Oxydothis ailaoshanensis **sp. nov. (Oxydothidaceae, Xylariales) from dead bamboo culms in Yunnan Province, China**

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Abstract

During the investigation of ascomycetes on Poaceae in Yunnan Province, China, a fungus was collected from dead bamboo culms in a terrestrial habitat in the Ailaoshan subtropical evergreen broad-leaved forest. Based on morphological characterization and phylogenetic analyses, this fungus was introduced as *Oxydothis ailaoshanensis* sp. nov*.* Maximum likelihood and Bayesian inference analyses of a concatenated dataset of internal transcribed spacer (ITS), large subunits (LSU) of the nuclear ribosomal RNA gene, small subunit (SSU) of the nuclear ribosomal RNA gene, and translation elongation factor 1-alpha (*tef*1-*α*) sequences were performed to clarify the phylogenetic affinities of the new species. Phylogenetically, *Oxydothis ailaoshanensis* forms an independent lineage, basal to *O. metroxylonis*. *Oxydothis ailaoshanensis* differs from *O. metroxylonis* in having smaller, immersed ascomata that become raised and superficial with the long axis horizontal to the host surface, shorter asci that are mostly straight, and longer ascospores that are elongated and fusiform. The new species was justified based on morphological traits and multigene phylogenetic analyses in comparison with closely related species. A detailed description, micrograph, and a phylogenetic tree of the new species are provided.

Citation: Dissanayake LS, Phookamsak R, Xu J, Wanasinghe DN. 2024. *Oxydothis ailaoshanensis* sp. nov. (Oxydothidaceae, Xylariales) from dead bamboo culms in Yunnan Province, China. *Studies in Fungi* 9: e016 [https://doi.org/10.48130/s](https://doi.org/10.48130/sif-0024-0016)i[f-0024-0016](https://doi.org/10.48130/sif-0024-0016)

Introduction

China is recognized as the most diverse country for bamboo, with 43 genera and 728 species^{[[1\]](#page-7-0)}. Southwest China, particularly Yunnan Province is the richest area of bamboo diversity in the country, accounting for 50% of all bamboo species diversity^{[[2\]](#page-7-1)}. Yunnan has three types of bamboo forests viz. cold-temperate, temperate, and tropical bamboo forests^{[\[3\]](#page-7-2)}. Since 2017, many studies of bambusicolous fungi have been conducted in Yunnan^{[[2](#page-7-1)[,4](#page-7-3)–10]}. However, studies on bambusicolous fungi in this region remain limited compared to other regions such as Hong Kong and Taiwan^{[[2,](#page-7-1)[11\]](#page-7-5)}. Among these studies, Xylariales has been relatively under-researched in Yunnan (comprising 14% of known species), compared to Pleosporales (39% of known species). Nonetheless, Sordariomycetes has emerged as the largest group of Ascomycota found on bamboo[\[2](#page-7-1)] .

The genus *Oxydothis* was introduced by Penzig & Saccardo^{[[12](#page-7-6)]} to initially accommodate three species (viz. *O*. *grisea*, *O*. *maculosa*, and *O*. *nigricans*) within the Amphisphaeriaceae, with *O*. *grisea* designated as the type species. The taxonomic placement of *Oxydothis* has been subject to extensive historical discussion[[13](#page-7-7)−[21](#page-7-8)] . A comprehensive study of *Oxydothis* was carried out by Konta et al.^{[[20](#page-7-9)]} who introduced Oxydothidaceae to accommodate the genus *Oxydothis* within Xylariales. Species of *Oxydothis* are characterized by solitary or aggregated ascomata that form in large groups, appearing as darkened, raised regions or dots on the host surface, and cylindrical asci with a

tion[[20](#page-7-9),[22](#page-7-10)] . The asexual morph of *Oxydothis* has been linked to Selenosporella species by Samuels & Rossman^{[[23](#page-7-11)]}, although the sexual-asexual connection between *Oxydothis* and *Selenosporella* remains unproven. Furthermore, Samuels & Rossman^{[[23](#page-7-11)]} reported that the asexual morph of *O. selenosporellae* sporulated *in vitro*, producing black stromatic masses with perithecia developing throughout the colony. This morph displays macronematous, mononematous conidiophores that are (1–)2–3 septate, unbranched or branched, brown to olivaceous, with finely denticulate conidiogenous cells. A minute refractive scar remains after the conical dehiscence, and the conidia are arcuate, hyaline, and unicellular. *Oxydothis* is a common genus mainly found on monoco-

