 (2.6-2.8)	2.4 ± 0.23 (2.2-2.6)
O	–	–	27.1 ± 1.8 (25.2-28.7)	23.9 ± 1.4 (22.5-25.2)	26.3 ± 2.4 (24.6-27.9)
Pharynx length	121 ± 1.4 (119-124)	–	109 ± 21.9 (82-132)	88 ± 8.9 (78-99)	95 ± 24.6 (72-121)
Ant. end to median bulb valve	–	–	69 ± 12.3 (53-78)	63 ± 7.0 (58-72)	71 ± 20.8 (56-86)
Ant. end to post. end of gland	133 ± 3.6 (128– 138)	–	128 ± 23.6 (91-148)	116 ± 17.6 (102-142)	122 ± 49 (88-157)
Maximal body diameter	27.4 ± 0.6 (25.9-28.1)	–	34 ± 5.2 (28.9-43)	32 ± 2.2 (29-34)	40 ± 5.5 (34-44)
Anal body diam.	24.2 ± 0.9 (22.8-25.2)	–	24.1 ± 1.3 (22.0-25.2)	23.6 ± 2.1 (22.3-26.8)	27.4 ± 3.7 (23.2-30)
Median bulb length	14.0 ± 0.5 (13.5-14.7)	–	14.7 ± 1.3 (13.5-16.5)	14.5 ± 0.0 (14.5-14.5)	–

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Table 4. (Continued.)

Character	*S. clathricaudatum* from chickpea in Ethiopia (this study)	*S. clathricaudatum* from cotton in Tanzania (Whitehead, 1959a)	*S. clathricaudatum* from yam in Ghana and Nigeria (Kolombia *et al.*, 2017)		
			Type A		Type D
			2NS35-9	L17	L28
Median bulb diam.	13.0 ± 1.1 (11.1-14.6)	–	12.6 ± 1.2 (11.0-14.0)	11.5 ± 0.0 (11.5-11.5)	–
Median bulb valve length	–	–	3.6 ± 0.22 (3.5-4.0)	3.0 ± 0.0 (3.0-3.0)	–
Median bulb valve width	–	–	2.6 ± 0.22 (2.5-3.0)	2.0 ± 0.0 (2.0-2.0)	–
Lip region diam.	8.7 ± 0.5 (7.9-9.4)	–	9.3 ± 0.43 (8.7-9.7)	8.7 ± 1.1 (7.6-10.1)	11.0 ± 1 (10.3-11.7)
Lip region height	7.4 ± 0.3 (6.9-7.8)	–	6.0 ± 0.72 (5.2-6.9)	5.9 ± 1.5 (4.2-7.9)	5.9 ± 0.8 (5.3-6.5)
Tail length	16.2 ± 0.5 (15.6-17.0)	–	18.4 ± 1.9 (16.5-21.5)	16.8 ± 1.7 (15.0-19.0)	32 ± 3.0 (29.5-35)
Scutellum length	4.8 ± 0.4 (4.0-5.2)	–	5.5 ± 0.36 (5.2-6.1)	4.1 ± 0.88 (3.0-5.1)	3.9 ± 0.93 (3.3-4.6)
Scutellum width	4.5 ± 0.2 (4.2-4.9)	–	5.0 ± 0.3 (4.6-5.4)	3.9 ± 0.89 (2.9-4.9)	3.3 ± 0.25 (3.1-3.5)
Spermatheca length	–	–	–	15.8 ± 0.78 (15.2-16.3)	–
Spermatheca diam.	–	–	–	15.1 ± 0.82 (14.6-15.7)	–
Gonad anterior length	–	–	56 ± 0.0 (56-56)	52 ± 14.2 (36-61)	91 ± 0.0 (91-91)
Gonad posterior length	–	–	–	59 ± 0.0 (59-59)	–
Ant. end to S-E/ pharynx length	0.9 ± 0.0 (0.9-1.0)	–	0.98 ± 0.02 (0.97-1.0)	1.1 ± 0.13 (0.89-1.2)	1.1 ± 0.03 (1.1-1.2)

750 bp) sequences were generated with 10-12 bp intraspecific sequence variations. The Ethiopian *R. parvus* sequences were found to be 67-96 bp (12-16%) different from the Tanzanian *R. parvus* sequences, and formed a well-supported clade (PP = 1.00) (data not shown).

REMARKS

As first reported on chickpea and from Ethiopia, this species was recovered from the rhizosphere soil samples from chickpea (Table 1). *Rotylenchulus parvus* has been already reported in other African countries, including Mauritius (cotton), Kenya (pigeon pea, maize), South Africa (soybean, sugarcane, groundnut), Tanzania (sugarcane), Zambia (cowpea) and Zimbabwe (tobacco), and from USA (barley, grass, cotton, cowpea, papaya, sugarcane and pearl millet) (Dasgupta & Raski, 1960; Williams, 1960a, b; Sharma *et al*., 1993; Robinson *et al*., 1997; Fourie *et al*., 2001; Singh *et al*., 2020).

Discussion

The production potential of chickpea is significantly constrained by various biotic factors, including insect pests, diseases, and nematodes (Zwart *et al*., 2019). However, despite the extensive presence of nematode infestations in chickpea-growing regions (Castillo *et al*., 2008), there have been no studies conducted on nematode-induced legume crop yield losses in Ethiopia (Abebe *et al*., 2015), although plant-parasitic nematodes are responsible for a 14.6% global reduction in chickpea production (Sharma & McDonald, 1990). Most plant-parasitic nematode genera identified in this study (*Pratylenchus*, *Roty-*

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Fig. 8. Light microscopy images of *Scutellonema clathricaudatum*. A: Total body; B, C: Anterior regions showing lip region and stylet; D: Lateral field showing lateral lines; E: Mid-body showing vulva region; F-H: Posterior regions showing tails, anus, tail annuli and scutella.

lenchulus, *Meloidogyne*, *Helicotylenchus*, *Hoplolaimus*, *Scutellonema*, *Quinisulcius*, *Criconemoides*, *Ditylenchus* and *Heterodera*) have been reported in association with chickpea in various parts of the world (Sharma & McDonald, 1990; Greco *et al*., 1992; Sharma *et al*., 1992; Di Vito *et al*., 1994; Abd-Elgawad & Askary, 2015; Sikora *et al*., 2018; Behmand *et al*., 2019). However, to the best of our knowledge, *Helicotylenchus caudatus*, *Scutellonema clathricaudatum* and *Rotylenchulus parvus* are reported for the first time from the rhizosphere of chickpea.

