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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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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. 2019, 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. 2019, 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, b, Yu et al. 2024) (Fig. 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. 2019, Gajanayake et al. 2021a, b, 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 review is to advance the existing comprehension of selected fungal diseases and competitor molds that affect the mushroom industry. This study also provides

insights into the current classification of selected mushroom pathogens. This work elucidates the taxonomic placement of pathogenic species at the generic/ family level with phylogenetic trees reconstructed from previously published DNA sequences available in GenBank. 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.

Fig. 1 – Fungi affecting mushroom cultivation. **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)

FUNGAL DISEASES AND COMPETITOR MOLDS ASSOCIATED WITH MUSHROOM CULTIVATION

Preparation of entries on fungal diseases and competitor molds

The content of each entry was prepared based on a literature survey (publications, theses, websites, checklists published until February 2025). The classification of the pathogens is based on the work of Hyde et al. (2024) and Index Fungorum (2025). Photographic plates illustrating disease symptoms and morphological characteristics of pathogens are included, for which the images were obtained by the authors. When images could not be obtained, they were adapted from previous literature, accompanied by appropriate citations.

Phylogenetic analyses

Sequence data from type, or authentic/reference/voucher strains for each species were obtained from the GenBank (https://ncbi.nlm.nih.gov/genbank/). Single-gene alignments were constructed using MAFFT v. 7.036 (http://mafft.cbrc.jp/ alignment/server/index.html) with default settings (Katoh et al. 2019). Subsequently, each alignment was trimmed using TrimAl with the "gappyout" option (Capella-Gutiérrez et al. 2009). Multigene alignments were obtained by combining the single-gene alignments using BioEdit v. 7.0.5.2 (Hall 1999). The optimal substitution models for the combined datasets were determined using jModelTest2 based on the Akaike information criterion (AIC) (Darriba et al. 2012). Phylogenetic analyses were performed to elucidate the taxonomic positions of pathogenic species within the genus/ family level. Maximum Likelihood (ML) analysis was conducted using IQ-Tree, and bootstrap support was assessed with 1,000 pseudo-replicates (Nguyen et al. 2014, Chernomor et al. 2016). Bayesian inference (BI) analysis was performed using MrBayes version 3.2.7a on XSEDE through the CIPRES Portal online platform. The BI analysis (Huelsenbeck & Ronquist 2001) involved running six simultaneous chains in two independent runs, each spanning 1,000,000 to 50,000,000 generations, with trees sampled every 10,000 generations. Phylogenetic trees were summarized, and posterior probabilities (PP) were calculated after discarding the initial 25% generations as burn-in (Miller et al. 2010, Ronquist et al. 2012). The resulting phylograms were visualized using FigTree v1.4.0 (Rambaut 2011) and further edited in Microsoft PowerPoint.

Phylogenetic analyses, encompassing both ML and BI methods, produced congruent topologies across all phylogenetic trees using their respective concatenated alignments. The ML analysis generated the highest-scoring tree, which was subsequently adopted as the backbone tree. The resulting ML parameters are presented alongside the figure legends corresponding to each phylogenetic tree.

Fungal diseases

Dry bubble disease

The initial documentation of dry bubble disease traces back to Constantin & Dufour (1892), who provided the first comprehensive report on various bubble diseases, collectively referred to as "la mole" 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) (Fig. 2).

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).

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, Largeteau et al. 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 (White 1981).

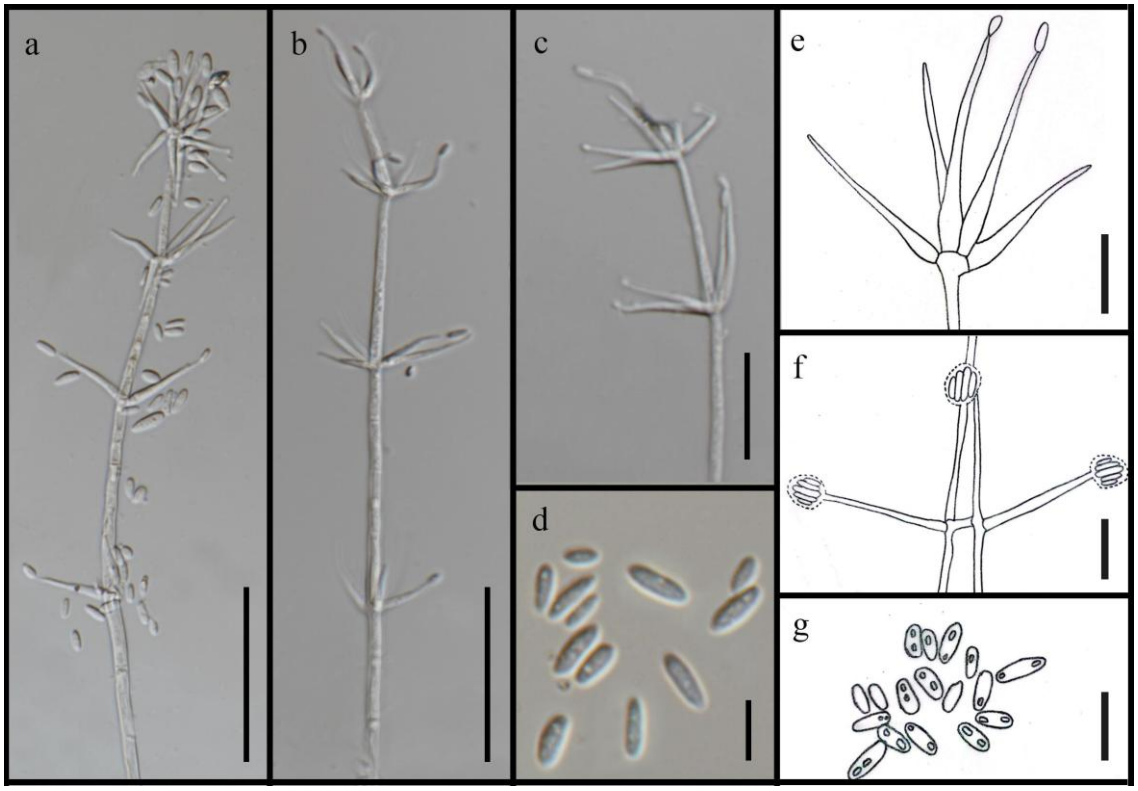


Fig. 2 – *Zarea* sp. (a-d). **a-c** Conidiophores and phialides. **d** Conidia. Scale bars: a, b = 50 µm, c, d = 10 µm. *Zarea fungicola* (e-g). **e, f** Conidiophores and phialides. **g** Conidia. Scale bars: e–g = 10 µm. (Redrawn from Khonsanit et al. (2024)

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 (Fig. 3).

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. 2016, Zhou et al. 2016, Li et al. 2019, 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) (Fig. 4).

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).

