



# First report of four dagger nematode species of the genus *Xiphinema* (Nematoda: Longidoridae) from banana in Syria using an integrative approach

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**Abstract** A nematological survey was conducted between 2021 and 2022 in banana fields distributed in two major banana-producing regions in the western coast of Syria. As a result, six populations of *Xiphinema* spp. identified as *X. diffusum*, *X. pachtaicum*, *X. simile*, *X. vuittenezi* and *X. zagrosense* were isolated from the rhizosphere of banana plants (*Musa* sp.) and characterized using morphological and molecular data based on two rRNA genes (D2–D3 expansion segments of the 28S, and ITS fragments) and partial region of the cytochrome oxidase I gene (*COI* mtDNA) sequences. Moreover, the molecular identification of the endosymbionts of these populations was also performed using the complete 16S rDNA gene. The phylogenetic relationships of the recovered species of nematodes and respective endosymbionts were reconstructed. *Candidatus* *Xiphinematobacter* sp.

(OR196969; OR196971) and *Ca. Xiphinematobacter* sp. (OR196970) were detected in *X. diffusum* and *X. simile*, respectively, and clustered together with other *Ca. Xiphinematobacter* sp.A and sp.I respectively. To our knowledge, this is the first report of *X. diffusum*, *X. simile*, *X. vuittenezi* and *X. zagrosense* parasitizing banana in Syria, extending the geographical distribution of these species within the Mediterranean Basin.

**Keywords** 16S rRNA gene · 28S rRNA gene · Bayesian inference · *COI* mtDNA · Endosymbionts · ITS rRNA · Longidorids · Molecular phylogeny · Taxonomy

## Introduction

Dorylaimida Pearse, 1942 is one of the most abundant and diverse orders within the phylum Nematoda Potts, 1932 (Potts, 1932; Pearse, 1942; Ahmed & Holovachov, 2021). The genus *Xiphinema* Cobb, 1913, commonly known as dagger nematode, belongs to the family Longidoridae Thorne, 1935 and to the sub-order Dorylaimina Pearse, 1936 (Ahmed & Holovachov, 2021; Gutiérrez-Gutiérrez et al., 2016; Pearse, 1936). According to morphological and biological features, members of *Xiphinema* are currently divided into two sub-groups: (*i*) *Xiphinema non-americanum* group, comprising around 237 species (172 species listed in original key by Loof & Luc, 1990, 11 species in the first and 31 species in the second supplement

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by Loof and Luc (1993) and Loof et al. (1996); till 2019, 60 species added to the genus or revalidated as listed by Mirzaie Fouladvand et al., 2019, and five species added to the genus since 2019 by Jahanshahi Afshar et al., 2019; Vazifeh et al., 2019; Archidona-Yuste et al., 2020a, b; Cai et al., 2020; Poureskandarian et al., 2023), mainly characterized by a wide morphological diversity: having a body J- to C-shaped after heat relaxation, a relatively long body (usually among 3.0 and 8.5 mm long) and odontostyle, female with high variation in the reproductive system, with or without any type of uterine differentiations (i.e. Z or pseudo-Z organ, crystal-like and/or spine-like structures in the tubular part of the uterus) and a wide diversity of tail shapes (Coomans et al., 2001; Loof & Luc, 1990; Taylor & Brown, 1997); and (ii) *Xiphinema americanum* group, accounted with 60 valid species (49 species listed by Lamberti et al., 2000, 11 extra species listed by Mobasseri et al., 2019a, b; three species added by Jahanshahi Afshar et al., 2021; Naghavi et al., 2022a; Gu et al., 2022), characterized by a spiral body after heat relaxation, a relatively small body (usually among 1.2 and 3.0 mm long), a female reproductive system with two equally developed genital branches, short uteri without uterine differentiations, endosymbiotic bacteria in intestinal cells and in the reproductive system in some species, and a conical tail with sharp to broadly rounded tip (Coomans et al., 2001; Lamberti et al., 2000; Palomares-Rius et al., 2016, 2021). *Xiphinema* species cause severe damage to plants by their direct feeding on root cells (Jones et al., 2013; Taylor & Brown, 1997). However, some of them retain/transmit economically important nepoviruses (genus Nepovirus, family Comoviridae) (Taylor & Brown, 1997; Trudgill et al., 1983). Furthermore, some of these *Xiphinema* species are included in the list of quarantine organisms of the European and Mediterranean Plant Protection Organization (EPPO) (OEPP/EPPO, 2022) which emphasizes the need for an accurate nematode identification at the species level.

An integrative taxonomic approach is the most efficient and accurate strategy to overcome practical issues with dagger nematodes (Gutiérrez-Gutiérrez et al., 2010, 2011b; 2013; Archidona-Yuste et al., 2016a, b; 2020b; Palomares-Rius et al., 2017; Cai et al., 2019, 2020; Mobasseri et al., 2019a, b). Until recently, *Xiphinema* spp. populations were usually only identified at the species-level using polytomous

diagnostic keys (Lamberti et al., 2000, 2004; Loof & Luc, 1990; Loof et al., 1996). Nowadays, sequencing RNA-based markers represents a powerful approach for species-level taxonomic identification within the genus *Xiphinema* and understanding of the evolutionary relationships within this genus (Gutiérrez-Gutiérrez et al., 2010, 2011b; 2013; Archidona-Yuste et al., 2016a, b; 2019; Cai et al., 2018, 2019; Mobasseri et al., 2019a, b; Naghavi et al., 2022a).

Members of the *X. americanum* group harbour bacterial endosymbionts belonging to 'Candidatus Xiphinematobacter' and 'Candidatus Xiphinematocola pachtaicus' species (Palomares-Rius et al., 2016, 2021; Brown, 2018; Mobasseri et al., 2019a, b). These endosymbionts are vertically transmitted from mother to offspring (Brown, 2018; Palomares-Rius et al., 2016, 2021). The 16S rRNA gene is useful for studying the taxonomy and genetic diversity of bacterial endosymbionts and resolving the nematode-endosymbiont bacteria coevolution (Lazarova et al., 2016a; Mobasseri et al., 2019a, b; Orlando et al., 2016; Palomares-Rius et al., 2016, 2021).

Previous studies have reported the occurrence and geographical distribution of dagger nematodes in Syria and to date a total of six *Xiphinema* species have been described, namely *X. americanum* sensu lato (s.l.) Cobb, 1913, *X. diversicaudatum* (Micoletzky, 1927) Thorne, 1939, *X. elongatum* Schuurmans Stekhoven & Teunissen, 1939, *X. index* Thorne & Allen, 1950, *X. italiae* Meyl, 1953, and *X. pachtaicum* (Tulaganov, 1938) Kirjanova, 1951 (Abdine et al., 2007; Al-Halabi & Al-Assas, 2021; Ali, 2023; Allouf, 2013; Greco et al., 1984, 1992; Kawas & Al-Assas, 2011; Khaleel et al., 2010; Lamberti, 1984; Lamberti et al., 1999a).

A precise and accurate diagnosis of dagger nematode species in Syria is a crucial requisite for the selection of effective control methods. However, updated information on the biological diversity including DNA data, geographical occurrence, and distribution of dagger nematodes in banana (*Musa* sp.) plantations and their associated endosymbiont bacteria is lacking. Thus, the objectives of this work were the following: (1) to characterize and describe *Xiphinema* populations obtained from nematode surveys from two major banana-growing regions of the West Coast of Syria using integrative taxonomy; (2) to update information on the diversity of *Xiphinema* spp. recorded from Syria; (3) to establish

phylogenetic relationships of the identified *Xiphinema* species with available sequenced species; and (4) to characterise the diversity and phylogeny of *Candidatus* Xiphinematobacter associated with populations of the *X. americanum*-group obtained from present survey.

## Material and methods

### Soil sampling and morphological studies

During two consecutive years (2021–2022) on the west coast of Syria, soil samples were collected from the rhizosphere of banana plants (*Musa* sp.) in 95 fields located in two of the main banana-growing regions (Latakia and Tartous). All sampling areas were arbitrarily chosen. Longidorid specimens were extracted from 500 cm<sup>3</sup> soil samples using the modified Cobb washing, sieving and flotation technique (Flegg, 1967). As a result, 18 populations of *Xiphinema* were isolated from soil samples from which six populations were considered for further characterization (Table 1). The other populations showed low density (less than two juveniles were recovered).

After observation under a stereoscope, adult specimens of each morphotypes (or putative species) were hand-picked, and kept in both TAF fixative solution (Triethanolamine) and ethanol 70% (v/v) for morphological and molecular analyses, respectively.

Subsequently, specimens maintained in TAF were processed to glycerol using Seinhorst's method (Seinhorst, 1959) as modified by De Grisse (1969). The light micrographs and measurements of the nematode population, including the main diagnostic key characteristics [i.e., De Man indices (de Man, 1880), Loof-Coomans indices (Loof & Coomans, 1968), and other measurements and morphological features (Coomans et al., 2001; Lamberti et al., 2000, 2004; Loof & Luc, 1990)] were performed using an Olympus BX50 light microscope equipped with an Olympus DP70 digital camera (Olympus BX50, Hamburg, Germany) and Cell software (Olympus Software Imaging for Life Sciences). All measurements were expressed in micrometers (µm). All abbreviations are as defined in Jairajpuri and Ahmad (1992). Etymology used to describe the female genital branches is accordace with Coomans et al. (2001).

### DNA sequencing and molecular methods

Total DNA isolation was performed using a thermodynamic and chemical approach according to Gutiérrez-Gutiérrez et al. (2020). DNA was extracted from a single individual adult specimen. Each individual nematode was placed in a 2 µL drop of sterile water on the flat cap of a PCR tube containing 20 µL of lysis buffer solution compounded by 10 µL ddH<sub>2</sub>O, 6 µL 10×PCR buffer, 2 µL Mg<sup>2+</sup> and 2 µL of proteinase K (20 mg/mL) (Nalgene®). Each specimen was cut into

**Table 1** Five species of *Xiphinema* Cobb, 1913 recovered from the West Coast of Syria, their species names, locality, related plants, sequenced loci and GenBank accession numbers

Species	Sample code	Locality	Host	GenBank accession			
				D2-D3	ITS1	<i>COI</i> mtDNA	16S
<i>Xiphinema dif-fusum</i>	M64	Hraisson, Baniyas, Tartous	banana trees ( <i>Musa</i> sp.)	OR196832, OR196837	OR197584	OR196695	OR196969, OR196971
<i>Xiphinema pachaicum</i>	M54	Siyannu, Jableh, Latakia	banana trees ( <i>Musa</i> sp.)	-	OR197587	OR196696	-
<i>Xiphinema simile</i>	M69	Hraisson, Baniyas, Tartous	banana trees ( <i>Musa</i> sp.)	OR196834	OR264513	-	OR196970
<i>Xiphinema vuittenezi</i>	M78	Hraisson, Baniyas, Tartous	banana trees ( <i>Musa</i> sp.)	OR196836, OR428495	OR197585	-	-
<i>Xiphinema vuittenezi</i>	M79	Hraisson, Baniyas, Tartous	banana trees ( <i>Musa</i> sp.)	OR196835, OR428496	OR197586	OR196697	-
<i>Xiphinema zagrosense</i>	M74	Hraisson, Baniyas, Tartous	banana trees ( <i>Musa</i> sp.)	OR196833	-	-	-

(-) Not obtained

several very small pieces, usually between three and five pieces, with surface-sterilized and pointed pins. Next, tubes were centrifuged at 12,000 rpm for 30 s to 1 min and frozen at  $-75\text{ }^{\circ}\text{C}$  (for 60 min). Samples were mixed for 10 s, centrifuged at 12,000 rpm for 30 s to 1 min, and incubated at  $57\text{ }^{\circ}\text{C}$  (2 h),  $65\text{ }^{\circ}\text{C}$  (2 h) and  $95\text{ }^{\circ}\text{C}$  (15 min). PCR amplification was performed in a final volume of  $25\text{ }\mu\text{L}$  containing:  $1\text{ }\mu\text{L}$  of DNA template,  $12.5\text{ }\mu\text{L}$  NZYTaq  $2\times$  Green Master Mix ( $1.25\text{ mM MgCl}_2$ ,  $200\text{ mM dNTPs}$ ,  $0.2\text{ U}/\mu\text{L}$  DNA Polymerase) (NZYTech, Lisbon, Portugal),  $0.6\text{ }\mu\text{L}$  of each primer ( $10\text{ mM}$ ), and  $10.3\text{ }\mu\text{L}$  of  $\text{ddH}_2\text{O}$ . Each rDNA (D2–D3 of 28S rRNA gene, the internal transcribed spacer 1 (ITS1) region, and 16S rRNA gene) and mtDNA (the partial portion of *COI* gene) fragment was amplified using one or several primer pairs (Table S1). All PCR assays were conducted as described by Gutiérrez-Gutiérrez et al. (2018, 2020). These PCR assays were conducted using DNA positive controls and a negative control containing sterile water. The PCR cycle conditions were followed as described by Gutiérrez-Gutiérrez et al. (2018, 2020) and Palomares-Rius et al. (2016, 2021). For a complete amplification of the 16S rRNA gene from the bacterial endosymbionts, specific PCR cycle conditions were used: initial denaturation at  $95\text{ }^{\circ}\text{C}$  for 3 min; followed by 30 amplification cycles of  $94\text{ }^{\circ}\text{C}$  for 30 s; an annealing temperature of  $50\text{ }^{\circ}\text{C}$  (27F/1492R; 27F/920R; 27F/800R) or  $55\text{ }^{\circ}\text{C}$  (360F/920R; 360F/1492R) for 30 s,  $72\text{ }^{\circ}\text{C}$  for 30–60 s; and final extension of  $72\text{ }^{\circ}\text{C}$  for 10 min. Each PCR product was purified and sequenced by STABVIDA (Caparica, Portugal). Additionally, 360R, 800R, 920R and 1100R primers (Table S1) were used to guarantee a robust and complete sequence. All new sequences of the Syrian populations of dagger nematode species were deposited into the GenBank database under the accession numbers indicated on the Table 1.

