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Deladenus posteroporus n. sp. (Nematoda: Neotylenchidae) Isolated from Packaging Wood from Canada and White Pine (*Pinus monticola*) Lumber from the United States and Intercepted in Ningbo, China

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Abstract: Deladenus posteroporus n. sp. isolated from packaging wood originated from Canada and from white pine lumber from the United States, both intercepted in the port of Ningbo, China, is described and illustrated. Both mycetophagous and infective forms were recovered from the Canadian sample, whereas only the mycetophagous form was found in the U.S. sample. The new species is characterized by the posteriorly positioned excretory pore relative to the hemizonid in both mycetophagous and infective forms, by a broadly rounded tail end in mycetophagous females and lateral fields with 11 to 12 lines midbody in both mycetophagous females and males. The partial 18S, complete internal transcribed spacer, and partial 28S D2/D3 rRNA genes were amplified and sequenced. Phylogenetic analyses of the genes grouped the new species with previously sequenced species of *Deladenus* in a fully supported clade. This is the first report of *Deladenus* species with a known infective stage to have the excretory pore positioned posterior to the hemizonid.

Key words: molecular, morphology, morphometrics, nematode, new species, taxonomy.

The genus *Deladenus* was erected by Thorne (1941) with *D. durus* (Cobb, 1922) Thorne, 1941 as its type species and was differentiated from other genera in the family Neotylenchidae by the location of the pharyngo-intestinal junction being situated immediately behind the nerve ring. *Deladenus* spp. had been considered to be mycetophagous until Bedding (1968, 1974) discovered seven entomophagous species from horntails (Siricidae), which could also reproduce on the symbiotic fungi. Those seven *Deladenus* species had two independent life cycles with two different forms: the free-living mycetophagous cycle in the form of neotylenchids and the insect-parasitic cycle in the form of allantonematids and sphaerularids for parasitic mature females. However, the taxonomy of the genus continued to be based on the mycetophagous (neotylenchid) forms because not all species have a known infective stage. Siddiqi (1986) expanded the definition of the genus by adding that the pharyngo-intestinal junction could be situated also anterior to the nerve ring. Chitambar (1991) reviewed the mycetophagous forms of the genus, synonymized *D. andrassyi* Vinciguerra, 1972 and *D. paradurus* Massey, 1974 with *D. durus* and *D. crassus* Zell, 1985 with *D. aridus* Andrassy, 1957, which resulted in a total of 18 nominal species. Siddiqi (2000) expanded *Deladenus* by transferring *D. aenea* (Rao and Reddy, 1983) Ebsary, 1991; *D. laricis* (Blinova and Korentchenko, 1986) Ebsary, 1991; *D. pakistanensis* Shahina and Maqbool, 1992; and *D. minimus* Chizhov and Sturhan, 1998 to the genus. Several species, including *D. lonchites* Massey, 1974; *D. ruehmi* Andrassy, 1958; and *D. saccatus* Andrassy, 1954, have been listed as species inquirendae (Chitambar, 1991; Siddiqi, 2000; Yu et al., 2014). Recently, six additional species have been described: *D. cocophilus* Nasira, Shahina and Firoza, 2013; *D. prorsus* Yu, Gu and Ye, 2013; *D. valveus* Yu, Popovic and Gu, 2014; *D. albizicus* Tomar, Somvanshi and Bajaj, 2015; *D. processus* Tomar, Somvanshi and Bajaj, 2015; and *D. nitobei* Kanzaki, Tanaka, Fitza, Kosaka, Slippers, Kimura, Tsuchiya and Tabata, 2016.

The position of the excretory pore relative to the hemizonid in mycetophagous females, either posterior or anterior, and the distance between the two structures are the most useful and reliable characters for the diagnosis of the species (Chitambar, 1991). Based on these features, all species can be grouped into two groups: those with posterior-positioned and those with anterior-positioned hemizonid, with the exception of *D. norimbergensis* Rühm, 1956 and *D. aenea* and *D. ulani* Sultanalieva, 1983, owing to the lack of information on the characters in the latter species. All species with a known infective stage belong to the anterior-positioned group, whereas those without an infective stage (with the exception of *D. apopkaetus* Chitambar, 1991) belong to the posterior-positioned group. The lateral fields at midbody are also diagnostically informative: all those with a known infective stage have 10 to 12 lines, whereas those without such a stage have 6 to 7 lines (with the exception of *D. obesus* Thorne, 1941, which has 8–10 lines).

In Canada, five species have been reported: *D. durus*, *D. canii* Bedding, 1968 and *D. wilsoni* Bedding, 1974, *D. siricidicola* Bedding, 1968, and *D. proximus* Bedding, 1974 (Das, 1964; Bedding and Akhurst, 1978; Yu et al., 2009, 2012). In the United States, *D. apopkaetus*, *D. durus*, *D. ipini* Massey, 1974, *D. obesus* Thorne, 1941, *D. proximus*, *D. siricidicola*, and *D. wilsoni* have been

