



Description of *Deladenus longicaudatus* n. sp. (Sphaerularioidea: Neotylenchidae) from Mazandaran province, northern Iran: A morphological and molecular phylogenetic study

Research Article

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Received 25 September 2025; Accepted 14 January 2026

Abstract: *Deladenus longicaudatus* n. sp. was recovered from decaying wood of a broad-leaf forest tree in the forests of Javaherdeh, Mazandaran province, northern Iran, and is herein described and illustrated based upon morphological, morphometric, and molecular characters. The new species is mainly characterized by its small to medium body size of free-living mycetophagous females (523–682 µm long) with an elongate conical tail ($c = 9.3$ – 11.0 and $c' = 3.9$ – 5.3), a relatively anterior vulval position ($V = 84.5$ – 89.0%), the pharyngo-intestinal junction at the level of the nerve ring, the secretory–excretory pore (S–E pore) posterior to the nerve ring, and at the same level as the hemizonid. It is further characterized by seven incisures in the lateral fields, a short stylet (5.0 – 6.5 µm), small lateral vulval flaps, and absence of a postvulval uterine sac (PUS). By having similarities in tail shape, c' ratio greater than 3, posterior position of the S–E pore and hemizonid to the nerve ring, and lack of PUS, the new species is comparable to four known species of the genus, namely, *D. gilanica*, *D. hyrcanus*, *D. zyzyphus*, and *D. parvus*. It is furthermore typologically comparable to mycetophagous phase of *Hexatylus vigissi*. In molecular phylogenetic analyses using partial small and large subunit (SSU and LSU D2–D3) rDNA sequences, the SSU sequences of the new species formed a moderately supported clade with sequences of *Howardula* spp. In LSU phylogeny, the newly generated sequences of the new species formed a clade with corresponding sequence of *D. hyrcanus*.

Keywords: *Deladenus gilanica* • *D. hyrcanus* • Mycetophagous phase • Iran • Javaherdeh • LSU rDNA D2–D3 • Phylogenetic relationships • Ramsar county • SSU rDNA

The genus *Deladenus* Thorne, 1941 comprises nematodes with two distinct main life phases: a free-living phase, feeding on fungi (the mycetophagous phase), and an insect-parasitic phase (the entomoparasitic phase). The infective and mycetophagous phases dwell in soil, decaying organic matter, wood, and the bark of trees (mostly dead and dying trees). Species identification in this genus relies on several morphological features, including body shape, vulva position, number of lateral lines, stylet length, the positions of the pharyngo-intestinal junction, secretory–excretory (S–E) pore and hemizonid, tail shape, and male characters. Due to morphological

and biological similarities in the mycetophagous phase of three genera *Deladenus*, *Hexatylus* Goodey, 1926, and *Rubzovinema* Slobodyanyuk, 1991, Rezaei et al. (2025) have recently urged that the mycetophagous *Deladenus*-like forms (species of the three aforementioned genera) need to be compared with all species under these genera when only free-living phase is available.

Since its establishment, *Deladenus* has attracted considerable attention of taxonomists. According to Aliramaji et al. (2024), a total of 42 valid species were described by 2024. Since then, the genus has been enriched by description of five more species, including *D. hebetocaudatus* Rezaei, Pourjam, Atighi, Kanzaki, Giblin-Davis and Pedram, 2025, *D. uljinensis* Mwamula, Bae, Kim and Lee,

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2025, *D. ramianensis* Ajoudani, Pourjam, Jahanshahi Afshar, Atighi and Pedram, 2025, *D. maraghensis* Saberi, Jahanshahi Afshar, Atighi, Kanzaki, Giblin-Davis and Pedram, 2025, and *D. hyrcanus* Agh Atabai, Aliramaji and Shokoohi, 2025. Eighteen species listed by Aliramaji et al. (2024), along with five species described after 2024, were characterized solely based on their free-living phase.

In Iran, the genus was first recorded by recovering *D. durus* (Cobb, 1922) Thorne, 1941 (Jahanshahi Afshar et al., 2014). Later, several species were described or reported from the country (Ajoudani et al., 2025). The species *D. ramianensis*, *D. maraghensis*, and *D. hyrcanus* represent the latest species added to the genus from Iran (Ajoudani et al., 2025; Saberi et al., 2025; Agh Atabai et al., 2025).