### Molecular phylogenetic analyses

The newly obtained rDNA sequences (D2–D3 expansion segments of 28S rRNA gene and partial ITS1) and mtDNA sequences (partial *COI* mtDNA gene) from all known dagger nematode species and complete 16S rRNA from all endosymbiotic bacteria found in this survey (Table 1), together with other available selected sequences from the National Center

for Biotechnology Information (NCBI) were used for phylogenetic analyses. Outgroup taxa for each studied gene was chosen according to previously published data by Archidona-Yuste et al. (2016a, b), Mobasseri et al. (2019a, b) and Palomares-Rius et al. (2016). MAFFT v. 7 (Kato et al., 2019) and ClustalX2 (Larkin et al., 2007) with default parameters used for aligning. After sequence alignment, ambiguous regions were removed with Gblocks v. 0.91b (Castresana, 2000) using less stringent parameters ([www.phylogeny.fr](http://www.phylogeny.fr)). Homogeneities of base frequencies and optional substitution models for 28S rRNA, ITS1, 16S rRNA, and COI mtRNA datasets were tested with Kakusan4 (Tanabe, 2011). Bayesian inference (BI) was performed using the software MrBayes v. 3.2.1 (Ronquist et al., 2012). For BI, the substitution model was selected by the Bayesian information criterion (BIC) and five different models were selected for our study. Convergence of the MCMC chains and burn-in length were assessed and checked in Tracer 1.7.1 (Rambaut et al., 2018). A number of 5,000,000 generations was performed for each BI analysis, sampling every 100th tree and discarding 25% of samples as ‘burn-in’. Finally, the final consensus trees were visualized using FigTree v. 1.4.3 (Rambaut, 2009).

## Results

Morphology and morphometrics of dagger nematode species of the genus *Xiphinema* recovered from the West Coast of Syria

Syrian population of *Xiphinema diffusum* Lamberti & Bleve-Zacheo, 1979 (Fig. 1; Table 2).

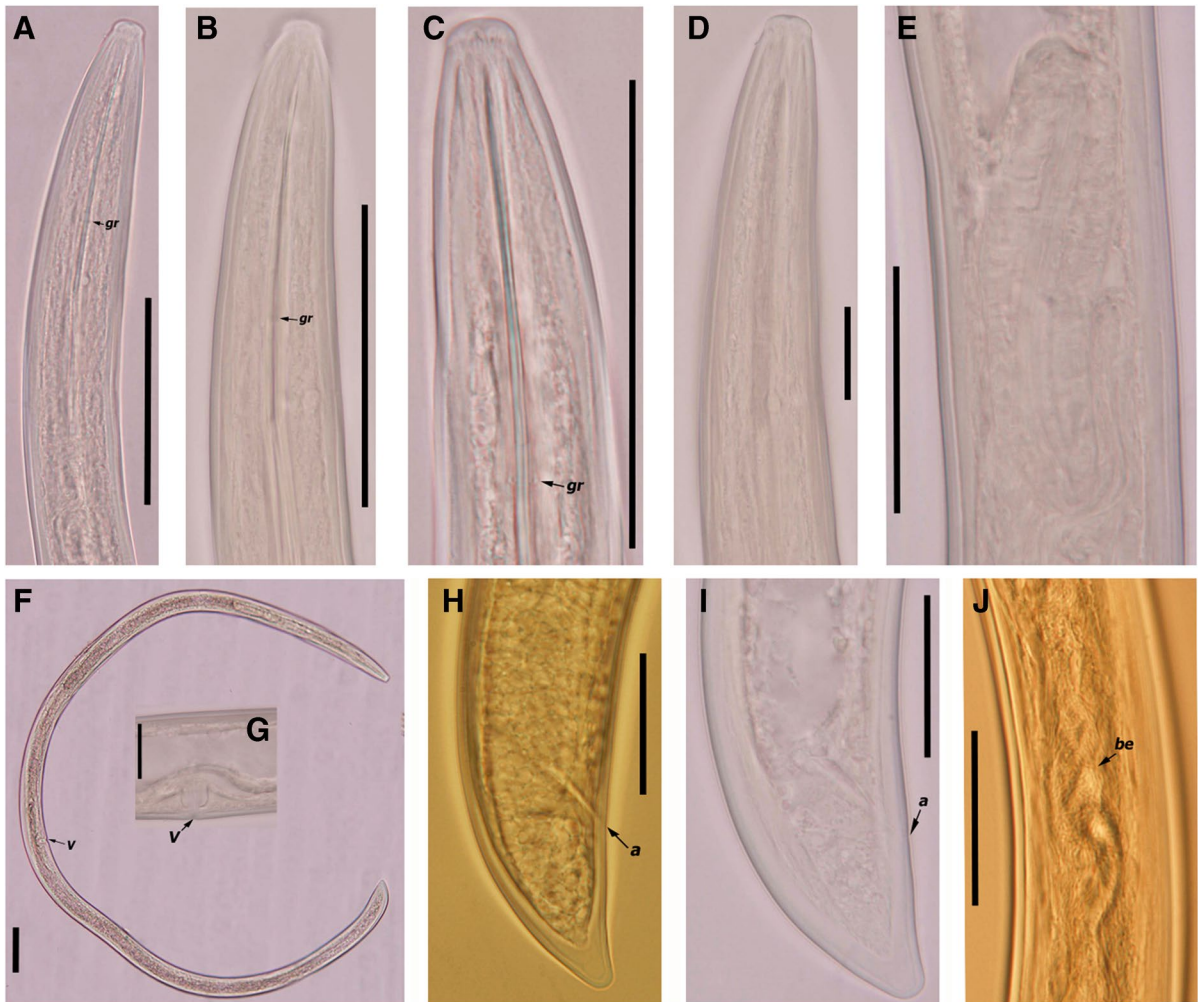
### Distribution

Collected from the rhizosphere of banana (*Musa* sp.) trees at Hraisson, Baniyas district, Tartous, Syria (Table 1).

### Brief description

The Syrian population of this species was characterised by a robust body, forming a close C-to open spiral when killed by heat. Cuticle appearing smooth,  $2.5\text{ (}2.4\text{--}2.6\text{)}\text{ }\mu\text{m}$  thick along body but thicker at the tail tip. Lip region expanded, rounded laterally and





**Fig. 1** Light micrographs of *Xiphinema diffusum* Lambert & Bleve-Zacheo, 1979 females from the rhizosphere of banana (*Musa* sp.) from Hraïsson (Baniyas, Tartous), Syria (A–J). A–B: Female anterior body region; C–D: Lip region; E: Basal bulb; F: Entire female specimen; G: Vulva region; H:

J4 tail region; I: Female tail region; J: Bacterial endosymbionts. Abbreviations: a=anus; be=bacterial endosymbionts; gr=guiding ring; v=vulva. (Scale bars: A–C=75  $\mu$ m; D, H=25  $\mu$ m; E, I=30  $\mu$ m; F=85  $\mu$ m; G=20  $\mu$ m; J=43  $\mu$ m)

slightly flattened frontally, separated from the rest of the body by a shallow constriction. Odontostyle robust 1.7 (1.6–1.8) times longer than the odontophore, the latter with well-developed flanges (Fig. 1). Guiding sheath typical of the genus with the guiding ring at about 75.8 (71.4–79.1)  $\mu$ m distance from anterior end. Basal bulb cylindrical, 4.0 (3.5–4.7) times longer than wide. Glandularium 3.6 (3.4–3.8) times longer than basal bulb width. Cardia with hemispherical shape, 4.3 (3.9–4.5)  $\mu$ m long. Prerectum often indistinct. Rectum clearly visible 27 (24.4–29.1)  $\mu$ m long. Reproductive system didelphic-amphidelphic

with equally developed branches, anterior branch 229 (213.2–246.5)  $\mu$ m long and posterior branch 258 (251.4–267.0)  $\mu$ m long, opposed, ovaries reflexed, and uteri short, without any differentiations. Ovaries showing bacterial endosymbionts (Fig. 1J). Vulva slightly post-equatorial, a transverse slit; vagina occupying two-third of the corresponding body width. Tail short, dorsally convex, slightly concave ventrally with rounded terminus. Males were not found for this species. Only fourth (J4) juvenile stages were found and they were distinguished from other stages according to Robbins et al. (1996) (Table 2). Fourth

**Table 2** Morphometrics of *Xiphinema diffusum* Lamberti & Bleve-Zacheo, 1979, *Xiphinema simile* Lamberti et al., 1983, *X. pachtaicum* (Tulaganov, 1938) Kirjanova, 1951, *X. vuittenezi* Luc et al., 1964, and *X. zagrosense* Ghaemi, Pourjam,Pedram, Robbins, Ye, & Decraemer, 2012 from the rhizosphere of banana (*Musa* sp.) from Latakia and Tartous, Syria. All measurements in  $\mu\text{m}$  and in the format: mean  $\pm$  s.d. (range)\*

