

MORPHO-MOLECULAR CHARACTERIZATION OF FUNGI ASSOCIATED WITH WILD MUSHROOMS AND MUSHROOM CULTIVATION, WITH DIGITAL DOCUMENTATION OF FUNGICOLOUS FUNGI

ACHALA JEEVANI GAJANAYAKE

DOCTOR OF PHILOSOPHY
IN
BIOLOGICAL SCIENCE

SCHOOL OF SCIENCE
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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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ABSTRACT

Fungicolous fungi that grow on or within other fungi represent an ecologically important but poorly understood group within the fungal kingdom. They play diverse ecological roles ranging from parasitism to commensalism and contribute significantly to fungal diversity and ecosystem dynamics. Despite their importance, knowledge of fungicolous fungi, particularly in tropical regions, remains limited. This study (1) identified fungicolous fungi associated with wild mushrooms from northern Thailand and southwest China, (2) investigated fungi associated with mushroom cultivation in northern Thailand and reviewed fungal diseases and competitor molds affecting global mushroom production, and (3) established a comprehensive digital platform to consolidate existing knowledge on fungicolous fungi.

During this study, a total of 32 fungicolous taxa were identified from wild mushrooms collected in northern Thailand and southwest China, representing 11 genera across the *Sordariomycetes*, *Dothideomycetes*, and *Mucoromycetes*. The *Sordariomycetes* genera included *Clonostachys*, *Diaporthe*, *Fusarium*, *Hypomyces*, *Hypoxylon*, *Mariannaea*, *Xenoacremonium*, and *Zarea*; *Lasiodiplodia* and *Neoroussoella* represented *Dothideomycetes*, while *Mucor* belonged to *Mucoromycetes*. Among these, four were newly described species (*Hypomyces chiangraiensis*, *Mucor yunnanensis*, *Zarea boleticola*, and *Z. thailandica*), five were newly proposed combinations (*Hypomyces chalcipori*, *H. laevigatus*, *H. novovarius*,

H. paravirescens, and *H. protrusus*), and 23 were new records (*Clonostachys rogersoniana*, *Diaporthe talong*, *Fusarium fabacearum*, *F. grosmichelii*, *F. mangiferae*, *F. pernambucanum*, *F. proliferatum*, *F. teslae*, *F. verticillioides*, *Hypomyces boletiphagus*, *H. chlorinus*, *H. cornea*, *H. protrusus*, *H. mycophilus*, *H. pseudocorticiicola*, *H. semicircularis*, *Hypoxylon fendleri*, *Lasiodiplodia thailandica*, *Mucor circinelloides*, *M. hiemalis*, *M. nederlandicus*, *Neoroussoella entadae*, and *Xenoacremonium allantoideum*). Morphological characterization combined with multi-locus phylogenetic analyses (Maximum Likelihood and Bayesian Inference) was conducted to confirm the identification of all fungal taxa. The presence of rare or unexpected genera such as *Diaporthe*, *Hypoxylon*, and *Lasiodiplodia* indicates ecological versatility and possible host-switching behavior of fungicolous fungi. Moreover, some species identified as fungicolous on wild mushrooms in this study, such as *Hypomyces protrusus*, *H. cornea*, *H. mycophilus*, *H. semicircularis*, and *H. pseudocorticiicola* are previously known mushroom pathogens on cultivated mushrooms, suggesting potential pathogenicity of fungicolous fungi on their living hosts.

During the investigation of fungi associated with mushroom cultivation in northern Thailand, *Daldinia eschscholtzii* and *Scedosporium apiospermum* were identified from oyster mushroom growing substrates. Whereas, *Aspergillus quadrilineatus*, *Fusarium sulawesiense*, and *Mucor irregulari* were isolated from cultivated *Phlebopus spongiosus*, *Hericium coralloides* and *Pleurotus* sp. fruiting bodies, respectively. Identification of these fungal taxa was also based on morphological characteristics and molecular phylogenetic analyses. The occurrence of *Daldinia eschscholtzii* on mushroom growing substrates highlights its potential for artificial cultivation and the large-scale harvesting of bioactive compounds produced by this species.

Fungal contaminations, manifesting as destructive diseases or rapidly spreading competitor molds, pose a major challenge to mushroom cultivation. These contaminants can arise at various stages of the cultivation process, causing growth inhibition, deformation, or decay of fruiting bodies, which leads to significant losses in both yield and quality. Addressing these impacts requires a clear understanding of

the causative agents and effective management strategies. In this study, four major fungal diseases, dry bubble, wet bubble, cobweb, and green mold, along with slippery scar and yellow rot, were comprehensively reviewed. The taxonomic placement of these pathogens was clarified through phylogenetic trees reconstructed from published DNA sequence data, and their morphological characteristics were illustrated. Additionally, nine competitor molds associated with mushroom cultivation were reviewed, with detailed accounts of their causal agents, symptoms, disease cycles, epidemiology, and management strategies compiled from available literature.

This study also compiled knowledge on 150 genera containing fungicolous species, including 108 in *Ascomycota*, 37 in *Basidiomycota*, and five in *Mucoromycota*. These generic notes include morphological, ecological, and host association information, accompanied by illustrations of morphological characters of each genus. A considerable number of these genera remain *incertae sedis*, indicating the need for further morpho-molecular studies to resolve their taxonomic placement. To integrate scattered data on this group of fungi, the fungicolous fungi webpage (https://www.fungicolousfungi.org/) was developed, providing an accessible platform for accurate identification, data sharing, and taxonomic updates. This marks a significant advancement in the documentation of fungal biodiversity and will serve as a valuable resource for mycologists, students, and other stakeholders interested in this group of fungi.

Overall, this study expands the current understanding of fungicolous fungal diversity, host associations, and ecological roles. The integrative approach combining morphological, molecular, and digital documentation provides a strong foundation for future research, including studies on host specificity, pathogenicity, evolution, and taxonomy of this remarkable fungal group.

Keywords: Fungicolous Fungi, Mushroom Diseases, Mycoparasites, Taxonomy and Phylogeny, Webpage

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CHAPTER 1

INTRODUCTION

1.1 Fungicolous Fungi: Diversity, Ecology, and Significance

Fungi represent a highly diverse group of eukaryotic organisms that play critical roles in ecosystem functioning, including nutrient cycling, mutualistic interactions, and pathogenesis (Bahram & Netherway, 2022; Niego et al., 2023a; Bhunjun et al., 2024). They interact with a wide range of hosts, such as plants, animals, and other microorganisms, exhibiting various ecological strategies (Jayawardena et al., 2019; Corbu et al., 2023; Fang et al., 2023; Pawlowska, 2024).

Within this vast kingdom, fungicolous fungi constitute a specialized ecological group that colonizes other fungi across multiple lineages (Gams et al., 2004; Sun et al., 2019a; Gajanayake et al., 2025a). They occupy a variety of habitats, including terrestrial and aquatic ecosystems, ranging from tropical and temperate zones to arctic environments (Põldmaa, 2011; Pintye et al., 2015). These fungi may inhabit the surfaces of their hosts or penetrate internal tissues, establishing interactions that can be mutualistic, commensal, parasitic, or saprotrophic (Lin et al., 2016; Sun et al., 2019a; Gajanayake et al., 2021a, 2023a, b; Angelova et al., 2023; Moore et al., 2011).

A wide array of terms has been used to describe fungicolous fungi, reflecting the nature of their host associations. These terms include mycoparasites, hyperparasites, mycophilic fungi, mycotrophic fungi, and sporocarp-inhabiting fungi (Barnett, 1963; Boosalis, 1964; Rudakov, 1978; Jeffries, 1995; Gams et al., 2004; Sun et al., 2019a; Bermúdez-Cova et al., 2023a, b). Fungicolous fungi exploit diverse substrates, such as fungal sporocarps, biotrophic plant parasites, mycelia, sclerotia, soil-borne spores, aquatic fungi, or fungus-like microorganisms (Gams et al., 2004). Their interactions with hosts may be biotrophic, necrotrophic, or hemibiotrophic. The mycoparasitic species can acquire nutrients via direct hyphal contact, specialized structures, or through the secretion of lytic enzymes such as chitinases and glucanases (Jeffries, 1995; Kirk et al., 2008; Sun et al., 2019a). Many fungicolous species employ

a combination of these strategies to exploit their hosts (Jeffries, 1995; Kirk et al., 2008; Sun et al., 2019a).

Global fungal diversity is estimated at 2–3 million species described (Niskanen et al., 2023; Hyde et al., 2024). However, only about 1,500 fungicolous taxa have been formally described (Sun et al., 2019a), indicating that this ecological group remains markedly underexplored. The majority of described fungicolous fungi belong to the *Ascomycota*, particularly within *Hypocreales* and *Helotiales* (Põldmaa, 2011; Maurice et al., 2021). *Hypomyces* is recognized as the ascomycetous genus which comprises the highest number of documented fungicolous species (Sun et al., 2019a; Gajanayake et al., 2025a). *Hypomyces* species often show host-specific parasitism on *Agaricomycetes* (Põldmaa, 2011; Maurice et al., 2021; Tamm & Põldmaa, 2013). Previous studies have highlighted biochemical diversity, host interactions, pathogenic mechanisms, and species richness of fungicolous fungi through both morphological and molecular analyses (Lin et al., 2016; Becker et al., 2020; Maurice et al., 2021).

Fungicolous fungi are ecologically and economically significant. They contribute to nutrient cycling by decomposing fungal substrates, playing a key role in ecosystem processes (Sun et al., 2019a; Gams et al., 2004; Maurice et al., 2021; Angelova et al., 2023; Niego et al., 2023b). Mycoparasitic and hyperparasitic fungi are also valuable in biocontrol, offering potential solutions against destructive fungal pathogens in agriculture. Well-studied examples include *Ampelomyces quisqualis*, *Aphanocladium album*, *Gjaerumia minor*, *Pseudozyma flocculosa* and *Moesziomyces rugulosus* which are effective against powdery mildew (Cesati, 1852; Hoch et al., 1979; Németh et al., 2023). *Trichoderma* spp. are widely applied in agricultural systems due to their biocontrol potential (Mukherjee et al., 2013). Moreover, fungicolous fungi serve as sources for bioactive compounds, including antifungal and anticancer agents, such as metabolites from *Hypomyces chrysospermus* (Vinale et al., 2008; Dikmen et al., 2020; Mukherjee et al., 2013). Some species, like *Naematelia aurantialba* and *Tremella* spp., are consumed as food, and the parasitized “lobster mushrooms” (*Hypomyces lactifluorum* on *Lactifluus piperatus* and *Russula brevipes*) are considered delicacies in many parts of the world (Bandoni & Zang, 1990; Bandoni & Boekhout, 2011; Laperriere et al., 2018; Wu et al., 2019).

Conversely, certain fungicolous fungi pose significant threats to mushroom cultivation, causing diseases that reduce yield and quality, with economic consequences (Hatvani et al., 2007; Sharma et al., 2007; Carrasco et al., 2017a; Bellettini et al., 2018). Additionally, some fungi growing on edible mushrooms, such as *Aspergillus*, *Fusarium*, *Penicillium*, and *Trichoderma* spp., can produce mycotoxins, raising concerns for food safety and human health (Jonathan & Esho, 2010; Ezekiel et al., 2013; Gajanayake et al., 2021a).

Despite the importance of fungicolous fungi, tropical regions, particularly Southeast Asia, remain underexplored (Senanayake et al., 2022; Stallman et al., 2024). Thailand is recognized as a hotspot for fungal diversity (Cheewangkoon et al., 2021; Suwannarach et al., 2022). However, yet the studies on fungicolous fungi in Thailand are limited (Põldmaa & Samuels, 2004; Sun et al., 2019b; Kobmoo et al., 2023). Therefore, Thailand represents a promising region for advancing research on the diversity, taxonomy, and ecological roles of fungicolous fungi. Exploring fungicolous fungi in these regions provides opportunities to discover novel taxa, understand ecological interactions, and identify potential biological resources. Integrating morphological and molecular approaches is essential for accurate identification, classification of these fungi.

1.2 Fungi Associated with Mushrooms Cultivation

Mushrooms are heterotrophic macro-fungi cultivated globally for their nutritional and medicinal importance (Chang & Miles, 1992; Bell et al., 2022; Kour et al., 2022; Yu et al., 2024). Mushroom cultivation is recognized as a valuable microbial technology that promotes large-scale recycling of agricultural waste and reduces the demand for arable land through controlled cultivation systems (Kouser & Shah, 2013). However, fungal contamination remains a persistent challenge, causing significant yield losses and economic impacts (Sun et al., 2019b; Ghimire et al., 2021; Yu et al., 2024). These contaminants include both pathogenic fungi and competitor molds that disrupt mushroom growth, often introduced through poor hygiene or inadequate sterilization (Okigbo & Anuagasi, 2021).

The majority of fungal pathogens associated with cultivated mushrooms belong to *Hypocreales* (*Sordariomycetes*), with *Hypomyces* (*Hypocreaceae*) being one of the most destructive genera (Põldmaa, 2000, 2011; Sun et al., 2019b; Yu et al., 2024). Major diseases such as cobweb, dry bubble, wet bubble, and green mold are caused by *Hypomyces/Cladobotryum*, *Zarea*, *Mycogone*, and *Trichoderma* species, respectively (Sharma et al., 2007; Fletcher & Gaze, 2008; Yu et al., 2024).

Other genera, including *Aspergillus*, *Fusarium*, *Penicillium*, *Chaetomium*, and *Cephalotrichum*, are recognized as competitor molds that reduce mushroom quality and productivity (Sharma et al., 2007; Gajanayake et al., 2021a, 2021b; Yu et al., 2024). Effective management of fungal diseases and competitor molds in mushroom cultivation relies on the proper sterilization of substrates, strict maintenance of hygiene, and careful regulation of environmental conditions (Gajanayake et al., 2021a; Gea et al., 2021; Ghimire et al., 2021; Rathod et al., 2024). Integrated approaches, including biological control and selective fungicide use, have been adopted to mitigate disease spread and yield loss in mushroom production systems worldwide (Gea et al., 2021; Pandey et al., 2025).

Understanding the fungal diversity associated with mushroom cultivation is essential for developing effective management strategies. Despite global progress, documentation on fungi associated with mushroom cultivation in Thailand remains limited (Pukahuta et al., 2000; Limtong et al., 2002; Seephueak et al., 2017; Ubolsuk & Pornsuriya, 2022). Moreover, a comprehensive synthesis of existing knowledge on fungal diseases and competitor molds affecting global mushroom cultivation is lacking; therefore, a compiled review is a timely need.

1.3 Taxonomic Approaches Related to Fungicolous Fungi: Morphological and Molecular Perspectives

Fungicolous fungi, which exist in association with other fungi, represent one of the oldest ecological interactions known among mycobiota. Based on fossil evidence, their evolution and divergence are estimated to have occurred approximately 400 million years ago (Krings et al., 2011). Scientific interest in these

fungi dates back nearly two centuries, with some of the earliest documented records (Von Esenbeck, 1817; Fries & Nordholm, 1817; Willdenow et al., 1833). The first described fungicolous ascomycete was *Cladobotryum agaricina* on *Agaricus* species (Fries & Nordholm, 1817), whereas *Asterophora agaricoides*, found growing on *Agaricus* fruiting bodies, was the earliest recorded fungicolous basidiomycete (Fries & Nordholm, 1817). In 1980s, the taxonomy of fungicolous fungi was characterized by significant advances such as the discovery of sexual–asexual morph connections in members of the *Hypocreales* and the discovery of novel mycoparasitic Heterobasidiomycetes (Reid, 1990; Helfer, 1991; Põldmaa & Samuels, 1999; Gams et al., 2004). Since these pioneering discoveries, numerous fungicolous taxa associated with a wide range of fungal hosts have been reported worldwide (Tubaki, 1955; Nicot, 1967; Samuels, 1993, 1994; Põldmaa, 2011; Ellenberger et al., 2014; Pintye et al., 2012; Sun et al., 2019a; Yu et al., 2020; Gajanayake et al., 2021a, 2023a, b, 2025a).

Accurate taxonomic identification of fungicolous fungi serves as the foundation for understanding their diversity, ecology, and evolutionary relationships. Historically, identification relied heavily on culture-dependent isolation and morphology-based descriptions (Pacioni et al., 2007). Morphological taxonomy remains important, as it enables detailed characterization of reproductive structures, host specificity, and ecological roles. However, morphology alone often fails to resolve cryptic species or to delineate taxa accurately, especially within morphologically conserved groups (Chethana et al., 2021; Jayawardena et al., 2021).

The advent of molecular techniques has transformed the taxonomy of fungicolous fungi. Integrative approaches combining morphological observations with multi-locus phylogenetic analyses now provide more reliable frameworks for species identification and classification. Molecular markers such as ITS, LSU, SSU, *tef*1-α, and *rpb*2 are routinely used to infer phylogenetic relationships and confirm species boundaries (Chethana et al., 2021; Jayawardena et al., 2021; Yu et al., 2024; Gajanayake et al., 2025a). These methods have clarified the placement of many previously ambiguous taxa and revealed extensive hidden diversity within fungicolous lineages (Sun et al., 2019a; Maurice et al., 2021; Yu et al., 2024; Gajanayake et al., 2025a).

In addition, recent developments in culture-independent techniques, particularly next-generation sequencing (NGS) and DNA metabarcoding, have revolutionized fungal biodiversity research. These high-throughput sequencing approaches enable the detection of multiple fungicolous taxa directly from fungal fruiting bodies, uncovering a far greater diversity than previously recognized through traditional isolation-based methods (Pacioni & Leonardi, 2016; Leonardi et al., 2018; Maurice et al., 2021). Consequently, integrating both culture-dependent and culture-independent techniques is crucial for future taxonomic and ecological studies, allowing for a more comprehensive understanding of fungicolous fungal diversity and their evolutionary patterns (Sun et al., 2019a; Maurice et al., 2021).

1.4 Digitalization in Mycology and Biodiversity Studies

Information on fungicolous fungi is widely scattered across publications, herbaria, and other repositories (Gajanayake et al., 2025b). Preserving these records and making data on fungal morphology, taxonomy, and diversity accessible is critical for mycology and broader biological research (Lange, 2010, Hyde et al., 2023).

Digitization has revolutionized mycology by enabling efficient storage, retrieval, and sharing of biodiversity data (Prakash et al., 2017; Lofgren & Stajich, 2021). Traditional taxonomic approaches, which relied heavily on herbarium specimens, monographs, and printed literature, are increasingly supplemented or replaced by digital platforms that consolidate morphological, molecular, and ecological information (Hyde et al., 2023). Online databases such as MycoBank, Index Fungorum, Species Fungorum, UNITE, and GenBank now serve as indispensable tools for accurate fungal identification and global data dissemination (Prakash et al., 2017; Lofgren & Stajich, 2021).

Modern researchers prefer digital resources over printed literature due to their efficiency, comprehensiveness, and ease of handling. Integrating images, DNA sequences, and ecological metadata into unified digital platforms enhances reproducibility, facilitates cross-disciplinary research, and supports accurate taxonomic work (Prakash et al., 2017; Lofgren & Stajich, 2021). Additionally, digital

imaging and web-based tools improve visualization and comparison of fungal structures, benefiting both research and education (Hyde et al., 2023; Gajanayake et al., 2025b).

Developing a specialized digital database for fungicolous fungi to consolidate taxonomic, molecular, and ecological data would provide a central resource for future studies. Thus, digital documentation has become a foundation for contemporary fungal taxonomy and biodiversity research, promoting collaboration, precision, and long-term accessibility of scientific knowledge (Hyde et al., 2024a, Gajanayake et al., 2025b).

1.5 Research Gaps

1.5.1 Research on fungicolous fungi associated with wild mushrooms in northern Thailand remains limited, with only a few studies documenting their diversity, host range, and ecological significance.

1.5.2 Investigations focusing on fungi associated with mushroom cultivation in northern Thailand are scarce, particularly concerning pathogenic and competitor species that influence mushroom yield and quality.

1.5.3 A comprehensive synthesis of existing knowledge on fungal diseases and competitor molds affecting global mushroom cultivation is lacking.

1.5.4 The available information on fungicolous fungi is highly fragmented and dispersed across various sources, including scattered publications, databases, and regional checklists. This fragmentation hinders accessibility and comparative research.

1.6 Research Objectives

1.6.1 To identify the fungicolous fungi on wild mushrooms from northern Thailand.

1.6.2 To identify the fungi associated with mushroom cultivation in northern Thailand and review fungal diseases and competitor molds affecting global mushroom cultivation.

1.6.3 To digitize the data on fungicolous fungi with updated information.

1.7 Research Contents

This thesis consists of six chapters.

Chapter 1 serves as the general introduction, providing background information on fungicolous fungi, fungi associated with mushroom cultivation, taxonomic approaches to fungicolous fungi, digitization in mycology, research gaps, research objectives, and the overall structure of the thesis.

Chapter 2 outlines the sampling, isolation, morphological and molecular procedures, and other methods used in this study.

Chapter 3 presents the morpho-molecular characterization of fungicolous fungi on wild mushrooms from northern Thailand and southwestern China during this study.

Chapter 4 details the morpho-molecular characterization of fungi associated with mushroom cultivation in northern Thailand and includes a review of fungal diseases and competitor molds affecting global mushroom cultivation.

Chapter 5 describes the compilation of scattered information on fungicolous fungi and the development of a digital database, including generic notes and illustrations for 150 genera containing fungicolous fungi.

Chapter 6 provides the conclusions derived from the study, research advantages and suggests directions for future research.

CHAPTER 2

MATERIAL AND METHODS

2.1 Specimen Collection

To investigate fungicolous fungi on wild mushrooms, mushrooms colonized by fungicolous fungi were collected from forest areas in northern Thailand (Chiang Rai, Chiang Mai, and Phayao Provinces) and southwest China (Yunnan Province). Collected mushrooms were wrapped in aluminium foil and transported to the laboratory for further examination and fungal isolation.

For the study of fungi associated with mushroom cultivation, contaminated mushroom grow bags and infected fruiting bodies were obtained from mushroom farms or cultivation trials conducted in northern Thailand (Chiang Rai and Phayao Provinces). In addition, edible mushrooms sold in local markets in Chiang Rai and Chiang Mai Provinces were collected. Contaminated mushroom grow bags were placed in sterilized polyethylene bags, whereas mushroom fruiting bodies were wrapped in aluminium foil, and all samples were brought to the laboratory for detailed observation and isolation.

2.2 Isolation of Fungi and Morphological Characterization

Specimens were initially examined using a stereomicroscope (Leica M205FCA-FA, Leica Microsystems Ltd., Hessen, Germany). For the isolation of fungicolous fungi from mushroom fruiting bodies, mycelia or spore masses present on the hosts were aseptically transferred to potato dextrose agar (PDA) or malt extract agar (MEA) plates using a sterile needle. When fruiting bodies of fungicolous fungi were observed on mushroom fruiting bodies, single spore isolation was performed on PDA to obtain pure cultures (Senanayake et al., 2020). Fungi growing on mushroom

cultivation substrates were isolated by aseptically transferring their mycelia or spore masses onto PDA or MEA using a sterile needle.

Inoculated plates were incubated at 25 °C for 3–4 days, and pure cultures were obtained through successive sub culturing. After one week of incubation, the colony characteristics of the fungal cultures were observed and documented. To induce sporulation in certain isolates, cultures were transferred onto carnation leaf agar (CLA), corn meal agar (CMA), oatmeal agar (OA), or water agar (WA), as appropriate. Host mushrooms were identified based on their morphological characteristics. After successful isolation of fungicolous fungi, the host mushroom specimens were dried in an electric dryer at 40 °C for 48 hours and later those were individually stored in zip-lock bags with silica gel to prevent moisture retention.

Micro-morphological examinations were carried out following the methodology of Senanayake et al. (2020). Observations were made using a Nikon Eclipse 80i compound microscope (Nikon, Tokyo, Japan), and images were captured with a Canon 750D digital camera (Canon Inc., Tokyo, Japan) mounted on the microscope. Morphological structures were measured with Tarosoft Image Framework v.0.9.7 (Informer Technologies Inc.), and images prepared for figures were processed using Adobe Photoshop CS6 Extended (Windows 10.0; Adobe Systems, USA).

Herbarium specimens and living cultures obtained from Thailand were deposited in the Mae Fah Luang University Fungarium (MFLU) and the Mae Fah Luang University Culture Collection (MFLUCC), Chiang Rai, Thailand. Specimens and cultures from China were deposited in the Zhongkai University of Agriculture and Engineering Herbarium (ZHKU) and the Zhongkai University of Agriculture and Engineering Culture Collection (ZHKUCC), Guangzhou, China. New species and new combinations were registered in Index Fungorum/ MycoBank, and numbers were obtained accordingly.

2.3 DNA Extraction, PCR Amplification, and Sequencing

For DNA extraction, approximately 50–100 mg of axenic mycelium was

scraped from 4-week-old cultures. Mycelia were finely ground into powder using liquid nitrogen, and genomic DNA was extracted with the Omega Bio-Tek E.Z.N.A. Forensic DNA Kit (Omega Bio-Tek, Inc., USA) according to the manufacturer's protocol.

Polymerase chain reaction (PCR) was performed using a standardized protocol. Each 25 μL reaction contained 12.5 μL DreamTaq Green PCR Master Mix (2×) (Thermo Fisher Scientific Inc., USA), 1 μL of each primer (10 μM), 2 μL of genomic DNA, and 8.5 μL of double-distilled water (ddH_2O). Targeted gene regions, primers, and corresponding PCR cycling conditions are listed in Table 2.1. PCR products were verified by electrophoresis on 1% agarose gels, with samples prepared using Invitrogen DNA Gel Loading Dye (6×) (Thermo Fisher Scientific Inc., USA).

Amplified fragments were purified and sequenced by SolGent Co., Ltd. (Daejeon, South Korea) following standard protocols. Newly obtained nucleotide sequences were deposited in GenBank for public access.

Table 2.1 Partial gene regions, primers and PCR conditions used in this study

Gene region	Primers	PCR condition	Reference
Internal transcribed spacer (ITS)	ITS5/ ITS4	94 °C: 5 min, (94 °C: 30 s, 54 °C: 50 s, 72 °C: 1 min) ×35 cycles, 72 °C: 10 min	White et al. (1990)
Large subunit nuclear ribosomal DNA region (LSU)	LROR/ LR5	94 °C: 5 min, (94 °C: 30 s, 55 °C: 50 s, 72 °C: 90 s) ×35 cycles, 72 °C: 10 min	Vilgalys and Hester (1990), Rehner and Samuels (1994)
Small subunit nuclear ribosomal DNA region (SSU)	NS1/ NS4	94 °C: 5 min, (94 °C: 30 s, 52 °C: 50 s, 72 °C: 1 min) ×35 cycles, 72 °C: 10 min	White et al. (1990)
Translation elongation factor 1-α (*tef1-α*)	983F/ 2218R	94 °C: 5 min, (94 °C: 30 s, 58 °C: 50 s, 72 °C: 1 min) ×40 cycles, 72 °C: 10 min	Rehner and Buckley (2005)
	EF1/ EF2	94 °C 90 s, (94 °C: 45 s, 55 °C: 45 s, 72 °C: 1 min) ×35 cycles, 72 °C: 10 min	Carbone and Kohn (1999)
Second largest subunit of RNA polymerase II (*rpb2*)	fRPB2-5F/ fRPB2-7cr	95 °C: 5 min, (95 °C: 45 s, 54 °C: 45 s, 72 °C: 2 min) ×40cycles, 72 °C: 10 min	Liu et al. (1999)
Beta (β) tubulin (*tub2*)	bt2a/ bt2b	94 °C: 3 min, (94 °C: 30 s, 58 °C: 1:30 min, 72 °C: 1:20 min) ×40 cycles, 72 °C: 10 min	Glass and Donaldson (1995)
	T1/T22	94 °C: 5 min, (94 °C: 30 s, 55 °C: 50 s, 72 °C: 1 min) ×35 cycles, 72 °C: 10 min	O'Donnell and Cigelnik (1997)
Calmodulin (*cmdA*)	228F/ 737R	95 °C: 5 min, (95 °C: 30 s, 54 °C: 50 s, 72 °C: 1 min) ×40 cycles, 72 °C: 10 min	Carbone and Kohn (1999)
Histone 3 (*his3*)	CYLH3f/ H3-1b	94 °C: 3 min, (95 °C: 30 s, 57 °C: 30 s, 72 °C: 1 min) ×40 cycles, 72 °C: 10 min	Glass and Donaldson (1995)

2.4 Sequence Alignment and Phylogenetic Analyses

Forward and reverse sequences were assembled into contigs using SeqMan v.7.1.0. The newly generated sequences were subjected to BLAST (Basic Local Alignment Search Tool) searches against the GenBank nucleotide database (https://blast.ncbi.nlm.nih.gov/Blast.cgi). Results from the BLAST searches, together with initial morphological observations, were used to validate and compare the sequences. Reference sequences for phylogenetic analyses were retrieved from GenBank based on previously published literature. Single-gene alignments were obtained using MAFFT v.7.036 (http://mafft.cbrc.jp/alignment/server/large.html; Katoh et al., 2019) with default settings. The resulting alignments were visualized and concatenated in BioEdit v.7.0.5.2 (Hall, 1999).

Maximum likelihood (ML) analyses were performed using IQ-TREE, with bootstrap support estimated from 1000 pseudo-replicates, or using RAxML-HPC2 on XSEDE (v.8.2.8) via the CIPRES Science Gateway platform, in which bootstrap support values were calculated from 1000 replicates (Stamatakis et al., 2008; Miller et al., 2010; Nguyen et al., 2014; Stamatakis, 2014; Chernomor et al., 2016). The optimal nucleotide substitution models for each dataset were determined using jModelTest2 under the Bayesian information criterion (Darriba et al., 2012).

Bayesian inference (BI) analyses were conducted using MrBayes v.3.2.7a on XSEDE through the CIPRES portal (Huelsenbeck & Ronquist, 2001; Miller et al., 2010). Phylogenetic trees were summarized, and posterior probabilities (BYPP) were estimated using Markov chain Monte Carlo (MCMC) methods. Two parallel runs were performed with six simultaneous Markov chains for 1,000,000 to 50,000,000 generations (depending on the dataset), with trees sampled every 1000th generation. Convergence was considered achieved when the standard deviation of split frequencies fell below 0.01. The first 25% of sampled trees, representing the burn-in phase, were discarded, and the remaining 75% were used to calculate posterior probabilities in the majority-rule consensus tree.

Phylogenetic trees were visualized with FigTree v1.4.0 (Rambaut, 2011) and further arranged in Microsoft PowerPoint. Genetic distances between strains of novel taxa and their sister taxa were calculated using the Kimura 2-parameter model in MEGA X, applying the pairwise deletion option.

2.5 Reviewing the Fungal Diseases and Competitor Molds Affecting Global Mushroom Cultivation

Information for each fungal disease or competitor mold was compiled through a comprehensive literature survey, including published articles, theses, websites, and checklists published until February 2025. Pathogen classification followed Hyde et al. (2024a) and nomenclature from Index Fungorum (2025). Photographic plates illustrating disease symptoms and morphological characteristics were included when images could be obtained by the author. In cases where images were unavailable, illustrations were adapted from previous literature with proper citation.

2.6 Preparation of Generic Notes and Illustrations of Fungicolous Fungi

Generic notes for 150 fungicolous genera were written based on a comprehensive literature survey, including publications, theses, websites, and checklists. Nomenclature followed Index Fungorum (2025), and the current species count for each genus was adopted from Species Fungorum (2025). The outline of taxonomic classification of the genera was organized in accordance with Hyde et al. (2024a). Photographic plates were included when images could be obtained by the authors, whereas line drawings were adapted or redrawn from previous literature with proper citation when photographs were unavailable. These visual materials were provided to illustrate the key morphological characteristics of each genus.

CHAPTER 3

FUNGICOLOUS FUNGI ON WILD MUSHROOMS

3.1 Introduction

Fungicolous fungi are a diverse and specialized ecological group associated with fungi across multiple lineages within the fungal kingdom (Gams et al., 2004; Sun et al., 2019a; Gajanayake et al., 2025a). These taxa coexist with their hosts in diverse environments, spanning both aquatic and terrestrial ecosystems, from temperate and tropical zones to arctic regions (Põldmaa, 2011; Pintye et al., 2015).

Fungicolous fungi can select a range of substrates as their biotopes, including fungal sporocarps, biotrophic plant parasites, mycelia, sclerotia, soil spores, aquatic fungi, or fungus-like microorganisms (Gams et al., 2004). They can grow on the surface of the host fungi as well as within the tissues of host fungi (Lin et al., 2016; Sun et al., 2019a; Gajanayake et al., 2021a, 2023a, b; Angelova et al., 2023). This group of fungi can exhibit a wide range of relationships, including mutualistic, commensal, parasitic, or saprotrophic interactions with their hosts (Moore et al., 2011; Sun et al., 2019a). Interactions between a fungicolous fungus and its host can be biotrophic, necrotrophic, or hemibiotrophic (Gams et al., 2004; Boddy, 2016). Mycoparasitic taxa derive nutrients from their hosts through direct physical interactions, such as forming haustoria or specialized hyphal structures, or by producing antifungal compounds and lytic enzymes like chitinase and glucanase (Jeffries, 1985, 1995; Jeffries & Young, 1994; Kirk et al., 2008; Sun et al., 2019a). These enzymes break down host cell walls and membranes, granting access to cellular contents. In many cases, mycoparasites employ a combination of these strategies (Jeffries, 1985, 1995; Jeffries & Young, 1994; Kirk et al., 2008; Sun et al., 2019a).

A study on the diversity of fungicolous fungi in sporocarps by Maurice et al., (2021) discovered that alpha diversity was consistently higher in short-lived, resupinate sporocarps compared to long-lived, pileate ones. Short-lived sporocarps are typically fleshy, spongy, and ephemeral with higher moisture content. Those provide

a more favorable niche that supports the germination and growth of fungicolous fungi. In contrast, tough, perennial sporocarps are often more resistant to the colonization by fungicolous fungi (Maurice et al., 2021). Therefore, the differences in structural complexity, biochemical makeup, and water content in sporocarps may affect the growth and specialization of fungicolous fungi. These traits can also lead to varying degrees of host specificity (Tamm & Põldmaa, 2013; Siozios et al., 2015; Hargreaves et al., 2018; Spirin et al., 2018), with some fungicolous fungi appearing limited to the geographic range of specific hosts due to their specialized relationships. Huo et al., (2024) showed that the diversity and composition of fungicolous fungi in host macrofungi varied according to the collection time and habitat of the host fungi. Lin et al. (2016) reported fifteen species of xylariaceous fungi isolated from basidiomata *Scytinopogon* species and also found that some of those xylariaceous fungai were endophytes in nearby plants. Therefore, Lin et al. (2016) suggested that these endophytic xylariaceous fungi might serve as sources of fungicolous fungi in *Scytinopogon* sp. within the forest. This observation also offers insights into potential lifestyle transitions of these fungi.

According to global fungal diversity estimation, 2 to 3 million fungal species exist (Niskanen et al., 2023; Hyde et al., 2024a). However, only about 1500 fungicolous taxa have been identified to date (Sun et al., 2019a). This number is significantly low as compared to overall fungal diversity (Sun et al., 2019a; Maurice et al., 2021). Tropical fungal diversity, particularly of fungicolous fungi, remains understudied compared to non-tropical regions (Stallman et al., 2024; Senanayake et al., 2022). Thailand is a tropical country, which is considered as a hotspot for discovering novel fungal taxa (Cheewangkoon et al., 2021; Suwannarach et al., 2022). Despite this, research on fungicolous fungi in Thailand and China is still limited.

Therefore, to address this research gap, this study was conducted focusing on the morpho-molecular characterization of fungicolous fungi on wild mushrooms in northern Thailand and southwest China. This study aimed to identify the fungicolous fungi on wild mushrroms in northern Thailand and southwest China.

3.2 Morpho-molecular Characterization of Fungicolous Fungi on Wild Mushrooms from Northern Thailand and Southwest China

This chapter documents four new species, five novel combinations, and 23 new records of fungicolous fungi associated with wild mushrooms, discovered from northern Thailand and southwest China during the present investigation. The identification of fungicolous isolates was carried out through an integrative approach, combining detailed morphological examinations with multi-locus phylogenetic analyses. The selection of gene regions followed the most suitable molecular markers recommended for each genus or family. To confirm the taxonomic placement of these fungi, both morphological illustrations and multi-gene phylogenetic reconstructions were produced, employing maximum likelihood (ML) and Bayesian inference (BI) methods. The findings are organized on a genus-wise basis.

3.2.1 *Clonostachys* Corda, Pracht-Fl. Eur. Schimmelbild. (Leipzig und Dresden): 31 (1839)

Clonostachys was first introduced by Corda (1839), based on the type species *C. araucaria*, which is now regarded as a synonym of *C. rosea* (basionym *Penicillium roseum*), the asexual morph of *Bionectria ochroleuca* (Schroers, 2001). According to Species Fungorum (2025), 104 species epithets are currently recognized under *Clonostachys*, which is classified within the *Bionectriaceae* (Hyde et al., 2024a).

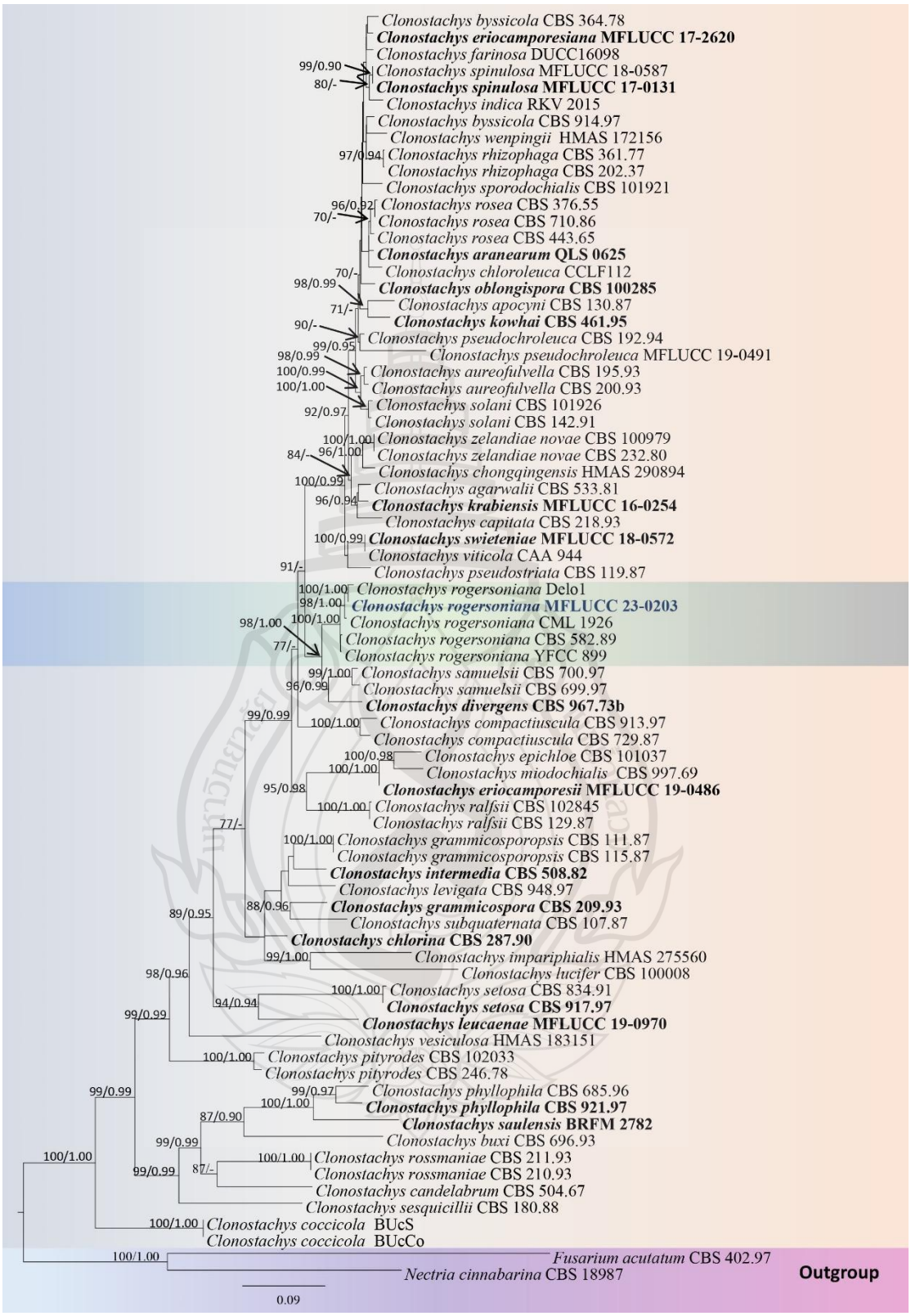


Figure 3.1 Phylogenetic tree generated from maximum likelihood analysis based on combined ITS and *tub2* sequence data representing the *Clonostachys* species

Figure 3.1, Related reference sequences were downloaded from GenBank based on previously published data from Perera et al., (2020) and Zeng and Zhuang (2022). Seventy-six taxa are included in the combined analyses. *Fusarium acutatum* (CBS 402.97) and *Nectria cinnabarina* (CBS 18987) are used as the outgroup taxa. The best scoring RAxML tree with a final likelihood value of −13,172.451 is presented. The matrix had 639 distinct alignment patterns, with 19.91% of undetermined characters or gaps. The proportion of invariable sites was 0.316. Estimated base frequencies were as follows: A = 0.250, C = 0.250, G = 0.250, T = 0.250; substitution rates: AC = 1.00000, AG = 2.80366, AT = 1.00000, CG = 1.00000, CT = 4.24917, GT = 1.00000; gamma distribution shape parameter α = 0.692. The value of the average standard deviation of the split frequencies of BYPP analysis was 0.008389. Bootstrap support values for ML equal to or greater than 70% and BYPP equal to or greater than 0.90 are given near the nodes. The newly generated sequence is in blue. The type strains are indicated in black bold.

Clonostachys rogersoniana Schroers, Studies in Mycology 46: 109 (2001)

Figure 3.2

Index Fungorum number: IF485131

Fungicolous on a bolete mushroom. Sexual morph: Not observed. Asexual morph**:** on the host, *Mycelium* white cottony mass. On PDA, hyphomycetous, *Hyphae* 1–3.5 μm ($\bar{x}$ = 2.5 μm, n = 30) wide, branched, septate, hyaline, hyphal coils observed. *Conidiophores* scattered on the agar media or arising from the aerial hyphae, mostly dominant towards the margin, hyaline, penicillate, septate, stipes 60–170 × 2–6 μm ($\bar{x}$ = 117 × 4 μm, n = 20). *Penicilli* 55–78 × 50–96 μm ($\bar{x}$ = 66.5 × 73 μm, n = 20), solitary to gregarious, bi- to quarter verticillate, non sporodochial; branches of the penicillus divergent, each branch terminating in metulae and adpressed phialides. *Phialides* 10–26 × 1.7–3.6 μm ($\bar{x}$ = 16.5 × 2.6 μm, n = 30), in whorls of 2–4, narrowly flask-shaped, slightly tapering toward the apex. *Intercalary phialides* not observed. *Conidial masses* white to light yellow. *Conidia* 5–9 × 1.5–4 μm ($\bar{x}$ = 6.5 × 2.5 μm, n = 40, broadly ellipsoidal to oval, rarely minutely curved, ends broadly rounded, hilum laterally displaced, almost median or invisible, hyaline, smooth-walled.

Colony characters – Colonies on PDA attaining 60–70 mm diameter after 14 days at 25 °C, velvety to lanose, dense, aerial mycelium with hyphae arranged in strands, colony front initially white and develops brown spots when getting older, colony reverse white to medium brown with irregular margins.

Material examined – Thailand, Chiang Mai province, Mae Tang, Pa Pae, Ban Pha Deng, isolated from the white mycelium growing on a bolete mushroom, 07 July 2021, AJ. Gajanayake, MR 01 (inactive dry culture, MFLU 23-0484), living culture, MFLUCC 23-0203.

GenBank numbers – ITS = OR473265; *tub*2 = OR804262.

Notes – As shown in Figure 3.1, the isolate (MFLUCC 23-0203), clusters within *Clonostachys rogersoniana* with bootstrap support of 100% ML, 1.00 BYPP. Furthermore, the morphology of our isolate (MFLUCC 23-0203) resembles the original description and illustrations of *C. rogersoniana* by Schroers (2001). However, when our strain is compared with the strain described by Schroers (2001), there are slight dimensional differences (conidiophores: 60–170 × 2–6 µm*vs* 60–200 µm × 3–5 µm, height of the penicilli: 55–78 µm *vs*. 50–100 µm, length of the phialides: 10–26 µm *vs*. 11.8–26.8 µm, conidia: 5–9 × 1.5–4 µm *vs*. 5.8–7.2 × 3–3.8 µm) in morphological structures. The reason may be the differences in the media in which the colonies were grown. *Clonostachys rogersoniana* has been commonly isolated from soil whereas it has also been isolated from bark of dead twigs, leaf litter and decaying seed pods (Schroers, 2001; Perera et al., 2020). This species has shown a cosmopolitan distribution while it has been mostly reported from warmer or tropical regions (Schroers, 2001). Therefore, most probably *C. rogersoniana* spores from the soil on the bolete mushroom would eventually lead to growth as a fungicolous fungus. Previously, *Clonostachys byssicola*, *C. subquaternata* and *C. rosea* have been reported as fungicolous species (Sun et al., 2019a). However, *C. rogersoniana* has been extensively studied for its potential to produce secondary metabolites whereby, a cordyceps-colonizing strain of *C. rogersoniana* was among them (Wang et al., 2017; Wang et al., 2019; Han et al., 2020; Tapfuma et al., 2023). To the best of our knowledge, this is the first report of *Clonostachys rogersoniana* as a fungicolous fungus on a bolete mushroom, from Thailand.

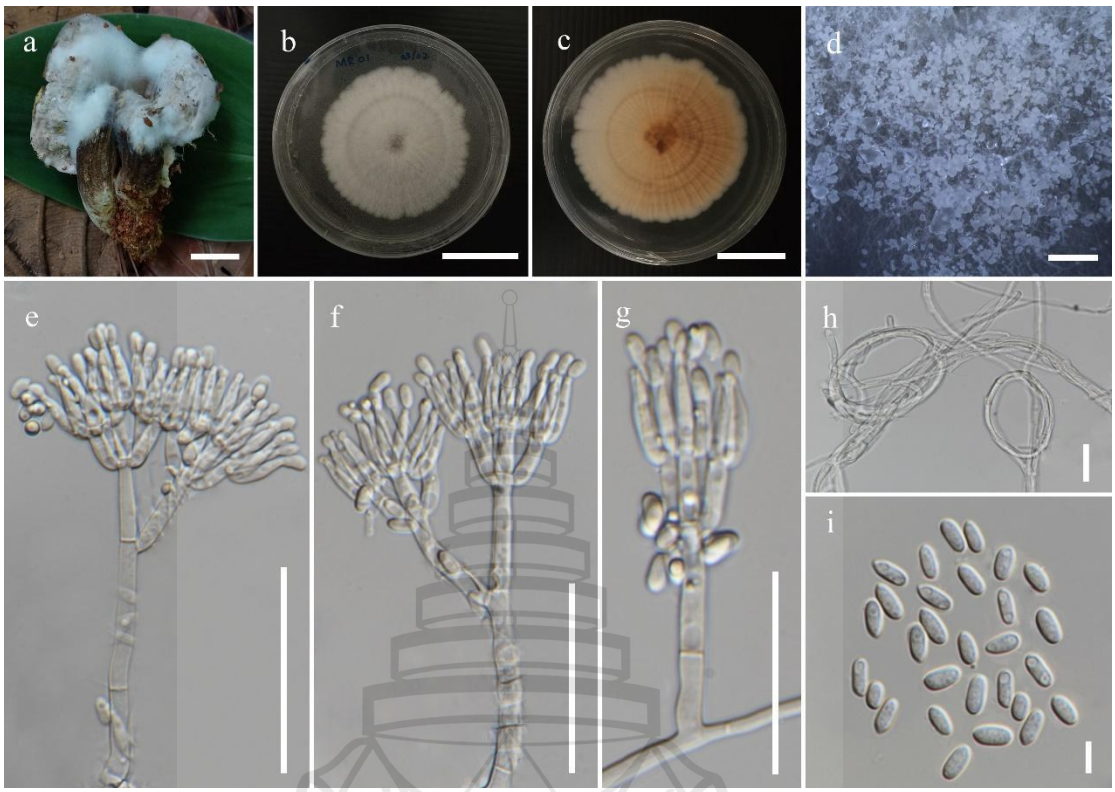


Figure 3.2 *Clonostachys rogersoniana* (MFLU 23–0203)

Figure 3.2, a Host. b, c 14 days old colony on PDA (b. above, c. below). d Sporulation on PDA. e–g Conidiophores with phialides and conidial attachments. h Hyphal coils. Hyphal coils. i Conidia. Scale bars: a = 2.5 cm, b, c = 40 mm, d = 200 µm, e, f = 45 µm, g = 30 µm, h = 25 µm, i = 5 µm.

3.2.2 *Diaporthe* Nitschke, Pyrenomyc. Germ. 1: 110 (1867)

Diaporthe was established by Nitschke (1870), with *D. eres* designated as the type species. To date, there are more than 400 species are listed under this genus and it is classified within *Diaporthaceae* (Dissanayake et al., 2024; Hyde et al., 2024a; Species fungorum 2025).

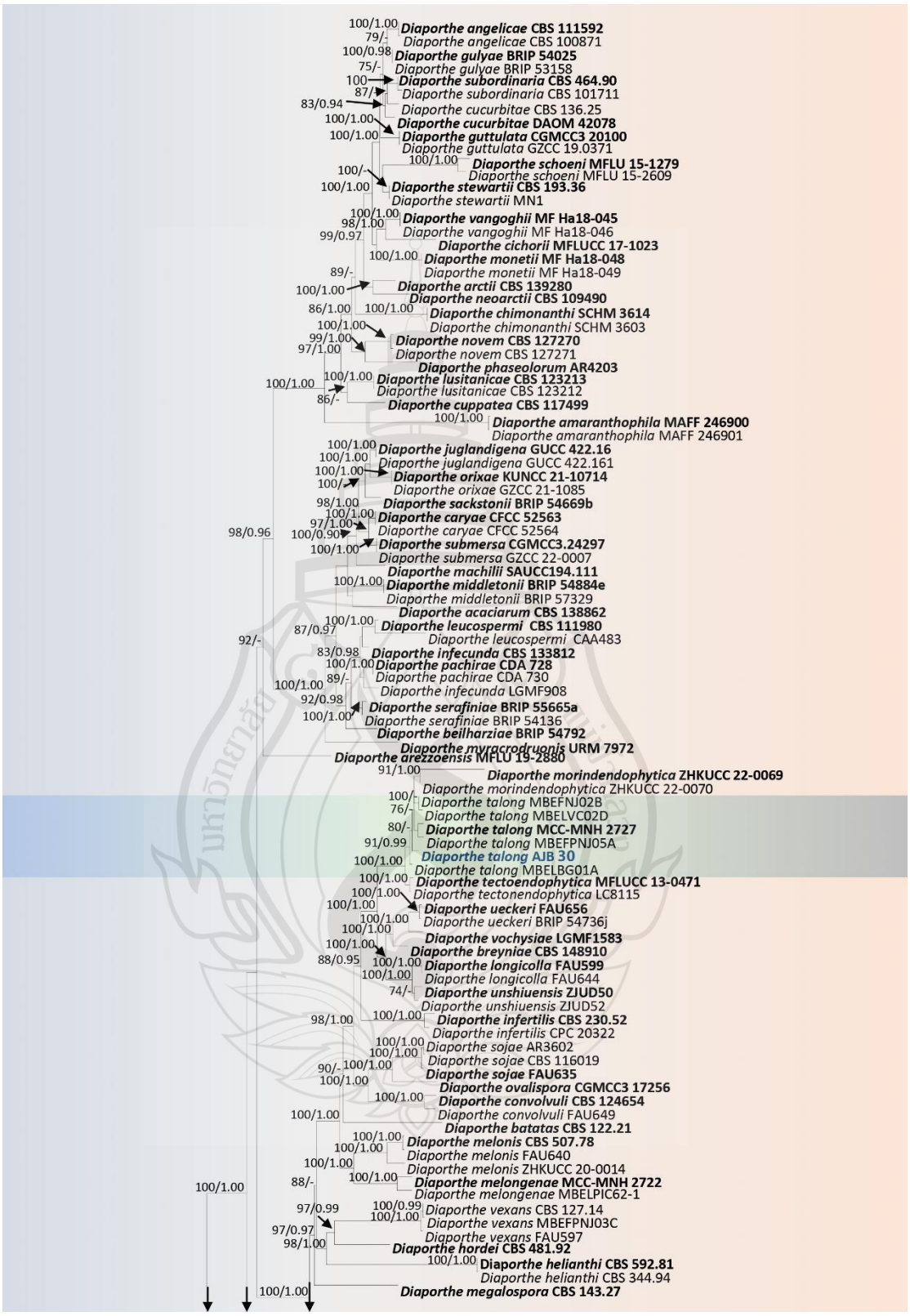


Figure 3.3 Phylogenetic tree generated by ML analysis of combined ITS, *tef*-1α, *tub*2, *cmdA*, and *his*3 sequence data of *Diaporthe sojae* species complex

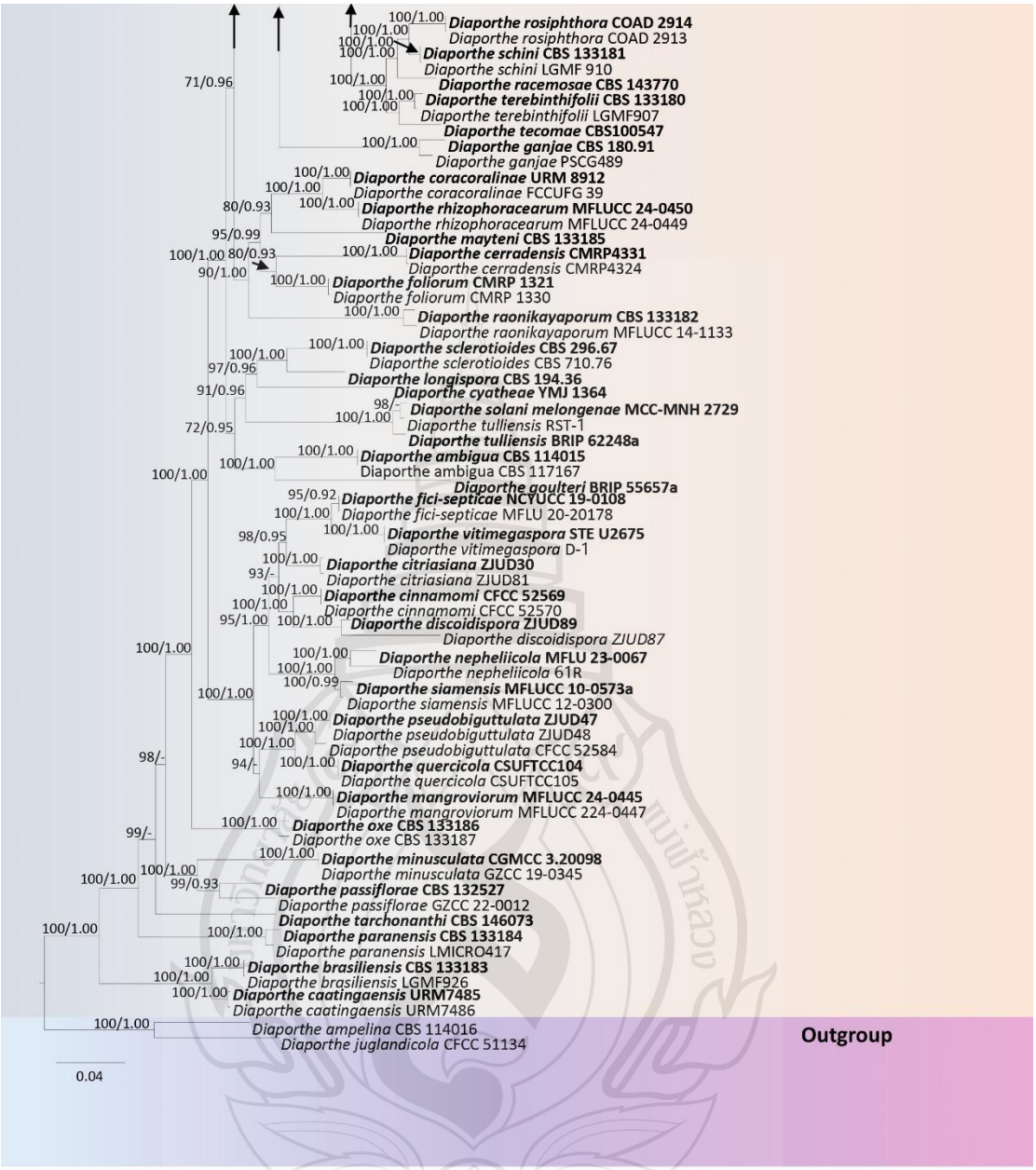


Figure 3.3 (continued)

Figure 3.3, A total of 161 strains were included in the analyses. The tree is rooted with *Diaporthe ampelina* (CBS 114016) and *Diaporthe juglandicola* (CFCC 51134). The best scoring ML tree with an optimal log-likelihood value of −39742.292 is presented. The matrix had 1633 distinct alignment patterns, with 26.69% of undetermined characters or gaps. Bootstrap support values for ML ≥ 70% and BYPP ≥ 0.90 values for BI (BS/BYPP) are shown respectively near the nodes. Type

(holotype/ex-type/isotype/paratype) strains are in bold. The strains reported in this study are in blue bold.

Diaporthe talong H.D. Aumentado & M.A. Balendres, Mycol. Progr. 23(no. 23): 16 (2024).

Figure 3.4

Index Fungorum number: IF 901481

Fungicolous on a polypore fruiting body. Sexual morph: not observed. Asexual morph: thck mass of white to grey mycelium growing on the host. on PDA, coelomycetous, *Mycelium* 1.5–2.5 μm ($\overline{x}$ = 2 μm, n = 30) wide, hyaline, septate, occasionally forming intercalary swellings, sometimes becoming brown-pigmented in mature colonies. *Conidiomata* superficial on agar media, pycnidial, aggregated, black, irregular in shape, sterile.

Colony characters – on PDA at 25 °C, 85–90 mm in 7 days. Colony front off-white to dark gray with concentric rings of dense to sparse hyphae, margin undulate to irregular, reverse of the colony is grey to olive-brown.

Material examined – Thailand, Chiang Rai, Muang, Tha Sai (19° 49′ 26.0292″N, 99◦ 52′ 18.966″E), isolated from mycelium on a polypore fruiting body, 20 September 2023, A.J. Gajanayake, AJB 30.

Notes – As shown in Figure 3.3, AJB 30, clustered within *Diaporthe talong* (MCC-MNH 2727, MBEFNJ02B, MBEFPNJ05A, MBELVC02D) in the phylogenetic analysis, with 76% BS and 0.75% BYPP. On the host, only dense mycelial growth was observed. Although colonies grown on CLA, CMA, and PDA produced pycnidia, they were sterile and did not show conidiogenesis. The colony charaters and the pycnidial structured formed on PDA are almost similar to description by Aumentado & Balendres (2024). Therefore, mainly based on existing morphological and phylogenetic evidence, we identified isolate AJB 30 as *D. talong*.

Diaporthe talong was originally isolated from blighted fruits of *Solanum melongena* in the Philippines (Aumentado & Balendres 2024). This study represents the first report of this species occurring on a mushroom, as well as the first record from Thailand. The polypore fruiting body hosting *D. talong* was found growing on a tree branch, suggesting that the conidiomata of *D. talong* on the plant substrate may have dispersed onto the polypore, leading to colonization. However, since the plant

host of the polypore was not examined in detail, we cannot confirm this hypothesis. Further collections and observations are needed to determine whether this occurrence reflects a true host association or incidental colonization.

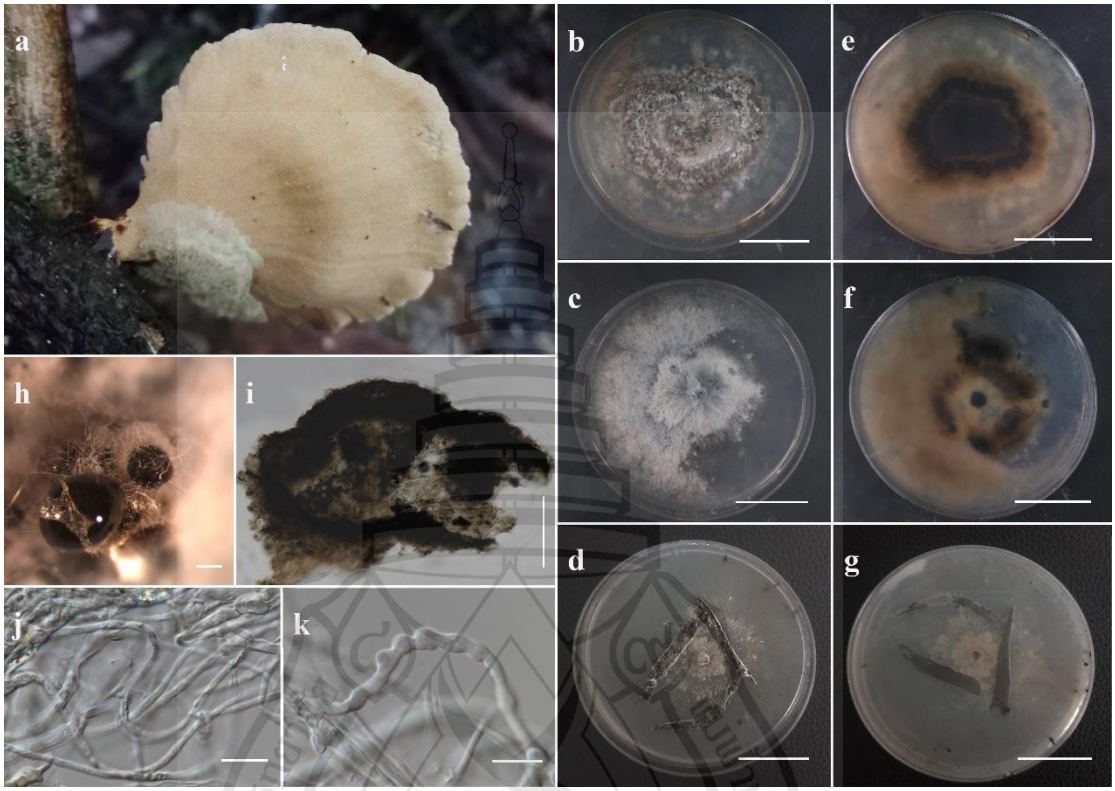


Figure 3.4 *Diaporthe talong* (AJB 30)

Figure 3.2, a. Host (Polypore fruiting body). b–d. Colony front on PDA, CMA and CLA. e–g. Colony reverse on PDA, CMA and CLA. h. Sterile conidiomata on PDA. i. Cross section of the sterile conidiomata. j. Mycelium on PDA. p. Swollen hyphae. Scale bars: b–g = 30 mm, h = 500 µm, i = 250 µm, j, k = 10 µm.

3.2.3 *Fusarium* Link, Mag. Gesell. naturf. Freunde, Berlin 3(1-2): 10 (1809)

Fusarium was established by (Link, 1809), with *F. roseum* designated as the type species. To date more than 400 species are listed under this genus and it is classified within *Nectriaceae* (Hyde et al., 2023, 2024a; Species Fungorum 2025).

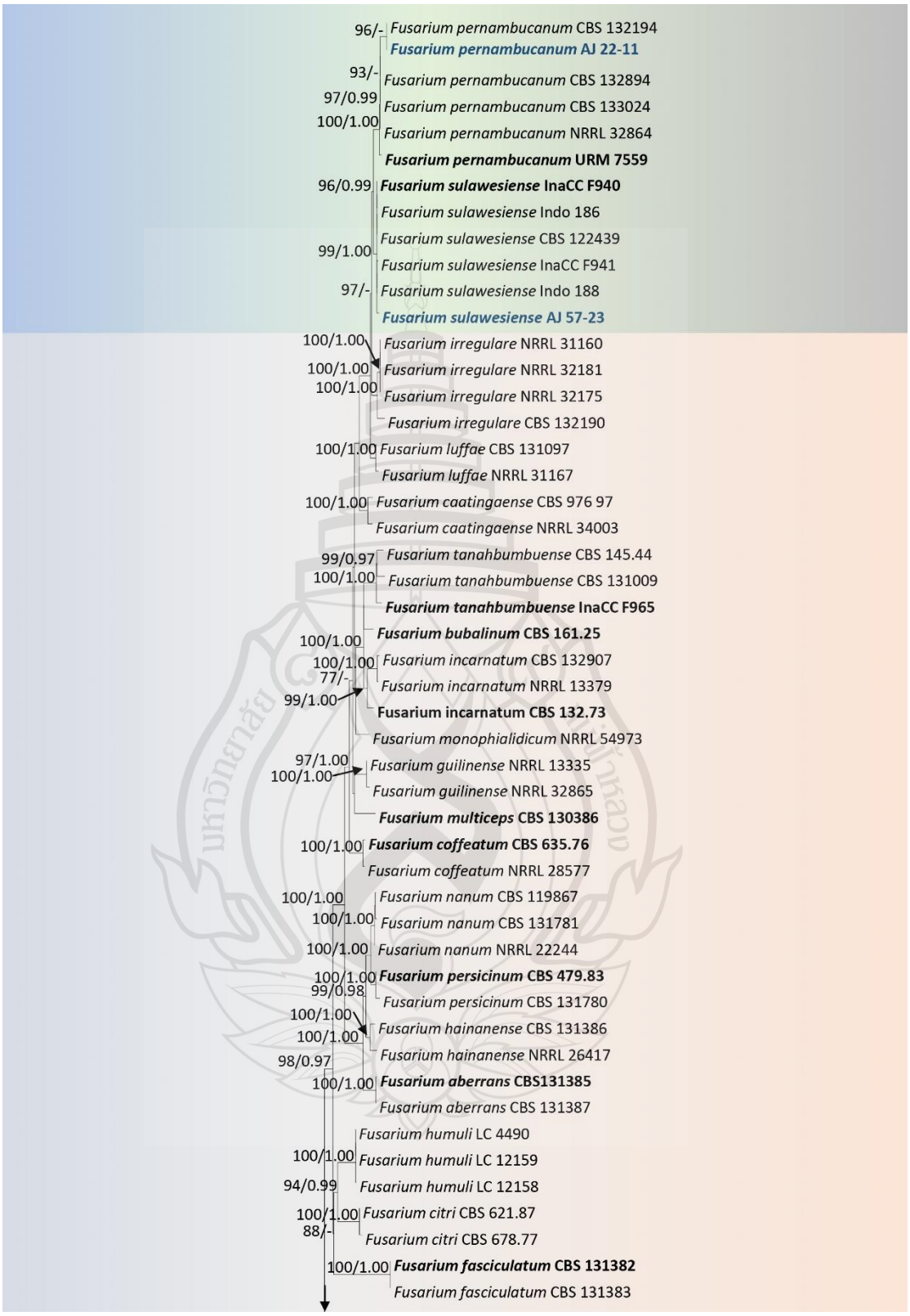


Figure 3.5 Phylogenetic tree generated by ML analysis of combined *tef-1α*, *cmdA* and *rpb2* sequence data of *Fusarium incarnatum-equiseti* species complex (FIESC)

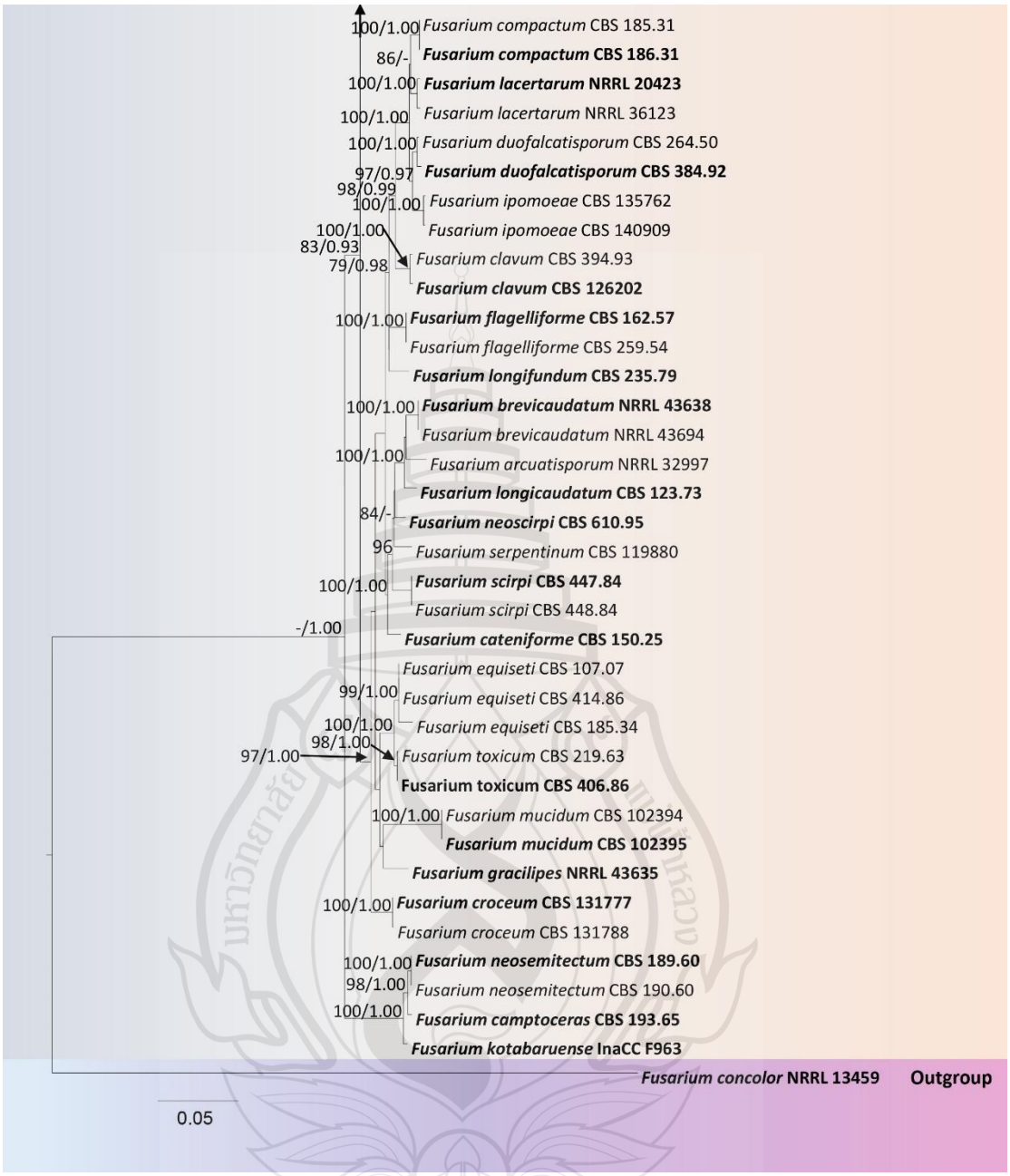


Figure 3.5 (continued)

Figure 3.5, A total of 86 strains were included in the analyses. The tree is rooted with *Fusarium concolor* (NRRL 13459). The best scoring ML tree with an optimal log-likelihood value of −11727.972 is presented. The matrix had 697 distinct alignment patterns, with 7.60% of undetermined characters or gaps. Bootstrap support values for ML ≥ 70% and BYPP ≥ 0.90 values for BI (BS/BYPP) are shown

respectively near the nodes. Type (holotype/ex-type/isotype/paratype) strains are in bold. The strains reported in this study are in blue bold.

Fusarium pernambucanum A.C.S. Santos, C.S. Lima, P.V. Tiago & N.T. Oliveira, Mycologia 111(2): 253 (2019)

Figure 3.6

Index Fungorum number: IF 825273

Fungicolous on a fruiting body of *Agaricus* sp. Sexual morph: not observed. Asexual morph: black powdery patches and white mycelium on a fruiting body of *Agaricus* sp. On CLA, hyphomycetous, *Mycelium* 1.5–3.5 μm ($\bar{x}$ = 2.5 μm, n = 30) wide, hyaline, septate, branched and occasionally forming hyphal coils. *Aerial conidiophores* 2–3.5 μm ($\bar{x}$ = 2.5 μm, n = 30) wide, hyaline, septate, simple or branched, bearing mono- or polyphialides with 2–3 conidiogenous openings. *Aerial conidia* 9–26 × 2–4 μm ($\bar{x}$ = 17 × 3 μm, n = 30), hyaline, long, straight to falcate, straight or slightly curved short-clavate, fusoid with rounded or pointed apices, or obovoid to pyriform, aseptate to 1–3 septate. *Sporodochia* pale orange to orange. *Sporodochial conidia* 19–44 × 2.5–4.5 μm ($\bar{x}$ = 28.5 × 3.5 μm, n = 30) straight to falcate, with curved apical cell and foot-shaped basal cell, 3–5 septate. *Chlamydospores* 4–9 μm ($\bar{x}$ = 6.5 μm, n = 20) in diameter, hyaline, formed in chains, terminal or intercalary, with smooth-walled.

Colony characters – on PDA at 25 °C, 55–80 mm in 7 days. The aerial mycelium sparse to abundant dense, and floccose. Colony front pale rose in the middle and white towards the margin Reverse pale orange to salmon.

Material examined – Thailand, Chiang Rai: Mueang, Nang Lae (20° 2' 24.6192" N, 99° 54' 2.2068" E), isolated from the mycelium growing on a fruiting body of an *Agaricus* sp., 22 April 2022, A.J Gajanayake, AJ 22-11.

Notes – Our isolate AJ 22-11, clustered within *Fusarium pernambucanum* (CBS 132194, CBS 132894, CBS 133024, NRRL 32864, URM 7559) with 96% BS, and 0.71 BYPP (Figure 3.5). The morphological features of AJ 22-11 match the original description and illustrations of *F. pernambucanum* provided by Santos et al. (2019a), except for slight differences in the dimensions of morphological structures. These variations are possible due to differences in the agar medium and cultural conditions used (Senanayake et al., 2020). Therefore, we confirmed that our isolate,

AJ 22-11, is both phylogenetically and morphologically consistent with *F. pernambucanum*.

Fusarium pernambucanum was initially described by Santos et al. (2019a) as an entomopathogenic fungus isolated from the insects *Aleurocanthus woglumi* and *Dactylopius opuntiae* in Brazil. Later, Diniz et al. (2022) expanded its known host range by reporting its entomopathogenic activity against *Nasutitermes corniger*. Beyond its entomopathogenic nature, *F. pernambucanum* has also been identified as a plant pathogen on various hosts in countries such as Brazil, China, and Thailand (Wang et al., 2024b; Silva et al., 2025; Wonglom et al., 2025). It has been reported to cause several plant diseases, including leaf blight on plum trees (Lu et al., 2022), fruit rot on muskmelon (Zhang et al., 2022), leaf yellow spot on melon (Gao et al., 2023), peduncle rot on grape (Wang et al., 2024b), root and stem rot on papaya (Silva et al., 2025), and postharvest fruit rot on mango (Li et al., 2023b). In Thailand, it has been documented as a leaf spot pathogen on the peach palm (*Bactris gasipaes* Kunth) (Wonglom et al., 2025) and associated with dry stems of *Asparagus setaceous* (Seifollahi et al., 2023). To the best of our knowledge, this study is the first to report *F. pernambucanum* as a fungicolous species on *Agaricus* sp. in Thailand and globally.

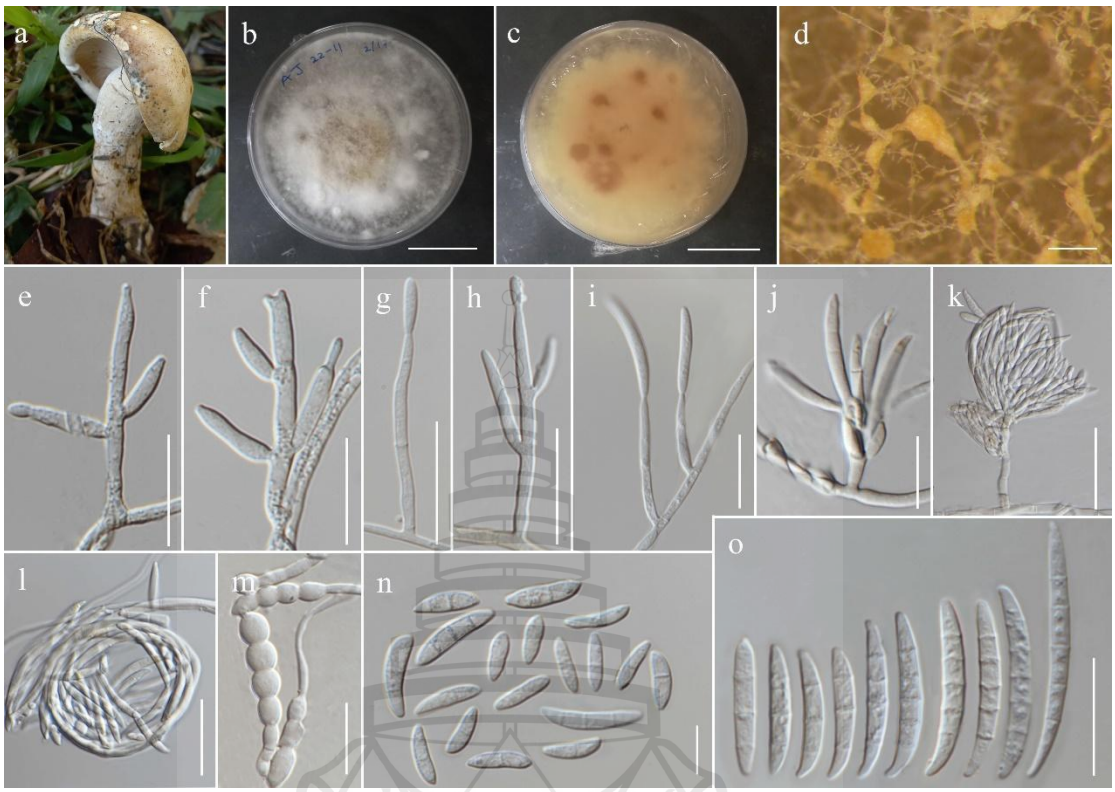


Figure 3.6 *Fusarium pernambucanum* (AJ 22-11)

Figure 3.6, a. Host (*Agaricus* sp.). b, c. Colony on PDA. d. Sporulation on CLA. e–k. Aerial conidiophores with conidial attachments. l. Hyphal coil. m. Chlamydospores. n, o. Conidia. Scale bars: b, c = 30 mm, d = 250 µm, k = 40 µm, l = 30 µm, g, h = 25 µm, e, f, i, j, m, o = 20 µm, n = 10 µm.

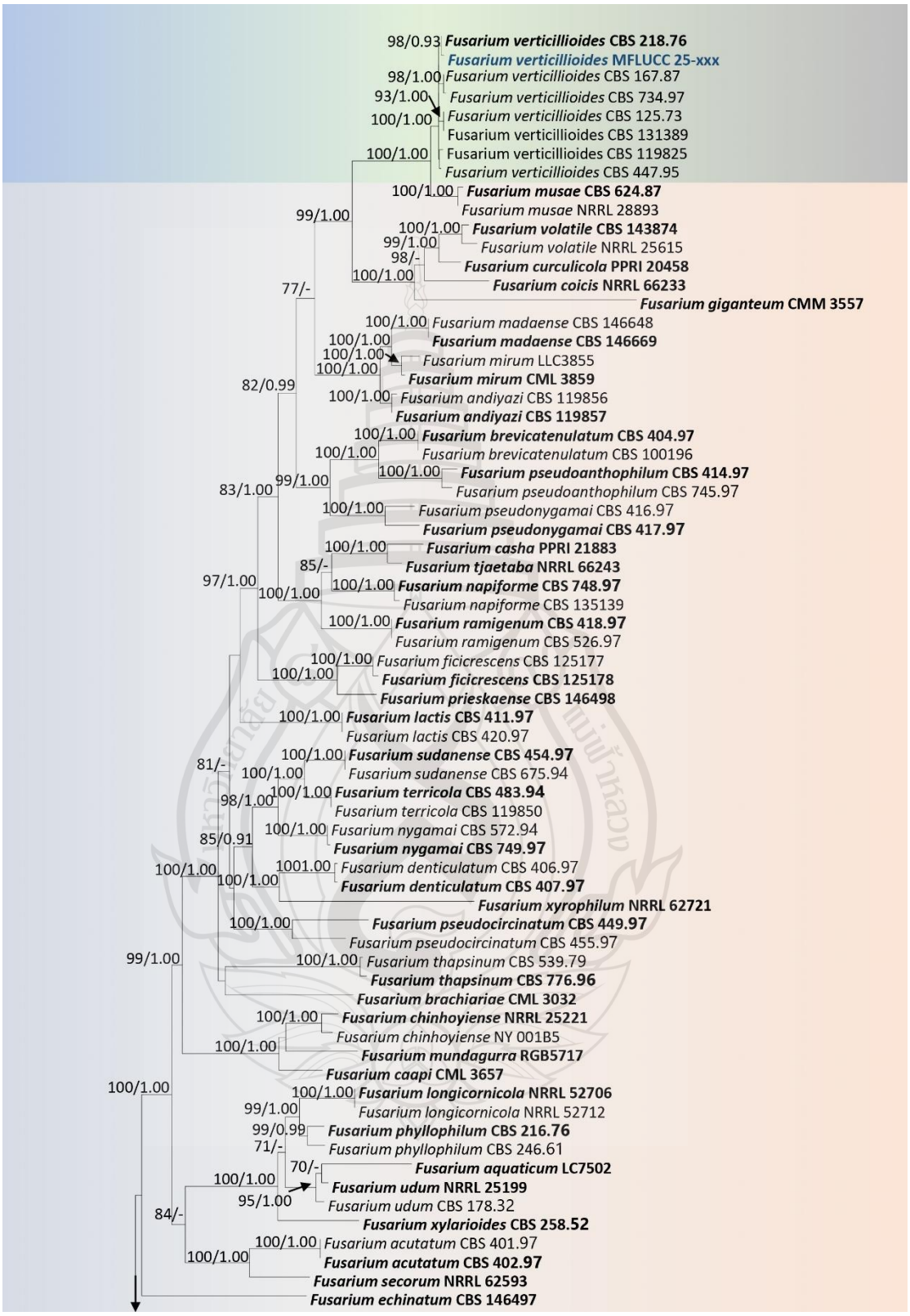


Figure 3.7 Phylogenetic tree generated by ML analysis of combined *tef-1α*, *rpb2*, *tub2*, and *cmdA* sequence data of *Fusarium fujikuroi* species complex (FFSC)

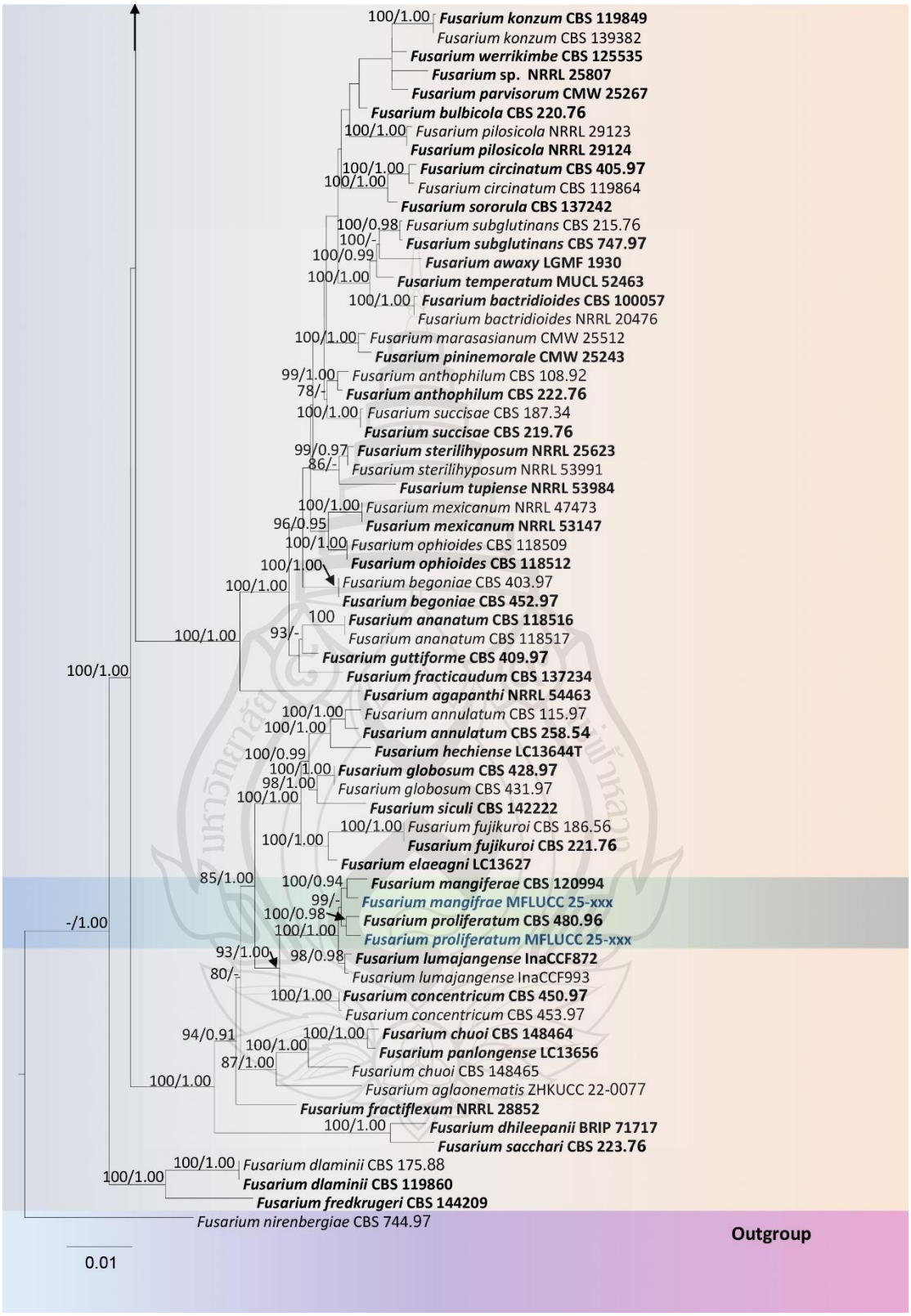


Figure 3.7 (continued)

Figure 3.7, A total of 133 strains were included in the analyses. The tree is rooted with Fusarium nirenbergiae (CBS 744.97). The best scoring ML tree with an optimal log-likelihood value of −18627.452 is presented. The matrix had 1223 distinct alignment patterns, with 13.64% of undetermined characters or gaps. Bootstrap support values for ML ≥ 70% and BYPP ≥ 0.90 values for BI (BS/BYPP) are shown respectively near the nodes. Type (holotype/ex-type/isotype/paratype) strains are in bold. The strains reported in this study are in blue bold.

Fusarium mangiferae Britz, M.J. Wingf. & Marasas, Mycologia 94(4): 725 (2002).

Fig. 3.8

Index Fungorum number: IF 484672

Fungicolous on a bolete fruiting body. Sexual morph: not observed. Asexual morph: white to pinkish mycelium covering the pores and mycelial patches on the cap of a bolete fruiting body. On CLA, hyphomycetous, *Conidiophores* 1.5–2.5 μm ($\overline{x}$ = 2 μm, n = 20) wide, erect and prostrate, phialides formed on the aerial conidiophores mostly mono-phialidic. *Microconidia* 5.5–14 × 1.5–3 μm ($\overline{x}$ = 9 × 2.5 μm, n = 35), variable in shape, obovoid conidia the most abundant type, oval to allantoid conidia occurring occasionally, mostly aseptate and occasionally 1 septate. *Sporodochia* cream to orange forming on carnation leaf with aggregated polyphialidic conidiophores. *Macroconidia* 15–39 × 2–3 μm ($\overline{x}$ = 25 × 2.5 μm, n = 35), long and slender, aseptate when immature and 3–5 septate at maturity. *Chlamydospores* terminal and elongated.

Colony characters – on PDA at 25 °C, 30–35 mm in 7 days. Aerial mycelium white, floccose. Reverse of the colony rosy buff,

Material examined – Thailand, Chiang Mai: Mae Taeng, Pa Pae (19° 7' 7.2444" N, 98° 44' 2.1228" E), isolated from the white to pinkish mycelium covering the pores and mycelial patches on the cap of a bolete fruiting body, 07 July 2022, A.J Gajanayake, MR 11.

Notes – Our isolate MR 11, clustered with the type strain of *Fusarium mangiferae* (CBS 120994) with 100% BS, and 0.94 BYPP (Figure 3.7). The morphological features of MR 11 match the original description and illustrations of *F.*

mangiferae provided by Britz et al. (2002). Therefore, we confirmed that our isolate, MR 11, is phylogenetically and morphologically consistent with *F. mangiferae*.

Fusarium mangiferae was first described in association with mango inflorescence malformation in Israel, and has also been recorded in Egypt, Malaysia, South Africa, and the USA (Britz et al., 2002). Additionally, it has been reported on mango from Australia, Brazil, China, India, Mexico, Oman, Spain, and Sri Lanka (USDA Fungal Databases, 2025). Beyond mango, this species has also been isolated from *Sansevieria trifasciata* in Malaysia and *Vanilla planifolia* in Indonesia (USDA Fungal Databases, 2025). In Thailand, *F. mangiferae* was previously isolated from durian tissues exhibiting die-back symptoms, however, its pathogenicity was not confirmed through Koch's postulates (Pongpisutta et al., 2023). This study represents the first record of *F. mangiferae* as a fungicolous species in Thailand, isolated from a bolete fruiting body, and constitutes the first global report of its fungicolous lifestyle.

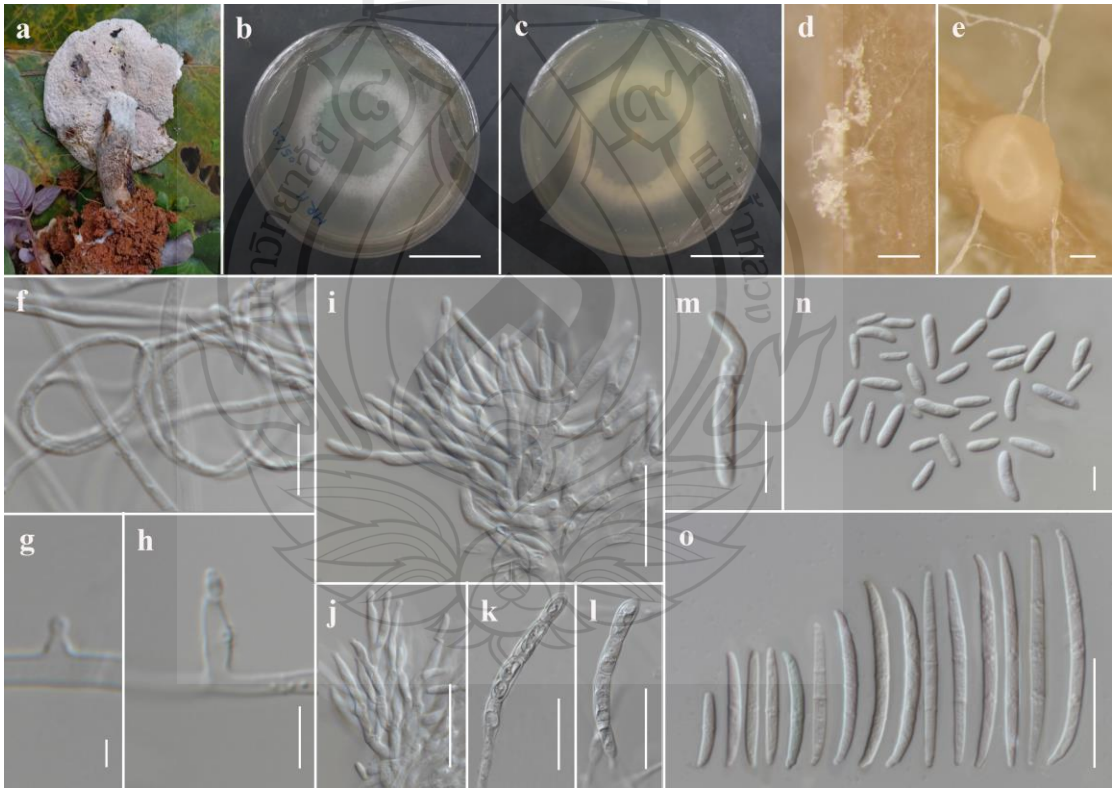


Figure 3.8 *Fusarium mangiferae* (MR 11)

Figure 3.8, a. Host (Bolete fruiting body). b, c. Colony on PDA. d, e. Sporulation on CLA. f. Hyphal coils. g–j. Phialides and conidial attachments. k, l.

Chlamydospores. m, n. Microconidia. l. Macroconidia. Scale bars: b, c = 30 mm, d, e = 250 µm, k, l = 25 µm, i, j, o = 20 µm, f, m = 10 µm, h = 6 µm, n = 5 µm, g = 2 µm.

Fusarium proliferatum (Matsush.) Nirenberg ex Gerlach & Nirenberg, Mitt. biol. BundAnst. Ld- u. Forstw. 169: 38 (1982)

Figure 3.9

Index Fungorum number: IF 509381

Fungicolous on fruiting bodies of *Cortinarius* sp. Sexual morph: not observed. Asexual morph: white mycelium on mushroom fruiting bodies. On CLA, hyphomycetous, *Conidiophores* 75–90 µm high ($\bar{x}$ = 82.5 µm, n = 20), infrequent and difficult to observe, arising sparsely from aerial mycelium, erect, straight to flexuous, smooth- and thin-walled, typically unbranched or irregularly branched, occasionally reduced to conidiogenous cells borne laterally on hyphae. *Conidiogenous* cells 13–22 × 1.5–3 µm ($\bar{x}$ = 17 × 2 µm, n = 20), mono to polyphialidic, subulate to subcylindrical, smooth- and thin-walled, lacking periclinal thickening. *Microconidia* 4–13.5 × 1.5–3 µm ($\bar{x}$ = 6 × 2 µm, n = 30), hyaline, ovoid to pyriform, smooth- and thin-walled, aseptate or rarely 1-septate, formed in discrete false heads at phialide apices. Sporodochia and chlamydospores not observed.

Colony characters – on PDA at 25 °C, 65–70 mm in 7 days. Colony surface floccose, white to pale pink. Reverse of the colony pale grey at centre fading into greyish towards the margin.

Material examined – Thailand, Chiang Mai: Mae Taeng, Pa Pae (19° 7' 7.2444" N, 98° 44' 2.1228" E), isolated from the white mycelium growing fruiting bodies of *Cortinarius* sp., 07 July 2022, A.J. Gajanayake, MR 29.

Notes – Our isolate MR 29, clustered with the type strain of *Fusarium proliferatum* (CBS 480.96) with 100% BS, and 0.98 BYPP (Figure 3.7). The morphological features of MR 29 match the original description and illustrations of *F. proliferatum* provided by Yilmaz et al. (2021). Therefore, we confirmed that our isolate, MR 29, is phylogenetically and morphologically consistent with *F. proliferatum*.

Fusarium proliferatum was originally described by Matsushima (1971) as *Cephalosporium proliferatum,* isolated from soil in Papua New Guinea. Later it was

identified as a *Fusarium* species (Gams & Lacey, 1972; Nirenberg, 1976). However, there was no viable ex-type culture to serve as a phylogenetic reference for *F. proliferatum*. Therefore, Yilmaz et al. (2021) designated the original illustration as the lectotype and selected CBS 480.96 as the epi-type for *F. proliferatum*. This species is widely distributed and known to infect a broad range of plant hosts (USDA Fungal Databases, 2025). It is primarily recognized as a plant pathogen, responsible for diseases such as garlic bulb dry rot, apple replant disease, sheath rot of rice, and peanut root rot (Prabhukarthikeyan et al., 2021; Duan et al., 2022; Gálvez & Palmero, 2022; Sun et al., 2023a). In addition to its plant pathogenicity, this species has been reported in human and animal infections, including cases of fungal keratitis, meningoencephalitis, and poultry mycosis (Sun et al., 2018; Alavi Darazam et al., 2022; Potekhina et al., 2023). *Fusarium proliferatum* has also been previously identified as a fungicolous species, associated with *Plasmopara viticola*, *Stereum hirsutum*, and a smut (Bakshi et al., 2001; Torbati et al., 2019, 2021). Notably, Bakshi et al. (2001) discovered it as a potential biocontrol agent against grape downy mildew. In Thailand, *F. proliferatum* has previously been isolated from sorghum (Nor et al., 2019). This study presents the first record of *F. proliferatum* as a fungicolous species, associated with fruiting bodies of *Cortinarius* sp. in Thailand.

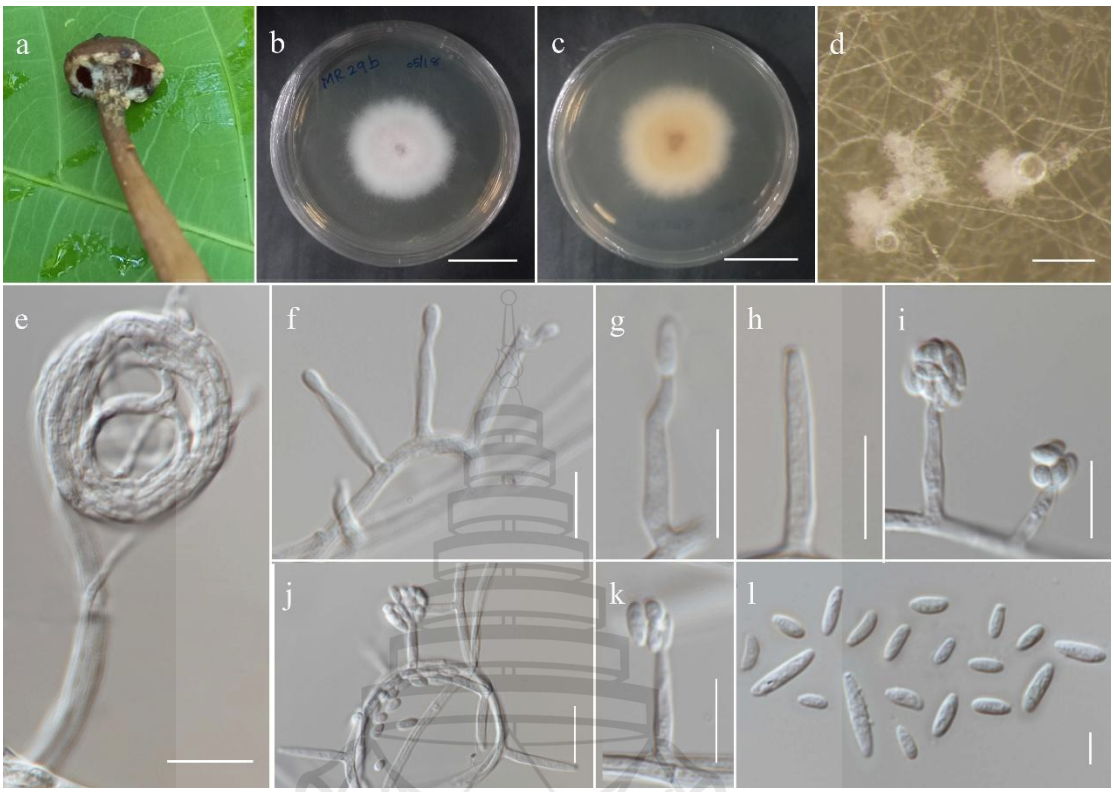


Figure 3.9 *Fusarium proliferatum* (MR 29)

Figure 3.9, a. Host (*Cortinarius* sp.). b, c. Colony on PDA. d. Sporulation on CLA. e. Hyphal coil. f–k. Conidiogenous cells and conidial attachments. l. Conidia. Scale bars: b, c = 30 mm, d = 250 μm, e, j = 15 μm, f–i, k = 10 μm, l = 5 μm.

Fusarium verticillioides (Sacc.) Nirenberg, Mitt. Biol. Bundesanst. Land-Forstw. 169: 26 (1976)

Figure 3.10

Index Fungorum number: IF 314223

Fungicolous on a fruiting body of *Lentinus* sp. Sexual morph: not observed. Asexual morph: white mycelium on a fruiting body of *Lentinus* sp. On CLA, hyphomycetous, *Conidiophores* 1–2 μm ($\bar{x}$ = 1.5 μm, n = 20) wide, arising from the aerial mycelium, unbranched or branched, bearing terminal or intercalary monophialides. *Phialides* 9.5–29.5 × 1.5–2.5 μm ($\bar{x}$ = 17 × 2 μm, n = 30), subulate to subcylindrical. *Microconidia* 4.5–8 × 1.5–3 μm ($\bar{x}$ = 6 × 2 μm, n = 40), hyaline, abundant, borne in short chains on monophialides of branched conidiophores, forming small false heads on the tips of the phialides, clavate, aseptate. Chlamydospores were

not observed, but swollen cells were present in the mycelium. Sporodochia not observed.

Colony characters – on PDA at 25 °C, 75–80 mm in 7 days. Colony surface white with abundant aerial mycelium. Reverse of the colony pale rose at the centre and dirty white towards the margin.

Material examined – Thailand, Chiang Mai: Doi Inthanon, isolated from the mycelium growing on a fruiting body of *Lentinus* sp., 02 December 2023, R.S. Jayawardena, AJ 58-4.

Notes – Our isolate AJ 58-4, cladded with the type strain of *Fusarium verticillioides* (CBS 218.76) with 98% BS, and 0.93 BYPP (Figure 3.7). The morphological features of AJ 58-4 match the original description and illustrations of *F. verticillioides* provided by Nirenberg (1981). Therefore, we confirmed that our isolate, MFLUCC AJ 58-4, is phylogenetically and morphologically consistent with *F. verticillioides*.

Fusarium verticillioides was originally described from maize in Italy as *Oospora verticillioides* (Saccardo, 1881). The taxonomic ambiguities surrounding this species was clarified and resolved through epitypification by Yilmaz et al. (2021). *Fusarium verticillioides* has been reported from several countries across the world, including Australia, Bangladesh, Belgium, Brazil, China, Cuba, France, India, Italy, Japan, Malaysia, Mexico, the Philippines, Poland, South Africa, Thailand, and the USA, commonly associated with a wide range of plant hosts (USDA Fungal Databases, 2025). This species is known as a significant pathogen of maize, leading to substantial yield and quality losses (Han et al., 2023). It is also a major producer of the mycotoxin, fumonisins that frequently contaminate maize (Chen et al., 2023a). In Thailand, *F. verticillioides* has been previously isolated from sorghum (Nor et al., 2019), corn, and soybean meal (Anukul et al., 2014). However, to date, there are no reports of this species exhibiting a fungicolous lifestyle.

This study presents the first documentation of *F. verticillioides* as a fungicolous species in Thailand, isolated from a fruiting body of *Lentinus* sp., and is the first such report globally.

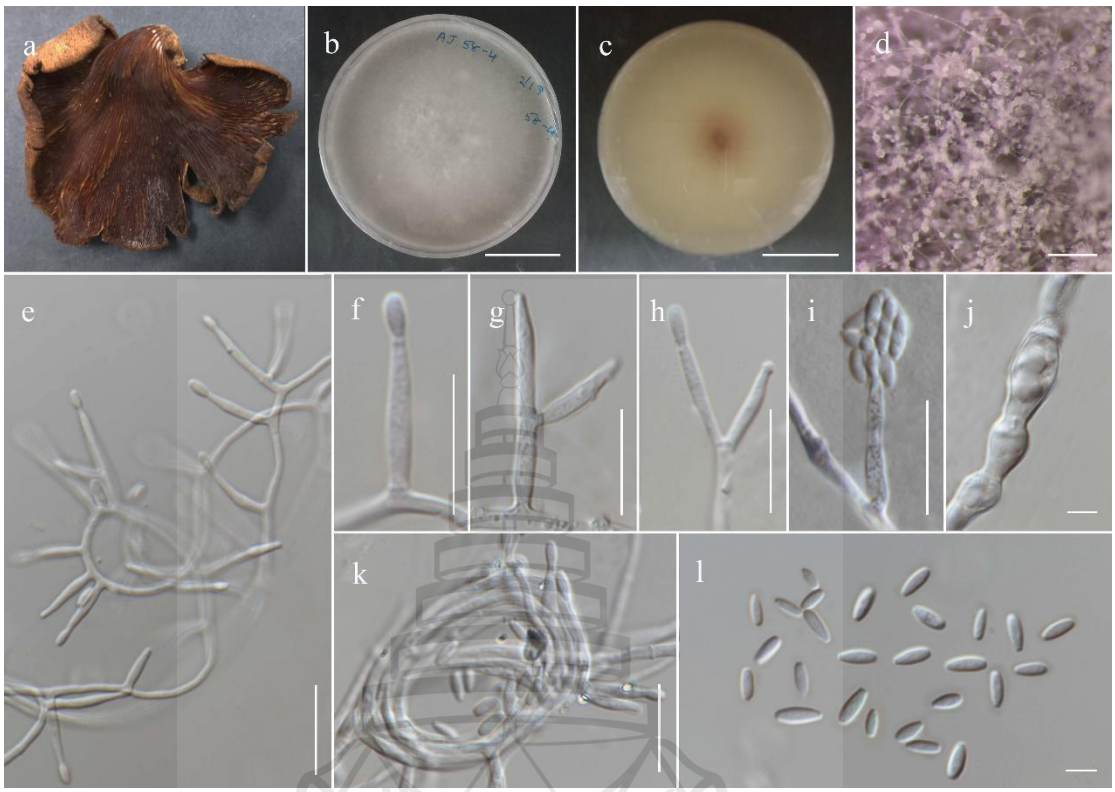


Figure 3.10 *Fusarium verticillioides* (AJ 58-4)

Figure 3.10, a. Host (*Lentinus* sp.). b, c. Colony on PDA. d. Sporulation on CLA. e–i. Phialides and conidial attachments. j. Swollen cell in the mycelium. k. Hyphal coil. l. Conidia. Scale bars: b, c = 30 mm, d = 250 µm, k = 35 µm, e = 20 µm, f–i = 15 µm, j, l = 5 µm.

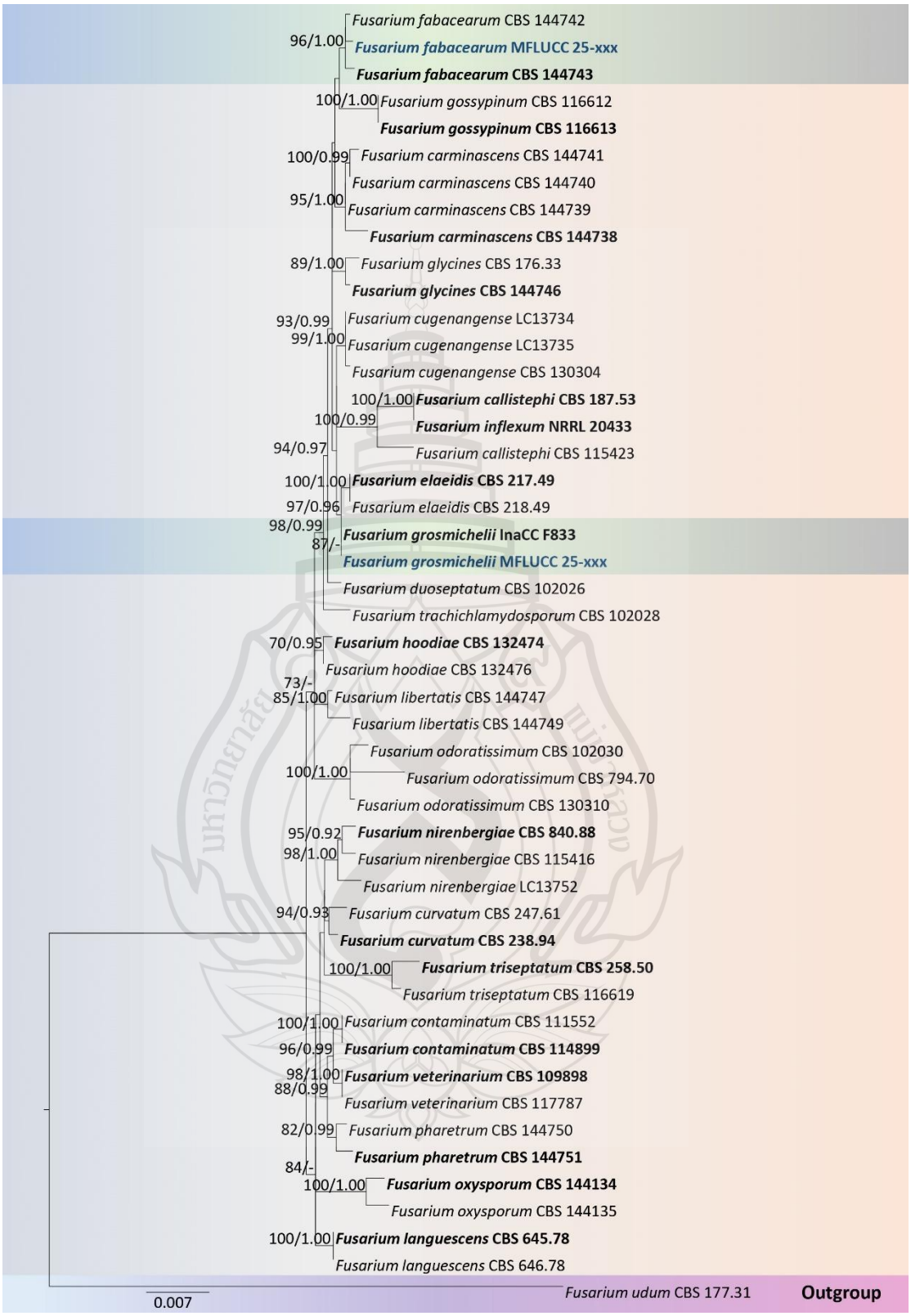


Figure 3.11 Phylogenetic tree generated by ML analysis of combined *tef-1α*, *rpb2*, and *tub2* sequence data of *Fusarium oxysporum* species complex (FOSC)

Figure 3.11, A total of 48 strains were included in the analyses. The tree is rooted with *Fusarium udum* (CBS 177.31). The best scoring ML tree with an optimal log-likelihood value of −4820.403 is presented. The matrix had 224 distinct alignment patterns, with 2.86% of undetermined characters or gaps. Bootstrap support values for ML ≥ 70% and BYPP ≥ 0.90 values for BI (BS/BYPP) are shown respectively near the nodes. Type (holotype/ex-type/isotype/paratype) strains are in bold. The strains reported in this study are in blue bold.

Fusarium fabacearum L. Lombard, Crous & Lampr., Persoonia 43: 24 (2019). Figure 3.12

Index Fungorum number: IF 826839

Fungicolous on a fruiting body of *Scleroderma* sp. Sexual morph: not observed. Asexual morph: white mycelium on a fruiting body of *Scleroderma* sp. On CLA, hyphomycetous, *Conidiophores* 1–2.5 μm ($\bar{x}$ = 2 μm, n = 20) wide, arising from the aerial mycelium, unbranched or sparingly branched, bearing terminal or intercalary monophialides, often reduced to single phialides. *Aerial phialides* 10–15 × 2–3.5 μm ($\bar{x}$ = 11.5 × 2.5 μm, n = 20), subulate to subcylindrical, smooth- and thin-walled, periclinal thickening inconspicuous or absent. *Aerial conidia* 5–9 × 1.5–3 μm ($\bar{x}$ = 6 × 2 μm, n = 40), forming small false heads on the tips of the phialides, hyaline, ellipsoidal to falcate, smooth- and thin-walled, aseptate or septate conidia: *Chlamydospores* 5.5–12 μm ($\bar{x}$ = 9 μm, n = 20) in diameter, hyaline, globose to subglobose, terminal or intercalary. Sporodochia not observed.

Colony characters – on PDA at 25 °C, 45–50 mm in 7 days. Colony surface white to pale rose, floccose with abundant aerial mycelium, colony margins irregular. Reverse of the colony pale rose.

Material examined – Thailand, Chiang Mai: Mae Taeng, Pa Pae (19° 7' 7.2444" N, 98° 44' 2.1228" E), isolated from the mycelium growing on a fruiting body of *Scleroderma* sp., 10 July 2023, S.A.D Thakshila, DL 11.

Notes – Our isolate DL 11, clustered within *Fusarium fabacearum* (CBS 144742, CBS 144743) with 96% BS, and 1.00 BYPP (Figure 3.11). The morphological features of DL 11 match the original description and illustrations of *F. fabacearum* provided by Lombard et al. (2019), except for slight differences in the

dimensions of morphological structures. These variations are possible due to differences in the agar medium and cultural conditions used (Senanayake et al., 2020). Therefore, we confirmed that our isolate, DL 11, is phylogenetically and morphologically consistent with *F. fabacearum*.

Fusarium fabacearum was described by Lombard et al. (2019) from *Glycine max* and *Zea mays* in South Africa. Since then, it has been reported in several countries as a pathogen on various plant hosts (Farias et al., 2021; Erima et al., 2025; Soufiani et al., 2025; Yarmeeva et al., 2025). This species has been identified as causing wilt of *Syzygium malaccensis* (Farias et al., 2021) and Fusarium wilt of common bean in Brazil (de Carvalho Paulino et al., 2022), root rot of common bean in Uganda (Erima et al., 2025), predominantly infecting cassava tubers in Brazil (Ono et al., 2023), associated with yellowing and wilting of grass pea in Iran (Soufiani et al., 2025), and as a pathogen on tomato in Russia (Yarmeeva et al., 2025).

To date, there are no reports of *F. fabacearum* from Thailand or this species exhibiting a fungicolous lifestyle globally. This study is the first to report *F. fabacearum* in Thailand and as a fungicolous species on a fruiting body of *Scleroderma* species.

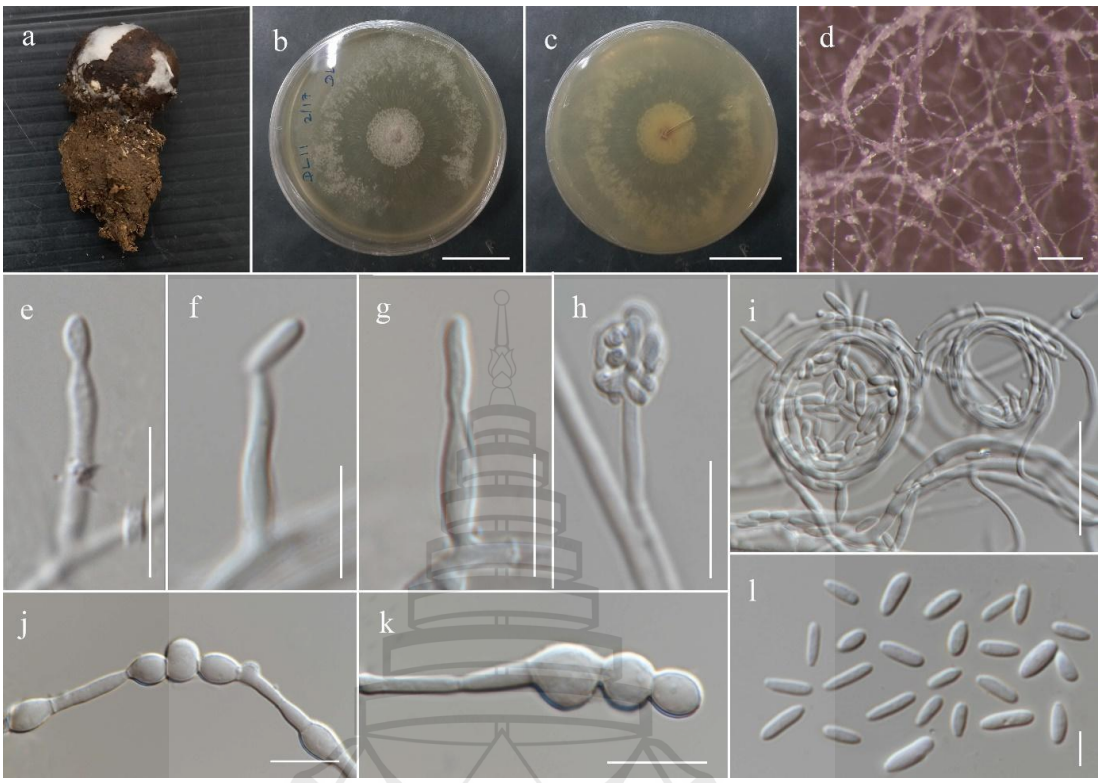


Figure 3.12 *Fusarium fabacearum* (DL 11)

Figure 3.12, a. Host (*Scleroderma* sp.). b, c. Colony on PDA. d. Sporulation on CLA. e–i. Aerial conidiophores with conidial attachments. j, k. Chlamydospores. l. Aerial conidia. Scale bars: b, c = 30 mm, d = 250 μm, i = 30 μm, e, h, j, k = 15 μm, f, g = 10 μm, l = 5 μm.

Fusarium grosmichelii Maryani, L. Lombard, Kema & Crous, Stud. Mycol. 92: 176 (2018)

Figure 3.13

Index Fungorum number: IF 826803

Fungicolous on a fruiting body of *Scleroderma* sp. Sexual morph: not observed. Asexual morph: white mycelial patches on a fruiting body of *Scleroderma* sp. On CLA, hyphomycetous, *Aerial conidiophores* 1.5–3 μm ($\bar{x}$ = 2 μm, n = 20) wide, unbranched or sparingly branched, bearing terminal or intercalarily phialides. *Conidiogenous cells* on aerial conidiophores: 8–24 × 2–4 μm ($\bar{x}$ = 14 × 3 μm, n = 30), often reduced to single phialides or as phialidic pegs, on sporodochia: mono- or polyphialidic on branched conidiophores, or formed directly from hyphae (lateral phialides). *Microconidia* 4–8 × 2–3 μm ($\bar{x}$ = 6 × 2.5 μm, n = 30), hyaline, ovoid to

ellipsoid, 0–1-septate, arranged in false heads on branched or lateral conidiophores carried on hyphae. *Macroconidia* 19–37 × 3–5 μm ($\overline{x}$ = 30 × 4 μm, n = 20), hyaline, formed on sporodochia and on aerial conidiophores, falcate, 3–5-septate, with apical cells papillate, basal cells foot-shaped. *Chlamydospores* 7–12 μm ($\overline{x}$ = 9 μm, n = 20) in diameter, hyaline, globose to subglobose, formed terminally or intercalarily, single or in clumps and rough-walled.

Colony characters – on PDA at 25 °C, 45–50 mm in 7 days. Colony surface pale rose to purple in the middle and white towards the margin. Colony surface dry, cottony white with filamentous margin. Aerial mycelium abundant and cottony.

Material examined – THAILAND, CHIANG MAI: Mae Taeng, Pa Pae (19° 7' 7.2444" N, 98° 44' 2.1228" E), isolated from the mycelium growing on a fruiting body of *Scleroderma* sp., 06 July 2021, A.J Gajanayake, MR 02.

Notes – Our isolate MR 02, clustered with the type strain of *Fusarium grosmichelii* (InaCC F833) with 87% BS (Figure 3.11). The morphological features of MR 02 match the original description and illustrations of *F. grosmichelii* provided by Maryani et al. (2019b), except for slight differences in the dimensions of morphological structures. These variations are possible due to differences in the agar medium and cultural conditions used (Senanayake et al., 2020). Therefore, we confirmed that our isolate MR 02, is phylogenetically and morphologically consistent with *F. grosmichelii*.

Fusarium grosmichelii was first described by Maryani et al. (2019b) as a pathogen on the banana variety Gros Michel in Indonesia. Since then, it has been reported in several countries, causing Fusarium wilt of banana in Malaysia (Ujat et al., 2021), sheath rot of rice in Indonesia (Pramunadipta et al., 2022), wilt of *Tibouchina seecandra* in China (Chen et al., 2023b), and cassava root rot in Brazil (da Silva et al., 2025).

To date, *F. grosmichelii* has not been reported from Thailand or documented with a fungicolous lifestyle. This study is the first to report *F. grosmichelii* in Thailand and as a fungicolous species on a fruiting body of *Scleroderma* species.

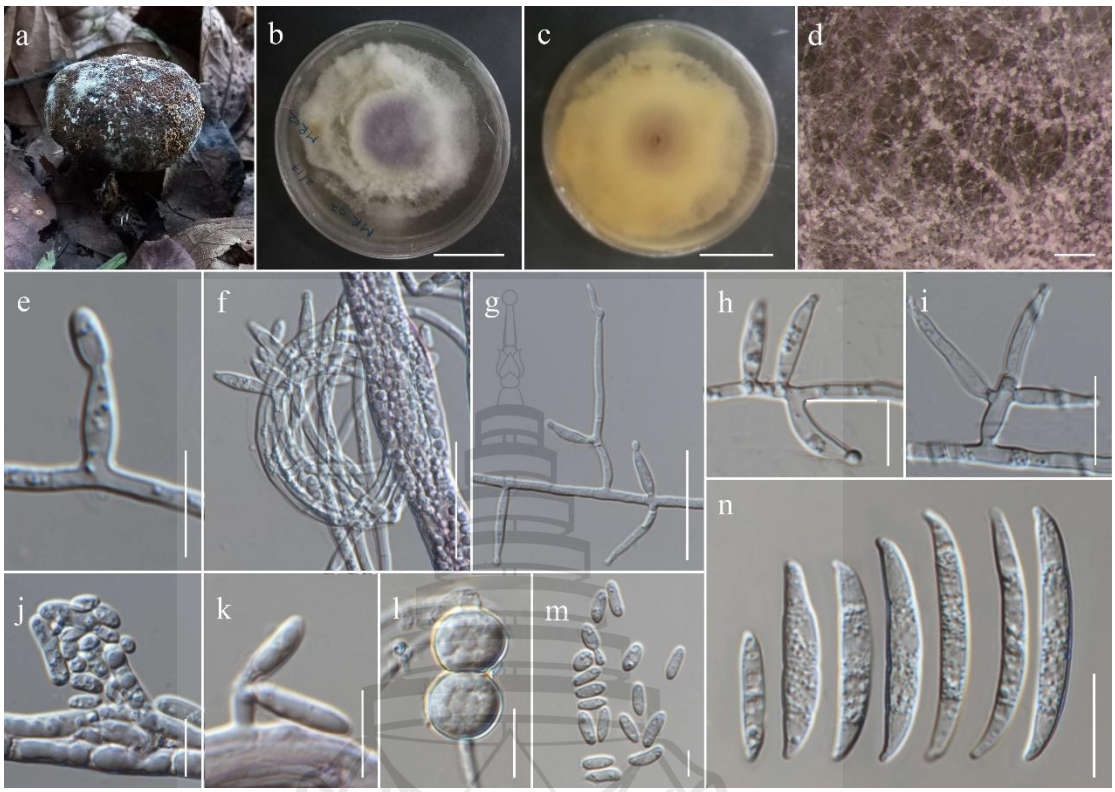


Figure 3.13 *Fusarium grosmichelii* (MR 02)

Figure 3.13, a. Host (*Scleroderma* sp.). b, c. Colony on PDA. d. Sporulation on CLA. e–i. Conidiogenous cells. j. False head on a lateral conidiophore. k. Phialidic peg. l. Chlamydospores. m. Microconidia. n. Macroconidia. Scale bars: b, c = 30 mm, d = 250 µm, g = 30 µm, f = 25 µm, i, n = 15 µm, e, h, j–l = 10 µm, m = 5 µm.

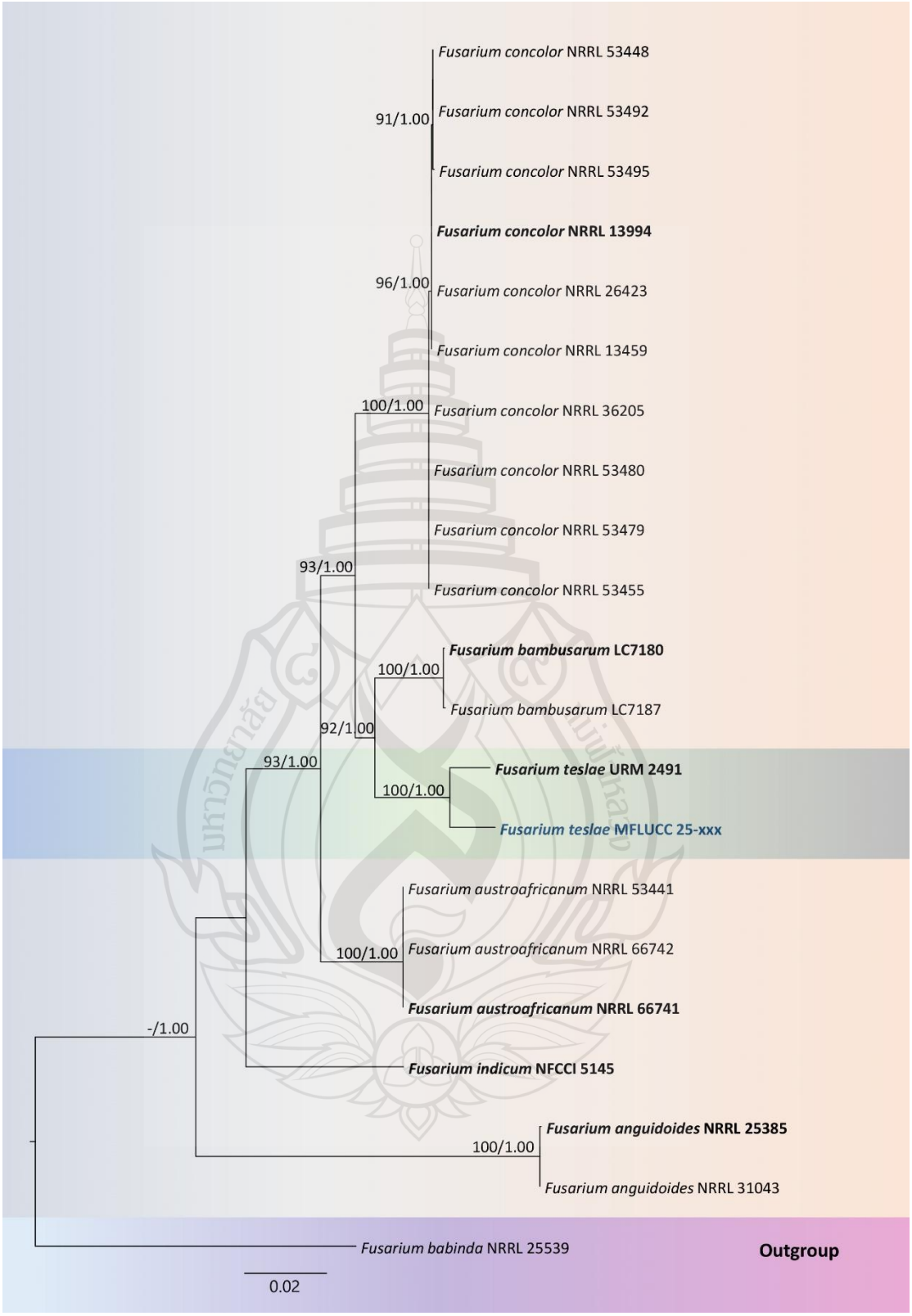


Figure 3.14 Phylogenetic tree generated by ML analysis of combined *cmdA, rpb1, rpb2,* and *tef-1α* sequence data of *Fusarium concolor* species complex (FCSC)

Figure 3.14, A total of 21 strains were included in the analyses. The tree is rooted with *Fusarium babinda* (NRRL 25539). The best scoring ML tree with an optimal log-likelihood value of −9506.049 is presented. The matrix had 449 distinct alignment patterns, with 20.00% of undetermined characters or gaps. Bootstrap support values for ML ≥ 70% and BYPP ≥ 0.90 values for BI (BS/BYPP) are shown respectively near the nodes. Type (holotype/ex-type/isotype/paratype) strains are in bold. The strains reported in this study are in blue bold.

Fusarium teslae A.C.S. Santos, S.K.B. Pedroso & P.V. Tiago, Mycol. Progr. 2: 4 (2025).

Figure 3.15

Index Fungorum number: IF 856892

Fungicolous on *Tricholoma* sp., Sexual morph: not observed. Asexual morph: white mycelium on the gills of the fruiting body. On PDA, hyphomycetous, *Aerial conidiophores* 1.5–2.5 μm ($\bar{x}$ = 2 μm, n = 20) wide, generally erect and simple, or sparingly sympodially branched. *Phialides* 10–28 × 1.5–3 μm ($\bar{x}$ = 18.5 × 2 μm, n = 20), terminal or lateral on aerial conidiophores, ampulliform, or subulate to sub-cylindrical form as monophialides, occasionally polyphialidic, with short and fared collarettes sometimes observed. *Microconidia* 5.5–12 × 1.5–3 μm ($\bar{x}$ = 9 × 2.5 μm, n = 30), formed on aerial conidiophores obovoid, oval to ellipsoidal, or allantoid, aseptate or rarely 1 septate. Chlamydospores elongated, slightly warty, hyaline, clusters and chains, terminal or intercalary. Sporodochia not observed.

Colony characters – on PDA at 25 °C, 60–65 mm in 7 days. Colony surface initially white, turning salmon with age, cottony, with dense aerial mycelium, margin entire to undulate. Reverse buff to honey.

Material examined – Thailand, Chiang Mai: Mae Taeng, Pa Pae (19° 7' 7.2444" N, 98° 44' 2.1228" E), covering the gills of the mushroom fruiting body, 7 July 2022, A.J. Gajanayake, MR 34.

Notes – Our isolate MR 34, clustered with the type strain of *Fusarium teslae* (URM 2491) with 100% BS, and 1.00 BYPP (Figure 3.14). The morphological features of MR 34 match the original description and illustrations of *F. teslae*

provided by da Silva Santos et al. (2025). Therefore, we confirmed that our isolate, MR 34, is phylogenetically and morphologically consistent with *F. teslae*.

Fusarium teslae was originally isolated from leaf litter in Brazil (da Silva Santos et al., 2025). This study represents the second global record of *F. teslae*, and the first report from Thailand. Additionally, this is the first documentation of *F. teslae* exhibiting a fungicolous lifestyle.

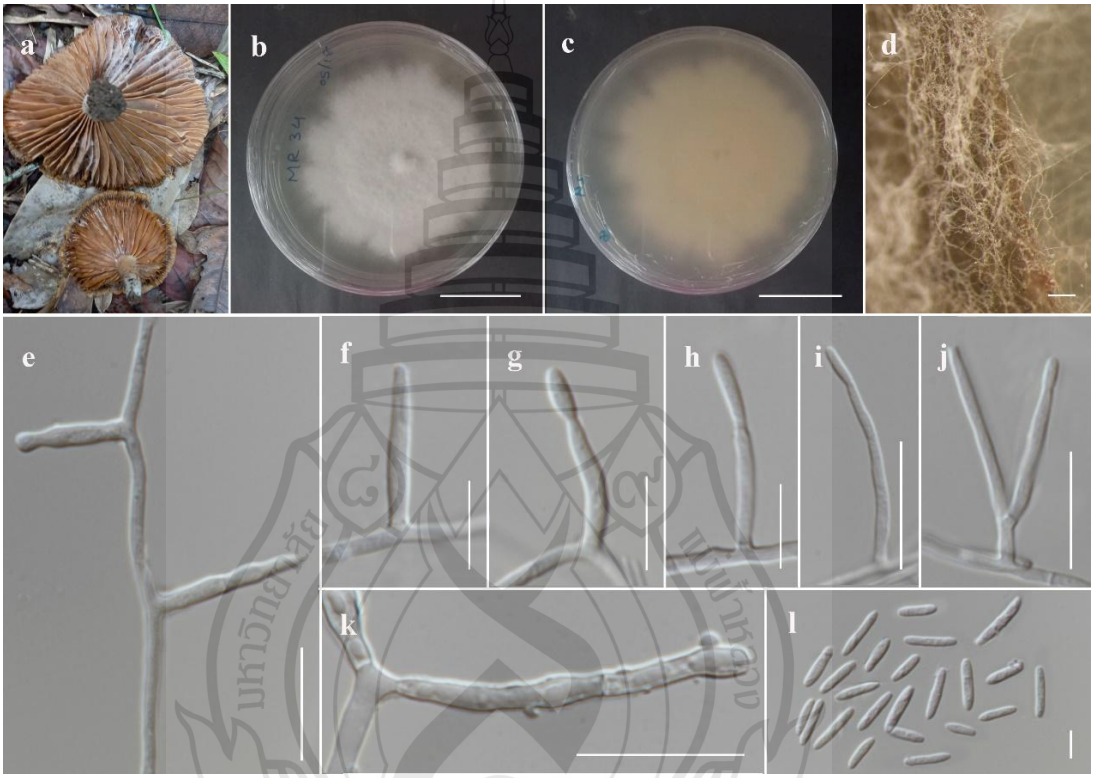


Figure 3.15 *Fusarium teslae* (MR 34)

Figure 3.15, a. Host. b, c. Colony on PDA. d. Mycelial cords on carnation leaf. e–j. Phialides and conidial attachments. k. Chlamydospore formation. l. Microconidia. Scale bars: b, c = 30 mm, d = 250 µm, i, k = 20 µm, e, j = 15 µm, f–h = 10 µm, l = 5 µm.

3.2.4 *Hypomyces* (Fr.) Tul. & C. Tul., Annls Sci. Nat., Bot., sér. 4 13: 11 (1860)

Hypomyces was originally described as a subgenus under *Hypocrea* Fr. Fries (1825), and it was later elevated to generic rank by Tulasne and Tulasne (1860). The designated type species is *Hypomyces lactifluorum* (Schwein.) Tul. & C. Tul. (Index

Fungorum, 2025). To date, 126 species are listed under *Hypomyces* in Species Fungorum (2025) and it is classified within *Hypocreaceae* (Hyde et al., 2024a).

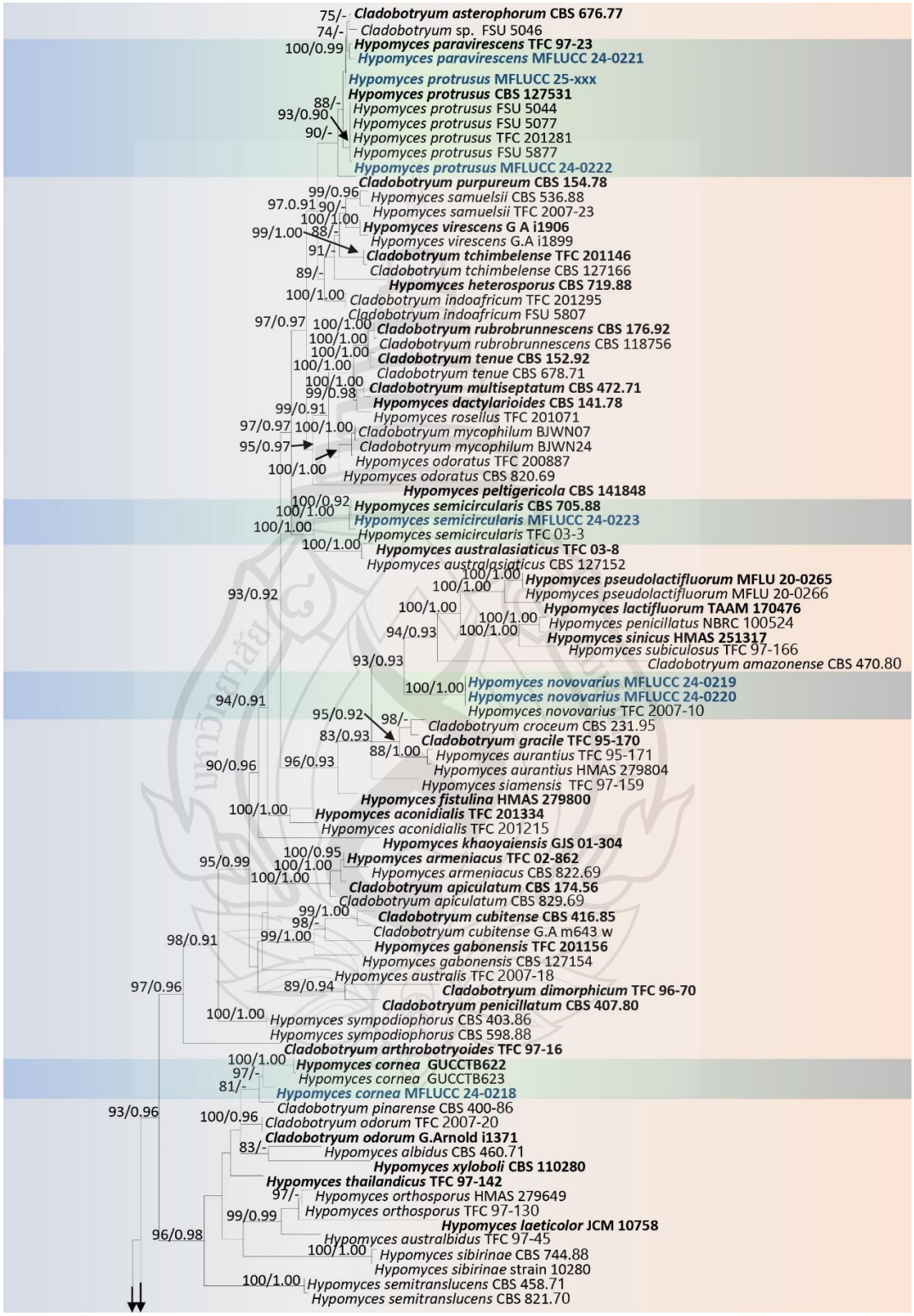


Figure 3.16 Phylogenetic tree generated by ML analysis of combined ITS, LSU, *tef-1α*, and *rpb2* sequence data of *Hypomyces* and related genera

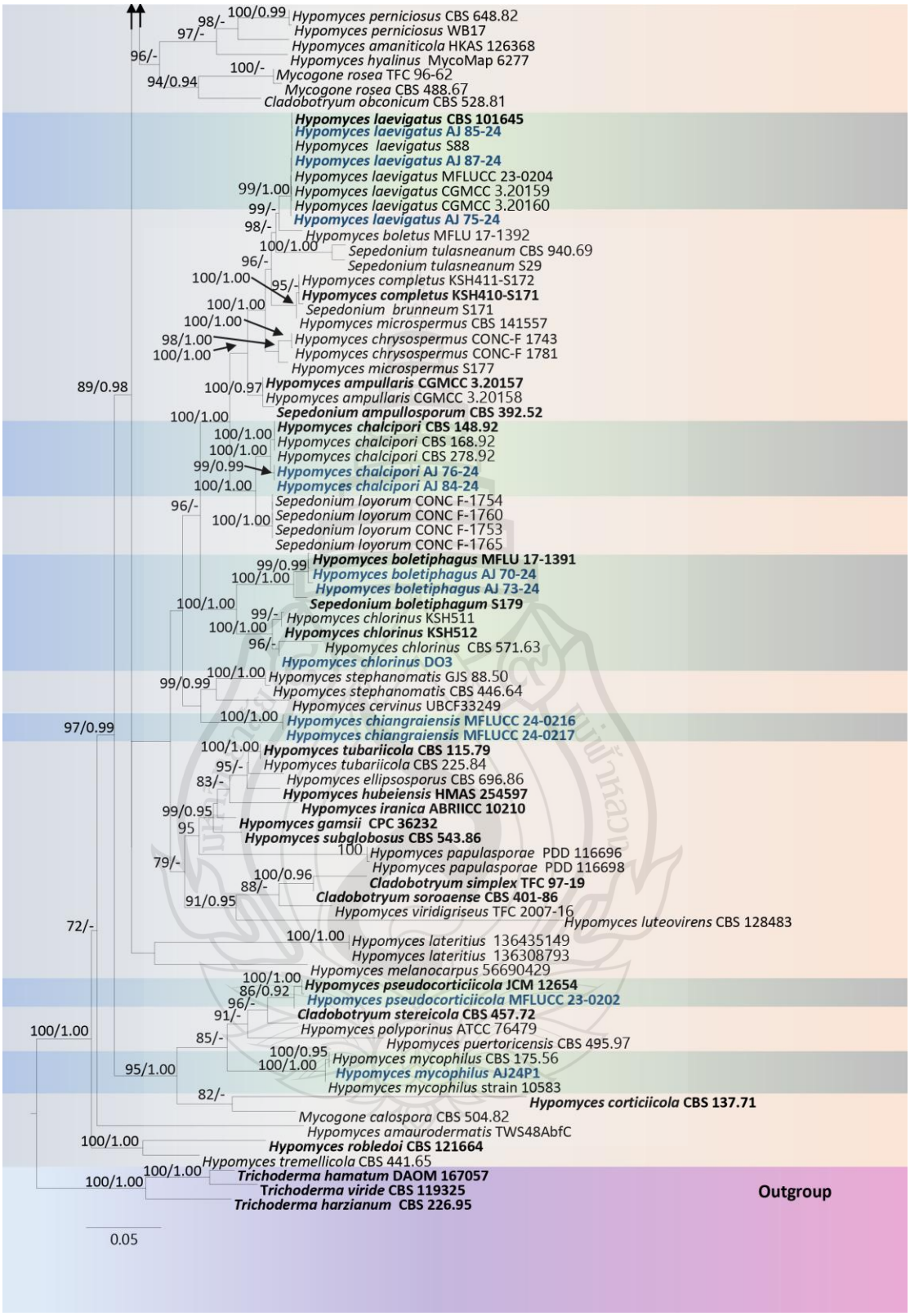


Figure 3.16 (continued)

Figure 3.16, A total of 170 strains were included in the analyses. The tree is rooted with *Trichoderma harzianum* (CBS 226.95), *T. hamatum* (DAOM 167057) and *T. viride* (CBS 119325). The best scoring ML tree with an optimal log-likelihood value of − 36071.578 is presented. The matrix had 1562 distinct alignment patterns, with 43.35% of undetermined characters or gaps. Bootstrap support values for ML ≥ 70% and BYPP ≥ 0.90 values for BI (BS/BYPP) are shown respectively near the nodes. Type (holotype/ex-type/isotype/paratype) strains are in bold. The strains reported in this study are in blue bold.

Hypomyces chiangraiensis Gajanayake, Jayaward. and K.D. Hyde, sp. *nov*. Figure 3.17

Index Fungorum number: IF 854920

Etymology – The epithet refers to the location "Chiang Rai" where the fungus was collected.

Diagnosis – Fungicolous on *Mycena* species. Characterized with conidiophores which are hyaline, septate, straight or flexuous, and repeatedly branching, either in a verticillate or irregular pattern. The conidiogenous cells arranged 2–5 in a verticil, elongated cylindrical to subulate, and monoblastic. Conidia on PDA measures 11.5–20 ×6–10 μm, hyaline, aseptate ellipsoidal, with some slightly obovoid, and mostly attenuated towards the base. Chlamydospores are hyaline, variable in size and shape, arranged in clusters.

Typification – Thailand, Chiang Rai, Muang, Nang Lae (20° 2' 24.9216"N, 99° 54' 2.1996"E), isolated from the sporulating mycelium growing on a fruiting body of *Mycena* sp., 10 August 2023, Gajanayake A.J, BO1a (Holotype MFLU 24-0220). Ex-holotype culture MFLUCC 24-0216.

GenBank numbers – ITS = PP472910; LSU = PP471503, *rpb*2 = PP982901; *tef1α* = PP982897.

Fungicolous on fruiting bodies of *Mycena* sp. Sexual morph: not observed. Asexual morph: white mycelium on host fruiting body. On PDA, hyphomycetous, *mycelium* hyaline, septate, branched. *Conidiophores* 3–9 μm ($\bar{x}$ = 6 μm, n = 50) wide, septate, straight or flexuous, hyaline, repeatedly branching, either in a verticillate or irregular pattern, producing side branches from an existing verticil, with additional branching at the apex, a verticil holding 2-5 conidiogenous cells. *Conidiogenous cells*

21–50 µm ($\bar{x}$ = 37 µm, n = 50) long, 3–6.5 µm ($\bar{x}$ = 5 µm, n = 50) wide near the base, attenuating to 0.8–2 µm ($\bar{x}$ = 1.5 µm, n = 50) at the apex, 2–5 in a verticil, elongated cylindrical to subulate, monoblastic. *Conidia* 11.5–20 × 6–10 µm ($\bar{x}$ = 16 × 8 µm, n = 60), hyaline, ellipsoidal, some slightly obovoid, mostly attenuated towards the base, aseptate. *Chlamydospores* 18–35 × 5–10 µm ($\bar{x}$ = 26.5 × 7.5 µm, n = 30), hyaline, variable in size and shape, arranged in clusters.

Colony characters – on PDA at 25 °C, 50–55 mm after 7 days. The aerial mycelium is moderate, cottony.

Additional material examined – Thailand, Chiang Rai, Muang, Nang Lae (20° 2' 24.9216"N, 99° 54' 2.1996"E), around 3.5 m away from the location where the holotype was collected, isolated from sporulating mycelium growing on a fruiting body of *Mycena* sp., 10 August 2023, Gajanayake A.J, BO1b (Paratype MFLU 24-0229). Ex-paratype culture MFLUCC 24-0217.

GenBank numbers – ITS = PP472911; LSU = PP471504; *rpb*2 = PP982902; *tef1α* = PP982898.

Notes – According to the Figure 3.16, *Hypomyces chiangraiensis* (MFLUCC 24-0216 and MFLUCC 24-0217) is phylogenetically closer to *H. cervinus* (UBC F33249). The genetic distance between *H. chiangraiensis* and *H. cervinus* (UBC F33249) in the trimmed ITS region (509 bp) is 8.49%. Morphologically, *H. chiangraiensis* is closer to *H. australasiaticus* K. Põldmaa. *Hypomyces australasiaticus* has so far been reported on polypores, such as, *Antrodiella* sp., *Earliella* sp., and *Microporus* sp. (Põldmaa, 2011). The morphological comparison of *H. chiangraiensis* with *H. australasiaticus* is shown in Table 3.1. Therefore, based on these morphological and phylogenetic evidence we introduce *H. chiangraiensis* as a novel species.

Table 3.1 The morphological comparison of *Hypomyces chiangraiensis* with *H. australasiaticus*

Character	***Hypomyces chiangraiensis***	***H. australasiaticus***
Conidiophores	Straight or flexuous, repeatedly branching, either in a verticillate or irregular pattern, hyaline, septate, 3–9 μm wide	Undifferentiated from aerial hyphae, ascending to suberect, hyaline, thin-walled, forming numerous short lateral branches, 2.5–3 μm wide
Conidia	Hyaline, aseptate ellipsoidal, with some slightly obovoid, mostly attenuated towards the base 11.5–20 × 6–10 μm L/W = 1.96	Hyaline, 1–3-septate, oblong clavate, clavate, ellipsoidal or cylindrical, occasionally long fusiform, mostly equilateral, straight or curved in lower half 15–35 × 3.5–6.5 μm, L/W = 3.7–5.1
Reference	This study	Põldmaa (2011)

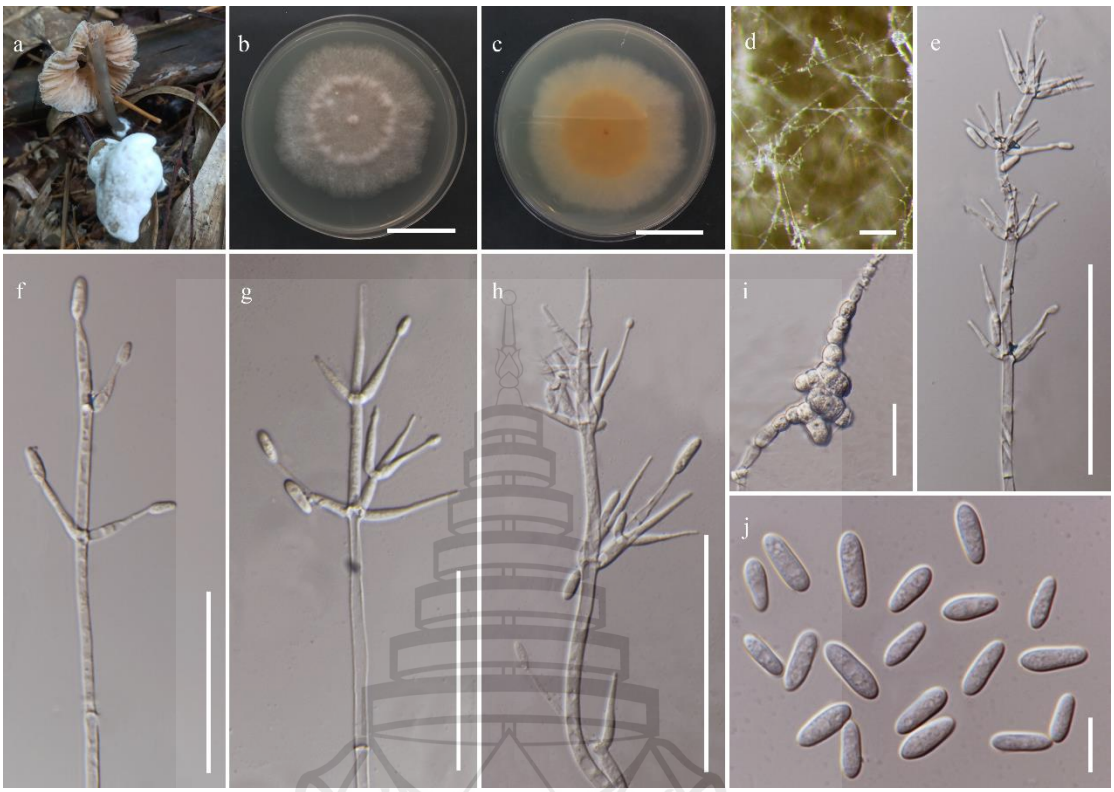


Figure 3.17 *Hypomyces chiangraiensis* (MFLU 24-0220)

Figure 3.17, a. Host (Mycena sp.). b, c. Colony on PDA. d. Sporulation on PDA. e–h. Conidiophores with conidiogenous cells and conidial attachments. i. Chlamydospores. j. Conidia. Scale bars: b, c = 30 mm, d = 100 µm, e, h = 80 µm, f, g = 50 µm, i = 30 µm, j = 10 µm.

Hypomyces chalcipori (Helfer) Gajanayake., Jayaward. & K.D. Hyde, comb. *nov*.

Figure 3.18

≡ *Sepedonium chalcipori* Helfer, Pilze auf Pilzfruchtkörpern. Untersuchungen zur Ökologie, Systematik und Chemie. Libri Botanici (Eching) 1: 73 (1991)

Fungicolous on a bolete fruiting body. Sexual morph: not observed. Asexual morph: white to yellow sporulated mycelial patch on a bolete fruiting body. On PDA, hyphomycetous, *Conidiophores* 3–4 µm ($\overline{x}$ = 3.5 µm, n = 20) wide, hyaline, septate, solitary or branched forming verticills of 2-4 phialides. *Phialides* 15–66 × 1.5–3 µm ($\overline{x}$ = 40 × 2 µm, n = 20), apex 0.8–1.2 µm. *Phialoconidia* 5–15 × 2–5.5 µm ($\overline{x}$ = 9 × 3.5 µm, n = 40), variable in size, oval to ellipsoidal, spindle-shaped or cylindrical,

slightly warty. *Aleurioconidia* 8–14.5 µm ($\bar{x}$ = 12 µm, n = 30) diameter, globose, bright yellow, tubercles up to 2.5 µm long, cylindrical, with apical depression, densely arranged.

Colony characters – on PDA at 25 °C, 25–28 mm in 7 days. Colony surface initially white with abundant aerial mycelium and later starts turning yellow from the centre towards margins with the formation of aleurioconidia.

Material examined – Thailand, Chiang Rai: Mae Salong Nok (20° 9' 59.4216"N, 99° 37' 34.7016"E), isolated from the mycelium growing on a bolete fruiting body, 12 June 2024, A.J Gajanayake, AJ 76-24 and AJ 84-24.

Notes – Our isolates MFLUCC AJ 76-24 and AJ 84-24 clustered as a sister lineage to *Sepedonium chalcipori* (CBS 148.92, CBS 168.92, CBS 278.92) with 100% BS and 1.00 BYPP within the clade comprising *S. chalcipori* and *S. loyorum* (Figure 3.16). Pairwise comparison of the trimmed ITS sequences (563 bp) revealed a genetic distance of 0.8% between our isolates (AJ 76-24 and AJ 84-24) and the type strain of *S. chalcipori* (CBS 148.92), while a 2.9% genetic distance was observed when compared to *S. loyorum* (CONC-F1754). No genetic distance (0%) was detected between our isolates and *S. chalcipori* (CBS 148.92) in the LSU region (838 bp). Sequence data for *tef* and *rpb2* are available for our isolates, but corresponding sequences for *S. chalcipori* are lacking, preventing further comparison at these loci. Morphologically, our isolates are consistent with the description of *S. chalcipori* provided by Sahr et al. (1999), with slight variations in the dimensions of morphological structures. These variations are possible due to differences in the agar medium and cultural conditions used (Senanayake et al., 2020). A comparative summary of morphological features of *S. chalcipori* as described by Sahr et al. (1999) and this study is provided in Table 3.2. Therefore, based on both phylogenetic and morphological evidence, we identify our isolates as *Sepedonium chalcipori*.

Sepedonium chalcipori was originally described by Helfer (1991) from *Chalciporus* sp. in Germany. Subsequently, Sahr et al. (1999) reported this species from *Chalciporus piperatus* in Germany and *Chalciporus* sp. in New Zealand. This study represents the first record of this species from Thailand, isolated from a bolete fruiting body.

According to the International Code of Nomenclature for Algae, Fungi, and Plants (ICN), the generic name *Hypomyces* has been proposed for conservation over earlier asexually typified genera: *Cladobotryum*, *Mycogone*, *Sepedonium*, and *Stephanoma* (Rossman et al., 2013). Given the absence of a sexual morph name for *Sepedonium chalcipori*, and following the current nomenclatural framework (("Nom. rej., but see Arts 14.6, Ex. 5 and 14.7" as mentioned in Index Fungorum (2025)), we propose the new combination *Hypomyces chalcipori* for this species.

Table 3.2 The morphological comparison of the species as described by Sahr et al. (1999) and this study

Morphological character	***Sepedonium chalcipori* (Sahr et al., 1999)**	***Hypomyces chalcipori* comb. *nov* (This study)**
Conidiophores and phialides	Conidiophores hyaline, septate, with verticills of 3-8 phialides, these 20–50 × 2–3 μm, apex 1 μm	Conidiophores hyaline, septate, solitary or branched forming verticills of 2-4 phialides, 3–4 μm ($\bar{x}$ = 3.5 μm, n = 20) wide, Phialides 15–66 × 1.5–3 μm ($\bar{x}$ = 40 × 2 μm, n = 20), apex 0.8–1.2 μm,
Phialoconidia	Oval, spindle-shaped or cylindrical, 8–12 × 3–7 μm, L/W ratio = 2	Variable in size, oval to ellipsoidal, spindle-shaped or cylindrical, slightly warty, 5–15 × 2–5.5 μm ($\bar{x}$ = 9 × 3.5 μm, n = 40), L/W ratio = 2.6
Aleurioconidia	Globose, bright yellow, 13–20 μm diameter, tubercles with reticulate ornament, up to 3 μm long, barrel-shaped, with apical depression	Globose, bright yellow, 14.5 μm ($\bar{x}$ = 12 μm, n = 30) diameter, tubercles up to 2.5 μm long, cylindrical, with apical depression

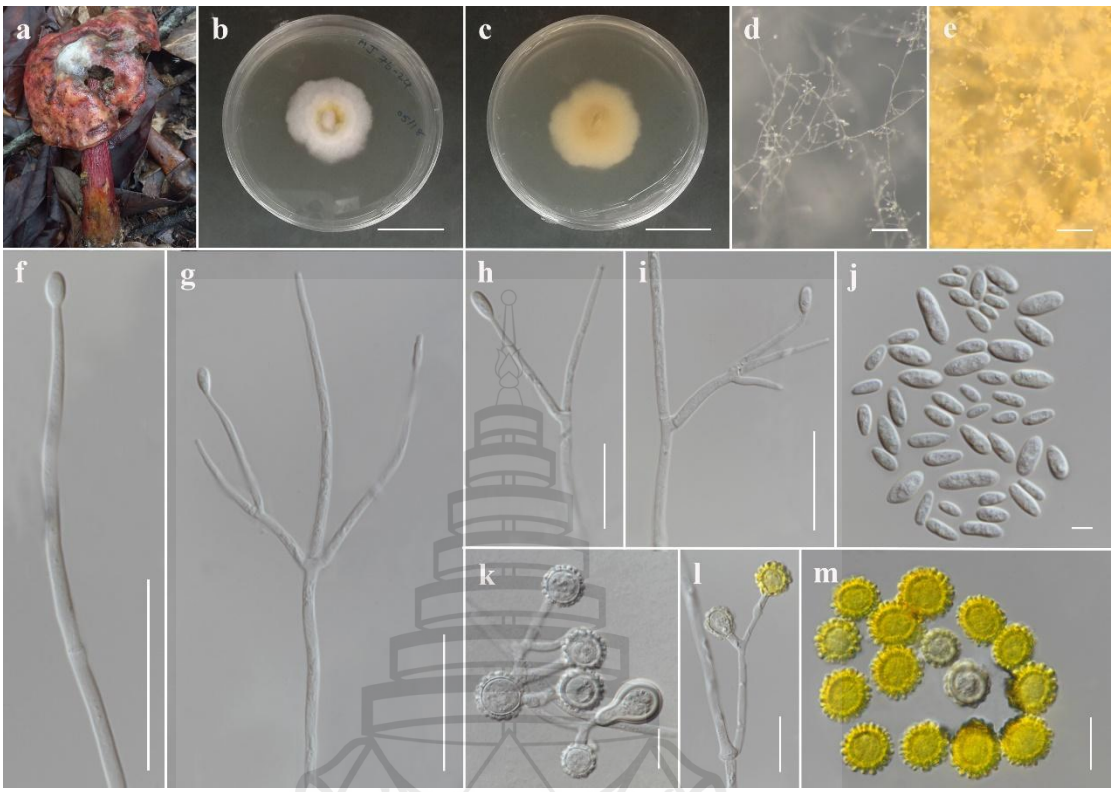


Figure 3.18 *Hypomyces chalcipori* (AJ 76-24)

Figure 3.18, a. Host (Bolete). b, c. Colony on PDA. d, e. Sporulation on PDA. f–i. Conidial attachments. j. Phialoconidia. k–m. Aleurioconidia. Scale bars: b, c = 30 mm, d, e = 250 µm, i = 40 µm, f, g = 35 µm, h, l = 20 µm, k, m = 15 µm, j = 5 µm.

Hypomyces laevigatus (Sahr & Ammer) Gajanayake., Jayaward. & K.D. Hyde, comb. *nov*.

Figure 3.19

≡ *Sepedonium laevigatum* Sahr & Ammer, Mycologia 91(6): 939 (1999)

≡ *Hypomyces sichuanensis* Jing Z. Sun, in Gu, Fu, Wang & Sun, Phytotaxa 516(1): 37 (2021)

Fungicolous on a bolete fruiting body. Sexual morph: not observed. Asexual morph: white to yellow mycelial patches on the fruiting body. On CMA, hyphomycetous, *Conidiophores* 2–4 µm ($\bar{x}$ = 3 µm, n = 20) wide, hyaline, septate, straight or flexuous, with verticills of 1-2 phialides or solitary. *Phialides* 70–210 × 2–3 µm ($\bar{x}$ = 140 × 2.5 µm, n = 20), comparatively long, reducing the width to 1–1.5 µm at the terminal ends. *Phialoconidia* 6–20.5 × 2.5–6.5 µm ($\bar{x}$ = 13.5 × 4 µm, n = 45),

hyaline, thin-walled, cylindrical, spindle shaped or cuneiform, highly variable in size. *Aleurioconidia* 10–14.5 μm ($\bar{x}$ = 12.5 μm, n = 30) diameter, on lateral hyphae, initially hyaline and later becoming yellow, thick-walled, globose, warted, tubercles 1–1.5 μm long, cylindrical, often with apical depression, densely arranged in the mycelium.

Colony characters – on PDA at 25 °C, 25–30 mm in 7 days. Colony surface initially white to pale rose with abundant aerial mycelium and later grows dense with an irregular margin. Reverse of the colony pale rose at the centre and faded to white towards the margin.

Materials examined – Thailand, Chiang Rai: Mae Salong Nok (20° 9' 59.4216"N, 99° 37' 34.7016"E), isolated from the sporulated mycelium growing on a bolete fruiting body, 12 June 2024, A.J Gajanayake, AJ 87-24, *ibid*. AJ 75-24 and AJ 85-24.

Notes– Our isolates AJ 75-24, AJ 85-24, and AJ 87-24 clustered with *Sepedonium laevigatum* (CBS 101645, S88) and *Hypomyces sichuanensis* (CGMCC 3.20159, CGMCC 3.20160, MFLUCC 23-0204) with 99% BS and 1.00 BYPP (Figure 3.16). Morphologically, these isolates match with the original descriptions and illustrations of *Sepedonium laevigatum* and *Hypomyces sichuanensis* provided by Sahr et al. (1999) and Gu et al. (2021), except for slight dimensional differences in the morphological structures. These variations are possible due to differences in the agar medium and cultural conditions used (Senanayake et al., 2020). A comparative summary of morphological features of *Hypomyces laevigatus* as described by Sahr et al. (1999), Gu et al. (2021), and this study is provided in Table 3.3. Therefore, based on both phylogenetic and morphological evidence, we identify our isolates as conspecific with *Sepedonium laevigatum* and *Hypomyces sichuanensis*.

Sepedonium laevigatum was described by Sahr et al. (1999) as a fungicolous species found on *Suillus punctipes* in the USA. Additional specimens were reported from Germany and New Zealand. The known host range includes several *Boletales*, such as *Leccinum* spp., *Boletus* spp., *Gomphidius roseus*, and *Gyrodon lividus* (Sahr et al., 1999). Subsequently, this species has been recorded from wild mushrooms in South Korea (Seung-Yoon, 2022), on *Rhizopogon roseolus* and *Suillus luteus* in Chile

(Binimelis-Salazar et al., 2021), and on *Octaviania asterosperma* in Poland (Mleczko et al., 2010).

Hypomyces sichuanensis was introduced by Gu et al., (2021), based on material collected from a *Boletus* sp. basidiocarp in China. It was later reported from a decaying bolete fruiting body in Thailand (Gajanayake et al., 2023a).

According to the International Code of Nomenclature for Algae, Fungi, and Plants (ICN), the generic name *Hypomyces* has been proposed for protection over earlier typified asexual genera *Cladobotryum*, *Mycogone*, *Sepedonium*, and *Stephanoma* (Rossman et al., 2013). Given the absence of a sexual morph name for *Sepedonium laevigatum* and in line with this nomenclatural framework ("Nom. rej., but see Arts 14.6, Ex. 5 and 14.7" as mentioned in Index Fungorum (2025)), we propose the new combination *Hypomyces laevigatus* for this species for nomenclatural reasons. Furthermore, based on both morphological comparisons and phylogenetic evidence, we synonymize *H. sichuanensis* under *H. laevigatus*.

Table 3.3 The morphological comparison of *Hypomyces laevigatus* as described by Sahr et al. (1999), Gu et al. (2021), and this study

Morphological character	***Sepedonium laevigatum*** **(Sahr et al., 1999)**	***Hypomyces sichuanensis*** **(Gu et al., 2021)**	***Hypomyces laevigatus*** **comb. *nov*** **(This study)**
Conidiophores and phialides	hyaline, septate, with verticills of 1–2 phialides, these very long, 120–250 × 3–4 µm	hyaline, aseptate, with verticills of 2– 3 phialides, or solitary, 65–180 × 2–3 µm, apex 1.0–2.0 µm	hyaline, septate, straight or flexuous, 2–4 µm wide, with verticills of 1-2 phialides, or solitary. Phialides comparatively very long, 70–210 × 2–3 µm, reducing the width to 1–1.5 µm at the terminal ends
Phialoconidia	colourless, thin-walled, cylindrical, spindle- shaped or cuneiform, very variable in size, 8–24 × 3.5–9.5 µm, L/W rstio = 2.5	hyaline, thin–walled, ellipsoid to clavate, sometimes cuneiform aseptate, 11.5–18 × 3–6 µm, L/W rstio = 3.3	hyaline, thin-walled, cylindrical, spindle-shaped or cuneiform, highly variable in size, 6–20.5 × 2.5–6.5 µm, L/W rstio = 2.9
Aleurioconidia	forms on lateral hyphae, colourless in the beginning, then becoming yellow, thick- walled, globose, warted, (13–) 14–19 (–22) µm diam, tubercles cylindrical, 1–1.5 µm long	golden yellow, subglobose to globose, thick-walled, aseptate, tuberculate, 12.5 × 12 µm, tubercles, densely arranged, cylindrical, 1–2 µm	forms on lateral hyphae, initially hyaline and later becoming yellow, thick-walled, globose, warted, 12.5 µm diameter, tubercles 1–1.5 µm long, cylindrical

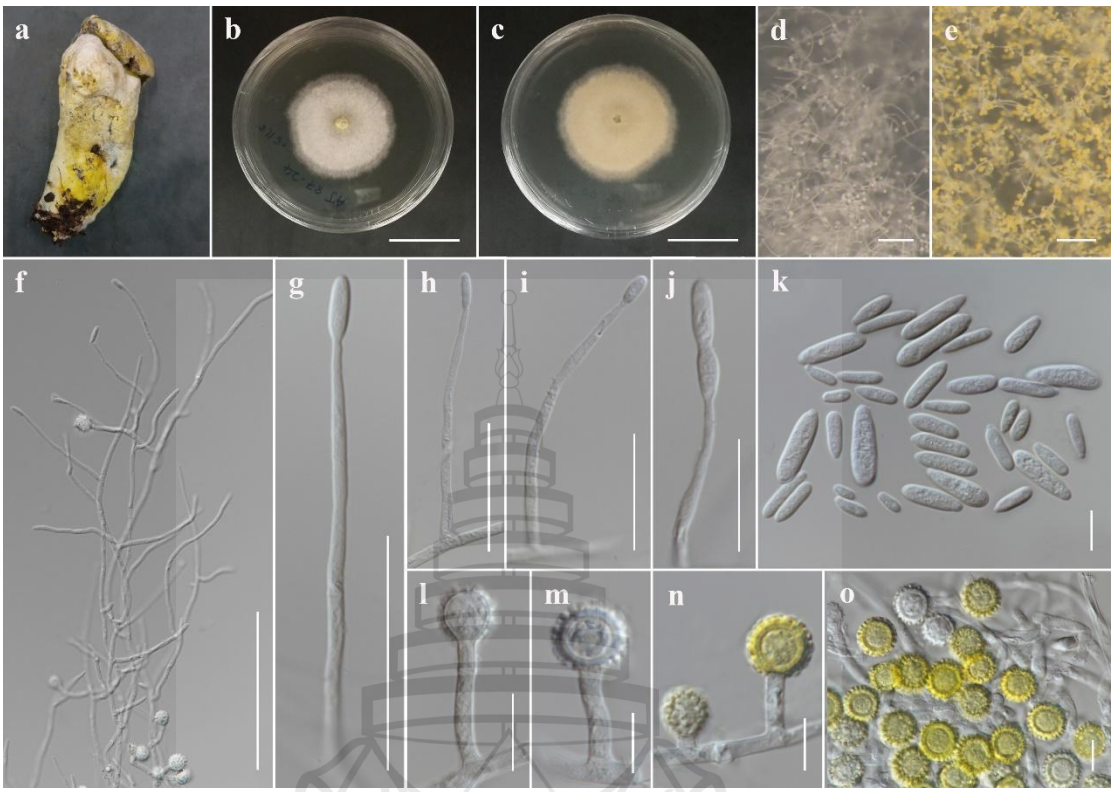


Figure 3.19 *Hypomyces laevigatus* (AJ 87-24)

Figure 3.19, a. Host (*Auricularia* sp.). b, c. Colony on PDA. d, e. Sporulation on CMA. f–j. Conidiophores with conidial attachments. k. Phialoconidia. l–n. Aleurioconidial attachments. o. Aleurioconidia. Scale bars: b, c = 30 mm, d, e = 500 µm, f = 120 µm, g = 45 µm, h = 40 µm, i = 30 µm, j = 20 µm, k–o = 10 µm.

Hypomyces novovarius (K. Põldmaa) Gajanayake., Jayaward. and K.D. Hyde, comb. *nov.*

Figure 3.20

Index Fungorum number: IF 854922

≡ *Cladobotryum novovarium* K. Põldmaa, Mycotaxon 102: 186 (2007)

Fungicolous on fruiting bodies of *Schizophyllum* sp. Sexual morph: not observed. Asexual morph: white powdery mycelium and yellow discolouration on host mushroom tissue. On PDA, hyphomycetous, *mycelium* hyaline, septate, branched. *Conidiophores* 3–9 µm ($\bar{x}$ = 6 µm, n = 50) wide, straight or flexuous, profusely branched, septate, main axis produces side branches, irregular or verticillate, main axis or the verticillate branches produces conidiogenous cells at the terminal. *Conidiogenous cells* 8–30 µm ($\bar{x}$ = 16 µm, n = 50) long, 3–6 µm ($\bar{x}$ = 4.5

μm, n = 50) wide near the base, attenuating to 0.8–2.5 μm ($\overline{x}$ = 1.5 μm, n = 50) at the apex with periclinal thickening, usually held by 3-4 verticils, occasionally the side branches may produce 1-2 verticils, subulate, aseptate or rarely septate. *Conidia* 9–20 × 5–9 μm ($\overline{x}$ = 13 × 7 μm, n = 60), hyaline, broadly ellipsoidal or subglobose to clavate, 1–2 septate, constricted at septa. *Chlamydospores* not observed.

Colony characters – on PDA at 25 °C, 60–70 mm in 5 days. The aerial mycelium is scarce to moderate, exhibiting even margins.

Material examined – Thailand, Chiang Rai, Muang, Tha Sai (19° 49' 26.0292"N, 99° 52' 18.966"E), isolated from the mycelium growing on fruiting bodies of *Schizophyllum* sp., 20 September 2023, Gajanayake A.J, AJB 31 (inactive dry culture MFLU 24-0222), living cultures MFLUCC 24-0219 and MFLUCC 24-0220.

GenBank numbers – MFLUCC 24-0219: ITS = PP472904, LSU = PP471497; *rpb2* = PQ037167; *tef1α* = PQ037169. MFLUCC 24-0220: ITS = PP472905; LSU = PP471498.

Notes – In the phylogenetic analyses (Figure 3.16), isolates MFLUCC 24-0219 and MFLUCC 24-0220, clustered with the type strain of *Cladobotryum novovarium* (TFC 2007-10) with with 100% BS and 1.00 BYPP. Furthermore, the morphological characteristics of our isolates MFLUCC 24-0219 and MFLUCC 24-0220 described herein are mostly similar to the original description and illustrations of *C. novovarium* (TFC 2007-10) provided by Põldmaa (2007). The width of conidiophores of MFLUCC 24-0219 described in this study are comparatively higher than those of TFC 2007-10 described by Põldmaa (2007): 3–9 μm *vs* 5–6 μm. The length, width at the base and width at the apex of the conidiogenous cells of MFLUCC 24-0219 is comparatively lower than those of TFC 2007-10 described by Põldmaa (2007): length of conidiogenous cells: 8–30 μm *vs* 30–50 μm, width of the conidiogenous cells at the base: 3–6 μm *vs* 3–6.5 μm, width of the conidiogenous cells at the apex: 0.8–2.5 μm *vs* 1.2–2.8 μm. The conidial size of MFLUCC 24-0219 is greater than those of TFC 2007-10 described by Põldmaa (2007): 9–20 × 5–9 μm *vs* 8.7–14.5 × 4.5–7.2 μm. The length to width ratio of conidia of MFLUCC 24-0219 described in this study are mostly similar to those of TFC 2007-10 described by Põldmaa (2007): 1.9 *vs* 1.6–2.4. These differences may have occurred due to the variations of the agar medium and the conditions used to obtain the cultures.

Therefore, we confirmed that our isolates (MFLUCC 24-0219 and MFLUCC 24-0220) are phylogenetically and morphologically similar to *C. novovarium*. Rossman et al. (2013) proposed *Hypomyces* to be protected against *Cladobotryum*. However, still, the *Cladobotryum* names are in use. Following Rossman et al. (2013), we propose *Hypomyces novovarius* over *Cladobotryum novovarium*. Furthermore, to the best of our knowledge, this is the first documented report of *H. novovarius* from Thailand.

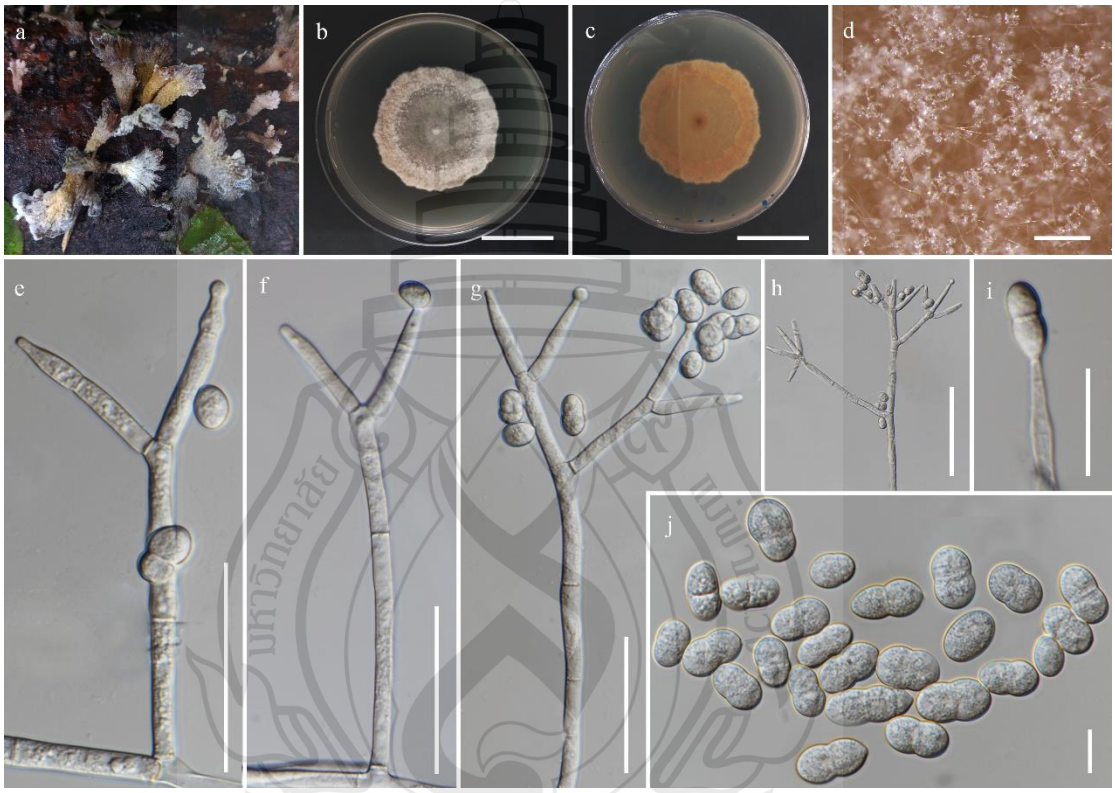


Figure 3.20 *Hypomyces novovarius* (MFLU 24-0222)

Figure 3.20, a. Host (*Schizophyllum* sp.). b, c. Colony on PDA. d. Sporulation on PDA. e–h. Conidiophores with conidiogenous cells and conidial formation. i. Close up of conidial attachment. j. Conidia. Scale bars: b, c = 30 mm, d = 250 µm, h = 100 µm, e-g = 50 µm, i = 25 µm, j = 10 µm.

Hypomyces paravirescens (K. Põldmaa) Gajanayake., Jayaward. and K.D. Hyde, comb. *nov*.

Figure 3.21

Index Fungorum number: IF 854923

≡ *Cladobotryum paravirescens* K. Põldmaa, Stud. Mycol. 68: 24 (2011)

Fungicolous on fruiting bodies of *Campanella* sp. Sexual morph: not observed. Asexual morph: white mycelium and dark green discolouration on host mushroom tissue. On PDA, hyphomycetous, *mycelium* hyaline, septate, branched. *Conidiophores* 3–9 μm ($\bar{x}$ = 6 μm, n = 50) wide, septate, sub erect or erect, moderate to profuse branching, either in a verticillate or irregular pattern, branching often arises as side branches from a verticil of conidiogenous cells, with additional branching at the apex, lateral branches support 1–3 conidiogenous cells. *Conidiogenous cells* 21–50 μm ($\bar{x}$ = 37 μm, n = 50) long, 3–6.5 μm ($\bar{x}$ = 5 μm, n = 50) wide near the base, attenuating to 0.8–2 μm ($\bar{x}$ = 1.5 μm, n = 50) at apex, frequently integrated into a pre-existing verticil, usually occurs in groups of 3–4 within a verticel, subulate, aseptate, create a single conidiogenous locus at the tip, occasionally, an additional locus may form on a small protrusion in the middle of the cell. *Conidia* 11.5–20 × 6–10 μm ($\bar{x}$ = 16 × 8 μm, n = 60), appear hyaline or pale yellowish-green, conidial masses in culture observed as with a pale green hue, ellipsoidal, with some slightly clavate, abundantly inequilateral while some are equilateral, exhibit straight or curved forms in the lower halves, mostly attenuated towards base, septate, septum median or sometimes sub median or supramedian, hilum is prominent, positioned centrally or laterally, narrow, and refractive. *Chlamydospores* not observed.

Colony characters – on PDA at 25 °C, 70–80 mm in 5 days. The aerial mycelium is moderate, exhibiting a cottony and buff appearance. Abundant conidiation, frequently occurring in patches. The colony acquires a greenish tinge with the formation of conidia.

Material examined – Thailand, Chiang Rai, Muang, Tha Sai (19° 49' 26.0292"N, 99° 52' 18.966"E), isolated from the mycelium growing on fruiting bodies of *Campanella* sp., 20 September 2023, Gajanayake A.J, AJB 35 (inactive dry culture MFLU 24-0223), living culture MFLUCC 24-0221.

GenBank numbers – ITS = PP472907; LSU = PP471500; *rpb2* = PQ037168; *tef1α* = PP982894.

Notes – In the phylogenetic analyses (Figure 3.16), our isolate MFLUCC 24-0221, clustered with the type strain of *Cladobotryum paravirescens* (TFC 97-23) with with 100% BS and 0.99 BYPP. Furthermore, the morphological characteristics of our isolate MFLUCC 24-0221 described herein are similar to the original description and

illustrations of *C. paravirescens* (TFC 97-23) provided by Põldmaa (2011). The width of conidiophores of MFLUCC 24-0221 and TFC 97-23 described by Põldmaa (2011) are mostly similar: 3–9 µm *vs* 6–9 µm. The length, width at the base and the width at the apex of the conidiogenous cells of MFLUCC 24-0221 is comparatively higher than those of TFC 97-23 described by Põldmaa (2011): length of conidiogenous cells: 21–50 µm *vs* 30–40 µm, width of the conidiogenous cells at the base: 3–6.5 µm *vs* 3–4.5 µm, width of the conidiogenous cells at the apex: 0.8–2 µm *vs* 0.7–1.3 µm. The conidial size of MFLUCC 24-0221 is lesser than those of TFC 97-23 described by Põldmaa (2011): 11.5–20 × 6–10 µm *vs* 18–27.5 × 6.5–10.0 µm. These differences may have occurred due to the variations of the agar medium and the conditions used to obtain the cultures. Therefore, we confirmed that our isolate MFLUCC 24-0221 is phylogenetically and morphologically similar to *C. paravirescens*. Following Rossman et al. (2013), we propose *Hypomyces paravirescens* over *Cladobotryum paravirescens*. To the best of our knowledge, this is the second documented report of *H. paravirescens* in Thailand and worldwide since its initial identification.

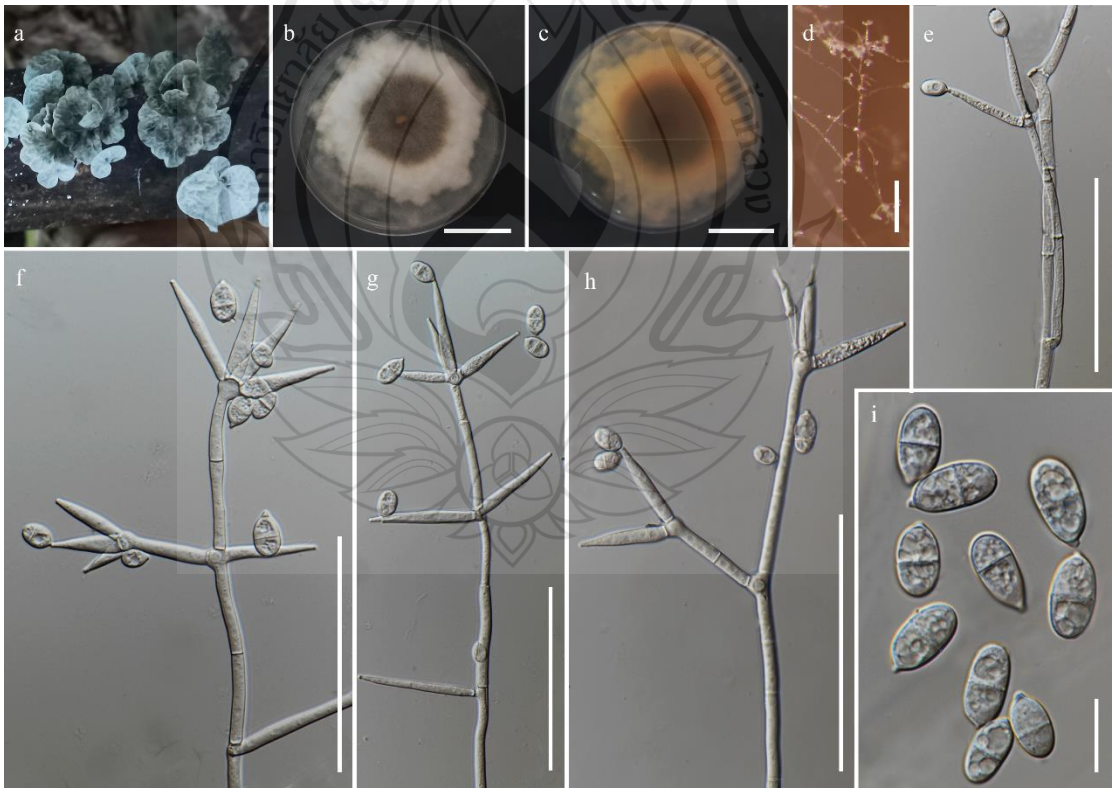


Figure 3.21 *Hypomyces paravirescens* (MFLU 24-0223)

Figure 3.21, A. Host (*Campanella* sp.). B, C. Colony on PDA. D. Sporulation on PDA. E–H. Conidiophores with conidiogenous cells and conidial attachments. I. Conidia. Scale bars: B, C = 30 mm, D–H = 100 μm, I = 15 μm.

Hypomyces protrusus (K. Põldmaa) Gajanayake., Jayaward. and K.D. Hyde, comb. *nov*.

Figure 3.22, 3.23

Index Fungorum number: IF 854924

≡ *Cladobotryum protrusum* K. Põldmaa, Stud. Mycol. 68: 24 (2011)

Fungicolous on a fruiting body of *Favolus* sp. Sexual morph: not observed. Asexual morph: white mycelium on the host mushroom tissue. On MEA, hyphomycetous, *mycelium* hyaline, septate, branched. *Conidiophores* 3–8 μm ($\overline{x}$ = 5 μm, n = 30) wide, septate, erect, moderately branched, either in a verticillate or occasionally drepanoid pattern, branches form at one to two levels, producing conidiogenous cells formed in a verticil. *Conidiogenous cells* 24–44 μm ($\overline{x}$ = 34 μm, n = 30) long, 3–4.5 μm ($\overline{x}$ = 3.5 μm, n = 30) wide near base, attenuating to 1–2 μm ($\overline{x}$ = 1.5 μm, n = 30) at apex, 2–5 in a vertical, subulate, conidiogenous locus bears protrusions at the tip. *Conidia* 14–25 × 7–10 μm ($\overline{x}$ = 18 × 8.5 μm, n = 40), appear hyaline to pale yellowish-green, ellipsoidal, sometimes cylindrical, long clavate or fusiform, attenuating at the base forming a narrow but prominent central to lateral, sometimes refractive hilum, inequi- or equilateral, often curved in lower half, aseptate to 1–3 septate, septum median or rarely sub- or supramedian, forms multiple conidia at the tip of a conidiogenous cell, some forms conidial anastomosis tubes. *Chlamydospores* ellipsoidal to subglobose, thick-walled, yellowish ochraceous.

Colony characters – on MEA at 25 °C, 50–60 mm in 7 days. The aerial mycelium is moderate, exhibiting a cottony and buff appearance in the middle, margin even, reverse initially yellowish, turns brick-brown with time.

Materials examined – Thailand, Chiang Rai: Muang, Tha Sai (19° 49' 26.0292"N, 99° 52' 18.966"E), isolated from the mycelium growing on a fruiting body of *Favolus* sp., 20 September 2023, Khyaju S, AJB 32 (inactive dry culture MFLU 24-0224), living culture MFLUCC 24-0222. Thailand, Chiang Mai: Mae Taeng, Pa Pae (19° 7' 7.2444" N, 98° 44' 2.1228" E), isolated from sporulated

mycelium growing on a polypore fruiting body, 19 July 2023, S.A.D Thakshila, DL 02.

GenBank numbers – MFLUCC 24-0222: ITS = PP472906; LSU = PP471499; *rpb2* = PP982903; *tef1α* = PP982899.

Notes – In the phylogenetic analyses (Figure 3.16), our isolate MFLUCC 24-0222 and DL 02, clustered within *Cladobotryum protrusum* strains (CBS 127531, FSU 5877, FSU 5044, FSU 5077 and TFC 201281). Furthermore, the morphological characteristics of our isolate MFLUCC 24-0222 described herein are similar to the original description and illustrations of the holotype of *C. protrusum* (CBS 127531) provided by Põldmaa (2011). Most of the dimensions of micro- morphological structures we have measured in MFLUCC 24-0222 are comparatively lesser than those of CBS 127531 described by Põldmaa (2011): conidiophore width: 3–8 μm *vs* 7–10 μm, length of conidiogenous cells: 24–44 μm *vs* 25–45 μm, width of the conidiogenous cells at the base: 3–4.5 μm *vs* 3.5–5 μm, conidial size: 14–25 × 7–10 μm *vs* 16–27 × 5.5–9 μm. Furthermore, we observed specialized hyphae known as conidial anastomosis tubes, which interconnect conidia. These structures are known to facilitate gene exchange and mediate heterokaryosis or recombination, particularly in cases where sexual reproduction is rare or absent (Gabriela et al., 2005). These differences may have occurred due to the variations of the agar medium and the conditions used to obtain the cultures. Therefore, we confirmed that our isolate MFLUCC 24-0222 is phylogenetically and morphologically similar to *C. protrusum*. Following Rossman et al. (2013), we propose *Hypomyces protrusus* over *Cladobotryum protrusum*.

Hypomyces protrusus was originally described as *Cladobotryum protrusum* by Põldmaa (2011), based on a specimen isolated from the basidioma of *Mycena* sp. in Madagascar. It was later transferred to *Hypomyces* for nomenclatural consistency (Gajanayake et al., 2025b). This species has been reported as a fungicolous fungus on various hosts including *Agaricus* sp., *Favolus* sp., *Morchella importuna*, *Neonothopanus* sp., *Pleurotus ostreatus*, and polypore in China, Madagascar, Thailand and Zimbabwe (Põldmaa 2011, Lan et al., 2020, Gajanayake et al., 2025b). Additionally, it has been found on the bark of *Eucalyptus* sp. in South Africa. *Hypomyces protrusus* is also notable for its ability to produce red pigments and as a

cobweb pathogen on cultivated mushrooms (Põldmaa, 2011; Lan et al., 2020). In Thailand, it was previously recorded on a decayed mushroom and *Favolus* sp. (Gajanayake et al., 2025b). This study also documents its DL 02 occurrence on a different polypore species, marking a new host record from Thailand.

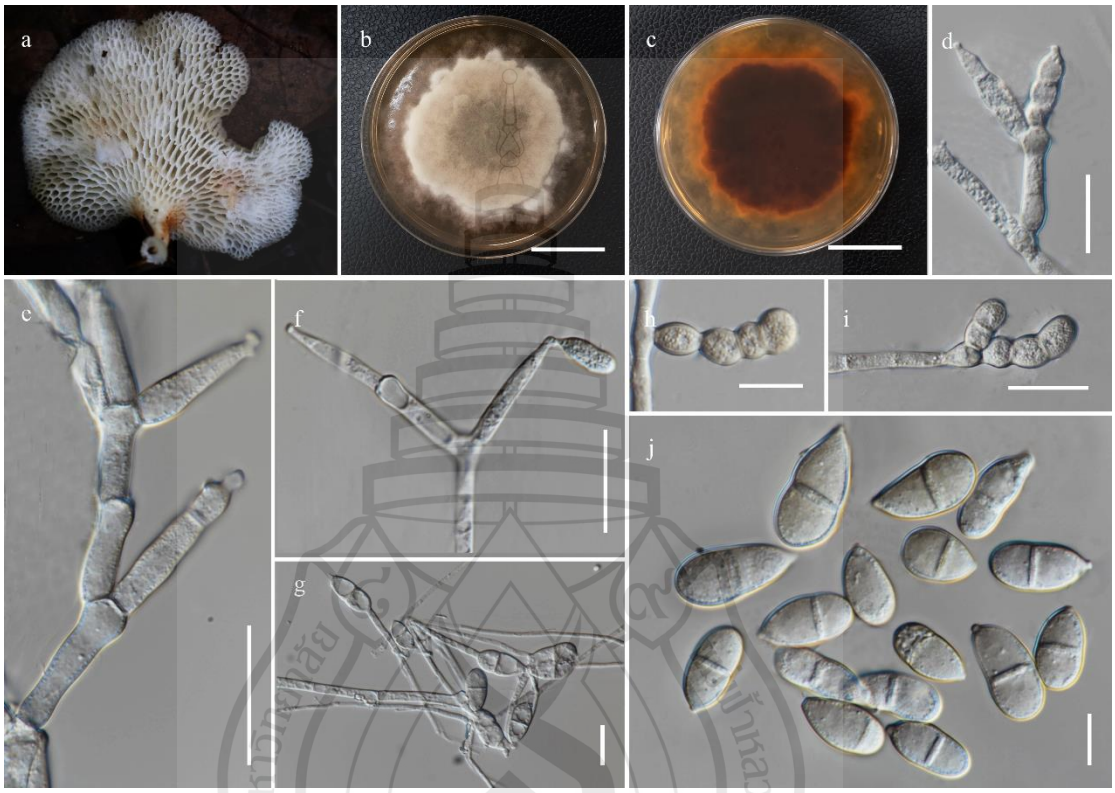


Figure 3.22 *Hypomyces protrusus* (MFLU 24-0224)

Figure 3.22, A. Host (*Favolus* sp.). B, C. Colony on PDA. D–F. Conidiogenous cells and conidial attachment. G. Conidia with anastomosis tubes. H, I. Chlamydospores. J. Conidia. Scale bars: B, C = 30 mm, I = 30 µm, D, E = 25 µm, F = 20 µm, G, H = 15 µm, J = 10 µm.