During a recent study on nematodes associated with deadwood in forests of Javaherdeh in Ramsar county, Mazandaran province, northern Iran, in 2024–2025, free-living stages of a *Deladenus*-like population *sensu* Rezaei et al. (2025) were recovered from decaying wood of a broad-leaf forest tree. Detailed morphological studies of this population after comparison with all species of relevant genera indicated that it represents an undescribed species. Thus, the aims of the present study are to describe this population using morphological features and to reconstruct its phylogenetic relationships with relevant species and genera using sequences of small subunit (SSU) and D2–D3 expansion segments of the large subunit (LSU) rDNA.

1. Materials and methods

1.1 Wood and bark sampling, nematode extraction, and morphological characterization

Decaying wood and bark samples were collected in natural forests of Javaherdeh, Ramsar county, Mazandaran province, northern Iran. Nematodes were extracted using the tray method (Whitehead and Hemming, 1965). Live specimens were handpicked under a Nikon SMZ1000 stereomicroscope, heat-killed in hot 4% formaldehyde solution, and processed to anhydrous glycerin following De Gisse (1969). Permanent slides were prepared and examined with a Nikon Eclipse E600 microscope. Photomicrographs were obtained using an Olympus DP72 digital camera attached to an Olympus BX51 microscope equipped with differential interference contrast optics. Line drawings were made with a drawing tube and digitally drawn in CorelDRAW® software version 2020.

Deladenus in its broad sense was accepted in this research (Chitambar, 1991). The new species was compared with the mycetophagous phases of three genera, *Deladenus*, *Hexatylus*, and *Rubzovinema*, according to Rezaei et al. (2025) [valid species of the latter two genera according to Siddiqi (2000)].

1.2 DNA extraction, polymerase chain reaction (PCR), and sequencing

Three live nematode specimens of the new species were picked out and transferred individually to a small drop of tris-ethylenediaminetetraacetic acid (TE) buffer (10 mM Tris-Cl; 0.5 mM ethylenediaminetetraacetic acid; pH 9.0; Qiagen) on a clean slide and gently squashed using a clean cover slip after photomicrographic documentation. The suspension from each specimen was collected by adding 35 µL of TE buffer. DNA samples were stored at –20°C until used as PCR templates. The partial SSU rDNA was amplified using forward primer 1813F (5'-CTGCGTGAGAGGTGA AAT-3') and reverse primer 2646R (5'-GCTACCTTGTTACGA CTTTT-3') (Holterman et al., 2006). The LSU rDNA D2–D3 expansion domains were amplified using the forward primer D2Ab (5'-ACAAGTACCGTGAGGGAAAGTTG-3') (De Ley et al., 1999) and reverse primer 1006R (5'-GTTTCGATTA GTCTTCGCCCT-3') (Holterman et al., 2008). PCR reactions were performed in 35 µL volumes with an annealing temperature of 52°C. The successfully amplified PCR products were sequenced with the same primers used in PCR by Pishgam Corporation (Tehran, Iran), using an ABI 3730XL sequencer. The newly obtained sequences were deposited in the GenBank database under the accession numbers PX106384 and PX106385 for SSU rDNA; and PX108876, PX108877, and PX108878 for LSU rDNA.

1.3 Phylogenetic analyses

The newly obtained SSU and LSU sequences of the new species were compared with those of other nematode species available in the GenBank database using the BLAST homology search program. For phylogenetic reconstruction, two independent datasets were prepared: the SSU and LSU. Sequences of both loci were aligned using MUSCLE implemented in MEGA7 (Kumar et al., 2016) and manually edited to remove poorly aligned or ambiguous positions. Model selection for nucleotide substitution was performed with MrModeltest v2 (Nylander, 2004), applying the Akaike information criterion. The analysis indicated that the general time reversible model, incorporating both a gamma distribution of rate heterogeneity

among sites and a proportion of invariant sites (GTR + G + I), was the most suitable, and was therefore used for further analyses. Bayesian inference was performed using MrBayes v3.1.2 (Ronquist and Huelsenbeck, 2003) for 5,000,000 generations for each dataset. Twenty-five percent of the samples were discarded as burn-in. The Markov chain Monte Carlo method within a Bayesian framework was used to estimate posterior probabilities of phylogenetic trees using the 50% majority rule. For the SSU phylogeny, sequences of *Acrobeloides maximus* Thorne, 1925 and *Acrobeles ciliatus* von Linstow, 1877 were used as outgroups, whereas for the LSU phylogeny, sequences of *Poikilolaimus oxycerca* de Man, 1895 and *P. piniperdae* Fuchs, 1930 served as outgroups. The resulting phylogenetic trees were visualized using Dendroscope v3.2.8 (Huson and Scornavacca, 2012) and subsequently digitally drawn in CorelDRAW® software version 2020.