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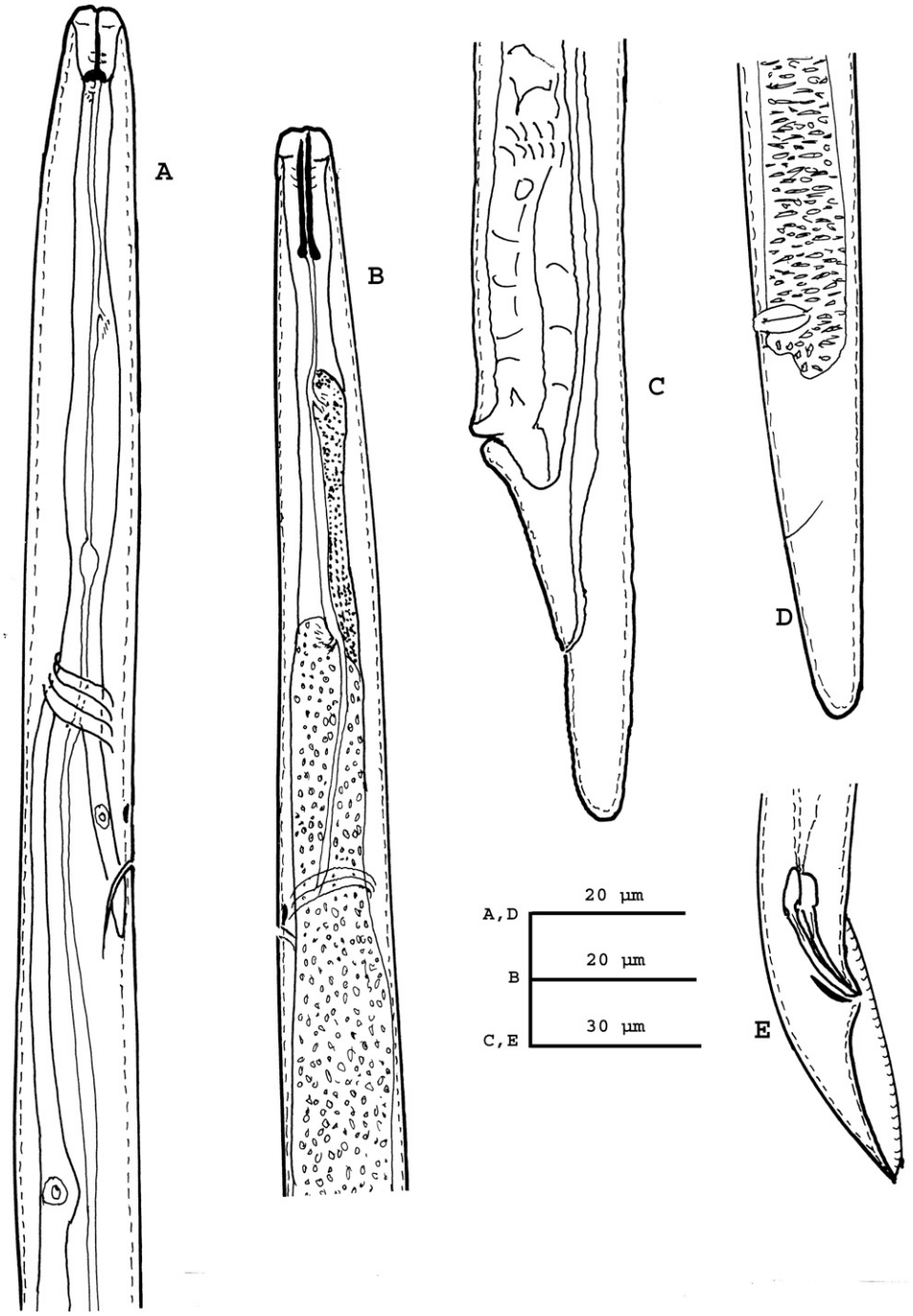

Fig. 1. Line drawings of *Deladenus posteroporus* n. sp. A. Head and pharynx of mycetophagous female. B. Head and pharynx of infective female. C. Vulva and tail of mycetophagous female. D. Vulva and tail of infective female. E. Tail of mycetophagous male.

reported (Thorne, 1941; Massey, 1974, Bedding and Akhurst, 1978, Chitambar, 1991; William et al., 2009). Here, we record a new species of *Deladenus* for the region. The objective of our study was to describe and illustrate *D. posteroporus* n. sp.

Materials and Methods

Nematode samples: Sawn wood samples intercepted in Ningbo port, China, were taken from packaging wood of lot no. 2078 from Canada, and white pine lumber of lot no. 8714 from the United States, in 2015 and 2016, respectively. The samples were cut into small pieces less than 1-cm long at the port of entry. Nematodes were extracted using the Baermann funnel technique for 24 hr. Efforts were made to obtain both mycetophagous and infective forms from the extractions among other species. The nematodes were then heat killed and kept in refrigerator at 5°C for both morphological and molecular studies.