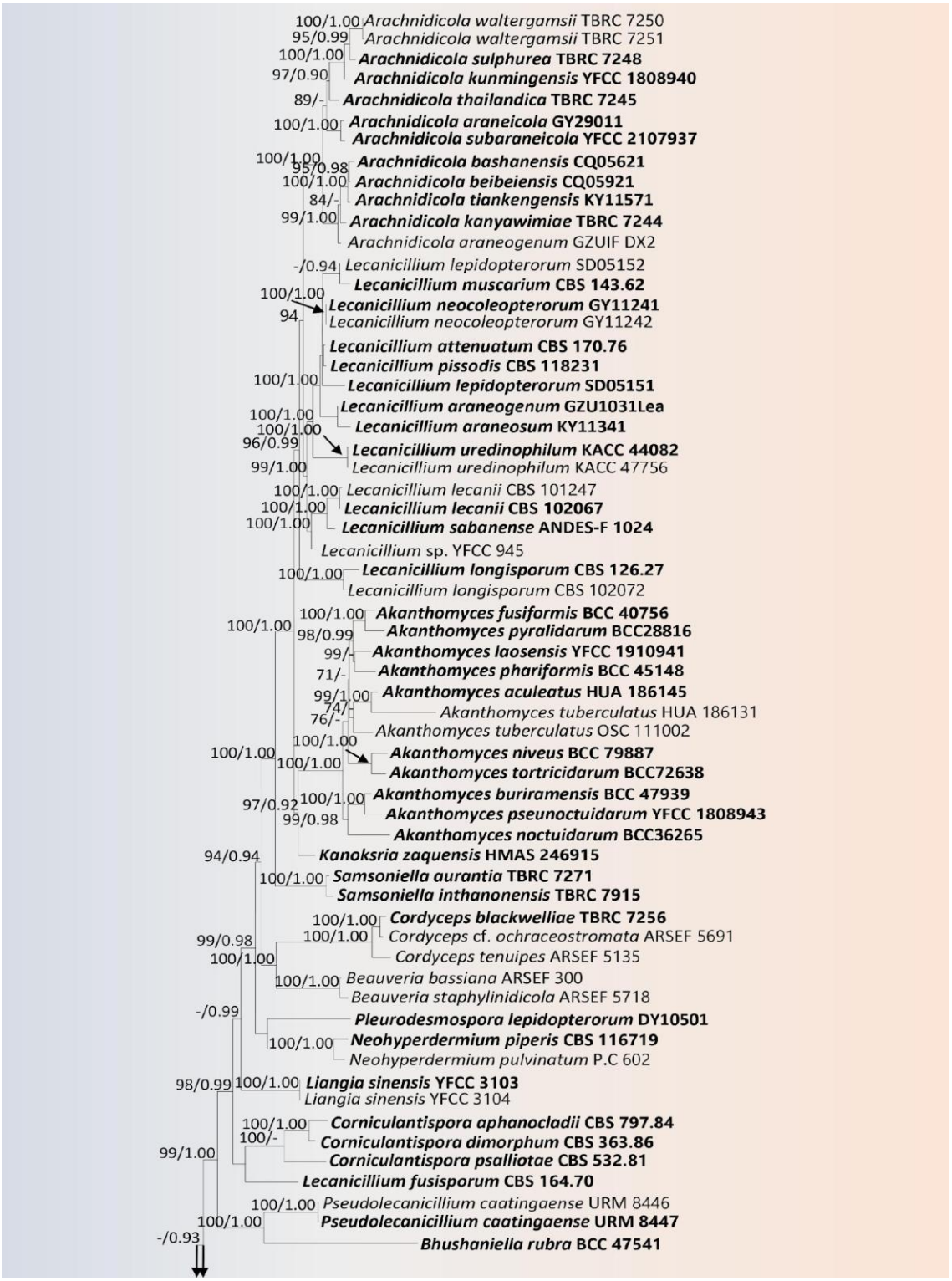


Fig. 3 − Phylogenetic tree generated by ML analysis of combined LSU, *tef*-1α, *rpb*1, and *rpb*2 sequence data of *Lecanicillium*, *Zarea,* and related genera in the *Cordycipitaceae*. Related sequences were obtained from previous publications and the GenBank database. A total of 111 strains were included 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.

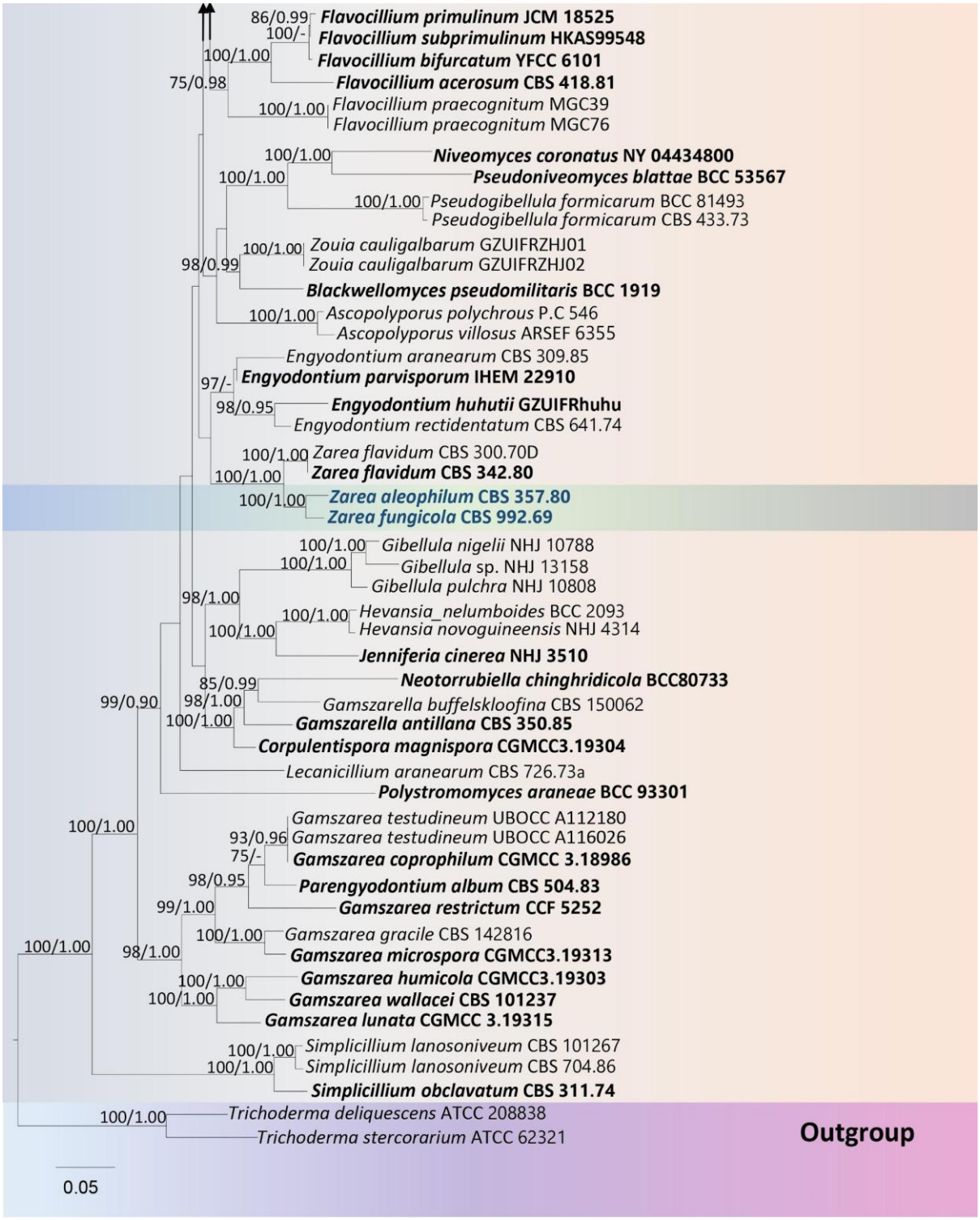


Fig. 3 − Continued.

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* (Potočnik 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 & 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 Fig. 8.

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).

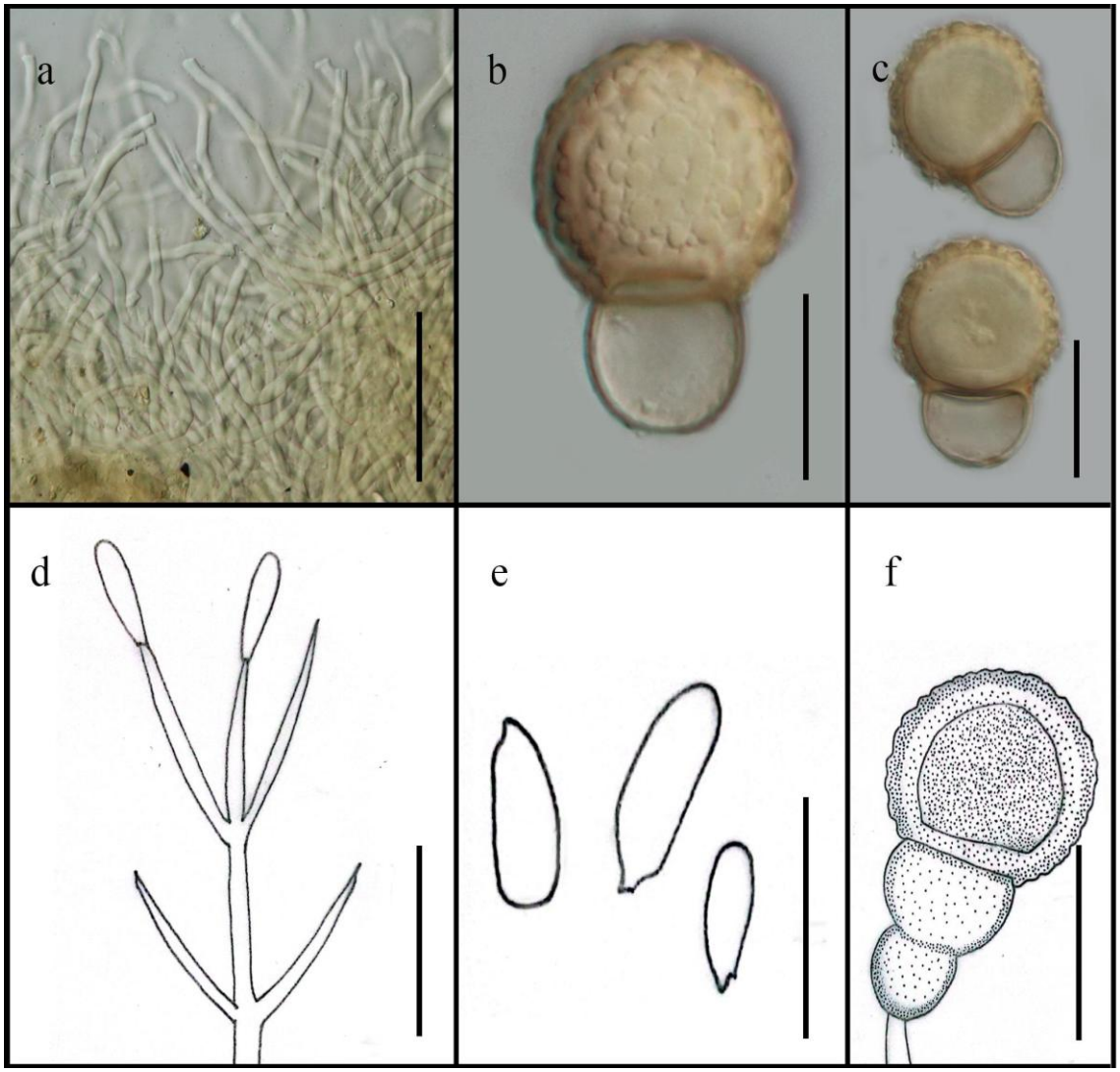


Fig. 4 – *Mycogone rosea* (a-c). **a** Hyphae. **b, c** Aleurioconidia. Scale bars: a = 50 µm, b, c = 20 µm (Photo credits: R.H. Perera). *Hypomyces perniciosus* (d-f). **d** Conidiophores. **e** Conidia. **f** Chlamydospore. Scale bars: d–f = 20 µm. (Adapted and redrawn from Du et al. (2021)

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) (Fig. 5–6).