2. Results

2.1 Description

2.1.1 The line drawings and photomicrographs of *Deladenus longicaudatus* n. sp. are presented in Figs. 1 and 2, respectively

2.1.2 The morphometrics of *Deladenus longicaudatus* n. sp. are shown in Table 1

Female (free-living mycetophagous phase):

Body small to medium-sized, almost fusiform, not obese, nearly straight to very slightly ventrally curved after fixation, gradually tapering toward both anterior and posterior ends, more at the posterior body region, with an elongate conical tail. Cuticle with fine annuli (1.3–1.5 µm wide at mid-body). Lateral field with seven lines at mid-body. Cephalic region low, 2.4–3.2 times wider than high, continuous with body contour, slightly depressed at base, anteriorly flattened to slightly concave. Stylet small, with three distinct posteriorly directed knobs, the conus occupying ca 31–40% of total stylet length. Dorsal gland orifice just posterior to stylet knobs. S–E pore posterior to nerve ring, at the same level with hemizonid. Deirid not observed. Pharynx without a distinct median bulb, lacking a chamber, its junction with intestine at the level with the nerve ring, dorsal pharyngeal gland forming a long overlap over intestine, subventral glands shorter, their orifice slightly posterior to mid-pharynx. Intestine simple, rectum and anus functional. Reproductive system monodelphic-prodelphic, with ovary outstretched, maturing oocytes in one or two rows, oviduct narrow, tube-like and long, spermatheca

not observed; crustoformeria with more than four cells in each row, uterus and vagina with moderately sclerotized wall, vulva in the shape of a wide slit, with lateral flaps (seen in ventro-lateral focus). Postvulval uterine sac (PUS) absent. Vulva-anus distance less than tail length (tail/vulva to anus 2–3). Tail elongate conical, gradually tapering to a finely rounded tip.

Male (free-living mycetophagous):
Not found.

2.2 Infective female

Not found.

2.3 Parasitic female

Not found.

2.4 Type habitat and locality

Decaying wood and bark of a dead broadleaf tree in forests of Javaherdeh, Ramsar county, Mazandaran province, northern Iran. GPS coordinates: 36°52'70"N, 50°33'39.5"E.

2.5 Type material

Holotype female and 11 paratype females were deposited at the WaNeCo nematode collection of Wageningen University, The Netherlands. The LSID code of this publication is: urn:lsid:zoobank.org:pub:800CA2DA-5C2C-47F8-9DED-95445BBDBCBO

2.6 Etymology

The specific epithet refers to the elongate conical tail of the new species.

2.7 Diagnosis and relationship

The mycetophagous females of the new species are mainly characterized by an elongate conical tail gradually tapering to a finely rounded terminus (51–63 µm long, $c = 9.3$ –11.0, $c' = 3.9$ –5.3), a relatively anterior vulval position ($V = 84.5$ –89.0%), and a tail length 2–3 times the vulva–anus distance long. *Deladenus longicaudatus* n. sp. is further characterized by 523–682 µm long females having the pharyngo-intestinal junction at the level with

