

***Quinisulcius salviae* sp. n. (Tylenchida: Telotylenchidae) from Mexico, with molecular characterisation of some stunt nematodes**

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Summary. Several stunt nematode species, including *Bitylenchus hispaniensis*, *B. maximus*, *B. ventrosignatus*, *Bitylenchus* sp. 1, *Paratrophurus striatus*, *Quinisulcius capitatus*, *Q. salviae* sp. n., *Tylenchorhynchus annulatus*, *T. claytoni*, *T. clarus*, *T. thermophilus*, *Tylenchorhynchus* spp. 1–3, *T. zaeae*, and *Paramerlinius* sp., were recovered from soil samples collected in Mexico, the USA (California, Florida, Minnesota, and North Dakota), India, Spain and South Korea and were characterised using morphological and molecular approaches. A new species, *Quinisulcius salviae* sp. n., isolated from the rhizosphere of *Salvia polystachia* in Mexico, is described herein. The new species is most similar to *Q. capitatus* but can be distinguished from it by a combination of morphological, morphometric and molecular characters. Phylogenetic relationships among the examined taxa and other representatives of the family were reconstructed using sequences of the D2-D3 expansion segments of the 28S rRNA gene, the ITS of rRNA gene, and the mitochondrial cytochrome *c* oxidase subunit I (*COI*) gene. In total, 43 new D2-D3 28S rRNA, thirteen new ITS rRNA, and nine new *COI* gene sequences were generated. The resulting phylogenetic analyses provided new insights into evolutionary relationships within the Telotylenchinae, revealed the non-monophyly of several currently recognised genera, and underscored the need for a comprehensive taxonomic reassessment of the group based on integrative analyses incorporating morphology and multilocus molecular data.

Key words: *Bitylenchus*, morphology, morphometrics, *Paramerlinius*, phylogeny, *Salvia polystachia*, *Telotylenchus*, *Tylenchorhynchus*.

Stunt nematodes (Nematoda: Dolichodoroidea) constitute a diverse group of migratory ectoparasites associated with the roots of cultivated and wild plants worldwide. Members of the family inhabit a wide range of terrestrial ecosystems and have been reported from agricultural, horticultural, grassland and forest habitats. Several species are economically important because they feed on root epidermal and cortical tissues, causing stunting, chlorosis, reduced root growth, and yield losses in numerous crops. Despite their broad distribution and agricultural significance, the taxonomy and phylogenetic relationships of many stunt nematodes remain insufficiently resolved owing to their conserved

morphology and overlapping morphometric characters (Fortuner & Luc, 1987; Siddiqi, 2000; Geraert, 2011; Bert & Hunt, 2025).

The superfamily Dolichodoroidea, as defined by Siddiqi (2000), comprises several families, including Telotylenchidae, which is the largest and encompasses the subfamilies Telotylenchinae Siddiqi, 1960, Meiodorinae Siddiqi, 1976, Macrotrophurinae Fotedar & Handoo, 1978, and Merliniinae Siddiqi, 1971. Taxon delimitation within these subfamilies has traditionally relied on a combination of morphological and morphometric characters, including the lip region structure morphology, incisure number in lateral field,

presence or absence of lateral field areolation, pharyngeal glands extending, reproductive structures and tail structures. However, many of these diagnostic features exhibit considerable intraspecific variation and, in some cases, may reflect convergent evolution. Consequently, their taxonomic utility may be limited, resulting in conflicting interpretations of species and generic boundaries.

The incorporation of molecular markers into stunt nematode systematics has substantially improved species identification and phylogenetic reconstruction. Ribosomal markers, particularly the D2-D3 expansion segments of the 28S rRNA gene and the internal transcribed spacer (ITS) region, together with the mitochondrial cytochrome *c* oxidase subunit I (*COI*) gene, have become standard tools for integrative taxonomy of tylenchid nematodes (Handoo *et al.*, 2014; Hosseinvand *et al.*, 2020; Azizi *et al.*, 2022). Molecular phylogenetic studies have demonstrated that several traditionally recognised genera are not monophyletic and have provided evidence supporting the reassessment of generic concepts within Telotylenchidae. Nevertheless, molecular data remain unavailable for numerous nominal species, while many existing sequences are based on geographically restricted populations, limiting our understanding of species boundaries, intraspecific variability, and evolutionary relationships.

Several populations of stunt nematodes were recovered during our surveys of plant-parasitic nematodes associated with natural vegetation in Mexico. To place these populations into a broader taxonomic and phylogenetic context, they were examined together with additional populations collected in the USA (California, Florida, and North Dakota), South Korea, Spain, and India. This geographically diverse material provided an opportunity to compare morphological variation across distant populations, evaluate patterns of molecular diversity, and infer phylogenetic relationships using multiple nuclear and mitochondrial markers.

Several genera of the subfamily Telotylenchinae have previously been reported from agricultural soils in Mexico, although their diversity and distribution remain poorly documented. Among species of the genus *Tylenchorhynchus*, those from Mexico include: *T. aspericutis* Knobloch, 1975a, *Tylenchorhynchus clarus* Allen, 1955, *T. claytoni* Steiner, 1937, *T. ewingi* Hopper, 1959, *T. mexicanus* Knobloch & Laughlin, 1973 and *T. paratriversus* Brzeski, 1991. There are also several species of the genus *Quinisulcius*: *Q. acutus* (Allen, 1955) Siddiqi, 1971, *Q. capitatus* (Allen, 1955) Siddiqi, 1971, *Q.*

obregonus Knobloch & Laughlin, 1973 and *Q. tarjani* Knobloch, 1975b (Knobloch & Laughlin, 1973; Knobloch, 1975a, b; Vazquez, 1976; Brzeski, 1991). All these available records are based exclusively on morphological identification; molecular characterisation has not yet been conducted for stunt nematodes from Mexico. This lack of molecular data limits the assessment of species boundaries, phylogenetic relationships, and the diversity of stunt nematodes in Mexico. More broadly, molecular data remain scarce for stunt nematode faunas in many regions of the world. As a result, the diversity, phylogenetic affinities, and biogeographic relationships of many regional populations remain poorly defined. Expanding integrative taxonomic studies to undersampled areas are therefore essential for improving species delimitation, testing the validity of existing genera, and establishing a more comprehensive framework for the systematics of Telotylenchidae.

The objectives of the present study were: (i) to provide an integrative characterisation of the new species *Quinisulcius salviae* sp. n. from Mexico based on morphology including scanning electron microscopy (SEM), morphometrics, and sequences of the D2-D3 expansion segments of the 28S rRNA, ITS rRNA, and mitochondrial *COI* genes; (ii) to characterise additional stunt nematode species collected in North America, Europe and Asia; (iii) to assess interspecific and intraspecific sequence divergence using nuclear and mitochondrial markers; and (iv) to reconstruct the molecular phylogeny of the subfamily Telotylenchinae to evaluate the evolutionary relationships among its principal genera and contribute to a more robust taxonomic framework for this economically important group of plant-parasitic nematodes.

MATERIALS AND METHODS

Nematode samples. Soil and root samples were collected from the rhizosphere of various cultivated and wild plant species in Mexico, the USA (California, Florida, Minnesota, and North Dakota), India, Spain and South Korea. Nematodes were extracted from soil and root samples using either the modified Baermann funnel technique or the modified Cobb sieving and flotation-centrifugation method (Jenkins, 1964). Extracted nematodes were examined under a stereomicroscope, and stunt nematodes were hand-picked individually from the mixed nematode suspensions. Specimens were heat-killed, fixed, and processed for morphological examination using light and SEM microscopy, while additional live specimens were preserved for molecular analyses.

Morphological study. For preliminary observations, live stunt nematodes were transferred to a drop of water on a glass slide, gently heat-relaxed, and examined under a compound microscope. Morphological and morphometric studies were conducted using specimens killed and fixed in Golden's fixative and processed to anhydrous glycerin following the ethanol-glycerin dehydration method of Seinhorst (1959), as modified by De Grisse (1969). Permanent microscope slides were prepared for detailed examination. Morphometric measurements and line drawings were made using a drawing tube attached to an American Optical compound microscope (Massachusetts, USA). Light micrographs were obtained with a Lumenera Infinity 2 digital camera (Ontario, Canada) mounted on an Olympus BX51 compound microscope (Tokyo, Japan) equipped with Nomarski differential interference contrast optics.

Scanning electron microscopy (SEM) was conducted at the Colegio de Postgraduados (Mexico) and Universidad Rey Juan Carlos (Spain). *Quinisulcius salviae* sp. n. specimens examined in Mexico were washed in 0.05 M magnesium buffer (pH 6.8) for 20 min and dehydrated through a graded ethanol series (10-100%) in ten steps of 15 min each. The specimens were subsequently critical-point dried, sputter-coated with gold/palladium (80:20) for 4 min, and examined with a JEOL JSM-6390 scanning electron microscope operated at an accelerating voltage of 10 kV (Cid del Prado Vera & Subbotin, 2012). *Tylenchorhynchus* sp.3 specimens were prepared according to Álvarez-Ortega and Peña-Santiago (2016). Briefly, specimens were rehydrated in distilled water, dehydrated through graded ethanol and acetone series, critical-point dried, sputter-coated with gold, and examined using a FEI Nova NanoSEM 230 scanning electron microscope.

Molecular study. Genomic DNA was extracted from individual or pooled nematode specimens using the proteinase K protocol. DNA extraction and PCR amplification were performed following the procedures described by Subbotin (2021). The following primer pairs were used: (i) D2A (5'-ACA AGT ACC GTG AGG GAA AGT TG-3') and D3B (5'-TCG GAA GGA ACC AGC TAC TA-3') to amplify the D2-D3 expansion segments of the 28S rRNA gene; (ii) TW81 (5'-GTT TCC GTA GGT GAA CCT GC-3') and AB28 (5'-ATA TGC TTA AGT TCA GCG GGT-3') to amplify the ITS rRNA gene; and (iii) JB3 (5'-TTT TTT GGG CAT CCT GAG GTT TAT-3') and JB5 (5'-AGC ACC TAA ACT TAA AAC ATA ATG AAA ATG-3') to

amplify a partial fragment of the mitochondrial *COI* gene (Subbotin, 2021).

