MYCOSPHERE 16(1): 2776–2847 (2025) www.mycosphere.org ISSN 2077 7019
Doi 10.5943/mycosphere/16/1/18

ARTICLE

Fungal community composition associated with the agarwood-producing tree, *Aquilaria sinensis*

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Citation – Du TY, Tibpromma S, Hyde KD, Wang YH, Jeewon R, Mapook A, Zhang X, Lu WH, Chen XM, Alfagham AT, Elgorban AM, Kumla J, Dai DQ, Suwannarach N, Karunarathna SC 2025 – Fungal community composition associated with the agarwood-producing tree, *Aquilaria sinensis*. Mycosphere 16(1): 2776–2847, Doi 10.5943/mycosphere/16/1/18

Abstract

Agarwood, a precious and rare resin, is primarily produced by *Aquilaria sinensis* of the plant family *Thymelaeaceae*. The fungi associated with *Aquilaria* are a rich source of secondary metabolites, demonstrating an exciting potential for drug discovery. However, despite its significance, there is a lack of comparative analysis of the fungal communities associated with different plant parts of *A. sinensis* and in different regions. In this study, we collected *A. sinensis* samples (agarwood resin, dead branches, healthy branches, and healthy leaves) from Maoming and Zhanjiang in Guangdong Province and Xishuangbanna and Yuanjiang in Yunnan Province, China. A total of 960 strains belonging to 64 genera of 44 families were successfully isolated. Among them, 142 strains had been previously reported in articles by our research team and were included in this study for community analysis. Based on a Venn diagram, the study revealed recombination relationships among fungal communities from plant parts and different collection sites. In addition, this study introduces new taxa belonging to the genera *Banksiophoma, Deniquelata, Fomitiporia,* and *Montagnula*, thereby enhancing our knowledge of the known fungal diversity in *Aquilaria sinensis*. At the same time, relevant notes on 64 genera are summarized, and their ecological

Submitted: 12 June 2025; **Accepted:** 21 August 2025; **Published:** 30 September 2025
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Accepted by: Artur Alves

functions, distribution, and relationships with *Aquilaria* spp. are discussed. For example, *Fusarium* is often reported to have the potential to induce the production of agarwood, providing valuable literature for further research. Overall, this study greatly enriches knowledge on the diversity of fungi associated with *Aquilaria*, providing potential "candidate fungal inducers", and lays a foundation for further exploring the ecological functions of agarwood and its associated fungi. Additionally, to avoid conceptual confusion, this study proposes that identifying fungi isolated from agarwood resin as 'agarwood-associated fungi', differentiating them from endophytic fungi in healthy tissues. This distinction is vital as it helps to clarify the ecological roles and origins of the fungi involved in agarwood formation. This study also underscores the need for more targeted research on their potential functions in agarwood resin production.

Keywords: agarwood-associated fungi, *Ascomycota*, *Banksiophoma*, *Deniquelata*, *Fomitiporia*, *Montagnula*, morphology, phylogeny

INTRODUCTION

Agarwood, also known as “Chenxiang” in China, is a highly valuable and fragrant resinous wood formed in certain species of trees, primarily *Aquilaria* and *Gyrinops,* within the family *Thymelaeaceae* (Faizal et al. 2020, 2022). In total, 14 *Aquilaria* species, *viz.*, *Aquilaria baillonii*, *A. beccariana*, *A. crassna*, *A. cumingiana*, *A. filaria*, *A. hirta*, *A. khasiana*, *A. malaccensis*, *A. microcarpa*, *A. rostrata*, *A. rugosa*, *A. sinensis*, *A. subintegra*, and *A. yunnanensis* and eight *Gyrinops* species *viz.*, *Gyrinops caudata*, *G. decipiens*, *G. ledermannii*, *G. moluccana*, *G. podocarpa*, *G. salicifolia*, *G. versteegii*, and *G. walla* have been reported to be able to produce agarwood (Li et al. 2022a). In China, there are two species of agarwood-producing trees, *viz.*, *A. sinensis* and *A. yunnanensis*, of which *A. sinensis* is the primary source of agarwood (Chinese Pharmacopoeia 2015, 2020, Tibpromma et al. 2021, CITES 2022).

Agarwood has a long history of use in religious activities due to its unique fragrance and holds cultural significance (Chen et al. 2017a, b, Wang et al. 2018, Adhikari et al. 2021). It can be processed into incense, jewelry, and carvings; additionally, agarwood essential oil has become a key raw material for high-end perfumes and cosmetics (Liu et al. 2013, Monggoot et al. 2017, Wang et al. 2018, CITES 2022, Ngadiran et al. 2023). It is worth noting that agarwood also plays a crucial role in traditional medicine in China, India, and Saudi Arabia (Liu et al. 2013, Liao et al. 2018, Wang et al. 2018). In modern pharmacology, the pharmacological effects of agarwood include anti-diabetic, anti-inflammatory, anti-cancer, anti-depressant, and antioxidant properties (Mei et al. 2008, Takemoto et al. 2008, Feng et al. 2011, Kumphune et al. 2011, Dahham et al. 2014, Tay et al. 2014, Adhikari et al. 2021, Li et al. 2025). Moreover, agarwood has also been used to treat rheumatism, arthritis, body pain, asthma, and gout (Borris et al. 1988, Li et al. 2024a).

The natural formation of agarwood in the wild is extremely rare, as it typically does not occur in healthy trees (Liu et al. 2013, Chhipa et al. 2017). Agarwood resin is produced as a defense response to biotic or abiotic stressors, including animal grazing, insect gnawing, strong winds, lightning, mechanical injury, or microbial invasion (Xu et al. 2013, Wang et al. 2018). Its unique fragrance, the rarity of its natural production, and its wide range of applications have all contributed to the increased economic value of agarwood. Agarwood oil had a global market value of USD 278.03 million in 2021 (Niego et al. 2023a), and a market analysis report has predicted that the agarwood essential oil market will reach a value of USD 345.5 million by 2030 (Agarwood Essential Oil Market 2021). Agarwood has a long history of trade, with its main markets currently including the United Arab Emirates, China, Japan, and Saudi Arabia (Nakashima et al. 2005).

Under the temptation of high-value agarwood, people have engaged in uncontrolled destruction and harvesting of wild agarwood, threatening its wild populations (Gogoi et al. 2022). Many agarwood-producing tree species are now classified as vulnerable or critically endangered by the International Union for Conservation of Nature (http://www.iucnredlist.org), and all species of *Aquilaria* and *Gyrinops* have been presented in Appendix II based on the data available in “Convention on International Trade in Endangered Species (CITES) in 2005” (CITES 2005, 2022).

To meet market demand and increase economic benefits while protecting wild resources, agarwood trees have been artificially cultivated in several countries, and the technology for inducing agarwood formation has emerged. Induction techniques have been continuously evolving, starting with basic physical damage to the trees, followed by a combination, or independent use of physical injury, biological induction, and chemical induction (Liu et al. 2013, Chen et al. 2017a, b, Chhipa et al. 2017, Monggoot et al. 2017, Wang et al. 2018, Ngadiran et al. 2023).

These technologies have been extensively researched and utilized; however, the mechanism by which agarwood resin is produced remains unclear. Currently, three main hypotheses have been proposed to explain the formation of agarwood (Zhang et al. 2010, Fu et al. 2024). 1) The "pathological" hypothesis, which proposes that agarwood formation is caused by disease, specifically resulting from fungal infection. 2) The "trauma/pathological" hypothesis, which suggests that physical trauma is the primary cause of agarwood formation, with fungal infections playing a secondary role. 3) The "nonpathological" hypothesis, which posits that physical and chemical damage are the primary contributors to agarwood formation (Fu et al. 2024). Based on these assumptions, while physical damage to the tree creates an opening, fungal infection has long been regarded as a key factor in the formation of agarwood (Rasool & Mohamed 2016).

Fungal induction has emerged as a promising technique for increasing agarwood production, and inoculating specific fungal strains has been shown to stimulate resin biosynthesis (Faizal et al. 2017, 2022, Subasinghe et al. 2019, Zheng et al. 2019, Liu et al. 2022a, b, Huang et al. 2023, Du et al. 2024b), and providing a controlled and sustainable approach to agarwood formation. Various fungal species, including those from the genera *Colletotrichum*, *Fusarium, Lasiodiplodia,* and *Trichoderma,* have been extensively employed in these processes with demonstrated efficacy (Du et al. 2022a, Li et al. 2022a, Ngadiran et al. 2023). However, the success of fungal induction depends on several complex factors, including the fungal strain, tree species, environmental conditions, and inoculation method. One key advantage of biological induction is its ability to foster progressive and systematic growth of fungal agents, resulting in continuous agarwood formation (Novriyanti et al. 2010). Recent studies have demonstrated that artificially induced agarwood exhibits similar chemical and pharmacological properties to those of wild agarwood, thereby further confirming its potential as a sustainable alternative (Huang et al. 2023). However, some endophytes display latent pathogenicity in plants, meaning they can act as pathogens under specific conditions (Nisa et al. 2015). In *Aquilaria*, this latent pathogenicity is economically beneficial, as it triggers the production of agarwood resin (Enshasy et al. 2019, Gogoi et al. 2022). Further research is necessary to optimize these variables for maximizing both the yield and quality of agarwood resin.

Li et al. (2022b) documented 67 fungal genera belonging to 42 families isolated and identified from eight agarwood-producing trees, and 82.8 % of fungal species belonged to *Ascomycota*. So far, some fungal genera, *viz.*, *Acremonium*, *Arthrinium*, *Aspergillus*, *Botryodiplodia*, *Botryosphaeria*, *Chaetomium*, *Cladosporium*, *Colletotrichum*, *Cylindrocladium*, *Diaporthe*, *Diplodia*, *Epicoccum*, *Fomitopsis*, *Fusarium*, *Hypocrea*, *Lasiodiplodia*, *Melanotus*, *Penicillium*, *Pestalotiopsis*, *Phaeoacremonium*, *Rhizopus*, *Rigidoporus*, *Trichoderma*, and *Xylaria*, have been reported to have the ability to promote agarwood formation (Du et al. 2022a, Li et al. 2022a, Gogoi et al. 2023). Additionally, the secondary metabolites produced by endophytic fungi in agarwood serve as sources of various pharmacological properties (Li et al. 2022a). More than 90 compounds were extracted from the endophytic fungi of agarwood-producing trees (Li et al. 2022a). Some fungal genera are responsible for the production of antimicrobial sesquiterpenes, e.g., *Acremonium*, *Arthrinium*, *Collectotrichum*, *Diaporthe*, *Fimetariella*, *Nemania*, *Nigrospora*, and *Nodulisporium* (Zhang et al. 2010, Wu et al. 2010, Tao et al. 2011, Li et al. 2014, Monggoot et al. 2017, Tibpromma et al. 2021).

Fungi are one of the most important microbial groups on Earth, widely distributed in various ecosystems, estimated to be of 1.5 to 3.8 million species (Niskanen et al. 2023, Hyde et al. 2024a), and have been extensively studied in recent years (Dong et al. 2024, Samarakoon et al. 2024, Manawasinghe et al. 2025). As decomposers (Sun et al. 2025), endophytes (Liao et al. 2025), and pathogens (Jayawardena et al. 2025), fungi are widely involved in carbon cycling, nutrient turnover, and biological interactions, profoundly affecting the natural environment and human society (Niego

et al. 2023b, Hyde et al. 2024b). Fungi exist in both terrestrial ecosystems and freshwater and marine environments, playing an irreplaceable role in maintaining ecological balance and promoting material cycling (Hyde & Lee 1998, Liu et al. 2024a, Ma et al. 2024, Ren et al. 2024, Shen et al. 2024, Tian et al. 2024, Wang et al. 2024a). Studying the diversity, ecological functions, and interaction mechanisms between fungi and their hosts can provide a theoretical basis for agricultural disease prevention and control, ecological restoration, and biotechnology applications (Hyde et al. 2019a, b, Ren et al. 2024). In recent years, an increasing number of studies have demonstrated that certain fungi play a crucial role in the formation of agarwood and are key drivers of its natural growth (Li et al. 2022a, Du et al. 2024b). Analyzing the relationship between fungi and agarwood formation can not only reveal the chemical mechanisms of plant-microbe interactions but also provide biotechnological strategies for sustainable agarwood production. Therefore, an in-depth exploration of the diversity and ecological functions of fungi, especially their involvement in the formation mechanism of agarwood, holds significant scientific value and application potential.

Previous studies have focused mainly on a limited number of fungal species associated with agarwood formation, and their diversity and ecological roles remain poorly understood, leaving substantial gaps in our knowledge of fungal communities across different parts of the *Aquilaria* tree. The primary purpose of this study is to explore the fungal diversity in different plant parts of agarwood trees, identify and analyze key fungal groups associated with resin production, and lay the foundation for understanding their interactions with hosts. This work, by providing potential fungal resources for agarwood induction strategies, is poised to optimize the approach to agarwood production and contribute to the sustainable development of the agarwood industry.

MATERIALS AND METHODS

Sample collection

Fresh samples of *Aquilaria sinensis* were collected from four sites across two provinces in China: Guangdong (Maoming, 21°71′32″ N, 111°24′01″ E, in June 2022; Zhanjiang, 21°49′48″ N, 111°40′12″ E, in December 2020) and Yunnan (Xishuangbanna, 22°21′09″ N, 101°01′06″ E, in September 2021; Yuanjiang, 23°60′14″ N, 102°02′11″ E, from September 2022 to September 2023). Samples from Guangdong Province are labeled as GDA, while those from Yunnan Province are labeled as YNA (Rathnayaka et al. 2024). Healthy leaves, healthy branches with agarwood resin, and decayed branches were collected by hand or with a pruning or chopping knife. All tools were cleaned with 75% alcohol before and after use. After collection, decayed branch samples were stored in dry envelopes. In contrast, fresh samples were placed in a thermal-insulated ice box, taken to the mycology laboratory at Qujing Normal University, and stored at 4°C until fungal strains could be isolated.

Fungal strain isolation

The isolation of endophytic fungi and agarwood-associated fungi from fresh samples followed the method described by Du et al. (2022b) and Tibpromma et al. (2021), with some modifications. First, dust from the surface of fresh leaves and the bark of fresh branches was removed under running tap water. These clean samples were transferred to a laminar flow hood and cut into small pieces (0.5 cm × 0.5 cm) using sterilized knives or blades. The surface sterilization procedure was as follows: the samples were washed with sterile water, then treated with 75% alcohol for 30 s, followed by immersion in 2.5% sodium hypochlorite (branches for 1 min, leaves for 30 s), and then rinsed with 75% alcohol for 30 s. Finally, the samples were washed three times with sterile water and placed on sterilized filter paper to absorb excess moisture. Five sterilized pieces were then placed on each 90 mm potato dextrose agar (PDA) plate (with ampicillin added: 50 mg/L) and incubated at 28 °C for 7 to 14 days. The plates were checked daily, and fresh mycelium was transferred to new 60 mm PDA plates to obtain pure cultures. The isolation, surface disinfection, and cultivation methods for samples of dead branches carrying saprobic fungi are the same as those of endophytic fungi. These pure cultures were used for DNA extraction. To promote sporulation, active mycelium from a new species was inoculated onto water agar (WA) plates (with or without bamboo sticks). Dried cultures of the new species were deposited at Guizhou Medical University (GMB-W), China, while living cultures

were stored in the Guizhou Medical University Culture Collection (GMBCC), the Zhongkai University of Agriculture and Engineering Culture Collection (ZHKUCC), and the Kunming Institute of Botany Culture Collection (KUMCC), China. Facesoffungi (FoF) numbers were registered as described in Jayasiri et al. (2015), and MycoBank numbers (MB) were registered as outlined in MycoBank (http://www.MycoBank.org). The data on taxa generated in this study were deposited in the Greater Mekong Subregion fungal database (Chaiwan et al. 2021).

Morphological observation

To observe the reproductive characteristics of the culture, it is necessary to attempt to induce sporulation. For sporulation induction, the strains were inoculated into PDA and WA culture media, respectively. Different groups were set up, including those with no addition of plant tissue, the addition of sterilized host leaves, the addition of sterilized host leaf grinds, sterilized host twigs, sterilized pine needles, and toothpicks. The cultures were grown at 25 °C in various environments, including darkness, ultraviolet light, direct sunlight, and –4 °C, for 4–12 weeks. The results were checked once a week, and important structures were recorded and photographed.

Morphological structures of the cultures were examined using an OPTEC SZ650 dissecting stereomicroscope (Chongqing, China). Microscopic fungal structures were captured with an OLYMPUS DP74 digital camera (Tokyo, Japan) mounted on an OLYMPUS optical microscope (Tokyo, Japan). Distilled water was used as the mounting solution, and cotton blue was employed to stain transparent tissues. All fungal micromorphological measurements were taken using the Tarosoft® Image Framework v. 1.3, while photo plates were created with Adobe Photoshop CS3 Extended (Adobe Systems, California, USA). Other details (tissue sectioning, slide preparation, observation, and photography) were followed as outlined in Senanayake et al. (2020).

DNA extraction, PCR amplification, and sequencing

Molecular phylogenetic studies were conducted according to the methods described by Dissanayake et al. (2020). Fresh mycelia, grown for 2–4 weeks on PDA plates, were scraped and transferred to a 1.5 ml centrifuge tube for DNA extraction using the Biospin Fungus Genomic DNA Extraction Kit–BSC14S1 (BioFlux, Hangzhou, China), following the manufacturer's instructions. Polymerase chain reaction (PCR) was performed to amplify the ITS region (including internal transcribed spacer 1, 5.8S ribosomal RNA gene, and internal transcribed spacer 2) using primers ITS5/ITS4 (White et al. 1990). PCR amplification was carried out according to Du et al. (2022b). For the new species, different multi-gene loci have been amplified, *viz.*, 28S nrRNA region (LSU) was amplified by using the primers LR0R and LR5 (Vilgalys & Hester 1990), 18S ribosomal RNA (SSU) was amplified using the primers NS1 and NS4 (White et al. 1990), and translation elongation factor 1-alpha (*tef*1-α) was amplified using the primers EF1-983F and EF1-2218R (Rehner 2001), *β*-tubulin (TUB) was amplified using the primers T1 and 2b (Trouillas et al. 2011), and RNA polymerase II second largest subunit (*rpb*2) was amplified using the primers fRPB2-5f and fRPB2–7cR (Liu et al. 1999). Finally, PCR products were purified and sequenced at the Tsingke Biotech Co. and Sangon Biotech Co., Kunming, China.

Phylogenetic analyses

In the identification of endophytic fungi, the ITS locus is commonly employed for genus-level identification (Guo et al. 2001, 2003). The forward and reverse sequences obtained were checked in BioEdit 7.2.6 (Hall 1999) and then merged using Geneious 9.1.8 (https://www.geneious.com) (Kearse et al. 2012), and the merged sequences were subjected to BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi?PAGE_TYPE=BlastSearch, accessed on 02 February 2025) to identify the most similar taxa. Additional sequences from different genera included in the analysis were gathered from recent publications. The FASTA files were generated using OFPT (Zeng et al. 2023) following the protocol for constructing Randomized Accelerated Maximum Likelihood (RAxML) and Bayesian Inference (BI) analyses. The FASTA format was then converted to PHYLIP (for RAxML) and NEXUS (for BI) formats using ALTER (http://www.sing-group.org/ALTER/) (Glez-Peña et al. 2010).

RAxML analysis was conducted based on the ITS region for 960 strains, and both RAxML and BI analyses were performed for multi-gene sequences of the new species described in this study. The RAxML tree was generated using the PHYLIP file in RAxML-HPC2 on XSEDE (8.2.12) (Stamatakis et al. 2008, Stamatakis 2014) via the CIPRES Science Gateway platform (https://www.phylo.org/portal2/home.action, accessed on 02 February 2025) (Miller et al. 2010), with 1000 bootstrap replicates under the GTR+I+G evolutionary model. The BI tree was generated using MrBayes on XSEDE (version 3.2.7a) (Ronquist et al. 2012), and the optimal evolutionary models were estimated with MrModeltest v. 2.3 (Nylander et al. 2008). Six simultaneous Markov chains were run for 1,000,000 to 2,000,000 generations, with trees sampled every 100th generation. The resulting phylogenetic trees of new species were visualized in FigTree v.1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/) (Rambaut 2012) and edited using Microsoft PowerPoint 2021 and Adobe Photoshop CS3 Extended (version 22.0.0) (Adobe Systems, California, USA). At the same time, the circular RAxML tree of 960 strains based on the ITS region was edited and visualized on Interactive Tree of Life (iTOL) v6 (https://itol.embl.de/, accessed on 02 February 2025) (Letunic and Bork 2024). All newly generated sequences from this study have been deposited in GenBank (https://www.ncbi.nlm.nih.gov/WebSub/?form=history&tool=genbank, accessed on 02 February 2025).

Phylogenetic species recognition by genealogical concordance analyses

Genealogical concordance phylogenetic species recognition (GCPSR) analysis serves as a model-based test for examining significant recombinant events within data sets. The combined data underwent analysis using the pairwise homoplasy index test (PHI) (Bruen et al. 2006), which was performed in SplitsTree v.4 (Huson & Bryant 2006; Quaedvlieg et al. 2014). This was done to ascertain the recombination level among closely related species. A PHI index lower than 0.05 ($\Phi w < 0.05$) implies that there is significant recombination within the data set. The relationships among closely related taxa were made visible by constructing split graphs from the concatenated data sets. This construction was carried out using the LogDet transformation and split decomposition options available in SplitsTree v.4. New species were established according to the recommendations outlined by Jeewon & Hyde (2016) and Pem et al. (2021).

Fungal community analysis

Community analysis of fungal strains in this study was primarily performed using an online microbial information platform (https://www.bioinformatics.com.cn/, accessed February 2, 2025) (Tang et al. 2023), with various charts constructed, including column charts, donut charts, Vertical stack bar charts, Link fill bar charts, and Venn diagrams. The Column chart with error lines visualizes the quantitative distribution of different genera, incorporating error bars to indicate variability and uncertainty in their relative frequencies. The Donut chart complements this by showing the proportional distribution of each genus, providing a clear overview of community composition. The Vertical stack bar and Link fill bar visually represent the distribution and abundance of genera across different samples, enabling a straightforward comparison of genus composition within each sample. The Venn diagram highlights the overlap and unique genera present in the various sample groups, helping to identify shared and distinct genera. Text editing and chart visualization were done using Adobe Photoshop CS3 Extended (version 22.0.0) (Adobe Systems, California, USA).

RESULTS

Fungal phylogenetic and community analyses in *Aquilaria sinensis*

This study collected agarwood resin, healthy branches, healthy leaves, and dead branch samples of *Aquilaria sinensis* from Guangdong (Maoming and Zhanjiang) and Yunnan (Xishuangbanna and Yuanjiang) provinces and isolated 960 fungal strains. These strains were identified at the genus level through ITS sequences and were classified as belonging to 64 genera of 44 families in three phyla: *Ascomycota* (951 strains, 99.06%), *Basidiomycota* (six strains, 0.63%), and *Mucoromycota* (three

strains, 0.31%). A phylogenetic tree showing the genus-level placements of the fungal taxa is presented in Fig. 1. The collection sites, times, isolation parts, classification status, and GenBank accession numbers for these strains are detailed in Supplementary Table 1.

Ascomycota is the dominant group in this study, comprising 951 sequences from 59 genera of 39 families, demonstrating its dominance in the *A. sinensis* ecosystem. These 951 sequences were distributed across five classes within *Ascomycota*: *viz.*, *Dothideomycetes* (38.28%, 363 strains), *Eurotiomycetes* (10.83%, 104 strains), *Leotiomycetes* (0.84%, eight strains), *Saccharomycetes* (0.21%, two strains), and *Sordariomycetes* (49.84%, 474 strains). *Sordariomycetes* is the most prominent class, followed by *Dothideomycetes*. The 59 genera identified within *Ascomycota* include *Acrocalymma* (two strains), *Allophoma* (three strains), *Alternaria* (23 strains), *Annulohypoxylon* (five strains), *Aspergillus* (42 strains), *Aureobasidium* (one strain), *Banksiophoma* (four strains), *Biscogniauxia* (one strain), *Botryosphaeria* (six strains), *Chaetomium* (five strains), *Cladorrhinum* (one strain), *Cladosporium* (four strains), *Colletotrichum* (57 strains), *Coniella* (two strains), *Corynespora* (one strain), *Crassiparies* (nine strains), *Curvularia* (six strains), *Daldinia* (16 strains), *Deniquelata* (three strains), *Diaporthe* (78 strains), *Didymella* (one strain), *Epicoccum* (eight strains), *Exophiala* (five strains), *Fonsecaea* (29 strains), *Fusarium* (172 strains), *Hermatomyces* (two strains), *Hypoxylon* (18 strains), *Lasiodiplodia* (170 strains), *Loculosulcatispora* (one strain), *Massaria* (five strains), *Medicopsis* (three strains), *Meyerozyma* (two strains), *Montagnula* (13 strains), *Nemania* (two strains), *Neodeightonia* (one strain), *Neofusicoccum* (one strain), *Neopestalotiopsis* (15 strains), *Neoscytalidium* (25 strains), *Nigrograna* (one strain), *Nigrospora* (41 strains), *Paracamarosporium* (23 strains), *Paraconiothyrium* (11 strains), *Paradictyoarthrinium* (one strain), *Penicillium* (23 strains), *Periconia* (five strains), *Pestalotiopsis* (one strain), *Phaeoacremonium* (28 strains), *Phyllosticta* (18 strains), *Pithomyces* (one strain), *Pseudofusicoccum* (two strains), *Pseudopithomyces* (three strains), *Pseudorobillarda* (one strain), *Rhytidhysteron* (one strain), *Scytalidium* (eight strains), *Talaromyces* (three strains), *Trichoderma* (18 strains), *Veronaea* (two strains), *Xenoroussoella* (four strains), and *Xylaria* (14 strains). Among them, *Fusarium* and *Lasiodiplodia* are the dominant genera, with 172 and 170 strains, respectively, followed by *Colletotrichum* (57 strains), *Diaporthe* (56 strains), *Aspergillus* (42 strains), and *Nigrospora* (41 strains). The remaining genera had fewer than 30 strains each.

Basidiomycota accounted for only 0.63% of all strains and formed well-independent clades in the phylogenetic tree (Fig. 1). Six strains from four genera of four families, isolated from agarwood resin, were identified within the *Basidiomycota*: *Fomitiporia* (three strains), *Phanerochaetella* (one strain), *Phlebiopsis* (one strain), and *Trichosporon* (one strain).

Mucoromycota is the least represented phylum, accounting for only 0.31% of the sequences. Its independent clade in the phylogenetic tree demonstrated significant evolutionary divergence (Fig. 1). Three strains of *Mucor* were isolated from agarwood resin or healthy branches.