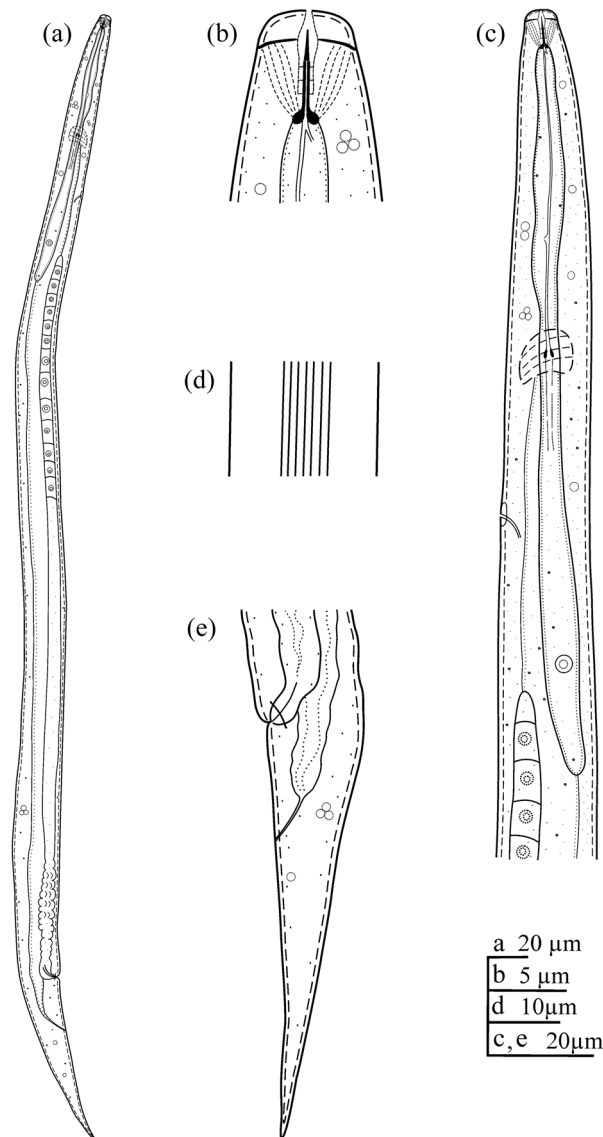


Figure 1. Line drawings of *Deladenus longicaudatus* n. sp. (mycetophagous female). (a) Total body. (b) Anterior body region. (c) Pharyngeal region. (d) Lateral lines. (e) Posterior body region.

the nerve ring, the S–E pore posterior to the nerve ring and at the level with the hemizonid, seven lines in the lateral fields, a short stylet (5.0–6.5 μm), small lateral vulval flaps, and absence of a PUS.

By having similarities in tail shape, c' ratio greater than 3 and position of S–E pore and hemizonid posterior to nerve ring as well as no PUS, the new species is comparable to four known species of the genus, namely, *D. gilanica* Jalalinasab, Esmaili, Ye and Heydari, 2020, *D. hyrcanus*, *D. parvus* Zell, 1985, and *D. zzyphus* Bajaj, 2015. The new species differs from *D. gilanica* by a longer body (523–682 vs

314–422 μm), shorter stylet (5.0–6.5 vs 7.5–8.0 μm), S–E pore 86–112 μm from anterior end (vs 61–76 μm), number of lateral field lines (seven vs eight), presence of lateral vulval flaps (vs absence), and longer tail (51–63 vs 27–32 μm); from *D. hyrcanus* by a shorter body (523–682 vs 718–806 μm), shorter stylet (5.0–6.5 vs 7.5–10.0 μm), shorter pharynx (51–69 vs 71–86 μm), vulva-anus distance (21–31 vs 28.5–46.0 μm), and presence of lateral vulval flaps (vs absence); from *D. parvus* by number of lateral field lines (seven vs four), a posterior vulval position ($V = 84.5$ – 89.0 vs 79.8 – 85.4%), presence of lateral vulval flaps (vs absence),

