

Taxonomy & Inventories

Drechslerella daliensis and D. xiaguanensis (Orbiliales, Orbiliaceae), two new nematodetrapping fungi from Yunnan, China

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Abstract

Background

Nematode-trapping fungi are a highly specialised group in fungi and are essential regulators of natural nematode populations. At present, more than 130 species have been discovered in Zygomycota (Zoopagaceae), Basidiomycota (*Nematoctonus*), and Ascomycota (Orbiliaceae). Amongst them, nematode-trapping fungi in Orbiliaceae have become the research focus of carnivorous fungi due to their abundant species. During the investigation of carnivorous fungi in Yunnan, China, four fungal strains isolated from burned forest soil were identified as two new nematode-trapping species in *Drechslerella* (Orbiliaceae), based on multigene phylogenetic analysis and morphological characters.

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New information

Drechslerella daliensis sp. nov. is characterised by its ellipsoid, 1–2-septate macroconidia, clavate or bottle-shaped, 0–1-septate microconidia and unbranched, simple conidiophores. *D. xiaguanensis* sp. nov. is characterised by fusiform or spindle-shaped, 2–4-septate conidia and unbranched, simple conidiophores. Both of them produce constricting rings to capture nematodes. The phylogenetic analysis, based on combined ITS, TEF1-α and RPB2 sequences, determined their placement in *Drechslerella*. *D. daliensis* forms a basal lineage closely nested with *D. hainanensis* (YMF1.03993). *D. xiaguanensis* forms a sister lineage with *D. bembicodes* (1.01429), *D. aphrobrocha* (YMF1.00119) and *D. coelobrocha* (FWY03-25-1).

Keywords

carnivorous fungi, constricting rings, new species, Orbiliaceae, taxonomy

Introduction

Nematode-trapping fungi are important predators that capture nematodes by specialised trap structures (Barron 1977, Li et al. 2006, Swe et al. 2011, Zhang and Hyde 2014). They play vital roles in maintaining energy balance and nutrient cycles in soil ecosystems and exhibit great potential for biocontrol application in agricultural management (Cooke 1962, Ulzurrun and Hsueh 2018, Zhang et al. 2020a). Most nematode-trapping fungi belong to Orbiliaceae, which have been extensively studied due to their abundant species and sophisticated trapping devices (Linford et al. 1938, Jaffee et al. 1993, Wolstrup et al. 1996, Jaffee et al. 1998, Morton et al. 2003, Liu et al. 2009, El-Borai et al. 2011, Kumar et al. 2011, Swe et al. 2011, Vilela et al. 2012). Currently, 116 predatory species in Orbiliaceae have been reported (Glockling and Dick 1994, Li et al. 2006, Wu et al. 2012, Li et al. 2013, Liu et al. 2014, Zhang and Hyde 2014, Quijada et al. 2020, Zhang et al. 2020, Zhang et al. 2020b, Zhang et al. 2022). They are classified into three genera according to their types of trapping structure: 1) Arthrobotrys (67 species), catching nematodes using adhesive networks; 2) Dactylellina (34 species), capturing nematodes by adhesive knobs, adhesive branches and non-constricting rings and 3) DrechsleIrella (15 species), trapping nematodes with constricting rings (Scholler et al. 1999, Li et al. 2005, Yang et al. 2007, Zhang and Hyde 2014).

Drechslerella was established by Subramanian (1963) with the type species *D. acrochaeta* (Drechsler) Subram. It is a small genus separated from *Monacrosporium*, based on conidia producing filamentous appendages at the apex, which are lacking in *Monacrosporium*. However, filamentous appendages are usually produced when conidia germinate and are also commonly found in some species of *Arthrobotrys*. Therefore, Liu and Zhang (1994) treated *Drechslerella* as a synonym of *Monacrosporium*, based on their similar conidial morphology. Subsequently, the generic concept of nematode-trapping fungi in Orbiliaceae