Species	<i>X. diffusum</i>		<i>X. simile</i>	<i>X. pachtaicum</i>	<i>X. vuittenezi</i>			<i>X. zagrosense</i>
Character	M64		M69	M54	M79			M74
Character	Females	J4	Females	Females	Females	J4	J3	Female
n	7	2	4	4	4	5	1	1
L	1564.8 $\pm$ 132.3 (1383.5–1702.8)	(1376.0, 1386.3)	1746.6 $\pm$ 43.3 (1703.5–1790.0)	2038.8 $\pm$ 61.7 (1989.7–2108.0)	2626.0 $\pm$ 172.0 (2369.0–2739.0)	1725.0 $\pm$ 112.4 (1836.0–2118.4)	1616.2	4131.6
a	37.1 $\pm$ 3.5 (32.5–40.7)	(33.9, 35.3)	62.6 $\pm$ 1.7 (60.9–64.4)	60.8 $\pm$ 1.0 (59.8–61.8)	45.9 $\pm$ 1.7 (44.1–48.0)	46.4 $\pm$ 1.3 (45.2–48.4)	40.4	59.3
b	6.1 $\pm$ 0.4 (5.6–6.5)	(4.4, 5.4)	6.9 $\pm$ 0.4 (6.5–7.4)	8.2 $\pm$ 0.0 (8.1–8.2)	5.6 $\pm$ 1.1 (4.0–6.5)	4.8 $\pm$ 8.3 (4.4–5.3)	4.9	6.7
c	58.0 $\pm$ 2.0 (56.4–60.3)	(44.4, 45.2)	61.4 $\pm$ 3.4 (57.7–64.4)	74.4 $\pm$ 2.1 (72.3–76.5)	75.8 $\pm$ 7.1 (68.3–82.2)	53.8 $\pm$ 4.9 (49.1–61.4)	38.9	107.4
c'	1.0 $\pm$ 0.0 (0.9–1.0)	(1.2, 1.2)	1.7 $\pm$ 0.0 (1.6–1.7)	1.4 $\pm$ 0.0 (1.4–1.4)	0.9 $\pm$ 0.1 (0.8–0.9)	1.1 $\pm$ 0.1 (1.0–1.2)	1.4	0.8
V (%)	54.3 $\pm$ 0.4 (53.9–54.9)	-	59.9 $\pm$ 0.7 (59.1–60.4)	56.4 $\pm$ 0.4 (56.1–56.9)	50.9 $\pm$ 0.8 (51.1–52.0)	-	-	48.5
G <sub>1</sub> (%)	14.3 $\pm$ 1.8 (12.5–16.1)	-	9.5 $\pm$ 1.1 (8.9–10.8)	9.8 $\pm$ 0.6 (9.3–10.2)	12.6 $\pm$ 0.3 (12.4–12.9)	-	-	11.6
G <sub>2</sub> (%)	16.1 $\pm$ 1.4 (14.8–17.4)	-	8.9 $\pm$ 0.3 (8.7–9.3)	8.5 $\pm$ 0.7 (8.0–9.0)	12.2 $\pm$ 0.2 (12.0–12.3)	-	-	12.2
Odontostyle length	90.9 $\pm$ 0.9 (89.8–92.2)	(74.0, 74.8)	72.6 $\pm$ 1.4 (71.5–74.2)	90.9 $\pm$ 0.4 (90.5–91.3)	138.3 $\pm$ 3.9 (133.0–141.5)	109.0 $\pm$ 3.0 (106.0–113.8)	91.8	155.0
Replacement odontostyle length	-	(85.9, 93.2)	-	-	-	132.7 $\pm$ 3.4 (127.8–135.5)	109.7	-
Odontophore length	52.7 $\pm$ 2.9 (49.6–55.8)	(45.7, 46.5)	40.3 $\pm$ 0.8 (39.4–41.0)	50.1 $\pm$ 0.3 (49.8–50.4)	67.8 $\pm$ 2.2 (65.4–70.5)	62.0 $\pm$ 3.7 (56.0–65.9)	56.9	102.5
Lip region width	12.2 $\pm$ 0.5 (11.5–12.7)	(10.2, 11.2)	9.2 $\pm$ 0.3 (8.9–9.4)	9.2 $\pm$ 0.2 (9.0–9.4)	13.5 $\pm$ 0.6 (12.9–14.2)	11.6 $\pm$ 0.3 (11.2–12.1)	10.5	13.6
Lip region height	4.4 $\pm$ 0.6 (3.7–4.9)	(3.7, 4.4)	3.7 $\pm$ 0.3 (3.3–4.0)	3.6 $\pm$ 0.4 (3.2–3.9)	5.2 $\pm$ 0.5 (4.6–5.5)	3.4 $\pm$ 0.3 (3.2–3.8)	3.0	4.6
Oral aperture-guiding ring	75.0 $\pm$ 3.8 (71.4–79.1)	(60.1, 60.4)	62.7 $\pm$ 0.7 (61.9–63.4)	75.1 $\pm$ 0.8 (74.3–75.9)	126.7 $\pm$ 10.2 (114.9–133.0)	99.9 $\pm$ 3.6 (94.5–103.4)	79.3	157.2
Pharynx length	258.9 $\pm$ 19.3 (225.0–273.6)	(257.1, 313.2)	254.2 $\pm$ 20.4 (230.6–267.4)	251.8 $\pm$ 11.6 (244.3–265.1)	478.0 $\pm$ 77.2 (419.0–591.5)	412.5 $\pm$ 12.5 (399.7–431.0)	332.0	612.9
Pharyngeal basal bulb length	71.6 $\pm$ 3.1 (69.1–75.4)	(64.4, 66.1)	71.8 $\pm$ 2.1 (69.8–74.0)	76.5 $\pm$ 1.3 (75.0–77.3)	98.4 $\pm$ 1.4 (97.4–100.0)	87.0 $\pm$ 8.4 (77.3–99.6)	65.7	169.8
Pharyngeal basal bulb width	18.2 $\pm$ 1.6 (16.0–19.9)	(17.0, 18.6)	11.3 $\pm$ 1.3 (10.0–12.5)	13.2 $\pm$ 0.6 (12.7–13.9)	20.9 $\pm$ 3.7 (17.0–24.3)	19.5 $\pm$ 2.8 (15.6–23.3)	20.1	21.35

**Table 2** (continued)

Species	<i>X. diffusum</i>		<i>X. simile</i>	<i>X. pachtaicum</i>	<i>X. vuittenezi</i>			<i>X. zagrosense</i>
Character	M64		M69	M54	M79			M74
Character	Females	J4	Females	Females	Females	J4	J3	Female
Gladularium length	63.1 ± 2.3 (60.9–65.0)	(50.2, 55.0)	60.3 ± 3.3 (56.5–62.7)	66.8 ± 0.2 (66.6–67.0)	86.0 ± 1.8 (84.0–87.4)	74.6 ± 4.0 (71.6–81.4)	-	148.2
Cardia length	4.3 ± 0.3 (3.9–4.5)	(3.3, 3.7)	3.2 ± 0.4 (2.8–3.6)	4.2 ± 1.1 (3.0–5.0)	6.2 ± 0.5 (5.8–6.5)	4.6 ± 1.3 (3.5–6.0)	-	7.08
Body width at mid-body	42.4 ± 4.7 (37.4–47.9)	(39.0, 40.6)	27.9 ± 0.1 (27.8–28.0)	33.2 ± 0.5 (32.7–33.6)	57.3 ± 5.6 (49–62.1)	42.2 ± 2.2 (39.0–44.6)	39.9	69.7
Body width at anus	27.68 ± 2.1 (24.8–30.2)	(24.6, 25.2)	17.1 ± 0.5 (16.6–17.6)	19.2 ± 0.5 (18.7–19.8)	39.9 ± 4.0 (33.9–42.3)	33.6 ± 1.9 (30.7–36.0)	29.1	48.1
Body width at guiding ring	30.5 ± 2.5 (27.6–33.6)	(26.1, 28.9)	18.7 ± 0.3 (18.4–18.9)	22.9 ± 0.2 (22.6–23.1)	43.3 ± 4.7 (37.2–48.8)	37.3 ± 1.4 (35.6–39.4)	31.5	47.8
Tail length	27.0 ± 2.6 (23.0–29.9)	(30.7, 31.0)	28.5 ± 0.9 (27.8–29.5)	26.7 ± 0.7 (26.2–27.5)	34.9 ± 4.7 (29.0–39.6)	36.6 ± 2.3 (33.7–38.8)	41.6	38.5
Vagina total	21.3 ± 1.5 (20.2–23.9)	-	15.8 ± 0.9 (15.3–16.6)	18.9 ± 0.8 (18.1–19.7)	29.8 ± 1.3 (28.7–31.6)	-	-	44.4
Cuticle wide at mid-body	2.5 ± 0.1 (2.4–2.6)	(1.9, 2.3)	1.4 ± 0.1 (1.3–1.5)	1.7 ± 0.2 (1.5–1.9)	3.3 ± 0.5 (2.6–3.8)	3.0 ± 0.3 (2.5–3.2)	2.1	3.57
Rectum length	25.4 ± 4.0 (19.3–29.1)	(18.0, 18.2)	16.7 ± 1.9 (14.5–18.0)	19.6 ± 1.2 (18.7–21.0)	41.4 ± 1.1 (40.6–42.1)	31.7 ± 1.5 (29.2–32.8)	24.0	49.9
J	9.3 ± 1.1 (7.5–10.3)	(8.2, 10.1)	5.7 ± 0.6 (5.3–6.4)	10.6 ± 1.2 (9.3–11.5)	13.4 ± 1.9 (12.2–16.2)	8.6 ± 0.6 (7.9–9.3)	6.9	13.4
Peg	-	-	-	-	4.8 ± 1.6 (3.0–5.9)	7.7 ± 1.7 (4.9–9.2)	12.2	-

\*Abbreviations are defined in Jairajpuri and Ahmad (1992)

(-) Not obtained

(J4) juvenile stages were similar to adult specimens, except for their smaller size, longer tail, higher index  $c'$ , and absence of sexual characteristics (Fig. 1H).

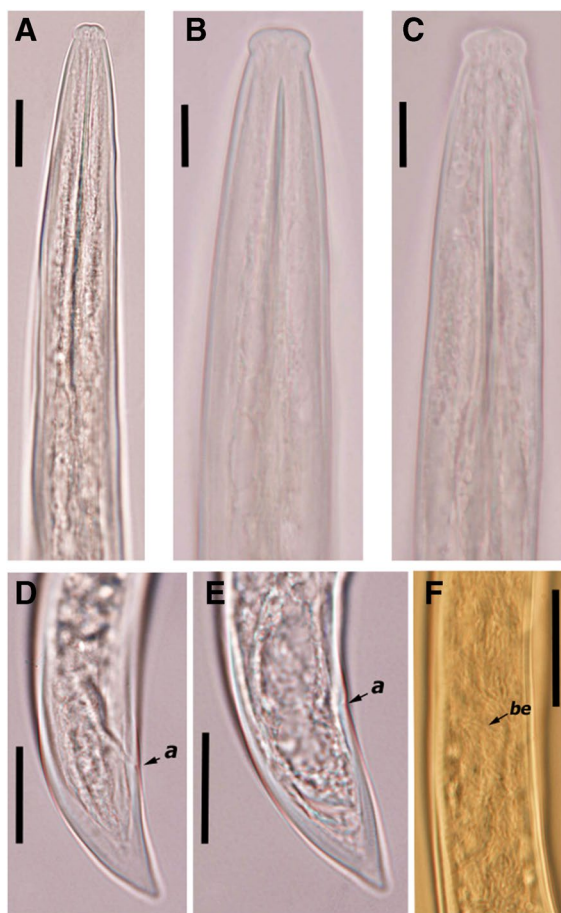
### Remarks

This species was found in a soil sample of banana (*Musa* sp.) trees (sample code: M64) at Hraisson, Baniyas district, Tartous, Syria (Table 1). The population presented low numbers of individuals in soil (20 individuals/500 cm<sup>3</sup> of soil). The morphological and morphometric traits of this population closely agree with those of the type population (Lamberti & Bleve-Zacheo, 1979) and other subsequent records of this species (Chen et al., 2005; Heyns & Coomans, 1994; Lamberti et al., 1991, 2002;

Lazarova et al., 2006; Luc et al., 1998; Shokoohi et al., 2021; Wang et al., 1996), except for minor intraspecific variations in the a and c ratios (e.g. 46–51 µm and 63–84 µm in the type population vs 33–41 µm and 56–60 µm), which may be because of geographical intraspecific variability. Apparently, our population of this species is almost indistinguishable from other species belonging to the *X. brevicolle* species complex (Lazarova et al., 2019), except by minor differences in morphological data, morphometric measures, but conspicuous differences in DNA sequences at level of the nematode and its associated bacterial endosymbionts. This species was originally described infecting *Pelargonium* plants in Réunion Island, Africa (Lamberti & Bleve-Zacheo, 1979) and later was reported from

cultivated and wild ecosystems worldwide (Lamberti et al., 2000, 2002; Chen et al., 2005; Oliveira et al., 2005; Lazarova et al., 2006, 2019; Gutiérrez-Gutiérrez et al., 2016; Shokoohi et al., 2021). To our knowledge, these findings represent the first record for this species associated with banana plants in Syria, extending its geographical distribution in Asia.

The Syrian population of *Xiphinema pachtaicum* (Tulaganov, 1938) Kirjanova, 1951 (Fig. 2; Table 2).



**Fig. 2** Light micrographs of *X. simile* Lamberti et al., 1983 (A–B, D, F) and *X. pachtaicum* (Tulaganov, 1938) Kirjanova, 1951 (C, E) from the rhizosphere of banana (*Musa* sp.) from Hraïsson (Baniyas, Tartous), and Siyannu (Jableh, Latakia), Syria (A–F). A: Female anterior body region; B–C: Lip region; D–E: Female tail region; F: Bacterial endosymbionts. Abbreviations: a=anus; be=bacterial endosymbionts. (Scale bars: A, E=18  $\mu$ m; B–C=9  $\mu$ m; D=17  $\mu$ m; F=28  $\mu$ m)

### Distribution

Collected from the rhizosphere of banana (*Musa* sp.) trees at Siyannu, Jableh district, Latakia, Syria (Table 1).