Successfully amplified PCR products were purified and sequenced by Azenta Life Sciences (Massachusetts, USA) using the same primer pairs employed for PCR amplification. The newly generated sequences were deposited in GenBank under accession numbers: PZ788139-PZ788176, PZ867569-PZ867572, QB031796 (D2-D3), PZ869697-PZ869705, PZ880654, PZ788177-PZ788179 (ITS), PZ869268-PZ869270, PZ867794, PZ867795, PZ793944, PZ793945, PZ888723, QB031795 (*COI*).

Newly generated sequences were aligned with selected homologous sequences of stunt nematodes of the subfamily Telotylenchinae retrieved from the GenBank (Handoo *et al.*, 2014; Hosseinvand *et al.*, 2020; Mwamula *et al.*, 2020; Abdolkhani & Azimi, 2021; Gu *et al.*, 2021; Munawar *et al.*, 2021; Shokoohi, 2021; Azizi *et al.*, 2022; Jumaah & Azimi, 2022; Kefelegn *et al.*, 2023; Peraza-Padilla *et al.*, 2024; Ansari & Ghaderi, 2026 and others) using ClustalX version 1.83 (Chenna *et al.*, 2003). Outgroup taxa for each dataset were chosen according to the results of previously published data (Handoo *et al.*, 2014). Representatives of the Merliniinae collected from Mexico were also added as outgroups. Phylogenetic analyses were conducted using Bayesian inference (BI) implemented in MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003). For each gene dataset, BI analyses were initiated from a random starting tree and run with four Markov chains for 2.0×10^6 generations. Posterior probability (PP) values are indicated on the corresponding clades. The alignment for ITS rRNA gene sequences was used to construct phylogenetic networks using statistical parsimony (SP) as implemented in POPART software (<http://popart.otago.ac.nz>) (Bandelt *et al.*, 1999). Sequence alignment analyses were performed using PAUP* 4b10 (Swofford, 2003). Pairwise genetic divergences among taxa were calculated as absolute distances and as mean percentage distances based on the complete alignments, with adjustments for missing data.

Species delimitation of the stunt nematodes examined in this study was based on an integrative taxonomic approach combining morphological and morphometric analyses with molecular phylogenetic inference and DNA sequence divergence analyses. Morphological identifications were evaluated in conjunction with phylogenetic relationships inferred from nuclear (D2-D3 expansion segments of the 28S rRNA gene and ITS rRNA gene) and mitochondrial (*COI*) sequence datasets, together with pairwise

genetic distance analyses, to delimit species and assess their phylogenetic relationships.

RESULTS

Using traditional morphological taxonomic characters integrated with molecular criteria, we distinguished several stunt nematode species within studied samples: *Bitylenchus hispaniensis* Handoo *et al.*, 2014, *B. maximus* (Allen, 1955) Siddiqi, 1986, *B. ventrosignatus* (Tobar-Jiménez, 1969) Jairajpuri, 1982, *Bitylenchus* sp. 1, *Paratrophurus striatus* Castillo, Siddiqi & Gomez Barcina, 1989, *Quinisulcius capitatus* (types A and B), *Q. salviae* sp. n., *Tylenchorhynchus annulatus* (Cassidy, 1930) Golden, 1971 (types A and B), *T. claytoni*, *T. clarus*, *T. thermophilus* Golden, Baldwin & Mundo-Ocampo, 1995, *Tylenchorhynchus* sp. 1, *Tylenchorhynchus* sp. 2, *Tylenchorhynchus* sp. 3, *T. zaeae* Sethi & Swarup, 1968 (type A) and *Paramerlinius* sp. (Table 1).

Quinisulcius capitatus (type A), *Q. salviae* sp. n., *Tylenchorhynchus* sp. 1 and *Paramerlinius* sp. were identified from soil samples collected in Mexico (Table 1). The description of the new species, together with morphometric data and photomicrographs of the stunt nematodes from Mexico, is provided below.

Quinisulcius salviae sp. n. (Figs 1-4)

Measurements. See Table 2.

Female. Body straight to spiral and ventrally arcuate in the posterior half of the body, after heat fixation. Cuticle annulated; annuli become wider (1.0 µm) at mid-body. Lateral field with five incisures, non-areolated, occupying about half of maximum body diameter, the middle three incisures extending past the phasmid. Labial disc not pronounced, lip region hemispherical bearing 7 to 8 fine annuli, slightly offset from body contour. Labial framework lightly sclerotised. Stylet knobs rounded, slightly posteriorly directed, 3.0 to 4.0 µm across. Median bulb oval with conspicuous valve plates. Isthmus slender, encircled with nerve ring, 107-132 µm from the anterior end. Hemizonid 3 to 4 body annuli anterior to excretory pore. Basal bulb elongate-pyriform. Cardia hemispherical. Reproductive system didelphic-amphidelphic, oocytes in a single row. Spermatheca inconspicuous, the anterior 10-14 µm long by 10-12 µm width and the posterior 8.0-15 µm long by 9.0-12 µm width, without sperm. Vagina about 9.0-11 µm long, vulva depressed, vulva lips inconspicuous. Anus prominent. Post-rectal intestinal sac present. Tail cylindrical, with a non-

annulated bluntly rounded terminus, bearing 43-44 annuli on lateral side. Phasmids close to middle of tail.

Male. Not found.

Etymology. The specific epithet was derived from genus name of the host plant, *Salvia*.

Type host and locality. Rhizosphere soil around wild sage *Salvia polystachia* Cav. (the mint family Lamiaceae). Samples were collected in an oak forest, Municipality of Ozumba, State of Mexico, Mexico.

Type material. Type specimens are deposited in the Laboratorio de Helmintología del Instituto de Biología, UNAM, Mexico: holotype female (CNHE-12360), and paratypes females (CNHE-1631). Other paratypes materials (A-129) were deposited in the Colegio de Postgraduados Nematode Collection. ZooBank: LSIDurn:lsid:zoobank.org:act: C81139D5-C9AF-45CF-9E66-5FA7F6488AF8.

Differential diagnosis. *Quinisulcius salviae* sp. n. can be identified by the following characteristics: body length 710-1190 µm, ventrally arcuate posterior to the vulva; stylet 17-22 µm long with rounded knobs; lip region offset, rounded with 7-8 fine annuli; basal bulb elongate-pyriform; post-rectal intestinal sac present, 15-28 µm long; lateral field not areolated; tail with 43-44 annuli, terminus bluntly rounded not striated.

Quinisulcius salviae sp. n. is distinguished from *Q. capitatus* (Hussain *et al.*, 2019; Peraza-Padilla *et al.*, 2024) by its longer body (710-1190 vs 605-911 µm), higher a ratio (36.8-62.4 vs 26.5-43.7) and tail terminus shape (broadly rounded vs bluntly rounded).

Quinisulcius salviae sp. n. differs from *Q. curvus* (Williams, 1960) Siddiqi, 1971 (Williams, 1960) by its longer body length (710-1190 vs 490-630 µm), longer tail (39-59 vs 39 µm), greater number of tail annuli (43-44 vs 15-20).

Quinisulcius salviae sp. n. is distinguished from *Q. obregonus* (Knobloch & Laughlin, 1973) by its longer body length (710-1190 vs 470-570 µm), higher a ratio (36.8-62.4 vs 26-36), longer stylet (17.0-22 vs 12-14 µm), greater number of tail annuli (43-44 vs 19-25), and the absence of males (vs presence in *Q. obregonus*).

Quinisulcius salviae sp. n. is distinguished from *Q. tarjani* (Knobloch, 1975b) by its longer body length (710-1190 vs 630-780 µm), higher a ratio (36.8-62.4 vs 30-32), fewer tail annuli (43-44 vs 44-60), and the absence of males (vs presence in *Q. tarjani*).

Other Telotylenchidae representatives

Light micrographs of female specimens are presented to document key morphological features

Table 1. Species and populations of the stunt nematodes characterised in this study.

Species	Location (coordinates)	Associated plants	Sample code	GenBank accession number		
				D2-D3 of 28S rRNA gene	ITS rRNA gene	COI gene
<i>Bitylenchus hispaniensis</i>	Spain, Toledo (40.05170° N, 4.07438° W)	Bramble, poplar, and wild asparagus	PP26A, PP26B	PZ788140, PZ788143	-	-
<i>B. hispaniensis</i>	Spain, Toledo (39.86068° N, 4.30907° W)	Olive trees	PP273A, PP273B	PZ788141, PZ788142	-	-
<i>B. maximus</i>	Spain, Granada (37.08952° N, 3.37688° W)	Unknown plants	SN1HA, SN1HB	PZ788147, PZ788148	-	-
<i>B. maximus</i>	USA, California, Santa Clara County, San Jose	<i>Iris</i> sp.	CD3464	PZ788149	PZ880654	-
<i>B. ventrosignatus</i>	India, Uttar Pradesh	Grasses	CD2089	PZ788139	-	PZ888723
<i>Bitylenchus</i> sp.1	USA, California, Monterey County, Monterey	<i>Poa</i> spp.	CD1254	PZ788144	-	-
<i>Paratrophurus striatus</i>	Spain, Guadalajara (40.67236° N, 1.92131° W)	<i>Pinus nigra</i> and <i>P. sylvestris</i>	RTERZ24PB, RTERZ24PC	PZ788145, PZ788146	-	-
<i>Quinisulcius capitatus</i> type A	Mexico, State of Mexico (19.09448° N, 98.74557° W)	<i>Solanum dulcamara</i>	CD2791, sample 8	PZ788152	-	PZ869269
<i>Q. capitatus</i> type A	USA, San Diego County, Escondido, Trinity Community Garden	Unknown plants	CD3686	QB031796		QB031795
<i>Q. capitatus</i> type B	USA	Unknown plants	CD2724	PZ788150	PZ788177	PZ869270
<i>Q. capitatus</i> type B	USA, North Dakota	Wheat	CD1900	PZ788151	PZ788178	PZ793945
<i>Q. salviae</i> sp. n.	Mexico, State of Mexico (19.0676° N, 98.8343° W)	<i>Salvia polystachia</i>	CD4620	PZ788153	PZ788179	PZ793944
<i>Telotylenchus</i> sp.	USA, California, Mono County (37.77317° N, 119.12600° W)	Unknown plants	BC858	PZ867571	-	-
<i>Telotylenchus</i> sp.	USA, California, Alpine County (38.67610° N, 119.62160° W)	Unknown plants	BC1303, BC1304	PZ867569, PZ867570	-	-
<i>Telotylenchidae</i>	USA, California, Santa Barbara County (34.41697° N, 119.83335° W)	Unknown plants	BC629	PZ867572	-	PZ869268
<i>Tylenchorhynchus annulatus</i> type A	USA, Florida	<i>Ficus benjamina</i>	CD974	PZ788154	PZ869698	-

Table 1 (continued). Species and populations of the stunt nematodes characterised in this study.