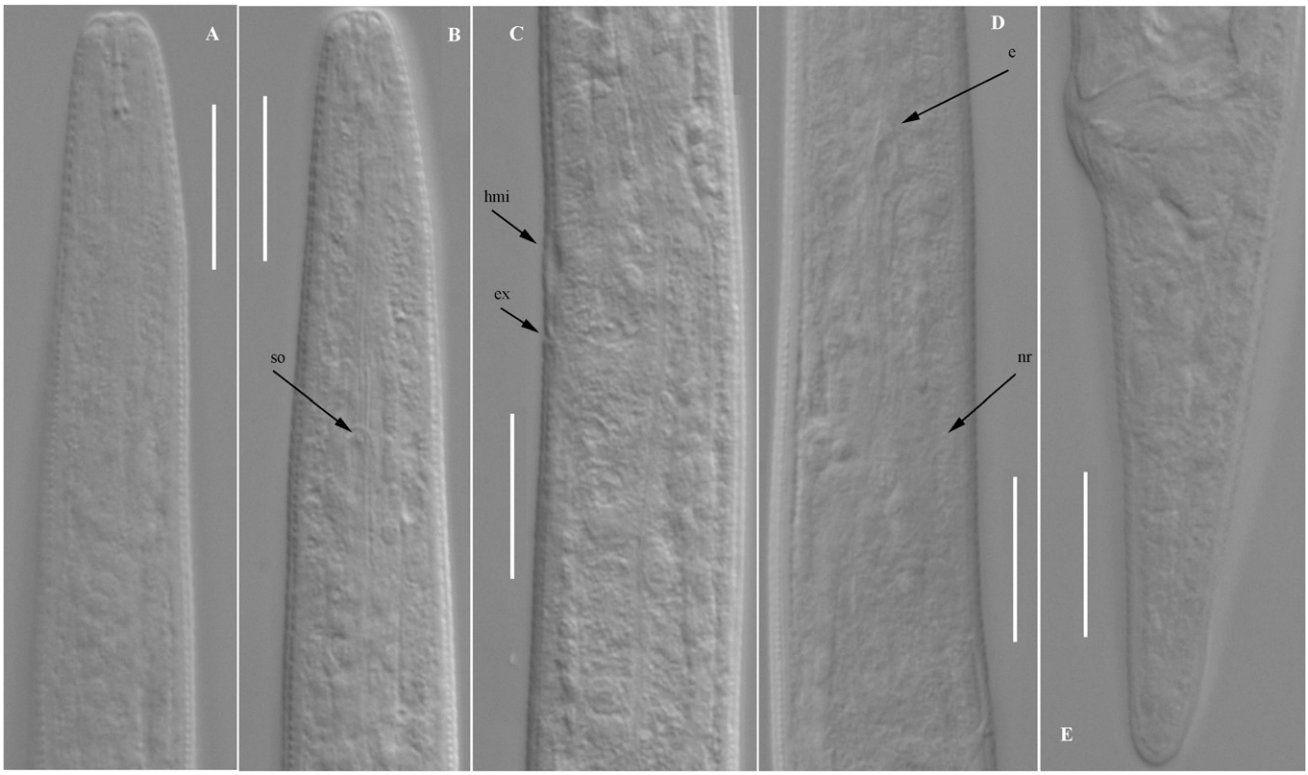

Fig. 2. Micrographs of mycetophagous females of *Deladenus posteroporus* n. sp. A. Head region. B. Pharynx (arrow pointing to the subventral gland orifice). C. Hemizonid (arrow labeled with *hmi*) and excretory pore (arrow labeled with *ex*). D. Pharynx, intestine region junction (arrow labeled with *e*), and nerve ring (arrow labeled with *nr*). E. Tail region (scale bar = 20 μm).

Morphological study: The nematodes were all fixed in TAF (20% triethanolamine, 7% of 37% formaldehyde, and 91% water) and mounted in dehydrated glycerin on slides for morphological studies. Specimens were examined using a Leica DM5500 B compound microscope using differential interference contrast (DIC) and pictures were taken with a Leica DFC 420 digital camera. Measurements were made using a Leica micro application system on the images. Details of observational techniques are given by Yu et al. (2014).

Molecular study: The method used for DNA extraction was developed by Gu and Wang (2010). A single nematode was cut into several fragments using a sterilized scalpel in 30 μl worm lysis buffer (20 mM Tris, pH 7.5; 50 mM EDTA; 200 mM NaCl; 0.5% SDS) (William et al., 1992). Proteinase K was added into the tubes, followed by incubation and then denaturing of the proteinase. A 2-μl aliquot was used for PCR amplification. Fragments of the rRNA gene including the small subunit (18S), the internal transcribed spacer (ITS) region, and the D2/D3 region of 28S were amplified. The primers and reaction conditions followed Powers et al. (2010) for the 18S region, Vrain et al. (1992) for the ITS region, and De Ley et al. (1999) for the 28S D2/D3 region. PCR products were purified for cloning and sequenced by Invitrogen (Shanghai, China).

Phylogenetic analysis was performed as described previously (Ye et al., 2007). The sequences were deposited in the GenBank database. The DNA sequences were aligned by Kalign (http://www.ebi.ac.uk/Tools/msa/kalign/) using default settings. The DNA sequences of *D. posteroporus* n. sp. were compared with those of the other nematode species available in GenBank using the BLAST homology search program. For phylogenetic analyses, the model of base substitution was first evaluated and selected using MODELTEST, and the Akaike-supported model, the base frequencies, the proportion of invariable sites and the gamma distribution shape parameters, and inferred substitution rates were specified in phylogenetic analyses. Bayesian analysis was performed to infer the tree topology for each gene separately using MrBayes 3.1.2 (Huelsenbeck and Ronquist, 2001) running a Markov chain Monte Carlo for 1×10^6 generations, discarding trees from the first 2,500 generations as burn-in after confirming convergence of chain. Node support was evaluated by their posterior probabilities of the phylogenetic trees using 50% majority rule.

