ENDOPHYTIC AND SAPROBIC FUNGI OF *AQUILARIA* SPP AND THEIR BIOACTIVE PROPERTIES

TIANYE DU

DOCTOR OF PHILOSOPHY
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THIS DISSERTATION IS A PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY IN BIOLOGICAL SCIENCE

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Author: Tianye Du

Examination Committee:

Associate Professor Hiran Anjana Ariyawansa, Ph. D.	Chairperson
Adjunct Professor Kevin David Hyde, Ph. D.	Member
Saowaluck Tibpromma, Ph. D.	Member
Thilini Chethana Kandawatte Wedaralalage, Ph. D.	Member
Professor Don Nalin Nilusha Wijayawardene, Ph. D.	Member

Advisors:

.....Advisor

(Adjunct Professor Kevin David Hyde, Ph. D.)

Saowaluck

.....Co-Advisor

(Saowaluck Tibpromma, Ph. D.)

Dean:

.....

(Professor Surat Laphookhieo, Ph. D.)

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Tianye Du

Dissertation Title	Endophytic and Saprobic Fungi of *Aquilaria* Spp and Their Bioactive Properties
Author	Tianye Du
Degree	Doctoral of Philosophy (Biological Science)
Advisor	Adjunct Professor Kevin David Hyde, Ph. D.
Co-Advisor	Saowaluck Tibpromma, Ph. D.

ABSTRACT

Aquilaria, known as a genus in the Thymelaeaceae family, is the primary source of agarwood and serves as a valuable resource in medicine and the fragrance industry. As a precious resin, agarwood has significant economic, cultural, and medicinal value. Given its medicinal and economic importance, understanding the fungal community associated with *Aquilaria* spp. is crucial. Currently, there are limited reports on saprobic fungi, whereas in the study of endophytic fungi, only some have been reported for their inducing potential or biological activities, and there are few reports on the fungal community of related fungi of *Aquilaria* spp.

In this study, we investigated the fungal communities associated with *Aquilaria sinensis* by collecting samples from four plantations in Guangdong and Yunnan provinces of China. Fungal isolation was conducted from different plant tissues, including agarwood resin, healthy branches, healthy leaves, and decaying branches, and separated into four parts in this study. First, 960 fungal strains were isolated and identified at the genus level, belonging to 64 genera within the Ascomycota, Basidiomycota, and Mucoromycota phyla. Those 64 genera are provided with detailed notes including information on their habitats, life strategies (e.g., endophytic, saprobic, pathogenic), distribution ranges, and known host associations. These comprehensive annotations serve as a reference for future taxonomic, ecological, and functional studies. In addition, five novel species were described, *viz.*, *Banksiophoma endophytica*, *Deniquelata aquilariae*, *Montagnula sinensis*, *M. yunnanensis*, and *Fomitiporia aquilariae* in this part. The second part, comprising 47 representative strains from part one, was tested for antagonistic activity against common plant pathogens (Bacterial pathogens: *Erwinia amylovora*, *Pseudomonas syringae*, and

Salmonella enterica; and fungal pathogens: *Alternaria alternata*, *Botrytis cinerea*, and *Penicillium digitatum*), and the results showed that 40 of 47 strains have biocontrol potential, with the most significant being *Lasiodiplodia* sp. (YNA-D3). The third part, 12 selected strains from part one, were used in artificial agarwood induction experiments. In this part, *Fusarium solani* (GDA-HC01) exhibited outstanding performance by successfully inducing the formation of key medicinal compounds, including agarotetrol, which met pharmacological standards as early as the sixth month. In the last part, we introduced one genus, 17 novel saprobic fungal species, and five new records, belonging to 14 genera in nine families, four orders, and two classes in Ascomycota.

This research fills critical gaps in the diversity and ecological roles of agarwood-associated fungi and saprobic fungi, and enriches the taxonomic foundation of the agarwood fungal ecosystem. Furthermore, several fungal strains with potential antagonistic activity against pathogens were identified. The study also provides important theoretical insights and practical support for elucidating the biological regulatory mechanisms underlying agarwood formation, developing effective biological induction techniques, and understanding the interactions between medicinal plants and fungi.

Keywords: 1 New Genus, 22 New Species, 6 New Records, Agarwood-saprobic Fungi, *Aquilaria*, Ascomycota, Basidiomycota, Biological Control, Biotechnology, Endophyte, Fungal Communities, Fungal Induction, *Fusarium solani*, Genera Notes, *Lasiodiplodia*, Mucoromycota

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ABBREVIATIONS AND SYMBOLS

diam.	diameter
e.g.	for example
et al.	and others
h	hours
gen.	genus/genera
ibid.	ibidem
min	minute
ML	maximum likelihood support
mL	milliliter
mm	millimetre
nov.	novum (Latin for new thing)
PP	posterior probabilities
sp.	species
spp.	species (plural)
viz.	that is
vs.	versus
$\overline{x}$	average
°C	degree centigrade
µm	micrometer
µL	microliter
%	percent

CHAPTER 1

INTRODUCTION

1.1 Background and Rationale

1.1.1 Overview of Agarwood: High-Value Resource

Agarwood is a highly valuable, fragrant, and dark resinous heartwood, formed after microorganisms invade tree wounds (Chen et al., 2017; Chhipa et al., 2017; Wang et al., 2018, 2019b; Tan et al., 2019). Agarwood is also known as ‘‘woods of the Gods’’, and it has been widely used as incense, decorations, jewelry, perfume (essential oils), medicine and religious ceremonies (Wang et al., 2018; CITES, 2022). In terms of economic status: the best agarwood price ranges from $100,000–800,000 per kilogram (https://tmhagarwood.com/agarwood-price/), and agarwood oil had a global market value of USD 278.03 million in 2021 (Niego et al., 2023a), with 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). In terms of medicinal value: agarwood plays important roles in traditional medicine in Arabia, China, and India, as well as in modern pharmacology (Liu et al., 2013; Liao et al., 2018; Du et al., 2022a; Ngadiran et al., 2023; Wang et al., 2018). The natural formation of agarwood is very slow and rare, and fungal induction has been reported as an effective method for artificially inducing agarwood formation (Laurence, 2013; Azren et al., 2018; Subasinghe et al., 2019). However, currently only a small number of fungal strains have been reported to be able to induce agarwood, and the characteristics of different fungal strains are different (Du et al., 2022a). This means that more research needs to be conducted to screen suitable stable fungal strains that can quickly induce agarwood. Research in this area can promote economic benefits, reduce dependence on chemical induction, and promote green and sustainable development.

1.1.2 The Central Role of *Aquilaria* in Agarwood Production and the Need for Mycological Insight

Aquilaria is the most important and common genera for the production of agarwood in Thymelaeaceae, it as a genus of evergreen broad-leaved trees in tropical and subtropical regions, mainly distributed in Southeast Asia (Borneo, Cambodia, China, India, Indonesia, Laos, Malaysia, New Guinea, Philippines, Thailand, and Vietnam) (Rasool & Mohamed, 2016; Wang et al. 2018, 2019). According to the latest CITES (2022) report, *Aquilaria* contains 21 accepted species, of which 13 species are reported to produce agarwood resin (Lee et al. 2016; POWO, 2021). In China, *Aquilaria sinensis* is the species that mainly produces agarwood, primarily planted in southern regions *viz.*, Fujian, Guangdong, Guangxi, Hainan, Hong Kong, Taiwan, and Yunnan provinces, while *A. yunnanensis* is only distributed in Yunnan Province (Cui et al., 2013; Tibpromma et al. 2021). The genus *Aquilaria* holds significant economic, medicinal, and ecological value. Research on *Aquilaria* spp. not only supports the sustainable use and conservation of agarwood resources but also provides a scientific foundation for the development of artificial induction technologies and high-value products.

Fungi are widely distributed across various ecological niches in terrestrial, freshwater, and marine ecosystems, where they exist in diverse forms such as pathogens, endophytes, saprobes, epiphytes, and symbionts (Ritz & Young, 2004; Hyde et al., 2020a, 2020b). They play vital ecological roles by decomposing organic matter, promoting nutrient cycling, and maintaining soil health, thereby indirectly supporting plant diversity and ecosystem stability (Hyde & Lee, 1995; Hyde et al., 2019a). Through interactions with host plants, fungi can establish mutualistic relationships that enhance plant resilience to environmental stresses such as drought and disease.

Research on pathogenic fungi associated with agarwood-producing trees has garnered significant interest because of the high value of agarwood (Li & Chen, 2008; Xu et al., 2012; Samsuddin et al. 2019; Syazwan et al., 2019). Several fungal species have been reported to contribute significantly to agarwood formation by stimulating resin production in *Aquilaria* spp. (e.g., *Fusarium solani* (Mart.) Sacc.) (Rasool & Mohamed, 2016; Subasinghe et al., 2019; Faizal et al., 2020; Du et al., 2022a; Du et al.,

2024b). Moreover, endophytic fungi isolated from *Aquilaria* spp. have demonstrated notable bioactivities, including antimicrobial and anti-inflammatory effects (e.g., *Nemania aquilariae* Tibpromma & Zhang Lu) (Azren et al., 2018; Tibpromma et al., 2021; Du et al., 2022a, c). However, studies on fungi associated with *Aquilaria* spp. remain limited and lack systematic investigation, and substantial variation often exists among strains of the same fungal species. Therefore, it is essential to identify and screen stable, effective, and highly bioactive fungal strains. In addition, research on saprobic fungi of *Aquilaria* spp. is extremely scarce, prior to this research, there were only eight records available—most lacking molecular data and comprehensive morphological descriptions. Therefore, in-depth research on plant-associated fungi—especially those associated with *Aquilaria* spp.—is crucial for advancing our understanding of plant–fungi interactions, expanding fungal biodiversity knowledge and for advancing our understanding of agarwood formation mechanisms, enhancing the medicinal potential of host plants, and promoting the sustainable development of biological resources.

1.1.3 Current Knowledge Gaps on the Functionality and Ecological Roles of Agarwood-associated Fungi

Southern China and Southeast Asia, as major distribution regions for *Aquilaria* spp., are known for their rich biodiversity and the extensive use of agarwood in traditional medicine and cultural practices (Azren et al., 2018; Wang et al., 2018). However, fungi inhabiting various tissues of *Aquilaria* spp.—particularly endophytes and saprobes—are still poorly understood in terms of community structure, ecological function, and specific roles in resin induction.

Endophytic fungi from agarwood have play attention, due to most of the fungi reported as inducers are endogenous, and some of the secondary metabolites isolated from endophytic fungi are similar to those in agarwood resin. Although previous studies have demonstrated that endophytic fungi play a key inductive role in agarwood resin formation (Rasool & Mohamed, 2016; Subasinghe et al., 2019; Du et al., 2022a, 2024b), systematic research on fungal communities associated with the genus *Aquilaria* remains limited, and strains with better induction effect, stronger biological activity, and more stable characteristics still need to be screened.

On the other hand, research on saprobic fungi is especially scarce, with only a few species reported to date, most lacking comprehensive morphological descriptions and molecular data. In-depth studies on the isolation, identification, and functional characterization of *Aquilaria*-associated fungi will not only enhance our understanding of fungal diversity and uncover potential new species, but also provide critical insights into the biological regulation of agarwood formation. Such research will support the development of efficient biological induction technologies and promote the sustainable utilization and industrial advancement of agarwood resources.

1.2 Significance of the Study

As a traditional medicinal resource, agarwood has long been valued for its therapeutic properties, including anti-inflammatory, analgesic, and sedative effects (Liao et al., 2018; Wang et al., 2018). It is also a precious aromatic material widely used in religious, cosmetic, and cultural practices across Asia and the Middle East (Du et al., 2022a). With increasing global demand, agarwood has become a high-value commodity, contributing significantly to international trade and rural economies (Azren et al., 2018; Rasool & Mohamed, 2016). Therefore, *Aquilaria* (the agarwood-producing genus) holds substantial importance across medical, economic, ecological, and cultural domains. In addition, *Aquilaria* species play an essential role in conserving subtropical and tropical biodiversity and form an integral part of sustainable forestry and agroforestry systems. As such, research on *Aquilaria* is closely linked to human health, cultural heritage, biodiversity conservation, and economic development.

Research on fungi associated with *Aquilaria* spp. is equally important. These fungi are believed to play a central role in inducing agarwood formation by activating the host's defense responses and promoting resin biosynthesis (Subasinghe et al., 2019; Du et al., 2022a, 2024b). Fungi isolated from *Aquilaria* spp. have demonstrated promising bioactivities, including antimicrobial and anti-inflammatory effects, indicating their potential for pharmaceutical and agricultural applications (Azren et al., 2018; Du et al., 2022c). However, comprehensive studies on the taxonomy, ecology, and functions of

Aquilaria-associated fungi remain limited—especially regarding saprobic fungi. Investigating these fungal communities not only enhances our understanding of plant–fungi interactions but may also lead to the discovery of novel fungal taxa and the identification of effective resin-inducing or biocontrol strains. Such research supports sustainable agarwood production, promotes biodiversity conservation, and provides new insights for the development of natural products.

1.3 Objectives

1.3.1 To isolate and identify endophytic fungi of *Aquilaria sinensis* and agarwood-associated fungi to the genus level, and analyze its community diversity.

1.3.2 To screen and test the ability of fungal strains to induce and promote agarwood formation by Agar-Wit and PIT methods.

1.3.3 To screen and test the antagonistic abilities of fungal strains against fungal and bacterial pathogens.

1.3.4 To identify and describe novel/known saprobic/endophytic/agarwood-associated fungi taxa of *Aquilaria* spp. in China based on morphology and phylogeny evidence.

1.4 Expected Outcomes

1.4.1 Endophytic fungi of *Aquilaria sinensis* and agarwood-associated fungi will be identified and described to the genus level, community diversity will be analyzed and discussed, and notes for each genus will be provided as literature materials.

1.4.2 The ability of fungal strains to induce and promote agarwood formation will be screen and test.

1.4.3 The antagonistic ability of fungal strains against fungal and bacterial pathogens will be screen and test.

1.4.4 This study will provide the host, lifestyle, and perform the taxonomy and phylogeny analyses of new taxa associated with *Aquilaria* spp.

1.5 Research Contents

This study focuses on the taxonomy, phylogeny, inducing ability, antagonistic ability, and community analysis of fungi associated with agarwood and agarwood-producing trees in southern China, comprising seven chapters.

In Chapter 1, a general introduction is provided, introducing the background and rationale for the study, discussing the importance of agarwood and *Aquilaria* spp. and their associated fungi in these biodiverse regions. It outlines the significance of the study, clearly stating the research objectives, expected outcomes and the outline of the thesis.

In Chapter 2, an in-depth overview of agarwood and agarwood-producing trees, along with a detailed review of fungi, and the relationships between them, is provided.

In Chapter 3, the research methodology of fungi in *Aquilaria sinensis*'s inside tissue is described. Including the isolation of endophytic and agarwood-associated fungal strains and preliminary identification, identification of new species based on multi-gene phylogenetic analyses and culture morphology, comparative analyses of community composition of 960 isolated strains based on circular phylogenetic trees and related charts, and summary of basic characteristics of 64 genera, such as lifestyle, habits, host and distribution range, and relationship with agarwood, as reference materials for literature.

In Chapter 4, the isolation, identification, and screening methods of induced fungal strains, as well as the detection and analysis methods of agarwood quality, are provided. A total of two experiments were conducted, and the preliminary screening experiment lasted for one year. Using 12 strains, a highly efficient strain was screened. In the extended experiment, the selected strains were used to conduct a six-month experiment using two common fungal induction methods. The results showed that the strain *Fusarium solani* (GDA-HC01) promoted the production of agarwood resin by

Agar-Wit method at the sixth month, which contained agarotetrol that could meet the medicinal standards.

In Chapter 5, the isolation, identification, and screening methods (Dual culture assay) of strains with antagonistic ability are provided. This study underwent pre experiments and formal experiments, and ultimately 40 out of 47 strains were considered to have inhibitory effects, with inhibition rates calculated and analyzed. *Lasiodiplodia* sp. (YNA-D3) showed the best inhibition effect on pathogens, with a more in-depth discussion and analysis were conducted.

In Chapter 6, research methodology of saprobic fungi are provided, including samples collection and isolation, observation and recording of morphological structures, acquisition of multi gene sequences, and construction of phylogenetic trees. Dealing with the taxonomic and phylogenetic study of saprobic fungi related to *Aquilaria* spp. in Guangdong and Yunnan provinces of China. Brief notes for each genus and species are given. The morphological structure of each species has been thoroughly examined and made photo plates. The phylogenetic analyses for each taxa are separately carried out based on the datasets of multi-gene sequences. The description and illustrations for each taxon are provided.

In Chapter 7, providing an overall conclusion, the research advantages, and future work.

CHAPTER 2

LITERATURE REVIEW

2.1 Overview of Agarwood

2.1.1 The Importance and Value of Agarwood

Agarwood is a highly valuable, fragrant, and dark resinous heartwood (Liu et al., 2017; Wang et al., 2018, 2019b; Tan et al., 2019). Agarwood is also known under different names in different regions, including agar (Hindi), akil (Tamil), aloe wood (Indonesian), chen xiang (Chinese), chim-hyuang (Korean), eaglewood (Papua New Guinea), gaharu (Malaysian), jin-koh (Japanese), mai ketsana (Lao), mai kritsana (Thai), oud (Arabic), oud or agar attar (Middle Eastern), sasi or sashi (Assamese), and tramhuong (Vietnamese) (Chen et al., 2012; Rasool & Mohamed, 2016; Chhipa et al., 2017). Agarwood has been referred to as the "woods of the Gods", and it has been widely used as incense, perfumes (essential oils), in medicine and religious ceremonies (Persoon, 2007; Zhang et al., 2012; Liu et al., 2013; National Pharmacopoeia Committee, 2015, 2020; Kalra & Kaushik, 2017; Wang et al., 2018).

Agarwood is well known as incense because it has a pleasant fragrance when it is burned, and the essential oil of agarwood is the most important ingredient in high-end perfume due to its unique fragrance (Zhang et al., 2012; Al-Hindi et al., 2018). Agarwood has been widely used in Buddhist, Hindu, and Islamic ceremonies (Wang et al., 2018). In the Middle East, agarwood is a famous incense, and the essential oil is being used as high demanding perfumes (Barden et al., 2000; Hashim et al., 2016). In addition, agarwood incense plays an important role in the Japanese "koh-doh" ceremony (Compton & Ishihara, 2006; Hashim et al., 2016).

Agarwood also plays an important role in both traditional and modern medicine (Liu et al., 2013; National Pharmacopoeia Committee, 2015, 2020; Wang et al., 2018). In traditional Chinese medicine, agarwood is used as a sedative, qi-regulating drug, and

carminative medicine, which can also alleviate stomach disease, cough, rheumatism, and high fever (Liu et al., 2013; National Pharmacopoeia Committee, 2015, 2020; Wang et al., 2018). In traditional Indian medicine, agarwood is used to treat diarrhea, dysentery, vomiting, anorexia, oral and dental diseases, facial paralysis, tremor, sprain, and fracture (Hashim et al., 2016). In traditional Arabian medicine, agarwood essential oil is often used in aromatherapy (Wang et al., 2018). Modern pharmacological research has shown that agarwood has the potential of inducing sedation, reducing nerve excitability as well as being antibacterial and antifungal, anti-inflammatory, having analgesic effects, gastrointestinal regulatory properties, antiasthma, anti-diabetes, and antioxidation (Guo et al., 2002; Wang et al., 2018).

The unique fragrance, rare production, and wide range of uses of agarwood have led to its very high market price, making it as the most expensive non construction timber forest product in the world. The price of agarwood varies with the quality of its resin, the best agarwood ranges from $100,000 to 800,000 per kilogram, and the essential oil of agarwood in the global market is sold for $30,000 per liter (https://tmhagarwood.com/agarwood-prices-updated-in-2021, accessed on 9 March 2022). The agarwood oil had a global market value of USD 278.03 million in 2021 (Niego et al., 2023a), with 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). Its preciousness and researchable value are self-evident.

2.1.2 Introduction of Agarwood-producing Trees

Woody plants that can produce agarwood are known as “agarwood-producing trees” or “incense-producing trees” (Rasool & Mohamed, 2016). The trees of Thymelaeaceae, are typical evergreen trees mainly distributed throughout Southeast Asia (Xu et al., 2016). Thymelaeaceae consists of many important incense-producing trees species, including those from the genera *Aetoxylon* (Airy Shaw) Airy Shaw, *Aquilaria*, *Gonystylus* Teijsm. & Binn., *Gyrinops*, and *Phaleria* Jack, while *Aquilaria* and *Gyrinops* are the two most important genera for the production of agarwood (Rasool & Mohamed, 2016). According to the latest CITES (2022) report, *Aquilaria* contains 21 accepted species (POWO, 2021), and in *Aquilaria*, 13 species are reported

to produce agarwood resin: *A. baillonii* Pierre ex Lecomte, *A. beccariana* Tiegh., *A. crassna* Pierre ex Lecomte, *A. filaria* (Oken) Merr., *A. hirta* Ridl., *A. khasiana* Hallier f., *A. malaccensis* Lam., *A. microcarpa* Baill., *A. rostrata* Ridl., *A. rugosa* K.Le-Cong & Kessler, *A. sinensis*, *A. subintegra* Ding Hou and *A. yunnanensis* (Lee et al., 2016). Excessive logging of agarwood is the biggest threat to agarwood-producing trees. Twenty species of *Aquilaria* have been assessed for the IUCN Red List, including *A. sinensis* and *A. yunnanensis* (IUCN, 2022). The main morphological difference between *A. yunnanensis* and *A. sinensis* is that the fruit of *A. yunnanensis* is oval, with short seed appendages, and the seed surface is densely covered with yellow pubescence, while *A. sinensis* has oblong fruit, seeds with long appendages, and smooth or covered with white pubescence on the surface (Kang, 2021). In China, *Aquilaria sinensis* is primarily planted in southern regions *viz.* Fujian, Guangdong, Guangxi, Hainan, Hong Kong, Taiwan, and Yunnan Provinces, while *A. yunnanensis* is only distributed in Yunnan Province (Cui et al., 2013; Tibpromma et al., 2021).

2.2 Overview of Fungi

Fungi are diverse and are the second largest group in the eukaryotes (Joshi & Chettri, 2019). Both microfungi and macrofungi are important in the functioning of ecosystems (Joshi & Chettri, 2019; Hyde et al., 2020), they are ubiquitous and play different roles as pathogens, endophytes, saprotrophs/decomposers, epiphytes, and symbionts in various diversified ecological niches in terrestrial, freshwater, and marine environments (Ritz & Young, 2004; Joshi & Chettri, 2019).

Endophytic fungi typically present as internal, unseen, microscopic hyphae, reside entirely within plant tissues, and may grow within roots, stems, or leaves (Stone et al., 2004; Rodriguez et al., 2009). Endophytic fungi are defined by Liao et al. (2025) 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”. Most of the endophytic fungi have been found to be non-sporulating, often remaining identified

as mycelia sterilia (Zhou & Hyde, 2001; Rashmi et al., 2019). Endophytic fungi have been reported to be capable of transforming into saprophytes or potential pathogens, depending largely on different environmental factors (Promputtha et al., 2010; Rashmi et al., 2019). Ecologically, endophytic fungi provide several benefits to plants; for example, grass endophytes provide their hosts with a number of benefits, such as resistance to herbivory and pathogens, thereby improving their fitness (Saikkonen et al., 1998; Stone et al., 2004); nongrass endophytes produce antifungal or antibacterial substances (Peláez et al., 2000; Du et al., 2022c), as well as insecticidal compounds (Johnson & Whitney, 1994; Stone et al., 2004). Some endophytic fungi have been reported to enhance economic benefits; for example, the endophytic fungi associated with *Aquilaria* plant genus can induce the production of agarwood resin (Du et al., 2022a, 2024b); on the other hand, natural products such as drugs are mainly produced by microbes, and various active metabolites and compounds used as antimicrobials, antivirals, cytotoxic and immunosuppressive drugs comprising about 23,000 active compounds are from microbes of which about 42% are derived from fungi (Demain, 2014; Joshi & Chettri, 2019).

Saprobic fungi, the largest group of fungi, are also known as decomposers (Hartl et al., 2012). Saprobic fungi represent essential organisms in soil microbial communities due to their wide array of metabolic processes and biotransformations, including the secretion of some enzymes to decompose dead organic matter, which makes them central in carbon recycling and as a crucial link in the ecosystem (Hartl et al., 2012; van der Wal et al, 2013; Eichlerová et al., 2015). Generally, saprobic fungi are believed not to be host-specific, but host-recurrence is a preferable term to host-preference for saprobic fungi (Zhou & Hyde, 2001). Saprobic fungi are generally identified at the species level, and mainly rely on morphological characteristics and phylogenetic analyses.

Pathogenic fungi are a significant group within the fungal kingdom that can infect various plant, animal, and human hosts. They play a crucial role in regulating population dynamics, community structure, and even ecosystem processes (Agrios, 2005; Hyde et al., 2020). In plants, fungal pathogens are major pathogens in agriculture

and forestry, leading to reduced productivity and loss of biodiversity (Dean et al., 2012; Fisher et al., 2012). These fungi invade their hosts through natural openings, mechanical penetration or enzymatic degradation of plant cell walls (Van Kan, 2006) and produce toxins, enzymes or effector proteins to suppress host defenses and promote colonization (Stergiopoulos & de Wit, 2009). These taxa include obligate biotrophs, necrotrophs and hemibiotrophs, and their interaction strategies with hosts are different (Horbache et al., 2011). The top ten pathogens listed in the molecular plant pathology list are *Magnaporthe oryzae* B.C. Couch, *Botrytis cinerea* Pers., *Puccinia* spp., *Fusarium graminearum* Schwabe, *Fusarium oxysporum* Schltdl., *Blumeria graminis* (DC.) Speer, *Mycosphaerella graminicola* (Fuckel) J. Schröt., *Colletotrichum* spp., *Ustilago maydis* (DC.) Corda, and *Melampsora lini* (Ehrenb.) Thüm (Dean et al., 2012). Pathogenic fungi are closely related to economic crops and human living environment, so research on them has received a lot of attention.

2.3 Studies of Fungi Associated with Agarwood

2.3.1 Endophytic Fungi Associated with Agarwood-producing Trees

Under natural conditions, the formation of agarwood is rare and very slow (Chen et al., 2017; Tibpromma et al., 2021). For the sustainable development of the agarwood industry, many agarwood-producing countries (Cambodia, China, Indonesia, Malaysia, Thailand, and Vietnam) are committed to developing artificial induction of agarwood resin (Rasool & Mohamed, 2016; Azren et al., 2018). Biological induction (fungal inoculation) is considered to be effective, especially in *Aquilaria sinensis*, and most of the fungi used for inoculation are endophytes that have been isolated from healthy or infected wood of agarwood-producing trees (Laurence, 2013; Azren et al., 2018; Subasinghe et al., 2019).

Therefore, many researchers are committed to isolating various endophytic fungi from different parts of agarwood-producing trees. Some endophytic fungi have been reported to have the ability to induce agarwood, such as *Aspergillus niger* Tiegh. (Subasinghe et al., 2019), *Fusarium solani* (Faizal et al., 2020; Du et al., 2024b), *F.*

oxysporum Schltdl. (Zhang et al., 2022b), *Lasiodiplodia theobromae* (Pat.) Griffon & Maubl. (Han et al., 2014), and *Melanotus flavolivens* (Sacc.) Singer (Qi et al., 1998). The strain of genus *Fusarium* has the highest number and frequency among all strains reported to have the inducing ability (Du et al., 2022a). However, the most widely used method on the market is chemical induction, and due to the rapid economic growth, the supply of agarwood is far less than the demand. Therefore, in order to balance supply and demand and achieve sustainable development, it is still necessary to study the ability of endophytic fungi to induce agarwood.

Besides, endophytic fungi have biological activity and are a source of many natural products (drugs) (Joshi & Chettri, 2019), especially endophytic fungi associated with agarwood, for examples, *Diaporthe* sp. - antioxidant capacity (Monggoot et al., 2017); *Nemania aquilariae* - antibacterial and antimicrobial activities (Tibpromma et al., 2021); and *Xylaria mali* Fromme - antimicrobial and antitumor activities (Tian et al., 2013). Endophytic fungi are a huge resource and an important source of secondary metabolites. The study of their biological activities is of great benefit to human life.

2.3.2 Saprobic Fungi Associated with Agarwood-producing Trees

The research on agarwood-producing trees associated fungi mainly focuses on endophytic fungi and their inducing ability and biological activity (Du et al., 2022a). A few studies have been carried out on saprobic fungi, only eight records were reported from *Aquilaria* spp., *viz. Cercosporella* sp., *Chaetomium spirale* Zopf*, Cladosporium* sp., *Phomopsis aquilariae* Punith. & I. A. S. Gibson, *Phialogeniculata* sp., *Pithomyces* sp., *Rhizopus* sp., and *Trichoderma* sp. (Punithalingam & Gibson, 1978; Subansenee et al., 1985). This has created a huge gap regarding the saprobic fungi study of agarwood-producing trees. Currently, the mechanism of agarwood formation is not clear (Sen et al., 2017), and it can be determined that the wound is the first factor and the second is microbial infection (Rasool & Mohamed, 2016). Therefore, it is of great significance to fill the gap of saprobic fungi associated with agarwood-producing trees.

2.3.3 Pathogenic Fungi Associated with Agarwood-producing Trees

Given the high economic value of agarwood, extensive research has been conducted on pathogenic fungi of agarwood-producing trees to identify their pathogens

and develop control methods (Li & Chen, 2008; Xu et al., 2012; Samsuddin et al. 2019; Syazwan et al., 2019). Unlike endophytic fungi in mutualistic symbiosis, pathogenic fungi invade and damage host tissues. For example, *Colletotrichum* spp., *Lasiodiplodia* spp., and *Rhizoctonia* spp., which known cause damage to the seedlings, branches, and leaves of agarwood trees (Liao et al., 2018; Liu et al., 2020). These infections may not only threaten the survival of the trees and decrease resin production, but they may also trigger complex wound responses and resin deposition, blurring the line between pathogenicity and induction under certain conditions.

CHAPTER 3

FUNGAL COMMUNITY COMPOSITION ASSOCIATED WITH THE AGARWOOD-PRODUCING TREE, *AQUILARIA SINENSIS*

3.1 Introduction

Agarwood, also known as "Chenxiang" in China, is a highly valuable and fragrant resinous wood formed in certain species of trees within the family Thymelaeaceae, primarily *Aquilaria* and *Gyrinops* (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., 2022b). 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, with significant cultural and religious meaning (Chen et al., 2017a, b; Wang et al., 2018; Adhikari et al., 2022). It can be processed into incense, jewelry, and carvings; additionally, agarwood essential oil has become one of the raw materials 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 plays essential roles in traditional medicine in Arabia, China, and India (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., 2022; 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 very rare, as it cannot 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, but the mechanism of producing agarwood resin is 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 argues that physical and chemical damage are the main 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, 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., 2022b; Ngadiran et al., 2023). However, the success of fungal induction depends on several complicated factors, such as fungal strains, tree species, environmental conditions, and inoculation methods. One key advantage of biological induction is its ability to foster progressive and systematic growth of fungal agents, leading to continuous agarwood formation (Novriyanti et al., 2010). Recent studies have shown that artificially induced agarwood exhibits similar chemical and pharmacological properties to wild agarwood, further confirming its potential as a sustainable alternative (Huang et al., 2023). However, some endophytes display latent pathogenicity in plants, which means they can act as pathogens under specific conditions (Nisa et al., 2015); in *Aquilaria*, this latent pathogenicity is economically beneficial, as it triggers agarwood resin production (Enshasy et al., 2019; Gogoi et al., 2022). Further research to optimize these variables is necessary 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., 2022b; Gogoi et al., 2023). Additionally, the secondary metabolites from endophytic fungi of agarwood lead the way as sources for various pharmacological properties (Li et al., 2022b). More than 90 compounds were extracted from the endophytic fungi of agarwood-producing trees (Li et al., 2022b). 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., 2009; 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, estimate of 1.5 to 3.8 million species (Niskanen et al., 2023; Hyde et al., 2024c), it has been extensively studied in recent years (Dong et al., 2024; Samarakoon et al., 2024). 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., 2024a). 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 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 shown that certain fungi play an important role in the formation of agarwood and are key driving factors for its natural growth (Li et al., 2022b; 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, in-depth exploration of the diversity and ecological functions of fungi, especially their involvement in the formation mechanism of agarwood, has important scientific value and application potential.

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

3.2 Research Methodology

3.2.1 Sample Collection and Fungal Strain Isolation

1. 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. Healthy leaves, healthy branches, branches with agarwood resin, and decayed branches

were collected by free hand or with a pruning or chopping knife, and 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 in Qujing Normal University, and stored at 4°C until fungal strains could be isolated.

2. Fungal strain isolation

The isolation of endophytic fungi (fresh healthy leaves and healthy branches) and agarwood-associated fungi (fresh branches with agarwood resin) 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 again 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 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 will be deposited in the Greater Mekong Subregion fungal database (Chaiwan et al., 2021).

3.2.2 Fungal Classification and Identification

1. Morphological observation

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 were followed as outlined in Senanayake et al. (2020).

2. DNA extraction, PCR amplification, and sequencing

Molecular phylogenetic studies were conducted according to 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 gene (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 gene (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.

3. 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 gene 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 with MrBayes on XSEDE (3.2.7a) (Ronquist et al., 2012), and the optimal evolutionary models were estimated using 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). While the circular RAxML tree of 960 strains based on the ITS gene was edited and visualized on Interactive Tree of Life (iTOL) v6

(https://itol.embl.de/, accessed on 02 February 2025) (Letunic & 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).

4. Phylogenetic species recognition by genealogical concordance analyses

Genealogical concordance phylogenetic species recognition (GCPSR) analysis serves as a model-based test applied for the examination of significant recombinant events within data sets. The combined data underwent analysis via the pairwise homoplasy index test (PHI) (Bruen et al., 2006), which was executed 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 by utilizing the LogDet transformation and split decomposition options available in SplitsTree v.4. New species are established as per recommendations outlined by Jeewon & Hyde (2016) and Pem et al. (2021).

3.2.3 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 on 2 February 2025) (Tang et al., 2023), with various charts constructed, including the Column chart, Donut chart, Vertical stack bar, Link fill bar, and Venn diagram. 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).

3.3 Results

3.3.1 Fungal Phylogenetic Analysis and Community Study in *Aquilaria sinensis*

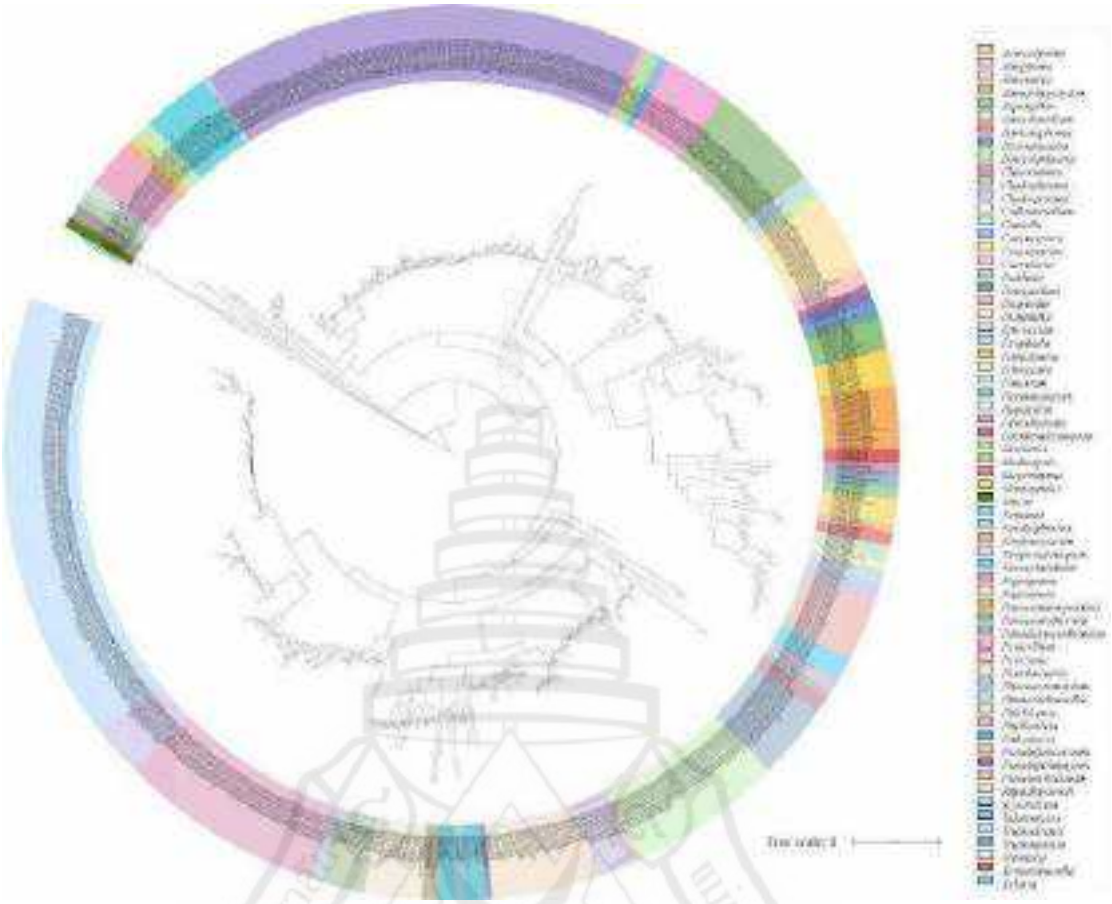
This study collected agarwood resin, healthy branches, healthy leaves, and dead branch samples of *Aquilaria sinensis* from Guangdong (Maoming and Zhanjiang) and Yunnan (Xishuangbanna and Yuanjiang) provinces and isolated 960 fungal strains. These strains were identified at the genus level through ITS 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 genus-level placements of the fungal taxa is shown in Figure 3.1.

Ascomycota is the dominant group in this study, comprising 951 sequences from 59 genera of 39 families, demonstrating its significant ecological 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 (Figure 3.1). Six strains from four genera of four families isolated from agarwood resin were identified within 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 (Figure 3.1). Three strains of *Mucor* were isolated from agarwood resin or healthy branches.



Note The tree was generated with maximum likelihood (RAxML) based on 1,031 ITS sequences and viewed 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 3.1 Circular phylogenetic tree showing the genus level

3.3.2 Analysis of Fungal Community Composition from Each Collection Site

1. 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 agarwood-associated 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 Figure 3.2, 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.

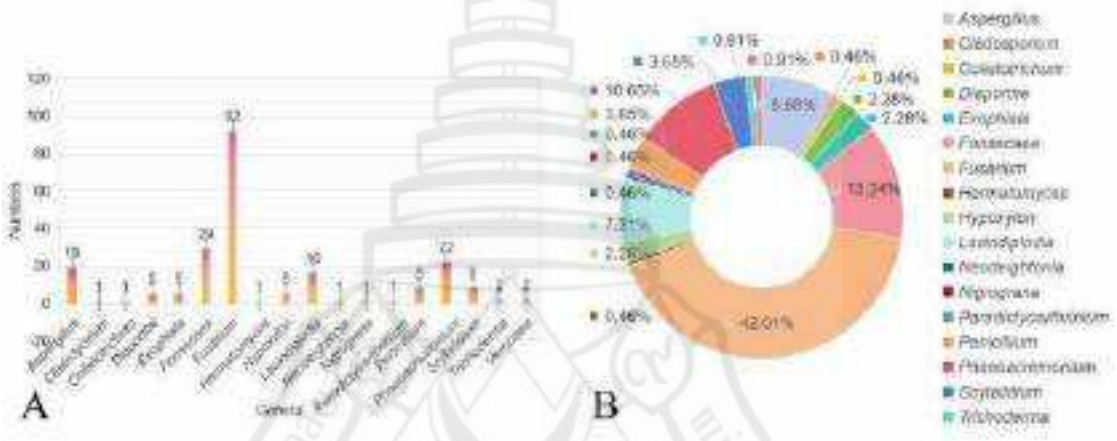


Figure 3.2 Column chart with error lines (A) and Donut chart (B) of the quantitative relationships of community composition among different genera in *Aquilaria sinensis*-associated fungi collected from Maoming

2. 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 Figure 3.3A, genus composition and strain distribution are shown in agarwood resins, healthy branches, and dead branches, displaying the number of shared strains and different genus compositions.

The distribution of genera in three different collection sites is shown in Figure 3.3B; 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.*

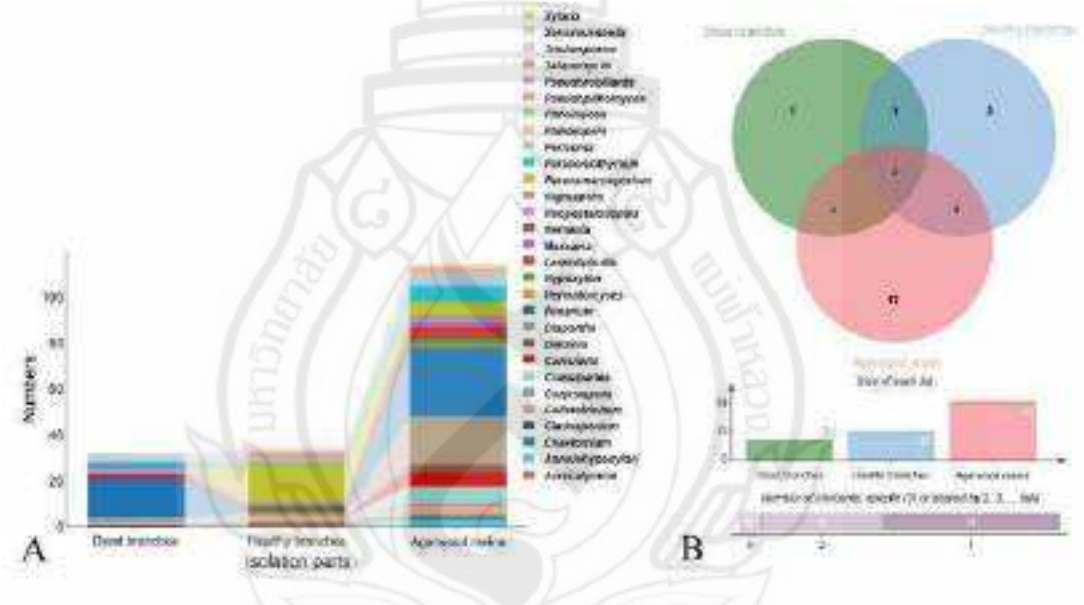


Figure 3.3 Link fill bar (A) and Venn diagram (B) of the genus composition in three isolation parts of *Aquilaria sinensis* collected from Zhanjiang

3. 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 isolated from different parts: 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 Figure 3.4A, 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 Figure 3.4B; 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.*

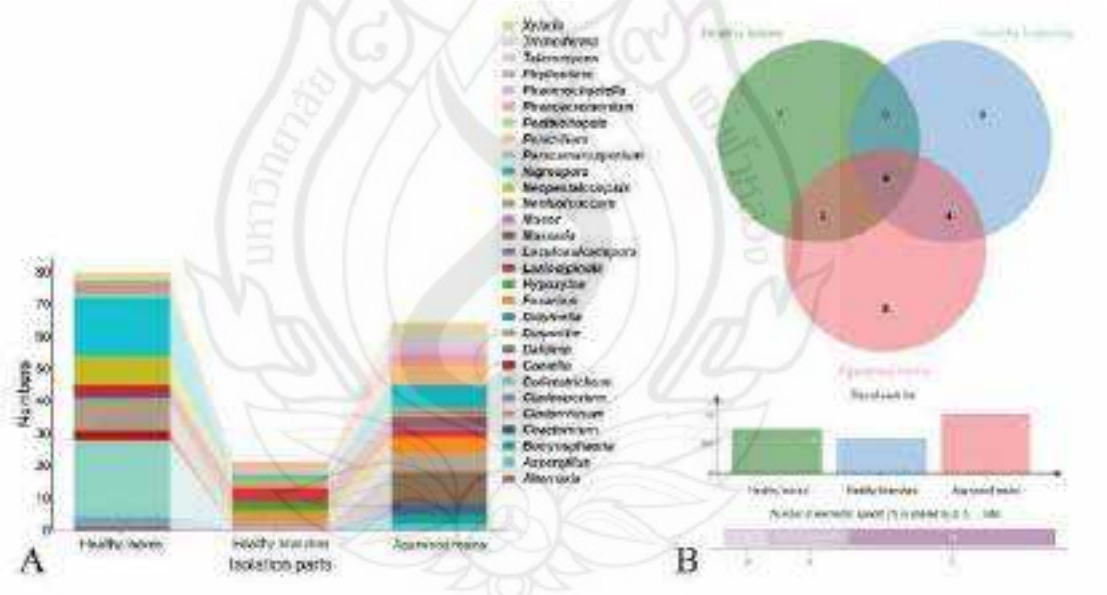


Figure 3.4 Link fill bar (A) and Venn diagram (B) of the genus composition in three isolation parts of *Aquilaria sinensis* collected from Xishuangbanna

4. 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 Figure 3.5A, 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 Figure 3.5B; 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.*

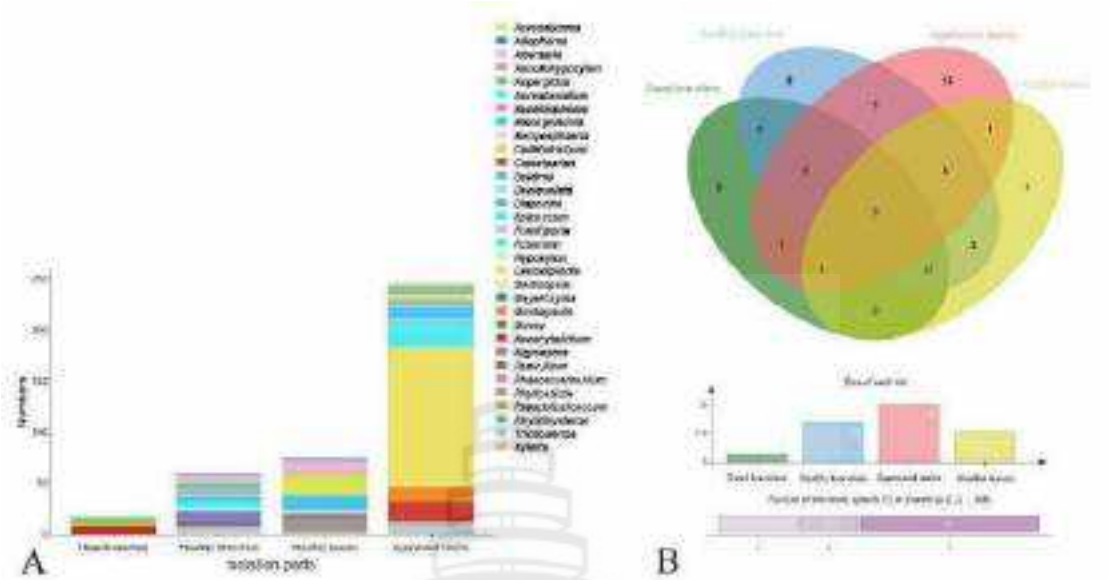


Figure 3.5 Vertical stack bar (A) and Venn diagram (B) of the genus composition in four isolation parts of *Aquilaria sinensis* collected from Yuanjiang

5. 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) (Figure 3.6A). 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 3.6B 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*.

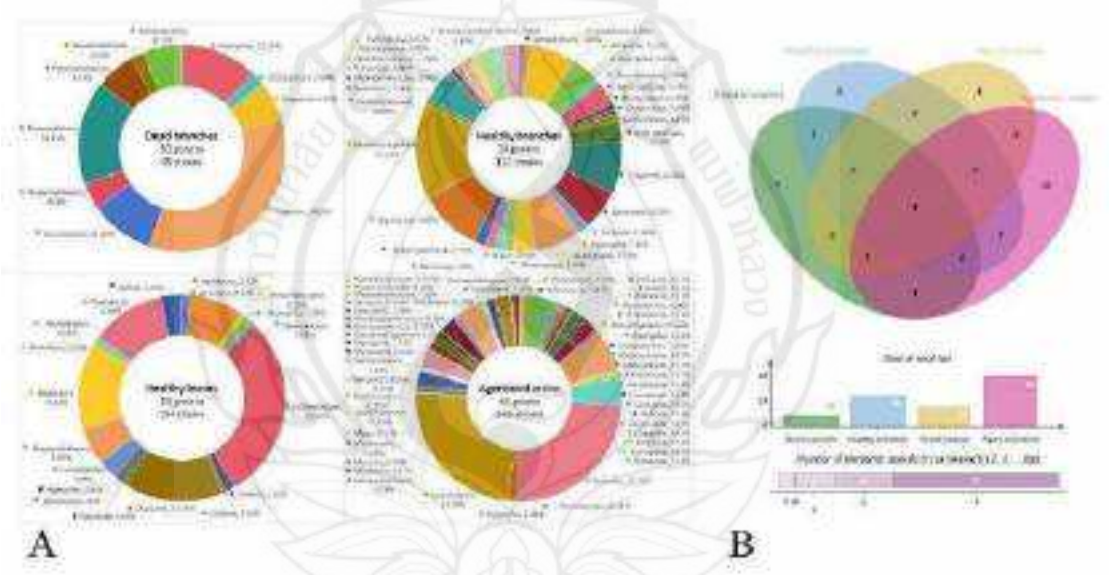


Figure 3.6 The Donut chart (A) and Venn diagram (B) of the genus composition of all *Aquilaria sinensis* strains in four isolation parts (agarwood resins, dead branches, healthy branches, and healthy leaves)

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

Agarwood resin samples were collected, and fungal strains were isolated from all four collection sites (Maoming, Zhanjiang, Xishuangbanna, and Yuanjiang) (Figure 3.7A). Therefore, the composition of agarwood-associated fungi from four different collection sites was analyzed. According to the Venn diagram in Figure 3.7B, the result is shown as the common genera in all four sites are *Diaporthe*, *Fusarium*, and *Lasiodiplodia*. While, *Daldinia* and *Xylaria* are presented 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.

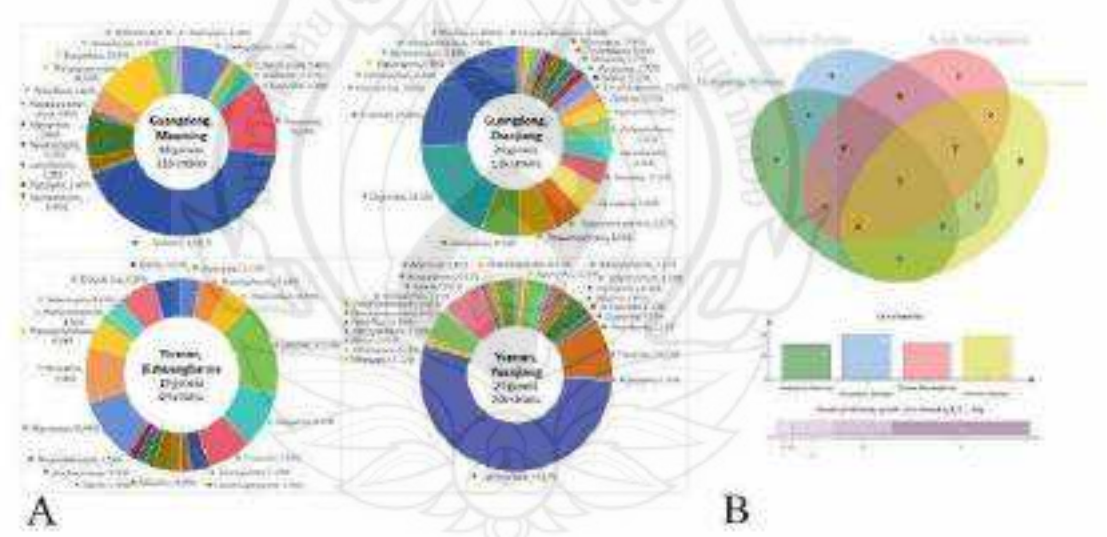


Figure 3.7 The Donut chart (A) and Venn diagram (B) of the genus composition of all agarwood-associated fungal strains in four collection sites (Maoming, Zhanjiang, Xishuangbanna, and Yuanjiang)

In summary, strains isolated in this study mainly belong to Dothideomycetes (38.28%) and Sordariomycetes (49.84%) of Ascomycota, 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). Regarding different isolation 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*.

3.3.3 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 isolated from the agarwood resin parts and healthy branches of *Aquilaria sinensis*, mainly belonging to Ascomycota, with only *Fomitiporia aquilariae* from Basidiomycota.

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

MycoBank number: MB XXXX; Facesoffungi number: FoF XXXX; Figure 3.8

Etymology: The species epithet “endophytica” refers to the strains isolated as endophytes.

Holotype: GMB-W1511

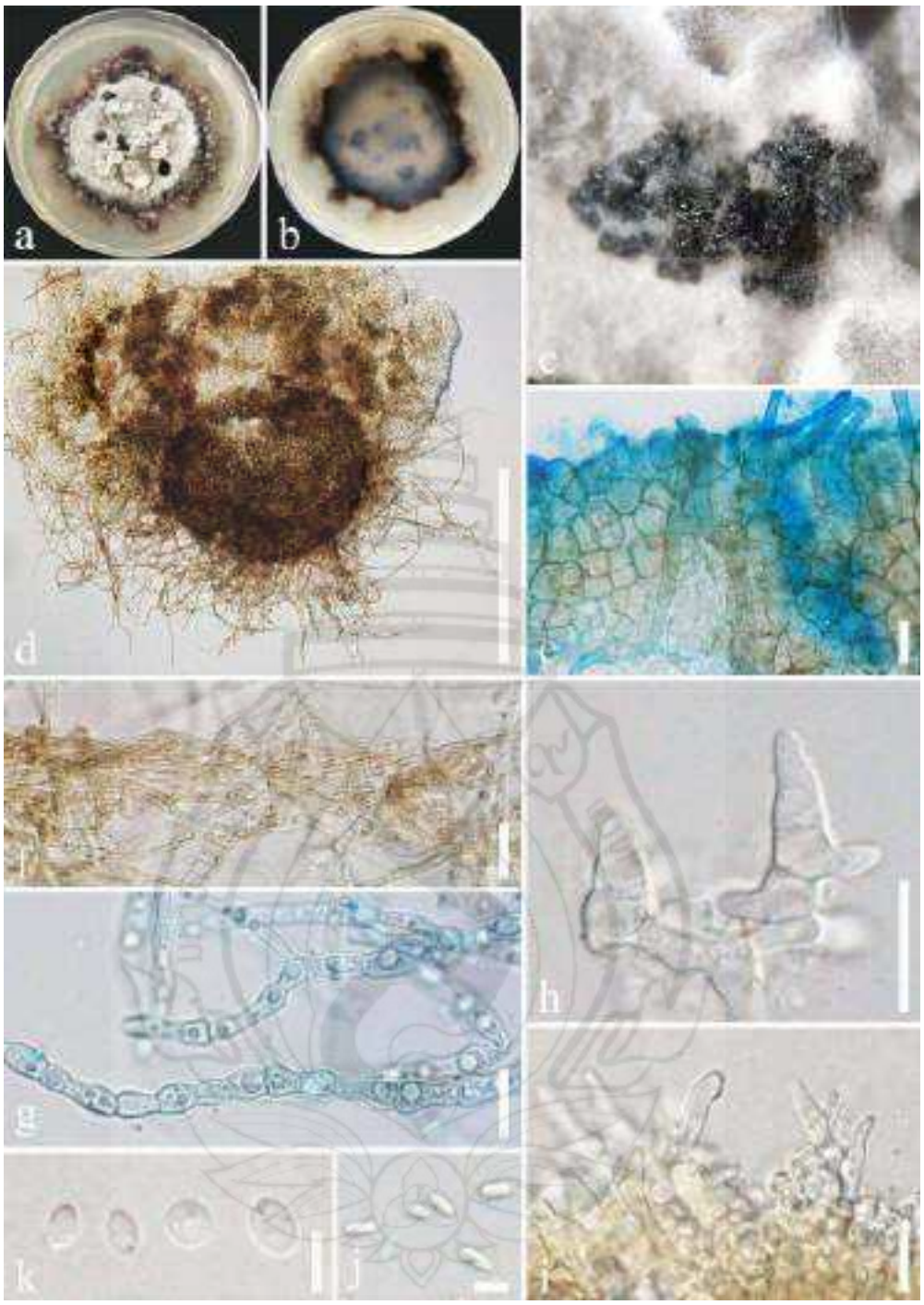
Endophytic on a healthy branch of *Aquilaria sinensis* (Thymelaeaceae). **Asexual morph:** on PDA media. *Mycelium* superficial. *Hyphae* 1.5–3 μm wide, brown, smooth- and thin-walled, septate, branched, partial mycelial have many partitions, some 4–6.5 μm wide, with guttulate. *Conidiomata* pycnidial, 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.

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); ex-type GMBCC1187; *ibid.,* YNA-YJA-BH-B06, living culture GMBCC1188.

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 (Figure 3.9). 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 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, SSU and *tef*1-α genes sequence of *B. australiensis* (CBS 142163, ex-type) are unavailable. The results of nucleotide base pair differences (without gaps) between our new strain 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) are 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.



Note 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.

Figure 3.8 *Banksiophoma endophytica* (GMB-W1511, holotype)

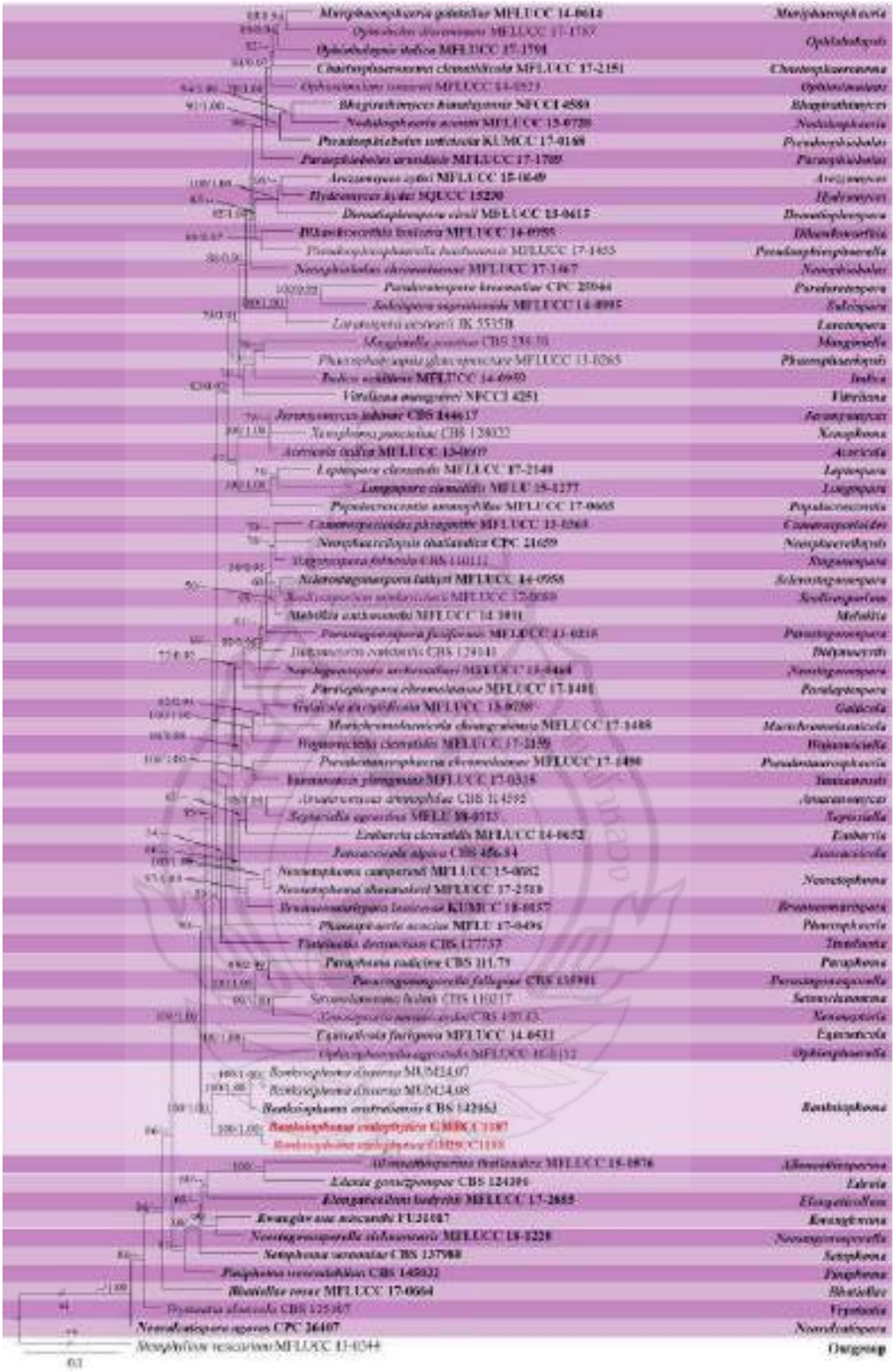


Figure 3.9 Phylogenetic tree of *Banksiophoma*

Figure 3.9 Bootstrap support values for ML greater than 50% and Bayesian posterior probabilities greater than 0.90 are given near the nodes, respectively. 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.

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

MycoBank number: MB XXXX; Facesoffungi number: FoF XXXX; Figure 3. 10.

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.

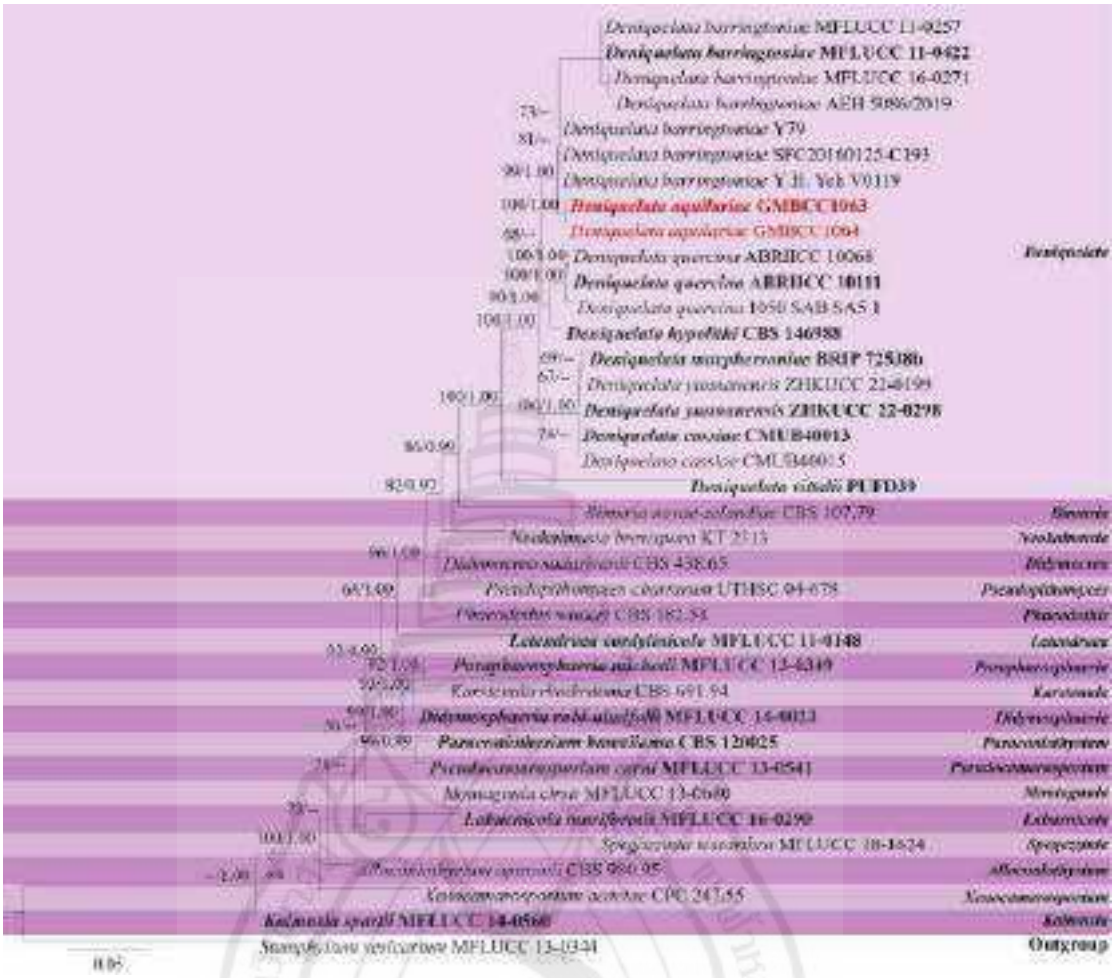
Material examined: CHINA, Yunnan Province, Yuxi City, Yuanjiang County, on agarwood resin part of *Aquilaria sinensis* (Thymelaeaceae), 18 September 2023, T. Y. Du, YNA-YJA-CA-C06 (GMB-W1513, dried culture, holotype), preserved in a metabolically inactive state at Guizhou Medical University (GMB-W);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

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% in ML and 1.00 in BYPP statistical support (Figure 3.11). The PHI test results (Figure 3.12) indicated no significant recombination events between *D. aquilariae* and its phylogenetically related taxa. The newly described strains did not sporulate in culture, so the morphological characteristics could not be compared with *D. barringtoniae*. The ITS, LSU, and SSU loci of nucleotide base pair differences (without gaps) between our new strain 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, 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.

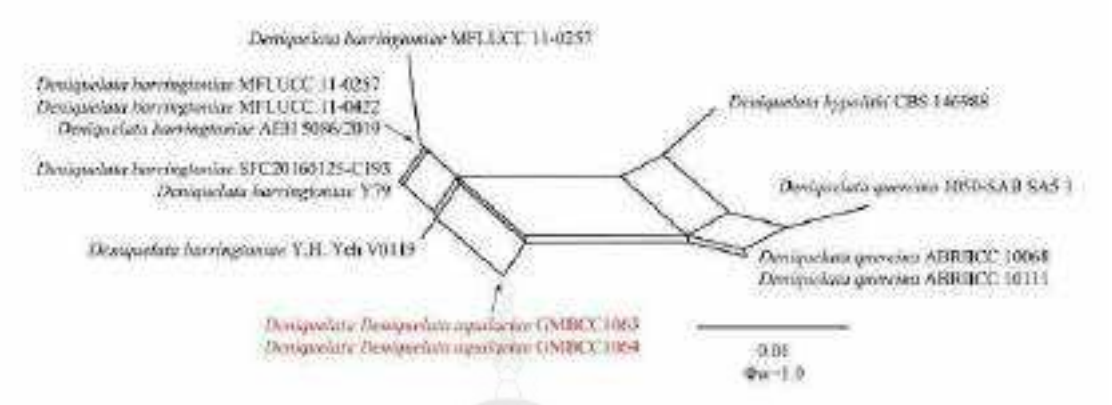
Note a, b, Colony on PDA at room temperature after one week from above and below. c, d, Mycelia masses. Scale bars: c, d = 10 μm.

Figure 3.10 *Deniquelata aquilariae* (GMB-W1513, holotype)



Note Bootstrap support values for ML greater than 50% and Bayesian posterior probabilities greater than 0.90 are given near the nodes, respectively. 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 3.11 Phylogenetic tree of *Deniquelata*



Note The PHI test result Φw ≤ 0.05 indicates that there is a significant recombination within the dataset. The new isolates are indicated in red.

Figure 3.12 Split graphs showing the results of the PHI test of *Deniquelata aquilariae* and closely related taxa using LogDet transformation and splits decomposition

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

MycoBank number: MB 834472. Figure 3.13

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); living culture, GMBCC1189.