Analysis of fungal community composition from each collection site

Community composition analysis of *Aquilaria sinensis*-associated fungi collected from Maoming, Guangdong Province

In total, 219 fungal strains were isolated from *A. sinensis* samples collected in June 2022 from Maoming. All isolated strains from the agarwood resinous parts were categorized as being associated with agarwood fungi. These strains were obtained and identified as belonging to 18 genera, *viz.*, *Aspergillus* (19 strains), *Cladosporium* (one strain), *Colletotrichum* (one strain), *Diaporthe* (five strains), *Exophiala* (five strains), *Fonsecaea* (29 strains), *Fusarium* (92 strains), *Hermatomyces* (one strain), *Hypoxylon* (five strains), *Lasiodiplodia* (16 strains), *Neodeightonia* (one strain), *Nigrograna* (one strain), *Paradictyoarthrinium* (one strain), *Penicillium* (eight strains), *Phaeoacremonium* (22 strains), *Scytalidium* (eight strains), *Trichoderma* (two strains), and *Veronaea* (two strains). As shown in Fig. 2, the most dominant genus is *Fusarium* (92 strains), followed by *Fonsecaea* (29 strains), *Phaeoacremonium* (22 strains), *Aspergillus* (19 strains), and *Lasiodiplodia* (16 strains); in contrast, other genera contain fewer fungal strains.

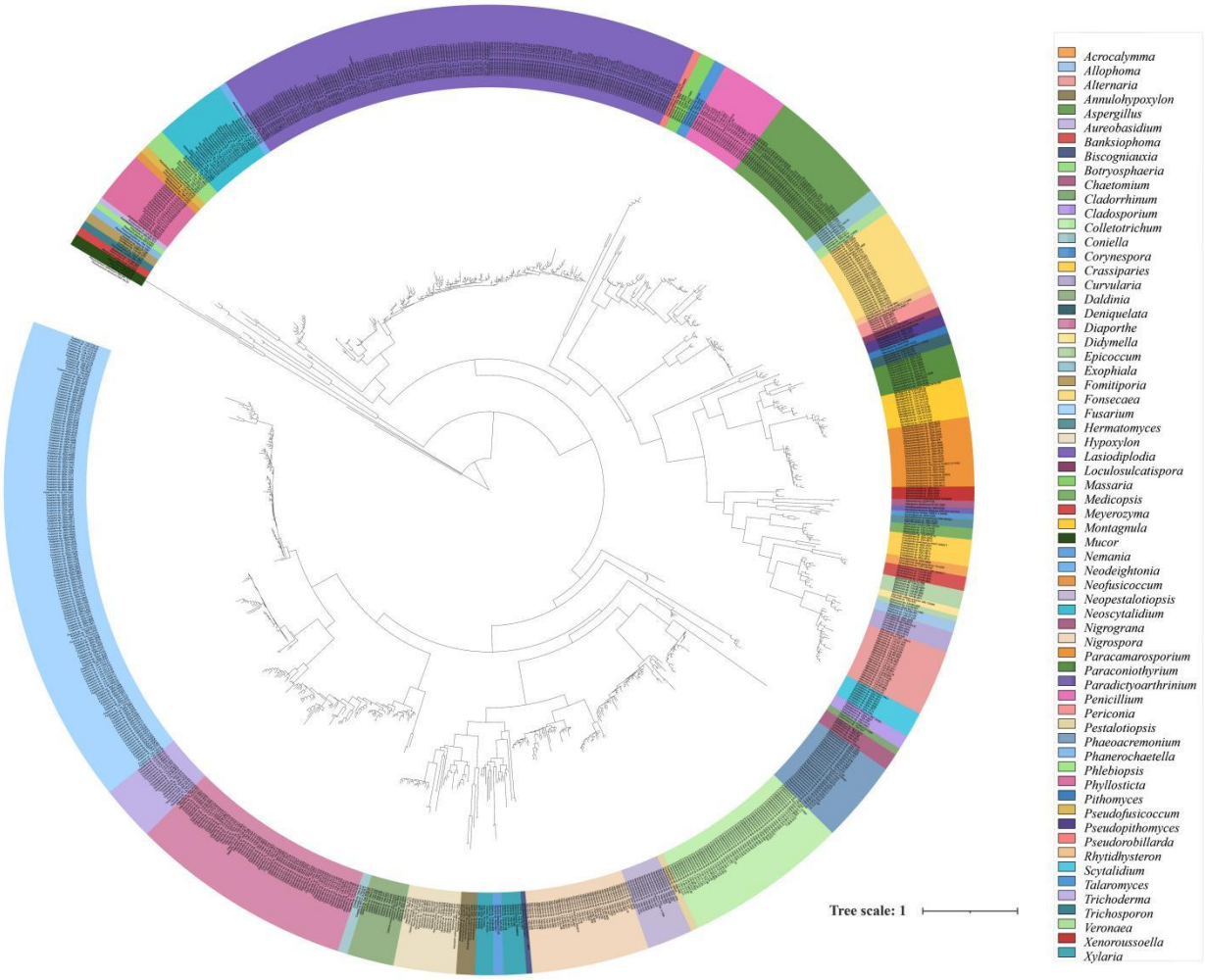

Figure 1 – Circular phylogenetic tree showing the placement of strains at the generic level. The tree was generated using maximum likelihood (RAxML) based on 1,031 ITS sequences and visualized in ITOL (Letunic & Bork, 2007). Different colors indicate independent genera, and the outgroups are *Phlyctochytrium californicum* (CBS 667.73) and *P. africanum* (CBS 454.65) (Chytridiomycota).

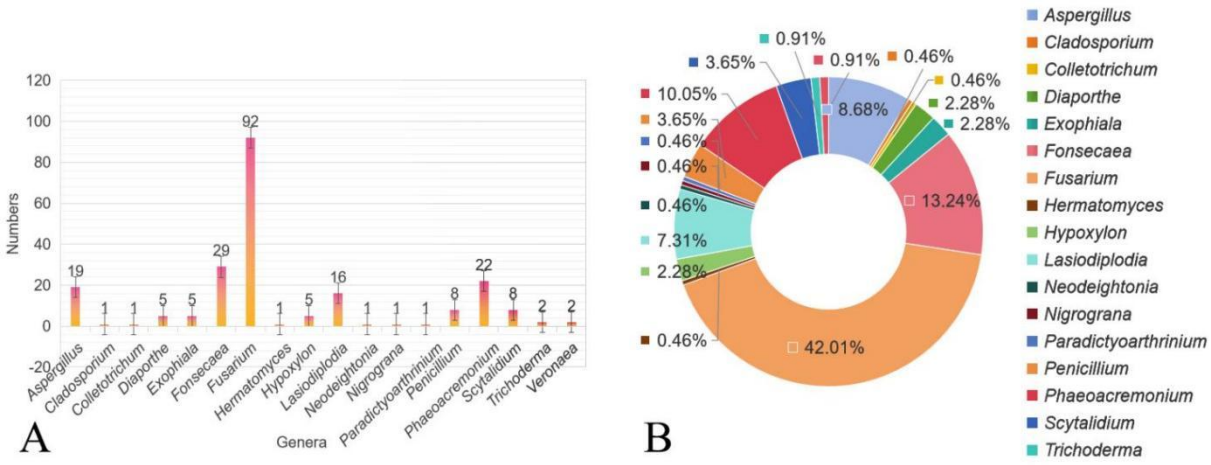

Figure 2 – Column chart with error lines (A) and Donut chart (B) of the quantitative relationships of community composition among different genera in *Aquilaria sinensis*-associated fungi collected from Maoming.

Community composition analysis of *Aquilaria sinensis*-associated fungi collected from Zhanjiang, Guangdong Province

A total of 180 fungal strains were isolated from *A. sinensis* samples collected in October 2020 from Zhanjiang, which were isolated from different parts: agarwood resins, healthy branches, and dead branches (decaying). These strains were identified as belonging to 29 genera: *viz.*, agarwood resins (116 strains of 24 genera), healthy branches (32 strains of 12 genera), and dead branches (32 strains of eight genera). In agarwood resins, the most dominant genus is *Fusarium* (30 strains), followed by *Diaporthe* (21 strains); in healthy branches, the most predominant genus is *Paracamarosporium* (16 strains); and in dead branches, the most dominant genus is *Fusarium* (17 strains). As shown in Fig. 3A, the genus composition and strain distribution are illustrated in agarwood resins, healthy branches, and dead branches, highlighting the number of shared strains and distinct genus compositions.

The distribution of genera in three different collection sites is shown in Fig. 3B; the common genera in all three parts (dead branches, healthy branches, and agarwood resins) are *Diaporthe* and *Paraconiothyrium*, the common genus in dead branches and healthy branches is *Xenoroussoella*, the common genera in dead branches and agarwood resins are *Cladosporium*, *Fusarium*, *Lasiodiplodia*, and *Neopestalotiopsis*, and the common genera in healthy branches and agarwood resins are *Chaetomium*, *Colletotrichum*, *Hypoxylon*, *Nigrospora*, *Paracamarosporium*, and *Pseudopithomyces.*

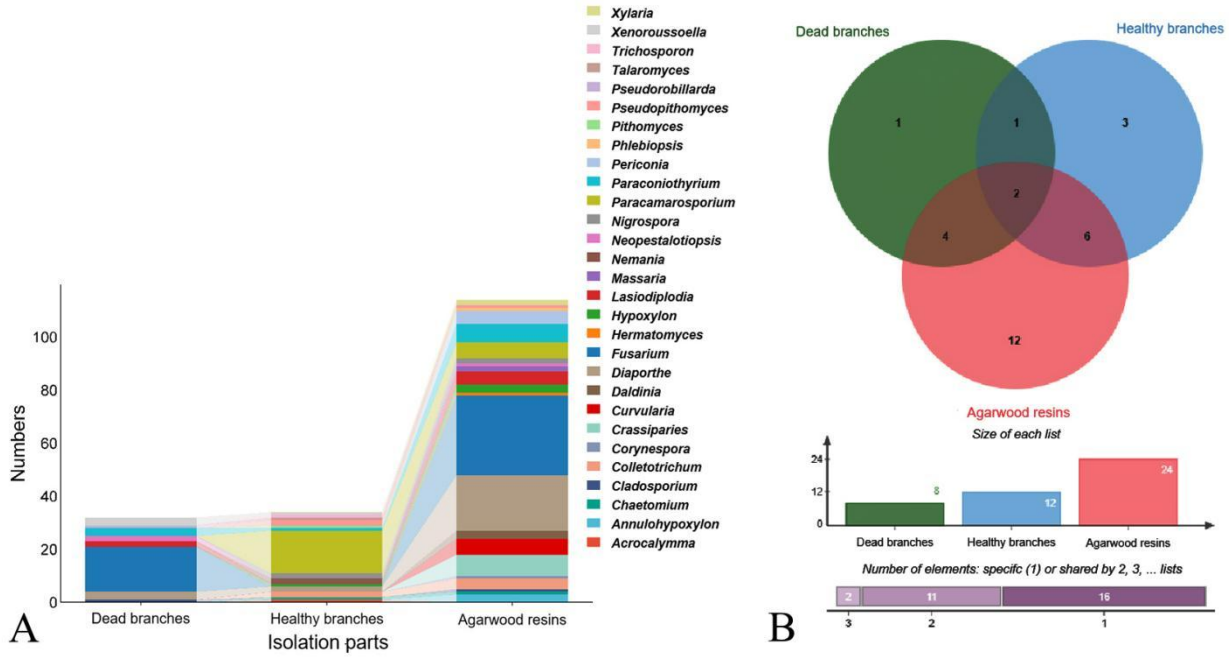

Figure 3 – Link fill bar (A) and Venn diagram (B) of the genus composition in three isolation parts of *Aquilaria sinensis* collected from Zhanjiang.

Community composition analysis of *Aquilaria sinensis*-associated fungi collected from Xishuangbanna, Yunnan Province

A total of 165 fungal strains were isolated from *A. sinensis* samples collected in September 2021 from Xishuangbanna, which were obtained from various parts, such as agarwood resins, healthy branches, and healthy leaves. These strains were identified as belonging to 29 genera: agarwood resins (64 strains of 19 genera), healthy branches (21 strains of 11 genera), and healthy leaves (80 strains of 14 genera).

In agarwood resins, the most dominant genus is *Daldinia* (10 strains); in healthy branches, the most dominant genus is *Lasiodiplodia* (four strains); and in healthy leaves, the most dominant genus

is *Colletotrichum* (24 strains). As shown in Fig. 4A, genus composition and strain distribution are shown in agarwood resins, healthy branches, and healthy leaves, displaying the number of shared strains and different genus compositions.

The distribution of genera in three different collection sites is shown in Fig. 4B; the common genera in all three parts (healthy leaves, healthy branches, and agarwood resins) are *Diaporthe*, *Lasiodiplodia*, *Neopestalotiopsis*, and *Nigrospora*; the common genera in healthy leaves and agarwood resins are *Aspergillus*, *Daldinia*, and *Xylaria*; and the common genera in healthy branches and agarwood resins are *Fusarium*, *Mucor*, *Penicillium*, and *Phaeoacremonium.*

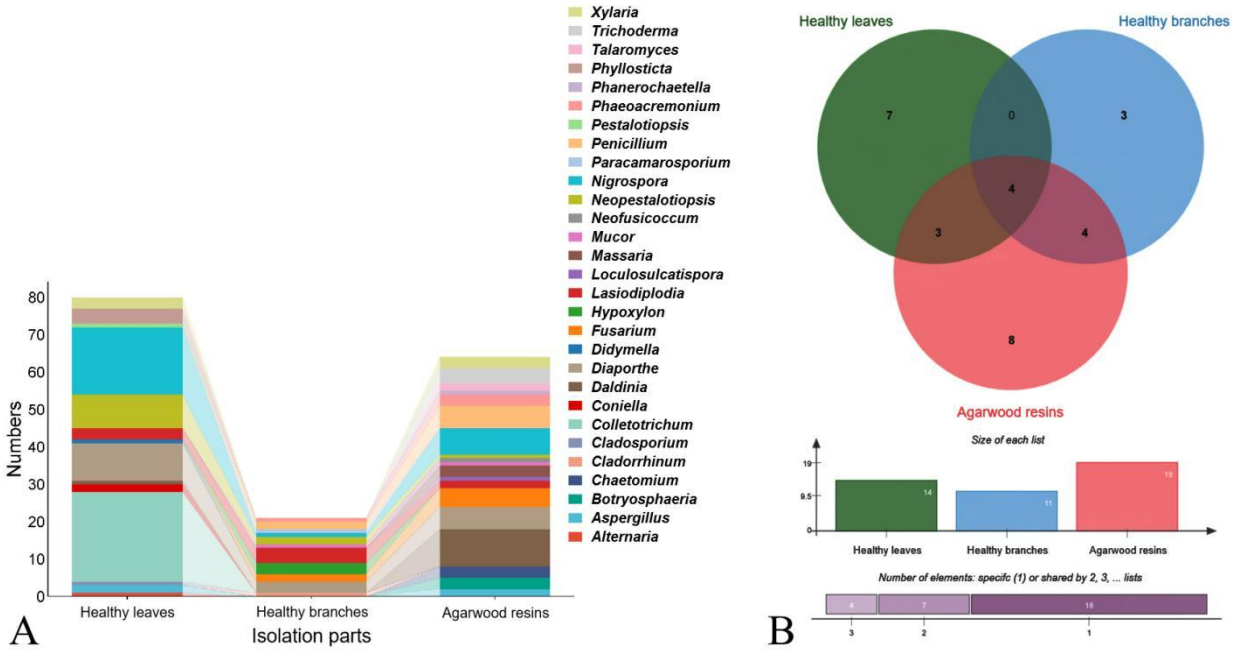

Figure 4 – Link fill bar (A) and Venn diagram (B) of the genus composition in three isolation parts of *Aquilaria sinensis* collected from Xishuangbanna.

Community composition analysis of *Aquilaria sinensis*-associated fungi collected from Yuanjiang, Yunnan Province

In total, 396 fungal strains were isolated from *A. sinensis* samples collected between December 2022 and September 2023 in Yuanjiang, which were isolated from different parts: agarwood resins, healthy branches, healthy leaves, and dead branches (decaying). These strains were identified as belonging to 32 genera: agarwood resins (246 strains of 23 genera), healthy branches (59 strains of 16 genera), healthy leaves (74 strains of 12 genera), and dead branches (17 strains of three genera). In agarwood resins, the most dominant genus is *Lasiodiplodia* (133 strains); in healthy branches, the most dominant genera are *Alternaria* and *Nigrospora* (eight strains); in healthy leaves, the most dominant genus is *Colletotrichum* (21 strains); and in dead branches, the most dominant genus is *Neoscytalidium* (eight strains). As shown in Fig. 5A, genus composition and strain distribution are shown in agarwood resins, healthy branches, healthy leaves, and dead branches, displaying the number of shared strains and different genus compositions.

The distribution of genera in four different collection sites is shown in Fig. 5B; the common genus in dead branches, healthy branches, and agarwood resins is *Aspergillus*; the common genus in dead branches, healthy leaves, and agarwood resins is *Lasiodiplodia*; the common genera in healthy branches, healthy leaves, and agarwood resins are *Alternaria*, *Colletotrichum*, *Diaporthe*, *Hypoxylon*, *Penicillium*, and *Xylaria*; the common genus in healthy branches and agarwood resins is *Trichoderma*; the common genus in dead branches and agarwood resins is *Neoscytalidium*, the

common genus in healthy leaves and agarwood resins is *Annulohypoxylon*, and the common genera in healthy branches and healthy leaves are *Allophoma*, *Epicoccum*, and *Nigrospora.*

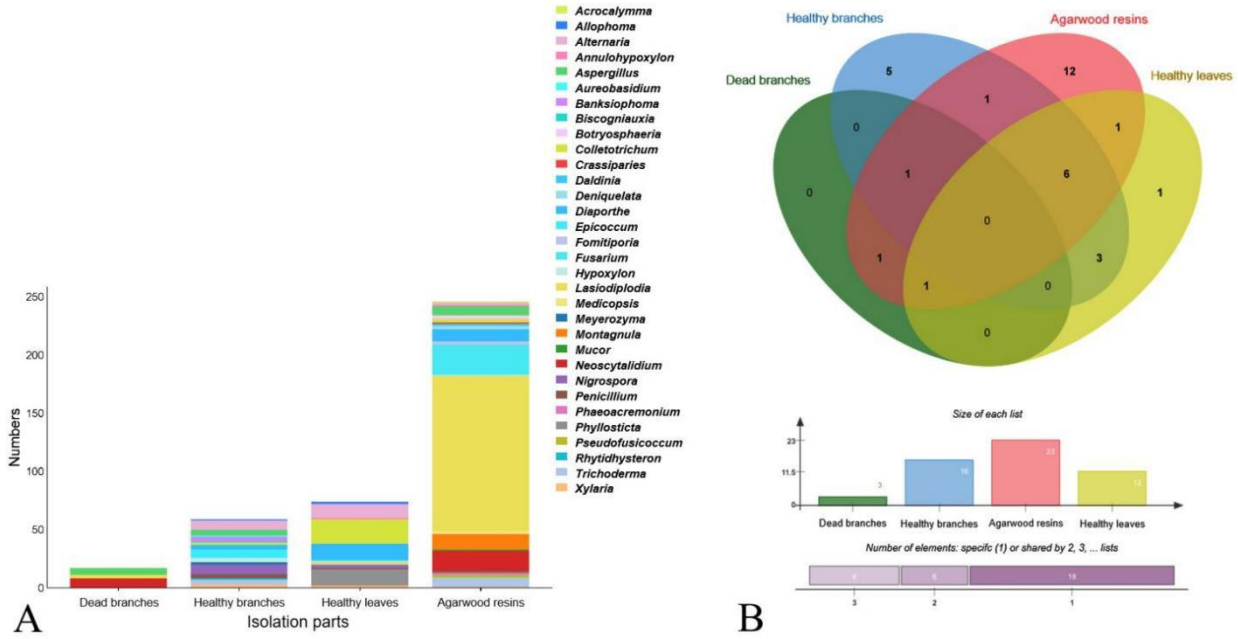

Figure 5 – Vertical stack bar (A) and Venn diagram (B) of the genus composition in four isolation parts of *Aquilaria sinensis* collected from Yuanjiang.

Community composition analysis of *Aquilaria sinensis*-associated fungi from four isolation parts

The 960 strains isolated in this study were isolated from four different parts (agarwood resins, dead branches, healthy branches, and healthy leaves) and subjected to data analysis. These strains were identified as belonging to 64 genera: agarwood resins (645 strains of 48 genera), healthy branches (112 strains of 30 genera), healthy leaves (154 strains of 19 genera), and dead branches (49 strains of 10 genera) (Fig. 6A).

In agarwood resins, the most dominant genera are *Lasiodiplodia* (156 strains) and *Fusarium* (153 strains), followed by *Diaporthe* (42 strains), *Aspergillus* (29 strains), *Fonsecaea* (29 strains), and *Phaeoacremonium* (27 strains); in healthy branches, the most dominant genus is *Paracamarosporium* (17 strains), followed by *Nigrospora* (11 strains) and *Diaporthe* (nine strains); in healthy leaves, the most dominant genus is *Colletotrichum* (45 strains), followed by *Diaporthe* (24 strains) and *Nigrospora* (21 strains); and in dead branches, the most dominant genus is *Fusarium* (17 strains), followed by *Neoscytalidium* (eight strains) and *Aspergillus* (six strains).

Figure 6B shows that the common genera in all four isolation parts are *Aspergillus*, *Diaporthe*, *Lasiodiplodia*, and *Neopestalotiopsis*; the common genera in agarwood resins, healthy branches, and healthy leaves are *Alternaria*, *Colletotrichum*, *Hypoxylon*, *Nigrospora*, *Penicillium*, and *Xylaria*; the common genera in agarwood resins, healthy branches, and dead branches are *Fusarium* and *Paraconiothyrium*; the common genus in agarwood resins, healthy leaves, and dead branches is *Cladosporium*; the common genera in agarwood resins and healthy branches are *Acrocalymma*, *Chaetomium*, *Mucor*, *Paracamarosporium*, *Phaeoacremonium*, *Pseudopithomyces*, and *Trichoderma*; the common genus in dead branches and healthy branches is *Xenoroussoella*; the common genera in healthy leaves and healthy branches are *Allophoma* and *Epicoccum*; the common genera in agarwood resins and healthy leaves are *Annulohypoxylon* and *Daldinia*; and the common genus in agarwood resins and dead branches is *Neoscytalidium*.

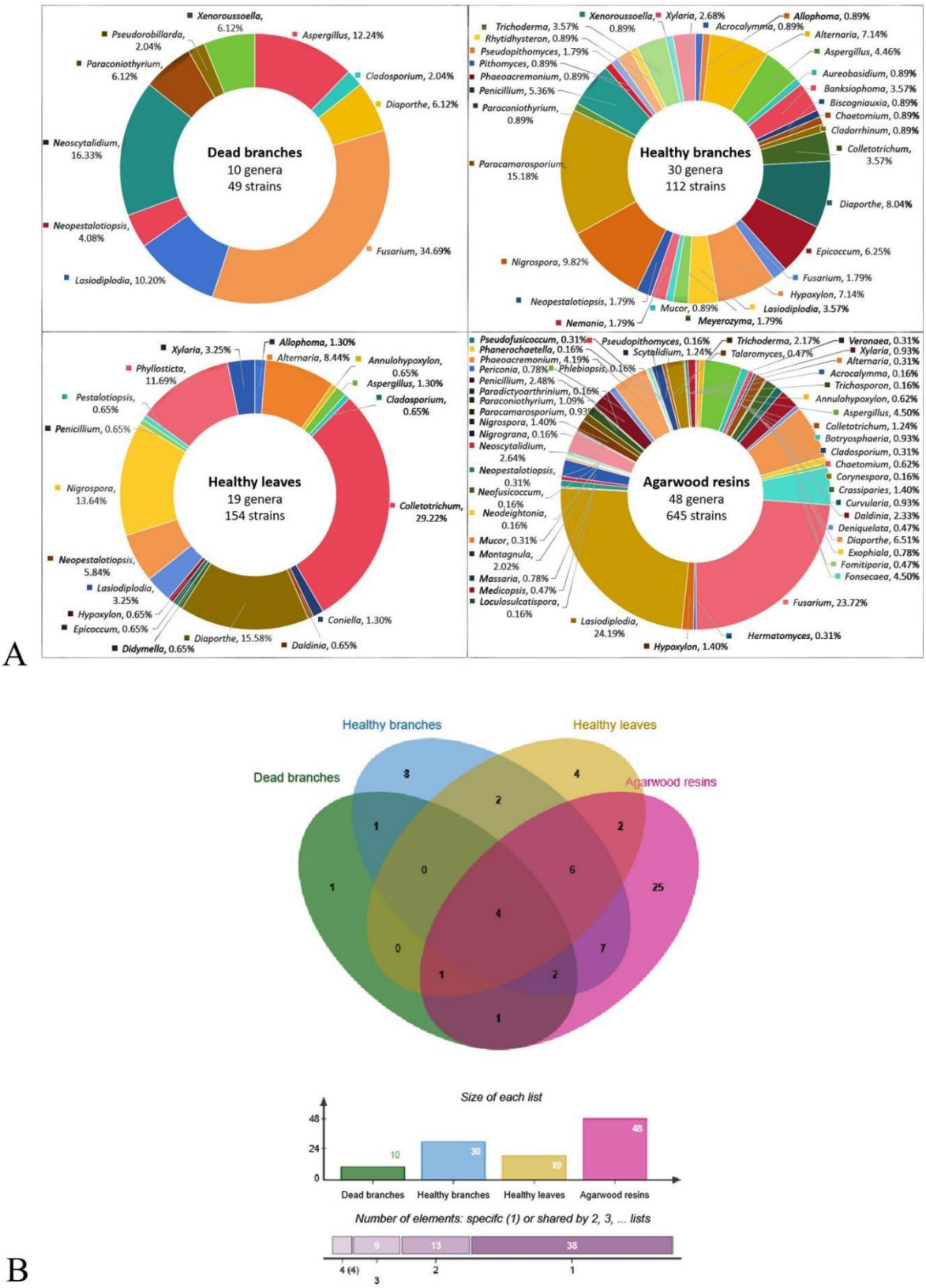

Figure 6 – The Donut chart (A) and Venn diagram (B) of the genus composition of all *Aquilaria sinensis* strains in four isolation parts (agarwood resins, dead branches, healthy branches, and healthy leaves).

Community composition analysis of agarwood-associated fungi from four collection sites

Agarwood resin samples were collected, fungal strains were isolated from all four collection sites (Maoming, Zhanjiang, Xishuangbanna, and Yuanjiang) (Fig. 7A), and the composition of agarwood-associated fungi was analysed.

According to the Venn diagram in Fig. 7B, the result shows that the common genera in all four sites are *Diaporthe*, *Fusarium*, and *Lasiodiplodia*. *Daldinia* and *Xylaria* are present in Zhanjiang, Xishuangbanna, and Yuanjiang; *Aspergillus*, *Penicillium*, *Phaeoacremonium*, and *Trichoderma* can be found in Maoming, Xishuangbanna, and Yuanjiang; *Colletotrichum* and *Hypoxylon* can be found in Maoming, Zhanjiang, and Yuanjiang; *Annulohypoxylon* and *Crassiparies* can be found in Zhanjiang and Yuanjiang; *Botryosphaeria* and *Mucor* can be found in Xishuangbanna and Yuanjiang; *Cladosporium* and *Hermatomyces* can be found in Maoming and Zhanjiang; *Chaetomium*, *Massaria*, *Neopestalotiopsis*, *Nigrospora*, and *Talaromyces* can be found in Zhanjiang and Xishuangbanna.