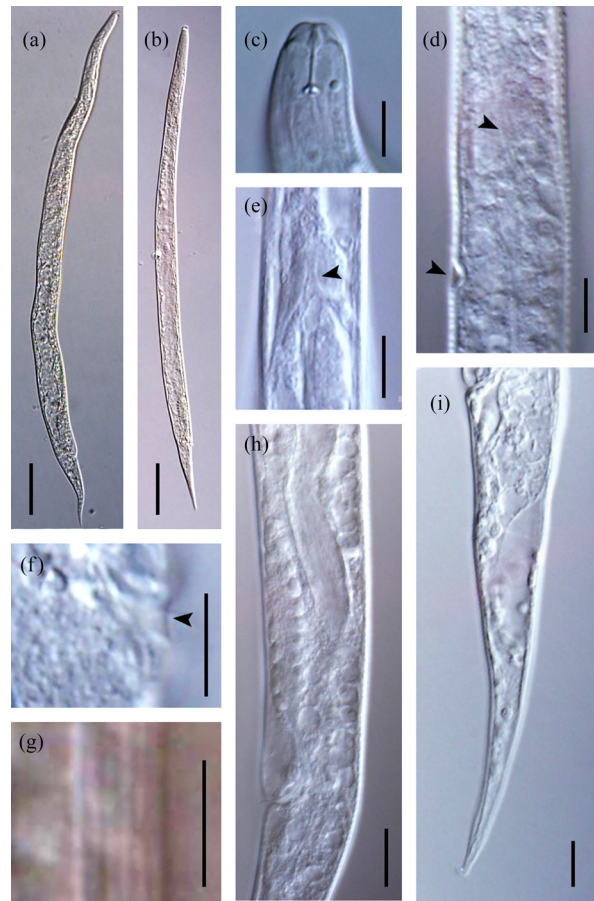


Figure 2. Photomicrographs of *Deladenus longicaudatus* n. sp. (mycetophagous female). (a and b) Total body. (c) Cephalic region and stylet (fresh sample in water). (d) Position of nerve ring (upper arrowhead) and hemizonid (lower arrowhead). (e) Position of pharyngo-intestinal junction at the level with the nerve ring (arrowhead). (f) Lateral vulval flap (arrowhead). (g) Lateral lines. (h) Part of reproductive system. (i) Posterior body region. (Scale bars: a and b = 40 μ m, c and g = 5 μ m, d–f, h and i = 10 μ m).

and a finely rounded tail tip (vs having a short hairy process); from *D. zyzyphus* by shorter body (523–682 vs 790–1,110 μ m), shorter stylet (5.0–6.5 vs 7–9 μ m), S–E pore at the level with hemizonid (vs posterior to hemizonid), number of lateral lines (seven vs four), lower a ratio (19.5–34.0 vs 45–51), lower c' ratio (3.9–5.3 vs 6.1–7.0), presence of lateral vulval flaps (vs absence), shorter tail (51–63 vs 69–90 μ m), and absence of males (vs presence).

Among the mycetophagous phases of the species under the genera *Hexatylus* and *Rubzovinema*, the new species is typologically comparable to *Hexatylus vigissi* Skarbilovich, 1952 (a poorly known species), but differs from it by a shorter body (523–682 vs 986–1,326 μ m), shorter stylet (5.0–6.5 vs 6–8 μ m), S–E pore 86–112 μ m from anterior end (vs 112–125 μ m), lower c ratio (9.3–11.0 vs 12.7–16.5), and shorter tail (51–63 vs 60–100 μ m).

2.8 Remark

Description of *Hexatylus vigissi* includes no data on the rectum acting as a feeding pump. This feature is regarded as one of the main generic characters of *Hexatylus*, as defined by Siddiqi (2000).

2.9 Molecular profiles and phylogenetic status

2.9.1 Partial SSU rDNA

The partial sequencing of SSU rDNA from two specimens of the new species yielded two fragments of 786 nucleotides which were identical after aligning. The BLAST

Table 1. Morphometrics of *Deladenus longicaudatus* n. sp.

Female		
Characters	Holotype	Paratypes
n	1	11
L	570	579 ± 51 (523–682)
a	26	27 ± 5 (19.5–34.0)
b	9.8	9.3 ± 1.0 (8–11)
b'	4.5	5 ± 1 (3.8–6.7)
c	9.8	10.1 ± 0.5 (9.3–11.0)
c'	4.6	4.7 ± 0.4 (3.9–5.3)
V	85.0	86.3 ± 1.2 (84.5–89.0)
Lip region height	2	2.0 ± 0.3 (1.8–2.5)
Lip region width	6	6.0 ± 0.2 (5.8–6.2)
Stylet	6.5	6.0 ± 0.5 (5.0–6.5)
Conus	2.5	2.3 ± 0.2 (2.0–2.5)
m	38	37.0 ± 3.1 (31.5 ± 40.5)
Nerve ring	57	61 ± 5 (51–67)
Hemizonid	89	97 ± 10 (84–110)
S–E pore	91	99 ± 10 (86–112)
Pharynx	58	62 ± 5 (51–69)
Anterior end to end of glands	126	121 ± 16 (102–142)
Overlapping	68	59 ± 13 (39–76)
Anterior end to vulva	485	500 ± 50 (442–607)
Maximum body diameter	22	22 ± 4 (16–27)

Table 1: *Continued*

Female		
Characters	Holotype	Paratypes
Vulval body width	19	17.5 ± 2.0 (14.5–20.5)
Anal body width	12.5	12.0 ± 1.5 (8.5–13.5)
Vulva-anus	27	25 ± 3 (21–31)
Tail	58	56.5 ± 4.0 (51–63)