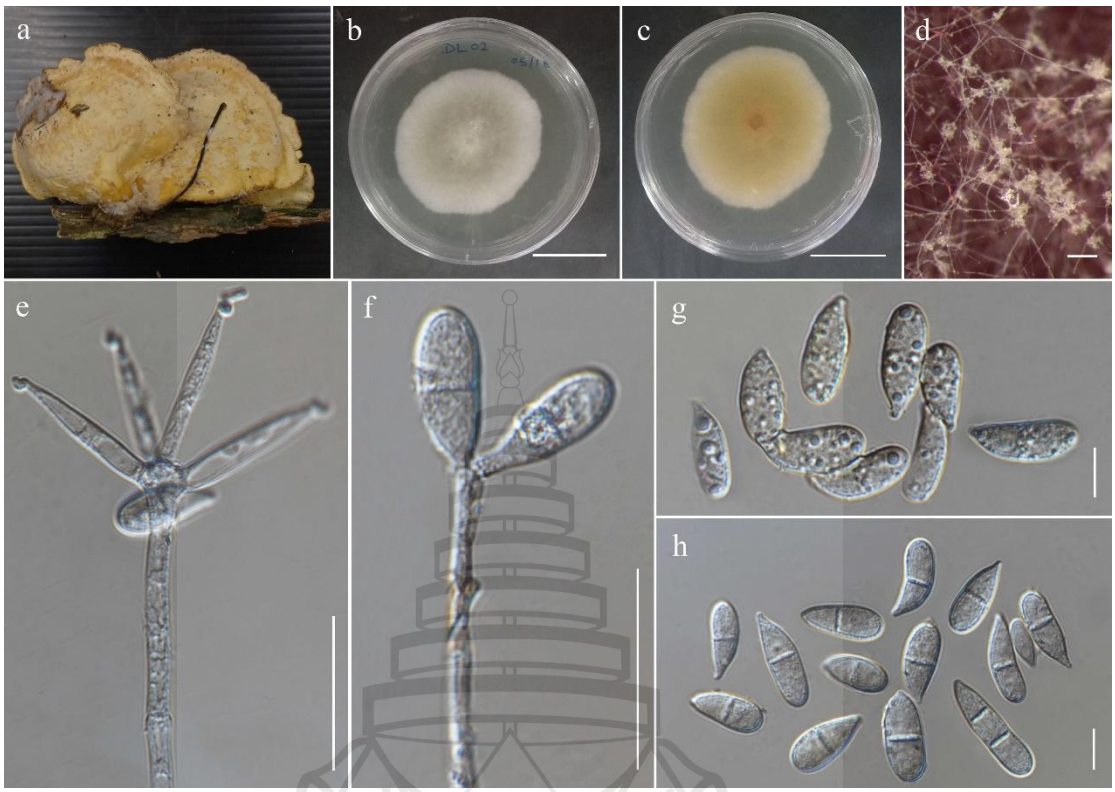


Figure 3.23 *Hypomyces protrusus* (DL 02)

Figure 3.23, a. Host (polypore). b, c. Colony on PDA. d. Sporulation on CLA. e, f. Conidiophores with conidiogenous cells. g, h. Conidia. Scale bars: b, c = 30 mm, d = 250 µm, e = 30 µm, f = 25 µm, g, h = 10 µm.

Hypomyces boletiphagus Rogerson & Samuels, Mycologia 81(3): 421 (1989) Figure 3.24, 3.25

Index Fungorum number: IF 136082

Fungicolous on a bolete fruiting body. Sexual morph: on the host, *Subiculum* initially white, becoming pale brown when drying. *Subicular hyphae* 1.5–4.5 µm ($\overline{x}$ = 3 µm, n = 30) wide. *Perithecia* 215–270 × 163–210 µm ($\overline{x}$ = 242 × 186 µm, n = 10), aggregated, semi-immersed to immersed in subiculum, globose to obovoid, papillate, papilla distinctly conical, dark orange-red to red-brown when dry. *Asci* 45–82 × 4–6 µm ($\overline{x}$ = 64 × 5 µm, n = 30), 8 spored, cylindrical, slightly thickened at apex, with apical pore. *Ascospores* 9–15 × 2–4 µm ($\overline{x}$ = 11.5 × 3 µm, n = 30), cylindric-fusiform to naviculate, uniseriate to partially biseriate in the ascus, smooth to verruculose, 1–septate, septum usually median but sometimes submedian, upper cell often slightly

wider than the lower cell, apex of upper cell acute, base of lower cell obtuse, not distinctly apiculate. Asexual morph: on PDA, hyphomycetous. *Conidiophores* 2–3.5 μm ($\overline{x}$ = 2.5 μm, n = 30) wide, hyaline, septate. *Phialides* solitary or ralely in verticills, 40–65 × 1.5–3 μm ($\overline{x}$ = 50 × 2 μm, n = 20), attenuating to 1.5–2 μm ($\overline{x}$ = 1.8 μm, n = 20). *Phialoconida* 6–16 × 3–6.5 μm ($\overline{x}$ = 9 × 4 μm, n = 30) ellipsoid, ovoid or base truncate or not, unicellular, hyaline, held in colorless slime heads. *Aleurioconidia* 21.5–36.5 × 15.5–26 μm ($\overline{x}$ = 25.5 × 21.5 μm, n = 30) formed as terminal swellings of short side branches of hyphae, at first ellipsoid, becoming globose or subglobose, at first longitudinally ribbed, portions of wall enlarging and forming obtuse elongated ridges, appearing wrinkled in side view.

Colony characters – on PDA, at 25 °C, reached 50–55 mm after 07 days of incubation, colony front grey to pale purple at the middle, reverse dark purple. Conidial fructifications developing as loosely floccose masses of white mycelium bearing robust conidiophores with white or yellowish spore masses.

Material examined – Thailand, Chiang Rai: Mae Salong Nok (20° 9' 59.4216"N, 99° 37' 34.7016"E), isolated from the sporulated mycelium growing on a bolete fruiting body, 12 June 2024, A.J Gajanayake, AJ 70-24 and AJ 73-24.

Notes – In our phylogenetic analyses (Figure 3.17), AJ 70-24 and AJ 73-24 clustered with *Hypomyces boletiphagus* (MFLU 17-1391) with 99% BS and 0.99 BYPP (Fig. 3.16). The morphological features of AJ 70-24 and AJ 73-24 match the original description and illustrations of *H. boletiphagus* provided by Rogerson and Samuels (1989), except for slight differences in the dimensions of morphological structures. These variations are possible due to differences in the agar medium and cultural conditions (Senanayake et al., 2020). Therefore, we confirmed that AJ 70-24 and AJ 73-24 are phylogenetically and morphologically consistent with *H. boletiphagus*.

Hypomyces boletiphagus was originally described by Rogerson and Samuels (1989) as a boleticolous species from the USA. Its known distribution includes Indonesia, Japan, New Zealand, Thailand, and the USA (Rogerson & Samuels, 1989; Sahr et al., 1999; Tokiwa et al., 2018; Sun et al., 2019b). This species has been reported in association with several bolete species, including *Austroboletus gracilis*,

Boletus sp., *Gyroporus castaneus*, *Pulveroboletus ravenelii*, and *Strobilomyces strobilaceus* (Rogerson & Samuels, 1989; Sahr et al., 1999; Sun et al., 2019b).

Hypomyces boletiphagus was first recorded in Thailand by Sun et al. (2019b) in association with a *Boletaceae* species. The present study constitutes the second report of this species from Thailand, with specimens collected from the same locality as the original record. Notably, this study provides the first documentation of the sexual morph of *H. boletiphagus* in Thailand, thereby offering additional morphological insight and further confirming its boleticolous nature.

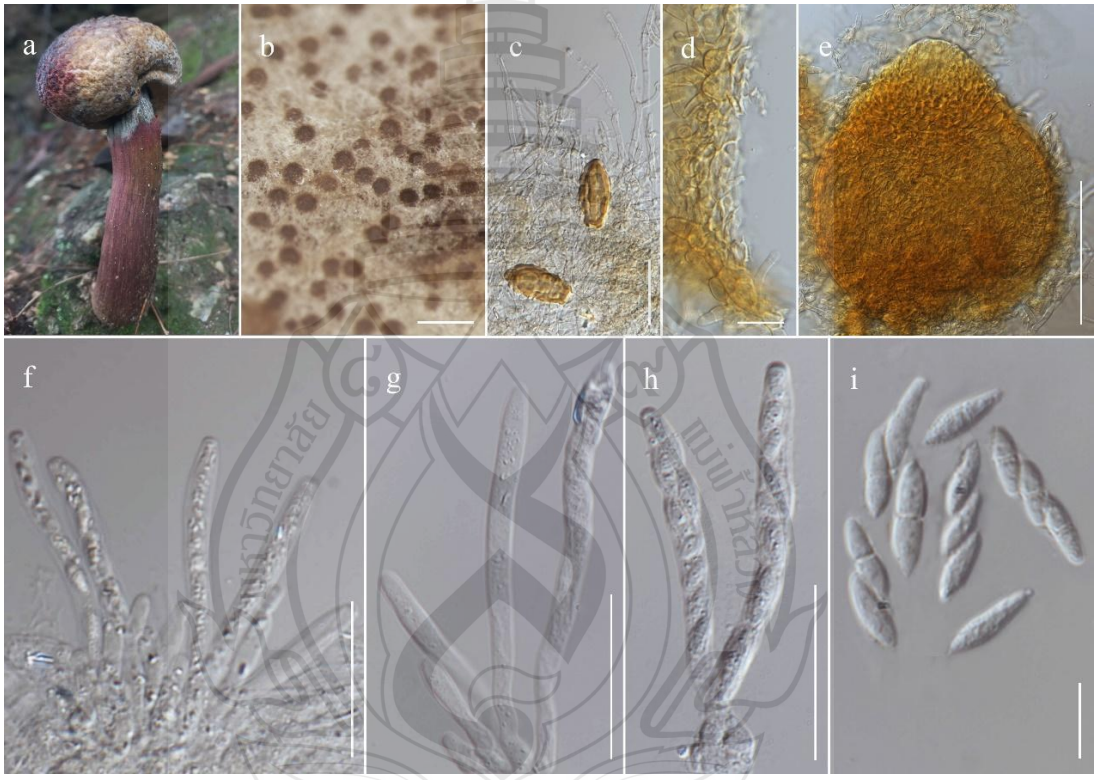


Figure 3.24 *Hypomyces boletiphagus*: sexual morph (AJ 70-24)

Figure 3.24, a. Host (bolete). b. Perithecia on host tissue. c. Subicular hyphae. d. Perithecial wall. e. Perithecium. f–h. Asci. i. Ascospores. Scale bars: b = 500 µm, e = 100 µm, c = 40 µm, f–h = 30 µm, d = 20 µm, i = 10 µm.

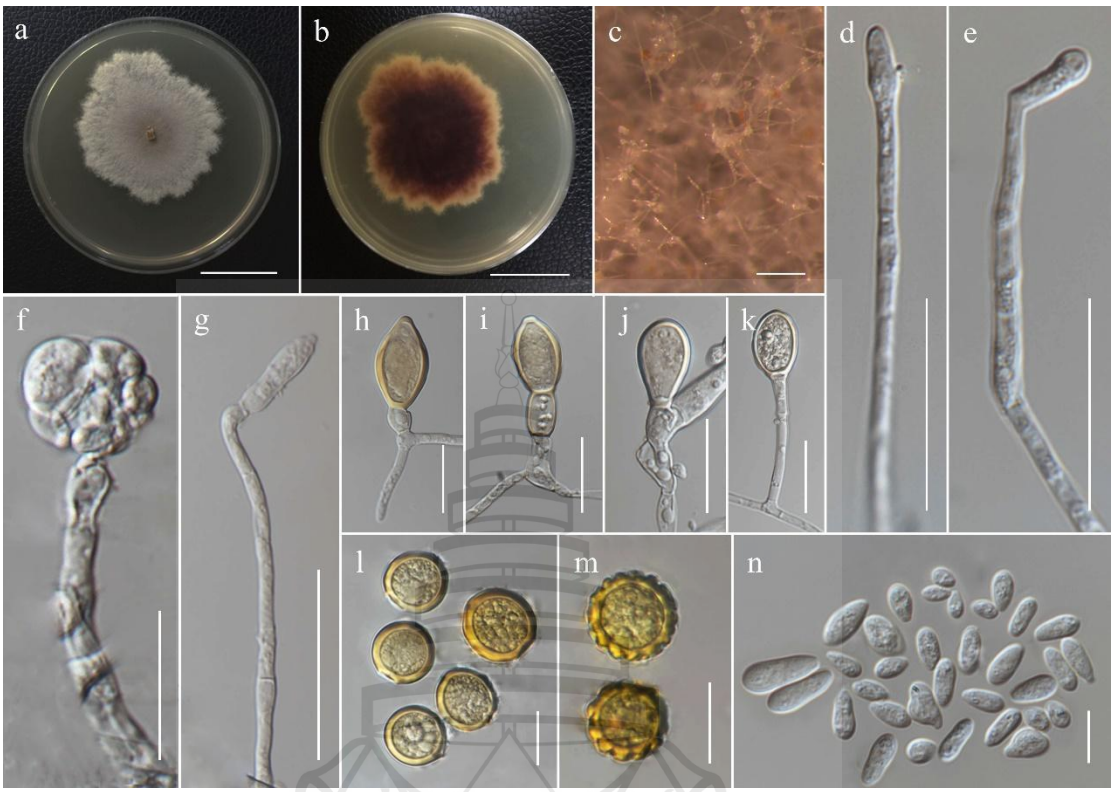


Figure 3.25 *Hypomyces boletiphagus*: asexual morph (AJ 73-24)

Figure 3.25, a, b. Colony on PDA. d. Sporulation on PDA. d–f. Conidiophores with conidial attachments. g–k. Aleurioconidia formation. l, m. Aleurioconidia. n. Phialoconida. Scale bars: a, b = 30 mm, c = 250 µm, g = 50 µm, d, h–k = 30 µm, e, f = 25 µm, l, m = 20 µm, n = 10 µm.

Hypomyces chlorinus Tul. & C. Tul., Annls Sci. Nat., Bot., sér. 4 13: 13 (1860). Figure 3.26

Index Fungorum number: IF 213291

Fungicolous on a bolete fruiting body. Sexual morph: not observed. Asexual morph: on the host, white mycelium on a bolete fruiting body. On PDA, hyphomycetous. *Mycelium* 1.5–3 µm ($\bar{x}$ = 2 µm, n = 30) wide, hyaline, septate, aerial hyphae short and conidiophores arising abundantly throughout the colony. *Conidiophores* 2–4.5 µm ($\bar{x}$ = 3 µm, n = 30) wide, hyaline, indefinite in length, smooth, colorless, macronematous, unbranched and terminating in a single phialide, or infrequently branched or branching several times, each branch produces a single phialide or a verticillate whorl of 2-4 phialides. *Phialides* 21–48 × 1.5–3 µm ($\bar{x}$ = 29.5

× 2 μm, n = 20), attenuating to 0.5–1.5 μm ($\overline{x}$ = 1 μm, n = 20), straight, smooth, subulate, with a slight periclinal thickening at the tip, collarette not flared. *Conidia* 5.5–12 × 2–4 μm ($\overline{x}$ = 8 × 2.5 μm, n = 30), ellipsoid, highly variable in size, lacking a visible basal abscission scar, unicellular, hyaline, held in colourless slime heads. Aleurioconidia not observed.

Colony characters – on PDA, at 25 °C, reached 35–40 mm after 07 days of incubation, aerial mycelium abundant, colony front initially white and turn to pale yellow with time, reverse pale yellow to pale orange.

Material examined – Thailand, Chiang Rai: Mae Salong Nok (20° 9' 59.4216"N, 99° 37' 34.7016"E), isolated from the sporulated mycelium growing on a bolete fruiting body, 12 June 2024, A.J Gajanayake, DO3.

Notes – Our isolate DO3, clustered within *Hypomyces chlorinus* (KSH511, KSH512, CBS 571.63) with 100% BS and 1.00 BYPP (Figure 3.16). The morphological features of DO3 match the description and illustrations of *H. chlorinus* provided by Rogerson and Samuels (1989), except for slight differences in the dimensions of morphological structures. These variations are possible due to differences in the agar medium and cultural conditions (Senanayake et al., 2020). Therefore, we confirmed that our isolate, DO3, is phylogenetically and morphologically consistent with *H. chlorinus*.

Hypomyces chlorinus was originally described by Tulasne (1860) as a fungicolous species associated with bolete basidiomata in France. *Hypolyssus chlorinus* (Tul. & C. Tul.) Kuntze, *Sepedonium chlorinum* (Tul. & C. Tul.) Damon, and *Leiosepium chlorinum* (Tul. & C. Tul.) A. Fontana are recognized as synonyms of *H. chlorinus* (Species Fungorum, 2025). Additionally, *Hypomyces chlorinigenus*, initially described as a distinct boleticolous species by Rogerson and Samuels (1989), was later synonymized with *H. chlorinus* (Species Fungorum, 2025). The known distribution of *H. chlorinus* includes Belgium, France, Germany, Guyana, Indonesia, Japan, New Zealand, and the USA (Rogerson & Samuels, 1989; Sahr et al., 1999; Index Fungorum, 2025). To the best of our knowledge, this study presents the first record of *H. chlorinus* in Thailand, further supporting its boleticolous nature.

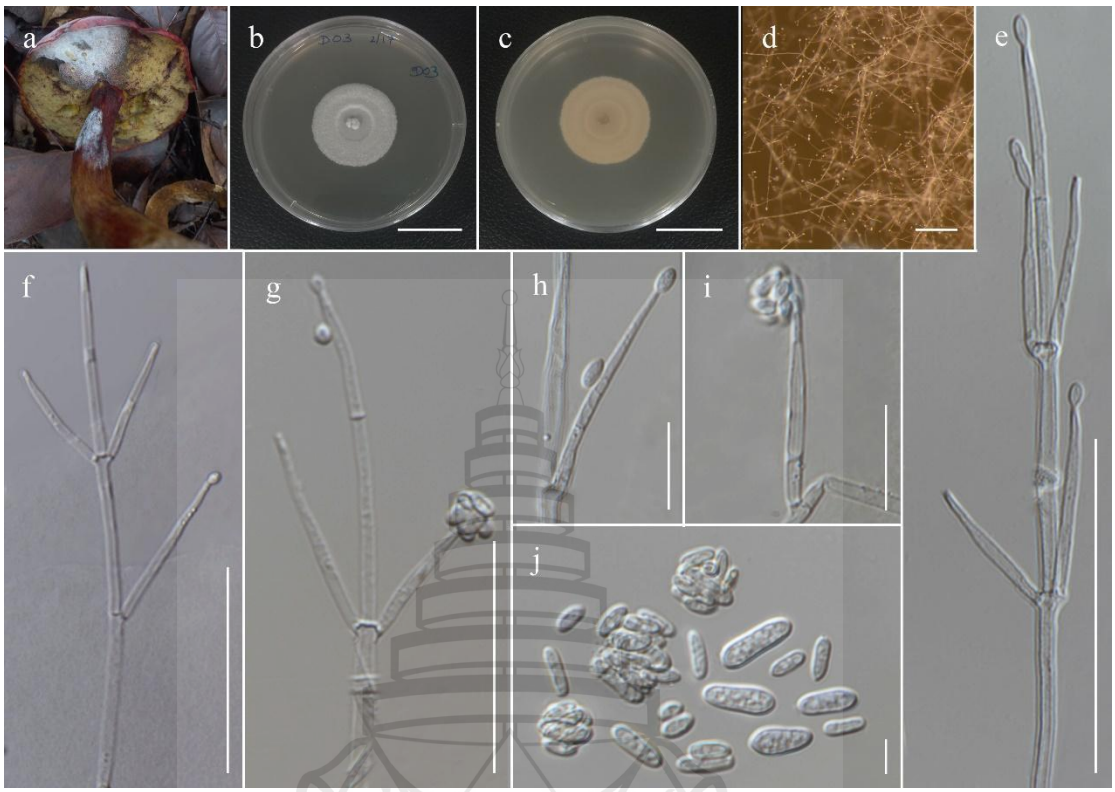


Figure 3.26 *Hypomyces chlorinus* (DO3)

Figure 3.26, a. Host (bolete) b, c. Colony on PDA. d. Sporulation on PDA. e–i. Conidiophores with conidial attachments. j. Conida. Scale bars: a, b = 30 mm, c = 250 µm, e, f = 50 µm, g = 35 µm, h, i = 15 µm, j = 5 µm.

Hypomyces cornea X.J. Xie, F.H. Tian & K.Q. Peng.

Figure 3.27

Index Fungorum number: IF 843972

Fungicolous on a fruiting body of *Hydnoporia* sp. Sexual morph: not observed. Asexual morph: white mycelium on host fruiting body. On PDA, hyphomycetous, *mycelium* hyaline, septate, branched. *Conidiophores* 2–5 µm ($\overline{x}$ = 3.5 µm, n = 60) wide, hyaline, septate, arising from aerial hyphae, straight or flexuous, producing conidiogenous cells in a penicillus. *Conidiogenous cells* 13–43 µm ($\overline{x}$ = 21 µm, n = 50) long, 1.5–4 µm ($\overline{x}$ = 2.5 µm, n = 50) wide near base, attenuating to 0.6–2 µm ($\overline{x}$ = 1 µm, n = 50) at apex, hyaline, solitary or 3–5 in a verticil, slender, cylindrical or elongated-ampulliform. *Conidia* 9–17 × 3–6 µm ($\overline{x}$ = 14 × 4 µm, n = 60), hyaline, ellipsoidal or cylindrical, straight or occasionally curved, hyaline,

aseptate or 1-septate. *Chlamydospores* 12–25 × 6–8 μm ($\bar{x}$ = 18.5 × 7 μm, n = 30), single or in chains, terminal or intercalary, hyaline, globose to subglobose.

Colony characters – on PDA at 25 °C, 40–45 mm in 7 days. The aerial mycelium is moderate, with conspicuous watery patches on the colony surface with the sporulation.

Material examined – Thailand, Phayao, Dok Khamtai, Dong Suwan (19° 13' 55.1964"N, 100° 5' 16.422"E), isolated from the mycelium growing on a fruiting body of *Hydnoporia* sp., 4 September 2023, Chaharmiri-Dokhaharani S, AJP 04 (inactive dry culture MFLU 24-0221). Living culture MFLUCC 24-0218.

GenBank numbers – ITS = PP472909; LSU = PP471502; *tef1α* – PP982895.

Notes – In the phylogenetic analyses (Figure 3.16), our isolate MFLUCC 24-0218 branches off from *Hypomyces cornea* (GUCCTB 622 and GUCCTB 623) within the subclade which also includes *Cladobotryum pinarense*. When considering the genetic distance between *H. cornea* (GUCCTB 622) and MFLUCC 24-0218 in the trimmed ITS (1.04%), LSU (0.61%), and *tef1α* (1.92%) sequences, are less. The conidiophores of MFLUCC 24-0218 are narrower than in *H. cornea* described by Xie et al. (2024b): 2–5 μm *vs* 6–9 μm. The conidiogenous cell length (7.1–45.3 μm *vs* 13–43 μm) and conidia (7.1–14.8 × 4.2–6.6 μm *vs* 9–17 × 3–6 μm) formed on verticillate conidiophores in *H. cornea* are smaller than those of MFLUCC 24-0218. However, the chlamydospores have not been observed in MFLUCC 24-0218. These differences may have occurred due to the variations of the agar medium and the conditions used to obtain the cultures. Therefore, we identify that our isolate MFLUCC 24-0218 is similar to *H. cornea*. To the best of our knowledge, this is the first report of *H. cornea* from Thailand and the first report of this species associated with a *Hydnoporia* species.

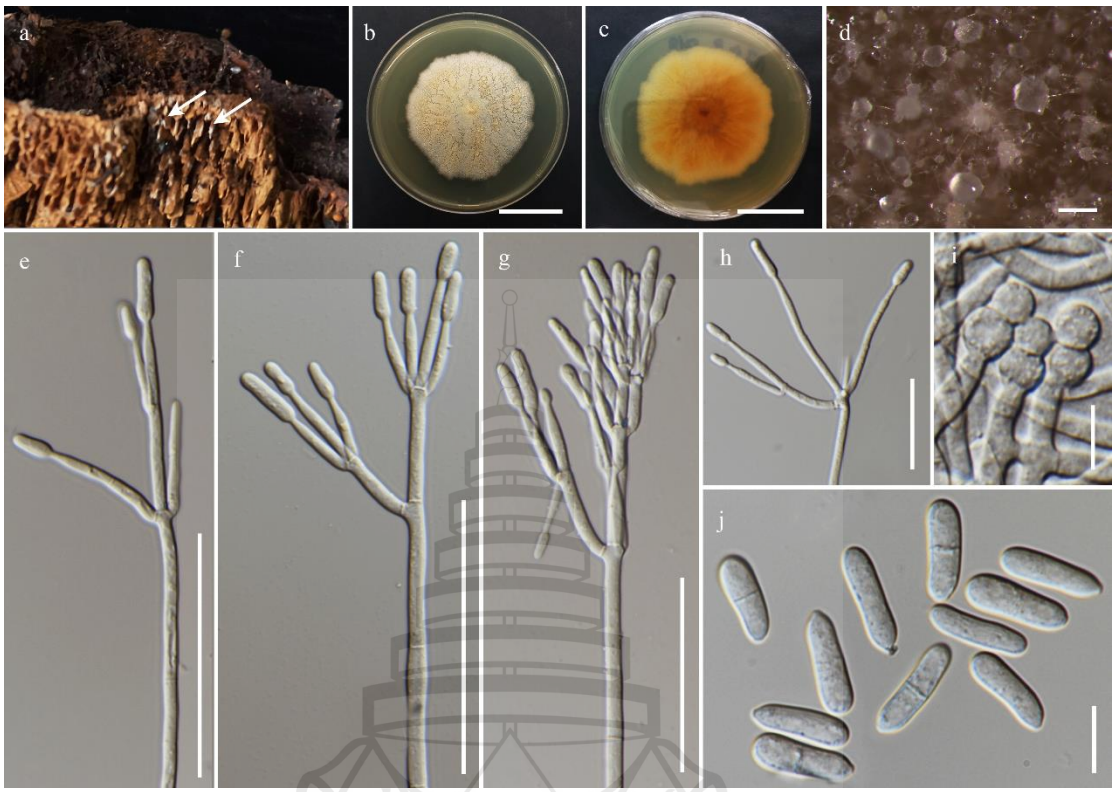


Figure 3.27 *Hypomyces cornea* (MFLU 24-0221)

Figure 3.27, a. Host (*Hydnoporia* sp.). b, c. Colony on PDA. d. Sporulation on PDA. e–h. Conidiophores with conidiogenous cells and conidial attachments. i. Chlamydospores. j. Conidia. Scale bars: b, c = 30 mm, d = 250 μm, h = 100 μm, e–g = 50 μm, i = 25 μm, j = 10 μm.

Hypomyces mycophilus Rogerson & Samuels 1993

Figure 3.28

Index Fungorum number: IF 359736

Fungicolous on the fruiting bodies of *Auricularia* sp. Sexual morph: not observed. Asexual morph: white to grey mycelial patches on fruiting bodies of *Auricularia* sp. On WA, hyphomycetous, *Conidiophores* arising in aerial mycelium, indefinite in length, main axis 4–7 μm ($\bar{x}$ = 5 μm, n = 20) wide, verticillately branched, each branch septate, each cell producing several denticulate conidiogenous loci over the terminal of the length of the conidiogenous branch, denticles 0.5–1 μm ($\bar{x}$ = 1 μm, n = 20) long and producing a single conidium. *Conidia* 11–23 × 7–10 μm ($\bar{x}$ = 15 × 8 μm, n = 35), hyaline, oblong to broadly ellipsoidal, 0-2 septate, with a low

and slightly frilled basal abscission scar, held singly along the length of the conidiogenous branch in a dry rachis. *Chlamydospores* 17–23 × 16–22 μm ($\overline{x}$ = 21 × 19.5 μm, n = 10) at the tip of the cell, Blastotrichum-like, forming from lateral branches of hyphae, each comprising 2-3 thick-walled cells, lightly pigmented.

Colony characters – on PDA at 25 °C, 25–30 mm in 7 days. Colony surface initially white to pale rose with abundant aerial mycelium and later growing dense with irregular margin. Reverse of the colony pale rose at the centre and fading to white towards the margin.

Material examined – Thailand, Phayao, Dok Khamtai, Dong Suwan (19◦ 13′ 55.1964″N, 100◦ 5′ 16.422″E), isolated from the white to grey mycelial patches on fruiting bodies of *Auricularia* sp., 4 September 2023, Gajanayake AJ, AJ24P1.

Notes – Our isolate, clustered within *Hypomyces mycophilus* with a bootstrap support of 100% ML, and 1.00 BYPP (Figure 3.16). The morphological features of AJ24P1 match the original description and illustrations of *H. mycophilus* provided by Rogerson and Samuels (1993). Therefore, we confirmed that our isolate, AJ24P1, is phylogenetically and morphologically consistent with *H. mycophilus*.

Hypomyces mycophilus was originally described by Rogerson and Samuels (1993) as a polyporicolous species on *Trametes versicolor*, in the United States. Its asexual morph is known as *Cladobotryum polypori* (Rogerson & Samuels, 1993).

Known distribution of *H. mycophilus* include China, Iran, Japan, Thailand, and the United States (Rogerson & Samuels, 1993; Asef & Mohammadi, 2002; Põldmaa & Samuels, 2004; Cao et al., 2023) Known hosts of *H. mycophilus* include *Armillaria mellea*, *Auricularia* spp., *Bulgaria* sp., *Lactifluus vellereus*, *Loweporus* sp., *Marasmius* sp., *Polyporus* spp., *Stereum* sp., and *Trametes versicolor* (Rogerson & Samuels, 1993; Asef & Mohammadi, 2002; Põldmaa & Samuels, 2004). This species has also been reported as a cobweb pathogen on *Auricularia cornea* and *A. heimuer* in China (Cao et al., 2023; Zhang et al., 2023). To the best of our knowledge, this is the first report of *H. mycophilus* on wild *Auricularia* sp. in Thailand.

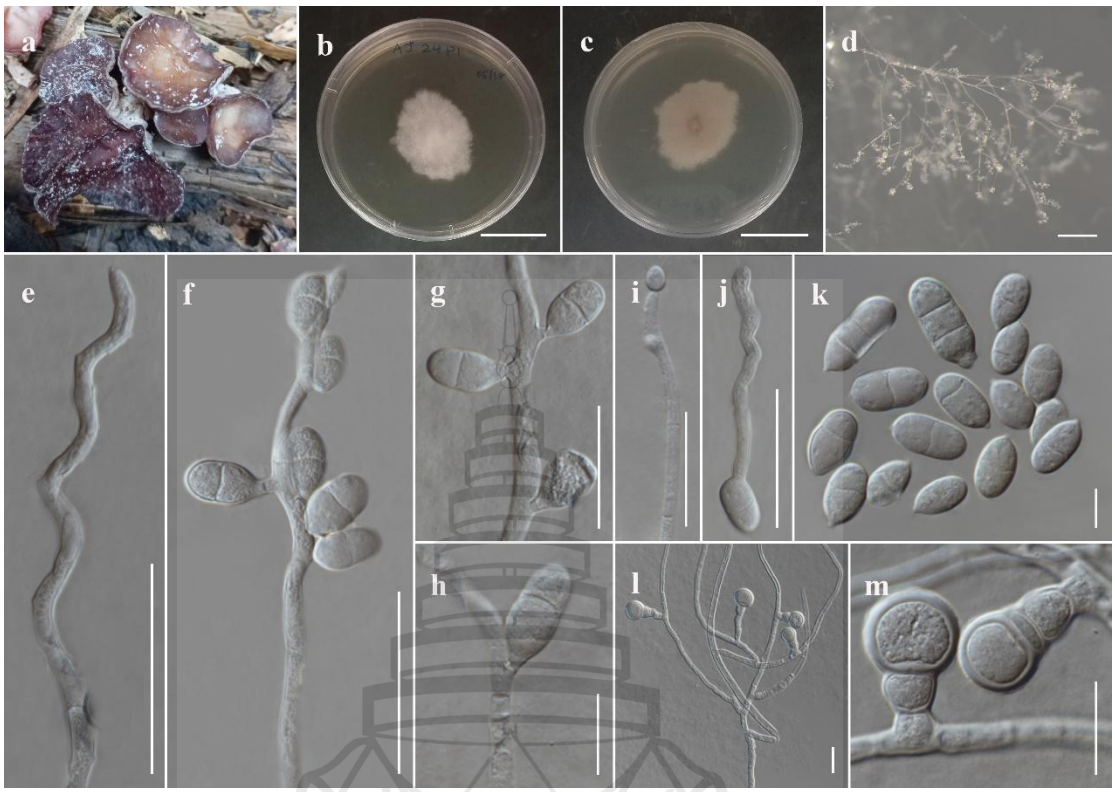


Figure 3.28 *Hypomyces mycophilus* (AJ24P1)

Figure 3.28, a. Host (*Auricularia* sp.). b, c Colony on PDA. d Sporulation on WA. e Fertile rachis of a conidiophore. f–i Conidial attachments. j, k Conidia. l Chlamydospores. Scale bars: b, c = 30 mm, d = 500 μm, e, f, j = 40 μm, i, l = 30 μm, g = 25 μm, m = 20 μm, h = 15 μm, k = 8 μm.

Hypomyces pseudocorticiicola Tokiwa & Okuda, Mycoscience 46(5): 295 (2005)

Figure 3.29

Index Fungorum number: IF 356471

Fungicolous on a fruiting body of *Auricularia* sp. Sexual morph: not observed. Asexual morph: on host, *Mycelium* white cottony mass. On PDA, hyphomycetous, *Hyphae* 3–7 μm ($\bar{x}$ = 5 μm, n = 40) wide, thick-walled, septate, hyaline. *Conidiophores* septate, semi macronematous, arising from aerial hyphae, irregularly branched, 70.5–418 × 2–7 μm ($\bar{x}$ = 193 × 4.5 μm, n = 20), initiating conidiogenous cells at the tip. *Conidiogenous cells* hyaline, slightly lanceolate, gradually tapered towards the apex, formed laterally or directly from conidiophores, solitary or as a

whorl, 2–3.5 μm ($\bar{x}$ = 2.5 μm, n = 30) wide. *Conidia* hyaline, (0–)2–3 septate, borne from the apex of conidiogenous cells, cylindrical to long ellipsoidal, smooth, 22–47 × 4–8.5 μm ($\bar{x}$ = 34 × 6.5 μm, n = 50). *Chlamydospores* hyaline, warty surface, subglobose to broadly ellipsoidal, formed in chains, laterally on the substrate hyphae or apically at the apex of the branches, 8.5–20 μm ($\bar{x}$ = 14 μm, n = 30) wide.

Colony characters – Colonies on PDA reaching 60–70 mm diameter after 5 days at 25 °C, floccose, margin uneven, front initially pale white to greyish-orange with time, reverse initially brownish-orange and turning yellowish-brown with time.

Material examined – Thailand, Chiang Rai province: Mueang, Tha sut, isolated from the white mycelium growing on a fruiting body of *Auricularia* sp., 20 February 2023, Sabin Khyaju, AJ 04-23 (metabolically inactive dry culture, MFLU 24-0226, new geographical record), metabolically active living culture, MFLUCC 23-0202.

GenBank numbers – ITS = OR473279; LSU = OR473293; *tef1-α* = OR887529; *rpb2* = OR887528.

Notes – Our isolate (MFLUCC 23-0202) clustered with the extype strain of *Hypomyces pseudocorticiicola* (JCM 12654) with a bootstrap support of 100% ML and 1.00 BYPP (Figure 3.16). Its morphology resembles the original description and illustrations for *H. pseudocorticiicola* by Tokiwa and Okuda (2005). However, the conidiophores, conidiogenous cells and conidia of MFLUCC 23-0202 are comparatively smaller than those of *H. pseudocorticiicola* strain described by Tokiwa and Okuda (2005) in having conidiophores 2–7 μm *vs* (6.5–)7.5–10.0 μm in width, conidiogenous cells 2–3.5 μm *vs* (2.5–)7.5–9.5 μm in width, conidia 22–47 × 4–8.5 μm *vs* (12.5–)32.5–37.5(–47.5) × (5.0–)7.5–9.0(–10.5) μm. These dimensional differences may be due to the variations of agar media and the conditions in which the colonies were grown.

Hypomyces pseudocorticiicola has been originally isolated from polypore fruiting bodies in Japan (Tokiwa & Okuda, 2005). Later, it was confirmed that *H. pseudocorticiicola* is the causal agent of cottony leak disease in cultivated *Auricularia nigricans* (Okuda et al., 2016). However, other than being a fungicolous fungus, published information on other host associations of *H. pseudocorticiicola* is scarce. Biochemical research on *H. pseudocorticiicola* has recently revealed it is a potential

source of compounds applicable in antifungal drug production (Watanabe et al., 2022; Watanabe et al., 2023). This is the first report of *H. pseudocorticiicola* from Thailand as a fungicolous fungus on wild *Auricularia* species.

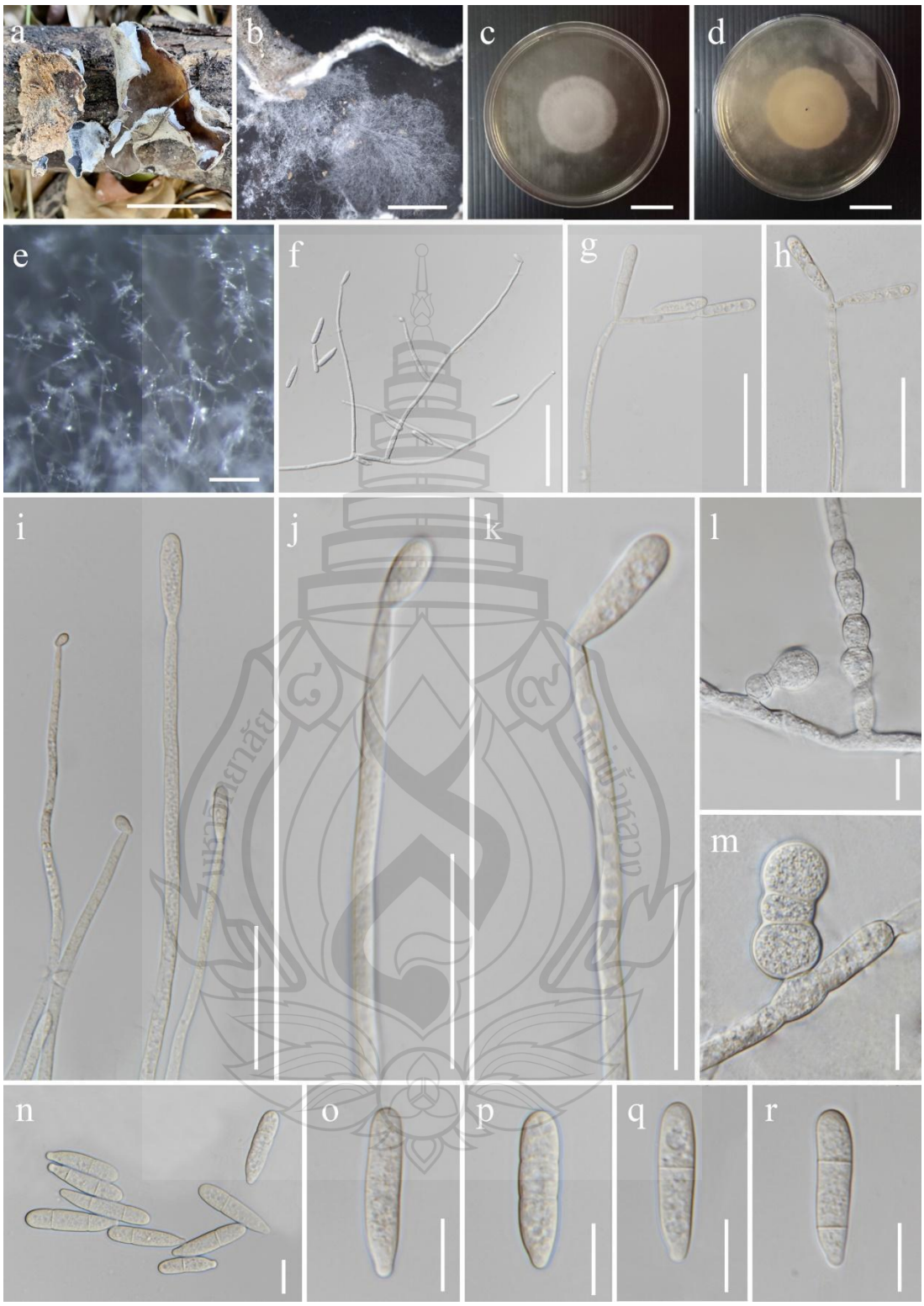


Figure 3.29 *Hypomyces pseudocorticiicola* (MFLU 24-0226)

Figure 3.29, a, b Host. c, d Colony on PDA. e Sporulation on PDA. f–k Conidiophores with conidial attachments. l, m Chlamydospores. n–r Conidia. Scale bars: a = 40 mm, c, d = 30 mm, b = 200 μm, e, f = 100 μm, g–k = 50 μm, l–r = 15 μm.

Hypomyces semicircularis (G.R.W. Arnold, R. Kirschner and Chee J. Chen) R. Kirschner, in Wei and Kirschner, Fungal Science, Taipei 32(1): 17 (2017)

Figure 3.30

Index Fungorum number: IF 356471

Fungicolous on a fruiting body of a polypore. Sexual morph: not observed. Asexual morph: white to grey mycelium on the host mushroom tissue. On PDA, hyphomycetous, *mycelium* hyaline, septate, branched. *Conidiophores* 4–7 μm ($\overline{x}$ = 5 μm, n = 30) wide, septate, erect to sub-erect, moderate branching, verticillate or irregular, evenly distributed for the most part, main axis produces side branches. *Conidiogenous cells* 10–35 μm ($\overline{x}$ = 20 μm, n = 30) long, 2–3 μm ($\overline{x}$ = 2.5 μm, n = 30) wide near base, attenuating to 0.8–1.5 μm ($\overline{x}$ = 1 μm, n = 30) at apex, subulate, produced on main axis of the conidiophores or lateral branches, 2–4 in a verticil, occasionally also formed singly just below verticil, aseptate or sometimes with one septum, often slightly curved at apex, forming one conidiogenous locus at apex. *Conidia* 11–25 × 3.5–5 μm ($\overline{x}$ = 18 × 4 μm, n = 40), hyaline, 1–3-septate, ellipsoidal, clavate, sigmoid or semicircular, occasionally with two shallow branches at tip; inequilateral, often curved or straight, base rounded or acuminate, sometimes slightly attenuated at ends, then sub-fusiform, with minute hilum of variable width, central or slightly off center. *Chlamydospores* formed among aerial mycelium, cells subglobose, thick wall, ochraceous, in short chains on supporting cells or forming irregular clusters.

Colony characters – on PDA at 25 °C, 60–70 mm in 7 days. The aerial mycelium abundant, colony growth exhibiting a cottony and buff appearance, margin even, reverse initially ivory or yellowish, turns reddish brown with time.

Material examined – Thailand, Chiang Rai, Muang (20° 3' 23.6772" N, 99° 52' 3.1872" E), isolated from the mycelium growing on a fruiting body of a Polypore, 16 September 2023, Thakshila S.A.D, AJDN 01 (inactive dry culture MFLU 24-0225), living culture MFLUCC 24-0223.

GenBank numbers – ITS = PP472908; LSU = PP471501; *rpb2* = PP982900; *tef1α* = PP982896.

Notes – In the phylogenetic analyses, our isolate MFLUCC 24-0223, clustered within *Hypomyces semicircularis* strains (CBS 705.88 and TFC 03-3) (Figure 3.16). Furthermore, the morphological characteristics of our isolate MFLUCC 24-0223 described herein are similar to the original description and illustrations of the holotype of *H. semicircularis* provided by Kirschner et al. (2007). Most of the dimensions of micro-morphological structures we have measured in MFLUCC 24-0223 are comparatively lesser than those of the type strain described by Kirschner et al. (2007): conidiophore width: 4–7 μm *vs* 8–10 μm, length of conidiogenous cells: 10–35 μm *vs* 28–48 μm, width of the conidiogenous cells at the base: 2–3 μm *vs* 4–6 μm, conidial size: 11–25 × 4–6 μm *vs* 10–33 × 2.5–4 μm. These differences may have occurred due to the variations of the agar medium and the conditions used to obtain the cultures. Therefore, we confirmed that our isolate MFLUCC 24-0223 is phylogenetically and morphologically similar to *H. semicircularis*. To the best of our knowledge, this is the first report of *H. semicircularis* from Thailand.

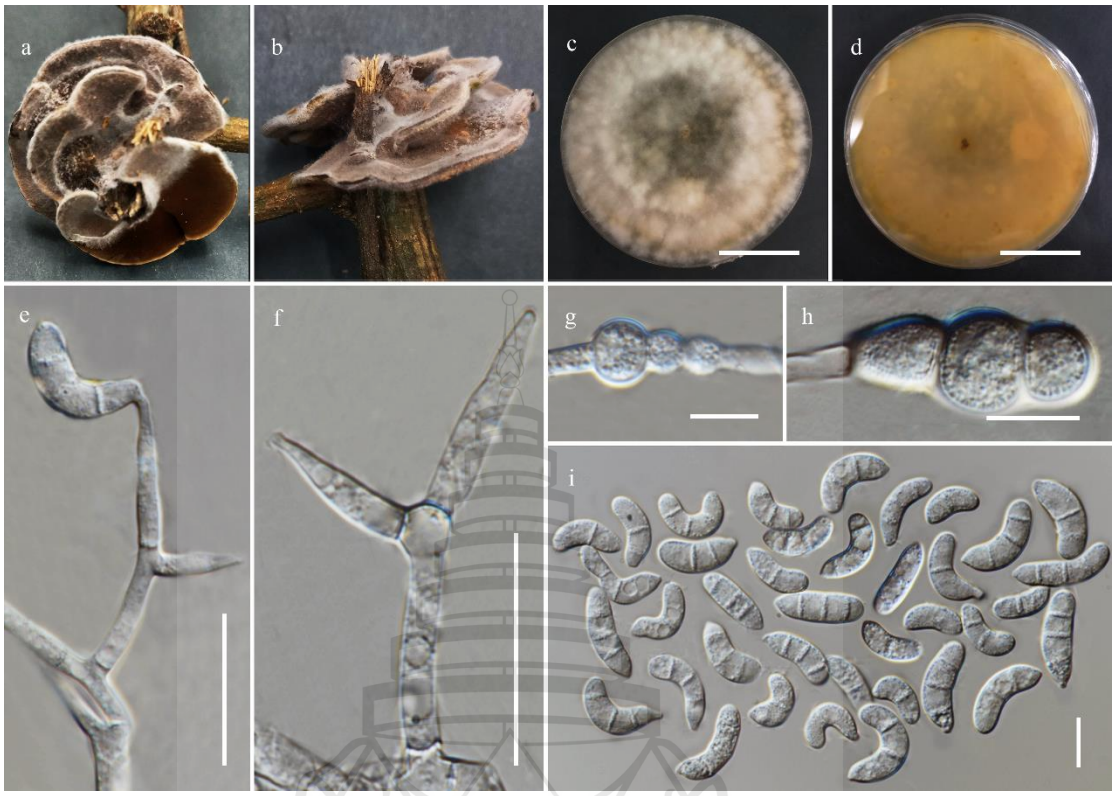


Figure 3.30 *Hypomyces semicircularis* (MFLU 24-0225)

Figure 3.30, a, b. Host (Polypore). c, d. Colony on PDA. e, f. Conidiogenous cells and conidial attachment. g, h. Chlamydospores. i. Conidia. Scale bars: c, d = 30 mm, f = 25 µm, e = 20 µm, h = 15 µm, g, i = 10.

3.25 *Hypoxylon* Bull., Hist. Champ. Fr. (Paris) 1(1): 168 (1791)

Hypoxylon was established by Bulliard (1791), with *H. fragiforme* designated as the type species. This comprises more than 200 species to date and it is classified within *Hypoxylaceae* (Hyde et al., 2024a; Species Fungorum, 2025).

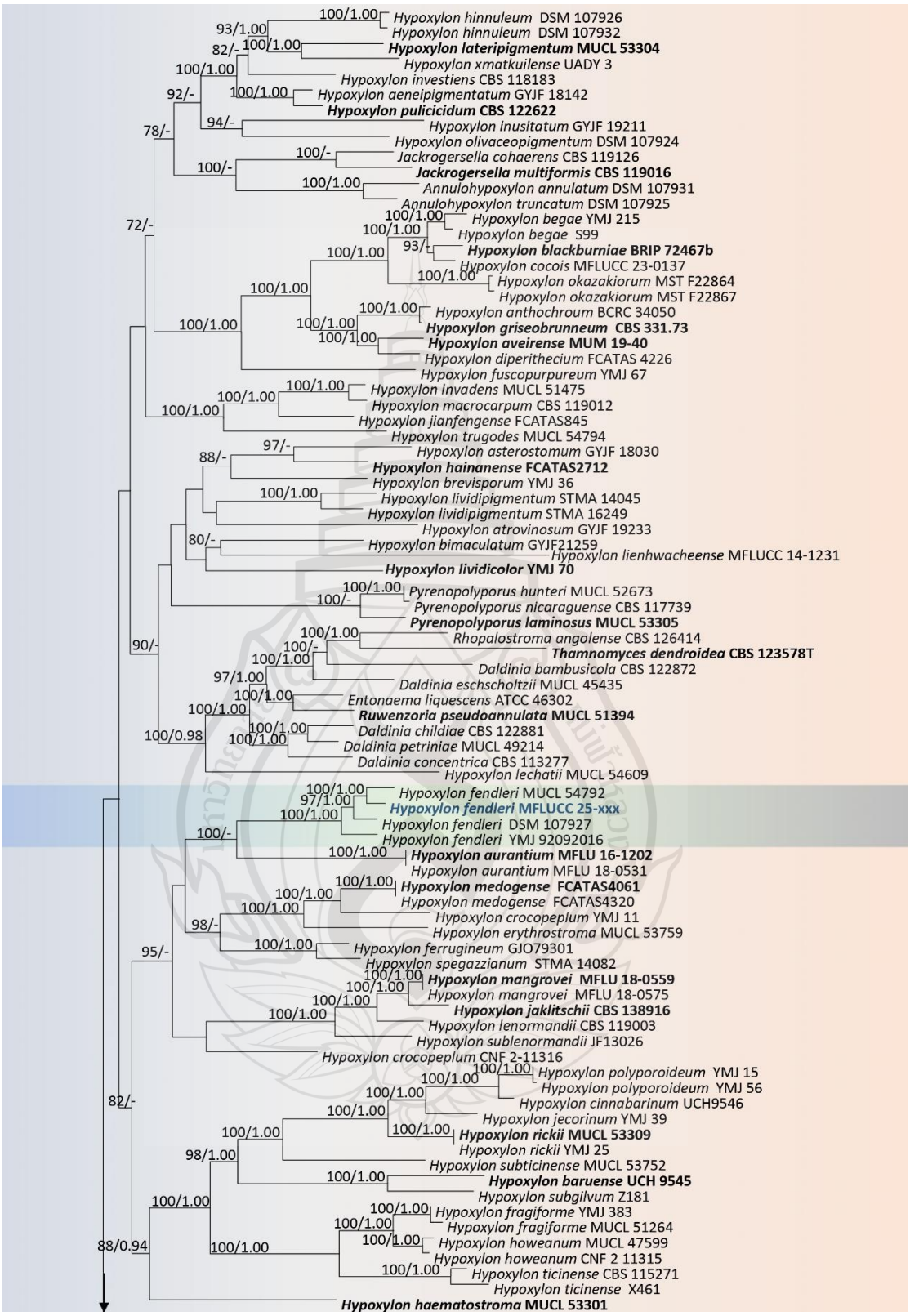


Figure 3.31 Phylogenetic tree generated by ML analysis of combined ITS, LSU, *rpb2* and *tub2* sequence data of *Hypoxylon* and related genera

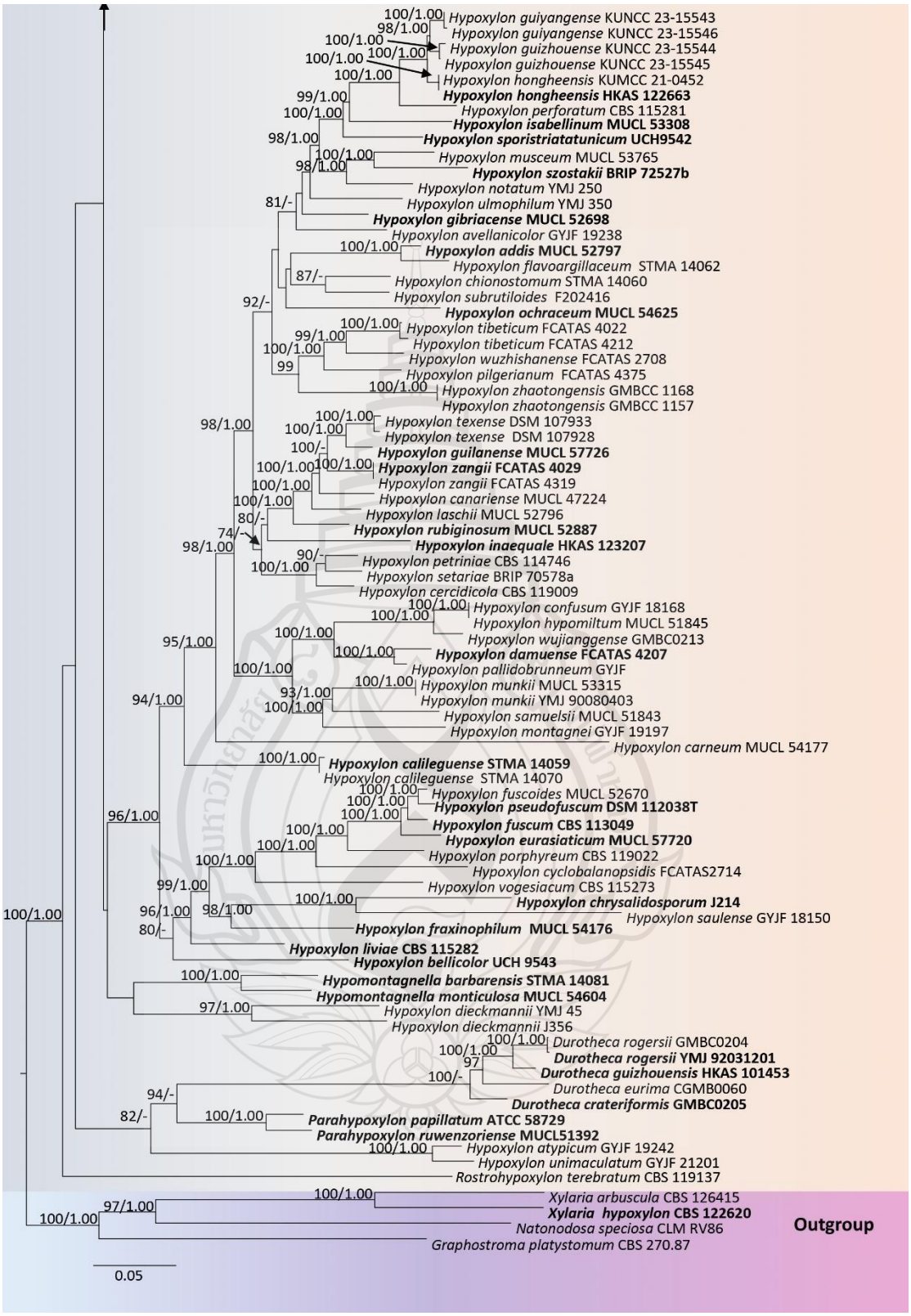


Figure 3.31 (continued)

Figure 3.31, A total of 164 strains were included in the analyses. The tree is rooted with *Graphostroma platystomum* (CBS 270.87), *Natonodosa speciose* (CLM-RV86), *Xylaria arbuscula* (CBS 126415), and *X. hypoxylon* (CBS 122620). The best scoring ML tree with an optimal log-likelihood value of −70600.272 is presented. The matrix had 1610 distinct alignment patterns, with 30.05% of undetermined characters or gaps. Bootstrap support values for ML ≥ 70% and BYPP ≥ 0.90 values for BI (BS/BYPP) are shown respectively near the nodes. Type (holotype/ex-type/isotype/paratype) strains are in bold. The strains reported in this study are in blue bold.

Hypoxylon fendleri Berk. ex Cooke, Grevillea 11(no. 60): 132 (1883)

Figure 3.32

Index Fungorum number: IF 206066

Fungicolous on a polypore fruiting body. Sexual morph: ascospore masses and black primordia observed on the polypore fruiting body. *Ascospores* 8–10.5 × 3.5–5.5 μm ($\overline{x}$ = 9 × 4.5 μm, n = 30), one-celled, brown to dark brown, with sigmoid germ slit spore-length, ellipsoid-inequilateral, with narrowly rounded ends, smooth or with inconspicuous coil-like ornamentation, perispore dehiscent in 10% KOH, epispore smooth. Asexual morph: thin white mycelium growing on the host. on CMA, chlamydosporus, *Mycelium* 1.5–2.5 μm ($\overline{x}$ = 2 μm, n = 30) wide, hyaline, septate, aerial mycelium sometimes forms hyphal coils. *Chlamydospores* 3–6 μm ($\overline{x}$ = 4.5 μm, n = 20) diameter, globose to subglobose, hyaline, intercalary, solitary or formed as chains.

Colony characters – on PDA at 25 °C, 30–35 mm in 7 days. Colony surface initially white with abundant aerial mycelium, velvety and later turns pale yellow at the centre. Reverse of the colony is pale brown.

Material examined – Thailand, Chiang Rai: Muang, Nang Lae (20° 2′ 24.9216″N, 99° 54′ 2.1996″E), isolated from mycelium on a polypore fruiting body, 17 October 2023, A.J. Gajanayake, AJ 48-23.

Notes – Our isolate AJ 48-23 clustered within *Hypoxylon fendleri* (MUCL 54792, DSM 107927, YMJ 92092016) with 100% BS and 1.00 BYPP (Figure 3.31). On the host substrate, only immature stromatal structures, ascospore masses, and mycelium were observed. Colonies on CMA, OA and PDA failed to produce

reproductive structures, with only chlamydospores formed in culture. Nonetheless, ascospore morphology matches the previous descriptions and illustrations of *H. fendleri* (Liu et al., 2015a; Cedeño-Sanchez et al., 2020). Therefore, based on the existing phylogenetic and morphological evidences we confirmed that our isolate, AJ 48-23, is *H. fendleri.*

Hypoxylon fendleri has previously been recorded in Thailand on decaying wood and dead bamboo clumps (Liu et al., 2015a). This study marks the first report of this species occurring on a mushroom. The polypore fruiting body hosting *H. fendleri* was growing on decaying wood, suggesting the possibility that ascospores from *H. fendleri* stromata on wood may have dispersed onto the polypore, initiating colonization. However, since the wooden host of the polypore was not examined in detail, we cannot confirm this hypothesis. Further collections and observations are necessary to confirm whether this represents a true host association or an incidental colonization.

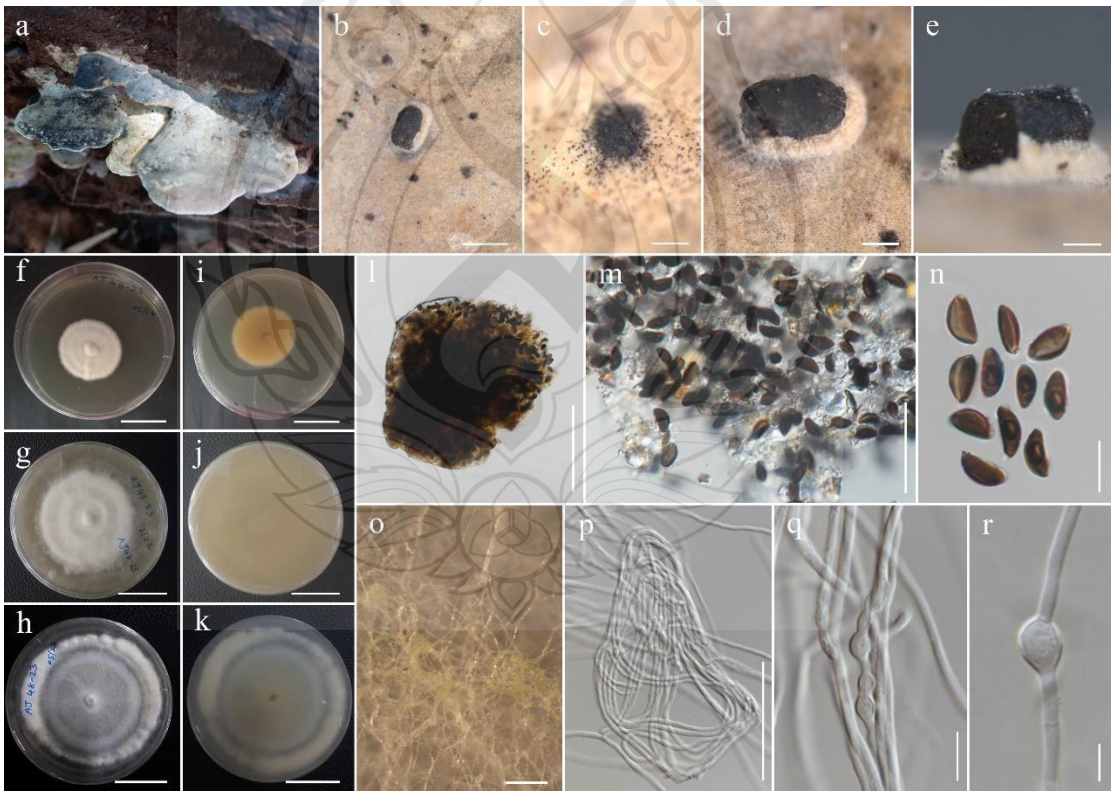


Figure 3.32 *Hypoxylon fendleri* (AJ 48-23)

Figure 3.32, a. Host (Polypore fruiting body). b–e. Ascospore masses and immature stromata on the host. f–h. Colony from above on PDA, OA and CMA. i–k. Colony from below on PDA, OA and CMA. l, m. Ascospore masses. N. Ascospores. o. Mycelium on CMA. p. Hyphal coil. q, r. Chlamydospores. Scale bars: b–e = 2.5 mm, f–k = 30 mm, o = 250 μm, l = 100 μm, p = 50 μm, m = 35 μm, n, q = 10 μm, r = 5 μm.

3.2.6 *Lasiodiplodia* Ellis & Everh., in Clendenin, Bot. Gaz. 21: 92 (1896)

Lasiodiplodia was introduced by Ellis and Everhart (1894), with a formal generic description later provided by Clendenin (1896). The genus was originally typified by *L. tubericola*, which is currently recognized as *L. theobromae* (Liu et al., 2012). There are 92 species listed under *Lasiodiplodia* in Species Fungorum (2025) and it is classified within *Botryosphaeriaceae* (Hyde et al., 2024a).

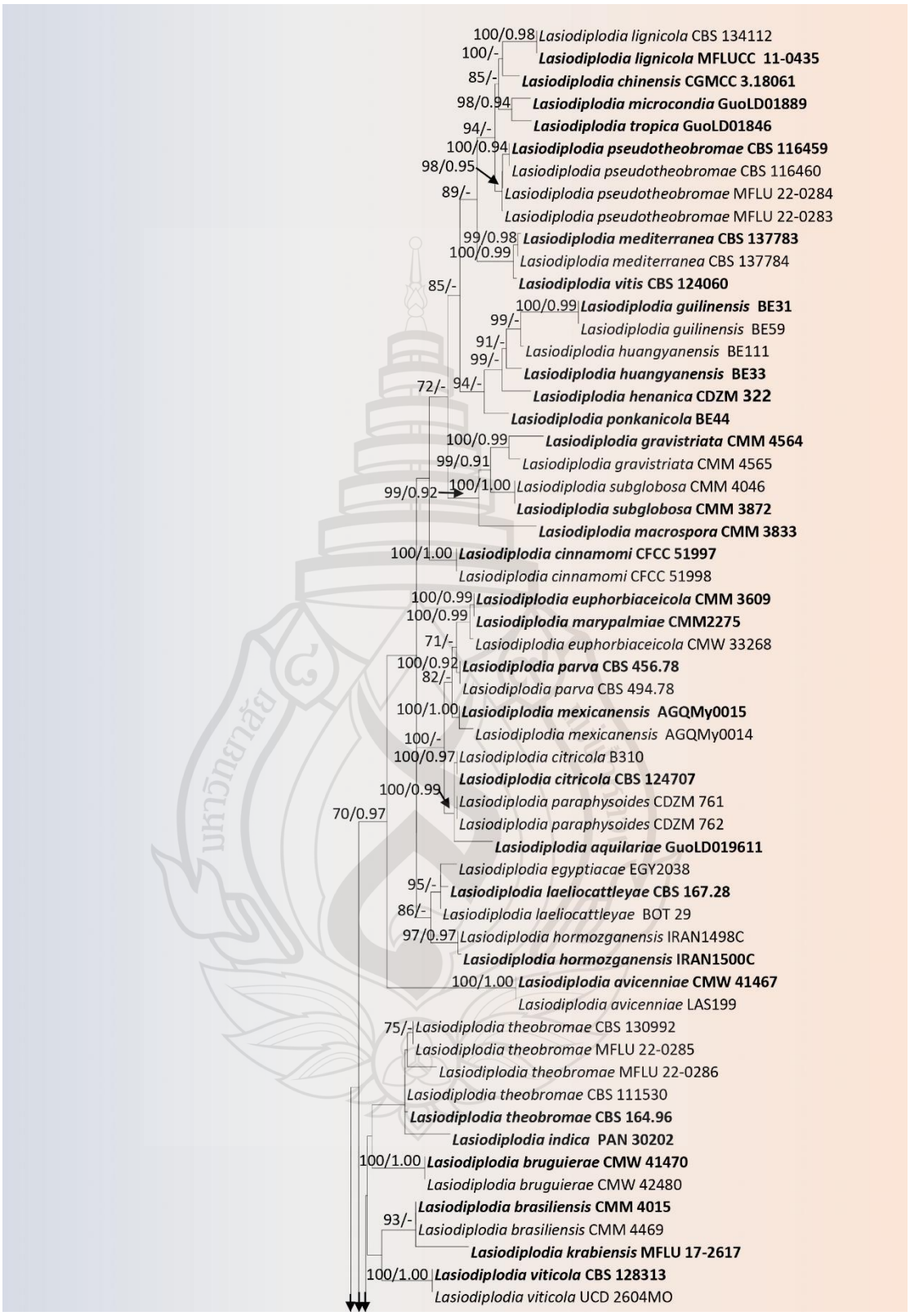


Figure 3.33 Phylogenetic tree generated by ML analysis of combined ITS, *tef-1α*, *tub2*, and *rpb2* sequence data of *Lasiodiplodia* taxa

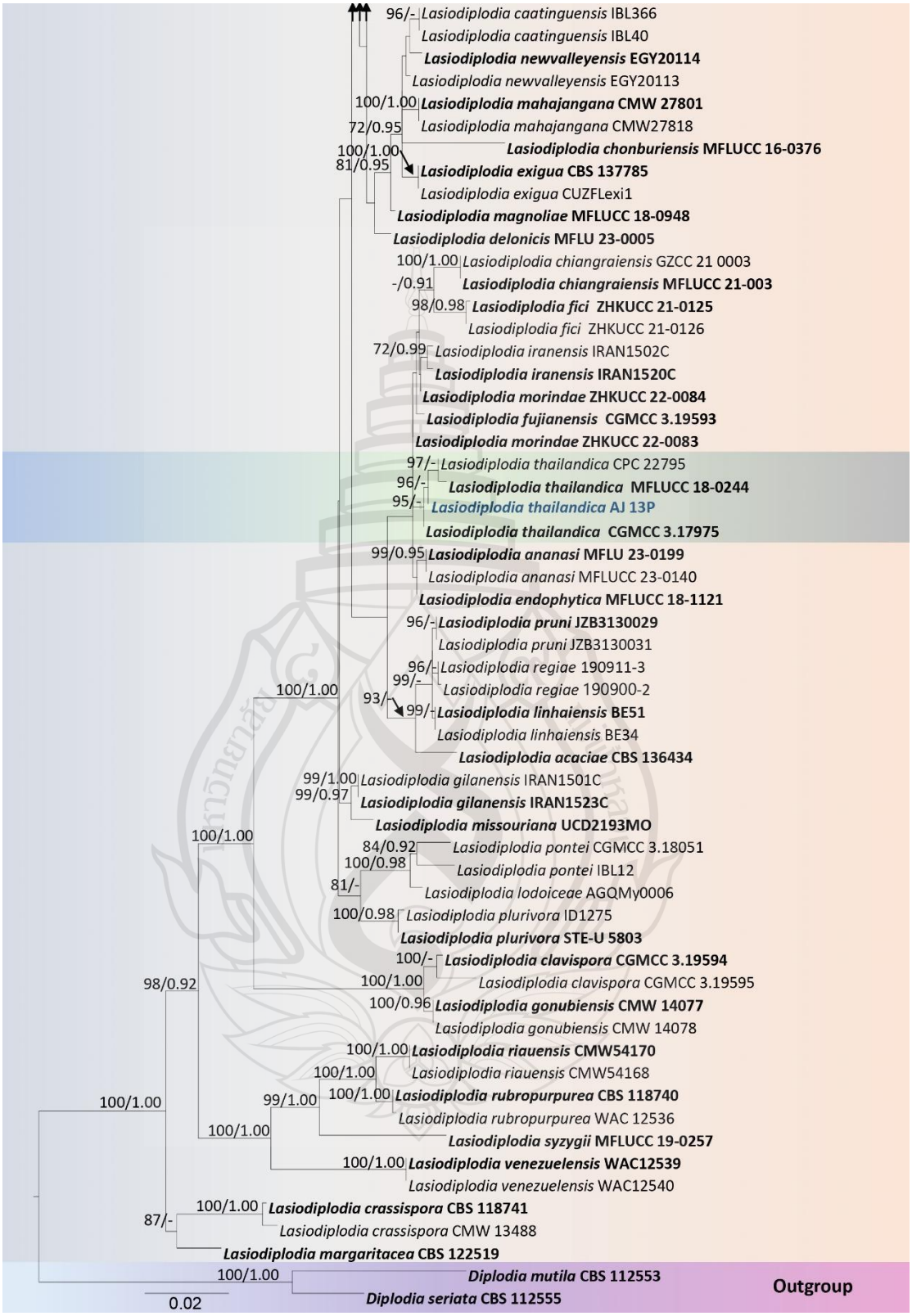


Figure 3.33 (continued)

Figure 3.33, A total of 115 strains were included in the analyses. The tree is rooted with *Diplodia mutila* (CBS 112553) and *Diplodia seriata* (CBS 112555). The best scoring ML tree with an optimal log-likelihood value of −8648.332 is presented. The matrix had 587 distinct alignment patterns, with 27.69% of undetermined characters or gaps. Bootstrap support values for ML ≥ 70% and BYPP ≥ 0.90 values for BI (BS/BYPP) are shown respectively near the nodes. Type (holotype/ex-type/isotype/paratype) strains are in bold. The strains reported in this study are in blue bold.

Lasiodiplodia thailandica Trakun., L. Lombard & Crous, Persoonia 34: 95 (2015)

Figure 3.34

Index Fungorum number: IF 810169

Fungicolous on a polypore fruiting body. Sexual morph: not observed. Asexual morph: white to grey fluffy mycelial patches on a polypore fruiting body. On PDA, coelomycetous. *Conidiomata* 150–300 × 120–250 μm ($\bar{x}$ = 225 × 185 μm, n = 10), pycnidial, semi-immersed, solitary or aggregated, dark brown to black, unilocular, with globose base, outer layers composed of dark brown *textura angularis*, becoming thin-walled and hyaline toward the inner region. *Hyphal hairs* 3–6 μm ($\bar{x}$ = 4.5 μm, n = 30) wide, brown, septate, with rounded tips covering the outer wall of fruiting body. *Ostiole* 30–50 μm diameter, central, circular, conidiomata papillate. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* 7–11 × 2–4 μm ($\bar{x}$ = 9 × 2.5 μm, n = 30), hyaline, smooth, thin-walled, discrete, cylindrical, holoblastic, proliferating percurrently from hyaline inner conidiomatal wall. *Paraphyses* 20–45 × 1–2 μm, hyaline, smooth, thin-walled, cylindrical, originating from the hyaline inner cells of pycnidial wall, the basal cells often slightly swollen, the apical cells with end-rounded tip, 1–3-septate. *Conidia* 1–1.5 μm thick, 16–23.5 × 9–14 μm ($\bar{x}$ = 20 × 12 μm, n = 50), initially hyaline, broadly ellipsoid, with granularcontent, and typically aseptate, upon release from pycnidia, a few conidia become pale brown, developing a single median septum and exhibiting longitudinal striations, while the majority remain hyaline.

Colony characters – on PDA at 25 °C, 70–80 mm in 7 days. Initially the colony is with white fluffy mycelium, with time mycelium becomes dense and

flattening at the centre, and turns smoky-grey to olivaceous-grey with age. Reverse of the colony turn greenish olivaceous to black-olivaceous with age.

Material examined – Thailand, Phayao: Dong Suwan, Dok Khamtai (19° 13' 55.1964" N, 100° 5' 16.422" E), isolated from the mycelium growing on a polypore fruiting body, 04 September 2023, A.J. Gajanayake, AJ 13P1.

Notes – Our isolate AJ 13P1, clustered within *Lasiodiplodia thailandica* (CPC 22795, CGMCC 3.17975, MFLUCC 18-0244) with 96% BS, and 0.80 BYPP (Figure 3.33). The morphological features of AJ 13P1 match the original description and illustrations of *L. thailandica* provided by Trakunyingcharoen et al. (2015), except for slight differences in the dimensions of morphological structures. These variations are possible due to differences in the agar medium and cultural conditions (Senanayake et al., 2020). Therefore, we confirmed that our isolate, AJ 13P1, is phylogenetically and morphologically consistent with *L. thailandica*.

Lasiodiplodia thailandica was originally described by Trakunyingcharoen et al. (2015) associated with *Mangifera indica* and *Phyllanthus acidus* in Thailand. Subsequently, this species has been reported on a wide range of plant hosts in Thailand including, *Cocos nucifera*, *Delonix regia, Hevea brasiliensis*, *Holmskioldia* sp., *Macaranga peltate, Magnolia lilifera, Musa* sp., *Swietenia mahagoni*, *Tectona grandis,* and *Wodyetia bifurcate* (Rathnayaka et al., 2023). Beyond Thailand, *L. thailandica* has also been recorded in China and Japan (Hattori et al., 2023; Rathnayaka et al., 2023). This study is the first to report *L. thailandica* as a fungicolous species on a polypore fruiting body in Thailand and globally.

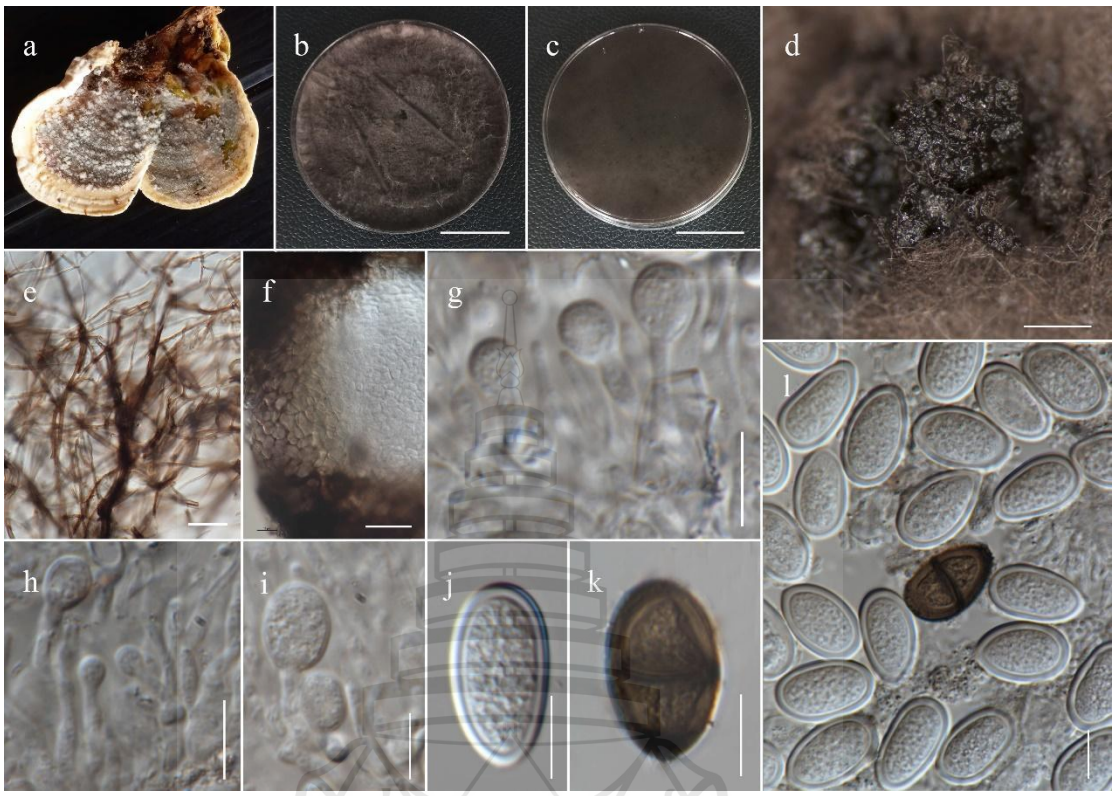


Figure 3.34 *Lasiodiplodia thailandica* (AJ 13P1)

Figure 3.34, a. Host (Polypore). b, c. Colony on PDA. d. Sporulation on PDA. e. Hyphyal hairs. f. Peridium. g–i. Conidiogenious cells with conidial attachment. j–l. Conidia. Scale bars: b, c = 30 mm, d = 750 μm, e = 40 μm, f = 20 μm, g–l = 10 μm.

3.2.7 *Mariannaea* G. Arnaud ex Samson, Stud. Mycol. 6: 74 (1974)

Mariannaea was initially proposed by Arnaud (1952) with the single species *M. elegans*, was subsequently redefined by Samson (1974). There are 23 species listed under *Mariannaea* in Species Fungorum (2025) and it is classified within *Nectriaceae* (Hyde et al., 2024a).

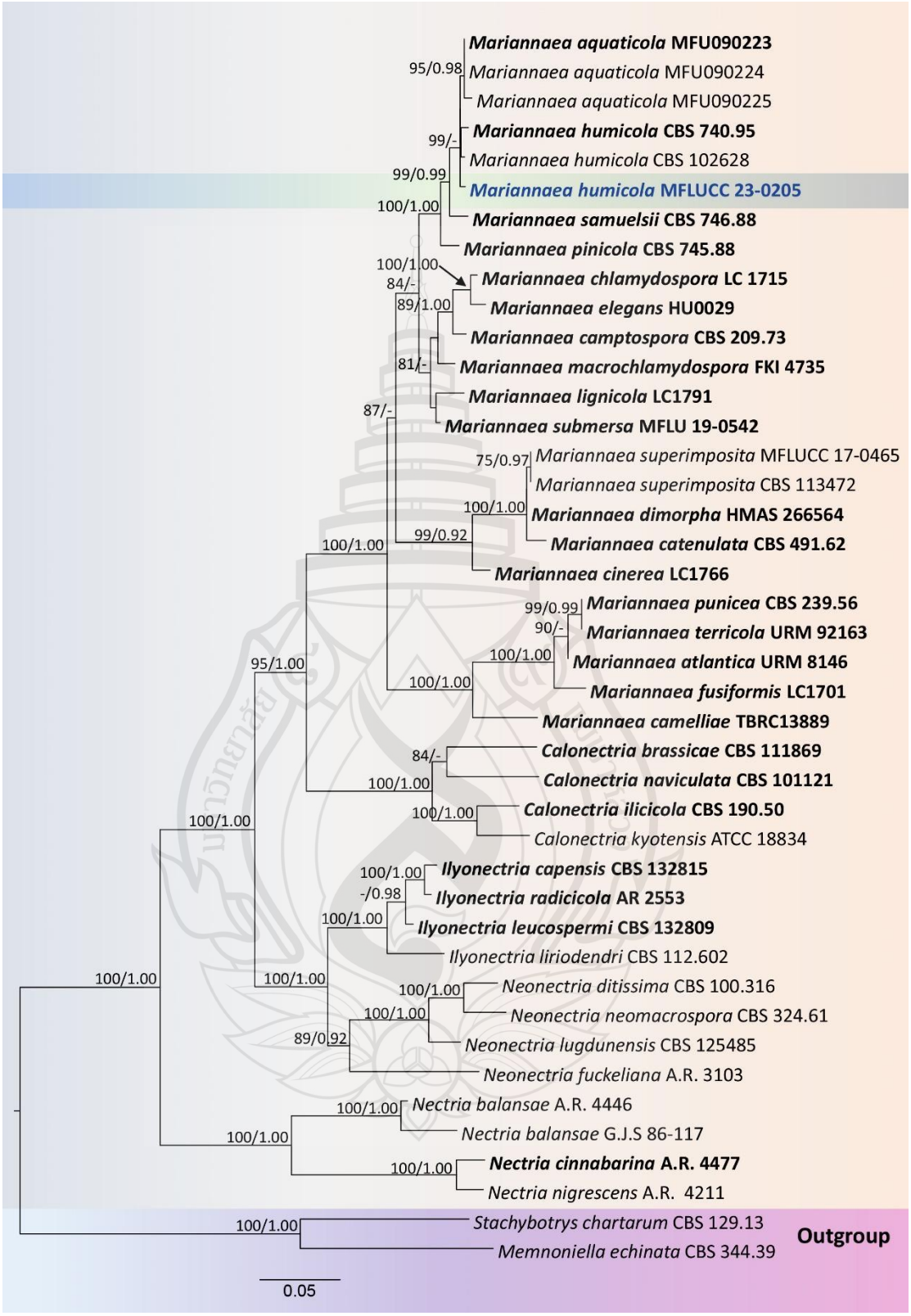


Figure 3.35 Phylogenetic tree generated from the maximum likelihood (ML) analysis based on ITS-LSU-*tub2*-*tef1α* sequence matrix with sequence data of *Mariannaea* and related genera

Figure 3.35, The combined ITS, LSU, *tub2* and *tef1α* matrix comprised 42 epithets that belong to *Nectriaceae* and two outgroup taxa, *Memnoniella echinata* (CBS 344.39) and *Stachybotrys chartarum* (CBS 129.13). The tree is rooted with *Memnoniella echinata* (CBS 344.39) and *Stachybotrys chartarum* (CBS 129.13). The concatenated alignments resulted in mostly similar topologies for both ML and BI analyses. The sequence matrix of four alignment files included ITS (401 bp), LSU (789 bp), *tub2* (619 bp), and *tef1α* (919 bp) sequence data (a total of 2728 characters). The best-scoring ML tree is shown in FIG. 2, with an optimal log-likelihood value of −16862.038. The matrix had 1051 distinct alignment patterns, with 33.30% of undetermined characters or gaps. The proportion of invariable sites was 0.552. Maximum likelihood bootstrap supports (≥75%), and BI posterior probabilities (≥0.90) are denoted near the respective nodes. The type strains are in black bold, whereas the strain reported in this study is in blue bold.

Mariannaea humicola L. Lombard & Crous, in Lombard, van der Merwe, Groenewald & Crous, Stud. Mycol. 80: 213 (2015) Figure 3.36

Index Fungorum number: IF 810165

Fungicolous on the fruiting bodies of *Marasmius* sp. Sexual morph: not observed. Asexual morph: on the host, Mycelium present as scattered white cottony masses. On PDA, hyphomycetous, *Hyphae* 3–6 μm ($\overline{x}$ = 4 μm, n = 30) wide, septate, hyaline. *Conidiophores* 100–310 × 2–5 μm ($\overline{x}$ = 204.5 × 3.5 μm, n = 20), rising from aerial hyphae or the agar surface, verticillately branching at 2–3 levels, with a terminal whorl of 1–6 phialides, and forming 1–2 lower nodes with 1–3 phialides or rarely with single phialides. *Phialides* 11–23 × 2–4 μm ($\overline{x}$ = 15.5 × 3 μm, n = 40), subulate, with a slightly swollen base, having an inconspicuous collarette. *Conidia* 3.5–7 × 2–4 μm ($\overline{x}$ = 5 × 3 μm, n = 45), produced in chains and later separated to be single, fusiform to ellipsoidal to obovoid, hyaline, some are slightly guttulate, with a hilum at both or at one end. *Chlamydospores* intercalary or terminal.

Colony characters – on PDA, at 25 °C, reached 50–60 mm after 7 days of incubation. Having a velutinous appearance, with age turning funiculose to fasciculate, slightly powdery nature due to sporulation, initially the surface of the

colony pale yellowish, later with age turning brown to dark brown, margin regular irregular.

Material examined – Thailand, Chiang Mai Province, Mae Tang, Pa Pae, Ban Pha Deng, isolated with the mycelium growing on a cap of *Marasmius* sp., 6 July 2021, Gajanayake A.J, MR 07 (inactive dry culture MFLU 23-0422), living culture MFLUCC 23-0205.

GenBank numbers – MFLUCC 23-0205: ITS = OR473193; LSU = OR473255; *tub2* = OR742383; *tef1α* = OR742382.

Notes – In the phylogenetic analyses (Figure 3.35), our isolate MFLUCC 23-0205 clustered with *Mariannaea humicola* strains CBS 740.95 and CBS 102628 with 99 % BS and 0.86 PP value. Additionally, the morphological characteristics of our isolate MFLUCC 23-0205, described herein, are similar to the original description and illustrations given in Lombard et al. (2015). The conidiophore length and the phialides length of MFLUCC 23-0205 are higher than those of *M. humicola*, described by Lombard et al. (2015): conidiophores: 100–310 × 2–5 μm *vs*. 80–100 × 3–7 μm, phialides: 11–23 × 2–4 μm *vs*. 10–20 × 2–4 μm. In contrast to *M. humicola* described in Lombard et al. (2015), chlamydospores and conidial chains were observed in MFLUCC 23-0205. These differences may have occurred due to the variations of the agar medium, the conditions used to obtain the cultures, and the time spent observing the morphology after isolation. Therefore, we confirmed that our isolate MFLUCC 23-0205 is *M. humicola*. There are previous reports of *M. humicola* being isolated from soil and the seagrass *Posidonia oceanica* as an epiphyte (Lombard et al., 2015; Le, 2019; Botta et al., 2020). To the best of our knowledge, this is the first report of *M. humicola* on a fruiting body of *Marasmius* sp. as a fungicolous fungus from Thailand.

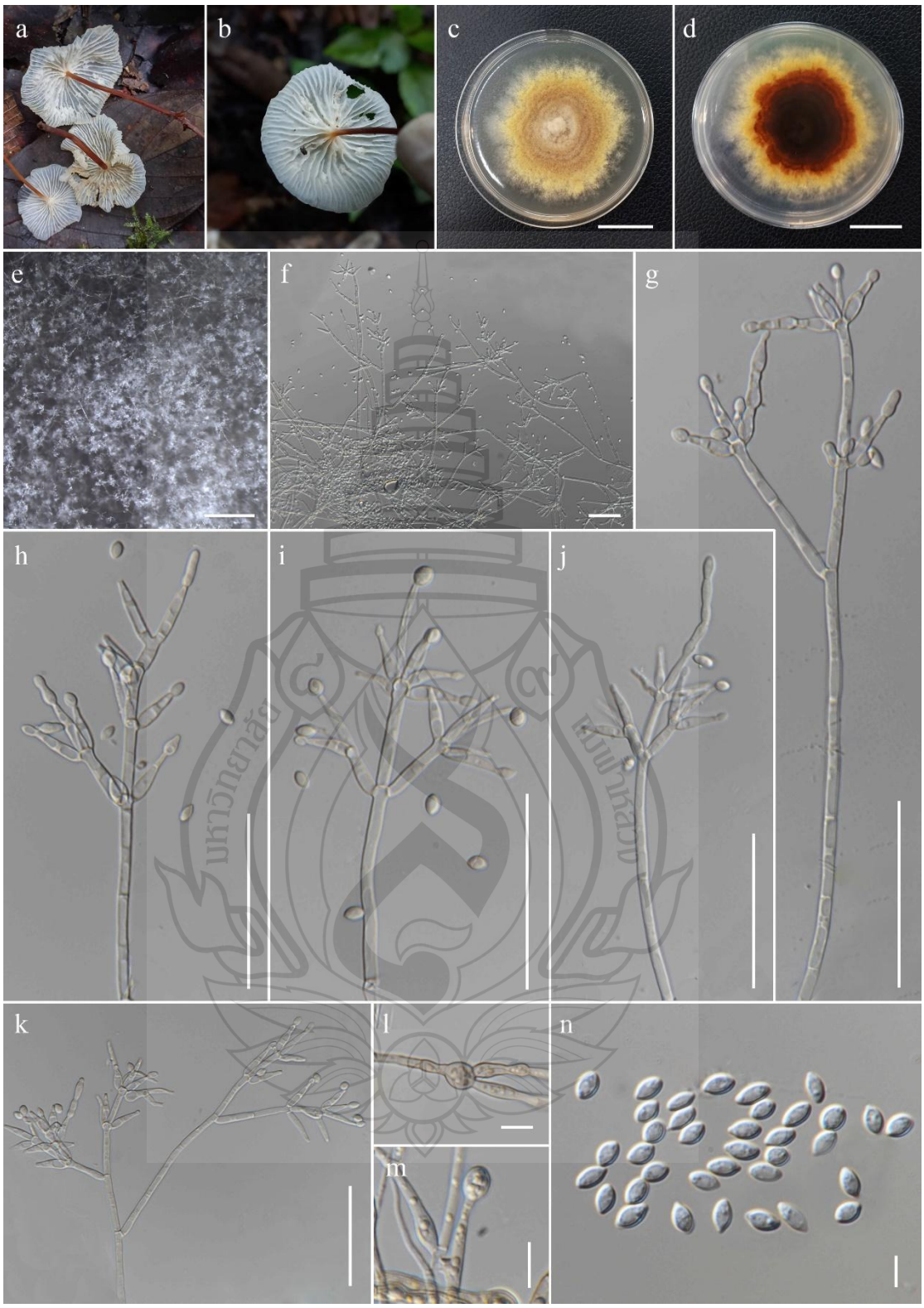


Figure 3.36 *Mariannaea humicola* (MFLU 23-0422)

Figure 3.36, a Host (*Marasmius* sp.) b Mycelium presents as scattered white cottony masses on the host (marked in black arrows). c, d Colony on PDA. e Sporulation on PDA. f–k Conidiophores with verticillate phialides. l, m Chlamydospores. n Conidia. Scale bars: c, d = 30 mm, e = 100 μm, f–k = 50 μm, l, m = 10 μm, n = 5 μm.

3.2.8 *Mucor* Fresen., Beitr. Mykol. 1: 7 (1850)

Mucor, the largest genus in *Mucorales* belonging to *Mucoromycotina*, was originally described by Fresenius (1850) and is typified by *M. mucedo* Fresen. (Nguyen et al., 2020; Walther et al., 2019; Wijayawardene et al., 2022). There are over 100 species accepted within *Mucor* and it is classified within *Mucoraceae* (Hyde et al., 2024a).

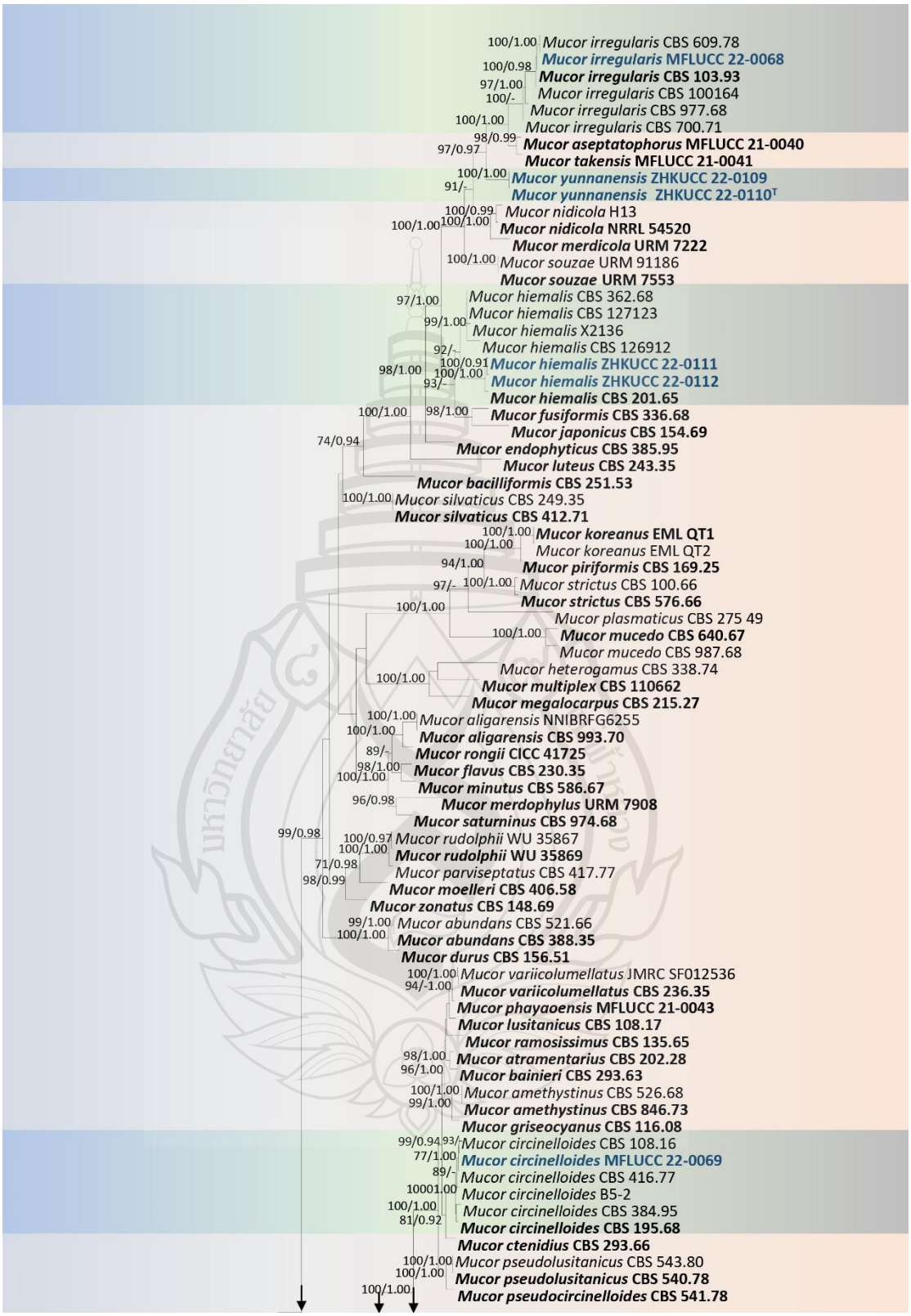


Figure 3.37 Phylogenetic tree generated from the maximum likelihood (ML) based on ITS-LSU sequence matrix

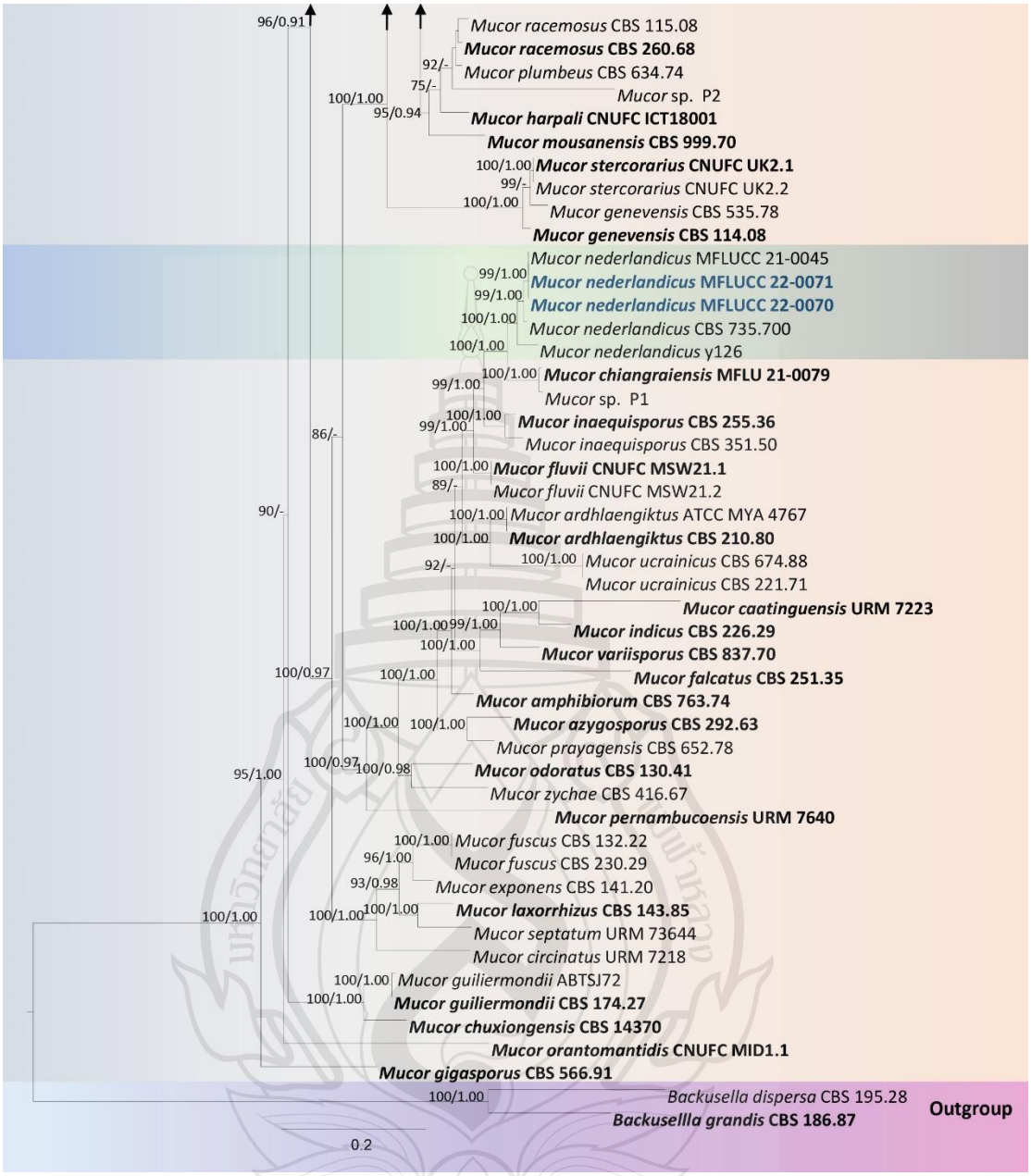


Figure 3.37 (continued)

Figure 3.37, The combined ITS and 28S matrix comprised 123 epithets that belong to *Mucor* and two outgroup taxa, *Backusella dispersa* (Hagem) Urquhart & Douch (CBS 195.28) and *B. grandis* (Schipper & Samson) Walther & de Hoog (CBS 186.87). The tree is rooted with *Backusella dispersa* (CBS 195.28) and *B. grandis* (CBS 186.87). The concatenated alignments resulted in mostly similar topologies for both ML and BI analyses. The best-scoring ML tree is with an optimal log-likelihood value of −20 887.925. The matrix had 741 distinct alignment patterns, with 9.47% of

undetermined characters or gaps. The proportion of invariable sites was 0.380. ML bootstrap supports (≥70%) and BI posterior probabilities (≥0.90) are denoted near the respective nodes. The type strains are in black bold while the strains reported in this study are in blue bold.

Mucor yunnanensis Gajanayake., Karun. & Jayaward, sp. *nov*.

Figure 3.38

Index Fungorum number: IF 845752

Typification – China, Yunnan, Lijiang, Shigu, isolated from the white mycelium growing on a fruiting body of *Armillara* sp., 03 June 2020, S.C. Karunarathna, SG 069 (holotype ZHKU 22-0058). Ex-holotype culture ZHKUCC 22-0110.

GenBank numbers – ITS = ON921544, LSU = ON921546.

Diagnosis – *Mucor yunnanensis* is phylogenetically distinct from all other *Mucor* species. Sporangia globose, Sporangiospores on PDA measures 2.3–7.2 × 1.5–4.4 μm, mostly ellipsoidal, occasionally oval or irregular, smooth-walled, hyaline with granular content in the middle.

Etymology – The epithet refers to the place "Yunnan Province" where the species was collected.

Fungicolous on a fruiting body of *Armillara* sp. Sexual morph: not observed. Asexual morph: on PDA, *Sporangiophores* up to 4.2–19.7 μm ($\overline{x}$ = 9.6 μm, n = 50) width, hyaline, occasionally curved, septate, sympodial or monopodial branches formed. *Sporangia* 20–38 × 21.8–37 μm ($\overline{x}$ = 29.6 × 30 μm, n = 12), globose, matured sporangial wall deliquescent, transparent and easily broken, hyaline. *Columellae* 13.5–31.5 × 10–30 μm ($\overline{x}$ = 21 × 19 μm, n = 35), mostly globose to sub globose, and rarely ellipsoid, collar present oftenly, hyaline to pale brown, smooth-walled. *Sporangiospores* 2.3–7.2 × 1.5–4.4 μm ($\overline{x}$ = 4.7 × 2.5 μm, n = 50), mostly ellipsoidal, occasionally oval or irregular, smooth-walled, hyaline with granular content in the middle. *Chlamydospores* abundant, intercalary and terminal, variable in shape and size. Hyphal bulges were frequently observed.

Colony characters – on PDA, at 25 °C, cultures are cottony and white to pale yellow. The colony reached 60 mm diam. after 5 days of incubation.

Additional materials examined – China, Yunnan, Lijiang, Shigu, isolated from the white mycelium growing on a fruiting body of *Boletus* sp., 29 June 2020, S.C. Karunarathna, SG 08B (paratype ZHKU 22-0057), Ex-paratype culture ZHKUCC 22-0109.

GenBank numbers – ZHKUCC 22-0109: ITS = ON921545; LSU = ON921549.

Notes – Based on our phylogenetic analyses it was observed that, *M. yunnanensis* is phylogenetically distinct from *M. irregularis*, *M. aseptatophorus* and *M. takensis* and the placement was stable in both ML and BI analyses. Two strains of *M. yunnanensis* form a sister clade to the clade formed by *M. irregularis*, *M. aseptatophorus*, *M. takensis* with 97% bootstrap support (Figure 3.37). The genetic distance between the newly described *Mucor* species and the respective sister taxa, in their trimmed ITS region 580 base pairs (bp) for *M. irregularis* (CBS 103.93), 601 bp for *M. aseptatophorus* (MFLUCC 21-0040), 607 bp for *M. takensis* (MFLUCC 21-0041), 452 bp for *M. nidicola* (NRRL 54520) and 574 bp for *M. merdicola* is shown in Table 3.4. Simultaneously, *M. yunnanensis* is clustered within the sister clade formed to the clade consisting *M. nidicola* and *M. merdicola*. The synopsis of morphological characteristics related to the taxon introduced in this study and relevant sister taxa are shown in Table 3.5. During the micro-morphologcal examination of *M. yunnanensis*, only 12 sporangia were measured as most of the sporangia were easily broken during the slide preparation due to the prevalence of deliquescent sporangial wall. In contrast to *M. irregularis*, highly variable shapes in columellae and sporangiospores were not observed in *M. yunnanensis* as it forms mostly globose to sub globose, and rarely ellipsoid columellae and mostly ellipsoidal, occasionally oval or irregular sporangiospores. Furthermore, the sizes of sporangia, sporangiospores and columellae are higher in *M. irregularis* when compared with *M. yunnanensis*. In contrast to *M. aseptatophorous*, septa were observed below sporangia in *M. yunnanensis*. The size of sporangia is higher in *M. aseptatophorous* when compared with *M. yunnanensis*. In contrast to *M. takensis*, sporangiophores were septate in *M. yunnanensis*. The size of sporangiospores is smaller in *M. takensis* compared to *M. yunnanensis* while granular content is observed in sporangiospores of *M. yunnanensis*

in contrast to *M. takensis*. Therefore, based on both phylogeny and morphology, *M. yunnanensis* is introduced as a new species.

Table 3.4 Genetic distance (%) of the trimmed ITS regions between the newly described *Mucor* species and the respective sister taxa. Distances were calculated using the Kimura2 parameter and gaps were considered as pairwise deletions

	% Genetic distance	
Sister taxa	*M. yunnanensis* (ZHKUCC 22-0109)	*M. yunnanensis* (ZHKUCC 22-0110)
M. aseptatophorus (MFLUCC 21-0040)	8.09	8.29
M. merdicola (URM 7222)	9.56	9.56
M. nidicola (NRRL 54520)	7.32	7.32
M. takensis (MFLUCC 21-0041)	8.95	9.15
M. irregularis (CBS 103.93)	8.11	8.11

Table 3.5 Synopsis of morphological characteristics related to the new taxon introduced in this study and relevant sister taxa

Taxon	**Sporangia**	**Sporangiospores**	**Columellae**	**Reference**
M. aseptatophorus	Globose to sub globose, smooth-walled, thick-walled and persistent, yellow to pale brown, 18–56.5 × 19–54 µm ($\bar{x}$ = 41.5 × 41.5 µm, n = 40)	Mostly ellipsoidal, occasionally oval to globose, some irregular, hyaline, 3.5–6 × 2–4 µm ($\bar{x}$= 4 × 3 µm, n = 70)	Globose, with a very short collar, hyaline to pale brown, non-collapsing, smooth-walled, 13–35 × 14–37.5 µm ($\bar{x}$= 19 × 20 µm, n = 40)	Hurdeal et al. (2021)

Table 3.5 (continued)

Taxon	Sporangia	Sporangiospores	Columellae	Reference
M. irregularis	Globose to slightly depressed globose, (23.5–) 35–106 μm in diam.	Variable in size and shape, ovoid, ellipsoid, oblong, sub globose, subtriangular or with other shapes, straight or curved, 2.5–11.5 (–16.5) × 2–7 μm	Very variable in size and shape, globose, sub globose, ovoid, ellipsoid, cylindrical, pyriform, conical, hemispherical, rarely degenerate, not frequently asymmetrical, sometimes longitudinally lobed, (15–) 23.5–59 μm in diam. or 23.5– 71× 26–82.5 μm	Zheng and Chen (1991)
M. merdicola	Globose (16–) 17.5–60 (–85) μm diam., initially yellow becoming greyish brown with diffluent wall, smooth-walled	Smooth-walled, hyaline, mostly ellipsoid to fusiform (2.5–)5–7×5–8.5 (–10.5), but also ellipsoid 4–7.5 × 3–7.5 (–10) μm or sub globose (2.5–)4–7.5(–8.5) μm diam.	Globose (12.5–)15–45 (–50) μm, subglobose and applanate (15–) 20–29 × 30–34 (–35) μm, hyaline or light to grey, smooth-walled; collar absent or little evident	Guo et al. (2016)
M. nidicola	Multisporate, globose, wall slowly dissolving or broken, 30–70 μm in diam., yellowish to brownish, smooth walled to warty.	Mostly ellipsoidal, but also kidney-shaped or irregular, 3–10 × 2–6 μm ($\bar{x}$ = 5.5 × 3.0 μm), pale greyish-brown, smooth- and thin- to thick walled	Globose to sub globose, non-collapsing, 15–40 × 20–45 μm, hyaline to pale brown, collar evident	Madden et al. (2012)

Table 3.5 (continued)

Taxon	Sporangia	Sporangiospores	Columellae	Reference
M. takensis	Globose, pale brown to brown, smooth-walled, and persistent, 12.5–46 × 13.5–47 µm ($\bar{x}$= 27 × 25 µm, n = 20)	Mostly ellipsoidal, occasionally globose, hyaline to pale yellow, abundant, smooth-walled, 3–5 × 2–3 µm ($\bar{x}$ = 4 × 2.5 µm, n = 32)	Globose to sub globose, hyaline to pale brown, with short collar, 7.5–38.5 × 11–45 µm ($\bar{x}$= 22 × 25 µm, n = 30)	Hyde et al. (2021)
M. yunnanensis	Globose, matured sporangia wall deliquescent, transparent and easily broken, hyaline, 20–38 × 21.8–37 µm ($\bar{x}$ = 29.6 × 30 µm, n = 12)	Mostly ellipsoidal, occasionally oval or irregular, smooth-walled, hyaline with granular content in the middle, 2.3–7.2 × 1.5–4.4 µm ($\bar{x}$ = 4.7 × 2.5 µm, n = 50)	Mostly globose to sub globose, and rarely ellipsoid, collar present in most of the times, hyaline to pale brown, smooth-walled, 13.5–31.5 × 10–30 µm ($\bar{x}$ = 21 × 19 µm, n = 35)	Current study

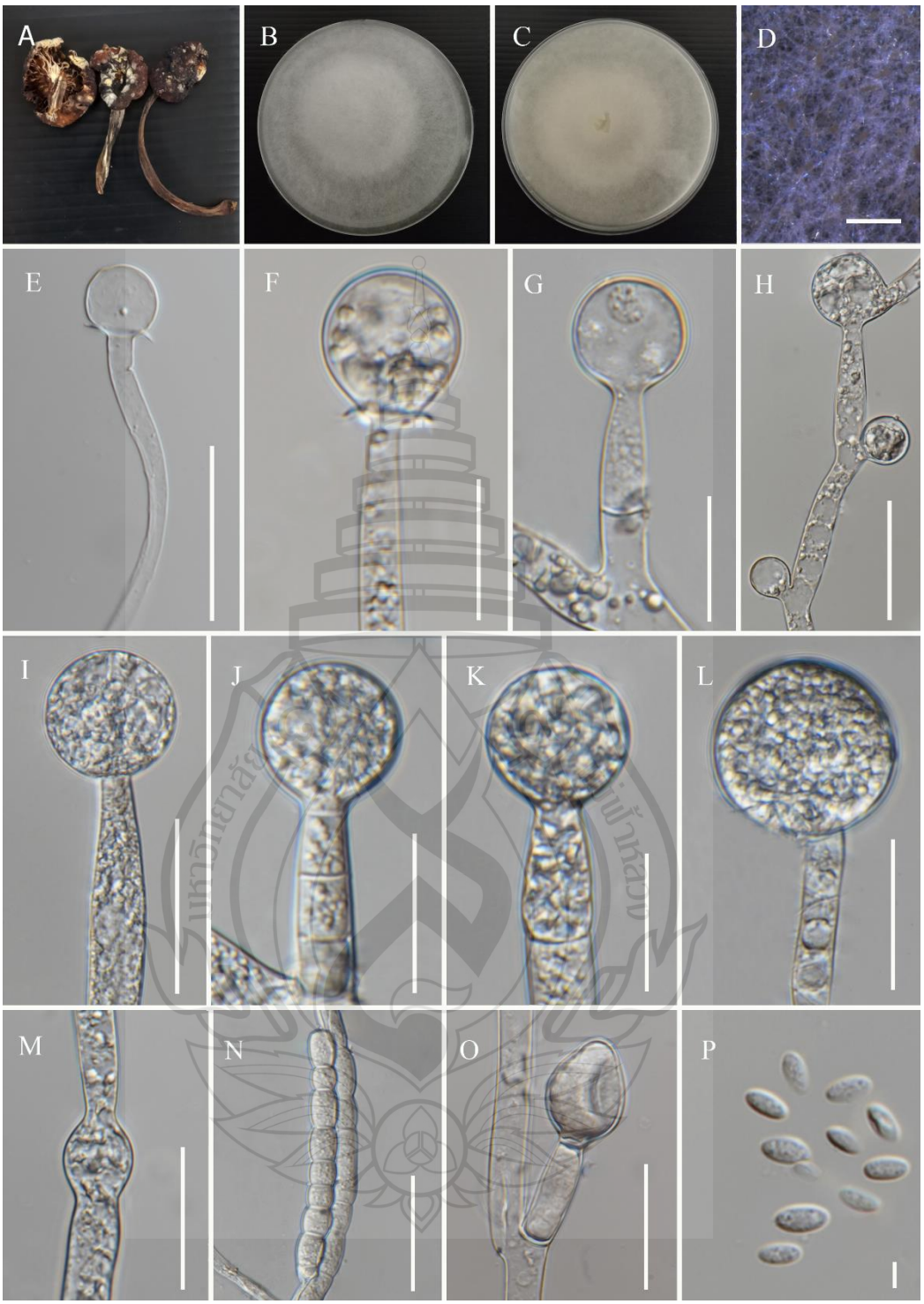


Figure 3.38 *Mucor yunnanensis* (ZHKUCC 22-0110)

Figure 3.38, a. Host (*Armillara* sp.). b-c. Colony on PDA. d. Sporulation on PDA. e-h. Columella with and without collars. i-l. Immature and mature sporangia. m.

Hyphal bulge. n, o. Chlamydospores. P. Sporangiospores. Scale bars: d = 100 μm, h, i, n = 40 μm, e, l, m = 30 μm, j, k = 25 μm, f, g, o = 20 μm, p = 5 μm.

Mucor circinelloides Tiegh., Annls Sci. Nat., Bot., sér. 6 1: 94 (1875) Figure 3.39

Index Fungorum number: IF 198947

Fungicolous on a fruiting body of *Phlebopus* sp. Sexual morph: not observed. Asexual morph: on PDA, *Sporangiophores* up to 12–20 μm ($\bar{x}$ = 15 μm, n = 20) in width, hyaline, repeatedly branched sympodially, having long and short branches, the latter infrequently circinate, short sporangiophores more profusely branched with short and often circinate branches, with slightly incrusted walls, the younger parts of the sporangiophores filled with granules, septate. *Sporangia* 40–53.5 × 39–53 μm ($\bar{x}$ = 46.5 × 48.5 μm, n = 10), globose to sub-globose, initially hyaline and turning yellowish to become brownish-grey at maturity, decreasing in diameter in order of arisal on each sporangiophore, slightly incrusted walls; walls of the larger sporangia deliquescent and leaving small collars, and of the smaller sporangia persistent and leaving large basal membranes. *Columellae* 16–44 × 15–35 μm ($\bar{x}$ = 30 × 25 μm, n = 20), obovoid to ellipsoidal in the larger sporangia, globose in the smaller sporangia, tinged a pallid brownish grey. *Sporangiospores* 4–7 × 3–6.2 μm ($\bar{x}$ = 5.4 × 4.5 μm, n = 40) μm, ellipsoidal, smooth-walled, hyaline to brownish. *Chlamydospores* intercalary and terminal, variable in shape and size. *Rhizoids* hyaline.

Colony characters – on PDA, at 25 °C, cultures are initially white and later turn pale brown in the middle with sporangia formation. The colony reached 70 mm diam. after 4 days of incubation.

Materials examined – Thailand, Chiang Rai, Muang, Tha sut, isolated from the white mycelium growing on a fruiting body of *Phlebopus* sp., 25 June 2020, A.J. Gajanayake, AJ 086, inactive dry culture MFLU 22-0156, living culture MFLUCC 22-0069.

GenBank numbers – ITS = ON911234; LSU = ON911284.

Notes – In the phologenetic analyses (Figure 3.37), MFLUCC 22-0069 is clustered within *M. circinelloides* with 93% BS. *Mucor circinelloides* strain MFLUCC 22-0069 reported in this study shares similar asexual morphologies with those observed from the ex-neotype (CBS 195.68) of *M. circinelloides* described by

Schipper (1976). During the micro-morphologcal examination, only 10 sporangia were measured as most of the sporangia were easily broken during the slide preparation due to the prevalence of deliquescent sporangial wall. The size of sporangia of MFLUCC 22-0069 (46.5 × 48.5 μm**)** is comparatively smaller than the sporangia of *M. circinelloides* (54 × 49 μm) described by Schipper (1976). The size of sporangiospores of MFLUCC 22-0069 (5.4 × 4.5 μm) is mostly similar to the sporangiospores of *M. circinelloides* (5.4 × 4 μm) described by Schipper (1976). The slight dimensional differences may have occurred due to the variations of agar medium and the conditions used to obtain the cultures. To the best of our knowledge, this is the first report of *M. circinelloides* on a fruiting body of *Phlebopus* sp. as a fungicolous fungus.

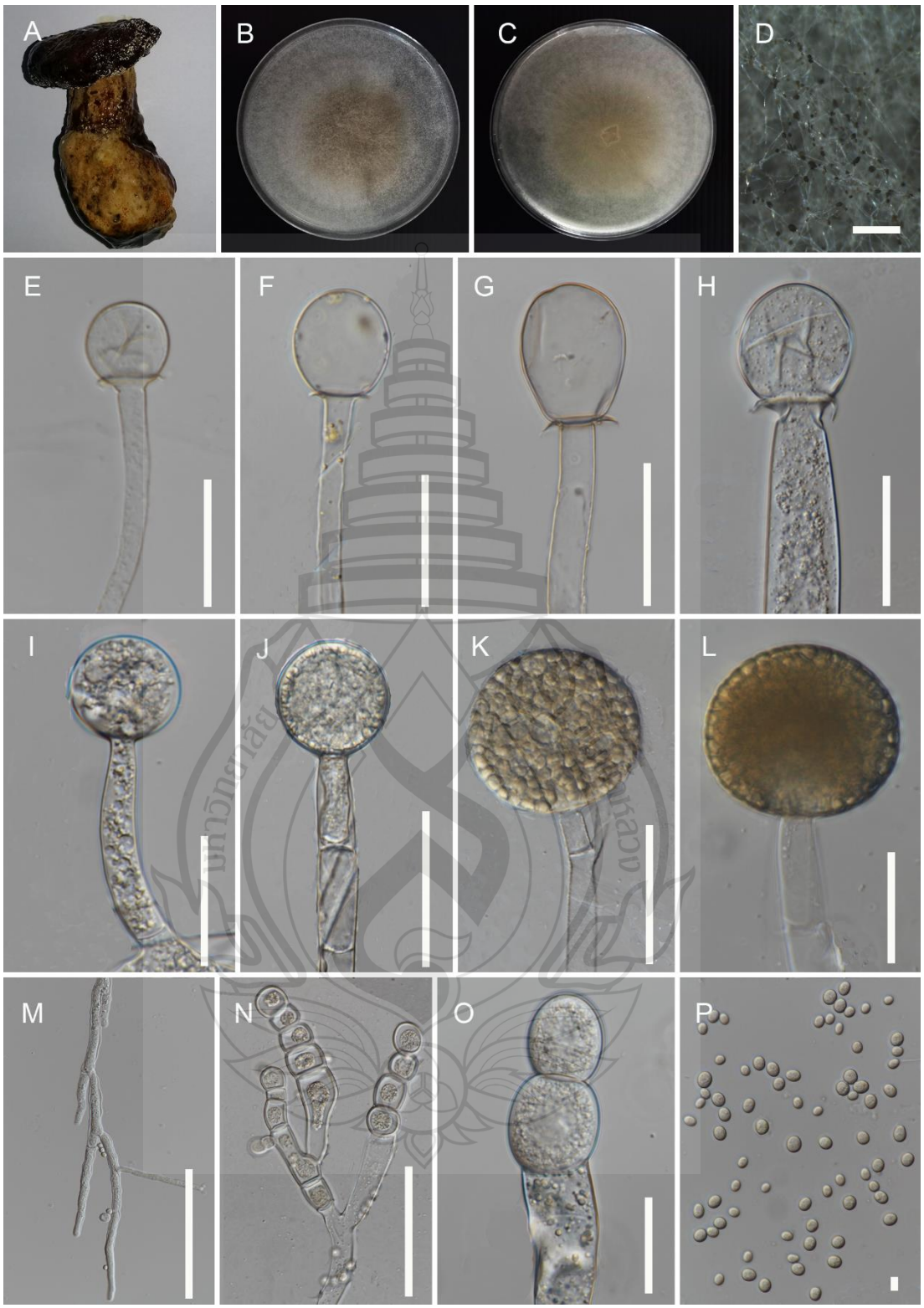


Figure 3.39 *Mucor circinelloides* (MFLUCC 22-0069)

Figure 3.39, a. Host. b-c. Colony on PDA. d. Sporulation on PDA. e-h. Columella with collars. i-l. Sporangia. m. Rhizoid. n-o. Chlamydospores. p.

Sporangiospores. Scale bars: d = 200 μm, m = 150 μm, g-h, j, k, n = 50 μm, f, i, l, o = 30 μm, e = 25 μm, p = 5 μm.

Mucor hiemalis Wehmer, Annls mycol. 1(1): 39 (1903)

Figure 3.40

Index Fungorum number: IF 249401

Fungicolous on a fruiting body of *Ramaria* sp. Sexual morph: not observed. Asexual morph: on PDA, *Sporangiophores* up to 12–23 μm ($\bar{x}$ = 12.5 μm, n = 20) width, slightly branched sympodially, septate. *Sporangia* 42–45 × 40–43 μm ($\bar{x}$ = 43.5 × 41.5 μm, n = 05) globose, initially hyaline to yellowish, then dark brown when matured, with deliquescent, slightly transparent walls. *Columellae* 28–38.5 × 26.5–30.5 μm ($\bar{x}$ = 33 × 30 μm, n = 20) ellipsoidal with truncate base, globose when young. *Sporangiospores* 3.7–7.8 × 2.5–5 μm ($\bar{x}$ = 3.5 × 5.5 μm, n = 45) ellipsoidal, containing a few scattered granules, variable in size. *Chlamydospores* intercalary, terminal, variable in shape and size.

Culture characteristics – on PDA, 25 °C, cultures are initially white and later turn yellowish. The colony reached 50 mm diam. after 4 days of incubation.

Materials examined – China, Yunnan, Lijiang, Shigu, isolated from the white mycelium growing on a fruiting body of *Ramaria* sp., 29 June 2020, S.C. Karunarathna, SG 039, Herbarium material ZHKU 22-0059, living culture ZHKUCC 22-0111; China, Yunnan, Lijiang, Shigu, isolated from the white mycelium growing on a fruiting body of *Boletus* sp., 29 June 2020, *S.C. Karunarathna*, *SG 071*, Herbarium material ZHKU 22-0060, living culture ZHKUCC 22-0112.

GenBank numbers – ZHKUCC 22-0111: ITS = ON911291; LSU = ON911297, ZHKUCC 22-0112: ITS = ON911297; LSU = ON911810.

Notes – In the phylogenetic analyses (Figure 3.37), ZHKUCC 22-0111 and ZHKUCC 22-0112 are clustered within *M. Hiemalis* with 100% BS and 0.91 BYPP. *Mucor hiemalis* strains ZHKUCC 22-0111 and ZHKUCC 22-0112 reported in this study share similar asexual morphologies with those observed from the ex-neotype (CBS 201.65) of *M. hiemalis* described by Schipper (1973). During the micro-morphologcal examination, only 05 sporangia were measured as most of the sporangia were easily broken during the slide preparation due to the prevalence of deliquescent sporangial wall. The sporangia, sporangiospores and columellae of

ZHKUCC 22-0111 and ZHKUCC 22-0112 are comparatively smaller than *M. hiemalis* described by Schipper (1973) as sporangia; 41.5 µm *vs* 70 µm in width, sporangiospores; 3.7–7.8 × 2.5–5 µm *vs* 5.7–8.7 × 2.7–5.4 µm and columellae; 33 × 30 µm *vs* 38 × 30 µm. The sporangiophores of ZHKUCC 22-0111 and ZHKUCC 22-0112 (up to 12–23 µm) are comparatively bigger than *M. hiemalis* (up to 10–12 (14) µm) described by Schipper (1973). Slight dimensional differences might have occurred due to the variations of agar medium and the conditions used to obtain the culture. To the best of our knowledge, this is the first report of *M. hiemalis* on a fruiting body of *Ramaria* sp. and *Boletus* sp. as a fungicolous fungus.

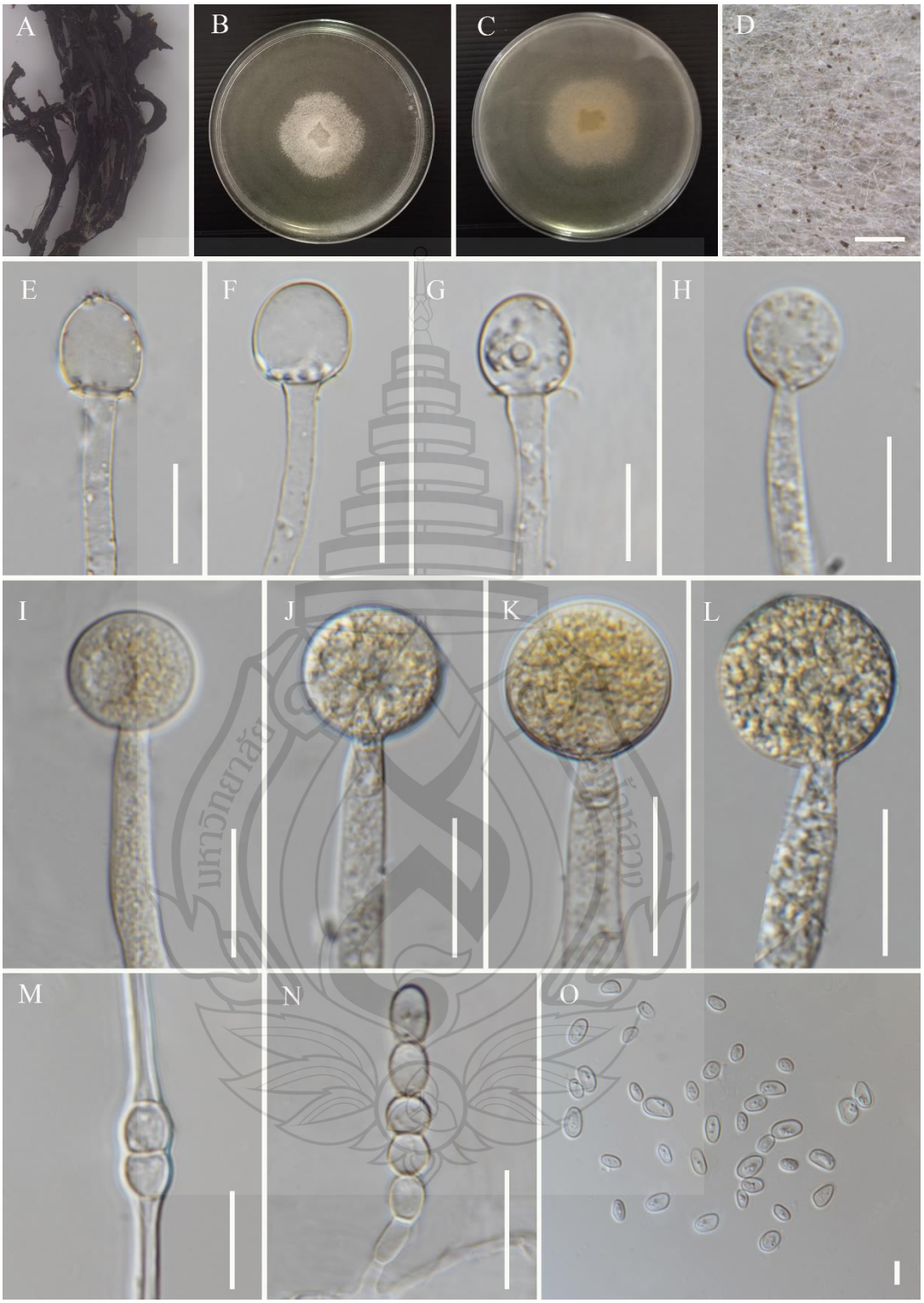


Figure 3.40 *Mucor hiemalis* (ZHKUCC 22-0111)

Figure 3.40, a. Host (*Ramaria* sp.). b-c. Colony on PDA. d. Sporulation on PDA. e-g. Columella with and without collars. h-l. Sporangia. m, n. Chlamydospores.

o. Sporangiospores. Scale bars: d = 200 μm, k, l = 30 μm, e-j, n = 20 μm, m = 10 μm, o = 5 μm.

Mucor nederlandicus Váňová, Česká Mykol. 45(3): 128 (1991)

Figure 3.41

Index Fungorum number: IF 354494

Fungicolous on a fruiting body of *Russula* sp. Sexual morph: not observed. Asexual morph: on PDA, *Sporangiophores* up to 3.2–9.5 μm ($\bar{x}$ = 6.5 μm, n = 20) width, hyaline, undulate, occasionally curved, irregular septate near the base, unbranched, sympodial branches formed. *Sporangia* 19.5–38.5 × 18.5–35.5 μm ($\bar{x}$ = 29 × 27 μm, n = 10), globose, thick-walled, wall echinulate, deliquescent in mature sporangia, hyaline to pale brown. *Columellae* 14.7–23.5 × 14.5–23 μm ($\bar{x}$ = 19 × 18.5 μm, n = 20), mostly globose to subglobose, and sometimes oblong, obovoid, and rarely ellipsoid, with or without short collar, hyaline to pale brown, smooth-walled. *Sporangiospores* 3.5–6.5 × 2.2–3.5 μm ($\bar{x}$ = 5 × 3 μm, n = 45), mostly ellipsoidal, sometimes flattened on one side, oval or cylindrical, smooth-walled, hyaline with one or more granules. *Chlamydospores* abundant, intercalary, terminal, variable in shape and size. *Rhizoids* absent.

Culture characteristics – on PDA, at 25 °C, cultures are cottony and white to pale yellow. The colony reached 60 mm in diam. after 4 days of incubation.

Materials examined – Thailand, Chiang Mai, Mae Tang, Pa Pae, Ban Pha Deng, isolated from the white mycelium growing on a fruiting body of *Russula* sp., 07 July 2021, A.J. Gajanayake, MR 30 inactive dry culture MFLU 22-0158, living cultures MFLUCC 22-0070; Thailand, Chiang Mai, Mae Tang, Pa Pae, Ban Pha Deng, isolated from the white mycelium growing on a fruiting body of *Russula* sp., 07 July 2021, A.J. Gajanayake, MR 33 inactive dry culture MFLU 22-0159, live cultures MFLUCC 22-0071.

GenBank numbers – MFLUCC 22-0070: ITS = ON911966; LSU = ON911967; MFLUCC 22-0071: ITS = ON911968; LSU = ON911983.

Notes – In the phylogenetic analyses (Figure 3.37), MFLUCC 22-0070 and MFLUCC 22-0071 clustered within *M. nederlandicus* with 99% BS and 1.00 BYPP. *Mucor nederlandicus* strains MFLUCC 22-0070 and MFLUCC 22-0071 reported in this study share similar asexual morphologies with those described by Oudem 1898 as

mentioned in Mycobank (2025). The sporangia, sporangiospores and columellae of MFLUCC 22-0070 and MFLUCC 22-0071 are comparatively smaller than ***M.*** *nederlandicus* described by Oudem 1898 as mentioned in Mycobank (https://www.mycobank.org/), as sporangia; 18.5–35.5 µm *vs* 40–45 µm in diam., sporangiospores; 5 × 3 µm vs 7 × 3 µm, columellae; 14.5–23 µm *vs* 25–35 µm in diam. These dimensional differences might have occurred due to the variations of agar medium and the conditions used to obtain the culture. To the best of our knowledge, this is the first report of *M. nederlandicus* on fruiting bodies of *Russula* sp. as a fungicolous fungus.

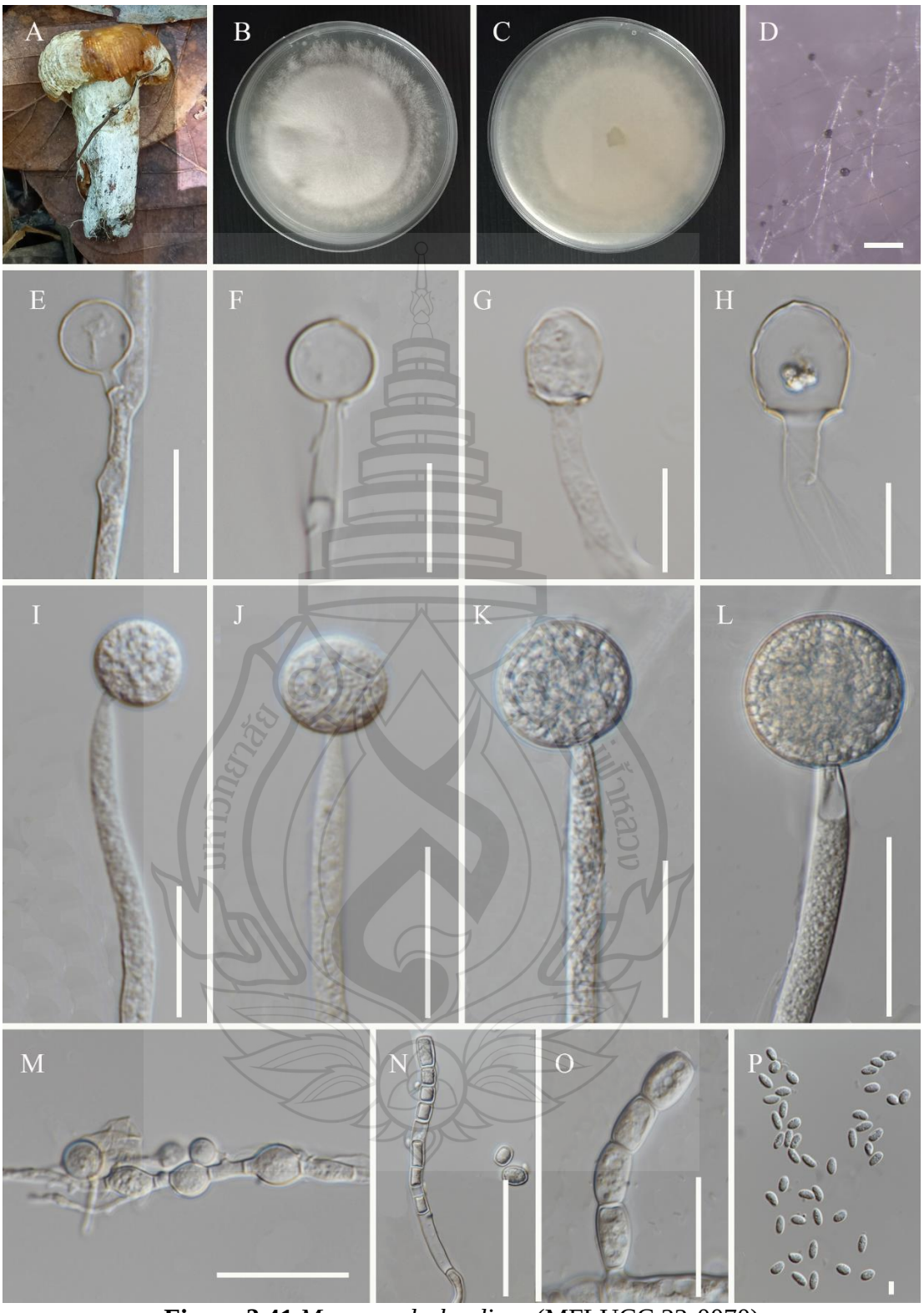


Figure 3.41 *Mucor nederlandicus* (MFLUCC 22-0070)

Figure 3.41, a. Host. b-c. Colony on PDA. d. Sporulation on PDA. e-h. Columella. i-l. Sporangia. m-o. Chlamydospores. p. Sporangiospores. Scale bars: d = 500 µm, l, n = 50 µm, i-k, m, o = 30 µm, e = 20 µm, f-h = 15 µm, p = 5 µm.

3.2.9 *Neoroussoella* Jian K. Liu, Phookamsak & K.D. Hyde, Phytotaxa 181(1): 21 (2014)

Neoroussoella was established by Liu et al. (2014), with *N. bambusae* designated as the type species. As of Species Fungorum (2025), eighteen species are listed under *Neoroussoella* and it is classified within *Roussoellaceae* (Hyde et al., 2024a).

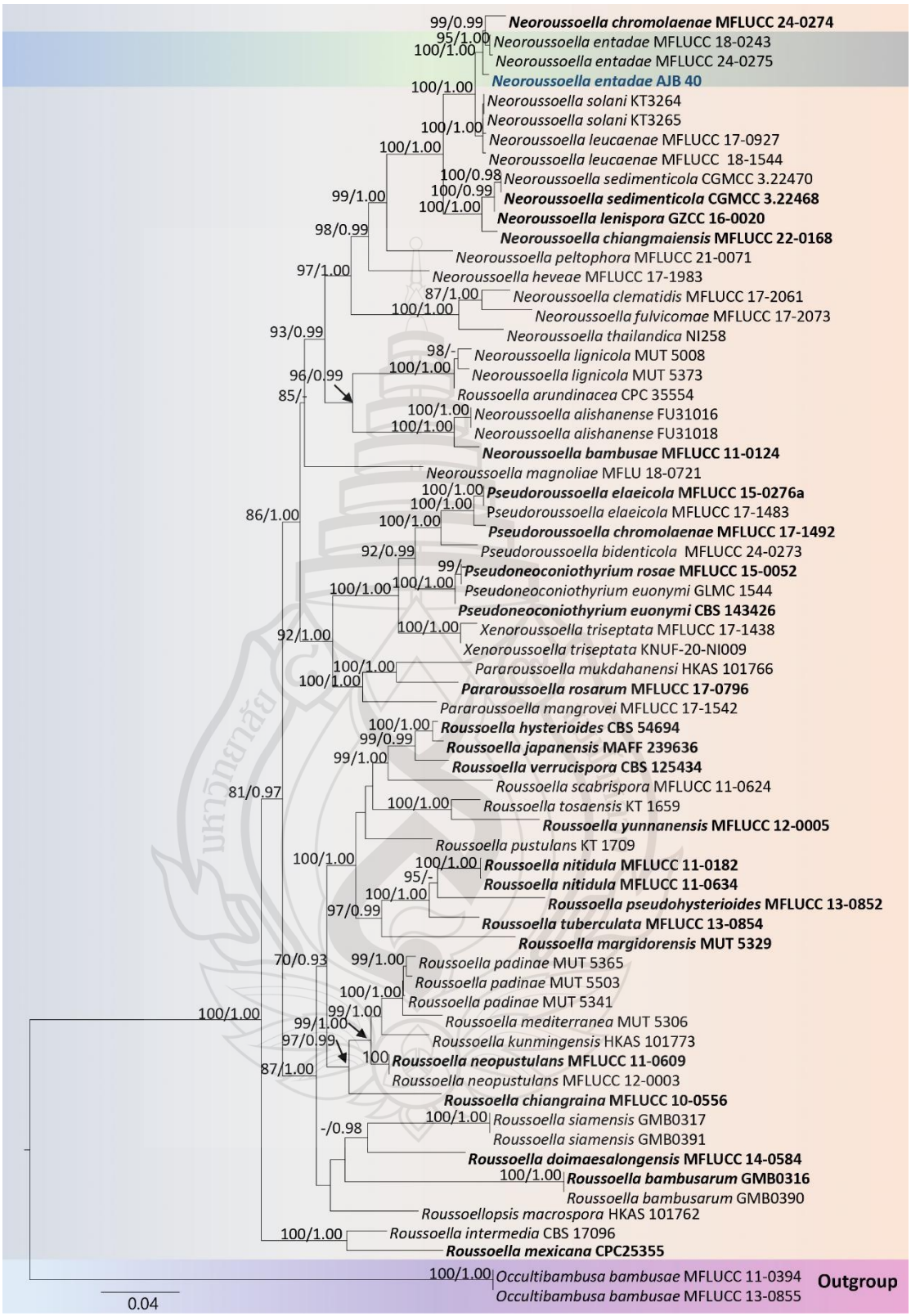


Figure 3.42 Phylogenetic tree generated by ML analysis of combined LSU, SSU, ITS, *tef-1α*, and *rpb2* sequence data of *Neoroussoella* and related genera

Figure 3.42, A total of 66 strains were included in the analyses. The tree is rooted with *Occultibambusa bambusae* (MFLUCC 11-0394 and MFLUCC 13-0855). The best scoring ML tree with an optimal log-likelihood value of −29737.191 is presented. The matrix had 1580 distinct alignment patterns, with 27.53% of undetermined characters or gaps. Bootstrap support values for ML ≥ 70% and BYPP ≥ 0.90 values for BI (BS/BYPP) are shown respectively near the nodes. Type (holotype/ex-type/isotype/paratype) strains are in bold. The strains reported in this study are in blue bold.

Neoroussoella entadae Jayasiri, E.B.G. Jones & K.D. Hyde, Mycosphere 10(1): 105 (2019)

Figure 3.43

Index Fungorum number: IF 555568

Fungicolous on a decaying polypore fruiting body. Sexual morph: not observed. Asexual morph: white hyphae on a decaying polypore fruiting body. On PDA, coelomycetous. *Conidiomata* 61–88 × 59–68.5 μm ($\overline{x}$ = 79 × 63 μm, n = 10), pycnidial, solitary to gregarious, unilocular, and ostiolate. *Ostiole* papillate, central, circular. *Conidiomata wall* 8–12 μm ($\overline{x}$ = 10 μm, n = 20) wide, composed of thick-walled, dark brown cells of *textura angularis*, inner layer thin, hyaline. *Conidiophores* usually reduced to conidiogenous cells. *Conidiogenous cells* 3–5 × 1.5–2.5 μm ($\overline{x}$ = 4 × 2 μm, n = 20), phialidic, ampulliform to cylindrical, hyaline, smooth-walled. *Conidia* 3–4 × 1.5–2.5 μm ($\overline{x}$ = 3.5 × 1.8 μm, n = 50), initially hyaline, becoming pale brown when mature, oblong to ovoid, both ends broadly rounded, aseptate.

Colony characters – on PDA at 25 °C, 25–30 mm in 7 days. Colony surface, slightly raised, dense and pale brown at the centre, and white to cram towards the margin. Reverse of the colony is pale brown at the centre and cream towards the margin.

Material examined – Thailand, Chiang Rai: Muang, Nang Lae (20°2′ 24.9216″N, 99°54′ 2.1996″E), isolated from the white mycelium on a Polypore fruiting body. 20 September 2023, Gajanayake A.J, AJB 40.

Notes – Our isolate AJB 40, clustered with *Neoroussoella entadae* with 100 % BS, and 1.00 BYPP (Figure 3.42). The morphological features of AJB 40 match the original description and illustrations of *N. entadae* provided by Jayasiri et al. (2019),

except for slight differences in the dimensions of morphological structures. These variations are possible due to differences in the agar medium and cultural conditions used (Senanayake et al., 2020). Therefore, we confirmed that our isolate, AJB 40, is phylogenetically and morphologically consistent with *N. entadae*.

Neoroussoella entadae was initially described by Jayasiri et al. (2019) as a saprobe on the pods of *Entada phaseoloides* and *Leucaena* sp. in Thailand. Subsequent studies documented it as a saprobe on *Chromolaena odorata, Magnolia* sp., and from forest soil in Thailand (De Silva et al., 2022; Htet et al., 2024; Yasanthika et al., 2025). This study presents the first record of *N. entadae* as a fungicolous species on a decaying polypore fruiting body, representing a novel ecological niche for this species.

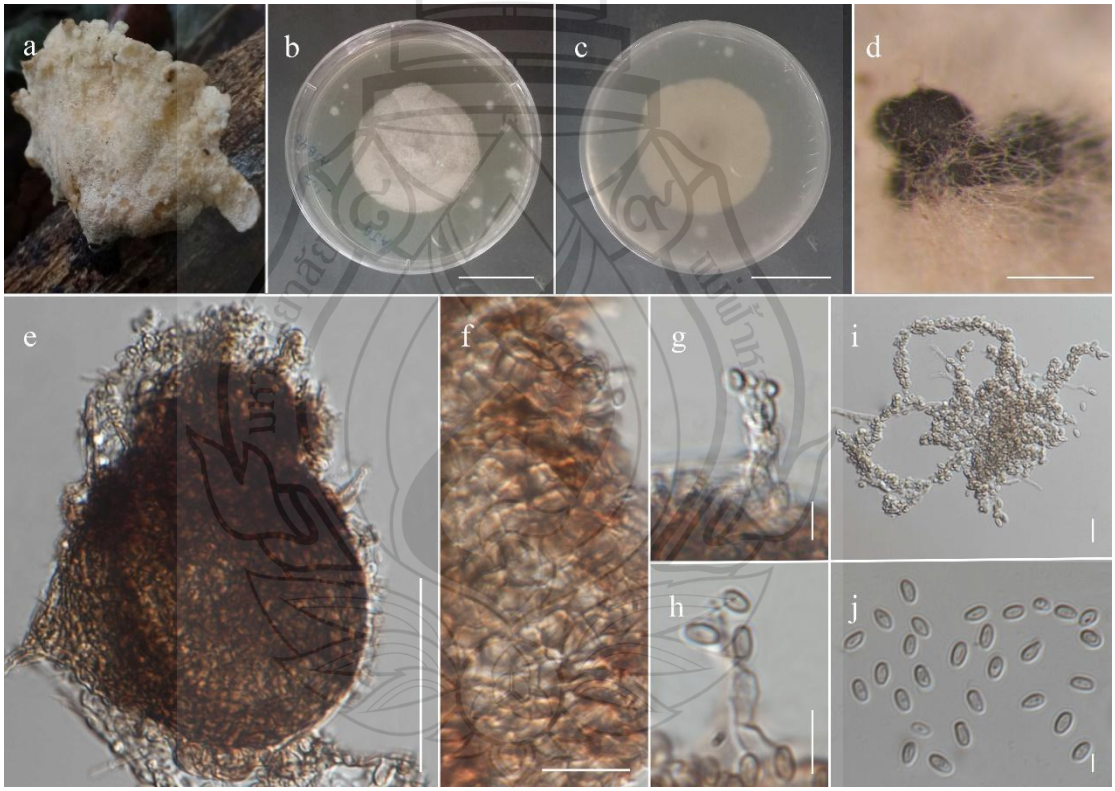


Figure 3.43 *Neoroussoella entadae* (AJB 40)

Figure 3.43, a. Host (decaying polypore). b, c. Colony on PDA. d. Formation of conidiomata on PDA. e. Conidiomata. f. Conidiomata wall. g, h. Conidiogenous cells with conidial attachments. i, j. Conidia. Scale bars: b, c = 30 mm, d = 250 µm, e = 45 µm, i = 10 µm, f–h = 5 µm, j = 3 µm.

3.2.10 *Xenoacremonium* L. Lombard & Crous, Stud. Mycol. 80: 234 (2015)

Xenoacremonium was established by Lombard et al., (2015), with *X. recifei* designated as the type species. According to Species Fungorum (2025), six species are recognized within *Xenoacremonium* and it is classified wihin *Nectriaceae* (Hyde et al., 2024).

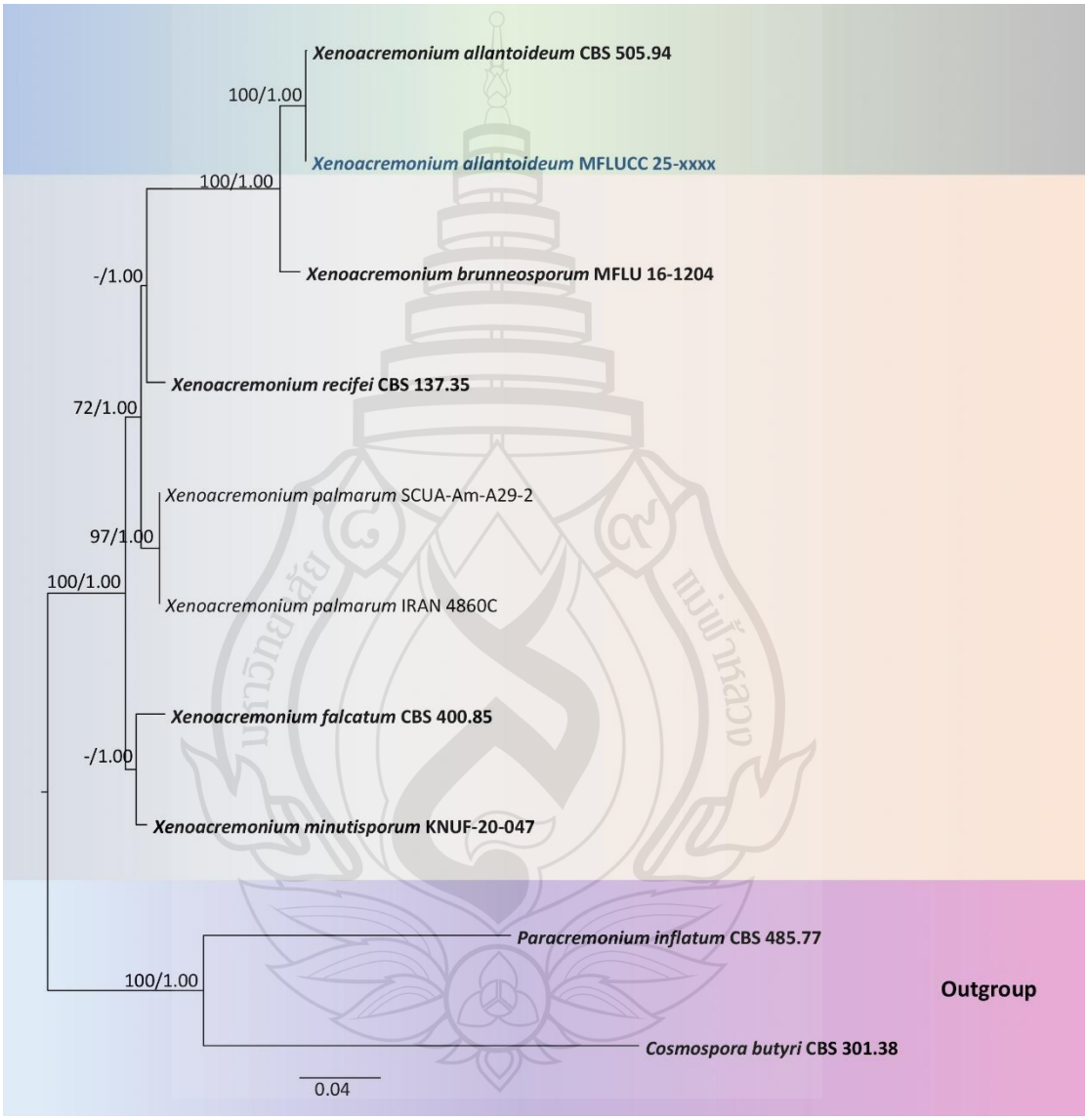


Figure 3.44 Phylogenetic tree generated by ML analysis of combined LSU, ITS, *rpb2*, *tef-1α*, and *tub2* sequence data of *Xenoacremonium*

Figure 3.44, A total of 10 strains were included in the analyses. The tree is rooted with *Cosmospora butyri* (CBS 301.38) and *Paracremonium inflatum* (CBS 485.77). The best scoring ML tree with an optimal log-likelihood value of −8681.270

is presented. The matrix had 460 distinct alignment patterns, with 28.52% of undetermined characters or gaps. Bootstrap support values for ML ≥ 70% and BYPP ≥ 0.90 values for BI (BS/BYPP) are shown respectively near the nodes. Type (holotype/ex-type/isotype/paratype) strains are in bold. The strains reported in this study are in blue bold.

Xenoacremonium allantoideum L.W. Hou, L. Cai & Crous, Stud. Mycol. 105: 56 (2023)

Figure 3.45

Index Fungorum number: 845808

Fungicolous on a fruiting body of *Auricularia* sp. Sexual morph: not observed. Asexual morph: white to grey sporulated hyphae on a fruiting body of *Auricularia* sp. On PDA, hyphomycetous, *Mycelium* 1.5–3 μm ($\overline{x}$ = 2 μm, n = 30) wide, branched, septate, hyaline, forms mycelial ropes and coils. Sporulation abundant, phalacrogenous, nematogenous, or plectonematogenous. *Conidiophores* 10–33 μm ($\overline{x}$ = 20 μm, n = 20) long, mostly aggregated, straight, arising directly from the mycelium, unbranched, basitonously branched, or repeatedly verticillate towards the apex, bearing 1–4 levels with 2–3 phialides per node, and hyaline. *Phialides* 18–30 μm ($\overline{x}$ = 25 μm, n = 20) long, 1.5–3 μm ($\overline{x}$ = 2 μm, n = 20) wide at base, solitary and in divergent whorls of 2–3, lateral, rarely terminal, subcylindrical, hyaline, commonly with conspicuous periclinal thickening and cylindrical collarette at conidiogenous loci, with short sterile outgrowths, polyphialides not observed. *Conidia* 3.5–6 × 1–2 μm ($\overline{x}$ = 5 × 1.5 μm, n = 30), aseptate, allantoid, with rounded ends, curved, hyaline, arranged in slimy heads. *Chlamydospores* 6–12 × 2.5–5 μm ($\overline{x}$ = 7.5 × 2.5 μm, n = 20), hyaline, terminal and ellipdoid to ovoid.

Colony characters – on PDA at 25 °C, 25–30 mm in 7 days. Colony surface white to dirty white, with moderate aerial mycelium, floccose at the centre, while periphery is thinly felty. Reverse of the colony is dirty white.

Material examined – Thailand, Chiang Rai: Muang, Nang Lae (20°2′ 24.9216″N, 99°54′ 2.1996″E), isolated from the sporulated hyphae on a fruiting body of *Auricularia* sp., 17 October 2023, A.J. Gajanayake, AJ 53-23.

Notes – Our isolate AJ 53-23, clustered with the type strain of *Xenoacremonium allantoideum* (CBS 505.94) with 100% BS, and 1.00 BYPP (Figure

3.44). The morphological features of AJ 53-23 match the original description and illustrations of *X. allantoideum* provided by Hou et al. (2023), except for slight differences in the dimensions of morphological structures. These variations are possible due to differences in the agar medium and cultural conditions used (Senanayake et al., 2020). Therefore, we confirmed that our isolate, AJ 53-23, is phylogenetically and morphologically consistent with *X. allantoideum*.

Xenoacremonium allantoideum was described as a novel species by Hou et al. (2023), but the origin and substrate of this species remain unknown. The ex-type culture of *X. allantoideum* (CBS 505.94) was initially identified as *Acremonium* cf. *curvulum* (Hou et al., 2023). The phylogenetic analyses revealed that CBS 505.94 forms a separate lineage related to *X. recifei* (Hou et al., 2023). Since its initial description, there have been no subsequent reports of this species. This study represents the second global report of *X. allantoideum* and the first record from Thailand, documenting it as a fungicolous species associated with the fruiting body of *Auricularia* species.

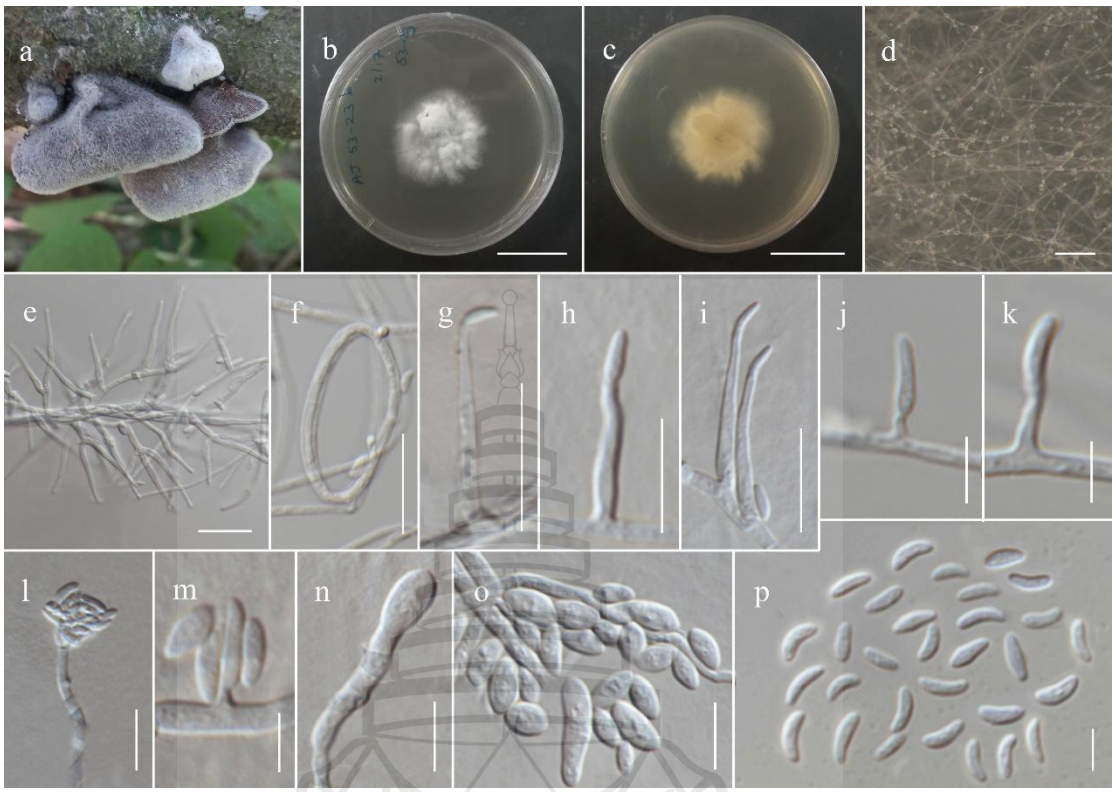


Figure 3.45 *Xenoacremonium allantoideum* (AJ 53-23)

Figure 3.45, a. Host (*Auricularia* sp.). b, c. Colony on PDA. d. Sporulation on PDA. e. Mycelial ropes with conidiophores. f. Hyphal coil. g–m. Conidial attachments. n. Chlamydospores. m. Conidia. Scale bars: b, c = 30 mm, d = 250 µm, e–g = 20 µm, i = 15 µm, h, l, n, o = 10 µm, j, k, p = 5 µm.

3.2.11 *Zarea* Khons., Thanakitp. & Luangsa-ard, Fungal Syst. Evol. 14: 300 (2024)

Zarea was estblished by Khonsanit et al. (2024) based on multigene phylogenetic analyses to accommodate certain species formerly placed within *Lecanicillium*. To date, *Zarea* comprises three species: *Z. fungicola*, the type species, along with *Z. aleophila* and *Z. flavida* (Khonsanit et al., 2024; Species Fungorum, 2025). *Zarea* is classified within *Cordycipitaceae* (Hyde et al., 2024a).

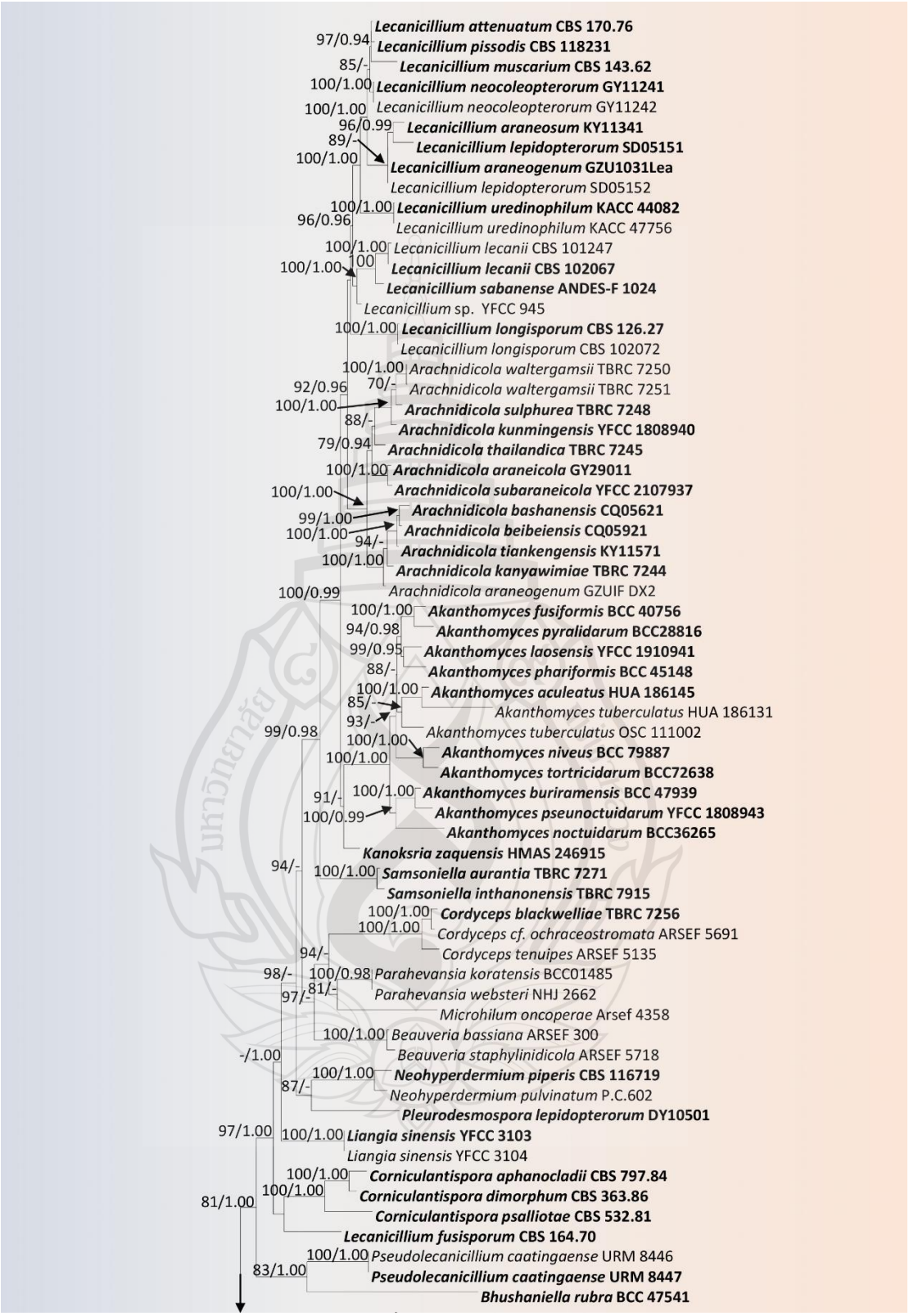


Figure 3.46 Phylogenetic tree generated by ML analysis of combined LSU, *tef-1α*, *rpb1* and *rpb2* sequence data of *Lecanicillium*, *Zarea* and related genera in the *Cordycipitaceae*

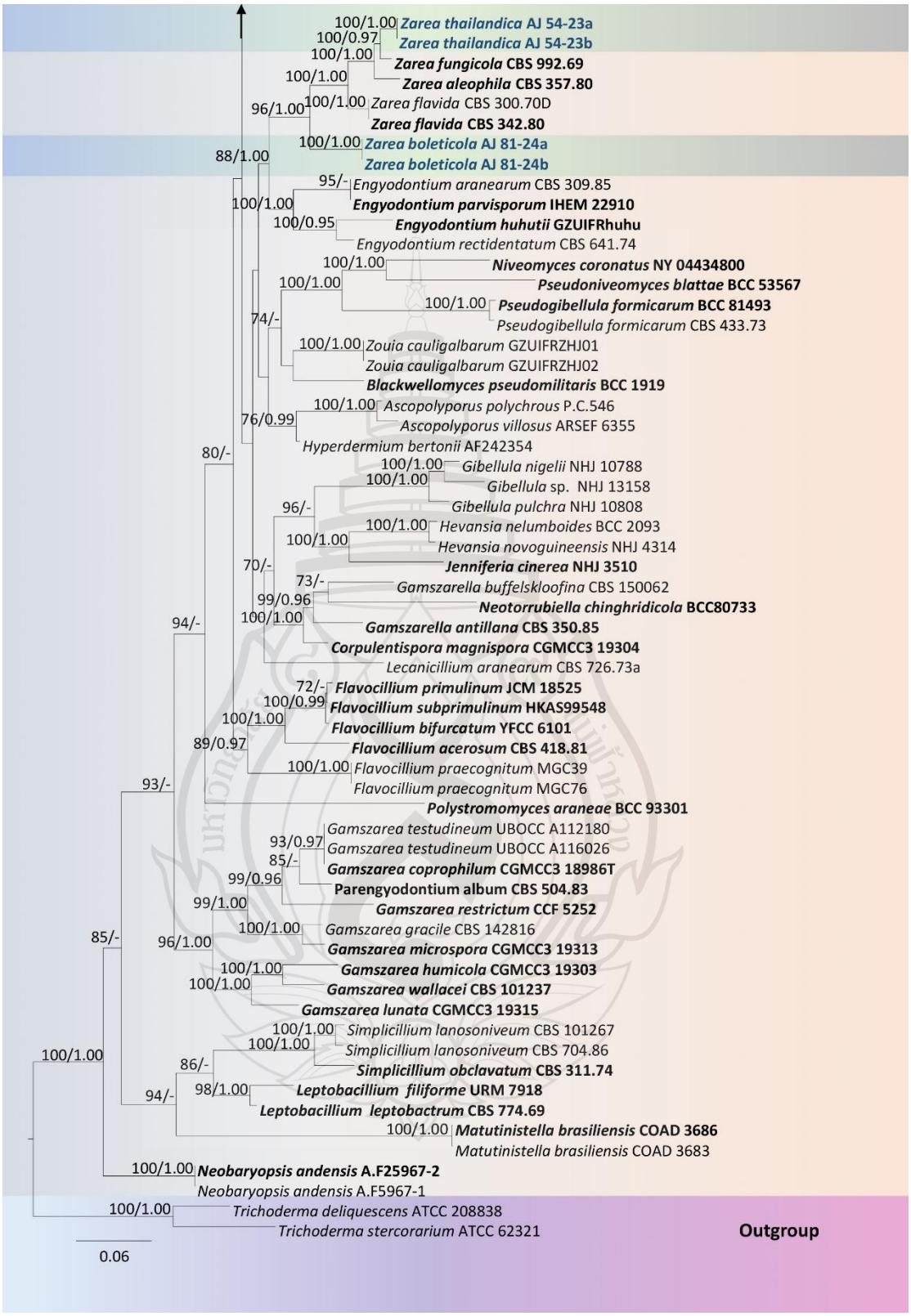


Figure 3.46 (continued)

Figure 3.46, A total of 125 strains were included in the analyses. The tree is rooted with *Trichoderma deliquescens* (ATCC 208838) and *T. stercorarium* (ATCC 62321). The best scoring ML tree with an optimal log-likelihood value of −44508.824 is presented. The matrix had 1615 distinct alignment patterns, with 24.73% of undetermined characters or gaps. Bootstrap support values for ML ≥ 70% and BYPP ≥ 0.90 values for BI (BS/BYPP) are shown respectively near the nodes. Type (holotype/ex-type/isotype/paratype) strains are in bold. The strains reported in this study are in blue bold.

Zarea boleticola Gajanayake., Jayaward. & K.D. Hyde, sp. *nov*.

Figure 3.47

Etymology – The epithet refers to the host "bolete" on which the fungus was growing.

Typification – Thailand, Chiang Rai: Mae Salong Nok (20° 9' 59.4216"N, 99° 37' 34.7016"E), isolated from white sporulated mycelial patches on a bolete fruiting body, 12 June 2024, A.J Gajanayake, AJ 81-24a (holotype).

Fungicolous on a bolete fruiting body. Sexual morph: not observed. Asexual morph: white sporulated mycelial patches on a bolete fruiting body. On PDA, hyphomycetous, *Vegetative hyphae* 1.5–2.5 μm ($\bar{x}$ = 2 μm, n = 30) wide, hyaline, septate. *Conidiophores* 2–3 μm ($\bar{x}$ = 2 μm, n = 20) wide, arising typically from the submerged hyphae, septate, mostly prostrate in younger colonies, rarely erect. Prostrate conidiophores are branched and solitary or few phialides are produced on the main axis or at the terminal of branches, while erect conidiophores bear 1–2 whorls of 2–3 phialides. *Phialides* on erect conidiophores 20.5–38 μm ($\bar{x}$ = 26 μm, n = 20) long, 1.5–2 μm at the base, gradually tapering to 0.7–1 μm at the tip, on prostrate conidiophores 18–60 μm ($\bar{x}$ = 28 μm, n = 20) long, 1.5–2.5 μm at the base, gradually tapering to 0.8–1.5 μm at the tip, occasionally shorter phialides arise directly from vegetative hyphae. *Conidia* are two types, hyaline. *Microconidia* 4–9 × 2–4 μm ($\bar{x}$ = 6 × 3 μm, n = 80), hyaline, smooth-walled, variable in size, oval to ellipsoidal, rarely slightly curved, inconspicuously guttulate, attenuated at the base, forming mostly globose slimy masses of conidia. *Macroconidia* 10–32 × 2–3 μm ($\bar{x}$ = 17 × 2.5 μm, n = 35), cylindrical to long-ellipsoidal, the basal end truncate, sometimes

septate, inconspicuously guttulate. *Chlamydospores* 3–5 µm diameter, aseptate, hyaline, globose, intercalary or terminal.

Colony characters – on PDA at 25 °C, 15–20 mm in 7 days. Colony surface white to pinkish with compact, flat mycelium and entire margin. Reverse of the colony yellowish at the centre and pinkish towards the margin.

Additional material examined – Thailand, Chiang Rai: Mae Salong Nok (20° 9' 59.4216"N, 99° 37' 34.7016"E), isolated from white sporulated mycelial patches on a bolete fruiting body, 12 June 2024, A.J Gajanayake, AJ 81-24b (isotype).

Notes – Based on morphological characteristics and multilocus phylogenetic analyses, *Zarea boleticola* (AJ 81-24a and AJ 81-24b) is introduced as a novel species. In the phylogenetic tree, *Z. boleticola* forms a distinct lineage basal to *Zarea flavida* (CBS 300.70D and CBS 342.80), with 96% BS and 1.00% BYPP (Figure 3.46). The pairwise comparison of the trimmed LSU sequences (812 bp) revealed a genetic divergence of 3.3% between *Z. boleticola* (AJ 81-24a) and the type strain of *Z. flavida* (CBS 342.80). Analysis of the *rpb2* region (813 bp) showed 9.6% genetic distance, while the *tef* region (879 bp) differed by 5.5%. The morphological comparison between *Z. boleticola* and *Z. flavida* is presented in Table 3.6. Following the guidelines of Aime et al. (2021) we introduce *Z. boleticola* as a new species.

Table 3.6 The morphological comparison of *Zarea boleticola* with *Z. flavida*

Morphological character	***Zarea boleticola* (This study)**	***Z. flavida* (Zare and Gams 2008)**
Conidiophores	Arising typically from the submerged hyphae, septate, 2–3 μm ($\bar{x}$ = 2 μm, n = 20) wide, mostly prostrate in younger colonies, rarely erect. Prostrate conidiophores are branched and solitary or few phialides are produced on the main axis or at the terminal of branches, while erect conidiophores are bearing 1–2 whorls of 2–3 phialides	Erect (later also procumbent), 2.5–3.5 μm wide at the base, with 2–6 whorls of 3–7 phialides. Many secondary branches occur along the conidiophores, some of them in whorls of 2–3
Phialides	On erect conidiophores 20.5–38 μm ($\bar{x}$ = 26 μm, n = 20) long, 1.5–2 μm at the base, gradually tapering to 0.7–1 μm at the tip, on prostrate conidiophores 18–60 μm ($\bar{x}$ = 28 μm, n = 20) long, 1.5–2.5 μm at the base, gradually tapering to 0.8–1.5 μm at the tip, occasionally shorter phialides arise directly from vegetative hyphae	Forming an oblique angle with the conidiophore stipe, 12–35 μm long, gradually tapering from 1.5–2.5 μm to 0.5–1 μm at the tips

Table 3.6 (continued)

Morphological character	***Zarea boleticola* (This study)**	***Z. flavida* (Zare & Gams, 2008)**
Conidia	Two types, hyaline. Microconidia 4–9 × 2–4 µm ($\bar{x}$ = 6 × 3 µm, n = 80), L/W ratio = 2, hyaline, smooth walled, variable in size, oval to ellipsoidal, rarely little bit curved, inconspicuously guttulate, attenuated at the base, form mostly globose slimy masses of conidia. Macroconidia 10–32 × 2–3 µm ($\bar{x}$ = 17 × 2.5 µm, n = 35), cylindrical to long-ellipsoidal, the basal end truncate, sometimes septate, inconspicuously guttulate, L/W ratio = 6.8	Adhering in slimy, mostly globose, but also some subglobose and ellipsoidal heads, conidia mostly fusiform, long-ellipsoidal to almost cylindrical, with the basal end indistinctly truncate, slightly sickle-shaped, smooth-walled, 4–8 × 1.5–2 µm, with 1–2 inconspicuous guttules, L/W ratio = 3.4

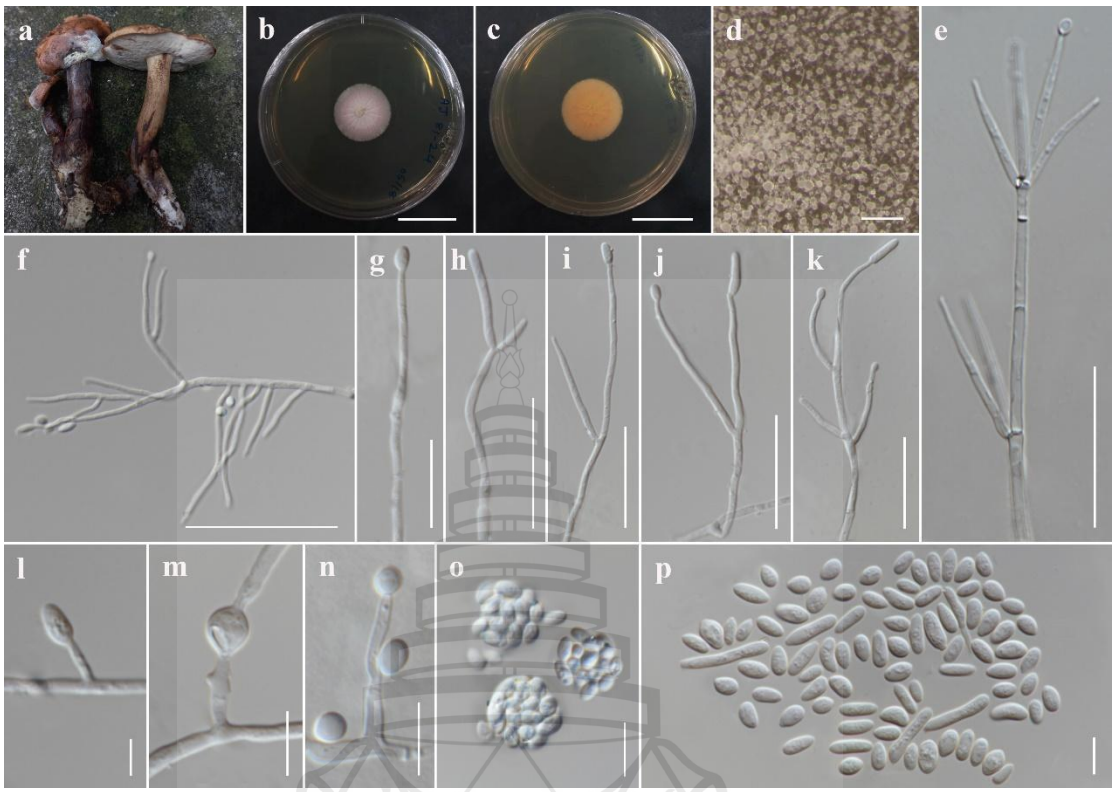


Figure 3.47 *Zarea boleticola* (AJ 81-24a)

Figure 3.47, a. Host (Bolete fruiting body). b, c. Colony on PDA. d, e. Sporulation on PDA. e–l. Conidial attachments. m, n. Chlamydospores. o. Slimy masses of conidia. p. Conidia. Scale bars: b, c = 30 mm, d = 250 µm, f = 65 µm, e, h–k = 30 µm, g = 20 µm, m–o = 10 µm, p = 8 µm, l = 5 µm.

Zarea thailandica Gajanayake., Jayaward. & K.D. Hyde, sp. *nov*.

Figure 3.48

Etymology – The epithet refers to the country “Thailand” where the fungus was collected.

Typification – Thailand, Chiang Rai: Muang, Nang Lae (20° 2′ 24.9216″N, 99° 54′ 2.1996″E), isolated from white sporulated mycelial patches on a fruiting body of *Marasmius* sp., 30 October 2023, S Phongeun, AJ 54-23a (holotype).

Fungicolous on a fruiting body of *Marasmius* sp. Sexual morph: not observed. Asexual morph: white sporulating mycelial patches on a fruiting body of *Marasmius* sp. On PDA, hyphomycetous, *Vegetative hyphae* 1–2 µm ($\bar{x}$ = 1.5 µm, n = 30) wide, hyaline, septate. *Conidiophores* 3–3.5 µm ($\bar{x}$ = 3 µm, n = 20) wide at the base, arising

typically from the submerged hyphae, erect septate, with 2–6 whorls of 3–7 phialides. *Phialides* 9.5–25 μm ($\bar{x}$ = 14.5 μm, n = 30) long, 1–2.5 μm at the base, gradually tapering to 0.5–1 μm at the tip, arising at an oblique angle from the conidiophore stipe. *Conidia* 3–8 × 1–2.5 μm ($\bar{x}$ = 4 × 2 μm, n = 50), hyaline, smooth- walled, fusiform, long-ellipsoidal to almost cylindrical, the basal end indistinctly attenuated, variable in size, with 1–2 or more inconspicuous guttules, forming mostly globose slimy masses of conidia. Chlamydospores not observed.

Colony characters – on PDA at 25 °C, 25–30 mm in 7 days. Colony surface white with abundant aerial mycelium, velvety. Reverse of the colony pale ochreous to light honey.

Additional material examined – Thailand, Chiang Rai: Muang, Nang Lae (20° 2′ 24.9216″N, 99° 54′ 2.1996″E), isolated from white sporulated mycelial patches on a fruiting body of *Marasmius* sp., 30 October 2023, S Phongeun, AJ 54-23b (isotype).

Notes – Based on morphological and phylogenetic evidence, herein *Zarea thailandica* (AJ 54-23a and AJ 54-23b) is introduced as a novel species. Phylogenetically, *Z. thailandica* forms a distinct lineage sister to the type strain of *Zarea fungicola* (CBS 992.69), with 100% BS and 0.97% BYPP, within the clade comprising *Z. fungicola* and *Z. aleophila* (Figure 3.46). Pairwise comparisons of the trimmed LSU sequences (812 bp) revealed a genetic distance of 0.4% between *Z. thailandica* and both *Z. fungicola* (CBS 992.69) and *Z. aleophila* (CBS 357.80). For the *rpb2* (813 bp), between *Z. thailandica* and *Z. fungicola* (CBS 992.69) the genetic distance was 3.7% while it was 7.2% between *Z. thailandica* and *Z. aleophila* (CBS 357.80). Similarly, comparisons of the *tef* sequences (879 bp) showed genetic distance of 1.5% to *Z. fungicola* (CBS 992.69) and 1.9% to *Z. aleophila* (CBS 357.80). The morphological comparison of *Z. thailandica* with closely related species are is summarized in Table 3.7 Following the guidelines of Aime et al. (2021) we introduce *Z. thailandica* as a new species.

Table 3.7 The morphological comparison of *Zarea thailandica* with *Z. fungicola* and *Z. aleophila*

Morphological character	***Zarea thailandica* (This study)**	***Z. fungicola* (Zare & Gams, 2008)**	***Z. aleophila* (Zare & Gams, 2008)**
Conidiophores	Erect septate, hyaline, with 2–6 whorls of 3–7 phialides, 3–3.5 μm ($\bar{x}$ = 3 μm, n = 20) wide at the base	Erect (later Sometimes also procumbent), thick-walled, with 2–5 (to over 10 in old colonies) whorls of 3–7 phialides, 3.5–4 μm wide at the base	Erect, thick-walled, bearing many whorls of 3–10 phialides, about 2.5(–3.5) μm wide at the base
Phialides	Arising at an oblique angle from the conidiophore stipe, 9.5–25 μm ($\bar{x}$ = 14.5 μm, n = 30) long, 1–2.5 μm at the base, gradually tapering to 0.5–1 μm at the tip	Arising at an oblique angle from the conidiophore stipe, 14–20(–45) μm long, from 1.5–3 μm at the base before gradually tapering to 0.5–1 μm at the tip	15–30 μm long, from 1.5–2.5 μm gradually tapering to 0.5–1.5 μm

Table 3.7 (continued)

Morphological character	***Zarea thailandica* (This study)**	***Z. fungicola* (Zare & Gams, 2008)**	***Z. aleophila* (Zare & Gams, 2008)**
Conidia	Forming mostly globose slimy masses of conidia, hyaline, smooth walled, fusiform, long-ellipsoidal to almost cylindrical, the basal end indistinctly attenuated, variable in size, 3–8 × 1–2.5 µm ($\bar{x}$ = 4 × 2 µm, n = 50), with 1–2 or more inconspicuous guttules, L/W ratio = 2	Adhering in mostly globose slimy heads, the heads of single phialides often coalescing to form large slimy masses, conidia fusiform, long-ellipsoidal to almost cylindrical, the basal end indistinctly truncate, sometimes curved along the longitudinal axis, asymmetrically biconvex to concave-convex to slightly sickle-shaped, smooth-walled, of very unequal size, 4–9(–12) × 1.5–2.5(–3.5) µm, with 1–2 or more inconspicuous guttules, L/W ratio = 3.25	Forming mostly globose heads, oblong, fusiform, long ellipsoidal to almost cylindrical but often with conically tapering and ultimately rounded tips, equal at both ends, usually straight, smooth-walled, of very irregular size, 4.5–8 × 1–2.5 µm, with two or more inconspicuous guttules, L/W ratio = 3.6

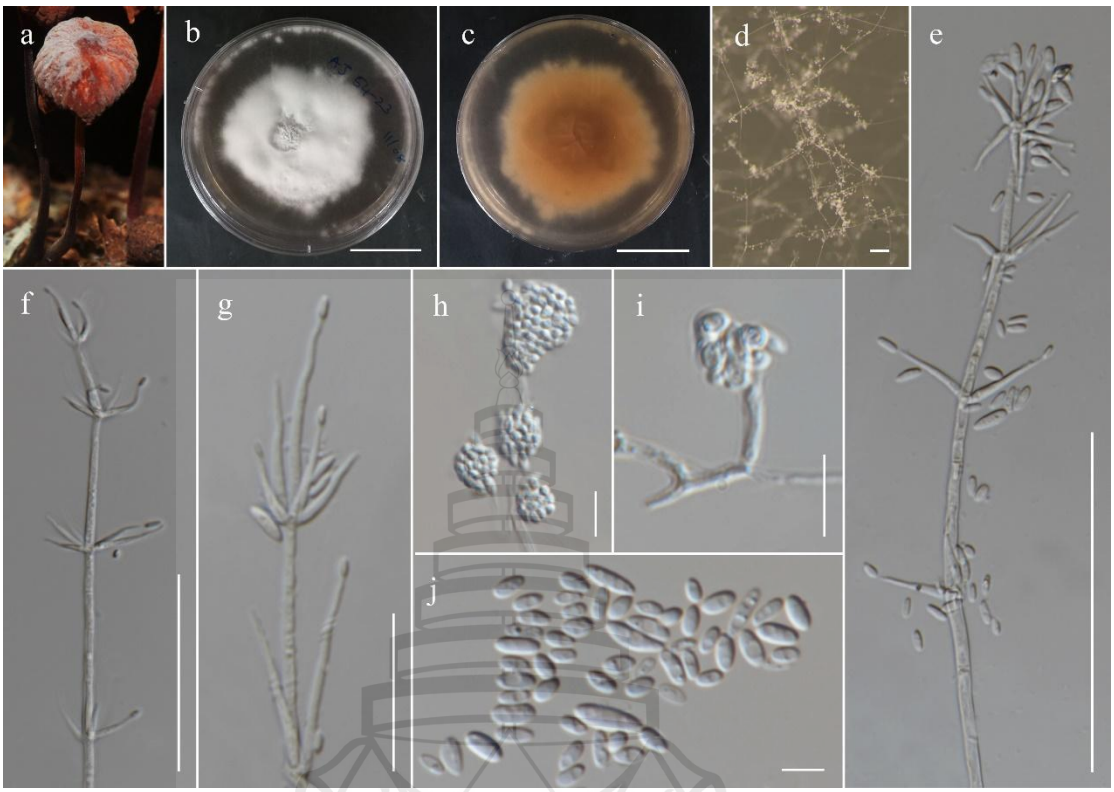


Figure 3.48 *Zarea thailandica* (AJ 54-23a)

Figure 3.48, a. Host (*Marasmius* sp.). b, c. Colony on PDA. d, e. Sporulation on PDA. e–g. Conidiophores, phialides and conidial attachments. h, i. Slimy masses of conidia. j. Conidia. Scale bars: b, c = 30 mm, d = 100 μm, e = 80 μm, f = 60 μm, g = 25 μm, h, i = 20 μm, j = 5 μm.

3.3 Discussion

Historically, fungal taxonomy depended on morphological features, however, these characters alone are often inadequate for resolving species boundaries due to phenotypic plasticity influenced by environmental variables, geographical distribution, host specificity, and ecological niche (Vasilyeva & Stephenson, 2010; Lücking, 2019; Jayawardena et al., 2021). Consequently, molecular data have become indispensable in achieving accurate species delimitation (Chethana et al., 2021; Gautam et al., 2022), and integrative approaches combining both morphological and molecular evidences are now standard in fungal systematics (Senanayake et al., 2020).

In this study, 33 fungicolous taxa were identified, belonging to 11 distinct genera classified within *Sordariomycetes* (08), *Dothideomycetes* (02), and *Mucoromycetes* (01). The genera identified within *Sordariomycetes* include *Clonostachys*, *Diaporthe*, *Fusarium*, *Hypomyces*, *Hypoxylon*, *Mariannaea*, *Xenoacremonium*, and *Zarea*, *Dothideomycetes* includes *Lasiodiplodia* and *Neoroussoella*, while *Mucoromycetes* include *Mucor*. Among the identified taxa, four represent novel species, five are newly proposed combinations, and 23 are new records. All the fungicolous taxa reported herein were identified based on both morphological characteristics and multi locus phylogenetic analyses.

3.3.1 Frequently Encountered Fungicolous Genera

Clonostachys, *Fusarium*, *Hypomyces*, *Mucor*, and *Zarea* are among the common genera previously identified as fungicolous fungi, and they were also recovered in this study. Species belonging to these genera have been reported as important pathogens affecting cultivated mushrooms (Yu et al., 2024).

The present study contributes two new species to *Zarea*, *Z. boleticola* and *Z. thailandica*, both isolated as fungicolous fungi associated with wild mushroom hosts. Members of *Zarea* are previously known to be fungicolous on a wide range of basidiomycetes, including *Agaricus* spp., *Allopsalliota geesterani*, *Coltricia perennis*, *Gomphidius glutinosus*, *Henningsomyces candidus*, *Hypholoma capnoides*, *Laccaria laccata*, *Marasmiellus ramealis*, *Russula nigricans*, and *Thelephora terrestris* (Khonsanit et al., 2024). Notably, *Z. fungicola* (syn. *Lecanicillium fungicola* var. *fungicola*) and *Z. aleophila* (syn. *Lecanicillium fungicola* var. *aleophilum*) are recognized pathogens that cause dry bubble disease in commercially cultivated mushrooms (Berendsen et al., 2010). Additionally, *Zarea* species have also been isolated from leaf litter and soil (Khonsanit et al., 2024).

Hypomyces is one of the genera which comprises numerous species that exhibit fungicolous lifestyle (Põldmaa, 2000). Some species of *Hypomyces* are also recognized as pathogens of cultivated mushrooms, responsible for economically significant diseases such as cobweb disease, wet bubble disease, and cottony leak disease (Jayawardena et al., 2025). In addition to their fungicolous lifestyle, *Hypomyces* species have been reported from a variety of other substrates, including plant material, moss, humus, rock surfaces, insect galls, and lichens (Lechat et al.,

2017; Farr et al., 2021; Jayawardena et al., 2025). It has been proposed to conserve *Hypomyces* over the asexual morph typified genera, *Cladobotryum*, *Mycogone*, *Sepedonium*, and *Stephanoma* (Rossman et al., 2013). However, this proposal remains unresolved, primarily due to the lack of a robust phylogenetic framework. Many of the relevant taxa lack molecular sequence data, and comprehensive herbarium-based studies have yet to be conducted. Therefore, future taxonomic studies integrating both detailed morphological observations and multigene phylogenetic analyses are essential for clarifying the delimitation and classification of *Hypomyces*. In the present study, following the current nomenclatural framework, five new combinations are proposed: *Hypomyces chalcipori*, *H. laevigatus*, *H. novovarius*, *H. paravirescens*, and *H. protrusus* over *Sepedonium chalcipori*, *S. laevigatum*, *Cladobotryum novovarium*, *C. paravirescens*, and *C. protrusum* respectively. *Hypomyces chiangraiensis* is introduced as a novel species. Furthermore, *H. chlorinus*, *H. cornea*, *H. pseudocorticiicola*, and *H. semicircularis* are reported for the first time from Thailand. The sexual morph of *H. boletiphagus* is described for the first time in Thailand, while *H. mycophilus* is recorded on wild *Auricularia* sp. in Thailand for the first time. Additionally, this study documents the first association of *H. cornea* with a *Hydnoporia* species and provides a new host record of *H. protrusus* in Thailand.

Fusarium species exhibit a cosmopolitan distribution and display a wide range of ecological lifestyles, functioning as endophytes, parasites, or pathogens of plants, as well as mutualists or pathogens of animals and insects (Torbati et al., 2021; Hyde et al., 2023). In addition to these roles, several species have been identified as fungicolous fungi (Torbati et al., 2021). Approximately 24 species of *Fusarium* have been reported as fungicolous, occurring on mushrooms, rusts, smuts, and various other micro fungi (Torbati et al., 2021). In the present study, seven *Fusarium* species representing four distinct species complexes (FIESC, FFSC, FOSC, and FCSC), were identified as fungicolous on mushroom hosts: *F. pernambucanum*, *F. mangiferae*, *F. proliferatum*, *F. verticillioides*, *F. fabacearum*, *F. grosmichelii*, and *F. teslae*. Of these, except *F. proliferatum*, seven other species are reported for the first time exhibiting a fungicolous lifestyle. Interestingly, *F. pernambucanum* have also been isolated from insects, suggesting a potential link between insect- and fungus-associated ecologies. This may be related to the presence of chitin in both fungal cell

walls and insect exoskeletons. To exploit fungi or insects as hosts, these *Fusarium* species may produce chitin-degrading enzymes, enabling colonization and nutrient acquisition from these substrates (Leger et al., 1986; Oliveira et al., 2018; Bakri et al., 2022).