J+ (rarely J-) subapical apparatus. The ascospores are filiform to fusiform, hyaline, 1-septate, and have pointed or blunt ends. In some species, ascospores produce appressoria upon germina-

tyledons, such as bamboo (Poaceae), palms (Arecaceae), and *Pandanus* (Pandanaceae) where it exists mainly as a saprobe^{[18–[20](#page-7-9)[,22](#page-7-10)[,24](#page-7-13)–29]}. A few species have been reported as phytopathogens^{[[30](#page-7-15)]} or as endophytes^{[\[31\]](#page-7-16)}. Hyde et al.^{[\[22\]](#page-7-10)} suggested that the *Oxydothis* species may serve as biological control agents against plant pathogens. Species in this genus with appressorium formation are involved in protein and amino acid degradation, as well as secondary metabolite synthesis i.e. melanin biosynthesis[\[32\]](#page-7-17) . *Neoxylaria*, *Oxydothis,* and *Xylaria* species collected from palms produce appressoria indicating they may have the ability to produce secondary metabolites especially when they live as endophytes^{[[24](#page-7-13)[,32\]](#page-7-17)}. Ninety-one

epithets are currently listed under the *Oxydothis* in Index Fungorum [\(https://indexfungorum.org/Names/Names.asp](https://indexfungorum.org/Names/Names.asp); accessed on 11 November 2024), though more than half of the described species lack molecular data to clarify their phylogenetic relationships. Among those that do have sequence data, most species are represented only by ITS, LSU, and SSU sequences. Recently, Zhang et al.^{[[29](#page-7-14)]} introduced five new *Oxydothis* species (*O. caryotae*, *O*. *foliata*, *O. palmae*, *O. pyriforme,* and *O. sinensis*) and improved the phylogenetic resolution of the genus using multigene phylogeny based on a concatenated dataset of ITS, LSU, SSU, *tef*1-*α*, and *rpb2* sequences. Unfortunately, only a few protein coding genes (i.e. *rpb2* and *tef*1-*α*) are currently available for *Oxydothis* species in GenBank, resulting in incomplete classification of the phylogenetic relationships within the genus.

During ongoing studies of Xylariomycetidae in Southwest China^{[33–[37](#page-7-19)]}, numerous new species have been reported. As part of this continuing effort, the new species *Oxydothis ailaoshanensis* was discovered in the Ailaoshan rain forest of Yunnan Province, China on dead bamboo culms. This is the second report of an *Oxydothis* species associated with a bamboo host in China. The new species is described based on its morphological characteristics and supported by multi-gene phylogenetic analyses.

Materials and methods

Sample collection and morphological examination

Dead bamboo culms were collected from the Ailaoshan subtropical evergreen broad-leaved forest (24.536944° N, 101.019444° E, 2,500 m), in Yunnan Province, China during the rainy season (April 2023). Specimens were processed accord-ing to the methods outlined by Senanayake et al.^{[[38](#page-7-20)]}. Observation and photography of the morphological features followed the procedure described in Dissanayake et al.^{[\[37\]](#page-7-19)}. Melzer's reagent was used to examine the apical apparatus of the asci. Measurements were taken using the Tarosoft (R) Image Framework software and photo plates representing the morphology were edited with Adobe Photoshop CS6 software (Adobe Systems, USA). Type specimens (holotype and isotype) were deposited in the Herbarium of Cryptogams, Kunming Institute of Botany, Chinese Academy of Sciences (KUN-HKAS), Kunming, China. The new taxon was registered in MycoBank (www.mycobank.org) and Facesoffungi^{[\[39\]](#page-7-21)}.