was revised, based on molecular phylogenetic analysis. Drechslerella is characterised by producing constricting rings to capture nematodes (Liou and Tzean 1997, Pfister 1997, Ahren et al. 1998, Scholler et al. 1999, Li et al. 2005). Drechslerella currently includes 15 accepted species, 13 of which have been reported in China (Zhang and Mo 2006, Zhang and Hyde 2014). They mainly occur in the soil or sediment of various ecosystems such as forests, mangroves, freshwater, brackish water, heavy metal polluted areas and even in tree trunks and animal faeces (Jansson and Autery 1961, Hao et al. 2005, Mo et al. 2006, Su et al. 2007, Swe et al. 2009, Zhang and Hyde 2014, She et al. 2020, Zhang et al. 2020). In soil, Drechslerella species are mainly distributed in the upper litter and humus layer and closely related to the density of soil nematodes (Burges and Raw 1967, Gray and Bailey 1985, Zhang and Hyde 2014). Drechslerella species lack nematodes mainly by the rapid expansion of the three cells that make up the constricting ring. This method of trapping nematodes mainly by mechanical force is significantly different from that of species in Arthrobotrys and Dactylellina (capture nematodes mainly with adhesive material) (Zhang and Mo 2006, Zhang and Hyde 2014). Therefore, Drechslerella is the most special genus amongst Orbiliaceae NTF and it is also a key group in studying the origin and evolution of carnivorous fungi.

The studies of nematode-trapping fungi have been poorly addressed in extreme habitats (Onofri and Tosi 1992, Mo et al. 2008, Swe et al. 2008). Our previous research investigated the succession of nematode-trapping fungi after fire disturbance in forests in China (She et al. 2020). Four strains were isolated and identified as two new nematode-trapping fungi in Orbiliaceae. The aim of this study is to introduce these two new species, *D. daliensis* and *D. xiaguanensis*, based on morphology and phylogenetic evidence. The discovery of these two species increased the diversity of nematode-trapping fungi and provided more valuable materials for studying the evolution and origin of carnivorous fungi, as well as more potential species for the biological control of plant and animal parasitic nematodes.

Materials and methods

Samples collection, isolation and morphology

The soil samples were collected from a burned forest in Cangshan Mountain, Dali City, Yunnan Province, China (100°07'44"N, 25°45'49"E). The sampling site information has been described by She et al. (2020). About 100 g of soil was collected from 10–20 cm depth using a 35 mm-diameter soil borer. The soil sample was placed into a zip lock bag and samples were brought back to the laboratory and stored at 4°C until processing.

The soil samples were sprinkled on corn meal agar (CMA) plates with sterile toothpicks. Free-living nematodes (*Panagrellus redivivus* Goodey) were added as bait to promote the germination of nematode-trapping fungi. After three weeks of incubation at 26°C, the plates were observed under a stereomicroscope to find the spores of nematode-trapping fungi. A single spore was transferred to a fresh CMA plate using a sterile toothpick, repeating this step until the pure culture was obtained.

Fungal isolates were transferred to fresh potato dextrose agar plate (PDA) using a sterile toothpick and incubated at 26°C for colony characteristics observation. The pure cultures were transferred to fresh CMA observation plates (an observation well of 2×2 cm was made by removing the agar from the centre of the CMA plate) and incubated at 26°C. When the mycelium overspread the observation well, about 500 nematodes (*P. redivivus*) were added to the well to induce the formation of trapping devices. The types of trapping devices were checked using a stereomicroscope. All morphological characters were captured and measured with an Olympus BX53 microscope (Olympus Corporation, Japan).

DNA extraction, PCR amplification and sequencing

The genomic DNA was extracted from the mycelium grown on PDA plates according to the method described by Jeewon et al. (2002). The primer pairs ITS4-ITS5 (White et al. 1990), 526F-1567R (O'Donnell et al. 1998) and 6F-7R (Liu et al. 1999) were used to amplify the ITS, TEF1-α and RPB2 genes, respectively. The PCR amplification was performed as follows: 4 minutes of pre-denaturation at 94°C, followed by 35 cycles of 45 seconds of denaturation at 94°C, 1 minute of annealing at 52°C (ITS), 55°C (TEF1-α), 54°C (RPB2), 1.5-2 minutes of extension at 72°C and a final extension of 10 minutes at 72°C. The PCR products were purified with a DiaSpin PCR Product Purification Kit (Sangon Biotech Company, Limited, Shanghai, China). ITS and RPB2 genes were sequenced in forward and reverse directions using PCR primers and the TEF1-α region was sequenced using the 247F-609R primer pair (Yang et al. 2007) (BioSune Biotech Company, Limited, Shanghai, China).