In line with previous research (Greco *et al*., 1984, 1992; Sharma & McDonald, 1990; Sharma *et al*., 1992; Di Vito *et al*., 1994; Behmand *et al*., 2019), *Pratylenchus*, *Rotylenchulus*, *Meloidogyne*, *Scutellonema*, *Helicotylenchus*, *Hoplolaimus*, *Ditylenchus*, *Heterodera* and *Quinisulcius* were among the plant-parasitic nematodes found in chickpea root and soil samples. These findings align with other studies of nematode diversity in Ethiopia (Meressa *et al*., 2014; Seid *et al*., 2019; Kidane *et al*., 2021; Tola *et al*., 2022; Singh *et al*., 2023). The current study also detected the genera *Criconemoides*, *Ditylenchus* and *Heterodera*, but all at relatively low densities. Notably, *Pratylenchus*, *Rotylenchulus* and *Meloidogyne* were found in high densities in almost all the analysed soil and root samples, posing a potential threat to chickpea production in Ethiopia. *Pratylenchus* and *Meloidogyne* species are already known for causing significant yield reductions in chickpea production elsewhere in the world (Castillo *et al*., 2008; Zwart *et al*., 2019). Remarkably, the observed high density of *Pratylenchus* (170 individuals (100 ml soil)$^{-1}$), and *Meloidogyne* (107 juveniles, males and females (10 g roots)$^{-1}$) indicates that both of these nematode genera

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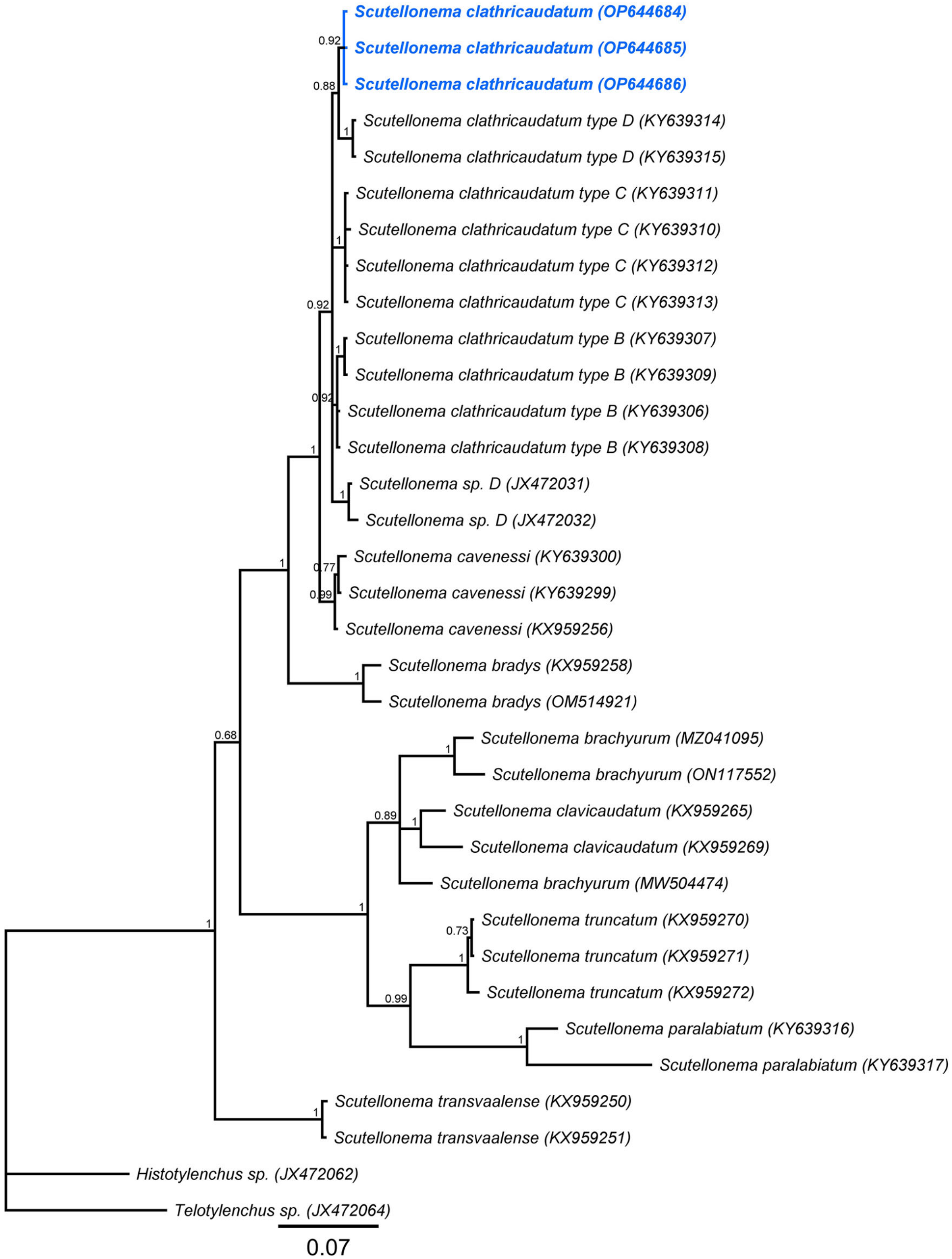

Fig. 9. Bayesian 50% majority rule consensus phylogeny of *Scutellonema clathricaudatum* from Ethiopia and related species based on D2-D3 of 28S of rDNA sequences using a GTR model. Branch support is indicated with PP. The sequences from this study are shown in blue.