### Brief description

The Syrian population of this species was characterised by a slender body, forming a close C to coiled spiral, when killed by heat. Cuticle appearing smooth, 1.7 (1.5–1.9)  $\mu$ m thick along body but thicker at tail tip. Lip region expanded and distinctly offset from the rest of the body. Odontostyle long, 1.8 times longer than the odontophore with weak flanges. Guiding sheath typical of the genus with the guiding ring near the base of the odontostyle. Basal bulb cylindrical, 5.8 (5.5–6.0) times longer than wide. Glandularium 5.0 (4.8–5.2) times longer than basal bulb width. Cardia conoid-rounded, 4.2 (3.0–5.0)  $\mu$ m long. Prerectum indistinct. Rectum visible, 19.6 (18.7–21.0)  $\mu$ m long. Reproductive system didelphic-amphidelphic with two short and equally developed genital branches, anterior branch 196.1 (188.6–203.9)  $\mu$ m long and posterior branch 170.6 (162.0–179.7)  $\mu$ m long, ovaries opposed and reflexed, and uteri without any differentiations. Ovaries darkened in fixed specimen, endosymbionts apparently absent under light microscope. Vulva, posterior to mid-body, a transverse slit; vagina occupying two-third of the corresponding body width. Tail conoid with pointed terminus. Males and juveniles were not found for this species.

### Remarks

This species was found in a soil sample of banana (*Musa* sp.) tree (sample code: M54) at Siyannu, Jableh district, Latakia, Syria (Table 1). This population presented low specimens density (14 individuals/500  $\text{cm}^3$  of soil). The morphological traits and morphometric data of females closely agree with those of the described population by Lamberti and Siddiqi (1977) and with other populations already reported (Barsi & Lamberti, 2002; Fadaei et al., 2003; Getaneh et al., 2015; Gutiérrez-Gutiérrez et al., 2011a, b; Kumari et al., 2005; Lamberti & Bleve-Zacheo, 1979; Lamberti et al., 1993; Mobasseri et al., 2019a, b; Vazifeh et al., 2019). Our population of this species is almost indistinguishable from other *X.*



*pachtaicum*-subgroup species (Gutiérrez-Gutiérrez et al., 2012; Archidona-Yuste et al., 2016b), except by some indiscernible morpho-anatomical differences, but notable differences in DNA sequences. Although this species has already been reported from Syria by Lamberti (1984) and Greco et al. (1992), no molecular and morphometric data were formerly provided for those populations. This species is widespread in the countries bordering the Mediterranean Sea, central and Eastern Europe, Africa and Asia (Gutiérrez-Gutiérrez et al., 2016; Lamberti et al., 2000, 2002; Taylor & Brown, 1997). To our knowledge, this is the first record of this species associated with banana plants in Syria. Furthermore, these findings confirm that it is widely distributed in the Middle Eastern.

The Syrian population of *Xiphinema simile* Lamberti et al., 1983 (Fig. 2; Table 2).

#### Distribution

Collected from the rhizosphere of banana (*Musa* sp.) trees at Hraisson, Baniyas district, Tartous, Syria (Table 1).

#### Brief description

The Syrian population of this species was characterised by a slender body, forming a close C to spiral shape when killed by heat. Cuticle smooth under light microscope, 1.4 (1.3–1.5)  $\mu\text{m}$  thick along body but thicker at tail tip. Lip region expanded, flat, rounded in corners, and offset from the rest of the body. Odontostyle 1.8 (1.8–1.9) times longer than the odontophore, the latter with weak flanges. Guiding ring 62.7 (61.9–63.4)  $\mu\text{m}$  from the anterior end. Basal bulb cylindrical, 6.4 (5.6–7.4) times longer than wide. Glandularium 5.4 (5.0–5.7) times longer than basal bulb width. Cardia conoid-rounded shape, 3.2 (2.8–3.6)  $\mu\text{m}$  long. Prerectum indistinct. Rectum 16.7 (14.5–18.0)  $\mu\text{m}$  long. Reproductive system didelphic-amphidelphic with two equally developed branches, anterior branch 165.3 (153.0–188.1)  $\mu\text{m}$  long and posterior branch 154.6 (150.1–160.2)  $\mu\text{m}$  long, opposed and reflexed ovaries with bacterial symbionts, and short uteri without any differentiation, vulva, posterior to mid-body, a transverse slit; vagina occupying 55–59% of the corresponding body diameter. Tail conical, dorsally convex, with finely rounded

terminus. Males and juveniles were not found for this species.

#### Remarks

This species was found in a soil sample of banana (*Musa* sp.) tree (sample code: M69) at Hraisson, Baniyas district, Tartous, Syria (Table 1) in low density (18 individuals/500  $\text{cm}^3$  of soil). The morphological features and morphometric measurements of females closely agree with those of the type population (Lamberti et al., 1983) and with other populations from Europe (Barsi & De Luca, 2008; Barsi & Lamberti, 2002, 2004; Barsi, 1994a; Kumari, 2006; Lamberti et al., 1999b; Lazarova et al., 2008; Lišková, 1995; Lišková & Brown, 1996; Lišková et al., 1993; Peneva & Choleva, 1992; Repasi et al., 2008) and outside Europe (Coomans & Heyns, 1997; Naghavi et al., 2022a). It is morphologically close to other members of *X. simile*-subgroup species (Lazarova et al., 2016a, b), except by some minor morphological and morphometric differences, but remarkable differences in DNA sequences. *Xiphinema simile* is widespread in the European countries in association with agricultural crops, and landscape trees and grasslands (Barsi & De Luca, 2008; Barsi & Lamberti, 2002, 2004; Barsi, 1994a; Kumari, 2006; Lamberti et al., 1999b, 2000; Lazarova et al., 2008; Lišková, 1995; Lišková & Brown, 1996; Lišková et al., 1993; Peneva & Choleva, 1992; Repasi et al., 2008; Taylor & Brown, 1997). Outside Europe, this species has been only reported from Kenya (Coomans & Heyns, 1997) and Iran (Naghavi et al., 2022a). To our knowledge this is the first record of this species infesting soils around banana trees in Syria, extending its geographical distribution in the Middle Eastern.

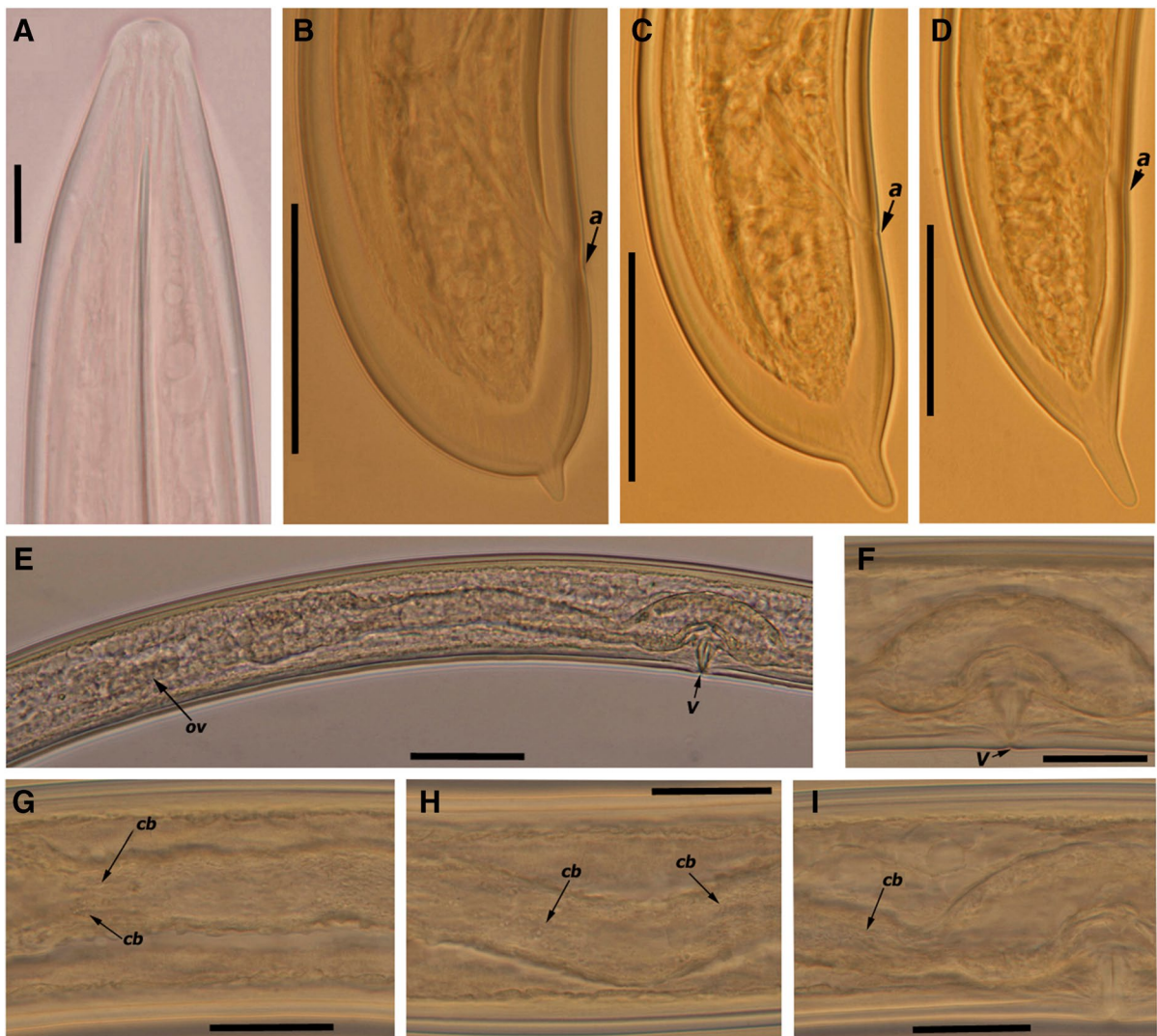
The Syrian populations of *Xiphinema vuittenezi* Luc, Lima, Weischer, Flegg, 1964 (Fig. 3; Table 2).

#### Distribution

It was recovered from two soil samples collected from the rhizosphere of banana (*Musa* sp.) trees at Hraisson, Baniyas district, Tartous, Syria (Table 1).

#### Brief description

The Syrian population of this species was characterised by a cylindrical body, forming a close C, when



**Fig. 3** Light micrographs of *Xiphinema vuittenezi* Luc, Lima, Weischer, Flegg, 1964 females from the rhizosphere of banana (*Musa* sp.) from Hraisson (Baniyas, Tartous), and Siyannu (Jableh, Lattakia), Syria (**A-I**). **A**: Lip region; **B**: Female tail region; **C**: J4 tail; **D**: J3 tail; **E**: Posterior reproductive branch;

**F**: Vulva region; **G-I**: detail of female genital track showing crystalloid bodies. Abbreviations: a=anus; cb=crystal bodies; gr=guiding ring; ov=ovary; v=vulva. (Scale bars: A=13  $\mu$ m; B=41  $\mu$ m; C-D=30  $\mu$ m; E: 58  $\mu$ m; F-I=29  $\mu$ m)

killed by heat. Cuticle smooth under light microscope, 3.3 (2.6–3.8)  $\mu$ m thick along body but thicker at tail tip. Lip region rounded, offset from the rest of the body by depression. Odontostyle robust, two times longer than the odontophore, the later with well-developed flanges. Guiding ring 126.7 (114.9–133.0)  $\mu$ m from the anterior end. Basal bulb cylindrical, 4.8 (4.0–5.9) times longer than wide. Glandularium 4.2 (3.6–4.9) times longer than basal bulb width. Cardia conoid-rounded, 6.2 (5.8–6.5)  $\mu$ m long. Prerectum

579.5 (573.7–585.3)  $\mu$ m long. Rectum as long as the anal body diameter. Reproductive system didelphic-amphidelphic with branches about equally developed without any Z-differentiation but containing crystalloid bodies distributed over the entire length (Fig. 3). Vulva a transverse slit, situated at mid-body; vagina usually occupying half of the corresponding body diameter. Tail short, broadly round, with a peg (Fig. 3). Males were not found for this species. Third (J3) and fourth (J4) juvenile stages were found and

they were similar to adult specimens, except for their smaller size, higher index  $c'$ , and absence of sexual characteristics (Fig. 3). All stages are distinguishable by relative body lengths, functional, and replacement odontostyle (Robbins et al., 1996) (Table 2). J3 characterized by a conical tail with a rounded end subdigitate extension (Fig. 3). J4 characterized by a tail bluntly rounded, slightly dorsally convex-conoid with a terminal peg (Fig. 3).