Phylogenetic analysis

The sequences generated in this study were compared against the NCBI GenBank database using BLASTn (BLASTn; https://blast.ncbi.nlm.nih.gov/Blast.cgi?PROGRAM= blastn&PAGE TYPE=BlastSearch&LINK LOC=blasthome; accessed on 16 July 2022). The morphological and BLASTn search results placed these two species in the genus Drechslerella. Drechslerella were searched in the Index Fungorum (http:// www.indexfungorum.org; accessed on 16 August 2022) and Species Fungorum (http:// www.speciesfungorum.org; accessed on 16 August 2022) and all relevant records were checked individually according to the relevant documents to ensure that all Drechslerella taxa were considered in this study (Li et al. 2013, Zhang and Hyde 2014). All reliable ITS, TEF1-α and RPB2 sequences of *Drechslerella* taxa were downloaded from the GenBank database (Table 1). The three genes datasets (including our two new species) were aligned using MAFFT online version (Madeira et al. 2022, https://www.ebi.ac.uk/Tools/msa/ mafft/), then manually adjusted and linked via BioEdit v.7.2.3 (Hall 1999) and MEGA6.0 (Tamura et al. 2013). Dactylaria sp. YNWS02-7-1 and Vermispora fusarina YXJ02-13-5 were selected as outgroups (Yang et al. 2007). Phylogenetic trees were inferred with Maximum Likelihood (ML), Maximum Parsimony (MP) and Bayesian Inference analyses (BI).

Table 1.

GenBank accession numbers of isolates included in this study. The type strains are marked with T at the end of the strain number. The newly-generated sequences are indicated in bold.

| Таха | Strain numbers | GenBank accession numbers | | | Reference |
|----------------------------|-------------------------|---------------------------|-----------------|-----------------|------------------------------|
| | | ITS | TEF1-α | RPB2 | |
| Arthrobotrys conoides | YMF1.00009 | MF948387 | MF948544 | MF948468 | Unpublished |
| Arthrobotrys guizhouensis | YMF1.00014 ^T | MF948390 | MF948547 | MF948471 | Unpublished |
| Arthrobotrys shizishanna | YMF1.00022 | MF948392 | MF948549 | MF948473 | Unpublished |
| Dactylaria sp. | YNWS02-7-1 | AY773457 | AY773399 | AY773428 | Yang et al. (2007) |
| Dactylellina appendiculata | CBS 206.64 ^T | <u>AF106531</u> | DQ358227 | DQ358229 | Hagedorn and Scholler (1999) |
| Dactylellina copepodii | CBS 487.90 ^T | U51964 | DQ999835 | DQ999816 | Liou and Tzean (1997) |
| Dactylellina mammillata | CBS229.54 ^T | AY902794 | DQ999843 | DQ999817 | Li et al. (2006) |
| Dactylellina yushanensis | CGMCC 3.19713 | MK372061 | MN915113 | MN915112 | Zhang et al. (2020) |
| Drechslerella anchonia | CBS109.37 | AY965753 | | | Li et al. (2006) |
| Drechslerella aphrobrocha | YMF1.00119 | MF948397 | | MF948477 | Unpublished |
| Drechslerella bembicodes | 1.01429 | MH179731 | | MH179835 | Unpublished |
| Drechslerella brochopaga | 701 | AY773456 | <u>AY773398</u> | <u>AY773427</u> | Yang et al. (2007) |
| Drechslerella brochopaga | 1.01829 | MH179750 | | MH179852 | Unpublished |
| Drechslerella brochopaga | CBS218.61 | U51950 | | | Liou and Tzean (1997) |
| Drechslerella brochopaga | ATCC 96710 | EF445987 | | | Smith and Jaffee (2009) |
| Drechslerella brochopaga | DHP 212 | U72609 | | | Pfister (1997) |
| Drechslerella brochopaga | BCRC 34361 | FJ380936 | | | Zhang et al. (2020b) |
| Drechslerella brochopaga | H.B.9925 | KT222412 | | | Zhang et al. (2020b) |
| Drechslerella brochopaga | H.B.9965 | KT380104 | | | Zhang et al. (2020b) |
| Drechslerella brochopaga | 6178 | DQ656615 | | | Zhang et al. (2020b) |
| Drechslerella coelobrocha | FWY03-25-1 | AY773464 | <u>AY773406</u> | <u>AY773435</u> | Yang et al. (2007) |
| Drechslerella coelobrocha | 1.0148 | MH179744 | | MH179847 | Unpublished |
| Drechslerella dactyloides | 1.00031 | MH179690 | MH179554 | MH179799 | Unpublished |
| Drechslerela dactyloides | expo-5 | AY773463 | <u>AY773405</u> | <u>AY773434</u> | Yang et al. (2007) |
| Drechslerella dactyloides | 1.00131 | MH179705 | | MH179813 | Unpublished |