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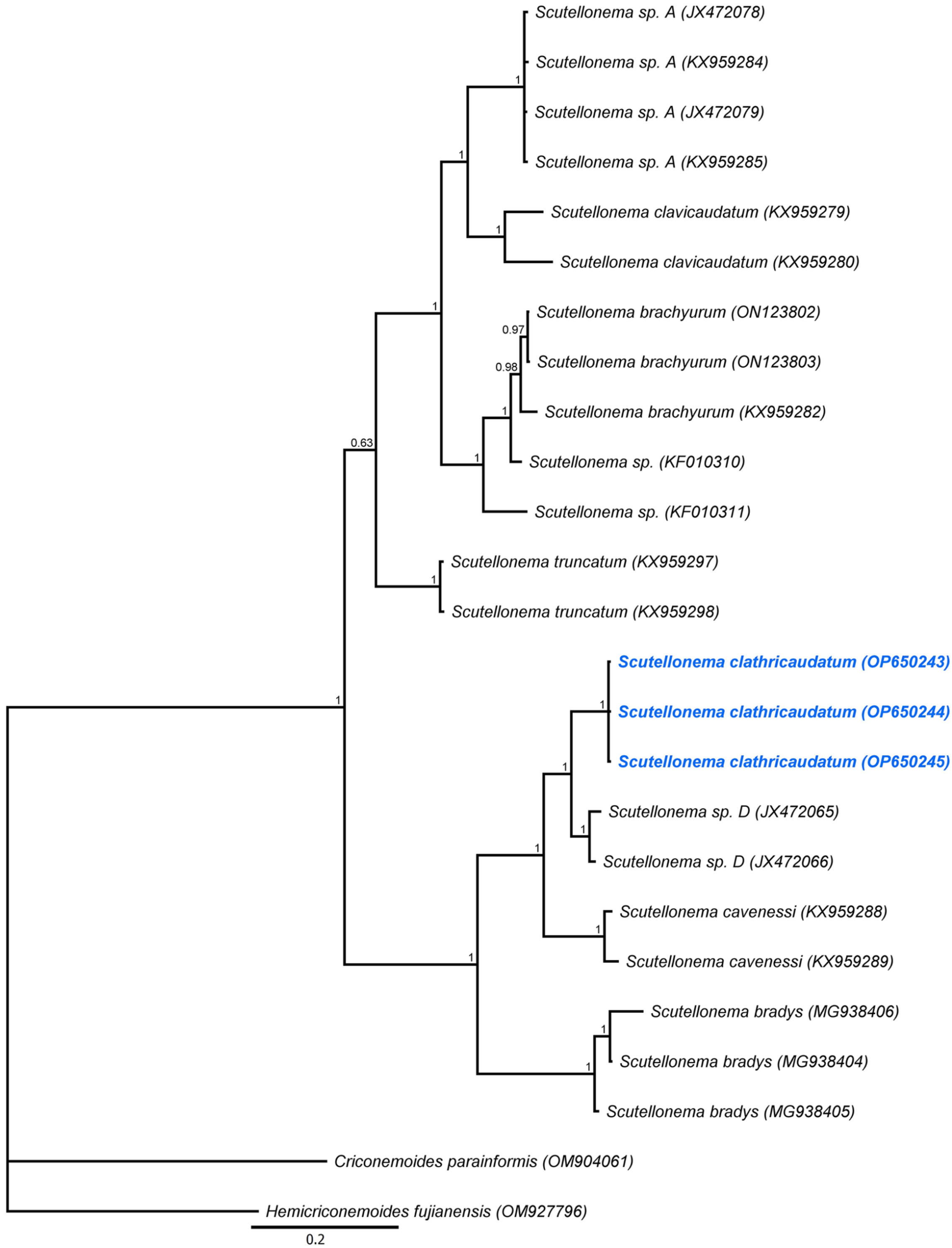

Fig. 10. Bayesian 50% majority rule consensus phylogeny of *Scutellonema clathricaudatum* from Ethiopia and related species based on ITS rDNA sequences using a GTR model. Branch support is indicated with PP. The sequences from this study are shown in blue.

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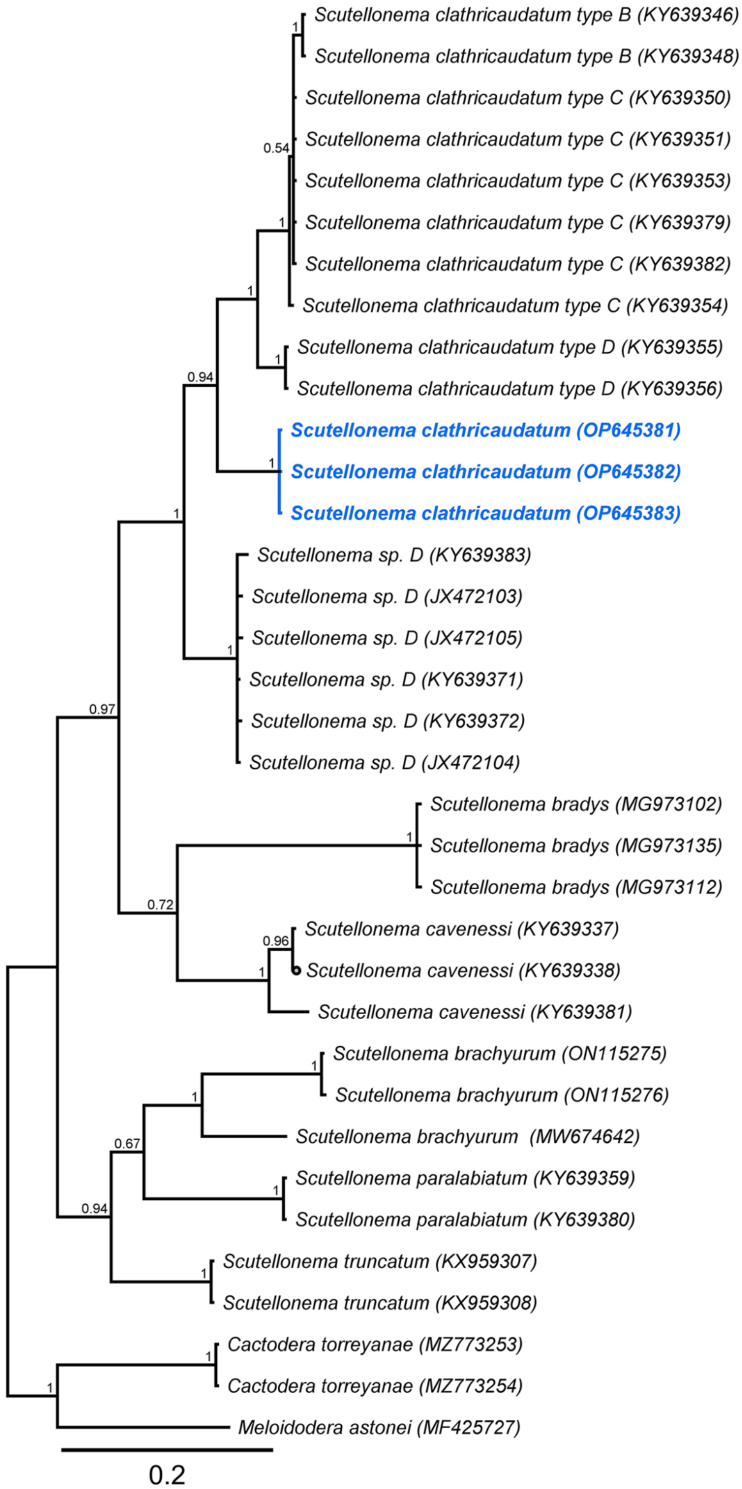