All measurements are in μm and in the form: Mean value $\pm$ standard deviation (range).

search using these two fragments revealed that all available sequences in GenBank shared less than 98% identity with them. A set of 80 sphaerularioid SSU sequences (including two sequences of the new species) and sequences of two classic rhabditids as outgroups were used in SSU phylogeny (accession numbers and species in the tree). Fig. 3 represents the SSU phylogeny resulting from this dataset. In this tree, SSU sequences assigned to *Deladenus* spp. occupied distant placements across the tree, indicating that the genus is polyphyletic based on this marker and currently available data. The SSU sequences of the new species clustered with sequences of *Howardula neocosmis* Poinar, Jaenike and Shoemaker, 1998 (AF519226), *H. cf. neocosmis* (AF519228), and *H. aoronymphium* Welch, 1959 (AY589304) inside a clade that also includes sequences of *Deladenus gilanic* (MF43926) and the sequence assigned to *D. durus* (JQ957898), with a moderate Bayesian posterior probability (BPP = 0.86).

2.9.2 D2–D3 fragments of LSU rDNA

Partial sequencing of the D2–D3 expansion segments of LSU rDNA of three individuals of the new species yielded three fragments of 724 nucleotides which were identical after aligning. The BLAST search revealed that all available sequences in GenBank shared less than 90% identity with them. For LSU phylogeny reconstruction, 92 sphaerularioid sequences (including three sequences of the new species) and sequences of two classic rhabditid taxa as outgroups were included (accession numbers and species in the tree). Fig. 4 represents the LSU phylogeny resulting