Hypomyces/*Cladobotryum* species are commonly known for their fungicolous lifestyle, and they can also persist in soil (Gajanayake et al. 2025, Jayawardena et al. 2025). Sharma et al. (2015a) 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. 2015a). 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).

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. 2015, Zuo et al. 2016, Wang et al. 2018, Wu et al. 2020, An et al. 2022a, Wang et al. 2024, 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 fruiting bodies (Carrasco et al. 2016, Carrasco et al. 2017a) (Fig. 7). 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 fruiting 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 & Põldmaa2013).

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 & Põldmaa 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).

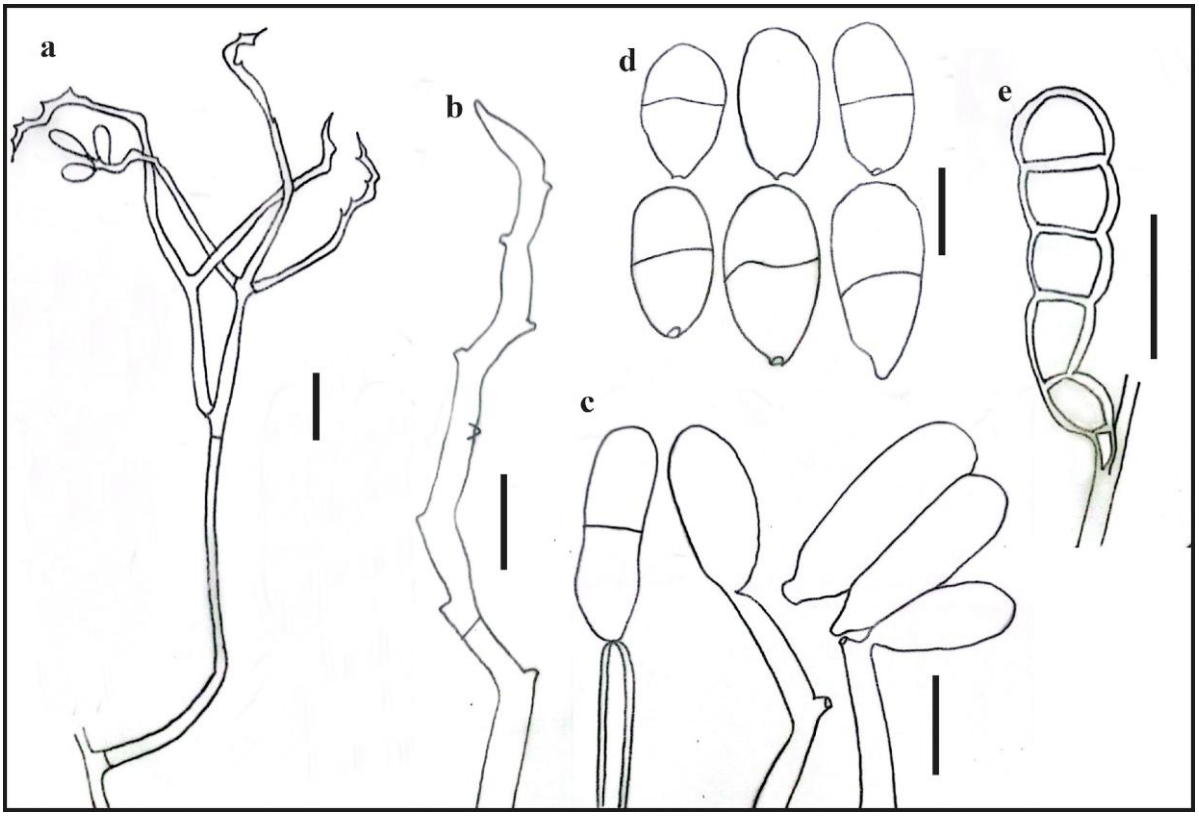


Fig. 5 – *Hypomyces mycophilus.* **a** Conidiophore. **b** Fertile rachis of a conidiophore. **c** Conidiogenous cells and conidiogenous loci. **d** Conidia. **e** Chlamydospore. Scale bars: a, e = 25 µm. b–d = 10 µm. (Redrawn from Rogerson & Samuels (1993)

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 65–70ºC 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 (17ºC) (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, 2017b). 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 Fig. 8.

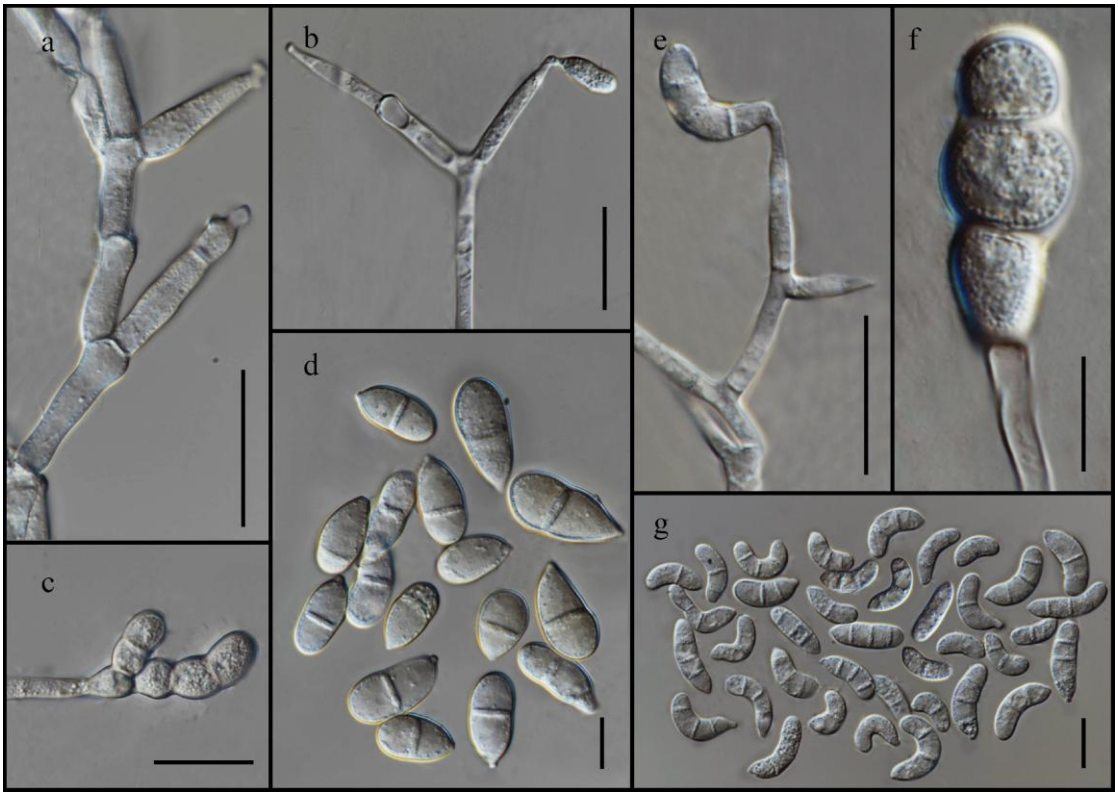


Fig. 6 − *Hypomyces protrusus* (a-d). **a, b** Conidiogenous cells and conidial attachment. **c** Chlamydospores. **d** Conidia. Scale bars: c = 30 µm, a = 25 µm, b = 20 µm, d = 10 µm. *Hypomyces semicircularis* (e-g). **e** Conidiogenous cells and conidial attachment. **f** Chlamydospores. **g** Conidia. Scale bars: e = 20 µm, f = 15 µm, g = 10.

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. 2023, Ajis et al. 2024, Tarafder et al. 2024a).

