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A *Trichodorus* (Triplonchida: Trichodoridae) Nematode from Thrips (Thysanoptera: Panchaetothripinae)

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Abstract: A thrips insect *Caliothrips* sp. (Thysanoptera: Panchaetothripinae) from persimmon fruit (Ebenaceae: *Diospyros* sp.) from an unknown origin, possibly Asia, was intercepted in a passenger bag in November 2012 at the Peace Arch Border Crossing from Canada to Blaine, WA, by a USDA-APHIS-PPQ port inspector. Nematodes were attached to the abdomen of the female insect and sent to us in saline. Seven nematodes (five females, two males) were measured and these and others were processed for permanent slides. An adult female and a female juvenile were prepared for PCR. Morphologically these nematodes belonged to the *Trichodorus sparsus* group, and the 28S rDNA D2-D3 sequence showed greatest similarity to *Trichodorus paragiennensis* (94%) and *T. giennensis* (93%), with greatest morphological similarity to the latter species. Among other morphological differences, the innermost uterus width is wider than in related species. *Trichodorus* spp. are normally found in soil, so this is the first population seen in the atypical habitat of an insect. Morphological and molecular characteristics of *Trichodorus* sp. are presented, but a putative new species name is not currently advisable because of relatively poor condition of specimens. Ecological associations are also discussed.

Key words: ecology, large subunit ribosomal DNA, stubby root nematode, systematics, taxonomy, virus vector.

A thrips insect (*Caliothrips* sp., Thysanoptera: Panchaetothripinae) from persimmon fruit (Ebenaceae: *Diospyros* sp.) was intercepted in a passenger bag in November 2012 at the Peace Arch Border Crossing from Surrey, British Columbia, Canada, to Blaine, Washington, by an APHIS-PPQ port inspector. The fruit was from an unknown origin, possibly Asia. Ten nematodes of only one type were attached by their head region, apparently phoretically, to the abdomen of the female insect (Fig. 1). They were carefully removed and sent to us in saline.

Up to this time, the only naturally occurring nematode associate of thrips insects (Thysanoptera: *Aptinothrips, Franklinella, Megaluriothrips, Taeniothrips*) were five species from the tylenchid genus *Thripinema* Siddiqi, 1986 (Hexatylina: Allantonematidae) (Siddiqi, 2000). *Thripinema* does not kill but sterilizes arboreal female thrips and reduces their life span (Murali, 2013). *Thripinema fuscum* Tipping & Nguyen parasitizes tobacco thrips and reduces insect feeding, which in turn reduces tomato spotted wilt virus transmission (Sims et al., 2009).

We were surprised to identify all nematodes from these thrips as a species of *Trichodorus* Cobb, 1913 (Dorylaimida: Trichodoridae), a plant parasitic nematode with a loose cuticular sheath. This genus is known commonly as the stubby root nematode that is typically found in soil. A few species vector tobraviruses to plants (Brown et al., 1989). Morphological and molecular features demonstrated to us that this insect associated nematode was a putative new species, partially described in this article without a name until better quality specimens become available.

Materials and Methods

The best-preserved nematodes from saline were imaged (five females, two males) at 40 to 60× on an Olympus BX51 microscope with DP71 camera (Olympus America, Inc., Center Valley, PA) equipped with polarization optics. Measurements in micrometers were taken with an ocular micrometer on a Zeiss Ultraphot II compound microscope with Nomarski optics before formalin fixation, and images were also measured with the calibrated measuring tool in the imaging program CellSens ver 1.6 (Olympus America). Six measured specimens and three specimens that were not imaged were processed for permanent slides according to the formalin-glycerine method (Golden, 1990). Measurements in micrometers and morphometrics were calculated on an Excel spreadsheet. Nematodes were morphologically identified with current literature (Decraemer et al., 1993; Decraemer and Baujard, 1998; Decraemer and Marais, 2000; Decraemer et al., 2013).

DNA analysis: An imaged female and a juvenile specimen were mechanically disrupted in 20 µl of extraction buffer (Thomas et al., 1997) then stored in PCR tubes at –80°C until needed. Extracts were prepared from thawed pools by incubating the tubes at 60°C for 60 min, followed by 95°C for 15 min to deactivate proteinase K. Two microliters of the extract was used for each 25-µl PCR reaction. The ribosomal LSU D3 expansion segment was amplified with primers D2A 5'-ACAAGTACCGT GAGGGAAAGTTG-3'and D3B 5'TCGGAAGGAACCAG CTACTA-3' (Nunn, 1996) using a previously published amplification procedure (Ye et al., 2007). PCR products were visualized with UV illumination after ethidium bromide staining. DNA was excised from the gels and purified with the QIAquick Gel Extraction Kit (Qiagen, Valencia, CA). Clean PCR products were directly sequenced by a local vendor (Genewiz, Inc.,