In summary, strains isolated in this study mainly belong to *Dothideomycetes* (38.28%) and *Sordariomycetes* (49.84%) of *Ascomycota*, a few in *Eurotiomycetes* (10.83%), *Leotiomycetes* (0.84%), and *Saccharomycetes* (0.21%), and some strains with small quantities were isolated from *Basidiomycota* (0.63%) and *Mucoromycota* (0.31%). The genera of strains isolated in different collection sites show an overlap. *Diaporthe*, *Fusarium*, and *Lasiodiplodia* were isolated from all four collection sites (Maoming, Zhanjiang, Xishuangbanna, and Yuanjiang). With regards to strains isolated from different plant parts, strains of *Aspergillus*, *Diaporthe*, *Lasiodiplodia*, and *Neopestalotiopsis* were isolated from all four parts (agarwood resins, dead branches, healthy branches, and healthy leaves). In addition, the genera commonly found in agarwood resins are *Aspergillus*, *Daldinia*, *Diaporthe*, *Fonsecaea*, *Fusarium*, *Lasiodiplodia*, and *Phaeoacremonium*; the genera commonly found in healthy branches are *Alternaria*, *Diaporthe*, *Lasiodiplodia*, *Nigrospora*, and *Paracamarosporium*; the genera commonly found in healthy leaves are *Colletotrichum*, *Diaporthe*, and *Nigrospora*; and the genera commonly found in decaying tree branches are *Aspergillus*, *Fusarium*, *Lasiodiplodia*, and *Neoscytalidium*.

Taxonomy of five new species

In this study, five new species (*Banksiophoma endophytica*, *Deniquelata aquilariae*, *Montagnula sinensis*, *M. yunnanensis*, and *Fomitiporia aquilariae*) are introduced and described based on morphology and phylogenetics. They were isolated from the agarwood resin parts and healthy branches of *Aquilaria sinensis*, mainly belonging to *Ascomycota*, with only *Fomitiporia aquilariae* from *Basidiomycota.*

Banksiophoma Crous 2017

The latest phylogenetic tree of *Banksiophoma* is shown in Fig. 8.

Banksiophoma endophytica T.Y. Du, Tibpromma, K.D. Hyde & Karun. sp. nov. Fig. 9

MycoBank number: MB860352; Facesoffungi number: FoF 18025.

Etymology – The species epithet “endophytica” refers to the endophytic nature of the species.

Holotype – GMB-W1511

Endophytic on a healthy branch of *Aquilaria sinensis* (*Thymelaeaceae*). Asexual morph: on PDA media. *Mycelium* superficial. *Hyphae* 1.5–3 μm wide, brown, smooth- and thin-walled, septate, branched, partial mycelial, with many partitions, some 4–6.5 μm wide, and with guttulate. *Conidiomata* pycnidial, 200–350 μm diam. ($\bar{x}$ = 268 μm), brown to dark brown, aggregated, superficial (on PDA), globose to subglobose, ostiolate. *Pycnidial wall* composed of hyaline to pale brown cells of *textura angularis*, flattened polygonal cells of 4–11 μm diam. ($\bar{x}$ = 7 μm). *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* 11–17 × 3–5.5 μm ($\bar{x}$ = 13.7 × 4 μm), phialidic, hyaline, smooth-walled, proliferating percurrently at apex. *Conidia* 3.5–6 × 1.5–3 μm ($\bar{x}$ = 4.5 × 2 μm), oblong or subglobose or oval, aseptate, hyaline, smooth- and thin-walled, guttulate. Sexual morph: undetermined.

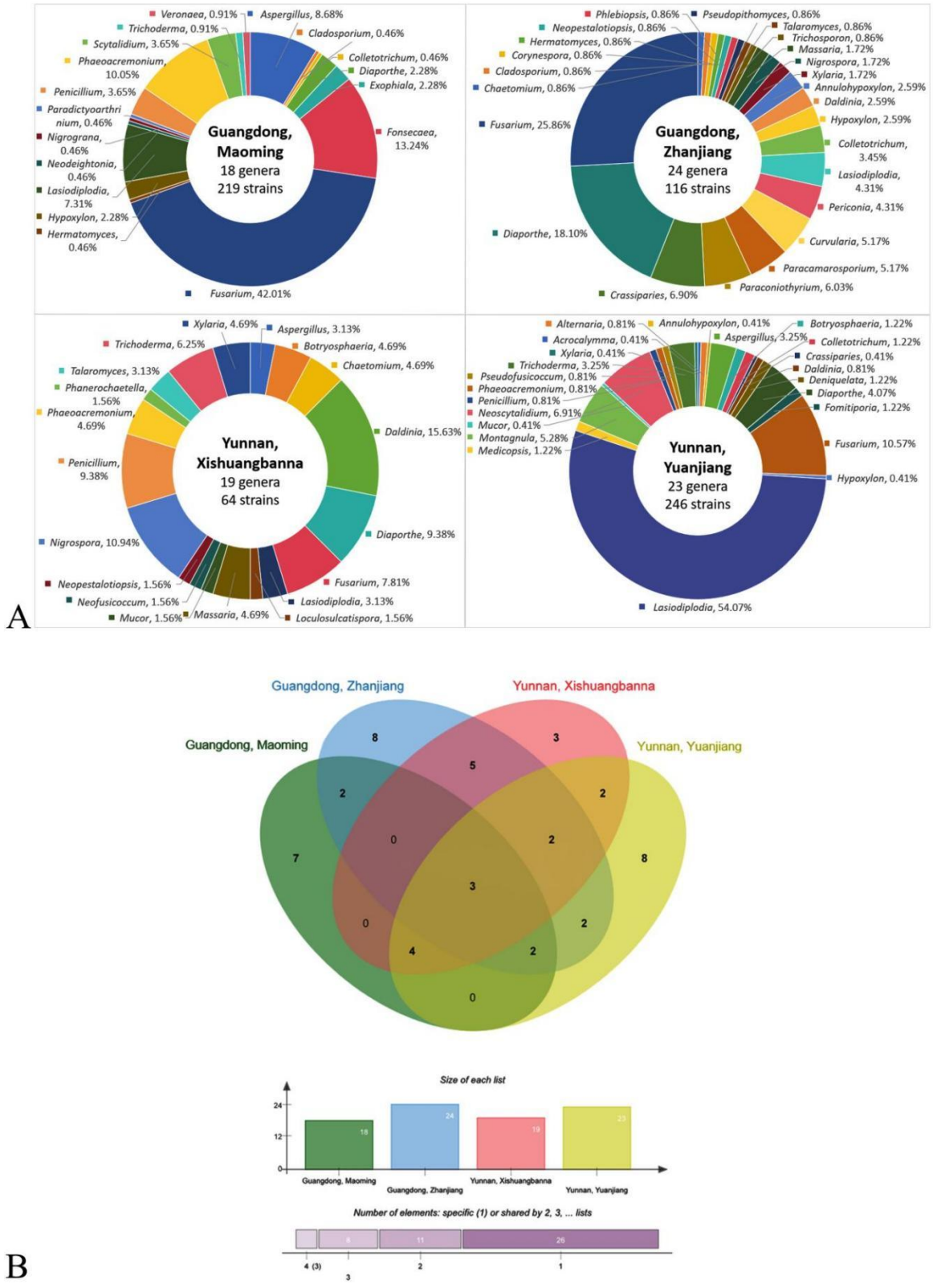

Figure 7 – The Donut chart (A) and Venn diagram (B) of the genus composition of all agarwood-associated fungal strains in four collection sites (Maoming, Zhanjiang, Xishuangbanna, and Yuanjiang).

Culture characteristics – Colonies on PDA at room temperature (23–28 °C) reaching 5 cm in one month; irregular, grey-white, with a dark grey-brown outer ring, irregular raised, lobate edge; grey to dark brown from below, irregular dark sediment. Sporulation in PDA after one month, and without pigmentation produced in PDA.

Material examined – CHINA, Yunnan Province, Yuxi City, Yuanjiang County, on a healthy branch of *Aquilaria sinensis* (*Thymelaeaceae*), 18 September 2023, T.Y. Du, YNA-YJA-BH-B04 (GMB-W1511 dried culture, holotype), preserved in a metabolically inactive state at Guizhou Medical University (GMB-W), China; ex-type GMBCC1187; *ibid.*, YNA-YJA-BH-B06, living culture GMBCC1188.

GenBank numbers – GMBCC1187: ITS = PQ346648, LSU = PX091384, SSU = PX091366, *rpb*2 = PX101317, *tef*1-α = PX101335; GMBCC1188: ITS = PQ346649, LSU = PX091385, SSU = PX091367, *rpb*2 = PX101318, *tef*1-α = PX101336.

Notes – In the phylogenetic analyses, *Banksiophoma endophytica* clustered with *B. australiensis* (CBS 142163, ex-type) and *B. dissensa* (MUM24.07: ex-type, MUM24.08) with 100% in ML and 1.00 in BYPP statistical support (Fig. 8). Morphologically, *B. endophytica* is consistent with the basic characteristics of *Banksiophoma* in having pycnidial conidiomata, brown, globose, and conidia solitary, hyaline, smooth, guttulate, aseptate (Crous et al. 2017). However, *B. endophytica* differs from *B. australiensis* (CBS 142163, ex-type) in having phialidic conidiogenous cells, oblong or subglobose or oval conidia, while *B. australiensis* (CBS 142163, ex-type) has subcylindrical to ampulliform conidiogenous cells and ellipsoid to globose or subglobose conidia (Crous et al. 2017). *Banksiophoma endophytica* differs from *B. dissensa* (MUM24.07, ex-type) in having conidiomata, conidiogenous cells, and solitary conidia, not in chains, while *B. dissensa* (MUM24.07, ex-type) has microsclerotia and conidia, mostly arthric, forming acropetal conidial chains (Paiva et al. 2025). The nucleotide base pair differences (without gaps) between our new strain (GMBCC1187, ex-type) and *B. australiensis* (CBS 142163, ex-type) were compared, and the results revealed 9.62% (ITS), 1.08% (LSU), and 17.17% (*rpb*2) base pair differences; in contrast, the SSU and *tef*1-α genes sequences of *B. australiensis* (CBS 142163, ex-type) are unavailable. The results of nucleotide base pair differences (without gaps) between our new strain (GMBCC1187, ex-type) and *B. dissensa* (MUM24.07, ex-type) revealed 9.15% (ITS), 1.08% (LSU), 0.13% (SSU), and 5.26% (*tef*1-α) base pair differences, while the *rpb*2 sequence of *B. dissensa* (MUM24.07, ex-type) is unavailable. Based on morphological and molecular evidence and following the guidelines of Pem et al. (2021), *B. endophytica* is introduced herein as a new species from Yunnan Province, China.

Deniquelata H.A. Ariy. & K.D. Hyde 2013

The latest phylogenetic tree of *Deniquelata* is shown in Fig. 10, and Fig. 11 is the PHI test results.

Deniquelata aquilariae T.Y. Du, Tibpromma, K.D. Hyde & Karun. sp. nov. Fig. 12.

MycoBank number: MB860353; Facesoffungi number: FoF 18026.

Etymology – Named after its host genus, *Aquilaria.*

Holotype – GMB-W1513

Diagnosis. Colonies on PDA at room temperature (23–28 °C) reaching 4–5 cm in one week; circular, white, flossy, velvety, raised, entire edge; from below: white to light yellow from the outer ring to the middle. Generative hyphae simple-septate, branched, septate, thin-walled, subhyaline, 1.5–2.5 µm wide. Not sporulating in WA and PDA media during the six-month observation period.

Material examined – CHINA, Yunnan Province, Yuxi City, Yuanjiang County, on agarwood resin part of *Aquilaria sinensis* (*Thymelaeaceae*), 18 September 2023, T.Y. Du, YNA-YJA-CA-C06 (GMB-W1513 dried culture, holotype), preserved in a metabolically inactive state at Guizhou Medical University (GMB-W), China; ex-type GMBCC1063; *ibid.*, YNA-YJA-CA-C04, living culture GMBCC1064.

GenBank numbers – GMBCC1063: ITS = PQ346638, LSU = PX091386, SSU = PX091368, *rpb*2 = PX101319, *tef*1-α = PX101337; GMBCC1064: ITS = PQ346639, LSU = PX091387, SSU = PX091369, *rpb*2 = PX101320, *tef*1-α = PX101338.

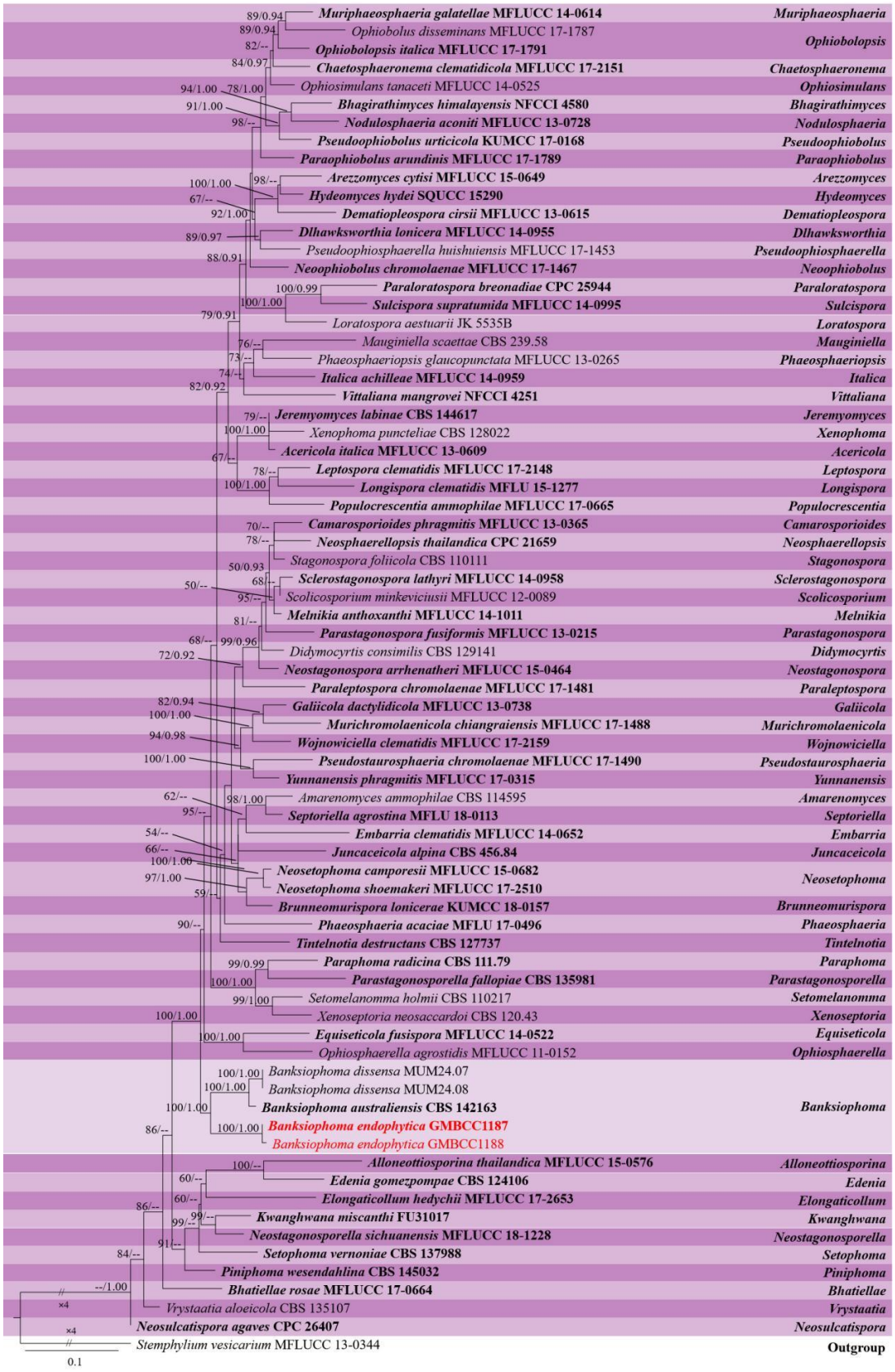

Figure 8 – Phylogram generated from maximum likelihood (ML) analysis based on combined ITS, LSU, *rpb*2, SSU, and *tef*1-α sequence data of 72 taxa, which comprised 4132 base pairs of ITS = 1–

426, LSU = 427–1307, *rpb*2 = 1308–2262, SSU = 2263–3264, *tef*1-α = 3265–4132. The best-scoring RAxML tree with a final likelihood value of -30781.965461 is presented. The matrix contained 1,551 distinct alignment patterns, with 33.90% of the characters being undetermined or gaps. Estimated base frequencies were as follows: A = 0.248134, C = 0.237194, G = 0.266257, T = 0.248415; substitution rates: AC = 1.183565, AG = 3.568373, AT = 2.178998, CG = 0.654796, CT = 7.023637, GT = 1.0; gamma distribution shape parameter α = 0.379670. Bootstrap support values for ML equal to or greater than 50% and clade credibility values equal to or greater than 0.90 from Bayesian inference analysis are labelled at each node. The tree is rooted with *Stemphylium vesicarium* (MFLUCC 13-0344). The new isolates are indicated in red, and the ex-type strains are in bold.

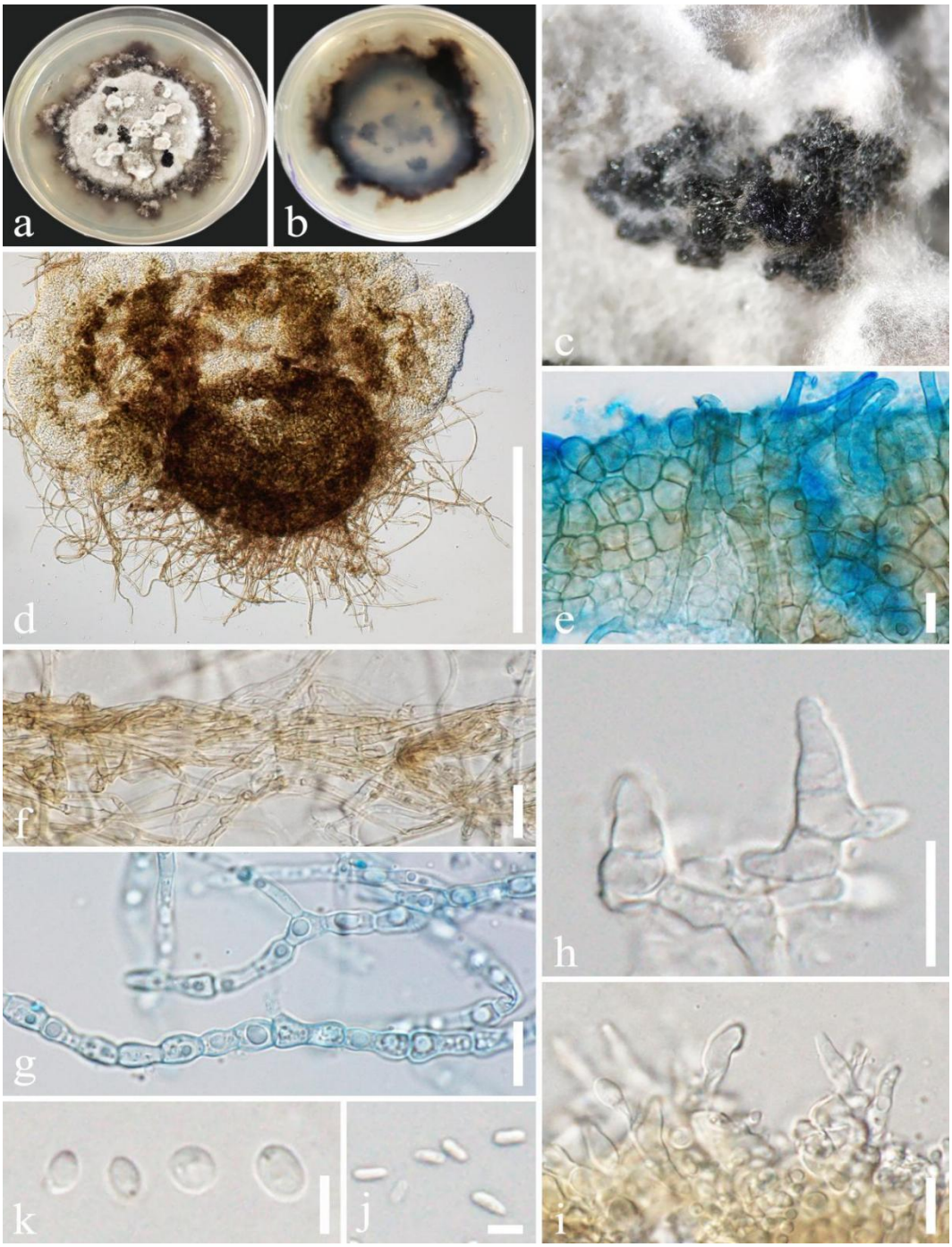

Figure 9 – ***Banksiophoma endophytica*** (GMBCC1187, ex-type). a, b Colony on PDA at room temperature after one month from above and below. c Gathered conidiomata grow on PDA. d Squash mount of conidiomata. e Peridium stained with cotton blue. f Mycelia masses. g Mycelia stained with cotton blue. h, i Conidiogenous cells. j, k Conidia. Scale bars: d = 300 µm, e-i = 10 µm, j, k = 5 µm.

Notes – Based on BLASTn searches of ITS, LSU, *rpb*2, SSU, and *tef*1-α sequence data, our new strain *Deniquelata aquilariae* showed a high similarity to *D. barringtoniae* (Y79, MN268538, 99.84%) in ITS, *D. barringtoniae* (MFLUCC 16-0271, MH260291, 99.29%) in LSU, *Deniquelata* sp. (20SA, MH316155, 99.70%) in SSU, *D. hypolithi* (CPC 38968, MZ078250, 96.89%) in *tef*1-α, *D. hypolithi* (CPC 38968, MZ078201, 93.85%) in *rpb*2. In the phylogenetic analyses, *D. aquilariae* is sister to seven strains of *D. barringtoniae*, with 99% ML and 1.00 BYPP statistical support (Fig. 10). Our strain also constitutes a highly supported independent lineage closely related to seven strains of *D. barringtoniae*. The PHI test results (Fig. 11) indicated no significant recombination events between *D. aquilariae* and its phylogenetically related taxa. The newly described strains did not sporulate in culture, so their morphological characteristics could not be compared with those of *D. barringtoniae*. The ITS, LSU, and SSU loci of nucleotide base pair differences (without gaps) between our new strain (GMBCC1063, ex-type) and *D. barringtoniae* (MFLUCC 11-0422, ex-type) were compared; the results revealed 0.15% in ITS, and no differences in LSU and SSU, while the *rpb*2 and *tef*1-α sequences of *D. barringtoniae* (MFLUCC 11-0422, ex-type) are unavailable. Therefore, the *rpb*2 and *tef*1-α genes of another strain, *D. barringtoniae* (MFLUCC 16-0271), were used to compare with our strain (GMBCC1063, ex-type), and the results revealed base pair differences of 10.8% in *tef*1-α and 1.58% in *rpb*2. Based on molecular evidence, *D. aquilariae* is introduced herein as a new species from the agarwood resin part of *Aquilaria sinensis* from Yunnan Province, China.

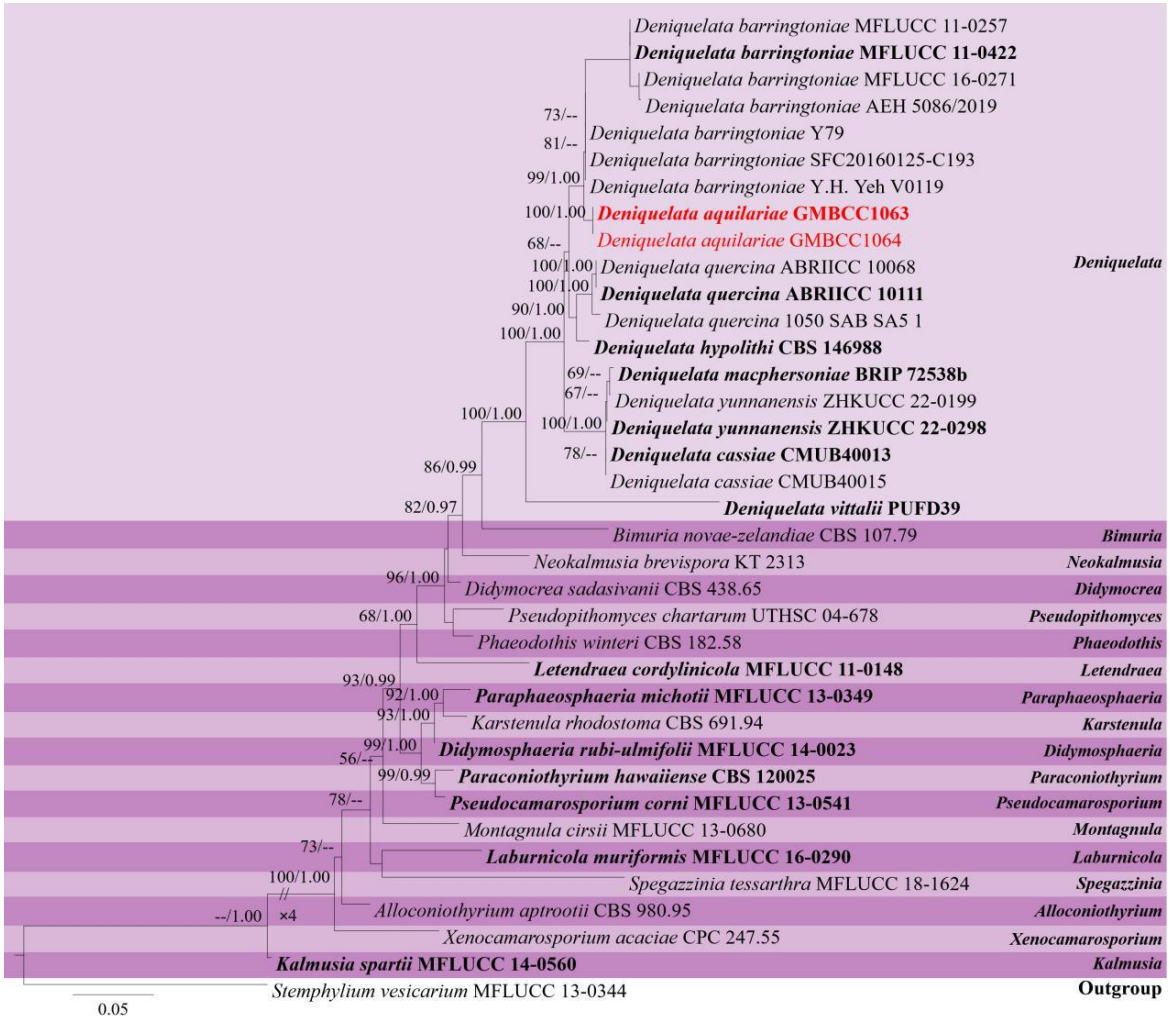

Figure 10 –Phylogram generated from maximum likelihood (ML) analysis based on combined ITS, LSU, *rpb*2, SSU, and *tef*1-α sequence data of 37 taxa, which comprised 4506 base pairs of ITS = 1–711, LSU = 712–1510, *rpb*2 = 1511–2660, SSU = 2661–3587, *tef*1-α = 3588–4506. The best-scoring

RAxML tree with a final likelihood value of -16492.242256 is presented. The matrix contained 1004 distinct alignment patterns, with 49.83% of the characters being undetermined or gaps. Estimated base frequencies were as follows: A = 0.232415, C = 0.256914, G = 0.278620, T = 0.232052; substitution rates: AC = 1.552719, AG = 2.595896, AT = 1.330019, CG = 0.986871, CT = 6.740942, GT = 1.0; gamma distribution shape parameter α = 0.532734. Bootstrap support values for ML equal to or greater than 50% and clade credibility values equal to or greater than 0.90 from Bayesian inference analysis are labelled at each node. The tree is rooted with *Stemphylium vesicarium* (MFLUCC 13-0344). The new isolates are indicated in red, and the ex-type strains are in bold.