Classification

Ascomycota, Pezizomycotina, Sordariomycetes, Hypocreales, Hypocreomycetidae, Hypocreaceae

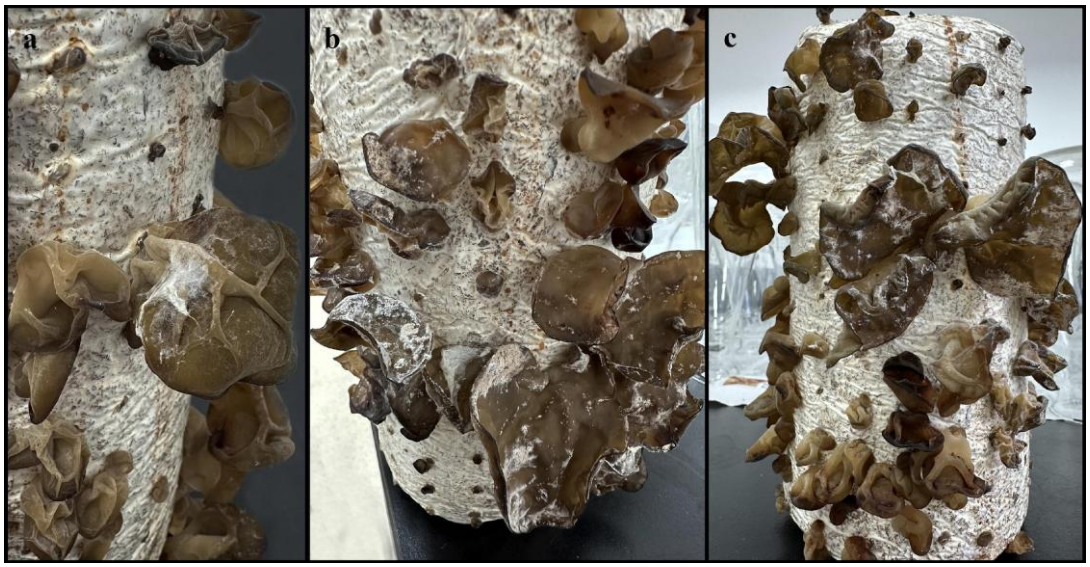


Fig. 7 − Signs and symptoms of cobweb disease of *Auricularia cornea* caused by *Hypomyces mycophilus* (a-c)

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) (Fig. 9).

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).

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. 2016, 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. 2023, Ajis et al. 2024, Tarafder et al. 2024a)

Distribution

Worldwide (Hatvani et al. 2012)

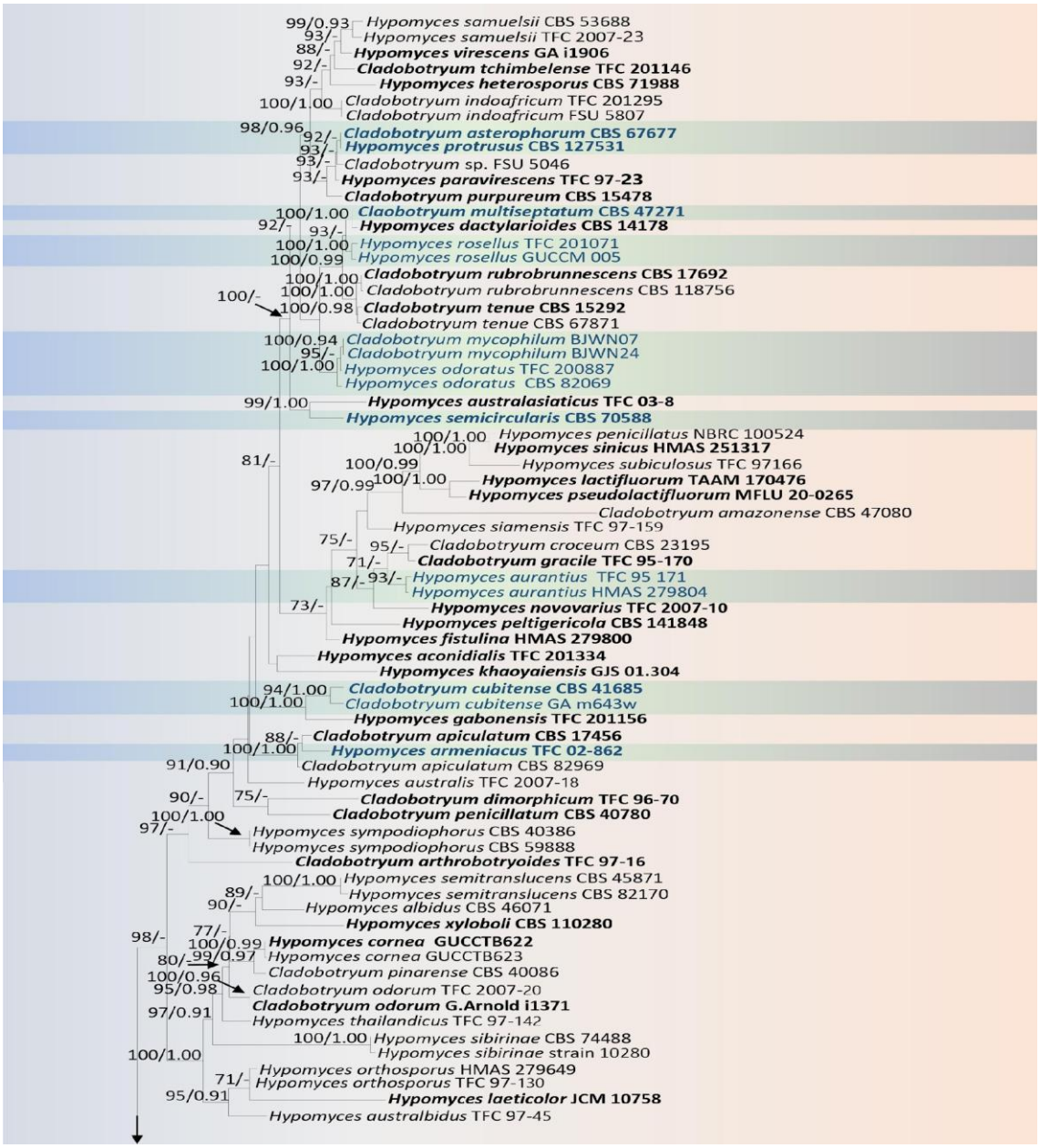


Fig. 8 − Phylogenetic tree generated by ML analysis of combined ITS, LSU, *tef*-1α, and *rpb*2 sequence data of *Hypomyces* and its allied genera. Related sequences were obtained from previous publications and the GenBank database. A total of 129 strains were included in the analyses. The tree is rooted 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.