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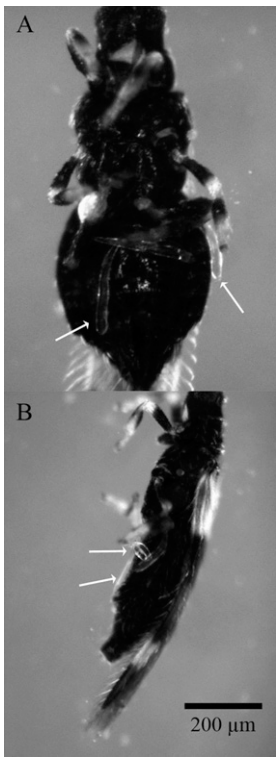

FIG. 1. A. Face view. B. Side view. Thrips (*Caliothrips* sp.) with nematodes (arrows) were intercepted by USDA-APHIS inspector William Carlson, from the Blaine, WA, port in November 2012.

Germantown, MD, and South Plainfield, NJ). Sequence was determined on both strands using internal D2A and D3B primers. It was submitted to GenBank with the accession number KM212949.

Phylogenetic analysis: DNA sequences were analyzed using BLASTN of nematode sequences contained in the EBI-EMBL parasite sequence database (http://www.ebi.ac.uk/blast2/parasites.html). Nematode sequences with highest e-values and morphologically similar nematode species that had GenBank sequences were subjected to ClustalW (Thompson et al., 1994) analysis with default parameters and a neighbor joining (NJ) distance tree, maximum parsimony (MP) tree, and a distance matrix was constructed with the PAUP* (Sinauer Associates, Sunderland, MA) plugin and ModelTest ver. 3.7 (Posada and Crandall, 1998) within Geneious ver 5.5.6 (Biomatters, Auckland, New Zealand). GenBank sequences were aligned with those determined in this study, including: *T. cedarus* ZJ8HM106502 (797 bp; Li, X, 2010, Institute of Biotechnology, Zhejiang University, Zhejiang, China), *T. giennensis* JQ716452 (753 bp; Decraemer et al., 2013), *T. iliplaensis* I37JQ716462 (787 bp; Decraemer et al., 2013), *T. paragiennensis* JQ716461 (807 bp; Decraemer et al., 2013), *T. sparsus* XT19JN123423 (786 bp; Kumari and Subbotin, 2012), and outgroup *T. viruliferus* XT21JN123426 (780 bp; Kumari and Subbotin, 2012). Sequences for somewhat morphologically similar taxa *T. iuventus* Decraemer and Marais, 2000 and *T. aequalis* Allen, 1957 were not available.

SYSTEMATICS

Trichodorus sp.
(Figs. 1–6, Table 1)

Description

Female (n = 5): Measurements are listed in Table 1.

Body cylindrical, ventrally curved, with prominent sheath, tapering increasingly from midbody to head. Tail terminus gently tapering, bluntly rounded with slight cuticular thickening at terminus with subterminal anus. Tubular stoma, expanded at base, with sclerotized rods; guide ring about 15% of the ventrally curved onchiostyle length from anterior. Onchium and onchiophore equal in length. Onchiostyle 33% of pharynx length. Two ventromedian cervical papillae at base and center levels of onchiostyle. Secretory-excretory pore (S-Epore) midway between nerve ring and pharyngeal-intestinal junction, 109 µm behind anterior end in one specimen. Basal pharyngeal bulb glands slightly overlap intestine ventrally. Vagina barrel to pear-shaped but with innermost diameter the widest. Vaginal length about 25% of body width. Vaginal sclerotized pieces in lateral view roughly triangular, small (2.3-µm length), closely apposed at one

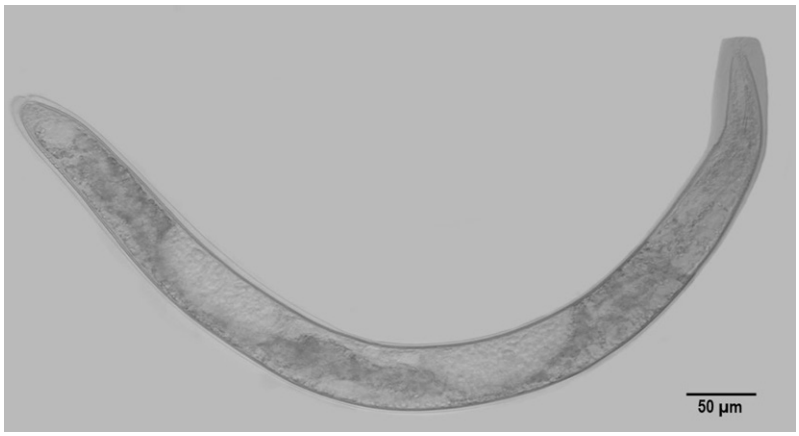

FIG. 2. *Trichodorus* sp. Female body stitched from 60× polarized images.