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 (Figure 3.16). Morphologically, our isolate resembles *M. cylindrospora* (UTHSC DI16-208, ex-type) in having pycnidial conidiomata, brown to dark brown, solitary, superficial, globose to subglobose, hyaline conidiogenous cells, phialidic, ampulliform to doliiform, smooth-walled, and hyaline conidia, aseptate (Crous et al., 2020). *Montagnula cylindrospora* was introduced by Crous et al. (2020) from a human skin sample in the USA and described its conidia as cylindrical; however, in this study, we also observed conidia 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.

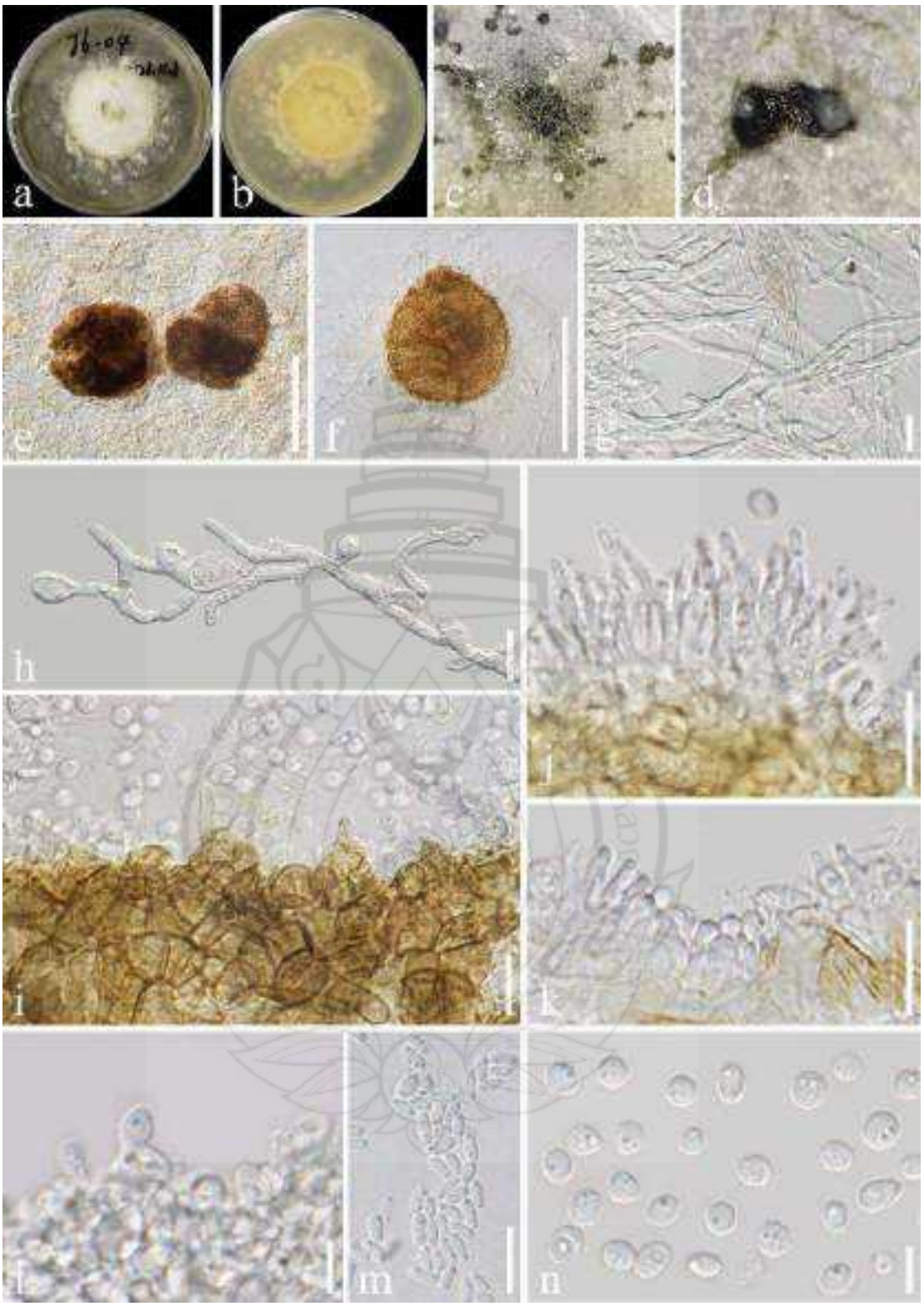


Figure 3.13 *Montagnula cylindrospora* (GMB-W1516)

Figure 3.13 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.

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

MycoBank number: MB XXXX; Facesoffungi number: FoF XXXX; Figure 3. 14.

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); ex-type, GMBCC1185; other living cultures, GMBCC1829, GMBCC1832, GMBCC1696, GMBCC1713, GMBCC1714, GMBCC1715, GMBCC1716, GMBCC1717, GMBCC1718, GMBCC1719.

Notes: *Montagnula sinensis* clustered sister to *M. cylindrospora* (UTHSC DI16-208, ex-type) and *M. yunnanensis* (GMBCC1174, ex-type) in the phylogenetic analyses (Figure 3.16). Morphologically, *M. sinensis* differs from *M. cylindrospora* (UTHSC DI16-208, ex-type) in conidiogenous cells phialidic, ampulliform with conical at the apex and cylindrical conidia, while *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 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, while the SSU sequence of *M. cylindrospora* (UTHSC DI16-208, ex-type) is unavailable. The results between our new strain and *M. sinensis* (GMBCC1185, 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 (Figure 3.17) 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.

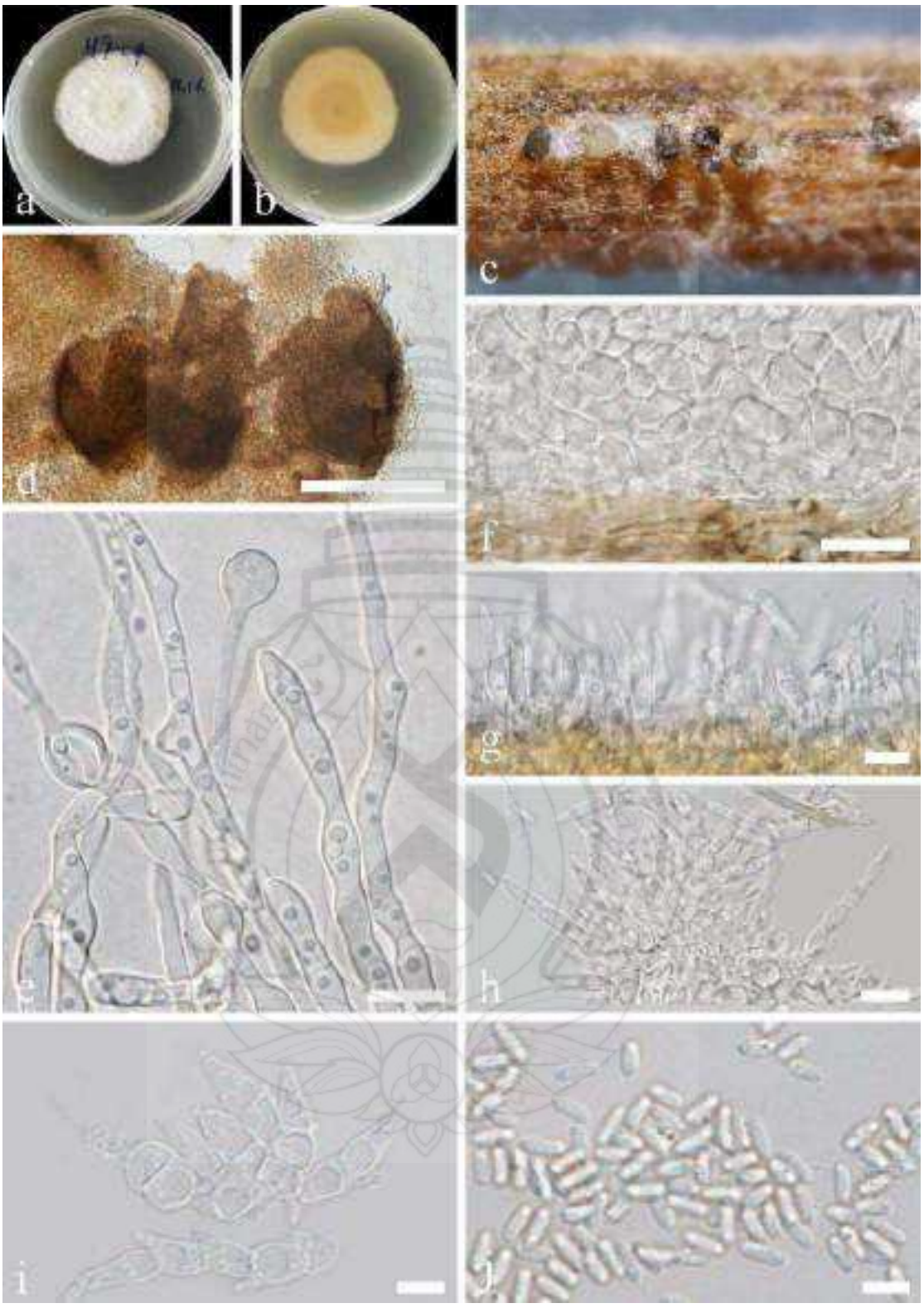


Figure 3.14 *Montagnula sinensis* (GMB-W1510, holotype)

Figure 3.14 a, b, Colony on PDA at room temperature after one week from above and below. c, Conidiomata grow on bamboo toothpicks on 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.

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

MycoBank number: MB XXXX; Facesoffungi number: FoF XXXX; Figure 3. 15.

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

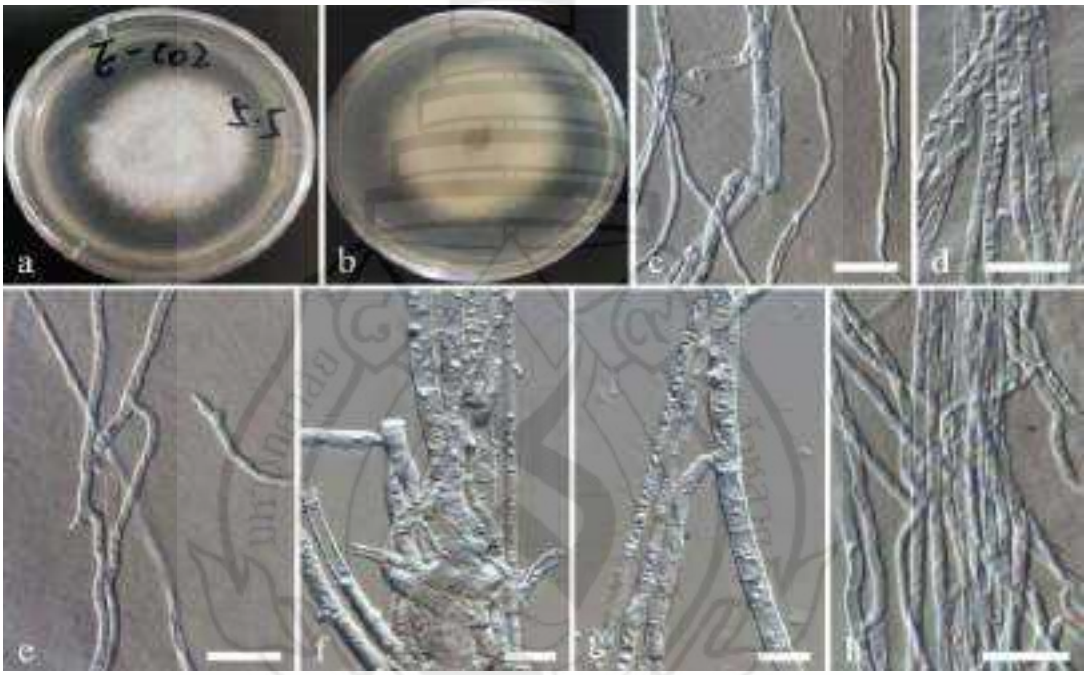
Holotype: GMB-W1512

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); ex-type living cultures, GMBCC1174=GMBCC1848.

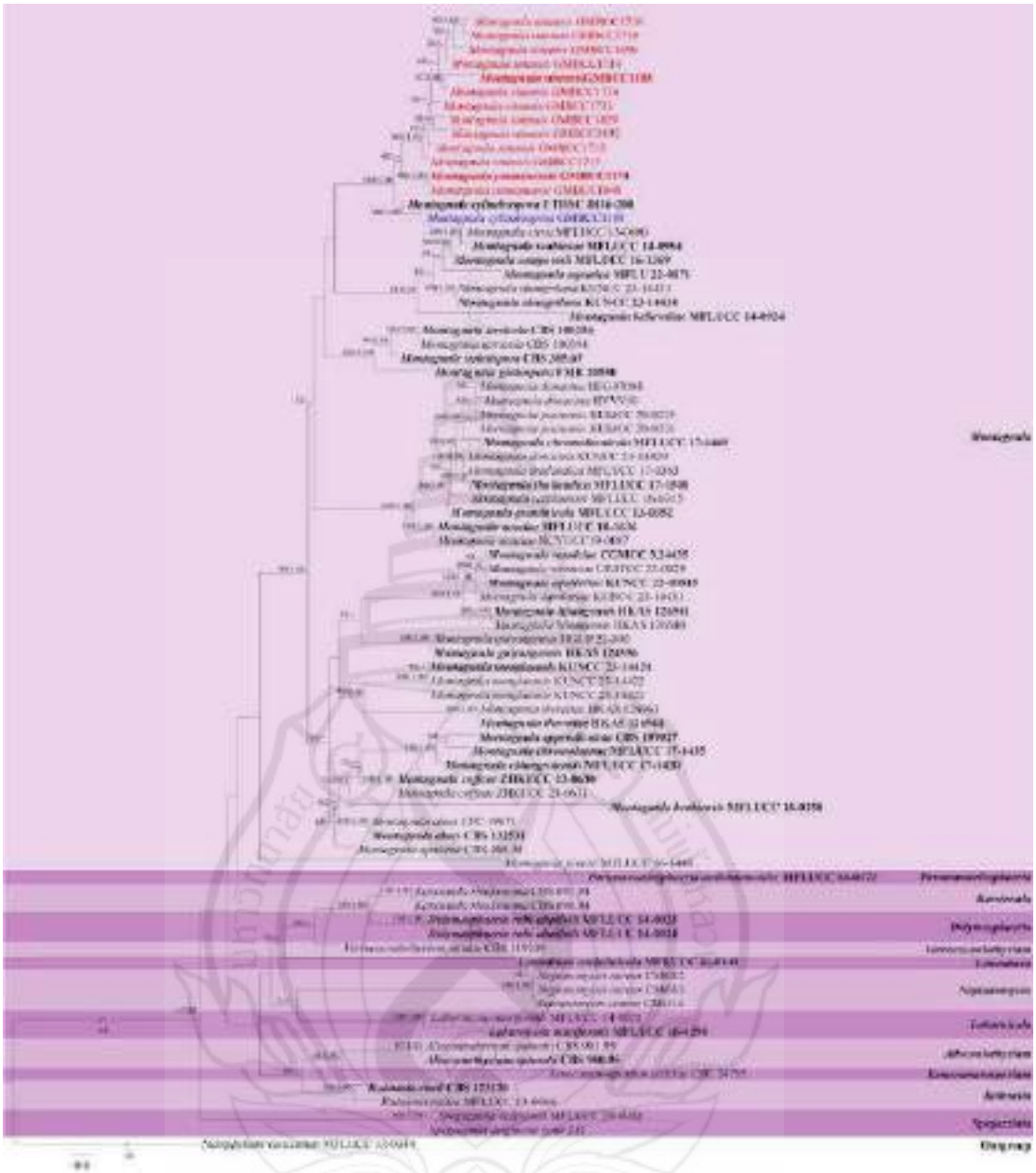
Notes: Based on BLASTn searches of ITS, LSU, *rpb*2, SSU, and *tef*1-α sequence data, our strain *Montagnula yunnanensis* showed a high similarity to *M. cylindrospora* (UTHSC DI16-208) (ITS = 98.73% (LT796834), LSU = 99.67% (LN907351), *rpb*2 = 97.42% (LT796994), and *tef*1-α = 98.54% (LT797074)), while SSU showed high similarity to *M. camporesii* (MFLUCC 16-1369, NG_068418) with 99.71%. In the phylogenetic analyses, *M. yunnanensis* clustered sister to *M. sinensis* (11 strains) and *M. cylindrospora* (UTHSC DI16-208, ex-type) (Figure 3.16). The newly described strains did not sporulate in WA and PDA media during the six-month observation period, so the morphological characteristics could not be compared with *M. cylindrospora* and *M. sinensis*. The nucleotide base pair differences (without gaps) between our new strain 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, while 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 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 (Figure 3.17) indicated no significant recombination events between *M. yunnanensis* and its phylogenetically related taxa. Based on significant statistical support in molecular phylogenetic studies, *M. yunnanensis* is introduced herein as a new species on agarwood resin part of *Aquilaria sinensis* from Yunnan Province, China.



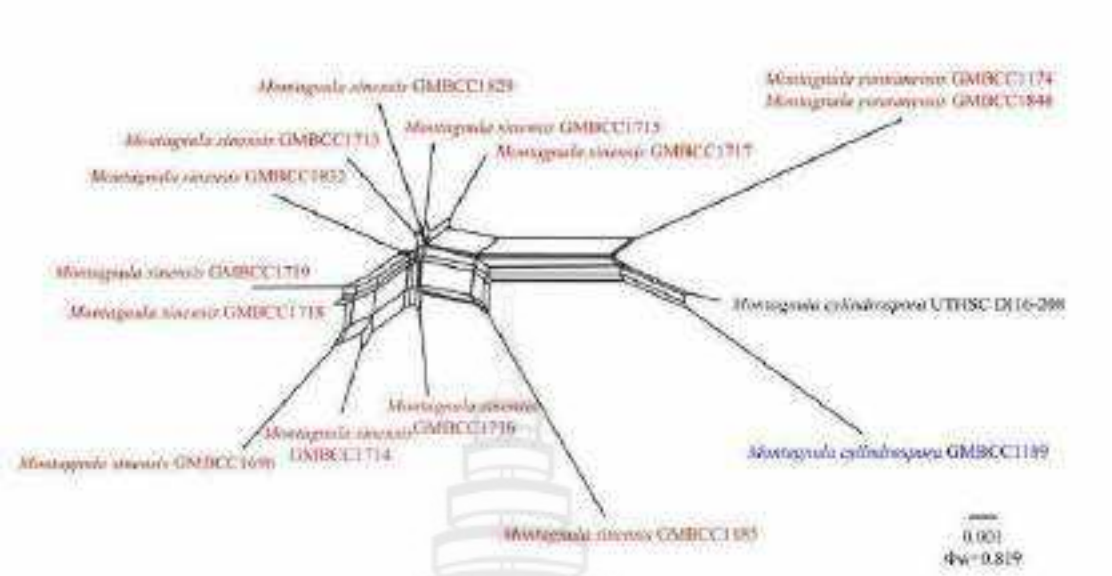
Note a, b, Colony on PDA at room temperature after one week from above and below. c–h, Mycelia masses. Scale bars: c–h = 10 μm.

Figure 3.15 *Montagnula yunnanensis* (GMB-W1512, holotype)



Note Bootstrap support values for ML greater than 50% and Bayesian posterior probabilities greater than 0.90 are given near the nodes, respectively. 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 3.16 Phylogenetic tree of *Montagnula*



Note The PHI test result Φw ≤ 0.05 indicates a significant recombination within the dataset. The new species are indicated in red, and the new record is indicated in blue.

Figure 3.17 Split graphs showing the results of the PHI test of *Montagnula cylindrospora* and closely related taxa using LogDet transformation and splits decomposition

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

MycoBank number: MB XXXX; Facesoffungi number: FoF XXXX; Figure 3. 18.

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

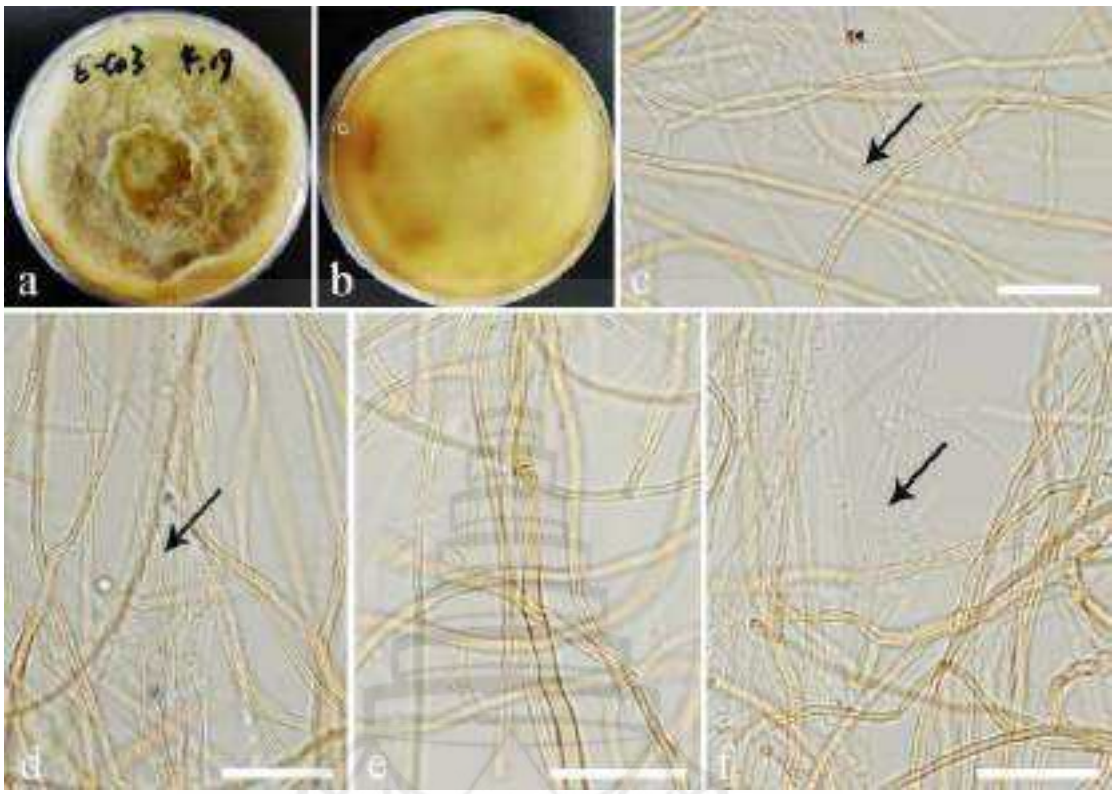
Holotype: GMB-W1514

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); ex-type, GMBCC1181; *ibid.,* YNA-YJA-CE-C04, living culture GMBCC1182; *ibid.,* YNA-YJA-CE-C05, living culture GMBCC1183.

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* has formed a distinct branch in *Fomitiporia* (Figure 3.19). The newly described strains belong to Basidiomycota and did not sporulate in culture, so morphological characteristics could not be compared with other *Fomitiporia* species. While our strains are similar to other *Fomitiporia* species with the 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 (Figure 3.19), *F. aquilariae* is introduced herein as a new species from the agarwood resin part of *Aquilaria sinensis* from Yunnan Province, China.



Note 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.

Figure 3.18 *Fomitiporia aquilariae* (GMB-W1514, holotype)

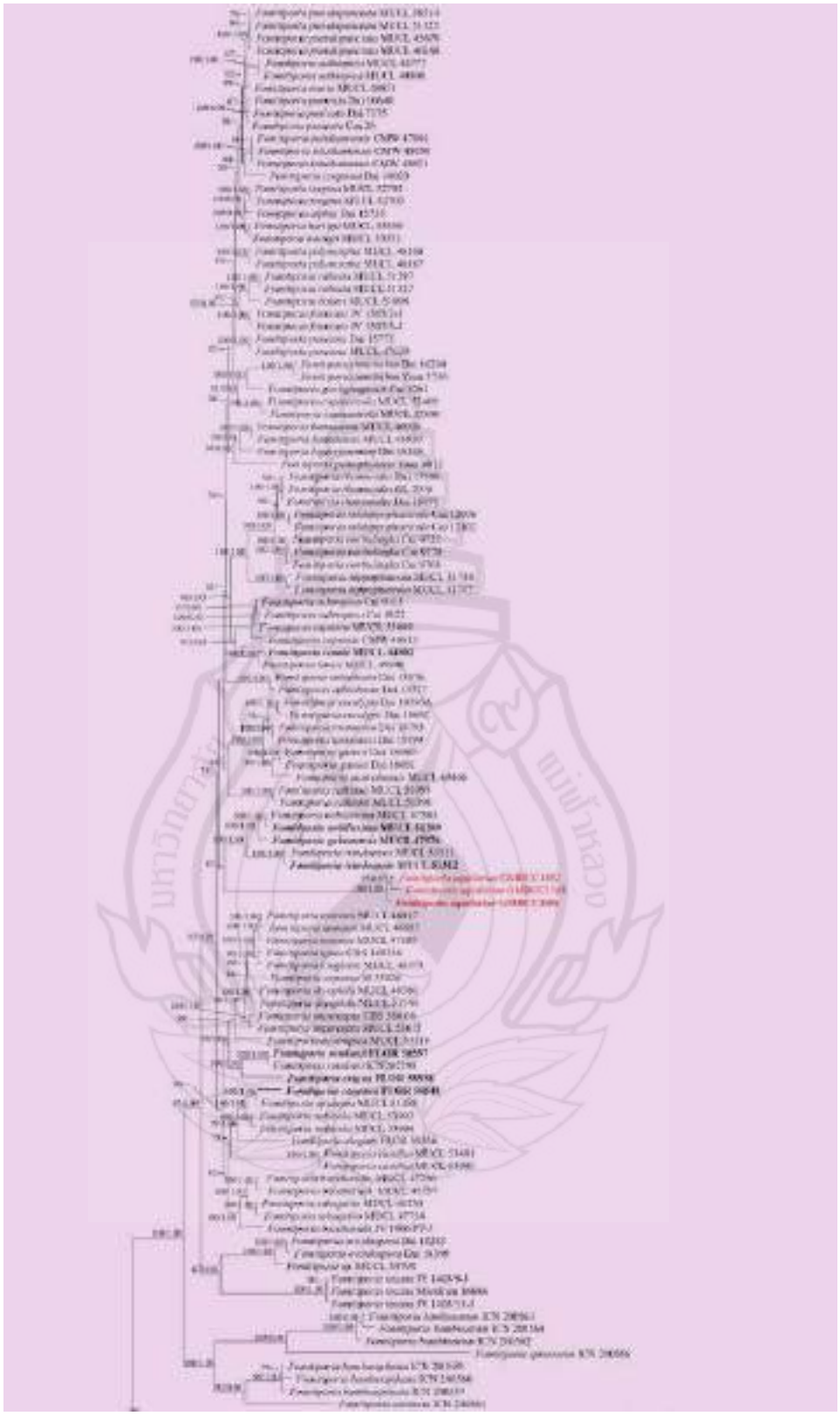
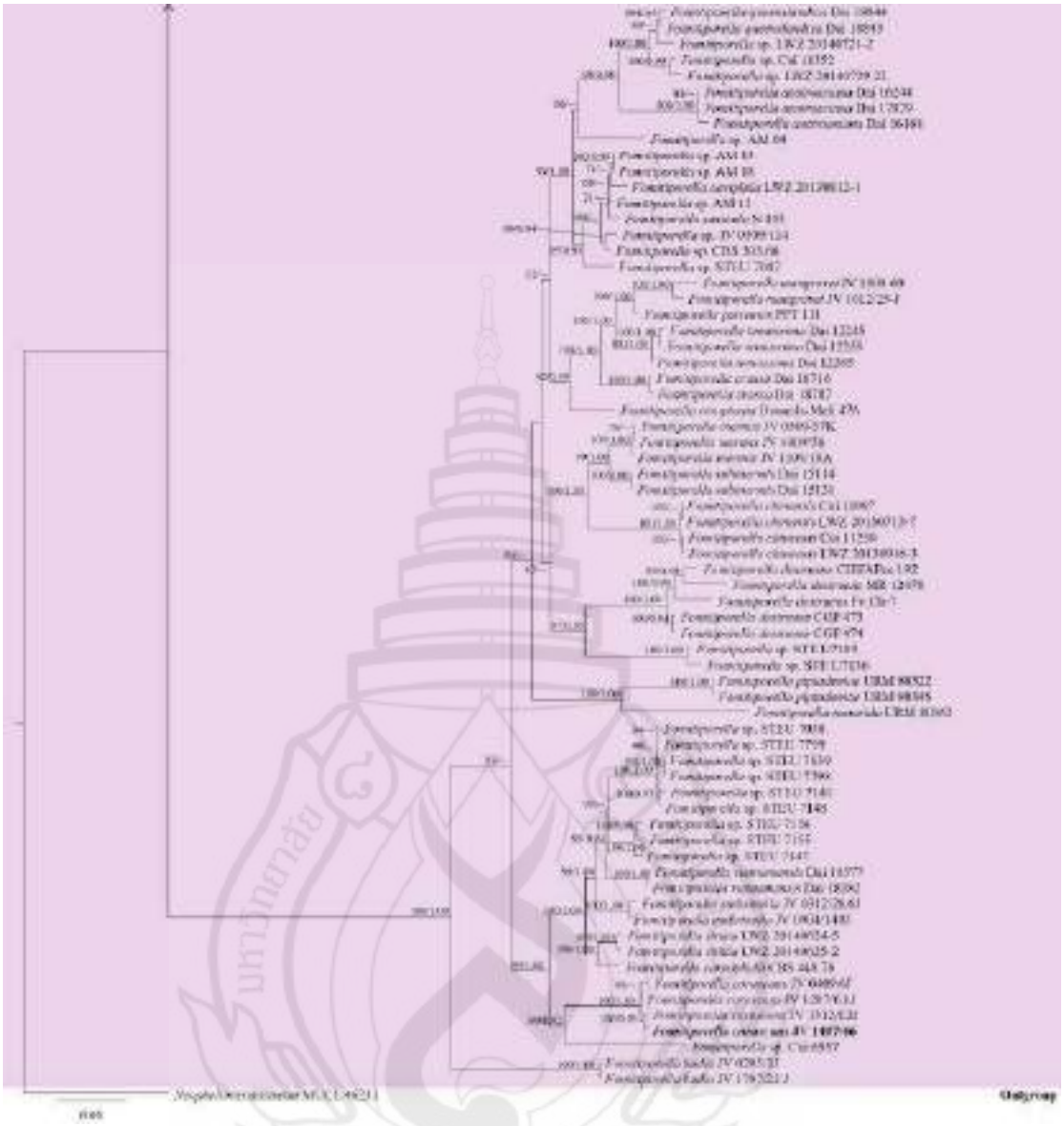


Figure 3.19 Phylogenetic tree of *Banksiophoma*



Note Bootstrap support values for ML greater than 50% and Bayesian posterior probabilities greater than 0.90 are given near the nodes, respectively. The tree is rooted with *Neophellinus uncisetus* (MUCL 46231). The new isolates are indicated in red, and the ex-type strains are in bold.

Figure 3.19 (continued)

3.3.4 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 of the 64 genera, including their species count, lifestyle, host, and geographic distribution, classification criteria, their roles in the *Aquilaria* genus, and their unique biological activities.

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

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 the species have available sequence data in GenBank, but mostly have only ITS and LSU sequences, while SSU and *tef*1-α sequences are absent (Liu & Zeng, 2022). In previous studies, some *Acrocalymma* strains were isolated from *Aquilaria sinensis* as agarwood-associated fungi from China (Du et al., 2024; Fu et al., 2024). In this study, we obtained two strains of *Acrocalymma* from *Aquilaria sinensis*, one of which was an endophytic fungus from a healthy tree branch and one from the agarwood resin part.

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

Allophoma was established by Hsieh et al. (2005). Totally 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., 2024b)

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 (Woudenberg et al., 2013; Ariyawansa et al., 2015; 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 were reported to be isolated from *Aquilaria* spp. from China and India (Premalatha et al., 2013; Tian et al., 2013; Lisdayani et al., 2015; Sen et al., 2020; Du et al., 2022a, d). In this study, we obtained 22 strains of *Alternaria* from *Aquilaria sinensis*, of which 20 strains were endophytic fungi from healthy tree branches or leaves, and two strains were from agarwood resin parts.

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

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 more strains of *Annulohypoxylon* from *Aquilaria sinensis*, of which one strain was an endophytic fungus from a healthy tree leaf, and one strain was from the agarwood resin part.

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

Aspergillus was described by Micheli (1729). More than 1110 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, 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 numerous existing endophytic fungi, *Aspergillus* strains are one of the most abundant sources of secondary metabolites with different biological activities (e.g., antibacterial, antifungal, antioxidant, anti-cancer, anti-plasmodial, anti-inflammatory, and immunosuppressive activities) (Hagag et al., 2022). The identification of *Aspergillus* species relies on standardized methods based on morphological characteristics, extrolite characterization, and multi-genes DNA sequence analyses (ITS, *rpb*2, CaM, and β-tubulin (BenA)) (Nguyen et al., 2020). In previous studies, there are some *Aspergillus* strains were reported to isolate 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., 2022d).

In this study, we obtained 40 strains of *Aspergillus* from *Aquilaria sinensis*, of which five strains were endophytic fungi from healthy tree branches or leaves, 29 strains were from agarwood resin parts, and six strains were from dead branches.

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

Aureobasidium was established by Viala & Boyer (1891). Totally 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) first carried out the molecular analysis. Subsequently, a large amount of molecular data became available based on the high accessibility of sequencing services (ITS and LSU) (Wu et al., 2023). The functional activities of *Aureobasidium* have been explored, such as: as biological control agents (Sharma et al., 2009; Prasongsuk et al., 2018), can produced commercial compounds (Wu et al., 2023), and *A. pullulans* can 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., 2024b)

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, there are no *Banksiophoma* strains 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., 2024b)

Biscogniauxia was introduced for the sexual morph of this genus by Pouzar (1979). In this genus, the asexual morph was 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., 2020b; Ma et al., 2020). This genus is well-studied in morphology, but only a few species have available DNA sequences (Hyde et al., 2020b; Li et al., 2021; 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 in *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., 2024b)

Botryosphaeria was described by Cesati & de Notaris (1863). Currently, more than 300 epithets are listed in Index Fungorum (2025). *Botryosphaeria* is cosmopolitan, and species of this genus 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 on host association, but these signs are not sufficient to distinguish them, later, molecular data is being 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* shows antimicrobial activity from China (Gong & Guo, 2009; Du et al., 2022d). 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., 2024b)

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 saprobic ascomycetes; species are well known as coprophilous, seed and soil fungi, and are also found in organic compost (Pornsuriya et al., 2008). Some species can act as both pathogenic and endophytic fungi, such as *C. globosum* (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 by morphological data; the study of molecular phylogeny is limited, and many species lack DNA sequences (ACT, ITS, *rpb2*, TUB, TUB, and CAL) (Sekhar et al., 2018). In previous studies, some *Chaetomium* strains were reported to isolate 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., 2024b)

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 pathogenic 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 morphology, but some of species without available DNA sequences (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 healthy tree branch of *Aquilaria sinensis*.

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

Cladosporium was established by Link (1816). More than 900 epithets are listed in this genus and most of *Cladosporium* species as plant pathogenic, and some of as saprobic, pathogenic in humans and animals, and endophytic or hyperparasitic in terrestrial environments, such as caves, soil, air, indoors, and marine environments, 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 biologically control agents against other fungi (Dutra et al., 2023; Lee et al., 2023; Yang et al., 2023). Previous studies reported some *Cladosporium* strains from *Aquilaria* spp. as endophytes and agarwood-associated fungi 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., 2024b)

Colletotrichum was initially described under the name *Vermicularia* by Tode (1790), while later revised as *Colletotrichum* by Corda (1837). More than 1,000 epithets are listed in Index Fungorum (2025). *Colletotrichum* species play 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, cause anthracnose in diverse hostplants (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 TUB2), and biochemical tests) (Sharma & Shenoy, 2016; Bhunjun et al., 2021; Zhang et al., 2024d). In previous studies, some *Colletotrichum* strains were reported to isolate from *Aquilaria* spp. as endophytes or agarwood-associated fungi, e.g., *C. gloeosporioides* from China (Tian et al., 2013; Du et al., 2022d). In this study, we obtained 49 strains of *Colletotrichum* from *Aquilaria sinensis*, of which 45 were endophytic fungi from healthy tree branches or leaves, and four were from agarwood resin parts.

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

Coniella was established by von Höhnel (1918). Totally 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., 2024b)

Corynespora was described by Güssow (1906). Currently, more than 200 epithets are listed in Index Fungorum (2025), and members of *Corynespora* play as saprobes, endophytes, and pathogens on a wide range of plants, 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., 2024b)

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 chinensi*) (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., 2024b)

Curvularia was established by Boedjin (1933). Totally 248 epithets are listed in this genus and most *Curvularia* species as saprobic and endophytes, and some species as epiphytes and pathogens (animal, human, and plants) in air, indoor environments, soil, water, or plant material (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 available 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., 2022d). 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* sp. 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., 2024b)

Daldinia was established by Cesati & de Notaris (1863). Totally, 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 available DNA sequences (Wongkanoun et al.,

2020; Yin et al., 2024a). *Daldinia* species can produce abundant secondary metabolites; those metabolites 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., 2024b)

Deniquelata was established by Ariyawansa et al. (2013). Seven epithets are listed in this genus and *Deniquelata* species 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., 2024b)

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). The polyphasic taxonomy is essential to identify and comprehensively characterize *Diaporthe,* and the phylogenetic analysis is based on muti-genes combined ITS, *tef*1-α, TUB, CAL, and HIS (Gomes et al., 2013; Norphanphoun et al., 2022; Zhu et al., 2023; 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 showed excellent antioxidant capacity from China and Thailand (Monggoot et al., 2017; Du et al., 2022a, 2022b, 2022d). In this study, we obtained 55 strains of *Diaporthe* from *Aquilaria*

sinensis, of which 31 strains were endophytic fungi from healthy tree leaves, 21 strains were from the agarwood resin part, and three strains were from dead branches.

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

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, and 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, such contain abundant metabolites (Yuan et al., 2023). This genus is well-studied in morphology and phylogeny based on multiple-loci (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., 2024b)

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, most of the species sequence data are unavailable (De Silva et al., 2021; Keirnan et al., 2021; Tian et al., 2024; Wang et al., 2024b). Some endophytic *Daldinia* species have biological control ability, and some species can produce mycotoxins (Oliveira et al., 2018; Bagy et al., 2019; Senanayake et al., 2023). In previous studies, *Epicoccum* strains were isolated from *Aquilaria* spp. as endophytes and agarwood-associated fungi from 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., 2024b)

Exophiala was established by Carmichael (1967). Totally 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, but 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., 2024b)

Fomitiporia was established by Murrill (1907). Totally, 101 epithets have been 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 nLSU) (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., 2024b)

Fonsecaea was described by Brumpt (1922) and Negroni (1936) (Ajello et al., 1988). Totally, 16 epithets are listed in this genus, and members of *Fonsecaea* have been reported as black yeasts, as pathogen 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, but 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., 2024b)

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, including 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 muti-genes include ITS, LSU, *tef1-α, rpb2,* TUB, and CaM (Ma et al., 2023; Afzalinia et al., 2025). In previous studies, there are many *Fusarium* strains were reported to isolate from *Aquilaria* spp., *Fusarium* is a dominant genus among fungi associated to *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, d, 2024b). In this study, we obtained 140 strains of *Fusarium* from *Aquilaria sinensis*, of which two strains were endophytic fungi from healthy tree branches, 122 strains were from agarwood resin parts, and 16 strains were from dead branches.

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

Hermatomyces was introduced by Spegazzini (1910). Totally, 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 were isolated from *Aquilaria sinensis* as agarwood-associated fungi in China (Song et al., 2021), and 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., 2024b)

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 live on dead and decaying wood of angiospermous plants (Stadler 2011; Song et al., 2022b), while some strains serve as plant pathogens (Nepolean et al., 2014). In addition, some species as endophytes may protect their host plants from pathogens (Song et al., 2022b). The identification of this genus is based on polyphasic taxonomic methods, and the phylogenetic analysis is based on multiple-loci (ITS, LSU, *tef*1-α, EPB2, and TUB) (Song et al., 2022b). In previous studies, some *Hypoxylon* strains were reported to isolate 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*, of which nine strains were endophytic fungi from healthy tree branches or leaves, and six were from agarwood resin parts.

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

Lasiodiplodia was described by Clendenin (1896). Currently, 92 epithets are listed in Index Fungorum (2025). *Lasiodiplodia* species are commonly 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, there are many *Lasiodiplodia* strains were reported to isolate from *Aquilaria* spp. as endophytes or agarwood-associated fungi, *Lasiodiplodia* is a common genus in *Aquilaria*-associated fungi, 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*, of which eight strains

were endophytic fungi from healthy tree branches or leaves, and 155 strains were from agarwood resin parts.

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

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., 2024b)

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 on *Acer* and Rosaceae plants through hemibiotrophic or weakly parasitic lifestyles, 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 or opportunistic growth in plants (Michalopoulos-Skarmoutsos & Skarmoutsos, 1999; Voglmayr & Jaklitsch; 2011; Hongsanan et al., 2020). Presently, there are 54 accepted species, of which only 19 species have molecular data (SSU, LSU, *tef*1-α, and *rpb*2); there are many species that lack molecular data (Hongsanan et al., 2020; Samarakoon et al., 2022; 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., 2024b)

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 pathogen of 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., 2024b)

Meyerozyma as one of genus of ascomycete yeasts was proposed by Kurtzman and Suzuki (2010). Eight epithets have been listed in this genus (Index Fungorum, 2025), and it can be distinguished well from another close genus in morphology and phylogeny (ITS and LSU) (Kurtzman & Suzuki, 2010; Yurkov et al., 2017). Most yeasts of *Meyerozyma* have been isolated from insect-related habitats and the 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 tree branches of *Aquilaria sinensis*.

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

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., 2014b; 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 isolate 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., 2024b)

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 collected in soil and dung (Walther et al., 2013; Zhao et al., 2023). Some species of *Mucor* are widely used in fermentation, biotransformation, and the pharmaceutical industry (Hong et al., 2012; Huang et al., 2014; Khan et al., 2019), and some species are well-known pathogens causing mucormycosis (Chibucos et al., 2016; Panthee et al., 2021). In this genus, only some species have molecular data (ITS and LSU), while most species lack it (GenBank, 2024). In previous studies, some *Mucor* strains were isolated from *Aquilaria sinensis* from China, India and Sri Lanka (Subasinghe et al., 2019; Gogoi et al., 2022; Du et al., 2024b). 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., 2024b)

Nemania was described by Gray (1821). Currently, 123 epithets are listed in Index Fungorum (2025). *Nemania* 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; Pietb al. 2021) and as pathogens of some plants (Wang et al., 2023a). In addition, *Nemania* species exhibits different biological activities as an endophytic fungus (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, and *N. aquilariae* showed antibacterial and antimicrobial properties from China

(Tibpromma et al., 2021). In this study, we obtained two strains of *Nemania* from healthy tree branches of *Aquilaria sinensis*.

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

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 causing leaf spots and leaf, rachis 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., 2024b)

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 and are known as endophytes and pathogens causing 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* are difficult to differentiate from one other since many morphological characters overlap between species; thus, the molecular data (ITS, *tef*1-α, *rpb*2, and TUB) are an indispensable part to distinguish 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 from China (Du et al., 2022d).

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

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 roughly 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). Also, 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, d). In this study, we obtained 13 strains of *Neopestalotiopsis* from *Aquilaria sinensis*, of which 10 strains were endophytic fungi from healthy tree branches or leaves, one strain was from the agarwood resin part, and two strains were from dead branches.

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

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 plant and human pathogens with 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 from China (Du et al., 2024). In this study, we obtained 25 strains of *Neoscytalidium* from *Aquilaria sinensis*, of which 17 strains were from agarwood resin parts, and eight strains were from dead branches.

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

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., 2024b)

Nigrospora was described by Zimmerman (1902). Currently, 52 epithets are listed in Index Fungorum (2025). This genus includes pathogens, endophytes, and saprobes, and it is 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 used for 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, d). In this study, we obtained 34 strains of *Nigrospora* from *Aquilaria sinensis*, of which 28 strains were endophytic fungi from healthy tree branches or leaves, and six strains were from agarwood resin parts.

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

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). And the species of *Paracamarosporium* have greater medicinal potential; a *Paracamarosporium* sp. has been reported to produce potent antimalarial compounds (Hayashi et al., 2019). It is difficult to morphologically distinguish the taxa in this genus (Crous et al., 2015), but can be well-studied by morphology and phylogeny (ITS and LSU) (Thuong et al., 2022). In previous studies, some *Paracamarosporium* strains were isolated from *Aquilaria sinensis* as agarwood-associated fungi from China (Du et al., 2022b, d, 2024b). In this study, we obtained 16 strains of *Paracamarosporium* from healthy tree branches of *Aquilaria sinensis*.

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

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 incorporated with 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 from 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., 2024b)

Paradictyoarthrinium was established by Matsushima (1996). There are five epithets have been listed in this genus (Index Fungorum, 2025). Members of *Paradictyoarthrinium* are mainly discovered as saprobes from 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 pathogen 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., 2024b)

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, with morphology and phylogeny (ITS, *rpb*2, BenA, and CaM) as the classification basis. In previous studies, there are several *Penicillium* strains 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*, of which seven strains were endophytic fungi from healthy tree branches or leaves, and 16 strains were from agarwood resin parts.

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

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, distributed widely in terrestrial habitats and rarely in aquatic and marine environments (Liao et al., 2024; Pem et al., 2024). And *Periconia* is also the 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* from China (Du et al., 2022b; Fu et al., 2024).

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

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 from 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., 2024b)

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) offers the standard for *Phaeoacremonium* 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*) from China and India (Le et al., 2017; Liu et al., 2022a; Li et al., 2023; Du et al., 2024b). In this study, we obtained 28 strains of *Phaeoacremonium* from *Aquilaria sinensis*, of which one strain was an endophytic fungus from a healthy tree branch, and 27 strains were from agarwood resin parts.

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

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., 2022a). This genus is well-studied in morphology and phylogeny (ITS and LSU) (Chen et al., 2021; Li et al., 2022a). In previous studies, *Phanerochaetella* was not reported from *Aquilaria* spp. In this study, we obtained one strain of *Phanerochaetella* from the agarwood resin part of *Aquilaria sinensis*.

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

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 from China (Liu et al., 2019a; Du et al., 2022b).

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

Phyllosticta was established by Persoon (1818). More than 3,200 epithets are listed in this genus (Index Fungorum, 2025) and most *Phyllosticta* species as saprobic, pathogenic, and endophytic fungi associated with variety of plants (e.g., *Citrus* spp., *Garcinia oblongifolia*, *Musa* spp., *Pterospermum heterophyllum*, and *Vitis* spp.) (Wang et al., 2012, 2023; Wong et al., 2012; Tran et al., 2019; Zhang et al., 2022a, 2024). 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., 2022a, 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 tree leaves of *Aquilaria sinensis*.

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

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, also found in soil, air, and clinical materiel (Da Cuncha et al., 2014; Walsh et al., 2018; Xiang et al., 2024). This genus is studied mostly based on morphology, and few species are supported by phylogeny analysis (ITS, LSU, SSU, and *rpb*2) (Pratibha & 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., 2024b)

Pseudofusicoccum was introduced by Crous et al. (2006). Nine epithets are listed in this genus (Index Fungorum, 2025), and *Pseudofusicoccum* species are known as saprobes, endophytes, and pathogens on different 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 from 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., 2024b)

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 and humans (e.g., *Acacia* sp., *Acoelorrhaphe wrightii*, *Entada*

phaseoloides, *Gnidia polycephala*, *Homo sapiens*, *Morus australis*, *Pandanus amaryllifolius*, Poaceae, *Rosa canina*, *Saccharum officinarum*, and *Zea mays*) (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 reported *Pseudopithomyces* strains as agarwood-associated fungi from *Aquilatia sinensis* from China (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., 2024b)

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* were well-studied in morphology and 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 from 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., 2024b)

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 isolate 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., 2024b)

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 others 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 from 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., 2024b)

Talaromyces was established by Benjamin (1955). A total of 296 epithets are listed in this genus (Index Fungorum, 2025) and *Talaromyces* species have been isolated as saprobes, endophytes, or pathogens from air, soil, food products, and leaf litter; *Talaromyces marneffei* is a pathogen association with HIV patients (Guevara-Suarez et al., 2017; Morales-Oyervides et al., 2020; Nguyen & Lee, 2023). This genus is well-studied in morphology and phylogeny (*BenA*, *cmdA*, 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 from 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., 2024b)

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; Nascimento 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, hemicelluloses, 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 & Kaushik, 2017; Du et al., 2022a, b). In this study, we obtained 16 strains of *Trichoderma* from *Aquilaria sinensis*, of which four strains were endophytic fungi from healthy tree branches or leaves, and 12 strains were from agarwood resin parts.

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

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 from 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* play a significant role due to its 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 from 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., 2024b)

Veronaea was established by Cifferi & Montemartini (1957). A total of 31 epithets are listed in this genus (Index Fungorum, 2025) and some *Veronaea* species saprobic on dead plant materials (e.g., *Carex pendula*, *Carlina vulgaris*, *Ficus hispida*, *Grewia asiatica, Hedychium coronarium, Thylacospermum caespitosum,* and bamboo), soil, and some *Veronaea* strains act as pathogens for human, animals or plants (Hyde & Goh, 1998; Kondo et al., 2007; Hosoya et al., 2015; Wijayawardene et al., 2020; Chandrasiri et al., 2021). The molecular data is not available for most *Veronaea* species, with only six species having 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 from 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., 2024b)

Xenoroussoella was established by Mapook et al. (2020). Up to now, only one species has been introduced 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) 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). In previous studies, *Xenoroussoella* was not 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., 2024b)

Xylaria is a large and the described genus of the Xylariaceae (Martin 1970). Currently, more than 930 epithets are listed in Index Fungorum (2025), most *Xylaria* are saprobes, endophytes and pathogens reported from multiple hosts (wood, sawdust, leaf, 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, the phylogenetic analysis of this genus has mainly been based on combining multiple loci (ITS, *rpb*2, and TUB) (Li et al., 2024b). Previous studies reported some *Xylaria* strains isolating from *Aquilaria* spp. as endophytes or agarwood-associated fungi from China (Du et al., 2022a, b, 2024b). In this study, we obtained 12 strains of *Xylaria* from *Aquilaria sinensis*, of which eight strains were endophytic fungi from healthy tree branches or leaves, and four strains were from agarwood resin parts.

3.4 Discussion

This study analyzed community composition data of 960 fungal strains representing 64 genera, which were 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, 2022d, 2024b) and are included in this study solely for data analysis. Therefore, a total of 818 strains are used in this study as newly reported *Aquilaria sinensis*-associated fungi. This study briefly documents the 64 genera and conducts meticulous phylogenetic and morphological analyses on five new species, 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 activity, e.g., antibacterial, anti-cancer, anti-inflammatory, antimalarial, antimicrobial, antioxidant, anti-plasmodial, antirheumatoid, antitumor, cytotoxic, enzyme inhibitory, and immunosuppressive, there is detailed information in the above text. 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*. 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 a pathogenic and saprobic fungal genus (Alves-Silva et al., 2020a, 2020b; Brown et al., 2020), has three strains reported in this study as an agarwood-associated fungus isolated from agarwood resin, further underlining 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 the 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. 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 saprobic 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 fungal distribution and the ecology of *Aquilaria sinensis* are significant, and further research is needed to fully understand these implications.

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 genera present 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.

Through a series of data analyses on 960 fungal strains, it was found that Ascomycota was the most dominant group, accounting for as much as 99.06%, while

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. Genera such as *Diaporthe*, *Fusarium*, and *Lasiodiplodia* were isolated from samples at four collection 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. 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 based on culture-dependent techniques across different isolation 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. 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 (from healthy tissues), agarwood-associated fungi (from agarwood resins), and saprobic fungi (from dead tissues) isolated from *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). And 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 agarwood resin be studied on these genera, but their secondary metabolites should also be extracted and their biological characteristics analyzed.

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, d, 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 the damage to economic 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 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, then, through which microorganisms invade and trigger the tree's defense mechanisms, leading to agarwood resin production to counter these external injuries. While, 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 has not yet been fully explained, and only some hypotheses remain unproven. The relationship between agarwood resin formation and the microbial community has also not been clarified. Therefore, to better understand and explore the relationship between agarwood's microbiota, agarwood resin, and the agarwood-producing tree genera, we suggest referring to fungi/bacteria isolated from the agarwood resin as “agarwood-associated fungi/bacteria,” while endophytic fungi/bacteria should specifically refer to those isolated from healthy tissues of the 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 the exploration of 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 strains of 14 new fungal genera isolated 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 genera such as *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 data analysis of fungi isolated from different parts of the plant, revealing their interactions and laying a solid foundation for the in-depth study of agarwood formation mechanisms. Future research is crucial to further explore 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.

3.5 Conclusion

This study provides a comprehensive overview of the fungal community associated with *Aquilaria sinensis*, highlighting its remarkable community composition diversity and ecological complexity. By analyzing 960 fungal strains representing 64 genera of 44 families, including 818 newly reported strains, this work significantly expands the current understanding of *Aquilaria*-associated mycobiota. 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 phylogenetic and morphological evidence underscores the taxonomic richness

uncovered. Furthermore, the proposed term “agarwood-associated fungi” offers a new perspective for distinguishing fungi linked to resin formation, potentially advancing future studies on the role of fungi in agarwood induction. 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.

CHAPTER 4

THE FUNGAL STRAIN PROMOTES RAPID AGARWOOD RESIN PRODUCTION WITH MEDICINALLY ACCEPTED AGAROTETROL LEVEL

4.1 Introduction

Agarwood is a dark resin heartwood, mainly produced by the plant genera *Aquilaria* Lam. and *Gyrinops* Gaertn. (Thymelaeaceae Juss.) (Xu et al., 2016; Azren et al., 2018; Chen et al., 2018; Wang et al., 2018, 2019). Agarwood has a unique fragrance produced by its rich secondary metabolites, sesquiterpenes, and chromones (Cui et al., 2013; Rasool & Mohamed, 2016; Sen et al., 2017). It is often traded as incense, carvings, and jewelry, and the essential oil of agarwood is used in high-grade perfume (Liu et al., 2013; Monggoot et al., 2017; CITES, 2022; Ngadiran et al., 2023). Due to the small amount of agarwood collected in the wild and its unique fragrance, agarwood has a high economic value in the global market (Azren et al., 2018; Wang et al., 2018; Niego et al., 2023a). At present, the global market of agarwood essential oil is estimated to be worth more than $200 million (Ngadiran et al., 2023; Niego et al., 2023a).

Nevertheless, agarwood possesses significant medicinal value in addition to its other attributes. Agarwood plays important roles in traditional medicine in Arabia, China, and India, as well as in modern pharmacology (Liu et al., 2013; Liao et al., 2018; Wang et al., 2018; Du et al., 2022a; Ngadiran et al., 2023). Takamatsu and Ito (2020) proposed that agarotetrol is a characteristic substance of medicinal-grade agarwood. National Pharmacopoeia Committee (2015, 2020) has set agarotetrol as the main standard for testing whether agarwood has a medicinal value, i.e., if the agarotetrol content in the agarwood reaches 0.10%, it indicates the agarwood has a medicinally accepted agarotetrol level. In China, only two species of agarwood-producing trees, *Aquilaria sinensis* (Lour.) Spreng. and *A. yunnanensis* S. C. Huang are currently

distributed, of which the main source of agarwood in China is *A. sinensis* (National Pharmacopoeia Committee 2015, 2020; Tibpromma et al., 2021; CITES 2022).

The natural formation of wild agarwood is slow, and yields are low because it unexpectedly occurs in over 20 years old trees as a defense mechanism against external damage (Liu et al., 2013; Wang et al., 2018; Du et al., 2022a; Ngadiran et al., 2023). Due to the extremely high economic value and strong market demand for agarwood, artificial induction methods have developed accordingly. Early physical methods involved using different tools to damage trees, which were simple and cost-effective, but required a significant amount of labor and time, resulting in low yields (Azren et al., 2018; Wang et al., 2018; Tan et al., 2019; Ngadiran et al., 2023). Later, chemical and biological methods were introduced, which involved creating wounds on trees and injecting inducers in different ways (Chen et al., 2017; Azren et al., 2018; Ngadiran et al., 2023). Chemical methods can quickly produce high-quality agarwood, there are some common compounds used to trigger the formation of agarwood, *viz.,* jasmonic acid, sulfuric acid, acetic acid, and alcohol, but the chemicals injected into the trees may be released back into the environment, causing water and soil pollution, causing safety issues (Zhang et al., 2012; Liu et al., 2013; Wang et al., 2018; Du et al., 2022a; Ngadiran et al., 2023). The biological induction method most commonly reported by fungi as induction factors, and fungal induction is considered effective; in recent years, some research has also been conducted on bacteria as induction factors (Wang et al., 2018; Fitriasari et al., 2020; Du et al., 2022a; Ngadiran et al., 2023). The use of bacteria as inducers has not been extensively studied; the methods and technologies are still immature, and only a few bacteria have been reported to promote the production of some characteristic compounds in agarwood, e.g., *Bacillus* sp., *Bacillus pumillus*, and *Pseudomonas* sp. (Fitriasari et al., 2020). Fungi which is environmentally friendly and can produce high-quality agarwood resins similar to wild agarwood, although the results may vary depending on the fungal strain used (Mohamed et al., 2014; Mohammed et al., 2021; Du et al., 2022a; Ngadiran et al., 2023). The fungal induction method was first proposed by Tunstall in 1929 (Gibson 1977) and scientists paid more attention to it with the development of science and technology. To date, 34 fungal

genera have been used to induce agarwood production (Du et al., 2022a; Ngadiran et al., 2023), out of which, the most reported are *Fusarium*, followed by *Lasiodiplodia*, then, *Aspergillus* and *Botryosphaeria*. *Fusaruim solani*, *Cunninghamella bainieri*, and *Lasiodiplodia theobromae* are commonly reported to be used in the fungal inoculation process (Rasool & Mohamed, 2016). *Fusarium solani* was found to be the most effective fungus in inducing agarwood resin (Faizal et al. 2022).

There are two most common fungal induction methods, *viz*., the pinholes-infusion technique (PIT) (Tian et al., 2013) and the Agar-Wit technique (Liu et al., 2013). The pinhole-infusion technique involves injecting the inducer using a syringe, which is simple and easy to complete, and consumes a small amount of inducer (Tian et al., 2013). For example, Faizal et al. (2020) used a DeWalt® bore injector to drill holes and injected *Fusarium solani* inoculant into the *Gyrinops versteegii* trunk to induce resin formation. The Agar-Wit technique involves transporting the inducer using an infusion device, which is low cost, high yield, and easy to operate and is the most widely used artificial fragrance technology in agarwood-producing regions (Liu et al., 2013). For example, Zheng et al. (2019) induced the production of agarwood resin by injecting fungal inducers (*Fusarium solani* and *Lasiodiplodia theobromae*) into *Aquilaria sinensis* using the same method as Agar-Wit.

We, as a collective of researchers, are tackling the challenge of precisely screening effective fungal species. In the forest environment where agarwood-producing trees grow, hundreds or even thousands of microorganisms are on the surface and inside the trunk and bark. It is difficult to screen out effective agarwood-inducing fungi from such a large microbial library. This study is based on collective previous research and has screened some potential fungal strains for validation experiments. We also mentioned several previous publications that provide details about agarwood resin-inducing fungi (Wang et al., 2018; Zheng et al., 2019; Faizal et al., 2020; Ngadiran et al., 2023). Our research aims to support and identify the use of biological inducers to reduce and avoid adverse effects on the environment, livestock, and human health.

In this study, we selected the PIT method (Tian et al., 2013) to test the induction ability of agarwood resin from 12 selected strains. The fungi selected for this study

were isolated from different parts of one of the agarwood-producing trees, *Aquilaria sinensis,* and were selected based on previous relevant reports. However, in previous studies, parallel experiments and analyses were not conducted on multiple strains. Therefore, this study analyzed the different induction effects and important agarwood characteristic compounds of the selected fungal strains. *Fusaruim* species have been used in the inoculation process (Akhsan et al., 2015; Faizal et al., 2017, 2020; Subasinghe et al., 2019; Zheng et al., 2019); *Fusarium solani* is considered the most effective fungus in promoting the production of agarwood resin (Turjaman et al., 2016; Herath & Jinendra 2023), accompanied by the production of characteristic agarwood compounds (Faizal et al., 2020).

This study used fungal inoculation to induce agarwood production, addressing a key research gap: the lack of strains that can promote the production of agarwood that meets medicinal standards in a short time. This variability hampers the large-scale and reliable production of agarwood. The main objectives are to identify a fungal strain that consistently and efficiently promotes agarwood resin formation while ensuring the product meets medicinal standards, a task that is urgently needed in the field. The study highlights the biological significance of developing scalable, efficient methods for sustainable agarwood production by focusing on these objectives. Understanding the interactions between fungal strains and host trees is essential for improving induction techniques. The detailed processes, data, and analyses emphasize the potential impact on future agarwood cultivation.

4.2 Research Methodology

4.2.1 Pre-Experiment - Screening and Identifying the Most Effective Fungal Strain for Agarwood Resin Induction

4.2.1.1 Isolation and identification of the agarwood associated fungal strains

Twelve fungal strains were isolated from the agarwood resin parts, healthy leaves, and branches of agarwood-producing trees (*Aquilaria sinensis*) in Yunnan and Guangdong provinces (Table 4.1). The strains were isolated according to Du et al. (2022b),

and pure cultures were used for genomic DNA extraction and deposited at Guizhou Medical University Culture Collection (GMBCC) in Guiyang, China.

These fungal strains were identified according to the description of Du et al. (2022b). Fungal mycelia on potato dextrose agar (PDA) aged one week were used to extract DNA and amplify polymerase chain reaction (PCR). The PCR products were purified and sequenced by Sangon Biotech Co., Kunming, China. The quality or chromatogram of the internal transcribed spacers (ITS) sequences obtained in the present study was checked in BioEdit v.7.2.6.1 (Hall, 1999), and the forward and reverse sequences were spliced with Geneious 9.1.8 (Kearse et al., 2012). The spliced sequences were blasted in GenBank (https://www.ncbi.nlm.nih.gov) for preliminary identification (Table 4.1). All newly generated sequences in this study were deposited to GenBank (https://www.ncbi.nlm.nih.gov) (Table 4.1).

Table 4.1 Collection site information and ITS Blast results of 12 *Aquilaria sinensis* associated fungi used in the present study

Fungal isolate	Collection site	Collection date	Plant Tissue (isolation part)	Culture collection number	GenBank accession number	BLAST search results				
						Closest match	Isolate number	GenBank accession number	Identity	Query coverage
GDA-2A9	Guangdong	October 2020	Agarwood resin	GMBCC1190	PQ573370	*Lasiodiplodia pseudotheobromae*	FV-13 69 DSM 56A	OR398670	99.94%	90%
GDA-3A25	Guangdong	October 2020	Agarwood resin	GMBCC1191	PQ573371	*Fusarium proliferatum*	KT207283	KT207283	100%	96%
GDA-3A26	Guangdong	October 2020	Agarwood resin	GMBCC1192	PQ573372	*Trichoderma harzianum*	SF_752	MT530028	100%	95%
GDA-3B17	Guangdong	October 2020	Agarwood resin	GMBCC1193	PQ573373	*Daldinia eschscholtzii*	NQU283	MN368169	99.96%	97%
GDA-HC01	Guangdong	June 2022	Agarwood resin	GMBCC1194	PQ573374	*Fusarium solani*	YZM1	KY245947	99.91%	92%
YNA-1B2	Yunnan	September 2021	Agarwood resin	GMBCC1195	PQ573375	*Botryosphaeria fusispora*	GBLZ17BO-001	MN540670	100%	90%
YNA-1C1	Yunnan	September 2021	Agarwood resin	GMBCC1196	PQ573376	*Trichoderma harzianum*	NTOU 4300	MZ423061	99.94%	95%
YNA-1C2	Yunnan	September 2021	Agarwood resin	GMBCC1197	PQ573377	*Lasiodiplodia theobromae*	CDFA145	KY229166	99.92%	97%
YNA-2C5	Yunnan	September 2021	Agarwood resin	GMBCC1199	PQ573378	*Trichoderma koningiopsis*	DAOM 233971	EU280131	99.88%	96%
YNA-A18	Yunnan	November 2020	Healthy leaf	GMBCC1200	PQ573379	*Aspergillus niger*	HC2	OR534536	100%	90%
YNA-A73	Yunnan	November 2020	Healthy leaf	GMBCC1201	PQ573380	*Aspergillus niger*	S2596	MG590099	100%	90%
YNA-D3	Yunnan	November 2020	Healthy branch	GMBCC1202	PQ573381	*Lasiodiplodia pseudotheobromae*	B0271	KM006441	100%	94%

4.2.1.2 Agarwood-producing tree

Thirteen healthy eight-year-old agarwood-producing *Aquilaria sinensis* trees were selected from agarwood plantations (Yunnan Yuanjiang Qinan Chenxiang Agricultural Technology Development Co., Ltd.) in Yunnan Province, China. Four healthy branches, each with a diameter ranging from 3–5 cm (from the first branch to the central branch), were selected from each tree for experimentation (modified from Faizal et al., 2020).

4.2.1.3 Determination of agarwood production

1. Preparation of fungal fermentation broth

Fungal fermentation broths were made according to the method described by Tibpromma et al. (2021). Fungal cultures were divided into small pieces (0.4 cm diam.) by sterilized straws; five pieces were placed in a conical flask containing 100 mL of sterile malt extract medium broth (MEB) (autoclaved at 121 °C, 20 mins and kept at room temperature 25±2 °C to cool it down). The conical flask mouth was sealed with cotton, and then the cotton was covered with tin foil to avoid contamination by other microorganisms. Finally, the conical flasks were incubated on a shaker (120 rpm, 28 °C) for five days in the darkness. Five days later, the mycelium blocks in the flasks were stirred by the sterilized glass rod and filtered by a filter to obtain fungal fermentation broth.

2. Inoculation method of fungal fermentation broth

This study used pinhole-infusion technology (PIT) to induce the production of agarwood (Tian et al., 2013). Thirteen healthy trees were selected for the experiment, with 12 trees as the experimental group labeled in order: A, B, C, D, E, F, G, H, I, J, K, and L. The 13th tree was the control group, marked as CK. Four branches are selected in each tree, and three holes (0.5 cm wide and 1–3 cm deep) are drilled on each selected branch using a disinfection drill. Three holes on each branch are evenly spaced (5 cm) and arranged in a straight line. In the experimental group, 12 different fungal fermentation broths were inoculated with 1 mL, thrice per hole, using sterile syringes for the experiment group (A-L). The control group was only drilled holes and was not inoculated with fermentation broth. Later, plastic films were used to seal the holes to avoid contamination by other microorganisms.

3. Agarwood analysis

1) The physical properties of agarwood

The total duration of this experiment was 12 months; one branch of each tree was cut off and observed every three months. The formation area and color of agarwood resin are crucial indicators of its quality. Typically, a larger formation area and a darker resin color suggest superior quality. The measurement and comparison of the formation area of agarwood resin forms were meticulously checked with a ruler tool, underscoring the precision and accuracy of the assessment. In contrast, agarwood resin's color observation and contrast were carried out through active visual engagement.

2) Detection of the content of three chromones in agarwood

Twelve-month-old agarwood samples were collected from each tree. All agarwood resins from each sample were cut into small pieces and mixed to make it homogenize, and then 0.2 g of each sample was selected for testing. The content of agarotetrol, 2-[2-(4-methoxyphenyl)ethyl]chromone (2-MC), and 2-(2-phenylethyl) chromone (2-PC) was detected by high-performance liquid chromatography (HPLC) following the established protocol (National Pharmacopoeia Committee, 2020; Quality Grade of Agarwood, 2017). According to the National Pharmacopoeia Committee (2020), a content of agarotetrol greater than 0.10% indicates that agarwood has medicinal value.