Results

Deladenus posteroporus n. sp.
(Figs. 1–4)

Multiple mycetophagous males and infective females, and one mycetophagous female were recovered from the Canadian sample and multiple mycetophagous

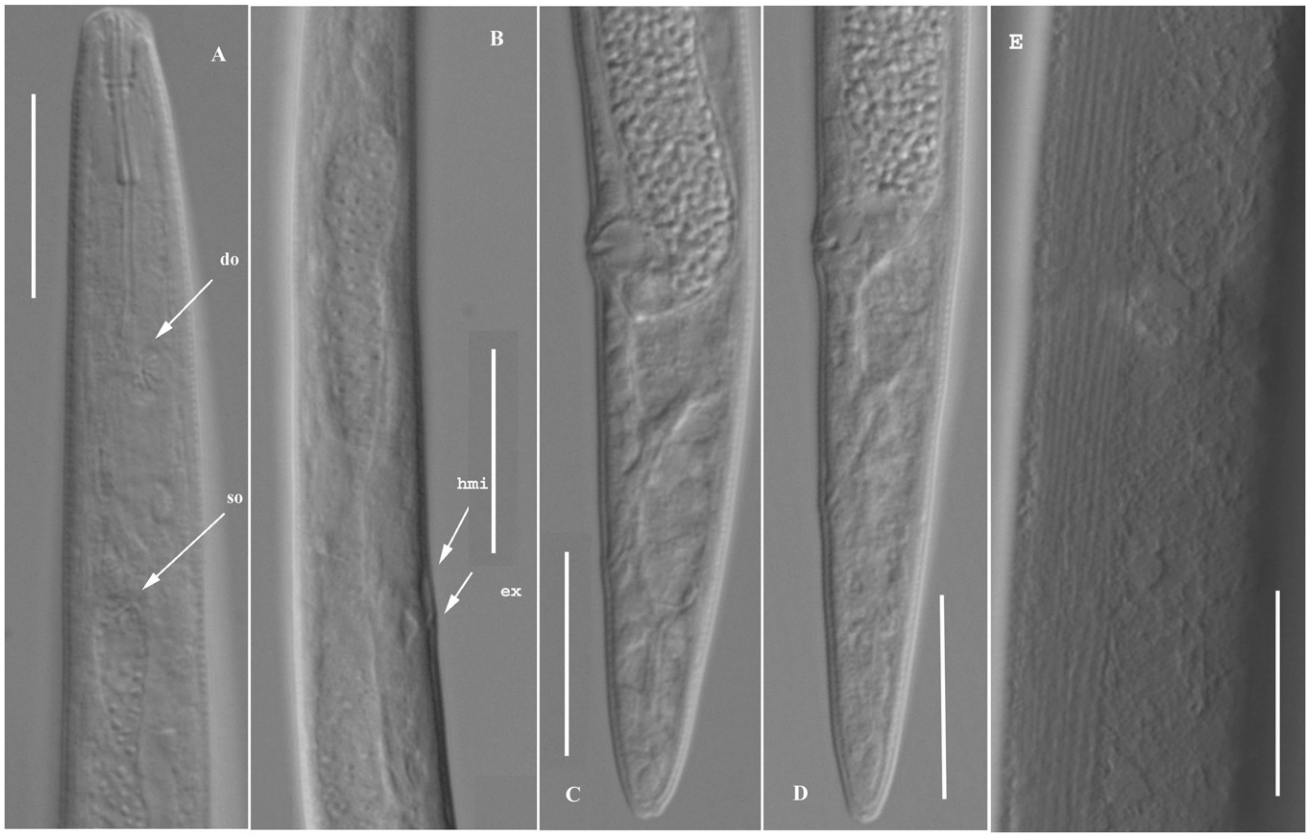

FIG. 3. Micrographs of infective females of *Deladenus posteroporus* n. sp. A. Head and pharynx (arrow labeled *do* and *so* pointing to the dorsal gland and subventral gland orifice, respectively). B. Hemizonid (arrow labeled *hmi*) and excretory pore (arrow labeled *ex*). C, D. Vulva and tail. E. Lateral field (scale bar = 20 μm).

males and three mycetophagous females were recovered from the U.S. sample.

Measurements

Measurements of the holotype, paratypes of mycetophagous females and males, and infective females of *D. posteroporus* n. sp. are given in Table 1.