Species	Location (coordinates)	Associated plants	Sample code	GenBank accession number		
				D2-D3 of 28S rRNA gene	ITS rRNA gene	COI gene
<i>Tylenchorhynchus annulatus</i> type A	USA, Florida	Palm	CD1378	PZ788155	-	-
<i>T. annulatus</i> type B	USA, California, Kern County (35.23560° N, 119.30025° W)	Unknown plants	BC288	PZ788162	PZ869697	-
<i>T. annulatus</i> type B	USA, California, Kern County, Wasco	Peach plum	CD4023	PZ788160	PZ869705	-
<i>T. annulatus</i> type B	USA, California, San Bernardino County, San Bernardino	<i>Poa annua</i>	CD1258	PZ788161	-	-
<i>T. claytoni</i>	South Korea	Grasses	CD1386	PZ788156	-	-
<i>T. clarus</i>	USA, California, Santa Cruz County (36.88610° N, 121.78215° W)	Unknown plants	BC126	PZ788173	-	-
<i>T. clarus</i>	USA, California, Madera County, Madera	Grasses	CD1220	PZ788172	-	-
<i>T. thermophilus</i>	USA, Florida	<i>Ficus</i> sp.	CD1368b	PZ788157	PZ869699	-
<i>Tylenchorhynchus</i> sp. 1	Mexico, Tlaxcala (19.38455° N, 97.92855° W)	<i>S. rostratum</i>	CD2783, sample 38	PZ788165, PZ788166	-	-
<i>Tylenchorhynchus</i> sp. 1	Mexico, State of Mexico (19.09263° N, 98.74487° W)	<i>S. dulcamara</i>	CD2787, sample 6	PZ788167	PZ869702	-
<i>Tylenchorhynchus</i> sp. 1	Mexico, Tlaxcala (19.38753° N, 97.92972° W)	<i>Solanum</i> sp.	CD2802, sample 43	PZ788168	-	-
<i>Tylenchorhynchus</i> sp. 2	USA, Minnesota	Unknown plants	CD1377	PZ788158	PZ869700	-
<i>Tylenchorhynchus</i> sp. 2	USA, North Dakota	Corn	CD1903	PZ788159	PZ869701	-
<i>Tylenchorhynchus</i> sp. 3	USA, California, Riverside County, Dripping Springs Campground	Trees and grasses	CD1808, CD1825	PZ788163, PZ788164	-	-
<i>T. zeae</i> type A	USA, California, Imperial County (33.04713° N, 115.35628° W)	Alfalfa	BC1481; BC1482; BC1485	PZ788169, PZ788170, PZ788171	-	-
<i>Paramerlinius</i> sp.	Mexico, Tlaxcala (19.38753° N, 97.92972° W)	<i>Solanum</i> sp.	CD2800, sample 43	PZ788176	PZ869703	PZ867794
<i>Paramerlinius</i> sp.	Mexico, Puebla (19.05558° N, 98.44692° W)	<i>S. dulcamara</i>	CD2803, sample 4 CD2816, sample 1	PZ788174, PZ788175	PZ869704	PZ867795

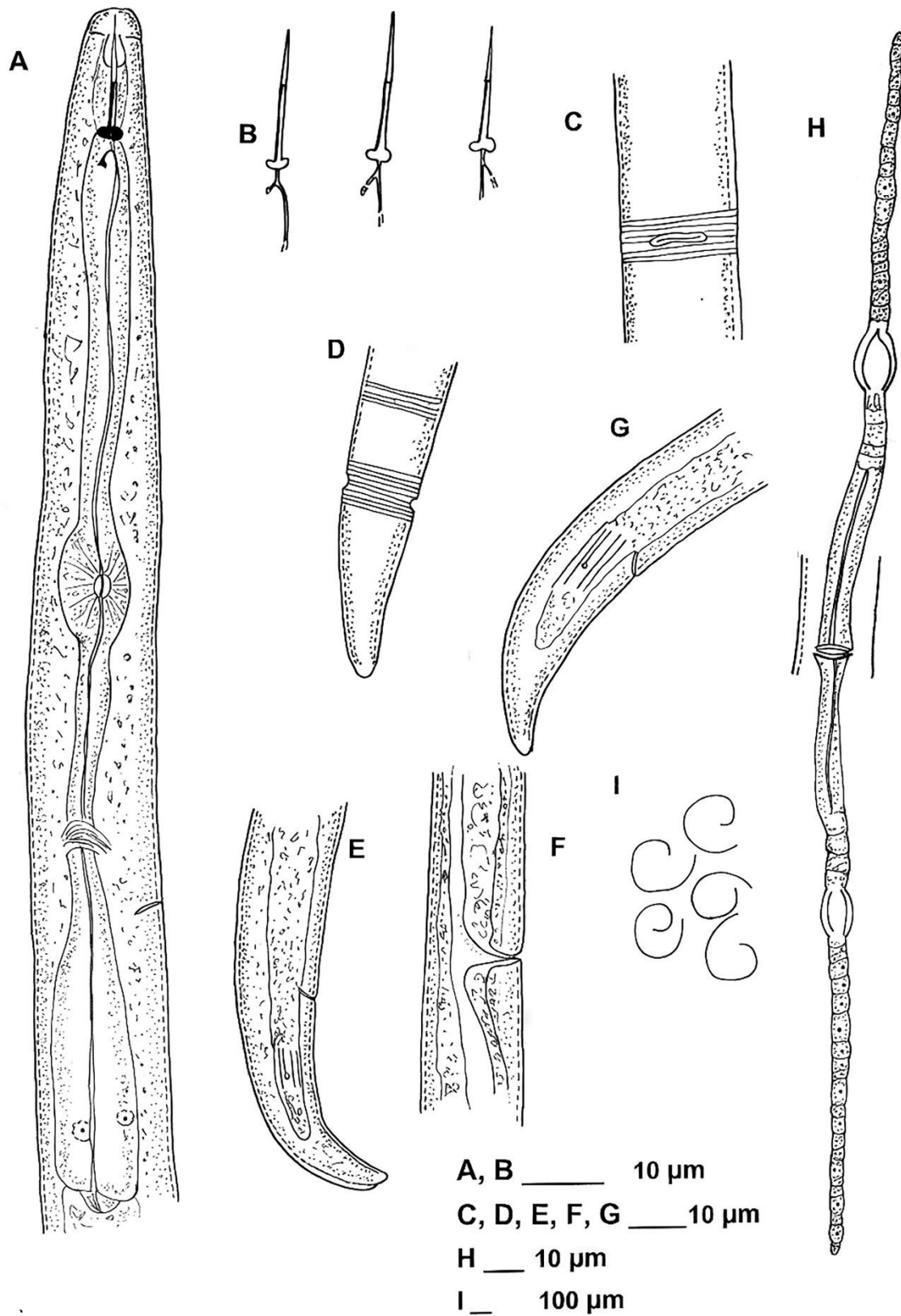


Fig. 1. *Quinisulcius salviae* sp. n. Female. A: Anterior region; B: Stylets; C: Vulva, ventral view; D: Tail, ventral view; E, G: Tail, lateral view; F: Vulva region, lateral view; H: Gonads; I: Body shape after fixation.