DNA extraction, PCR amplification, and sequencing

Fungal DNA was extracted from 15–20 fresh fruiting bodies of the fungus as described in Wanasinghe et al.^{[\[40\]](#page-8-0)} using Forensic DNA Kit (Omega®, Norcross, GA, USA). LSU, SSU, ITS, and *tef*1*-α* gene were amplified with primer pairs LR0R/LR5[\[41\]](#page-8-1) , NS1/NS4^{[[42](#page-8-2)]}, ITS5/ITS4^[42], and EF1-983F/EF1-2218R^{[[43](#page-8-3)]} respectively. The thermal cycling program was followed by Konta et al.^{[\[20\]](#page-7-9)} and Hu et al.^{[[26](#page-7-22)]}. The amplified PCR fragments were sent to a commercial sequencing provider (BGI, Ltd Shenzhen, PR China). All the sequ[ences g](#page-2-0)enerated in this study were deposited in GenBank ([Table 1](#page-2-0)).

Phylogenetic analysis

Newly generated sequences were subjected to BLAST search in the NCBI GenBank database and sequences of closely related

taxa were downloaded. Phylogenetic analysis was performed using ITS, LSU, SSU, and *tef*1-*α* sequences [\(Table 1](#page-2-0)). Multiple alignments, including both consensus sequences and reference sequences, were generated using MAFFT v. $7^{[44]}$ $7^{[44]}$ $7^{[44]}$ and manually refined using BioEdit v. 7.0.5.2^{[[45](#page-8-5)]}. The individual datasets were combined into a concatenated dataset and further refined with BioEdit. Combined and individual datasets were subjected to maximum likelihood (ML) and Bayesian inference (BI) analyses. The best-fit substitution models were evalu-ated using MrModeltest v. 2.3^{[\[46\]](#page-8-6)} with the Akaike Information Criterion (AIC) as the selection criteria executed in PAUP v. 4.0b10^{[\[47\]](#page-8-7)}. ML and BI analyses were performed on the CIPRES Science Gateway platform^{[[48\]](#page-8-8)}. For ML analyses, RAxML-HPC2 on XSEDE v. 8.2.10^{[[49](#page-8-9)[,50\]](#page-8-10)} was used, applying the GTR + I + G model with 1000 bootstrap repetitions. The BI analysis was executed with MrBayes on XSEDE v.3.2.7a^{[51–[53\]](#page-8-12)} under the GTR + I + G, with one million generations and sampling every 100 generations. The analysis stopped automatically once the standard deviation of split frequencies fell below 0.01, with a burn-in fraction of 0.25. Phylogenetic results were considered significant if ML bootstrap values (MLB) $\geq 60\%$ and Bayesian posterior (BYPP) ≥ 0.95, which were displayed above each node in the resulting tree. The phylogram was visualized using the FigTree v1.4.0 program^{[[54](#page-8-13)]}, and final reorganization was done in Microsoft PowerPoint (2019).

Results

Phylogenetic analysis

The combined ITS, LSU, SSU, and *tef*1*-α* matrix comprised 34 strains, including *Vialaea mangiferae* (MFLUCC 12-0808) and *V. minutella* (BRIP 56959) as outgroup taxa. The concatenated alignment consisted of 3,421 characters (ITS: 1–680 bp, LSU: 681–1,510 bp, SSU: 1,511–2,512 bp, *tef*1-*α*: 2,513–3,421 bp), including gaps. The species-level relationships within *Oxydothis* in both ML and BI trees were similar in topology. The bestscoring RAxML tree was selected to represent the ta[xa rela](#page-3-0)tionship with a final likelihood value of –15,291.6517[57 \(Fig. 1](#page-3-0)). The phylogenetic tree obtained from ML anal[ysi](#page-7-23)[s](#page-7-14) in [Fig. 1](#page-3-0) showed a topology consistent with previous work^{[\[28,](#page-7-23)[29](#page-7-14)]}. The matrix had 990 distinct alignment patterns with 33.64% of characters being undetermined or gaps. The proportion of invariable sites $I = 0.453933$, the gamma distribution shape parameter alpha = 0.576006 and the Tree-Length = 1.338729. The Bayesian analysis ran for one million generations, with the average standard deviation of split frequencies reaching below 0.01 (0.009728). This analysis generated 1,922 trees, from which 721 were sampled after discarding the 25% as burn-in. The alignment contained a total of 995 unique site patterns.