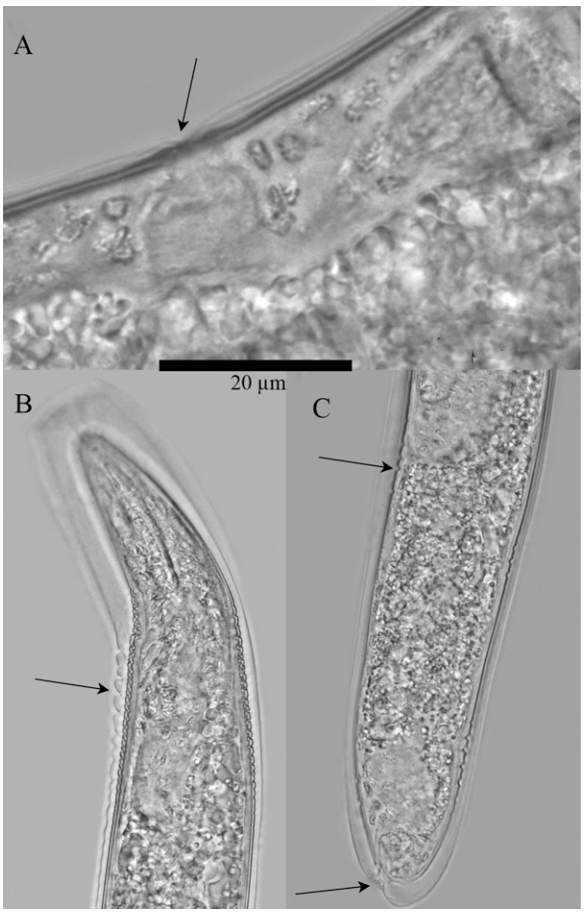

FIG. 3. *Trichodorus* sp. Female A. Vulva (arrow), barrel-shaped vagina, anterior uterus. B. Head, excretory pore (arrow), 110 µm from head. C. Tail and posterior ovary, arrows at anus, ovary tip. Scale bar applies to A to C.

vertex to each other, obliquely adjacent to external vulval cuticle, oblique to vaginal walls. Reproductive system paired, symmetrical, outstretched, 35% of body length, with crescent-shaped ovaries in lateral view. Spermatheca oval between bellows-shaped oviduct and uterus, containing oval sperm throughout. Cuticular pores near vulva not clearly observed, but one possible posterior advulvar pore within the cuticle noted slightly more than one body width from vulva. Vulval anal distance (VAD) = 274 ± 50 (204 to 331) µm, VAD/t = 43.5 ± 17.3 (23.1 to 63.7) µm.

Male (n = 2): Measurements are listed in Table 1.

Body cylindrical, ventrally curved, strongly to loosely J-shaped, with prominent sheath. Tail terminus gently tapering, flat at tip. Outer labial papillae interrupt otherwise rounded lip region. Tubular stoma, expanded at base, with sclerotized rods; guide ring about 15% onchiostyle length from anterior. Two ventromedian cervical papillae anterior to excretory pore, at level of base and midpoint of onchiostyle; S-E pore positioned at level of anterior pharyngeal bulb. Onchiostyle 43% of pharynx length. Reproductive system with a single outstretched testis reaching well anterior to midbody. Large sperm with sausage-shaped nuclei (6.7 × 2.8 µm) in distal testis. Three precloacal tail supplements nearly equidistant

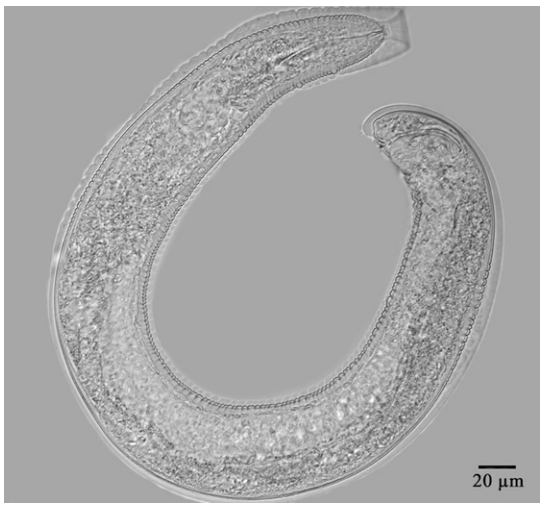

FIG. 4. *Trichodorus* sp. Male body, stitched from 60× polarized images.