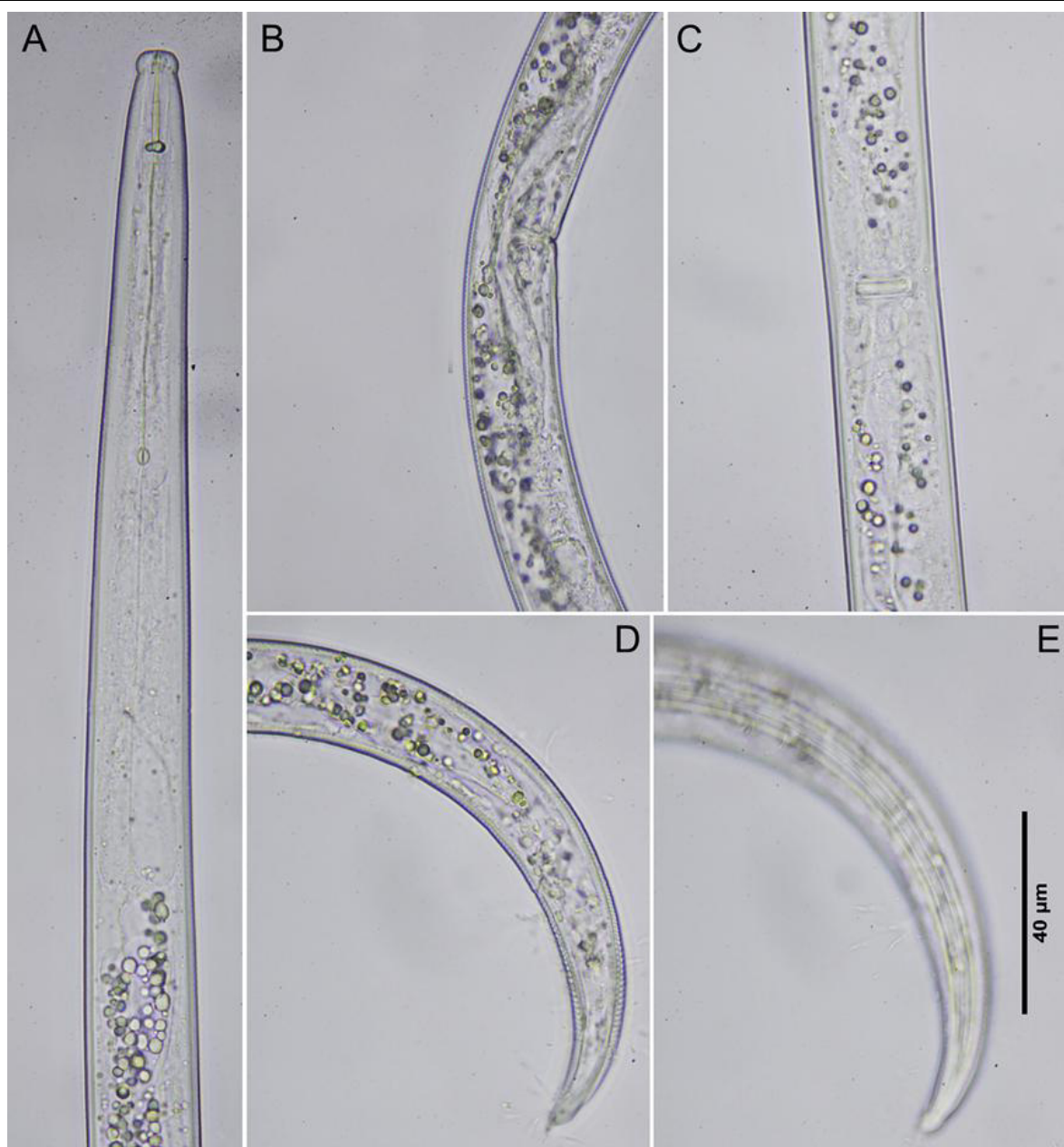


Fig. 2. *Quinisulcius salviae* sp. n. Light microscopy photographs. Female. A: Anterior region; B: Lateral view midbody at vulva region; C: Midbody at vulva level, ventral view; D, E: Tail region, lateral view.

and to facilitate future comparisons of *Quinisulcius capitatus* type A (CD2791) (Fig. 3) and *Tylenchorhynchus* sp. 1 (CD2783, CD2787) (Fig. 5), both collected in Mexico. Scanning electron micrographs are provided for *Tylenchorhynchus* sp. 3 (CD1825) from California, USA (Fig. 6). These images highlight diagnostic morphological characters, including the lip region, stylet morphology, and tail shape. Additional sampling and integrative taxonomic analyses will be necessary to determine whether these unidentified taxa correspond to previously described species or

represent novel species.

Molecular characterisation and phylogenetic relationships of the stunt nematodes. D2-D3 expansion segments of 28S rRNA gene. Forty-three new sequences were generated in the present study. The alignment comprised 119 sequences representing members of the family Telotylenchidae, along with two outgroup taxa, and had a total length of 777 bp. The inferred phylogenetic relationships of Mexican Telotylenchidae species to related taxa from geographic regions are shown in Figure 7. Molecular

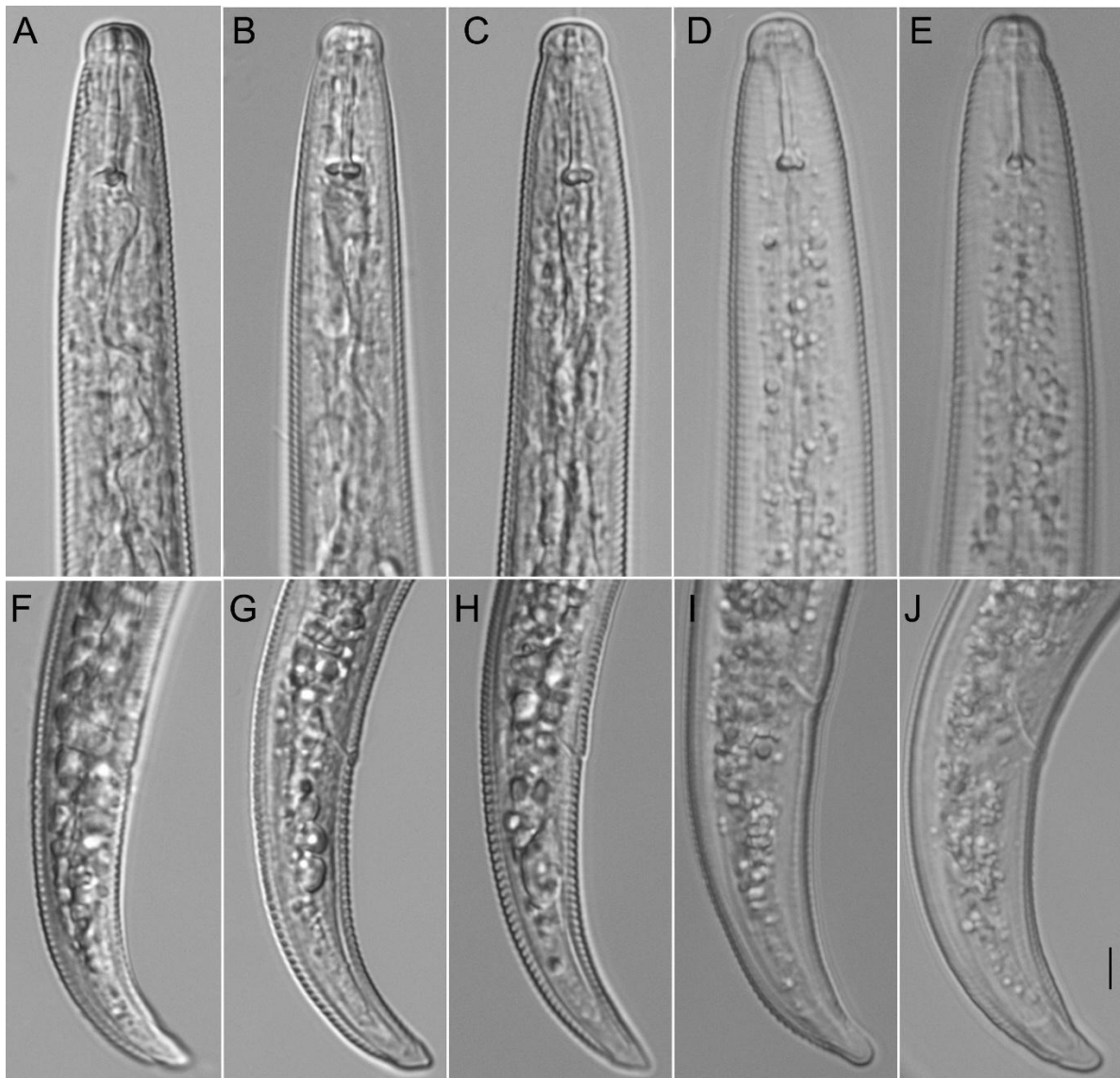


Fig. 3. *Quinisulcius salviae* sp. n. (A-C, F-H) and *Q. capitatus* (type A) (D, E, I, J) from Mexico. Light microscopy photographs. Female. A-E: Anterior regions; F-J: Posterior regions. Scale = 10 μ m.

characteristics indicate that the genera: *Bitylenchus*, *Neodolichorhynchus*, *Paratrophurus*, *Quinisulcius*, *Telotylenchus* and *Tylenchorhynchus* are non-monophyletic. *Tylenchorhynchus* and *Bitylenchus* exhibit pronounced polyphyly, with multiple strongly supported subclades.

The sequences of the *Quinisulcius* species formed a clade with *Neodolichorhynchus*. The genus *Quinisulcius* was divided into four well-resolved lineages corresponding to: (i) *Q. capitatus* (type A) from Spain, Costa Rica, Netherlands, Mexico, Pakistan, USA, Ethiopia, (ii) *Q. salviae* sp. n. from Mexico, (iii) *Q. capitatus* (type B) from USA and Canada and (iv) *Q. curvus* from China. *Quinisulcius salviae* sp. n. was recovered as a distinct lineage sister to *Q. capitatus* type A with strong support (PP = 1.00)

and differed from it in 3.1-3.9% (19-24 bp). Intraspecific variation for *Q. capitatus* (type A) was up to 0.3% (2 bp) and *Q. capitatus* (type B) was 1.1-1.4% (8-10 bp). Interspecific differences between type A and B of *Q. capitatus* was 10-11%.

Intraspecific sequence variations were up to 4.3% (27 bp) for *Tylenchorhynchus aduncus*, 4.2% (28 bp) for *Bitylenchus ventrosignatus*, 3.5% (20 bp) for *Paramerlinius* sp., 2.6% (18 bp) for *B. maximus*, 1.3% (9 bp) for *Tylenchorhynchus* sp.1, 0.6% (4 bp) for *Paratrophurus striatus* and 0.3% (2 bp) for *T. zeae* (type A).

ITS rRNA gene. Three new *Quinisulcius* sequences and ten sequences from other representatives of the family Telotylenchidae were generated in the present study. Two ITS rRNA

Table 2. Morphometrics of females of *Quinisulcius salviae* sp. n.
All measurements are in μm and in the form: range (mean $\pm$ S.D.).