#### Remarks

This species was found in two soil samples collected from the rhizosphere of banana (*Musa* sp.) trees (sample codes: M78 and M79) at Hraisson, Baniyas district, Tartous, Syria (Table 1). The only one adult specimen that was detected in the sample M78 was checked under light microscope before sequencing it. Then, this population (M78) was only molecularly characterized. The code 79 showed low nematode density (14 individuals/500 cm<sup>3</sup> of soil). The morphological features and morphometric measurements of the fixed females closely agree with those of the type population (Luc et al., 1964), in which their authors did not consider the presence of crystalloids in this species (Coomans et al., 2001). It matches well with other populations from Europe and Middle East (i.e. Mojtahedi et al., 1980; Barsi, 1989, 1994b; Roca et al., 1989, 1991; Coiro et al., 1989, 1992; Barsi & Lamberti, 2000; Kumari et al., 2005; Groza et al., 2013; Gutiérrez-Gutiérrez et al., 2016; Vazifeh et al., 2019; Naghavi et al., 2022b), except for minor differences in the body length and b ratio (e.g. 2800–3400 µm and 6.7–7.0; 3008–4109 µm and 6.0–8.7; 3250–3760 µm and 7.3–7.9 vs 2369–2739 µm, 4.0–6.5) (Kumari et al., 2005; Roca et al., 1989; Vazifeh et al., 2019) which may be because of geographical intraspecific variability. This species is widespread in the European countries, especially Central Europe (Mojtahedi et al., 1980; Lamberti et al., 1983; Barsi, 1989, 1994b; Roca et al., 1989, 1991; Taylor & Brown, 1997; Coiro et al., 1989, 1992; Barsi & Lamberti, 2000; Coomans et al., 2001; Walker, 2004; Kumari et al., 2005; Groza et al., 2013; Vazifeh et al., 2019; Naghavi et al., 2022b). To our knowledge this is the first record of this species associated with banana plants. Furthermore, these findings represent the first detection of this species in Syria.

The Syrian population of *Xiphinema zagrosense* Ghaemi, Pourjam, Pedram, Robbins, Ye & Decraemer, 2012 (Fig. 4; Table 2).

#### Distribution

Collected from the rhizosphere of banana (*Musa* sp.) trees at Hraisson, Baniyas district, Tartous, Syria (Table 1).

#### Brief description

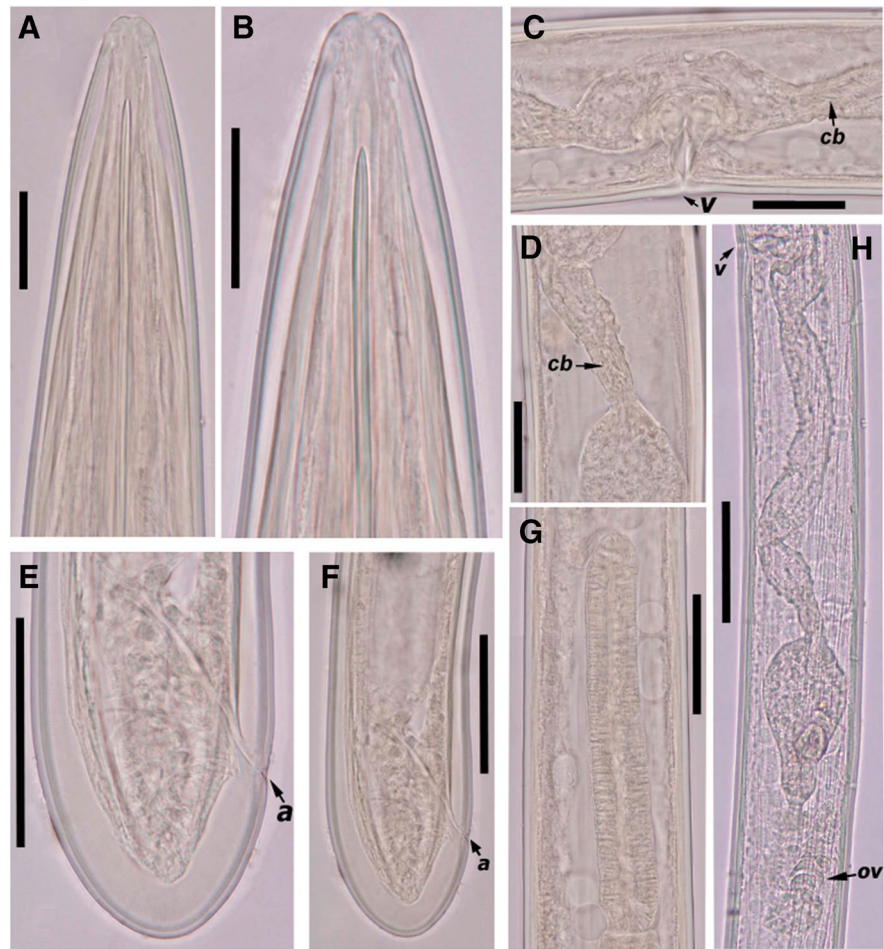
The Syrian population of this species is characterised by a cylindrical body, forming an open C shape when killed by heat. Cuticle smooth under light microscope, 3.57 µm thick at mid-body. Lip region rounded, separate from the rest of the body by a slight depression. Odontostyle robust, 1.5 times longer than the odontophore, the later with well-developed flanges. Guiding ring 157.2 µm from the anterior end. Basal bulb cylindrical, eight times longer than wide. Glandularium seven times longer than basal bulb width. Cardia semi-circular, 7.1 µm long. Prerectum 11 times the anal body diameter and rectum as long as the anal body diameter. Reproductive system didelphic-amphidelphic with branches about equally developed without Z-differentiation, uterus bipartite which is composed of *pars dilatata uteri* and tubular portion with crystalloids (Fig. 4). Vulva a transverse slit, situated at mid-body; vagina occupying more than half of the corresponding body diameter. Tail convex conoid with a broadly rounded terminus (Fig. 4). Male and juveniles were not found for this species.

#### Remarks

This dagger nematode species was found in a soil sample of banana (*Musa* sp.) tree (sample codes: M74) at Hraisson, Baniyas district, Tartous, Syria (Table 1). It showed a low density (2 individuals/500 cm<sup>3</sup> of soil). The morphological and morphometric features of females closely agree with those of the type population (Ghaemi et al., 2012), except for minor differences in the lip region diameter and height (15.0–18.0 µm and 7.0–9.0 µm vs 13.6 µm and 4.6 µm), which should be considered as an intraspecific variability. This species is morphologically close to members of *X. pyrenaicum* complex (Gutiérrez-Gutiérrez et al., 2010; Lamberti et al., 1992; Pedram



**Fig. 4** Light micrographs of *Xiphinema zagrosense* Ghaemi, Pourjam, Pedram, Robbins, Ye & Decraemer, 2012 female from the rhizosphere of banana (*Musa* sp.) from Hraisson (Baniyas, Tartous), Syria (A–H). **A–B**: Lip regions; **C**: Vulva region; **D**: detail of female genital track showing crystalloid bodies; **E–F**: Female tail region; **G**: Detail of basal bulb; **H**: posterior uterine branch. Abbreviations: a = anus; cb = crystalloid bodies; ov = ovary; v = vulva. (Scale bars: A–B = 22  $\mu$ m; C–D = 35  $\mu$ m; E–F: 48  $\mu$ m; G = 42  $\mu$ m; H: 70  $\mu$ m)



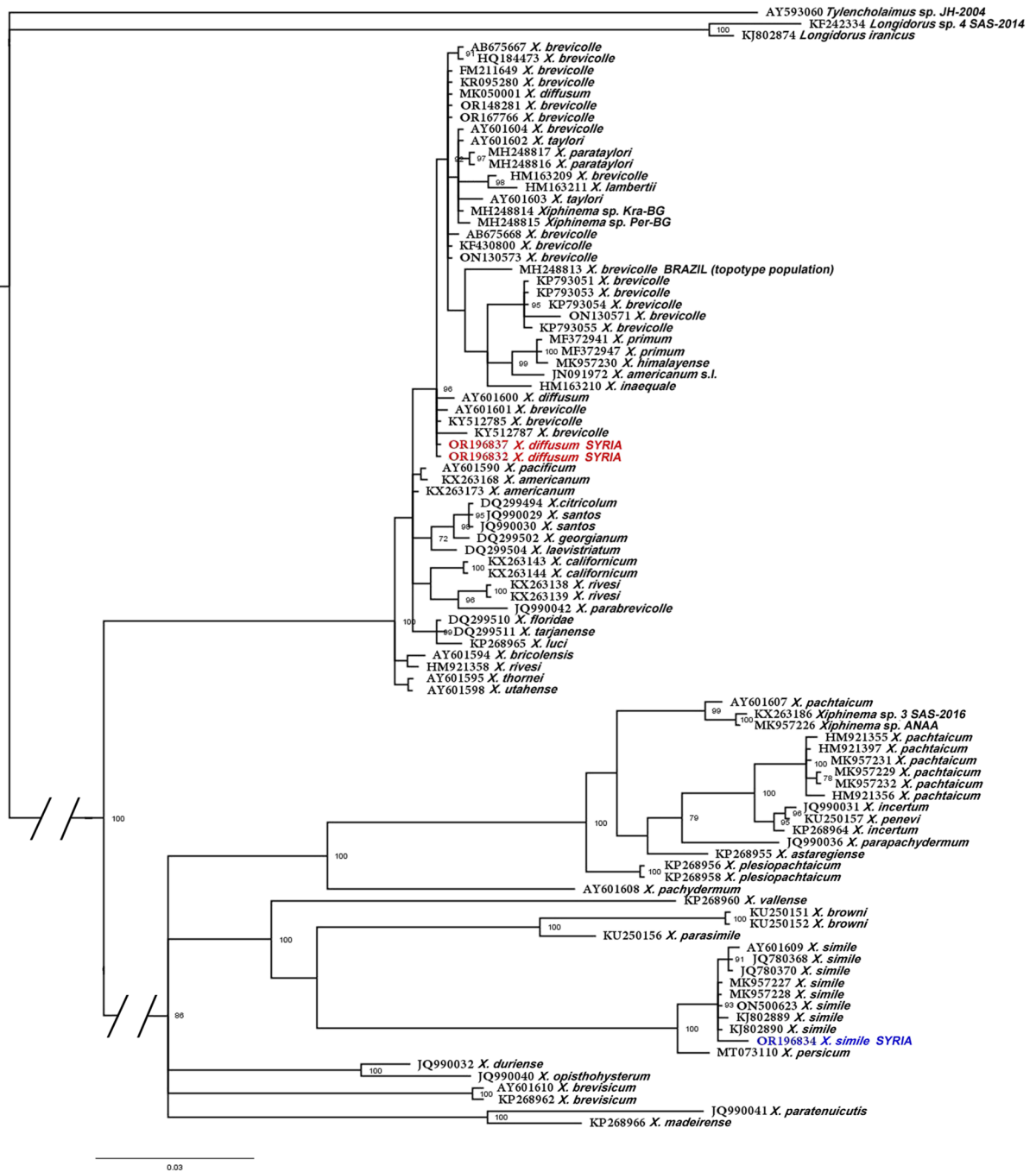
et al., 2009, 2012), except by some indiscernible morpho-anatomical differences, but notable differences in DNA sequences. This species was described in association with grasses in natural environments from Iran (Ghaemi et al., 2012). To our knowledge, this is the first record of this species outside its type locality, extending its distribution in the world, and first report of its association with banana plants.