when tail outstretched, with distance between supplement 2 and 3 (43 µm ± 1.6) slightly greater than 1 and 2 (37 ± 1.5 µm) and the cloaca and supplement 1 (27 ± 2.6). Distinctly ensheathed spicule suspensor muscles forming capsule around proximal end of paired spicules. Discrete, although not offset, wide anterior manubrium, about one-sixth the length of the spicule. Spicules moderately curved with median notch at midpoint of nonstriated shaft. Keel-like gubernaculum about half spicule length, distal to capsule.

Diagnostic key coding with letter for feature and number for dominant character state (Decraemer and Baujard, 1998) for females is A1, B2, C1, D1, H3, N2, K3, L1, M1, N1, O1, P2. For males, codes are A1, B2, C1, D0, E2, F3, G0, H3, I2, J5, K3, L4, M1, N1, P2.

Locality and host: Original locality unknown, possibly China, primary host *Caliothrips* sp. (Moritz et al., 2004), secondary host *Diospyros* sp.

Specimen designation and deposition: United States Department of Agriculture Nematode Collection: one female USDANC#G21497; one female, USDANC#G21498; one male USDANC#G21499 (tail lost in processing); two females, two males, two juveniles USDANC#G21500. Image vouchers for all specimens measured in saline are available. All formalin fixed specimens in glycerin are of poor quality.

Differential diagnosis: Morphology (Figs. 1–6) and morphometrics (Table 1) demonstrate that this species fits within the *Trichodorus sparsus* morphospecies group (Table 1, Fig. 7). A distinctive combination of features of *Trichodorus* sp. include wide barrel-shaped vaginal walls, triangular sclerotized pieces near the vulval lips (Figs. 4,6A), two cervical papillae at the level of the onchiostyle (Figs. 4,5A), nearly equidistant spacing of male tail supplements and discrete, wide manubrium and median notch of spicules (Figs. 5B,6B).

Trichodorus sp. had a relatively longer spicule manubrium relative to spicule length than in *T. cedarus*

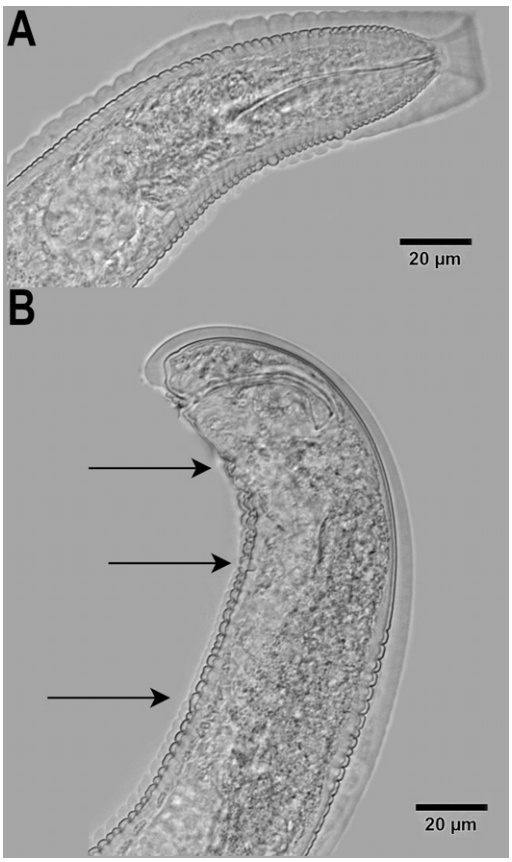

Fig. 5. *Trichodorus* sp. Male A. Head with stylet, pharynx, two cervical papillae. B. Spicule, anterior supplements (arrows).

Yokoo, 1964 and *T. iliplaensis* Decraemer et al., 2013. The male spicules were longer (48 ± 3 vs. 39 ± 2 µm) than in *T. paragiennennensis* Decraemer et al., 2013. The female stylet was shorter (43.8 ± 1.7 vs. 52.5 ± 3 µm), 'a' ratio shorter in both sexes (12.1 to 15.7 vs. 17.5 to 27.5 F; 11.9 to 16.2 vs. 17 to 31 M) and upper range of body length (720 vs. 1176 µm F; 646 vs. 1004 µm M) than in *T. giennensis* Decraemer et al., 1993. The upper range of body length was somewhat smaller in *Trichodorus* sp. than in *T. paragiennennensis* (720 vs. 956 µm F; 646 vs. 813 µm M). Although the qualitative morphology of spicules and vulva are most similar to *T. giennensis*, the vaginal walls are more expanded in *Trichodorus* sp. population (Figs. 3,6) than in both species.