Characters	Holotype	Paratypes Fixed	Immobilized by heating
n	1	20	21
L	873	900 $\pm$ 0.10 (710-1070)	1030 $\pm$ 0.11 (770-1190)
a	45.9	46.3 $\pm$ 4.4 (38.2-53.6)	43.8 $\pm$ 5.8 (36.8-62.4)
b	5.6	5.6 $\pm$ 0.5 (4.6-6.4)	5.8 $\pm$ 0.6 (4.5-6.6)
c	21.3	20.2 $\pm$ 2.4 (16.4-25.4)	21.2 $\pm$ 1.9 (17.3-24)
c'	2.9	3.2 $\pm$ 0.3 (2.8-4.0)	2.9 $\pm$ 0.7 (1.2-3.9)
Stylet length	18	18.8 $\pm$ 1.0 (18-22)	19.1 $\pm$ 1.0 (17-21)
Conus length	9	9.3 $\pm$ 0.89 (8.0-11)	8.7 $\pm$ 0.72 (8.0-10)
Lip region width	8	8.0	8.8 $\pm$ 0.6 (7.0-9)
Lip region height	5	4.7 $\pm$ 0.4 (4.0-5.0)	4.8 $\pm$ 0.4 (4.0-5.0)
Lip diameter / lip high	1.6	1.7 $\pm$ 0.18 (1.6-2.0)	1.8 $\pm$ 0.2 (1.6-2.3)
DGO	2	2.0	2.3 $\pm$ 0.5 (1.5-3.0)
o	11.1	10.6 $\pm$ 0.5 (9.0-11.1)	12.0 $\pm$ 2.5 (8.3-16.7)
Median bulb valve to anterior end distance	80	75.3 $\pm$ 3.1 (69-80)	83.1 $\pm$ 3.7 (77-90)
Median bulb length	13	15.5 $\pm$ 1.2 (13-18)	16.4 $\pm$ 1.0 (15-19)
Median bulb diameter	9	9.4 $\pm$ 0.8 (7.0-10)	10.5 $\pm$ 0.8 (9.0-12)
Median bulb length/diameter	1.4	1.7 $\pm$ 0.2 (1.4-2.1)	1.6 $\pm$ 0.2 (1.1-1.9)
Pharynx length	155	158 $\pm$ 5.9 (147-169)	176 $\pm$ 6.7 (164-187)
Glandular bulb length	37	36.7 $\pm$ 2.9 (32-42)	40.0 $\pm$ 4.7 (35-55)
Body width (maximum)	19	19.4 $\pm$ 0.8 (18-21)	24.1 $\pm$ 3.1 (20-31)
Excretory pore to anterior end distance	124	129.2 $\pm$ 8.4 (108-145)	135.3 $\pm$ 13.7 (103-153)
Hemizonid to anterior end	117	123.8 $\pm$ 11.5 (101-160)	134.8 $\pm$ 3.9 (130-140)
Vulval body diameter	18	18.4 $\pm$ 0.8 (17-20)	22.7 $\pm$ 3.2 (18-27)
V%	54.4	52.6 $\pm$ 3.5 (45.6-59.1)	52.4 $\pm$ 3.2 (44-56.4)
Vagina length	9	9.3 $\pm$ 1.1 (6.0-10)	9.9 $\pm$ 0.6 (9.0-11)
Anterior gonad length	172	174.9 $\pm$ 10.3 (160-203)	194.3 $\pm$ 10.8 (173-215)
Posterior gonad length	169	169.4 $\pm$ 8.1 (150-185)	183.9 $\pm$ 19.4 (154-210)
Tail length	41	44.7 $\pm$ 3.7 (40-54)	47.6 $\pm$ 5.4 (39-59)
Tail width	14	13.8 $\pm$ 0.7 (12-15)	15.4 $\pm$ 1.4 (12-18)
Phasmid to anus	15	16.2 $\pm$ 3.1 (12-25)	18.3 $\pm$ 3.7 (13-25)
Intestine sac	22	20.5 $\pm$ 3.3 (15-28)	25 (n=2)
Nerve ring to anterior end	102	108.9 $\pm$ 6.8 (99-123)	117.4 $\pm$ 6.9 (106-132)

sequence alignments were constructed: (i) an alignment including representatives of the family Telotylenchidae, and (ii) an alignment including representatives of the genus *Quinisulcius*.

The Telotylenchidae alignment contained 178 sequences and was 829 bp in length. A statistical parsimony network showing the phylogenetic relationships among the ITS rRNA gene sequences is presented in Figure 8. The ITS sequences representing the genus *Quinisulcius* clustered together, whereas sequences of species of the genera *Bitylenchus* and *Paratrophurus* were distributed across different parts of the network. The sequences identified as *T. annulatus* and *T. leviterminalis* showed a wide distribution throughout the network.

The *Quinisulcius* alignment comprised 17

sequences of the genus along with two sequences of outgroup taxa, and had a total length of 826 bp. Phylogenetic relationships of representatives of the genus *Quinisulcius* as inferred from Bayesian analysis is given in Figure 9. The genus was divided into four well-resolved lineages corresponding to: (i) *Q. capitatus* (type A) from China, Pakistan, Ethiopia, (ii) *Q. salviae* sp. n. from Mexico, (iii) *Q. capitatus* (type B) from USA and Canada and (iv) *Q. curvus* from China. *Quinisulcius salviae* sp. n. had a sister relationship with the *Q. capitatus* type A and differed from it in 9.0-9.4% (68-69 bp). Interspecific differences between type A and B of *Q. capitatus* was 21.4-22.6% (139-158 bp).

COI gene. Nine new sequences were generated in the present study. The alignment comprised 15

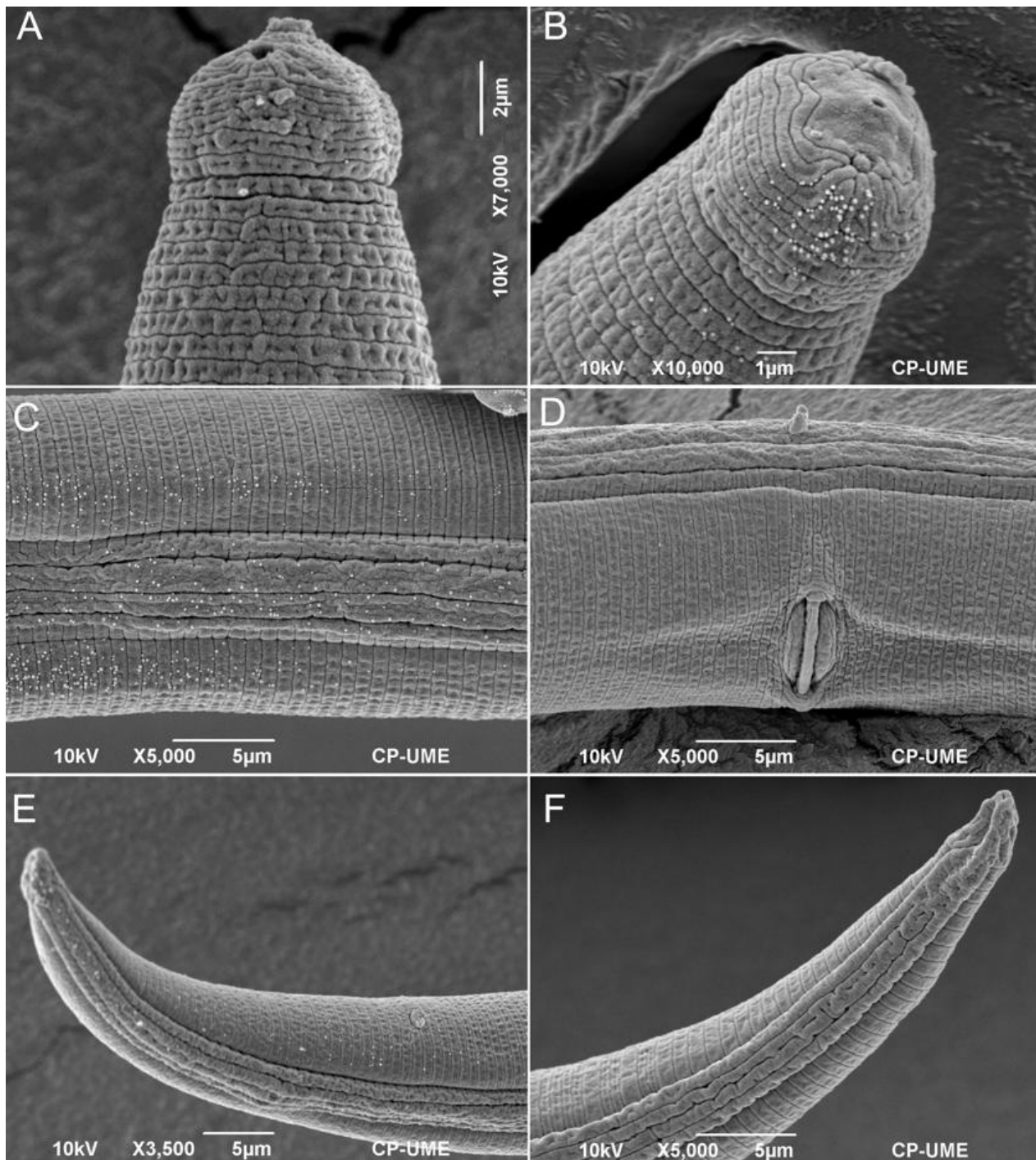


Fig. 4. *Quinisulcius salviae* sp. n. Scanning electron micrographs. Female. A, B: Cephalic region; C: Lateral field; D: Vulval region; E, F: Tail regions.

sequences and had a total length of 396 bp. Phylogenetic relationships of representatives of the genus *Quinisulcius* are given in Figure 10. *Quinisulcius salviae* sp. n. had a sister relationship with the *Q. capitatus* type A and differed from it in 13.4-13.9% (43-47 bp). Interspecific differences between type A and B of *Q. capitatus* was 24-28%

(74-101 bp).