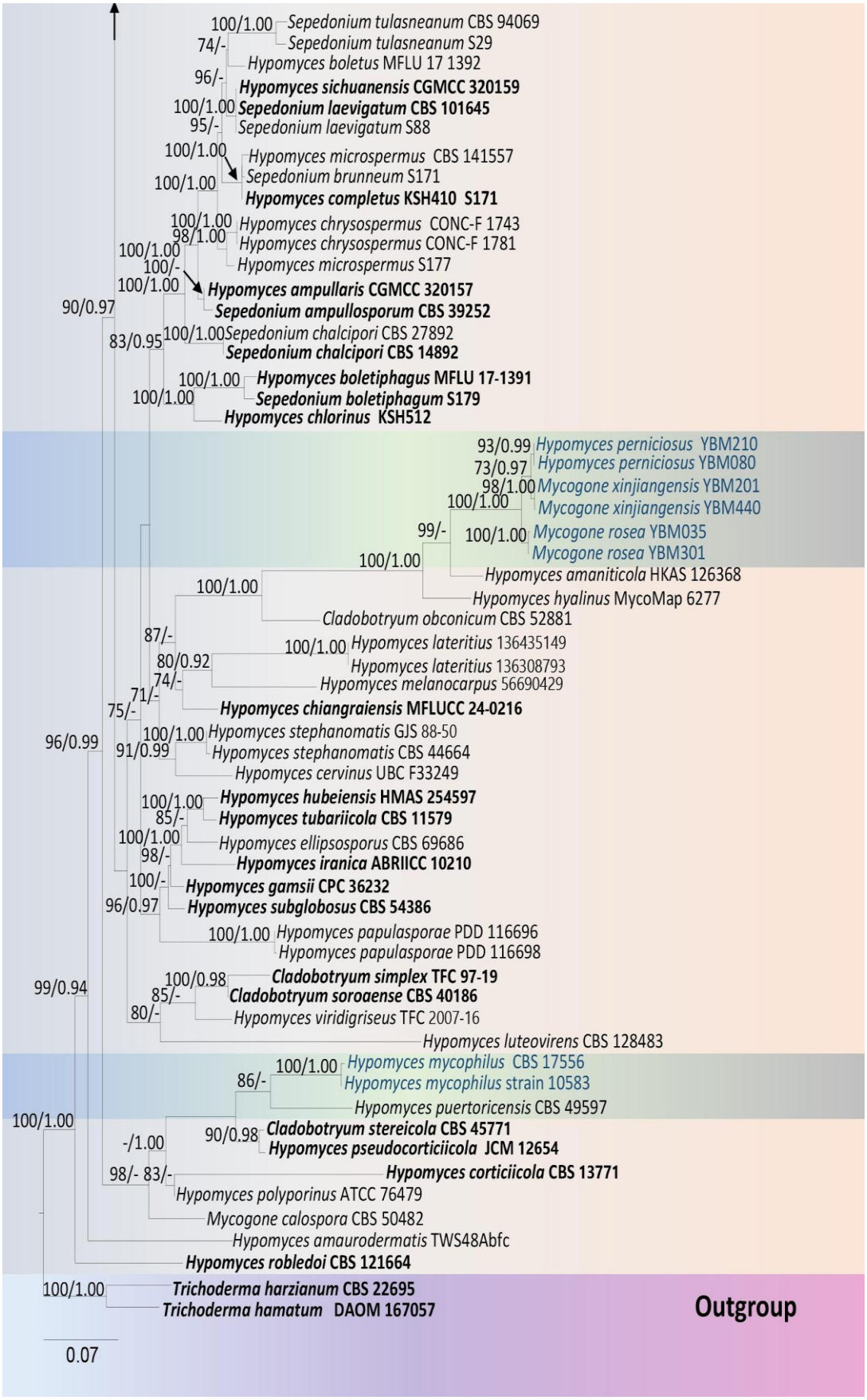


Fig. 8 − Continued

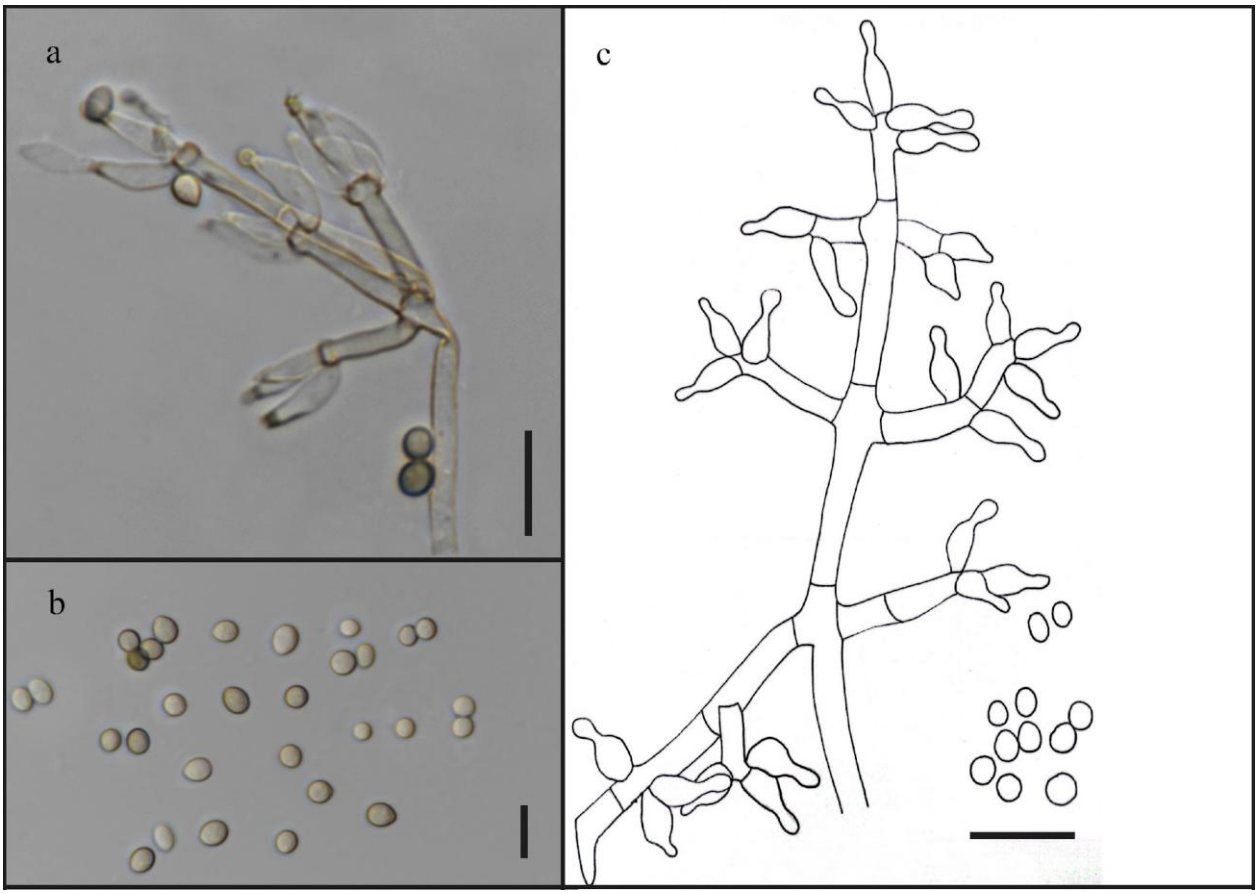


Fig. 9 − *Trichoderma* sp. (a-b). **a** Conidiophore with conidiogenous cells. **b** conidia. Scale bars: a = 10 µm, b = 5 µm. *Trichoderma harzianum*. **c** Conidiophore with conidiogenous cells, and conidia. Scale bar c = 10 µm. (Redrawn from Chaverri & Samuels (2003)

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) (Fig. 10). 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).

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.

Fig. 10 − Signs and symptoms of green mold disease. **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 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. 2023). 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 Fig. 11.

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 & Bian (2012) identified *Scytalidium lignicola* as the cause; however, Peng et al. (2014) later argued that the pathogen described by Sun & 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) (Fig. 12). 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).