Description

Mycetophagous female (holotype, Canadian population): Body cylindrical, almost straight when relaxed, gradually tapered toward both ends, swollen near vulva. Cuticle finely annulated, annulations 1 μm apart, lateral fields prominent, extending almost entire body length, 11 to 12 straight lines at midbody, 8 to 10 lines anterior to deirids, and 3 to 5 lines from vulva to tail terminus. Deirids prominent and papilla shaped, near the position of never ring. Amphids invisible; head low, lip region not offset from body contour; stylet with well-developed, rounded basal knobs, cone slightly longer than shaft, which has two guild rings. Dorsal gland orifice close to the basal knobs of the stylet, corpus of pharynx cylindrical, nonmuscular, and pharyngeal median bulb not obvious, lumen narrow, without valvular apparatus, subventral gland orifice located half way between the stylet basal knobs and the pharynx–intestine junction. The pharyngo-intestinal junction as swelling of lumen about 20 μm anterior to the anterior edge of nerve ring. Hemizonid 113 μm from anterior end. Excretory pore 4 μm posterior to hemizonid. Dorsal gland tube shaped, swollen at bottom section, subventral glands reduced to much narrower and shorter tube than dorsal gland. Intestine lumen wide. Reproductive system well developed, ovary prodelphic, without postuterine sac, outstretched, not overlapping dorsal gland, multiple rows of oocytes, oviduct long with 14 cells, spermatheca from round to ovoid in shape, empty in holotype specimen or filled with round sperms at 3 μm in diameter, crustaformeria typical with four columns of cells, uterus narrow and long, uterine sac elongated, cylindrical, surrounded with a few large cells, vagina deep, vulva a wide transverse slit with protuberant lips. Rectum not broadened. Tail gradually tapered, with broadly rounded end. Phasmids not observed by DIC microscopy.

Although the diagnostic characteristics of the U.S. population, namely the posterior position of the excretory pore relative to the hemizonid, a rounded tail end, and 11 to 12 lines in the lateral fields, matched those of the Canadian population, some minor intraspecific differences were observed, i.e., a smaller body, shorter distance from the excretory pore to the hemizonid (immediate vs. 4 μm), longer distance to

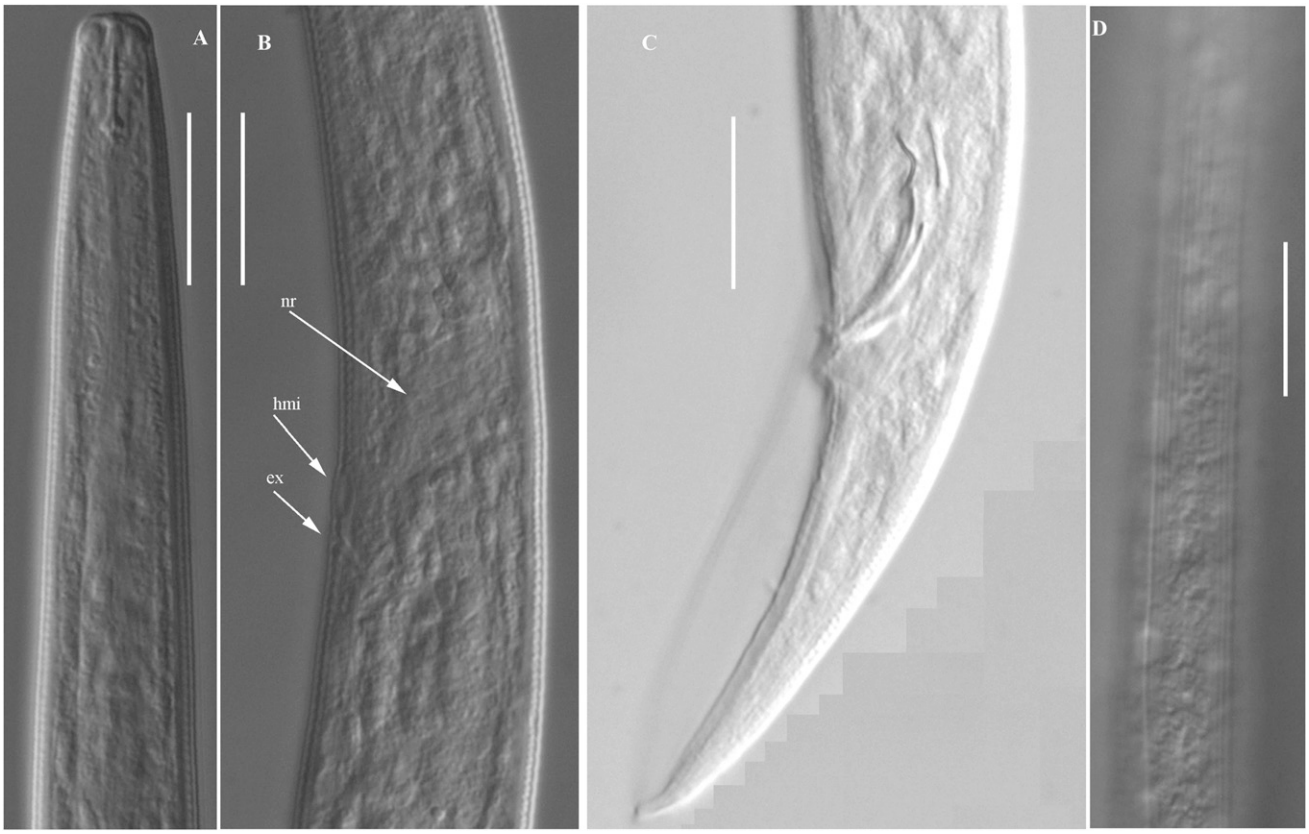

Fig. 4. Micrographs of mycetophagous males *Deladenus posteroporus* n. sp. A. Head region. B. Hemizonid (arrow labeled *hmi*), excretory pore (arrow labeled *ex*), and nerve ring (arrow labeled *nr*). C. Tail. D. Lateral field (scale bar = 20 μm).

the subventral gland openings from the anterior end (44–47 vs. 42 μm), and a spermatheca filled with round sperm about 3 μm in diameter (as observed in two specimens).