Based on the results of multigene phylogeny, two strains of the new collection (*Oxydothis ailaoshanensis* sp. nov.) formed a robust subclade withi[n the](#page-3-0) monophyletic clade of *Oxydothis* (60% MLB, 0.99 BYPP, [Fig. 1](#page-3-0)). *Oxydothis ailaoshanensis* (HKAS 130464 and HKAS 130465) formed an independent lineage that is basal to *O. calamicola* (MFLUCC 14-1165), *O. coperniciae* (CMUB 40043), *O. caryota* (HKAS 115712), *O. cyrtostachicola* (MRC-007), *O. metroxylonicola* (MFLUCC 15-0281), *O. metroxylonis* (MFLUCC 15-0283), *O. palmicola* (MFLUCC 15-0806), *O. palmae* (HKAS 115711), *O. phoenicis* (MFLUCC 18-0269, MFLUCC 18-0270), and *O. rhapidicola* (MFLUCC 14-0616).

*Oxydothis ailaoshanensis*sp. nov.

Table 1. Names, strain numbers, and GenBank accession numbers of the taxa used in the phylogenetic analyses.

Superscripts 'T' and 'IST' represent the type and isotype strains. Newly generated sequences are indicated in bold. 'NA' sequences are unavailable.

Taxonomy

Oxydothis ailaoshanensis L.S. Dissan., Phookamsak & Wanas. sp. nov. ([Fig. 2\)](#page-4-0)

MycoBank: MB856009; *Facesoffungi number*: FoF 14917

Etymology − The specific epithet is derived from the locality, Ailaoshan, where the holotype was collected

Holotype − HKAS 130464

Asco*mata* 450–550 μm high \times 130–150 μm diameter ($\overline{\text{x}}$ = 508 \times $(\bar{x} = 75 \times 140 \mu m, n = 5)$, central, broad neck, open-ended. *Saprobic* on dead bamboo culms (Poaceae). Sexual morph: 140 μ m, n = 5), solitary or aggregated in groups, immersed in host's exodermis, becoming raised, superficial, visible as black, shiny knobbed, long axis horizontal to flat on the host, hemispherical (dome-shaped) to subconical, with flattened, wedgeshaped base, uniloculate, somewhat clustered, forming pseudostromatic, with 3–6 in groups of ascomata, glabrous, ostiolate, papillate. *Ostiole* 50–100 μm long × 40–50 μm diameter *Peridium* 15–20 μm wide, composed of several layers of flattened, inside thin cell layers, composed, hyaline, *textura prismatica*, outside, thin, light brown to dark brown, *textura prismatica*, merged with host tissues. *Paraphyses* are cylindrical, fragmented, hyaline, branched, or non-branched. *Asci* 100–120 ×

10-15 μm (\bar{x} = 110 × 13 μm, n = 15), 8-spored, unitunicate, with a J+, apical apparatus. *Ascospores* 55–75 \times 3–5 μ m ($\overline{\text{x}}$ = 65 cylindrical to elongated fusiform, with blunt apex, slightly tapering towards both ends, mostly straight, short pedicillate, \times 4 μ m, n = 15), overlapping 1-3-seriate, elongated fusiform, with acute ends, hyaline, obliquely 1-septate, tapering gradually from the center to the ends, with multi-guttules in each cell, pointed processes. Asexual morph: Undetermined.

Material examined – CHINA, Yunnan Province, Ailaoshan Forest Mountain (24.536944° N, 101.019444° E, 2,500 m), on dead culms of bamboo, 7 April 2023, L.S. Dissanayake, ALF23- 10 (HKAS 130464, holotype), *ibid*., ALF23-10A (HKAS 130465, isotype).