DISCUSSION

The genus *Quinisulcius* Siddiqi, 1971 is characterised by the presence of five lateral incisures, an offset, rounded, and finely annulated cephalic region, a robust stylet with rounded basal knobs, and

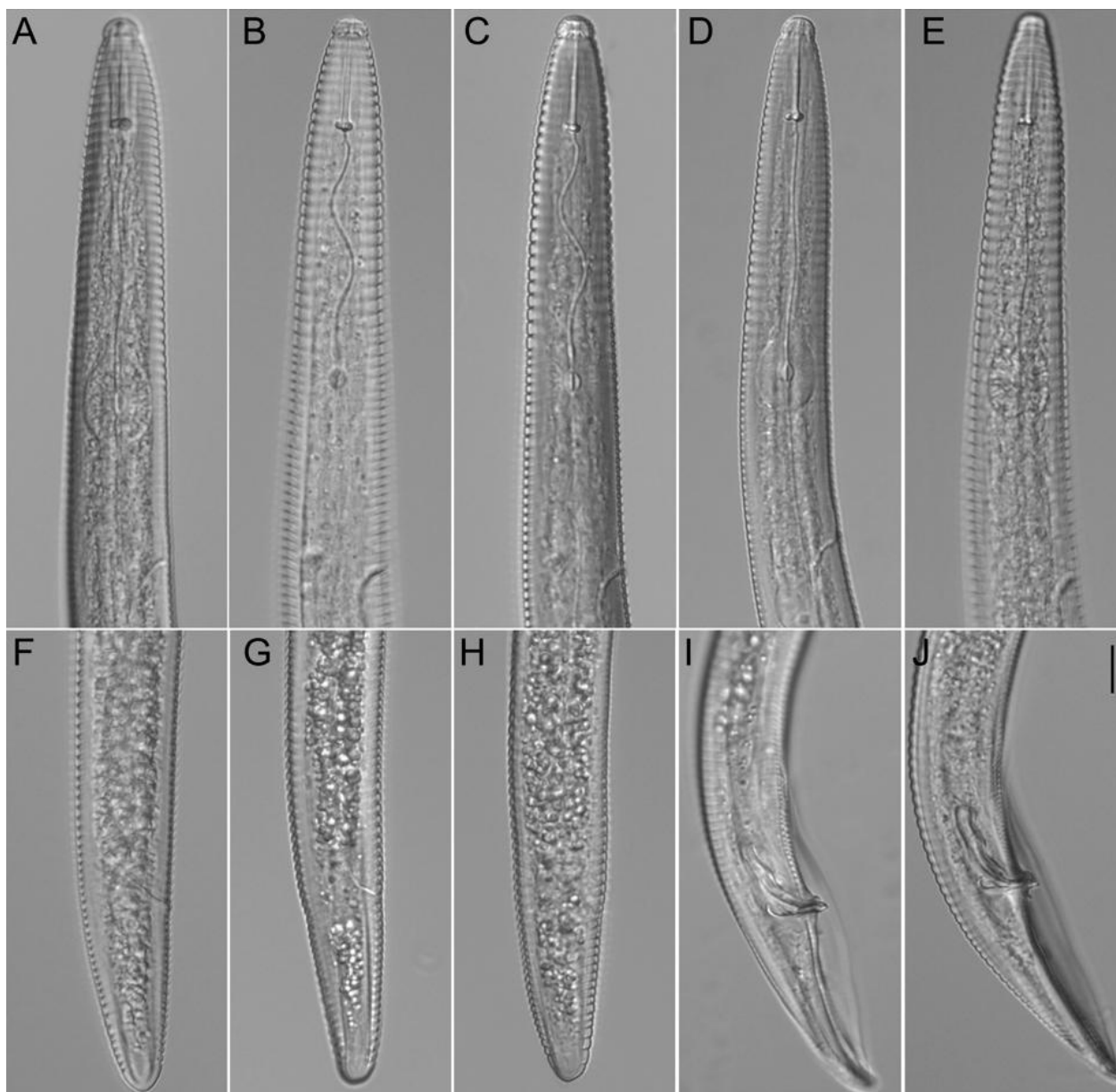


Fig. 5. *Tylenchorhynchus* sp. 1. (CD2783: A, B, D, F, G, I; CD2787: C, E, H, J). Light microscopy photographs. Female (A-C; F-H). Males (D, E, I, J). A-C: Anterior regions; F-J: Posterior regions. Scale = 10 μ m.

a conoid tail that is usually ventrally arcuate and terminates in a smooth or finely striated tip. Males are either rare or absent in most species. Members of the genus are distributed throughout tropical and subtropical regions, where they occur in association with a wide range of cultivated crops and natural vegetation (Siddiqi, 1971; 2000; Geraert, 2011; Hussain *et al.*, 2019).

With the description of *Q. salviae* sp. n., the genus now comprises 18 valid species. Morphologically, the new species most closely resembles *Q. capitatus*, sharing the general body form, cephalic region, stylet, and tail morphology that characterise the

genus. However, *Q. salviae* sp. n. can be distinguished from *Q. capitatus* by a combination of a few morphological and morphometric differences, together with clear molecular divergence in the D2-D3 expansion segments of the 28S rRNA gene, ITS rRNA region, and mitochondrial *COI* gene. The concordance between morphological observations and molecular phylogenetic evidence supports the recognition of *Q. salviae* sp. n. as a distinct species.

Quinisulcius capitatus is one of the most widely reported species of the genus and has been recorded from a broad range of cultivated crops and natural vegetation across North and South America, Asia,

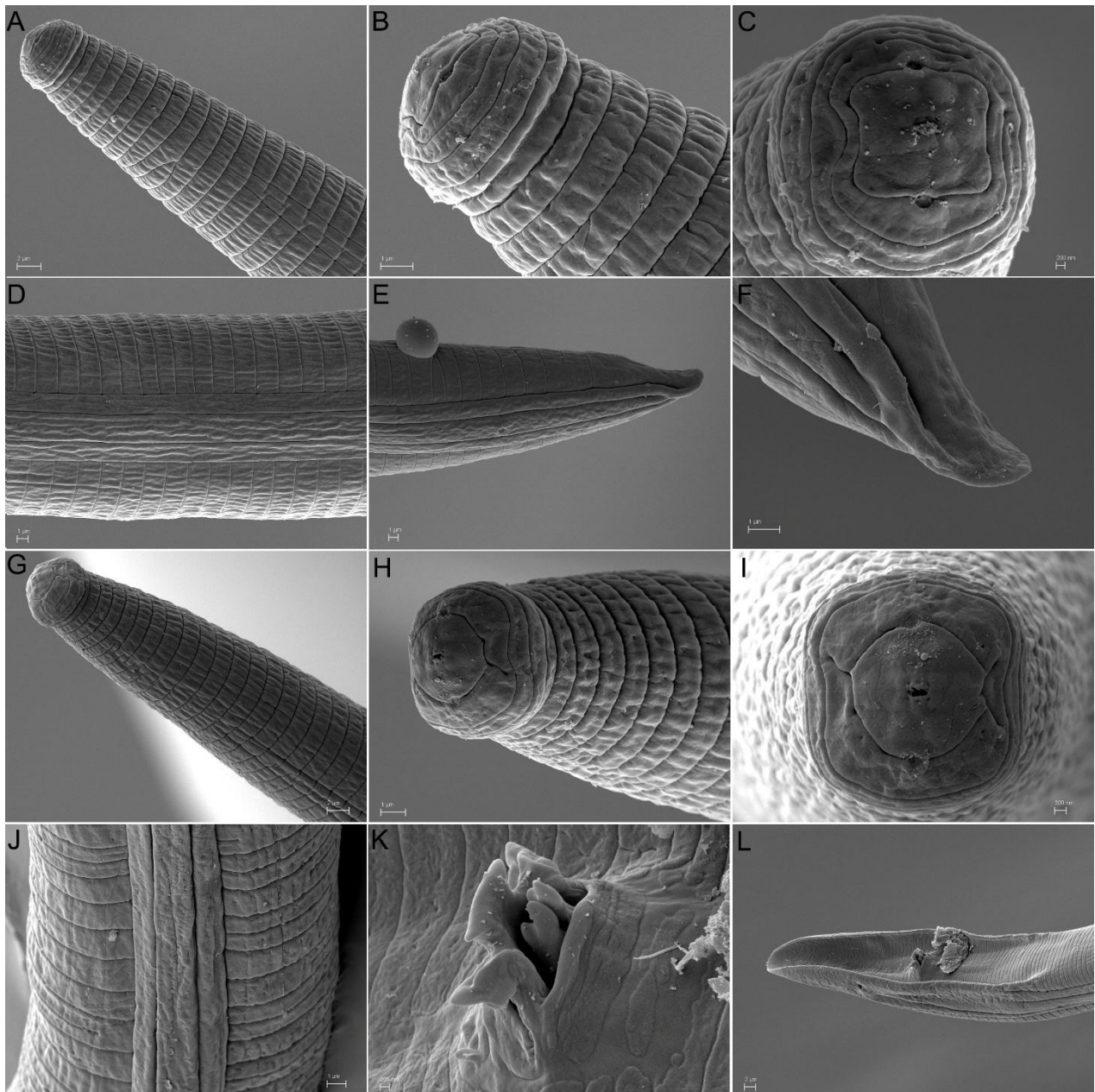


Fig. 6. *Tylenchorhynchus* sp. 3. (CD1825). Scanning electron micrographs. Female (A-F). A, B: Anterior region; C: Cephalic region; D: Lateral field; E: Tail region; F: Tail terminus; Males (G-L). G, H: Anterior region; I: Cephalic region; J: Lateral field; K: Spicule tips; L: Posterior region.