Mycetophagous male: Body thinner than that of mycetophagous female and slightly ventrally arcuate when relaxed, lateral fields prominent with 11 to 12 lines at midbody. Lip region not offset from body. Stylet and pharynx structure similar to that of mycetophagous female. Excretory pore 1 to 4 μm posterior to the hemizonid. Testis outstretched, comprising single row of germ cells, vesicular seminalis long, vas deferens short, sperm cells round and about 1 μm in diameter. Spicules and gubernaculum typical tylenchoid, i.e., each spicule divided into three sections: cylindrical head (manubrium), tubelike shaft (calomus), and flattened blade (lamina). Bursa peloderan and well developed. Tail tapered to sharp, pointed terminus. Mycetophagous males of the U.S. population shorter than those in the Canadian population (810–920 vs. 1010–1035 μm) and with a smaller ratio (31–38 vs. 54–68).

Infective female: Form significantly different from mycetophagous female. Body slender, and shorter with finer annulations. Lateral fields 11 to 12 lines at midbody. Lips appear fused, stylet moderate short for the genus with thick stylet walls, long, dorsal side one slightly longer than ventral side, and with moderate wide lumen cone, shaft and knobs amalgamated, and accompanied by three guide rings. Dorsal gland orifice clearly visible at about one stylet length posterior to stylet knobs. Subventral gland orifice clearly visible at two-thirds of pharynx length posterior to stylet; pharynx not muscular, forming broad tube, without distinct median bulb; the pharyngo-intestinal junction not apparent. Excretory pore immediately posterior to hemizonid. Both dorsal and subventral glands massive, extending to more than half of body length. Reproductive system small and immature, ovary a single row of cells, oviduct narrow, and spermathecal elongate, filled with sperm cells of different shapes ranging from circular to elongate, uterus short and reduced, vagina narrow and shallow, vulva small and comprising narrow and short slit, a short postuterine sac present and about 5- to 10-μm long; anus easily observed and located halfway between vulva and posterior end; tail narrowed to rounded end.

Infective male: Not found.

Type host and locality: Packaging wood from Canada, as intercepted in Ningbo Entry-Exit Inspection and Quarantine Bureau, China, in 2015.

TABLE 1. Morphometrics of *Deladenus posteroporus* n. sp. All measurements are in μm and in the form: mean ± standard deviation (range).

	Measurements				
	Canadian population			U.S. population	
Character	Holotype (mycetophagous female)	Mycetophagous male	Infective female	Mycetophagous female	Mycetophagous male
n	1	20	20	3	20
L	1,026	1,020 ± 20.5 (1010–1035)	615 ± 15.8 (530–627)	988 ± 61.5 (889 –1020)	865 ± 50.6 (810–920)
a	39.5	59.7 ± 12.2 (54.1–68.1)	35.8 ± 3.1 (33.7–37.5)	40.3 ± 2.4 (38–43)	35.8 ± 3.5 (31.1–38.2)
b	10.3	14.4 ± 0.4 (13.3–15.1)	11.6 ± 0.4 (10.5–12.3)	11.2 ± 1.9 (10.1–12.8)	9.9 ± 1.2 (9.1–10.6)
c	35.4	28.2 ± 1.9 (26.4–35.8)	30.4 ± 2.1 (29.3–32.8)	33.2 ± 3.2 (31.3–37.1)	24.5 ± 2.5 (22.3–25.1)
c'	2.5	2.6 ± 0.8 (2.1–2.8)	2.4 ± 1.8 (2.2–2.6)	2.8 ± 0.5 (2.7–3.0)	3.1 ± 0.6 (2.3–3.5)
G_1 or T	76.0	55.4 ± 2.4 (49.8–58.2)	54.5 ± 2.5 (52.5–56.9)	60.4 ± 5.6 (55.7–66.8)	45.5 ± 4.5 (37.5–51.5)
V	94.0	-	88.7 ± 2.4 (84.3–91.2)	94.4 ± 1.1 (93.5–95.9)	-
Stylet	10	11.6 ± 0.6 (10.4–12.0)	14.1 ± 1.7 (12–16)	9.0 ± 1.4 (8–11)	11.5 ± 0.5 (9–12)
Body diam.	26	17.5 ± 1.5 (17–19)	17.5 ± 0.9 (16–20)	24.1 ± 1.5 (19–25)	20.3 ± 1.5 (19–22)
Excretory pore from the anterior end	117	113.7 ± 3.5 (110–119)	84.2 ± 1.6 (81–89)	110.0 ± 11.5 (105–120)	105.3 ± 15.5 (90–120)
Excretory pore anterior to the hemizonid	4	1 ± 0 (1.0–1.0)	1 ± 0 (1–1)	1 ± 0 (1–1)	3 ± 0.5 (1–4)
Dorsal gland orifice from anterior end	12	13 ±1.5 (12–14)	32.4 ± 4.4 (30–38)	11.5 ± 0.6 (10–12)	12.0 ± 1.5 (11–13)
Subventral gland orifice from anterior end	42	42.3 ± 3.3 (40–46)	61.5 ± 5.1 (55–66)	45 ± 5.7 (44–47)	45.5 ± 3.5 (44–48)
Vulva to anus	31	-	29.3 ± 2.1 (27–31)	27.2 ± 3.2 (26–30)	-
Tail length	29	36.5 ± 3.4 (30–41)	20.5 ± 1.5 (18–23)	28.3 ± 2.5 (27–29)	30.3 ± 3.4 (28–34)
Spicules	-	23.5 ± 2.4 (21–25)	-	-	23 ± 2.1 (19–24)

Distribution: In addition to the type host and locality, the new species was isolated from lumber of white pine (*Pinus monticola*) from the United States, as intercepted in Ningbo Entry-Exit Inspection and Quarantine Bureau, China, 2016.