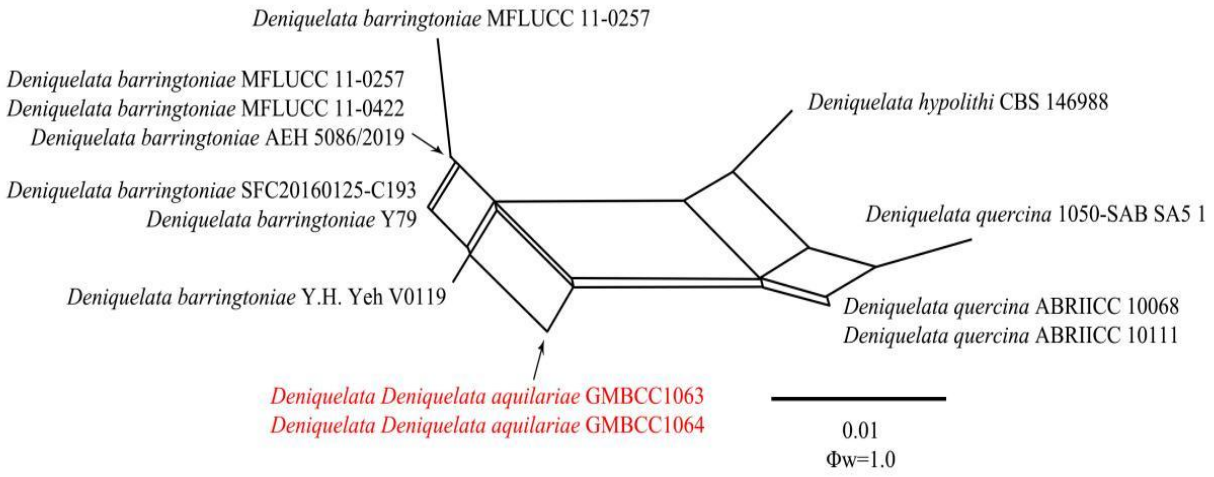

Figure 11 – Split graphs showing the results of the PHI test of *Deniquelata aquilariae* and closely related taxa using LogDet transformation and splits decomposition. The PHI test result, $\Phi w \leq 0.05$, indicates a significant recombination within the dataset. The new isolates are indicated in red.

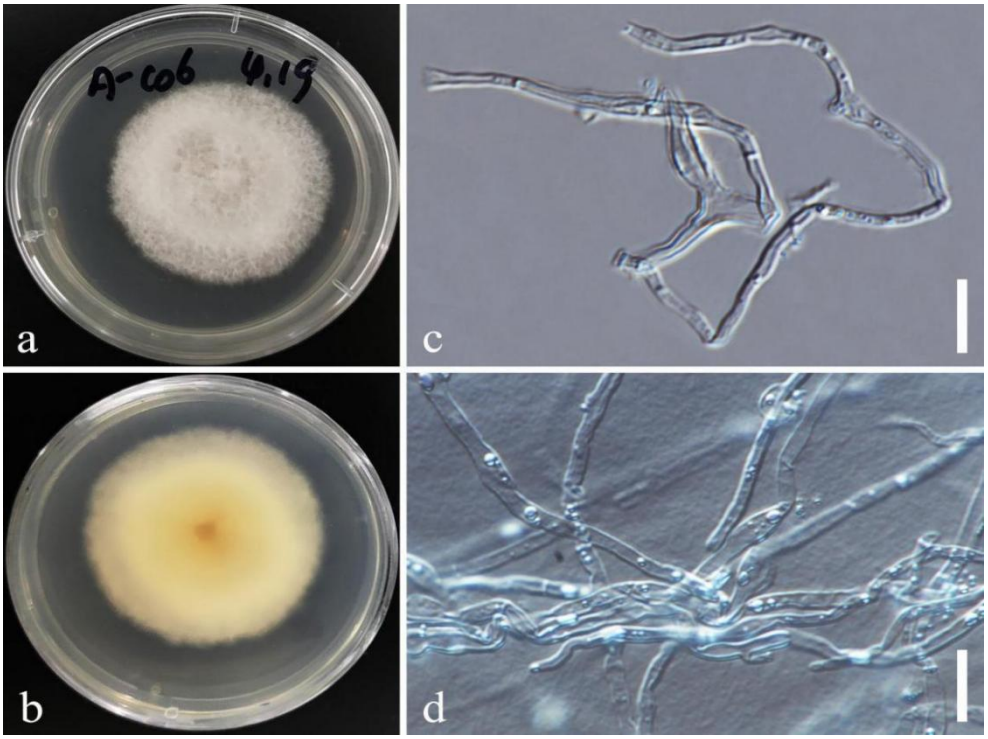

Figure 12 – ***Deniquelata aquilariae*** (GMBCC1063, ex-type). a, b Colony on PDA at room temperature after one week from above and below. c, d Mycelia masses. Scale bars: c, d = 10 µm.

Montagnula Berl. 1896

The latest phylogenetic tree of *Montagnula* is shown in Fig. 13, and Fig. 14 is the PHI test results.

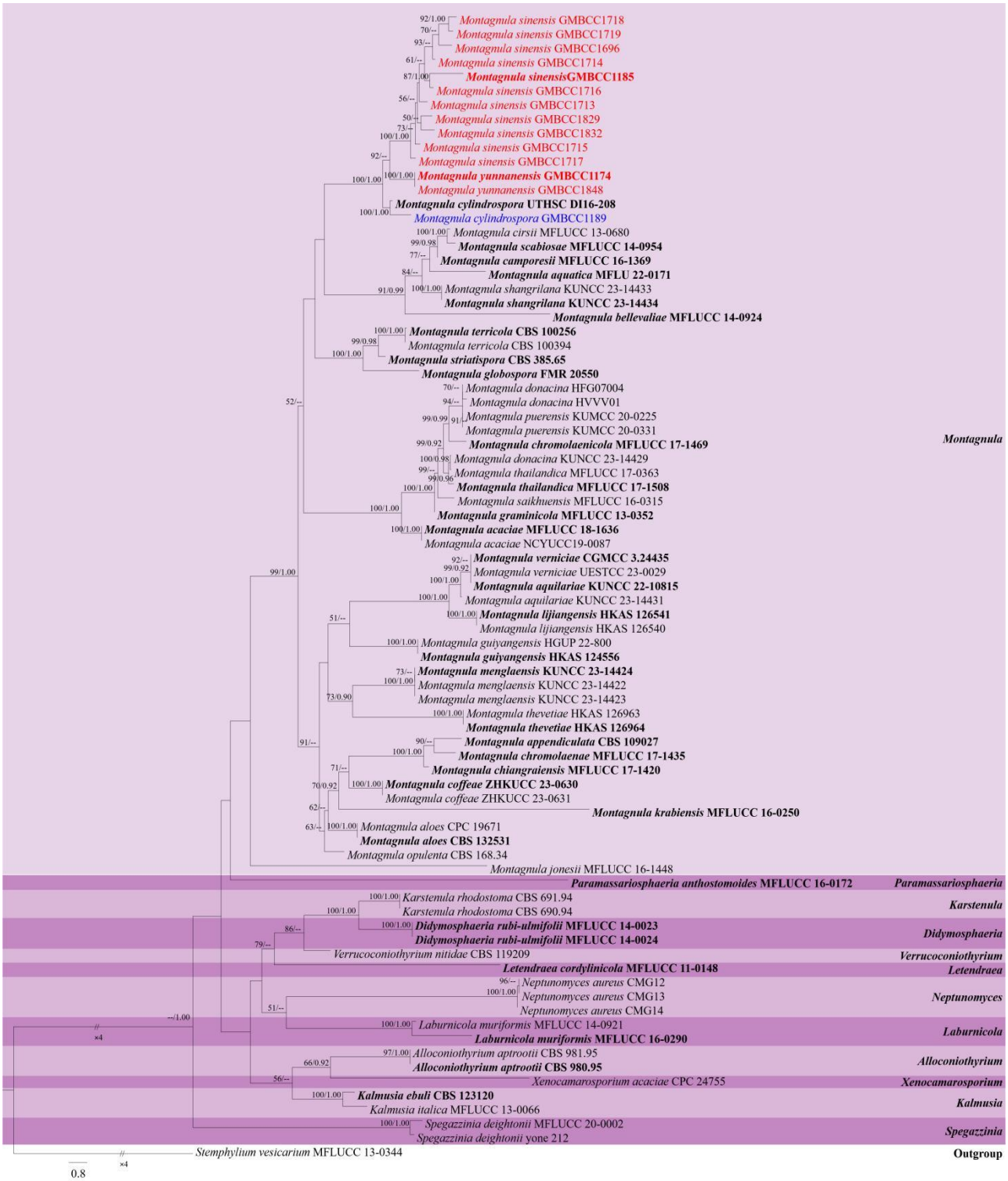

Figure 13 –Phylogram generated from maximum likelihood (ML) analysis based on combined ITS, LSU, *rpb*2, SSU, and *tef*1-α sequence data of 81 taxa, which comprised 4441 base pairs of ITS = 1–531, LSU = 532–1477, *rpb*2 = 1478–2432, SSU = 2433–3404, *tef*1-α = 3405–4441. The best-scoring RAxML tree with a final likelihood value of -22038.568199 is presented. The matrix contained 1,470 distinct alignment patterns, with 32.20% of the characters being undetermined or gaps. Estimated base frequencies were as follows: A = 0.241950, C = 0.253294, G = 0.270082, T = 0.234673; substitution rates: AC = 1.019692, AG = 2.294466, AT = 1.102568, CG = 0.914410, CT = 5.540507, GT = 1.0; gamma distribution shape parameter α = 0.436674. Bootstrap support values for ML equal

to or greater than 50% and clade credibility values equal to or greater than 0.90 from Bayesian inference analysis are labelled at each node. The tree is rooted with *Stemphylium vesicarium* (MFLUCC 13-0344). The new species are indicated in red; the new record is indicated in blue, and the ex-type strains are in bold.

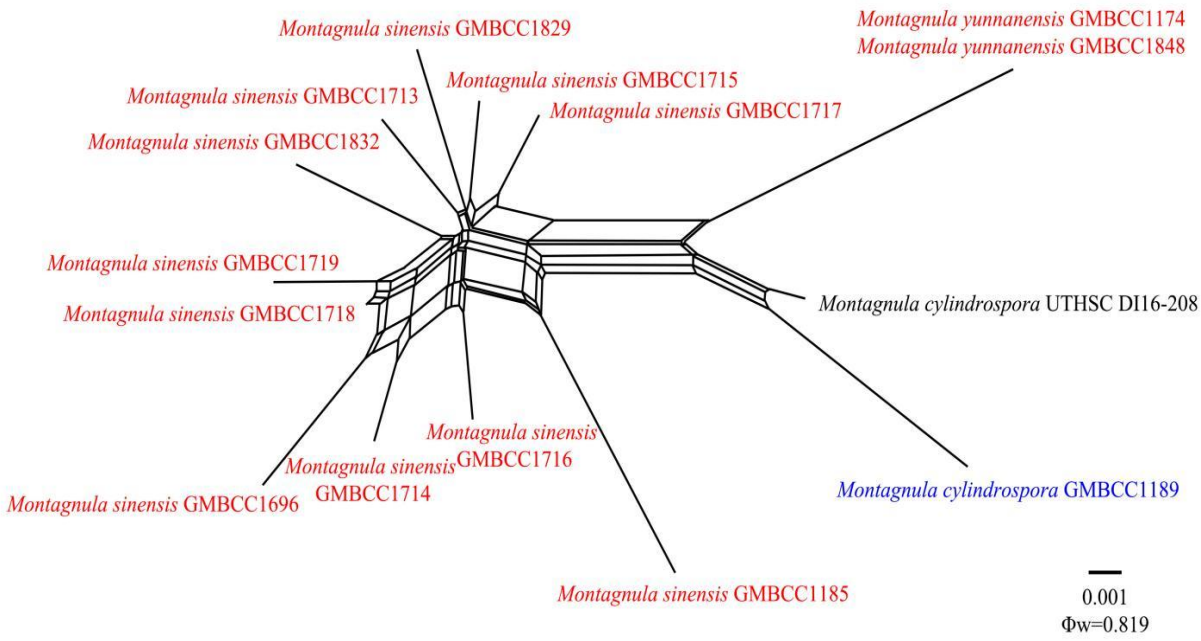

Figure 14 – Split graphs showing the results of the PHI test of *Montagnula cylindrospora* and closely related taxa using LogDet transformation and splits decomposition. The PHI test result, $\Phi w \leq 0.05$, indicates a significant recombination within the dataset. The new species are indicated in red, and the new record is indicated in blue.

Montagnula cylindrospora Valenz.-Lopez, Cano, Guarro & Stchigel (2020) Fig. 15

MycoBank number: MB 834472.

Endophytic on agarwood resin part of *Aquilaria sinensis* (*Thymelaeaceae*). Asexual morph: on WA media. *Mycelium* superficial. *Hyphae* 4–7 µm wide, hyaline to pale brown, smooth- and thin-walled, septate, branched, partial mycelial ends swell into spherical shapes. *Conidiomata* pycnidial, 100–150 µm diam. ($\bar{x}$ = 125 µm), brown to dark brown, solitary, individual or aggregated, superficial (on water agar, WA), globose to subglobose, ostiolate. *Pycnidial wall* composed of brown to dark brown cells of *textura angularis*, flattened polygonal cells of 4.5–11 µm diam. ($\bar{x}$ = 7.1 µm). *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* 6–14 × 1.5–3 µm ($\bar{x}$ = 10 × 2.2 µm), phialidic to ampulliform, hyaline, smooth-walled. *Conidia* 3–5(–6) × 1.8–4 µm ($\bar{x}$ = 3.9 × 2.8 µm), cylindrical or globose to subglobose, solitary, aseptate, hyaline, smooth- and thin-walled, guttulate. Sexual morph: undetermined.

Culture characteristics – Colonies on PDA at room temperature (23–28 °C) reaching 3 cm in one month; circular, white, flossy, raised, irregular edge, part of the mycelia grow irregularly in the peripheral culture medium; peripheral white, inner part yellow from below. Sporulation in WA after one month, and without pigments produced in WA.

Material examined – CHINA, Yunnan Province, Yuxi City, Yuanjiang County, on agarwood resin part of *Aquilaria sinensis* (*Thymelaeaceae*), 22 June 2023, T.Y. Du, YNA-YJA-TJ06-04 (GMB-W1516), preserved in a metabolically inactive state at Guizhou Medical University (GMB-W), China; living culture GMBCC1189.

GenBank numbers – GMBCC1189: ITS = PQ346643, LSU = PX091388, *rpb*2 = PX101321, SSU = PX091370, *tef*1-α = PX101339.

Notes – In the phylogenetic analyses, our strain clustered with *M. cylindrospora* (UTHSC DI16-208, ex-type) with 100% in ML and 1.00 in BYPP statistical support (Fig. 13). Morphologically, our isolate resembles *M. cylindrospora* (UTHSC DI16-208, ex-type) in having pycnidial conidiomata that are brown to dark brown, solitary, superficial, globose to subglobose, with hyaline conidiogenous cells, phialidic, ampulliform to doliiform, smooth-walled, and hyaline conidia, all of which are aseptate (Crous et al. 2020). *Montagnula cylindrospora* was introduced by Crous et al. (2020) from a human skin sample in the USA, where its conidia were described as cylindrical. However, in this study, we also observed conidia with shapes ranging from globose to subglobose. Based on morphological and molecular evidence, our isolate is introduced herein as a new geographical and host record on the agarwood resin part of *Aquilaria sinensis* from Yunnan Province, China.

Montagnula sinensis T.Y. Du, Tibpromma, K.D. Hyde & Karun. sp. nov. Fig. 16

MycoBank number: MB860355; Facesoffungi number: FoF 18027.

Etymology – The epithet "*sinensis*" refers to the type locality "China".

Holotype – GMB-W1510

Endophytic on agarwood resin part of *Aquilaria sinensis* (*Thymelaeaceae*). Asexual morph: on WA media. *Mycelium* superficial. *Hyphae* 3.5–5.5 μm wide, hyaline, smooth- and thin-walled, septate, branched, partial mycelial ends swell into spherical shapes. *Conidiomata* pycnidial, 150–400 μm diam. ($\bar{x}$ = 285 μm), brown to dark brown, solitary, individual or aggregated, superficial, globose to subglobose, ostiolate. *Pycnidial wall* composed of hyaline to pale brown cells of *textura angularis*, flattened polygonal cells of 2.8–7.5 μm diam. ($\bar{x}$ = 4.4 μm). *Conidiophores* 17–35 × 2.5–4 μm ($\bar{x}$ = 23.5 × 3.2 μm), subcylindrical, septate, hyaline. *Conidiogenous cells* 6–12 μm long ($\bar{x}$ = 8.5 μm), phialidic, ampulliform with conical apex, hyaline, smooth-walled. *Conidia* 3.5–5 × 1.5–2 μm ($\bar{x}$ = 4.1 × 1.7 μm), solitary, cylindrical, aseptate, hyaline, smooth- and thin-walled, guttulate. Sexual morph: undetermined.

Culture characteristics – Colonies on PDA at room temperature (23–28 °C) reaching 3 cm in one week; circular, white, flossy, flat, entire edge; outer ring white to cream, inner ring yellow in reverse. Sporulation in WA after one month, and without pigments produced in WA.

Material examined – CHINA, Yunnan Province, Yuxi City, Yuanjiang County, on agarwood resin part of *Aquilaria sinensis* (*Thymelaeaceae*), 22 June 2023, T.Y. Du, YNA-YJA-TH09-04 (GMB-W1510 dried culture, holotype), preserved in a metabolically inactive state at Guizhou Medical University (GMB-W), China; ex-type GMBCC1185; *ibid.*, other living cultures: YNA-YJA-CA-C02, GMBCC1829; YNA-YJA-CA-C05, GMBCC1832; YNA-YJA-TA12-06, GMBCC1696; YNA-YJA-TF12-01, GMBCC1713; YNA-YJA-TF12-02, GMBCC1714; YNA-YJA-TF12-03, GMBCC1715; YNA-YJA-TF12-04, GMBCC1716; YNA-YJA-TF12-05, GMBCC1717; YNA-YJA-TF12-06, GMBCC1718; YNA-YJA-TF12-07, GMBCC1719.

GenBank numbers – GMBCC1185: ITS = PQ346644, LSU = PX091389, *rpb*2 = PX101322, SSU = PX091371, *tef*1-α = PX101340; GMBCC1829: ITS = PX088640, LSU = PX091390, *rpb*2 = PX101323, SSU = PX091372, *tef*1-α = PX101341; GMBCC1832: ITS = PX088643, LSU = PX091391, *rpb*2 = PX101324, SSU = PX091373, *tef*1-α = PX101342; GMBCC1696: ITS = PX070383, LSU = PX091392, *rpb*2 = PX101325, SSU = PX091374, *tef*1-α = PX101343; GMBCC1713: ITS = PX070400, LSU = PX091393, *rpb*2 = PX101326, SSU = PX091375, *tef*1-α = PX101344; GMBCC1714: ITS = PX070401, LSU = PX091394, *rpb*2 = PX101327, SSU = PX091376, *tef*1-α = PX101345; GMBCC1715: ITS = PX070402, LSU = PX091395, *rpb*2 = PX101328, SSU = PX091377, *tef*1-α = PX101346; GMBCC1716: ITS = PX070403, LSU = PX091396, *rpb*2 = PX101329, SSU = PX091378, *tef*1-α = PX101347; GMBCC1717: ITS = PX070404, LSU = PX091397, *rpb*2 = PX101330, SSU = PX091379, *tef*1-α = PX101348; GMBCC1718: ITS = PX070405, LSU = PX091398, *rpb*2 = PX101331, SSU = PX091380, *tef*1-α = PX101349; GMBCC1719: ITS = PX070406, LSU = PX091399, *rpb*2 = PX101332, SSU = PX091381, *tef*1-α = PX101350.

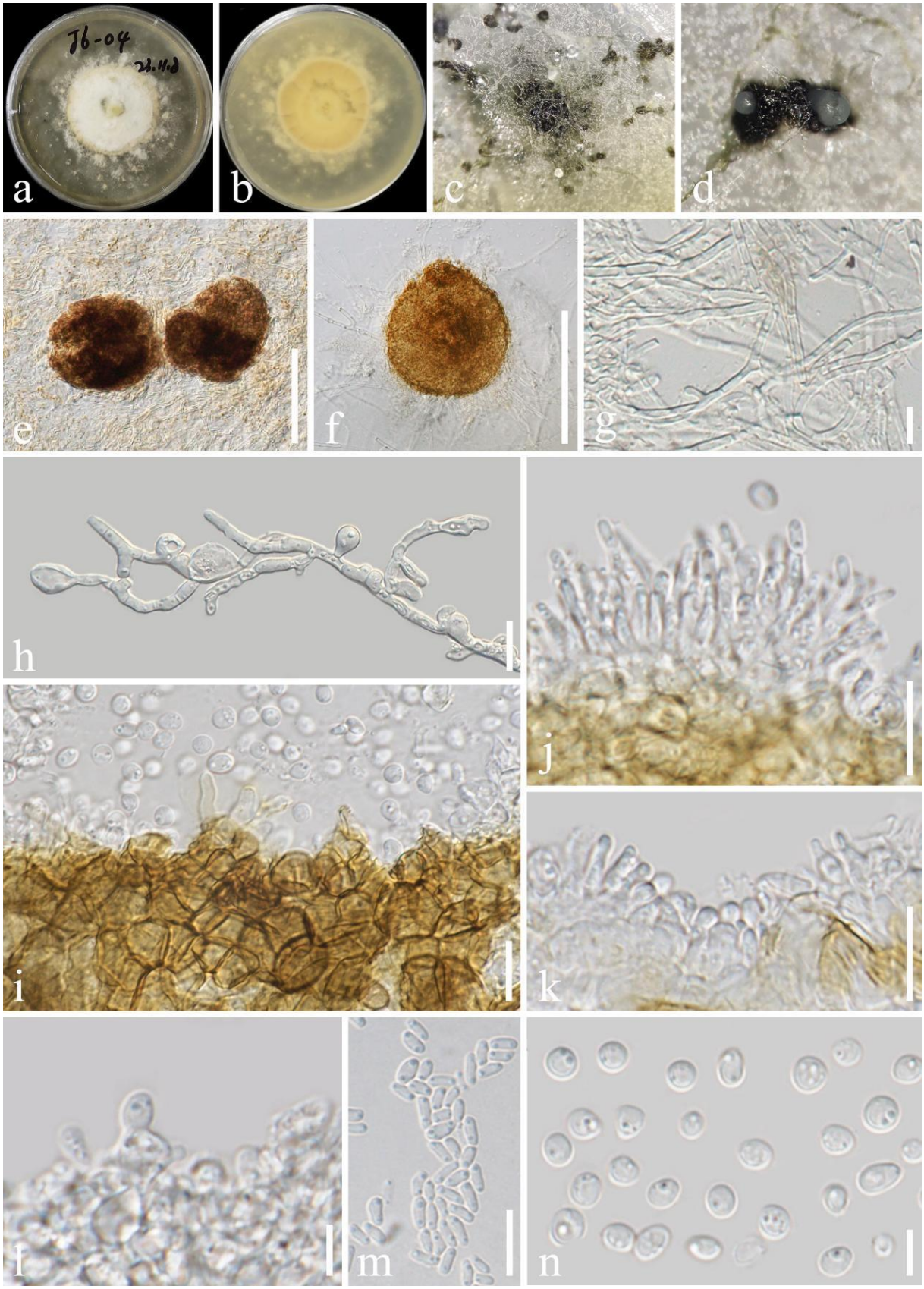

Figure 15 – ***Montagnula cylindrospora*** (GMBCC1189). a, b Colony on PDA at room temperature after one month from above and below. c, d Conidiomata grow on WA with exuding conidia in hyaline masses. e, f Squash mount of conidiomata. g, h Mycelia masses. i Peridium. j-l

Conidiogenous cells. m, n Conidia. Scale bars: e, f = 100 µm, g, h = 20 µm, i-k, m = 10 µm, l, n = 5 µm.

Notes – *Montagnula sinensis* clustered with *M. cylindrospora* (UTHSC DI16-208, ex-type) and *M. yunnanensis* (GMBCC1174, ex-type) in the phylogenetic analyses (Fig. 13). Morphologically, *M. sinensis* differs from *M. cylindrospora* (UTHSC DI16-208, ex-type) in conidiogenous cells phialidic, ampulliform with conical apices, and cylindrical conidia. In contrast, *M. cylindrospora* (UTHSC DI16-208, ex-type) has phialidic, ampulliform to doliiform conidiogenous cells, and *M. cylindrospora* has cylindrical, globose to subglobose conidia. Additionally, *M. sinensis* has longer conidiogenous cells (8.5 µm *vs.* 4 µm) than *M. cylindrospora* (UTHSC DI16-208, ex-type) (Crous et al. 2020). The nucleotide base pair differences (without gaps) between our new strain (GMBCC1185, ex-type) and *M. cylindrospora* (UTHSC DI16-208, ex-type) were compared; the results revealed 0.38% (ITS), 0.56% (LSU), 2.22% (*rpb*2), and 1.85% (*tef*1-α) base pair differences. The SSU sequence of *M. cylindrospora* (UTHSC DI16-208, ex-type) is unavailable. The results between our new strain (GMBCC1185, ex-type) and *M. yunnanensis* (GMBCC1174, ex-type) (without gaps) revealed 0.95% (ITS), 0.89% (LSU), 3.04% (*rpb*2), and 1.77% (*tef*1-α) base pair differences, while no difference in the SSU locus. The PHI test results (Fig. 14) indicated no significant recombination events between *M. sinensis* and its phylogenetically related taxa. Based on morphological and molecular evidence, *M. sinensis* is introduced as a new species on the agarwood resin part of *Aquilaria sinensis* from Yunnan Province, China.

Montagnula yunnanensis T.Y. Du, Tibpromma, K.D. Hyde & Karun. sp. nov. Fig. 17

MycoBank number: MB860357; Facesoffungi number: FoF 18028.