#### Sequence analysis and phylogeny of 28S rRNA gene

##### *Xiphinema americanum*-group spp.

The two 28S sequences of the Syrian isolate of *X. diffusum* (OR196832, OR196837) obtained showed high homology (99–100%) with *X. brevicolle* complex, such as *X. diffusum* (e.g., AY601600, MK050001, and MK050002) and *X. brevicolle* Lordello & Da Costa 1961 (e.g., KY512785–KY512787 and AY601601),

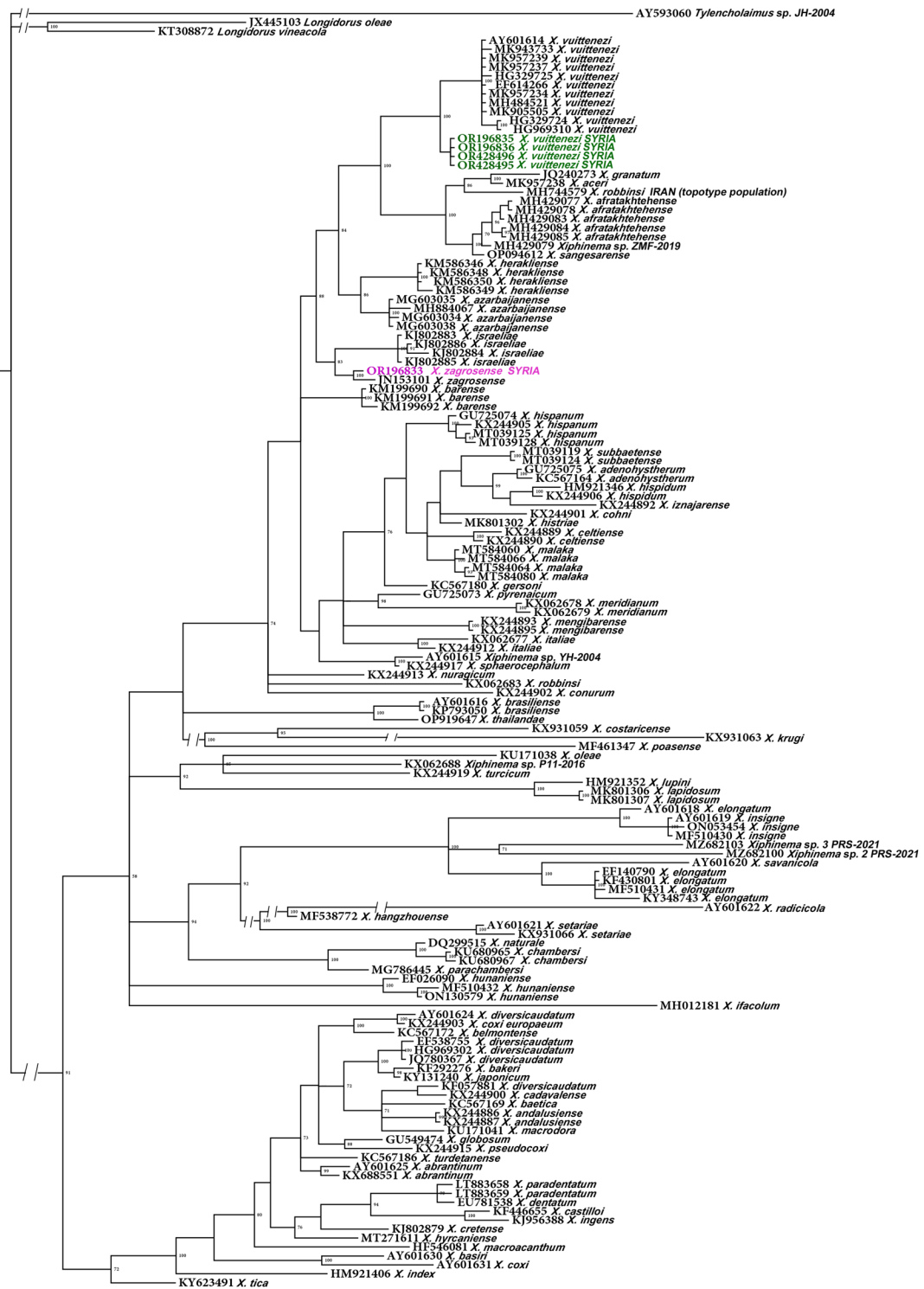
but presented less than 98% homology with the topotype population of *X. brevicolle* (MH248813). The 28S sequence of *X. simile* (OR196834) showed a high homology (99–100%) with sequences of the same species, namely *X. simile* (AY601609, JQ780368–JQ780370, KJ802889–KJ802890, ON500623, MK957227–MK957228). For these species, the respective Bayesian phylogenetic tree (Fig. 5) showed that *X. diffusum* and *X. brevicolle* were grouped together within the well-supported clade of these same species and clearly separated from the topotype population of *X. brevicolle* (MH248813). These results could be due to a possible misidentification of the species in GenBank. Although the Syrian isolate of *X. simile* was phylogenetically closest to European and Asian populations of the same species (e.g. AY601609, JQ780368–JQ780370, KJ802889–KJ802890), the



**Fig. 5** Phylogenetic relationships of *Xiphinema diffusum* Lamberti & Blevé-Zacheo, 1979 and *X. simile* Lamberti et al., 1983. Bayesian 50% majority rule consensus trees was inferred from 96 sequences of D2-D3 expansion segments (713 bp) of

28S rRNA sequences aligned under the SYM+G model. Posterior probabilities more than 70% are given for appropriate clades. Newly obtained sequences in this study are coloured in red and navy blue. Scale bar = expected changes per site





◀**Fig. 6** Phylogenetic relationships of *Xiphinema vuittenezi* Luc et al., 1964, and *X. zagrosense* Ghaemi, Pourjam, Pedram, Robbins, Ye, & Decraemer, 2012. Bayesian 50% majority rule consensus trees was inferred for 143 sequences of D2-D3 expansion segments (673 bp) of 28S rRNA sequences aligned under the GTR + G model. Posterior probabilities more than 70% are given for appropriate clades. Newly obtained sequences in this study are coloured in green and pink. Scale bar = expected changes per site

length of all these sequences were different, yielding intraspecies cladogenesis and varied branch lengths inside this species clade.

#### *Xiphinema non americanum*-group spp.

The 28S sequences from Syrian populations of *X. vuittenezi* (OR196835–OR196836, OR428495–OR428496) matched closely (more than 99% of similarity) to an Iran population of the same species (MK905505), varying in 4–13 nucleotides and 0–5 indels. Our sequences matched also with other world isolates with 98–99% similarity (e.g. HG329724–HG329724, HG969310, AY601614, MK943733, MK957234, EF614266, MK957237, MK957239). Little intra-specific variation between the 28S sequences from the two Syrian populations of *X. vuittenezi* from Hraïsson (M78 and M79, banana) was recorded (0–2 nucleotides and 0–1 indel) (Table 1). The 28S sequence of *X. zagrosense* (OR196833) showed high homology (99–100%) with *X. zagrosense* (JN153101, Iran population) with low sequence variations (only 4 nucleotides with no indels). The Bayesian phylogenetic tree of *X. vuittenezi* and *X. zagrosense* is presented in Fig. 6. The Syrian isolates of *X. vuittenezi* were closest to isolates of the same species from different world populations but not within the same clade (Fig. 6), mostly due to the intraspecific variations of the 28S sequences from isolates that distinguished Hungarian, Iranian, Romanian, Czech and Russian populations from the Syrian, yielding intraspecies cladogenesis with two subclades inside this species clade. In relation to *X. zagrosense*, the Iranian (JN153101) and Syrian (OR196833) populations clustered in a well-supported sub-clade.

#### Sequence analysis and phylogeny of ITS rRNA

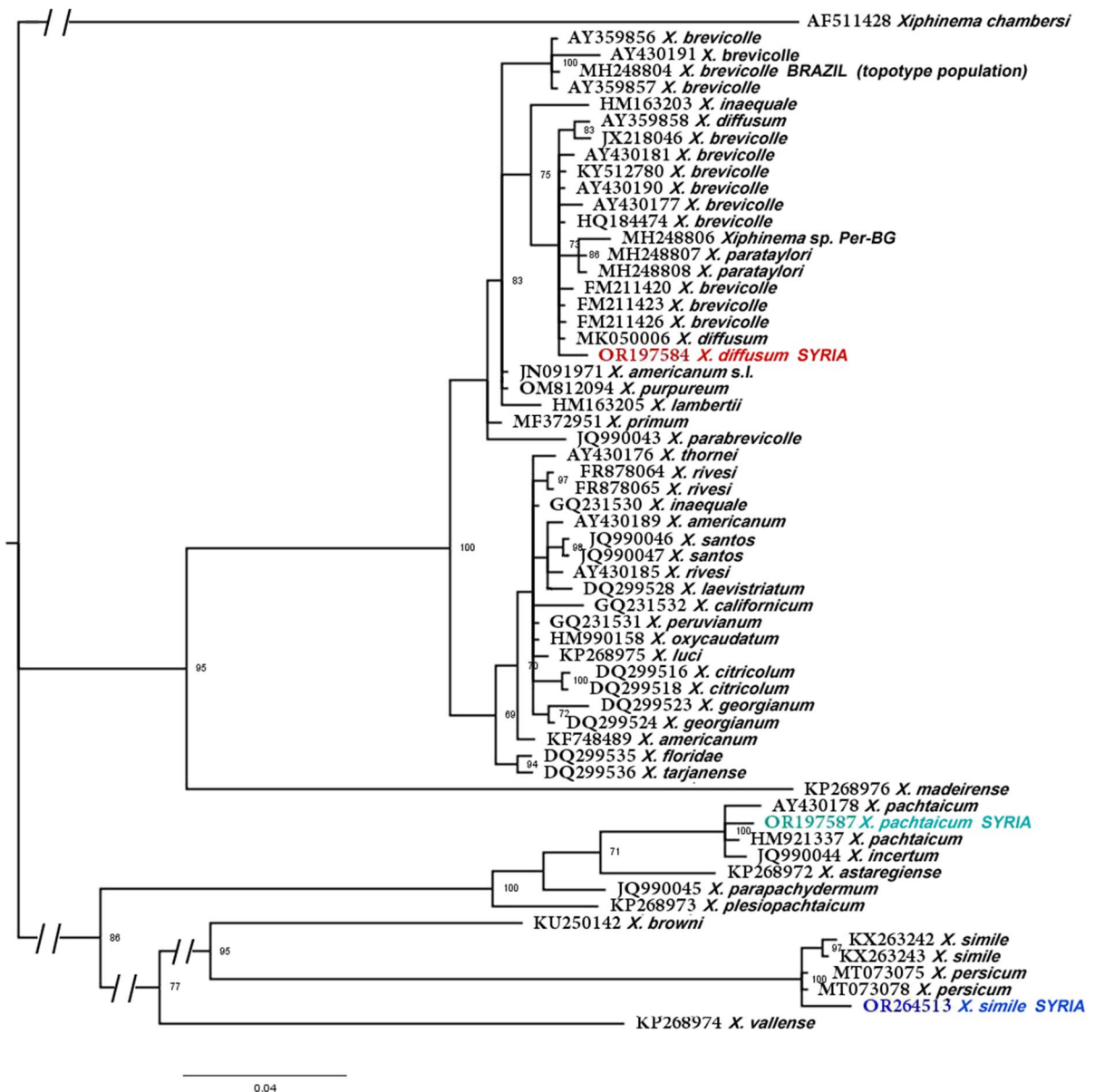
##### *Xiphinema americanum*-group spp.

Concerning the ITS region, the Syrian population of *X. diffusum* (OR197584) presented 95–96% sequence

similarity with other *X. brevicolle* complex sequences, such as *X. diffusum* (e.g., AY359858, MK050006) and *X. brevicolle* (e.g., FM211423, FM211420, FM211426, HQ184474, KY512780), with a considerable intra-species variability recording 21–48 nucleotide differences and 8–13 indels. For *X. pachtaicum*, the Syrian ITS sequence (OR197587) showed more than 99% match with other sequences from the same species (e.g. AY430178, KU250149), presenting little sequence polymorphisms (0–5 nucleotides and 0–3 indels). The ITS sequence of *X. simile* (OR264513) showed 95% sequence similarity with the Spanish *X. simile* isolates (KX263242–KX263243), followed by Iranian isolates of *X. persicum* Jahanshahi Afshar et al. (2021) (94% of similarity) (MT073075, MT073077–MT073078). Our ITS sequences of *X. simile* showed an intraspecific variability with 30–29 nucleotides and 10–11 indels. As for their phylogenetic inference (Fig. 7), the Syrian populations of *X. diffusum* (OR197584) were closely related with several isolates of the *X. brevicolle* complex from different countries and clearly separated from the topotype population of *X. brevicolle* (MH248804). All ITS sequences of *X. diffusum* clustered together within the same clade; however, Korean and Syrian isolates (e.i. OR197584, MK050006) were separated from the South African isolate (AY359858). This could be due to *X. diffusum* has variation among some isolates for this marker. The ITS sequences of *X. pachtaicum* and *X. incertum* Lamberti et al., 1983 were clustered in the same clade, mostly because the sequences were shorter and poor quality in the database. The ITS sequences of *X. simile* and *X. persicum* were also grouped in the same clade, probably due to the high intraspecific variation among some populations.