3) Identification of the fungal strains occurring during the agarwood production

To confirm whether the original inoculated strain induced the fungi from agarwood samples, each sample collected every three months was re-isolated. The isolation and identification methods were followed according to the methodology described in 2.1.1. ITS sequences were used to compare with the sequences of the original strains separately.

4.2.2 Extended Experiment - Agarwood Production by Fusarium Solani (GDA-HC01)

4.2.2.1 Source of fungal strains

The best strains identified and screened during the pre-experiment were used for further experiment expansion.

4.2.2.2 Agarwood-producing tree

The artificial plantation of agarwood-producing trees was the same as 2.1.2. The experiment was conducted on 8-year-old trees with a diameter of 15–20 cm (nine trees), which were healthy (no pests and diseases) and in good growth conditions in a tropical monsoon climate. According to the plantation, in 8-year-old trees, a diameter of 15–20 cm is a common size to conduct the experiment.

4.2.2.3 Determination of agarwood production

1. Preparation of fungal fermentation broth

The fungal fermentation broths were the same as mentioned in section 2.1.3.1., prepared according to the method described by Tibpromma et al. (2021). After five days of cultivation; they were obtained.

2. Inoculation method of fungal fermentation broth

Two standard fungal inoculation methods were selected as a comparison, aiming to find a fast and efficient way to induce agarwood for six months. The two methods used in this experiment were the pinholes-infusion technique (PIT) (Tian et al., 2013) and the Agar-Wit technique (Liu et al., 2013). Nine trees were divided into three groups (three trees in each group) and tested in the PIT, Agar-Wit, and control groups. Each tree was drilled with three holes (0.5 cm diam., 6–8 cm deep) using a sterilized electric drill.

In the PIT group, each tree was arranged in a vertical straight line, with the first hole at a height of 50 cm above the ground, and the distance between each hole is 8 cm. Fungal fermentation broth was injected into the holes by using sterile syringes, injecting 1 mL into each hole three times (total of 3 mL/hole) and plastic films were used to seal the holes to avoid contamination by other microorganisms.

In the Agar-Wit group, the three holes on each tree were arranged in a vertical spiral pattern, with the first hole located 30 cm above the ground and a distance of 10 cm between each hole. The Agar-Wit groups were injected with fungal fermentation broth into the holes using infusion bags and tubes. First, 500 mL of fermentation broth was put in each infusion bag, and each infusion bag was equipped with three infusion tubes. Then the infusion tubes were inserted into the holes respectively. Finally, the flow rate was adjusted to be input into the tree trunk within 3–5 days. Finally, plastic films were used to

seal the holes to avoid contamination by other microorganisms.

The control groups were only drilled holes and were not inoculated with fermentation broth. Plastic films were used to seal the holes to avoid contamination by other microorganisms.

3. Agarwood analysis

The inspection method for inoculation results was the same as in section 2.1.3.3. The results were checked after six months.

4. Statistical Analysis

To evaluate the effect of different treatments on agarotetrol, one-way ANOVA was used. This experiment set up three treatment groups: The Agar-Wit, PIT, and the control. The analysis of variance was conducted using IBM SPSS v. 27 statistical software, with a significance level set at 0.05. Use one-way analysis of variance to test the differences in agarotetrol content between groups. At the same time, to visually demonstrate the impact of different processing methods on agarotetrol content, this study used IBM SPSS v. 27 statistical software to draw box plots.

5. Identification of the fungal strains occurring during the agarwood production

To confirm whether the original inoculated strain induced the fungi from agarwood samples, each sample collected every six months was re-isolated. The isolation and identification methods followed the methodology described in section 2.1.1. ITS sequences were used to compare with the sequences of the original strains, separately.

4.3 Results

4.3.1 Isolation and Identification Results of the Agarwood Associated Fungal Strains

Twelve fungi strains isolated from *Aquilaria sinensis* are listed in Table 4.1 with relevant information (collection site, date, and isolation part). The preliminary identification based on ITS BLAST search in NCBI resulted in *Aspergillus niger* Tiegh. (Identity: 100%, YNA-A73 and 100%, YNA-A18), *Botryosphaeria fusispora*

Boonmee, Jian K. Liu & K.D. Hyde (identity: 100%, YNA-1B2), *Daldinia eschscholtzii* (Ehrenb.) Rehm (Identity: 99.66%, GDA-3B17), *Fusarium proliferatum* (Matsush.) Nirenberg (Identity: 100%, GDA-3A25), *F. solani* (Mart.) Sacc. (Identity: 99.81%, GDA-HC01), *Lasiodiplodia pseudotheobromae* A.J.L. Phillips, A. Alves & Crous (Identity: 99.64%, GDA-2A9 and identity: 100%, YNA-D3), *L. theobromae* (Pat.) Griffon & Maubl. (Identity: 99.82%, YNA-1C2), *Trichoderma harzianum* Rifai (identity: 100%, GDA-3A26 and 99.84%, YNA-1C1) and *T. koningiopsis* Samuels, Carm. Suárez & H.C. Evans (identity: 99.68%, YNA-2C5). In addition, YNA-D3 and GDA-2A9 were identified as *Lasiodiplodia pseudotheobromae*; even though they were isolated from different host parts (YNA-D3 from a healthy branch while GDA-2A9 from agarwood resin part).

4.3.2 Analysis of Induction Results of 12 Fungal Strains on Agarwood Resin (Pre-Experiment)

Notably, previous studies revealed that fungal infections accelerate the process of agarwood formation when compared to the traditional method of inducing agarwood, and these fungi were isolated from agarwood resin or agarwood-producing trees (Ngadiran et al., 2023). Therefore, this study selected 12 fungal strains isolated from *Aquilaria sinensis* to investigate their agarwood resin formation potential.

After 12 months, 12 *Aquilaria sinensis* trees inoculated by fermentation broths of 12 fungal strains formed black-brown layers of agarwood resin around the hole. All groups in the pre-experiment showed their ability to induce agarwood resins, including the control group; the results are meticulously recorded in Table 4.2 and visually represented in Figure 4.1. According to the comparison of the colors of the samples collected in the 12th month, the 12 groups are arrayed in descending order from darken to clarity pigment: G > A > B > C > F > I > J > D > K >L >H > E. There are significant differences among them (Figure 4.1).

Group G exhibited the most effective induction effect (Table 4.2 and Figure 4.1). Its average growth width expanded to 8.5 cm by the third month, demonstrating a continuous increase over time, ultimately reaching 13.5 cm by the 12th month. Moreover, by the 12th month of compound testing, group G exhibited significantly

medicinally accepted agarotetrol level and other two chromones (2-MC and 2-PC) content compared to the other groups. Specifically, its agarotetrol content was 37.7 times higher than that of the control group, and its 2-MC and 2-PC content was 3.8 times higher than that of the control group. Notably, the experimental observations for group G indicated the absence of wound healing or death of central tissue (around the hole). The original strain was successfully obtained during the re-isolation.

Regarding formation area and compound content (Table 4.2, Figure 4.1 and 4.2), groups A and H showed more significant results than the other ten groups (including the control group). Neither group A nor group H manifested any discernible signs of wound healing; instead, the central regions exhibited pronounced desiccation and necrosis. Particularly, the observation of group H was noteworthy, wherein the area formed by 12 months witnessed a substantial reduction compared to the measurements taken in the ninth month.

The induction effects of the other six groups (B, C, D, E, J, and L) were not significantly different from those of the control group. All six experimental groups had wounds that healed over time, and three groups showed wound healing and central tissue death (groups B, C, and E). The size of the area formed by agarwood in these groups remained unchanged or decreased over time.

In addition, groups D and L showed a mortality rate of 75% in all collections. A total of four branches were collected, of which three died. Fungal species of these two groups all belong to *Aspergillus niger*. While the other three groups (F, I, and K) did not obtain the original strains during the re-isolation.

Therefore, based on the pre-experiment results mentioned above, Group G showed significant positive results compared to other experimental groups (Table 4.2 and Figure 4.1). Therefore, Group G strain *Fusarium solani* (GDA-HC01) was selected for further agarwood induction experiments.

Table 4.2 Agarwood induction results (Pre-experiment)

Agarwood tree inoculated by fungal isolate	The 3rd month			The 6th month			The 9th month			The 12th month						
	Original strain re-isolated	Wound healing	Average width (cm)	Original strain re-isolated	Wound healing	Average width (cm)	Original strain re-isolated	Wound healing	Average width (cm)	Original strain re-isolated	Wound healing	Average width (cm)	Agarotetrol content (%)	Improvement rate	Content of 2-MC and 2-PC (%)	Improvement rate
YNA-D3 (group A)	Y	N	4.12	Y	N	4.8	Y	N	6	Y	N	6.5	0.0003%	0.4	0.0164%	0.9
YNA-1C1 (group B)	Y	Y	0.7	Y	Y	1.1	Y	Y	0.68	N	Y	0.5	0.0004%	0.5	0.0037%	0.2
GDA-2A9 (group C)	N	Y	0.36	Y	Y	1.5	Y	Y	1.1	Y	Y	0.8	0.0025%	3.6	0.0326%	1.7
YNA-A18 (group D)	Y	N	1.34	Y	Y	1.15	N	Y	0.7	N	Y	0.6	0.0009%	1.2	0.0098%	0.5
YNA-1B2 (group E)	Y	N	0.24	Dead	N	0.4	Dead	N	0.35	Dead	N	0.4	/	/	0.0043%	0.2
GDA-3A25 (group F)	N	Y	0.35	N	Y	0.3	N	Y	0.5	N	Y	0.48	0.0014%	2.0	0.0060%	0.3
GDA-HC01 (group G)	Y	N	8.5	Y	N	9.8	Y	N	12.3	Y	N	13.5	0.0267%	37.7	0.0710%	3.8
YNA-1C2 (group H)	Y	N	3.5	Y	N	4.5	Y	N	4.8	Y	N	2.7	0.0040%	5.6	0.0203%	1.1
YNA-2C5 (group I)	N	N	0.22	N	N	0.55	N	N	1.2	Y	Y	0.8	0.0012%	1.7	0.0078%	0.4
GDA-3A26 (group J)	N	Y	0.23	Y	Y	0.4	N	N	1.1	N	N	0.78	0.0027%	3.8	0.0169%	0.9
GDA-3B17 (group K)	N	N	0.18	N	N	0.2	N	N	1.5	N	N	0.23	0.0013%	1.8	0.0040%	0.2
YNA-A73 (group L)	Dead	N	0.1	Dead	N	0.18	Dead	N	0.16	N	N	1.6	0.0067%	9.4	0.0083%	0.4
CK	/	N	0.34	/	N	0.36	/	N	0.41	/	N	0.46	0.0007%	1.0	0.0189%	1.0

Note "Y" = Yes, "N" = No, "/" = Inapplicable, "CK" = Control group, "Dead" refers to this sample that had already died when it was collected, Average width = The average width that extends longitudinally along the xylem (sum of the upper and lower sides of the hole).

Note Ck–1,–2 and –3, Control groups. A–L, Group A–L (White is the normal color of the xylem, while brown to dark brown is the agarwood resin part).

Figure 4.1 Induction results of agarwood resin, after one year of inoculation with 12 different fungal fermentation broths

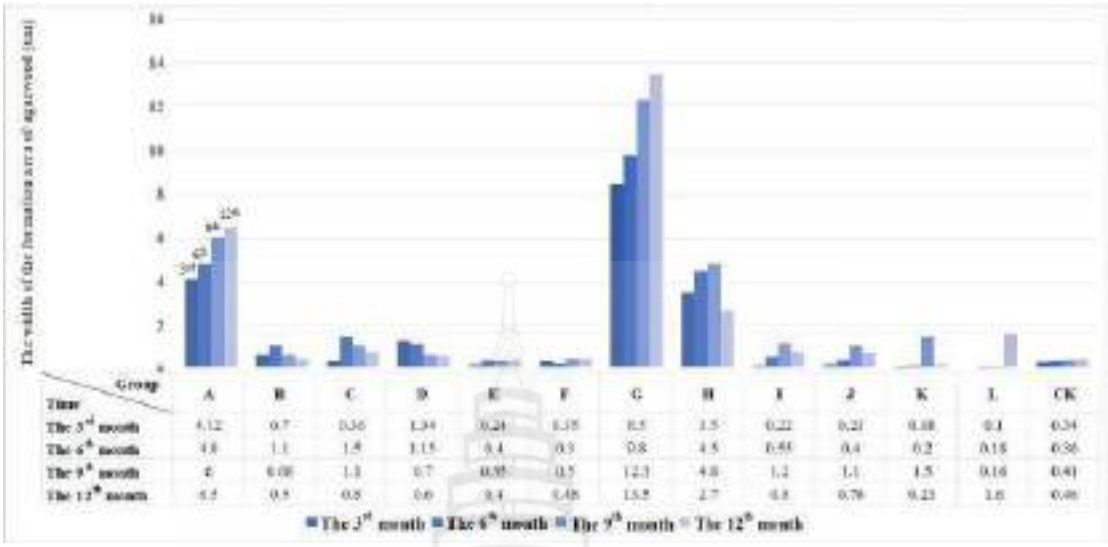


Figure 4.2 Comparison of the agarwood resin formation area width collected in 12 groups and control groups at different periods

4.3.3 Analysis of Agarwood Resin Induction Results of *Fusarium Solani* (GDA-HC01) (Extended Experiment)

The pre-experiment results showed that group G (*F. solani* GDA-HC01) had the best effect, as it had a darker, wider resin area and higher chromone content compared to other experimental groups (Table 4.2 and Figure 4.1); therefore, this strain was selected as the best strain for the extended experiment.

According to the six-month results, the growth width of agarwood infused with infusion bags in Agar-Wit is 2.2 times larger than that in PIT and 6.6 times larger than that in the control group (Table 4.3, Figure 4.3). Regarding the colors, Figure 4.3-B (control group) appears black, a color that only forms after the tissue necrosis. In contrast, Figure 4.3-C (PIT) displayed brown resin, while Figure 4.3-D (Agar-Wit) showed brown to black, brown resin. The darker color of Agar-Wit's resin compared to PIT's indicated higher quality. At the same time, in terms of texture, the resin content of PIT was relatively low, the oil lines were sparse, the oil distribution was uneven, the hand feel was light, it felt slightly rough, the woody feeling was more obvious, and the fragrance was weak and not long-lasting when burned; while, the Agar-Wit had a higher resin content, especially in the central part, with abundant internal oil and clear and full oil lines, a harder texture, a heavier hand feel, and a smoother texture; when burned,

the smoke was light and soft and lasted longer.

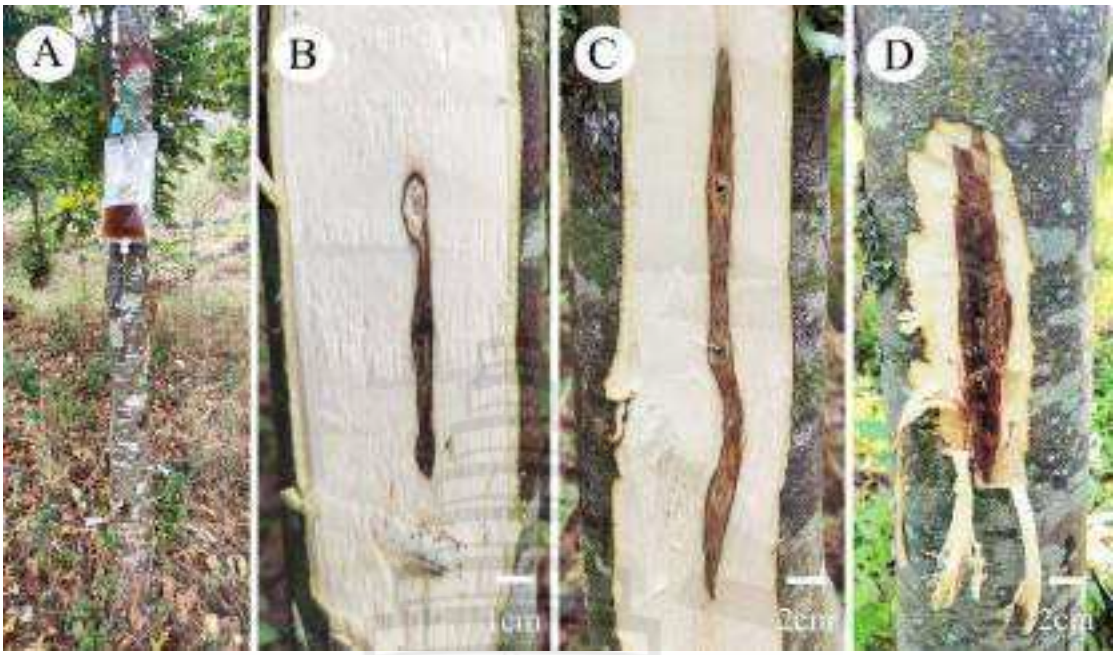
The agarotetrol content in Agar-Wit is 3.4 times that of PIT and 216.6 times that of the control group, while the 2-MC and 2-PC content of Agar-Wit is 1.5 times that of PIT and 40.4 times that of the control group (Table 4.3). The structures of agarotetrol, 2-MC, and 2-PC are shown in Figure 4.4, and the peak plot of High-performance liquid chromatography (HPLC) is shown in Figure 4.5.

The statistical analysis results showed that there is a significant difference in the effect of different treatment methods on the content of agarotetrol ($F = 1220.2$, $p = 1.37 \times 10^{-14}$, far less than 0.05). The specific analysis is as follows:

Agar-Wit has the highest content of agarotetrol, with an average of 0.140%. The agarotetrol in this treatment group was significantly higher than that in other groups ($p<0.001$), indicating that the Agar-Wit method has the strongest promoting effect on the synthesis of agarotetrol. PIT: The agarotetrol content was 0.040%, second only to the Agar-Wit method and significantly higher than the control group ($p<0.001$). This indicates that the PIT method can also promote the synthesis of agarotetrol to a certain extent, but its effect is not as good as the Agar-Wit method. Control: Agarotetrol has the lowest content, averaging only 0.001%, which is almost negligible. The agarotetrol content in the control group was significantly lower than that in the treatment group ($p<0.001$), indicating that the natural generation of agarwood resin is extremely limited under no treatment conditions. In summary, the Agar-Wit method has the strongest promoting effect on the synthesis of agarotetrol; in contrast, the PIT method, although less effective, is still significantly higher than the control group, indicating that it also has a certain effect on increasing the content of agarwood resin. The box plot (Figure 4.6) further illustrates the significant differences among the three groups: the data distribution of the Agar-Wit group is completely higher than the other two groups, followed by the PIT group, and the Control group has the lowest and tighter distribution. These results indicate that there are significant differences in the induction effect of different fungal treatment methods on agarotetrol, with the Agar-Wit method being the most effective.

In addition, the agarotetrol content in Agar-Wit exceeds the National Pharmacopoeia Committee (2020) requirement (0.1%) by 1.4 times. From this, it can be seen that strain *F. solani* (GDA-HC01) can quickly induce agarwood through Agar-

Wit within six months and meet the medicinally accepted agarotetrol level.



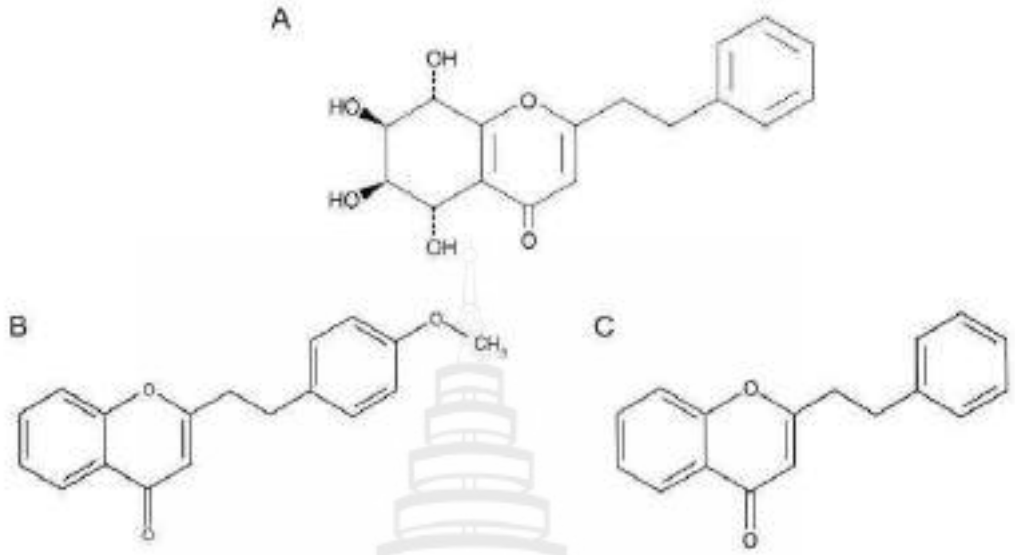
Note A, Field experiment site in the plantation. B, Control group (the black part represents decaying tissue). C, PIT. D, Agar-Wit.

Figure 4.3 The results of the extended experiment in the sixth month. (A) Field experiment site in the plantation

Table 4.3 Comparison of agarwood induction results of different methods after six months

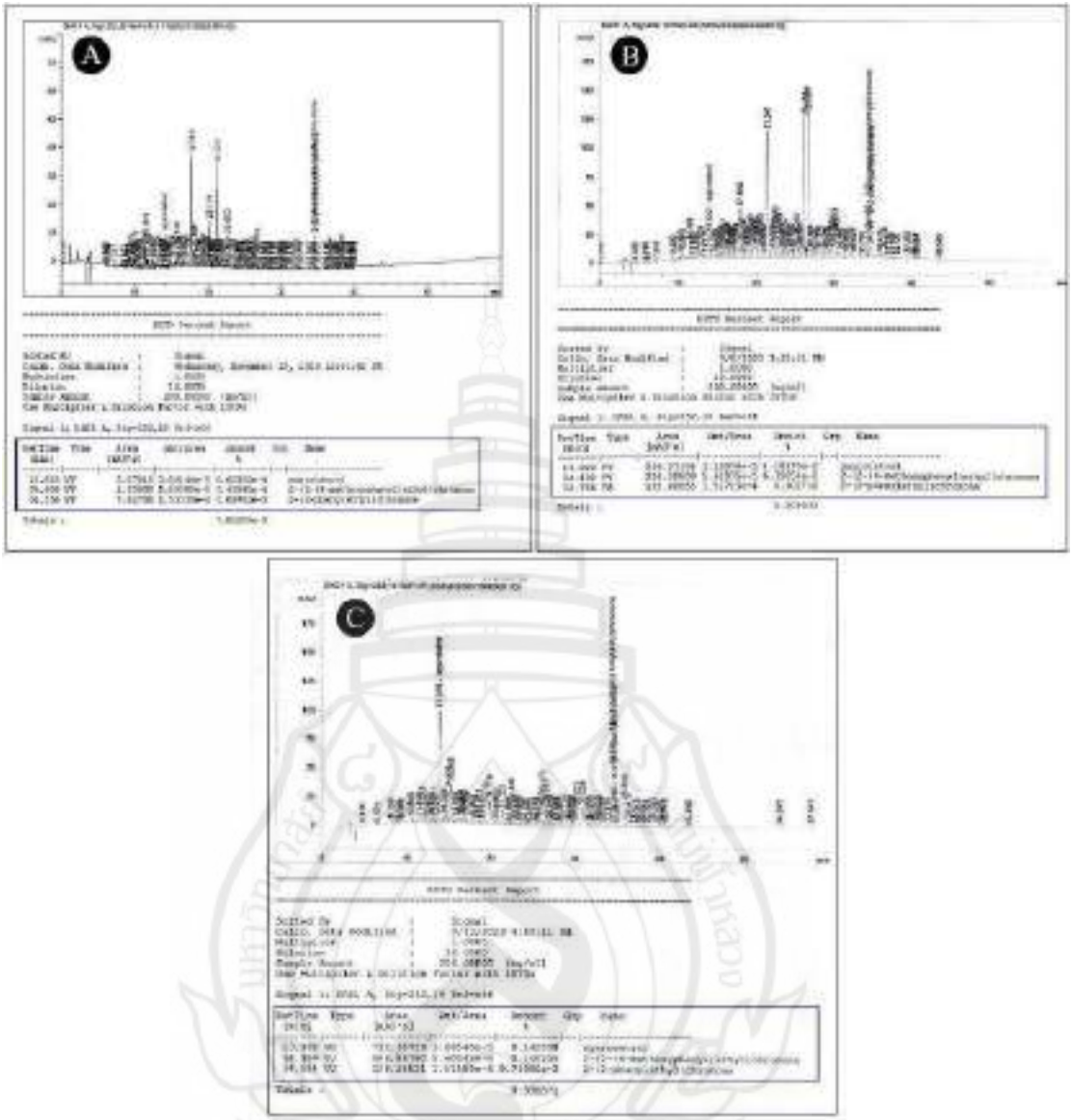
Methods	Original strain re-isolated	Wound healing	Average width (cm)	Agarotetrol content (%)	Improvement rate	Content of 2-MC and 2-PC (%)	Improvement rate
Agar-Wit	Y	N	3.3	0.14%	216.6	0.26%	40.4
PIT	Y	N	1.5	0.04%	63.4	0.17%	26.2
Control	/	N	0.5	0.001%	1.0	0.01%	1.0

Note "Y" = Yes, "N" = No, "/" = Inapplicable, Average width = Horizontal expansion average width.



Note (A) Agarotetrol. (B) 2-[2-(4-methoxyphenyl)ethyl]chromone (2-MC). (C) 2-(2-phenylethyl)chromone (2-PC).

Figure 4.4 Structures of agarwood chromones that were obtained in this study



Note (A) Control group. (B) PIT. (C) Agar-Wit. The blue box indicates the content of three main compounds.

Figure 4.5 High-performance liquid chromatography (HPLC) results of agarwood resin induced by three treatments

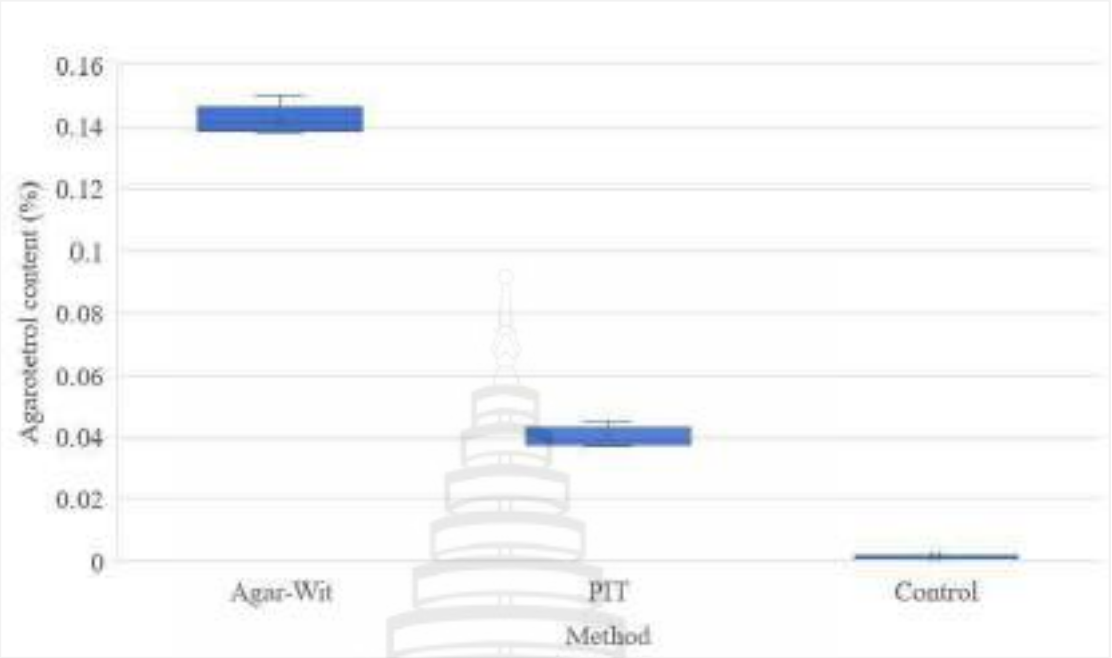


Figure 4.6 The agarotetrol content under different treatments

4.3.4 Analysis of Fungal Strains in the Induction Process of Agarwood

In the results of strain re-isolation, all re-isolated strains were compared with the original strain in terms of bases, and the results showed that, except for the inevitable impact of peaks at both ends of the ITS gene, most were not different from the original strain. Some strains had a 1 or 2 bp base difference, which is less than 0.5%. Except for the original strains, other strains belonging to 20 genera were also isolated *viz., Acrocalymma* Alcorn & J.A.G. Irwin, *Alternaria* Nees, *Aspergillus*, *Camarosporium* Schulzer, *Colletotrichum*, *Crassiparies* M. Matsum., K. Hiray. & Kaz. Tanaka, *Daldinia* Ces. & De Not., *Deniquelata* Ariyaw. & K.D. Hyde, *Diaporthe* Nitschke, *Fusarium*, *Hypoxylon* Bull., *Lasiodiplodia*, *Medicopsis* Gruyter, Verkley & Crous, *Montagnula* Berl., *Mucor* P. Micheli, *Neoscytalidium* Crous & Slippers, *Penicillium* Link, *Phaeoacremonium* W. Gams, Crous & M.J. Wingf., *Pseudofusicoccum* Mohali, Slippers & M.J. Wingf. and *Xylaria*. *Lasiodiplodia* was the most prominent genus, accounting for 50% of all the above.

4.4 Discussion

This study conducted pre- and extended experiments to screen the best fungal strain and explore the most suitable inoculation method for inducing agarwood resin formation.

In the pre-experiment, 12 strains were selected to undergo PIT induction on the small branches of 12 trees. The pre-experiment results indicated that all available strains can induce agarwood formation, but their effects vary greatly. This PIT causes minimal damage to the host and uses less inoculum, so it is the most appropriate method for inoculation experiments on small branches. In this experiment, an agarwood-associated fungal strain (*Fusarium solani* GDA-HC01) showed the best result: an increase in the formation area of agarwood resin over time, and no signs of wound healing or tissue death around the wound were observed. Therefore, this strain was selected for the extended experiments on tree trunks, and the results showed that after only six months, the content of agarotetrol in agarwood resin induced by the *F. solani* (GDA-HC01) was 1.4 times higher than the required standard.

Species of *Fusarium* are commonly reported as endophytic fungi or agarwood resin-associated fungi in agarwood-producing trees (Chhipa et al., 2017; Azren et al., 2018; Du et al., 2022a; Ngadiran et al., 2023). *Fusarium solani* has been proven to be an effective fungus in inducing the formation of agarwood resin in previous studies. For example, Faizal et al. (2020) reported that *Gyrinops versteegii* (Gilg.) Domke produced a large area of agarwood after being inoculated with a fungal solution of *F. solani* (strains GSL1 and GSL2) for three months, while the study did not detect the content of agarotetrol. In previous studies, Chen et al. (2018) reported that the content of agarotetrol induced by *Rigidoporus vinctus* (Berk.) Ryvarden could meet the medicinal standards in the sixth month. This study reports for the first time that qualified agarotetrol can be detected on induced wood after six months of inoculation with *F. solani* (GDA-HC01) on *A. sinensis*. These pieces of evidence indicate that this strain has a high potential in inducing agarwood resin formation and is expected to be developed into a highly efficient, low-cost, pollution-free, and environmentally friendly fungal inducer.

In addition, both group A (*Lasiodiplodia pseudotheobromae* strain YNA-D3) and group H (*L. theobromae* strain YNA-1C2) were able to significantly induce the production of agarwood resin; but both showed signs of central tissue necrosis, with group H being more severe. *Lasiodiplodia pseudotheobromae* was first reported to have the ability to induce agarwood production in this study. This may be worth further research.

Additionally, in groups F (*Fusarium proliferatum* strain GDA-3A11), I (*Trichoderma koningiopsis* strain YNA-2C5), and K (*Daldinia eschscholtzii* strain GDA-3B13), original strains were not obtained during re-isolations. The possible reason could be that these three strains could not settle in *A. sinensis* trees. This might be because those fungi are related to the inherent characteristics of the strain, host, temperature, humidity, and other factors. Therefore, further research is needed to explore why these three strains cannot settle on *A. sinensis* trees to induce agarwood resin.

Moreover, in this experiment, four experimental groups (groups B, C, D, and J) showed healing of tree wounds, and two groups (groups B and C) showed healing of tree wounds and central tissue death. These two situations produced small resin regions and did not accumulate more resins over time, resulting in gradual wound healing and less damage to the tree. Groups A and H experienced severe central tissue death without healing, causing certain damage to the tree, while E and L groups had a mortality rate of up to 75% for tree branches. However, group G did not show any sound healing or central tissue death; over time, it promoted the formation of more agarwood resin. Therefore, this study indicates that some strains (from groups B, C, D, and J) that have no effect on the tree or cause too weak damage have minimal damage to the tree, making it easy for the tree to produce callus tissue for wound healing. The strains (from groups A, E, H, and L) that cause too serious damage to the tree will cause the tree to die or wither around the inoculation hole, so neither of these strains is suitable for inducing agarwood production.

In the extended experiment, two methods *viz.,* PIT and Agar-Wit were used to explore the suitable methods for fungal induction of agarwood. After six months, PIT significantly promoted the production of agarwood resin compared to the control group, although the agarotetrol content did not meet the required standard. In contrast, the

Agar-Wit method not only significantly enhanced agarwood resin formation but also resulted in agarotetrol amount that meets the medicinally accepted agarotetrol level. This may be because Agar-Wit can inject a large amount of fungal fermentation broth (500 mL/tree) simultaneously, and a large amount of fungal fermentation broth is input into the lower base of the tree trunk, facilitating the colonization of the fermentation broth. Then, through transpiration, it continuously infects and induces the trees to accelerate the formation of a large amount of agarwood resin. However, the volume content of the fermentation broth used by Agar-Wit is relatively high, and further experiments are needed to determine the most suitable volume of fermentation broth for inoculation. In addition, using fermentation broth with different concentration gradients to determine the optimal concentration for agarwood induction is also a worthy topic for future research. Subsequent research should further focus on exploring other methods of fungal agent production to reduce costs, making it easier for pollution-free fungal inducers to be promoted and used in the market, and promoting sustainable development of the green economy.

The results of strain re-isolation showed that *Lasiodiplodia* is the most prominent genus except for the original strains. These fungi may contribute to the formation of agarwood resin, which is one of the many factors.

Our research has revealed significant differences in the induction results of the 12 strains through pre-experiments. These findings are closely related to the interactions between fungi and plants. The effects vary depending on the strain, and the difference in induction effect may be due to the different secondary metabolic pathways of different strains. These pathways produce different types and contents of secondary metabolites during growth, which play a crucial role in interacting with fungi and host plants. For strains with good induction effects, the secondary metabolites produced may be more conducive to activating genes related to agarwood formation in the host plant. The formation mechanism of agarwood is currently unclear and presents an exciting opportunity for further research. The data and strains provided in this study can assist subsequent research and fuel curiosity in this field.

The advantage of this study is the identification of an effective strain capable of inducing agarwood resin formation, which achieved significant results within six months. *Lasiodiplodia pseudotheobromae* was first reported to have the ability to

induce agarwood production in this study. However, some strains didn't have the ability to colonize on trees (*Fusarium proliferatum* strain GDA-3A11, *Daldinia eschscholtzii* strain GDA-3B13, and *Trichoderma koningiopsis* strain YNA-2C5), while, some strains caused severe tissue damage (*Aspergillus niger* strain YNA-A73 and *Botryosphaeria fusispora* strain YNA-1B2), restricting their applicability. Although the Agar-Wit method is applicable in this study, further research is needed to optimize inoculation volume and concentration to maximize efficiency and reduce costs.

The significance of this study lies in the potential for utilizing *Fusarium solani* and other strains for fungal induction. This approach can significantly shorten the formation cycle of agarwood and boost its yield while reducing dependence on chemical agents in production, thereby reducing environmental pollution and protecting soil microbial communities. To mitigate damage to the ecological environment, we can develop low-damage induction techniques and precise inoculation techniques when promoting the use of these strains in agarwood production. These technical techniques can improve the effective interaction between strains and agarwood trees by controlling the depth, dosage, and location of inoculation while reducing negative impacts on trees and the surrounding environment. Moreover, the application of modern biotechnology, such as gene editing, can enable strains to more accurately target specific tissues or cells within the agarwood-producing tree, thereby enhancing the induction efficiency of agarwood while reducing the risk of strain spread in the environment. To ensure the sustainability of these methods, it is crucial to stress the importance of regularly monitoring soil, air, and water quality during fungal inoculation. This will prevent strain spread or negative impacts on soil microbial communities. If necessary, soil disinfection or fungal control treatment can be carried out to maintain the stability of the surrounding ecosystem. At the same time, a corresponding ecological management system should be established, and strict operational norms and standards should be formulated. This will ensure that agarwood production does not cause excessive damage to the surrounding ecological environment, and will help us achieve sustainable production.

In this study, we successfully identified *Fusarium solani* (GDA-HC01) as an efficient fungal strain that induces agarwood resin formation, demonstrating its potential to meet and exceed medicinal standards in just six months. This discovery

provides valuable insights for optimizing fungal inoculation to achieve sustainable and efficient agarwood production; and it has the potential to develop a low-cost, environmentally friendly inducer that can be widely applied in the industry. Future research will focus on optimizing inoculation volume and fermentation broth concentration to increase agarwood yield further while reducing costs and promoting green production in the agarwood industry.

4.5 Conclusions

The innovation part of this study is the discovery of *Fusarium solani* (GDA-HC01) with good agarwood resin induction potential, which was tested on *A. sinensis* in field experiments. The fungal strain *F. solani* (GDA-HC01) is patented under patent number 7067418 (https://pss-system.cponline.cnipa.gov.cn/conventionalSearch) (Du et al., 2024c).

The conclusions are as follows:

4.5.1 *Fusarium solani* (GDA-HC01) can quickly and stably induce the formation of agarwood resin in *A. sinensis*. Within six months, the content of agarotetrol in agarwood resin can meet the medicinally accepted agarotetrol level, and it does not cause the tree's wound to heal or wither around the wound.

4.5.2 *Lasiodiplodia pseudotheobromae* (YNA-D3) and *L. theobromae* (YNA-1C2) significantly induced agarwood resin. This is the first report of *L. pseudotheobromae* that can induce agarwood production, but they cause the central tissue to wither.

4.5.3 *Aspergillus niger* (YNA-A73) and *Botryosphaeria fusispora* (YNA-1B2) showed direct withering of the tested branches, with a mortality rate of up to 75%. Therefore, we suggest that if *A. niger* and *B. fusispora* will be used to conduct relevant induction experiments on *A. sinensis* trees, it is recommended to conduct a pre-experiment on small tree branches first to avoid unnecessary and unpredictable damage to the trees.

CHAPTER 5

ENDOPHYTIC FUNGI ASSOCIATED WITH *AQUILARIA SINENSIS* (AGARWOOD) FROM CHINA SHOW ANTAGONISM AGAINST BACTERIAL AND FUNGAL PATHOGENS

5.1 Introduction

Aquilaria Lam. (Thymelaeaceae Juss.) is the main genus that can produce agarwood (Kalra & Kaushik, 2017). Agarwood, a fragrant, dark, and resinous heartwood is the most expensive non-construction wood product in the world (Azren et al., 2018; Naziz et al., 2019). In China, agarwood is used in traditional Chinese medicine, and only *A. sinensis* (Lour.) Spreng. is the main agarwood tree species cultivated in Guangdong, Guangxi, Hainan, and Yunnan Provinces (Cui et al., 2013; National Pharmacopoeia Committee, 2015; Rasool & Mohamed, 2016; Azren et al., 2018; Lv. et al., 2019). Current research on endophytic fungi associated with *A. sinensis* mainly focuses on the agarwood formation ability of the endophytic fungi (Tibpromma et al., 2021; Du et al., 2022a), and only a few of the *A. sinensis* associated endophytic fungi have been studied for antimicrobial activities via dual culture assay (Hidayat et al., 2019). In a previous study, 38 endophytic strains have been reported to have antimicrobial activities, for example, *Botryosphaeria rhodina* (Berk. & M.A. Curtis) Arx, *Cladosporium edgeworthiae* H. Zhang & Z.Y. Zhang, *Fusarium oxysporum* Schltdl., and *Guignardia mangiferae* A.J. Roy showed antimicrobial activities (Gong & Guo, 2009); and a variety of important secondary metabolites with antibacterial and antimicrobial activities have been extracted from *Nemania aquilariae* Tibpromma & Zhang Lu (Tibpromma et al., 2021). However, the microorganisms that can be inhibited by agarwood are not clear enough, thus it is necessary to continue the research on the microbial spectrum of agarwood (Wang et al., 2018).

In this study, endophytic fungi associated with agarwood isolated from different plant tissues were used to test their antagonistic abilities against three pathogenic

bacteria viz. *Erwinia amylovora* (Burrill) Winslow et al., *Pseudomonas syringae* van Hall, and *Salmonella* enterica (ex Kauffmann and Edwards) Le Minor and Popoff; and three pathogenic fungi viz. *Alternaria alternata* (Fr.) Keissl., *Botrytis cinerea* Pers., and *Penicillium digitatum* (Pers.) Sacc.

5.2 Research Methodology

5.2.1 Sample Collection and Isolation

5.2.1.1 Sample Collection

Fresh samples of *A. sinensis* were collected three times; i.e., two times in Yunnan Province (21°55′48″ N, 101°15′36″ E, in November 2020; 22°21′09″ N, 101°01′06″ E, in September 2021) and one time in Guangdong Province (21°49′48″ N, 111°40′12″ E, in December 2020). Samples from Yunnan Province are denoted YNA, while from Guangdong Province are denoted GDA. The leaves and twigs of healthy plants, and the branches and twigs with agarwood dark resin were collected. Branch cutters, knives, and saws were used to cut the samples and they were cleaned with 75% alcohol before and after use. After collection, the fresh samples were placed in a thermal insulation ice box, brought back to the laboratory, and placed in the 4°C refrigerators until the endophytic fungi are isolated.

5.2.1.2 Isolation of Endophytic Fungi

Du et al. (2022b) with some adjustments was followed for the isolation of endophytic fungi in fresh agarwood samples. The bark of fresh samples was removed and then washed under running water, transferred to a laminar flow hood and the samples were cut into small pieces (0.5 cm × 0.5 cm) by sterilized knives and blades (sterilized with 75% alcohol). The surface disinfection steps of each sample are washed in sterile water, 75% alcohol for 30 s, 2.5% sodium hypochlorite for 1 min, and 75% alcohol for 30 s, finally, samples were washed in sterile water three times, and transferred to the sterilized filter paper to absorb the water. All tools were dipped in 95% alcohol and flamed before and after use. All the steps were done in a laminar flow hood. Five sterilized small pieces were placed in each 90 mm potato dextrose agar (PDA) plate (Ampicillin was added), and incubated at 28°C for 14 days. During incubation,

plates were checked every two days and the fresh mycelia were transferred to new 60 mm PDA plates to get pure cultures. The pure cultures were used for DNA extraction. Living pure cultures were deposited in the Zhongkai University of Agriculture and Engineering Culture Collection (ZHKUCC), China.

5.2.2 Endophytic Fungi Identification

5.2.2.1 DNA Extraction, PCR Amplification and Sequencing

Ten days old fresh mycelia were used for DNA extraction using the Biospin Fungus Genomic DNA Extraction Kit–BSC14S1 (BioFlux, Hangzhou, China), following the manufacturer's instructions (Dissanayake et al., 2020). Polymerase chain reaction (PCR) was used to amplify the ITS gene (internal transcribed spacer 1, 5.8S ribosomal RNA gene and internal transcribed spacer 2), using primers ITS5/ITS4 (White et al., 1990). The PCR amplification was followed Du et al., (2021), and the total volume of PCR mixtures for amplifications was 25 μL, with 94°C: 3 min, (94°C: 30 s, 55°C: 50 s, 72°C: 90 s) × 35 cycles, 72°C: 10 min, final 4°C. Finally, PCR products were purified and sequenced by Qinke Biotech Co., Kunming, China.

5.2.2.2 Phylogenetic Analyses

Phylogenetic analyses are widely used in the identification of endophytic fungi, and the ITS gene is commonly used to primarily identify endophytic fungi to genus level (Guo et al., 2001, 2003; Ko et al., 2011; Tibpromma et al., 2018, 2022). In this study, to confirm the endophytic fungal genera, the ITS phylogenetic analyses were performed by Randomized Accelerated Maximum Likelihood (RAxML) analyses according to the parameters described in Dissanayake et al. (2020). The obtained sequences of the forward and reverse were merged in Geneious (9.1.2), and the merged sequences were subjected to BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi?PAGE_TYPE=BlastSearch, accessed on 18 September 2022). Based on the BLAST search, the closest sequences were retrieved from the aNationl Center for Biotechnology Information (NCBI) (https://www.ncbi.nlm.nih.gov/, accessed on 18 September 2022). The sequences were aligned in the online website MAFFT v.7 (https://mafft.cbrc.jp/alignment/server/, accessed on 18 September 2022) (Katoh & Standley, 2013), and automatic cutting was done in trimAl.v1.2rev59. BioEdit v. 7.0.5.2 (Hall, 1999) was used to manually combine the sequences, and subsequently, multiple sequence alignments were converted from FASTA to PHYLIP in ALTER (http://www.sing-

group.org/ALTER/, accessed on 18 September 2022) (Glez-Peña et al., 2010). The RAxML tree was run using the PHYLIP file, in RAxML-HPC BlackBox (8.2.12) (Stamatakis et al., 2008; Stamatakis 2014) on the CIPRES Science Gateway platform (https://www.phylo.org/portal2/home.action, accessed on 18 September 2022) (Miller et al., 2010), with the GTR+I+G model of evolution. The final tree was visualized in FigTree v. 1.4.2 (http://tree.bio.ed.ac.uk/software/figtree/, accessed on 18 September 2022) (Rambaut, 2012), and edited in Microsoft PowerPoint 2010. The sequences generated in this study were uploaded to NCBI (https://submit.ncbi.nlm.nih.gov/ subs/, accessed on 18 September 2022) to obtain the GenBank numbers (Table 5.1).

Table 5.1 Original code, strain name, strain number, ITS GenBank accession number, class in Ascomycota, plant tissue, collection site, and date of collection of 47 fungal strains associated with *Aquilaria sinensis* used in this study. The contents in the table are arranged according to the genus of endophytic fungi

Original Code	Strain Name	Strain Number	ITS GenBank Accession Number	Plant Tissue	Collection Site	Collection Date
Dothideomycetes						
YNA-A40	*Alternaria* sp.	ZHKUCC 22-0248	OP445267	Health leaves	Yunnan	November 2020
YNA-1B2	*Botryosphaeria* sp.	ZHKUCC 22-0249	OP450949	Agarwood resins	Yunnan	September 2021
GDA-3A20	*Corynespora* sp.	KUMCC 21-0302	OL455852	Agarwood resins	Guangdong	December 2020
GDA-3A5	*Curvularia* sp.	KUMCC 21-0287	OL455828	Agarwood resins	Guangdong	December 2020
GDA-3A9	*Curvularia* sp.	KUMCC 21-0291	OL455842	Agarwood resins	Guangdong	December 2020
GDA-1A7	*Lasiodiplodia* sp.	KUMCC 21-0224	OL548888	Agarwood resins	Guangdong	December 2020
GDA-2A9	*Lasiodiplodia* sp.	KUMCC 21-0252	OL455795	Agarwood resins	Guangdong	December 2020
GDA-2B1	*Lasiodiplodia* sp.	KUMCC 21-0254	OL455797	Agarwood resins	Guangdong	December 2020
GDA-3C2	*Lasiodiplodia* sp.	KUMCC 21-0324	OL548897	Agarwood resins	Guangdong	December 2020
YNA-1C2	*Lasiodiplodia* sp.	ZHKUCC 22-0251	OP450951	Agarwood resins	Yunnan	September 2021
YNA-D3	*Lasiodiplodia* sp.	ZHKUCC 22-0270	OP445276	Health branches	Yunnan	November 2020
YNA-1C3	*Neofusicoccum* sp.	ZHKUCC 22-0252	OP450952	Agarwood resins	Yunnan	September 2021
GDA-5A7	*Paracamarosporium* sp.	ZHKUCC 22-0247	OP439521	Health branches	Guangdong	December 2020
GDA-4C2	*Pseudopithomyces* sp.	ZHKUCC 22-0246	OP439520	Health branches	Guangdong	December 2020

Table 5.1 (continued)

Original Code	Strain Name	Strain Number	ITS GenBank Accession Number	Plant Tissue	Collection Site	Collection Date
Eurotiomycetes						
YNA-A18	*Aspergillus* sp.	ZHKUCC 22-0258	OP445263	Health leaves	Yunnan	November 2020
YNA-A41	*Aspergillus* sp.	ZHKUCC 22-0262	OP445268	Health leaves	Yunnan	November 2020
Saccharomycetes						
GDA-1B3	*Trichosporon* sp.	KUMCC 21-0230	OL455772	Agarwood resins	Guangdong	December 2020
Sordariomycetes						
GDA-2A3	*Annulohypoxylon* sp.	KUMCC 21-0246	OL455788	Agarwood resins	Guangdong	December 2020
YNA-A22	*Colletotrichum* sp.	ZHKUCC 22-0260	OP445265	Health leaves	Yunnan	November 2020
YNA-A42	*Colletotrichum* sp.	ZHKUCC 22-0263	OP445269	Health leaves	Yunnan	November 2020
YNA-A55	*Colletotrichum* sp.	ZHKUCC 22-0264	OP445270	Health leaves	Yunnan	November 2020
YNA-A60	*Colletotrichum* sp.	ZHKUCC 22-0265	OP445271	Health leaves	Yunnan	November 2020
GDA-3A11	*Daldinia* sp.	KUMCC 21-0293	OL455844	Agarwood resins	Guangdong	December 2020
YNA-A21	*Daldinia* sp.	ZHKUCC 22-0259	OP445264	Health leaves	Yunnan	November 2020
GDA-2A1	*Diaporthe* sp.	KUMCC 21-0244	OL455786	Agarwood resins	Guangdong	December 2020
GDA-2A2	*Diaporthe* sp.	KUMCC 21-0245	OL455787	Agarwood resins	Guangdong	December 2020
GDA-2C2	*Diaporthe* sp.	KUMCC 21-0271	OL455832	Agarwood resins	Guangdong	December 2020
YNA-A29	*Diaporthe* sp.	ZHKUCC 22-0261	OP445266	Health leaves	Yunnan	November 2020
YNA-C4	*Diaporthe* sp.	ZHKUCC 22-0269	OP445275	Health leaves	Yunnan	November 2020
GDA-1A2	*Fusarium* sp.	KUMCC 21-0219	OL548884	Agarwood resins	Guangdong	December 2020

Table 5.1 (continued)

Original Code	Strain Name	Strain Number	ITS GenBank Accession Number	Plant Tissue	Collection Site	Collection Date
GDA-2A8	*Fusarium* sp.	KUMCC 21-0251	OL455794	Agarwood resins	Guangdong	December 2020
GDA-2B7	*Fusarium* sp.	KUMCC 21-0260	OL455811	Agarwood resins	Guangdong	December 2020
GDA-2C9	*Fusarium* sp.	KUMCC 21-0278	OL455819	Agarwood resins	Guangdong	December 2020
GDA-2F9	*Fusarium* sp.	ZHKUCC 22-0244	OP439518	Agarwood resins	Guangdong	December 2020
GDA-3C4	*Fusarium* sp.	KUMCC 21-0326	OL548899	Agarwood resins	Guangdong	December 2020
YNA-2C10	*Fusarium* sp.	ZHKUCC 22-0253	OP450965	Agarwood resins	Yunnan	September 2021
YNA-2C3	*Fusarium* sp.	ZHKUCC 22-0254	OP450953	Agarwood resins	Yunnan	September 2021
YNA-2C6	*Fusarium* sp.	ZHKUCC 22-0256	OP450955	Agarwood resins	Yunnan	September 2021
YNA-A1	*Neopestalotiopsis* sp.	ZHKUCC 22-0257	OP445262	Health leaves	Yunnan	November 2020
GDA-2B6	*Nigrospora* sp.	KUMCC 21-0259	OL455810	Agarwood resins	Guangdong	December 2020
GDA-4C1	*Nigrospora* sp.	ZHKUCC 22-0245	OP439519	Health branches	Guangdong	December 2020
YNA-2C4	*Nigrospora* sp.	ZHKUCC 22-0255	OP450954	Agarwood resins	Yunnan	September 2021
YNA-A61	*Nigrospora* sp.	ZHKUCC 22-0266	OP445272	Health leaves	Yunnan	November 2020
YNA-A67	*Nigrospora* sp.	ZHKUCC 22-0267	OP445270	Health leaves	Yunnan	November 2020
YNA-A71	*Nigrospora* sp.	ZHKUCC 22-0268	OP445274	Health leaves	Yunnan	November 2020
YNA-1C1	*Trichoderma* sp.	ZHKUCC 22-0250	OP450949	Agarwood resins	Yunnan	September 2021
GDA-2B15	*Xylariaceae* sp.	KUMCC 21-0268	OL455829	Agarwood resins	Guangdong	December 2020

5.2.3 Pre Dual Culture Assay for Antibiosis Test (Pretest)

The ability of endophytic fungal isolates to inhibit the growth of pathogens was evaluated by the dual culture technique (Rahman et al., 2009). The six pathogens (three bacterial pathogens viz. *E. amylovora*, *P. syringae*, and *S. enterica*; and three fungal pathogens viz. *A. alternata*, *B. cinerea*, and *P. digitatum*) used in this study were obtained from the China General Microbiological Culture Collection Center (CGMCC).

The pretest is a screening test conducted before the formal test. We used 47 strains from all isolated strains for the pretest. The 47 endophytic fungi strains and six pathogenic strains (Table 5.2) were incubated at 28°C for 10 days before the test. Fungi were cultivated on PDA, while bacteria were cultivated in nutrient agar (NA). After 10 days of incubation, the fungal colonies were cut into 0.4 cm diameter discs (sterilized plastic straw) in the laminar flow cabinet, then endophytic fungi and pathogenic fungi were inoculated in the same 90 mm PDA plates, and endophytic fungi and pathogenic bacteria (bacteria scraped with 0.4 cm wide strip) were inoculated in the same 90 mm NA plates. The control was inoculated with only pathogens. All the plates were incubated at 28°C for 10 days. After 10 days, the colony growth of the test group and the control group were checked and recorded. According to the test results, we compared the colony diameters of the test group and the control group, and then endophytic fungi that can inhibit three pathogenic fungi or three pathogenic bacteria were selected. These selected strains with antagonistic activities were used for formal testing.

Table 5.2 Six pathogens were purchased from China General Microbiological Culture Collection Center (CGMCC). The PB (pathogenic bacteria) and PF (pathogenic fungi) are new codes created in this study to distinguish pathogenic bacteria and pathogenic fungi

Pathogen	New Code	Strain Name	Strain Number	Effects of Pathogens	References
Pathogenic bacteria	PB1	*Erwinia amylovora*	CGMCC 1.7276	*Erwinia amylovora* causes a destructive plant disease that endangers many host species of Rosaceae Juss. (e.g., apple, blackberry, cotoneaster, pear, pyracantha, and raspberry)	Bonn and van der Zwet (2000), Thomson (2000), Vanneste (2000), Oh and Beer (2005), Van der Zwet et al. (2012), Born et al. (2014), Piqué et al. (2015), Kharadi et al. (2021)
	PB2	*Pseudomonas syringae*	CGMCC 1.3333	*Pseudomonas syringae* mainly harms plant hosts, including fruit trees (such as apples, hazelnuts and plums) and some field crops (such as beets, cabbage, cucumbers, oats, peas, rice, tobacco, and tomatoes), which cause major economic losses	Horst (1990), Hwang et al. (2005), Kennelly et al. (2007)
	PB3	*Salmonella enterica*	CGMCC 1.10603	*Salmonella enterica* is a zoonotic pathogenic bacterium. It can cause acute gastroenteritis, and it causes other symptoms such as septicaemia, fever and/or abortion. The resistance of this pathogen to multiple antibiotics is a public threat to most Asian countries	Schwartz (1991), Rice et al. (1997), Uzzau et al. (2000), Knodler and Elfenbein (2019), Patra et al. 2021
Pathogenic fungi	PF1	*Alternaria alternata*	CGMCC 3.15535	*Alternaria alternata* is a pathogenic fungus, that infects important cash crops and lead to human and animal diseases. In the field of human diseases, *A. alternata* is considered to be one of the most important fungal allergens in the world, which are related to severe asthma and respiratory status	Twaroch et al. (2015), Woudenberg et al. (2015), Gabriel et al. (2016), Lawrence et al. (2016), Wang et al. (2020), Sánchez et al. (2022)
	PF2	*Botrytis cinerea*	CGMCC 3.3790	*Botrytis cinerea* is one of the most destructive pathogens, especially for food and fruits obtained in the field and storage room. Because the pathogen is resistant to commonly used synthetic fungicides, a number of research activities have been carried out, focusing on the development of biological control strategies for the pathogen	Abbey et al. (2019), Bolívar-Anillo et al. (2020)
	PF3	*Penicillium digitatum*	CGMCC 3.15410	*Penicillium digitatum* is a main pathogenic fungus of postharvest decay of fruits belonging to Rutaceae Juss. This high host specificity leads to the loss of citrus fruits	Poppe et al. (2003), Ghooshkhaneh et al. (2018), Costa et al. (2019)

5.2.4 Dual Culture Assay for Antibiosis Test (Formal Test)

5.2.4.1 Methods of Dual Culture Assay

The test method is similar to the pretest. According to the results of the pretest, among 47 endophytic fungi, 25 strains were able to inhibit pathogenic bacteria, 40 strains were able to inhibit pathogenic fungi, and 18 strains were able to inhibit both pathogenic fungi and bacteria. Therefore, 47 endophytes and six pathogens were incubated at 28°C for 10 days before the formal test. Fungi were incubated on PDA, while bacteria were incubated in NA.

The endophytic and pathogenic fungi grown on PDA plates were cut into small fungal discs (0.4 cm diam.) using a sterilized plastic straw in laminar. Then, the 25 selected endophytic fungal strains were inoculated with three pathogenic bacteria (0.4 cm wide strip) in the same NA plates, and each test was replicated three times (total of 25 × 3 × 3 = 225 plates). The 40 selected endophytic strains were inoculated with three pathogenic fungi in the same PDA plates, and each test was replicated three times (total of 40 × 3 × 3 = 360 plates). The pathogens were inoculated on the left of the petri dish, while the endophytic fungi were inoculated on the right by keeping a space of 6 cm between the pathogens and endophytes. Negative controls were set in the antibiosis tests of each pathogen. The control group used the same culture medium as the test group. The pathogen was inoculated on the left of the medium, while nothing was inoculated on the right. Controls were incubated under the same conditions as the test groups. After inoculation, petri dishes were incubated at 28°C for 10 days. While incubating, they were observed, photographed and the diameter of the pathogens in the test group and the control group was measured every two days.

5.2.4.2 Calculation and Analysis of Inhibition Rate

According to the test results, the data were processed and analyzed. The antibiosis effects and the degree of endophytic fungi effect on pathogens can be expressed by calculating the inhibition rate of endophytic fungi on the growth diameter of pathogens. The inhibition rate was calculated according to the method described in Gao et al. (2017) and Rajani et al. (2021), and the calculation formula used is as follows:

$$\text{Inhibition\%} = (Cd\text{-}Td)/(Cd\text{-}0.4) \times 100$$

Notes: Cd = radial growth of the pathogen in pure control culture, Td =radial growth of the pathogen in dual culture. The width of the original fungal discs and bacterial strip in this test is 0.4 cm.

5.2.4.3 Statistical Analyses

The statistical analyses of the inhibition rate were carried out in Microsoft Excel 2010. The measured data (colony diameter) were recorded in an excel table. The inhibition rate and average inhibition rate were obtained by the formula. The standard deviation (SD) reflects the dispersion degree of a data set, and the values were obtained by inserting the function (STDEV) of standard deviation into the excel table. In addition, clustered column graphs were inserted in the excel table based on the average inhibition rate and edited in Microsoft Excel 2010.

5.3 Results

5.3.1 Results of Sample Collection and Isolation

In this study, agarwood samples were collected from Guangdong and Yunnan Provinces. The fresh samples were isolated to obtain pure cultures for molecular analyses and antibiosis tests. In Table 5.1, we list the host, collection site, and other information of 47 endophytic fungi used in this study.

5.3.2 Single Gene Phylogenetic Analyses

The single-gene phylogenetic analyses were carried out by constructing an RAxML phylogenetic tree based on ITS. The RAxML analyses gave a final ML optimization likelihood value of −12,190.561600. The matrix had 567 distinct alignment patterns, with 19.72% of undetermined characters or gaps. Parameters for the GTR+I+G model of the ITS were as follows: estimated base frequencies A = 0.249972, C = 0.260278, G = 0.245555, T = 0.244194; substitution rates AC = 1.190651, AG = 3.363586, AT = 2.316682, CG = 1.153165, CT = 3.693909, GT = 1.000000; proportion of invariable sites I = 0.105968; and gamma distribution shape parameter α = 0.446892.

The final RAxML tree is shown in Figure 5.1. The 47 strains are distributed in four classes in Ascomycota, viz. Dothideomycetes, Eurotiomycetes, Saccharomycetes, and Sordariomycetes. According to the BLAST results and phylogenetic analyses, 46 strains were identified at the genus level, and they belong to 18 genera. While one of our strains (GDA-2B15) is closest to two strains of Xylariaceae viz. (CHTAE14) and (PB-85), therefore, GDA-2B15 was identified as a member of Xylariaceae in this paper.

The results can be summarized as 47 endophytic fungi strains belong to Ascomycota Caval.-Sm., of which 30 strains belong to Sordariomycetes O.E. Erikss. & Winka (63.83%), 14 strains belong to Dothideomycetes O.E. Erikss. & Winka (29.79%), two strains belong to Eurotiomycetes O.E. Erikss. & Winka (4.26%), and one strain belongs to Saccharomycetes G. Winter (2.13%).

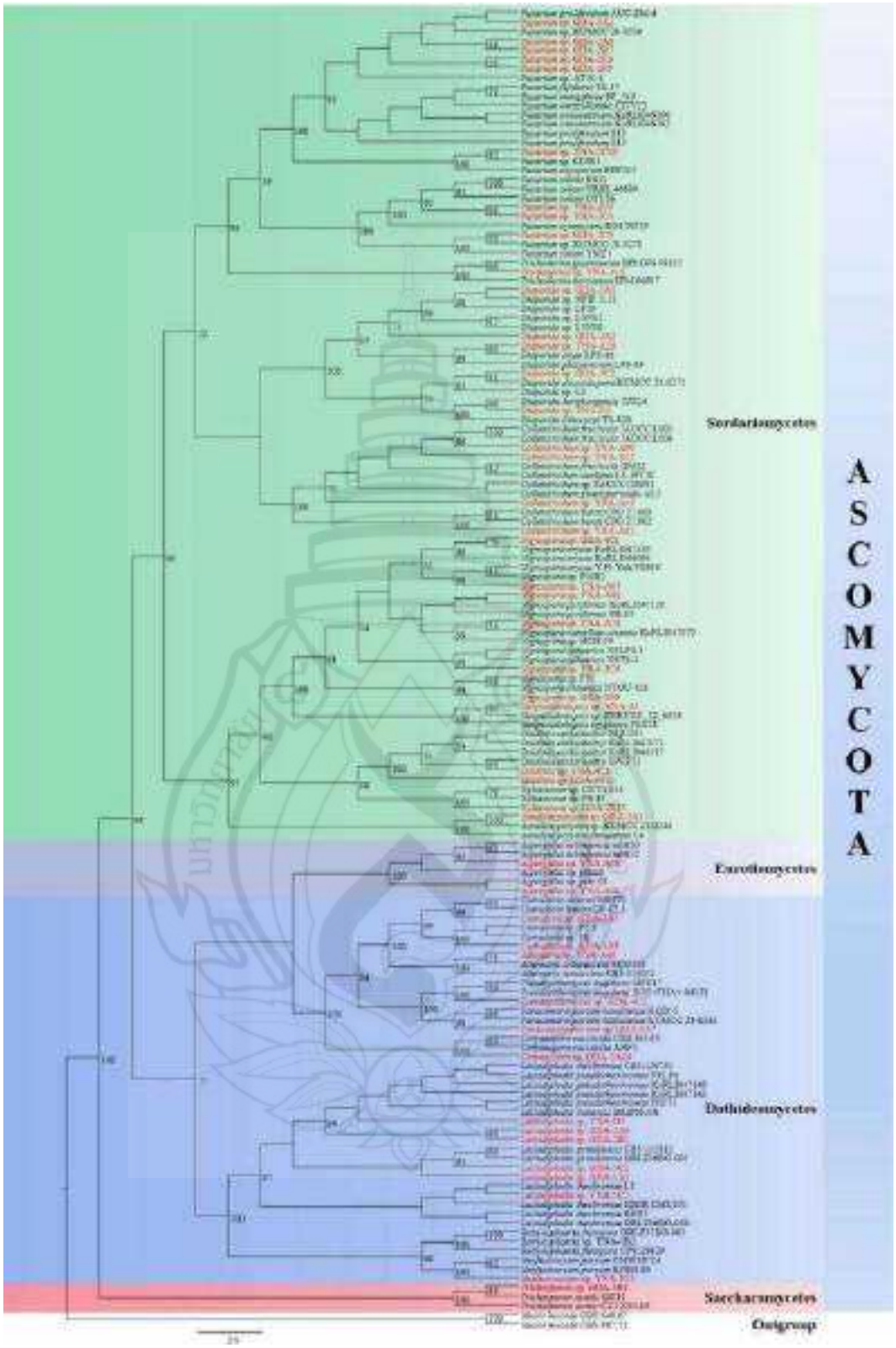


Figure 5.1 A RAxML single gene phylogenetic tree of 47 endophytic fungi strains and their related sequences based on ITS

Figure 5.1 Bootstrap support values for maximum likelihood (ML) equal to or higher than 50% are indicated above the branches. The endophytic fungi with original strain numbers isolated in this study are marked with red font.

5.3.3 Dual Culture Assay for Antibiosis Test (Pretest)

A total of 47 endophytic fungi strains were tested on six pathogens under the same conditions. The results showed that 18 strains had inhibitory effects on all six pathogens, seven strains had inhibitory effects on all three pathogenic bacteria, and 22 strains had inhibitory effects on all three pathogenic fungi. Therefore, 25 strains had inhibitory effects on all three pathogenic bacteria, and 40 strains had inhibitory effects on all three pathogenic fungi. Therefore, 25 strains and 40 strains were used to conduct formal tests on three pathogenic bacteria and three pathogenic fungi respectively.

5.3.4 Dual Culture Assay for Antibiosis Test (Formal Test)

Through the results of the pretest, we carried out the formal test with the selected strains (25 endophytic fungi for pathogenic bacteria, and 40 endophytic fungi for pathogenic fungi) By calculating the inhibition rate through the formula, the strains whose inhibition rate was more than 60% were considered to have an inhibition effect, and the results recorded in Table 5.3 and only *Lasiodiplodia* sp.(YNA-D3) can inhibit all six pathogens, and its inhibition rate to pathogenic fungi is higher than bacteria pathogens (Inhibition rate: 93.30% to PF2-*B. cinerea*, 76.73% to PF3-*P. digitatum*, 75.90% to PF1-*A. alternata*, 74.07% to PB2-*P. syringae*, 63.33% to PB3-*S. enterica*, 63.64% to PB1-*E. amylovora*). Figure 5.2 shows the pictures of several endophytic fungi with significant inhibition rates to pathogens in the dual culture assay.