| Taxa | Strain numbers | GenBank accession numbers | | | Reference |
|-------------------------------|----------------|---------------------------|-----------------|----------|-----------------------|
| | | ITS | TEF1-α | RPB2 | |
| Drechslerella daliensis | CGMCC 3.20131 | MT592896 | OK556701 | OK638157 | This study |
| Drechslerella daliensis | DLU22-1 | OK643974 | OK556700 | OK638158 | This study |
| Drechslerella doedycoides | YMF1.00553 | MF948401 | | MF948481 | Unpublished |
| Drechslerella doedycoides | CBS 586.91 | MH862283 | | | Vu et al. (2019) |
| Drechslerella doedycoides | CBS175.55 | MH857432 | | | Liou and Tzean (1997) |
| Drechslerella effusa | YMF1.00583 | MF948405 | MF948557 | MF948484 | Unpublished |
| Drechslerella effusa | CBS 774.84 | MH861835 | | | Vu et al. (2019) |
| Drechslerella hainanensis | YMF1.03993 | KC952010 | | | Li et al. (2013) |
| Drechslerella heterospora | YMF1.00550 | MF948400 | MF948554 | MF948480 | Unpublished |
| Drechslerella polybrocha | CBS 319.56 | MH857657 | | | Vu et al. (2019) |
| Drechslerella polybrocha | CCRC 32872 | U51973 | | | Vu et al. (2019) |
| Drechslerella polybrocha | DHP 133 | U72606 | | | Zhang et al. (2020b) |
| Drechslerella polybrocha | H.B. 8317 | KT222361 | | | Unpablished |
| Drechslerella stenobrocha | YNWS02-9-1 | AY773460 | <u>AY773402</u> | AY773431 | Yang et al. (2007) |
| Drechslerella xiaguanensis | CGMCC 3.20132 | MT592900 | OK556699 | OK638159 | This study |
| Drechslerella xiaguanensis | DLU23-1 | OK643975 | OK556698 | OK638160 | This study |
| Drechslerella yunnanensis | 1.01863 | MH179759 | | MH179861 | Unpublished |
| Drechslerella yunnanensi | YMF1.03216 | HQ711927 | | | Yu et al. (2009) |
| Vermispora fusarina | YXJ02-13-5 | AY773447 | AY773389 | AY773418 | Yang et al. (2007) |

SYM+I+G, GTR+I+G and GTR+I+G models were selected as best-fit optimal substitution models for ITS, TEF1- α and RPB2, respectively, via jModelTest v.2.1.10 (Posada 2008) under the Akaike Information Criterion (AIC).

MrBayes v. 3.2.6. (Huelsenbeck and Ronquist 2001) was used to perform the Bayesian Inference (BI) analysis. The multiple sequence alignment file was converted into the MrBayes compatible NEXUS file via Fasta Convert (Hall 2005). The dataset was partitioned and the optimal substitution models of each gene were equivalently replaced to conform to the setting of MrBayes. Six simultaneous Markov Chains were run for 10,000,000 generations and trees were sampled every 100 generations (a total of 100,000 trees). The first 25% of trees were discarded and the remaining trees were used to calculate the posterior probabilities (PP) in the majority rule consensus tree. All the above parameters are edited into the MrBayes block in the NEX file.

IQ-Tree v.1.6.5 (Nguyen et al. 2014) was used to perform the Maximum Likelihood (ML) analysis. The dataset was partitioned and each gene was analysed with its corresponding model. The rapid bootstrapping method with 1000 replicates (Felsenstein 1985) was used to compute the bootstrap support values (BS).

Maximum Parsimony (MP) analysis was performed via the web CIPRES Science Gateway v. 3.3 (Miller et al. 2010, https://www.phylo.org) by PAUP 4. a168 on XSEDE using the heuristic search option with 1000 random sequence additions. Max-trees were set up at 5000 and no increase. Clade stability was assessed using a bootstrap analysis with 1,000 replicates (Felsenstein 1985). Descriptive tree statistics tree length (TL), consistency index (CI), retention index (RI), rescaled consistency index (RC) and homoplasy index (HI) were calculated for all trees generated under different optimality criteria. All the above parameters are edited into the PAUP block in the NEX file.

The trees were visualised with FigTree v.1.3.1 (Rambaut 2009). The backbone tree was edited and reorganised by Microsoft PowerPoint (2013) and Adobe Photoshop CS6 software (Adobe Systems, USA). Sequences derived from this study were deposited in GenBank (Table 1).