The S-E pore is normally just below two (in *T. giennensis*) or three (in *T. paragiennennensis*) cervical papillae in related nematodes, but two cervical papillae were positioned more anteriorly at the levels of basal and middle onchiostyle (Figs. 4,5A). This was similar to the position of two of the three papillae present in *T. viruliferus* (Hooper, 1963).

Molecular alignment and phylogeny: The 28S rDNA alignment of *Trichodorus* sp. sequence KM212949 with one of the two closest sequences in GenBank (Table 2) showed a 94% Blast similarity to *Trichodorus paragiennennensis* from Spain, but a 92.5% similarity within the ClustalW alignment distance matrix of Table 2. *T. giennensis* had a slightly greater 93% similarity in the Clustal alignment. *T. paragiennennensis* had 97% similarity to *T. giennensis*, and 96% to *T. iliplaensis* Decraemer et al., 2013 (Decraemer et al., 2013), so this thrips population sequence is clearly distinct from that species group (Table 2).

On the 810 character Clustal alignment, Geneious ran the ModelTest program where settings corresponded to the GTR+G model, with distribution of rates at variable sites = gamma (continuous) with shape parameter (alpha) = 0.3439. Besides the NJ distance tree (Fig. 7) created to assist with visualizing sequence difference between species, a MP tree (not shown) of the Clustal alignment had 89 parsimony informative characters, and *T. cedarus* and *T. sparsus* formed a clade. In both NJ and MP trees *Trichodorus* sp. was basal to *T. giennensis, T. paragiennennensis,* and *T. iliplaensis*, the three of which formed a clade with 100% bootstrap support. *T. cedarus* was basal to this clade.

Discussion

This report of unusual *Trichodorus* specimens from a thrips insect contains information that should allow the future identification of another conspecific population based on molecular sequence of 28S rDNA. The

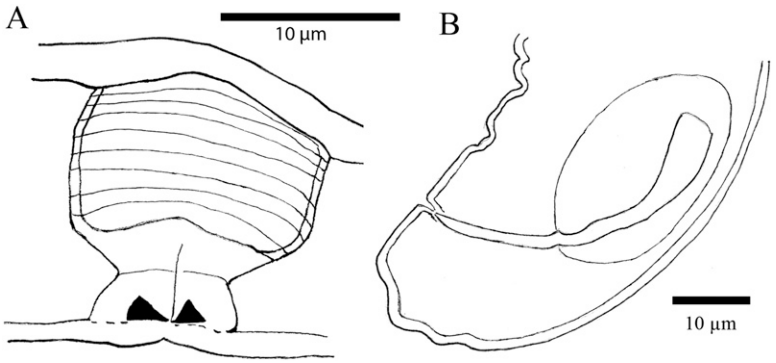

Fig. 6. A. Female vaginal region with closely aligned, triangular sclerotized pieces near vulva and barrel-shaped vaginal walls. B. Male tail with spicule shaft notched at midpoint, proximally surrounded by muscular capsule.

TABLE 1. Morphometrics of female and male *Trichodorus* sp. and morphologically similar *T. giennensis* and *T. paragiennensis*.

Character	Female *Trichodorus* sp.	Male *Trichodorus* sp.	Female *T. giennensis*	Male *T. giennensis*	Female *T. paragiennensis*	Male *T. paragiennensis*
n	5	2	57 (5 pops.)	66 (5 pops.)	10	10
Body L µm	630 ± 54 (588-720)	620 ± 37 (594-646)	700-1176	550-1004	790 ± 95 (627-956)	735 ± 39.4 (688-813)
Body W µm	49 ± 3 (46-52)	45 ± 7 (40-50)	28−49	29-46		
Stylet µm	43.8 ± 1.7 (42-45)	55 ± 1 (54-56)	48-62	45-60	49.4 ± 2.5 (45-52)	49.6 ± 2.9 (44-54)
Pharynx L µm	136 ± 20 (117-164)	127 ± 0 (127-128)	119-194	112-222	152.9 ± 11.7 (141-174)	153.2 ± 18.9 (130-190)
Lip-vulva µm	371 ± 23 (348-404)					
Tail L µm	9.0 ± 2.7 (5.0-11.6)	13.5 ± 0.7 (13-14)				12.3 ± 0.7 (11-14)
'a'	12.8 ± 1.6 (12.1-15.7)	14.0 ± 3.02 (11.9-16.2)	17.5-27.5	17-31	24.9 ± 4.0 (19.6-29.8)	24.7 ± 2.1 (21.2-30.4)
'b'	4.7 ± 0.3 (4.4-5.0)	4.9 ± 0.3 (4.7-5.1)	4-8	4-7.5	5.2 ± 0.9 (4.2-6.7)	4.8 ± 0.6 (3.6-5.9)
V/spicule µm	59 ± 5 (56-64)	48 ± 3 (46-50)	49-62	40-50	55.7 ± 1.2 (53.8-57.1)	39.3 ± 2.1 (34.5-41.5)