Clonostachys represents a taxonomically diverse group that includes soil-inhabiting fungi with multiple ecological roles, functioning as mycoparasites, endophytes, epiphytes, pathogens and saprotrophs (Schroers, 2001; Moreira et al., 2016). Species of *Clonostachys* are cosmopolitan, with their highest diversity reported from tropical regions. They are frequently encountered in soils, litter, and on both decaying and living plant substrates (Torcato et al., 2020). However, there are reports of mycoparasitism and a mycophilic habit exhibited by several *Clonostachys* taxa (Samuels 1976; Schroers et al., 1999; Schroers, 2001). While there have been occasional reports highlighting parasitic interactions of *C. rosea* with myxomycetes, nematodes, ticks, molluscs, and leafhoppers (Schroers, 2001; Toledo et al., 2006; Zhang et al., 2008). The species such as, *Clonostachys rogersoniana*, *C. rosea*, *C. subquaternata* and *C. farinosa* (syn. *C. byssicola*) have been reported as fungicolous fungi (Sun et al., 2019a; Manawasinghe et al., 2024). Due to the mycoparasitic activity of *C. rosea*, it has been explored for biological control of plant diseases as well (Jensen et al., 2022). This study is the first to reports *Clonostachys rogersoniana* as a fungicolous fungus on a bolete mushroom in Thailand.

Mucor species are cosmopolitan in distribution, frequently encountered in a wide range of natural habitats (Morin-Sardin et al., 2017; Hurdeal et al., 2021). While species of *Mucor* are predominantly saprobic, it also includes endophytes, parasites, and pathogens (Rashmi et al., 2019; Wagner et al., 2020). They are frequently isolated from substrates such as soil, dung, decomposing plant material, and other moist environments (Walther et al., 2013). Several species have been identified as opportunistic pathogens in both humans and animals (Hoffmann et al., 2013; Morin-Sardin et al., 2017). In addition, some *Mucor* species exhibit fungicolous behaviour, growing on or in association with other fungi (Gajanayake et al., 2023b). Previousely reported fungicolous associations include *Mucor circinelloides* on *Rhizopus stolonifer*, and *M. luteus* on *Amanita muscaria*, (Sun et al., 2019a). This study contributes several new records of fungicolous *Mucor* species. These include *M.*

circinelloides on *Phlebopus* sp. in Thailand, *M. hiemalis* on *Ramaria* sp. and *Boletus* sp. in China, and *M. nederlandicus* on *Russula* sp. in Thailand. Furthermore, *M. yunnanensis* is introduced as a novel species, associated with *Armillaria* sp. and *Boletus* sp. in China.

3.3.2 Rarely Fungicolous/ Uncommon Genera on Mushroom Hosts

Unlike *Clonostachys*, *Fusarium*, *Hypomyces*, *Mucor*, and *Zarea* this study reveals six more uncommon genera associated with mushrooms. Those are *Diaporthe*, *Hypoxylon, Lasiodiplodia*, *Mariannaea*, *Neoroussoella*, and *Xenoacremonium.*

Diaporthe is well known for its plant-pathogenic members, though species also occur as endophytes and saprobes (Hongsanan et al., 2023; Dissanayake et al., 2024). In the holotype material of *D. baptisiae*, it was reported alongside *D. arctii* (Rehm, 1908), though the fungicolous nature of *D. baptisiae* has not been conclusively verified (Hongsanan et al., 2023). Beyond this, there have been no confirmed reports of *Diaporthe* species exhibiting a fungicolous lifestyle. Rather, *Diaporthe* has been recorded as a host for fungicolous fungi such as *Unguiculella jamaicensis*, *Nectriopsis septofusidiae*, and *Woswasia atropurpurea* (Sun et al., 2019a). In this study, *Diaporthe talong* is reported for the first time as a fungicolous species, isolated from a polypore fruiting body.

Hypoxylon species are predominantly saprobic, commonly found on dead wood, and are distributed globally (Ju & Rogers, 1996, Wendt et al., 2018). Some species have also been reported as endophytes or facultative parasites on weakened hosts, and has been isolated from soil (Ju & Rogers 1996; Kuhnert et al., 2014; Preedanon et al., 2023). Fungicolous behavior has been infrequently reported for *Hypoxylon*. For instance, *H. invadens* was described from aborted primordia of *H. fragiforme* (Fournier, 2014), and *H. aeruginosum* has been observed growing on stromata of other *Hypoxylon* species (Læssøe et al., 2010). Additionally, *H. parasiticum* was reported on reduced stromata of a *Hypoxylon* species and later confirmed to be *H. jecorinum* parasitizing *H. duranii* (Fournier, 2014). In the present study, we report *Hypoxylon fendleri* for the first time occurring on a polypore fruiting body. Given the limited records of fungicolous behaviour in this genus, it is plausible that *H. fendleri* exhibits such an ecological role. However, as noted under the species

description, further collections and detailed observations are required to determine whether this represents a true host-specific association or an incidental colonization.

Species of *Lasiodiplodia* are globally distributed and occur on a wide variety of plant hosts (Rathnayaka et al., 2023). While most members of the genus are known as plant pathogens, they have also been reported as endophytes or saprobes on plant material, and has been isolated from soil (Rathnayaka et al., 2023; Jayawardena et al., 2025, Yasanthika et al., 2025). Although *Lasiodiplodia theobromae* has been reported as a host for parasitic microfungi such as *Dendrodochium parasiticum* Chevaug. and *Hansfordia alba* J.A. Mey. (Sun et al., 2019a), no other species of *Lasiodiplodia* has previously been documented exhibiting a fungicolous lifestyle. In the present study, *L. thailandica* is described as a fungicolous species associated with a polypore fruiting body, representing the first such record for the genus both in Thailand and globally.

Members of *Mariannaea* are discovered to be distributed in terrestrial and aquatic habitats. *Mariannaea* species have been previously recognized as mainly associated with soil, wood/ submerged wood, bark, and pine needles (Samson, 1974; Cai et al., 2010; Farr et al., 2021; Watanabe & Dai, 2021). The study is the first to report of *M. humicola* on a fruiting body of *Marasmius* sp. as a fungicolous fungus from Thailand. *Mariannaea humicola* was originally described by Lombard et al. (2015), and it was isolated from rhizosphere soil under *Araucaria angustifolia* in Sao Paulo, Brazil. So far, *M. humicola* has been reported from terrestrial and aquatic habitats (Lombard et al., 2015; Pasqualetti et al., 2020). During our study, fruiting bodies of *Marasmius* sp. were collected from the wild. As *M. humicola* has been previously reported from the soil, likely, the natural introduction of *M. humicola* from the soil onto the fruiting bodies of *Marasmius* sp. may have led to its development as a fungicolous fungus. Recently, it was discovered that a strain of *M. humicola* isolated from a marine environment produces two bioactive terpenoids. Those compounds exhibit noteworthy antifungal properties against *Aspergillus flavus*, *Penicillium griseofulvum*, and *Trichoderma pleuroticola*, which belong to toxicogenic/pathogenic genera that encompass a significant number of species holding considerable agronomical, clinical, ecological and economic importance (Botta et al., 2020).

The majority of *Neoroussoella* species have been isolated from decaying plant material, with some also reported from sediments and soil (Index Fungorum, 2025). In this study, *N. entadae* is documented for the first time as a fungicolous species occurring on a decaying polypore fruiting body, thereby expanding the known ecological range of the genus and highlighting a novel niche association.

Most of the *Xenoacremonium* species have been isolated from plant substrates, although some have been found in different habitats, for example, *X. minutisporum* was originally isolated from a female *Dorcus titanus castanicolor*, and *X. recifei* from a human mycetoma (Index Fungorum, 2025). In the present study, *X. allantoideum* is described as a fungicolous species associated with *Auricularia* sp., marking the first fungicolous record for the genus both in Thailand and globally. This finding extends the ecological range of *Xenoacremonium*.

3.3.3 The Danger of Fungicolous Fungi on Wild Mushroom to Mushroom Cultivation

Wild mushrooms can serve as natural reservoirs of fungicolous fungi which may pose significant risks to mushroom cultivation by causing destructive diseases. Several common genera, including *Fusarium*, *Hypomyces*, *Trichoderma*, and *Zarea*, harbour species recognized as pathogens in mushroom farms, and these fungi have also been reported from wild mushrooms (Yu et al., 2024; Gajanayake et al., 2025b). For example, *Hypomyces protrusus, H. semicircularis* are causal agents of cobweb disease in cultivated mushrooms (Yu et al., 2024), and both species have been detected on wild mushrooms (Gajanayake et al., 2025b). These fungi are capable of spreading from wild hosts to cultivated mushrooms through airborne spores, insect vectors, contaminated substrates, or inadequate farm hygiene. Once introduced, they can cause severe infections that lead to significant yield losses, reduced mushroom quality, and substantial economic damage.

Therefore, documenting fungicolous fungi associated with wild mushrooms is crucial for predicting potential threats to cultivated species. Early detection of related fungi and continuous monitoring can support the development of effective management strategies, such as strict sanitation, substrate sterilization, and environmental control, thereby reducing the likelihood of pathogen transfer from natural ecosystems to commercial mushroom cultivation systems.

3.3.4 Challenges Implications and Future Directions

Studying fungicolous fungi presents numerous challenges, from field collection to species identification. In tropical regions like northern Thailand, rapid decomposition due to high humidity and microbial activity shortens the window for effective sampling. The rainy season proved most suitable for collecting mushroom-associated fungicolous taxa. To ensure successful isolation, specimens must be processed promptly, as delayed or dried samples often fail to yield viable fungicolous isolates. Many fungicolous fungi grow slowly and can be easily overrun by fast-growing contaminants. Additionally, sporulation is sometimes absent *in-vitro*, making morphological identification difficult. Sporulation can be induced using different media or sterilized host tissues, even sporulating isolates often show reduced or overlapping features that complicate taxonomy. Molecular techniques are essential for identification, but reference sequences for some fungicolous groups remain limited in public databases.

The isolates from previously known fungicolous genera such as *Zarea*, *Hypomyces*, *Mucor*, and *Fusarium* in this study were obtained from living mushroom fruiting bodies. Given previous records of pathogenicity in these genera on cultivated mushrooms (Yu et al., 2024), some species may be potential pathogens on specific hosts.

The detection of fungicolous taxa in less-expected genera such as *Diaporthe*, *Hypoxylon*, *Lasiodiplodia*, *Neoroussoella*, and *Xenoacremonium* during this study suggests possible ecological flexibility or early-stage host shifts. These genera, commonly associated with plants or wood, may opportunistically colonize mushroom hosts under suitable environmental conditions. In this study, such fungi were consistently isolated from polypores and wild *Auricularia* species growing on decaying logs or tree branches, or *Marasmius* sp. on soil, where shared microhabitats likely facilitate cross substrate colonization. Due to the limited number of studies targeting fungicolous taxa, such interactions may be remaining unrevealed. However, some associations may be incidental, but repeated recovery from multiple studies may clarify their ecological relevance.

Future studies should investigate the pathogenicity and seasonal dynamics of fungicolous fungi, utilizing both culture-dependent and culture-independent

approaches, such as metagenomic analyses. These methods will enhance the detection of additional fungicolous taxa and contribute to a more comprehensive understanding of their ecological roles in both natural and cultivated systems.

CHAPTER 4

FUNGI ASSOCIATED WITH MUSHROOM CULTIVATION

4.1 Introduction

Mushrooms are heterotrophic macrofungi with either hypogeal or epigeal growth habits (Chang & Miles, 1992). They are renowned for their numerous nutritional and medicinal properties, and are globally cultivated (Bell et al., 2022; Kour et al., 2022; Yu et al., 2024). Mushroom production stands out as a vital microbial technology, offering significant commercial value by facilitating large-scale recycling of agricultural waste (Kouser & Shah, 2013). Moreover, it helps to alleviate pressure on arable land by enabling cultivation under controlled conditions (Kouser & Shah, 2013). Over the past decade, the mushroom industry has emerged as a rapidly expanding and thriving sector in numerous countries worldwide (Singh et al., 2020). According to Li et al. (2021), there exist over 2,000 species of edible mushrooms worldwide. The total estimated global production of mushrooms and truffles in 2023 was 50,010,109 tons (FAO Stat, 2023). Asia is the leading region in global mushroom production, with China as the primary producer (Li & Xu, 2022; Sangeeta et al., 2024; Ling et al., 2025).

The proliferation of fungal contaminants, including both pathogenic species and competitor molds, remains a persistent challenge and poses a major obstacle to the growth of the mushroom industry (Sun et al., 2019b; Ghimire et al., 2021; Yu et al., 2024). Contamination in mushroom cultivation often occurs due to poor hygiene practices and inadequate sterilization (Okigbo & Anuagasi, 2021). Yu et al. (2024) reported more than 130 fungal pathogens/competitor molds, displaying significant taxonomic diversity across 58 genera affecting the growth and development of major cultivated mushroom species. These fungal pathogens affecting mushrooms show the highest diversity within *Hypocreales* (*Sordariomycetes*), with *Hypomyces* (*Hypocreaceae*) being the most impactful (Põldmaa 2000, 2011; Sun et al., 2019a; Yu et al., 2024). The major fungal pathogens encountered in mushroom cultivation

include *Hypomyces*/*Cladobotryum* spp., *Zarea* spp., *Mycogone* spp., and *Trichoderma* spp. (Sharma et al., 2007; Fletcher & Gaze, 2008; Yu et al., 2024). These are responsible for economically significant diseases such as cobweb, dry bubble, wet bubble, and green mold (Sharma et al., 2007; Fletcher & Gaze, 2008). In addition, other species such as *Pseudodiploospora longispora*, which causes white mold disease on *Morchella* spp., *Hypomyces pseudocorticiicola*, which causes cottony leak disease on *Auricularia nigricans*, and *Scytalidium* spp., which cause slippery scar on *Auricularia* spp. and yellow rot on *Ganoderma* spp., have also been reported as confirmed pathogens on cultivated mushrooms (Kang et al., 2010; Peng et al., 2014; Okuda et al., 2016; Xie et al., 2024a; Yu et al., 2024; Jayawardena et al., 2025). Moreover, several other species, such as *Aspergillus* spp., *Cephalotrichum* spp., *Chaetomium* spp., *Daldinia* sp., *Fusarium* spp., *Penicillium* spp., along with many others, act as competitor molds that negatively impact mushroom cultivation (Sharma et al., 2007; Gajanayake et al., 2021a, 2021b; Yu et al., 2024) (Figure 4.1).

The presence of fungal pathogens or competitor molds can lead to a decreased yield and/or compromised quality of mushroom fruiting bodies, resulting in significant economic losses (Sun et al., 2019b; Gajanayake et al., 2021a, 2021b; Yu et al., 2024). Fungal pathogens often exhibit distinct characteristics in terms of symptomatology on substrates, disease cycle, epidemiological prerequisites, and the extent of yield reduction (Ghimire et al., 2021). Inadequately sterilized substrates are the primary source of most contaminants in mushroom cultivation (Gajanayake et al., 2021a; Ghimire et al., 2021; Rathod et al., 2024; Jayawardena et al., 2025). Moreover, the poor management practices and insect infestations can also exacerbate the spread of diseases (Sharma et al., 2007; Gea et al., 2021; Yu et al., 2024).

Key strategies for managing fungal pathogens and competitor molds in mushroom cultivation include the use of properly sterilized substrates, strict hygiene practices, and careful control of environmental conditions (Gajanayake et al., 2021a; Gea et al., 2021 ;Ghimire et al., 2021; Rathod et al., 2024). Integrated disease management approaches, such as the use of biological control agents and selective fungicide applications, are increasingly employed to suppress both pathogens and competitor molds, thereby reducing yield losses and maintaining mushroom quality worldwide. (Gea et al., 2021; Pandey et al., 2025).

The primary objective of this study was to discover the fungi associated with mushroom cultivation in northern Thailand and to review the fungal diseases and competitor molds that affect the global mushroom industry.



Figure 4.1 Fungi affecting mushroom cultivation

Figure 4.1, a Oyster mushroom growing bags contaminated with *Daldinia eschscholtzii*. b Cultivated *Auricularia cornea* fruiting bodies infected by *Hypomyces*/*Cladobotryum* sp. (Photo credits: Mr. Arttapon Walker). c Cultivated Oyster mushrooms contaminated by *Penicillium* sp. (Photo credits: Mr. Sabin Khyaju). d Cultivated *Morchella* sp. infected by *Pseudodiploospora longispora* (Photo credits: Dr. Lu Caige).

4.2 Morpho-molecular Characterization of Fungi Associated with Mushroom Cultivation from Northern Thailand

This section presents the fungal species identified in association with mushroom cultivation in northern Thailand during the present study. *Daldinia eschscholtzii* and *Scedosporium apiospermum* were discovered for the first time from oyster mushroom cultivation substrates in northern Thailand. In addition, *Aspergillus quadrilineatus, Fusarium sulawesiense,* and *Mucor irregulari* were isolated from cultivated *Phlebopus spongiosus, Hericium coralloides* and *Pleurotus* sp. fruiting bodies, respectively for the first time in northern Thailand.

The identification of all the fungal isolates was carried out through an integrative approach, combining detailed morphological examinations with multi-locus phylogenetic analyses. The selection of gene regions followed the most suitable molecular markers recommended for each genus or family. To confirm the taxonomic placement of these fungi, both morphological illustrations and multi-gene phylogenetic reconstructions were produced, employing maximum likelihood (ML) and Bayesian inference (BI) methods.

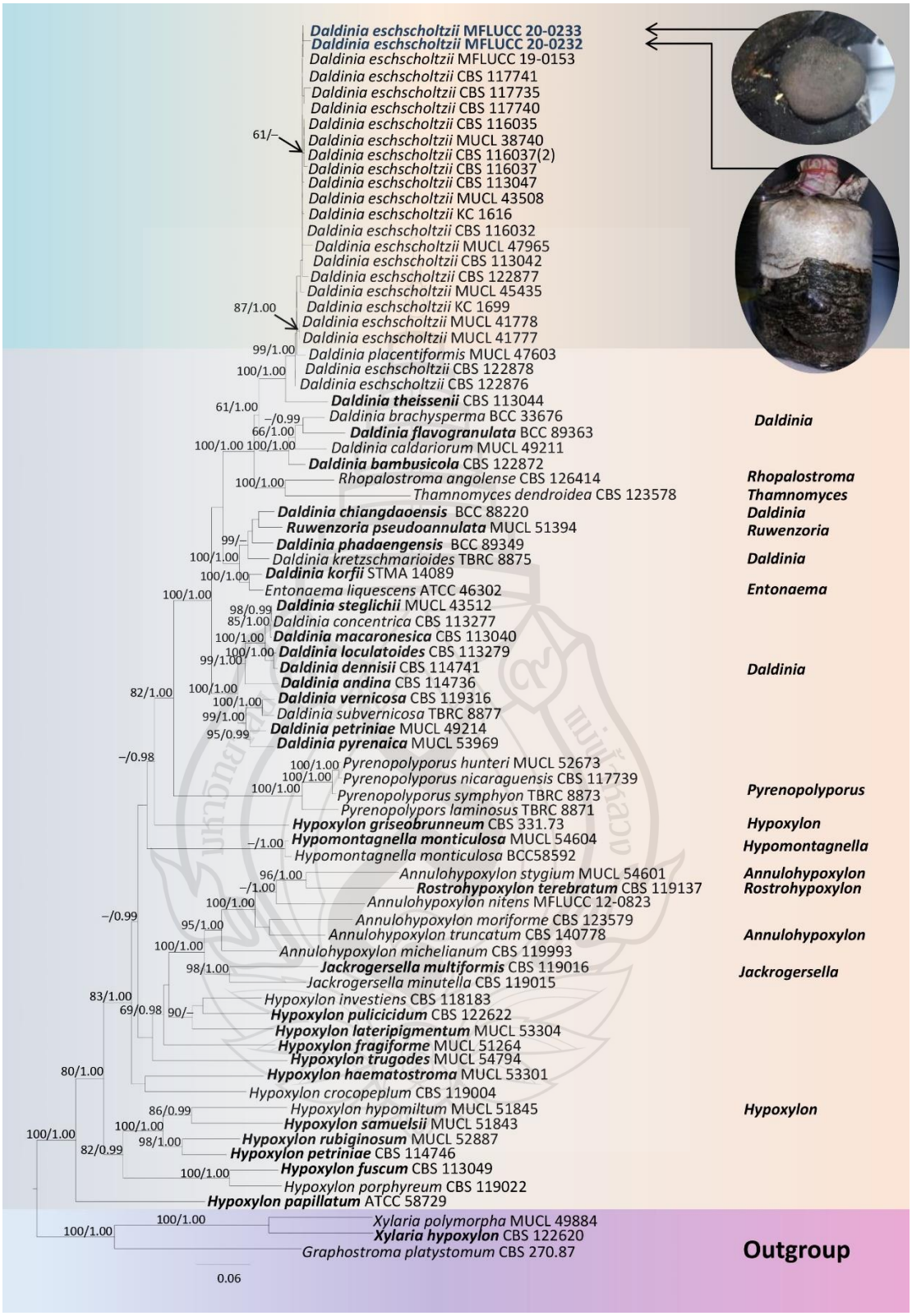


Figure 4.2 RAxML tree based on the analysis of LSU, ITS, *rpb*2 and *tub*2 combined data set of selected genera in *Hypoxylaceae*

Figure 4.2, The combined LSU, ITS, *rpb*2 and *tub*2 matrix comprised 79 epithets including selected genera in *Hypoxylaceae* and three outgroup taxa. The tree is rooted using *Graphostroma platystomum*, *Xylaria hypoxylon* and *X. polymorpha*. Single and concatenated alignments resulted similar topologies for both ML and BI analyses. The value of average standard deviation of the split frequencies of BI analysis was 0.009485.The best scoring RAxML tree had a final ML optimization likelihood value of –38238.950864. The matrix had 1670 distinct alignment patterns, with 33.46% of undetermined characters or gaps. Bootstrap support values for ML values equal to or >60% and BYPP values equal to or >0.95 are shown as ML/BYPP above the nodes. The isolate used for the present study is shown in blue bold. Type strains are indicated in black bold. The scale bar represents the expected number of nucleotide substitutions per site.

Daldinia eschscholtzii (Ehrenb.) Rehm, Annls mycol. 2(2): 175 (1904)

Figure 4.3–4.5

Index fungorum number: IF 544992

Facesoffungi Number: FoF02990

Growing on oyster mushroom grow substrate. Sexual morph: *Stromata* 1.2–2 × 1–1.5 cm, placentiform to turbinate, rarely depressed–hemispherical, sessile to short–pedicellate, perithecial outlines on surface inconspicuous; dark brick, greyish sepia, or vinaceous grey when immature, black and smooth on maturity, brown granules underneath the surface, fresh and young stromata producing livid purple or vinaceous purple with KOH–extractable pigments; tissue between perithecia brown, pith like to woody, tissue beneath perithecial layer comprising alternate dark and light zones, darker area made of dark brown, pithy to woody tissue 0.1–0.3 mm thick, lighter area grey to greyish brown, initially soft, becoming hard when dry, persistent, 0.2–0.3 mm thick. *Perithecia* 0.9–1.2 × 0.3–0.4 mm ($\overline{x}$ = 1.05 × 0.35 mm). *Asci* 96–124 × 5 – 8 µm ($\overline{x}$ = 110 × 6.5 µm, n = 15), 8–spored, long–pedicellate, amyloid, with discoid apical ring, 2–3 × 0.4–0.6 µm. *Ascospores* 8.2–12.7 × 3.8–6.1 µm ($\overline{x}$ = 10.4 × 4.9 µm, n=30), uniseriate, dark brown, unicellular, ellipsoid-inequilaterally with narrowly rounded at the ends, comprising a straight germ slit spore length on convex side; perispore dehiscent in 10% KOH smooth, at times showing conspicuous transverse striations, epispore smooth. Asexual morph: Observed on the ten weeks old

culture, *hyphomycetous*. *Conidiophores* 2–3 × 0.8–1.2 µm ($\overline{x}$ = 2.5–1 µm, n = 10), hyaline, mononematous, synonymous, with dichotomous or trichotomous conidiogenous apparatus bearing nodulisporium–like branching pattern, 1–3 conidiogenous cells originating from each end. *Conidiogenous cells* 2.4–4.5 × 1.8–5 µm ($\overline{x}$ = 3.45–3.4 µm, n = 10), hyaline, holoblastic, terminal or intercalary, cylindrical, with rounded apices, collaret or opening width. *Conidia* 3.2–5 × 2.5–4.5 µm ($\overline{x}$ = 4.1–3.5 µm, n = 40), hyaline, obovoid to ellipsoid, aseptate, smooth, often with a truncate base. *Mycelium* 1.5–3.5 µm ($\overline{x}$ = 2.5 µm) wide, superficial, septate, branched, have melanized hyphae with brownish exudates in old cultures.

Colony characters – Colonies on PDA reaching 90 mm diam. with a diffused margin after 14 days at 25 ^{o}C, colony circular. Front, initially white, turning into gray with olive green to dull green patches with time; reverse black at the center and whitish gray at the periphery.

Material examined – Thailand, Phayao province, growing out of the substrate of oyster mushroom grow bags, 10 July 2020, AJ. Gajanayake, AJ 061 (MFLU 21–0021), living cultures (MFLUCC 20–0232) and (MFLUCC 20–0233).

GenBank numbers – MFLUCC 20–0232: ITS = MW672318; *tub*2 = MW682336; MFLUCC 20–0233: ITS = MW672319; LSU = MW672325; *tub*2 = MW682337.

Notes – Our isolates (MFLUCC 20–0232 and MFLUCC 20–0233) clustered within *D. eschscholtzii* clade (Figure 4.2). *Daldinia eschscholtzii* (MFLU 21–0021, MFLUCC 20–0232 and MFLUCC 20–0233) reported in this study shares similar sexual and asexual morphologies with the epitype of *D. eschscholtzii* (MBT177380) described in Stadler et al. (2014). The stromata, perithecia, asci and ascospores of MFLU 21–0021 are comparatively smaller than the *D. eschscholtzii* described in Stadler et al., (2014) as, (1.2–2 × 1–1.5 *vs* 1–7 × 1–4.5 cm, stromata; 0.9–1.2 × 0.3–0.4 *vs* 0.9–1.8 × 0.3–0.6 mm, perithecia; 96–124 × 5–8 *vs* 160–210 × 7–10 µm, asci; 8.2–12.7 × 3.8–6.1 *vs* (10–)11–13(–14) × 5–6.5 µm, ascospores). These dimensional differences are probably due to the environmental and substrate variations.

In this study, *D. eschscholtzii* is reported for the first time associated with oyster mushroom growing substrate in northern Thailand. Usually the growers discard the grow bags due to visual observations such as, black mycelium growth on the

substrate and lack of mushroom growth. In our study, we isolated fungal mycelia from blackened grow bags and allowed that mycelium to grow further. With time, stromata were observed on contaminated substrate (Figure 4.3). Morphological and phylogenetic evidence revealed that the fungus growing on grow bag substrate was *D. eschscholtzii*.

Previous studies have reported that *Daldinia* species are commonly found on woody substrates (Stadler et al., 2014; Ng et al., 2016). Stadler et al. (2014) examined *D. eschscholtzii* specimens associated with dead rubber tree, while Seephueak (2012) reported *D. concentrica* and *D. eschscholtzii* from old rubber wood logs in Thailand. Oyster mushroom grow bags used in this study was filled with rubber saw dust, lime, gypsum salts, mushroom supplement, rice bran, molasses and spawn made from sorghum and were sterilized (personal communication with the grower). *Daldinia* spores or hyphal fragments probably entered the grow bags with rubber sawdust during inoculation of *Pleurotus* spawn. The other possibility is, bags may not have been properly sterilized. Such occurrence causes fungal contamination of grow bags resulting loss of productivity in the mushroom cultivation and is a challenge to overcome.

Therefore, Selection of quality substrates and following the processing guidelines strictly are important to prevent substrate contaminations in mushroom production. A useful spin–off of this study is that, we are now aware that *Daldinia* can be grown in a similar way of *Pleurotus* growing. Since *Daldinia* are high in valuable chemical compounds, this methodology is useful in artificial production of *Daldinia* and using them in industrial application.

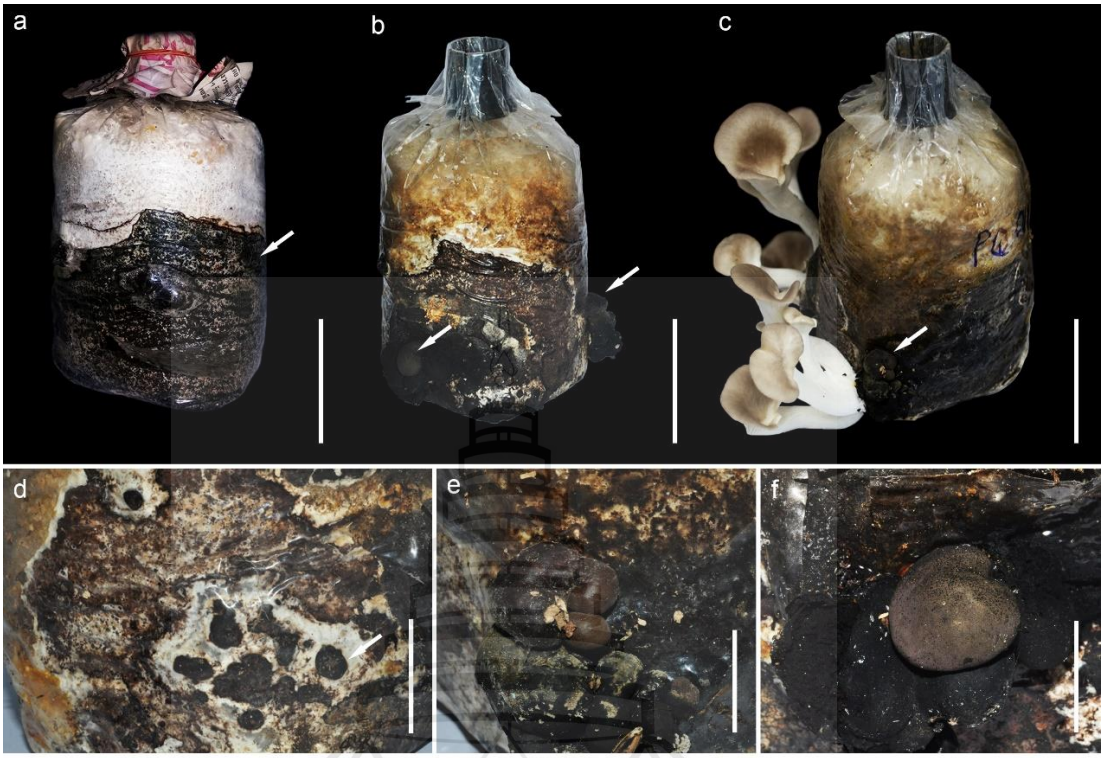


Figure 4.3 Contaminated oyster mushroom grow bags and development of stromata

Figure 4.3, a. Black, cottony masses of fungal mycelium. b, c, e, f. Stromata on grow bags (shown by arrow heads). d. Initial patches on the substrate prior to stromatal growth (shown by arrow heads). Scale bars: a–c = 5cm, d–f = 2 cm.



Figure 4.4 *Daldinia eschscholtzii*: sexual morph (MFLU 21–0021)

Figure 4.4, a. Stromata. b. Stroma in longitudinal section showing internal concentric zones and perithecial layer. c. Close up of internal concentric zones and perithecial layer with ostioles. d–f. Asci. g,h. Apical ring bluing in Melzer's reagent. i–k. Ascospores (j in 10% KOH, showing dehiscing perispore, k germ slit in arrow). l. KOH–extractable pigments. Scale bars: a,b = 1 cm, c = 1 mm, d–f = 50 µm, g,h,k = 10 µm, i,j = 5 µm.

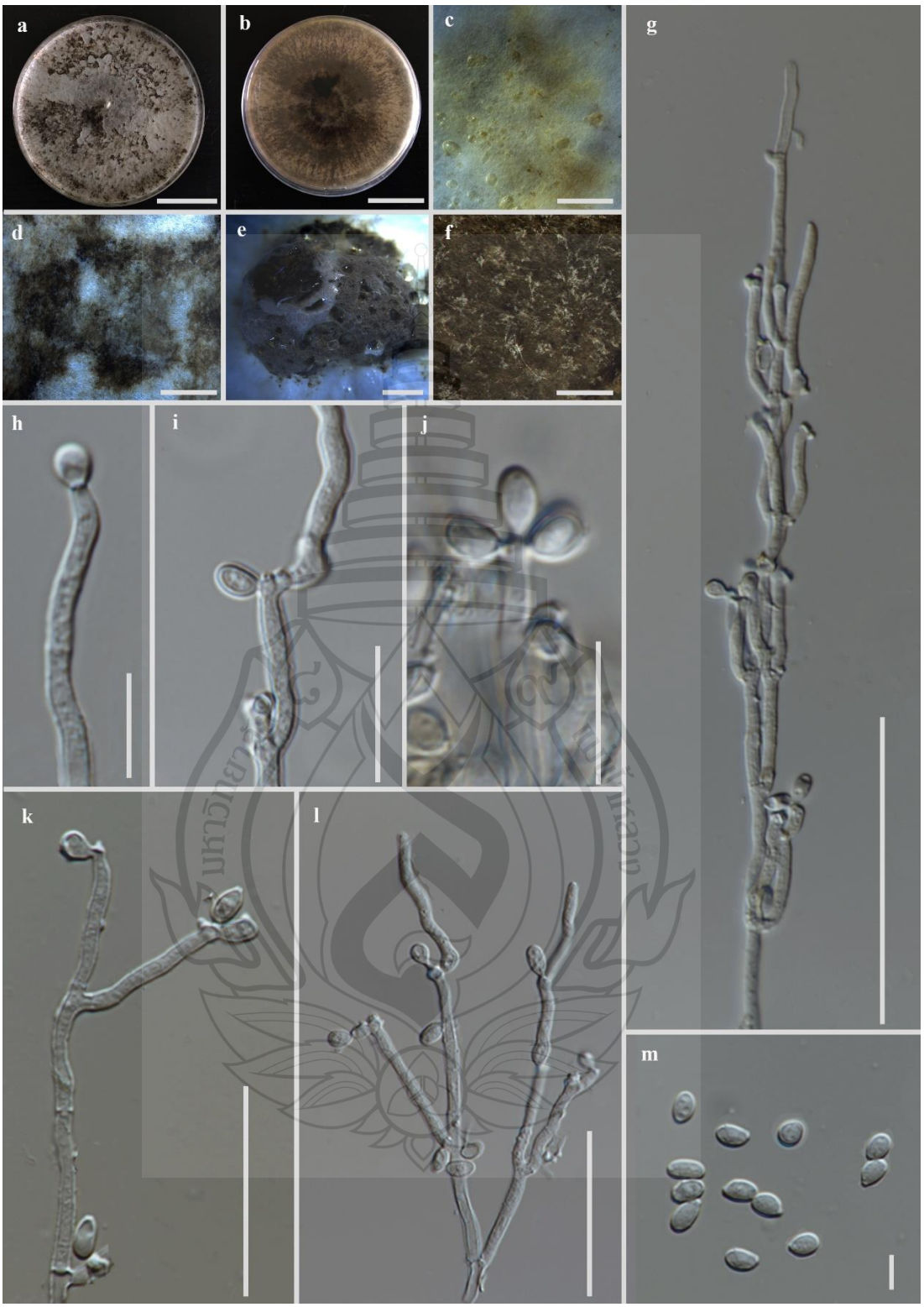


Figure 4.5 *Daldinia eschscholtzii*: sexual morph (MFLUCC 20–0232)

Figure 4.5, a,b. Colony on PDA after four weeks. c. Greenish patches on PDA after two weeks. d. Dark patches on PDA after four weeks. e. Sterile stromatic

structures on PDA after ten weeks. f. Sporulation of the colony on PDA. g. Conidial attachments and conidiogenous cells showing nodulisporium-like branching pattern. h–l. Conidial attachments and conidiogenous cells. m. Conidia. Scale bars: a,b = 30 mm, c,d,f = 500 µm, e= 1 mm, g,l = 30 µm, h–j = 10 µm, k= 25 µm, m= 4 µm.

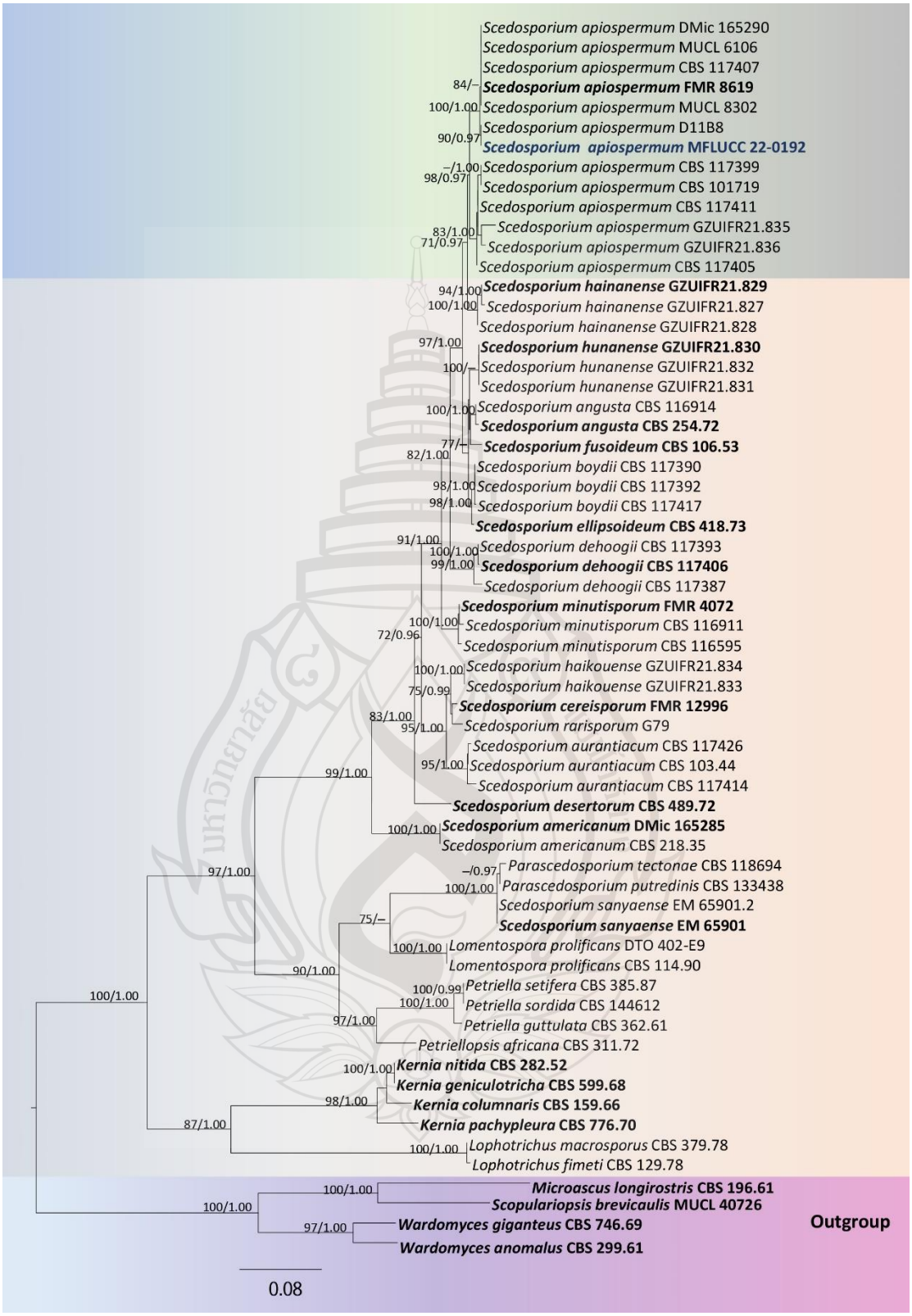


Figure 4.6 Phylogram generated from maximum likelihood analysis based on combined ITS and *tub2* sequence data representing the species of *Scedosporium* and related genera

Figure 4.6, Related sequences are taken from Zhang et al., (2021). Sixty-two taxa are included in the combined analyses. *Microascus longirostris* (CBS 196.61), *Scopulariopsis brevicaulis* (MUCL 40726), *Wardomyces anomalus* (CBS 299.61) and *Wardomyces giganteus* (CBS 746.69) are used as the outgroup taxa. Bootstrap support values for ML equal to or greater than 70% and BYPP equal to or greater than 0.95 are given near the nodes. The newly generated sequence is in blue. The type strains are indicated in black bold.

Scedosporium apiospermum Sacc. ex Castell. & Chalm., Manual of tropical medicine (London): 1122 (1919)

Figure 4.7

Index Fungorum number: IF432048

Facesoffungi number: FoF 11704

Growing on Oyster mushroom grow substrate. Sexual morph: Not observed. Asexual morph: on host, *Mycelium* black powdery mass. On *PDA*, hyphomycetous, *Hyphae* 1.5–3.5 μm ($\overline{x}$ = 2.2 μm) wide, branched, septate, hyaline. *Conidiophores* solitary or synnematous, solitary conidiophores 75–128 × 1.8–3 μm ($\overline{x}$ = 102.5 × 2.6 μm, n = 10) hyaline, branched, forms 1–3 conidiogenous cells at the end. synnematous conidiophores 132–352 × 8.2–17.5 μm ($\overline{x}$ = 288.4 × 12.7 μm, n = 15) cylindrical stipe, erect, forms conidia at the end. *Conidiogenous cells* 4.8–25 × 1.2–2.5 μm ($\overline{x}$ = 15.2 × 1.3 μm, n = 10) lateral or terminal formation on solitary conidiophores, hyaline, cylindrical. *Conidia* hyaline, guttulate, conidia arising from conidiogenous cells 6.2–8.2 × 2–4.5 μm ($\overline{x}$ = 7.4 × 3.3 μm, n = 30) obvoid to ellipsoidal, conidia arising from synnematous conidiophores 6.4–9.2 × 1.7–3.5 μm ($\overline{x}$ = 7.5 × 2.8 μm, n = 35) cylindrical or claviform with a truncate base, conidia from undifferentiated hyphae 6–7.5 × 5.2–6.6 μm ($\overline{x}$ = 6.4 × 5.2 μm, n = 20) sessile, globose to subglobose.

Colony characters – colonies on PDA attaining 65–75 mm diameter after 14 days at 25 °C, cottony, dense, lanose, light gray to dark grey, margins fimbriate and irregular; reverse dark grey to brown, grey to white margins.

Material examined – Thailand, Phayao province, growing on the oyster mushroom growing substrate, 06 June 2020, AJ. Gajanayake, AJ 072 (inactive dry culture, MFLU 22-0160, new host record), living culture, MFLUCC 22-0192.

GenBank numbers – ITS = ON714510; LSU = ON714511; *tub2* = ON730889.

Notes – Our isolate MFLUCC 22-0192, clusters within *Scedosporium apiospermum* with a boostrap support of 90% ML, 0.97 BYPP (Figure 4.6). Furthermore, the morphology of our isolate MFLUCC 22-0192 resembles the original description and illustrations for *Scedosporium apiospermum* by Saccarado in Castellani and Chalmers (1919) and the description and morphological illustrations by Gilgado et al. (2010). However, there are size differences of conidiophores, conidiogenous cells and conidia, when we compare our strain with the strains described in Castellani and Chalmers (1919) and Gilgado et al. (2010). The reason for this may be the differences in the media in which the colonies were grown.

Scedosporium apiospermum has been mainly identified as an opportunistic clinical pathogen relevant to many infections which commonly occur in the bones, central nervous system, lungs, paranasal sinuses, skin and soft tissues (Shinohara et al., 2009; Goldman et al., 2016). Seaphueek et al. (2017) isolated 21 fungal species from spent mushroom substrate of *Pleurotus* sp. collected from mushroom farms in southern Thailand. Among those 21 fungal species there were, *Alternaria* spp., *Aspergillus* spp., *Chaetomium* sp., *Cunninghamella* spp., *Fusarium* spp., *Lasiodiplodia* sp., *Neurospora* sp., *Penicillium* spp., *Rhizoctonia* sp. and *Trichoderma* spp. (Seaphueek et al., 2017). Suada et al. (2015) have reported *Aspergillus* spp., *Fusarium* spp., *Gliocladium* sp., *Mucor* spp., *Neurospora* spp., *Paecilomyces* sp., *Penicillium* spp., *Pythium* sp., *Stachybotrys* spp. and *Trichoderm*a spp. as contaminants from oyster mushroom growing substrate. According to best our knowledge this is the first report of *Scedosporium apiospermum* as a contaminant of oyster mushroom growing substrate.

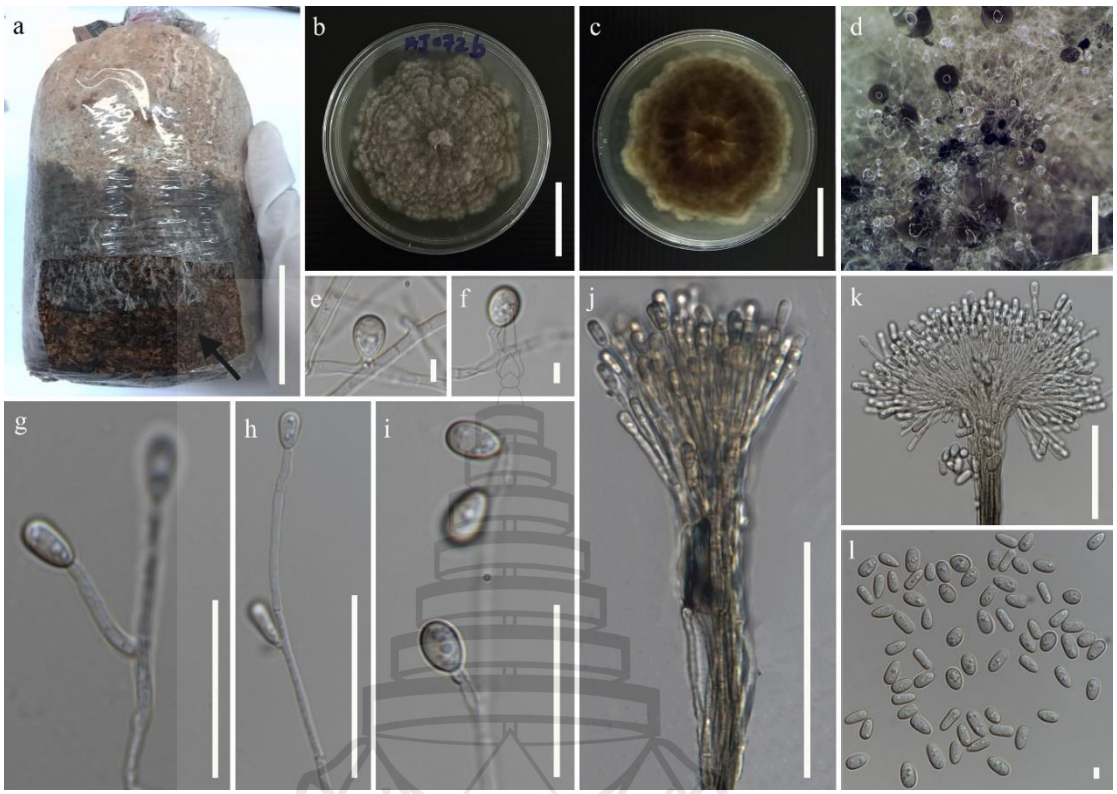


Figure 4.7 *Scedosporium apiospermum* (MFLU 22-0192)

Figure 4.7, a. Contaminated oyster mushroom grow substrate. b,c. Colony on PDA. d. Sporulation of the colony on PDA. e-i. Conidial attachments and conidiogenous cells. j,k. Synnema with conidia. l. Conidia. Scale bars: a = 5 cm, b,c = 30 mm, d = 200 µm, e, f, l = 4 µm, g = 20 µm, h = 35 µm, i = 25 µm, j = 65 µm, k = 40 µm.

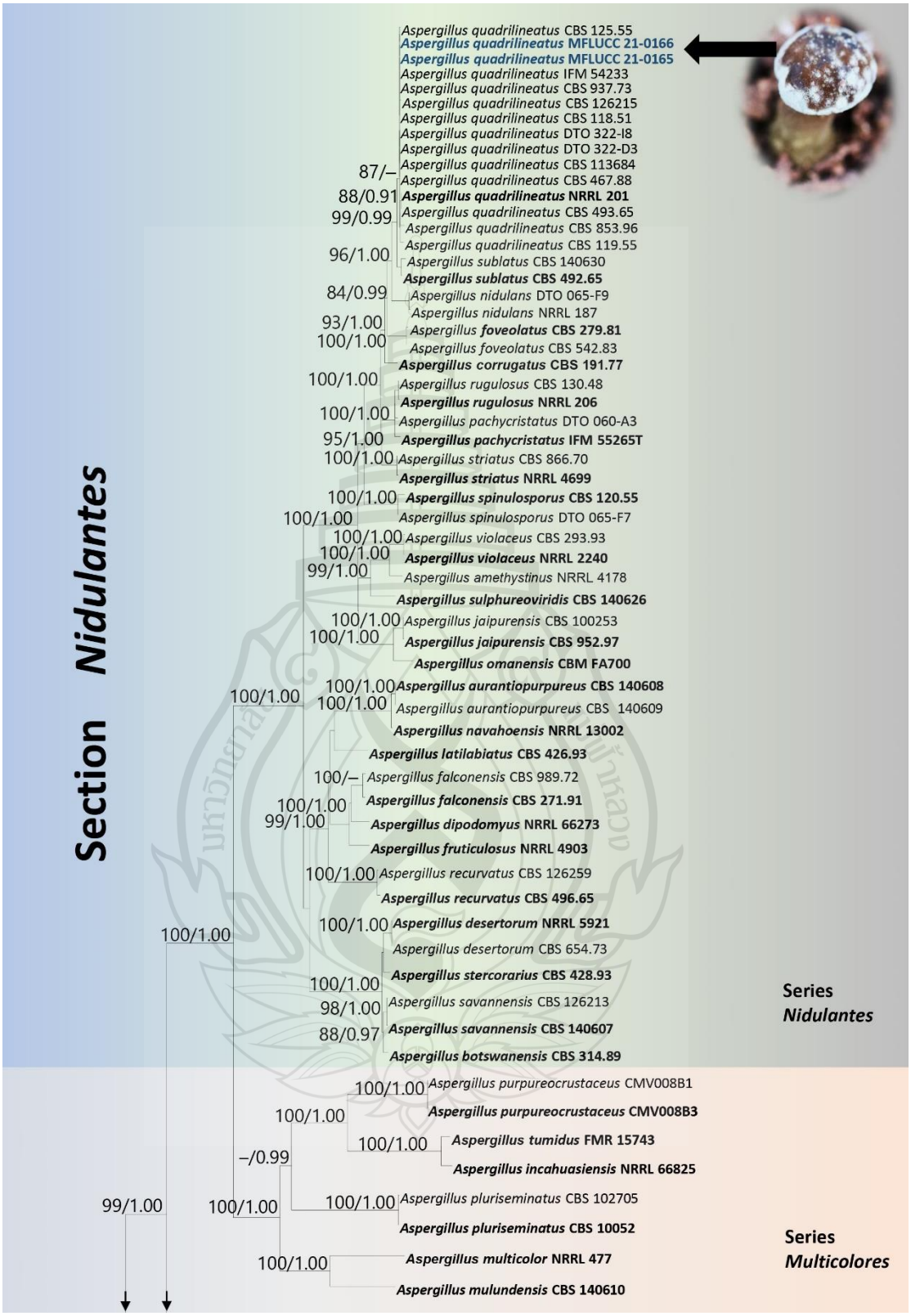


Figure 4.8 The best scoring RAxML tree based on the analysis of ITS, *tub*2, *cmdA* and *rpb*2 combined dataset for *Aspergillus* section *Nidulantes*

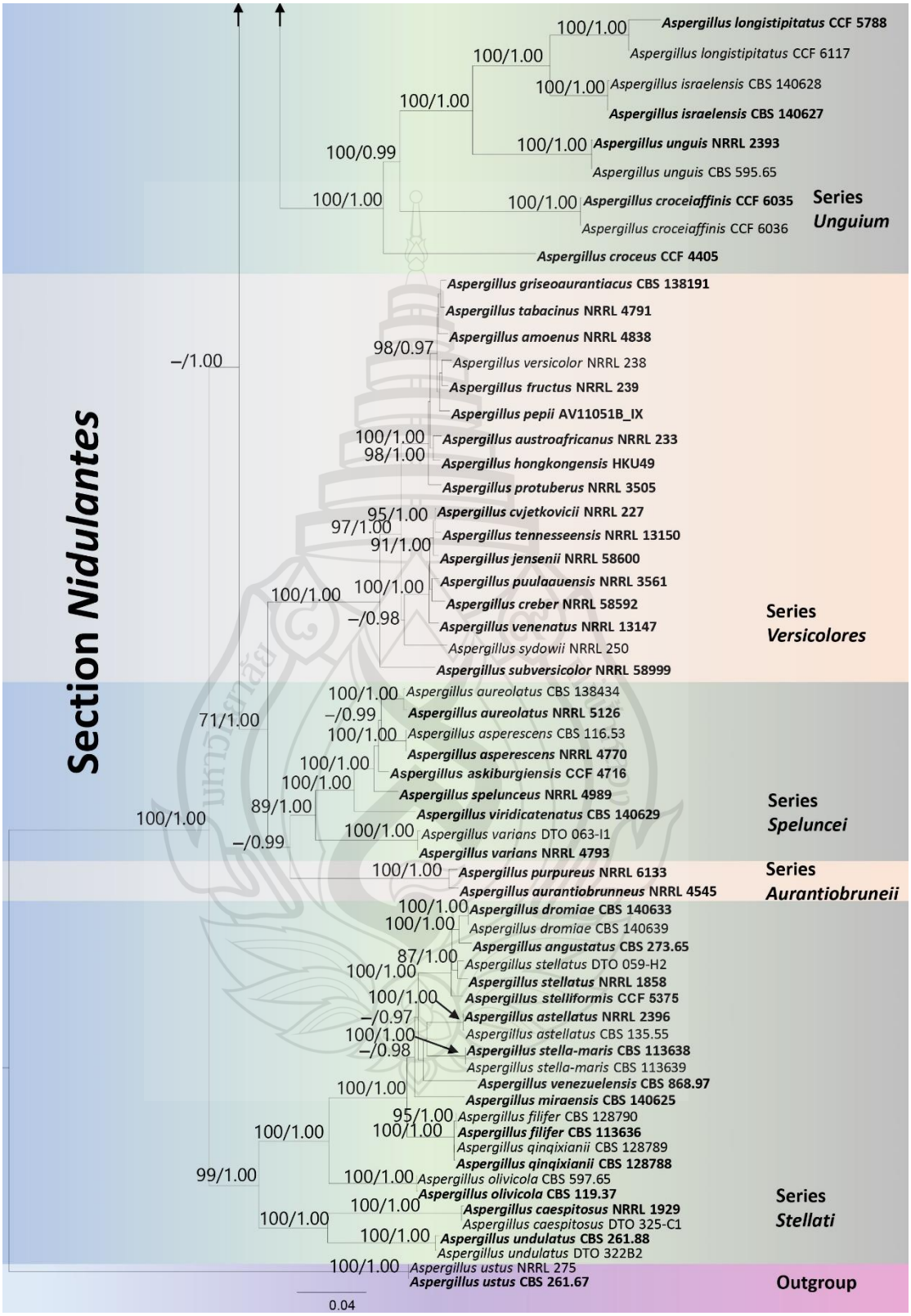


Figure 4.8 (continued)

Figure 4.8, The combined ITS, *tub*2, *cmdA* and *rpb*2 matrix comprised 122 strains including selected taxa in *Aspergillus* section *Nidulantes* and *Aspergillus ustus* (which belongs to *Aspergillus* section *Usti*) as the outgroup. The tree is rooted with *Aspergillus ustus* (NRRL 275 and CBS 261.67). The concatenated alignment resulted in similar topologies for both ML and BYPP. The value of the average standard deviation of the split frequencies of BYPP analysis was 0.009970. The best scoring RAxML tree is shown hhad a final ML optimization likelihood value of –28316.145006. The matrix had 1261 distinct alignment patterns, with 11.16% of undetermined characters or gaps. Bootstrap support values for ML values equal to or >70% and BYPP values equal to or >0.95 are shown as ML/BYPP near the nodes. The isolates used for the present study are shown in blue bold. The type-derived sequences are given in black bold. The scale bar represents the expected number of nucleotide substitutions per site.

Aspergillus quadrilineatus Thom & Raper, Mycologia 31: 660. (1939)

Figures 4.9, 4.10

Index Fungorum number: IF 275888

Facesoffungi Number: FoF 10610

Fungicolous on the fruiting body of *Phlebopus spongiosus* Pham and Har. Takah. Sexual morph: on PDA, *Ascomata* 190–310 × 160–300 μm ($\bar{x}$ = 227.6 × 221.6 μm, n = 5), cleistothecial, developing throughout the colony, reddish-brown, globose to subglobose, surrounded by numerous Hülle cells; *Hülle cells* 12.5–23 × 11.5–22 μm ($\bar{x}$ = 17.5 × 17.3 μm, n = 30), hyaline to brown, globose to ovoid. *Asci* 9–11 × 8–11 μm ($\bar{x}$ = 10.1 × 9.9 μm, n = 15), 8-spored, globose to subglobose. *Ascospores* 3–4 × 3–4 μm ($\bar{x}$ = 3.8 × 3.4 μm, n = 40), orange to reddish-brown, globose to subglobose in surface view, spore bodies smooth, lenticular in lateral view, with two plaited equatorial crests about 0.5-1 μm in width paralleled by a secondary narrower pair which are sometimes indistinct, crests are entire, defective or with irregular protuberance. Asexual morph: on host, *Mycelium* powdery mass, white to green; sporulation light green to dark green. PDA: *Conidiophores* 80–165 × 3–6 μm ($\bar{x}$ = 122.2 × 4.3 μm, n = 15) macronematous, mononematous, erect, simple, with septate to aseptate stipes, pale brown; *Vesicles* 9–12 μm ($\bar{x}$ = 10.6 μm, n = 15) wide, pale brown, globose to subglobose; *Metulae* 3–4.5 × 1–2 μm ($\bar{x}$ = 3.7 × 1.5 μm, n = 20)

hyaline; *Phialides* 4.5–6 × 1–2 μm ($\overline{x}$ = 5.7 × 1.4 μm, n = 20) hyaline, flask-shaped; *Conidia* 2.5–4 × 2–4 μm ($\overline{x}$ = 3.2 × 3.3 μm, n = 50) slightly echinulate, globose to subglobose, hyaline to light green.

Colony characters – on PDA, 25 °C, 14 days: Colonies moderately deep, marginally sulcate; margins slightly irregular; mycelium buff and white, later turns to reddish-brown; texture floccose; sporulation sparse; soluble pigments absent; exudates clear droplets; reverse dark brown.

Material examined – Thailand, Chiang Rai Province, isolated using the mycelium growing on the fruiting body of *Phlebopus spongiosus* cultivated in soil, 29 November 2019, Bhavesh Raghoonundon, AJ 044 (inactive dry culture MFLU 21-0261), living cultures MFLUCC 21-0165 and MFLUCC 21-0166.

GenBank numbers – MFLUCC 21-0165: ITS = OL615082; *tub2* = OL625674. MFLUCC 21-0166: ITS = OL615089; *tub2* = OL625675.

Notes – Our isolates (MFLUCC 21-0165 and MFLUCC 21-0166) clustered within *Aspergillus quadrilineatus* (Figure 4.8). *Aspergillus quadrilineatus* strains MFLUCC 21-0165 and MFLUCC 21-0166 reported in this study share similar sexual and asexual morphologies with those observed from the culture of the neotype of *A. quadrilineatus* (NRRL201) described by Chen et al. (2016). The ascomata, Hülle cells, ascospores, vesicles, metulae and phialides of MFLU 21-0261 are comparatively smaller than those of *A. quadrilineatus* described in Chen et al. (2016) as shown in Table 4.1. These dimensional differences occurred probably due to the variations of agar medium used to obtain the culture.

During this study, all four loci namely, ITS, *tub*2, *cmdA* and *rpb*2 were amplified and sequenced using methods and primers as previously described in Houbraken and Samson (2011) and Samson et al. (2014). However, only the ITS and *tub*2 sequence results were obtained successfully. There were no base pair differences of ITS and *tub*2 sequences between the neotype of *A. quadrilineatus* (NRRL 201) described by Chen et al. (2016) and *Aspergillus quadrilineatus* strains MFLUCC 21-0165 and MFLUCC 21-0166 reported in this study.

Herein, *A. quadrilineatus* is reported for the first time as a fungicolous fungus on cultivated *Phlebopus spongiosus* in northern Thailand. It has also been formerly documented to be associated with *Elaeis guineensis*, *Lens culinaris*, *Lupinus termis*,

Pisum sativum and human infections (Chadiesh et al., 2017; Seyedmousavi et al., 2018; Farr & Rossman 2021). *Aspergillus quadrilineatus* is a soil fungus commonly isolated in tropical countries (Polacheck et al., 1992). Therefore, most probably the primary inoculation of *A. quadrilineatus* spores may be from the soil used for cultivation or the surrounding air. This ultimately led to fungal contamination on the mushroom cultivation.

Aspergillus section *Nidulantes* are able to produce mycotoxins such as aflatoxins, asteltoxins, emestrin, fumitremorgins, paxillin, sterigmatocystin and other extrolites useful as drugs or drug lead candidates such as calbistrins, echinocandins, mulundocandins, terrain, variecolins and varitriols (Chen et al., 2016). Sterigmatocystin is a carcinogenic mycotoxin, while aflatoxin has become a major problem in the agricultural and food industries (Nieto et al., 2018). *Aspergillus quadrilineatus* has been reported to produce extrolites such as asperthecin, asperugins, echinocandins, emestrin, emericellin, emindols, quadrilineatin, shamixanthone, sterigmatocystin and violaceols. (Chen et al., 2016).

Phlebopus spongiosus is an edible fungus (Kumla et al., 2020). *Aspergillus quadrilineatus* growing on *P. spongiosus* as a fungicolous fungi is able to produce carcinogenic mycotoxins such as sterigmatocystin. Therefore, this may be a food safety issue and it is a challenge to overcome during the cultivation of *P. spongiosus* on soil. Furthermore, *Aspergillus quadrilineatus* would be able to cause both yield and quality losses in commercial cultivation of *P. spongiosus* on soil resulting economic losses for mushroom farmers. As we were able to isolate *A. quadrilineatus* from a live fruiting body, it can be potentially pathogenic on *P. spongiosus*; future studies are required with pathogenicity tests for confirmation. The screening of potential biocontrol agents to control *A. quadrilineatus* on *P. spongiosus* also would be important in commercial scale cultivation of *P. spongiosus* on soil.

Table 4.1 The comparison of the sizes of fungal structures

Fungal structure	**Chen et al. (2016)**	**This study**
Ascomata	100–700 µm	190–310 × 160–300 µm
Hülle cells	10–24 µm	12.5–23 × 11.5–22 µm
Ascospores	4–4.5 × 3–4.5 µm	3–4 × 3–4 µm
Vesicles	10–13 µm	9–12 µm
Metulae	5–7 × 2–4.5 µm	3–4.5 × 1–2 µm
Phialides	5–7 × 2–4 µm	4.5–6 × 1–2 µm

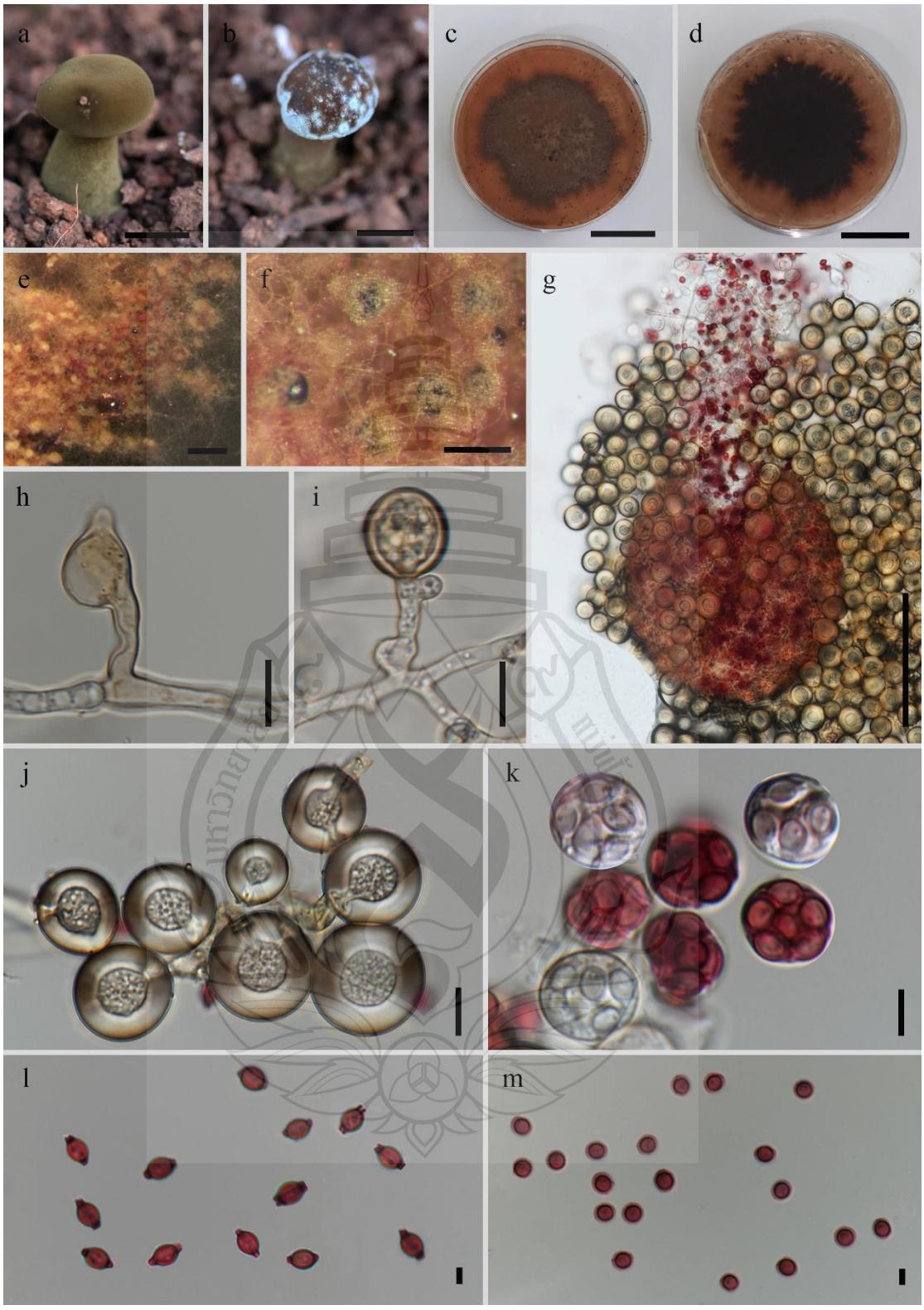


Figure 4.9 *Aspergillus quadrilineatus*: sexual morph (MFLU 21-0261)

Figure 4.9, a Healthy mushroom, *Phlebopus spongiosus* growing in soil. b The mushroom affected by *Aspergillus quadrilineatus*. c, d Colony on PDA. e, f Cleistothecial ascomata formation in the colony on PDA. g Cleistothecium covered with Hülle cells. h, i Formation of Hülle cells. j Hülle cells. k Immature and mature asci. l Side view of ascospores. m Surface view of ascospores. Scale bars: a, b = 2 cm, c, d = 30 mm, e = 300 μm, f = 500 μm, g = 100 μm, h–j = 10 μm, k = 5 μm, l, m = 3 μm.

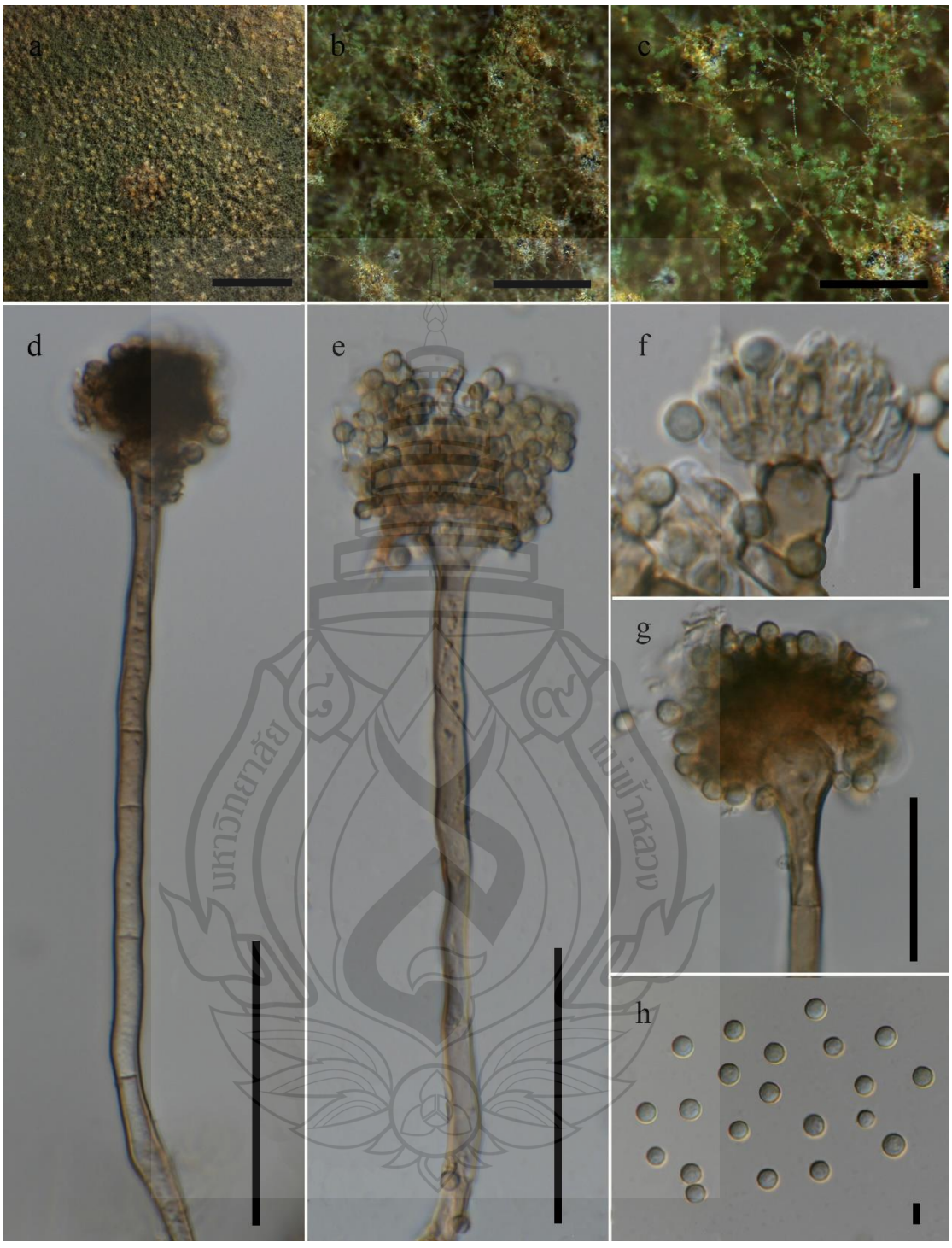


Figure 4.10 *Aspergillus quadrilineatus*: asexual morph (MFLU 21-0261)

Figure 4.10, a Colony of Aspergillus on PDA. b, c Sporulation on PDA. d, e Mononematous conidiophores with conidia. f, g Apex of conidiogenous cell. h Conidia. Scale bars: a = 5 mm, b = 1 mm, c = 500 μm, d, e = 50 μm, f = 10 μm, g = 25 μm, h = 3 μm.

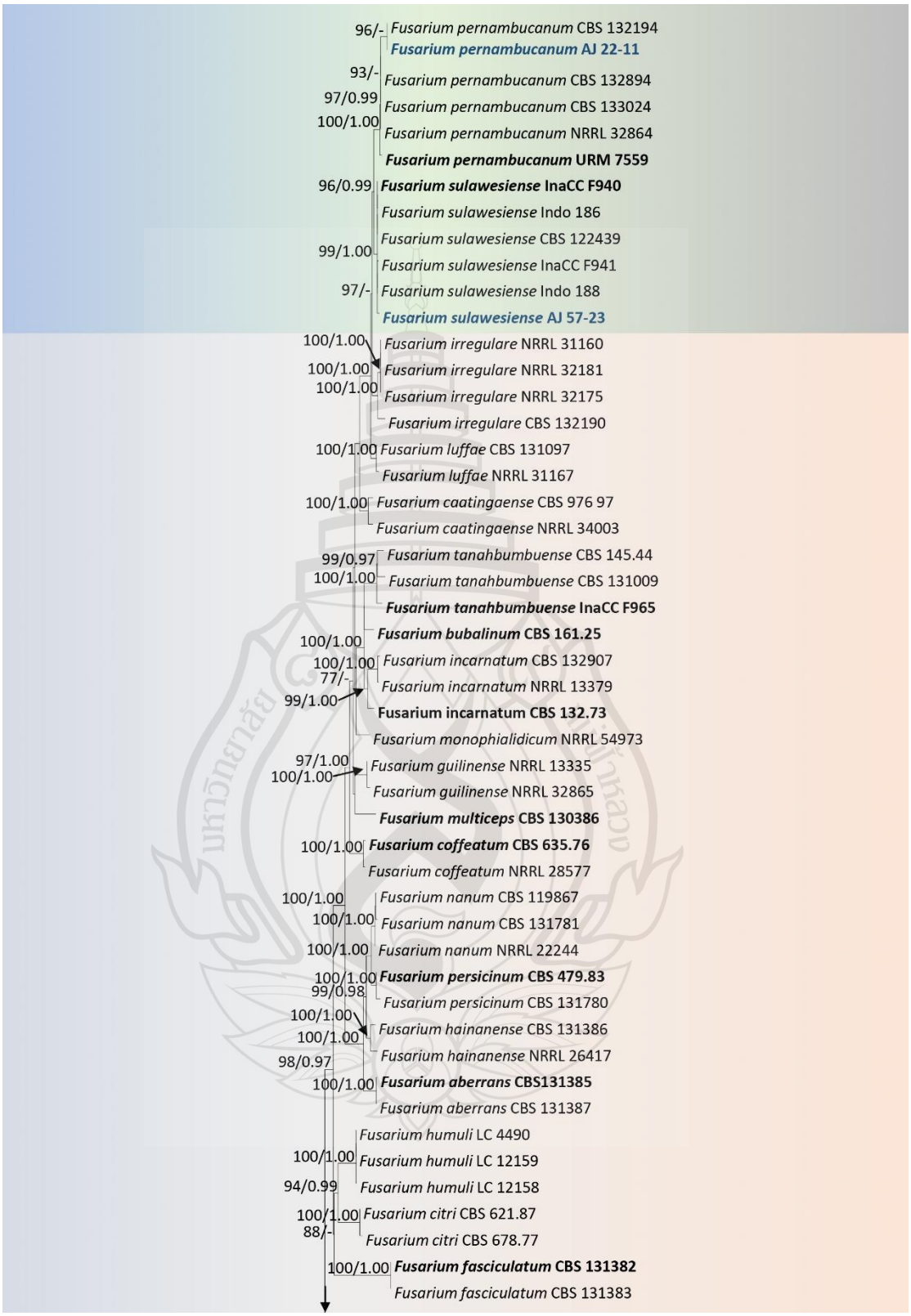


Figure 4.11 Phylogenetic tree generated by ML analysis of combined *tef-1α*, *cmdA* and *rpb2* sequence data of *Fusarium incarnatum-equiseti* species complex (FIESC)

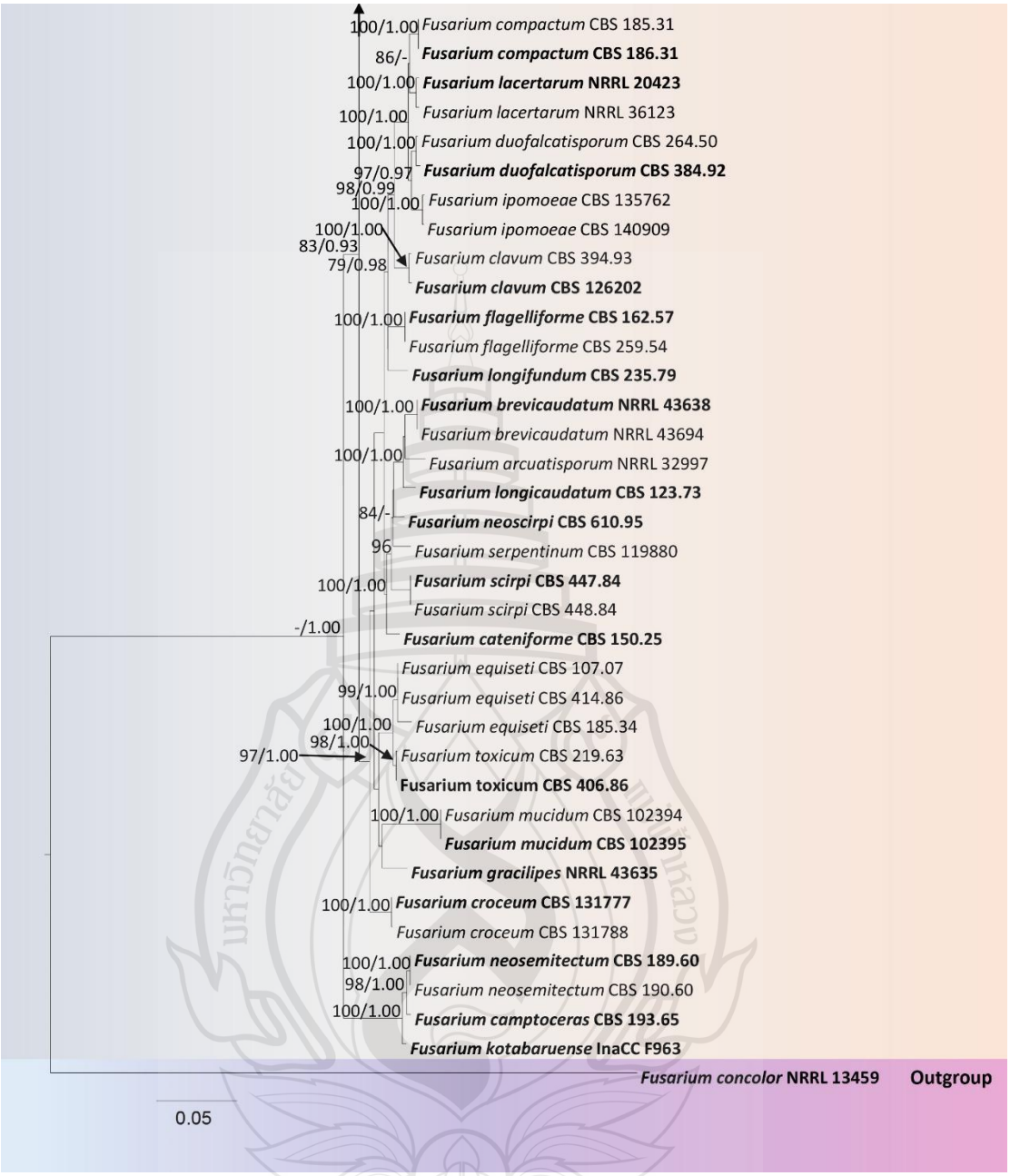


Figure 4.11 (continued)

Figure 4.11, A total of 86 strains were included in the analyses. The tree is rooted with *Fusarium concolor* (NRRL 13459). The best scoring ML tree with an optimal log-likelihood value of −11727.972 is presented. The matrix had 697 distinct alignment patterns, with 7.60% of undetermined characters or gaps. Bootstrap support values for ML ≥ 70% and BYPP ≥ 0.90 values for BI (BS/BYPP) are shown

respectively near the nodes. Type (holotype/ex-type/isotype/paratype) strains are in bold. The strains reported in this study are in blue bold.

Fusarium sulawesiense Maryani, Sand. -Den., L. Lombard, Kema & Crous [as 'sulawense'], Persoonia 43: 65 (2019)

Figure 4.12

Index Fungorum number: IF 830777

Fungicolous on a fruiting body of *Hericium coralloides*. Sexual morph: not observed. Asexual morph: red inky patches and white to grey mycelium on a fruiting body of *Hericium coralloids*. On CLA, hyphomycetous. *Mycelium* 2–3.5 μm ($\overline{x}$ = 2.5 μm, n = 30) wide, hyaline, septate, and branched. *Aerial conidiophores* 2–4 μm ($\overline{x}$ = 3 μm, n = 30) wide, hyaline, septate, and irregularly or verticillately branched. *Conidiogenous cells* 8–18 × 2–3.5 μm ($\overline{x}$ = 13 × 3 μm, n = 30), mono- or polyphialidic, subulate to subcylindrical, formed laterally or terminally, smooth- and thin-walled. *Conidia* of one type (macroconidia) 13–35.5 × 2.5–4 μm ($\overline{x}$ = 20 × 3 μm, n = 30), hyaline, falcate, 3–5 septate, apical cells papillate, basal cells indistinct or foot-shaped, formed on both mono- and polyphialides. *Conidia* of other type (microconidia) 6–13.5 × 2–3.5 μm (x = 10 × 2.5 μm, n = 30), obovoid to ellipsoidal, straight to slightly curved, hyaline and septate to aseptate. *Chlamydospores* 3.5–7 μm ($\overline{x}$ = 5 μm, n = 10) diameter, hyaline, globose to ellipsoidal, intercalary or terminal. *Sporodochia* not observed

Colony characters – on PDA at 25 °C, 50–55 mm in 7 days. The aerial mycelium sparse to abundant and cottony. Colony surface dry, cottony, saffron and reverse rosy buff becoming white towards the margins.

Material examined – Thailand, Chiang Rai: Mueang, Nang Lae, isolated from the mycelium growing on a fruiting body of *Hericium coralloids* at a cultivation trial, 27 November 2023, Didsanutda Gonkhom, AJ 57-23.

Notes – Our isolate AJ 57-23, clustered within *Fusarium sulawesiense* (CBS 122439, InaCC F940, InaCC F941, Indo 186, Indo 188) with 99% BS, and 1.00 BYPP (Figure 4.11). The morphological features of AJ 57-23 match the original description and illustrations of *F. sulawesiense* provided by Maryani et al. (2019a), except for slight differences in the dimensions of morphological structures. These variations are possible due to differences in the agar medium and cultural conditions

(Senanayake et al., 2020). Therefore, we confirmed that our isolate, AJ 57-23, is phylogenetically and morphologically consistent with *F. sulawesiense*.

Fusarium sulawesiense was identified from infected pseudo stems of *Musa acuminata* var. Pisang Cere in Indonesia (Maryani et al., 2019a). This species has since been recognized as a plant pathogen responsible for various plant diseases across multiple regions, including Brazil, China, Indonesia, Mexico, Pakistan, and Thailand (Kamran et al., 2020; Leyva-Mir et al., 2022; Lu et al., 2022; Pramunadipta et al., 2022; de Almeida Nogueira et al., 2023; Suwannarach et al., 2024). Documented pathogenicities of *F. sulawesiense* include, Fusarium head blight on wheat (Leyva-Mir et al., 2022), leaf blight on plum trees (Lu et al., 2022), sheath rot in rice (Pramunadipta et al., 2022), fruit rot in melons (de Almeida Nogueira et al., 2023), and stem rot in sesame (Kamran et al., 2020).

Beyond plant pathogenicity, this species has also been isolated from the insect *Aleurocanthus woglumi* in Brazil (da Silva Santos et al., 2024), and Diniz et al. (2022) has proved its pathogenic effects against *Nasutitermes corniger*. In Thailand, *F. sulawesiense* has been reported to cause postharvest fruit rot on muskmelons (Suwannarach et al., 2024), associated with diseased pineapple stalk (Abeywickrama et al., 2023), saprobic on *Asplenium nidus* leaves (Seifollahi et al., 2023), and as a saprobe on the panicles of *Oryza sativa* (Absalan et al., 2025). To the best of our knowledge, this study represents the first report of *F. sulawesiense* as a fungicolous species on cultivated *Hericium coralloides* in Thailand and worldwide.

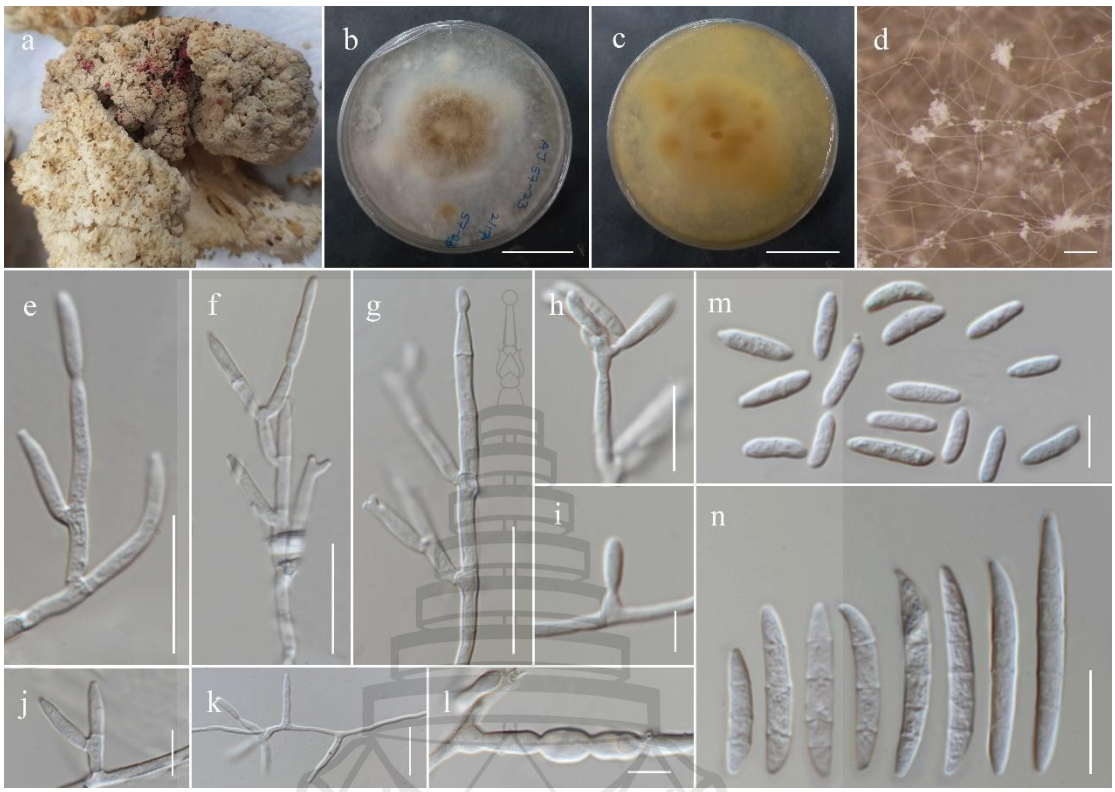


Figure 4.12 *Fusarium sulawesiense* (AJ 57-23)

Figure 4.12, a. Host (*Hericium coralloides*). b, c. Colony on PDA. d. Sporulation on CLA. e–k. Aerial conidiophores with conidiogenious cells and conidial attachments. l. Chlamydospores. m, n. Conidia. Scale bars: b, c = 30 mm, d = 250 µm, f, g = 25 µm, e, k = 20 µm, h, n = 15 µm, j, l, m = 10 µm, i = 5 µm.

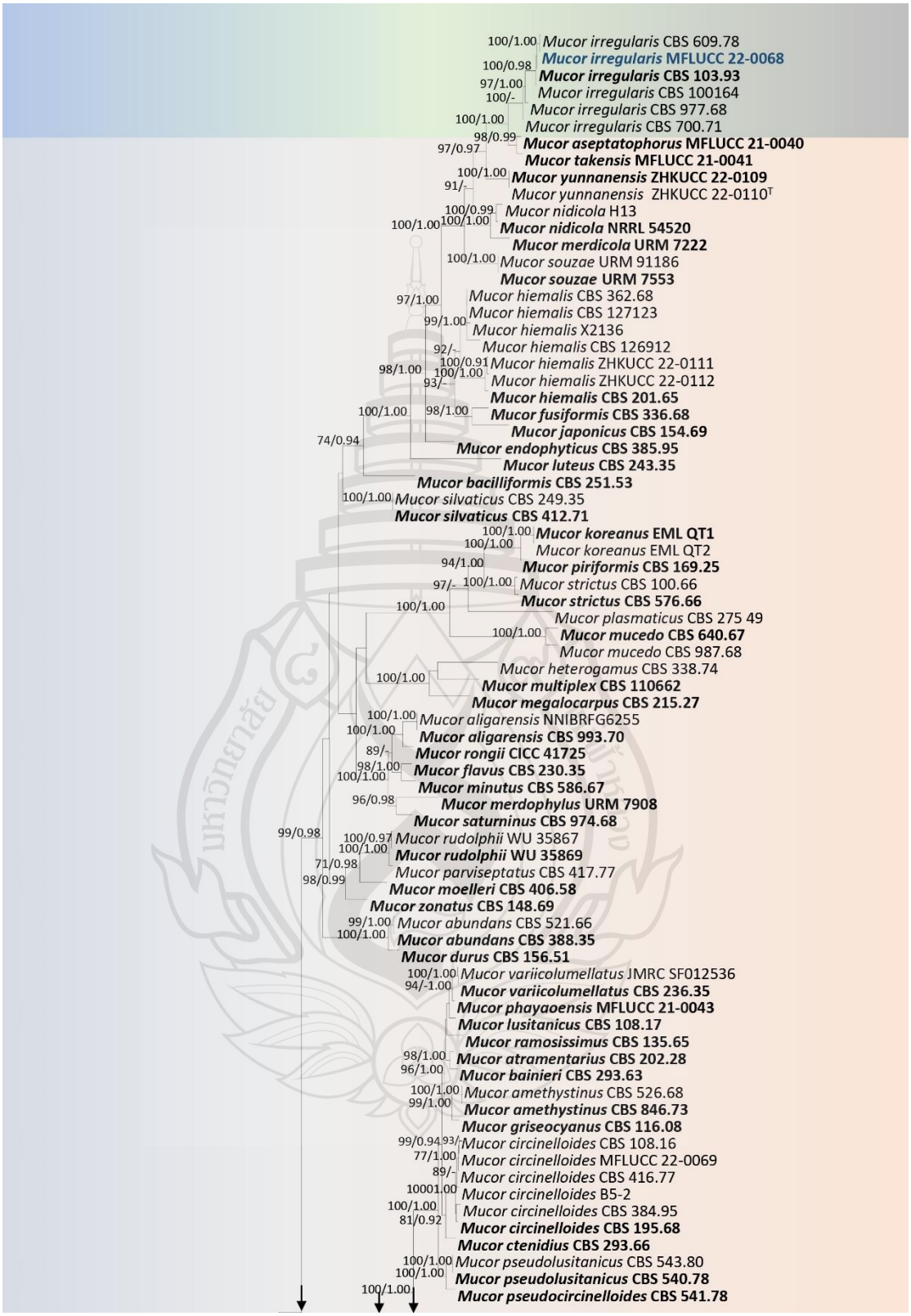


Figure 4.13 Phylogenetic tree generated from the maximum likelihood (ML) based on ITS-LSU sequence matrix of *Mucor* species

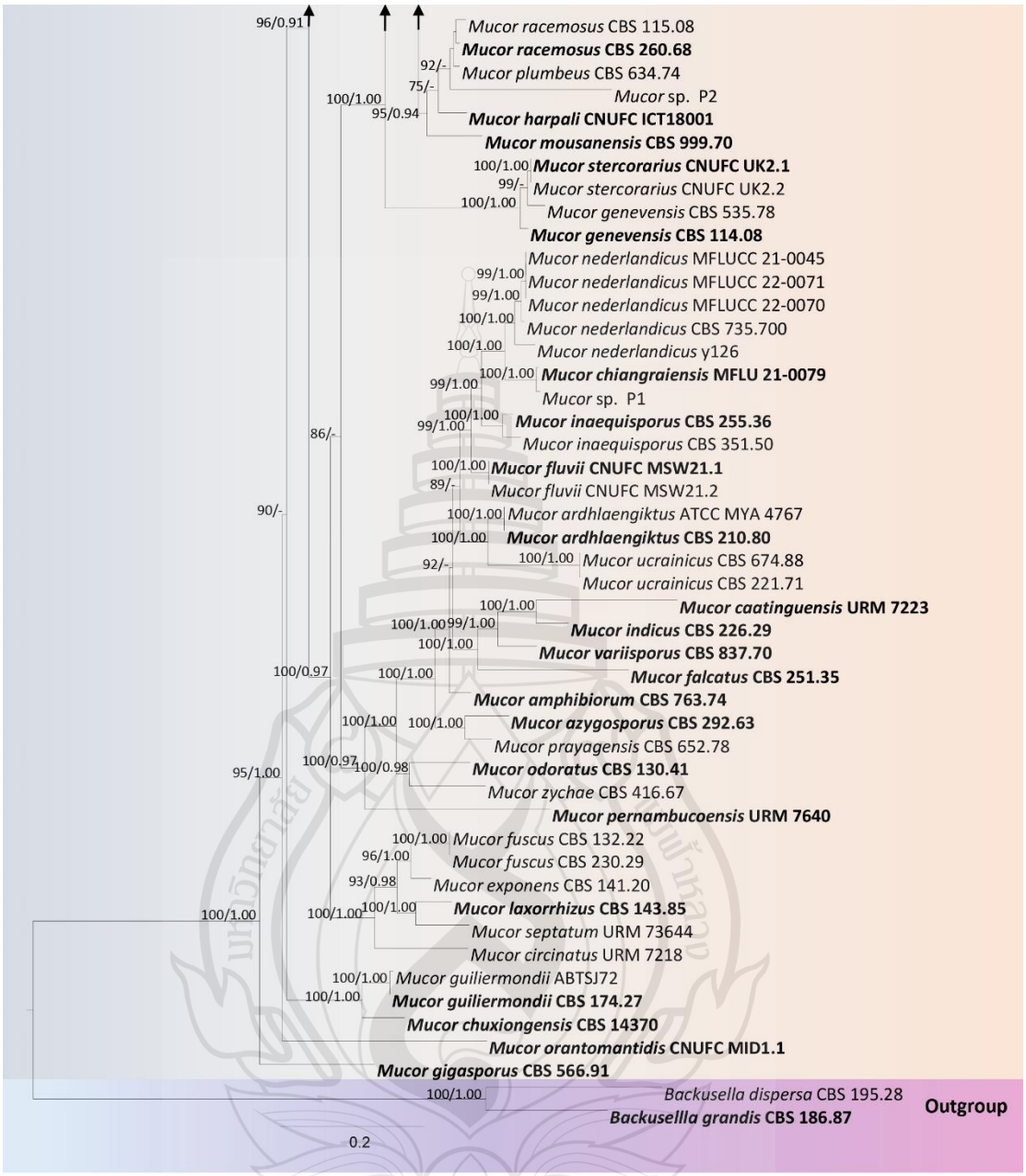


Figure 4.13 (continued)

Figure 4.13, The combined ITS and 28S matrix comprised 123 epithets that belong to *Mucor* and two outgroup taxa *Backusella dispersa* (Hagem) Urquhart & Douch (CBS 195.28) and *B. grandis* (Schipper & Samson) Walther & de Hoog (CBS 186.87). The tree is rooted with *Backusella dispersa* (CBS 195.28) and *B. grandis* (CBS 186.87). The concatenated alignments resulted in mostly similar topologies for both ML and BI analyses. The best scoring ML tree is shown in Fig. 1, with an optimal log-likelihood value of –20887.925. The matrix had 741 distinct alignment

patterns, with 9.47% of undetermined characters or gaps. The proportion of invariable sites was 0.380 ML bootstrap supports (≥70%) and BI posterior probabilities (≥0.90) are denoted near the respective nodes. The type strains are in black bold while the strain reported in this study is in blue bold.

Mucor irregularis Stchigel, Cano, Guarro & E. Álvarez, in Álvarez et al.,, Medical Mycol. 49(1): 71 (2011)

Figure 4.14

Index Fungorum number: IF 546922

Fungicolous on a fruiting body of *Pleurotus* sp. Sexual morph: not observed. Asexual morph: on PDA, *Sporangiophores* up to 4–10.5 μm ($\bar{x}$ = 7.5 μm, n = 20) width, hyaline, septate, erect, sympodially and monopodially branched. *Sporangia* 22–38 × 21–37 μm ($\bar{x}$ = 30 × 29 μm, n = 20), globose to sub-globose, grayish-brown, with diffluent wall. *Columellae* 13.5–30 × 12.5–29 μm ($\bar{x}$ = 22 × 21 μm, n = 20), globose or ellipsoidal to cylindrical, rarely conical, smooth-walled, have small or no clear collars. *Sporangiospores* 3–7 × 1.5–3 μm ($\bar{x}$ = 4.5 × 2 μm, n = 45), hyaline, smooth-walled, mostly ellipsoidal to ovoid, or globose, some irregularly shaped. Rhizoids not observed. *Chlamydospores* vary in shape and size.

Colony characters – on PDA, at 25 C, cultures are initially white and later turn yellowish with sporangia formation. The colony reached 84 mm in diam. after 4 days of incubation.

Specimen examined – Thailand, Chiang Rai, Muang, Ban Du (20°02′41″ N, 99°49′24″ E, elevation 418 m) isolated from the black patches in white mycelium grown on a fruiting body of *Pleurotus* sp., 28 October 2021, A.J. Gajanayake, AJ 010 inactive dry culture MFLU 22-0157, living culture MFLUCC 22-0068.

GenBank numbers – ITS = ON911811; LSU = ON911814.

Notes – Our strain MFLUCC 22-0068 is clustered within *M. irregularis* with 100% BS and 1.00 BYPP (Figure 4.13). The morphological characteristics of *Mucor irregularis* (MFLUCC 22-0068) described here are similar to the original description given by Zheng and Chen (1991), as *Rhizomucor variabilis* R.Y. Zheng & G.Q. Chen which has later been synonymized to *M. irregularis* in Alvarez et al. (2011). The sporangia, sporangiospores and columellae MFLUCC 22-0068 are smaller than *M. irregularis*, described by Zheng and Chen (1991) as sporangia; 21–37 μm *vs* (23.5–)

35–106 μm in diam., sporangiospores; 3–7 × 1.5–3 μm *vs* 2.5–11.5 (–16.5) × 2–7 μm and columellae; 13.5–30 × 12.5–29 μm *vs* 23.5**–** 71× 26–83 μm**.** In contrast to *M. irregularis* described in Zheng and Chen (1991), highly variable shapes of columellae and sporangiospores were not observed in MFLUCC 22-0068. These dimensional and shape differences may have been occurred due to the variations of agar medium and the conditions used to obtain the cultures**.** To the best of our knowledge, this is the first report of *M. irregularis* on a fruiting body of *Pleurotus* sp. as a fungicolous fungus**.**

Mucor irregularis was isolated from *Pleurotus* sp. purchased from a local market. Although *Pleurotus* is a cultivated mushroom, it is possible that in village-based simple grow-houses, which are often exposed to soil, the sporangiospores of *M. irregularis* originated from the surrounding soil environment. Since *M. irregularis* was isolated directly from a living fruiting body of *Pleurotus* sp., it may represent a potential pathogen of this host. However, pathogenicity needs to be confirmed through targeted infection and pathogenicity assays in future studies.



Figure 4.14 *Mucor irregularis* (MFLUCC 22-0068)

Figure 4.14, a. Host (*Pleurotus* sp.). b-c. Colony on PDA. d. Sporulation on PDA. e-h. Columella with and without collars. i-l. Sporangia. m. Granular content inside hyphae. n-o. Chlamydospores. p. Sporangiospores .Scale bars :d =200 μm, e-g, j-m =30 μm, h-i = 20 μm, n-o = 10 μm, p = 5 μm.

4.3 Fungal Diseases and Competitor Molds Affecting Global Mushroom Cultivation

In this section, four prevalent fungal diseases (dry bubble, wet bubble, cobweb, and green mold), along with slippery scar and yellow rot, are reviewed. The taxonomic classification of the major fungal pathogens on mushrooms is summarized at the family/genus levels, using phylogenetic trees reconstructed from previously published DNA sequences available in GenBank to illustrate their current phylogenetic placement. The morphological features of the pathogens are also illustrated. Additionally, nine competitor molds associated with mushroom cultivation are reviewed. Furthermore, for each disease and competitor mold, details on their causative agents, signs and symptoms, disease cycles, epidemiology, and management strategies are provided based on the available literature.

This work would enable an accurate understanding of fungal diseases/competitor molds, as well as the causative agents associated with mushrooms. Such insights could support the development and implementation of precise control strategies.

4.3.1 Fungal Diseases Affecting Global Mushroom Cultivation

1. Dry Bubble Disease

The initial documentation of dry bubble disease traces back to Constantin and Dufour (1892), who provided the first comprehensive report on various bubble diseases, collectively referred to as 'la môle' disease at the time (Berendsen et al., 2010). This disease poses a significant threat to the mushroom industry (Berendsen et al., 2010). It results in substantial losses in commercial cultivation. *Agaricus bisporus* is considered the main host affected by the disease (Berendsen et al., 2010). This

disease is estimated to result in an annual loss of revenue for mushroom growers ranging from 2% to 4% (Berendsen et al., 2010).

Pathogens − *Zarea fungicola* (syn. *Lecanicillium fungicola* var. *fungicola*), and *Zarea aleophila* (syn. *Lecanicillium fungicola* var. *aleophilum*)

Note − Khonsanit et al. (2024), based on multigene phylogenetic analyses, proposed new combinations *Zarea fungicola* (syn. *Lecanicillium fungicola* var. *fungicola*) and *Zarea aleophila* (syn. *Lecanicillium fungicola* var. *aleophilum*) for the pathogen previously known as *Lecanicillium fungicola*. However, since the existing literature predominantly references the pathogen under its former name, we will adhere to using *Lecanicillium fungicola* to maintain consistency with prior records.

Classification − *Ascomycota, Pezizomycotina, Sordariomycetes, Hypocreales, Hypocreomycetidae, Cordycipitaceae*

Pathogen morphology and biology − The asexual morphology of *Lecanicillium fungicola* can be identified by its characteristic, erect, and discernible conidiophores, which bear unequally sized conidia arranged in large, slimy globose heads. The conidiophores exhibit a verticillate arrangement, featuring two to five whorls composed of three to seven phialides each (Zare & Gams, 2008) (Figure 4.15).

Infection by *Lecanicillium fungicola* likely occurs in the casing layer, as evidence suggests that *L. fungicola* cannot infect the vegetative mycelium of *Agaricus bisporus* in the compost (Cross & Jacobs, 1968; Bernardo et al., 2004; Calonje et al., 2000). However, in the casing layer, *L. fungicola* spores do not germinate immediately. Instead, they appear to remain dormant until *Agaricus* colonizes the casing. They only germinate when conditions become favourable for the growth of the pathogen (Berendsen et al., 2010). Infection commences with the attachment of *L. fungicola* to the hyphae. This attachment to the hyphae of *A. bisporus* may be initiated through specific and nonspecific interactions between surface molecules of both fungi (Dragt et al., 1996; Calonje et al., 1997, 2000; Shamshad et al., 2009; Berendsen et al., 2010). Following the initial attachment, *L. fungicola* can grow both inter- and intracellularly on the hyphae of *A. bisporus* fruiting body. Invasion of *A. bisporus* occurs through a combination of mechanisms. It includes weakening of the cell wall via the production of lytic enzymes and mechanical pressure exerted by the formation of appressoria and peg penetration structures (Dragt et al., 1996; Calonje et al., 1997).

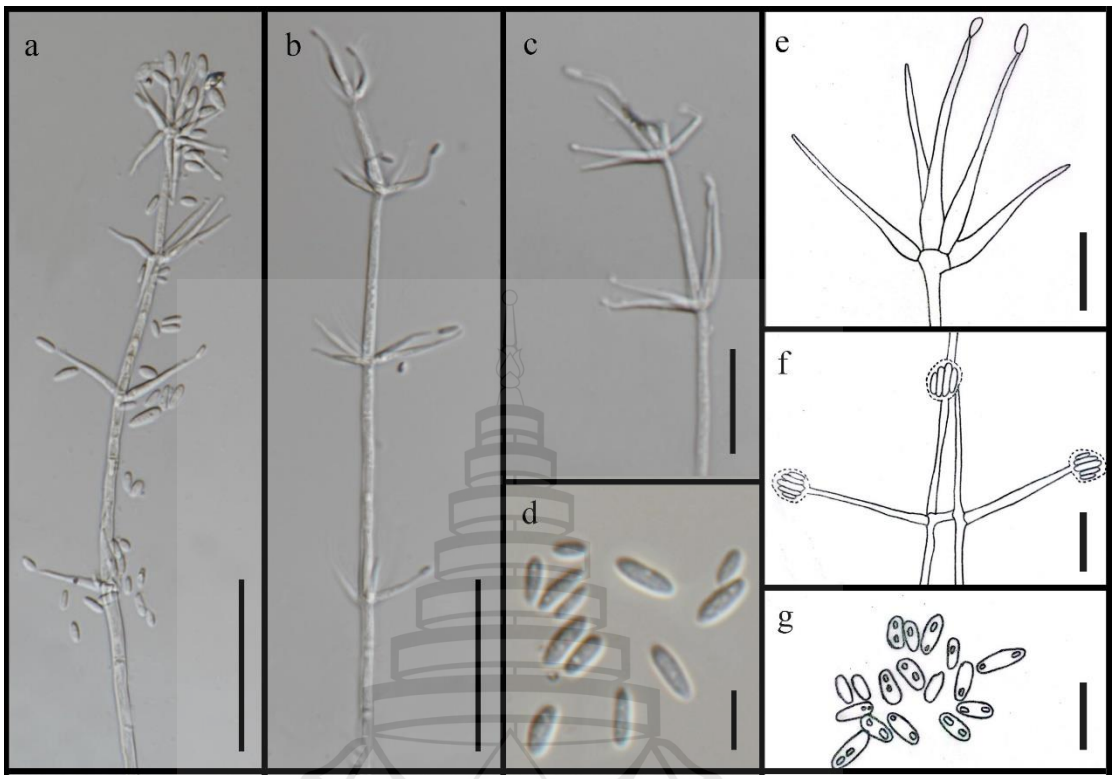


Figure 4.15 *Zarea* sp. (a-d) and *Zarea fungicola* (e-g)

Figure 4.15, *Zarea* sp. (a-d). a-c. Conidiophores and phialides. d. Conidia. Scale bars: a, b. = 50 μm, c, d = 10 μm. *Zarea fungicola* (e-g). e, f. Conidiophores and phialides. g. Conidia. Scale bars: e–g. = 10 μm. (Redrawn from Khonsanit et al., 2024).

Hosts − *Agaricus bitorquis*, *Agaricus bisporus*, *Pleurotus ostreatus*, *Coltricha perennis*, *Marasmiellus ramealis*, *Thelephora terrestris*, *Henningsomyces candidus*, *Hypholoma capnoides*, and *Laccaria laccata* (Marlowe, 1982; Gea et al., 2003; Berendsen et al., 2010)

Distribution − China, Europe, and North America (Berendsen et al., 2010)

Signs and symptoms − The symptoms of mushroom diseases encompass a spectrum ranging from small necrotic lesions on the caps of the fruiting bodies (cap spotting) to partially deformed structures, termed stipe blow-out, or completely malformed and undifferentiated masses of mushroom tissue, known as dry bubble (Sharma et al., 2007; Berendsen et al., 2010). The manifestation and severity of these symptoms depend on the timing of the infection. Late infections typically yield small necrotic lesions on the fruiting bodies, whereas interactions between the pathogen and

the host within the casing layer led to stipe blow-out and dry bubble (Berendsen et al., 2010). The occurrence of dry bubbles and stipe blow-out indicates the interference of *L. fungicola* in the differentiation of host tissues (Largeteau et al., 2007, 2010). The brown, light brown, or grey discolorations on the cap or stipe that appear after the infection are attributed to the formation of melanin in the infected mushroom tissue (Berendsen et al., 2010).

Disease cycle and epidemiology − The viability of *Lecanicillium* spores in soil can persist for over a year (Cross & Jacobs, 1968). Under dry conditions, *L. fungicola* spores can persist for 7–8 months on a mushroom farm (Fekete, 1967). Consequently, the presence of *L. fungicola* on a farm establishes a reservoir of inoculum on-site, facilitated by inadequate hygiene practices or the dispersion of wind-blown dust and soil. This reservoir poses a continual risk of infection for subsequent crops (Berendsen et al., 2010). The presence of *L. fungicola* in compost delivered to farms is improbable due to the spores' susceptibility to temperatures above 40 °C, rendering them nonviable during the composting process, which typically reaches temperatures of 70–80 °C (Van Griensven, 1988). Consequently, it was hypothesized early on that the casing material, rather than the compost, was more likely the source of infection (Ware, 1933). Infected mushrooms, whether occurring naturally in the wild or cultivated on nearby mushroom farms, could represent a significant source of primary inoculation (Gams et al., 2004; Zare & Gams 2008). Contaminated equipment also presents a potential source of infection (Berendsen et al., 2010).

Ware (1933) noted an association between the occurrence of dry bubble disease and the presence of insects. Fly populations originating from an infected farm could effectively serve as vectors for transmitting dry bubble disease (Berendsen et al., 2010). It has been observed that the spores can disperse through splashing water (Cross & Jacobs, 1968). The dispersal of spores by farm employees and equipment also plays a significant role in disease outbreaks (Fekete, 1967; Wong & Preece, 1987). According to White (1981), there is a correlation between the initial percentage of dry bubble disease in the first break of mushrooms and the initial population density of flies carrying *L. fungicola* spores. However, the rapid spread of the disease in subsequent breaks was primarily attributed to watering.

Disease management − Management of *Lecanicillium fungicola* primarily hinges on rigorous hygiene practices and the judicious application of fungicides. However, controlling dry bubble disease poses a challenge due to the host's sensitivity to fungicides (Berendsen et al., 2010). Consequently, only a limited selection of chemicals can be effectively utilized for its management (Berendsen et al., 2010). The management of dry bubble disease heavily relies on the application of Prochloraz-manganese, commonly known as Sporgon (Gea et al., 2005; Grogan 2008). However, reports indicate a reduced sensitivity to this fungicide (Gea et al., 2005; Grogan 2008). On behalf of the application of chemical control methods it has been discovered that biological methods such as usage of plant extracts (Ex: *Azadirachta indica*, Cinnamon, Clove, Thyme), spent mushroom substrate teas and biocontrol agents (Ex: *Bacillus amyloliquefaciens*) are potential and efficient alternatives in the control of dry bubble disease (Gea et al., 2014; Singh et al., 2016; Santos et al., 2017). Romaine et al. (2002) has developed a PCR-based diagnostic test for *Verticillium fungicola* var. *aleophilum*. Hayes et al. (2024) proposed a hypothesis suggesting that the production of cis-α-bisabolene by *A. bisporus* serves as a defensive response to infection by *L. fungicola*. This phenomenon warrants further investigation, with the potential to develop protective treatments against dry bubble disease (Hayes et al., 2024).

The taxonomic classification of the pathogens is presented at the family level, utilizing an updated phylogenetic tree based on available DNA sequence analyses (Figure 4.16).



Figure 4.16 Phylogenetic tree generated by ML analysis of combined LSU, *tef*-1α, *rpb*1, and *rpb*2 sequence data of *Lecanicillium*, *Zarea*, and related genera in the *Cordycipitaceae*

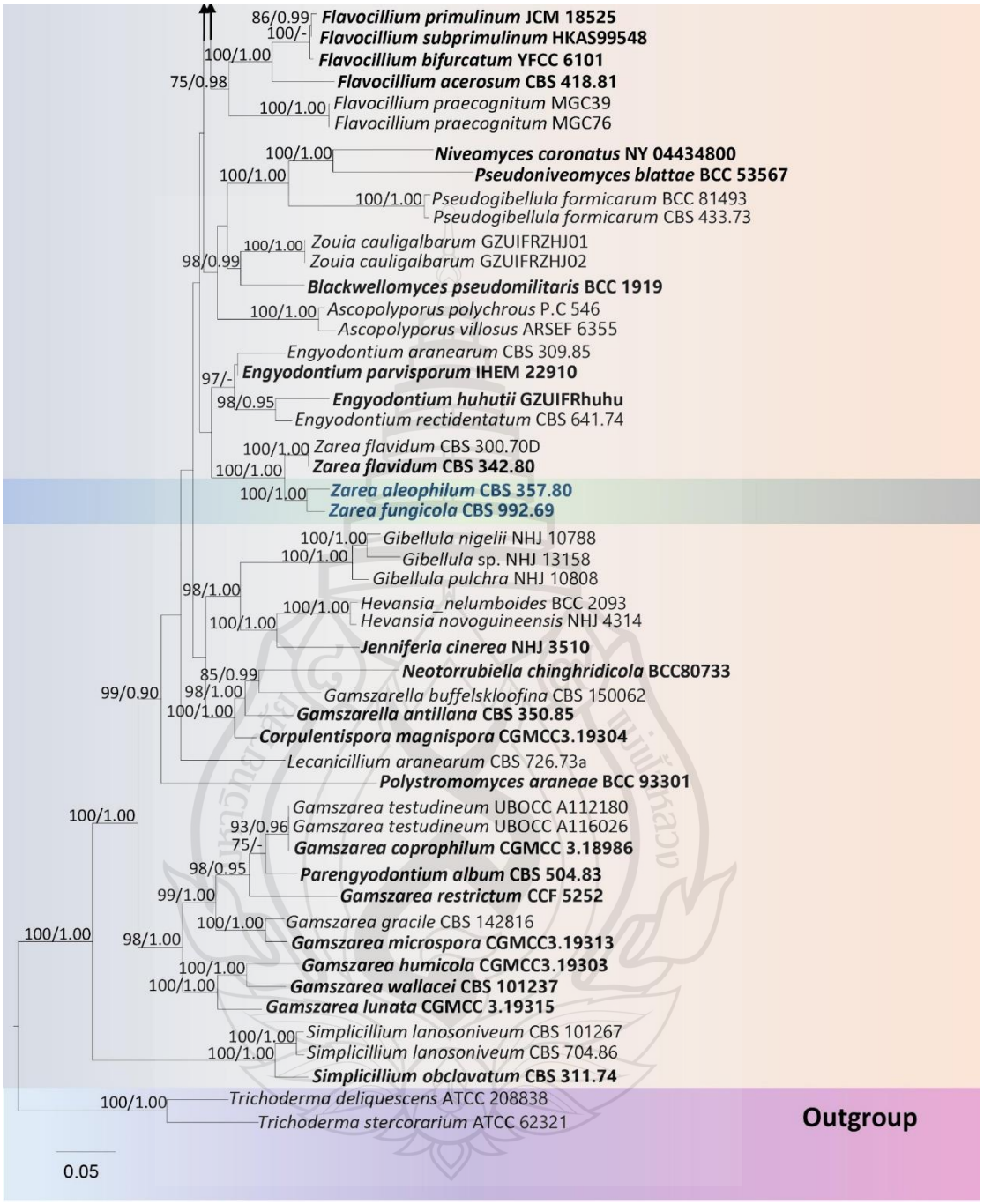


Figure 4.16 (continued)

Figure 4.16, Related sequences were obtained from previous publications and the GenBank database. A total of 111 strains were included in the analyses. The tree is rooted with *Trichoderma deliquescens* (ATCC 208838) and *T. stercorarium* (ATCC 62321). The tree topology of the ML analysis was similar to the Bayesian

analyses. The best-scoring ML tree with an optimal log-likelihood value of −46868.388 is presented. The matrix contained 1,827 distinct alignment patterns, with 24.21% of the characters being undetermined or gaps. Bootstrap support values for ML ≥ 70% and PP ≥ 0.90 (ML/ PP) are shown, respectively, near the nodes. Type (holotype/ex-type/isotype/paratype) strains are in bold, and the dry bubble causing pathogenic species are in blue text.

2. Wet Bubble Disease

Wet bubble disease is increasingly emerging as a significant challenge in mushroom cultivation worldwide (Kouser & Shah, 2013; Navarro et al., 2023). Infected mushrooms undergo complete deformation, rendering them unmarketable (Kumar et al., 2020). It has been documented to result in yield decreases ranging from 15 to 30% in button mushroom cultivation (Wang et al., 2016a; Zhou et al., 2016; Li et al., 2019a; Shi et al., 2020). Traditionally, *Hypomyces perniciosus* (previously classified as *Mycogone perniciosa*) has been attributed as the primary cause of wet bubble disease. However, recent investigations have revealed the potential involvement of other pathogens, including *Mycogone rosea* and *M. xinjiangensis,* which can infect mushrooms and induce disease symptoms (Du et al., 2021; Shi et al., 2023).

Pathogens − *Hypomyces perniciosus* (syn. *Mycogone perniciosa*), *M. rosea* and *M. xinjiangensis.*

Classification − *Ascomycota, Pezizomycotina, Sordariomycetes, Hypocreales, Hypocreomycetidae, Hypocreaceae*

Pathogen morphology and biology − *Mycogone perniciosa* is characterized by the production of small, thin-walled phialoconidia on verticillate to sub-verticillate, branched, hyaline, slender conidiophores. Additionally, it produces large bi-cellular aleuriospores, comprising a dark, spherical, thick-walled, verrucose apical cell and a thin-walled basal cell (Holland & Cooke, 1990; Kouser & Shah, 2013; Shaheen et al., 2015). The mycelium of *M. perniciosa* is white, compact, and felt-like. The hyphae are hyaline, septate, branched, and interwoven (Shaheen et al., 2015) (Figure 4.17).

Mycogone perniciosa is not limited to a specific host. However, among cultivated mushrooms, *Agaricus bisporus* appears to be its primary host globally (Shaheen et al., 2015). The pathogen has been observed to target button mushrooms at

all stages of growth, with immature mushrooms exhibiting greater susceptibility than mature ones (Kouser & Shah, 2013). Zhang et al. (2017a), conclude that *Hypomyces perniciosus* does not have pathogenic activity during the mycelial stage of *A. bisporus*. Zhang et al. (2024) concluded, by analyzing physiological and transcriptomic data together, that *H. perniciosus* primarily causes malformations in *A. bisporus* fruiting bodies by affecting the levels of certain phytohormones, rather than using toxins. According to Sharma et al. (2017), the thermal lethality threshold for *Mycogone* spp. Has been observed at temperatures ranging from 44 °C to 45 °C. Casing soil with moisture levels below 60% during pasteurization is conducive to the survival of *M. perniciosa*. Conversely, *Mycogone* sp. failed to persist in casing soil with a moisture content of 60% or higher when subjected to temperatures of 60 °C or higher (Sharma et al., 2017).

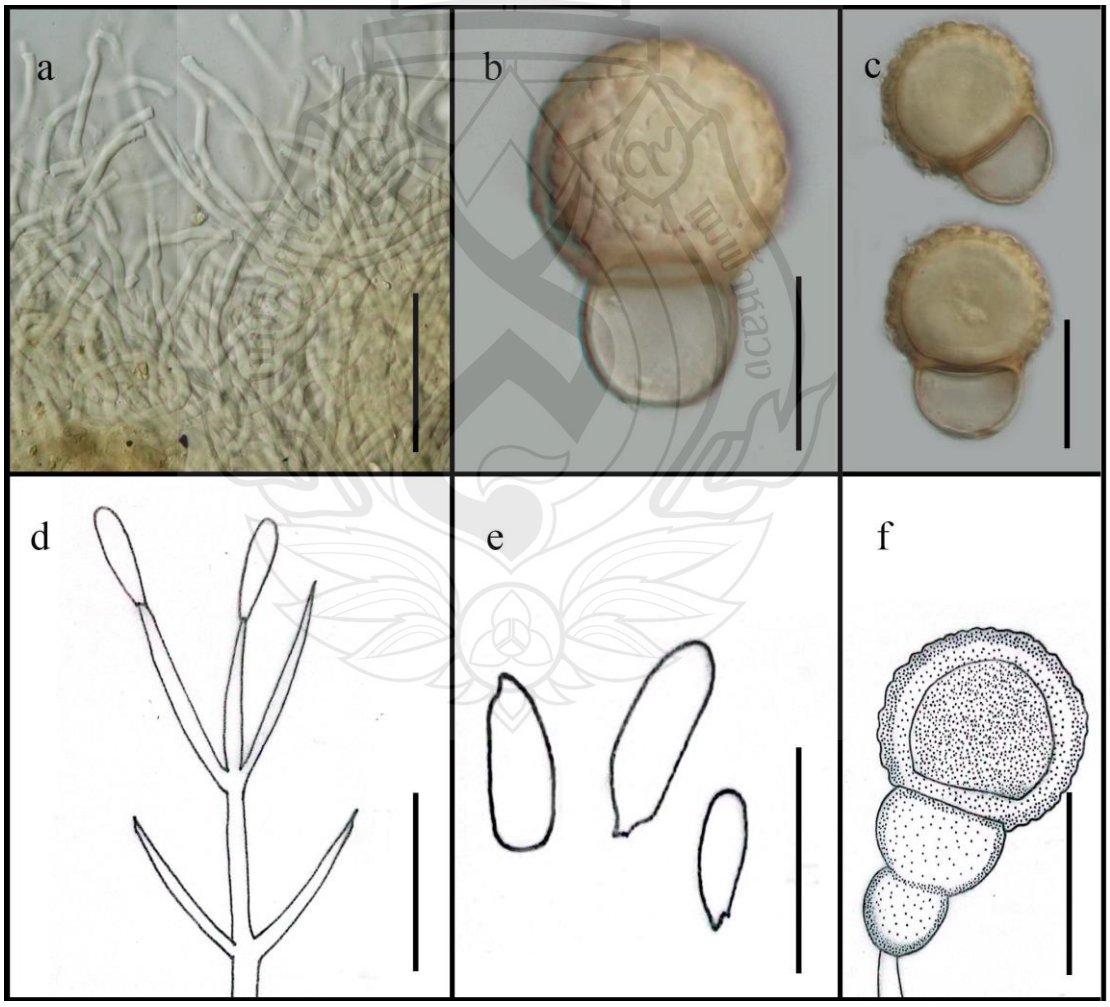


Figure 4.17 *Mycogone rosea* (a-c) and *Hypomyces perniciosus* (d-f)

Figure 4.17, *Mycogone rosea* (a-c). a. Hyphae. b, c. Aleurioconidia. Scale bars: a. = 50 μm, b, c. = 20 μm (Photo credits: R.H. Perera). *Hypomyces perniciosus* (d-f). d. Conidiophores. e. Conidia. f. Chlamydospore. Scale bars: d–f. = 20 μm. (Adapted and redrawn from Du et al. (2021)).

Hosts − *Agaricus bisporus, A. campestris, Pleurotus citrinopileatus, P. eryngii, P. nebrodensis, P. ostreatus,* and *Volvariella volvacea* (Figueiredo & Mucci, 1985; Zhang et al., 2017b)

Distribution − Worldwide (Shaheen et al., 2015; Kumar et al., 2021)

Signs and symptoms − The pathogen/s disrupts the morphogenesis of mushroom fruiting bodies, resulting in the emergence of clusters of deformed tissue lacking discernible differentiation (sclerodermoid mushrooms) (Fletcher et al., 1995; Kouser & Shah, 2013). This phenomenon occurs when the initial stage of sporophores undergoes infection before the differentiation of mushroom tissue into stipe and cap structures (Fletcher et al., 1995; Kouser & Shah, 2013). At the outset, the wet bubbles exhibit a white, porous texture before transitioning to a brown hue, exuding foul-smelling amber-coloured droplets atop their surface (Kouser & Shah, 2013). Examination of cross-sections of distorted sporophores reveals the presence of black circular regions situated just beneath the outer layer (Fletcher et al., 1995).

Disease cycle and epidemiology − Traditionally, casing contamination has been regarded as the primary inoculum of *M. perniciosa* (Fletcher & Ganney, 1968; Shaheen et al., 2015). Therefore, it is crucial to meticulously maintain the cleanliness of casing materials, storing them in environments shielded from potential contamination by debris, dust originating from cropping houses, drainage water, or soil from proximate regions (Sharma et al., 2007; Fletcher & Gaze, 2008). The dispersal of *M. perniciosa* can occur through water splashes and air currents onto adjacent mushrooms; however, it's noteworthy that its spores are generally non-adhesive, diminishing the significance of flies and pickers as potential vectors (Gea et al., 2010; Shaheen et al., 2015).

Disease management − The effective prevention of wet bubble disease can be achieved through the implementation of proper hygiene and sanitation practices, coupled with the judicious application of fungicides (Sharma et al., 2007; Gea et al., 2021). Importantly, these measures can be employed without adversely impacting the

growth of mushrooms (Gea et al., 2021). Shi et al. (2023) have designed three sets of species-specific primers for the detection and identification of *M. perniciosa*, *M. rosea*, and *M. xinjiangensis* utilizing differences in *tef-1α* gene sequences. This holds significant potential for practical applications, particularly in the early detection of *Mycogone* species in soil and the effective management of wet bubble disease (Shi et al., 2023). The oils extracted from lemon verbena and thyme have been identified as having potential applications as fungicides against *M. perniciosa*, without adversely affecting the growth of the button mushroom (Regnier & Combrinck, 2010). Al-Balushi et al. (2022) suggested that the essential oil from *Zataria multiflora* (thyme), holds potential as a viable option for combating wet bubble disease. *In vitro* trials have demonstrated that Prochloraz-manganese and Carbendazim exhibit the highest efficacy compared to Iprodione in suppressing the mycelial growth of *M. perniciosa* (Potocnik et al., 2008; Gea et al., 2010). During field trials, Prochloraz-manganese and Thiabendazole have demonstrated consistent efficacy in managing wet bubble disease while exerting minimal impact on mushroom growth (Shi et al., 2020). It has also been revealed that Fludioxonil, Diniconazole, Fenbuconazole, and Imazalil possess the potential to serve as alternatives for controlling wet bubble disease (Shi et al., 2020). Sharma et al. (2017) has observed that bacterial isolates of *Bacillus* sp. and *Alcaligenes* sp., have significant potential as biocontrol agents for effective management of wet bubble disease in both *in vivo* and *in vitro* conditions. Novikova and Titova (2023) revealed that utilizing *Bacillus subtilis* strains is an effective strategy for controlling the development of *M. perniciosa*.

The taxonomic classification of the pathogens is presented in an updated phylogenetic tree based on available DNA sequence analyses in Figure 4.21.

3. Cobweb Disease

During the 1990s, cobweb disease emerged as a significant challenge in mushroom cultivation within the UK and Ireland, resulting in considerable crop production losses of up to 40% (Adie et al., 2006). The disease manifested through severe spotting symptoms and premature crop terminations, reaching its peak during the epidemic (Adie et al., 2006). Cobweb disease ranks among the most serious fungal diseases affecting commercially cultivated mushrooms (Carrasco et al., 2016). This results in both qualitative and quantitative losses in commercial mushroom crops,

compromising mushroom quality and leading to a substantial decrease in profitability within the crop cycle (Carrasco et al., 2016). This disease appears to persist as an ongoing issue across numerous countries worldwide, such as Australia, Belgium, China, Canada, France, India, Ireland, Japan, Korea, New Zealand, Poland, Serbia, South Africa, Spain, Turkey, and the USA (Carrasco et al., 2017a).

Pathogens − *Cladobotryum asterophorum, C. cubitense, C. dendroides* (sexual morph: *Hypomyces rosellus*), *C. multiseptatum, C. mycophilum* (sexual morph: *Hypomyces odoratus*), *C. varium* (sexual morph: *Hypomyces aurantius*), *C. verticillatum, Hypomyces cornea, H. mycophilus, H. protrusus*, and *H. semicircularis*.

Classification − *Ascomycota, Pezizomycotina, Sordariomycetes, Hypocreales, Hypocreomycetidae, Hypocreaceae*

Pathogen morphology and biology − *Hypomyces/Cladobotryum* spp. are generally characterized by hyaline, septate, conidiophores that branch either in a verticillate or irregular manner, and produce three to four conidiogenous cells. The conidia produced are hyaline, globose to subglobose, and elongated, with pointed bases, exhibiting 1-3 septa, and a slight constriction is observed at the septa (Sharma et al., 2007; Tamm & Põldmaa, 2013). These fungi are capable of generating dark, thin-walled microsclerotia (Carrasco et al., 2016). Additionally, multicellular, globose structures known as chlamydospores have been documented in association with these microsclerotia (Carrasco et al., 2016). Both microsclerotia and chlamydospores typically represent survival structures of the fungus during adverse environmental conditions, as part of its life cycle (Rogerson & Samuels, 1993) (Figure 4.18–4.19).

Hypomyces/*Cladobotryum* species are commonly known for their fungicolous lifestyle, and they can also persist in soil (Gajanayake et al., 2025b; Jayawardena et al., 2025). Sharma et al. (2015) conducted assays of extracellular enzymes from ten isolates of *Cladobotryum*, associated with cobweb disease in various edible mushrooms. They observed that elevated levels of chitinase and pectinase enzymes were associated with increased yield losses in mushroom crops (Sharma et al., 2015). Among the identified pathogens, *Hypomyces rosellus*, *H. odoratus*, and *C. multiseptatum* are attributed as species capable of producing aurofusarin (Potočnik et al., 2008; Tamm & Põldmaa, 2013).

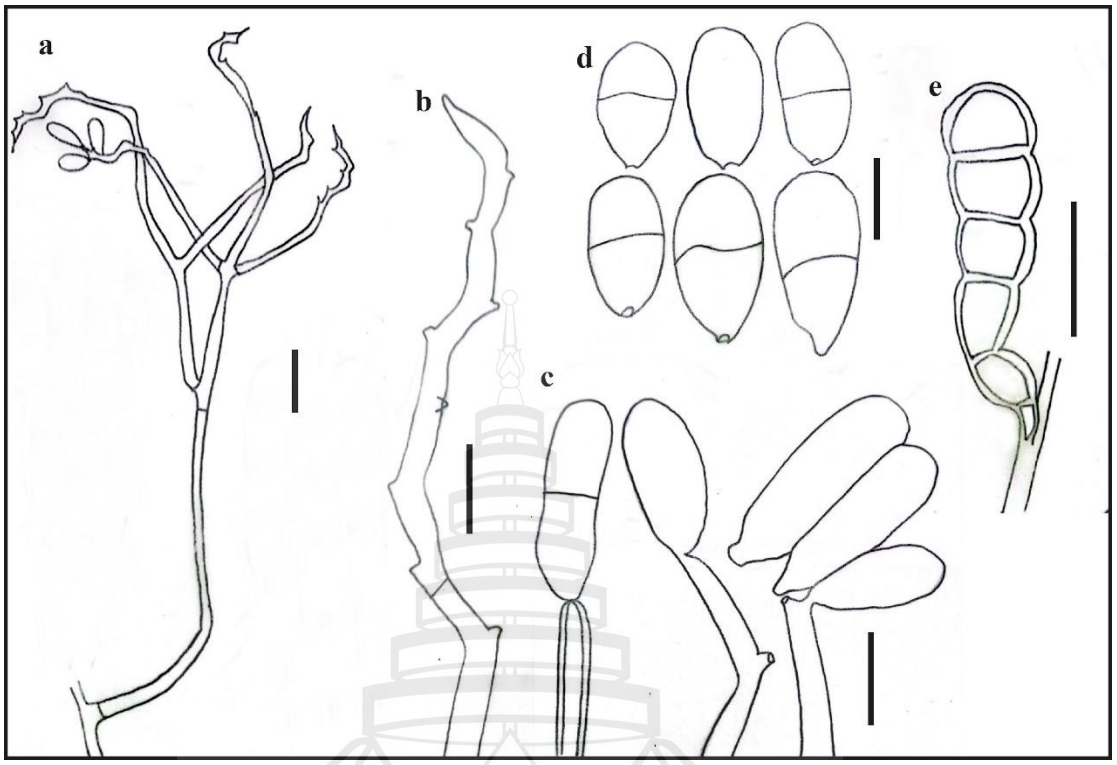


Figure 4.18 *Hypomyces mycophilus*

Figure 4.18, a. Conidiophore. b. Fertile rachis of a conidiophore. c. Conidiogenous cells and conidiogenous loci. d. Conidia. e. Chlamydospore. Scale bars: a, e = 25 μm. b–d = 10 μm. (Redrawn from Rogerson & Samuels, 1993).

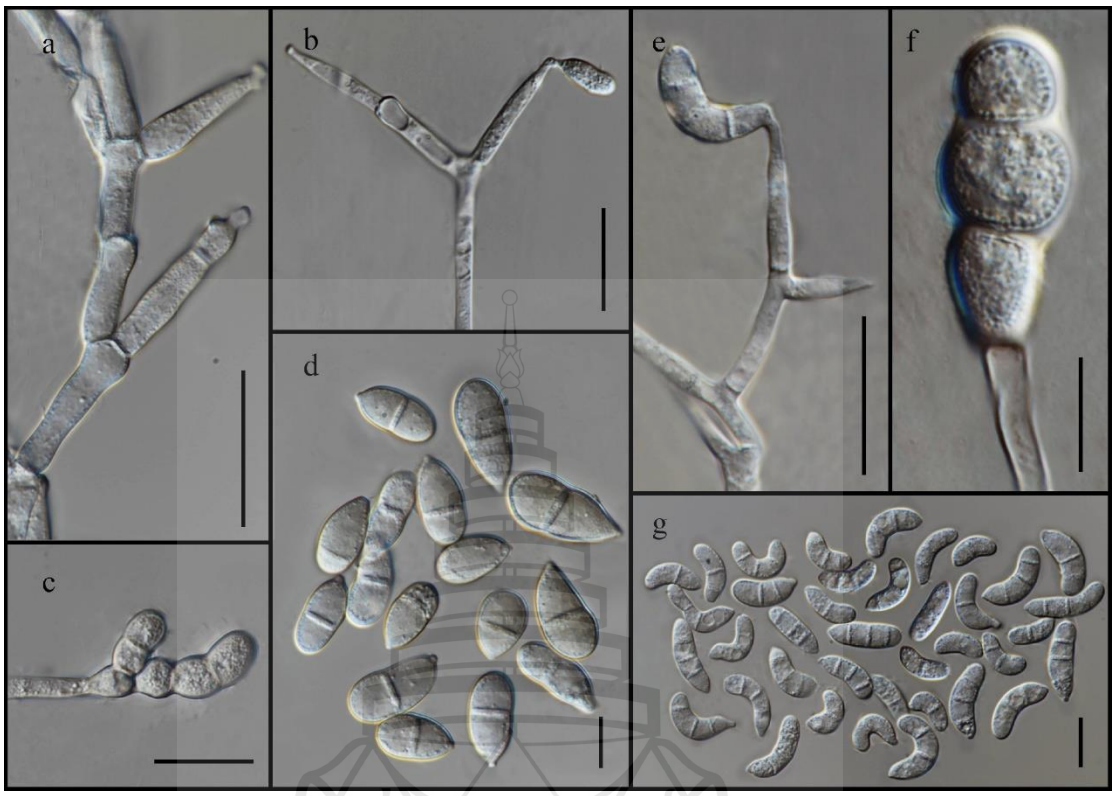


Figure 4.19 *Hypomyces protrusus* (a-d) and *Hypomyces semicircularis* (e-g)

Figure 4.19, *Hypomyces protrusus* (a-d). a, b. Conidiogenous cells and conidial attachment. c. Chlamydospores. d. Conidia. Scale bars: c = 30 μm, a = 25 μm, b = 20 μm, d = 10 μm. *Hypomyces semicircularis* (e-g). e Conidiogenous cells and conidial attachment. f Chlamydospores. g Conidia. Scale bars: e = 20 μm, f = 15 μm, g = 10 μm.

Hosts − *Auricularia cornea, Auricularia polytricha, Agaricus bisporus, Coprinus comatus, Flammulina velutipes, Ganoderma lingzhi, G. lucidum, Hypsizygus marmoreus, Lentinula edodes, Morchella sextelata, Paxillus involutus, Pleurotus eryngii,* and *P. ostreatus* (Potočnik et al., 2008; Back et al., 2012; Kim et al., 2012; Wang et al., 2015c; Zuo et al., 2016; Wang et al., 2018; Wu et al., 2020; An et al., 2022a; Wang et al., 2024a; Xie et al., 2024b, 2024c)

Distribution − Worldwide (Carrasco et al., 2017a; Gea et al., 2019)

Signs and symptoms − The outbreaks of cobweb disease are typified by the emergence of a cobweb-like white, fluffy cottony mycelium growth on the surface of the casing layer, along with the invasion of primordia and developing fruit bodies

(Carrasco et al., 2016; Carrasco et al., 2017a) (Figure 4.20). Affected mushrooms often exhibit discoloration and eventual decay (Carrasco et al., 2016; Carrasco et al., 2017a). Spore dissemination within growing rooms facilitates the rapid colonization of the casing layer. Spores landing on developing mushrooms can result in yellowish brown cap spotting, while fruit bodies overtaken by mycelium may undergo soft wet rot, turning the fruiting bodies dark brown and shrunken (Lee et al., 2011; Tamm & Põldmaa, 2013). Without proper control measures, localized outbreaks tend to expand radially outward across the casing layer, progressively colonizing a larger area of the crop surface and consequently reducing its size. Initially, the light invasive mycelium swiftly transforms into a dense white mass with a mealy texture due to extensive sporulation (Adie, 2000). At times when the colonies mature, they typically develop pink-red hues (Tamm & Poldmaa, 2013).

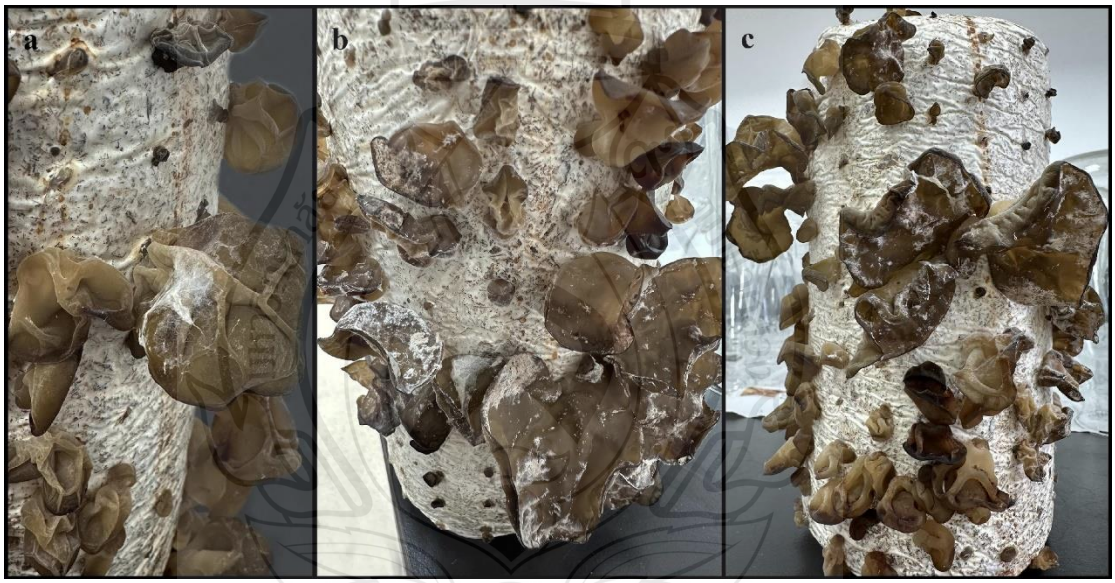


Figure 4.20 Signs and symptoms of cobweb disease of *Auricularia cornea* caused by *Hypomyces mycophilus* (a-c)

Disease cycle and epidemiology − The casing contamination is often regarded as a primary source of infection (Fletcher & Gaze, 2008). Occasionally, the wild specimens, possibly infected in proximity to the farm, could serve as a primary source of infection (Tamm & Poldmaa, 2013). Alternative sources of primary infection may include contaminated packages and containers, contaminated water, external visits, and vehicles (Carrasco et al., 2017a). The principal factor influencing

the occurrence and intensity of the disease in commercial mushroom cultivation is the dissemination of detrimental conidia (Adie et al., 2006; Fletcher & Gaze, 2008). Pathogenic spores are abundant, dry, and prone to detachment upon physical contact (Adie & Grogan, 2000). Upon release, these conidia rapidly disperse through air-conditioning systems. Previous studies indicate that primary causes of conidia release include splashing and runoff during watering (Adie & Grogan, 2000).

Disease management − Implementing stringent hygiene measures to prevent the dispersion of conidia plays a crucial role in managing cobweb disease (Adie et al., 2006). Covering the affected area with a thick, damp paper towel to prevent the release of conidia and preventing irrigation over or closer to cobweb patches is advisable to halt the spread of the disease (Pyck & Grogan, 2015). Implementing measures such as turning off fans during the removal of spent mushroom compost, tightly sealing the doors of growing rooms, and employing high-efficiency particulate air filters (HEPA) can also be effective strategies to prevent the dispersal of conidia (Fletcher & Gaze, 2008; Pyck & Grogan, 2015). The conclusion of the crop cycle represents a critical period for eliminating any remaining disease residues. Therefore, conducting *in situ* thermal disinfection after the crop cycle via "cooking-out" (at temperatures of 65–70 ºC for 9–12 hours) is recommended as the most effective method for ensuring proper disinfection (Fletcher & Gaze, 2008). Alternatively, when thermal disinfection is not feasible, it is advisable to clean the vacant facility using water and appropriate disinfectants (Fletcher & Gaze, 2008). Preventing disease outbreaks can also be achieved by regulating humidity and temperature levels within mushroom facilities (Desrumeaux, 2005). It has been observed that a few spores of *Cladobotryum dendroides* are capable of germination at relative humidity levels below 85%, and disease development and spread are unlikely at low temperatures (17 ºC) (Desrumeaux, 2005). Navarro et al. (2021) proposed that effective management of the moisture level in casing materials could enhance crop yield and mitigate the incidence of cobweb disease. However, the control of cobweb disease continues to heavily rely on the regular application of fungicides from various chemical groups such as Prochloraz-Mn, Chlorothalonil, and Metrafenone (Carrasco et al., 2017a, b). Gea et al. (2019) proposed that essential oils from *Thymus vulgaris* and *Satureja montana* could be valuable products in managing cobweb disease when

incorporated into an integrated pest management program. Muhammad et al. (2019) observed that *Syzygium aromaticum* has potential for biocontrol of cobweb disease. Potočnik et al. (2014) suggested peracetic acid as an environmentally sustainable casing soil disinfectant to combat cobweb disease in *Agaricus bisporus*. Nmom et al. (2022) discovered that treating cobweb disease, induced by *Cladobotryum mycophilium* on *Pleurotus ostreatus*, with seed extract of *Piper guineense* is efficacious.

The taxonomic classification of the pathogens is presented in an updated phylogenetic tree based on available DNA sequence analyses in Figure 4.21.

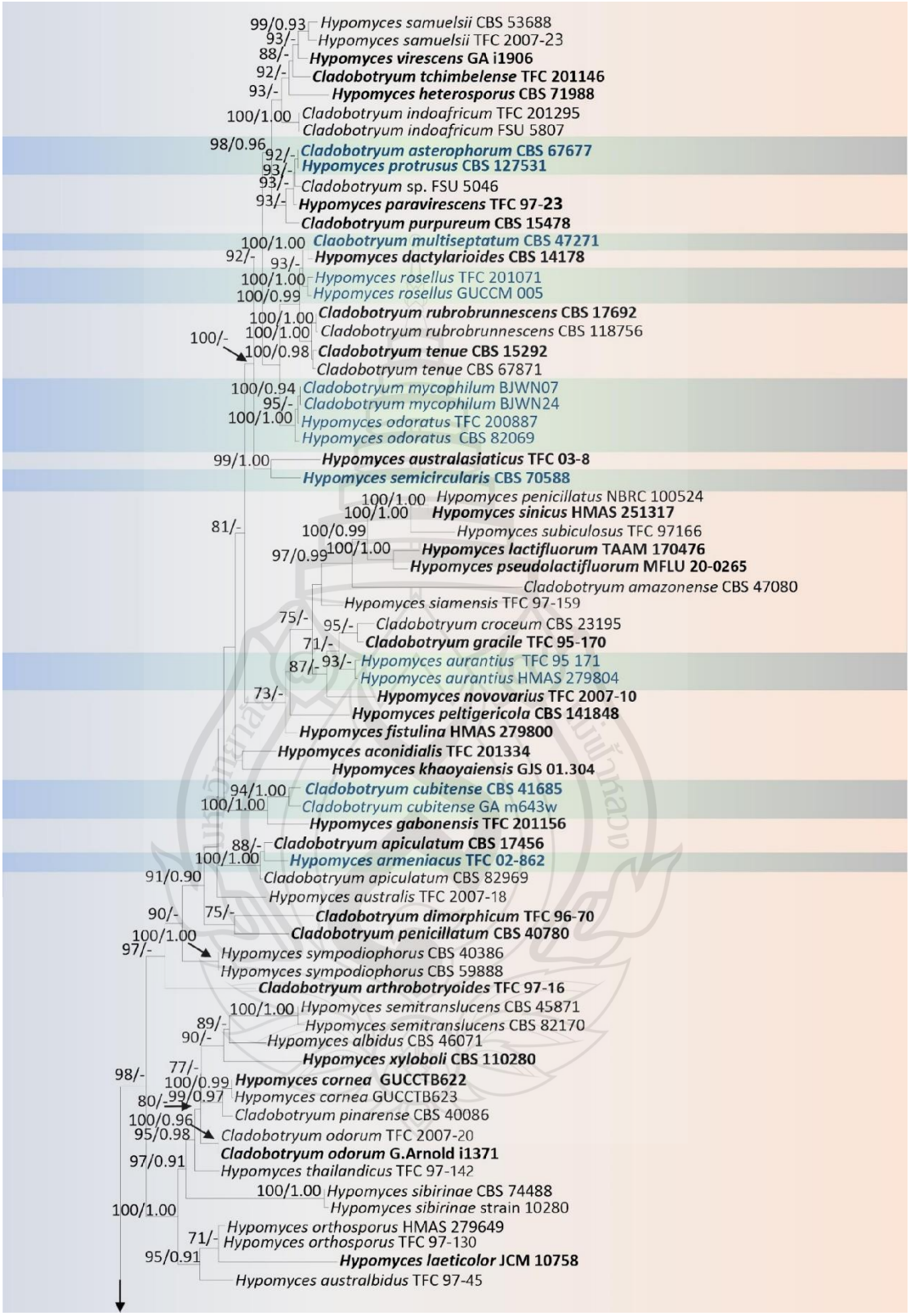


Figure 4.21 Phylogenetic tree generated by ML analysis of combined ITS, LSU, *tef*-1α, and *rpb*2 sequence data of *Hypomyces* and its allied genera

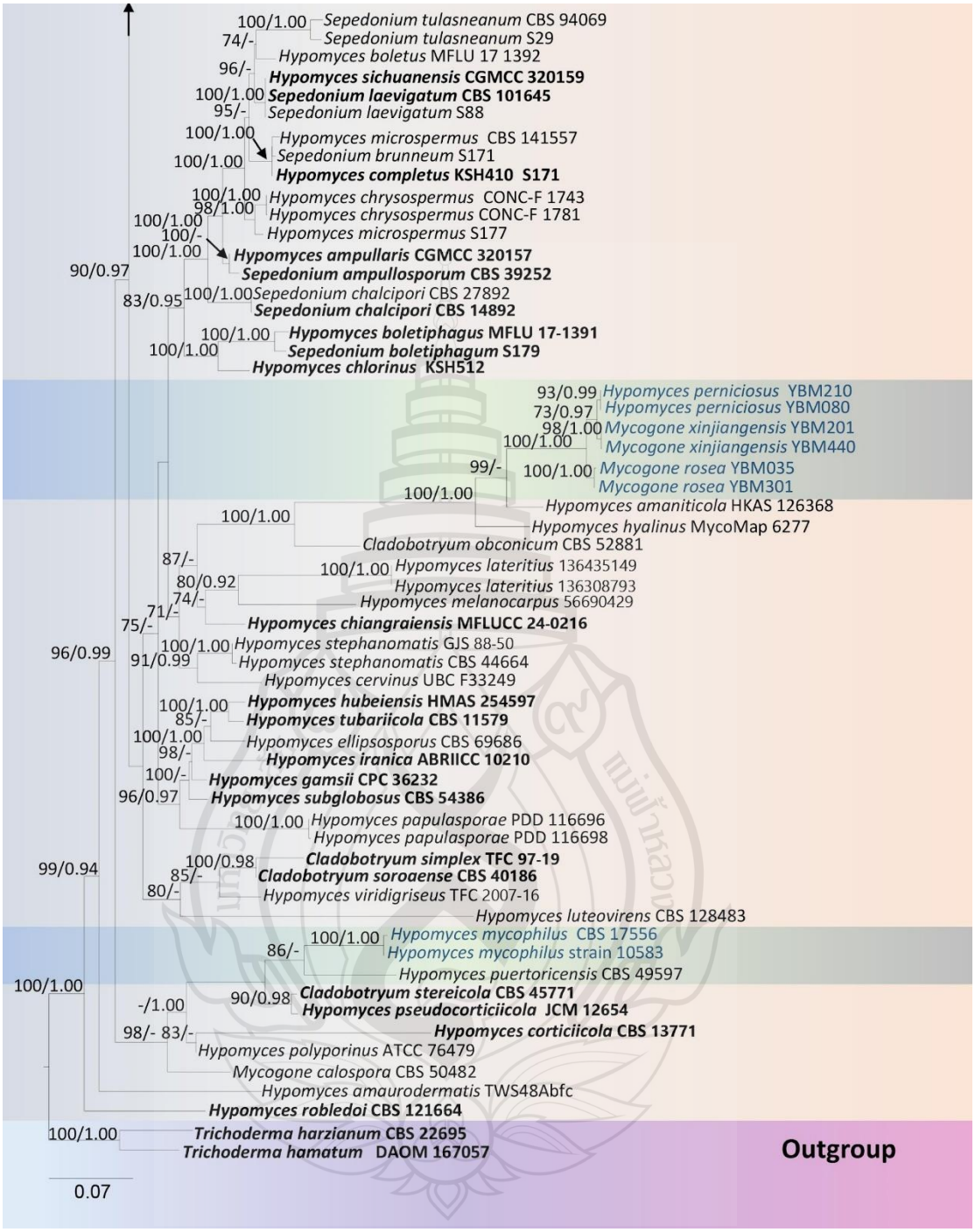


Figure 4.21 (continued)

Figure 4.21, A total of 129 strains were included in the analyses. The tree is rooted with *Trichoderma harzianum* (CBS 22695) and *T. hamatum* (DAOM 167057). The tree topology of the ML analysis was similar to the Bayesian analyses. The best-scoring ML tree with an optimal log-likelihood value of −34558.104 is

presented. The matrix contained 1,489 distinct alignment patterns, with 45.19% of the characters being undetermined or gaps. Bootstrap support values for ML ≥ 70% and PP ≥ 0.90 (ML/ PP) are shown, respectively, near the nodes. Type strains are in bold, and the pathogenic species associated with wet bubble and cobweb diseases are in blue text.

4. Green Mold

Green mold disease, attributed to *Trichoderma* species, poses a significant global-scale challenge for mushroom cultivators (Hatvani et al., 2012; Jayawardena et al., 2021). This is also known as Trichoderma blotch, Trichoderma mildew, and Trichoderma spot, among other names, and is responsible for significant losses, ranging from 63% to 65%, in cultivated mushroom production (Bhatt & Singh, 2000; Kumar et al., 2017).

Pathogens − *Trichoderma aggressivum, T. asperellum, T. atroviride, T. citrinoviride, T. ganodermatigerum, T. ghanese, T. guizhouense, T. hamatum, T. harzianum, T. hengshanicum, T. hymenopellicola, T. koningiopsis, T. longibrachiatum, T. oblongisporum, T. paratroviride, T. pleuroti, T. pleuroticola, T. strophariensis, T. virens,* and *T. viridistromatis* (Hatvani et al., 2012; Bellettini et al., 2018; Šantrić et al., 2018; Cai et al., 2020; An et al., 2022b; Zeng et al., 2022; Li et al., 2023a; Ajis et al., 2024; Tarafder et al., 2024a).

Classification − *Ascomycota, Pezizomycotina, Sordariomycetes, Hypocreales, Hypocreomycetidae, Hypocreaceae*

Pathogen morphology and biology − Generally, the asexual morph of *Trichoderma* spp. is hyphomycetous. It is characterized by conidiophores that are conspicuously curved to sinuous, with or without a well-defined main axis. These conidiophores are branched, displaying irregular, verticillate, or sometimes tree-like branching patterns. They are hyaline, smooth, and septate in structure. The phialides are hyaline, either divergent or parallel, occurring singly or in whorls, and sometimes arranged in repetitive patterns to form chains. The conidia are typically unicellular and exhibit various shapes, such as globose, subglobose, ovoid, ellipsoidal, or oblong, and may appear green or hyaline (Siddiquee et al., 2017; Perera et al., 2023) (Figure 4.22).

Trichoderma species are characterized as asexual, filamentous fungi that inhabit soil environments (Bellettini et al., 2018; Aydoğdu & Kurbetli, 2021). Mycoparasitism represents an ancestral trait of *Trichoderma* (Mukherjee et al., 2022). This phenomenon involves a complex physiological process that entails the synthesis and secretion of enzymes, such as chitinases, glucanases, and proteases, as well as secondary metabolites, by *Trichoderma*, which contributes to its ability to parasitize other fungi (Mukherjee et al., 2022). *Trichoderma* species have also been reported as secondary pathogens associated with plants (Kredics et al., 2009; Jayawardena et al., 2021).

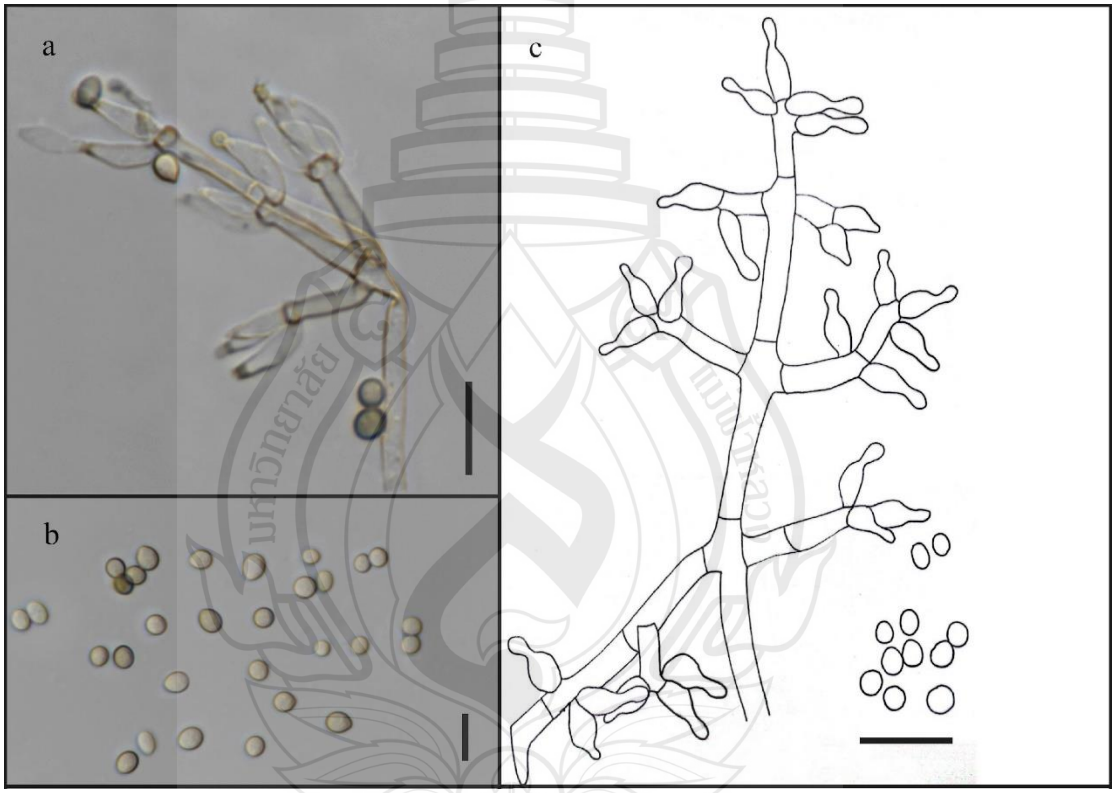


Figure 4.22 *Trichoderma* sp. (a-b)

Figure 4.22, a. Conidiophore, conidiogenous cells. b. conidia. Scale bars: a = 10 µm, b = 5 µm. *Trichoderma harzianum*. c Conidiophore, conidiogenous cells, and conidia. Scale bar c = 10 µm. (Redrawn from Chaverri & Samuels (2003)).

Hosts − *Agaricus bisporus*, *A. bitorquis*, *Auricularia auricula*, *Calocybe indica*, *Dictyophora rubrovolvata*, *Ganoderma lingzhi*, *G. lucidum*, *G. sichuanense*, *Hymenopellis raphanipes*, *Lentinula edodes*, *Pleurotus eryngii*, *P. pulmonarius*, *P.*

ostreatus, P. sajor-caju, Stropharia rugosoannulata, and *Volvariella volvacea* (Singh et al., 2006; Hatvani et al., 2012; Wang et al., 2016b; Zhang et al., 2019; Cai et al., 2020; Allaga et al., 2021; Chen et al., 2021; Zeng et al., 2022; Dang et al., 2023; Li et al., 2023a; Ajis et al., 2024; Tarafder et al., 2024a)

Distribution − Worldwide (Hatvani et al., 2012)

Signs and symptoms − *Trichoderma* pathogens initially develop as white and compact mycelia, which undergo colour transformation during sporulation, ultimately turning dark green and becoming noticeable on the mushroom-growing substrate (Sharma et al., 2007; Luković et al., 2020) (Figure 4.23). Mushrooms growing within or near this mycelium exhibit brown discoloration, potential cracking, and distortion, and may also display stipe peels (Sharma et al., 2007). Moreover, it induces the formation of brown spots, characterized by necrotic tissue and lesions on the fruiting bodies of mushrooms (Sharma et al., 2007; Luković et al., 2020).



Figure 4.23 Signs and symptoms of green mold disease

Figure 4.23, a. Green mold infection in cultivated *Ganoderma sichuanense*. b. Green mold infection in a grow bag of *Auricularia cornea.* c. Green mold infection in the substrate of *Lentinus edodes*.

Disease cycle and epidemiology − Various sources of primary inoculum for *Trichoderma* spp. include dust particles, contaminated clothing, animal vectors

such as the mite, mice, and sciarid flies, airborne transmission, contaminated spawn, surface spawning, and compost contamination resulting from handling and machinery/equipment usage at mushroom farms (Sharma et al., 2007). The spores of the pathogen can also be disseminated through water droplets (Gea & Navarro, 2017). Ajis et al. (2024) detected *Trichoderma* in water, air within the production facility, and on cleaning tools. These findings indicate that water may act as a primary source of *Trichoderma* contamination in mushroom farms.

Green mold typically manifests in compost that is rich in carbohydrates but deficient in nitrogen (Sharma et al., 2007). Factors such as excessive compaction of compost in beds or overly high filling weights can impede the initiation of peak heating during composting (Sharma et al., 1999; Sharma et al., 2007). This issue is particularly pronounced in compost with a shorter texture and potentially elevated moisture content, leading to inadequate pasteurization and conditioning. Additionally, frequent application of formalin has been observed to encourage the proliferation of green molds (Sharma et al., 1999; Sharma et al., 2007). Moreover, the temperature of the compost plays a pivotal role in the progression of the infection, as excessively high temperatures, such as 28 °C, can accelerate the growth of *T. aggressivum* mycelium up to ten times that of the mushroom (Gea & Navarro, 2017). Consequently, meticulous monitoring and control of substrate colonization stage temperatures are imperative to mitigate the risk of infection (Gea & Navarro, 2017). Mazin et al. (2019) confirmed the previously anecdotal evidence that mushroom sciarid flies (*Lycoriella ingenua*) are indeed involved in the epidemiology of green mold disease, serving as vectors for the fungal pathogen. Aydoğdu & Kurbetli (2021) demonstrated that the occurrence of *Trichoderma aggressivum* f. *aggressivum* within casing soil may exert a more pronounced adverse effect on the yield of *Agaricus bisporus* compared to its presence in compost. Additionally, they observed that the brown strain of *A. bisporus* exhibited a higher level of resistance to *T. aggressivum* f. *aggressivum* when compared to the white strain.

Disease management − The timely detection of *Trichoderma* during the initial stages of infection is crucial for effectively preventing and controlling the spread of green mold disease in commercial mushroom cultivation (Šašić et al., 2023). Therefore, alongside stringent hygiene practices and disinfectant treatments as

primary measures for preventing green mold disease, early screening of mushroom-growing substrate should be incorporated as a routine component of control procedures (Šašić et al., 2023). Colavolpe et al. (2014) noted that immersing the substrate in hot water at 60 °C for 30 minutes or in alkalinized water for 36 hours was an effective treatment for reducing contamination with *Trichoderma* spp. during the spawning phase in the cultivation of lignicolous mushroom species. Coles et al. (2024) concluded that implementing mechanical filling techniques and adopting measures to minimize contact with the floor and between beds can effectively mitigate the spread of green mold within the context of commercial mushroom production. The commercial fungicides Prochloraz and Carbendazim have demonstrated efficacy against the disease (Hatvani et al., 2012; Altaf et al., 2022a; Li et al., 2023a). According to Luković et al. (2020), Metrafenone exhibited satisfactory efficacy and could potentially be recommended for managing green mold disease in mushroom cultivation. Altaf et al. (2022b), demonstrated that incorporating botanical and bacterial antagonists into the casing of *Agaricus bisporus* mushrooms infected with pathogens effectively reduces green mold infection, leading to increased yields as a result. It has been discovered that *Bacillus amyloliquefaciens* exhibits promising potential for biocontrol of compost green mold, suggesting its suitability for further evaluation in commercial-scale trials (Mwangi et al., 2016; Stanojević et al., 2019). Milijašević-Marčić et al. (2017) proposed the utilization of *Bacillus subtilis* strains as a viable alternative to chemical fungicides for managing green mold disease in *Agaricus bisporus* cultivation. The biofungicide derived from *Bacillus subtilis* Ch-13 has demonstrated superior efficacy in controlling green mold caused by *Trichoderma aggressivum* on *Agaricus bisporus*, exerting a positive influence on mushroom production (Potočnik et al., 2021). Šantrić et al. (2018) noted that *Streptomyces flavovirens* exhibits potential for enhancing mushroom yield and aiding in disease management against the aggressive compost green mold disease induced by *Trichoderma aggressivum*. Hatvani et al. (2007) developed a polymerase chain reaction (PCR)-based method for the rapid detection of *T. pleurotum* and *T. pleuroticola*. Lee et al. (2020) devised a molecular marker capable of swiftly detecting a broad spectrum of *Trichoderma* spp. This marker relies on DNA sequence alignment of the ITS1 and ITS2 regions, which are specific to *Trichoderma* spp.

The taxonomic classification of the pathogens is presented in an updated phylogenetic tree based on available DNA sequence analyses in Figure 4.24.

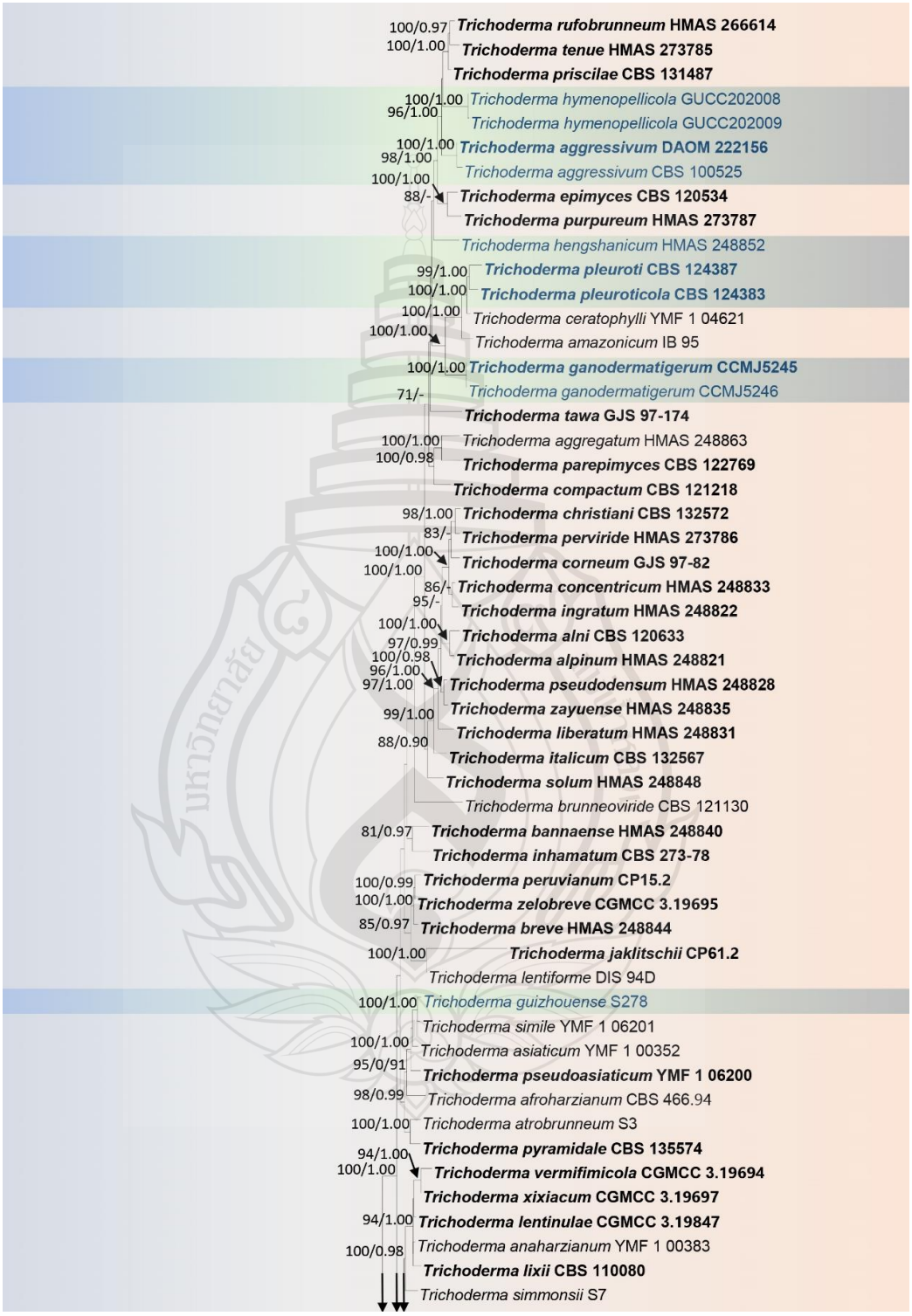


Figure 4.24 Phylogenetic tree generated by ML analysis of combined ITS, *rpb2*, and *tef-1α* sequence data of *Trichoderma* species

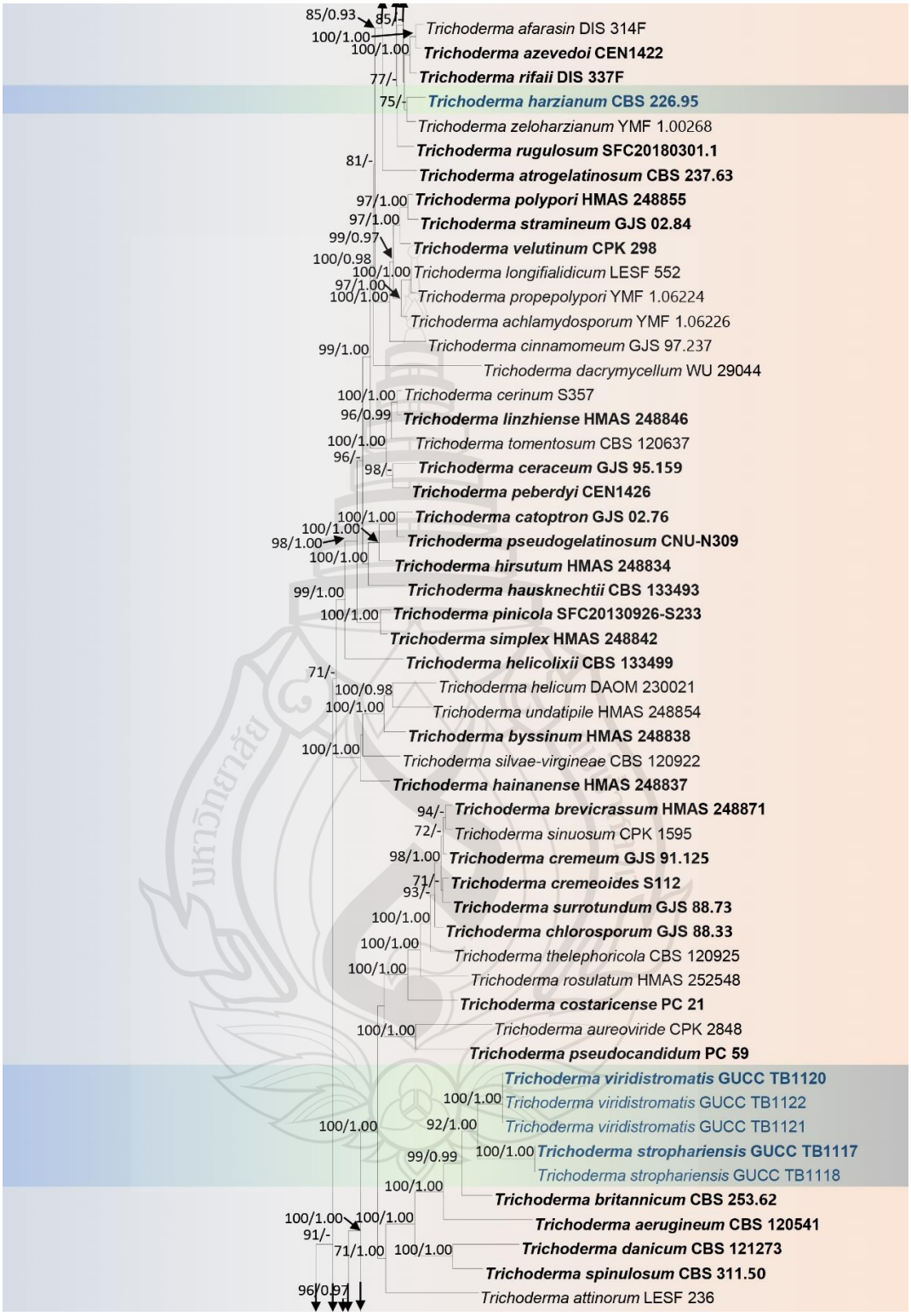


Figure 4.24 (continued)

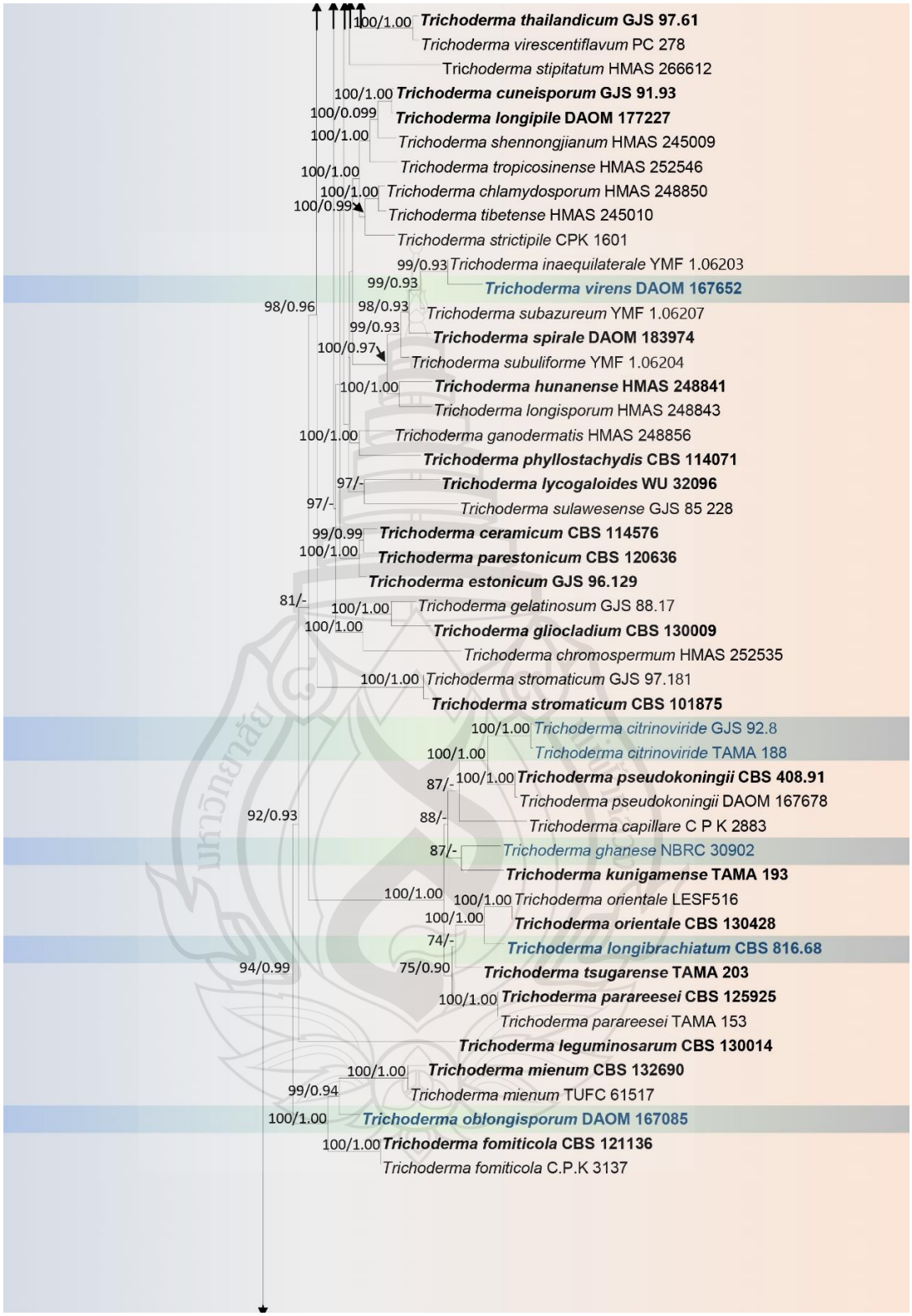


Figure 4.24 (continued)

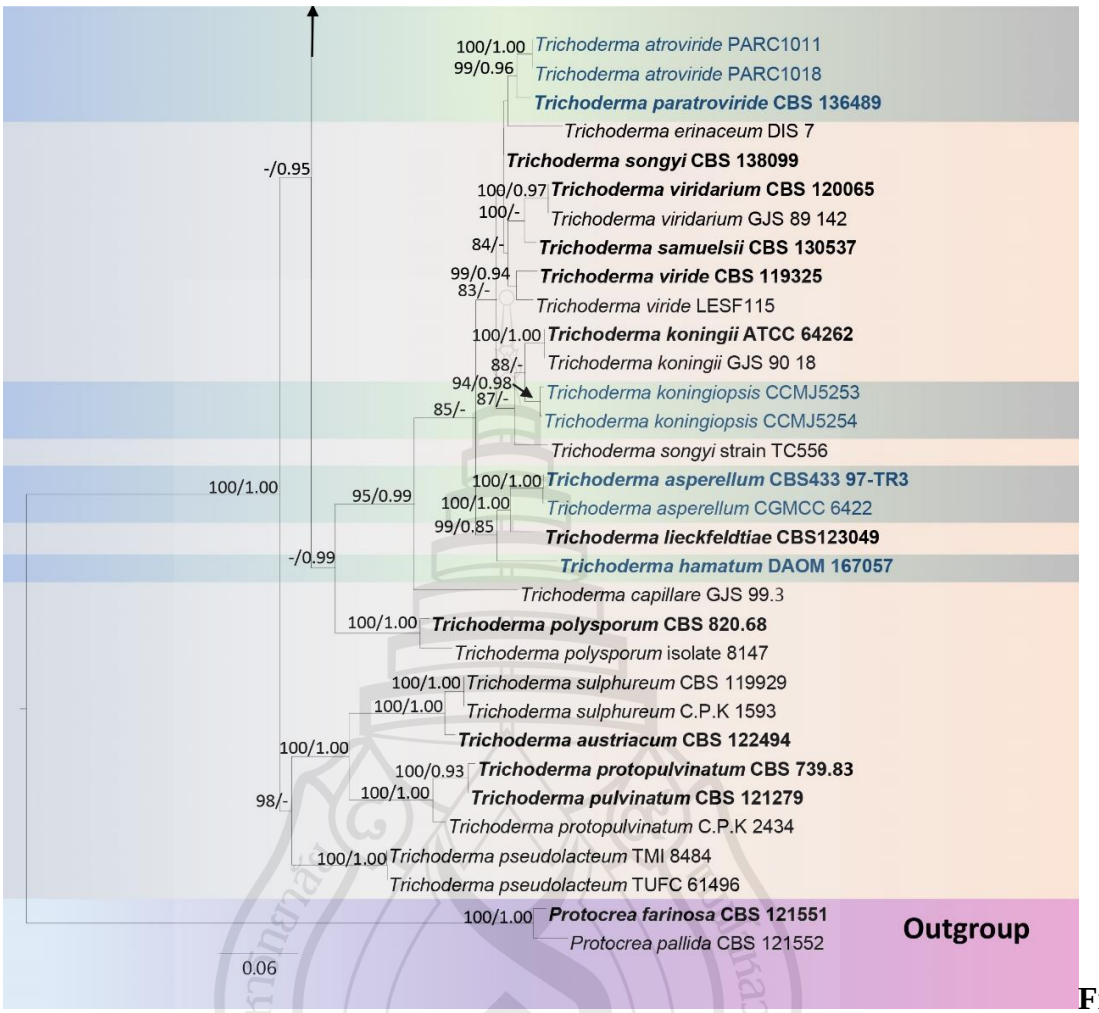


Figure 4.24 (continued)

Figure 4.24, A total of 186 strains were included in the analyses. The tree is rooted with *Protocrea farinosa* (CBS 121551) and *P. pallida* (CBS 121552). The tree topology of the ML analysis was similar to the Bayesian analyses. The best-scoring ML tree with an optimal log-likelihood value of −45105.730 is presented. The matrix contained 1,223 distinct alignment patterns, with 22.59% of the characters being undetermined or gaps. Bootstrap support values for ML ≥ 70% and PP ≥ 0.90 (ML/ PP) are shown, respectively, near the nodes. Type strains are in bold, and the pathogenic species associated with green mold disease are in blue text.

5. Slippery Scar

Since the 1990s, this disease has been a widespread and damaging issue in China, affecting *Auricularia polytricha* (Peng et al., 2014). However, the exact

identity of the pathogen responsible for the slippery scar remained uncertain for a long time. Sun and Bian (2012) identified *Scytalidium lignicola* as the cause; however, Peng et al. (2014) later argued that the pathogen described by Sun and Bian was not *S. lignicola*. Based on morphological and phylogenetic analysis, Peng et al. (2014) found that the pathogen differed from other existing *Scytalidium* species, leading them to propose a new species, *S. auriculariicola*, to classify the pathogenic strains. This disease has resulted in a decline in the annual *Auricularia polytricha* yield by approximately 20-30% (Sun & Bian, 2012).

Pathogen − *Scytalidium auriculariicola* (Peng et al., 2014).

Classification − *Ascomycota*, *Pezizomycotina*, *Leotiomycetes*, *Leotiomycetidae*, *Helotiales*, *Helotiaceae*

Pathogen morphology and biology − The hyphae of *Scytalidium auriculariicola* are septate, sub-hyaline to brown, with one or several oil globules. Conidiogenesis is thallic (Peng et al., 2014). Conidia are cylindrical and rectangular, varying in length based on the parent hypha, and are often catenate, with both ends truncated. Chlamydoconidia are also catenate, pale brown to brown, barrel-shaped to oblong, with thick walls (Peng et al., 2014) (Figure 4.25). The compost, even though it is located far from the mushroom mycelia, also showed the slippery scar symptom. This observation suggests that the pathogen may also act as a saprobe (Sun & Bian, 2012).

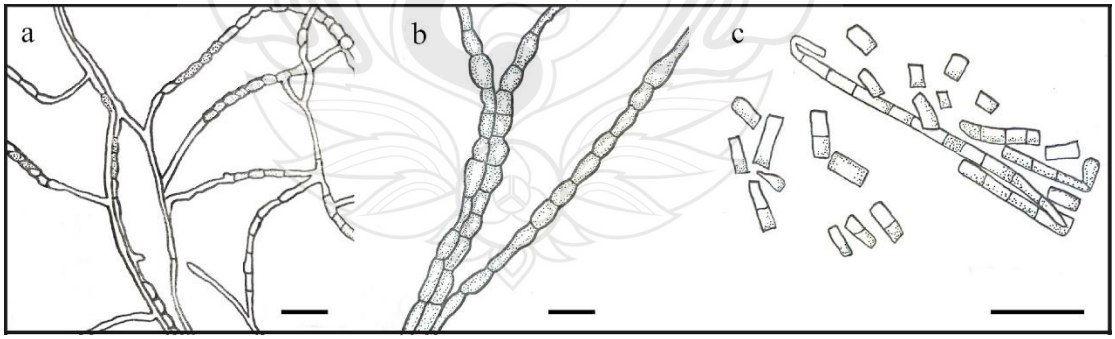


Figure 4.25 *Scytalidium auriculariicola*

Figure 4.25, a Branched hyphae with developing chlamydoconidia b Catenate and thick-walled chlamydoconidia. c Conidia of variable length. Scale bars: a, c = 20 μm, b = 10 μm (Adapted and redrawn from Peng et al. (2014)).

Hosts − Mycelia of *Auricularia polytricha* (Sun & Bian, 2012; Peng et al., 2014)

Distribution − China (Sun & Bian, 2012; Peng et al., 2014)

Signs and symptoms − The pathogen infects only the mycelia of *Auricularia polytricha*, whether during their growth phase or when they have fully colonized the bags, but does not affect the mushroom fruiting bodies (Sun & Bian, 2012). Infected mycelia develop slippery, glossy, dark-brown scars on their surface. A red-brown antagonistic line forms between the infected and healthy mycelia, with the margin of this line being irregular (Sun & Bian, 2012). The infected scar spreads rapidly until it covers the entire bag. The pathogen inhibits the growth of mushroom mycelia, and the infection thoroughly corrodes the mycelia (Sun & Bian, 2012).

Disease cycle and epidemiology − The primary cause of this issue is often due to insufficient sterilization of the compost or the rupture of cultivation bags during the growing process (Sun & Bian, 2012). The infection rate rose with higher temperatures. When temperatures exceeded 25 °C, pathogen reproduction accelerated, resulting in a rapid increase in the number of scars (Sun & Bian, 2012). When the shed's humidity was excessively high due to frequent spraying or watering, the pathogen spread rapidly (Sun & Bian, 2012). Once the mushrooms started to be harvested, the primary route of infection was through the openings in the cultivated bags (Sun & Bian, 2012).

Disease management − Effective methods for controlling slippery scar in *A. polytricha* remain elusive, primarily due to the prolonged uncertainty about the precise identity of the pathogen causing the condition (Peng et al., 2014). Nevertheless, proper sterilization of the compost, along with careful management of temperature and humidity in grow houses, can be beneficial in controlling the disease (Sun & Bian, 2012; Peng et al., 2014).

The taxonomic classification of the pathogens is presented in an updated phylogenetic tree based on available DNA sequence analyses in Figure 4.27.

6. Yellow Rot

Yellow rot stands as the most devastating disease affecting *Ganoderma lucidum* cultivation in Korea (Lee et al., 1996; Oh et al., 1998; Kang et al., 2010). The disease leads to significant yield loss and hinders the ongoing cultivation of the

mushroom in the same location. The exact identity of the yellow rot pathogen remained uncertain for an extended period (Kang et al., 2010). Lee et al. (1996) initially identified *Xylogone sphaerospora* (asexual morph *Scytalidium sphaerosporum*) as the yellow rot pathogen. Oh et al. (1998) identified *Arthrographis cuboidea* (syn. *Scytalidium cuboideum*) as the causative agent. However, Kang et al. (2010) later confirmed *Xylogone ganodermophthora* (with the asexual morph *Scytalidium ganodermophthorum*) as the causal agent of yellow rot. Pathogenicity tests by Kang et al. (2010) showed that only *X. ganodermophthora* was capable of causing the disease in *Ganoderma lucidum.*

Pathogen − *Scytalidium ganodermophthorum* (Kang et al., 2010).

Classification − *Ascomycota, Pezizomycotina, Leotiomycetes, Leotiomycetidae, Helotiales, Helotiaceae*

Pathogen morphology and biology − The ascomata of the pathogen, which arise from coiled ascogenous hyphae, are globose, non-ostiolate, and lack appendages. They start off pale brown and turn dark brown upon maturity, featuring a wall of *textura epidermoidea* (Kang et al., 2010). Asci are subglobose or globose and dispersed in the centrum. Those are eight-spored, thin-walled, and quickly evanescent. Ascospores have refractive walls, are hyaline, smooth, and range from subglobose to globose (Kang et al., 2010). The fertile hyphae emerge laterally on simple conidiophores. Initially, these hyphae have few septa, but over time, they develop numerous septa and eventually break into arthroconidia (Kang et al., 2010). Arthroconidia are typically rectangular to cylindrical, hyaline to yellow, and may be wider than they are long. They do not have separating cells or disjunctors (Kang et al., 2010) (Figure 4.26).

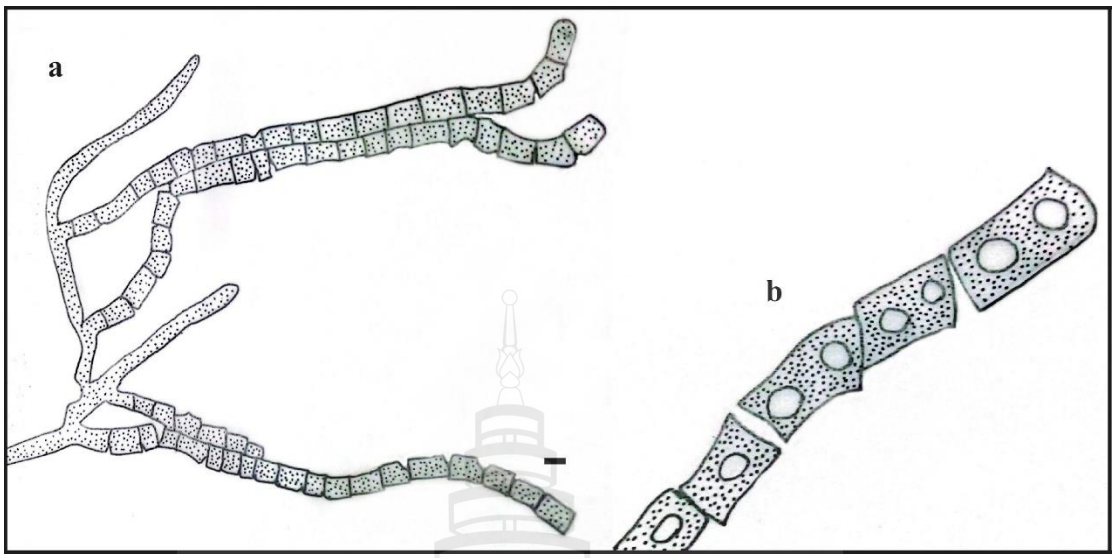


Figure 4.26 *Scytalidium ganodermophthorum*

Figure 4.26, a, b Arthroconidia without disjunctors. (Oil immersion objective). Scale bar: a = 2 µm. (Adapted and redrawn from Kang et al. (2010)).

Hosts − *Ganoderma lucidum* and *Ganoderma sichuanense* (Kang et al., 2010; Li et al., 2024)

Distribution − China, and Korea (Lee et al., 1996; Oh et al., 1998; Kang et al., 2010; Liu et al., 2019; Li et al., 2024)

Signs and symptoms − The pilei of infected fruiting bodies were malformed (Kang et al., 2010). The disease predominantly affects the mature stage of the fruiting body. Symptoms initially present as small, white, circular spots on the diseased hymenium of the pileus (Li et al., 2024). These spots gradually enlarge, covering up to three-quarters of the hymenium and changing to grey (Li et al., 2024). As the disease advances, the grey spots become black, impacting spore production. The stipes of the infected fruiting bodies showed greenish-yellow discoloration, and the usual white mycelial mat was absent (Kang et al., 2010; Li et al., 2024). Additionally, the interior tissue of oak logs producing healthy fruiting bodies had white mycelium, while the wood of contaminated logs displayed a greenish-yellow discoloration (Kang et al., 2010).

Disease cycle and epidemiology − The pathogen overwinters as ascocarps and/or mycelia primarily within the tissues of infected logs previously hosting *G. lucidum* or inside infected *G. lucidum* fruiting bodies (Kang et al., 2011).

Additionally, it can overwinter as ascocarps and mycelia in the soil (Kang et al., 2011). *Scytalidium ganodermophthorum* has occasionally been found in soil at cultivation sites of *Ganoderma lucidum* (Oh et al., 1998). During the spring, ascospores are likely carried by the wind to the inoculum (spawn) of *G. lucidum*, where they infect the developing young mycelia of the mushroom (Kang et al., 2011). The overwintered ascocarps, ascospores, and mycelia of *S. ganodermophthorum* in the soil directly infect the young mycelia of *G. lucidum*, which then colonize the oak logs (Kang et al., 2011). It appears to be a wood-associated pathogen, as it extensively colonizes and causes staining in the mushroom cultivating logs (Kang et al., 2010). The numerous arthroconidia primarily formed beneath the bark of oak logs and at the base of the mushroom fruiting bodies can be spread to other uninfected logs through irrigation water, tools, insects, or other agricultural activities (Kang et al., 2011). Ascocarps develop in the tissues of infected logs and mushroom fruiting bodies 2 to 3 months following infection (Kang et al., 2011). They can persist in the tissues of oak logs and mushroom fruiting bodies for 1 to 3 years or even longer. Once the diseased logs and mushroom fruiting bodies have decomposed, the ascocarps can persist for several years within the decayed tissue in the soil (Kang et al., 2011). They can be carried over long distances by adhering to equipment used in the cultivation of *G. lucidum*, potentially initiating another cycle of the disease (Kang et al., 2011).