Taxon treatments

Drechslerella daliensis Fa Zhang, Xiao-Yan Yang, Kevin D Hyde, sp. nov.

- IndexFungorum http://www.indexfungorum.org/Names:IF558120
- Species-ID <u>Facesoffungi number:FOF 10565</u>

Materials

Holotype:

a. scientificName: *Drechslerella daliensis*; kingdom: Fungi; phylum: Ascomycota; class: Orbiliomycetes; order: Orbiliales; family: Orbiliaceae; taxonRank: species; genus: *Drechslerella*; specificEpithet: *daliensis*; scientificNameAuthorship: Fa Zhang, Xiao-Yan Yang, Kevin D. Hyde; country: China; countryCode: CHN; stateProvince: Yunnan; county: Dali; locationRemarks: China, Yunnan Province, Dali City, Cangshan Mountain, burned forest soil, 25 July 2017; occurrenceRemarks: Isolated from burned forest soil; identifiedBy: Fa Zhang; language: English; collectionID: CGMCC3.20131; occurrenceID: 82BE156C-BBA2-57F5-B468-EA13407B9F19

Isotype:

a. scientificName: Drechslerella daliensis; kingdom: Fungi; phylum: Ascomycota; class: Orbiliomycetes; order: Orbiliales; family: Orbiliaceae; taxonRank: Species; genus: Drechslerella; specificEpithet: daliensis; country: China; countryCode: CHN; stateProvince: Yunnan Province; county: Dali; locationRemarks: China, Yunnan Province, Dali City, burned forest soil; occurrenceRemarks: Isolated from burned forest soil; identifiedBy: Fa Zhang; language: English; collectionID: DLU22-1; occurrenceID: 9A5F7D25-49A6-5CC9-925B-595C9BB01673

Description

Colonies white, cottony, slow-growing on PDA medium, reaching 50 mm diameter after 18 days at 26°C. **Mycelium** hyaline, septate, branched, smooth. **Conidiophores** 125–335 µm (\overline{x} = 216.5 µm, n = 50) long, 3–6.5 µm (\overline{x} = 4.5 µm, n = 50) wide at the base, 2–3.5 µm (\overline{x} = 3 µm, n = 50) wide at the apex, hyaline, erect, septate, unbranched, bearing a single conidium at the apex. Conidia two types: **Macroconidia** 20–49.5 × 8.5–15 µm (\overline{x} = 38.5–12 µm, n = 50), hyaline, smooth, ellipsoid, broadly rounded at the apex, truncate at the base, 1–2-septate, mostly 2-septate. **Microconidia** 6.5–22 × 3.5–7 µm (\overline{x} = 15.5–5 µm, n = 50), hyaline, smooth, clavate or bottle-shaped, broadly rounded at the apex, truncate at the base, 0–1-septate. **Chlamydospores** not observed. Capturing nematodes with three-celled **constricting rings**, in the nonconstricted state, the outer diameter is 21–32 µm (\overline{x} = 26 µm, n = 50), the inner diameter is 12–21 µm (\overline{x} = 15.5 µm, n = 50) stalks 5.5–11 µm (\overline{x} = 8.5µm, n = 50) long and 4–6.5 µm (\overline{x} = 5µm, n = 50) wide (Fig. 1).

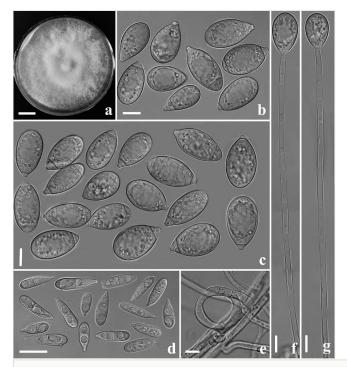


Figure 1. doi

Drechslerella daliensis (holotype, CGMCC3.20131). **a** Culture colony; **b**, **c** Macroconidia; **d** Microconidia; **e** Constricting rings; **f**, **g** Conidiophores. Scale bars: $\mathbf{a} = 1$ cm; $\mathbf{b} - \mathbf{g} = 10$ μ m.

Diagnosis

D. daliensis differs from D. hainanensis by its thinner macroconidia and shorter microconidia.

Etymology

The species name "daliensis" refers to the locality (Dali) of the type specimen.

Distribution

China, Yunnan Province, Dali City, from burned forest soil.