distinct spicule and vaginal shapes were very similar to *T. giennensis*, a species with 93% similar DNA sequence to this thrips population. Although the partial list of possible morphological measurements for *Trichodorus* given in this study are accurate for the best specimens among poorly preserved material, it is possible that morphometrics will differ in some significant fashion when better-preserved specimens become available. The poor condition of specimens may account for difficulty in detecting lateral advulvar pores in these specimens, although these pores were rare in *T. paragiennensis* (Decraemer et al., 2013). Therefore it is not prudent now to provide a name for what is clearly a unique species of *Trichodorus*.

The distance tree (Fig. 7) is sparsely populated with only species that are morphologically similar, but not necessarily phylogenetically close to the unique *Trichodorus* species described in this work. Simple pairwise similarity for two taxa in isolation will have a different value than the support value for the same taxon pair in a tree clade. The difference depends on the composition of other taxa and the different nature of possible alignment methods. For instance, the relatively high support of 97% for pairwise similarity of *T. giennensis* and *T. paragiennensis* (Table 2) changed when compared in an alignment of multiple taxa for a tree. Clade support is only 91% for *T. giennensis* and *T. paragiennensis* in a Clustal alignment tree (Fig. 7) and is lowered to 86% with a MUSCLE (Edgar, 2004) alignment-based tree (not shown). The lowest support node in the Clustal-based tree of 59% (Fig. 7) would change to 78% with a MUSCLE alignment, but a more internal

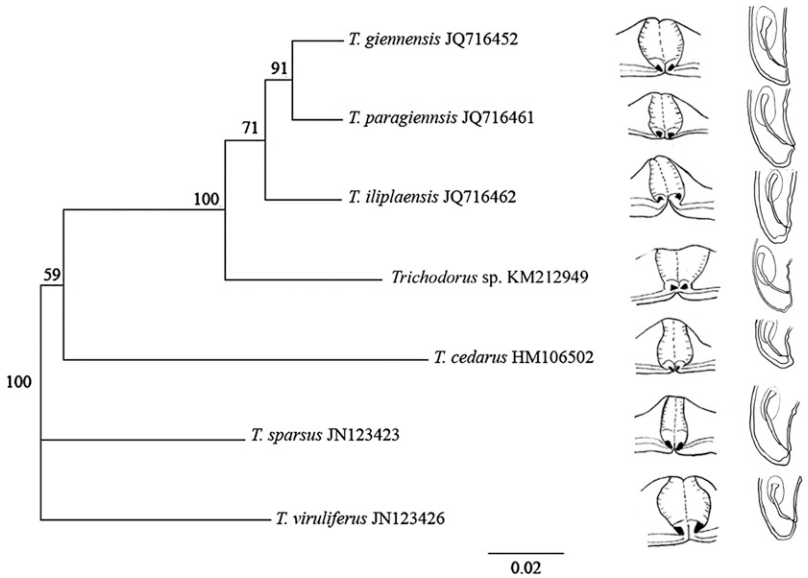

FIG. 7. NJ distance tree, bootstrapped 1,000 times, of members of the *Trichodorus sparsus* morphospecies group, including *Trichodorus* sp. from thrips. *T. viruliferus* was specified as the outgroup. ModelTest settings used to create the phylogenetic tree corresponded to the GTR+G model. Branch support percentage values from bootstrapping are given on the tree. Diagnostically important vulval and male tail regions redrawn from Decraemer and Baujard, 1998 and original descriptions for *T. viruliferus* (Hooper, 1963), *T. cedarus* (Yokoo, 1964), *T. sparsus* (Szczygiel, 1968), *T. giennensis* (Decraemer et al., 2013), *T. iliplaensis* (Decraemer et al., 2013), and *T. paragiennensis* (Decraemer et al., 2013).