Africa, and Europe (Hussain *et al.*, 2019; Munawar *et al.*, 2021; Peraza-Padilla *et al.*, 2024). The species was originally described from soil collected in a pear orchard near Watsonville, California, USA (Allen, 1955), and is now among the best-characterised members of the genus, with both morphological and molecular information available from multiple populations. Nevertheless, the molecular analyses presented here indicate that *Q. capitatus* may represent a species complex. Phylogenetic analyses consistently recovered at least two well-

differentiated lineages: a broadly distributed 'type A' lineage exhibiting relatively low intraspecific sequence variation and a more divergent 'type B' lineage represented by populations from North America and closely related isolates. The level of genetic divergence between these lineages is comparable to that observed among closely related species in other plant-parasitic nematode groups and may therefore reflect the presence of cryptic species. However, because the available evidence is based on a limited number of molecular markers and only

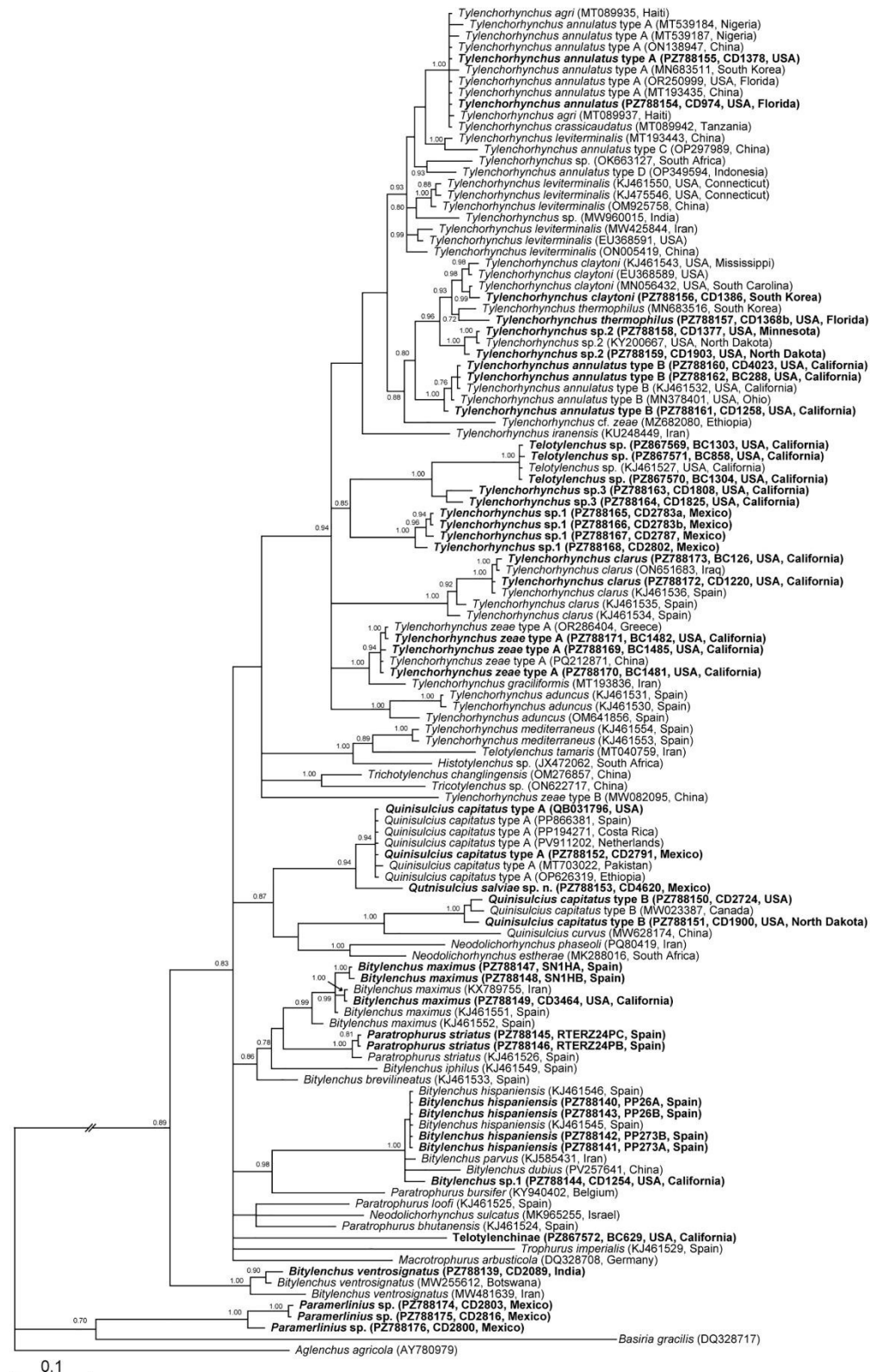


Fig. 7. Phylogenetic relationships of representatives of the subfamily Telotylenchinae from Mexico with other species as inferred from Bayesian analysis of the D2-D3 of the 28S rRNA gene sequences under the GTR + I + G model. Posterior probabilities equal to or greater than 70% are given for appropriate clades. The new sequences are indicated in bold.

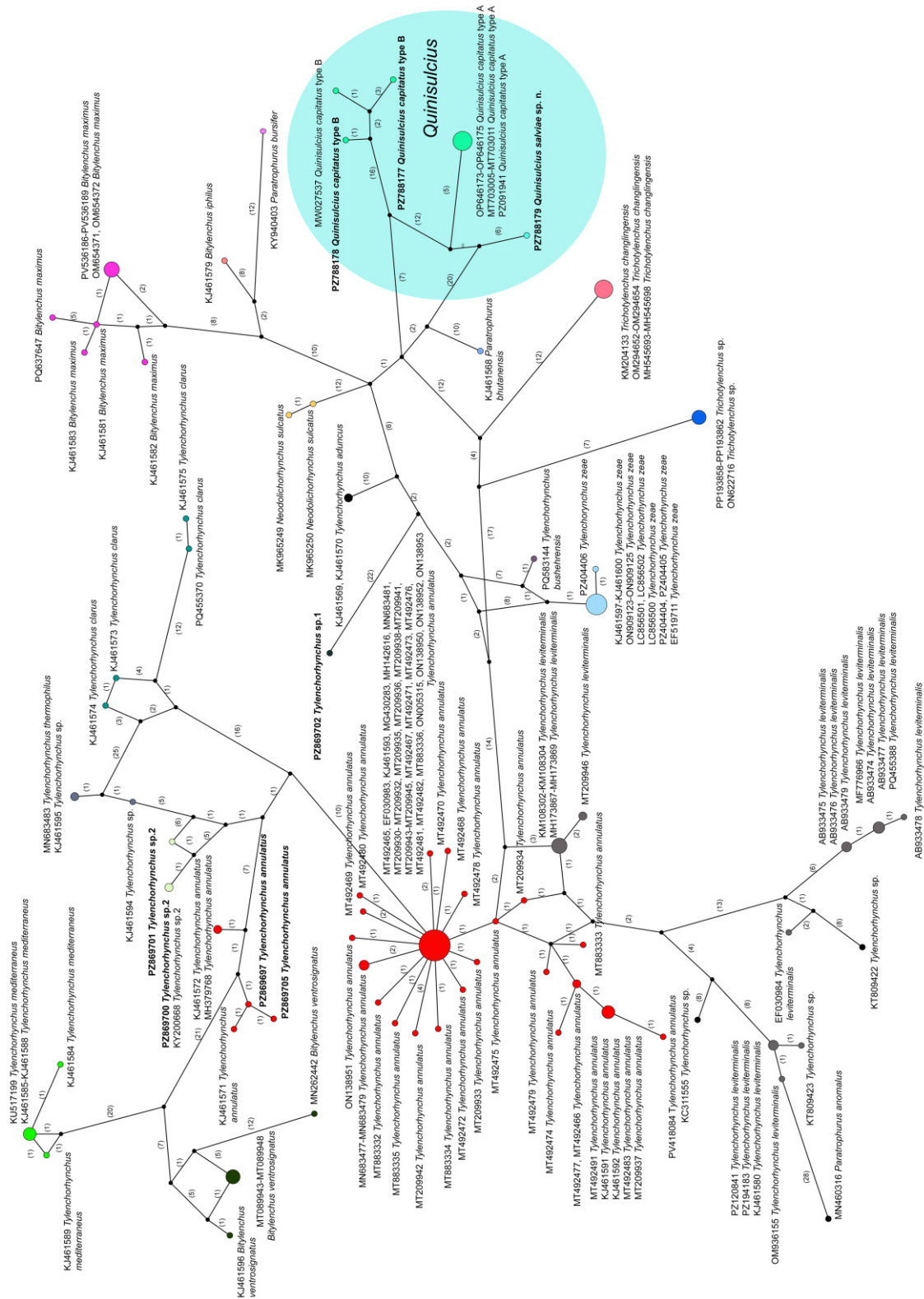


Fig. 8. Statistical parsimony network showing the phylogenetic relationships between ITS rDNA gene sequences of representatives of the genus *Quinisulcius* and other stunt nematodes. Pie (circle) sizes are proportional to the number of samples with a particular ITS haplotype. The new sequences are indicated in bold.