Drechslerella xiaguanensis Fa Zhang, Xiao-Yan Yang, Kevin D. Hyde, sp. nov.

- IndexFungorum http://www.indexfungorum.org/Name:IF558121
- Species-ID <u>Facesoffungi number: FOF10566</u>

Materials

Holotype:

a. scientificName: Drechslerella xiaguanensis; kingdom: Fungi; phylum: Ascomycota; class: Orbiliomycetes; order: Orbiliales; family: Orbiliaceae; taxonRank: Species; genus: Drechslerella; specificEpithet: xiaguanensis; scientificNameAuthorship: Fa Zhang, Xiao-Yan Yang, Kevin D. Hyde; country: China; countryCode: CHN; stateProvince: Yunnan; county: Dali; locationRemarks: China, Yunnan Province, Dali City, Cangshan Mountain, burned forest soil, 25 July 2017; occurrenceRemarks: Isolated from burned forest soil; identifiedBy: Fa Zhang; language: English; collectionID: CGMCC3.20132; occurrenceID: 7D732B1B-4091-549C-97B3-64CC0D42FFC0

Isotype:

a. scientificName: Drechslerella xiaguanensis; kingdom: Fungi; phylum: Ascomycota; class: Orbiliomycetes; order: Orbiliales; family: Orbiliaceae; taxonRank: Species; genus: Drechslerella; specificEpithet: xiaguanensis; country: China; countryCode: CHN; stateProvince: Yunnan Province; county: Dali; locationRemarks: China, Yunnan Province, Dali City, Cangshan Mountain, burned forest soil; occurrenceRemarks: Isolated from burned forest soil; identifiedBy: Fa Zhang; language: English; collectionID: DLU23-1; occurrenceID: A14AF229-0901-5266-92D8-8950A34DCCDF

Description

Colonies white, cottony, slow-growing on PDA medium, reaching 50 mm diameter after 15 days at 26° C. **Mycelium** hyaline, smooth, septate, branched. **Conidiophores** $145-315 \ \mu m \ (\overline{x}=208.5 \ \mu m, \ n=50) \ long, 3-6 \ \mu m \ (\overline{x}=4 \ \mu m, \ n=50) \ wide at the base, 2-3 \ \mu m \ (\overline{x}=2.5 \ \mu m, \ n=50) \ wide at the apex, hyaline, erect, septate, unbranched, bearing a single conidium at the apex.$ **Conidia** $<math>33-52\times9.5-28\ \mu m \ (\overline{x}=42.5-15.5\ \mu m, \ n=50)$, hyaline, smooth, fusiform, spindle-shaped, rounded and swollen at the both ends, 2-4-septate, mostly 3-septate, germinating tubes produced from both ends. **Chlamydospores** not observed. Capturing nematodes with three-celled **constricting rings**, in the non-constricted state, the outer diameter is $19-27.5 \ \mu m \ (\overline{x}=24 \ \mu m, \ n=50)$, the inner diameter is $12.5-20.5 \ \mu m \ (\overline{x}=17 \ \mu m, \ n=50)$, stalks $5-11.5 \ \mu m \ (\overline{x}=9 \ \mu m, \ n=50)$ long and $4.5-6 \ \mu m \ (\overline{x}=5 \ \mu m, \ n=50)$ wide (Fig. 2).

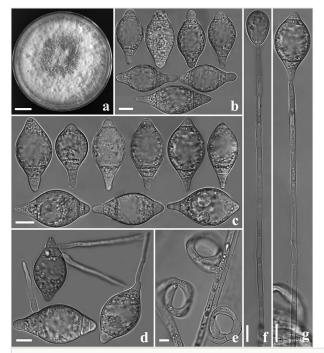


Figure 2. doi Drechslerella xiaguanensis (holotype, CGMCC3.20132). a Culture colony; b, c Conidia; d Germinating conidia; e Constricting rings; f, g Conidiophore. Scale bars: a = 1 cm; b-g = 10 μ m.

Diagnosis

D. xiaguanensis differs from D. aphrobrocha by its smaller conidia and swollen cells at both ends of conidia.

Etymology

The species name "xiaguanensis" refers to the locality (Xiaguan) of the type specimen.

Distribution

China, Yunnan Province, Dali City, Cangshan Mountain, from burned forest soil.