##### *Xiphinema non americanum*-group spp.

The two ITS sequences from Syrian populations of *X. vuittenezi* (OR197585–OR197586), that shared in-between 99% similarity, showed 89–91% sequence similarity with several isolates of *X. vuittenezi* (e.g. HG329722–HG329723, HG969308–HG969308; MK909917; AJ437028) and 89% similarity with *X. iranicum* Pedram et al., 2009 (EU477386); presenting an intraspecific variation of 3–46 nucleotide mismatches and 0–15 indels. The corresponding Bayesian phylogenetic tree is represented in Fig. 8. The Syrian ITS sequences of *X. vuittenezi* clustered

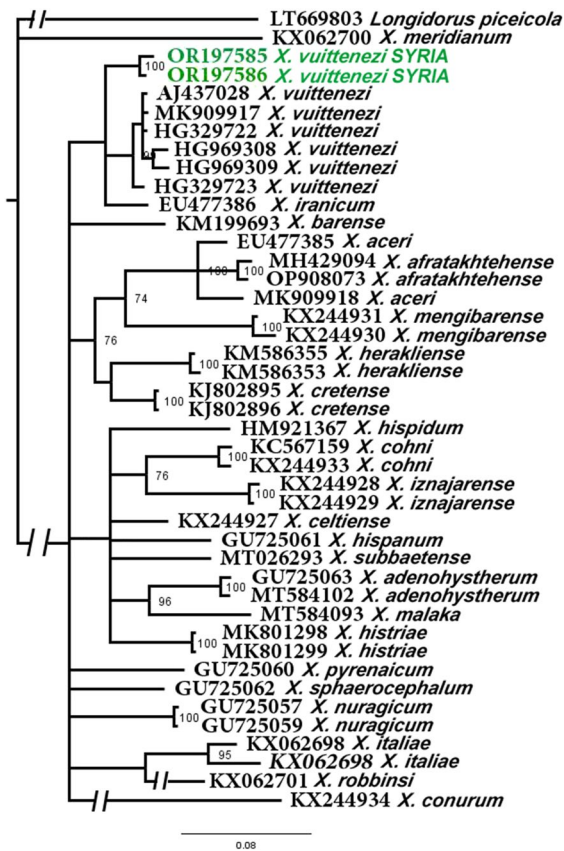


**Fig. 7** Phylogenetic relationships of *Xiphinema diffusum* Lambert & Blevé-Zacheo, 1979, *X. simile* Lambert et al., 1983, and *X. pachtaicum* (Tulaganov, 1938) Kirjanova, 1951. Bayesian 50% majority rule consensus trees was inferred from 61 sequences of ITS1 rRNA (381 bp) aligned under the K80+G

model. Posterior probabilities more than 70% are given for appropriate clades. Newly obtained sequences in this study are coloured in red, navy blue, and sky blue. Scale bar=expected changes per site

together in a well-supported subclade within the clade of *X. vuittenezi* (e.i. OR197585– OR197585, AY359858, HG969308– HG969309, MK909917, HG329722–HG329723, AJ437028) and *X. iranicum*

(EU477386), probably due to *X. vuittenezi* shows a high intraspecific variation for this marker as well as the shorter and poor quality in some sequences deposited in the database.



**Fig. 8** Phylogenetic relationships of *Xiphinema vuittenezi* Luc et al., 1964. Bayesian 50% majority rule consensus trees was inferred from 61 sequences of ITS1 rRNA (260 bp) aligned under the K80+G model. Posterior probabilities more than 70% are given for appropriate clades. Newly obtained sequences in this study are coloured in green. Scale bar = expected changes per site

## Sequence analysis and phylogeny of COI mtDNA

### *Xiphinema americanum*-group spp.

The Syrian COI sequences of *X. diffusum* (OR196695) showed a sequence similarity of 97–100% to sequences from the *X. brevicolle* complex, such as *X. diffusum* (e.g., AM086698–AM086701) and *X. brevicolle* (e.g., ON107524, ON107526–ON107529), with intraspecific variation of 1–9 nucleotides. For *X. pachtaicum*, our COI sequence (OR196696) showed high homology (98–100% of similarity) with other sequences of this species (e.g. KX263112–KX263113, HM921378), with 0–8 nucleotides mismatches. Regarding the phylogenetic tree

(Fig. 9), the Syrian COI sequences of *X. diffusum* and *X. brevicolle* grouped together in the well-supported clade and clearly separated from the topotype population of *X. brevicolle* (AM086707, MH248818). This could be due to a plausible misidentification of these species for some sequences available in GenBank. Moreover, all COI sequences of *X. pachtaicum* also clustered in a well-supported sub-clade, however, the length of some sequences was different, yielding different branch lengths inside this species clade.

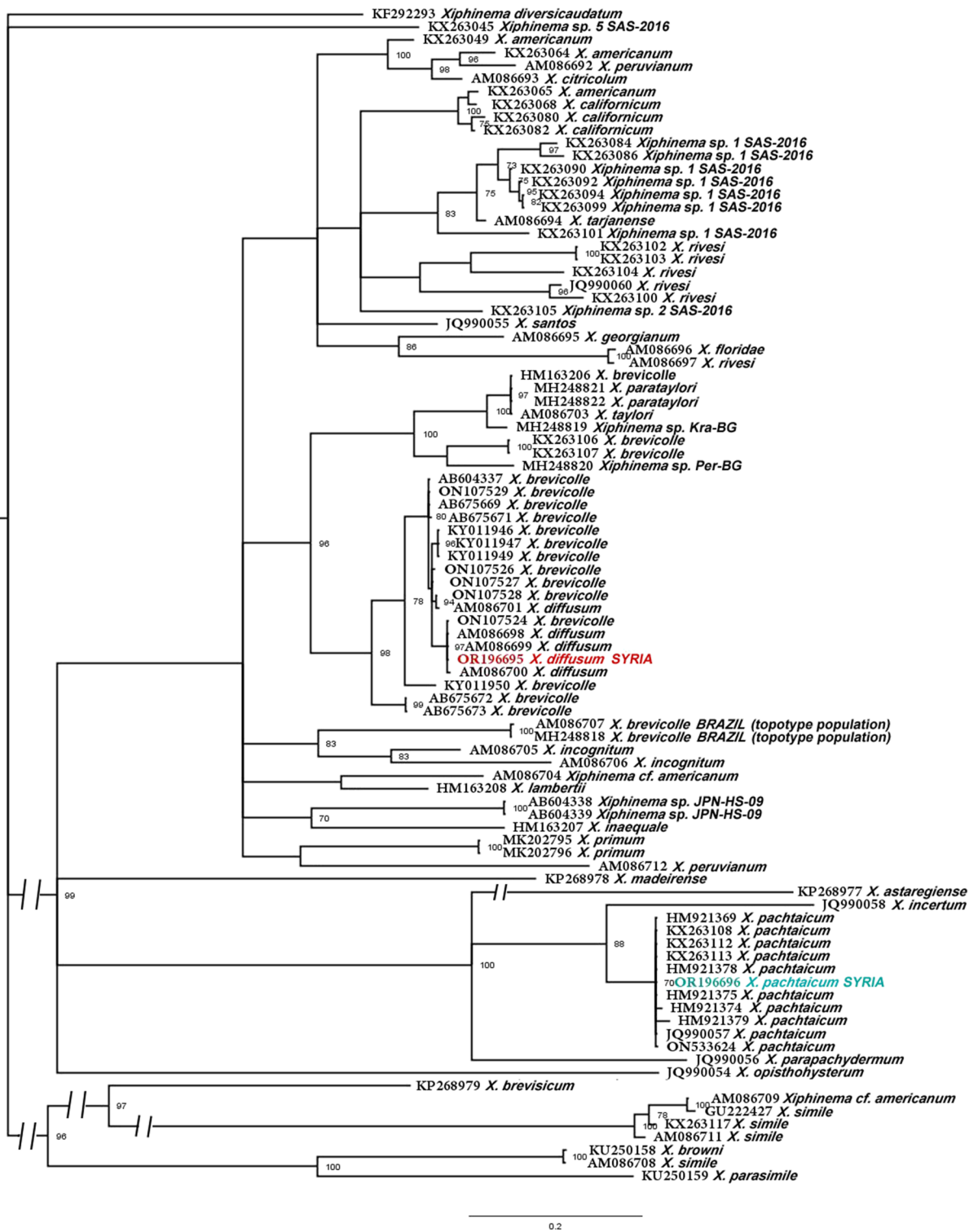
### *Xiphinema non americanum*-group spp.

The COI sequence from Syrian population of *X. vuittenezi* (OR196697) showed 83% similarity to the Russian isolate of this species (OQ699231) and less than 79% similarity with other *Xiphinema* species. Regarding the phylogenetic inference (Fig. 10) showed that our *X. vuittenezi* COI sequence was clustered, with good support, in-between *X. afratakhtehense* (MH429098) and the cluster of the Russian and Czech isolates of *X. vuittenezi* (OQ699231 and EF614265). This could be due to a poor quality of these sequences and overlapping peaks, yielding intraspecific cladogenesis.

## Phylogenetic analysis of the bacterial endosymbionts 'Candidatus Xiphinematobacter' and correlation with host phylogeny

The complete 16S rRNA gene of the bacterial endosymbionts 'Candidatus Xiphinematobacter' were successfully amplified from *X. diffusum* (OR196699, OR196971) and *X. simile* (OR196970), with an approximate size of 1400 bp. Both sequences from *X. diffusum* were 100% identical and matched closely (99–100% identity) with several sequences of Chinese, Brazilian, and Australian Xiphinematobacter species reported from *X. diffusum* populations (KJ614450–KJ614453). A sequence of South African population of Xiphinematobacter from *X. brevicolle* complex (AF217462) also grouped in this cluster. When compared with Xiphinematobacter species detected in topotype population of *X. brevicolle* (KJ614447), the latter sequence had only 96% identity. The other endosymbiont from *X. simile* (OR196970) matched closely (99–100% identity) with two sequences of a Greek population of this same species (KT735097–KT735098) from *X.*







◀**Fig. 9** Phylogenetic relationships of *Xiphinema diffusum* Lamberti & Bleve-Zacheo, 1979 and *X. simile* Lamberti et al., 1983 and *X. pachtaicum* (Tulaganov, 1938) Kirjanova, 1951. Bayesian 50% majority rule consensus trees was inferred from 91 sequences of *COI* mtDNA (341 bp) aligned under the HKY85+G model. Posterior probabilities more than 70% are given for appropriate clades. Newly obtained sequences in this study are coloured in red and sky blue. Scale bar=expected changes per site

*simile*. Figure 11 presents the BI tree (50% majority rule consensus tree) of 70 sequences of 16S rRNA for ‘*Ca. Xiphinematobacter*’ and three outgroup species [Uncultured *Eubacterium* spp. WCHD3-88 (AF050561), *Spartobacteria bacterium* (AB245341) and *Terrimicrobium sacchariphilum* (GU129926)]. The phylogenetic analysis within the genus ‘*Candidatus Xiphinematobacter*’ differentiated 18 well-supported clades corresponding to the 18 species denoted as species A through species R (Fig. 11). In exception of ‘*Candidatus Xiphinematobacter*’ sp. A, which was isolated from two *X. americanum* s.s., *X. pachtaicum*, and *X. simile* from Europe (KT735098, KJ614457, KJ614458) and Asia (MT568602, OR196970, KX263187), and ‘*Candidatus Xiphinematobacter*’ sp. R, which was isolated from *X. americanum* s. str., *X. americanum* s. s., *X. rivesi* Dalmaso, 1969, *X. peruvianum* Lamberti & Bleve-Zacheo, 1979, *X. georgianum* Lamberti & Bleve-Zacheo, 1979, the other ‘*Candidatus Xiphinematobacter*’ species were all isolated from one or two host nematode species. ‘*Candidatus Xiphinematobacter*’ sp. I included two sequences of one population of *X. diffusum* from Syria, which grouped in the well-supported clade with other populations from Asia, Australia, Africa, and South America, and one population of *X. brevicolle* complex from South Africa, with high clade support (0.95 BPP), clearly separated of the sequence of ‘*Candidatus Xiphinematobacter*’ sp. G of the toptype population of *X. brevicolle*. ‘*Candidatus Xiphinematobacter*’ from *X. simile* from Syria clustered in the sub-clade of ‘*Candidatus Xiphinematobacter*’ sp. A, jointly with other sequences of the bacterium from populations of *X. simile* from other origins.