Disease management − Choi et al. (1998) tested 37 fungicides, including Benomyl, and found that 21 effectively inhibited the growth of *Scytalidium ganodermophthorum in vitro*. This study suggested that most of these fungicides also negatively impacted the growth of the mushroom. However, Li et al. (2024) indicated that Chlorothalonil, Carbendazim, Prochloraz, and Prochloraz-manganese can effectively manage the yellow rot pathogen without substantially inhibiting the growth of *Ganoderma sichuanense* mycelium, even at low concentrations. To effectively control this disease, it is essential to implement good hygiene practices, such as eliminating contaminated wood and removing diseased *Ganoderma* fruiting bodies from the cultivation areas (Kang et al., 2010).

The taxonomic classification of the pathogens is presented in an updated phylogenetic tree based on available DNA sequence analyses in Figure 4.27.

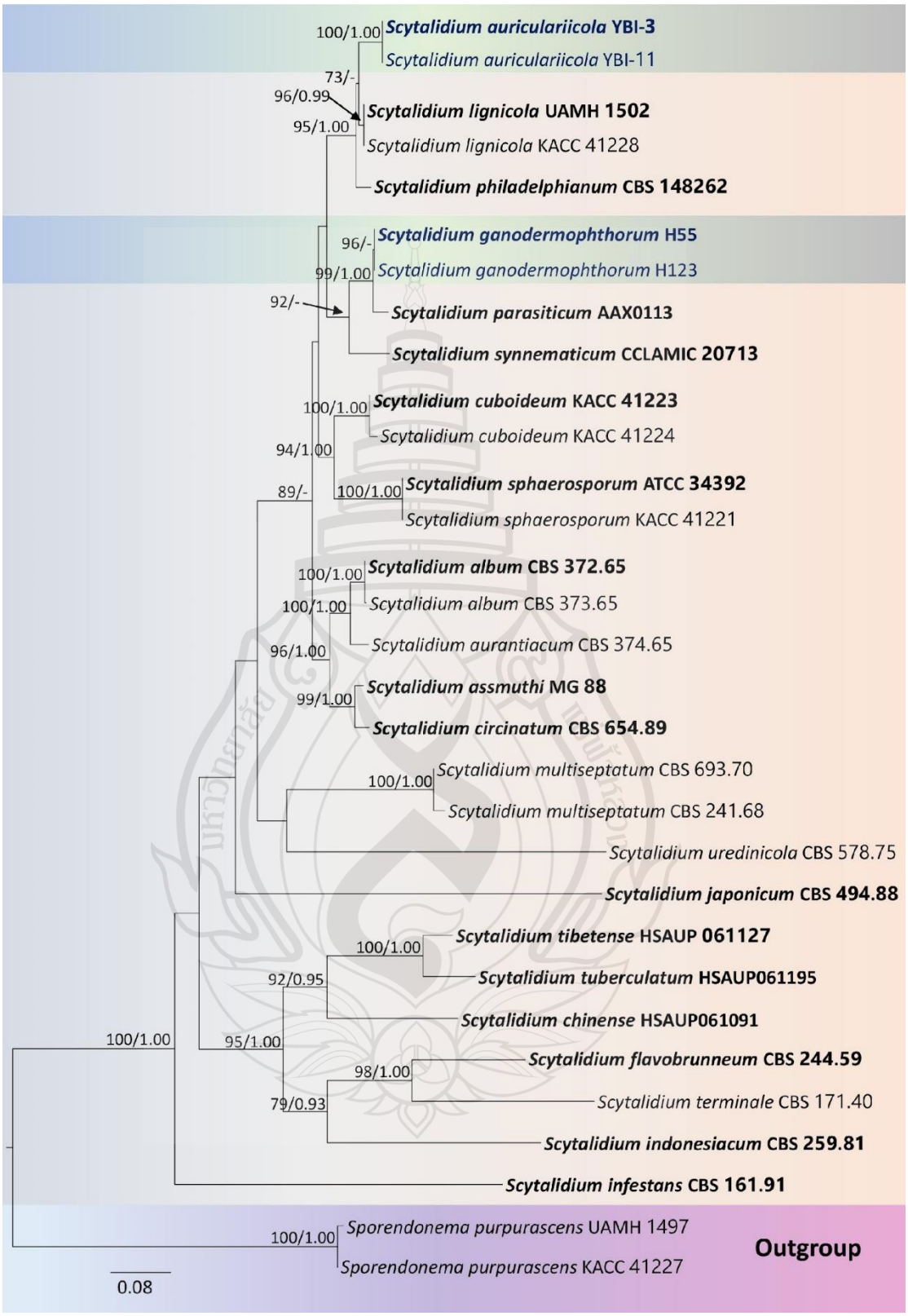


Figure 4.27 Phylogenetic tree generated by ML analysis of ITS sequence data of *Scytalidium* species

Figure 4.27, Related sequences were obtained from previous publications and the GenBank database. Twenty-nine strains are included in the analyses. The tree is rooted with *Sporendonema purpurascens* (UAMH 1497 and KACC 41227). The tree topology of the ML analysis was similar to the Bayesian analyses. The best-scoring ML tree with an optimal log-likelihood value of −5621.080 is presented. The matrix contained 349 distinct alignment patterns, with 3.14% of the characters being undetermined or gaps. Bootstrap support values for ML ≥ 70% and PP ≥ 0.90 (ML/ PP) are shown, respectively, near the nodes. Type strains are in bold, and the slippery scar and yellow rot-causing pathogens are in blue text.

4.3.2 Competitor Molds Affecting Global Mushroom Cultivation

1. White Plaster Mold

White plaster mold can inhibit or delay the harvest by competing with the mushroom mycelium (Gea & Navarro, 2017). This is caused by *Scopulariopsis coprophila* (syn. *Scopulariopsis fimicola*) (*Microascales, Microascaceae*) (Yu et al., 2024). The causal agent was originally described from dung as *Monosporium coprophilum*. Several subsequent taxonomic revisions have led to its current designation as *Scopulariopsis coprophila* (Sandoval-Denis et al., 2016).

White plaster mold has been reported to be associated with the cultivation of *Agaricus bisporus, Calocybe indica,* and *Flammulina velutipes* from countries such as India, China, and Iraq (Bhardwaj et al., 1989; Kumar et al., 2024a; Yu et al., 2024).

The fungus initially appears densely on the casing and compost of mushrooms, starting as a white fluffy growth that develops into a dense mat of mycelium, which resembles plaster (Bhardwaj et al., 1989; Chandhrapati et al., 2021; Aminuzzaman et al., 2022). As it progresses, the colour of the fungus changes from white to pink, then to red. Eventually, the spots turn yellow, which ultimately reduces mushroom production (Chandhrapati et al., 2021; Aminuzzaman et al., 2022).

Bhardwaj et al. (1989) found that the disease exhibited greater severity in compost that was either under-composted or over-composted, retaining an ammonia odor and having a pH greater than 7.5 at the time of spawning. Excessive water during the anaerobic peak heating phase of composting also promotes the growth of pathogens (Aminuzzaman et al., 2022). The emergence of mold is also associated with low temperatures and insufficient pasteurization duration (Gea & Navarro,

2017). The presence of mold is typically more prevalent early in the growth cycle, often attributed to the utilization of materials from the previous year's composting (Gea & Navarro, 2017). When mold does manifest, it tends to be widespread across most substrate packages originating from the same pile and pasteurization room. In instances of severe infestation, it can substantially impede the incubation of mushroom mycelium (Gea & Navarro, 2017).

Proper hygiene practices, combined with the careful removal of stray patches and subsequent treatment with 4% formalin, can help to protect crops against the disease (Bhardwaj et al., 1989). Maintaining a temperature of 60 °C throughout the compost during the peak heat phase of pasteurization completely eradicated the pathogen (Bhardwaj et al., 1989). Thoroughly mixing the compost piles during the composting process to prevent anaerobic zones and ensuring uniform pasteurization throughout the compost mass are beneficial practices for controlling the disease (Gea & Navarro, 2017). The addition of optimal amounts of water and gypsum to the compost is also recommended to facilitate disease control (Sharma et al., 2007). According to Kumar et al. (2024b), Tulsi leaf extract demonstrates high efficacy in controlling white plaster mold under *in vitro* conditions when applied at a concentration of 20%. Re-casing combined with surface treatment using Neem leaf extract was found to be effective in managing white plaster mold in *Calocybe indica* (milky mushroom) cultivation (Kumar et al., 2024b).

2. Brown Plaster Mold

Brown plaster mold can lead to a total crop loss, resulting in 100% yield loss upon infestation (Thakur et al., 1967). It is caused by *Myriococcum praecox* (syn. *Papulaspora byssina*) (*Agaricomycetes, Incertae sedis*) (Yu et al., 2024). Brown plaster mold has been reported to be associated with the cultivation of *Agaricus bisporus, Calocybe indica,* and *Pleurotus* spp., in countries such as India and Iraq (Thakur et al., 1967; Sharma et al., 2007; Binit et al., 2013; Murmu et al., 2014; Yu et al., 2024).

This mold is initially observed as a whitish mycelial growth on the exposed surface of the compost and casing soil (Sharma et al., 2007; Gea & Navarro, 2017). As the colony matures, it forms extensive, dense aggregations that progressively alter in colour. This transition initiates at the center of the colony and

extends towards the periphery, evolving through hues of tan and light brown to cinnamon brown, ultimately achieving a rust-coloured appearance (Thakur et al., 1967). Mushroom mycelium does not grow in areas where plaster mold is present (Thakur et al., 1967). Disease outbreaks are easily recognizable as the spots resemble a granular texture due to the presence of brown spherical structures (bulbils), which form on the compost and casing material (Gea & Navarro, 2017).

The initial infection typically occurs via airborne bulbils or contaminated containers, compost, casing soil, or human workers (Thakur et al., 1967). Optimal conditions for the pathogen's proliferation include excessive moisture and inadequately prepared compost. Elevated temperatures during the spawn run and cropping stages promote the growth of mold (Thakur et al., 1967). In the compost with excessive moisture and insufficient oxygen during fermentation, mold development is facilitated. Furthermore, the inclusion of insufficient gypsum and excessive greasiness in the compost fosters the progression of the disease (Thakur et al., 1967). The pH value above 8.0 also facilitates the mold growth (Gea & Navarro, 2017).

Adhering to stringent hygiene protocols and implementing effective environmental control measures constitutes the most effective strategy for combating the disease (Gea & Navarro, 2017). Throughout the composting process, it is crucial to ensure that peak heating occurs for an adequate duration and at appropriate temperatures (Thakur et al., 1967). Application of Carbendazim (0.05%) via spraying at 7-day intervals is also recommended to control the disease (Thakur et al., 1967).

3. False Truffle

This is regarded as one of the most significant competitors in the cultivation of *Agaricus brasiliensi*s (Nascimento & Eira, 2003). Substantial losses in crop yield can occur when the cultivation is affected either before or during the incubation period, resulting in yield reductions of up to 75% (Gea & Navarro, 2017). This is caused by *Diehliomyces microspores* (syn. *Pseudobalsamia microspora*) (*Eurotiales, Incertae sedis*) (Yu et al., 2024). False truffle has been reported associated with the cultivations of *Agaricus bisporus, A. bitorquis,* and *A. brasiliensis* in countries such as India, the Netherlands, and the United Kingdom (Thakur et al., 1967; Sahrma et al., 2007; do Nascimento et al., 2003; Kakraliya et al., 2022).

Initially, a dense mycelium appears white and subsequently transitions to a creamy yellow as it matures. It manifests as small clusters of white to cream-colored mycelium in both compost and casing soil, typically becoming more noticeable at the interface between the compost and the casing mixture, as well as on the casing itself (Thakur et al., 1967; Sharma et al., 2007; Gea & Navarro, 2017). Over time, the mycelial growth thickens and transforms into whitish, solid, wrinkled, and irregular fungal masses, resembling small brains (calves' brains) or peeled walnuts (ascocarps of the fungus). Upon reaching maturity, these fungal masses become dry, reddish, and eventually disintegrate into a brown powdery mass that emits a chlorine-like odour (Thakur et al., 1967; Sharma et al., 2007; Gea & Navarro, 2017). The reported thermal death point for ascospores is 70 °C for 1 hour, while for mycelium, it is 45 °C for 30 minutes (Sharma, 1998).

The primary sources of infection include casing soil and residual ascospores/mycelium present in wooden trays from previous crop cycles (Sharma et al., 2007). The ascospores of the pathogen have the capability to endure for up to five years in soil and spent compost, while the mycelium can persist for approximately six months (Sharma, 1998), thus representing a significant reservoir of primary inoculum. The stage of infection and temperature are critical factors influencing the severity of the disease (Sharama et al., 2007). Ascospores of *Diehliomyces microsporus* often initiate germination concurrent with the development of *Agaricus* mycelium, as their germination is induced by the presence of actively proliferating mushroom mycelium (Gea & Navarro, 2017). Optimal germination occurs at temperatures exceeding 26–30 °C (Sharma, 1998). Following germination, the pathogen's mycelium thrives at lower temperatures; however, growth halts below 15–16 °C, which explains the rarity of *D. microsporus* occurrences during winter. Conversely, its prevalence increases during summer when maintaining temperatures below 20 °C within mushroom farms proves challenging (Gea & Navarro, 2017).

The composting process induces a temperature rise, activating any pathogen ascospores present in the soil. As a precaution, compost preparation should occur on a concrete floor and never on uncovered soil (Thakur et al., 1967; Sharma et al., 2007, Gea & Navarro, 2017). Temperatures exceeding 26–27 °C should be avoided during both the spawn run and after casing. Throughout the cropping phase,

temperatures should be maintained below 18 °C (Thakur et al., 1967; Sharma et al., 2007). Conducting a thorough cooking-out process, with compost temperatures maintained at 70 °C for 12 hours, is recommended at the conclusion of the crop cycle. This procedure can effectively eliminate the mycelium and spores of the pathogen present in the compost (Thakur et al., 1967; Sharma et al., 2007). At the conclusion of a crop affected by false truffle disease, it is recommended to treat wooden structures such as trays or side-boards of shelf-beds with a solution of sodium pentachlorophenolate. Additionally, air-drying the woodwork for 2–3 months may help to eradicate the pathogen (Sharma et al., 2007). *In vitro* evaluation of various botanicals by Sharma and Jarail (2000) revealed that water hyacinth (*Eichhornia crassipes*), neem cake, and neem leaves significantly inhibited *Diehliomyces microsporus*. Accordingly, incorporating these botanicals into the compost, particularly water hyacinth, led to a substantial reduction in the incidence of false truffle, regardless of the type of inoculum. Additionally, there was a notable increase in the yield of both *Agaricus bisporus* and *Agaricus bitorquis* (Sharma & Jarail, 2000).

4. Inky Caps

Ink caps, also known as ink weed, primarily affect compost and substrates used in mushroom cultivation (Sharma et al., 2007). This fungus depletes the nutrients in compost, impeding the spawn run and yields of cultivated mushrooms (Thakur et al., 1967; Sharma et al., 2007). This is caused by *Coprinus comatus* and *C. lagopus* (*Agaricales, Agaricaceae*) (Sharma et al., 2007; Aminuzzaman et al., 2022). Inky caps have been reported to be associated with the compost and substrate of *Agaricus bisporus*, *Pleurotus* spp., and *Volvariella volvacea* cultivations (Kaul et al., 1978; Garcha, 1984; Sohi, 1986; Sharma et al., 2007; Chinara & Mohapatra, 2014; Sharma et al., 2015; Chakraborty & Archana, 2021).

The presence of mushroom fruiting bodies, covered with scales at their young stages and featuring a long, cylindrical stalk and a small, thin, bell-shaped cap that is initially cream-colored but eventually transforms into a bluish-black, indicates that the compost has been affected by inky caps (Thakur et al., 1967; Sharma et al., 2007; Aminuzzaman et al., 2022). Several days after their appearance, ink caps undergo auto-digestion, decaying into a blackish, slimy mass. Sometimes, inky caps

are found growing in clusters within mushroom beds, featuring long, robust stems that frequently extend deep into the compost layer (Thakur et al., 1967). This also indicates the presence of excess ammonia in compost (Thakur et al., 1967; Sharma et al., 2007; Aminuzzaman et al., 2022). Ink caps appear in compost during the spawn run or in newly cased beds, or even outside manure piles during fermentation (Thakur et al., 1967; Sharma et al., 2007). Their mycelium closely resembles that of button mushrooms, posing a challenge in distinguishing it from the mycelium of cultivated mushrooms (Thakur et al., 1967).

Infection typically occurs through unpasteurized or partially pasteurized compost or casing soil, as well as through airborne sources. Ink caps thrive in compost with excessive amounts of nitrogen, often resulting from overuse of chicken manure, or an insufficient peak heating period during composting (Sharma et al., 2007). Inky caps serve as genuine indicator molds that thrive in conditions where nitrogen-containing constituents, such as ammonia, are insufficiently converted. Ink caps can also manifest symptoms if insufficient gypsum is added to the compost, if peak heating occurs at too low a temperature, or if the compost is excessively wet and lacks proper texture (Sharma et al., 2007). Ink caps can efficiently utilize free ammonium and are proficient in decomposing cellulose, as well as lipids and lignin. Their occurrence has also been reported when old straw is utilized in the composting (Thakur et al., 1967). The substantial quantities of spores released during the inking of ink caps can readily infect freshly prepared compost (Sharma et al., 2007).

Utilizing properly pasteurized compost and casing soil and avoiding over watering would be helpful to manage the problem. Removing young fruiting bodies of the weed fungus would prevent the further spread of inky caps (Thakur et al., 1967; Sharma et al., 2007). Compost trays should be cleared of ammonia. This can be achieved by re-pasteurizing the spawn trays at 60°C for 2 hours, followed by re-spawning and re-casing (Aminuzzaman et al., 2022).

5. Cinnamon Mold

Cinnamon mold is also referred to as brown mold (Sharma et al., 2007). It has been reported in countries such as India, South Africa, and the USA, particularly in association with the cultivation of *Agaricus bisporus* and *A. brunnescens* (Fergus, 1978; Coetzee & Eicker, 1990; Eicker & Greuning, 1991; Sharma et al., 2007; Yu et

al., 2024). This is caused by *Chromelosporium fulvum* (*Pezizales, Pezizaceae*) (Sharma et al., 2007).

The mold initially manifests as expansive, circular patches of white, aerial mycelium on the compost or casing surface. Within a few days, spores develop, causing the colour to shift from white to light yellow or pale golden brown (Sharma et al., 2007). As the spores mature, the colour transitions to golden brown or cinnamon, and the colony develops a granular texture. The fungus also produces many cup-shaped, fleshy fruit bodies on the mushroom beds (Thakur et al., 1967; Sharma et al., 2007).

Soil, casing mixtures, and damp wood serve as the primary sources of inoculum. Inoculum can be carried through open doors by wind or splashed from the floor during cleaning (Thakur et al., 1967; Sharma et al., 2007). The spores of the fungus are easily dispersed in the air. Factors such as over-pasteurized compost, overheated areas during spawn run, high moisture levels, and excessive ammonia in the compost create favourable conditions for the disease to develop (Thakur et al., 1967; Sharma et al., 2007).

Avoiding the complete sterilization of the casing soil with steam or formaldehyde, applying Carbendazim to newly cased beds, and ensuring proper moisture levels in the casing layer would be helpful to manage the disease (Thakur et al., 1967; Sharma et al., 2007).

6. Pink Mold

Pink mold is caused by *Trichothecium roseum* (*Hypocreales, Myrotheciomycetaceae*) (Sharma et al., 2007; Ghimire et al., 2021). *Trichothecium roseum* is an asexually reproducing, soil-borne fungus with an unknown sexual form. It is widely recognized for causing postharvest diseases in various fruits and vegetables worldwide (Summerbell et al., 2011; Harishchandra et al., 2023). Additionally, it has been reported as a fungicolous species on fungal fruiting bodies and sometimes displays mycoparasitic behaviour (Sun et al., 2019a; Yu et al., 2024). Pink mold in mushroom cultivation has been reported to cause yield losses of up to 90%, and in some cases, it can lead to complete crop failure (Sharma et al., 2007). This contamination has been mainly reported to be associated with the cultivation of *Agaricus* spp. (Ghimire et al., 2021).

At the early stages of contamination, this mold appears as a white growth on the casing soil, which gradually turns pink over time (Sohi & Upadhyaya, 1989; Singh & Singh, 2012; Ghimire et al., 2021).

The optimal conditions for the growth and development of the fungus are a temperature of 25 °C and a pH of 6.0. However, a combination of lower temperatures (15 °C) and a pH range of 4.0 to 6.5 promotes rapid sporulation (Domsch et al., 1980; Ghimire et al., 2021). Air serves as the primary pathway for fungal infection in mushroom cultivation (Domsch et al., 1980).

Mold can be controlled by spraying Thiram or Captan (0.04%) on the casing soil twice at 10-day intervals (Guleria & Seth, 1977; Sharma et al., 2007).

7. Lipstick mold

Lipstick mold is caused by *Sporendonema purpurascens* (*Gymnoascaceae, Onygenales*) and has been reported in association with the cultivation of *Agaricus bisporus* (Thakur et al., 1967; van Greuning & Eicker, 1991; Sharma et al., 2007; Largeteau & Savoie, 2010; Yu et al., 2024).

This mold contamination initially appears in the spawned compost as a white, crystalline-like growth difficult to distinguish from the spawn (Thakur et al., 1967; Sharma et al., 2007). As the mold's spores mature, the colour changes from white to pink, cherry red, and eventually to a dull orange or buff. The white mycelial growth is more prominent in loose areas of the casing and can easily colonize well-conditioned compost (Thakur et al., 1967; Sharma et al., 2007).

The primary sources of inoculum are casing mixtures, soil, and spent compost. The mold is further spread by water splashes or by pickers (Thakur et al., 1967; Sharma et al., 2007). It has also been linked to the use of chicken manure in compost formulations, as the litter is known to harbour the fungus (Thakur et al., 1967, Sharma et al., 2007).

Maintaining good hygiene is crucial for controlling mold. Proper pasteurization and conditioning of the compost are effective in eliminating the pathogen (Sharma et al., 2007).

8. Yellow mold

Yellow mold is known to be caused by *Myceliophthora lutea* (*Sordariales, Chaetomiaceae*), *Hypomyces chrysospermus* (*Hypocreales, Hypocreaceae*),

Sepedonium maheshwarianum (*Hypocreales, Hypocreaceae*), and *S. niveum*, primarily associated with the cultivation of *Agaricus bisporus* (Kamal et al., 2000; Sharma et al., 2007; Largeteau & Savoie, 2010; Singh & Singh, 2012; Yu et al., 2024).

This mold is primarily observed in compost, where it initially appears white and gradually turns yellow or tan as it matures (Sharma et al., 2007; Singh & Singh, 2012). It is typically found in the lower layers of the compost or at the bottom of cropping bags. Distortions in fruit bodies occur, likely due to the production of volatile substances or toxins by the mold (Sharma et al., 2007; Singh & Singh, 2012). These toxins inhibit the growth of the spawn, eventually leading to the disappearance of mushroom mycelium from the compost (Sharma et al., 2007; Singh & Singh, 2012).

The primary sources of inoculum are likely soil, spent compost, air, or improperly sterilized wooden trays (Sharma et al., 2007; Singh & Singh, 2012). The thick-walled chlamydospores are heat-resistant. Therefore, the fungus is capable of surviving peak heat conditions in this spore form. Spores can be dispersed by air currents (Sharma et al., 2007; Singh & Singh, 2012). Higher nitrogen content, particularly from chicken manure, has been reported to favour mold development (Vijay et al., 1993). The presence of mold in the lower layers of the compost has been associated with increased moisture (Sharma et al., 2007; Singh & Singh, 2012).

Ensuring thorough pasteurization of compost and using air filters during the spawning and spawn run phases can help minimize the risk of spore contamination (Sharma et al., 2007; Singh & Singh, 2012). Adding 0.5% Carbendazim to the compost is an effective method for controlling the mold (Vijay et al., 1993). Sharma et al. (2019) reported that extracts from *Cannabis sativa* could be utilized to control yellow mold due to their demonstrated antifungal properties against the specific molds.

9. Olive Green Mold

Olive green mold is caused by *Chaetomium globosum* (*Sordariales, Chaetomiaceae*), which has been primarily documented in association with the cultivation of *Agaricus bisporus* (Sharma et al., 2007; Singh & Singh, 2012; Yu et al., 2024).

The initial signs of mold include an inconspicuous, greyish-white fine mycelium within the compost or a delicate aerial growth on the compost surface, which appears approximately 10 days after spawning (Sharma et al., 2007; Singh & Singh, 2012). Often, the initial growth of the spawn is delayed and diminished. By the later stages of the spawn run, fruiting structures of *Chaetomium globosum* resembling grey-green cockleburs, approximately 1/16 inch in diameter, begin to form on straw in isolated areas of the affected compost, which also develops a musty odour (Sharma et al., 2007; Singh & Singh, 2012).

The primary sources of infection are compost and casing soil (Sharma et al., 2007; Singh & Singh, 2012). The ascospores of *Chaetomium globosum* can be dispersed through air currents, clothing, and other materials used in the farm. This mold can survive in environments with high ammonia levels, and also the growth of *C. globosum* is enhanced by the alkalinity of the compost (Sharma et al., 2007; Singh & Singh, 2012).

Olive green mold can be prevented through effective composting in Phase I and by controlling environmental conditions during Phase II (Singh & Singh, 2012). Controlling peak heat conditions is crucial to prevent anaerobic conditions. Ensuring adequate time for peak heating and a sufficient supply of fresh air during pasteurization would also be helpful in controlling mold growth. Temperatures above 60 °C should be avoided for extended periods (Sharma et al., 2007; Singh & Singh, 2012). Spraying with 0.2% Zineb (Dithane Z-78) is recommended for the effective control of mold spread (Sohi, 1986).

4.4 Discussion

4.4.1 Fungal Diseases/Competitor Molds: A Major Challenge for Mushroom Growers

Mushroom cultivation presents a promising opportunity as a profitable agribusiness (Okuda, 2022; Bijla & Sharma, 2023) and has become prolific in China (Ling et al., 2025). It addresses modern-day concerns, promotes efficient resource use, fosters a circular economy, creates jobs, enhances sustainability, builds resilience to

unpredictable weather, and improves nutritional security (Okuda, 2022, Bijla & Sharma, 2023, Jayaraman et al., 2024).

Fungal diseases and competitor molds pose a significant obstacle to worldwide mushroom cultivation (Sharma et al., 2007; Sun et al., 2019a; Chakraborty & Archana, 2021; Gea et al., 2021; Ghimire et al., 2021; Yu et al., 2024). The competitor molds negatively impact the spawn run, while pathogens target the fruiting bodies at different stages of crop development, resulting in specific disease symptoms (Sharma et al., 2007). Based on existing literature, a generalized disease cycle for fungal pathogens affecting mushroom cultivation is illustrated in Figure 4.28.

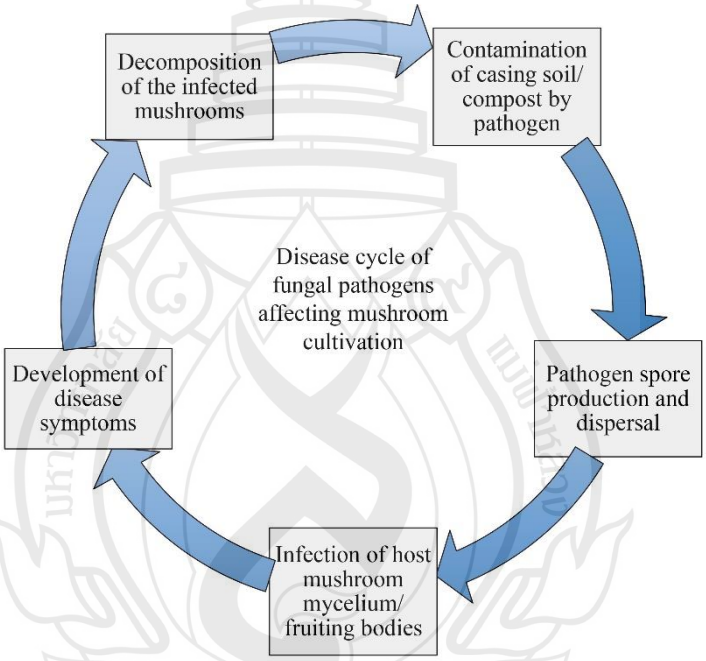


Figure 4.28 Generalized disease cycle for fungal pathogens affecting mushroom cultivation

Uncontrolled fungal diseases/competitor molds in mushroom cultivation led to growth retardation, deformities, and decay. Results show significant yield losses and reduced product quality (Sun et al., 2019b; Gajanayake et al., 2021a, 2021b; Yu et al., 2024). This results in costly control measures, threatening the sustainability of the industry, especially for small-scale farmers. The economic impact extends beyond yield loss, with increased expenses on fungicides, labour, and substrate replacement

(Fletcher & Gaze, 2008). For large producers, these costs reduce profitability, while smaller growers face potential financial devastation. Additionally, frequent chemical treatments raise concerns for both environmental and human health, further challenging long-term sustainability (Potočnik et al., 2015; Ahmad et al., 2024).

4.4.2 Disease Detection, Identification of Pathogens, and Host-pathogen Interactions

Early detection of disease outbreaks is crucial in preventing most economic losses. Regular and careful inspection of mushroom bags or beds helps to recognize mushroom diseases at an early stage (Okigbo & Anuagasi, 2021). Typically, monitoring the infection status of growing mushrooms relies on visual inspection. Advancements in technology have led to the proposal of automated fungal disease detection systems for mushroom cultivation (Jareanpon et al., 2024; Sangeetha et al., 2024). The application of machine learning, image processing, and sensor technologies can facilitate the early identification of fungal diseases (Jareanpon et al., 2024; Sangeetha et al., 2024). These innovations enhance the accuracy and speed of disease detection. This reduces reliance on manual inspections and enables the implementation of timely management strategies (Jareanpon et al., 2024). These systems could significantly reduce losses from fungal pathogens and improve production efficiency. However, further research is necessary to refine these technologies and ensure accessibility for small-scale farmers.

Once a disease outbreak is detected, accurate identification of the responsible pathogenic species is crucial for determining the suitable control and management strategies (Jayawardena et al., 2021). In the past, the classification of pathogenic taxa was largely based on morphological traits. However, this approach is unreliable because distinct species can have overlapping morphological characteristics (Jayawardena et al., 2021). With the introduction of the phylogenetic species concept, based on molecular phylogenetic reconstructions, fungal pathogens were primarily identified through sequence similarity of the internal transcribed spacer (ITS) gene region, often lacking substantial morphological evidence (Choi et al., 2010; Sun et al., 2023). Studies have confirmed that ITS and small-subunit ribosomal RNA (SSU) datasets alone are inadequate to provide optimal resolution in certain *Sordariomycetes* (Hyde et al., 2020; Chethana et al., 2021). Whenever possible, the identification of

pathogenic species should rely on a polyphasic approach, incorporating morphology, phylogeny, ecology, and pathogenicity (Jayawardena et al., 2021).

Mushroom pathogens interact with their hosts through a combination of specific molecular recognition, enzymatic degradation, and mechanical pressure (Berendsen et al., 2010; Zhang et al., 2017a). The extent and nature of these interactions can vary depending on the specific pathogen involved. The initial attachment of pathogens to mushroom hyphae may involve both specific and nonspecific interactions between surface molecules of both fungi (Calonje et al., 1997, 2000; Dragt et al., 1996; Shamshad et al., 2009; Berendsen et al., 2010; Zhang et al., 2017a). Once attached, pathogens can grow both inter- and intracellularly, utilizing lytic enzymes such as chitinase and pectinase to weaken the host cell walls (Sharma et al., 2015). Mechanical pressure from structures like appressoria also facilitates the pathogen's invasion of the host (Dragt et al., 1996; Calonje et al., 1997). These combined mechanisms enable the pathogens to establish and propagate within the mushroom tissue.

Transcriptomic and metabolomic profile analyses provide a comprehensive approach to understanding the complex dynamics of mushroom-pathogen interactions (Yang et al., 2023; Zhang et al., 2024). These analyses reveal the defense responses via key genetic and metabolic pathways in both hosts and pathogens (Wang et al., 2023). It would provide new opportunities for targeted disease control strategies, including the development of resistant strains, early detection systems, and novel antifungal treatments, thereby improving yields and sustainability in mushroom cultivation (Gea et al., 2021; Wang et al., 2023; Tarafder et al., 2024b; Zhang et al., 2024).

4.4.3 Disease Management

The management of mushroom diseases predominantly relies on integrated control programs (Gea & Navarro, 2017; Pandey et al., 2025). Improved hygiene practices, varietal selection, vector management, and the use of phytosanitary products, especially fungicides, are some of the economic measures to prevent infection (Gea & Navarro, 2017; Ghimire et al., 2021). The rising demand for organic products, coupled with the emergence of resistant pathogenic fungal strains, highlights the need for innovative and sustainable crop protection strategies (Grogan,

2008; Carrasco et al., 2017b). The wide variability in fungicides with different modes of action underscores the need of research to identify complementary active substances (Gea et al., 2021). Such treatments can help to prevent over-reliance on a single product and reduce the risk of emerging resistant pathogenic strains (Gea et al., 2021). To reduce dependence on fungicides, environmentally friendly alternatives, such as aromatic plant extracts, have been explored. Unfortunately, their efficacy in controlling fungal diseases in mushroom crops has been inconsistent, with occasional negative impacts on the host itself (Gea et al., 2014; Geösel et al., 2014; Mehrparvar et al., 2016). Compost teas derived from various agricultural wastes can also serve as effective alternatives for controlling fungal diseases, due to the high activity of the microbial communities present in these solutions (Gea et al., 2021). Biocontrol using selected bacterial strains also offers a promising green alternative (Carrasco & Preston, 2020). Notably, many of these strains have demonstrated effective biocontrol activity against parasites of *Agaricus bisporus* (Berendsen et al., 2012; Kosanović et al., 2013; Beyer et al., 2016; Milijašević-Marčić et al., 2017). However, the cost-effectiveness of alternative treatments to chemical fungicides must be considered. Both types of preventive treatments should coexist in the short and medium term (Gea et al., 2021).

4.4.4 Future Directions and Research Gaps

While significant progress has been made in identifying and managing fungal diseases, several research gaps remain. With the large number of new mushroom species being cultivated in China (Ling et al., 2025), it is likely that new diseases will emerge. There is a need for continued development of resistant mushroom strains through advanced breeding techniques informed by genomic and transcriptomic data (Tarafder et al., 2024b). Moreover, future research should focus on refining automated detection systems to make them more accessible and cost-effective for a broader range of growers, particularly those in low-resource settings. Emerging biocontrol agents and natural antifungal compounds also represent promising avenues for reducing chemical dependence in disease management. Continued exploration of phylogenetic relationships among fungal pathogens could provide new insights into pathogen evolution and adaptation, potentially revealing weaknesses that can be targeted for more effective control measures. By integrating modern technologies

such as transcriptomics, metabolomics, and automated detection systems, growers and researchers can collaborate to develop more effective and sustainable strategies for managing these diseases. The mushroom industry must continue to evolve in response to the challenge of fungal contamination. It should find a balance between achieving high production yields and reducing losses from fungal diseases/competitor molds.

CHAPTER 5

DIGITAL DOCUMENTATION OF FUNGICOLOUS FUNGI

5.1 Introduction

Fungicolous fungi are a widespread group of organisms that belong to many ecological categories found in both, terrestrial and aquatic habitats (Gams et al., 2004; Sun et al., 2019a; Hyde et al., 2023). They are the fungi consistently having associations between different lineages across the fungal kingdom as saprotrophs, mycoparasites or neutrals (Gams et al., 2004; Põldmaa, 2011; Lin et al., 2016; Sun et al., 2019a; Hyde et al., 2023).

According to the estimation of global fungal diversity by Niskanen et al. (2023), 2 to 3 million fungal species exist on Earth, although much work is required before this figure can be considered accurate (Hyde et al., 2024a). So far, about 140,000 fungal taxa have been described (Hyde et al., 2024b) and around 1500 are fungicolous taxa (Sun et al., 2019a). When compared with the global fungal diversity, the discovered number of fungicolous species is perhaps low (Sun et al., 2019a; Maurice et al., 2021).

The first studies on fungicolous fungi were conducted around two centuries ago (Von Esenbeck, 1817; Fries & Nordholm, 1817; Willdenow et al., 1833). The first ascomycete discovered to be fungicolous was *Cladobotryum agaricina* on *Agaricus* species (Fries & Nordholm, 1817). *Asterophora agaricoides* on a fruiting body of *Agaricus* sp. was the first discovered fungicolous basidiomycete (Fries & Nordholm, 1817). Since the 1980s, there has been considerable progress related to the taxonomy of fungicolous fungi with many discoveries on asexual–sexual morph connections in the *Hypocreales*, and the discovery of novel mycoparasitic Heterobasidiomycetes (Reid, 1990; Helfer, 1991; Põldmaa & Samuels, 1999; Gams et al., 2004). Krings et al. (2011) reported the first convincing fossil evidence for mycoparasitism in sporocarps.

Most earlier studies on fungicolous taxa commonly used culture-dependent approaches and morphology-based identification (Pacioni et al., 2007). However, since the 2000s accurate identification of fungicolous taxa has been based on both morphological and molecular evidence such as internal transcribed spacer (ITS), partial 28S large subunit (LSU), partial fragments of the calmodulin (*cal*), partial 18S small subunit (*ssu*), partial beta-tubulin (*tub*2), translation elongation factor (*tef*), DNA directed RNA polymerase II (*rpb*2) sequence data, genomic analyses and transcriptome analyses (Liu et al., 2020; Gajanayake et al., 2021a, 2023a; Yu et al., 2024). Recent studies conducted with culture-independent approaches, such as next-generation sequencing and DNA metabarcoding based on high-throughput sequencing of amplified markers have shown fungal fruiting bodies contain many more fungicolous taxa than expected (Leonardi et al., 2018; Maurice et al., 2021). Therefore, the combination of both culture-dependent and culture-independent approaches may reveal a greater diversity of fungicolous taxa in the future (Sun et al., 2019a; Maurice et al., 2021).

The available information on fungicolous fungi is highly fragmented and dispersed across various sources, including scattered publications, databases, and regional checklists. This fragmentation hinders accessibility and comparative research. Therefore, there is a pressing need to consolidate and digitize the existing data on fungicolous fungi to facilitate a clearer understanding of their taxonomy, biology, and ecological interactions. Therefore, to compile the dispersed published information on fungicolous fungi, a webpage (https://www.fungicolousfungi.org/) has been established. Moreover, this study consolidated knowledge on 150 genera that include fungicolous fungi (*Ascomycota*: 108 genera, *Basidiomycota*: 37 genera, *Mucoromycota*: 5 genera), providing generic notes and morphological illustrations. This provides a robust foundation for understanding the taxonomic diversity of fungicolous fungi, improves the identification accuracy, and ensure proper documentation. This in turn, will aid in assessing their ecological significance, identifying research gaps, and outlining future directions for the study of this group of organisms.

5.2 Need of a Database for Fungicolous Fungi

To date, various types of research related to fungicolous fungi such as, biochemical innovation, fungal host interactions, pathogenic mechanisms and species diversity have been conducted based on both morphological and molecular evidence (Lin et al., 2016; Maurice et al., 2021; Yu et al., 2024). Accordingly, fungicolous fungi represent a variety of lineages within the fungal tree of life, although a significant portion has been poorly represented with reference sequences in databases (Maurice et al., 2021). Further research combining the existing DNA sequence data with morphological characters is expected to provide important information concerning ecology, distribution, and fungal systematics. Conserving scientific records and dissemination of knowledge on fungal morphology, taxonomy and diversity is a valuable process for mycology and also for other fields of biological studies (Lange, 2010; Raghoonundon et al., 2021; Phonemany et al., 2022; Hyde et al., 2023; Hyde et al., 2024b).

Therefore, developing a database to gather all of the scattered knowledge on fungicolous fungi would be a strong foundation to identify research gaps, and future perspectives in mycology. With the improvement of modern technology, all the information can be made available on an online platform, which would be more practical and flexible for researchers worldwide, both now and in the future (Hyde et al., 2023). Therefore, the web page (https://fungicolousfungi.org/), aims to provide an up-to-date outline and all relevant information on fungicolous fungi in a single platform.

5.3 The Web Page on Fungicolous Fungi

This (https://fungicolousfungi.org/) is a freely accessible, user-friendly interface dedicated for compiling the scattered published knowledge on taxonomy, phylogeny, ecology, host range, distribution and industrial relevance of fungicolous fungi. Other online databases, such as “Fungalpedia” (Hyde et al., 2023), “Outline of

Fungi" (Wijayawardene et al., 2020), "Faces of Fungi" (Jayasiri et al., 2015) will be linked to the new website to expand the related information on fungicolous taxa.

5.3.1 Construction of the Webpage

The taxonomic information for known fungicolous species is gathered from reliable sources. Next, fungicolous taxa from various lineages within the fungal kingdom are listed on the website. Subsequently, entries for these genera/taxa are uploaded and will be continuously updated with the latest available information. Each entry includes the Index Fungorum, FacesofFungi, MycoBank and/or herbaria numbers. The database will be continuously updated as new information related to fungicolous taxa becomes available. Mycological experts have been assigned as curators to share their knowledge and suggestions as well as to monitor the web page (Table 5.1).

Table 5.1 Curators for the webpage

Position	Name	Contact details
Head	Kevin D. Hyde	kdhyde3@gmail.com
curators	Ruvishika Shehali Jayawardena	ruvishika.jay@mfu.ac.th
Managing curator	Achala Jeevani Gajanayake	achalajeevani@gmail.com
Curators	Feng-Ming Yu	fm_yu2018@163.com
	Sun Jing-Zu	sunjz@im.ac.cn
	Thatsanee Luangharn	thatsanee.lua@mfu.ac.th
	Naritsada Thongklang	naritsada.tho@mfu.ac.th

5.3.2 Database Interface and Visualization

The opening webpage comprises the following main features and functions:

Home: Provides a brief introduction to the database (Figure 5.1).

Introduction: Provides insight to fungicolous fungi.

Outline: Gives an overall idea of the taxonomic classification to which the fungicolous taxa belong. Clicking on this feature unfolds the main phyla to which fungicolous taxa belong and under each phylum, the species are

arranged according to their taxonomic ranks. The genus/species names direct to the relevant information (Figure 5.2).

Diseases: Provides a list of fungal diseases caused by fungicolous taxa on mushrooms together with literature references.

Archives: Summarizes the taxonomic classification of the fungicolous taxa from order to species level and directs to read more about the fungicolous taxa (Figure 5.3).

Curators: Provides a list and contact details of the curators of the webpage.

Citation: Includes recommended citation of the web page.

News: Communicates important events and information related to mycology.

Contact: Provides contact details of the website and offers interested users the opportunity to contribute their comments and suggestions.

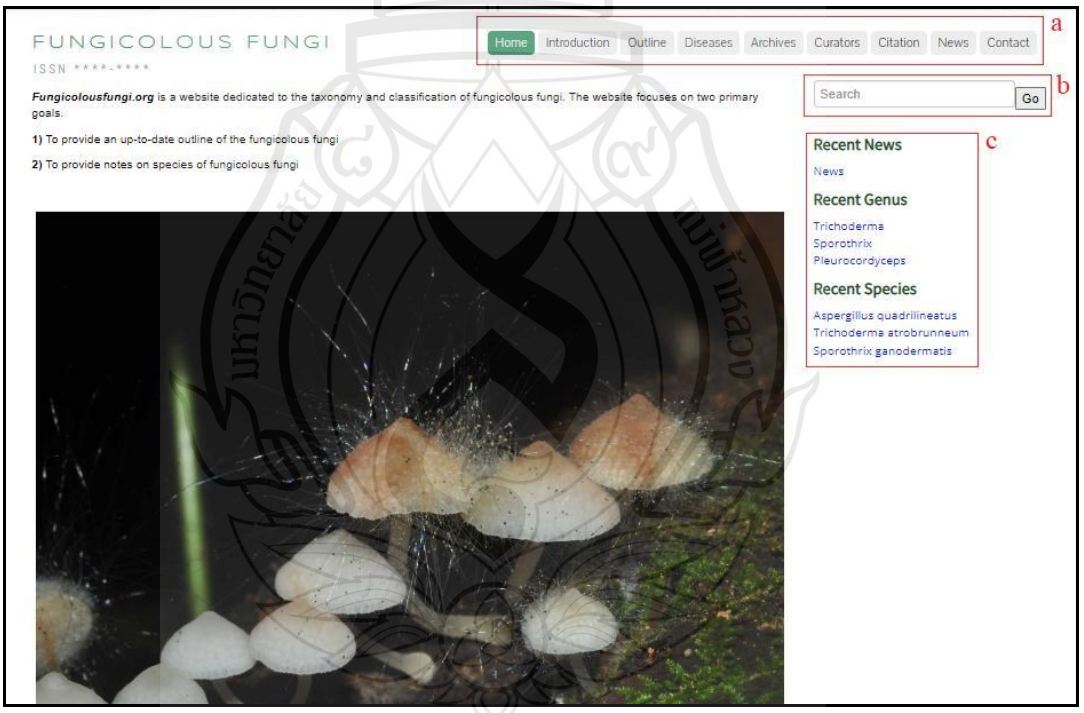


Figure 5.1 View of the Fungicolous Fungi web homepage

Figure 5.1, a Tabs. b Search box. c Recently updated information.

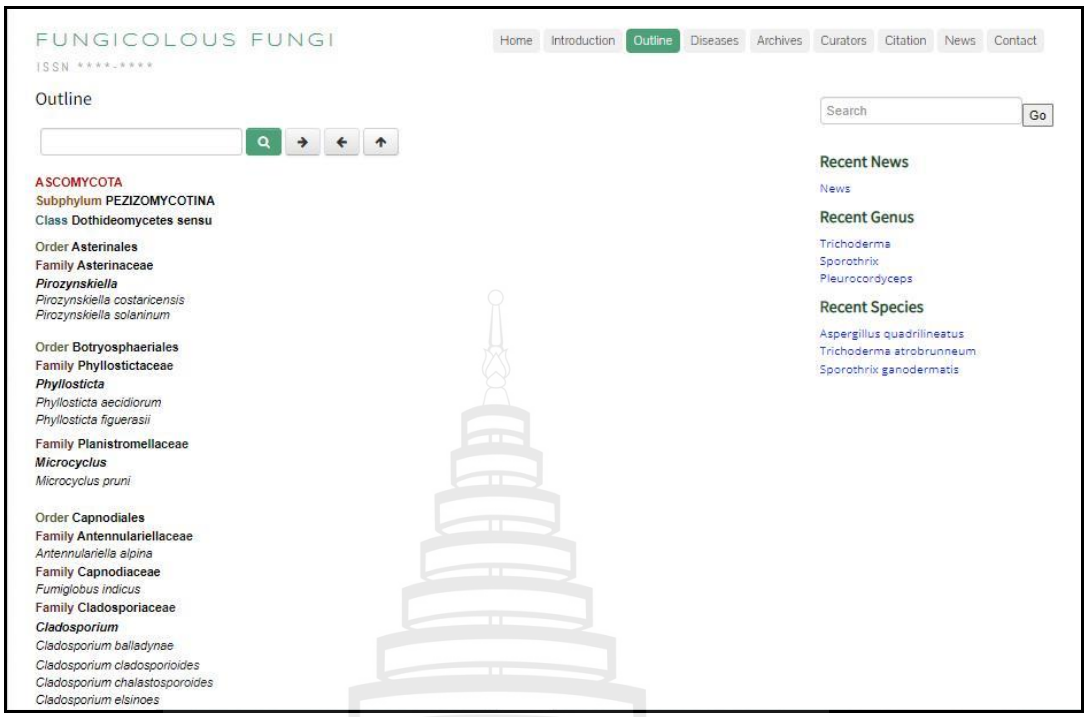


Figure 5.2 Outline classification of fungiolous fungi

Figure 5.2, Outline of fungicolous fungi is based on Sun et al. (2019a) which will be updated as new information becomes available.

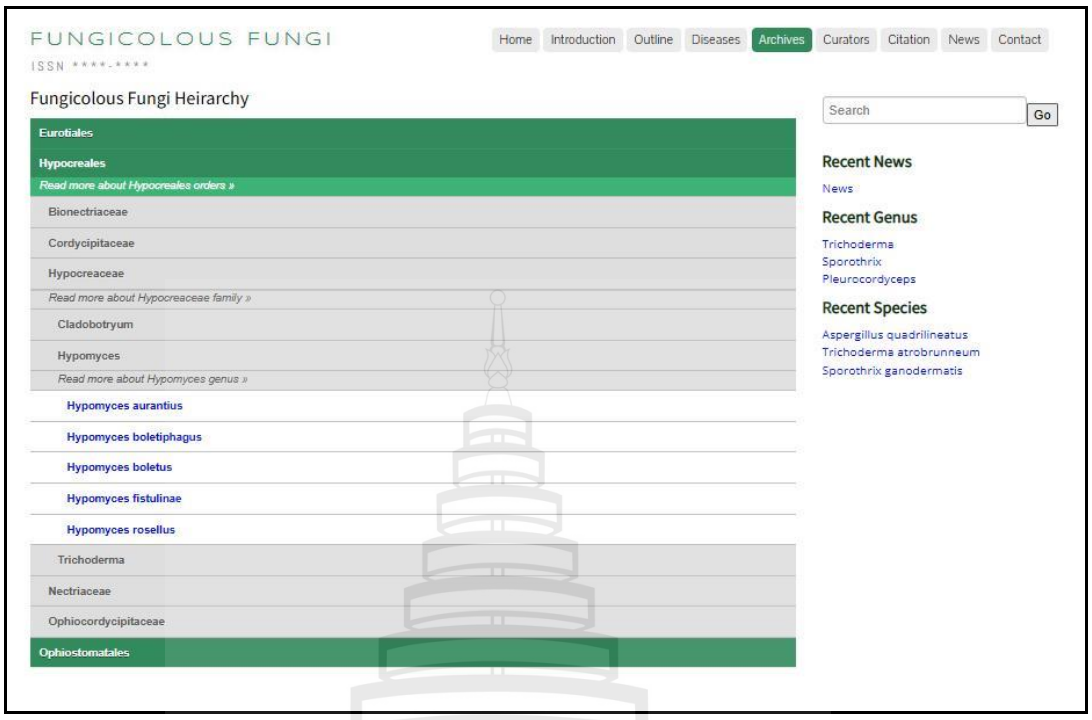


Figure 5.3 View of the "Archives"

Figure 5.3, This reveals the taxonomic classification of fungicolous taxa.

5.4 Notes and Illustrations for Fungicolous Genera

This study consolidates knowledge on 150 genera that include fungicolous fungi (*Ascomycota*: 108 genera, *Basidiomycota*: 37 genera, *Mucoromycota*: 5 genera), providing generic notes and morphological illustrations.

5.4.1 Outline of the Genera

The notes are arranged as in the Outline of Fungi and fungus-like organisms (Hyde 2024). For synonyms for each genus, see Species Fungorum (2025).

Phylum *Ascomycota* Caval.-Sm.

Subphylum *Pezizomycotina* O.E. Erikss. & Winka

Class *Dothideomycetes* O.E. Erikss & Winka

Subclass *Dothideomycetidae* P.M. Kirk, P.F. Cannon, J.C. David & Stalpers ex C.L. Schoch, Spatafora, Crous & Shoemaker

Cladosporiales Abdollahz. & Crous

Cladosporiaceae Chalm. & R.G. Archibald

1. ***Cladosporium*** Link

Mycosphaerellales (Nannf.) P.F. Cannon

Mycosphaerellaceae Lindau

2. ***Ramularia*** Unger

Teratosphaeriaceae Crous & U. Braun

3. ***Acrodontium*** de Hoog

Myriangiales Starbäck

Myriangiaceae Nyl.

4. ***Uleomyces*** Henn.

Subclass *Pleosporomycetidae* C.L. Schoch, Spatafora, Crous & Shoemaker

Pleosporales Luttr. ex M.E. Barr

Cucurbitariaceae G. Winter

5. ***Parafenestella*** Jaklitsch & Voglmayr

Didymosphaeriaceae Munk

6. ***Letendraea*** Sacc.

7. ***Pseudotrichia*** Kirschst.

Leptosphaeriaceae M.E. Barr

8. ***Sphaerellopsis*** Cooke

Phaeosphaeriaceae M.E. Barr

9. ***Ampelomyces*** Ces. ex Schltdl.

10. ***Eudarluca*** Speg.

Roussoellaceae Jian K. Liu, Phook., D.Q. Dai & K.D. Hyde

11. ***Immotthia*** M.E. Barr

Dothideomycetes* orders *incertae sedis

Acrospermales Minter, Peredo & A.T. Watson

Acrospermaceae Fuckel

12. ***Pseudovirgaria*** H.D. Shin, U. Braun, Arzanlou & Crous

Dothideomycetes* families *incertae sedis

Paranectriellaceae Boonmee & K.D. Hyde

13. ***Paranectriella*** (Henn. ex Sacc. & D. Sacc.) Magnus

Trichothyriaceae Theiss.

14. ***Pachythyrium*** G. Arnaud ex Spooner & P.M. Kirk

Dothideomycetes **genera** ***incertae sedis***

15. ***Acanthostigmella*** Höhn.

16. ***Catulus*** Malloch & Rogerson

17. ***Chaetocrea*** Syd.

18. ***Chionomyces*** Deighton & Piroz.

19. ***Malacaria*** Syd.

20. ***Phragmogibbera*** Samuels & Rogerson

Class ***Eurotiomycetes*** O.E. Erikss. & Winka

Subclass ***Chaetothyriomycetidae*** Doweld

Chaetothyriales M.E. Barr

Herpotrichiellaceae Munk

21. ***Capronia*** Sacc.

Class ***Leotiomycetes*** O.E. Erikss. & Winka

Helotiales Nannf. ex Korf & Lizoň

Cordieritidaceae Sacc.

22. ***Unguiculariopsis*** Rehm

Hyphodiscaceae Ekanayaka & K.D. Hyde

23. ***Hyphodiscus*** Kirschst.

Helotiales **genera** ***incertae sedis***

24. ***Scytalidium*** Pesante

Phacidiales C.E. Bessey

Helicogoniaceae Baral

25. ***Eleutheromyces*** Fuckel

26. ***Gelatinipulvinella*** Hosoya & Y. Otani

27. ***Helicogonium*** W.L. White

Leotiomycetes **genera** ***incertae sedis***

28. ***Gelatinopsis*** Rambold & Triebel

Class ***Lichinomycetes*** V. Reeb, Lutzoni & Cl. Roux

Coniocybales M. Prieto & Wedin

Coniocybaceae Rchb.

29. ***Chaenotricha*** Suija, McMullin & P. Lõhmus

Class *Sordariomycetes* O.E. Erikss. & Winka

Subclass *Diaporthomycetidae* Senan., Maharachch. & K.D. Hyde

Ophiostomatales Benny & Kimbr.

Ophiostomataceae Nannf.

30. ***Sporothrix*** Hektoen & C.F. Perkins

Diaporthomycetidae* families *incertae sedis

Woswasiaceae H. Zhang, K.D. Hyde & Maharachch.

31. ***Woswasia*** Jaklitsch, Réblová & Voglmayr

Subclass *Hypocreomycetidae* O.E. Erikss. & Winka

Coronophorales Nannf.

Ceratostomataceae G. Winter

32. ***Scopinella*** Lév.

33. ***Syspastospora*** P.F. Cannon & D. Hawksw.

Glomerellales Chadef. ex Réblová, W. Gams & Seifert

Ascocodinaceae D.F. Bao, K.D. Hyde & Z.L. Luo

34. ***Ascocodinaea*** Samuels, Cand. & Magni

Hypocreales Lindau

Albomorchellophilaceae F.M. Yu, K.D. Hyde & Q. Zhao

35. ***Albomorchellophila*** F.M. Yu, K.D. Hyde & Q. Zhao

Bionectriaceae Samuels & Rossman

36. ***Clonostachys*** Corda

37. ***Nectriopsis*** Maire

Calcarisporiaceae Jing Z. Sun, X.Z. Liu & K.D. Hyde

38. ***Calcarisporium*** Preuss

Clavicipitaceae (Lindau) Earle ex Rogerson

39. ***Epicrea*** Petr.

40. ***Neobarya*** Lowen

41. ***Tyrannicordyceps*** Kepler & Spatafora

Cordycipitaceae Kreisel ex G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora

42. ***Corniculantispora*** Khons., Thanakitp. & Luangsa-ard

43. ***Matutinistella*** F.A. Custódio & O.L. Pereira

44. ***Niveomyces*** J.P.M. Araújo & de Bekker

45. ***Pseudoniveomyces*** Tasan., Noisrip. & Kobmoo

46. ***Zarea*** Khons., Thanakitp. & Luangsa-ard

Flammocladiellaceae Crous, L. Lombard & R.K. Schumach.

47. ***Flammocladiella*** Crous, L. Lombard & R.K. Schumach.

Hypocreaceae **De Not.**

48. ***Hypocreopsis*** P. Karst.

49. ***Hypomyces*** (Fr.) Tul. & C. Tul.

50. ***Mycogone*** Link

51. ***Protocrea*** Petch

52. ***Sphaerostilbella*** (Henn.) Sacc. & D. Sacc.

53. ***Sporophagomyces*** K. Põldmaa & Samuels

54. ***Trichoderma*** Pers.

Myrotheciomycetaceae Crous

55. ***Trichothecium*** Link

Nectriaceae Tul. & C. Tul.

56. ***Cosmospora*** Rabenh.

57. ***Fusarium*** Link

58. ***Fusicolla*** Bonord.

59. ***Macroconia*** (Wollenw.) Gräfenhan, Seifert & Schroers

60. ***Nectria*** (Fr.) Fr.

61. ***Pseudocosmospora*** C.S. Herrera & P. Chaverri

62. ***Stylonectria*** Höhn.

63. ***Thyronectria*** Sacc.

Niessliaceae Kirschst.

64. ***Circinoniesslia*** Samuels & M.E. Barr

Ophiocordycipitaceae G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora

65. ***Tolypocladium*** W. Gams

66. ***Torrubiellomyces*** J.P.M. Araújo & de Bekker

Pseudodiploösporaceae Jing Z. Sun, X.Z. Liu & H.W. Liu

67. ***Pseudodiploöspora*** Jing Z. Sun, Xing Z. Liu & H.W.

Sarocladiaceae L. Lombard

68. ***Sarocladium*** W. Gams & D. Hawksw.

Tilachlidiaceae Lombard & Crous

69. ***Tilachlidium*** Preuss

Subclass *Sordariomycetidae* O.E. Erikss. & Winka

Cephalothecales Maharachch. & K.D. Hyde

Cephalothecaceae Höhn.

70. ***Albertiniella*** Kirschst.

Chaetosphaeriales Huhndorf, A.N. Mill. & F.A. Fernández

Helminthosphaeriaceae Samuels, Cand. & Magni.

71. ***Helminthosphaeria*** Fuckel

Sordariomycetidae* genera *incertae sedis

72. ***Phaeotrichosphaeria*** Sivan.

Subclass *Xylariomycetidae* O.E. Erikss & Winka

Xylariales Nannf.

Hansfordiaceae Crous

73. ***Hansfordia*** S. Hughes

Hypoxylaceae DC.

74. ***Chlorostroma*** A.N. Mill., Lar.N. Vassiljeva & J.D. Rogers

Sordariomycetes* genera *incertae sedis

75. ***Immersisphaeria*** Jaklitsch

76. ***Scotiosphaeria*** Sivan.

Ascomycota* families *incertae sedis

Eoterfeziaceae G.F. Atk.

77. ***Eoterfezia*** G.F. Atk.

Ascomycota* genera *incertae sedis

78. ***Annellodochium*** Deighton

79. ***Atractilina*** Dearn. & Barthol.

80. ***Colletoconis*** de Hoog & Aa

81. ***Ctenosporium*** R. Kirschner

82. ***Dennisographium*** Rifai

83. ***Denticularia*** Deighton

84. ***Didymopsis*** Sacc. & Marchal

85. ***Digitopodium*** U. Braun, Heuchert & K. Schub.

86. ***Domingoella*** Petr. & Cif.
87. ***Engelhardtiella*** A. Funk
88. ***Entropezites*** Poinar & R. Buckley
89. ***Eriocercospora*** Deighton
90. ***Gonatobotryum*** Sacc.
91. ***Hoornsmania*** Crous
92. ***Irpicomyces*** Deighton
93. ***Laterispora*** Uecker, W.A. Ayers & P.B. Adams
94. ***Paraphaeoisaria*** de Hoog & Morgan-Jones
95. ***Redbia*** Deighton & Piroz.
96. ***Rhinotrichella*** G. Arnaud ex de Hoog
97. ***Spermosporella*** Deighton
98. ***Sphaerulomyces*** Marvanová
99. ***Spiropes*** Cif.
100. ***Stellospora*** Alcorn & B. Sutton
101. ***Stenospora*** Deighton
102. ***Tetraposporium*** S. Hughes
103. ***Trichoconis*** Clem.
104. ***Tuberculispora*** Deighton & Piroz.
105. ***Tympanosporium*** W. Gams
106. ***Veracruzomyces*** Mercado, Guarro, Heredia & J. Mena
107. ***Zakatoshia*** B. Sutton

Subphylum *Saccharomycotina* O.E. Erikss. & Winka

Class *Saccharomycetes* O.E. Erikss. & Winka

Saccharomycetales Kudryavtsev

Saccharomycetales* genera *incertae sedis

108. ***Phialoascus*** Redhead & Malloch

Phylum *Basidiomycota* R.T. Moore

Subphylum *Agaricomycotina* Doweld

Class *Agaricomycetes* Doweld

Order *Agaricales* Underw.

Suborder *Agaricineae* Fr.

Squamanitaceae Jülich

109. ***Squamanita*** Imbach

Suborder *Tricholomatineae* Aime, Dentinger & Gaya

Lyophyllaceae Jülich

110. ***Asterophora*** Ditmar

Sebacinales M. Weiss, Selosse, Rexer, A. Urb. & Oberw.

Serendipitaceae M. Weiss, Waller, A. Zuccaro & Selosse

111. ***Serendipita*** P. Roberts

Class *Tremellomycetes* Doweld

Filobasidiales Jülich

Filobasidiaceae L.S. Olive

112. ***Syzygospora*** G.W. Martin

Tremellales Fr.

Naemateliaceae X. Z. Liu, F. Y. Bai, M. Groenew. & Boekhout

113. ***Naematelia*** Fr.

Phaeotremellaceae A.M. Yurkov & Boekhout

114. ***Phaeotremella*** Rea

Phragmoxenidiaceae Oberw. & R. Bauer

115. ***Phragmoxenidium*** Oberw.

Sirobasidiaceae Lindau

116. ***Sirobasidium*** Lagerh. & Pat.

Tremellaceae Fr.

117. ***Tremella*** Pers.

Trimorphomycetaceae X. Z. Liu, F.Y. Bai, M. Groenew. & Boekhout

118. ***Trimorphomyces*** Bandoni & Oberw.

Tremellales* genera *incertae sedis

119. ***Tremellina*** Bandoni

120. ***Sigmogloea*** Bandoni & J.C. Krug

121. ***Sirotrema*** Bandoni

122. ***Xenolachne*** D.P. Rogers

Trichosporonales Boekhout & Fell

Tetragoniomycetaceae Oberw. & Bandoni

123. ***Tetragoniomyces*** Oberw. & Bandoni

Tremellomycetes **genera** ***incertae sedis***

124. ***Heteromycophaga*** P. Roberts

Subphylum ***Pucciniomycotina*** R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Class ***Agaricostilbomycetes*** R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Agaricostilbales Oberw. & R. Bauer

Agaricostilbales **genus** ***incertae sedis***

125. ***Mycogloea*** L.S. Olive

Class ***Classiculomycetes*** R. Bauer, Begerow, J. P. Samp., M. Weiss & Oberw.

Classiculales R. Bauer, Begerow, Oberw. & Marvanová

Classiculaceae R. Bauer, Begerow, Oberw. & Marvanová

126. ***Classicula*** R. Bauer, Begerow, Oberw. & Marvanová

127. ***Jaculispora*** H.J. Huds. & Ingold

Class ***Cryptomycocolacomycetes*** R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Cryptomycocolacales Oberw. & R. Bauer

Cryptomycocolacaceae Oberw. & R. Bauer

128. ***Colacosiphon*** R. Kirschner, R. Bauer & Oberw.

129. ***Cryptomycocolax*** Oberw. & R. Bauer

Class ***Cystobasidiomycetes*** R. Bauer, Begerow, J. P. Samp., M. Weiss & Oberw.

Cystobasidiales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Cystobasidiaceae Gäum.

130. ***Cystobasidium*** (Lagerh.) Neuhoff

131. ***Occultifur*** Oberw.

Naohideales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Naohideaceae Denchev

132. ***Naohidea*** Oberw.

Cystobasidiomycetes **families** ***incertae sedis***

Microsporomycetaceae Q.M. Wang, F. Y. Bai, M. Groenew. & Boekhout

133. ***Obvidator*** Schoutt.

Class ***Microbotryomycetes*** R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Heterogastridiales Oberw. & R. Bauer

Heterogastridiaceae Oberw. & R. Bauer

134. ***Krieglsteinera*** Pouzar

Microbotryomycetes **families** ***incertae sedis***

Colacogloeaceae Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout

135. ***Colacogloea*** Oberw. & Bandoni

Mycogloiocolacaceae Schoutteten & Yurkov

136. ***Mycogloiocolax*** Schoutt. & Rödel

Microbotryomycetes **genera** ***incertae sedis***

137. ***Slooffia*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout

Class ***Pucciniomycetes*** R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Helicobasidiales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Helicobasidiaceae P.M. Kirk

138. ***Helicobasidium*** Pat.

Platygloeales R.T. Moore

Platygloeaceae Racib.

139. ***Achroomyces*** Bonord.

Class ***Spiculogloeomycetes*** Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout

Spiculogloeales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Spiculogloeaceae Denchev

140. ***Spiculogloea*** P. Roberts

Pucciniomycotina **genera** ***incertae sedis***

141. ***Kryptastrina*** Oberw.

142. ***Zygogloea*** P. Roberts

Basidiomycota **genera** ***incertae sedis***

143. ***Celatogloea*** P. Roberts

144. ***Cystogloea*** P. Roberts

145. ***Tectobasidium*** Spirin, Malysheva & H. Nilsson

Phylum ***Mucoromycota*** Doweld

Subphylum *Mucoromycotina* Benny

Class *Mucoromycetes* Doweld

Mucorales Dumort.

Mucoraceae Dumort.

146. ***Dicranophora*** J. Schröt.

147. ***Mucor*** Fresen.

Phycomycetaceae Arx

148. ***Spinellus*** Tiegh.

Syzygitaceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu, Yuan Yuan & X.Y. Liu

149. ***Syzygites*** Ehrenb.

Mucoromycota **genus *incertae sedis***

150. ***Nothadelphia*** Degawa & W. Gams

5.4.2 Genera notes and illustrations

Phylum *Ascomycota* Caval.-Sm.

Subphylum *Pezizomycotina* O.E. Erikss. & Winka

Class *Dothideomycetes* O.E. Erikss & Winka

Subclass *Dothideomycetidae* P.M. Kirk, P.F. Cannon, J.C. David & Stalpers ex C.L. Schoch, Spatafora, Crous & Shoemaker

Cladosporiales Abdollahz. & Crous

Cladosporiaceae Chalm. & R.G. Archibald

Cladosporium Link, Mag. Gesell. naturf. Freunde, Berlin 7: 37 (1816) [1815]

Figure 5.4

Index Fungorum number: IF 7681

Facesoffungi number: FoF 06967

Cladosporium was established by Link (1816), comprising four species. Later, *C. herbarum* was designated as the lectotype species by Clements and Shear (1931), a decision that was subsequently endorsed by De Vries (1952) and Hughes (1958). *Cladosporium* represents one of the most extensive and heterogeneous genera within the hyphomycetes with more than 772 names (Dugan et al. 2004). Numerous researchers have explored the heterogeneity of *Cladosporium sensu lato* and suggested new, more natural delineations for this genus (Morgan-Jones & Jacobsen, 1988; McKemy & Morgan-Jones, 1990; Morgan-Jones & McKemy, 1990; Partridge

& Morgan-Jones, 2002, 2003). David (1997) revised *Cladosporium* species that were previously classified under *Heterosporium*. His work demonstrated that *Cladosporium* is well-characterised and readily identifiable by the distinct structure of conidiogenous loci and conidial hila. Crous et al. (2001) made initial efforts to revise and create a monograph for *Cladosporium sensu lato* Braun et al. (2003) conducted the first molecular analysis of *Cladosporium sensu lato*, providing definitive evidence that underscores the considerable heterogeneity within this genus. Over the past two decades, multiple genera exhibiting cladosporium-like morphologies have been distinguished from *Cladosporium sensu stricto*., utilizing re-evaluations of morphological characteristics alongside molecular data (De Hoog et al., 1995; Seifert et al., 2004; Heuchert et al., 2005; Crous et al., 2006, 2007; Braun et al. 2008; Bezerra et al. 2017). Efforts aimed at elucidating the phylogeny and taxonomic organisation of *Cladosporium* species and related fungi have led to a contemporary redefinition of the genus (Crous et al., 2007; Schubert et al., 2007; Zalar et al., 2007; Bensch et al., 2010, 2012, 2018). Three primary species complexes, *C. herbarum*, *C. sphaerospermum*, and *C. cladosporioides* are acknowledged within the genus, primarily based on morphology, and are employed for practical categorization of the species (Bensch et al., 2012, 2015; Marin-Felix et al., 2017). However, distinguishing specific species of *Cladosporium* within a given species complex based solely on morphological traits is often challenging due to overlapping characteristics among many species. Therefore, employing polyphasic approaches, which include multilocal (the internal transcribed spacers of the rDNA genes, as well as partial actin and translation elongation factor 1-α gene sequences) phylogenetic analyses, becomes imperative for accurate species delimitation and identification (Bensch et al., 2012, 2015, 2018).

The species of *Cladosporium* are dematiaceous hyphomycetes. The asexual morph is characterized by, branched, septate, and pigmented hyphae. The conidiophores are mononematous, subhyaline to typically distinctly pigmented, occurring either singly or in clusters. The conidiogenous cells are integrated into the hyphae, occurring at both terminal and intercalary positions. They typically follow a sympodial pattern, bearing one to several scars. Conidiogenesis is holoblastic. The conidiogenous loci are coronated, characterized by being more or less protuberant, consisting of a central convex dome encircled by a raised periclinal rim. The conidia

are either solitary or arranged in short to long, simple to branched acropetal chains. They can be amero- to phragmosporous, ranging from subhyaline to typically distinctly pigmented. Conidial hila are coronated, typically more or less protuberant (adapted from Crous et al. 2007). The sexual morphs, previously classified under *Davidiella*, are documented for only a limited number of species within *Cladosporium* (Bhunjun et al., 2024).

Members of *Cladosporium* are ubiquitous and have a global distribution (Heuchert et al., 2005; Crous et al., 2007). They inhabit both aquatic and terrestrial ecological niches as endophytes, fungicolous species, human pathogens, phytopathogens, and saprobes (Heuchert et al., 2005; Crous et al., 2007; Bensch et al., 2012, 2018). Certain species hold medical significance in clinical laboratories and have the potential to induce allergic lung mycoses (de Hoog et al. 2000). *Cladosporium* species are commonly found on various types of plants, fungi, and other debris. They are frequently isolated from soil, air, food, paint, textiles, and other organic materials. Additionally, they often act as secondary invaders, colonizing leaf lesions caused by plant pathogenic fungi (Ellis, 1971, 1976; Farr et al., 1989; Flannigan, 2001; Mullins, 2001; Ma et al., 2017; Iturrieta-González et al., 2021).

The fungicolous species have been found associated with different mushroom species and rust fungi (Heuchert et al., 2005; Sun et al., 2019a). The species such as, *Cladosporium balladynae* (colonized *Balladyna magnifica* (*Parmulariaceae*)), *C. cladosporioides* (parasitized rust fungi), *C. chalastosporoides* (associated with the fruiting bodies of *Teratosphaeria proteae-arboreae* (*Teratosphaeriaceae*)), *C. elsinoes* (colonized *Elsinoe wisconsinensis* (*Elsinoaceae*)), *C. exile* (parasitized the chasmothecia of *Phyllactinia guttata* (*Erysiphaceae*)), *C. gallicola* (colonized the galls of *Endocronartium harknessii* (*Cronartiaceae*)), *C. herbarum* (parasitized powdery mildew and rust fungi), *C. gerwasiae* (colonized *Gerwasia* sp. (*Phragmidiaceae*)), *C. lophodermii* (colonized the apothecia of *Lophodermium pinastri* (*Rhytismataceae*)), *C. pseudocladosporioides* (parasitized powdery mildew and rust fungi) and *C. phyllactiniicola* (colonized *Phyllactinia guttata* (*Erysiphaceae*)) have been documented in fungicolous contexts (Heuchert et al., 2005; Sun et al. 2019a).These species are potent biocontrol agents (Heuchert et al., 2005; Sun et al. 2019a).

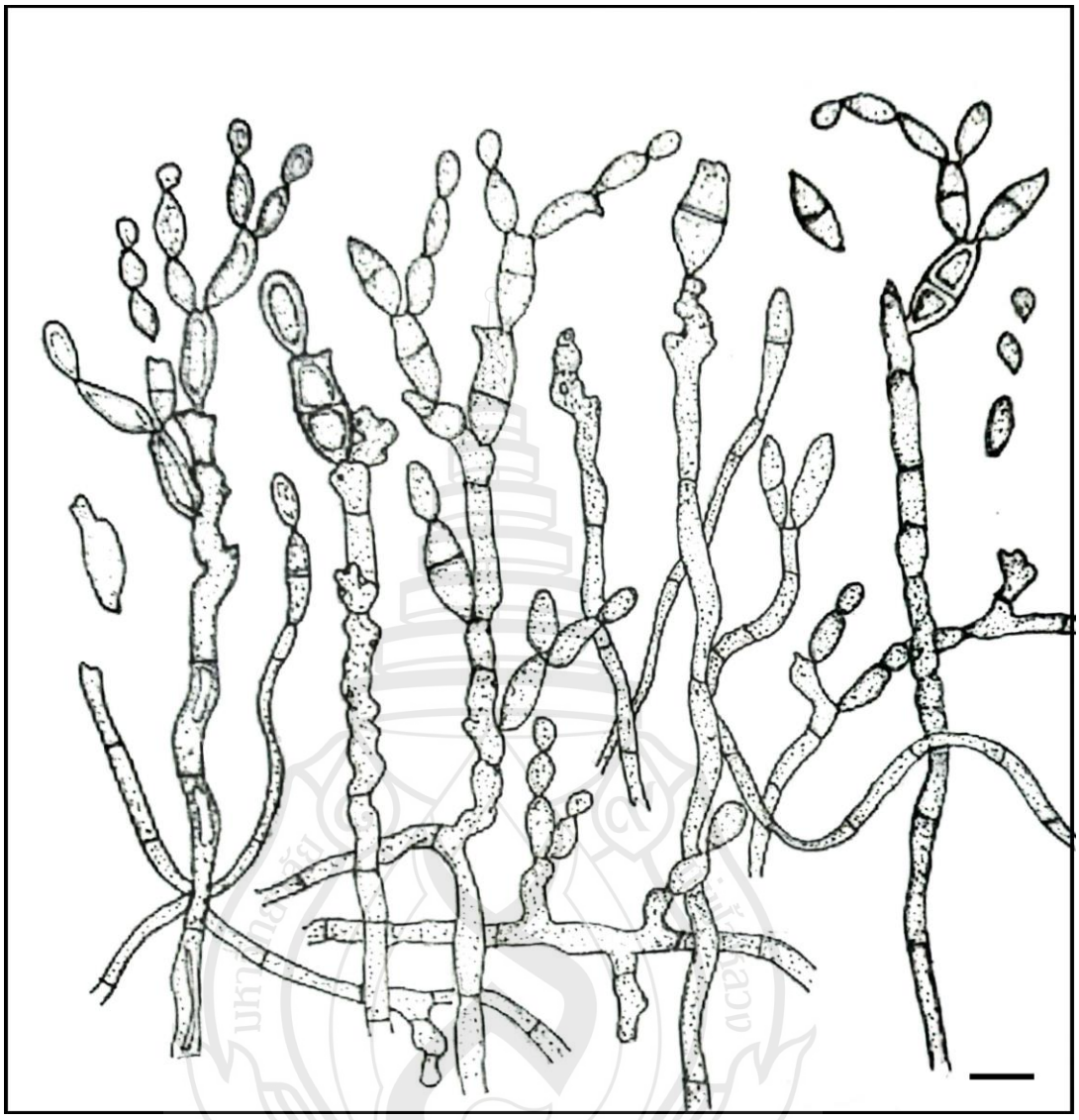


Figure 5.4 *Cladosporium herbarum*

Figure 5.4, Macronematous and micronematous conidiophores with conidia. Scale bar = 10 μm. (Redrawn from Schubert et al., 2007).

Mycosphaerellales (Nannf.) P.F. Cannon

Mycosphaerellaceae Lindau

Ramularia Unger, Exanth. Pflanzen (Wien): 119 (1832) [1833]

Figure 5.5

Index Fungorum number: IF 9691

Facesoffungi number: FoF 09222

Ramularia was proposed by Unger (1833), with *R. pusilla* as its type species. Previously, the taxonomy of *Ramularia* and its related genera relied on morphological attributes (Braun, 1995, 1998). Videira et al. (2016), employed a polyphasic methodology encompassing multi-locus phylogeny of DNA sequences, morphological and cultural traits, as well as host data, to refine the delineation of *Ramularia* from closely related genera and enhance the demarcation of species within this genus. *Ramularia* was previously regarded as monophyletic but was found later to exhibit genetic heterogeneity. Despite remaining a sizable genus, certain species, which are not congruent with the type species, were reassigned to new genera, including *Xenoramularia* and *Teratoramularia* (Videira et al., 2016). Some of these ramularia-like genera even formed clusters outside *Mycosphaerellaceae*, yet retained the ramularia-like morphology (Videira et al., 2016). Moreover, multigene phylogenetic analyses unveiled several cryptic species within species complexes such as *R. endophylla* and *R. eucalypti* (Videira et al., 2015a, b; Bakhshi & Arzanlou, 2017).

Ramularia is characterized as a hyphomycetes, possessing hyaline conidiophores and conidia featuring distinctive, thickened, darkened, refractive conidiogenous loci and conidial hila (Videira et al., 2016). The sexual morphs of *Ramularia* species belong in *Mycosphaerella*. However, only a limited number of lifecycles have been experimentally validated. Therefore, it is suggested that certain species may solely exist as asexual holomorphs (Braun, 1995, 1998; Videira et al., 2015b).

The members of *Ramularia* are distributed worldwide. They are predominantly phytopathogenic, typically linked to leaf spots, necrosis, or chlorosis accountable for yield reductions in numerous significant crops, such as barley, sugar beet, and strawberry (Videira et al., 2016). However, certain species may exhibit saprobic, endophytic and a mycophilic/fungicolous nature. The species such as, *Ramularia butomi*, *R. coleosporii*, *R. cylindriopsis*, *R. dichosciadii*, *R. uredinearum*, *R. uredinicola*, and *R. uredinis* have been documented as fungicolous, forming associations with various rust fungi (Braun, 1998; Khodaparast & Braun, 2005; Sun et al., 2019a; Bakhshi et al., 2021).

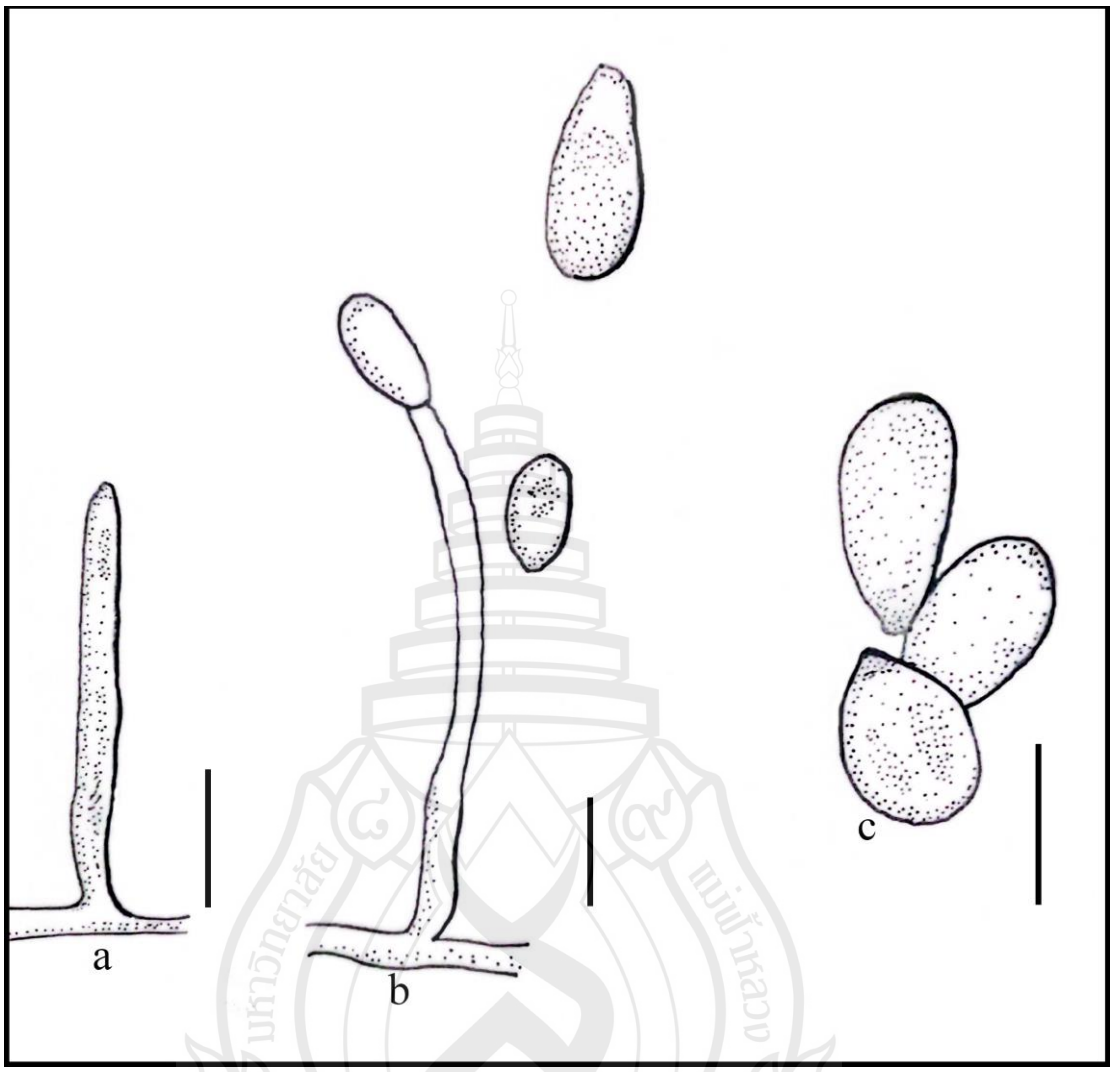


Figure 5.5 *Ramularia pusilla*

Figure 5.5, a–c. Conidiophores and conidia. Scale bars = 10 μm. (Adapted from Videira et al., 2016).

Teratosphaeriaceae Crous & U. Braun

Acrodontium de Hoog, Stud. Mycol. 1: 23 (1972)

Figure 5.6

Index Fungorum number: IF 7035

Facesoffungi number: FoF 06994

Acrodontium was established by De Hoog (1972), with the type species *A. crateriforme*. Videira et al. (2016), revised *Acrodontium* and resolved its phylogenetic placement in *Teratosphaeriaceae*.

The members of *Acrodontium* have been commonly isolated from soil and different plant substrates collected from countries such as, Australia, France, Germany, Indonesia, Korea, the Netherlands, the UK, the USA and South Africa (De Hoog, 1972; Videira et al., 2016; Crous et al., 2021a; Farr et al., 2021). Moreover, species such as *A. crateriforme* (parasitized powdery mildew and rust fungi), *A. intermissum* (parasitized rust fungi), *A. luzulae* (*Puccinia* sp. (*Pucciniaceae*)), and *A. simplex* (on *Oligoporus rennyi* (*Dacryobolaceae*) are fungicolous species (De Hoog, 1972; Videira et al., 2016; Sun et al., 2019a; Wasiatus, 2022).

The asexual morph of *Acrodontium* is characterized by mycelium composed of subhyaline, brownish, or olivaceous, septate, thin-walled, hyphae. Conidiophores emerge from the hyphae. They can be erect or procumbent, occasionally thick-walled and dark brown at the base, gradually becoming paler brown towards the apex. These conidiophores may branch verticillately or dichotomously. Conidiogenous cells are integrated, often terminal in conidiophores, forming whorls or reduced to conidiogenous cells. They arise from hyphae, with the basal part being flask-shaped or elongated, tapering towards the apex to form a sympodial denticulate rachis, which can be straight to flexuous. Conidia are produced singly, and they can be hyaline or pigmented, smooth, subglobose to fusiform, featuring an apiculate base (adapted from De Hoog, 1972). There are no records on the sexual morph of this genus.

To date, there are 17 species listed under *Acrodontium* in Species Fungorum (2025) whereas, ten of these species have molecular data available in GenBank (2025).

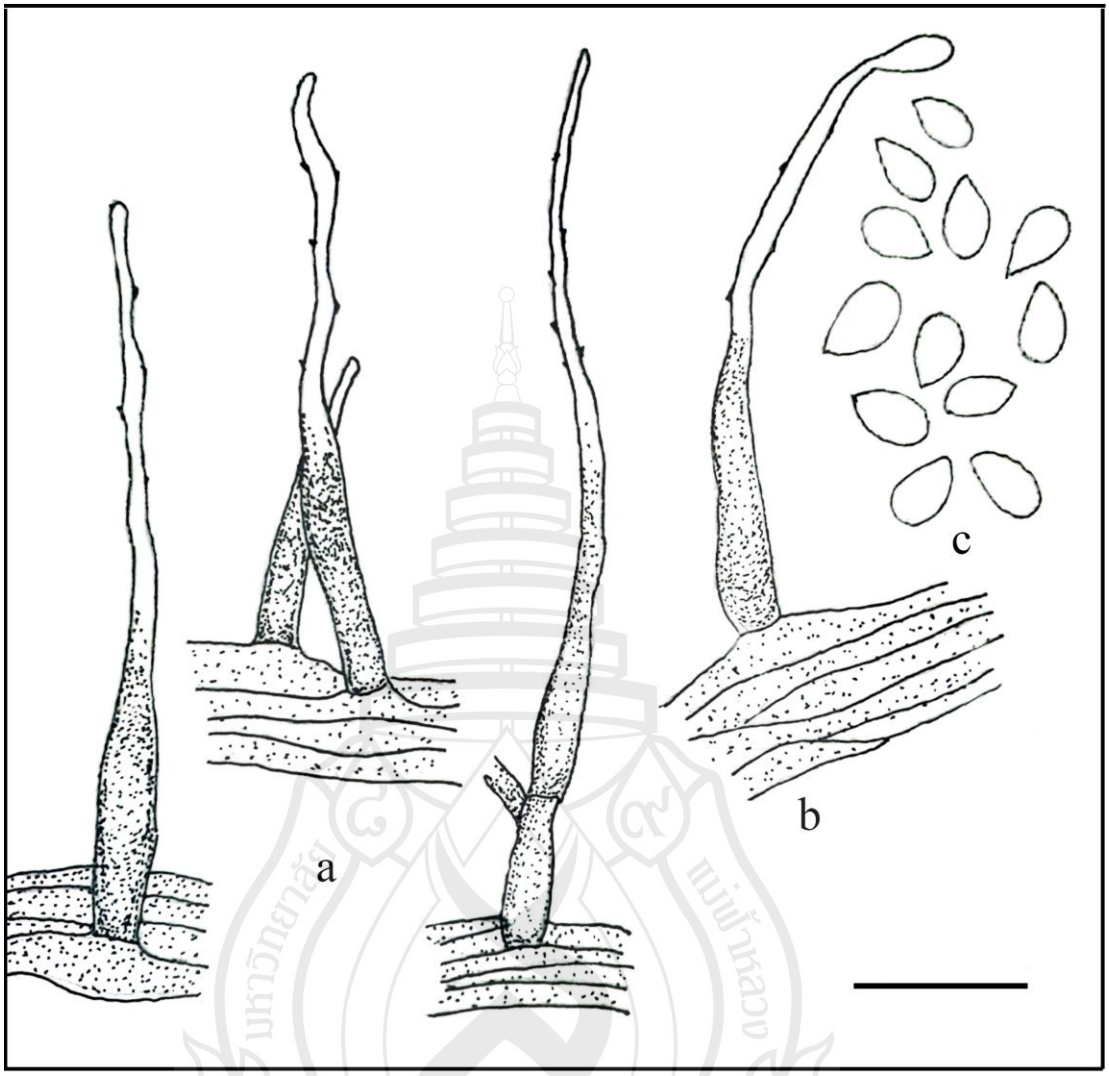


Figure 5.6 *Acrodontium crateriforme*

Figure 5.6, a. Conidiophores. b, c. Conidiogenous cells and conidia. Scale bar = 10 μm. (Redrawn from De Hoog 1972).

Myriangiales Starbäck

Myriangiaceae Nyl.

Uleomyces Henn., Hedwigia 34: 107 (1895)

Figure 5.7

Index Fungorum number: IF 5657

Facesoffungi number: FoF 03682

Uleomyces was introduced by Hennings (1895) with *U. parasiticus* as the type species and was placed in *Hypocreaceae*. Moreau (1953) proposed *Uleomycetaceae*

to accommodate the genus, although this was not validly published. Von Arx and Müller (1975) transferred *Uleomyces* to *Cookellaceae* (*Dothideales*) based on morphology and it was followed by Barr (1997), who accepted *Uleomyces* in *Cookellaceae* but within *Myriangiales*. Lumbsch and Huhndorf (2010) also listed *Uleomyces* under *Cookellaceae* (*Dothideomycetes*, order *incertae sedis*). Boonmee et al. (2017) re-evaluated the morphology and placed *Uleomyces* in *Myriangiaceae* (*Myriangiales*), where it is currently accepted in recent classifications (Hyde et al., 2024a; Pem et al., 2024). According to Species Fungorum (2025), 11 species epithets are presently recognized in the genus, although no molecular data are available in GenBank (2025).

Uleomyces is distinguished by irregular, effuse ascostromata embedded in a parasitic matrix, which are crustose, pulvinate, tuberculate, or hump-like, and lack a hypostroma. Stromata are semi-immersed, subglobose, and contain locules with individual asci, without pseudoparaphyses, and with a dark red stromatal context. Asci are 8-spored, bitunicate, sessile, and subellipsoid to broadly clavate. Ascospores are multi-seriate, conglobate, oblong-clavate to subperiform, muriform, multi-septate, sometimes constricted at the septa, and brown to dark red (Boonmee et al., 2017; Pem et al., 2024; Index Fungorum, 2025).

Species of *Uleomyces* are mostly fungicolous or hyperparasitic, occurring on other fungi and occasionally on living leaves (Boonmee et al., 2017; Pem et al., 2024; Index Fungorum 2025). Reported associations include *U. brenesii* (on uredinia of *Prospodium amphilophii* (*Uropyxidaceae*)), *U. comedens* (on stromata of *Hysterostomella phoebes* (*Parmulariaceae*)), *U. japonicus* (on stromata of *Coccoidea quercicola* (*Coccoideaceae*)), and *U. parasiticus* (on *Parmularia styracis* (*Parmulariaceae*)) (Index Fungorum 2025). The genus has been recorded from Brazil, Costa Rica, El Salvador, Guyana, Japan, Papua New Guinea, and the USA (Pem et al., 2024; Index Fungorum, 2025).

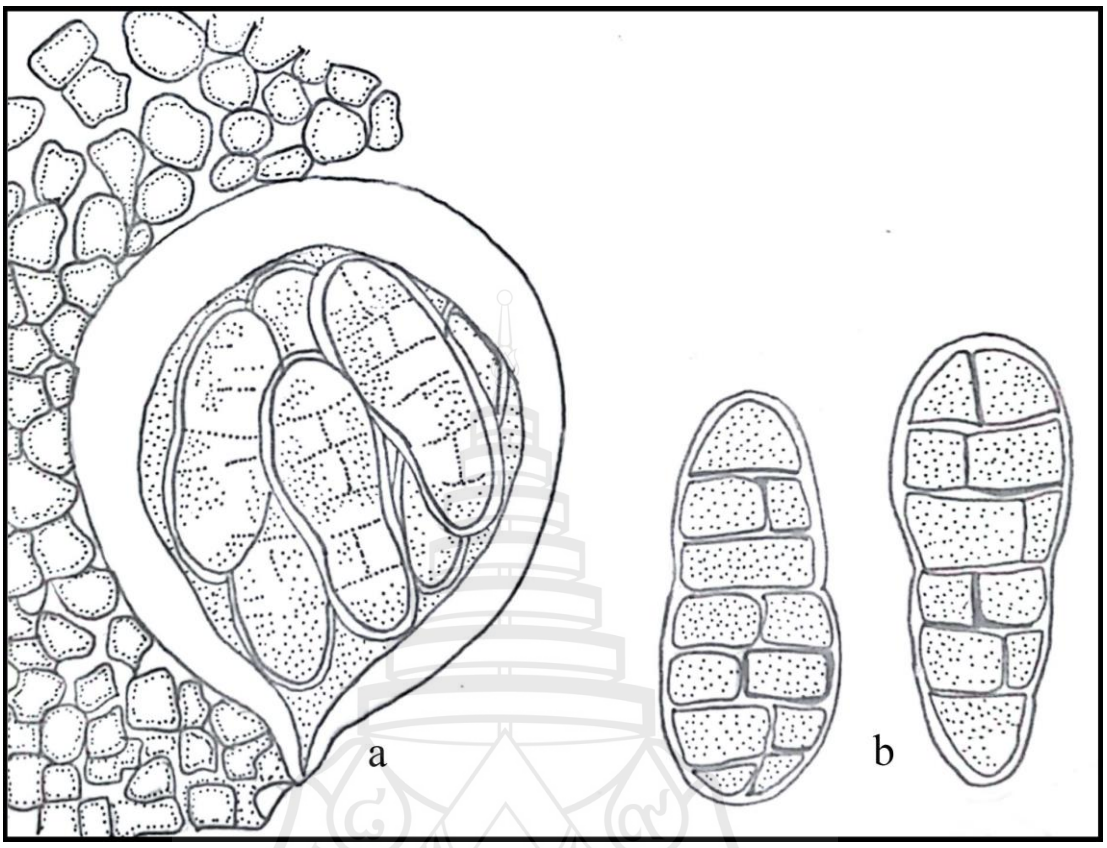


Figure 5.7 *Uleomyces parasiticus*

Figure 5.7, a. Ascus and sub-globose cells. b. Ascospores. (Redrawn from Boonmee et al., 2017).

Subclass *Pleosporomycetidae* C.L. Schoch, Spatafora, Crous & Shoemaker

Pleosporales Luttr. ex M.E. Barr

Cucurbitariaceae G. Winter

Parafenestella Jaklitsch & Voglmayr, Stud. Mycol. 90: 108 (2017)

Figure 5.8

Index Fungorum number: IF 823014

Facesoffungi number: FoF 08186

Jaklitsch et al. (2018) established *Parafenestella*, designating *P. pseudoplatani* as its type species. *Parafenestella pseudoplatani* was identified as a fungicolous species growing on *Diaporthe* (*Diaportheceae*) pseudostromata, which was found on dead branches of *Acer pseudoplatanus* collected in Austria (Jaklitsch et al., 2018). The name *Parafenestella* was chosen considering its close phylogenetic relationship with *Fenestella* (Jaklitsch et al., 2018).

The sexual morph of *Parafenestella* is distinguished by its subglobose, globose to pyriform ascomata, which are typically surrounded by subicular hyphae. The asci are cylindrical, bitunicate, and fissitunicate, with thick walls and an ocular chamber, containing 6–8 ascospores arranged in a uniseriate manner. The ascospores are ellipsoid, slightly wider at the upper part, and possess several transverse and longitudinal septa. They are constricted at the median primary septum and range from hyaline to pale or yellowish-brown when immature, eventually becoming greyish-brown and finally dark to blackish-brown upon maturity (adapted from Jaklitsch et al., 2018). The asexual morph of *Parafenestella* in culture produces pycnidia that are more or less globose, with surfaces often roughened by hyphal appendages. The phialides are produced on hyaline base cells or at the apex of short, simple, or basally branched conidiophores. The conidia are single-celled, oblong or allantoid, occasionally tapering towards one end or pinched, hyaline, containing guttules, and with a smooth surface (adapted from Jaklitsch et al., 2018).

Species Fungorum (2025) lists 18 species of *Parafenestella*. The species of *Parafenestella* are mainly fungicolous and can be saprobic or necrotrophic on woody plants (Jaklitsch et al., 2018; Jaklitsch et al., 2020). The fungicolous species of *Parafenestella* include *P. austriaca* (associated with perithecial fungi on *Rosa canina*), *P. faberi* (on *Cytospora* sp. (*Cytosporaceae*)), *P. germanica* (on *Diaporthe decedens* (*Diaporthaceae*)), *P. parasalicum* (on *Cytospora* sp.), *P. pseudoplatani* (on *Diaporthe* pseudostromata), *P. rosacearum* (associated with other perithecial fungi), *P. salicis* (on *Cytospora* sp.), *P. tetratrupha* (on or in conidiomata of *Melanconis alni* (*Melanconidaceae*)) and *P. vindobonensis* (on *Cytospora* sp.) (Jaklitsch et al., 2018, 2020). These species have been documented in Austria, Canada, China, France, Germany, Italy, Russia and the UK (Jaklitsch et al., 2018, 2020; Ilyukhin et al., 2022; Su et al., 2022).

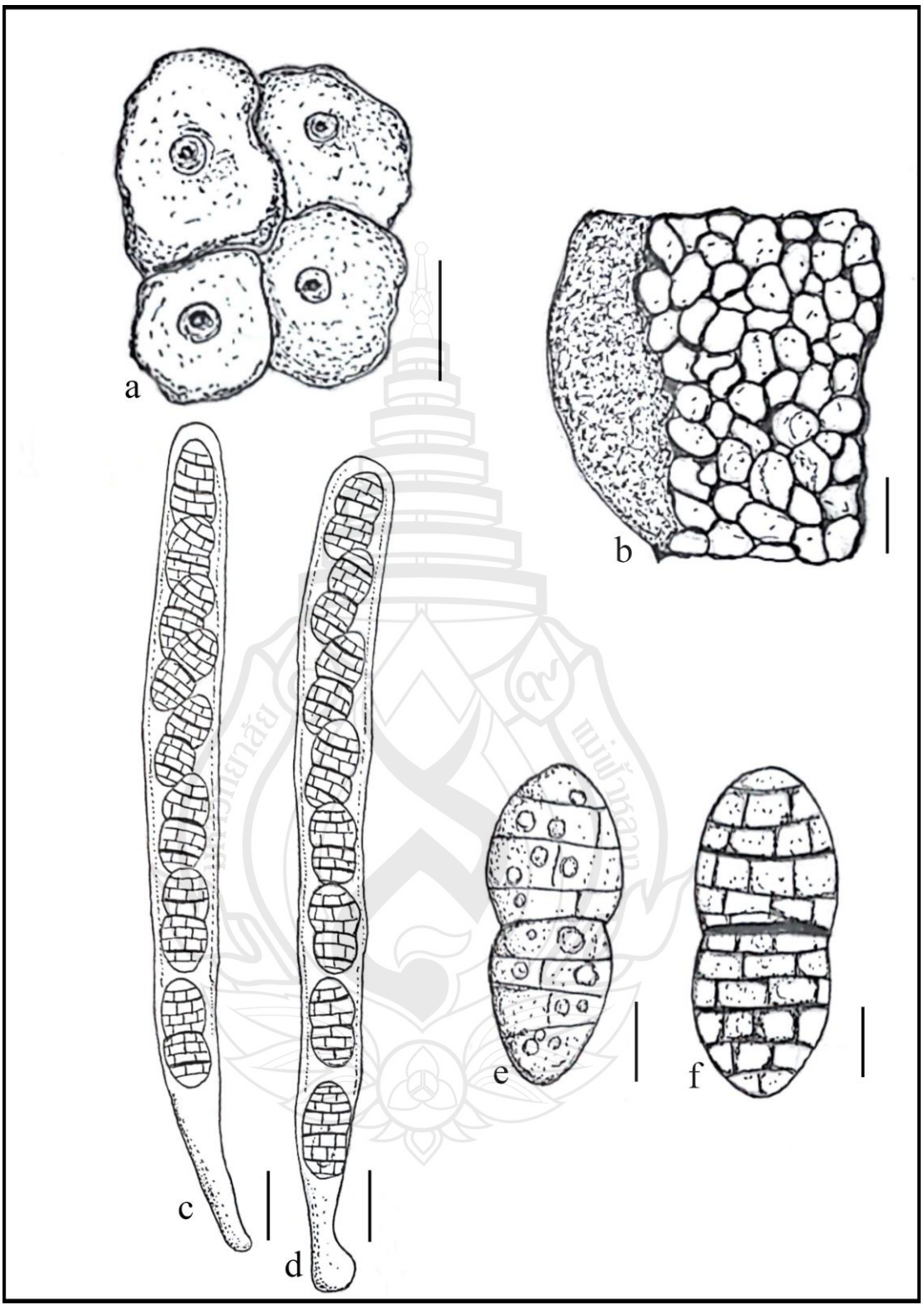


Figure 5.8 *Parafenestella pseudoplatani*

Figure 5.8, a. Ascomata in face view. b. Peridium and subicular hyphae in vertical section. c, d. Asci. e, f. Ascospores. Scale bars: a = 200 μm, b–d = 20 μm, e, f = 7 μm. (Adapted from Jaklitsch et al., 2018).

Didymosphaeriaceae Munk

Letendraea Sacc., Michelia 2(no. 6): 73 (1880)

Figure 5.9

Index Fungorum number: IF 2812

Facesoffungi number: FoF 00044

Letendraea was established by Saccardo (1880), with *L. eurotioides* as the type species. It was found on dead branches of *Alnus glutinosa*, *Rubus fruticosus*, and *Salix* in Italy. There are 15 species listed under this genus in Species Fungorum (2025). *Letendraea* species have been identified as saprobes, endophytes, and associated with leaf spot disease in terrestrial environments (Ariyawansa et al., 2014; Jie et al., 2021; De Silva et al., 2021). Some species, such as *L. helminthicola* and *L. kamatii*, are fungicolous on *Helminthosporium* spp. (*Massarinaceae*) (Petch, 1938; Akulov, 2015; Sun et al., 2019a). *Letendraea* species have also been isolated from the gut of a marine crab (Xu et al., 2019) and as an insect-associated fungus (Xu et al., 2020). These species have been documented across several countries worldwide, including Austria, Brazil, Cameroon, China, Hungary, India, Indonesia, Italy, Mauritius, Mexico, Portugal, Thailand, Ukraine, the UK and the USA (Ariyawansa et al., 2014; Akulov, 2015; Jie et al., 2021; De Silva et al., 2021; Index Fungorum, 2025).

Letendraea is characterized by superficial, globose to conical ascomata. It possesses filiform pseudoparaphyses and obclavate to cylindrical, 8-spored asci. The ascospores are fusoid to oblong and 1-septate (Ariyawansa et al., 2014). *Letendraea* has been assigned to different families by taxonomists based on morphological characteristics. The multi-gene phylogenetic analysis by Ariyawansa et al. (2014) placed *Letendraea* within *Didymosphaeriaceae*.



Figure 5.9 *Letendraea helminthicola*

Figure 5.9, a. Perithecium. b. Ascus. c. Ascospore. (Redrawn from Petch, 1938).

Pseudotrichia Kirschst., Annls mycol. 37(1/2): 125 (1939)

Figure 5.10

Index Fungorum number: IF 4497

Facesoffungi number: FoF 00784

Pseudotrichia was established by Kirschstein (1939), with *P. stromatophila* as the type species. This species was described as fungicolous, occurring on the stroma of *Diatrypella* (*Diatrypaceae*) in the Czech Republic (Kirschstein, 1939). Additional fungicolous species include *P. minor*, reported on *Diaporthe larseniana* in Denmark,

and *P. mutabilis*, found parasitizing stromata of hosts within the *Xylariales*, such as *Hypoxylon crocopeplum* and *Rosellinia corticium* (Akulov, 2022; Index Fungorum, 2025). According to Species Fungorum (2025), the genus currently comprises 12 accepted species. Most members of *Pseudotrichia* are saprobes or parasites on plant substrates, occurring primarily in terrestrial environments and are occasionally found in aquatic habitats (Pem et al., 2024). Species of the genus have been documented from Austria, Canada, the Czech Republic, Estonia, Finland, France, Germany, Italy, Japan, Lithuania, New Zealand, Norway, Pakistan, Poland, Slovakia, Sri Lanka, Sweden, Switzerland, Ukraine, the UK, the USA, and Venezuela (Akulov, 2022; Pem et al., 2024; Index Fungorum, 2025).

The sexual morph of *Pseudotrichia* is characterized by carbonaceous, ostiolate perithecial ascomata that occur either solitarily or in groups and are superficially positioned. Asci are clavate to cylindrical, each containing eight ascospores and accompanied by numerous paraphyses. The ascospores are fusiform, hyaline, and possess multiple transverse septa (Kirschstein, 1939; Akulov, 2022; Pem et al., 2024). The taxonomic placement of *Pseudotrichia* has been a subject of debate over past years (Thambugala et al., 2014; Tian et al., 2015). However, the study by Jaklitsch & Voglmayr (2017) supported the inclusion of *Pseudotrichia* within *Melanommataceae*. Molecular data for some *Pseudotrichia* species is available in GenBank (2025), with sequence records for multiple loci including ITS, LSU, SSU, *actin*, *tub*2, *cmdA*, *his*, *rpb*2, and *tef-1*.

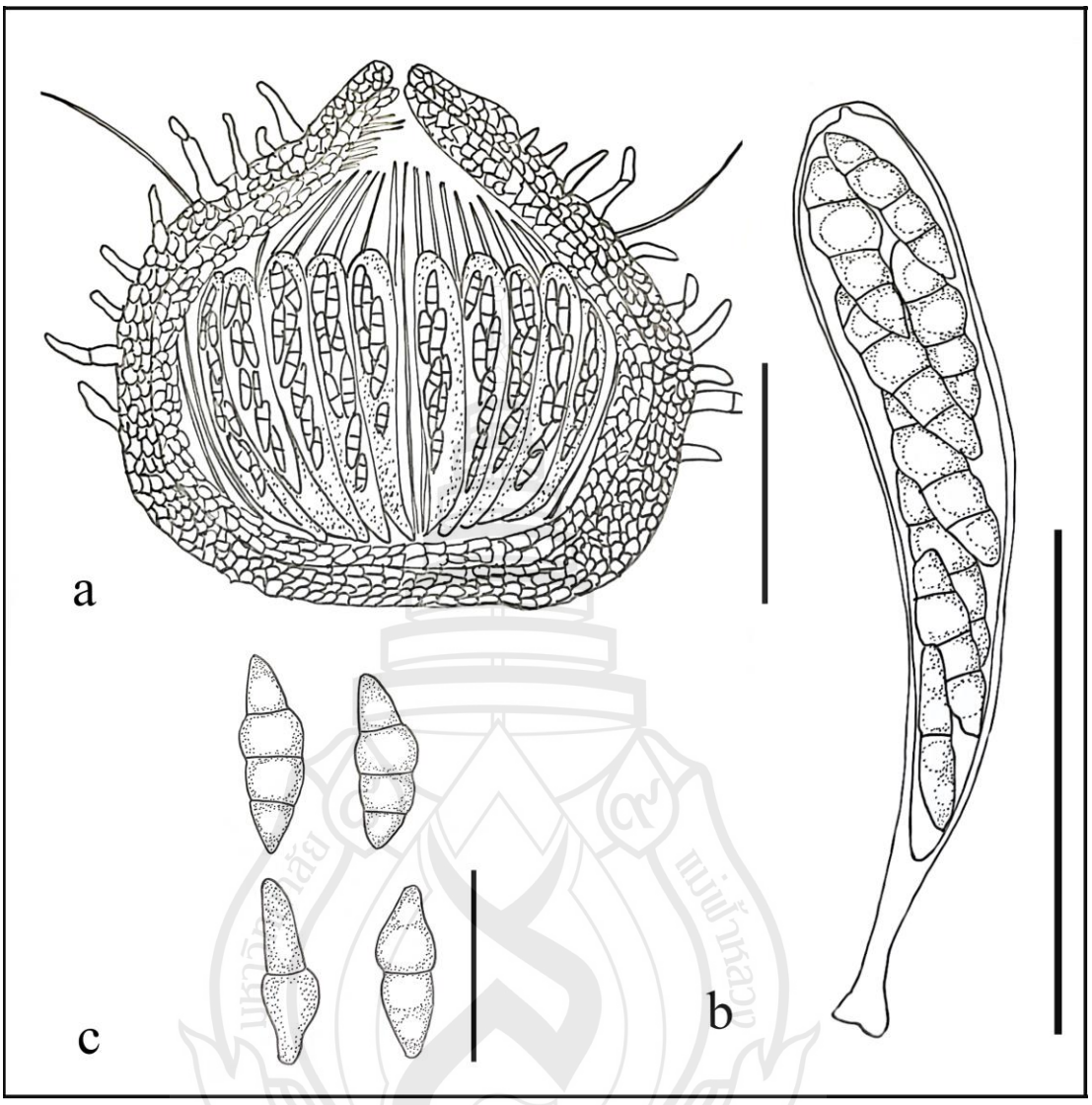


Figure 5.10 *Pseudotrichia mutabilis*

Figure 5.10, a. Vertical section of pseudothecium. b. Ascus. c. Ascospores. Scale bars: a = 300 μm, b = 60 μm, c = 35 μm. (Redrawn from Akulov 2022).

Leptosphaeriaceae M.E. Barr

Sphaerellopsis Cooke, Grevillea 12(no. 61): 23 (1883)

Figure 5.11

Index Fungorum number: IF 9976

Facesoffungi number: FoF 06405

Sphaerellopsis was established with *S. filum* as its type species (Sutton, 1977). Based on molecular phylogenetic analyses, *Sphaerellopsis* was re-circumscribed by Trakunyingcharoen et al. (2014) and Ariyawansa et al. (2015). *Sphaerellopsis* taxa are

predominantly encountered in their asexual state, with the sexual morph rarely observed (Gómez-Zapata et al., 2024). Although *Sphaerellopsis* and *Eudarluca* are considered to be congeneric, however, some uncertainty remains regarding their precise taxonomic relationship (Phookamsak et al., 2019; Gómez-Zapata et al., 2024).

The asexual morph of *Sphaerellopsis* is characterized by conidiomata which are eustromatic, pycnidioid, initially immersed but becoming erumpent. They appear dark brown to black *in vivo* and pale brown to brown *in vitro*. They may be uni- or multilocular, with each locule possessing a distinct, simple ostiole. Paraphyses, when present, are hyaline, filiform, septate, sometimes branching, and end in a rounded apex. Conidiophores are typically reduced to conidiogenous cells, occasionally accompanied by a supporting cell. Conidia are hyaline to pale brown and irregularly verruculose, with 0–1(–3) eusepta and constricted at the septa. They are fusoid-ellipsoidal, occasionally Y-shaped or digitate, with an obtuse apex, and a truncate base, sometimes bearing mucoid polar appendages. Microconidia are subcylindrical to ellipsoid or globose, aseptate, smooth, and hyaline (Trakunyingcharoen et al., 2014; Phookamsak et al., 2019; Gómez-Zapata et al., 2024).

The sexual morph of *Sphaerellopsis* is characterized by, stromata that develop associated with rust sori, with a brown outer zone and a hyaline inner zone. Loci are immersed, subglobose to ampulliform, featuring a protruding papillate neck and ostiole. The stromatal wall is composed of a few layers of *textura prismatica*. Pseudoparaphyses are cellular, septate, branched, and hyaline. Asci are numerous, 8-spored, bitunicate, fissitunicate, cylindrical-clavate, and short-stipitate. Ascospores are irregularly biseriate, fusoid, occasionally isthmosporous, hyaline to pale yellow, and septate, with constrictions at the septa. They are sometimes guttulate and may possess a mucoid cupula at each polar end or lack it (Trakunyingcharoen et al., 2014; Phookamsak et al., 2019; Gómez-Zapata et al., 2024).

Sphaerellopsis taxa are widely recognized as cosmopolitan mycoparasites on a broad range of rust fungi (Trakunyingcharoen et al., 2014; Phookamsak et al., 2019; Gómez-Zapata et al., 2024). Therefore, these mycoparasitic species are tentatively regarded as potential biological control agents against rust fungi, which cause severe disease epidemics and substantial yield losses worldwide (Kolmer et al., 2009; Lidwell-Durnin & Lapthorn, 2020; Gómez-Zapata et al., 2024). *Sphaerellopsis*

comprises nine species (Species Fungorum, 2025), with a worldwide distribution (Gómez-Zapata et al., 2024). Among these, six taxa namely, *Sphaerellopsis anomala* (on *Puccinia* sp. (*Pucciniaceae*)), *S. filum* (on *Melampsora* sp. (*Melampsoraceae*), *Puccinia* spp., *Tranzschelia discolour* (*Tranzscheliaceae*)), *S. hakeae* (on *Uromyces ehrhartae*), *S. macroconidialis* (on *Phakopsora* spp. (*Phakopsoraceae*), *Puccinia* spp., *Ravenelia* spp. (*Raveneliaceae*), *Uromyces* spp.), *S. melampsorinearum* (on *Coleosporium* spp. (*Coleosporiaceae*), *Melampsora* spp., *Puccinia* spp., *Uromyces* spp.), and *S. paraphysata* (on *Melampsora* spp., *Puccinia* spp., *Ravenelia macowania*, *Uromyces* spp.) are mycoparasites of rust fungi: (Nag Raj, 1993; Trakunyingcharoen et al., 2014; Crous et al., 2016; Gómez-Zapata et al., 2024). In contrast, *Sphaerellopsis artemisiae* and *S. isthmospora*, are recognized only as saprobes on plant substrates (Doilom et al., 2021; Phookamsak et al., 2019).

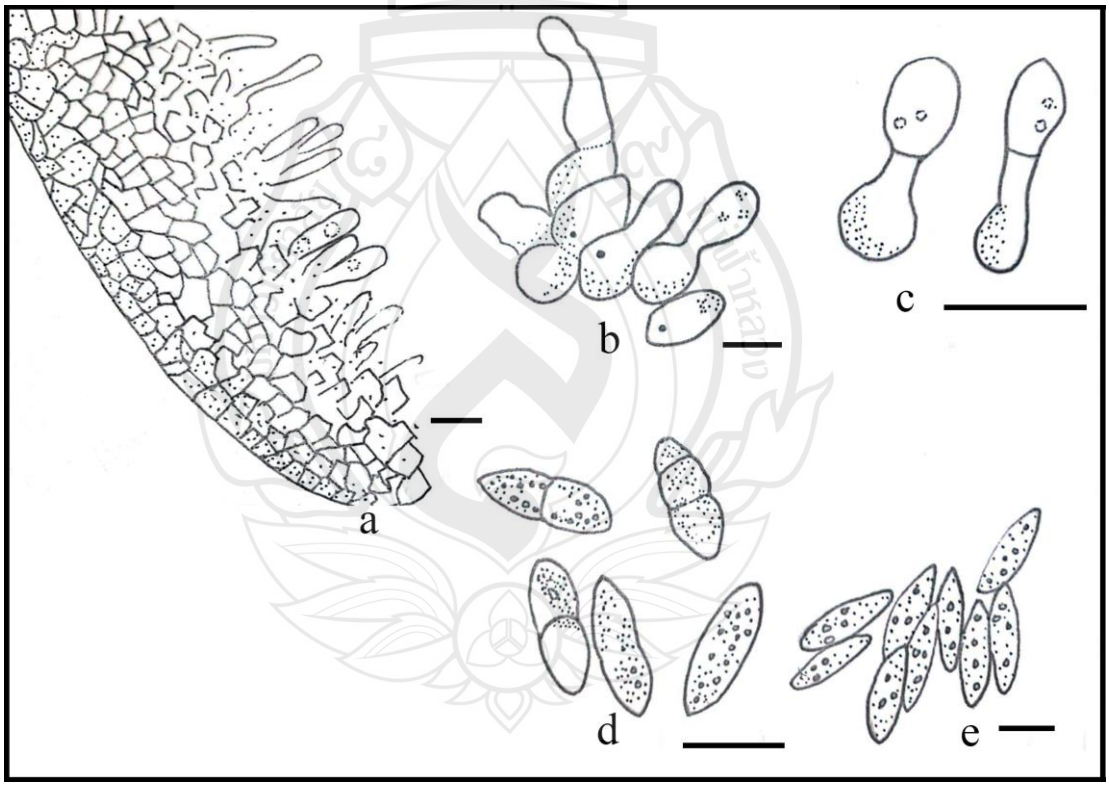


Figure 5.11 *Sphaerellopsis paraphysata*

Figure 5.11, a. Section through conidiomatal wall, showing conidiogenous cells. b, c. Conidiogenous cells. d, e. Conidia. Scale bars a–e = 10 μm. (Adapted from Trakunyingcharoen et al., 2014).

Phaeosphaeriaceae M.E. Barr

Ampelomyces Ces. ex Schltdl., in Klotzsch, Bot. Ztg. 10: 301 (1852)

Figure 5.12

Index Fungorum number: IF 7129

Facesoffungi number: FoF 00291

Ampelomyces was established by Cesati (1852), with *A. quisqualis* as the type species. This species was described from the powdery mildew fungus *Erysiphe necator* (*Erysiphaceae*) (Cesati, 1852). Members of *Ampelomyces* are mycoparasites, primarily targeting powdery mildews and are distributed globally (Gautam & Avasthi, 2016; Manjunatha et al., 2020; Prahl et al., 2023; Pem et al., 2024). *Ampelomyces* species represent one of the earliest groups of mycoparasites employed as biological control agents against powdery mildews, owing to their ability to suppress mycelial development and reduce the survival of overwintering inoculum in host fungi (Prahl et al., 2023).

The asexual morph of *Ampelomyces* is characterized by solitary, superficial, uniloculate pycnidial conidiomata, which are scattered and vary from globose to elongated or pyriform. These structures are pale brown, ostiolate, and occasionally papillate. The conidiomatal wall is thick and composed of pale brown cells arranged in a *textura angularis* (Sutton, 1980; Phookamsak et al., 2014). Conidiophores are typically reduced to conidiogenous cells. The conidiogenous cells are enteroblastic, phialidic, determinate, and discrete, being doliiform to ampulliform. They are hyaline, smooth-walled, with minute channels and collarettes, and a periclinally thickened apex. Conidia are amerosporous, cylindrical to fusiform, straight to slightly curved, aseptate, very pale brown, thin-walled, smooth-walled, and often contain guttules (Sutton, 1980; Phookamsak et al., 2014).

According to Species Fungorum (2025), 16 species epithets are listed under *Ampelomyces*. Available molecular markers for this genus include LSU, SSU, ITS, and actin (*act1*) sequences (GenBank, 2025). Phookamsak et al. (2014) redefined *Ampelomyces* based on phylogenetic analysis and placed it within *Phaeosphaeriaceae*. Despite these efforts, the taxonomy of *Ampelomyces* remains unresolved (Németh et al., 2023; Prahl et al., 2023; Pem et al., 2024). Several described species may be conspecific, underscoring the need for a comprehensive taxonomic revision (Németh et al., 2023). An integrative approach that combines

detailed morphological assessment with multigene phylogenetic analyses is lacking and is essential to clarify species boundaries within *Ampelomyces*.

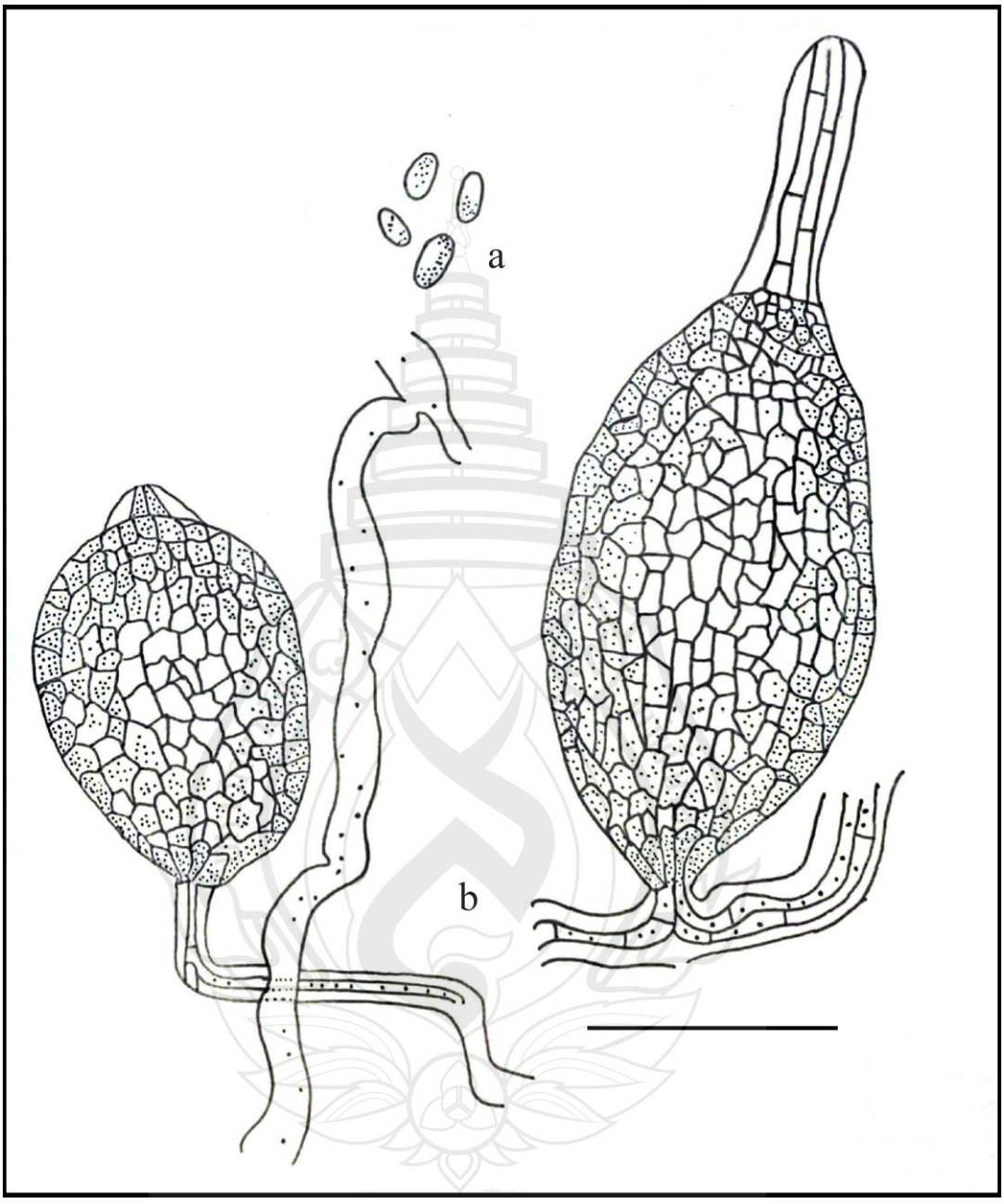


Figure 5.12 *Ampelomyces quisqualis*

Figure 5.12, a Conidia. b Pycnidia. Scale bar = 20 μm. (Redrawn from Gautam & Avasthi, 2016).

Eudarluca Speg., Revta Mus. La Plata 15(2): 22 (1908)

Figure 5.13

Index Fungorum number: IF 1921

Facesoffungi number: FoF 00245

Spegazzini (1908) introduced *Eudarluca*, with *E. australis* as the type species. This species was found associated with the uredinia of *Uredo cannae* on living leaves of *Canna* (Spegazzini, 1908). To date, *Eudarluca* comprises nine species (Species Fungorum, 2025).

All species are fungicolous or hyperparastic. These include *E. biconica*, found on the stromata of *Botryosphaeria* (*Botryosphaeriaceae*), *E. brenesii*, associated with *Phyllachora* (*Phyllachoraceae*), *E. caricis*, which occurs on various rust fungi (Ex: *Puccinia* spp., *Uredo* spp,), *E. connata* reported on the stroma of *Cyclostomella oncophora*, *E. indica*, associated with *Uredo amomi*, *E. mycophila*, inhabits rust fungi, *E. quinqueseptata* observed on the stromata of *Botryosphaeria dothidea*, and *E. venezuelana* reported on a hyphomycete (Kajamuhan et al., 2015; Sun et al., 2019a; Index Fungorum, 2025).

The sexual morph of *Eudarluca* is characterized by scattered, solitary to gregarious ascomata that are immersed to semi-immersed, uni- to multi-loculate, and are subglobose to irregular. These structures are glabrous, dark brown to black, and possess a central ostiole with a minute papilla. The peridium is thin-walled and composed of brown to dark brown, flattened, pseudo-parenchymatous cells arranged in a *textura angularis*. The hamathecium consists of numerous filamentous, distinctly septate, and frequently anastomosing broadly cellular pseudoparaphyses. The asci are bitunicate, fissitunicate, cylindrical, and short-pedicellate, containing eight spores. They have rounded apices with a well-developed ocular chamber. The ascospores are phragmosporous, arranged in a biseriate manner, and are fusiform to oblong with rounded ends. They are pale brown, septate, and possess smooth walls (adapted from Phookamsak et al., 2014).

Eriksson (1966) classified *E. australis* as a synonym of *E. caricis*, which is primarily known in its asexual form as *Sphaerellopsis*. Studies, including morphological and ITS sequence comparisons, suggest that *Eudarluca* belongs in *Leptosphaeriaceae*, but a definitive connection between *Eudarluca* and *Sphaerellopsis* remains unconfirmed (Zhang et al., 2012; Phookamsak et al., 2014).

Sequence data is available only for *E. caricis* in GenBank (2025). *Eudarluca* is classified within *Phaeosphaeriaceae* (Phookamsak et al., 2014; Hyde et al., 2024a).

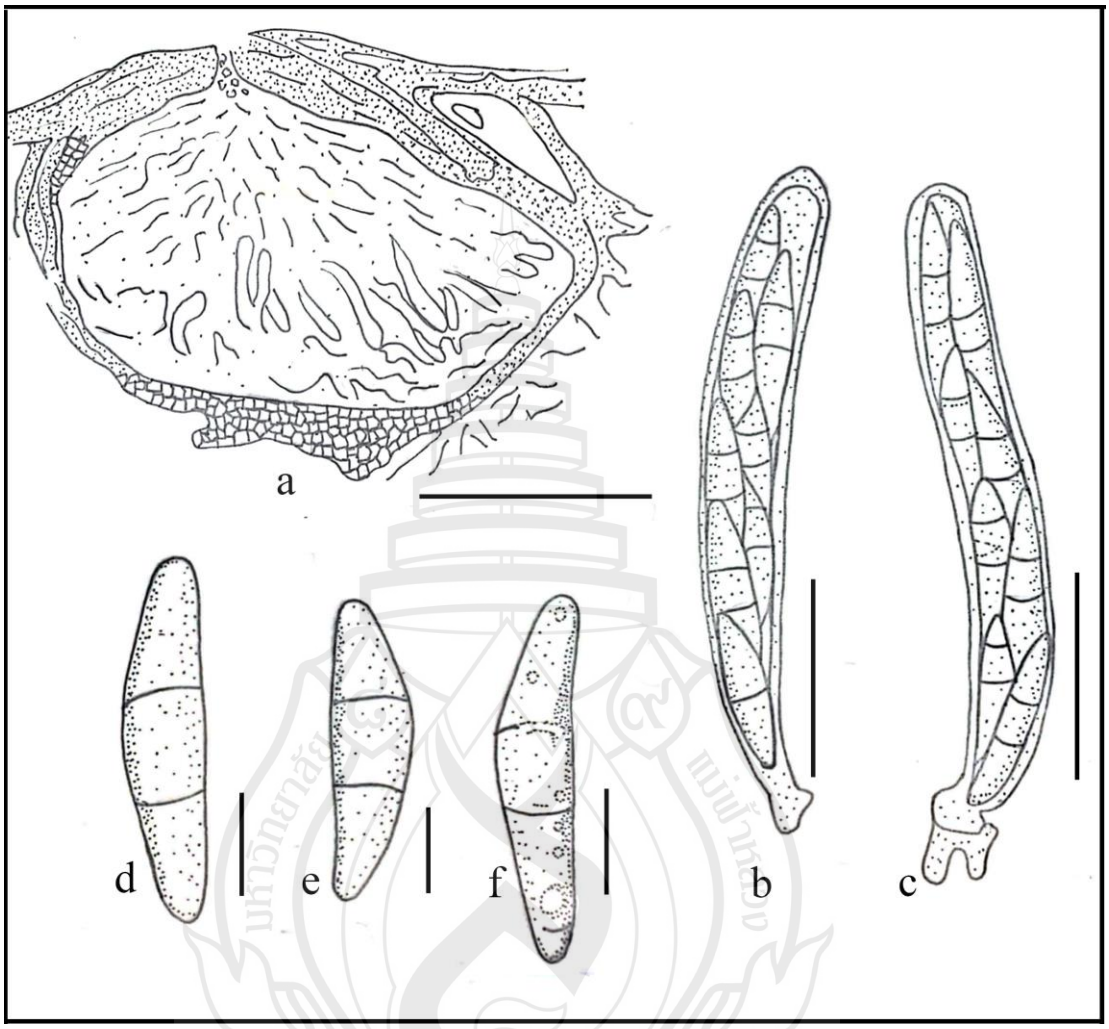


Figure 5.13 *Eudarluca australis*

Figure 5.13, a. Section through ascoma. b, c. Asci. d–f. Ascospores. Scale bars: a =100µm, b, c =20µm, d–f = 5µm (Adapted from Phookamsak et al., 2014).

Roussoellaceae Jian K. Liu, Phook., D.Q. Dai & K.D. Hyde

Immotthia M.E. Barr, Mycotaxon 29: 504 (1987)

Figure 5.14

Index Fungorum number: IF 25106

Facesoffungi number: FoF 08362

Barr (1987) established *Immotthia*, designating *I. hypoxylon*, formerly *Amphisphaeria hypoxylon*, as the type species. *Immotthia atrograna* and *I.*

atroseptata were also included in the genus (Barr 1993, 2002). Upon re-examining the type specimens, Jaklitsch et al. (2002) concluded that *I. hypoxylon* is conspecific with *I. atrograna*. Jiang et al. (2021) subsequently added *Immotthia bambusae* to the genus. There are four species listed under *Immotthia* in Species Fungorum (2025). These species are hyperparasitic on *Annulohypoxylon* spp. (*Hypoxylaceae*), *Hypoxylon* spp. (*Hypoxylaceae*), and *Pestalopezia rhododendri* (*Helotiales*), or as saprobes on decorticated wood (Barr 1993, 2002; Jaklitsch et al., 2002; Akulov & Hayova, 2016; Jiang et al., 2021). They have been found in Austria, Belgium, China, France, Italy, Lithuania, the Netherlands, Norway, Poland, Puerto Rico, Russia, Sweden, Switzerland, Thailand, the USA, Ukraine, and Venezuela (Jaklitsch et al., 2002; Akulov & Hayova, 2016; Jiang et al., 2021).

The sexual morph of *Immotthia* is characterized by small to medium-sized, globose to subglobose ascomata that form on a blackened hypostroma. The asci are bitunicate, fissitunicate, and cylindrical. The ascospores are, brown to reddish-brown, ellipsoidal to fusiform, 1-septate, smooth or slightly verrucose (Hyde et al., 2017; Hongsanan et al., 2020). The asexual morph of *Immotthia* has been described as coelomycetous and identified as *Coniothyrium parasitans*. This form produces enteroblastic, phialidic, doliiform to ampulliform, or cylindrical, smooth and hyaline conidiogenous cells. The conidia are brown, ellipsoidal, smooth-walled, and aseptate (Hyde et al., 2017; Hongsanan et al., 2020). The connection between the sexual and asexual morphs of *Immotthia* has not been definitively established (Jiang et al., 2021). Due to the lack of available DNA sequence data, the family-level classification of *Immotthia* has been uncertain, relying solely on morphological characteristics. This has led to its placement in different families by various authors (Barr 1987, 2002; Jaklitsch et al., 2002; Akulov & Hayova, 2016; Hyde et al., 2017; Doilom et al., 2018; Jiang et al., 2021). Currently, *Immotthia* is placed within *Roussoellaceae*, in *Pleosporales* (Hyde et al., 2024a).

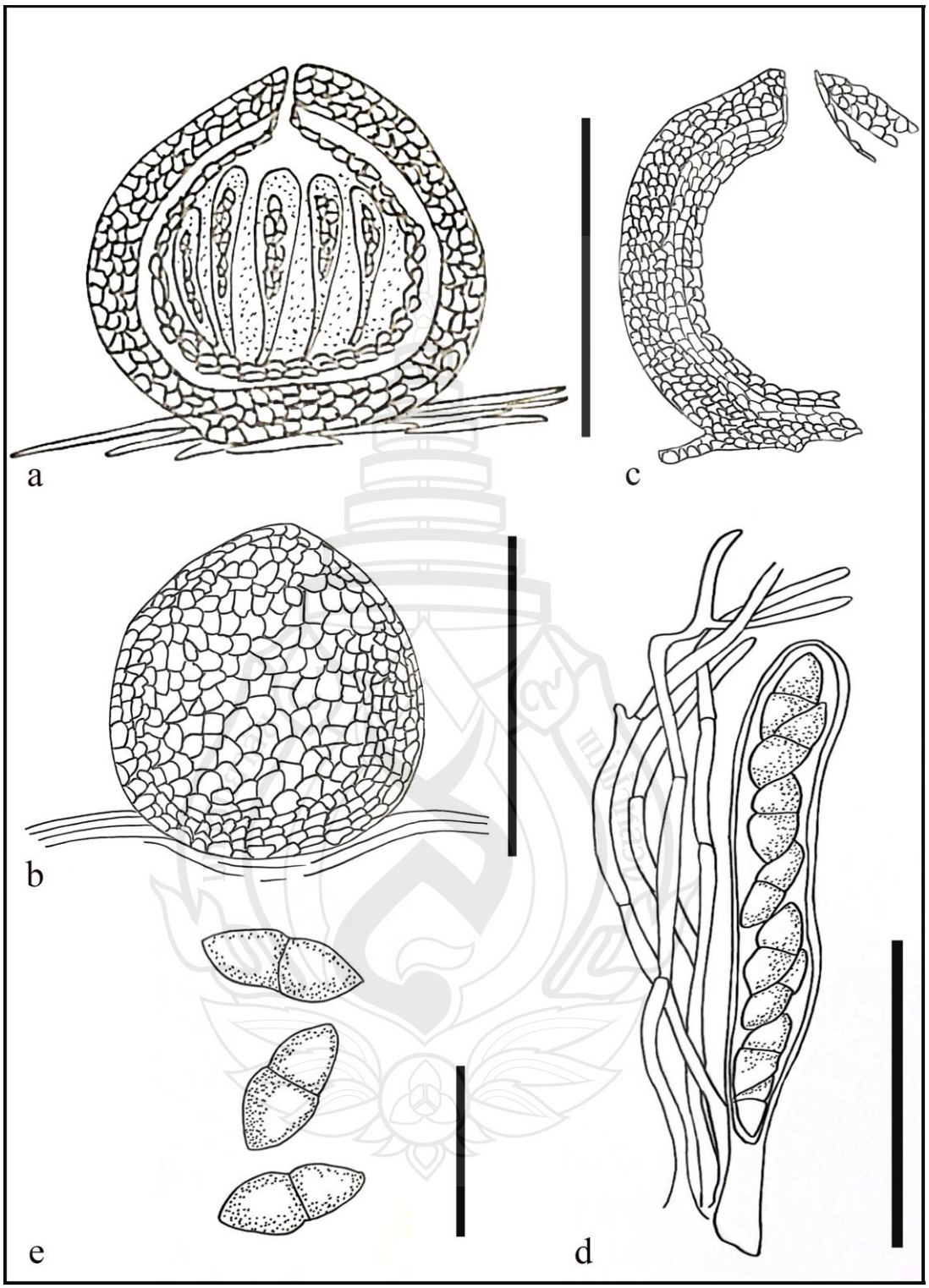


Figure 5.14 *Immotthia atrograna*

Figure 5.14, a. Vertical section of the ascomata. b. Surface view of ascomata. c. Peridium. d. Ascus and part of the hamathecium. e. Ascospores. Scale bars a, b, c = 250 μm, d = 40 μm, e = 13 μm. (Redrawn from Akulov & Hayova, 2016).

Dothideomycetes* orders *incertae sedis

Acrospermales Minter, Peredo & A.T. Watson

Acrospermaceae Fuckel

Pseudovirgaria H.D. Shin, U. Braun, Arzanlou & Crous, Stud. Mycol. 58: 87 (2007)

Figure 5.15

Index Fungorum number: IF 504564

Facesoffungi number: FoF 06487

Pseudovirgaria was established by Arzanlou et al. (2007), with *P. hyperparasitica* as the type species. Braun et al. (2011) added *Pseudovirgaria grisea* which was previously known as *Rhinotrichum griseum* to the genus. *Pseudovirgaria* is recognized for its hyperparasitic nature on rust fungi (Arzanlou et al., 2007; Braun et al., 2011). *Pseudovirgaria hyperparasitica*, was found on *Frommeëlla* sp., *Phragmidium* sp. (*Phragmidiaceae*) and *Pucciniastrum agrimoniae* (*Pucciniastraceae*) in Korea (Arzanlou et al., 2007), whereas *P. grisea* was reported on *Phragmidium* spp. in Austria and Italy (Braun et al., 2011). *Pseudovirgaria* comprises two species (Species Fungorum, 2025). Molecular phylogenetic analyses have placed *Pseudovirgaria* within *Acrospermaceae* (Hudson et al., 2019).

Pseudovirgaria is characterized by branched, septate, smooth, thin-walled, hyaline to pale brown hyphae. The conidiogenous cells are hyaline to pale brown, integrated into creeping hyphae, terminal or intercalary, polyblastic, and exhibit sympodial proliferation with a subcylindrical to geniculate rachis. The conidiogenous loci are conspicuous. Conidia are solitary, formed holoblastically, more or less obovoid, straight to slightly curved, asymmetrical, aseptate, and vary from hyaline to subhyaline or very pale olivaceous-brown. They have a conspicuous hilum that is truncate to rounded, unthickened, and either not or slightly darkened-refractive. Conidial secession is schizolytic (Arzanlou et al., 2007).

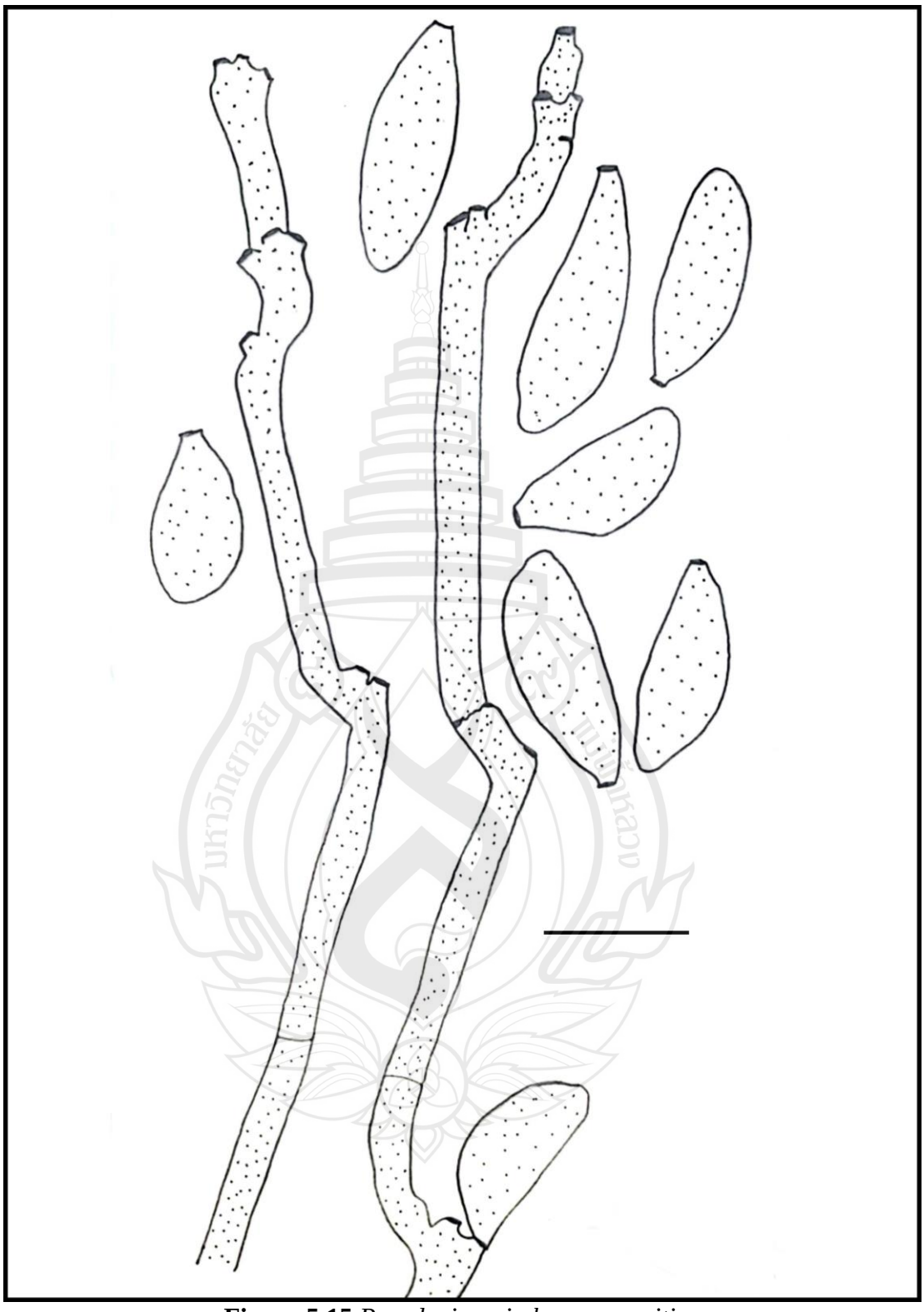


Figure 5.15 *Pseudovirgaria hyperparasitica*

Figure 5.15, Scale bar = 10 μm. (Redrawn from Arzanlou et al., 2007)

Dothideomycetes* families *incertae sedis

Paranectriellaceae Boonmee & K.D. Hyde

Paranectriella (Henn. ex Sacc. & D. Sacc.) Magnus, Botan. Zbl. 98: 587 (1905)

Figure 5.16

Index Fungorum number: IF 3708

Facesoffungi number: FoF 07887

Paranectriella was introduced as a subgenus of *Paranectria* (Hennings, 1904). It was validated by Saccardo and Saccardo (1905). Von Höhnel (1910) elevated *Paranectriella* to the rank of a distinct genus. There are eight species listed under *Paranectriella* in Species Fungorum (2025). All of these species have been documented as mycoparasites/hyperparasites: *Paranectriella arcuata* on *Asterina* sp. (*Asterinaceae*), *P. hemileiae* on *Hemileia* sp. (*Zaghouaniaceae*), *P. imperconspicua* on *Discodothis filicum (Parmulariaceae*), *P. juruana* on the stroma of *Auerswaldia miconiae*, *P. meliolicola* on *Meliola* species, *P. miconiae* on *Microthyriaceae*, *P. minuta* on *Meliola* spp. (*Meliolaceae*), and *P. stromaticola* on a fungal stroma growing on the leaves of *Berlinia* (Sun et al., 2019a; Bermúdez-Cova et al., 2023b; Index Fungorum, 2025). These species have been reported in several countries, including Benin, Brazil, China, Indonesia, Panama, Puerto Rico, Tanzania, and Uganda (Bermúdez-Cova et al., 2023b; Pem et al., 2024; Index Fungorum, 2025).

The sexual morph of *Paranectriella* is characterized by superficial, crustose, solitary, and scattered ascostromata, which are white to light orange and have a fleshy texture. These structures are soft and surrounded by sparse, hyaline hairs. They are multi-loculate, with the ascomata positioned in a peripheral outer layer. The asci are 8-spored, bitunicate, fissitunicate, cylindrical to oblong-clavate, apedicellate, and rounded at the apex. The ascospores are broadly fusiform, arranged in a bi-seriate manner, and hyaline. They are narrowed at both ends, 3-septate, slightly constricted at the septa, and exhibit apical spine-like appendages (Hyde et al., 2013; Hongsanan et al., 2020). The asexual morph is hyphomycetous and staurosporous (Hyde et al., 2013; Hongsanan et al., 2020).

Wijayawardene et al. (2014) synonymized *Araneomyces* under *Paranectriella*. Rossman et al. (2015) proposed the conservation of *Paranectriella* over *Araneomyces*.

Previously, *Paranectriella* was classified within *Tubeufiaceae* (Barr, 1980; Rossman 1987). Based on morphology, Hyde et al. (2013) excluded *Paranectriella* from *Tubeufiaceae* and established *Paranectriellaceae*, to accommodate this genus. *Paranectriellaceae* is placed among the *Dothideomycetes* families *incertae sedis* (Wijayawardene et al., 2020). In terms of molecular data for this genus, only the LSU sequence data for *Paranectriella minuta* is available in GenBank (2025). Additional sequence data are necessary to confirm the placement of *Paranectriella* within *Paranectriellaceae*.

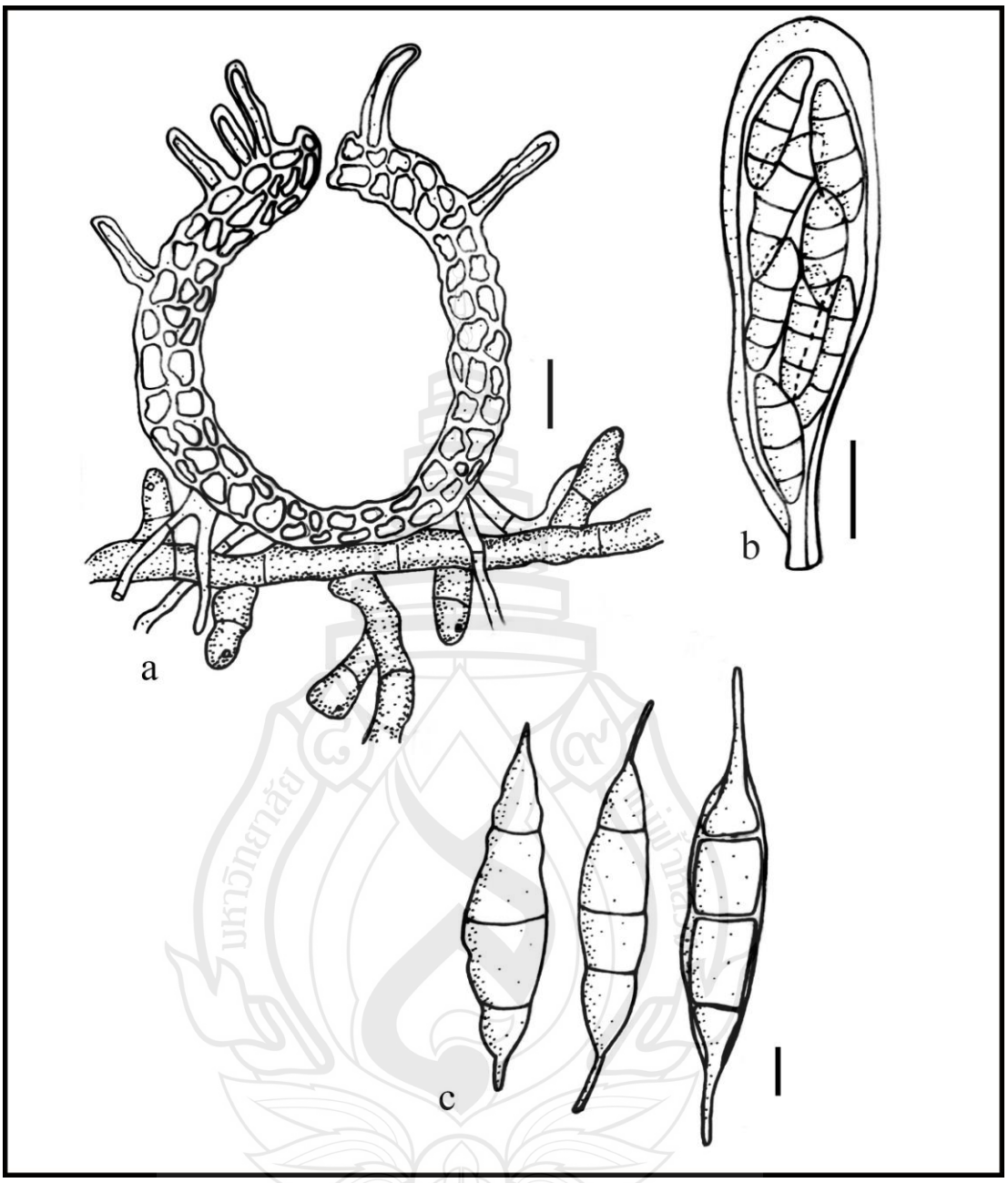


Figure 5.16 *Paranectriella minuta*

Figure 5.16, a. Pseudothecium on hyphae of *Meliola* sp. b. Ascus with ascospores. c. Ascospores. Scale bars: a = 15 µm, b = 10 µm, c = 3 µm. (Redrawn from Bermúdez-Cova et al., 2023b).

Trichothyriaceae Theiss.

Pachythyrium G. Arnaud ex Spooner & P.M. Kirk, Mycol. Res. 94(2): 228 (1990)

Figure 5.17

Index Fungorum number: IF 25378

Facesoffungi number: FoF 06897

Arnaud (1953) introduced the name *Pachythyrium* for *Bertia parasitica* (syn: *Trichothyrina parasitica*), which was found as a fungicolous species on *Eutypa lata* (*Diatrypaceae*) in France. However, this combination was not validly published at that time. Therefore, Spooner and Kirk (1990) validated the generic name "*Pachythyrium*" with *P. parasiticum* as the type species. *Pachythyrium* is characterized by, flat-turbinate, ostiolate ascomata. The asci are eight-spored, and the ascospores are hyaline, uniseptate, and setulate (Spooner & Kirk, 1990). Hawksworth et al. (1995) and Lumbsch and Huhndorf (2010) classified *Pachythyrium* as a member of the *Microthyriaceae*. Wu et al. (2011) assigned it to *Trichothyriaceae* based on thyriothecial characteristics. *Pachythyrium* remains monotypic (Species Fungorum, 2025). There is no molecular data available for *Pachythyrium* in GenBank (2025).

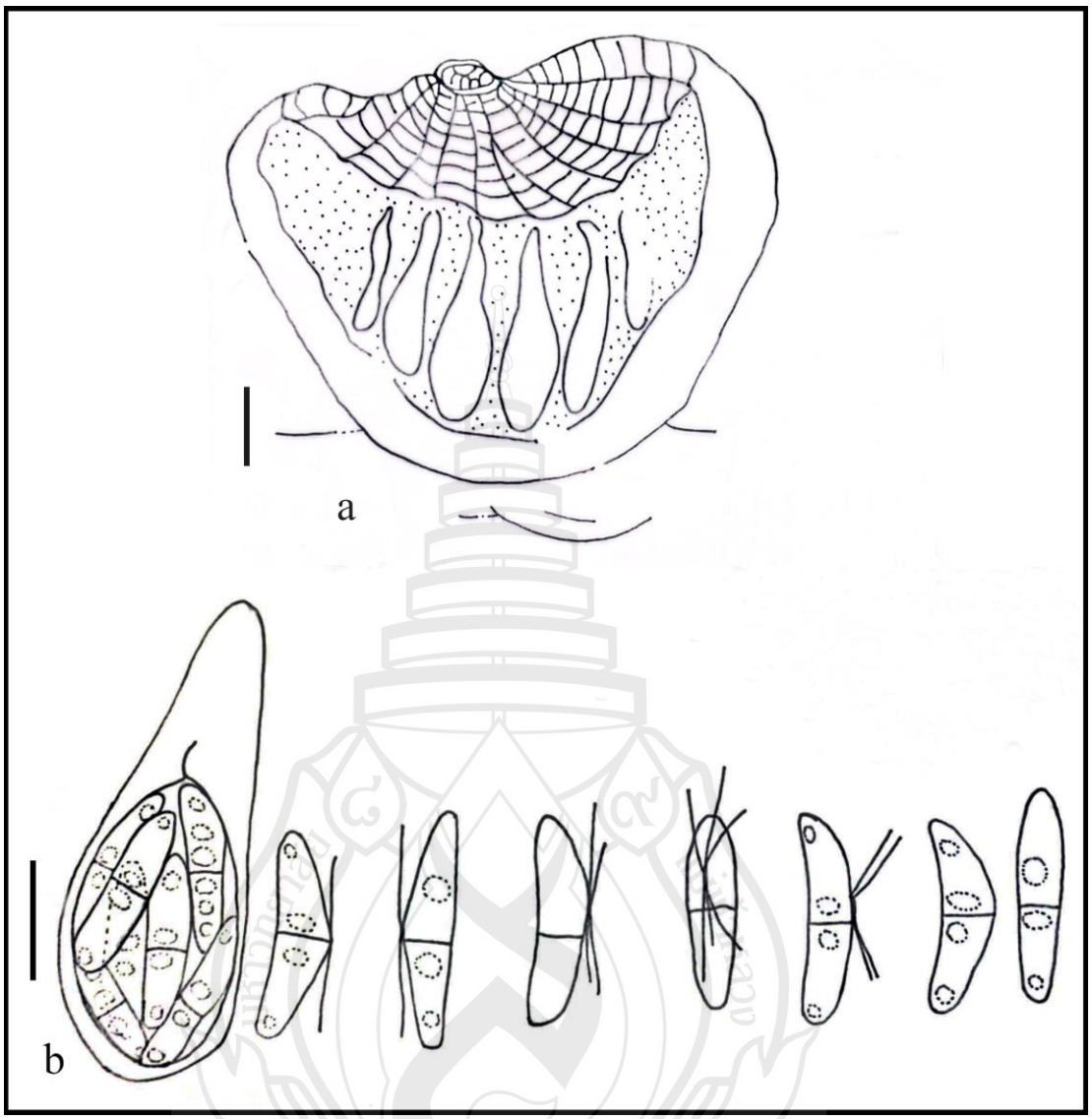


Figure 5.17 *Pachythyrium parasiticum*

Figure 5.17, a. Diagrammatic section through young thyriothecium. b. Ascus and ascospores. Scale bars = 10 µm. (Redrawn from Ellis 1977 (as *Trichothyrina parasitica*)).

Dothideomycetes* genera *incertae sedis

Acanthostigmella Höhn., Annls mycol. 3(4): 327 (1905)

Figure 5.18

Index Fungorum number: IF 17

Acanthostigmella was described by von Höhnel (1905), with the type species, *A. genuflexa* collected from Austria. Species of this genus are saprobes associated

with different plant hosts from Austria, Canada, Tobago and the UK (Farr et al., 2021). Moreover, *A. pallida* has been reported from the UK as a fungicolous species colonizing the stromata of *Hypoxylon mammatum* (*Hypoxylaceae*) (Sun et al., 2019a; Farr et al., 2021). Watanabe et al. (2001) has reported that bioactive compounds from *Acanthostigmella* sp. have potent antifungal activity.

However, the taxonomic placement of this genus has been debatable. *Acanthostigmella* is distinguished from all genera in *Tubeufiaceae* by its small ascomata, featuring a distinct papilla surrounded by setae, the absence of pseudoparaphyses, largely obovoid to fusoid asci, and 2–3-septate, yellow-brown ascospores (von Höhnel, 1905; Barr, 1977). The asexual morph of *Acanthostigmella* are hyphomycetous, helicosporous, dictyosporous, and xenosporium-like, as noted by Hyde et al. (2011). However, any asexual morph has not yet been linked to the generic type of *Acanthostigmella*.

Barr (1977, 1980) and Rossman (1987) proposed placing *Acanthostigmella* in *Herpotrichiellaceae* (*Chaetothryriales*) instead of *Tubeufiaceae*. Untereiner et al. (1995) assigned *Acanthostigmella* to *Dothideomycetes*. Subsequently, Boonmee et al. (2014) re-evaluated the holotype specimen of *A. genuflexa* and designated the genus as *incertae sedis* within *Dothideomycetes*. To date, there are six species listed under *Acanthostigmella* in Species Fungorum (2025), whereas *A. brevispina* has molecular data available in GenBank (2025). Therefore, to accurately place the genus taxonomically, DNA sequence data is required.

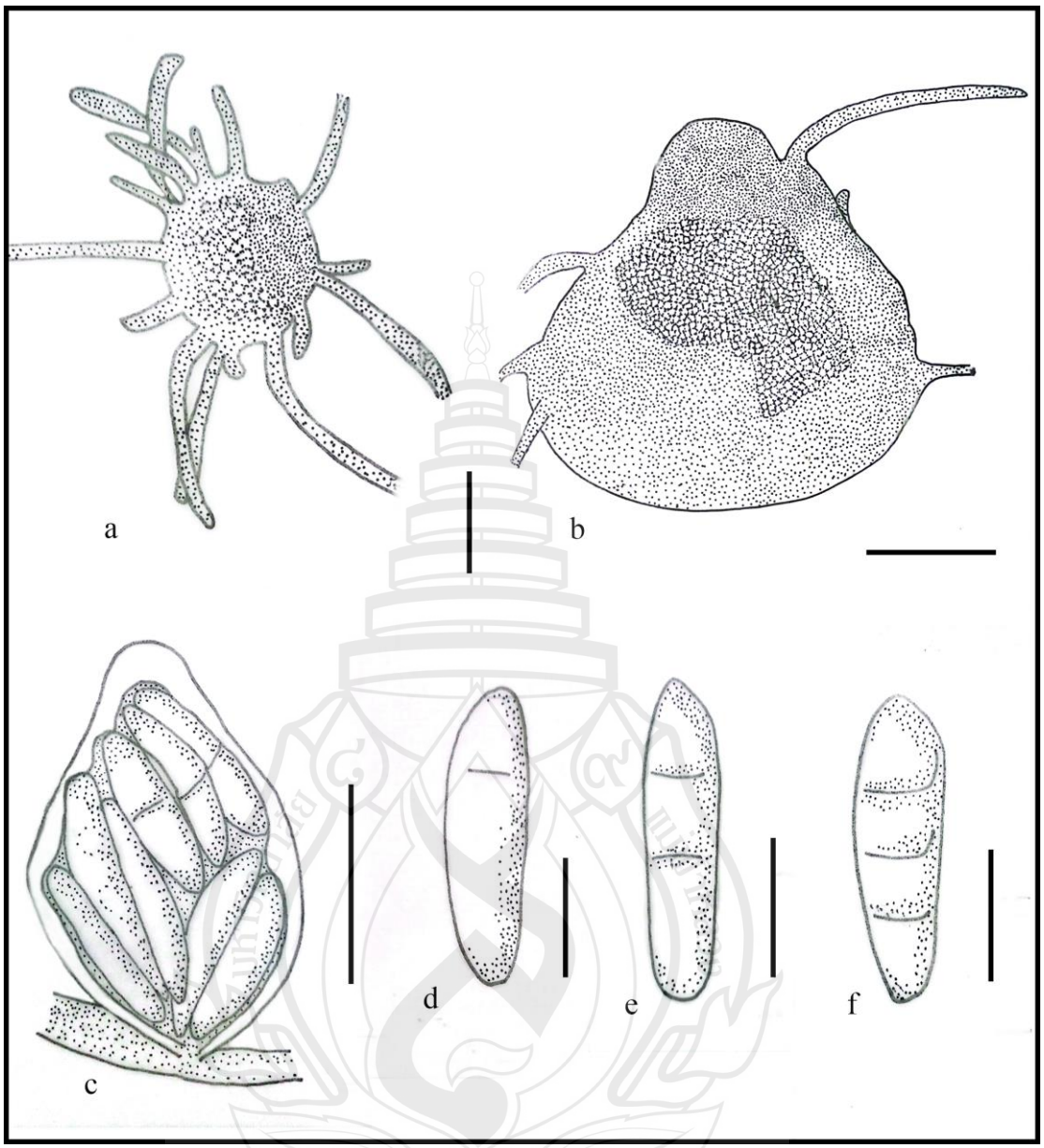


Figure 5.18 *Acanthostigmella genuflexa*

Figure 5.18, a. Ascomata with long setae. b. Peridial wall. c. Ascus. d–f. Ascospores. Scale bars: b = 40 μm, a = 20 μm, c =10 μm, d–f = 5 μm. (Adapted from Boonmee et al., 2014).

Catulus Malloch & Rogerson, Canad. J. Bot. 56(19): 2344 (1978)

Figure 5.19

Index Fungorum number: IF 851

Catulus was introduced by Malloch and Rogerson (1978), with *C. aquilonius* as the type species. This species was discovered as a hyperparasite on the stromata of

Seuratia millardetii (*Seuratiaceae*), which was growing on living needles of *Abies balsamea* in Canada (Malloch & Rogerson, 1978). To date, *Catulus* remains monotypic (Species Fungorum, 2025), with no sequence data currently available in GenBank (2025). It is classified under the *Dothideomycetes* genera *incertae sedis* (Hyde et al., 2024a).

The sexual morph of *Catulus* is characterized by ovoid, pale yellow-brown, ostiolate ascomata with a prosenchymatous peridial wall. Asci develop from a basal hymenium, are clavate to cylindrical, inamyloid, and lack a differentiated apical ring. Paraphyses are absent. The ascospores are clavate, hyaline, two-celled, and bear three distinctive apical setae resembling whiskers (adapted from Malloch & Rogerson, 1978). The asexual morph of the genus remains unknown.

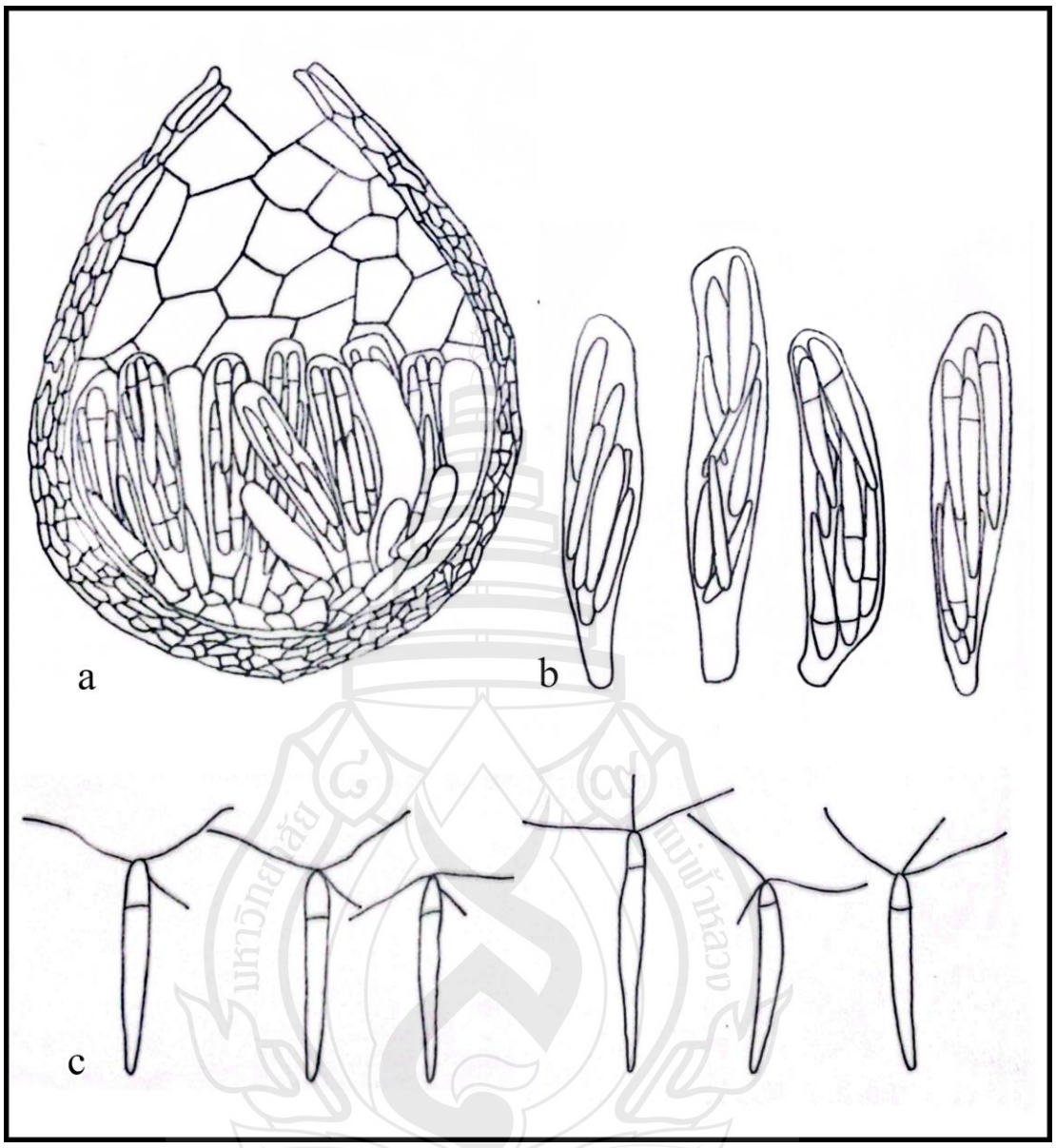


Figure 5.19 *Catulus aquilonius*

Figure 5.19, a. Longitudinal section through a nearly matured ascoma. b. Asci. c. Ascospores. (Redrawn from Malloch & Rogerson, 1978).

Chaetocrea Syd., Annls mycol. 25(1/2): 18 (1927)

Figure 5.20

Index Fungorum number: IF 943

The genus *Chaetocrea* was established by Sydow (1927), with *C. parasitica* as the type species. This species was described as a mycoparasite on *Cyclostomella*

disciformis (syn. *Peltistroma disciforme*), which parasitized the leaves of *Nectandra sanguinea* in Costa Rica (Sydow, 1927).

The asexual morph of *Chaetocrea* has not yet been observed or described. The sexual morph of *Chaetocrea* is characterized by superficial ascomata that are solitary or gregarious, globose to subglobose, membranous, and white to pale yellow. These structures are typically covered with apically branched setae. The peridium consists of whitish-yellow cells of *textura angularis*. The hamathecium is composed of filiform, septate, branched, hyaline pseudoparaphyses that develop over the asci. Asci are bitunicate, cylindrical, short-pedicellate, and contain eight spores. The ascospores are elongate-clavate, often slightly curved, hyaline, and pluriseptate (Sydow, 1927; Boonmee et al., 2014).

As of Species Fungorum (2025), *Chaetocrea* remains monotypic. No DNA sequence data are available for this genus in GenBank (2025). *Chaetocrea* was classified within the *Hypocreaceae*, and it was transferred to *Tubeufiaceae* by Rossman et al. (1999). However, based on detailed morphological examination, Boonmee et al. (2014) reassigned the genus to the *Dothideomycetes* genera *incertae sedis*, a placement that has since been adopted by subsequent authors (Hyde et al., 2024a; Pem et al., 2024).

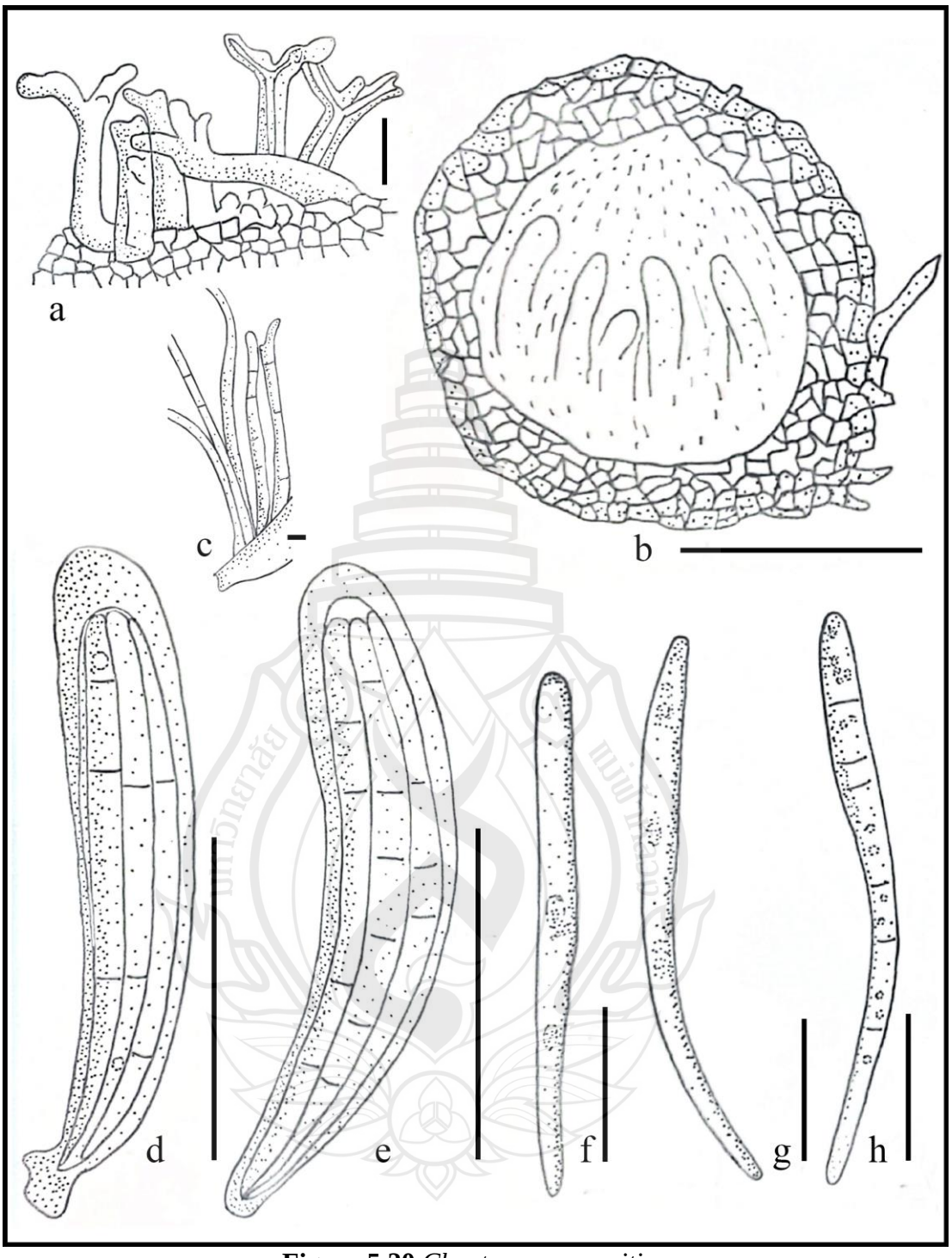


Figure 5.20 *Chaetocrea parasitica*

Figure 5.20, a. Apically branching setae. b. Section of an ascoma. d Peridium. c. Pseudoparaphyses. d, e. Asci. f–h. Ascospores. Scale bars: b = 100µm, d, e = 50µm, a, f–h = 20µm, c = 5µm (Adapted from Boonmee et al., 2014).

Chionomyces Deighton & Piroz., Mycol. Pap. 128: 74 (1972)

Figure 5.21

Index Fungorum number: IF 7619

Deighton and Pirozynski (1972) established *Chionomyces*, designating *C. meliolicola* (syn. *Monacrosporium meliolicola*) as the type species. *Chionomyces* comprises seven recognized species (Species Fungorum, 2025).

Chionomyces meliolicola is a hyperparasite on *Amazonia* spp., *Irenopsis* spp., and *Meliola* spp. in tropical regions of East and West Africa and the Dominican Republic (Deighton & Pirozynski, 1972). Similarly, *Chionomyces chorleyi* and *Chionomyces sclerochitonis* were described as hyperparasites on *Meliola* spp. (*Meliolaceae*), *C. chorleyi* occurs in East and West Africa, while *C. sclerochitonis* is found in East and West Africa as well as in Brunei (Deighton & Pirozynski, 1972). Matsushima (1975) expanded the genus by adding *C. vacuocellularis*, isolated from the rotting bark of *Quercus* in Japan. Matsushima (1983) described two additional species: *C. ontariensis*, isolated from submerged leaves of *Acer saccharum* in Ontario, Canada, and *C. ponapensis*, found on rotten bark of *Artocarpus communis* in the Federated States of Micronesia. Sutton (1993) further contributed to the genus with *C. ellipsoideus*, a fungicolous species found on ascomata grown on dead stems in Malawi.

Chionomyces is characterized by a whitish, superficial mycelium composed of hyaline, septate, and branched hyphae. The conidiophores are hyaline, smooth, erect, and may be continuous or septate. They exhibit both percurrent and sympodial growth patterns, often within the same conidiophore. Old conidial scars are very slightly and evenly thickened. The conidia are hyaline, fusiform, navicular, or obclavate, tapering towards the apex and frequently rostrate, with a truncate, unthickened hilum. They are typically smooth and three or more septate (Deighton & Pirozynski, 1972). No sequence data for *Chionomyces* is available in GenBank (2025).

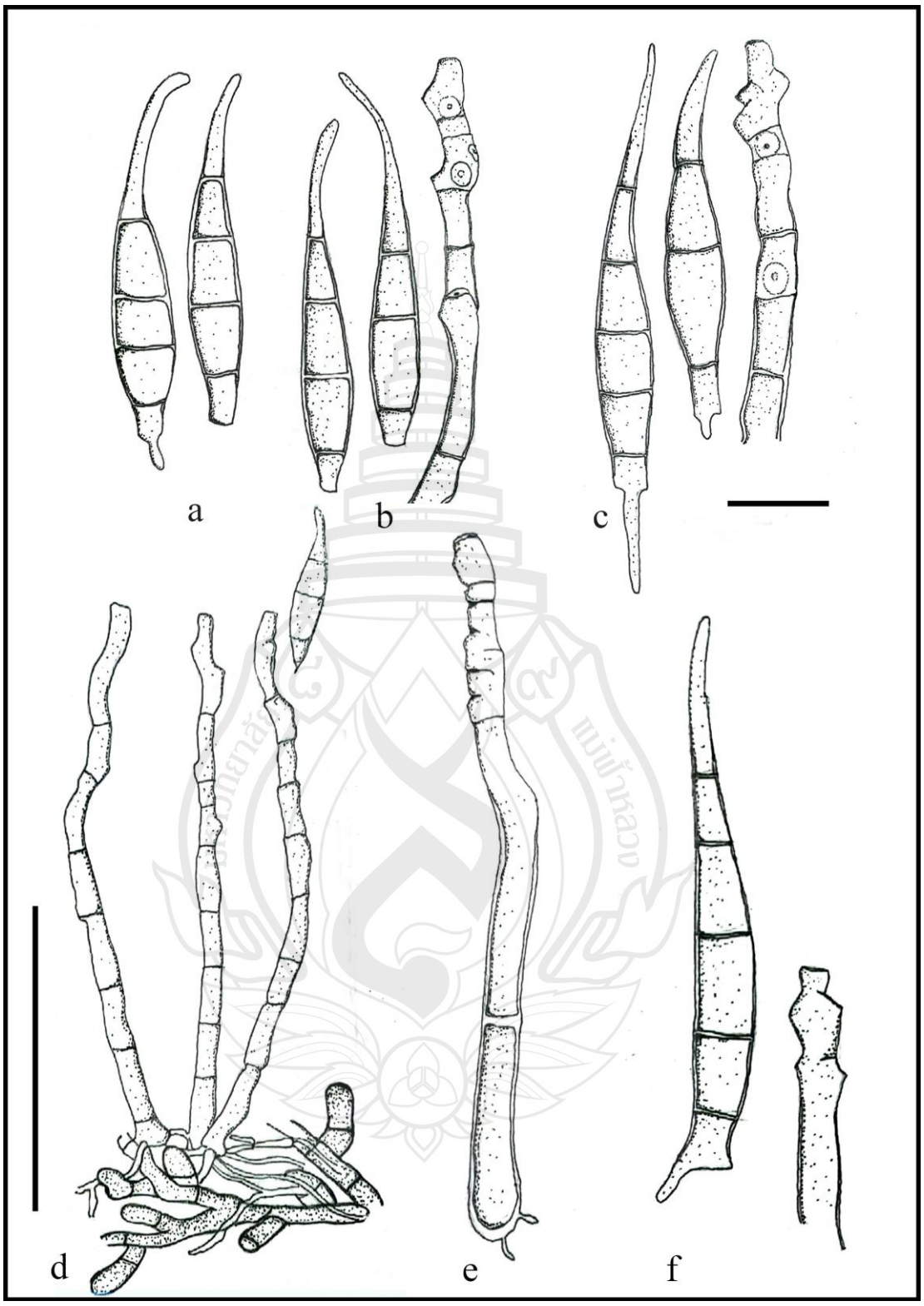


Figure 5.21 *Chionomyces meliolicola*

Figure 5.21, a–f. Conidiophores and conidia. Scale bars: c = 20 μm, d = 100 μm. (Redrawn from Deighton & Pirozynski, 1972).

Malacaria Syd., Annls mycol. 28(1/2): 69 (1930)

Figure 5.22

Index Fungorum number: IF 2983

Malacaria was established by Sydow (1930), with *M. meliolicola* as the type species. This species is a parasite on the mycelium of *Meliola* sp. (*Meliolaceae*) growing on the leaves of *Hamelia erecta* in Venezuela. According to Species Fungorum (2025), seven species epithets are currently recognized within *Malacaria*, all of which are associated with *Meliolales* species (Index Fungorum, 2025). *Malacaria australiensis* was recorded on *Asteridiella fraseriana* (syn. *Irenina fraseriana*) in New South Wales, while *M. entebbeensis* was described from *Meliola artabotrydis* in Uganda (Index Fungorum, 2025). *Malacaria flagellata* was found on *Asteridiella glabra* (syn. *Irenina glabra*), also in Uganda (Index Fungorum, 2025). *Malacaria luxurians* was recorded from *Meliola maesae* and *Meliola panici* in the Philippines (Index Fungorum, 2025). *Malacaria meliolinae* and *M. ugandensis* were both described from hosts in Uganda, with the former found on *Meliolina octospora* and the latter on unidentified *Meliola* species (Index Fungorum, 2025).

The asexual morph of *Malacaria* has not yet been observed. The sexual morph is characterized by superficial, solitary, globose to subglobose ascomata that are pale brown to orange-brown, soft in texture, and possess a membranous wall with a central ostiole. The peridium consists of 3–5 layers of pale orange cells arranged in a *textura angularis*. Asci are 8-spored, bitunicate, oblong to subclavate, rounded at the apex, and obtuse at the base. Ascospores are fasciculate, elongate-fusiform, slightly curved, 3–(−4)-septate, slightly constricted at the septa, pale brown, smooth-walled, apically subacute, and continuous with a basal filiform or thread-like, hyaline appendage (Sydow, 1930; Boonmee et al., 2014).

Based on morphological characteristics, *Malacaria meliolicola* was placed in *Tubeufiaceae*, but was treated as *Dothideomycetes* genera *incertae sedis* by Boonmee et al. (2014), a placement that has been followed by subsequent authors (Hyde et al., 2024a; Pem et al., 2024). LSU sequence data for *M. meliolicola* is currently available in GenBank (2025).

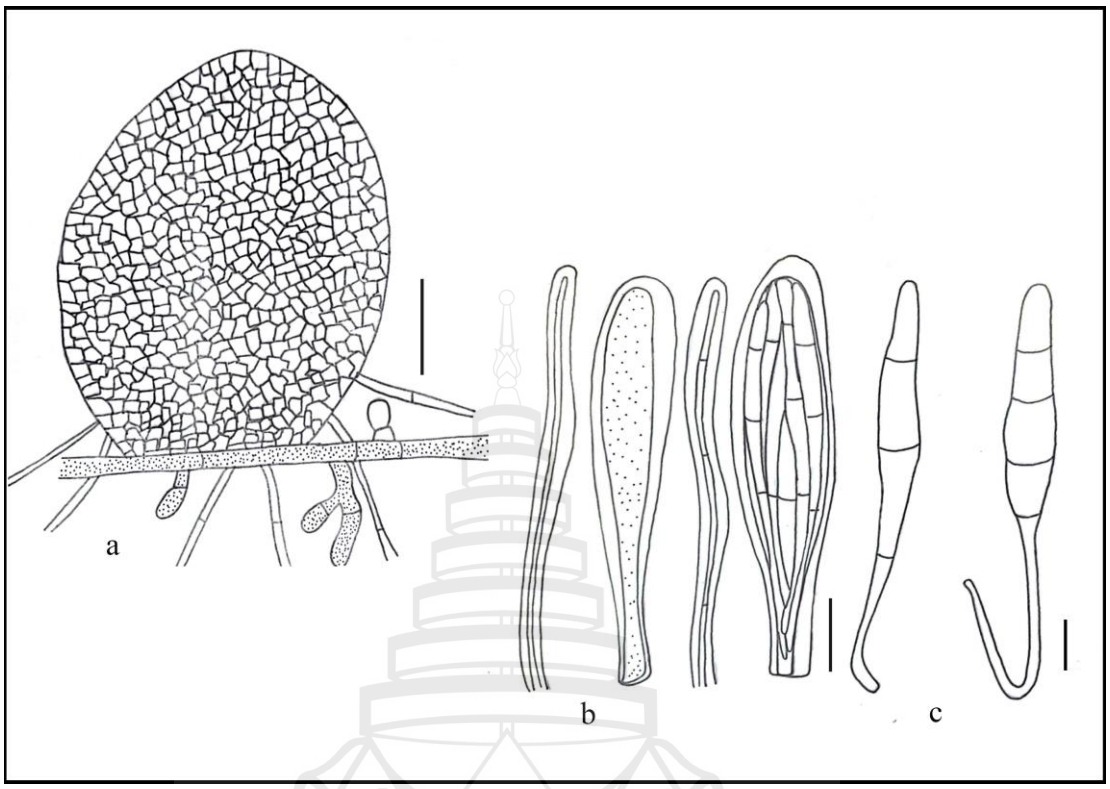


Figure 5.22 *Malacaria meliolicola*

Figure 5.22, a. Pseudothecium on a hypha of *Meliola* sp. b. Young and mature asci with pseudoparaphyses. c. Ascospores. Scale bars: approx. a = 40 μm, b = 10 μm, c = 5 μm. (Redrawn from Bermudez-Cova et al., 2023).

Phragmogibbera Samuels & Rogerson, Mem. N. Y. bot. Gdn 64: 178 (1990)

Figure 5.23

Index Fungorum number: IF 25543

Phragmogibbera was established by Samuels and Rogerson (1990), with *P. xylariicola* as the type species. This species was described as fungicolous on a *Xylaria* sp. (*Xylariaceae*) in Venezuela. A second species, *P. herbicola*, was added to the genus by Zhuang and Li (2009) based on morphological characteristics. However, recent phylogenetic evidence led to the transfer of *P. herbicola* to *Praeclarispora* by Xu et al. (2024). As of Species Fungorum (2025), *Phragmogibbera* remains monotypic, and no molecular data are available for *P. xylariicola* in GenBank (2025). The genus is currently placed under *Dothideomycetes* genera *incertae sedis* (Hyde et al., 2024a).

The sexual morph of *Phragmogibbera* is defined by globose, black, carbonaceous, apapillate ascomata. Asci are bitunicate, 8-spored, broadly cylindrical to narrowly clavate, and possess a prominent ocular chamber. Ascospores are narrowly fusoid, curved, arranged partially to completely in a biseriate manner, with hyaline terminal cells and brown multi-septate central cells, constricted at each septum (adapted from Zhang et al., 2011).

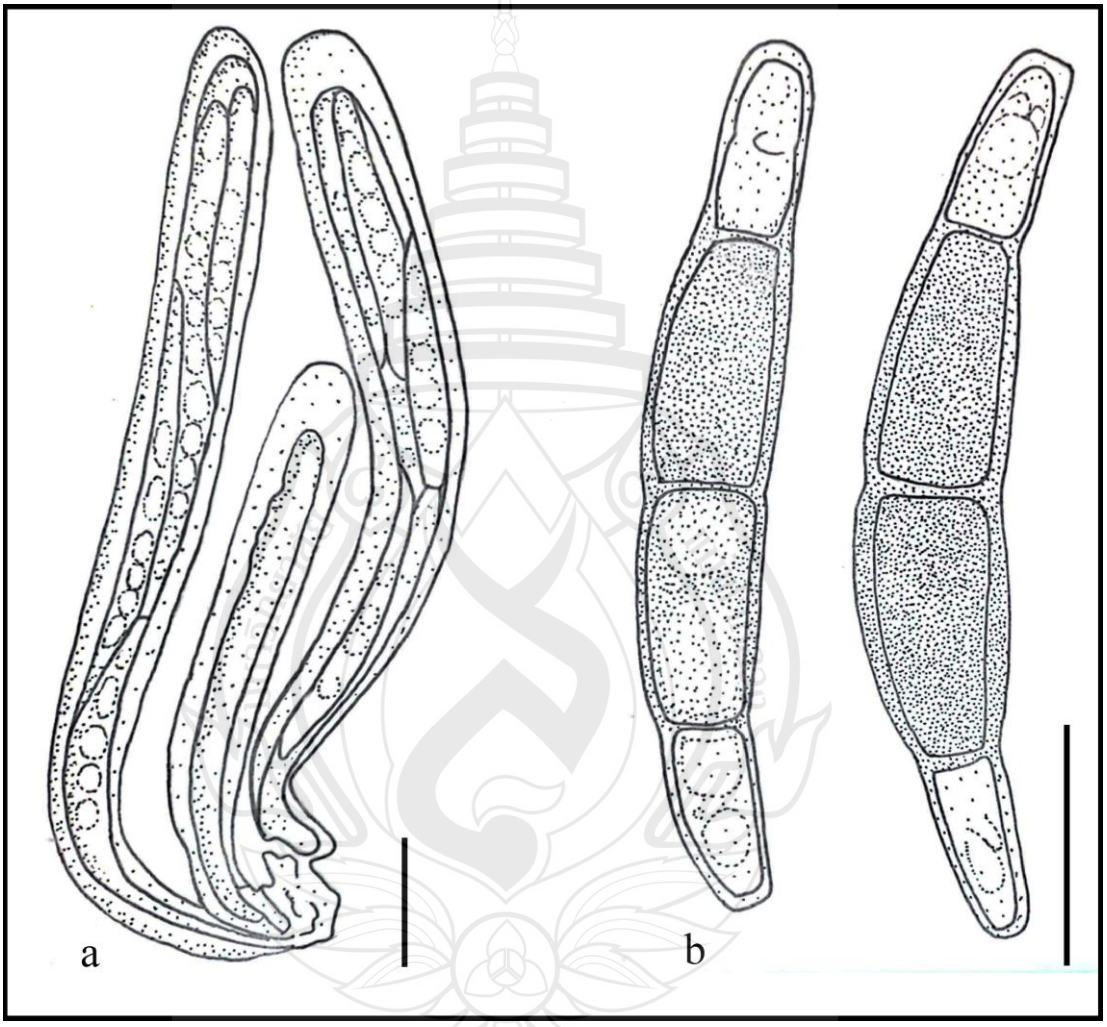


Figure 5.23 *Phragmogibbera xylariicola*

Figure 5.23, a. Clavate immature asci. b. Narrowly fusoid ascospores. Scale bars: a, b =10 μm. (Adapted from Zhang et al., 2011).

Class *Eurotiomycetes* O.E. Erikss. & Winka

Subclass *Chaetothyriomycetidae* Doweld

Chaetothyriales M.E. Barr

Herpotrichiellaceae Munk

Capronia Sacc., Syll. fung. (Abellini) 2: 288 (1883)

Figure 5.24

Index Fungorum number: IF 815

Facesoffungi number: FoF 10371

Capronia (*Chaetothyriales*, *Herpotrichiellaceae*) was introduced by Saccardo (1883), with *C. sexdecimspora* serving as its type species. *Capronia* stands as the largest genus within *Herpotrichiellaceae*, encompassing over 80 species (Phookamsak et al., 2019). According to Species Fungorum (2025), there are a total of 83 epithets listed under *Capronia*.

This is recognized as a homothallic sexual genus that generates asexual morphs resembling black yeasts, which are associated with species found in *Exophiala*, *Ramichloridium*, *Rhinocladiella* species complex, as well as phialophora-like and cladophialophora-like species (Müller et al., 1987; Untereiner et al., 1995; Réblová, 1996; Untereiner, 2000; Phukhamsakda et al., 2022). The sexual morph of the genus is characterised by setose ascomata, devoid of paraphyses, fissitunicate asci, and containing septate or muriform ascospores, which may be hyaline or pigmented (Sánchez et al., 2019; Tian et al., 2021).

Members of *Capronia* have a cosmopolitan distribution. The majority exist as saprotrophs, thriving on decaying wood, bark, and leaves, although some may exhibit fungicolous or lichenicolous habits (Munk, 1957; Müller et al., 1987; Untereiner 1997, 2000; Halici et al., 2010; Untereiner et al., 2011). This fungicolous genus has been frequently encountered on pyrenomycetes (Untereiner et al., 1995). *Capronia baeomycetis* (apothecia of *Baeomyces heteromorphus* (*Baeomycetaceae*)), *C. castlerockii* (associated with *Rhytidhysteron* (*Patellariaceae*)), *C. fungicola* (old pyrenomyetous ascomata), *C. dactylotricha* (associated with *Hapalopilus rutilans* (*Phanerochaetaceae*)), *C. epimyces* (associated with *Nectria* sp.(*Nectriaceae*)), *C. mycophila* (associated with *Antrodia xanthan* (*Fomitopsidaceae*)), *C. nigerrima* (associated with *Diatrype speciebus* (*Diatrypaceae*)), *C. parasitica* (associated with *Hypoxylon cohaerens* (*Hypoxylaceae*)), and *C. porothelia* (associated with pyrenomycetes) are fungicolous species (Sun et al., 2019a).