Fig. 11. Bayesian 50% majority rule consensus phylogeny of *Scutellonema clathricaudatum* from Ethiopia and related species based on *COI* of mtDNA using a G + T + R model. Branch support is indicated with PP. The sequences from this study are shown in blue.

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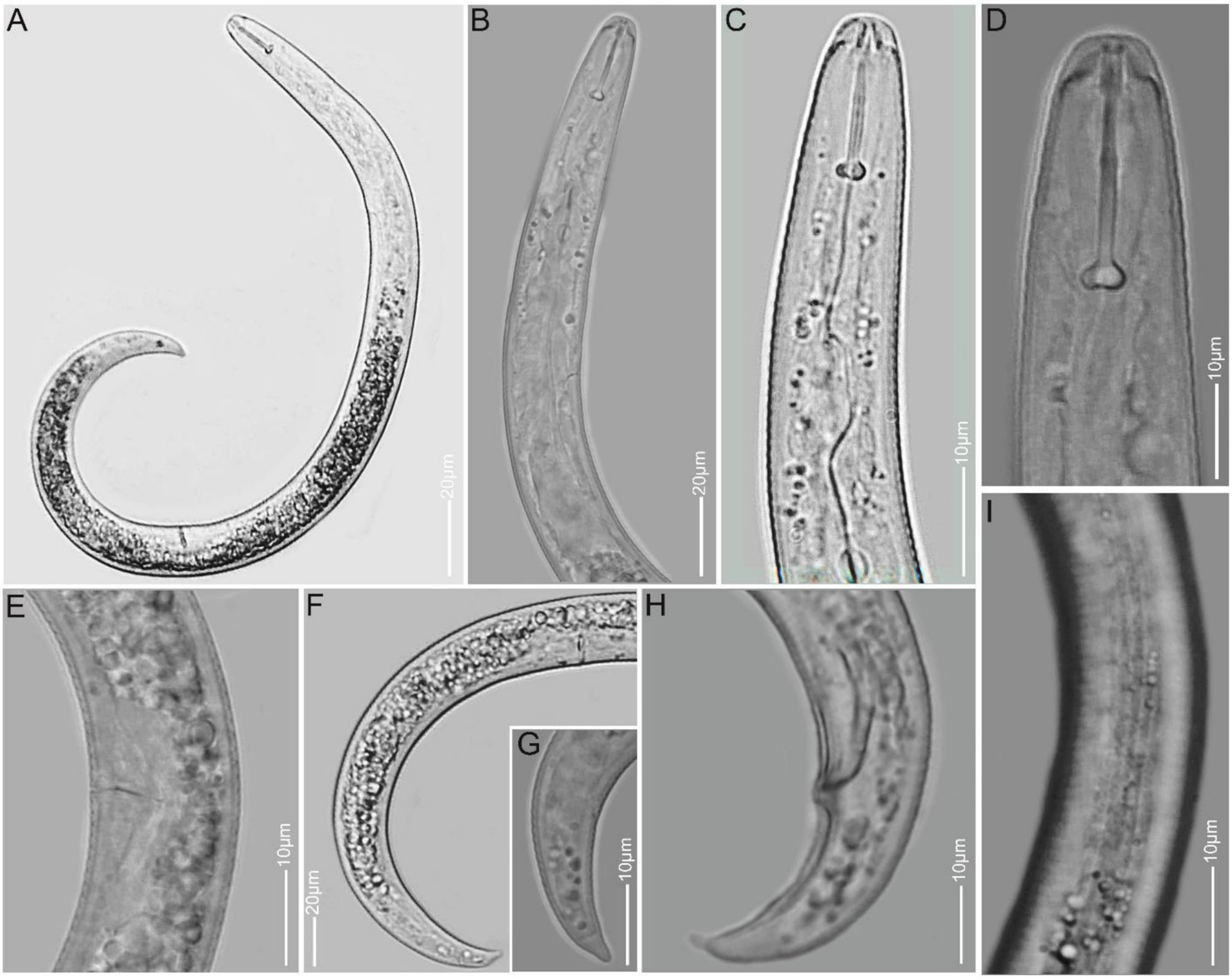

Fig. 12. Light microscopy images of *Rotylenchulus parvus*. A: Total body; B: Anterior region up to the median bulb; C: Lip region, stylet and dorsal gland orifice; D: Lip region and conus; E: Vulva region; F: Vulva-tail region; G: Tail region showing tail tip; H: Cloacal and tail region of male showing spicule; I: Lateral field showing lateral lines.

should be considered important for chickpea in Ethiopia. Previously, species of *Pratylenchus*, such as *P. delattrei*, *P. thornei*, *P. neglectus*, *P. mediterraneus*, *P. penetrans*, *P. zeae*, *P. brachyurus*, *P. alleni* and *P. alkan* (Greco *et al*., 1992; Di Vito *et al*., 1994; Sikora *et al*., 2018; Behmand *et al*., 2019; Kefelegn *et al*., 2023) and *M. arenaria*, *M. artiellia*, *M. javanica* and *M. incognita* (Greco *et al*., 1984; Sharma & McDonald, 1990; Sharma *et al*., 1992), were reported to be pathogens of chickpea elsewhere in the world. The detection of *Meloidogyne javanica* in chickpea roots across various sampling locations is consistent with reports from other parts of the world (Sharma & McDonald, 1990; Sharma *et al*., 1992) as well as in other crops in Ethiopia (Mandefro & Mekete, 2002; Seid *et al*., 2019). Root-knot nematode species are considered economically to be the most important nematodes; they also cause substantial losses in grain legumes globally (Sharma & McDonald, 1990), have a broad host range (Jones *et al*., 2013), and are known to represent a major biotic threat to crop production in SSA (Coyne *et al*., 2018).