Etymology – Named after the type location, "Yunnan Province of China".

Holotype – GMB-W1512

Culture characteristics – Colonies on PDA at room temperature (23–28 °C) reaching 5 cm in one week; circular, white, flossy, velvety, raised, filamentous edge; white to cream from below. Generative hyphae simple-septate, branched, subhyaline, cells with guttules, thick-walled with 1.3–2 µm wide, and some 4–5.5 µm wide. Not sporulating in WA and PDA media during the six-month observation period.

Material examined – CHINA, Yunnan Province, Yuxi City, Yuanjiang County, on agarwood resin part of *Aquilaria sinensis* (*Thymelaeaceae*), 18 September 2023, T.Y. Du, YNA-YJA-CE-C02 (GMB-W1512 dried culture, holotype), preserved in a metabolically inactive state at Guizhou Medical University (GMB-W), China; ex-type GMBCC1174=GMBCC1848.

GenBank numbers – GMBCC1174: ITS = PQ346645, LSU = PX091400, *rpb*2 = PX101333, SSU = PX091382, *tef*1-α = PX101351; GMBCC1848: ITS = PX088659, LSU = PX091401, *rpb*2 = PX101334, SSU = PX091383, *tef*1-α = PX101352.

Notes – Based on BLASTn searches of ITS, LSU, *rpb*2, SSU, and *tef*1-α sequence data, our strain *Montagnula yunnanensis* showed a high similarity to *M. cylindrospora* (UTHSC DI16-208) (ITS = 98.73% (LT796834), LSU = 99.67% (LN907351), *rpb*2 = 97.42% (LT796994), and *tef*1-α = 98.54% (LT797074)), while SSU showed high similarity to *M. camporesii* (MFLUCC 16-1369, NG_068418) with 99.71%. In the phylogenetic analyses, *M. yunnanensis* clustered as the sister species to *M. sinensis* (11 strains) and *M. cylindrospora* (UTHSC DI16-208, ex-type) (Fig. 13). The newly described strains did not sporulate in WA and PDA media during the six-month observation period; therefore, their morphological characteristics could not be compared with those of *M. cylindrospora* and *M. sinensis*. The nucleotide base pair differences (without gaps) between our new strain (GMBCC1174, ex-type) and *M. cylindrospora* (UTHSC DI16-208, ex-type) were compared; the results revealed 0.57% (ITS), 0.33% (LSU), 2.59% (*rpb*2), and 1.38% (*tef*1-α) base pair differences. The SSU sequence of *M. cylindrospora* (UTHSC DI16-208, ex-type) is unavailable. The results of nucleotide base pair differences (without gaps) between our new strain (GMBCC1174, ex-type) and *M. sinensis* (GMBCC1185, ex-type) revealed 0.95% (ITS), 0.89% (LSU), 3.04% (*rpb*2), and 1.77% (*tef*1-α) base pair differences, while no difference in the SSU gene. The PHI test results (Fig. 14)

indicated no significant recombination events between *M. yunnanensis* and its phylogenetically related taxa. Based on significant statistical support from phylogenetic studies, *M. yunnanensis* is introduced herein as a new species of agarwood resin from a part of *Aquilaria sinensis* found in Yunnan Province, China.

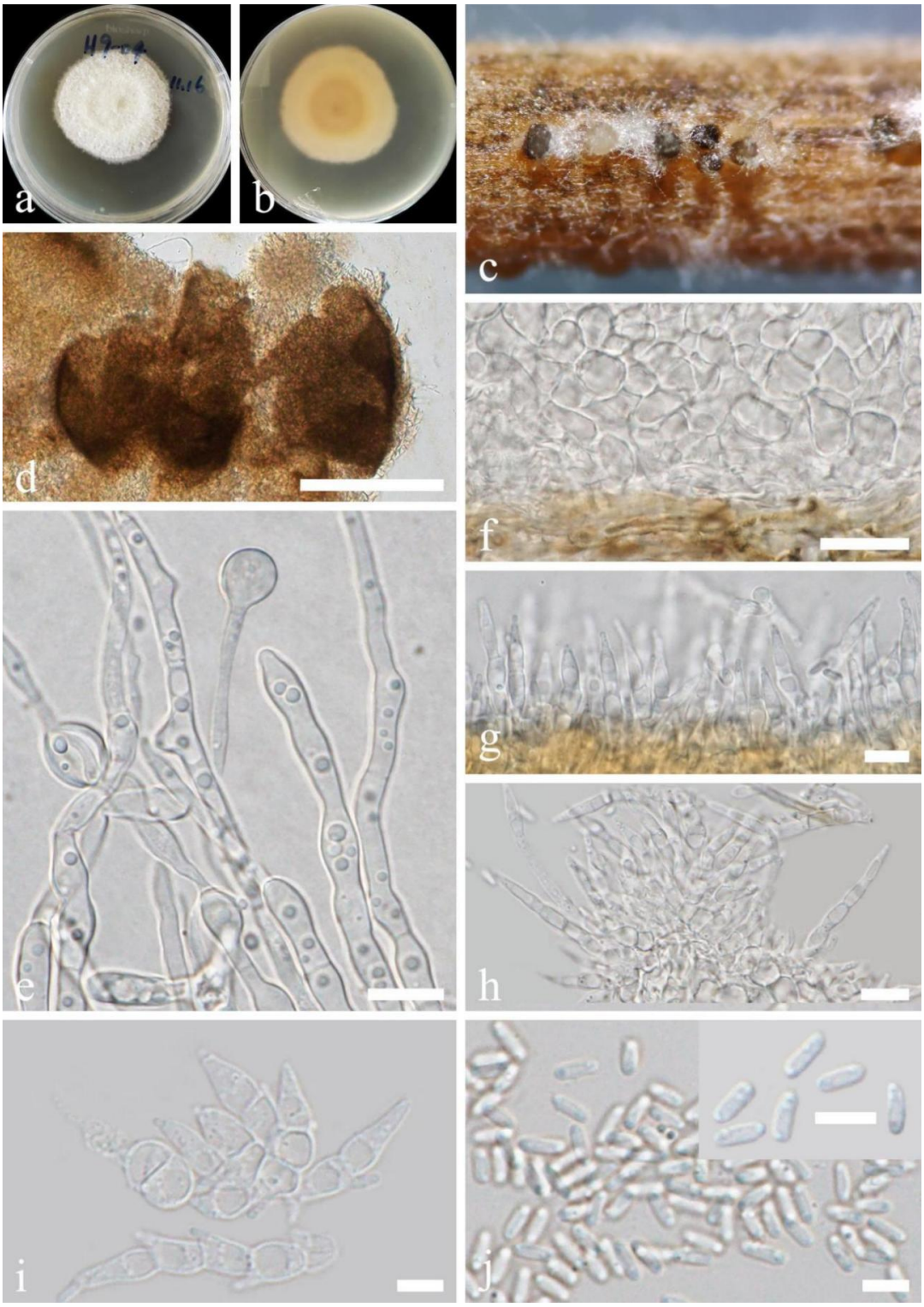

Figure 16 – ***Montagnula sinensis*** (GMBCC1185, ex-type). a, b Colony on PDA at room temperature after one week from above and below. c Conidiomata grow on bamboo toothpicks in WA. d Squash mount of conidiomata. e Mycelia masses. f Peridium. g-i Conidiogenous cells. j Conidia. Scale bars: d = 200 µm, e-h = 10 µm, i, j = 5 µm.

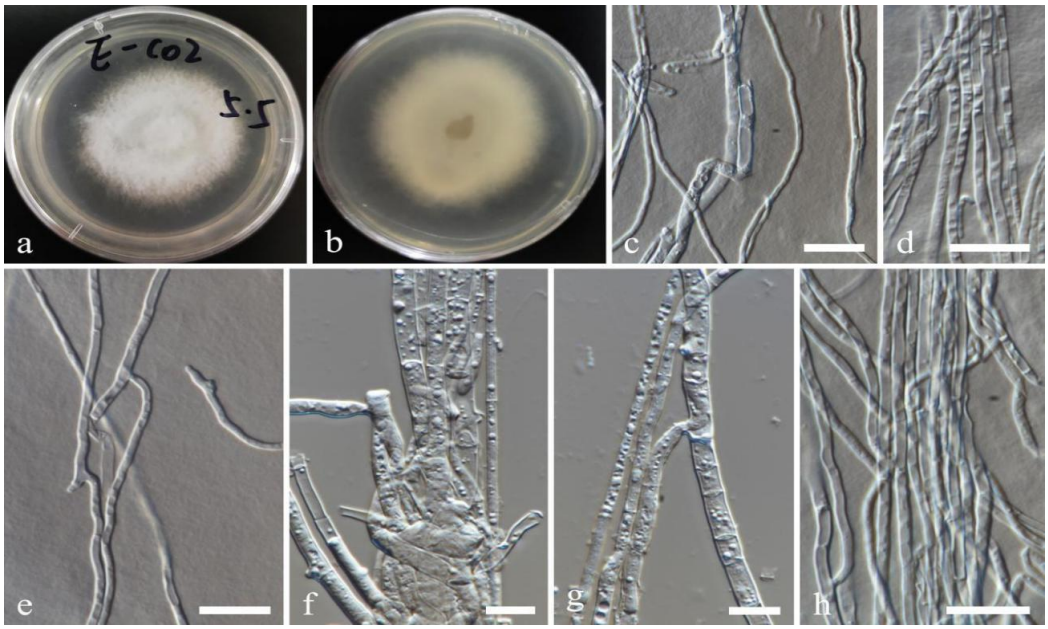

Figure 17 – ***Montagnula yunnanensis*** (GMBCC1174, ex-type). a, b Colony on PDA at room temperature after one week from above and below. c–h Mycelia masses. Scale bars: c–h = 10 µm.

Fomitiporia Murrill 1907

The latest phylogenetic tree of *Fomitiporia* is shown in Fig. 18**.**

Fomitiporia aquilariae T.Y. Du, Tibpromma, K.D. Hyde & Karun. sp. nov. Fig. 19

MycoBank number: MB860358; Facesoffungi number: FoF 18029.

Etymology – Named after its host genus, *Aquilaria.*

Holotype – GMB-W1514

Culture characteristics – Colonies on PDA at room temperature (23–28 °C) reaching 6 cm in one month; circular, light yellow to yellow, dense, raised, entire edge; yellow from below. Skeleton hyphae with few branches, few septa, thick-walled, yellow, 1.5–2.5 µm wide; generative hyphae simple-septate, branched, septate, thin-walled, subhyaline, 1.5–3.5 µm wide. Clamp connection: absent. Not sporulating in WA and PDA media during the six-month observation period.

Material examined – CHINA, Yunnan Province, Yuxi City, Yuanjiang County, on agarwood resin part of *Aquilaria sinensis* (*Thymelaeaceae*), 18 September 2023, T.Y. Du, YNA-YJA-CE-C03 (GMB-W1514 dried culture, holotype), preserved in a metabolically inactive state at Guizhou Medical University (GMB-W), China; ex-type GMBCC1181; *ibid.*, YNA-YJA-CE-C04, living culture GMBCC1182; *ibid.*, YNA-YJA-CE-C05, living culture GMBCC1183.

GenBank numbers – GMBCC1181: ITS = PQ346640, LSU = PX091402; GMBCC1182: ITS = PQ346641, LSU = PX091403; GMBCC1183: ITS = PQ346642, LSU = PX091404.

Notes – Based on BLASTn searches of ITS and LSU sequence data, our strain *Fomitiporia aquilariae* showed a similarity to *F. tasmanica* (Dai 18799, MH971174, 86.45%) in ITS and *F. punctata* (MUCL 47629, GU461982, 97.71%) in LSU. In the phylogenetic analyses, *F. aquilariae* forms a distinct and highly supported subclade within *Fomitiporia* (Fig. 18). The newly described strains belong to the *Basidiomycota* and did not sporulate in culture, so their morphological characteristics could not be compared with those of other *Fomitiporia* species. Our strains are similar to other *Fomitiporia* species in terms of mycelial morphology (dense, raised) and color (yellow) on PDA media, which were isolated from wood and grapevines affected by rot disease (Rajaiyan et al. 2014, Mirsoleymani & Mostowfizadeh-Ghalamfarsa 2018). Based on phylogenetic analysis (Fig. 18)*, F. aquilariae* is introduced herein as a new species from the agarwood resin part of *Aquilaria sinensis* from Yunnan Province, China.

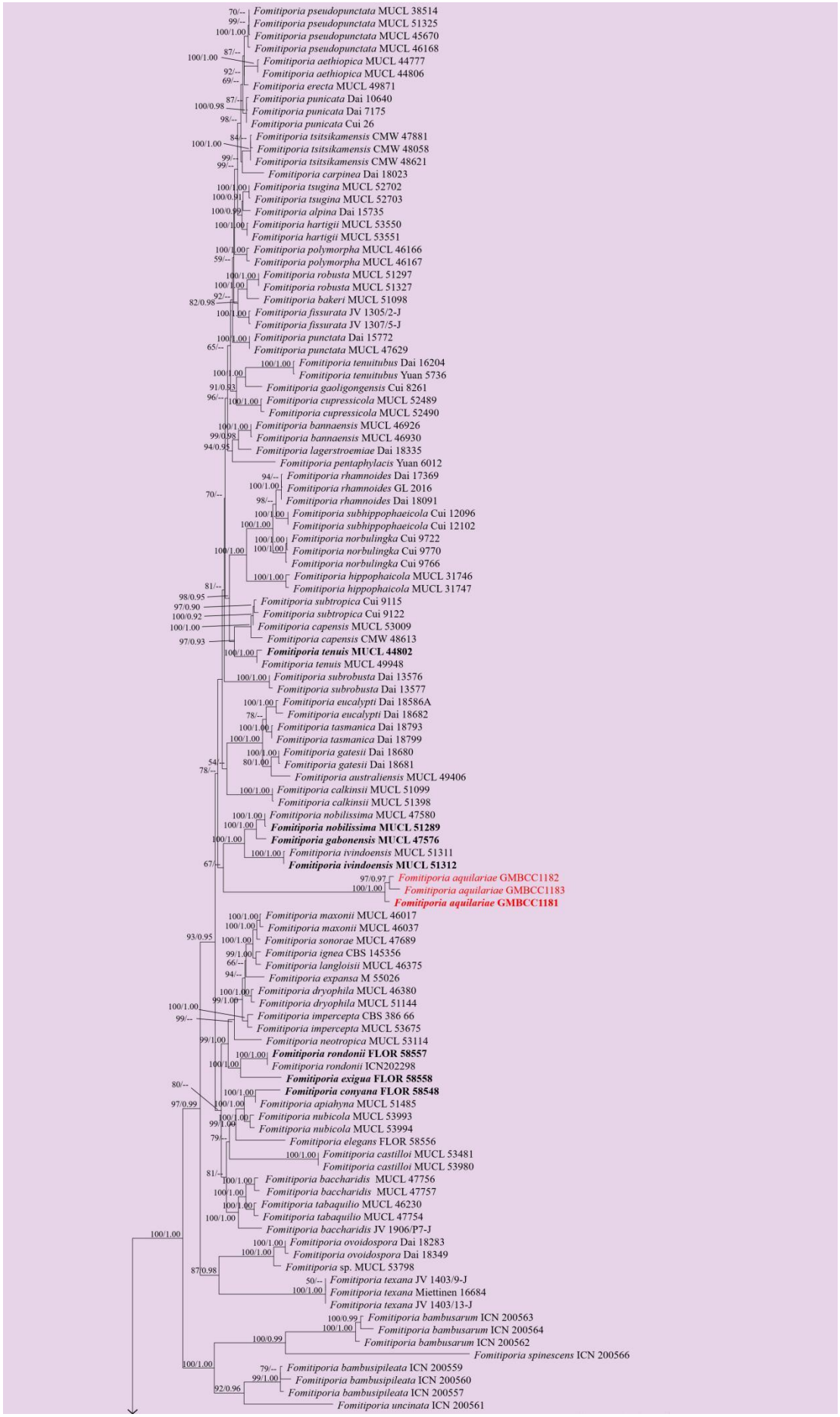

Figure 18 – Continued

Figure 18 – Phylogram generated from maximum likelihood (ML) analysis based on combined ITS and LSU sequence data of 181 taxa, which comprised 1558 base pairs of ITS = 1–686, LSU = 687–2038. The best-scoring RAxML tree with a final likelihood value of -21069.917864 is presented. The matrix contained 961 distinct alignment patterns, with 27.90% of the characters being undetermined or gaps. Estimated base frequencies were as follows: A = 0.247124, C = 0.215256, G = 0.268157, T = 0.269464; substitution rates: AC = 1.140190, AG = 4.531739, AT = 1.165343, CG = 0.747045, CT = 5.860242, GT = 1.0; gamma distribution shape parameter α = 0.576017. Bootstrap support values for ML equal to or greater than 50% and clade credibility values equal to or greater than 0.90 from Bayesian inference analysis are labelled at each node. The tree is rooted with *Neophellinus uncisetus* (MUCL 46231). The new isolates are indicated in red, and the ex-type strains are in bold.

Notes for 64 genera

In this study, we report a total of 960 strains from 64 genera, a significant and impactful contribution to the field. Among these, 142 strains from six genera were reported in our team's

previous articles, and 818 strains from 58 genera are newly reported in this article. This article provides a concise summary and introduction to the 64 genera, including their species counts, lifestyles, hosts, geographic distribution, classification criteria, roles on the *Aquilaria* plants, and biological activities.

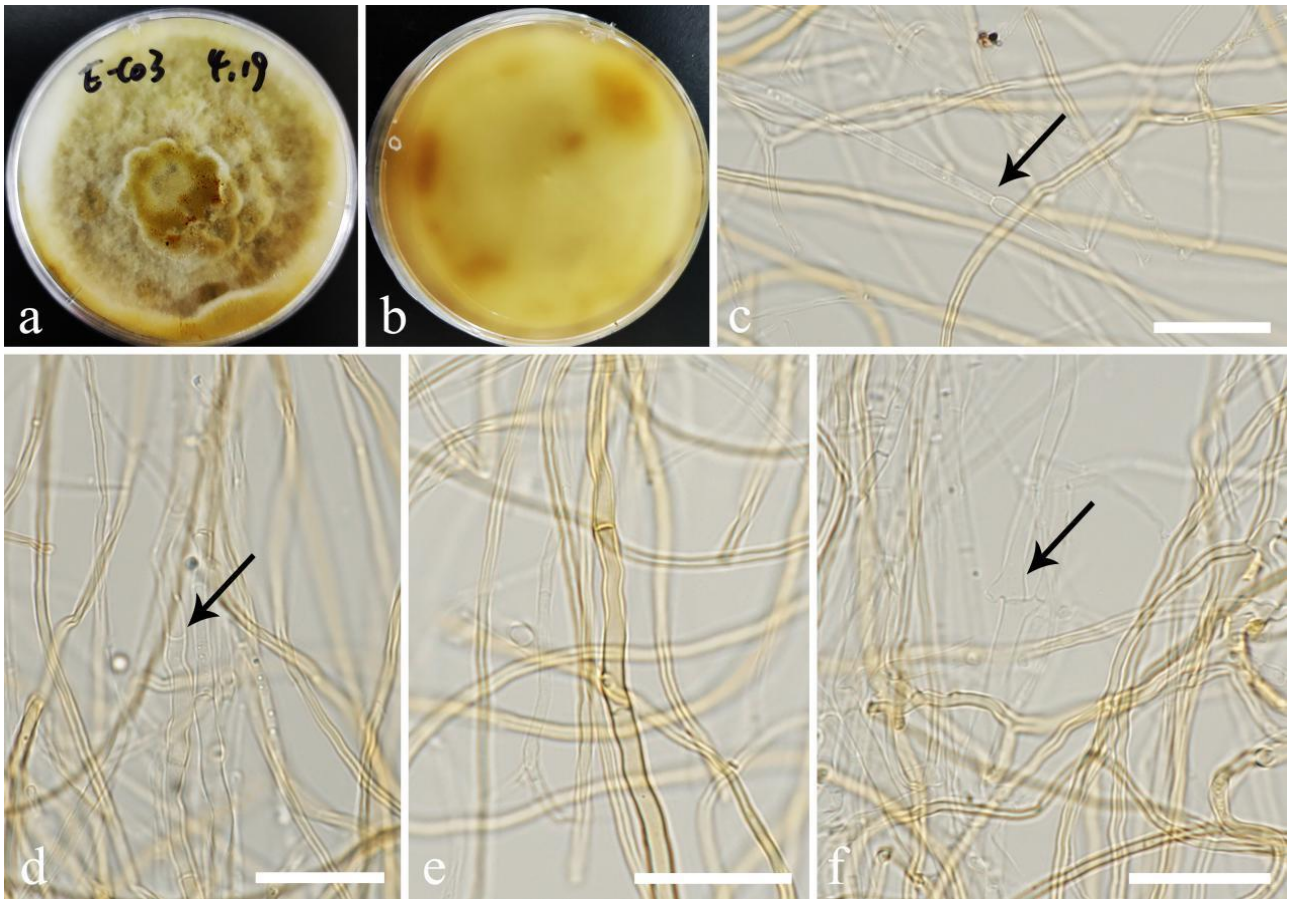

Figure 19 – ***Fomitiporia aquilariae*** (GMBCC1181, ex-type). a, b Colony on PDA at room temperature after one month from above and below. c–f Mycelia masses (The arrows indicate generative hyphae). Scale bars: c–f = 20 µm.

1- ***Acrocalymma*** (*Acrocalymmaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Acrocalymma was established by Alcorn & Irwin (1987). Currently, 18 epithets are listed in this genus (Index Fungorum 2025). *Acrocalymma* species are found as endophytes, saprobes and pathogens on wood, root, leaf litter, and seed pods in terrestrial and freshwater habitats (e.g., *Arenga pinnata*, *Cucumis melo*, *Cucumis* sp., *Cycas calcicola*, *Eleiodoxa conferta*, *Ficus ampelas*, *Ficus* sp., *Magnolia liliifera*, *Medicago sativa*, *Paeonia suffruticosa*, *Perilla frutescens*, *Pterocarpus indicus*, *Quercus* sp., and *Trachycarpus fortune*) reported from five countries (*viz.*, Australia, China, Egypt, India, and Thailand) (Alcorn & Irwin 1987, Zhang et al. 2012, Dong et al. 2020, Liu & Zeng 2022, Shao et al. 2022, Li et al. 2023, Pem et al. 2024). This genus is well-studied in morphology, and all species have available sequence data in GenBank; however, most have only ITS and LSU sequences, while SSU and *tef*1-α sequences are largely absent (Liu & Zeng 2022). In previous studies, some *Acrocalymma* strains were isolated from *Aquilaria sinensis* as agarwood-associated fungi in China (Du et al. 2024, Fu et al. 2024). In this study, we obtained two strains of *Acrocalymma* from *Aquilaria sinensis*: one was an endophytic fungus isolated from a healthy tree branch, and the other was isolated from the agarwood resin part.

2- ***Allophoma*** (*Didymellaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Allophoma was established by Hsieh et al. (2005). A total of 18 epithets are listed in this genus and members of *Allophoma* species are found in soil, air and regarded as endophytes, saprobes or regarded as pathogens on different herbaceous and woody plants (e.g., *Acanthus ilicifolius*, *Acropora formosa*, *Bambusa vulgaris*, *Cicer arietinum*, *Coffea arabica*, *Cyperus aromaticus*, *Lantana camara*, *Lycopersicon esculentum*, *Peperomia pereskiifolia*, *Piper longum*, *Pterospermum xylocarpum*, *Radermachera sinica*, *Saintpaulia ionantha*, *Syzygium aromaticum*, *Thunbergia grandiflora*, and *Yucca gigantea*), bat flies, even human eye lesions (Chen et al. 2015, 2017a, b, Babaahmadi et al. 2017, Jayasiri et al. 2019, Hou et al. 2020, Yuan et al. 2021, Carvalho et al. 2022, Aumentado et al. 2024, Oliveira et al. 2024, Pem et al. 2024, Index Fungorum 2025). This genus is well-studied in morphology and phylogeny (ITS, LSU, *rpb*2, and TUB) (Chen et al. 2015, Hou et al. 2020, Aumentado et al. 2024). In previous studies, *Allophoma* has not been reported in *Aquilaria* spp. In this study, we obtained three strains of *Allophoma* from *Aquilaria sinensis*, three of which were endophytic fungi from healthy tree branches or leaves.

3- ***Alternaria*** (*Pleosporaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Alternaria was described by Nees (1816). Currently, 850 epithets are listed in Index Fungorum (2025). *Alternaria* is a common fungal genus, with saprobic, endophytic, and pathogenic species that have been reported from seeds, plants, agricultural products, animals, soil, and the atmosphere (Ariyawansa et al. 2015, Woudenberg et al. 2013, Wanasinghe et al. 2018b, He et al. 2024). This genus is well-studied based on morphology and phylogeny (ITS, LSU, SSU, GAPDH, *rpb*2, *tef*1-α, Alt a1, endoPG, and OPA10-2), and the use of DNA sequence data is very important in resolving *Alternaria* taxonomy (He et al. 2024). In previous studies, some *Alternaria* strains have been reported from *Aquilaria* spp. in China and India (Premalatha et al. 2013, Tian et al. 2013, Lisdayani et al. 2015, Sen et al. 2020, Du et al. 2022a, c). In this study, we obtained 22 strains of *Alternaria* from *Aquilaria sinensis*, comprising 20 endophytic fungi from healthy tree branches or leaves, and two strains from agarwood resin parts.

4- ***Annulohypoxylon*** (*Hypoxylaceae*, *Xylariales*, *Sordariomycetes*, *Ascomycota*, Hyde et al. 2024c)

Annulohypoxylon was established by Hsieh et al. (2005). More than 90 epithets are listed in this genus, and most *Annulohypoxylon* species are saprobic on wood. Some species are endophytes of herbaceous plants (e.g., *Dendrobium aphyllum*, *D. chrysotoxum*, *D. crystallinum*, *D. falconer*, and *Stanhopea trigrina*) (Chen et al. 2013, Daranagama et al. 2018, Ma et al. 2022, Liu et al. 2024b, Index Fungorum 2025). This genus has been studied extensively in morphology and phylogeny (ITS, LSU, ACT, and TUB) (Liu et al. 2024b). In previous studies, three *Annulohypoxylon* strains were isolated from *Aquilaria sinensis* as agarwood-associated fungi from China (Du et al. 2022b). In this study, we obtained two additional strains of *Annulohypoxylon* from *Aquilaria sinensis*, one of which was an endophytic fungus isolated from a healthy tree leaf, and the other was from the agarwood resin part.