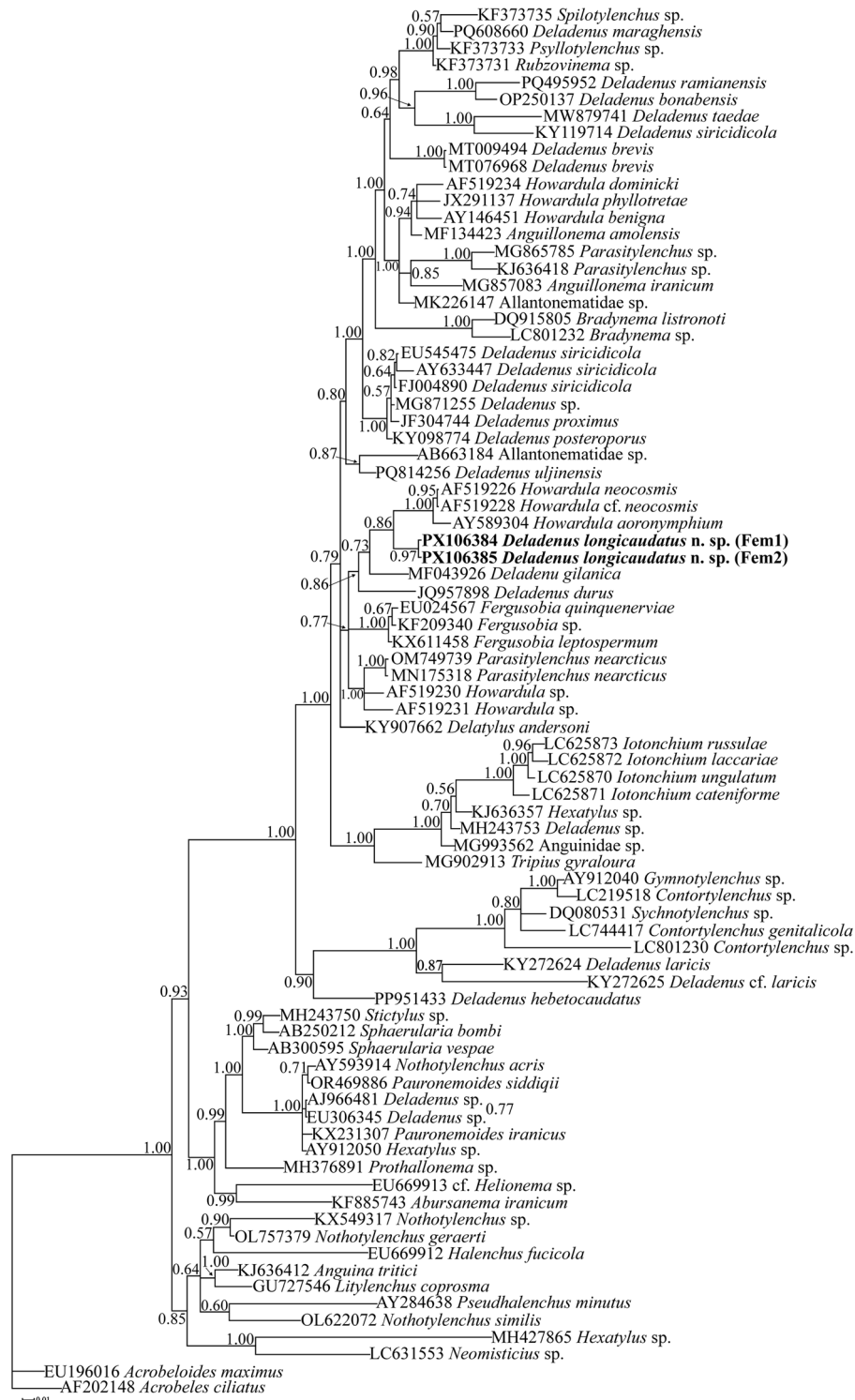


Figure 3. Bayesian 50% majority rule consensus tree of *Deladenus* spp. and other related species from various genera based on SSU rDNA sequences under GTR + I + G model. BPP values more than 0.50 are given for appropriate clades. The newly generated sequences are indicated in bold.