Type specimens: Holotype mycetophagous female, 10 paratype mycetophagous males, and 10 paratype infective females of *D. posteroporus* n. sp. were deposited in the Canadian National Collection of Nematodes, Ottawa, ON, Canada, under the accession number T546. Three paratype mycetophagous males and infective females were deposited in each of the following collections: USDA Nematode Collection, Beltsville, MD, under the accession numbers T6853p to T6858p. Additional paratypes have were deposited in the Ningbo Entry-Exit Inspection and Quarantine Bureau Nematode Collection, Ningbo, China.

Diagnosis: Deladenus posteroporus n. sp. is distinguished from all other species of the genus by the combination of the posteriorly positioned excretory pore relative to the hemizonid, a broadly rounded tail end, and the 11 to 12 lines of the lateral fields in mycetophagous females.

Relationships: General morphology of the new species is most similar to *D. siricidicola*, *D. wilsoni*, and *D. nitobei*. The new species differs from the latter species, as well as all other species with a known infective stage, including *D. canii*, *D. imperialis* Bedding, 1974, *D. rudyi* Bedding, 1974, *D. nevexii* Bedding, 1974, *D. proximus*, *D. albizicus, D. cocophilus, D. laricis*, *D. prorsus*, *D. valveus*, *D. indicus* Singh, 1976, *D. nitobei*, and from two species without known infective stage, namely *D. apopkaetus* and *D. ipini* Massey, 1974, by the excretory pore being posteriorly positioned vs. anteriorly positioned relative to the hemizonid. Compared to the species that have their excretory pore posteriorly positioned to the hemizonid, which include *D. aridus*, *D. parvus* Zell, 1985, *D. megacondylus* (Mulvey, 1969), Sumenkova, 1975, *D. durus*, *D. processus*, and *D. pakistanensis*, the new species differs from them by having lateral fields with 11 to 12 lines vs. 6 to 7 lines. The new species differs from *D. obesus* by its lateral fields having 11 to 12 vs. 8 to 10 lines, a mycetophagous female having a nonobese body, specifically having a ratio of 38 to 43 vs. 16 to 22, and a tail end that is broadly rounded vs. narrowly rounded. Compared with species in which information is lacking on the position of excretory pore relative to the hemizonid, the new species differs from *D. norimbergensis* by a broadly rounded vs. narrowly rounded tail end and by a shorter body (1,026 µm in the holotype Canadian population) and 889 to 1020 µm (paratypes, U.S. population) vs. 1,364 to 1,628 µm in mycetophagous females, and 1,010 to 1,035 µm (Canadian population) and 810 to 920 (U.S. population) µm vs. 1,254 to 1,364 µm in mycetophagous males. The new species differs from *D. ulani* by its lateral fields having 10 to 11 vs. 6 lines and by a broadly rounded vs. narrowly rounded tail end. The new species differs from *D. aenea* by its longer body, specifically being 1,026 µm (holotype Canadian population) and 889 to 1,020 µm (paratypes, U.S. population) vs. 524 to 567 µm and 531 to 627 µm vs. 417 to 450 µm; its longer stylet, specifically at 13 to 16 vs. 9 to 10 µm in infective females and 8 to 11 µm vs. 3 to 4 µm in mycetophagous males, a broadly rounded vs. sharply pointed tail end in both mycetophagous and infective females.

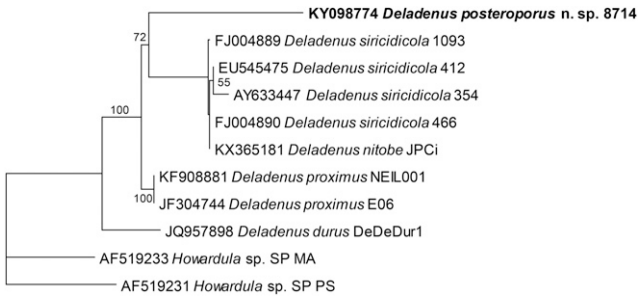

Fig. 5. Phylogeny of *Deladenus* species inferred from partial 18S rRNA gene sequences by Bayesian analysis. Phylogeny was inferred under a GTR + I + G model (-lnL = 6333.834; AIC = 12687.668; freqA = 0.2384; freqC = 0.2036; freqG = 0.267; freqT = 0.2911; R(a) = 1.1233; R(b) = 3.698; R(c) = 2.4739; R(d) = 0.7402; R(e) = 5.1375; R(f) = 1; Pinva = 0.6096; Shape = 0.8015). Posterior probability values exceeding 50% are given on appropriate clades.