Given the high population densities of plant-parasitic nematodes obtained, it is apparent that these nematodes pose a significant threat to chickpea production in Ethiopia. This situation mirrors the broader context in sub-Saharan Africa, where nematodes are recognised as

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Table 5. Comparison of morphometrics of the Ethiopian *Rotylenchulus parvus* from chickpea in Ethiopia with the original description from Mauritius (Williams, 1960a), and other population from sugarcane fields in Tanzania. All measurements are in μm and in the form: mean ± s.d. (range).

Character	*R. parvus* from chickpea in Ethiopia (this study)		*R. parvus* from sugarcane in Mauritius (Williams, 1960)	*R. parvus* from sugarcane in Tanzania (Singh *et al*., 2020)	
	Immature female	Male	Immature female	Immature female	Male
n	10	4	6	28	5
L	322 ± 9.2 (315-345)	344 ± 4.5 (338-348)	210-270	327 ± 29 (271-352)	393 ± 38 (342-426)
a	21.8 ± 0.6 (21.1-22.7)	31.2 ± 1.5 (29.4-32.9)	19.0-24.0	24.9 ± 1.6 (21.9-26.8)	31.1 ± 1.6 (29.4-33.2)
b	3.2 ± 0.1 (3.1-3.5)	3.2 ± 0.0 (3.1-3.2)	2.9-3.3	3.2 ± 0.5 (2.6-3.9)	3.7 ± 0.2 (3.5-3.9)
c	17.1 ± 1.1 (16.1-19.7)	17.2 ± 0.3 (16.7-17.5)	16.0-20.0	15.3 ± 0.4 (12.3-17.5)	17.0 ± 0.9 (16.0-18.1)
DGO	15.9 ± 1.6 (13.0-17.6)	–	–	17.3 ± 1.1 (16.6-18.0)	–
V	64.5 ± 1.7 (62.4-66.5)	–	61-65	62 (60-66)	–
Stylet length	14.7 ± 0.7 (13.8-15.8)	12.1 ± 0.2 (11.8-12.3)	*ca*. 12.5	14.5 ± 0.4 (13.1-15.4)	11.9 ± 0.3 (11.7-12.3)
Metenchium length	–	–	–	6.4 ± 0.3	5.2 ± 0.1
Telenchium length	–	–	–	8.1 ± 0.2 (6.3-8.7)	6.6 ± 0.2 (6.4-6.9)
Stylet knob width	2.6 ± 0.2 (2.1-2.9)	1.6 ± 0.1 (1.5-1.6)	–	2.7 ± 0.3 (2.5-2.9)	1.5 ± 0.2 (1.4-1.6)
Stylet knob height	1.7 ± 0.2	1.0 ± 0.1	–	1.6 ± 0.3	0.9 ± 0.1
Pharyngeal length	100 ± 1.0	108 ± 0.5	–	102 ± 8.7	109 ± 1.1
S-E pore from anterior end	75.7 ± 1.8 (72.5-77.7)	78.2 ± 0.2 (77.9-78.5)	–	75.4 ± 3.2 (74.0-77.0)	77.9 ± 0.6 (77.5-78.5)
Mid-body diam.	14.8 ± 0.4 (13.9-15.2)	11.0 ± 0.4 (10.5-11.5)	–	12.7 ± 1.6 (12.7-13.4)	12.6 ± 1.1 (11.2-13.8)
Median bulb length	9.3 ± 0.4 (8.5-9.8)	8.2 ± 0.4 (7.8-8.5)	–	9.1 ± 0.8 (8.6-9.8)	8.0 ± 0.9 (7.4-8.6)
Median bulb diam.	7.6 ± 0.2 (6.9-7.6)	5.1 ± 0.1 (4.9-5.2)	–	7.0 ± 0.2 (6.9-7.6)	5.1 ± 0.3 (4.9-5.3)
Lip region diam.	3.6 ± 0.3 (3.1-4.0)	3.3 ± 0.1 (3.2-3.5)	–	3.8 ± 0.8 (3.1-4.2)	3.5 ± 0.2 (3.4-3.5)
Lip region height	2.5 ± 0.1 (2.2-2.6)	2.0 ± 0.1 (1.8-2.1)	–	2.4 ± 0.3 (2.2-2.6)	2.1 ± 0.5 (1.6-2.7)
Tail length	18.9 ± 0.8 (17.5-19.8)	20.0 ± 0.2 (19.8-20.2)	–	21.4 ± 0.8 (18.5-25.3)	23.1 ± 2.0 (20.3-25.0)
Hyaline tail (h)	–	–	–	2.5 ± 0.4 (1.3-3.1)	3.4 ± 0.5 (2.9-3.9)
Spicule length	–	16.8 ± 0.3 (16.4-17.1)	–	–	16.7 ± 1.2 (16.0-17.5)
Gubernaculum length	–	5.6 ± 0.4 (5.1-6.0)	–	–	5.6 ± 0.5 (5.0-6.0)

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economically important pests affecting most crops (Coyne *et al*., 2018). However, there is still a lack of awareness regarding nematodes as pests and their management. Farmers in Ethiopia, for instance, seem to have little to no awareness of nematode pests, especially compared to other chickpea pests such as fungi and insects (pers. comm.). The findings of this study should serve as a foundational source of information on the occurrence and distribution of plant-parasitic nematode species in chickpeas, raising awareness among farmers and an incentive to establish the population dynamics and damage thresholds of these pest species. This, in turn, can inform the development of effective management strategies, set priorities for further research, and draw the attention of policymakers and agricultural officers to the importance of addressing nematode-related problems in various legume-producing regions in Ethiopia, including chickpeas.