Table 5.3 The results and inhibition rate percentage ± standard deviation of dual culture assay-formal test (10 days). "–" indicates that the dual culture assay-formal test of endophytic fungi against the pathogen has not been carried out. Taxa are arranged according to the alphabetical order of generic names

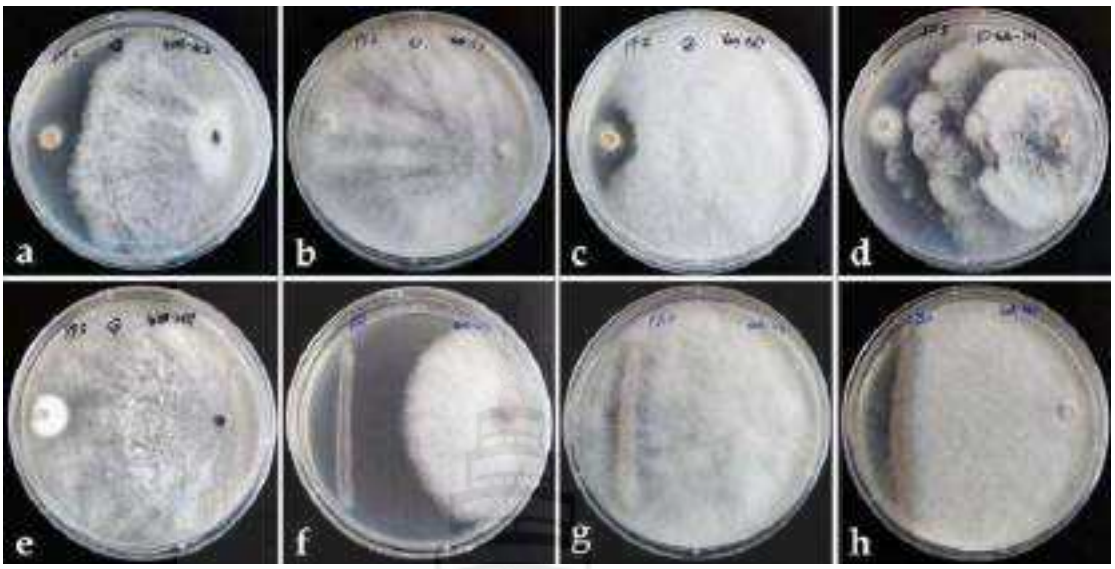
Original Code	Strain Name	PB1-*Erwinia amylovora* (CGMCC 1.7276)	PB2-*Pseudomonas syringae* (CGMCC 1.3333)	PB3-*Salmonella enterica* (CGMCC 1.10603)	PF1-*Alternaria alternata* (CGMCC 3.15535)	PF2-*Botrytis cinerea* (CGMCC 3.3790)	PF3-*Penicillium digitatum* (CGMCC 3.15410)
YNA-A40	*Alternaria* sp.	–	–	–	48.27 ± 2.76	64.82 ± 0.07	64.15 ± 1.14
GDA-2A3	*Annulohypoxylon* sp.	26.94 ± 1.67	33.33 ± 0.00	46.67 ± 0.22	70.61 ± 0.03	61.47 ± 1.74	72.96 ± 0.58
YNA-A18	*Aspergillus* sp.	40.64 ± 0.42	37.04 ± 0.27	36.67 ± 1.56	58.85 ± 0.53	63.71 ± 1.24	72.33 ± 0.03
YNA-A41	*Aspergillus* sp.	49.77 ± 0.42	48.15 ± 1.10	40.00 ± 0.00	–	–	–
YNA-1B2	*Botryosphaeria* sp.	–	–	–	57.08 ± 0.63	81.02 ± 0.19	72.33 ± 0.03
YNA-A22	*Colletotrichum* sp.	–	–	–	56.50 ± 2.02	80.46 ± 0.04	71.70 ± 0.02
YNA-A42	*Colletotrichum* sp.	–	–	–	47.09 ± 2.63	69.85 ± 0.90	65.41 ± 1.10
YNA-A55	*Colletotrichum* sp.	–	–	–	58.85 ± 1.25	81.57 ± 0.00	71.07 ± 0.81
YNA-A60	*Colletotrichum* sp.	36.07 ± 2.92	33.33 ± 0.00	30.00 ± 0.67	48.85 ± 1.18	75.43 ± 0.31	70.44 ± 0.72
GDA-3A20	*Corynespora* sp.	–	–	–	42.39 ± 2.95	70.97 ± 0.10	71.07 ± 0.01
GDA-3A5	*Curvularia* sp.	–	–	–	62.96 ± 0.44	52.54 ± 2.18	67.30 ± 0.13
GDA-3A9	*Curvularia* sp.	86.30 ± 0.00	74.07 ± 0.27	56.67 ± 0.22	77.07 ± 0.02	91.62 ± 0.02	75.47 ± 0.17
GDA-3A11	*Daldinia* sp.	–	–	–	46.50 ± 0.17	76.55 ± 0.00	72.33 ± 0.13
YNA-A21	*Daldinia* sp.	–	–	–	53.56 ± 0.44	78.22 ± 0.07	72.33 ± 0.03
GDA-2A1	*Diaporthe* sp.	–	–	–	71.19 ± 0.01	84.92 ± 0.13	79.87 ± 0.01
GDA-2A2	*Diaporthe* sp.	–	–	–	65.90 ± 0.03	79.90 ± 0.24	75.47 ± 0.07
GDA-2C2	*Diaporthe* sp.	–	–	–	49.44 ± 2.08	81.02 ± 0.01	74.21 ± 0.01
YNA-A29	*Diaporthe* sp.	–	–	–	50.03 ± 0.50	69.85 ± 0.69	68.55 ± 0.22
YNA-C4	*Diaporthe* sp.	–	–	–	63.55 ± 0.01	74.87 ± 0.24	77.99 ± 0.01
GDA-1A2	*Fusarium* sp.	31.51 ± 1.25	11.11 ± 2.47	46.67 ± 0.22	58.26 ± 1.38	70.41 ± 2.89	72.33 ± 0.06

Table 5.3 (continued)

Original Code	Strain Name	PB1-*Erwinia amylovora* (CGMCC 1.7276)	PB2-*Pseudomonas syringae* (CGMCC 1.3333)	PB3-*Salmonella enterica* (CGMCC 1.10603)	PF1-*Alternaria alternata* (CGMCC 3.15535)	PF2-*Botrytis cinerea* (CGMCC 3.3790)	PF3-*Penicillium digitatum* (CGMCC 3.15410)
GDA-2A8	*Fusarium* sp.	45.21 ± 0.00	44.44 ± 0.82	43.33 ± 0.22	55.91 ± 1.93	63.71 ± 3.11	64.78 ± 0.22
GDA-2B7	*Fusarium* sp.	54.34 ± 1.67	48.15 ± 0.27	36.67 ± 0.22	–	–	–
GDA-2C9	*Fusarium* sp.	49.77 ± 0.42	33.33 ± 0.00	46.67 ± 0.89	–	–	–
GDA-2F9	*Fusarium* sp.	54.34 ± 0.42	48.15 ± 1.10	46.67 ± 0.89	–	–	–
GDA-3C4	*Fusarium* sp.	36.07 ± 1.67	22.22 ± 0.82	33.33 ± 0.89	55.32 ± 2.52	81.57 ± 0.58	72.33 ± 0.01
YNA-2C10	*Fusarium* sp.	54.34 ± 0.42	55.56 ± 0.00	56.67 ± 0.22	–	–	–
YNA-2C3	*Fusarium* sp.	81.74 ± 0.42	44.44 ± 0.82	36.67 ± 0.22	62.38 ± 0.13	56.45 ± 2.38	56.60 ± 1.23
YNA-2C6	*Fusarium* sp.	49.77 ± 0.42	62.96 ± 1.10	46.67 ± 1.56	–	–	–
GDA-1A7	*Lasiodiplodia* sp.	86.30 ± 1.25	59.26 ± 0.27	46.67 ± 0.22	74.13 ± 0.03	91.07 ± 0.02	79.25 ± 0.17
GDA-2A9	*Lasiodiplodia* sp.	63.47 ± 0.42	55.56 ± 0.00	60.00 ± 0.00	70.61 ± 0.03	89.39 ± 0.01	78.62 ± 0.13
GDA-2B1	*Lasiodiplodia* sp.	77.17 ± 0.42	48.15 ± 1.92	53.33 ± 1.56	72.96 ± 0.17	93.30 ± 0.00	73.58 ± 0.31
GDA-3C2	*Lasiodiplodia* sp.	49.77 ± 0.42	62.96 ± 0.27	50.00 ± 0.67	65.90 ± 0.30	93.30 ± 0.00	72.96 ± 0.06
YNA-1C2	*Lasiodiplodia* sp.	68.04 ± 0.42	70.37 ± 0.27	56.67 ± 0.89	75.31 ± 0.15	92.18 ± 0.01	75.47 ± 0.17
YNA-D3	*Lasiodiplodia* sp.	63.47 ± 0.42	74.07 ± 0.27	63.33 ± 0.89	75.90 ± 0.09	93.30 ± 0.00	76.73 ±0.10
YNA-1C3	*Neofusicoccum* sp.	49.77 ± 0.42	70.37 ± 0.27	46.67 ± 0.22	71.19 ± 0.13	92.18 ± 0.02	69.18 ± 0.15
YNA-A1	*Neopestalotiopsis* sp.	–	–	–	48.27 ± 1.69	64.82 ± 1.40	71.07 ± 0.06
GDA-2B6	*Nigrospora* sp.	40.64 ± 0.42	29.63 ± 0.27	40.00 ± 0.67	–	–	–
GDA-4C1	*Nigrospora* sp.	68.04 ± 0.42	62.96 ± 0.27	46.67 ± 3.56	64.73 ± 0.06	71.52 ± 1.70	71.70 ± 0.07
YNA-2C4	*Nigrospora* sp.	–	–	–	65.31 ± 1.38	79.34 ± 0.31	72.33 ± 0.03
YNA-A61	*Nigrospora* sp.	–	–	–	52.97 ± 0.01	78.78 ± 0.16	64.78 ± 0.10
YNA-A67	*Nigrospora* sp.	–	–	–	47.09 ± 0.08	93.30 ± 0.00	69.81 ± 0.00
YNA-A71	*Nigrospora* sp.	–	–	–	61.20 ± 0.02	68.73 ± 2.36	71.70 ± 0.02
GDA-5A7	*Paracamarosporium* sp.	–	–	–	50.62 ± 2.57	59.80 ± 1.40	71.70 ± 0.00

Table 5.3 (continued)

Original Code	Strain Name	PB1-*Erwinia amylovora* (CGMCC 1.7276)	PB2-*Pseudomonas syringae* (CGMCC 1.3333)	PB3-*Salmonella enterica* (CGMCC 1.10603)	PF1-*Alternaria alternata* (CGMCC 3.15535)	PF2-*Botrytis cinerea* (CGMCC 3.3790)	PF3-*Penicillium digitatum* (CGMCC 3.15410)
GDA-4C2	*Pseudopithomyces* sp.	36.07 ± 5.42	62.96 ± 0.27	33.33 ± 0.89	51.79 ± 1.50	65.38 ± 0.47	58.49 ± 1.45
YNA-1C1	*Trichoderma* sp.	45.21 ± 0.00	62.96 ± 0.27	60.00 ± 0.67	77.07 ± 0.02	92.74 ± 0.04	75.47 ± 0.17
GDA-1B3	*Trichosporon* sp.	–	–	–	51.21 ± 3.20	46.40 ± 1.74	74.21 ± 0.03
GDA-2B15	*Xylariaceae* sp.	–	–	–	54.14 ± 1.18	78.78 ± 0.16	72.33 ± 0.25



Note Left: pathogen. Right: endophytic fungus. **a–c**, Endophytic fungi dominate against the pathogenic fungus PF2. **d**,**e**, Endophytic fungi dominate against pathogenic fungus PF3. **f**, Endophytic fungi dominate against pathogenic bacterium PB1. **g**,**h**, Endophytic fungi dominate against pathogenic bacterium PB2.

Figure 5.2 Dual culture assay

5.3.4.1 Inhibition of 25 Endophytic Fungi on Three Pathogenic Bacteria

The inhibitory effect (≥60%) of 25 endophytic fungi on pathogenic bacteria is shown in Figure 5.3 and Table 5.3, and the inhibitory effect is ranked as *E. amylovora* (CGMCC 1.7276) > *P. syringae* (CGMCC 1.3333) > *S. enterica* (CGMCC 1.10603). For *S. enterica* (CGMCC 1.10603), there is almost no inhibitory effect.

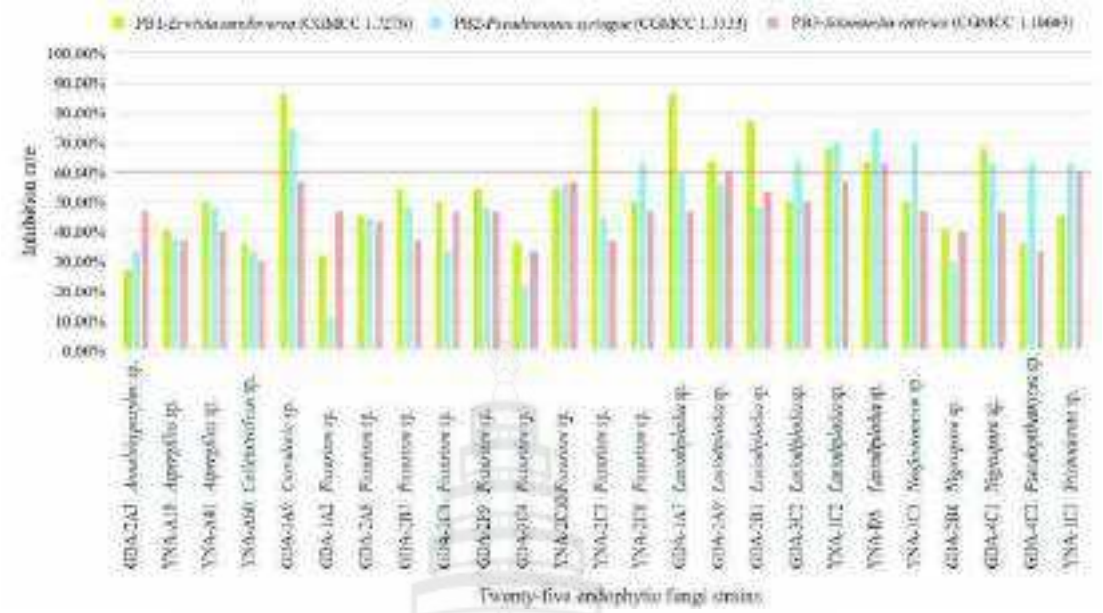


Figure 5.3 Inhibition rate of 25 endophytic fungi to three pathogenic bacteria. The inhibition ≥60% is considered a good inhibition effect

For PB1-*E. amylovora* (CGMCC 1.7276), eight strains showed inhibitory effects (Table 5.3 and Figure 5.3), and the three strains with the highest inhibition rate are *Curvularia* sp. (GDA-3A9, 86.36%), *Lasiodiplodia* sp. (GDA-1A7, 86.36%), and *Fusarium* sp. (YNA-2C3, 81.82%). Among the eight strains, the genus *Lasiodiplodia* Ellis & Everh. has the highest number of strains (five strains).

For PB2-*P. syringae* (CGMCC 1.3333), nine strains showed inhibitory effects (Table 5.3 and Figure 5.3), and the three strains with the highest inhibition rate are *Curvularia* sp. (GDA-3A9, 74.07%), *Lasiodiplodia* sp. (YNA-D3, 74.07%), and *Lasiodiplodia* sp. (YNA-1C2, 70.37%). Among the nine strains, the genus *Lasiodiplodia* has the largest number of strains (three strains).

For PB3-*S. enterica* (CGMCC 1.10603), three strains showed inhibitory effects (Table 5.3 and Figure 5.3), and *Lasiodiplodia* sp. (YNA-D3, 63.33%) had the strongest inhibitory effect, followed by *Lasiodiplodia* sp. (GDA-2A9, 60.00%), and *Trichoderma* sp. (YNA-1C1, 60.00%). Among the three strains, the genus *Lasiodiplodia* has the largest number of strains (two strains).

5.3.4.2 Inhibition of 40 Endophytic Fungi on Three Pathogenic Fungi

The inhibitory effect (≥60%) of 40 endophytic fungi on pathogenic fungi shows some good results in Figure 5.4 and Table 5.3, and the inhibitory effect is ranked as *B. cinerea* (CGMCC 3.3790) > *P. digitatum* (CGMCC 3.15410) > *A. alternata* (CGMCC 3.15535).

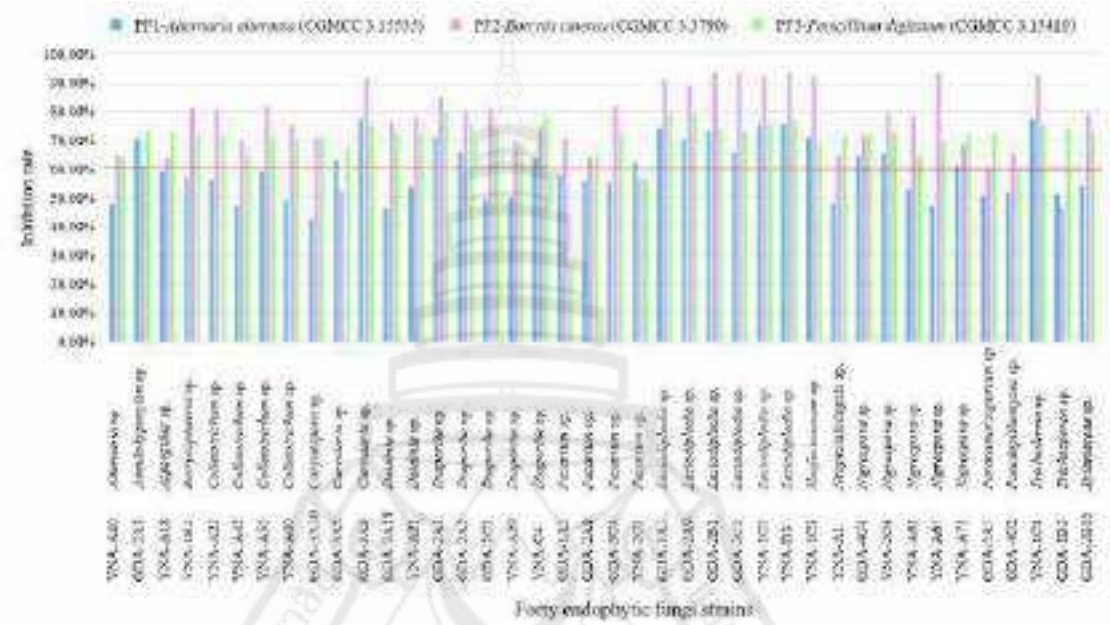


Figure 5.4 Inhibition rate of 40 endophytic fungi to three pathogenic fungi. The inhibition ≥60% is considered a good inhibition effect

For PF1-*A. alternata* (CGMCC 3.15535), 18 strains showed inhibitory effects (Table 5.3 and Figure 5.4), among them, the three strains with the highest inhibition rate are *Curvularia* sp. (GDA-3A9, 77.07%), *Trichoderma* sp. (YNA-1C1, 77.07%), and *Lasiodiplodia* sp. (YNA-D3, 75.90%). Among the 18 strains, the genus *Lasiodiplodia* has the largest number of strains (six strains).

For PF2-*B. cinerea* (CGMCC 3.3790), 36 strains showed inhibitory effects (Table 5.3 and Figure 5.4), among them, the three strains with the highest inhibition rate are *Lasiodiplodia* sp. (GDA-3C2, 93.30%), *Lasiodiplodia* sp. (YNA-D3, 93.30%), and *Lasiodiplodia* sp. (GDA-2B1, 93.30%). Among the 36 strains, the genus *Lasiodiplodia* has the largest number of strains (six strains).

For PF3-*P. digitatum* (CGMCC 3.15410), 38 strains showed inhibitory effects (Table 5.3 and Figure 5.4), among them, the three strains with the highest inhibition

rate are *Diaporthe* sp. (GDA-2A1, 79.87%), *Lasiodiplodia* sp. (GDA-1A7, 79.25%), and *Lasiodiplodia* sp. (GDA-2A9, 78.62%). Among the 38 strains, the genus *Lasiodiplodia* has the largest number of strains (six strains).

To sum up, the endophytic fungi used in this test have a good inhibitory effect on PF2-*B. cinerea* (CGMCC 3.3790), which can reach a 93.30% inhibition rate, however, for PB3-*S. enterica* (CGMCC 1.10603), there was almost no inhibitory effect, and the highest inhibitory rate was 63.33%. Among the inhibition results of endophytic fungi on these six pathogens, it can be seen that most fungi with inhibitory effect belong to the genus *Lasiodiplodia*, and *Lasiodiplodia* sp. (YNA-D3) showed the best inhibition effect on pathogens (anti-PB1 63.47%, anti-PB2 74.07%, anti-PB3 63.33%, anti-PF1 75.90%, anti-PF2 93.30%, and anti-PF3 76.73%).

5.4 Discussion

The 47 endophytic fungal strains isolated from agarwood were tested against six bacterial and fungal pathogens. The reasons for selecting these six pathogens are: few studies have been carried out on the pathogens of *A. sinensis* trees, thus no pathogenic strains of *A. sinensis* are available to be used, and these six pathogens can cause severe damages, their hosts and distribution are very wide and common (Schwartz, 1991; Poppe et al., 2003; Woudenberg et al., 2015; Abbey et al., 2019).

The results of the dual culture assay showed that 40 endophytic fungi strains with antimicrobial activities out of 47 strains belong to 18 genera viz. *Alternaria* Nees, *Annulohypoxylon* Y.M. Ju, J.D. Rogers & H.M. Hsieh, *Aspergillus* P. Micheli ex Haller, *Botryosphaeria* Ces. & De Not., *Colletotrichum* Corda, *Corynespora* Güssow, *Curvularia* Boedijn, *Daldinia* Ces. & De Not., *Diaporthe* Nitschke, *Fusarium* Link, *Lasiodiplodia*, *Neofusicoccum* Crous, Slippers & A.J.L. Phillips, *Neopestalotiopsis* Maharachch., K.D. Hyde & Crous, *Nigrospora* Zimm., *Paracamarosporium* Wijayaw. & K.D. Hyde, *Pseudopithomyces* Ariyaw. & K.D. Hyde, *Trichoderma* Pers., and *Trichosporon* Behrend while one strain was identified as Xylariaceae Tul. & C. Tul., while their inhibitory effects on different pathogens were identified as different (Table 5.3). Among them, the strains of six genera (*Curvularia*, *Diaporthe*, *Lasiodiplodia*,

Neofusicoccum, *Nigrospora*, and *Trichoderma*) showed relatively significant inhibition effects (Table 5.3) and the most significant of which is *Lasiodiplodia* sp. (YNA-D3), which can inhibit all six pathogens.

In previous studies, some agarwood endophytic fungal strains have been shown to have antimicrobial properties that are consistent with our results viz. *Botryosphaeria rhodina* (Gong & Guo, 2009), *Colletotrichum* sp. (Gong & Guo, 2009), *Diaporthe* sp. (Monggoot et al., 2017), *Fusarium equiseti* (Corda) Sacc. (Cui et al., 2011), *F. oxysporum* (Gong & Guo, 2009; Cui et al., 2011), *F. solani* (Mart.) Sacc. (Cui et al., 2011), *F. verticillioides* (Sacc.) Nirenberg (Chi et al., 2016), *Lasiodiplodia theobromae* (Pat.) Griffon & Maubl. (Cui et al., 2011), and *Xylaria mali* Fromme (Tian et al., 2013).

In addition, in this study, this is the first time that 13 genera of agarwood endophytic fungi are reported for antimicrobial activities viz. *Alternaria*, *Annulohypoxylon*, *Aspergillus*, *Corynespora*, *Curvularia, Daldinia*, *Neofusicoccum*, *Neopestalotiopsis*, *Nigrospora*, *Paracamarosporium*, *Pseudopithomyces*, *Trichoderma*, and *Trichosporon*. At the same time, nine genera viz. *Alternaria*, *Annulohypoxylon*, *Corynespora*, *Daldinia*, *Neofusicoccum*, *Neopestalotiopsis*, *Paracamarosporium*, *Pseudopithomyces*, and *Trichosporon* were reported as endophytic fungi of agarwood for the first time.

In this study, some potential fungal strains that can be used as biocontrol agents were screened (Table 5.3). *Botrytis cinerea* (CGMCC 3.3790) is one of the most destructive pathogens with a large number of hosts (Abbey et al., 2019). This pathogen is resistant to commonly used synthetic fungicides, so it is necessary to carry out more research on biological control strategies (Abbey et al., 2019; Bolívar-Anillo et al., 2020). In this study, strains of the five genera viz. *Curvularia* sp., *Lasiodiplodia* sp., *Neofusicoccum* sp., *Nigrospora* sp., and *Trichoderma* sp. with inhibition rates to *B. cinerea* (CGMCC 3.3790) more than 90% were identified. These strains have the potential to be developed into fungicides against *B. cinerea* (CGMCC 3.3790).

In conclusion, this study enriches the diversity of the endophytic fungi of agarwood and their antagonistic potential against bacterial and fungal pathogens. The most significant fungal strain is *Lasiodiplodia* YNA-D3 which can inhibit all pathogens and needs further studies to identify and analyze its secondary metabolites with antimicrobial effects. In addition, in-depth studies on the endophytic fungi associated with agarwood are needed to develop effective biocontrol agents.

CHAPTER 6

THE POLYPHASIC APPROACH REVEALS FIFTEEN NOVEL AND TWO KNOWN ASCOMYCOTA TAXA FROM TERRESTRIAL AGARWOOD PRODUCING TREES

6.1 Introduction

Agarwood, a rare and highly valuable dark resin with a unique fragrance, is produced by the defense mechanism of Thymelaeaceae Juss. plants after being damaged by external factors such as animals, insects, lightning, and microorganisms (Chhipa et al., 2017; Wang et al., 2018). Agarwood is a multipurpose wood sold in the market as wood chips, powder, prayer beads, and wood carvings; and it also plays an essential role in Chinese traditional medicine (National Pharmacopoeia Committee, 2015, 2020; CITES, 2022). Agarwood chips and essential oils have created enormous economic value in the market; for example, agarwood oil had a global market value of USD 278.03 million in 2021 (Niego et al., 2023a). Members of Thymelaeaceae are well known for their ability to produce agarwood and are distributed in tropical and subtropical regions (Xu et al., 2016; Azren et al., 2018; Kang, 2021). These plants are native to Southeast Asia and are distributed in Borneo, Cambodia, China, India, Indonesia, Laos, Malaysia, Myanmar, Papua New Guinea, Sri Lanka, Thailand, the Philippines, and Vietnam (Rasool & Mohamed, 2016; Xu et al., 2016; Kang, 2021). The family Thymelaeaceae contains of many important agarwood-producing tree species, including those from the genera *Aetoxylon* Airy Shaw, *Aquilaria* Lam., *Gonystylus* Teijsm. & Binn., *Gyrinops* Gaertn., and *Phaleria* Jack, and these tree species that can produce agarwood are called “agarwood-producing trees” (Rasool & Mohamed, 2016). *Aquilaria* is an important genus of agarwood-producing tree genera due to its unique and precious fragrant resins (Rasool & Mohamed, 2016). There are 21 accepted species, of which 13 are reportedly capable of producing agarwood, including two native Chinese species – *Aquilaria sinensis* (Lour.) Spreng. and *Aquilaria yunnanensis* S. C. Huang (Su et al., 2016; CITES, 2022). *Aquilaria sinensis* is the main source of agarwood in China (National Pharmacopoeia Committee,

2015, 2020), and is mainly distributed in Fujian, Guangdong, Guangxi, Hainan, Hong Kong, Taiwan, and Yunnan provinces/regions (Cui et al., 2013) while *A. yunnanensis* is found only in Xishuangbanna, Yunnan Province, China (Su et al., 2016). The main morphological difference between *A. yunnanensis* and *A. sinensis* is that the fruit of *A. yunnanensis* is oval, with short seed appendages, and the seed surface is densely covered with yellow pubescence, while *A. sinensis* has oblong fruit, seeds with long appendages, and smooth or covered with white pubescence on the surface (Kang, 2021).

Studies of the microfungi associated with agarwood- producing trees have been carried out over a long time, but those studies were focused mainly on endophytic and pathogenic fungi (Liao et al., 2018; Wang et al., 2018, 2019b; Liu et al., 2020; Du et al., 2022a, 2022b; Li et al., 2022c). In the studies of endophytic fungi associated with *A. sinensis* and other agarwood-producing tree species, *Fusarium* is the most significant genus among the endophytic fungi (Du et al., 2022a; Li et al., 2022c). In the past 20 years, endophytic fungi associated with agarwood-producing trees have been extensively studied for their induction potential and their biological activity (Azren et al., 2018; Wang et al., 2018; Subasinghe et al., 2019; Tibpromma et al., 2021; Du et al., 2022d). Studies of pathogenic fungi associated with agarwood-producing trees have also received considerable attention due to the highly valuable agarwood (Li & Chen, 2008; Xu et al., 2012; Samsuddin et al. 2019; Syazwan et al., 2019). The most commonly reported pathogenic fungi genus of *A. sinensis* is *Colletotrichum* Corda, followed by *Lasiodiplodia* Ellis & Everh. and *Rhizoctonia* DC., which cause damage to the seedling, branches, and leaves (Liao et al., 2018; Liu et al., 2020). With respect to the study of saprobic fungi associated with agarwood-producing trees, Punithalingam and Gibson (1978) described *Phomopsis aquilariae* Punith. & I. A. S. Gibson from the dead wood of *Aquilaria malaccensis* Lam. Later, Subansenee et al. (1985) reported seven saprobic fungi on *Aquilaria* spp., viz. *Cercosporella* sp., *Chaetomium* spirale Zopf, *Cladosporium* sp., *Phialogeniculata* sp., *Pithomyces* sp., *Rhizopus* sp., and *Trichoderma* sp. but lacked complete morphological characteristics and sequence data. With only eight records, research on saprobic fungi associated with agarwood-producing trees is limited compared to studies of endophytes and diseases.

As a continuation of fungal diversity studies in the Greater Mekong Subregion (GMS) (Chaiwan et al., 2021), we collected specimens of *Aquilaria* spp. with fungal

fruiting bodies present from Guangdong and Yunnan provinces of China. One new genus and nine new species are described herein, based on morphology, multigene phylogeny, and multiple gene sequences are provided for a known species, *Camarographium clematidis* for the first time. Full descriptions, illustrations, photo plates, and phylogenetic trees to indicate the placement of new taxa are provided.

6.2 Research Methodology

6.2.1 Sample Collection, Morphological Study, and Single Spore Isolation

Dead twigs of *Aquilaria* spp. with fungal fruiting bodies present were collected from Guangdong and Yunnan provinces in China during 2021–2023. Morphological structures of the fungi were examined with an OPTEC SZ650 dissecting stereomicroscope (Chongqing, China), and microscopic fungal structures were photographed with an OLYMPUS DP74 (Tokyo, Japan) digital camera on an OLYMPUS optical microscope (Tokyo, Japan). Distilled water was used as a mounting slide solution, India ink was used to examine the sheath of ascospores, and Melzer's reagent was used to stain the apical ring structure in members of Sordariomycetes. All fungal micromorphological structures were measured by the Tarosoft Image Framework program v. 1.3, and photo plates were made by Adobe Photoshop CS3 Extended version 10.0 software (Adobe Systems, San Jose, CA, USA).

Single spore isolations were carried out following the methods outlined by Senanayake et al. (2020). The fruiting bodies of the fungi were observed under a stereomicroscope (Chongqing, China). A sterile blade was used for lateral cutting of the fruiting bodies, and a sterile needle was used to pick and place spores in 1 mL of sterile water. Then, the sterile needle was used to mix the sterile water and spores to form a mixture. Later, the sterile water with spores was transferred to a potato dextrose agar (PDA) culture plate by pipette gun and incubated at 23°C–28°C for 12–48 h. After the spores germinated, sterile needles were used to pick up the germinated individual spores and transfer them to new PDA plates under sterile conditions. Pure cultures were obtained after 5–7 days of incubation (23°C–28°C), then the culture characteristics were observed and recorded.

The specimens were deposited in the Guizhou Medical University (GMB-W), Kunming Institute of Botany Academia Sinica (HKAS), and Mycological Herbarium of

Zhongkai University of Agriculture and Engineering (MHZU), China. Living cultures were deposited in the Kunming Institute of Botany Culture Collection (KUNCC), Guizhou Medical University Culture Collection (GMBCC), Guizhou Culture Collection (GZCC), and Zhongkai University of Agriculture and Engineering Culture Collection (ZHKUCC), China. Facesoffungi (FoF) numbers were registered as described in Jayasiri et al. (2015), and MycoBank (MB) numbers were registered as outlined in MycoBank (http://www.MycoBank.org).

6.2.2 DNA Extraction, PCR Amplification, and Sequencing

Molecular phylogenetic studies were carried out according to Dissanayake et al. (2020). Fresh mycelia grew for 2–4 weeks on PDA plates were scraped and placed in a 1.5 mL centrifuge tube. Genomic DNA of mycelia was extracted using DNA Extraction Kit-BSC14S1 (BioFlux, Hangzhou, PR China), following the manufacturer's protocol. The partial nuclear genes and primers were used in polymerase chain reaction (PCR) amplification and sequencing: 28S nrRNA gene (LSU) was amplified by using the primers LR0R and LR5 (Vilgalys & Hester, 1990), the internal transcribed spacer (ITS) regions gene was amplified by using the primers ITS5 and ITS4 (White et al., 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). The total volume of the PCR mixture for amplifications was 25 μL containing 12.5 μL 2xMaster Mix (mixture of Easy Taq TM DNA Polymerase, dNTPs, and optimized buffer [Beijing Trans Gen Biotech Co., Beijing, China]), 8.5 μL ddH2O, 2 μL of DNA template, and 1 μL of each forward and reverse primer (10 pM). The conditions for the PCR of LSU, ITS, SSU, *tef*1-α and *rpb*2 followed Dai et al. (2022), while conditions for TUB followed Du et al. (2022c). Purification and sequencing of PCR products were carried out by Sangon Biotech Co. (Kunming, China).

6.2.3 Phylogenetic Analyses

All sequences obtained in this study were checked in BioEdit v.7.2.6.1 (Hall, 1999), and the forward and reverse sequences were spliced with Geneious 9.1.8 (Kearse et al., 2012). The spliced sequences were subjected to nucleotide BLAST searches to identify

closely related sequences available in the NCBI (http://blast.ncbi.nlm.nih.gov/). Sequence data for the phylogenetic analyses were searched from GenBank based on recent publications. Sequences were aligned by MAFFT v.7 (http://mafft.cbrc.jp/alignment/server/) (Katoh et al., 2019), and automatic optimization by TrimAl.v1.2rev59 (Capella-Gutiérrez et al., 2009). The sequence data sets were automatically combined using Sequence Matrix 1.7.8 (Vaidya et al., 2011), and were converted FASTA to PHYLIP and NEXUS formats in AliView (Larsson, 2014) or ALTER (http:// www.sing-group.org/ALTER/) (Glez-Peña et al., 2010).

Randomized accelerated maximum likelihood (RAxML) and Bayesian inference (BI) analyses were carried out in the CIPRES Science Gateway platform (https://www.phylo. org/portal2/login!input.action) (Miller et al., 2010). The RAxML trees analyzed with 1000 bootstrap replicates were generated using RAxML-HPC2 on XSEDE (8.2.12) (Stamatakis et al., 2008; Stamatakis, 2014) with the different models of evolution generated from different data sets. Bayesian analyses were performed with MrBayes on XSEDE (3.2.7a) (Ronquist et al., 2012) by the Markov chain Monte Carlo (MCMC) method to evaluate posterior probabilities (BYPP) (Richard & Lippmann, 1991; Rannala & Yang, 1996; Zhaxybayeva & Gogarten, 2002). According to different data sets, six simultaneous Markov chains were run for 1 000 000– 10 000 000 generations, and trees were sampled every 100th generation. Max-trees were set to 5000, and clade robustness was assessed with a bootstrap (BT) analysis of 1000 replicates. The phylogenetic trees were visualized in FigTree v.1.4.2 (Rambaut, 2012), and edited by Microsoft Office PowerPoint 2021. All novel sequences generated in this study were deposited to the GenBank (https://www.ncbi.nlm.nih. gov/WebSub/?form=history&tool=genbank).

6.3 Results

The new taxa described according to the guidelines outlined in Chethana et al. (2021a), Pem et al. (2021), and Maharachchikumbura et al. (2021). Taxa illustrated below are in alphabetical order. They represent 22 species, 14 genera in nine families, four orders and two classes in Ascomycota. There species name with their taxonomic placement are provided in the Table 6.1.

Table 6.1 Taxonomic placement of the taxa presents in this study

Phylum	Class	Order	Family	Genus	Species
Ascomycota	Dothideomycetes	Dyfrolomycetales	Pleurotremataceae	*Melomastia*	*Melomastia aquilariae*
					Melomastia guangdongensis
					Melomastia maomingensis
					Melomastia sinensis
					Melomastia yunnanensis
		Pleosporales	Corynesporascaceae	*Corynespora*	*Corynespora aquilariae*
			Didymosphaeriaceae	*Camarographium*	*Camarographium clematidis*
				Montagnula	*Montagnula aquilariae*
			Nigrograna ceae	*Nigrograna*	*Nigrograna aquilariae*
			Phaeoseptaceae	*Phaeoseptum*	*Phaeoseptum aquilariae*
			Thyridariaceae	*Aquilariomyces*	*Aquilariomyces aquilariae*
					Aquilariomyces maomingensis
				Parathyridariella	*Parathyridariella aquilariae*
				Pseudothyridariella	*Pseudothyridariella aquilariae*
			Torulaceae	*Torula*	*Torula fici*
			Pleosporales genera *incertae sedis*	*Mangifericomes*	*Mangifericomes aquilariae*
	Sordariomycetes	Sordariales	Podosporaceae	*Triangularia*	*Triangularia aquilariae*
		Xylariales	Diatrypaceae	*Allocryptovalsa*	*Allocryptovalsa aquilariae*
					Allocryptovalsa rabenhorstii
				Peroneutypa	*Peroneutypa aquilariae*
					Peroneutypa maomingensis
	Ascomycota genera *incertae sedis*				*Pseudoacrodictys deightonii*

6.3.1 Dothideomycetes

Dyfrolomycetales K. L. Pang, K. D. Hyde & E. B. G. Jones 2013

Pleurotremataceae Walt. Watson 1929

Melomastia Nitschke ex Sacc. 1875

Notes: *Melomastia* was introduced by Saccardo (1875) to accommodate *Melomastia mastoidea* (Fr.) J. Schröt. (=M. friesii Nitschke) as the type species. *Melomastia* was previously classified under Ascomycota as incertae sedis based only on morphology (Maharachchikumbura et al., 2016). Later, Norphanphoun et al. (2017) assigned *Melomastia* in Pleurotremataceae (Dothideomycetes) based on molecular data (LSU and SSU) and introduced a new species (*Melomastia italica* Norph., Camporesi, T. C. Wen & K. D. Hyde) and also transferred *Dyfrolomyces maolanensis* J. F. Zhang, J. K. Liu, K. D. Hyde & Z. Y. Liu to *Melomastia*. Subsequently, Li et al. (2022c) synonymized *Dyfrolomyces* under *Melomastia* and transferred 11 species in *Dyfrolomyces* to *Melomastia* based on molecular phylogeny and morphology. Kularathnage et al. (2023) recently maintained *Dyfrolomyces* to accommodate *Dibamus tiomanensis* (K. L. Pang, Alias, K. D. Hyde, Suetrong & E. B. G. Jones) W. L. Li, Maharachch. & Jian K. Liu (type) and *Dyfrolomyces chromolaenae* (Mapook & K. D. Hyde) W. L. Li, Maharachch. & Jian K. Liu based on their ascospore morphology and septation that differ from that of *Melomastia*. Currently, 72 epithets of *Melomastia* are listed in Index Fungorum (http:// www.indexfungorum.org/Names/Names.asp, accessed on 1 May 2025). *Melomastia* is characterized by coriaceous to carbonaceous, globose ascomata with erumpent and conical apex, bitunicate asci, short pedicel, cylindrical, and ascospores overlapping uniseriate, ovoid, ellipsoid to fusiform, hyaline, one to 10-septate, with or without a mucilaginous sheath, while the asexual morph of this genus has not been determined (Li et al., 2022c). Members of *Melomastia* are often saprobes on decaying wood in terrestrial, freshwater, and mangrove habitats (Li et al., 2022c). However, *Melomastia septemseptata* Muxfeldt & Aptroot was recently reported as a new species in Brazil based on morphology without sequence data, which has been reported from living tree bark in a dry terrestrial environment, and the authors mentioned that it is likely not a saprobe but rather a weak parasite of the tree (Muxfeldt Naziazeno & Aptroot, 2023).

Melomastia guangdongensis T. Y. Du, K.D. Hyde, Tibpromma & Karun., ***sp. nov.***

MycoBank number: MB 856407; Facesoffungi number: FoF 16958; Figure 6.1

Etymology: Named after the type locality "Guangdong, China".

Holotype: MHZU 23-0021.

Saprobic on a dead branch of *Aquilaria sinensis.* **Sexual morph:** *Ascomata* (excluding neck) 180–360 µm high × 200–300 µm diam. ($\bar{x}$ = 267 × 245 µm, n = 10), visible as black dots on the host surface, black, solitary, scattered to gregarious, semi-immersed to immersed, uniloculate, globose to subglobose, coriaceous to carbonaceous, ostiolate. *Ostiolar canal* 190–240 µm high × 120–160 µm wide ($\bar{x}$ = 214 × 140 µm, n = 10), central, black, cylindrical, coriaceous to carbonaceous, filled with hyaline cells. *Peridium* 30–60 µm wide ($\bar{x}$ = 40 µm, n = 20), comprising dense, several layers, outer layers brown to dark brown, thick-walled cells of *textura angularis* to *textura globulosa*, inner layers hyaline, thin-walled cells of textura angularis to textura prismatica, not fusion well with host tissue. *Hamathecium* comprising 1.5–3 µm wide, numerous filamentous, filiform, septate, sometimes branched, hyaline, pseudoparaphyses, attached to the base and between the asci, embedded in a gelatinous matrix. *Asci* 120–168 × 5.5–7.5 µm ($\bar{x}$ = 144 × 6.5 µm, n = 30), bitunicate, 8-spored, cylindrical, short pedicel, rounded in apex, with an obvious ocular chamber. *Ascospores* (18.7–)20–26 × 5–7 µm ($\bar{x}$ = 23 × 6 µm, n = 30), overlapping-uniseriate, hyaline, 3-septate at maturity, fusiform with acute ends, slightly constricted at the middle septum, smooth-walled, not surrounded by a mucilaginous sheath. **Asexual morph:** Undetermined.

Culture characteristics: Ascospores germinated on PDA after 24 hours, germ tubes were produced from both ends. Colonies on PDA reaching 3 cm diam., after two weeks at 23–28°C. Colonies obverse: dense, circular, white, velvety, slightly raised at the center, entire edge. Colonies reverse: yellow, cream at the margin.

Material examined: CHINA, Guangdong Province, Maoming City, Dianbai District, Poxin, 21°34′28″N, 111°7′39″E, on a dead branch of *Aquilaria sinensis* (Thymelaeaceae), 3 June 2022, T. Y. Du, MMA14, (MHZU 23-0021, **holotype**), ex-type, GMBCC1046, other living culture, ZHKUCC 23-0040.

Notes: In the phylogenetic analyses, our new collection, *M. guangdongensis* formed a sister branch with *M. thamplaensis* strains (HKAS122773, KUMCC 21-0671, and MFLUCC 15-0635) in *Melomastia sensu lato* clade (Figure 6.5) with a 75% ML/0.91

PP bootstrap support. NCBI BLASTn searches of our collection, *M. guangdongensis* showed 99.88% similarity to *M. thamplaensis* (HKAS122773) in the LSU sequence, 100% similarity to *M. thamplaensis* (AND9) in the SSU sequence, and 98.17% similarity to *M. thamplaensis* (KUMCC 21-0671) in the *tef*1-α sequence. Our new collection, *M. guangdongensis* shares similar morphology with *M. thamplaensis* in the shape of asci and ascospores. However, *M. thamplaensis* differs from *M. guangdongensis* in having clypeate, raised spots, immersed, subglobose to obpyriform, some with broad, flattened base ascomata, and three strata of peridium (Zhang et al., 2017), while *M. guangdongensis* has semi-immersed to immersed, globose to subglobose ascomata, and two strata of peridium. Base pair differences of the LSU and SSU genes between our new collection *M. guangdongensis* (GMBCC1046, ex-type) and *M. thamplaensis* (MFLUCC 15-0635, ex-type) showed that there are no nucleotide differences, while the *tef*1-α has 1.6% nucleotide differences (14/865 bp, without gaps), and a comparison of the *tef*1-α nucleotides between new collections and another strain of *M. thamplaensis* (KUMCC 21-0671) resulted in 1.7% differences (15/865 bp, without gaps) (Zhang et al., 2017; Ren et al., 2024). Therefore, we introduce our collection, *M. guangdongensis*, as a new species on a dead branch of *Aquilaria sinensis* from terrestrial habitats in China, based on both morphology and phylogenetic analyses following the guidelines of Maharachchikumbura et al. (2021).

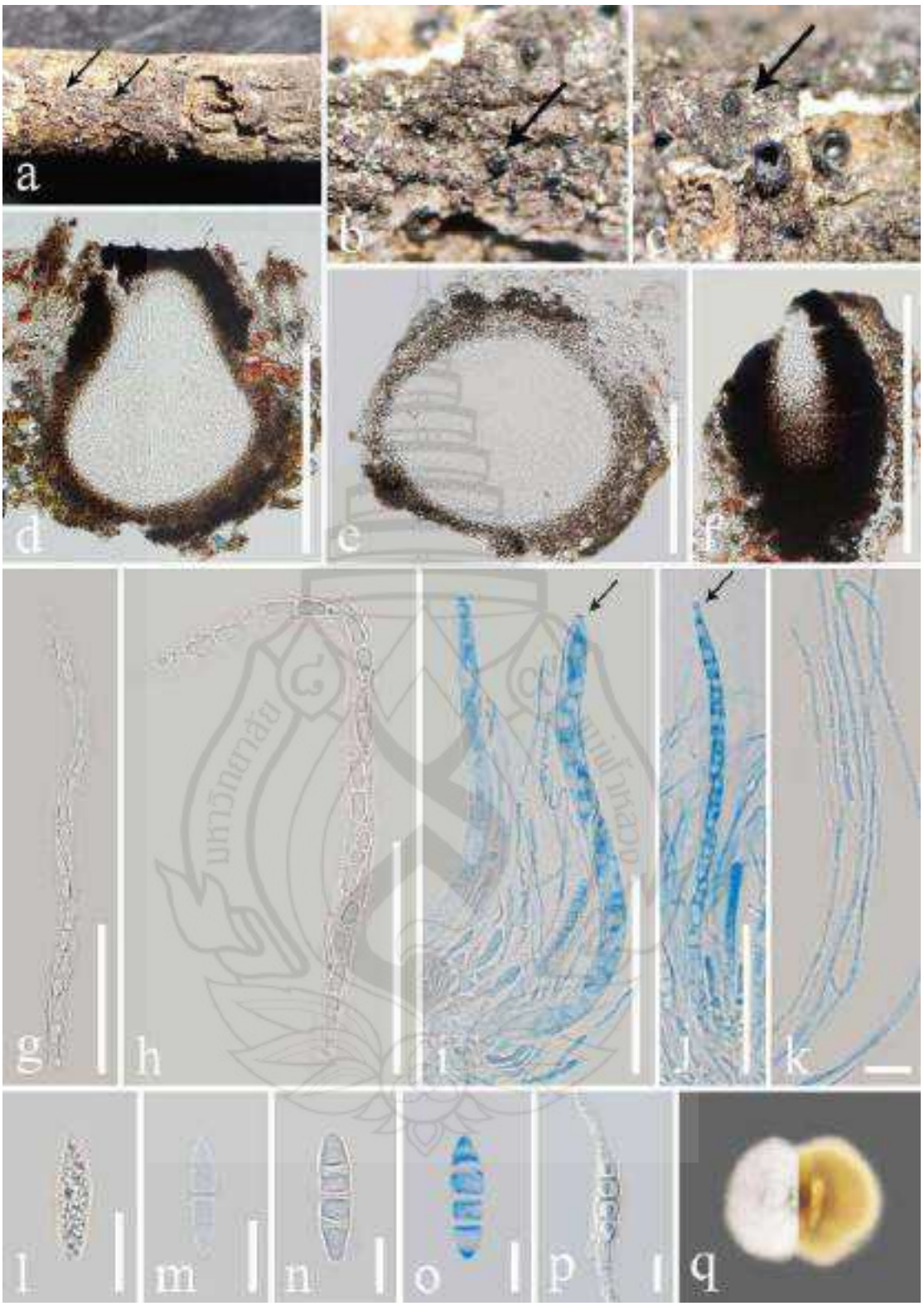


Figure 6.1 *Melomastia guangdongensis* (MHZU 23-0021, holotype)

Figure 6.1 a–c, Appearance of ascomata on the host (the arrows indicate ascomata). d, e, Vertical sections through the ascomata. f, Ostiole. g–j, Asci (i, j asci stained with cotton blue, and arrows indicate ocular chambers). k, Pseudoparaphyses stained with cotton blue. l–o, Ascospores (o ascospore stained with cotton blue). p, Germinated ascospore. q, Colony on PDA obverse and reverse view. Scale bars: d–f = 200 µm, g–j = 50 µm, k–p = 10 µm.

Melomastia maomingensis T. Y. Du, Tibpromma & Karun. ***sp. nov.***

MycoBank number: MB 853997; Facesoffungi number: FoF 15261; Figure 6.2

Etymology: Named after the place of the holotype collection, Maoming.

Holotype: MHZU 23-0019.

Saprobic on a dead branch of *Aquilaria sinensis.* **Sexual morph:** *Ascomata* (excluding neck) 300–550 µm high × 250–500 µm diam. ($\bar{x}$ = 410 × 400 µm, n = 10), solitary, semi- immersed to immersed, visible as black dots on the host surface, obvious, raised spots, black, uniloculate, globose to subglobose, coriaceous to carbonaceous. *Ostiolar canal* 120–280 µm high × 100–220 µm wide ($\bar{x}$ = 230 × 175 µm, n = 10), black, cylindrical, or conical, carbonaceous, papillate with periphyses. *Peridium* 35–100 µm wide ($\bar{x}$ = 67 µm, n = 10), comprising dense, thick-walled, brown to dark brown cells of textura angularis, fusion with host tissue. *Hamathecium* comprising 1.5–3.5 µm wide, numerous filamentous, hyaline, septate, sometimes branched, pseudoparaphyses, longer than asci, attached to the base and between the asci. *Asci* 180–200 × 7–9 µm ($\bar{x}$ = 192 × 8.5 µm, n = 30), bitunicate, eight-spored, cylindrical, short pedicel, rounded in apex, with a minute ocular chamber, J-apical ring. *Ascospores* (23–) 24.5–29 × 6–8 µm ($\bar{x}$ = 26.5 × 7 µm, n = 30), overlapping uniseriate, one to three-septate, mostly three-septate, hyaline, fusiform with acute ends, constricted at the septum, smooth- walled, with a large guttule in each cell when mature, not surrounded by a mucilaginous sheath. **Asexual morph:** Undetermined.

Culture characteristics: Ascospores germinated on PDA after 24 h, germ tubes were produced from both ends. Colonies on PDA reaching 2–3 cm diam., after 2 weeks at 23°C–28°C. Colonies obverse: dense, oval, grayish white to light brown, raised at the center, entire edge. Colonies reverse: brown, cracked at the center, cream to light yellow at the margin.

Material examined: CHINA, Guangdong Province, Maoming City, Dianbai District, Poxin, 21°34′25″ N, 111°7′43″ E, on dead branch of *Aquilaria sinensis* (Thymelaeaceae), June 3, 2022, T. Y. Du, MMA12 (MHZU 23-0019, **holotype**), ex-type, ZHKUCC 23-0038, other living culture, GZCC 23-0619.

Notes: In the present phylogenetic analyses, our new collection *Melomastia maomingensis* formed a sister lineage to *M. beihaiensis* (KUMCC 21-0084) in *Melomastia Sensu lato* with 93% ML, 0.97 BYPP statistical support (Figure 6.5). Morphologically, *M. maomingensis* shares similar morphology with *M. beihaiensis* in asci and ascospores. However, *Melomastia beihaiensis* differs from *M. maomingensis* in having solitary or aggregated, clypeate to wide subglobose ascomata, ostiolar canal filled with hyaline cells, periphyses absent, peridium comprising cells of *textura angularis* to *textura prismatica*, unbranched pseudoparaphyses, smaller asci and ascospores than *M. maomingensis* (asci: 163 × 5.9 µm vs. 186 × 8.5 µm; ascospores: 22 × 5.8 µm vs. 26.5 × 7 µm) (Senanayake et al., 2023). In addition, the base pair differences of the LSU and SSU genes between our new collection and *M. beihaiensis* (KUMCC 21-0084, ex-type) were compared, and the results showed that there are no nucleotide differences, while *tef*1-α has 1.7% nucleotide differences (15/874 bp, without gaps), which reveals that they belong to different species. Therefore, we introduce our new collection, *M. maomingensis*, as a new species based on both morphological study and phylogenetic analyses.

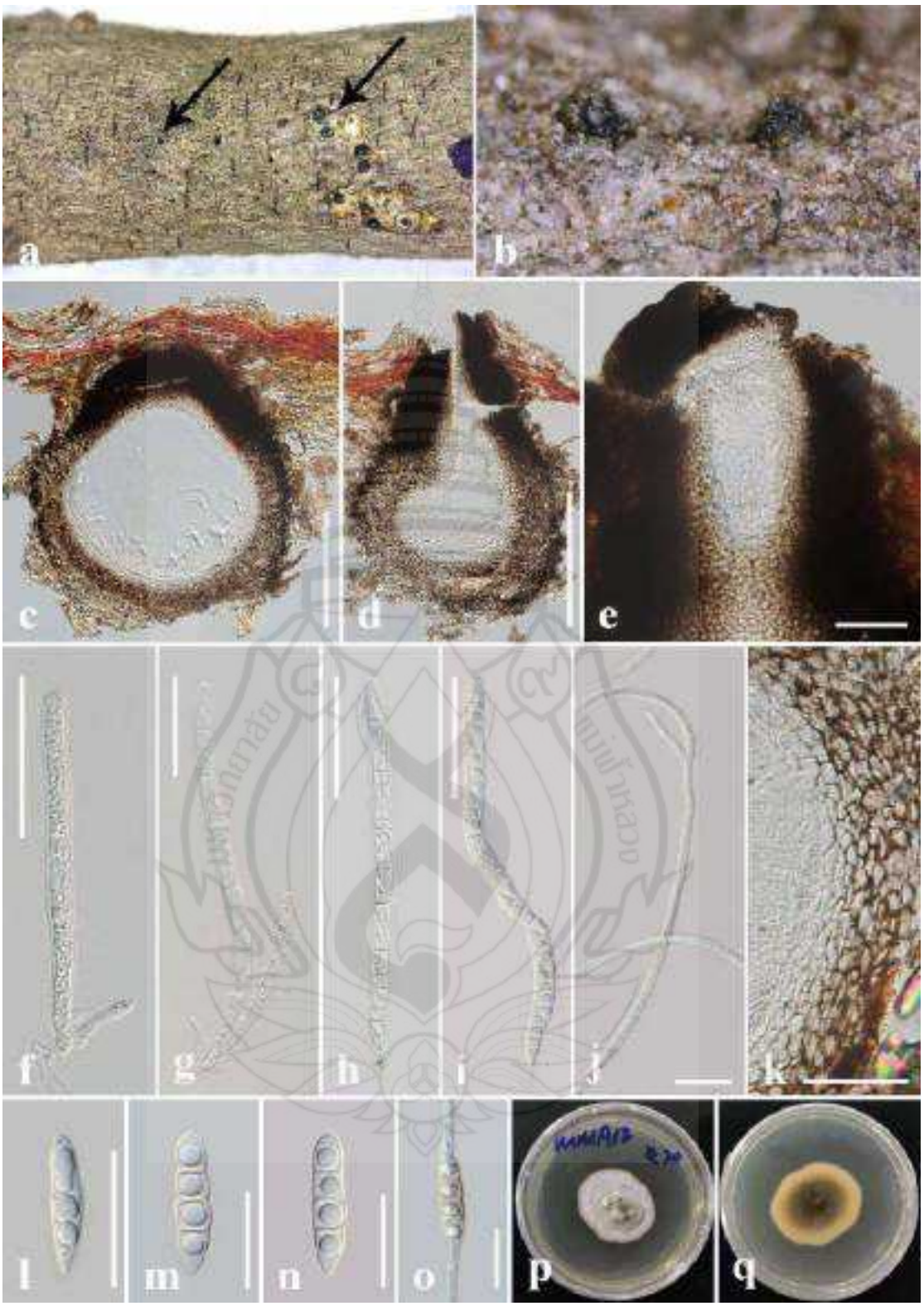


Figure 6.2 *Melomastia maomingensis* (MHZU 23-0019, holotype)

Figure 6.2 a, b, Appearance of ascomata on the host. c, d, Vertical sections through the ascomata. e, Ostiole with periphyses. f–i, Asci. j, Pseudoparaphyses. k, Peridium. l–n, Ascospores. o, Germinated ascospore. p, q, Colony on potato dextrose agar (PDA) obverse and reverse view. Scale bars: c, d = 200 µm, e–i, k = 50 µm, j = 10 µm, l–o = 20 µm.

Melomastia sinensis (M.C. Samar., Tennakoon & K.D. Hyde) W.L. Li, Maharachch. & Jian K. Liu 2022

MycoBank number: MB 842093; Facesoffungi number: FoF 03935; Figure 6.3

Saprobic on a dead branch of *Aquilaria* sp. **Sexual morph:** *Ascomata* (excluding neck) 400–600 µm high × 430–580 µm diam. ($\bar{x}$ = 515 × 520 µm, n = 10), solitary, scattered to gregarious, semi-immersed to immersed, erumpent through host tissue, globose to subglobose, black, coriaceous to carbonaceous, ostiolate. *Ostiolar canal* 230–365 µm high × 200–260 µm wide ($\bar{x}$ = 303 × 230 µm, n = 10), central, black, conical, coriaceous to carbonaceous, filled with hyaline sparse periphyses. *Peridium* 30–120 µm wide ($\bar{x}$ = 75 µm, n = 20), comprising dense, several layers of thick-walled cells of textura angularis to textura prismatica, outer layers brown to dark brown, becoming lighter inwardly. *Hamathecium* comprising 2.5–6.5 µm wide, numerous filamentous, filiform, septate, unbranched, hyaline pseudoparaphyses, attached to the base and between the asci, embedded in a gelatinous matrix. *Asci* 175–220 × 8.5–11.5 µm ($\bar{x}$ = 195 × 10.5 µm, n = 30), bitunicate, 8-spored, cylindrical, long pedicel, thickened and rounded apex, with an obvious ocular chamber. *Ascospores* (17.5–)20–26.5 × 7–9 µm ($\bar{x}$ = 24 × 8 µm, n = 30), overlapping-uniseriate, hyaline, when ascospores gather together, they appear light yellow, mostly 6–7-septate at maturity, cylindrical, with rounded ends, slightly constricted at the septum, often similar width of cells with several small guttules, not surrounded by a mucilaginous sheath. **Asexual morph:** Undetermined.

Culture characteristics: Ascospores germinated on PDA after 24 hours, germ tubes were produced from most cells, germinated ascospores appear light yellow. Colonies on PDA reaching 3 cm diam., after two weeks at 23–28°C. Colonies obverse: dense, circular or irregular, umbonate, cream, light yellow at the center, entire or undulate edge. Colonies reverse: dark gray, yellow at the margin.

Material examined: CHINA, Yunnan Province, Xishuangbanna, Jinghong City, Naban River Nature Reserve, 22°7′48″N, 100°40′24″E, on a dead branch of *Aquilaria* sp. (Thymelaeaceae), 14 September 2021, T. Y. Du, YNA41 (GMB-W 1006, new host and geographical record), living culture, GMBCC1008.

Host and distribution: *Aquilaria* sp. (China; this study), *Camellia sinensis* (Thailand; Hyde et al., 2018a), and *Hevea brasiliensis* (Thailand; Senwanna et al., 2021).

Notes: In the phylogenetic analyses, our new collection (GMBCC1008) isolated from a dead branch of *Aquilaria* sp. grouped with *Melomastia sinensis* strains (MFLUCC 17-1344, MFLUCC 17-2606 and MFLU 17-0777) in *Melomastia sensu lato*, with a 99% ML/0.93 PP bootstrap support (Figure 6.5). NCBI BLASTn searches of our collection showed 99.78% similarity to *M. sinensis* (MFLUCC 17-2606) in the LSU sequence, 99.21% similarity to *M. oleae* (UESTCC 21.0006) in the SSU sequence, and 99.67% similarity to *M. sinensis* (MFLUCC 17-2606) in the *tef*1-α sequence.

Melomastia sinensis (=*Dyfrolomyces sinensis* Samarak., Tennakoon & K.D. Hyde) was introduced by Hyde et al. (2018) as a saprobic on *Camellia sinensis* (L.) Kuntze stems. Our new collection shares a similar morphology with *M. sinensis* (MFLU 17-0777, holotype) in cylindrical ascospores with 6–7-septate ascospores. Our new collection has semi-immersed to immersed ascomata, differs from *M. sinensis* (MFLU 17-0777, holotype) in having superficial ascomata (Hyde et al., 2018a) and differs from immersed ascomata in *M. sinensis* (MFLU 19-0232) (Senwanna et al., 2021). However, the nucleotide base pair differences between our new collection (GMBCC1008) and *M. sinensis* (MFLUCC 17-1344, ex-type) showed that the LSU and SSU gene has no nucleotide differences, while the *tef*1-α gene of *M. sinensis* (MFLUCC 17-1344, ex-type) is unavailable in NCBI (Hyde et al., 2018a). The comparison of the *tef*1-α nucleotides between the new collection and another strain of *M. sinensis* (MFLUCC 17-2606) resulted in 0.3% differences (3/873 bp, without gaps) (Senwanna et al., 2021). This study first discovered *M. sinensis* on *Aquilaria* sp. in China. Therefore, we introduce our new collection as a new host and geographical record of *M. sinensis* based on both morphological study and phylogenetic analyses.

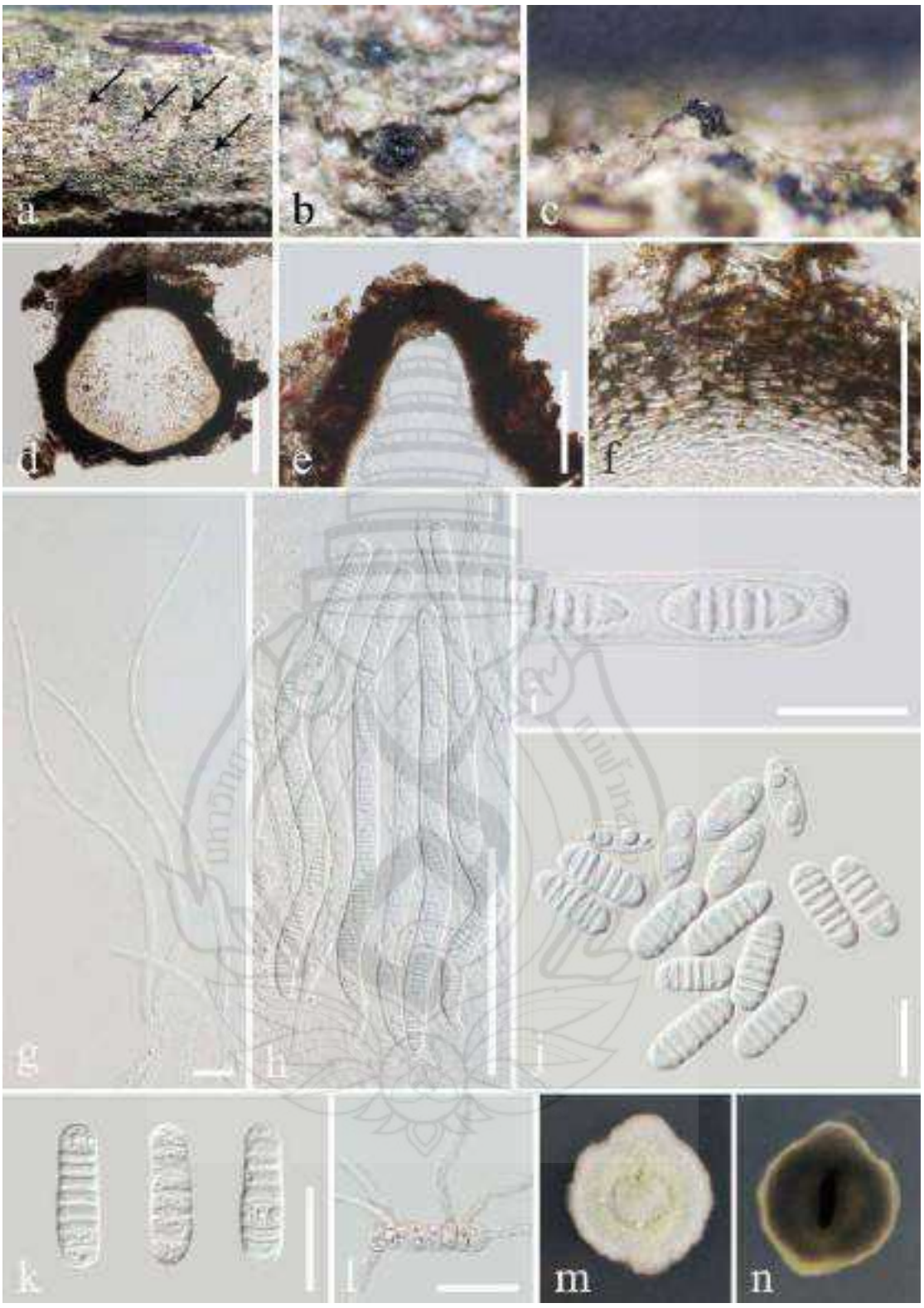


Figure 6.3 *Melomastia sinensis* (GMB-W 1006, new host and geographical record)

Figure 6.3 a–c, Appearance of ascomata on the host (a the arrows indicate ascomata). d, Vertical sections through the ascoma. e, Ostiole. f, Peridium. g, Pseudoparaphyses. h, Asci. i, Ascus with an ocular chamber. j, k, Ascospores. l, Germinated ascospore. m, n, Colony on PDA obverse and reverse view. Scale bars: d, e = 200 µm, h = 100 µm, f = 50 µm, i–l = 20 µm, g = 10 µm.

Melomastia yunnanensis T. Y. Du, K.D. Hyde, Tibpromma & Karun., ***sp. nov.***

MycoBank number: MB 856408; Facesoffungi number: FoF 16959; Figure 6.4

Etymology: Named after the type location "Yunnan, China".

Holotype: GMB-W 1007.

Saprobic on a dead branch of *Aquilaria* sp. **Sexual morph:** *Ascomata* (excluding neck) 400–500 µm high × 300–480 µm diam. ($\bar{x}$ = 458 × 395 µm, n = 10), solitary, scattered to gregarious, immersed to erumpent through host tissue, globose, black, carbonaceous, ostiolate. *Ostiolar canal* 100–160 µm high × 120–230 µm wide ($\bar{x}$ = 130 × 184 µm, n = 10), central, black, conical, carbonaceous, filled with hyaline sparse periphyses. *Peridium* 25–75 µm wide ($\bar{x}$ = 55 µm, n = 10), comprising of dense, several layers of brown to dark brown, thick-walled cells of *textura angularis* to *textura prismatica*. *Hamathecium* comprising 2.5–7.5 µm wide, numerous filamentous, filiform, septate, sometimes branched, hyaline pseudoparaphyses, attached to the base and between the asci, embedded in a gelatinous matrix. *Asci* 180–220 × 7.5–10.5 µm ($\bar{x}$ = 195.5 × 9 µm, n = 30), bitunicate, 8-spored, cylindrical, short pedicel, thickened and rounded apex, with an obvious ocular chamber. *Ascospores* 20–24.5 × 6–8 µm ($\bar{x}$ = 22.5 × 7 µm, n = 30), overlapping-uniseriate, hyaline, when ascospores gather together, they appear light yellow, mostly 6–8-septate at maturity, mostly 7-septate, cylindrical, with rounded ends, slightly constricted at the septum, often similar width of cells with several small guttules, not surrounded by a mucilaginous sheath. **Asexual morph:** Undetermined.