Hosts

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

Distribution

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

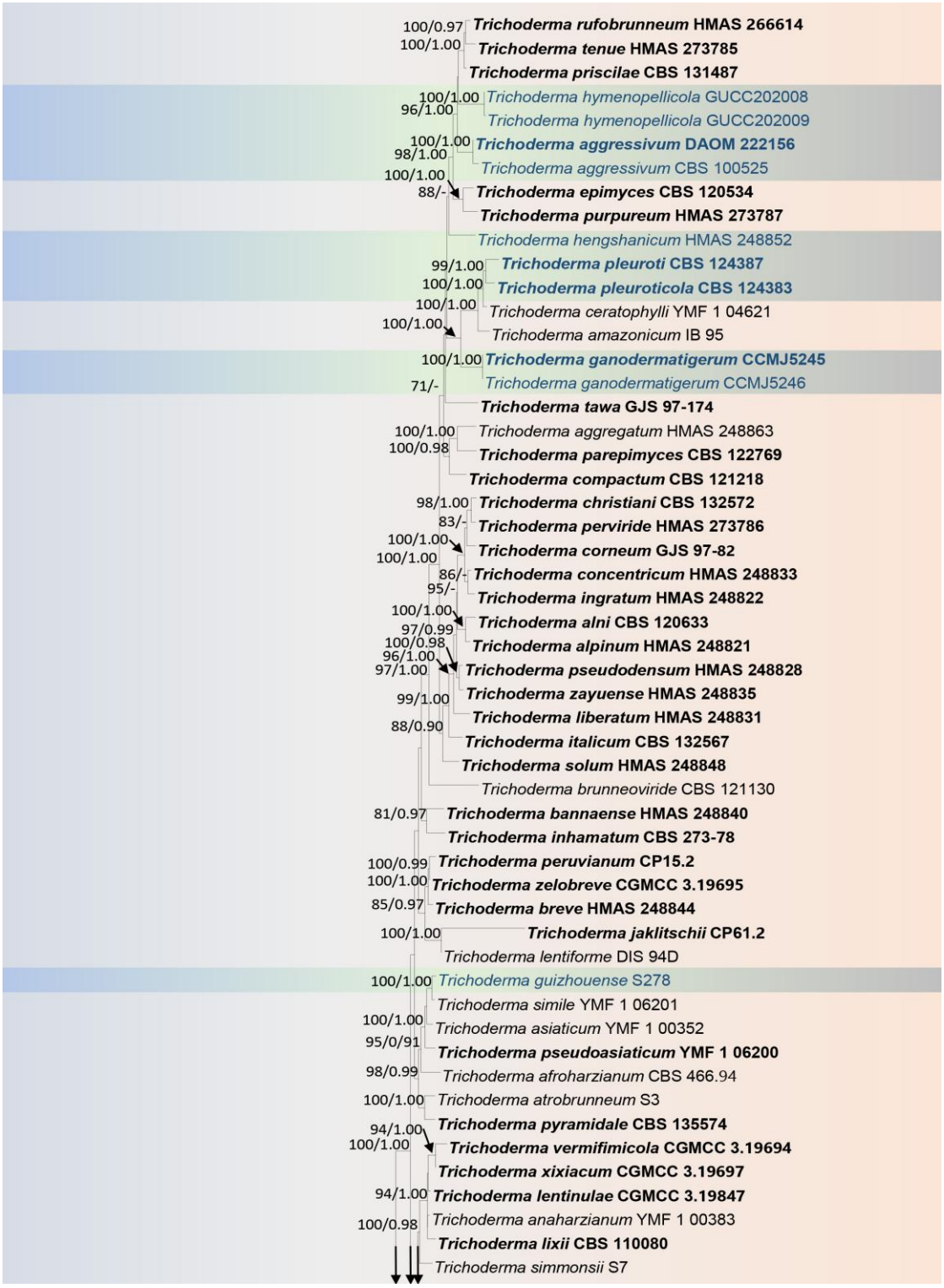
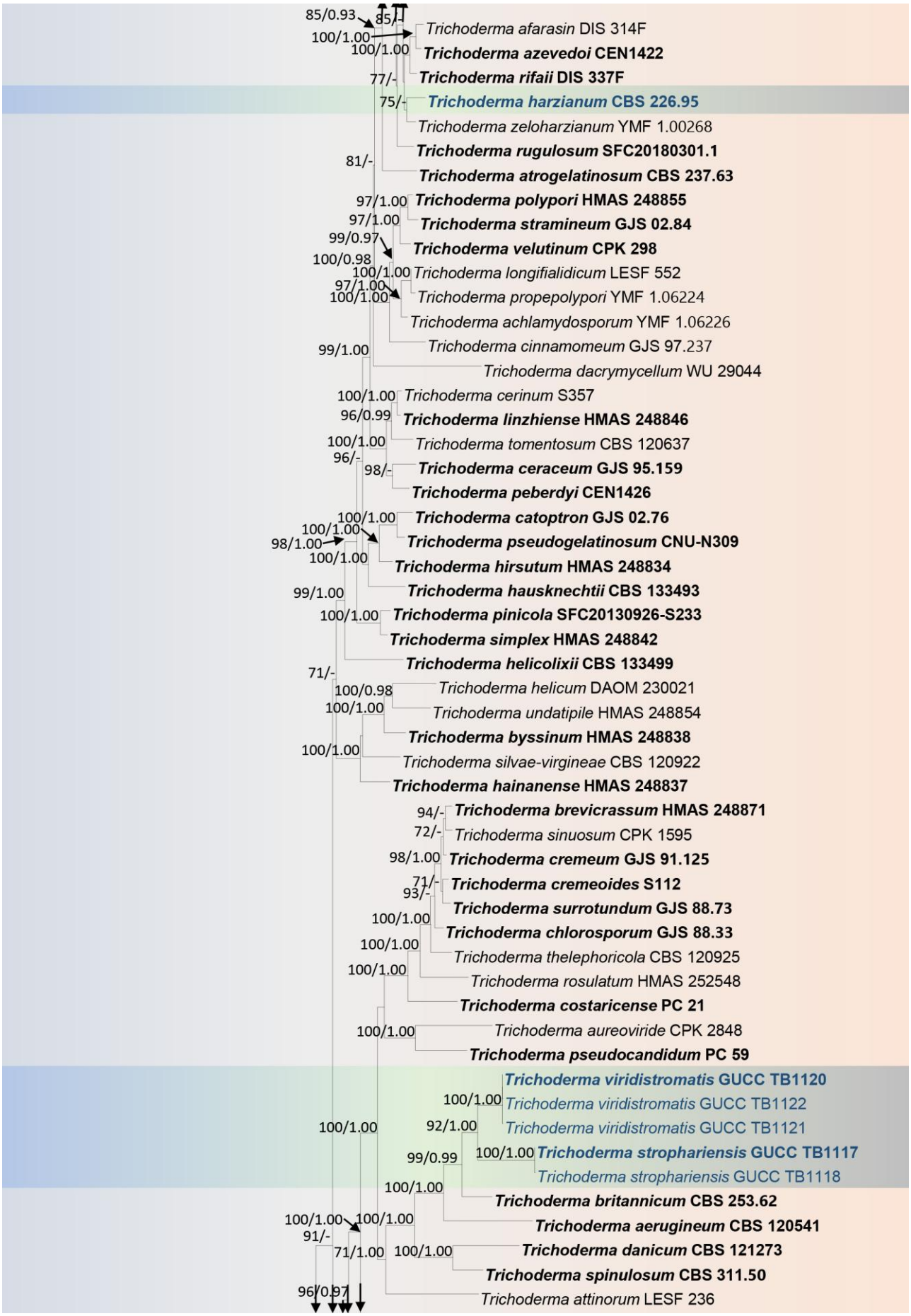


Fig. 11 − Phylogenetic tree generated by ML analysis of combined ITS, *rpb2*, and *tef-1α* sequence data of *Trichoderma* species. Related sequences were obtained from previous publications and the GenBank database. A total of 186 strains were included in the analyses. The tree is rooted with *Protocrea 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.



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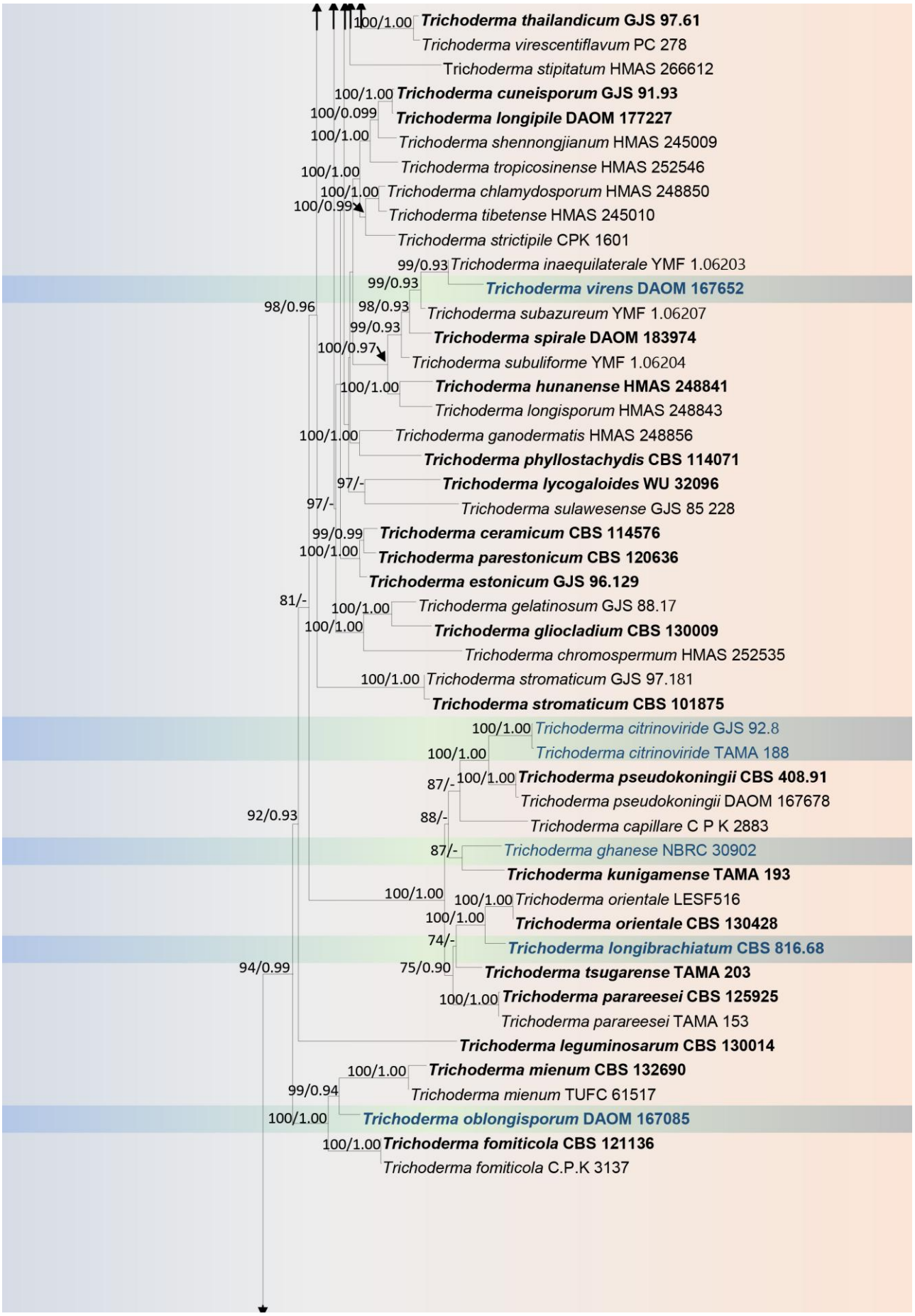