Analysis

Phylogenetic analyses

A total of 15 *Drechslerella* related taxa were listed in Index Fungorum (http://www.indexfungorum.org; accessed on 16 August 2022) and Species Fungorum (http://www.indexfungorum.org; accessed on 16 August 2022) and Species Fungorum (http://www.indexfungorum.org; accessed on 16 August 2022) and Species Fungorum (http://www.indexfungorum.org; accessed on 16 August 2022) and Species Fungorum (http://www.indexfungorum.org; accessed on 16 August 2022) and Species Fungorum (http://www.indexfungorum.org; accessed on 16 August 2022) and Species Fungorum (http://www.indexfungorum.org; accessed on 16 August 2022) and Species Fungorum.

www.speciesfungorum.org; accessed on 16 August 2022), representing 15 valid *Drechslerella* species. Amongst them, 13 species have available molecular data. The combined ITS, TEF1-α and RPB2 sequence dataset contained 42 nematode-trapping taxa in Orbiliaceae (3 *Arthrobotrys* species, 4 *Dactylellina* species and 35 *Drechslerella* taxa representing 15 species). The final dataset comprised 1939 characters (ITS = 591, TEF1-α = 534 and RPB2 = 814), including 807 conserved characters, 1072 variable characters and 748 parsimony-informative characters. After Maximum Likelihood (ML) analysis, a best-scoring likelihood tree was obtained with a final ML optimisation likelihood value of -7146.589745. For Bayesian analysis (BI), the first 25% of trees were discarded in a burn-in period, the consensus tree was calculated with the remaining trees and the Bayesian posterior probabilities were evaluated with a final average standard deviation of the split frequency of 0.009547. Within Maximum Parsimony (MP) analysis, a strict consensus tree was obtained from the two equally most parsimonious trees (TL = 2817, CI = 0.471, RI = 0.514, RC = 0.296, HI = 0.404). The trees inferred by ML, MP and BI showed similar topologies. Therefore, the best-scoring ML tree was selected for presentation (Fig. 3).

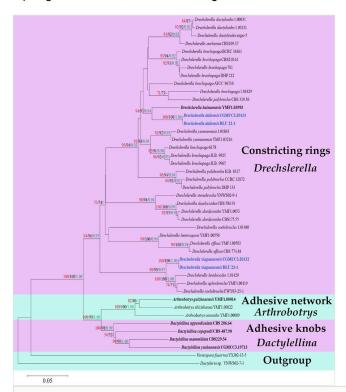


Figure 3. doi

Maximum Likelihood tree, based on combined ITS, TEF1- α and RPB2 sequence data from 42 nematode-trapping taxa in Orbiliaceae. Bootstrap support values for Maximum Parsimony (red) and Maximum Likelihood (black) equal or greater than 50% and Bayesian posterior probabilities values (green) greater than 0.90 are indicated above the nodes. New isolates are in blue, ex-type strains are in bold.

The phylogram inferred from the ITS+TEF1-α+RPB2 dataset clustered 42 Orbiliaceae nematode-trapping fungi into two large clades according to their mechanisms for catching nematodes: 1) The genus *Drechslerella* that captures nematodes by mechanical force (Zhang and Hyde 2014); 2) The genera *Arthrobotrys* and *Dactylellina* capture nematode by adhesive material (Zhang and Hyde 2014). Our two new species *D. daliensis* and *D. xiaguanensis* clustered in *Drechslerella* with high statistical support. *D. daliensis* forms a basal lineage closely nested with *D. hainanensis* (YMF1.03993) with 94% MPBS, 93% MLBS and 0.94 BYPP support. *D. xiaguanensis* forms a sister lineage with *D. bembicodes* (1.01429), *D. aphrobrocha* (YMF1.00119) and *D. coelobrocha* (FWY03-25-1) with 98% MPBS, 99% MLBS and 0.97 BYPP support (Fig. 3).

Discussion

Drechslerella daliensis and *D. xiaguanensis* produce constricting rings to capture nematodes, which is consistent with the genus *Drechslerella* (Zhang and Hyde 2014). The multi-genes phylogenetic analysis also confirmed that they are members of *Drechslerella*.