Culture characteristics: Ascospores germinated on PDA after 24 hours, germ tubes were produced from both ends, germinated ascospores appear light brown. Colonies on PDA reaching 2 cm diam., after two weeks at 23–28°C. Colonies obverse: dense, circular, umbonate, gray at the center, cream, and entire edge. Colonies reverse: gray brown, light brown at the margin.

Material examined: CHINA, Yunnan Province, Xishuangbanna, Jinghong City, Naban River Nature Reserve, 22°7′51″N, 100°40′21″E, on a dead branch of *Aquilaria* sp. (Thymelaeaceae), 14 September 2021, T. Y. Du, YNA51 (GMB-W 1007, **holotype**), ex-type, GMBCC1009, other living culture, GZCC 23-0621.

Notes: In the phylogenetic analyses, our new collection, *M. yunnanensis* formed a sister branch with *M. sinensis* (MFLUCC 17-1344, MFLUCC 17-2606, MFLU 17-0777, and GMBCC1008) in *Melomastia sensu lato* with a 100% ML/1.00 PP bootstrap support (Figure 6.5). NCBI BLASTn searches of our collection *M. yunnanensis* showed 99.23% similarity to *M. sinensis* (MFLUCC 17-2606) in the LSU sequence, 98.92% similarity to *M. thamplaensis* (AND9) in the SSU sequence, and 96.34% similarity to *M. sinensis* (MFLUCC 17-2606) in the *tef*1-α sequence. Our new collection, *M. yunnanensis* shares similar morphology with *M. sinensis* in cylindrical and septate ascospores. However, *M. sinensis* differs from *M. yunnanensis* in having superficial, semi-immersed to immersed ascomata, cylindrical or conical ostiolar canal, and unbranched pseudoparaphyses (Hyde et al., 2018a), while our *M. yunnanensis* has immersed ascomata, conical ostiolar canal, and pseudoparaphyses sometimes branched. In addition, the nucleotide base pair differences between our new collection *M. yunnanensis* (GMBCC1009, ex-type) and *M. sinensis* (MFLUCC 17-1344, ex-type) showed the LSU gene has 0.5% nucleotide differences (4/760 bp, without gaps), the SSU gene has 0.5% nucleotide differences (4/813 bp, without gaps), while the *tef*1-α gene of *M. sinensis* (MFLUCC 17-1344, ex-type) is unavailable (Hyde et al., 2018a). We compared the *tef*1-α nucleotides between the new collection and another collection of *M. sinensis* (MFLUCC 17-2606), which resulted in 3.8% differences (33/873 bp, without gaps) (Senwanna et al., 2021). Therefore, we introduce our new collection, *M. yunnanensis*, as a new species on a dead branch of *Aquilaria* sp. from terrestrial habitats in China, based on both morphological study and phylogenetic analyses following the guidelines of Maharachchikumbura et al. (2021).

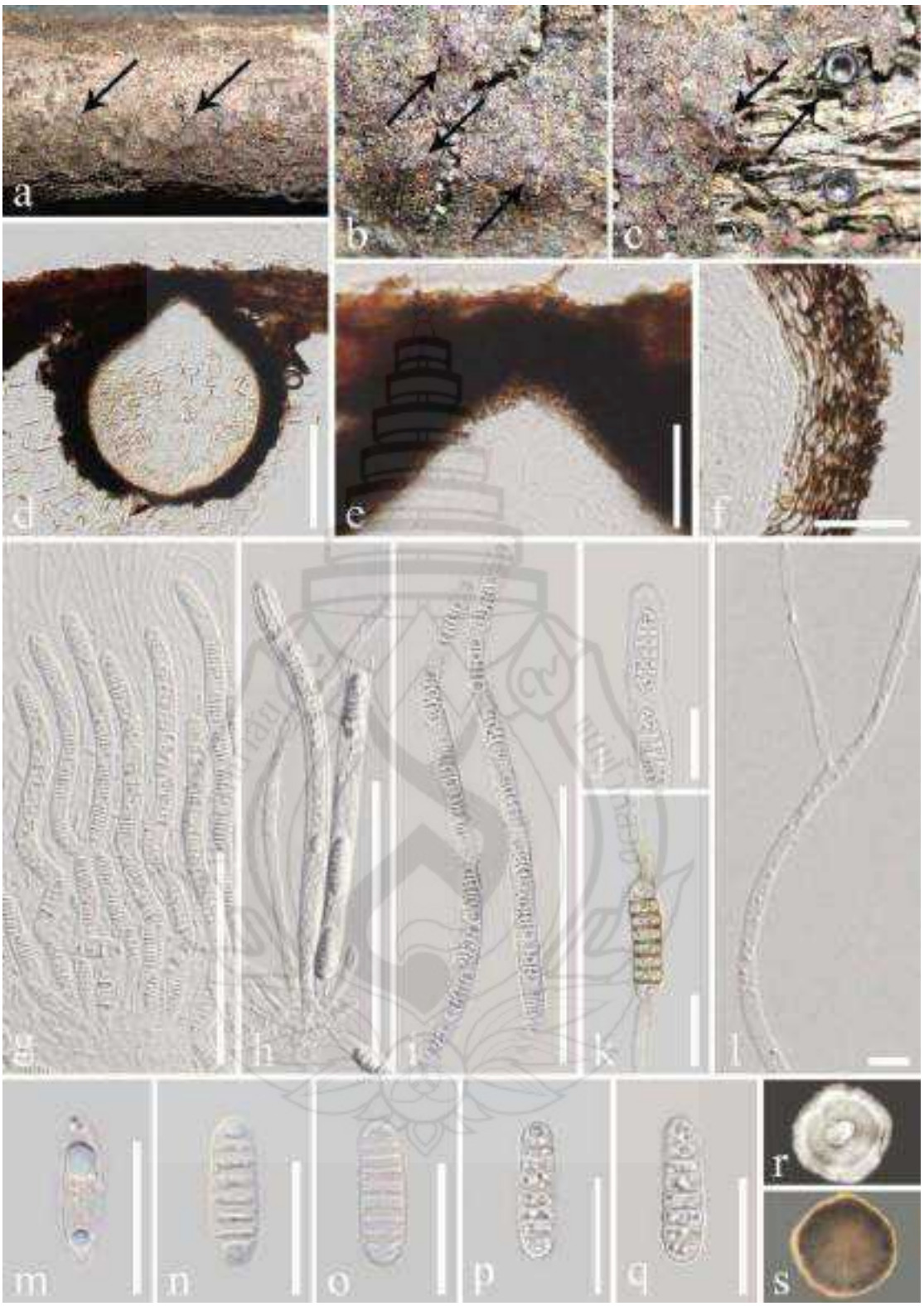
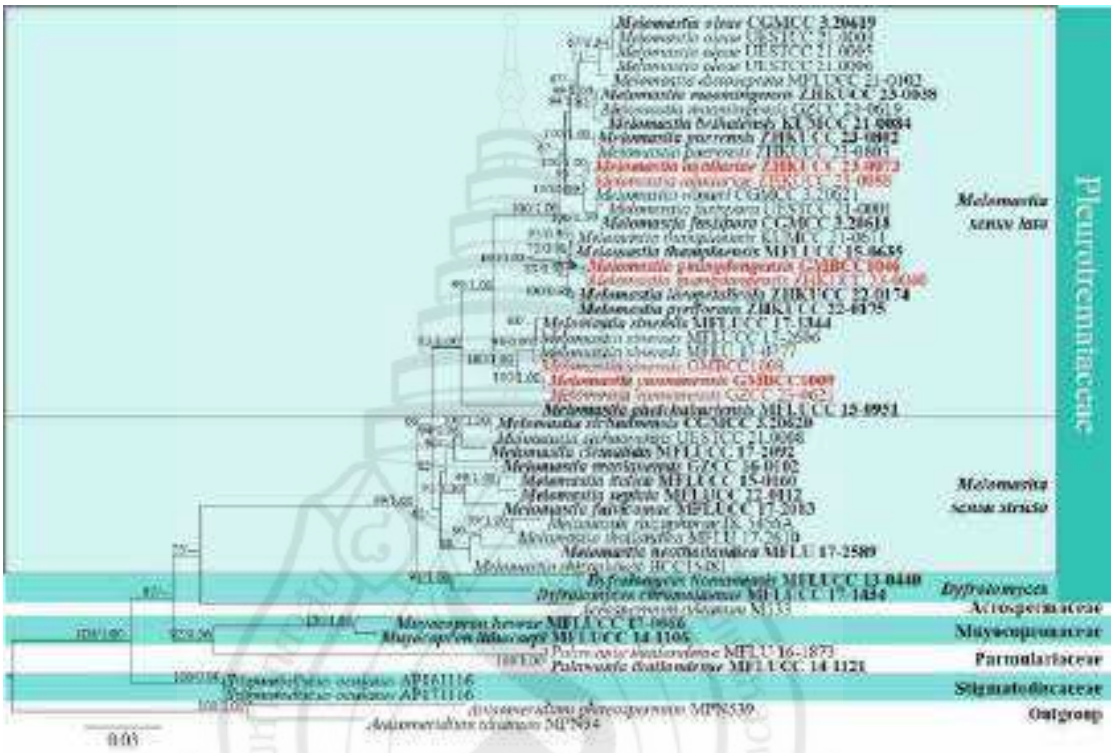


Figure 6.4 *Melomastia yunnanensis* (GMB-W 1007, holotype)

Figure 6.4 a–c, Appearance of ascomata on the host (the arrows indicate ascomata). d, Vertical sections through the ascoma. e, Ostiole. f, Peridium. g–i, Asci. j, Asci ocular chamber. k, Germinated ascospore. l, Pseudoparaphyses. m–q, Ascospores. r, s, Colonies on PDA obverse and reverse view. Scale bars: d = 200 µm, g–i = 100 µm, e, f = 50 µm, J, k, m–q = 20 µm, l = 10 µm.



Note Bootstrap support values for ML greater than 60% and Bayesian posterior probabilities greater than 0.90 are given near the nodes, respectively. The tree is rooted with *Anisomeridium phaeospermum* (MPN539) and *A. ubianum* (MPN94). The new isolates are indicated in red, and the ex-type strains are in bold.

Figure 6.5 Phylogenetic tree of *Melomastia*

Pleosporales Luttr. ex M. E. Barr 1987

Corynesporascaceae Sivan. 1996

Corynespora Güssow 1906

Notes: *Corynespora* was described by Güssow (1906) with the type species *Cor. mazei* Güssow. Wei, a synonym of *Cor. cassiicola*. Voglmayr and Jaklitsch (2017) assigned *Cor. cassiicola* and *Cor. smithii* to Corynesporascaceae based on phylogenetic analyses and morphology. Currently, more than 200 epithets of *Corynespora* have been recorded in Index Fungorum (2025). However, there are only 14 species in this genus with DNA sequence data (Crous et al., 2019; Hyde et al., 2020; Li et al., 2023; Liu et al., 2023a). This genus is characterized by conidiophores with integrated, terminal, monotretic conidiogenous cells, and acrogenous, solitary or catenate, distoseptate conidia, while the sexual morph is characterized by *Cor. caryotae* with cultural studies (Wei, 1950; Sivanesan, 1996; Xu et al., 2020; Liu et al., 2022c). Species of *Corynespora* live as saprobes, pathogens, and endophytes on a wide range of hosts, including woody and herbaceous plants, other fungi, nematodes, and human skin (Dixon et al., 2009; Kumar et al., 2012; Hyde et al., 2020; Li et al., 2023). This study introduces a new saprobic species, *Corynespora aquilariae*, collected from *Aquilaria yunnanensis* in terrestrial habitats based on morphology and multigene phylogenetic analyses.

Corynespora aquilariae T. Y. Du, Tibpromma & Karun. ***sp. nov.***

MycoBank number: MB 853998; Facesoffungi number: FoF 15262; Figure 6.6

Etymology: Named after its host genus *Aquilaria*.

Holotype: MHZU 23-0035

Saprobic on a dead branch of *Aquilaria yunnanensis*. **Sexual morph:** undetermined. **Asexual morph:** hyphomycetous. *Colony* on natural substrate effuse, hairy, black. *Mycelium* partly superficial and mostly immersed in the substratum composed of branched, septate, pale brown, smooth-walled. *Conidiophores* 145–255 × 6.5–10.5 µm ($\bar{x}$ = 192 × 8 µm, n = 50), macronematous, mononematous, erect, straight or flexuous, mostly flexuous, septate, unbranched, cylindrical, brown to dark brown, thick-walled. *Conidiogenous cells* 16–22 × 7–11 µm ($\bar{x}$ = 19 × 9 µm, n = 50) monotretic, integrated, terminal, determinate, cylindrical, brown to dark brown, often percurrently proliferating. *Conidia* (73–)85–110(–130) × 13–15.5(–17.5) µm ($\bar{x}$ = 99 × 14 µm, n = 50), acrogenous,

solitary, simple, obclavate, straight or slightly curved, subhyaline to brown, 10–16-distoseptate, guttulate, thick-walled, smooth-walled, slender at the apex, and truncate at the base, with a dark basal scar, wide at middle and lower part, narrow and elongated at the upper part.

Culture characteristics: Conidia germinated on PDA after 24 h, and germ tubes were produced from both ends. Colonies on PDA reaching 2–3 cm diam., after 2 weeks at 23°C–28°C. Colonies obverse: dense, oval, white, raised, entire edge. Colonies reverse: yellow to light brown at the center, cream at the margin.

Material examined: CHINA, Yunnan Province, Xishuangbanna, Jinghong City, Gasa, Naban River Basin National Nature Reserve, 22°7′50″ N, 100°40′29″ E, on dead branches of *Aquilaria yunnanensis* (Thymelaeaceae), September 14, 2021, T. Y. Du, YNA40 (MHZU 23-0035, **holotype**), ex-type, ZHKUCC 2-0071; other living culture, GZCC 23-0615.

Notes: In the present phylogenetic analyses, our new collection *Corynespora aquilariae* formed a well-separated and sister lineage to *Cor. citricola* (CBS 169.77, Nursery PG FL and CABI211585) with 97% ML and 1.00 PP statistical support (Figure 6.7). Additionally, *Cor. citricola* differs from *Cor. aquilariae* in having subcylindrical or obovate, subhyaline, 4–18 pseudoseptata conidia (Ellis, 1957), while conidia of *Cor. aquilariae* is obclavate, subhyaline to brown, 10–16-distoseptate. Morphologically, *Cor. aquilariae* share similar cylindrical conidiophores and acrogenous, solitary conidia with *Cor. nabanheensis* J. W. Liu & J. Ma (Liu et al., 2023a). However, *Cor. aquilariae* differs from *Cor. nabanheensis* in having longer conidia (99 × 14 μm), subhyaline to brown, 10–16-distoseptate, while *Cor. nabanheensis* has shorter conidia (66.5 × 13 μm), brown to golden brown, nine to 13-distoseptate (Liu et al., 2023a). Overall, we introduce our new collection, *Cor. aquilariae*, as a new species based on both morphological study and phylogenetic analyses. Due to this genus's limited molecular sequence data, more research is needed.

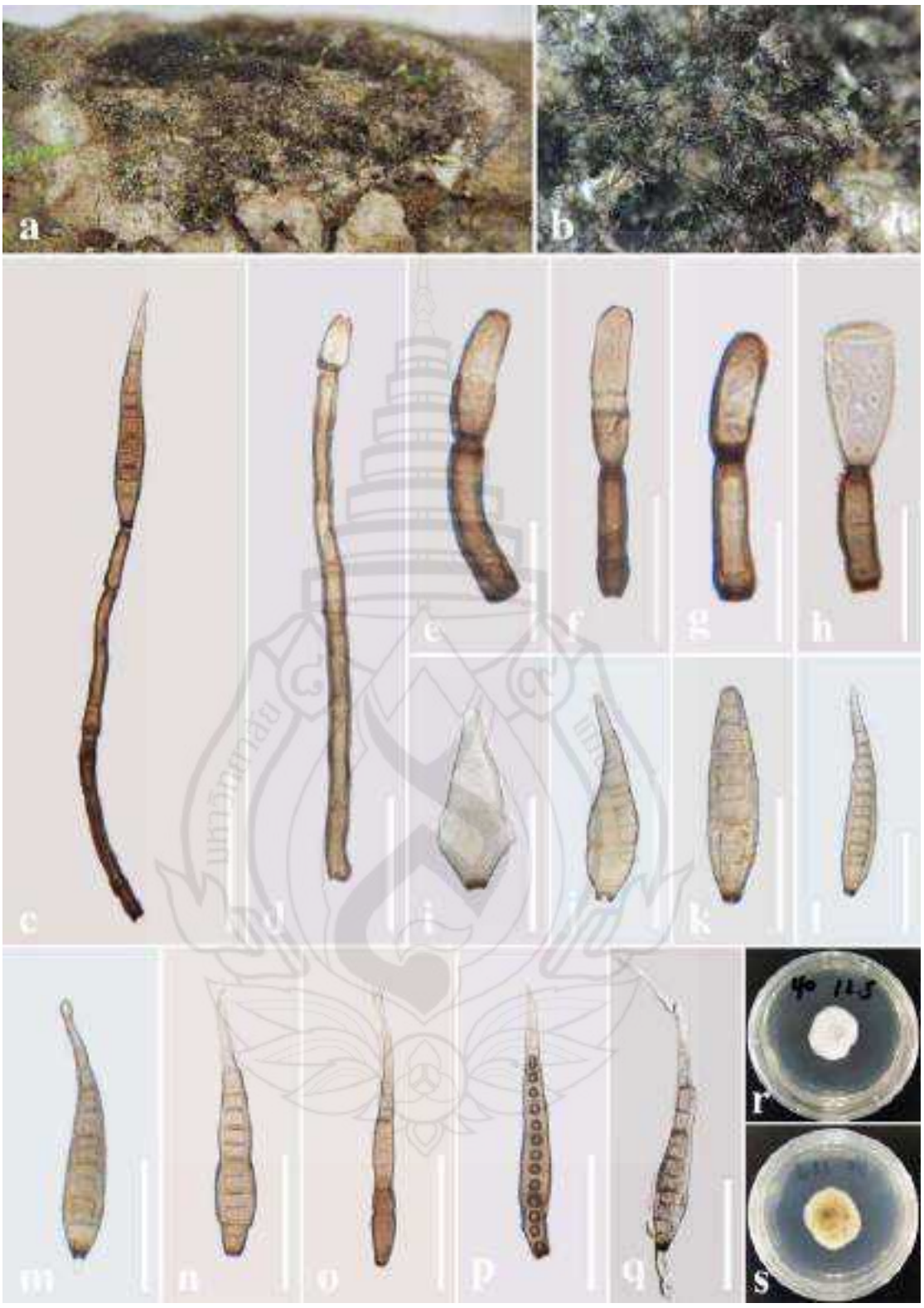


Figure 6.6 *Corynespora aquilariae* (MHZU 23-0035, holotype)

Figure 6.6 a, b, Appearance of hyphomycetes on the host. c–h, Conidiophores, conidiogenous cells, and conidia. i–p, Conidia. q, Germinated conidium. r, s, Colony on potato dextrose agar (PDA) obverse and reverse view. Scale bars: c, d = 50 µm, e–i = 20 µm, j–q = 50 µm.

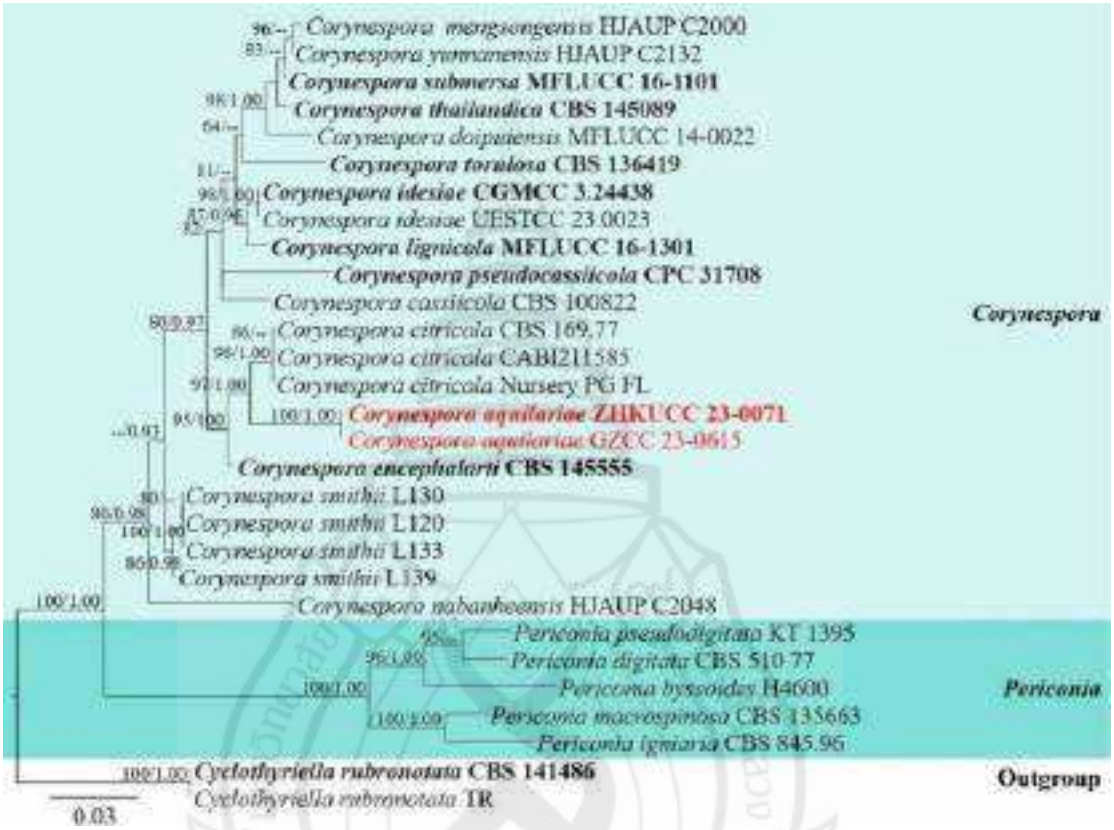


Figure 6.7 Phylogenetic tree of *Corynespora*

Figure 6.7 Bootstrap support values for ML greater than 60% and Bayesian posterior probabilities greater than 0.90 are given near the nodes, respectively. The tree is rooted with *Cyclothyriella rubronotata* (CBS 141486 and TR). The new isolates are indicated in red, and the ex-type strains are in bold.

Didymosphaeriaceae Munk 1953

Camarographium Bubák 1916

Notes: *Camarographium* was introduced by Bubák (1916) to accommodate *Cam. stephensii* (Berk. & Broome) Bubák as type species. Crous et al. (2022) designated a neotype of *Cam. stephensii* due to the type material of *Cam. stephensii* has presumably been lost and gave the phylogenetic placement of *Cam. stephensii* in Didymosphaeriaceae. *Camarographium* is characterized by asexual morph (two types of conidia): conidiomata globose, unilocular, conidiogenous cells enteroblastic, phialidic, ampulliform to doliiform, macroconidia globose, ellipsoid or irregular in shape, brown, with up to five transverse septa, numerous longitudinal or oblique septa; microconidiogenous cells phialidic, holoblastic, ampulliform to doliiform, microconidia subglobose to ellipsoidal, truncate at base, rounded at apex. While sexual morph is undetermined (Sutton & Rizwi, 1980; Verkley et al., 2005; Crous et al., 2011; Wijayawardene et al., 2016; Crous et al., 2022). Members of *Camarographium* were found as saprobes on a wide range of hosts (e.g., *Acacia sphaerocephala* Cham. and Schltdl., *Ammophila* sp., *Betula papyrifera* Marshall, *Carpinus betulus* L., *Clematis vitalba* L., *Cornus kousa* F. Buerger ex Hance, *Pteridium aquilinum* (L.) Kuhn, *Scorzonera pusilla* Pall., and *Stachytarpheta jamaicensis* (L.) Vahl) (Wijayawardene et al., 2016; Crous et al., 2022). Currently, nine epithets of *Camarographium* are listed in Index Fungorum (2025), while only *Cam. stephensii* has molecular data in NCBI (https://www.ncbi.nlm. nih.gov/, accessed on November 29, 2023). In this study, based on morphological comparisons, we introduce a new host (*Aquilaria sinensis*) and geographic record (China) of *Cam. clematidis* Wijayaw., Camporesi, McKenzie & K. D. Hyde, and provide molecular data for *Cam. clematidis* for the first time.

Camarographium clematidis Wijayaw., Camporesi, McKenzie & K. D. Hyde

MycoBank number: MB 551767; Facesoffungi number: FoF 01447; Figure 6.8

Saprobic on dead branch of *Aquilaria sinensis*. **Sexual morph:** undetermined. **Asexual morph:** coelomycetous. *Conidiomata* 450–820 µm long × 200–500 µm wide × 300–650 µm high ($\bar{x}$ = 610 × 346 × 400 µm, n = 10), pycnidial, immersed, slightly rising causing bark cracking, the mature conidia scattered around the ostioles, solitary or scattered in small groups, uniloculate, obpyriform, elliptical or irregular, brown to dark brown. *Ostiolar canal* 120–150 µm high × 80–110 µm wide ($\bar{x}$ = 134 × 100 µm,

n = 10), single, central, circular, brown to dark brown, cylindrical, without periphyses. *Conidiomata walls* 20–45 µm wide, composed of several light brown to dark brown cells of textura angularis. *Hamathecium* comprising hyaline, filiform, septate, unbranched, pseudoparaphyses. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* short, holoblastic, hyaline, discrete, determinate, cylindrical to elliptical, unbranched, aseptate, smooth, arising from the inner cavity of the conidioma wall, disappear after the conidia maturity. *Conidia* (35–)40–50(–54) × (17–)20–29 (–31) µm ($\overline{x}$ = 46.5 × 24.5 µm, n = 30), hyaline when young, with transverse-septate when immature, becoming yellow brown to dark brown, oblong to ellipsoidal, or asymmetrical, muriform, not constricted at the septum, thin and smooth- walled, guttulate.

Culture characteristics: Conidia germinated on PDA after 12 h, germ tubes were produced from each cell of the conidia. Colonies on PDA reaching 3–4 cm diam., after 1 week at 23°C–28°C. Colonies obverse: soft, circular, white aerial hypha, raised at the center and the outermost circle, entire edge. Colonies reverse: brown at the center, cream at the margin.

Material examined: CHINA, Guangdong Province, Maoming City, Dianbai District, Poxin, 21°34′25″ N, 111°7′43″ E, on dead branch of *Aquilaria sinensis* (Thymelaeaceae), June 3, 2022, T. Y. Du, MMA13 (MHZU 23-0020, Paratype), living cultures, ZHKUCC 23-0039; other living culture, GZCC 23-0610.

Known distribution: Italy (Wijayawardene et al., 2016).

Known hosts: *Clematis vitalba* (Wijayawardene et al., 2016).

Notes: *Camarographium clematidis* was introduced by Wijayawardene et al. (2016) based on morphology. Our collection and *Cam. clematidis* exhibit high similarities in morphological characteristics, such as the shape and color of conidiomata, conidiogenous cells and conidia, and the separation of conidia. Therefore, our collection is identified here as *Cam. clematidis*. Wijayawardene et al. (2016) mentioned that the single spore isolation of *Cam. clematidis* was successful, but the germinated spores did not continue to grow on the medium. In this study, pure cultures were successfully obtained from the single spores, thus multigene sequence data for *Cam. clematidis* are provided. In addition, pseudoparaphyses were seen in our collection, which were not seen in Wijayawardene et al. (2016). Moreover, this study discovered *Camarographium* species on *Aquilaria sinensis* in China for the first time, therefore,

our *Cam. clematidis* collection is reported as a new host and geographical record. In the present phylogenetic analyses, our collection forms a well-separated sister lineage to *Anastomitrabeculia didymospora* (MFLUCC 16-0412 and MFLUCC 16-0417) (Anastomitrabeculiaceae), which is distant from *Cam. stephensii* (CPC 41923 and 41598) (Didymosphaeriaceae) in the phylogenetic tree (Figure 6.9). Therefore, in this study, we place *Cam. clematidis* in *Camarographium sensu lato*, due to only *Cam. stephensii* and *Cam. clematidis* having available molecular data. When molecular data of other *Camarographium* species are available, the placement of *Cam. clematidis* can accurately be determined. Due to the lack of molecular data for most species in *Camarographium*, more collections from different geographical regions should be collected and sequenced in order to resolve the taxonomic uncertainties in the genus.

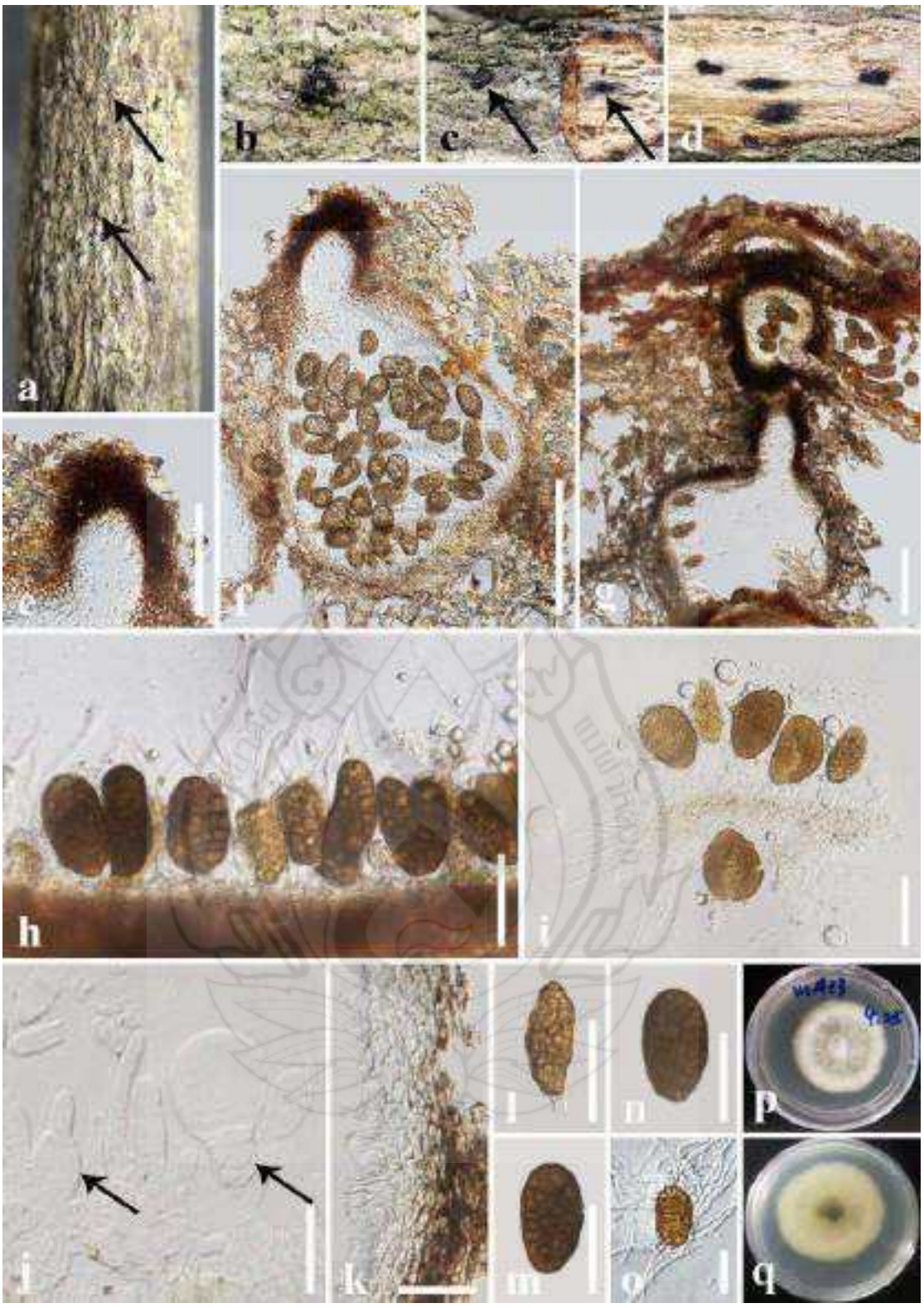


Figure 6.8 *Camarographium clematidis* (MHZU 23-0020 paratype)

Figure 6.8 a–c, Appearance of conidiomata on the host. d, Transverse sections through conidiomata on the host. e, Ostiole. f, g, Vertical sections through the conidiomata. h, i, Conidiogenous cells, conidia, and pseudoparaphyses. j, Conidiogenous cells. k, Conidioma wall. l–n, Conidia. o, Germinated conidium. p, q, Colony on potato dextrose agar (PDA) obverse and reverse view. Scale bars: e = 100 µm, f, g = 200 µm, h, i = 40 µm, j, k = 20 µm, l–o = 40 µm.

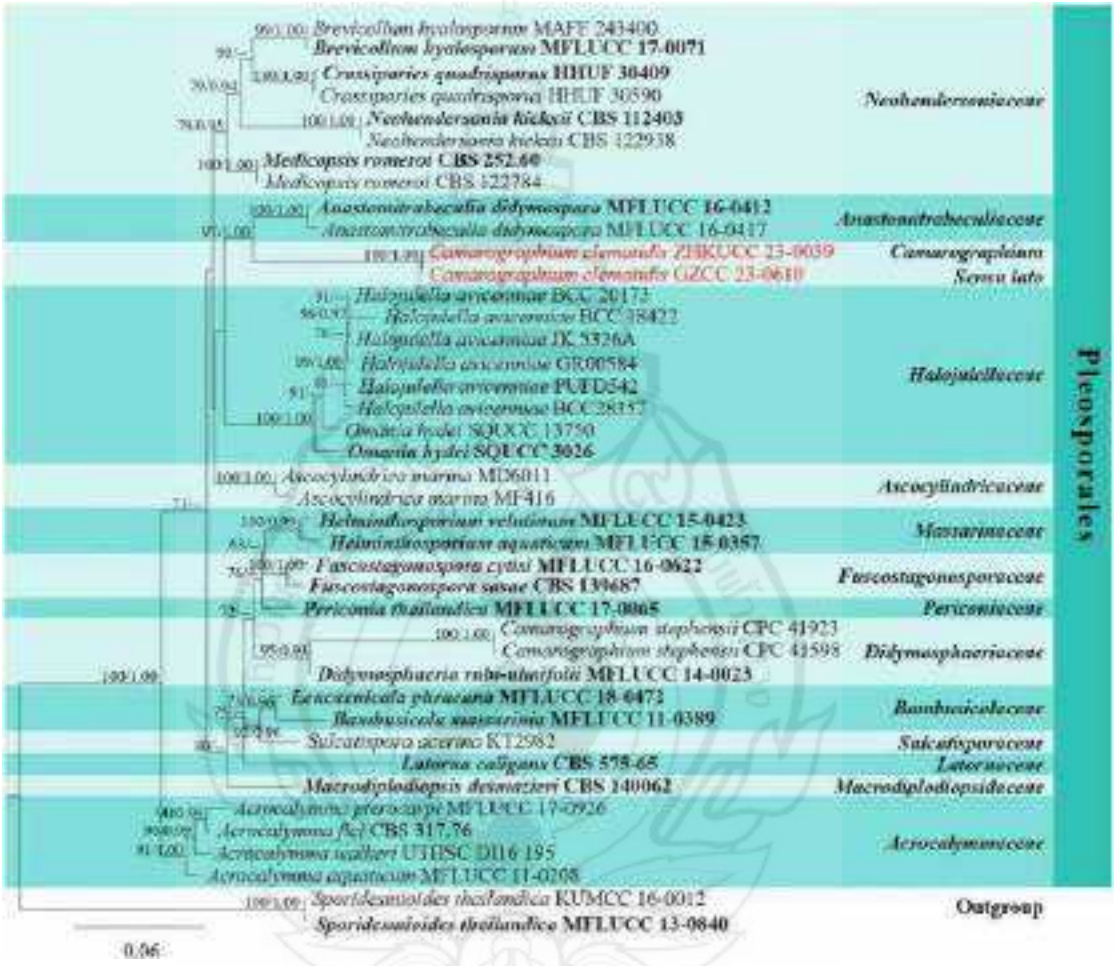


Figure 6.9 Phylogenetic tree of *Camarographium*

Figure 6.9 Bootstrap support values for ML greater than 60% and Bayesian posterior probabilities greater than 0.90 are given near the nodes, respectively. The tree is rooted with Sporidesmioides thailandica (KUMCC 16-0012 and MFLUCC 13-0840). The new isolates are indicated in red, and the ex-type strains are in bold.

Nigrogranaceae Jaklitsch & Voglmayr 2016

Nigrograna Gruyter, Verkley & Crous 2013

Notes: *Nigrograna* was introduced as a new genus by De Gruyter et al. (2013) and typified by *Nigrograna mackinnonii* (Borelli) Gruyter, Verkley & Crous (=*Pyrenochaeta mackinnonii* Borelli), which was isolated from human mycetomata (Jaklitsch & Voglmayr, 2016). However, Ahmed et al. (2014) synonymized *Nigrograna* under Biatriospora K. D. Hyde & Borse based on the phylogenetically closely related *N. mackinnonii* with the type species of *Biatriospora* (*B. marina* K. D. Hyde & Borse). Subsequently, Jaklitsch and Voglmayr (2016) established the family Nigrograna ceae to accommodate *Nigrograna* based on its unique morphological characteristics. While, Jaklitsch and Voglmayr (2016) mentioned all *Nigrograna* species are morphologically very similar that, can be interpreted as cryptic species. In 2018, four endophytic species of *Biatriospora* were synonymized under *Nigrograna* (Kolařík, 2018). Lu et al. (2022) introduced three new saprobic species in *Nigrograna*. Recently, Li et al. (2023) introduced four new species in this genus. Currently, 45 epithets of *Nigrograna* are listed in Index Fungorum (2025). Members of this genus have been recorded from marine and terrestrial habitats as saprobes, endophytes, and human pathogens (Hyde et al., 2017; Tibpromma et al., 2017; Kolařík, 2018; Zhao et al., 2018; Dayarathne et al., 2020; Zhang et al., 2020; Boonmee et al., 2021; Lu et al., 2022; Li et al., 2023). *Nigrograna* is characterized by black, globose to subglobose, ostiolate ascomata, clavate, fissitunicate, short pedicellate asci, and pale to chocolate brown, fusoid to narrowly ellipsoid, asymmetric, septate ascospores (Zhang et al., 2020; Boonmee et al., 2021; Lu et al., 2022). Asexual morph is characterized by pycnidia similar to ascomata and usually co- occurring with ascomata, branched conidiophores, filiform, with pegs, phialides terminal, one-celled conidia, oblong, cylindrical or allantoid, hyaline or subhyaline, smooth (Jaklitsch & Voglmayr, 2016). This study introduces one new saprobic species, *Nigrograna aquilariae*, collected from *Aquilaria sinensis* in terrestrial habitats based on morphology and multigene phylogenetic analyses. In addition, this is the first record of *Nigrograna* species on *Aquilaria sinensis*.

Nigrograna aquilariae T. Y. Du, Tibpromma & Karun., ***sp. nov.***

MycoBank number: MB 853999; Facesoffungi number: FoF 15263; Figure 6.10

Etymology: Named after its host genus *Aquilaria*.

Holotype: MHZU 23-0034

Saprobic on dead branches of *Aquilaria sinensis*. **Sexual morph:** *Ascomata* (excluding neck) 180–270 µm high × 200–300 µm diam. ($\overline{x}$ = 205 × 225 µm, n = 10), solitary, immersed in the substrate, globose to subglobose, dark brown to black, appearing as black ostiolar canal, surrounded by brown hair-like setae. *Ostiolar canal* 150–200 µm long × 50–100 µm wide ($\overline{x}$ = 175 × 82 µm, n = 10), straight or slightly curved, without periphyses. *Peridium* 15–40 µm wide, comprising several layers, thick-walled cells, comprising brown to dark brown cells of *textura angularis*. *Hamathecium* comprising 2–3 µm wide, hyaline, filiform, branched, septate, pseudoparaphyses. *Asci* (51–)56–64(–67) × 7–9(–11) µm ($\overline{x}$ = 59 × 8.5 µm, n = 20), bitunicate, fissitunicate, eight- spored, clavate, straight or slightly curved, with a 5–9 µm long pedicel, apically rounded. *Ascospores* 10–13 × 3.5–4.5 µm ($\overline{x}$ = 11 × 4 µm, n = 30), uniseriate to biseriate, fusiform or inequilateral, asymmetric, with slightly obtuse ends, the two cells in the upper part are larger than those in the lower part, hyaline to brown with age, one- (two to three)-septate when mature, slightly constricted at the septum, curved, guttulate, without sheath and appendages. **Asexual morph:** undetermined.

Culture characteristics: Ascospores germinated on PDA after 24 h, germ tubes were produced from both ends. Colonies on PDA reaching 2–3 cm diam., after 1 week at 23°C–28°C. Colonies obverse: dense, circular, annular, white, raised at the center, entire edge light reddish brown. Colonies reverse: the center is brown, and the outer circle is light reddish brown.

Material examined: CHINA, Yunnan Province, Xishuangbanna, Menghai City, agarwood plantation, 22°3′22″ N, 100°40′2″ E, on dead branches of *Aquilaria sinensis* (Thymelaeaceae), September 15, 2021, T. Y. Du, YNA38 (MHZU 23-0034, **holotype**), ex-type living culture, ZHKUCC 23-0070; other living culture, GZCC 23-0614.

Notes: In the present phylogenetic analyses, our new collection *Nigrograna aquilariae* formed a well-separated and sister lineage to *N. lincangensis* (ZHKUCC 23-0798 and ZHKUCC 23-0798) with 73% ML, 0.90 BYPP statistical support (Figure 6.11). Morphologically, *N. lincangensis* can be distinguished from *N. aquilariae* in

having globose or ellipsoid ascomata without brown hair- like setae, unbranched pseudoparaphyses and fusoid to narrowly ellipsoid ascospores (Xu et al., 2024), while the globose to subglobose ascomata of *N. aquilariae* are surrounded by brown hair-like setae, branched pseudoparaphyses and fusiform or inequilateral, asymmetric ascospores. In addition, the base pair differences of the LSU, SSU, and *tef*1-α genes between our new collection and *N. lincangensis* (ZHKUCC 23-0798, ex-type) were compared, and the results showed that there are insignificant nucleotide differences, while ITS has 1.04% nucleotide differences (5/476 bp, without gaps), and *rpb*2 has 2.91% nucleotide differences (30/1031 bp, without gaps) which reveals that they belong to different species. Therefore, based on phylogenetic analyses and morphological comparison, *N. aquilariae* is described herein as a new species from terrestrial habitats. In addition, some species of this genus have only provided partial gene sequences in NCBI (https://www.ncbi.nlm.nih. gov/), such as *Nigrograna schinifolii* (ITS and *tef*1-α), *Nigrograna trachycarpi* (ITS and *tef*1-α) and *Nigrograna verniciae* (LSU, ITS, and *tef*1-α). Due to all *Nigrograna* species are morphologically very similar (Jaklitsch & Voglmayr, 2016), phylogenetic analysis is very important in the taxonomy of this genus. In order to better classify the *Nigrograna* taxa, we suggest to carry out multigene phylogenetic analyses (LSU, ITS, SSU, *tef*1-α, and *rpb*2), together with the morphological study.

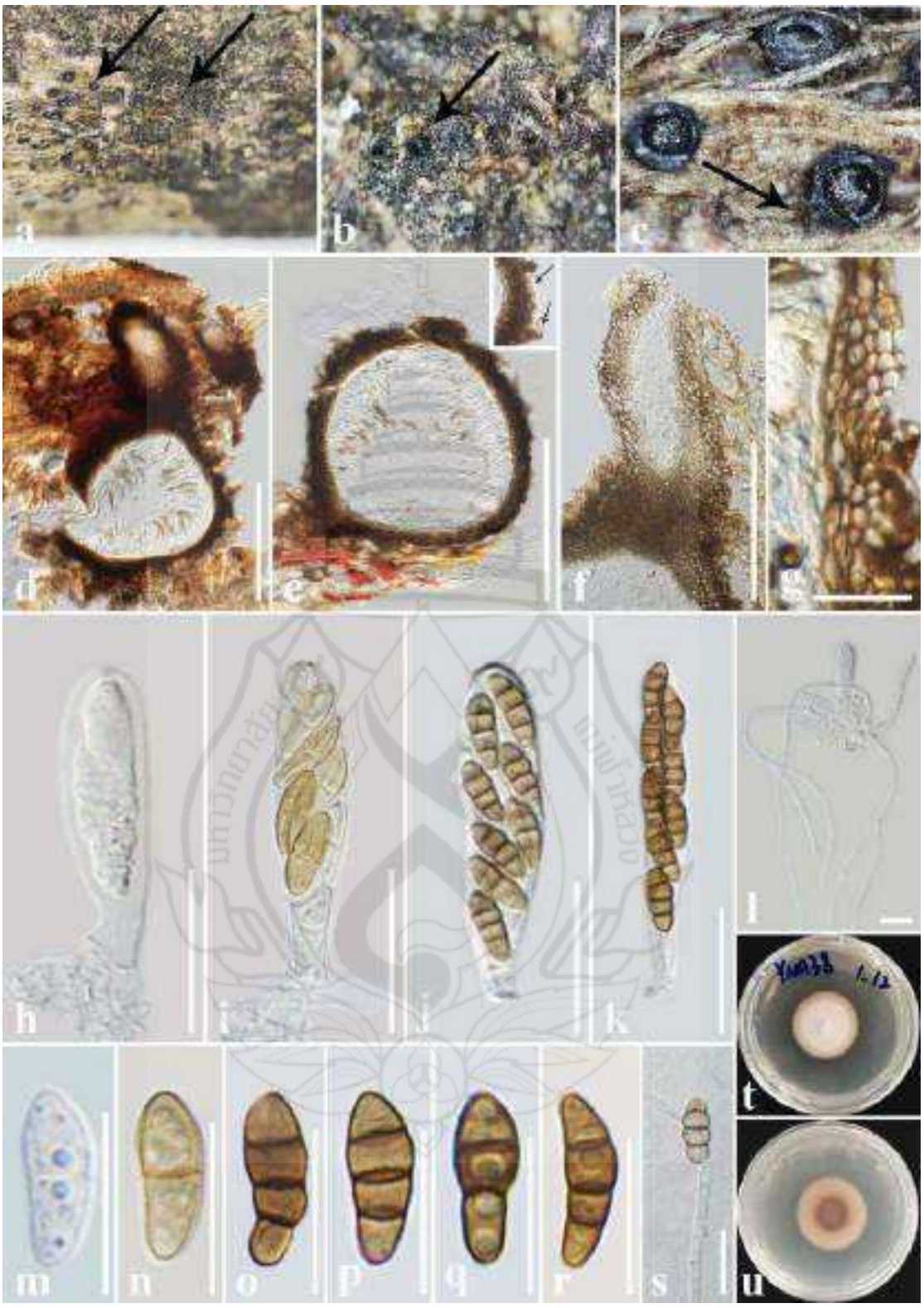


Figure 6.10 *Nigrograna aquilariae* (MHZU 23-0034, holotype)

Figure 6.10 a, b, Appearance of ascomata on the host. c, Transverse sections through the ascomata on the host (the arrow points towards the brown hair-like setae on the surface of the ascomata). d, e, Vertical sections through the ascomata (the arrow points towards the brown hair-like setae on the surface of the ascomata). f, Ostiole without periphyses. g, Peridium. h–k, Asci. l, Pseudoparaphyses. m–r, Ascospores. s, Germinated ascospore. t, u, Colony on potato dextrose agar (PDA) obverse and reverse view. Scale bars: d, e = 200 µm, f = 100 µm, g–k = 20 µm, l–s = 10 µm.

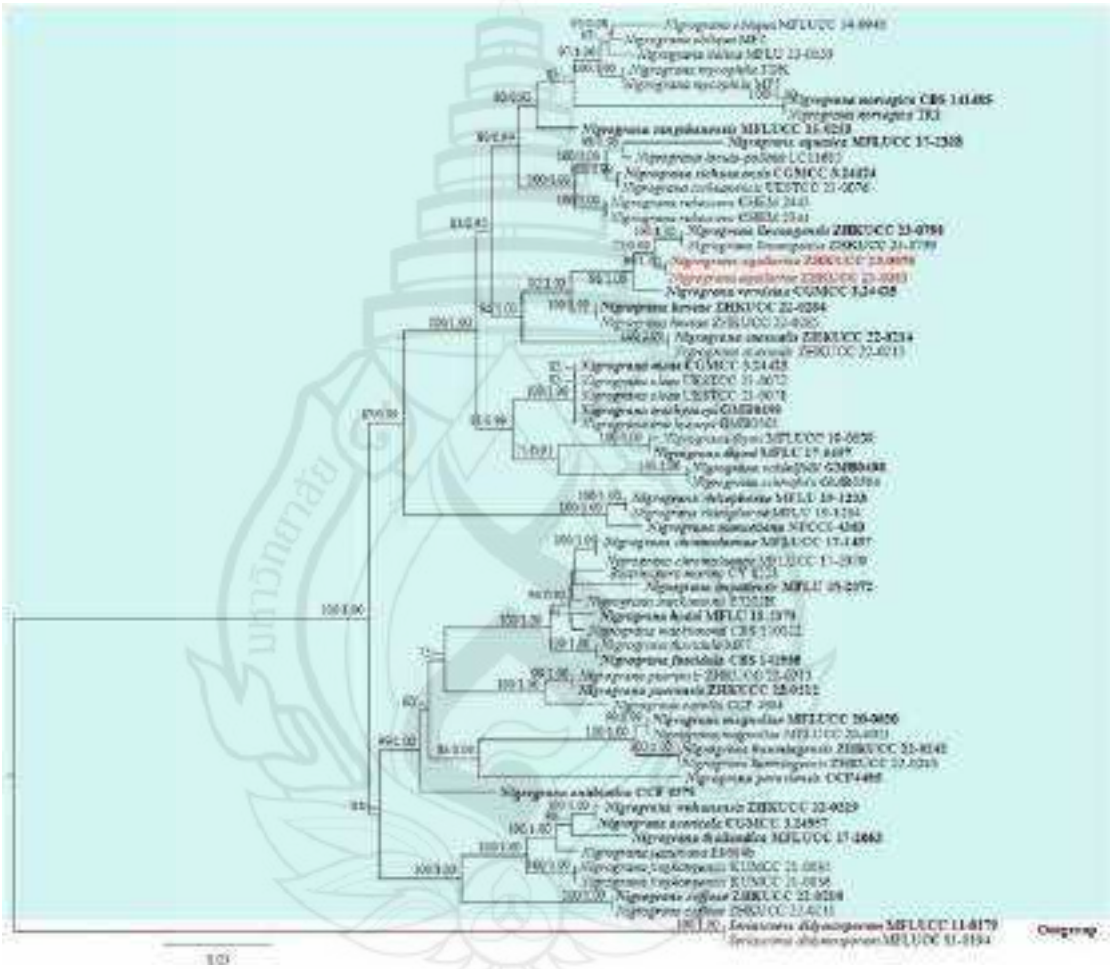


Figure 6.11 Phylogenetic tree of *Nigrograna*

Figure 6.11 Bootstrap support values for ML greater than 60% and Bayesian posterior probabilities greater than 0.90 are given near the nodes, respectively. The tree is rooted with Seriascoma didymospora (MFLUCC 11-0179, MFLUCC 11-0194). The new isolates are indicated in red, and the ex-type strains are in bold.

Phaeoseptaceae S. Boonmee, Thambugala & K. D. Hyde 2018

Phaeoseptum Ying Zhang, J. Fourn. & K. D. Hyde, in Zhang 2013

Notes: *Phaeoseptum* was introduced by Zhang et al. (2013) to accommodate *Pha. aquaticum* Ying Zhang, J. Fourn. & K. D. Hyde as the type species, collected from freshwater habitats. *Phaeoseptum* was placed in Halotthiaceae based on LSU sequence data by Zhang et al. (2013). Later, Hyde et al. (2018) introduced the second species *Pha. terricola* S. Boonmee & K. D. Hyde as a saprobe from Thailand, and based on their multigene phylogenetic analysis, *Phaeoseptum* was transferred from Halotthiaceae to a new family Phaeoseptaceae. Currently, nine epithets of *Phaeoseptum* are listed in Index Fungorum (2025). *Phaeoseptum* is characterized by ascomata immersed under pseudoclypeus, scattered to gregarious, depressed globose, bitunicate asci, cylindrical-clavate or broadly fusoid, eight-spored, with a small ocular chamber, fusiform ascospores; while the asexual morph of this genus has not been determined (Zhang et al., 2013; Hyde et al., 2018; Jayawardena et al., 2022). Later, Wanasinghe et al. (2020) found the asci of *Pha. hydei* Wanas., Senwanna & Mortimer with 32-spored, and *Pha. thailandicum* Samarak. & K. D. Hyde introduced by Jayawardena et al. (2022), possesses both eight-spored and 32-spored asci, which is extremely rare. This study introduces the new species *Phaeoseptum aquilariae*, which was collected from *Aquilaria yunnanensis* in terrestrial habitats of China based on morphological comparisons and phylogenetic analyses. Additionally, this is the first report of a *Phaeoseptum* species on *Aquilaria yunnanensis*.

Phaeoseptum aquilariae T. Y. Du, Tibpromma & Karun., ***sp. nov.***

MycoBank number: MB 854000; Facesoffungi number: FoF 15264; Figure 6.12

Etymology: Named after its host genus *Aquilaria*.

Holotype: MHZU 23-0032

Saprobic on dead branches of *Aquilaria yunnanensis*. **Sexual morph:** *Ascomata* 200–400 µm high × 500–1000 µm long × 200–400 µm diam. ($\bar{x}$ = 265 × 715 × 275 µm, n = 10), scattered to gregarious, depressed-spherical, laterally fattened, fully immersed under a small blackened pseudoclypeus, appearing on host surface as black irregular spots or elongated regions, with an apical ostiole, short papillate, ostiole with transverse cells, without periphyses. *Pseudoclypeus* is composed of host cells with black deposits. *Peridium* 15–55 µm ($\bar{x}$ = 28 µm, n = 20) wide, pseudoparenchymatous, comprising

several layers of thin-walled cells, outer layers dark brown to black, somewhat angular cells of *textura angularis*; inner layers hyaline to lightly pigmented angular cells of *textura angularis*. *Hamathecium* comprising 2 µm wide, septate, branched pseudoparaphyses, embedded in a gelatinous matrix between and above the asci. *Asci* (109–) 121–131(–136) × 26–30 µm ($\overline{x}$ = 124 × 28 µm, n = 30), bituni-cate, fissitunicate, eight-spored, cylindrical-clavate, long with club-like pedicellate, apically rounded with a small ocular chamber. *Ascospores* (25–)27–30(–32) × (7–)8–10 µm ($\overline{x}$ = 28 × 9 µm, n = 30), uniseriate to slightly overlapping two-seriate, hyaline to yellow when young, yellow-brown with age, allantoid, broadly fusoid, slightly curved, muriform, with broadly rounded ends, smooth-walled, 10–12-transverse septa, with one to five longitudinal septa in nearly all median cells, not constricted at the septa, the septa thickened and heavily pigmented at maturity, without sheath or appendages. **Asexual morph:** undetermined.

Culture characteristics: Ascospores germinated on PDA after 24 h, germ tubes were produced from both ends. Colonies on PDA reaching 2–3 cm diam., after 2 weeks at 23°C–28 °C. Colonies obverse: dense, circular, white, aerial hypha raised at the center, entire edge light brown. Colonies reverse: dark brown, cracked at the center, light brown at the margin.

Material examined: CHINA, Yunnan Province, Xishuangbanna, Jinghong City, Gasa, Naban River Basin National Nature Reserve, 22°7′50″ N, 100°40′29″ E, on dead branches of *Aquilaria yunnanensis* (Thymelaeaceae), September 14, 2021, T. Y. Du, YNA32 (MHZU 23-0032, **holotype**), ex-type living culture, ZHKUCC 23-0068; other living culture, GZCC 23-0613.

Notes: In the present phylogenetic analyses, our new collection *Pha. aquilariae* formed a well-separated and sister lineage to *Pha. terricola* (MFLUCC 10-0102) (Figure 6.13). Morphologically, *Pha. aquilariae* share similar asci and ascospores shapes and branched, septate, anastomosed pseudoparaphyses with *Pha. terricola* (Hyde et al., 2018). However, *Pha. terricola* differs from *Pha. aquilariae* in having globose to subglobose ascomata, ascospores with 9–10(–11) transverse septa, and one or two longitudinal septa in each cell, and smaller ascomata, asci, and ascospores than *Pha. aquilariae* (ascomata: 172 × 183.5 µm vs. 265 × 275 µm; asci: 79 × 16 µm vs. 124 × 28 µm; ascospores: 22 × 6 µm vs. 28 × 9 µm) (Hyde et al., 2018). In addition,

the base pair differences of the LSU, ITS, and SSU genes between our new collection and *Pha. terricola* (MFLUCC 10-0102, ex- type) were compared, and the results showed that there are no nucleotide differences, while *tef*1-α has 7.6% nucleotide differences (61/798 bp, without gaps), which reveals that they belong to different species of the same genus. Therefore, we introduce our new collection as a new species *Pha. aquilariae* based on morphological study and phylogenetic analyses.

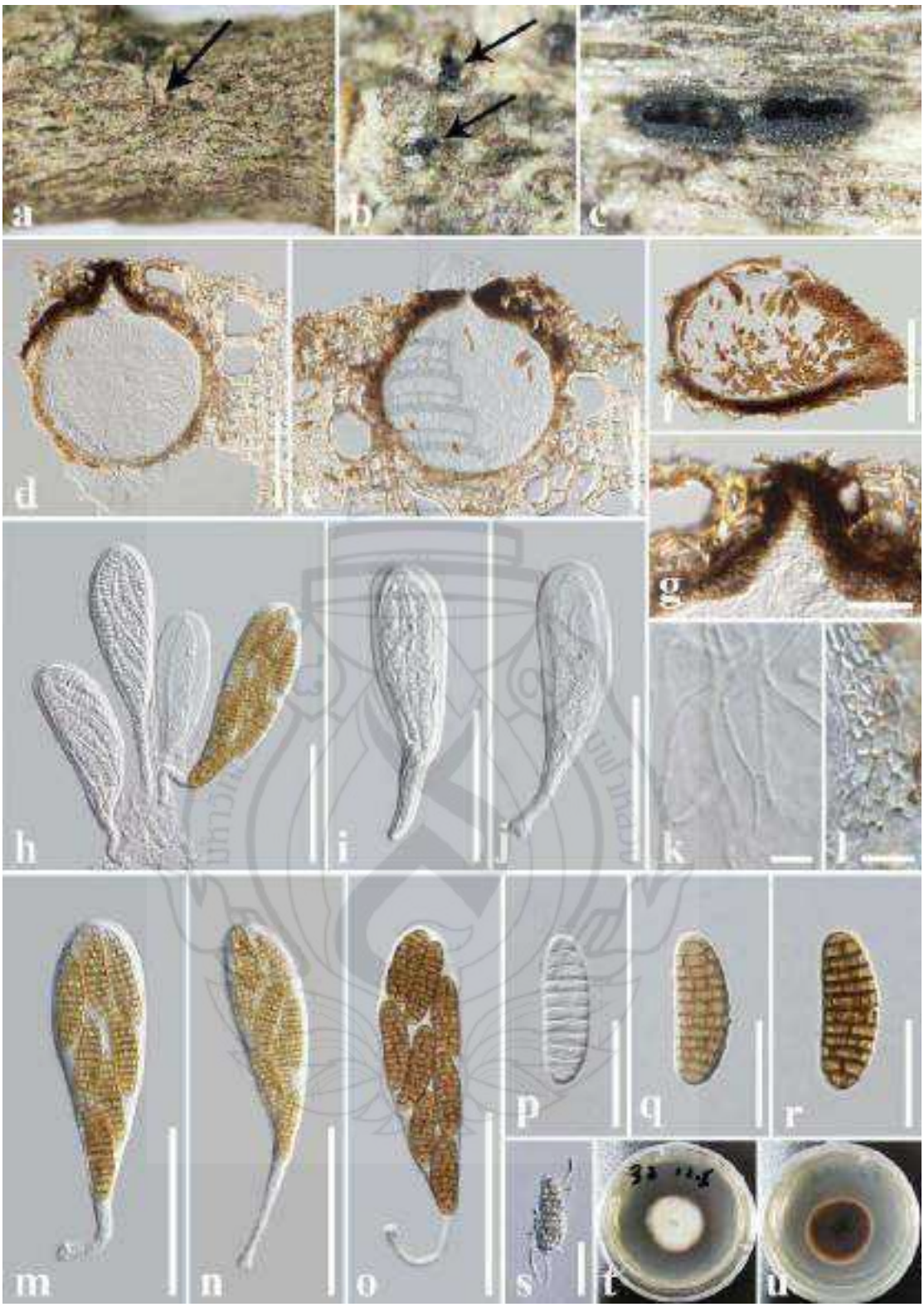


Figure 6.12 *Phaeoseptum aquilariae* (MHZU 23-0032, holotype)

Figure 6.12 a, b, Appearance of ascomata on the host. c, Transverse sections through ascomata on the host. d–f, Vertical sections through the ascomata. g, Ostiole without periphyses. h–j, m–o, Asci. k, Pseudoparaphyses. l, Peridium. p–r, Ascospores. s, Germinated ascospore. t, u, Colony on potato dextrose agar (PDA) obverse and reverse view. Scale bars: d–f = 200 µm, g–j = 50 µm, k, l = 10 µm, m–o = 50 µm, p–s = 20 µm.

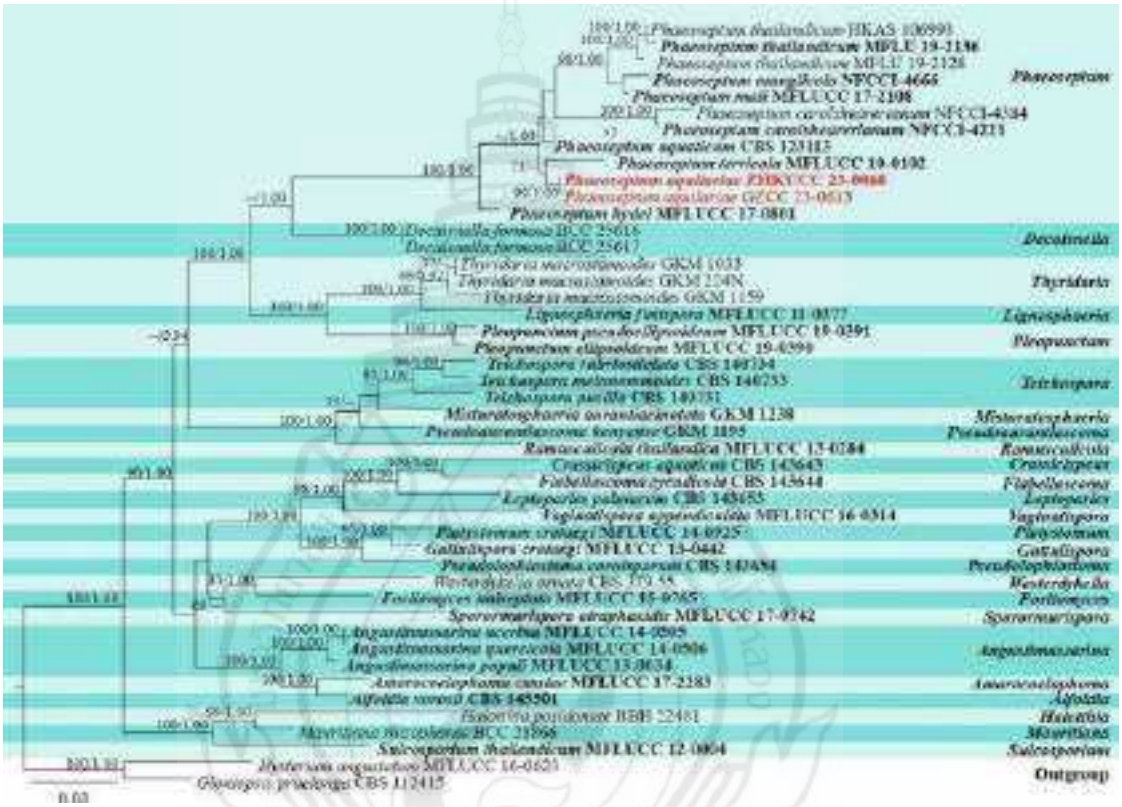


Figure 6.13 Phylogenetic tree of *Phaeoseptum*

Figure 6.13 Bootstrap support values for ML greater than 60% and Bayesian posterior probabilities greater than 0.90 are given near the nodes, respectively. The tree is rooted with Gloniopsis praelonga (CBS 112415) and Hysterium angustatum (MFLUCC 16-0623). The new isolates are indicated in red, and the ex-type strains are in bold.

Thyridariaceae Q. Tian & K. D. Hyde 2013

Aquilariomyces T. Y. Du, Tibpromma & Karun. ***gen. nov.***

MycoBank number: MB 854001; Facesoffungi number: FoF 15265

Etymology: Named after its host genus *Aquilaria*, combined with "myces" refers to the fungus.

Saprobic on decaying wood in terrestrial habitats. **Sexual morph:** *Ascomata* solitary, or gregarious in small groups, brown to dark brown, surrounded by long brown to black fluff, immersed under the bark, inconspicuous, globose to subglobose, apapillate ostioles, with pore-like opening. *Peridium* comprising three to five layers, hyaline to brown cells of *textura angularis*, fusing with the host tissue. *Hamathecium* comprising numerous, hyaline, septate, branched, pseudoparaphyses, embedded in a gelatinous matrix. *Asci* eight-spored, bitunicate, fissitunicate, thick-walled, clavate, with short pedicel, club-shaped, apically rounded, with an ocular chamber. *Ascospores* uniseriate, slightly overlapping, hyaline, one- transverse septate, constricted at the septum, fusiform to ellipsoidal, above cells are slightly larger than below cells, rough-walled, several guttulate and granules, surrounded by mucilaginous sheath. **Asexual morph:** undetermined.

Type species: ***Aquilariomyces aquilariae*** T. Y. Du, Tibpromma & Karun.