Note: The multigene phylogenetic analyses indicate that *Oxydothis ailaoshanensis* is closely related to *O. metroxylonis* ([MFLU](#page-3-0)CC 15-0283), with 60% MLB, 0.99 BYPP statistical support ([Fig. 1](#page-3-0)). The nucleotide difference between *O. ailaoshanensis* and *O. metroxylonis* in ITS, LSU, SSU, and *tef*1-*α* are 124/555 bp (22.3%), 37/826 bp (4.5%), 13/981 bp (1.3%), and 95/906 bp (10.5%) respectively. *Oxydothis ailaoshanensis* differs from *O. metroxylonis* in having smaller, immersed ascomata (450–550 × 130–150 μm) that become raised and superficial with the long

Fig. 1 RAxML tree based on a combined dataset of analyzed ITS, LSU, SSU, and *tef*1-*α* sequences. Bootstrap support values for ML equal to or greater than 60%, Bayesian posterior probabilities (BYPP) equal to or greater than 0.95 are shown as MLB/BYPP above the nodes. The new isolate is in red; ex-type strains are in bold. The scale bar represents the expected number of nucleotide substitutions per site.

axis horizontal to the host surface, shorter asci (100-120 \times 10–15 μm) that are mostly straight, and longer ascospores $(55-75 \times 3-5 \mu m)$ that are elongated and fusiform. In contrast, *O. metroxylonis* has larger ascomata (716–1,580 μm diam), with an axis oblique or perpendicular to the host surface, longer asci (165–181 \times 9–15µm) with a cylindrical-clavate shape, and shorter ascospores (47–57 \times 4–6 μ m) with central curve^{[\[20\]](#page-7-9)}. Morphologically, *O. ailaoshanensis* is similar to *O. bambusicola* sharing characteristics such as solitary or aggregated ascomata with a central papilla, 8-spored, unitunicate, cylindrical asci with a J+, apical apparatus and elongated fusiform, 1-septate, hyaline ascospores^{[[18](#page-7-12)]}. Both species were isolated from bamboo hosts[[18](#page-7-12)] . However, *O. ailaoshanensis* can be distinguished from *O. bambusicola* by its larger ascomata (450–550 × 130–150 μm vs 130–375 × 90–160 μm), shorter asci (100–120 × 10–15 μm vs 240 \times 23 μm), and shorter ascospores (55–75 \times 3–5 μm vs 93 \times 7 μm) which taper gradually from the center to the pointed ends. In contrast, *O. bambusicola* ascospores are gradually tapering to the rounded apices and are covered with small amounts of mucilage. Based on the phylogenetic evidence and morphological differences, we describe our new collection as a distinct species, *O. ailaoshanensis*.

Discussion

This study listed 89 accepted *Oxydothis* species in [Table 2](#page-5-0) with their hosts. Among them nearly all host species for *Oxydothis* belong to Arecaceae, except *Oxydothis aequalis*, *O.* *bambusicola,* and *O. miscanthicola*, recorded from Poaceae[\[18](#page-7-12)[,31,](#page-7-16)[55](#page-8-14)] . Notably, *O. aequalis* and *O. bambusicola* were recorded on bamboo hosts in the Philippines and the Hong Kong region in China respectively. In the current study, *O. ailaoshanensis* is introduced also from a bamboo host in China marking a new record for Poaceae hosts in Yunnan Province. Other *Oxydothis* species, i.e. *Oxydothis caryotae*, *O. chinensis*, *O. fortunei*, *O. palmae*, *O. pyriforme,* and *O. sinensis* were introduced from an Arecaceae host in China, Guangdong Province and Guizhou Province^{[[26](#page-7-22)[,27](#page-7-24)[,29\]](#page-7-14)}. Based on the findings in [Table 2](#page-5-0), *Oxydothis* appears to exhibit host specificity primarily within Arecaceae and Poaceae with a distribution across both temperate and tropical regions.

Despite the substantial diversity within this genus, only 23 species currently have sequence data available in GenBank. Some species lack informative genetic markers such as ITS for *Oxydothis calamicola*, *O. hohnelli*, and *O. rhapidicola*, or LSU and SSU sequences data for *O. chinensis*, *O. cyrtostachicola*, *O. daemonoropsicola*, *O. fortunei*, *O. inaequalis,* and *O. yunnanensis*. Previous studies on *Oxydothis* taxonomy relied on ITS, LSU, and SSU sequences^{[\[20,](#page-7-9)[22](#page-7-10),[26](#page-7-22)[,28](#page-7-23)[,56\]](#page-8-15)}. However, recent advancements in phylogenetic studies such as that by Zhang et al.^{[\[29\]](#page-7-14)}, introduced five new *Oxydothis* species using a multigene dataset including ITS, LSU, SSU, *tef*1*-α,* and *rpb2*. Only nine species incorporate *tef*1*-α* in their datasets, further supporting the phylogenetic placement of *Oxydothis* species in Oxydothidaceae. In the present study, we contribute to this approach by providing a combined ITS, LSU, SSU, and *tef*1-*α* phylogeny