TABLE 2. Similarity values and number of nucleotide differences of 28S rDNA D2–D3 sequences between *Trichodorus* sp. and related species.

	T. giennensis	*T. paragiennensis*	*T. iliplaensis*	*Trichodorus* sp.	*T. sparsus*	*T. viruliferus*	*T. cedarus*
T. giennensis	–	21	37	52	99	104	127
T. paragiennensis	97.2%	–	35	58	102	105	137
T. iliplaensis	95.0%	95.6%	–	65	95	108	126
Trichodorus sp.	93.1%	92.5%	91.5%	–	107	111	129
T. sparsus	86.9%	87.1%	87.8%	85.9%	–	85	116
T. viruliferus	86.2%	86.7%	86.1%	85.3%	89.1%	–	126
T. cedarus	83.2%	83.0%	84.1%	83.0%	85.3%	84%	–

node would lose support. Therefore the distribution of high and low clade support values is not especially noteworthy with such a sparse assemblage of taxa.

Just how *Trichodorus,* phylogenetically distant from *Thripinema*, might encounter thrips is difficult to imagine. The approximately 125 species within Thysanoptera subfamily Panchaetothripinae all feed on leaves (Tillekaratne et al., 2007). Within the 10 or so species within *Caliothrips*, none are found in Europe (Hoddle et al., 2012). This is important because Spain appears to be a center of radiation for this *Trichodorus* species group (Decraemer et al., 2013) to which *Trichodorus* sp. from thrips belongs. No species of *Caliothrips* are known to transmit viruses (Jones, 2005), nor are other thrips known to transmit tobraviruses (Jones, 2005) vectored by nematodes of the Trichodoridae. Among trichodorid nematodes, five species are known to transmit tobraviruses (Brown et al., 1989) and are given special phytosanitary importance for that reason (Singh et al., 2013). Perhaps the coincidence of the ability of both certain thrips and some *Trichodorus* species to vector viruses may shed some light on optimum conditions for virus transmission. Major gaps in knowledge of virus vector relationships still exist (Bragard et al., 2013).

This insect association could represent an occasional case of mechanical transmission of these nematodes. Some environmental factor could conceivably be responsible for temporary attachment. However, three different live dorylaim nematodes were recently found for the first time within the haemocoel of a beetle and weevil (Namjou et al., 2013). If this insect association is not exceptional, *Trichodorus* might be vectored within a field or a region in a way that could impact its distribution in a unique pattern relative to spottier distribution of other nematodes. It could also provide an obscure means of transport between states or countries, making this an issue of regulatory concern.

The 28S rDNA sequence of this thrips population was only 92% to 93% similar to *T. paragiennensis* and *T. giennensis* (97% similar to each other), the closest *Trichodorus* species for which a sequence was available for comparison. *Trichodorus* sp. was morphologically very similar to *T. giennensis*, but had shorter body length, onchiostyle, and smaller 'a' ratio and more anteriorly positioned cervical papillae than both these species. This thrips population with a wide uterine-vaginal region and unique molecular sequence represents a putative new *Trichodorus* species from an atypically dry habitat for which its cuticular sheath may be adaptive.

LITERATURE CITED

Bragard, C., Caciagli, P., Lemaire, O., Lopez-Moya, J. J., Macfarlane, S., Peters, D., Susi, P., and Torrance, L. 2013. Status and prospects of plant virus control through interference with vector transmission. Annual Review of Phytopathology 51:177–201.

Brown, D. J. F., Ploeg, A. T., and Robinson, D. J. 1989. A review of reported associations between *Trichodorus* and *Paratrichodorus* species (Nematoda: Trichodoridae) and tobraviruses with a description of laboratory methods for examining virus transmission by trichodorids. Revue de Nématologie 12:235–241.

Decraemer, W., and Baujard, P. 1998. A polytomous key for the identification of species of the family Trichodoridae Thorne, 1935 (Nematoda: Triplonchida). Fundamental and Applied Nematology 21:37–62.

Decraemer, W., Roca, F., Castillo, P., Pena-Santiago, R., and Gomez-Barcina, A. 1993. Trichodoridae from southern Spain, with description of *Trichodorus giennensis* n. sp. (Nemata: Trichodoridae). Fundamental and Applied Nematology 16:407–416.

Decraemer, W., and Marais, M. 2000. A new *Trichodorus* species from South Africa with notes on T. *vandenbergae* (Triplonchida: Diphtherophorina). Annales Zoologici 50:193–203.