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Supplementary Table S1. Site-level details for the roots.

Site no	District	Locality	Genus	PD	FO (%)	PV
1	Abeshegie	Bekota	*Meloidogyne*	8	40	5
2	Abeshegie	Bekota	*Pratylenchus*	56	90	53
3	Abeshegie	Beido	*Meloidogyne*	0	0	0
4	Abeshegie	Beido	*Pratylenchus*	40	38	25
5	Abeshegie	Gebi yebari	*Meloidogyne*	12	56	9
6	Abeshegie	Gebi yebari	*Pratylenchus*	18	56	13
7	Adea'a	Bekajou	*Meloidogyne*	41	63	33
8	Adea'a	Bekajou	*Pratylenchus*	6	63	5
9	Adea'a	Gollodhertu	*Meloidogyne*	3	25	2
10	Adea'a	Gollodhertu	*Pratylenchus*	3	25	2
11	Adea'a	Diree	*Meloidogyne*	1	13	0
12	Adea'a	Diree	*Pratylenchus*	7	50	5
13	Chekolla	Dollo.Jilla	*Meloidogyne*	6	25	3
14	Chekolla	Dollo.Jilla	*Pratylenchus*	3	25	2
15	Chekolla	Wara jarssa	*Meloidogyne*	7	25	3
16	Chekolla	Wara jarssa	*Pratylenchus*	0	0	0
17	Lemmen	Lemmen zurai	*Meloidogyne*	19	50	13
18	Lemmen	Lemmen zurai	*Pratylenchus*	33	75	28
19	Mesekan	Jolle-1	*Meloidogyne*	1	21	0
20	Mesekan	Jolle-1	*Pratylenchus*	38	64	30
21	Mesekan	Jolle-2	*Meloidogyne*	2	21	1
22	Mesekan	Jolle-2	*Pratylenchus*	9	57	6
23	Mesekan	Jolle-3	*Meloidogyne*	9	88	8
24	Mesekan	Jolle-3	*Pratylenchus*	18	50	13
25	Minjar	Adama	*Meloidogyne*	19	100	19
26	Minjar	Adama	*Pratylenchus*	76	88	71
27	Minjar	Dire amba	*Meloidogyne*	6	75	5
28	Minjar	Dire amba	*Pratylenchus*	37	88	34
29	Minjar	Chele	*Meloidogyne*	106	88	99
30	Minjar	Chele	*Pratylenchus*	21	75	18
31	Minjar	Kitecha	*Meloidogyne*	68	63	54
32	Minjar	Kitecha	*Pratylenchus*	71	100	71
33	Minjar	Korema	*Meloidogyne*	334	88	312
34	Minjar	Korema	*Pratylenchus*	41	88	39
35	Sodo	Abuno	*Meloidogyne*	6	30	3
36	Sodo	Abuno	*Pratylenchus*	55	100	55
37	Sodo	Frish	*Meloidogyne*	0	0	0
38	Sodo	Frish	*Pratylenchus*	7	67	5
39	Sodo	Genbella	*Meloidogyne*	2	40	1
40	Sodo	Genbella	*Pratylenchus*	42	70	35
41	Sodo	Negessa	*Meloidogyne*	5	35	3
42	Sodo	Negessa	*Pratylenchus*	6	38	4
43	South Sodo	Kella	*Meloidogyne*	0	0	0
44	South Sodo	Kella	*Pratylenchus*	0	0	0
45	South Sodo	Gogeti-1	*Meloidogyne*	4	14	2
46	South Sodo	Gogeti-1	*Pratylenchus*	6	50	5
47	South Sodo	Gogeti-2	*Meloidogyne*	11	36	6
48	South Sodo	Gogeti-2	*Pratylenchus*	7	50	5
49	South Sodo	Gogeti-3	*Meloidogyne*	0	0	0
50	South Sodo	Gogeti-3	*Pratylenchus*	22	50	16

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Supplementary Table S2. Site-level details for the soil.