Notes: In the present phylogenetic analyses based on a combined data set of LSU, ITS, SSU, *tef*1-α, and *rpb*2 sequence data show that our new collection is well-separated and formed an independent lineage with the two strains of *Thyridariella mangrovei* Devadatha, V. V. Sarma, K. D. Hyde, D. N. Wanas. & E. B. G. Jones (NFCCI 4213 and NFCCI 4214), one strain of *Pseudothyridariella chromolaenae* Mapook & K. D. Hyde (MFLUCC 17-1472), two strains of *Pse. aquilariae* T. Y. Du, Tibpromma & Karun. (ZHKUCC 23-0044 and ZHKUCC 23-0061), and one strain of *Pse. idesiae* W. L. Li & Jian K. Liu (CGMCC 3.24439) with 98% ML, 1.00 BYPP statistical support (Figure 6.18). Our new collection shares comparable characteristics with *Th. mangrovei* in having globose to subglobose ascomata, clavate, pedicellate, eight-spored asci, and hyaline, fusiform to ellipsoidal ascospores surrounded by a sheath (Devadatha et al., 2018). However, our new collection differs from *Th. mangrovei* by its immersed ascomata, apapillate ostioles, and one-transverse septate ascospore, while *Th. mangrovei* has immersed to erumpent ascomata, ostiolate with reddish-brown

neck, and muriform ascospore (Devadatha et al., 2018). Our new collection shares similar characteristics with *Pse. chromolaenae* in having immersed ascomata, clavate, pedicellate, eight-spored asci, and fusiform to ellipsoidal ascospores surrounded by a sheath (Mapook et al., 2020). However, our new collection differs from *Pse. chromolaenae* by its globose to subglobose ascomata, hyaline, one-transverse septate ascospore, while *Pse. chromolaenae* has obpyriform ascomata, brown or olivaceous-brown to dark brown, muriform ascospore (Mapook et al., 2020). While *Pse. aquilariae* has been found only as an asexual morph, our new collection has been found as a sexual morph, so a morphological comparison is improbable. Additionally, our new collection shares a similar morphology to *Chromolaenomyces appendiculatus* Mapook & K. D. Hyde in having immersed, globose to subglobose ascomata, and uniseptate, hyaline ascospores (Mapook et al., 2020). However, our new collection differs from *Chr. appendiculatus* by its clavate asci and ascospore surrounded by a mucilaginous sheath, with no appendages formed. In contrast, *Chr. appendiculatus* has cylindrical asci, and ascospores with a narrow sheath drawn out to form polar appendages from both ends of the ascospores (Mapook et al., 2020). *Aquilariomyces* can be distinguished from *Parathyridaria* and *Thyridaria* in having uniseptate, hyaline, and fusiform to ellipsoidal ascospores, while the sexual morph of *Cycasicola*, *Liua* and *Parathyridariella* have not been reported. Therefore, we introduce a new genus *Aquilariomyces* from dead branches of *Aquilaria yunnanensis* in China.

Aquilariomyces aquilariae T. Y. Du, Tibpromma & Karun. ***sp. nov.***

MycoBank number: MB 854002; Facesoffungi number: FoF 15266; Figure 6.14

Etymology: Named after its host genus *Aquilaria*.

Holotype: MHZU 23-0036

Saprobic on decaying wood of *Aquilaria yunnanensis*. **Sexual morph:** *Ascomata* 200–350 µm high × 200–300 µm diam. ($\overline{x}$ = 285 × 265 µm, n = 10), solitary, or gregarious in small groups, brown to dark brown, surrounded by long brown to black fluff, immersed under the bark, inconspicuous, globose to subglobose, apapillate ostioles, with a pore-like opening. *Peridium* 10–55 µm ($\overline{x}$ = 30 µm, n = 20) wide, comprising three to five layers of hyaline to brown cells of *textura angularis*, fusing with the host tissue. *Hamathecium* comprising 1–2 µm wide, numerous, hyaline, septate, branched, pseudoparaphyses, embedded in a gelatinous matrix. *Asci* (65–) 90–110(–

128) × 23.5–32 µm ($\overline{x}$ = 100 × 27 µm, n = 30), eight-spored, bitunicate, fissitunicate, thick-walled, clavate, with short pedicel, club-shaped, apically rounded, with an ocular chamber. *Ascospores* 27–31.5 × 11–14 µm ($\overline{x}$ = 29 × 12.5 µm, n = 30), uniseriate, slightly overlapping, hyaline, 1- septate, constricted at the septum, fusiform to ellipsoidal, above cells are slightly larger than below cells, rough-walled, several guttulate and granules, surrounded by mucilaginous sheath, and the sheath of immature ascospores is significantly wider than that of mature ascospores. **Asexual morph:** undetermined.

Culture characteristics: Ascospores germinated on PDA after 24 h, and germ tubes were produced from both ends. Colonies on PDA reaching 2–3 cm diam., after 2 weeks at 23°C–28°C. Colonies obverse: dense, circular, white, raised at the center, entire edge. Colonies reverse: dark brown to black at the center, cream to light brown at the margin.

Material examined: CHINA, Yunnan Province, Xishuangbanna, Jinghong City, Gasa, Naban River Basin National Nature Reserve, 22°7′50″ N, 100°40′29″ E, on dead branches of *Aquilaria yunnanensis* (Thymelaeaceae), 14 September 2021, T. Y. Du, YNA43 (MHZU 23-0036, **holotype**), ex-type living culture, ZHKUCC 23-0072; other living culture, GZCC 23-0616.

Notes: In the present phylogenetic analyses, our new collection *Aquilariomyces aquilariae* formed a well-separated sister lineage to the strains of *Thyridariella mangrovei*, *Pseudothyridariella chromolaenae*, *Pse. idesiae*, and *Pse. aquilariae* with 98% ML, 1.00 BYPP statistical support (Figure 6.18). *Aquilariomyces aquilariae* shares similar characteristics with *Th. mangrovei* and *Pse. chromolaenae* in having clavate, pedicellate, eight-spored asci, and fusiform to ellipsoidal ascospores surrounded by a sheath (Devadatha et al., 2018; Mapook et al., 2020). However, *Aqu. aquilariae* differs from *Th. mangrovei* and *Pse. chromolaenae* by its one-septate ascospore, while *Th. mangrovei* and *Pse. chromolaenae* have muriform ascospores (Devadatha et al., 2018; Mapook et al., 2020). Therefore, we introduce our new collection as a new species *Aqu. aquilariae* based on morphological comparison and phylogenetic analyses.

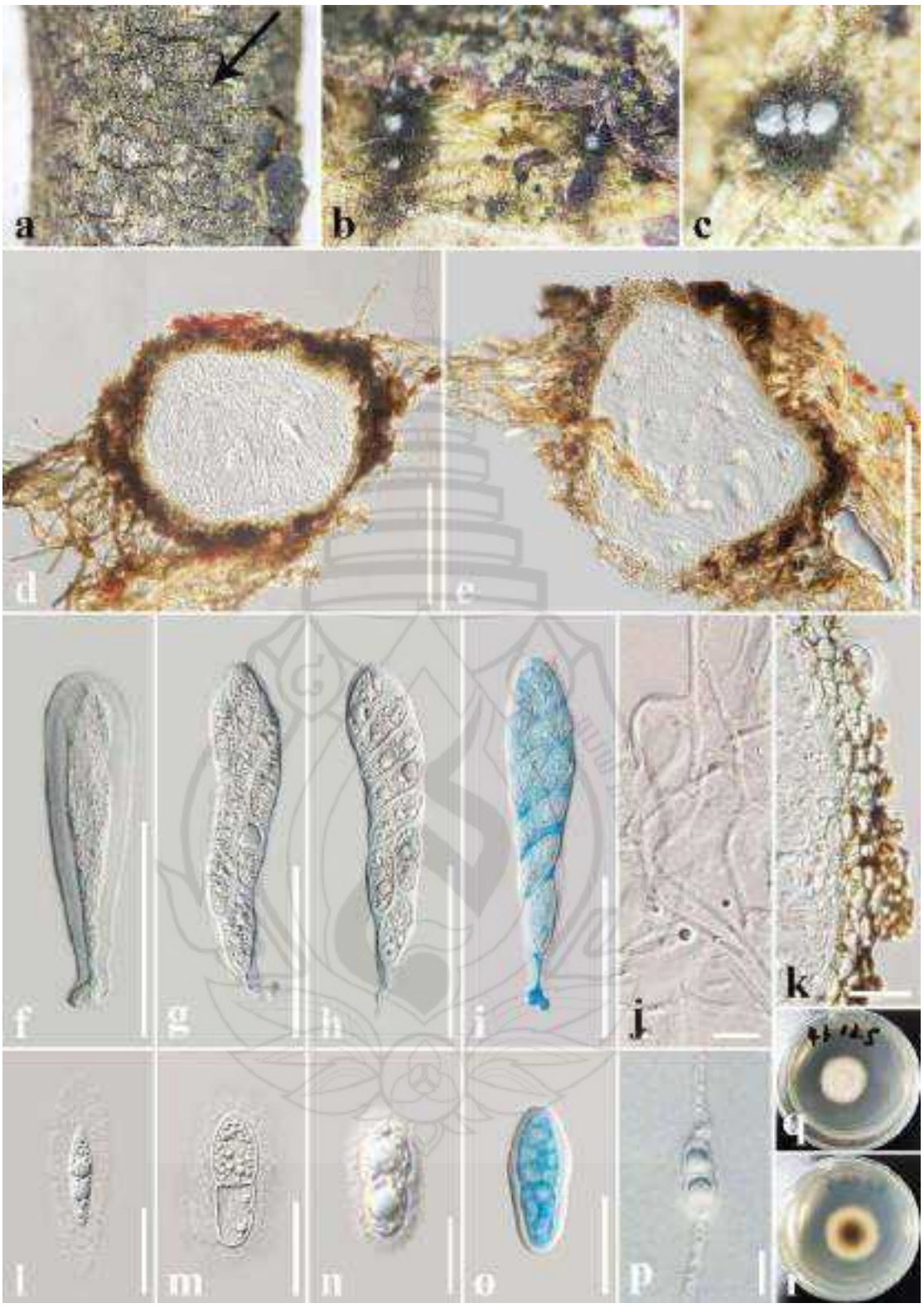


Figure 6.14 *Aquilariomyces aquilariae* (MHZU 23-0036, holotype)

Figure 6.14 a, b, Appearance of ascomata on the host. c, Transverse sections through ascomata on the host. d, e, Vertical sections through the ascomata. f–i, Asci (i an ascus stained with cotton blue). j, Pseudoparaphyses. k, Peridium. l–o, Ascospores (o, An ascospore stained with cotton blue). p, Germinated ascospore. q, r, Colony on potato dextrose agar (PDA) obverse and reverse views. Scale bars: d, e = 200 µm, f–i = 50 µm, j = 10 µm, k–p = 20 µm.

Aquilariomyces maomingensis T. Y. Du, K.D. Hyde, Tibpromma & Karun. ***sp. nov.***

MycoBank number: MB 856409; Facesoffungi number: FoF 16960; Figure 6.15

Etymology: Named after the location "Maoming" where the holotype was collected.

Holotype: MHZU 23-0022

Saprobic on decaying branch of *Aquilaria sinensis*. ***Sexual morph:*** *Ascomata* (excluding necks) 250–450 µm high × 200–500 µm diam. ($\overline{x}$ = 366 × 350 µm, n = 5), solitary, or gregarious in small groups, brown to dark brown, surrounded by short brown to black fluffs, immersed, slightly raised under the bark, globose to subglobose, sometimes ovoid, ostiolate. *Ostiolar canal* 250–280 µm long × 150–200 µm wide ($\overline{x}$ = 263 × 180 µm, n = 10), cylindrical to elliptical, usually straight, dark-brown to black necks, with periphyses. *Peridium* 15–70 µm ($\overline{x}$ = 31 µm, n = 30) wide, comprising 3–5 layers of pale brown to brown cells of *textura angularis* to *textura prismatica*, fusing with the host tissue. *Hamathecium* comprising 1 µm wide, hyaline, septate, branched, numerous, trabeculate pseudoparaphyses (*sensu* Liew et al. 2000), embedded in a gelatinous matrix. *Asci* 100–140 × 21–25 µm ($\overline{x}$ = 123 × 23 µm, n = 30), bitunicate, 8-spored, thick-walled, clavate, apically rounded, with an ocular chamber, short pedicel, some club-shaped. *Ascospores* 20–36 × 9–15 µm ($\overline{x}$ = 30 × 13 µm, n = 30), uniseriate, 1-septate, fusiform to ellipsoidal, conical at both ends or round, constricted at the septum, upper cells are slightly larger than below cells, rough-walled, with several guttules and granules, hyaline to pale yellow when immature and surrounded by a mucilaginous sheath, later become yellow-brown and without a mucilaginous sheath. ***Asexual morph:*** Undetermined.

Culture characteristics: Ascospores germinated on PDA after 12 hours, and germ tubes were produced from one or both ends. *Colonies* on PDA reaching 2–3 cm diam. after two weeks at 23–28°C. Colonies obverse: dense, circular, or irregular, cream to brown, umbonate, raised at the center, filamentous edge. Colonies reverse dark brown to black at the center, and cream to light brown at the margin.

Material examined: CHINA, Guangdong Province, Maoming City, Dianbai District, Poxin Town, 21°34′25″N, 111°7′43″E, on a dead branch of *Aquilaria sinensis* (Thymelaeaceae), 3 June 2022, T. Y. Du, MMA15 (MHZU 23-0022, **holotype**), ex-type, GMBCC1047, other living culture, ZHKUCC 23-0041.

Notes: In the present phylogenetic analyses, our new collection *Aquilariomyces maomingensis* formed a well-separated sister lineage to *Aqu. aquilariae* (ZHKUCC 23-0072 and GZCC 23-0616) with 100% ML, 1.00 BYPP statistical support (Figure 6.18). *Aquilariomyces maomingensis* shares similar morphological characteristics with *Aqu. aquilariae* (MHZU 23-0036, holotype) in having immersed, globose to subglobose ascomata, numerous, septate, branched, trabeculate pseudoparaphyses in a gelatinous matrix, clavate asci, with short and club-shaped pedicel, and uniseriate fusiform to ellipsoidal, 1-septate, ascospores, constricted at the septum, and surrounded by a mucilaginous sheath (Du et al., 2024). However, *Aqu. maomingensis* (MHZU 23-0022) differs from *Aqu. aquilariae* (MHZU *23-0036*) from its ascomata and ascospore characters. *Aquilariomyces maomingensis* has ascomata surrounded by short fluffs, slightly raised under the bark, and brown mature ascospores; while *Aqu. aquilariae* (MHZU *23-0036*) has inconspicuous ascomata, surrounded by long fluffs, and hyaline mature ascospores (Du et al., 2024).

According to the phylogenetic analysis of the present study, both *Aquilariomyces* species clustered in Thyridariaceae, a family characterized by trabeculate or cellular pseudoparaphyses. Trabeculate pseudoparaphyses are characterized by narrow, thread-like, apparently nonseptate, branched and anastomosing or unbranched above the asci and embedded in a gelatinous matrix (Liew et al., 2000; Hongsanan et al., 2020). Trabeculae were considered important at the Dothideomycetes O.E. Erikss. & Winka in earlier classifications; thus, Melanommatales was defined as having trabeculae (Barr, 1983). However, Liew et al. (2000) showed that trabeculae were not important at the order level and probably were important at the family level (or even species). Thyridariaceae

comprises nine genera: *Aquilariomyces*, *Chromolaenomyces* Mapook & K.D. Hyde, *Cycasicola* Wanas., E.B.G. Jones & K.D. Hyde, *Liua* Phookamsak & K.D. Hyde, *Parathyridaria* Jaklitsch & Voglmayr, *Parathyridariella* Prigione, A. Poli, E. Bovio & Varese, *Pseudothyridariella* Mapook & K.D. Hyde, *Thyridaria* Sacc., and *Thyridariella* Devadatha, V.V. Sarma, K.D. Hyde, Wanas. & E.B.G Jones (Wijayawardene et al., 2022; Du et al., 2024). Among these genera, *Aquilariomyces* (Du et al., 2024), *Parathyridaria* (Jaklitsch & Voglmayr, 2016), and *Thyridaria* (Jaklitsch & Voglmayr, 2016) have trabeculate pseudoparaphyses; *Chromolaenomyces* (Mapook et al., 2020), *Pseudothyridariella* (Mapook et al., 2020), and *Thyridariella* (Devadatha et al., 2018) have cellular pseudoparaphyses, while, pseudoparaphyses type has not been reported yet in other genera *viz., Cycasicola, Liua*, and *Parathyridariella*. We believe pseudoparaphyses type is one of the important characters in the genus level.

The base pair differences in the LSU, ITS, SSU, *tef*1-α, and *rpb*2 genes (without gaps) between our new collection and *Aqu. aquilariae* (ZHKUCC *23-0072*, ex-type) were also compared. The results showed that there are 3.1% nucleotide differences (28/912 bp) in LSU; in comparison, ITS has 12.3% nucleotide differences (67/544 bp), SSU has 0.3% nucleotide differences (3/873 bp), *tef*1-α has 7.5% nucleotide differences (76/1008 bp), and *rpb*2 has 10.6% nucleotide differences (109/1025 bp). These comparisons indicate minor differences in SSU and LSU, while considerable base differences in ITS, *tef*1-α, and *rpb*2. Therefore, we introduce our new collection as a new species, *Aqu. maomingensis* based on a polyphasic approach, according to the guidelines of Maharachchikumbura et al. (2021).

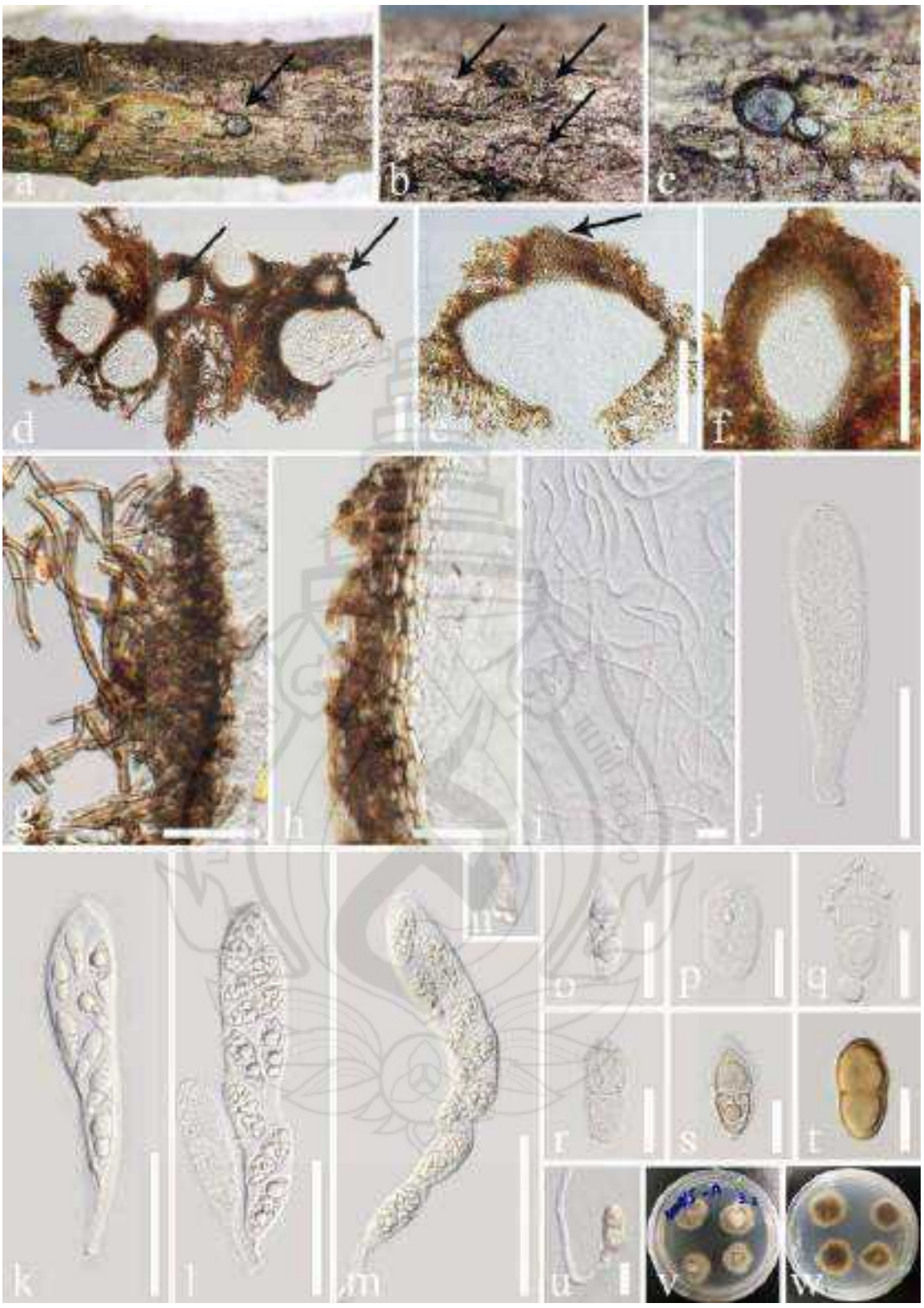


Figure 6.15 *Aquilariomyces maomingensis* (MHZU 23-0022, holotype)

Figure 6.15 a–c, Appearance of ascomata on the host (the arrows indicate ascomata). d, e, Vertical sections through the ascomata (the arrows indicate ostioles). f, Ostiole with periphyses. g, Short fluffs around the periphery of the ascomata. h, Peridium. i, Trabeculae pseudoparaphyses. j–m, Asci. n, A club-shaped pedicel. o–t, Ascospores (s, stained with Indian ink). u, Germinated ascospore. v, w, Colonies on PDA obverse and reverse views. Scale bars: d–f = 200 µm, g, h = 30 µm, i = 10 µm, j–m = 50 µm, o–u = 20 µm.

Parathyridariella Prigione, A. Poli, E. Bovio & Varese 2020

Notes: Poli et al. (2020) established the monotypic genus *Parathyridariella* within Thyridariaceae to accommodate *Par. dematiacea* Prigione et al., as the type species. *Parathyridariella dematiacea* is characterized by having hyphae septate, hyaline to lightly pigmented, and numerous, globose to subglobose chlamydospores, mostly in chains, intercalary or solitary, from brownish to dark brown, not observed the sexual morph and asexual morph with differentiated conidiogenesis (Poli et al., 2020). *Parathyridariella* is distributed in green alga *Flabellia petiolata* and seagrass *Posidonia oceanica* (Poli et al., 2020). In this study, we introduce a new species, *Parathyridariella aquilariae*, collected from the dead branches of *Aquilaria yunnanensis* in terrestrial habitats from China based on molecular evidence. This study is the first to define an asexual *Parathyridariella* morph and the first to describe a species of *Parathyridariella* on *Aquilaria yunnanensis*.

Parathyridariella aquilariae T. Y. Du, Tibpromma & Karun. ***sp. nov.***

MycoBank number: MB 854003; Facesoffungi number: FoF 15267; Figure 6.16

Etymology:Named after its host genus *Aquilaria*.

Holotype: MHZU 23-0038

Saprobic on dead branches of *Aquilaria yunnanensis*. **Sexual morph:** undetermined. **Asexual morph:** coelomycetous. *Conidiomata* 200–500 µm high × 300–550 µm diam. ($\overline{x}$ = 323 × 380 µm, n = 10), pycnidial, surrounded by short brown fluff, solitary or scattered in small groups, individual or aggregated, uniloculate, immersed under the bark, inconspicuous, slightly raised through the bark, globose to subglobose, dark brown to black, ostioles with slightly papillate. *Conidiomata walls* 20–50 µm wide, light brown to dark brown, soft, thick-walled, composed of five to eight cell layers, somewhat angular pseudoparenchymatous cells of *textura angularis*. *Hamathecium* lacking. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous*

cells 4.5–6 µm × 4–6 µm ($\overline{x}$ = 5.1 × 4.9 µm, n = 30), holoblastic, discrete, determinate, phialidic, cylindrical to ampulliform, unbranched, aseptate, smooth-walled, hyaline, arising from the inner cavity of the conidioma wall. *Conidia* (3.5–)4–5 × (2.7–)3–4 µm ($\overline{x}$ = 4.5 × 3.5 µm, n = 30), hyaline when immature, brown at maturity, oval, apex broadly rounded, aseptate, guttulate, with longitudinal striations when mature.

Culture characteristics: Conidia germinated on PDA after 48 h, and germ tubes were produced from both ends. Colonies on PDA reaching 1 cm diam., after 1 week at 23°C–28°C. Colonies obverse: dense, circular or oval, white, raised at the center, entire edge. Colonies reverse: brown at the center, light brown at the margin.

Material examined: CHINA, Yunnan Province, Xishuangbanna, Jinghong City, Gasa, Naban River Basin National Nature Reserve, 22°7′50″ N, 100°40′29″ E, on dead branches of *Aquilaria yunnanensis* (Thymelaeaceae), September 14, 2021, T. Y. Du, YNA59 (MHZU 23-0038, **holotype**), ex-type, ZHKUCC 23-0074, other living culture, GZCC 23-0617.

Notes: In the present phylogenetic analyses, our new collection *Parathyridariella aquilariae* formed a well-separated and sister lineage to four strains of *Par. dematiacea* with 81% ML, 0.96 BYPP statistical support (Figure 6.18). Additionally, the base pair differences of the LSU, ITS, and *rpb*2 genes between our strain (ZHKUCC 23-0074, ex-type) and *Par. dematiacea* (MUT 4884, ex-type) were compared, and the results showed that LSU has 2.2% nucleotide differences (21/937 bp, without gaps), ITS has 4.2% nucleotide differences (22/525 bp, without gaps), and *tef*1-α has 10% nucleotide differences (46/462 bp, without gaps), which reveals that they belong to different species of the same genus. Morphologically, *Par. dematiacea* has been only reported by numerous chlamydospores, mostly in chain, there was also no evidence of a sexual or asexual morph with distinct conidiogenesis (Poli et al., 2020). In contrast, our new collection has complete conidiomata, conidiogenous cells, and conidia. And the striped conidia in our latest collection set it apart from other genera in Thyridariaceae. Therefore, we introduce our new collection, *Par. aquilariae*, as a new species based on molecular data and phylogenetic analyses. Because of the type species, *Par. dematiacea*, lacks asexual morphological characteristics; additional samples containing different species morphs in this genus must be collected in the future to determine a more precise phylogeny of *Par. aquilariae*.

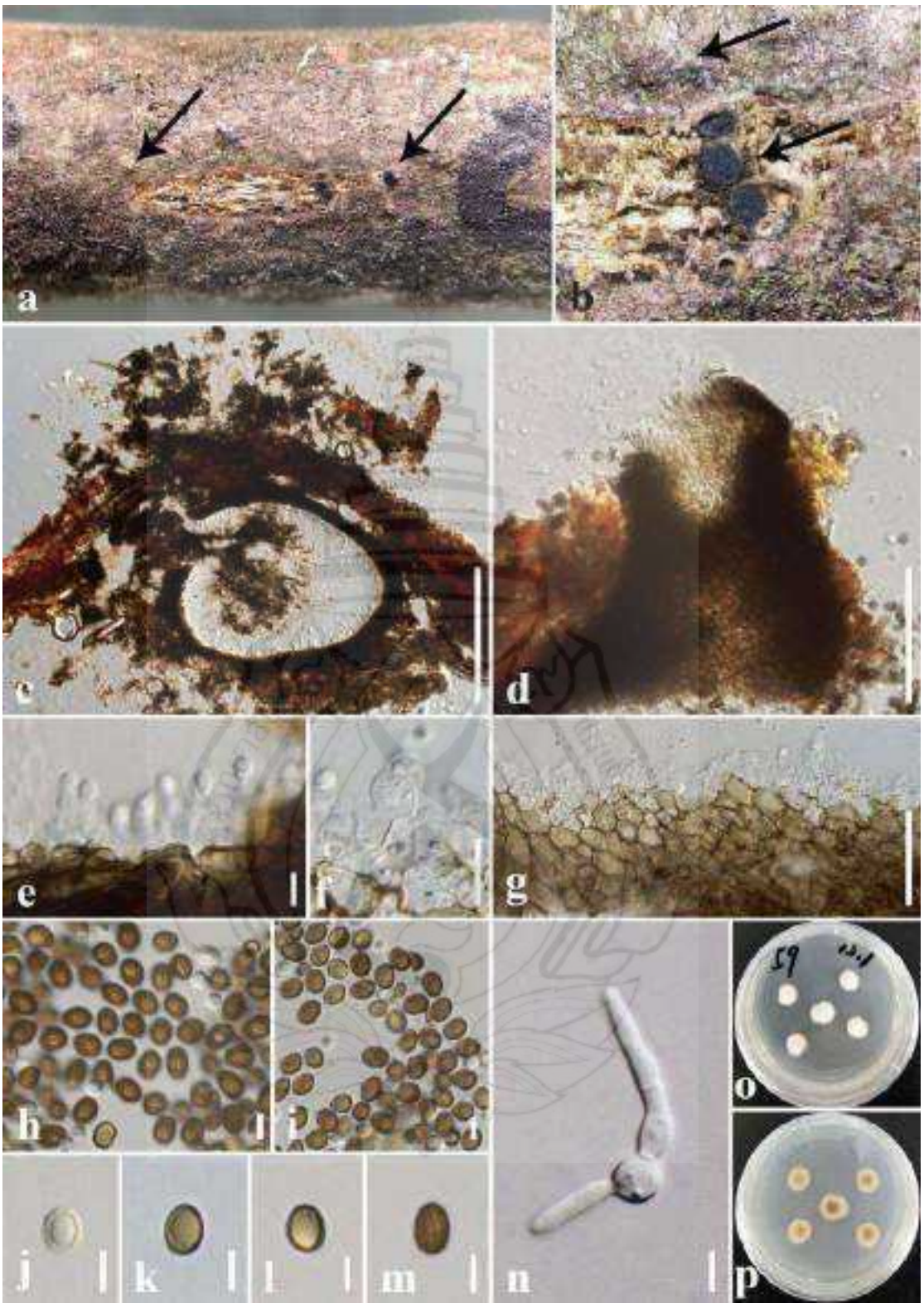


Figure 6.16 *Parathyridariella aquilariae* (MHZU 23-0038, holotype)

Figure 6.16 a, Conidiomata on the host. b, Transverse section of conidiomata. c, Vertical sections through the conidioma. d, Ostiole. e, f, Conidiogenous cells developing conidia. g, Conidioma wall. h–m, Conidia. N, Germinated conidium. o, p, Colonies on potato dextrose agar (PDA) obverse and reverse view. Scale bars: c = 300 µm, d = 100 µm, e, f = 5 µm, g = 20 µm, h–n = 3 µm.

Pseudothyridariella Mapook & K. D. Hyde 2020

Notes: *Pseudothyridariella* was introduced by Mapook et al. (2020) to accommodate *Pse. chromolaenae* Mapook & K. D. Hyde as the type species. Mapook et al. (2020) transferred *Pse. mahakashae* (Devadatha, V. V. Sarma, D. N. Wanas., K. D. Hyde & E. B. G. Jones) Mapook & K. D. Hyde (≡ *Thyridariella mahakoshae* Devadatha, V. V. Sarma, D. N. Wanas., K. D. Hyde & E. B. G. Jones) from *Thyridariella* to *Pseudothyridariella* based on its relatedness with *Pse. chromolaenae* in phylogeny and also based on morphological similarity (Mapook et al., 2020). Recently, Li et al. (2023) introduced a new species *Pse. idesiae* with the asexual morph in this genus based on molecular evidence. Currently, four *Pseudothyridariella* species are listed in Index Fungorum (2025) (accessed on May 1, 2025). *Pseudothyridariella* is characterized by sexual morph having immersed to erumpent, coriaceous, globose or subglobose to obpyriform ascomata, septate, branching pseudoparaphyses, eight-spored, fissitunicate, bitunicate, cylindrical, clavate, pedicellate asci, ellipsoid to broadly fusiform, one to two seriate, hyaline to brown or olivaceous-brown to dark brown, muriform ascospores, surrounded by a hyaline gelatinous sheath (Mapook et al., 2020). The asexual morph of this genus is characterized by subglobose to globose conidiomata, unilocular, surrounded by yellow, hair-like setae, conidiophores reduced to conidiogenous cells, conidia cylindrical to ellipsoidal, with transverse septate and longitudinal or oblique septa, dark brown, straight (Li et al., 2023). *Pseudothyridariella* species was reported as saprobes from *Avicennia marina* (Forsk.) Vierh. in India (Devadatha et al., 2018), *Chromolaena odorata* (Linnaeus) R. M. King & H. Robinson in Thailand (Mapook et al., 2020), and *Idesia polycarpa* Maxim. in China (Li et al., 2023). In this study, we introduce a new species, *Pseudothyridariella aquilariae*, collected from the dead branch of *Aquilaria sinensis* in terrestrial habitats from China based on morphological and molecular evidence. This study is the first to describe a *Pseudothyridariella* species on *Aquilaria yunnanensis*.

Pseudothyridariella aquilariae T. Y. Du, Tibpromma & Karun. ***sp. nov.***

MycoBank number: MB 854004; Facesoffungi number: FoF 15268; Figure 6.17

Etymology:Named after its host genus *Aquilaria*.

Holotype: MHZU 23-0025

Saprobic on dead branch of *Aquilaria sinensis*. **Sexual morph:** undetermined. **Asexual morph:** coelomycetous. *Conidiomata* 220–350 µm high × 200–400 µm diam. ($\overline{x}$ = 251 × 253 µm, n = 10), pycnidial, surrounded by white to brown hair-like setae, solitary or scattered in small groups, uniloculate, individual or aggregated, immersed under the bark, inconspicuous, globose to subglobose, brown to dark brown, apapillate ostioles, with a pore-like opening. *Conidiomata walls* 15–35 µm wide, light brown to dark brown, soft, thin-walled with equal thickness, composed of three to five cell layers, somewhat angular pseudoparenchymatous cells of *textura angularis*. Hamathecium not observed. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* 5.5–10 µm × 4–9 µm ($\overline{x}$ = 7.5 × 6.5 µm, n = 30), holoblastic, discrete, determinate, phialidic, ampulliform, unbranched, aseptate, smooth-walled, hyaline, arising from the inner cavity of the conidioma wall. *Conidia* 11–12.5(–13) × 4.5–6.5 µm ($\overline{x}$ = 11.7 × 5.5 µm, n = 30), aseptate, hyaline when immature, becoming brown to dark brown, oblong to ellipsoidal, three transverse septate with age, not constricted at the septum, straight, guttulate, rough-walled. Culture characteristics: Conidia germinated on PDA after 48 h, and germ tubes were produced from both ends. Colonies on PDA reaching 1 cm diam. after 1 week at 23°C–28 °C. Colonies obverse: dense, oval, white, raised at the center, entire edge. Colonies reverse: light brown at the center, cream at the margin.

Material examined: CHINA, Guangdong Province, Maoming City, Dianbai District, Poxin, 21°34′25″ N, 111°7′43″ E, on a dead branch of *Aquilaria sinensis* (Thymelaeaceae), June 3, 2022, T. Y. Du, MMA18 (MHZU 23-0025, **holotype**), ex-type living culture, ZHKUCC 23-0044; other living culture, GZCC 23-0611.

Notes: In the present phylogenetic analyses, our new collection *Pseudothyridariella aquilariae* formed a well-separated and sister lineage to *Pse. chromolaenae* (MFLUCC 17-1472) and *Pse. idesiae* (CGMCC 3.24439) with 100% ML, 1.00 BYPP statistical support (Figure 6.18). Morphologically, *Pse. aquilariae* shares a similar shape and color to conidiomata and conidia of *Pse. idesiae* (Li et al., 2023). However, *Pse. aquilariae* differs from *Pse. idesiae* in having immersed

conidiomata, surrounded by white to brown hair-like setae, apapillate, conidiomatal wall composed cells of textura angularis, and conidia with three transverse septate, no longitudinal septum. Whereas *Pse. idesiae* has superficial conidiomata, surrounded by yellow hair-like setae, papillate, conidiomatal wall composed cells of *textura intricata* to *textura epidermoidea*, and conidia 0 to four transverse septate, one to two longitudinal or oblique septa in the apical or second cell (Li et al., 2023).

Pseudothyridariella chromolaenae is only known from its sexual morph (Mapook et al., 2020), and our new collection *Pse. aquilariae* has only the asexual morph; thus, the morphological characteristics cannot be compared. However, the base pair differences of the LSU, ITS, SSU, *tef*1-α, and *rpb*2 genes between our strain (ZHKUCC 23-0044, ex- type) and *Pse. chromolaenae* (MFLUCC 17-1472, ex-type) were compared. The results showed that LSU has 0.2% nucleotide differences (2/809 bp, without gaps), ITS has 6.4% nucleotide differences (32/497 bp, without gaps), SSU has 12.5% nucleotide differences (75/601 bp, without gaps), *tef*1-α has 1.5% nucleotide differences (13/893 bp, without gaps), and *rpb*2 has 3.6% nucleotide differences (26/726 bp, without gaps), which reveals that they belong to different species of the same genus. Therefore, we introduce our new collection as a new species *Pse. aquilariae* based on morphological and molecular data.

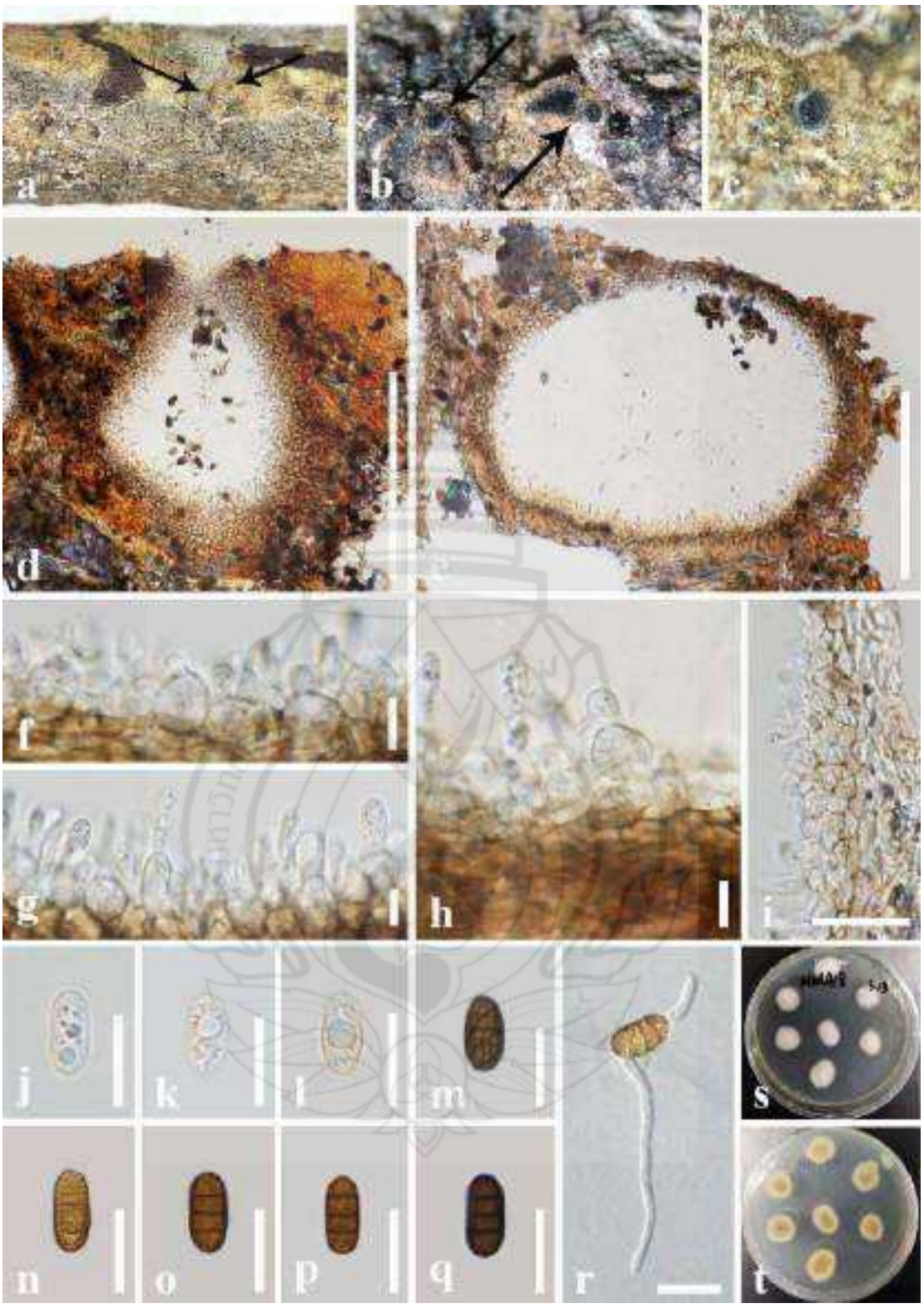


Figure 6.17 *Pseudothyridariella aquilariae* (MHZU 23-0025, holotype)

Figure 6.17 a, Conidiomata on the host. b, c, Transverse section of conidiomata. d, e, Vertical sections through the conidiomata. f–h, Conidiogenous cells developing conidia. i, Conidioma wall. j–q, Conidia. R, Germinated conidium. s, t, Colonies on potato dextrose agar (PDA) obverse and reverse view. Scale bars: d, e = 200 µm, f–h = 5 µm, i = 20 µm, j–r = 10 µm.

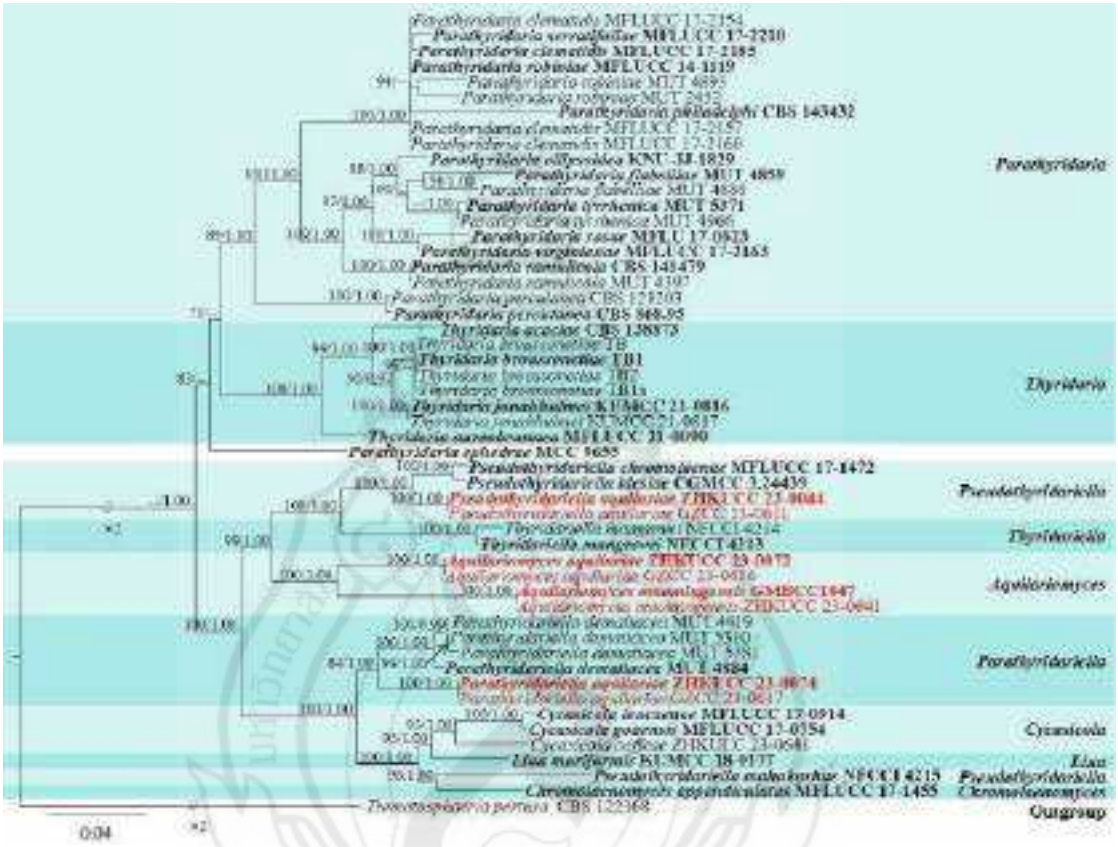


Figure 6.18 Phylogenetic tree of *Aquilariomyces*, *Parathyridariella* and *Pseudothyridariella*

Figure 6.18 Bootstrap support values for ML greater than 60% and Bayesian posterior probabilities greater than 0.90 are given near the nodes, respectively. The tree is rooted with *Trematosphaeria pertusa* (CBS 122368). The new isolates are indicated in red, and the ex-type strains are in bold.

Pleosporales genera *incertae sedis*

Mangifericomes E.F. Yang and Tibpromma 2022

Notes: *Mangifericomes* was established by Yang et al. (2022) as a monotypic genus in Pleosporales genera *incertae sedis* to accommodate *Man. hongheensis* E.F. Yang and Tibpromma as type species, which was isolated from *Mangifera indica* L. in China. *Mangifericomes* is characterized by immersed or semi-immersed, globose to subglobose, dark brown to black ascomata with or without ostioles; a hamathecium comprising filiform, hyaline, septate, branched cellular pseudoparaphyses (*sensu* Liew et al., 2000); 8-spored, bitunicate, cylindrical-clavate, pedicellate asci; and ellipsoid, muriform, pale brown to brown ascospores, wrapped in a gelatinous sheath (Yang et al., 2022).

Mangifericomes aquilariae T. Y. Du, K.D. Hyde, Tibpromma & Karun. ***sp. nov.***

MycoBank number: MB 856410; Facesoffungi number: FoF 16961; Figure 6.19

Etymology: Named after the host genus "*Aquilaria*" from which the holotype was collected.

Holotype: GMB-W 1008

Saprobic on decaying branch of *Aquilaria* sp. **Sexual morph:** *Ascomata* 280–460 µm high × 250–510 µm diam. ($\overline{x}$ = 375 × 380 µm, n = 10), globose to subglobose, brown to dark brown, gregarious, immersed, inconspicuous on host surface, ostiolate. *Peridium* 20–70 µm ($\overline{x}$ = 40 µm, n = 20) wide, comprising 5–7 layers of hyaline to pale brown cells of *textura angularis* to *textura prismatica*, fusing with the host tissue. *Hamathecium* 2.5 µm wide, hyaline, fascicular, septate, branched, numerous, cellular pseudoparaphyses, embedded in a glutinous matrix. *Asci* 170–265 × 32–50 µm ($\overline{x}$ = 216 × 40 µm, n = 30), bitunicate, fissitunicate, 8-spored, cylindric-clavate, with short pedicel, apically rounded, with an ocular chamber. *Ascospores* 40–53 × 18–23 µm ($\overline{x}$ = 47 × 20 µm, n = 30), muriform, uniseriate, hyaline and later become golden yellow, pale-brown to dark brown, ellipsoid, slightly curved to straight, rough-walled, slightly wider near apex, apically rounded, 10–13-transversally septate, and 3–6-longitudinal septa, slightly constricted at the septum, surrounded by a 6.5–15 µm wide gelatinous sheath. **Asexual morph:** Undetermined.

Culture characteristics: Ascospores germinated on PDA after 24 hours, and germ tubes were produced from each cell. *Colonies* on PDA reaching 5 cm diam., after four weeks at 23–28 °C. Colonies obverse: loose, circular or irregular, white-cream, slightly raised at the center, filamentous edge. Colonies reverse reddish-brown at the center, and cream to light yellow towards the periphery.

Material examined: CHINA, Yunnan Province, Nujiang Prefecture, Lushui City, Liuku Town, 25°48′30″N, 98°51′5″E, on a dead branch of *Aquilaria* sp. (Thymelaeaceae), 21 April 2023, T. Y. Du, NJT41 (GMB-W 1008, **holotype**), ex-type, GMBCC1010, other living culture, GZCC 23-0628.

Notes: In the present phylogenetic analyses, our new collection, *Mangifericomes aquilariae* formed a well-separated sister lineage to *Man. hongheensis* (KUMCC 21-0342 and KUMUCC 21-0345) with 100% ML, 1.00 BYPP statistical support (Figure 6.20). *Mangifericomes aquilariae* shares similar morphological characteristics with *Man. hongheensis* (HKAS 1221888, holotype) in having globose to subglobose, brown to dark brown, ostiolate ascomata, bitunicate asci with fissitunicate, 8-spored, cylindrical-clavate, and muriform ascospores, ellipsoid, pale-brown to dark brown, slightly wider near apex, surrounded by a gelatinous sheath (Yang et al., 2022). However, *Man. aquilariae* (GMB-W 1008) differs from *Man. hongheensis* (HKAS 1221888) by its immersed ascomata, peridium comprising *textura prismatica* to *textura angularis* cells, fascicular, numerous pseudoparaphyses, and ascospores are 10–13-transversally septate, 3–6-longitudinal septa; while ascomata of *Man. hongheensis* (HKAS 1221888) are semi-immersed to fully immersed, peridium comprising *textura angularis* to *textura globosa* cells, sparse pseudoparaphyses, and ascospores are 7–11-transversally septate, 5–8-longitudinal septa (Yang et al., 2022). In addition, the base pair differences of the LSU, ITS, *tef*1-α, and *rpb*2 genes (without gaps) between our new collection and *Man. hongheensis* (KUMCC 21-0342, ex-type) were compared, while SSU of our new collection is not available. The results showed that there are 0.8% nucleotide differences (7/864 bp) in LSU, while ITS has 3.4% nucleotide differences (18/533 bp), *tef*1-α has 3.2% nucleotide differences (31/962 bp), and *rpb*2 has 4.5% nucleotide differences (41/905 bp). These comparisons indicate that they display minor differences on LSU, while displaying significant base differences on ITS, *tef*1-α, and *rpb*2. Therefore, we introduce our new collection (from *Aquilaria*

sp. in China) as a new species, *Man. aquilariae*, based on a polyphasic approach according to the guidelines of Maharachchikumbura et al. (2021). In addition, this study introduces the second *Mangifericomes* species in the genus and the first *Mangifericomes* species collected from *Aquilaria.*

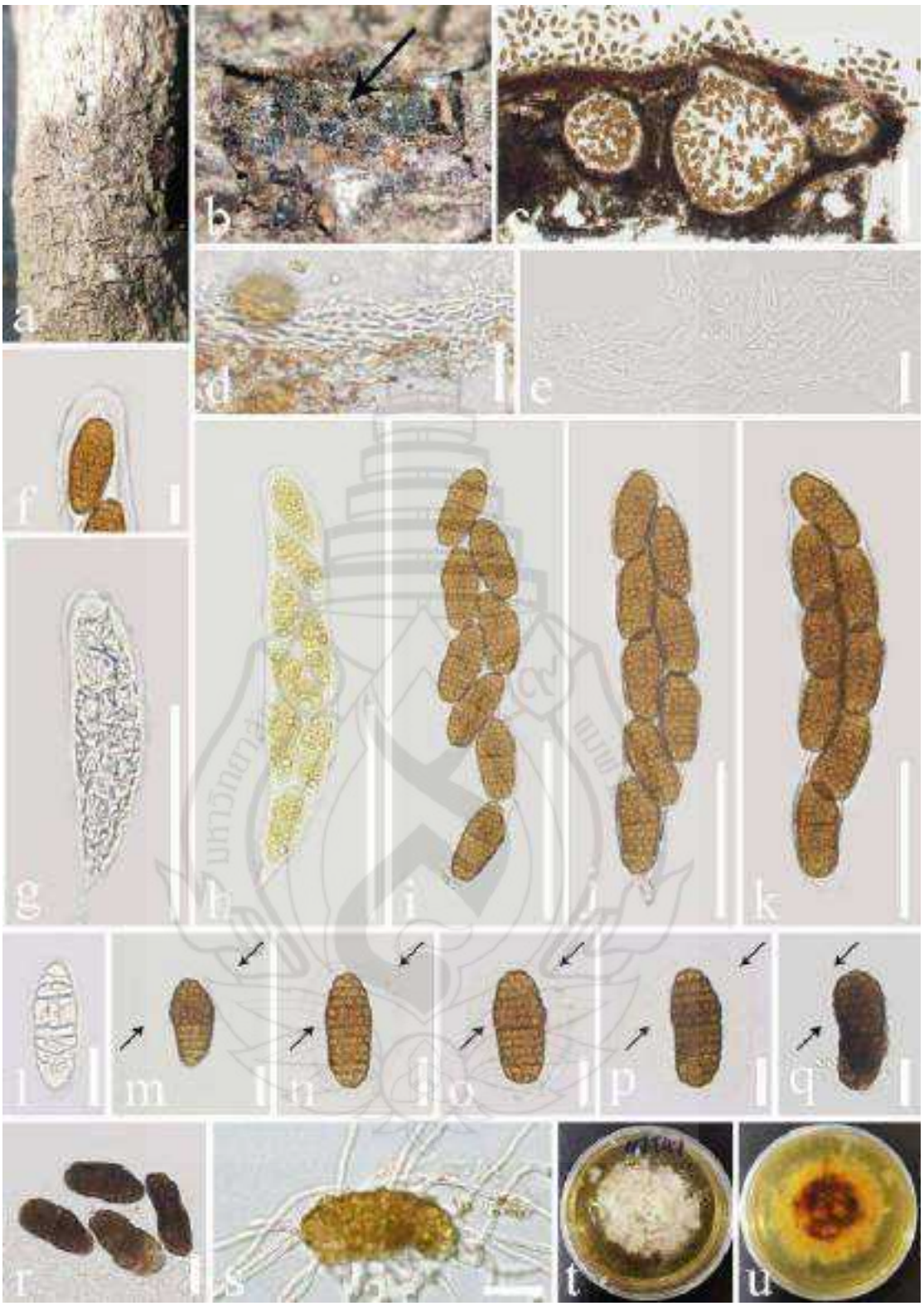


Figure 6.19 *Mangifericomes aquilariae* (GMB-W 1008, holotype)

Figure 6.19 a, b, Ascomata on the host (the arrow indicates the cross-section of the ascomata). c, Vertical sections through the ascomata. d, Peridium. e, k, Cellular pseudoparaphyses (e, stained with cotton blue). f, Ocular chamber of asci. g–j, Asci. l–r, Ascospores (the arrows indicate the sheath of the ascospores). s, Germinated ascospore. t, u, Colony on PDA obverse and reverse views. Scale bars: c = 200 μm, d, g, l–s = 20 μm, e, k = 10 μm, f, h–j = 100 μm.

Figure 6.20 Phylogenetic tree of *Mangifericomes*

Figure 6.20 (continued)

Figure 6.20 Bootstrap support values for ML greater than 60% and Bayesian posterior probabilities greater than 0.90 are given near the nodes, respectively. The tree is rooted with *Orbilia auricolor* (AFTOL-ID 906) and *O. vinosa* (AFTOL-ID 905). The new isolates are indicated in red, and the ex-type strains are in bold.

6.3.2 Sordariomycetes

Sordariales Chadef. ex D. Hawksw. & O. E. Erikss. 1986

Podosporaceae X. Wei Wang & Houbraken 2019

Triangularia Boedijn 1934

Notes: *Triangularia* was transferred from *Trigonia* J. F. H. Beyma and introduced as a new genus by Boedijn (1934), is typified by *Tr. bambusae* (J. F. H. Beyma) Boedijn (Guarro & Cano, 1988; Huang et al., 2021). This genus was previously classified in Lasiosphaeriaceae Nannf. by Wijayawardene et al. (2018). Subsequently, Wang et al. (2019a) redefined *Triangularia* in Podosporaceae, and synonymized *Apiosordaria* under *Triangularia* based on phylogenetic analysis. Further, Marin-Felix et al. (2020) transferred three species to *Triangularia*, and Huang et al. (2021) transferred seven species to *Triangularia* based on morphological and phylogenetic studies. Currently, 38 epithets are listed in Index Fungorum (2025). The genus is characterized by ascomata cleistothecial or perithecial, obpyriform to pyriform, black, glabrous or surrounded by hairs or setae, ostiole with papilla; unitunicate asci four to eight-multispored, clavate to cylindrical, pedicellate, evanescent or persistent until ascospores mature; ascospores aseptate, hyaline when young, becoming one-septate at maturity, upper cell brown, ellipsoidal to polygonal, with an apical or subapical germ pore; lower cell smaller than upper cell, hyaline, elongated fusiform, sometimes collapsing, rarely early evanescent, guttulate, gelatinous appendages absent or present; and asexual morph (Hyphomycetous): conidiophores reduced to conidiogenous cells, aseptate conidia, hyaline, globose to oval, smooth-walled (Boedijn, 1934; Guarro & Cano, 1988; Wang et al., 2019a; Huang et al., 2021). Most members of this genus are isolated from soil, animal dung, sand, and decaying plants (Wang et al., 2019a; Huang et al., 2021; Index Fungorum, 2025). In this study, we introduce a new species, *Triangularia aquilariae*, collected from a dead branch of *Aquilaria sinensis* in China's terrestrial habitats based on morphological comparison and phylogenetic analyses.

Triangularia aquilariae T. Y. Du, Tibpromma & Karun. ***sp. nov.***

MycoBank number: MB 854005; Facesoffungi number: FoF 15269; Figure 6.21

Etymology: Named after its host genus *Aquilaria*.

Holotype: MHZU 23-0028

Saprobic on dead branch of *Aquilaria sinensis*. **Sexual morph:** *Ascomata* (excluding neck) 250–550 µm high × 230–500 µm diam. ($\bar{x}$ = 335 × 325 µm, n = 10), membranaceous to coriaceous, immersed, solitary or loosely aggregated, subglobose to obpyriform, glabrous, black, not obvious, not easily detected, ostiolate, periphysate, neck conical. *Peridium* 20–40 µm wide ($\bar{x}$ = 27 µm, n = 10), membranaceous, outer layer composed of dark brown cells, inner layer composed of three to five layers of elongated to flattened, hyaline cells of *textura angularis* to *textura prismatica*. Hamathecium comprising 2.5–3.5 µm wide, filiform, septate, branched, hyaline, persistent, paraphyses. *Asci* (148–)160–195(–215) µm long × (9–)11–16(–21) µm wide ($\bar{x}$ = 178 × 13 µm, n = 20), unitunicate, thin-walled, biseriate to triseriate, elongated clavate or fusiform, slightly curved, eight- spored, pedicellate, evanescent or persistent until ascospores mature. *Ascospores* hyaline, aseptate when immature, becoming transversely uniseptate, two-celled, gelatinous bipolar appendages present at maturity, upper cell 15–19 µm long × 8–11 µm wide ($\bar{x}$ = 16.5 × 9.5 µm, n = 30), ellipsoid, truncate at the base, conical at the apex, dark brown, with an apical germ pore, and lower cell (primary appendage or pedicel) 25–40 µm long × 4.5–7 µm wide ($\bar{x}$ = 32 × 5.5 µm, n = 30), elongated and narrow, slightly sigmoid, hyaline to pale brown, with gelatinous secondary appendages, guttulate, smooth, without ornamented. **Asexual morph:** Undetermined.

Culture characteristics: Ascospores germinated on PDA after 12 h, germ tubes were produced from both ends of immature ascospores. Colonies on PDA reaching 2–3 cm diam. after 1 week at 23°C–28°C. Colonies obverse: soft, oval, white, flat in the center with sparse hyphae, abundant aerial hyphae raised at the margin, entire edge. Colonies reverse: near transparent in the center, white to cream at the margin. Material examined: CHINA, Yunnan Province, Xishuangbanna, an agarwood plantation, 21°50′1″ N, 100°29′31″ E, on dead branches of *Aquilaria sinensis* (Thymelaeaceae), September 15, 2021, T. Y. Du, YNA05 (MHZU 23-0028, **holotype**), ex-type, ZHKUCC 23-0064, other living culture, GZCC 23-0612.

Notes: In the present phylogenetic analyses, our new collection *Tr. aquilariae* formed a distinct clade in *Triangularia* (Figure 6.22). Morphologically, *Tr. aquilariae* share similar shape of asci and ascospores with *Triangularia striata* (Ellis & Everh.) Y. Marín, A. N. Mill. & Stchigel (Miller & Huhndorf, 2001). However, *Tr. striata* differs from *Tr. aquilariae* in having superficial ascomata, surface upon drying covered with white to grayish granules or crystalline flakes below the neck, and unbranched paraphyses. Whereas, *Tr. aquilariae* has immersed, not obvious ascomata, surface without granules or crystalline flakes, and branched paraphyses (Miller & Huhndorf, 2001). Additionally, the base pair differences of the LSU, *rpb*2 and TUB genes between our new collection and *Tr. striata* (SMH 3431) were compared, and the results showed that LSU has 1.9% nucleotide differences (16/837 bp, without gaps), *rpb*2 has 16.8% nucleotide differences (185/ 1098 bp, without gaps), TUB has 54% nucleotide differences (555/1028 bp, without gaps), which reveals that they belong to different species of the same genus. Therefore, we introduce our collection as a new species, *Tr. aquilariae* based on morphological and phylogenetic analyses.

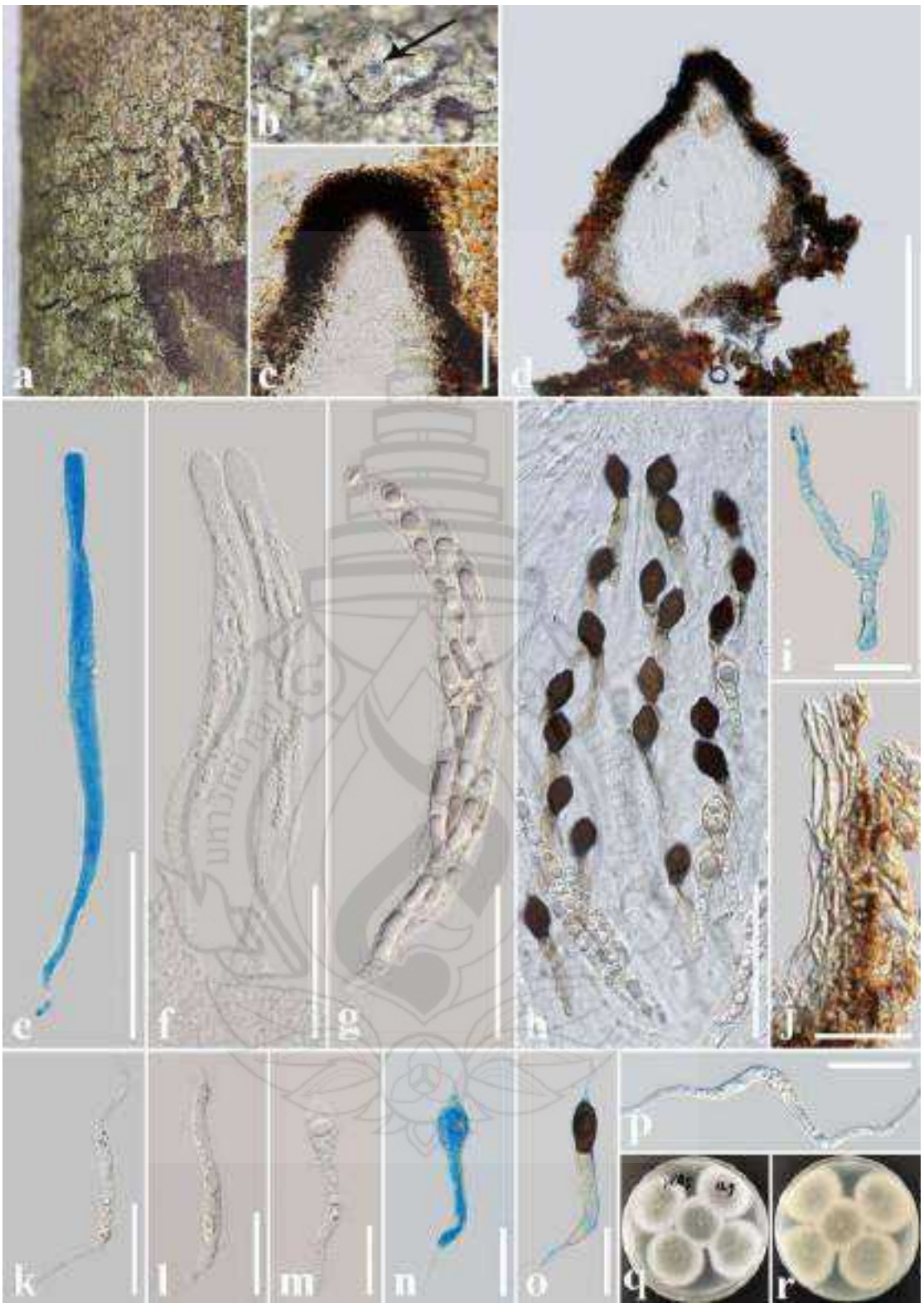


Figure 6.21 *Triangularia aquilariae* (MHZU 23-0028, holotype)

Figure 6.21 a, b, Ascomata on the host. c, Ostiole with periphyses. d, Vertical sections through an ascoma. e–h, Asci (e, An ascus stained with cotton blue). i, Paraphyses stained with cotton blue. j, Peridium. k–o, Ascospores (n, o, an ascospore stained with cotton blue). p, Germinated ascospore. q, r, Colonies on potato dextrose agar (PDA) obverse and reverse view. Scale bars: c = 50 µm, d = 200 µm, e–h = 50 µm, i = 10 µm, j–p = 20 µm.

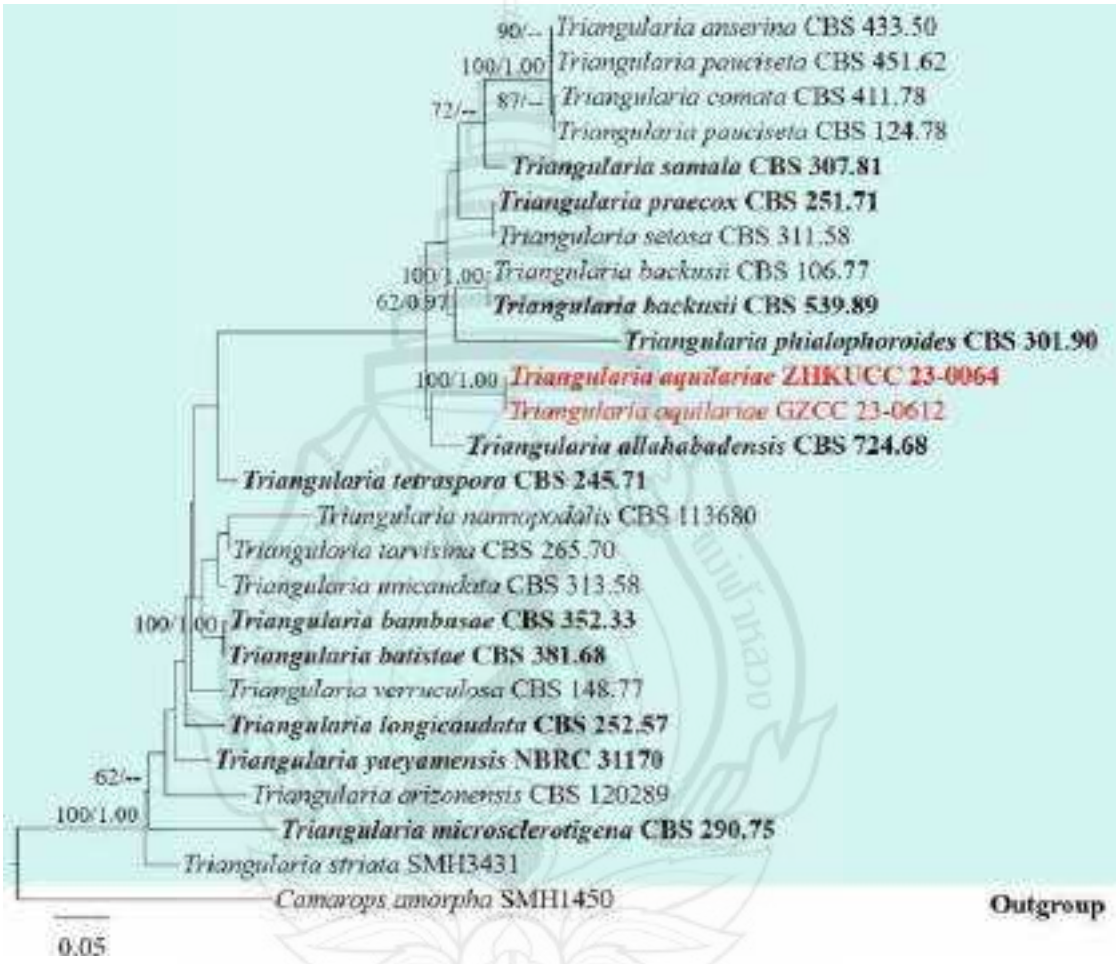


Figure 6.22 Phylogenetic tree of *Triangularia*

Figure 6.22 Bootstrap support values for ML greater than 60% and Bayesian posterior probabilities greater than 0.90 are given near the nodes, respectively. The tree is rooted with Camarops amorpha (SMH1450). The new isolates are indicated in red, and the ex-type strains are in bold.