Phylogenetically, D. daliensis (CGMCC3.20131) forms a sister lineage to D. hainanensis (YMF 1.03993) with 97% MLBS, 96% MPBS and 0.95 BYPP support (Fig. 3). A comparison of ITS nucleotide shows 10.15% difference (60/591 bp) between them. Morphologically, amongst 17 species in Drechslerella (plus our two new species), D. daliensis, D. effusa, D. hainanensis and D. heterospora produce ellipsoid 0-3 septate conidia (Li et al. 2013, Zhang and Hyde 2014). The difference between D. daliensis and D. effusa is that the conidiophores of *D. daliensis* produce only a single conidium at the apex, while the conidiophores of D. effusa usually bear two or more conidia (Zhang and Hyde 2014). D. daliensis can be easily distinguished from D. heterospora by their microconidia size and the apex characteristic of conidiophore: the microconidia of D. daliensis are significantly smaller than those of D. heterospora (6.5–22 \times 3.5–7 μm vs. 23–40 \times 5.3–8 µm), the conidiophores of D. heterospora usually swollen and spherical at the apex, while those of D. daliensis are not swollen. In addition, D. daliensis does not produce chlamydospores, while D. heterospora produces chlamydospores in chains (Zhang and Hyde 2014). It is challenging to distinguish D. daliensis and D. hainanensis according to their shape characteristics. The difference between them is that the macroconidia of D. daliensis are thinner than those of D. hainanensis (20-49.5 × 8.5-15 µm vs. 32.5-43 × 17-25 µm) and the microconidia are shorter than those of D. hainanensis (6.5–22 × 3.5–7 µm vs. $18.2-22.8 \times 4.2-5.3 \mu m$) (Li et al. 2013).

In the phylogenetic analysis, *D. xiaguanensis* (CGMCC3.20131) forms a sister lineage to *D. bembicodes* (1.01429), *D. aphrobrocha* (YMF1.00119) and *D. coelobrocha* (FWY03-25-1) with 100% MLBS, 100% MPBS and 1.00 BYPP support (Fig. 3). Comparison of ITS nucleotide shows 2.6% (15/577 bp), 5.2% (30/577 bp) and 3.6% (20/556 bp) between *D. xiaguanensis* and *D. bembicodes*, *D. aphrobrocha* and *D. coelobrocha*, respectively. Morphologically, they can be distinguished by their conidia size: the conidia of *D. xiaguanensis* are thinner than those of *D. bembicodes*, shorter than those of *D. coelobrocha* and smaller than those of *D. aphrobrocha* (*D. xiaguanensis* 33–52 (42.5)

 \times 9.5–28 (15.5) μm vs. *D. bembicodes* 36–43.2 (40) \times 16.8–21.6 (20.5) μm vs. *D. coelobrocha* 45.6–55.2 (49.5) \times 16.8–21.6 (19.8) μm vs. *D. aphrobrocha* 40–57.5 (51) \times 15.5–35 (24.6) μm). In addition, the cells at both ends of some conidia of *D. xiaguanensis* are swollen, while *D. bembicodes*, *D. aphrobrocha* and *D. coelobrocha* are not (Drechsler 1950, Zhang and Mo 2006, Zhang and Hyde 2014). Based on the above, we propose *D. daliensis* and *D. xiaguanensis* as two new species of *Drechslerella*.

Amongst nematode-trapping fungi, species in Arthrobotrys are the dominant group in most ecosystems due to their strong reproductive and saprophytic ability, while the species in Dactylellina and Drechslerella, with weaker competitive abilities were rare (Jaffee et al. 1998, Hao et al. 2005, Elshafie et al. 2006, Su et al. 2007, Mo et al. 2008, Yang et al. 2008, Swe et al. 2009, Wachira et al. 2009, Yang et al. 2011). However, many species of Dactylellina and Drechslerella have been isolated from the burning forest in Cangshan, Yunnan (She et al. 2020). Amongst them, two new Dactylellina species (Zhang et al. 2020) and two new Drechslerella species (this paper) have been identified. We speculate that the reasons for this unusual phenomenon may be as follows: in normal habitat, Arthrobotrys species usually occupy the main living resources and are mainly distributed in the upper soil where humus, air and space are abundant due to their strong reproductive and saprophytic ability, while those species of Dactylellina and Drechslerella are mainly distributed in the lower soil where humus is scarce. When a fire occurs, Arthrobotrys species distributed in the upper soil are more vulnerable to the fire and are wiped out and then the habitat plaques form. In contrast, the rare species distributed in the lower layer are protected by the upper soil and preserved. In the subsequent recovery stage, these species can grow in large numbers and occupy the habitat plaque to form the dominant population in the area. Based on the above, we speculate that we would find more rare nematode-trapping fungi in burned forests. In addition, according to this principle, we speculate that other saprophytic fungi also have similar laws. Further research is underway and will be reported later.

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