Site no.	District	Locality	Genus	PD	FO (%)	PV
1	Abeshegie	Bekota	*Pratylenchus*	82	85	75
2	Abeshegie	Bekota	*Rotylenchulus*	8	10	3
3	Abeshegie	Bekota	*Meloidogyne*	22	45	15
4	Abeshegie	Bekota	*Helicotylenchus*	6	35	3
5	Abeshegie	Bekota	*Scutellonema*	90	90	85
6	Abeshegie	Bekota	*Hoplolaimus*	3	25	1
7	Abeshegie	Biedo	*Pratylenchus*	131	81	118
8	Abeshegie	Biedo	*Rotylenchulus*	9	50	6
9	Abeshegie	Biedo	*Meloidogyne*	28	69	23
10	Abeshegie	Biedo	*Helicotylenchus*	14	44	10
11	Abeshegie	Biedo	*Scutellonema*	2	19	1
12	Abeshegie	Biedo	*Hoplolaimus*	1	6	0
13	Abeshegie	Biedo	*Ditylenchus*	3	25	1
14	Abeshegie	Gibi.Yebari	*Pratylenchus*	53	69	44
15	Abeshegie	Gibi.Yebari	*Rotylenchulus*	4	13	1
16	Abeshegie	Gibi.Yebari	*Meloidogyne*	9	50	6
17	Abeshegie	Gibi.Yebari	*Helicotylenchus*	1	13	0
18	Abeshegie	Gibi.Yebari	*Scutellonema*	46	88	43
19	Abeshegie	Gibi.Yebari	*Hoplolaimus*	3	31	2
20	Adea'a	Bekajou	*Rotylenchulus*	18	50	13
21	Adea'a	Bekajou	*Pratylenchus*	7	50	5
22	Adea'a	Bekajou	*Meloidogyne*	3	38	2
23	Adea'a	Bekajou	*Scutellonema*	3	25	1
24	Adea'a	Bekajou	*Criconemodies*	1	25	1
25	Adea'a	Bekajou	*Quinisulcius*	1	25	1
26	Adea'a	Diree	*Rotylenchulus*	26	88	24
27	Adea'a	Diree	*Pratylenchus*	31	88	29
28	Adea'a	Diree	*Meloidogyne*	1	13	0
29	Adea'a	Diree	*Scutellonema*	3	25	2
30	Adea'a	Diree	*Hoplolaimus*	6	13	2
31	Adea'a	Diree	*Criconemodies*	1	13	0
32	Adea'a	Diree	*Ditylenchus*	1	13	0
33	Adea'a	Gollodhertu	*Rotylenchulus*	16	63	12
34	Adea'a	Gollodhertu	*Pratylenchus*	17	38	10
35	Adea'a	Gollodhertu	*Meloidogyne*	19	75	17
36	Adea'a	Gollodhertu	*Scutellonema*	30	38	18
37	Adea'a	Gollodhertu	*Hoplolaimus*	8	13	3
38	Adea'a	Gollodhertu	*Quinisulcius*	8	25	4
39	Chekolla	Dollo.Jilla	*Rotylenchulus*	6	38	3
40	Chekolla	Dollo.Jilla	*Pratylenchus*	11	63	9
41	Chekolla	Dollo.Jilla	*Meloidogyne*	3	25	1
42	Chekolla	Dollo.Jilla	*Quinisulcius*	1	13	0
43	Chekolla	Dollo.Jilla	*Helicotylenchus*	2	38	1
44	Chekolla	Jara.gorro	*Rotylenchulus*	14	63	11
45	Chekolla	Jara.gorro	*Pratylenchus*	17	63	13
46	Chekolla	Jara.gorro	*Meloidogyne*	4	38	3
47	Chekolla	Jara.gorro	*Scutellonema*	13	63	10
48	Chekolla	Jara.gorro	*Hoplolaimus*	6	38	3
49	Chekolla	Jara.gorro	*Criconemodies*	3	38	2
50	Chekolla	Wara.Jarssa	*Rotylenchulus*	8	63	6
51	Chekolla	Wara.Jarssa	*Pratylenchus*	39	88	37

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Supplementary Table S2. (Continued.)

Site no.	District	Locality	Genus	PD	FO (%)	PV
52	Chekolla	Wara.Jarssa	*Meloidogyne*	5	63	4
53	Chekolla	Wara.Jarssa	*Scutellonema*	2	25	1
54	Lemmen.zuria	Lemmen.zuria	*Pratylenchus*	58	100	58
55	Lemmen.zuria	Lemmen.zuria	*Meloidogyne*	49	100	49
56	Lemmen.zuria	Lemmen.zuria	*Ditylenchus*	1	11	0
57	Mesekan	Jolle-1	*Pratylenchus*	162	100	162
58	Mesekan	Jolle-1	*Rotylenchulus*	273	100	273
59	Mesekan	Jolle-1	*Meloidogyne*	93	79	82
60	Mesekan	Jolle-1	*Scutellonema*	6	71	5
61	Mesekan	Jolle-1	*Helicotylenchus*	7	50	5
62	Mesekan	Jolle-1	*Quinisulcius*	191	100	191
63	Mesekan	Jolle-1	*Criconemodies*	1	21	1
64	Mesekan	Jolle-2	*Pratylenchus*	167	100	167
65	Mesekan	Jolle-2	*Rotylenchulus*	248	100	248
66	Mesekan	Jolle-2	*Meloidogyne*	13	79	11
67	Mesekan	Jolle-2	*Scutellonema*	4	36	2
68	Mesekan	Jolle-2	*Quinisulcius*	136	71	115
69	Mesekan	Jolle-2	*Criconemodies*	3	43	2
70	Mesekan	Jolle-2	*Ditylenchus*	1	7	0
71	Mesekan	Jolle-3	*Pratylenchus*	136	93	131
72	Mesekan	Jolle-3	*Rotylenchulus*	191	93	184
73	Mesekan	Jolle-3	*Meloidogyne*	31	64	25
74	Mesekan	Jolle-3	*Scutellonema*	8	57	6
75	Mesekan	Jolle-3	*Helicotylenchus*	6	43	4
76	Mesekan	Jolle-3	*Quinisulcius*	19	71	16
77	Mesekan	Jolle-3	*Criconemodies*	1	21	1
78	Minjar	Adama	*Rotylenchulus*	32	100	32
79	Minjar	Adama	*Pratylenchus*	169	100	169
80	Minjar	Adama	*Meloidogyne*	79	100	79
81	Minjar	Adama	*Scutellonema*	30	88	28
82	Minjar	Adama	*Hoplolaimus*	49	100	49
83	Minjar	Adama	*Criconemodies*	8	63	6
84	Minjar	Chele	*Rotylenchulus*	76	100	76
85	Minjar	Chele	*Pratylenchus*	269	100	269
86	Minjar	Chele	*Meloidogyne*	111	100	111
87	Minjar	Chele	*Scutellonema*	1	13	0
88	Minjar	Chele	*Hoplolaimus*	4	50	3
89	Minjar	Chele	*Criconemodies*	4	50	3
90	Minjar	Chele	*Quinisulcius*	1	13	0
91	Minjar	Dire.Amba	*Rotylenchulus*	55	100	55
92	Minjar	Dire.Amba	*Pratylenchus*	119	100	119
93	Minjar	Dire.Amba	*Meloidogyne*	29	100	29
94	Minjar	Dire.Amba	*Scutellonema*	25	88	23
95	Minjar	Dire.Amba	*Hoplolaimus*	38	88	35
96	Minjar	Dire.Amba	*Criconemodies*	3	50	2
97	Minjar	Kitecha	*Rotylenchulus*	167	100	167
98	Minjar	Kitecha	*Pratylenchus*	224	100	224
99	Minjar	Kitecha	*Meloidogyne*	40	100	40
100	Minjar	Kitecha	*Scutellonema*	3	38	2
101	Minjar	Kitecha	*Hoplolaimus*	1	13	0
102	Minjar	Kitecha	*Criconemodies*	4	38	2

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Supplementary Table S2. (Continued.)