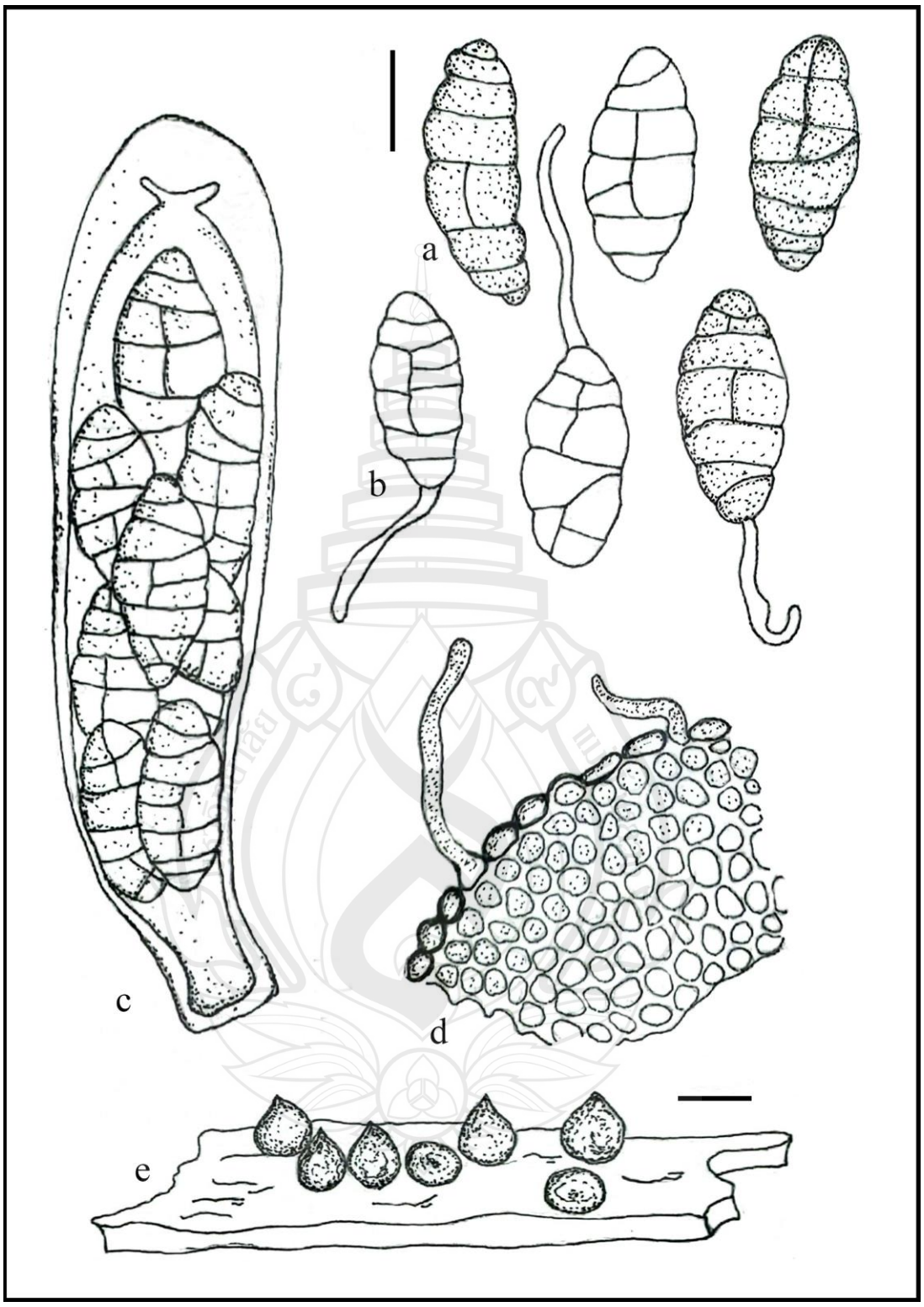


Figure 5.24 *Capronia perpusilla*

Figure 5.24, a. Ascospores. b. Ascospores with germinating hypha. c. Ascus. d. Vertical section of the peridium. e. Ascomata on the substrate. Scale bars: a = 10 μm, e = 100 μm. (Redrawn from Réblová 1996).

Class *Leotiomycetes* O.E. Erikss. & Winka

Helotiales Nannf. ex Korf & Lizoň

Cordieritidaceae Sacc.

Unguiculariopsis Rehm, Annls mycol. 7(5): 400 (1909)

Figure 5.25

Index Fungorum number: IF 5676

Unguiculariopsis Rehm (1909) was established with *U. ilicincola* as the type species. Members of *Unguiculariopsis* are distributed across tropical, subtropical, and temperate regions, occurring on fungi, lichens, and dead plant material (Zhuang, 1988, 2000; Etayo & Sancho, 2008; Kondratyuk et al., 2016; Etayo, 2017). Known fungicolous *Unguiculariopsis* species include: *U. adirondackensis* (associated with *Lachnellula* (*Lachnaceae*)), *U. australiensis* (on *Mollisiella ilicincola* (*Mollisiaceae*) and *Myriangium* sp. (*Myriangiaceae*)), *U. changbaiensis* (associated with a pyrenomycete on decorticated wood), *U. dimorpha* (on a pyrenomycete), *U. godroniicola* (on apothecia of *Godronia confertus* (*Godroniaceae*)), *U. hamatopilosa* (on *Didymosphaeria* sp. (*Didymosphaeriaceae*)), *U. hysterigena* (on *Rhytidhysteron rufulum* (*Patellariaceae*)), *U. ilicincola* (on *Myriangium* sp. (*Myriangiaceae*)), *U. livida* (on *Karstenula* sp. (*Didymosphaeriaceae*)), *U. parasitica* (on *Eutypa lata* (*Diatrypaceae*)), *U. ravenelii* (on *Rhytidhysteron hysterinum*), *U. rehmii* (on *Cucurbitaria berberidis* (*Cucurbitariaceae*)), and *U. subravenelii* (on *Rhytidhysteron* sp.) (Zhuang, 1988; Index Fungorum, 2025; Yu et al., 2025).

The sexual morph of *Unguiculariopsis* features cupulate to discoid or infundibuliform apothecia, sometimes unequal-sided and often strongly enrolled at the margin when dry, usually sessile but occasionally with a short, broad stipe. Receptacle hairs have a swollen base and a fine, curved apex. Asci are inoperculate, inamyloid, cylindrical to fusoid-clavate, containing unicellular, spherical or ellipsoid, hyaline, sub hyaline to pale yellow ascospores. Paraphyses are filiform, septate, branched, and occasionally deformed at the apex (Rehm, 1909; Zhuang, 1988, 2000; Etayo & Sancho, 2008; Kondratyuk et al., 2016; Etayo 2017; Yu et al., 2025).

According to Species Fungorum (2025), there are currently 30 accepted species epithets within *Unguiculariopsis*. The generic delimitation and taxonomic placement of this genus have long been uncertain and the subject of debate (Zhuang, 1988; Suija et al., 2015; Pärtel et al., 2017). *Unguiculariopsis* was assigned to *Hyaloscyphaceae* by Korf (1973). Zhuang (1988) transferred it to *Encoelioideae* within *Leotiaceae* and also introduced *Deltosperma* to represent its asexual morph. Following the adoption of the "One Fungus—One Name" principle, the earlier name *Unguiculariopsis* was retained in preference to *Deltosperma* (McNeill et al., 2012; Johnston et al., 2014). Molecular phylogenetic analyses have shown that the lichenicolous representatives of *Unguiculariopsis* fall within the *Encoelioideae*, *Helotiales*, based on phylogenetic analysis of the combined SSU, LSU, and the 5.8S regions of the ITS (Suija et al., 2015). Subsequently, Pärtel et al. (2017) accepted the placement of *Unguiculariopsis* in *Cordieritidaceae*, supported by analyses of combined SSU, LSU, *rpb1*, *rpb2*, and *tef* sequences. Based on the phylogenetic analyses of a different dataset comprising combined LSU, SSU, ITS, *tef* and *rpb2*, Ekanayaka et al. (2019) excluded *Cordieritidaceae* from the *Helotiales* and reassigned it to the *Cyttariales*. Haelewaters et al. (2021), based on a multi-locus phylogeny involving 15 gene regions, treated *Cyttariales* as a synonym of *Helotiales*. In the latest classification, *Unguiculariopsis* is recognized as a member of *Cordieritidaceae* within the *Helotiales* (Hyde et al., 2024a). Yu et al. (2025) further considered the genus as polyphyletic based on the phylogenetic analyses of a combined LSU, ITS, and SSU dataset.

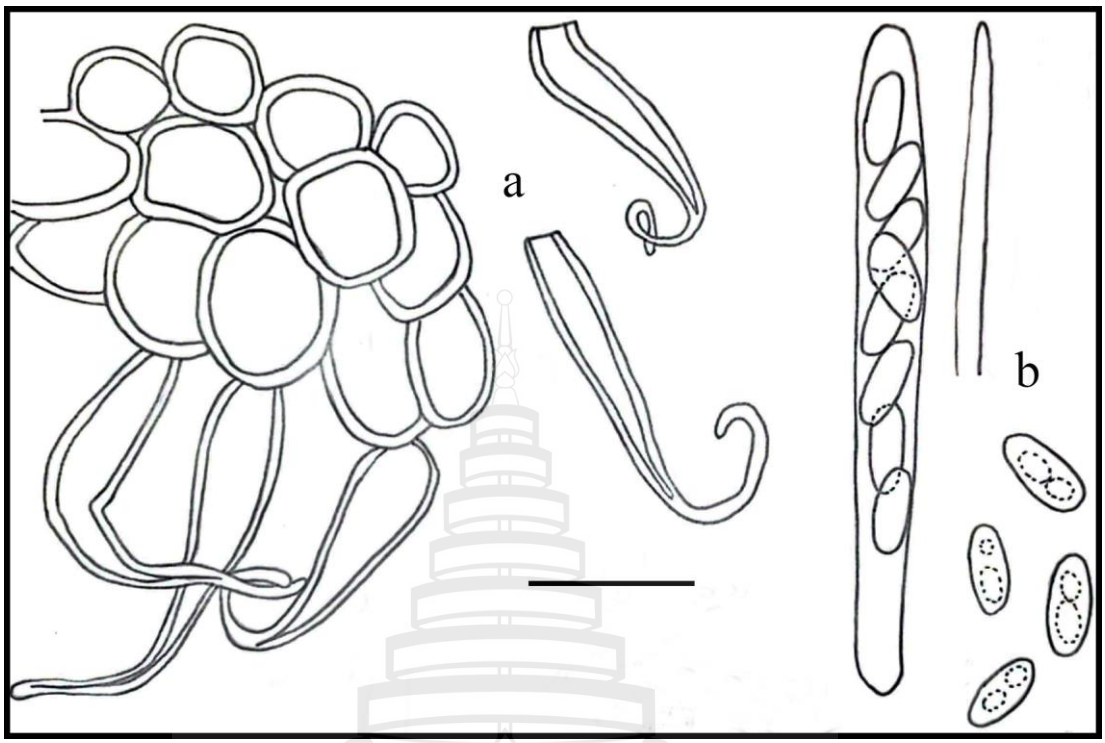


Figure 5.25 *Unguiculariopsis changbaiensis*

Figure 5.25, a. Ectal excipular structure and hairs. b. Ascus, ascospores and paraphyses apex. Scale bars: a, b = 10 µm. (Redrawn from Zhuang 2000).

Hyphodiscaceae Ekanayaka & K.D. Hyde

Hyphodiscus Kirschst., Verh. bot. Ver. Prov. Brandenb. 48: 44 (1906) [1907]

Figure 5.26

Index Fungorum number: IF 2421

Kirschstein (1907) established *Hyphodiscus*, designating *H. gregarius* as the type species. This species was discovered on decaying wood of *Rhamnus frangula* in Germany. Subsequently, Zhuang (1988) determined that *H. gregarius* is identical to *Lachnellula theiodea*. Since the basionym of *L. theiodea* was published prior to *H. gregarius*, a new combination, *H. theiodeus*, was proposed for the type species of *Hyphodiscus* (Zhuang, 1988). Hosoya (2002) proposed *Catenulifera* for the asexual stages of *Hyphodiscus*. The proper classification of *Hyphodiscus* has been a topic of extensive debate for an extended period (Eriksson & Hawksworth, 1993; Baral, 1994; Hosoya, 2002; Hosoya et al., 2011). Ekanayaka et al. (2019) introduced *Hyphodiscaceae*, designating *Hyphodiscus* as its type genus.

Hyphodiscus species are characterized by their small, sessile or short-stalked apothecial ascomata, which may sometimes be gelatinized and hairy. Their paraphyses are hyaline, filiform, septate, and slightly enlarged at the apices. The asci are 8-spored, cylindric-clavate, and either amyloid or non-amyloid, while the ascospores are hyaline, guttulate, and ellipsoid (Hosoya, 2002; Hosoya et al., 2011; Pärtel & Põldmaa, 2011; Ekanayaka et al., 2019). These species typically grow on dead, often decorticated wood of deciduous or coniferous trees (Pärtel & Põldmaa, 2011). *Hyphodiscus ucrainicus* are lichenicolous species associated with *Cladonia* spp. (Suija et al., 2018). Several species in this genus have also been found as fungicolous, growing on decaying polypore fruiting bodies and corticioid fungi (Pärtel & Põldmaa, 2011). Hosoya et al. (2011) suggested that the fungicolous association may be an intrinsic feature of *Hyphodiscus*, promoting ascomata formation. *Hyphodiscus* species have been recorded in several countries worldwide, including Austria, Belarus, Estonia, Finland, Germany, Japan, Mexico, the Netherlands, Russia, Spain, Switzerland, Ukraine, and the USA (Hosoya, 2002; Hosoya et al., 2011; Pärtel & Põldmaa, 2011; Suija et al., 2018; Index Fungorum, 2024). The fungicolous species of this genus include *H. brevicollaris* (associated with *Phellinus* sp. (*Hymenochaetaceae*)), *H. hymeniophilus* (on decaying basidiomata of *Antrodia serialis* (*Fomitopsidaceae*), *Antrodiella hoehnelii* (*Steccherinaceae*), *Piptoporus betulinus* (*Fomitopsidaceae*), *Polyporus* spp. (*Polyporaceae*), and *Trametes versicolor* (*Polyporaceae*)), *H. incrustatus* (on old *Polyporus* spp. (*Polyporaceae*)), *H. stereicola* (on dead basidiomata of *Stereum* spp. (*Stereaceae*)), and *H. theiodeus* (on *Peniophora* spp. (*Peniophoraceae*)) (Raitviir, 2004; Pärtel & Põldmaa, 2011). As of Species Fungorum (2025), there are 16 species listed within *Hyphodiscus*. The DNA sequence data for the ITS, LSU, SSU, *tef*, *tub2*, *rpb1*, and *rpb2* regions for this genus are available in GenBank (2025).

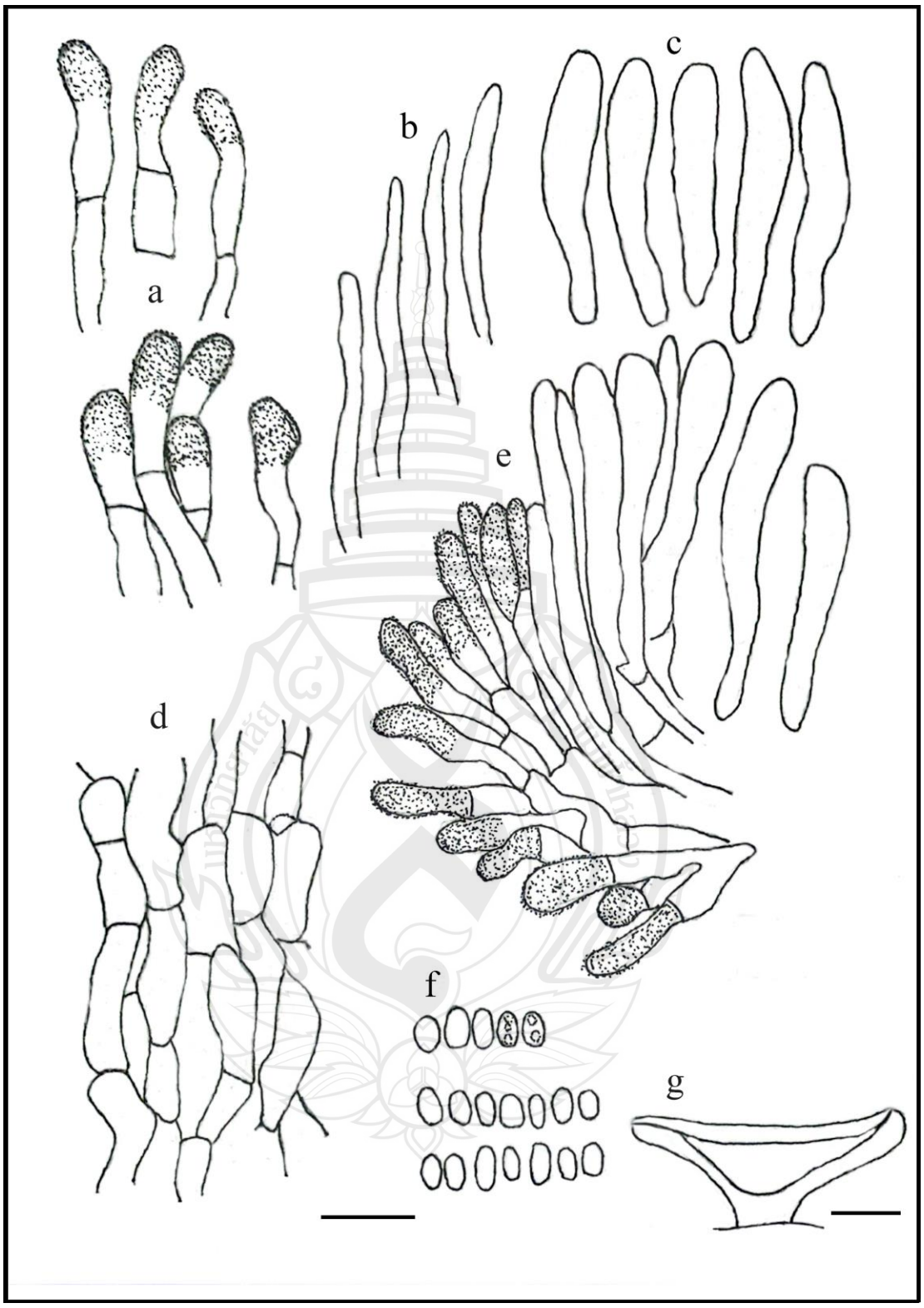


Figure 5.26 *Hyphodiscus hymeniophilus*

Figure 5.26, a. Hairs. b. Paraphyses. c. Asci. d. Ectal cells in squash mount. e. Vertical section showing the margin. f. Ascospores. g. Schematic drawing of an apothecial section showing the outline of the structure without hairs. Scale bars: a–f = 10 μm, g = 100 μm. (Redrawn from Hosoya, 2002).

Helotiales* genera *incertae sedis

Scytalidium Pesante, Annali Sper. agr., N.S. 11(2, Suppl.): cclxiv (1957)

Figure 5.27

Index Fungorum number: IF 9862

Pesante (1957) established *Scytalidium* (*Helotiales, Helotiaceae*) with the type species *S. lignicola*. *Scytalidium* species exhibit a cosmopolitan distribution with a broad host range, being associated with humans, insects, plants, soil, and mushrooms (Dickinson et al., 1983; Carnaúba et al., 2007; Gautam et al., 2015; Peng et al., 2014). *Scytalidium parasiticum* on basidiomata of *Ganoderma* sp. (*Polyporaceae*) and *Scytalidium uredinicola* in aecia of rust fungi (*Cronartium fusiforme* (*Cronartiaceae*)), are myco-parasites (Kuhlman et al., 1976; Goh et al., 2015). *Scytalidium ganodermophthorum* is responsible for the yellow rot on *Ganodorma lucidium* whereas, *Scytalidium auriculariicola* is the causal agent of slippery scar in *Auricularia polytricha* (*Auriculariaceae*) (Kang et al., 2010; Peng et al., 2014).

The asexual morph of *Scytalidium* species is dematiaceous and hyphomycetous. It is characterized by the presence of intercalary or terminal arthroconidia and chlamydospores, as described by Gautam et al. (2015). On the other hand, the sexual morphology has been observed specifically in *Scytalidium parasiticum*. In this species, cleistothecial ascomata develop from coiled ascogenous hyphae. Initially, they are subhyaline to pale yellowish-brown, maturing into dark brown, and possess a wall of *textura epidermoidea*. These ascomata are globose, lack appendages, and have a two-layered wall. The asci are dispersed in the centrum, subglobose to globose, thin-walled, quickly evanescent, eight-spored, and the ascospores are hyaline. They exhibit a greenish fluorescence pigment, have smooth reflective walls, and are globose to subglobose (Goh et al., 2015). To date, there are 29 species listed under *Scytalidium* in Species Fungorum (2025).

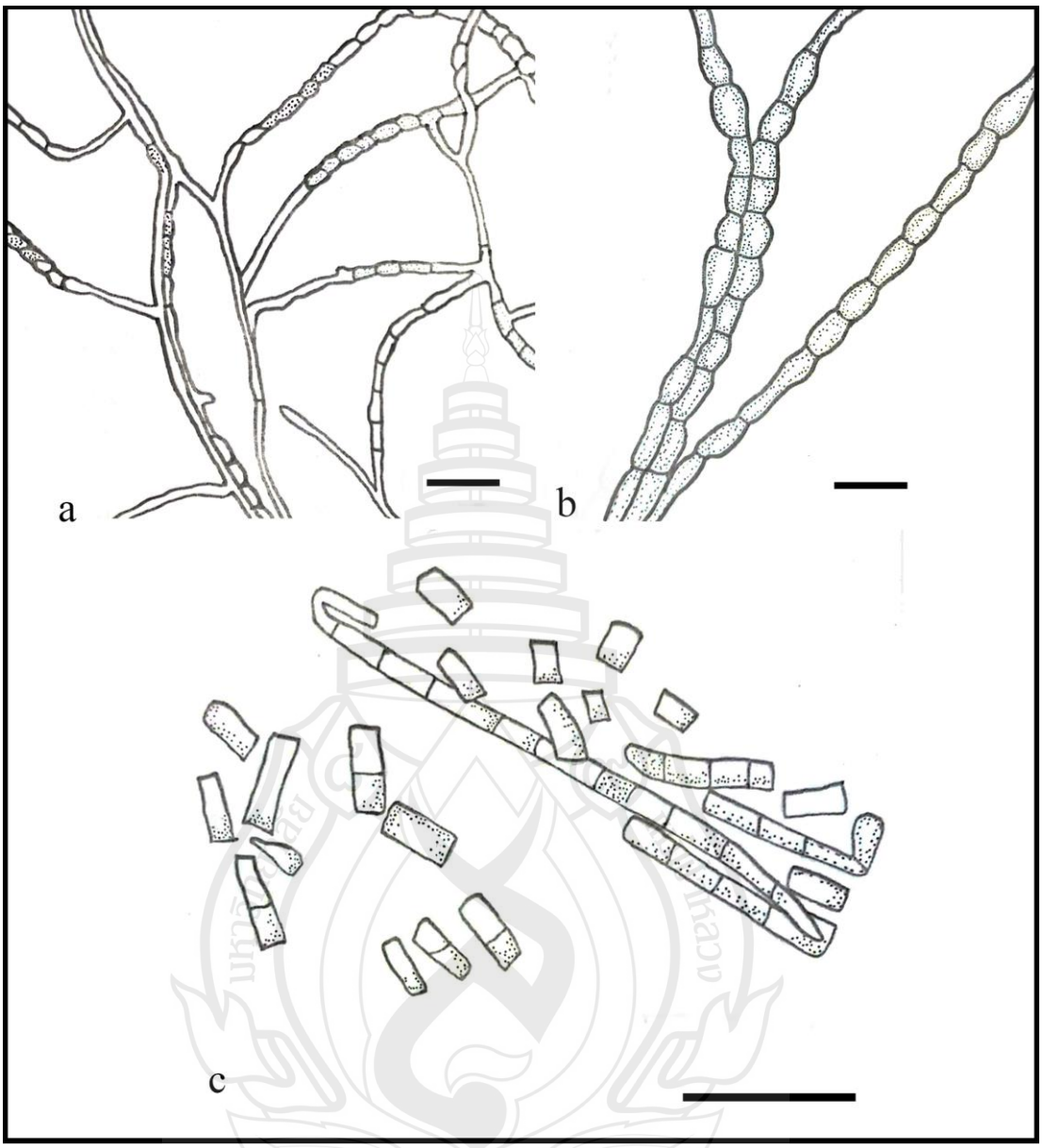


Figure 5.27 *Scytalidium auriculariicola*

Figure 5.27, a. Branched hyphae with developing chlamydoconidia b. Catenate and thick-walled chlamydoconidia. c. Conidia. Scale bars: a, c = 20 μm, b = 10 μm. (Adapted from Peng et al., 2014).

Phacidiales C.E. Bessey

Helicogoniaceae Baral

Eleutheromyces Fuckel, Jb. nassau. Ver. Naturk. 23-24: 183 (1870) [1869-70]

Figure 5.28

Index Fungorum number: IF 8139

Eleutheromyces was proposed by Fuckel (1870) to accommodate *E. subulatus*. Seeler (1943) re-described *Eleutheromycella* and distinguished it from *Eleutheromyces* based on morphological characters. This concept was supported by Sutton (1980). However, Nag Raj (1993) disagreed and considered the *Eleutheromyces* and *Eleutheromycella* to be congeneric. Crous et al. (2014) designated an epitype for *E. subulatus*. Whereas, Crous et al. (2015) introduced an additional species, *E. pseudosubulatus,* to *Eleutheromyces*. However, Li et al. (2020), upon re-examining the type species of *E. mycophila*, suggested that *E. pseudosubulatus* should be synonymized with *E. mycophila*. Consequently, Li et al. (2020) accepted only two species: *E. mycophila* and *E. subulatus* within *Eleutheromyces*. These species are fungicolous on agarics (Crous et al., 2015). *Eleutheromyces subulatus* has been reported on hosts such as *Lentinula edodes* (*Omphalotaceae*), while *E. mycophila* is associated with decaying basidiomata of *Trametes versicolor* (*Polyporaceae*) and *Lactarius scrobiculatus* (*Russulaceae*) (Nag Raj, 1993; Tsuneda et al., 1997; Crous et al., 2015). *Eleutheromyces* species occur in Austria, Canada, Germany, France, Latvia, Sweden, and the UK (Nag Raj, 1993; Crous et al., 2014, 2015; Li et al., 2020).

The asexual morph of *Eleutheromyces* is characterized by yellowish-brown, salmon, or black, pycnidial conidiomata. Conidiomata are oval or globose to subglobose, unilocular, gelatinous, papillate and ostiolate. Conidiophores emerge from all around the cavity of the conidiomata. They are hyaline, often branched, septate, and are encased in mucus. Conidiogenous cells are hyaline, enteroblastic, and phialidic, and range from subcylindrical to lageniform. They are integrated with the conidiogenous loci just below the septa. Conidia are hyaline and can be ellipsoidal, lenticular, or cylindrical. They are unicellular and feature tubular, tapered appendages at each end, which are separated from the main conidium body by septa (adapted from Crous et al., 2014, 2015; Li et al., 2020).

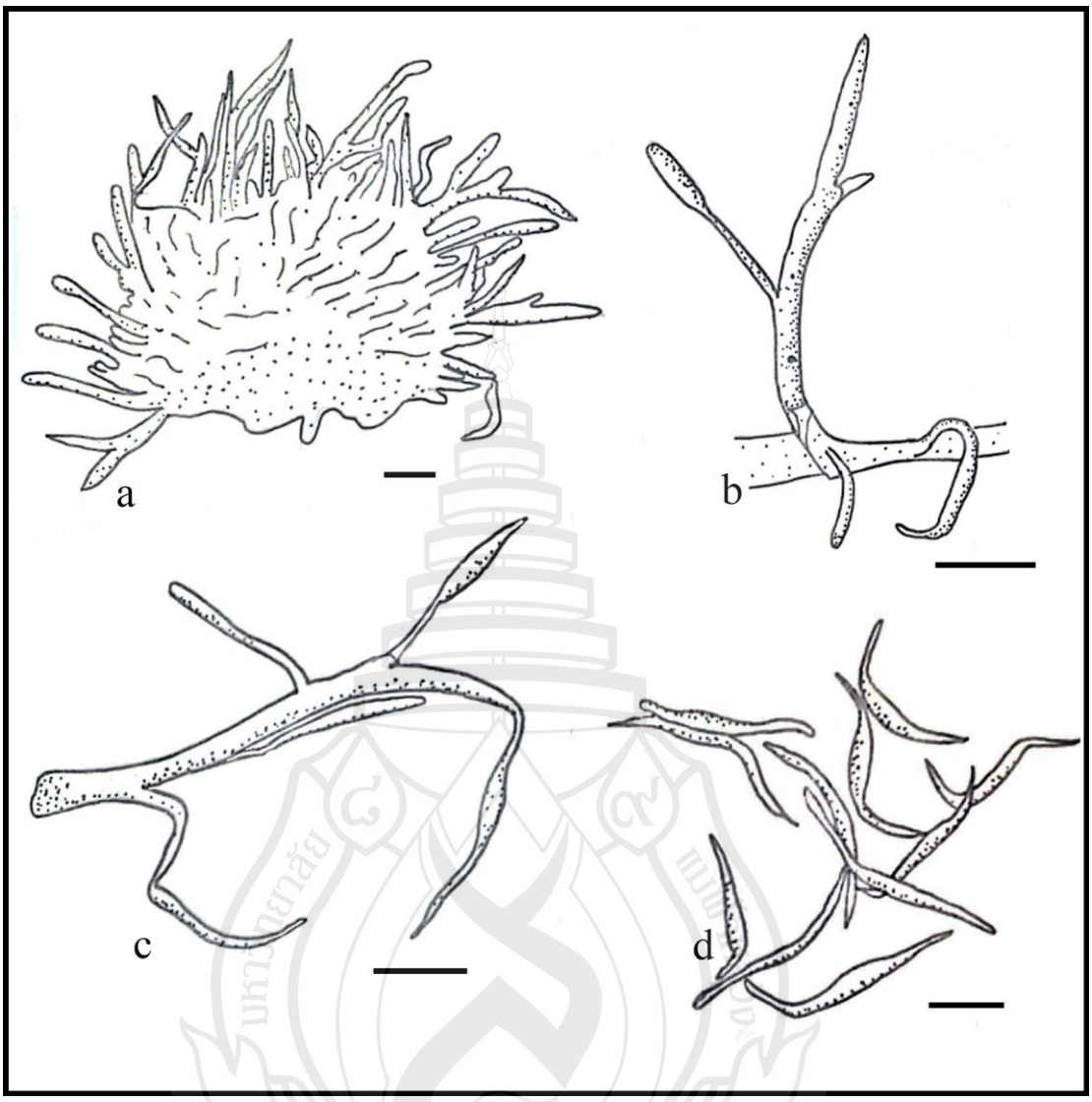


Figure 5.28 *Eleutheromyces subulatus*

Figure 5.28, a–c. Conidiophores giving rise to conidia. d. Conidia. Scale bars: a–d = 10 μm. (Adaped from Crous et al., 2015).

Gelatinipulvinella Hosoya & Y. Otani, Mycologia 87(5): 690 (1995)

Figure 5.29

Index Fungorum number: IF 27591

Hosoya and Otani (1995) established *Gelatinipulvinella*, designating *G. astraeicola* as the type species. This species is fungicolous on *Astraeus hygrometricus* (*Diplocystidiaceae*) in Japan. In the same study, Hosoya and Otani (1995) proposed *Aureohyphozyma* as the asexual morph name for the same species. Since the type species of both genera represent the same species, those two generic names are

synonyms with equal taxonomic standing. However, given the historical preference for naming based on sexual morphs and the wider usage of *Gelatinipulvinella* in the literature, it was recommended that *Gelatinipulvinella* be adopted as the valid name (Johnston et al., 2014). Since the establishment, *Gelatinipulvinella* has remained monotypic (Species Fungorum, 2025).

The sexual morph of *G. astraeicola* is characterized by apothecia that develop on the gelatinous inner surface of the recurved peridial rays of *Astraeus* species (*Diplocystidiaceae*). These apothecia are minute, hyaline, and range in color from gray or brownish-gray to orange-gray when fresh, and become orange-gray upon drying. They are convex, superficial, and weakly embedded in the gelatinous matrix of the host's peridium. The apothecia lack an epithecium, with the hymenium composed of asci and paraphyses, while the subhymenium is undifferentiated. Paraphyses are filiform, septate, simple or branched, and often bent or circinate at the apices. Asci are clavate, thick-walled, eight-spored, and arise from repetitive croziers. Ascospores are ellipsoid, aseptate, hyaline, and smooth-walled, with a multiguttulate to spumose appearance. They are typically biseriate in the upper portion of the ascus, although this arrangement may be indistinct or shift to uniseriate in mature asci (adapted from Hosoya & Otani, 1995).

The asexual morph of *G. astraeicola* is characterized by hyphae that are predominantly immersed or creeping along the substrate, with fine aerial hyphal strands that are straight. Submerged hyphae are slightly thickened and torulose near the center, hyaline, and exhibit even or slightly narrowed apices. Conidiogenous cells are integrated, either intercalary or terminal, and only rarely discrete, appearing as ampulliform cells. These cells more commonly become free, resulting in a yeast-like phase. Conidial production is holoblastic, occurring percurrently in a basipetal order through scars left by previously liberated conidia. These scars form inconspicuous annelations on the conidiogenous cells. The conidia are ellipsoidal, one-celled, hyaline, and may possess a protuberant hilum or lack it (adapted from Hosoya & Otani, 1995).

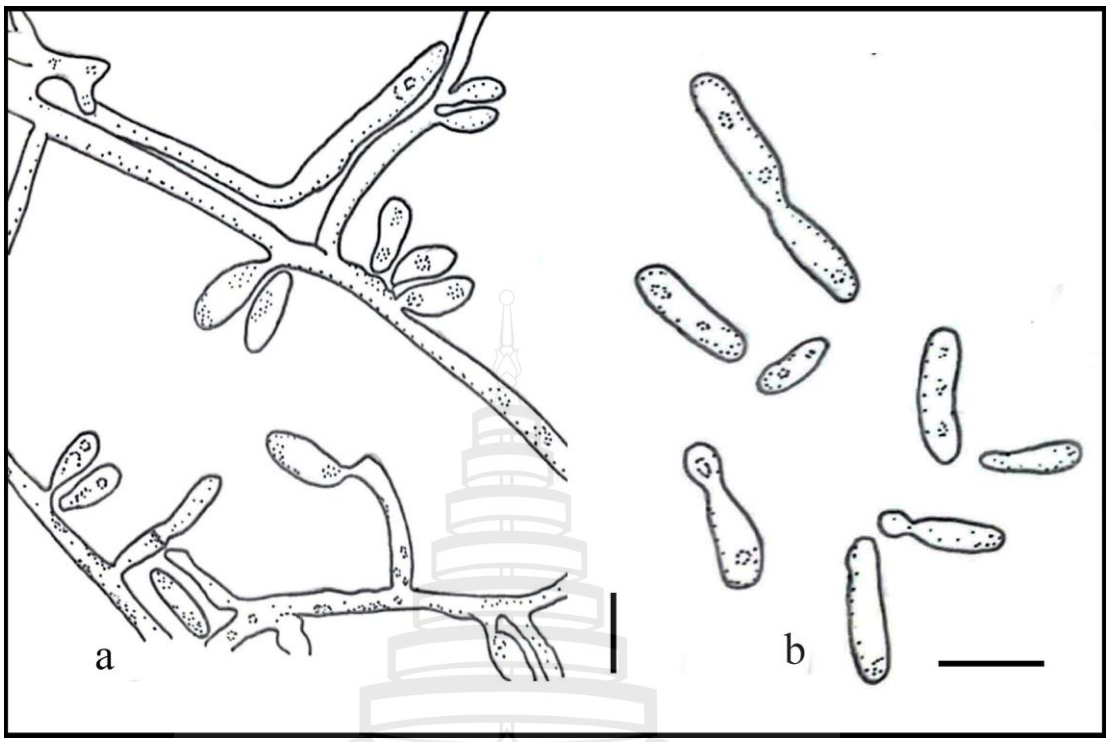


Figure 5.29 *Gelatinipulvinella astraeicola*

Figure 5.29, a. Conidia produced on hyphae. b. Yeast-like budding conidia. Scales bars: a, b = 10 µm. (Adapted from Hosoya & Otani, 1995).

Helicogonium W.L. White, Canadian Journal of Research, Section C 20: 390 (1942)

Figure 5.30

Index Fungorum number: IF 2257

White (1942) established *Helicogonium* (*Phacidiales, Helicogoniaceae*) with *H. jacksonii* as the type species. *Helicogonium jacksonii* was collected as a fungicolous species on *Corticium microsporum* (*Corticiaceae*) collected in Ontario, Canada (White, 1942). Members of *Helicogonium* are fungicolous within the hymenia of other fungi, where they inhibit the development of meiosporangia (Baral, 1999). *Helicogonium* was classified under the *Saccharomycetales* due to the lack of fruiting bodies (Eriksson & Hawksworth, 1993). However, Baral (1999) suggested that *Helicogonium* likely evolved from a lineage within the *Leotiales* that does not produce apothecia. Most species within *Helicogonium* are believed to exhibit drought tolerance (Baral, 1999). This assumption is based on certain morphological

characteristics, including the presence of inamyloid asci and ascoconidia (Baral, 1999).

The sexual morph of *Helicogonium* is distinguished by the absence of apothecia, with ascogenous hyphae growing among the subhymenial hyphae of the host's fruiting body. Asci form among the host's hymenial elements (cystidia and paraphyses), are cylindrical to clavate, and typically contain eight ascospores. Upon maturity, each ascus may contain 30-60 ascoconidia. The asci have hemispherical or conical apices with an inconspicuous to pronounced apical dome, lacking amyloid rings. The ascospores are globose, ellipsoid, or clavate, and rarely filiform or helicoid. They are aseptate or occasionally 1–3-septate, hyaline, and smooth-walled. Ascoconidia often form directly on the ascospores, with each ascospore producing 4 to 8 ascoconidia, which cluster around the ascospore within the living asci (adapted from Baral, 1999).

The asexual morph is characterized by the growth of conidiophores within the hymenium of the host. These conidiophores are hyaline and consist of long, cylindrical, frequently branched cells. Conidiogenous cells form at the upper level of the hymenium and are more or less verticillate, cylindrical, or often lageniform to subulate. The conidiogenous loci exhibit minute internal wall thickening. Conidia are produced acrogenously, are enteroblastic, monophialidic, and lack a collarette (adapted from Baral, 1999).

According to Species Fungorum (2025), there are 29 species of *Helicogonium* listed. The documented species of *Helicogonium* are mycoparasites, having associations mostly with discomycetes of various *Leotiomycetes*, *Orbiliomycetes* and basidiomycetes (Sun et al., 2019, Baral & Perić 2024). These associations occur in Austria, Canada, France, Germany, Lithuania, Luxembourg, Switzerland, and the USA (Baral, 1999; Baral & Kutorga, 2010; Sun et al., 2019a). To date, no molecular data for *Helicogonium* is available in GenBank (2025).

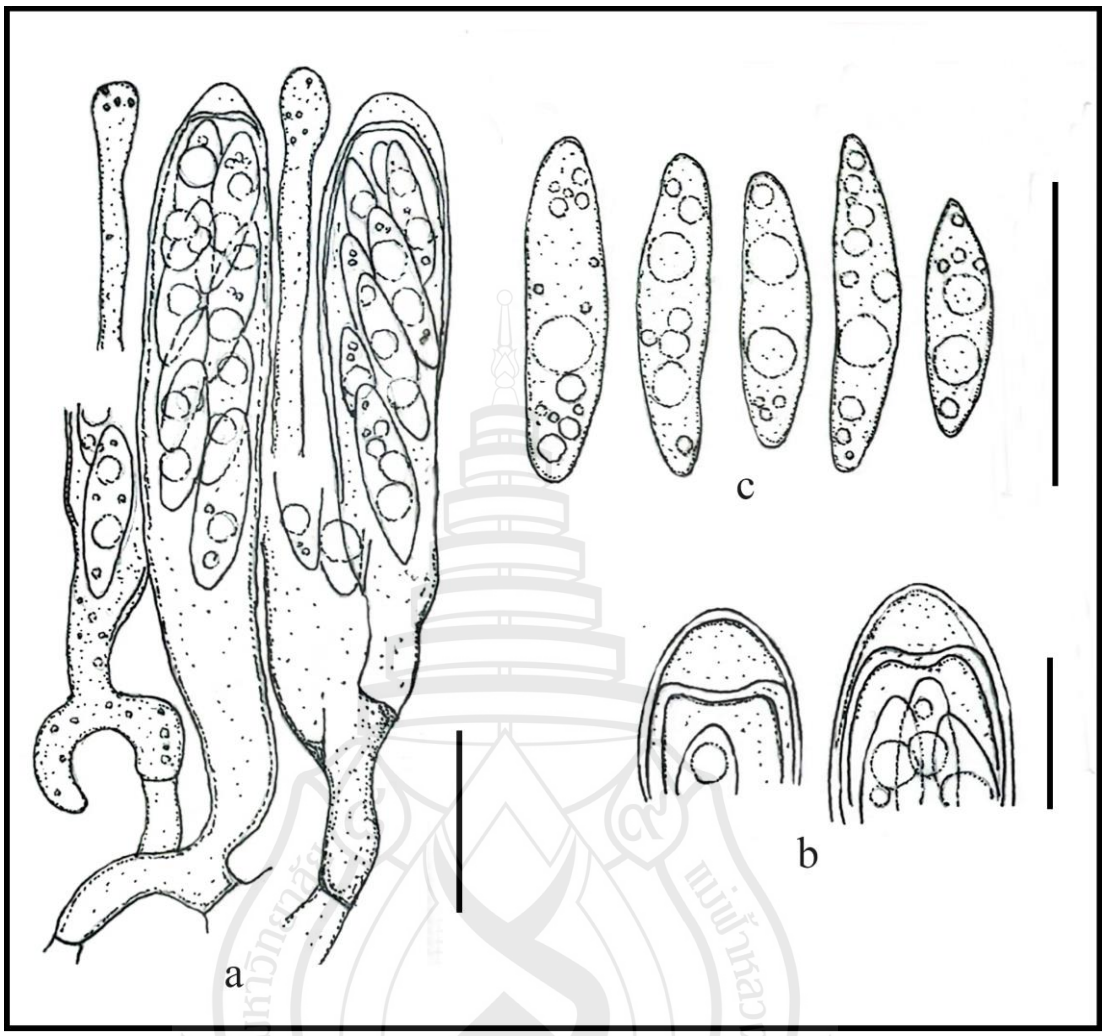


Figure 5.30 *Helicogonium fusisporum*

Figure 5.30, a. Asci (between paraphyses of *Orbilia eucalypti*). b. Ascus apices. c. Ascospores containing lipid bodies. Scale bars: a, c = 10 μm, b = 5 μm. (Redrawn from Baral & Kutorga 2010).

Leotiomycetes* genera *incertae sedis

Gelatinopsis Rambold & Triebel, Notes R. bot. Gdn Edinb. 46(3): 375 (1990)

Figure 5.31

Index Fungorum number: IF 25361

Gelatinopsis was established by Rambold and Triebel (1990) to replace *Micropyxis*, accommodating two species formerly treated as *Micropyxis geoglossi* and *Nesolechia ericetorum*, which were transferred as *G. geoglossi* and *G. ericetorum*, respectively. *Gelatinopsis geoglossi* was designated as the type species (Rambold &

Triebel, 1990). The placement of *G. ericetorum* in *Gelatinopsis* was tentative but accepted by Baral & Marson (2001). Diederich et al. (2010) transferred *G. ericetorum* to *Rhymbocarpus*. Currently, eight species are recognized within *Gelatinopsis* (Species Fungorum, 2025), and it is classified in *Leotiomycetes* genera *incertae sedis* (Hyde et al., 2024a).

Gelatinopsis is characterized by gelatinous apothecia, which typically exhibit diffuse pale yellow to pale green pigmentation in the inner tissue. The paraphyses are relatively thick and have a distinctive ascus structure, in which the lateral wall is thin and slightly thickened apically. Asci are cylindrical to clavate, short-stalked, 8-spored, while ascospores are hyaline, aseptate, smooth, and ellipsoid to oblong (adapted from Rambold & Triebel, 1990).

Species of *Gelatinopsis* are typically fungicolous or lichenicolous and have been recorded from Belgium, France, Germany, Luxembourg, and the USA (Rambold & Triebel, 1990; Aptroot et al., 1997; Baral & Marson, 2001; Ertz & Diederich, 2006; Sun et al., 2019a; Index Fungorum, 2025). Reported fungicolous associations include *G. exidiophila* (on *Exidia recisa* (*Auriculariaceae*)), *G. geoglossi* (on *Geoglossum* sp. (*Geoglossaceae*), *Trichoglossum farlowii*, *T. rasum*, and *T. walteri* (*Geoglossaceae*)), *G. hysteropatellae* (in apothecia of *Hysteropatella elliptica* (*Hysteriaceae*)), *G. polyconidiata* (on *Trechispora* (*Hydnodontaceae*)), *G. septata* (on *Merulius* (*Hydnaceae*)), and *G. tryblidariae* (in the hymenium of *Tryblidaria* (*Tryblidaria*)) (Rambold & Triebel, 1990; Aptroot et al., 1997; Baral & Marson, 2001; Sun et al., 2019a; Index Fungorum, 2025).

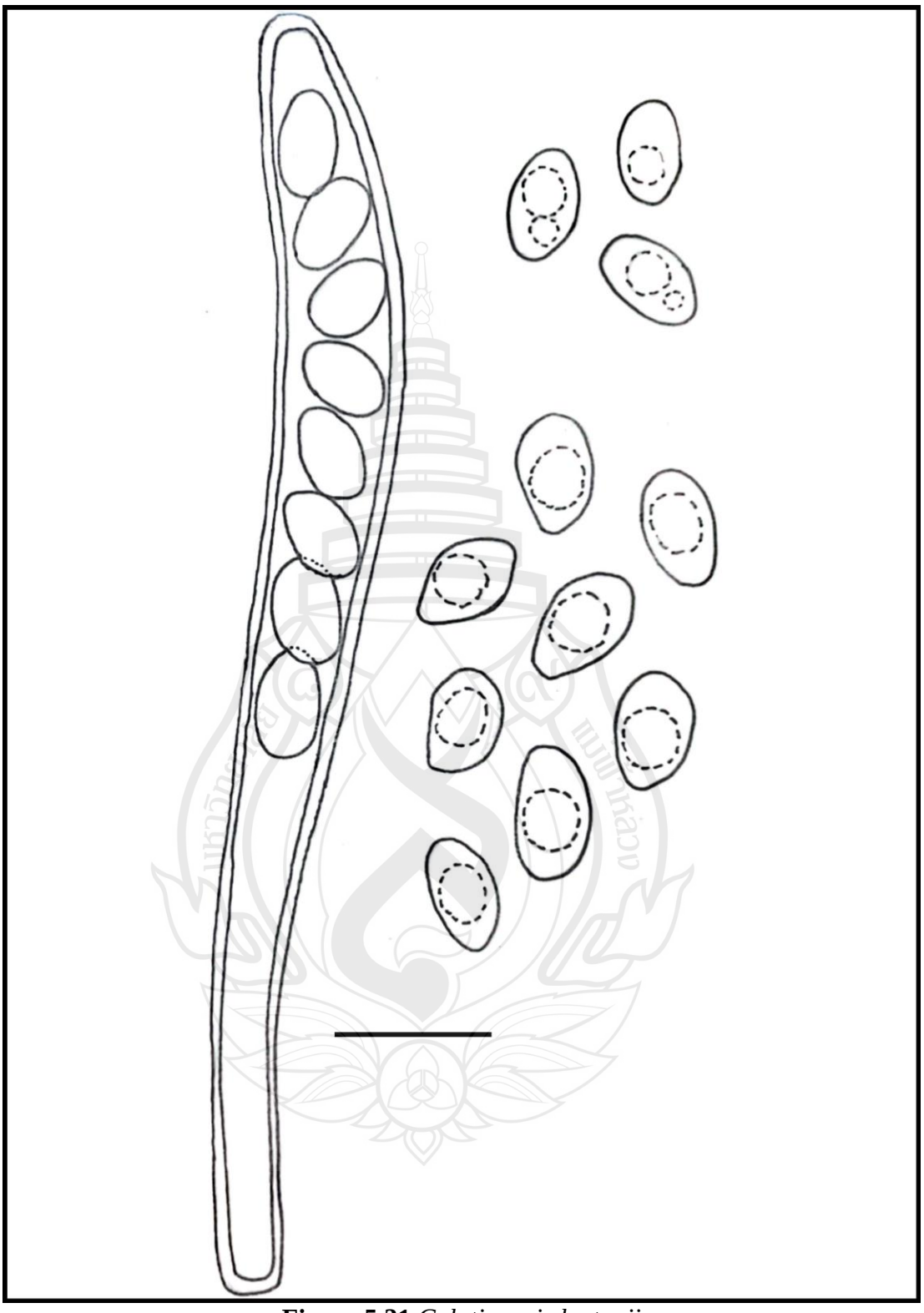


Figure 5.31 *Gelatinopsis leptogii*

Figure 5.31, Ascus and ascospores. Scale bar =10 μm. (Redrawn from Ertz & Diederich, 2006).

Class *Lichinomycetes* V. Reeb, Lutzoni & Cl. Roux

Coniocybales M. Prieto & Wedin

Coniocybaceae Rchb.

Chaenotricha Suija, McMullin & P. Lõhmus, Fungal Syst. Evol. 12: 261 (2023)

Figure 5.32

Index Fungorum number: IF 850355

Suija et al. (2023) established *Chaenotricha* to accommodate *Chaenotricha obscura*, previously known as *Calicium obscurum*, and it is the type species. In the same study, an epitype for *C. obscura* was designated. Alongside this, another species *Chaenotricha cilians* was also included (Suija et al., 2023). Both species were described as fungicolous taxa associated with the sporocarps of *Trichaptum* spp. (*Hymenochaetales*), and have been reported from Canada, Denmark, Estonia, Latvia, Lithuania, Norway, Russia, Sweden, and the USA (Suija et al., 2023).

The sexual morph of *Chaenotricha* is defined by stalked ascomata, with the stalks appearing dark brown to black, typically shiny, and ranging from straight to slightly curved. The stalks are composed of periclinally arranged brown hyphae, presenting an uneven surface, and may exhibit a K– or K+ red reaction, with coloration sometimes bleeding from the tissue. The capitulum is spherical to obconical and lacks pruina. The mazaedium is powdery in texture. Both the true excipulum and hypothecium are well-developed, brown to dark brown, and continuous with the stalk, sharing the same hyphal structure. The hamathecium comprises asci that disintegrate early in development, along with paraphyses. Asci are cylindrical, arise singly and directly from ascogenous hyphae without croziers, and contain eight uniseriate, stalked ascospores. Paraphyses are hyaline, straight, aseptate, and not expanded at the apices. Ascospores are initially hyaline and become brown at maturity. They are aseptate, smooth-walled, and range from spherical to irregularly spherical. To date, the asexual morph has not been observed (adapted from Suija et al., 2023).

As of Species Fungorum (2025), two species are currently listed within *Chaenotricha*. DNA sequence data, including ITS, LSU, and SSU regions for this genus, are available in GenBank (2025). *Chaenotricha* is placed within *Coniocybaceae*, in *Coniocybales* (Hyde et al., 2024a).

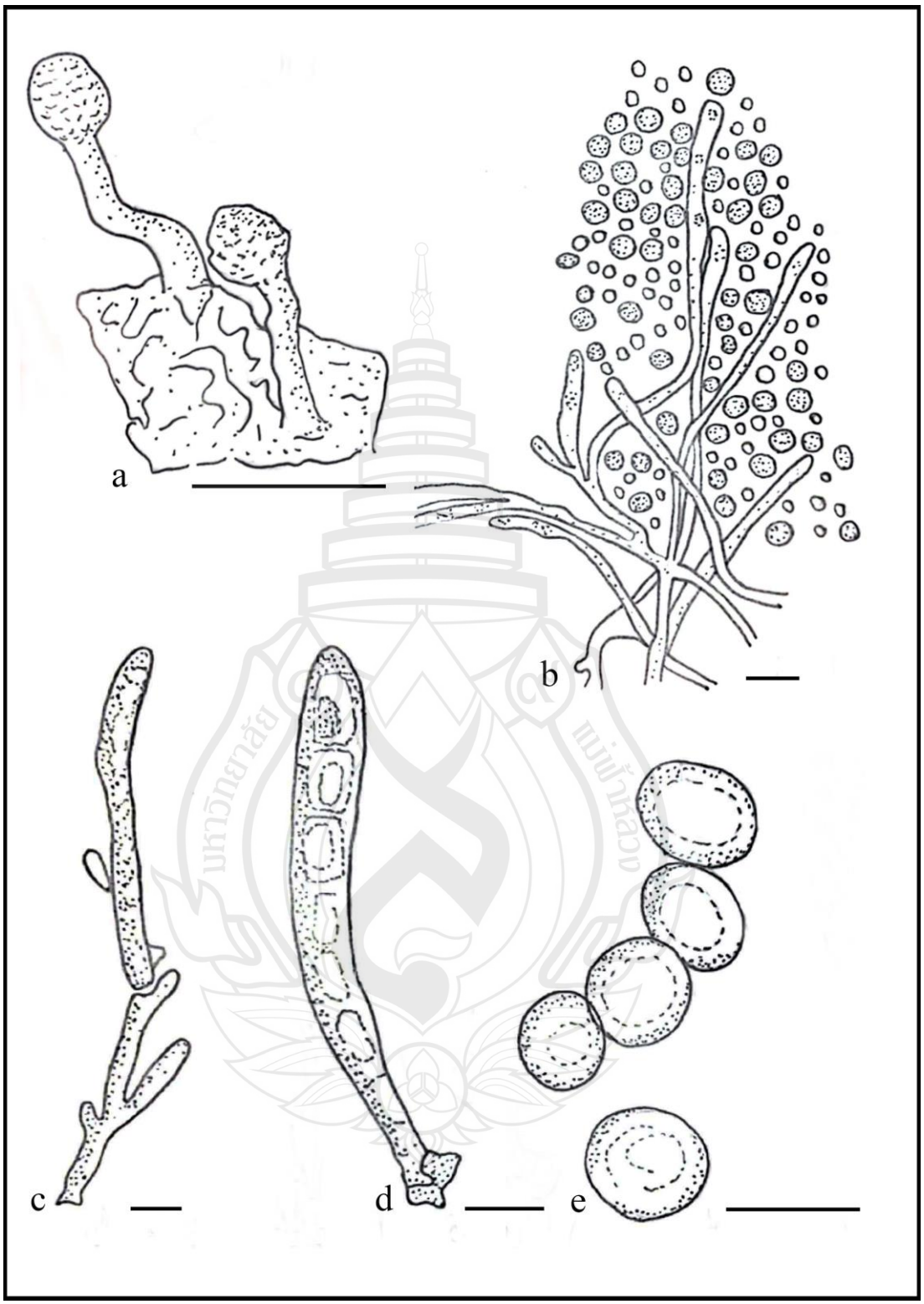


Figure 5.32 *Chaenotricha cilians*

Figure 5.32, a. Ascomata (observed from electron microscopy). b. Developing asci, paraphyses and ascospores. c. Ascus (immature) developing singly from the

ascogenous cells. d. Immature ascus with developing ascospores. e. Mature ascospores. Scale bars: a = 300 µm, b = 10 µm, c–e = 5 µm. (Adapted from Suija et al., 2023).

Class *Sordariomycetes* O.E. Erikss. & Winka

Subclass *Diaporthomycetidae* Senan., Maharachch. & K.D. Hyde

Ophiostomatales Benny & Kimbr.

Ophiostomataceae Nannf.

Sporothrix Hektoen & C.F. Perkins, J. Exp. Med. 5: [77] (1900)

Figure 5.33

Index Fungorum number: IF 10046

Facesoffungi number: FoF 10509

Sporothrix was established by Hektoen and Perkins (1900), with *S. schenckii* as the type species. *Sporothrix schenckii* is the etiological agent of human sporotrichosis (Barros et al., 2011). Over the past century, the asexual morphs of numerous *Ophiostoma* species have also been classified within *Sporothrix* (de Beer et al., 2016). The first comprehensive monograph of the genus was produced by de Hoog (1974), who treated 12 *Sporothrix* species alongside the asexual morphs of 12 *Ophiostoma* species, providing illustrations. Molecular phylogenetic analyses indicated that species of *Sporothrix* and *Ophiostoma* cluster within a single lineage, historically referred to as *Ophiostoma sensu lato* (de Beer & Wingfield, 2013; de Beer et al., 2016). In accordance with the "One Fungus, One Name" principle adopted in the Melbourne Code, application to *Ophiostoma sensu lato* conferred nomenclatural priority to *Sporothrix* over *Ophiostoma* (de Beer et al., 2016). To resolve the phylogenetic relationship between *Ophiostoma* and *Sporothrix*, de Beer et al. (2016) analyzed LSU, ITS, *btub*, and *cmdA* sequence data from 65 isolates. Their results supported *Sporothrix* as a distinct, well-resolved monophyletic lineage separate from *Ophiostoma sensu stricto*. Furthermore, to aid species-level classification, six species complexes were proposed within *Sporothrix* (de Beer et al., 2016). Currently, 94 species epithets are listed within *Sporothrix* in Species Fungorum (2025), with molecular data available for most taxa in GenBank (2025). The genus is classified in *Ophiostomataceae*, *Ophiostomatales* (de Beer et al., 2022; Hyde et al., 2024a).

The sexual morph of *Sporothrix* produces ascomata with dark brown to black, globose bases and necks that are straight or flexuous, cylindrical, and slightly tapering towards the apex, reaching up to 1,600 μm in length. The necks are brown to black, and the ostiole is often surrounded by divergent ostiolar hyphae, though these may be absent. Asci are 8-spored, evanescent, and range from globose to broadly clavate. Ascospores are hyaline, aseptate, and lunate, allantoid, reniform, or orange section-shaped, lacking a sheath (de Beer et al., 2016). The asexual morph is micronematous and mycelial, with hyaline or occasionally pigmented conidia produced holoblastically from denticulate conidiogenous cells (de Beer et al., 2016).

Sporothrix comprises species occurring across a wide range of climatic regions worldwide (de Beer & Wingfield 2013; de Beer et al., 2016). These species occupy varied habitats, with the most recorded on bark, within infructescences of *Protea* spp., and in the wood of various forest trees (de Errasti et al., 2016; Ostafińska et al., 2021). Additional substrates include soil, bark beetles, ambrosia beetles, mites, and other fungi (de Beer et al., 2016; de Errasti et al., 2016; Ostafińska et al., 2021; Bilański et al., 2023). Fungicolous representatives include *Sporothrix echinospora* (on *Meliola millettiae-rhodanthae* (*Meliolaceae*)), *S. epigloea* (on *Tremella fuciformis* (*Tremellaceae*)), *S. insectorum* (on *Hirsutella citriformis* (*Ophiocordycipitaceae*)), *S. phellini* (on the carpophore of *Phellinus* (*Hymenochaetaceae*)), *S. polyporicola* (on *Fomitopsis pinicola* (*Fomitopsidaceae*)), and *S. tuberi* (on *Tuber* sp. (*Tuberaceae*)) (Sun et al., 2019a; Pérez-González et al., 2023). Several species are also recognized as significant pathogens of humans and animals (Barros et al., 2011; Teixeira et al., 2014; Ostafińska et al., 2021).

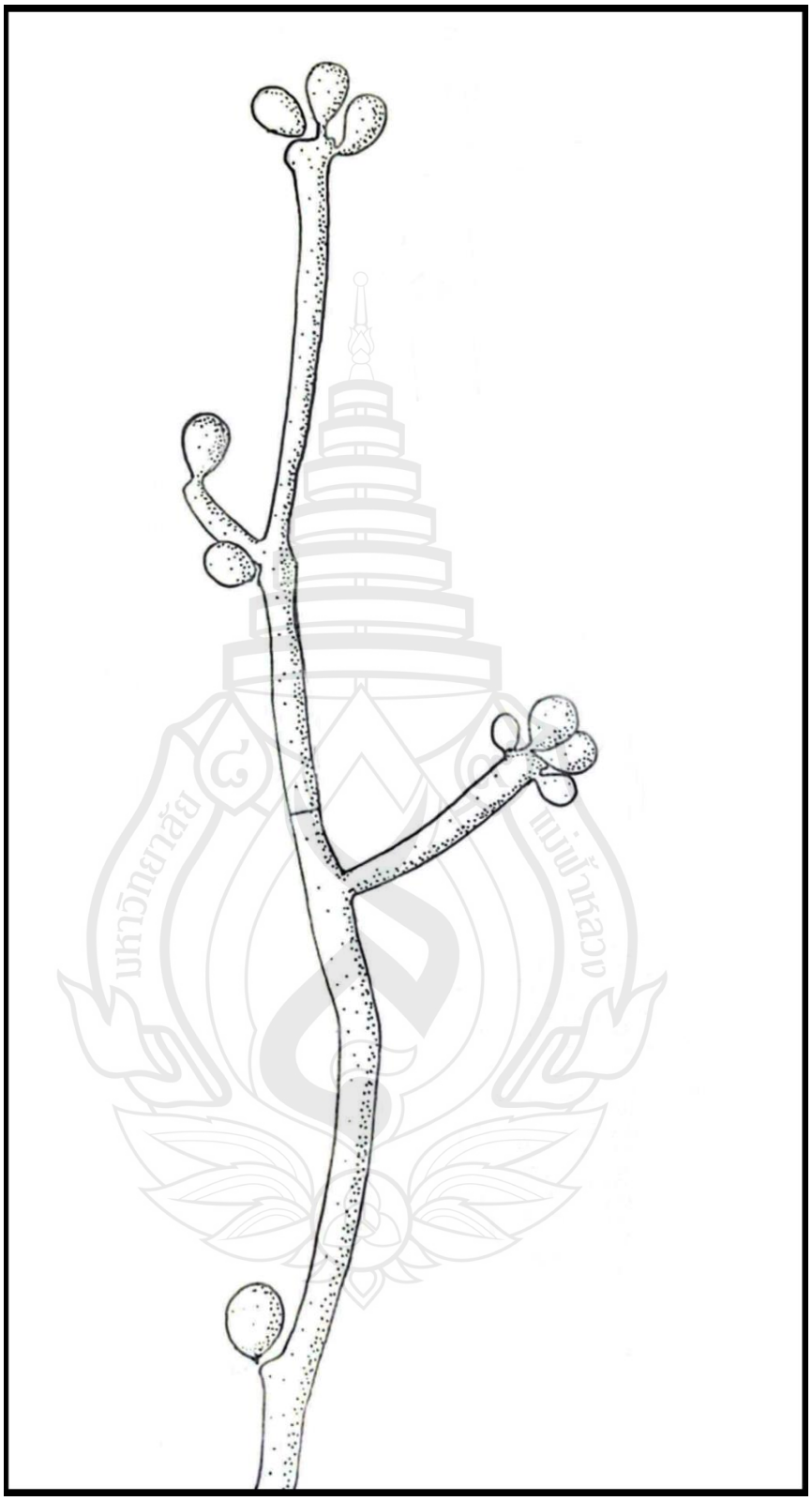


Figure 5.33 *Sporothrix* sp.

Figure 5.33, Conidiophore, conidiogenous cells and conidia (Adapted from de Beer et al., 2022).

Diaporthomycetidae* families *incertae sedis

Woswasiaceae H. Zhang, K.D. Hyde & Maharachch.

Woswasia Jaklitsch, Réblová & Voglmayr, Mycologia 105(2): 479 (2013)

Figure 5.34

Index Fungorum number: IF 800841

Facesoffungi number: FoF 04920

Woswasia was proposed by Jaklitsch et al. (2013), with *W. atropurpurea* as the type species. This species was described as hyperparasitic or hypersaprotrophic on the stromata of *Diaporthe oncostoma* (*Diaportheaceae*). *Woswasia* was placed within *Sordariomycetidae incertae sedis* (Jaklitsch et al., 2013). Subsequently, based on phylogenetic analyses and divergence time estimates, *Woswasiaceae* was established within *Diaporthomycetidae* families *incertae sedis* to accommodate *Woswasia* along with *Xylochrysis* and *Cyanoannulus* (Zhang et al., 2017c). As of Species Fungorum (2025), *Woswasia* remains monotypic. Sequence data for ITS, LSU, and *rpb2* genes are available in GenBank (2025).

The sexual morph of *Woswasia* is characterized by perithecia with elongated necks immersed in a stroma that exhibits a conspicuous pH-dependent colour reaction. Asci are cylindrical, stipitate, and possess an inamyloid apical annulus that stain blue in aqueous cotton blue. Ascospores are hyaline, globose to subglobose, unicellular, and bear a distinctly verruculose epispore (adapted from Jaklitsch et al., 2013). The asexual morph comprises branched, subhyaline to hyaline conidiophores with terminal, sympodial conidiogenous cells. Conidia are holoblastic, hyaline, ellipsoid to obovoid, and tapering towards the base (adapted from Jaklitsch et al., 2013).

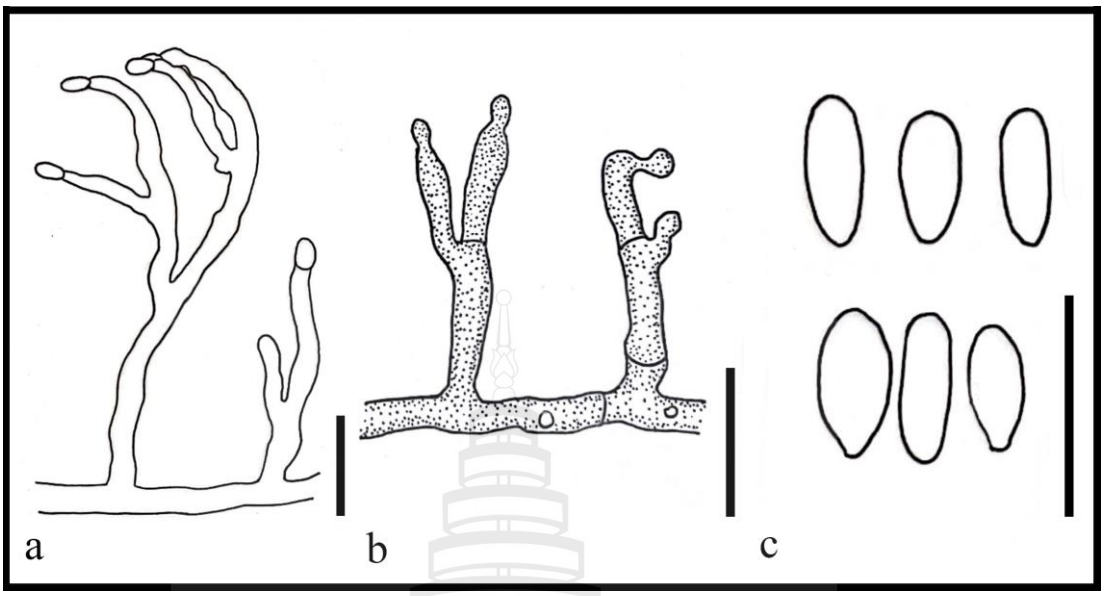


Figure 5.34 *Woswasia atropurpurea*

Figure 5.34, a, b. Conidiophores with terminal sympodial conidiogenous cells. c. Conidia. Scale bars: a–c = 10 µm (Adapted from Jaklitsch et al., 2013).

Subclass *Hypocreomycetidae* O.E. Erikss. & Winka

Coronophorales Nannf.

Ceratostomataceae G. Winter

Scopinella Lév., in Orbigny, Dict. Univ. Hist. Nat. 8: 493 (1846)

Figure 5.35

Index Fungorum number: IF 4962

Facesoffungi number: FoF 10522

Léveillé (1847) established *Scopinella* to accommodate the single species *S. barbata*. Saccardo (1891) included another species, *S. pleiospora* which was classified as *Melanospora pleiospora*. *Scopinella pleiospora* was identified as the type species of this genus, having been discovered growing on the dung of a rabbit (*Oryctolargus cuniculus*) in Norway (Index Fungorum, 2025). *Scopinella* is characterized by ascomata with long necks and globose bodies. The asci are evanescent, and the cuboid-ellipsoidal ascospores feature two prominent longitudinal germ slits (Cannon & Hawksworth, 1982; Stchigel et al., 2006).

Species Fungorum (2025) lists nine species of *Scopinella*. These species have been reported in Argentina, Canada, Costa Rica, the Czech Republic, Germany,

Norway, Lithuania, Pakistan, Slovakia, the UK, the USA, and Tunisia (Farr & Rossman, 2024; Index Fungorum, 2025). These species have been documented as saprobes on plant substrates, coprophilous fungi, or fungicolous species (Hawksworth, 1975; Sanchez et al., 2013). *Scopinella gallicola* (on the gall of *Endocronartium harknessii* (*Cronartiaceae*)) and *S. sphaerophila* (on ascomata of *Sphaeria morbosa* (*Hypoxylaceae*)) are fungicolous species in the genus (Sanchez et al., 2013; Sun et al., 2019a).

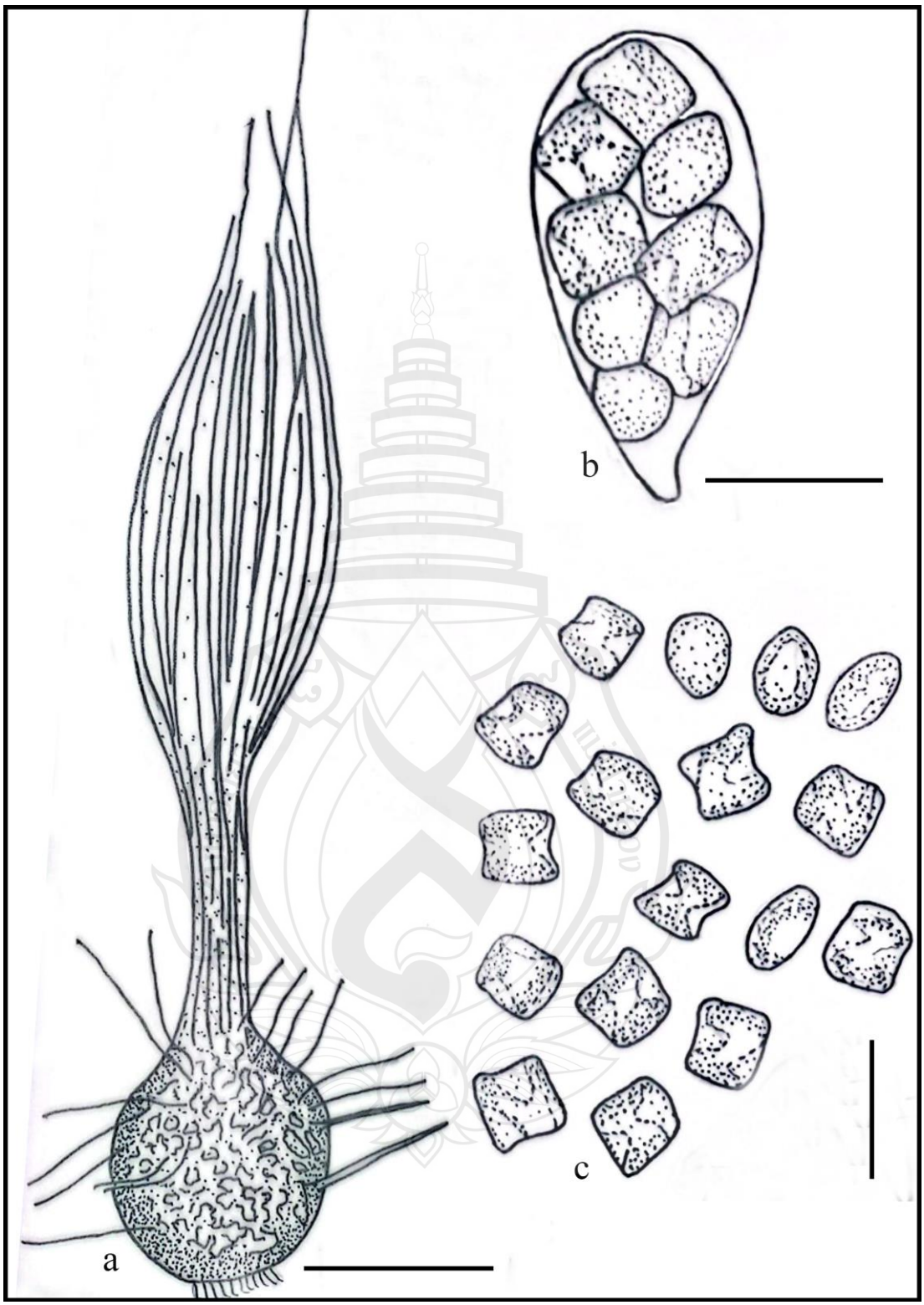


Figure 5.35 *Scopinella barbata*

Figure 5.35, a. Ascoma. b. Ascus. c. Ascospores. Scale bars: a = 200 µm, b, c = 10 µm (Redrawn from Hawksworth, 1975).

Syspastospora P.F. Cannon & D. Hawksw., Bot. J. Linn. Soc. 84(2): 152 (1982)

Figure 5.36

Index Fungorum number: IF 5345

Facesoffungi number: FoF 10524

Syspastospora was established by Cannon and Hawksworth (1982) to include *S. parasitica*, previously known as *Melanospora parasitica* (= *Sphaeronaema parasiticum*), found on *Isaria* (*Cordycipitaceae*) species in France. Species of *Syspastospora* are characterized by ascomata that are either perithecial or lack an external opening. They vary from superficial to immersed, are globose to subglobose, and sometimes have elongated necks. The ascomata are pale brown to brown, membranaceous, and may be glabrous, setose, or hairy, with or without ostioles. The asci are 8-spored, unitunicate, clavate, and evanescent. Mature ascospores are brown to olivaceous brown, broadly fusiform to cylindrical to doliiform, truncate at both ends, aseptate, and have a large, depressed germ pore at each end. The asexual morph is hyphomycetous, characterized by mycelium consisting of hyaline to yellowish-brown, branched, septate hyphae. Chlamydospores are terminal or intercalary, globose to ovoid, and vary in color from hyaline to brown. (Cannon & Hawksworth, 1982; Horie et al., 1986; García et al., 2002; Etayo & Sancho, 2008).

There are four species of *Syspastospora* listed in Species Fungorum (2025). Members of this genus have been recorded in Argentina, Cuba, France, Japan, Nepal, Nigeria, Spain, and Ukraine (Horie et al., 1986; Lee & Nam, 2000; García et al., 2002; Posada et al., 2004; Akulov, 2011a; Coste & Pinault, 2018; Georgieva et al., 2020). *Syspastospora boninensis* and *S. tropicalis* have been documented as soil fungi (Horie et al., 1986; García et al., 2002), while *S. cladoniae* is lichenicolous (Etayo & Sancho, 2008; Coste & Pinault, 2018). *Syspastospora parasitica* has been identified as a hyperparasite on the entomopathogenic species, *Beauveria pseudobassiana*, *B. varroae* (*Cordycipitaceae*), and *Paecilomyces tenuipes* (*Aspergillaceae*) (Lee & Nam, 2000; Posada et al., 2004; Georgieva et al., 2020). According to GenBank (2025), molecular data for ITS, LSU, and SSU regions are available only for *Syspastospora parasitica*.

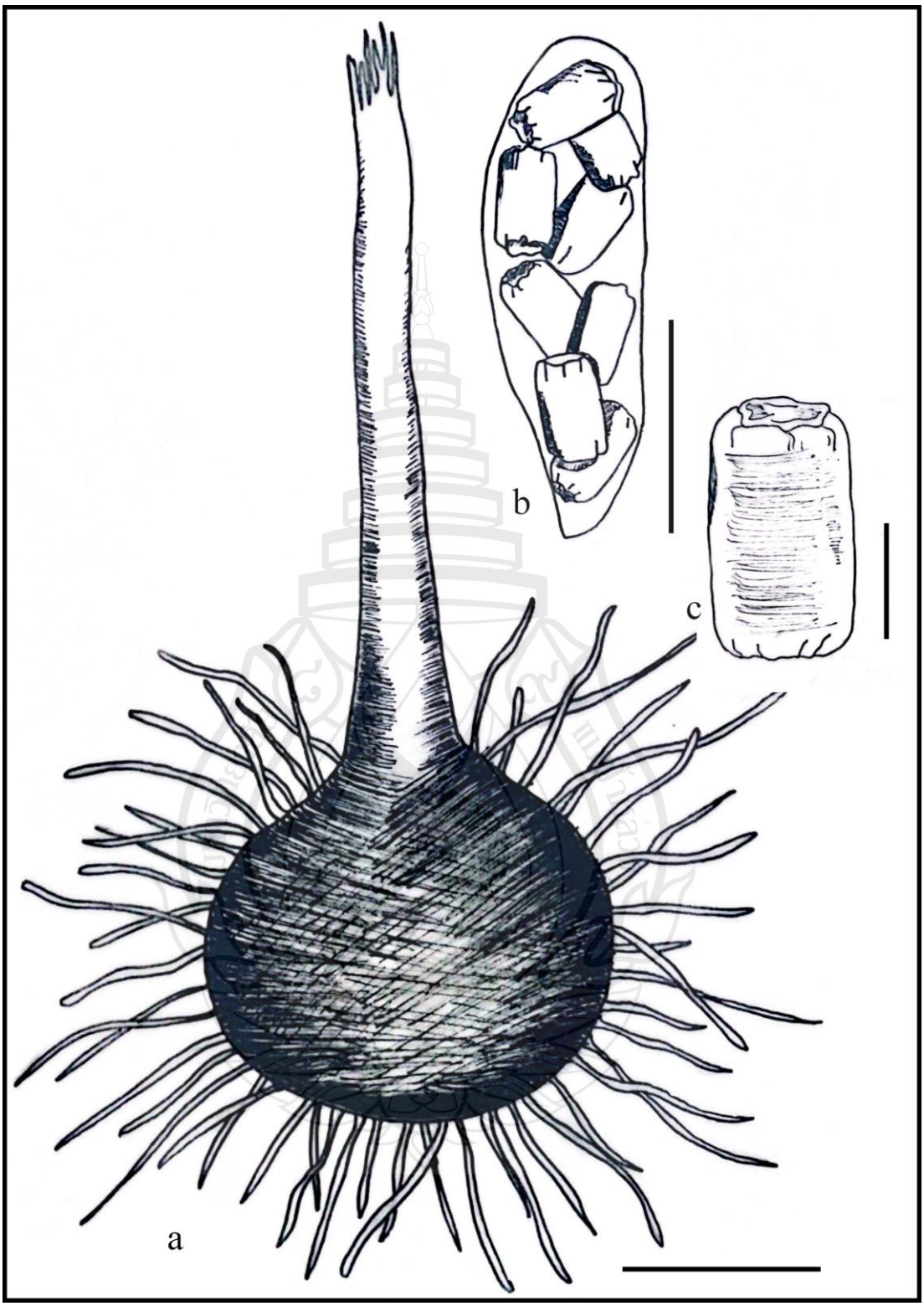


Figure 5.36 *Syspastospora parasitica*

Figure 5.36, a. Ascoma. b. Ascus. c. Ascospores. Scale bars: a = 100 µm, b = 15 µm, c = 3 µm (Redrawn from Akulov, 2011a).

Glomerellales Chadef. ex Réblová, W. Gams & Seifert

Ascocodinaceae D.F. Bao, K.D. Hyde & Z.L. Luo

Ascocodinaea Samuels, Cand. & Magni, Mycologia 89(1): 156 (1997)

Figure 5.37

Index Fungorum number: IF 27833

Facesoffungi number: FoF 13622

Ascocodinaea was introduced by Samuels et al. (1997a) with the type species *A. stereicola*. It was isolated as a fungicolous species associated with a basidiomata of *Stereum* sp. (*Stereaceae*) collected from Kentucky, USA. At the same time as establishing *Ascocodinaea,* Samuels et al. (1997a) introduced another species *A. polyporicola* found on old basidiomata of *Polyporus* sp. (*Polyporaceae*) collected from the USA. Other than the USA, these two species have been recorded as fungicolous from France and Sweden (Samuels et al., 1997a; Farr et al., 2021). To date, *Ascocodinaea* is classified under the *Glomerellales* genus *incertae sedis* (Wijayawardene et al., 2022).

The sexual morph of *Ascocodinaea* is characterized by ostiolate, setose, and black perithecia. The paraphyses are filiform and septate. Asci are cylindrical, 8 spored, J- and with an apical ring. The ascospores are uniseriate with overlapping ends inside the asci. Ascospores are ellipsoidal to fusiform, slightly curved, 3-septate, central cells are translucent brown and end cells are hyaline (adapted from Samuels et al., 1997a). The asexual morph of *Ascocodinaea* is considered to be *Codinaea* spp. with unbranched macronematous to mononematous, septate, unbranched, and black conidiophores. Each conidiophore bears a single, terminal, integrated conidiogenous cell. The conidiogenous cells are monophialidic, enteroblastic, proliferating percurrently or sympodially, apex not flared, with slight periclinal thickening at the conidiogenous locus. Conidia are broadly ellipsoidal, cylindrical, or inequilateral, often slightly curved, 0-1-septate, hyaline, lacking a visible basal abscission scar, smooth-walled, held in a drop of hyaline slime at the apex of each conidiophore (adapted from Samuels et al., 1997a).

To date, there are only two species (*A. stereicola*, *A. polyporicola*) listed under *Ascocodinaea* in Species Fungorum (2025), whereas only *A. stereicola* has LSU molecular data available in GenBank (2025).

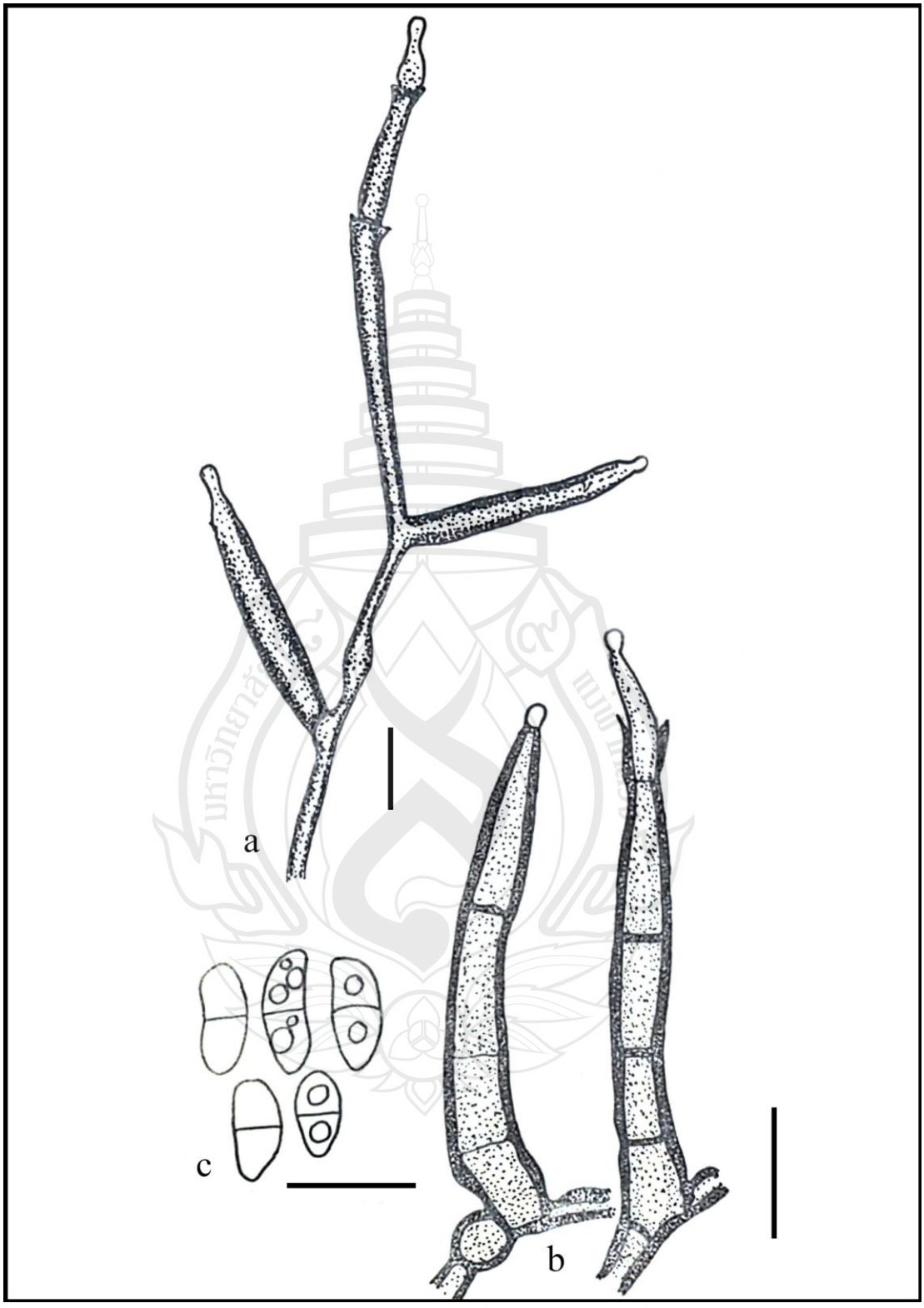


Figure 5.37 *Ascocodinaea stereicola*

Figure 5.37, a, b. Conidiophores and conidiogenous cells. c. Conidia. Scale bars a–c = 10 μm. (Redrawn from Samuels et al., 1997a).

Hypocreales Lindau

Albomorchellophilaceae F.M. Yu, K.D. Hyde & Q. Zhao

Albomorchellophila F.M. Yu, K.D. Hyde & Q. Zhao, Fungal Diversity 125: 167 (2024)

Figure 5.38

Index Fungorum number: IF 901517

Facesoffungi number: FoF 15282

Albomorchellophila was introduced by Yu et al. (2024), based on both morphological characteristics and phylogenetic evidence, with *A. morchellae* as the type species. *Albomorchellophila morchellae* was described as fungicolous on the fruiting bodies of cultivated *Morchella* (*Morchellaceae*) species (Yu et al., 2024).

The asexual morph of *Albomorchellophila* is characterized by micronematous conidiophores, which are typically reduced to conidiogenous cells that emerge terminally or laterally from hyphae. These structures are hyaline and smooth-walled. The conidiogenous cells are holoblastic, polyblastic, terminal or intercalary, and phialidic. Conidia are aseptate, smooth-walled, and ellipsoidal to oval or subglobose. The sexual morph has not yet been observed (adapted from Yu et al., 2024).

Phylogenetic analyses placed *Albomorchellophila* as a distinct lineage within *Hypocreales*, forming a sister clade to *Calcarisporium* within *Calcarisporiaceae*. However, it differs morphologically from *Calcarisporium* in having phialidic conidiogenous cells and conidiophores that are reduced to conidiogenous cells (Yu et al., 2024).

As of Species Fungorum (2025), *Albomorchellophila* remains monotypic. Sequence data for the ITS, LSU, SSU, and *tef* regions are available in GenBank (2025). The genus is currently placed within the *Albomorchellophilaceae*, in *Hypocreales* (Hyde et al., 2024a).

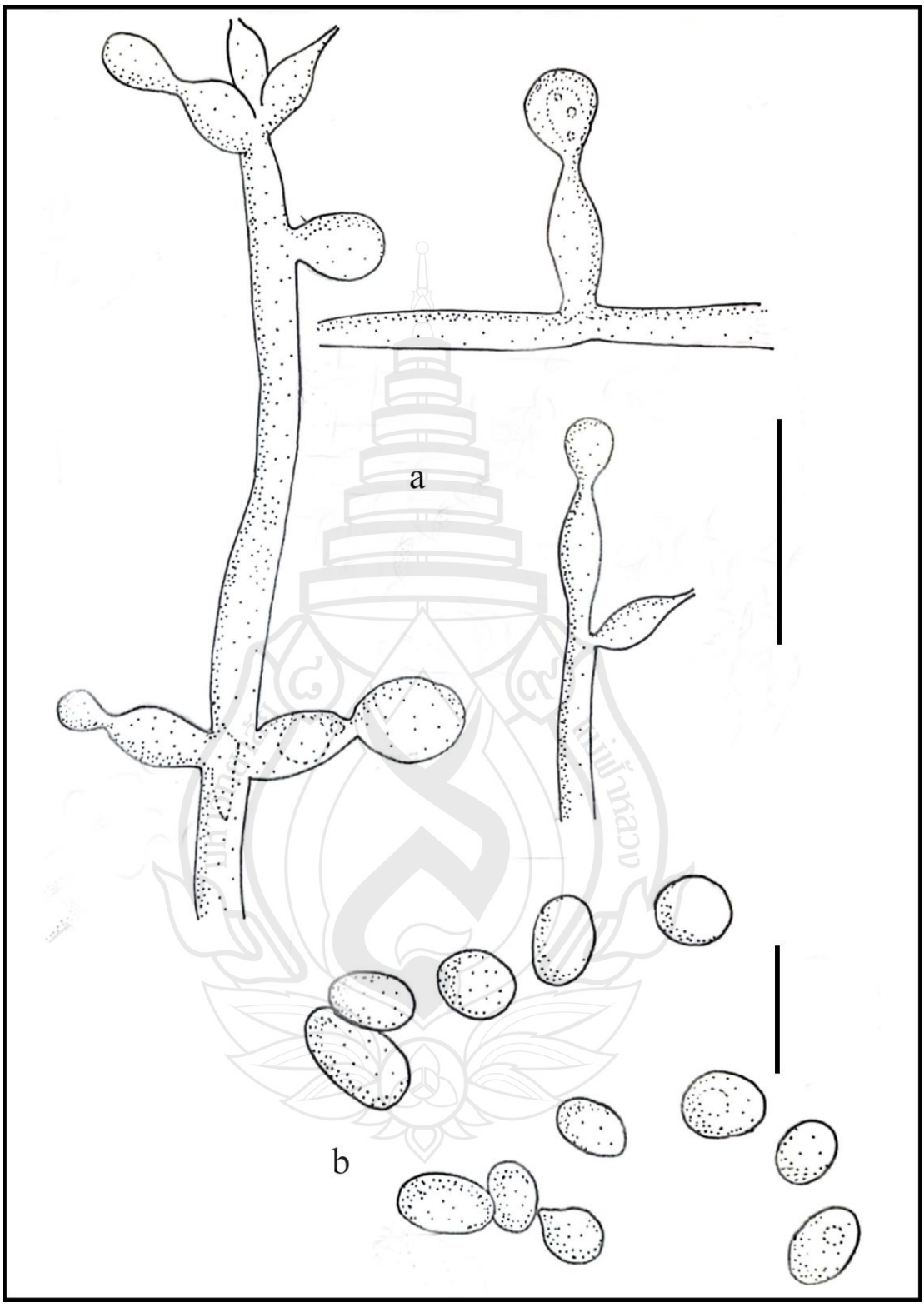


Figure 5.38 *Albomorchellophila morchellae*

Figure 5.38, a. Conidiogenous structure and conidia. b. Conidia. Scale bars: a, b = 10 μm. (Adaped from Yu et al., 2024).

Bionectriaceae Samuels & Rossman

Clonostachys Corda, Pracht-Fl. Eur. Schimmelbild. (Leipzig und Dresden): 31 (1839)

Figure 5.39

Index Fungorum number: IF 7701

Facesoffungi number: FoF 02102

Corda (1839) described *Clonostachys* based on the type species *C. araucaria*, which is currently considered as a synonym of *C. rosea* (basionym *Penicillium roseum*), the asexual morph of *Bionectria ochroleuca* (Schroers, 2001). Formerly, in accordance with the dual nomenclatural concepts, Schroers (2001) chose the sexual morph-typified *Bionectria* as the generic name, while encouraging the use of binominals for the asexual morph-typified *Clonostachys*. Schroers (2001) divided *Bionectria* into six newly distinguished subgenera: *Astromata*, *Bionectria*, *Epiphloea*, *Myronectria*, *Uniparietina*, and *Zebrinella*. This division was due to the considerable diversity of morphological patterns observed, primarily in the sexual morphs of these fungi. However, with the cessation of dual nomenclature, it was recommended that *Clonostachys* should be conserved as the preferred name over *Bionectria* (Rossman et al., 2013). Zhao et al. (2023a) conducted a generic revision for *Clonostachys* based on morphological and molecular phylogenetic analyses. The phylogenetic analyses were based on ITS, LSU combined with *rpb2*, *tef*, and *tub2* to reconstruct a phylogenetic backbone and to define robust species boundaries within, *Clonostachys*. Accordingly, Zhao et al. (2023a) concluded that *Clonostachys* encompasses the subgenera *Astromata*, *Bionectria*, *Myronectria*, and *Zebrinella*. Within these subgenera, they identified 19 new species and confirmed the existence of 49 species. Additionally, Zhao et al. (2023a) resurrected *Sesquicillium*, which is now recognized as a separate genus from *Clonostachys*. *Sesquicillium* has been established to accommodate the subgenera *Epiphloea* and *Uniparietina*, previously considered as of *Clonostachys* (Zhao et al., 2023a).

Clonostachys is a diverse genus that comprises soil-borne species, which can be mycoparasites, endophytes, epiphytes and saprotrophs (Schroers, 2001; Moreira et

al., 2016). Members of *Clonostachys* are widely distributed across the world, with the greatest species diversity observed in tropical regions. These taxa are commonly associated with soils, litter, and decaying and living plant materials (Torcato et al., 2020). However, there are reports of mycoparasitism and a mycophilic habit exhibited by several *Clonostachys* species (Samuels, 1976; Schroers et al., 1999; Schroers, 2001). While there have been occasional reports highlighting parasitic interactions of *C. rosea* with myxomycetes, nematodes, ticks, molluscs, and leafhoppers (Schroers, 2001; Toledo et al., 2006; Zhang et al., 2008). The species such as, *C. farinosa*, *C. rosea*, *C. rogersoniana*, and *C. subquaternata* are fungicolous (Sun et al., 2019a; Manawasinghe et al., 2024). Due to the mycoparasitic activity of *C. rosea*, it has been explored for biological control of plant diseases (Jensen et al., 2022). Although *C. rosea* has been extensively studied, there is a lack of comprehensive data for many other species within *Clonostachys* (Jayawardena et al., 2025).

Clonostachys species are distinguished by their sexual morphs, which feature globose to subglobose perithecial ascomata. The asci are narrowly clavate and contain ellipsoidal ascospores (Schroers, 2001). Regarding the asexual morphs, the conidiophores can be penicillate, sporodochial and in many cases, they exhibit a dimorphic pattern. The primary conidiophores are mononematous and can have either a verticillium-like arrangement or a narrowly penicillate structure. The secondary conidiophores often produce imbricate conidial chains, which can collapse, forming slimy masses. The phialides are arranged in whirls. The conidia are typically hyaline, but in some cases, they may appear greenish or olivaceous (Schroers, 2001; Perera et al., 2023; Zhao et al., 2023a).

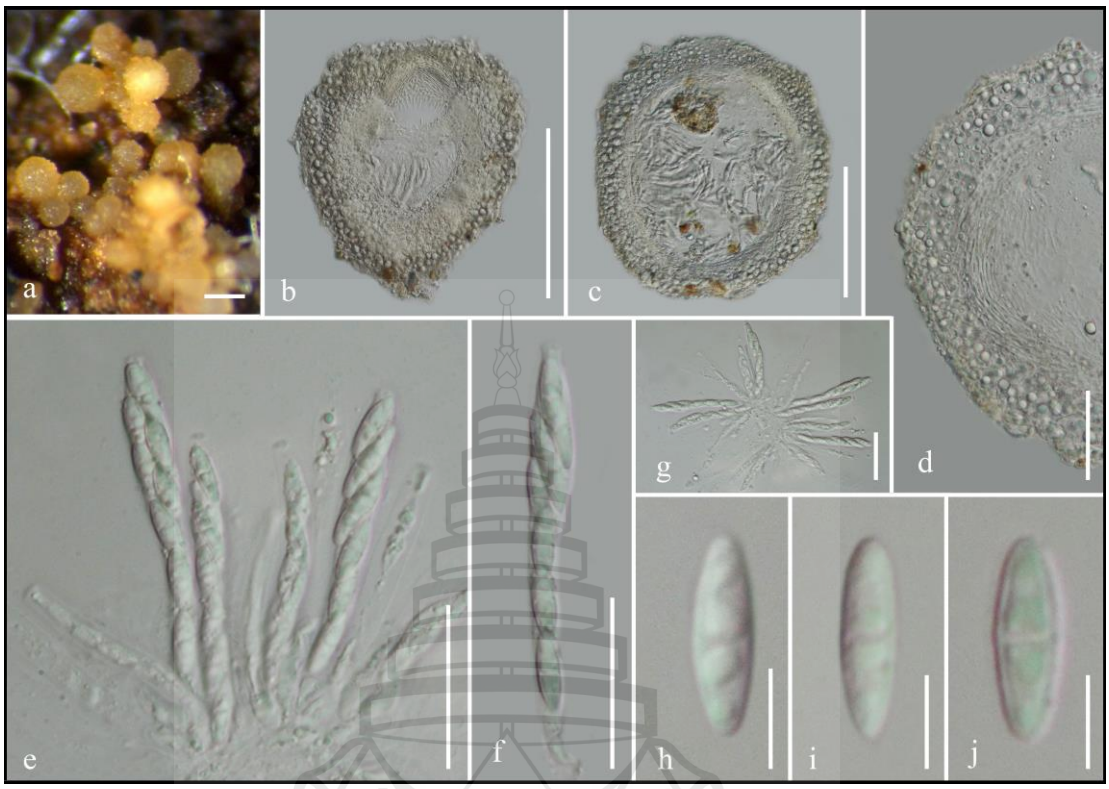


Figure 5.39 *Clonostachys rosea* (MFLU 18-2770)

Figure 5.39, a. Ascomata on the host. b, c. Section of ascomata. d. Section of peridium. e–g. Asci. h–j. Ascospores. Scale bars: b, c = 100 µm, a, d = 50 µm, e–g = 20 µm, h–j = 5 µm. (Photo credits: R.H Perera).

Nectriopsis Maire, Annls mycol. 9(4): 323 (1911)

Figure 5.40

Index Fungorum number: IF 3434

Facesoffungi number: FoF 13002

Nectriopsis was established to encompass four hypocrealean species characterized by ascomata within a byssoid stroma which were regarded as intermediate forms between *Nectria* and *Hypomyces* (Maire, 1911; Rossman et al., 1999). The genus is typified by, *Nectriopsis violacea*. According to Species Fungorum (2025), *Nectriopsis* comprises 72 distinct epithets.

The sexual morph of *Nectriopsis* is characterised by either superficial or immersed, nearly white to pale yellow or orange, KOH-, perithecia within the substratum. Those can be rarely inconspicuously stromatic. The cells on the surface of the perithecial wall form a *textura epidermoidea* (Rossman et al., 1999; Zhao et al.,

2023a). Asci are cylindrical to clavate, with either a simple apex or an apex with a ring, and contain eight spores. Ascospores are ellipsoidal, hyaline, and (0–)1-septate. The asexual morphs resemble those of *Acremonium*, *Gliocladium*, or *Verticillium* (Rossman et al., 1999; Zhao et al., 2023a).

The members of *Nectriopsis* have been found on free-living fungi, lichens, and myxomycetes, and less frequently on herbaceous substrates (Samuels, 1988; Rossman et al., 1999). *Nectriopsis* have been so far reported from China, Brazil, Japan, the UK, the USA, New Zealand, Venezuela, France, and Denmark (Samuels, 1988; Hou et al., 2023). *Nectriopsis ellipsoidea* (on *Polyporus pargamenus* (*Polyporaceae*)), *N. epimyces* (colonized *Omphalina* (*Agaricales*)), *N. epinectria* (colonized Ascomycetes species), *N. hyperbiota* (on the perithecia of *Nectria pseudotrichia* (*Nectriaceae*)), *N. lasiodermopsis* (colonized the perithecia of *Nectria*), *N. macroephichloe* (colonized the stroma of *Hypocrella cyperacearum* (*Clavicipitaceae*)), *N. oxyspora* (colonized *Nectria*), *N. septofusidiae* (colonized *Diaporthe* (*Diaporthaceae*)), *N. sibicola* (colonized *Nectria*), *N. sororicola* (colonized the perithecia of *Nectria*), and *N. uredinophila* (colonized rust fungi) are among the fungicolous species reported to be associated with various ascomycetes and basidiomycetes (Samuels, 1988; Sun et al., 2019a; Hou et al., 2023).

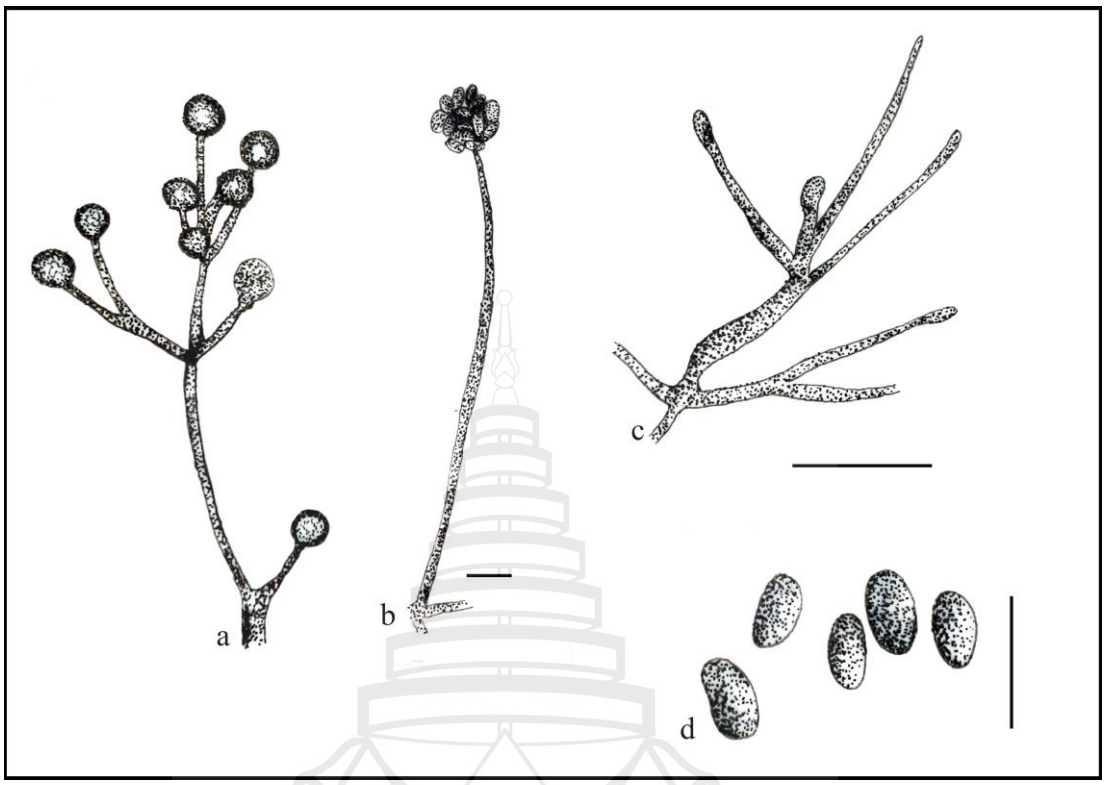


Figure 5.40 *Nectriopsis ellipsoidea*

Figure 5.40, a. Conidiophores and conidial heads. b. Unbranched conidiophore. c. Branched conidiophores. d. Conidia. Scale bars: b–d = 10 μm. (Adaped from Hou et al., 2023).

Calcarisporiaceae Jing Z. Sun, X.Z. Liu & K.D. Hyde

Calcarisporium Preuss, Linnaea 24: 124 (1851)

Figure 5.41

Index Fungorum number: IF 7465

Facesoffungi number: FoF 08843

Calcarisporium was defined by Preuss (1851) and was typified by *C. arbuscula*. Thereafter over time, the classification of *Calcarisporium* species relied on morphological characters. Therefore, the taxonomic position at a higher rank was uncertain due to the lack of phylogenetic analysis. De Hoog (1974) placed *Calcarisporium* in *Sordariomycetes* based on its morphological features while Maharachchikumbura et al. (2015, 2016) confirmed the placement based on phylogenetic analysis. Hausner and Reid (2004) confirmed *Calcarisporium* within *Hypocreales*, family *incertae sedis*, providing SSU sequence data for *C. arbuscula*.

Maharachchikumbura et al. (2015) categorized it as *Sordariomycetes*, genera *incertae sedis*. Sun et al. (2017) conducted a comprehensive multi-gene analysis including SSU, ITS, LSU, *tef*, and *rpb2* sequence data from *Calcarisporium* species and representative taxa from other Hypocrealean families. This analysis revealed that *Calcarisporium* forms a distinct clade within *Hypocreales*. Consequently, Sun et al. (2017) established a new family *Calcarisporiaceae* within *Hypocreales*, to accurately classify *Calcarisporium* at the family level.

The sexual morph of *Calcarisporium* has not yet been observed. The asexual morphology of *Calcarisporium* is hyphomycetous. It is characterized by, hyaline, erect, verticillate conidiophores with sympodial and denticulate, polyblastic conidiation (Hughes, 1951a; De Hoog, 1974). The conidia are aseptate, unicellular, hyaline, globose or subglobose, or acerose to narrowly obclavate, straight to curved (Sun et al., 2017).

The members of *Calcarisporium* such as, *C. arbuscula, C. cordycipiticola, C. griseum, C. guizhouense*, *C. ovalisporum*, *C. xylariicola*, and *C. yuanyangense* are fungicolous (Sun et al., 2019a; Index Fungorum, 2025). They have been associated with, various higher basidiomycetes such as *Agaricus* (*Agaricaceae*), *Cortinarius* (*Cortinariaceae*), *Hypholoma* (*Strophariaceae*), *Laccaria* (*Hydnangiaceae*), *Lactarius* (*Russulaceae*), *Mycena* (*Mycenaceae*), Polyporus (*Polyporaceae*), Russula (Russulaceae), and Trichaptum (*Hymenochaetales, Incertae sedis*) as well as certain ascomycetes including *Cordyceps* (*Cordycipitaceae*), *Nemania* (*Xylariaceae*), *Ophiocordyceps* (*Ophiocordycipitaceae*), *Rosellinia* (*Xylariaceae*), and *Xylaria* (*Xylariaceae*) (Anke & Sterner, 1988; Akulov, 2011b; Sun et al., 2016, 2017, 2019a; Perera et al., 2023; Index Fungorum, 2025). Additionally, these taxa have also been recorded as endophytes or saprobes associated with plant hosts (Somrithipol & Jones, 2006). There are ten distinct taxa listed under *Calcarisporium* in Species Fungorum (2025). The molecular data is available for *Calcarisporium* species in GenBank (2025).

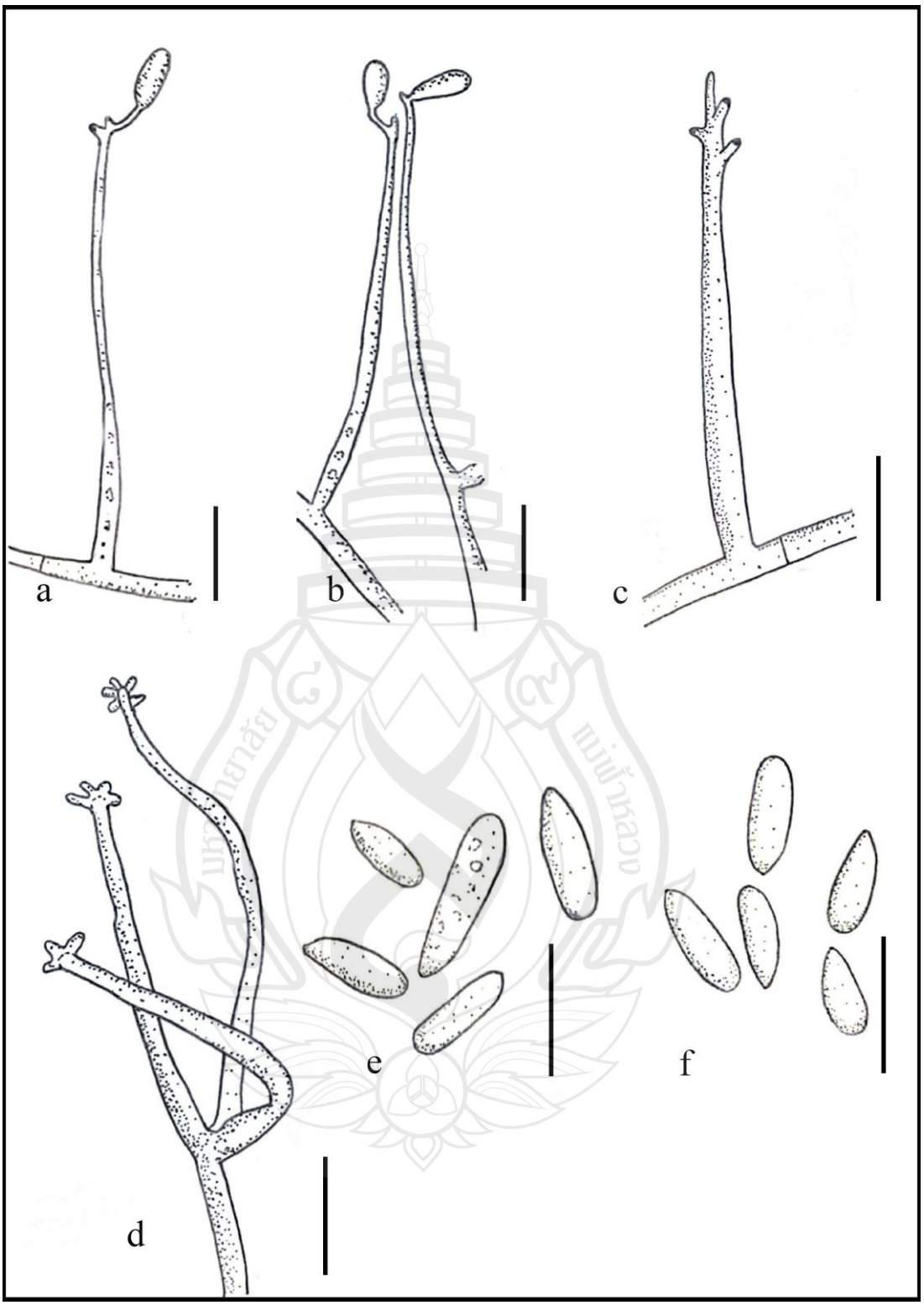


Figure 5.41 *Calcarisporium arbuscula*

Figure 5.41, a, b. Conidiophores with conidia. c, d. Conidiophores without conidia. e, f. Conidia. Scale bars: a–f = 10 μm. (Adapted from Sun et al., 2017).

Clavicipitaceae (Lindau) Earle ex Rogerson

Epicrea Petr., Sydowia 4(1-6): 325 (1950)

Index Fungorum number: IF 1857

Facesoffungi number: FoF 13077

Epicrea was established by Petrak (1950), with *E. insignis* as the type species. This species was described as a mycoparasite on *Hypocrella chusqueae* (*Clavicipitaceae*) in Ecuador (Petrak, 1950). According to Species Fungorum (2025), *Epicrea* remains monotypic, and no molecular sequence data are currently available in GenBank (2025).

Epicrea is characterized by dense, ovoid to ellipsoid, brightly colored, gelatinous perithecia. The asci are clavate to cylindrical, with a long stipe, and are 8-spored. Ascospores are typically straight and hyaline (adapted from Petrak, 1950). Additional records or morphological illustrations for the genus remain scarce to date.

Neobarya Lowen, in Eriksson & Hawksworth, Syst. Ascom. 5(1): 121 (1986)

Figure 5.42

Index Fungorum number: IF 25587

Facesoffungi number: FoF 13090

Barya was described by Fuckel (1870) with the type species *B. parasitica*. Based on the morphology, *Barya* was classified in *Clavicipitaceae* by later researchers, including Saccarado (1883), Rogerson (1970), and Candoussau et al. (2007). *Neobarya* (*Hypocreales*, *Clavicipitaceae*) was suggested as a new designation for *Barya* by Lowen (as mentioned in Eriksson & Hawksworth, 1986). This change was necessary as the name *Barya* was already in use for a genus of flowering plants in Bignoniaceae (Candoussau et al., 2007). However, when *Neobarya* was proposed with *N. parasitica* as the type species, not all species within *Barya* were transferred to the new genus. Specifically, *Barya montana* and *B. salaccensis* were excluded from *Neobarya* (Candoussau et al., 2007).

The sexual morph of *Neobarya* is distinguished by the production of soft, superficial, light-colored (white or shades of yellow) sessile ascomata on a pseudoparenchymatous stroma or within a subiculum. It features unitunicate, cylindrical, or narrowly clavate asci with an enlarged, thickened apical cap that is penetrated by a pore. The ascospores are filiform, often flexuous, hyaline, guttulate,

aseptate or septa obscure, remaining entire (Candoussau et al., 2007). The asexual morph of *Neobarya* is diverse as they can be acremonium-like, calcarisporium-like, lecanicillium-like or paeciliomyse-like (Candoussau et al., 2007).

These species have a fungicolous or lichenicolous habit and are reported from Argentina, Australia, Canada, Colombia, Denmark, France, Germany, New Zealand, Puerto Rico, Ukraine, the UK and the USA (Candoussau et al., 2007). As of date, there are 11 *Neobarya* species listed in Species Fungorum (2025). Among those, *Neobarya agaricicola* (on *Agaricus* spp. (*Agaricaceae*)), *N. aurantiaca* (parasitized *Claviceps purpurea* (*Clavicipitaceae*)), *N. danica* (colonized a corticioid fungus), *N. lutea* (colonized *Xylaria*), *N. parasitica* (parasitized *Bertia moriformis* (*Bertiaceae*) and *Cucurbitaria* (*Cucurbitariaceae*)) and *N. xylariicola* (colonized *Xylaria* (*Xylariaceae*)) are fungicolous species (Candoussau et al., 2007; Sun et al., 2019a). However, GenBank (2025) contains limited molecular data for the species of this genus.

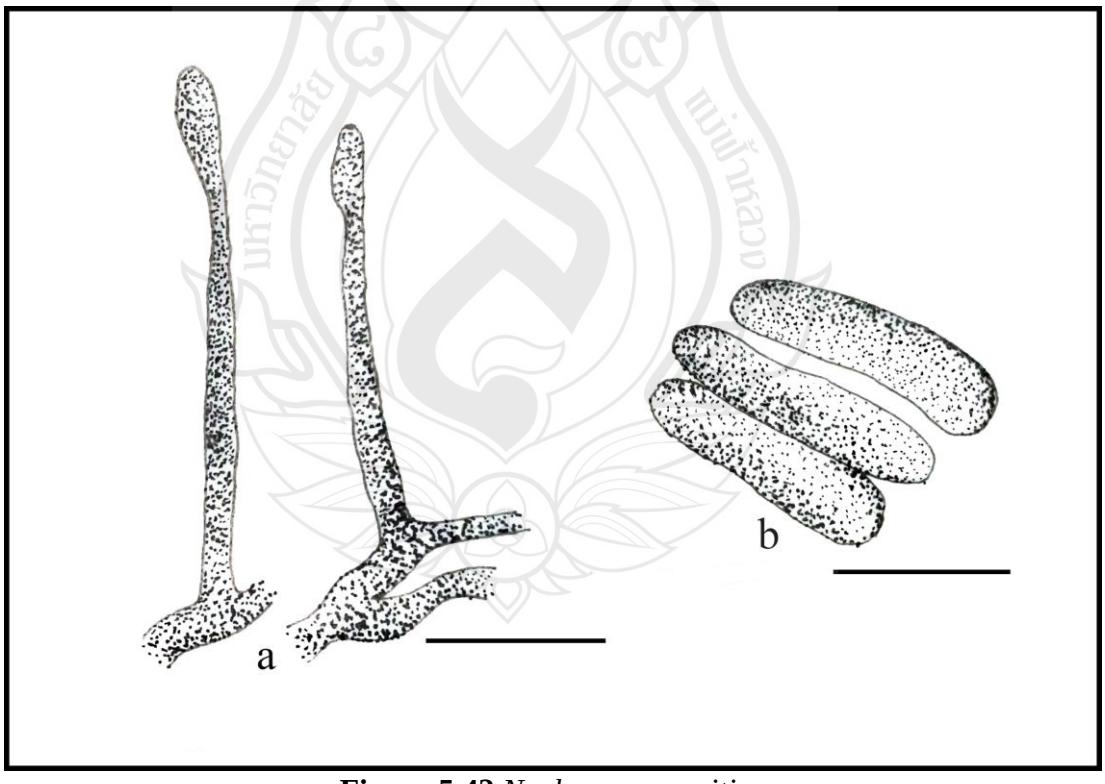


Figure 5.42 *Neobarya parasitica*

Figure 5.42, a. Conidiophores with attached conidia. b. Conidia. Scale bars: a = 20 μm, b = 10 μm (Adapted from Candoussau et al., 2007).

Tyrannicordyceps Kepler & Spatafora, Index Fungorum 12: 1 (2012)

Figure 5.43

Index Fungorum number: IF 550079

Facesoffungi number: FoF 13112

Tyrannicordyceps was established by Kepler et al. (2012) to accommodate five species formerly placed in *Cordyceps*, based on morphological features and a multigene phylogeny incorporating SSU, LSU, *tef1*, *rpb1*, and *rpb2* sequence data. The genus currently comprises *T. clavicipiticola*, *T. clavicipitis*, *T. ergoticola*, *T. fratricida* (type species), and *T. sclerotium* (Kepler et al., 2012; Species Fungorum, 2025; Index Fungorum, 2025). To date, molecular sequence data are available only for *T. fratricida* in GenBank (2025). Fungicolous associations have been reported for *T. clavicipiticola*, *T. clavicipitis*, *T. ergoticola*, and *T. fratricida*, all occurring on *Claviceps* spp. (*Clavicipitaceae*), whereas *T. sclerotium* has been recorded on the sclerotia of *Cordyceps* (*Cordycipitaceae*) (Sun et al., 2019a; Index Fungorum, 2025). In addition to their fungicolous nature, species of *Tyrannicordyceps* can infect both plants and insects (Kepler et al., 2012).

Tyrannicordyceps is characterized by pallid, yellow, or occasionally vermilion stroma arising from the sclerotia of *Claviceps* species. Perithecia may be scattered along the stipe or aggregated at the apex. Asci are cylindrical and possess an apical cap. Ascospores are filiform, septate, and may fragment into part-spores (adapted from Kepler et al., 2012). *Tyrannicordyceps* is placed in *Clavicipitaceae*, within *Hypocreales* (Hyde et al., 2024a).

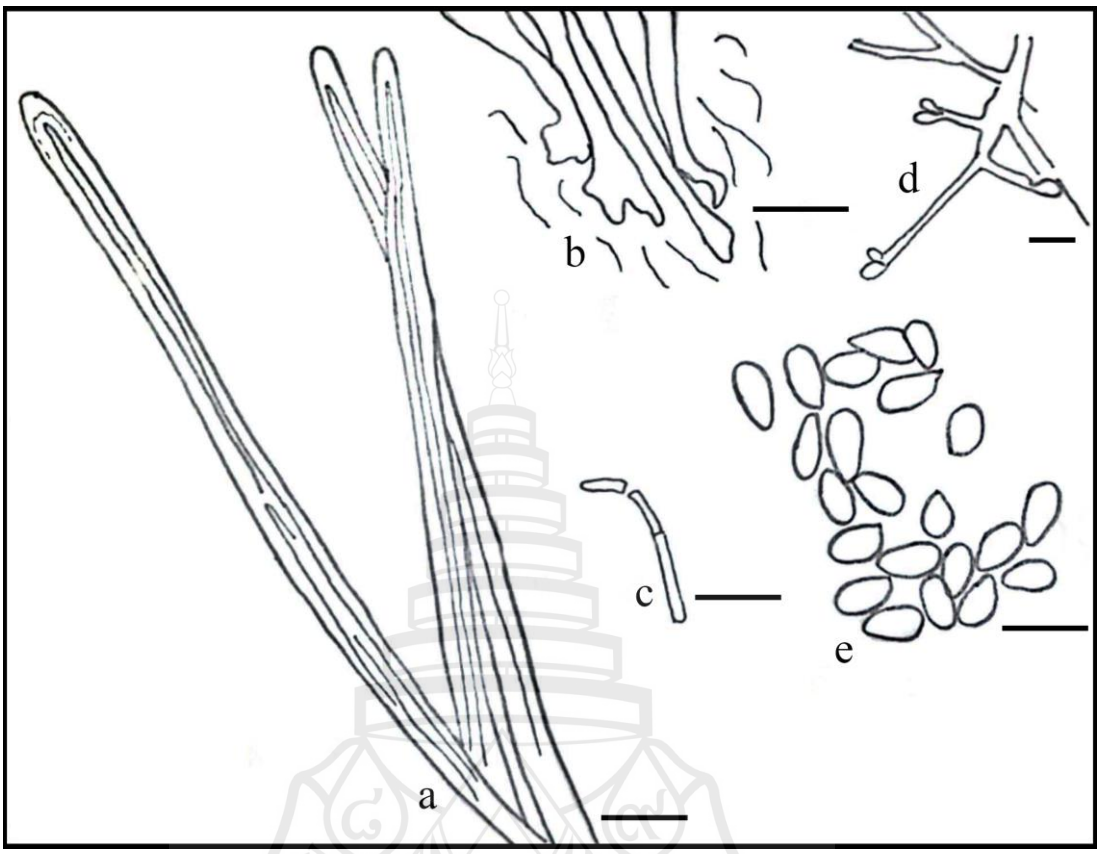


Figure 5.43 *Tyrannicordyceps fratricida*

Figure 5.43, a. Apices of asci. b. Foot of asci. c. Part-spores. d. Phialides of verticillium-like anamorph, showing conida in droplet at apices. e. Conidia. Scale bars: a–e = 10 µm (Adapted from Kepler et al., 2012).

Cordycipitaceae Kreisel ex G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora

Corniculantispora Khons., Thanakitp. & Luangsa-ard, Fungal Syst. Evol. 14: 296 (2024)

Figure 5.44

Index Fungorum number: IF 851978

Khonsanit et al. (2024) proposed *Corniculantispora* to accommodate three species which were previously assigned to *Lecanicillium*. This was based on multigene phylogenetic analyses of LSU, *tef1*, *rpb1*, and *rpb2* sequence data. Khonsanit et al. (2024) included *Corniculantispora aranearum* (syn. *Lecanicillium aphanocladii*), *C. dimorpha* (syn. *Lecanicillium dimorphum*), and *C. psalliotae* (syn. *Lecanicillium psalliotae*) within the genus, with *C. psalliotae* as the type species.

According to Species Fungorum (2025), *Corniculantispora* currently includes three species. Molecular sequence data for all accepted species are available in GenBank (2025).

The sexual morph of *Corniculantispora* remains unknown. The asexual morph is characterized by aculeate, verticillate aphanophialides that originate from undifferentiated, prostrate conidiophores. These phialides are initially flask-shaped with thread-like necks that collapse over time, becoming reduced to fine denticles bearing solitary conidia or small whorls of three to six. Conidia are dimorphic, produced from phialides, solitary or in small clusters. Macroconidia are crescent-shaped, slightly curved, 1-celled, and sharply pointed at both ends. Microconidia are ranging from ellipsoidal to subglobose, slightly curved to nearly straight. Octahedral crystals may be present or absent (adapted from Khonsanit et al., 2024).

Members of *Corniculantispora* have been isolated from a wide range of substrates, including fungi, plants, insects, leaf litter, and soil (Khonsanit et al., 2024). All the three species exhibit fungicolous lifestyles and have been reported on fungal hosts such as *Agaricus bisporus*, *A. bitorquis* (*Agaricaceae*), *Puccinia coronata* (*Pucciniaceae*), *Sphaerotheca fuliginea*, and *S. pannosa* (*Pucciniaceae*) (Khonsanit et al., 2024). These taxa have been documented across diverse geographic regions including Bulgaria, China, Cuba, Germany, Ghana, the Netherlands, India, Indonesia, Israel, Sri Lanka, South Africa, Spain, the UK, and the USA (Khonsanit et al., 2024).

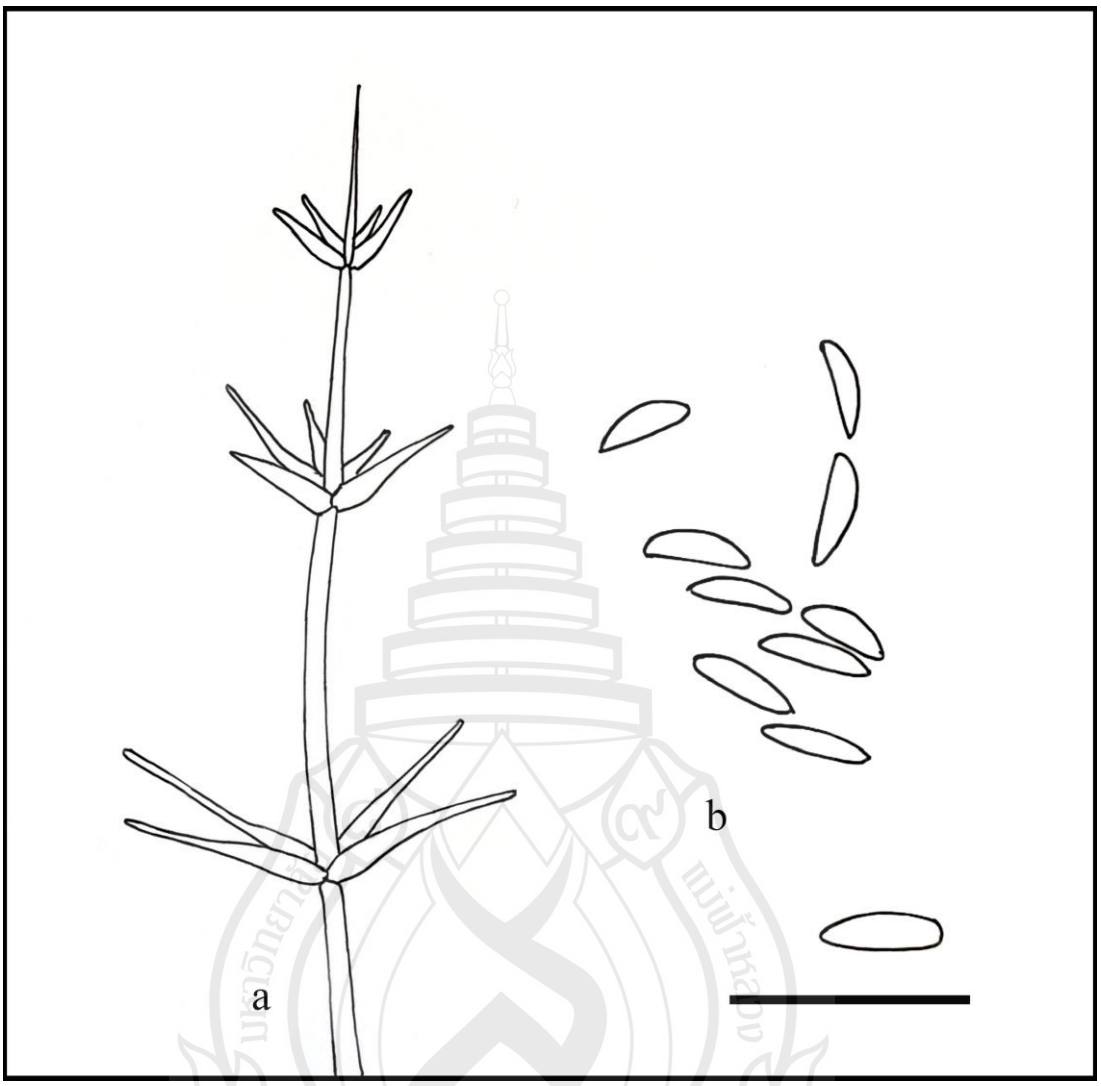


Figure 5.44 *Corniculantispora psalliotae*

Figure 5.44, a. Conidiophore with conidiogenous cells. b. conidia. Scale bar: a, b = 10 μm. (Redrawn from Khonsanit et al., 2024).

Matutinistella F.A. Custódio & O.L. Pereira, Fungal Syst. Evol. 15: 146 (2024)

Figure 5.45

Index Fungorum number: IF 854041

Matutinistella was established by Custódio and Pereira (2025), with *M. brasiliensis* as the type species. This species was isolated as fungicolous on *Pseudocercospora fijiensis* (*Mycosphaerellaceae*) in Brazil (Custódio & Pereira, 2025). As of Species Fungorum (2025), *Matutinistella* is monotypic. Sequence data

for ITS, LSU, SSU, *rpb1*, *rpb2*, and *tef* for *M. brasiliensis* are available in GenBank (2025).

The asexual morph of *Matutinistella* is characterized by septate, branched, smooth-walled, hyaline mycelium. Conidiophores are typically unbranched, occasionally branched or reduced to conidiogenous cells, they are erect, flexuous, septate, and hyaline. Conidiogenous cells are terminal, usually swollen at the apex, and are formed through proliferation of numerous denticles. Conidia are ellipsoid to slightly fusoid, tapering towards the base, hyaline, smooth-walled, and aseptate (adapted from Custódio & Pereira, 2025). The sexual morph of *Matutinistella* remains unknown.

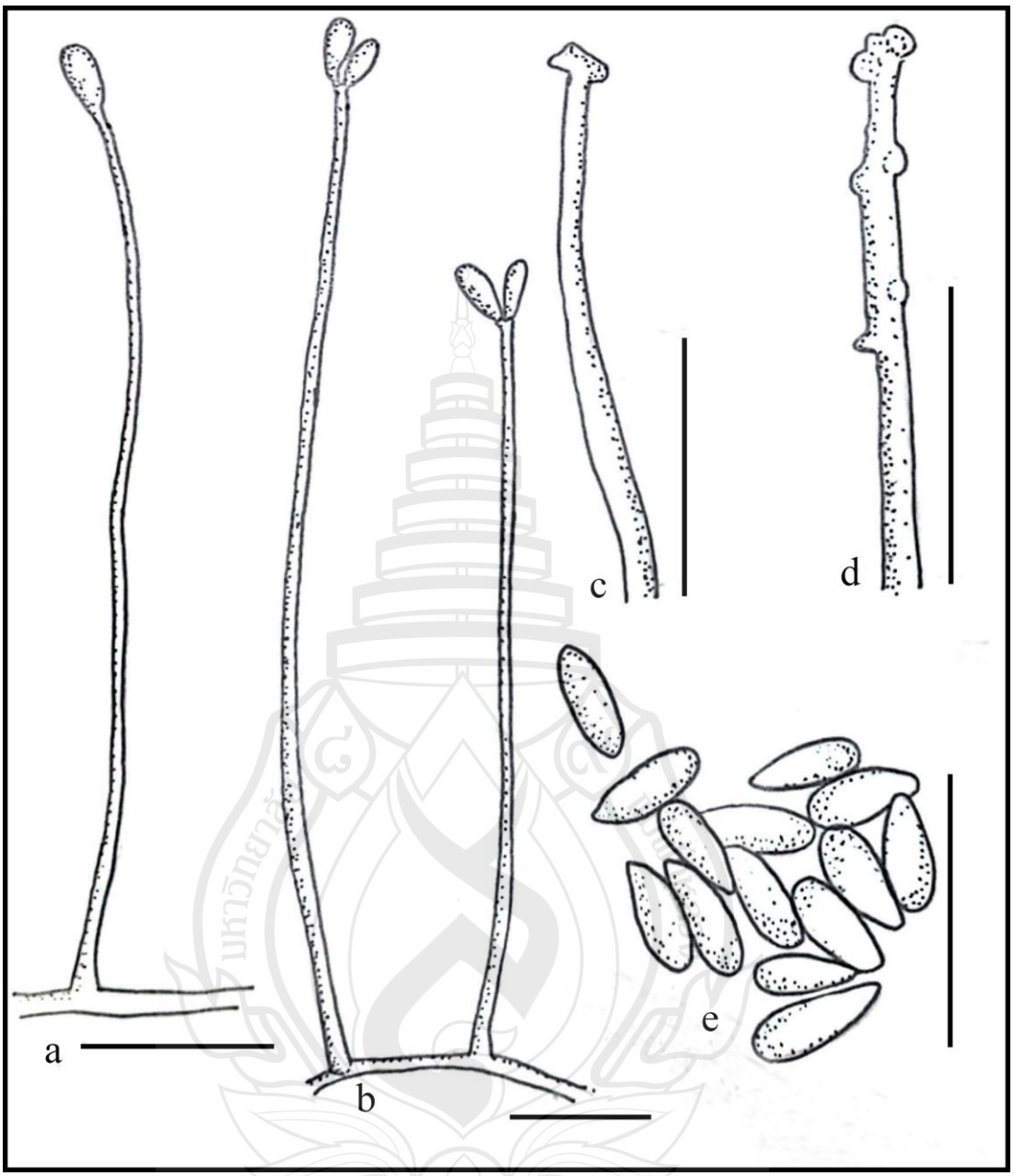


Figure 5.45 *Matutinistella brasiliensis*

Figure 5.45, a, b. Conidiophores and conidiogenous cells. c. Conidiogenous cells with swollen apex. d. Conidiogenous cells with swollen apex and denticles. e. Conidia. Scale bars a–e = 10 µm. (Adapted from Custódio & Pereira, 2025).

Niveomyces J.P.M. Araújo & de Bekker, Persoonia 49: 186 (2022)

Figure 5.46

Index Fungorum number: IF 839229

Niveomyces was introduced by Araújo et al. (2022), with *N. coronatus* as the type species. *Niveomyces coronatus* was described as a mycoparasite on *Ophiocordyceps camponoti-floridani* (*Ophiocordycipitaceae*), an entomopathogen infecting *Camponotus floridanus* in the USA. As of Species Fungorum (2025), five species are listed under *Niveomyces*. Sequence data for ITS, LSU, SSU, *rpb1*, *rpb2*, and *tef* are available in GenBank (2025) for several *Niveomyces* species.

The asexual morph of *Niveomyces* is characterized by septate, hyaline vegetative hyphae and the production of multiple, erect, spiky, and slightly sinuous to straight synnemata, which are unbranched and taper towards the apex. These synnemata are covered by a hymenium-like layer of conidiogenous cells. The conidiogenous cells are polyblastic, elongated, irregular, hyaline, cylindrical, and bear characteristic denticles that are densely arranged apically and sparser towards the base. Conidia are globose to ovoid and are formed singly on the denticles (adapted from Araújo et al., 2022). The sexual morph of *Niveomyces* remains unknown.

Kobmoo et al. (2023) expanded *Niveomyces* by describing five additional species: *N. albus*, *N. formicidarum*, *N. hirsutellae*, *N. insectorum*, and *N. multisynnematus*. *Niveomyces albus* is a mycoparasite on *Ophiocordyceps dipterigena sensu lato* growing on *Diptera* in Thailand and was also observed parasitizing a fungal pathogen of a spider (Kobmoo et al., 2023). *Niveomyces formicidarum* was described from *Ophiocordyceps polyrhachis-furcata* infecting *Polyrhachis furcata* (*Hymenoptera*) and has also been observed on *Hymenoptera* in Thailand (Kobmoo et al., 2023). *Niveomyces hirsutellae* is a mycoparasite on *Hirsutella* aff. *versicolor* infecting *Hemiptera* (leafhoppers, Cicadellidae), and has also been observed on *Hemiptera* (leafhopper, Cicadellidae) in Thailand (Kobmoo et al., 2023). *Niveomyces insectorum* was proposed as a new combination for *Sporothrix insectorum*, based on phylogenetic evidence showing that the ex-type culture of *S. insectorum* clusters within *Niveomyces* (Kobmoo et al., 2023). However, this combination is currently considered invalid in Species Fungorum (2025) and MycoBank (2025). *Niveomyces multisynnematus* was described as a mycoparasite on *Ophiocordyceps* aff. *flavida* infecting *Hemiptera* (leafhoppers) in Thailand, and has also been observed on *Hemiptera* (leafhopper) (Kobmoo et al., 2023).

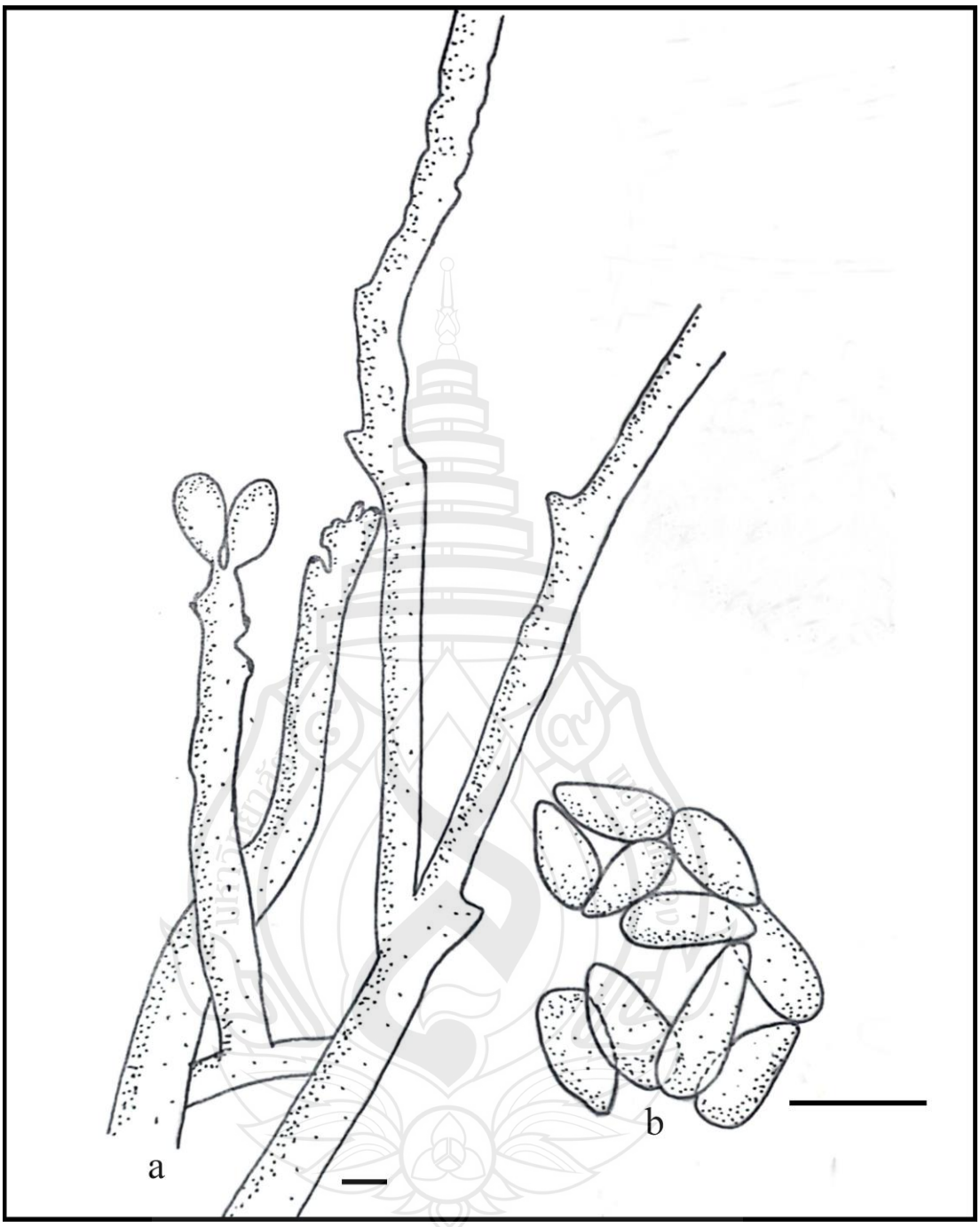


Figure 5.46 *Niveomyces multisynnematus*

Figure 5.46, a. Conidiogenous cells with characteristic of denticles and conidial attachment. b. Conidia. Scale bars: a = 1 μm, b = 4 μm. (Adapted from Kobmoo et al., 2023).

Pseudoniveomyces Tasan., Noisrip. & Kobmoo, Fungal Syst. Evol. 12: 101 (2023)

Figure 5.47

Index Fungorum number: IF 846491

Pseudoniveomyces was established by Kobmoo et al. (2023), with *P. blattae* as the type species. *Pseudoniveomyces blattae* was discovered as a fungicolous species on the stromata of an *Ophiocordyceps* sp. (*Ophiocordycipitaceae*) growing on a cockroach in Thailand. In the same study, Kobmoo et al. (2023) also described *P. arachnovorum*, which was found parasitizing spider eggs within an egg sac.

The asexual morph of *Pseudoniveomyces* is characterized by septate, hyaline vegetative hyphae. Conidiogenous cells arise from undifferentiated hyphae and are elongate or cylindrical, bearing characteristic denticles that are densely clustered at the apex and more sparsely distributed towards the base. Two conidial types are observed. Type I conidia (microconidia) are hyaline, aseptate, smooth- and thin-walled, ovoid to ellipsoid, and are formed singly on denticles, which are produced both in nature and on solid media. Type II conidia (macroconidia) are hyaline, aseptate, smooth, thin-walled, and fusoid, and are produced only on solid media (adapted from Kobmoo et al., 2023). The sexual morph of *Pseudoniveomyces* remains unknown. As of Species Fungorum (2025), two species are listed under *Pseudoniveomyces*. Sequence data for ITS, LSU, *rpb2*, and *tef* are available for *Pseudoniveomyces* in GenBank (2025).

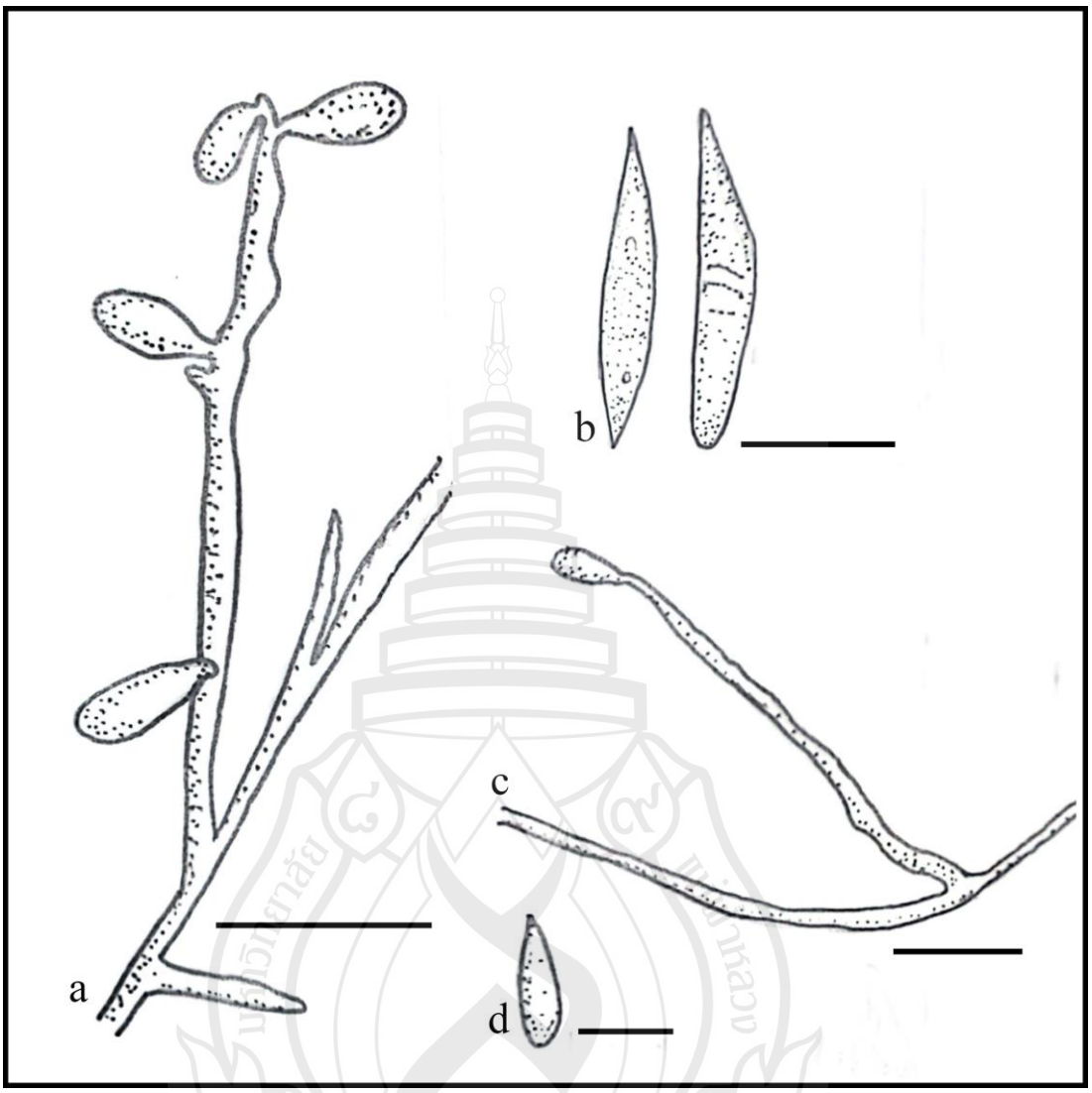


Figure 5.47 *Pseudoniveomyces blattae*

Figure 5.47, a. Conidiogenous cells and Type I conidia on PDA. b. Type II conidia on PDA. c. Conidiogenous cells and Type I conidia on OA. d. Type I conidium on OA. Scale bars: a, c = 10 μm, b = 5 μm, d = 4 μm. (Adaped from Kobmoo et al., 2023).

Zarea Khons., Thanakitp. & Luangsa-ard, Fungal Syst. Evol. 14: 300 (2024)

Figure 5.48

Index Fungorum number: IF 851990

Khonsanit et al. (2024) proposed *Zarea* to accommodate certain species that were previously classified under *Lecanicillium*. This reclassification was based on a multigene phylogenetic analysis using LSU, *tef*, *rpb*1, and *rpb*2 combined sequence

data (Khonsanit et al., 2024). The genus name was designated in honor of Dr. Rasoul Zare, who, alongside Dr. Walter Gams, made significant contributions to the understanding of the genus *Lecanicillium* (Khonsanit et al., 2024). Zare and Gams (2008) proposed transferring members of the *Verticillium fungicola* species complex to *Lecanicillium* based on their close phylogenetic relationship. During their revision of this species complex, var. *flavidum* was elevated to species level, while var. f*ungicola* and var. *aleophilum* were retained as varieties due to their indistinguishable morphological characteristics and minimal ITS sequence variations (Zare & Gams, 2008). However, multigene phylogenetic analyses conducted by Khonsanit et al. (2024) revealed that var. *fungicola* and var. *aleophilum* possess distinct characteristics comparable to *Z. flavidum*, supporting their elevation to the species level within *Zarea*. Consequently, *Zarea* now comprises three species: *Z. aleophila*, *Z. flavida*, and *Z. fungicola* (Khonsanit et al., 2024).

Zarea is characterized by conidiophores that typically emerge from submerged hyphae. These structures are erect, though they may become procumbent over time, and possess thick walls. Conidiophores bear 2–5 whorls of 3–7 phialides, with older colonies sometimes exhibiting more than 10 whorls. The phialides arise at an oblique angle from the conidiophore stipe. Conidia are arranged in mostly globose, slimy heads, with the heads of individual phialides often merging to form large, mucilaginous masses. They are fusiform to long-ellipsoidal or nearly cylindrical, with a basal end that is indistinctly truncate. Some conidia may appear curved along the longitudinal axis, displaying an asymmetrically biconvex, concave-convex, or slightly sickle-shaped form. The conidial surface is smooth-walled, and the conidia vary greatly in size, typically containing one or two, or occasionally more, inconspicuous guttules (adapted from Khonsanit et al., 2024). To date, the sexual morph of *Zarea* has not been observed (adapted from Khonsanit et al., 2024).

Zarea species are fungicolous and associated with a diverse range of mushroom hosts, including *Agaricus* spp. (*Agaricaceae*), *Allopsalliota geesterani* (*Agaricaceae*), *Coltricia perennis* (*Hymenochaetaceae*), *Gomphidius glutinosus* (*Gomphidiaceae*), *Henningsomyces candidus* (*Agaricales incertae sedis*), *Hypholoma capnoides* (*Strophariaceae*), *Laccaria laccata* (*Hydnangiaceae*), *Marasmiellus ramealis* (*Omphalotaceae*), *Russula nigricans* (*Russulaceae*), and *Thelephora terrestris*

(*Thelephoraceae*) (Khonsanit et al., 2024). Additionally, these species can be found in leaf litter and soil (Khonsanit et al., 2024). Notably, *Z. aleophila* and *Z. fungicola* are recognized as pathogens responsible for dry bubble disease in cultivated mushrooms (Berendsen et al., 2010; Yu et al., 2024). These species have been reported from Australia, Belgium, Germany, Finland, France, Iran, the Netherlands, Scotland, UK, and the USA (Khonsanit et al., 2024).

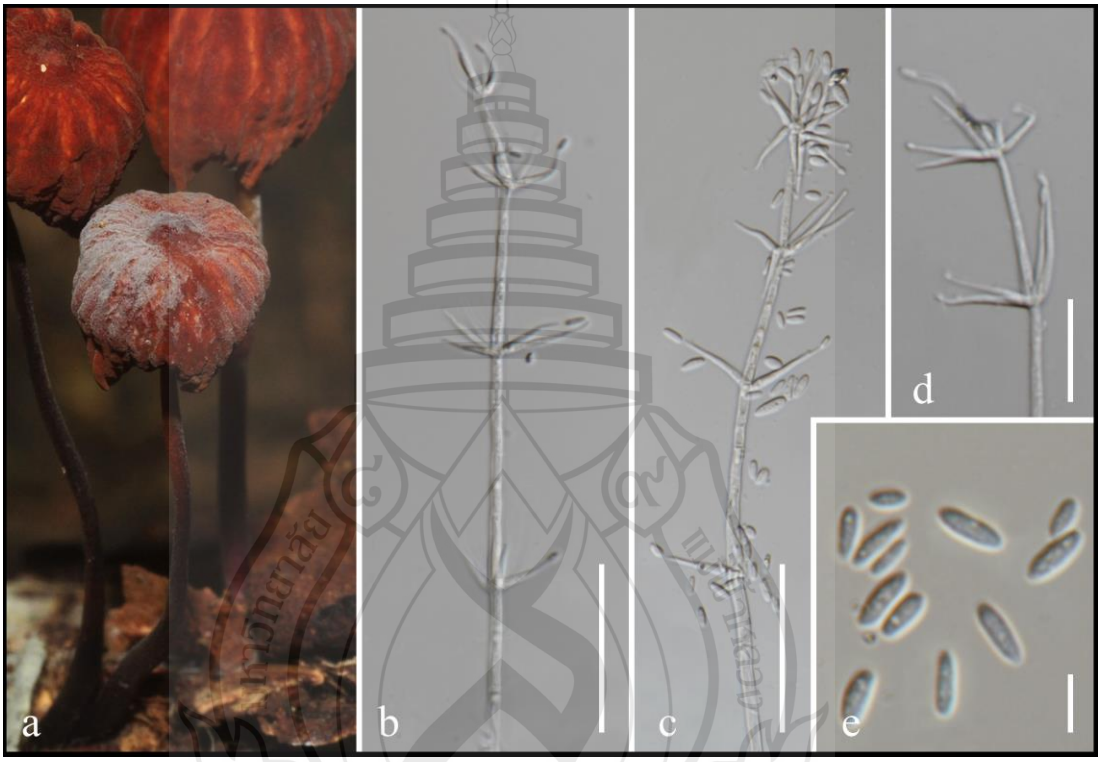


Figure 5.48 *Zarea* sp.

Figure 5.48, a. Fruiting body of *Marasmius* sp. covered with sporulated hyphae b–d. Conidiophores and conidiogenous cells e. Conidia. Scale bars: b, c = 50 μm, d, e = 10 μm.

Flammocladiellaceae Crous, L. Lombard & R.K. Schumach.

Flammocladiella Crous, L. Lombard & R.K. Schumach., Sydowia 67: 103 (2015)

Figure 5.49

Index Fungorum number: IF 812530

Facesoffungi number: FoF 09183

Crous et al. (2015) established *Flammocladiella*, with *F. aceris* (current name *F. decora*) as the type species, which was collected from twigs of *Acer platanoides* in Germany. The genus name "*Flammocladiella*" is derived from the flame-like appearance of the conidial masses that form on the sporodochia (Crous et al., 2015). Lechat and Fournier (2018) proposed *F. decora* as a new combination to *Nectria decora*, whose taxonomic position had been uncertain. Simultaneously, they also pointed out that *F. aceris* should be regarded as a synonym of *F. decora* due to their identical morphology and their classification within the *Flammocladiaceae* clade, affirming that both specimens represent the same species. Lechat et al. (2019) added *F. anomiae* to *Flammocladiella*.

The sexual morph of *Flammocladiella* is characterized by, perithecial, pale luteous to yellow-orange ascomata typically clustered together and connected by a stromatic base. Asci are hyaline, fasciculate, unitunicate and 8-spored. Ascospores are hyaline, guttulate to granular, septate, and fusoidal to ellipsoidal with obtuse ends (adapted from Crous et al., 2015). The asexual morph is characterized by, determinate, sporodochial conidiomata which sporulate in orange, erect flame-like masses. Conidiophores are subcylindrical, septate, straight to flexuous, and branched. Conidiogenous cells are also subcylindrical, hyaline, terminal and intercalary. They proliferate sympodially at the apex. Conidia are hyaline, granular to guttulate, with a slimy texture. They are solitary, subcylindrical to narrowly obclavate, straight to slightly curved, featuring an obtuse apex and a long base, obconically truncate to truncate (adapted from Crous et al., 2015).

Flammocladiella includes only two species: *F. anomiae* and *F. decora* (Species Fungorum, 2025). Both species are fungicolous associated with microfungi, *F. decora* is found on the ascomata of *Massaria* spp. (*Massariaceae*), while *F. anomiae* has occurred on the ascomata of *Massaria anomia* (*Massariaceae*) and on the conidiomata of *Diaporthe oncostoma* (*Diaporthaceae*) (Lechat & Fournier, 2018; Lechat et al., 2019; Crous et al., 2021b). These species have been recorded in Bulgaria, France, Germany, and Ukraine (Crous et al., 2015; Lechat & Fournier, 2018; Lechat et al., 2019; Crous et al., 2021b).

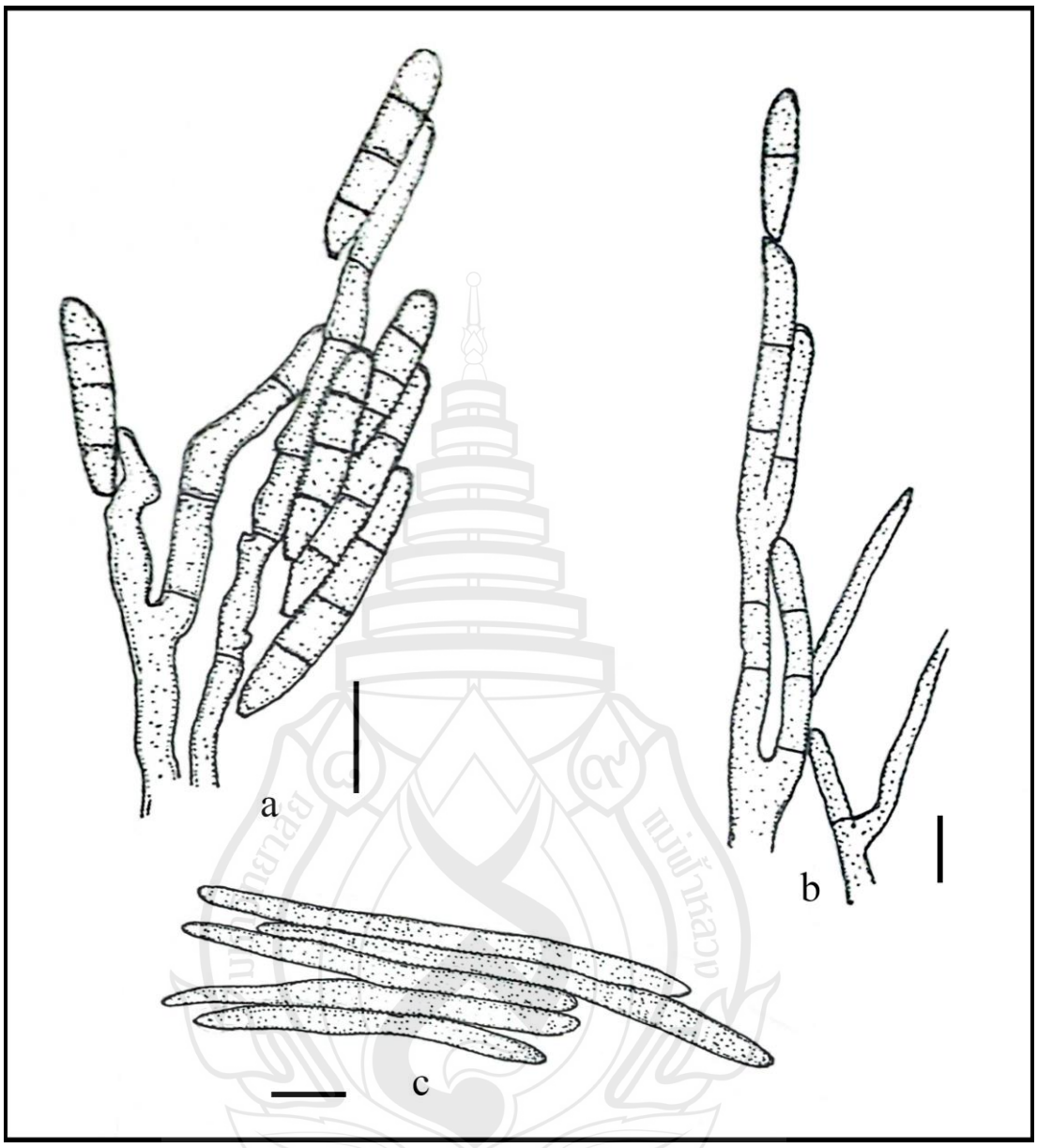


Figure 5.49 *Flammocladiella anomiae*

Figure 5.49, a, b. Conidiogenous cells giving rise to conidia. c. Conidia. Scale bars: a, b, c = 10 μm. (Adapted from Crous et al., 2021b).

Hypocreaceae De Not.

Hypocreopsis P. Karst., Bidr. Känn. Finl. Nat. Folk 23: [251] (1873)

Figure 5.50

Index Fungorum number: IF 2436

Facesoffungi number: FoF 13217

Hypocreopsis was established to include *Sphaeria riccioidea*, reclassified as *Hypocreopsis riccioidea* (Index Fungorum, 2025). Subsequently, *H. riccioidea* was synonymized with *H. lichenoides* (Index Fungorum, 2025). *Hypocreopsis* species are typically found on decaying wood and resupinate basidiomycetes (Stasinska, 2004; Johnston et al., 2007). They are characterized by globose, white to pale yellow perithecial ascomata. They are embedded in a well-developed, radially shredded, often lobate, reddish-brown to grey stromata. The asci are cylindrical, while the ascospores are ellipsoid to fusiform, 1–3- septate, hyaline, and minutely to coarsely warted (Stasinska 2004; Johnston et al., 2007).

Species of *Hypocreopsis* have been reported globally, including in Australia, Austria, Belgium, Canada, China, the Czech Republic, Denmark, Estonia, Finland, France, Germany, Guyana, Indonesia, Ireland, Italy, Japan, Luxembourg, the Netherlands, New Zealand, Norway, Poland, Russia, Spain, Sweden, the UK, and the USA (Johnston et al., 2007; Grundy et al., 2012; Bondartseva & Zmitrovich, 2016; Cannon & Minter, 2019a, 2019b). To date, ten species are listed under *Hypocreopsis* in Species Fungorum (2024). *Hypocreopsis amplectens*, *H. lichenoides*, and *H. rhododendri* are fungicolous associated with *Hymenochaete* spp. (*Hymenochaetaceae*) (Johnston et al., 2007; Grundy et al., 2012; Bondartseva & Zmitrovich, 2016; Cannon & Minter 2019a, 2019b). Grundy et al. (2012) observed that *H. rhododendri* does not form mycelia within woody substrates, suggesting that it is parasitic on the wood decay fungus *Hymenochaete corrugata* (*Hymenochaetaceae*). *Hypocreopsis xylariicola* is fungicolous on *Xylaria* sp. (*Xylariaceae*) in Guyana (Sun et al., 2019a). Only three species, *H. amplectens*, *H. lichenoides*, and *H. rhododendri* currently have ITS sequence data available in GenBank (2025).

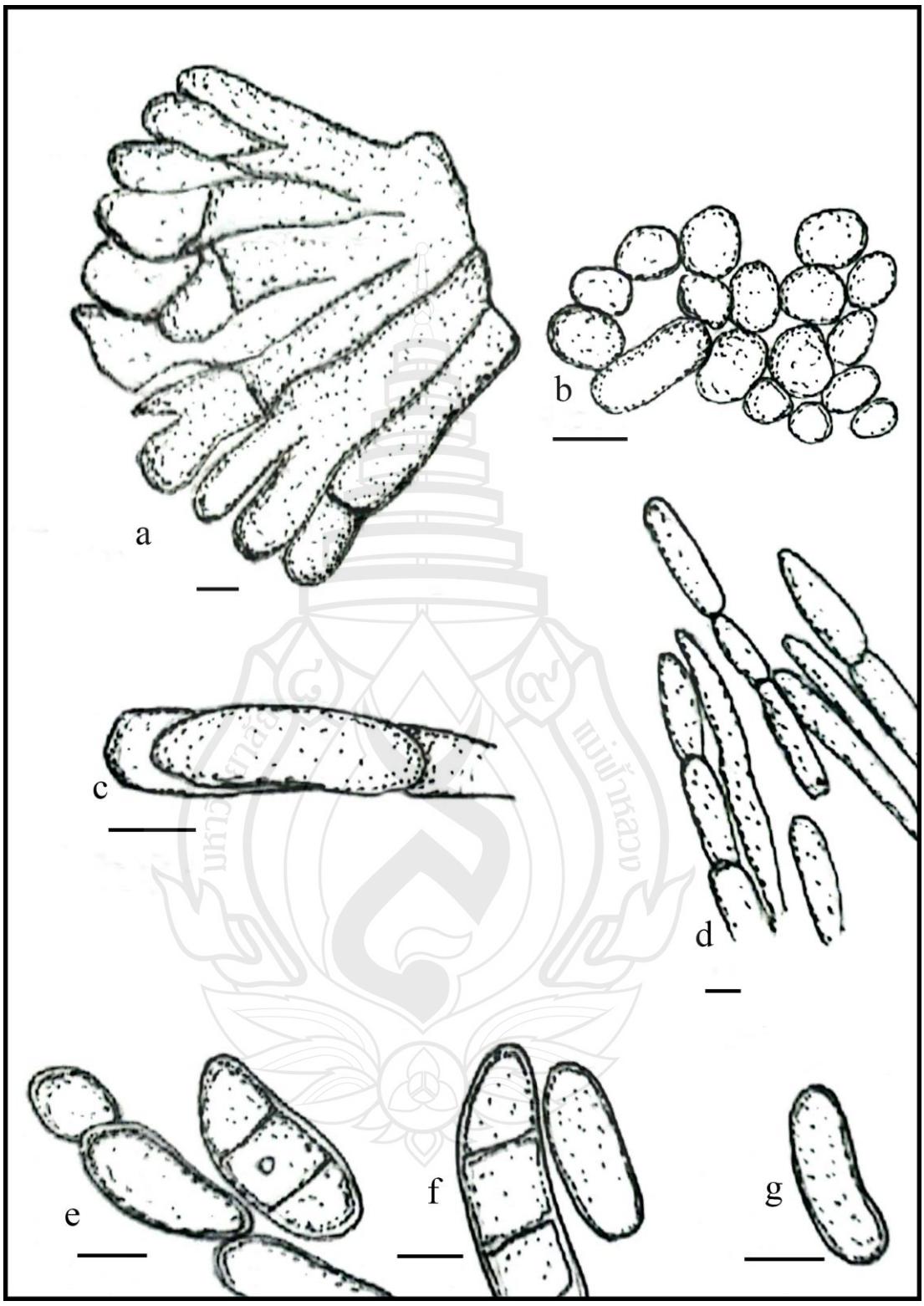


Figure 5.50 *Hypocreopsis amplectens*

Figure 5.50, a. Portion of the whole stroma. b. More or less loose, globose cells on the stromatal surface. c. Ascus apex. d. 3-spored ascus with immature

ascospores. e–g. Ascospores. Scale bars: a = 1 mm, c–g = 10 μm. (Adapted from Johnston et al., 2021).

Hypomyces (Fr.) Tul. & C. Tul., Annls Sci. Nat., Bot., sér. 4 13: 11 (1860)

Figure 5.51

Index Fungorum number: IF 2446

Facesoffungi number: FoF 10847

Hypomyces was treated as a subgenus of *Hypocrea* by Fries (1825), but was elevated to genus level by Tulasne and Tulasne (1860). The genus is typified by *H. lactifluorum*, which was described from collections in the USA (Index Fungorum, 2025). A comprehensive taxonomic revision by Arnold (1971) distinguished *Hypomyces* from related genera such as *Arachnocrea*, *Apiocrea*, and *Peckiella*. Subsequent studies further explored the taxonomy of *Hypomyces*, revealing its morphological relationship with *Cladobotryum* (Rogerson & Samuels, 1985, 1989, 1993, 1994; Põldmaa, 1996, 2003, 2011; Põldmaa et al., 1997, 2000). This relationship was confirmed through multigene phylogenetic analyses (Põldmaa et al., 2000; Põldmaa, 2011). Rossman et al. (2013) formally proposed the connection between the sexual morph *Hypomyces* and the asexual morph *Cladobotryum*, and this concept has been widely accepted in subsequent taxonomic studies (Perera et al., 2023). In accordance with the International Code of Nomenclature for Algae, Fungi, and Plants (ICN), the name *Hypomyces* has also been proposed for conservation over, asexually typified genera such as *Mycogone*, *Sepedonium*, and *Stephanoma* (Rossman et al., 2013).

The sexual morph of *Hypomyces* is characterized by perithecial ascomata, which may be superficial or partially to entirely embedded within a concolorous subiculum. The asci are cylindrical, containing eight ascospores. These ascospores are hyaline, uniseriately arranged, partially overlapping, fusiform with either blunt or acute ends, and possess spinulose to verrucose ornamentation (Rossman et al., 1999; Põldmaa, 2011; Perera et al., 2023). The asexual morph is hyphomycetous, with conidiophores that are generally micronematous, though they can range from semi-macronematous to macronematous. These structures may be aseptate or septate and often bear verticils of conidiogenous cells. The conidia are produced singly and are

ellipsoidal to fusiform, cylindrical, ovoid, obovoid, or clavate and are hyaline to green (Rossman et al., 1999; Põldmaa, 2011; Perera et al., 2023).

Hypomyces species are globally distributed and occur across temperate, tropical, and subtropical ecosystems. Within this broad geographic range, many taxa function as either saprobes or pathogens (Rogerson & Samuels, 1993, 1994; Rossman et al., 1999; Põldmaa, 1996, 2003, 2011). According to Species Fungorum (2025), the genus currently comprises 126 accepted species. Nearly all *Hypomyces* species are fungicolous, predominantly associated with mushroom hosts (Sun et al., 2019a; Gajanayake et al., 2025b). However, exceptions exist, such as *H. iranicus*, which was isolated from submerged branches of *Fagus* sp. in freshwater habitats, and *H. peltigericola*, a lichenicolous species growing on the thallus of *Peltigera canina* (Lechat et al., 2017; Karimi et al., 2022).

Species of *Hypomyces* often exhibit a parasitic relationship with the fruiting bodies of mushrooms, especially those within the *Agaricomycetes* (Tamm & Põldmaa, 2013). Several species show notable host-specificity when parasitizing boletes or agarics (Rogerson & Samuels, 1989; Tamm & Põldmaa, 2013). In commercial mushroom cultivation, certain *Hypomyces* taxa are considered significant pathogens responsible for major diseases (Jayawardena et al., 2025). For instance, *H. rosellus* and *H. odoratus* are the primary agents of cobweb disease, *H. perniciosus* causes wet bubble disease, and *H. pseudocorticiicola* is associated with cottony leak disease (Jayawardena et al., 2025).

Beyond their fungal hosts, *Hypomyces* species have also been reported from a variety of substrates and habitats, including bark, wood, leaves, moss, humus, rock surfaces, insect galls, and lichens (Rogerson & Samuels 1993, 1994; Lechat et al., 2017; Farr et al., 2021; Karimi et al., 2022; Perera et al., 2023). Additionally, some members of the genus produce bioactive secondary metabolites with potential pharmaceutical applications. Notably, metabolites produced by *Hypomyces chrysospermus* have demonstrated anticancer, antimicrobial, and antioxidant activities, including anti-metastatic and anti-proliferative effects (Chakraborty et al., 2016; Dikmen et al., 2020).

The identification and classification of *Hypomyces* species currently rely on a combination of morphological features and multigene phylogenetic analyses. DNA

sequence data for numerous taxa within the genus are available in GenBank (2025). Commonly used molecular markers for resolving species boundaries in *Hypomyces* include ITS, LSU, *rpb1*, *rpb2*, and *tef1-α* (Rehner & Samuels, 1995; Põldmaa et al., 2000; Põldmaa, 2000, 2011; Zare & Gams, 2016). Taxonomically, *Hypomyces* is classified within the *Hypocreaceae*, in *Hypocreales* (Hyde et al., 2024a).

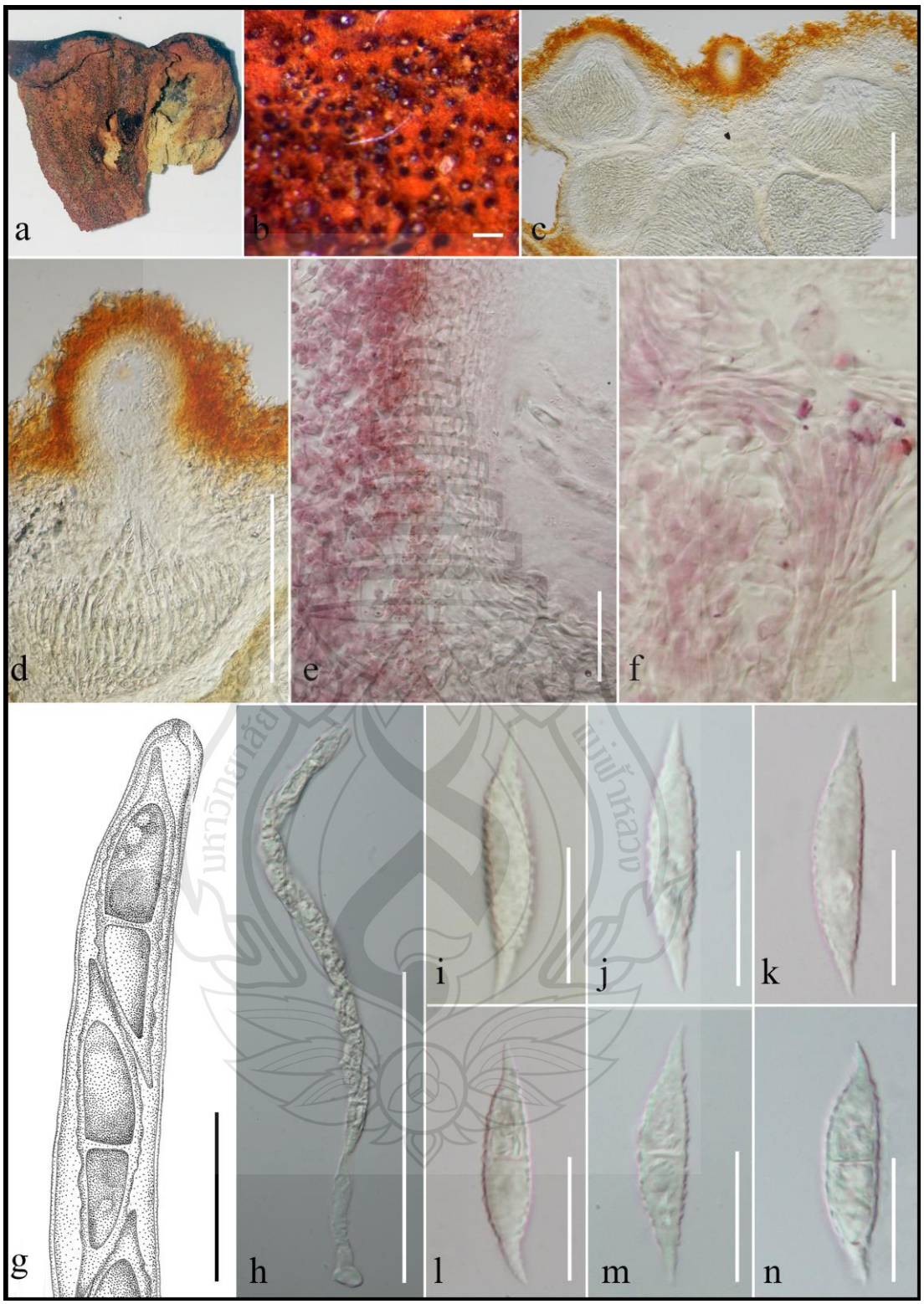


Figure 5.51 *Hypomyces lactifluorum*

Figure 5.51, a. Host *(Lactarius* sp.). b. Ascomata on the host. c, d. Vertical section of ascoma. e. Section of peridium in 3% KOH. f. Hyphae of the subiculum in

3% KOH. g. Illustration of ascal apex (Redrawn from Rogerson & Samuels, 1994). h. Ascus. i–n. Ascospores. Scale bars: b, c, d = 200 μm, h = 80 μm, f = 50 μm, e, g, i–n = 20 μm. (Photo Credits: R.H. Perera).

Mycogone Link, Mag. Gesell. naturf. Freunde, Berlin 3(1-2): 18 (1809)

Figure 5.52

Index Fungorum number: IF 9026

Facesoffungi number: FoF 10849

Mycogone was documented by Link (1809), and the type species is *M. rosea*. Subsequently, numerous species were included in *Mycogone* based on their morphological characteristics. As of the present, there are 23 distinct taxa listed under *Mycogone* in Species Fungorum (2025). The molecular data are available only for a few species. Based on the morphology, *Mycogone* was considered as an allied asexual genus of *Hypomyces* (Rossman et al., 2013). However, to date, the link between *Hypomyces* and *Mycogone* has not been conclusively established through molecular data (Perera et al., 2023).

Mycogone taxa such as *M. calospora*, *M. jaapii*, *M. novae-zelandiae*, *M. rosea*, *M. rufa* and *M. simplex* are fungicolous species (Sun et al., 2019a). Whereas, some are documented associated with decomposing plant substrates (Perera et al., 2023). Members of *Mycogone* have a worldwide distribution. *Mycogone* spp. are pathogens on cultivated mushrooms which cause wet bubble disease (Du et al., 2021; Shi et al., 2023).

The sexual morphology of *Mycogone* has not been determined. Only the asexual morphology has been observed. The conidiophores are semimacronematous, with a straight or flexuous, hyaline and verticillate during the phialidic stage. The conidiogenous cells are monophialidic, discrete, subulate, ampulliform and are arranged in a verticillate pattern. The resulting phialoconidia are clustered in shiny heads and exhibit variation in shape, ranging from ovoid to oblong, ellipsoid, obpyriform or clavate. These phialoconidia can be aseptate or have a single septum, and they are hyaline and smooth-walled. Hyphae are either micronematous or semimacronematous, short, branched, or unbranched and bear aleurioconidia. The aleurioconidia-bearing cells are monoblastic, determinate, can be cylindrical or ampulliform and emerge terminally on laterally from branches of vegetative hyphae

or intercalary positions. The aleurioconidia are solitary and dry, forming at the apex. They are either globose or pyriform and consist of two cells, with one septum dividing them. The upper cell is larger and can be yellow-brown or black, with a thick, tuberculate, or spinose wall. In contrast, the lower cell is smaller, conical or barrel-shaped, and has a thin wall that is either smooth or finely warted (Perera et al., 2023).

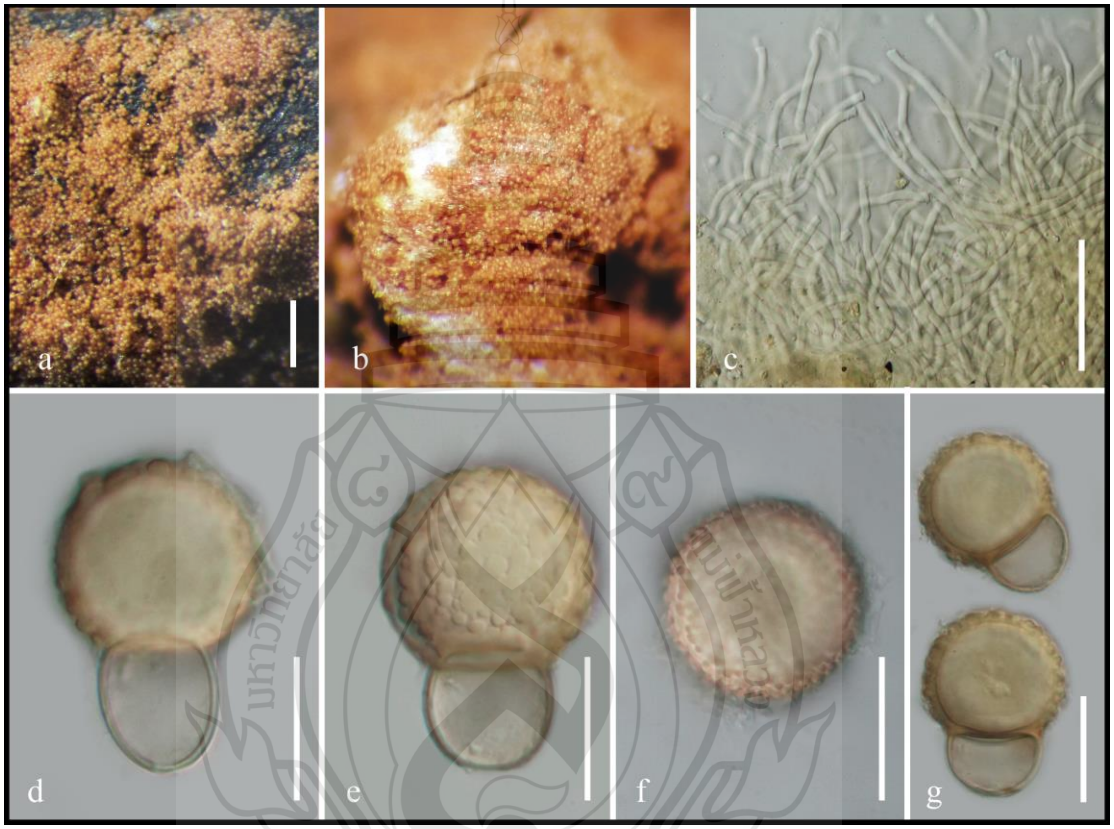


Figure 5.52 *Mycogone rosea*

Figure 5.52, a, b. Large, nodular fruit body covered by fluffy mycelium. c. Hyphae. d–g. Aleurioconidia. Scale bars: a = 500 µm, c = 50 µm, d–g = 20 µm. (Photo credits: R.H Perera).

Protocrea Petch, J. Bot., Lond. 75: 219 (1937)

Figure 5.53

Index Fungorum number: IF 4383

Facesoffungi number: FoF 13220

Petch (1937) established *Protocrea*, which included *Hypocrea farinosa*, *H. delicatula*, and *H. stipata*. Notably, Petch (1937) did not designate a specific type

species for the genus. Moravec (1956) designated *P. farinosa* as the lectotype for *Protocrea*, while maintaining *P. delicatula* within *Protocrea* but transferred *P. stipata* to his newly established *Arachnocrea*.*Protocrea delicatula* was replaced by *Hypocrea* (Jaklitsch et al., 2008). Overton et al. (2006) epitypified *Protocrea*. However, the subsequent examination by Jaklitsch et al. (2008) revealed that the epitypification by Overton et al. (2006) was based on misidentified material. Therefore, *Protocrea* was reconsidered by Jaklitsch et al. (2008) based on morphology and phylogenetic analyses.

The sexual morph of *Protocrea* is characterized by perithecial ascomata, which are either immersed within or erupting from a continuous or discontinuous, broadly effuse subiculum. Asci are cylindrical and contain 2-celled ascospores that disarticulate at the septum into globose, oblong, or wedge-shaped cells. The asexual morph is *Gliocladium* like (Jaklitsch et al., 2008).

The members of *Protocrea* have been documented associated with plant substrates (bark, decaying wood) and fungal hosts (basidiomycetes) in Argentina, Austria, Denmark, Estonia, Finland, France, Germany, Japan, the Netherlands, Slovenia, the UK and the USA (Rossman et al., 1999; Põldmaa, 2000; Jaklitsch et al., 2008). There are six species of *Protocrea* listed in Species Fungorum (2025). Among those species, *Protocrea farinosa* (on decayed *Stereum* (*Stereaceae*)), *P. fungicola* (on a polypore), *P. illinoensis* (on a hymenophore of *Skeletocutis nivea* (*Incrustoporiaceae*)), *P. pallida* (on decaying *Polyporus caesius* (*Polyporaceae*)) are fungicolous (Põldmaa, 2000; Jaklitsch et al., 2008; Index Fungorum, 2025).

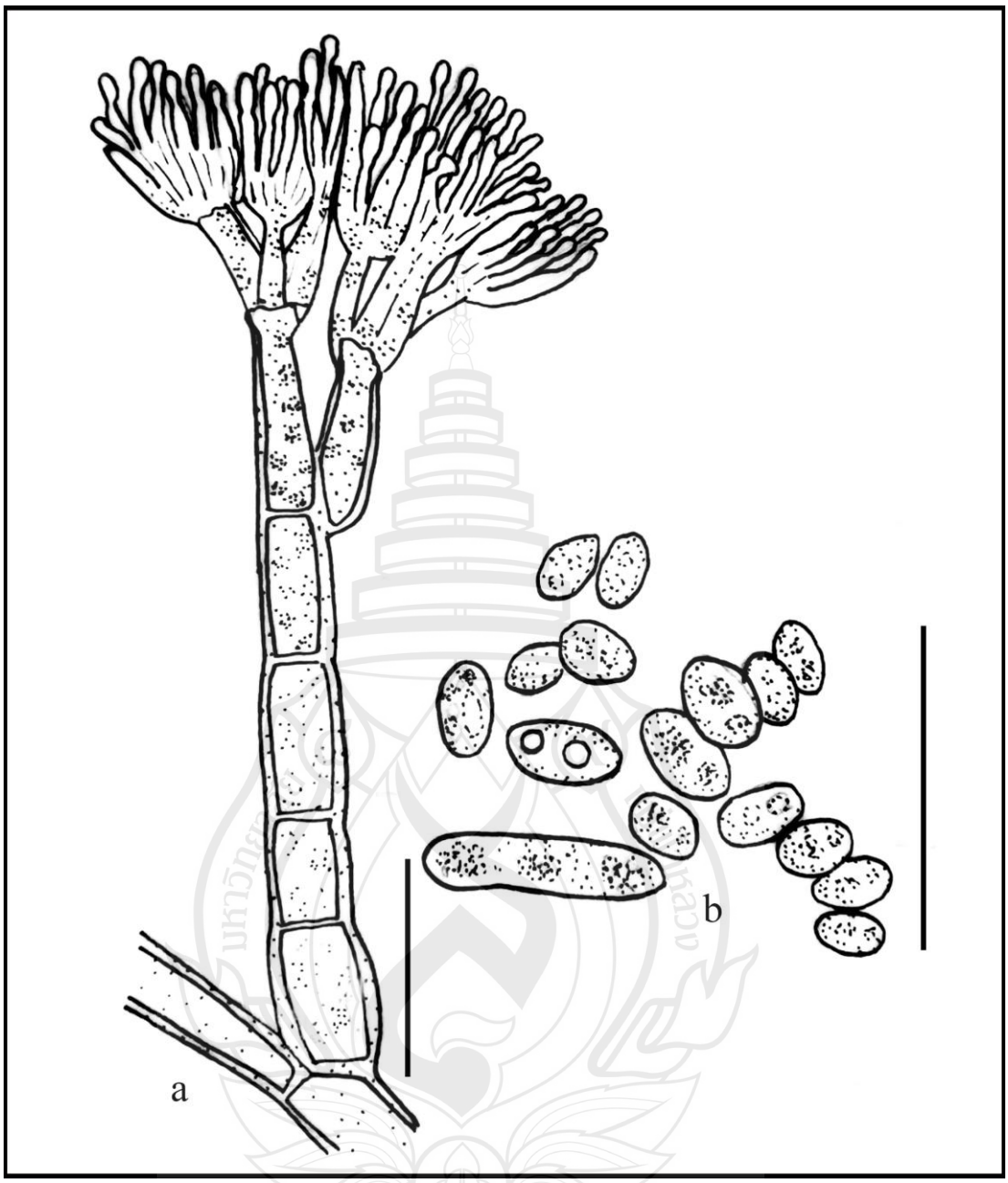


Figure 5.53 *Protocrea farinosa*

Figure 5.53, a. Conidiophores on corn meal agar. b. Conidia. Scale bars: a, b = 15 μm (Adapted from Jaklitsch et al., 2008).

Sphaerostilbella (Henn.) Sacc. & D. Sacc., Syll. fung. (Abellini) 17: 778 (1905)

Figure 5.54

Index Fungorum number: IF 5122

Facesoffungi number: FoF 10851

Sphaerostilbella, was classified as a subgenus within *Sphaerostilbe* and consisted of a single species, *Sphaerostilbe lutea*. Seifert (1985) reaffirmed *Sphaerostilbella*. Rehner and Samuels (1994) combined the asexual morphic *Gliocladium* with *Sphaerostilbella* based on phylogenetic evidence. Rossman et al. (2013) proposed *Sphaerostilbella* over *Gliocladium. Sphaerostilbella* has also been considered as one of the allied genera of *Hypomyces*. Rossman et al. (1999, 2001) confirmed the placement of *Sphaerostilbella* in *Hypocreaceae* by phylogenetic analyses. *Sphaerostilbella aurifila* is considered as the type species of this genus. Previously identified *Sphaerostilbe lutea* was named *Sphaerostilbella aurifila* after several synonyms (Lombard et al., 2015). The existence of *Sphaerostilbella* was further confirmed by taxonomic studies (Maharachchikumbura et al., 2016; Hyde et al., 2020). As of the present, there are 12 distinct taxa listed under *Sphaerostilbella* in Species Fungorum (2025). Recently ITS, LSU, and *tef* molecular markers have been used for the multigene phylogenetic analyses of *Sphaerostilbella*; Põldmaa et al., 2019).

Members of *Sphaerostilbella* have a worldwide distribution occurring as fungicolous associated with basidiomycetes and rarely on decaying wood (Rossman et al., 1999; Poldmaa et al., 2019). The fungicolous species include *S. appalachiensis* (on *Heterobasidion irregular* (*Bondarzewiaceae*)), *S. aurifila* (on *Daedalea unicolor* (*Fomitopsidaceae*)), *S. berkeleyana* (on dead *Stereum hirsutum* (*Stereaceae*)), *S. broomeana* (on *Heterobasidion* sp.), *S. ganodermatis* (on *Ganodermataceae*), *S. himalayensis* (on *Dichostereum effuscatum* (*Peniophoraceae*)), *S. micropori* (on *Microporus xanthopus* (*Polyporaceae*)), *S. novae-zelandiae* (on basidiomata of polypore), *S. parabroomeana* (on polypore), *S. penicillioides* (on *Thelephora hirsute* (*Thelephoraceae*)), and *S. toxica* (on *Gloeophyllum striatum* (*Gloeophyllaceae*)) (Poldmaa et al., 2019; Sun et al., 2019a; Index Fungorum, 2025).

The sexual morph of *Sphaerostilbella* is characterized by, perithecial ascomata which can be superficial or semi-immersed in the subiculum. Ascomata can be solitary to gregarious, ivory, yellowish white to ochraceous while it is occasionally covered with white mycelial weft and lacks paraphyses. Asci are 8-spored, cylindrical, with slightly thickened apex. Ascospores are uniseriate with ends

overlapping, fusiform to naviculate or ellipsoid, 1-septate, hyaline, finely spinulose or grossly warted-tuberculate (Rossman et al., 1999; Perera et al., 2023). The asexual morph is characterized by, micronematous conidiophores/ conidiogenous branches which arises from hyphae on the host or aerial hyphae in the culture. Conidiophores are branched or unbranched, septate, and hyaline to pale ochraceous, bear one to a few phialides, or form conidia directly from simple conidiophores. Conidiogenous cells are phialidic, almost cylindrical, tapering gradually to the apex. Conidial masses are translucent, and globose. Conidia are variable in size and shape, ellipsoidal to oblong or allantoid, narrow clavate or narrow obclavate, 0–1(−3)-septate, straight to curved or bent, sometimes apiculate, base flattened or rounded, hilum inconspicuous or rarely pronounced (Rossman et al., 1999; Perera et al., 2023).



Figure 5.54 *Sphaerostilbella aurifila*

Figure 5.54, a, b. Synnemata on host. c. Synnema mounted in water. Hyphae. d. Hyphae of conidiophores. e. Conidiogenous cells and conidia. f. Conidia. Scale bars: a = 1 mm, b, c = 500 µm, d = 100 µm, f = 10 µm. (Photo credits: R.H Perera).

Sporophagomyces K. Põldmaa & Samuels, Canad. J. Bot. 77(12): 1765 (2000) [1999]

Figure 5.55

Index Fungorum number: IF 28375

Facesoffungi number: FoF 13223

Põldmaa et al. (2000) proposed *Sporophagomyces* to accommodate three species formerly placed in *Hypomyces*, namely *H. chrysostomus*, *H. lanceolatus*, and *H. moellerianus*. These were combined as *Sporophagomyces chrysostomus* (type species), *S. lanceolatus*, and *S. moellerianus*, respectively. Among them, *S. chrysostomus* and *S. lanceolatus* are typically growing on polypores of *Ganodermataceae*, while *S. moellerianus* is commonly found on members of *Polyporaceae* (Põldmaa et al., 2000). These taxa likely derive nutrients from detached basidiospores (Põldmaa et al., 2000).

The sexual morph of *Sporophagomyces* include obpyriform, papillate perithecia that are buff to yellow, semi-immersed, gregarious, and embedded within a hyphal tomentum. The hyphae may be smooth-walled or spinulose, often with free ends. The perithecial wall comprises interwoven hyphae, with clavate terminal cells in papillar hyphae. Asci are cylindrical, with slightly thickened apices and lacking a visible apical pore. Ascospores are arranged in an obliquely uniseriate manner, fusiform to lanceolate or naviculate, (0–)1-septate with median or submedian septation, smooth or minutely verrucose, non-apiculate or bearing minute apiculi (<1 μm). Upon discharge, mature ascospores often fragment into part-spores (Põldmaa et al., 2000).

The asexual morph has only been described for *S. chrysostomus*, previously known as *Acremonium lindtneri*. It features simple conidiogenous cells formed directly on vegetative hyphae, each producing conidia singly at the apex within a droplet of clear liquid. Conidia are primarily three-septate, thick-walled and resting spores are absent (Põldmaa et al., 2000).

To date, *Sporophagomyces* comprises three species (Species Fungorum, 2025), although molecular sequence data are currently available only for *S. chrysostomus* in GenBank (2025).