5- ***Aspergillus*** (*Aspergillaceae*, *Eurotiales*, *Eurotiomycetes*, *Ascomycota*, Hyde et al. 2024c)

Aspergillus was described by Micheli (1729). More than 1,110 epithets are listed in Index Fungorum (2025). All members of this genus live largely as saprobes (Pennerman et al. 2020), and some *Aspergillus* species are common and important plant pathogens as they can affect agricultural crops in the field as well as after harvest (e.g., coffee beans, corn ear, cotton boll, peanut, onion, garlic, fruit of grapes, pomegranates, olives, citrus, and apples) (Zakaria 2024). Among the numerous existing endophytic fungi, *Aspergillus* strains are one of the most abundant sources of secondary metabolites with diverse biological activities (e.g., antibacterial, antifungal, antioxidant, anticancer, antimalarial, anti-inflammatory, and immunosuppressive activities) (Hagag et al. 2022). The identification of *Aspergillus* species relies on standardized methods that incorporate morphological characteristics, extralite characterization, and multi-gene DNA sequence analyses (ITS, *rpb*2, CaM, and β-tubulin (BenA)) (Nguyen et al. 2020). In previous studies, some *Aspergillus* strains have been isolated from *Aquilaria* spp. as endophytes or agarwood-associated fungi, e.g., *A. niger* from China

and Sri Lanka (Subasinghe et al. 2019, Du et al. 2022c). In this study, we obtained 40 strains of *Aspergillus* from *Aquilaria sinensis*, comprising five endophytic fungi from healthy tree branches or leaves, 29 strains from agarwood resin parts, and six strains from dead branches.

6- ***Aureobasidium*** (*Saccotheciaceae*, *Dothideales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Aureobasidium was established by Viala & Boyer (1891). A total of 69 epithets are listed in this genus, and members of *Aureobasidium* species are often found as saprobes, endophytes, and pathogens in various plant tissues, water, soil, ice, air, marine sediments, swamps, and high osmotic environments (Wu et al. 2023, da Silva et al. 2024, Pem et al. 2024, Index Fungorum 2025). Zalar et al. (2008) was the first to carry out phylogenetic analysis. Subsequently, a large amount of molecular data became available due to the high accessibility of sequencing services (ITS and LSU) (Wu et al. 2023). The functional activities of *Aureobasidium* have been explored in various ways, such as: as biological control agents (Sharma et al. 2009, Prasongsuk et al. 2018); production of commercial compounds (Wu et al. 2023), and *A. pullulans* as a natural alternative to chemical fungicides in agricultural practices (Podgórska-Kryszczuk 2023, da Silva et al. 2024). In previous studies, *Aureobasidium* has not been reported in *Aquilaria* spp. In this study, we obtained one strain of *Aureobasidium* from a healthy tree branch of *Aquilaria sinensis*.

7- ***Banksiophoma*** (*Phaeosphaeriaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Banksiophoma was described by Crous et al. (2017). Currently, two epithets are listed in Index Fungorum (2025), and *Banksiophoma* species have been isolated from limestone and the leaves of *Banksia coccinea* (Crous et al. 2017, Pem et al. 2024, Paiva et al. 2025). This genus is well-studied in morphology and phylogeny (ITS, LSU, *tef*1-α, *rpb*2, and TUB) (Crous et al. 2017). In previous studies, no *Banksiophoma* strains have been reported from *Aquilaria* spp. In this study, we obtained four *Banksiophoma* strains from healthy *Aquilaria sinensis* tree branches.

8- ***Biscogniauxia*** (*Graphostromataceae*, *Xylariales*, *Sordariomycetes*, *Ascomycota*, Hyde et al. 2024c)

Biscogniauxia was introduced for the sexual morph of this genus by Pouzar (1979). In this genus, the asexual morph has been recorded as *Nummularia*, and the sexual morph as *Biscogniauxia* (Tulasne & Tulasne 1863; Li et al. 2021). Totally, 133 epithets are listed in this genus, and members of *Biscogniauxia* species are pathogens on some angiosperm genera (e.g., *Acacia*, *Acer*, *Alnus*, *Artocarpus*, *Carya*, *Celtis*, *Coprosma*, *Eucalyptus*, *Fagus*, *Fraxinus*, *Gluta*, *Lithocarpus*, *Padus*, *Phyllirea*, *Pisnia*, *Populus*, *Psidium*, *Quercus*, *Rhamnus*, *Rubus*, and *Tilia*) and endophytes reported from oak trees (Raimondo et al. 2016, Hyde et al. 2020, Ma et al. 2020). This genus is well-studied in morphology, but only a few species have available DNA sequences (Li et al. 2021, Hyde et al. 2020, Samarakoon et al. 2022a, Qiao et al. 2024). *Biscogniauxia* species can produce more than 40 secondary metabolites (Liu et al. 2019b, Sritharan et al. 2019, Ma et al. 2020). In previous studies, *Biscogniauxia* has not been reported from *Aquilaria* spp. In this study, we obtained one strain of *Biscogniauxia* from a healthy tree branch of *Aquilaria sinensis*.

9. ***Botryosphaeria*** (*Botryosphaeriaceae*, *Botryosphaeriales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Botryosphaeria was described by Cesati & de Notaris (1863). Currently, more than 300 epithets are listed in Index Fungorum (2025). *Botryosphaeria* is a cosmopolitan genus, and its species have been reported in many woody plants as endophytes, saprobes, and pathogens (Liu et al. 2012, Dissanayake et al. 2016, Slippers et al. 2017, Sun et al. 2022, Pem et al. 2024). In the past, the species of *Botryosphaeria* were mainly identified through morphological characters alone or by host association, but these aspects are insufficient to distinguish them. Later, molecular data have been studied, but only some species have DNA sequences (ITS, LSU, *tef*1-α, *rpb*2, and TUB) (Sun et al. 2022). In previous studies, some *Botryosphaeria* strains were reported to isolate from *Aquilaria* spp.

as endophytes or agarwood-associated fungi, and *B. rhodina* (from China) has been reported to possess antimicrobial activity (Gong & Guo 2009, Du et al. 2022c). In this study, we obtained five strains of *Botryosphaeria* from agarwood resin parts of *Aquilaria sinensis*.

10- ***Chaetomium*** (*Chaetomiaceae*, *Sordariales*, *Sordariomycetes*, *Ascomycota*, Hyde et al. 2024c)

Chaetomium was described by Gustav Kunze in 1817 (Kunze & Schmidt 1817). Currently, more than 440 epithets are listed in Index Fungorum (2025). *Chaetomium* is one of the largest genera of saprophytic ascomycetes; species are well known as coprophilous, seed, and soil fungi, and are also found in organic compost (Pornsuriya et al. 2008). Some species, such as *C. globosum* can act as both pathogenic and endophytic fungi (Zhai et al. 2018, Hassan et al. 2022). The biological activity of *Chaetomium* is also worth noting (e.g., antitumor, antimalarial, cytotoxic, enzyme inhibitory, antimicrobial, phytotoxic, and antirheumatoid activities) (Abdel-Azeem 2019). *Chaetomium* species were traditionally identified based on morphological data; however, the study of molecular phylogeny is limited, and many species lack DNA sequences (ACT, ITS, *rpb*2, TUB, and CAL) (Sekhar et al. 2018). In previous studies, some *Chaetomium* strains have been reported to be isolated from *Aquilaria* spp. as endophytes or agarwood-associated fungi, e.g., *C. globosum* from India (Tamuli et al. 2000, 2005). In this study, we obtained four strains of *Chaetomium* from *Aquilaria sinensis*, of which one strain was an endophytic fungus from a healthy tree branch, and three strains were from agarwood resin parts.

11- ***Cladorrhinum*** (*Podosporaceae*, *Sordariales*, *Sordariomycetes*, *Ascomycota*, Hyde et al. 2024c)

Cladorrhinum was introduced by Marchal (1885). A total of 23 epithets are listed in this genus and members of *Cladorrhinum* species as saprobes in soil, dung, or plant material, as endophytes in roots, and some species as pathogens on humans and animals (Carmarán et al. 2015, Huang et al. 2021, Crous et al. 2024, Index Fungorum 2025). This genus is well-studied in terms of morphology; however, for some species, no DNA sequences are available (Wang et al. 2019a). Some *Cladorrhinum* species exhibit biocontrol potential, promote plant growth, produce phytases, or generate enzymes beneficial for animal feed (Carmarán et al. 2015). In previous studies, *Cladorrhinum bulbillosum* was reported as a novel inoculant for agarwood formation in *Aquilaria sinensis* from China (Ma et al. 2021). In this study, we obtained one strain of *Cladorrhinum* from a healthy tree branch of *Aquilaria sinensis*.

12- ***Cladosporium*** (*Cladosporiaceae*, *Cladosporiales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Cladosporium was established by Link (1816). More than 900 epithets are listed in this genus and most *Cladosporium* species are plant pathogens, and some are saprophytic, pathogenic in humans and animals, and endophytic or hyperparasitic in terrestrial environments, such as caves, soil, air, indoors, and marine environments, and known to colonise many habitats such as seawater, sediment and marine organisms (Dutra et al. 2023, Yang et al. 2023, Pereira et al. 2024, Index Fungorum 2025). This genus is well-studied in morphology and phylogeny (ACT, ITS, and *tef*1-α) (Dutra et al. 2023, Lee et al. 2023, Yang et al. 2023). *Cladosporium* species can produce diverse secondary metabolites of medical interest or as potential biocontrol agents for other plant diseases, and also can act as biological control agents against other fungi (Dutra et al. 2023, Lee et al. 2023, Yang et al. 2023). Some *Cladosporium* strains have been reported as endophytes and agarwood-associated fungi in *Aquilaria* spp. from China (Du et al. 2022a, b). In this study, we obtained three strains of *Cladosporium* from *Aquilaria sinensis*, of which one strain was an endophytic fungus from a healthy tree leaf, one strain was from an agarwood resin part, and one strain was from a dead branch.

13- ***Colletotrichum*** (*Glomerellaceae*, *Glomerellales*, *Sordariomycetes*, *Ascomycota*, Hyde et al. 2024c)

Colletotrichum was initially described under the name *Vermicularia* by Tode (1790), and later revised by Corda (1837) as *Colletotrichum*. More than 1,000 epithets are listed in Index Fungorum

(2025). *Colletotrichum* species exist as plant pathogens, saprobes, or endophytes on a wide variety of plant hosts (Than et al. 2008, Jayawardena et al. 2021, Zhang et al. 2024d) and are considered as one of the top 10 economically important fungal pathogens, causing anthracnose in diverse host plants (e.g., fruit plants, vegetables, and ornamentals) (Dean et al. 2012, Sharma & Shenoy 2016), and some species reportedly infect humans (Natarajan et al. 2013). A polyphasic approach is needed to identify new taxa (e.g., morphology, phylogenetics (ACT, ITS, CHS-1, GAPDH, and TUB), and biochemical tests) (Sharma & Shenoy 2016, Bhunjun et al. 2021, Zhang et al. 2024d). In previous studies, some *Colletotrichum* strains were reported to be isolated from *Aquilaria* spp. as endophytes or agarwood-associated fungi, e.g., *C. gloeosporioides* from China (Tian et al. 2013, Du et al. 2022c). In this study, we obtained 49 strains of *Colletotrichum* from *Aquilaria sinensis*, comprising 45 endophytic fungi from healthy tree branches or leaves and four from agarwood resin parts.

14- ***Coniella*** (*Schizoparmaceae*, *Diaporthales*, *Sordariomycetes*, *Ascomycota*, Hyde et al. 2024c)

Coniella was established by von Höhnel (1918). A total of 65 epithets are listed in this genus and members of *Coniella* species as plant pathogens, endophytes and saprobes (e.g., *Castanea mollissima*, *Daemonorops margaritae*, *Eucalyptus grandis*, and *Punica granatum*) (Zhang et al. 2023b). This genus is well-studied in morphology and phylogeny (ITS, *tef*1-α, and *rpb*2) (Tennakoon et al. 2021, Zhang et al. 2023b). In previous studies, *Coniella* has not been reported in *Aquilaria* spp. In this study, we obtained two strains of *Coniella* from healthy tree leaves of *Aquilaria sinensis* as endophytic fungi.

15- ***Corynespora*** (*Corynesporascaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Corynespora was described by Güssow (1906). Currently, more than 200 epithets are listed in Index Fungorum (2025), and members of *Corynespora* exist as saprobes, endophytes, and pathogens on a wide range of plants, on other fungi, nematodes, and human skin (Dixon et al. 2009, Kumar et al. 2012, Li et al. 2023, Du et al. 2024a, Pem et al. 2024). This genus is poorly studied in phylogeny, mostly due to a lack of molecular data for species. In previous studies, two *Corynespora* species were reported to isolate from *Aquilaria* spp., e.g., *C. aquilariae* as saprobe from China (Du et al. 2024a), *C. cassiicola* as agarwood-associated fungi from China (Du et al. 2022b) and as pathogen from India (Borah et al. 2012).

16- ***Crassiparies*** (*Neohendersoniaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Crassiparies was established by Li et al. (2016). Three epithets are listed in this genus and *Crassiparies* species are saprobic on wood (e.g., *Acer* sp., *Arabica coffee*, *Machilus japonica*, *Hevea brasiliensis*, *Mangifera indica*, and *Litchi chinensis*) (Li et al. 2016, Senwanna et al. 2021, Lu et al. 2022c, Yang et al. 2024, Index Fungorum 2025). This genus is well-studied in morphology and phylogeny (ITS, LSU, SSU, *tef*1-α, and *rpb*2; Lu et al. 2022c, Yang et al. 2024). In previous studies, *Crassiparies* strains were isolated from *Aquilaria sinensis* as agarwood-associated fungi from China (Du et al. 2022b, 2024). In this study, we obtained one strain of *Crassiparies* from the agarwood resin part of *Aquilaria sinensis*.

17- ***Curvularia*** (*Pleosporaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Curvularia was established by Boedjin (1933). A total of 248 epithets are listed in this genus and most *Curvularia* species exist as saprobic and endophytes, and some species exist as epiphytes and pathogens (animal, human, and plants); isolated from air, indoor environments, soil, water, or plant materials (Ferdinandez et al. 2021, 2023, Yasanthika et al. 2023, Van Vuuren et al. 2024, Wang et al. 2024c). This genus is well-studied in morphology, but some species lack DNA sequences (Van Vuuren et al. 2024, Wang et al. 2024c). *Curvularia* strain has been reported to have inhibitory potential against various pathogens (Du et al. 2022c). In previous studies, some *Curvularia* strains were reported from *Aquilaria* spp. as agarwood-associated fungi from China and Malaysia

(Mohamed et al. 2010, Du et al. 2022a, b), and *Curvularia* is a potential fungal inoculant that can promote the production of dark agarwood resin (Naziz et al. 2023).

18- ***Daldinia*** (*Hypoxylaceae*, *Xylariales*, *Sordariomycetes*, *Ascomycota*, Hyde et al. 2024c)

Daldinia was established by Cesati & de Notaris (1863). A total of 111 epithets are listed in this genus, and members of *Daldinia* have been reported as endophytes, saprobes, and pathogens on dicots and monocots plants (Sir et al. 2016, Lee et al. 2019, Wongkanoun et al. 2020, Yin et al. 2024a). This genus is well-studied in morphology, but some species lack DNA sequences (Wongkanoun et al. 2020, Yin et al. 2024a). *Daldinia* species can produce abundant secondary metabolites, which can be used as taxonomic markers (Wongkanoun et al. 2020, Yin et al. 2024a). In previous studies, *Daldinia* strains were isolated from *Aquilaria sinensis* as agarwood-associated fungi from China (Du et al. 2022b, 2024). In this study, we obtained 12 strains of *Daldinia* from agarwood resin parts of *Aquilaria sinensis*.

19- ***Deniquelata*** (*Didymosphaeriaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Deniquelata was established by Ariyawansa et al. (2013). Seven epithets are listed in this genus and *Deniquelata* species exist as pathogens, saprobes, and endophytes on *Barringtonia asiatica, Cassia fistula*, *Coffea* sp., Persian oak, stone, *Suaeda monoica* (Ariyawansa et al. 2013, Devadatha et al. 2018, Alidadi et al. 2019, Crous et al. 2021, 2023, Lu et al. 2022b). This genus is well-studied in morphology and phylogeny (ITS, LSU, SSU, and *tef*1-α) (Crous et al. 2021, 2023, Lu et al. 2022b). In previous studies, *Deniquelata* strains were isolated from *Aquilaria sinensis* as agarwood-associated fungi from China (Du et al. 2024). In this study, we obtained three strains of *Deniquelata* from agarwood resin parts of *Aquilaria sinensis*.

20- ***Diaporthe*** (*Diaporthaceae*, *Diaporthales*, *Sordariomycetes*, *Ascomycota*, Hyde et al. 2024c)

Diaporthe was described by Nitschke (1870). More than 1,300 epithets are listed in Index Fungorum (2025). *Diaporthe* (*Phomopsis*) species have often been reported as plant pathogens, endophytes, or saprobes, commonly isolated from various hosts (Gomes et al. 2013, Dissanayake et al. 2017). A polyphasic taxonomic approach is essential for identifying and comprehensively characterizing *Diaporthe,* and phylogenetic analysis should be based on multiple loci (e.g., ITS, *tef*1-α, TUB, CAL, and HIS) (Gomes et al. 2013, Zhu et al. 2023, Norphanphoun et al. 2022, Dissanayake et al. 2025). In previous studies, some *Diaporthe* strains were reported to isolate from *Aquilaria* spp. as endophytes or agarwood-associated fungi, and some strains from China and Thailand showed excellent antioxidant capacity (Monggoot et al. 2017, Du et al. 2022a, b, c). In this study, we obtained 55 strains of *Diaporthe* from *Aquilaria sinensis*, comprising 31 endophytic fungi from healthy tree leaves, 21 strains from the agarwood resin part, and three strains from dead branches.

21- ***Didymella*** (*Didymellaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Didymella was described by Saccardo (1880). Currently, more than 600 epithets are listed in Index Fungorum (2025); most of the *Didymella* species are usually found as saprobes from herbaceous and woody plants, but many are also important plant pathogens (Magaña-Dueñas et al. 2021, Chen et al. 2022, Luo et al. 2024, Pem et al. 2024). Some endophytic species contain a high abundance of metabolites (Yuan et al. 2023). This genus is well-studied in terms of morphology and phylogeny (based on multiple loci of ITS, LSU, *rpb*2, and TUB) (Luo et al. 2024). In previous studies, no *Didymella* strains were reported from *Aquilaria* spp. In this study, we obtained one strain of *Didymella* from a healthy tree leaf of *Aquilaria sinensis*.

22- ***Epicoccum*** (*Didymellaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Epicoccum was established by Link (1815). Totally, 178 epithets are listed in this genus, and members of the *Epicoccum* have been reported as saprobes, pathogens, and endophytes from air, soil, on human toenails, in various plant parts, and in water (Senanayake et al. 2023, Pem et al. 2024, Tian

et al. 2024). This genus is well-studied in morphology; however, sequence data are unavailable for most species (de Silva et al. 2021, Keirnan et al. 2021, Tian et al. 2024, Wang et al. 2024b). Some endophytic *Daldinia* species possess biological control abilities, and certain species can produce mycotoxins (Oliveira et al. 2018, Bagy et al. 2019, Senanayake et al. 2023). In previous studies, *Epicoccum* strains have been isolated from *Aquilaria* spp. as endophytes and agarwood-associated fungi in China (Du et al. 2022a). In this study, we obtained eight strains of *Epicoccum* from healthy tree branches or leaves of *Aquilaria sinensis* as endophytic fungi.

23- ***Exophiala*** (*Herpotrichiellaceae*, *Chaetothyriales*, *Eurotiomycetes*, *Ascomycota*, Hyde et al. 2024c)

Exophiala was established by Carmichael (1966). A total of 97 epithets are listed in this genus and members of *Exophiala* as black yeast-like fungi isolated from various habitats worldwide, such as air, biological crusts, bulk soil, infected animals and human tissue, natural water masses, plant tissues, rhizosphere, and rock surfaces (Yang et al. 2021, Lv et al. 2022, Thitla et al. 2022). This genus is well-studied in morphology; however, some of the species' sequence data are unavailable (Lv et al. 2022, Thitla et al. 2022, Ide-Pérez et al. 2024). In previous studies, *Exophiala* has not been reported in *Aquilaria* spp. In this study, we obtained five strains of *Exophiala* from agarwood resin parts of *Aquilaria sinensis*.

24- ***Fomitiporia*** (*Hymenochaetaceae*, *Hymenochaetales*, *Agaricomycetes*, *Basidiomycota*, Hyde et al. 2024c)

Fomitiporia was established by Murrill (1907). A total of 101 epithets are listed in this genus, and *Fomitiporia* species have been reported as pathogens and saprobes (Alves-Silva et al. 2020a, b, Brown et al. 2020). This genus is well-studied in morphology and phylogeny (ITS and LSU) (Alves-Silva et al. 2020a, b, Brown et al. 2020, Wu et al. 2022). In previous studies, *Fomitiporia* has not been reported in *Aquilaria* spp. In this study, we obtained three strains of *Fomitiporia* from agarwood resin parts of *Aquilaria sinensis*.

25- ***Fonsecaea*** (*Herpotrichiellaceae*, *Chaetothyriales*, *Eurotiomycetes*, *Ascomycota*, Hyde et al. 2024c)

Fonsecaea was described by Brumpt (1922) and Negroni (1936) (Ajello et al. 1988). A total of 16 epithets are listed in this genus, and members of *Fonsecaea* have been reported as black yeasts, as pathogens in humans and animals, and potential etiologic agents of human chromoblastomycosis (Najafzadeh et al. 2010a, b, Vicente et al. 2012, 2013, de Azevedo et al. 2015). This genus is well-studied in morphology; however, some of the species' sequence data are unavailable (de Hoog et al. 2004, Najafzadeh et al. 2009, 2010a b, Vicente et al. 2012, 2013, de Azevedo et al. 2015). In recent studies, Fu et al. (2024) considered *Fonsecaea* isolated from China potentially associated with agarwood formation in *Aquilaria sinensis.* In this study, we obtained 29 strains of *Fonsecaea* from agarwood resin parts of *Aquilaria sinensis*.

26- ***Fusarium*** (*Nectriaceae*, *Hypocreales*, *Sordariomycetes*, *Ascomycota*, Hyde et al. 2024c)

Fusarium was described in 1809 by Link (Nelson et al. 1981). Currently, more than 1,800 epithets are listed in Index Fungorum (2025). *Fusarium* is a common fungal genus in nature, existing as saprobic, endophytic, and pathogenic species reported from air and soil, usually associated with plants, and some also associated with humans (Ma et al. 2013, Aoki et al. 2014, Wu 2014, Ekwomadu et al. 2018, Torbati et al. 2021, Ekwomadu & Mwanza 2023, Song et al. 2023, Zhang et al. 2023c). There are many species in this genus, which are divided into multiple complex groups. Common loci used in their systematics include ITS, LSU, *tef*1-α*, rpb*2, TUB, and CaM (Ma et al. 2023, Afzalinia et al. 2025). In previous studies, many *Fusarium* strains were reported to be isolated from *Aquilaria* spp., *Fusarium* is a dominant genus among fungi associated with *Aquilaria*, and *F. solani* has been repeatedly reported as an excellent inducer from China, India, Indonesia, Malaysia, Sri Lanka, Sumatra island, and Vietnam (Tabata et al. 2003, Tamuli et al. 2005, Gong & Guo 2009, Cui et al.

2011, Premalatha et al. 2013, Subasinghe et al. 2019, Du et al. 2022a, b, c, 2024b). In this study, we obtained 140 strains of *Fusarium* from *Aquilaria sinensis*, comprising two endophytic strains from healthy tree branches, 122 strains from agarwood resin parts, and 16 strains from dead branches.

27- ***Hermatomyces*** (*Hermatomycetaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Hermatomyces was introduced by Spegazzini (1910). A total of 35 epithets are listed in this genus, and most *Hermatomyces* species are saprobic on various plants (de Silva et al. 2022) and have a worldwide distribution (Hashimoto et al. 2017, de Silva et al. 2022, Zhang et al. 2023a, Pem et al. 2024, Index Fungorum 2025). Currently, this genus is well-studied based on morphology and phylogeny (ITS, LSU, SSU, *tef*1-α, and *rpb*2) (Delgado et al. 2022, Zhang et al. 2023a). In previous studies, *Hermatomyces* strains have been isolated from *Aquilaria sinensis* as agarwood-associated fungi in China (Song et al. 2021). Zhang et al. (2024b) proposed that the abundance of *Hermatomyces* was correlated with the formation of the sesquiterpene constituents of agarwood. In this study, we obtained one strain of *Hermatomyces* from the agarwood resin part of *Aquilaria sinensis*.

28- ***Hypoxylon*** (*Hypoxylaceae*, *Xylariales*, *Sordariomycetes*, *Ascomycota*, Hyde et al. 2024c)

Hypoxylon was described by the world monograph of *Hypoxylon* (Miller 1961). Currently, more than 1,200 epithets are listed in Index Fungorum (2025). *Hypoxylon* species are mainly saprobes that inhabit the dead and decaying wood of angiospermous plants (Stadler 2011, Song et al. 2022b), while some strains act as plant pathogens (Nepolean et al. 2014). Additionally, some endophytic species may protect their host plants from pathogens (Song et al. 2022b). The identification of species is based on polyphasic taxonomic approaches, and the phylogenetic inferences are usually based on multiple loci (ITS, LSU, *tef*1-α, *rpb*2, and TUB) (Song et al. 2022b). In previous studies, some *Hypoxylon* strains have been reported from *Aquilaria sinensis* as agarwood-associated fungi from China (Du et al. 2022b, 2024b). In this study, we obtained 15 strains of *Hypoxylon* from *Aquilaria sinensis*, comprising nine endophytic fungi from healthy tree branches or leaves and six from agarwood resin parts.

29- ***Lasiodiplodia*** (*Botryosphaeriaceae*, *Botryosphaeriales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Lasiodiplodia was described by Clendenin (1896). Currently, 92 epithets are listed in Index Fungorum (2025). *Lasiodiplodia* species are common saprobes and pathogens on woody hosts (Wu et al. 2021). This genus is well-studied in morphology and phylogeny (ITS, *tef*1-α, and TUB) (Wu et al. 2021). In previous studies, many *Lasiodiplodia* strains have been reported from *Aquilaria* spp. as endophytes or agarwood-associated fungi. *Lasiodiplodia* is a common genus associated with *Aquilaria*; some *Lasiodiplodia* strains are also considered to have strong induction potential, e.g., *L. theobromae* from China and Laos (Zhang et al. 2014, Chen et al. 2017a, Huang et al. 2017, Wang et al. 2019b, Du et al. 2024b). In this study, we obtained 163 strains of *Lasiodiplodia* from *Aquilaria sinensis*, comprising eight endophytic fungal strains from healthy tree branches or leaves, and 155 strains from agarwood resin parts.

30- ***Loculosulcatispora*** (*Sulcatisporaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Loculosulcatispora was introduced by Ren et al. (2020). Currently, four epithets are listed in *Loculosulcatispora* (Index Fungorum 2025), and all of *Loculosulcatispora* species were reported as saprobes on *Juglans regia*, *Paeonia suffruticosa*, *Vernicia fordii*, and decaying wood or twigs of unidentified plants in China and Thailand (Ren et al. 2020, Xu et al. 2022, Wanasinghe et al. 2022, Li et al. 2023, Wang et al. 2023b). This genus is well-studied in morphology and phylogeny (ITS, LSU, SSU, *tef*1-α, and *rpb*2) (Li et al. 2023, Wang et al. 2023b). In previous studies, no *Loculosulcatispora* species have been isolated from *Aquilaria* spp. In this study, we obtained one strain of *Loculosulcatispora* from the agarwood resin part of *Aquilaria sinensis*.