Fig. 2 *Oxydothis ailaoshanensis* (HKAS 130464, holotype). (a) Substrate. (b), (c) Ascomata on the host surface. (d) Section of an ascoma. (e) Close up of ostiole. (f) Peridium. (g) Paraphyses. (h)–(j) Asci (j = Asci in Melzer's reagent showing J+, apical apparatus, arrow showing short pedicel). (k)–(o) Ascospores. (o = Ascospore in Congo Red). Scale bars: (c) 200 μm, (e) 50 μm, (f, g) 10 μm, (h–j) 50 μm, (k–o) 20 μm.

for introducing *O. ailaoshanensis*. The use of multiple gene markers in phylogenetic analyses has enhanced our ability to resolve species-level relationships within *Oxydothis*.

While ITS, LSU, and SSU have previously been used as the primary markers for differentiating species, the addition of protein-coding genes such as *tef*1-*α* and *rpb*2 has improved resolution by increasing phylogenetic signal and reducing ambiguities in species placement[\[29\]](#page-7-14) . For *Oxydothis ailaoshanensis*, the multigene analysis including *tef*1-*α*, coupled with morphological data such as the unique ascomata and spore characteristics([Fig. 2](#page-4-0)), has successfully differentiated it from close relatives such as *O*. *metroxylonis*. Nevertheless, some *Oxydothis* species still lack sequences for key informative gene regions, limiting comprehensive phylogenetic analyses. Future studies should focus on obtaining missing sequence data, especially for protein-coding genes, across more species in this genus. This could further clarify phylogenetic relationships and species boundaries within *Oxydothis*.

An ITS BLAST search of the sequences linked *Oxydothis* to some leaf-litter-based ascomycetes (i.e., AF502894, AF502896, AF502740) and various uncultured fungal strains (i.e., KT328718, GU174316, AM999626, KC222801). However, these strains lack associated morphological data, which limits deeper insights into their morpho-phylogenetic relationships. This absence of morphological connections emphasizes the need for comprehensive morphological and molecular

Table 2. Host occurrences and distribution of all known *Oxydothis* species.

(to be continued)

*Oxydothis ailaoshanensis*sp. nov.

Table 2. (continued)

characterization of these strains. The present findings suggest that *Oxydothis* diversity remains underexplored in this region, with potentially numerous species still awaiting discovery.

Author contributions

The authors confirm contribution to the paper as follows: conceptualization, formal analysis, writing – original draft: Dissanayake LS; data curation: Dissanayake LS, Wanasinghe DN; methodology: Dissanayake LS, Phookamsak R; resources, project administration: Wanasinghe DN, Xu J; supervision: Xu J; writing – review and editing: Wanasinghe DN, Phookamsak R. All authors reviewed the results and approved the final version of the manuscript.

Data availability

The datasets generated for this study can be found in the NCBI, GenBank and MycoBank.

Acknowledgments

Rungtiwa Phookamsak sincerely acknowledges the Introducing Talents Start-up Fund of Kunming Institute of Botany, Chinese Academy of Sciences, Yunnan Revitalization Talent Support Program 'Young Talent' Project (Grant No. YNWR-QNBJ-2020-120), Yunnan Revitalization Talent Support Program "High-end Foreign Expert" Project and the Independent Research Department of Economic Plants and Biotechnology, Yunnan Key Laboratory for Wild Plant Resources, Kunming Institute of Botany, Chinese Academy of Sciences (Grant No. Y537731261). Jianchu Xu thanks the Yunnan Department of Sciences and Technology of China (Grant No. 202302AE090023, 202303AP140001). Dhanushka N. Wanasinghe is funded by the Distinguished Scientist Fellowship Program (DSFP), King Saud University, Kingdom of Saudi Arabia.

Conflict of interest

The authors declare that they have no conflict of interest.

Dates

Received 12 November 2024; Revised 5 December 2024; Accepted 5 December 2024; Published online 20 December 2024

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