Decraemer, W., Palomares-Rius, J. E., Cantalapiedra-Navarrete, C., Landa, B. B., Duarte, I., Almeida, T., Vovlas, N., and Castillo, P. 2013. Seven new species of *Trichodorus* (Diphtherophorina, Trichodoridae) from Spain, an apparent centre of speciation. Nematology 15:57–100.

Edgar, R. C. 2004. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Research 32:1792–1797.

Golden, A. M. 1990. Preparation and mounting nematodes for microscopic observation. Pp. 197–205 *in* B. M. Zuckerman, W. F. Mai, and L. R. Krusberg, eds. Plant nematology laboratory manual. Amherst, MA: University of Massachusetts Agricultural Experiment Station.

Hoddle, M. S., Mound, L. A., and Paris, D. L. 2012. Thrips of California. CBIT Publishing, Queensland. http://keys.lucidcentral.org/keys/v3/thrips_of_california/identify-thrips/key/california-thysanoptera-2012/Media/Html/browse_species/Caliothrips_phaseoli.htm.

Hooper, D. J. 1963. *Trichodorus viruliferus* n. sp. (Nematoda: Dorylaimida). Nematologica 9:200–204.

Jones, D. R. 2005. Plant viruses transmitted by thrips. European Journal of Plant Pathology 113:119–157.

Kumari, S., and Subbotin, S. A. 2012. Molecular characterization and diagnostics of stubby root and virus vector nematodes of the family Trichodoridae (Nematoda: Triplonchida) using ribosomal RNA genes. Plant Pathology 61:1021–1031.

Moritz, G., Mound, L. A., Morris, D. C., and Goldarazena, A. 2004. Pest thrips of the world—visual and molecular identification of pest thrips. CD-Rom published by OBIT, Brisbane. http://wwwcbit.uq.edu.au/software/pestthrips/default.htm.

Murali, S. 2013. Nematode infecting thrips and their utilization in pest management: A review. Trends in Biosciences 6:227–229.

Namjou, S., Pedram, M., Poinar, G. O., Pourjam, E., and Atighi, M. R. 2013. Novel host associations for dorylaim nematodes (Nematoda: Dorylaimida). International Journal of Nematology 23:111–114.

Nunn, G. B., Theisen, B. F., Christensen, B., and Arctander, P. 1996. Simplicity-correlated size growth of the nuclear 28S ribosomal RNA D3 expansion segment in the crustacean order Isopoda. Journal of Molecular Evolution 42:211–223.

Posada, D., and Crandall, K. A. 1998. MODELTEST: Testing the model of DNA substitution. Bioinformatics 14:817–818.

Siddiqi, M. R. 2000. Tylenchida, parasites of plants and insects. 2nd ed. Wallingford, UK: CABI Publishing.

Sims, K., Funderburk, J., Reitz, S. R., and Boucias, D. 2009. The impact of a parasitic nematode *Thripinema fuscum* (Tylenchida: Allantonematidae) on the feeding behavior and vector competence of *Frankliniella fusca* (Thysanoptera: Thripidae). Entomologia Experimentalis et Applicata 132:200–208.

Singh, S. K., Hodda, M., and Ash, G. J. 2013. Plant-parasitic nematodes of potential phytosanitary importance, their main hosts and reported yield losses. EPPO Bulletin 43:334–374.

Szczygiel, A. 1968. *Trichodorus sparsus* sp. n. (Nematoda: Trichodoridae). Bulletin de l'Academie Polonaise des Sciences 16:695–698.

Thomas, W. K., Vida, J. T., Frisse, L. M., Mundo, M., and Baldwin, J. G. 1997. DNA sequences from formalin-fixed nematodes: Integrating molecular and morphological approaches to taxonomy. Journal of Nematology 29:250–254.

Thompson, J. D., Higgins, D. G., and Gibson, T. J. 1994. CLUSTAL W: Improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. Nucleic Acids Research 22:4673–4680.

Tillekaratne, K., Mound, L. A., Zur Strassen, R., and Edirisingh, J. P. 2007. List of thrips (Thysanoptera) recorded from Sri Lanka. Journal of the National Science Foundation of Sri Lanka 35:197–205.

Ye, W., Giblin-Davis, R. M., Davies, K. A., Purcell, M. F., Scheffer, S. J., Taylor, G. S., Center, T. D., Morris, K., and Thomas, W. K. 2007. Molecular phylogenetics and the evolution of host plant associations in the nematode genus *Fergusobia* (Tylenchida: Fergusobiinae). Molecular Phylogenetics and Evolution 45:123–141.

Yokoo, T. 1964. On the stubby root nematodes from the western Japan. Agricultural Bulletin of Saga University 20:57–62.