Site no.	District	Locality	Genus	PD	FO (%)	PV
103	Minjar	Kitecha	*Quinisulcius*	3	13	1
104	Minjar	Kitecha	*Ditylenchus*	4	50	3
105	Minjar	Korema	*Rotylenchulus*	138	100	138
106	Minjar	Korema	*Pratylenchus*	70	100	70
107	Minjar	Korema	*Meloidogyne*	56	88	53
108	Minjar	Korema	*Scutellonema*	3	38	2
109	Minjar	Korema	*Hoplolaimus*	6	38	4
110	Minjar	Korema	*Criconemodies*	9	63	7
111	Minjar	Korema	*Ditylenchus*	1	13	0
112	Sebeta	Sebeta.hawas	*Pratylenchus*	34	89	32
113	Sebeta	Sebeta.hawas	*Rotylenchulus*	13	67	10
114	Sebeta	Sebeta.hawas	*Meloidogyne*	17	67	14
115	Sebeta	Sebeta.hawas	*Scutellonema*	3	33	2
116	Sebeta	Sebeta.hawas	*Quinisulcius*	5	22	2
117	Sebeta	Sebeta.hawas	*Ditylenchus*	2	11	1
118	Sebeta	Sebeta.hawas	*Helicotylenchus*	1	11	0
119	Sebeta	Sebeta.hawas	*Heterodera*	6	44	4
120	Sodo	Abuno	*Pratylenchus*	41	100	41
121	Sodo	Abuno	*Rotylenchulus*	21	50	14
122	Sodo	Abuno	*Meloidogyne*	6	40	4
123	Sodo	Abuno	*Scutellonema*	2	40	1
124	Sodo	Abuno	*Quinisulcius*	1	20	0
125	Sodo	Abuno	*Ditylenchus*	1	10	0
126	Sodo	Abuno	*Helicotylenchus*	23	70	19
127	Sodo	Frish	*Pratylenchus*	354	100	354
128	Sodo	Frish	*Rotylenchulus*	133	71	112
129	Sodo	Frish	*Meloidogyne*	9	29	5
130	Sodo	Frish	*Scutellonema*	8	43	5
131	Sodo	Frish	*Ditylenchus*	1	14	1
132	Sodo	Frish	*Helicotylenchus*	14	43	9
133	Sodo	Genbella	*Pratylenchus*	51	100	51
134	Sodo	Genbella	*Rotylenchulus*	18	60	14
135	Sodo	Genbella	*Meloidogyne*	8	40	5
136	Sodo	Genbella	*Scutellonema*	2	30	1
137	Sodo	Genbella	*Quinisulcius*	3	10	1
138	Sodo	Genbella	*Criconemodies*	1	10	0
139	Sodo	Genbella	*Ditylenchus*	2	20	1
140	Sodo	Genbella	*Helicotylenchus*	23	100	23
141	Sodo	Negesessa	*Pratylenchus*	42	92	40
142	Sodo	Negesessa	*Rotylenchulus*	4	42	3
143	Sodo	Negesessa	*Meloidogyne*	62	92	60
144	Sodo	Negesessa	*Scutellonema*	5	38	3
145	Sodo	Negesessa	*Hoplolaimus*	4	27	2
146	Sodo	Negesessa	*Criconemodies*	2	27	1
147	Sodo	Negesessa	*Ditylenchus*	12	46	8
148	Sodo	Negesessa	*Helicotylenchus*	18	69	15
149	Soouth.Sodo	Gogeti-1	*Pratylenchus*	52	93	50
150	Soouth.Sodo	Gogeti-1	*Rotylenchulus*	126	79	111
151	Soouth.Sodo	Gogeti-1	*Meloidogyne*	9	50	7
152	Soouth.Sodo	Gogeti-1	*Helicotylenchus*	190	64	152
153	Soouth.Sodo	Gogeti-1	*Scutellonema*	31	93	30

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Supplementary Table S2. (Continued.)

Site no.	District	Locality	Genus	PD	FO (%)	PV
154	Soouth.Sodo	Gogeti-1	*Criconemodies*	1	7	0
155	Soouth.Sodo	Gogeti-1	*Hoplolaimus*	1	14	0
156	Soouth.Sodo	Gogeti-1	*Quinisulcius*	1	21	0
157	Soouth.Sodo	Gogeti-2	*Pratylenchus*	85	86	79
158	Soouth.Sodo	Gogeti-2	*Rotylenchulus*	86	79	76
159	Soouth.Sodo	Gogeti-2	*Meloidogyne*	13	71	11
160	Soouth.Sodo	Gogeti-2	*Helicotylenchus*	8	57	6
161	Soouth.Sodo	Gogeti-2	*Scutellonema*	11	64	9
162	Soouth.Sodo	Gogeti-2	*Criconemodies*	0	7	0
163	Soouth.Sodo	Gogeti-2	*Hoplolaimus*	3	29	2
164	Soouth.Sodo	Gogeti-2	*Quinisulcius*	7	36	4
165	Soouth.Sodo	Gogeti-3	*Pratylenchus*	49	86	45
166	Soouth.Sodo	Gogeti-3	*rotylenchulus*	198	93	190
167	Soouth.Sodo	Gogeti-3	*Meloidogyne*	15	64	12
168	Soouth.Sodo	Gogeti-3	*Helicotylenchus*	3	21	1
169	Soouth.Sodo	Gogeti-3	*Scutellonema*	14	71	11
170	Soouth.Sodo	Gogeti-3	*Hoplolaimus*	1	14	0
171	Soouth.Sodo	Gogeti-3	*Quinisulcius*	1	14	0
172	Soouth.Sodo	Gogeti-3	*Ditylenchus*	1	21	1
173	Soouth.Sodo	Kella	*Pratylenchus*	9	56	7
174	Soouth.Sodo	Kella	*Rotylenchulus*	12	100	12
175	Soouth.Sodo	Kella	*Meloidogyne*	21	78	18
176	Soouth.Sodo	Kella	*Helicotylenchus*	16	78	14
177	Soouth.Sodo	Kella	*Scutellonema*	25	67	20
178	Soouth.Sodo	Kella	*Criconemodies*	1	22	1

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