Xylariales Nannf. 1932

Diatrypaceae Nitschke 1869

Peroneutypa Berl. 1902

Notes: *Peroneutypa* was introduced by Berlese (1902) to accommodate *Per. bellula* (Desm.) Berl., *Per. corniculata* (Ehrh.) Berl and *Per. heteracantha* (Sacc.), and without designating the type species. Later, Rappaz (1987) proposed *Per. bellula* as the type of *Peroneutypa* and synonymized *Peroneutypa* with *Eutypella* (Nitschke) Sacc. However, Carmarán et al. (2006) reinstated *Peroneutypa* as an independent genus based on morphology and phylogeny. Subsequent phylogenetic analyses have also shown that *Peroneutypa* is an independent genus within Diatrypaceae (Shang et al., 2017; Mehrabi et al., 2019; Du et al., 2022c; Li et al., 2023). Currently, 72 epithets of *Peroneutypa* are listed in Index Fungorum (2025). Members of this genus are characterized by valsoid ascostromata, perithecial ascomata with long necks, clavate asci, sessile to subsessile, eight-spored or polysporous, allantoid ascospores, hyaline or yellowish. In contrast, the asexual morph of this genus is undetermined (Carmarán et al., 2006; Shang et al., 2017; Dayarathne et al., 2020; Du et al., 2022c; Li et al., 2023). *Peroneutypa* is widely distributed in both terrestrial and marine habitats as saprobes or pathogens (Lumbsch & Huhndorf, 2010; Maharachchikumbura et al., 2015; Luo et al., 2019; Dayarathne et al., 2020). In this study, we introduce a new species, *Peroneutypa maomingensis* collected from a dead branch of *Aquilaria sinensis* in China based on morphological comparison and phylogenetic analyses.

Peroneutypa aquilariae T. Y. Du & Tibpromma, ***sp. nov.***

MycoBank number: MB845438; Facesoffungi number: FoF12744; Figure 6.23

Etymology: named after the host genus, *Aquilaria.*

Saprobic on dead twigs of *Aquilaria sinensis* (Thymelaeaceae). **Sexual morph:** *Ascostromata* 0.5–1.5 mm wide, well-developed interior, solitary to gregarious, mostly solitary, immersed, long ostiolar canal raised through host tissue, black, irregular in shape, arranged irregularly, 1–6 locules. *Ascomata* (excluding necks) 300–570 µm diam., perithecial, immersed in ascostromata, subglobose to globose, dark brown to black. *Ostiolar canal* 20–40 µm wide, without periphysis, filled with hyaline cells, with 200–300 µm long, cylindrical, straight, dark-brown to black necks. *Peridium* 35–70 µm wide, composed of outer layer thick-walled, dark brown to pale brown cells of *textura*

angularis, and inner layer thin-walled, hyaline cells of *textura prismatica. Paraphyses* absent. *Asci* 15–20 × 5–7 µm ($\bar{x}$ = 18 × 6 µm, n = 20), unitunicate, 8-spored, clavate to cylindrical, thin-walled, short pedicellate or non-pedicellate, apically rounded to truncate with indistinct J-apical ring. *Ascospores* (5–)5.5–7(–7.5) × (1.6–)1.8–2.2 µm ($\bar{x}$ = 6 × 2 µm, n = 30), overlapping 1–3-seriate, hyaline to pale yellow, oblong to allantoid, slightly curved, aseptate, smooth-walled, with granules, ascospores turn yellow after being stained by Melzer's reagent. **Asexual morph:** Undetermined.

Culture characteristics: Ascospores germinated on PDA within 24 h at a constant temperature incubator (28°C). Colonies on PDA reaching 6 cm diam., after one week at 28°C, mycelium white, flossy, circular with entire edge, with filiform margin. After one month, mycelium becomes white to light yellow from above and light brown to brown from below.

Material examined: CHINA, Yunnan Province, Xishuangbanna, on dead twigs of *Aquilaria sinensis* (Thymelaeaceae), 15 September 2021, T. Y. Du, YNA03 (holotype, HKAS 124185), ex-type, KUNCC 22-10817=KUNCC 22-10818.

Notes: The BLASTn search of ITS sequences of our strains is 87.67% similar to *Per. mackenziei* (MFLUCC 16-0072, NR_154363). In the present phylogenetic analyses (Figure 6.25), our strains formed a sister branch with *Per. mackenziei* (MFLUCC 16-0072) with a low bootstrap support (63% ML). However, they differ in morphological characteristics i.e. stromata of *Per. aquilariae* have well-developed interior, ostiolar canal without periphyse, peridium inner layer comprises of 3–5 hyaline cell layers of *textura prismatica*, and paraphyses absent; while *Per. mackenziei* has poorly developed interior stromata, ostiolar canal periphysate, peridium inner layer comprises 8–10 hyaline cell layers of *textura angularis*, and hamathecium is composed of paraphyses (Shang et al., 2017). Furthermore, a comparison of ITS nucleotides between *Per. aquilariae* and *Per. mackenziei* (MFLUCC 16-0072) resulted in 13.8% differences (67/487 bp, without gaps), and 54.1% differences (173/320 bp, without gaps) respectively in TUB. Based on both morphological characteristics and multigene phylogenetic analyses results, we introduce *Peroneutypa aquilariae* as a distinct new species and this is the first report of *Peroneutypa* from *Aquilaria sinensis*.

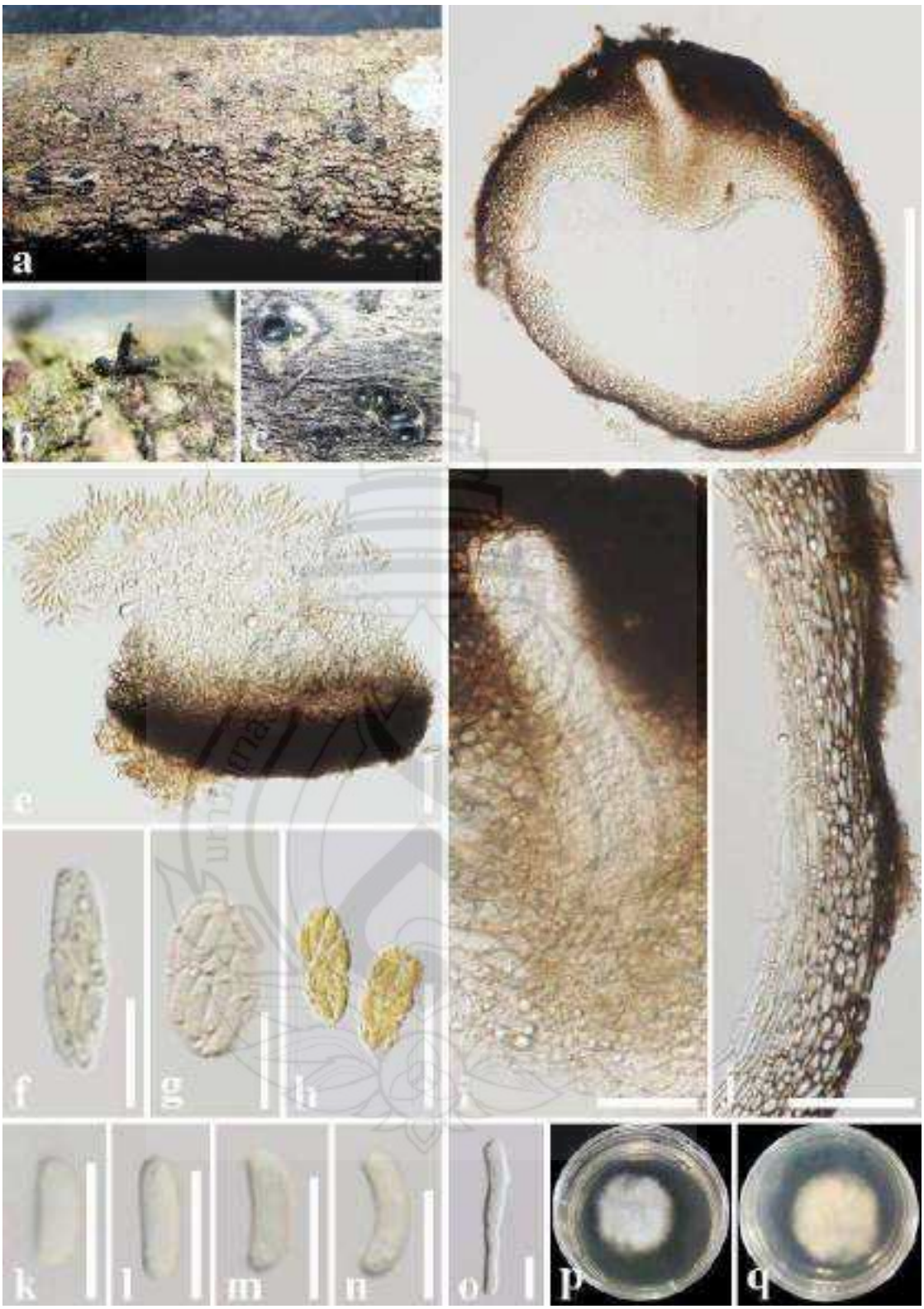


Figure 6.23 *Peroneutypa aquilariae* (HKAS 124185, holotype)

Figure 6.23 a-c Appearance of ascomata on the substrate. d A section through an ascoma. e-h Asci (g, An ascus stained with Congo red reagent, h, Asci stained with Melzer's reagent). i Ostiole. j Peridium. k-n Ascospores. o A germinating ascospore. p, q Colony on PDA medium (after one week in culture). Scale bars: d = 300 μm, e, j = 50 μm, f, g = 10 μm, h = 20 μm, i = 30 μm, k-o = 5μm.

Peroneutypa maomingensis T. Y. Du, Tibpromma & Karun. ***sp. nov.***

MycoBank number: MB 854006; Facesoffungi number: FoF 15270; Figure 6.24

Etymology: Named after the location "Maoming" where the holotype was collected.

Holotype: MHZU 23-0011

Saprobic on dead branch of *Aquilaria sinensis*. **Sexual morph:** *Ascostromata* well-developed interior, solitary to gregarious, immersed, ostiolar canal raised through host tissue, black, arranged irregularly, one to seven locules. *Ascomata* (excluding necks) 250–480 μm high × 200–450 μm diam. ($\bar{x}$ = 307 × 285 μm, n = 10), perithecial, immersed in ascostromata, globose, dark brown to black. *Ostiolar canal* 150–850 μm long × 85–150 μm wide ($\bar{x}$ = 510 × 110 μm, n = 10), cylindrical, curved, dark-brown to black necks, with periphysis. *Peridium* 20–45 μm wide, composed of an outer layer of thick-walled, pale brown to dark brown cells of *textura angularis*, and inner part comprising thin-walled, hyaline cells of *textura angularis* to *textura prismatica*. *Paraphyses* absent. *Asci* (40–)43–46(–47.5) × (6–)7–10(–13) μm ($\bar{x}$ = 44.5 × 8.5 μm, n = 30), spore-bearing part length 17–24 μm ($\bar{x}$ = 21.5 μm, n = 30), unitunicate, eight-spored, oval to cylindrical, thin- walled, 20–26 μm long pedicel, apically rounded to truncate with indistinct J-apical ring. *Ascospores* 5–7 × 1.3–2 μm ($\bar{x}$ = 6 × 1.5 μm, n = 30), uniseriate, oblong to allantoid, pale yellow when mature, slightly curved, aseptate, smooth-walled, with granules at ends, ascospores turn yellow after being stained by Melzer's reagent. **Asexual morph:** undetermined.

Culture characteristics: Ascospores germinated on PDA after 12 h, and germ tubes were produced from one end or both ends. Colonies on PDA reaching 6 cm diam., after 1 week at 23°C–28°C. Colonies obverse: soft, circular, flat or effuse, filiform margin, white, with a light yellow ring. Colonies reverse: white, no pigmentation.

Material examined: CHINA, Guangdong Province, Maoming City, Dianbai District, Poxin, 21°34′25″ N, 111°7′43″ E, on a dead branch of *Aquilaria sinensis* (Thymelaeaceae), June 3, 2022, T. Y. Du, MMA01 (MHZU 23-0011, **holotype**), ex-type, ZHKUCC 23-0030, other living culture, GZCC 23-0618.

Notes: The present phylogenetic analyses show that our new collection *Per. maomingensis* clustered in *Peroneutypa* and formed a well-separated branch with other species of *Peroneutypa* (Figure 6.25). Morphologically, *Per. maomingensis* shares similar ascomata and asci morphology with *Per. scoparia* (Dayarathne, 2020). However, *Per. scoparia* differs from *Per. maomingensis* in having uniseriate to biseriately arranged ascospores, and smaller ascomata, asci, and ascospores than *Per. maomingensis* (ascomata: 257 × 185 μm vs. 307 × 285 μm; asci: 20 × 4 μm vs. 21.5 × 8.5 μm; ascospores: 4 × 1 μm vs. 6 × 1.5 μm) (Dayarathne et al., 2020). Additionally, the base pair differences of the ITS and TUB genes between our new collection and Per. scoparia (MFLUCC 17-2143) were compared, and the results showed ITS has 14.2% nucleotide differences (68/480 bp, without gaps), while TUB has 22.4% nucleotide differences (76/340 bp, without gaps). Therefore, we introduce our new collection as a new species *Per. maomingensis* based on both morphological study and phylogenetic analyses.

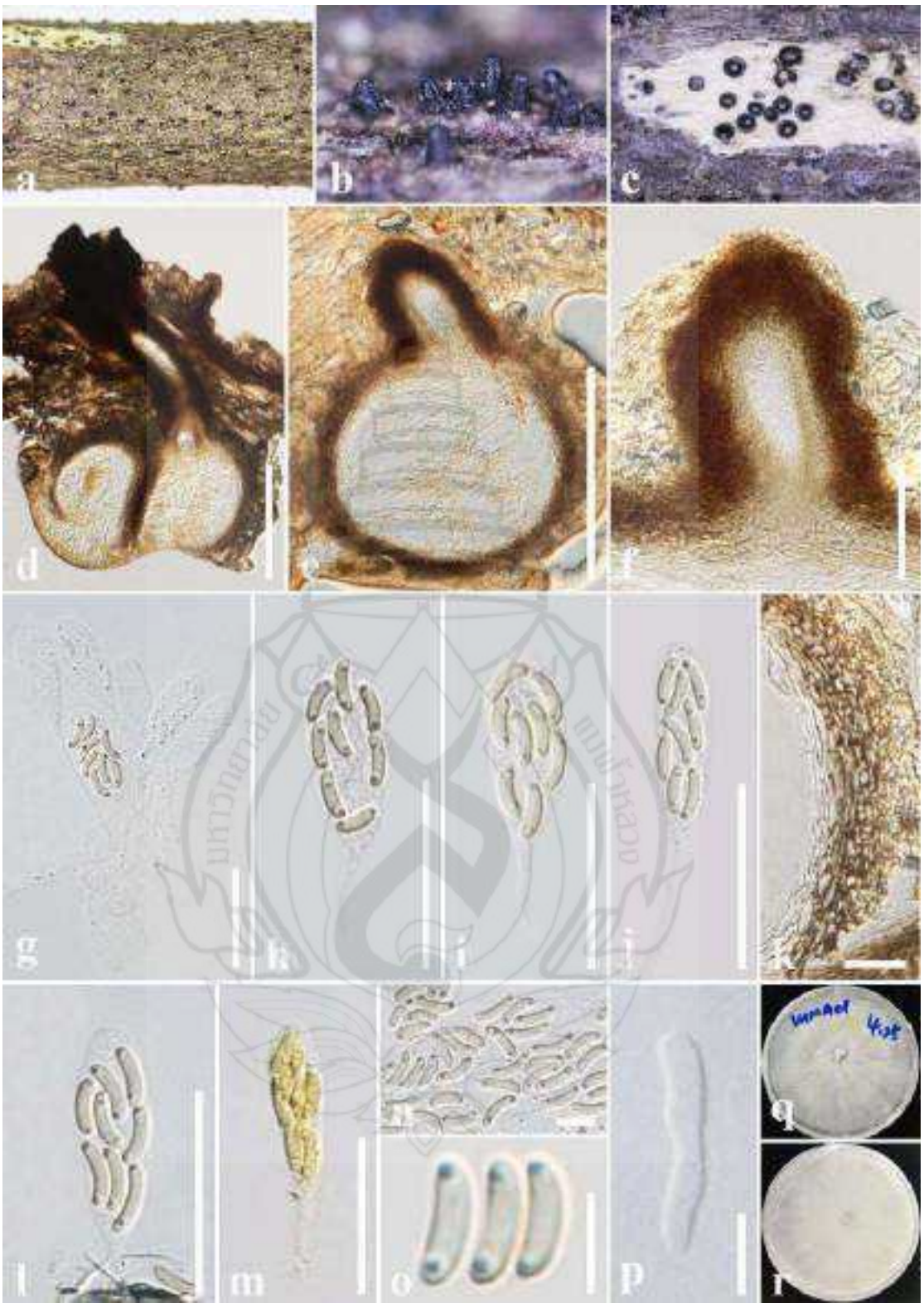


Figure 6.24 *Peroneutypa maomingensis* (MHZU 23-0011, holotype)

Figure 6.24 a, b, Ascostromata on the host. c, Transverse sections through ascostromata. d, e, Vertical sections through the ascomata. f, Ostiole with periphyses. g–j, l, m, Asci (m, asci stained with Melzer's reagent). k, Peridium. n–o, Ascospores. p, Germinated ascospore. q, r, Colony on potato dextrose agar (PDA) obverse and reverse view. Scale bars: d, e = 300 µm, f = 100 µm, g–m = 20 µm, n–p = 5 µm.

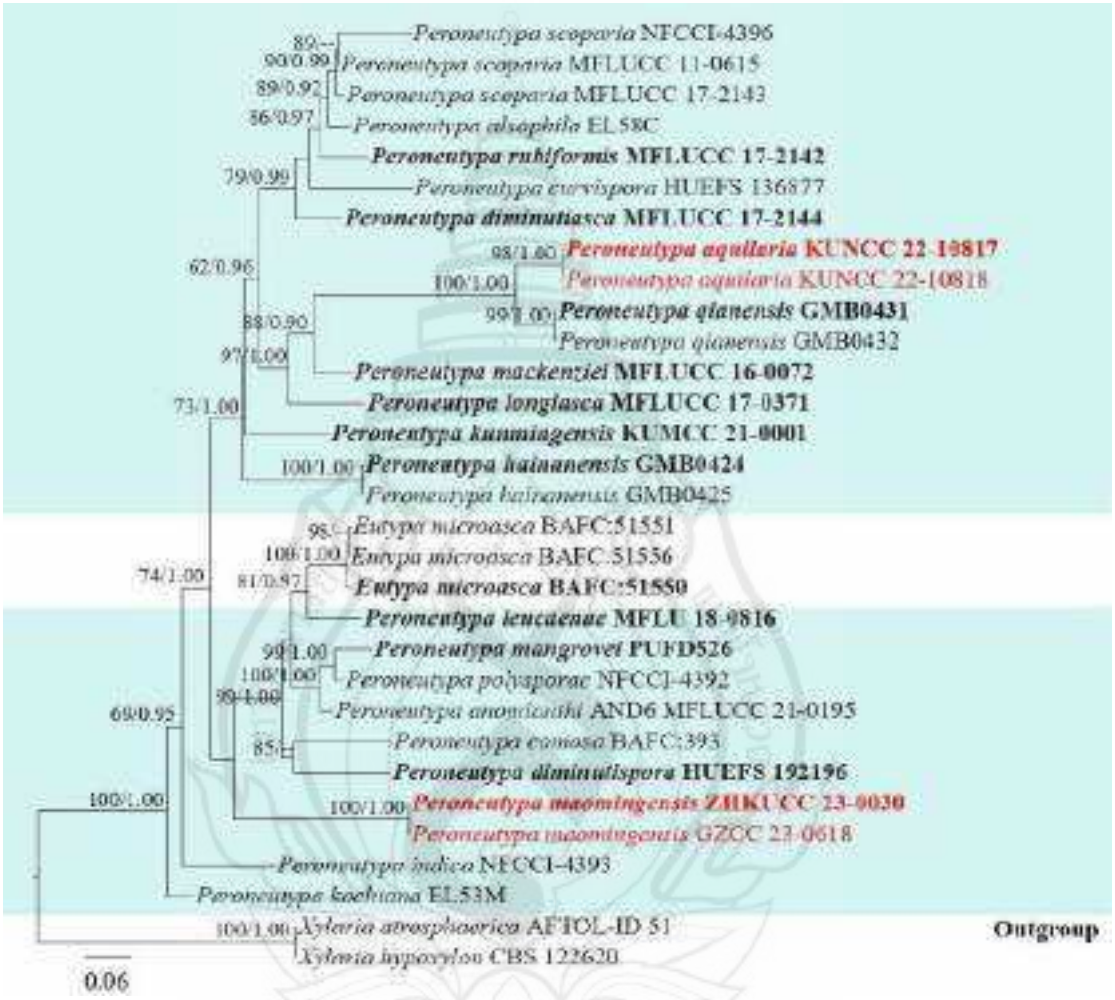


Figure 6.25 Phylogenetic tree of *Peroneutypa*

Figure 6.25 Bootstrap support values for ML greater than 60% and Bayesian posterior probabilities greater than 0.90 are given near the nodes, respectively. The tree is rooted with Xylaria atrosphaerica (AFTOL-ID 51) and X. hypoxylon (CBS 122620). The new isolates are indicated in red, and the ex-type strains are in bold.

6.3.3 Other Work

Saprobic fungi of *Aquilaria* spp. were contributed to the co-authors and published in the article.

Dyfrolomycetales K.L. Pang, K.D. Hyde & E.B.G. Jones 2013

Pleurotremataceae Walt. Watson 1929

Melomastia Nitschke ex Sacc. 1875

Notes: *Melomastia* was introduced by Saccardo (1875) and typified by *M. mastoidea* (Fr.) J. Schröt. *Melomastia* was classified under Ascomycota *genera incertae sedis* due to the lack of molecular data, and it was difficult to determine the placement of *Melomastia* based on only morphology (Maharachchikumbura et al., 2015). Later, Norphanphoun et al. (2017) assigned *Melomastia* in Pleurotremataceae based on molecular data (LSU and SSU). Subsequently, Li et al. (2022) synonymized *Dyfrolomyces* under *Melomastia* based on molecular phylogeny and morphology and transferred 11 *Dyfrolomyces* species to *Melomastia*. However, Kularathnage et al. (2023) reinstated *Dyfrolomyces* to accommodate two species (*D. tiomanensis* (K.L. Pang, Alias, K.D. Hyde, Suetrong & E.B.G. Jones) W.L. Li, Maharachch. & Jian K. Liu (type) and *D. chromolaenae* (Mapook & K.D. Hyde) W.L. Li, Maharachch. & Jian K. Liu). Currently, 73 epithets of *Melomastia* are listed in Index Fungorum (2025). *Melomastia* is characterized by ascomata solitary, coriaceous to carbonaceous, with conical, periphysate papilla; septate pseudoparaphyses; asci bitunicate, cylindrical, short pedicel; ascospores overlapping uniseriate, hyaline, ellipsoid to fusiform, 1–10-septate, mucilaginous sheath with or without; and asexual morph unknown (Li et al., 2022). Members of this genus are saprobic on branches, twigs, and culms of decaying wood, distributed in terrestrial, freshwater, and mangrove habitat (Li et al., 2022).

A new species was published in the following co-authored article:

Manawasinghe, I. S., Hyde, K. D., Wanasinghe, D. N., Karunarathna, S. C., Maharachchikumbura, S. S. N., Samarakoon, M. C., . . . Xu, B. (2024). Fungal diversity notes 1818–1918: Taxonomic and phylogenetic contributions on genera and species of fungi. *Fungal Diversity,* 1–261. https://doi.org/10.1007/s13225-024-00541-y

Melomastia aquilariae T. Y. Du & Karun. ***sp. nov.***

Index Fungorum number: IF 902121; Facesoffungi number: FoF 15849; Figure 6.26

Etymology: Named after the host genus, *Aquilaria*.

Holotypy: HKAS 126527

Saprobic on dead stems of *Aquilaria sinensis*. **Sexual morph:** *Ascomata* (excluding neck) 350–700 µm high × 300–450 µm diam. ($\overline{x}$ = 524 × 377 µm, n = 10), solitary, semi-immersed to immersed, visible on the host surface as dark, raised spots, dark brown to black, uniloculate, globose to subglobose (wide at the base), carbonaceous. *Ostiolar canal* 100–150 µm high, black, conical, carbonaceous, papillate, with periphyses. *Peridium* 35–150 µm wide ($\overline{x}$ = 85 µm, n = 10), comprising dense, brown to darkbrown cells of *textura angularis* to *textura prismatica*, fusion with host tissue. *Hamathecium* 1–3 µm wide, comprising numerous, hyaline, branched, septate pseudoparaphyses, longer than asci, attached at the base and between the asci. *Asci* 145–220 × 7.5–9 µm ($\overline{x}$ = 186 × 8.5 µm, n = 30), bitunicate, 8-spored, cylindrical, cylindrical pedicellate 7–14 µm long, rounded in apex, J- apical ring. *Ascospores* 21.5–28 × 7–8µm ($\overline{x}$ = 25 × 7.5µm, n = 30), 3-septate, overlapping-uniseriate, hyaline, fusiform with acute ends, slightly constricted at the septum, smooth-walled, with a large guttule in each cell when mature, not surrounded by a mucilaginous sheath. **Asexual morph:** Not observed.

Culture characteristics: Colonies on PDA reaching 6 cm diam., after one month at 28℃; grey, soft, irregular shape, middle protrusion, filiform margin; pale yellow to dark grey, smooth in reverse.

Specimen examined: China, Yunnan Province, Xishuangbanna, Jinghong City, Naban River Nature Reserve, 22° 7′50″ N, 100° 40′ 29″ E, on dead stems of *Aquilaria sinensis* (Thymelaeaceae), 14 September 2021, T.Y, YNA52, (HKAS 126527, **holotype**), ex-type ZHKUCC:23-0073, ex-isotype ZHKUCC:23-0088.

Notes: Based on the results of BLAST analysis in NCBI GenBank, in LSU, *Melomastia aquilariae* gave 99.65% closest match to *M. oleae* (CGMCC 3.20619), 99.90% for SSU with the closest match *M. fusispora* (CGMCC 3.20618) and 98.86% for *tef*1-α with the closest matches *M. winteri* (CGMCC 3.20621). In the phylogenetic analyses of this study, *M. aquilariae* formed a sister branch with *M. winteri* (CGMCC

3.20621) with 97% ML bootstrap support (Figure 6.27). However, *M. aquilariae* is different from *M. winteri* in having solitary, globose to subglobose ascomata, branched pseudoparaphyses, and colonies grey, soft, irregular shape in PDA; while *M. winteri* has solitary, gregarious, globose ascomata, unbranched pseudoparaphyses, and colonies white, dense, circular in PDA (Li et al., 2022). In addition, *M. aquilariae* can be distinguished from *M. winteri* by its wider ascomata (524 × 377 µm *vs.* 352 × 387 µm), wider range of peridium (35–150 µm *vs.* 55–62.5 µm), larger asci (186 × 8.5 µm *vs.* 177 × 7.5 µm) and longer cylindrical pedicellate (7–14 µm *vs.* 4.8–6.5 µm) (Li et al., 2022). Furthermore, a comparison of *tef*1-α nucleotides between *M. aquilariae* and *M. winteri* (CGMCC 3.20621) resulted in 1.18% differences (10/845bp, without gaps). In this study, *M. aquilariae* was collected from *Aquilaria sinensis* in China, while *M. winteri* was introduced from *Olea europaea* in China. Therefore, we introduce our collection as a new species based on both morphological study and phylogenetic analyses.

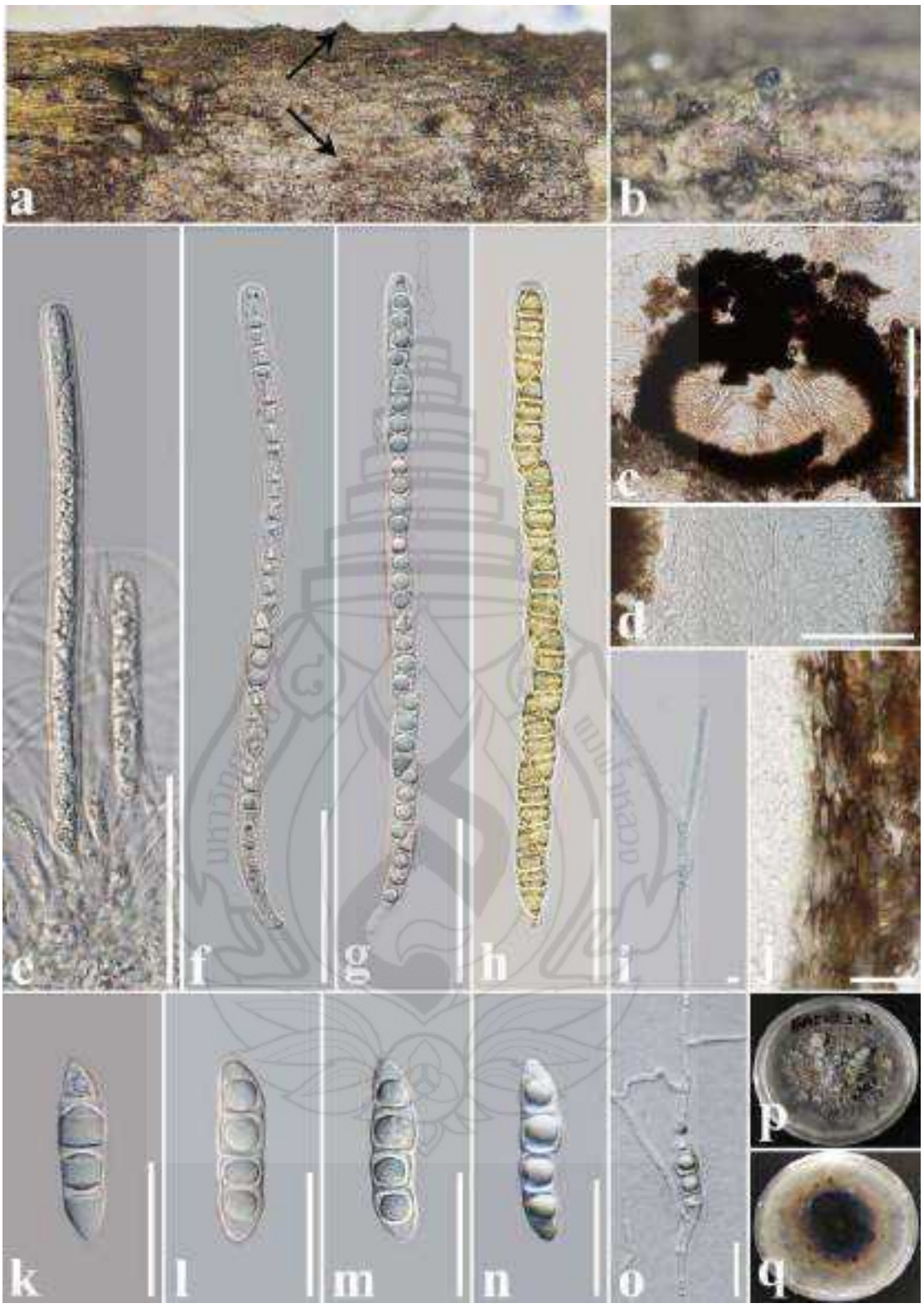


Figure 6.26 *Melomastia aquilariae* (HKAS 126527, holotype)

Figure 6.26 a, b Appearance of ascoma on the host. c Vertical sections through the ascoma. d Ostiole with periphyses. e–h Asci (h ascus stained with Melzer's reagent). i Pseudoparaphyses. j Peridium. k–n Ascospores. o Germinated ascospore. p, q Colony on PDA surface and reverse view. Scale bars: c=300 µm, d=50 µm, e–h=50 µm, i=2 µm, j–o=20µm

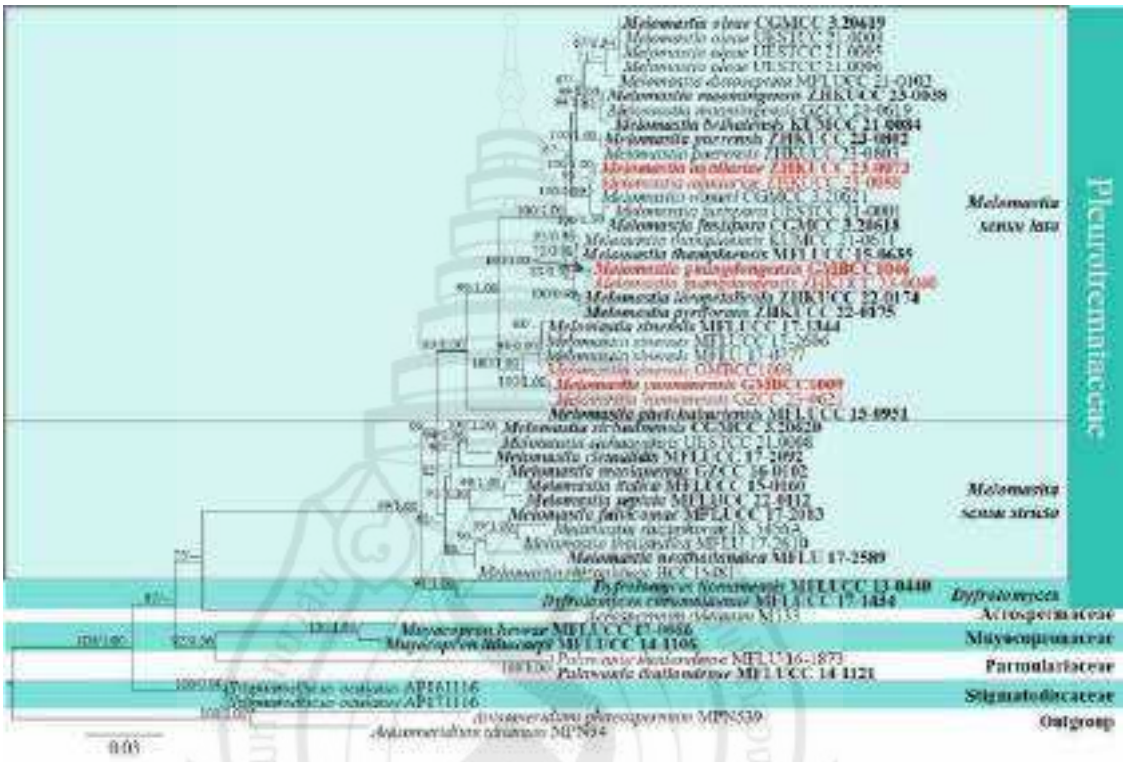


Figure 6.27 Phylogenetic tree of *Melomastia*

Figure 6.27 Bootstrap support values for ML greater than 60% and Bayesian posterior probabilities greater than 0.90 are given near the nodes, respectively. The tree is rooted with *Anisomeridium phaeospermum* (MPN539) and *A. ubianum* (MPN94). The new isolates are indicated in red, and the ex-type strains are in bold.

Pleosporales Luttr. ex M.E. Barr 1987

Didymosphaeriaceae Munk 1953

Montagnula Berl. 1896

Notes: *Montagnula* was introduced by Berlese (1896), with *M. infernalis* as the type species. According to Barr (2001), *Montagnula* was placed in Montagnulaceae based on morphological characteristics. Later, *Montagnula* was transferred from Montagnulaceae to Didymosphaeriaceae by Ariyawansa et al. (2014). Subsequently, Wanasinghe et al. (2016) transferred two species of *Munkovalsaria* (*M. appendiculata* and *M. donacina*) to *Montagnula* based on phylogenetic analyses. Recently, two new species *M. aquatica* and *M. guiyangensis* have been introduced into *Montagnula*, and four species *viz., M. chromolaenicola*, *M. puerensis*, *M. saikhuensis*, and *M. thailandica* have been synonymized under *M. donacina* based on morphological examination and molecular data (Sun et al., 2023). *Montagnula* has 61 records in Index Fungorum (2025). Species of genus *Montagnula* are characterized by immersed to erumpent, gregarious or grouped, globose or spherical, black ascomata, mostly cylindric-clavate to clavate asci with long pedicels, and straight or slightly curved, and fusoid or ellipsoid ascospores (Barr, 1990; Ariyawansa et al., 2014; Tennakoon et al., 2016; Tibpromma et al., 2018; Hongsanan et al., 2020). *Montagnula* plays a vital role as saprobes on a wide range of hosts in various countries (Ariyawansa et al., 2014; Du et al., 2021).

A new species was published in the following co-authored article:

Hyde, K. D., Norphanphoun, C., Ma, J., Yang, H. D., Zhang, J. Y., Du, T. Y., . . . Zhao, Q. (2023). Mycosphere notes 387–412 – novel species of fungal taxa from around the world. *Mycosphere, 14*(1), 663–744. https://doi.org/10.5943/mycosphere/14/1/8

Montagnula aquilariae T. Y. Du & Tibpromma, ***sp. nov.***

MycoBank number: MB846332; Facesoffungi number: FoF12850; Figure 6.28

Etymology: Named after the host genus *Aquilaria* from which the holotype was collected.

Holotype: HKAS 124186

Saprobic on dead twigs of *Aquilaria sinensis*. **Sexual morph:** *Ascomata* 300–450 × 300–420 μm ($\overline{x}$ = 380 × 360 μm, n = 5), immersed, solitary to gregarious, mostly gregarious, subglobose to globose, black, with a long ostiole. *Ostiole* 100–180 × 60–160 μm ($\overline{x}$ = 147 × 117 μm, n = 5), central, straight, dark brown to black, without periphysate. *Peridium* 20–60 μm wide, fused with host tissues, thick-walled, pale brown to dark brown cells of *textura angularis*. *Hamathecium* comprising 1.5–2 μm wide, numerous filamentous, branched, septate, guttulate, trabeculate pseudoparaphyses. *Asci* 45–75(–88) × (13–)15–20 μm ($\overline{x}$ = 60 × 18 μm, n = 30) (spore-bearing part), bitunicate, 8-spored, elongate-clavate, slightly curved, with a furcate, 45–70 μm long pedicel. *Ascospores* 17–20 × 7–10 μm ($\overline{x}$ = 19 × 8 μm, n = 30), uni-to bi-seriate, fusoid or ellipsoid, straight or slightly curved, 1-septate, slightly or strongly constricted at the septum, widest at the centre, tapering towards ends, hyaline to yellow when immature, become brown to dark brown when mature, turns reddish-brown in Melzer's reagent, guttulate, with a thin mucilaginous sheath. **Asexual morph:** Undetermined.

Culture characteristics: Ascospores germinating on PDA within 24 h at 28°C, germ tubes produced from both upper and lower cells. Colonies on PDA reaching 6 cm diam., after one week at 28°C, mycelium white, flossy, circular with the entire edge, with filiform margin; white in reverse.

Material examined: China, Yunnan Province, Xishuangbanna, on dead twigs of *Aquilaria sinensis* (Thymelaeaceae), 13 September 2021, T. Y. Du, YNA25 (HKAS 124186, **holotype**), ex-type living cultures, KUNCC 22-10815 = KUNCC 22-10816.

Notes: In the NCBI BLASTn search, the ITS sequences of *Montagnula aquilariae* matched with *M. opulenta* (MW187736) in 98.39% similarity; the LSU sequences of *M. aquilariae* matched with *M. aloes* (NG_042676) in 97.55% similarity; the SSU sequences of *M. aquilariae* matched with *M. thailandica* (OL780525) in 96.61% similarity; and the *tef*1-α sequences of *M. aquilariae* matched with

M. thailandica (MT235774) in 96.94% similarity. In the phylogenetic analyses, *M. aquilariae* forms a sister branch with *M. guiyangensis* (HGUP 22-0800, HKAS 124556) with moderate statistical support (Figure 6.29). However, they differ in morphological characteristics i.e., ascospores of *M. aquilariae* with a thin mucilaginous sheath, not form polar appendages; while ascospores of *M. guiyangensis* with sheath drawn out to form polar appendages, from both ends of the ascospores. In morphology, *M. aquilariae* resembles *M. opulenta* in having immersed ascomata, branched and septate pseudoparaphyses, and ascospores with a mucilaginous sheath. However, they are different because *M. aquilariae* has trabeculate pseudoparaphyses (sensu Liew et al., 2000), and ascospores uni or bi-seriate, slightly or strongly constricted at the septum, while *M. opulenta* has cellular pseudoparaphyses, ascospores bi-seriate, and strongly constricted at the septum (Aptroot, 1995b; Wang, 2000). In addition, the ascomata in *M. aquilariae* are smaller than those of *M. opulenta* (300–450 μm *vs.* 400–1200 μm) (Aptroot, 1995b). Therefore, based on phylogenetic analyses and morphological characteristics, *M. aquilariae* is introduced as a new species from China.

Figure 6.28 *Montagnula aquilariae* (HKAS 124186, holotype)

Figure 6.28 a, b, Appearance of ascomata on the host. c, Section of an ostiole. d, Section of an ascoma. e–g, Asci. h, Ascus stained by Melzer's reagent. i–n, Ascospores. o, Pseudoparaphyses. p, Peridium. q, Ascospore stained by Indian ink. r, A germinating ascospore. s, t, Colonies on PDA medium (after one week in culture). Scale bars: c = 100 µm, d = 200 µm, e–h = 50 µm, i–o = 10 µm, p = 20 µm, q = 10 µm, r = 20 µm.

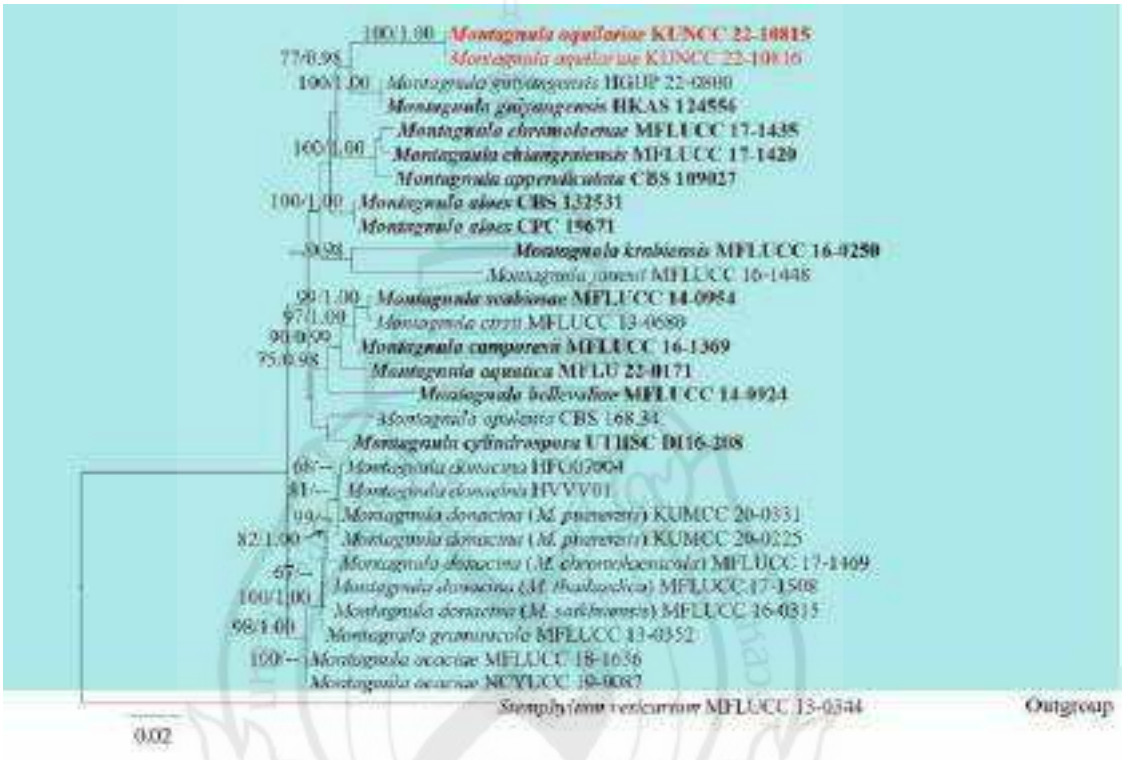


Figure 6.29 Phylogenetic tree of *Montagnula*

Figure 6.29 Bootstrap support values for ML greater than 60% and Bayesian posterior probabilities greater than 0.95 are given near the nodes, respectively. 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.

Torulaceae Corda 1829

Torula Pers. 1795

Notes: *Torula* is an asexual hyphomycetous genus, initially introduced by Persoon (1794), with *T. herbarum* as the type species (Tian et al., 2023). The genus is characterized by terminal or lateral, monoblastic or polyblastic conidiogenous cells and acrogenous conidia, dark brown, cylindrical to subcylindrical, solitary to catenate, septate (Crane & Miller, 2016; Li et al., 2017; De Silva et al., 2022). Morphologically, the different species of *Torula* can be distinguished by conidial size and the number of septa and chains (Tian et al., 2023). Recently, Tian et al. (2023) introduced four new species to the genus and provided molecular data and complete morphological characteristics. Currently, 561 species epithets are listed in Index Fungorum (2025).

A new record was published in the following co-authored article:

Hyde, K. D., Wijesinghe, S. N., Amuhenage, T. B., Bera, I., Bhunjun, C. S., Chethana, K. W. T., . . . Zhao, H. J. (2024). Current Research in Applied and Environmental Mycology Fungal Profiles 1–30. *Current Research in Environmental & Applied Mycology (Journal of Fungal Biology), 14*(1), 167–266. https://doi.org/10.5943/cream/14/1/11

Torula fici Crous 2015

Index Fungorum number: IF 816154; Facesoffungi number: FoF 02712; Figure 6.30

Saprobic on dead branch of *Aquilaria* sp. **Sexual morph:** Undetermined. **Asexual morph:** Hyphomycetous. *Colonies* effuse on natural substrate, black, powdery. *Mycelium* partly immersed to superficial on the host, composed of pale brown to light brown, septate, branched hyphae. *Conidiophores* 2–5 µm wide, macronematous, mononematous, arising from hypha, solitary, erect, or slightly flexuous, subcylindrical, pale brown to brown, thick-walled. *Conidiogenous cells* 3.5–6.5 × 4–5.5 µm ($\overline{x}$ = 5 × 4.5 µm, n = 10), monoblastic to polyblastic, terminal, doliiform to subglobose, dark brown to black, thick-walled. *Conidia* 12–17 × 5–8.5 µm ($\overline{x}$ = 15 × 7 µm, n = 30), acrogenous, phragmosporous, 1–5-septate (mostly 3-septate), catenate, branched, oblong, elongated, constricted at the septa, brown to dark brown, verrucose, straight or sometimes slightly curved, easily separate, rough-walled.

Culture characteristics: Conidia germinated on PDA within 24 h at 28℃ and germ tubes were produced from each cell. Colony on PDA reached 4–5 cm diam. after two weeks at 28℃. Colonies obverse: flat, irregular, floccose, white to pale grey, medium dense, irregular margin, and dark brown in reverse pale, edge is brown.

Material examined: China, Yunnan Province, Xishuangbanna, Menghai City, Agarwood plantation, on a dead branch of Aquilaria sp., 15 September 2021, T. Y. Du, YNA34 (MHZU 23-0033), living cultures (ZHKUCC 23-0069).

Known distribution (based on molecular data): China (Su et al., 2018; Jayasiri et al., 2019; Samarakoon et al., 2021a; Yang et al., 2022b; this study), Cuba (Crous et al., 2015), South Africa (Spies et al., 2020), and Thailand (Li et al., 2017; Tibpromma et al., 2018; Jayasiri et al., 2019; Mapook et al., 2020; Senwanna et al., 2021; Jayawardena et al., 2023).

Known hosts (based on molecular data): *Aquilaria* sp. (This study), *Chromolaena odorata* (Li et al., 2017; Mapook et al., 2020), *Ficus ampelas* (Tennakoon et al., 2021), *Ficus religiosa* (Crous et al., 2015), Freshwater habitat (Su et al., 2018), *Garcinia* sp. (Jayasiri et al., 2019), *Hevea brasiliensis* (Senwanna et al., 2021), *Magnolia grandiflora* (Jayasiri et al., 2019), *Mangifera indica* (Yang et al., 2022b), *Musa* sp. (Samarakoon et al., 2021a; Jayawardena et al., 2023), *Olea europaea* (Spies et al., 2020), and *Pandanus* sp. (Tibpromma et al., 2018).

Notes: According to the phylogenetic analyses, our strain (ZHKUCC 23-0069) clusters with *Torula fici* strains (CBS 595.96, KUMCC 16-0038, UESTCC 22.0123, UESTCC 22.0124 and KUMCC 15-0428), with 73% ML bootstrap support (Figure 6.31). Our fungal collection shares similar morphology with *T. fici* in macronematous and mononematous conidiophores, monoblastic to polyblastic conidiogenous cells, and acrogenous, phragmosporous, catenate, brown, verrucose conidia (Su et al., 2018, Mapook et al., 2020). Based on morphology and phylogenetic analyses, we conclude our collection as *T. fici* found on *Aquilaria* sp., and it is a new host record.

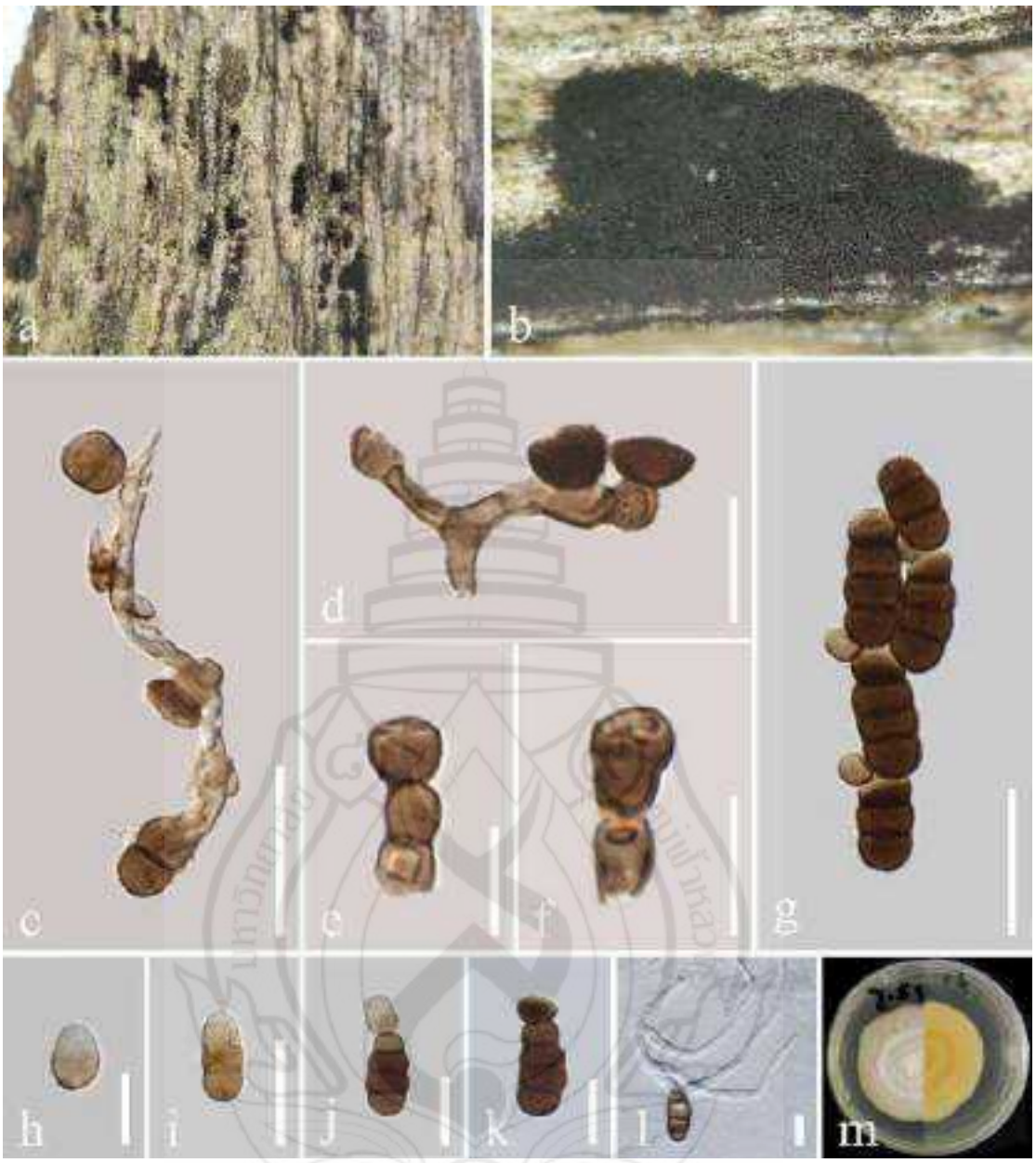


Figure 6.30 *Torula fici* (MHZU 23-0033, a new host record)

Figure 6.30 a, b, Appearance of colonies on the natural substrate. c–f, Conidiophores, conidiogenous cells and conidia. g, Conidia in chains. h–k, Conidia. l, A germinated conidium. m, Colonies on PDA from above and below (two weeks). Scale bars: c = 20 µm, d–f = 10 µm, g = 20 µm, h = 5 µm, i–l = 10 µm.

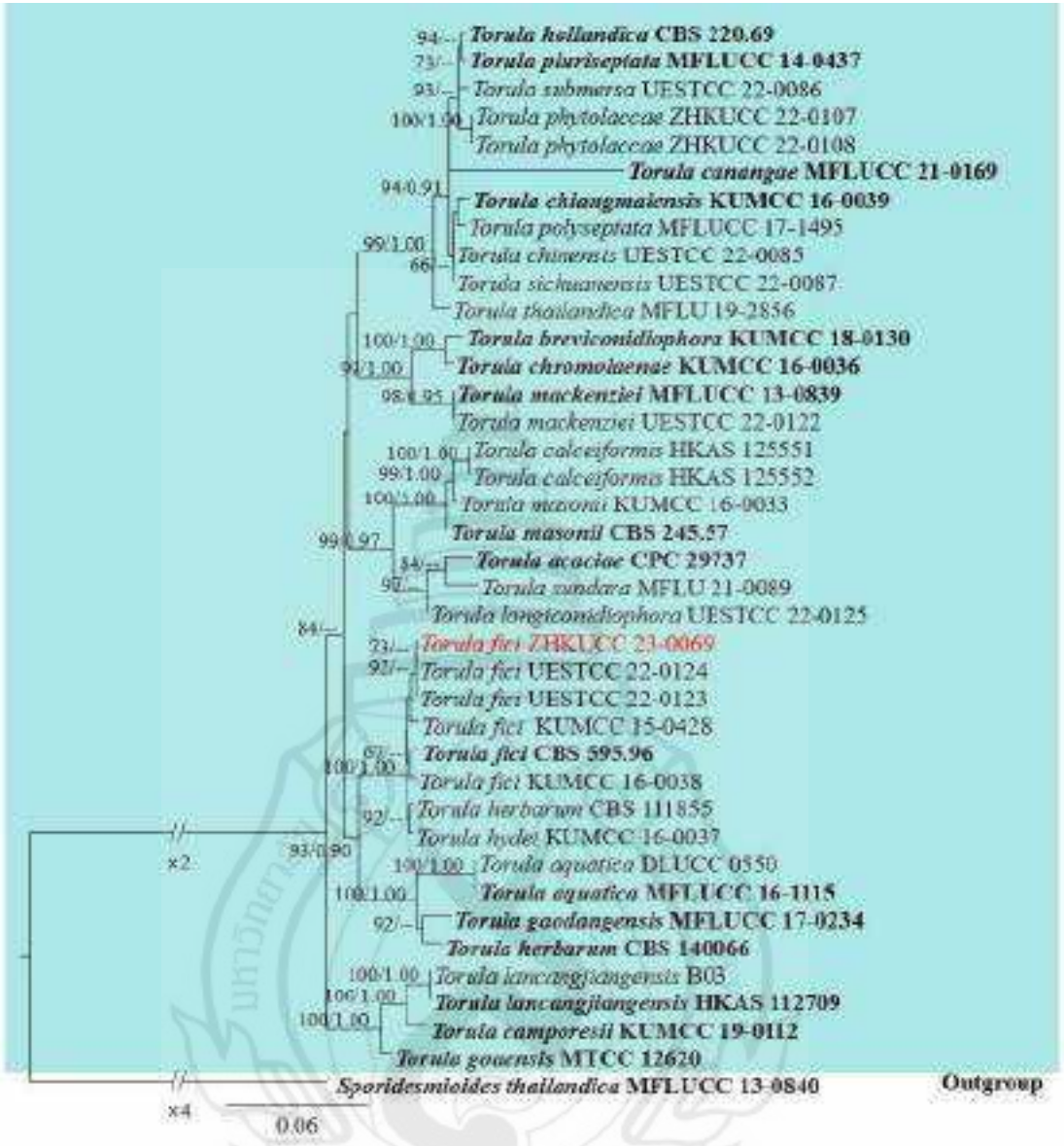


Figure 6.31 Phylogenetic tree of *Torula*

Figure 6.31 Bootstrap support values for ML greater than 60% and Bayesian posterior probabilities greater than 0.90 are given near the nodes, respectively. The tree is rooted with *Sporidesmioides thailandica* (MFLUCC 13-0840). The new isolate is indicated in red, and the ex-type strains are in bold.

Sordariomycetes

Xylariales Nannf. 1932

Diatrypaceae Nitschke 1869

Allocryptovalsa Senwanna, Phookamsak & K.D. Hyde 2017

Notes: *Allocryptovalsa* was introduced by Senwanna et al. (2017) with *Allocryptovalsa polyspora* as the type species. Senwanna et al. (2017) transferred *Eutypella cryptovalsoidea* and *Cryptovalsa rabenhorstii* to *Allocryptovalsa* based on morphological and phylogenetic analyses. The general features of this genus are immersed stromata, ostiolar with periphyses, unbranched, septate paraphyses, polysporous asci and oblong to allantoid ascospores, while the asexual morph was reported with hyaline, elongate-allantoid conidia (Senwanna et al., 2017; Zhu et al., 2021). To date, 11 species have been recorded in Index Fungorum (2025).

A new species was published in the following co-authored article:

Chethana, K. W. T., Rathnayaka, A. R., Samarakoon, B. C., Wu, N., Wijesinghe, S. N., Yasanthika, W. A. E., . . . Hyde, K. D. (2023). AJOM new records and collections of fungi: 151–200. *Asian Journal of Mycology, 6*(2), 89–243. https://doi.org/10.5943/ajom/6/2/7

Allocryptovalsa aquilariae T. Y. Du & Tibpromma ***sp. nov.***

MycoBank number: MB 846167; Facesoffungi number: FoF 12954; Figure 6.32

Etymology: Named after the host genus, *Aquilaria* from which it was collected.

Holotype: HKAS 124187

Saprobic on dead twigs of *Aquilaria sinensis* (Lour.) Spreng. **Sexual morph:** *Ascostromata* gregarious with small black dots, immersed, the surrounding white host tissue without bark, 1–12-loculate. *Ascomata* (excluding the neck) 320–550 µm high × 250–650 µm diam. ($\overline{x}$ = 380 × 410 µm, n = 10), perithecial, solitary to gregarious, immersed in substrate, globose to ampuliform, dark brown to black, not wrapped in white entostroma, the surrounding tissue is black after sectioning, ostiolate, papillate. *Ostiolar canal* 150–330 µm high × 85–150 µm diam. ($\overline{x}$ = 203 × 112 µm, n = 10), central, not protrude or protrude slightly to outside from the substrate, cylindrical or irregular, straight, dark brown to black, periphysate. *Peridium* 35–95 µm wide, composed of several layers of thick-walled, hyaline to brown cells of *textura angularis* to *textura prismatica*, which are not fully fused with the host tissue. *Hamathecium* 2–9

μm wide, hyaline, with granulate, filamentous, unbranched, septate paraphyses, slightly constricted at the septa. *Asci* 130–190 × 10–20 μm ($\overline{x}$ = 167.8 × 15.4 μm, n = 30), spore-bearing part length 65–100 μm ($\overline{x}$ = 87 μm, n = 30), unitunicate, thin-walled, polysporous, clavate, J- apical ring, with 64–102 μm, apically rounded, narrowing towards lower region, with long and fragile pedicels, and some pedicels with subglobose or irregular structure. *Ascospores* (8–)9.5–11.5 × 2–3.5 μm ($\overline{x}$ = 10.2 × 2.8 μm, n = 30), crowded, oblong to allantoid, pale yellowish at maturity, aseptate, slightly curved, smooth-walled. **Asexual morph:** Undetermined.

Culture characteristics: Colonies on PDA reaching 6 cm diam., after seven days at 28℃, flattened, filiform margin, with white aerial mycelia, flossy, velvety, reverse white, smooth.

Material examined: China, Yunnan Province, Xishuangbanna, dead twigs of Aquilaria sinensis, 13 September 2021, T. Y. Du, YNA27 (HKAS 124187, **holotype**), ex-type cultures, KUNCC 22-10819 = KUNCC 22-12389.

GenBank accession numbers: KUNCC 22-10819: ITS: OP454035, TUB: OP572197; KUNCC 22-12389: ITS: OP456373, TUB: OP572198.

Notes: In the phylogenetic tree (Figure 6.34), our isolates formed an inconspicuous branch with no support similar to *Allocryptovalsa cryptovalsoidea*, *A. elaeidis*, *A. polyspora,* and *A. truncata*. *Allocryptovalsa cryptovalsoidea* has ostioles often perforated, emerging through the bark, while our species do not protrude or protrude slightly to the outside from the substrate, mostly immersed (Trouillas et al., 2011). The ascomata of our collection are 1–12-loculate, wrapped in white powder, which differs from the ascomata of *A. elaeidis* which has 1–2-loculate ascomata, delimited by a black zone in host tissues (Konta et al., 2020). Also, our species differs from *A. polyspora* by having 1–12-loculate, larger ascomata (320–550 × 250–650 μm *vs.* 80–425 × 100–400 μm), whereas the ascomata of *A. polyspora* are 1–3-loculate (Senwanna et al., 2017). *Allocryptovalsa truncata* has superficial ascostromata and individual ascomata, which differ from our collection by having 1–12-loculate, immersed ascostromata (Hyde et al., 2020). Based on the multi-gene phylogenetic tree, and its unique morphological characteristics, *Allocryptovalsa aquilariae* is identified as a new species.

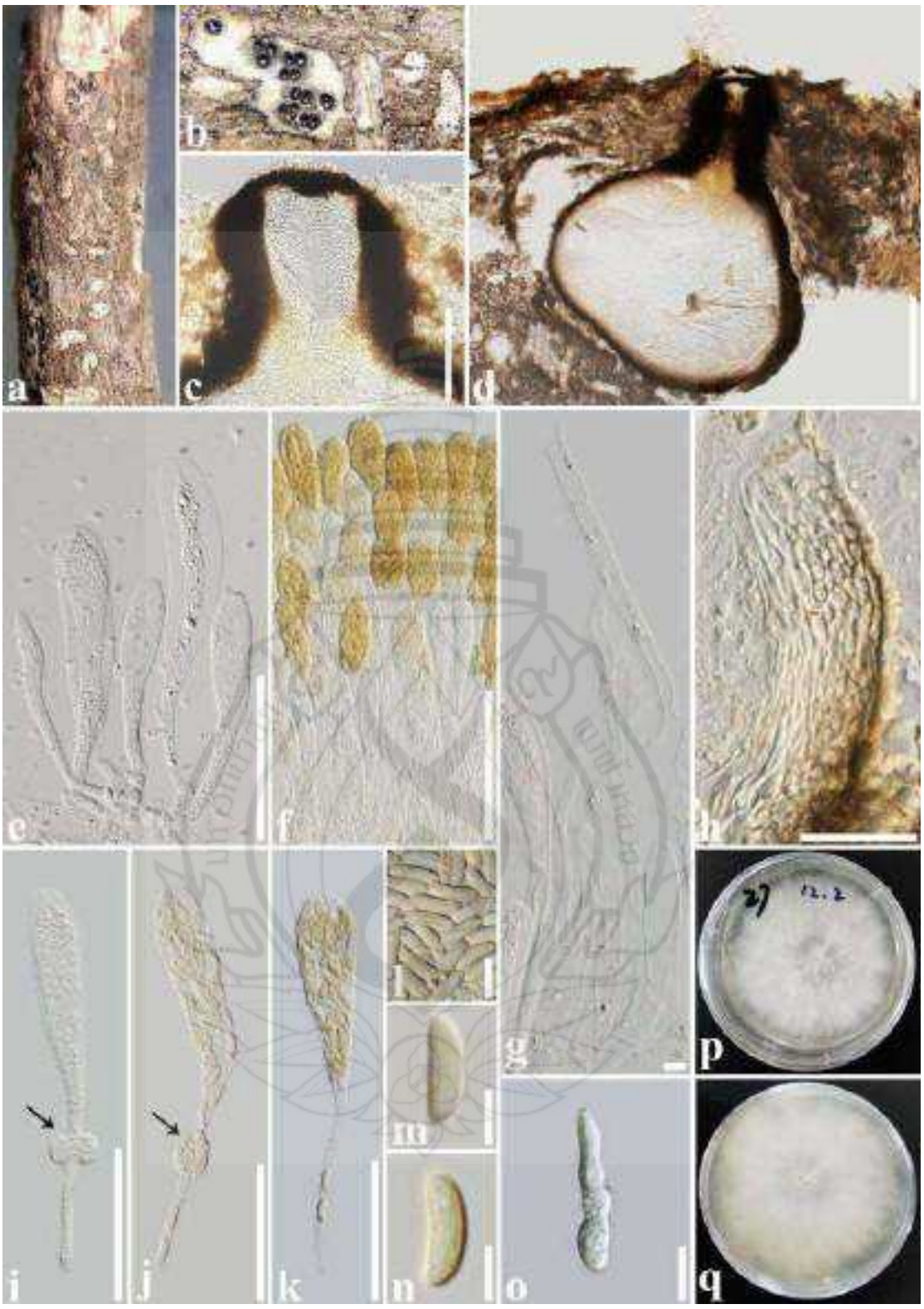


Figure 6.32 *Allocryptovalsa aquilariae* (HKAS 124187, holotype)

Figure 6.32 a, b, Appearance of ascostromata on the host. c, Ostiolar periphysate. d, Section through an ascoma. e, f, i–k, Asci (arrows pointed towards subglobose structures at the pedicel). g, Paraphyses. h, Peridium. l–n, Ascospores. o, Germinated ascospore. p, q, Culture characteristics on PDA after seven days (p, front view, q, reverse view). Scale bars: c, f = 100 µm, d = 200 µm, e, h–k = 50 µm, g, m, n = 5 µm, l, o = 10 µm.

A new record was published in the following co-authored article:

Hyde, K. D., Wijesinghe, S. N., Afshari, N., Aumentado, H. D., Bhunjun, C. S., Boonmee, S., . . . Zhang, J. Y. (2024). Mycosphere Notes 469–520. *Mycosphere, 15*(1), 1294–1454. https://doi.org/10.5943/mycosphere/15/1/11

Allocryptovalsa rabenhorstii (Nitschke) Senwanna, Phookamsak & K.D. Hyde 2017

Index Fungorum number: IF553864; Facesoffungi number: FoF14962; Figure 6.33

Saprobic on a dead branch of *Aquilaria* sp. **Sexual morph:** *Ascostromata* poorly developed, scattered or gregarious, 1–4-loculate, immersed through the substrate, inconspicuous, only the ostioles exposed to the surface. *Ascomata* 250–500 µm high × 300–600 µm diam. ($\bar{x}$ =375 × 400 µm, n = 10) (excluding neck), perithecial, solitary or gregarious, immersed, ampuliform, brown to dark brown, not wrapped in white entostroma, the surrounding tissue is light yellow after section, ostiolate. *Ostiolar canal* 200–350 µm high × 60–200 µm diam. ($\bar{x}$ = 280 × 140 µm, n = 10), central, slightly cylindrical, straight, not protruding or protruding slightly from the substrate, the upper part is wider than the lower part, dark brown to black, periphysate. *Peridium* 30–85 µm wide, composed of several layers, from outer toward inner layers with thick-walled, pale brown to thin-walled, hyaline to cells of *textura angularis* to *textura prismatica*. *Hamathecium* comprising 3–9 µm wide, filamentous, unbranched, hyaline, granular, septate paraphyses, slightly constricted at the septa, enlarged base, gradually tapers towards the tip. *Asci* (150–)155–175(–180) × (12.5–)14–15.5(–17) µm ($\bar{x}$ = 165.5 × 15 µm, n = 30), spore-bearing part (60–)65–85(–90) µm length ($\bar{x}$ = 75.5 µm, n = 30), unitunicate, thin-walled, polysporous, clavate, with Japical ring, 70–100 µm long pedicellate, some pedicel with subglobose structure, apically rounded, narrowing

towards lower region. *Ascospores* (9.5–)11–14(–16) × 3–4.5 µm ($\overline{x}$ = 13 × 3.8 µm, n = 30), crowded, sub-allantoid, initially hyaline, turning pale yellow at the maturity, aseptate, curved, smooth-walled. **Asexual morph:** Undetermined.