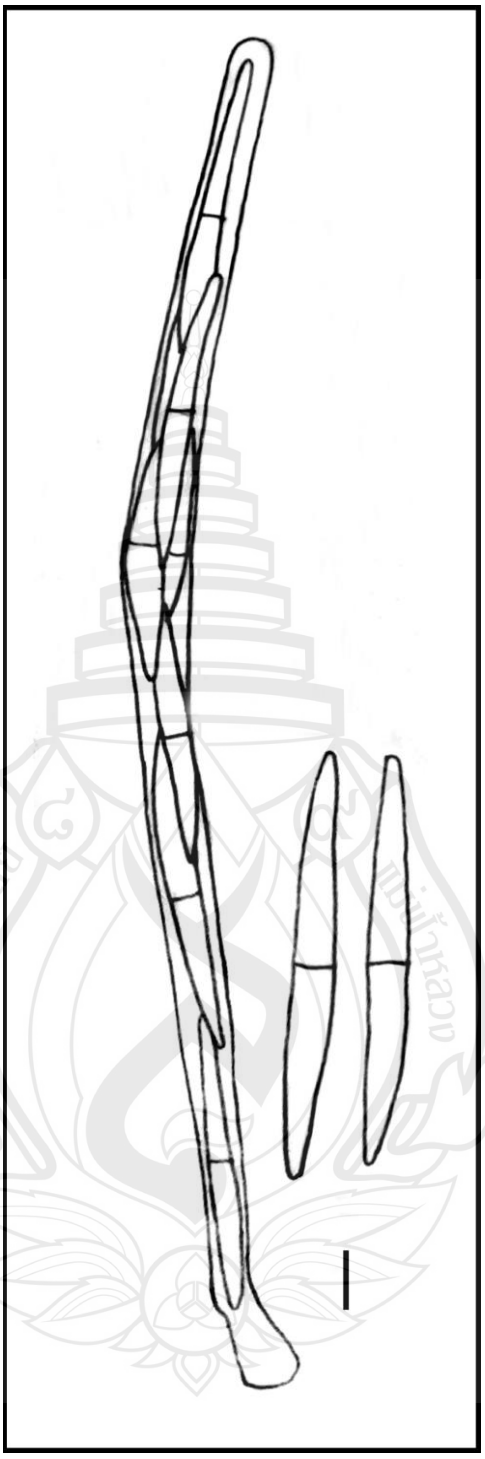


Figure 5.55 *Sporophagomyces lanceolatus*

Figure 5.55, Ascus and ascospores. Scale bar = 10 µm. (Redrawn from Rogerson & Samuels, 1993).

Trichoderma Pers., Neues Mag. Bot. 1: 92 (1794)

Figure 5.56

Index Fungorum number: IF 10282

Facesoffungi number: FoF 02075

Trichoderma was introduced by Persoon (1794) with *T. viride* as the type species. *Trichoderma* is an asexual morph typified generic name which is currently used over *Hypocrea*. *Hypocrea* is typified by *H. rufa*, a sexual morph typified generic name (Rossman et al., 2013; Jaklitsch & Voglmayr, 2014a). *Hypocreaceae* was established based on *Hypocrea*. The members of *Hypocrea*/*Trichoderma* were identified to be monophyletic. Therefore, following the Melbourne Code of Nomenclature (ICN) rules, Rossman et al. (2013) proposed to conserve *Trichoderma* over *Hypocrea*.

The members of *Trichoderma* have a cosmopolitan distribution (Jayawardena et al., 2021). They have been commonly found on different plant hosts with an abundant presence in soils and decaying wood, in various environments (Sharma et al., 2019; Oliveira et al., 2023). *Trichoderma* species are considered as typical mycoparasites on a diverse array of hosts, encompassing pathogens and saprobes which represent Ascomycota and Basidiomycota (Krauss et al., 2013; Mukherjee et al., 2013; Swain & Mukherjee, 2020; Jayawardena et al., 2021). Therefore, *Trichoderma* possesses various biotechnological applications such as bio-fungicide and biofertilizer production (Sharma et al., 2019a; Swain & Mukherjee, 2020). Many species such as, *T. aggressivum*, *T. americanum*, *T. asperellum*, *T. austriacum*, *T. atroviride*, *T. hamatum*, and *T. koningii* are fungicolous (Sun et al., 2019a). However, some fungicolous *Trichoderma* species are also responsible for causing green mold disease which is a significant and substantial threat to mushroom cultivation on a global scale (Jayawardena et al., 2021; Yu et al., 2024). Mushroom growers worldwide view *Trichoderma* as a grave concern due to its potential to result in substantial economic losses and reduced yields within the mushroom industry (Gea et al., 2021; Jayawardena et al., 2021; Altaf et al., 2022a, b; Šašić et al., 2023).

It has been recommended that the species identification of *Trichoderma* should be based on a polyphasic approach (ecology, morphology, phylogeny, pathogenicity) whenever the data are available (Jayawardena et al., 2021). As of the

present, over 400 distinct taxa are listed under *Trichoderma* in Species Fungorum (2025). Molecular data for most of the species are available in GenBank (2025). The recommended molecular markers for *Trichoderma* are, ITS, LSU, *rpb2* and *tef* (Jaklitsch & Voglmayr, 2014a; Cai & Druzhinina, 2021).

The sexual morph of *Trichoderma* is characterized by, stromata discrete to effused, with or without a true cortex, composed of pseudoparenchyma cells and/ or highly compacted hyphae. Ascomata are embedded in the stroma, perithecial, flask-shaped, globose, subglobose to ellipsoidal. Peridium hyaline, subhyaline or yellow, sometimes yellow-brown, yellow-orange, dull green or brown. Paraphyses usually are apically deliquescent. Asci are 8-spored, unitunicate, cylindrical, sometimes with a J-, apical ring. Ascospores are uniseriate or sometimes obliquely biseriate, bi-cellular, disarticulating into two equal or unequal parts, subglobose, globose, ovoid, oblong or wedge-shaped part ascospores, guttulate, hyaline or green, sometimes dull green to brown-green, typically spinulose or warted, rarely smooth-walled (Maharachchikumbura et al., 2016; Perera et al., 2023). The asexual morph is hyphomycetous, mostly formed in pustules, on natural substrates associated with stroma. The conidiophores are simple, conspicuously curved to sinuous or conspicuously curved, without or with weakly developed or well-developed main axis, branched, branching irregular, verticillate or sometimes tree-like, hyaline, smooth, septate. The phialides are divergent or parallel, solitary or originating in whorls, sometimes repetitive, forming chains, lageniform, ampulliform, cylindrical or subulate, symmetric or inequilateral, curved to sinuous or straight, hyaline, smooth. The conidia unicellular, globose to subglobose, ovoid, ellipsoidal, oblong, green or hyaline, usually guttulate, rarely aguttulate, scar indistinct or indistinct, smooth-walled or verruculose, spinulose or warted. The chlamydospores can be absent or present, terminal and/or intercalary, globose, subglobose, oblong or ellipsoid or oblong, usually aseptate, sometimes 1-septate (Maharachchikumbura et al., 2016; Perera et al., 2023).

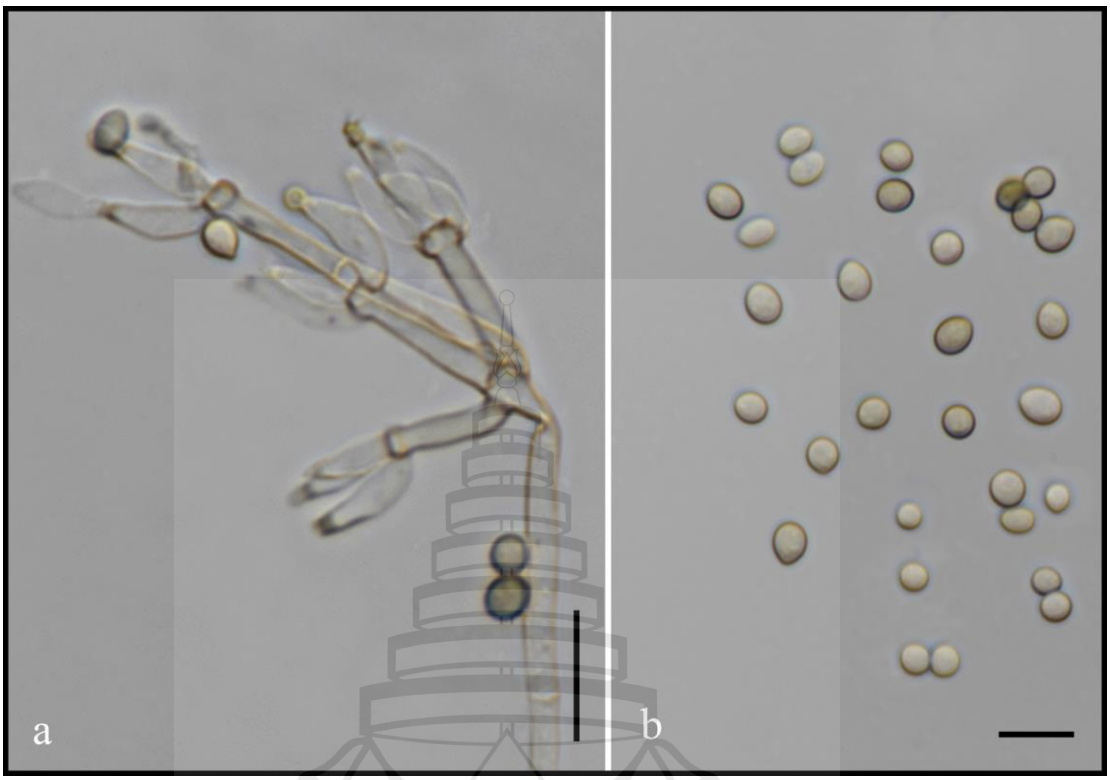


Figure 5.56 *Trichoderma* sp.

Figure 5.56, a. Conidiophore, conidiogenous cells. b. Conidia. Scale bars: a = 10 μm, b = 5 μm.

Myrotheciomycetaceae Crous

Trichothecium Link, Mag. Gesell. naturf. Freunde, Berlin 3(1-2): 18 (1809)

Figure 5.57

Index Fungorum number: IF 10303

Facesoffungi number: FoF 13427

Trichothecium was described by Link in 1809 and was revised by Summerbell et al. (2011). This revision revealed five *Trichothecium* species with three distinct asexual forms. These forms are currently classified as *Acremonium*, *Spicellum*, and *Trichothecium* (Summerbell et al., 2011). *Trichothecium roseum* (Pers.) Link is the type species of this genus.

Trichothecium roseum has been globally recognized as a common pathogen causing post-harvest rots in a wide range of fruits and vegetables including, avocado, grapes, purple passion, strawberry, and tomato (Dal Bello et al., 2008; Kwon et al., 2010; Sharma et al., 2016; Li et al., 2022; Harishchandra et al., 2023). It is also a leaf

spot pathogen on crops such as mango and cherry (He et al., 2011; Ashraf et al., 2020). Furthermore, *T. roseum* is associated with rose dieback, trunk disease in *Sapindus mukorossi*, maize ear rot, alfalfa root rot, and apple core rot (Wright et al., 2007; Gao et al., 2013; Tang et al., 2016; Xue et al., 2016; Dan et al., 2022). Moreover, *T. roseum* exhibits an entomopathogenic effect against *Pauropsylla buxtoni* immatures infesting *Ficus carica* leaves (Batta, 2020). As a fungicolous species, it acts as a hyper-parasite of rusts and on conidia of *Pestalotiopsis funerea* (*Amphisphaeriacese*) (Ahmad, 1970; Urbasch, 1992). Due to the hyper-parasitic activity on rusts *T. roseum* has been studied as a potential agent for the biological control of soybean rust (Kumar & Jha, 2002). *Trichothecium roseum* also has an antagonistic behaviour against wheat powdery mildew (*Blumeria graminis* (*Erysiphaceae*)) (Zhu et al., 2022). The compound trichothecin produced by *T. roseum* has been revealed to demonstrate a strong antifungal activity (Freeman, 1955; Zhang et al., 2010). Additionally, *T. roseum* is a pathogen on *Coprinus comatus*, causing stipe canker and as a mycoparasite of *Sclerotinia sclerotiorum* (Huang & Kokko, 1993; Dong & Bian, 2013). Moreover, *T. crotocinigenum* (on *Trametes versicolor*) and *T. fusarioides* (on *Phyllachora peribebuyensis* (*Phyllachoraceae*)) are fungicolous taxa (Index Fungorum, 2025).

The asexual morph of *Trichothecium* exhibits variability in the conidiogenous apparatus among species. Conidiophores can be septate and unbranched, producing hyaline, obovate, oblong, or cylindrical phialoconidia. Alternatively, conidiophores may be unbranched or occasionally branched, exhibiting a retrogressive pattern with each conidial production. In this case, conidia are septate, ellipsoidal or ovate, with a decurved, abruptly narrowed basal hilum ending in a distinct truncate apex. Another type of conidiophore ranges from unicellular to multicellular, with multiple rebranched structures that extend indefinitely. These structures show sympodial proliferation of the conidiogenous rachis, producing oval to ellipsoidal, cylindrical, or allantoid conidia (adapted from Summerbell et al., 2011). The sexual morph of *Trichothecium* is characterized by colorless or slightly pink, spherical or nearly spherical, non-ostiolate ascomata. The asci are 8-spored and clavate to spherical. Ascospores are smooth or finely striate, ellipsoidal, or reniform, with a broad gelatinous sheath (adapted from Summerbell et al., 2011). To date, there are 25

Trichothecium species listed in Species Fungorum (2025). As most of the species have been described before the molecular data came into use, to date only seven species among them have molecular data in GenBank (2025). Therefore, Summerbell et al. (2011) suggested a thorough investigation to elucidate the phylogenetic relationship of those species within *Trichothecium*.

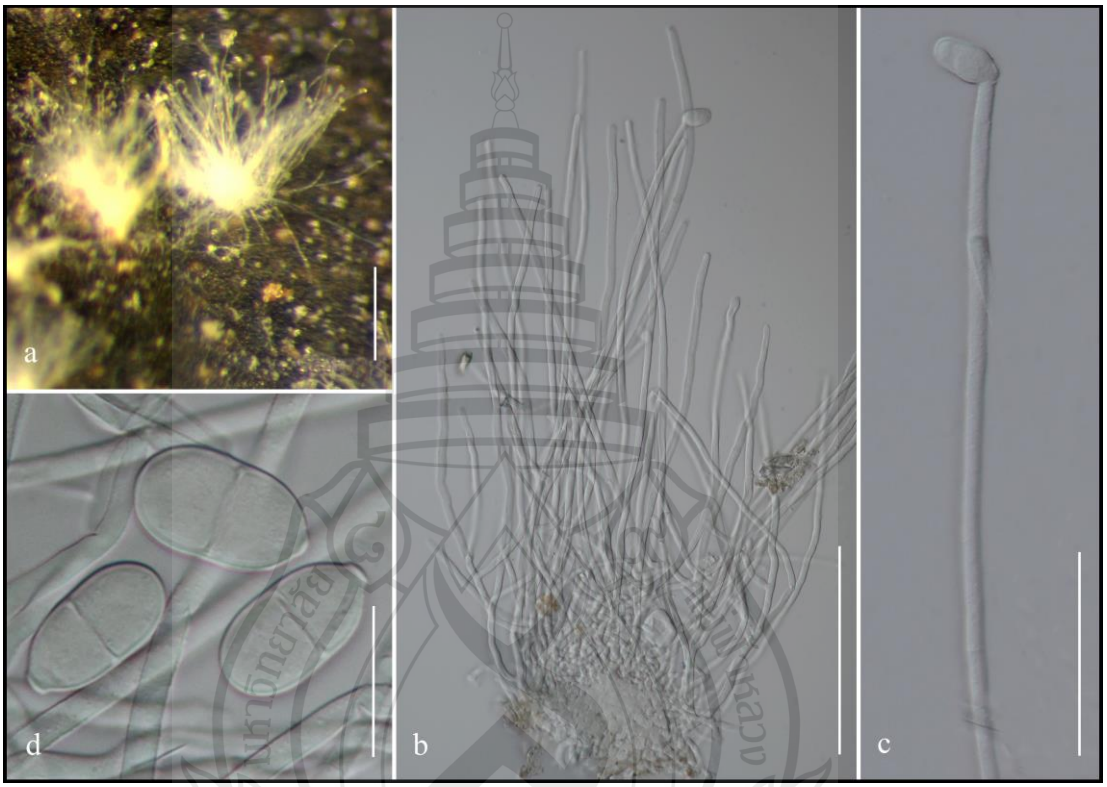


Figure 5.57 *Trichothecium roseum*

Figure 5.57, a. Conidiophores on host. b, c. Conidiophore with conidia. d. Conidia. Scale bars: a = 200 μm, b = 100 μm, c = 50 μm, d = 20 μm. (Photo credits: R.H Perera).

Nectriaceae Tul. & C. Tul.

Cosmospora Rabenh., Hedwigia 2: 59 (1862)

Figure 5.58

Index Fungorum number: IF 1273

Facesoffungi number: FoF 10977

Rabenhorst (1862) established *Cosmospora* with *C. coccinea* as the type species. The generic concept of *Cosmospora* remained relatively broad. It encompassed a broad range of asexual morphologies, though sexual morphology was

more conserved. Species typically exhibit small, orange to reddish, KOH+ perithecia with thin walls, cylindrical asci (with or without an apical ring), and uniseriate, 1-septate ascospores. Stroma development is typically limited (Gräfenhan et al., 2011).

Gräfenhan et al. (2011) proposed a more restricted concept for *Cosmospora*, limiting it to species closely related to *C. coccinea*, characterized by acremonium-like asexual morphs and predominantly fungicolous lifestyles. This revision led to the acceptance of eight species in the genus, with 12 subsequently added, reaching a current total of 20 recognized species (Gräfenhan et al., 2011; Herrera et al., 2015; Zeng & Zhuang, 2016; Luo et al., 2019; Lechat & Fournier 2021; Bao et al., 2023). These species have been documented globally, including in Argentina, Brazil, Canada, China, Costa Rica, Denmark, Finland, France, Germany, Guyana, India, Japan, the Netherlands, Portugal, Puerto Rico, Switzerland, the UK, the USA, Ukraine, and Venezuela (Hirooka et al., 2008; Gräfenhan et al., 2011; Herrera et al., 2015; Zeng & Zhuang, 2016; Luo et al., 2019; Lechat & Fournier, 2021; Bao et al., 2023).

Cosmospora species are characterized by superficial, solitary to gregarious, orange-red to bright red, pyriform perithecia. The asci are cylindrical to narrowly clavate with ellipsoidal, multi-septate, verrucose, or tuberculate yellow–brown ascospores. Their conidia are ellipsoidal, oblong, clavate, or allantoid and aseptate (Gräfenhan et al., 2011; Herrera et al., 2015; Zeng & Zhuang, 2016).

Cosmospora species are typically fungicolous on basidiomycetous or xylariaceous hosts, though they have also been found in soil, plant substrates, and occasionally butter (Gräfenhan et al., 2011; Herrera et al., 2015). Documented fungicolous associations include: *C. annulohypoxyli* on *Annulohypoxylon cohaerens* (*Hypoxylaceae*), *C. arxii* on *Hypoxylon* sp. (*Hypoxylaceae*), *C. berkeleyana* on *Stereum hirsutum* (*Stereaceae*), *C. clavi* on *Kretzschmaria clavus* (*Xylariaceae*), *C. cymosa* on decaying *Inonotus radiatus* (*Hymenochaetaceae*), *C. fomiticola* on *Fomes fomentarius* (*Polyporaceae*), *C. inonoticola* on *Inonotus* sp. (*Hymenochaetaceae*), *C. micropedis* on *Kretzschmaria micropus* (*Xylariaceae*), *C. novozelandica* on *Annulohypoxylon bovei* (*Hypoxylaceae*), *C. scruposae* on *Xylaria scruposa* (*Xylariaceae*), *C. stilbohypoxyli* on *Stilbohypoxylon quisquiliarum* (*Xylariaceae*), *C. ustulinae* on *Kretzschmaria deusta* (*Xylariaceae*), *C. viridescens* on a black

pyrenomycete, and *C. xylariae* on *Xylaria* spp. (*Xylariaceae*) (Gräfenhan et al., 2011; Herrera et al., 2015; Zeng & Zhuang 2016; Lechat & Fournier 2021).

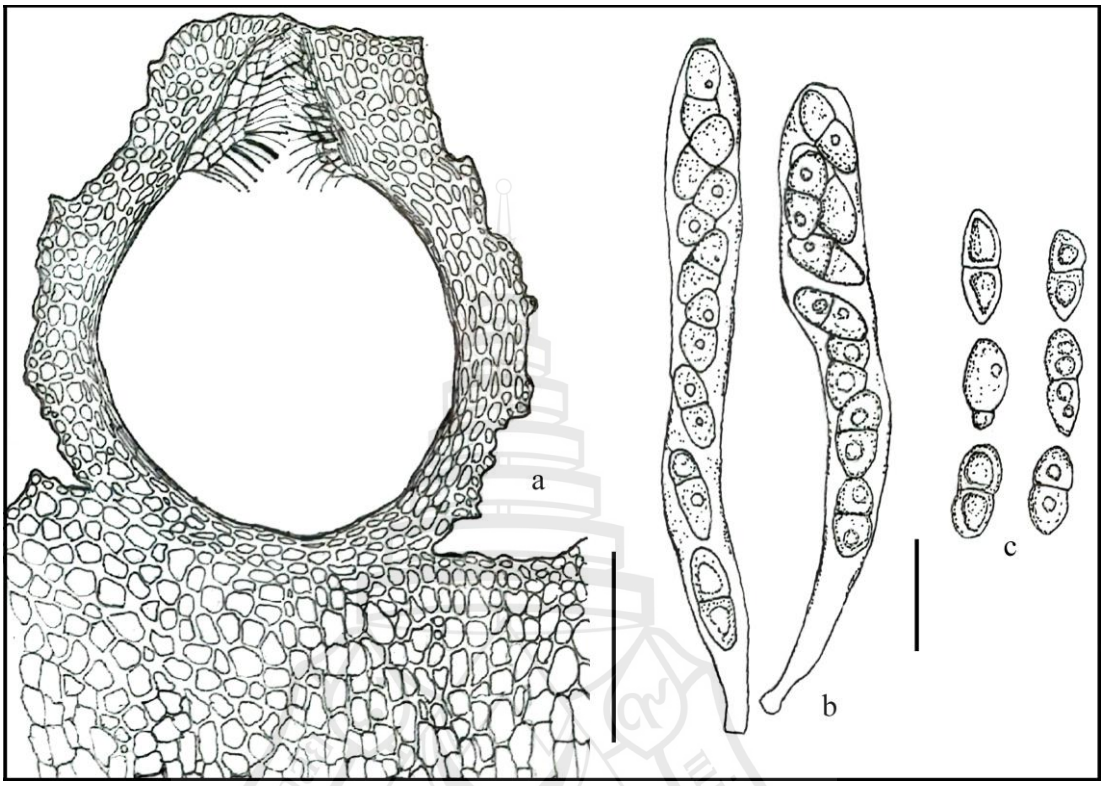


Figure 5.58 *Cosmospora japonica*

Figure 5.58, a. Median section of perithecium. b. Asci. c. Ascospores. Scale bars: a = 100 μm, b, c = 20 μm (Redrawn from Hirooka et al., 2008).

Fusarium Link, Mag. Gesell. naturf. Freunde, Berlin 3(1-2): 10 (1809)

Figure 5.59

Index Fungorum number: IF 8284

Facesoffungi number: FoF 00149

Fusarium was described by Link (1809), with *F. roseum* as the type species. Since its original description, *Fusarium* has undergone extensive taxonomic and nomenclatural revisions, often accompanied by debate and conflicting interpretations (Wollenweber, 1935; Booth, 1971; Nelson et al., 1983; Geiser et al., 2013; Lombard et al., 2015; Sandoval-Denis et al., 2019; Crous et al., 2021c; Wang et al., 2022a). Species delimitation in *Fusarium* based solely on morphological traits has proven challenging due to high phenotypic variability in culture, ambiguous or overlapping species descriptions across studies, and a historically complex subspecies level ranks

(Leslie & Summerell, 2006; Lombard et al., 2019a, b; Wang et al., 2019). Molecular phylogenetics has increasingly contributed to clarifying *Fusarium* taxonomy (Lombard et al., 2019a, b). Comprehensive analysis using a concatenated ITS–LSU–*rpb1–rpb2–tef1* dataset, Crous et al. (2021) re-evaluated fusarioid taxa within *Nectriaceae*, revealing that the Wollenweber concept of *Fusarium* actually comprises 20 distinct genera. This phylogenetic framework was subsequently refined by Wang et al. (2022a) and Han et al. (2023), who further updated the taxonomy of *Fusarium sensu stricto*. However, differing viewpoints on the appropriate taxonomic circumscription persist.

The sexual morph of *Fusarium* is characterized by perithecial ascomata that are typically gregarious, astromatic or borne on a thin stroma, and erumpent through the epidermis. The ascomata are superficial, subglobose to globose or broadly pyriform, and apapillate. Asci are clavate, with a simple apex, 8-spored, and frequently contain an apical ring, the arrangement of ascospores is biseriate to pluriseriate. Ascospores are ellipsoidal to cylindrical, 1–3-septate, not or only slightly constricted at the septa, pale tan, and smooth-walled (Crous et al., 2021c). The asexual morph comprises conidiophores that may be mononematous (aerial) or aggregated into sporodochia. Conidiogenous cells are mono- or polyphialidic, subulate to subcylindrical, smooth- and thin-walled, occasionally proliferating percurrently, with periclinal thickening inconspicuous or absent. Aerial conidia are hyaline, smooth- and thin-walled, and occur in three forms: microconidia, mesoconidia, and macroconidia. Microconidia are ellipsoidal, fusoid, ovoid, obovoid, reniform, allantoid, clavate, napiform, pyriform, or limoniform, 0–5-septate, produced in false heads or chains on phialides. Mesoconidia (present in certain species or species complexes) are falcate, slender, ranging from straight to moderately curved with parallel walls, 1–5-septate, tapering towards both ends, with the apical cell pointed to blunt and the basal cell obtuse to flattened. Macroconidia are typically produced on sporodochia, falcate, slightly to strongly dorsiventrally curved, 1-septate to multiseptate, with a long, tapering apical cell that may be pointed, blunt, hooked, or elongate, and a basal cell that may be obtuse, poorly-developed, well-developed, or elongate and foot-shaped (Crous et al., 2021c).

Fusarium species are cosmopolitan in distribution and exhibit diverse ecological roles, functioning as endophytes, parasites, or pathogens of plants, as well as mutualists or pathogens of animals and insects (Torbati et al., 2021; Wang et al., 2022a; Hyde et al., 2023). Members of this genus are plant pathogens, affecting a broad range of crops and cause diseases such as rots, blights, wilts, and cankers (Samiksha & Kumar, 2021; Hyde et al., 2023). Many species produce mycotoxins that are harmful to both humans and animals (Watanabe et al., 2011; Samiksha & Kumar, 2021). *Fusarium* species have been isolated from air, water, and soil (Wang et al., 2022a; Nikitin et al., 2023; Hyde et al., 2023) and are also utilized in various industrial sectors, including biofuel production, cosmetics, food processing, and pharmaceuticals (Samiksha & Kumar, 2021).

Several *Fusarium* taxa are reported for their fungicolous lifestyle (Torbati et al., 2021). These species have been reported growing on mushrooms, rusts, smuts, and other microfungi (Torbati et al., 2021). Examples include *F. acuminatum* (on *Boletus* sp.), *F. avenaceum* (on *Sclerotinia borealis* (*Sclerotiniaceae*) and *Botrytis cinerea* (*Sclerotiniaceae*)), *F. bactridioides* (on *Cronartium conigenum* (*Cronartiaceae*)), *F. chlamydosporum* (on *Puccinia arachidis* (*Pucciniaceae*)), *F. clavus* (on *Coprinus* sp. (*Agaricaceae*)), *F. compactum* (on *Stereum hirsutum* (*Stereaceae*)), *F. concentricum* (on *Austropuccinia psidii* (*Sphaerophragmiaceae*)), *F. dominicanum* (on *Meliola byrsonimae* (*Meliolaceae*)), *F. gamsii* (on *Agaricus bisporus* (*Agaricaceae*)), *F. graminearum* (on *Sclerotinia sclerotiorum* (*Sclerotiniaceae*)), *F. heterosporum* (on *Claviceps purpurea* (*Clavicipitaceae*) and *Sclerotinia sclerotiorum*), *F. incarnatum* (on *Sclerospora graminicola* (*Peronosporaceae*) and *Pseudocercospora mori* (*Mycosphaerellaceae*)), *F. iranicum* (on *Agaricus bisporus*), *F. lateritium* (on *Polyporus radiates* (*Polyporaceae*), *Fomes fomentarius* (*Polyporaceae*), and *Suillus luteus* (*Suillaceae*)), *F. longipes* (on *Sclerospora graminicola*), *F. oxysporum* (on *Agaricus bisporus*, *Botrytis cinerea*, and *Rhizoctonia solani* (*Ceratobasidiaceae*)), *F. pallidoroseum* (on *Hemileia vastatrix* (*Zaghouaniaceae*)), *F. persicinum* (on *Ganoderma* sp. (*Polyporaceae*), *Stereum hirsutum*, and smut), *F. proliferatum* (on *Plasmopara viticola* (*Peronosporaceae*), *Stereum hirsutum*, and smut), and *F. udum* (on *Mortierella subtilissima* (*Mortierellaceae*)) (Torbati et al., 2021). In the present

study, seven additional *Fusarium* species are documented for the first time as fungicolous associated with mushrooms.

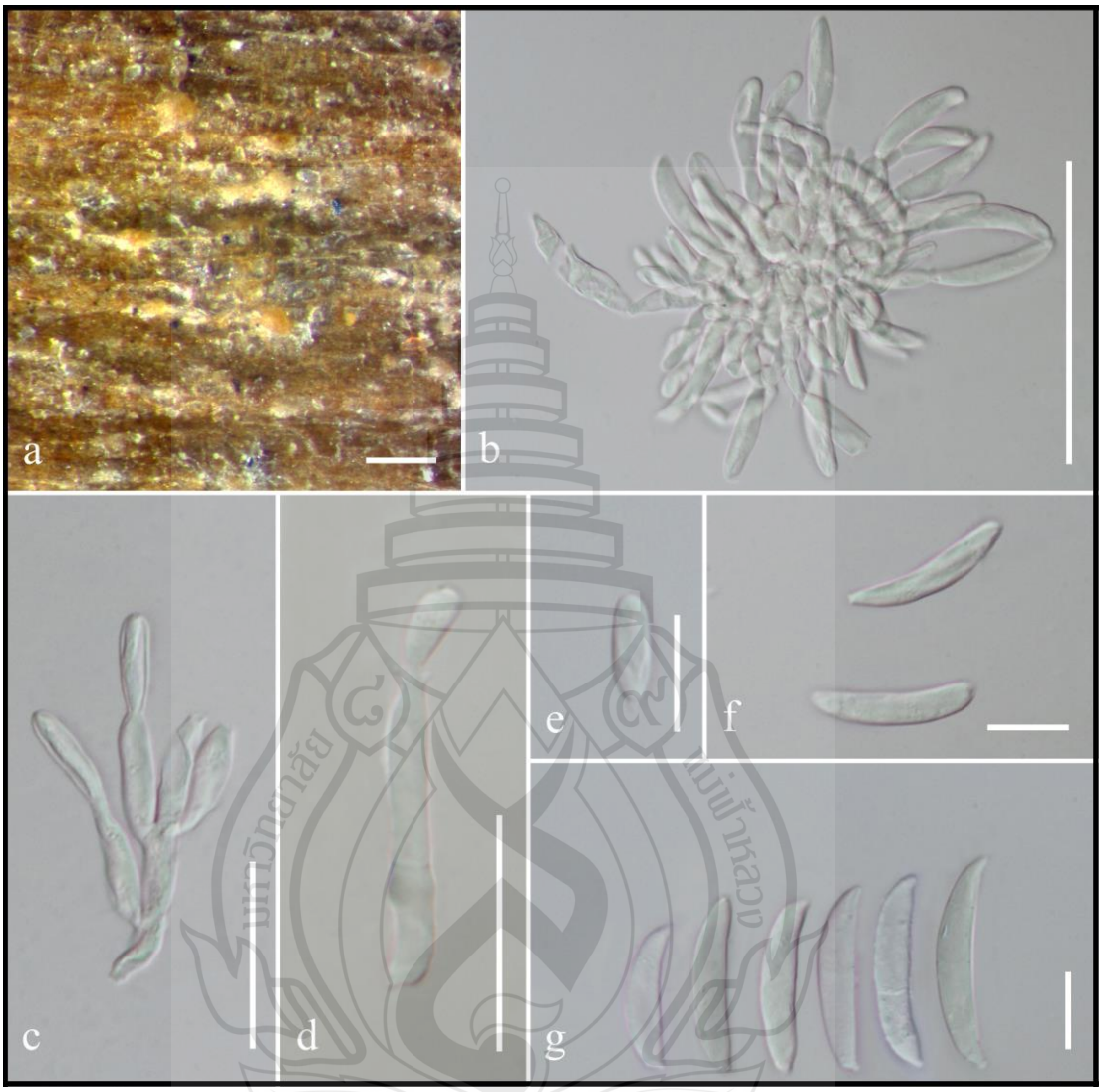


Figure 5.59 *Fusarium sambucinum*

Figure 5.59, a. Sporodochia on the host. b–d. Conidiophores with conidia. e–g. Conidia. Scale bars: a = 200 µm, b = 50 µm, c, d = 20 µm, e–g = 10 µm. (Photo credits: R.H Perera).

Fusicolla Bonord., Handb. Allgem. Mykol. (Stuttgart): 150 (1851)

Figure 5.60

Index Fungorum number: IF 8294

Facesoffungi number: FoF 10954

Bonorden (1851) established *Fusicolla* (*Hypocreales, Nectriaceae*) with the type species *Fusicolla betae* isolated from rotten roots of *Beta* sp. in France.*Fusicolla* was considered synonymous with *Fusarium* (Wollenweber, 1916). However, Gräfenhan et al. (2011) redefined *Fusicolla* designating a lectotype for *Fusicolla betae*. The members of *Fusicolla* have a worldwide distribution being discovered from soil or plant debris near soil, on wood surfaces, slime flux of trees and in flowing water (drinking water and sewage) (Gräfenhan et al., 2011). Occasionally *Fusicolla* spp. are fungicolous on stromata of other fungi (Gräfenhan et al., 2011).

The sexual morph of *Fusicolla* is characterized by, globose to pyriform, yellow, pale buff to orange, perithecial ascomata. These ascomata can be fully or partially submerged in the stroma while being scattered, in small groups, or arranged gregariously. The asci are cylindrical to narrowly clavate, featuring an apical ring and containing 8 uniseriate ascospores. These ascospores are hyaline to pale brown, 1-septate, and exhibit a smooth surface or may become slightly verrucose as they mature (adapted from Gräfenhan et al., 2011 and Perera et al., 2023). Distinguishing characteristics between *Fusicolla* and *Fusarium* include the coloration of their perithecia. *Fusicolla* exhibits yellow to orange perithecia, whereas *Fusarium* produces perithecia in a dark blue to black hue (Crous et al., 2021c).

The asexual morph of *Fusicolla* is characterized by conidiophores which initially appear as lateral phialides on somatic hyphae. Occasionally, they can be monochasial, verticillate, or penicillate, and are hyaline. The phialides are hyaline, monophialidic and cylindrical to subulate. Microconidia are either sparse or absent, and when present, they are ellipsoidal to allantoid, aseptate, and hyaline. Macroconidia are falcate, more or less straight, or moderately to clearly curved. They are slightly narrowed towards each end, with the apical cell often hooked and possessing a more or less pointed tip. The basal cell is slightly pedicellate. Macroconidia are predominantly 1–3-septate, or 3–5-septate, and in one species, they can be up to 10-septate. They are hyaline, mostly thin-walled. Chlamydospores are either absent, sparse, or abundant. When present, they are globose, occurring singly, in pairs or chains, and sometimes found within macroconidia (adapted Gräfenhan et al., 2011 and Lombard et al., 2015). To date, there are 34 species listed under *Fusicolla* in Species Fungorum (2025).

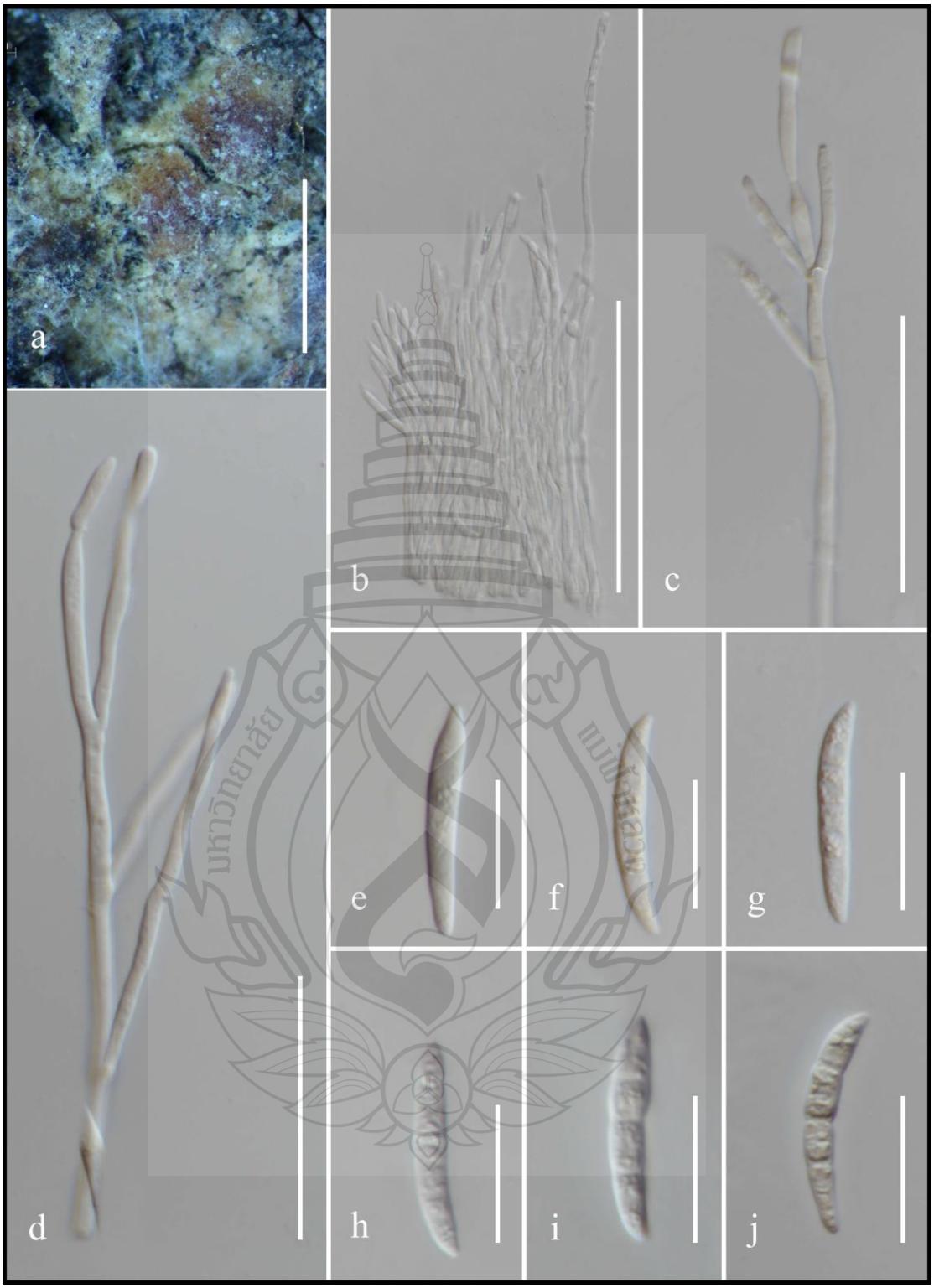


Figure 5.60 *Fusicolla betae*

Figure 5.60, a. Sporodochium on the host. b–d. Conidiophores with conidiogenous cells. e–j Conidia. Scale bars: a = 1 mm, b = 100 μm, c = 50 μm, d = 40 μm, e–j = 20 μm (Photo credits: R.H Perera).

Macroconia (Wollenw.) Gräfenhan, Seifert & Schroers, Stud. Mycol. 68: 101 (2011)

Figure 5.61

Index Fungorum number: IF 519441

Facesoffungi number: FoF 10968

Macroconia, was introduced by Gräfenhan et al. (2011) delineating it with the inclusion of *Nectria leptosphaeriae* and four other taxa that were previously classified under *Cosmospora*, *Fusarium*, and *Nectria*. *Macroconia leptosphaeriae* previously known as *Nectria leptosphaeriae* is the type species of the genus (Gräfenhan et al., 2011). Through phylogenetic analysis, *Macroconia* is identified as closely related to *Fusicolla* and *Microcera* (Lombard et al., 2015; Perera et al., 2023). The members of *Macroconia* have been collected from Canada, China, Germany, Italy, the Netherlands, South Africa, and the USA associated with plant and fungal hosts (Gräfenhan et al., 2011). The fungicolous associations include, *M. bulbipes* (associated with *Dimerosporiopsis engleriana* (*Metacapnodiaceae*)), *M. cupularis* (on fruiting bodies of *Stylodothis* (*Dothideaceae*)), *M. leptosphaeriae* (on *Leptosphaeria* sp.), *M. podocarpi* (on fungal ascomata), and *M. sphaeriae* (on *Leptosphaeria* sp.(*Leptosphaeriaceae*)) (Gräfenhan et al., 2011; Crous et al., 2021c; Visagie et al., 2024; Index Fungorum, 2025).

The sexual morph of *Macroconia* comprises an inconspicuous stroma or stroma can be absent. The perithecia are solitary, subglobose, with or without a small apical papilla, andcupulate when dry. They range from orange to carmine red, turning dark red to violet with KOH, and sometimes have hyphal hairs emerging from the outer wall. Asci are cylindrical to narrowly clavate, featuring a simple apex and containing 8 uniseriate to partially biseriate ascospores. The ascospores are yellowish, 1-septate, initially smooth but may develop striations as they mature (Gräfenhan et al., 2011; Perera et al., 2023).

The asexual morph of *Macroconia* comprises conidiophores which begin as lateral phialides on somatic hyphae, later transitioning to being monochasial to

verticillate, and are hyaline. Phialides are monophialidic, cylindrical to subulate, and hyaline. Microconidia are either absent or very rare, and when present, they are ellipsoidal to allantoid and hyaline. Macroconidia are robust, subcylindrical to moderately curved, with a conical or hooked apical cell and a conspicuously pedicellate basal cell. They typically have 3–7(–14) septa and appear hyaline, mostly thick-walled. Chlamydospores are either absent or rare, and when present, they are globose, occurring singly, in pairs, or chains within the hyphae (Gräfenhan et al., 2011). To date, there are nine species listed under *Macroconia* in Species Fungorum (2025).

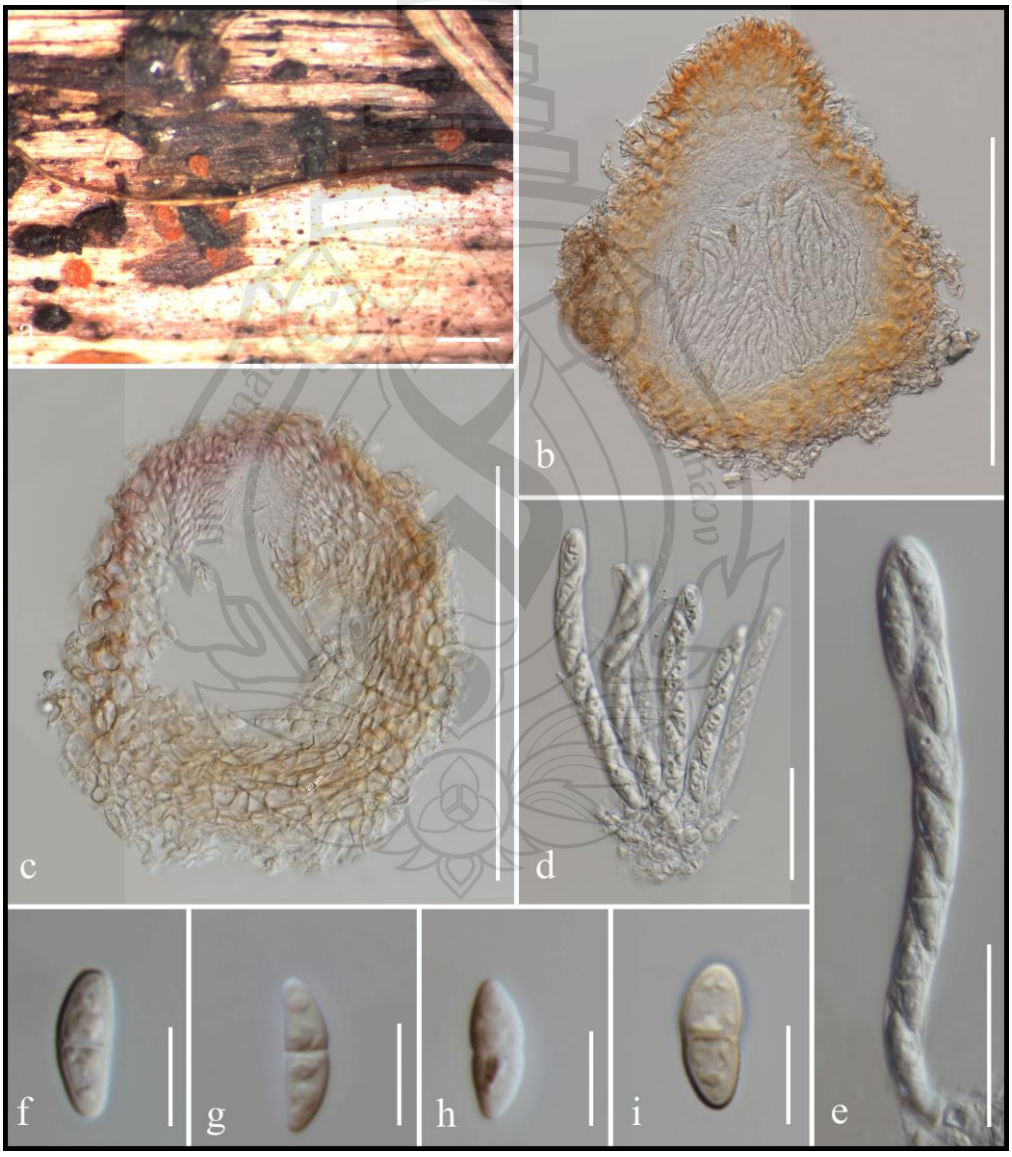


Figure 5.61 *Macroconia leptosphaeriae*

Figure 5.61, a. Ascomata on host. b, c. Sections of ascomata. d, e. Asci. f–i Ascospores. Scale bars: a = 500 μm, b, c = 200 μm, d, e = 50 μm, f–i = 10 μm. (Photo credits: R.H Perera).

Nectria (Fr.) Fr., Summa veg. Scand., Sectio Post. (Stockholm): 387 (1849)

Figure 5.62

Index Fungorum number: IF 3431

Facesoffungi number: FoF 02122

Fries (1825), proposed *Nectria* as an infra-generic section of *Hypocrea*. Subsequently, Fries (1849) elevated *Nectria* to the rank of a genus (Booth, 1959; Schroers, 2001). The initial valid typification of the genus *Nectria* was performed by Clements and Shear (1931), in which *Nectria cinnabarina* was designated as the lectotype. Since the introduction, the taxonomic concept of *Nectria* has been broadly defined for many years, resulting in the description and classification of over 1000 species within *Nectria sensu lato* (Hirooka et al., 2012). Therefore, after several amendments, *Nectria sensu lato* has been divided into several genera based on morphology, in conjunction with phylogenetics (Saccardo, 1878, 1883; Samuels, 1976; Rossman, 1989; Rehner & Samuels, 1995; Rossman et al., 1999, 2001; Schroers, 2001; Brayford et al., 2004; Hirooka et al., 2010; Lombard et al., 2015; Lechat & Fournier, 2017; Forin et al., 2020).

The sexual morph of *Nectria* is characterised by, perithecial ascomata, situated either on or nearly completely immersed in an erumpent stroma. They range from red to bay to sienna, which change to bright red, blood red, or purple when treated with KOH. The ascomata shape varies from subglobose to globose, with a smooth to warted surface texture. Asci are cylindrical to narrowly clavate or clavate, featuring an inconspicuous ring and containing eight spores (Lombard et al., 2015). The asexual morph of *Nectria* is tubercularia-like (Rossman, 2000; Hirooka et al., 2012). The conidiophores are pycnidial, sporodochial, with lateral phialidic pegs or acropleurogenous. Microconidia are hyaline, ellipsoid to fusoid, rarely curved, and aseptate. Macroconidia are hyaline and exhibit a variety of shapes, including ellipsoidal, oblong, cylindrical, allantoid, or subglobose to ellipsoidal. They are 0–1-septate, smooth, straight to slightly curved, and rounded at both ends (Lombard et al., 2015).

Members of *Nectria* typically act as parasites on woody plants. They are found on hardwood trees and shrubs in tropical, subtropical, and temperate regions around the globe (Rossman et al., 1999; Hirooka et al., 2012). Moreover, some species of *Nectria* such as *N. asakawaensis* (parasitized *Armillaria* (*Physalacriaceae*)), *N. cytosporae* (on the pycnidia of *Cytospora pinastri* (*Cytosporaceae*)), *N. ganymede* (parasitized *Zeus olympius* (*Rhytismataceae*)), and *N. munkii* (colonized *Aplosporella* (*Aplosporellaceae*)), are fungicolous species (Minter et al., 1987; Sun et al., 2019a).

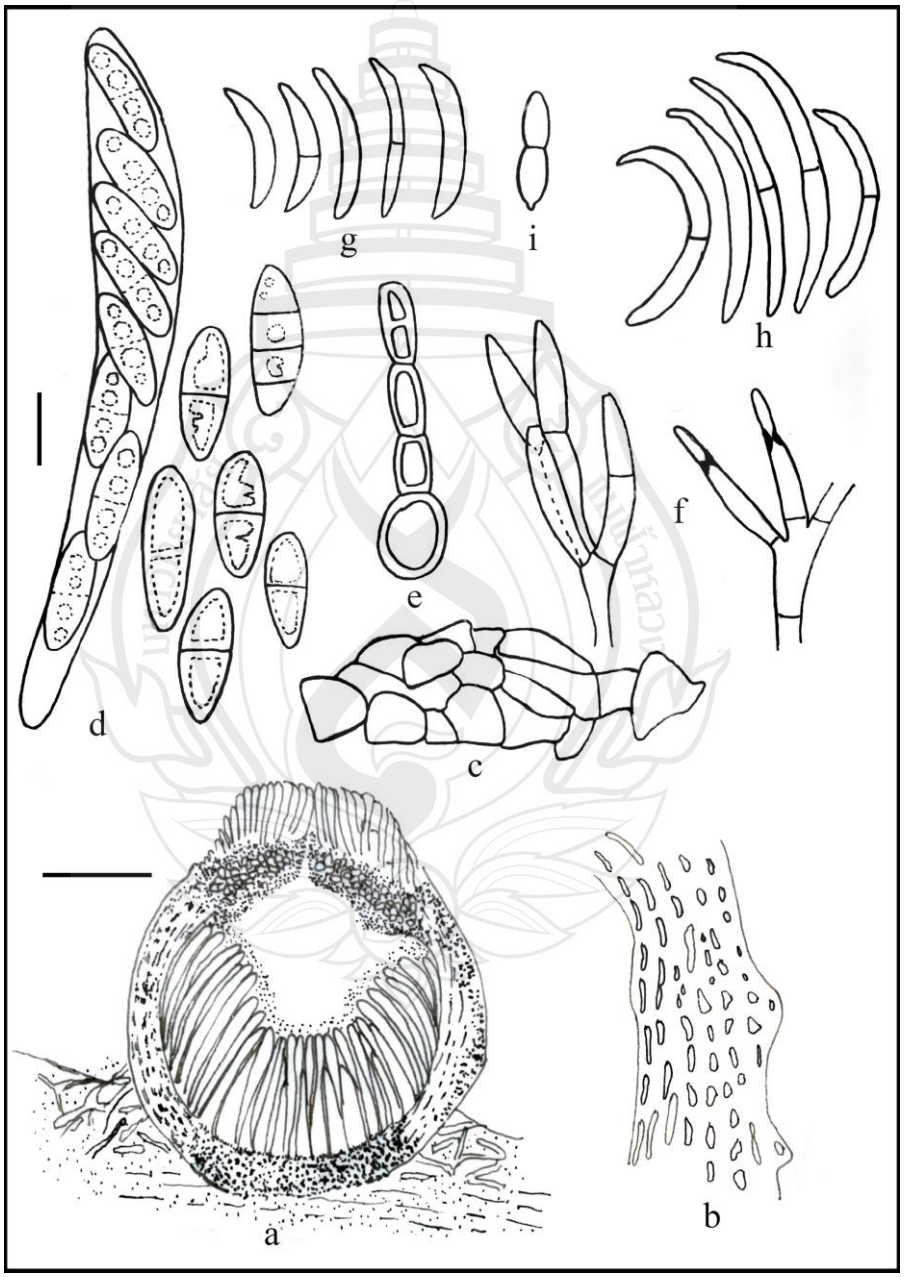


Figure 5.62 *Nectria ganymede*

Figure 5.62, a. Vertical transverse section of ascoma. b. Wall of ascoma. c. Surface view of the ascoma cells. d. Ascus and ascospores. e. Thickened hyphal cells. f. Conidiophores. g, h. Macroconidia. i. Distorted old conidium. Scale bars: a = 100 μm, c–g = 10 μm. (Redrawn from Minter et al., 1987).

Pseudocosmospora C.S. Herrera & P. Chaverri, Mycologia 105(5): 1291 (2013)

Figure 5.63

Index Fungorum number: IF 802432

Facesoffungi number: FoF 13451

Cosmospora sensu traditionally comprised nectroid fungi characterized by small, reddish, smooth, thin-walled perithecia (Rossman et al., 1999). It was discovered to be polyphyletic, leading to its division into several distinct genera (Gräfenhan et al., 2011; Schroers et al., 2011). However, many fungi that resemble *Cosmospora*, including species such as *C. vilior* and various other specimens often referred to as "*Cosmospora* sp.," were not systematically studied. Herrera et al., (2013) aimed to confirm the identity of *C. vilior* by designating an epitype based on a recent collection that matches the type specimen in terms of morphology, host, and geographic location. Additionally, they sought to clarify its phylogenetic position within *Cosmospora sensu lato* and *Nectriaceae*. The multilocus phylogenetic analyses carried out by Herrera et al. (2013) revealed that *C. vilior* forms a monophyletic group with other cosmospora-like fungi that have an acremonium-like anamorph and display a mycoparasitic lifestyle. This group was found to be phylogenetically distinct from other previously recognized genera. Consequently, Herrera et al. (2013) proposed *Pseudocosmospora*, designating *P. eutypellae* as the type species, along with nine additional species within this clade.

The sexual morph of *Pseudocosmospora* is characterized by the uniloculate perithecia either superficial or slightly immersed in the fungal stroma, which are typically subglobose to obpyriform with a blunt papilla. They turn blood red in KOH and yellow in lactic acid. The asci are unitunicate and cylindrical to narrowly clavate. They lack a conspicuous apical ring and have eight spores arranged uniseriately. The ascospores are ellipsoidal, one-septate, slightly constricted at the septum, yellow-brown, verrucose, and sometimes smooth at maturity (adapted from Herrera et al.,

2013). The asexual morph of *Pseudocosmospora* is either acremonium-like or verticillium-like. Conidiophores are generally simple and unbranched but can occasionally be verticillately branched or rarely densely aggregated. The phialides are monophialidic, cylindrical, and hyaline. Conidia are hyaline, ellipsoidal, ovoid, or reniform, smooth, sometimes guttulate, and aseptate (adapted from Herrera et al., 2013).

Seventeen species are identified within *Pseudocosmospora* (Species Fungorum, 2025). Most of these species are fungicolous, with specific associations such as: *Pseudocosmospora beijingensis* (on rotten bark associated with other fungi), *P. curvispora* (on dead ascomata of *Diatrypaceae*), *P. eutypae* (on *Eutypa lata* (*Diatrypaceae*)), *P. eutypellae* (on *Eutypella* sp. (*Diatrypaceae*)), *P. henanensis* (associated with beaked ascomycete), *P. hypoxylicola* (on *Hypoxylon fuscum* (*Hypoxylaceae*)), *P. joca* (on *Biscogniauxia* sp. (*Graphostromataceae*) and on *Hypoxylon* sp. (*Hypoxylaceae*)), *P. metajoca* (on *Eutypa* sp.), *P. metepisphaeria* (on *Eutypella* sp.), *P. nummulariae* (on *Biscogniauxia* sp.), *P. pithoides* (on *Eutypella* sp.), *P. pseudepisphaeria* (on *Eutypella* sp.), *P. rogersonii* (on *Eutypella* sp.), *P. shenongjiana* (on old fruiting bodies of an unidentified fungus), *P. triqua* (on *Eutypella* sp.), and *P. vilior* (on *Eutypella* sp.) (Herrera et al., 2013; Zeng & Zhuang, 2017, 2021, 2022; Lechat & Fournier, 2020). They are distributed in Argentina, Brazil, Canada, China, France, New Zealand, the UK, the USA, and Venezuela (Herrera et al., 2013; Zeng & Zhuang, 2017, 2021, 2022; Lechat & Fournier, 2020; Index Fungorum, 2025). It is anticipated that the species diversity of *Pseudocosmospora* would be particularly high in warm temperate and tropical regions (Herrera et al., 2013).

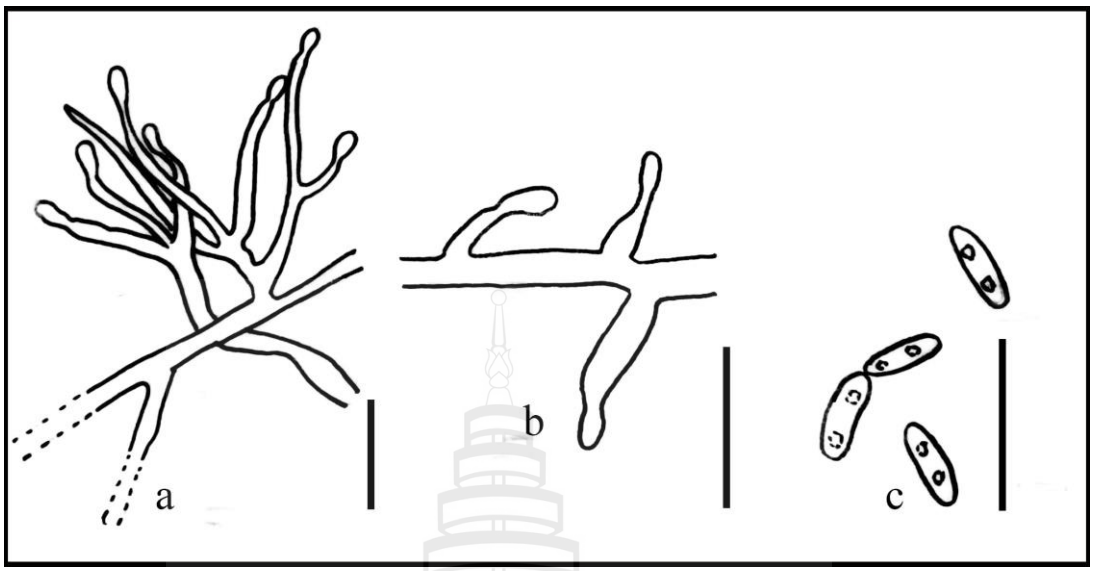


Figure 5.63 *Pseudocosmospora eutypellae*

Figure 5.63, a, b. Phialides and conidial attachments. c. Conidia. Scale bars: a–c = 10 μm. (Adapted from Herrera et al., 2013).

Stylonectria Höhn., Sber. Akad. Wiss. Wien, Math.-naturw. Kl., Abt. 1 124: 52 (1915)

Figure 5.64

Index Fungorum number: IF 5301

Facesoffungi number: FoF 11010

Stylonectria was proposed by Höhnel (1915) to include what was believed to be a pycnidial, phialidic asexual morph of *Nectria applanata*. As determined by Booth (1959) and confirmed by Rossman et al. (1999) and Gräfenhan et al. (2011), the structures initially identified as pycnidia were perithecia containing discharged ascospores. This finding made the name *Stylonectria* applicable to a sexual morph rather than an asexual one. Booth (1959) included *Stylonectria* within his broad concept of *Nectria* but Rossman et al. (1999) synonymized *Stylonectria* with *Cosmospora*. Gräfenhan et al. (2011) conducted a phylogenetic revision of *Cosmospora*, which revealed its polyphyletic nature. As a result, several genera were resurrected, including *Stylonectria*.

Stylonectria is characterized by its perithecia, which are gregarious, often found in groups of up to 20 on a thin, white to yellow, hyphal or subiculum-like

stroma. The perithecia are superficial, subglobose, pyriform to subcylindrical, and vary in color from pale yellow, to orange-brown, to pale or dark red. When treated with KOH, they turn dark red to purple. Asci are cylindrical to clavate, containing 8 spores, with a simple apex or an apical ring. Ascospores are cylindrical, allantoid, or ellipsoidal, septate, hyaline to yellow or pale brown (adapted from Höhnel (1915) and Gräfenhan et al. (2011)). Conidiophores initially develop as unbranched phialides on somatic hyphae. They may occasionally become loosely branched or form small sporodochia. Conidiogenous cells are monophialidic, cylindrical to subcylindrical, and feature a distinct collarette. Microconidia are sparse, allantoid to lunulate, slightly or strongly curved, aseptate, and occur in slimy heads. Macroconidia are orange in mass, 0- or 1-septate, subcylindrical to moderately or strongly curved, and falcate (adapted from Höhnel (1915) and Gräfenhan et al. (2011).

Species Fungorum (2025) lists nine *Stylonectria* species. These taxa are primarily fungicolous, occurring on the stromata of ascomycetes (Gräfenhan et al., 2011; Lechat et al., 2015). Those include *S. applanata* (found on an ascomycete), *S. alpina* (associated with dead stromata of *Diplodia* (*Botryosphaeriaceae*)), *S. corniculata* (on an ascomycete), *S. hetmanica* (on ascomata of *Diaporthe* (*Diaportheceae*)), *S. norvegica* (on dead sporodochia of *Fusarium* (*Nectriaceae*) and on *Amphiporthe* (*Gnomoniaceae*)), *S. qilianshanensis* (on decayed ascoma), and *S. tuedensis* (on dead stromata of *Eutypella* (*Diatrypaceae*) and associated with the asexual morph of *Ascocoryne* (*Gelatinodiscaceae*)) (Gräfenhan et al., 2011; Lechat et al., 2015; Zeng et al., 2020; Crous et al., 2021c; Lechat et al., 2021). Additionally, some *Stylonectria* species are associated with plant hosts (Index Fungorum, 2024). *Stylonectria* species have been reported from Austria, Canada, China, Germany, France, Norway, and Ukraine (Gräfenhan et al., 2011; Lechat et al., 2015; Zeng et al., 2020; Crous et al., 2021c; Lechat et al., 2021; Index Fungorum, 2025).

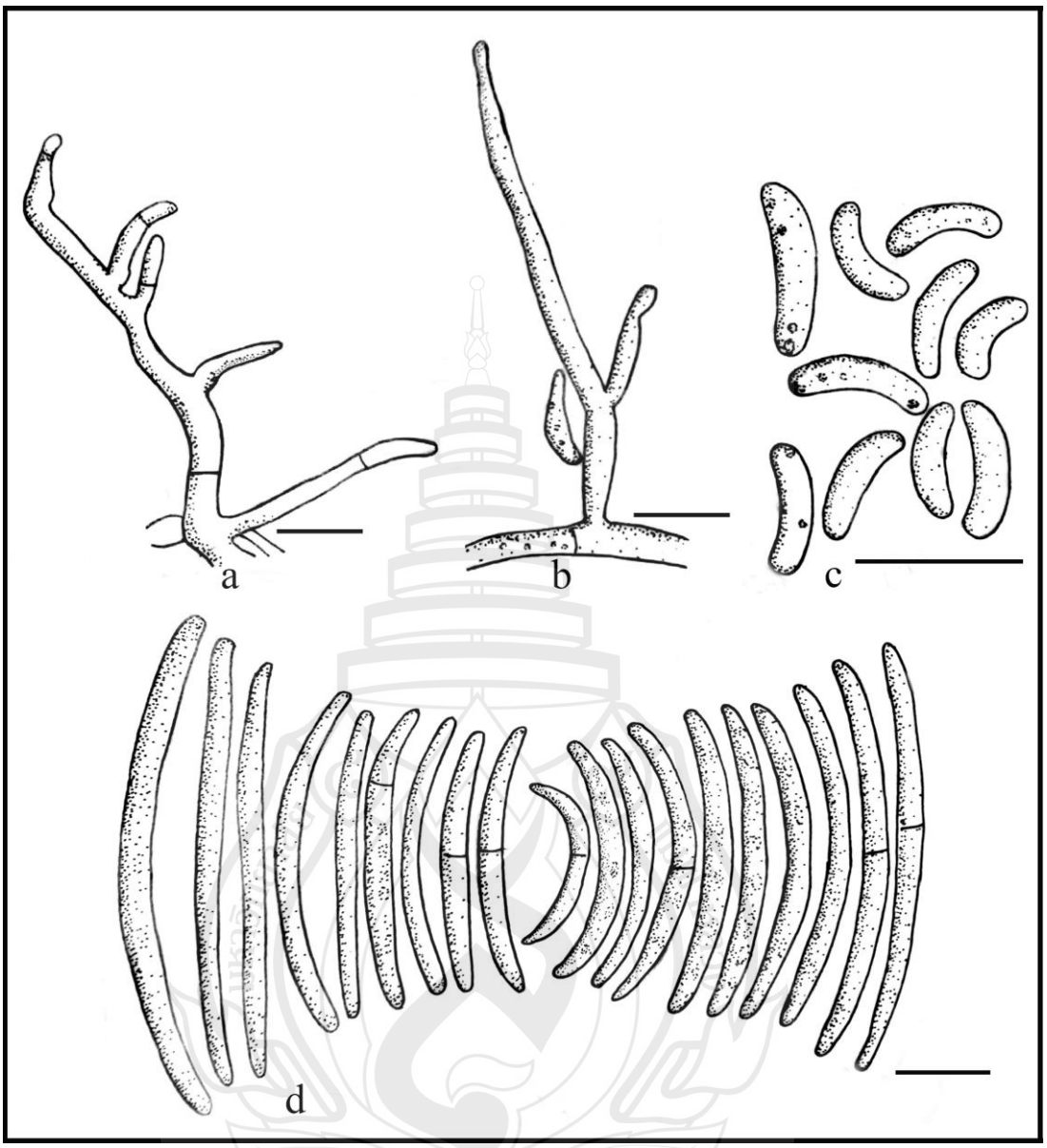


Figure 5.64 *Stylonectria corniculata*

Figure 5.64, a, b. Conidiophores and conidiogenous cells. c. Microconidia. d. Macroconidia. Scale bars: a–d = 10 μm.

Thyronectria Sacc., Grevillea 4(no. 29): 21 (1875)

Figure 5.65

Index Fungorum number: IF 5469

Facesoffungi number: FoF 07713

Thyronectria was established by Saccardo (1875). The generic name "*Thyronectria*" was based on the superficial resemblances of the immersed stromata

and muriform ascospores to *Thyridium*. Additionally, the nectriaceous perithecial context and the hyaline ascospores are similar to *Nectria* or *Calonectria* (Saccardo, 1875). Thereafter, several studies were conducted on *Thyronectria* and various taxonomic revisions occurred and *T. rhodochlora* was designated as the type species of the genus (Seeler, 1940; Rossman et al., 1999; Hirooka et al., 2012; Checa et al., 2013). However, based on comprehensive investigations involving multigene phylogenies, type studies and recently collected specimens, Jaklisch and Voglmayr (2014) re-established *Thyronectria* within *Nectriaceae*. At the same time, Jaklisch and Voglmayr (2014) synonymized *Mattirola*, *Pleonectria* and *Thyronectroidea* with *Thyronectria*.

The members of *Thyronectria* are distributed worldwide mainly in temperate and subtropical regions (Hirooka et al., 2012; Jaklitsch & Voglmayr, 2014b; Perera et al., 2023). Those species are saprobes associated with plants while some species are fungicolous (Hirooka et al., 2012; Jaklitsch & Voglmayr, 2014b). The fungicolous species include *T. asturiensis* (from *Cyclothyriella rubronotata* (*Cyclothyriellaceae*)), while *T. giennensis* and *T. pistaciae* have been described as possibly fungicolous, associated with *Diplodia* sp. (*Botryosphaeriaceae*) (Checa et al., 2015; Index Fungorum, 2025).

The sexual morph of *Thyronectria* is characterized by, immersed-erumpent stromata with single to multiple ascomata. The ascomata are perithecial, immersed in a stroma or superficial and typically densely aggregated on a hypostroma, usually globose to flask-shaped, often collapsed cupulate upon drying, with an obtuse apex. The peridium consists of 2–4 cell layers, outer layer(s) pigmented, subhyaline, yellow, orange, red or light brown in section, yellow-orange when dry, shades of red to brown or black, thickened around the ostiole. Hamathecium present as periphyses in the ostiole and as apical paraphyses, branched and anastomosing, descending from an apical cushion to the bases of asci, usually present at maturity, cylindrical or as submoniliform bands. Asci are 8-spored, unitunicate, oblong or clavate, with an undifferentiated apex. Ascospores are uni or biseriate, ellipsoid, oblong, fusiform, globose, clavate or vermiform, 1- to several- septate or muriform, hyaline, yellowish, rosy, green or brown, with eusepta and/or distosepta becoming indistinct in KOH,

smooth or striate-walled, sometimes budding in the ascus to produce oblong to allantoid, aseptate, hyaline, ascoconidia (adapted from Jaklisch & Voglmayr, 2014).

The asexual morph is pycnidial and/or effuse conidial masses form on white mycelium and conidiophores. Pycnidia are associated with perithecia on the same hypostroma or occurring separately, solitary or aggregated in groups, erumpent-superficial, subglobose to irregularly discoid to cupulate or elongate and erect, rosy, orange, red, violaceous brown to nearly black. Conidiophores are densely aggregated, simple, irregularly or verticillately branched, conidia formed on minute pegs or cylindrical to subulate phialides. The conidial formation is enteroblastic. In cultures lageniform to ampulliform phialides are formed on simple, unbranched or branched, sometimes verticillate conidiophores or formed in pycnidia on mostly lageniform to subulate phialides on densely aggregated, simple, asymmetrically or verticillately branched, often shrub- or fan-shaped conidiophores. Conidia are oblong, ellipsoid or (sub)allantoid, aseptate or rarely 1- or 2-sepate, hyaline, smooth-walled (adapted from Jaklisch & Voglmayr, 2014). To date, 48 species are listed under *Thyronectria* in Species Fungorum (2025).

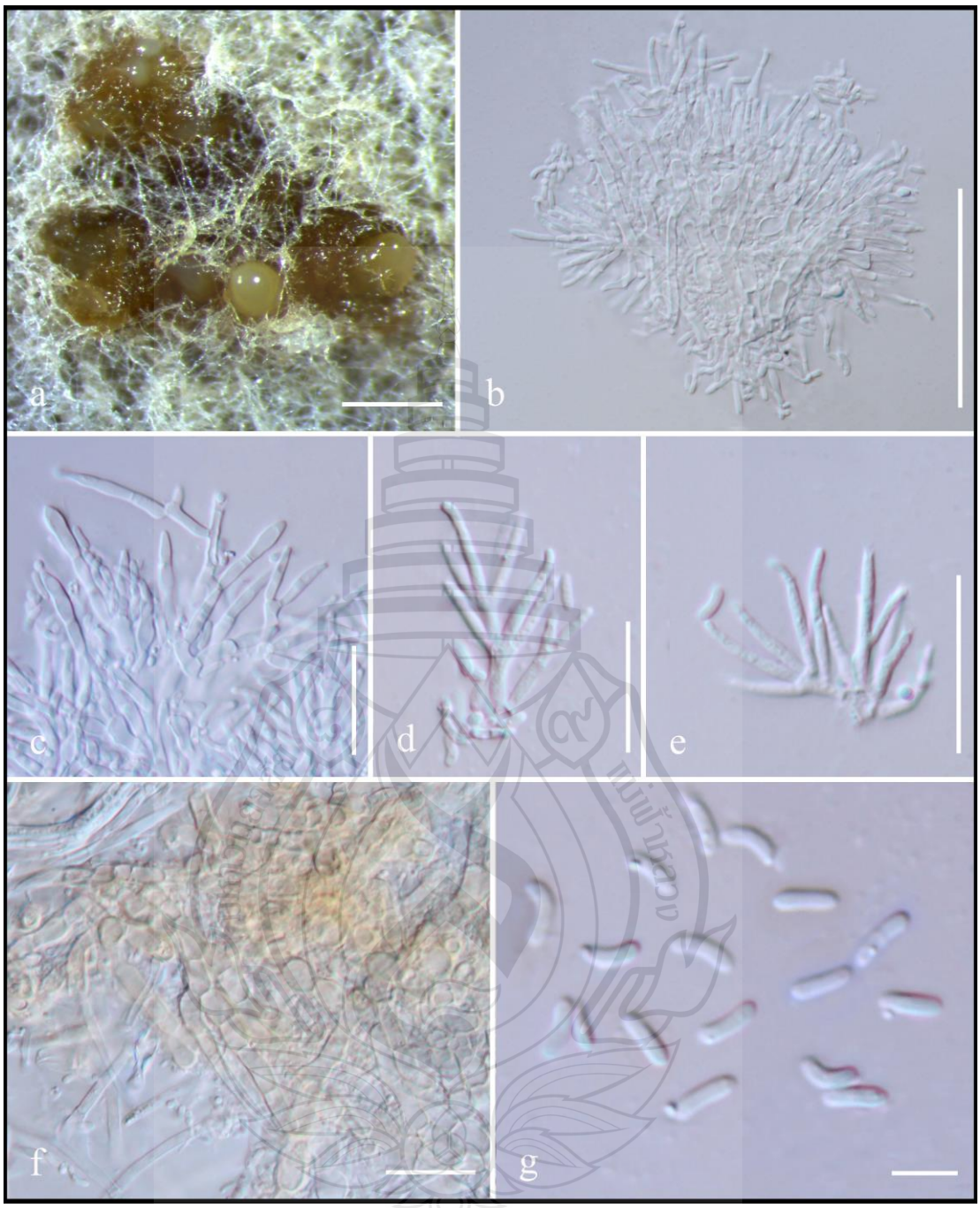


Figure 5.65 *Thyronectria sinopica*

Figure 5.65, a. Sporodochial conidiomata on MEA. b, c. Conidiophores and phialides. d, e. Phialides and conidia. f. Chlamydospores. g. Conidia. Scale bars: a = 500 µm, b = 50 µm, c–f = 20 µm, g = 5 µm. (Photo credits: R.H Perera).

Niessliaceae Kirschst.

Circinoniesslia Samuels & M.E. Barr, Canad. J. Bot. 75(12): 2166 (1998) [1997]

Figure 5.66

Index Fungorum number: IF 27818

Facesoffungi number: FoF 13457

Samuels and Barr (1997) established *Circinoniesslia* with the type species *C. nectriae*. It was found as fungicolous on ascomata of *Bionectria* or *Nectria* (*Nectriaceae*) species on decayed wood in Guyana and Puerto Rico (Samuels & Barr, 1997). *Circinoniesslia* remains monotypic and as of GenBank (2025), molecular data is not available.

The sexual morph of *Circinoniesslia* is characterized by, solitary or scattered, superficial, globose, yellow, membranaceous, perithecial ascomata which are surrounded by white, circinately coiled appendages. Asci are 8-spored, unitunicate, cylindrical, and pedicellate. Ascospores are bi-seriate, hyaline, striate, 1-septate, ellipsoidal, either straight or slightly curved, and guttulate. The asexual morph of *Circinoniesslia* has not yet been observed (adapted from Samuels & Barr, 1997; Huang et al., 2021a).

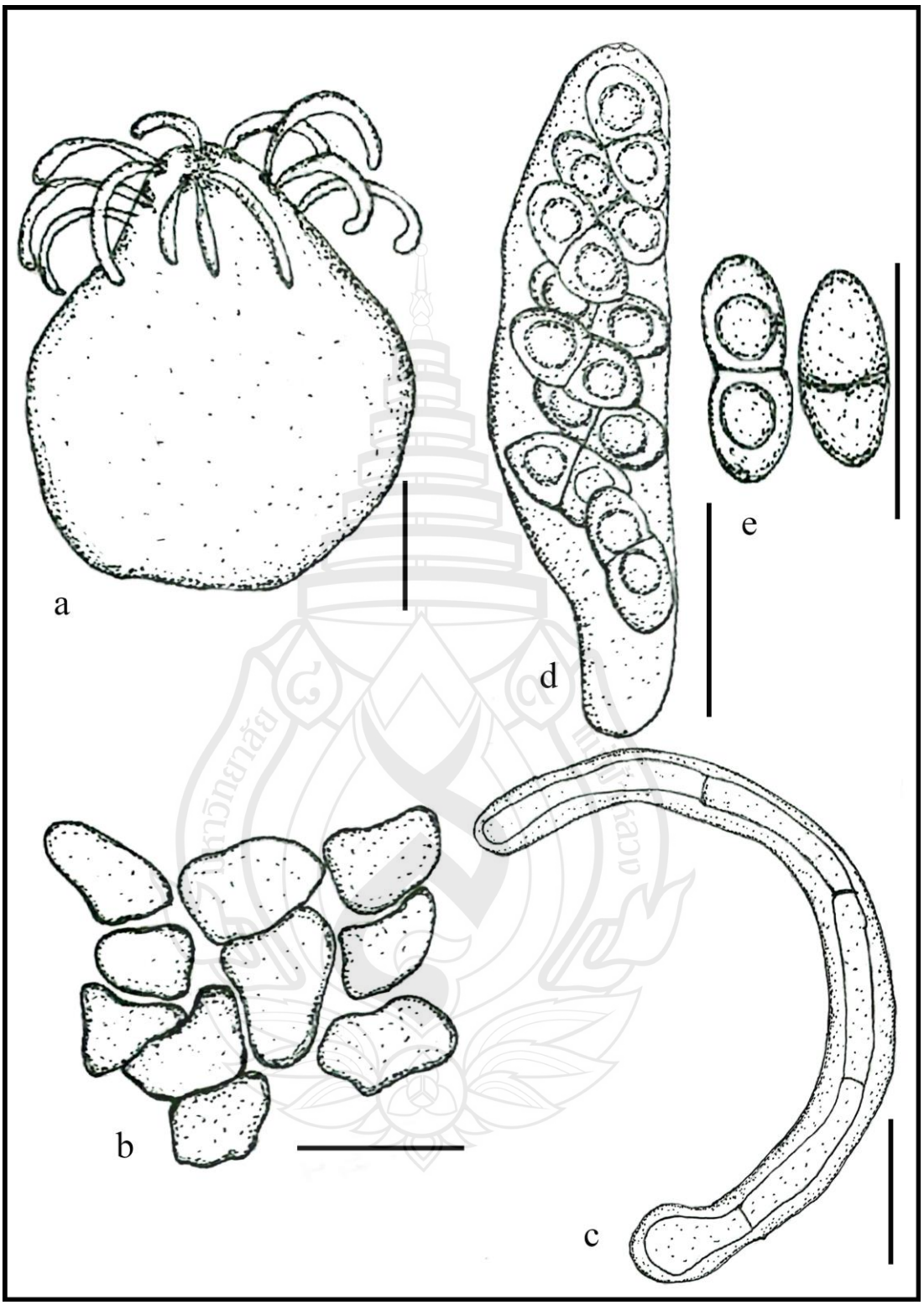


Figure 5.66 *Circinoniesslia nectriae*

Figure 5.66, a. Habit sketch of an ascoma.b. Cells at surface of peridium. c. Setae from ascomal apex. d. Ascus. e. Ascospores. Scale bars: a–e = 10 μm. (Redrawn from Samuels & Barr, 1997).

Ophiocordycipitaceae G.H. Sung, J.M. Sung, Hywel-Jones & Spatafora

Tolypocladium W. Gams, Persoonia 6(2): 185 (1971)

Figure 5.67

Index Fungorum number: IF 10242

Facesoffungi number: FoF 10425

Tolypocladium was established by Gams (1971a), with *T. inflatum* as the type species. Hodge et al. (1996) demonstrated the asexual-sexual connection between *Tolypocladium inflatum* and *Cordyceps subsessilis* through cultural studies. *Elaphocordyceps* was introduced to accommodate a subclade within *Ophiocordycipitaceae* that includes *Cordyceps* species parasitizing *Elaphomyces* (*Elaphomycetaceae*) and some related arthropod-associated taxa (Sung et al., 2007). *Chaunopycnis*, a genus exhibiting conidiogenesis similar to *Tolypocladium*, was described by Gams (1980). In line with the "One Fungus, One Name" principle, Quandt et al. (2014) proposed the protection of *Tolypocladium* over both *Chaunopycnis* and *Elaphocordyceps*. A comprehensive revision of *Tolypocladium* was undertaken by Dong et al. (2022) using a multigene phylogeny based on SSU, LSU, *tef1-α, rpb1*, and *rpb2* sequence data, and provided a key to 48 accepted *Tolypocladium* species worldwide. There are 52 species recognized within the genus (Species Fungorum, 2025), with molecular data available for most taxa in GenBank (2025). The genus is classified in *Ophiocordycipitaceae*, *Hypocreales* (Hyde et al., 2024a).

The sexual morph of *Tolypocladium* produces solitary to multiple, stipitate stromata that are fleshy or fibrous to tough in texture, with clavate to capitate fertile heads. Perithecia are immersed within the stromata. Asci are cylindrical, with a thickened apex, and contain filiform, multiseptate ascospores that disarticulate into part-spores (Quandt et al., 2014; Yu et al., 2021). The asexual morph is *Tolypocladium*-, *Chaunopycnis*-, or verticillium-like. Conidiophores bear whorls of phialides either laterally or terminally. Phialides typically possess a cylindrical to swollen base and a slender, often bent neck. Conidia are hyaline, globose to oval,

aseptate, smooth-walled, and aggregate into globose heads at the phialide apices (Gams, 1971; Yu et al., 2021).

Tolypocladium species occur in terrestrial and humid environments worldwide (Yu et al., 2021). They occupy a wide range of hosts and substrates, including insects, lichens, nematodes, bdelloid rotifers, other fungi, soil, and plant substrates (Yu et al., 2021; Dong et al., 2022; Wang et al., 2022b; Das et al., 2023). Many fungicolous species, such as *T. capitatum*, *T. delicatistipitatum*, *T. flavonigrum*, *T. fractum*, *T. guangdongense*, *T. intermedium*, *T. japonicum*, *T. jezoense*, *T. longisegmentatum*, *T. minazukiense*, *T. miomoteanum*, *T. ophioglossoides*, *T. ramosum*, *T. rouxii*, *T. valliforme*, *T. valvatistipitatum*, and *T. virens*, are associated with *Elaphomyces* spp. In addition, *T. inflatum* has been recorded on the sclerotia of *Ophiocordyceps gracilis* (*Ophiocordycipitaceae*), and *T. sinense* on the stromata and sclerotia of *Ophiocordyceps sinensis* (Sun et al., 2019a; Yu et al., 2021). Moreover, *Tolypocladium* species produce bioactive secondary metabolites, including cyclosporin A, tolypoalbin, tolypin, cyclosporin D hydroperoxide, and tolyprolinol, which have significant pharmaceutical and biocontrol applications (Leung et al., 2006; Fukuda et al., 2015; Fukasawa et al., 2018; Niu et al., 2024).

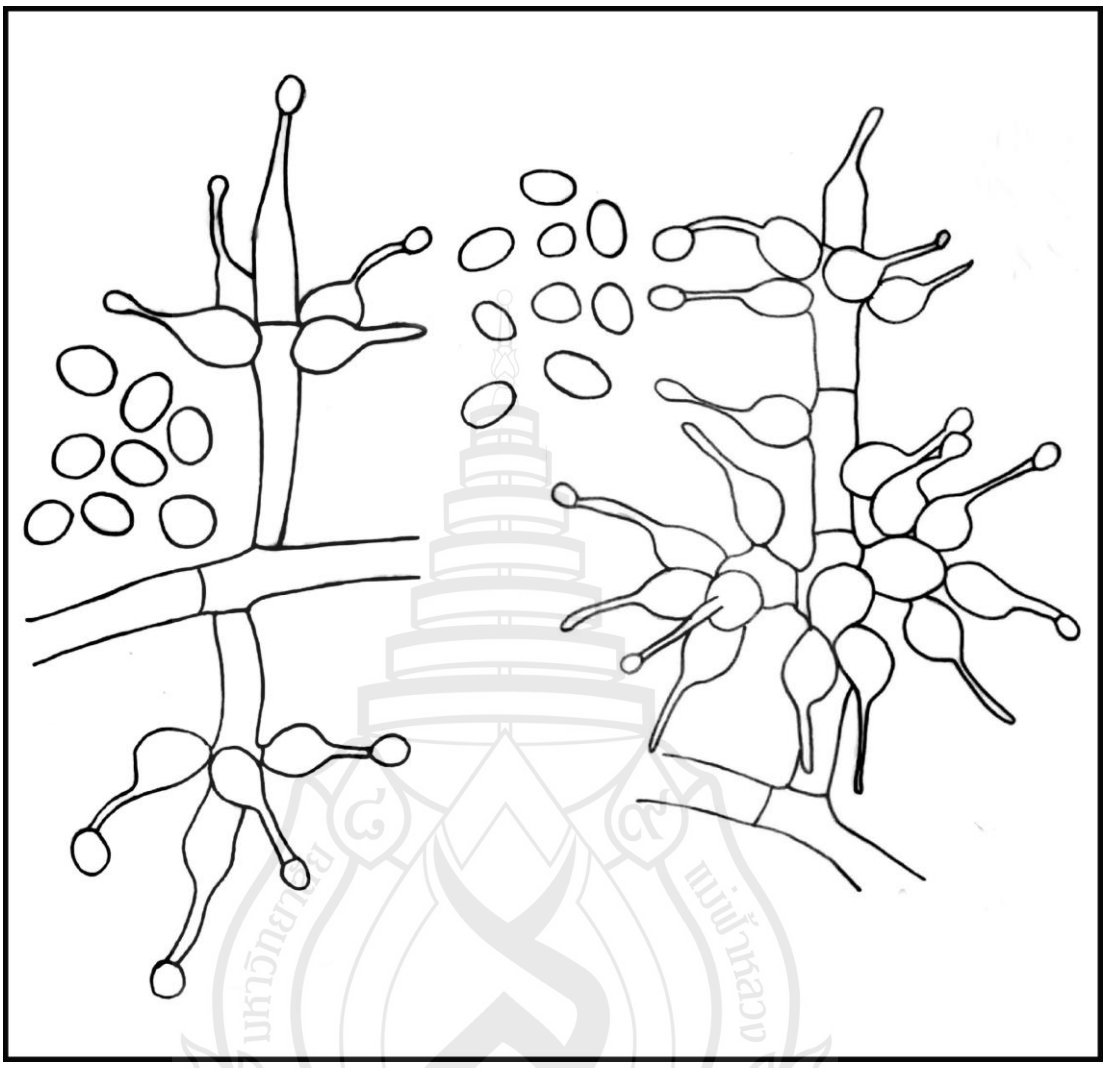


Figure 5.67 *Tolypocladium inflatum*

Figure 5.67, Conidiophore with conidia. (Redrawn from Gams, 1971a).

Torrubiellomyces J.P.M. Araújo & de Bekker, Persoonia 49: 188 (2022)

Figure 5.68

Index Fungorum number: IF 844048

Araújo et al. (2022) introduced *Torrubiellomyces* with *T. zombiae* as the type species. *Torrubiellomyces zombiae* was described as a mycoparasite on *Ophiocordyceps camponoti-floridani* (*Ophiocordycipitaceae*), an entomopathogen of *Camponotus floridanus* in the USA (Araújo et al., 2022). To date, *Torrubiellomyces* remains monotypic (Species Fungorum, 2025). Sequence data for LSU, SSU, *rpb1*, and *tef* of *T. zombiae* are available in GenBank (2025).

The sexual morph is characterized by solitary or clustered superficial perithecia that become black and powdery with age, without the formation of synnemata or stalks on the host or in culture. Ascospores are filiform and disarticulate into part-spores at maturity (adapted from Araújo et al., 2022). The asexual morph produces light cream-colored mycelium, with masses of viscous conidia formed in sporodochia, with no synnemata observed. Only a single type of conidiogenous cell has been reported (adapted from Araújo et al., 2022).

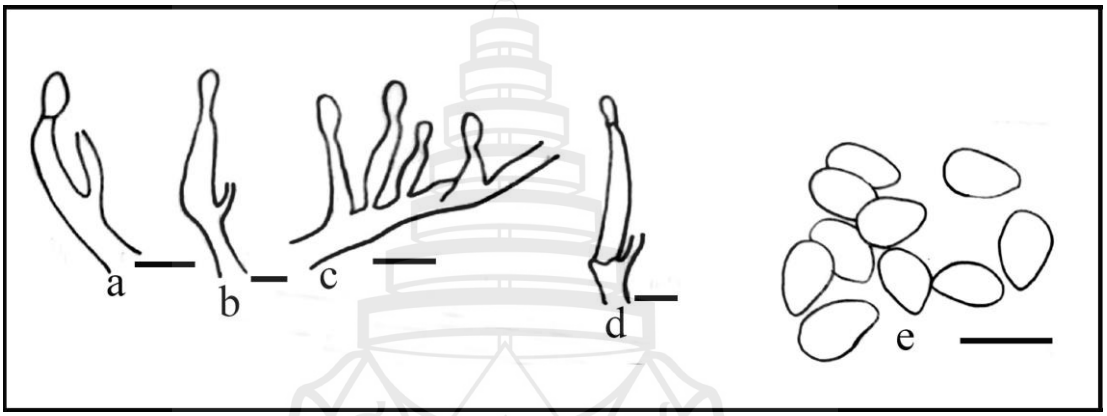


Figure 5.68 *Torrubiellomyces zombiae*

Figure 5.68, a–d. Phialides with attached conidia. e. conidia. Scale bars: a–d = 5 μm, e = 3 μm. (Adapted from Araújo et al., 2022).

Pseudodiploösporaceae Jing Z. Sun, X.Z. Liu & H.W. Liu

Pseudodiploöspora Jing Z. Sun, Xing Z. Liu & H.W. Liu, Mycology 14(1): 67 (2022)

Figure 5.69

Index Fungorum number: IF 571281

Pseudodiploöspora was established by Sun et al. (2023b) based on both morphological and phylogenetic analyses to accommodate several species previously misclassified under *Diploöspora*. The type species, *Pseudodiploöspora longispora* (syn. *Diploöspora longispora*), was described as a saprobic fungus growing on dead leaves of *Colocasia esculenta* var. *antiquorum* in Japan. It is a fungicolous species on cultivated *Morchella* (*Morchellaceae*) species in China (Sun et al., 2023b). In addition to *P. longispora*, three other species were transferred into the genus: *P. cubensis* (syn. *Diploöspora longispora* var. *cubensis*), *P. fungicola* (syn. *Diploöspora fungicola*),

and *P. zinniae* (syn. *Diploöspora zinnia*). *Pseudodiploöspora cubensis* was isolated from fallen leaves of *Leguminosae* in Cuba and has also been recorded from porcupine dung (Castañeda, 1987; Sun et al., 2023b). *Pseudodiploöspora fungicola* was described as a fungicolous on the decaying basidiomata of *Auricularia* spp. (*Auriculariaceae*) in Cuba (Castañeda, 1987). *Pseudodiploöspora zinniae* was documented from seeds of *Zinnia elegans* in Japan (Matsushima, 1981).

The asexual morph of *Pseudodiploöspora* is characterized by branched, septate, hyaline hyphae. Conidiophores range from micronematous to macronematous and may be aseptate or septate. Conidiogenous cells are hyaline, sympodial, and exhibit acropetal development. Conidia are hyaline, smooth-walled, and are cylindrical, ellipsoidal or fusiform. They are typically produced in simple or branched chains. Ramoconidia are hyaline, cylindrical to fusiform, truncate at the base, and bear terminal scars (adapted from Sun et al., 2023b).

According to Species Fungorum (2025), four species are accepted within *Pseudodiploöspora*. Molecular sequence data for this genus are available in GenBank (2025). *Pseudodiploöspora* is classified within *Pseudodiploösporeaceae* in *Hypocreales* (Hyde et al., 2024a).

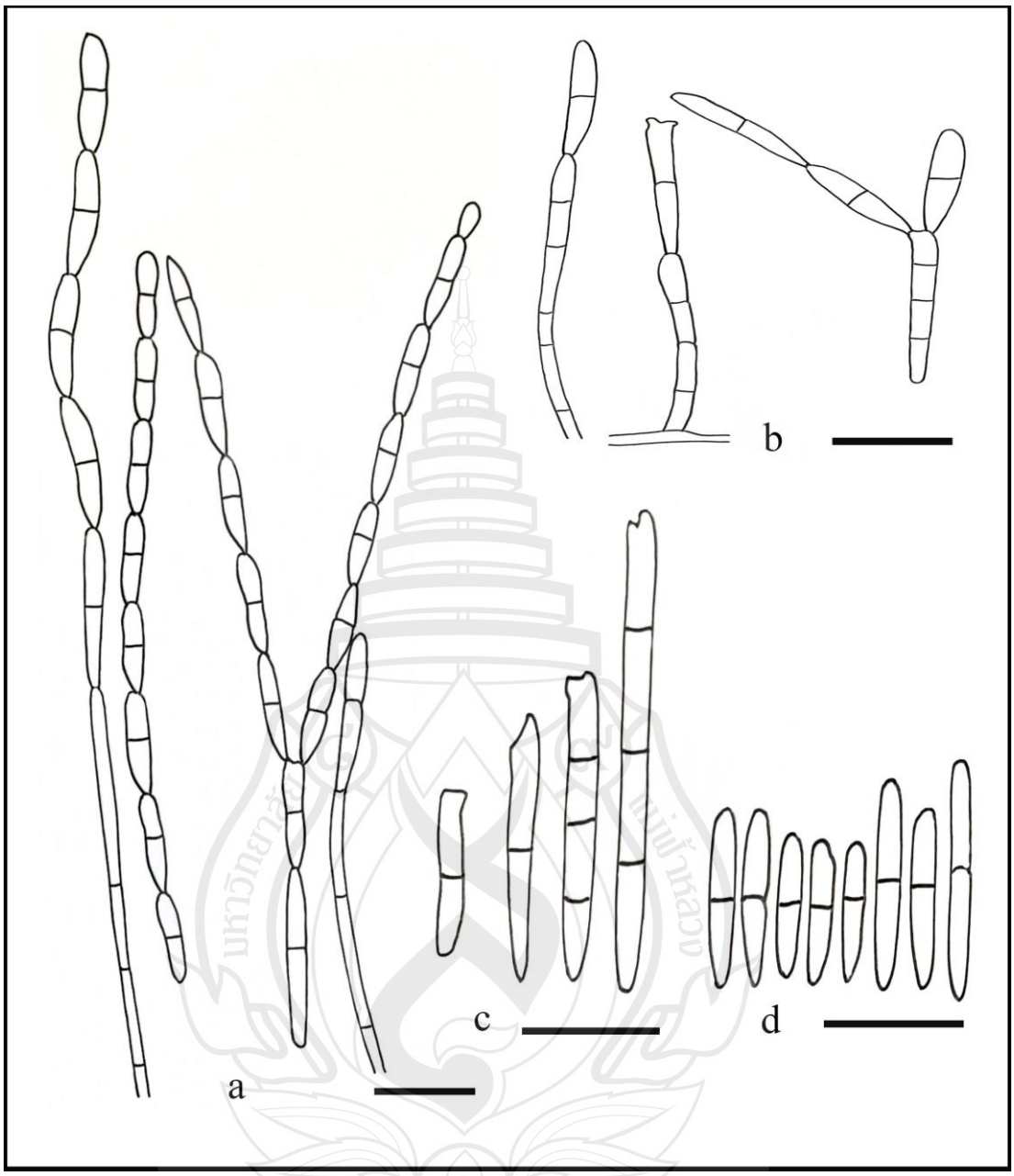


Figure 5.69 *Pseudodiploöspora longispora*

Figure 5.69, a, b. Conidiophores with conidia. c. Conidiogenous cells. d. Conidia. Scale bars: a–e = 20 μm. (Redrawn from Sun et al., 2023b).

Sarocladiaceae L. Lombard

Sarocladium W. Gams & D. Hawksw., Kavaka 3: 57 (1976) [1975]

Figure 5.70

Index Fungorum number: IF 9790

Facesoffungi number: FoF 06266

Gams and Hawksworth (1975) established *Sarocladium* with *S. oryzae* serving as the type species. *Sarocladium* is characterised by cylindrical conidiogenous phialides emerging solitarily from undifferentiated hyphae or conidiophores, which may exhibit sparse to dense branching and bear ellipsoidal conidia formed in pseudo-heads (Gams & Hawksworth, 1975). Summerbell et al. (2011) initiated a revision of *Sarocladium*, which was further examined by Giraldo et al. (2015). Additional species were identified and added by subsequent authors (Yeh & Kirschner, 2014; Liu et al., 2017; Crous et al., 2018). There are 40 species listed within *Sarocladium* in Specie Fungorum (2025).

Sarocladium encompasses endophytes, plant/human pathogens, saprobes, and mycoparasites distributed worldwide (Rivera-Varas et al., 2007; Yeh & Kirschner, 2014; Liu et al., 2017; Ou et al., 2020; Afolabi et al., 2023). Numerous members of *Sarocladium* are associated with gramineous hosts, with notable pathogens such as, *S. oryzae* causing rice sheath rot worldwide (Chen et al., 1986; Ou et al., 2020). *Sarocladium strictum* (associated with *Botrytis cinerea* (*Sclerotiniaceae*)) and *S. mycophilum* associated with *Cortinarius subsertipes* (*Cortinariaceae*)) are mycoparasites (Rivera-Varas et al., 2007; Sun et al., 2019a).



Figure 5.70 *Sarocladium oryzae*

Figure 5.70 Conidiophores, phialides and conidia. Scale bars: a, b = 10 μm. (Redrawn from Gams & Hawksworth, 1975).

Tilachlidiaceae Lombard & Crous

Tilachlidium Preuss, Linnaea 24: 126 (1851)

Figure 5.71

Index Fungorum number: IF 10236

Facesoffungi number: FoF 02138

Tilachlidium was established by, Preuss (1851) based on *T. pinnatum*. Gams (1971b) accepted *Tilachlidium* within *Hypocreales incertae sedis*. Subsequently, Lombard et al., (2015) introduced *Tilachlidiaceae* to encompass *Tilachlidium* and *Septofusidium* and considered *T. brachiatum* as the type species for *Tilachlidium*. Until now, only the asexual stage of *Tilachlidium* has been documented (Lombard et al., 2015; Liang et al., 2016).

The asexual morph is characterized by, cylindrical synnemata which are either simple or branched and taper towards the apex. They are composed of bundles of parallel, longitudinal hyphae, typically closely packed together. The phialides are scattered throughout the synnema. They are hyaline, subulate and often terminate the hyphae of the synnema. Phialides can also occur as lateral cells of the hyphae, either individually or in groups. The conidia produced by this organism are oblong to ellipsoidal, aseptate, hyaline, and smooth. They are covered by a mucoid layer and tend to aggregate into large spherical or irregular masses (adapted from Lombard et al., 2015).

The members of *Tilachlidium* are saprobes associated with fungal insect hosts and soil (Preuss, 1851; Mains, 1951; Lombard et al., 2015). The fungicolous species include *T. brachiatum* (on *Trametes versicolor* (*Polyporaceae*), *Hypholoma fasciculare* (*Strophariaceae*), *Mycena galericulata* (*Mycenaceae*), and *Lactarius deterrimus* (*Russulaceae*)), *T. pinnatum* (on dry basidiomata of *Agaricus galericulatus* (*Agaricaceae*)), and *T. setigerum* (on old *Xeromphalina campanella* (*Mycenaceae*)) (Sun et al., 2019a; Index Fungorum, 2025). To date, there are 15 species listed under *Tilachlidium* in Species Fungorum (2025). Sequence data are available for *T. brachiatum* and *T. poneraticum* in GenBank (2025).



Figure 5.71 *Tilachlidium brachiatum*

Figure 5.71, a. Synnemata on the host. b. Base of a synnema. c. Arrangement of hyphae in synnema and phialides. d. Conidial mass attached to a phialide. e. Close-up view of hyphae of synnemata. f. Conidia. Scale bars: b = 500 µm, a = 200 µm, c, d = 100 µm, e = 50 µm, i = 5 µm. (Photo credits: R.H Perera).

Subclass *Sordariomycetidae* O.E. Erikss. & Winka

Cephalothecales Maharachch. & K.D. Hyde

Cephalothecaceae Höhn.

Albertiniella Kirschst., Annls mycol. 34(3): 183 (1936)

Figure 5.72

Index Fungorum number: IF 109

Facesoffungi number: FoF 13018

Kirschstein (1936) established *Albertiniella* to include *A. reticulata* (type species), which was found in Germany on a fruiting body of *Ganoderma applanatum*. The name *Albertiniella* was chosen to honour the distinguished mycologist Albertini (Kirschstein, 1936). Malloch and Cain (1972) synonymised *Cephalotheca polyporicola*, which was also collected from Russia on the hymenium of *Ganoderma applanatum* (*Polyporaceae*), under *Albertiniella*, as *A. polyporicola*. *Albertiniella polyporicola* has also been reported on the basidiomata of *Ganoderma lucidum* (*Polyporaceae*) and *G. resinaceum* (*Polyporaceae*) (Akulov, 2013). The distribution of *Albertiniella* species includes Austria, the Czech Republic, Denmark, Estonia, Germany, Japan, Norway, Russia, Ukraine, and Sweden, (Akulov, 2013). Specifically, *Albertiniella polyporicola* is identified as a specialised parasite that forms its fruiting bodies exclusively on the hymenia of *Ganoderma* species, infecting the host mycelium (Akulov, 2013).

The sexual morph of *Albertiniella* is characterized by, gregarious, superficial, carbonaceous, black, stomatal, and globose cleistothecia (Kirschstein, 1936). The asci are subglobose to globose, sessile, and octosporous. The ascospores range from hyaline to yellowish (Kirschstein, 1936). The asexual morph of *Albertiniella* is acremonium-like, characterised by spreading, undifferentiated, irregularly branched hyphae, with simple conidiogenous cells called adelophialides located laterally (Akulov, 2013). The phialides are cylindrical, sometimes slightly expanded at the base and pointed at the apex. The conidia are single-celled, hyaline, sausage-shaped and are collected in slimy spherical masses (Akulov, 2013).

As of date, *Albertiniella* includes only *A. reticulata* and *A. polyporicola* (Species Fungorum, 2025). Among these, molecular data is available solely for *A. polyporicola* in GenBank (2025).

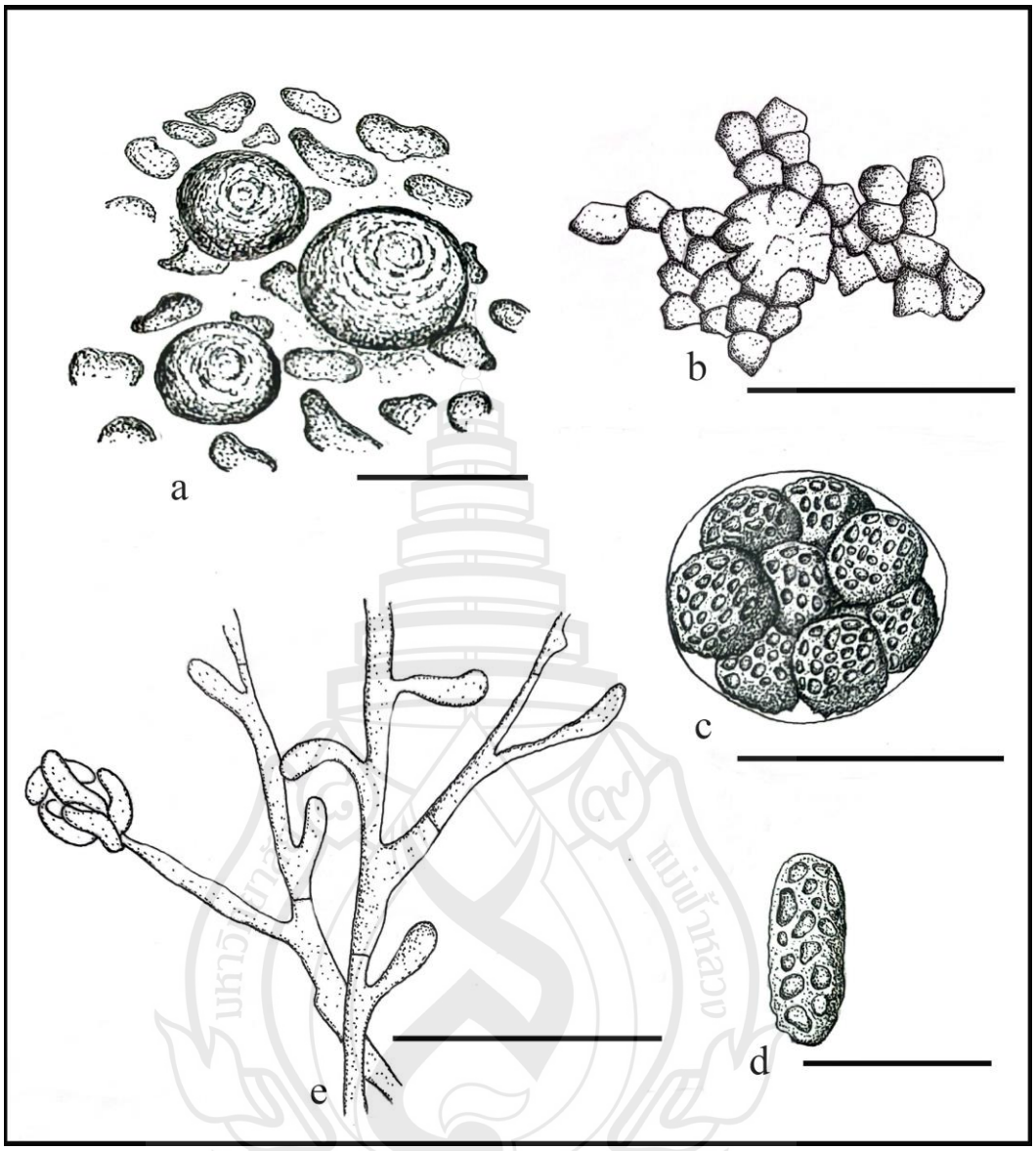


Figure 5.72 *Albertiniella polyporicola*

Figure 5.72, a. General view of cleistothecia on the *Ganoderma applanatum* hymenium. b. Remains of the peridium shell. c, d. Ascus and ascospores. e. Asexual morph. Scale bars: b = 800 µm, a = 400 µm, e = 15 µm, c = 7 µm, d = 3 µm. (Redrawn from Akulov, 2013).

Chaetosphaeriales Huhndorf, A.N. Mill. & F.A. Fernández

Helminthosphaeriaceae Samuels, Cand. & Magni.

Helminthosphaeria Fuckel, Jb. nassau. Ver. Naturk. 23-24: 166 (1870) [1869-70]

Figure 5.73

Index Fungorum number: IF 2263

Facesoffungi number: FoF 01143

Fuckel (1870) proposed *Helminthosphaeria* with the type species *H. clavariarum*, which was described by Desmazières (1837) as *Peziza clavariarum*. *Helminthosphaeria* was regarded as a member of *Sordariales* due to similarities in the ontogeny of the ascomata and the presence of 1-septate ascospores with germ pores, akin to those found in *Sordaria* (Parguey-Leduc, 1960; Lundqvist, 1972; Eriksson & Hawksworth, 1993). Following this, Samuels et al. (1997b) conducted a monograph on this genus and established *Helminthosphaeriaceae*, designating *Helminthosphaeria* as its type genus. Additionally, Samuels et al. (1997b) observed the co-occurrence of *Helminthosphaeria* species with hyphomycetous *Diplococcium* or heteroconium-like asexual morphs on the substrate. Subsequently, Miller et al. (2014) delineated multiple lignicolous *Helminthosphaeria* species through phylogenetic investigation. They noted that the polyphyletic nature of *Helminthosphaeria* includes *Diplococcium* and *Selenosporella* asexual morphs in natural habitats. However, these associations were not confirmed through culture characteristics or phylogenetic analyses. Huang et al. (2021b) noted the association of *Helminthosphaeria* with *Endophragmiella dimorphospora* and *Hilberina* species, within the *Helminthosphaeriaceae*. Nevertheless, they were unable to verify the asexual morph of *Helminthosphaeria* due to insufficient culture characteristics and molecular data. As of the latest update on Species Fungorum (2025), there are 21 species names documented under *Helminthosphaeria*. It is classified within *Helminthosphaeriaceae* in *Chaetosphaeriales* (Hyde et al., 2024a).

The members of *Helminthosphaeria* exhibit fungicolous and lignicolous lifestyles (Huang et al., 2021b). *Helminthosphaeria clavariarum* (associated with *Clavaria fuliginea* (*Clavariaceae*) and *Clavulina cristata* (*Hydnaceae*)), *H. corticiorum* (associated with Aphyllophorales), *H. hyphodermae* (associated with *Hyphoderma puberum* (*Hyphodermataceae*)) and *H. hispidissima* (on *Hypoxylon investiens* (*Xylariaceae*)) have been documented as fungicolous (Crous et al., 2019a; Sun et al., 2019a). The species of *Helminthosphaeria* possesses superficial or immersed ascomata, cylindrical asci containing hyaline to brown ascospores, and

associated asexual morphs characterized by smooth-walled or verrucose, septate conidia (Samuels et al., 1997b; Goh & Hyde, 1998; Réblová, 1999; Hernández-Restrepo, et al., 2017).

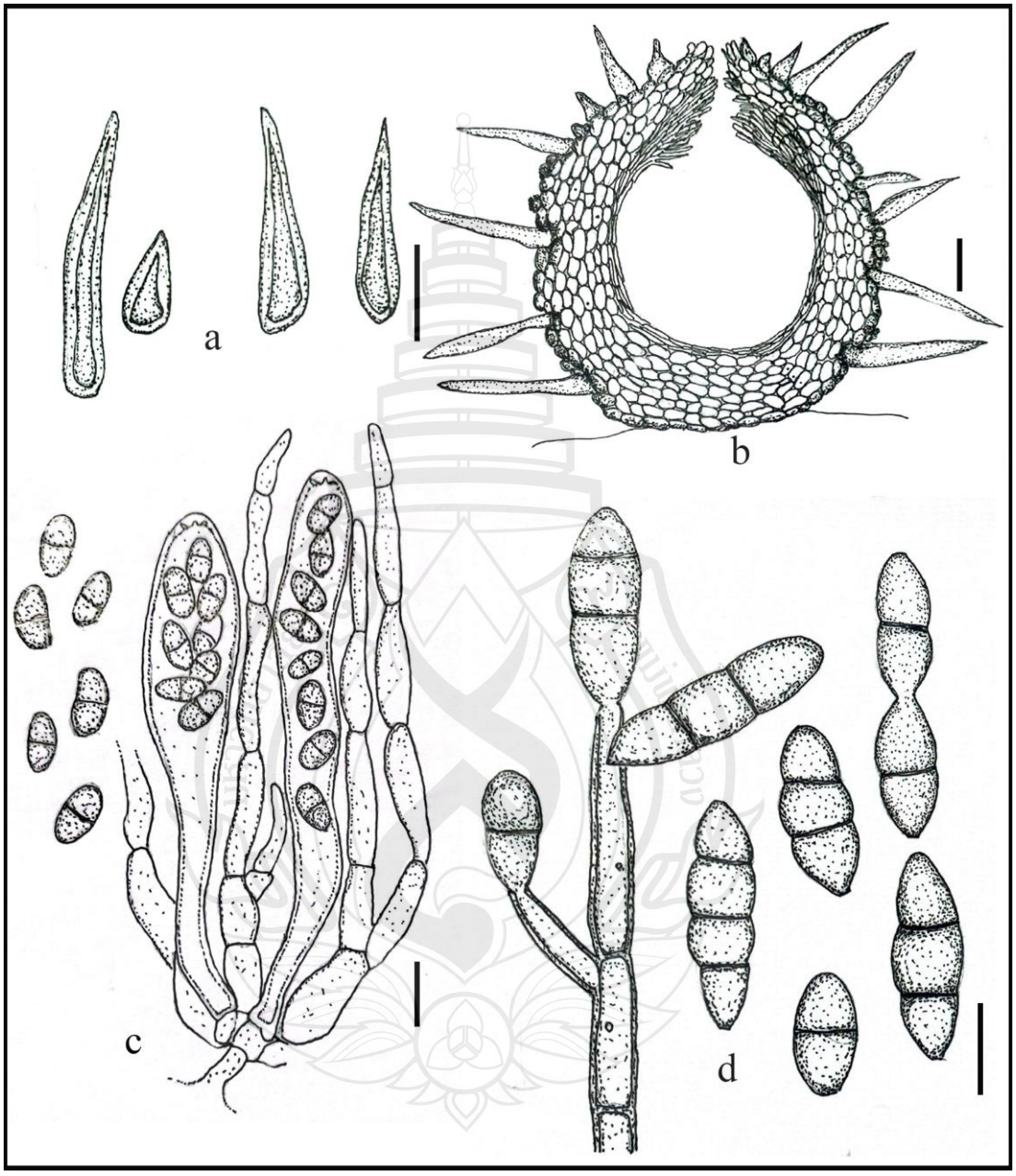


Figure 5.73 *Helminthosphaeria pilifera*

Figure 5.73, a. Perithecial setae. b. Median, longitudinal section of perithecium. c. Asci with paraphyses and ascospores. d. Conidiophore and conidia. Scale bars: b = 20 μm, a, c, d = 10 μm. (Redrawn from Réblová, 1999).

Sordariomycetidae* genera *incertae sedis

Phaeotrichosphaeria Sivan., Trans. Br. mycol. Soc. 81(2): 313 (1983)

Figure 5.74

Index Fungorum number: IF 25837

Facesoffungi number: FoF 13727

Sivanesan (1983) established *Phaeotrichosphaeria* to encompass specific unitunicate pyrenomycetes with *Endophragmiella* asexual morphs. *Phaeotrichosphaeria indica*, identified on the stems of *Lawsonia alba*, was designated as the type species. Sivanesan (1983) described two other species: *P. britannica*, found on *Quercus* branches and *Fagus* wood in the UK, and *P. hymenochaeticola*, a fungicolous species isolated from *Hymenochaete mougeotii* (*Hymenochaetaceae*) in New Zealand. Subsequently, Romero and Carmarán (2003) expanded *Phaeotrichosphaeria* by adding *P. minor*, discovered on a fallen branch in Argentina.

The sexual morph of *Phaeotrichosphaeria* is characterized by its perithecia, which are superficial and occur either solitarily or in small, scattered to aggregated groups. These perithecia are globose, subglobose, or ovoid, setose, and feature a short, papillate ostiole at the apex, internally lined with hyaline, filiform periphyses. The perithecial wall is constructed of polygonal, brown cells that become thinner-walled, subhyaline to hyaline, compressed, and elongated towards the interior. Paraphyses are hyaline and filiform. The asci are cylindrical, short-stalked, 8-spored, thin-walled, and unitunicate, with evanescent characteristics and an indistinct, non-amyloid apical structure. The ascospores are smooth, ovoid, pale brown to brown at maturity, and 0-1 septate (adapted from Sivanesan, 1983).

Phaeotrichosphaeria comprises four species (Species Fungorum, 2025). The sequence data for the genus is not available in GenBank (2025). *Phaeotrichosphaeria* is currently classified within *Sordariomycetidae* genera *incertae sedis* (Hyde et al., 2024a).

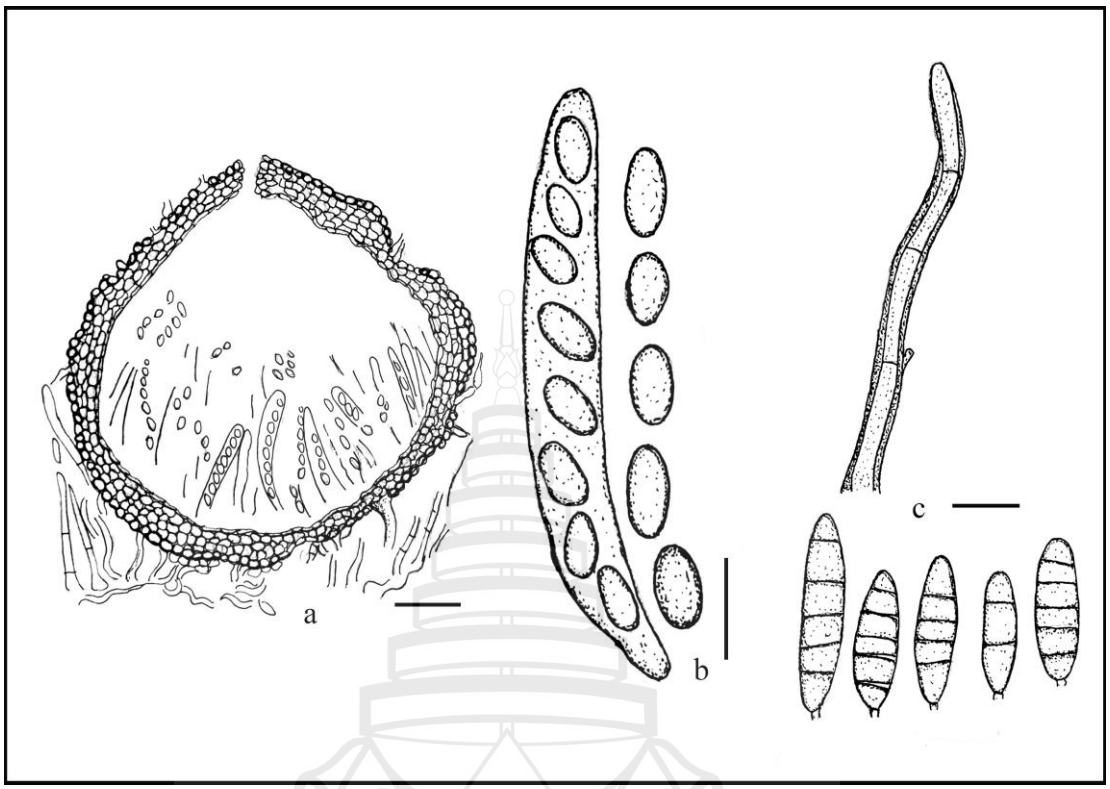


Figure 5.74 *Phaeotrichosphaeria hymenochaeticola*

Figure 5.74, a. Vertical section of the perithecium. b. Ascus and ascospores. c. Conidiophore and conidia. Scale bars: a = 45 μm, b, c = 10 μm. (Redrawn from Sivanesan, 1983).

Subclass *Xylariomycetidae* O.E. Erikss & Winka

Xylariales Nannf.

Hansfordiaceae Crous

Hansfordia S. Hughes, Mycol. Pap. 43: 15 (1951)

Figure 5.75

Index Fungorum number: IF 8423

Facesoffungi number: FoF 06207

Hughes (1951a) established *Hansfordia* with the type species *H. ovalispora*, which was collected from dead leaves of *Saccharum officinarum* in Ghana. Crous et al. (2019b) proposed *Hansfordiaceae* to accommodate *Hansfordia* as its type genus. As of Species Fungorum (2024), there are 13 species listed under *Hansfordia*. The sexual morph of *Hansfordia* has not yet been observed. The asexual morph of *Hansfordia* is characterised by, straight to flexuous, medium brown, solitary, erect

and branched conidiophores which arises from superficial mycelium (adapted from Crous et al., 2019b). The conidiogenous cells are subcylindrical or club-shaped and subhyaline. They have subdenticulate apices where conidia are formed through rhexolytic conidiogenesis. The conidia are hyaline to pale brown, solitary and aseptate. They are dry, globose to ellipsoid to fusoid, with smooth or finely roughened surfaces and possess a minute basal frill derived from the apex of the separating cell (adapted from Crous et al., 2019b).

Hansfordia species have been documented in Australia, Congo, Germany, Ghana, India, Italy, Japan, Java, New Zealand, Pakistan, Papua New Guinea, Thailand, the UK, the USA and Venezuela (Crous et al., 2019b; Farr & Rossman, 2024). These species have been found on various plant substrates and in soil, primarily as saprobes (Wu et al., 2015; Crous et al., 2019b). Moreover, some species such as *H. alba* (colonized *Lasiodiplodia theobromae* (*Botryosphaeriaceae*)), *H. parasitica* (colonized, *Botryosphaeria* (*Botryosphaeriaceae*), *Coniothyrium* (*Coniothyriaceae*), culture of *Dothiorella quercina* (*Botryosphaeriaceae*), and *Physalospora* (*Hyponectriaceae*)) and *H. pulvinata* (associated with *Fulvia fulva* (*Mycosphaerellaceae*) on tomatoes) are mycoparasites (Hepperly, 1969; Peresse & Le Picard, 1980; Crous et al., 2019b; Sun et al., 2019a). *Hansfordia pulvinata* has also been proposed as a potential biological control agent for plant pathogenic fungi (Mitchell & Taber, 1986; Crous et al., 2019b).

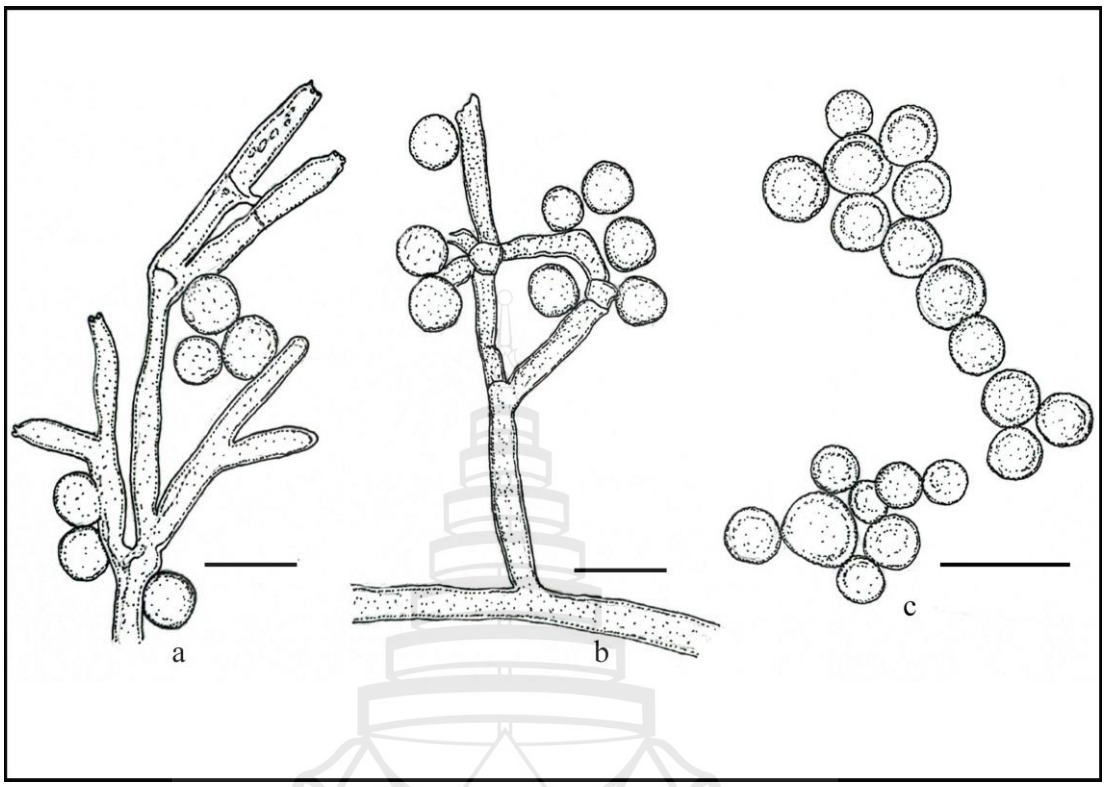


Figure 5.75 *Hansfordia pulvinata*

Figure 5.75, a, b. Conidiophores and conidiogenous cells. c. Conidia. Scale bars: a–c = 10 μm. (Adapted from Crous et al., 2019b).

Hypoxylaceae DC.

Chlorostroma A.N. Mill., Lar.N. Vassiljeva & J.D. Rogers, Sydowia 59(1): 142 (2007)

Figure 5.76

Index Fungorum number: IF 29126

Facesoffungi number: FoF 02986

Chlorostroma was established by Miller et al. (2007), with *C. subcubisporum* as the type species. *Chlorostroma subcubisporum* was described as fungicolous growing on the stromata of *Hypoxylon perforatum* (*Hypoxylaceae*) in the USA (Miller et al., 2007). Subsequently, two additional species, *C. cyaninum* and *C. vestlandicum*, were added to the genus (Læssøe et al., 2010; Nordén et al., 2014). *Chlorostroma cyaninum* is fungicolous on immature stromata of *Hypoxylon* sp. in Thailand, while *C. vestlandicum* was recorded from *Hypoxylon vogesiacum* in Norway. Additional records of *Chlorostroma* species remain scarce, although *C. vestlandicum* has been

reported from Russia (Popov et al., 2021). As of Species Fungorum (2025), three species are currently accepted under *Chlorostroma*. However, no DNA sequence data for *Chlorostroma* are available in GenBank (2025).

Chlorostroma is characterized by green stromata containing embedded perithecia. The asci are unitunicate, cylindrical, 8-spored, and uniseriate, with a J- or J+ apical ring. Ascospores are brown, more or less cuboid or broadly ellipsoid, sometimes guttulate and possess a germination slit (Miller et al., 2007; Læssøe et al., 2010; Nordén et al., 2014). Miller et al. (2007) noted that the taxonomic placement of *Chlorostroma* was uncertain and tentatively placed it in *Xylariaceae*. It was transferred to the *Hypoxylaceae* based on the morphological similarity to *Hypoxylon aeruginosum* and comparable secondary metabolite profiles (Læssøe et al., 2010).

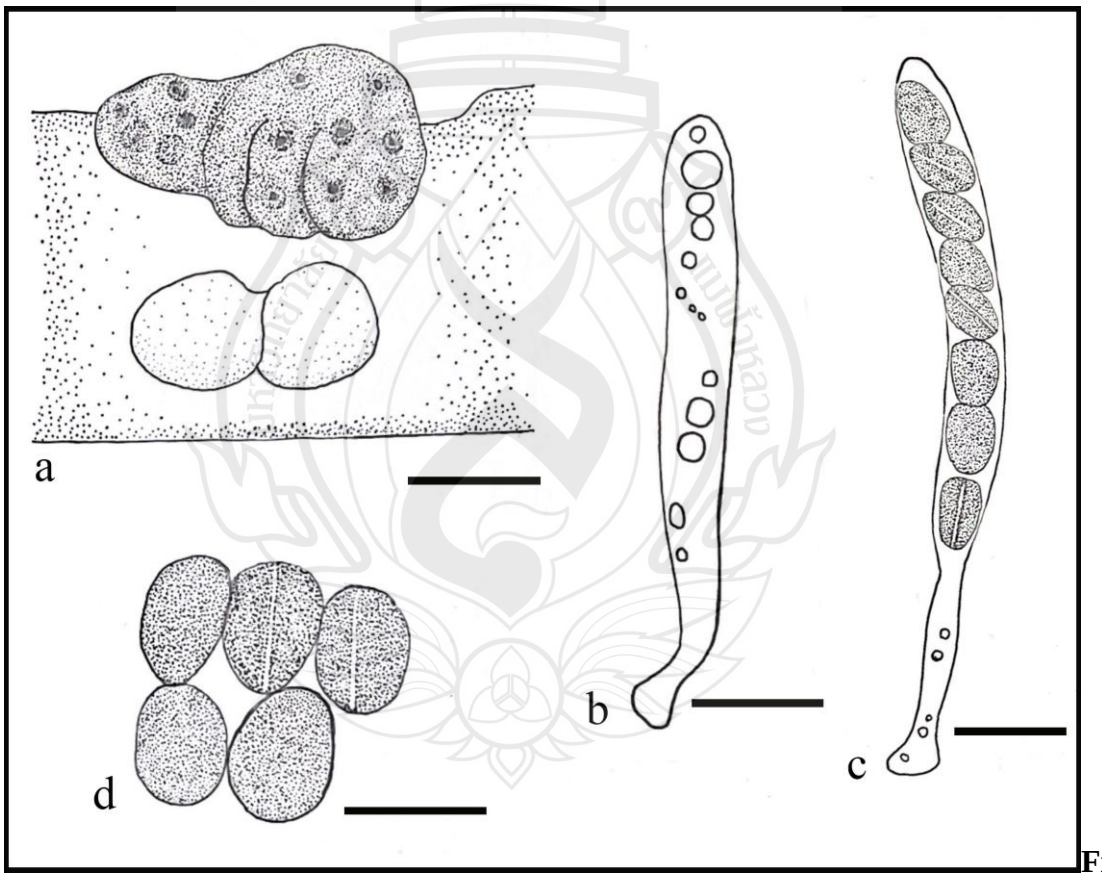


Figure 5.76 *Chlorostroma subcubisporum*

Figure 5.76, a. Stromata. b. Immature ascus. c. Ascus with eight spores. d. Ascospores. Scale bars: a = 2 mm, b, c = 15 μm, d = 10 μm. (Adapted from Miller et al., 2007).

Sordariomycetes* genera *incertae sedis

Immersisphaeria Jaklitsch, Mycotaxon 101: 18 (2007)

Figure 5.77

Index Fungorum number: IF 510734

Facesoffungi number: FoF 01359

Jaklitsch (2007) introduced *Immersisphaeria* to accommodate *Hypocrea eichleriana* (as *Immersisphaeria eichleriana*) based on morphological assessments and a comparative study of its type specimen. This species was described as fungicolous, associated with the corticioid basidiomycete *Phanerochaete tuberculata* (*Phanerochaetaceae*) in Poland (Jaklitsch, 2007).

The sexual morph of *Immersisphaeria* is distinguished by its pulvinate, fleshy pseudostromata, which are yellowish-brown. The ascomata are immersed, globose to subglobose in cross-section, and occur solitarily, with dark brown to black ostiolar dots. The peridium is thin and composed of hyaline pseudoparenchymatous cells of *textura angularis*. The hamathecium consists of periphyses originating from the upper part of the peridium, accompanied by sparse, hyaline paraphyses. Asci are unitunicate, cylindrical, short-stipitate, 8-spored, with a thickened base and lacking an apical apparatus. The ascospores are uniseriate, light brown, 2-celled, ellipsoid, smooth-walled, and feature a straight to sigmoid germ slit. The asexual morph has not yet been observed (Jaklitsch, 2007; Daranagama et al., 2016).

Since its establishment, *Immersisphaeria* has remained monotypic (Species Fungorum, 2025). To date, sequence data for *I. eichleriana* is not available in GenBank (2025). *Immersisphaeria* is currently placed within *Sordariomycetes* as genera *incertae sedis* (Hyde et al., 2024a).

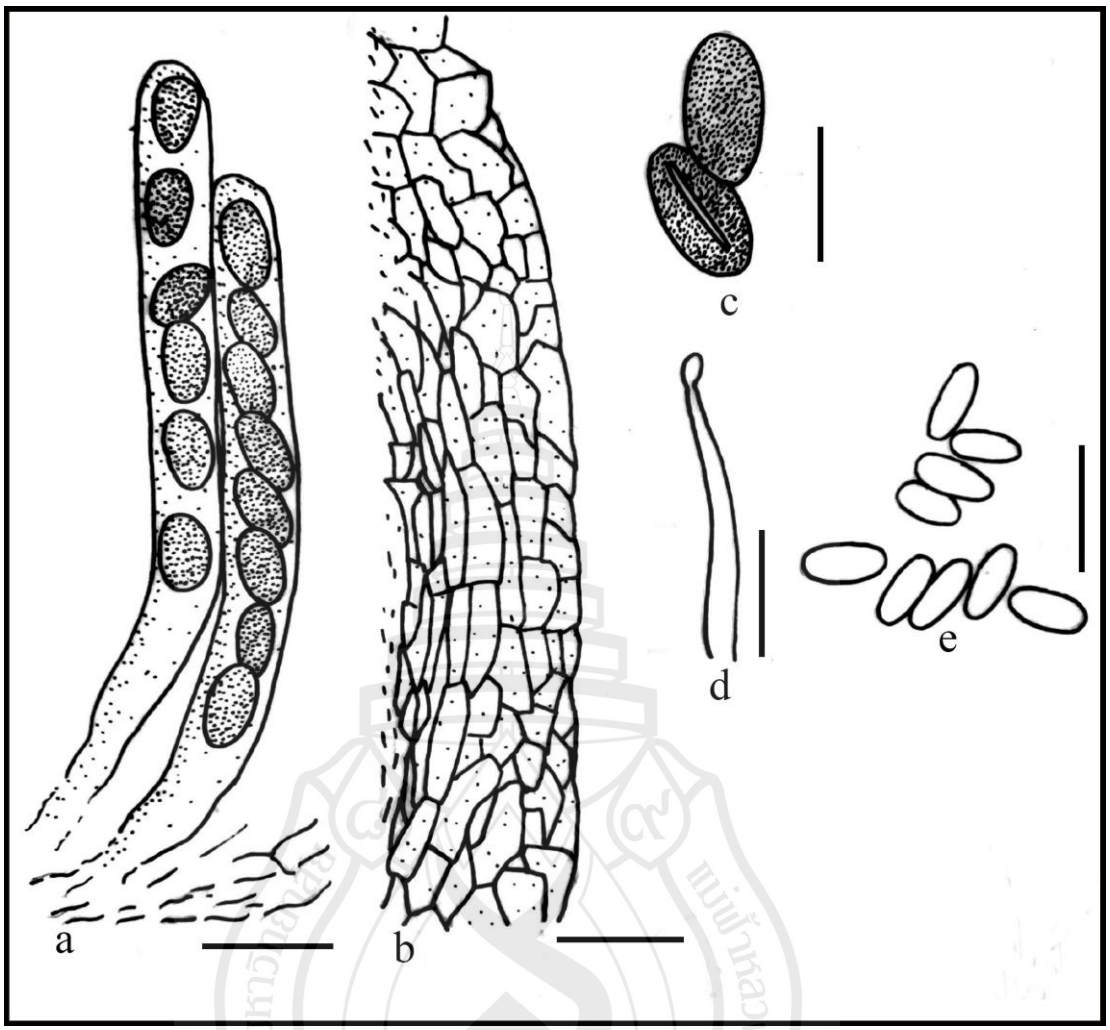


Figure 5.77 *Immersisphaeria eichleriana*

Figure 5.77, a. Asci. b. Peridium. c. Ascospores. d. Phialide from the host surface. e. Conidia from the host surface. Scale bars: b, d = 15 μm, a = 11 μm, c = 6 μm, e = 8 μm. (Adapted from Jaklitsch, 2007).

Scotiosphaeria Sivan., Trans. Br. mycol. Soc. 69(1): 119 (1977)

Figure 5.78

Index Fungorum number: IF 4971

Facesoffungi number: FoF 13820

Sivanesan (1977) established *Scotiosphaeria*, designating *S. endoxylinae* as the type species. This species was described as a fungicolous sphaeriaceous ascomycete associated with the perithecia of *Endoxylina pini* (*Sordariomycetes incertae sedis*) in Scotland (Sivanesan, 1977). The sexual morph of *S. endoxylinae* is

characterized by densely aggregated perithecia that are either superficial or partially immersed within a stromatic complex associated with the necks of *E. pini*. The perithecia are black, globose, and possess a short, papillate ostiole internally lined with hyaline, filiform periphyses. The paraphyses are numerous, filiform, and hyaline. The asci are cylindrical, pedicellate, unitunicate, and 8-spored. The ascospores are ellipsoid, brown, and one-septate (adapted from Sivanesan, 1977).

Since its establishment, *Scotiosphaeria* has remained monotypic (Species Fungorum, 2025). No sequence data for *S. endoxylinae* is available (GenBank, 2025). This genus is currently classified within the *Sordariomycetes* genera *incertae sedis* (Hyde et al., 2024a).

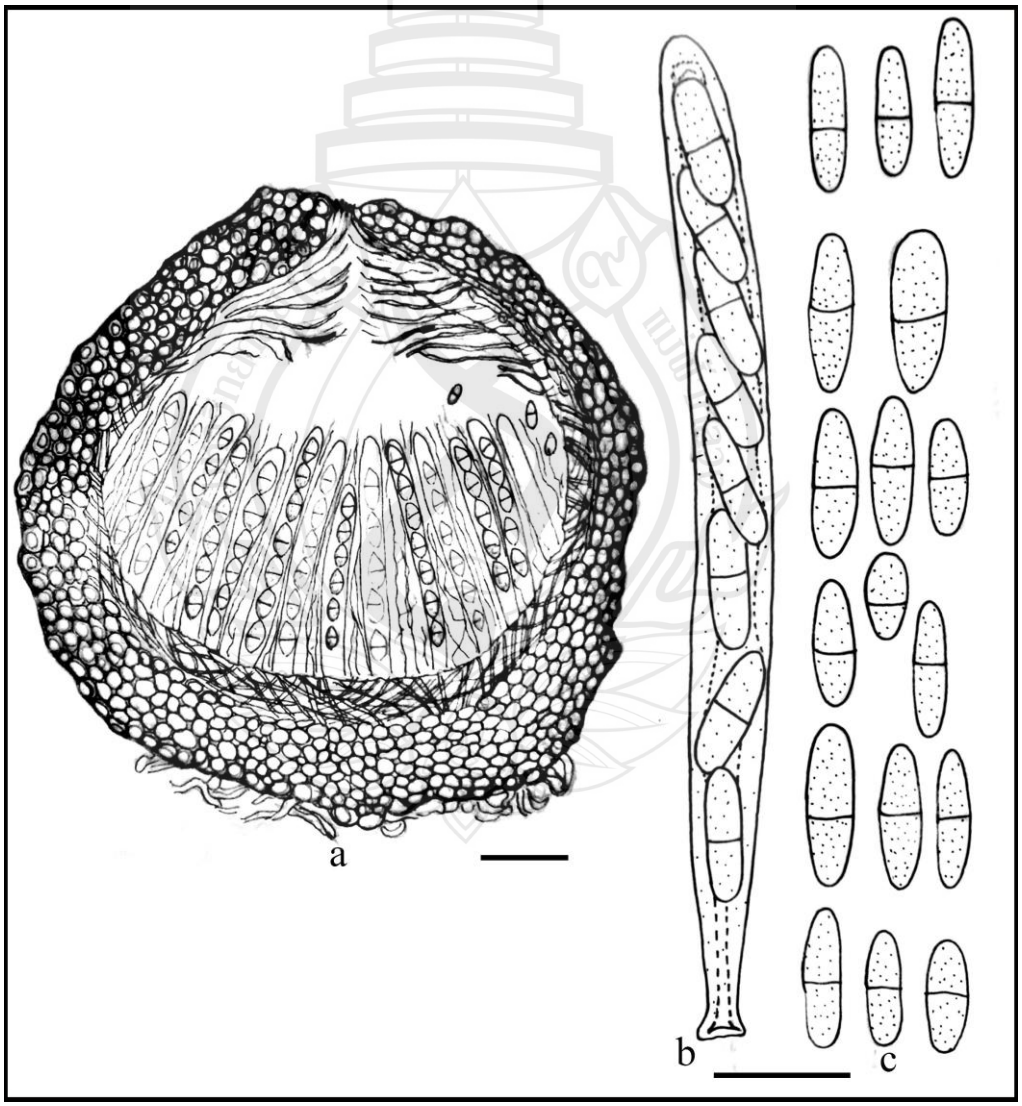


Figure 5.78 *Scotiosphaeria endoxylinae*

Figure 5.78, a. Vertical section of the perithecium. b. Ascus. c. Ascospores. Scale bars: a = 25 μm, b, c = 10 μm. (Redrawn from Sivanesan, 1977).

Ascomycota* families *incertae sedis

Eoterfeziaceae G.F. Atk.

Eoterfezia G.F. Atk., Bot. Gaz. 34: 40 (1902)

Figure 5.79

Index Fungorum number: IF 1844

Atkinson (1902) established *Eoterfezia* with the type species *E. parasitica.* To accommodate this genus, he also proposed *Eoterfeziaceae*. Jeng and Cain (1976) expanded the *Eoterfezia* by adding *E. perlucida*. *Eoterfezia* consists two species (Species Fungorum, 2025). *Eoterfezia parasitica* was discovered as a mycoparasitic on *Sordaria* (*Sordariaceae*) in the USA (Atkinson, 1902), while *Eoterfezia perlucida* was discovered on *Podospora communis* (*Podosporaceae*) in Venezuela (Jeng & Cain, 1976).

The sexual morph of *Eoterfezia* is characterized by, initially globose, subglobose, later kidney-shaped, fleshy, perithecial ascomata with a membranaceous peridium. The ascomata are closely attached to the perithecia of the host. The asci are elliptical to oblong or globose and contain 8 spores. The ascospores are biseriate, elliptical to oblong or ellipsoidal, hyaline and smooth (adapted from Atkinson, 1902, Jeng & Cain, 1976). The asexual morph of *Eoterfezia* has not yet been observed. No molecular data is available for *Eoterfezia* (GenBank, 2025).

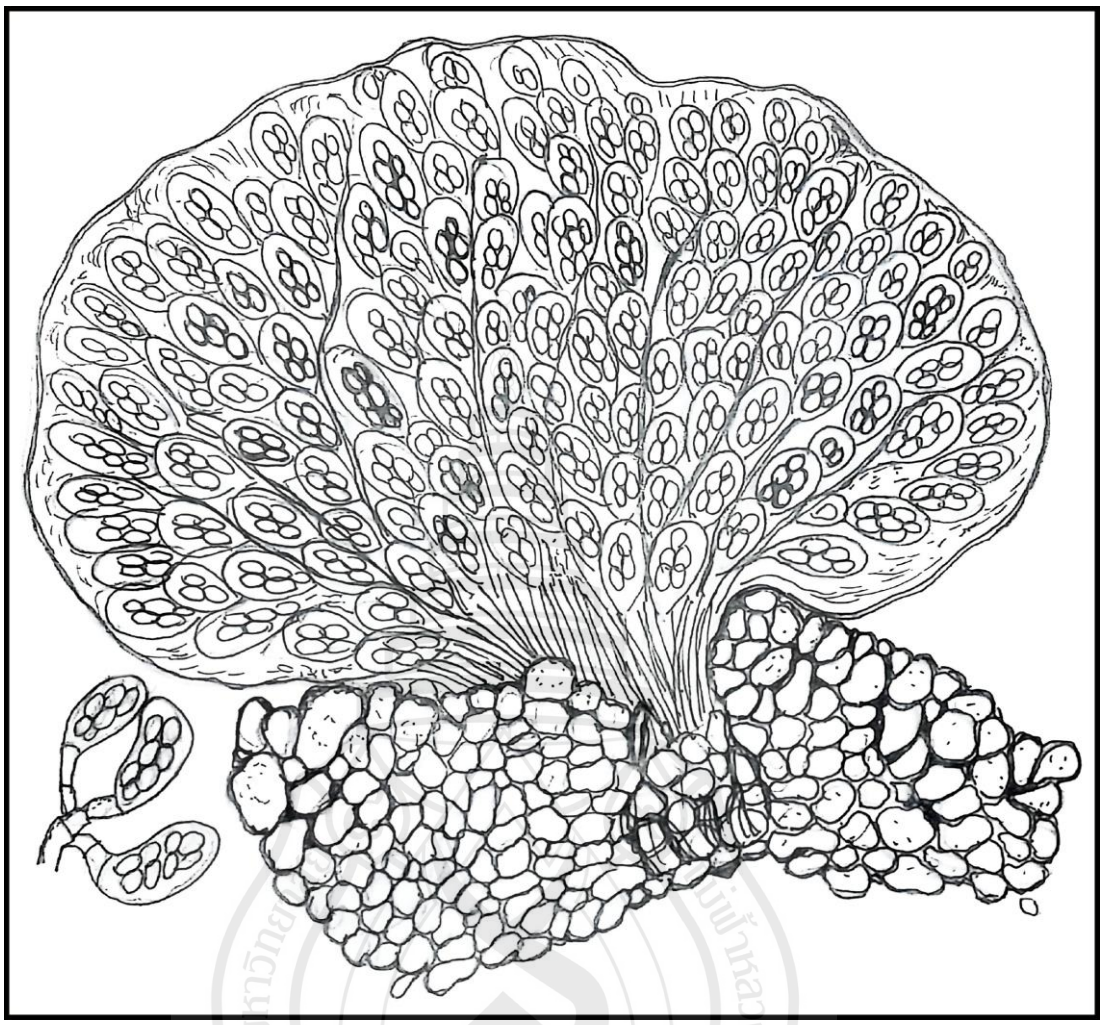


Figure 5.79 *Eoterfezia parasitica*

Figure 5.79, Section of ascomata and portion of the perithecial wall of *Sordaria* (Redrawn from Atkinson 1902).

Ascomycota* genera *incertae sedis

Annellodochium Deighton, Mycol. Pap. 118: 28 (1969)

Figure 5.80

Index Fungorum number: IF 7160

Annellodochium was introduced by Deighton (1969), with *A. ramulisporum* as the type species. *Annellodochium ramulisporum* was described as a hyperparasite on *Diatrype* sp. (*Diatrypaceae*) in Sierra Leone (Deighton, 1969).

Annellodochium is characterized by pulvinate, stromatic sporodochia composed of branched hyphae radiating from the center of the base towards the

margin, and surrounded by a peripheral palisade-like layer of parallel conidiophores. The conidiophores are cylindrical, pale brown, thin-walled, and annellate, bearing conidia (blastospores) terminally and proliferating through the old apical scars. Conidia are pale brown, thin-walled, catenulate, one-septate, with the apical cell small and producing the second conidium as a lateral branch (adapted from Deighton, 1969).

Since the original discovery, additional records on this genus remains scarce, however, *A. ramulisporum* has also been recorded from Venezuela on decorticated, unidentified wood (Crane & Dumont, 1975). As of Species Fungorum (2025), *Annellodochium* remains monotypic. Sequence data for the genus are unavailable in GenBank (2025). *Annellodochium* is presently classified within *Ascomycota*, genera *incertae sedis* (Hyde et al., 2024a).

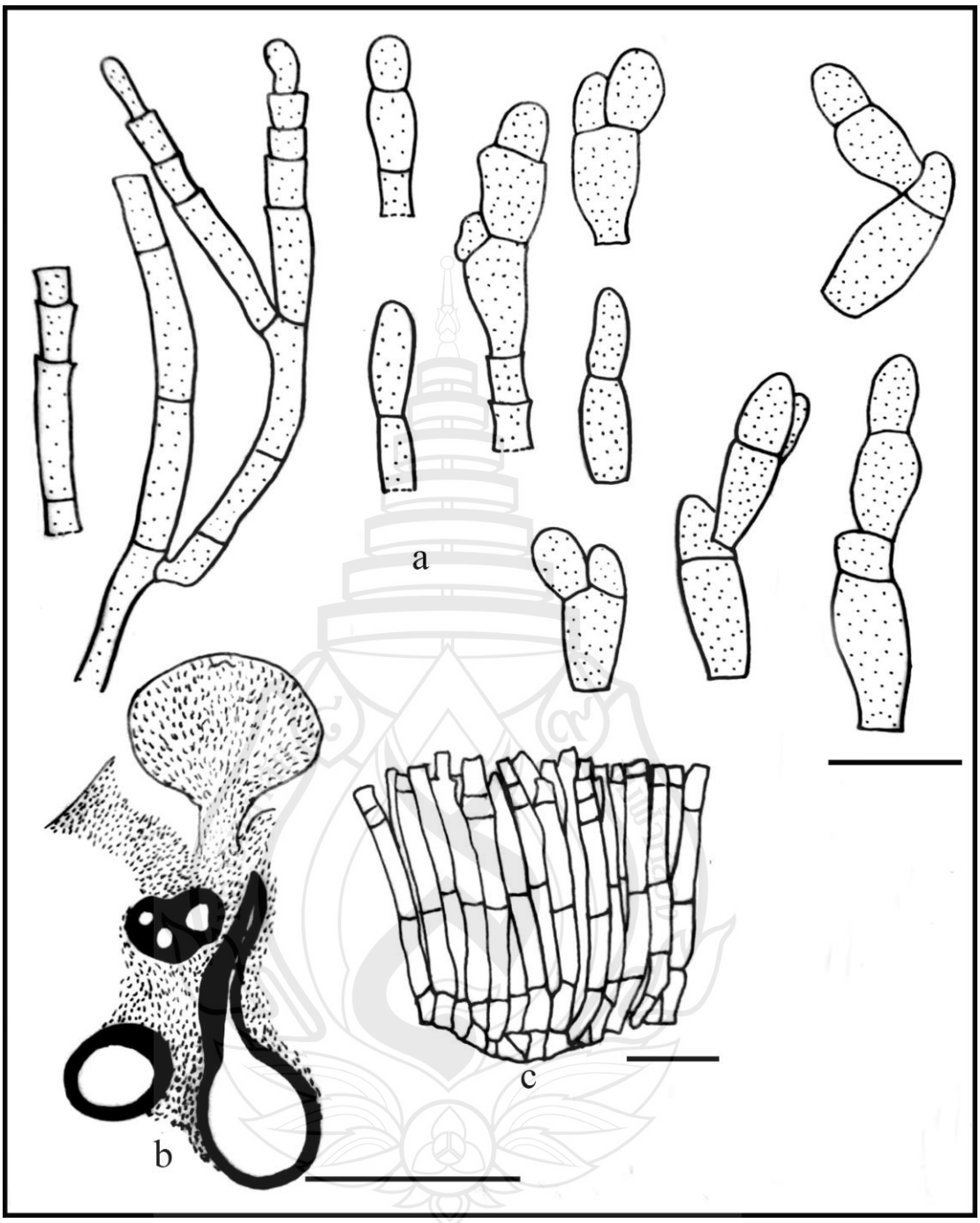


Figure 5.80 *Annellodochium ramulisporum*

Figure 5.80, a. Conidiophores and conidial attachments. b. Sporodochia on *Diatrype* sp. c. Layer of parallel conidiophores. Scale bars: b = 500 μm, a, c = 10 μm. (Redrawn from Deighton, 1969).

Atractilina Dearn. & Barthol., Mycologia 16(4): 175 (1924)

Figure 5.81

Index Fungorum number: IF 7289

Dearness (1924), established *Atractilina* with *A. callicarpae* as the type species (Deighton & Pirozynski, 1972). As of Species Fungorum (2025), *Atractilina* comprises seven species. Members of *Atractilina* are predominantly hyperparasitic hyphomycetes associated with *Meliolales* and *Asterinales* (Bermúdez-Cova et al., 2024). These species have been documented in Benin, Cuba, India, Uganda, the USA and Vietnam (Bermúdez-Cova et al., 2024; Index Fungorum, 2025).

Atractilina parasitica is characterized by true synnemata, denticulate conidiogenous loci, and pale pluriseptate conidia (Deighton & Pirozynski, 1972; Mel'nik & Braun, 2013; Bermúdez-Cova et al., 2024). Considering these traits, only *A. alinae*, *A. biseptata* and *A. calycini* are classified as congeneric with *A. parasitica* (Castañeda-Ruiz, 1986; Jana et al., 2006; Mel'nik & Braun, 2013). *Atractilina asterinae*, hyperparasitic on *Asterinales* is characterized by solitary conidiophores and distoseptate conidia (Deighton & Pirozynski, 1972). *Atractilina hymenaeae*, hyperparasitic on *Meliolales* is distinguished by its non-synnematous conidiophores and conidia which possess a variable number of septa (Batista & Bezerra, 1961). Therefore, *Atractilina* represents heterogeneous species. It may need to be split in the future as taxonomic concepts are further validated through morphological and molecular sequence data (Bermúdez-Cova et al., 2024). Based on molecular analysis of the nrLSU rDNA region from *Atractilina parasitica*, Bermúdez-Cova et al. (2024) confirmed it belongs to *Pleosporales, Dothideomycetes*. Bermúdez-Cova et al. (2024) also confirmed the asexual-sexual connection between *A. parasitica* and *Malacaria meliolicola*. However, in Hyde et al. (2024a) *Atractilina* is placed within the *Ascomycota* genera *incertae sedis*.

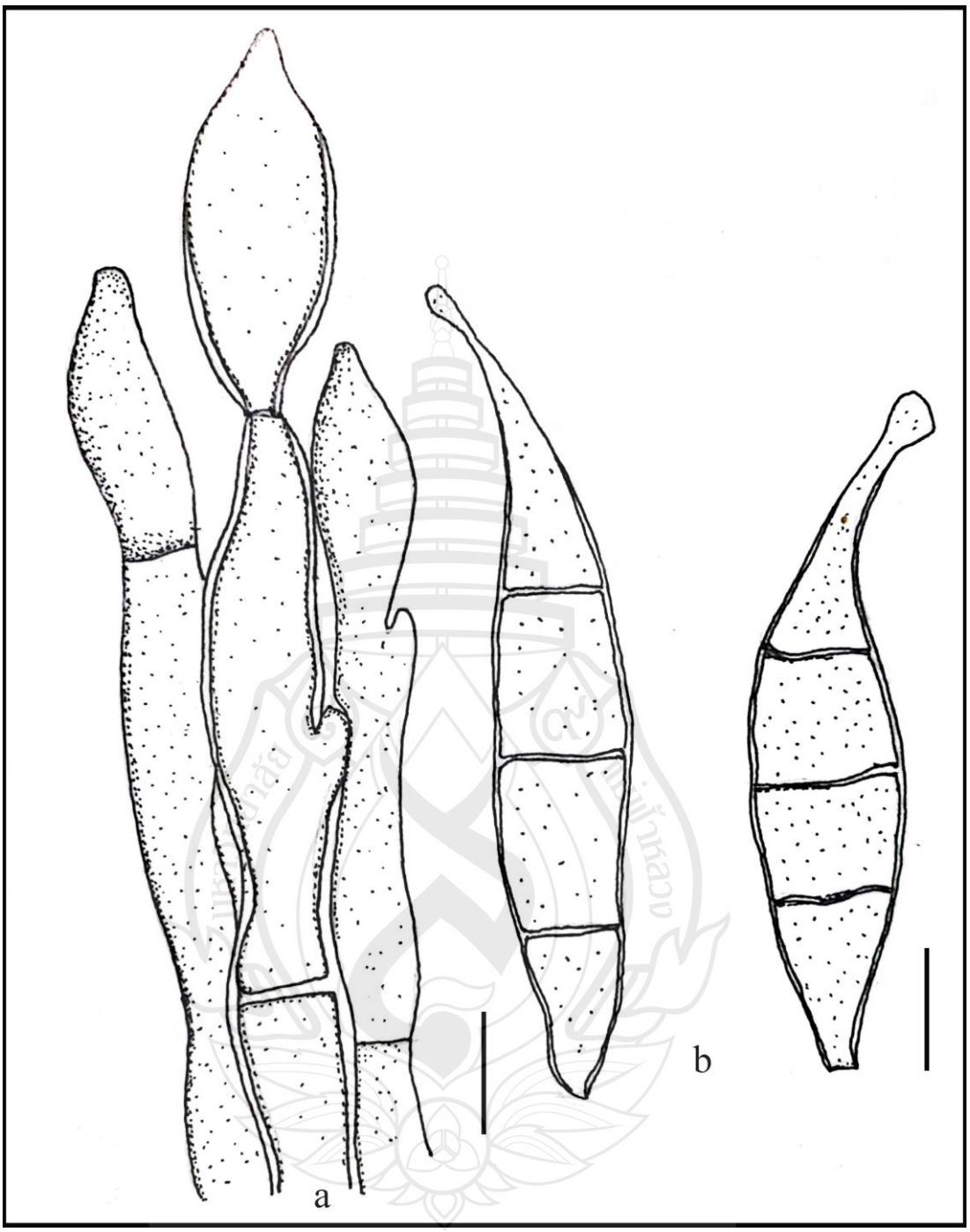


Figure 5.81 *Atractilina parasitica*

Figure 5.81, a. Conidiophores. (thickness of the wall is indicated only in the drawing in the middle). b. Conidia. Scale bars: a, b = 8 μm (Redrawn from Bermúdez-Cova et al., 2024).

Colletoconis de Hoog & Aa, Persoonia 10(1): 48 (1978)

Figure 5.82

Index Fungorum number: IF 7732

de Hoog (1978) established *Colletoconis* to include *Gloeosporium aecidiophilum*, which was reclassified as *Colletoconis aecidiophila*. *Colletoconis* remains monotypic (Species Fungorum, 2025). *Colletoconis aecidiophila* is a fungicolous species associated with rust fungi (*Puccinia* spp. (*Pucciniaceae*)) in the West Indies and India (de Hoog, 1978).

Colletoconis is characterized by conidiomata that are either flat or pulvinate, melanconiaceous, and lack setae. They are hyaline and composed of a basal prosenchyma, an intermediate parenchyma, and a hymenium formed by parallel, cylindrical conidiogenous cells. The conidiogenous cells produce conidia in basipetal succession. Conidial dimorphism is present, with one type being thin-walled, hyaline, and subcylindrical, and the other being relatively thick-walled, pale brown, and broadly ellipsoidal (adapted from de Hoog, 1978). ITS and LSU molecular data for *C. aecidiophila* are available in GenBank (2025).

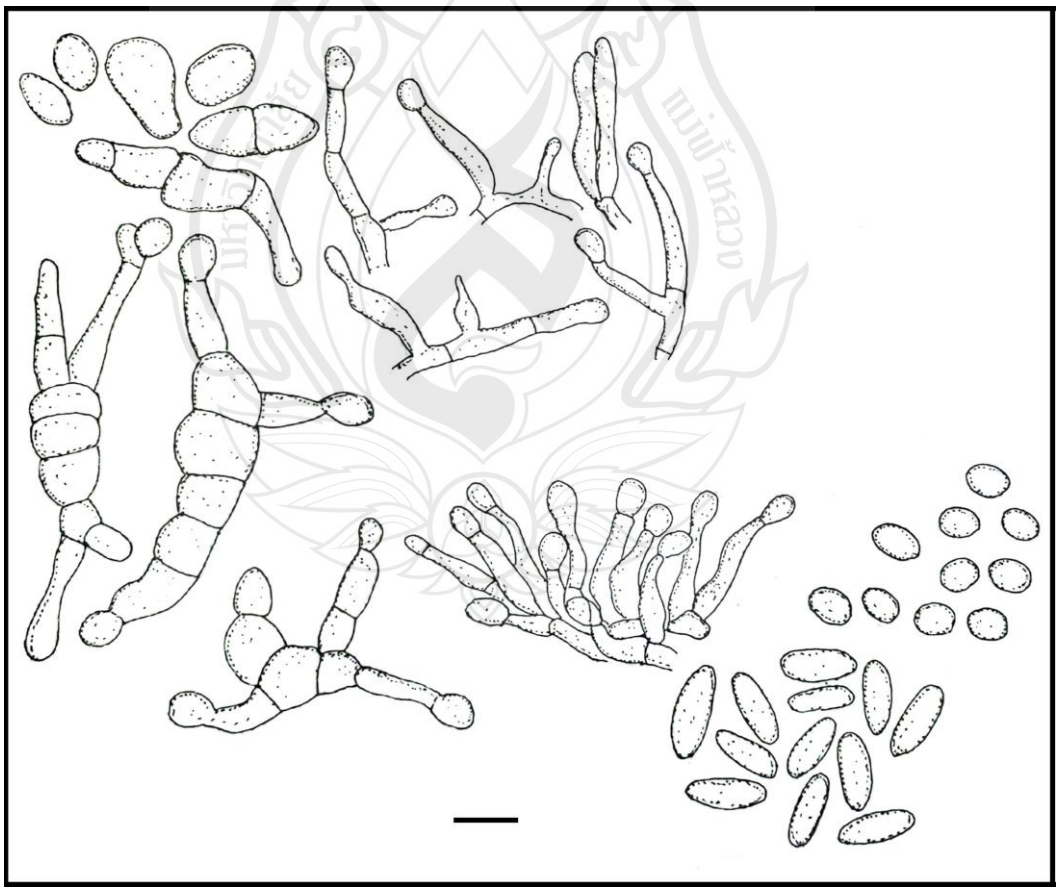


Figure 5.82 *Colletoconis aecidiophila*

Figure 5.82, Scale bar = 10 μm. (Redrawn from de Hoog 1978).

Ctenosporium R. Kirschner, Mycol. Progr. 5(3): 136 (2006)

Figure 5.83

Index Fungorum number: IF 500777

Ctenosporium was established by Kirschner and Piepenbring (2006), with *C. pectinatum* as the type species. *Ctenosporium pectinatum* was described as a fungicolous species overgrowing old conidiophores of *Dischloridium* sp. (*Australiascaceae*) and occurring on dead fern rachis in Panama (Kirschner & Piepenbring, 2006).

Ctenosporium is characterized by micronematous, hyaline conidiophores bearing monoblastic conidiogenous cells. Conidia are hyaline, solitary, and pectinate, composed of a basal, distally curved main axis with unilateral, parallel, septate branches (adapted from Kirschner & Piepenbring, 2006).

As of Species Fungorum (2025), *Ctenosporium* remains monotypic. Sequence data for the genus are currently unavailable in GenBank (2025). *Ctenosporium* is presently classified within *Ascomycota*, genera incertae sedis (Hyde et al., 2024a).

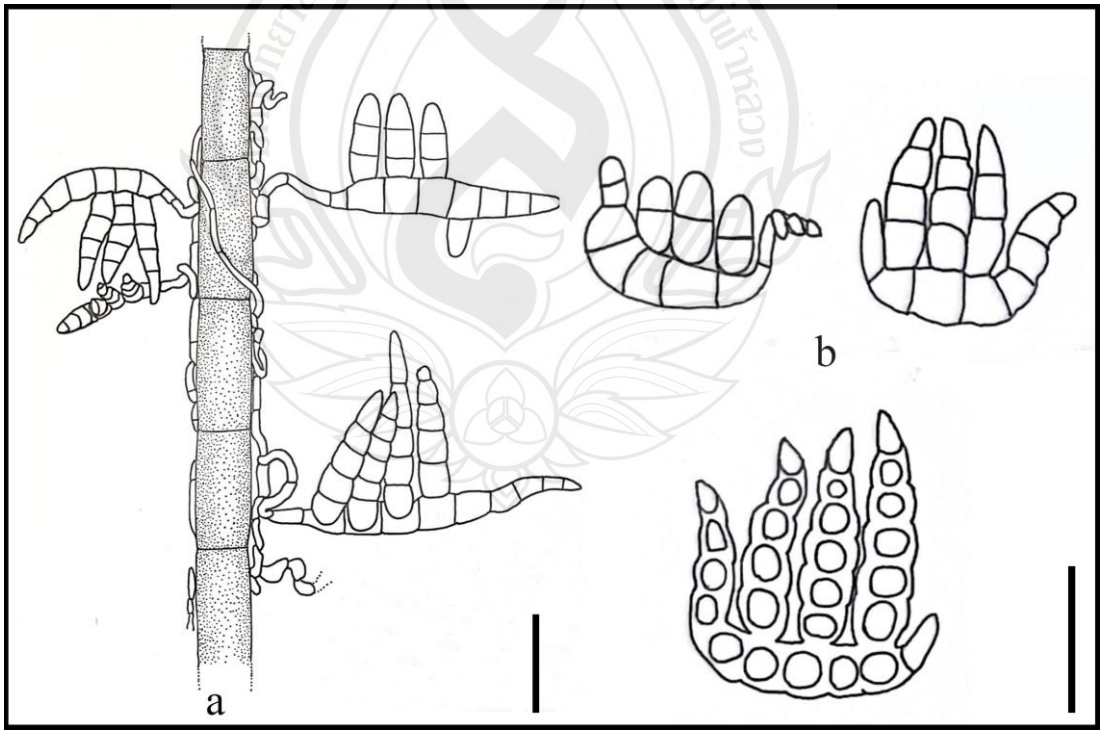


Figure 5.83 *Ctenosporium pectinatum*

Figure 5.83, a. Hyphae overgrowing an old, pigmented conidiophore of *Dischloridium* sp., conidiogenous cells and developing conidia. b. Detached conidia. Scale bars: a, b = 10 μm (Redrawn from Kirschner & Piepenbring, 2006).

Dennisographium Rifai, Kew Bull. 31(3): 726 (1977)

Figure 5.84

Index Fungorum number: IF 7955

Dennisographium was established by Rifai (1977), with *D. episphaeriae* as the type species. *Dennisographium episphaeriae* was documented as a mycoparasite on *Ustulina deusta* (*Xylariaceae*) in Java and it was also found on *Xylaria* species (Rifai, 1977). A second species, *D. ustulinae*, previously identified as *Stilbum ustulinae* was transferred to the genus by Seifert (1985). This species was described on stromata of *Ustulina vulgaris* in France (Index Fungorum, 2025).

The members of *Dennisographium* are primarily synnematous, irregularly branched, occasionally exhibiting tubercularioid forms, and composed of light brown, septate, smooth-walled, and sparsely branched hyphae. The conidiophores are formed by diverging, branched hyphae, with the terminal cells produced as conidiogenous cells or annellides. These conidiogenous cells are typically monoblastic, percurrently proliferating, and may be integrated or discrete, with shapes ranging from lageniform to narrowly ninepin. Conidia are produced acrogenously in short, loosely aggregated chains, and are hyaline, aseptate, smooth-walled, and obovoidal to ellipsoidal, usually with a truncate base (adapted from Rifai, 1977).

According to Species Fungorum (2025), the genus comprises two species. No DNA sequence data for *Dennisographium* is available in GenBank (2025). This genus is placed within the *Ascomycota* genera *incertae sedis* (Hyde et al., 2024a).

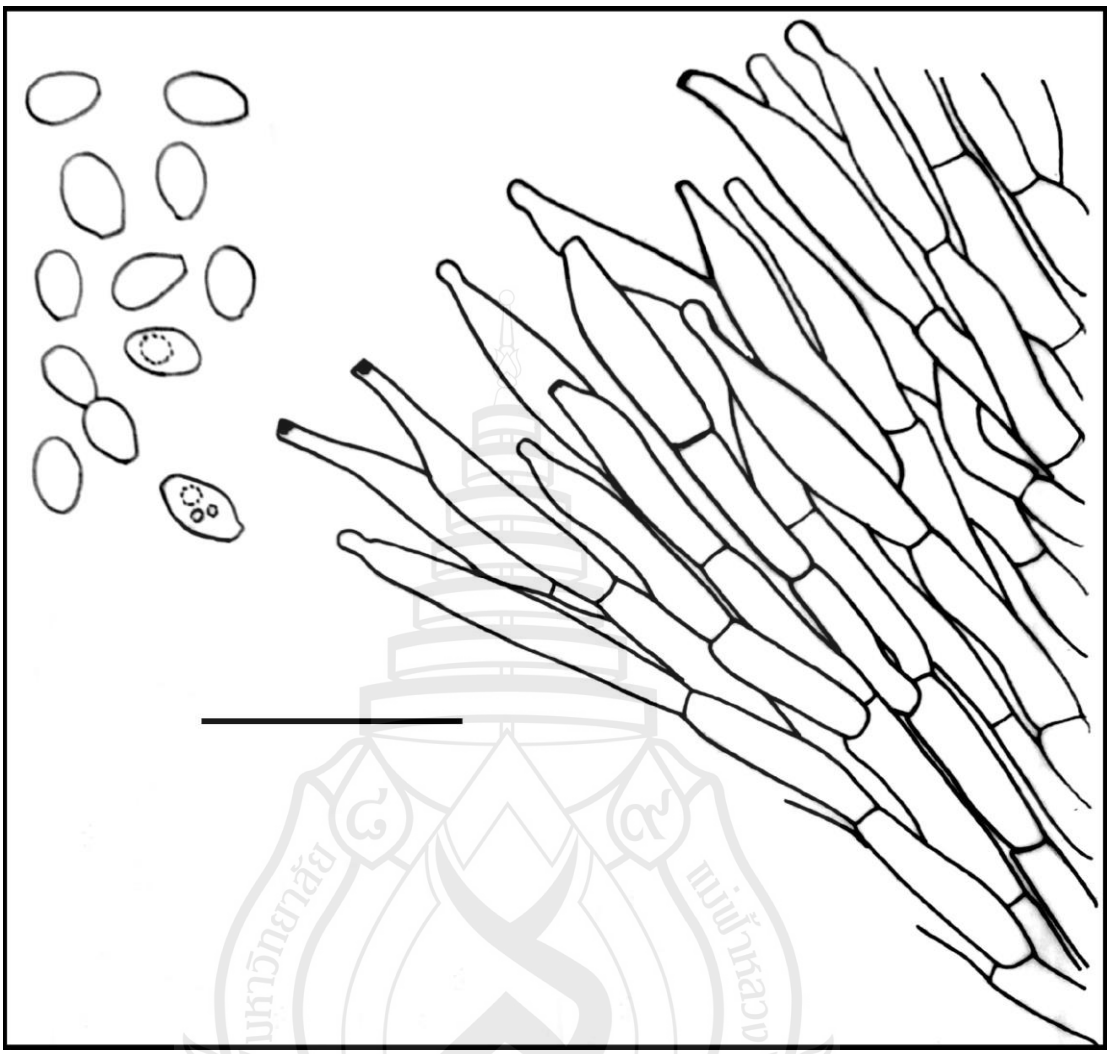


Figure 5.84 *Dennisographium episphaeriae*

Figure 5.84, Annellides and conidia. Scale bar = 10 μm. (Redrawn from Rifai, 1977).

Denticularia Deighton, Trans. Br. mycol. Soc. 59(3): 421 (1972)

Figure 5.85

Index Fungorum number: IF 7956

Facesoffungi number: FoF 08598

Denticularia was established by Deighton (1972), with *Denticularia modesta* as the type species. This species was previously referred to as *Cladosporium modestum*. There are seven species listed under this genus in Species Fungorum (2024). Among them, *D. limoniformis* is a fungicolous species on *Xylodon brevisetus* (syn. *Hyphodontia breviseta*) (*Schizoporaceae*) while the remaining species have been

associated with various plant hosts (Deighton, 1972; Videira et al., 2017; Adikaram & Yakandawala, 2020; Index Fungorum, 2025). The distribution of *Denticularia* species spans several countries, including Cuba, India, Japan, Sierra Leone, Sri Lanka, Sweden, and the USA (Deighton, 1972; Ellis, 1976; Videira et al., 2017; Adikaram & Yakandawala, 2020; Index Fungorum, 2025).

Denticularia species are characterized by an immersed mycelium, with conidiophores arising from stromata. The conidiophores are densely crowded, brown, predominantly unbranched, smooth, thin-walled, and may be continuous or occasionally septate. They exhibit sympodial growth and produce polyblastic, denticulate structures, with the denticles being short, subcylindrical, and having a truncate, unthickened apex. The conidia are pale brown, fusiform, and form in chains (catenulate). They possess unthickened hila and scars, with thin walls that are either smooth or minutely roughened and can be continuous or 1-septate (Deighton, 1972; Videira et al., 2017). No molecular data is available for *Denticularia* in GenBank (2025).

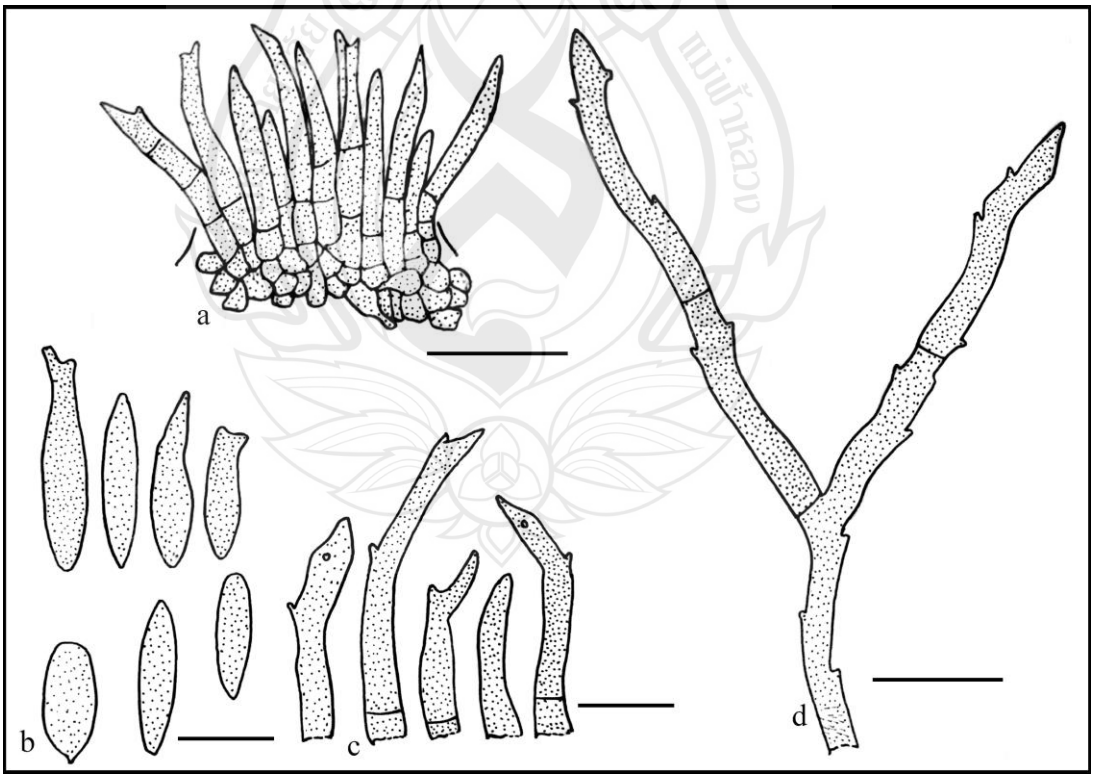


Figure 5.85 *Denticularia modesta*

Figure 5.85, a. Section through conodiophore fascicle. b. Conidia. c, d. Conidiophores. Scale bars: a, d = 20 μm, b, c = 10 μm. (Redrawn from Deighton, 1972).

Didymopsis Sacc. & Marchal, Bull. Soc. R. Bot. Belg. 24(1): 61 (1885)

Figure 5.86

Index Fungorum number: IF 8014

Didymopsis was established with the type species *D. perexigua* (Marchal, 1885). This species was discovered in Belgium as fungicolous growing on *Philocopra pleiospora* (Marchal, 1885). *Didymopsis* species are characterized by having short, slender hyaline conidiophores and oblong to clavate, hyaline, 1-septate conidia (Marchal, 1885). Four species are accepted within *Didymopsis* (Hyde et al., 2024a).

Didymopsis helvellae and *D. phyllachorae* are fungicolous on the ascomata of *Helvella* spp. (*Helvellaceae*) and on *Phyllachora* sp. (*Phyllachoraceae*) respectively (Index Fungorum, 2025). *Didymopsis locustanae* is associated with the insect *Locusta anapardalina* (Prinsloo, 1962). The distribution of these species includes Belgium, the Czech Republic, South Africa, Uganda and Ukraine (Index Fungorum, 2025; Dudka et al., 2004). There is no molecular data available for this genus in GenBank (2025).

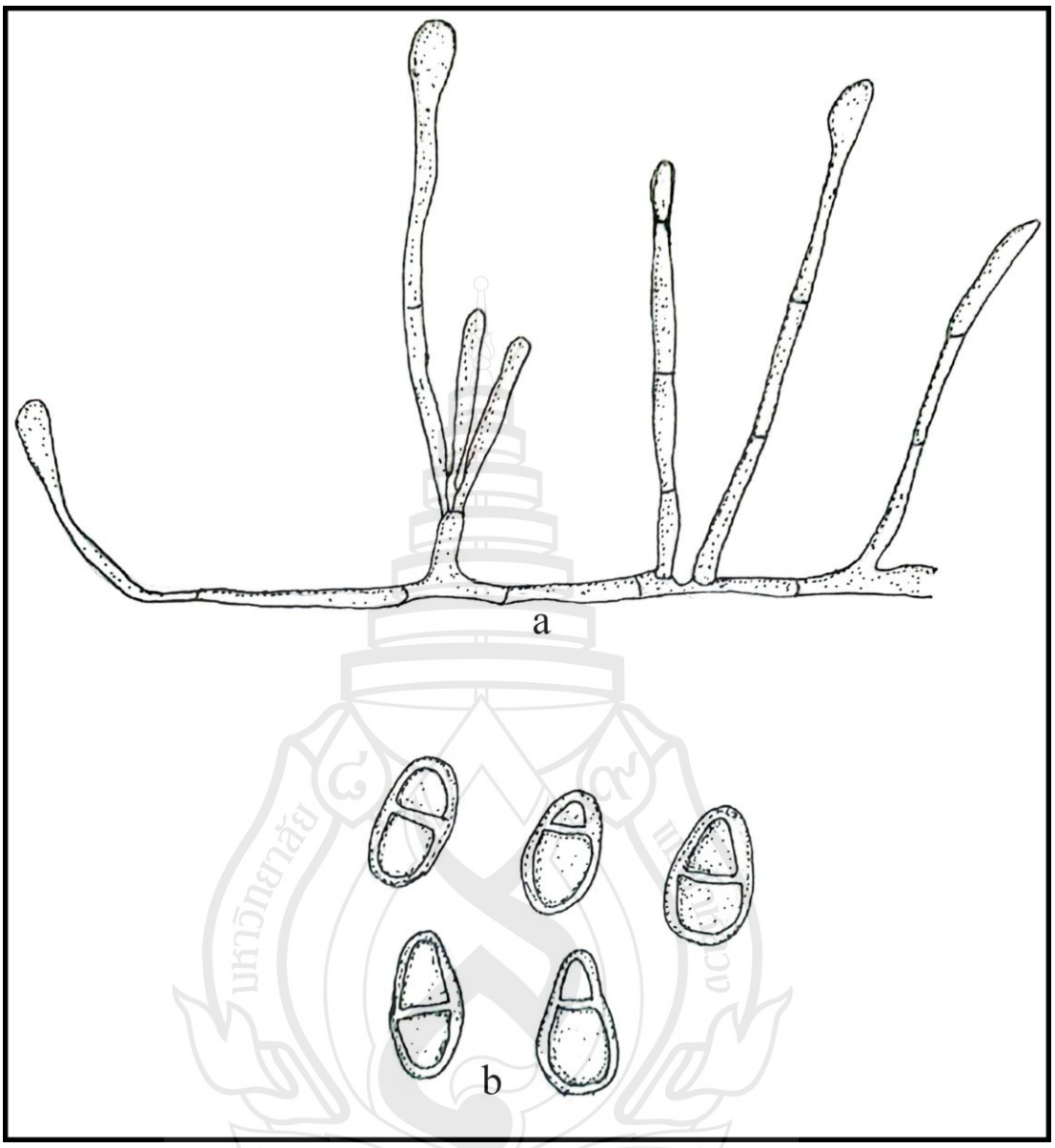


Figure 5.86 *Didymopsis locustanae*

Figure 5.86, a. Conidiophores with conidial attachments. b. Conidia. (Redrawn from Prinsloo, 1962).

Digitopodium U. Braun, Heuchert & K. Schub., Schlechtendalia 13: 65 (2005)

Figure 5.87

Index Fungorum number: IF 500749

Digitopodium was established to accommodate *D. hemileiae*, which was previously known as *Cladosporium hemileiae* (Heuchert et al., 2005). This species was discovered as a mycoparasite of the coffee leaf rust *Hemileia vastatrix*

(*Zaghouaniaceae*) in the Democratic Republic of the Congo (Colmán et al., 2021). *Digitopodium* is distinguished from *Cladosporium* by inconspicuous or slightly visible, non-coronate conidiogenous scars on the conidiogenous cells, the presence of conidiogenous cells which are not conspicuously sympodial and the presence of short, digitate or rhizoid protuberances at the base of the conidiophores (Heuchert et al., 2005). There are five *Digitopodium* species listed in Species Fungorum (2025).

Digitopodium canescens is a mycoparasite on rust colonies of *Puccinia thaliae* (Colmán et al., 2021). *Digitopodium cannae* was reclassified from *Hyalocladosporiella cannae*, described in India, where a possible but uncertain connection to *Puccinia thaliae* was noted (Crous et al., 2017). *Digitopodium tectonae* has been found parasitizing the rust fungi *Neoolivea tectonae* (syn. *Olivea tectonae*) and *Hemileia vastatrix* in Brazil and Ethiopia, respectively (Colmán et al., 2021). *Digitopodium citri*, is an endophyte from *Citrus* species in China (Liang et al., 2023). *Digitopodium* is placed in *Herpotrichiellaceae* based on molecular data (Colmán et al., 2021). There are ITS and LSU sequence data available for this genus in GenBank (2025).

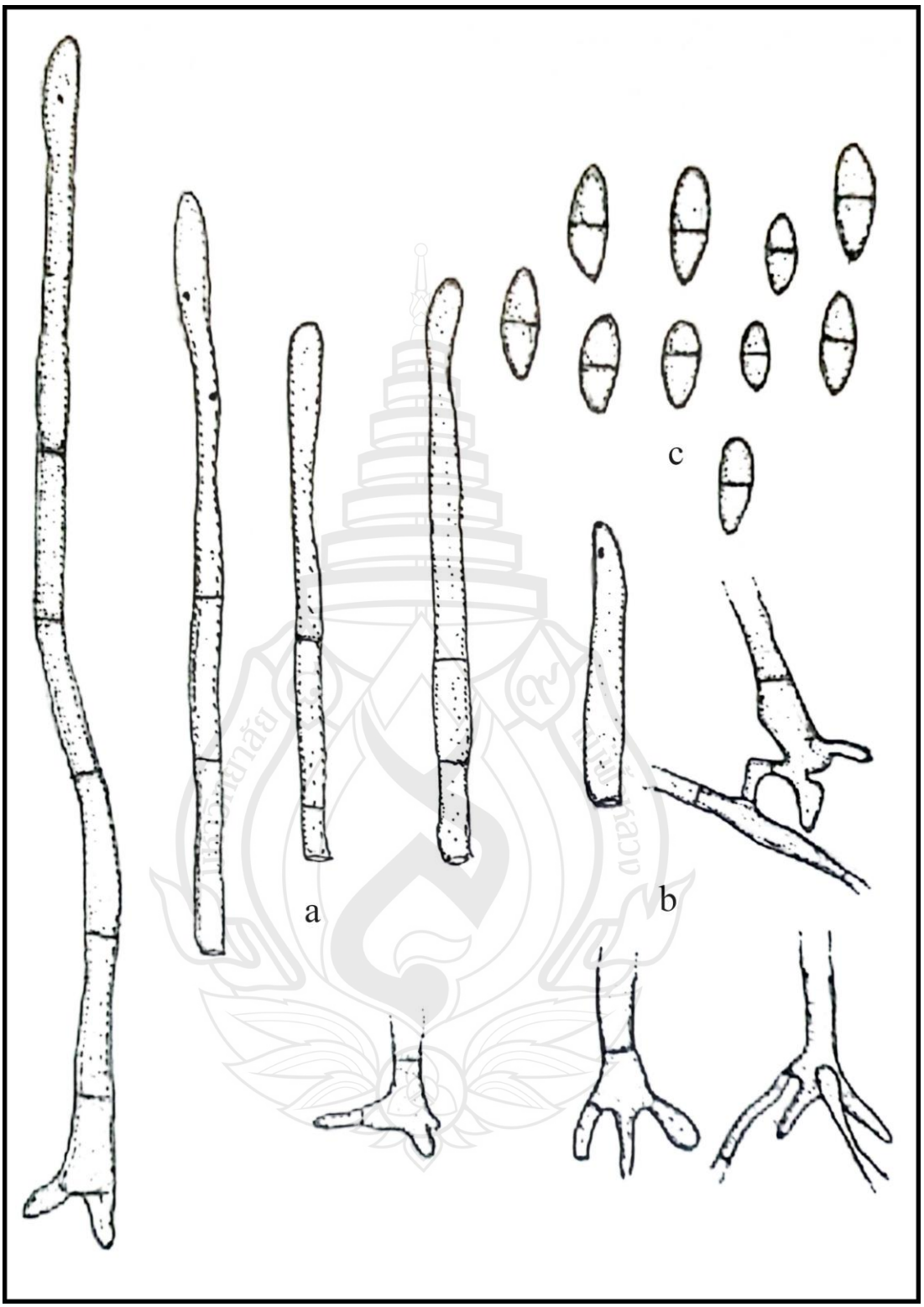


Figure 5.87 *Digitopodium hemileiae*

Figure 5.87, a. Conidiophores. b. Digitate or rhizoid protuberances. c. Conidia. (Redrawn from Heuchert et al., 2005).

Domingoella Petr. & Cif., Annls mycol. 30(3/4): 339 (1932)

Figure 5.88

Index Fungorum number: IF 8092

Petrak and Ciferri (1932) established *Domingoella* with *D. asterinarum* as the type species. *Domingoella asterinarum* is a fungicolous on *Asternilaes* hosts such as *Asterina* spp., *Asterolibertia* spp., *Hysterostomella* spp., and *Diedickea* spp. in tropical and subtropical countries (Petrak & Ciferri, 1932; Deighton & Pirozynski, 1972). There are four *Domingoella* species listed under this genus in Species Fungorum (2025). *Domingoella pycnopeltarum* is fungicolous on *Pycnopeltis conspicua* (*Elsinoaceae*) in Brazil (Sun et al., 2019a; Index Fungorum, 2025). *Domingoella arctostaphyli* and *D. caesalpiniae* are associated with plant hosts (Kirk, 1986; Index Fungorum, 2025). The distribution of *Domingoella* species extends across Brazil, the Dominican Republic, Ghana, India, Indonesia, Nigeria, Tanzania, Uganda, South Africa, Sierra Leone, Solomon Islands and the UK (Petrak & Ciferri, 1932; Deighton & Pirozynski, 1972; Index Fungorum, 2025).

The asexual morph of *Domingoella* species is hyphomycetous. They are characterized by superficial, pale brown to dark brown, thin-walled, septate hyphae. Conidiophores arise as lateral patent branches from the mycelial hyphae. The conidia are borne singly and terminally on the conidiophores. They are subglobose to globose and pale to dark brown (Petrak & Ciferri, 1932; Deighton & Pirozynski, 1972). There is no molecular data available for this genus in GenBank (2025).

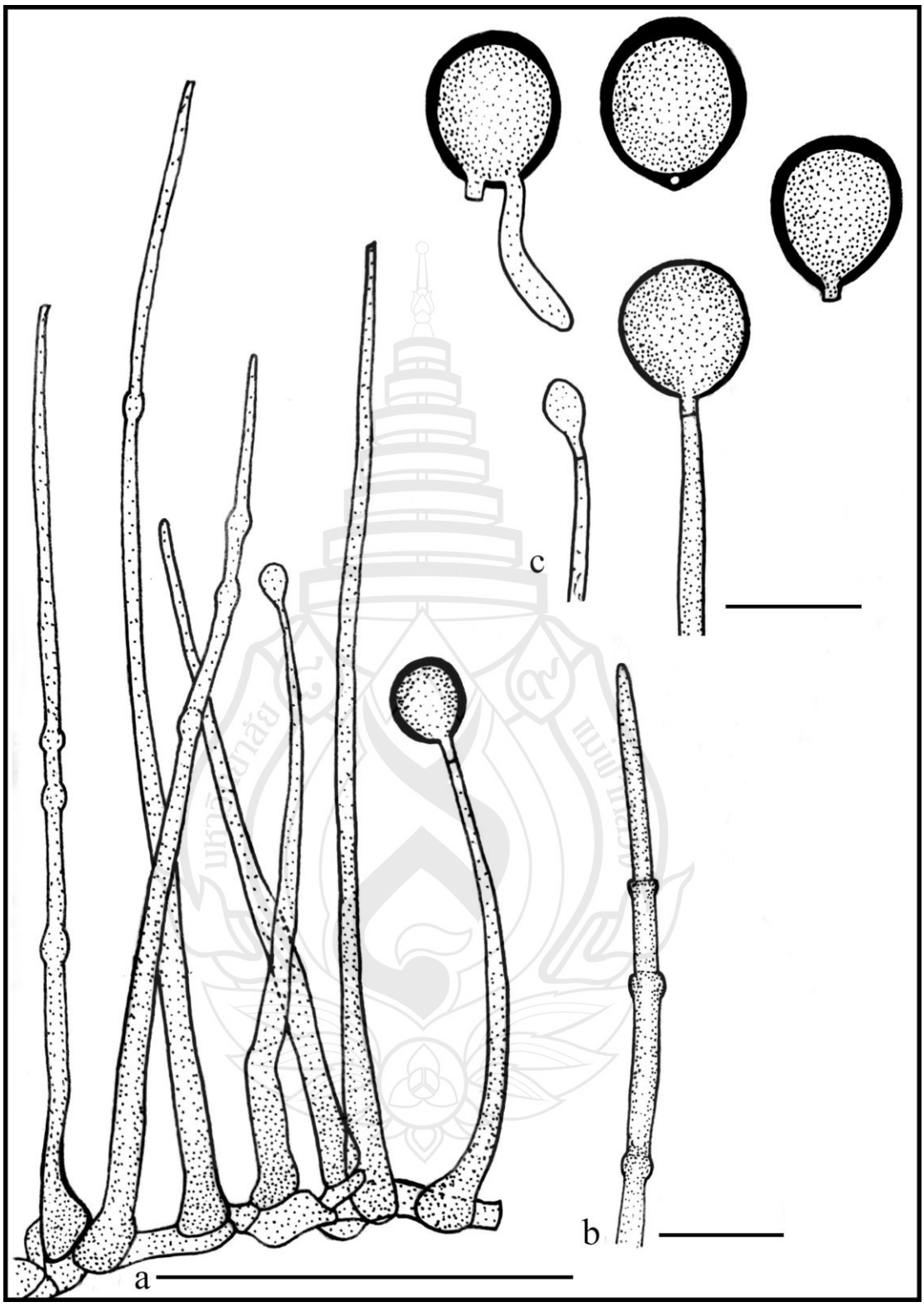


Figure 5.88 *Domingoella asterinarum*

Figure 5.88, a, b. Conidiophores. c. Conidial attachments and conidia. Scale bars: a = 50 μm, b, c = 10 μm. (Redrawn from Deighton & Pirozynski, 1972).