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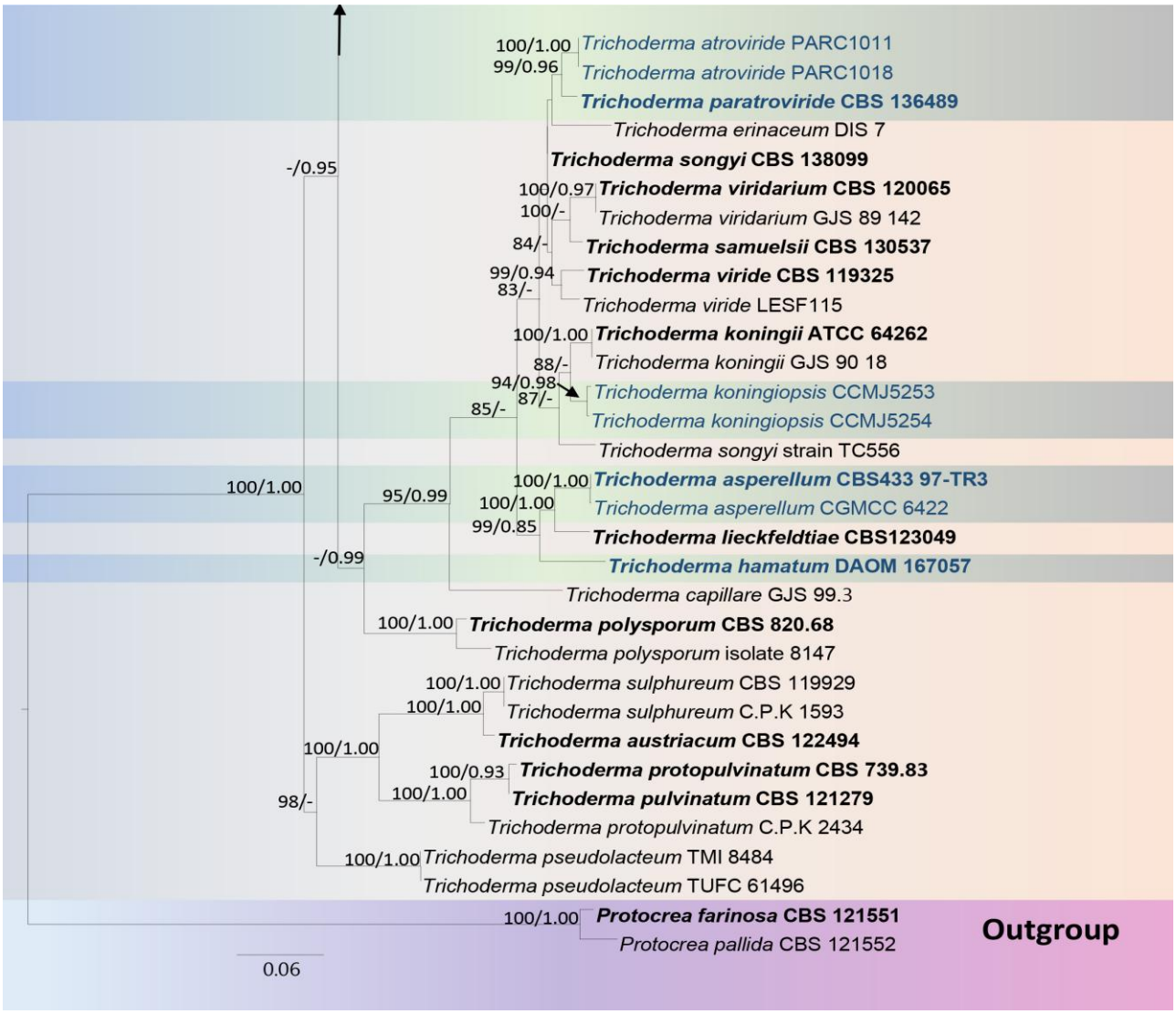

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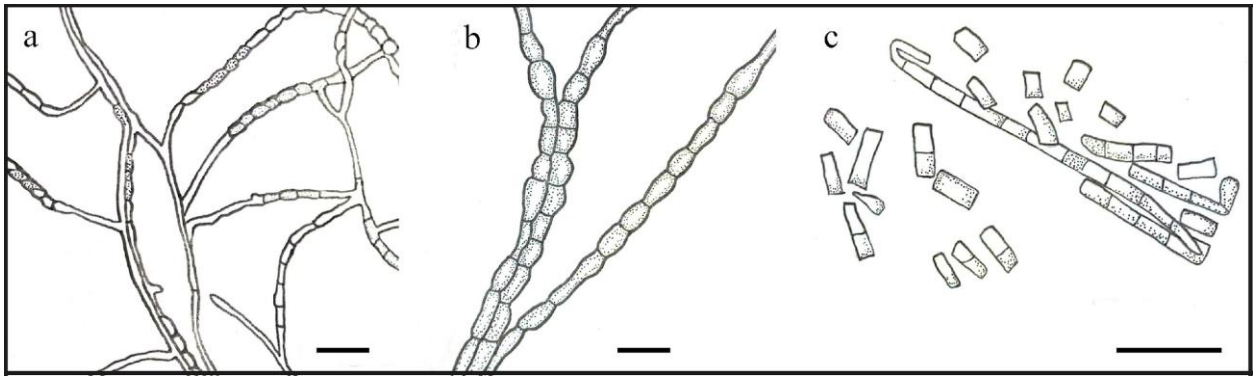

Fig. 12 − *Scytalidium auriculariicola* **a** Branched hyphae with developing chlamydoconidia **b** Catenate and thick-walled chlamydoconidia. **c** Conidia of variable length. Scale bars: a, c = 20 µm, b = 10 µm (Adapted and redrawn from Peng et al. (2014)

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 Fig. 14.

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) (Fig. 13).

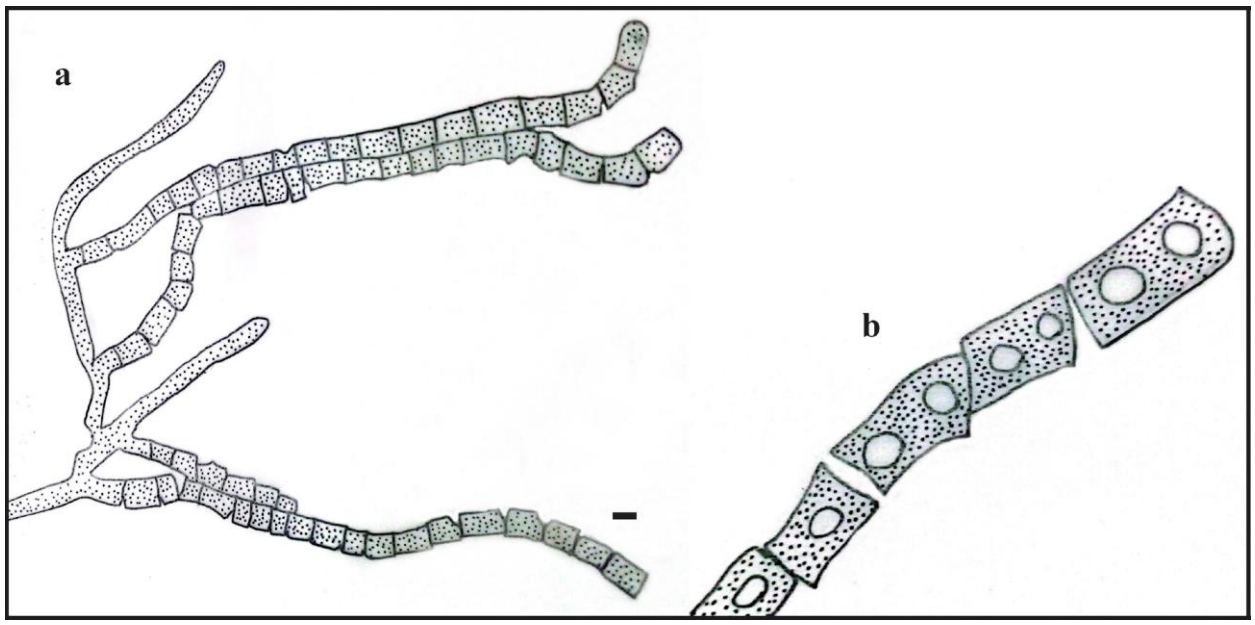

Fig. 13 − *Scytalidium ganodermophthorum*. **a, b** Arthroconidia without disjunctors. (Oil immersion objective). Scale bar: a = 2 μm. (Adapted and redrawn from Kang et al. (2010)

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 Fig. 14.

Competitor molds

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 odour 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).