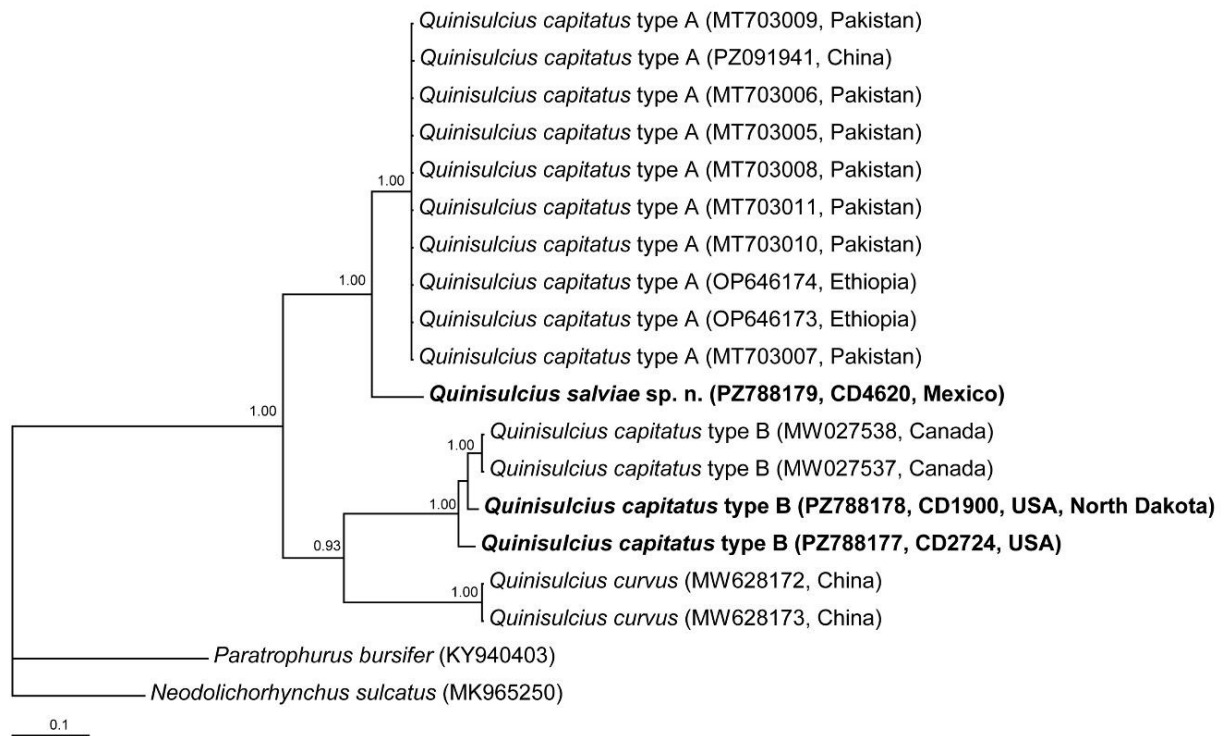


Fig. 9. Phylogenetic relationships of representatives of the genus *Quinisulcius* as inferred from Bayesian analysis of the ITS of rRNA gene sequences under the GTR + I + G model. Posterior probabilities equal to or greater than 70% are given for appropriate clades. The new sequences are indicated in bold.

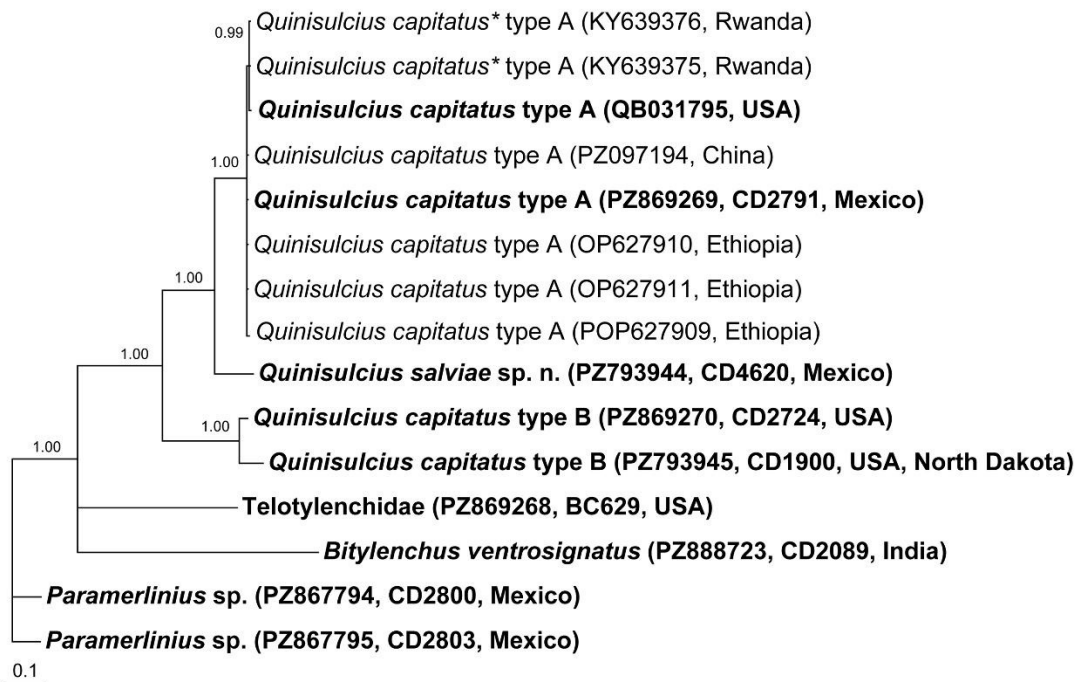


Fig. 10. Phylogenetic relationships of representatives of the genus *Quinisulcius* as inferred from Bayesian analysis of the COI gene sequences under the GTR + I + G model. Posterior probabilities equal to or greater than 70% are given for appropriate clades. The new sequences are indicated in bold. *- identified as *Tylenchorhynchus* sp. in the GenBank.

minor morphological differences, additional sampling, multilocus phylogenetic analyses, and detailed morphometric comparisons will be required before formal taxonomic conclusions can be drawn.

It is important to emphasise that the accurate identification and taxonomic interpretation of species within the Telotylenchidae require confirmation through integrated morphological and molecular analyses of topotype populations. In particular, additional studies involving *Quinisulcius capitatus* and other representatives of the family, including *Tylenchorhynchus annulatus*, *T. claytoni*, *T. clarus*, *T. leviterminalis*, *T. thermophilus*, *T. zaeae*, and *Bitylenchus ventrosignatus*, collected from their respective type localities are essential. Examination of these populations using detailed morphometric analyses, high-resolution morphological techniques, and multilocus molecular markers will provide a critical framework for evaluating the reliability of current species concepts and for confirming or revising the identifications applied in the present study. Such topotype-based investigations are especially important for taxa with broad geographical distributions and complex genetic variation, where cryptic diversity or historical misidentifications may influence phylogenetic interpretations and taxonomic conclusions.

The present phylogenetic analyses provide further insight into relationships within the Telotylenchinae and have important implications for the classification of the group. Handoo *et al.* (2014) tested alternative phylogenetic hypotheses and found support for the monophyly of both *Tylenchorhynchus* and *Bitylenchus* under the classification of Siddiqi (2000), while rejecting the broader concept of *Tylenchorhynchus* proposed by Fortuner and Luc (1987). However, the expanded molecular dataset analysed in the present study provides evidence that may challenge these earlier conclusions. The phylogenetic analyses based on the D2-D3 expansion segments of the 28S rRNA gene consistently indicate that several genera currently recognised within the Telotylenchinae, including *Bitylenchus*, *Neodolichorhynchus* and *Telotylenchus*, are not monophyletic. Rather, representatives of these genera are interspersed throughout the phylogeny, indicating that the morphological characters traditionally used for generic delimitation may not reliably reflect evolutionary history and may have evolved independently in different lineages. Consequently, the present molecular evidence does not support the concept of the subfamily Telotylenchinae as proposed by Siddiqi (2000). Instead, the inferred relationships are more consistent with the broader generic concept advocated by

Fortuner and Luc (1987), who regarded *Bitylenchus*, *Telotylenchus*, *Quinisulcius*, *Trilineellus*, *Neodolichorhynchus* and several other nominal genera as junior synonyms of *Tylenchorhynchus*. In the 28S rRNA gene phylogeny, representatives of these genera fail to form distinct, well-supported monophyletic lineages, suggesting that many diagnostic morphological characters used to separate these genera might be homoplastic. If these relationships are further confirmed by broader taxon sampling, multilocus phylogenetic analyses, and comprehensive morphological reassessments, these genera could likewise be treated as junior synonyms of *Tylenchorhynchus*. Such a taxonomic framework would support a broader, phylogenetically informed circumscription of *Tylenchorhynchus*, encompassing substantially greater morphological diversity. Nevertheless, because the present conclusions are based primarily on limited number of molecular markers, additional integrative studies incorporating multiple independent nuclear and mitochondrial loci, together with detailed morphological and morphometric analyses, will be essential before a comprehensive revision of generic boundaries within the Telotylenchidae can be confidently proposed.

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I. Cid del Prado Vera, E. Sosa Pérez, J. H. Ruiz Ibarra, H. Ferris, S. Álvarez-Ortega, A. Michaud and S. A. Subbotin. *Quinisulcius salviae* sp. n. (Tylenchida: Telotylenchidae) из Мексики с молекулярно-генетической характеристикой некоторых видов нематод.

Резюме. Несколько видов нематод из семейства Telotylenchidae, включая *Bitylenchus hispaniensis*, *B. maximus*, *B. ventrosignatus*, *Bitylenchus* sp. 1, *Paratrophurus striatus*, *Quinisulcius capitatus*, *Q. salviae* sp. n., *Tylenchorhynchus annulatus*, *T. claytoni*, *T. clarus*, *T. thermophilus*, *Tylenchorhynchus* spp. 1–3, *T. zeeae* и *Paramerlinius* sp., были обнаружены в образцах почвы, собранных в Мексике, США (Калифорния, Флорида, Миннесота и Северная Дакота), Индии, Испании и Южной Корее, и охарактеризованы с использованием морфологических и молекулярных методов. В настоящей работе описан новый вид *Quinisulcius salviae* sp. n., выделенный из ризосферы *Salvia polystachia* в Мексике. Новый вид наиболее близок к *Q. capitatus*, но отличается от него сочетанием морфологических, морфометрических и молекулярных признаков. Филогенетические взаимоотношения между исследованными таксонами и другими представителями семейства были реконструированы с использованием последовательностей D2-D3-расширяющихся сегментов гена 28S рРНК, ITS-области гена рРНК и митохондриального гена цитохром с оксидазы субъединицы I (COI). Всего было получено 43 новые последовательности D2-D3 28S рРНК, 13 новых последовательностей ITS рРНК и 9 новых последовательностей гена COI. Полученные результаты филогенетического анализа позволили получить новые данные об эволюционных взаимоотношениях внутри подсемейства Telotylenchinae, выявили немонофилетичность нескольких родов, признаваемых в настоящее время, и подчеркнули необходимость всестороннего таксономического пересмотра этой группы на основе комплексного анализа, объединяющего морфологические признаки и многолокусные молекулярные данные.