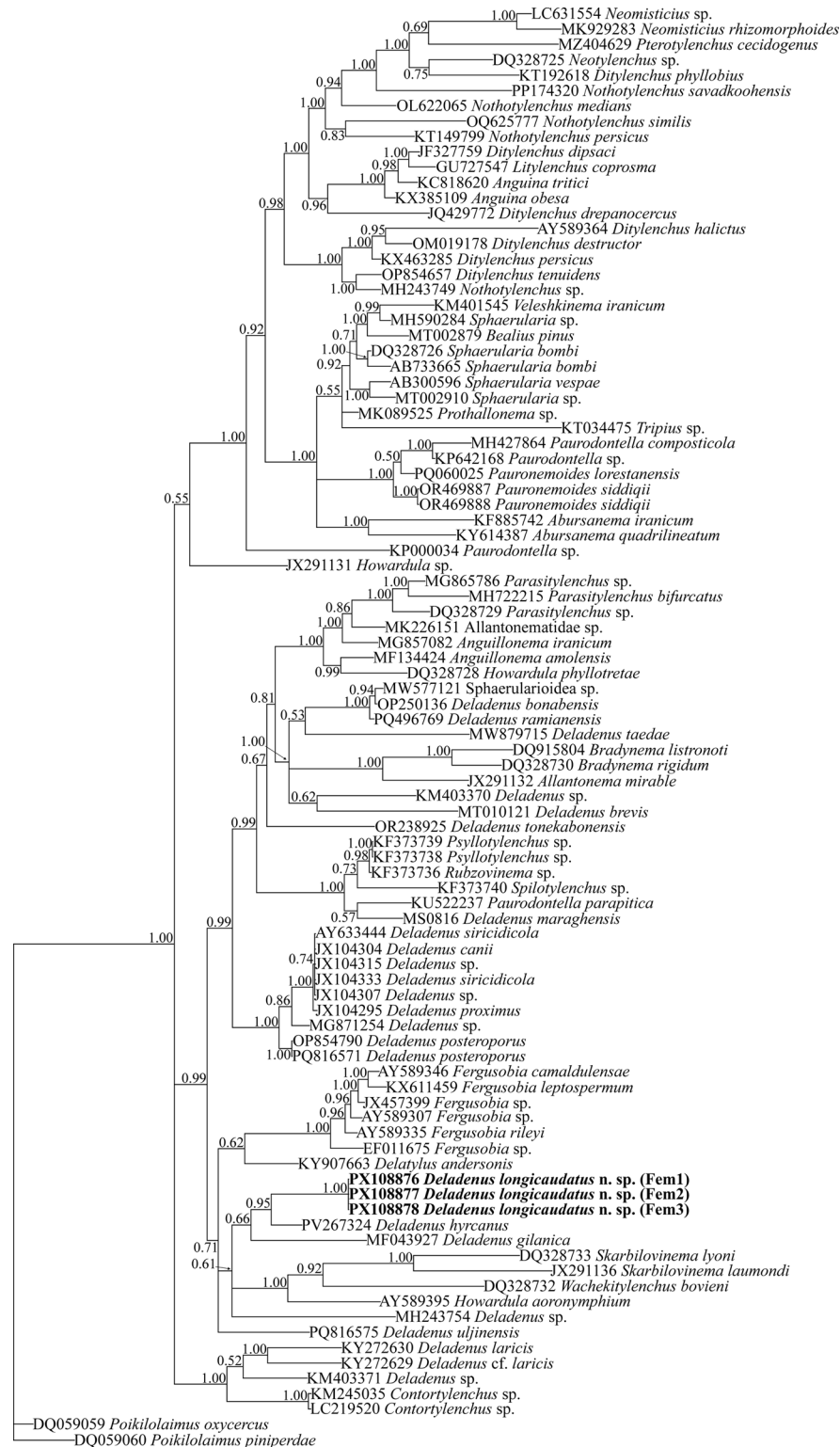


Figure 4. Bayesian 50% majority rule consensus tree of *Deladenus* spp. and other related species from various genera based on LSU rDNA D2–D3 sequences under GTR + I + G model. BPP values more than 0.50 are given for appropriate clades. The newly generated sequences are indicated in bold.

from this dataset. In this tree, LSU sequences assigned to *Deladenus* spp. were scattered across different clades, indicating that the genus is polyphyletic based on the LSU marker and currently available data. The LSU sequences of the new species formed a clade with the corresponding sequence of *Deladenus hyrcanus* (PV267324), and the relationship of this clade with the LSU sequence of *D. gilanica* (MF043927) was not supported (BPP = 0.66).

2.10 Remark

Attempts to amplify the cytochrome c oxidase subunit 1 gene of the new species failed.

3. Discussion

In this study, a new species of the genus *Deladenus* was described and characterized using an integrative approach, combining morphological and molecular data. To date, six species of genus *Deladenus*, characterized by a long conical tail (the c' ratio ≥ 3) ending in a pointed or finely rounded terminus, have been described. Among them, *D. megacondylus* (Mulvey, 1969) Sumenkova, 1975 and *D. saccatus* Andr ssy, 1954 possess a PUS and were therefore excluded from comparisons with the new species. The remaining four species have already been morphologically compared with the new species in diagnosis and relationships.

As emphasized by Rezaei et al. (2025), most species currently placed in the genus *Hexatylus* are poorly described. Although its type species is well delimited by the morphology of its stylet knobs, the descriptions of other species lack details on the basal cephalic sectors and the rectum acting as a feeding tube, which have been emphasized as generic traits by Siddiqi (2000). At the current status, no taxonomic changes are proposed for the species currently placed in *Hexatylus*, as it is beyond the scope of this study.

The reconstructed SSU and LSU phylogenies in the present study revealed that, in line with previous analyses (e.g., Amiri Bonab et al., 2023; Saberi et al., 2025; Ajoudani et al., 2025), ribosomal sequences of *Deladenus* and other sphaerularioid genera do not form monophyletic groups based on the currently available data. Although several independent phylogenetic genera could be proposed based on the varying positions of currently sequenced species in phylogenetic trees, such an action would further complicate the taxonomy of *Deladenus*. In that case, the generic status of *Deladenus*-like species would become entirely dependent on sequencing results. Moreover, the parasitic

stages and molecular data of many species remain unknown or insufficiently studied. Therefore, any tentative revision of *Deladenus* requires additional data in the future. The description of the present new species supports the findings of Saberi et al. (2025), Ajoudani et al. (2025), and Agh Atabai et al. (2025), highlighting the potentially high diversity of the genus *Deladenus* in Iran.

Acknowledgments

The authors gratefully acknowledge the financial support provided by Tarbiat Modares University.

Funding information

Authors state that no funding information.

Author contributions

Mehdi Salemi: Sampling, methodology, writing. Farahnaz Jahanshahi Afshar: Methodology, writing, review and editing, data curation, financial support in part. Mohammad Reza Atighi: Methodology, writing, review and editing, data curation. Majid Pedram: Methodology, writing, review and editing, data curation, resources, project administration, investigation, funding acquisition, conceptualization.

Conflict of interest statement

Authors state no conflict of interest.

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