Engelhardtiella A. Funk, Canad. J. Bot. 51(9): 1643 (1973)

Figure 5.89

Index Fungorum number: IF 8177

Engelhardtiella was introduced by Funk (1973), with *E. alba* as the type species. This species is hyperparasite on the pycnidia of *Cytospora pinastri* (syn. *Cytospora abietis*) (*Cytosporaceae*) in Canada and was also recorded on *Pestalotia funerea* (*Pestalotiopsidaceae*) (Funk, 1973).

Engelhardtiella is distinguished by its white, compact, and irregular sporodochia. The mycelium is hyaline, septate, and sparsely branched. Setae are erect, septate, unbranched or occasionally branched at the base, and tapered at the apex. Conidiophores are hyaline, erect, septate, and mostly unbranched, terminating in a bulbous apex. Blastoconidia are hyaline, four-celled, comprising a basal and central cell along with two superior lateral, bicorniform cells. These conidia are typically botryose on the swollen apices of the conidiophores, but may also be pleurogenous (adapted from Funk, 1973).

As of Species Fungorum (2025), *Engelhardtiella* remains monotypic. No DNA sequence data are available for this genus in GenBank (2025). Taxonomically, it is classified within *Ascomycota*, genera *incertae sedis* (Hyde et al., 2024a).

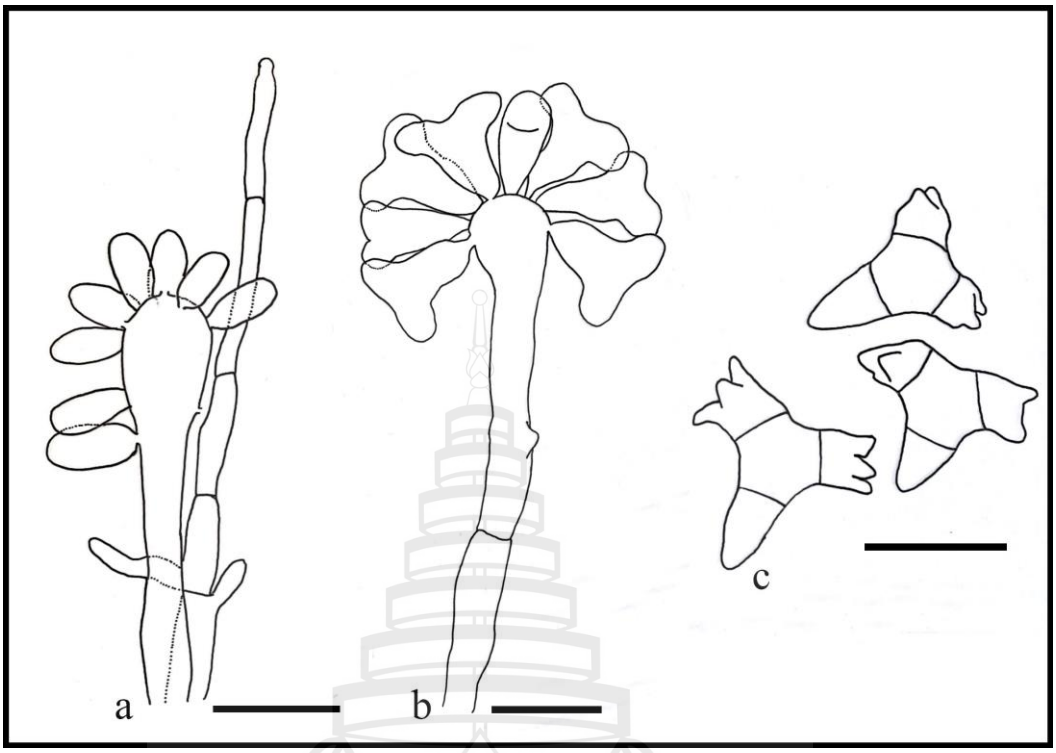


Figure 5.89 *Engelhardtiella alba*

Figure 5.89, a. Conidiophore with immature conidia and seta. b. Conidiophore with semi-mature conidia. c. Mature conidia. Scale bars: a–c = 35 μm. (Redrawn from Funk, 1973).

Entropezites Poinar & R. Buckley, Mycol. Res. 111(4): 504 (2007)

Index Fungorum number: IF 501250

Entropezites was established by Poinar and Buckley (2007), with *E. patricii* as the type species. This species was described as a hyperparasite colonizing the hyphae of *Mycetophagites atrebora* (fossil *Basidiomycota*) in Myanmar (Poinar & Buckley, 2007).

Entropezites is characterized by delicate, hyaline, aseptate, and branched vegetative hyphae that penetrate and grow internally within the host hyphae. The conidiophores are short, simple, erect, and hyaline, bearing conidia in basipetal chains. Conidia are minute, single-celled, hyaline, and spherical to cylindrical. Additionally, zygospore-like structures are produced (adapted from Poinar & Buckley, 2007).

According to Species Fungorum (2025), *Entropezites* remains monotypic. No molecular sequence data for *Entropezites* are available in GenBank (2025). Taxonomically, it is placed within *Ascomycota*, genera *incertae sedis* (Hyde et al., 2024a).

Eriocercospora Deighton, Mycol. Pap. 118: 5 (1969)

Figure 5.90

Index Fungorum number: IF 8200

Facesoffungi number: FoF 08605

Deighton (1969) established *Eriocercospora* to include *E. balladynae*, which was previously classified as *Helminthosporium balladynae*. Species within *Eriocercospora* are fungicolous, hyperparasitic dematiaceous hyphomycetes (Braun et al., 2013; Pem et al., 2024). There are only three species of *Eriocercospora* listed in Species Fungorum (2024). *Eriocercospora balladynae* was found on *Balladyna* sp. (*Balladynaceae*) and *Asterina* sp. (*Asterinaceae*), while *E. olivacea* was reported on *Meliolina mollis* (*Meliolinaceae*) (Sun et al., 2019a; Index Fungorum, 2025). *Eriocercospora palustris* has been reported on dead leaves of *Chrysobalanus icaco*. These species have been recorded in Brazil, Cuba, India, Papua New Guinea, and Uganda (Pem et al., 2024; Index Fungorum, 2025).

The sexual morph of *Eriocercospora* has not yet been documented (Pem et al., 2024). The asexual morph is distinguished by macronematous, mononematous, and solitary conidiophores. They emerge laterally from superficial hyphae. These conidiophores are erect, generally unbranched, septate or aseptate, and pigmented. The conidiogenous cells are integrated, either terminal or intercalary, and proliferate sympodially, though they typically do not exhibit a distinctly geniculate appearance. The conidiogenous loci are subtle, unthickened, and either non-protuberant or only slightly so, with minimal or no darkened-refractive features. Conidia are solitary, scolecosporous, transversely euseptate, pigmented, thin-walled, and smooth or nearly smooth. The hila remain unthickened and show little to no darkened-refractive characteristics (Braun et al., 2013; Pem et al., 2024).

No molecular data is available for *Eriocercospora* (GenBank, 2025). It has been suggested that *Eriocercospora* is potentially synonymous with *Pseudocercospora* (Braun et al., 2013). However, definitive confirmation requires

molecular DNA sequence analysis, and until such evidence is available, a conclusive decision remains pending (Braun et al., 2013; Pem et al., 2024). *Eriocercospora* is classified within *Ascomycota* genera *incertae sedis* (Hyde et al., 2024a).

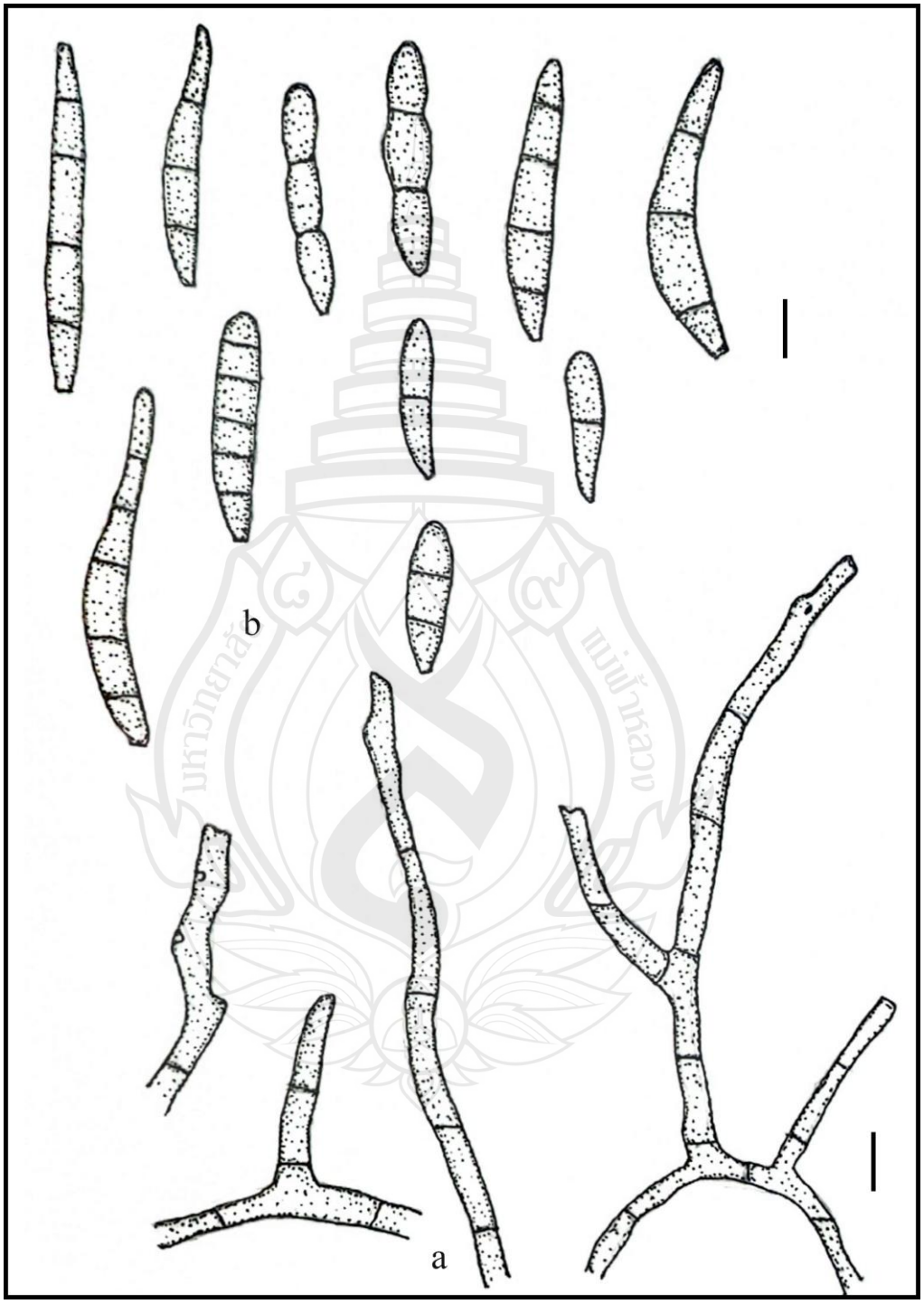


Figure 5.90 *Eriocercospora balladynae*

Figure 5.90, a. Conidia. b. Conidiophores. Scale bars: a, b = 10 μm. (Redrawn from Braun et al., 2013).

Gonatobotryum Sacc., Michelia 2(no. 6): 24 (1880)

Figure 5.91

Index Fungorum number: IF 8375

Gonatobotryum was established by Saccardo with *G. fuscum* as the type species (Gao et al., 2020). Walker and Minter (1981) conducted a morphological review of the genus, which led to the exclusion of five species. As of Species Fungorum (2025), 11 species are listed within *Gonatobotryum.*

Gonatobotryum is characterized by hyaline to dark brown, septate, mycelium. The conidiophores are hyaline to dark brown, mononematous, macronematous, erect, unbranched or occasionally branched and septate. The conidiogenous cells are terminal, often becoming intercalary due to continuous or percurrent proliferation or by percurrent regeneration. These cells are integrated, hyaline to dark brown, smooth or roughened, and thin-walled, and globose, and produce conidia from up to 100 loci. The conidia are hyaline to pale brown, mostly aseptate but occasionally with a single septum, and are smooth or roughened, forming simple chains of 2–3 conidia or branched chains of up to 8 conidia. Conidial development is holoblastic and polyblastic, with proximal conidia forming synchronously. Conidial secession occurs via separating cells, and in at least one species, it is rhexolytic, leaving conspicuous, unblackened or blackened denticles on both conidia and conidiogenous cells (Walker & Minter, 1981).

Gonatobotryum species are distributed across Austria, China, India, Italy, Ukraine, the UK and the USA. These have been identified on plant substrates, where they function as endophytes, pathogens, saprobes, or mycoparasites (Walker & Minter, 1981; Jacob & Bhat, 2000; Akulov, 2011b; Gao et al., 2020). *Gonatobotryum fuscum* (found on hosts such as *Ceratocystis* sp. (*Ceratocystidaceae*), *Chalaropsis* sp. (*Ceratocystidaceae*), *Graphium* sp. (*Graphiaceae*), and *Leptographium* sp. (*Ophiostomataceae*)) and *G. parasiticum* (found on decaying *Hypocrea* sp. (*Hypocreaceae*), *Ganoderma* sp. (*Polyporaceae*), *Hypomyces* sp. (*Hypocreaceae*), *Polyporus* sp. (*Polyporaceae*), *Tremella* sp. (*Tremellaceae*), and *Trichoderma* sp.

(*Hypocreaceae*)) are recognized as fungicolous (Walker & Minter, 1981; Akulov, 2011b).

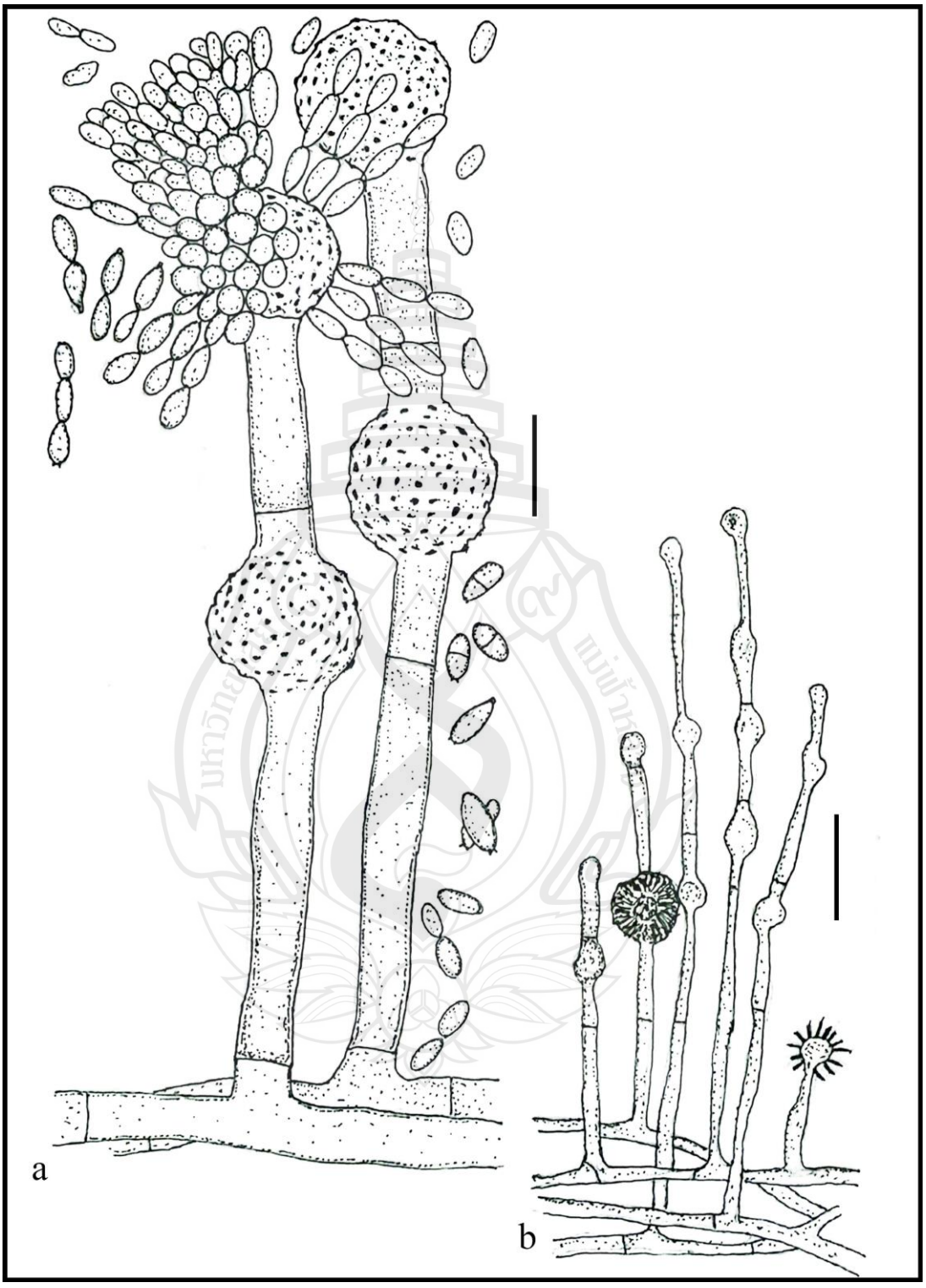


Figure 5.91 *Gonatobotryum parasiticum*

Figure 5.91, a, b. Conidiophores, conidiogenous cells and conidia. Scale bars: a = 20 μm, b = 150 μm. (Redrawn from Walker & Minter, 1981).

Hoornsmania Crous, Fungal Planet, A Global Initiative to Promote the Study of Fungal Biodiversity 11-21: 11: [2] (2007)

Figure 5.92

Index Fungorum number: IF 501110

Facesoffungi number: FoF 06632

Crous (2007) introduced *Hoornsmania*, designating *H. pyrina* as its type species. *Hoornsmania pyrina* was described as a hyperparasite on the perithecia of *Neonectria ditissima* (*Nectriaceae*) in the Netherlands (Crous, 2007). Attempts to culture this species on various nutrient media under different incubation conditions and temperatures were unsuccessful (Crous, 2007).

The asexual morph of *H. pyrina* is hyphomycetous and characterized by solitary, brown, septate conidiophores that emerge from superficial hyphae. Its conidiogenous cells are brown, smooth to finely verruculose, and are elongate-ellipsoid to fusoid with one to two truncate loci that are somewhat thickened and darkened, though not highly refractive. The conidia are brown, smooth to finely verruculose, broadly ellipsoidal to slightly fusoidal, and occur in branched, acropetal chains, with scars that are somewhat darkened and thickened but lack strong refractiveness (adapted from Crous, 2007). To date, the sexual morph of this species has not been observed. Morphologically, *Hoornsmania* shares similarities with *Hormoconis* (Crous, 2007).

Since its establishment, *Hoornsmania* has remained monotypic (Species Fungorum, 2025). Efforts to amplify DNA directly from the spore masses of *H. pyrina* have been unsuccessful (Crous, 2007). As a result, no sequence data for this genus is currently available in GenBank (2025). *Hoornsmania* is presently classified within *Ascomycota* under *incertae sedis* (Hyde et al., 2024a).

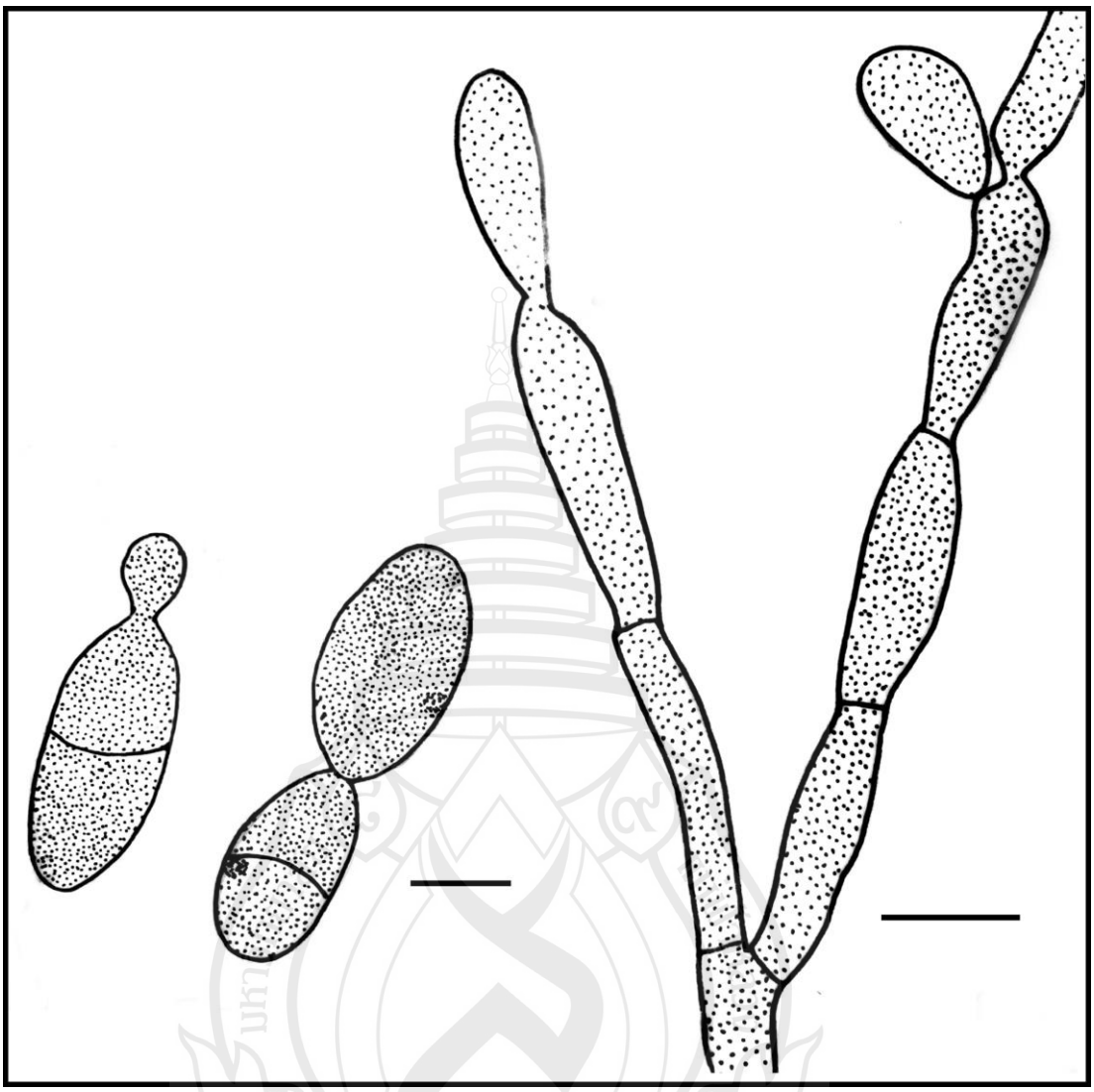


Figure 5.92 *Hoornsmania pyrina*

Figure 5.92, Conidiophores and developing conidial chains. Scale bars = 10 μm (Redrawn from Crous, 2007).

Irpicomyces Deighton, Mycol. Pap. 118: 24 (1969)

Figure 5.93

Index Fungorum number: IF 8635

Irpicomyces was established by Deighton (1969), with *I. schiffnerulae* as the type species. This species was described as a hyperparasite on *Schiffnerula solani* (*Englerulaceae*), which was growing on leaves of *Solanum melongena* (Deighton, 1969). Another species, *I. cornicola*, isolated from stems of *Cornus florida* in Japan, was added to the genus (Watanabe & Narita, 1994).

Irpicomyces is characterized by pale brown, septate, and branched hyphae. Conidiophores arise laterally from selected hyphal cells, with one or several conidiophores per cell. They are cylindrical, short, narrow, concolorous, continuous, thin-walled, and each terminates in a single conidium. Conidial scars are truncated and lack thickening. Conidia are concolorous, obclavate to filiform, smooth-walled, and indistinctly pluriseptate, with a truncate and unthickened hilum (adapted from Deighton, 1969).

As of Species Fungorum (2025), *Irpicomyces* comprises two accepted species. Molecular data are limited, with ITS sequence data available only for *I. cornicola* in GenBank (2025). The genus is classified within *Ascomycota*, genera *incertae sedis* (Hyde et al., 2024a).

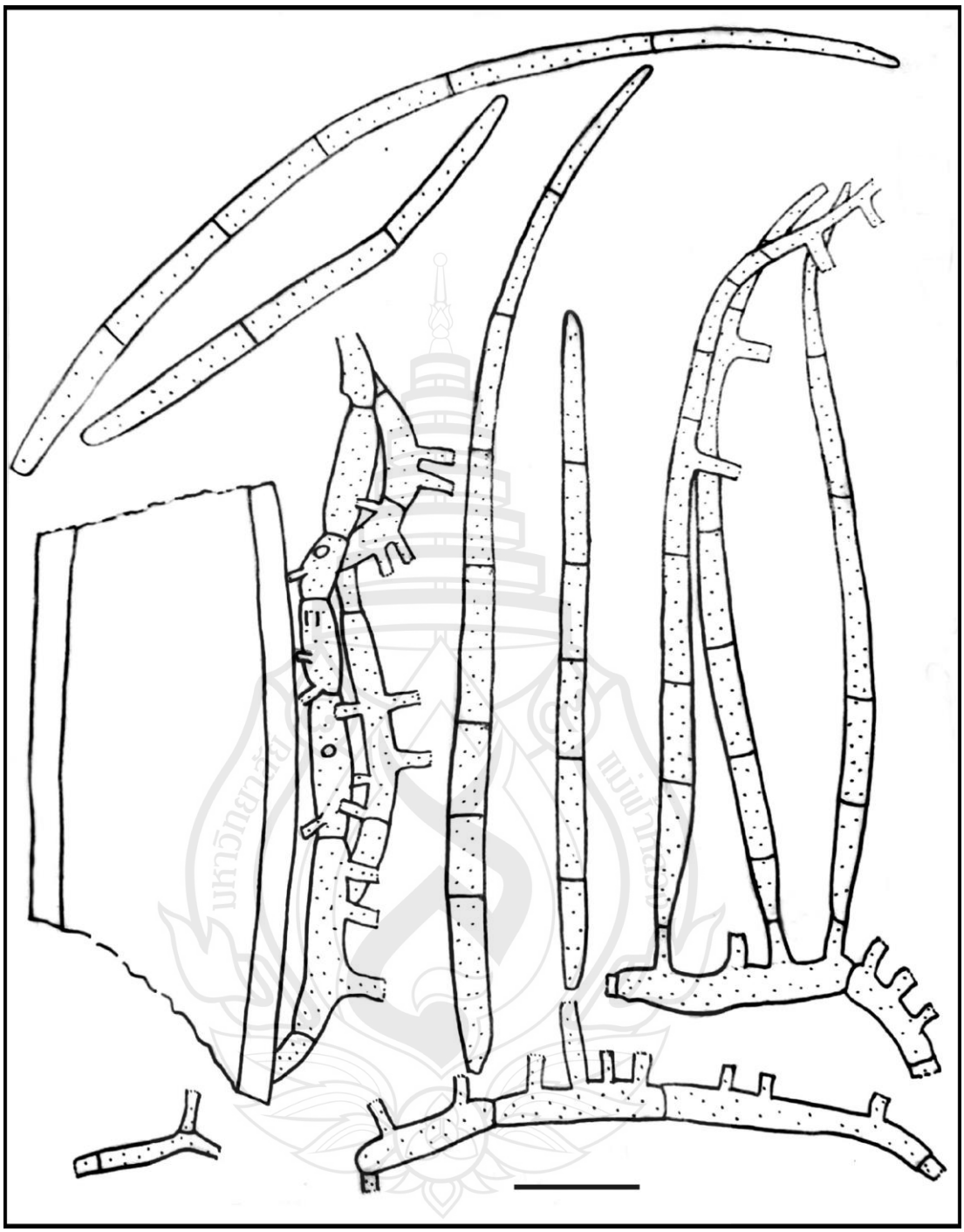


Figure 5.93 *Irpicomyces schiffnerulae*

Figure 5.93, Repent hyphae bearing conidiophores, conidial attachments and conidia. Scale bar = 10 μm. (Redrawn from Deighton, 1969).

Laterispora Uecker, W.A. Ayers & P.B. Adams, Mycotaxon 14(2): 492 (1982)

Figure 5.94

Index Fungorum number: IF 8717

Uecker et al. (1982) established *Laterispora*, designating *L. brevirama* as the type species. *Laterispora brevirama* was discovered as a fungicolous, dematiaceous hyphomycete on the sclerotia of *Sclerotinia minor* (*Sclerotiniaceae*) in the USA. *Laterispora* is characterized by discrete, determinate, stable conidiogenous cells with a terminal appendage and a single fixed conidiogenous locus. The conidia are erect, dematiaceous, phragmoseptate, holoblastic, and are produced laterally from the conidiogenous cell (adapted from Uecker et al., 1982). Since its establishment, *Laterispora* has remained monotypic (Species Fungorum, 2025). No molecular data is available for *Laterispora* in GenBank (2025).

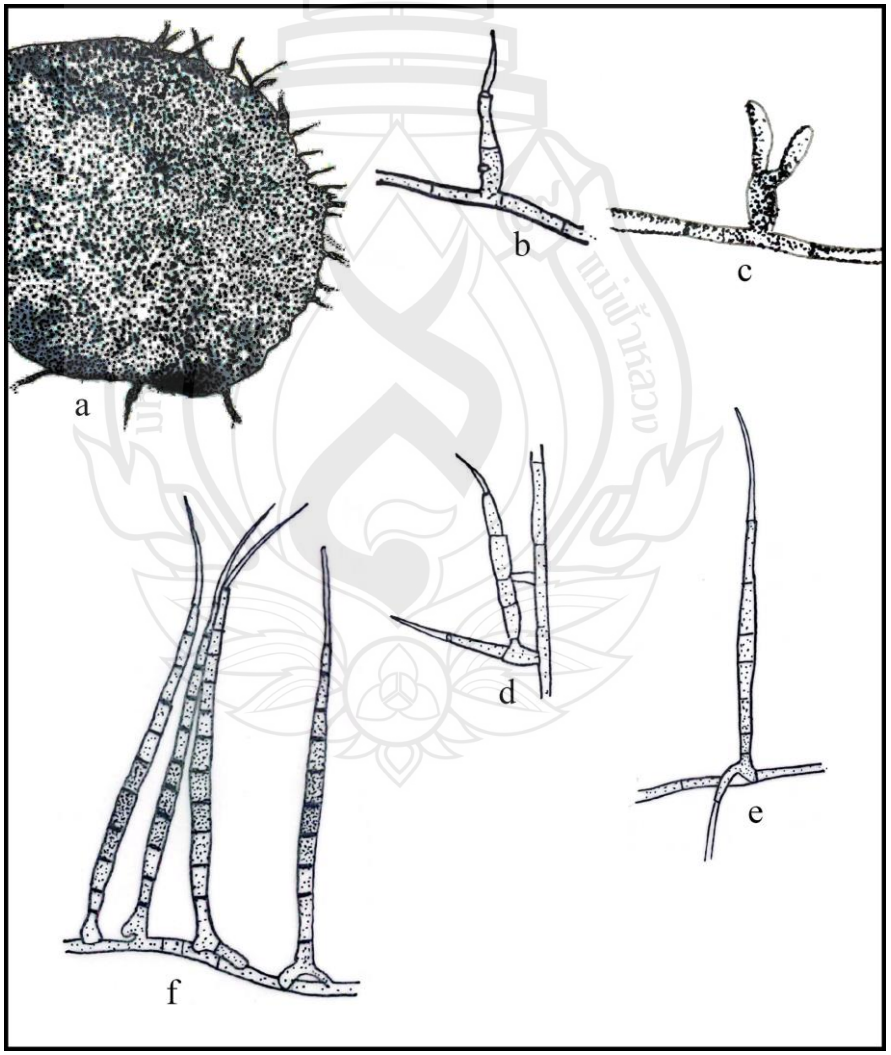


Figure 5.94 *Laterispora brevirama*

Figure 5.94, a. Conidia on sclerotium of *Sclerotinia sclerotiorum*. b. Conidiogenous cell with a short lateral conidiogenous locus. c. Young conidium initially delimited by a septum. d. Three-septate conidium at the initial stage. e. Mature conidium with terminal a hyaline appendage. f. Mature conidia. (Adapted from Uecker et al., 1982).

Paraphaeoisaria de Hoog & Morgan-Jones, Mycotaxon 7(1): 133 (1978)

Figure 5.95

Index Fungorum number: IF 9217

Paraphaeoisaria was established by de Hoog and Morgan-Jones (1978), with *P. alabamensis* as the type species. This species was isolated as fungicolous from aecial galls of *Cronartium quercuum* (*Cronartiaceae*) in Alabama, USA (de Hoog & Morgan-Jones, 1978).

Paraphaeoisaria is characterized by profusely branched, submerged hyphae that are smooth, olivaceous, and become thick-walled upon maturation. In contrast, the aerial hyphae are fasciculate and have roughened walls due to encrusted pigmentation. Conidiogenous cells are intercalary and arise from undifferentiated hyphae, each bearing one or more conidiiferous pegs, which may branch subtly in an inconspicuously sympodial manner. Conidia are hyaline, smooth, thin-walled, and are short cylindrical to fusiform (adapted from de Hoog & Morgan-Jones, 1978).

According to Species Fungorum (2025), *Paraphaeoisaria* remains monotypic. Sequence data for the ITS and LSU loci are available for *P. alabamensis* in GenBank (2025). It is currently placed within *Ascomycota* genera *incertae sedis* (Hyde et al., 2024a).

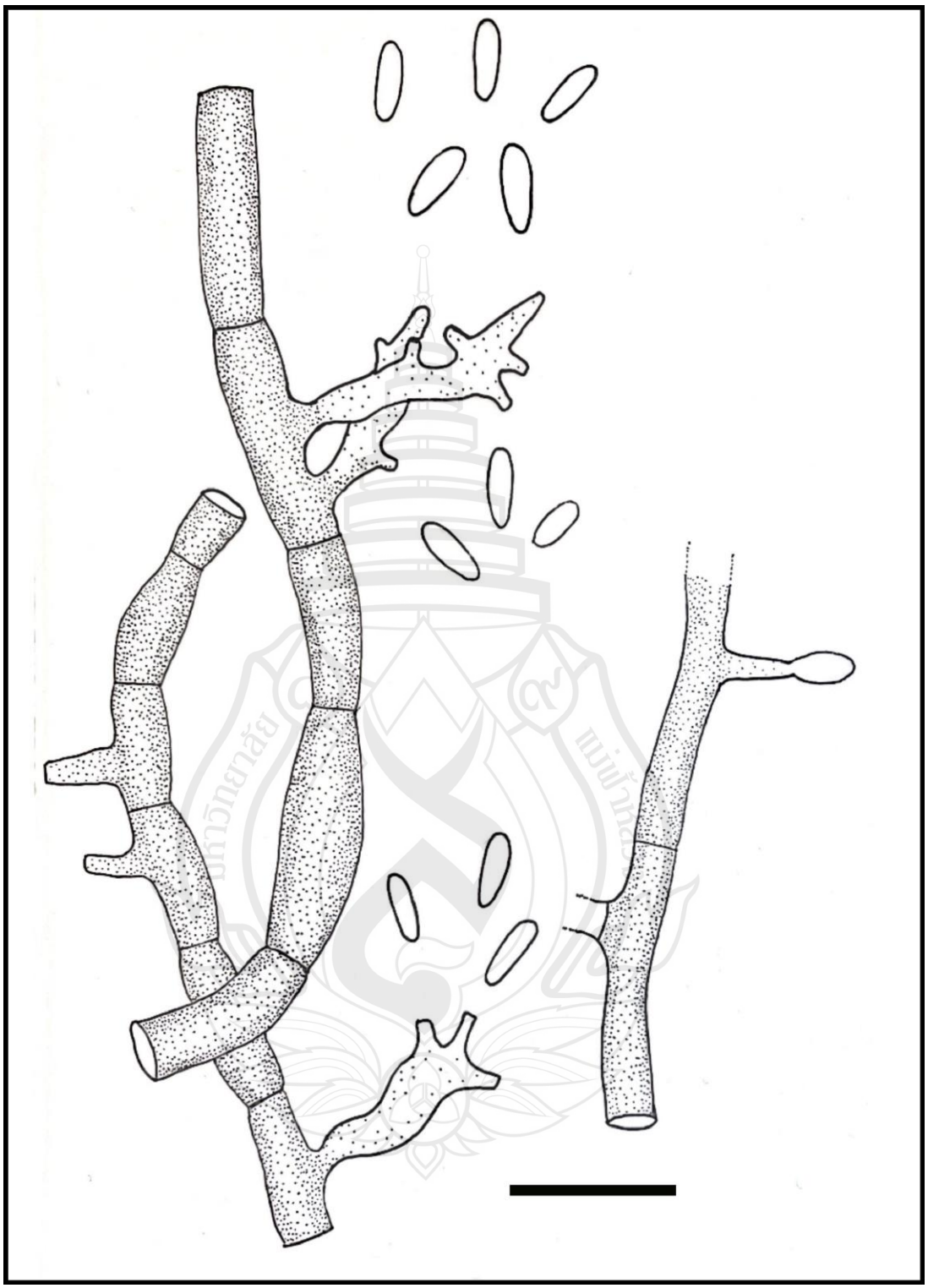


Figure 5.95 *Paraphaeoisaria alabamensis*

Figure 5.95, Conidiogenous cells, conidial attachments and conidia. Scale bar = 10 μm. (Redrawn from de Hoog & Morgan-Jones, 1978).

Redbia Deighton & Piroz., Mycol. Pap. 128: 83 (1972)

Figure 5.96

Index Fungorum number: IF 9700

Redbia was established by Deighton and Pirozynski (1972), with *R. pucciniicola* as the type species. *Redbia pucciniicola* was identified as fungicolous associated with *Puccinia holosericea* (*Pucciniaceae*) in Tanzania (Deighton & Pirozynski, 1972). Since its establishment, four additional species have been added to the genus: *R. elegans*, *R. inflata*, *R. laxa*, and *R. trichomambusta* (Index Fungorum, 2025).

Redbia elegans was described from fallen leaves of *Persea borbonia* in South Carolina, USA (Pirozynski & Hodges, 1973), while *R. inflata* was discovered on decaying leaves of a *Lauraceae* species in Veracruz, Mexico (Castañeda-Ruíz et al., 2013). *Redbia laxa* was identified on fallen leaves of *Dendropanax arboreus* in Cuba (Index Fungorum, 2025), and *R. trichomambusta* was recorded on leaves of *Chromolaena odorata* in Brazil (Barreto & Evans, 1994).

Redbia is characterized by macronematous, mononematous conidiophores that arise as lateral branches from the vegetative hyphae. These conidiophores are erect, smooth, thin-walled, septate, and typically branched. They exhibit a dark olivaceous brown coloration at the base, becoming progressively paler towards the apex, which is often nearly hyaline. The conidiophores taper towards the apex and usually terminate with denticulate, polyblastic conidiogenous cells. Denticles are minute, truncate, and lack apical thickening. Conidia are holoblastic, hyaline, smooth-walled, and thin, ranging from narrowly ellipsoid to fusiform or subclavate. They are aseptate to three-septate (Deighton & Pirozynski, 1972; Pirozynski & Hodges, 1973; Barreto & Evans, 1994; Castañeda-Ruíz et al., 2013).

According to Species Fungorum (2025), five species are currently accepted within *Redbia*. To date, no DNA sequence data are available for this genus in GenBank (2025). It is currently placed within the *Ascomycota* genera *incertae sedis* (Hyde et al., 2024a).

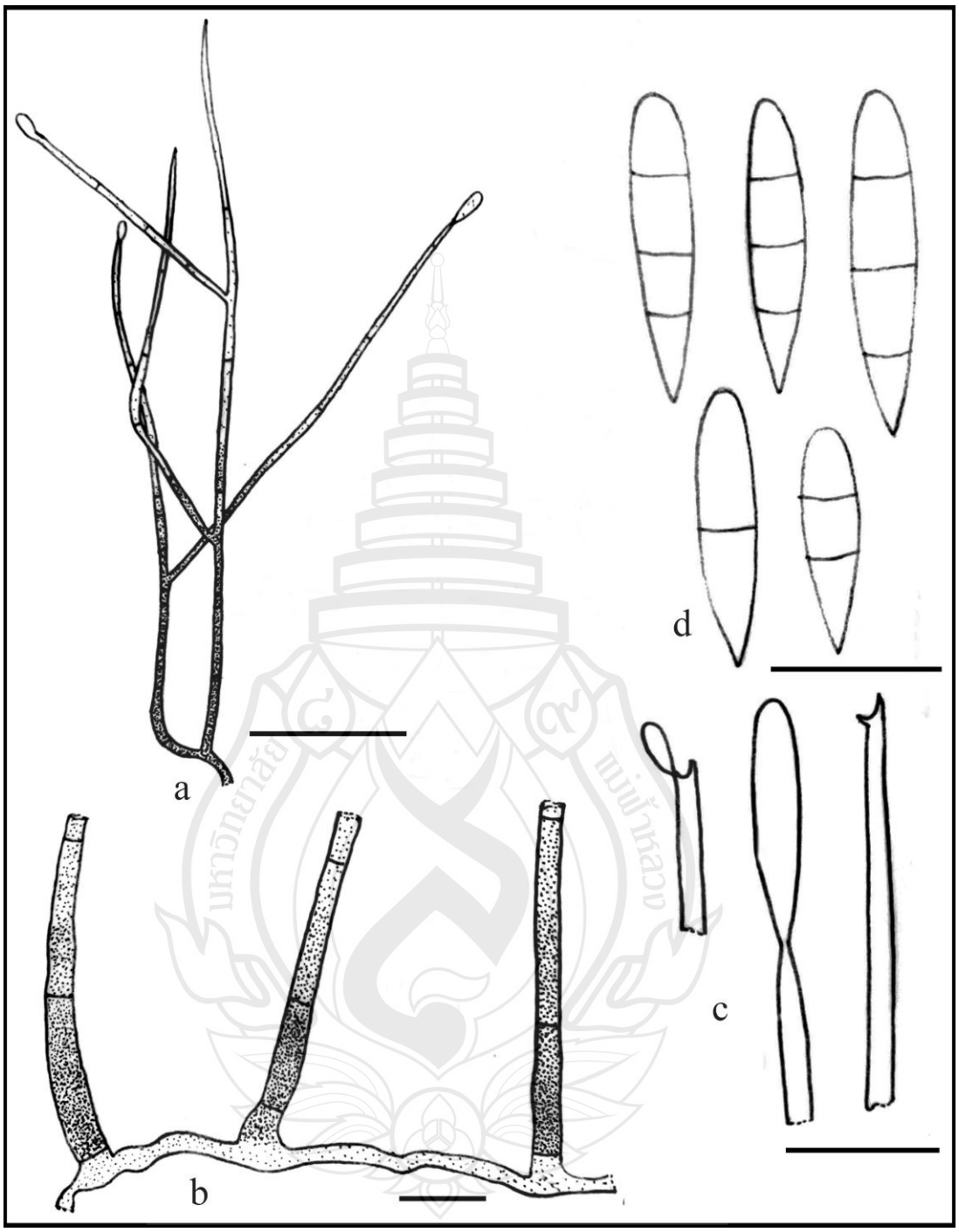


Figure 5.96 *Redbia pucciniicola*

Figure 5.96, a–c. Conidiophores and conidial attachments. d. Conidia. Scale bars: a = 50 μm, b–d =. 10 μm. (Redrawn from Deighton & Pirozynski, 1972).

Rhinotrichella G. Arnaud ex de Hoog, Stud. Mycol. 15: 86 (1977)

Figure 5.97

Index Fungorum number: IF 9691

Facesoffungi number: FoF 09222

Rhinotrichella was proposed by Arnaud (1953) but was not validly described. Subsequently, de Hoog (1977) validated the genus, designating *R. globulifera* as the type species.

Rhinotrichella is characterized by colonies that exhibit a flocculose and whitish appearance. The hyphae are smooth, thin-walled, hyaline, and relatively broad. Conidiophores are erect, fragile, thin-walled, and hyaline, consisting of straight, multicellular stalks and flexuous conidiiferous rachides with scattered conidium bearing denticles. The conidia are hyaline, smooth or verrucose, and globose (adapted from de Hoog, 1977).

Rhinotrichella includes three valid species (Species Fungorum, 2025). Among these, *R. globulifera* was isolated as fungicolous on *Ganoderma tsugae* (*Polyporaceae*) in Japan, while *R. elegans* was obtained from leaf litter of *Podocarpus elongatus* in Cape Province, South Africa, and *R. macrospora* was identified from a dead leaf of *Caryota mitis* in Taiwan, China (de Hoog, 1977; Index Fungorum, 2025). In GenBank (2025), only LSU sequence data for *R. globulifera* is available. *Rhinotrichella* is currently classified within the *Ascomycota* genera *incertae sedis* (Hyde et al., 2024a).

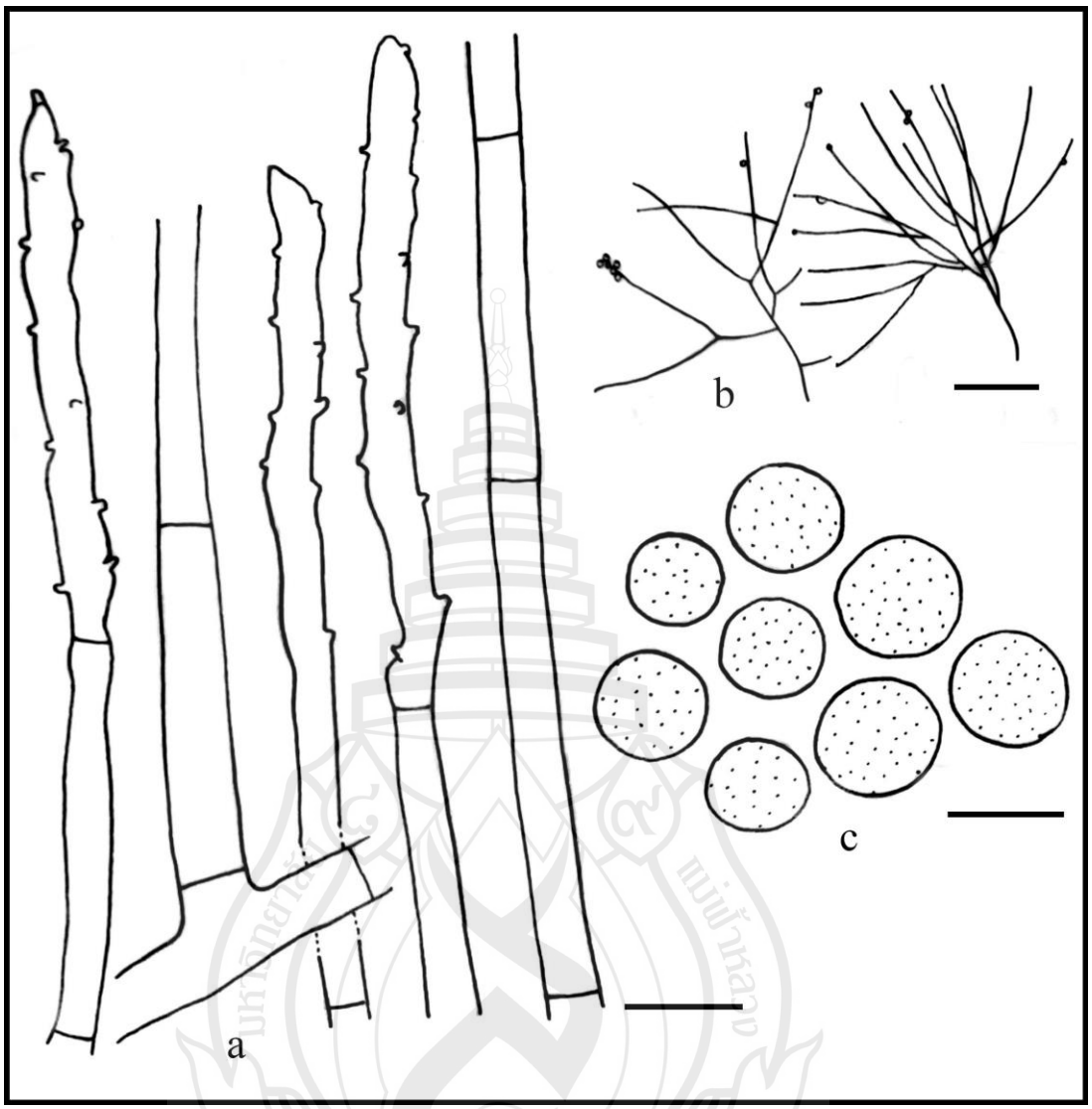


Figure 5.97 *Rhinotrichella globulifera*

Figure 5.97, a, b. Conidial apparatus. c. Conidia. Scale bars: b = 100 μm, a, c = 10 μm. (Redrawn from de Hoog, 1977).

Spermosporella Deighton, Mycol. Pap. 118: 21 (1969)

Figure 5.98

Index Fungorum number: IF 9971

Deighton (1969) introduced *Spermosporella*, with *S. aggregata* as the type species. It was identified as a hyperparasite on *Meliola* sp. in Sierra Leone. Deighton and Pirozynski (1972) added *S. pulvinata*, which was also found as a hyperparasite on *Meliola* sp. in Uganda and Sierra Leone. Sutton (1973) described *S. elegans* as fungicolous found on old conidiophores of *Haplographium delicatum* (syn.

Dematioscypha dematiicola (*Hyaloscyphaceae*)) in Canada. Additionally, *S. flagelliformis* is fungicolous on conidiophores of *Pleurothecium recurvatum* (*Pleurotheciaceae*)) in Japan (Sun et al., 2019a). Santos et al. (2019b) proposed *S. irenopsidis*, found on *Irenopsis vincensii* (*Meliolaceae*) in Brazil. However, only four species of *Spermosporella* except *S. irenopsidis* are listed in Species Fungorum (2025) and MycoBank (2025).

Spermosporella species are characterized by hyaline, smooth, septate, and branched hyphae. Their conidiophores are produced singly as lateral branches of the mycelial hyphae. They are often densely clustered, hyaline, ampulliform, short, simple, continuous, smooth, and sympodial, with unthickened conidial scars. The conidia are hyaline, obclavate-fusiform, smooth, 2–3-septate, with a truncate, unthickened hilum, and an apical cell that narrows into a slender rostrum (adapted from Deighton, 1969). No molecular data for *Spermosporella* is available in GenBank (2025).

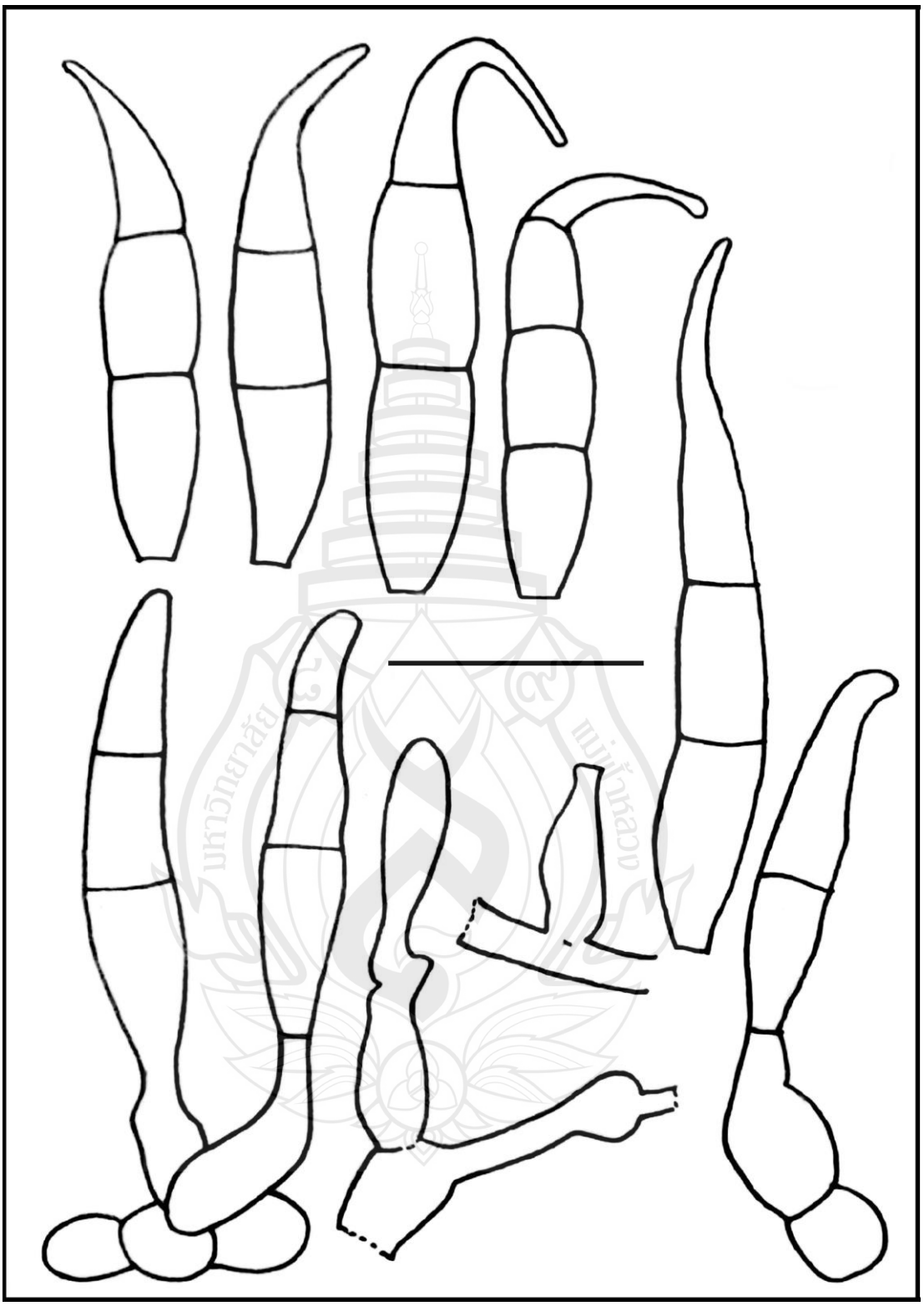


Figure 5.98 *Spermosporella aggregata*

Figure 5.98 Conidial attachments and conidia. Scale bar = 10 μm. (Redrawn from Deighton, 1969).

Sphaerulomyces Marvanová, Trans. Br. mycol. Soc. 68(3): 485 (1977)

Figure 5.99

Index Fungorum number: IF 9994

Marvanová (1977) established *Sphaerulomyces*, designating *S. coralloides* as its type species. *Sphaerulomyces coralloides* was described as a contact biotrophic mycoparasite of aquatic hyphomycete conidia, isolated from foam collected in a small brook in the Little Carpathian Mountains, Slovakia (Marvanová, 1977).

Sphaerulomyces is characterized by a mono- to polycellular, hyaline, sparsely branched, moniliform thallus. The vegetative cells are rounded or lobed, while the fertile cells are apiculate. Conidia are produced individually at the apices of conidiogenous cells, and upon maturity, they become deciduous and non-motile. The conidia are rounded or ellipsoidal, glabrous, and aseptate (adapted from Marvanová, 1977). *Sphaerulomyces coralloides* has been observed parasitizing the conidia of *Anguillospora crassa*, *Tricladium splendens*, and *Varicosporium elodeae* (Marvanová, 1977).

Since its establishment, *Sphaerulomyces* has remained monotypic (Species Fungorum, 2025). As of GenBank (2025), no sequence data for *S. coralloides* is available. This genus is currently classified within the *Ascomycota* genera *incertae sedis* (Hyde et al., 2024a).

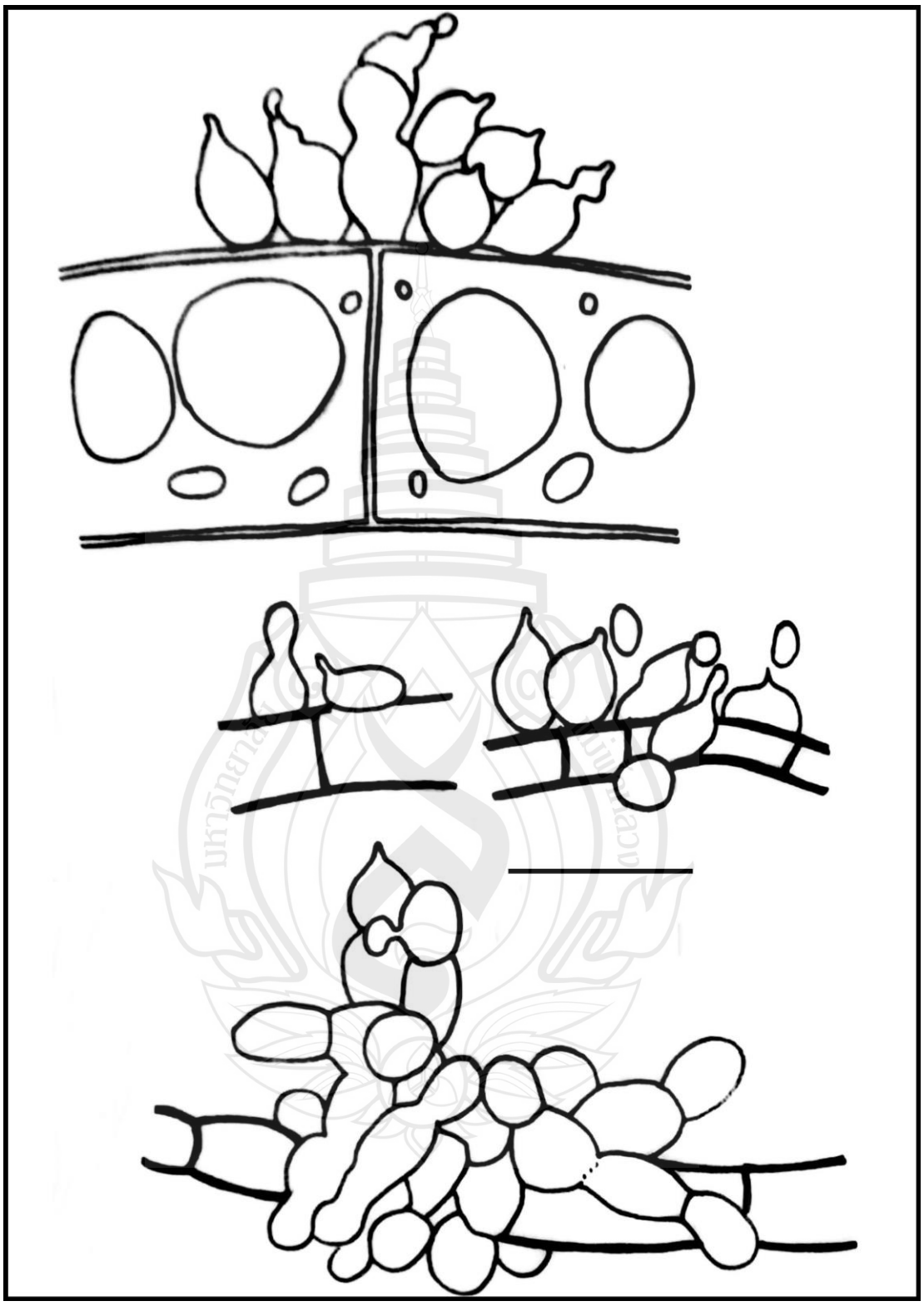


Figure 5.99 *Sphaerulomyces coralloides*

Figure 5.99, Thalli with conidial attachments. Scale bar = 10 μm. (Redrawn from Marvanová, 1977).

Spiropes Cif., Sydowia 9(1-6): 302 (1955)

Figure 5.100

Index Fungorum number: IF 10012

Ciferri (1955) proposed *Spiropes*, designating *S. guareicola* as the type species. *Spiropes* is a dematiaceous asexual genus, with its members commonly recognized as hyperparasites of black mildews in tropical regions (Bermúdez-Cova et al., 2024). For *Spiropes*, the widely accepted generic diagnosis was provided by Ellis (1968, 1971) and amended by subsequent authors such as Seifert and Hughes (2000) and McTaggart et al. (2007).

The species of *Spiropes* are characterized by, mononematous, fasciculate or synnematous conidiophores and conidiogenous cells with conspicuous, flat, and numerous scars. The conidia are pigmented and possess 1–9 septa or pseudosepta (Ellis, 1968, 1971, 1976; Seifert & Hughes, 2000; Bánki et al., 2023). *Spiropes* comprises 36 species (Species Fungorum, 2025). The species delimitation in *Spiropes* has thus far relied solely on morphology, as most of these species were described before the molecular era, and due to the challenges associated with isolating DNA from mixed infections (Bermúdez-Cova et al., 2022, 2023a, 2023b). For molecular-based identification of *Spiropes* species, the availability of DNA sequences in publicly accessible databases is currently lacking. Consequently, species within the genus remain "*incertae sedis*" at many taxonomic ranks (Bermúdez-Cova et al., 2022, 2023a). The initial DNA sequences for *Spiropes* have been generated by Bermúdez-Cova et al. (2024) suggested that *Spiropes* may be polyphyletic within the *Leotiomycetes*. However, to confirm this, continuous generation of new DNA sequences from various species within the genus is recommended (Bermúdez-Cova et al., 2024).

Spiropes species have been reported, in Benin, Brazil, China, Cuba, India, Japan, Malaysia, Nepal, New Caledonia, New Zealand, Panama, Paraguay, Puerto Rico, Sierra Leone, Sri Lanka, the USA, Tanzania, Trinidad Tobago, and Uganda (Bermúdez-Cova et al., 2024; Index Fungorum, 2025). They parasitize fungi and are associated with plant substrates (Bermúdez-Cova et al., 2024). The species such as

Spiropes angylocalycis (on *Meliola* (*Meliolaceae*)), *S. armatellae* (on colonies of *Armatella cinnamomicola* (*Armatellaceae*)), *S. armatellicola* (on colonies of *Armatella* sp.), *S. asterinae* (on *Asterina pulchella* (*Asterinaceae*)), *S. bakeri* (on *Halbaniella* sp. (*Trichothyriaceae*)), *S. balladynae* (on *Balladyna velutina* (*Balladynaceae*)), *S. caribensis* (on *Meliola* sp.), *S. carpolobiae* (on *Meliola carpolobiae*), *S. croissantiformis* (on *Meliola xylopiae*), *S. curvatus* (on ascomata of *Hemisphaeriales*), *S. deightonii* (on *Meliola borneensis*), *S. dictyosporus* (on conidiomata of *Euantennaria mucronata* (*Euantennariaceae*)), *S. echidnodis* (on *Echidnodes quercina* (*Asterinaceae*)), *S. guareicola* (on *Meliola guareicola*), *S. helleri* (on *Meliola helleri*), *S. lembosiae* (on *Lembosia ampulligera* (*Asterinaceae*)), *S. leonensis* (on *Meliola garciniae*), *S. limoniformis* (on *Armatella litseae*), *S. penicillium* (on mycelium of *Meliola*), *S. pirozynskii* (on *Irenopsis* sp. (*Meliolaceae*)), and *S. shoreae* (on *Microthyriaceae*) have been recorded as fungicolous within this genus (Sun et al., 2019a; Bermúdez-Cova et al., 2024; Index Fungorum, 2025).

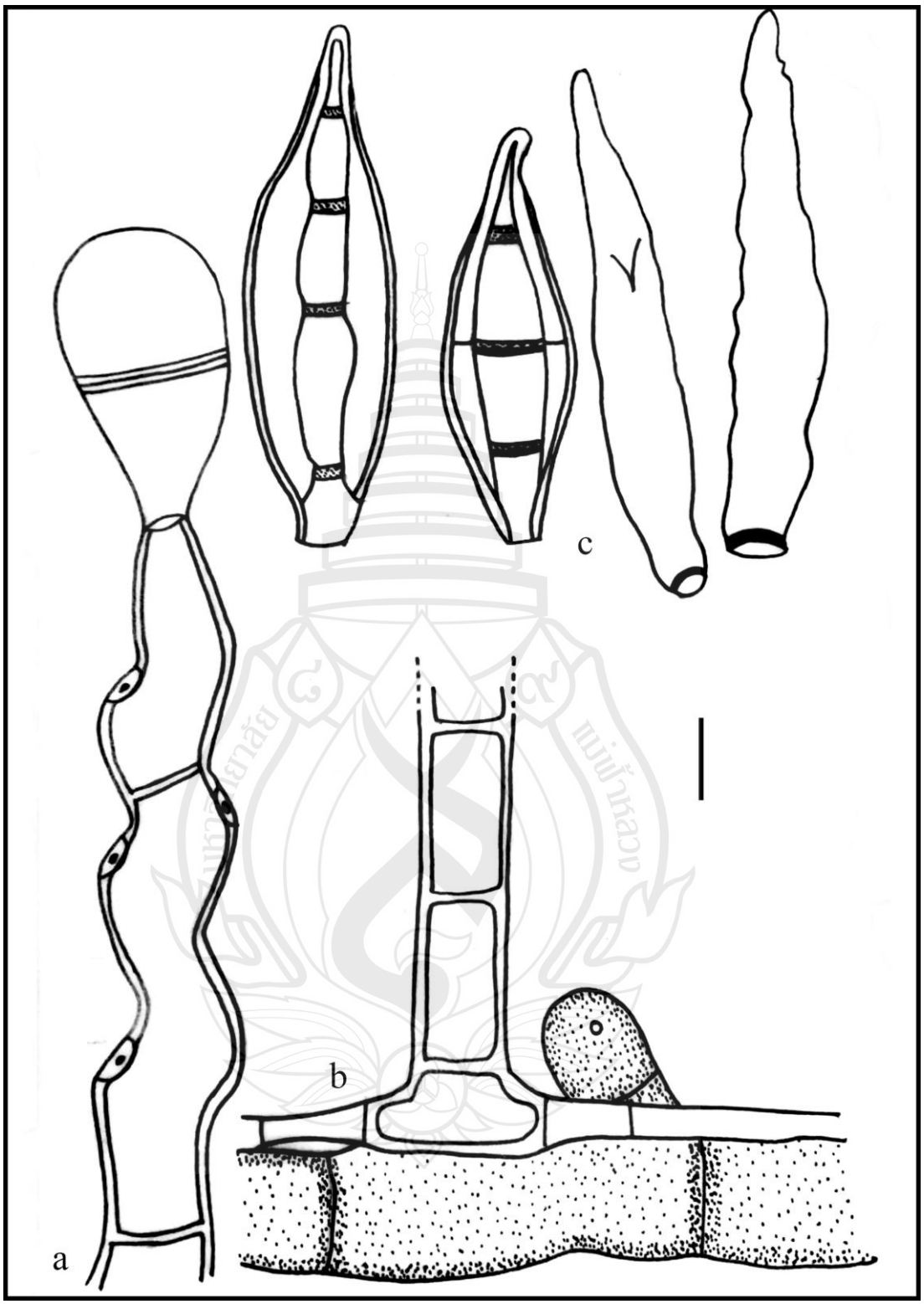


Figure 5.100 *Spiropes guareicola*

Figure 5.100, a. Conidiophore with scars and a young conidium. b. Base of a conidiophore growing on a hypha of *Meliola* sp. c. Conidia. Scale bar = 8 μm. (Redrawn from Bermúdez-Cova et al., 2024).

Stellospora Alcorn & B. Sutton, Mycotaxon 20(1): 45 (1984)

Figure 5.101

Index Fungorum number: IF 11196

Alcorn and Sutton (1984) established *Stellospora* with *S. appendiculellae* as the type species. *Stellospora appendiculellae* is a fungicolous overgrowing *Appendiculella calostroma* (*Meliolaceae*) in Australia and the Philippines (Alcorn & Sutton, 1984). Another species, *S. tricornuta*, found on a dead leaf of a broad-leaved tree, in stagnant water in Peninsular Malaysia was added to the genus (Matsushima & Matsushima, 1996). *Stellospora* comprises two species (Species Fungorum, 2025), and no molecular data for the genus is currently available in GenBank (2025).

Stellospora appendiculellae is characterized by sparse, hyaline to subhyaline, septate, and branched hyphae. The conidiophores are macronematous, mononematous, unbranched or occasionally once-branched near the base, straight or flexuous, hyaline to subhyaline, smooth, tapered cylindrical, and sometimes swollen at the base, with 1–4 septa. The conidiogenous cells are monophialidic, integrated, terminal, determinate, hyaline, and tapered, featuring a flared and sometimes recurved collarette (Alcorn & Sutton, 1984). Conidiogenous cells exhibit internal thickening at the conidiogenous locus, basal septum, subapex, and apex. Conidial initials are endogenous, becoming semi-endogenous as they mature. The conidia are hyaline, unicellular, initially globose with short blunt projections, and eventually develop a stellate form with typically six blunt to more or less acute papillae, though some conidia may appear elongate. Conidia aggregate into globose heads at the apices of the conidiogenous cells (Alcorn & Sutton, 1984).

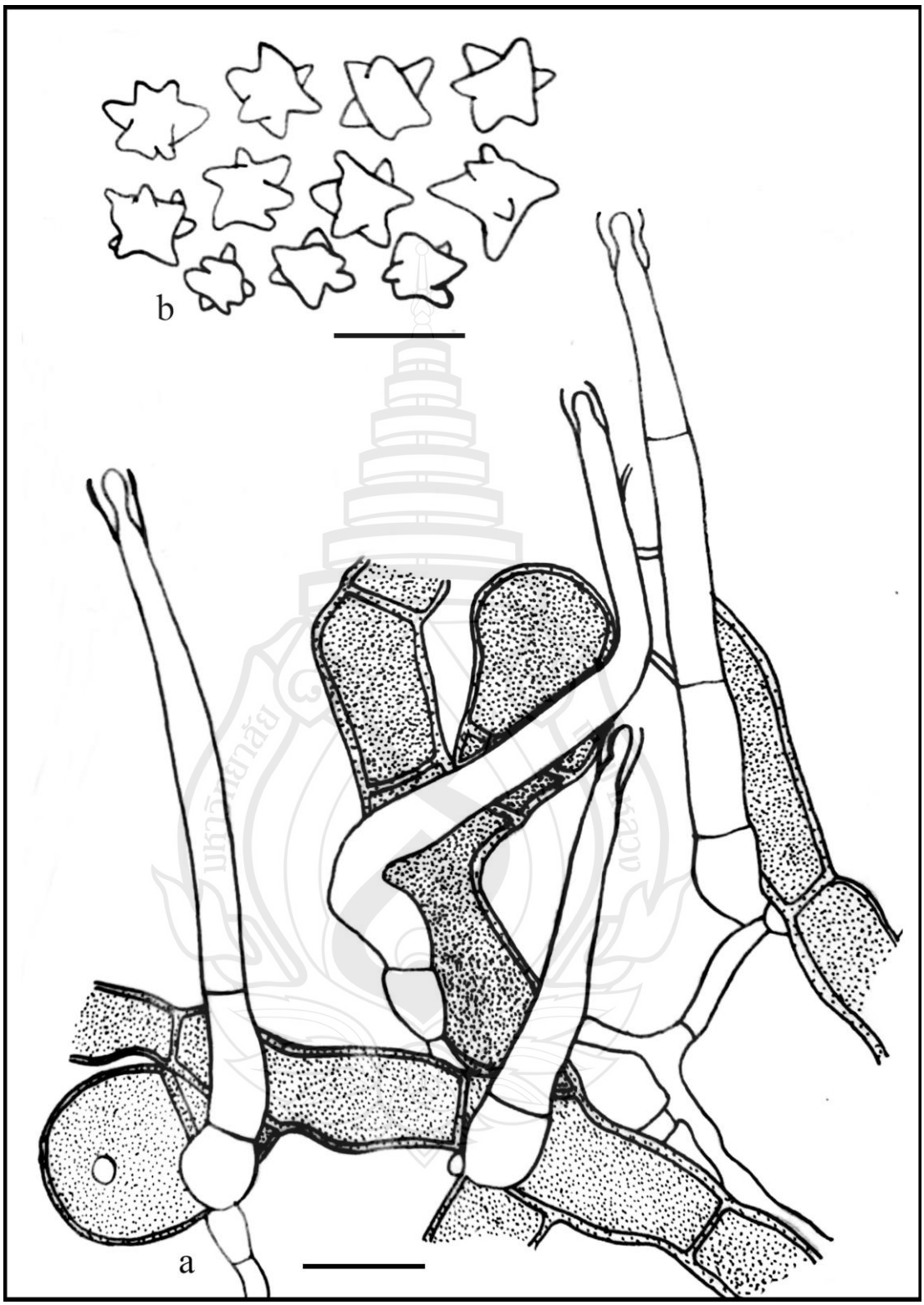


Figure 5.101 *Stellospora appendiculellae*

Figure 5.101, a. Conidiophores. b. Conidia. Scale bars: a, b = 10 µm. (Redrawn from Alcorn & Sutton, 1984).

Stenospora Deighton, Mycol. Pap. 118: 22 (1969)

Figure 5.102

Index Fungorum number: IF 10086

Facesoffungi number: FoF 08663

Deighton (1969) established *Stenospora* with *S. uredinicola* as the type species. *Stenospora uredinicola* was discovered to be hyperparasitic on the sori of *Puccinia kraussiana* (*Pucciniaceae*) in Sierra Leone (Deighton, 1969).

Stenospora is characterized by conidiophores that arise as lateral branches of the mycelial hyphae. These conidiophores are short, smooth, simple or branched, and septate, with conidial scars that are very slightly but distinctly thickened, refractive, and slightly prominent. The conidia are hyaline, acicular, smooth, and pluriseptate, resembling those of *Cercospora*, but distinguished by a very slightly but distinctly thickened and refractive truncate hilum (Deighton, 1969). Since its establishment, *Stenospora* has remained monotypic (Species Fungorum, 2025), and no molecular data for the genus is currently available in GenBank (2025).

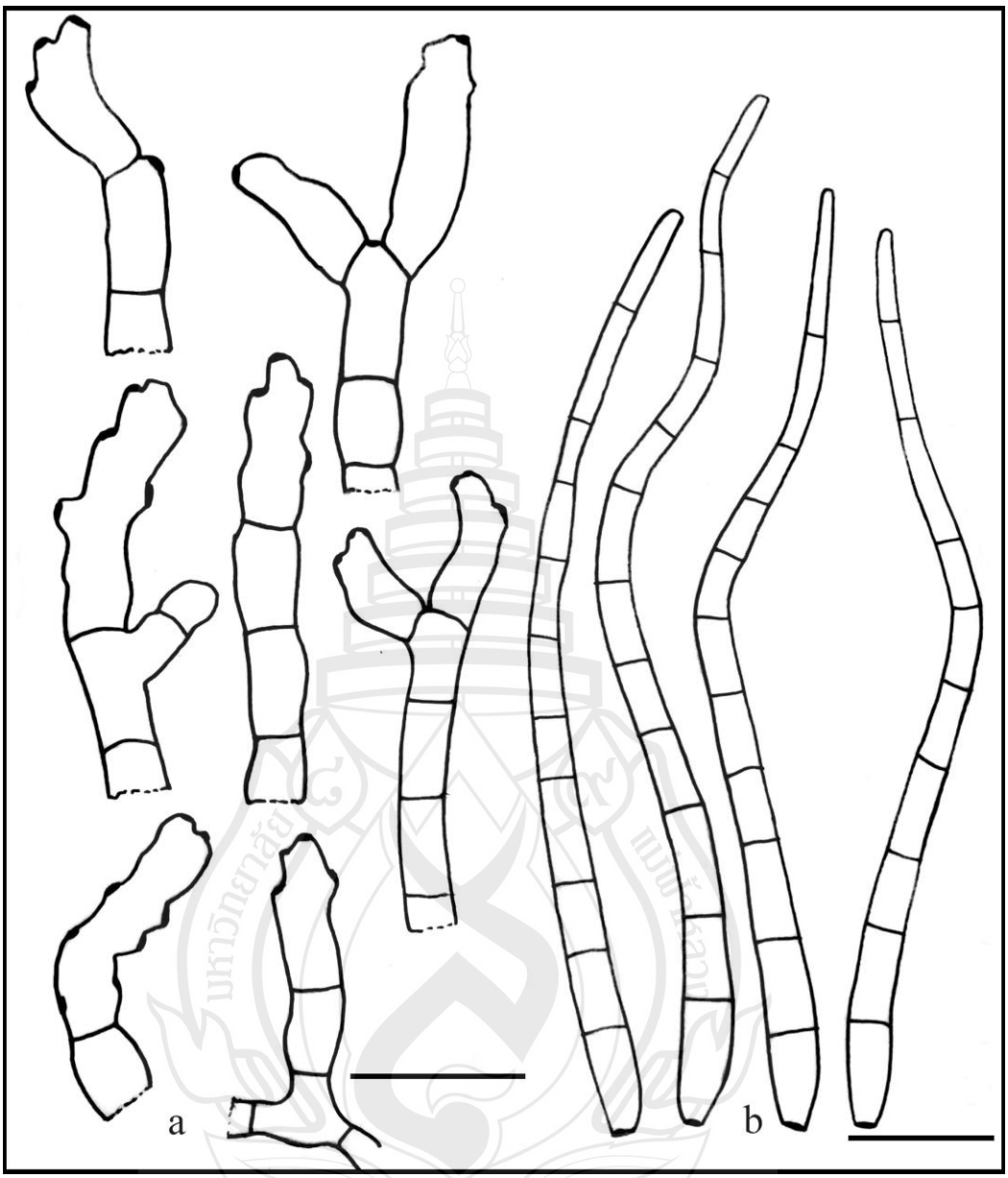


Figure 5.102 *Stenospora uredinicola*

Figure 5.102, a. Conidiophores. b. Conidia. Scale bars: a, b = 10 μm. (Redrawn from Deighton, 1969).

Tetraposporium S. Hughes, Mycol. Pap. 46: 25 (1951)

Figure 5.103

Index Fungorum number: IF 10200

Tetraposporium was established by Hughes (1951b), with *T. asterinearum* as the type species. This species was described as a hyperparasite on *Asterina funtumiae*

(*Asterinaceae*) in Ghana (Hughes, 1951b). Hughes (1951b) also transferred *Triposporium ravenelii* to the genus as *T. ravenelii*, a species reported from the bark of *Platanus* in North America.

Tetraposporium is characterized by superficial, branched, septate hyphae that are pale brown to subhyaline. Conidia are produced singly at the apex of short conidiophores and are stauriform, consisting of one terminal and three lateral, septate arms. At maturity, the conidia are pale brown, with paler apices of the arms (adapted from Hughes, 1951b).

As of Species Fungorum (2025), two species are recognized within the genus. No molecular sequence data for *Tetraposporium* are available in GenBank (2025). *Tetraposporium* is presently classified within *Ascomycota*, genera *incertae sedis* (Hyde et al., 2024a).

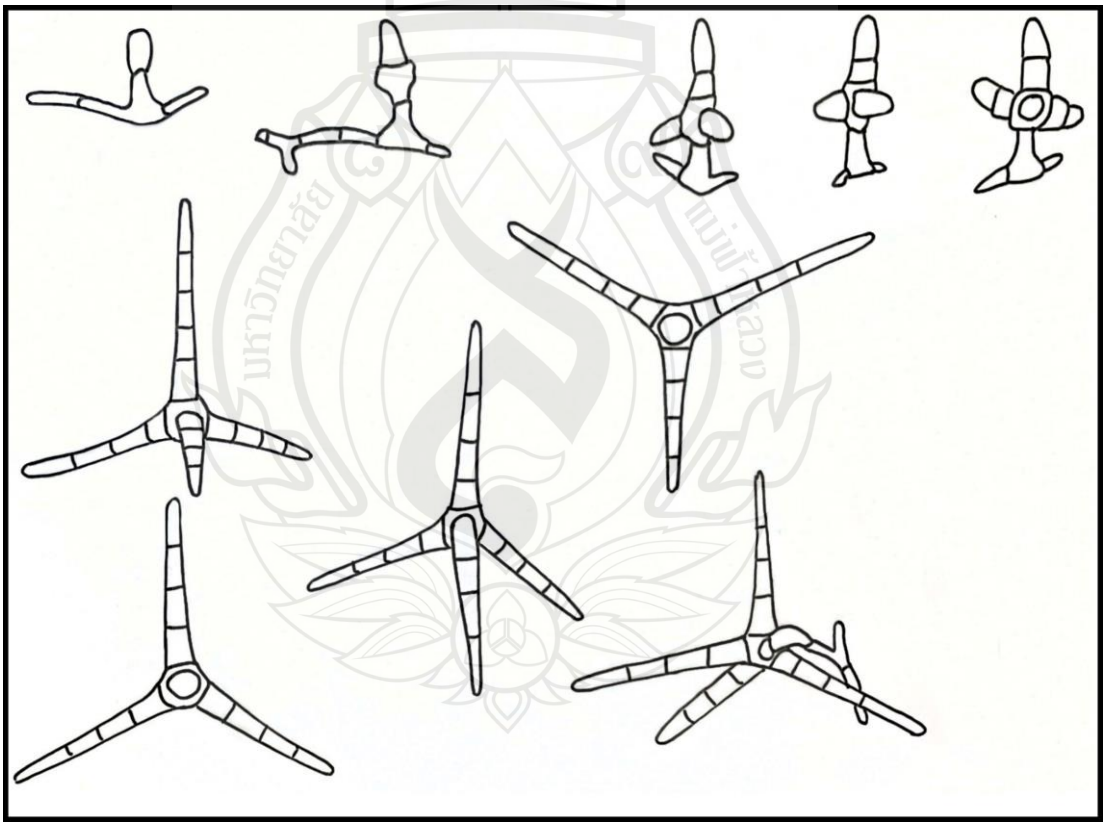


Figure 5.103 *Tetraposporium asterinearum*

Figure 5.103, Conidial development and mature conidia. (Redrawn from Hughes, 1951b).

Trichoconis Clem., Gen. fung. (Minneapolis): 145 (1909)

Figure 5.104

Index Fungorum number: IF 10280

Clements (1909) established *Trichoconis* to accommodate *T. caudata*, discovered on deceased fruits of *Theobroma cacao* in Cameroon and identified as *Pyricularia caudate*. This genus comprises lichenicolous, fungicolous, and saprobic species associated with plant substrates (Braun et al., 2016). Species identification within *Trichoconis* has been primarily dependent on morphological characteristics thus far (Braun et al., 2016).

Trichoconis species are characterized by distinct, colorless conidiophores that are either solitary or branched. Conidiogenous cells are polyblastic, sympodial, and denticulate, featuring cylindrical denticles that separate cells through rhexolytic secession. The conidia are solitary and vary in shape from fusiform, obclavate, clavate, ellipsoid, subcylindrical, to navicular. They are rostrate, with apical and lateral septation, and are colorless (Deighton & Pirozynski, 1972). The phylogeny of *Trichoconis*, as determined from the genetic sequences of its type species *T. caudata*, remains poorly understood due to the absence of comparable sequences for phylogenetic analysis (Braun et al., 2016). To date, there are 23 species within *Trichoconis* (Silva et al., 2015a; Braun et al., 2016; Species Fungorum, 2025).

Trichoconis species have been reported from Australia, Brazil, Cuba, Germany, Ghana, Ireland, North Solomons, Peru, Sierra Leone, Uganda, and Ukraine (Deighton & Pirozynsky, 1972; Index Fungorum, 2024). The species such as, *Trichoconis africana* (on colonies of *Asterina* (*Asterinaceae*)), *T. angustispora* (on colonies of *Hysterostomella tetracerae* (*Parmulariaceae*)), *T. antillana* (on setae of *Beltrania rhombica* (*Beltraniaceae*)), *T. appendiculata* (on *Asterinella tecleae* (*Microthyriaceae*)), *T. capitata* (on *Meliolina mollis* (*Meliolinaceae*)), *T. caudata* (colonized *Lasiodiplodia theobromae* (*Botryosphaeriaceae*)), *T. englerulae* (on *Meliola macarangicola*), *T. hamata* (on *Meliola* spp.), *T. hibernica* (on *Appendiculella calostroma* (*Meliolaceae*)), *T. pedicephora* (on setae of coelomycete), *T. schiffnerulae* (on colonies of *Schiffnerula mirabilis* (*Englerulaceae*)), *T. sigmoidea* (on *Meliola kawandensis*), *T. trichiliae* (on colonies of *Asterina*), and *T. viridula* (on *Clypeolella ricini* (*Englerulaceae*)) have been recorded as fungicolous within this genus (Deighton & Pirozynsky, 1972; Sun et al., 2019a, Index Fungorum, 2025).

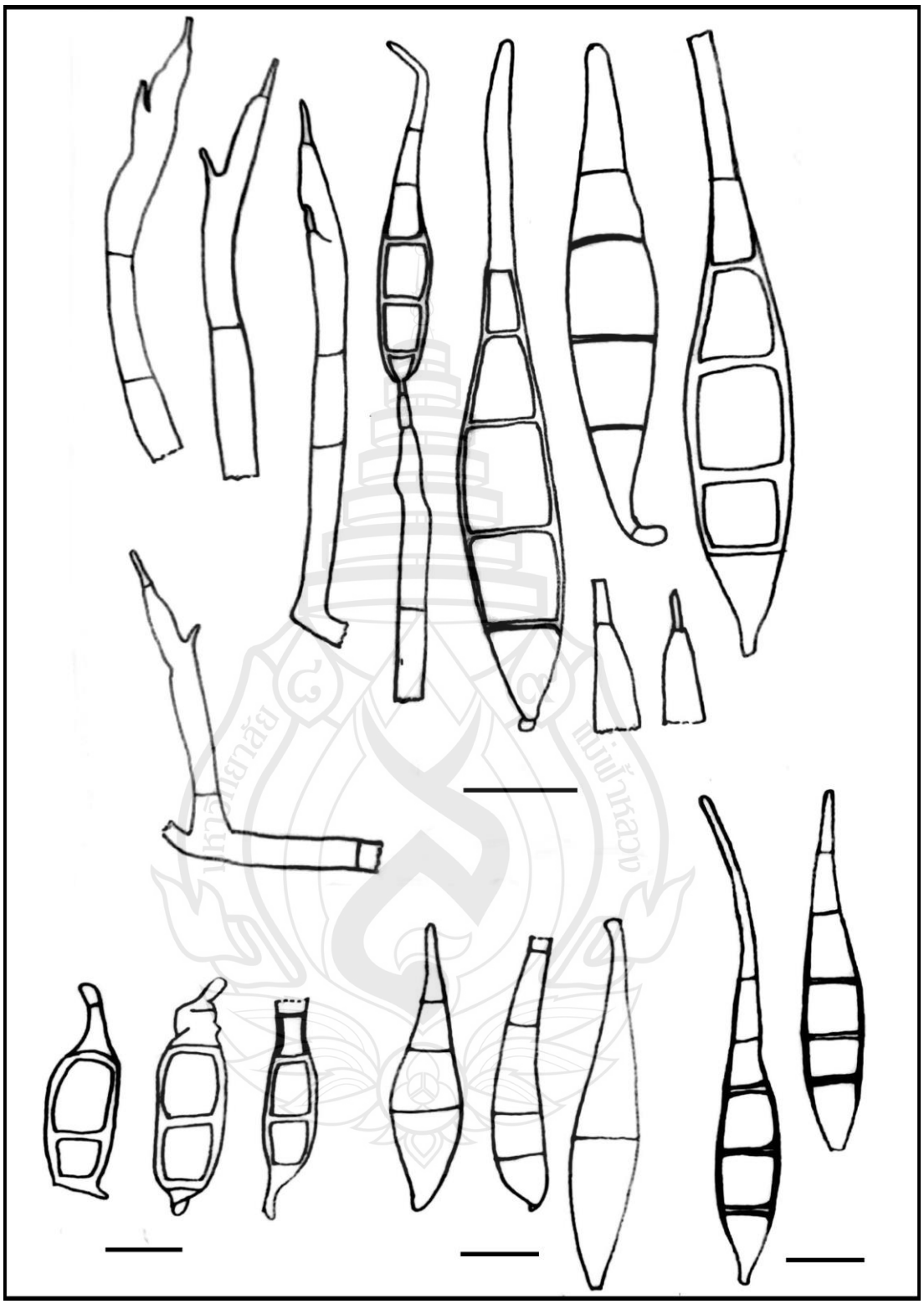


Figure 5.104 *Trichoconis caudata*

Figure 5.104, Conidiophores, Conidial attachment and conidia. Scale bars = 10 µm. (Redrawn from Deighton & Pirozynski, 1972).

Tuberculispora Deighton & Piroz., Mycol. Pap. 128: 92 (1972)

Figure 5.105

Index Fungorum number: IF 10337

Deighton and Pirozynski (1972) established *Tuberculispora* with the type species, *T. jamaicensis* which is fungicolous on *Irenopsis aciculosa* (*Meliolaceae*) in Jamaica and *I. cryptocarpa* in the USA. *Tuberculispora* remains monotypic (Species Fungorum, 2025). There is no molecular data available for *Tuberculispora* in GenBank (2025).

Tuberculispora is characterized by, superficial, hyaline, septate, hyphae which bear conidiophores as lateral branches. Conidiophores are hyaline, straight, sympodial, and narrowed towards the apex. The old apices are eventually displaced to one side and persist as elongated, peg-like structures. The conidial scars are truncate and unthickened. The conidia are subglobose, hyaline, and thin-walled, with large conical warts covering their surface (adapted from Deighton & Pirozynski, 1972).

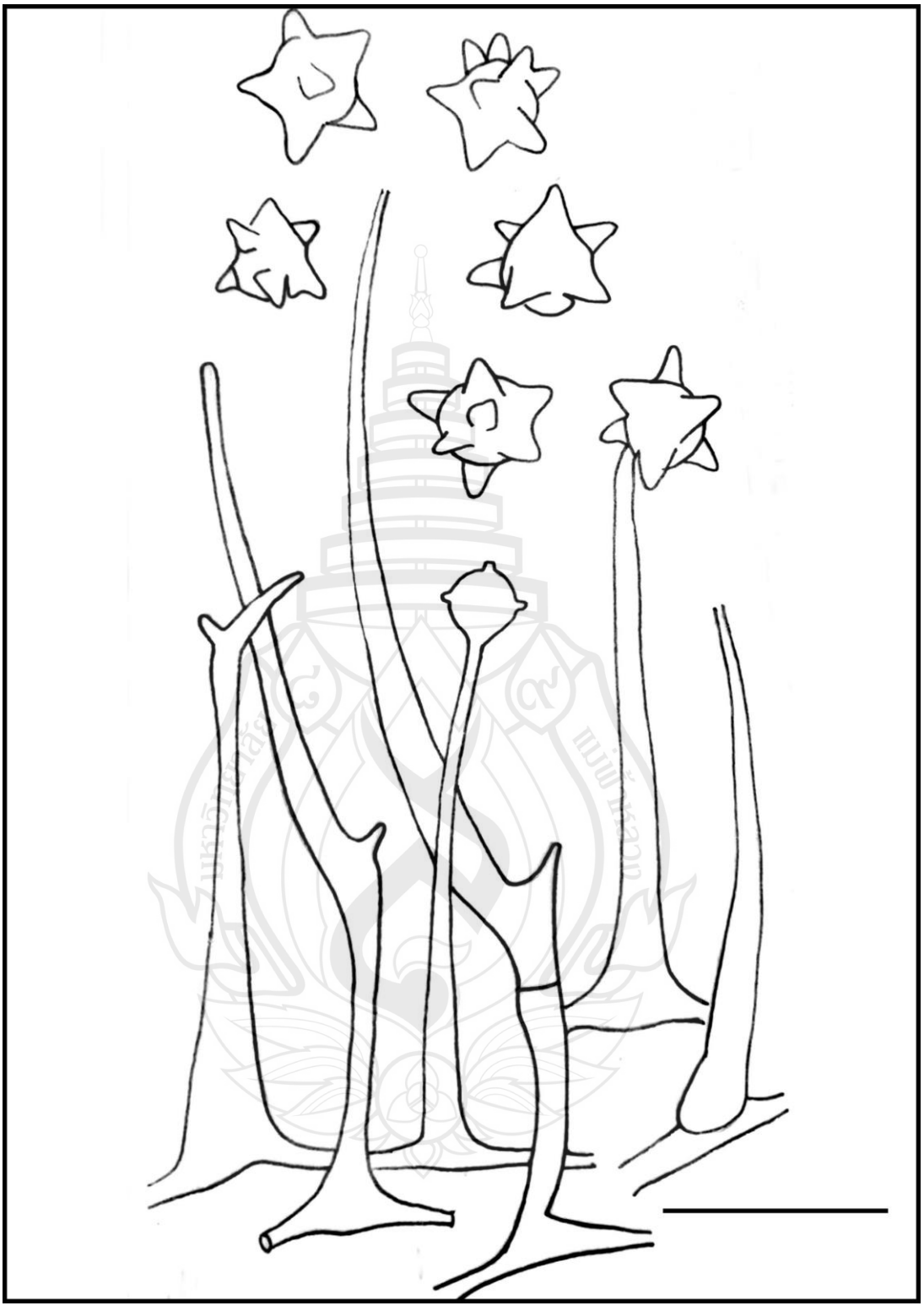


Figure 5.105 *Tuberculispora jamaicensis*

Figure 5.105, Conidiophores, conidial attachments, and conidia. Scale bar = 10 μm. (Redrawn from Deighton & Pirozynski, 1972).

Tympanosporium W. Gams, Antonie van Leeuwenhoek 40: 478 (1974)

Figure 5.106

Index Fungorum number: IF 10343

Gams (1974) established *Tympanosporium* with the type species *T. parasiticum*. This species was recognized as a mycoparasite on *Tubercularia vulgaris* in the Netherlands (Gams. 1974). *Tympanosporium* remains monotypic (Species Fungorum, 2025). It is characterized by annellated conidiogenous cells that produce short, cylindric (tympaniform) conidia within white sporodochia on the host. On agar media, the conidia form short necks and generate narrow secondary conidia in a phialidic manner. The aerial mycelium forms sporodochia, bearing short, truncate conidia similar to those found on the natural substrate (Gams, 1974). There is no molecular data available for *Tympanosporium* (GenBank, 2025).

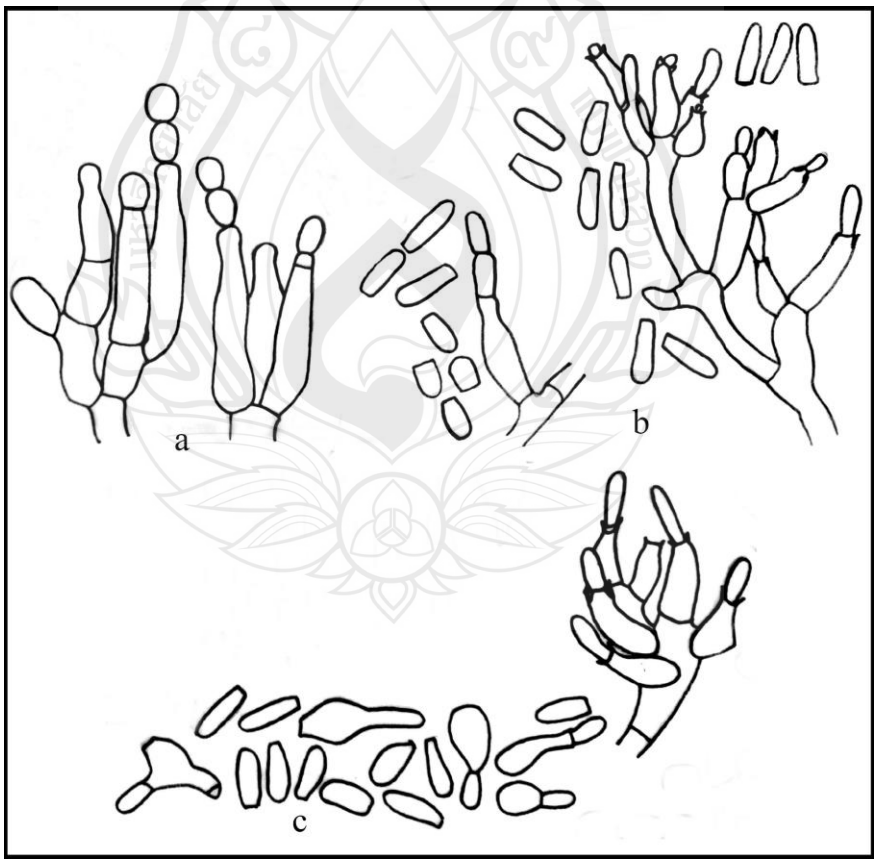


Figure 5.106 *Tympanosporium parasiticum*

Figure 5.106, a. Annellate conidiogenous cells. b. Conidiophores with phialides. c. Yeast-like germination of the conidia in the absence of the host fungus. (Redrawn from Gams, 1974).

Veracruzomyces Mercado, Guarro, Heredia & J. Mena, Nova Hedwigia 75(3-4): 534 (2002)

Figure 5.107

Index Fungorum number: IF 28698

Mercado-Sierra et al. (2002) established *Veracruzomyces*, with *V. obclavatus* as the type species. This fungus was discovered growing on old conidiophores of *Helminthosporium velutinum* (*Massarinaceae*) in Veracruz, Mexico (Mercado-Sierra et al., 2002). *Veracruzomyces* is characterized by mycelium that are immersed in the substrate. The conidiophores are macronematous, mononematous, brown to dark brown or blackish-brown, simple, short, and smooth, sometimes with a broad base. The conidiophores often proliferate percurrently one or more times, exhibiting a lateral, enlarged, paler protuberance that bends downward. Conidiogenous cells are monoblastic, percurrent, and cylindrical. Conidia are solitary, dry, simple, obclavate, rostrate, smooth, muriform, and brown, with a protuberant and very dark basal cell (Mercado-Sierra et al., 2002). Since its establishment, *Veracruzomyces* has remained monotypic (Species Fungorum, 2025), and no molecular data for the genus is currently available in GenBank (2025).

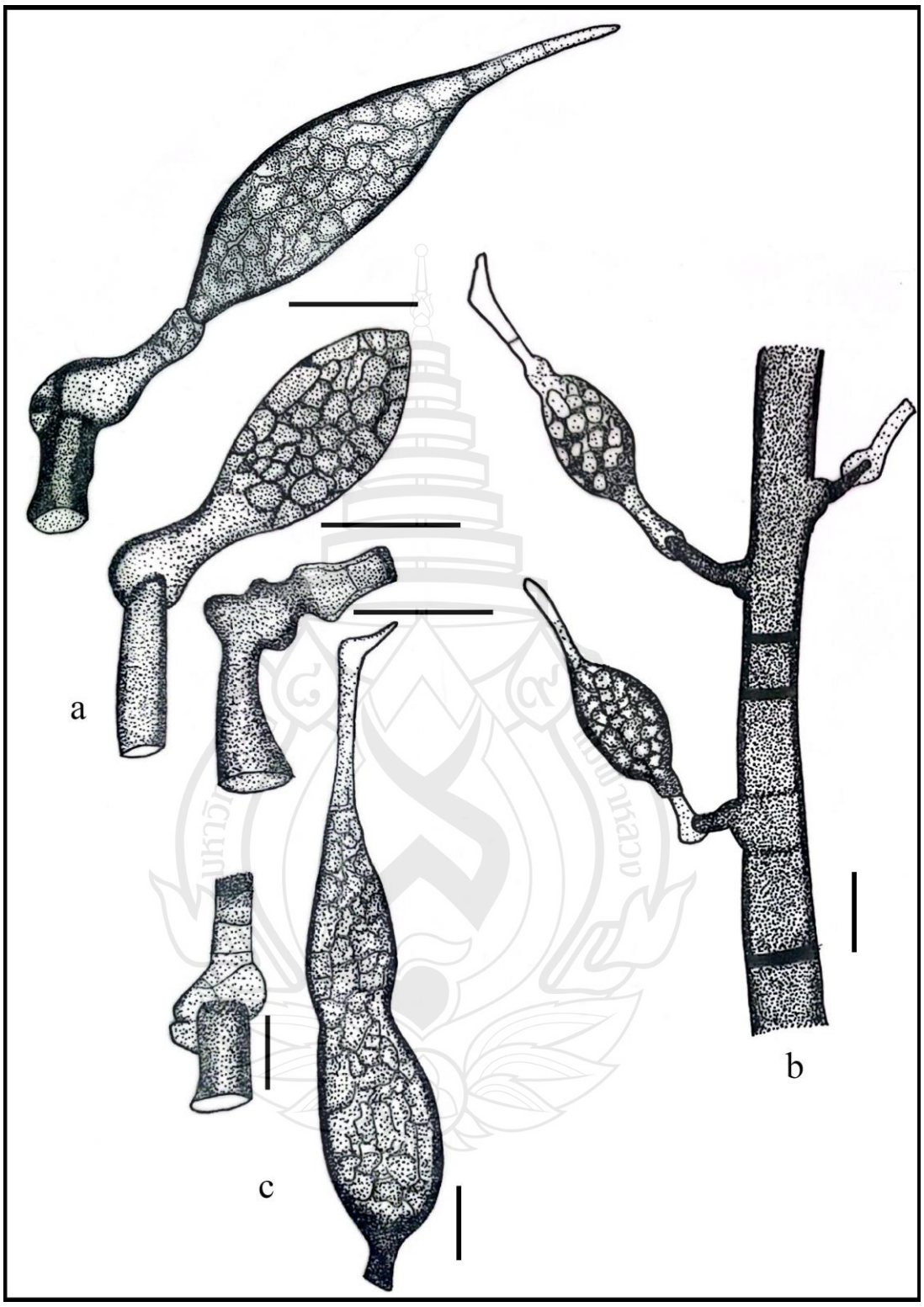


Figure 5.107 *Veracruzomyces obclavatus*

Figure 5.107, a. Conidiophores, conidiogenous cells and attached conidia. b. Conidiophores with attached conidia. c. Conidium with a pedicel in the basal cell and apical rostrum. Scale bars = 20 μm. (Redrawn from Mercado-Sierra et al., 2002).

Zakatoshia B. Sutton, Mycol. Pap. 132: 129 (1973)

Figure 5.108

Index Fungorum number: IF 10466

Sutton (1973) introduced *Zakatoshia*, with *Z. hirschiopori* as the type species. This species was found on basidiocarps of *Hirschioporus abietinus* (*Hirschioporaceae*) in Canada. Gams (1986) included *Z. erikssonii* in *Zakatoshia* which was discovered on *Sistotrema brinkmannii* (*Hydnaceae*) in Austria.

The asexual morph of *Zakatoshia* is hyphomycetous. It is characterized by conidiophores that arise directly from the immersed mycelium and are macronematous, mononematous, straight or flexuous, unbranched, brown, septate, and smooth. Conidiogenous cells are monophialidic, integrated, and can be apical or intercalary. They are determinate and cylindrical, becoming smaller towards the conidiophore apices, and are primarily located in the apical region of the conidiophore. These cells possess a well-defined collarette. Conidia are aseptate, slimy, semi-endogenous, acropleurogenous, simple to ovoid, hyaline, and smooth-walled (adapted from Sutton, 1973).

Zakatoshia comprises only these two fungicolous species, and its classification remains within the *Ascomycota* genera *incertae sedis* (Species Fungorum, 2025). Molecular data for these species is not available in GenBank (2025). Further research is needed to clarify the phylogenetic placement and ecology of the genus.

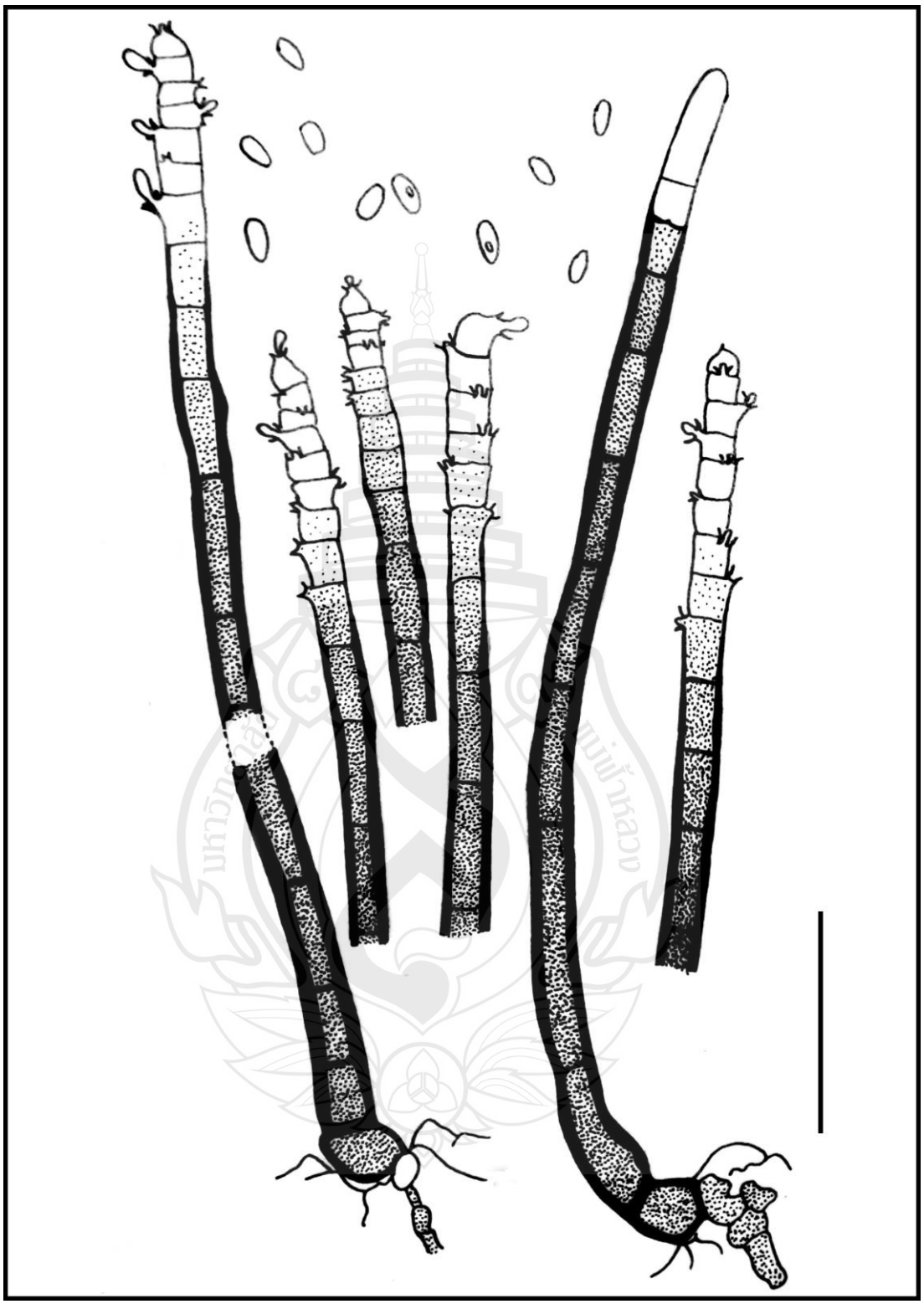


Figure 5.108 *Zakatoshia hirschiopori*

Figure 5.108, Conidiophores, conidial attachments and conidia. Scale bar = 20 μm. (Redrawn from Sutton, 1973).

Subphylum *Saccharomycotina* O.E. Erikss. & Winka

Class *Saccharomycetes* O.E. Erikss. & Winka

Saccharomycetales Kudryavtsev

Saccharomycetales* genera *incertae sedis

Phialoascus Redhead & Malloch, Canad. J. Bot. 55(13): 1703 (1977)

Figure 5.109

Index Fungorum number: IF 3989

Phialoascus was introduced by Redhead and Malloch (1977), with *P. borealis* as the type species. *Phialoascus borealis* was isolated as a mycoparasite on the hymenium of *Cortinarius huronensis* (*Cortinariaceae*) in Canada. As of Species Fungorum (2025), *Phialoascus* remains monotypic. Sequence data for this genus are unavailable in GenBank (2025). *Phialoascus* is currently classified within *Saccharomycetales*, genera *incertae sedis* (Hyde et al., 2024a).

Phialoascus is characterized by submerged, interbasidial, septate, branched, hyaline, thin-walled vegetative hyphae. Ascomata are absent. Ascophores are aseptate, scattered, and project perpendicularly from the host hymenium. They are hyaline, moderately thick-walled, tapering apically, swollen basally, occasionally forked, and often bear a clamp-like structure at the base. Ascophores may be intercalary or terminal and resemble collared phialides, initially bearing a single terminal ascus. Asci are clavate to short-cylindrical or ellipsoidal, thin-walled, hyaline, and dissolve or rupture at the apex, typically containing four spores. Ascospores are lunate to wedge-shaped, enclosed in a thin gelatinous sheath, hyaline, inamyloid, and are extruded through the ascus apex, often adhering in groups of 4–12 on the ascophore (adapted from Redhead & Malloch, 1977).

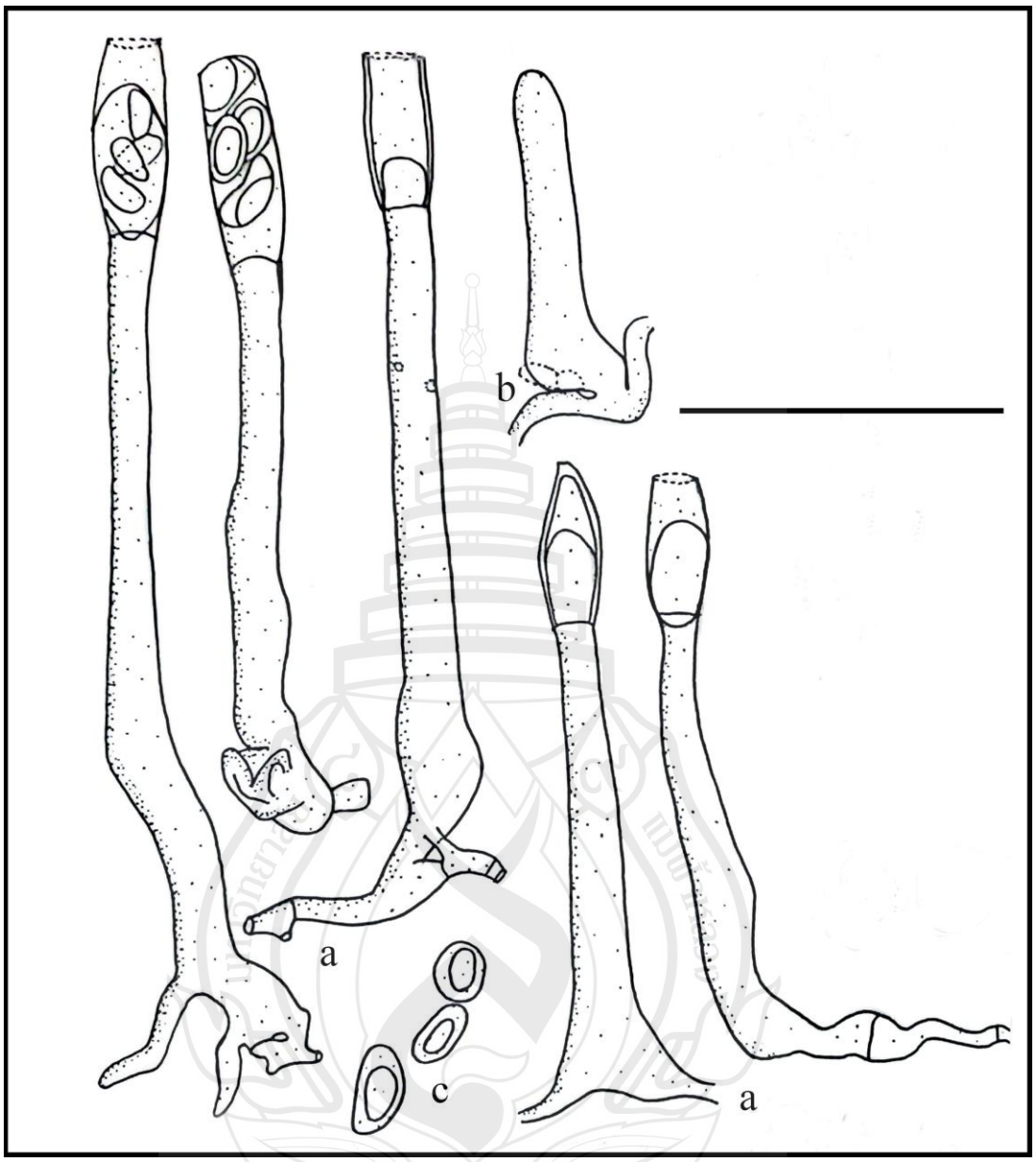


Figure 5.109 *Phialoascus borealis*

Figure 5.109, a. Ascophores. b. Immature ascophore. c. Ascospores. Scale bar = 30 μm. (Redrawn from Redhead & Malloch, 1977).

Phylum *Basidiomycota* R.T. Moore

Subphylum *Agaricomycotina* Doweld

Class *Agaricomycetes* Doweld

Order *Agaricales* Underw.

Suborder *Agaricineae* Fr.

Squamanitaceae Jülich

Squamanita Imbach, Mitt. naturf. Ges. Luzern 15: 81 (1946)

Figure 5.110

Index Fungorum number: IF 18578

Imbach (1946) introduced *Squamanita* with *Squamanita schreieri* from Switzerland as its type species. Previously, this genus has been assigned to various families, including *Squamanitaceae* and *Cystodermataceae* based on morphological characteristics (Singer, 1975, 1986). Through phylogenetic analysis of combined nuclear ribosomal RNA genes, Matheny and Griffith (2010) proposed that *Squamanita*, *Cystoderma*, and *Phaeolepiota* form a monophyletic clade. Subsequent molecular studies referred *Squamanita* in *Squamanitaceae* together with *Cystoderma*, *Floccularia*, *Leucopholiota*, and *Phaeolepiota* (Matheny et al., 2015; Griffith et al., 2019; Vizzini et al., 2019; Kalichman et al., 2020; Liu et al., 2021).

Squamanita species are characterized by collybioid, tricholomatoid to even mycenoid basidiomata, which emerge from infected and transformed host basidiomata/ tissue. Frequently, infected host basidiomata are so strongly altered, that their identification based on morphological characteristics is difficult or even impossible. *Squamanita* basidiomata feature a bulbous stipe base or gall, from which one or multiple *Squamanita* basidiomata may appear. These galls have been described using various terms such as "sclerotial body", "protocarpic tuber", "cecidiocarp", or "mycocecidium" (Bas, 1965; Singer, 1986; Bas & Thoen, 1998; Griffith et al., 2019). *Squamanita* species usually produce hyaline basidiospores, although some areas of the gills may comprise pigmented basidiospores, and produce a whitish to greyish spore deposit. Due to the unusual growth pattern of *Squamanita* species, which usually grow out of transformed host basidiomata, their original descriptions sometimes included morphological characteristics of the host fungus.

Currently, 17 *Squamanita* species are listed in Species Fungorum (2025). Nearly all of these species are considered as biotrophic mycoparasites, dependent on other agaric species such as *Amanita*, *Cystoderma*, *Galerina*, *Hebeloma*, *Inocybe*, *Kuehneromyces*, *Phaeolepiota*, and possibly *Mycena* (Bas, 1965; Gulden et al., 1977; Reid, 1983; Singer, 1986; Harmaja, 1988; Nagasawa et al., 1990; Redhead et al., 1994; Vizzini & Girlanda, 1997; Bas & Læssøe, 1999; Holden, 2005; Mondiet et al., 2007; Cervini et al., 2009; Matheny & Griffith, 2010; Henrici, 2013; Halama, 2016;

Griffith et al., 2019). The host species of *Squamanita* have primarily been identified based on morphological characteristics and ecological evidence (Bas, 1965; Mondiet et al., 2007), with a few exceptions where molecular phylogenetic techniques were employed to identify the hosts (Mondiet et al., 2007; Matheny & Griffith 2010; Griffith et al., 2019; Liu et al., 2021; Saar et al., 2022). Details about the nature of the interaction and ultrastructure of the host-parasite interface of *Squamanita* species are currently lacking and remain to be investigated. The members of *Squamanita* are considered as rare species, and have been reported from Belgium, Cameroon, China, Germany, Guyana, Italy, Japan, New Zealand, the UK and the USA (Holden, 2005; Matheny & Griffith 2010; Griffith et al., 2019; Fraiture et al., 2019).

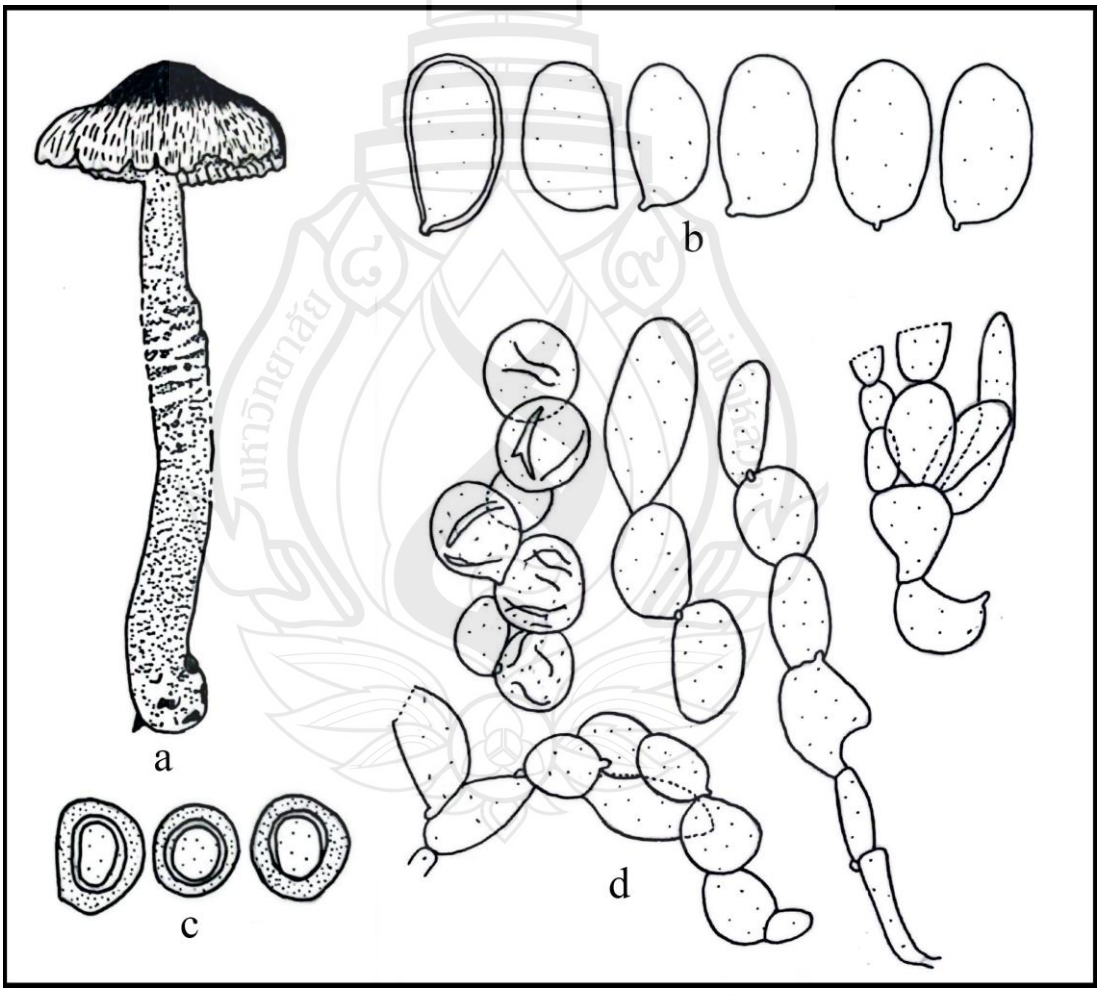


Figure 5.110 *Squamanita paradoxa*

Figure 5.110, a. Fruiting body. b. Spores. c. Chlamydospores. d. Chains of cells on limbs of volva (Redrawn from Bas, 1965).

Suborder *Tricholomatineae* Aime, Dentinger & Gaya

Lyophyllaceae Jülich

Asterophora Ditmar, Neues J. Bot. 3(1, 2): 56 (1809)

Figure 5.111

Index Fungorum number: IF 7267

Facesoffungi number: FoF 14369

Ditmar (1809) established *Asterophora*, with *A. lycoperdoides* as its type species. *Asterophora* species usually grow on the (decaying) basidiomata of other fungi (Redhead et al., 2001; Blanco-Dios, 2011; Chethana et al., 2023). The most frequent hosts are *Russulaceae* species, particularly those within *Lactarius* and *Russula* (Redhead et al., 2001; Blanco-Dios, 2011). Currently, it includes four recognized species: *A. lycoperdoides*, *A. mirabilis*, *A. parasitica*, and *A. salvaterrensis* (Blanco-Dios, 2011; Chethana et al., 2023; Species Fungorum, 2025). The nature of the interaction between *Asterophora* species and their hosts is unclear, and a true parasitic interaction remains to be proven. Oberwinkler (2012) studied the host-parasite interface and showed that the hyphae of *Asterophora* penetrate hyphae of the russuloid host.

Asterophora species are characterized by their production of chlamydospores. *Asterophora salvaterrensis* features a zonate, greenish-brown to brownish cap and smooth chlamydospores (Blanco-Dios, 2011). *Asterophora mirabilis* has a smooth cap, with chlamydospores formed in both the lamellar trama and the pileal trama above the lamellae (Blanco-Dios, 2011). *Asterophora parasitica* displays relatively larger basidiospores and smooth chlamydospores (Blanco-Dios, 2011). *Asterophora* species have been documented worldwide, including Australia, China, India, Turkey, Russia, Spain, Sweden, and Thailand (Wang et al., 2004; Sharma et al., 2007; Uzun et al., 2010; Chethana et al., 2023; Index Fungorum, 2025).

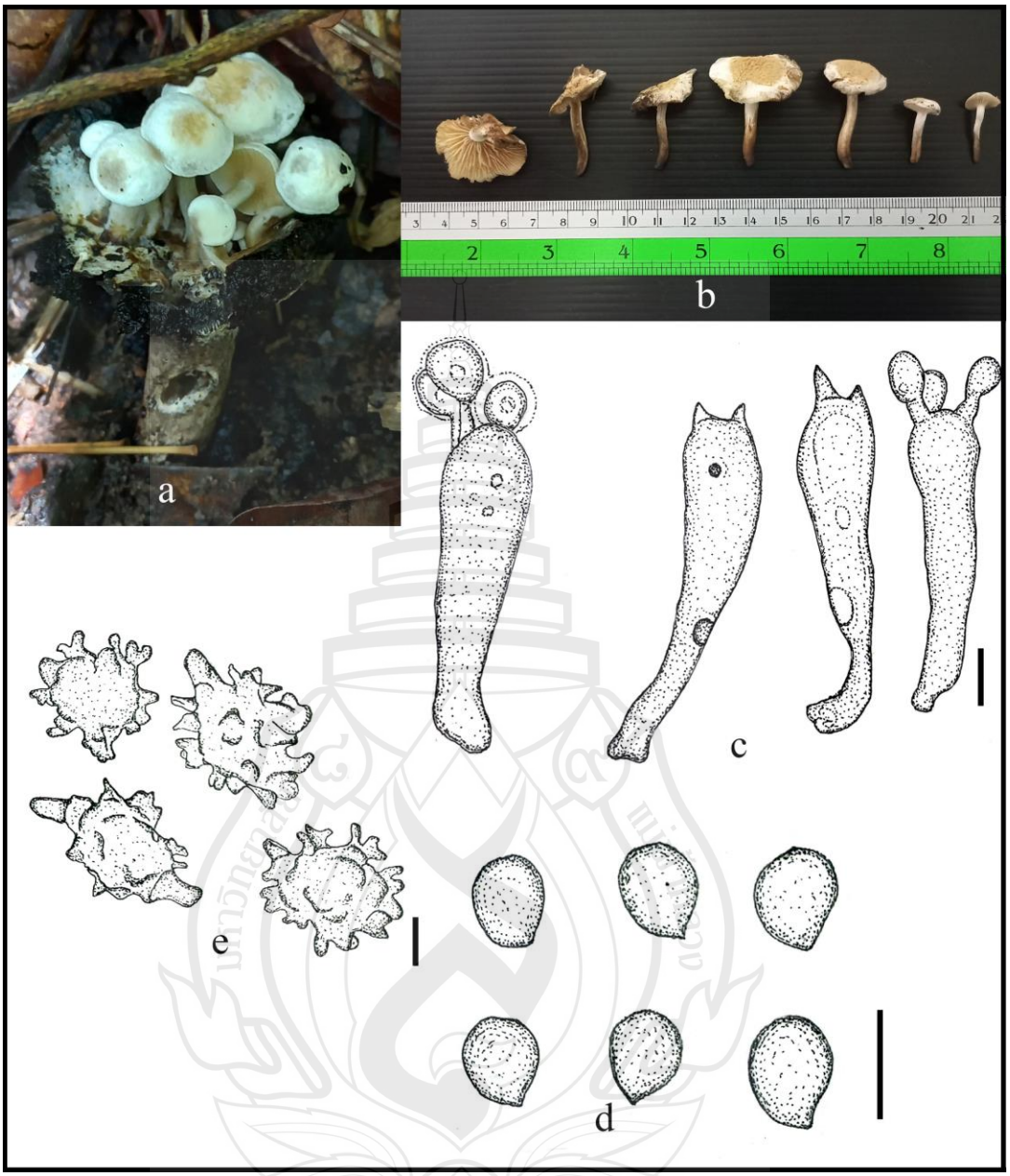


Figure 5.111 *Asterophora lycoperdoides*

Figure 5.111, a, b. Basidiomata. c. Basidia. d. Basidiospores. e Chlamydospores. Scale bars: e = 10 µm, c, d = 5 µm. (Adapted from Chethana et al., 2023).

Sebacinales M. Weiss, Selosse, Rexer, A. Urb. & Oberw.

Serendipitaceae M. Weiss, Waller, A. Zuccaro & Selosse

Serendipita P. Roberts, Mycol. Res. 97(4): 474 (1993)

Figure 5.112

Index Fungorum number: IF 22442

Roberts (1993) proposed four new genera to reclassify species that needed to be excluded from *Exidiopsis* during its revision. One of these newly proposed genera is *Serendipita*, which includes the type species *Serendipita vermifera* along with six additional species (Roberts, 1993). The name *Serendipita* was derived from the English word "serendipity," which refers to a chance discovery made while searching for something else (Roberts, 1993).

Serendipita species are characterized by basidiomes which are not visible to the unaided eye. They consist of sparsely branched, basidia-bearing hyphae that trail over the surface of decaying wood. The hyphae are exceptionally thin, either damped or undamped, hyaline, and have thin, refractive walls. Hyphidia are absent. The basidia are 2- to 4-septate, globose or ovoid when young, and become broadly ellipsoid as they mature. They typically arise singly on short side branches or sub-basidial cells at right angles to the main hyphae, eventually proliferating to form small clusters. Each basidium bears 1-4 sterigmata, which are tubular, sinuous, and generally short, often producing subsidiary sterigmata. The spores are often elongated (adapted from Roberts, 1993).

As of Species Fungorum (2025), there are 24 species within *Serendipita.* These species have been reported from Australia, Germany, China, Denmark, France, India, and the UK (Roberts, 1993; Index Fungorum, 2025). The members of *Serendipita* function as mycobionts in a diverse array of plant hosts worldwide, including grasses, ericoids, liverworts, and orchids (Weiss et al., 2016). *Serendipita* species have also been found in soil and as fungicolous taxa. For example, *Serendipita inclusa* (intrahymenial in *Botryobasidium botryosum*), *S. interna* (intrahymenial in *Hyphoderma obtusum*), and *S. vermifera* (in *Uthatobasidium fusisporum*) (Roberts, 1993; Index Fungorum, 2025).

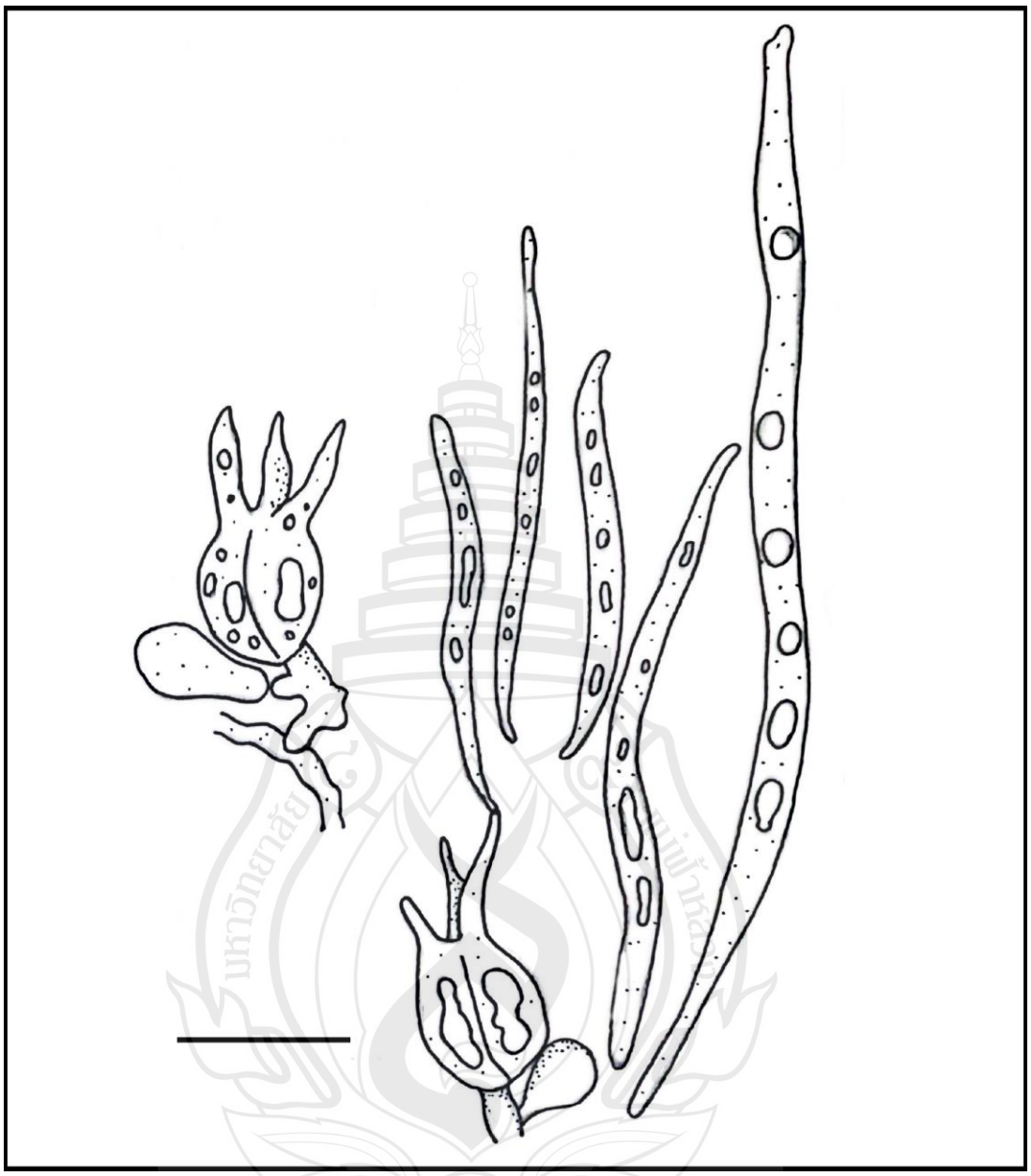


Figure 5.112 *Serendipita vermifera*

Figure 5.112, Basidia and spores. Scale bar = 10 μm. (Redrawn from Roberts 1993).

Class *Tremellomycetes* Doweld

Filobasidiales Jülich

Filobasidiaceae L.S. Olive

Syzygospora G.W. Martin, J. Wash. Acad. Sci. 27: 112 (1937)

Figure 5.113

Index Fungorum number: IF 18627

Martin (1937) introduced *Syzygospora* to accommodate *S. alba*, which he described as a peculiar tremella-like fungus growing on wood. This fungus is characterised by holobasidia and conidial structures, comprising paired blastogenous cells that fuse and detach from the conidiogenous cells. However, Martin (1937) did not recognize the holobasidia, and misinterpreted the conidiogenous cells of *S. alba*, describing them as a unique form of an auriculariaceous basidium. Kao (1956) examined *S. alba* collections from Martin, and revealed that the structures described by Martin were in fact conideogenous structures. Moreover, he found that these conidiogenous structures were linked to generative hyphae which are giving rise to holobasidia. Kao (1956) also clarified the nuclear behavior during the formation of conidia. Oberwinkler and Lowy (1981) recognized *S. alba* as a mycoparasite of a corticioid fungus, interacting with tremelloid haustorial cells of which the apices attach to host hyphae. Also, the authors discussed the basidiomycete affinity of *S. alba*, and its potential relationship to *Filobasidiales* based on the ultrastructure of its septal pore complexes, comprising dolipores without parenthesomes (Oberwinkler & Lowy, 1981).

Syzygospora species are characterized by basidiomata which are gelatinous and subhyaline when moist, but become glossy and crust-like upon drying (Oberwinkler & Lowy, 1981; Oberwinkler et al., 1984; Ginns 1986). They are typically visible as smooth to cerebriform galls on host basidiomata. The hyphae are hyaline and thin-walled, with some species exhibiting clamp connections. The basidia are holobasidiate, sometimes incompletely cruciately septate at the apex, suburniform to cylindrical-clavate, and contain up to 6 sterigmata. Basidiospores are thin-walled, smooth, and germinate by secondary spores or yeast budding. In some species, blastoconidia are produced from conidiogenous cells. The host parasite interface of *Syzygospora* species comprises tremelloid haustorial cells, of which the apices attach to, or partially invaginate host hyphae (Bauer & Oberwinkler, 1990; Bauer 2004). To date, the best studied species is *S. pallida*, a mycoparasite of *Phanerochaete cremea*. The life cycle of *S. pallida* was investigated by Oberwinkler et al. (1984), and the ultrastructure of its host-parasite interface was investigated by Bauer and Oberwinkler (1990).

Most *Syzygospora* species are known from morphological descriptions only, and molecular DNA sequence data are available only for a limited number of *Syzygospora* species (Millanes et al., 2011; Diederich et al., 2022; Schoutteten et al., 2024a). Molecular phylogenetic studies have revealed that *Syzygospora* is polyphyletic, and the included species belong to various clades in *Filobasidiales* and *Tremellales* (Millanes et al., 2011; Liu et al., 2015b). Based on these insights, only *S. alba* and *S. pallida* belong to *Syzygospora sensu stricto*, and it remains to be investigated to which clades the currently unsequenced *Syzygospora* species belong.

Currently, 12 *Syzygospora* species are listed in Species Fungorum (2025). These species have been documented across a diverse geographical range, including countries such as Austria, Canada, Costa Rica, Denmark, Finland, Germany, Mexico, Norway, Panama, Sweden, Switzerland, Taiwan, China and the USA. *Syzygospora* species are presumed mycoparasitic on agaricoid and corticioid fungi. Schoutteten et al. (2024a) summarize the host-parasite associations of the currently known *Syzygospora sensu lato* species. Several species with a syzygospora-like morphology have been found in association with lichens (Diederich, 1996, 2022). These species were assigned to *Syzygospora* (Diederich, 1996). Based on molecular phylogenetic reconstructions, Diederich et al. (2022) introduced *Zyzygomyces* to accommodate these syzygospora-like lichenicolous fungi. Due to the lack of DNA sequence data, two lichenicolous syzygospora-like species are tentatively assigned to *Syzygospora* (Diederich et al., 2022). The nature of the interaction between *Zyzygospora* species and their lichen hosts remains to be investigated (Diederich et al., 2022).

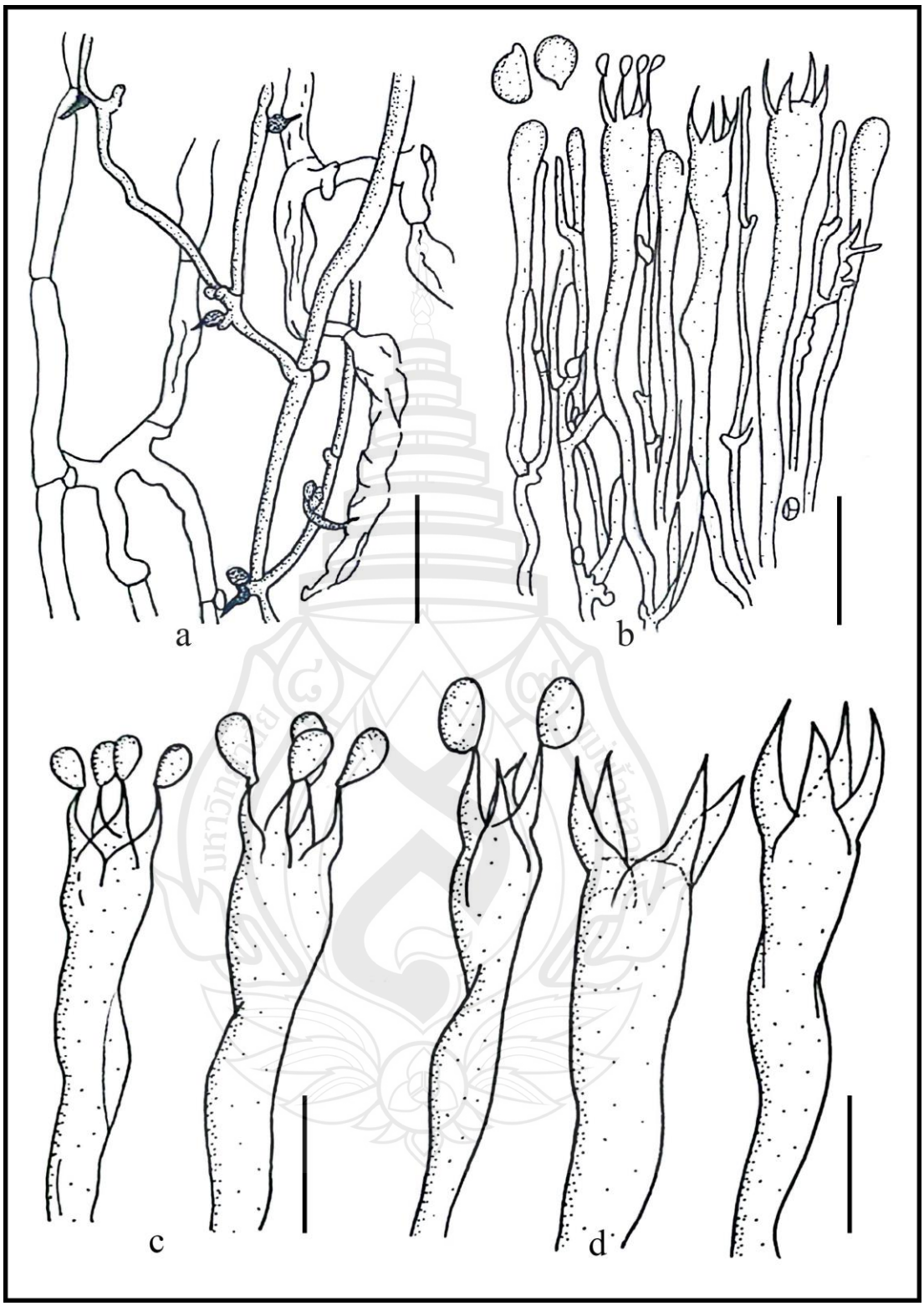


Figure 5.113 *Syzygospora alba*

Figure 5.113, a. Hyphal context of the inner part of the basidiocarp, hyphae of the parasite connected to the host cells with tremelloid haustoria. b. Part of the

hymenium with different stages of basidial development, and basidiospores. c. Apical parts of basidia with young basidiospores. d. Apical details of mature basidia with central figure showing a partial septum. Scale bars: a, b = 20 μm, c, d = 10 μm. (Redrawn from Oberwinkler & Lowy, 1981).

Tremellales Fr.

Naemateliaceae X. Z. Liu, F. Y. Bai, M. Groenew. & Boekhout

Naematelia Fr., Observ. mycol. (Havniae) 2: 370 (1818)

Figure 5.114

Index Fungorum number: IF 18113

Naematelia was introduced in Fries's contribution to Liljeblad (1816), where *N. encephala* and *N. fragiformis* were included. However, this initial publication lacked a clear generic diagnosis and thus *Naematelia* was not validly published. The valid publication of *Naematelia* is credited to Fries (1818). *Naematelia* was lectotypified with *N. encephala* (Clements & Shear, 1931; Hawksworth et al., 2016). Following several taxonomic revisions, *Naematelia* was resurrected to accommodate species within the *Tremella aurantia* clade based on molecular phylogenetic analysis (Chen, 1998; Millanes et al., 2011; Liu et al., 2015b). Liu et al. (2015b) also established *Naemateliaceae* to include *Naematelia*.

Naematelia is characterized by basidiomata that are cerebriform, caespitose, tuberculate, or spherical to thickly foliaceous or crumpled, with colors ranging from ivory to yellow, bright orange, or reddish. Basidia are subglobose to ovoid, four-celled, and have vertical or occasionally transverse septa. The hyphal system is monomitic, with clamp connections at all septa. Basidiospores germinate by secondary spores, hyphae or yeast budding (Roberts, 1995, 1999; Weiss et al., 2014).

Four species are assigned to *Naematelia* (Bandoni & Zang, 1990; Chen, 1998). Three *Naematelia* species are considered mycoparasites of *Stereum* species (*Russulales*). For *N. microspora*, the host is unknown, but most likely the mycoparasite is also associated with a *Stereum* species (Schoutteten et al., 2024a). The host-parasite interface of all four species comprises basally clamped tremelloid haustorial cells (Schoutteten et al., 2024a). Zugmaier et al. (1994) showed that nanometer size fusion pores are produced in the apex of its haustorial cells connecting to host hyphae. Remarkably, the central part of *Naematelia* basidiomata comprises a

white area which has been shown to represent tissue of the host fungus, probably enlarging the contact surface between host and parasite (Roberts, 1995, 1999). *Naematelia aurantialba* is also valued as both a tonic food and a medicinal product (Sun et al., 2023c; Huang et al., 2024; Tang & Yang, 2024). *Naematelia* species have been reported in most European countries, China, and the USA (Hawksworth et al., 2016).

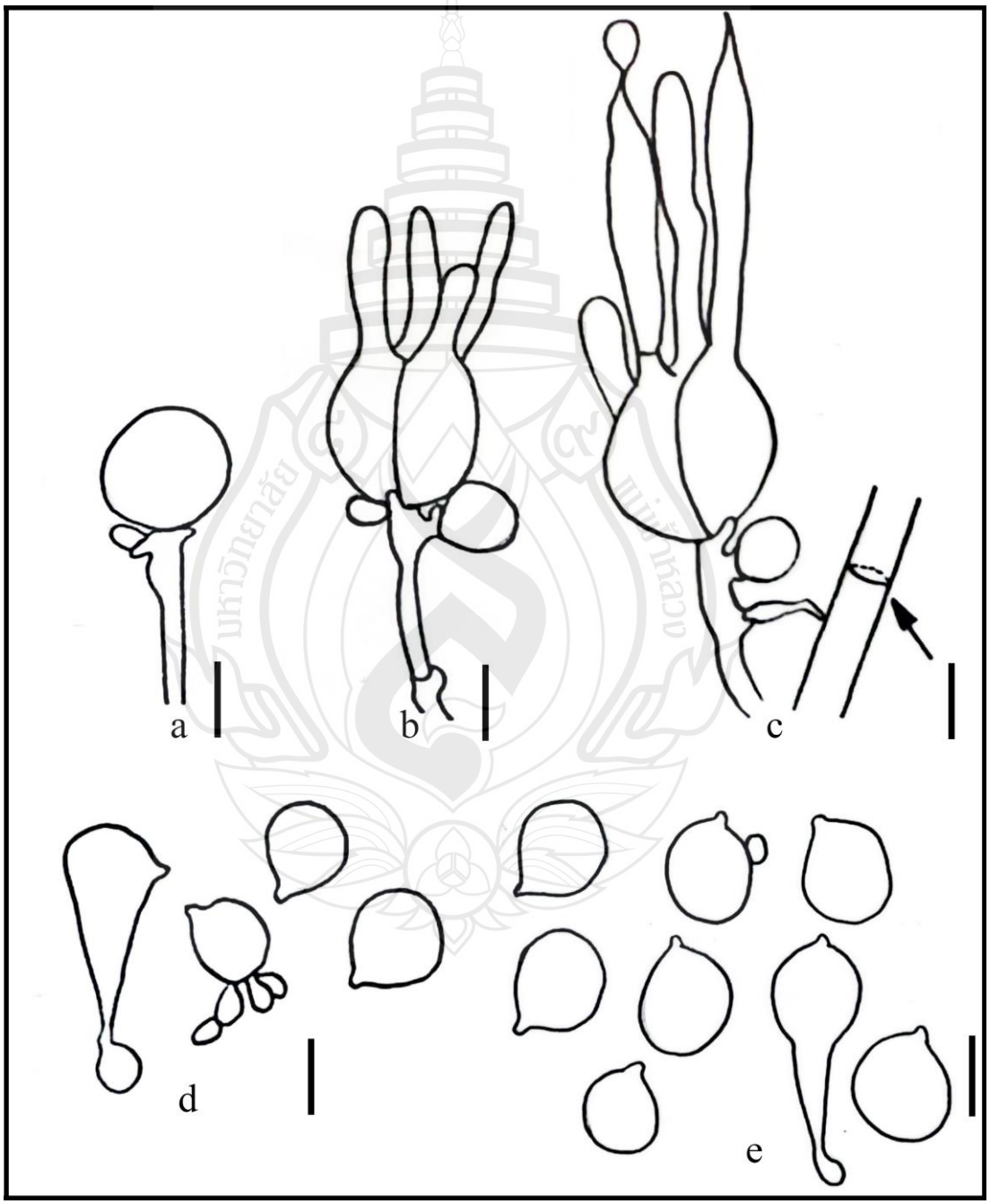


Figure 5.114 *Naematelia aurantialba*

Figure 5.114, a–c. Basidia at different stages of development (a haustorium attached to a host hypha is shown by arrow in “c”). d, e. Basidiospores germinating by budding or by repetition. Scale bars: a–e = 10 µm. (Redrawn from Tang & Yang 2024).

Phaeotremellaceae A.M. Yurkov & Boekhout

Phaeotremella Rea, Trans. Br. mycol. Soc. 3(5): 377 (1912) [1911]

Figure 5.115

Index Fungorum number: IF 18243

Rea (1912) described *Phaeotremella* to include *P. pseudofoliacea*. *Phaeotremella pseudofoliacea* was considered synonymous with *Tremella foliacea* (Roberts, 1999a). However, the taxonomy of *Tremella foliacea* remained controversial. Wedin et al. (2016) recombined *T. foliacea* into *Phaeotremella* without revising the species concept or clearly distinguishing it from morphologically similar species and potential taxonomic synonyms. *Phaeotremella* was resurrected and emended to accommodate the *Tremella foliacea* group, which was recognized as a well-supported monophyletic clade (Liu et al., 2015b; Spirin et al., 2018). Liu et al. (2015b) established *Phaeotremellaceae* to accommodate *Phaeotremella* in it.

Phaeotremella species are commonly known as jelly fungi which produce conspicuous foliar, gelatinous basidiomata with clustered lobes. Their hyphae exhibit clamp connections. The basidia are globose to ellipsoidal, four-celled, and septate. The basidiospores are subglobose to broadly ellipsoidal, and germinate by secondary spores, hyphae, or yeast budding (Rea, 1912; Liu et al., 2015b; Spirin et al., 2018; Lebeuf et al., 2023).

There are 22 species listed under *Phaeotremella* in Species Fungorum (2025). These species have been recorded in several countries, including Canada, China, the Czech Republic, Finland, Germany, Japan, the Netherlands, Norway, Russia, Sweden, the UK, and the USA (Spirin et al., 2018; Index Fungorum, 2025). *Phaeotremella* species are reported to associate with fungal hosts, plant substrates, lichens, and water (Spirin et al., 2018; Li et al., 2019c; Sun et al., 2020; Lebeuf et al., 2023; Kachalkin et al., 2024). When considering the fungicolous taxa, several *Phaeotremella* species, including *P. dejopia*, *P. fimbriata*, *P. foliacea*, *P. frondosa*, and *P. fuscosuccinea*, are identified as mycoparasites on *Stereum* species (Roberts, 1999a; Spirin et al., 2018;

Lebeuf et al., 2023). *Phaeotremella translucens* is associated with *Lophodermium conigenum*, while *P. mycetophiloides*, *P. mycophaga*, and *P. simplex* are parasitic on *Aleurodiscus* species (Kobayasi, 1939; Martin, 1940; Bandoni & Ginns, 1993).

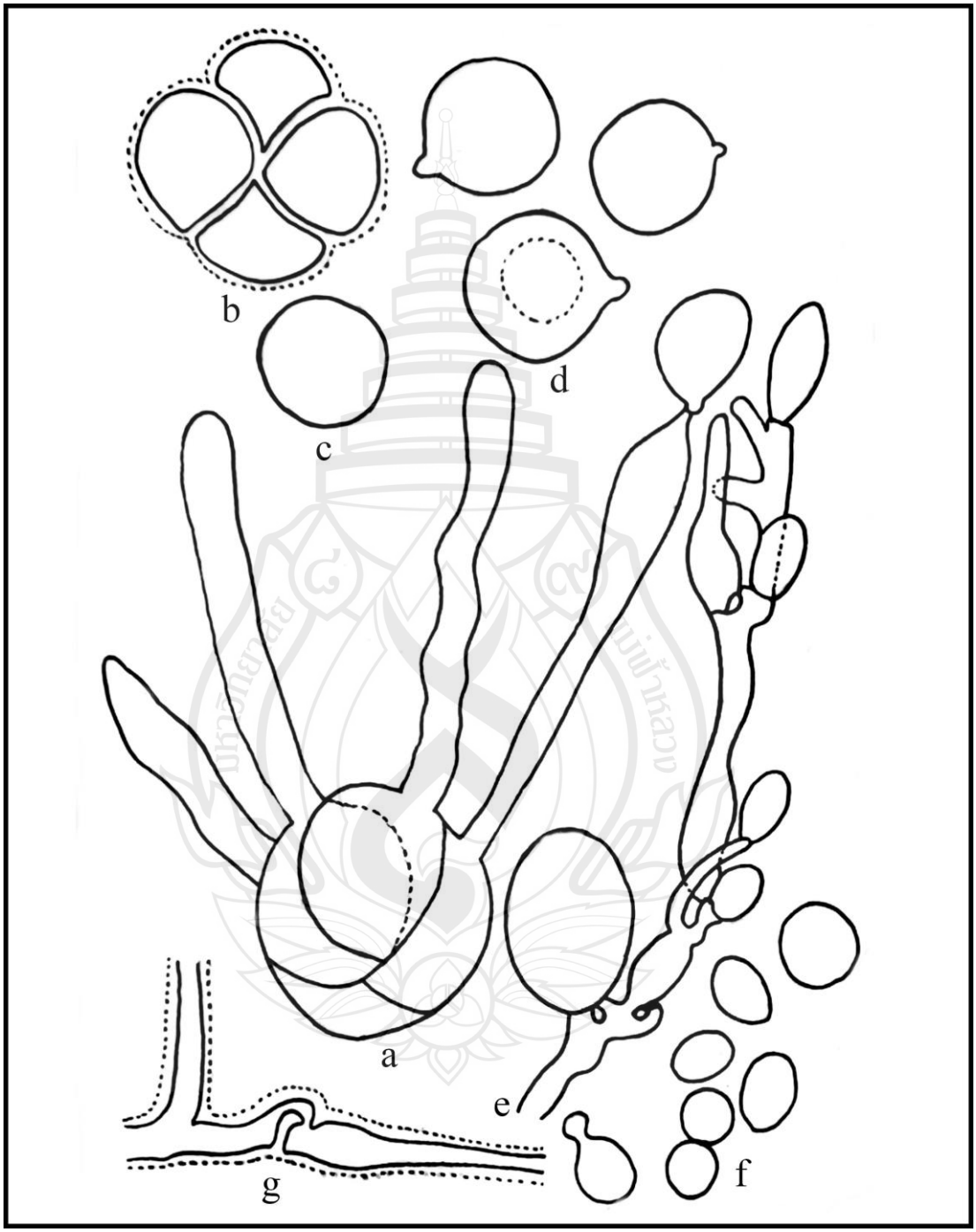


Figure 5.115 *Phaeotremella mycophaga*

Figure 5.115, a. Detached basidium. b. Septate, thick walled, hypobasidium. c. Basidiospore like body apparently derived from segment of a hypobasidium. d.

Basidiospores. e. Hypha with clamp connections bearing probasidium and conidia. f. Detached conidia. g. Internal hypha with clamp connections. (Redrawn from Martin, 1940).

Phragmoxenidiaceae Oberw. & R. Bauer

Phragmoxenidium Oberw., Syst. Appl. Microbiol. 13: 187 (1990)

Figure 5.116

Index Fungorum number: IF 25109

The monotypic genus *Phragmoxenidium* was introduced by Oberwinkler et al. (1990a), to accommodate *P. mycophilum*, an intrahymenial mycoparasite of *Rhizoctonia fusispora* (syn. *Uthatobasidium fusisporum*), collected in Switzerland. *Phragmoxenidium mycophilum* is known from the type locality in Switzerland. A second collection was reported from Norway, developing in the same host (Spirin et al., 2016).

Phragmoxenidium mycophilum develops completely intrahymenial. The hyphal system is monomitic, with unclamped septa. The basidia are transversely 3-septate, with each cell bearing a single sterigma. The basidiospores are subglobose to ellipsoid, thin-walled, and smooth, and germinate by secondary spores or globose microconidia (Oberwinkler et al., 1990). Yeast budding was not observed. The host-parasite interface is unusual, and comprises closely attached hyphae of host and mycoparasite, associated with the formation of small pores. However, no cytoplasmic continuity was observed (Oberwinkler et al., 1990a). The septal pores are dolipores that lack parenthosomes. Based on the septal pore morphology, this species was tentatively assigned to *Tremellomycetes* (Oberwinkler et al., 1990a). However, no molecular data are available for this fungus (GenBank, 2025), and its classification remains to be assessed by molecular phylogenetic reconstructions.

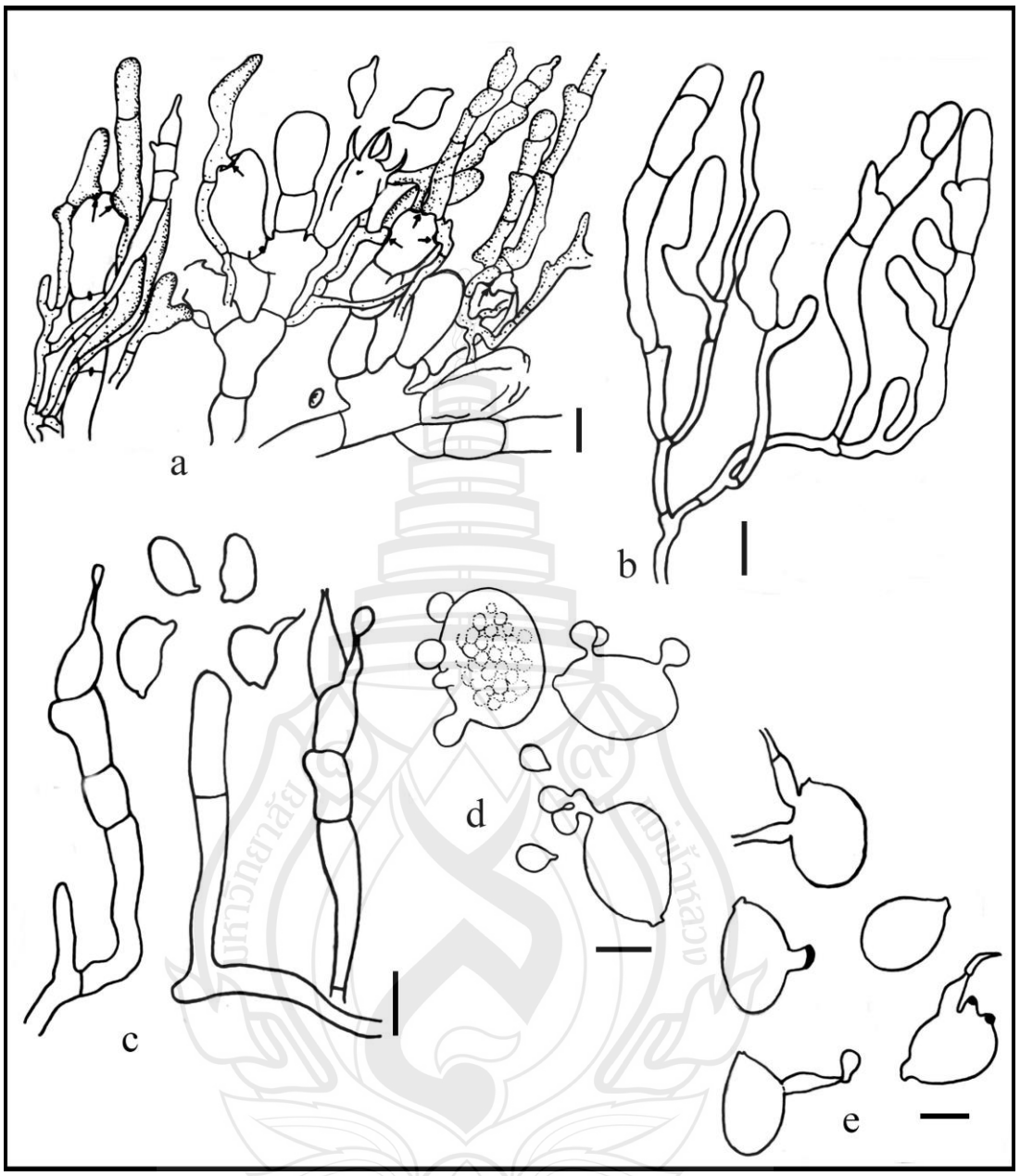


Figure 5.116 *Phragmoxenidium mycophilum*

Figure 5.116, a. Sections through fructifications of *Uthatobasidium fusisporum*, parasitized by *Phragmoxenidium mycophilum* with hyphae, basidia and basidiospores. (*Uthatobasidium fusisporum* with broad hyphae, holobasidia and naviculate basidiospores, two germinating by repetition. *Phragmoxenidium mycophilum* with small hyphae, transversely septate basidia and subglobose to ellipsoid basidiospores. Tight attachments of host and parasite are shown by arrows). b, c. Basidia of in different developmental stages and basidiospores. d, e.

Basidiospores of germinating with microconidia and secondary spores. Scale bars: a–c = 10 µm, d, e= 5 µm. (Redrawn from Oberwinkler et al., 1990a).

Sirobasidiaceae Lindau

Sirobasidium Lagerh. & Pat., J. Bot., Paris 6: 468 (1892)

Figure 5.117

Index Fungorum number: IF 18549

Sirobasidium was established by Lagerheim and Patouillard (1892) to encompass two species, *S. albidum* and *S. sanguineum*, which were collected in Ecuador. Möller (1895) added another species, *S. brefeldianum*, and also established *Sirobasidiaceae* to accommodate *Sirobasidium*.*Sirobasidiaceae* was validated by Lindau in 1897 (Dämon & Hausknecht, 2002). Based on morphological characteristics, there has been considerable debate regarding species delimitation and the taxonomic placement of *Sirobasidium* at higher ranks (Dämon & Hausknecht, 2002). There are 10 species recognized within *Sirobasidium* (Yamada et al., 2022; Schoutteten et al., 2024a). Molecular phylogenetic analyses have revealed that *Sirobasidium* is polyphyletic within the *Tremellales* (Liu et al., 2015b; Kachalkin et al., 2019; Yamada et al., 2022). In current classifications, *Sirobasidium* is placed within *Tremellales, Incertae sedis* (Wijayawardene et al., 2022; Index Fungorum, 2025).

Sirobasidium species are distinguished by their basidiomes, which range from pustulate to cerebriform. They produce two- or four-celled basidia arranged in chains, and exhibit a dimorphic life cycle (Lagerheim & Patouillard, 1892; Bandoni, 1957; Bandoni et al., 2011; Yamada et al., 2022; Schoutteten et al., 2024a). *Sirobasidium* species have been reported worldwide, including Australia, Austria, Belgium, Brazil, Costa Rica, Ecuador, France, Germany, Indonesia, Japan, the Netherlands, and the USA (Boedijn, 1934; Dam & Dam, 2014; Dämon & Hausknecht, 2002; Bandoni et al., 2011; Kisimova-Horovitz et al., 2000; Kobayashi, 1962; Rödel & Putzmann, 2015; Van de Put, 1994, 1995; Index Fungorum, 2025). Most of these species have been typically associated with woody substrates. However, some species such as *S. indicum* (on *Eutypa*), *S. magnum* (associated with pyrenomycetous stromata), and *S. sandwicense* (on *Diatrypella favacea*) have been identified as fungicolous (Dämon & Hausknecht, 2002; Bandoni et al., 2011; Rödel & Putzmann, 2015; Schoutteten et al.,

2024a). However, no previous studies reported on the host-parasite interface of *Sirobasidium* species, and the nature of the interaction between *Sirobasidium* and the associated fungi remains to be investigated (Schoutteten et al., 2024a).

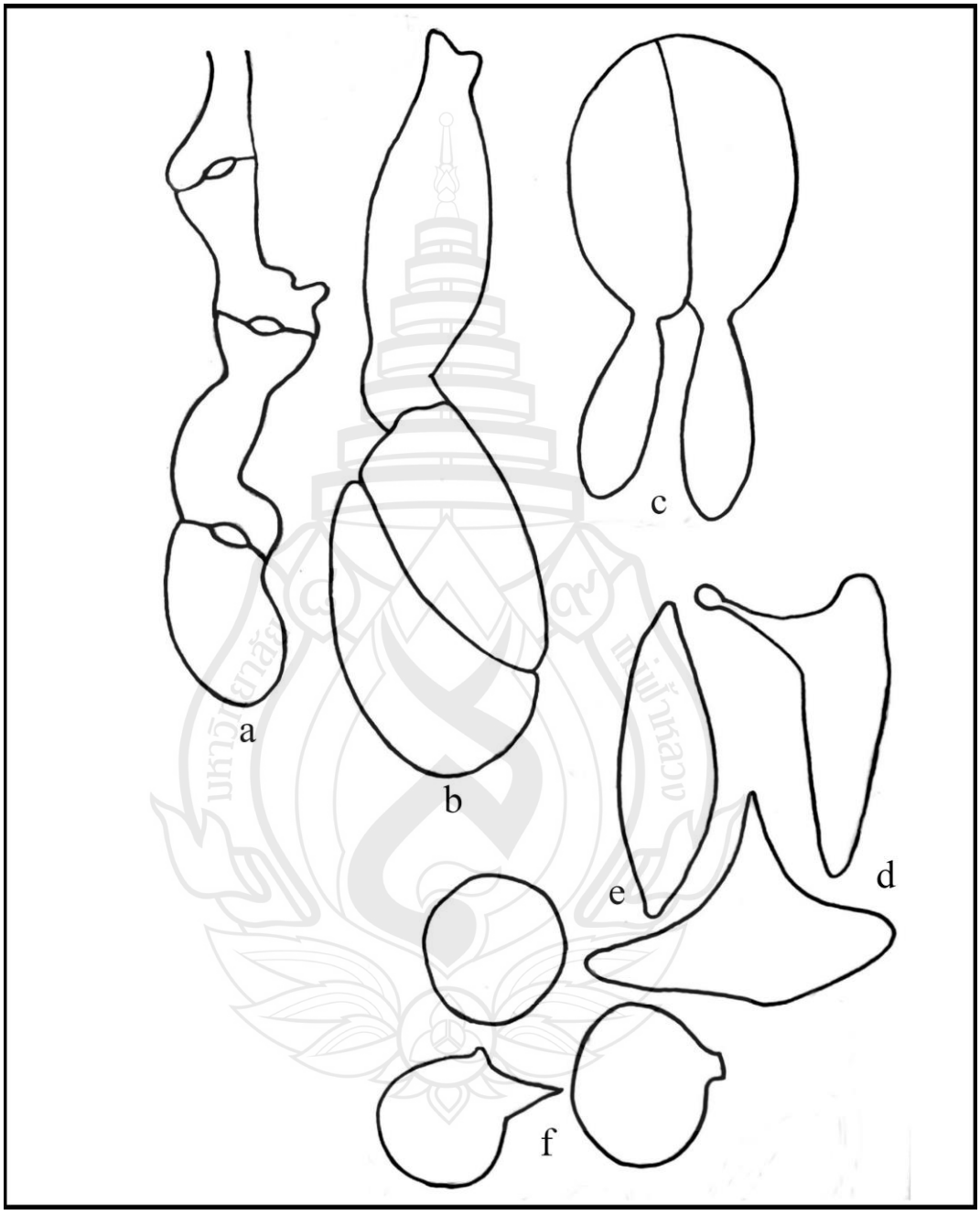


Figure 5.117 *Sirobasidium sanguineum*

Figure 5.117, a. Fertile hypha showing development of cells destined to become basidia. b. Probasidia. c. Mature basidium before epibasidia have been shed.

d. Epibasidium e. Two epibasidia germinating by production of tubes tipped with sterigmata. f. Basidiospores. (Redrawn from Bandoni, 1957).

Tremellaceae Fr.

Tremella Pers., Syn. meth. fung. (Göttingen) 2: 622 (1801)

Figure 5.118

Index Fungorum number: IF 18665

Tremella sensu lato, typified by *T. mesenterica*, is considered the largest genus within the *Tremellales* (Boekhout et al., 2011; Weiss et al., 2014; Liu et al., 2015b, c). Based on morphological and molecular phylogenetic studies, Chen (1998) already recognized five distinct groups within *Tremella sensu lato*, which he referred to as the *T. mesenterica*, *T. fuciformis*, *T. indecorata*, *T. foliacea*, and *T. aurantia* groups. These groups were also recognized as distinct clades in later studies, where it became clear that the morphological genus concept of *Tremella* is in fact a polyphyletic gathering. Phylogeny-informed classification of the *Tremellomycetes* species within the *Mesenterica* and *Fuciformis* groups were assigned to *Tremella sensu stricto*, while those in the Indecorata, Foliacea, and Aurantia groups were reclassified into *Pseudotremella*, *Phaeotremella*, and *Naematelia*, respectively (Liu et al., 2015c; Wedin et al., 2016; Spirin et al., 2018).

The members of *Tremella sensu lato* are dimorphic fungi characterized by two distinct life stages: a haploid unicellular yeast phase and a dikaryotic filamentous phase (Zhao et al., 2019). The basidiocarps of *Tremella* species range in size from minute to large and exhibit variable coloration, including whitish-yellow, cream, yellowish-orange, brown, reddish, or black hues. Dikaryotic hyphae are characterized by the presence of clamp connections and haustorial branches (Liu et al., 2015c). The basidia are globose, subglobose, ellipsoid, oval, clavate, or pyriform, and are typically two- or four-celled with longitudinal or oblique septa, though transverse septa may occasionally occur. Basidiospores are globose to ellipsoid, and budding cells develop from germinating basidiospores. Yeast states lack fermentation capability, and nitrate is not utilized. The primary coenzyme Q (CoQ) systems are CoQ-9 or CoQ-10 (Liu et al., 2015c).

The taxa within *Tremella* are found to be lichenicolous, fungicolous, or associated with plant substrates, and they exhibit a worldwide distribution (Kout et

al., 2015; Lindgren et al., 2015; Bera et al., 2018; Spirin et al., 2018; Diederich et al., 2022; Zhao et al., 2019; Fan et al., 2021). Several species demonstrate a fungicolous lifestyle, including *Tremella abrothalli* (on apothecia of *Abrothallus parmeliarum*), *T. basidiomaticola* (on basidiomata of *Tremella fuciformis*), *T. brodoae* (on *Brodoa intestiniformis*), *T. caloceraticola* (on *Calocera cornea*), *T. dactylobasidia* (on *Dendrothele macrospora*), *T. discicola* (in the hymenium of *Mollisia*), *T. episphaerica* (on *Diatrype*), *T. flava* (on ascocarps of *Hypoxylon*), *T. fuciformis* (on a pyrenomycete), *T. hymenophaga* (on *Scytinostroma odoratum*), *T. invasa* (in *Trechispora microspora*), *T. occultifuroidea* (in basidiomata of *Dacrymyces*), *T. penetrans* (on *Dacrymyces stillatus*), *T. poilkavensis* (on ascomata of *Biscogniauxia*), *T. rhytidhysterii* (on ascocarps of *Rhytidhysteron rufulum*), *T. resupinata* (on stromata of *Hypoxylon*), *T. sarniensis* (in the hymenium of *Phanerochaete sordida*), *T. silvae-dravedae* (on an unidentified fungus), *T. spicifera* (on *Massarina arundinacea*), *T. subencephala* (on *Acanthophysium lividocoeruleum*), *T. telleriae* (on *Oligoporus leucomallellus*), and *T. versicolor* (on *Corticium nudum*) (Schoutteten et al., 2024a).

In addition to its ecological diversity, *Tremella* includes edible and medicinal species, such as *T. fuciformis*, which is known for its rich bioactive compounds, including proteins, polysaccharides, dietary fiber, and trace elements (Wu et al., 2019; Yang et al., 2019). The hydrocolloids derived from *Tremella* have shown potential applications as food texture modifiers, antioxidants, and anti-aging agents in the food industry (Zhang et al., 2023). The genus comprises around 170 recognized species (Hyde et al., 2024a).

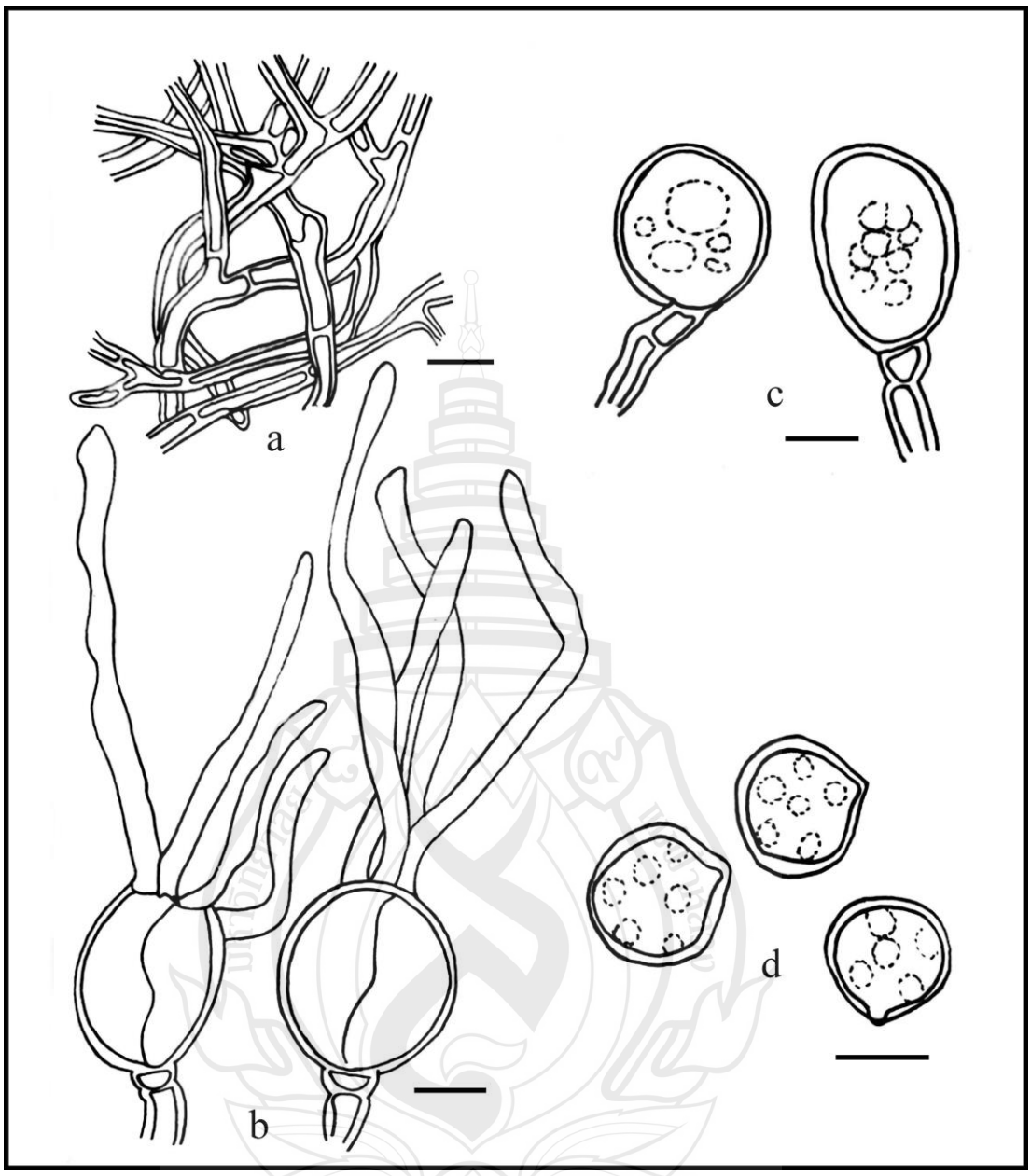


Figure 5.118 *Tremella mesenterica*

Figure 5.118, a. Hyphae. b. Basidia. c. Swollen cells. d. Basidiospores. Scale bars: a–d = 10 μm. (Redrawn from Bera et al., 2018).

Trimorphomycetaceae X. Z. Liu, F.Y. Bai, M. Groenew. & Boekhout

Trimorphomyces Bandoni & Oberw., Syst. Appl. Microbiol. 4(1): 106 (1983)

Figure 5.119

Index Fungorum number: IF 25672

Trimorphomyces was introduced by Oberwinkler and Bandoni (1983) to accommodate *T. papilionaceus*, a dimorphic mycoparasite of *Arthrinium* species (*Xylariales*, *Sordariomycetes*), developing small, pulvinate, slimy basidiomata engulfing host structures on gramineous plants (Oberwinkler & Bandoni, 1983).

Trimorphomyces species develop pulvinate, slimy basidiomata. Monomytic, hyphae hyaline, smooth, clamped. Conidiogenous cells clavate to phialide-like, giving rise to blastogenous conidia developing in pairs. Conidia elliptic to cylindrical in early development, later fusing together resulting in a H-shaped zygoconidium prior to release. Zygoconidia dikaryotic, germinating by hyphae (in presence of the host), or dikaryotic yeast cells. Basidia develop from clavate, thin-walled probasidia, thin-walled, longitudinally septate, four-celled at maturity, stalked, basally clamped, bearing four sterigmata. Basidiospores subglobose to broadly oval, germinating by secondary spore production or budding, giving rise to haploid yeast cells. The host-parasite interface comprises basally clamped haustorial cells, which attach with their globular apex to host hyphae. At the contact surface, a nanometer fusion pore is produced, establishing a cytoplasmic connection between the host hypha and the mycoparasite haustorial cell (Oberwinkler & Bandoni, 1983).

The morphologically similar *Trimorphomyces nebularis* was described by Kirschner and Chen (2008) from Taiwan, China. However, molecular phylogenetic reconstructions have shown that the ex-type culture belongs to *Vishniacozyma* (Liu et al., 2015b, c). It is unclear whether Kirschner and Chen isolated the trimorphomyces-like fungus or a contaminant belonging to *Vishniacozyma*. The latter genus comprises various species that are frequently isolated from a multitude of substrates, including other fungi. If Kirschner and Chen (2008) isolated the correct trimorphomyces-like fungus, then the unique morphology of *Trimorphomyces* occurs in at least two, distinctly related genera of *Tremellomycetes*.

Trimorphomyces species are known from Belgium, Canada, the Netherlands, and the UK (Oberwinkler & Bandoni, 1983; Spooner, 1994; Van de Put, 2001). In most reported collections, only the conidial stage was observed and none of the collections reported after the formal description were deposited in culture collections and the identity confirmed by molecular methods.

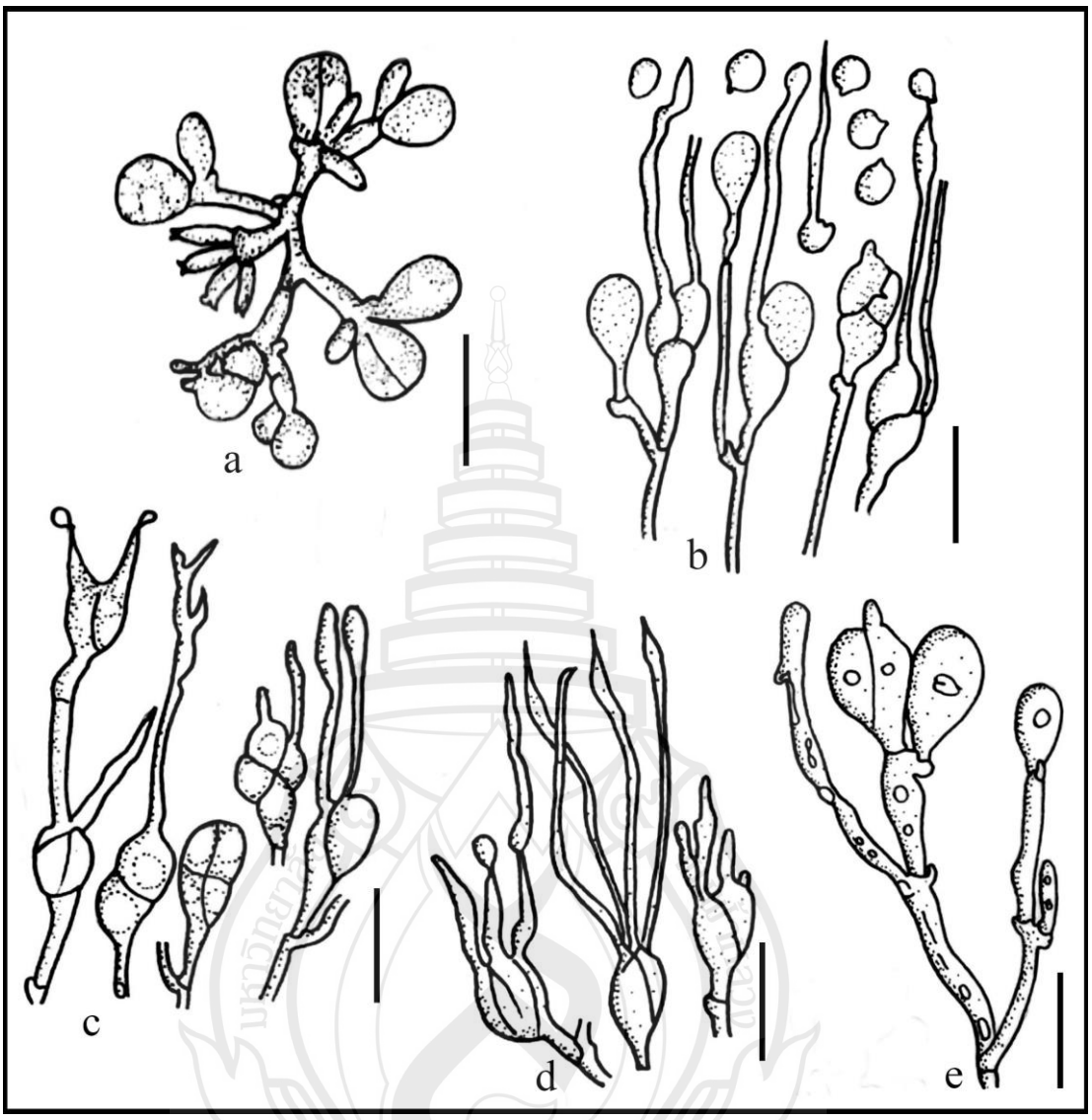


Figure 5.119 *Trimorphomyces papilionaceus*

Figure 5.119, a–e. Fertile hyphae with basidia, developing basidiospores, and mature basidiospores. Scale bars: a–d = 20 μm, e = 10 μm. (Redrawn from Oberwinkler & Bandoni, 1983).

Tremellales* genera *incertae sedis

Tremellina Bandoni, Windahlia 16: 53 (1986)

Index Fungorum number: IF 25079

The monotypic genus *Tremellina* was introduced by Bandoni (1986) to accommodate *T. pyrenophila*, a sporodochia-producing mycoparasite engulfing ascomata of *Ceratocystis* sp. on a decaying palm leaf.

Tremellina pyrenophila produces (sub)globose sporodochia-like basidiomata, sometimes fusing together producing a gelatinous layer. Monomytic, hyphae thin-walled, comprising short hyphal cells, with infrequent clamp connections. Basal hyphae with irregular shapes, described as 'pseudoparenchymata-like'. Conidiogenous cells bear finger-like clamp vestiges at sites of conidiogenesis. Conidia holoblastic, single or in clusters, sometimes formed in acropetal chains, thick-walled, globose to ellipsoid to ovoid. No structures for sexual reproduction observed (Bandoni, 1986a).

The host-parasite interface comprises (basally clamped) tremelloid haustorial cells, which attach to host hyphae (Bandoni, 1986a). No ultrastructural details about the host-parasite interface were reported. *Tremellina pyrenophila* is known exclusively from the type locality in the USA. There are no molecular DNA sequence data available for *Tremellina* in GenBank (2025).

Sigmogloea Bandoni & J.C. Krug, Mycoscience 41(4): 376 (2000)

Figure 5.120

Index Fungorum number: IF 28447

Bandoni and Krug (2000) established the monotypic genus *Sigmogloea*, to accommodate *S. tremelloidea*. This species is a presumed mycoparasite, associated with perithecia of *Coniochaeta* sp. (*Coniochaetales*) and was collected in Canada (Bandoni & Krug, 2000).

Sigmogloea tremelloidea is characterized by its gelatinous, thin basidiomata, developing as an effused layer over the host. The hyphal system is monomitic, with hyaline, thin-walled hyphae with clamp connections. Probasidia initially appear ellipsoid to obovoid, then develop into pyriform structures, sometimes umbonate, later elongating into bent cylindrical forms that are typically sigmoid, and transversally 2- to 3-septate. The basidiospores are ovoid to ellipsoidal, smooth, hyaline, thin-walled, inamyloid, and germinate by secondary spores (adapted from Bandoni & Krug, 2000). No yeast budding was observed. Conidiophores give rise to blastic single- and zygoconidia. The host-parasite interface comprises short, basally clamped haustorial cells attaching to host hyphae, but their ultrastructure was not previously investigated. There are no molecular DNA sequence data available for *Sigmogloea* (GenBank, 2025).



Figure 5.120 *Sigmogloea tremelloidea*

Figure 5.120, a. Basidia with developing epibasidia. b, c. Basidia with developing epibasidia and basidiospores. d. Mature basidium. e. basidiospores. f.

Basidiospores germinating by repetition. g. Young probasidia with thickened umbos are shown by arrows. h. Mature sigmoid probasidium. i. Spent basidium. j. Mature probasidium. k. Paired mature probasidia. l, m. Probasidia with the basal septum. n. Mature probasidia with chlamydospores. o. Mature probasidium with the attachment. p. Basidiospores. q. Conidiogenous cells with single and paired blastic conidia. r. Conidia. s. Haustorial branches attached to host cells. Scale bars: a– f, g–s = 10 μm. (Redrawn from Bandoni & Krug, 2000).

Sirotrema Bandoni, Canad. J. Bot. 64(3): 668 (1986)

Figure 5.121

Index Fungorum number: IF 25776

Bandoni (1986) introduced *Sirotrema* to include three species, i.e., *S. parvula*, *S. pusilla*, and the previously described *S. translucens*, that parasitize rhytismataceous fungi. *Sirotrema pusilla*, which was found developing in the ascomata of *Hypoderma pacificensis* collected in British Columbia (Canada), was designated as the type species of the genus. *Sirotrema parvula* grows on ascomata of *Lophodermium pinastri*, also collected in British Columbia (Canada). Yamada et al. (2022), combined *S. translucens* to *Phaeotremella translucens* based on a molecular phylogenetic reconstruction. *Sirotrema* species share basidiome characteristics with those in *Sirobasidium* and *Tremella*, which was the reason for naming the genus "*Sirotrema*" (Bandoni, 1986b).

Sirotrema species are characterized by, minute, gelatinous, hyaline to faintly colored basidiomata. The hyphal system is monomitic, with clamp connections. Basidia occur singly or occasionally in chains, are usually subglobose to elongated, display irregular septation patterns which may be longitudinally oblique, to even transversally, and produce up to four basidiospores at maturity. Sometimes, blastospores are produced on basidia-like cells. Basidiospores are subglobose to ellipsoid, thin-walled, smooth, and germinate by yeast budding. The haploid state of these species exists as yeasts. The host-parasite interface comprises basally clamped tremelloid haustorial branches, which are primarily located in the basal regions of the basidiomata (Bandoni, 1986b).

Currently, only *S. parvula* and *S. pusilla* are listed within *Sirotrema* in Species Fungorum (2025). Since molecular DNA sequence data are lacking for both species,

the phylogenetic placement of *Sirotrema* within *Tremellomycetes* remains unresolved (Yamada et al., 2022; GenBank, 2025).

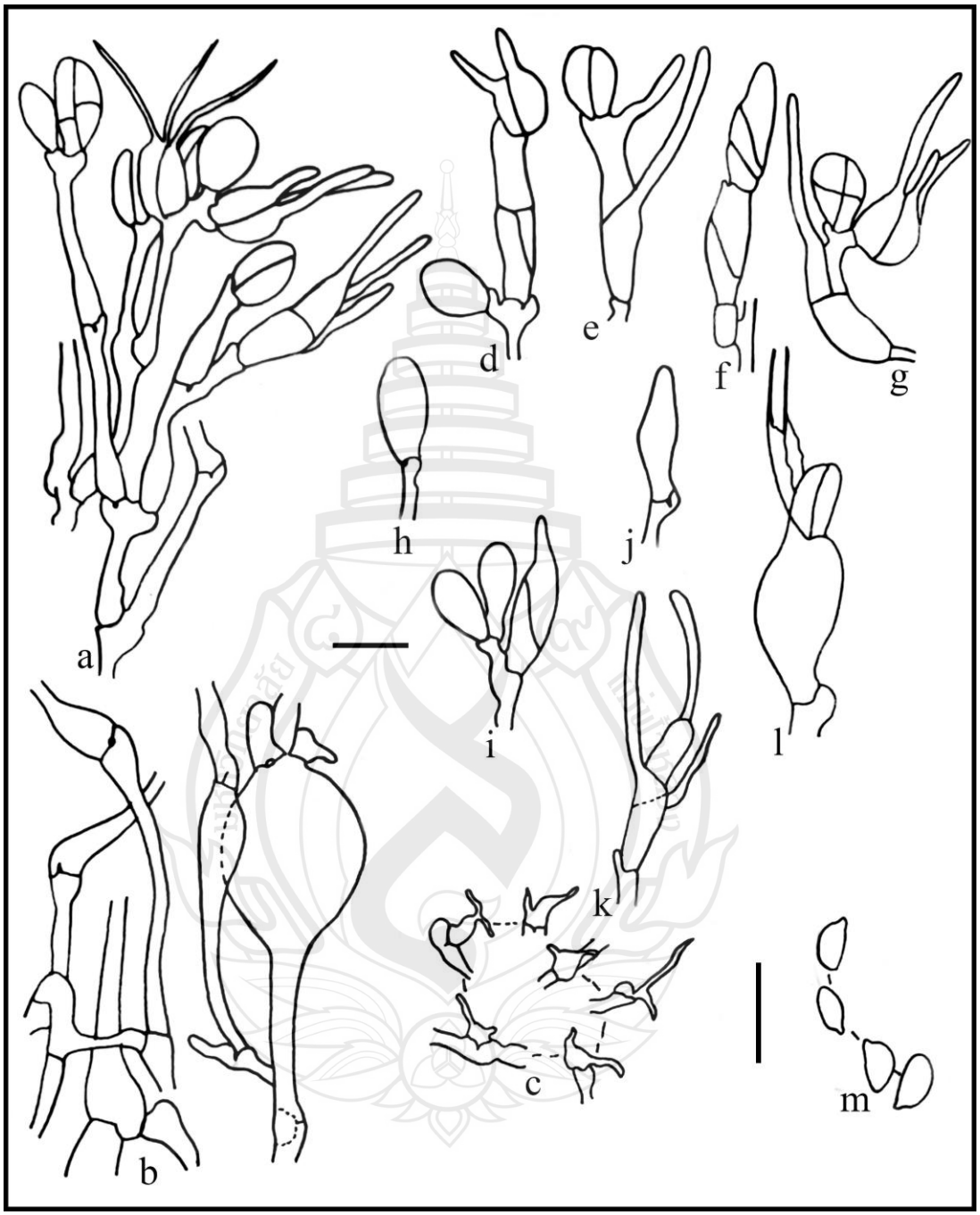


Figure 5.121 *Sirotrema pusilla*

Figure 5.121, a. Portion of hymenium. b. Hyphae of context, one with a vesiculose swelling. c. Haustorial branches. d–g. Paired basidia developed from contiguous hyphal cells. h–j. Probasidia in various stages of development. k.

Subcylindric basidium with transverse septation. l. Collapsed basidium and mature probasidium borne on vesiculose fertile cell. m. Basidiospores. Scale bars: a–l, m = 10 µm. (Redrawn from Bandoni, 1986b).

Xenolachne D.P. Rogers, Mycologia 39(5): 561 (1947)

Figure 5.122

Index Fungorum number: IF 18758

Rogers (1947) introduced the genus *Xenolachne* to accommodate *X. flagellifera*, a fungicolous tremelloid fungus developing on the hymenium of *Hyaloscypha atomaria*, which was found in the USA. Hauerslev (1977) added a second species, *Xenolachne longicornis*, which was found on the apothecia of a *Cudoniella clavus* collection from Denmark.

Xenolachne species do not produce basidiomata, but develop as a white pruinose layer on the host. Monomitic, hyphae thin-walled, hyaline, with clamp connections at the septa. Basidia usually in clusters, with or without a short stalk, basally clamped and longitudinally or obliquely uniseptate. Each compartment gives rise to a straight sterigma, reaching up to 60 µm. Basidiospores thin-walled, hyaline, symmetrically attached to the sterigmata, and germinate by repetition or clamped hyphae. The host-parasite interface of *Xenolachne* species comprises short, basally clamped, tremelloid haustorial cells attaching to host hyphae (Hauerslev, 1977; Antonissen & Van de Put, 1994). Whereas *X. flagellifera* is restricted to the USA, *X. longicornis* has been reported from various European countries, including Belgium, Denmark, Germany, France, and the Netherlands (Hauerslev, 1977; Grauwinkel, 1993; Antonissen & Van de Put, 1994; Van Vooren & Gaignon, 2002; Jagers, 2009). *X. longicornis* has also been reported to parasitize *Hymenoscyphus vernus* (Grauwinkel, 1993; Jagers, 2009). There are no molecular DNA sequence data available for *Xenolachne* in GenBank (2025).