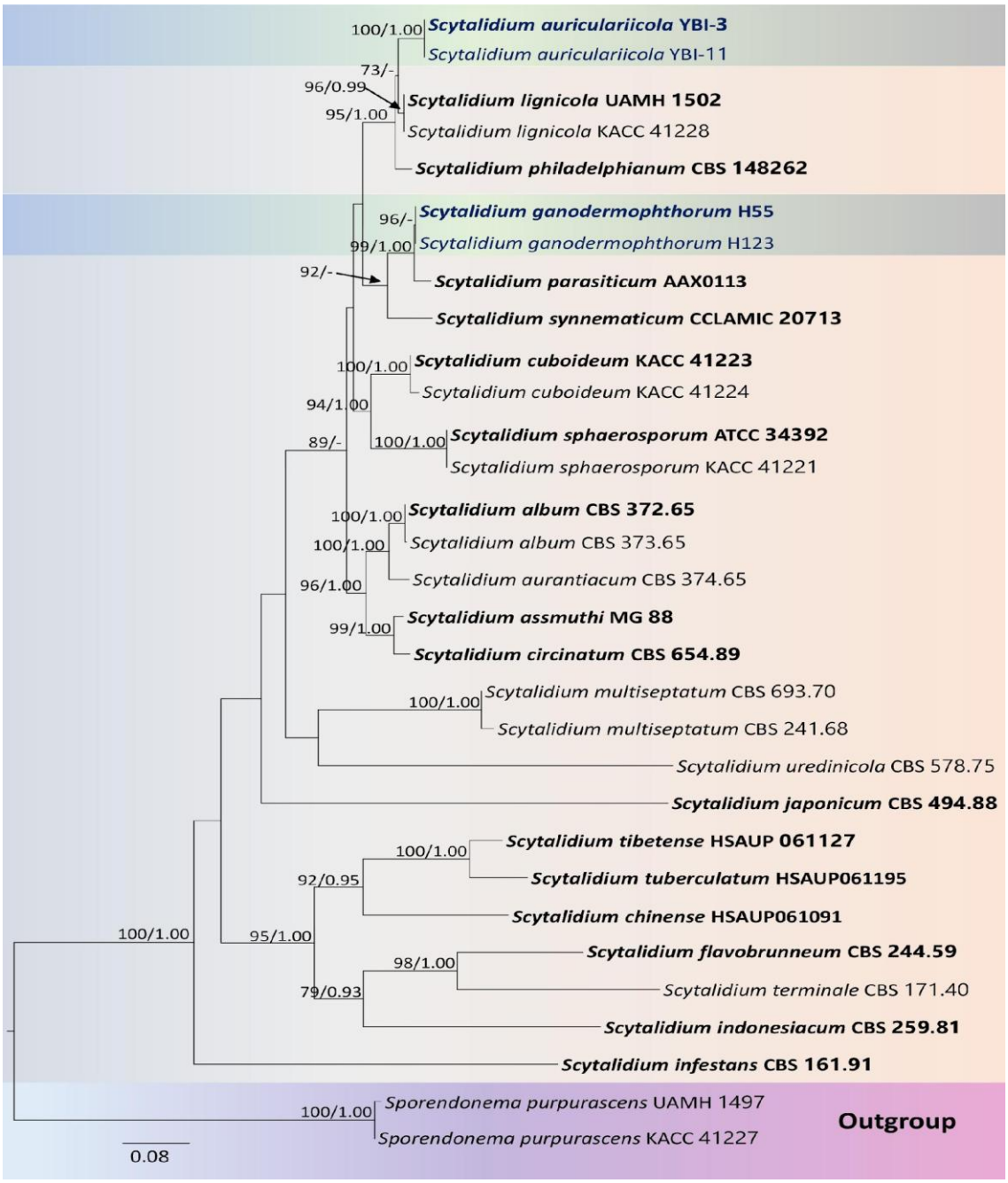

Fig. 14 − Phylogenetic tree generated by ML analysis of ITS sequence data of *Scytalidium* species. Related sequences were obtained from previous publications and the GenBank database. Twenty-nine strains are included in the analyses. The tree is rooted with *Sporendonema purpurascens* (UAMH 1497 and 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.

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).

False truffle

This is regarded as one of the most significant competitors in the cultivation of *Agaricus brasiliensi*s (do Nascimento & da 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 UK (Thakur et al. 1967, Sahrma et al. 2007, do Nascimento & da Eira 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 & 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).

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. 2015b, 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 a too low 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).

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 fruiting 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).

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. 2019, 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).

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).

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 fruiting 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.

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).

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. 2019, Chakraborty & Archana 2021, Gea et al. 2021, Ghimire et al. 2021, Yu et al. 2024). This review covers four common fungal diseases, namely dry bubble, wet bubble, cobweb, and green mold, as well as slippery scar, yellow rot, and nine competitor molds associated with mushroom cultivation. 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 Fig. 15.

Uncontrolled fungal diseases/competitor molds in mushroom cultivation lead to growth retardation, deformities, and decay. Results show significant yield losses and reduced product quality (Sun et al. 2019, Gajanayake et al. 2021a, b, 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).

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.

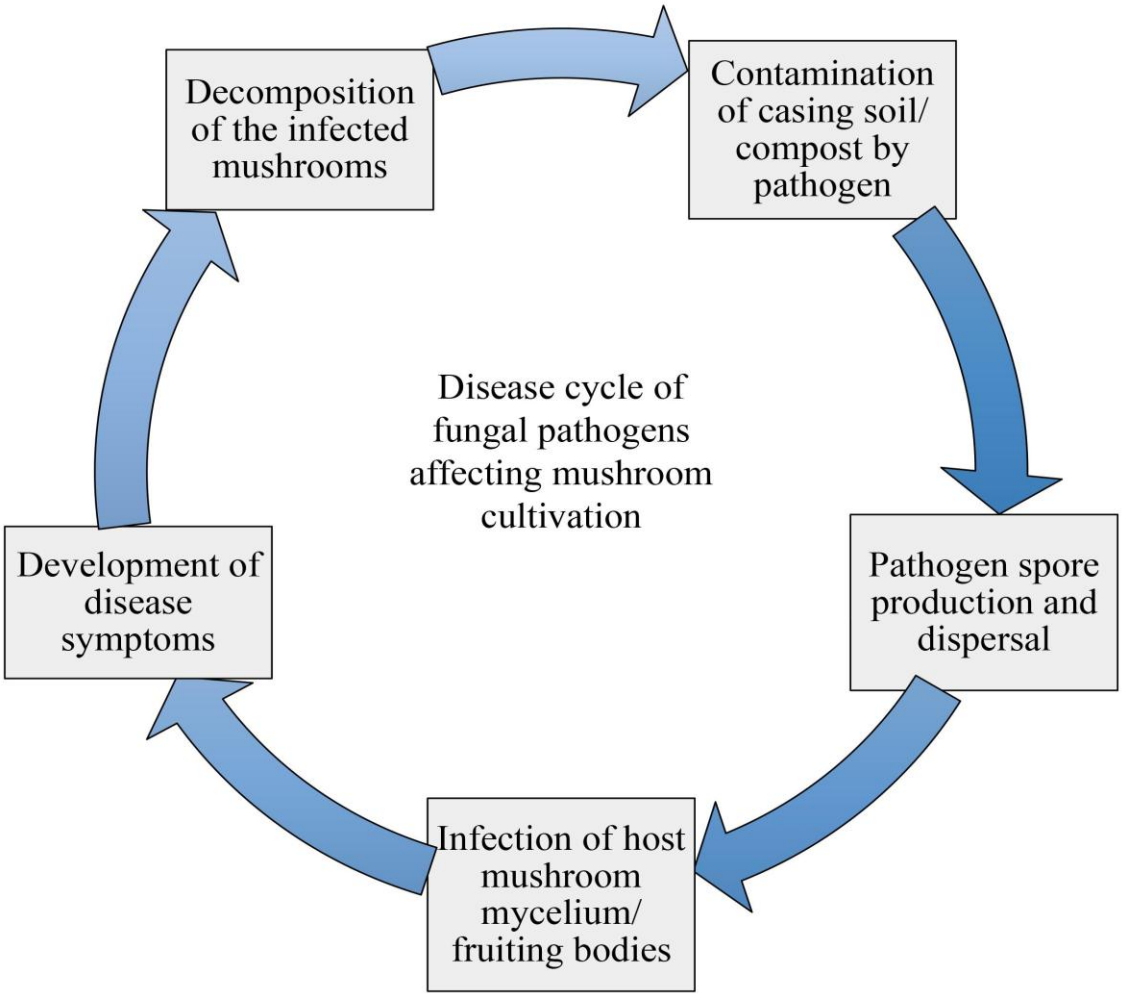

Fig. 15 Generalized disease cycle for fungal pathogens affecting mushroom cultivation

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. 2015a). 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).

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. 2017). 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).

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.

CONCLUSION

Fungal diseases pose a substantial threat to mushroom cultivation, with wide-ranging impacts on yield, quality, and economic viability. 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.

AUTHORS' CONTRIBUTIONS

All authors participated in the conception and design of the study. Achala J. Gajanayake conducted data collection, data analyses, prepared figures, and drafted the manuscript. Ruvishika S. Jayawardena, Kevin D. Hyde, Thatsanee Luangharn, Wasanatha K. K. Liyanage, Lu Caige, and Qi Zhao provided feedback on previous drafts to enhance the manuscript. Qi Zhao and Kevin D. Hyde secured the necessary funding for the research. All authors reviewed and approved the final version of the manuscript.

DECLARATION OF COMPETING INTEREST

No potential conflict of interest was reported by the author(s).

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