31- ***Massaria*** (*Massariaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Massaria was introduced by de Notaris (1844). A total of 193 epithets are listed in this genus (Index Fungorum 2025). The *Massaria* species are highly host-specific to *Acer* and *Rosaceae* plants exhibiting hemibiotrophic or weakly parasitic lifestyles, and are distributed in northern temperate climatic regions (Voglmayr & Jaklitsch 2011, Hongsanan et al. 2020, Samarakoon et al. 2022b, Pem et al. 2024). Some species, including *M. campestris*, *M. gigantispora*, and *M. vindobonensis* have been identified from dead branches attached to trees, indicating their weak pathogenicity in plants (Michalopoulos-Skarmoutsos & Skarmoutsos 1999, Voglmayr & Jaklitsch 2011, Hongsanan et al. 2020). Currently, there are 54 accepted species, of which only 19 species have molecular data (SSU, LSU, *tef*1-α, and *rpb*2); many species lack molecular data (Hongsanan et al. 2020, Samarakoon et al. 2022b, Index Fungorum 2025). In previous studies, some *Massaria* strains were isolated from *Aquilaria sinensis* as agarwood-associated fungi from China (Du et al. 2022b). In this study, we obtained three strains of *Massaria* from agarwood resin parts of *Aquilaria sinensis*.

32- ***Medicopsis*** (*Neohendersoniaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Medicopsis was introduced by de Gruyter et al. (2013). Currently, two epithets have been listed in this genus (Index Fungorum 2025), and members of *Medicopsis* can be found as pathogens in humans, endophytes, and saprobes on plants (Badali et al. 2010, Khan et al. 2011, de Gruyter et al. 2013, Ahmed et al. 2014, Jeddi et al. 2020, Garofalo et al. 2022, Want et al. 2022). This genus is well-studied in morphology and phylogeny (ITS, LSU, and SSU) (de Gruyter et al. 2013, Hyde et al. 2018). In previous studies, some *Medicopsis* strains were isolated from *Aquilaria sinensis* as agarwood-associated fungi from China (Du et al. 2024). In this study, we obtained three strains of *Medicopsis* from agarwood resin parts of *Aquilaria sinensis*.

33- ***Meyerozyma*** (*Debaryomycetaceae*, *Saccharomycetales*, *Saccharomycetes*, *Ascomycota*, Hyde et al. 2024c)

Meyerozyma was proposed by Kurtzman and Suzuki (2010) as one of the genera of ascomycete yeasts. Eight epithets have been listed in this genus (Index Fungorum 2025), and it can be distinguished from other similar species based on morphology and phylogeny (ITS and LSU) (Kurtzman and Suzuki 2010; Yurkov et al. 2017). Most yeasts of *Meyerozyma* have been isolated from insect-related habitats and plant materials in the forest (*Carpinus betulus*). In previous studies, no *Meyerozyma* have been isolated from *Aquilaria* spp. In this study, we obtained two strains of *Meyerozyma* from healthy branches of *Aquilaria sinensis* trees.

34- ***Montagnula*** (*Didymosphaeriaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Montagnula was described by Berlese (1896). Currently, 57 epithets are listed in Index Fungorum (2025). Most *Montagnula* species have been reported as saprobes on a wide range of hosts (dead wood, bark, or leaves) in various countries (Ariyawansa et al. 2014, Du et al. 2021, Pem et al. 2024), and *M. cylindrospora* was reported from a human skin sample (Crous et al. 2020). This genus is well-studied in morphology and phylogeny (ITS, LSU, SSU, *tef*1-α, and *rpb*2) (Hyde et al. 2023, Wanasinghe et al. 2024). In previous studies, only *M. aquilariae* was reported to be isolated from *Aquilaria sinensis* as a saprobe from China (Hyde et al. 2023). In this study, we obtained 13 strains of *Montagnula* from agarwood resin parts of *Aquilaria sinensis*.

35- ***Mucor*** (*Mucoraceae*, *Mucorales*, *Mucoromycetes*, *Mucoromycota*, Hyde et al. 2024c)

Mucor was designated by Fresenius (1850). More than 770 epithets are listed in this genus (Index Fungorum 2025). *Mucor* species are distributed worldwide and commonly found in soil and dung (Walther et al. 2013, Zhao et al. 2023). Some species of *Mucor* are widely utilized in fermentation, biotransformation, and the pharmaceutical industry (Hong et al. 2012, Huang et al.

2014, Khan et al. 2019). Additionally, some species are well-known pathogens that cause mucormycosis (Chibucos et al. 2016, Panthee et al. 2021). In this genus, only some species have DNA sequence (mostly ITS and LSU). In previous studies, some *Mucor* strains were isolated from *Aquilaria sinensis* in China, India, and Sri Lanka (Subasinghe et al. 2019, Gogoi et al. 2022, Du et al. 2024). In this study, we obtained three strains of *Mucor* from *Aquilaria sinensis*, of which one strain was an endophytic fungus from a healthy tree branch, and two strains were from agarwood resin parts.

36- ***Nemania*** (*Xylariaceae*, *Xylariales*, *Sordariomycetes*, *Ascomycota*, Hyde et al. 2024c)

Nemania was described by Gray (1821). Currently, 123 epithets are listed in Index Fungorum (2025). *Nemania* species are more diverse in temperate zones than tropical zones, and mainly distributed on the rotting wood of angiosperms (Ju & Rogers 2002, Tang et al. 2007, Pi et al. 2021) and as pathogens of certain plants (Wang et al. 2023a). In addition, endophytic *Nemania* species possess different biological activities (Kumarihamy et al. 2019, Tibpromma et al. 2021). The species of this genus are mainly identified through morphology, as most species lack molecular data (ITS, LSU, *rpb*2, and TUB) (Pourmoghaddam et al. 2022). In previous studies, *N. aquilariae* and *N. yunnanensis* were isolated from *Aquilaria sinensis* as agarwood-associated fungi in China, and *N. aquilariae* showed antibacterial and antimicrobial properties (Tibpromma et al. 2021). In this study, we obtained two strains of *Nemania* from healthy branches of *Aquilaria sinensis* trees.

37- ***Neodeightonia*** (*Botryosphaeriaceae*, *Botryosphaeriales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Neodeightonia was reported by Punithalingam (1969). A total of 15 epithets are listed in this genus (Index Fungorum 2025). Mostly members of *Neodeightonia* are associated with palms, bamboos, and other plants (Punithalingam 1969, Phillips et al. 2008, Liu et al. 2012, Adamčík et al. 2015, Dai et al. 2017, Pereira & Phillips 2023, Zhang et al. 2024a), and primarily reported as saprobes, although a few have been reported as pathogens on rachis, causing leaf spots and root rot (Ligoxigakis et al. 2013, Bengyella et al. 2015, Nishad & Ahmed 2020, Shabong & Kayang 2022, Zhang & Song 2022, Pereira & Phillips 2023). This genus is well-studied in morphology and phylogeny (ITS, LSU, *tef*1-α, and TUB). In previous studies, no *Neodeightonia* species were isolated from *Aquilaria* spp. In this study, we obtained one strain of *Neodeightonia* from the agarwood resin part of *Aquilaria sinensis*.

38- ***Neofusicoccum*** (*Botryosphaeriaceae*, *Botryosphaeriales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Neofusicoccum was reported by Crous et al. (2006). A total of 71 epithets are listed in this genus (Index Fungorum 2025). The members of *Neofusicoccum* have a worldwide and cosmopolitan distribution, occurring as endophytes and pathogens that cause shoot blight, cankers, and dieback on a wide range of woody hosts, including wild, ornamental, and economically important species (Slippers & Wingfield 2007, Diniz et al. 2021, Si et al. 2023). *Neofusicoccum* species are difficult to differentiate from one another due to the overlap of many morphological characters between species; therefore, molecular data (ITS, *tef*1-α, *rpb*2, and TUB) are indispensable for distinguishing species (Crous et al. 2006, Phillips et al. 2008, Phillips et al. 2013, Zhang et al. 2021). In previous studies, some *Neofusicoccum* species were isolated from *Aquilaria sinensis* as agarwood-associated fungi in China (Du et al. 2022c).

39- ***Neopestalotiopsis*** (*Sporocadaceae*, *Amphisphaeriales*, *Sordariomycetes*, *Ascomycota*, Hyde et al. 2024c)

Neopestalotiopsis was introduced by Maharachchikumbura et al. (2014). A total of 119 epithets are listed in this genus (Index Fungorum 2025). Members of *Neopestalotiopsis* are important plant pathogens and are ubiquitous in agricultural settings, causing several diseases and losses on various hosts worldwide (Maharachchikumbura et al. 2014, Jayawardena et al. 2016, Norphanphoun et al.

2019, Farr & Rossman 2023, Sun et al. 2023). Several species have been reported as saprobes and endophytes (Chethana et al. 2021, Sun et al. 2023). The species of *Neopestalotiopsis* can be distinguished from *Pseudopestalotiopsis* and *Pestalotiopsis* by morphology and phylogeny (ITS, *tef*1-α, and TUB). In previous studies, *Neopestalotiopsis* spp. were isolated from *Aquilaria sinensis* as agarwood-associated fungi from China (Du et al. 2022b, c). In this study, we obtained 13 strains of *Neopestalotiopsis* from *Aquilaria sinensis*, comprising 10 endophytic fungi from healthy tree branches or leaves, one strain from the agarwood resin part, and two strains from dead branches.

40- ***Neoscytalidium*** (*Botryosphaeriaceae*, *Botryosphaeriales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Neoscytalidium was introduced by Crous et al. (2006). Eight epithets are listed in this genus (Index Fungorum 2025). Species of *Neoscytalidium* have been reported as pathogens of both plants and humans, with a worldwide distribution. (Crous et al. 2006, Calvillo-Medina et al. 2018, Wonglom et al. 2023). This genus can be distinguished from other genera based on morphology and phylogeny (ITS, *tef*1-α, and TUB) (Wonglom et al. 2023). In previous studies, some *Neoscytalidium* strains were isolated from *Aquilaria sinensis* as agarwood-associated fungi in China (Du et al. 2024). In this study, we obtained 25 strains of *Neoscytalidium* from *Aquilaria sinensis*, comprising 17 strains from agarwood resin parts and eight strains from dead branches.

41- ***Nigrograna*** (*Nigrograna*ceae, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Nigrograna was described by De Gruyter et al. (2013). Currently, 43 epithets are listed in Index Fungorum (2025), and *Nigrograna* species have been reported as saprobes, endophytes, and human pathogens distributed in marine and terrestrial habitats (Jaklitsch & Voglmayr 2016, Dayarathne et al. 2020, Lu et al. 2022a, Du et al. 2024a). This genus is well-studied in morphology and phylogeny (ITS, LSU, SSU, *tef*1-α, and *rpb*2) (Du et al. 2024a). In previous studies, only *N. aquilariae* was reported from *Aquilaria sinensis* as a saprobe from China (Du et al. 2024a). In this study, we obtained one strain of *Nigrograna* from the agarwood resin part of *Aquilaria sinensis*.

42- ***Nigrospora*** (*Apiosporaceae*, *Amphisphaeriales*, *Sordariomycetes*, *Ascomycota*, Hyde et al. 2024c)

Nigrospora was described by Zimmerman (1902). Currently, 52 epithets are listed in Index Fungorum (2025). This genus includes pathogens, endophytes, and saprobes, which are usually isolated from various substrates like plants, soil, and air (Zhang et al. 2024c). This genus is well-studied in morphology and phylogeny (ITS, *tef*1-α, and TUB) (Zhang et al. 2024c). *Nigrospora* is considered a natural product source and is utilized in industrial applications (Metwaly et al. 2014, Zhong et al. 2016, Zhang et al. 2024c). In previous studies, some *Nigrospora* strains were reported to isolate from *Aquilaria* spp. as endophytes or agarwood-associated fungi, and some strains show a high inhibition rate to *Botrytis cinerea* from China (Li et al. 2014, Huang et al. 2018, Du et al. 2022a, b, c). In this study, we obtained 34 strains of *Nigrospora* from *Aquilaria sinensis*, comprising 28 endophytic fungi from healthy tree branches or leaves and six strains from agarwood resin parts.

43- ***Paracamarosporium*** (*Didymosphaeriaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Paracamarosporium was introduced by Wijayawardene et al. (2014). Nine epithets are listed in this genus (Index Fungorum 2025). Members of *Paracamarosporium* are found as endophytes and saprobes on leaves, twigs, branches, and stems of various plants (Wijayawardene et al. 2014, Pelo et al. 2020, Thuong et al. 2022). Species of *Paracamarosporium* have medicinal potential, and a *Paracamarosporium* sp. has been reported to produce potent antimalarial compounds (Hayashi et al. 2019). It is challenging to morphologically distinguish the taxa in this genus (Crous et al. 2015), but this can be achieved through multi-locus phylogeny (using ITS and LSU) (Thuong et al. 2022). In previous studies, some *Paracamarosporium* strains were isolated from *Aquilaria sinensis* as

agarwood-associated fungi in China (Du et al. 2022b, c, 2024). In this study, we obtained 16 strains of *Paracamarosporium* from healthy branches of *Aquilaria sinensis* trees.

44- ***Paraconiothyrium*** (*Didymosphaeriaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Paraconiothyrium was introduced by Verkley et al. (2004). A total of 36 epithets are listed in this genus (Index Fungorum 2025). The genus is reported as a phytopathogen, saprobe, and endophyte in a wide range of hosts and substrates worldwide (Lu et al. 2022b, Pem et al. 2024). The species delineation of this genus should be based on a combination of morphology and molecular phylogeny (ITS, LSU, SSU, *tef*1-α, and *rpb*2) (Xiong et al. 2023). In previous studies, some *Paraconiothyrium* strains were isolated from *Aquilaria sinensis* as agarwood-associated fungi in China (Du et al. 2022a, b). In this study, we obtained four strains of *Paraconiothyrium* from *Aquilaria sinensis*, of which one strain was from the agarwood resin part, and three strains were from dead branches.

45- ***Paradictyoarthrinium*** (*Paradictyoarthriniaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Paradictyoarthrinium was established by Matsushima (1996). Five epithets have been listed in this genus (Index Fungorum 2025). Members of *Paradictyoarthrinium* are mainly discovered as saprobes in terrestrial, freshwater, and marine environments in China, India, South Africa, and Thailand (Htet et al. 2023, Pem et al. 2024). This genus has also been reported as endophytes (Kristiani et al. 2023), and pathogens in humans (Kang et al. 2024). The genus can be identified by morphology and phylogeny (ITS, LSU, and *rpb*2) (Liu et al. 2018, Htet et al. 2023). In previous studies, no *Paradictyoarthrinium* species have been isolated from *Aquilaria* spp. In this study, we obtained one strain of *Paradictyoarthrinium* from the agarwood resin part of *Aquilaria sinensis*.

46- ***Penicillium*** (*Aspergillaceae*, *Eurotiales*, *Eurotiomycetes*, *Ascomycota*, Hyde et al. 2024c)

Penicillium was established by Link (1809). More than 1400 epithets are listed in this genus (Index Fungorum 2025). Members of *Penicillium* can be isolated from various substrates and reported across the world (Wang et al. 2023d). *Penicillium* species are ubiquitous in all kinds of environments, and they are of industrial, agricultural and clinical importance (Wang et al. 2023d). There are many species in this genus, which have been classified based on morphology and phylogeny (ITS, *rpb*2, BenA, and CaM). In previous studies, there were several *Penicillium* strains that were isolated as endophytes, and agarwood-associated fungi were isolated from *Aquilaria* spp. in China and Bangladesh (Tian et al. 2013, Du et al. 2022a, 2024, Zafrin et al. 2024). In this study, we obtained 23 strains of *Penicillium* from *Aquilaria sinensis*, comprising seven endophytic fungi from healthy tree branches or leaves and 16 strains from agarwood resin parts.

47- ***Periconia*** (*Periconiaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Periconia was introduced by Tode (1791). More than 200 epithets are listed in this genus (Index Fungorum 2025). The members of *Periconia* have been reported as saprobes, endophytes, and plant and human pathogens, with a wide distribution in terrestrial habitats and a rare presence in aquatic and marine environments (Liao et al. 2024; Pem et al. 2024). *Periconia* is also a source of many economically important bioactive compounds (Azhari & Supratman 2021). More than 100 compounds have been isolated from *Periconia* species (Liu et al. 2020a, Azhari & Supratman 2021). Currently, this genus is well-studied based on morphology and phylogeny (ITS, LSU, SSU, and *tef*1-α) (Liao et al. 2024, Yu et al. 2024). In previous studies, some *Periconia* species were isolated from *Aquilaria sinensis* in China (Du et al. 2022b, Fu et al. 2024).

48- ***Pestalotiopsis*** (*Sporocadaceae*, *Amphisphaeriales*, *Sordariomycetes*, *Ascomycota*, Hyde et al. 2024c)

Pestalotiopsis was proposed by Steyaert (1949). More than 400 epithets have been listed in this genus (Index Fungorum 2025) and most *Pestalotiopsis* species are known as endophytes, saprobes and can cause severe human, animal, and plant diseases, and are mainly found in the host of *Araceae*, *Ericaceae*, *Fagaceae*, *Garryaceae*, *Hypericaceae*, *Oleaceae*, *Theaceae*, and *Winteraceae* (Razaghi et al. 2024). This genus is well-studied in morphology and phylogeny (ITS, *tef*1-α, and TUB) (Tibpromma et al. 2018, Li et al. 2024c, Razaghi et al. 2024, Yin et al. 2024b). In previous studies, several *Pestalotiopsis* strains were isolated from *Aquilaria* spp. as agarwood-associated fungi in China and Thailand (Tian et al. 2013, Monggoot et al. 2017, Du et al. 2022a, Li et al. 2023). In this study, we obtained one strain of *Pestalotiopsis* from a healthy tree leaf of *Aquilaria sinensis*.

49- ***Phaeoacremonium*** (*Togniniaceae*, *Togniniales*, *Sordariomycetes*, *Ascomycota*, Hyde et al. 2024c)

Phaeoacremonium was established by Crous et al. (1996). A total of 74 epithets are listed in this genus (Index Fungorum 2025), and most *Phaeoacremonium* species were associated with human and plant infections, and the majority have also been isolated as saprobes or endophytes from woody hosts (terrestrial or aquatic habitats), soil, and air (Mostert et al. 2006, Damm et al. 2008, Gramaje et al. 2015, Spies et al. 2018, Halleen et al. 2020, Calabon et al. 2024, Mostert et al. 2024). The combination of morphology and phylogeny (ACT, ITS, LSU, TUB, and *tef*1-α) is essential for *Phaeoacremonium* species identification (Calabon et al. 2024, Mostert et al. 2024). In previous studies, several *Phaeoacremonium* strains were isolated from *Aquilaria* species as agarwood-associated fungi and reported to promote agarwood sesquiterpene accumulation (e.g., *P. parasiticum* and *P. rubrigenum*) in China and India (Le et al. 2017, Liu et al. 2022a, Li et al. 2023, Du et al. 2024). In this study, we obtained 28 strains of *Phaeoacremonium* from *Aquilaria sinensis*, comprising one endophytic fungus isolated from a healthy tree branch and 27 strains from agarwood resin parts.

50- ***Phanerochaetella*** (*Irpicaceae*, *Polyporales*, *Agaricomycetes*, *Basidiomycota*, Hyde et al. 2024c)

Phanerochaetella was established by Chen et al. (2021). Eight epithets are listed in this genus (Index Fungorum 2025), and most *Phanerochaetella* species are plant pathogens that cause white rot on hardwood and conifers in China, India, Italy, Japan, Mexico, and the United States (Chen et al. 2021, Li et al. 2022b). This genus is well-studied in morphology and phylogeny (ITS and LSU) (Chen et al. 2021, Li et al. 2022b). In previous studies, *Phanerochaetella* has not been reported from *Aquilaria* spp. In this study, we isolated a strain of *Phanerochaetella* from the agarwood resin part of *Aquilaria sinensis*.

51- ***Phlebiopsis*** (*Phanerochaetaceae*, *Polyporales*, *Agaricomycetes*, *Basidiomycota*, Hyde et al. 2024c)

Phlebiopsis was introduced by Jülich (1978). A total of 41 epithets are listed in this genus (Index Fungorum 2025), and most *Phlebiopsis* species are saprobic on wood, and some species are used as biocontrol agents (*P. gigantea*) (Gaitnieks et al. 2020, Zhao et al. 2021). This genus is well-studied in morphology and phylogeny (ITS and LSU) (Miettinen et al. 2016, Zhao et al. 2021). In previous studies, *Phlebiopsis* strains were isolated from *Aquilaria sinensis* as agarwood-associated fungi in China (Liu et al. 2019a, Du et al. 2022b).

52- ***Phyllosticta*** (*Phyllostictaceae*, *Botryosphaeriales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Phyllosticta was established by Persoon (1818). More than 3,200 epithets are listed in this genus (Index Fungorum 2025), and most *Phyllosticta* species are saprobic, pathogenic, and endophytic fungi associated with a variety of plants (e.g., *Citrus* spp., *Garcinia oblongifolia*, *Musa* spp., *Pterospermum heterophyllum*, and *Vitis* spp.) (Wang et al. 2012, 2023c, Wong et al. 2012, Tran et al. 2019, Zhang et al. 2022, 2024a). This genus is well-studied in morphology and phylogeny (ACT, ITS, LSU, *tef*1-α, and GAPDH) (Wikee et al. 2013, Norphanphoun et al. 2020, Zhang et al. 2022, 2024b, Wang et al. 2023c). In previous studies, many *Phyllosticta* strains were isolated from

Aquilaria spp. as agarwood-associated fungi from China (Chen 2007, Zhang et al. 2015, Li et al. 2018). In this study, we obtained 18 strains of *Phyllosticta* from healthy leaves of *Aquilaria sinensis* trees.

53- ***Pithomyces*** (*Astrosphaeriellaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Pithomyces was proposed by Berkeley & Broome (1873). More than 50 epithets are listed in this genus (Index Fungorum 2025), and most *Pithomyces* species are known as saprobes, endophytes, pathogens on wood, leaf, and are also found in soil, air, and clinical material (Da Cunha et al. 2014, Walsh et al. 2018, Xiang et al. 2024). This genus is studied mostly based on morphology, and classification of a few species is supported by phylogenetic analysis (ITS, LSU, SSU, and *rpb*2) (Pratibha and Ashish 2015, Wanasinghe et al. 2018a). In previous studies, *Pithomyces* strains were isolated from *Aquilaria* sp. as agarwood-associated fungi from Thailand (Subansenee et al. 1985). In this study, we obtained one strain of *Pithomyces* from a healthy tree branch of *Aquilaria sinensis*.

54- ***Pseudofusicoccum*** (*Phyllostictaceae*, *Botryosphaeriales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Pseudofusicoccum was introduced by Crous et al. (2006). Nine epithets are listed in this genus (Index Fungorum 2025), and *Pseudofusicoccum* species are known to be saprobes, endophytes, and pathogens on various hosts (Marques et al. 2012, Phillips et al. 2013, Jayasiri et al. 2019, Iantas et al. 2023). This genus is well-studied in morphology and phylogeny (ITS, LSU, and *tef*1-α) (Crous et al. 2006, Jayasiri et al. 2019). In previous studies, some *Pseudofusicoccum* strains were isolated from *Aquilaria sinensis* as agarwood-associated fungi in China (Du et al. 2024). In this study, we obtained two strains of *Pseudofusicoccum* from agarwood resin parts of *Aquilaria sinensis*.

55- ***Pseudopithomyces*** (*Didymosphaeriaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Pseudopithomyces was established by Ariyawansa et al. (2015). A total of 13 epithets have been listed in this genus (Index Fungorum 2025) and most *Pseudopithomyces* species are saprobic, endophytic or parasitic on dead leaves, and stems of plants (e.g., on *Acacia* sp., *Acoelorrhaphe wrightii*, *Entada phaseoloides*, *Gnidia polycephala*, *Morus australis*, *Pandanus amaryllifolius*, Poaceae, *Rosa canina*, *Saccharum officinarum*, and *Zea mays*) and also reported on human specimens (Crous et al. 2016, Hyde et al. 2017, Tibpromma et al. 2018, Tennakoon et al. 2021, García-Latorre et al. 2024). This genus is well-studied in morphology and phylogeny (ITS, LSU, SSU, and *tef*1-α) (Ariyawansa et al. 2015, Tibpromma et al. 2018, Tennakoon et al. 2021). Previous studies from China reported *Pseudopithomyces* strains as agarwood-associated fungi from *Aquilaria sinensis* (Du et al. 2022a, b). In this study, we obtained one strain of *Pseudopithomyces* from a healthy tree branch of *Aquilaria sinensis*.

56- ***Pseudorobillarda*** (*Pseudorobillardaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Pseudorobillarda was established by Morelet (1968). A total of 21 epithets are listed in this genus (Index Fungorum 2025) and most *Pseudorobillarda* species are saprobic on wood, dead leaves, stems, barks, and some species are endophytes of plants (e.g., *Asparagus*, *Bambusa*, *Bolusanthus*, *Camellia*, *Dicotyledon*, *Eucalyptus*, and *Setaria*) (Vujanovic & St-Arnaud 2003, Tangthirasunun et al. 2014, Li et al. 2020, Nag Raj et al. 1972, Vujanovic et al. 2003, Plaingam et al. 2005, Crous et al. 2018, Rathnayaka et al. 2021). Ten species of *Pseudorobillarda* have been extensively studied based on morphology and multi-locus phylogeny (ITS, LSU, SSU, and *rpb*2) (Crous et al. 2018, Li et al. 2020, Rathnayaka et al. 2021, Song et al. 2022a). In previous studies, *Pseudorobillarda* strains were isolated from *Aquilaria* spp. as agarwood-associated fungi in China and Greece (Song et al. 2021, Theologidis et al. 2023). In this study, we obtained one strain of *Pseudorobillarda* from a dead branch of *Aquilaria sinensis*.

57- ***Rhytidhysteron*** (*Hysteriaceae*, *Hysteriales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Rhytidhysteron was described by Spegazzini (1881). Currently, 43 epithets are listed in Index Fungorum (2025), and most members of *Rhytidhysteron* are known as saprobes, some also as endophytes and weak pathogens on woody plants distributed on a wide range of hosts in many countries, and some are rarely found as human pathogens (Thambugala et al. 2016, de Silva et al. 2020, Wanasinghe et al. 2021, Ren et al. 2022, Du et al. 2023). This genus is well-studied in morphology and phylogeny (ITS, LSU, SSU, and *tef*1-α) (Du et al. 2023). In previous studies, only *R. thailandicum* was reported to be isolated from *Aquilaria sinensis* as a saprobe from China (Du et al. 2023). In this study, we obtained one strain of *Rhytidhysteron* from a healthy tree branch of *Aquilaria sinensis*.