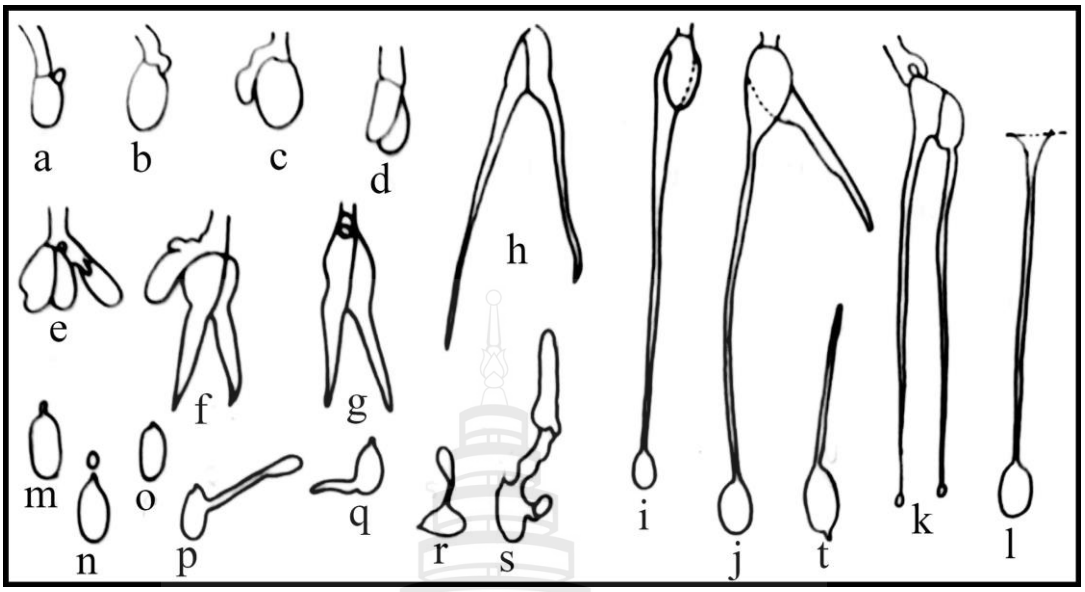


Figure 5.122 *Xenolachne flagellifera*

Figure 5.122, a–d. Young basidia. e–g. Development of epibasidia. h–k. Basidia with sterigmata and developing spores. l. Mature spore. m–o. Abstricted spores. p–r. Germination by secondary spores. s. Germination by the mycelium. t. Spore germinating by a sterigma like that of the basidium. (Redrawn from Rogers 1947).

Trichosporonales Boekhout & Fell

Tetragoniomycetaceae Oberw. & Bandoni

Tetragoniomyces Oberw. & Bandoni, Canad. J. Bot. 59(6): 1034 (1981)

Figure 5.123

Index Fungorum number: IF 10197

Oberwinkler & Bandoni (1981) investigated Canadian and German material of *Tremella uliginosa*, described by Karsten (1833) from Finland, where it was found growing on decaying plant remnants. Due to the deviating morphological characteristics of this species, the authors introduced the monotypic genus *Tetragoniomyces* to accommodate this species, as well as *Tetragoniomycetaceae* (Oberwinkler & Bandoni, 1981).

Tetragoniomyces does not produce basidiomata, but grows as a thin layer on the surfaces of hollow sclerotium-like structures of its host fungus (Oberwinkler & Bandoni, 1981; Van de Put et al., 2000). The hyphal system is monomitic, comprising

hyphae with clamp connections. Branched basidiophores give rise to basally clamped basidia, which originate from probasidia. Probasidia are ellipsoid, globose to pyriform and thin-walled. In later developmental stages, probasidia become thick-walled, after which they become longitudinally septate and transform into four-celled basidia. Each of the four compartments may become secondarily thick-walled. At maturity, basidia are rhomboidal, and detach from the basidiophore. Released, mature basidia do not produce basidiospores, but instead germinate through dikaryotic hyphae or germ tubes that may conjugate (Oberwinkler & Bandoni, 1981; Van de Put, 2000). The deciduous nature of the basidia and their four-lobed, thickened form, along with their outer porous wall, was interpreted as an adaptation to water dispersal (Oberwinkler & Bandoni, 1981).

Tetragoniomyces uliginosus was recognized as a mycoparasite by Koske (1972), who illustrated haustorial cells attaching to host hyphae, but was unable to identify the host. Oberwinkler and Bandoni (1981) investigated the interaction in more detail, and suggested that the host is a species within the *Rhizoctonia* complex (Cantharellales) based on the ultrastructure of the septal pore complexes comprising dolipores. Bauer and Oberwinkler (1990) studied the host-parasite interface between *Tetragoniomyces uliginosus* and its host fungus. *T. uliginosus* produces tremelloid haustorial cells of which the apices attach to host hyphae, after which nanometer-fusion pores are produced, establishing a cytoplasmic connection between host and parasite cells (Bauer & Oberwinkler, 1990). *Tetragoniomyces uliginosus* has been reported from Belgium, Canada, Denmark, Germany, Finland, Switzerland, and the Netherlands (Koske, 1972; Oberwinkler & Bandoni, 1981; Clemençon, 1990; Van de Put et al., 2000; Keizer & Enzlin, 2024).

Molecular DNA sequence data for *T. uliginosus* is available in GenBank (2025). Millanes et al. (2011) sequenced a basidiome of *T. uliginosus*, and showed by their phylogenetic analysis that it is a member of *Trichosporonales* (*Tremellomycetes*). Based on current knowledge, it is the only known mycoparasite in this order, which is dominated by animal and human pathogenic fungi (Schoutteten et al., 2024a).

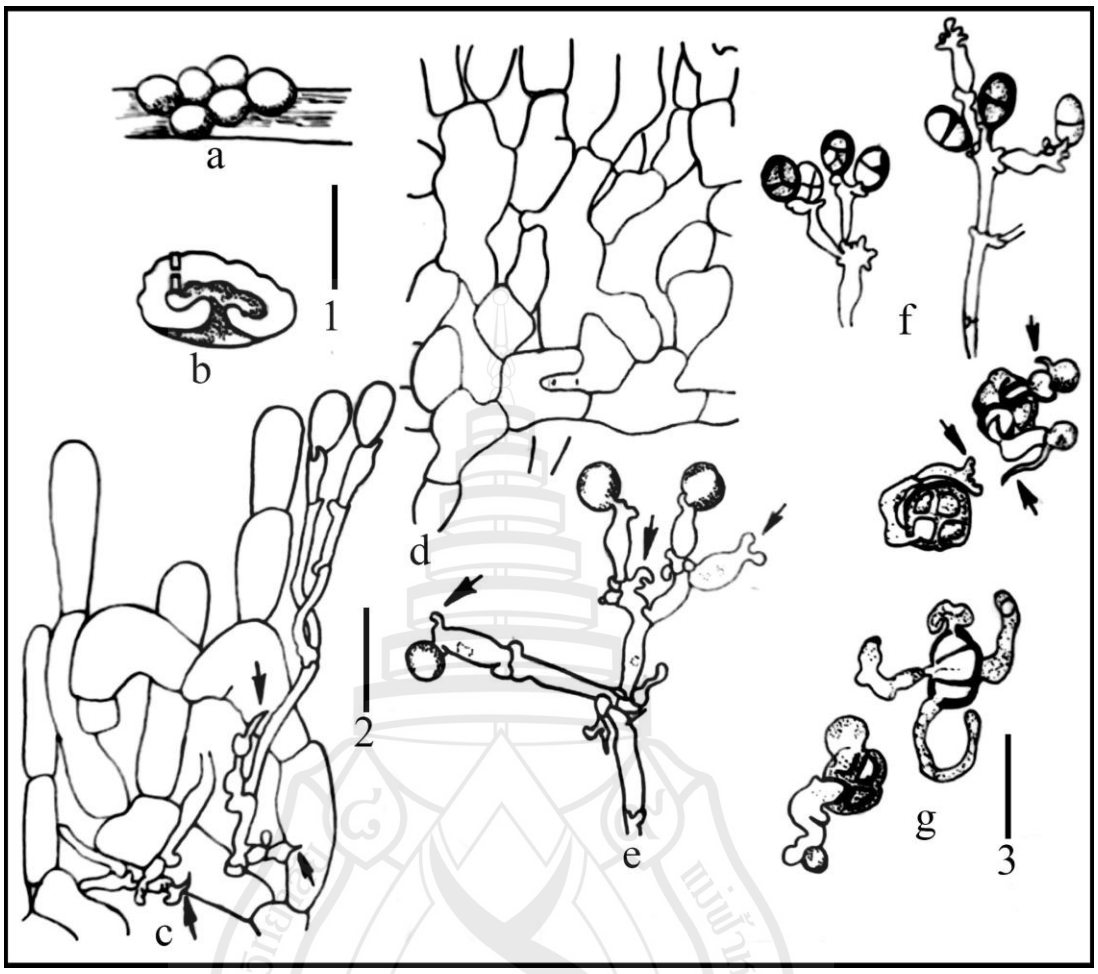


Figure 5.123 *Tetragoniornyces uliginosus*

Figure 5.123, a. Habit of host sclerotium infected by *T. uliginosus*. b. Section of mature host sclerotium with hollow central region. (Upper rectangle indicates source for fig. c, lower rectangle for fig. d.) c. Peripheral portion of host sclerotium showing hyphae of *T. uliginosus* attached by haustoria (arrows) to sclerotial cells. d. Uninfected internal portion of host sclerotium. e. Young basidiophore showing branching and clamp vestiges (arrows) where basidia have been released. f. Basidiophore with nearly mature and developing basidia, note also the numerous fingerlike clamp vestiges. g. Germinating basidia in culture (arrows indicate haustoria). Scale bars: 1 = 1 mm, 2 = 20 μm, 3 = 10 μm. (Redrawn from Oberwinkler & Bandoni, 1981).

Tremellomycetes* genera *incertae sedis

Heteromycophaga P. Roberts, Mycotaxon 63: 210 (1997)

Figure 5.124

Index Fungorum number: IF 27781

Roberts (1997) proposed *Heteromycophaga* with the type species *H. glandulosae*, developing as galls on basidiomata of *Exidia glandulosa* in the UK. This species has also been reported from Belgium, France, Germany, and the Netherlands (Van de Put, 2001; Kruse et al., 2013; Bruggeman & Kremer, 2014). Remarkably, in the Netherlands this species was detected on two different hosts: *Exidia glandulosa* and *Exidia plana* (Bruggeman & Kremer, 2014). As of Species Fungorum (2025) there are three species listed within *Heteromycophaga*. The second species, *H. tremellicola* was described from Brunei by Roberts (1998). This mycoparasite develops in the hymenium of *Tremella philippinensis*. This species was also reported in Brazil, associated with the same host (Roberts & de Meijer, 1997). The third species introduced is, *H. cladoniae* discovered on *Cladonia cervicornis* in France (Index Fungorum, 2025). No ultrastructural studies detailing the host-parasite interface have been reported so far, but there are indications that both species produce tremelloid haustorial cells (Chen & Oberwinkler, 2000; Bruggeman & Kremer, 2014). According to GenBank (2025), there is no molecular data for *Heteromycophaga*.

Heteromycophaga species are characterized by gelatinous, pustule-like conidiomata or by intrahymenial growth without the formation of conidiomata. They possess tubular conidiophores with clamp connections, producing one or more terminal, basally clamped conidia. The conidia can be clavate to oblong, ellipsoid, broadly fusiform, or cylindrical, with or without remnants of subtended clamp connections attached (adapted from (Roberts, 1997; Roberts & Spooner, 1998).

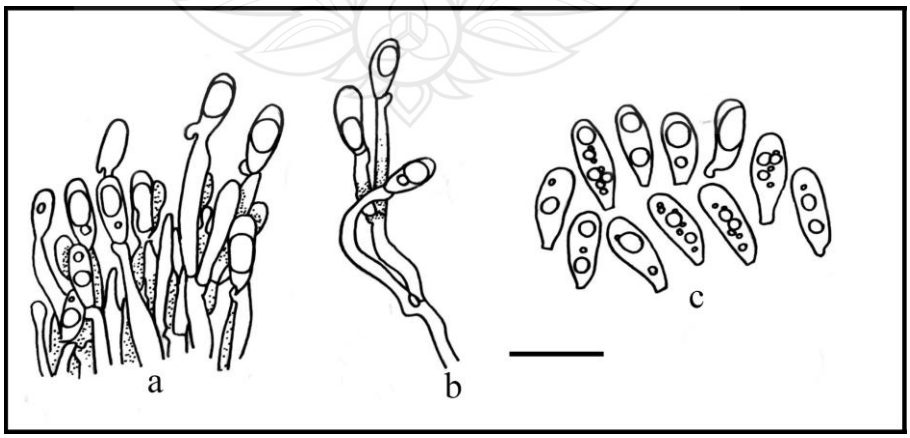


Figure 5.124 *Heteromycophaga glandulosae*

Figure 5.124, a. Section of the gall surface. b. Conidiophores. c. Conidia. Scale bar = 10 μm. (Redrawn from Roberts, 1997).

Subphylum *Pucciniomycotina* R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Class *Agaricostilbomycetes* R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Agaricostilbales Oberw. & R. Bauer

Agaricostilbales* genus *incertae sedis

Mycogloea L.S. Olive, Mycologia 42(3): 385 (1950)

Figure 5.125

Index Fungorum number: IF 18096

Mycogloea was proposed by Olive (1950), to accommodate *M. carnosa*, a heterobasidiomycetous species with pustulate basidiomata and transversely septate, deciduous basidia. This species develops pustulate, gelatinous basidiomata which eventually fuse together, forming a gelatinous layer covering a pyrenomycete growing on a fallen corticated branch of an unidentified deciduous tree species (Olive, 1950; Schoutteten et al., 2024a). Basidia develop from probasidia, from which they eventually detach prior to producing sterigmata and basidiospores (Olive, 1950). This character was interpreted by Bandoni (1998) as an adaptation to aquatic dispersal. Most *Mycogloea* species produce hyphidia and comprise a monomitic fibulate or efibulate hyphal system. The other known *Mycogloea* species were assigned to this genus based on morphological similarities.

Mycogloea comprises seven species, six of which are known only from morphological data. *Mycogloea macrospora* was reported on *Diatrype stigma* (syn. *Sphaeria stigma*) in the UK (Berkeley & Broom 1873; McNabb, 1965). *Mycogloea nipponica* was observed on a thin stromatic layer, possibly belonging to a *Hypoxylon* sp. on decaying bark, with *Diatrype* stromata nearby, in Japan (Bandoni, 1998). *Mycogloea amethystina* was reported growing on the stromata of *Diaporthe sociabilis* in Canada, and *Mycogloea bullatospora* was associated with the apothecia of a *Rhytidhysteton* species in Thailand (Bandoni, 1998).

Mycogloea species are fungicolous due to their association with pyrenomycetes, but no cellular interaction structures were previously reported (Aime

et al., 2014; Schoutteten et al., 2024a). A dimorphic life cycle was observed for *M. nipponica*, the only species for which DNA sequence data are available (Kirschner et al., 2003). The other *Mycogloea* species are known only in their filamentous morph (Schoutteten et al., 2024a). It is likely that all *Mycogloea* species are dimorphic, but these species are in need of recollection to investigate their life cycles, host-parasite interface, and evolutionary relationships.

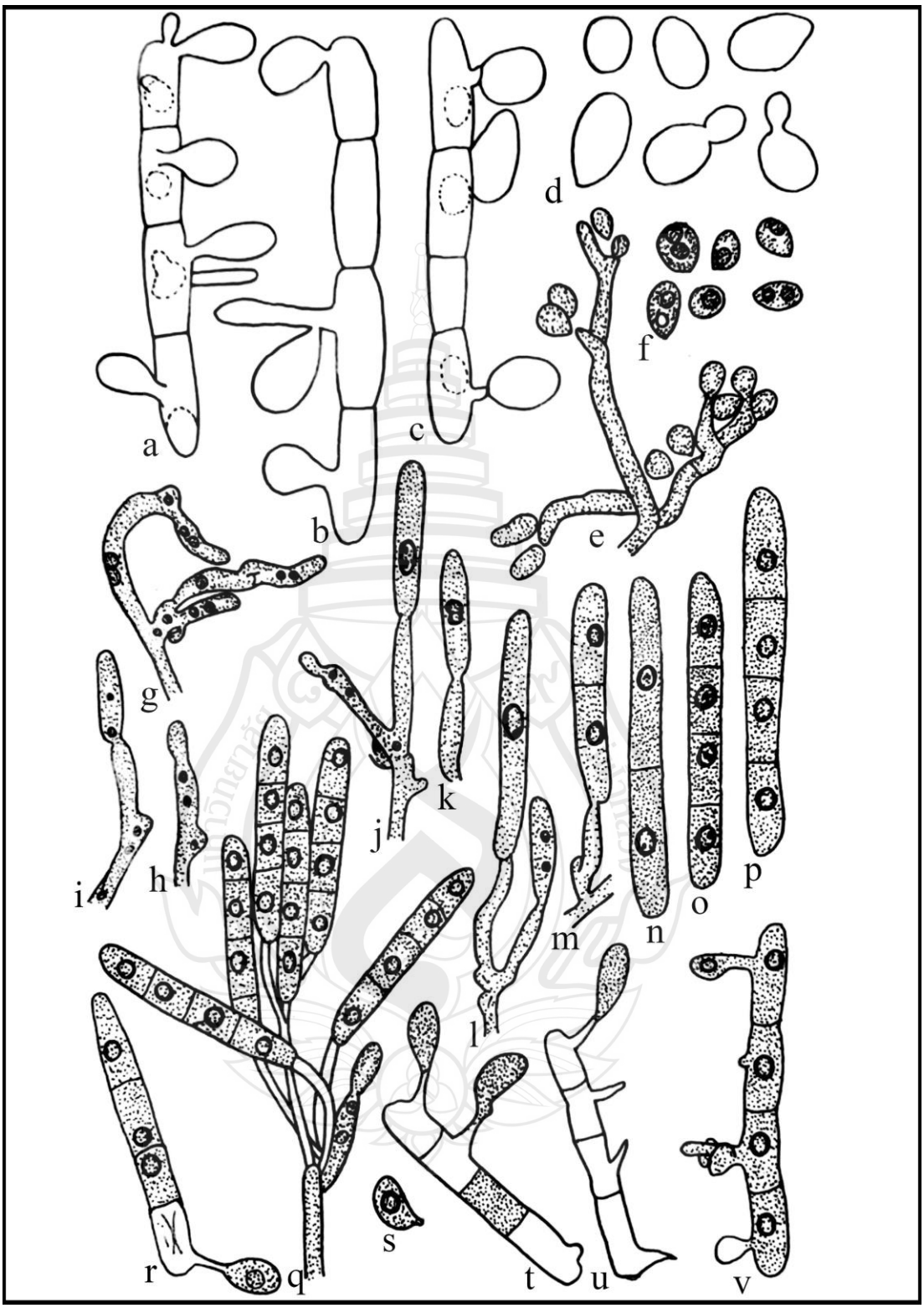


Figure 5.125 *Mycogloea carnosa*

Figure 5.125, a–c. Basidia giving rise to conidia on agar. d. Basidial conidia (two showing budding). e. Conidiophores producing conidia. f. Conidia. g. Hyphae

with clamp connections and binucleate cells. h, i. Binucleate cells bussing out basidia. j, k. Nuclear fusion in young basidia. l. Young basidium with a fusion nucleus, binucleate probasidium. m, n. Two-celled basidia after the first meiotic division. o, p. Mature 4-celled, 4- nucleate basidia after second meiotic division. q. Cluster of mature basidia attached to empty sub-basidial cells. r–u. Basidia germination and producing uninucleate basidiospores. v. Basidium budding out uninucleate conidia. (Redrawn from Olive, 1950).

Class *Classiculomycetes* R. Bauer, Begerow, J. P. Samp., M. Weiss & Oberw.

Classiculales R. Bauer, Begerow, Oberw. & Marvanová

Classiculaceae R. Bauer, Begerow, Oberw. & Marvanová

Classicula R. Bauer, Begerow, Oberw. & Marvanová, Mycologia 95(4): 757 (2003)

Figure 5.126

Index Fungorum number: IF 28760

Classicula was introduced by Bauer et al. (2003), to accommodate the sexual morph of *Naiadella fluitans*, which was previously described by Marvanová and Bandoni (1987). Since the higher classification of this group is based on the name *Classicula*, a later synonym of *Naiadella*, Aime et al. (2018) recommended for the protection of *Classicula*. A second *Classicula* species, *C. sinensis*, was described by Qiao et al. (2018). To date, *Classicula* contains two species only, both of which were isolated from freshwater aquatic habitats from Canada, the Czech Republic, and China (Bauer et al., 2003; Qiao et al., 2018; Schoutteten et al., 2004a; Species Fungorum, 2024). *Classicula fluitans* is recognized as a presumed mycoparasite producing tremelloid haustorial cells, of which the apex attached to hyphae of its own mycelium in pure culture, although no formation of nanopores was observed (Bauer et al., 2003, 2006). The host fungus is unknown for both *Classicula* species.

Members of *Classicula* are characterized by transversely septate basidia with subapically swollen sterigmata, fusiform basidiospores with 3–4 bristle-like lateral branches, and clamped hyphae with tremelloid haustorial cells (adapted from Marvanová & Bandoni, 1987; Bauer et al., 2003). *Classicula* species share morphological similarities with *Jaculispora submersa*, such as the navicular, setose conidia with 2-3 branches, and the presence of tremelloid haustorial cells (Bauer et

al., 2003). Bauer et al. (2003) examined the evolutionary relationships of both genera in *Basidiomycota* based on the small subunit ribosomal DNA (18S rDNA). This phylogenetic analysis revealed a well-supported sister relationship between *Classicula fluitans* and *Jaculispora submersa*, nested with strong support in *Pucciniomycotina*. As a result, Bauer et al. (2003) proposed *Classiculaceae* and *Classiculales* to accommodate these two species. Later studies, including analyses of both SSU and LSU sequences, further confirmed that the two genera are closely related and belong to *Classiculomycetes* (Bauer et al., 2006; Schell et al., 2011).

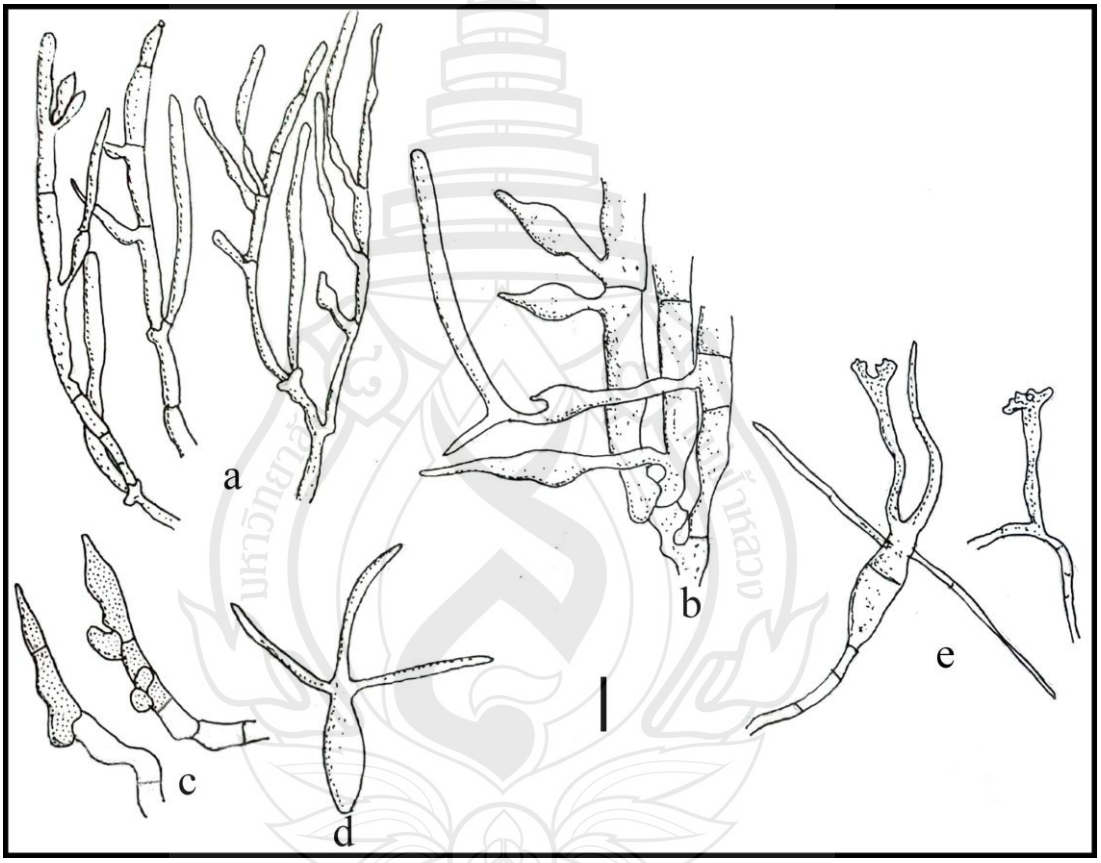


Figure 5.126 *Classicula fluitans*

Figure 5.126, a. Cluster of basidia. Note the subapically swollen sterigmata and the fusiform basidiospores. b. Sterigmata in detail. Note that one sterigma is furcate. c. Tremelloid haustorial cells. d. Conidium. e. Germination of conidia with coralloid, appressorium-like structures on glass. Scale bar: a, d, e = 10 μm, b, c = 5 μm. (Redrawn from Bauer et al., 2003).

Jaculispora H.J. Huds. & Ingold, Trans. Br. mycol. Soc. 43(3): 475 (1960)

Figure 5.127

Index Fungorum number: IF 2522

Hudson and Ingold (1960) proposed *Jaculispora* to accommodate *J. submersa*. This species was isolated from rotten, submerged leaves in a river in Jamaica (Hudson & Ingold, 1960). *Jaculispora submersa* is characterized by narrow, delicate conidiophores and obclavate conidia that bear 0–3 hair-like lateral appendages (Hudson & Ingold, 1960). Hyphae of this species are characterized by clamp connections, and produce basally clamped tremelloid haustorial cells (Matsushima 1987; Bauer et al., 2003). Comparative studies suggest a common ancestral lineage shared between *Classicula* and *Jaculispora* (Bauer et al., 2003, 2006). *Jaculispora submersa* is considered an aquatic mycoparasite, however the host range remains unknown (Bauer et al., 2003, 2006; Schoutteten et al., 2024a).

Since the establishment, *Jaculispora* has remained monotypic (Species Fungorum, 2025). DNA sequence data for the LSU, SSU and *tub2* of *J. submersa* are available in GenBank (2025).

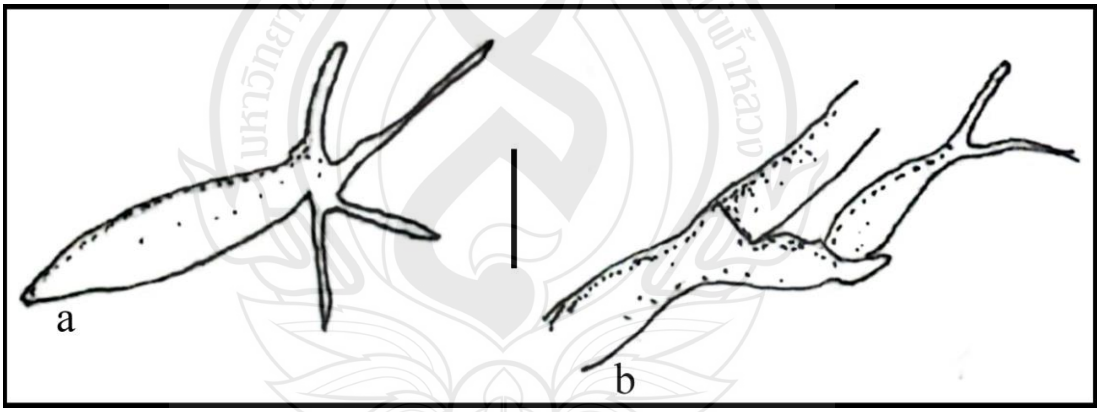


Figure 5.127 *Jaculispora submerse*

Figure 5.127, a. Conidium. b. Trmrlloid haustorial cell. Scale bar: a = 10 μm, b = 5 μm. (Redrawn from Bauer et al., 2003).

Class *Cryptomycocolacomycetes* R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Cryptomycocolacales Oberw. & R. Bauer

Cryptomycocolacaceae Oberw. & R. Bauer

Colacosiphon R. Kirschner, R. Bauer & Oberw., Mycologia 93(4): 643 (2001)

Figure 5.128

Index Fungorum number: IF 28508

The monotypic genus *Colacosiphon* was introduced by Kirschner et al. (2001) to accommodate *C. filiformis*. *Colacosiphon filiformis* is currently known only from Germany. This species was discovered in mixed cultures derived from bark beetles (*Ips sexdentatus*) occurring in a felled *Pinus sylvestris* log. *Colacosiphon filiformis* is a colacosome-interacting mycoparasite of an unidentified ascomycetous host. The hyphae of the host invaginate the hyphae of the mycoparasite, and colacosomes are produced by the mycoparasite along the contact surface (Kirschner et al., 2001).

Colacosiphon is characterized by mononematous, macronematous, filiform, erect, and aseptate conidiophores, reaching up to 870 µm in length. The conidia are cylindrical, sessile, produced at the apex, hyaline, and aseptate. The hyphae of *C. filiformis* are hyaline, lack clamp connections, and contain colacosomes at the contact surface with host hyphae. In some places, chlamydospores are produced. The septal pores have a simple morphology, and are associated with microbodies that contain globose, electron-dense inclusions and putative Woronin bodies (Kirschner et al., 2001). In molecular phylogenetic reconstructions, *Colacosiphon* clusters with *Cryptomycocolax* with strong support (Bauer et al., 2006). However, their relationship to other members of *Basidiomycota* remains unresolved (Schoutteten et al., 2024a). Sequence data for the D1/D2 region of the LSU of *Colacosiphon filiformis* is available in GenBank (2025).



Figure 5.128 *Colacosiphon filiformis*

Figure 5.128, a. Habitat sketch of a cluster of conidiophores. b. Apical parts of three conidiophores with developing conidia (arrows) and conidium secession scars. c. Conidia. d. Conidia producing germ tubes (arrows) and colacosomes developed within two of the conidia (arrows). Scale bars: a = 100 μm, b–d = 10 μm. (Redrawn from Kirschner et al., 2001).

Cryptomycocolax Oberw. & R. Bauer, Mycologia 82(6): 672 (1990)

Figure 5.129

Index Fungorum number: IF 25576

Oberwinkler and Bauer (1990) established *Cryptomycocolax* for *C. abnormis*. This species was detected as a thin, slimy layer overgrowing ascomata of an unidentified ascomycetous host, growing on decaying stems of *Cirsium subcoriaceum* in Costa Rica. *Cryptomycocolax abnormis* is currently only known from the type

locality. *Cryptomycocolax abnormis*, a colacosome-interacting mycoparasite, was studied in detail for its lifecycle, micromorphology and ultrastrucural properties (Oberwinkler & Bauer, 1990). This species displays unique characteristics, and even the similarities with the closely related *Colacosiphon* are limited (Oberwinkler & Bauer, 1990; Schoutteten et al., 2023, 2024a). Since its establishment, *Cryptomycocolax* has remained monotypic (Species Fungorum, 2025).

The structures for sexual reproduction of *Cryptomycocolax* are deviating from those of other *Basidiomycota*, and basidial development involves an initial phragmobasidial stage, followed by a holobasidial stage (Oberwinkler & Bauer, 1990). The first meiotic division occurs in the phragmobasidial stage, after which each of the two daughter nuclei migrates to a different compartment of the uniseptate basidium. Subsequently, the upper compartment of the basidium is abscised, and the second meiotic division takes place in the remaining compartment of the basidium, which now represents a holobasidium. After elongation of the basidial cell, the successive production of basidiospores takes place. Basidiospores germinate by hyphae or budding off yeast cells. Hyphae are clamped, thin walled, and contain colacosomes along the contact surface with host hyphae. In some places, thick-walled chlamydospores are formed. The septal pores of *C. abnormis* are surrounded by microbodies and Woronin body-like structures. Remarkably, *C. abnormis* comprises two distinct types of colacosomes, but further research is needed to clarify the difference between these two types (Schoutteten et al., 2024a).

Due to these strongly deviating characteristics, Oberwinkler and Bauer (1990) proposed *Cryptomycocolacaceae* and *Cryptomycocolacales* to accommodate this species. In molecular phylogenetic reconstructions, *Cryptomycocolax* clusters with *Colacosiphon* with strong support (Aime et al., 2006; Bauer et al., 2006). However, their relationship to other members of *Basidiomycota* remains unresolved. Sequence data for the D1/D2 region of the LSU of *C. abnormis* is available in GenBank (2025).

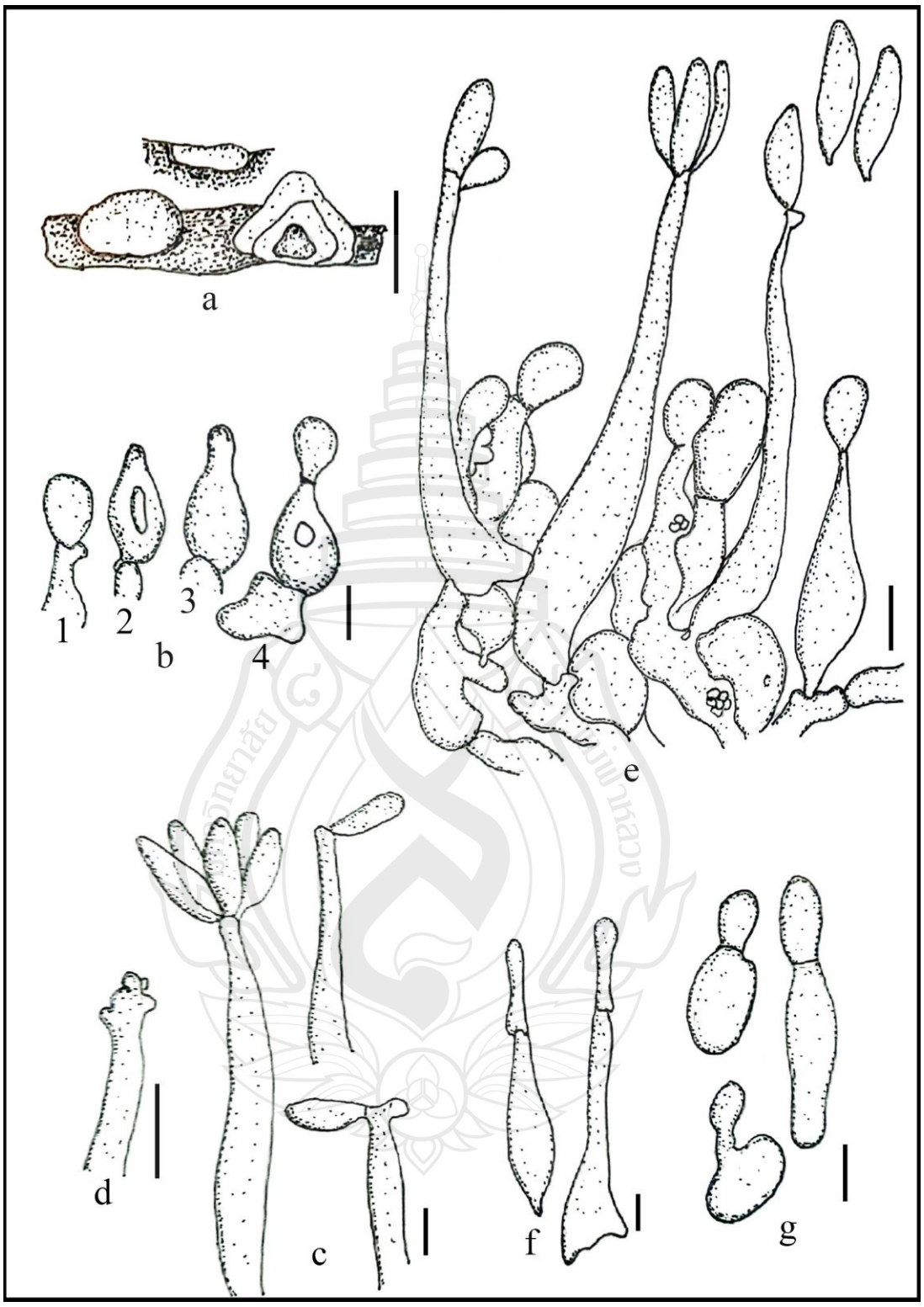


Figure 5.129 *Cryptomycocolax abnormis*

Figure 5.129, a. Habit sketch of fructification growing in and on sclerotia of the host. b. Basidial development (1. Globose probasidium. 2, 3. Apical elongation of

young basidium. 4. Two-celled basidium.). c. Basidial apices of mature, one-celled holobasidia with sessile basidiospores at different development stages. d. Old apex of basidium with bases of spore attachments. e. Sectional view of sclerotium with hyphae of the host, unclamped, and hyphae and basidia of the parasite with clamps. f. Germination of basidiospores by hyphae. g. Budding of basidiospores. Scale bars: a = 1 mm, b–g = 10 μm. (Redrawn from Oberwinkler & Bauer, 1990).

Class *Cystobasidiomycetes* R. Bauer, Begerow, J. P. Samp., M. Weiss & Oberw.

Cystobasidiales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Cystobasidiaceae Gäum.

Cystobasidium (Lagerh.) Neuhoff, Bot. Arch. 8: 272 (1924)

Figure 5.130

Index Fungorum number: IF 17446

Cystobasidium was proposed by Lagerheim (1898) as a subgenus of *Jola*, to accommodate *Jola lasioboli*, a pustulate, auricularioid heterobasidiomycete growing on cow dung. This species was described by Schumacher (1803) as *Tremella fimetaria*, after which it was combined into *Helicobasidium* (Boudier, 1887) and *Platygloea* (Von Höhnel, 1917) based on the auricularioid basidia and texture of the basidiomata. Roberts (1999) finally proposed the combination of *Cystobasidium fimetarium*, which is the type of the genus. Rödel and Bender (2016) illustrated this species, and provided a detailed taxonomic and nomenclatural history of this taxon.

Cystobasidium fimetarium is a dimorphic mycoparasite, producing small waxy, pustulate basidiomata on dung of different herbivores (cow, rabbit, goat dung was previously reported as substrates). This species is characterized by transversely three-septate basidia emerging from a swollen, thin-walled, basally clamped probasidium. Basidiospores germinate by hyphae or by budding off yeast cells. The host-parasite interface comprises tremelloid haustorial cells, of which the apex attaches to host hyphae and through which nanometer fusion pores are formed (Bauer, 2004; Sampaio & Oberwinkler, 2011a; Schoutteten et al., 2024a). The septal pores of this species are sometimes occluded by cystosomes, special pore-associated structures found exclusively in filamentous morphs of specific *Cystobasidiomycetes* (Bauer et al., 2006).

The majority of the other accepted *Cystobasidium* species were isolated as yeasts from a variety of substrates, such as soil, plant leaves, human tissues, aquatic and marine environments. To date, *C. fimetarium* is the only known *Cystobasidium* species of which the full life cycle is known, and the only species that is interpreted as a mycoparasite. Two more *Cystobasidium* species are known from a filamentous morph, namely *C. sebaceum* and *C. proliferans*. However, it is unlikely that these taxa represent members of *Cystobasidium*. Schoutteten et al. (2023) already found that *C. sebaceum* is a colacosome-interacting mycoparasite that shows more similarity to the genus *Slooffia*. As of Species Fungorum (2025) there are 24 species listed within *Cystobasidium.*

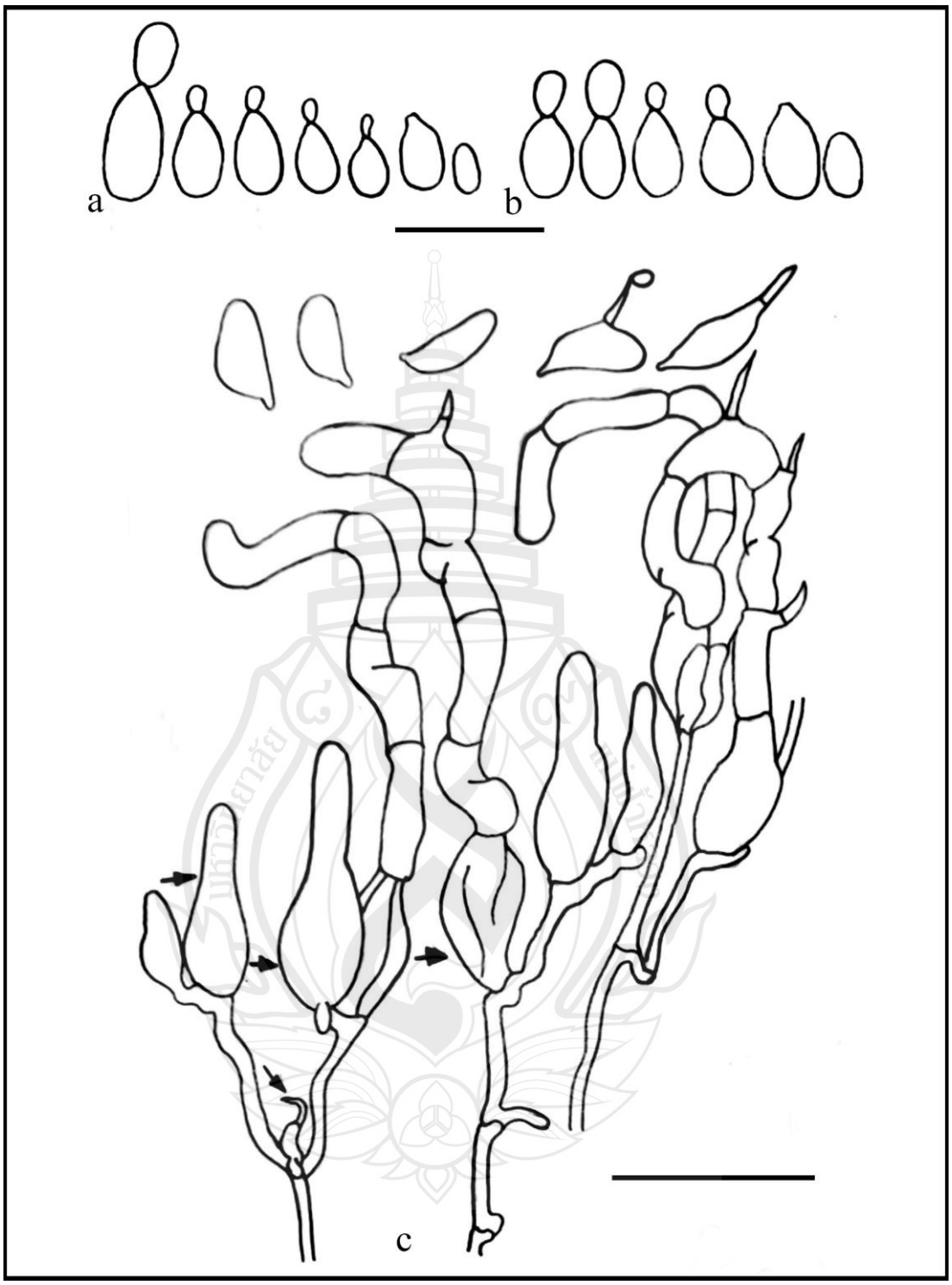


Figure 5.130 *Cystobasidium fimetarium*

Figure 5.130, a, b. Budding cells. c. Young and mature basidia and basidiospores, the probasidia in different developmental stages (arrow heads) and one

haustorium (arrow heads). Scale bars: c = 20 μm a, b = 10 μm. (Redrawn from Sampaio & Oberwinkler, 2011a).

Occultifur Oberw., Rep. Tottori Mycol. Inst. 28: 119 (1990)

Figure 5.131

Index Fungorum number: IF 25570

Oberwinkler (1990) introduced *Occultifur* to accommodate *O. internus*, a dimorphic, intrahymenial mycoparasite of *Dacrymyces* sp. (*Dacrymycetes, Agaricomycotina*). This species was earlier described by Olive (1954) from the USA as *Platygloea peniophorae var. interna*. The mycoparasite *O. internus* develops completely intrahymenially in its host fungus, and most often the infection is not visible to the naked eye. *O. internus* is characterised by a monomitic hyphal system with clamped hyphae, basally clamped conidiophores producing thick-walled conidia, basally clamped transversely 3-septate basidia, and ellipsoid, thin-walled basidiospores that germinate by secondary spores, hyphae, or yeast budding (Oberwinkler, 1990). Yeast cells are subglobose to ellipsoid, budding is predominately polar. Cultures are characterized by pink to orange pigments due to the synthesis of carotenoids and mycosporines (Schoutteten et al., 2024b). The host-parasite interface of *O. internus* comprises basally clamped tremelloid haustorial cells emerging from hyphae, of which the apices attach to host hyphae. In these apices, a nanometer fusion pore is formed, to establish cystoplasmic continuity between the host and mycoparasite (Bauer et al., 2006; Schoutteten et al., 2024a, b). The septal pores of *O. internus* have a simple morphology, and are frequently occluded by cystosomes (Sampaio et al., 1999; Bauer et al., 2006; Schoutteten et al., 2024b). Sampaio et al. (1999) described *O. externus*, and assigned it to *Occultifur* based on the presence of such cystosomes, which were then thought to be specific for *Occultifur*. Their conclusion was not supported by a molecular phylogenetic reconstruction, because molecular DNA sequence data were long unavailable for *O. internus*, the generic type (Schoutteten et al., 2024b). However, cystosomes also occur in other filamentous members of *Cystobasidiomycetes*, such as *Cystobasidium fimetarium* (Bauer et al., 2006). Schoutteten et al. (2024b) showed in their phylogenetic analysis of *Cystobasidiomycetes* that *O. internus* and *O. externus* are not congeneric, and a large evolutionary distance exists between them. Therefore,

Cystastrum was introduced to accommodate the previous *O. externus* clade, comprising five additional species, only known from yeast morphs that were isolated from various substrates and habitats (Sampaio & Oberwinkler, 2011b; Schoutteten et al., 2024b).

Based on the insights from Schoutteten et al. (2024b), *Occultifur* comprises five species, two of which are dimorphic intrahymenial mycoparasites of dacrymycetous hosts, namely *O. internus* and *O. cerinomycicola*. The other three species are only known from yeast morphs, and were all isolated from lichen thalli (Černajová & Škaloud, 2019; Kachalkin et al., 2024). Two species, namely *Occultifur corticiorum* (parasitizing *Peniophorella praetermissa*), and *O. rivoirei* (parasitizing *Hyphodontia arguta*) were assigned to *Occultifur* based on superficial morphological similarities (Roberts, 1997, 2016). However, this conclusion should be interpreted with caution, given that the morphological characters of these species occur in various clades of *Pucciniomycotina* and their correct assignment awaits molecular DNA sequence data (Schoutteten et al., 2024a, b). *Occultifur* species were previously reported from Belgium, the Czech Republic, Denmark, Finland, France, Germany, Hungary, the Netherlands, Norway, Russia, Slovakia, Spain, Sweden, the UK, Ukraine, and the USA (Oberwinkler, 1990; Van de Put, 2001; Trichies, 2006; Černajová & Škaloud, 2019; Schoutteten et al., 2024b).

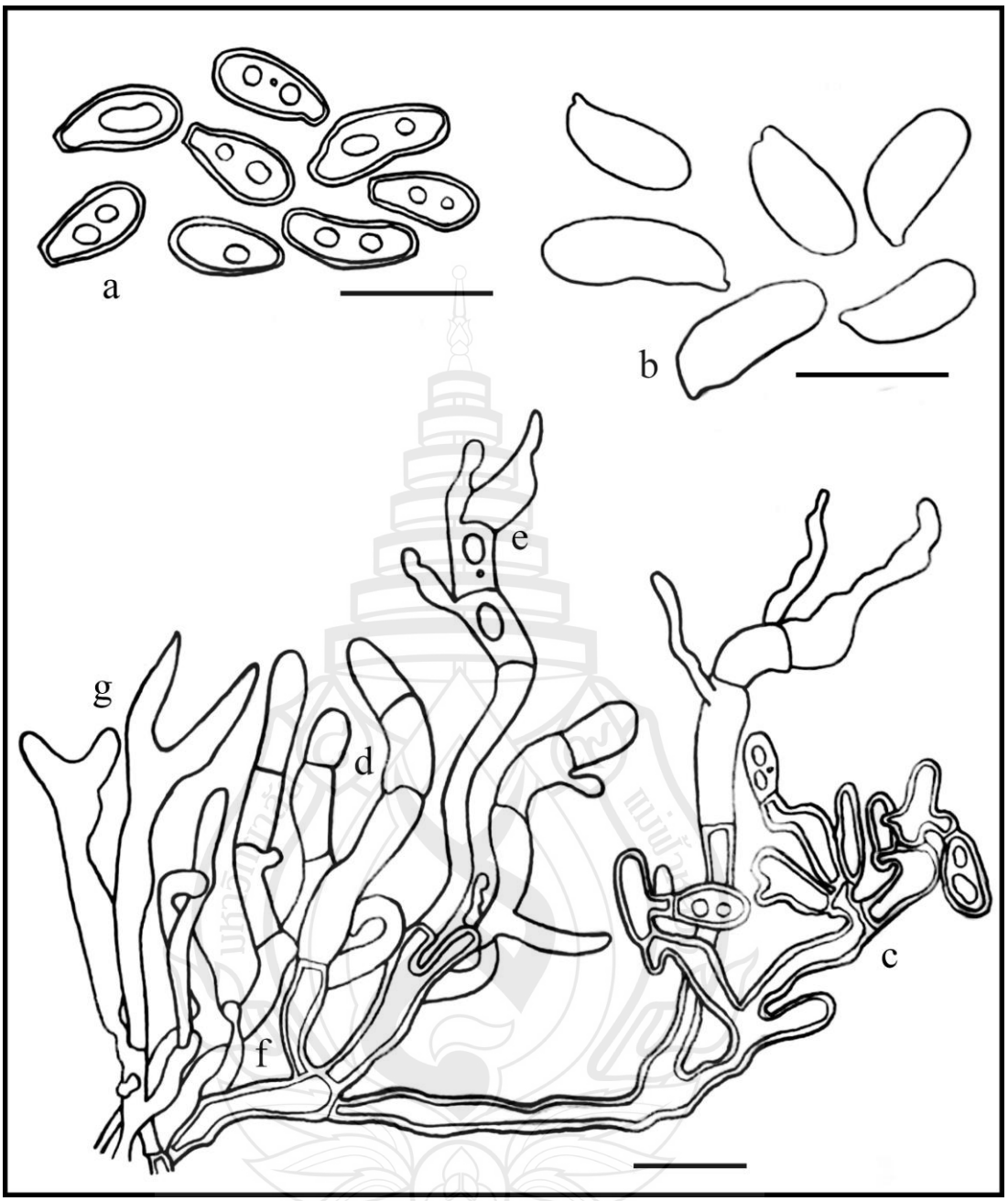


Figure 5.131 *Occultifur cerinomycicola*

Figure 5.131, a. Thick-walled conidia. b. Basidiospores. c. Thick-walled conidiogenous cells giving rise to conidia. d. Cluster of transversally-septate basidioles. e. Transversally 3-septate basidium. f. Haustorial cell attaching to a host hypha. g. Host basidia. Scale bars: a–g = 10 µm. (Redrawn from Schoutteten et al., 2024b).

Naohideales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Naohideaceae Denchev

Naohidea Oberw., Rep. Tottori Mycol. Inst. 28: 114 (1990)

Figure 5.132

Index Fungorum number: IF 25560

Oberwinkler (1990) introduced the monotypic genus *Naohidea* to accommodate *N. sebacea*, described as *Dacrymyces sebaceus* by Berkeley and Broome (1871). The first collections of *N. sebacea* were reported from twigs of ash and maple found in the UK, without the notion of an association with other fungi (Berkeley & Broome, 1871). After the original description, the same species was also described by Bresadola (1903) as *Platygloea miedzyrzecensis*.

Naohidea is characterized by soft gelatinous, inconspicuous and film-like basidiocarps, often overgrowing ascomata of its host (*Botryosphaeriales*). The hyphal system is monomitic, with clamp connections. Basidia are unusually long, reaching up to 200µm in length, are transversely septate, develop directly from the mycelium without forming probasidia. Basidiospores are hyaline, thin-walled, smooth, subglobose to broadly naviculate and are formed at the end of a tubular sterigma (Oberwinkler, 1990; Sampaio & Chen, 2011). Oberwinkler (1990) also reported the formation of so-called endospores in mature basidial cells. Basidiospores germinate by secondary spores, hyphae, or yeast budding. Yeast cells are globose and are capable of producing multiple buds on each cell (Oberwinkler, 1990; Sampaio & Chen, 2011).

Naohidea sebacea has been recognized as a mycoparasite of members of the *Botryosphaeriales* (*Botryodiplodia* spp., *Botryosphaeria* spp., *Dothiorella iberica*) (Schoutteten et al., 2024a). *Naohidea sebacea* produces haustoria that partially invaginate host hyphae with the haustorium's apical part, after which multiple nanometer fusion pores are produced between the haustorial apex and host hypha, connecting the cytoplasm of host and mycoparasite (Bauer, 2004; Bauer et al., 2006; Schoutteten et al., 2024a). *Naohidea sebacea* was previously reported from Canada, France, Japan, Poland, Ukraine, the Netherlands, and the USA (Oberwinkler, 1990; Piątek, 2002; Sampaio & Chen, 2011; Oberwinkler, 2017; Sun et al., 2019a; Akulov et al., 2022). Phylogenetically, *Naohidea* represent a basal lineage within the

Cystobasidiomycetes (Bauer et al., 2006; Schoutteten et al., 2024b). Molecular DNA sequence data for *Naohidea sebacea* are available in GenBank (2025).



Figure 5.132 *Naohidea sebacea*

Figure 5.132, a. Part of the hymenium with hyphidia, basidia of different ages, basidiospores, and yeast cells in hyphae (“endospores”). b. Basidia of different

developmental stages and spores, one basidial cell with a sessile, yeast-like spore (arrowhead). Scale bars: a = 30 µm, b = 20 µm. (Redrawn from Oberwinkler, 2017).

Cystobasidiomycetes* families *incertae sedis

Microsporomycetaceae Q.M. Wang, F. Y. Bai, M. Groenew. & Boekhout

Obvidator Schoutt., Stud. Mycol. 109: 467 (2024)

Figure 5.133

Index Fungorum number: IF 854576

Obvidator was introduced by Schoutteten et al. (2024b) to accommodate *O. incarnatae*, *O. mycophilus*, and *O. quercinae*, three intrahymenial mycoparasites of *Peniophora* species (*Russulales, Agaricomycetes*) with dimorphic life cycles. *Obvidator mycophilus* which was previously known as *Platygloea mycophila* was described from the USA by Burdsall and Gilbertson (1974).

Obvidator species do not produce basidiomata, but develop completely intrahymenially in their host. Their presence can easily be detected due to the formation of hollow galls (up to 0.5 cm diam.) in the host basidiome in the locations where the mycoparasite develops. Monomytic, hyphae hyaline, smooth, thin- to thick-walled, unclamped. Hyphidia and cystidia absent. Terminal cells thick-walled, usually clavate, sometimes constricted or curved, sometimes apically bifurcating. Basidia transversally septate, two-celled at maturity, developing from a thick-walled and often slightly thickened probasidium, unclamped, upper sterigma apically inserted. Basidiospores broadly ellipsoid to (sub)globose, inamyloid, non-cyanophilous, thin-walled, smooth, germinating by hyphae, budding or secondary spore production (Schoutteten et al., 2024b). Yeast cells are typically thick-walled, and yeast colonies of *Obvidator* species have orange carotenoid pigments (Schoutteten et al., 2024b). The host-parasite interface comprises short finger-like outgrowths, up to 4 µm long, of hyphae adjacent to host hyphae and touching host cells. Ultrastructural observations have shown a rupture of the host cell wall at places of contact, but no formation of fusion pores and establishment of cytoplasmic connections were observed (Schoutteten et al., 2024b). Therefore, it remains unclear how nutrients are transfer from host to parasite (Schoutteten et al., 2024b).

Obvidator species have been reported from Belgium, Denmark, Germany, the Netherlands, and the USA. *Obvidator mycophilus* is known only from Arizona

(USA), and *O. incarnatae* has been reported only from the type locality in the Netherlands. *Obvidator quercinae* is known from Belgium, Denmark, Germany, and the Netherlands (Schoutteten et al., 2024b).

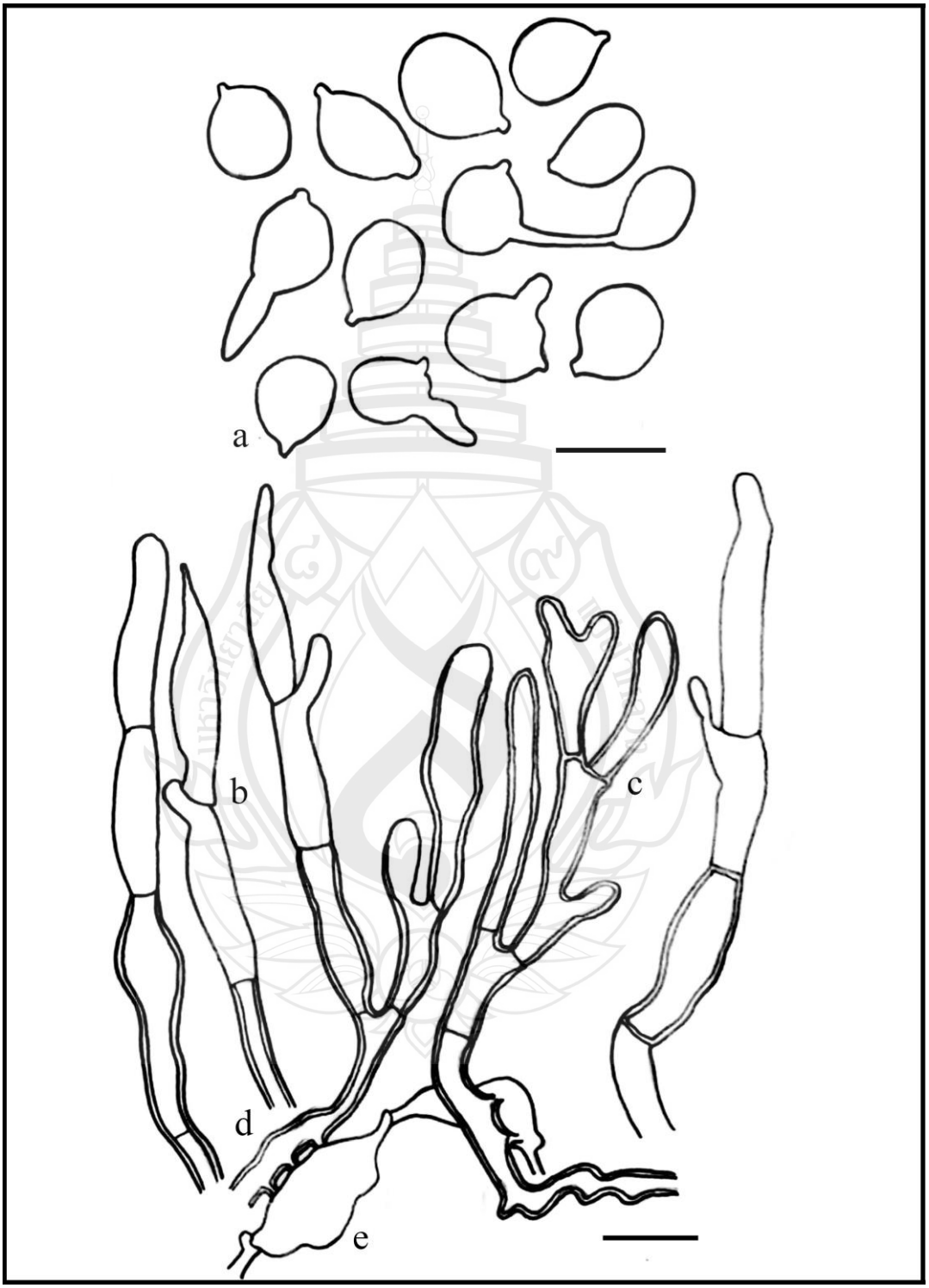


Figure 5.133 *Obvidator quercinae*

Figure 5.133, a. Basidiospores. b. Cluster of transversally 2-septate basidia with thick-walled, slightly swollen probasidia, and outgrowing sterigmata. c. Cluster of terminal cells with variable morphology. d. Thick-walled parasite hypha producing interaction protrusions. e. Clamped host cell adjacent to host protrusions. Scale bars a, b–e = 10 µm. (Redrawn from Schoutteten et al., 2024b).

Class *Microbotryomycetes* R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Heterogastridiales Oberw. & R. Bauer

Heterogastridiaceae Oberw. & R. Bauer

Krieglsteinera Pouzar, Beitr. Kenntn. Pilze Mitteleur. 3: 404 (1987)

Figure 5.134

Index Fungorum number: IF 25260

The monotypic genus *Krieglsteinera* was proposed by Pouzar (1987) to accommodate *K. lasiosphaeriae*, a peculiar mycoparasite growing on perithecia of *Lasiosphaeria ovina* (*Sordariales*, *Ascomycota*) (Pouzar, 1987; Miller et al., 2003; Oberwinkler, 2017; Schoutteten et al., 2023). This species was previously illustrated and invalidly described as *Jacobia conspicua* by Arnaud (1951), who misinterpreted the nature of the stalks and spores. This species was collected in the former Czechoslovakia and has since been reported in several other countries, including, Germany, Norway, Russia, the UK and the USA (Miller et al., 2003; Rödel, 2005).

Macroscopically, this species is visible as thin stalks, adorned with slimy droplets at their apices, developing on the perithecia of its host (Miller et al., 2003). The micromorphology of *Krieglsteinera* is distinguished by basidia that are transversely three-septate. They arise from basidiophores featuring a prominent clamp connection in the middle of the stalk. Each basidiophore exhibits a tri- to tetrapodal structure, with a basal clamp connection supporting each basidium. The basidiospores are ellipsoid to obpyriform. They are hyaline, thin-walled, and are produced successively in large clusters that coalesce to form slimy droplets (Miller et al., 2003; Schoutteten et al., 2024a). Basidiospores can germinate by forming yeast-like cells via a budding process (Oberwinkler, 2017). Attempts to obtain cultures from *Krieglsteinera* have been unsuccessful (Schoutteten et al., 2023, 2024a). Ultrastructural studies on the host-parasite interface showed that *K. lasiosphaeriae* is

a colacosom-interacting mycoparasite producing gall-like cells which are invaginated by host hyphae. Colacosomes are produced along the contact surface in these cells (Bauer, 2004; Schoutteten et al., 2024a).

There is no DNA sequence data available for *Krieglsteinera* in GenBank (2025). *Krieglsteinera* has been tentatively classified within *Heterogastridiales* based on micro morphological similarities and the presence of colacosomes (Bauer et al., 2006; Schoutteten et al., 2023). Due to the absence of DNA sequence data, Schoutteten et al. (2023) advocated categorizing *Krieglsteinera* as *Microbotryomycetes incertae sedis*.

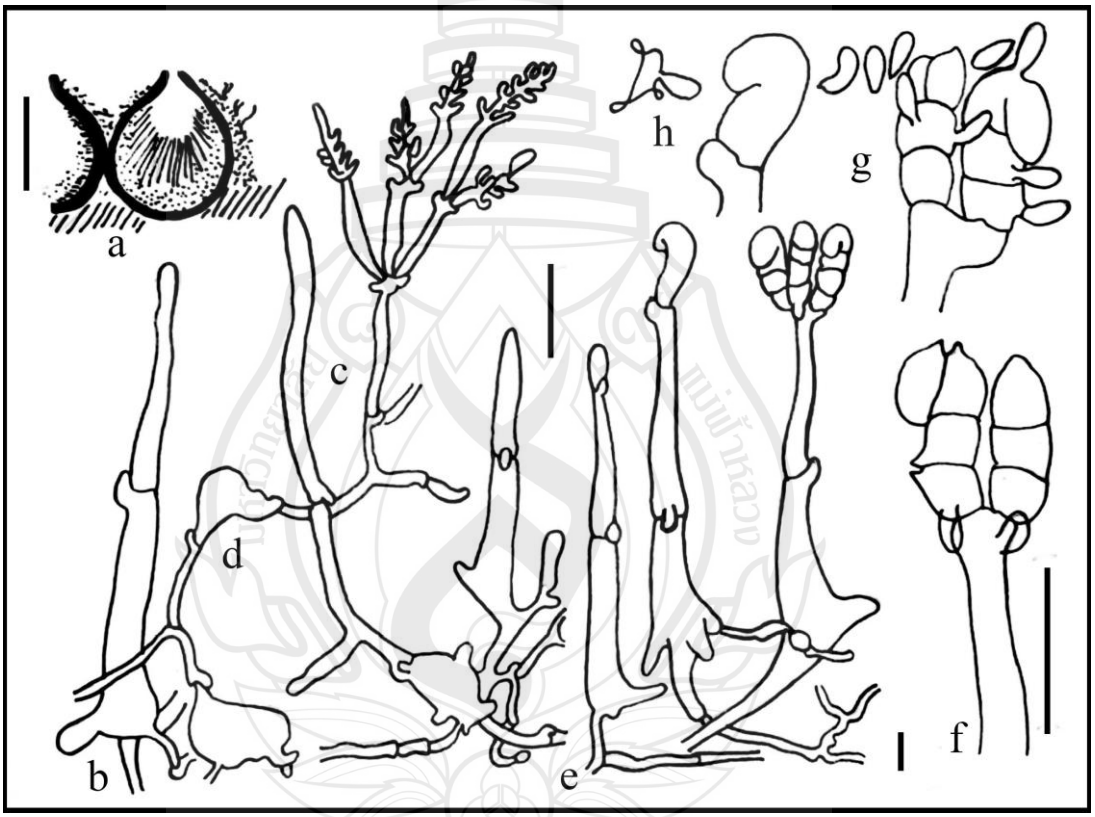


Figure 5.134 *Krieglsteinera lasiosphaeriae*

Figure 5.134, a. Longitudinal section of *Lasiosphaeria ovina* covered with the mycoparasite. b. Young basidiophore. c. Basal hyphae and initial stages of basidiophores. d. Conidiophores. e. Development of basidia on top of the basidiophore. f. Septate basidia. g. Basidia with basidiospores. h. Budding basidiospore. Scale bars: a = 0.5 mm, b–e = 20 μm, f–h = 20 μm. (Redrawn from Oberwinkler ,2017).

Microbotryomycetes* families *incertae sedis

Colacogloeaceae Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout

Colacogloea Oberw. & Bandoni, Canad. J. Bot. 68(12): 2532 (1991) [1990]

Figure 5.135

Index Fungorum number: IF 25562

Oberwinkler et al. (1990b) introduced *Colacogloea* to accommodate *Platygloea effusa* [*as Platygloea peniophorae*] (synonym: *Colacogloea peniophorae*) (Malysheva et al., 2021; Schoutteten et al., 2023). The authors compared spore germination patterns and the ultrastructural organization of the septal pores and the host-parasite interface of *P. effusa* with those of the genus type (*Platygloea disciformis*), types of information that were previously not applied to investigate the heterogeneity of the genera *Achroomyces* and *Platygloea*. The clear differences in ecology, macro- and micromorphology, ultrastructure, and spore germination patterns clearly separated both species, and justified the creation of a new genus to accommodate the dimorphic, intrahymenial mycoparasite *Colacogloea effusa*. The most striking feature of *Colacogloea* was the presence of colacosomes, unique structures produced by the mycoparasite along the host-parasite interface (Oberwinkler et al., 1990b; Bauer & Oberwinkler, 1991). Early phylogenetic studies showed that *Colacogloea* is a member of *Microbotryomycetes*, *Pucciniomyctina* (Weiß et al., 2004; Bauer et al., 2006).

Several researchers assigned more species to the genus, based on ultrastructural and/or morphological similarities of the filamentous morphs of (presumed) mycoparasites (Oberwinkler et al., 1999; Kirschner & Oberwinkler, 2000; Bandoni et al., 2002). Based on molecular phylogenetic reconstructions, Wang et al. (2015a, b) assigned various so-called ‘white *Rhodotorula*’ species to *Colacogloea*, all of which are only known from their yeast morphs. Several new yeasts, isolated from various habitats, were assigned to *Colacogloea* based on molecular phylogenetic reconstructions and physiological profiles (Yurkov et al., 2016; Li et al., 2020; Wang et al., 2021; Lu et al., 2024). *Colacogloea* yeast morphs are characterized by subglobose to ovoid or allantoid cells and reproduce by polar budding (Hamamoto et al., 2011; Sampaio, 2011; Wang et al., 2015b). These yeasts have primarily been isolated from various plant materials, including leaves, fruits, tree bark, and plant

residues. They have occasionally been isolated from soil, lichens, insects, and their tunnels (Belloch et al., 2007; Hamamoto et al., 2011; Sampaio, 2011; Sampaio et al., 2011; Yurkov et al., 2016; Li et al., 2020; Wang et al., 2021; Kachalkin et al., 2024). Physiologically, *Colacogloea* yeast cultures lack fermentative capabilities and contain Q-10 as the dominant ubiquinone (Hamamoto et al., 2011; Sampaio, 2011; Sampaio et al., 2011; Wang et al., 2015b).

Schoutteten et al. (2023) showed that at least seven distinct *Colacogloea* species, i.e., *C. bettinae*, *C. biconidiata*, *C. bispora*, *C. effusa*, *C. fennica*, *C. microspora*, *C. philyla*, and *C. universitatis-gandavensis*, alternate between a yeast morph and a mycoparasitic filamentous morph. These filamentous morphs are characterized by transversely septate basidia, thick-walled conidia, and thin-walled basidiospores that germinate by hyphae, secondary spores, or yeast budding. The host-parasite interface of all studied species comprises colacosomes (Schoutteten et al., 2023). The filamentous morphs of *Colacogloea* species develop in the corticioid basidiomata of specific *Peniophorella* species (*Polyporales*, *Agaricomycotina*) (Oberwinkler et al., 1990b; Sampaio et al., 2011; Schoutteten et al., 2023). It remains to be investigated if *Colacogloea bispora* and *C. allantospora*, both parasites of *Tubulicrinis* spp. (*Hymenochaetales, Agaricomycotina*), are true *Colacogloea* species. To date, 27 species have been recognized within *Colacogloea* (Wang et al., 2021; Schoutteten et al., 2023; Kachalkin et al., 2024; Lu et al., 2024; Species Fungorum, 2025).

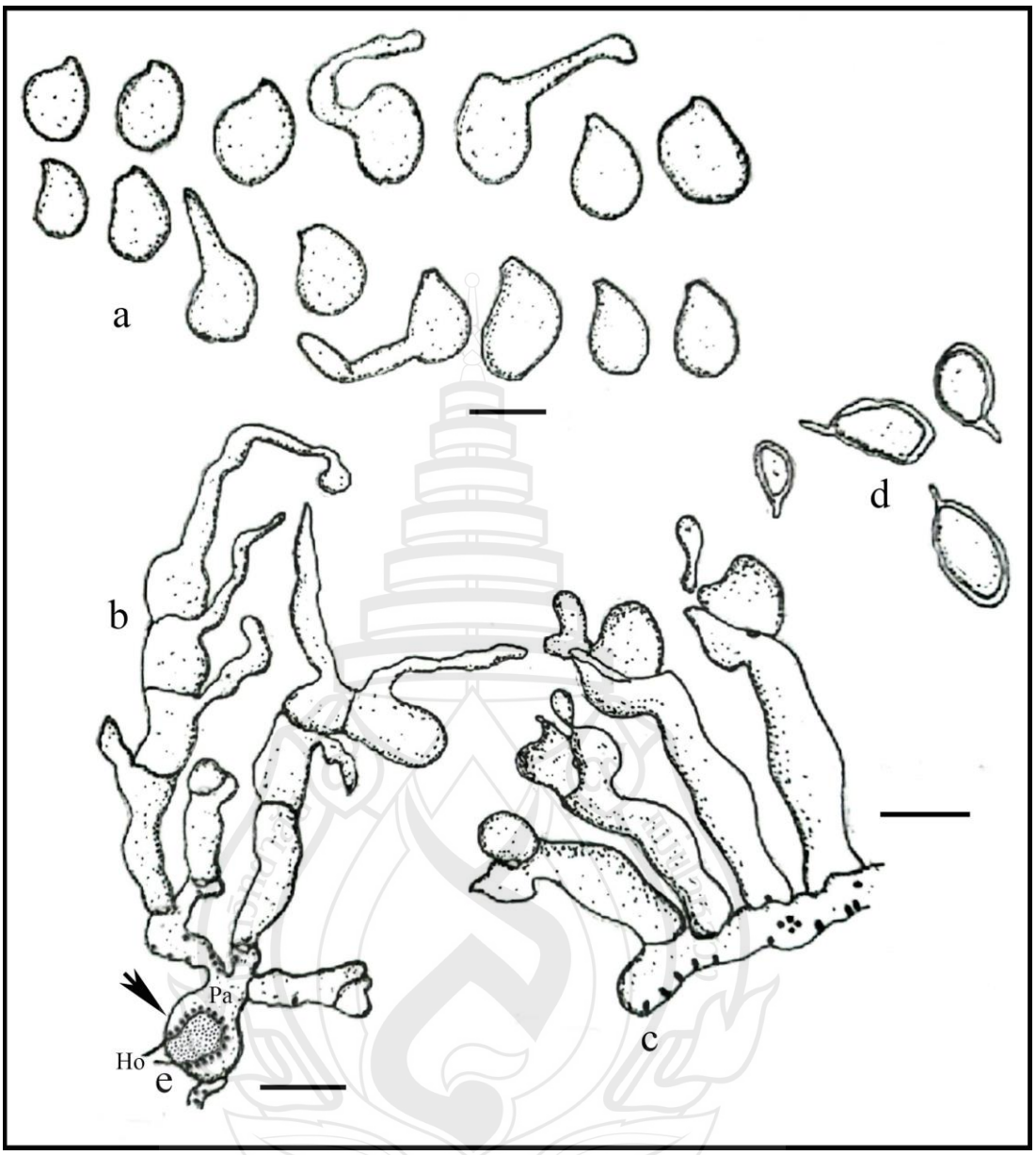


Figure 5.135 *Colacogloea bettinae*

Figure 5.135, a. Basidiospores and germinating basidiospores with secondary spores. b. Cluster of basidia and conidiophores. c. Cluster of conidiophores, showing subsequent stages of conidiogenesis. d. Conidia. e. Gall-like cell of the parasite (Pa) enveloping a host hyphae (Ho) (lack dots represent colacosomes). Scale bars = 10 µm. (Redrawn from Schoutteten et al., 2023).

Mycogloiocolacaceae Schoutteten & Yurkov

Mycogloiocolax Schoutt. & Rödel, Stud. Mycol. 106: 83 (2023)

Figure 5.136

Index Fungorum number: IF 848662

The monotypic genus *Mycogloiocolax* was introduced by Schoutteten et al. (2023), to accommodate *M. gerardii*, a dimorphic, intrahymenial mycoparasite of *Xenasmatella tulasnelloidea* (Schoutteten et al., 2023).

The filamentous morph of *Mycogloiocolax gerardii* develops intrahymenially in its host, and is visible as a hyaline, slimy layer covering the thin host basidiome in fresh condition. Upon drying, it becomes a nearly invisible dried layer. *Mycogloiocolax gerardii* is characterized by a monomitic hyphal system comprising thin-walled hyphae with clamp connections at all septa. Hyphidia and cystidia are absent. The basidia are basally clamped, cylindrical to tubular-clavate, often curved or sinuous, and transversely septate, with mature basidia being 2 to 3 celled. Basidiospores are fusiform to amygdaliform, possess a prominent apiculus, and can germinate via hyphae, budding, or secondary spores. Conidia are ellipsoid to subfusiform and thin-walled. *M. gerardii* engages in colacosome interaction, and colacosomes are scattered in host hyphae along the host-parasite contact surface (Schoutteten et al., 2023). *Mycogloiocolax gerardii* is known from France, Germany and Sweden (Schoutteten et al., 2023, 2024a). Molecular data for *M. gerardii* is available in GenBank (2025).

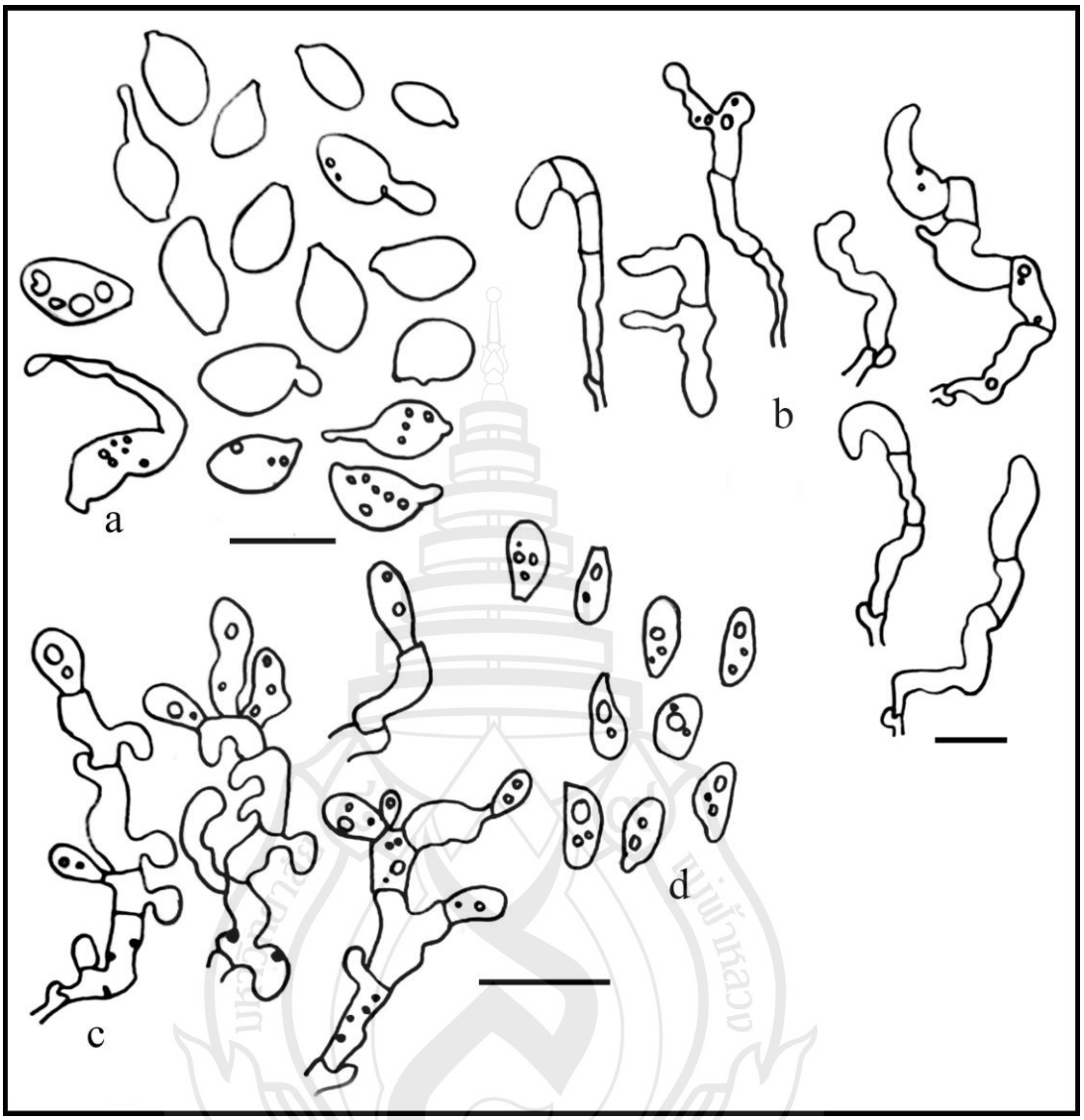


Figure 5.136 *Mycogloiocolax gerardii*

Figure 5.136, a. Basidiospores and germinating basidiospores by budding, hyphae and secondary spores. b. Basidia and basidioles. c. Conidiophores. d. Conidia (black dots represent colacosomes). Scale bars = 10 μm. (Redrawn from Schoutteten et al., 2023).

Microbotryomycetes* genera *incertae sedis

Slooffia Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout, Stud. Mycol. 81: 186 (2015)

Figure 5.137

Index Fungorum number: IF 813202

Slooffia was introduced by Wang et al. (2015b) to accommodate fungi exclusively known from yeast morphs from the *Sporobolomyces tsugae* clade, which was recovered in multilocus phylogenetic reconstructions (Wang et al., 2015a). The filamentous morph in *Slooffia* was discovered by Schoutteten et al. (2023), who showed that *Platygloea micra* Bourdot and Galzin (1924), a dimorphic intrahymenial mycoparasite of *Myxarium podlachicum*, belongs to *Slooffia*. The nutritional strategy of the other known *Slooffia* species remains to be investigated. Currently, these species are only known from yeast morphs but it can be expected that they also represent dimorphic fungi which are mycoparasites in their filamentous morph. It is likely that *Cystobasidium sebaceum* also represents a colacosome-interacting *Slooffia* species (Martin, 1939; Schoutteten et al., 2023). Unfortunately, no living cultures of the latter species are available.

Slooffia micra does not produce basidiomata, but develops intrahymenial in the host basidiome. Infected areas are sometimes visible as a whitish pruinose layer on the host basidiome. Monomitic, hyphae hyaline, thin-walled, smooth, clamped. Probasidia are thin-walled, collapsing after maturation of the basidium. Basidia are narrowly clavate, frequently curved, transversally septate, mature basidia four-celled. Basidiospores are irregular, ellipsoid-angular to drop- or comma-shaped, germinating by hyphae, budding or secondary spores. Conidiophores are stalked, with numerous apical appendages. Conidia are irregular, ellipsoid to curved, often with one flattened side, thick-walled, cyanophilous. The host-parasite interface of *S. micra* comprises hyphae with colacosomes which coil around host hyphae (Schoutteten et al., 2023). *Slooffia micra* has been reported from Belgium, Denmark, Germany, France, Norway and the Netherlands (Schoutteten et al., 2023).

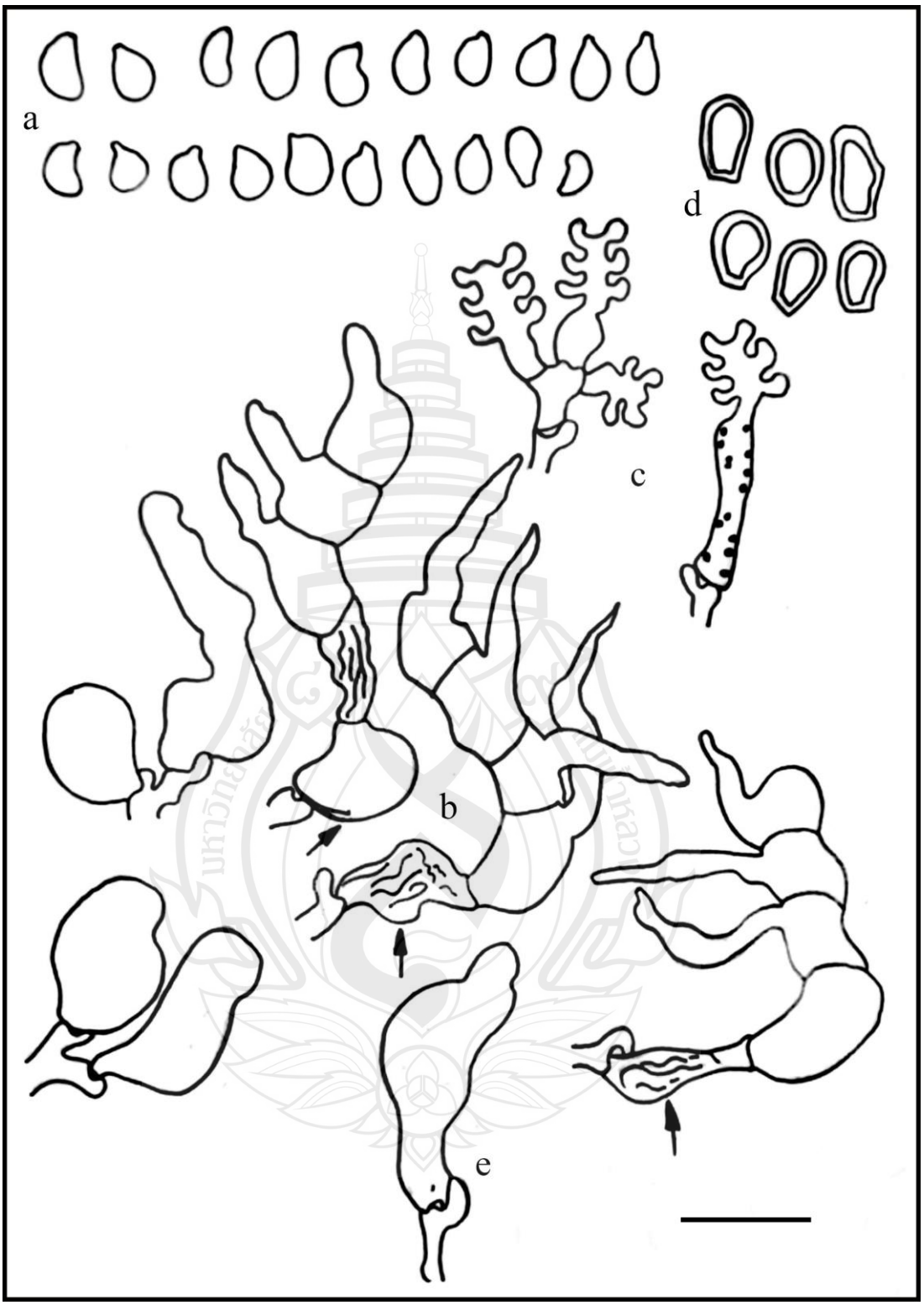


Figure 5.137 *Slooffia micra*

Figure 5.137, a. Basidiospores. b. Basidia. c. Cluster of conidiophores. d. Conidia. e. Basidioles (arrows indicate probasidia and black dots represent colacosomes). Scale bar = 10 µm. (Redrawn from Schoutteten et al., 2023).

Class *Pucciniomycetes* R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Helicobasidiales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Helicobasidiaceae P.M. Kirk

Helicobasidium Pat., Bull. Soc. bot. Fr. 32: 172 (1885)

Figure 5.138

Index Fungorum number: IF 17727

Helicobasidium was introduced by Patouillard (1885) to accommodate *Hypochnus purpureus*, a corticioid fungus developing on plants with purplish basidiomata, and one of the causal agents of violet root rot. *Helicobasidium* species have complex life cycles, alternating between a sexual, dikaryotic plant parasitic stage (*Helicobasidium*-stage) and an asexual, haploid mycoparasitic stage (*Tuberculina*-stage). No yeast morph is known from *Helicobasidiales* (Roberts, 1999b). The different stages of the life cycle were interpreted as distinct organisms belonging to various fungal genera, due to their strongly differing ecology and morphology. Plant parasitic stages were referred to as *Helicobasidium*, and the mycoparasitic stages as *Tuberculina*. The complexity of the life cycle was shown by Lutz et al. (2004b), who were able to link these different stages by means of molecular phylogenetic reconstructions.

The dikaryotic, plant parasitic, *Helicobasidium*-stage, which includes the sexual part of the life cycle, has been reported from a multitude of plant hosts. The sexual stage is characterized by corticioid, hypochnoid to membranaceous, purple to purple-brown basidiomata when fresh. Monomytic, hyphae thin- to thick-walled, unclamped. Basidia cylindrical, often strongly curved, transversally septate, two-celled at maturity. Basidiospores hyaline, ellipsoid to reniform, smooth, thin-walled, and germinate by hyphae. No secondary spore formation has been reported for *Helicobasidium* species (Roberts, 1999b). An anamorphic stage, morphologically similar to the mycelium of the *Helicobasidium*-stage, is known comprising sclerotia, i.e. the *Thanatophytum*-stage (Roberts, 1999b; Lutz et al., 2004b).

The haploid, mycoparasitic *Tuberculina*-stage comprises pulvinate sporodochia developing on the aecia of various *Pucciniales*. Within these sporodochia, conidiogenous cells are organised in a palisade-like arrangement, and each conidiophore produces one conidium (Aghayeva et al., 2016). Based on infection experiments, Lutz et al. (2004c) showed a high degree of host-specificity in the mycoparasitic *Tuberculina*-stage. This contrasts to the apparently host-unspecific plant parasitic *Helicobasidium*-stages of the same organisms, but these inferences are based on a tiny sampling and more studies are needed in this group (Schoutteten et al., 2024a).

The host-parasite interface comprises fusion pores between host and parasite hyphae (Bauer et al., 2004; Bauer, 2004). However, the diameter of the fusion pores is in the range of micrometers, unlike any other mycoparasite in Basidiomycota engaging in fusion pore interaction of which the fusion pores typically are about 20 nm in diameter (Bauer, 2004). More details on the host-parasite interaction mechanism are given in Schoutteten et al. (2024a).

Helicobasidium species have been reported from most regions of the world, either in association with plant hosts (in the *Helicobasidium*-stage) or in a mycoparasitic interaction with *Pucciniales* (*Tuberculina*-stage) (Roberts, 1999b; Lutz et al., 2004a, b, c; Zhao et al., 2017).

Nomenclaturally, the oldest available name for this genus is *Thanatophytum*. However, Aime et al. (2018) argued that the name *Helicobasidium* is much more commonly used for these species and called for the protection of the latter name, as well as for the protection of the type species *Helicobasidium purpureum*.

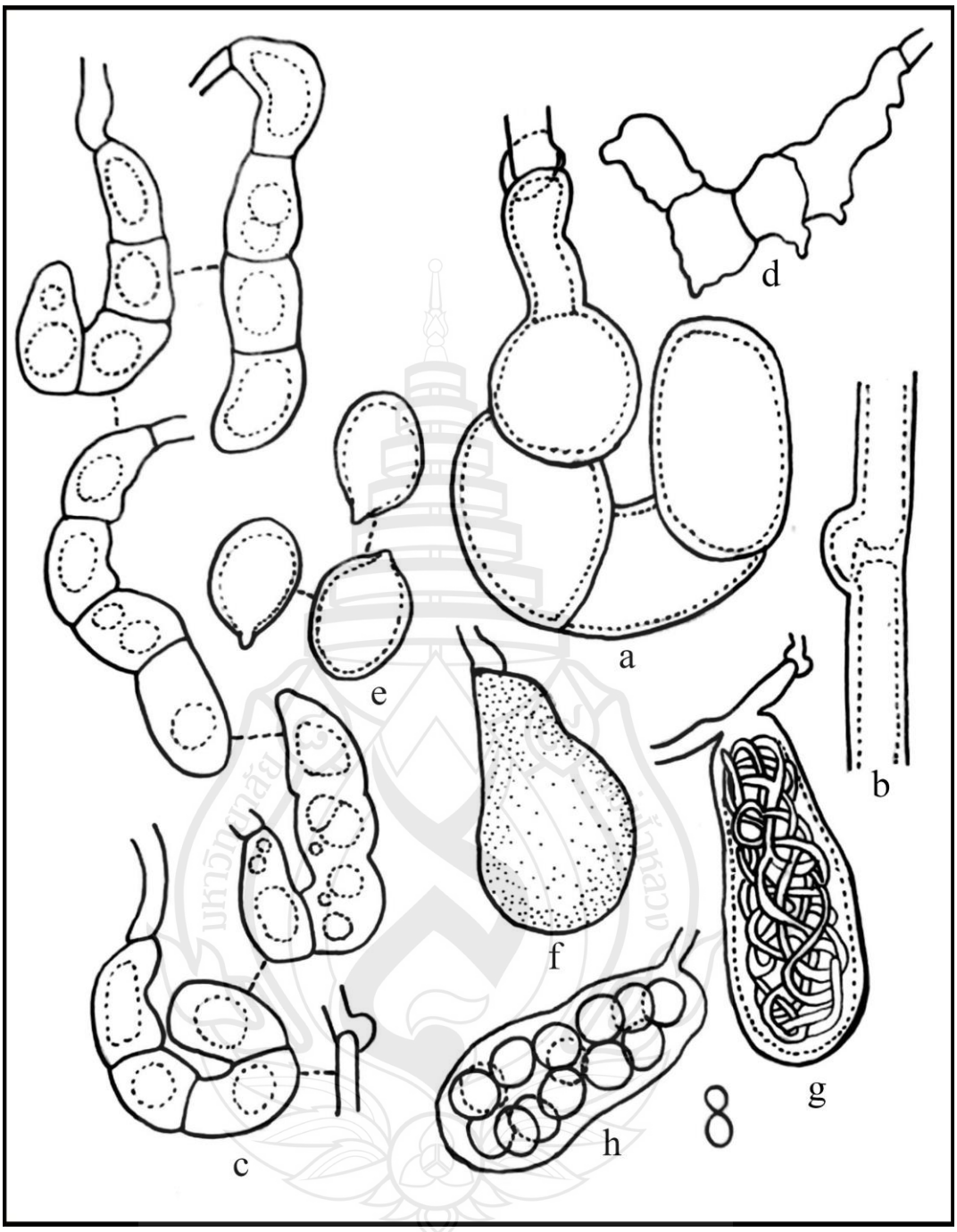


Figure 5.138 *Helicobasidium candidum*

Figure 5.138, a. Basidium. b. Clamp connection. c. Basidia and clamp connection. d. Spent basidium. e. Basidiospores. f. Parasite, early homogeneous stage. g. Same, intermediate stage. h. Same, late stage. (Redrawn from Martin, 1940).

Platygloeales R.T. Moore

Platygloeaceae Racib.

Achroomyces Bonord., Handb. Allgem. Mykol. (Stuttgart): 135 (1851)

Figure 5.139

Index Fungorum number: IF 17007

Achroomyces was introduced by Bonorden (1851), with the type species, *A. tumidus*, presumably collected from Germany. *Achroomyces tumidus* was reported to produce erumpent pustulate, cushion-shaped, basidiomata on *Betula* twigs, which develop from below the bark of its substrate and eventually break through. *Achroomyces tumidus* was not recognized as a basidiomycetous fungus, and it was only Von Höhnel (1904) who correctly recognized the transversely septate reproductive cells as basidia. As outlined by Donk (1958, 1966), this species was described by various authors and various synonyms are available. This species is most likely congeneric, or even conspecific, with *Achroomyces disciformis* (Fr.) Donk and *Platygloea nigricans* (Fr.) J. Schröt., both reported to produce pustulate basidiomata on *Tilia* branches. Since *P. nigricans* is the type species of *Platygloea* J. Schröt., the latter genus represents a later synonym of *Achroomyces*. However, not all authors shared this interpretation and believe that Bonorden's *A. tumidus* represents a distinct taxon and treat the name as a *nomen dubium*. Because of these contrasting views on the application of generic names, both *Achroomyces* and *Platygloea* remain in use, and many species were moved from one genus to the other. Most of these species share few characters, except for the presence of transversely septate basidia, a character that occurs in many lineages of Basidiomycota. Bandoni (1956) already reported the heterogeneity of this group of species, and traditional macro- and micromorphological characteristics proved to be insufficient to come to a more natural classification. The heterogeneity of this group is also displayed in differences at the ultrastructural level and in spore germination patterns (Oberwinkler, 1987; Oberwinkler et al., 1990b).

Several species in *Achroomyces* and *Platygloea* are known for their mycoparasitic lifestyle, most of which do not produce distinct basidiomata, but exhibit intrahymenial growth in their fungal host (Oberwinkler, 1964; Schoutteten et al., 2023). Following *Achroomyces* species are mycoparasites or fungicolous species: *A. arachidosporus, A. chlamydospora, A. dennisii, A. henricii, A. insignis, A. lotharingus, A. lumbricifer, A. lunaticonidiatus,* and *A. soranus* (Schoutteten et al.,

2024a). All of these species are only known from morphological descriptions based on one or a few specimens, of which no living cultures were derived. Consequently, no molecular data are available, and ultrastructural insights about the host-parasite interface are lacking. For some species, tremelloid haustorial cells were observed by means of light microscopy and a nanometer fusion pore host-parasite interface may be assumed, but for other species the host-parasite interaction type remains unknown. The latter group of species may either comprise colacosome-interacting mycoparasites, or species with previously undiscovered types of host-parasite interfaces. The latter scenario was the case for *Platygloea mycophila* (currently *Obvidator mycophilus*), in which Schoutteten et al. (2024b) discovered a *hitherto* unknown type of host-parasite interface.

Molecular phylogenetic reconstructions have shown that all previously sequenced mycoparasitic and fungicolous species that were originally assigned to *Achroomyces* and *Platygloea* based on morphological similarities, belong to distinct orders, classes and subphyla of Basidiomycota. Remarkably, none of these previously studied fungicolous taxa belongs to *Platygloeales*. Good examples are *A. insignis*, which was transferred to the genus *Slooffia* (*Microbotryomycetes*, Schoutteten et al., 2023), *A. soranus*, which was combined into *Occultifur* (*Cystobasidiomycetes*, Schoutteten et al., 2024b), and *A. chlamydospora*, for which the genus *Tectobasidium* was introduced (*Basidiomycota Incertae sedis*, Spirin et al., 2024). Consequently, the name *Achroomyces* should be applied only for a small group of species around *A. tumidus* (syn. *A. disciformis*), which most likely solely comprises saprobic fungi, and no mycoparasites. However, many fungicolous species are retained in *Achroomyces* and *Platygloea* because of the lack of molecular and ultrastructural data. Further disentangling of the genus *Achroomyces* will involve culture studies of mycoparasites and fungicolous taxa, combined with molecular phylogenetic reconstructions and detailed microscopy. To date, *Achroomyces* comprises 13 species which are presumed mycoparasites or fungicolous species, whereas *Platygloea* comprises five of these (Schoutteten et al., 2024b). For none of these mycoparasites and fungicolous species currently assigned to these two genera, DNA sequence data are available in GenBank (2025) or living cultures are available in public culture collections.

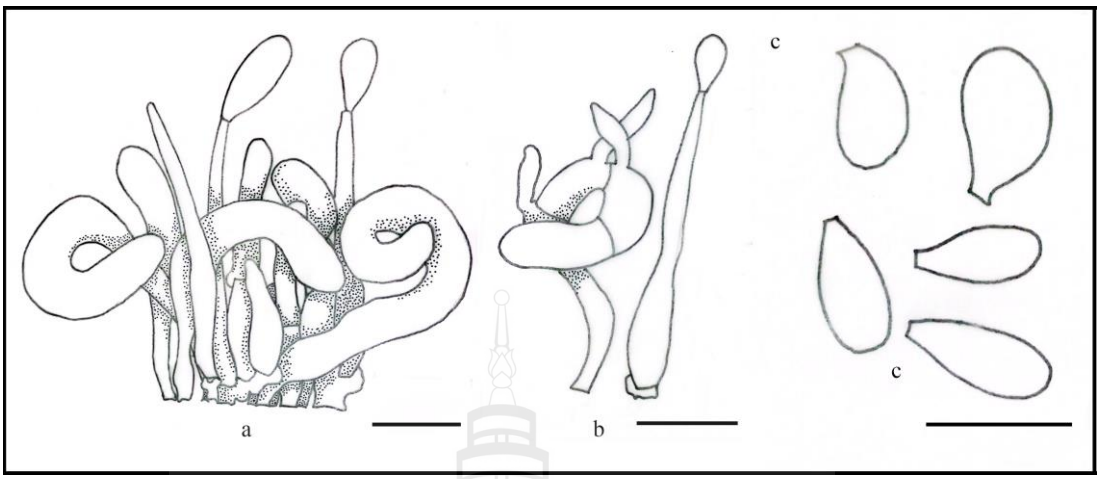


Figure 5.139 *Achroomyces lumbricifer*

Figure 5.139, a. Section of hymenium, showing intermixed conidiophores and coiled basidia b. coiled basidia and conidiophore c. basidiospores and conidiospores. Scale bars: a, b, c = 10 μm. (Redrawn from Roberts, 2001).

Class *Spiculogloeomycetes* Q.M. Wang, F.Y. Bai, M. Groenew. & Boekhout

Spiculogloeales R. Bauer, Begerow, J.P. Samp., M. Weiss & Oberw.

Spiculogloeaceae Denchev

Spiculogloea P. Roberts, Mycotaxon 60: 112 (1996)

Figure 5.140

Index Fungorum number: IF 27829

Roberts (1996) introduced *Spiculogloea* to accommodate *S. occulta*, an intrahymenial mycoparasite of *Kurtia argillacea*, collected in Majorca (Spain). The most remarkable characteristic of this species was the strongly ornamented (spiculated), cyanophilous, transversely three-septate basidia, which originate from small probasidia. These ornamented basidia were used to distinguish this genus from *Achroomyces*/*Platygloea* (Roberts, 1996). Roberts (1997) described *S. minuta* from the UK, an intrahymenial mycoparasite of *Tulasnella violea*. This species was also reported from some other fungi, including *Tubulicrinis accedens*, *Tulasnella saveloides, T. eichleriana,* and *Helicogloea* sp., but it remains to be assessed if it truly comprises the same taxon. Hauerslev (1999) described *S. subminuta* from Denmark, as an intrahymenial mycoparasite of *Botryobasidium subcoronatum*. Trichies (2006) described *S. limonispora* from France, as an intrahymenial mycoparasite of *Kurtia*

argillacea. Finally, Schoutteten et al. (2018), introduced *S. inaequalis*, an intrahymenial mycoparasite of *Sistotrema oblongisporum*, collected in Belgium. *Spiculogloea* species have been documented in Belgium, Canada, Finland, France, Germany, Russia, Spain, and Sweden (Bandoni et al., 2002; Trichies, 2002; Kotiranta, 2009; Rödel, 2014; Spirin et al., 2016; Van de Put, 1998, 2005).

Spiculogloea species are characterized by monomitic hyphal systems with narrow, clamped hyphae, stalked spiculate cyanophilous transversely three-septate basidia, sometimes emerging from small probasidia, subglobose, ellipsoid, navicular or subfusiform basidiospores that germinate by repetition, hyphae or yeast budding, and basally clamped tremelloid haustorial cells of which the apices attach to host hyphae (Roberts, 1996; Langer & Oberwinkler, 1998; Schoutteten et al., 2018; Schoutteten et al., 2024a). Conidial structures are present in some species. The septal pore complexes in hyphae of *Spiculogloea* species have a simple morphology, without the presence of associated microbodies or other structures (Bauer et al., 2006). All five currently described *Spiculogloea* species are presumed mycoparasites, interacting with tremelloid haustorial cells, of which the apices attach to host hyphae. Bauer et al. (2006) showed the formation of a nanometer fusion pore at the apex region of a haustorial cell of *Spiculogloea subminuta* connecting to a host hypha, establishing cytoplasmic contact between host and mycoparasite.

Roberts (1996) provisionally assigned *Spiculogloea* within *Platygloeales*, while acknowledging the heterogeneity of the group. To date, molecular DNA sequence data for *Spiculogloea* species remains limited to the LSU and SSU sequences derived from a single *Spiculogloea* isolate, used in Weiss et al. (2004) and Bauer et al. (2006). Weiss et al. (2004) conducted molecular studies utilizing D1/D2 (LSU) DNA sequence data, and found that this *Spiculogloea* sp. isolate clustered with a *Mycogloea* sp. isolate. These two isolates formed a well-supported clade sister to *Agaricostilbales*. This topology was also retrieved by Bauer et al. (2006), who used LSU and SSU DNA sequence data. Bauer et al. (2006) also found that several *Sporobolomyces* species (the *S. subbruneus* group) cluster with the two *Spiculogloea* and *Mycogloea* isolates. Bauer et al. (2006), introduced *Spiculogloeales* to accommodate this *Spiculogloea*-clade sister to *Agaricostilbales*. Multilocus molecular phylogenetic reconstructions by Wang et al. (2015a) confirmed the findings by Bauer

et al. (2006), and suggested that *Spiculogloeales* might represent a deep or ancient lineage, basal to other members of *Agaricostilbomycetes*. Therefore, Wang et al. (2015b) raised this clade to class level, introducing *Spiculogloeomycetes*.

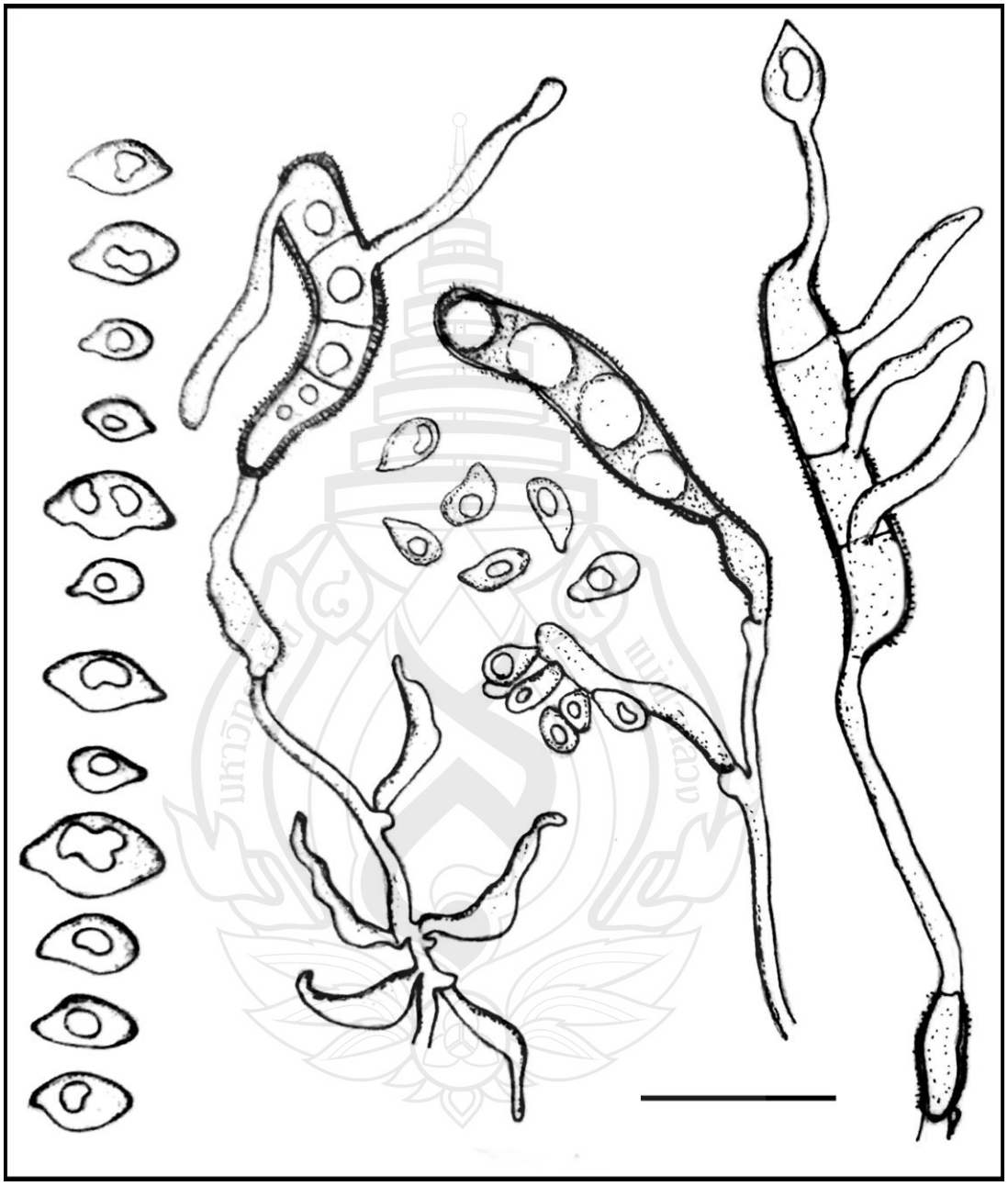


Figure 5.140 *Spiculogloea occulta*

Figure 5.140, Basidiospores from print, basidia showing haustorial cells, conidiophore, conidia and swollen probasidia. Scale bar = 10 μm. (Redrawn from Roberts, 1996).

Pucciniomycotina* genera *incertae sedis

Kryptastrina Oberw., Rep. Tottori Mycol. Inst. 28: 118 (1990)

Figure 5.141

Index Fungorum number: IF 25572

Oberwinkler (1990) introduced the monotypic genus *Kryptastrina*, to accommodate *K. inclusa*, an intrahymenial mycoparasite of an unidentified corticioid fungus found in Colombia. To date, *K. inclusa* is only known from the type locality. *Kryptastrina* is characterized by hyaline, somewhat indistinct hyphae, which produce basally clamped haustorial cells. The generative hyphae produce solitary, scattered, transversally three-septate basidia. Each basidial cell bears one short sterigma to which a spore is attached asymmetrically. Mature basidiospores are pyramidally tetrahedral, thin-walled, hyaline, and non-amyloid (Oberwinkler, 1990). The presence of tetrahedic basidiospores is a unique characteristic among heterobasidiomycetous taxa. No ultrastructural studies were reported on the host-parasite interface. There are no DNA sequence data available for *Kryptastrina* in GenBank (2025).

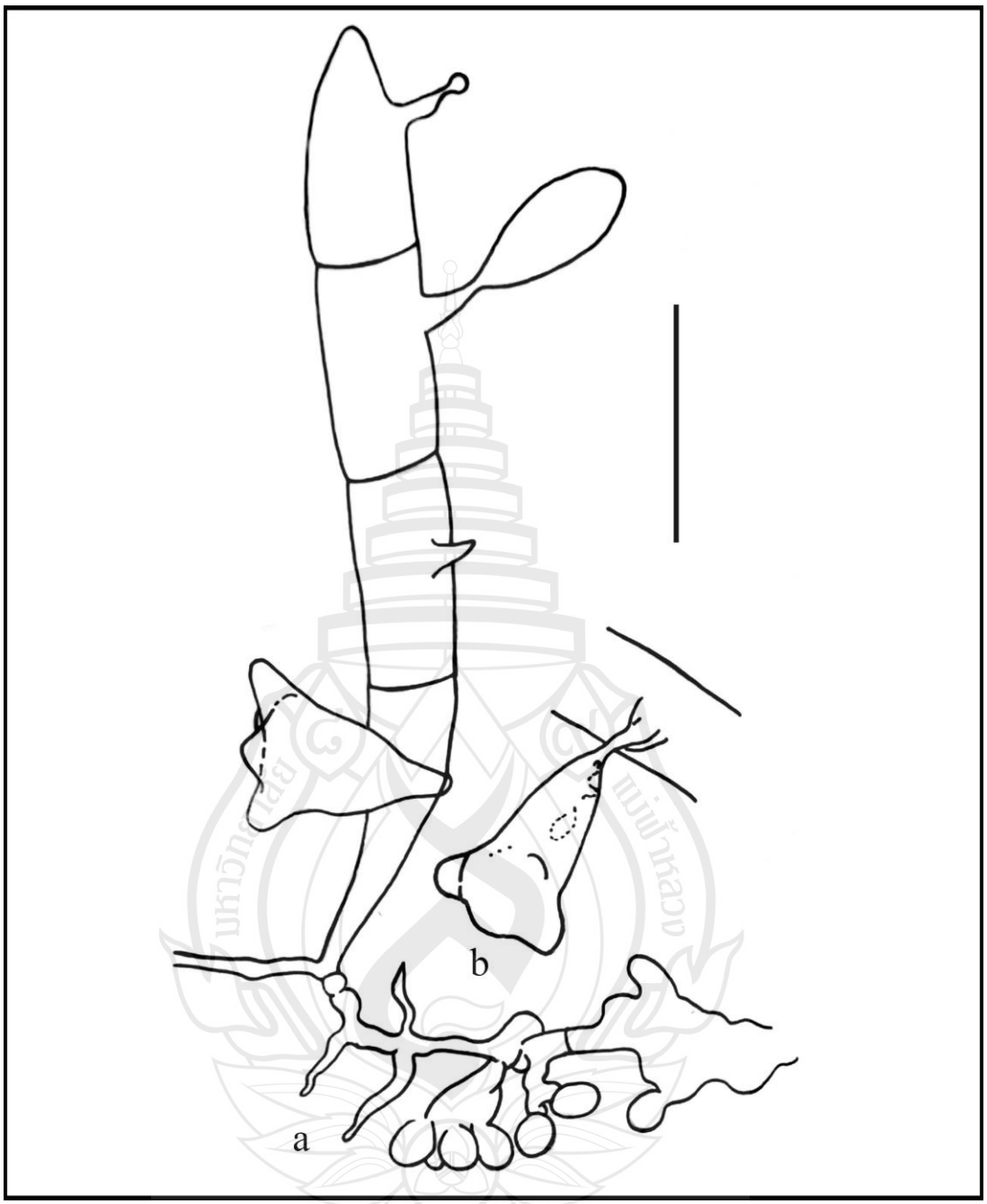


Figure 5.141 *Kryptastrina inclusa*

Figure 5.141, a. Mature, transversely septate basidium with sterigmata and attached spores and thin, branched, basal hypha.b. Basidiospore attached to sterigma. Scale bar = 10 μm. (Redrawn from Oberwinkler, 1990).

Zygogloea P. Roberts, Mycotaxon 52(1): 241 (1994)

Figure 5.142

Index Fungorum number: IF 27297

The monotypic genus *Zygogloea* was introduced by Roberts (1994) to accommodate *Z. gemellipara*, an intrahymenial mycoparasite found in *Myxarium nucleatum* collections from the UK.

Zygogloea gemellipara does not produce basidiomata, but develops completely intrahymenial in its host. Infections are not visible to the naked eye. Monomitic, hyphae thin-walled, hyaline, with clamp connections. Basidia basally clamped, transversely septate, stalked or not, cylindrical, sinuous. Basidiospores allantoid, thin-walled, 1- to 3-septate at maturity, with acute apex on one side, with a clear apiculus, germination pattern unknown. Conidiophores basally clamped, two-celled, each cell with a prominent incurving outgrowth where conidiogenesis of zygoconidia takes place. Zygoconidia are born singly, and fuse during the maturation process, prior to abscission (Roberts, 1994; Van de Put, 2005). The host-parasite interface of *Z. gemellipara* comprises basally clamped tremelloid haustorial cells, frequently found in clusters (Roberts, 1994; Van de Put, 2005). There are no studies reporting on the ultrastructure of the host-parasite interface.

Zygogloea gemellipara has been reported from Belgium, Denmark, the Netherlands and the UK (Roberts, 1994; Van de Put, 2005). There are no molecular DNA sequence data available for *Zygogloea* in GenBank (2025).

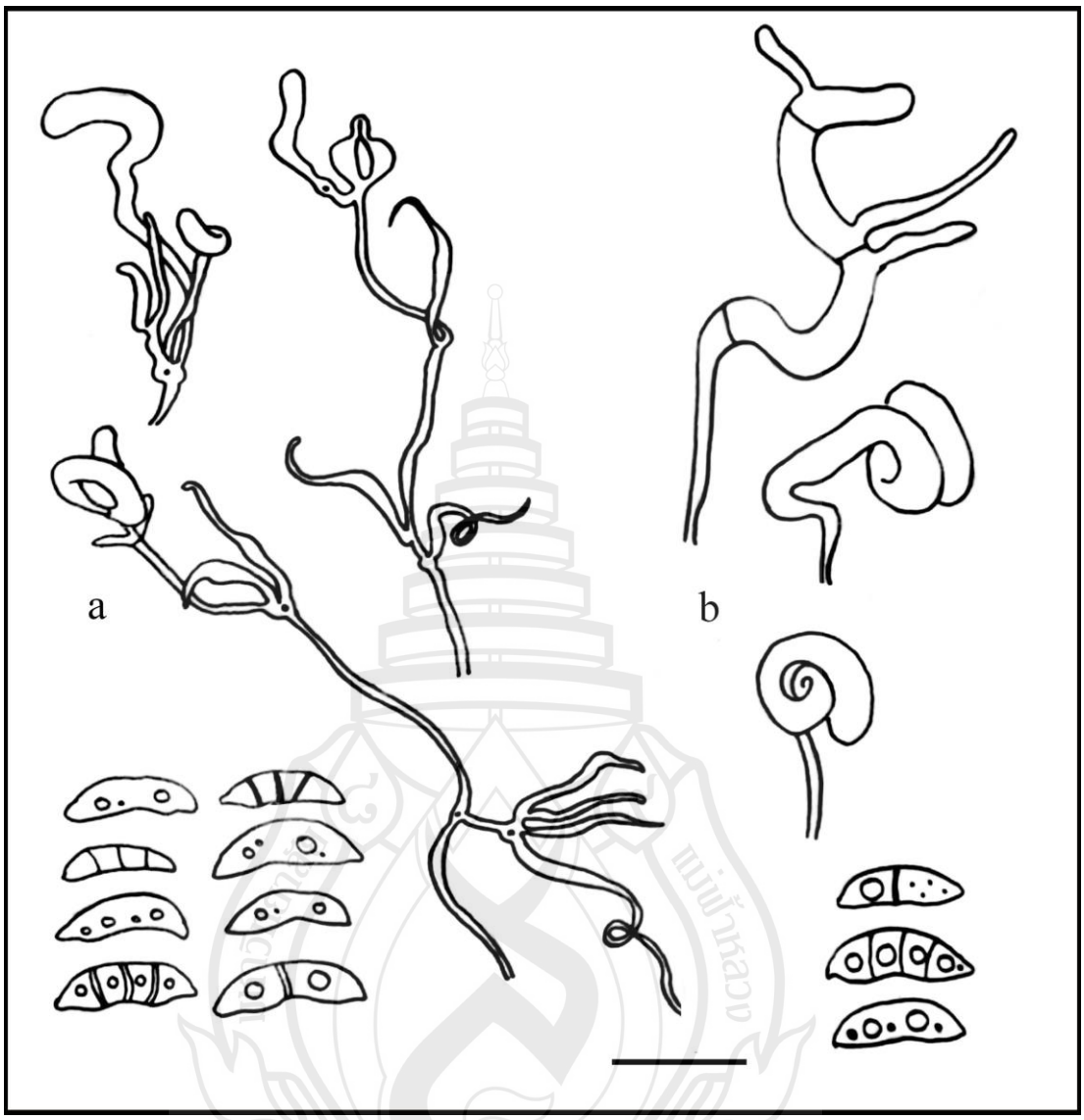


Figure 5.142 *Zygogloea gemellipara*

Figure 5.142, a. Basidia bearing hyphae showing haustorial cells and basidiospores from print. b. Spiralling basidia and basidiospores from print. Scale bar = 10 μm. (Redrawn from Roberts, 1994).

Basidiomycota* genera *incertae sedis

Celatogloea P. Roberts, Mycologist 19(2): 69 (2005)

Figure 5.143

Index Fungorum number: IF 28923

Roberts (2005) introduced the monotypic genus *Celatogloea* to accommodate *C. simplicibasidium*, a dimorphic, intrahymenial mycoparasite of *Corticium roseum*.

Celatogloea simplicibasidium was previously described as *Laeticorticium simplicibasidium*, but this represented a misinterpretation of the host and parasite as one fungal species (Lindsey & Gilbertson, 1977). *Celatogloea simplicibasidium* does not produce its own basidiomata, and is characterized by aseptate, monosterigmate basidia that arise from swollen, thick-walled, basally clamped probasidia. The basidiospores germinate by secondary spore production and producing yeast cells (Roberts, 2005). The host-parasite interface comprises basally clamped haustorial cells. Since the establishment, *Celatogloea* has remained monotypic (Species Fungorum, 2025). *Celatogloea simplicibasidium* has been collected in the UK and the USA (Lindsey & Gilbertson, 1977; Roberts, 2005). No molecular data are available for *Celatogloea* in GenBank (2025).

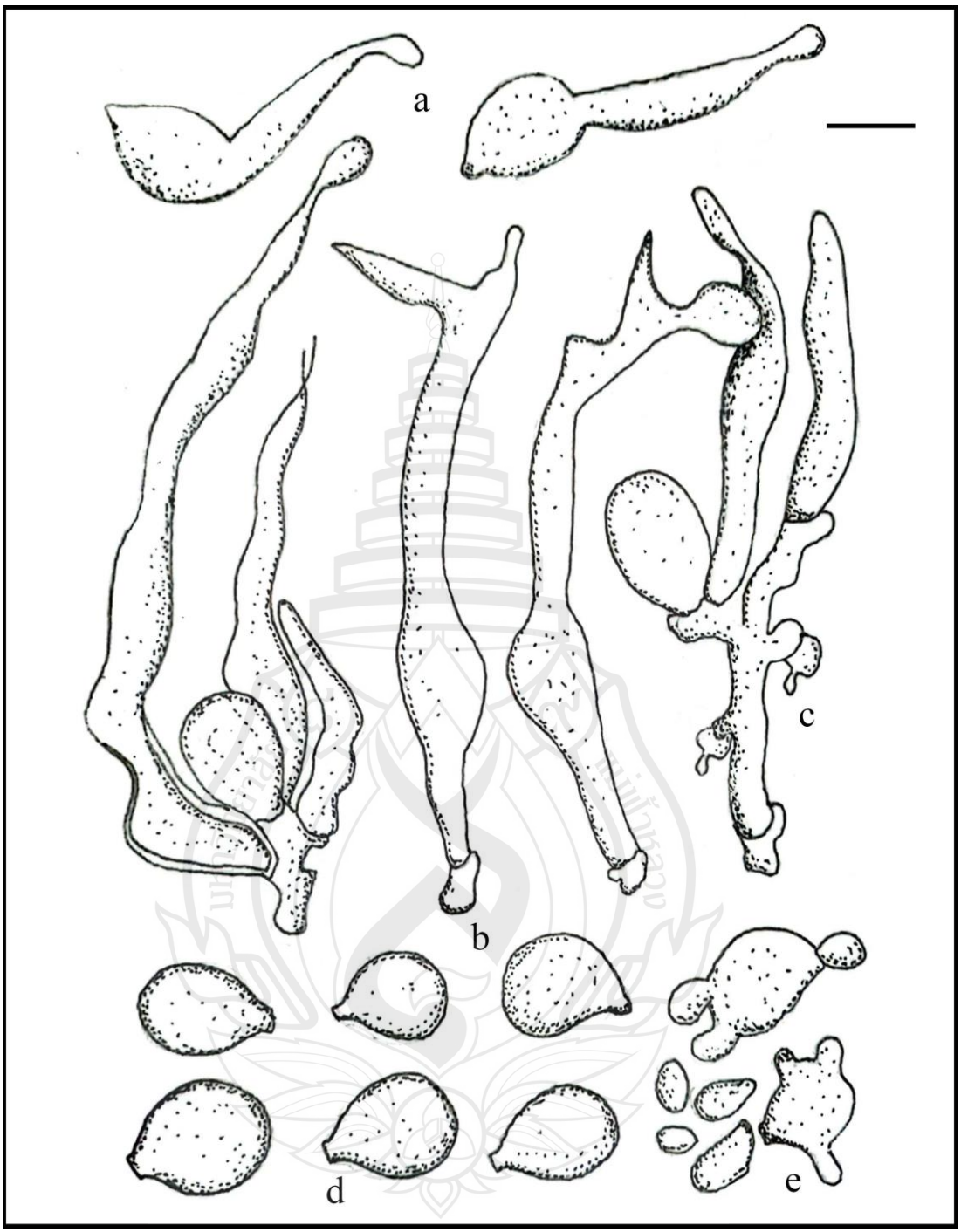


Figure 5.143 *Celatogloea simplicibasidium*

Figure 5.143, a. Basidiospores producing secondary spores. b. Basidia, some producing secondary sterigmata, arising from thin- to thick- walled probasidia. c. Haustorial cell. d. Basidiospores. e. Basidiospores germinating by yeast cells. Scale bar = 10 μm. (Redrawn from Roberts, 2005).

Cystogloea P. Roberts, Acta Mycologica, Warszawa 41(1): 25 (2006)

Figure 5.144

Index Fungorum number: IF 510654

The monotypic genus *Cystogloea* was introduced by Roberts (2006) to accommodate *C. oelandica*. This species was detected as a gelatinous layer overgrowing perithecia of *Pseudotrichia minor*, which themselves developed on old stromata of *Amphiporthe leiphaemia* (syn. *Dendrostoma leiphaemia*) (Roberts, 2006).

Cystogloea oelandica is characterized by the production of gelatinous basidiomes, in which three-septate auricularioid basidia arise from conspicuous, swollen probasidia. These probasidia develop from disarticulated segments of moniliform hyphae, resembling rhizoctonia-like chains, and seem to collapse upon maturity of the basidium (Roberts, 2006). Basidia give rise to ellipsoid to fusiform basidiospores, of which the germination pattern is unknown (Roberts, 2006). Details about the host-parasite interface are known (Schoutteten et al., 2024a). There is no molecular data available for *Cystogloea* in GenBank (2025).

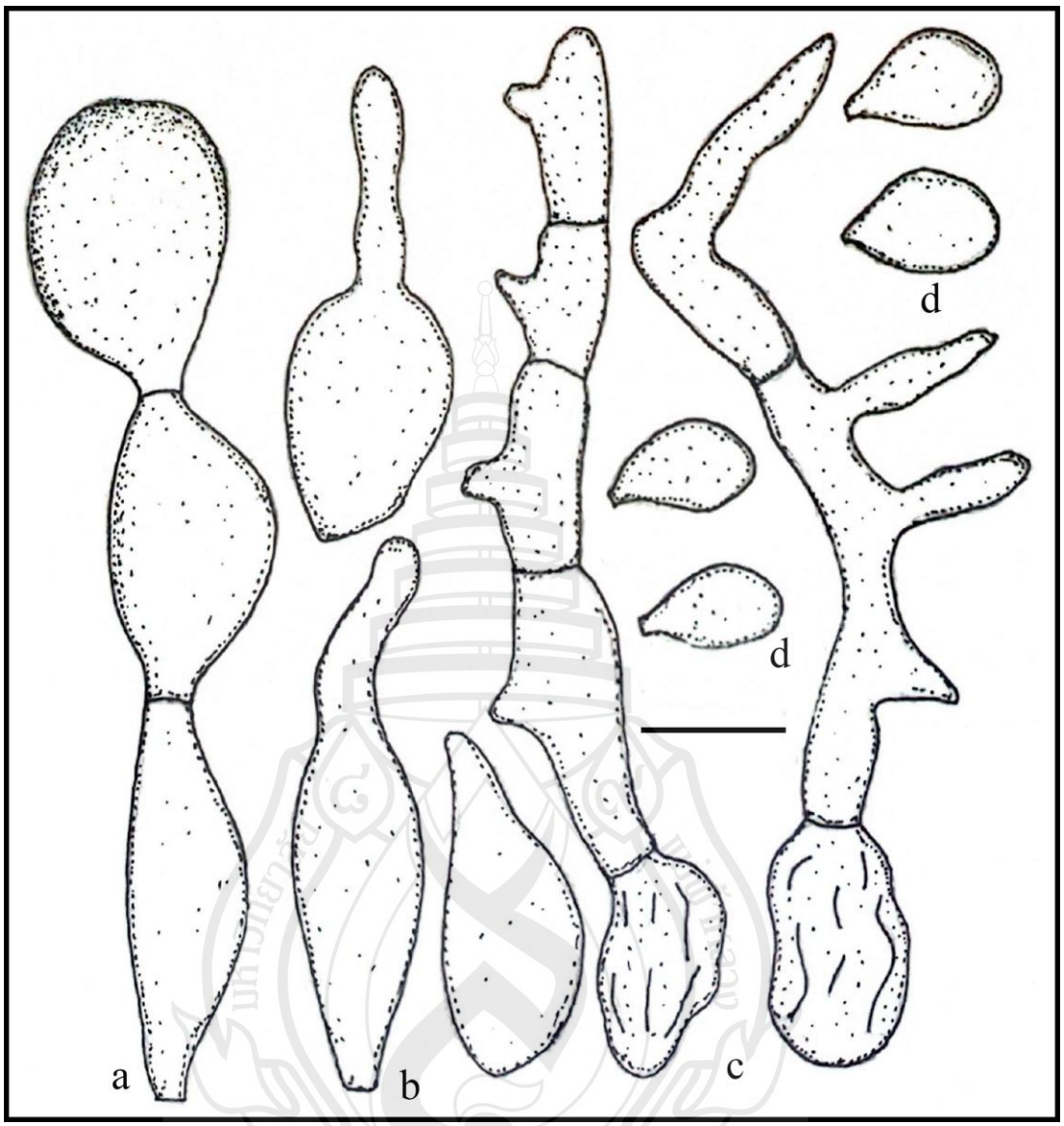


Figure 5.144 *Cystogloea oelandica*

Figure 5.144, a. Moniliform hyphae. b. Disarticulated hyphal compart ments (probasidia) starting to produce epibasidia. c. Mature, septate epibasidia arising from collapsed hyphal compartments (probasidia). d. Basidiospores. Scale bar = 10 μm. (Redrawn from Roberts, 2006).

Tectobasidium Spirin, Malysheva & H. Nilsson, Mycol. Progr. 23(no. 77): 2 (2024)

Figure 5.145

Index Fungorum number: IF 854998

Tectobasidium was introduced by Spirin et al. (2024) to accommodate *T. chlamydosporum* and *T. cornutum*, two intrahymenial heterobasidiomycetes growing in *Helicogloea* and *Myxarium* species. *Tectobasidium chlamydosporum* was described as *Achroomyces chlamydosporus* by Roberts (2002).

Tectobasidium species do not produce basidiomata, but develop intrahymenially in their hosts. Monomitic, hyphae hyaline, clamped, slightly cyanophilous. Basidia transversally septate, two-celled at maturity. Basidiospores hyaline, thin-walled, cylindrical, germinating by hyphae. Chlamydospores hyaline, truncate-ellipsoid to almost turbinate, thick-walled, cyanophilous, with blunt or acute outgrowths (Spirin et al., 2024). No distinct host-parasite interface was reported so far. *Tectobasidium* species do not produce typical tremelloid haustorial cells or colacosomes. Given the absence of a distinct host-parasite interface, it is questionable if *Tectobasidium* species engage in mycoparasitism (Spirin et al., 2024). The nutritional strategy of these species remains to be investigated. *Tectobasidium* species have been reported from Norway and Sweden (Spirin et al., 2024).

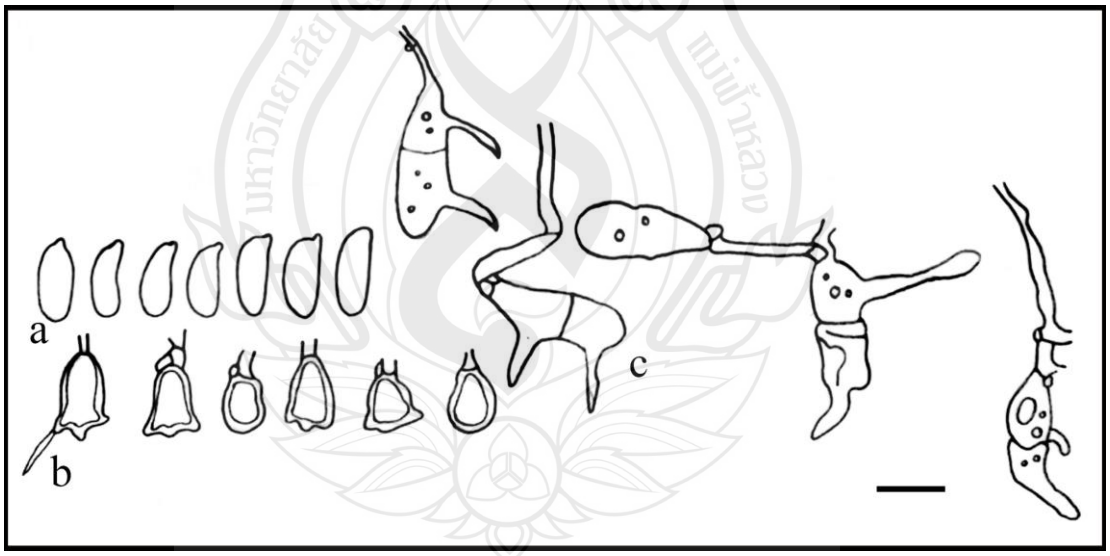


Figure 5.145 *Tectobasidium chlamydosporum*

Figure 5.145, a. Basidiospores. b. Chlamydospores. c. Basidia. Scale bar = 10 μm. (Redrawn from Spirin et al., 2024).

Phylum *Mucoromycota* Doweld

Subphylum *Mucoromycotina* Benny

Class *Mucoromycetes* Doweld

Mucorales Dumort.

Mucoraceae Dumort.

Dicranophora J. Schröt., Jber. schles. Ges. vaterl. Kultur 64: 184 (1886)

Figure 5.146

Index Fungorum number: IF 20175

Dicranophora was established by Schröter (1886), with *D. fulva* as the type species. This species was described as fungicolous on *Paxillus involutus* (*Paxillaceae*) in Germany. Subsequently it has been reported mainly on the senescent fruiting bodies of various *Boletales* members across several countries, including Austria, France, Germany, Greece, Italy, and the USA (Voglmayr & Krisai-Greilhuber, 1996).

Dicranophora is distinguished by the presence of two types of sporangia: tree-like sporangiophores that bear predominantly unisporous sporangiola on saddle-shaped, bifurcate columellae, and typical mucoralean sporangia. Additional features include golden-yellow colonies, clearly defined anisogamy, and the formation of zygospores with irregularly creviced surfaces (adapted from Voglmayr & Krisai-Greilhuber, 1996).

As of Species Fungorum (2025), *Dicranophora* remains monotypic. Sequence data for *D. fulva* are available in GenBank (2025), including ITS, LSU, SSU, and TEF regions. The genus is currently classified within *Mucoraceae*, in *Mucorales* (Hyde et al., 2024a).

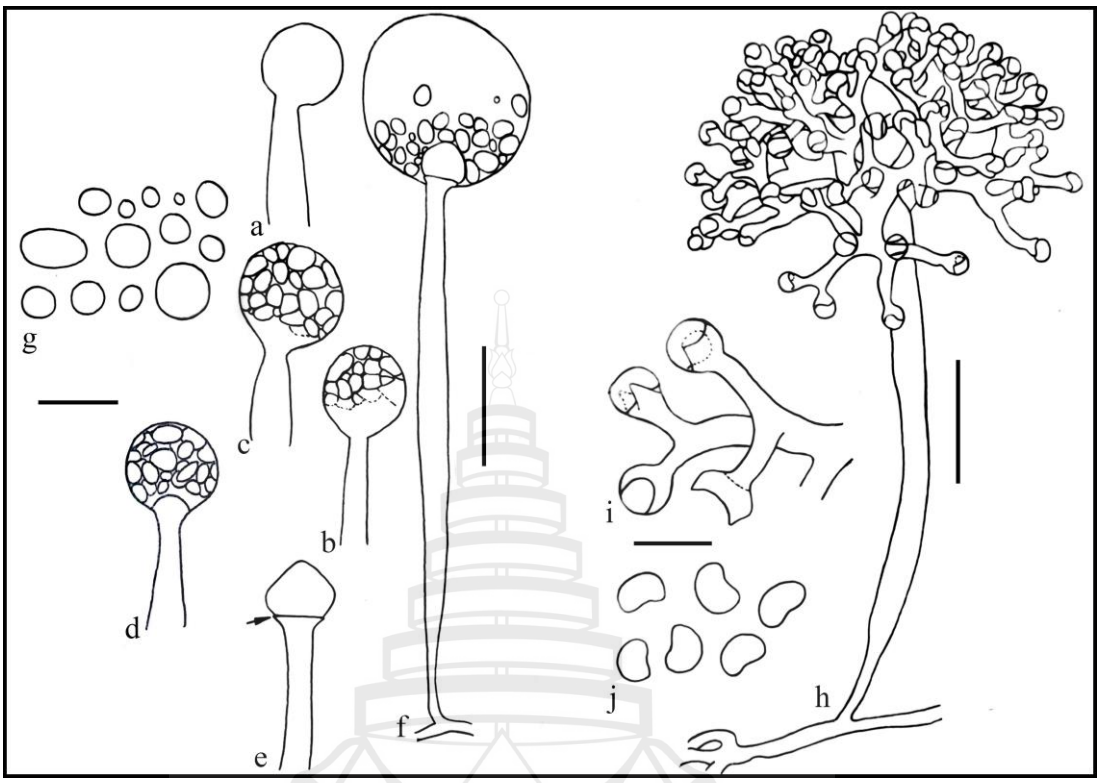


Figure 5.146 *Dicranophora fulva*

Figure 5.146, a. Young sporangium. b–d. Successive stages in sporangiospore production. e. Sporangium with columella after release of the spores (arrow indicates the insertion mark of the dissolved sporangium wall). f. Whole sporangium after dissolving of the sporangium wall, the spores being distributed in the sporangial drop exuded by the columella. g. Sporangiospores. h. Dichotomously branched sporangiophore with unisporous sporangiola on the apices of sporangiophore branches. i. Outermost part of the sporangiophore branch. j. Reniform spores of typical unisporous sporangiola. Scale bars: f, h = 100 μm, a–e, g = 50 μm, i, j = 30 μm. (Redrawn from Voglmayr & Krisai-Greilhuber, 1996).

Mucor Fresen., Beitr. Mykol. 1: 7 (1850)

Figure 5.147

Index Fungorum number: IF 25484

Mucor is the largest genus within *Mucorales* and was established by Fresenius (1850), with *M. mucedo* as the type species (Walther et al., 2019; Nguyen et al., 2020; Zhao et al., 2023b). The genus comprises primarily heterothallic species, although homothallic forms are also known. These fungi typically form zygospores or

azygospores lacking appendages (Benny et al., 2016; Lima et al., 2020). Colonies of *Mucor* grow rapidly and are defined by simple or branched sporangiophores, globose sporangia with an incrusted and deliquescent wall, and zygospores borne on opposed or tongue-like suspensors. In addition, some species may develop sporangiola, apophyses, and rhizoids (Benny et al., 2016; Walther et al., 2019; Lima et al., 2020; Nguyen et al., 2020; Hurdeal et al., 2021).

Mucor species are cosmopolitan in distribution, frequently encountered in a wide range of natural habitats (Morin-Sardin et al., 2017; Hurdeal et al., 2021). While species of *Mucor* are predominantly saprobic, it also includes endophytes, parasites, and pathogens (Rashmi et al., 2019; Wagner et al., 2020). They are frequently isolated from substrates such as soil, dung, decomposing plant material, and other moist environments (Walther et al., 2013). Several species have been identified as opportunistic pathogens in both humans and animals (Hoffmann et al., 2013; Morin-Sardin et al., 2017). In addition, some *Mucor* species exhibit fungicolous behaviour, growing on or in association with other fungi (Gajanayake et al., 2023b). Reported fungicolous associations include *Mucor circinelloides* on *Rhizopus stolonifer* (*Rhizopodaceae*) and *Phlebopus* sp. (*Boletinellaceae*), *M. hiemalis* on *Ramaria* sp. (*Gomphaceae*) and *Boletus* sp. (*Boletaceae*), *M. irregularis* on *Pleurotus* sp. (*Pleurotaceae*), *M. luteus* on *Amanita muscaria* (*Amanitaceae*), *M. nederlandicus* on *Russula* sp. (*Russulaceae*), and *M. yunnanensis* on *Armillaria* sp. (*Physalacriaceae*) and *Boletus* sp. (Sun et al., 2019a; Gajanayake et al., 2023b).

Mucor species have been recognized for their diverse biotechnological applications, including the production of enzymes (Lee et al., 2011; Huang et al., 2014), biofuels (Carvalho et al., 2018), and fermented food products (Morin-Sardin et al., 2017). Additionally, they play roles in bioremediation (Jabasingh & Pavithra, 2010) and biotransformation processes with potential applications in pharmaceutical and energy industries (Oliveira Silva et al., 2013; Silva et al., 2015b; Morin-Sardin et al., 2017).

This genus includes over 100 accepted species (Species Fungorum, 2025), and DNA sequence data for many of these taxa are available in GenBank (2025). Taxonomically, *Mucor* is placed within *Mucoraceae*, in *Mucorales* (Hyde et al., 2024a).

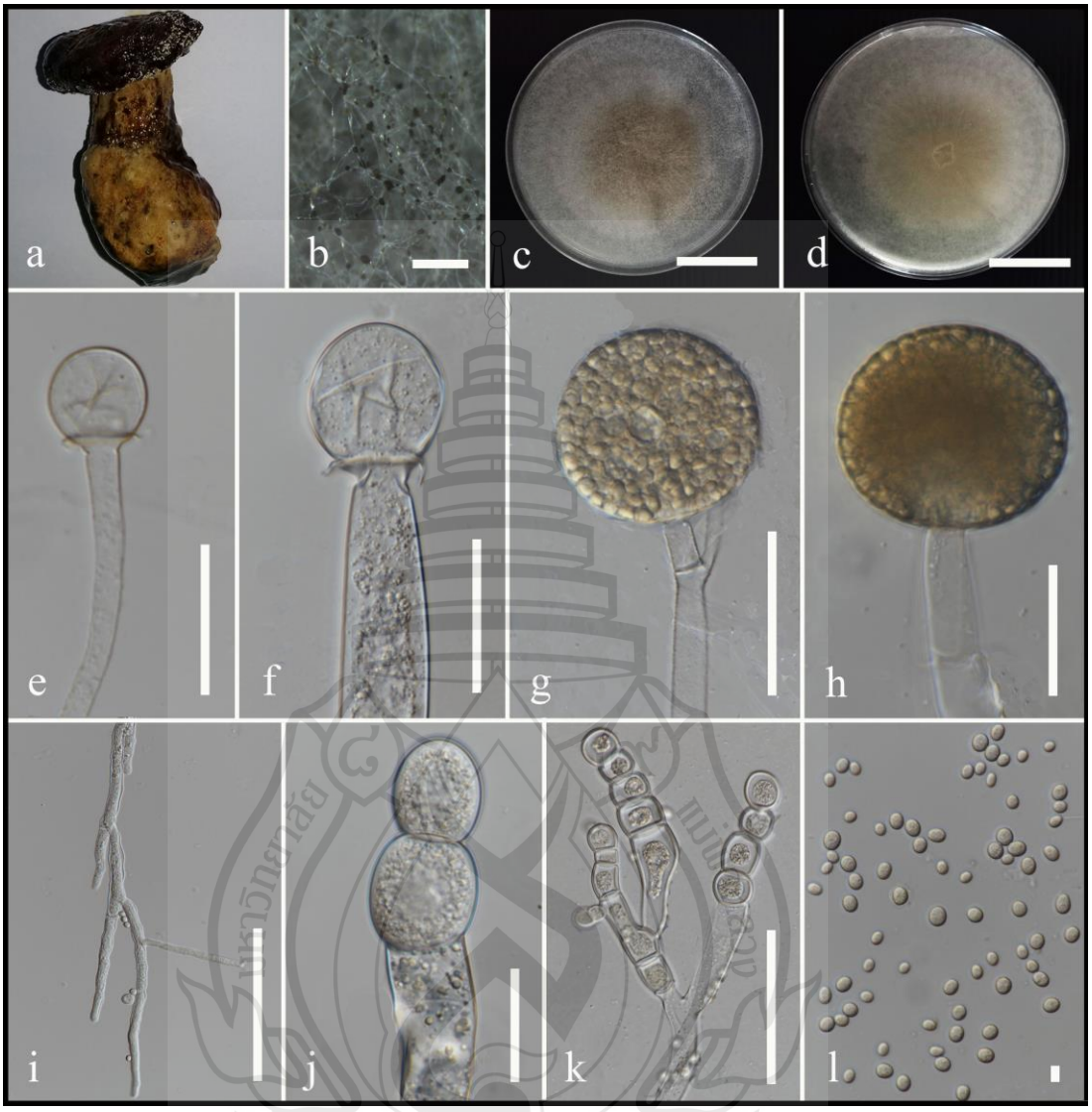


Figure 5.147 *Mucor circinelloides*

Figure 5.147, a. Host (*Phlebopus* sp.). b. Sporulation on PDA. c, d. Colony on PDA. e, f. Columella with collars. g, h. Sporangia. i. Rhizoid. j, k. Chlamydospores. l. Sporangiospores. Scele bars: c, d = 30 mm, b = 200 µm, i = 150 µm, f, g, k = 50 µm, h, j = 30 µm, e = 25 µm, h, j = 30 µm, l = 5 µm.

Phycomycetaceae Arx

Spinellus Tiegh., Annls Sci. Nat., Bot., sér. 6 1: 66 (1875)

Figure 5.148

Index Fungorum number: IF 20539

Spinellus was established by van Tieghem (1875) and is typified by *S. fusiger* (Hesseltine, 1955). Species of *Spinellus* are mycoparasites, primarily infecting basidiomata of *Mycena* spp. (*Mycenaceae*), though they have also been reported on other agarics such as *Amanita* (*Amanitaceae*), *Collybia* (*Clitocybaceae*), and *Hygrophorus* (*Hygrophoraceae*) (Gams et al., 2004). Members of this genus exhibit a broad global distribution (Voigt et al., 2021), yet detailed information regarding their morphology, ecology, and biogeography remains limited.

Spinellus is characterized by unbranched sporangiophores, spinose, apophysate, and multi-spored zygospores (Zycha et al., 1969; Overton, 1997; Zhao et al., 2023b).

According to Species Fungorum (2025), five species are currently recognized within the genus. Molecular data for *S. fusiger*, including ITS, LSU, *btub*, and *tef* sequences, are available in GenBank (2025). Taxonomically, *Spinellus* is placed within *Phycomycetaceae*, in *Mucorales* (Hyde et al., 2024a).



Figure 5.148 *Spinellus* sp.

Figure 5.148, a. Host. b–d. Sporangiophores on the host. e. Sporangiospores. Scale bars: b = 750 μm, c = 250 μm, d = 200 μm, e = 20 μm.

Syzygitaceae H. Zhao, Y.C. Dai, B.K. Cui, F. Wu, Yuan Yuan & X.Y. Liu

Syzygites Ehrenb., Sylv. mycol. berol. (Berlin): 25 (1818)

Figure 5.149

Index Fungorum number: IF 20561

Syzygites was established by Ehrenberg (1818), with *S. megalocarpus* as the type species. *Syzygites* remains monotypic (Species Fungorum, 2025). *Syzygites megalocarpus* is a homothallic species, distinguished by its erect, dichotomously branched sporangiophores, which bear columellate, multispored globose to irregularly globose sporangia at the apices. The sporangiospores are hyaline to pale brown, broad, varying from globose to irregularly globose or ovoid, and have a verrucose surface (Fries, 1832; Hesseltine, 1957; Benny & O'Donnell, 1978; O'Donnell, 1979; Kovacs & Sundberg, 1999).

Syzygites megalocarpus is recognized as a parasite on a wide range of basidiomycetes and occasionally on ascomycetes (Kovacs & Sundberg, 1999). It's myco-hosts include *Agaricus* spp. (*Agaricaceae*), *Boletus* spp. (*Boletaceae*), *Boletinellus merulioides* (*Boletinellaceae*), *Cortinarius* sp., (*Cortinariaceae*), *Calvatia cyathiformis* (*Lycoperdaceae*), *Ganoderma lucidum* (*Polyporaceae*), *Lactarius piperatus* (*Russulaceae*), *Lentinus edodes* (*Polyporaceae*), *Lycoperdon pyriforme* (*Lycoperdaceae*), *Morchella esculenta* (*Morchellaceae*), *Omphalotus olearius* (*Omphalotaceae*), *Pluteus cervinus* (*Pluteaceae*), *Psathyrella* sp. (*Psathyrellaceae*), *Russula* sp. (*Russulaceae*), *Suillus americanus* (*Suillaceae*), *Tricholoma* spp. (*Tricholomataceae*) and *Tylopilus* sp. (*Boletaceae*) (Kovacs & Sundberg, 1999). Additionally, *S. megalocarpus* is a pathogen of *Agaricus bisporus* (button mushroom) (Beyer et al., 2013; De Soto, 2019). This species has been reported in Korea, Poland, and the USA (Ka et al., 1999; Kovacs & Sundberg, 1999; Mulenko et al., 2008).

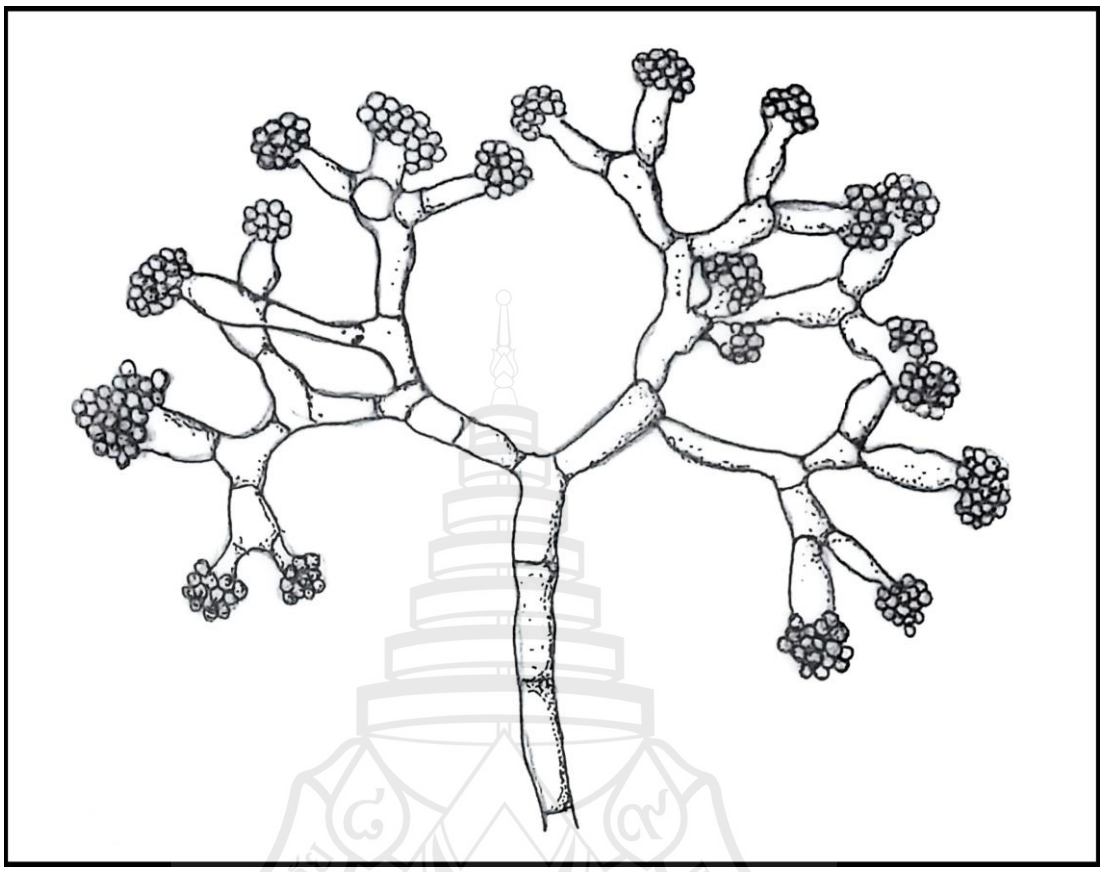


Figure 5.149 *Syzygites megalocarpus*

Figure 5.149, Dichotomously branched shorangiophore after spore release. (Adapted from Zygomycetes.org. (n.d.). Syzygites. Retrieved on 29th September 2025, from https://zygomycetes.org/index.php?id=66).

Mucoromycota* genus *incertae sedis

Nothadelphia Degawa & W. Gams, Stud. Mycol. 50(2): 569 (2004)

Figure 5.150

Index Fungorum number: IF 28862

Nothadelphia was established by Degawa and Gams (2004), with *N. mortierellicola* as the type species. This species was described as a haustorial biotroph on *Mortierella hypsicladia* (*Mortierellaceae*) and was also found on bat dung in Japan (Degawa & Gams, 2004).

Nothadelphia is characterized by fasciculate, erect, unbranched sporangiophores that arise from basal vesicles. The sporangia are hyaline and multispored, initially fusiform but becoming spherical at maturity. The sporangial

wall is deliquescent and lacks a columella, leaving behind a minute collarette following dehiscence. Sporangiospores are hyaline, ranging from cylindrical to irregular in shape, with some appearing swollen and nearly globose, oily droplets are often visible prior to haustorium formation. Chlamydospores are hyaline to slightly yellow, thick-walled, papillate, and intercalary, typically bearing a short, free distal hyphal segment (adapted from Degawa & Gams, 2004).

As of Species Fungorum (2025), *Nothadelphia* remains monotypic. Molecular data for *N. mortierellicola* are not available in GenBank (2025). Taxonomically, *Nothadelphia* is currently placed within *Mucoromycota* genera *incertae sedis* (Hyde et al., 2024a).

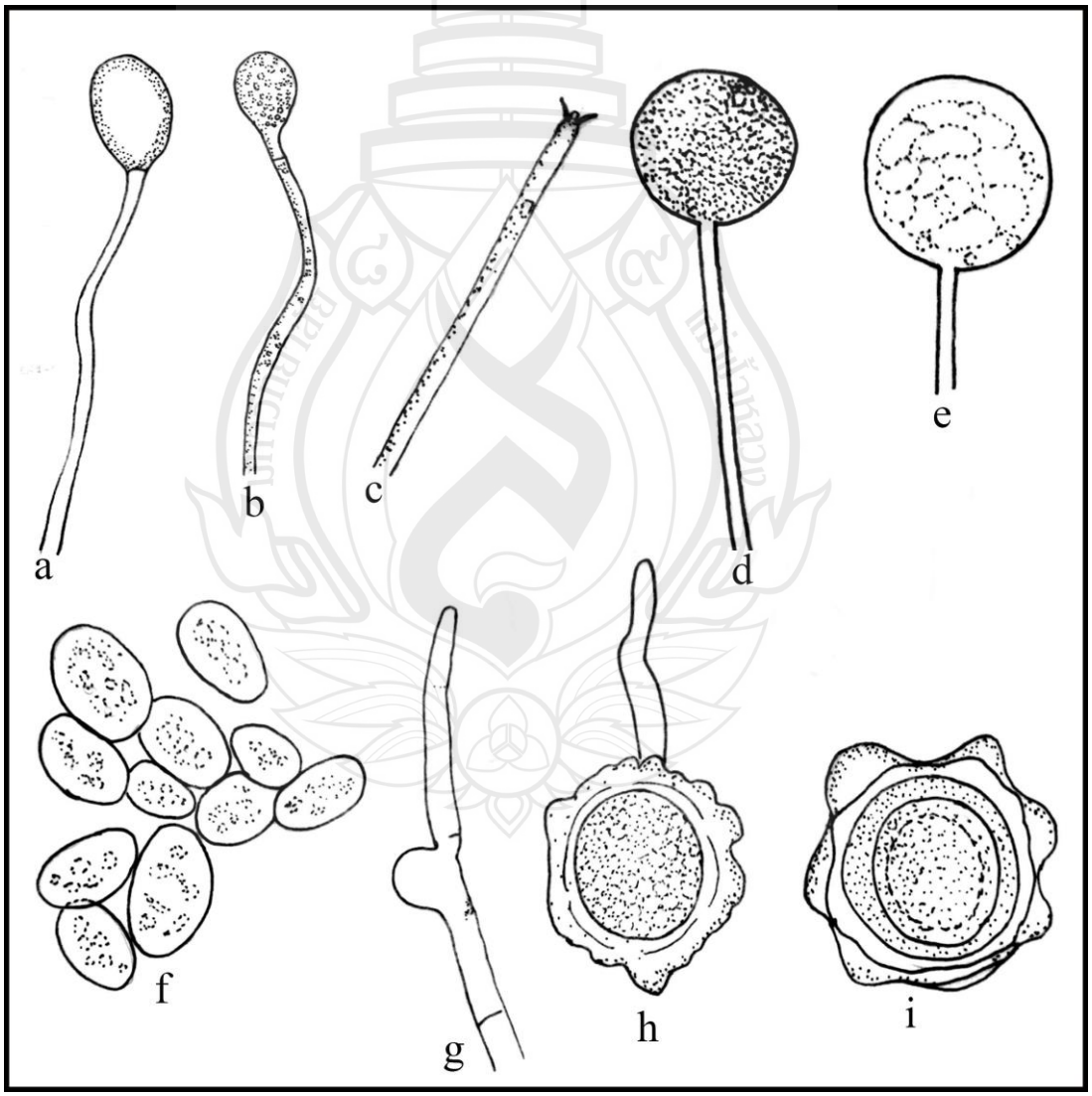


Figure 5.150 *Nothadelphia mortierellicola*

Figure 5.150, a, b. Young vesicles, with vegetative hypha. c. Apex of a sporangiophore. d. Sporangium. e. Mature sporangium containing sporangiospores. f. Sporangiospores. g. Young stage of chlamydospore. h, i. Mature chlamydospores (i, stained by phloxine in KOH). (Adapted from Degawa & Gams, 2004).

5.5 Discussion

The establishment of a digital database for fungicolous fungi, together with the compilation of a considerable number of generic notes and illustrations genera that includes fungicolous fungi, represents a significant step toward improving access to and dissemination of knowledge on this ecologically important group of fungi. Fungicolous fungi have historically been understudied compared to plant-associated fungi, and much of the available information is fragmented across publications, theses, and herbarium records. By consolidating these data into a single platform, this study provides a comprehensive resource that supports taxonomy, ecology, biodiversity studies, and applied research.

A key strength of this work lies in its integration of both morphological and molecular information for 150 genera which includes fungicolous fungi. For each genus, diagnostic features, taxonomic placement, host associations, and geographical distribution were summarized, while photographic plates or redrawn illustrations provide visual references to facilitate identification. The inclusion of updated nomenclature and species counts based on reliable sources ensures that the information is taxonomically reliable and aligned with current frameworks (Hyde et al., 2024a; Index Fungorum, 2025; Species Fungorum, 2025). This makes the database valuable not only for taxonomists but also for ecologists, pathologists, and mycologists involved in applied fields such as mushroom cultivation.

The preference of modern researchers is increasingly to refer to databases rather than printed books or dispersed publications to gather scattered knowledge. Databases are technically easier to handle, searchable, and significantly less time-consuming to use. Therefore, compiling morphological and ecological data into a single digital tool provides a flexible, efficient, and time-saving method for

researchers, enabling quicker access to comprehensive information compared to conventional resources. This highlights the importance of digitization in advancing mycological research and promoting wider accessibility of biodiversity data.

Digitization also addresses one of the persistent challenges in mycology: the limited accessibility of fungal knowledge. Many descriptions of fungicolous fungi are locked in older literature, often not readily accessible online, or are published in languages that restrict their global use. By creating a digital and illustrated resource, this study enhances the visibility of fungicolous fungi and provides a foundation for building open-access, user-friendly platforms that can be updated as new taxa and records are discovered. Such efforts are in line with broader global initiatives promoting the digitization of biodiversity data to support conservation and sustainable utilization.

This database can serve as a foundation for future expansions. With continuous updating, it could evolve into a global reference hub for fungicolous fungi, integrating species descriptions, host-fungus interaction data, ecological metadata, and sequence-based phylogenies. Linking the database to platforms such as GBIF, Index Fungorum, or MycoBank would enhance its reach and interoperability with existing biodiversity repositories. Moreover, the resource could have direct applied significance, particularly in the mushroom industry, by providing rapid access to knowledge on competitor molds and potential pathogens.

CHAPTER 6

CONCLUSION

6.1 Overall Conclusion

This study was aimed on three major components: (1) the identification of fungicolous fungi on wild mushrooms from northern Thailand and southwest China, (2) the identification of fungi associated with mushroom cultivation in northern Thailand and a comprehensive review of fungal diseases and competitor molds affecting global mushroom production, and (3) the digitalization and compilation of existing data on fungicolous fungi. Collectively, these studies contribute to a more comprehensive understanding of fungal diversity, ecology, and taxonomy, while also bridging the gap between traditional taxonomic research and modern digital documentation.

6.1.1 The Identification of Fungicolous Fungi on Wild Mushrooms from Northern Thailand and Southwest China

This study successfully identified a total of 32 fungicolous taxa associated with wild mushrooms in northern Thailand and southwest China, representing 11 genera across three fungal classes: *Sordariomycetes* (8 genera), *Dothideomycetes* (2 genera), and *Mucoromycetes* (1 genus). The *Sordariomycetes* genera included *Clonostachys*, *Diaporthe*, *Fusarium*, *Hypomyces*, *Hypoxylon*, *Mariannaea*, *Xenoacremonium*, and *Zarea*; *Dothideomycetes* comprised *Lasiodiplodia* and *Neoroussoella*; and *Mucoromycetes* was represented by *Mucor*. Among these, four taxa were newly described species (*Hypomyces chiangraiensis*, *Mucor yunnanensis*, *Zarea boleticola*, and *Z. thailandica*), five were new combinations (*Hypomyces chalcipori*, *H. laevigatus*, *H. novovarius*, *H. paravirescens*, and *H. protrusus*), and 23 were new records (*Clonostachys rogersoniana*, *Diaporthe talong*, *Fusarium fabacearum*, *F. grosmichelii*, *F. mangiferae*, *F. pernambucanum*, *F. proliferatum*, *F. teslae*, *F. verticillioides*, *Hypomyces boletiphagus*, *H. chlorinus*, *H. cornea*, *H. protrusus*, *H. mycophilus*, *H. pseudocorticiicola*, *H. semicircularis*, *Hypoxylon*

fendleri, *Lasiodiplodia thailandica*, *Mucor circinelloides*, *M. hiemalis*, *M. nederlandicus*, *Neoroussoella entadae*, and *Xenoacremonium allantoideum*).

Species delimitation was based on an integrative taxonomic approach, combining morphological characteristics with multi-locus phylogenetic analyses. Most specimens originated from northern Thailand, with a few from southwest China. While common fungicolous genera such as *Clonostachys*, *Fusarium*, *Hypomyces*, *Mucor*, and *Zarea* were represented, several less commonly reported genera *viz. Diaporthe*, *Hypoxylon*, *Lasiodiplodia*, *Mariannaea*, *Neoroussoella*, and *Xenoacremonium* were also identified. These findings indicate potential ecological adaptability or host-shift events among these taxa. Many of these genera, typically known as soil, plant or wood-associated fungi, may opportunistically colonize mushroom hosts under suitable environmental conditions. Given the scarcity of research on fungicolous taxa, such associations remain largely underexplored, and continued investigations may help clarify their ecological roles and evolutionary pathways.

Interestingly, several fungi identified in this study as fungicolous on wild mushrooms have previously been documented as mushroom pathogens of cultivated mushrooms. For instance, *Hypomyces protrusus*, *H. cornea*, *H. mycophilus*, and *H. semicircularis* are known agents of cobweb disease, while *H. pseudocorticiicola* is known for cottony leak disease. This suggests that some fungicolous taxa occurring on living wild mushrooms may possess pathogenic potential toward their hosts.

Moreover, based on the fungal collections obtained from wild mushrooms during this study, together with the literature review on fungi associated with mushroom cultivation, it was clear that the species diversity of fungicolous fungi associated with wild mushrooms is higher than that found in cultivated systems. Mushrooms grown under controlled environmental conditions support a comparatively limited range of fungal taxa, whereas natural ecosystems with their heterogeneous substrates and fluctuating environmental conditions, provide a wider array of niches that facilitate greater fungal diversity.

6.1.2 Fungi Associated with Mushroom Cultivation in Northern Thailand and Global Review of Fungal Diseases and Competitor Molds

This study reports *Daldinia eschscholtzii* and *Scedosporium apiospermum* for the first time from oyster mushroom cultivation substrates in northern Thailand. Additionally, *Aspergillus quadrilineatus*, *Fusarium sulawesiense*, and *Mucor irregularis* was recorded from cultivated *Phlebopus spongiosus*, *Hericium coralloides* and *Pleurotus* sp. respectively for the first time in northern Thailand. These findings broaden the known diversity of fungi associated with mushroom cultivation and highlight the potential for unexpected taxa to emerge as opportunistic pathogens. Notably, the discovery that *Daldinia* can be grown under conditions similar to *Pleurotus* cultivation opens possibilities for artificial production of *Daldinia* species, which are rich in bioactive secondary metabolites with industrial relevance. All isolates were identified through an integrative taxonomic framework combining morphology and multi-locus phylogenetic analyses.

Furthermore, this study provides a global review of major fungal diseases and competitor molds impacting mushroom cultivation. Four key diseases *viz.* dry bubble, wet bubble, cobweb, and green mold, along with slippery scar and yellow rot, were reviewed in detail, including their causal agents, morphological features, disease cycles, epidemiology, and management practices. Phylogenetic analyses based on published DNA sequences were used to illustrate the current taxonomic placement of these pathogens. Nine additional competitor molds were also documented.

Fungal pathogens and competitor molds remain a major constraint to mushroom production, reducing both yield and quality. Integrating modern biotechnological approaches such as transcriptomics, metabolomics, and automated diagnostic tools may enhance early detection and sustainable disease management. The mushroom industry must therefore adopt a balanced strategy that ensures productivity while minimizing losses due to fungal contamination.

6.1.3 Digitization and Compilation of Data on Fungicolous Fungi

To consolidate the scattered data on fungicolous fungi, a webpage “https://www.fungicolousfungi.org/” was established as part of this study. This platform compiles and standardizes morphological, molecular, and ecological information from published sources and repositories, improving accessibility, data

accuracy, and taxonomic consistency. The establishment of the fungicolous fungi database represents a crucial step toward integrating traditional taxonomy with digital biodiversity informatics, supporting taxonomists, ecologists, and database curators in advancing global fungal systematics.

Moreover, this study consolidated knowledge on 150 genera that include fungicolous fungi across *Ascomycota* (108 genera), Basidiomycota (37 genera), and *Mucoromycota* (05 genera) and provided comprehensive generic notes and morphological illustrations. These notes encompass morphological traits, ecological roles, and known host associations of each genus. Importantly, a considerable number of these genera remain *incertae sedis* within higher taxonomic classifications, indicating unresolved phylogenetic positions. Therefore, future research focusing on fungicolous taxa is essential to clarify their evolutionary relationships and refine their systematic placement.

6.2 Research Advantages

This study provides multiple scientific and practical advantages that contribute significantly to mycology, fungal ecology, and biodiversity. This work exemplifies how traditional morphology-based taxonomy can be effectively integrated with molecular and digital tools, promoting reproducibility, accessibility, and long-term preservation of fungal knowledge.

This study expands the known diversity of fungicolous fungi in tropical Asia, particularly from northern Thailand and southwest China in where previous records on fungicolous fungi were lacking. The discovery of new species, new combinations, and new records enhances current understanding of fungal biodiversity and biogeography. By applying an integrative taxonomic framework, combining morphological characters with multi-locus phylogenetic data, the study ensures accurate species identification and strengthens the reliability of taxonomic conclusions. This approach also helps clarify species boundaries and evolutionary relationships among fungicolous taxa.

The identification of *Daldinia eschscholtzii*, *Scedosporium apiospermum*, *Aspergillus quadrilineatus*, and *Mucor irregularis* associated with mushroom cultivation provides novel insights into fungal ecology within artificial cultivation systems. These findings are valuable for both taxonomy and applied mycology, with implications for disease management and the potential utilization of bioactive *Daldinia* species.

The comprehensive review of fungal diseases and competitor molds affecting global mushroom production provides a valuable resource for both mycologists and mushroom growers. It facilitates the early identification of major fungal threats and supports the implementation of effective management and control strategies, thereby minimizing production losses and improving overall cultivation efficiency.

The establishment of the fungicolous fungi webpage (https://www.fungicolousfungi.org/) represents a significant advancement in mycology by integrating previously scattered information into a centralized and accessible digital platform. This resource enhances the accuracy of fungal identification, promotes data sharing, and supports future taxonomic and ecological studies. It serves as an invaluable tool for researchers, students, and other stakeholders interested in fungicolous fungi, fostering continued progress in this underexplored area of mycology.

The compilation of 150 genera, which include fungicolous fungi, with detailed notes and morphological illustrations, serves as a valuable reference for researchers. The inclusion of numerous *incertae sedis* genera highlights gaps in current taxonomy and provides a roadmap for future systematic studies.

6.3 Future Directions

Although this study has advanced the understanding of fungicolous fungi and fungal diseases associated with mushrooms, numerous avenues remain for future research.

Taxonomic clarification is another key priority. Many fungicolous genera within both *Ascomycota* and *Basidiomycota* remain classified as *incertae sedis*.

Therefore, comprehensive morphological and molecular investigations are needed to resolve their phylogenetic placements and refine their taxonomic frameworks.

Future research should aim to investigate host affiliations of fungicolous fungi, including patterns of host specificity and host switching, to better understand their ecological roles and evolutionary dynamics. A monographic study on fungicolous *Hypomyces* species is also recommended, focusing on species diversity, cryptic lineages, host associations, and the linkage between sexual and asexual morphs.

Moreover, pathogenicity studies should be expanded to examine the interactions between fungicolous fungi and their mushroom hosts, both in wild and cultivated systems. Integrating genomic, transcriptomic, and metagenomic approaches will help reveal molecular mechanisms of pathogenicity and host defense, as well as seasonal dynamics and ecological functions of fungicolous fungi.

As new fungicolous taxa are continually being discovered, it is essential to update the fungicolous fungi webpage with an outline and notes for each genus. This will ensure that the database remains a comprehensive and up-to-date resource reflecting the expanding knowledge in this field.

With the increasing diversity of mushroom species being cultivated globally, there is a possibility that new fungal diseases will continue to emerge. Thus, developing resistant mushroom strains through advanced breeding programs informed by genomic and transcriptomic data should be a research priority. Additionally, refinement of automated detection systems is essential to enhance accessibility and cost-effectiveness, especially for small-scale growers in low-resource settings.

Exploring biocontrol strategies and natural antifungal compounds offers a promising pathway toward sustainable disease management. Further phylogenetic and evolutionary studies of fungal pathogens will also shed light on their adaptation mechanisms and may reveal novel targets for more effective control measures.

Collectively, these future directions will strengthen the integration of taxonomy, ecology, and molecular biology in the study of fungicolous fungi, fostering improved understanding and management of fungal interactions in both natural and cultivated environments.

6.4 Publications

Worked on nine papers as the first author during this study, and contributed for 17 other papers as a co-author.

6.4.1 First Author Publications

Gajanayake, A. J., Samarakoon, M. C., Bundhun, D., Jayawardena, R. S., Luangharn, T., & Hyde, K. D. (2021). A challenge for mushroom growers: *Daldinia eschscholtzii* associated with oyster mushroom growing substrate. *Chiang Mai Journal of Science*, *48*(3), 774–786.

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6.4.2 Co-author Publications

Jayawardena, R. S., Hyde, K. D., Aumentado, H. D., Abeywickarama, P. D., Avasthi, S., Dissanayake, A. J., . . . Wang, Y. (2025). One stop shop V: taxonomic update with molecular phylogeny for important phytopathogenic genera: 101–125 (2024). *Fungal Diversity, 130*: 263–429.

Jayawardena, R. S., Hyde, K. D., Wang, S., Sun, Y. R., Suwannarach, N., Sysouphanthong, P., . . . Wang, Y. (2022). Fungal diversity notes 1512–1610: taxonomic and phylogenetic contributions on genera and species of fungal taxa. *Fungal Diversity*, *117*(1), 1–272.

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Fungalpedia notes- 2018. Hongsanan et al., (In prep)

Cream Notes. Wijesinghe et al., (In prep)

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APPENDIX A

CHEMICAL REAGENTS AND MEDIA

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

Potato starch (from infusion) 4 g

Dextrose 20 g

Agar 15 g

Suspend 40 g of Potato dextrose agar in distilled water and mix thoroughly. Heat with frequent agitation and boil for 1 minute to completely dissolve the powder and bring volume up to 1000 ml. Autoclave at 121^{o}C for 15 minutes

APPENDIX B

PUBLICATIONS

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ARTICLE

Fungal threats to global mushroom cultivation: diseases, competitor molds, and management strategies – a review

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Abstract

Mushroom cultivation, with its significant potential, not only enhances food and nutritional security but also contributes to environmental sustainability by recycling agricultural waste materials. However, this promising industry is under threat from fungal contaminations, which can manifest as destructive diseases or rapidly spreading competitor molds. These contaminants, which emerge at various stages of the cultivation process, can cause growth retardation, deformation, or decomposition of mushrooms, leading to substantial losses in both the quality and quantity of mushroom production. The economic impact of these losses underscores the importance of a comprehensive understanding of fungal diseases and competitor molds, which is crucial for developing effective management strategies to mitigate these challenges. Herein, four prevalent fungal diseases (dry bubble, wet bubble, cobweb, and green mold), along with slippery scar and yellow rot, are reviewed. The taxonomic classification of the major fungal pathogens on mushrooms is summarized at the family/genus levels, using phylogenetic trees reconstructed from previously published DNA sequences available in GenBank to illustrate their current phylogenetic placement. The morphological features of the pathogens are also illustrated. Additionally, nine competitor molds associated with mushroom cultivation are reviewed. Furthermore, for each disease and competitor mold, details on their causative agents, signs and symptoms, disease cycles, epidemiology, and management strategies are provided based on the available literature.

Keywords – Fungal pathogens – morphology – mushroom disease management – mycoparasites – phylogeny – signs and symptoms

INTRODUCTION

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Additions to fungicolous *Hypomyces* from northern Thailand: A novel species, combinations and new records

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ABSTRACT

Hypomyces species are recognized for their fungicolous lifestyle. These species are globally distributed across various habitats from temperate to tropical and subtropical regions. This study introduces a novel fungicolous *Hypomyces* species, *Hypomyces chiangraiensis* associated with *Mycena* sp. in northern Thailand. Three new combinations within the genus, *Hypomyces novovarius*, *Hypomyces paravirescens* and *Hypomyces protrusus* are proposed. Additionally, new geographical records for *Hypomyces cornea*, *Hypomyces novovarius* and *Hypomyces semicircularis* are documented. A new host record for *Hypomyces cornea* is documented. All species identifications relied on morphological features coupled with phylogenetic analyses of the combined internal transcribed spacer region (ITS1-5.8S-ITS2), partial 28S large subunit (nc LSU rDNA), partial translation elongation factor (*TEF1α*), and partial second largest subunit of the DNA-directed RNA polymerase II (*RPB2*) sequence matrix. Comprehensive descriptions, illustrations, and a phylogenetic tree to show the placements of taxa are provided. The morphological characters of the novel species are compared with sister taxa.

1. Introduction

Fungicolous fungi are specialized organisms that grow on or are associated with other fungi (Gams et al., 2004; Sun et al., 2019a, 2019b; Hyde et al., 2023). Fungi within this category consistently form associations across various lineages throughout the fungal kingdom, acting as mycoparasites, saprotrophs or neutrals (Gams et al., 2004; Põldmaa, 2011; Lin et al., 2016; Sun et al., 2019a; Hyde et al., 2023). They play a crucial role in ecological balance by influencing the population dynamics of fungal communities in both aquatic and terrestrial ecosystems (Marano et al., 2011; Parratt and Laine, 2018).

In earlier classification, *Hypomyces* (Fr.) Tul. & C. Tul. was considered a subgenus within *Hypocrea* Fr. by Fries (1825). Later it was promoted to the status of a distinct genus by Tulasne and Tulasne (1860). The type species for *Hypomyces* is *Hypomyces lactifluorum* (Schwein.) Tul. and C. Tul., originally collected in the United States (Index Fungorum, 2025).

Arnold (1971) differentiated *Hypomyces* from its closely related genera *Arachnocrea* Z. Moravec, *Apiocrea* Syd. & P. Syd., and *Peckiella* (Sacc.) Sacc. by conducting a comprehensive taxonomic study. Subsequently, various studies on *Hypomyces* followed whereas, a connection between *Hypomyces* and *Cladobotryum* Nees was revealed based on morphology (Rogerson and Samuels, 1985, 1989, 1993, 1994; Põldmaa, 1996, 2003, 2011; Põldmaa et al., 1997, 2000). This link was further

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Fungicolous *Mucor* on mushrooms: One novel species and six host records from southwest China and northern Thailand

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ABSTRACT

Mucor species are a group of common soil-borne fungi, known to cause infections on humans and animals, interfere in food production, and act as useful agents in biotechnological applications. This study reports one new *Mucor* species, *M. yunnanensis*, which was found to be fungicolous on an *Armillaria* sp. from southwest China. Further, *M. circinelloides* on *Phlebopus* sp., *M. hiemalis* on *Ramaria* sp. and *Boletus* sp., *M. irregularis* on *Pleurotus* sp., *M. nederlandicus* on *Russula* sp., and *M. yunnanensis* on *Boletus* sp. are reported as new host records. *Mucor yunnanensis* and *M. hiemalis* have been collected from Yunnan Province in China, whereas *M. circinelloides, M. irregularis*, and *M. nederlandicus* have been collected from Chiang Mai and Chiang Rai Provinces in Thailand. All the *Mucor* taxa reported herein were identified based on both morphology and phylogenetic analyses of a combined nuc rDNA internal transcribed spacer region ITS1-5.8S-ITS2 (ITS) and partial nuc 28S rDNA (28S) sequence matrix. Comprehensive descriptions, illustrations, and a phylogenetic tree are provided for all the taxa reported in the study to show the placements of taxa, and the new taxon is compared with its sister taxa.

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Fungicolous fungi; molecular phylogeny; Mucorales; Mucoromycota; taxonomy; 1 new taxon

INTRODUCTION

Fungicolous fungi are an ecologically and economically important, richly diverse group (Maurice et al. 2021; Sun et al. 2019). This fungal group is widely dispersed throughout the fungal kingdom's different lineages in both aquatic and terrestrial habitats (Gams et al. 2004; Põldmaa 2011; Sun et al. 2019). To date, more than 1500 taxa have been identified and more are to be revealed (Sun et al. 2019). Most of the previously identified fungicolous taxa belong to Ascomycota, whereas others belong to Basidiomycota, Blastocladiomycota, Chytridiomycota, Entomophthoromycota, Glomeromycota, Kickxellomycota, Mortierellomycota, Mucoromycota, Rozellomycota, and Zoopagomycota (Gams et al. 2004; Sun et al. 2019).

Mucor, the largest genus in Mucorales belonging to Mucoromycotina, was originally described by Fresenius (1850) and is typified by *M. mucedo* Fresen. (Nguyen et al. 2020; Walther et al. 2019; Wijayawardene et al. 2022). Most of the *Mucor* species are heterothallic, but some homothallic species also exist and they produce nonappendaged zygospores or azygospores (Benny et al. 2016; Lima et al. 2020). *Mucor* species produce rapidly growing colonies that could be characterized by the presence of simple or branched sporangiophores, globose sporangia with the incrusted, deliquescent sporangial wall, and zygospores on opposed or tong-like suspensors, and some species may form sporangiola, apophyses, and rhizoids (Benny et al. 2016; Hurdeal et al. 2021; Lima et al. 2020; Nguyen et al. 2020; Walther et al. 2019).

It has been revealed that *Mucor* species are important for the production of enzymes (Huang et al. 2014; Lee et al. 2011), production of biofuel (Carvalho et al. 2018), fermentation of some food products (Morin-Sardin et al. 2017), bioremediation (Jabasingh and Pavithra 2010), and biotransformation usable for drug or energy production (Morin-Sardin et al. 2017; Oliveira Silva et al. 2013; Silva et al. 2015).

Mucor species are ubiquitous in natural environments (Hurdeal et al. 2021; Morin-Sardin et al. 2017).

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Revealing new records of hypocrealean fungicolous fungi from northern Thailand

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Abstract

Hypocreales comprise a diverse group of fungi that exhibit a wide range of lifestyles in both aquatic and terrestrial environments. A significant number of the identified fungicolous taxa belong to *Hypocreales*. Samples were collected from Chiang Rai and Chiang Mai Provinces during an investigation on fungicolous fungi in northern Thailand. Based on morphological characteristics and multi-gene phylogenetic analyses of ITS-LSU-*tef1α*-*rpb2* and ITS-LSU-*tub2*-*tef1α*, two isolates were identified as *Hypomyces sichuanensis* (*Hypocreaceae*) and *Mariannaea humicola* (*Nectriaceae*) respectively. This study marks the first documentation of *Hypomyces sichuanensis* and *Mariannaea humicola* as fungicolous species from Thailand. Additionally, the study reveals a novel host record for *M. humicola* on *Marasmius* sp.

Key words: Geographical records, Host record, *Hypomyces*, *Mariannaea*, Phylogeny, Taxonomy

Introduction

Fungicolous fungi are a distinct ecological group of organisms that are consistently found in association with various species across different lineages within the fungal kingdom (Gams *et al.* 2004, Põldmaa 2011, Sun *et al.* 2019, Maurice *et al.* 2021). These fungi can be found in aquatic and terrestrial habitats (Gams *et al.* 2004, Põldmaa 2011, Sun *et al.* 2019, Bao *et al.* 2023). There is a high taxonomic diversity among fungicolous fungi; most of these organisms belong to the *Ascomycota* (Sun *et al.* 2019, Maurice *et al.* 2021). Within the *Ascomycota*, *Sordariomycetes* exhibit a significant diversity, specifically within *Hypocreales* (Sun *et al.* 2019). Fungicolous taxa are predominantly found in *Calcarisporiaceae* and *Hypocreaceae*, while some species from *Nectriaceae* and *Bionectriaceae* within *Hypocreales* also exhibit fungicolous lifestyles (Sun *et al.* 2019). Within the *Hypocreaceae*, there are several fungicolous taxa (Põldmaa 2000). *Hypomyces* and its allied asexual genera *Cladobotryum*, *Mycogone*, and *Sepedonium* are common fungicolous taxa recorded from many countries (Põldmaa *et al.* 2000, Sun *et al.* 2019).

Hypomyces belong to *Hypocreales, Hypocreaceae*, *Sordariomycetes* (Wijayawardene *et al.* 2022a). The genus was initially classified as a subgenus of *Hypocrea* Fr. by Fries (1825) and was later elevated to the genus level by Tulasne & Tulasne (1860). A total of 118 *Hypomyces* names are listed in the Species Fungorum (2023). The type species of *Hypomyces* is *H. lactifluorum* (Schwein.) Tul. & C. Tul., originally collected from the USA (Index Fungorum 2023). *Hypomyces* species specifically parasitize the fruiting bodies of mushrooms, particularly those belonging to the *Agaricomycetes* (Tamm & Põldmaa 2013). *Hypomyces* species that parasitize boletes or agarics exhibit host specificity (Rogerson & Samuels 1989, Tamm & Põldmaa 2013). *Hypomyces* species have been reported to occur occasionally in association with various plant substrates such as bark, wood, and leaves, as well as other substrates including moss, humus, rock, insect galls, and lichens (Rogerson & Samuels 1993, 1994, Lechat *et al.* 2017, Farr *et al.* 2021, Karimi *et al.* 2022, Perera *et al.* 2023). Members of *Hypomyces* have a wide distribution and can be found in temperate, tropical, and subtropical regions (Põldmaa 1996, 2003, 2011, Põldmaa *et al.* 2000). They are often encountered as pathogens or saprobes, playing a role in decomposing organic matter and cause disease (Rogerson & Samuels 1993, 1994, Rossman *et al.* 1999, Põldmaa 1996, 2003, 2011).

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Research Article

An Online Database on Fungicolous Fungi: https://www.fungicolousfungi.org

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ABSTRACT

Fungicolous fungi represent an ecologically and economically significant group of organisms, with potential applications in biological control and various industrial processes. Accurate identification and comprehensive investigation of the taxonomic diversity of fungicolous taxa are essential for understanding their ecological roles and harnessing their potential applications. Compiling the dispersed published information on fungicolous fungi provides a robust foundation for understanding their taxonomic diversity, improving identification accuracy, and ensuring proper documentation. This in turn, will aid in assessing their ecological significance, identifying research gaps, and outlining future directions for the study of this group of organisms. The website (https://www.fungicolousfungi.org/) serves as a user-friendly platform, continuously updated to provide information on aspects such as morphology, phylogeny, ecology, hosts/substrates, distribution, and industrial relevance of fungicolous fungi.

Keywords: hyperparasites, mycoparasites, mycophilic fungi, taxonomy, webpage

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1. INTRODUCTION

Fungicolous fungi are a widespread group of organisms that belong to many ecological categories found in both, terrestrial and aquatic habitats [1–3]. They are the fungi consistently having associations between different lineages across the fungal kingdom as saprotrophs, mycoparasites or neutrals [1–5]. The interaction between a fungicolous fungus and its host can be biotrophic, necrotrophic or hemibiotrophic [1,6]. Mycoparasitic taxa obtain nutrients from their hosts through physical interactions, by forming specialized structures in hyphae or producing chemical compounds such as enzymes or antibiotics, which are able to attack the host cells [1,2,6]. The substrates colonized by fungicolous fungi can be fungal sporocarps, biotrophic plant parasites, mycelia, sclerotia, spores in soil, aquatic fungi or fungus-like microorganisms [1]. The highest diversity of fungicolous fungi is observed in ascomycetes, with the majority found in *Hypocreales* and *Helotiales* [4,7,8].

The first studies on fungicolous fungi were conducted around two centuries ago [9–11]. The first ascomycete discovered to be fungicolous

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Contributed Paper

A Challenge for Mushroom Growers: *Daldinia eschscholtzii* Associated with Oyster Mushroom Growing Substrate

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ABSTRACT

Mushroom growing substrates are important for the quality, quantity and nutritional value of mushrooms produced. However, the fungal contamination in substrates is known as a major problem in mushroom cultivation. Therefore, accurate identification of contaminants may be important in order to improve mushroom cultivation to increase mushroom yield. Oyster mushroom grow bags in a mushroom farm at northern Thailand were contaminated with a *Daldinia* species. Contaminated oyster mushroom grow bags were brought to mycology laboratory of Center of Excellence in Fungal Research. Multi-locus phylogenies from combined LSU, ITS, RPB2 and TUB2 sequence data indicated that the contaminant *Daldinia* species clusters with *Daldinia eschscholtzii*. In this paper, *D. eschscholtzii* is described with a full description, color images and a phylogenetic tree of *Hypoxylaceae* to show the placement of the taxon. This is the first report of *D. eschscholtzii* associated with oyster mushroom growing substrate.

Keywords: grow bag contamination, host, mushroom growing, *Sordariomycetes*, taxonomy

1. INTRODUCTION

Mushrooms are fleshy, spore bearing fruiting bodies which can be epigeous or hypogeous in formation [1]. Due to nutritional and therapeutic values, mushrooms have been used for human consumption since ancient times [2,3]. Mushroom industry has expanded globally and especially in Asia where commercial cultivation has greatly increased [3,4].

Oyster (*Pleurotus* spp.) mushrooms are one of the main commercialized edible mushrooms in the global market [4] especially in Asia. They are prolific sources of biologically active compounds [5], important functional foods or nutraceuticals [2] and are used in cosmetics [6]. They have anti-cancer, anti-diabetic, anti-obesity, anti-oxidant and hepatoprotective activities [2,7,8]. China, India, Japan, South Korea, Taiwan, Thailand and Vietnam are the main consumers and producers of oyster mushrooms in Asia [4,9]. Mushroom growers usually choose oyster mushroom cultivation due to the easiness of cultivation and increased profitability, as they convert a higher percentage



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Pathogenic *Diaporthe* from Italy and the first report of *D. foeniculina* associated with *Chenopodium* sp.

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Abstract

Diaporthe is an important genus composed of pathogenic, saprobic and endophytic species. A *Diaporthe* species was collected from a dead aerial branch of *Chenopodium* sp. from Italy. Multi-locus phylogeny of ITS, CAL, HIS, TEF1–α and TUB2 sequence data showed that our strain clusters with *Diaporthe foeniculina* with good statistical support. A comprehensive description, photographs of micromorphological characteristics and phylogenetic trees to show the placement of the taxon are provided. This is the first report of *D. foeniculina* on *Chenopodium* sp. from Italy. Previously, *Diaporthe foeniculina* has been recorded from Italy as a pathogen on different plant species. Based on the previous findings, a list of known pathogenic *Diaporthe* species reported from Italy is provided.

Keywords – Coelomycetes – Diaportheceae – New record – Sordariomycetes – Taxonomy

Introduction

Chenopodium species are morphologically variable and comprise herbaceous and bushy annual or perennial plants growing in worldwide arid and semiarid zones (Bonifacio 2003). Most of the species of this genus are able to survive in adverse climatic and edaphic conditions (Bonifacio 2003, Fuentes-Bazan et al. 2012). This genus has important cultivable species which play diverse roles like crops for food (*C. album*, *C. giganteum*, *C. murale*, *C. quinoa*), animal feed production (*C. album*, *C. murale*, *C. opulifolium*) and medicinal uses (*C. album*, *C. amaranticolor*, *C. botrys*) (Bonifacio 2003, Fuentes-Bazan et al. 2012). *Chenopodium* sp. also constitutes major classes of phyto-constituents such as phenolics, ecdysteroids, flavonoids, triterpenoids and saponins (Bonifacio 2003, Kokanova-Nedialkova et al. 2009, de la Cruz Torres et al. 2013).

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Article

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Aspergillus quadrilineatus revealed to be fungicolous on *Phlebopus spongiosus* from northern Thailand

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Abstract

Fungicolous fungi are able to grow on both cultivable and wild mushrooms as saprotrophs, mycoparasites or symbionts. These taxa are capable of causing deformations or decomposition of mushrooms and can also be potential pathogens on cultivable mushrooms, thereby causing both yield and quality losses. Therefore, accurate identification and investigation of taxonomic diversity of the fungicolous taxa associated with mushrooms would be beneficial for disease management strategies and quarantine purposes in the mushroom industry. During a cultivation trial to grow *Phlebopus spongiosus* on soil, the mushrooms were contaminated with an *Aspergillus* species. Multi-locus phylogeny based on combined ITS, *tub*2, *cam* and *rpb*2 sequence data and morphological characters revealed the fungicolous contaminant to be *A. quadrilineatus*. Herein *A. quadrilineatus* is described with complete descriptions, illustration and a phylogenetic tree of *Aspergillus* section *Nidulantes* to show its placement. This study is the first report of *A. quadrilineatus* as a fungicolous species on *Phlebopus spongiosus*.

Keywords – *Aspergillaceae* – *Eurotiales* – *Eurotiomycetes* – host record – taxonomy

Introduction

Phlebopus spongiosus Pham and Har. Takah., is an ectomycorrhizal mushroom which is edible and native to southern Vietnam (Kumla et al. 2020, Raghoonundon et al. 2021). It produces medium to large, dark yellowish-brown fruiting bodies with a sponge-like tissue more or less similar to *P. portentosus*, but can be distinguished by its dark brown spore print and distinctive hymenial cystidia (Pham et al. 2012). Chuankid et al. (2020) recognized a series of pulvinic acid derivatives from liquid cultivation of *P. spongiosus*, whereas some of them had significant antimicrobial and cytotoxic activities. Kumla et al. (2020) were the first to report *P. spongiosus* from northern Thailand and its capability to produce fruiting bodies without a host plant.

Fungicolous fungi are a diverse group of organisms associated with species of different lineages across the fungal kingdom (Sun et al. 2019a, Maurice et al. 2021). They have a wide range of distribution and principally exist as saprotrophs, mycoparasites, symbionts and even neutrals (Sun et al. 2019a). They can be primary consumers with special and often rapid life cycles, which may result in a decrease of certain nutrients in the food webs (Maurice et al. 2021). Several fungicolous fungi have been reported to cause deformation, decomposition or serious diseases in

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