Fig. 6. Phylogeny of *Deladenus* species inferred from 28S D2/D3 rRNA gene sequences by Bayesian analysis. Phylogeny was inferred under a TrN + G model (-lnL = 2644.97; AIC = 5301.9399; freqA = 0.2103; freqC = 0.1993; freqG = 0.3249; freqT = 0.2655; R(a) = 1; R(b) = 3.0953; R(c) = 1; R(d) = 1; R(e) = 7.2585; R(f) = 1; Pinva = 0; Shape = 0.3542). Posterior probability values exceeding 50% are given on appropriate clades.

Etymology: The species epithet denotes the posterior position of the excretory pore relative to the hemizonid in both mycetophagous and infective forms.

Molecular characterization and phylogenetic analysis: The 765 bp sequences of the 28S D2/D3 of the Canada and U.S. populations were identical. Additionally, 2,657 bp of the 18S, ITS1, and 5.8S rRNA gene was sequenced for the U.S. population. Sequences have been deposited in GenBank with accession numbers KX094978 (28S D2/D3) and KY098774 (18S and ITS sequences). The BLAST search of 18S of *D. posteroporus* n. sp. showed between 5 and 21 (of 1,768 total) nucleotide differences from all other deposited *Deladenus* sequences, specifically showing a 98% to 99% identity with *D. siricidicola*, *D. proximus*, and *D. nitobei*. The inferred phylogeny, when rooted using *Howardula* sp. as outgroup, *D. posteroporus* n. sp. forms a lineage separate from other clades of *Deladenus* species and is specifically closer to *D. siricidicola* and *D. nitobei* than to *D. proximus* and *D. durus* (Fig. 5). Based on the 28S D2/D3 sequence, the closest matches were isolates of *D. siricidicola*, *D. proximus*, and *D. canii* isolated from *Sirex* in northeastern North America (Morris et al., 2013) and *D. nitobei* from Japan (Kanzaki et al., 2016) having 95% identity to the latter. In the phylogenetic tree inferred from 28S D2/D3, shown in Fig. 6, *D. posteroporus* n. sp. was grouped as a sister group to *D. canii*, *D. nitobei*, *D. proximus*, *D. siricidicola*, and several unidentified *Deladenus* species in a clade supported by 100% posterior probability. As expected, the ITS1 and 5.8S sequences are variable among *Deladenus* species, with the highest match is in the 5.8S region with 85% to 86% identity. In the phylogenetic tree (Fig. 7) inferred from the sequence of the ITS1 and 5.8 fragment, *D. posteroporus* n. sp. is separate from all other inferred clades of other *Deladenus* species. Although posterior probability support was not high for any *Deladenus* clade besides that for the two isolates of *D. prorsus*, the inferred tree largely agrees with the tree by Kanzaki et al. (2016). Unfortunately, the vast majority of described *Deladenus* species have not yet been sequenced, and thus inference phylogenetic relationships will require molecular characterization of further species.

Remarks: Species diagnosis should be clearly defined in nematode taxonomy. However, the intraspecific variation of mycetophagous females of *D. posteroporus* n. sp. is not thoroughly studied due to limited specimen in this study. Although this new genus/species is well separated from *Deladenus* species based on molecular data, further study is needed to examine the morphology of this nematode group.

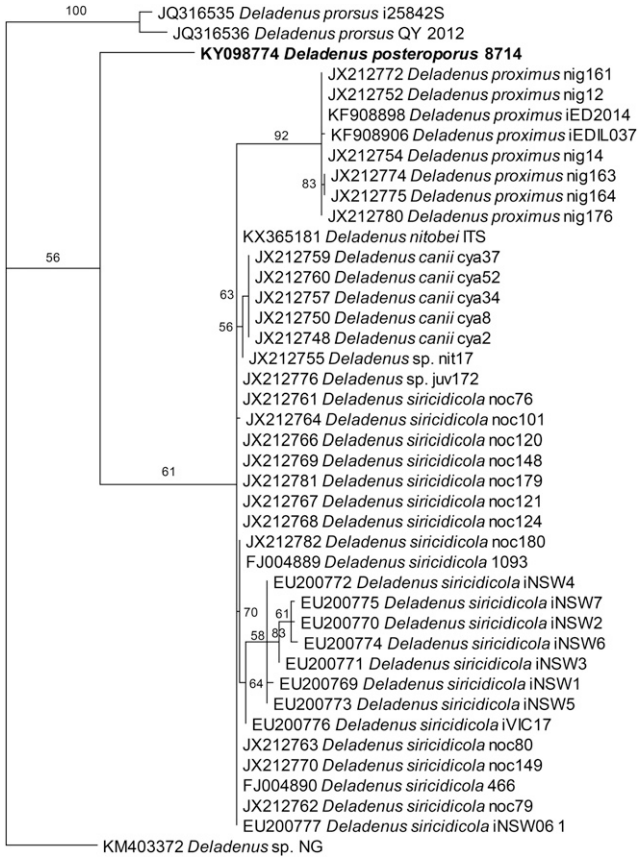

Fig. 7. Phylogeny of *Deladenus* species inferred from ITS1 and 5.8S rRNA gene sequences by Bayesian analysis. Phylogeny was inferred under HKY + G model (-lnL = 2372.4062; AIC = 4754.8125; freqA = 0.1782; freqC = 0.211; freqG = 0.3059; freqT = 0.3049; Pinva = 0; shape = 0.3098). Posterior probability values exceeding 50% are given on appropriate clades.

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