58- ***Scytalidium*** (*Helotiaceae*, *Helotiales*, *Leotiomycetes*, *Ascomycota*, Hyde et al. 2024c)

Scytalidium was established by Pesante (1957). A total of 39 epithets are listed in this genus (Index Fungorum 2025), and most *Scytalidium* species are quite common saprobic, endophytic or parasitic on soil, plants, animals, and other fungal members (e.g., *Betula alba*, *Globodera rostochiensis*, *Picea abies*, *Pinus*, and *Platanus*) (Klingstrom & Beyer 1965, Ellis 1971, Dickinson et al. 1983, Holubova-Jechova 1990, Egger & Sigler 1993, Kang et al. 2010, Gautam et al. 2015). Only ten species of *Scytalidium* have molecular data (ITS and LSU) (Crous et al. 2022, 2023). Previous studies isolated *Scytalidium* strains from *Aquilaria* spp. as agarwood-associated fungi in China and Indonesia (Lisdayani et al. 2015, Gong & Guo 2009, Fauzi et al. 2024). In this study, we obtained eight strains of *Scytalidium* from agarwood resin parts of *Aquilaria sinensis*.

59- ***Talaromyces*** (*Trichocomaceae*, *Eurotiales*, *Eurotiomycetes*, *Ascomycota*, Hyde et al. 2024c)

Talaromyces was established by Benjamin (1955). A total of 296 epithets are listed in this genus (Index Fungorum 2025). *Talaromyces* species have been isolated as saprobes, endophytes, or pathogens from air, soil, food products, and leaf litter, while *Talaromyces marneffei* is a pathogen associated with HIV patients (Guevara-Suarez et al. 2017, Morales-Oyervides et al. 2020, Nguyen & Lee 2023). This genus is well-studied in morphology and multi-locus phylogeny (*BenA*, *CAM*, ITS, *rpb*2, and TUB; Alves et al. 2022, Nguyen & Lee 2023, Paiva et al. 2024, Tian et al. 2024). In previous studies, some *Talaromyces* strains were isolated from *Aquilaria sinensis* as agarwood-associated fungi in China (Du et al. 2022b, Pang et al. 2024). In this study, we obtained two strains of *Talaromyces* from agarwood resin parts of *Aquilaria sinensis*.

60- ***Trichoderma*** (*Hypocreaceae*, *Hypocreales*, *Sordariomycetes*, *Ascomycota*, Hyde et al. 2024c)

Trichoderma was established by Persoon (1794). A total of 549 epithets are listed in this genus (Index Fungorum 2025), and most *Trichoderma* species are pathogenic or saprobic in dead wood and bark, other fungi, soil, bats, and some species are endophytes of plants (Prameeladevi et al. 2021, Zheng et al. 2021, Liu et al. 2023, Brito et al. 2023, Zhao et al. 2024). This genus is well-studied in morphology and phylogeny (*tef*1-α and *rpb*2) (Zhao et al. 2024). *Trichoderma* species are extensively utilized in industrial applications as producers of enzymes such as cellulases, hemicellulases, and proteases, which are essential for biofuel production, food processing, and textile manufacturing (Bustamante et al. 2021, Cai & Druzhinina 2021, Liu et al. 2023). In previous studies, *Trichoderma* was found as the main genus isolated from *Aquilaria* spp. as agarwood-associated fungi from China, India, and Malaysia (Mohamed et al. 2010, Li et al. 2012, Chhipa and Kaushik 2017, Du et al. 2022a, b). In this study, we obtained 16 strains of *Trichoderma* from *Aquilaria sinensis*, comprising four endophytic fungi from healthy tree branches or leaves and 12 strains from agarwood resin parts.

61- ***Trichosporon*** (*Trichosporonaceae*, *Trichosporonales*, *Tremellomycetes*, *Ascomycota*, Hyde et al. 2024c)

Trichosporon was established by Doweld (2001). More than 130 epithets are listed in this genus (Index Fungorum 2025), and most *Trichosporon* species have been found in soil, water, plants,

clinical specimens, and insects as pathogens, endophytes, or saprobes (Sheikh et al. 1974, Molnar et al. 2004, Sugita 2011, Kunthiphun et al. 2016, Francisco et al. 2019). Species of *Trichosporon* are medically important due to their antifungal resistance, especially to echinocandins and amphotericin B, with azoles like voriconazole being the preferred treatment (Colombo et al. 2011, Francisco et al. 2019, Guo et al. 2019, Nobrega de Almeida et al. 2021). This genus is well-studied in morphology and phylogeny (ITS, IGS1, and LSU) (Nováková et al. 2015, Guo et al. 2019, Nobrega de Almeida et al. 2021, Francisco et al. 2019). In previous studies, some *Trichosporon* strains were isolated from *Aquilaria* spp. as agarwood-associated fungi in Brunei Darussalam and China (Mohammad et al. 2021, Du et al. 2022a, b, Zhang et al. 2024b).

62- ***Veronaea*** (*Herpotrichiellaceae*, *Chaetothyriales*, *Eurotiomycetes*, *Ascomycota*, Hyde et al. 2024c)

Veronaea was established by Cifferi & Montemartini (1957). A total of 31 epithets are listed in this genus (Index Fungorum 2025). While some *Veronaea* species are saprobic on dead plant materials (e.g., *Carex pendula*, *Carlina vulgaris*, *Ficus hispida*, *Grewia asiatica*, *Hedychium coronarium*, *Thylacospermum caespitosum*, and bamboo), others colonise soil, and some *Veronaea* strains act as pathogens for humans, animals, or plants (Hyde and Goh 1998, Kondo et al. 2007, Wijayawardene et al. 2020, Hosoya et al. 2015, Chandrasiri et al. 2021). Molecular data is not available for most *Veronaea* species, with only six species having DNA sequence data (Wijayawardene et al. 2020, Chandrasiri et al. 2021, Su et al. 2023). In previous studies, *Veronaea* strains were isolated from *Aquilaria* spp. as agarwood-associated fungi in China (Liu et al. 2019a, Zhang et al. 2024b). In this study, we obtained two strains of *Veronaea* from agarwood resin parts of *Aquilaria sinensis*.

63- ***Xenoroussoella*** (*Roussoellaceae*, *Pleosporales*, *Dothideomycetes*, *Ascomycota*, Hyde et al. 2024c)

Xenoroussoella was established by Mapook et al. (2020). Up to now, only one species has been described in this genus (Mapook et al. 2020, Index Fungorum 2025). This genus has been reported to have both sexual and asexual morphs (Mapook et al. 2020, de Silva et al. 2022) and exists mainly as saprobes on *Anomianthus dulcis*, *Chromolaena odorata*, and *Desmos chinensis* in Thailand (Pem et al. 2024). This genus is well-studied in morphology and phylogeny (ITS, LSU, SSU, *tef*1-α, and *rpb*2) (Mapook et al. 2020, de Silva et al. 2022). *Xenoroussoella* has not been previously reported from *Aquilaria* spp. In this study, we obtained four strains of *Xenoroussoella* from *Aquilaria sinensis*, of which one strain was from the agarwood resin part, and three strains were from dead branches.

64- ***Xylaria*** (*Xylariaceae*, *Xylariales*, *Sordariomycetes*, *Ascomycota*, Hyde et al. 2024c)

Xylaria is a large and well-described genus of the Xylariaceae (Martin 1970). Currently, more than 930 epithets are listed in Index Fungorum (2025). Most *Xylaria* species are reported to be saprobes, endophytes, and pathogens that occur on multiple hosts (wood, sawdust, leaves, dung, or soil), and are highly diverse in the tropics and subtropics (Rogers 1979, de Vega et al. 2010, Wangsawat et al. 2021, Zhu et al. 2024). So far, phylogenetic analysis of species has mainly been based on multiple loci (ITS, *rpb*2, and TUB) (Li et al. 2024b). Previous studies reported some *Xylaria* strains isolated from *Aquilaria* spp. as endophytes or agarwood-associated fungi in China (Du et al. 2022a, b, 2024b). In this study, we obtained 12 strains of *Xylaria* from *Aquilaria sinensis*, comprising eight endophytic strains isolated from healthy tree branches or leaves, and four strains from agarwood resin parts.

DISCUSSION

This study analyzed community composition data of 960 fungal strains representing 64 genera, isolated from *Aquilaria sinensis* samples collected in Guangdong and Yunnan provinces. Among these, 142 strains have previously been reported by our research team (Du et al. 2022b, c, 2024b) (Supplementary Table 1) and are included in this study solely for data analysis purposes. Therefore,

a total of 818 strains are used in this study, which are newly reported *Aquilaria sinensis*-associated fungi. This study provides a brief overview of the 64 genera and conducts meticulous phylogenetic and morphological analyses on five new species, thereby ensuring the robustness and reliability of our findings.

In this study, 64 genera are documented, including information on their habitats, lifestyles, specific roles, and relationships with *Aquilaria* spp. Among these, 50 genera have been previously reported on *Aquilaria* spp., with some genera considered to be associated with the formation of agarwood resin, e.g., *Cladorrhinum, Curvularia*, *Fonsecaea*, *Fusarium*, *Hermatomyces*, *Lasiodiplodia*, and *Phaeoacremonium* (Du et al. 2022a). Some genera (e.g., *Aspergillus*, *Aureobasidium*, *Chaetomium*, *Curvularia*, *Diaporthe*, *Epicoccum*, *Nemania*, *Paracamarosporium*, *Phaeoacremonium*, and *Trichoderma*) exhibit rich secondary metabolites or biological activities, e.g., antibacterial, anti-cancer, anti-inflammatory, antimalarial, antimicrobial, antioxidant, anti-plasmodial, antirheumatoid, antitumor, cytotoxic, enzyme inhibitory, and immunosuppressive, and there is detailed information for each genus. The potential of these secondary metabolites for various applications is a promising area for future research. Additionally, 14 genera (21.88%) are reported for the first time in *Aquilaria*, *viz.*, *Allophoma*, *Aureobasidium*, *Banksiophoma*, *Biscogniauxia*, *Coniella*, *Didymella*, *Exophiala*, *Fomitiporia*, *Loculosulcatispora*, *Meyerozyma*, *Neodeightonia*, *Paradictyoarthrinium*, *Phanerochaetella*, and *Xenoroussoella*. The strains within these genera may also possess a similar potential for producing secondary metabolites or promoting agarwood formation, warranting further research in the future.

This study isolated 960 fungal strains of 64 genera in 44 families, a substantial number that provides a comprehensive view of the fungal community composition in our study area. At the same time, most of these strains belong to known taxa and are primarily concentrated in a few common genera, such as *Fusarium* and *Lasiodiplodia* (Fig. 1). The proportion of unknown taxa is relatively low; we describe five new taxa: *Banksiophoma endophytica*, *Deniquelata aquilariae*, *Montagnula sinensis*, *M. yunnanensis*, and *Fomitiporia aquilariae.* These taxa, with their distinct phylogenetic lineages or morphological differences compared to their sister branches in the phylogenetic analyses, represent a significant contribution to the field of fungal biology. *Banksiophoma* and *Fomitiporia* genera are reported for the first time in *Aquilaria* spp., providing new insights into their ecological roles, host range, and their potential roles in the formation process of agarwood. The genus *Fomitiporia*, a basidiomycete previously reported as both pathogenic and saprobic (Alves-Silva et al. 2020a, b; Brown et al. 2020), has three strains identified in this study (Figs. 18, 19) as agarwood-associated fungi isolated from agarwood resin, further underscoring the importance of our findings.

In previous studies, *Montagnula* has often been reported as a saprobic genus on various hosts, including *M. aquilariae*, found on *Aquilaria sinensis* as a saprobe (Hyde et al. 2023). The discovery of asexual morphs of *Montagnula* has been limited, with only *M. cylindrospora* and *M. menglaensis* identified to date (Crous et al. 2020, Wanasinghe et al. 2024). In this study, 13 strains of *Montagnula* were isolated and identified as two new species and one new record based on molecular and morphological analyses (Figs 13-17); all of these strains clustered with *M. cylindrospora* in an independent clade. The 13 strains of *Montagnula* in this study were isolated from the agarwood resins of samples collected from Yuanjiang, Yunnan, and are considered agarwood-associated fungi. Among them, 11 strains were identified as the same species, although they were not isolated from the same tree and were collected at different times. This suggests that the isolation of *Montagnula* strains from *Aquilaria sinensis* is not incidental and is not limited by the survival state of the plant material, as the species of *Montagnula* can live in *Aquilaria* as saprophytic and agarwood-associated fungi. However, *Montagnula* strains have so far been discovered only on *Aquilaria sinensis* from Yunnan, and the saprobic fungus *M. aquilariae* has also been reported only in Yunnan. The potential implications of these findings for the distribution and ecology of *Aquilaria sinensis* are significant, and further research is necessary to fully understand their significance.

Additionally, strains of the genera *Corynespora*, *Nigrograna*, and *Rhytidhysteron* were also found in fresh plant material in this study. In previous research, these genera have primarily been described as saprobic, occurring on various plants, including records on *Aquilaria* spp. (Du et al.

2023, 2024a). This evidence suggests that some common saprobic fungal groups are capable of living within healthy plant tissues and may alter their lifestyle in response to changes in the plant's health. These lifestyle transitions could be closely associated with the formation of agarwood resin, underscoring the importance of future studies on these genera and intriguing research topics.

In this study, despite extensive attempts to induce sporulation, reproductive structures were not observed in the three new species (*Deniquelata aquilariae*, *Montagnula yunnanensis*, and *Fomitiporia aquilariae*). This is not uncommon in endophytic strains and certain sterile fungal taxa, particularly those of the *Basidiomycota*. However, we fully delimited these strains using a combination of multi-locus phylogenetic analysis, base pair comparison, and mycelial morphology and cultural characteristics. Therefore, we believe the species delineation is reasonable, but the lack of reproductive traits is a limitation, and further induction methods should be explored to fully characterize these strains. Furthermore, for several species in which sporulation structures were observed, we found that they primarily sporulated naturally on PDA or WA medium at 25 °C in the dark. In contrast, culture conditions supplemented with host tissue promoted rapid mycelial expansion and growth but did not induce spore formation. This is presumably due to an overabundance of nutrients, which inhibited the initiation of meristematic reproduction. Therefore, future studies could explore stimulating sporulation potential by adjusting medium composition, limiting specific nutrients, or inducing specific factors to obtain more comprehensive morphological evidence.

Through a series of data analyses on 960 fungal strains (Fig. 1), it was found that *Ascomycota* was the most dominant group, accounting for approximately 99.06%. At the same time, *Basidiomycota* and *Mucoromycota* made up only a small proportion. This dominance of *Ascomycota* in *Aquilaria sinensis* suggests that it occupies the primary ecological niche, demonstrating both dominance and community diversity. These findings align with previous studies, which also identified *Ascomycota* as the major group, whether as saprobes or pathogens associated with *Aquilaria* spp. (Liao et al. 2018, Liu et al. 2020b, Du et al. 2024a). Data analysis revealed some overlap in fungal community composition between agarwood samples from two different provinces (Fig. 7). Genera such as *Diaporthe*, *Fusarium*, and *Lasiodiplodia* were isolated from samples collected at four sites in Guangdong and Yunnan, and these genera have been frequently reported in prior studies (Du et al. 2022a). This suggests that the fungal taxa associated with *Aquilaria sinensis* do not exhibit significant geographic variation. However, some genera were “region-specific”. For instance, *Cladosporium* and *Hermatomyces* were found only in two sites in Guangdong, while *Botryosphaeria* and *Mucor* were detected only in two sites in Yunnan. These differences may stem from insufficient sampling or variations in the *Aquilaria sinensis* cultivars. Given that the physiological functions and defense mechanisms of each tree are not entirely consistent, variations in microbial communities are understandable. These differences contribute to the rich biodiversity associated with *Aquilaria sinensis*.

Notably, all samples collected from Maoming were agarwood resins, from which 219 fungal strains belonging to 18 genera were isolated (Fig. 2). Most of these fungal genera have been extensively reported in previous studies, with only three genera, *viz*., *Exophiala, Neodeightonia*, and *Paradictyoarthrinium*, being reported for the first time in *Aquilaria*. Previous studies on agarwood and its associated fungi have revealed their richness in secondary metabolites, with some strains shown to promote agarwood resin formation (Wang et al. 2018, Du et al. 2022a). Therefore, the strains isolated from the Maoming agarwood resins, particularly those belonging to the newly discovered genera, may represent potential candidates for enhancing resin formation. These findings underscore the hopeful prospect of enhancing resin formation and suggest significant research potential for these genera in the future.

Additionally, in this study, we primarily analyzed the fungal community composition using culture-dependent techniques across different parts of *Aquilaria sinensis*. Data analysis revealed that fungal strains from various parts of the tree showed a certain degree of overlap, a finding that underscores the interconnectedness of these organisms (Fig. 6). For instance, *Aspergillus*, *Diaporthe*, *Lasiodiplodia*, and *Neopestalotiopsis* were found in agarwood resins, dead branches, healthy

branches, and healthy leaves in four parts, representing common genera. This suggests that the endophytic fungi (isolated from healthy tissues), agarwood-associated fungi (isolated from agarwood resins), and saprobic fungi (isolated from dead tissues) associated with *Aquilaria sinensis* are not entirely distinct or unrelated. For example, *Fusarium* and *Paraconiothyrium* were present in healthy branches, agarwood resins, and dead branches, while *Cladosporium* was a common genus in agarwood resins, healthy leaves, and dead branches. These overlaps might result from lifestyle transitions among these fungi, indicating their adaptability to different environments or their broad presence on *Aquilaria sinensis*, regardless of the tissue's survival state. At the same time, we observed that the strains and genera of fungi isolated from agarwood resin were the highest (645 strains of 48 genera). Among the 48 genera, 12 genera have been reported in previous studies to promote the formation of agarwood resin, *viz.*, *Aspergillus*, *Botryosphaeria*, *Chaetomium*, *Cladosporium*, *Colletotrichum*, *Diaporthe*, *Fusarium*, *Lasiodiplodia*, *Penicillium*, *Phaeoacremonium*, *Trichoderma*, and *Xylaria*. Among the other 36 genera, 30 genera have been reported as isolated from agarwood or *Aquilaria* spp. in previous studies, *viz.*, *Acrocalymma*, *Alternaria*, *Annulohypoxylon*, *Corynespora*, *Crassiparies*, *Curvularia*, *Daldinia*, *Deniquelata*, *Fonsecaea*, *Hermatomyces*, *Hypoxylon*, *Massaria*, *Medicopsis*, *Montagnula*, *Mucor*, *Neofusicoccum*, *Neopestalotiopsis*, *Neoscytalidium*, *Nigrograna*, *Nigrospora*, *Paracamarosporium*, *Paraconiothyrium*, *Periconia*, *Phlebiopsis*, *Pseudofusicoccum*, *Pseudopithomyces*, *Scytalidium*, *Talaromyces*, *Trichosporon*, and *Veronaea*; Only six genera have been reported for the first time on *Aquilaria*, *viz.*, *Exophiala*, *Fomitiporia*, *Loculosulcatispora*, *Neodeightonia*, *Paradictyoarthrinium*, and *Phanerochaetella*. Due to the rich fungal community and abundant secondary metabolites (sesquiterpenes and chromones) in agarwood resin, these genera are worthy of development and utilization research. Not only should the induction effect of these genera on agarwood resin be studied, but secondary metabolites such as sesquiterpenes and chromones should also be extracted to conduct in-depth *in vitro* studies of their antibacterial, antioxidant, and neuroprotective biological activities, providing a theoretical basis and application potential for the development of natural medicines and the regulation of agarwood quality.

Aquilaria sinensis, as an important economic plant, is undoubtedly a hot research topic. In previous studies, *Fusarium* has been the most widely studied genus due to its abundant presence as an endophytic or agarwood-associated fungus in *Aquilaria* spp. (Tabata et al. 2003, Tamuli et al. 2005, Gong & Guo 2009, Cui et al. 2011, Premalatha et al. 2013, Subasinghe et al. 2019, Du et al. 2022a, b, c, 2024b). Some *Fusarium* strains have shown excellent potential for inducing agarwood formation, such as *F. solani* (Du et al. 2024b). Du et al. (2024b) reported that *F. solani* could induce agarwood that meets medicinal standards within six months. Moreover, *Lasiodiplodia* is another genus that has been extensively studied. Zheng et al. (2019) reported that *F. solani* and *Lasiodiplodia theobromae* were used as inducers to promote agarwood production. These two genera are also the most frequently isolated in this study, indicating their widespread presence in *Aquilaria* spp., which aligns with previous research. Additionally, *Aspergillus* and *Botryosphaeria*, as common pathogens, are also frequently found as *Aquilaria*-associated fungi (Wang et al. 2018, Du et al. 2022a). Furthermore, *Aspergillus niger* and *Botryosphaeria* spp. have been reported to promote agarwood formation (Gong & Guo 2009, Tian et al. 2013, Subasinghe et al. 2019). However, in Du et al. (2024b), *A. niger* and *Botryosphaeria fusispora* showed a 75% mortality rate in the tested samples (small branches). This could be due to differences in biochemical characteristics between strains or variations in host defense mechanisms. Therefore, this study recommends that researchers investigate the characteristics of the strains before conducting related experiments to minimize damage to economically important plants.

In fungal induction of agarwood, endophytic fungi are often used as fungal inducers and have been reported to be effective (Laurence 2013, Azren et al. 2018, Subasinghe et al. 2019). Additionally, the formation of aromatic compounds in agarwood is believed to be closely related to the presence of endophytic fungi (Pang et al. 2024). However, the definition of endophytic fungi in agarwood research has been unclear in previous studies. For example, in the study by Li et al. (2022), fungi isolated from agarwood resin were considered endophytic fungi, and several other studies have

also classified fungi isolated from agarwood resin as endophytic fungi (Wang et al. 2009, Premalatha & Kalra 2013, Chen et al. 2018, Pang et al. 2024). However, this is unreasonable. Firstly, the formation of agarwood requires the presence of a wound, through which microorganisms invade and trigger the tree's defense mechanisms, leading to the production of agarwood resin to counter these external injuries. Endophytic fungi are defined as "asymptomatic microbial partners that are intimately associated and co-inhabit within healthy internal plant tissues with the ability to confer benefits, co-evolve, and alter their lifestyle depending upon plant life stages and adverse conditions" (Liao et al. 2025). Therefore, fungi isolated from resin cannot be definitively identified as endophytic fungi originally residing in healthy trees, nor as exophytic fungi that have invaded through the wound. The mechanism of agarwood formation remains incompletely understood, and only a few hypotheses remain unproven. The relationship between agarwood resin formation and the microbial community remains unclear. Therefore, to better understand and explore the relationship between the microbiota of agarwood, agarwood resin, and the agarwood-producing tree genera, we suggest referring to fungi and bacteria isolated from the agarwood resin as "agarwood-associated fungi/bacteria." In contrast, endophytic fungi and bacteria should specifically refer to those isolated from the healthy tissues of agarwood-producing trees. This approach will help to more clearly define the microbial community of agarwood in future studies, avoid confusion between microorganisms from different sources, and provide more accurate evidence for exploring the mechanism of agarwood formation. Future research should focus on the diversity, functional characteristics, and relationship of agarwood-associated fungi and bacteria with agarwood resin synthesis in order to reveal the potential role of microorganisms in agarwood formation. Meanwhile, through precise microbial classification and functional analysis, more scientifically grounded theoretical support and practical guidance can be provided for the artificial induction and quality control of agarwood.

This study is the first to conduct a community analysis of a large number of agarwood-producing tree strains and reports the isolation of 14 fungal genera from *Aquilaria*, significantly increasing the community richness of fungi related to *Aquilaria sinensis* and providing valuable data support for future research. The results indicate that *Ascomycota* are the dominant taxa, playing a significant role in the formation of agarwood resin, particularly the genera *Fusarium* and *Lasiodiplodia*, which have been widely reported, with some strains showing potential in inducing agarwood resin formation. Additionally, this study is the first to perform a comprehensive data analysis of fungi isolated from various parts of the plant, revealing their interactions and laying a solid foundation for an in-depth study of the mechanisms underlying agarwood formation. Future research is crucial for exploring the biochemical characteristics and ecological functions of different strains to reveal their specific roles in the formation of agarwood resin. Moreover, with the continuous development of agarwood cultivation techniques, optimizing the use of fungi to improve the quality and yield of agarwood resin will become a key issue that needs to be addressed. In particular, for those fungal genera with potential, in-depth functional research and applied exploration may reveal their specific roles in agarwood resin synthesis, thereby promoting the sustainable development of the agarwood industry.

CONCLUSION

This study provides a comprehensive overview of the fungal community associated with *Aquilaria sinensis*, highlighting its remarkable diversity of community composition and ecological complexity. By analyzing 960 fungal strains representing 64 genera of 44 families, including 818 newly reported strains, this study significantly expands the current understanding of the mycobiota associated with *Aquilaria*. The dominance of *Ascomycota*, alongside the presence of *Basidiomycota* and *Mucoromycota*, reflects distinct fungal distribution patterns across different plant parts and geographic locations. Identifying 14 genera newly associated with *Aquilaria* and five novel species, supported by both phylogenetic and morphological evidence, underscores the taxonomic richness uncovered. In this study, most of the fungi were identified based on ITS sequence data. To study the complete taxonomy, a future study will need to incorporate morphology and sequences of additional genes to identify them to the species level. Notably, some fungal genera with species complexes (e.g., *Aspergillus*, *Colletotrichum*, *Diaporthe*, *Fusarium*, *Penicillium*, and *Trichoderma*) cannot be

identified correctly without the ITS gene. In addition, the proposed term “agarwood-associated fungi” provides a new perspective for distinguishing fungi linked to resin formation, potentially advancing future studies on the role of fungi in inducing agarwood. With its significant contribution to the field, this research provides valuable insights into fungal ecology, systematics, and plant-fungal interactions in economically important tree species, underscoring the importance and impact of the findings.

FUNDING

The “Yunnan Revitalization Talents Support Plan” (Young Talents Program and High‐End Foreign Experts Program), the Key Laboratory of Yunnan Provincial Department of Education of the Deep‐Time Evolution on Biodiversity from the Origin of the Pearl River, the National Natural Science Foundation of China (No. 32260004 and 31760013), the Yunnan Provincial Department of Science and Technology “Zhihui Yunnan” Plan (202403AM140023), Ongoing Research Funding Program (ORF-Ctr-2025-6), King Saud University, Riyadh, Saudi Arabia and Chiang Mai University.

ACKNOWLEDGEMENTS

Tian-Ye Du extends her heartfelt gratitude to Mae Fah Luang University for granting her the tuition scholarship for her Ph.D. studies. Dr. Shaun Pennycook, Manaaki Whenua - Landcare Research, New Zealand, is thanked for his assistance in selecting species epithets for the new species. We express our gratitude for the experimental materials provided by Beijing Zhongke Qinan Technology Co., Ltd., Zhanjiang, Guangdong Province; Yunnan Yuanjiang Qinan Agarwood Agricultural Technology Development Co., Ltd., Yuanjiang, Yunnan Province; Maoming Shushangbao Agarwood Culture Co., Ltd., Maoming, Guangdong Province; and Maoming Xiangtaotao Agarwood Industry Development Co., Ltd., Maoming, Guangdong Province. The authors extend their appreciation to the Ongoing Research Funding Program (ORF-Ctr-2025-6), King Saud University, Riyadh, Saudi Arabia. Nakarin Suwannarach and Jaturong Kumla thank Chiang Mai University for the support. The University of Mauritius and the PIFI (2026PVB0047) are also acknowledged.

DECLARATION ON CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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