Culture characteristics: Ascospores germinated on PDA within 24 h at 28°C and germ tubes were produced from both ends. Colonies on PDA reached 6 cm diam. after one week at 28°C. Colonies obverse: flat, circular, flossy, filiform margin, and white to cream, smooth in reverse.

Material examined: China, Yunnan Province, Xishuangbanna, Menghai City, Agarwood plantation, on a dead branch of *Aquilaria* sp. (Thymeleaceae), 15 September 2021, T. Y. Du, YNA22 (MHZU 23-0030, living culture ZHKUCC 23-0066).

Known distribution: Australia (Trouillas et al., 2011; Jayawardena et al., 2018b), China (this study), England (Mejia et al., 2011), Iran (Mehrabi et al., 2019), Japan (Kobayashi, 2007), Pakistan (Ahmad, 1969), South Africa (Moyo et al., 2019), United States of America (Trouillas et al., 2011), Ukraine (Dudka et al., 2004).

Known hosts: *Acacia farnesiana* (Ahmad, 1969), *Aquilaria* sp. (this study), *Betula* sp. (Mejia et al., 2011), *Citrus* sp. (Mehrabi et al., 2019), *Dalbergia sissoo* (Ahmad, 1969), *Echinops echinatus* (Ahmad, 1978), *Morus alba* (Ahmad, 1978), *Morus* sp. (Kobayashi, 2007), *Robinia pseudoacacia* (Dudka et al., 2004), *Sambuscus nigra* (Trouillas et al., 2011), *Viburnum* sp. (Ahmad, 1978), *Vitis* sp. (Jayawardena et al., 2018b), *Vitis vinifera* (Trouillas et al., 2011).

Notes: According to the phylogenetic analyses, our strain (ZHKUCC 23-0066) clustered with *A. rabenhorstii* (WA08CB) with 100% ML and 1.00 BYPP bootstrap support (Figure 6.34). Our fungal collection share similar morphology to *A. rabenhorstii* in color, shape, and size of asci and ascospores (Trouillas et al., 2011). Our collection has thinner (14–15.5 µm wide *vs.* 18–22 µm wide) pedicels of asci than *A. rabenhorstii* (WA07CO) (Trouillas et al., 2011). This might depend on different environmental factors and host plants. Based on morphology and multi-gene phylogeny we identified our collection as *A. rabenhorstii*. This is the first report of *Allocryptovalsa* species on *Aquilaria* plants, and it is reported for the first time in China. Therefore, this study presents a new host and geographical record of *A. rabenhorstii*.

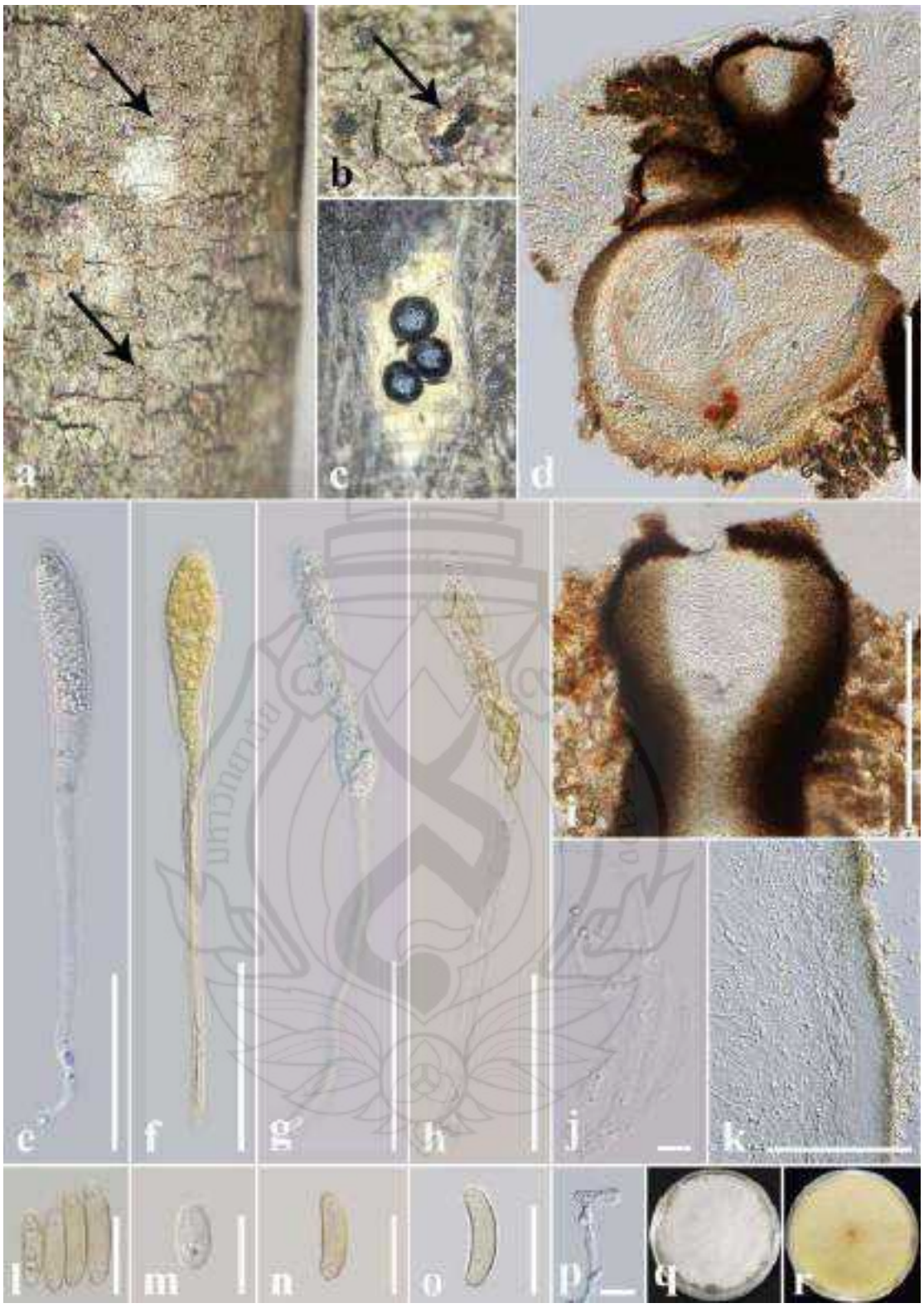


Figure 6.33 *Allocryptovalsa rabenhorstii* (MHZU 23-0030, a new host and a geographical record)

Figure 6.33 a, b, Appearance of ascostromata on the host. c, Transverse section of an ascostroma. d, Section through an ascoma. e–h, Asci (f is an ascus stained with Melzer's reagent). i, Ostiole with periphyses. j, Paraphyses. k, Peridium. l–o, Ascospores. p, A germinating ascospore. q, r, Colonies on PDA after two weeks (q, obverse view; r, reverse view). Scale bars: d = 300 µm, e–h = 50 µm, i = 200 µm, j = 10 µm, k = 50 µm, l–p = 10 µm.

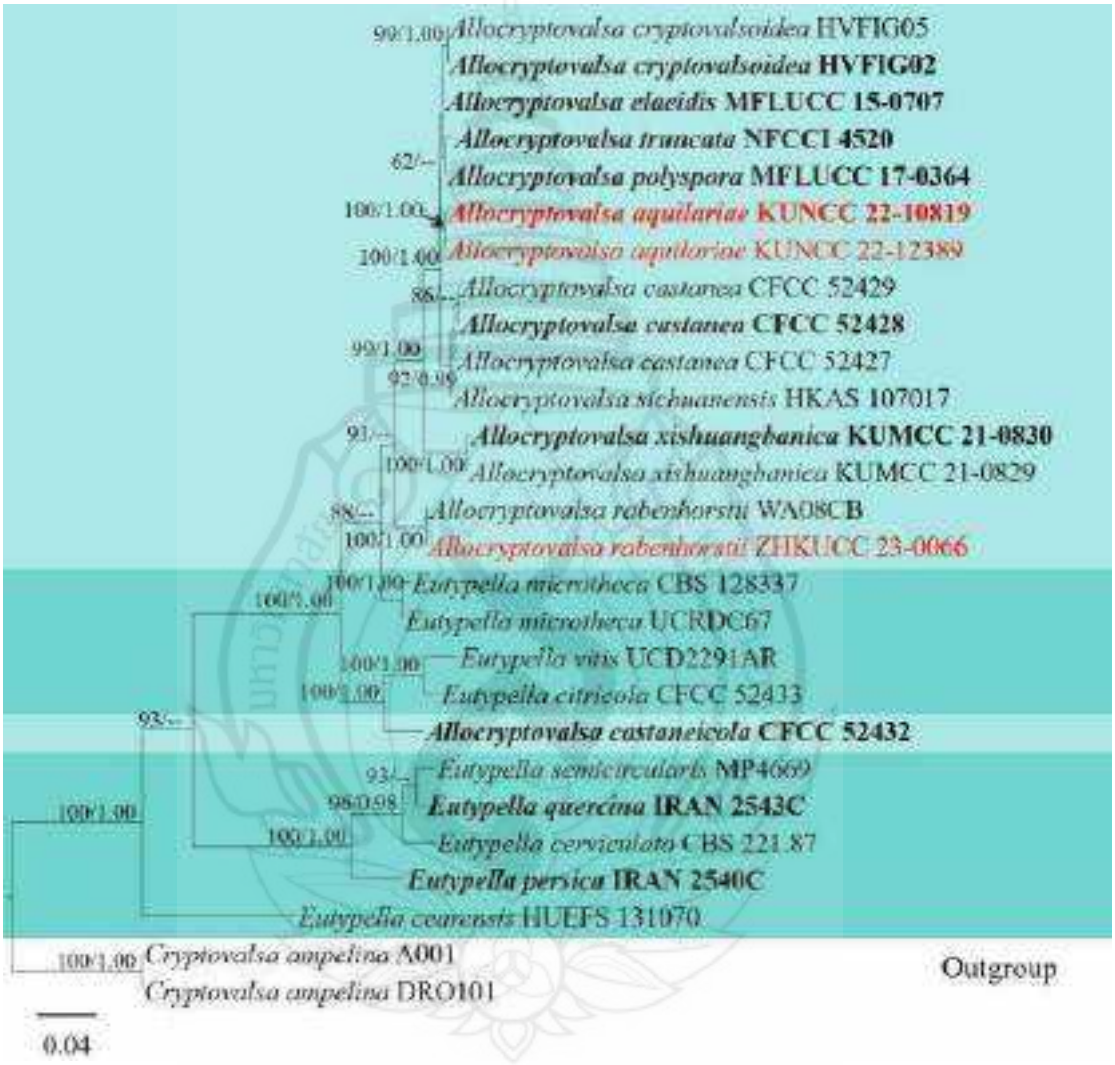


Figure 6.34 Phylogenetic tree of *Allocryptovalsa*

Figure 6.34 Bootstrap support values for ML greater than 60% and Bayesian posterior probabilities greater than 0.95 are given near the nodes, respectively. The tree is rooted with *Cryptovalsa ampelina* (A001 and DRO101). The new isolates are indicated in red, and the ex-type strains are in bold.

Ascomycota *genera incertae sedis*

Pseudoacrodictys W.A. Baker & Morgan-Jones 2003

Notes: *Pseudoacrodictys* was introduced by Baker and Morgan-Jones (2003) to accommodate seven species of *Acrodictys*, including *P. eickeri* as the type species. The genus is characterized by solitary, acrogenous, subglobose, broadly pyriform to turbinate, brown conidia that are somewhat irregular, with brown undulate appendages (Gao et al., 2016). Currently, 14 species belong to this genus (Wijayawardene et al., 2022); however, molecular data in GenBank (https://www.ncbi.nlm.nih.gov/) is only available for two species (*P. balansae* and *P. deightonii*).

A new record was published in the following co-authored article:

Hyde, K. D., Wijesinghe, S. N., Afshari, N., Aumentado, H. D., Bhunjun, C. S., Boonmee, S., . . . Zhang, J. Y. (2024). Mycosphere Notes 469–520. *Mycosphere, 15*(1), 1294–1454. https://doi.org/10.5943/mycosphere/15/1/11

Pseudoacrodictys deightonii *(M.B. Ellis) W.A. Baker & Morgan-Jones 2003*

Index Fungorum number: IF373226; Facesoffungi number: FoF15260; Figure 6.35

Saprobic on dead branch of *Aquilaria* sp. Sexual morph: Undetermined. Asexual morph: Hyphomycetous. *Colonies* on natural substrate effuse, dark brown. *Mycelium* partly superficial to immersed, composed of septate, branched, brown hyphae. *Conidiophores* 150–250 × 7–14(–17.5) µm, macronematous, mononematous, erect, straight or slightly curved, septate, thick-walled, dark brown. *Conidiogenous cells* integrated, terminal, monoblastic, indeterminate, cylindrical, smooth, dark brown, truncate at the apex after schizolytic conidial secession. *Conidia* 40–120 × 50–130 µm, acrogenous, solitary, subglobose or irregular, brown, dictyoseptate, with numerous obscure oblique septa, thick-walled, dry, sometimes cracking.

Culture characteristics: Conidia germinated on PDA within 48 h at 28°C and germ tubes were produced from each cell. Colonies on PDA reached 2 cm diam. after two weeks at 28°C. Colonies obverse: flat, irregular, floccose, white to pale grey, medium dense, irregular margin, and dark brown in reverse pale, edge is brown.

Material examined: China, Yunnan Province, Xishuangbanna, Menghai City, Agarwood plantation, on a dead branch of *Aquilaria* sp. (Thymeleaceae), 15 September 2021, T. Y. Du, YNA01 (GZAAS 23-0616, living culture ZHKUCC 23-0989).

Known distribution: China (Zhao et al., 2011; this study), Sierra Leone (Ellis, 1961).

Known hosts: *Aquilaria* sp. (this study), *Cassia fruticosa* (Ellis, 1961), *Gardenia nitida* (Ellis, 1961), *Rauwolfia vomitoria* (Ellis, 1961).

Notes: According to the phylogenetic analyses, our fungal strain (ZHKUCC 23-0989) clustered with *P. deightonii* strains (HMAS 42892, HMAS 43152, HMAS 44636, HSAUP myr4732, and HSAUP myr4737) with 100% ML and 1.00 BYPP bootstrap support (Figure 6.36). Our fungal collection shares morphology with *P. deightonii* in having similar conidiophores, conidiogenous cells and conidial characteristics (Zhao et al. 2011). This collection has longer conidiophores and larger conidia (conidiophores: 150–250 μm; conidia: 40–120 × 50–130 μm) than those of *P. deightonii* (HMAS 90312) (conidiophores: 40–120 μm; conidia: 30–61 × 25–55 μm) (Zhao et al., 2011). This may depend on different environmental factors and host plants. This study is the first *Pseudoacrodictys* species found on *Aquilaria* species. Therefore, our fungal collection is identified as *P. deightonii* and we introduced a new host record based on morphological and phylogenetic analyses.

Figure 6.35 *Pseudoacrodictys deightonii* (GZAAS 23-0616, a new host record)

Figure 6.35 a, b, Colonies on natural host substrate. c–i, Conidiophores, conidiogenous cells and developing conidia. j, A germinating conidium. l–o, Conidia. k, p, Colonies on PDA after two weeks (k, above; p, below). Scale bars: c–h = 100 µm, i, j, l–o = 50 µm.

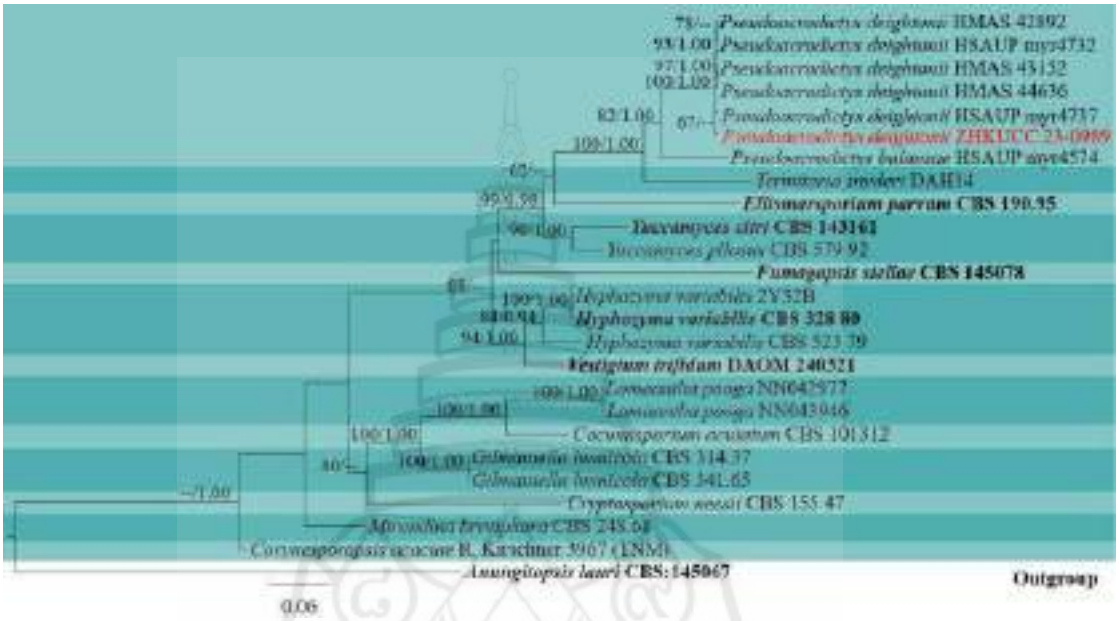


Figure 6.36 Phylogenetic tree of *Pseudoacrodictys*

Figure 6.36 Bootstrap support values for ML greater than 60% and Bayesian posterior probabilities greater than 0.90 are given near the nodes, respectively. The tree is rooted with *Anungitopsis lauri* (CBS:145067). The new isolate is indicated in red, and the ex-type strains are in bold.

6.4 Discussion

This study reports 22 taxa of saprobic fungi associated with dead branches of *Aquilaria* spp. (Thymelaeaceae) from Guangdong and Yunnan provinces, China. One new genus, 17 new species, and five known species that belong to four orders of Ascomycota (Dyfrolomycetales, Pleosporales, Sordariales, and Xylariales) are described based on morphological studies and phylogenetic analyses. These 22 taxa belong to 14 different genera, *viz., Allocryptovalsa*, *Aquilariomyces*, *Camarographium*, *Corynespora*, *Mangifericomes*, *Melomastia*, *Montagnula*, *Nigrograna*, *Parathyridariella*,

Peroneutypa, *Phaeoseptum*, *Pseudothyridariella*, *Torula*, and *Triangularia*.

In this study, one new genus *Aquilariomyces* is introduced. *Aquilariomyces* is established in Thyridariaceae (Pleosporales) to accommodate *Aqu. aquilariae*, and it differs from the closely related taxa in phylogeny by its one-transverse septate ascospores. In addition, two new species (*Parathyridariella aquilariae* and *Pseudothyridariella aquilariae*) with asexual morphs in Thyridariaceae are also introduced. Interestingly, the ascomata of these three species are immersed in the bark and surrounded by fluff. *Pseudothyridariella aquilariae* is found as an asexual *Pseudothyridariella* morph, while *Pseudothyridariella* has been reported only as a sexual morph (Mapook et al., 2020). Therefore, due to the lack of comparison of morphological characteristics, more research is needed to determine the placement of *Pse. aquilariae*. This is the first report of a member of Thyridariaceae on *Aquilaria*.

Camarographium was placed in the Didymosphaeriaceae by Crous et al. (2022), based on the phylogenetic analyses of *Cam. stephensii*. In this study, we provided the sequences of *Cam. clematidis*, but *Cam. clematidis*, and *Cam. stephensii* grouped far apart in the phylogenetic tree. Therefore, due to limited molecular data, in this study, *Cam. clematidis* is temporarily classified in Didymosphaeriaceae *sensu lato*. In previous studies (Crous et al., 2011; Wanasinghe et al., 2016), *Camarographium* species were mainly classified using the key to *Camarographium*. The main classification criteria are the shape (linear or pycnidial) of stromata, the size of conidia, and different hosts. This study suggests adding more morphological features, such as shape and color of conidia and number and type of separations, for distinguishing species in this genus. With very few molecular sequences in *Camarographium*, detailed descriptions of its species can help with better classification. More fresh collections of *Camarographium* in different geographical regions should be collected and sequenced in the future to understand the phylogenetic placement of the genus better.

The other new species are introduced based on morphological comparisons and molecular phylogenetic studies. The phylogenetic trees of this study were constructed multiple times, and the topological structure of the trees is consistent with previous studies.

Agarwood is an important economic wood, and the endophytic fungi and pathogenic fungi of agarwood-producing trees (*Aquilaria* spp.) have been extensively studied. Based on the literature, more than 170 strains of endophytic fungi have been

reported, and some of them have been further studied for their biological activity, induction ability, and secondary metabolites (Wang et al., 2018, 2019b; Du et al., 2022a, 2022b; Li et al., 2022c). Pathogenic fungi mainly infect the seedling stage of *Aquilaria* spp., and sometimes they also cause branch blight and leaf spot disease. More than 15 species of pathogenic fungi have been reported in literature, and these pathogenic strains have been investigated, isolated, identified, and studied for disease prevention and control (Borah et al., 2012; Pandey et al., 2019; Sun et al., 2021). However, the saprobic fungi of species of *Aquilaria* have been poorly studied. Punithalingam & Gibson (1978) were the first to report a saprobic fungus on *Aquilaria malaccensis* Lam. Subsequently, Subansenee et al. (1985) recorded seven saprobic fungi collected from *Aquilaria* spp. To date, only 30 taxa of saprobic fungi (including this study) were found on *Aquilaria* plants. Undoubtedly, this is a knowledge gap in the research on saprobic fungi associated with *Aquilaria* plants. In addition, since 96% taxa belong to Ascomycota, it can be considered that the members of Ascomycota are the primary saprobic fungi found on *Aquilaria*. Furthermore, among the 14 genera considered in this study, it is reported that most of these fungal genera are common taxa such as *Melomastia*, *Corynespora*, *Nigrograna*, and *Peroneutypa*. Therefore, the saprobic fungi reported on *Aquilaria* may not be host-specific. This hypothesis requires more relevant research on saprobic fungi. Additional research is necessary to complete the research gap regarding saprobic fungi associated with *Aquilaria* and understand the fungal diversity associated with *Aquilaria* plants in their natural habitats.

This work collected saprobic fungi associated with *Aquilaria* and classified and identified them using morphology and multigene phylogenetic analyses. Seventeen new fungal taxa were identified, enriching the diversity of saprobic fungi in *Aquilaria*. This article's research methods can be applied to the classification and identification of saprobic fungi associated with any plant, and the cultures generated in this study can be used for further research in secondary metabolite analysis.

As mentioned above, this work was planned based on the research gap that the saprobic fungi associated with *Aquilaria* need to be better studied. From an ecological perspective, saprobic fungi, as decomposers, play an essential role in decomposing plant materials and recycling them (Alexopolous & Mims, 1979; Sudharsan et al., 2023; Boswell, 2024). Research on saprobic fungi requires a rich and solid accumulation of biological knowledge, combining traditional morphology with modern molecular phylogenetics to

classify and identify them. This challenge is common in other disciplines, such as botany and zoology.

Fungi associated with economically important crops such as apples, coffee, corn, mangoes, rice, and other plants, including *Aquilaria*, help to understand the potential fungal pathogens, industrially important fungi, plant growth promoting and disease controlling fungi and improve economic benefits, which is of great significance to people's lives (Doehlemann et al., 2017; Peng et al., 2021; Akram et al., 2023; Deresa & Diriba, 2023; Singh & Kumar, 2023; Qin et al., 2024). Not only in plants, studying fungi associated with humans and animals also provides many benefits, especially in controlling fungal diseases and understanding the importance of beneficial fungi (Guégan et al., 2023; Lionakis et al., 2023; Macias-Paz et al., 2023).

CHAPTER 7

CONCLUSIONS

7.1 Overall Conclusion

This study explores the fungal communities associated with agarwood and agarwood-producing trees (*Aquilaria* spp.) from Guangdong and Yunnan provinces. It collects and isolates fungi and analyzes them with functional screening and taxonomic identification. In addition, this study reports the composition of fungal genera and identifies strains with potential agarwood-inducing and antimicrobial properties. Overall, this study is divided into four parts, followed by a conclusion.

The first part of this study isolated 960 fungal strains from *Aquilaria sinensis* samples collected in Guangdong and Yunnan provinces from four parts (agarwood resins, dead branches, healthy branches, and healthy leaves), representing 64 genera across 44 families. Among them, 818 strains of 14 genera was first recorded on *Aquilaria* spp. Five new species were introduced based on morphology and phylogenetics, *viz.*, *Banksiophoma endophytica*, *Deniquelata aquilariae*, *Montagnula sinensis*, *M. yunnanensis*, and *Fomitiporia aquilariae*. Community analysis showed that Ascomycota dominated the fungal assemblage (99.06%), followed by Basidiomycota and Mucoromycota (Figure 7.1). The most frequently isolated genera were *Fusarium* and *Lasiodiplodia*. A total of 645 strains from 48 genera were isolated from agarwood resins, with 12 genera previously reported to induce agarwood formation, *viz.*, *Aspergillus*, *Botryosphaeria*, *Chaetomium*, *Cladosporium*, *Colletotrichum*, *Diaporthe*, *Fusarium*, *Lasiodiplodia*, *Penicillium*, *Phaeoacremonium*, *Trichoderma*, and *Xylaria*. Thirty-six genera were also reported from *Aquilaria* spp. in earlier studies, and six genera were newly recorded, *viz.*, *Exophiala, Fomitiporia, Loculosulcatispora, Neodeightonia, Paradictyoarthrinium,* and *Phanerochaetella*. Samples from different plant parts (agarwood resins, dead branches, healthy branches, and healthy leaves) revealed overlapping genera, of which *Aspergillus*, *Diaporthe*, *Lasiodiplodia*, and *Neopestalotiopsis* were found in all four parts. In terms of

geographical location, the composition of fungal communities did not show significant differences. In addition, all 64 genera were annotated with ecological notes, including habitat, lifestyle, and host information. This work expands the known fungal diversity of *Aquilaria sinensis* and provides a strain dataset for further functional and applied research.

Figure 7.1 Multi-level doughnut chart showing the taxonomic distribution of fungal strains by phylum, class, and genus

Second part, among the isolated fungal strains, 12 strains were selected based on literature reports to evaluate their potential in inducing agarwood formation. Through systematic screening and comparative analysis, *Fusarium solani* (GDA-HC01) was identified as a highly efficient fungus for agarwood induction. In the preliminary experiment, this strain successfully induced distinct agarwood resin formation on small branches within 12 months, without causing wound healing or tissue necrosis—significantly outperforming other strains. In the extended experiment on tree trunks, it also exhibited excellent inducing capacity, with the agarotetrol content reaching 1.4 times the pharmacopeial standard. This highlights its considerable potential as a microbial inducer for commercial agarwood production. In contrast, other strains such as *Lasiodiplodia pseudotheobromae* also demonstrated resin-inducing ability but

caused notable tissue necrosis, indicating a need for optimization of application method or inoculum dosage. Regarding inoculation methods, the study found that the Agar-Wit technique, which involves injecting a larger volume of fungal fermentation broth and enables sustained infection, facilitated better colonization and induction in tree trunks. However, it also revealed issues such as higher fermentation liquid volume and associated costs, suggesting that future research should focus on optimizing inoculum volume and concentration for a balance between efficacy and cost-efficiency. Additionally, certain strains like *Fusarium proliferatum* and *Trichoderma koningiopsis* failed to colonize the host, indicating distinct ecological adaptability among different fungal species. In summary, this study not only identified promising fungal strains for agarwood induction but also provided empirical data on inoculation techniques and host responses, offering a solid foundation and theoretical support for further research on fungal induction mechanisms, microbial agent development, and the green industrialization of agarwood production. In this study, an invention patent was published due to the outstanding performance of *Fusarium solani* (GDA-HC01).

In the third part of this study, 47 strains were preliminarily screened and used for testing their antagonistic ability and belonging to 18 genera. Thirteen of these genera are reported for the first time to have antimicrobial activity in agarwood, *viz.*, *Alternaria*, *Annulohypoxylon*, *Aspergillus*, *Corynespora*, *Curvularia, Daldinia*, *Neofusicoccum*, *Neopestalotiopsis*, *Nigrospora*, *Paracamarosporium*, *Pseudopithomyces*, *Trichoderma*, and *Trichosporon.* And nine genera are newly recorded in *Aquilaria sinensis*, *viz.*, *Alternaria*, *Annulohypoxylon*, *Corynespora*, *Daldinia*, *Neofusicoccum*, *Neopestalotiopsis*, *Paracamarosporium*, *Pseudopithomyces*, and *Trichosporon*. Among them, *Lasiodiplodia* sp. (YNA-D3) showed strong inhibitory effects against all six tested pathogens and was the most effective strain. Additionally, fungal strains from five genera (*Curvularia*, *Lasiodiplodia*, *Neofusicoccum*, *Nigrospora*, and *Trichoderma*) exhibited over 90% inhibition rates against *Botrytis cinerea*, a major plant pathogen, highlighting their potential for development as biocontrol agents. These findings significantly enrich the antimicrobial resources of agarwood-associated fungi and provide candidate strains and theoretical support for future pharmaceutical development and the creation of eco-friendly microbial pesticides.

The last part of this study introduced 17 new and five known saprobic fungal collections associated with dead branches of *Aquilaria* spp. from Guangdong and Yunnan provinces, China. These include one new genus, 14 new species, and two new records, all classified within four orders of Ascomycota: Dyfrolomycetales, Pleosporales, Sordariales, and Xylariales (Figure 7.2). The 22 taxa belong to 14 different genera, *viz*., *Allocryptovalsa*, *Aquilariomyces*, *Camarographium*, *Corynespora*, *Mangifericomes*, *Melomastia*, *Montagnula*, *Nigrograna*, *Parathyridariella*, *Peroneutypa*, *Phaeoseptum*, *Pseudothyridariella*, *Torula*, and *Triangularia*, all recorded on *Aquilaria* genus for the first time. The new genus *Aquilariomyces*, placed in the family Thyridariaceae, is established based on phylogenetic analysis and its distinct ascospore morphology; two additional new species, *Parathyridariella aquilariae* and *Pseudothyridariella aquilariae*, are also described in Thyridariaceae, with unique asexual morphs. Several species show distinctive features such as ascomata immersed in bark and surrounded by fluff. The study also provides sequence and addresses the provisional placement of *Camarographium clematidis*. This research employs detailed morphological and multigene phylogenetic analyses to fill the knowledge gap in saprobic fungi on *Aquilaria* spp. Prior to this study, there were only eight records and a lack of complete morphological descriptions and molecular data, therefore, this study alone contributes 17 new taxa, significantly enriching the understanding of fungal diversity associated with this economically important plant.

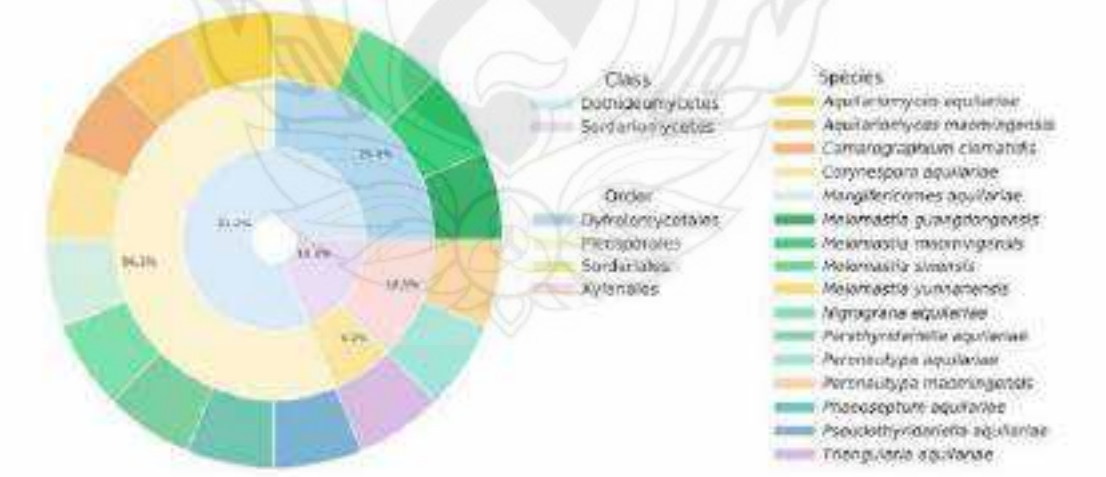


Figure 7.2 Multi-level doughnut chart showing the taxonomic distribution of saprobic fungi by class, order, and species

There is compelling evidence that endophytic fungi can adapt their lifestyle to become pathogenic or saprobic under specific conditions (Bhunjun et al., 2024). In this study, we identified four genera, *Corynespora*, *Montagnula*, *Nigrograna*, and *Rhytidhysteron*, as saprobic fungi on *Aquilaria* spp. These fungi were also found to be endophytic or agarwood resin fungi in the fresh tissues of *Aquilaria* spp. This transformation in lifestyle could be a key factor in agarwood production. The unclear mechanism of agarwood production has long puzzled researchers, but our findings provide valuable data that could significantly advance our understanding of this process. The future holds promise for further isolation, identification, and analysis of endophytic, pathogenic, and saprobic fungi associated with agarwood-producing trees, which will undoubtedly deepen our understanding of the intricate interaction mechanisms between fungi and plants.

Together, these findings establish a foundational reference for understanding the fungal communities associated with *Aquilaria*. They contribute novel taxa, identify promising microbial inducers for agarwood production, and reveal antagonistic strains with potential for eco-friendly plant protection-laying a solid groundwork for sustainable, fungi-assisted agarwood industry development.

7.2 Research Advantages

7.2.1 Systematic Exploration of Agarwood-Associated Fungi Expands the Foundation of Fungal Diversity

This study conducted extensive sampling across major agarwood-producing regions in Guangdong and Yunnan provinces, resulting in the isolation of 960 fungal strains belonging to 64 genera. Among them, 14 genera were reported for the first time from *Aquilaria* spp., and five novel species were identified. In addition, detailed notes were compiled for each genus. These findings significantly enhance the understanding of fungal diversity within the agarwood ecosystem and provide a solid foundation for the establishment of a comprehensive microbial database related to agarwood. More importantly, these isolates represent a rich microbial resource pool for future functional screening, bioinducer development, and natural product discovery. This work bridges

the gap between ecological identification and applied microbial utilization, offering valuable materials for the sustainable development of the agarwood industry.

7.2.2 Biodiversity Insight: Classification of Saprobic Fungi

This study is the first to systematically focus on saprobic fungal communities inhabiting decaying *Aquilaria* spp. branches, resulting in the discovery and description of 14 novel species and 2 new records. These findings substantially broaden the taxonomic scope and diversity knowledge of fungi associated with agarwood. By integrating morphological characteristics with multilocus phylogenetic analyses, a more comprehensive classification framework was established. These discoveries provide not only scientific support for fungal taxonomy and biodiversity conservation, but also a foundational basis for understanding the ecological roles of saprobic fungi within the agarwood microecosystem.

7.2.3 Screening of Antagonistic Fungi Supports the Development of Green Biocontrol Agents

Through antagonism assays on 47 representative strains, several fungal strains were identified with strong potential for plant disease suppression. These strains can be further explored for the extraction of antimicrobial secondary metabolites and developed into biopesticides with high inhibitory activity. When combined with modern fermentation and formulation technologies, such biocontrol agents may partially replace chemical pesticides in agricultural settings, thereby reducing environmental pollution and phytotoxicity. For agarwood plantations, these microbial agents not only offer disease control but may also be co-applied with resin inducers, facilitating an integrated “induction + protection” management strategy.

7.2.4 Discovery of High-Efficiency Induction Strains Promotes Sustainable Agarwood Production

Among the strains tested, *Fusarium solani* (GDA-HC01) was able to induce the formation of pharmacologically active compounds in agarwood that meet Chinese Pharmacopoeia standards within just six months—significantly reducing the production cycle. This strain exhibits stable induction performance and simple application, making it a promising solution to the long-standing challenges of low yield, high labor demand, and destructive practices in artificial agarwood production. It has strong potential to be developed into a microbial formulation for commercial use, enabling low-injury, rapid

resin formation. With further optimization of fermentation processes and the development of user-friendly products (e.g., powders, granules, or sustained-release pellets), this research paves the way for a scalable, low-cost, and environmentally friendly induction system, contributing to the green and standardized upgrading of the agarwood value chain.

7.3 Future Work

7.3.1 Exploring Fungal Diversity Associated with *Aquilaria* spp. Using High-Throughput Sequencing

Current studies on fungi associated with *Aquilaria* spp. mainly focus on culturable strains, which limits our understanding of the true diversity of its fungal communities. In the future, culture-independent approaches such as high-throughput sequencing should be employed to systematically investigate the fungal communities in different tissues (e.g., healthy bark, resinous wood, rhizosphere soil). This approach will help identify dominant unculturable taxa, key functional groups, and novel fungal species, providing a more comprehensive view of the symbiotic interactions between *Aquilaria* spp. and its associated microbes. Furthermore, predictive functional profiling and ecological network analysis can be used to evaluate the potential roles of different fungal taxa in resin induction and plant health, thereby enhancing our ecological and applied understanding of these fungal resources.

7.3.2 Collection and Characterization of Saprobic Fungi: Taxonomy, Induction Ability, and Bioactivity

Research on saprobic fungi associated with *Aquilaria* spp. is still in its infancy, with very few species reported and limited taxonomic data. Future work should focus on the systematic collection and isolation of saprobic fungi from decaying tissues of *Aquilaria* spp. These strains should be identified and described using multi-locus phylogenetic analyses and morphological observations. In addition to increasing known fungal diversity, the functional potential of these saprobes should be explored, especially their ability to induce agarwood formation under simulated wound conditions. Furthermore, their secondary metabolites should be evaluated for biological

activities such as antimicrobial or antioxidant effects. Such efforts would not only uncover new taxa but also contribute to the biotechnological exploitation of these fungi in medicine and agriculture.

7.3.3 Investigation of Antagonistic Strains for Secondary Metabolites and Biocontrol Applications

Several strains in this study showed strong antagonistic effects against common plant pathogens, indicating their potential use in sustainable plant disease management. Future research should focus on the extraction, purification, and structural characterization of their secondary metabolites to identify active compounds and clarify their mechanisms of action. Metabolomics and genomic analyses could be employed to unravel biosynthetic pathways, enabling pathway engineering and optimized production. In addition, bioassays should be extended to greenhouse or field trials to evaluate efficacy in real-world conditions. These efforts will support the development of eco-friendly alternatives to chemical pesticides and advance the application of fungal-based biocontrol agents in agriculture.

7.3.4 Functional Optimization of Induction Strains and Innovation in Artificial Agarwood Induction

The high-performance agarwood-inducing strains identified in this study offer promising application prospects. Future research should investigate the optimal conditions (e.g., carbon source, temperature, pH, oxygen levels) for maximizing their resin-inducing efficiency. Further development of artificial induction technologies is also necessary, including reducing induction time, improving yield and quality of active compounds, and enhancing aroma profiles. In terms of the application form, efforts should focus on transforming liquid fermentation products into more stable and user-friendly formulations, such as pellets, powders, or controlled-release granules, thereby enabling large-scale, efficient, and environmentally friendly applications in agarwood plantations. To improve the efficiency of agarwood induction, future research can investigate the combined effects of fungal and bacterial inoculation. For example, high-performing fungal strains (e.g., *Lasiodiplodia* spp., *Fusarium* spp., *Trichoderma* spp.) can be combined with endophytic bacteria known to promote plant growth, suppress pathogens, or activate host defense responses (e.g., *Bacillus subtilis*, *Pseudomonas fluorescens*, *Streptomyces* spp.). These microbial agents can be co-cultured in liquid

fermentation or formulated into mixed preparations for application, using methods such as sequential inoculation, co-encapsulation, or multi-point injection to maximize effectiveness. This strategy is expected to shorten the induction period, increase resin yield and bioactive compound content, improve aroma quality, and enhance consistency across treated trees. All microbial strains should undergo safety evaluation and non-pathogenicity verification to ensure ecological safety and controllability in field applications.

7.4 Publications

List of publications

7.4.1 First Author

Du, T. Y., Hyde, K. D., Mapook, A., Mortimer, P. E., Xu, J. C., Karunarathna, S. C., & Tibpromma, S. (2021). Morphology and phylogenetic analyses reveal *Montagnula puerensis* sp. nov. (Didymosphaeriaceae, Pleosporales) from southwest China. *Phytotaxa, 514* (1), 001–025. https://doi.org/10.11646/phytotaxa.514.1.1

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Du, T. Y., Zhang, X., Dai, D. Q., Liu, X. F., Karunarathna, S. C., & Tibpromma, S. (2024). *Fusarium solani* (HC01), a fungal strain capable of inducing the rapid production of a medicinally accepted amount of agarotetrol in *Aquilaria sinensis* agarwood resin. In *Proceedings of the 12th YSF Symposium - 2024. National Science and Technology Commission* (pp. 59–65). Sri Lanka.

Du, T. Y., Tibpromma, S., Hyde, K. D., Mapook, A., Dai, D. Q., Zhang, G. Q., . . . Karunarathna, S. C. (2024). The polyphasic approach reveals 10 novel and one known Ascomycota taxa from terrestrial agarwood-producing trees. *Journal of Systematics and Evolution,* 1–38. https://doi.org/10.1111/jse.13128

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Du, T. Y., Karunarathna, S. C., Tibpromma, S., Hyde, K. D., Nilthong, S., Mapook, A., . . . Wang, H. H. (2024). *Melomastia* (Dothideomycetes, Ascomycota) species associated with Chinese *Aquilaria* spp. *MycoKeys, 111*, 65–86. https://doi.org/10.3897/mycokeys.111.137898

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APPENDIX A

MEDIA

1. Malt Extract Broth (MEB) fungal liquid culture and fermentation

Malt extract 30 g

Peptone 5.0 g

Suspend 20 g of malt extract agar in distilled water and mix thoroughly to completely dissolve the power and bring volume to 1000 mL. Autoclave at 121°C for 20 min.

2. Potato dextrose agar (PDA) used for fungal cultivation

Potato starch (from the infusion) 4 g

Dextrose 20 g

Agar 15 g

Suspend 39 g of Potato dextrose agar in distilled water and mix thoroughly. Heat with frequent agitation and boil for 1 min to completely dissolve the powder and bring volume to 1000 mL. Autoclave at 121 °C for 20 min.

3. Water Agar (WA) Used for Fungal Isolation

Agar 20 g

Suspend 20 g of agar in distilled water and mix thoroughly. Heat with frequent agitation and boil for 1 min to completely dissolve the powder and bring volume to 1000 mL. Autoclave at 121 °C for 20 min.

4. **Indian ink** used for observing gelatinous appendages of ascospores in some species

5. Cotton blue used to make hyaline structures appear colored in some species

6. **Melzer reagent** used to detect amyloid or amyloid like reactions in some species

APPENDIX B

ABSTRACT OF PUBLICATIONS

Journal of *Fungi*

MDPI

Article

Endophytic Fungi Associated with *Aquilaria sinensis* (Agarwood) from China Show Antagonism against Bacterial and Fungal Pathogens

Tian-Ye Du [1,2,3], Samantha C. Karunarathna [4], Xiao Zhang [1], Deng-Qin Dai [1], Ausana Mapook [5], Nakarin Suwannarach [6], Jian-Chu Xu [4,*], Steven L. Stephenson [7], Abdallah M. Elgorban [8], Sallin Al-Rejaie [9] and Saisamorn Tibpromma [4,*]

1 Center for Yunnan Plateau Biological Resources Protection and Utilization, College of Biological Resource and Food Engineering, Qujing Normal University, Qujing 655011, China
2 Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100, Thailand
3 School of Science, Mae Fah Luang University, Chiang Rai 57100, Thailand
4 Research Center of Microbial Diversity and Sustainable Utilization, Faculty of Science, Chiang Mai University, Chiang Mai 50200, Thailand
5 Center for Mountain Futures, Kunming Institute of Botany, Kunming 650201, China
6 Department of Biological Sciences, University of Arkansas, Fayetteville, AR 72701, USA
7 Department of Botany and Microbiology, College of Science, King Saud University, Riyadh 11451, Saudi Arabia
8 Department of Plant Production & Technology, College of Planning, King Saud University, Riyadh 11451, Saudi Arabia
* Correspondence: jcxu@mail.kib.ac.cn (J.-C.X.); saisamorn.t@cmu.ac.th (S.T.)

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Abstract: Agarwood is the most expensive non-construction wood product in the world. As a therapeutic agent, agarwood can cure some diseases, but few studies have been carried out on the antagonistic abilities of endophytic fungi associated with agarwood. Agarwood is mainly found in the genus *Aquilaria*. The objectives of this study are to understand the antibacterial activities and their potential as biocontrol agents of the endophytic fungi of *Aquilaria sinensis*. First, fresh samples of *A. sinensis* were collected from Yunnan and Guangdong Provinces in 2020–2021, and the endophytic fungi were isolated and identified to genus level based on the phylogenetic analyses of the Internal Transcribed Spacer (ITS) region. In this research, 47 endophytic strains were selected to check their bioactivities against three bacterial pathogens viz. *Erwinia amylovora*, *Pseudomonas syringae*, and *Salmonella enterica*; and three fungal pathogens viz. *Alternaria alternata*, *Botrytis cinerea*, and *Fusarium fujikuroi*. The antibiosis test was carried out by hyphal collision assay (10 days), and among the 47 strains selected, 10 strains belonging to 10 genera viz. *Alternaria*, *Arcopilus/Arcopilaceae*, *Aspergillus*, *Beauveriaceae*, *Colletotrichum*, *Corynespora*, *Curvularia*, *Diaporthe*, *Epicoccum*, *Lasiodiplodia*, *Xylariaceae*, *Nectriaceae* sp., *Nigrospora*, *Pleosporaceae* sp., *Pseudocercospora*, *Pyrenochaeta*, *Talaromyces* and one strain belonging to *Xylariaceae* had antimicrobial activities. In particular, *Lasiodiplodia* sp. (YNAA-D3) showed the inhibition of all the bacterial and fungal pathogens with a significant inhibition rate. In addition, the strains viz. *Curvularia* sp. (GDBA-D3), *Diaporthe* sp. (GDAA-D2), *Lasiodiplodia* sp. (YNAA-D2), *Nectriaceae* sp. (YNAA-C7), *Nigrospora* sp. (GDBA-C1), and *Talaromyces* sp. (YNAA-C1) showed significant antibacterial activities and are considered worthy of further studies to identify the bacterial fungal species and their bioactive compounds. This study enriches the diversity of endophytic fungi associated with agarwood, and their potential antagonistic effects against bacterial and fungal pathogens.

Key words: agarwood; ascbacterial activities; antifungal activities; antimicrobial activities; Lasiodiplodia

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The fungal strain promotes rapid agarwood resin production with medicinally accepted agarotetrol level

Tian-Ye Du [a,b,c,1], Saowaluck Tibpromma [a,c,**], Kevin D. Hyde [b,c], Yue-Hu Wang [d], Putarak Chomnunti [e], Ekachai Chukeatirote [e], Wen-Hua Lu [a,b,c], Aussana Mapook [e], Dong-Qin Dai [a,f], Douglas S.A. Wijesundara [g], Abdallah M. Elgorban [h], Nakarin Suwannarach [i,j], Jaturong Kumla [i,j], Ihab M. Moussa [k], Hao-Han Wang [b,c], Samantha C. Karunarathna [a,b,c,*]

[a] Center for Yunnan Plateau Biological Resources Protection and Utilization, College of Biological Resource and Food Engineering, Qujing Normal University, Qujing, 655011, PR China
[b] Key Laboratory of Yunnan Provincial Department of Education for the Conservation and Sustainable Use of Fungal Resources, Qujing Normal University, Qujing, 655011, PR China
[c] Research Center of Microbial Diversity and Sustainable Utilization, College of Biological Resources and Food Engineering, Qujing Normal University, Qujing, 655011, PR China
[d] Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai, 57100, Thailand
[e] School of Science, Mae Fah Luang University, Chiang Rai, 57100, Thailand
[f] Yunnan Key Laboratory for Fungal Diversity and Green Development, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, 650201, PR China
[g] Center of Excellence in Microbial Diversity and Sustainable Utilization, Chiang Mai University, Chiang Mai, 50200, Thailand
[h] National Institute of Biodiversity, Horana Road, Kurulu, 10206, Sri Lanka
[i] Center of Excellence in Biotechnology Research (CEBIO), King Saud University, Riyadh, 11451, Saudi Arabia
[j] Office of Research Administration, Chiang Mai University, Chiang Mai, 50200, Thailand
[k] Department of Botany and Microbiology, College of Science, King Saud University, Riyadh, 11451, Saudi Arabia

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Aquilaria sinensis
Fusarium solani
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ABSTRACT

Agarwood, a highly valued, fragrant, dark, resinous heartwood, commands an estimated market value of over US $100 million. With the increasing market demand for agarwood, artificial induction methods have been a subject of study. Fungal induction is one of the methods that can effectively induce agarwood formation and is eco-friendly to the environment and humans. This study, however, brings a new perspective by focusing on identifying and screening fungal strains capable of rapidly inducing agarwood formation in *Aquilaria sinensis*. The bole-infusion technique (BIT) was used as a pre-experiment, and *Fusarium solani* (QJA-HC02) was the most effective strain among 12 tested fungal species. A subsequent experiment using the *Agar-Wit* method was used to confirm *Fusarium solani* (QJA-HC02), and results showed *Fusarium solani* (QJA-HC02) can induce agarwood resin containing 2.0 times the agarotetrol content required by the Chinese Pharmacopeia within six months. Other strains: *Lasiodiplodia pseudotheobromae* (YNA-TH) and *Lasiodiplodia theobromae* (YNA-LC2), also showed some induction ability, while other strains had minimal effects. This is the first report demonstrating the rapid and consistent production of agarwood with medicinally accepted agarotetrol level in *Aquilaria sinensis* using *Fusarium solani* (QJA-HC02). With its potential for market application, this discovery is a significant step forward in the field and a valuable contribution to developing a sustainable green economy, offering a promising future for agarwood production.

* Corresponding author. Center for Yunnan Plateau Biological Resources Protection and Utilization, College of Biological Resource and Food Engineering, Qujing Normal University, Qujing, 655011, PR China.
** Corresponding author. Center for Yunnan Plateau Biological Resources Protection and Utilization, College of Biological Resource and Food Engineering, Qujing Normal University, Qujing, 655011, PR China.
Email addresses: saowaluck.tib@gmail.com (S. Tibpromma), samantha.karunarathna@gmail.com (S.C. Karunarathna)

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Research Article

The polyphasic approach reveals ten novel and one known Ascomycota taxa from terrestrial agarwood-producing trees

Tian-Ye Du[1,2,3], Saowaluck Tibpromma[3*], Kevin D. Hyde[4,5], Ausana Mapook[3], Dong-Qin Dai[6], Gui-Qing Zhang[1], Steven L. Stephenson[6], Nakarin Suwannarach[7], Jaturong Kumla[7], Abdallah M. Elgorban[8], Kunhiraman C. Rajeshkumar[9], Sajeewa S. N. Maharachchikumbura[10], Qiang Li[1], and Samantha C. Karunarathna[1,3*]

[1]Center for Yunnan Plateau Biological Resources Protection and Utilization, College of Biological Resource and Food Engineering, Qujing Normal University, Qujing 655011, China
[2]Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100, Thailand
[3]School of Science, Mae Fah Luang University, Chiang Rai 57100, Thailand
[4]Department of Biological Sciences, University of Arkansas, Fayetteville 72701, USA
[5]Center of Excellence in Microbial Diversity and Sustainable Utilization, Faculty of Science, Chiang Mai University, Chiang Mai 50200, Thailand
[6]Department of Botany and Microbiology, College of Science, King Saud University, PO 2455, Riyadh 11451, Saudi Arabia
[7]National Fungal Culture Collection of India (NFCCI), Biodiversity and Palaeobiology (Fungi) Gr, MACS-Agharkar Research Institute, G. G. Agarkar Road, Pune 411004, India
[8]School of Life Science and Technology, University of Electronic Science and Technology of China, Chengdu 611731, China
[9]National Institute of Fundamental Studies, Hanguranketha, Kandy 20000, Sri Lanka
*Authors for correspondence: Samantha C. Karunarathna. Email: samanthakarunarathna@gmail.com; Saowaluck Tibpromma. Email: saowaluck14@gmail.com.
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Abstract Aquilaria (Thymelaeaceae), a tropical and subtropical plant, is one of the main genera that can produce agarwood. Aquilaria sinensis and Aquilaria yunnanensis are native Chinese tree species, and A. sinensis is China's main agarwood source. Agarwood is a nontimber forest product with high economic and medicinal value. First-grade agarwood is sold as much as USD 600 000 per kilogram. There has been little research on the saprobic fungi associated with Aquilaria, with only 11 records having been reported. In the present study, 10 terrestrial saprobic fungi associated with A. sinensis and A. yunnanensis were collected in China. Based on morphological and phylogenetic studies, these 10 collections are introduced herein as one new genus (*Aquilariomyces*), nine new species – *Aquilariomyces aquilariae*, *Corynelyppa aquilariae*, *Melomastia muiangensis*, *Nigrograna aquilariae*, *Parathyridariella aquilariae*, *Peroneutypa mucilaginosa*, *Phaeoseptum aquilariae*, *Pseudothyridariella aquilariae*, and *Triangularia aquilariae*, and one known species (*Ganoderma clemensiae*). Descriptions, illustrations of morphological characteristics, photo plates, phylogenetic trees, and the results of a pairwise homoplasy index test (PHI) test results are provided.

Key words: agarwood fungi, Aquilaria, Dothideomycetes, morphology, saprobes, Sordariomycetes, two new taxa, Thymelaeaceae.

1 Introduction

Agarwood, a rare and highly valuable dark resin with a unique fragrance, is produced by the defense mechanism of Thymelaeaceae Juss. plants after being damaged by external factors such as animals, insects, lightning, and microorganisms (Chhipa et al., 2017; Wang et al., 2018). Agarwood is a multipurpose wood sold in the market as wood chips, powder, prayer beads, and wood carvings; and it also plays an essential role in Chinese traditional medicine (National Pharmacopoeia Committee, 2015, 2020; Convention on International Trade in Endangered Species of Wild Fauna and Flora [CITES], 2022). Agarwood chips and essential oils have created enormous economic value in the market, for example, agarwood oil had a global market value of USD 278.03 million in 2021 (Naeja et al., 2023). Members of Thymelaeaceae are well known for their ability to produce agarwood and are distributed in tropical and subtropical regions (Xu et al., 2016; Azren et al., 2018; Kang, 2021). These plants are native to Southeast Asia and are distributed in Borneo, Cambodia, China, India, Indonesia, Laos, Malaysia, Myanmar, Papua New Guinea, Sri Lanka, Thailand, the Philippines, and Vietnam (Rasool & Mohamed, 2016; Xu et al., 2016; Kang, 2021). The family Thymelaeaceae contains of many important agarwood-producing tree species, including those from the genera Aetoxylon Airy Shaw,

Studies in Fungi

ARTICLE

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Morphology and multigene phylogeny revealed *Peroneutypa aquilariae* sp. nov. (Diatrypaceae, Xylariales) from *Aquilaria sinensis* in Yunnan Province, China

Tian-Ye Du[1,2,3], Samantha C. Karunarathna[1], Xian Zhang[1], Dong-Qin Dai[1], Ying Gao[2,3], Ausana Mapook[2], and Saowaluck Tibpromma[1*]

[1] Center for Yunnan Plateau Biological Resources Protection and Utilization, College of Biological Resource and Food Engineering, Qujing Normal University, Qujing 655011, Yunnan, China
[2] Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100, Thailand
[3] School of Science, Mae Fah Luang University, Chiang Rai 57100, Thailand
* Corresponding author, E-mail: saowaluck1fah@gmail.com

Abstract

Dead twigs of *Aquilaria sinensis* (Thymelaeaceae) with fungal fruiting bodies were collected from Xishuangbanna, Yunnan Province, China. After initial morphological observations, an interesting fungus whose morphologically resembled *Peroneutypa* was isolated. Molecular phylogeny of combined ITS and *tub2* showed our fungal collection is phylogenetically closely related to *P. mackenziei*. However, in morphology, our fungal collection is distinct from *P. mackenziei* in having an ostiolar canal without periphyses and the absence of paraphyses. Based on unique morphological characteristics and multigene phylogenetic analyses results, our fungal isolate is described in this paper as *Peroneutypa aquilariae* sp. nov. In addition, this is the first report of the genus *Peroneutypa* from the host *A. sinensis*. Full description, illustrations, and a phylogenetic tree to show the placement of the new species are provided. A synoptic table of morphological characteristics in *Peroneutypa* reported worldwide is also provided.

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INTRODUCTION

Sordariomycetes O.E. Erikss. & Winka, is the second largest class in Ascomycota Cavel.-Sm, characterized by unitunicate asci and are widely distributed in almost all ecosystems as endophytes, pathogens, or saprobes[1]. Hyde et al.[2], accepted 45 orders, 167 families, 1,499 genera and 308 genera *incertae sedis* in Sordariomycetes, while in the latest outline by Wijayawardene et al.[3], the numbers were increased to 46 orders, 184 families, 1,598 genera and 346 genera *incertae sedis*. In Sordariomycetes, there are seven subclasses viz. Diaporthomycetidae Senan., Maharachch. & K.D. Hyde, Hypocreomycetidae O.E. Erikss. & Winka, Lulworthiomycetidae Dayar., E.B.G. Jones & K.D. Hyde, Phaeosporidiomycetidae Bundhun, Maharachch. & K.D. Hyde, Savoryellomycetidae Hongsanan, K.D. Hyde & Maharachch., Sordariomycetidae O.E. Erikss & Winka, and Xylariomycetidae O.E. Erikss & Winka[2].

Xylariales Nannf. is a large order and the only order in the subclass Xylariomycetidae which was accepted by Maharachchikumbura et al.[3] and later Amphisphaeriales and Xylariales were accepted in Xylariomycetidae by Samarakoon et al.[4] and Hongsanan et al.[5] based on phylogenetic analyses and divergence time estimations. Later, Delonicicolales R.H. Perera, Maharachch. & K.D. Hyde was introduced into Xylariomycetidae based on phylogenetic analyses by Perera et al.[6]. According to Wijayawardene et al.[3] currently, 20 families are listed in this order.

Diatrypaceae Nitschke is one important family of higher ascomycetes that belongs to Xylariales[7,8]. Diatrypaceae was introduced by Nitschke[7] and is typified by *Diatrype* Fr. Diatrypaceae is characterized by perithecial black stroma, ascomata usually embedded in stroma, cylindric-clavate to clavate asci and allantoid ascospores in its sexual morph[9–12]. The asexual morph is characterized by coelomycetous; acervuli conidiomata, erumpent, with branched conidiophores, conidiogenous cells in dense palisades, cylindrical with filiform conidia, curved, flattened base, blunt apex, and hyaline[8,9]. Zhu et al.[13] showed that Diatrypaceae has high diversity, and the members of this family are usually wood inhabiting fungi in China. According to Wijayawardene et al.[3], currently, 22 genera are listed in this family.

Peroneutypa Berl. was introduced by Berlese[14] to accommodate *P. bellula* (Desm.) Berl., *P. comiculata* (Ehrh.) Berl and *P. heteracantha* (Sacc.), without designating the type species until Rappaz[15] designated *P. bellula* as the type species and considered *Peroneutypa* as a synonym of *Eutypella* (Nitschke) Sacc. Later, based on morphological characteristics and phylogenetic analyses of Acero et al.[16], Carmarán et al.[17] resurrected *Peroneutypa* as an independent genus, and transferred eight species from *Eutypella* and *Echinomyces* Rappaz to *Peroneutypa* viz: *P. alsophila* (Durieu & Mont.) Carmarán & A.I. Romero, *P. arecae* (Syd. & P. Syd.) Carmarán & A.I. Romero, *P. comosa* (Speg.) Carmarán & A.I. Romero, *P. curvispora* (Starbäck) Carmarán & A.I. Romero, *P. glirioides*

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Research Article

Melomastia (Dothideomycetes, Ascomycota) species associated with Chinese *Aquilaria* spp.

Tian-Ye Du[1,2], Samantha C. Karunarathna[1], Saowaluck Tibpromma[1], Kevin D. Hyde[2,3], Somrudee Nilthong[3], Ausana Mapook[2], Xiang-Fu Liu[1,2,4], Dong-Qin Dai[1], Chen Niu[4], Abdallah M. Elgorban[5], Ekachai Chukeatirote[2], Hao-Han Wang[1]

1 *Research Center of Natural History and Culture, Center for Yunnan Plateau Biological Resources Protection and Utilization, Key Laboratory of Yunnan Provincial Department of Education for the Deep-Time Evolution on Biodiversity from the Origin of the Pearl River, College of Biological Resource and Food Engineering, Qujing Normal University, Qujing 655011, China*
2 *Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100, Thailand*
3 *School of Science, Mae Fah Luang University, Chiang Rai 57100, Thailand*
4 *Spice and Beverage Research Institute, Chinese Academy of Tropical Agricultural Sciences, Wanning 571533, China*
5 *Department of Botany and Microbiology, College of Science, King Saud University, Riyadh 11451, Saudi Arabia*

Corresponding authors: Ekachai Chukeatirote (ekachai@mfu.ac.th), Hao-Han Wang (wanghaohan-mail@qjnu.edu.cn)

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Abstract

This study is based on three terrestrial saprobic fungi associated with *Aquilaria* in Guangdong and Yunnan provinces in China. All isolated species matched with generic concepts of *Melomastia*. Detailed morphological characteristics and combined multi-gene phylogeny of LSU, SSU, and TEF revealed that the new isolates represent two new species (*Melomastia guangdongensis* and *M. yunnanensis*), and one new host and geographical record (*M. sinensis*). *Melomastia guangdongensis* is distinct from the phylogenetically closest species in having semi-immersed to immersed, globose to subglobose ascomata, and two strata of the peridium. *Melomastia yunnanensis* differs from the phylogenetically closest species in having immersed ascomata, conical ostiolar canals, and branched pseudoparaphyses. The discovery of these two new species and one new record collected expands the number of saprobic species associated with *Aquilaria* from 28 to 31. Descriptions, photo plates, and phylogenetic analyses of taxa are provided.

Key words: 2 new species, Dyfrolomycetales, new records, Pleurotremataceae, saprobes, Thyridiaceae

Introduction

Pleurotremataceae Walt. Watson was introduced by Watson (1929) to accommodate *Pleurotrema* Müll. Arg. with *P. polysemum* (Nyl.) Müll. Arg. as the type species. The familial placement of *Pleurotrema* has been controversial, as the mature asci are neither typically unitunicate nor bituncate (Mathiassen 1989; Hyde 1992). The placement of *Pleurotrema* has been confirmed based on the re-examined feature of the type of species *P. polysemum*, and Maharachchikumbura et al. (2016) transferred Pleurotremataceae from Sordariomycetes O.E. Erikss. & Winka to Dothideomycetes O.E. Erikss. & Winka and synonymized

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New *Aquilariomyces* and *Mangifericomes* species (Pleosporales, Ascomycota) from *Aquilaria* spp. in China

Tian-Ye Du[1,2], Samantha C. Karunarathna[1], Kevin D. Hyde[2,3], Somrudee Nilthong[3], Ausana Mapook[2], Dong-Qin Dai[1], Kunhiraman C. Rajeshkumar[4], Abdallah M. Elgorban[5], Li-Su Han[1], Hao-Han Wang[1], Saowaluck Tibpromma[1]

1 *Research Center of Natural History and Culture, Center for Yunnan Plateau Biological Resources Protection and Utilization, Key Laboratory of Yunnan Provincial Department of Education of the Deep-Time Evolution on Biodiversity from the Origin of the Pearl River, College of Ecology and Food Engineering, Qujing Normal University, Qujing 655011, China*

2 *Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100, Thailand*

3 *School of Science, Mae Fah Luang University, Chiang Rai 57100, Thailand*

4 *National Fungal Culture Collection of India (NFCCI), Biodiversity and Palaeobiology (Fungi) Gr, MACS Agharkar Research Institute, G. G. Agarkar Road, Pune 411004, India*

5 *Department of Botany and Microbiology, College of Science, King Saud University, Riyadh 11451, Saudi Arabia*

Corresponding authors: Saowaluck Tibpromma (saowaluck@gmail.com); Hao-Han Wang (wanghh@eastern-himalaya.cn)

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Abstract

Saprobic fungi are known for their critical role in decomposition and nutrient cycling. The study of saprobic fungi is equally important, as it helps in understanding their ecological roles and identifying their hidden diversity. This study focused on saprobic fungi on *Aquilaria*, which is poorly studied compared to economically important hosts like coffee, tea, and rubber. Our rigorous process led to the collection of two new terrestrial saprobic fungi from the Guangdong and Yunnan provinces in China. After extensive phylogenetic analyses and detailed comparison of morphological characteristics, the two collections were identified as two new species belonging to Pleosporales, Ascomycota. *Aquilariomyces maomingensis* **sp. nov.** was isolated from *Aquilaria sinensis* in Guangdong Province, while *Mangifericomes aquilariae* **sp. nov.** was isolated from *Aquilaria* sp. in Yunnan Province. Full descriptions, photo plates, and phylogenetic analyses (maximum likelihood and Bayesian inference analyses based on LSU, ITS, SSU, *tef1-α*, and *rpb2* gene combinations) of the new species are provided, along with a comprehensive list of saprobic fungi associated with *Aquilaria* spp.

Key words: 2 new species, agarwood, saprobes, Thymeleaceae, Thyridariaceae

Introduction

Aquilaria Lam. (Thymeleaceae) is the main plant genus capable of producing agarwood (Lee and Mohamed 2016; Wang et al. 2018; Li et al. 2021). Currently, there are 21 accepted species in *Aquilaria*, of which 13 have been reported to produce agarwood (Hashim et al. 2016). These trees are tropical and subtropical evergreen broad-leaved trees (Rasool and Mohamed 2016; Xu et al. 2016), widely distributed in Asia, such as Borneo, Cambodia, China, India, Indonesia, Laos, Malaysia, New Guinea, the Philippines, Thailand, and Vietnam, (Wang et

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NAME Tianye Du

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PUBLICATIONS

First Author Publications

Du, T. Y., Hyde, K. D., Mapook, A., Mortimer, P. E., Xu, J. C., Karunarathna, S. C., & Tibpromma, S. (2021). Morphology and phylogenetic analyses reveal *Montagnula puerensis* sp. nov. (Didymosphaeriaceae, Pleosporales) from southwest China. *Phytotaxa, 514* (1), 001–025. https://doi.org/10.11646/phytotaxa.514.1.1

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