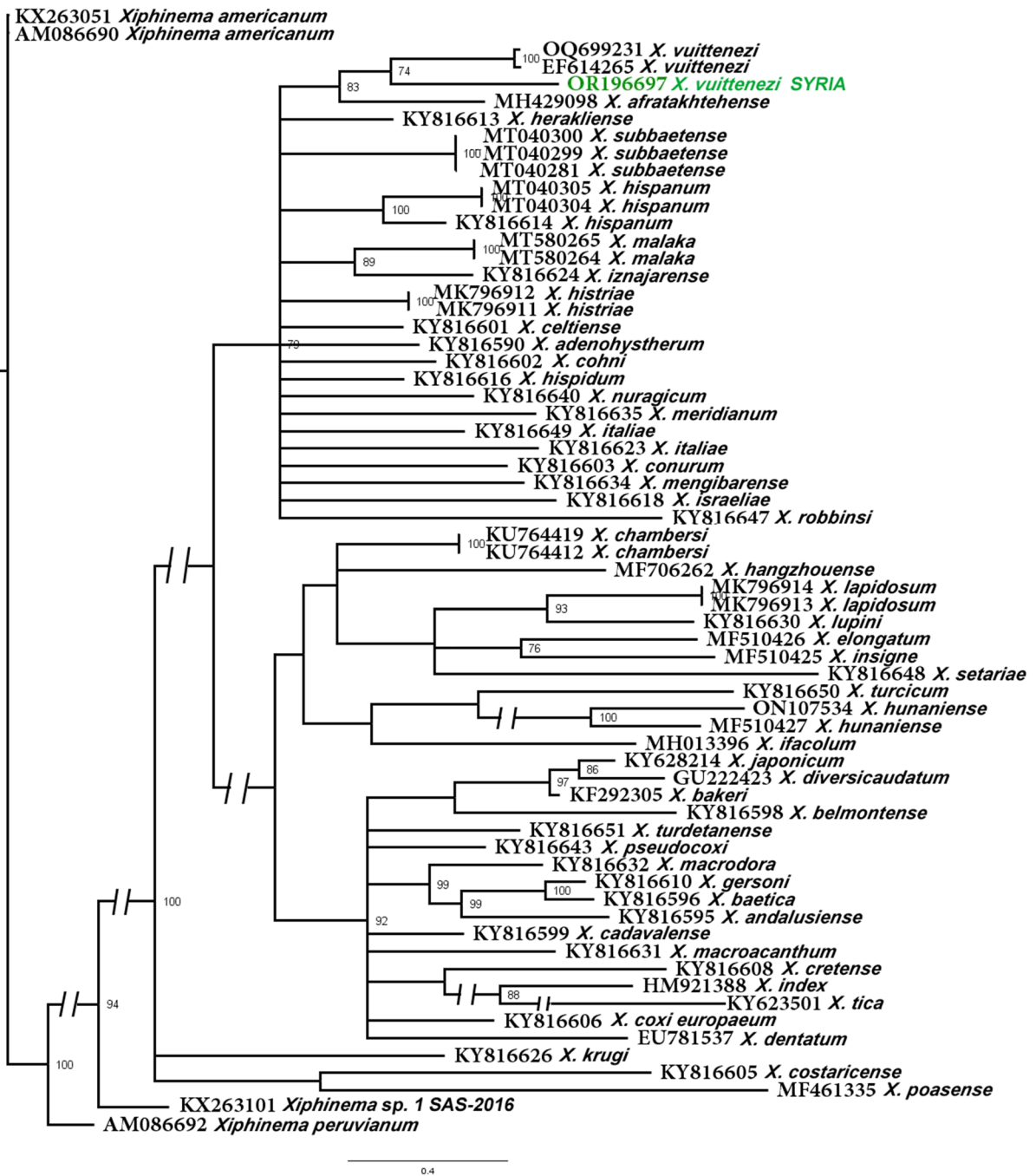
## Discussion

In this study, six *Xiphinema* populations were recovered and identified from Syria belonging to

five species, namely *X. diffusum*, *X. pachtaicum*, *X. simile*, *X. vuittenezi* and *X. zagrosense* by integrating morphological and molecular data. Using an integrative approach to identify species in this specious genus has already well documented (Gutiérrez-Gutiérrez et al., 2012; Ghaemi et al., 2012; Archidona-Yuste et al., 2016b, 2020a; Lazarova et al., 2019; Mobasserri et al., 2019a, b; Vazifeh et al., 2019; Naghavi et al., 2022a; Gu et al., 2022). The endosymbiont bacterias were also sequenced for two *X. americanum*-group species, *X. diffusum* and *X. simile*. Four species including *X. diffusum*, *X. simile*, *X. vuittenezi*, and *X. zagrosense* are new records from Syria, increasing the geographical distribution points of these species.

In accordance with other taxonomic studies (Lazarova et al., 2008, 2016b; Gutiérrez-Gutiérrez et al., 2011b; 2013; Archidona-Yuste et al., 2016a, b; 2020a, b; Mobasserri et al., 2019a, b; Vazifeh et al., 2019; Naghavi et al., 2022a), our results showed that the D2–D3 of the 28S rRNA and the *COI* mtDNA regions were the most conclusive molecular markers for species-level identification within genus *Xiphinema* in exception of some species within the subgroup *X. brevicolle*. Our study corroborates other studies (Lazarova et al., 2016a; Mobasserri et al., 2019a, b; Palomares-Rius et al., 2016) emphasizing that 16S rRNA gene is a useful molecular marker for discerning among *Candidatus Xiphinematobacter* species and so, as a result of their closely related *Xiphinema* hosts. In our phylogenetic, representative sequences for some species occupied different positions. An accurate way to resolve this problem is to sequence toptype specimens. Currently, most populations of *X. brevicolle* have identified only based on molecular data without morphological and morphometric analysis, occupying distant placements from the sequences of the toptype population of the species, and possibly indicating misidentification. Furthermore, recently Jahanshahi Afshar (2019) sequenced the D2–D3 fragments of 28S rRNA gene of the toptype population of *X. robbinsi* Pedram, Niknam & Decraemer, 2008 revealing a mistake identification of a Tunisian population.

Nowadays, exploring the molecular evolution and phylogenetic relationships of ‘*Ca. Xiphinematobacter*’ species using the 16S rRNA gene is at its peak (Brown, 2018; Lazarova et al., 2016a, b; Mobasserri et al., 2019a, b; Palomares-Rius et al., 2016, 2021).



**Fig. 10** Phylogenetic relationships of *Xiphinema vuittenezi* Luc et al., 1964. Bayesian 50% majority rule consensus trees was inferred from 65 sequences of *COI* mtDNA (335 bp) sequences aligned under the GTR+G+I model. Posterior

probabilities more than 70% are given for appropriate clades. Newly obtained sequences in this study are coloured in green. Scale bar = expected changes per site

Still, there is knowledge gap on the nematode-endosymbiont bacteria co-evolution in the *X. americanum* group. Our results agree with other authors (Mobasser et al., 2019a, b; Palomares-Rius et al., 2016, 2021) that proposed a plausible host-endosymbiont co-speciation and suggest an adaptative role during the process of natural selection in the host *Xiphinema* species.

In conclusion, our work revealed a high biodiversity of the dagger nematode species in banana gardens of Syria. The recovered species could be regarded potential threats and monitoring of their population could prevent their outbreak.

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## Declarations

**Research involving human participants and/or animals** No specific permits were required for the described fieldwork studies. Permission for sampling the banana fields was granted by the landowner. However, the sites are not protected in any way.

**Informed consent** All the authors certify that this work carried out in this research followed the principles of ethical and professional conduct have been followed. The funding source had no role the design of this study and not had any role during its execution, data collection, analyses, interpretation of the data, decision to publish, or preparation of the manuscript.

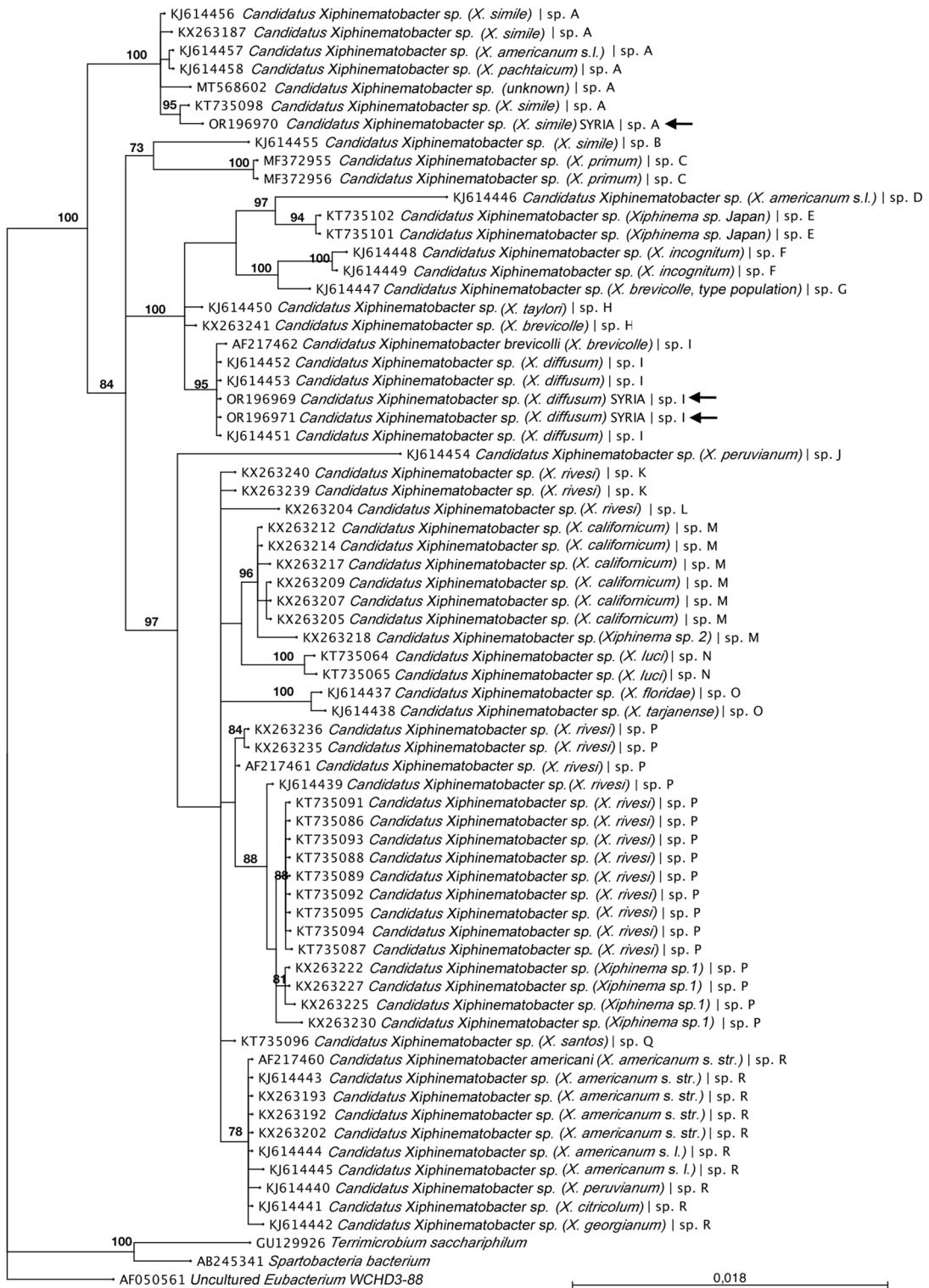
**Conflict of interest** All authors declare no conflict of interest.

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◀**Fig. 11** Phylogenetic relationships of the endosymbiont bacteria, isolated from *Xiphinema diffusum* Lamberti & Bleve-Zacheo, 1979 and *X. simile* Lamberti et al., 1983 within 'Candidatus Xiphinematobacter'. Bayesian 50% majority rule consensus tree was inferred from 16S rRNA sequence alignment under the K80+G model. Posterior probabilities more than 70% are given for appropriate clades. Newly obtained sequences in this study are targeted with an arrow. Scale bar = expected changes per site

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